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## Review of the Biology of Panurgine Bees, with Observations on North American Forms (Hymenoptera, Andrenidae)

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The Panurginae are a rather large subfamily of minute- to moderate-sized bees found in all biogeographic areas of the world except the Oriental and Australian regions. With the notable exception of *Perdita*, a genus that contains perhaps 700 forms, the species in the genera tend to be few or moderate in number. From all evidence on hand, be it adult anatomy, structures of the larvae and pupae, or biology, these genera almost certainly represent a monophyletic assemblage, even though there is considerable diversity among them. The subfamily has been divided from time to time into two tribes, the Melitturgini, containing only *Melitturga*, and the Panurgini. It is doubtful that this division expresses accurately either the phenetic or the phylogenetic relationships of the genera, and a review of the higher classification of the subfamily is needed.

The present paper, believed to be the first attempt to treat the biology of this subfamily as a whole, has two purposes: (1) to record original observations on the biology of North American Panurginae; and (2) to synthesize and compare all available information on the biology of the group for the world. As a result of the latter, it is possible to present

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some tentative ideas concerning the evolutionary trends in the subfamily as revealed by the biological data.

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## EVOLUTIONARY CONSIDERATIONS

Panurgine bees beyond a doubt shared a common ancestor with the essentially holarctic Andreninae. From all evidence on hand, we can assume that this ancestor more closely resembled the Andreninae than the Panurginae. The andrenines have not diversified greatly, whereas the panurgines have undergone considerable evolutionary radiation. The resulting diversity is revealed in the anatomy of the adults (Rozen, 1951) and in that of the larvae (Rozen, 1966b).

Most of this paper is devoted to demonstrating the biological similarities and differences among the panurgine genera. Not only is it possible to show that in many respects the subfamily is a diverse group biologically, but we can deduce in which direction some of the biological traits seem to have evolved. The rationale of the deductions is based on the fact that some of the panurgines share various biological features with the Andreninae. Therefore it is likely that these features

of the panurgines are primitive and that modifications of them found in other panurgines represent recent evolutionary steps away from the primitive condition. All cells of *Andrena* that I have seen possess a conspicuous shiny lining as do the cells of most panurgines. The less visible lining of *Nomadopsis* cells and the complete absence of one from *Perdita* cells therefore seem to represent a recent evolutionary development. Similarly the stored provisions of many species of *Andrena*<sup>1</sup> are somewhat flattened as are those of most panurgines (figs. 6–8). Consequently, the completely spherical provisions known only for *Nomadopsis*, *Calliopsis* (figs. 9, 10), and *Perdita* (fig. 11) probably are a specialized condition for the Andrenidae (though pollen spheres are found in other families of bees). The provisions of *Calliopsis*, *Nomadopsis*, and *Perdita* are unique in that they possess a waterproof coating, undoubtedly a feature derived from the non-coated provisions of the andrenines and the other panurgines. The position of the egg on top of the pollen mass is primitive, whereas the forward position found in *Panurginus* (fig. 8) and the rear position in *Perdita* (fig. 11) are separate derivations.

## REVIEW OF PANURGINE BIOLOGY

This section attempts to summarize all available information on the biology of the Panurginae of the world, with special emphasis on comparative data so that contrasts and similarities between taxa can be noted. The bulk of the information is concerned with various aspects of nesting behavior. This review is based upon the following sources, listed by taxa:

Panurginae	Nielsen, 1936
<i>Psaenythia</i> ( <i>Psaenythia</i> ) <i>interrupta</i> Friese	Claude-Joseph, 1926; Janvier, 1933
<i>Psaenythia</i> ( <i>Protandrena</i> ) <i>bancrofti</i> (Dunning)	Chandler, 1962
<i>Psaenythia</i> ( <i>Protandrena</i> ) <i>bicolor</i> Timberlake	Rozen, present paper
<i>Panurgus</i> Panzer	Bischoff, 1927; Buttel-Reepen, 1915; Lepeletier, 1841; Malyshev, 1916, 1935; Nielsen, 1934; Rudow, 1901, 1905, 1913
<i>Panurgus banksianus</i> (Kirby)	Friese, 1891, 1897, 1901, 1922–1923, 1926; Micheli, 1931; Nielsen, 1934; Shuckard, 1866 (may also refer to <i>calcaratus</i> )

<sup>1</sup> The peculiar shape of the provisions of *Andrena* (*Cryptandrena*) *viburnella* Graenicher (Stephen, 1966) does not have a homologue in the Panurginae and presumably is derived from the flattened pollen sphere of other species of *Andrena*.

- Panurgus calcaratus* (Scopoli) Friese, 1891 (as *lobatus* Panzer), 1897, 1901, 1922-1923, 1926; Hohndorf, 1932; Malyshev, 1933, 1935; Micheli, 1936; Nielsen, 1934; Shuckard, 1866 (may refer only to *banksianus*); Smith, 1846, 1855; Stoeckhert, 1954
- Pseudopanurgus* (*Pseudopanurgus*) *aethiops* (Cresson) Hicks, 1931; Rozen, present paper
- Pseudopanurgus* (*Pseudopanurgus*) *aethiops*? Rozen, present paper
- Pseudopanurgus* (*Pseudopanurgus*) *timberlakei* Cockerell Rozen, present paper
- Pseudopanurgus* (*Pseudopanurgus*) species A Rozen, present paper
- Pseudopanurgus* (*Pseudopanurgus*) species B Rozen, present paper
- Pseudopanurgus* (*Heterosarus*) *boylei* (Cockerell) Rozen, present paper
- Pseudopanurgus* (*Heterosarus*) *piercei* (Crawford) Hicks, 1936; Pierce, 1904
- Panurginus* Nylander Bischoff, 1927; Friese, 1926; Malyshev, 1916, 1935; Nielsen, 1934
- Panurginus hispanicus* Giraud Grandi, 1931
- Panurginus labiatus* (Eversmann) Malyshev, 1924, 1933, 1935
- Panurginus montanus* Giraud Friese, 1891, 1901, 1922-1923
- Panurginus potentillae* (Crawford) Rozen, present paper
- Panurginus romani* Aurivillius Erlandsson, 1958
- Panurginus* species Stephen, Bohart, and Torchio (in press)
- Camptopoeum* Spinola Nielsen, 1934
- Camptopoeum friesei* Mocsáry Friese, 1901, 1922-1923, 1926
- Camptopoeum frontale* (Fabricius) Friese, 1891, 1901, 1922-1923, 1926
- Calliopsis* (*Calliopsis*) *andreniformis* Smith Ainslie, 1937; Rozen, present paper
- Calliopsis* (*Calliopsima*) *coloradensis* Cresson Hicks, 1926
- Calliopsis* (*Calliopsima*) *crypta* Shinn Rozen, present paper; Shinn, 1965
- Calliopsis* (*Calliopsima*) *rozeni* Shinn Rozen, present paper; Shinn, 1965
- Calliopsis* (*Verbenapis*) *nebraskensis* Crawford Rau, 1922; Rau and Rau, 1916
- Nomadopsis*, numerous species Rozen, 1958
- Nomadopsis*, several species Rozen, 1963
- Nomadopsis* (*Macronomadopsis*) *zebrata* Cockerell, 1915; Hicks, 1936
- Nomadopsis* (*Micronomadopsis*) *australior* (Cockerell) [may also be *scitula* (Cresson); see Rozen, 1958] Custer, 1927
- Nomadopsis* (*Micronomadopsis*) *beamerorum* Rozen Kerfoot (MS)
- Nomadopsis* (*Micronomadopsis*) *scitula* Cockerell, 1906
- Spinoliella maculata* (Spinola) Claude-Joseph, 1926

" <i>Camptopoeum herbsti</i> Friese" <sup>1</sup>	Claude-Joseph, 1926
<i>Acamptopoeum submetallicum</i> (Spinola)	Claude-Joseph, 1926
<i>Melitturga clavicornis</i> (Latreille)	Bischoff, 1923, 1927, 1952; Friese, 1891, 1896, 1919, 1922-1923, 1926; Malyshev, 1925, 1933, 1935; Nielsen, 1934, 1936; Rozen, 1965b
<i>Melitturga clavicornis</i> ? (probably not <i>clavicornis</i> ; see Rozen, 1965b)	Ferton, 1920
<i>Melitturga praestans</i> Giraud	Rudow, 1901
<i>Melitturgula braunsi</i> Friese	Brauns, 1913
<i>Perdita</i> ( <i>Perdita</i> ) <i>confusa</i> Timberlake	Rozen, present paper
<i>Perdita</i> ( <i>Perdita</i> ) <i>maculigera maculipennis</i> Graenicher	Michener and Ordway, 1963
<i>Perdita</i> ( <i>Cockerellula</i> ) <i>opuntiae</i> Cockerell	Custer, 1928, 1929a, 1929b
<i>Perdita</i> ( <i>Perdita</i> ) <i>sexmaculata</i> Cockerell	Rozen, present paper
<i>Perdita</i> ( <i>Perdita</i> ) <i>zebrata zebrata</i> Cresson	Custer, 1929a; Rozen, present paper
<i>Perdita</i> ( <i>Cockerellia</i> ) <i>lingualis</i> Cockerell	Michener, 1963
<i>Perdita</i> species A	Rozen, present paper
<i>Liphanthus sabulosus</i> Reed	Claude-Joseph, 1926
<i>Rhophitulus niger</i> (Spinola)	Janvier, 1933

#### CHARACTERISTICS OF NESTING AREA

All panurgines nest in the ground and prefer sites that have little vegetation and are exposed to the sun. Most species choose areas that are horizontal or nearly so, such as dirt roadways, paths, and bare areas on a field; such choice is made by the following: *Psaenythia* (all species); *Pseudopanurgus* (all species); *Panurginus labiatus*, *montanus*, and *potentillae*; *Calliopsis andreniformis*, *crypta*, *rozeni*, and *nebraskensis*; *Nomadopsis* (all species); *Spinoliella maculata*; "*Camptopoeum herbsti*"; *Melitturga clavicornis* and *clavicornis*?; *Melitturgula braunsi*; and apparently *Acamptopoeum submetallicum*. Some species, however, have been discovered nesting in oblique slopes (*Liphanthus sabulosus*, *Rhophitulus niger*, and apparently *Camptopoeum frontale*) or even in vertical walls (*Camptopoeum friesei*).

At least in the case of *Nomadopsis*, the nesting habits of enough species are known to indicate that a horizontal or nearly horizontal nesting site

<sup>1</sup> Moure (*in litt.*) states that *Camptopoeum herbsti* Friese is a synonym of *Spinoliella maculata*. However, the larva of "*C. herbsti*" drawn by Claude-Joseph (1926, fig. 59) is clearly distinct from that of *S. maculata* (fig. 57). This fact suggests that one or the other of Claude-Joseph's species was misidentified. Accordingly they are treated here as separate species.

is probably characteristic of the genus. Further, it would not be surprising if all species of *Pseudopanurgus*, *Calliopsis*, and perhaps other genera had similar requirements. However, members of the genus *Perdita* differ one from another in their selection of slope: *P. sexmaculata*, *opuntiae*, and *confusa* preferred nearly horizontal sites; *P. maculigera maculipennis*, moderately sloping ones; *P. zebrata zebrata*, a gradual to moderately steep one; and *P. lingualis*, a vertical bank. The information on *Panurgus banksianus* and *calcaratus* is somewhat contradictory; *P. banksianus* presumably nests in horizontal areas, whereas *P. calcaratus* has been discovered making use of both horizontal and vertical sites.

The texture of the soil of the nesting sites differs greatly among the Panurginae, though the soil contains little organic matter. Some species (e.g., *Nomadopsis larreae* Timberlake and *Perdita maculigera maculipennis*) nest in loose sand, one (*Perdita opuntiae*) presumably is restricted to sandstone, and burrows of another (*Nomadopsis beamerorum*) have been found in gypsum rock. However, most seem to select sites that range from moderately hard packed to hard packed soil at the depth of the cells. The surface layer of soil is usually rather stable and undisturbed, but in some instances (*Nomadopsis micheneri* Rozen and *Spinoliella maculata*) the surface was so trodden by animals and man that there was no indication of the burrow entrances.

Where more than one nesting site of a species has been observed, the data seem to suggest that at least some species are somewhat specific in their choice of soil texture. However, it is difficult to determine whether the soil hardness attracts the bees directly or whether some correlated ecological factor is involved. For example, *Perdita maculigera maculipennis* may nest in sand not because it prefers sand, but because it nests near its pollen plant, *Salix nigra*, which grows in sandy soils along streams. At least in *Nomadopsis* and *Perdita* there is no generic constancy in choice of soil texture, as is indicated by the above examples.

In most panurgine nests that I have excavated, the soil is visibly moist at the cell level during the nesting period, even in desert regions. In some instances, the soil dries out during the estivating-hibernating period.

#### NESTING ACTIVITY

The subfamily Panurginae has long been considered to be composed solely of solitary bees, and most of them exhibit no indication of a truly social way of life. However, Stoeckhert (1954) observed that females of *Panurgus calcaratus* from a single colony varied in size to a considerable extent and that some were worn and tattered although others were fresh. The small females reminded him of workers of social halictids; therefore

he presented the tentative hypothesis that some members of the species may be social. It is hoped that someone will examine the ovaries of a series of females to ascertain if any of the females are indeed workers.

No other suspected case of social behavior appears in the literature. However, a variety of species, in addition to *P. calcaratus*, have several or more females sharing a common nest entrance, often a characteristic of social or subsocial bees, including *Psaenythia interrupta*, *Panurginus labiatus*, "*Camptopoeum herbsti*," *Perdita opuntiae*, and *Perdita lingualis*. Because of the widespread condition of this trait in the subfamily and because so few panurgines have been investigated, the possibility of social behavior cannot be excluded from consideration.

At least most panurgines tend to nest gregariously. When the population size is sufficiently large, the females build their nests near one another and thereby form loose nesting aggregations. This behavior has been recorded for the following: *Psaenythia interrupta*; *Panurgus banksianus* and *calcaratus*; *Pseudopanurgus aethiops*, species A, species B, and *boylei*; *Panurginus montanus* and *potentillae*; *Calliopsis andreniformis* and *nebraskensis*; almost all species of *Nomadopsis*; *Spinoliella maculata*; "*Camptopoeum herbsti*"; *Acamp-topoeum submetallicum*; *Rhophitulus niger*; *Melitturga clavicornis* and *clavicornis?*; *Melitturgula braunsi*; *Perdita maculigera maculipennis*, *opuntiae*, *sexmaculata*, *zebrata*, and *lingualis*. Such nest groups are not so limited that other burrows cannot be discovered at some distance from the main concentration. When the population size is small, the gregarious nesting tendency may not be obvious. Although a few authors claimed that a species was solitary in its nesting habit, others reported the same species nesting in groups; for example, Nielsen (1934) stated that *Panurgus calcaratus* is solitary, but both Friese (1897) and Micheli (1936) discovered it nesting in small aggregations.

Although the phenomenon of the use by several females of a single nest entrance has been noticed here and there throughout the Panurginae (as indicated above), most species have but a single female to a nest. There is little specific information as to how many nests a female constructs, but it would seem that in most species she is responsible for only one nest under normal conditions. A female of a species that constructs only a single cell in a nest obviously excavates a number of nests during her adulthood.

There is usually only a single entrance to a nest, but the following species, at least in some instances, tunnel out several openings: *Panurgus banksianus*, *Perdita maculigera maculipennis*, *opuntiae*, and *zebrata*. Nielsen (1934) provided a meticulous account of the complex construction of the double entrance to the burrow of *Panurgus banksianus*. The details sug-

gest that similar studies should be carried out on other bees, for a considerable amount of information is perhaps being overlooked. My observations indicate that some species start burrows near such features on the ground as small stones, clumps of vegetation, or edges of depressions: *Psaenythia bicolor*, *Pseudopanurgus aethiops*, *timberlakei*, species B, *boylei*, *Calliopsis andreniformis*, *rozeni*, *Nomadopsis edwardsii* (Cresson), *linsleyi* Rozen, and *trifolii* Timberlake. This habit which probably in most cases serves to hide the nest entrance may occur in other species but apparently has been overlooked by authors. Some species, such as *Panurginus potentillae*, do not attempt to conceal their nest entrances.

No panurgine constructs a turret at the nest entrance as do some of the anthophorids. However, the entrances of most species are surrounded by a usually symmetrical tumulus of soil that results from the nest construction. In a few species, namely, "*Camptopoeum herbsti*" and *Perdita zebata zebata*, the tumulus is found on only one side of the entrance. Burrow entrances of *Panurginus potentillae*, *Melitturga clavicornis*, and *Perdita opuntiae* in some cases are found with tumuli and, in other cases, without such mounds. The single nest entrance definitely assigned to *Psaenythia bicolor* was without a tumulus.

The burrow entrances of apparently all species of *Calliopsis* and *Nomadopsis* are plugged with loose earth, as are those of *Perdita maculigera maculipennis*, *zebrata zebata*, and the various species of *Pseudopanurgus* nesting on the grounds of the Southwestern Research Station. One of these, *Pseudopanurgus boylei*, when found nesting 2 miles northeast of Portal, Arizona, had most of the burrow entrances open. In *Panurginus potentillae*, the entrances are found either open or closed, the condition depending perhaps on a specific unknown activity of the female at the time of observation. Malyshev (1924) claimed that females of *Panurginus labiatus* have their entrances closed when they are in the nests. The entrances of *Psaenythia bancrofti*, *interrupta*, *bicolor*, *Spinoliella maculata*, "*Camptopoeum herbsti*," *Acamptopoeum submetallicum*, *Melitturga clavicornis*, and *Liphanthus sabulosus* are presumably open. The main tunnels of *Nomadopsis* and of *Perdita lingualis* are partly filled with loose soil; those of *Psaenythia bicolor* and *interrupta* have earthen septa at various points along the way, and a somewhat similar condition may apply to the tunnels of *Pseudopanurgus*.

Because most observations on panurgine bees are made during the season when the nests are being constructed and provisioned, there is relatively little information on the main tunnels of completed nests. Micheli (1931) reported that the burrows of *Panurgus banksianus* were open while being provisioned but were closed the following month when the nests were inactive. The main tunnel of *Pseudopanurgus aethiops*?, when



excavated the year after construction, was found to be open at the surface but closed below.

The main tunnels of most panurgines are circular in cross section. However, the roughly horizontal burrows of *Perdita lingualis* are flattened on the lower side. The main burrows lack any sort of special lining, although Malyshev (1935) reported that the main tunnel of *Melitturga clavicornis* is lined with soil. This lining may be referable to the filled exit burrow of a scarab, as Rozen (1965b) reported for the same bee. The diameter of the main tunnel corresponds approximately to the size of the bee. The main burrow of bees nesting in horizontal sites descends more or less sinuously, depending to some extent on the rock inclusions of the soil. *Perdita opuntia* is the only species for which we know that main burrows of nests anastomose; this feature may be found in other species in which more than one female uses a common nest entrance.

There is no indication that a female uses water in constructing a nest.

The cells of panurgines are connected to the main burrow by distinct lateral tunnels which are circular in cross section. These tunnels are presumably always somewhat narrower than the main one and always lack a special lining of any sort. Their lengths vary within a single nest. They are commonly more or less horizontal, in some cases curved, and lead off from the main burrow in various directions. With some species, namely, *Nomadopsis edwardsii*, *zonalis sierrae* Rozen, and, perhaps, *Panurginus potentillae*, each tunnel dips and rises again before joining the cell. Such features have not been well studied, however, because side tunnels of panurgines are filled with soil after their cells have been closed. *Perdita opuntiae* is apparently unique in having many of its cells in the filled main burrow, which is in sandstone.

The cells of most species are arranged singly. However, those of a few species (*Nomadopsis helianthi*, *Lipanthus sabulosus*, and, perhaps, *Psaenythia bicolor*) are built in a linear series. At least in the case of *N. helianthi*, the nest contains a number of such series.

The cells seem similar in shape throughout the Panurginae, although those of some species may be slightly flattened on the bottom. Their size is approximately proportional to the body size of the species. The cells of most panurgines are roughly horizontal, with the rear end somewhat lower than the front end. In some species of *Pseudopanurgus* the tilting of the cell is often more pronounced, but only the cells of the South American *Psaenythia interrupta* are truly vertical.

In preparing cells the females of all panurgines excavate a cavity the same size as the completed cell. They do not therefore cement in a special wall of earth and adhesive as do, for example, some anthophorids. *Per-*

*dita opuntiae* is the only apparent exception in that its cells are reported to have "smooth mud walls." The cell wall of the panurgine is smooth, in some cases extremely so. The smoothing, at least in the case of *Nomadopsis hesperia equina* (Cockerell), apparently results from a tamping of the wall by the female with her pygidial plate. The walls of *Perdita* cells presumably receive no further treatment, as there is no indication of any secretion. Such a wall almost instantaneously absorbs a drop of water placed on the surface. The walls of all other panurgines examined by the author have been treated with some waterproofing secretion. With some species the lining is not visible, but it will retard the absorption of a water droplet. With most species (including many of *Nomadopsis*) a visible shiny lining is present beneath which the cell wall has been impregnated with an adhesive. The shiny lining found in such diverse genera as *Psaenythia*, *Pseudopanurgus*, *Panurginus*, and *Calliopsis* can be peeled in small transparent patches from the cell wall and appears to be a silklike substance in that it does not melt when heated and does not dissolve in wax solvents. When thickly applied, it is impervious to water droplets. The adhesive beneath the lining may not be the same substance. It is rarely sufficiently strong to hold the cell wall completely intact while the entomologist excavates the nest.

So far as known, all panurgines close their cells with a spiral partition of earth. The closure is concave on the cell side.

The rather scanty data suggest that the Panurginae (with the exception of those that build composite nests) construct relatively few cells to a nest. The following species excavate only single-celled nests: *Calliopsis andreniformis*,<sup>1</sup> *Nomadopsis edwardsii*, *zonalis sierrae*, and *Perdita maculigera maculipennis*. According to Nielsen (1934) *Panurgus banksianus* digs a burrow with one or two cells. Other species congeneric with these excavate nests with numerous cells, a fact that suggests that the behavior responsible for a single cell nest has evolved a number of times. *Panurginus labiatus* (presumably when not occupying a composite nest) builds a nest with not more than five cells. A complete nest of *Nomadopsis barbata* Timberlake had 13 cells. A nest of *Nomadopsis helianthi* had 12, whereas one of *N. anthidia* had six, but neither may have been complete. *Melitturga clavicornis* is reported to construct a nest of eight or more cells. *Rhophitulus niger* presumably has about 12 cells. *Pseudopanurgus aethiops*? holds the maximum record of 26 cells.

Insofar as known, all panurgines construct a cell, provision it, deposit

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<sup>1</sup> C. D. Michener (*in litt.*) states that this species usually constructs several cells to a nest. Also, see Shinn (1967).

an egg, and close the cell before constructing the next one. The order of cell construction has been reported for some, as follows: *Psaenythia interrupta*; *Nomadopsis* (probably all species); *Spinoliella maculata*; "*Camptopoeum herbsti*"; *Acamptopoeum submetallicum*; and *Melitturga clavicornis*. In all, the cells closer to the surface of the ground are the older. The considerable data on the depths of nests demonstrate that panurgines nest shallowly, in some cases extremely so, e.g., *Panurginus potentillae* (table 1). The cells of most panurgines with vertical burrows are found at depths of 5 to 20 cm., although a nest of *Pseudopanurgus boylei* descended 32 cm. Nests of *Panurginus*, *Calliopsis*, and *Nomadopsis* are not known to descend more than 10 cm. The essentially horizontal composite nest of *Perdita lingualis* extended into a bank 85 cm., whereas the horizontal nest of *Camptopoeum friesei* ran for, at most, about 15 cm.

Although vacated cells from previous years are often encountered during excavations of panurgine nests, such cells are not part of the active nests, and there is no indication that old nests are re-used.<sup>1</sup>

There is a considerable amount of interesting variation among the Panurginae regarding the shape, consistency, position, and other aspects of the provisions. The completed pollen-nectar mass is formed into a more or less spherical shape. With the following species a flattened sphere is molded: *Psaenythia bicolor* (fig. 61), *Panurgus banksianus*, *Pseudopanurgus* (fig. 7) (species listed in table 2), *Panurginus potentillae* (fig. 8), and *Melitturga clavicornis*. The provisions are a perfect sphere in the following: *Calliopsis* (figs. 9, 10), *Nomadopsis*, and *Perdita* (fig. 11). *Panurginus labiatus* is unique in that the pollen nectar mixture is only partly formed and is placed at the end of the cell (Malyshev, 1924).

The provisions of *Pseudopanurgus aethiops* and *boylei* are very moist on the outside, dry inside, and lack a special coating; those of *Pseudopanurgus* species B, *Panurginus potentillae*, and *Melitturga clavicornis* are firm, moist throughout, and do not have a special coating. The pollen balls of *Calliopsis* and *Nomadopsis* are firm, moist, homogeneous, but are coated with a shiny, transparent, waterproof substance that appears to be identical with the inner layer of the cell. The provisions of *Perdita zebrata zebrata* and *sexmaculata* were more moist than those of *Calliopsis* and *Nomadopsis* and had a thin, transparent, special coating, whereas those of *P. maculigera maculipennis* were firm, and no obvious coating was noted though it may have been overlooked.

A number of pollen loads (apparently two in the case of *Perdita macu-*

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<sup>1</sup> After reading this manuscript, C. D. Michener (*in litt.*) stated that he suspected that cells of *lingualis* are re-used.

*ligera maculipennis*) are required for the manufacture of the pollen-nectar mass. With *Panurgus calcaratus*, *Pseudopanurgus boylei*, *Melitturga clavicornis*, *Perdita maculigera maculipennis*, and *opuntiae* the pollen is stored as an unworked mass until the entire quantity is brought in to form the total provisions. In contrast, the incomplete provisions of *Nomadopsis* and *Calliopsis* are formed into a small homogeneous ball, to which pollen from subsequent forays is later added to make the completed sphere.

The position of the pollen mass in the cell varies, apparently depending on the genus. Unfortunately this feature has been overlooked by most workers. In *Psaenythia bicolor* (fig. 6), *Pseudopanurgus aethiops* (fig. 7), *boylei*, *timberlakei*, species B, *Panurginus labiatus*, *potentillae* (fig. 8), and *Melitturga clavicornis* the flattened sphere is at, or almost at, the rear of the cell. However, the pollen spheres of *Calliopsis andreniformis*, *crypta*, *rozeni*, *Nomadopsis*, and *Perdita zebrata zebrata* are situated on the floor of the cell more toward the center.

The consistency of the stored provisions of most panurgines does not change before being consumed. However, those of *Panurginus labiatus* swell and acquire water, whereas the inner portion of the pollen mass of both *Pseudopanurgus aethiops* and *boylei* (and probably *Psaenythia bicolor*) becomes more moist, perhaps as a result of liquefaction of the nectar. I have not noticed the odor of fermentation in any panurgine nest.

The eggs of all panurgines (e.g., figs. 6–11) are elongate, curved, whitish, and possess a very thin chorion. They apparently always rest in the sagittal plane of the cell and do not touch the cell wall. The posterior end of the egg seems always to be closest to the rear of the cell and is somewhat more pointed than the anterior. Whereas the posterior end is attached to the provisions, the rest of the egg may rise in the cell so that the anterior end does not touch the provisions (e.g., figs. 8, 10); in some cases both ends rest on the provisions, though the middle may be elevated (figs. 6, 7, 9). The significance of these different positions is not fully understood but apparently is not specific or generic in nature. It may relate in part to the ontogeny of the egg: newly laid eggs being often erect; as the embryo develops, the egg bends down until, at the time of hatching, its full length adheres to the pollen ball. More detailed studies need to be carried out on this matter, and the relationship of drops of moisture on the egg (as, for example, in *Panurginus potentillae*) to the development of the embryo and early instar should also be investigated.

Although the observations of some authors have not been sufficiently critical for a comparison of oviposition sites, there is no question but that the eggs of panurgines are affixed to the provisions. Some evidence has now come to light to suggest that the place where the egg is placed

may have some taxonomic significance. The eggs of *Psaenythia bicolor* (fig. 6), *Pseudopanurgus* (fig. 7), *Calliopsis andreniformis* (fig. 9), *crypta* (fig. 10), *rozeni*, *Nomadopsis*, and *Melitturga clavicornis* rest on top of the pollen masses. Those of *Panurginus labiatus* and *potentillae* (fig. 8) hang forward of the top of the food, so that when the newly hatched larva feeds, it attacks the front of the pollen mass (fig. 12). The eggs of *Perdita zebrata zebrata* (fig. 11) and possibly of *sexmaculata* are attached to the rear of the pollen ball, as probably are the eggs of *P. opuntiae*, though Custer (1928) stated that the egg is "along the side" of the ball. The duration of the egg stage is short in panurgines (and in most other bees), but there are few data indicating the exact time between deposition and hatching. Claude-Joseph (1926) stated that the various Chilean panurgines he studied took eight days to two weeks to hatch. Rozen (1958) reported that the duration of the egg stage in *Nomadopsis* was perhaps a week or less, and elsewhere in this paper I claim that the period for *P. aethiops* was not much more than four to five days.

As indicated in the treatment of *Pseudopanurgus* in this paper, the larvae of panurgines that I have studied increase very rapidly in size, too fast to be attributable solely to the consumption of food. The rapid growth apparently is a result of the intake of water. The duration of the larval stadium is short, but again exact figures are scanty. Michener and Ordway (1963) indicated that *Perdita maculigera maculipennis* probably consumes the entire provisions in about two weeks. Claude-Joseph (1926) stated that the larvae of various Chilean species are active for five to six weeks. One larva of *Nomadopsis anthidia anthidia* (Fowler) started defecating 12 days after hatching.

The larvae of at least *Calliopsis*, *Nomadopsis*, and *Melitturga clavicornis* (and presumably most other panurgines) do not move around the provisions—they merely rest on the pollen mass and eat the food beneath their heads. The only known probable exception is in the genus *Panurginus*; the partly grown larva of *P. potentillae* apparently moves on the pollen ball, possibly with the aid of the spiculated venter of its tenth abdominal segment. Although the other panurgines do not move in relation to the food upon which they sit, they do move in the cell so that the larger larvae are found on their dorsa and cradle the provisions on their venter, as I have described, for example, for a number of species of *Nomadopsis*. The literature is not clear as to how the various panurgine groups accomplish this maneuver, but the dorsal tubercles play an important role in *Nomadopsis* and probably in other groups as well. Detailed observations are needed before the problem can be elucidated.

With the apparent exception of the larvae of the subgenus *Pseudo-*

*panurgus*, which may overwinter as predefecating forms, panurgine larvae defecate a short time after consuming their provisions. Except for the genus *Perdita*, panurgines deposit their feces at the rear of the cells (not known for *Pseudopanurgus*). For this reason, it is easy to distinguish a cell occupied by a panurgine from one that has been taken over by a parasitic bee such as *Oreopasites*, for the feces of many of the nomadine parasitic bees are applied to a large part of the inner cell surface. *Panurginus potentillae* is the only bee I observed that usually has its terminal body segment glued to the meconial mass. Because of the elongate median dorsal tubercle on the last abdominal segment, *Perdita* larvae are incapable of depositing feces at the tip of the cell, and the fecal mass rests on the venter of the larva. At the time of defecation panurgine larvae (including those of *Perdita*) lie on their dorsa with their heads closest to the cell opening.

Having finished defecating, the univoltine species overwinter on their dorsa as quiescent larvae. Cocoons are not spun by members of the Panurginae. The integument of the overwintering postdefecating larva is tough and apparently is coated with a waterproof secretion.

Almost all literature states that panurgines overwinter as larvae; the only exception is the *Panurginus* described by Stephen, Bohart, and Torchio (in press) which overwinters as an adult.

The duration of the pupal stadium averages 12 days for *Perdita maculiger maculipennis*, 18 days for *Calliopsis andreniformis*, and approximately two weeks for *Nomadopsis*. It would be surprising if other panurgines had a pupal stadium of appreciably longer duration.

#### ADULT ACTIVITIES

The nesting sites of known univoltine species of panurgines are active for only about one month. This means that the life span of an adult is at most of the same duration. During this period, mating occurs, nests are constructed and provisioned, and eggs are deposited.

Very little comparative information is available on mating behavior in the Panurginae. The work of Rozen (1958) demonstrated that marked differences in behavior pattern exist in *Nomadopsis*, and that these differences may vary from species to species and from group to group. Clearly, investigations on copulatory and precopulatory behavior of other genera can be expected to yield considerable data for both systematic and behavior studies.

The Panurginae as a group visit a wide variety of plants for pollen, a fact that is evident from my 1958 work on *Nomadopsis*, from Timberlake's (1954-1964) taxonomic treatises on the genus *Perdita*, from the

catalogue of Muesebeck *et alii* (1951), as well as from the literature in general. It has often been suggested, and my observations confirm, that a species of bee may visit a wide range of plant species for nectar, whereas its pollen collecting is restricted to relatively few kinds of flowers. For this reason, records attached to museum specimens may not give a correct impression as to whether a bee is monolectic, oligolectic, or polylectic. The works cited above, in addition to the observations presented in this paper, point out that many, and probably most, panurgines tend to be oligolectic or monolectic. Further, in some instances related species of bees collect pollen from the same genus of plant and in other instances closely related species visit dissimilar species of plants.

There are only scanty observations on the "sleeping" habits of these bees. Females presumably of all spend the night in their burrows. I have found that it is desirable to excavate nests in the evening because, for one reason, the adult bee can be taken in the burrow and the identity of the nest therefore is assured. Males of *Panurgus* sleep on the flowers; those of *Meliturgula braunsi*, on dry plants. In contrast, males of *Perdita maculigera maculipennis* and of *Nomadopsis* spend the night in short burrows that they excavate in the nests of females, and, in the case of *Nomadopsis*, in crevices in the ground.

#### CYCLES OF ACTIVITY

Most panurgines are univoltine, but *Perdita lingualis* has two generations a year, and a number of species (but not all) of the *Nomadopsis* subgenus *Micronomadopsis* and possibly *Calliopsis rozeni* are multivoltine. Univoltinism can often be detected on the basis of museum specimens because the collection dates fall within a period of about a month. Because the adults appear with the blooming of the pollen plants, the mechanism of synchronization of the two events, though apparently unknown, is a matter of considerable interest, especially in regard to the desert biota, which is subjected to seasonal rains. It should be noted that univoltine species (except for *Panurginus* sp.) spend nearly 10 months of the year as quiescent larvae in diapause. For such species, most of the life span is devoted to "marking time" in a suspended physiological state, until suitable ecological conditions again appear with the advent of the breeding season.

Bees are usually regarded as insects that prefer the warmth of the day for their flower-visiting activities. This pattern holds for most panurgines, but with *Nomadopsis puellae* (Cockerell) and *nigromaculata* Timberlake the daily flight period apparently depends either on the temperature, the opening of the flowers of the pollen plant, or both, for their activities

were restricted to the morning hours, as reported by Rozen (1958). Since those observations, I have seen *N. puellae* flying in numbers in the afternoon on cool days. Several species of *Perdita*, with enlarged ocelli, are crepuscular in their flower visitations.

Knowledge is lacking concerning the activities of the bees in the nests during that part of the diel when the cells are not being provisioned.

#### CUCKOO-BEE PARASITISM

The nests of panurgine bees are attacked by a number of genera of the cleptoparasitic Nomadinae. It has long been known that certain species of the widespread genus *Nomada* parasitize the nests of several European *Panurgus* (Friese, 1926) and that *Ammobatooides* is apparently restricted to *Melitturga*. Several species of *Parammobatooides* have been associated with *Camptopoeum* by Popov (1951), though he listed another species as a possible parasite of *Nomioides*. *Schmiedeknechia* is, so far as known, a parasite of *Epimethea* (Popov, 1951). In North America, the various species of *Oreopasites* are apparently all obligatoryinquilines in the nests of *Perdita* (new information) and *Nomadopsis*, and *Holcopasites*, long considered a cleptoparasite solely of *Calliopsis*, has now been associated also with *Pseudopanurgus* (Linsley, MacSwain, and Smith, 1956). It seems likely that *Neolarra*, recently recovered from the nest of *Perdita* (Rozen, 1965a), is restricted to that genus.

Insofar as known, the mode of parasitism of all Nomadinae is the same. The cuckoo-bee female enters the open cell of the host while the cell is being provisioned, deposits one or, more probably, several eggs in the cell wall, and then departs. After the host female closes the cell, the eggs of the cuckoo bee hatch into small ambulatory larvae with elongate, sharp-pointed mandibles. These larvae kill (or are killed by) their siblings, similarly destroy the egg or early instar of the host, and then the survivor develops on the provisions.

The only other group of cuckoo bees known to attack panurgines is the halictine genus *Sphecodes*. Though thought primarily parasites of halictines, some species have been associated with *Melitturga* (Rozen, 1965b) and *Calliopsis* (Rau, 1922; and probably Michener, 1953, as "*Neopasites* sp.?"), as well as with other groups. The mode of parasitism is apparently unknown for *Sphecodes*, though the first-stage larva presumably does not have abnormally elongate mandibles.



BIOLOGICAL OBSERVATIONS ON NORTH  
AMERICAN PANURGINAE*PSAENYTHIA* GERSTAECKER*Psaenythia (Protandrena) bicolor* Timberlake

LOCALITY AND DATE: This species nested 2 miles northeast of Portal, Cochise County, Arizona, on the outwash plain of Cave Creek. Although first discovered by Mont A. Cazier on September 14, the site was studied on September 20 to 23, 1963. The area gently sloped to the east, and the nests were not shaded by the few low-growing desert herbs that sparsely covered the ground. Devoid of large rocks, the soil was easy to dig and moist except at the surface. Numerous bees were found in the area, including *Pseudopanurgus aethiops*, *boylei*, and also *Nomadopsis helianthi* (Swenk and Cockerell). Most females collected pollen from the yellow-flowered composite *Bahia*, but some landed occasionally on the similar-appearing *Verbesina* heads. Both plants grew in the immediate vicinity of the nests.

NESTING ACTIVITY: The three burrows associated with this species were about 25 feet apart, and each was in a somewhat different situation. The opening of the only one containing a female of *Psaenythia bicolor* was in a depression approximately 2 feet long and 6 inches deep. Without a tumulus, the open hole lay at the base of the wall of the depression. The open entrance of the second nest was at the bases of herbaceous plants, and that of the third was situated on a 5-inch-high mound of recently excavated earth. Because of the possibility that these last two burrows might have belonged to *Pseudopanurgus boylei*, which also nested in the vicinity, the following description and the dimensions in table 1 refer only to the first. The main tunnel descended as an open shaft more or less vertically though with several turns. It seemed to widen into an antechamber at a depth of 5.5 cm., below which it was filled with 1 cm. of loose soil held in place by a septum of more consolidated soil. Immediately below this plug, the burrow was open for 1 cm., then was filled with a similar plug, below which it was again open. The nest was occupied by a single female that had constructed two cells possibly arranged in a linear series. The front end of the only cell exhumed intact (fig. 6) seemed to be elevated well above the rear, and the cell possessed both a very shiny waterproof lining that could be peeled in small patches and an earthen wall distinctly harder than the surrounding soil. Closed with a spiral plug, the cell was similar in shape and appearance to that of *Pseudopanurgus*.

The bright orange, flattened, pollen ball (fig. 6) resembled in appear-



FIGS. 1, 2. Southwestern Research Station near Portal, Cochise County, Arizona. 1. Parking lot where *Pseudopanurgus* and *Calliopsis* nested. Pollen plants can be seen in front of cabins. 2. Roadway where *Pseudopanurgus* nested. Area in front of figure is where burrows of *P. boylei* (Cockerell) and *aethiops* (Cresson) were concentrated.

ance the balls of *Pseudopanurgus aethiops* and *boylei*, in that it was situated at the posterior end of the cell and was coated with a very moist layer of pollen at least 0.5 mm. thick. Although in some places the moisture penetrated farther into the interior of the ball than in the case of that of *Pseudopanurgus aethiops* and that of *boylei*, the interior pollen was completely dry. Pollen on the legs of females is dry next to the tibia, but the outermost pollen on the anterior tibial surface of a fully loaded female is somewhat moist. How this moist pollen is employed in the construction of the final food masses is not understood.

A white egg (fig. 6) attached by its posterior end, but also touching at the anterior end, occupied the flattened top of the pollen mass. As with other panurgines, its long axis lay in the sagittal plane of the cell; its chorion was smooth and shiny.

**ADULT ACTIVITY:** Unlike other known members of the subfamily, these females exhibit a strange behavior pattern while collecting pollen and nectar. After landing on a flower head, the female raises one pollen-laden hind leg and then the other, or both, at nearly right angles to her body. The legs may be lowered momentarily, only again to be erected. The gymnastics are performed while she collects the provisions and only after she is secure on the flower. Though such behavior suggests a sex-recognition signal, no males were encountered during the course of the observations.

#### *PSEUDOPANURGUS* COCKERELL<sup>1</sup>

The species in this genus are treated together, because so many of them nested in the same area.

**LOCALITY AND DATE:** *Pseudopanurgus (Pseudopanurgus) aethiops* (Cresson), (*Pseudopanurgus*) *timberlakei* Cockerell, (*Heterosarus*) *boylei* (Cockerell), and an undescribed species of the subgenus *Pseudopanurgus* referred to as species A by Rozen (1966b) were observed nesting in the parking lot (fig. 1) and dirt roadways (fig. 2) of the Southwestern Research Station near Portal, Cochise County, Arizona, between August 28 and September 10, 1962. All nesting areas were nearly horizontal, devoid of even moderately sparse vegetation, and exposed to the sun during most of the day. The soil was rocky, containing stones several inches in diameter. Numerous bees, including two species of *Calliopsis* and several of *Perdita*, nested in the same roadways and parking lot. Two species of *Nomadopsis* were collected as adults but were not found nesting, and four other species of *Pseudopanurgus*, all undescribed, were encountered on the flow-

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<sup>1</sup> All species identified by P. H. Timberlake.



FIG. 3. One mile north of Rodeo, Hidalgo County, New Mexico. Several burrows of *Pseudopanurgus* species B were found near equipment on ground.

ers. The eight species of *Pseudopanurgus* collected pollen from yellow- or orange-flowered composites: *P. aethiops* and *boylei*, from *Verbesina encelioides*; *P. timberlakei*, from *Aplopappus* species; and the various undescribed species, from *Verbesina encelioides*, *Aplopappus*, *Heterotheca subaxillaris*, and other yellow composites. The pollen plants of the three named *Pseudopanurgus* grew adjacent to the nesting areas.

Another nesting site of *P. boylei* was discovered 2 miles northeast of Portal, Cochise County, Arizona, on September 23, 1963. Most of the nests were concentrated along the margins of a wash, 1 foot deep, that sloped gently to the east. The soil here was moist, claylike, and even-grained without rocks. The associated bee fauna is discussed above under *Psaenythia (Protandrena) bicolor*. Females gathered pollen from both *Bahia* and *Verbesina* which grew abundantly in the immediate vicinity.

An undescribed species in the subgenus *Pseudopanurgus*, species B (Rozen, 1966b), nested 1 mile north of Rodeo, Hidalgo County, New Mexico (fig. 3), where nesting activities were briefly observed for several days late in August, 1964. A number of burrows were found on nearly level ground in impressions made by the hooves of cattle during a previous wet period. The vegetation here consisted of a few low shrubs and scattered herbs, none of which shaded the nest entrances for an extended period during the day.

NESTING ACTIVITIES: The nests of *P. aethiops*, *timberlakei*, *boylei*, and



FIG. 4. Fallon, Prairie County, Montana, where *Perdita zebrata zebrata* Cresson nested in bank in foreground. Pollen plant, *Cleome*, can be seen on top of embankment.

species A at the Southwestern Research Station were widely distributed though grouped into local loose aggregations which usually consisted of a number of species. Burrow entrances of *P. aethiops* and *boylei*, the two most abundant species, were usually found either at the edge of, or actually under, stones on the surface of the ground. Frequently entrances of both species could be found under one stone. Hicks (1931) reported that females of *P. aethiops* tried to start nests near "natural depressions," and he described in some detail how the females dig. The single burrow entrance of *P. timberlakei* was among the creeping stems of a puncture vine (*Tribulus terrestris*). At 2 miles northeast of Portal, numerous nest openings of *P. boylei* were situated along the wash, especially where the sloping and terraced walls met the sandy floor and in the corners formed by the small terraces on the walls. In some cases the openings were surrounded by an abundant dark tumulus. Rarely were nests seen in the sandy bed of the wash. The nest entrances of *P. species B* were usually in the sloping wall of cattle tracks; as many as four individuals used a single print.

The nest dimensions of all species are given in table 1. In no case was more than one female associated with a nest.

The main tunnels of all species (fig. 17) are circular in cross section, unlined, and generally descended vertically, though they turn and twist if there are rock inclusions. The main burrows of *P. boylei* 2 miles north-east of Portal, where the soil is even-textured, were much straighter than those of the same species at the Southwestern Research Station, where the soil is rocky. During the nesting season the burrows of the species at the Southwestern Research Station were plugged with loose soil at the surface, as were those of *P. species B*. Hicks (1931) stated that the nest entrances of *P. aethiops* were closed only part of the time. Although some of the main tunnels of *P. boylei* 2 miles northeast of Portal were plugged, most were found open. In one instance a burrow of this species

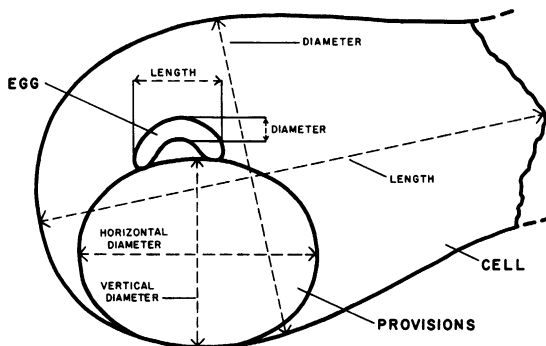


FIG. 5. Diagram of the cells, pollen masses, and eggs of the Panurginae, to show how measurements were made for tables 1 and 2.

was open, but, when the female returned with provisions, she descended and closed it with a centimeter of loose soil. In the case of *P. species B*, plugs of loose earth were occasionally encountered at varying depths along the main tunnel. This situation may have been overlooked in the nests of the other species.

In only one instance was a completed nest of a species of *Pseudo-panurgus* excavated. Constructed in the previous year, the nest was studied on April 21, 1961, 2 miles northeast of Portal, Arizona. It almost certainly belonged to *P. aethiops*, because it had the same dimensions as nests of this species, the largest in the genus. At the time of excavation, the main burrow was opened at the surface but was filled at lower levels.

Lateral tunnels leading from the main burrow to the cells are present in all species but vary in length even within a species. Although they meandered to some extent, the straight-line distance from the cell to the main tunnel ranged from 2 to 3.5 cm. for *P. aethiops* and *boylei* at

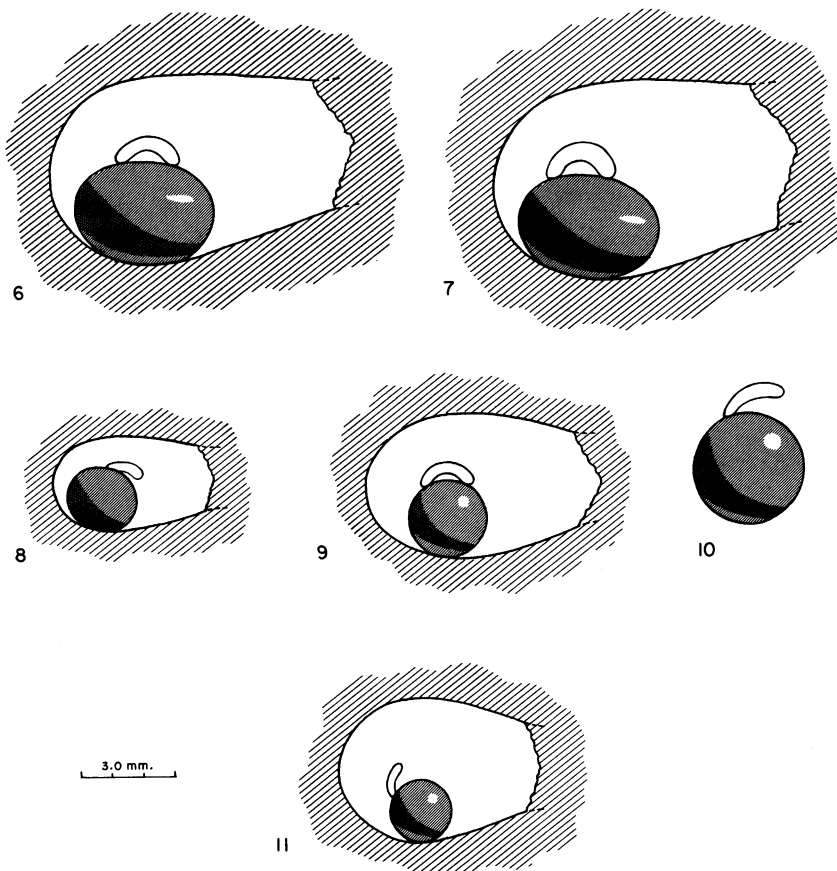
the Southwestern Research Station. For *P. boylei*, 2 miles northeast of Portal, the distances were approximately 3 to 5 cm. A single lateral tunnel of *P. timberlakei* measured 1 cm. in length; tunnels of *P. species B* ranged from 1 to 4 cm. The side tunnels are circular in cross section, unlined, and apparently usually slope downward to the cells. After the female provisions and closes the cell, the side tunnel is filled with earth and remains that way until the following year when the offspring emerge.

All species (not known for *P. timberlakei*) construct more than one cell to a nest. The total number of cells in a completed nest has been recorded only for *P. aethiops*? from 2 miles northeast of Portal, where 26 cells were counted; all but three contained mature, live, predefecating larvae. There is but a single cell at the end of each side tunnel in all cases. The cells of *P. boylei* and presumably of the other species are excavated and provisioned consecutively, with the cell closest to the surface being the oldest. The cell wall is essentially smooth, although that of *P. aethiops* and perhaps of the others is slightly wavy. In spite of the fact that the cell wall is not built into the excavation, as is the case, for example, with many anthophorids, it is definitely tougher than the surrounding soil, probably as a result of the female's impregnating it with some secretion. Though difficult to measure, the thickness of the rigid layer is more than 0.5 mm. in the case of *P. aethiops*. This wall is sufficiently strong so that a cell usually can be removed from the soil and brought intact into the laboratory if some care is taken. The cells of *Nomadopsis*, *Perdita*, and *Calliopsis* are too fragile to be treated in such a way.

The cells of all species studied are lined with a thin, shiny, plastic-like, waterproof coating that can be peeled from the wall. It appears to be identical to that found in cells of *Calliopsis*, *Psaenythia bicolor*, and *Panurginus potentillae*. The chemical nature of the substance is not known, but it will not readily dissolve in xylene, chloroform, ether, isopropyl alcohol, or benzene, and, when heated to 200° F., becomes brittle.

The cells (fig. 7) of *Pseudopanurgus* are elongate spheroids, similar in shape to those of other panurgines. They are oriented with the front end somewhat higher than the rear end. With both *P. aethiops* and *timberlakei* they were tilted about 20 degrees from the horizontal, but with *P. boylei*, as much as 45 degrees, and with *P. species B*, 40 degrees. The cell closure in all was an uncoated spiral.

The females of *P. aethiops* and *boylei* transport the pollen unmoistened to the cell, but some species in the genus may moisten the pollen before returning to the nest. The female *Pseudopanurgus* shapes it into a flattened ball (fig. 7), with the height invariably less than the width (table



FIGS. 6-11. Cells, pollen masses, and eggs of the Panurginae. 6. *Psaenythia bicolor* Timberlake. 7. *Pseudopanurgus aethiops* (Cresson). 8. *Panurginus potentillae* (Crawford). 9. *Calliopsis andreniformis* Smith. 10. Pollen ball and egg only of *C. crypta* Shinn. 11. *Perdita zebrata zebrata* Cresson.

2). The provisions are not coated with a shiny, transparent, plastic-like coating as in *Calliopsis* and *Nomadopsis*. However, at least in the case of *P. aethiops* and *boylei*, the outer 0.3 to 0.5 mm. is evenly and abundantly moistened, probably with nectar, whereas the inner part is dry. As the larva eats the ball, the inner part also becomes moistened, perhaps as a result of liquefaction of the nectar. One open cell of *P. boylei* contained an amorphous mass of pollen; another, a flattened but unmoistened ball of pollen. These facts suggest that the provisioning female stores pollen loads in the cell until the entire amount is present; she then shapes it



into a ball, and, lastly, coats it with liquid. *Pseudopanurgus* species B differs from *P. aethiops* and *boylei* in that its pollen masses are uniformly moist throughout. In at least *P. aethiops*, *boylei*, *timberlakei*, and species B the pollen mass is placed toward the posterior end of the cell (fig. 7).

The egg (fig. 7) is deposited on the flattened top of the pollen mass. In *P. timberlakei* and presumably in *P. boylei*, the egg is oriented with its long axis parallel to that of the cell and with its anterior end closest to the closure. In *P. aethiops*, *boylei*, and *timberlakei* the eggs are elongate, curved, and translucent white, with a blunt anterior end and a more pointed and slightly thinner posterior end. They are identical in these respects to those of other panurgines. Their dimensions are given in table 2. Whereas the eggs of *P. aethiops* and *timberlakei* are shiny and have at most an indistinctly wrinkled chorion, those of *P. boylei* possess a distinctly reticulated chorion. The reticulation consists of raised ridges that outline the smooth, somewhat elongate, five- to six-sided "cells." The greatest length of an average "cell" was 0.037 mm.

The eggs of at least *P. aethiops*, *boylei*, and *timberlakei* are attached at both their anterior and posterior ends, so that the middle part curves above the pollen. The posterior attachment is the more secure, the chorion seemingly glued to the pollen.

One egg of *P. aethiops* collected in the field hatched in the laboratory in four days. It seemed freshly deposited when excavated, so that the duration of the egg stage is probably not much more than four or five days, during which time the development of the embryo can be seen through the chorion. Toward the end of this stage, the thin chorion becomes appressed to the embryo, as in *Nomadopsis* (Rozen, 1958), so that the shedding of the chorion is difficult to observe. At about the time of eclosion, pulsating motions of the head take place, probably indicating ingestion of the amniotic fluid and perhaps of liquid on the egg and on the surface of the pollen.

The first instar of *Pseudopanurgus* has a head similar in appearance to that of *Nomadopsis* (Rozen, 1958, figs. 2, 3), though the antennae are more pronounced. The dorsal body tubercles are nearly absent, though the ventrolateral lobes are well developed.

Panurgine larvae in general increase in size extremely rapidly just after emerging. However, the amount of provisions that they consume is too small to account for this rapid growth. After attempting to mark a freshly emerged larva of *P. timberlakei* with blue vegetable coloring so that the number of larva instars could be recorded, I noticed that the larva was ingesting the blue dye placed on its back. The liquid ran forward to the creases where the head attached to the body and then, after

running down the creases, it seemed to be directed forward along hypostomal grooves (or the grooves between the maxillae and the labium) to the mandibles. As it was gulped into the alimentary canal, the blue liquid could easily be seen through the semitransparent larva. As the liquid was being consumed, the head of the young larva pulsed, presumably as a result of the muscular contractions associated with swallowing. A strip of minute spicules that runs along the middorsal line of the body probably assists water droplets to flow toward the head. The dyed larva increased to very large proportions without consuming an appreciable amount of the food mass. It is suggested, therefore, that the rapid growth of young panurgine larvae is caused by the swallowing of liquid that forms on the larva or that is on the surface of the food mass.

The feeding period is normally short, lasting for only a few weeks. Having finished eating, the larva of *P. (Heterosarus) boylei* defecates, in contrast to the larva of *P. (Pseudopanurgus) aethiops*, which does not defecate for a long time. The larvae of *P. aethiops*? from 2 miles northeast of Portal were all predefecating forms resting on their dorsa with their heads closest to the cell closure when they were found in the spring following the year that the nest was constructed. No member of the subgenus *Pseudopanurgus* has been collected as a postdefecating larva, nor has one defecated in the laboratory after being collected. (None has survived in the laboratory until the following year.) In contrast the mature *Holcopasites* larvae taken from the nests of *P. aethiops* and *boylei* have been either postdefecating, quiescent forms, or have defecated subsequently in the laboratory. Furthermore, with other panurgine bees some postdefecating forms are almost always encountered in the nests, even during the height of activity of the nesting season. These facts suggest that members of the subgenus *Pseudopanurgus* probably overwinter in the predefecating stage.

From evidence on hand it seems likely that at least *P. aethiops*, *boylei*, and species A have a single generation a year.

**ADULT ACTIVITY:** Few observations were made on the mating behavior of *Pseudopanurgus* at both the Southwestern Research Station and 2 miles northeast of Portal. Males belonging to this genus occasionally encountered females at the flower heads, but they did not search the ground of the nesting site for mates.

**PARASITISM:** Rozen (1965a) discussed the relationships of a number of species of cuckoo bees belonging to the genus *Holcopasites* with the *Pseudopanurgus* found at the Southwestern Research Station. *Holcopasites (Trichopasites) insoletus* (Linsley) was also seen in the vicinity of nests of *P. boylei* at 2 miles northeast of Portal, although no larvae were col-

lected from the few nests that were excavated. The same species of cuckoo bee was discovered investigating the nest of *P.* species B. In addition, at the Southwestern Research Station a first instar of a mutillid was found feeding on a mature larva of *P. boylei*, and a first-stage larva of a rhipiphorid was seen within the head capsule of a large but still feeding larva of *P. aethiops*. The beetle larva, dark in color, could easily be observed as it moved its head, legs, and abdomen. Unfortunately the host and parasite died before maturing.

*PANURGINUS* NYLANDER

*Panurginus potentillae* (Crawford)

**LOCALITY AND DATE:** This species was found nesting in Closter, Bergen County, New Jersey, on May 18, 1963. The site was surveyed numerous times, and excavations began May 24. When last visited on June 18, it had become inactive, and was abandoned the following year. The nesting site was near first base in an infrequently used, essentially horizontal, baseball field. The site itself sloped somewhat more than the surrounding field. Although a wild cherry tree shaded the area until 9:30 A.M., Eastern Standard Time, the site was otherwise unshaded during the day. Its surface at first was sparsely covered with short dead grass but before it became inactive, small sprouts of crab grass appeared here and there over most of it. The soil consisted of easily excavated, even-grained, moist sand with few pebbles. At the time these bees were active, *Colletes*, *Andrena*, *Lasioglossum*, *Halictus*, and associated parasitic bees nested in the baseball field, but none had burrows in the nest area of *P. potentillae*. The pollen plant, *Potentilla*, grew profusely in areas adjacent to the ball field though few flowers occurred in the field itself.

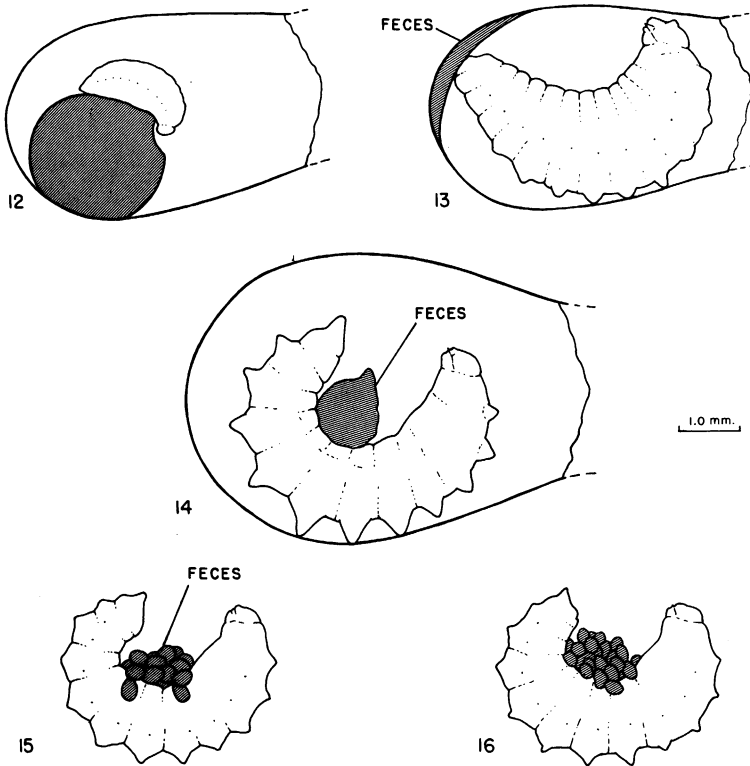
**NESTING ACTIVITY:** Though not very densely populated, the 3-by-5-foot nesting site was sufficiently occupied to suggest strongly that *Panurginus potentillae* nests gregariously. Some of the burrows seemed to be free of tumuli and open, whereas others were definitely plugged and surrounded by rather high tumuli. The cause of this variability is not understood, though future observations may prove that the bee tends to dig and close its burrows in the evening and to leave them open during the heat of the day. The burrow openings are not situated near or under rocks, pebbles, or other debris or at the bases of plants. A centimeter below the surface the rather winding main burrows are open and unlined. The side tunnels, also unlined, are somewhat narrower than the main burrows and are filled with soil after cell closure. Their direction could not be definitely determined, though several seemed to dip between

the cell and the main burrow. Several measured approximately 2 mm. long. The cells (fig. 8), arranged singly, are nearly horizontal, with the front end slightly higher than the rear. With the spheroid shape of the cells of other panurgines, they are supplied with a distinct, shiny, waterproof lining that can be peeled from the surface, and they are closed with a spiral plug. The dimensions of the nest are given in table 1.

The yellow-orange pollen masses (fig. 8) are nearly spherical, their height being slightly less than their horizontal diameter (table 2). There may be a tendency for the smaller masses to be more spherical than the larger ones. The provisions are not coated, for, when dropped in water, they quickly and evenly "melt." They are quite firm (perhaps more so than those of *Nomadopsis*), moist, and of an even consistency, i.e., they are not moist on the outside and dry on the inside as are those of *Pseudopanurgus aethiops*, *boylei*, and *Psaenythia bicolor*. As are the pollen balls of *Pseudopanurgus* and *Psaenythia bicolor*, the pollen ball is situated toward the posterior end of the cell (fig. 8). The egg (table 2) rests on the upper surface of the provisions and has its long axis parallel to that of the cell. The posterior end of the egg is attached to the top of the mass, with the consequence that the rest of the egg lies forward of center. Although the anterior end of the egg usually projects into the cell, occasionally it touches the anterior surface of the provisions. As with other genera, the egg is curved, with its posterior end more sharply pointed than the anterior end. The chorion is smooth, and usually several droplets of liquid were noticed on the egg and on the cell wall.

After hatching, the larva maintains the same position as the egg, with the result that its anterior end is lower than the posterior. Consequently the front surface of the provisions is eaten (fig. 12). Later the larva reorients itself but apparently not as does *Nomadopsis* which lies on its back so that the pollen is cradled on its venter. Though additional observations should be made, the larva of *P. potentillae* apparently moves on the pollen ball and even rests on its side while feeding. No later-stage larva was discovered on its dorsum with partly consumed pollen masses on its venter. If the larva does move on the provisions, this is the first such case that I have observed in the Panurginae. The last larval instar of this species (but not of other species of *Panurginus* of which the larvae are known) possesses a patch of spicules on the venter of the tenth abdominal segment (Rozen, 1966b). This feature suggests that the segment may be used as a pygopod to push the larva on the pollen ball.

Larvae that have just finished feeding are oriented on their dorsa, with their heads toward the rear of the cell. Before defecating, an action



FIGS. 12, 13. *Panurginus potentillae* (Crawford). 12. Young larva feeding on front of pollen ball. 13. Postdefecating larva with tip of abdomen cemented to feces.

FIGS. 14-16. Postdefecating larvae of *Perdita*, showing feces resting on venter. 14. *P. zebrata zebrata* Cresson. 15. *P. confusa*?. 16. *P. sexmaculata* Cockerell.

that takes place soon after feeding, they again change so that their heads are at the cell closure and the feces are deposited at the back end of the cell. In most (fig. 13) but not all cases, the tenth abdominal segment of the larva was attached to the feces. This attachment (perhaps with the assistance of mold hyphae that grow out from the feces) provided enough support so that the larvae were suspended from the feces when the front end of the cell was broken away. This species hibernates as entirely quiescent, postdefecating larvae.

**ADULT ACTIVITY:** Males were not encountered about the nesting site, though they were discovered on the flowers. Consequently mating probably takes place on the flowers. As only very young larvae and eggs were

encountered on May 24, and, as the site was inactive by June 18, the seasonal duration of adult activity is approximately one month.

PARASITISM: No cleptoparasitic bees were associated with the nesting site.

*CALLIOPSIS SMITH*<sup>1</sup>

*Calliopsis (Calliopsima) crypta* Shinn

LOCALITY AND DATE: The following observations, all referring to a single nest, were made on September 16, 1962, at the Southwestern Research Station, near Portal, Cochise County, Arizona. The nest was discovered in the nearly horizontal parking lot, which at that place was unshaded during most of the day. The soil contained numerous pebbles and rocks and was sparsely covered with scattered low-growing plants. The pollen plant, *Heterotheca subaxillaris*, grew profusely on the margins of the parking area. Numerous other species of bees nested in the area, including, among the Panurginae, at least three species of *Pseudopanurgus* (discussed above), one other species of *Calliopsis*, and several of *Perdita*.

ADULT ACTIVITY: A single female was uncovered from the nest, which, though not complete, contained six cells and a plugged entrance surrounded by a dry tumulus. The cells were arranged singly at the end of lateral tunnels, two of which were 1.5 cm. long. The cells sloped to the rear at about 20 degrees from the horizontal, though one sloped as much as 35 degrees. Similar in shape to those of the other Panurginae discussed here, they possessed a smooth, shiny lining. Peeled strips of lining reacted to heating, as did those of *Pseudopanurgus* (above). All cells were closed with a spiral plug. The various dimensions of this nest are given in table 1.

The provisions of this species consist of a spherical, homogeneous, yellow-orange mass (fig. 10), perhaps somewhat more moist than the pollen balls of *Nomadopsis* though not so moist as those of *Perdita zebrata zebrata*. The ball, provided with a shiny waterproof coating, rested on the floor of the cell. Its connection with the floor was supplied with a drop of moisture, the source of which is not known. The whitish egg, situated on top of the pollen-nectar ball, is characteristic of the Panurginae and possesses a smooth, non-reticulated chorion. It is oriented in the sagittal plane of the cell, and its anterior end faces the cell closure.

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<sup>1</sup> Identified by Alvin F. Shinn. Shinn's revision of the genus (1967) appeared after this paper had been submitted for publication; consequently his valuable data and interpretations could not be included here.

The posterior end was attached to the ball, whereas the anterior end usually did not touch (fig. 10). The dimensions of the egg (fig. 10) are given in table 2.

As seems to be characteristic of larvae of at least *Pseudopanurgus* and *Nomadopsis*, the young larva of this species (and probably all other species of *Calliopsis*) quickly ingests large quantities of liquid but almost no food after hatching, a fact that can be dramatically demonstrated by feeding small larvae colored water. The larvae of these genera increase rapidly in size because of their liquid intake. Defecation occurs in *C. crypta* shortly after the food has been consumed.

**ADULT ACTIVITY:** Almost no observation regarding adult behavior was noted. However, a female of this species mounted by the male of *C. rozeni* was collected in flight on the pollen plant. At the time, not knowing that two species were represented, I assumed that the pair were flying *in copula* as do the members of the subgenus *Nomadopsis*. I did not therefore look to see if their genitalia were engaged.

**PARASITISM:** Three species of *Holcopasites* were found on the grounds of the Southwestern Research Station at the time these observations were made (Rozen, 1965a). No eggs were found in the cells of this nest, but another nest of *C. crypta* with a single cell contained six eggs of *Holcopasites*. A female of *H. knulli* had been captured while leaving the nest.

*Calliopsis (Calliopsima) rozeni* Shinn and *C. rozeni*?

**LOCALITY AND DATE:** A single nest definitely assigned to this species was discovered 3 miles north of Apache, Cochise County, Arizona, by Marjorie Statham Favreau on April 29, 1966. The area was nearly horizontal, exposed to the sun for the entire day, and sparsely covered with grasses, *Malacothrix*, *Gaillardia*, *Phacelia*, and a number of other low-growing plants. The burrow entrance was found in the footprint of a cow in a barren area. The soil was loose at the surface but became hard-packed sand with few pebbles beneath the surface layer. No other individuals of the species were seen at this time.

Unfortunately in 1962, when I studied the biology of *Calliopsis* on the grounds of the Southwestern Research Station near Portal, Arizona, I did not distinguish between the two sibling species that were active. A female of *C. crypta* found in a nest made possible the identification of the nest and its larvae. As a *Calliopsis* larva unlike that of *C. crypta* was taken from the nest on September 9, 1962, this larva and nest are tentatively assigned to *C. rozeni* (i.e., *C. rozeni*?). This larva was recovered from a slightly sloping, flat section of a wash which was elevated above

the main part of the wash and thereby subjected to flooding only during severe rains. Surrounded by trees, the nest area nonetheless was exposed to the sun during the heat of the day. The somewhat sandy soil was devoid of vegetation, rather hard packed, and contained some stones, though not so many as at the nesting site of *C. crypta*.

The pollen source of *C. rozeni*, like that of *C. crypta*, was *Heterotheca subaxillaris* in the late summer of 1962. The source in the spring of 1966 was not determined.

**NESTING ACTIVITY:** Each burrow opening was surrounded by a tumulus, and at least the entrance of *C. rozeni*? was closed. The tunnel of *C. rozeni* descended in a meandering fashion and four filled side tunnels branched off; the main burrow of *C. rozeni*? was short and ended in a single cell. All cells, closed with a concave spiral plug, were inclined about 20 degrees from the horizontal, with the rear end lowest. The cell lining was moderately thin but still shiny and waterproof to a drop-let of water. Cell measurements for both *C. rozeni* and *C. rozeni*? are given in table 1. The yellow provisions (table 2) were spherical, moist, firm, homogeneous, and possessed a thin transparent coating. The coating on the provisions of *C. rozeni* seemed to be thinner than, and not so shiny as, that found on pollen balls of other species of *Calliopsis* and of *Nomadopsis*. The balls did not touch the rear end of the cell; their diameters are given in table 2.

The smooth shiny egg of *C. rozeni* rested on top of the ball in the sagittal plane of the cell, and the anterior end was closest to the cell closures. The larva of *C. rozeni*? defecated soon after consuming its food and then became quiescent. The fact that *C. rozeni* has been found nesting in April and also in late summer suggests that it may be multi-voltine.

**PARASITISM:** No parasitic bees were associated with the nest near Apache; three species of *Holcopasites* (Rozen, 1965a) flew at the site of *C. rozeni*? though none was definitely associated with this species of *Calliopsis*.

*Calliopsis (Calliopsis) andreniformis* Smith

**LOCALITY AND DATE:** The following brief observations on the early nesting activity of this species were made in Closter, Bergen County, New Jersey, on June 18, 1963. Though in the same baseball field as the nesting site of *Panurginus potentillae* (see description above), this site was separated from the other by approximately 60 feet and, further, the *Panurginus* site had become inactive by the time the *Calliopsis* began flying. The burrow openings were situated in barren, unshaded patches



of horizontal ground between clumps of grass. *Trifolium*, the pollen source, grew within 80 feet of the site. Ainslie (1937) provided a fairly detailed account of the nesting habits of this species in Iowa.

**NESTING ACTIVITY:** Although relatively few burrows were found, and these were sparsely distributed, they were restricted to one part of the field, a fact suggesting gregarious nesting habits. The openings, at the bases of young shoots of crab grass, were plugged and provided with tumuli. All nests excavated (dimensions given in table 1) had only a single cell (fig. 9), but, as the nesting activity of the species had just commenced, additional cells may have been added later. However, Ainslie (1937) clearly stated that "each nest provides for only a single egg." The unlined main tunnel, open below the entrance plug, twisted considerably but did not dip lower than the cell. Nearly horizontal, the elongate spheroid cell tilted slightly to the rear and possessed a distinct shiny lining. The completed provisions (fig. 9; table 2) were gray-green, spherical, and coated with a thin transparent substance identical to that found on the pollen balls of other species of *Calliopsis* and *Nomadopsis*. Molded from the moist pollen found on the legs of the female, the provisions were a homogeneous moist solid. As do the pollen balls of *Nomadopsis* and of the other species of *Calliopsis*, those of *C. andreniformis* rest on the cell floor and do not touch the posterior wall of the cell. The incomplete provisions were also spherical, a situation noted in *Nomadopsis* (Rozen, 1958, 1963). The single egg encountered (table 2) rested on top of the ball. With its long axis paralleling the long axis of the cell, its blunt anterior end pointed toward the cell closure (fig. 9). The anterior end and more pointed posterior end both touched the pollen mass, but the middle was elevated. With the exception of a very faintly muricate chorion, the egg had no characteristics by which it differed from most of the other panurgine eggs. The bee hibernates as a mature larva.

**ADULT ACTIVITY:** Few males were seen at the nesting site, and none attempted copulation there. Because numerous males patrolled the clover patches, I assume that mating takes place on or near the flowers. As I excavated a burrow, a female attempted to plug the burrow opening by repeatedly climbing up the tunnel backward with loads of loose soil which were then deposited at the opening. These actions perhaps indicate the method by which soil is excavated during normal tunnel construction. No cells from the previous year were discovered during the course of excavation.

**PARASITISM:** A single, freshly emerged specimen of *Holcopasites* (*Holcopasites*) *calliopsidis* (Linsley) was collected at the site. Ainslie (1937)

found *Sphecodes* flying about the nest area as well as *H. Calliopsidis* (as *stevensi*) entering the burrows.

PERDITA SMITH<sup>1</sup>

*Perdita (Perdita) zebrata zebrata* Cresson

**LOCALITY AND DATE:** The following observations were made on August 8, 1962, at the nesting site of the species, ½ mile northeast of Fallon, Prairie County, Montana (fig. 4). The site occupied a long roadside embankment that sloped 30 to 45 degrees from the horizontal and that by facing west-southwest was exposed to the hot afternoon sun. At most 4 feet high, the sloping surface here and there supported herbaceous vegetation. Between the vegetated patches there were variable-sized, nearly barren stretches, the larger ones of which were occupied by *Perdita*. Only one of the barren areas was studied, and it was completely devoid of plants with the exception of a few, small, leafless herbs. Its soil was fine, sandy, light in color, and easily excavated. Dry on the surface, it became moist at the depth of 10 cm. and was moist at the level where *Perdita* cells were encountered. No other pollen-collecting bees were noticed nesting there. The pollen plant, a purple-flowered *Cleome*, grew abundantly at the top of and at the foot of the bank as well as in the vegetated areas on the bank itself. Custer (1929a) provided considerable information on various aspects of the biology of this bee in Colorado.

**NESTING ACTIVITY:** Numerous burrow entrances, observed on the slope, were not associated with pebbles, stems, or other such objects. The openings, plugged but distinct, bore tumuli only on the downhill sides. The main burrows descended vertically in a somewhat meandering fashion. The essentially horizontal cells (fig. 11), arranged singly, were unlined so far as could be seen and were closed with a spiral cap. Unfortunately the number of females using the nest, or whether there was more than one cell to a burrow, could not be determined, but the impression was that only a single female occupied a nest that consisted of a number of cells. Custer (1929a) stated that there is but one female to a nest, that a nest consists of five to eight cells, and that there are usually two to three entrances to each nest. Dimensions of the Montana nest are given in table 1.

The provisions consisted of a spherical, gray-brown, pollen-nectar mass (fig. 11; table 2) that rested on the middle of the floor of the cells. Unlike the provisions of *Nomadopsis* and *Calliopsis*, those of *P. zebrata zebrata*

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<sup>1</sup> All species identified by P. H. Timberlake.

are moist, and the shiny, plastic-like coating is extremely thin. This coating was definitely detected only when observed under the microscope.

The position of the egg on the pollen ball (fig. 11) was seen in only three cases, but in each the egg was attached by its posterior end to the back of the ball. It projected upward, and its anterior end did not touch the pollen ball. The curved egg (table 2) is similar in appearance to

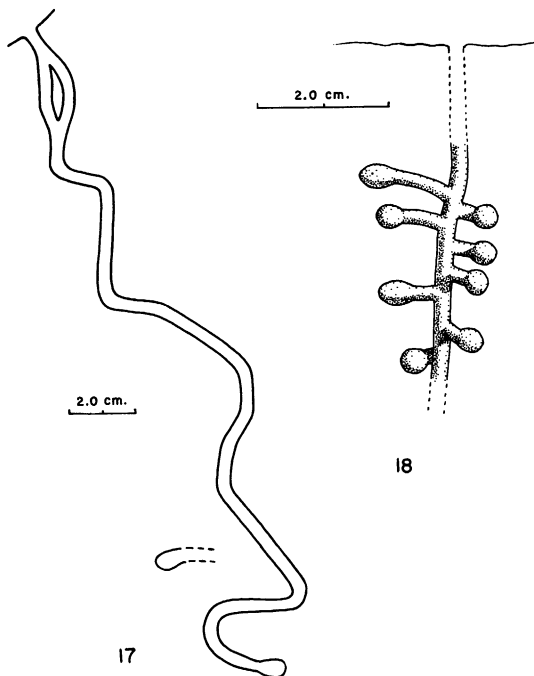


FIG. 17. Nest of *Pseudopanurgus* species B. The double segment of the main tunnel shown here is atypical.

FIG. 18. Segment of nest of *Perdita sexmaculata* Cockerell.

the eggs of other species of the Panurginae. All the mature or nearly mature larvae were found resting on their dorsa, and the one found still eating had the food cradled on its venter, as is characteristic of most panurgines. The species defecates soon after consuming the provisions. The only postdefecating individual encountered rested on its dorsum and held the meconial mass of one large pellet on its venter near the anus (fig. 14). Consequently the feces were not applied to the posterior end of the cell as in other panurgine genera.

**ADULT ACTIVITY:** Males, though common on the pollen plant, were

TABLE 1  
DIMENSIONS OF THE NESTS OF PANURGINE BEES

Species	Diameter of Main Burrow		Cell Depth		Cell Length <sup>a</sup>		Cell Diameter <sup>a</sup>	
	Num- ber of Data	Measure- ments (mm.)	Num- ber of Data	Measure- ments (mm.)	Num- ber of Data	Measure- ments (mm.)	Num- ber of Data	Measure- ments (mm.)
<i>Psacanthia</i>								
<i>bicolor</i>	1	4.0	2	14.0	1	9.0	1	5.5
<i>Pseudopanurgus</i>								
<i>boylei</i>	3	3.5-4.0	7	6.0-32.0	4	7.0-8.0	7	4.0-5.0
species A	—	—	1	8.0	—	—	—	—
species B	5	3.5-4.5	8	14.0-25.0	3	7.5-8.0	5	4.5-5.0
<i>aethiops</i> <sup>b</sup>	6	5.0	9	9.5-20.0	4	9.0-10.0	6	6.0-6.5
<i>timberlakei</i>	1	4.0	2	8.5	2	7.5	2	5.0
<i>Panurginus</i>								
<i>potentillae</i>	2	2.0-2.5	11	4.0-7.5	3	5.0	5	2.8-3.2
<i>Calliopsis</i>								
<i>andreniformis</i>	3	3.0-3.5	3	5.0-6.0	3	7.0-8.0	3	4.5-5.0
<i>crypta</i>	1	3.5	6	5.0-6.5	4	7.0-8.0	5	5.0
<i>rozeni</i>	1	3.0	4	7.0-10.0	1	8.0	3	5.5-6.0
<i>rozeni?</i>	—	—	1	3.5	—	—	—	—

TABLE 1—(Continued)

Species	Diameter of Main Burrow		Cell Depth		Cell Length <sup>a</sup>		Cell Diameter <sup>a</sup>	
	Num- ber of Data	Measure- ments (mm.)	Num- ber of Data	Measure- ments (cm.)	Num- ber of Data	Measure- ments (mm.)	Num- ber of Data	Measure- ments (mm.)
<i>Pardilia</i>								
<i>zebrata zebrata</i>	1	2.5	Several	Ca. 18 <sup>c</sup>	2	6.0-7.0 <sup>c</sup>	2	4.5-5.0
<i>confusa</i>	—	—	1	16.0	1	4.0	1	2.3
<i>confusa?</i>	1	2.0	2	9.0-17.5	1	4.0	2	2.5-3.0
species A	1	2.5	1	23.0	—	—	1	4.0
<i>sexmaculata</i>	1	2.5	7	1.8-4.3 <sup>d</sup>	5	5.0-6.0	6	3.5

<sup>a</sup> Measured as in figure 5.

<sup>b</sup> Somewhat comparable figures were given by Hicks (1931) for this species.

<sup>c</sup> Somewhat comparable figures were given by Custer (1929a).

<sup>d</sup> Below surface layer of loose dust 3-4 cm. thick.

not seen at the nesting site. Mating probably occurs on or near the plants.

PARASITISM: Adults of *Neolarra* (*Neolarra*) *pruinosa* Ashmead flew over the nesting site, and their larvae were found in the cells. The habits and larvae of this parasitic bee were discussed by Rozen (1965a, 1966a).

*Perdita* (*Perdita*) *confusa* Timberlake and *P. confusa*?

LOCALITY AND DATE: While studying a nesting site of *Nomadopsis helianthi* (Swenk and Cockerell) on August 30, 1963, 16 miles northeast of Douglas, Cochise County, Arizona, we came upon the burrows of several species of *Perdita*, some at the *Nomadopsis* site and others a short distance away. *Perdita confusa* was abundant on the flowers of *Lepidium* which grew profusely in the area. Only one cell, that which contained a pupa that later developed sufficiently far to be identified, can positively be attributed to this species, though several others (including one with a larva) can tentatively be assigned here.

All burrows, which were widely scattered, occurred in gently sloping, unshaded ground, where the soil was sandy, dry, and hard below the soft surface layer of dust.

NESTING ACTIVITY: The dimensions of the nest definitely identified, and of the nests tentatively identified, are given in table 1. All cells were nearly horizontal and lacked any visible indication of lining. A post-defecating larva held 17 small fecal pellets on its venter (fig. 15).

*Perdita* (*Perdita*) *sexmaculata* Cockerell

LOCALITY AND DATE: Most of the observations on the nests of this species were made on September 22, 1963, 3 miles east of Apache, Cochise County, Arizona, when the site was inactive and all the larvae were postdefecating forms. This nesting area occupied the gently sloping top of an embankment that was nearly barren of vegetation. The soil, dusty at the surface, contained few stones and was moderately hard packed below 3 to 4 cm. The nests were encountered while I excavated the inactive nests of *Nomadopsis puellae* (Cockerell). Although larvae of the latter species were more abundant, sufficient *Perdita* larvae were discovered to suggest that the species may nest gregariously, as does *N. puellae*.

A single nest of the same species was encountered 3 miles south of Rodeo, Hidalgo County, New Mexico, on May 4, 1966. This nest, agreeing with the one excavated earlier, allowed me to make brief observations on the provisions of the species.

TABLE 2  
DIMENSIONS OF POLLEN MASSES AND OF EGGS OF PANURGINE BEES

Species	Pollen Mass Dimensions <sup>a</sup>			Egg Dimensions <sup>a</sup>		
	Num- ber of Data	Horizontal Diameter (mm.)	Vertical Diameter (mm.)	Num- ber of Data	Length (mm.)	Width (mm.)
<i>Psaenythia</i>						
<i>bicolor</i>	1	4.4	3.5	1	2.2	0.5
<i>Pseudopanurgus</i>						
<i>boylei</i>	1	3.8	3.0	1	1.9	0.5
species B	2	3.3	2.5-2.8	—	—	—
<i>aethiops</i>	3	4.5-5.3	3.5-3.8	3	1.8-2.1	0.5-0.6
<i>timberlakei</i>	1	3.7	2.9	1	1.9	0.5
<i>Panurginus</i>						
<i>potentillae</i>	6	2.1-2.7	2.0-2.3	4	1.3-1.4	0.3-0.4
<i>Calliopsis</i>						
<i>andreniformis</i>	2	2.5 (Spherical)		1	1.7	0.4
<i>crypta</i>	6	3.5-3.8 (Spherical)		3	1.9-2.0	0.5
<i>rozeni</i>	3	3.5-3.8 (Spherical)		—	—	—
<i>Perdita</i>						
<i>zebrata zebrata</i>	3	2.0-2.5 <sup>b</sup> (Spherical)		3	1.1-1.2	0.3

<sup>a</sup> Measured as in figure 5.  
<sup>b</sup> Custer (1929a) stated that the spheres are 2 mm. in diameter.

NESTING ACTIVITY: At the Apache site, a section of the main tunnel and associated cells were removed intact to the laboratory, where they were carefully dissected and diagrammed (fig. 18). The dimensions are given in table 1. The open main tunnel descended more or less vertically, and the filled side tunnel had a diameter of 2.0 mm., that is, somewhat less than that of the main burrow. The cells, dipping slightly to the rear, were completely without a lining, lacked a hardened wall, and possessed an inner surface of the same smooth texture and appearance as that of the main burrow. The cell closure consisted of earth too poorly compacted to reveal a spiral structure. All larvae recovered were overwintering forms, resting on their dorsa, with their heads facing the closure, and with the fecal pellets heaped on their venters (fig. 16).

The provisions uncovered at the Rodeo site were spherical, quite moist, and definitely coated with a waterproof layer. Because the coating was thin, the provisions were not so shiny as those of *Nomadopsis* and *Calli-*

*opsis*. No eggs were discovered, but the young larvae in the sagittal plane of the cells rested on top of the balls a little to the rear. Their position suggested that the egg may be deposited somewhat toward the rear of the ball.

### *Perdita* Species A

This species was found nesting at the same time and place as *P. confusa*. Though only a single larva was recovered, it was obviously different from that of *P. confusa*?, so the few data on its habits are given to provide a more complete understanding of the nesting habits of the genus.

NESTING ACTIVITY: The nest dimensions are given in table 1. The cell, as did those of the other species of *Perdita* discussed here, lacked any indication of a shiny lining. This species, as did *P. confusa*?, held the feces as pellets on its venter.

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