

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024  
Number 3138, 19 pp., 22 figures, 1 table  
May 26, 1995

## Foraging and Nesting Biology of the Bee *Anthemurgus passiflorae* (Hymenoptera: Apoidea), Descriptions of Its Immature Stages, and Observations on Its Floral Host (Passifloraceae)

JOHN L. NEFF<sup>1</sup> AND JEROME G. ROZEN, JR.<sup>2</sup>

### ABSTRACT

Information on the nesting, foraging, and mating biology of *Anthemurgus passiflorae* Robertson is presented based on observations of a population in Austin, Texas. The population is multivoltine with the late spring-summer flight period bounded by the flowering period of *Passiflora lutea*, its only known floral host. Nest arrangement indicates that the bee is weakly gregarious, with one female per nest. Nest architecture is simple, differing from that of its close putative relatives only in features related to nest reuse within a season. Females average six pollen trips per day, apparently provisioning one cell per day during peak *Passiflora* bloom. In behavior novel for panurgine bees, females scrape pollen from the *Passiflora* anthers with their mandibles. Despite gregarious nesting,

mating and mating attempts were observed only at *Passiflora* flowers. Data on nectar and pollen production of *P. lutea* are presented.

The mature larva of *Anthemurgus passiflorae* is described, illustrated, and compared with larvae of other known panurgines. It resembles closely those of other Anthemurgini (*Protandrena*, *Pseudopanurgus*, *Pterosarus*, *Heterosarus*, *Parasarus*, *Cephalurgus*, *Metapsaenythia*, *Psaenythia*, *Rhopitulus*, *Anthrenoides*, and apparently *Liphanthus*) and *Melitturga*. However, phylogenetic analysis of the panurgines based on larvae will be attempted only after new South American taxa are named and described. The pupa of *A. passiflorae*, also discussed, is similar to known anthemurgine pupae.

<sup>1</sup> Director and Curator, Central Texas Melittological Institute, 7307 Running Rope, Austin, Texas 78731.

<sup>2</sup> Curator, Department of Entomology, American Museum of Natural History.

## INTRODUCTION

We present information on foraging and mating behavior and on nesting biology of *Anthemurgus passiflorae* Robertson (Andrenidae: Panurginae: Anthemurgini<sup>3</sup>) and describe its mature larva and pupa. We hope that these data, not previously recorded, will further elucidate the phylogenetic relationships of this monotypic genus with other members of the andrenid subfamily Panurginae.

The Panurginae is a large group of small bees which reaches its greatest diversity in temperate and subtropical North and South America. It is also represented in Africa and the Palearctic but is absent from Australia. The subfamily has long been of biological and evolutionary interest because of the prevalence of oligolecty and structural diversity among its members. Analysis of host relationships was hampered by the poorly resolved phylogeny of the group, and investigations on the phylogeny were inhibited because of the subfamily's large size (probably more than 2000 species) and diversity (37 genera).

Recently, however, Ruz (1986) undertook a morphological analysis of the Panurginae. She demonstrated that *Anthemurgus* belongs to a largely unresolved clade including *Heterosarus*, *Pseudopanurgus*, *Pterosarus*, *Metapsaenythia*, and several South American genera. Excluding the basal genera *Liphanthus* and *Protandrena*, this clade is the sister group to the rest of the Panurginae. Ruz's work invites further analysis of the subfamily, and the data that we present should provide additional clues to the relationships within the clade.

*Anthemurgus* is an infrequently collected monotypic genus of the southern and central regions of the United States. Individuals are small, black, 7.5–8.5 mm long, and are the only bees believed to be restricted to the Pas-

sifloraceae as a pollen host. Beyond a few reports of floral records (Robertson, 1902; Mitchell, 1960), nothing has been published on the biology of *A. passiflorae*.

Information on foraging, nesting biology, and the floral host was prepared by the first author (JLN). The immature stages were described by the second author (JGR).

## ACKNOWLEDGMENTS

The late G. E. Eickwort identified *Trochometridium*, and J. Manley identified *Pseudomethoca*. We would like to acknowledge our appreciation to Bryan N. Danforth and James H. Cane for taking the time to read the manuscript and for their helpful comments.

## FORAGING AND NESTING BIOLOGY

All observations and nest excavations were undertaken at the Brackenridge Field Laboratory (BFL) of the University of Texas, Austin (30°17.10'N, 97°46.83'W). Foraging and mating behavior were timed to the nearest second with hand-held digital watches. Observations of activity (or, more commonly, inactivity) at flowers at BFL totaled 11 hours. Mating and pollen collecting activities at flowers were recorded with an 8 mm video camera. Individual females were marked with dots of quick-drying enamel on the thorax. Nest entrances were covered with clear plastic cups to facilitate timing of provisioning behavior. This technique permits large numbers of nests to be monitored at one time but decreases precision since movements to remove the cups altered the bees' behavior, often significantly delaying entry to or departure from the nests.

Bees, pollen loads, and anthers were weighed to 0.1 mg with a Cahn 25 Microbalance. Pollen production per anther was estimated by compound microscope counts of glycerin squashes of intact mature anthers. We used 1 ml pipettes to extract nectar from previously bagged flowers. Nectar concentration was calculated with hand-held refractometers and the readings converted from the Brix scale to weight by volume for estimating total sugars (Cruden and Hermann, 1983).

<sup>3</sup> Ruz (1986) developed two classifications on the basis of a cladistic study of the Panurginae. The strictly monophyletic classification results in nine tribes, with five of them being monogeneric. The other, consisting of six tribes, places four of the basal clades in a single paraphyletic tribe, the Anthemurgini, and leaves only a single monogeneric tribe. It is in the latter sense that *Anthemurgini* is used in the current study.



Fig. 1. Nest site of *Anthemurgus passiflorae* at the Brackenridge Field Lab, Austin, Texas. Nests are scattered in bare areas on margins of path.

Nectar composition was determined by High Performance Liquid Chromatography (see Neff and Simpson, 1990, for methods). Floral UV reflectance was checked by photographs with a Kodak 18A filter. Data are presented as mean  $\pm$  1 SD followed by sample size and range. All times are Central Daylight Savings Time. Sunrise during May through July in Austin ranged from 0626 to 0644 hrs.

All studied nests were clustered along a 3 m long portion of a dirt path through little bluestem (*Schizachyrium scoparium* [Michx.] Nash) grassland in oak-juniper woodland at BFL. The soil is a deep, fine-grained, hard-packed, red, sandy loam with numerous tree roots and limestone inclusions. Surrounding plateau live oak (*Quercus fusiformis* Small) and Ashe juniper (*Juniperus ashei* Buchh.) shaded most of the nest area until noon each day. A few nests were found on the flat floor of the path but the majority were on the bare, gently sloping sides of the slightly sunken path (fig. 1). All of the nests were initiated in bare ground, none being closely associated with

vegetation or rocks, although falling leaves later covered the entrances of several active nests.

*Anthemurgus* nests were first noted at BFL at the site described above in 1979, and additional nests were active in 1980 and 1981. Nests likely to have been those of *Anthemurgus* were present at this site each year from 1982 through 1993 but were not confirmed as such until 1992. The earliest observation of activity was 5 May 1981, and the latest was 20 July 1992. In the best-studied year (1992), total flight season was a minimum of 56 days (26 May [although it almost certainly began earlier] through 20 July). Seven females were still active on 20 July when we had to leave the study area. No females were active when we returned on 29 July, and none was observed at any time later that year. A maximum of 15 nests was active at any one time along the path.

Although only a single female is ever associated with a particular nest at any one time, individual nests may be reused within a sea-

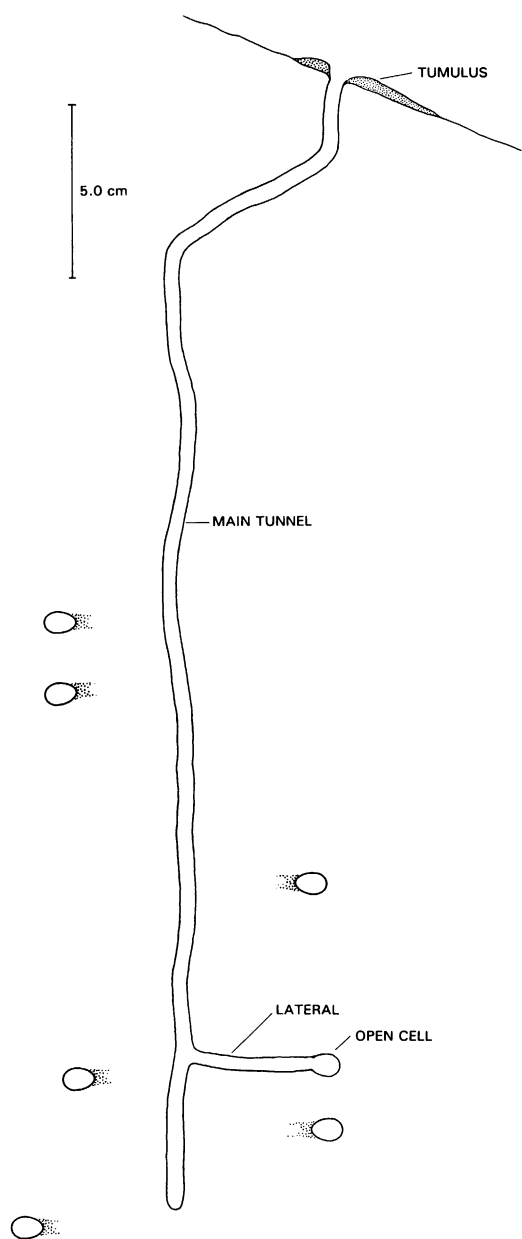


Fig. 2. Nest of *Anthemurgus passiflorae*, side view.

son. At three nests with marked females, provisioning was initiated by new unmarked females 7 to 16 days after the marked original occupant was last seen. Reuse of several other nests was likely but not confirmed since the occupants were not marked.

The long flight season and the pattern of nest reuse suggest multivoltinism, although this could simply be caused by greatly extended emergence of a single generation. Evidence from nest excavations and monitoring of individual nests indicates *Anthemurgus passiflorae* is at least partially bivoltine. Excavations (18 and 20 July 1992) during the provisioning season yielded a mix of older empty cells, cells with developing larvae, hibernating larvae, and larvae initiating pupation. A nest (B-5) excavated 13 November 1992, well after the cessation of all adult activity, contained 23 cells, 12 of which were infested by fungi and mites. Of the remainder, six cells were old, empty cells with fecal smears, four contained quiescent, defecated prepupae, while the last cell was empty with a dead female *Anthemurgus* in the lateral. Provisioning activity at this nest was continuous from 29 June through 7 July 1992. Since the second occupant made only enough trips to provision a single cell, the mix of old cells and prepupae suggests partial bivoltinism although the older cells may have been from a previous year. The maximum number of generations per year was not determined.

The adult lifespan of individual bees appears to be relatively brief, although available data are still sparse. The longest period of continuous activity for an individual nest was 19 days, but most nests were continuously active for no more than 10 days. The only female observed to initiate a new burrow made two nectar trips on her first day but failed to return from her second pollen foraging trip on the following day.

The architecture of nests of *Anthemurgus passiflorae*, like that of the related panurgines *Pseudopanurgus* and *Heterosarus* (Rozen, 1967, 1989), is quite simple (fig. 2). Newly constructed nests occurring on flat surfaces have a low, roughly conical tumulus about the entrance. The tumulus tends to be asymmetrical when the nest is initiated on a sloping surface, with most of the tumulus down-slope from the entrance. Older nests usually lack a tumulus, indicating that excavated soil is simply relocated within the nest.

Entrance diameters averaged  $3.5 \pm 0.6$  mm (2.6–4.5 mm,  $N = 12$ ). In several cases the entrance was clearly constricted relative to

the width of the main burrow. In one case the burrow diameter of 4.3 mm at a depth of 15 mm decreased to 3.5 mm at the entrance. The main burrow descends vertically for the first 1 to 2 cm from the nest entrance before turning at a roughly 45° angle for 5 to 7 cm before again continuing a roughly vertical descent. The main burrow is circular in cross section with a diameter of 3.5 to 4.3 mm. Although there was no indication of a secreted lining to the main burrow, walls of the upper portions of the main burrow of several nests had been extensively reworked with a soil type different from that of the substrate at that depth. The nests had all been reused within a season.

Cells are normally placed singly at the end of short, horizontal laterals off the main burrow. A single instance of two cells in a linear series was observed. Virtually all cells were 1 to 3 cm from the main burrow. Few open laterals were discovered, as laterals are filled with soil after cell closure. Diameters of the three open laterals examined were all slightly less than that of the main burrow at that depth. Cells were found at depths of 11 to 41 cm with an average depth of  $23.2 \pm 7.3$  cm ( $N = 67$ ) (fig. 7). Of these cells, 78% occurred at a depth between 15 and 30 cm. Individual cells are elongate spheroids, primarily horizontal in orientation, but sometimes slightly descending from the entrance. Measurements from seven cells indicated an average cell length of  $8.9 \pm 0.8$  mm (8.3–10.0 mm) and an average maximum width of  $5.2 \pm 0.4$  mm (4.7–5.6 mm) with an average cell entrance width of  $3.4 \pm 0.2$  mm (3.2–3.7). Cell walls are completely coated with a thin, smooth, shining, waterproof lining. The cell closure is unlined and formed of an earthen spiral of 2 to 3 turns.

The order of cell construction appears to be progressive in newly initiated nests but more complex in older nests. In two reused nests, the main burrow was open considerably below the lateral to the cell currently being provisioned. There was no clear order to the placement of recently provisioned cells within the nest relative to the most recently provisioned cell (fig. 2). Although the nest entrance and upper portions of the burrow may fill with soil after the cessation of female

activity, the lower portions remain open. Due to the pattern of nest reuse and extensive mortality from mite infestation, the maximum number of cells provisioned per female was not determined with certainty. The only nest excavated after the cessation of foraging (B-5) contained 23 cells of which the first occupant probably constructed 21 (assuming none was from a previous year).

**HOST PLANT:** *Passiflora lutea* L., the plant on which Robertson first collected the type series of *Anthemurgus* (Robertson, 1902), produced the only flowers utilized by males and females of *Anthemurgus passiflorae* at BFL. It is a perennial, herbaceous climbing vine occurring in rich forests and woodlands throughout the southeastern United States, extending as far north as Pennsylvania and Illinois and reaching its southwesterly limits in central Texas (Killip, 1939). Flowering occurs from May through October in central Texas, peaking in June and July.

Individual vines are widely scattered at BFL, and we had great difficulty finding plants in bloom. The bees were apparently much more successful in locating hosts. The floral display of *Passiflora lutea* vines at BFL is rarely conspicuous. Individual vines normally have only two to four flowers open per day, although occasional very large vines, typically quite high in the canopy, had 30 or more flowers open at one time. Individual flowers, with a corolla diameter of 1 to 2 cm, are relatively small for a *Passiflora*, weakly scented, and relatively inconspicuous in the understory with their pale yellow, green, and white coloration. Strong UV reflection is absent.

Greenhouse crosses indicate *Passiflora lutea* is self-incompatible. Forty-four of 45 hand cross-pollinations set fruit, but none of 18 hand self-pollinations did so. Like those of many other *Passiflora* species (Janzen, 1968), flowers of *P. lutea* are strongly herkogamous and functionally protandrous. Under normal Central Texas summer conditions, the flowers typically open between 0800 and 0900 hrs. The stigmas are held well above the anthers at anthesis and typically do not descend to anther level until after 1200 hrs (fig. 3). The flowers last a single day and close in the late afternoon or evening. Most flowers on a



Figs. 3-6. 3. Flower of *Passiflora lutea*, side view of early male phase ( $2.4\times$ ). 4-6. Female of *Anthemurgus passiflorae*. 4. With mounted male, foraging on flower of *Passiflora lutea* ( $2.4\times$ ). 5. Collecting pollen of newly opened flower of *Passiflora lutea* ( $3.5\times$ ). 6. Collecting pollen of *Passiflora lutea* ( $2.4\times$ ). Pollen evident on clypeus and mandibles.

vine are functionally hermaphroditic, but in some flowers the stigmas never descend. This makes the flowers functionally male and the plant functionally andromonoecious, a condition noted for a number of other *Passiflora* species (McGregor, 1976; May and Spears, 1988).

Flowers of *Passiflora lutea* produce a sucrose-dominant nectar ( $90.1 \pm 9.1\%$  S [N = 4, 80–100%]). Analysis of nectar accumulation in bagged flowers indicates a constant rate of sugar production of 0.106 mg sucrose per hour (least squares regression analysis of 34 samples,  $r^2 = 0.759$ ,  $p < .0001$ ) from anthesis (0800–0900) to 1800 hrs. Nectar sugar concentration in bagged flowers increases from a mean of  $29.4 \pm 5.2$  mg/ml (N = 5) in the early morning (0830–0930 hrs) to  $52.1 \pm 19.6$  mg/ml (N = 16) in the afternoon (1500–1830 hrs).

The subprolate pollen grains of *Passiflora lutea* are relatively large (expanded long axis length of 65  $\mu$ m), have simple exine sculpturing, and stain strongly with iodine indicating starchy pollen reserves. Individual anthers produce an average of  $1715.6 \pm 176.7$  grains (N = 7, 1548–2086 grains) or  $0.142 \pm 0.012$  mg fresh wt (N = 12, 0.125–0.157 mg) yielding an average total production of 8578 grains or 0.708 mg pollen per flower.

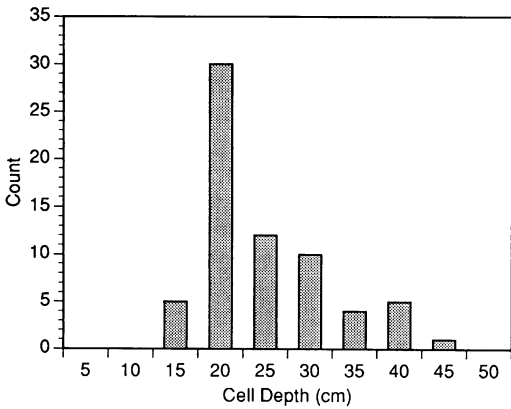
**INTRAFLORAL BEHAVIOR:** Female *Anthemurgus passiflorae* employ a distinctive mode of pollen collection. Upon arriving at a *Passiflora* flower the female usually first moves under the anthers to gather nectar from the hidden nectarial disc. Duration of nectaring averaged  $11.3 \pm 4.6$  sec (N = 12, 5–22 sec). The bee rarely contacts an anther during this activity. The female then crawls up a stamen and suspends herself under an anther by grasping it with her mid- and hind legs (figs. 5, 6). She then typically scrapes pollen from the anther by moving her open mandibles along the staminal thecae with a forward motion of her head. This motion is repeated two to three times per anther. Pollen accumulates on the mandibles, clypeus, and labrum during this maneuver and is rapidly transferred, first from the forelegs to midlegs and then from the midlegs to the sparse simple scopal hairs of the anterior face of the flattened hind tibia and basitarsus. In some cases females used only their forelegs to extract pollen from

the anthers. The foretarsi of female *Anthemurgus* have an array of sparse, simple hairs which may facilitate pollen collection, but the mandibles are unmodified (at least relative to those of other related panurgines which do not use mandibular pollen collection). Both the labrum and clypeus lack distinctive setal arrays likely to facilitate pollen collection.

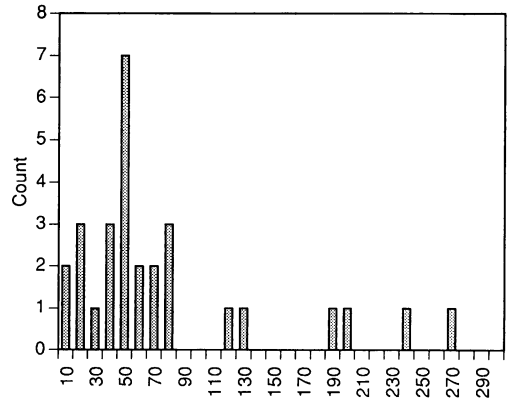
Following extraction of pollen from an anther, the female usually moved to an adjacent stamen on the same flower. Pollen is initially loaded in a dry state into the scopa of long, simple hairs on the outer face of the hind tibiae and basitarsi. When sufficient pollen has been collected, nectar is added to the outer portions of the provision mass before the female leaves the vine on which it is currently foraging. Regurgitated nectar is added to the outer portions of the scopal mass by transfer from the mouthparts to the forelegs, forelegs to midlegs, and then midlegs onto the scopal pollen mass as the female hangs under the anther before departing from a flower.

A female typically visited each of the five anthers of a flower only once on a given floral visit. Floral visits were highly variable in duration, averaging  $66.3 \pm 63.2$  sec (N = 28, 3–278 sec) (fig. 8). Visual inspection indicated that most pollen is removed on the first visit to an anther with twice-visited anthers having only a few remaining pollen grains. First visits to individual flowers averaged  $83.6 \pm 64.7$  sec (N = 17 (32–278 sec) and were always longer than second visits to the same flower.

**PROVISIONING BEHAVIOR:** Females make one or two prolonged nectar-only trips on the first day or two before beginning to forage for pollen (mean =  $96.4 \pm 54.6$  min, N = 11, 16.00–204.70 min). Females forage for pollen on each day thereafter (weather permitting). Except for the earliest part of the season when some females only made one or two pollen trips per day, most females apparently provision one cell per day. In the only case where initiation of a nest was confirmed, the female made one nectar trip on the day the nest was initiated and began foraging for pollen on the following day. Female *Anthemurgus passiflorae* averaged  $6.00 \pm 1.01$  pollen trips per day (N = 54, 3–9) (fig. 9). These included  $5.5 \pm 1.1$  (N = 54, 3–8) trips with large pollen loads (full scopae) and  $0.5 \pm 0.7$



7



8

Figs. 7, 8. Histogram of depth of (7) *Anthemurgus passiflorae* nests; (8) duration of visits to flowers of *Passiflora lutea* by females of *Anthemurgus passiflorae*, in 10 second increments.

(N = 54, 0–3) trips where the female returned with small, partial pollen loads. The likelihood of a daily provisioning sequence including one or more small loads decreased as the number of large loads per sequence increased. Four of five sequences (80%) with only three or four large loads included at least one small load. However, only 38% (14 of 37) of series with five or six large loads included at least one small load, and only 8% (1 of 12) of series with seven or eight large loads did so. The modal number of pollen trips per day was six (or five for large loads only). Nest entrances were consistently plugged with soil after the completion of foraging for the day during the early portion of the foraging season, but later in the season nest entrances remained open at all times.

Excavations after the completion of foraging on a given day indicated that these nests did have hidden plugs in the main burrow at depths of 3 to 5 cm.

The pollen load of a 15.19 mg female was 4.20 mg (both fresh wt). Assuming that, as in other panurgine bees (Danforth, 1990; Neff and Danforth, 1992; Neff, unpubl. obs.), *Anthemurgus* females must collect at least their own fresh weight in pollen (and usually considerably more) to form a pollen ball, it is likely that females need to collect a minimum of four to five pollen loads to make a pollen ball (i.e., provision mass). Given per anther pollen production of 0.142 mg and ignoring (probably perilously) the contribution of added nectar, a female would have to collect all the pollen from 7 flowers to complete a pollen load. If a pollen mass requires 5 pollen loads, a female would need to collect all the pollen from 35 flowers to provision a cell. We had difficulty finding more than 8 flowers of *Passiflora lutea* open at any one time within 100 m of the nest site. While a requirement of 35 flowers per cell may well be an overestimate, it still suggests the considerable prowess of these bees in finding widely scattered inconspicuous flowers.

If we use a criterion of a five-trip minimum to indicate a complete provisioning sequence, females took an average of  $136.0 \pm 35.0$  min (N = 35, 84.9–243.3 min) to provision a cell. More time is required to provision a nest cell early in the season (May)

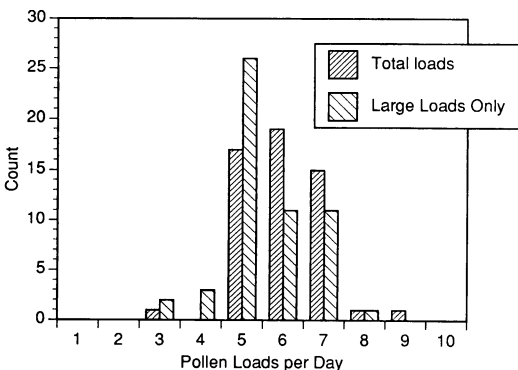


Fig. 9. Histogram of number of pollen loads per day by females of *Anthemurgus passiflorae*.



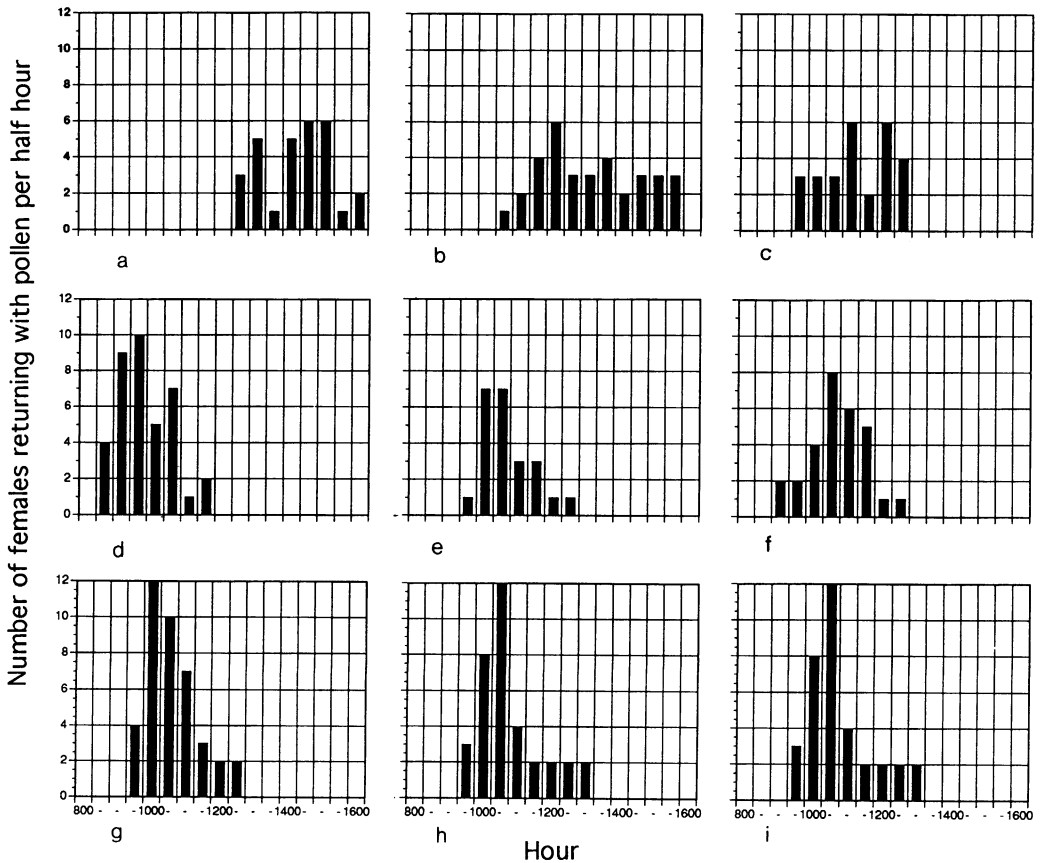
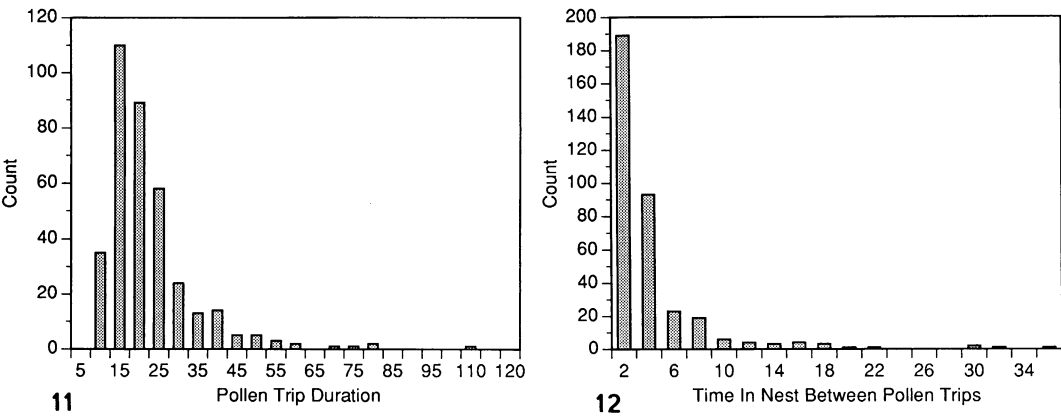


Fig. 10. Diel provisioning activity of female *Anthemurgus passiflorae* at BFL, 1992. Number of females returning with pollen per half hour. a. 27 May, b. 28 May, c. 11 June, d. 2 July, e. 4 July, f. 14 July, g. 15 July, h. 16 July, i. 18 July.

( $202.8 \pm 25.8$  min,  $N = 5$ , 177.0–243.0 min) than later (June–July) ( $124.8 \pm 21.1$  min,  $N = 30$ , 84.9–183.4 min).

Limited observations for early season bees indicated that most did not begin foraging before 1030 hrs with some pollen foraging continuing to 1500 hrs or later (fig. 10, a–c), but, during June and July, virtually all pollen foraging occurred between 0830 and 1200 hrs (fig. 10, d–i). The later starting and more extended foraging in May probably was due to a combination of relatively cool conditions and a paucity of *Passiflora* flowers. Females appeared to require a minimum air temperature of 20°C for foraging. The daily minimum temperature exceeds 20°C in June and July in Austin, but it was not reached until after 1000 hrs during the May observation dates.

Duration of pollen trips was highly variable, ranging from 5.50 to 109.00 min with an average of  $21.19 \pm 13.21$  min ( $N = 390$ ) and a median of 17.12 min (fig. 11). Some of this variation is seasonal since early-season trips are much longer (mean duration of  $37.45 \pm 19.28$  min,  $N = 58$ , 11.08–109.00 min) than those later in the season ( $19.31 \pm 13.13$  min,  $N = 332$ , 5.50–57.87 min). There was no consistent pattern in the duration of foraging trips within a provisioning sequence by a particular female other than the tendency of the last provisioning trip to be longer than the penultimate provisioning trip (39 of 63 cases) even though neither was necessarily the longest trip of the series. Time in the nest between provisioning trips averaged  $3.47 \pm 5.03$  min ( $N = 350$ , 0.47–34.37 min), but the median was only 1.88 min (fig. 12). This fig-



Figs. 11, 12. Histograms of (11) duration of pollen trips by female *Anthemurgus passiflorae*, in 5 min increments; (12) duration of time spent in the nest between pollen trips by *Anthemurgus passiflorae*, in 2 min increments.

ure is skewed by a few long periods since 70% of the within-nest periods were less than 2.2 min. Many females made one or two presumed nectar-only trips after completing pollen provisioning. These trips averaged  $33.70 \pm 36.07$  min ( $N = 49$ , 4.55–187.13 min) with the interval between the last pollen trip and the first nectar-only trip averaging  $22.19 \pm 22.14$  min ( $N = 38$ , 1.18–99.45 min).

**PROVISIONS AND DEVELOPMENT:** Females deposit their pollen loads on the floor of the cell as unshaped masses after each foraging trip. The provisions are molded into an uncoated, uniformly moist, slightly flattened, subspherical provision mass after the completion of foraging. The only two pollen masses recovered intact had heights of 3.1 and 3.3 mm and diameters of 3.7 and 4.0 mm, respectively. The smooth, strongly arched, 1.6 mm long egg is placed on top of the provision mass with both ends contacting the provisions, the posterior end inserted into the provision mass and the anterior end barely contacting the provision surface. Details of larval development were not obtained. Larvae defecate after completion of feeding, the feces being laid down as a series of strips on the rear of the cell. Accumulation of these fecal smears results in a single fecal mass adhering to the rear of the cell. Quiescent, post-defecating, overwintering larvae rest in a C-shaped position on their dorsal tubercles with the head nearest the closure.

**MALE BEHAVIOR:** Males were regularly seen at flowers of *Passiflora lutea* L. where they patrolled or held territories. Males commonly perched for long periods on *Passiflora* flowers or on nearby vegetation. Male-male interactions were not observed, as there rarely was more than one male present at a vine and most vines had no males present. Males were never observed patrolling the nest site. Males were observed mounting pollen-foraging females throughout the nesting season (fig. 4). Average duration of such mountings was  $28.8 \pm 16.3$  sec ( $N = 8$ , 10–50 sec). The male remained mounted as the female foraged within a flower but released the female, or was dislodged, before the female moved between flowers. Males attempting to remount a female immediately after being dislodged were usually rebuffed by kicking motions of the female. There was no clear indication of any courtship behavior before or during mountings. Attempts at genitalic insertion were commonly observed, but it was very difficult to tell if successful copulation regularly took place. Successful genitalic insertion was confirmed for only a single early season (5 May 1981) instance.

**ANTHEMURGUS AS A POLLINATOR:** Although *Anthemurgus passiflorae* was by far the most common visitor to flowers of *Passiflora lutea* at BFL, its role as a pollinator may be quite limited, and in many cases it is more likely to be simply a pollen thief. Due to their mod-

est size, females rarely contact either the anthers or stigmas while nectaring and very rarely contact the stigmas while harvesting pollen. Their failure to contact the stigmas during pollen collection results from the stigmas remaining at a distance above the anthers during the morning periods when the bees collect pollen most actively. Males may actually play a more important role as pollinators. Like females, they do not normally contact the anthers or stigmas while nectaring, but males mounted on females are at the proper height to receive a dorsal pollen load when the female is nectaring. Pollination via dorsally deposited pollen could occur later in the day during nectaring at flowers in which the stigmas have descended to an appropriate height. Males also contact both anthers or stigmas during their perching behavior on flowers; pollen deposition in this case is ventral. Pollen was deposited on stigmas during male activity, but no fruit-set resulted from these pollinations. However, these vines set no fruit at all, so it was impossible to tease apart questions of pollinator efficacy and resource limitation. Since males tend to be territorial, it remains to be established if their activity yields any significant levels of effective pollination in *Passiflora lutea*, a self-incompatible species requiring cross pollination. More effective pollinators are likely to be infrequent but more robust visitors such as *Bombus pennsylvanicus* (Degeer) workers, females of *Xylocopa micans* Lepeletier and *Augochloropsis metallica* (Fabricius), and males of *Colletes latitarsus* Robertson. These bees are of sufficient size to contact both anthers and descended stigmas while nectaring.

**NEST ASSOCIATES:** Although several species of *Holcopasites* and *Sphecodes* known to attack nests of panurgine bees are present at BFL, no cleptoparasitic bees were at any time associated with nests of *Anthemurgus passiflorae* during the course of this study. The small mutillid, *Pseudomethoca simillima* (Smith) was reared from cocoons found in three cells of nest 92-15 (excavated 20 July 1992), a 10-cell nest (including four empty cells with fecal smears). This is the first host record for *Pseudomethoca simillima*, but its broad geographic range (Texas to Florida to Maine) suggests it is not restricted to *Anthe-*

*murgus*. Several other small mutillid species were present in the nest area, but none was observed closely investigating *Anthemurgus* nests.

Two female *Anthemurgus passiflorae* were captured at the nest area with phoretic mites (*Trochometridium tribulatum* Cross) on their propodeal areas plus a few scattered mites grasping hairs near the leg bases and tegulae. Dense infestations of these mites were found in 12 fungally infected cells in a 23-cell nest excavated 13 November 1992. No bee larvae were found in any of the infested cells. The phoretic female mites kill the eggs or early-stage larvae, and their offspring feed primarily on fungi which were transported by the mites and infested the pollen mass within the closed cell (Cross, 1965; Lindquist, 1985). This mite is not host specific, as it attacks a wide range of ground-nesting bees.

## DISCUSSION OF BIOLOGY

The nesting biology of *Anthemurgus passiflorae* yields little of value in understanding its phylogenetic relationships within the Panurginae. Features such as nest architecture, egg placement, shape of the provision mass, and fecal placement are all similar to that found in other primitive<sup>4</sup> panurgines (Rozen, 1989) and thus are consistent with the proposed close relationship of *Anthemurgus* to these bees. Unfortunately, these characters all appear to be plesiomorphic within the Panurginae and thus are not phylogenetically informative. Multivoltinism and nest reuse have not previously been reported among any of the North American primitive panurgines although multivoltinism appear likely in some South American *Liphanthus* and *Cephalurgus* and nest reuse is likely in *Cephalurgus* (Rozen, 1989). In addition, *Pterosarus ornatipes* (Cresson) and *P. albitarsis* (Cresson) both appear to be multivoltine in the Austin area, as both have distinct spring and fall flight periods (JLN, personal obs.) In any case, the phylogenetic significance of multivoltinism is questionable since the interaction of

<sup>4</sup> We used the term "primitive" for convenience to refer to this group, but, of course, we do not imply that they necessarily possess primitive features, only that they were apparently an early branching of the Panurginae.

genetic and environmental factors in its determination is poorly understood among most bees (Rozen, 1989). The secondary soil lining of the main burrow appears to be unique among the primitive panurgines. This may simply reflect nest reuse since a similar soil lining is found in burrows of *Panurginus polytrichus* Cockerell, another noncommunal panurgine with nest reuse (JLN, unpubl. obs.).

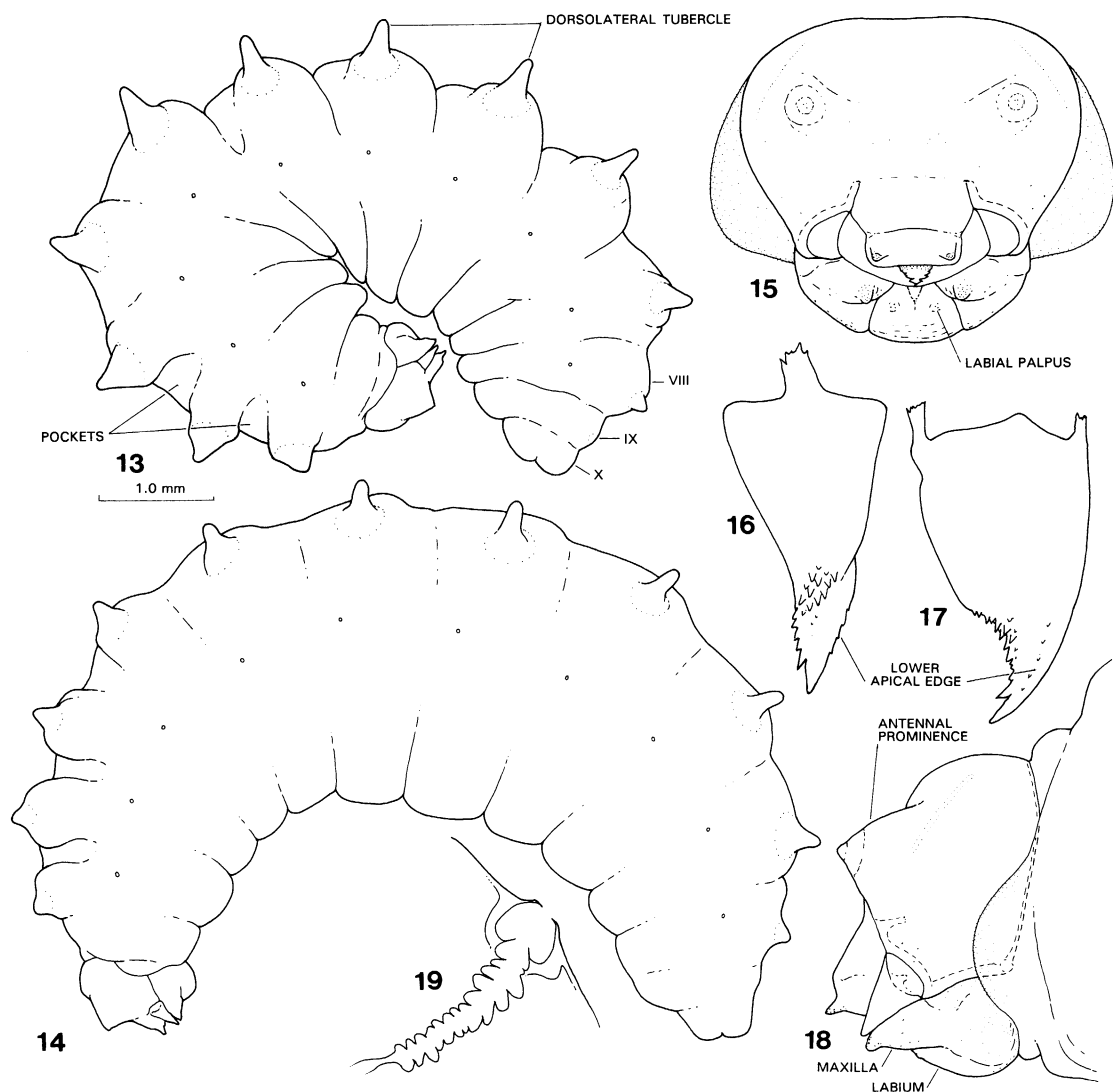
As there are no other long-term (throughout the flight season) studies of either mating or provisioning behavior for any of the other primitive panurgines, it is clearly premature to draw any conclusions from our observations. Our unpublished observations from long-term studies of *Pseudopanurgus rugosus* (Robertson) and *Ps. aethiops* (Cresson) suggest mating exclusively at flowers despite gregarious nesting. This may be a distinctive behavioral feature uniting *Anthemurgus* with *Pseudopanurgus*.

There are few reports on the details of pollen harvesting behavior of panurgine bees, but the mandibular pollen collection behavior of *Anthemurgus passiflorae* appears to be unique within this group. *Protandrena mexicanorum* (Cockerell) does use its mandibles during its "buzz-milking" pollen collecting behavior from flowers of *Solanum* (Cane and Buchmann, 1989), but this behavior is quite dissimilar from that of *Anthemurgus*. Our personal observations of various species of *Pseudopanurgus* (*P. rugosus*, *P. aethiops*, and *P. texanus* Timberlake), *Pterosarus* (*P. albittarsis* and *P. ornatipes*), and *Heterosarus illinoiensis* (Cresson) indicate all use a combination of passive collection of pollen while nectaring plus active collection with the forelegs in their pollen collecting repertoires. *Metapsaenythia abdominalis* (Cresson) uses only its forelegs in harvesting pollen from the anthers in the upper lip of the corolla of *Monarda* (Lamiaceae) flowers.

Although *A. passiflorae* has been observed only at flowers of *Passiflora lutea*, its specialized mandibular pollen-collecting behavior would also be appropriate for collecting pollen from other small-flowered species such as *Passiflora suberosa* L., *P. tenuiloba* Engelm., *P. filipes* Benth., or *P. affinis* Engelm. Of this group, only *P. affinis* is known to be sympatric with *Anthemurgus passiflorae*. On the other hand, mandibular pollen-collecting behavior appears to be ill-suited for pollen-

collection from the very large anthers of large-flowered *Passiflora* taxa such as the maypop, *Passiflora incarnata* L. Indeed, *A. passiflorae* has never been reported at flowers of *P. incarnata* even though that plant occurs through much of the range of *A. passiflorae*.

The restriction of pollen collection to *Passiflora lutea* and its unusual pollen-collecting methods appear to be the most distinctive aspects of the biology of *Anthemurgus passiflorae*. In fact, *A. passiflorae* is the only bee known to restrict its pollen collection to a member of the large (530+ spp) family Passifloraceae. This situation may change when the biologies of the diverse tropical and subtropical bee faunas are better known, but *A. passiflorae* is almost certainly the only temperate-zone species with such a diet. *Passiflora* has traditionally been placed in the Dilleniidae. Floral host relations are poorly known for the majority of the *Pseudopanurgus-Psaenythia* clade but none, other than *A. passiflorae*, appears to be restricted to any member of the Dilleniidae. However, a recent analysis of angiosperm relationships based on *rbcL* sequence data has confirmed earlier suspicions that the Dilleniidae is highly polyphyletic and instead places the Euphorbiaceae as the closest relative of the Passifloraceae (Chase et al., 1993). A number of species of *Heterosarus*, including *H. euphorbiae*, appear to be oligolectic on the Euphorbiaceae, but there is nothing to suggest that they are particularly closely related to *Anthemurgus*. All species of *Pseudopanurgus* and *Pterosarus* apparently are oligolectic on the Asteraceae while *Metapsaenythia* restricts its pollen collecting to *Monarda* (Lamiaceae). Some *Heterosarus* species are oligolectic on a variety of distantly related taxa such as *H. illinoiensis* on the Asteraceae or *H. virginicus* (Cockerell) on *Hedyotis* (Rubiaceae), but others are almost certainly polylectic (*H. bakeri* [Cockerell], *H. neomexicanus* [Cockerell]). Polylecty is also known among some *Lipanthus* and *Protandrena*. Coupled with the fact that *Anthemurgus* is at best only an incidental pollinator of *Passiflora*, oligolecty on *Passiflora* by *Anthemurgus* likely reflects not an extended close bee-plant coevolutionary history but rather either a major host shift from an oligolectic ancestor or an evolutionary restriction of diet from a polylectic progenitor. Better resolution of the relationships



Figs. 13–19. Mature larva of *Anthemurgus passiflorae*. 13. Live postdefecating larva, lateral view. 14. Recently killed predefecating larva, lateral view. 15. Head, frontal view. 16, 17. Right mandible, inner and ventral views. 18. Head, lateral view. 19. Spiracle, side view. Scale refers to figures 13 and 14.

of the primitive panurgines and more complete information on their floral relationships are needed to resolve this question.

#### IMMATURE STAGES OF *ANTHEMURGUS PASSIFLORAE*

##### MATURE LARVA Figures 13–19

The following diagnosis is based on recent descriptions of mature panurgine larvae (see

McGinley, 1989, for references; see also Ruz and Rozen, 1993, for the larval description of *Parasarus atacamensis* Ruz; Rozen, 1988, for that of *Camptopoeum bakeri* Rozen) and on larvae yet to be described, indicated in table 1.

**DIAGNOSIS:** The mature larva of *Anthemurgus passiflorae* and larvae of *Protandrena*, *Pseudopanurgus*, *Pterosarus*, *Heterosarus*, *Parasarus*, *Cephalurgus*, *Metapsaenythia*, *Psaenythia*, *Rhopitulus*, *Anthren-*

TABLE 1

**Immature Stages of Panurgine Species Examined**  
(Specimens, marked "+", are in the American Museum of Natural History. Not included are species whose immatures have already been described; see text for further explanation.)

Species	Larva	Pupa
<i>Lipanthus alicahue</i> Toro and Ruz	+	+
<i>Heterosarus nanulus</i> (Timberlake)	+	+
<i>Rhopitulus</i> sp.	+	—
<i>Cephalurgus anomalus</i> Moure and Oliveira	+	+
<i>Metapsaenythia abdominalis</i> (Cresson)	+	—
<i>Anthemurgus passiflorae</i> Robertson	+	+
<i>Psaenythia</i> 2 spp.	+	+
<i>Anthrenoides</i> species near <i>wagneri</i> (Vachal)	+	+
<i>Melitturga penrithorum</i> Eardley	+	+
<i>Calliopsis</i> (C.) <i>teucii</i> (Cockerell)	+	+
( <i>Micronomadopsis</i> ) <i>foleyi</i> (Timberlake)	+	+
( <i>M.</i> ) <i>larrae</i> (Timberlake)	+	+
( <i>M.</i> ) <i>australior</i> (Cockerell)	+	+
( <i>Liopoeum</i> ) <i>hirsutula</i> (Spinola)	+	+
( <i>L.</i> ) <i>trifasciata</i> (Spinola)	+	+
( <i>Ceroliopoeum</i> ) <i>laeta</i> (Vachal)	+	+
( <i>Verbenapis</i> ) <i>nebraskensis</i> (Crawford)	+	+
<i>Arhysosage flava</i> Moure	+	—
<i>Spinoliella herbsti</i> (Friese)	+	—
<i>Callonychium</i> ( <i>Callonychium</i> ) <i>pentuniae</i> Cure and Wittmann	+	+
( <i>Callonychium</i> ) sp.	+	+
(C.) sp.	+	—
( <i>Paranychium</i> ) sp.	+	+
<i>Perdita</i> (P.) <i>kiowi</i> Griswold	+	—
(P.) <i>luciae</i> Cockerell	+	—
(P.) <i>mentzeliae</i> Cockerell	+	+
(P.) <i>obsurella</i> Timberlake	+	+
(P.) <i>sexmaculata</i> Cockerell	+	—
(P.) <i>stathamae</i> Timberlake	+	—
(P.) <i>zebrata</i> Cresson	+	+
( <i>Epimacrotera</i> ) <i>biguttata</i> Timberlake	+	—
( <i>Hexaperdita</i> ) <i>asteris</i> Cockerell	+	+
( <i>Macrotera</i> ) <i>pipyolin</i> Snelling and Danforth	+	+
( <i>Macroteropsis</i> ) <i>portalis</i> Timberlake	+	+
( <i>M.</i> ) <i>laticornis</i> Cockerell	+	+
( <i>Macroterella</i> ) <i>mellea</i> Timberlake	+	+
( <i>Perditella</i> ) <i>minima</i> Cockerell	+	+
(P.) <i>cladothricis</i> Cockerell	+	—
( <i>Cockerellia</i> ) <i>coreopsidis collaris</i> Cockerell	+	+

*oides*, *Melitturga*, and *Lipanthus*<sup>5</sup> share the peculiar modifications of the bases of the thoracic dorsolateral tubercles which form lateral pockets between the prothorax and mesothorax and between the mesothorax and metathorax (figs. 13, 14). This unique feature characterizes these genera. Furthermore, their paired dorsolateral abdominal tubercles, although not always large, rise abruptly from the segments (figs. 13, 14). These genera also have large, strongly projecting maxillary apices with large palpi and usually a strongly recessed labium (fig. 18). With the exception of the Old World *Melitturga* (Rozen, 1971: fig. 36), their antennal prominences project strongly (fig. 18).

Excluding three genera (*Arhysosage*, *Spinoliella*, and *Callonychium*), none of the other panurgine genera whose larvae are known (*Melitturgula*, *Camptopoeum*, *Panurgus*, *Panurginus*, *Calliopsis* sensu lato, and *Perdita*) exhibit these thoracic pockets (Rozen, 1971: figs. 17, 27), their maxillae tend to be more reduced (Rozen, 1966: figs. 31, 39, 43, 49) (though not in *Panurgus* and *Panurginus*), and, with some, the labium projects nearly as far as the maxillae in lateral view (Rozen, 1966: figs. 43, 49; Rozen, 1988: fig. 7). With the exception of *Panurginus*, which has reduced paired dorsolateral abdominal tubercles and down-curved maxillary palpi, the antennal prominences of these same genera are quite low. While some species of *Perdita* also have strongly projecting dorsolateral abdominal tubercles (Rozen, 1966: figs. 41, 47, 50, 51, 52), the other genera tend to have lower, more rounded tubercles (Rozen, 1966: figs. 17, 21, 24, 24, 29; Rozen, 1968: figs. 13, 14; Rozen, 1988: fig. 5). *Perdita* uniquely almost always has a short or long, dorsal median tubercle on abdominal segment X.

*Arhysosage*, *Spinoliella*, and *Callonychium* possess highly modified dorsolateral thoracic

<sup>5</sup> The condition of this character in *Lipanthus alicahue* is uncertain because the lateral pockets seem less well defined even though all dorsolateral body tubercles are large, rounded, and conspicuous. Before final judgment can be made on this species, it should be carefully studied, particularly because the genus is the sister group to all other panurgines and misinformation concerning it could be misleading.

tubercles which may (or may not) be derived from the condition found in the Anthemurgini and *Melitturga*. With these three genera, the prothoracic tubercles and sometimes the mesothoracic tubercles are greatly elongate and much more robust than the elongate, slender metathoracic and abdominal dorso-lateral tubercles. Furthermore the prothoracic tubercles recline backward (Claude-Joseph, 1926: fig. 59) thereby forming a pocketlike enclosure between the pro- and mesothorax. Because the elongate, backward condition of the tubercles is unlike the tubercles of the Anthemurgini and *Melitturga*, larvae of the two groups are very dissimilar in appearance.

The larvae of *Anthemurgus* closely resemble those of the *Melitturga* and the Anthemurgini, which, however, have not been fully studied. With respect to those that have been described, *Anthemurgus* can be distinguished from Old World *Melitturga* because the latter (Rozen, 1965: figs. 10, 13) has a pronounced projection (tooth) arising from the mandibular cuspal area and low antennal prominences. The nonserrate (nondentate) lower apical edge of the mandible of *Pseudopanurgus* (Rozen, 1966: fig. 13) and *Pterosarus* (Rozen, 1966: fig. 3) seems to be diagnostic when contrasted with the serrated lower edge of the mandible of *Anthemurgus* (figs. 16, 17). The dorsal body tubercles of *Protandrena verbesinae* (Timberlake) (Rozen, 1970: fig. 9, as *Psaenythia bicolor* Timberlake) are shorter and not as slender as those of *Anthemurgus* (figs. 13, 14). Furthermore, spiracles of *Protandrena verbesinae* are larger and exhibit a rim (Rozen, 1970: figs. 9, 10) in contrast to those of *Anthemurgus* (figs. 13, 14, 19). The mature larva of *Anthemurgus* can be distinguished from that of *Parasarus atacamensis* because the former has longer paired dorsal body tubercles on most segments (figs. 13, 14), because these tubercles are virtually absent on abdominal segment IX, and because the antennal prominences, though projecting, are not globose (fig. 18).

Larvae of the other Anthemurgini have not been sufficiently studied to determine how they differ from those of *Anthemurgus*, if at all. Features in boldface below are those that appear to be characteristic of (although not

in all cases restricted to) the Anthemurgini and *Melitturga*.

**HEAD** (figs. 15, 18): Integument of head capsule with very few sensilla, some minutely setiform; some sensilla of mouthparts setiform; integument of both pre- and postdefecating larvae unpigmented except for mandibular apices.

Head size moderately small in relation to rest of body of postdefecating larva; head capsule much wider than maximum length from vertex to lower clypeal margin. Tentorium including dorsal arms well developed; anterior pits in normal position on face; posterior tentorial pit normal in position; posterior thickening of head capsule moderately thin, only slightly curving forward medially as seen in dorsal view; posterior margin of head capsule normal in position; median longitudinal thickening of head capsule absent; hypostomal ridge well developed, without ramus; pleurostomal ridge well developed; epistomal ridge well developed between anterior mandibular articulations and anterior tentorial pits, absent mesad of these pits; epistomal depression vague between pits. Parietal bands distinct. **Antennal prominences well developed** but not globose like those of *Parasarus*; antennal disc and papilla moderate in size, with three sensilla. Vertex in lateral view (fig. 18) evenly rounded, without projections or elevations; frontoclypeal area normal in length and configuration, not projecting strongly, as is characteristic of *Panurgus*. Labrum normal in size and shape for Panurginae, without sclerite; paired labral tubercles arising from labral disc, moderate in size, apically more slender than those of *Parasarus*; epipharyngeal integument rough but apparently not spiculate.

**Mandible** (figs. 16, 17) moderately slender; dorsal surface nonspiculate, smooth (contrasting with that of *Parasarus*); outer surface without tubercle; apex tapering, slender, simple, but with distinct subapical tooth somewhat larger than other teeth on dorsal apical edge; ventral apical edge with distinct small teeth; cusp moderately weakly produced, with moderately large, evenly spaced teeth, not produced ventrally as in *Panurgus* and without large cuspal tooth as in *Melitturga*. Labiomaxillary region recessed, and, except for

maxillary apices, fused. **Maxilla as seen in lateral view (fig. 18) projecting well beyond labial apex; cardo and stipes unpigmented, vague integumental thickening (best seen on cleared specimen); articulating arm of stipital sclerite not evident; palpus large, clearly stouter than labral tubercle, not directed downward as in *Panurginus* but dorsal surface curving downward; this surface with conspicuous spicules some of which extend onto dorsal surface of maxilla. Labium not divided into prementum and postmentum; premental sclerite not evident; labral apex recessed in comparison to maxillary apices (fig. 18), unlike those in *Camptopoeum*; labial palpus only vaguely represented as slight swelling, much smaller than maxillary palpus.** Salivary opening in weakly expressed, curved groove. Hypopharynx bulging, spiculate.

**BODY:** Integument without obvious setae and without spicules except for lateral pronotal swellings; fine nonsetiform sensilla present on dorsal body tubercles; posteroventral area on abdominal segment X with band of short, setiform sensilla; spicules of lateral pronotal swelling fine, sharp-pointed, less evident than those of *Parasarus*. Body form (figs. 16, 17) moderately robust; intersegmental lines well incised on postdefecating larva; intrasegmental lines not evident; paired dorsal body tubercles (figs. 13, 14) long, attenuate on most body segments; these tubercles with their apices faintly sclerotized (though unpigmented) and smooth; **dorsal prothoracic tubercles apically somewhat forward projecting; bases of pro- and mesothoracic tubercles and meso- and metathoracic dorsal tubercles forming lateral pockets on each side of body (figs. 13, 14) (see Remarks, below); dorsal abdominal tubercles rounded (i.e., not transverse), nonspiculate; pleural region elsewhere not produced; abdominal segment IX and X without paired tubercles; segment X with dorsal surface slightly bulging compared with ventral area as seen in lateral view (figs. 13, 14); segment X attached centrally to IX, not produced posteriorly or ventrally. Spiracles (fig. 19) small, unpigmented, but evident under normal magnification; spiracles subequal in size; peritreme present; atrium projecting**

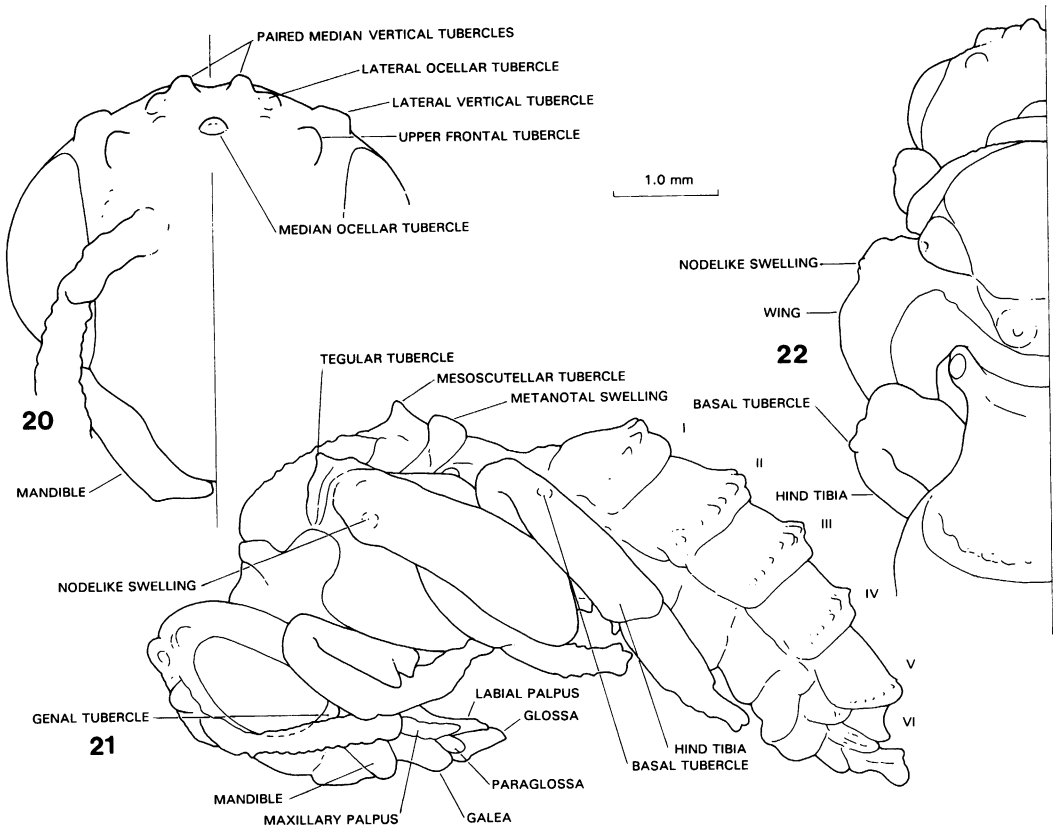
slightly above body wall but apparently without rim; atrial wall unornamented; primary tracheal opening with collar; subatrium of moderate length, consisting of approximately 12 chambers. Male sex characters on cleared specimens consisting of median, transverse, dumbbell-shaped cuticular scar near posterior margin of abdominal segment IX; on un-cleared specimen, pale imaginal disc immediately above this scar; female sex characters unknown.

**MATERIAL STUDIED:** Four postdefecating larvae, Austin, Travis Co., Texas, July 20, 1992 (J. Neff); 1 predefecating larva, same data except June 20, 1992.

**REMARKS:** The pockets formed on each side of the body in the area between the pro- and mesothoracic tubercles and between the meso- and metathoracic tubercles are features shared by a number of panurgines, as enumerated above. They will probably be found in other panurgine genera, but they are lacking in *Meliturgula*, *Camptopoeum*, *Panurgus*, *Calliopsis* (sensu Ruz, 1991), *Panurginus*, and *Perdita*, among others. Until now they were thought to be a modification of the tubercles themselves. However, the sclerotization of the apices of all of the dorsal body tubercles in *Anthemurgus* suggests that the pockets are a modification of the thoracic segments basad of the tubercles. JGR has seen these pockets cupping a clear, darkish, viscous liquid in at least some of the genera. It seems likely that the pockets and the liquid are functionally interrelated, and they are probably a synapomorphy attesting to the relationship of their bearers because such features are unknown among other bees. The chemical composition, source, and function of the liquid are not understood and should be investigated.

As indicated in Ruz and Rozen (1993), these two authors plan a series of papers to describe and name a number of new genera of South American panurgine bees. Where possible they will also describe the immature stages. At the end of that series, the roster of known panurgine genera will be much more complete and, at that time, an attempt will be made to analyze the phylogenetic relationships of all panurgine genera using data





Figs. 20–22. Pupa of *Anthemurgus passiflorae*. 20. Head, frontal view. 21. Entire pupa, lateral view. 22. Left side of anterior part of pupa, dorsal view. Scale refers to figures 21 and 22.

derived from all life stages. The description of the mature larva of *Anthemurgus* (and also that of the pupa) will be grist for that analysis.

#### PUPA

##### Figures 20–22

**DIAGNOSIS:** This preliminary diagnosis is possible because of comparative published accounts of panurgine pupae (McGinley, 1989) and because pupae of other panurgines were available for study, as listed in table 1. The pupa of *A. passiflorae* can be distinguished from pupae of *Perdita*, *Callonychium*, *Heterosarus*, *Melitturga penrithorum*, some species of *Panurginus*, and *Panurgus* because the latter lack tegular tubercles. Pupae of *Calliopsis* sensu Ruz (1986) also lack these tubercles except for the monotypic sub-

genus *Ceroliopoeum* and some members of the subgenus *Calliopsis* (Yager and Rozen, 1966: fig. 12). Both of these subgenera, however, have small paired scutal tubercles, whereas *A. passiflorae* does not (figs. 21, 22). *Melitturga braunsi* Friese and *Melitturga clavicornis* (Latreille) also have tegular tubercles. Because *M. clavicornis* (Yager and Rozen, 1966: figs. 15, 16) (as well as *M. penrithorum*) lacks a distinct tubercle at the base of the outer surface of the hind tibia, it can be distinguished from *Anthemurgus* (figs. 21, 22). *Melitturga* (Rozen, 1968: figs. 26, 27), unlike *Anthemurgus*, has a relatively long basal spine on the hind tibia. It is unclear at this time, however, how to separate the pupa of *Anthemurgus* from pupae of *Protandrena verbesinae*, *Panurginus albopilosus* Lucas, two species of *Psaenythia*, *Lipanthus alicahue*,

*Cephalurgus anomalus*, *Anthrenoides* sp. near *wagneri*, and two undescribed genera of South American *Anthemurgini*.

The format below follows that used in Yager and Rozen (1966).

**DESCRIPTION:** Length 7.0 mm; body without setae.

**HEAD:** Outer surface of scape scarcely swollen; pedicel with small rounded tubercle on outer surface. Ventral surface of mandible with vague tubercle near base. Vertex and upper part of frons bearing large and small rounded tubercles; these tubercles positioned as those of *Protandrena verbesinae* (Rozen, 1970) and no doubt homologous with them; gena with tubercle.

**MESOSOMA:** Lateral angles and posterior lobes of pronotum scarcely produced; mesoscutum without tubercles but with low varicosities; mesoscutellum with pair of distinct but not large acute tubercles; axillae not swollen; metanotum produced on each side; mesepisternum without tubercle. Tegula with small but distinct tubercle. Anterior part of wing base produced and with a nodelike swelling (this swelling is more basal than wing

tubercle of Halictinae which is associated with the costal wing fold of the pharate imago). Each coxa with small apical tubercle; fore and mid (but not hind) trochanters each with small apical tubercle; base of hind tibia with low tubercle on outer surface.

**METASOMA:** Terga I to V (female) each with transverse apical row of moderately large tubercles. Terminal spine short, apically rounded.

**MATERIAL STUDIED:** 1 female pupa, Austin, Travis Co., Texas, larva collected July 20, 1992, pupa preserved August 5, 1992 (J. Neff).

**REMARKS:** The close agreement between the pupa of *Anthemurgus passiflorae* and pupae of some of the taxa indicated in the Diagnosis suggests that the pupal features of *A. passiflorae* are primitive in the Panurginae. They more closely correspond to pupal characters of the more basal clades in the subfamily than to the pupal characters of the remaining clades, as determined by Ruz (1986). The evolutionary relationships of *Anthemurgus* to other andrenids as revealed by pupal characters will be dealt with in a separate paper.

## REFERENCES

- Cane, J. H. and S. L. Buchmann  
1989. Novel pollen-harvesting behavior by the bee *Protandrena mexicanorum*. (Hymenoptera: Andrenidae). *J. Insect Behav.* 2: 431–436.
- Chase, M. W. et al.  
1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcL*. *Ann. Missouri Bot. Gard.* 80: 528–580.
- Claude-Joseph, F.  
1926. Recherches biologiques sur les hyménoptères du Chili (mellifères). *Ann. Sci. Nat., Zool. ser. 10*, 9: 113–268.
- Cross, E. A.  
1965. The generic relationships of the family Pyemotidae (Acarina: Trombidiformes). *Univ. Kansas Sci. Bull.* 45: 29–275.
- Cruden, R. W., and S. M. Hermann  
1983. Studying nectar? Some observations on the art. In B. Bentley and T. Elias (eds.), *The biology of nectaries*, 223–241. New York: Columbia Univ. Press.
- Danforth, B. N.  
1990. Provisioning behavior and estimation of investment ratios in a solitary bee, *Calliopsis (Hypomacrotera) persimilis* (Cockerell) (Hymenoptera: Andrenidae). *Behav. Ecol. Sociobiol.* 27: 159–168.
- Janzen, D. H.  
1968. Reproductive behavior in the Passifloraceae and some of its pollinators in Central America. *Behaviour* 32: 33–48.
- Killip, E. P.  
1939. The American species of Passifloraceae. *Field Mus. Nat. Hist. Publ. Bot. ser.* 19: 1–63.
- May, P. G., and E. E. Spears, Jr.  
1988. Andromonoecy and variation in phenotypic gender of *Passiflora incarnata* (Passifloraceae). *Am. J. Bot.* 75: 1830–1841.
- McGinley, R. J.  
1989. A catalog and review of immature Apoidea (Hymenoptera). *Smithson. Contrib. Zool.* 494: 24 pp.
- McGregor, S. E.  
1976. Insect pollination of cultivated plant crops. *U.S. Dep. Agric. Handbook* 496: 411 pp.

- Mitchell, T. B.  
1960. Bees of the Eastern United States, Vol. 1. North Carolina Agric. Exp. Stn. Tech. Bull. 141: 538 pp.
- Neff, J. L., and B. N. Danforth  
1992. The nesting and foraging behavior of *Perdita texana* (Cresson) (Hymenoptera: Andrenidae). J. Kansas Entomol. Soc. 64: 394–405.
- Neff, J. L., and B. B. Simpson  
1990. The roles of phenology and reward structure in the pollination biology of wild sunflower (*Helianthus annuus* L., Asteraceae). Israel J. Bot. 39: 197–221.
- Robertson, C.  
1902. Some new or little known bees.—IV. Can. Entomol. 34: 321–325.  
1929. Phenology of oligolectic bees and favorite flowers. Psyche 36: 112–118.  
1930. Proterandry and flight of bees (Hymen.: Apoidea). III. Entomol. News 41: 331–336.
- Rozen, J. G., Jr.  
1965. 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). Am. Mus. Novitates 2224: 18 pp.  
1966. Systematics of the larvae of North American panurgine bees (Hymenoptera, Apoidea). Ibid., 2259: 22 pp.  
1967. Review of the biology of panurgine bees, with observations on North American forms (Hymenoptera: Andrenidae). Ibid., 2297: 44 pp.  
1968. Biology and immature stages of the aberrant bee genus *Meliturgula* (Hymenoptera, Andrenidae). Ibid., 2331: 18 pp.
1970. Biology and immature stages of the panurgine bee genera *Hypomacrotera* and *Psaenythia* (Hymenoptera, Apoidea). Ibid., 2416: 16 pp.
1971. Biology and immature stages of Moroccan panurgine bees (Hymenoptera, Apoidea). Ibid., 2457: 37 pp.
1988. Ecology, behavior, and mature larva of a new species of the Old World bee genus *Camptopoeum* (Andrenidae: Panurginae). Ibid., 2926: 12 pp.
1989. Life History Studies of the “Primitive” Panurgine Bees (Hymenoptera: Andrenidae: Panurginae). Ibid., 2692: 27 pp.
- Ruz, L.  
1986. Classification and phylogenetic relationships of the panurgine bees (Hymenoptera—Andrenidae). Ph.D. thesis, Univ. Kansas, Lawrence.  
1991. Classification and phylogenetic relationships of the panurgine bees: the Calliopsini and allies (Hymenoptera: Andrenidae). Univ. Kansas Sci. Bull. 54: 209–256.
- Ruz, L., and J. G. Rozen, Jr.  
1993. South American panurgine bees (Apoidea: Andrenidae: Panurginae), Part I. Biology, mature larva, and description of a new genus and species. Am. Mus. Novitates 3057: 12 pp.
- Yager, K., and J. G. Rozen, Jr.  
1966. Preliminary systematic study of the pupae of andrenid bees (Hymenoptera, Apoidea). Am. Mus. Novitates 2265: 13 pp.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates*, *Bulletin*, and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: [scipubs@amnh.org](mailto:scipubs@amnh.org)