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Biology and Immature Stages of the Bee Genus *Meganomia* (Hymenoptera, Melittidae)

JEROME G. ROZEN, JR.[1]

ABSTRACT

The hibernating, postdefecating larva and pupa of *Meganomia binghami* (Cockerell) are described and compared with similar stages of other melittid bees. Biological information on this species and on an undescribed species of *Meganomia* includes the following information: nest ecology, nest configuration and structure, provisioning, development, number of generations a year, mating, sound production and daily activity of adults. The placement of the genus in the Melittidae cannot be evaluated on the basis of larvae because the numerous similarities shared by *Meganomia*, *Melitta*, and *Macropis* are symplesiomorphic. However, there are no larval characteristics that would exclude *Meganomia* from the family. Cladistic analysis of features of the mature larva indicates that *Meganomia* is a sister group to all other melittids whose immatures are known.

INTRODUCTION

Meganomia is a southern African genus of large-bodied, conspicuously marked bees that had been placed in the halictid subfamily Nomiinae until Stage (1971) demonstrated that it belonged to the Melittidae on the basis of numerous structural features of adults. Transferring it to that family, he stated that "it fit nicely" in the Melittinae although he did not enumerate what characters he used for this decision. More recently Rozen and McGinley (1974) investigated the phylogeny and systematics of the Melittidae using mature larvae as the data source. Although larvae of a number of taxa were described and analyzed, including representatives of all subfamilies except for Ctenoplectrinae, the immatures of *Meganomia* were then unknown.

On a trip of South West Africa in 1976, my wife and I made a special effort to find and recover larvae of this genus, partly to confirm Stage's taxonomic placement of the genus and partly to see how the larvae would fit Rozen and McGinley's hypothesized phylogenetic relationships within the family. Not only did we collect larvae and pupae of *Meganomia binghami* (Cockerell) we also obtained considerable biological information on the same species and a limited amount of such information on another, distinctive species of *Meganomia* yet to be named

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and described. The present paper describes the immature stages of *M. binghami* and reports on all biological information that was gathered; conclusions regarding relationships and placement of the genus are offered.

I thank my wife, Barbara, who helped in all aspects of the field investigations. Drs. Mary-Louise and Michael Penrith and Director C. G. Coetzee of the State Museum, Windhoek, South West Africa, extended many courtesies and advice while we were in southern Africa, for which we are grateful. Most of the manuscript was dictated on tape in noisy hotel rooms or still noisier airplanes. My thanks go to Ms. Phyllis Browne who painstakingly deciphered these tapes as she has done for many other similar studies. Dr. Vincent Whitehead, South African Museum, Capetown, and Dr. L. Vari, of the Transvaal Museum, Pretoria, kindly permitted me to examine their respective collections in connection with this study. This investigation was partly supported by National Science Foundation grant no. GB32193.

Specimens of adults, immatures, and cocoons described here are deposited in the collections of the American Museum of Natural History.

BIOLOGY

Description of Area. We commonly encountered *Meganomia binghami* in central South West Africa in thorn scrub savanna where its pollen plant, *Crotalaria podocarpa* (Leguminosae), occured in sandy situations. We found the bees in large numbers at 17 km. east of Usakos, S.W.A.; 8 and 26 km. north of Karibib, S.W.A.; 52 and 58 km. southwest of Omaruru, S.W.A.; and 62 km. west of Omaruru. Nesting sites were discovered at all localities except the two north of Karabib and were studied between March 18 and 27, 1976.

At 17 km. east of Usakos, another species of *Meganomia* flew in the same vicinity as *M. binghami*, and collected pollen from *Indigofera*, also a legume; currently unnamed, I call it *Meganomia* species B. Because its nests were not found, most of the following biological information refers to *M. binghami.*

The nesting season was early for *M. binghami* although some nesting sites were farther advanced than others. At 17 km. east of Usakos, we saw no pollen-bearing females entering nests; at 62 km. west of Omaruru, only a few pollen carrying females were observed and no fresh cells were uncovered. However, at 52 and 58 km. southwest of Omaruru pollen-laden females were abundant, and provisioned cells were encountered although none was occupied by last instar larva. *Meganomia* species B apparently flies somewhat earlier than *M. binghami*, for we often saw pollen-laden females with frayed wings, whereas females of *M. binghami*, all fresh, were just beginning to appear.

Abundant rains had fallen in South West Africa during the late summer so that vegetation at all sites was green and flowers plentiful. Late summer rains also had been moderately heavy for several preceding years.

Description of Sites. All nesting sites of *M. binghami* were in nearly horizontal ground where the soil was sandy, moist below the surface, and partly or completely barren on the surface. At 17 km. east of Usakos (fig. 1) and 62 km. west of Omaruru (fig. 2), the sites were in a partly denuded area a few meters from a graded dirt roadway, whereas at the two localities southwest of Omaruru (fig. 3) most nests were actually in the margin of a dirt roadway although some nests occurred on adjacent ground. We excavated nests only at 62 km. west and 52 km. southwest of Omaruru. At the former locality the soil was compact, moderately fine, and easily excavated sand; from here we gathered information regarding cocoons and postdefecating larvae. At the latter, the surface soil was drier and harder, but the subsurface soil was fairly easy to excavate. The soil texture differed primarily by being coarser. This locality yielded data on eggs, pollen masses, and early larval instars.

Nesting Activity. Females constructed nests in open horizontal ground, under low plants (including *Indigofera*) growing on flat surfaces, and in the sloping surfaces of low banks along the edges of roadways. Where abundant, nests were in large, loose aggregations, which at 58 km. southwest of Omaruru (fig. 3), the largest nesting site, extended along the roadway and its margins for approximately 150 meters. Within aggregations, nests were irregularly distributed, and, when dense, were often less than 10 cm. apart.

FIGS. 1-3. Nesting sites of *Meganomia binghami* in South West Africa. 1. At 17 km. east of Usakos. 2. At 62 km. west of Omaruru. 3. At 58 km. southwest of Omaruru. In figures 1 and 2, burrows were most common in middle foreground; in figure 3, dark tumuli of burrows can be seen along edge of road.

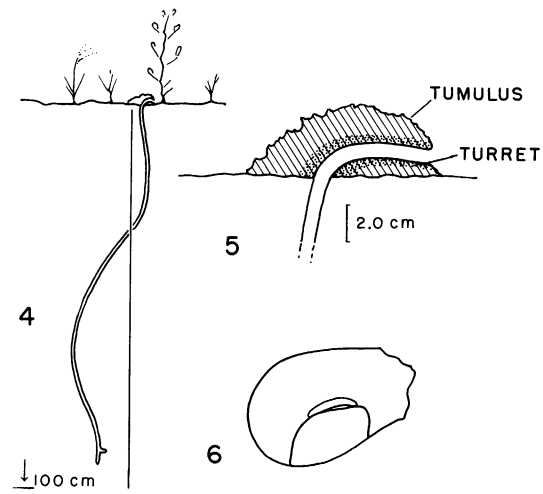
At 58 km. southwest of Omaruru, the adjacent tumuli formed a striking, continuous row of freshly excavated soil along the edge of the road, somewhat darker than the roadway (fig. 3).

Our casual observations indicated that most nests were occupied by only one female, but two nests at 62 km. west of Omaruru had two females each. Although these two nests may have

been entered by females searching for places to begin nests, both females from one nest had somewhat frayed wings, suggesting that neither had just begun nesting. All entrances were surrounded by copious tumuli, measuring approximately 10 cm. in diameter and 5 to 8 cm. high in cases of horizontal surfaces. The tumulus was loose, except that most incorporated a curved entrance turret (fig. 5) of consolidated sand buried in the soft excavated material. The turret rose from the nest, curved, then extended horizontally as much as 5 cm. so that the entrance was near the edge of the tumulus. Nest entrances with or without turrets appeared open most of the time although several were found plugged, perhaps by females bringing soft soil to the surface. Holes without tumuli, encountered at some nest sites, were emergence openings.

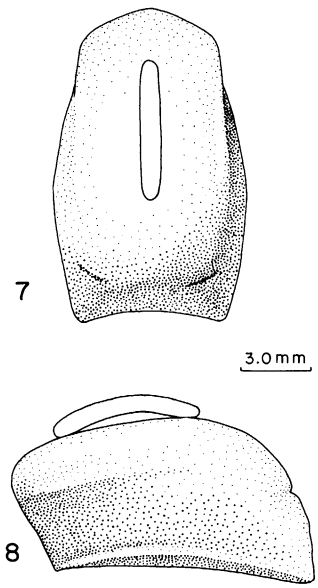
Main tunnels and branches, circular in cross section and about 10 mm. in diameter, possessed smooth, seemingly uncoated walls. Several main burrows excavated carefully at 62 km. west of Omaruru descended not quite vertically in a slightly irregular path to depths of as much as 114 cm. (fig. 4) but as yet lacked cells. At this locality, numerous cells from previous generations were encountered at depths commonly between 70 and 120 cm. At 52 km. southwest of Omaruru the main burrows at first descended vertically, seemed to angle horizontally in more cases than those at the other locality, and branched. Cells occurred more shallowly there, some at depths of only 50 cm. Perhaps the harder surface or coarser soil accounted for these shallow nests, which also had smaller tumuli. Some branches, apparently leading to closed cells, were filled with somewhat coarser soil than that of the substrate.

Cells (fig. 6) ranged from 12 to 13 mm. in maximum diameter and 19 to 23 mm. in maximum length. Oriented with their long axis 20 to 45 degrees from horizontal, the rear of the cell was always lower than the front. The cell floor was somewhat flatter than the ceiling so that the cell was not symmetrical around its long axis. No special "built-in" lining (i.e., consisting of soil mixed with secretions) had been constructed and the cell surface was uniformly smooth and dull. A droplet of water placed on the surface was absorbed very slowly, indicating that the female had applied a waterproof lining. The cell closure was a deeply concave spiral on the inside. That it was composed of very fine sand, finer than the surrounding soil, proves that the female somehow was able to extract fine particles from the heterogeneous substrate to construct the closure.



FIGS. 4-6. Nest components of *Meganomia binghami*. 4. General configuration of main burrow at 62 km. west of Omaruru. 5. Nest entrance. 6. Diagram of cell showing orientation, orientation of provisions, and position of egg. Scale refers to figure 5 only.

Provisioning. Females of both *Meganomia binghami* and species B may be oligoleges on their respective pollen plants because at 17 km. east of Usakos *M. binghami* was never seen collecting pollen from *Indigofera*, the pollen source of species B, which grew abundantly in the nesting area of *M. binghami*. Both species transported pollen in a moist condition on the hind legs. In the cell the provisions of *M. binghami* were shaped into an elongate form 11 to 14 mm. long (six measurements), 5.5 to 6 mm. at a maximum height (five measurements), and 7 to 8 mm. at a maximum width (five measurements) (figs. 7, 8); these measurements were taken from dried specimens that showed no signs of shrinking. The bottom surface of the provisions rested on and assumed the curvature of the cell floor. The top surface was rounded with its front edge projecting slightly beyond the base. The top surface



FIGS. 7, 8. Provisions and egg of *Meganomia binghami*, top and side views, respectively.

curved smoothly toward the rear of the mass, and the rear base was produced on each side forming angles that extended farther backward than the middle. This form, more clearly depicted by diagram, was essentially identical in more than 10 cases. Distinctly greenish, the provisions were homogeneously soft, lightweight, mealy-moist, without any special surface coating of either nectar or waterproofing material. Even when fresh they emitted a slightly sour, fermented odor; they were not noticeably sweet to taste, a surprising fact considering the amount of moisture they contained and raising a question as to whether the moisture was nectar as would be normally assumed.

Development. Elongate, white, curved eggs, 5.0 to 5.5 mm. long and almost 0.8 to 1.0 mm. in diameter (two measurements) and newly hatched larvae were encountered on the tops of the pollen masses. Although little is known about larval activity and growth, larvae increased rapidly in size without consuming appreciable amounts of provisions, indicating that they may ingest considerable quantities of water as has been observed in other bees. Developing larvae, at least during early instars, maintained an elongate form and apparently could crawl. Partly grown larvae encircled the pollen mass while feeding much as do the larvae of New World *Diadasia.*

At least five larval instars were identified. Only the last instar, described in detail below, possesses the strongly produced labiomaxillary area characteristic of cocoon-spinning larvae.

A mystery surrounds larval defecation. Approximately 100 cells containing cocoons, all from the last generation, were examined from the nesting site at 62 km. west of Omaruru. No feces, either in the cell, within the cocoon, or in the fabric of the cocoon, were detected. I assume that the pollen grains either were digested or more probably broke down through microbial activity during the year after cocoon spinning (assuming one generation a year).

All postdefecating larvae were encased in large cocoons (fig. 9) that presumably had been spun at the end of the larval feeding the previous year. The cocoon occupied the entire cell, conformed to its dimensions and shape, and did not adhere to the cell wall. Although somewhat thicker at the front end, the cocoon fabric elsewhere was approximately 0.5 mm. thick and consisted of two layers. The outer, dull reddish brown one was composed of indistinct sheets of loose fibers and accounted for the thickness of the casing. The inner layer, shiny brown on the interior, was parchment-like, very thin, and fenestrated in some areas.

Adult Activity. Meganomia binghami apparently has a single generation per year, because no

FIG. 9. Cocoon of *Meganomia binghami*, side view, anterior end to the left.

active postdefecating larvae were found as would be expected if the adults were from the second generation. Although the adults might have represented the first generation of a bivoltine life history, the season (early fall in South West Africa) probably would have been too short to permit the development of a second generation before the onset of cool weather. As indicated above, the nesting activity was not completely synchronized from one site to another even though all sites were within 75 km. of one another and had the same climatic conditions.

Subjective population censuses taken in late morning at three sites indicated (1) at 17 km. east of Usakos, the earliest in seasonal activity, males far exceeded females; (2) at 62 km. west of Omaruru, the next earliest in seasonal activity, males still predominated but relatively more females were present than at the preceding site; and (3) at 52 km. southwest of Omaruru, the site farthest along in adult activity, females were as abundant as males. The sites were visited within nine days of one another. These facts suggest that during adult activity, males reach peak abundance first, then decline, and that females predominate late in the period.

Mating of *M. binghami* occurred in association with the pollen plant and with the nesting site. The two nesting sites first discovered were initially identified by the loud buzzing noise caused by males flying swiftly 10 to 15 cm. over both ground and plants, in search of females. At 62 km. west of Omaruru, the large number of males could be heard 20 meters away. The male's flight over the nesting site was usually so swift that the insects could scarcely be seen. Females generally flew somewhat slower, perhaps because they were searching for potential nest sites or for their nests. The male's flight suggested that of *Bembix* except the males of *M. binghami* almost never alighted on the ground to rest, a rather remarkable feature considering the rapidity of their flight. They did stop on the flowers for nectar from time to time.

At the nesting site and on the flowers, as many as four males were seen swiftly pursuing a single female, sometimes for a distance of more than 6 meters. Clumps of four to 10 males were occasionally seen flying in a swift, tight, meandering fashion near copulating pairs on the ground (fig. 10) or near emergence holes on the ground, presumably when females were about to appear. Males seemingly attempted to nudge and thereby to break apart both clasping and mating couples.

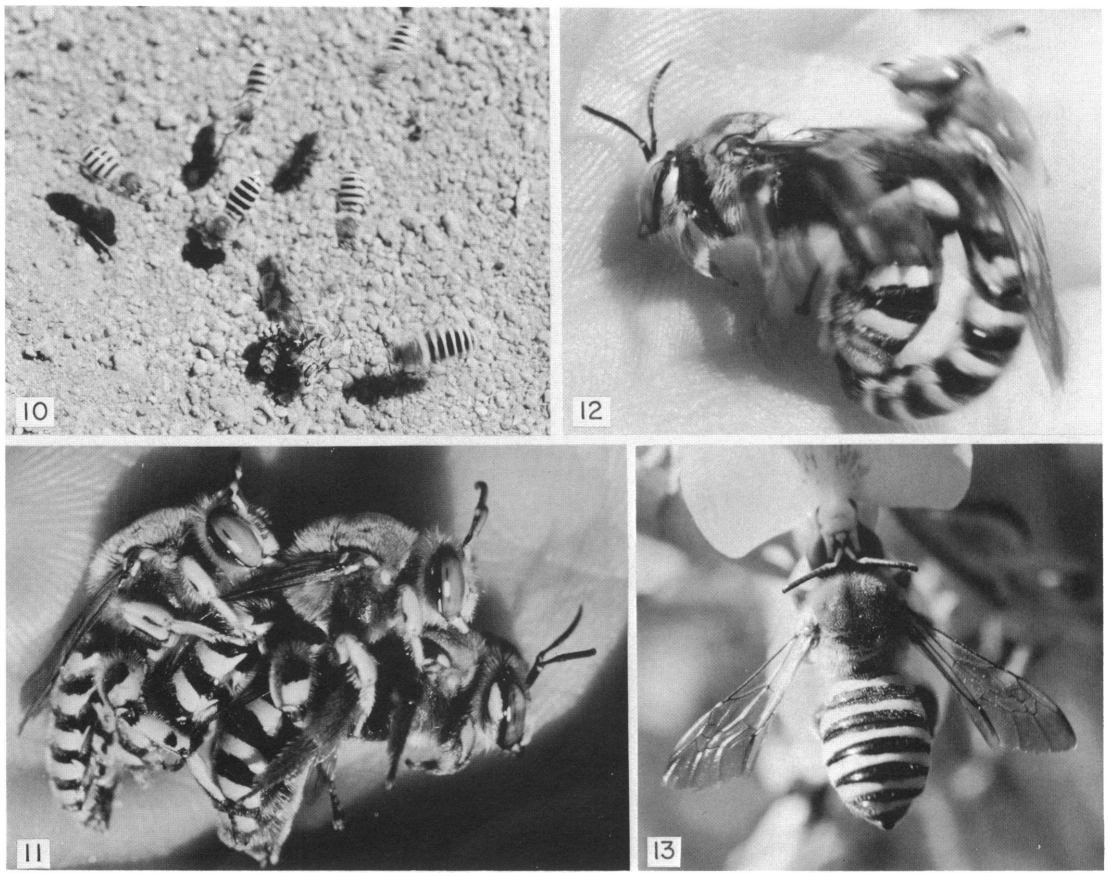
No particular behavior of the female appeared to signal willingness to mate. Indeed, she seemed pursued by males at all times, i.e., when leaving the nesting area, when starting to excavate a nest, when returning with pollen, and while feeding or collecting pollen.

One remarkable aspect of the mating sequence was that I could invariably pick up clasping pairs of *M. binghami* without their disengaging or without the female attempting to sting. Holding them in my palm I could photograph them while they proceeded to clasp (the term is defined below) and on one occasion (fig. 12) to initiate copulation. Several times while clasping and intermittently tumbling in my hand, they fell to the ground (about 1.5 meters) and I was able to pick them up again without their separating. In one case (fig. 11) a clasping pair was mounted by a second male and the *ménage à trois* was picked up without being disturbed. Because of this remarkable behavior pattern and because of very large body size, this species would be ideal for more detailed analysis of mating using slow-motion moving pictures and tape recorder.

The mating sequence was divided into a clasping period, lasting for 60 seconds or more, followed by a copulatory period of 5 to 20 seconds. We never saw mating sequences being initiated, but mating pairs were easily seen because of the numerous males flying around the pair, the female's buzzing as she tried to escape from the clasping male, and the rasping squeak produced during copulation. Mating occurred normally on the ground but occasionally while the pair clung to vegetation.

In clasping, the male wrapped his enlarged, modified hind femora and tibiae around the female's waist so that his venter was against her dorsum and they both faced the same direction. His hind tarsi directed forward along her venter usually paralleled each other although they sometimes crossed. His other legs seemed to be employed in pinioning her wings and legs. This posture is exhibited in figure 11 in a normal fashion; the presence of the second male was not seen in any other matings.

Clasping pairs were often found tumbling on

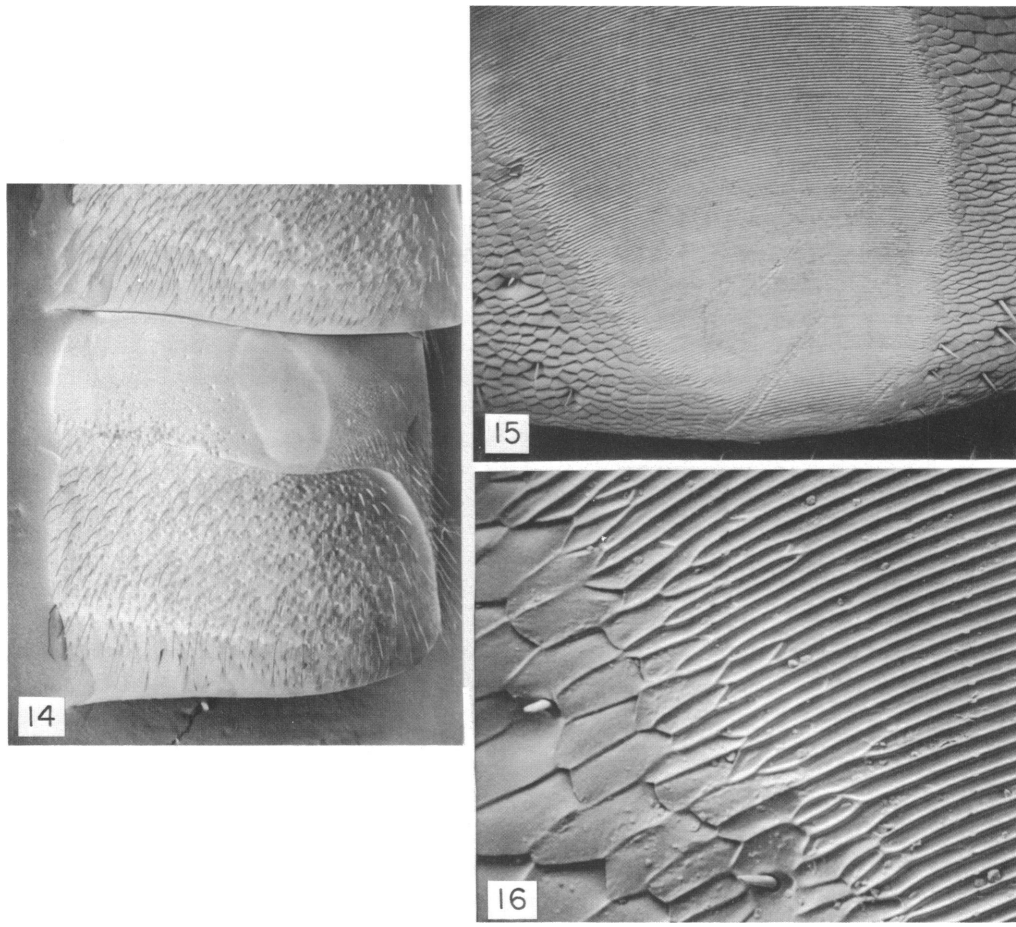


FIGS. 10-13. Adults of *Meganomia binghami*. 10. Six males circling clasping pair (center bottom) on ground. 11. Female (bottom) clasped by male, which in turn is mounted by second male, all held in author's hand. 12. Copulating pair, held in palm. 13. Male with mandibles extended, prying keel of *Crotalaria* flower downward.

their sides or backs as the female intermittently attempted to free herself. On several occasions females worked themselves loose before copulation. Usually, however, the pair clasped for approximately one minute and then initiated copulation (fig. 12) as the genitalia and apical metasomal sterna of the male extended and engaged the tip of the female's metasoma. Copulation was easily identified because, as the male rhythmically and spasmodically contracted his metasoma, a clearly audible rasping squeak was produced. The noise emission lasted approximately 0.5 second at 1 second intervals during the full period of copulation (5 to 20 seconds).

This sound almost certainly is produced by a pair of large oval lateral pregradular stridulatory areas (figs. 14-16) on each of male metasomal terga IV and V and by a smaller similar pair on VI. These areas seem to be scraped by the posterior margin of the preceding segment, apparently as a male contracts or extends his metasoma. Although I first thought that the male alone produced the sound, females also possess well-developed stridulatory patches on metasomal terga IV and V and therefore may contribute to sound production. By extending and contracting the metasoma on recently killed and still soft males I was able to generate a somewhat similar though softer sound.

As he copulates, the male seems to slide pos-



FIGS. 14-16. Pregradular stridulatory area on right side of male metasomal tergum IV. 14. 26×. 15. 130×. 16. 680×.

teriorly and looses his grasp, at times enabling the female to break free either by crawling or flying. On several occasions males with genitalia still engaged were dragged over the ground for approximately 10 cm. before they separated. Similarly several females flew into the air for 10 to 15 cm. before the males disengaged and the females flew on. However, several couples were observed to disengage by the male releasing the female without her struggling. After mating, males and females sometimes flew away immediately and other times one or the other cleaned itself while resting on the ground.

Males of *Meganomia* species B flew swiftly from one flower clump of *Indigofera* to another, presumably searching for females; rarely was more than one male seen at a time. The sound they emitted, like that of females of the same species, was higher pitched than that of *M. binghami* and was about as loud and at the same pitch as that of a honey bee. Although no matings were seen probably they occurred in the vicinity of the pollen plant.

The daily activity of males of *M. binghami* was observed at 62 km. west of Omaruru. Between 9:00 and 10:00 a.m. on a clear, warm day, males flew in great numbers over the nesting site and surrounding pollen plants. By early afternoon their numbers had decreased appreciably and by 5:00 p.m. far fewer males were present,

although some were still seen stopping at flowers to feed, chasing females, and mating. Both here and at 52 km. southwest of Omaruru female abundance appeared to be constant during the day.

Males and females fed on the *Crotalaria* flowers in a similar fashion. The bee landed on the nearly horizontal keel of the flower and faced the banner; it then forced the keel downward with its body by prying the extended mandibles (fig. 13) against the banner, thus causing the longitudinal slit of the keel to open. The bee then extended its mouth parts into the slit and presumably imbibed nectar. This also seems to be the mode of feeding of other large bees visiting *Crotalaria.*

Nesting females probably sleep in their burrows, as is characteristic of most ground-nesting bees. Males were never seen entering burrows in the late afternoon, a fact suggesting that they do not spend the night in the ground.

At 62 km. west of Omaruru all cocoons encountered, both occupied and vacated, were retrieved and examined. A tally of their contents follows:

Vacated cocoons	37
Cocoons containing live *M. binghami* (or individuals accidentally killed while being excavated):	
Adults	1
Pupae	9
Postdefecating larvae	27
Total	37
Cocoons containing dead *M. binghami*:	
Cause of death unknown	23
Killed by clerid larvae	2
Total	25
Total cocoons retrieved	99

All cocoons seemed to belong to the last generation as judged by lack of deterioration. If this is true, then of all individuals of *M. binghami* that survived until the date of excavation (March 25, 1976), exactly half (37) had emerged, leaving their vacated cocoons in the ground. Of the 37 live individuals that remained in the ground as of my excavation, 10 (1 adult, 9 pupae) probably would have emerged in the current season. The other 27 probably would have remained in diapause another year, a deduction based upon the fact that none of the 15 postdefecating larvae brought back to the United States had pupated by April 25, 1976, more than one month after being collected, and none of the larvae preserved at the time of excavation seemed to be near pupation. A conclusion from these figures is that, even in a year of abundant moisture and flowering, slightly more than one-third of the offspring of the previous generation still surviving (i.e., 27 of 74) do not break diapause; presumably they would appear the following year.

An adult male emerged on July 13, 1976 from one of the 15 postdefecating larvae brought to the United States. Two other male larvae had pupated by that date. The significance of these facts is hard to assess, but presumably such an emergence would not have taken place in the climatic conditions of South West Africa in July.

IMMATURE STAGES

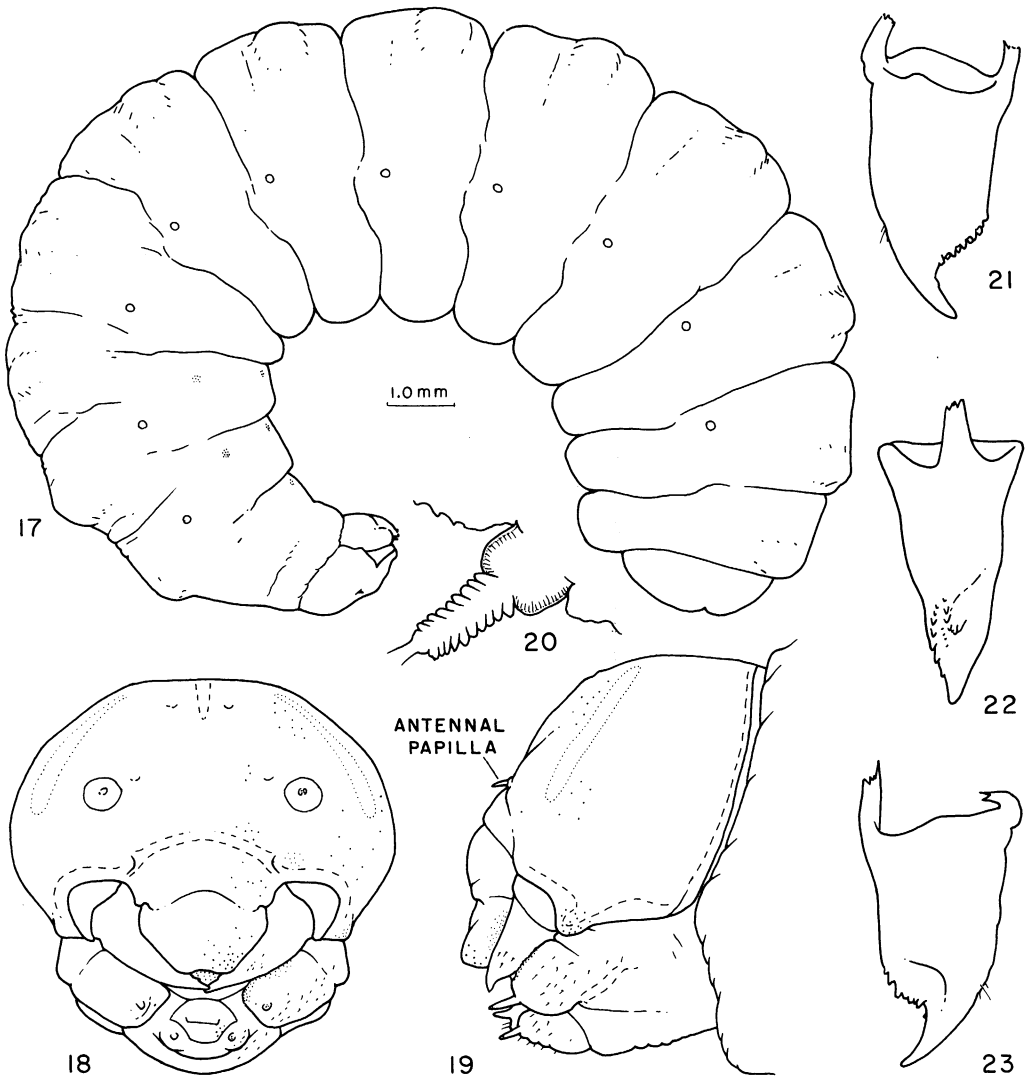
Mature Larva

Figures 17-23

The larva of this species is compared with the larvae of other melittids described by Rozen and McGinley (1974).

Diagnosis. This species can be separated from all other melittids except for *Macropis* and *Melitta* on the basis of the strongly produced labiomaxillary region of the mature larva, an indication of its cocoon-spinning abilities. It can be separated from both *Macropis* and *Melitta* because of its spinose subatrial wall, elongate antennal papillae, scarcely noticeable galeae, and various features of the mandible.

Head (figs. 18, 19). As described for *Macropis europaea* Weke (Rozen and McGinley, 1974) except for the following: Not only epipharynx and upper part of hypopharynx finely spiculate but also dorsal surface of maxilla; entire head capsule darkly pigmented by comparison with that of *Macropis* and *Melitta.* Supraclypeal area not quite so flat as that of *Macropis* as seen in lateral view (fig. 19). Longitudinal thickening of head capsule well developed above; parietal band pronounced; unlike in either *Macropis* or *Melitta* area immediately behind posterior mandibular articulation somewhat projecting, beset with numerous sensilla, and apparently rubbing against swollen area at base of maxilla. Antennal prominences slightly more evident than those of



FIGS. 17-23. Mature larva of *Meganomia binghami*. 17. Live larva, lateral view. 18. Head, front view. 19. Same, lateral view. 20. Spiracle, side view. 21-23. Right mandible, dorsal, inner, and ventral views, respectively. Scale refers to figure 17.

Macropis; antennae situated slightly higher on face compared with those of *Macropis*; papilla elongate, more so than that of any other known melittid, approximately one and one-half times basal diameter, bearing three to four sensilla. Clypeus not quite so narrow as that of *Macropis*. Mandible (figs. 21-23) normally elongate, longer than that of *Macropis*, tapering to simple apex; cusp well developed with many moderately large teeth extending apically along dorsal adoral surface; dorsal inner edge well defined and bearing a number of moderately large teeth; ventral edge also well defined but without teeth; apical concavity moderately expressed. Maxillary apex bent about as strongly mesiad as that of *Macropis*; galea very small, scarcely noticeable. Labium

distinctly divided into prementum and postmentum; labial palpi large and conspicuous, slightly smaller than maxillary palpi.

Body. Integument conspicuously wrinkled except where spiculate; spiculation on most dorsal tubercles, dorsal surfaces of abdominal segments IX and X and venter of IX; scattered fine setae present on dorsal tubercles; integument associated with imaginal discs of legs and wings darkly pigmented, hence position of discs easily definable. Dorsal tubercles (fig. 17) less pronounced than those of *Macropis*, not causing caudal annulets to appear noticeably higher than cephalic annulets; lateral swellings below spiracles indistinct; dorsal intrasegmental lines present. Abdominal segment IX with venter slightly protuberant though not elongate; segment X slightly dorsal in attachment to IX, moderately short and rounded; venter of segment X not elongate; anus apical in position, distinctly transverse; perianal area very faintly wrinkled; dorsal limit of area not identified by ridge but rather by the appearance of spicules anterior to area. Spiracles (fig. 20) not on elevations; atrial rim present and produced above body surface; peritreme present but very narrow, narrower than in other melittids; atrial wall thickly beset with spines; primary tracheal opening with jagged collar; subatrial chamber with collar also jagged; subatrium moderate in length. Male with deep median, slightly transverse, cuticular invagination on abdominal sternum IX approximately one-fourth to one-third distance from posterior margin of segment. Female with paired cuticular scars evident on venter of abdominal segments VII, VIII, and IX, their location approximately same as imaginal discs of *Macropis*.

Material Studied. Fourteen postdefecating larvae, 62 km. west of Omaruru, South West Africa, March 25, 1976 (J. G. and B. L. Rozen).

Pupa

Figures 24-26

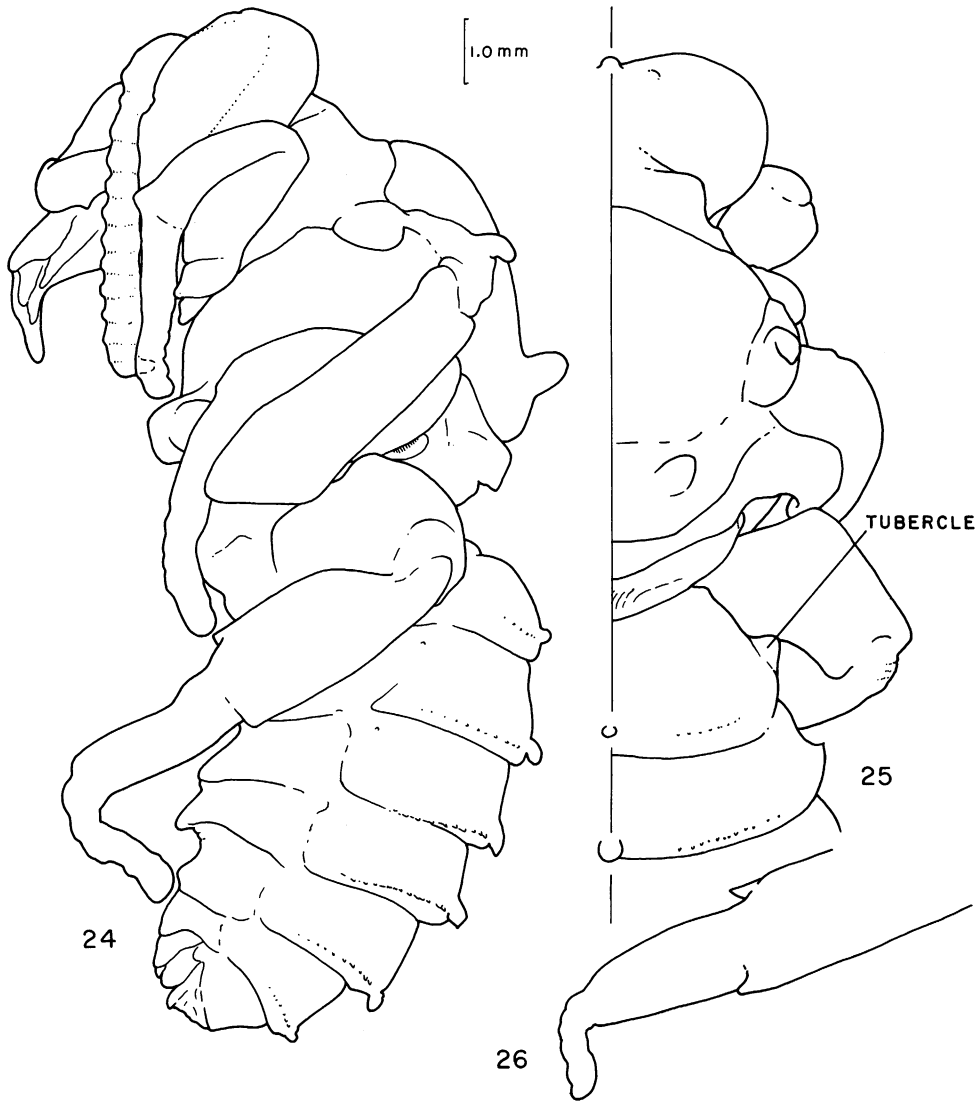
The following is comparative with the treatment of the pupae of *Melitta leporina* (Panzer) and *Macropis europaea* Weke in Rozen and McGinley (1974).

Diagnosis. The pupa of *Meganomia binghami* is easily distinguished from those of the above taxa by the placement and size of various tubercles and spines, as described below.

Head. Integument without setae or spicules. Scape, frons, and vertex without tubercles; pedicel without tubercles; apical flagellar segment of male abruptly bent at right angles to long axis of flagellum, corresponding to the modification of the same segment in adult; flagellar apex of female normal. Gena with short spine immediately behind mandibular base; mandible simple, with small tubercle on ventral surface.

Mesosoma. Integument without setae or spicules. Lateral angles of pronotum scarcely produced; posterior lobe of pronotum only moderately produced, rounded posteriorly; mesepisternum without tubercles; mesoscutum without tubercles; axilla not produced and undifferentiated; scutellum with pair of large, well-differentiated, dorsally projecting tubercles; metanotum with median swelling but without tubercles; propodeum without tubercles. Tegula with large dorsal tubercle (in *Melitta leporina* and *Macropis europaea* tubercle absent); wing without tubercle. Fore coxa with short apical spine; fore trochanter with very short, less distinct apical spine; fore femur with outer basal angle acute, spinelike. Mid-coxa with inner apical angle strongly produced in male (corresponding to peculiar modification of adult), somewhat less produced in female; mid-trochanter only slightly produced in male, more conspicuously produced in female; mid-femur with outer basal angle having slight swelling in female, unmodified in male. Hind coxa with very small apical tubercle in both sexes; hind trochanter with small apical swelling in male, larger swelling in female; femur of male greatly enlarged, corresponding to same condition in adult, and with distinct swelling midway on anterior surface of segment; hind femur of female unmodified; hind tibia in male with vague posterior apical swelling, in female this swelling a distinct tubercle; hind basitarsus of male somewhat concave on ventral surface corresponding to modification of area in adult; basitarsus of female (fig. 26) normal.

Metasoma. Integument without setae. Terga I through VI (male) and I through V (female), each with conspicuous median apical tubercle in



FIGS. 24-26. Pupa of *Meganomia binghami*. 24. Male, lateral view. 25. Right side of male, dorsal view. 26. Apex of hind leg of female, lateral view.

contrast to the lack of such tubercles in *Melitta leporina* and *Macropis europaea*; same terga also with apical transverse row of very small tubercles; lateral part of segment I with pronounced tubercle in both sexes when pupa is in early stages of development; this tubercle becoming less pronounced as adult features develop; sterna without tubercles; terminal spine absent.

Material Studied. Three males, two females, 62 km. west of Omaruru, South West Africa, March 25, 1976 (J. G. and B. L. Rozen).

CONCLUSIONS

Rozen and McGinley (1974) reported that the larvae of both *Melitta* (Melittinae) and *Macropis* (Macropidinae) possess numerous character states that are primitive in contrast to the larvae of the

Dasypodinae, which have undergone extensive evolutionary change. Although *Meganomia* larvae are similar to those of *Melitta* or *Macropis*, the shared similarities are almost all symplesiomorphies, as defined in table 1 of their paper; specifically these characters are 1-6, 8, 10-19. Characters 7 and 20 are somewhat intermediate in *Meganomia* and are therefore excluded from interpretation in this section. In evaluating the taxonomic placement of *Meganomia* in the family, I conclude that information about its larva in no way contradicted Stage's (1971) transfer of the genus to the Melittidae. However, supportive proof of this placement cannot be forthcoming from studies of larvae because of the absence of synapomorphies among larvae of *Meganomia*, *Melitta*, and *Macropis*. No characteristics of *Meganomia* larvae indicate that the genus is more closely related to other families of bees than to the Melittidae, and, of course, there is ample evidence, presented by Stage (1971) to include *Meganomia* in the Melittidae on the basis of adult features.

An analysis of the characters of the larva of *Meganomia* provides an interesting picture of the relationship of the genus to other members of the family (fig. 27). (Characters 23-26 are new in the present paper; other characters are in Rozen and McGinley, 1974.) The elongate antennal papilla is more primitive than in any other melittid the larva of which is known because elongate antennal papillae are thought to be more primitive in bee larvae than short ones (with the exception of certain cleptoparasitic forms such as *Dioxys*). If this is true, then all other known melittid larvae share a derived character state (fig. 27, Character 26), namely short antennal papillae, and hence, *Meganomia* seems to be a sister group to the other melittids.

Meganomia does not share the specialized condition of the spiracular subatrial chambers of *Melitta* (Rozen and McGinley, 1974, table 1, Character 15) or a short mandible (Character 8), a derived feature of *Macropis*. It differs from both these genera and the hypothetical primitive melittid by having the following synapomorphies:

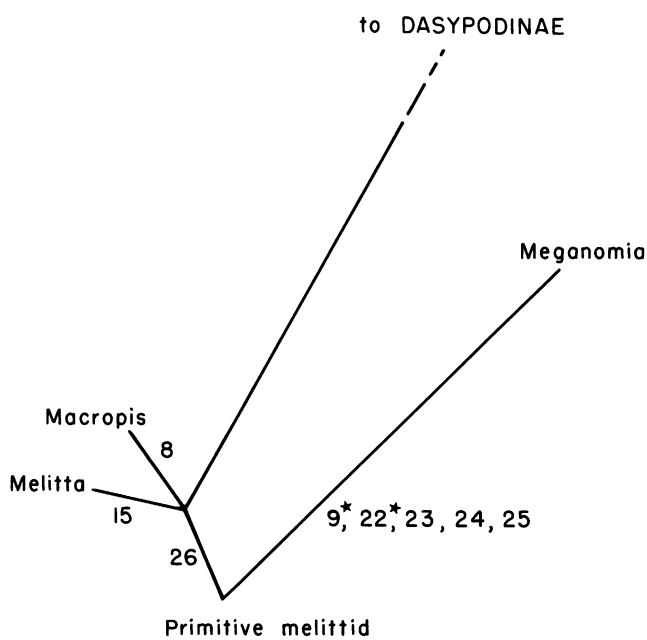


FIG. 27. Hypothesized phylogeny of the Melittidae, modified from figure 5 in Rozen and McGinley (1974). Numbers refer to characters as discussed in text; length of line approximates amount of character change; number with asterisks indicates that feature had multiple origin in family. For further explanation see text.

simple mandibular apex (Character 9) (also occurring *de novo* in some Dasypodinae); area behind posterior mandibular articulation projecting and apparently rubbing against adjacent swollen area of maxilla (Character 23); perianal area without dorsal transverse ridge (Character 22) (also occurring *de novo* in some Dasypodinae); atrial wall beset with elongate spines (Character 24); and collar of primary tracheal opening jagged as are the collars on subatrial chambers (Character 25). The synapomorphic condition of Characters 9, 23, 24, and 25 has been determined by comparisons with other groups of bees; that of Character 22 was deduced after the completion of the cladistic analysis of Characters 1-15 (Rozen and McGinley, 1974).

Figure 27, a modification of figure 5 in Rozen and McGinley (1974), presents this information in terms of the most probable phylogeny within the family excluding the Ctenoplectrinae, the larva of which is yet unstudied.

A cladistic classification of the family if adopted would dictate that *Meganomia*, as a sister group to all other melittids, should be placed in its own subfamily.

LITERATURE CITED

Rozen, Jerome G., Jr., and Ronald J. McGinley
1974. Phylogeny and systematics of Melittidae based on the mature larvae (Insecta, Hymenoptera, Apoidea). Amer. Mus. Novitates, no. 2545, pp. 1-31, figs. 1-82.

Stage, Gerald I.
1971. Family placement of the African genus *Meganomia* Cockerell with a review of the included species (Hymenoptera: Apoidea). Proc. Ent. Soc. Washington, vol. 73, no. 3, pp. 306-313, figs. 1-10.