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Biology and Immature Stages of Moroccan Panurgine Bees (Hymenoptera, Apoidea)

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INTRODUCTION

While on a field trip to Morocco in the spring of 1968, I studied the biology of representatives of three genera belonging to the subfamily Panurginae—*Panurgus*, *Panurginus*, and *Melitturga*. The results of this investigation are presented herein with descriptions of larvae and pupae. The present paper is part of a continuing series treating the bionomics and immature stages of the subfamily. The purpose of the series is to provide information for the evaluation of the phylogeny and systematics of the subfamily.

The genus *Panurgus*, which has a circum-Mediterranean distribution, consists of 40 to 45 species. Although the group is replete with species characteristics, particularly in the males, it has not been revised in modern times. A revision is badly needed, judging from the confusion in collections of various institutions. The genus *Panurginus* is distributed through the Holarctic region. The South American species assigned to the genus probably belong to other genera. *Melitturga* ranges from Europe to the Orient and to the southern tip of Africa. In addition to these three genera, the Moroccan panurgine fauna includes the Old World genus *Camptopoeum*.

The field work was carried out with the cheerful assistance of Mr. Eli

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Suissa. I would like to thank Prof. Jean B. Panouse and Dr. H. Choumara of the Institut Scientifique Chérifien, Rabat, and their staff for their hospitality and assistance while I was in Morocco. The following people kindly permitted me to examine collections in their charge, making possible the identifications of Moroccan specimens: Dr. S. Kelner Pillault, Muséum National D'Histoire Naturelle, Paris; Dr. Eberhard Königsmann, Institut für Spezielle Zoologie und Zoologisches Museum, Humboldt-Universität, Berlin; and Dr. I. H. H. Yarrow, British Museum (Natural History), London.

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IDENTIFICATION OF SPECIES

The following species are treated in the present paper:

Panurgus oraniensis Pérez

Panurgus intermedius, new species

Panurgus podagricus Pérez

Panurginus albopilosus Lucas

Melitturga caudata Pérez

Because there are no modern taxonomic revisions treating Moroccan panurgines, identification of species has been difficult. The excellent co-operation of the scientists noted above has been a major factor in increasing the reliability of the names, but doubts remain concerning the correct names of some species. All specimens, including immatures and samples of cells, collected by me in Morocco are deposited in the American Museum of Natural History and are available should additional biological work be undertaken or should the genera be revised.

The name for specimens herein called *Panurgus oraniensis* is somewhat in doubt. Both *P. oraniensis* and *maroccanus* were proposed by Pérez in 1895 for two similar-appearing species. The description of *oraniensis* seems to fit my specimens more closely than does the description of *maroccanus*. Unfortunately, Pérez did not select types and I found no specimens labeled *oraniensis* in his collection in the Muséum National D'Histoire Naturelle, Paris. However, a male specimen, identified by Pérez as *maroccanus* (and possibly the undesigned allotype), was not conspecific with my specimens. Therefore, *P. oraniensis* is probably the correct name even though identifications of specimens of the two species in the various institutions I visited were often reversed.

Specimens of *Panurgus podagricus* were not found in the Pérez collection and the type, therefore, is presumably lost. However, the distinctive ventral projection on the hind basitarsus of the male leaves little doubt as to the correct name of my specimens. A survey of the identified collections and of the descriptions of species indicates that *Panurgus intermedius* (description appended) is a heretofore undescribed species.

Although the original description of *Panurginus albopilosus* gives no information that is of diagnostic value, my specimens agreed with material identified as *P. albopilosus* in many institutions.

Pérez, who described *Melitturga caudata* from France, had in his collection a female and numerous males from Barcelona identified as this species. The female is conspecific with the Moroccan specimens and the males are conspecific with a male from Marseille in the Pérez collection which is perhaps the type. So far as I know, *M. caudata* is the only species from North Africa in which the female has black hairs at the apex of the metasoma; it has a completely dark face with no yellow, or even light brown, areas on the clypeus.

BIOLOGY

Insofar as possible, the sequence of presentation of biological features follows that of Rozen (1967).

PANURGUS PANZER

This genus is abundant in Morocco; the following notes concern three species, *P. oraniensis* Pérez, *intermedius* Rozen, and *podagricus* Pérez.

DESCRIPTION OF HABITAT: We found several burrows of *P. oraniensis* on the slightly sloping ground next to the shoulder of a road 33 kilometers southwest of Rabat near Oued Cherrat on April 23, 1968. The site, about 150 feet from the main nesting area of *Panurginus albopilosus*, was shaded only by scattered herbaceous plants several inches high. The ground was rocky, moderately hard, and with visible moisture at the cell level. The pollen plant, a yellow composite, *Picris cupuligera*,¹ grew abundantly adjacent to the nesting site.

Only a few feet from the burrows of *P. oraniensis*, *P. intermedius* nested in a vertical, southeast-facing cliff of conglomerate and limestone 1 meter or more in height (fig. 1). A number of burrows, discovered on April 24, 1968, entered a stratum of rock that had decomposed to such an extent that it was more easily excavated than the soil around the nesting site of *P. oraniensis*. The cliff face was fully exposed to the sun until early

¹ Kindly identified by J. Mathez, Institut Scientifique Chérifien, Rabat, Morocco.

afternoon, by which time the bees had virtually ceased collecting pollen from *Picris cupuligera*. We also located several burrows of *P. intermedius* in a south-facing, 2-foot-high bank of soil along a road 32 kilometers south of Ben Slimane on April 13, 1968 (fig. 15). This bank was devoid of vegetation, was moderately hard and moist at the cell level, and contained some scattered stones. Here, too, the pollen plant grew abundantly next to the site. The bank sloped at about 45 degrees where the burrow entered it.

In the same bank and on the same day, we discovered two nesting areas of *P. podagricus* (fig. 15). In one area most burrows entered where the bank was vertical but some were constructed in slightly sloping sections, and even in the nearly horizontal top of the bank. The pollen plant of this species, a yellow-orange composite, grew profusely along the roadway and in adjoining open places.

NEST STRUCTURE: Both *P. oraniensis* and *intermedius* apparently normally have more than one female in a nest. Two nests of *P. oraniensis* each contained three females while 20 females were collected from one nest of *P. intermedius*. All were dissected in the laboratory, and each was found to contain three normal ovarioles per ovary. Hence there is no indication of the development of social casts in spite of the bee having composite nests. The nests of *P. podagricus* may also be composite but this point was not verified; two females, collected from flowers, had ovaries similar to those of *P. oraniensis* and *intermedius*.

Two nests of *P. oraniensis* were supplied with an abundant eccentric tumulus, in one case measuring 8.0 cm. in diameter. During the time of flight, the entrances were open; in the afternoon when the females were in the nests and no longer collecting pollen the entrances were closed with soil. The main tunnel of the nest excavated descended vertically in a meandering fashion to a depth of about 8 cm. Unfilled except for the entrance plug, it branched into a number of meandering rami which were loosely or partly filled. These branches extended primarily horizontally for a considerable distance; some cells were as far as 23 cm. from the main tunnel. There was no indication of a lining in either the main tunnel or its branches, all of which had diameters of about 5.0 mm. Each of two open cells was connected to a branch by a lateral 3.5 cm. long that rose more than 1 cm. before opening into the cell with an entrance aperture of 4.0 mm. Laterals are filled after cell closure so that they cannot be traced, but all cells seemed to be far removed from the main branches.

Cells of *P. oraniensis* (dimensions given in table 1) were at depths of 9 to 15 cm.; all were tilted downward to the rear at about 15 to 20



FIG. 1. Thirty-three kilometers southwest of Rabat near Oued Cherrat, Morocco. *Panurgus oraniensis* and *intermedius* nested in bank on right side of picture, and *Panurginus albopilosus* nested in horizontal areas nearby.

FIG. 2. Female of *P. oraniensis* collecting pollen from *Picris cupuligera*.

degrees from the horizontal. The floor may have been slightly flattened compared with the ceiling. The lining was apparently not “built-in” but

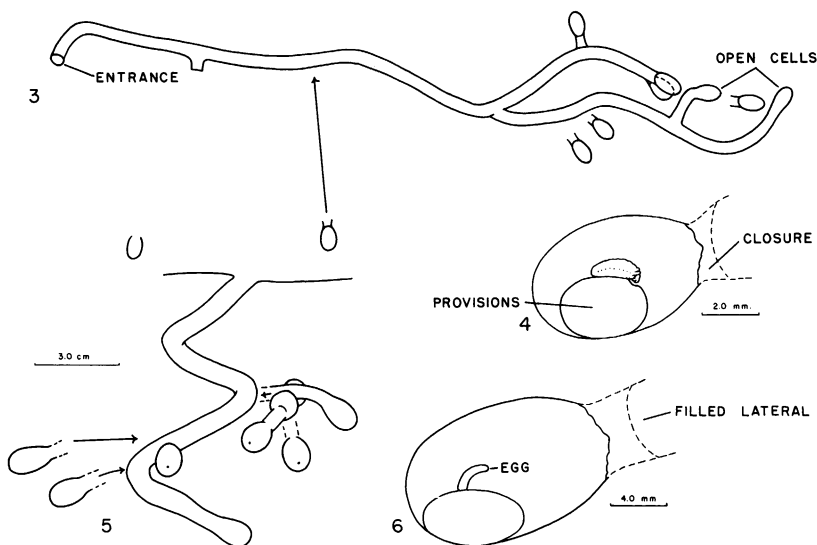


FIG. 3. Diagram of nest of *Panurgus intermedius* occupied by four females, top view.

FIG. 4. Cell of *Panurgus podagricus* containing first instar and provisions, side view.

FIG. 5. Nest of *Melitturga caudata*, side view.

FIG. 6. Cell of *M. caudata* containing egg and provisions, side view.

Scales refer to figures 3 and 5, 4 and 6, respectively.

was coated with a shiny, waterproof, silklike layer. The closure was a concave spiral on the inside and a concave smooth surface on the outside. Normally the outer surface was obscured by the fill in the lateral.

The nest entrances of *P. intermedius* from Oued Cherrat were open but had no tumuli because they were in a vertical bank. The two nests of this species from 32 kilometers south of Ben Slimane were also open, except in the afternoon, and lacked tumuli. One of these nests (fig. 3) occupied by four females was excavated with care. With most cells about 4 to 6 cm. deep, the nest was similar in configuration to that of *P. oranien-sis*. The diameter of the main burrow and branches was 3.5 to 4.0 mm. and that of the cell entrance, 2.5 mm. Cell dimensions are given in table 1. In addition to a shiny, waterproof coating, the cell wall may have had a "built-in" lining but, if so, the lining was thin and fused with the surrounding soil.

The burrow entrances of *P. podagricus* were open, at least during the period when females were flying, and some displayed excavated soil on the downhill side. The main burrow, about 2.5 mm. in diameter, headed downward into the bank, meandered, and at least in some cases

TABLE 1
 DIMENSIONS (IN MILLIMETERS) OF CELLS OF MOROCCAN PANURGINAE
 (Figures in parentheses indicate the number of measurements)

Species	Cell Length	Cell Diameter
<i>Panurgus oraniensis</i>	10.0–12.0 (4)	6.0–6.5 (3)
<i>Panurgus intermedius</i>	8.0–9.0 (2)	4.5–5.0 (3)
<i>Panurgus podagricus</i>	6.0 (3)	3.5–4.5 (3)
<i>Panurginus albopilosus</i>	5.0 (5)	2.75 (2)
<i>Melitturga caudata</i>	14.0–15.0 (8)	8.0–9.0 (6)

branched. Because of the difficulty of excavating the nest, the general configuration was not apparent but numerous cells, perhaps from a number of nests, occurred horizontally from 3 to 10 cm. into the bank.

The cells of *P. podagricus* (dimensions given in table 1) had an entrance diameter of not more than 2.0 mm. They seemed to have a more spherical shape than those of the other two species of *Panurgus*, but, like them, had a shiny lining and perhaps a "built-in" wall. The closure was a concave indistinct spiral on the inside and a concave smooth surface on the outside against which the soil plug of the lateral was placed.

PROVISIONING, OVIPOSITION, AND DEVELOPMENT: All three species transported the pollen dry with the extensive scopa of long, plumose hairs on the hind legs (fig. 2) and placed it loose in the bottom of the cell until a sufficient quantity was on hand for it to be shaped into the form of the food mass. The shaped provisions in each case were a flattened sphere roughly proportional to the size of the adult (table 2). Lacking a coating, the spheres were homogeneously moist and mealy, and were placed at the rear of the cell floor so that they were more or less horizontal. Apparently because of the somewhat spherical form of the cell (fig. 4), the provisions of *P. podagricus* were placed more toward the middle of the cell than were those of the other two species.

In all three species the eggs were deposited in the sagittal plane of the cell on top of the provisions, and with their anterior ends toward the cell closure. The eggs were white, shiny, and arched so that in each case the anterior and posterior ends, but not the middle, touched the provisions. The approximate lengths of the eggs were as follows: *Panurgus oraniensis* 2.5 mm., *intermedius* 2.5 mm., *podagricus* 2.2 mm.

The eggs hatched quickly and the small larvae, sitting in the positions occupied by the eggs, fed on the provisions beneath their heads, as do other Panurginae. However, as the larvae grew, their activities apparently departed from those of most panurgines and although some evi-

TABLE 2

DIMENSIONS (IN MILLIMETERS) OF POLLEN BALLS OF MOROCCAN PANURGINAE
(Figures in parentheses indicate the number of measurements)

Species	Maximum Diameter	Minimum Diameter
<i>Panurgus oraniensis</i>	4.2–5.0 (6)	3.0–3.6 (6)
<i>Panurgus intermedius</i>	4.0–4.5 (6)	3.0 (6)
<i>Panurgus podagricus</i>	3.5–3.8 (4)	2.2–3.0 (4)
<i>Panurginus albopilosus</i>	2.25–2.50 (3)	1.75 (4)
<i>Melitturga caudata</i>	7.2×6.0 ¹ (1)	4.0 (1)

¹ These provisions were elongate so that the length was greater than the width.

dence indicates there may be specific differences in their feeding behavior, sufficient information is not on hand for a complete analysis of these actions. Even the moderately small larvae of *P. intermedius* and *oraniensis* began to feed along the top edge of the entire anterior half of the pollen ball by moving the anterior half of their bodies. At least in the case of *P. intermedius* the larva ate even farther around the top edge but whether this was accomplished by moving only the anterior half of its body was not clear. In contrast, young larvae of other known panurgines consume only the food directly beneath their heads (Rozen, 1965, fig. 4).

The activities and orientation of intermediate and last stage feeding larvae are not understood, but predefecating forms were found on their backs facing the rear of the cell. At least in the case of *P. oraniensis* and *intermedius* they reoriented before defecating so that in each case the head was next to the cell closure. Several intermediate larvae of *P. podagricus* were noticed to have consumed the entire anterior part of the pollen mass before reorienting.

In the case of *P. oraniensis* and *intermedius*, and presumably also *podagricus*, the larva defecates after finishing the food supply. The period between completing the provisions and defecating may be longer than it is with most panurgines, at least in the case of *P. intermedius*, for on April 28, 1968 we excavated more than 25 predefecating larvae and only one postdefecating larva. Most larvae of *P. oraniensis* and *intermedius* pupated a short time after defecating. The majority of the postdefecating larvae continued to be active and developed the characteristic constriction between the mesosoma and metasoma well before pupating. Some, however, became quiescent after defecating and presumably were overwintering forms. This transformation may have been

a result of the laboratory conditions under which they were kept. The feces of *P. oraniensis*, applied to the upper rear of the cell, quickly became moldy and adhered only loosely to the cell wall. Although the meconial mass was thicker and not so extensive as that of *Panurginus albopilosus*, it occupied the same position in the cell (fig. 13). As is the case with all panurgines, no cocoons were spun.

ADULT ACTIVITY: Because males of all three species were found inactive on the heads of Compositae on cool cloudy days, they apparently slept there. Females normally passed the night in the burrows although some inactive females bearing pollen were observed on the flowers during cloudy conditions in the morning.

Mating in the case of *P. intermedius* and *podagricus*, and presumably also of *oraniensis*, takes place when the female lands on the flowers. Whether the males merely wait on the flowerheads until the female lands or whether the males fly from flower to flower in search of females is not certain.

Some larvae of all three species transformed into quiescent, post-defecating, overwintering forms under laboratory conditions, and some of *P. intermedius* and *podagricus* were still in diapause in January, 1970. The fact that many pupae of *P. oraniensis* and *intermedius* developed in the laboratory or were collected from the field indicates that these two species, and also very possibly *podagricus*, have more than one generation a year.

PARASITISM: Various species of *Nomada* of body sizes corresponding to those of presumed hosts were found flying around the nesting entrances of all three species of *Panurgus*, but only two *Nomada* larvae and one egg were recovered, all from the cells of *P. intermedius*. The *Nomada* egg was inserted about halfway into a hole in the cell wall but was not cemented in the hole. Its chorion was clear and shiny, and the chorion in the other cells remained behind after the larva hatched. One first instar was found on the dead first instar of the host.

SUMMARY OF THE BIOLOGY OF *Panurgus*: The works of Münster-Swendsen (1968) and Rozen (1967), together with the current study, make possible tentative generalizations regarding the life history of bees in the genus *Panurgus*. Although biological information is available on only five [*P. banksianus* (Kirby), *calcaratus* (Scopoli), *intermedius*, *oraniensis*, and *podagricus*] of approximately 45 species in the genus, these five represent diverse taxonomic elements.

Like many other panurgines, *Panurgus* nests in barren or nearly barren ground. The genus differs from most other genera in that it has broad tolerances with respect to the degree of slope of the nesting site,

with some species nesting in nearly horizontal ground, others in vertical banks, and some in both situations. All species nest in soil that is more or less hard packed even though the nests of *P. intermedius* at Oued Cherrat seemed at first to enter limestone. *Panurgus calcaratus* as well as *P. oraniensis* and *intermedius* at times use composite nests, a habit that may be widespread among other *Panurgus*. However, an examination of the ovaries of Moroccan panurgines gives no reason to assume that the genus has developed a social system with casts.¹ It seems likely that all species will be found to nest at times in loose aggregations, as is the case with *P. calcaratus*, *podagricus*, *banksianus*, and, indeed, most panurgines.

So far only *P. banksianus* is known to construct several openings to a nest. Tumuli are apparently formed when the ground is sufficiently horizontal to hold the excavated material, and burrow entrances are open during the time that females are foraging, at least so far as *P. banksianus* and the three Moroccan species are concerned. The cells of *Panurgus* are arranged singly and are tilted only slightly from the horizontal. They are lined with a waterproof, shiny lining and there is a possibility that beneath this lining there may be a special "built-in" wall in the cells of some species. Such walls are difficult to detect, for they blend with the surrounding soil. Although *P. banksianus* has been reported to have only one or two cells to a nest (Nielsen, 1934), Münster-Swendsen (1968) stated that the species constructs a number of cells to a nest. Cell closures for all species in the genus will probably be found to be a concave spiral on the inside, as is the case with all the Panurginae. The nests of *P. oraniensis*, *intermedius*, and possibly other *Panurgus* are shallow, like those of most panurgines, but tend to branch and extend laterally over a greater area than do the nests of other genera.

In all known *Panurgus* the provisions are shaped into a mealy moist, flattened sphere that is not coated with a waterproof lining. At least in the Moroccan species, but probably in others as well, the sphere is placed toward the rear of the cell, and the female deposits an egg on top of the food.

The young larvae of at least the Moroccan species are able to move the anterior part of their body to a greater extent than can most other of the Panurginae. Probably, larvae of all species apply the feces to the rear of the cell. The three Moroccan species apparently pass through more than one generation a year, but the European *P. banksianus*

¹ At the time dissections were being performed on series of *Panurgus* females, similar dissections were made on series from two composite nests of *Perdita utahensis* Cockerell from Rodeo, New Mexico. Both series, one of four females and the other of eight, showed that the ovaries of all individuals were identical and functional.

(Münster-Swendsen, 1968) apparently has only one. So far as known, all *Panurgus* hibernate as quiescent postdefecating larvae.

Mating of the Moroccan species takes place on the flowers, but Münster-Swendsen (1968) discussed the mating of *P. banksianus* over the nesting area. Adults seem to prefer composites as a source of food for their offspring, and males sleep on the blossoms although Münster-Swendsen stated that those of *P. banksianus* also slept in short burrows.

The European and Moroccan *Panurgus* are attacked by the cuckoo bees of the genus *Nomada*.

PANURGINUS NYLANDER

Panurginus albopilosus Lucas

DESCRIPTION OF HABITAT: We discovered this species nesting at Oued Cherrat, 33 kilometers southwest of Rabat, Morocco, on April 10, 1968 and studied its biology from time to time over a three-week period. Most nesting sites occurred on horizontal to slightly sloping, sparsely vegetated areas, and each consisted of numerous nests. The species was the most abundant bee in the area.

The nest area examined in greatest detail occurred along the shoulder of the paved main road leading from Rabat to Casablanca, close to where *Panurgus* nested (fig. 1). The low surface vegetation, consisting of the pollen plant, *Diplotaxis tenuisiliqua*¹ (Cruciferae), and other species, grew sparsely so that the ground was clearly visible although shaded slightly in the morning. Eucalyptus trees grew nearby, shading the area of the site 50 to 60 per cent in the afternoon.

Burrows, occurring over a slightly sloping area about 20 feet long and 6 to 7 feet wide, were little disturbed by man or domestic animals. The soil was hard and difficult to dig, and in some places contained many small stones. Although appearing dry, the soil was quite moist because of recent rains.

NEST STRUCTURE: The nests of *P. albopilosus* were occupied by one or more females; the maximum number of females counted was five to a nest although larger assemblages probably existed. Composite nests seemed to be more common than nests occupied by single females. Four females taken from one nest and two from another all had their ovaries normally developed with three ovarioles per ovary. Hence this species apparently has not developed a cast system.

Nest entrances were irregularly spaced and either had tumuli of loose, fine, dry soil or lacked them. The burrow openings varied from

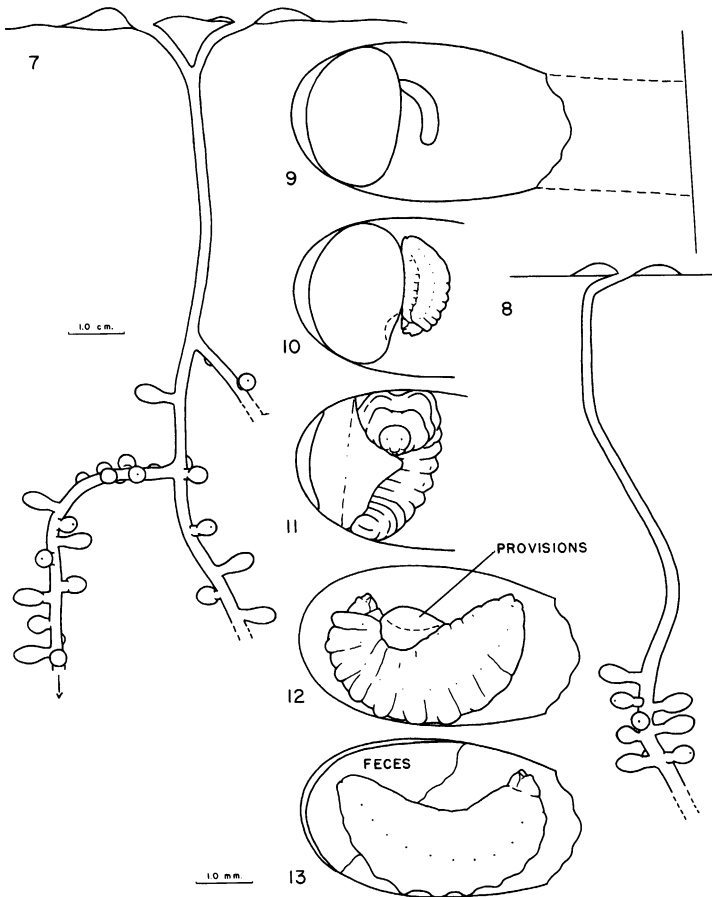
¹ Kindly identified by J. Mathez, Institut Scientifique Chérifien, Rabat, Morocco.

being centrally situated in the tumuli to being on the edge of the tumuli, and females occasionally began nests under twigs or next to stones. In most cases the main tunnel (figs. 7, 8) entered the ground at only a slight angle from the horizontal, but after 0.5 to 1.0 cm., became nearly vertical and descended moderately straight. The diameter of the main burrow was approximately 1.75 mm. at the entrance and part way to the cell level, but then gradually increased to 2.0 to 2.5 mm. at the cell level. This is the first observed case in the Panurginae in which the main tunnel has not been of uniform diameter for its entire length. However, other panurgine nests should be checked for this kind of variation. Why the tunnels are narrower toward the surface is not clear but at least in one case seemed to be the result of a special "built-in" lining of soft earth in the upper part of the burrow. This lining was thicker on one side than on the opposite side and was suggestive of a lining in the burrows of *Melitturga clavicornis* (Latreille) (Rozen, 1965) although in *Melitturga* the lining was harder than the substrate and was tentatively thought to be what remained of a filled-in beetle burrow. The constricted upper burrow of *P. albopilosus* may assist in excluding cuckoo bees and other parasitic insects from gaining entrance to the cell area.

Nests of single females (fig. 8) consisted of only one entrance and a single main tunnel, whereas the one nest occupied by five females (fig. 7) had two entrances and at least three branches. The main tunnel and branches on all nests were open but in one of the single nests, a short plug was found near the surface. In cases where main tunnels branched, one ramus continued to descend vertically, whereas the other descended at least, at first, obliquely. All cells were connected to the main tunnel by laterals (figs. 7-9) of nearly uniform length, 2.0 to 2.5 mm., and with a diameter of about 2.0 mm. These laterals were filled after the cell was provisioned and closed so that no laterals were visible on the wall of the main tunnel.

Cells (fig. 9) with dimensions given in table 1 were arranged singly at the end of laterals and were apparently symmetrical around their long axis. Some were oriented horizontally and others tilted as much as 20 degrees. In those that tilted the closure was lower than the rear in most cases but perhaps some had the closure slightly higher than the rear. All were lined with a conspicuous, shiny, waterproof lining which was more pronounced toward the rear of the cell than toward the front. This lining was thicker than I have seen for any other panurgine and peeled easily from the cell wall. Semi-transparent, it was suggestive of, although not so developed as, the lining of colletid cells. The closure was an indistinct spiral, concave on the inside.

The cells were arranged around the main tunnel or its branches from



FIGS. 7-13. *Panurginus albopilosus*. 7. Partial diagram of nest containing five females. 8. Nest containing one female. 9. Cell containing egg and pollen mass, side view. 10. Rear part of cell with young feeding larva. 11. Rear part of cell with reoriented larva feeding on central core of provisions. 12. Cell with last instar consuming central core. 13. Cell containing postdefecating larva and feces.

Scales refer to figures 7 and 8, and 9 to 13, respectively.

about 5 cm. below the surface to a depth of more than 11 cm. A number of cells were sometimes attached to a main tunnel at almost the same depth so that shallow nests contained a good many cells even if the tunnels were not branched. One nest of a single female contained nine irregularly spaced cells, all between the depth of 7 to 10 cm. Sequence of cell construction in single nests seemed to be from top to bot-

tom, as older cells were found above. However, in the large composite nests, the order of cell construction was mixed so that even on a single branch cells with eggs were above or at the same level as those containing mature larvae. In both composite and single nests a female constructed a cell and provisioned and closed it before starting the next one.

PROVISIONING, OVIPOSITION, AND DEVELOPMENT: Females transported the provisions to the nest as a large moist mass surrounding each hind tibia, in contrast to all known species of *Panurgus* which transport the pollen dry. The provisions, homogeneously moist and without a waterproof coating, were formed into a flattened sphere (fig. 9), with dimensions as given in table 2. These spheres were wedged into the rear of the cells so that their maximum diameter was approximately vertical. The surface closest to the cell closure was somewhat flatter than the one toward the rear of the cell.

The females deposited arched eggs, about 1.75 mm. long (fig. 9), in the sagittal plane of the cell on the front surface of the provisions. The more pointed posterior end of the egg was attached and the anterior end extended into the lumen of the cell. The eggs were translucent white and the chorion was smooth and shiny. As with other panurgines, the eggs hatched in a few days and the early instars were immobile. The newly emerged larvae rested, head down, on the pollen mass and consumed the provisions beneath their heads (fig. 10). As a consequence, the lower part of the provisions was eaten first. Young larvae quickly became robust compared with other panurgine larvae, a condition that persisted through the last larval instar.

Unlike most of the panurgines, the larvae of *P. albopilosus* moved about the food supply after they had become intermediate in size. Once a larva reached this critical size, it shifted its position but remained in contact with the provisions. In the new attitude, the sagittal plane of its body was at approximate right angles to the long axis of the cell, and its dorsum came in contact with the cell wall. It then fed circularly around the provisions, apparently moving by pushing its back against the cell wall. The ambulation was apparently assisted by a sticky secretion that caused the larva to adhere to the cell lining. The secretion, although not visible, was easily detected when larvae were picked up by forceps. The larva moved around the front of the provisions, eating the food in front of it, so that a central, pointed core of pollen remained as the periphery of the provisions was consumed (fig. 11). When the provisions were eaten so that they no longer adhered to the sides of the cell, the larva reoriented so that it rested on its back and faced the rear of the

cell. It then consumed the central core (fig. 12) which was cradled on its venter.

The provisions were consumed in a week or two. A short time thereafter the larvae reoriented, for by the time they defecated they faced the cell closure. All postdefecating larvae, totally quiescent, robust, and white (fig. 13), were found on their backs with their heads toward the future exit.

The feces were applied as a thin layer (fig. 13) to the upper rear of the cells. Yellow at first, the feces darkened quickly. The posterior tip of the abdomen of the larva did not stick to the mass as was the case with *Panurginus potentillae* (Crawford) (Rozen, 1967). This species, like other panurgines, did not spin a cocoon. There is apparently but one generation a year, for after defecating all larvae became totally quiescent.

ADULT ACTIVITY: Both males and females were active and abundant during the field observations. Males slept on the flowers of three species of Compositae which grew among the pollen plant. One of these species, *Picris cupuligera*, was the pollen plant for *Panurgus oraniensis* and *intermedius*, the biologies of which are treated above. As many as 25 males could be found hiding under the ray flowers of a single head (fig. 14), whereas other flowers of the same species were unoccupied even though they grew close by. Although males did not "ball," as is the case with some bees and wasps, their grouping on certain flowers indicated communication between individuals. Females were never found inactive on the flower plants and spent the night and periods of inclement weather in their nests.

During cool, cloudy weather and at night the bees were inactive but as soon as the weather warmed and became sunny, both sexes flew actively around the pollen plant. On a warm sunny day males and females were on the wing before 9 A.M.

Mating occurred on the flowers; females, returning to the nest, were never pursued by males even though the males were abundant in the vicinity. Numerous males were observed flying about the pollen plants in an erratic weak flight. Copulation was apparently very swift, for in spite of numerous individuals of both sexes, no certain copulations were noticed though many brief encounters were observed.

PARASITISM: Parasitic insects were not commonly found in the nesting area and none was recovered from a cell. However, a number of very small *Nomada* were collected from the vicinity of one nesting site. Because of the close agreement in size between them and *P. albopilosus*, the latter may well have been parasitized by this species. If so, the rate of parasitism



FIG. 14. Males of *Panurginus albopilosus* congregated for the night on the flower-head of *Picris cupuligera*. A single beetle sits in the middle of the head.

is extremely low, perhaps as a result of more than one female *Panurginus* using a single nest.

SUMMARY OF THE BIOLOGY OF *Panurginus*: The biology of *P. albopilosus* agrees closely with what is known about other species in the genus (Rozen, 1967). All species nest in nearly horizontal ground in aggregations. *Panurginus albopilosus* is similar to *labiatus* (Eversmann) in that a number of females share a nest; some species in the genus have solitary nests.

Panurginus albopilosus may construct more than one opening to a composite nest, a situation not reported heretofore for the genus. Nest entrances of this species were in some cases hidden near stones or twigs on the ground, whereas those of *P. potentillae* were not. The two species are similar in that entrances may or may not have tumuli. The lined main tunnel of *P. albopilosus* has not been reported for other species in the genus although this condition is perhaps similar to that occurring in *Melitturga*. A main tunnel that has a greater diameter at the cell level

than at its upper part is not known for any other panurgine. Females of this genus construct cells (arranged singly) that are nearly horizontal, lined with a conspicuous shiny lining, and closed with a spiral plug.

There is considerable variation from species to species with respect to the provisions, which are mealy moist in all known cases. The food mass of *P. potentillae* is almost spherical and placed on the floor of the cell, but the food of *P. albopilosus* is flattened and placed vertically in the cell, a condition that is somewhat similar to that described for *P. labiatus* by Malyshev (1924). The eggs of both *P. albopilosus* and *labiatus* are placed on the anterior flattened surface of the spheres, whereas in *P. potentillae* the egg is forward to the center of the top of the sphere.

Panurginus is unusual in that the intermediate larvae, at least of *P. albopilosus* and *potentillae*, are capable of moving in relation to the food mass. The feces are applied to the rear of the cell by the larvae of *P. albopilosus* and *potentillae*, and both of these species overwinter as robust postdefecating larvae. One unidentified species of this genus (Rozen, 1967) apparently overwinters as an adult.

MELITTURGA LATREILLE

Melitturga caudata Pérez

DESCRIPTION OF HABITAT: We discovered a cluster of five nests of this species 32 kilometers south of Ben Slimane, Morocco, on April 25, 1968. Four nests in early stages of construction were excavated the same day, the fifth, three days later. The cluster occupied the slightly sloping ground on top of a foot-high bank next to a dirt road (fig. 15). The site, 100 feet from the nesting areas of *Panurgus podagricus* and *intermedius*, discussed above, was unshaded during the day, well drained but moist at the cell level, and of moderately hard soil containing some rocks.

NEST STRUCTURE: The five nests were grouped within an area of less than 30 cm. in diameter. Four entrances were not constructed at the edges of stones or beneath twigs; the fifth was not discovered. Three nests were totally devoid of tumulus but the other, in the process of being constructed, had a symmetrical tumulus about 4 cm. in diameter and 1.5 cm. high. One female was recovered from each nest.

Main burrows of all nests were open and about 7.0 mm. in diameter, and meandered to a considerable extent. One nest, excavated so that it could be diagrammed (fig. 5), consisted of a meandering main burrow, at the end of which was a recently constructed, unprovisioned cell. Eight other cells were associated with the nest; three of these were arranged singly and one of the three had been completely filled in after being

constructed though there was no indication of parasites or of the eggs of cuckoo bees in the cell wall. The remaining five cells formed a cluster and were interconnected by their laterals or were in series. Of these



FIG. 15. Nesting site of *Melitturga caudata* marked with X at 32 kilometers south of Ben Slimane, Morocco. *Panurgus podagricus* and *intermedius* nested 100 feet away in the same low bank.

cells, the closest was 1.5 cm. to the main burrow and all were separated by 1.5 cm. or less.

Laterals, filled after the cells were provisioned, seemed to have a special "built-in" lining of fine soil. Neither they nor the main burrows are waterproof. The laterals, although sometimes curved, ran directly

to the cells without dipping first and narrowed to about 5.0 mm. in diameter at the cell opening.

The cells (fig. 6), with dimensions as given in table 1, were apparently symmetrical around their long axis. Found at depths between 4.0 and 9.0 cm., they were tilted 20 to 80 degrees from the horizontal, with the front end always being higher than the rear. Like the laterals, the cells may have had a "built-in" wall of about 1.0 mm. in thickness. This wall was intimately bound to the substrate. The female applied a thin waterproof coating of silklike material over the wall except for the front part of the cell. This imparted a smooth, but not very shiny, appearance to the surface; elsewhere the wall was duller and less smooth. The cell closures, about 3.0 mm. long, were distinct concave spirals with four to five rows to the radius on the inside and a smooth concave surface on the outside. Each cell was constructed, provisioned, and closed before the next one was started.

PROVISIONING, OVIPOSITION, AND DEVELOPMENT: The female transported the pollen to the nest in a moist condition and deposited each load as an amorphous mass in the bottom of the cell. When a sufficient quantity was on hand, she shaped it into an orange, flattened spheroid which in one case was longer than wide (see table 2). In other cases the length and width seemed more equal. The provisions were homogeneous and very moist, and were unusual in that they had a sticky consistency rather than a mealy one. This consistency prevented their removal as a sphere with forceps and they did not crack open when jabbed with pointed forceps. The difference between the length and width of the pollen mass may have been the result of the semi-liquid quality of the food, causing the mass to conform to the elongate shape of the cell. The food mass did not normally liquefy while being consumed although a considerable quantity of moisture may have existed at the juncture of the food and the floor of the cell when the larvae were intermediate in size.

The female placed the provisions to the rear of the cell (fig. 6) and deposited the egg on top of the provisions so that its posterior end was attached at right angles to the rear half of the provisions. The front end of the egg rose into the cell. As in other Panurginae, the egg is in the sagittal plane of the cell.

The arched egg (fig. 6), 2.7 mm. long, had a rounded anterior end and a slightly thicker posterior end. The translucent chorion was white and smooth. In some cells no eggs or larvae were evident and the provisions had begun to liquefy. Mature predefecating larvae were uncovered from one nest that also contained a cell recently completed, a



FIG. 16. Intermediate larva (probably second instar) of *Melitturga caudata* on top of provisions.

fact that indicated that hatching and larval development were rapid. Young larvae (fig. 16) were slender and not so robust as those of *Panurginus albopilosus*. They did not move on the pollen mass as they fed but merely consumed the food beneath their heads. One larva, nearly finished eating, rested on its side while completing the provisions that projected upward like a pillar from the cell floor to which it adhered. Soon after feeding, predefecating larvae voided from the anus a considerable quantity of clear liquid, the significance of which is not understood at this time. With apparently one generation a year, *M. caudata* overwintered as a postdefecating larva.

ADULT ACTIVITY: Females, as they came to their burrow entrances, hovered in a stationary position longer than most panurgines and emitted a conspicuous buzzing sound. A single male, hovering in a stationary position in the vicinity of this site, gave a loud buzzing sound before darting rapidly away.

SUMMARY OF THE BIOLOGY OF *Melitturga*: The biology of *M. caudata*

agrees closely with that of *M. clavicornis* (Latreille) and "*clavicornis*?" (Ferton, 1920; Rozen, 1965, 1967), the only species in the genus about which we have substantial biological data.

All three species nest in nearly horizontal, mostly barren, ground in loose nesting aggregations. In the case of *M. caudata* there seems to be only one female to a nest, but in *M. clavicornis* a nest may be occupied by two females. At least in the case of *M. clavicornis* and *caudata*, tumuli are sometimes lacking around nest entrances and the meandering main tunnels are open in the day during the nesting season. The main tunnels of these two species seem to possess a lining. Heretofore this phenomenon seemed unusual for the Panurginae, but now there are also suggestions of such linings in *Panurginus albopilosus*. Lateral tunnels of different lengths within a nest are filled with soil after the nest has been closed, as is the case with all panurgines. Some cells of *M. caudata* were arranged in linear series, but those of *M. clavicornis* are arranged singly, so far as is known. Cells of *M. caudata* and *clavicornis* tip to the rear in varying amount. The cells of *M. clavicornis*, and apparently of *caudata*, may have a special wall, but whether it is "built-in" is not clear. *Melitturga* has numerous cells to a nest and seems to nest shallowly, although Tigrari (1965) found cells of *M. clavicornis* as deep as 35 cm. Cell closures are a concave spiral on the inside.

The provisions of *M. clavicornis* and many other panurgines are flattened spheres, but the food mass of *M. caudata* also is in some cases longer than wide, a feature not reported heretofore for the subfamily. The consistency of this food in *M. caudata* was moist and sticky, whereas in *M. clavicornis* it was firm. In both species the food mass is uncoated and is placed toward the rear of the cell. Moisture is evident where the sphere adheres to the cell floor. Before being shaped into the food loaf, the pollen and nectar are stored as an amorphous mass on the rear of the floor.

The eggs and egg orientation of *M. clavicornis* and *caudata* are similar (fig. 6). The feeding habits of the larvae of the three species of *Melitturga* seem to differ (Ferton, 1920; Rozen, 1965). *Melitturga caudata* and *clavicornis* overwinter as postdefecating larvae (Tigrari, 1965) and apparently have a single generation a year.

MATURE LARVAE

The larvae treated below agree in most respects with the congeneric larvae which have been described previously (Rozen, 1965, 1966; Rozen and Rozen, 1966), and indicate that *Panurgus*, *Panurginus*, and *Melitturga*, as genera, are quite distinct from one another in larval stage. All Moroc-

can species described here key out to their congeners in Rozen (1966).

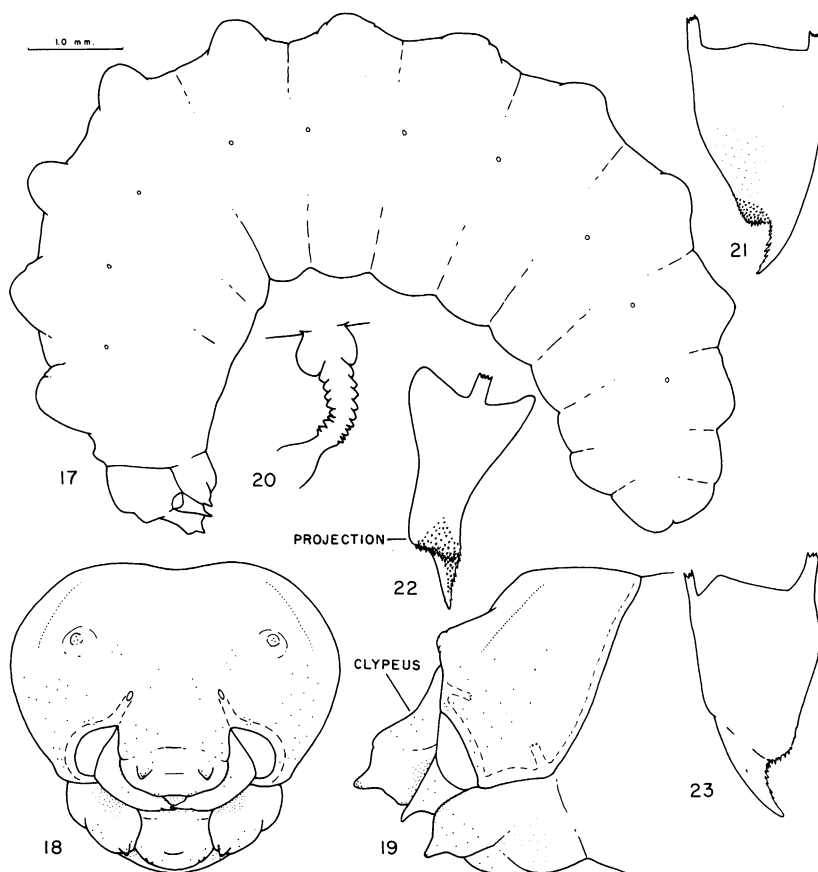
PANURGUS PANZER

The mature larvae of *Panurgus* are quite similar, as revealed not only by the study of the three species described below, but also by the work of Rozen (1966) and by an examination of the larvae of *P. banksianus* (Kirby) (kindly donated by Dr. Mikael Münster-Swendsen). The elongate clypeus and ventrally produced cuspal region of the mandible (as seen in adoral view) are unique features for the Panurginae; neither characteristic is found in any other genus. At the present stage of our knowledge the species of *Panurgus* cannot be distinguished on the basis of mature larvae.

Panurgus oraniensis Pérez

Figures 17–23

HEAD (FIGS. 18, 19): Integument without setae but with scattered sensilla; integument unpigmented except for mandibular apices, antennal papillae, and internal ridges. Vertex produced moderately on each side above antennae but degree of expression of vertical prominences somewhat variable so that vertex of some specimens more pronounced than on specimen illustrated (fig. 19); antennae arising from moderately projecting prominences; clypeus abnormally elongate compared with that of other panurgine genera; gena produced slightly just above posterior mandibular articulation. Tentorium complete and well developed; each posterior pit situated at juncture of hypostomal ridge and posterior thickening of head capsule; posterior thickening of head capsule well developed; hypostomal ridge well developed; pleurostomal ridge well developed; epistomal ridge below anterior tentorial pits moderately well developed, mesiad of pits absent; parietal bands faint. Each antenna a low convexity bearing three sensilla. Labrum bearing two prominent tubercles; epipharynx spiculate laterally. Mandible (figs. 21–23) moderately slender; apex slender and simple (i.e., without subapical tooth); upper apical margin serrate; lower margin nonserrate except for one or two minute denticles on some specimens; cusp strongly produced adorally (fig. 21) and also ventrally (fig. 22); cuspal teeth numerous; dorsal surface faintly spiculate basad of cusp. Maxilla, as seen in lateral view, projecting at most slightly beyond apex of labium (specimen drawn in fig. 19 has apical part of labium somewhat retracted); palpus well developed, approximately equal in size to labral tubercle; palpus perhaps directed somewhat downward but not so much as in *P. dentipes* (Rozen, 1966); dorsal surface of maxilla, but not of palpus, spiculate. Hypo-



FIGS. 17-23. Mature larva of *Panurgus oraniensis*. 17. Postdefecating larva, lateral view. 18, 19. Head, frontal and lateral views, respectively. 20. Spiracle, side view. 21-23. Left mandible, dorsal, inner, and ventral views, respectively.

Scale refers to figure 17.

pharynx spiculate; hypopharyngeal groove indistinct. Labium divided into prementum and postmentum; palpus evident but much smaller than maxillary palpus. Salivary opening a slightly curved slit not extending to hypopharyngeal groove.

BODY (FIG. 17): Color of preserved larvae whitish. Much of integument finely spiculate; tenth abdominal segment nonspiculate ventrally but with some spicules just below anus. Paired dorsal tubercles low, rounded; their apices at most indistinctly spiculate; on predefecating

larvae tubercles scarcely evident on posterior body segments (as in *P. podagricus*, fig. 26); on postdefecating larvae (fig. 17) tubercles evident on most segments; tenth abdominal segment not produced as median tubercle; pleural regions not produced; intersegmental lines normally to shallowly incised. Spiracles (fig. 20) with atrium projecting above body wall; atrial wall without teeth; peritreme present; primary tracheal opening with collar; subatrium moderate in length. Predefecating female larva with imaginal disks on venter, as described for *Meliturgula braunsi* Friese (Rozen, 1968); sexual characteristics of male larva not known.

MATERIAL STUDIED: Three postdefecating larvae, two predefecating larvae, Oued Cherrat, 33 kilometers southwest of Rabat, Morocco, April 24, 1968, all from burrow no. 1 (J. G. Rozen); one postdefecating larva, same, except April 23, 1968, no burrow information.

Panurgus intermedius Rozen¹

Figure 24

HEAD: As described for *P. oraniensis* except for following: Maxillary palpi slightly smaller in relation to head size; serrations on upper apical mandibular edge perhaps somewhat larger.

BODY: (FIG. 24): As described for *P. oraniensis* except for following: Live postdefecating larva yellowish, with body wall rigid; spiracular subatrium somewhat longer than that of *P. oraniensis*; sexual characteristics of ninth abdominal segment of male as described for *Meliturgula braunsi* (Rozen, 1968).

MATERIAL STUDIED: Eight predefecating larvae, Oued Cherrat, 33 kilometers southwest of Rabat, Morocco, April 24, 1968, from burrow no. 4 (J. G. Rozen); one postdefecating larva, same, except no burrow indication; eight postdefecating larvae, 32 kilometers south of Ben Slimane, Morocco, April 28, 1968 (J. G. Rozen).

Panurgus podagricus Pérez

Figures 25, 26

HEAD: As described for *P. oraniensis* except mandibular denticles somewhat larger and fewer.

BODY (FIGS 25, 26): As described for *P. oraniensis* except for following: Color of live postdefecating larva yellow, with body wall rigid; integument somewhat more distinctly spiculate; spiracular subatrium even

¹Description appended.

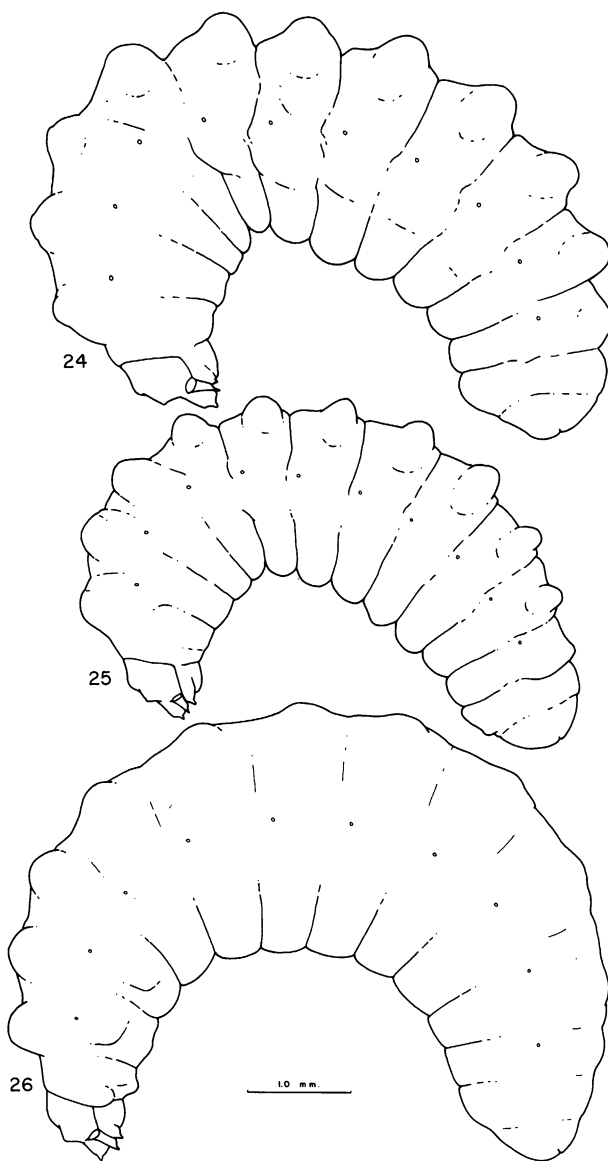


FIG. 24. *Panurgus intermedius*. Live postdefecating larva, lateral view.

FIG. 25. *Panurgus podagricus*. Live postdefecating larva, lateral view.

FIG. 26. Same, except predefecating larva preserved.

Scale refers to all figures.

longer than that of *P. intermedius*; live postdefecating larva with distinct modification of integument below imaginal disks of female.

MATERIAL STUDIED: One postdefecating larva, six predefecating larvae, 32 kilometers south of Ben Slimane, Morocco, April 25–28, 1968 (J. G. Rozen).

PANURGINUS NYLANDER

Low vertex, presence of the median section of the epistomal ridge, anterior tentorial pits situated slightly above the epistomal ridge, short clypeus, receding labium, down-curved maxillary palpus with enlarged spicules, and reduced dorsal tubercles on the posterior abdominal segments make the larvae of *Panurginus* distinctive among the Panurginae.

Panurginus albopilosus Lucas

Figures 27–33

The larva of this species is nearly identical to those of other known members of the genus (Rozen, 1968).

HEAD (FIGS. 29, 30): As described for *Panurginus potentillae* (Crawford) (Rozen, 1966) except for following: Pleurostomal ridge well developed; epistomal ridge moderately well developed below anterior tentorial pits although fading toward median line mesiad of pits; maxillary apex not directed mesiad (re-examination of *P. potentillae* shows that this structure is not directed mesiad in that species either); hypopharynx with distinct spicules above; although labium reduced and receding, maxillae not unusually close, as seen in frontal view.

BODY: As described for *P. potentillae* except for following: Imaginal disks on venter of both female and male larvae as described for *Melitturga braunsi* (Rozen, 1968) but cuticle beneath disks only faintly modified.

MATERIAL STUDIED: Numerous postdefecating and predefecating larvae, Oued Cherrat, 33 kilometers southwest of Rabat, Morocco, April 10–25, 1968 (J. G. Rozen and E. Suissa).

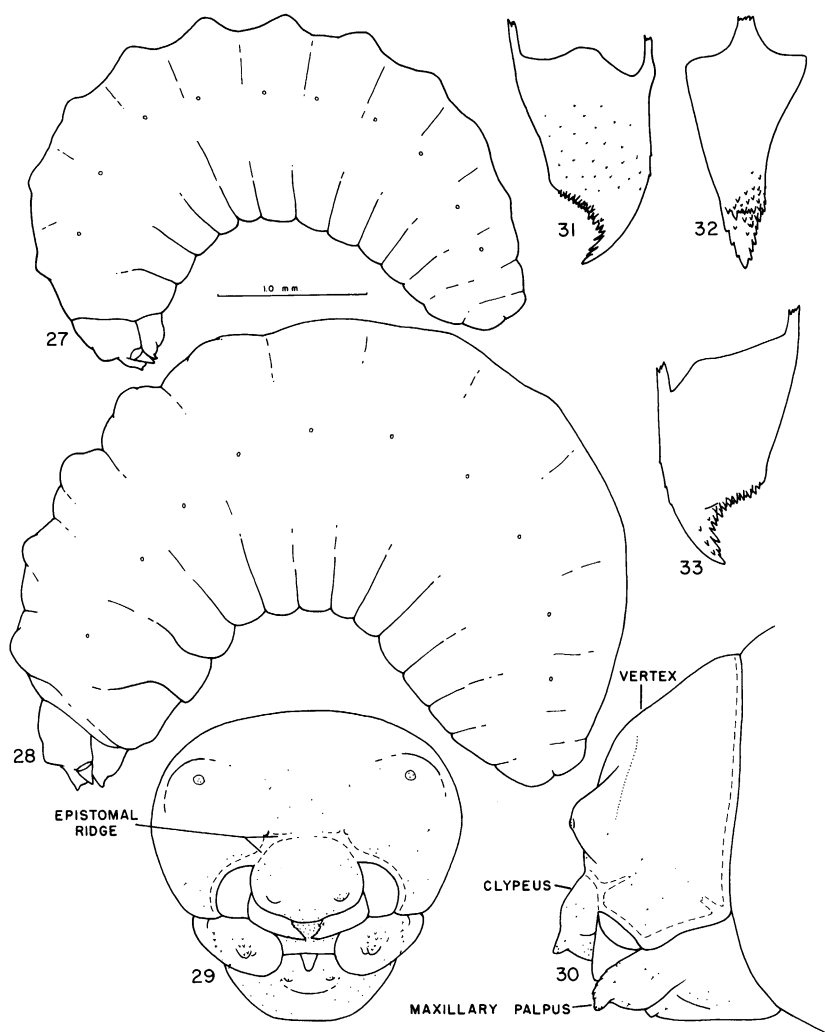
MELITTURGA LATREILLE

Melitturga can be distinguished from other panurgines by the spiculate apices of most of the dorsal abdominal tubercles and also by the very large cuspal tooth.

Melitturga caudata Pérez

Figures 34–36

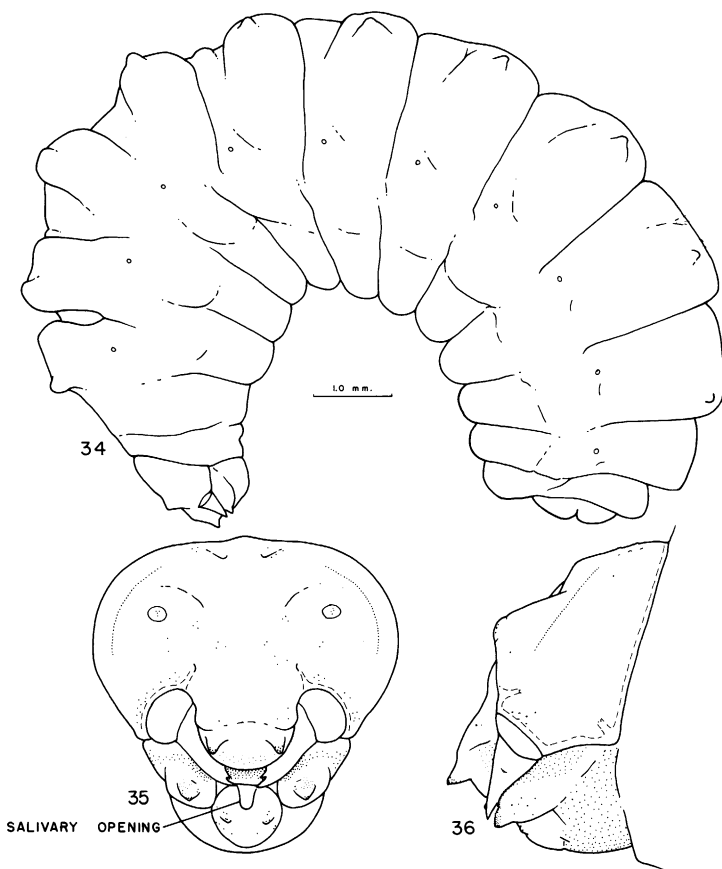
The larva of this species agrees closely with that of *Melitturga clavicornis*



FIGS. 27-33. *Panurginus albopilosus*. 27. Live postdefecating larva, lateral view. 28. Predefecating larva, lateral view. 29, 30. Head, frontal and lateral views, respectively. 31-33. Left mandible, dorsal, inner, and ventral views, respectively.

Scale refers to figures 27 and 28.

(Latreille), the only other member of the genus, the larva of which has been studied. The larvae of *M. clavicornis* and *caudata* can apparently be separated by the fact that the area enclosed by the salivary opening in *M. clavicornis* is spiculate, whereas in *M. caudata* it is nonspiculate.



FIGS. 34–36. *Melitturga caudata*. 34. Live postdefecating larva, lateral view. 35, 36. Head, frontal and lateral views.

Scale refers to figure 34.

HEAD (FIGS. 35, 36): As described for *M. clavicornis* (Rozen, 1965) except for following: Mandibular teeth (including cuspal tooth) somewhat more sharply pointed; mandibular denticles fewer; area surrounded by salivary opening nonspiculate; hypopharyngeal groove distinct (as also true of *M. clavicornis*).

BODY (FIG. 34): As described for *M. clavicornis* (Rozen, 1965) except for following: Ninth abdominal segment of male with cuticular scar on venter, as described for *Melitturgula braunsi* (Rozen, 1968); other sexual characteristics of mature larvae not known.

MATERIAL STUDIED: Two predefecating larvae and four postdefecating

larvae, 32 kilometers south of Ben Slimane, Morocco, April 25–28, 1968 (J. G. Rozen and E. Suissa).

PUPAE

There should be no confusion in the generic placement of pupae of the three genera of Moroccan panurgines treated here; immatures of *Camp-topoeum* are unknown. Because of the elongate pigmented tubercle on the base of the hind tibia, the pupae of the two species of *Panurgus* are easily distinguished from the pupa of *Panurginus albopilosus* which possesses only a short tibial tubercle. In this and other respects, *P. albopilosus* agrees closely with a North American species of *Panurginus* described by Yager and Rozen (1966). The pupa of *Melitturga caudata* was not recovered. However, because of the numerous similarities between the adults and larvae of *M. caudata* and *clavicornis*, the pupa of *M. caudata* will probably prove to be nearly identical to that of *M. clavicornis*. The total lack of a tubercle at the base of the hind tibia and the extremely short terminal metasomal spine combined make the pupa of *M. clavicornis* unique among the Panurginae.

Knowledge of pupal features of the panurgines is not sufficient as yet to enable an interpretation of the phylogenetic relationships of the three genera treated here with other genera of the subfamily.

PANURGUS PANZER

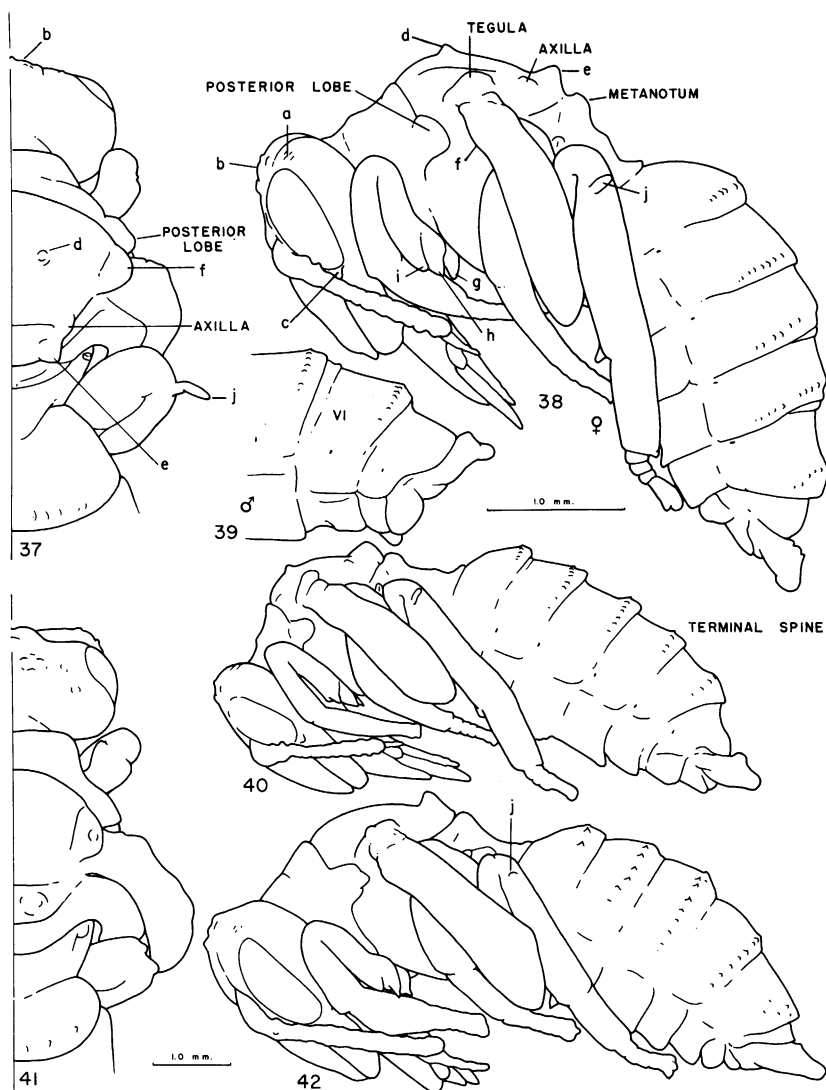
Because of the elongate pigmented tubercle at the base of the hind tibia (j, figs. 37, 38, 40), the pupae of the two species of *Panurgus* described below can be separated from those of other known panurgine bees. These two species can be distinguished from each other in the pupal stage on the basis of the presence or absence of apical spines on the fore and middle trochanters.

Panurgus oraniensis Pérez

Figures 37–39

Length 8.0 to 9.0 mm. Body without setae.

HEAD: Outer apical surface of scape and pedicel faintly, if at all, pigmented, not swollen and without tubercles; inner surface of pedicel with small tubercle. Ventral surface of mandible with small tubercle. Vertex with series of very small, indistinct tubercles above each compound eye (a, fig. 38); median part of head above ocelli somewhat swollen and bearing minute indistinct tubercles (b, figs. 37, 38); tubercles present over each ocellus; vertical tubercles tending to be less pronounced on megacephalic male; genal tubercle distinct (c, fig. 38).



FIGS. 37-42. Pupae. 37. *Panurginus oraniensis*, female, dorsal view of anterior part of body. 38. Female, lateral view. 39. Male, apex of metasoma. 40. *Panurginus intermedius*, female, lateral view. 41. *Panurginus albopilosus*, female, anterior part of body, dorsal view. 42. Female, lateral view.

Scales refer to figures 37-40 and 41 and 42, respectively.

MESOSOMA: Lateral angles of pronotum slightly produced; posterior lobes of pronotum somewhat produced; mesoscutum with pair of paramedian tubercles (d, figs. 37, 38); mesoscutellum with large pair of paramedian tubercles (e, figs. 37, 38); axillae somewhat produced; metanotum somewhat swollen medially; mesepisternum without tubercles. Tegula slightly produced. Anterior part of anterior wing base slightly produced (f, fig. 38). Each coxa with pointed apical spine (g, fig. 38); fore and middle trochanters with short apical spine (h, fig. 38); hind trochanter without apical spine; base of fore femur somewhat produced (i, fig. 38); other femora not produced; base of hind tibia with pigmented elongate spine (j, figs. 37, 38) approximately four times length of basal diameter.

METASOMA: Terga I through V (female) (figs. 37, 38) and I through VI (male) (fig. 39) with irregular rows of small tubercles, none of which is sharply pointed; sterna without tubercles; terminal spine moderately short and rounded apically.

MATERIAL STUDIED: Two male, four females pupae, Oued Cherrat, 33 kilometers southwest of Rabat, Morocco, April 23, 1968 (J. G. Rozen); one male and one female pupa, same, except April 24, 1968, all from burrow no. 1.

Panurgus intermedius Rozen¹

Figure 40

Length 6.0 to 8.5 mm. Body without setae.

HEAD: As described for *P. oraniensis*.

MESOSOMA: As described for *P. oraniensis* except for following: Tubercles of mesoscutum and mesoscutellum somewhat less pronounced and tegula at most indistinctly swollen; trochanters without distinct apical spine.

METASOMA: As described for *P. oraniensis*.

MATERIAL STUDIED: Two female pupae, one male pupa, 32 kilometers south of Ben Slimane, Morocco, April 28, 1968 (J. G. Rozen and E. Suissa); one male pupa, Oued Cherrat, 33 kilometers southwest of Rabat, Morocco, April 24, 1968 (J. G. Rozen).

PANURGINUS NYLANDER

Panurginus albopilosus Lucas

Figures 41, 42

Except for size, the pupa of this species agrees closely with that of

¹ Description appended.

Panurginus species A (Yager and Rozen, 1966). The two species can apparently be distinguished on the basis of the tegular tubercle and outer apical protuberances on the hind tibia, as discussed below.

Length 5.5 mm. Body without setae.

HEAD: Outer apical surface of scape slightly swollen and faintly pigmented; pedicel with small tubercle on outer surface and one on inner surface. Ventral surface of mandible with small tubercle (also present in *P. species A* [Yager and Rozen, 1966]). Vertex with several pairs of inconspicuous tubercles mesiad of compound eyes and with somewhat more conspicuous tubercles in vicinity of lateral ocelli; gena without tubercle.

MESOSOMA: Lateral angles of pronotum not produced; posterior lobes produced; mesoscutum without tubercles; mesoscutellum with pair of pointed tubercles; axillae not swollen; metanotum perhaps slightly produced; mesepisternum without tubercle. Tegula, unlike that of *P. species A* (Yager and Rozen, 1966), with small tubercle. Anterior part of wing base produced as a low swelling. Each coxa with long, pointed, apical spine; fore- and mid-trochanters with long apical spines; hind trochanter with apical pointed projection; base of fore femur produced; other femora not produced; base of hind tibia with low tubercle (j, fig. 42) on outer surface but without outer apical protuberance found in *P. species A* (Yager and Rozen, 1966).

METASOMA: Terga I through V (female) (fig. 42) with irregular rows of small tubercles, largest of which are sharply pointed; tubercles tending to be somewhat more conspicuous than those of *P. species A*; sterna without tubercles; apical spine of moderate length, rounded apically.

MATERIAL STUDIED: One female pupa, Oued Cherrat, 33 kilometers southwest of Rabat, Morocco, April, 1968, pupated in laboratory January 4, 1970 (J. G. Rozen).

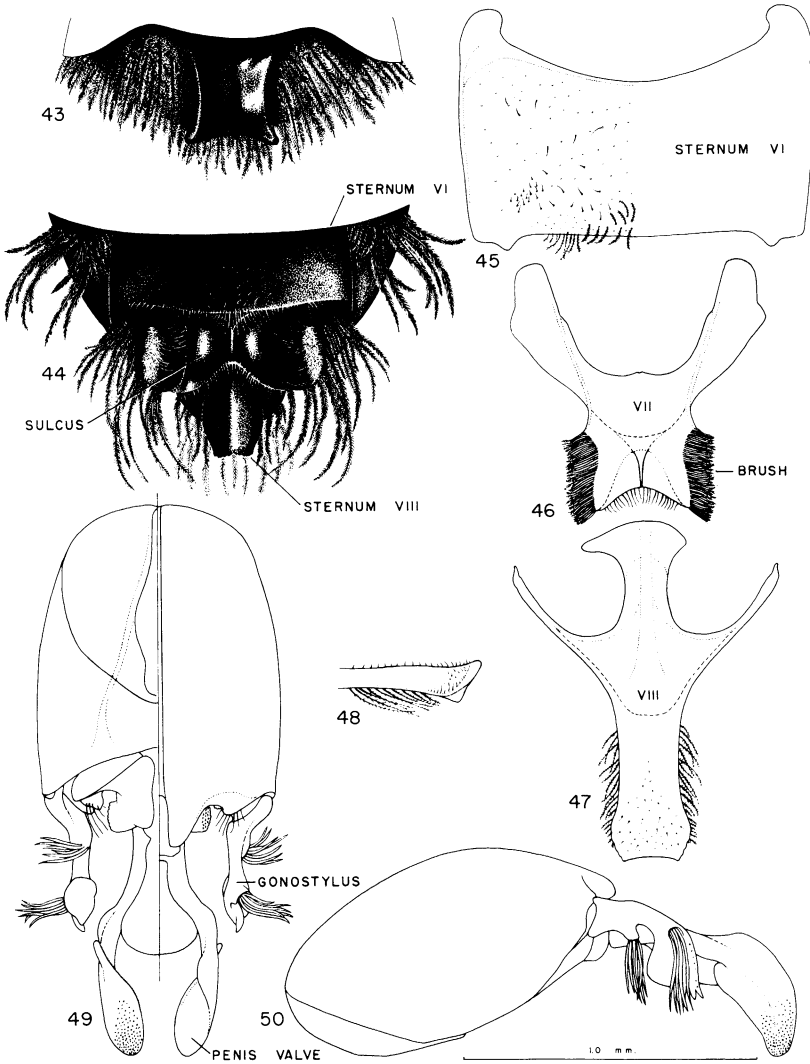
APPENDIX

Panurgus intermedius, new species¹

Figures 43–50

DIAGNOSIS: This species is of medium size and agrees with many species of *Panurgus* in that it has no yellow integumental markings and in

¹When the manuscript was in galley proof, I had an opportunity to examine the type of *Panurgus vachali* var. *villosiclypeus* Strand, lent by the Deutsches Entomologisches Institut, Eberswalde, East Germany. This unique specimen, a male from Algeria, agrees in many ways with *P. intermedius*, most significantly with respect to the shape of sternum VII and more or less to the configuration of the labral glabrous area. It differs in that the body is more slender and in that the width of the head is disproportionately small in relation to body size compared with that of *P. intermedius*. Furthermore, the median carina separating the sulci of sternum VII appears lower than that of *P. intermedius*. Unfortunately the genitalia are not visible. *Panurgus vachali* var. *villosiclypeus* and *P. intermedius*, though similar, seem to be distinct, but the two should be compared carefully when the genus is revised.



FIGS. 43-50. Adult of *Panurgus intermedius*. 43. Labrum, frontal view. 44. Apex of metasoma of male, ventral view. 45. Sternum VI of male, ventral view. 46. Sternum VII, same. 47. Sternum VIII, same. 48. Apex of sternum VIII, lateral view. 49. Genital capsule of male, ventral (left, dorsal) right view. 50. Same, lateral view.

Scale refers to figures 45-50.

that the setae on head and mesosoma are black to dark brown. The shape of the apical sternal plates and the genitalia of the male (figs. 44–50) will separate *P. intermedius* from other members of the genus. Males can be recognized without being dissected because of the relatively unmodified hind legs, the shape of the labral glabrous area (fig. 43), and the hidden penis valves and gonostyli, all in combination with intermediate body size, dark setae, and totally dark integument. Females will prove to be more difficult to identify as they are similar to such well-known species as *P. dentipes* and *calcaratus*. The shape of the labral glabrous area (fig. 43) should prove to be the most satisfactory recognition feature.

DESCRIPTION, MALE: Body length 6.5 to 8.0 mm. [about same size as *P. calcaratus* (Scopoli), *canescens* Latreille, *dentipes* Latreille, *scutellaris* Pérez, *unicolor* Spinola, but smaller than *banksianus* (Kirby), *cephalotes* Latreille, *maroccanus* Pérez, *oraniensis* Pérez, *perezii* Saunders, *siculus* Morawitz, *trochantericus* Pérez, and somewhat larger than *cavannae* Griboodo, *calceatus* Pérez, and *podagricus* Pérez]; forewing length 5.0 to 5.5 mm.

HEAD: Maximum width variable (as is the case with many male *Panurgus*), ranging from 2.15 to 2.60 mm. Integument entirely black; flagellum dark brown to black. Setae dark brown to black. Inner orbits subparallel to diverging slightly below [i.e., not converging as in *marginalis* (Pérez)]. Interantennal keel simple, moderately sharp, but not strongly projecting. Clypeus, like that of *P. calcaratus*, evenly rounded, moderately densely but evenly punctate, and bearing long setae. Labrum with medium glabrous area, distinctive, in that it is almost always troughlike and with sides subparallel (fig. 43). Galea with dorsal surface strongly papillate from base of palpus to apex. Labial palpus with sclerotized part of first segment approximately twice the length of sclerotized part of second segment and length of last two segments combined subequal to length of second segment.

MESOSOMA: Integument black; that of mesoscutum and mesoscutellum polished, with widely scattered punctures, which are approximately four to six puncture widths apart on disks; tegulae transparent brown; legs brown to black. Setae brown to black even on legs; dorsal mesosomal setae long. Wings with veins brown to dark brown and with membranous areas slightly infuscated. Hind trochanter with apical angle slightly produced but without large spoon-shaped projection of *P. dentipes* and without projections such as found in *P. calcaratus*; hind tibia normally straight and at most indistinctly widened near apex (therefore not like that of *P. dentipes*); tibia without ventral tooth; hind basitibial plate

elongate, acutely angled apically; hind basitarsus linear, i.e., without ventral projection such as found in *P. podagricus*.

METASOMA: Integument black to dark brown; punctation of terga moderately fine and sparse; punctation of sterna moderately dense. Setae brown to black and apical setae brown. Sternum VI with posterior margin unmodified, i.e., nearly straight (fig. 45); sternum VII (figs. 44, 46) with posterior lobes separated by median notch of only moderate depth; lobes with brushes of dark hairs; integument mesiad of brushes forming two moderately shiny sulci separated by median longitudinal carina; these sulci normally exposed on dried specimen (fig. 44); sternum VIII as illustrated (figs. 44, 47, 48). Shape of genitalia diagnostically distinct (figs. 49, 50); penis valves and gonostyli not visible externally on dried specimens.

FEMALE: Body length 6.5 to 8.0 mm.; forewing length 4.5 to 5.25 mm.

HEAD: As described for male except for following: Maximum width 1.8 to 2.2 mm. Setae on clypeus not so long as those of male.

MESOSOMA: As described for male except for following: Setae on body brown to black; setae on forelegs brown on basal segments but becoming paler on apical segments so that tarsal setae pale buff colored; setae of middle legs pale buff colored on tibia and tarsus; scopa on hind tibia and basitarsus very pale buff, almost white. Hind legs without any apical modifications, indistinguishable from hind legs of female of such species as *P. dentipes* and *calcaratus*.

METASOMA: Integument as described for male except for following: Depressed posterior margins of most segments more distinctly, finely striated than those of female *P. calcaratus* and *dentipes* so that margins slightly less shiny than in other species; margins with some punctures but these fewer than those of *P. dentipes* but more abundant than those of *calcaratus*. Setae like those of *P. dentipes* and *calcaratus*, moderately fine brownish; setae at apex of metasoma buff colored, somewhat darker than scopa.

MATERIAL STUDIED: Holotype male, allotype, Oued Cherrat, 33 kilometers southwest of Rabat, Morocco, April 9, 1968 (J. G. Rozen and E. Suissa); nine male paratypes, 49 female paratypes (20 of which are in alcohol), same, except dates ranging from April 9 to 24, 1968; 11 male paratypes (two in alcohol), six female paratypes, 32 kilometers south of Ben Slimane, Morocco, April 13 and 14, 1968 (J. G. Rozen and E. Suissa). The holotype and allotype are in the collection of the American Museum of Natural History.

SUMMARY

The present paper, which is intended to shed light on the phylogeny and systematics of the bees belonging to the subfamily Panurginae, treats the biology and immature stages of three genera found in Morocco—*Panurgus*, *Panurginus*, and *Melitturga*.

(1) Observations on the environment of the nesting site, flower relationships, nest structure, provisioning, oviposition, development, adult activity, and parasitism by cuckoo bees are presented; comparisons are made with panurgines from other parts of the world.

(2) The mature larvae of the three genera are described and contrasted with those of other panurgines.

(3) Pupae of *Panurgus* and *Panurginus* are described.

(4) Appended is a description of a new species, *Panurgus intermedius*.

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