

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2962, 27 pp., 16 figs., 3 tables November 30, 1989

Life History Studies of the "Primitive" Panurgine Bees (Hymenoptera: Andrenidae: Panurginae)

JEROME G. ROZEN, JR.¹

ABSTRACT

As a result of field investigations in North and South America, comparative life history information is presented on the following genera of panurgine bees which comprise the basal three clades in the Panurginae according to Luisa Ruz: *Liphanthus*, *Protandrena*, *Pseudopanurgus*, *Heterosarus*, *Cephalurgus*, *Metapsaenythia*, and *Psaenythia*. Subjects include ecology of nesting sites, nest architecture and dimensions, provisioning, development, larval behavior, mating behavior, voltinism, diapausing, food sources, diurnal and seasonal phenology, and nest cleptoparasites.

The diverse biological attributes of the Panurginae that are potentially useful for phylogenetic analysis are summarized, discussed, and evaluated

in light of information offered in the current paper, derived from previous literature, and/or incorporated in the author's unpublished fieldnotes. Comparisons are made with biological features of *Andrena*, the only genus of the Andreninae for which there are published accounts. Although of obvious phylogenetic value, biological data concerning the Panurginae are still too limited and poorly understood to permit an analysis at this time. Furthermore, too few taxa have been observed and outgroup comparisons are limited to *Andrena*.

A formal synoptic overview of the biological features of the Andrenidae is presented.

INTRODUCTION

I have been compiling life history information on the large andrenid subfamily Panurginae for many years. The recent study by Ruz (1987) presented a classification of the genera of these bees based on a careful analysis of the anatomy of the adults. Because

many of the genera for which I have notes belong to the basal three clades in the subfamily, it seems convenient to present this information here. Integrated with these new data are previous literature accounts on the life histories of the assemblage. Immature

¹ Curator, Department of Entomology, American Museum of Natural History.

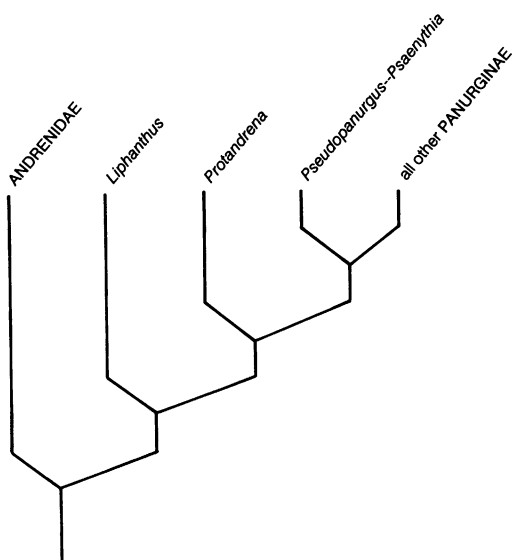


Fig. 1. Simplified cladogram of the bee family Andrenidae, from Ruz (1987). The clade *Pseudopanurgus-Psaenythia* includes the genera *Pseudopanurgus*, *Pterosarus*, *Heterosarus*, *Xenopanurgus*,* *Pseudosarus*,* *Rhophitulus*, *Chaeturginus*,* *Cephalurgus*, *Metapsaenythia*, *Anthemurgus*,* *Parapsaenythia*,* *Anthrenoides*,* and *Psaenythia*. Asterisks indicate that no nesting biologies within the genus are known.

stages from the field studies will be examined systematically and treated elsewhere, as will the biologies and immatures of the more highly derived panurgine genera.

Data presented below were gathered not only to expand our understanding of the life histories of the Panurginae but also to aid in determining the phylogenetic relationships within the subfamily. A phylogenetic analysis of the Panurginae is not attempted here because available information is still too incomplete (too few panurgine taxa, insufficient outgroup studies, and poorly understood biological features). Nonetheless, a discussion of characteristics that lend themselves to such a study is presented to direct attention to data of potential value.

Because I had to assemble biological information about the Andreninae in order to evaluate features of the Panurginae, I drafted a summary statement encompassing the biological traits of the entire family. This profile, obviously preliminary in nature, is offered at the end.

The genera covered in this paper are listed in table 1. Ruz's analysis (fig. 1) recognized

Liphanthus as the sister group of all other Panurginae, *Protandrena* as the sister group of the remaining Panurginae, and the assemblage *Pseudopanurgus* to *Psaenythia* (as listed in table 1) the sister group for all Panurginae except for *Liphanthus* and *Protandrena*. These genera occur only in the New World. Belonging to the basal clades of the subfamily does not, of course, necessarily mean that these genera are plesiomorphic. However, Ruz's study demonstrated that these genera, in fact, exhibit fewer adult apomorphies than the remaining genera, as also seems to be true with respect to the biological features discussed here. For convenience I refer to these genera as the "primitive" panurgines.

I follow the generic nomenclature used by Ruz (1987) with two exceptions: She combined *Calliopsis* (and its four subgenera), *Nomadopsis* (and its three subgenera), *Hypomacrotera*, and *Liopoeum* into one genus, *Calliopsis*. I continue to follow the more traditional usage of considering these genera distinct until the interrelationships of their taxonomic elements (i.e., the subgenera, genera, and certain troublesome subgenerically unassigned species) are better understood (which is not to say that I believe the traditional usage is more meritorious). Also, I continue to recognize *Poecilomelitta* as distinct from *Meliturgula* because I refer to my unpublished notes on the nesting and mating biology of the type species, *P. flavida* Friese. However, biological information in these notes seems to support Warncke's (1985) synonymizing of the two genera and Ruz's (1987) acceptance of the synonymy.

Table 2 presents the dimensions of nest components, provision masses, and eggs of the panurgines treated here.

ACKNOWLEDGMENTS

I gratefully acknowledge the field assistance of the following persons, named in association with the bee genus studied: *Liphanthus*: L. E. Peña; *Protandrena*: M. Favreau; *Pseudopanurgus*: E. Quinter; *Heterosarus*: M. Favreau, K. C. Rozen; *Cephalurgus*: J. S. Moure and F. C. Thompson; *Metapsaenythia*: B. L. Rozen; *Psaenythia*: S. Laroca, J. S. Moure, and F. C. Thompson.

The investigations in Brazil on *Cephalurgus* and *Psaenythia* were carried out while I worked in the laboratory of Padre J. S. Moure, Departamento de Zoologia, Universidade

Federal do Paraná, Curitiba. Dr. P. Noguiera-Neto, São Paulo, Brazil, provided living accommodations for my party at his plantation near Cosmopolis where we discovered and excavated the nests of *Cephalurgus*. Señor Luis E. Peña G., Santiago, Chile, guided me on two expeditions to northern Chile where I was able to pursue the biology of many Chilean bees including *Liphanthus*. Research on *Heterosarus* and *Pseudopanurgus* was conducted while I was in residence at the Southwestern Research Station, near Portal, Cochise Co., Arizona, administered by Vincent D. Roth and later by Wade C. Sherbrooke. The studies recorded here would have been impossible without the hospitality and assistance of these persons.

I would also like to acknowledge the cooperation of Dr. Luisa Ruz and Professor Haroldo Toro, of the Laboratorio de Zoología, Universidad Católica de Valparaíso, Chile. Their keen interest in and knowledge about panurgine bees aided the investigations. They identified specimens and named new species involved in the study; their publications on panurgines of Chile were a significant source of background information concerning the subfamily; and Dr. Ruz's thesis provided a meaningful framework for the report of these studies.

Field investigations were partly supported by the National Science Foundation GB5407 and GB32193.

This manuscript was critically reviewed by the following specialists: Bryan N. Danforth, Wallace E. LaBerge, Charles D. Michener, and Luisa Ruz, to whom I extend my sincere thanks.

LIPHANTHUS

Claude-Joseph (1926) briefly described the nest of *Liphanthus sabulosus*, the only previous account of the nesting biology of this genus. Friese (1916), Rozen (1970b), and Ehrenfeld and Rozen (1977) identified several species as hosts of the nomadine cuckoo bee *Kelita*. Ruz and Toro (1983) summarized previous information on the life histories of *Liphanthus* and listed the known flower preferences of the species.

Liphanthus (*Leptophanthus*) *alichahue*
Ruz and Toro

HABITAT: Approximately ten nests of *Liphanthus alichahue* were excavated along a

TABLE 1

The "Primitive" Panurgine Genera Treated in This Paper, as Identified by Ruz's (1987) Study
Bibliographic references are to biologies (other than pollen preference) of the species. Rozen (1967), Hurd and Linsley (1972), and Ruz and Toro (1983) provided summary accounts of some aspects of the natural histories of these bees.

Taxon	Biology
<i>Liphanthus</i>	
<i>alichahue</i>	Ehrenfeld and Rozen, 1977; present paper
<i>parvulus</i>	Rozen, 1970b; present paper
<i>sabulosus</i>	Friese, 1916; Claude-Joseph, 1926; present paper
<i>Protandrena</i>	
<i>bancrofti</i>	Chandler, 1962; present paper
<i>bicolor</i>	Rozen, 1967
<i>verbesinae</i>	Rozen, 1970a (as <i>Psaenythia bicolor</i>)
<i>Pseudopanurgus</i>	
<i>aethiops</i> (Cresson)	Hicks, 1931; Rozen, 1967
<i>fraterculus timberlakei</i>	Rozen, 1965a, 1967, present paper; Hurd and Linsley, 1972
<i>verticalis</i> Timberlake	Rozen, 1967 (as sp. B)
<i>Pterosarus</i>	
<i>boylei</i> (Cockerell)	Rozen, 1967
<i>occidus</i> (Timberlake)	Rozen, 1965a (as unnamed <i>Pseudopanurgus</i>), 1967 (as <i>Pseudopanurgus</i> sp. A); Hurd and Linsley, 1972
<i>perlaevis</i> (Cockerell)	Rozen, 1965a; Hurd and Linsley, 1972
<i>p. piercei</i> (Crawford)	Pierce, 1904; Hicks, 1936
<i>Heterosarus</i>	
<i>nanulus</i>	present paper
<i>Xenopanurgus</i>	
<i>Pseudosarus</i>	
<i>Rhophitulus</i>	
<i>niger</i> (Spinola)	Janvier, 1933 (as <i>Camptopoeum nigris</i>)
<i>Chaeturginus</i>	
<i>Cephalurgus</i>	
<i>anomalous</i>	present paper
<i>Metapsaenythia</i>	
<i>abdominalis</i>	present paper
<i>Anthemurgus</i>	
<i>Parapsaenythia</i>	
<i>Anthrenoides</i>	
<i>Psaenythia</i>	
<i>interrupta</i>	Claude-Joseph, 1926; Janvier, 1933
<i>annulata</i>	Rozen, 1977b; present paper

TABLE 2
Dimension of Nest Components, Provisions, and Eggs of the "Primitive" Panurgine Genera
(Numbers in parentheses are number of data.)

	Main burrow diameter (mm)	Cell depth (cm)	Cell length (mm)	Maximum cell diameter (mm)	Closure diameter (mm)	Provision, horizontal diameter (mm)	Provision, height (mm)	Egg length ^a (mm)	Maximum egg diameter ^a (mm)
<i>Lipanthus alicahue</i>	2.0	4-9	4.5-5.0 (10)	2.5-3.0 (12)	-	1.8 (3)	1.5 (3)	1.35 (1)	0.4 (1)
<i>Lipanthus parvulus</i>	2.3-2.5	5	5.5 (1)	3.5 (1)	2.15 (1)	-	-	-	-
<i>Lipanthus sabulosus</i>	-	6.5	7.0 (1)	4.0-4.5 (2)	-	3.5 (1)	2.5 (1)	-	-
<i>Protandrena bancrofti</i>	-	-	-	7.0-8.0 (1)	-	4.3 (1)	3.6 (1)	1.7 (1)	0.4 (1)
<i>Pseudopanurgus f. timberlakei</i>	3.5-4.0	10-14	6.8-8.4 (3)	4.8-5.2 (5)	2.8-3.2 (6)	-	-	-	-
<i>Heterosarus nanulus</i>	1.5-1.8	8-9	4.3 (1)	2.3-2.5 (2)	1.3 (1)	1.7-2.1 (2)	1.3-1.5 (2)	-	-
<i>Cephalurgus anomalus</i>	2.5-3.0	16-50	7.0-7.5 (6)	4.1-5.0 (6)	2.5 (2)	3.0-3.5 (10)	2.7-2.8 (9)	1.3-1.45 (4)	0.35-0.4 (4)
<i>Metapsaenythia abdominalis</i>	3.8-4.0	11-47	7.0-8.0 (10)	5.0-5.5 (9)	3.0-3.5 (5)	-	-	-	-
<i>Psaenythia annulata</i>	3.5	15-21	9.0-9.5 (2)	5.2 (2)	-	3.5-3.8 (2)	3.5-4.3 (2)	2.0 (2)	0.55 (2)

^a To closest 0.05 mm.

nearly horizontal earthen path (fig. 2) near Paipote, Atacama Province, Chile, between October 15 and 18, 1969. On October 20, 1971, another nesting site (fig. 3) (discovered on October 12) approximately 100 m away was excavated. The cuckoo bee *Kelita tuberculata* Ehrenfeld and Rozen (Nomadini) flew abundantly over the second site and seemed to be attacking the *Lipanthus* nests. *Kelita* larvae, however, were recovered only from one nest of an undescribed genus and species of panurgine intermixed with those of *Lipanthus*. In 1971 *Lipanthus* was not flying at its former nesting area which had apparently become inactive. The following discussion refers to the 1969 study unless otherwise indicated.

The path in which the bees nested bordered a plowed, irrigated field, sparsely vegetated with low herbs, including *Melilotus*. The sub-surface soil was moist, even-grained, moderately compact, without stones, with little organic material, and easily excavated. The pollen plant was not discovered; many males and some females flew over the nesting area, and males hovered around the flowers of *Melilotus*. The 1971 population was in a barren horizontal area, dry on the surface and exposed to the sun.

NESTS: Most nest entrances were scattered along the path on the sides of small depressions or elevations on the ground surface. Nest entrances usually had inconspicuous tumuli on the downhill sides. In 1971 most of the scattered entrances were in an area of a square meter. Main burrows descended diagonally in a meandering fashion. Those of nests being provisioned were open throughout, and those of completed nests were filled with soil just below the surface or were filled above but open below where the laterals connected. Laterals (3-6 mm long), of the same diameter as main burrows, branched from the main tunnel at irregular intervals and in random directions. Those leading to closed cells were filled with soil.

One completed nest (fig. 4) contained seven cells. Cells were arranged singly or in linear series of two, but in 1971 all cells seemed to be arranged singly. Completed cells in series were separated by short, soil-filled tunnels 1.25-1.5 mm long (N = 2). Cells were symmetrical around their long axes and lined with



Figs. 2, 3. Nesting areas of *Lipanthus alicahue* near Paipote, Atacama Province, Chile. 2. Nests in path in foreground. 3. Nest restricted to small, bare area by camera bag, left foreground.

a waterproof, clear, shiny coating. They tilted from 10 to 45° from horizontal, the rear lower than the front. Those containing food masses possessed a clear, silklike partial lining covering the rear and rear floor, in addition to the normal lining. The pollen sphere was affixed to it, apparently with nectar. This partial lining was thick, not unlike that of a *Colletes*, although less extensive, and could be peeled from the other lining. The coating and lining were appressed to each other, there being no fine, silk threads between them as in *Colletes*. Both linings were waterproof when tested with water droplets. This unusual, partial separate lining was overlooked in 1971, perhaps because most cells contained older larvae.

The cell closure was a concave spiral of three to four coils on the inside, was smooth and concave on the outside, so that the closure was 1.25 mm thick at the rim and 0.63 mm thick at the center, in one case. Cells arranged in linear series were separated from one another by a tunnel approximately 1.5 mm long.

Older offspring in nests were found in the upper cells, the younger ones in the lower cells.

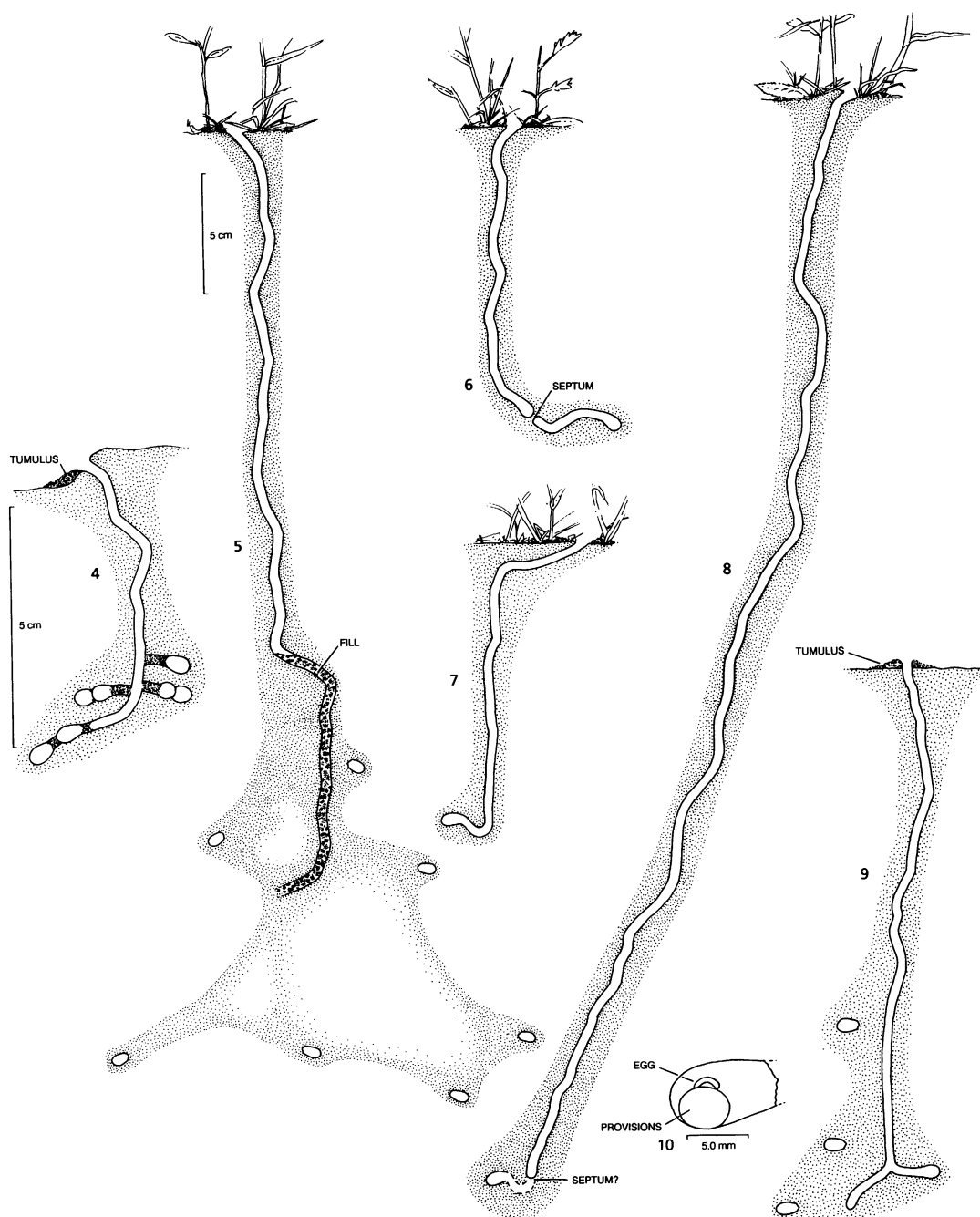
PROVISIONING AND DEVELOPMENT: Females transported moist pollen on their hind legs, and shaped the provisions into flattened homogeneously moist spheres in the nest. The orange spheres, uncoated and shiny, were

placed on the special inner coatings at the rear of the cells. Some cells emitted a fermented odor, suggesting that the provisions of this species may normally ferment.

The white, shiny, curved eggs were placed on top of the food masses with their long axes parallel to those of the cells. At least in two cases the posterior end of the egg was attached to the food mass while the anterior end rose above the mass. Eggs had a smooth chorion and were blunt at both ends.

As with most other panurgines, young larvae fed on top of the provisions and were unable to crawl. After eating the front one-half of the provisions, the larva reached the last instar. It then reoriented and, while facing the cell rear on its back, consumed the provisions still attached to its venter. After ingesting all food it again reoriented and faced the cell closure on its back; it defecated, appressing the meconial mass against the upper rear of the cell. Because a single nest contained both eggs and pupae, the species apparently has a number of generations annually. All postdefecating larvae were active, exhibiting no diapause. As indicated elsewhere, no parasitic bees were associated with these nests in that no immatures of *Kelita* were recovered from a nest.

ADULT ACTIVITY: I discovered the 1971 site when I noticed males flying at 11:30 a.m. They ceased their activity at about 2:00 p.m. I had seen no males the day before when I



Figs. 4-10. Nests of some "primitive" panurgines, side views. 4. *Liphanthus alicahue*. 5-8. *Metap-saenythia abdominalis*. 9. *Psaenythia annulata*. 10. Cell of same, showing egg and provisions. Three scales refer respectively to fig. 4, figs. 5-9, and fig. 10.

visited the site at 2:30 p.m. Males flew over the ground in a zigzag fashion and thrust their antennae forward and somewhat upward

when they alighted. A single pair mated, for approximately 5 seconds while they tumbled on the ground.



Figs. 11, 12. Nesting sites of *Liphanthus*. 11. *L. parvulus* at Peñuelas, Valparaíso Province, Chile, L. E. Peña excavating nest in path. 12. *L. sabulosus* at Tilama, Coquimbo Province, Chile; nest entrances in barren surface, left foreground.

Liphanthus (Xenoliphanthus) parvulus
(Friese)

HABITAT: Numerous males of this species patrolled unvegetated, essentially horizontal areas such as paths at Peñuelas, Valparaíso Province, Chile (fig. 11). I observed them both on October 6, 1969, and again on October 28, 1969, when they seemed equally abundant. Females, less numerous than males, were occasionally seen on the flowers of two species of *Adesmia*. (One *Adesmia* was no longer in bloom on October 28.) The region was dominated by herbaceous plants and a few scattered trees. A single nest was discovered on a gently sloping barren ground exposed to the sun. The soil, containing no rocks, was hard packed above and moist and soft below a depth of 3 to 4 cm.

NESTS: The nest, containing an open, unprovisioned cell, was in the early stages of construction. Its main tunnel entered the raised side of a crack in the soil at an oblique angle and then bent nearly vertically. A loose tumulus occurred on the lower side of the crack. The main tunnel was open to a depth of about 5 cm where it was blocked by loose soil for a short distance. Just below this material it opened, became nearly horizontal, and connected to the cell. Although the cell was essentially horizontal, exact orientation was uncertain. (Another cell from a nest of a previous generation was tilted about 15° from the horizontal with the rear part lower than

the front.) Its lining consisted of a thick transparent shiny waterproof coating over the entire surface and bore faint polar-directed ridges toward the rear. The cell was empty except for the egg of *Kelita chilensis*, discussed below.

ADULT ACTIVITY: Adults, especially males, were abundant at 11 a.m. on October 28, a warm, sunny day. By 2 p.m. their activity was much reduced, though some bees were flying even at 2:45 p.m. Males flew swiftly, close to the ground, and landed often on bare areas. Females both with and without pollen also landed in the same areas at which time several brief attempted (or actual) copulations were seen. Although many females were on the flowers of *Adesmia* on October 6, only a few were seen there on October 28. Males did not attempt copulation with females on the flowers.

CLEPTOPARASITISM: Many individuals of *Kelita chilensis* (Friese) patrolled the same barren areas as the *Liphanthus* males, and the egg of this nomadine was discovered in the open cell (Rozen, 1970b).

Liphanthus (Liphanthus) sabulosus
Reed

HABITAT: Several burrows within a few centimeters of each other were in a barren area adjacent to an irrigated wheat field (fig. 12) at El Naranjo, Tilama, Coquimbo Province, Chile, on October 24, 1969. Nests of

the panurgines *Liopoeum trifasciatum* (Spinola) and *Spinoliella herbsti* (Friese) were in the same area although the nests of these three species seemed segregated. The combined nesting area, bordered by short trees on one side and low vegetation elsewhere, was unshaded during the main part of the day. Dry, loose, and without stones on the surface, the soil was moist just below. The surface sloped about 10° from the horizontal.

NESTS: Hasty excavations revealed two nearly horizontal cells exhibiting a conspicuous waterproof coating over the entire inner surface and a rounded rear end. Claude-Joseph (1926) depicted the cells of this species in a linear series of four at the end of a short open main tunnel.

PROVISIONING AND DEVELOPMENT: One pollen mass, uncoated and homogeneously moist, was recovered from the rear of a cell. A small larva on top was feeding on the front end of the mass.

ADULT ACTIVITY: A number of males flew over the surface of the nesting area and along the earthen path leading to it. When they alighted they characteristically clung to the sides of small rocks so that they faced upward, exposing their large yellow faces to the sky. This behavior pattern was apparently associated with territorial behavior or with mating activity, although matings were not seen.

CLEPTOPARASITISM: We saw no cuckoo bees, but Friese (1916) suggested that *Kelita chilensis* might attack the nests of this species.

PROTANDRENA

This North American genus until recently was considered a subgenus of the South American genus *Psaenythia*. Chandler (1962) briefly described the nest of *Protandrena bancrofti* as did Rozen (1967) for *P. bicolor* (Timberlake). Rozen (1970a) later reported on the larva and pupa as well as the nest of *P. verbosinae* (Timberlake) (misidentified as *P. bicolor*).

Protandrena bancrofti (Dunning)

HABITAT: Marjorie Favreau discovered a single nest of this species at the Southwestern Research Station, 5 mi west of Portal, Cochise Co., Arizona, on August 26, 1973.

NESTS: The cell, with a maximum diameter of 7–8 mm, possessed a wall that was indistinguishable from the substrate and lined with a moderately smooth, shiny, waterproof coating. The closure was a concave spiral of three coils on the inside.

PROVISIONING AND DEVELOPMENT: A pollen mass shaped as a flattened sphere was orange, mealy moist throughout, and was not coated with either a sticky surface (nectar) or a waterproof covering. The curved, translucent white egg possessed a shiny smooth chorion.

PSEUDOPANURGUS

Many of the species formerly placed in this genus were recently assigned to other genera, so that in fact we have biological information about only three of the currently included species (table 2). Fragmentary information suggests that a thorough examination of at least one species might reveal why some larvae seem to overwinter as predefecating forms (Rozen, 1967) whereas others overwinter as postdefecating forms (present study).

Pseudopanurgus fraterculus timberlakei (Cockerell)

HABITAT: Females of this species nested at 2 mi east of Apache, Cochise County, Arizona, in late August 1988, and we excavated a number of burrows on August 24 and 30. All nests were situated on nearly horizontal surfaces on grazing land that contained a mixture of low-growing xerophilous herbaceous plants including the main food source, *Haplopappus gracilis* Nuttall,² as well as scattered shrubs (fig. 13).

NESTS: Entrances were widely scattered over an area of more than 100 m in diameter, and we found three as close as 3 cm apart. Adults of its cleptoparasite, *Holcopasites insoletus* (Linsley), throughout this same area helped draw our attention to some of the burrows. Although open when the females foraged, entrances were usually filled with several millimeters of soil in the evening and during inclement weather when the females were in the nest. The clogged entrances appeared narrower than the open, nearly vertical burrows beneath. All cells, arranged singly, were shal-

² Kindly identified by A. Cronquist, New York Botanical Garden.



Figs. 13, 14. 13. Nesting site of *Pseudopanurgus fraterculus timberlakei* at 2 mi east of Apache, Cochise Co., Arizona; nests widely scattered in lower half of picture, E. Quinter pointing to one entrance. 14. Nesting area of *Cephalurgus anomalus* at Cosmopolis, São Paulo, Brazil; F. C. Thompson sitting on ground digging nest, J. S. Moure looking for nest entrances.

low and tilted slightly to the rear (ca. 20°). Their dimensions (table 2) were consistent with those given in Rozen (1967). Cell walls were notably thick (ca. 5 mm) and substantially harder than, but otherwise indistinguishable from, the substrate. They possessed a conspicuous waterproof coating of transparent material over their entire surface. Cell closures were concave spirals on the inner surface and consisted of 3 to 4 coils of moderately loose, coarse soil. Laterals were variable in length (2–5 cm; $N = 3$) and filled after cell closure. Each nest was occupied by a single female.

PROVISIONING AND DEVELOPMENT: Females shaped provisions into uncoated, flattened spheres and deposited eggs on the tops. A larva, perhaps early last stage, sat on the top of one pollen mass that had its front half eaten away, an indication that larvae do not crawl over their food masses as they feed. We recovered several postdefecating larvae still able to slowly curl and uncurl their bodies, as has been reported for postdefecating *Proandrena verbesinae* (Rozen, 1970a) and *Metapsaenythia abdominalis* (present paper). We also found predefecating larvae, one of which was still alive and responsive to touch (far more so than the postdefecating larvae) more than four months later; it defecated and became more active during the first 10 days of April 1989. Hence, larvae of this species seem to overwinter as both predefecating and post-

defecating forms, contrary to preliminary conclusions (Rozen, 1967) suggesting that all *Pseudopanurgus* overwinter as predefecating larvae. As is the case with most panurgines, feces were applied as single masses to the upper rear wall of the cells, the first such observation for the genus.

CLEPTOPARASITISM: Although *Holcopasites insoletus* had been tentatively associated with both *Pseudopanurgus* and *Pterosarus* (Hurd and Linsley, 1972), the recovery of its first- and last-stage larvae from the brood cells of *Pseudopanurgus f. timberlakei* now confirms the association with *Pseudopanurgus*. The last instars of this cuckoo bee were completely quiescent in contrast to the postdefecating host larvae.

HETEROSARUS

This is the only genus of "primitive" panurgines to occur in both North and South America. In spite of its wide distribution, its nesting biology has not been described before.

Heterosarus nanulus (Timberlake)

HABITAT: We studied the nesting of this species and its parasite, *Holcopasites tegularis* Hurd and Linsley, August 20 to September 1, 1971, at 13 mi southwest of Apache, Cochise County, Arizona, the type locality for both species. Burrows of *Heterosarus*

nanulus occurred on barren and semibarren stretches of unpaved roads that bordered Route 80 (Rozen, 1984b: fig. 25). Although predominantly grassland, the region offered numerous herbaceous plants, particularly along the disturbed roadsides, and the area adjacent to the nesting area consisted of several species of *Euphorbia* (the food source for this species) as well as other low-growing herbs. None of the nests were shaded by vegetation in spite of scattered mesquite trees and other shrubs. The soil, volcanic in origin, was moist because of recent rains and moderately pebbly, both on the surface and at the cell level. It was difficult to dig because the soil fractured unevenly. The surface sloped only barely at most of the nest entrances although one nest was found on the side of a sloping embankment about 3 m high.

NESTS: Of the approximately 15 nests of *Heterosarus nanulus* discovered, none was surrounded by a tumulus. The open main tunnels, circular in cross section, descended nearly vertically although in a few cases they meandered slightly, presumably because of hard soil inclusions. Because of the nature of the soil and the small diameter of the main tunnel, the nest structure was difficult to examine. Cells, arranged singly, were found from 8 to 9 cm deep though presumably some occurred at lower depths.

Several laterals were 1.3–1.5 mm in diameter; their walls were rough and embossings from the females' pygidial plates were evident. Laterals were filled with soil after cell closure. One nest contained four cells, with the oldest larva highest in the series. The cells were nearly horizontal but tipped somewhat to the rear. Their smooth walls possessed conspicuous, shiny, waterproof linings over their entire surface. The closure of coarse particles was a concave spiral on the inside.

PROVISIONING AND DEVELOPMENT: Females transported pollen as moist masses on their hind tibiae. They deposited the food in the rear of the cells as amorphous masses and shaped it into flattened spheres only when all supplies had been accumulated. Fully formed masses were visibly moist on the outside and seemed to be uniformly moist on the inside. An egg had been deposited on the top of one mass, and an intermediate-stage larva sat on top of another, both in positions typical of

other panurgines. Of three mature larvae uncovered, one was defecating, applying the feces as elongate, parallel strips to the upper rear of the cell; another began defecating within several days of being discovered; the third had not started defecating by August 29, 1971, when observations ceased. The two larvae pupated after defecating, suggesting that the species undergoes more than one generation a year.

CLEPTOPARASITISM: Female *Holcopasites tegularis* examined or entered the burrows of the species on at least ten occasions during our observations. *Holcopasites* entered several nests twice before we excavated them. Because of the difficulty of excavating nests, we uncovered few cells of *H. nanulus* intact. One, however, contained a first instar of *Holcopasites* biting an egg of *Heterosarus*, and another, a first instar *Holcopasites* ambulating by pushing itself with the tip of its abdomen over the cell wall. Not infrequently, it stopped and raised the anterior part of its body in the air. One first instar was approximately 0.6 mm long, and both were semitransparent, white, possessing distinct but unpigmented head capsules with sharp-pointed but not very long mandibles. Egg insertion holes were discovered in the walls of both cells. Similar to the insertion holes described by Rozen (1965a), each consisted of a hinged flap beneath which was a cavity approximately 0.3 mm long. The vacated chorions were visible but had collapsed after eclosion.

CEPHALURGUS

Cephalurgus anomalus Moure and Oliveira

HABITAT: This species nested at Cosmopolis, São Paulo, Brazil, on January 26, 1974, and was studied over a three-day period. The region was originally forested but tropical agriculture, primarily sugar cane plantations, had long dominated so that none of the original forest survived. The nesting site was in a large field (fig. 14) that had been recently bulldozed. As a consequence, plants generally less than one meter tall, including the food plant, *Sida* (Malvaceae), covered much of it. Bare areas, some resulting from recent scrapings, appeared randomly over the field. Al-

though we searched for nests in many of these bare patches, we found them only in two.

Both sites sloped gently and consisted of soil which when dry was hard but when wet was easily excavated. The soil lacked a powdery surface layer because of the heavy rains that occurred every afternoon during the field investigations which took place in the rainy season. We were impressed by seeing so much rain during the nesting period of a panurgine, and the moist condition of the food masses of these bees and unusually plump predefecating larvae (discussed below) may have been connected to the high relative humidity and abundant water. Homogeneous, the earth contained no stones or pebbles, only fine roots, and was dry on the surface early in the morning before the rains but moist below the surface at all times.

The pollen plant was abundant throughout the field but was especially prevalent near the larger of the two bare areas. The appearance of the flowers and their time of opening and closing suggested that several species of *Sida* may have been represented. Flowers opened between 8:00 and 9:00 a.m. and closed shortly after noontime.

NESTS: The smaller nesting site contained a single nest whereas the larger one, approximately 30 m away, was composed of 10 to 20 nests. We excavated the nest from the small site and three from the larger one, and each contained a number of foraging females as well as callow males and females. Most, if not all, other nests were also composite. The first nest excavated contained 12 females and undoubtedly a number of others escaped detection. Of these 12, 5 were teneral, lacked large oöcytes and had no pollen in their alimentary tracts; 5 contained large oöcytes and pollen in their alimentary tracts; 1 (not dissected) was carrying pollen; and 1 though not obviously teneral lacked pollen and had no large oöcytes. These facts suggest that there is no caste system and that there is probably no division of labor (but see comments on teneral females, below). This same nest yielded 4 males, all fresh and apparently teneral. Although males of this species have large heads, there is little variation in head width and these 4 males gave no indication of being subterranean, i.e., they did not have extra large heads, reduced compound eyes, or pale

coloration. Such macrocephalic forms have been found in the nests of some *Perdita*.

During the height of foraging (9:00 to 10:30 a.m.) 40 pollen-laden females entered another nest during a half hour period and 9 females entered a smaller nest nearby. We did not monitor exiting females in either case, so that the colony size could not be estimated. Nest entrances occurred on horizontal ground and along the sloping side of a low earthen embankment, 20 to 40 cm high. Most were not surrounded by tumuli because of afternoon rains and sloping surfaces, but one, on the flat, was surrounded on all sides by a tumulus 3 cm in diameter and 0.7 to 0.8 cm high. Entrances were open during morning foraging but were closed around noon after the females had returned. There was only a single entrance for each nest.

Circular in cross section and open, burrows descended with little meandering. Burrow walls were rough. The main burrow of one nest, containing 13 females and 1 male, did not branch, but in the other three nests each branched a number of times, with each branch tending to descend more or less vertically so that branches never diverged widely. In one nest a short tunnel 12 mm long branched at a depth of 13 cm and ended abruptly. This vestibule may have permitted females to pass one another. Main tunnels and branches were open for their entire lengths. Even though burrows of separate nests approached one another, they did not anastomose. Females always filled laterals after cell provisioning and closure. We were unable to trace open laterals, so that their configuration is unknown. However, many cells were as far as 7 cm from the main tunnels, indicating that laterals were of considerable length, perhaps averaging 5 to 6 cm.

Cells were arranged singly rather than in linear series. Tipped slightly to the rear, they were essentially horizontal and appeared similar to the diagrammed cell of *Protandrena verbesinae* (Rozen, 1967: fig. 6; misidentified as *P. bicolor*). The closure was a coarse, indistinct spiral, concave on the inner surface with about three coils. The cell wall was extremely smooth, without pygidial plate markings, and indistinguishable from the substrate. Cell linings were thick, waterproof, conspicuous, covered all cell surfaces except

for the closure, and could be easily peeled with forceps.

PROVISIONING: Females transported yellow-orange pollen of *Sida* as large moist sticky masses on the anterior surfaces of their hind tibiae and to some extent on their hind femora. The finished loaf formed a flattened sphere, homogeneously sticky-moist throughout. Its surface appeared coarse because of the large size of the pollen grains and lacked a waterproof coating.

DEVELOPMENT: The female placed a white, elongate, curved egg with a shiny transparent chorion on the top of the loaf as diagrammed for *Protandrena verbesinae* (Rozen, 1967: fig. 6). Eggs were attached only at their anterior and posterior ends. The anterior end was blunter than the posterior end and faced the cell closure, as is characteristic of all panurgines.

Young larvae and even last instars sat stationary on top of the pollen masses while they fed on the loaf beneath. Very small larvae ingested considerable quantities of liquid before eating pollen, revealed by viewing the liquid-to-pollen ratio in the stomach contents of recently preserved specimens. With almost all panurgines (*Panurginus* is the exception), larvae consume approximately half their provision by eating away the front half of the food mass while sitting on top of it. Then, after reaching the last instar, they reorient and, resting on their dorsa, finish the food hemispheres cradled on their venters. Larvae of *Cephalurgus* were always encountered perched on the loaf even when two-thirds of the food had been eaten and only a small crescentic part (seen in side view) remained. We found no larvae resting on their dorsa while they completed the provisions. Failure to observe larvae on their dorsa was, therefore, probably not the result of too small a sample. The feeding activities of this species need further research, but the species appears atypical for the subfamily.

The fully fed larva (to be illustrated and described in a subsequent paper) was unusual because of its very large abdominal region, a feature not seen before in panurgines. The postdefecating larva, in contrast, was much smaller than the predefecating form and had proportions typical of other panurgines.

Feces were always voided on the upper rear

of the cell as is the case with all panurgines except most *Perdita*. Feces were unusual in that they were deposited as approximately 15 elongate pellets, each about 2 mm long, roughly in the sagittal plane of the cell. These pellets were not flattened so that the surface of the deposited meconial mass was uneven. With aging, pellets lost their identity, perhaps because of the moisture in the cell or mold. Older fecal masses therefore appeared as single unconsolidated bodies of loose pollen grains.

We encountered very active postdefecating forms, six pupae, but no inactive postdefecating larvae; hence diapausing did not occur during the season of these observations. As with all panurgines, no cocoon was spun. After emerging, adults apparently spend time in the nest while their integument hardens and colors. It is unknown if teneral adults function in the nest while they harden, but several were encountered at the ends of burrows suggesting they may assist in digging tunnels.

PHENOLOGY: Adult activity outside the nest during the day was synchronized with the diurnal blooming period of the pollen plant. On one day, nests were opened between 8:45 and 9:30 a.m. and females started foraging. The first flowers opened at about 8:00 a.m. and all flowers were in full bloom by 9:45. Bee activity on the flowers diminished substantially by 11:30 a.m. with only scattered females to be seen. The flowers closed between 12:30 and 2:00 p.m.

Because we encountered no diapausing larvae and found all ontogenetic stages, this species must have a number of generations per year or have continuous generations throughout the year. Numerous old vacated cells excavated from at least three of the nests indicate that nests are used by members of successive generations.

ADULT ACTIVITY: Mating was not observed, but the absence of males over the nesting area indicated that mating does not take place in association with the nests. Males were numerous on the *Sida* flowers and flying from one blossom to another, a possible indication that copulation is initiated on the food plant. Padre Moure (personal commun.) stated that mating is initiated on the flowers and that the pairs then drop to the ground. I



Figs. 15, 16. 15. Nesting site of *Metapsaenythia abdominalis* at 2 mi WSW of Osceola, Hill Co., Texas; nests widely scattered throughout lower half of picture, taken on August 10, 1988, when adult bees no longer active. 16. *Psaenythia annulata* at Furnas, Vila Velha, Paraná, Brazil; nests to the left of J. S. Moure, middle foreground.

would have noticed pairs flying in copula if such were the mating mode.

CLEPTOPARASITISM: No cuckoo bees have been associated with this species either at the nesting site or at numerous other localities where the bees flew.

METAPSAENYTHIA

This genus contains two described species. *Metapsaenythia abdominalis*, biology described below, occurs from Kansas and Texas to the east coast of the United States. *Metapsaenythia sonorana* Timberlake is known only from the type specimen from Sonora, Mexico (Timberlake, 1969). Nothing has been recorded about the life histories of either species except that Timberlake (1969) reported that females of *M. abdominalis abdominalis* collect pollen from *Monarda* (although they have been taken at flowers of a number of other plants) and the type of *M. sonorana* was captured on *Tidestromia lanuginosa*. Mitchell (1960) recorded that *Metapsaenythia a. tricolor* (Cockerell), an eastern dark form, has been collected only from *Monarda punctata*.

Metapsaenythia abdominalis (Cresson)

HABITAT: I discovered the nesting site (fig. 15) of *Metapsaenythia abdominalis* 2 mi WSW of Osceola, Hill County, Texas, on June 26, 1988, and studied it during the next four

days. Because the nesting season had just begun, I returned to the site on August 10, 1988, to recover mature larvae from a nest previously marked but left to be excavated later. The site was now quiescent; no adults of either *Metapsaenythia* or its cleptoparasitic bee were evident although a few scattered blossoms persisted on the pollen plant.

The nesting area occupied the east side of a fenced pasture bordered by shrubs and trees. Pasture plants of low-growing herbs and grasses were generally no more than 15 cm tall, but the pollen plant, *Monarda punctata* L., affinity towards var. *stanfieldii* (Small) Cory,³ was widely distributed throughout the pasture and tended to be taller, with some plants being nearly a half meter high. Live ground cover was greater than 80 percent, and dead plant material, cattle feces, and oak leaves obscured the surface further. Only rodent mounds offered barren surfaces which, however, were unused by nesting *Metapsaenythia*. The low-growing vegetation at the nesting area was similar to the mixture described above, except *Monarda* was scarcer and part of the area near an oak tree was more uniformly covered with grasses. Whereas the ground surface gently sloped in most areas of the pasture, the nesting site was on the high part of the pasture near two large oaks. These

³ Kindly identified by Thomas J. Starbuck, New York Botanical Garden.

trees cast an open, sun-flecked shade over all but one of the nest entrances until about 11 a.m. Afterwards all entrances except one at the boundary of the open shade were exposed to full sun. The soil at nest excavations was uniformly moist, moderately fine, even-grained, moderately compact sand that tended to remain in clumps after drying. The soil contained few pebbles but was penetrated by fine roots.

NESTS: I first discovered the nest area because of adults of the cleptoparasite, *Holcopasites eamia* (Cockerell), searching it. Five nests were eventually identified scattered over an area about 4 m long and 2 m wide, with a sixth nest occurring 30 m away. Although nests probably occurred elsewhere as evidenced by *Holcopasites* searching more widely, *Holcopasites* activity and therefore nest occurrence was restricted to only a small part of the pasture. Two nests were a third of a meter apart but others were more widely distributed.

Only a single *Metapsaenythia* female was associated with each nest, and the nest entrances were hidden among the growing vegetation, dry grass, and dead leaves, so that they could not be detected unless these plant materials were removed or parted. Each was discovered because I observed a returning female trying to enter her burrow. In spite of being hidden, these entrances were open and not clearly surrounded by tumuli. Excavated soil, apparently intermixed with surface debris, was rained upon and therefore lost its identity quickly.

Except in one nest (fig. 7) that had a nearly horizontal upper segment 4 cm long, all main burrows descended more or less vertically with slight bending. The deepest burrow (fig. 8), 47 cm long, angled from the vertical so that its terminus was 10 cm from a vertical line passing through its entrance. Main burrows excavated in June were approximately 4.0 mm in diameter although one was slightly smaller (3.75 mm) near its entrance. Main burrows were not filled with soil but two nests (figs. 6, 8) (and possibly all) contained a thin septum of fine dry soil immediately above the junction with the lateral which led to the open cell. The upper surface of the septum was concave and the area immediately above it was 6.0 mm and 5.5 mm in diameter in

both cases. The enlargement of the burrow may have resulted from the female taking soil from the burrow wall to construct the septum. Septa may assist in excluding *Holcopasites* females from finding open cells; neither cell so walled off contained *Holcopasites* eggs. The single completed nest (fig. 5) studied in August had an open burrow to the depth of 25 cm but was filled with loose, fine-grained soil from there to about the 30 cm level, below which it was lost. Burrow walls were dull, moderately rough, nonwaterproof when tested with a water droplet, and presumably unlined.

All laterals leading to open cells were circular in cross section, open, and invariably curved upward before widening at the cell entrance (figs. 6–8). Their walls were unlined, dull, and smoother than those of the main burrows. Laterals leading to the closed cells were soil-filled and undetectable. Laterals measured by the horizontal distance between the cell entrance and main tunnel terminus ranged from 1.5 to 4.5 cm, but the seven cells seemingly (but not certainly) belonging to the closed nest (fig. 5) were distributed over a horizontal area 20 cm in diameter.

All cells were arranged singly (that is, not in linear series) and were nearly horizontal, sloping toward the rear by 10 to 20°. They were elongate ovals with their rear ends rounded. They appeared symmetrical around their long axis so that the ceiling was not more highly vaulted than the floor. The cell wall, at least in one case, was slightly harder than the surrounding substrate, but no other features distinguish the wall from the substrate. The wall was coated with a distinct shiny lining, darker than the substrate on freshly excavated cells (but when exposed soon dried to be concolorous with the substrate). The lining covered all surfaces of the cell, but at least in one cell it ended 1 mm from the narrowest point of the cell mouth. Whether this uncoated area would have been covered by the closure is uncertain.

The cell closures of loose soil were uncoated and consisted of a deeply concave spiral of 3–4 coils on the inner surface.

An unusual feature of the nests studied in June was the variability in cell depth, some open cells being only 11 cm deep and the deepest, 47 cm. In the nest with two cells, the

completed cell was above the open one. The completed nest excavated in August presumably had seven cells, ranging in depth from 28 to 40 cm.

PROVISIONING: Females transported pollen as a moist solid on the hind tibiae. Each of the five nests excavated in June contained a partly provisioned open cell. In all these cases, stores were sufficiently liquid so that their upper surfaces were horizontal and some clear fluid (presumably nectar) was discernible intermixed with pollen grains. Such fluid provisions are unknown among other panurgines, whose provisions are either removed from hind legs as irregular semisolid masses or shaped into small spheres to which additional loads are subsequently added. The liquid early loads in *Metapsaenythia* may have resulted from females depositing moist pollen and then adding nectar. On the other hand, each of the five nests excavated had remained open overnight (females had been either collected the day before or excluded from the nest) so that the nectar in the provisions may have acquired water from the visibly moist substrate. The single completed food loaf, on the floor of the cell, was a formed semisolid with a sticky surface to which sand had adhered as a result of excavation. Its exact shape could not be detected but it was unquestionably more solid than the preliminary provisions in the open cells.

DEVELOPMENT: Cells from the nest excavated in August yielded five postdefecating larvae of *Metapsaenythia* and two of *Holcopasites*. Whereas the *Holcopasites* larvae were totally quiescent, all *Metapsaenythia* were able to slowly curl and uncurl their bodies, an unusual feature for postdefecating, overwintering larvae of the Panurginae. They continued these movements for months, although by the end of January 1989 they could no longer be induced to move. All *Metapsaenythia* postdefecating larvae were discovered resting on their prominent dorsal tubercles, with their heads near the cell entrances and their fecal material plastered at the upper rear wall of the cell. Their integument was coated with an oily material that caused sand to adhere to it, in contrast to the dry integument of *Holcopasites* overwintering larvae.

PHENOLOGY: In an attempt to analyze the relative ages of the individuals in the *Metap-*

saenythia and *Holcopasites* populations, I studied the wing wear along the outer edge of the forewing of all individuals (41 *Metapsaenythia* and 17 *Holcopasites*) collected in June. The individuals were assigned to one of four categories, each reflecting the percentage of the wing edge worn away. The figures are presented in table 3, on the basis of combining the sexes of each species and then of separating the sexes of each. If one assumes that the rate of wear of the wing of the species and of the sexes is not altered by the obvious differences (discussed below) in their flight behaviors, then the relative ages of the individuals are reflected by the degree of wing wear: i.e., the more wing wear, the older the individual. Table 3 suggests that the *Metapsaenythia* population had emerged later than that of *Holcopasites* in that 73% of the *Metapsaenythia* had 0–25% wing wear whereas only 29% of the *Holcopasites* fell into this category and 41% exhibited excessive wing wear (75–100%). The disparity between the two populations may actually have been greater since many of the *Metapsaenythia* (but few of the *Holcopasites*) showed almost no wing wear (that is 0%) and some of the *Holcopasites* (but none of the *Metapsaenythia*) exhibited wing wear in which much of the wing distad of the veins had disappeared [that is to say, a more precise classification might have included yet two more categories to recognize: (1) 0% wing wear only and (2) wear beyond the total destruction of the original wing edge]. Eighty-four percent of the female *Metapsaenythia* had 0–25% wing wear, and the remaining 16% had 25–50% wing wear, whereas males of the same species had 64% in the 0–25% bracket and the remaining males fell into all of the three other categories. These figures probably reflect the fact that the species is protandrous. Although the figures for males of *Holcopasites* are too few for analysis, the fact that only three *Holcopasites* males were captured may be an indication that the species is also protandrous and many of the males had already died. Comparison of the females of the two species reveals that the *Holcopasites* population was substantially further advanced with only 36% of individuals in the 0–25% category and 64% in the other three categories, whereas 84% of the *Metapsaenythia* females were in the 0–25% category and

TABLE 3

Analysis of Wear of Outer Edge of Forewing of All *Metapsaenythia* and *Holcopasites* Collected 2 Miles WSW Osceola, Hill County, Texas, in June 1988

The four categories represent percentages of wear (removal) of normal outer edge. For explanation, see text.

	0–25% category	25–50% category	50–75% category	75–100% category
Sexes combined:				
<i>Metapsaenythia</i>				
Individuals (N = 41)	30	5	2	4
Percentage of sample	73%	12%	5%	10%
<i>Holcopasites</i>				
Individuals (N = 17)	5	4	1	7
Percentage of sample	29%	24%	6%	41%
Sexes separated:				
<i>Metapsaenythia</i>				
Males				
Individuals (N = 22)	14	2	2	4
Percentage of sample	64%	9%	9%	18%
Females				
Individuals (N = 19)	16	3	0	0
Percentage of sample	84%	16%	—	—
<i>Holcopasites</i>				
Males				
Individuals (N = 3)	0	1	0	2
Percentage of sample	—	33%	—	67%
Females				
Individuals (N = 14)	5	3	1	5
Percentage of sample	36%	21%	7%	36%

the remaining 16% fell only into the 25–50% category.

The earliness of the *Metapsaenythia* nesting season in June was also reflected in the fact that, of the five nests excavated at that time, only one contained a completely provisioned and closed cell. All four females associated with the nests fell into the 0–25% wing wear category.

Metapsaenythia abdominalis and *Holcopasites eamia* have a single generation per year, as revealed by the presence of postdefecating larvae in the nest excavated in August and by the pollen source being essentially exhausted at the same time.

ADULT ACTIVITY: I saw male *Metapsaenythia* around the flowers throughout the field from when I arrived at 10:20 a.m. until I departed at about 4:30 p.m., although the activity was reduced at 4:15 p.m. on June 27. In general, males were more abundant than females, and females were uncommonly seen on the mornings of June 27 and 28, days

which later became partly cloudy to cloudy. During the afternoons of these two days, females became so abundant on the flowers after 1:30 p.m. that I thought that their activity might normally be restricted to the afternoon; however, on June 29 and 30, days that remained clear, females were observed in the late morning, and no surge of females occurred in midafternoon as had been perceived on the two previous days. Future monitoring of flight activity will perhaps explain the observations.

Male flight activity primarily involved mate searching. Males flew moderately swiftly from one pollen plant clump to another, and they also scouted the nesting area where they probably were looking for females leaving and returning to nests. Males occasionally approached females at the flowers and at the site, but all observed meetings ended nearly instantaneously as the female quickly avoided the male. Several times a male would again approach the same female but was again

avoided. Unless the nearly momentary encounters were matings, no copulations were detected.

The female foraging flight was moderately slow and deliberate. A female often circled a flower stalk of *Monarda* and alighted on one or more blossoms to forage before departing to another stalk. Not infrequently a female departed from one stalk to forage on another only to return to the first stalk, suggesting that females could not recognize flower stalks they had recently visited.

Some females landed only to take nectar from flowers, others only to collect pollen, but, if a female visited a flower for nectar and pollen, she invariably gathered nectar first and pollen second. A nectaring female was immediately identifiable because she inserted her head and mesosoma into the corolla while her metasoma extended from the corolla and her hind legs held down the lower lip of the corolla, while her wings, longitudinally plaited and darkly infuscated, conspicuously diverged from each side of the flower. In this posture her head and part of the mesosoma were hidden within the corolla. A pollen-gathering female, on the other hand, clung to the lower surface of the upper lip of the flower and faced away from the corollar base so that her head appeared face up at the apex of the upper lip where the anthers extruded. Females presumably raked pollen from the anthers with their foretarsi, although the brief motion of their heads seemed to suggest that they were chewing the pollen from the anthers. Nectaring on a flower took approximately five seconds; pollen gathering only several seconds.

An unusual feature of the females (and perhaps of males) of this species is their ability to fold their wings longitudinally. Whereas such wing folding is characteristic of the Vespidae, it has been recorded in bees only for the paracolletine genus *Eulonchopria* where it may be a mimetic trait (Danforth and Michener, 1988).

Live females held between the fingers emitted an oil-of-lemon odor, characteristic of many panurgines.

Because females have a well-developed external stinging apparatus, I investigated their ability to sting by holding a live female against the inner surface of my forearm. No certain

stinging sensation resulted, but within several minutes hard welts appeared in the two areas where the female had been positioned, indicating that venom had penetrated my skin and that the bee can use its sting as a defense mechanism.

Females almost certainly spend the night in their nests. Males presumably sleep in crevices and unoccupied burrows, for I observed a male digging into a loose rodent mound one afternoon and another male searched the same mound.

CLEPTOPARASITISM: During the three days of observations in June, *Holcopasites eamia* females were abundant. They flew slowly close to the ground in a meandering flight. Several males had a similar slow flight so that I was uncertain of gender of flying *Holcopasites*. Not infrequently, a female flew back and forth over a limited area, perhaps 10 cm in diameter, and alighted occasionally, suggesting that she was assessing whether a hidden burrow was present or occupied. No matings were observed and males seemed uncommon or absent toward the end of the study period in June.

Of the five nests excavated in June, only the one consisting of two cells contained *Holcopasites* immatures. The closed cell yielded five first instars (two alive and three dead, apparently killed by the live ones) and the dead white egg of *Metapsaenythia*. The vacated chorions of some of these larvae were visible in the cell wall. The open cell contained a single live egg inserted into the unlined part of the wall at the cell entrance. One end, protruding 0.2 mm into the lumen, appeared narrow and therefore may have been the egg's posterior end, but this orientation needs to be checked because anterior ends of nomadine eggs normally are at the cell surface. This egg was not inserted under a flap as reported by Rozen (1965a) and Hurd and Linsley (1972) for several other species of *Holcopasites*, but, like that of other *Holcopasites* and of *Nomada*, it was not cemented into the hole as is characteristic of some other genera of Nomadinae.

Removed from the fragment of cell wall by being placed in water, the translucent white egg was 0.5 mm long, 0.2 mm in maximum diameter. Its anterior end (as identified by the head capsule of the embryo) was broadly

rounded and the posterior end tapering. Its chorion was unsculptured, shiny, and transparent. A noteworthy feature was its small size, also reflected in the small size of the first instars. One first instar that had consumed no pollen was 0.8 mm long.

The two postdefecating larvae from the completed nest were totally quiescent, and at least one rested on its dorsum with its head pointed toward the cell closure. The feces were centered at the upper rear of the cell, but they covered more of the rear wall than did those of *Metapsaenythia*.

First instars possessed sclerotized, only faintly pigmented head capsules, sharp-pointed mandibles, and elongate labral tubercles, and they used the tip of the abdomen as a pygopod to push themselves along.

PSAENYTHIA

Claude-Joseph (1926) diagrammed and described the nest of *Psaenythia interrupta* Friese, and Janvier (1933) briefly mentioned its nest in conjunction with describing the mature larva.

Psaenythia annulata (Gerstaecker)

HABITAT: We found two nests of *Psaenythia annulata* at Furnas, Vila Velha, Paraná, Brazil (fig. 16), on February 9, 1974. They were a meter apart in a seldom-used earthen roadway that bordered a large grass area with numerous low-growing herbaceous plants. On the other side of the road were low trees far enough removed so as not to shade the site. Sparse plants grew on the roadway providing less than 50 percent coverage. The surface of the nesting site was sandy and sloped slightly; dry on the surface, the soil was moist immediately below. It was easily excavated, containing no rocks and only small roots.

NESTS: A single female and no males were associated with each nest. Neither nest was started near objects on the surface. The entrance of the first burrow was surrounded by a small loose tumulus, and its tunnel descended vertically to a depth of 6 cm where it ended. Filled with loose soil, the burrow presumably was in the early stage of construction.

The second burrow (fig. 9), with a concentric tumulus 2.0 cm in diameter, also descended vertically and was unfilled its entire length. Laterals, filled after cell closure, varied in length from 1 to 4 cm, and the one leading to an open cell descended slightly before reaching the cell.

Nearly horizontal cells (fig. 10), arranged singly and randomly around the burrow, had walls indistinguishable from the substrate. The inner wall surface was smooth and completely coated with a shiny, presumably waterproof lining. The closure was a spiral, concave on the inside. The uppermost cell was filled with soil.

PROVISIONING: Females transported pollen in a moist condition on their hind legs. Pollen-laden females visited a variety of plants, both at this locality and at others, suggesting the species may be polylectic. The open cell contained four irregular-shaped but nearly identical, compact, pollen-nectar masses deposited from the female's tibiae; thus the female had already made two foraging trips. Because I captured her returning with yet another load, she would have made at least three trips to provision the cell. Of the two completed pollen masses, one was a perfect sphere, 3.5 mm in diameter; the other was a flattened sphere, 3.75 mm high and with a horizontal diameter of 4.25 mm. Both were homogeneously mealy-moist, somewhat shiny, but without either a waterproof coating or a special layer of liquid on the outside. When they were removed, the cell floors were moist where they had rested toward the rear of the cells (fig. 10).

DEVELOPMENT: Two curved eggs were positioned slightly anterior of the top of the pollen masses in the plane of the long axis of the cell. More rounded on the anterior end than the posterior end, they were white and had a smooth shiny chorion. No larvae were recovered.

ADULT ACTIVITY: Because we observed males flying around flowers and not around nest entrances, we presumed that mating takes place on the flower.

CLEPTOPARASITISM: Rozen (1977b) has reported on the association of a species of *Brachynomada* near *argentina* Holmberg with the nesting site of this species.

POTENTIAL OF BIOLOGICAL FEATURES IN PHYLOGENETIC ANALYSIS OF THE PANURGINAE

Unless otherwise noted, biological data concerning the Panurginae referenced below come from the current study, Rozen (1958, 1965b, 1967 [summarizing all previous literature], 1968, 1970a, 1971a, 1988), my unpublished fieldnotes (mostly regarding South American and African genera), Eickwort (1977), Hirashima (1962), Rust (1976, 1988), Shinn (1967), and Torchio (1975).

The Andreninae, the other subfamily in the Andrenidae, is the obvious choice for out-group comparisons. It comprises only six disparate genera (in contrast to the approximately 35 genera [sensu Ruz, 1987] of the Panurginae): the huge, primarily Holarctic *Andrena*, the two small Nearctic *Megandrena* and *Ancylandrena*, and the three small Neotropical *Euherbstia*, *Orphana*, and *Alocandrena* (Rozen, 1971b; Michener, 1986). Whereas *Andrena* contains approximately 2000 species, the other genera together account for a mere 10 species. *Andrena* is the only genus about which there is available biological information. Nesting biologies of *Andrena* come from selected references, especially Packard (1889), Parker and Böving (1925), Malyshev (1926, 1935), Michener and Rettenmeyer (1956), Linsley and MacSwain (1956, 1959), Hirashima (1962), Stephen (1966), Youssef and Bohart (1968), Thorp and Stage (1968), Thorp (1969), Linsley, MacSwain, Raven, and Thorp (1973), Rozen (1973), Davis and LaBerge (1975), and Schrader and LaBerge (1978). There is also extensive literature dealing with flower relationships.

NUMBER OF FEMALES OCCUPYING A NEST: Nest occupancy by a single female is unquestionably plesiomorphic in the Apoidea. The apomorphic condition of nest sharing (i.e., composite nests) has developed a number of times among a few species of *Andrena*, *Cephalurgus anomalus*, *Psaenythia interrupta*, *Melitturga*, *Meliturgula*, *Poecilomelitta*, *Panurginus*, and certain groups of *Perdita*.

MALE NEST INHABITANTS: I have found megacephalic, small-eyed, flightless males (of

the same species as the females) in composite nests of two species of *Perdita*, *P. portalis* Timberlake and *P. mellea* Timberlake (not formerly reported in entomological literature); normal males (though exhibiting variability in head size) flew around flowers in the vicinity of the nests. Such striking male dimorphism is unknown elsewhere in the family and is an apomorphy of considerable interest both systematically and behaviorally. Males of other species of *Perdita* and of *Panurgus* show variability in head size suggesting that this phenomenon should be looked for in other species that nest communally.

DEPTH OF NESTS: This character is of limited use, partly because most of the nests studied are still incomplete so that the deepest cells are not yet constructed. Furthermore, very small bees tend to have shallower nests, and composite nests (containing numerous females) of *Andrena* and *Perdita* are generally deeper than nests of related bees containing only single females. Also, we can assume that bees that nest in very compact soil have a difficult time in constructing deep nests, so that depth of nests may depend to some extent on the nature of the substrate. Most *Andrena* bees have the lowest cells well below 15 cm. The "primitive" panurgines exhibit considerable variation in depth of nests (depth of lowest cell). However, the very shallow nests of *Liphanthus* are almost certainly derived, and the shallow nests of such bees as *Nomadopsis*, *Calliopsis*, and *Hypomacrotera* are therefore a separately derived synapomorphy.

TUMULI: Nest entrances of most *Andrena* species and all of the "primitive" panurgine genera treated here either lack tumuli or, if excavated soil is present, it surrounds but does not hide the entrance. The hidden entrances of *Andrena erythronii* Robertson (Michener and Rettenmeyer, 1956) and *A. vaga* Panzer (as *ovina* Klug) appear to be an evolutionary development separate from that in the Panurginae. In contrast to the plesiomorphic condition, entrances that are hidden by tumuli (or by loose surface sand or soil) are derived (*Nomadopsis*, *Calliopsis*, some *Hypomacrotera*, and related South American genera). Nests with such hidden entrances

have the main burrows clogged with loose soil (see below). Nests of some species seem to be devoid of any tumulus or, if soil is present, the nests are thought to be in early stages of construction. Entrances of most composite nests are without tumuli of any sort.

TURRETS: Panurgine nests are not known to have turrets, and such features are uncommon in *Andrena* species. However, conical, hardened turrets have been reported within tumuli of several species of *Andrena* (summarized by Youssef and Bohart, 1968). These structures may be the result of the female impregnating the tumulus with some liquid so that tumulus soil does not collapse into the entrance, possibly an indication of how the hardened cell walls are formed in *Andrena* and the "primitive" panurgines (see below). Turrets of this sort are clearly not behavioral homologs of those of *Anthophora* and the Emphorini (Anthophoridae). In the Andrenidae, these turrets at first appear as derived because of their uncommon occurrence. However, they raise the question as to whether *Andrena* and the "primitive" panurgines normally apply heretofore undetected stabilizing liquid (perhaps secretions or nectar) to burrow walls.

SPECIAL MAIN BURROW WALLS AND DIAMETERS: Special water-absorbent walls in main burrows of Old World *Panurginus* and *Melitturga* have been discussed by Rozen (1971a) and may be related to situations where the burrow diameters are not constant in a single nest, as in the narrowed entrances to the nests of *Pseudopanurgus f. timberlakei*. These are presumably apomorphic conditions and need further study.

MAIN BURROW FILL: Most *Andrena* species (but not *erythronii*, Michener and Rettenmeyer, 1956) and the "primitive" panurgines do not have the main nest tunnels filled with soil during nest construction and provisioning. Sometimes soil is encountered at the lower end of otherwise open tunnels and presumably is a result of cell construction. The plesiomorphic open condition is distinct from totally filled burrows, the apomorphic state seen in *Nomadopsis*, *Calliopsis*, *Hypomacrotera* and relatives. (Because my early studies on the "primitive" panurgines at the Southwestern Research Station [Rozen, 1967] were

often carried out at night, I confused nests closed for the night with the apomorphic condition of totally filled burrows; so far as I know, none of the "primitive" panurgines have filled burrows.)

BURROW SEPTA: Septa (thin partitions of soil blocking main tunnels) have been noted deep in the nests of some of the "primitive" panurgines (*Metapsaenythia*, *Protandrena bicolor*, and perhaps *Psaenythia interrupta*). This is presumably an apomorphic condition but needs further investigation.

FILLED LATERALS: Tunnels leading to closed cells are filled in almost all andrenid nests, certainly a plesiomorphic condition for the family. Hence open laterals (except for septa) of *Psaenythia interrupta* as reported by Claude-Joseph (1926), if true, are apomorphic.

NUMBER OF CELLS IN A NEST: Completed nests of almost all andrenids consist of a number of cells. Single-celled nests, known or suspected in several *Nomadopsis* species and one of *Perdita*, must be considered apomorphic. Because second and third nests of females of some *Andrena* (Michener and Rettenmeyer, 1956) are known to have reduced numbers of cells compared with first nests, an investigator must sample a number of nests before drawing conclusions about numbers of cells per nest for any andrenid.

ORDER OF CELL CONSTRUCTION: So far as is known, all panurgines have progressive nests; that is, the youngest cells are always deepest where there is only one female to a nest and cells are arranged singly. Literature accounts suggest the same is true for *Andrena* with the exception of *A. perplexa* Smith (Stephen, 1966). Nests of this species are regressive; the entire main burrow is constructed, and the lowest cell is the first built while subsequent cells are closer to the surface. Although progressive nests seem plesiomorphic for the family, more observations are required.

CELL ARRANGEMENT: Cells arranged singly rather than in linear series are generally found in *Andrena* (the "linear-branched" arrangement in nests of *A. bimaculata* [Kirby] is an interesting exception [Malyshev, 1926, 1935]) and in most of the Panurginae, and therefore are thought to be primitive. Linear series have been reported for four Japanese *Andrena*

species (Hirashima, 1962), but this reporting may be suspect because the author thought that such an arrangement was characteristic of the genus. End-to-end linear series of cells have been noted for several species of *Liphanthus*, one species of *Melitturga*, and *Nomadopsis helianthi* (Swenk and Cockerell), an indication that the apomorphic condition has arisen independently a number of times in the Panurginae.

CELL ORIENTATION: Most andrenids build cells that are nearly horizontal but tipped slightly toward the rear, the presumed primitive condition. Within some species (e.g., *Pseudopanurgus verticalis* Timberlake, *Pterosarus boylei* (Cockerell), and some *Andrena*) tilting may vary from 0 to 45°. Other species of *Andrena* have cells that uniformly tilt approximately 45°. In *Andrena perplexa* (Parker and Böving, 1925; Stephen, 1966) and *Psaeonnythia interrupta* (Claude-Joseph, 1926) cells are vertical, almost certainly a condition derived independently in each of these taxa.

CELL WALLS: Beneath the shiny cell linings of *Andrena*, the "primitive" panurgines, and some Old World genera, the immediate substrate tends to be harder than the surrounding substrate as a result of the female applying some substance to the soil. The literature is ambiguous as to whether this wall results from the female permitting a hardening liquid to soak into the soil, the soil and liquid being worked into a mixture that is cemented into a rough cavity, or some intermediate process taking place. Because I have been unable to detect a sharp line separating the cell wall from the substrate, I suspect that a female moistens the substrate with the hardening liquid and then tamps and rubs the softened soil with her pygidial plate to form a smooth surface. The source of the liquid needs to be determined (whether a secretion or nectar, and, if a secretion, from what gland or glands). The liquid is presumably different from the shiny material that coats and waterproofs the cell wall. Because the hard, thick cell walls of at least some *Protandrena*, *Pseudopanurgus*, and *Pterosarus* species resemble those of *Andrena*, conspicuous cell walls are thought to be plesiomorphic. The thinner, less conspicuous walls of *Perdita* and other more specialized panurgines are judged to be apomorphic. Unfortunately, detection of this

character depends on the hardness of the substrate, size of cells, and subjective judgment of the observer.

CELL LININGS: Conspicuous shiny waterproof cell linings that uniformly cover all inner surfaces of the cell except for the closure are characteristic of *Andrena* and the "primitive" panurgines dealt with here and therefore are primitive in the family. A reduction in the lining so that it is relatively inconspicuous or so that only the cell floor upon which the food mass rests is waterproof occurs in *Nomadopsis*, *Calliopsis*, *Hypomacrotera*, related South American genera and also *Perdita* and is a synapomorphy. So inconspicuous is the lining in some species in these genera that it can be easily overlooked although the cell wall has a smooth inner surface. Intermediate reduction of the cell lining has been documented for *Melitturgula* (Rozen, 1968). Reduction in cell lining in New World genera seems correlated with presence of a clear waterproof coating over the food mass (see below). The peculiar extra partial lining under the food mass of *Liphanthus alicahue* in addition to the conspicuous cell lining seems to be a unique apomorphy, although this feature should be analyzed in light of the "inner lining to the basal two fifths of the cell" of *A. perplexa* (Stephen, 1966).

TRANSPORTED PROVISIONS: Among the Andrenidae, there is considerable variation as to how and in what condition pollen is carried to the nests. For example, females of at least some *Andrena* carry pollen unmoistened on the trochanters, femora, and tibiae of the hind legs, in corbiculae on the propodeum, and attached to the ventral base of the metasoma. In the "primitive" panurgines, pollen is often carried in a moistened condition on the anterior surface of the hind tibiae, but, in some taxa, females on the foraging trip first apply dry pollen to their hind legs and then, before returning, cover the dry pollen with moist pollen. In some of the more specialized panurgines like *Nomadopsis* and *Calliopsis*, females transport very moist pollen in masses that surround the tibiae. This mode of transport is almost certainly an apomorphy, for it is not encountered in other bees and seems to be correlated with absence of keirotrichia on the posterior surfaces of the hind tibiae (Ruz, 1987). However, the mode of pollen

transport including body parts involved, plumes of scopal hairs, and wetness or dryness of the food seems so variable from one group of andrenids to the next that it is currently possible only to highlight this matter for further study.

FORMS OF EARLY DEPOSITS OF PROVISIONS: Females of the "primitive" panurgines, for which there are data, store the food from each foraging trip on the cell floor as irregular masses that are unshaped until the last load is brought into the cell. At least some species of the Old World genus *Meliturgula* (including *Poecilomelitta*) form the first loads into small spheres, as do all *Nomadopsis*, *Calliopsis*, *Hypomacrotera* species in North America and their South American relatives. Surprisingly, most reports on *Andrena* indicate that early loads of provisions are shaped into small spheres (with the possible exception of *A. regularis* Malloch [Schrader and LaBerge, 1978]). No Old World genera except for *Meliturgula* and *Poecilomelitta* are known to shape early food loads. This matter remains an unresolved conundrum.

FORMS OF COMPLETED PROVISIONS: Among the New World Panurginae, food masses are either spheres or flattened spheres (with their height less than their horizontal diameter). (In the Old World genus *Melitturga*, food masses of at least some species are longer than wide. Other Old World genera have either spheres or flattened spheres, so far as known.) In all of the "primitive" panurgines (which are New World), the masses are flattened spheres (except for the smaller of the two food masses of *Psaenythia annulata*). In many species of *Andrena* food masses are flattened spheres, but in some species the top of the food mass is hollowed (cratered) and in still others the upper and lower halves of the food masses are strongly asymmetrical. Because neither of these situations is found in the Panurginae, the simple flattened sphere, found in both subfamilies, is believed plesiomorphic in the "primitive" panurgines; complete spheres, found in *Perdita*, *Nomadopsis*, *Calliopsis*, *Hypomacrotera*, and their South American relatives, apparently represent the derived condition. However, it should be noted that Hirashima (1962) found provisions of *Andrena knuthi* Alfken to be "quite spherical."

CONSISTENCY AND COATING OF STORED

PROVISIONS: Provisions of most panurgines are homogeneously moist and firm, but in some *Protandrena*, *Pseudopanurgus*, and *Pterosarus* species provisions are very moist on the outside and dry inside. Those of *Cephalurgus* are sticky and very moist throughout. Although of potential phylogenetic value, such data are still too incompletely understood for use. On the other hand, clear, plasticlike, waterproof coatings on provisions of most *Perdita*, *Nomadopsis*, *Calliopsis*, *Hypomacrotera*, and South American allies are certainly a unique synapomorphy, in contrast to uncoated provisions of the "primitive" panurgines, the Old World panurgine genera, and *Andrena*.

POSITION OF PROVISIONS IN CELL: Some variation exists as to where females place fully formed food masses in their cells, but precise placements are difficult to observe and therefore data are incomplete. Positioning food masses toward the rear end of cells seems to be characteristic of most panurgines and *Andrena* and is presumably the plesiomorphic condition. Food masses applied to the very rear of the cell, as in some *Panurginus*, is almost certainly a derived feature.

POSITIONS OF EGGS: Panurgine eggs (including those of the "primitive" panurgines) are usually found on the top of food masses, as also has been reported for *Andrena* and for many other bees with shaped food masses. Hence, other placements such as the rear (*Perdita*) or front (some *Panurginus*) of the food mass are believed to be apomorphies.

LARVAL AMBULATIONS: Of all the panurgines whose nests have been studied, only larval *Panurginus* apparently is capable of crawling over its food mass during feeding. All others sit on top of provisions and (except perhaps for *Cephalurgus*) reorient when they have attained the last larval stage, presumably by crawling with their projecting dorsal body tubercles. Repositioned on their dorsa, the larvae then consume the remaining food. Some *Panurgus* apparently move the front part of their bodies back and forth as they feed, a condition perhaps intermediate between the typical panurgine feeding behavior and that of *Panurginus* (Rozen, 1971a). Unfortunately outgroup comparisons have yet to be made to determine the polarity of this character.

PLACEMENT OF FECES: Scanty reports in-

dicate that *Andrena* either places its feces at the upper rear or lower rear of the cell. All panurgines except for most *Perdita* apply their feces to the upper rear of the cell, the plesiomorphic condition for the subfamily. All known *Perdita* except for *P. portalis* cradle the feces on their venter, a unique apomorphy among bees.

VOLTINISM: Some of the "primitive" panurgines studied have one generation per year (*Protandrena*, *Pseudopanurgus*, *Heterosarus*) whereas others are suspected or known to have more than one (*Lipanthus*, *Cephalurgus*). Elsewhere in the Panurginae both univoltine and multivoltine taxa are known. The value of this character for phylogenetic interpretation is questionable because we do not know whether internal factors, external factors, or both control voltinism. Furthermore, although most *Andrena* are single brooded, double broods have been reported for a number of species (see Linsley, 1937).

DIAPAUSING LARVAE: All panurgines spend the winter as larvae, and most overwintering larvae are totally quiescent. However, larvae of *Metapsaenythia* and at least some *Protandrena*, *Pseudopanurgus*, and *Meliturgula* curl and uncurl slowly in a semidiapause. Furthermore some *Pseudopanurgus* overwinter as predefecating, nondiapausing larvae. Out-group comparisons with *Andrena* are probably invalid because *Andrena* species overwinter as adults (with the possible exception of *A. accepta* Viereck [Rozen, 1973]) that are not in a physiological diapause. Perhaps studies of other genera of Andreninae will establish the polarity of these features.

MATING BEHAVIOR: Patterns in panurgine bees have been studied only in a few cases but, if better documented, appear to be potentially useful for phylogenetic analysis. Certainly the ability of some *Perdita* females to forage while in copula is apomorphic as is the ability of paired couples of some *Perdita* and of the species of the subgenus *Nomadopsis* to fly from flower to flower and to their nesting sites. However, there are undoubtedly many different aspects of mating behaviors that need to be factored before they can be studied.

CUCKOO BEE ASSOCIATES: The associations between taxa of nomadine cleptoparasitic bees and their andrenid host taxa reveal interesting, complex, and presently inexplicable pat-

terns. As one example: Species of *Holcopasites* are nest parasites of species of the "primitive" panurgine genera *Heterosarus*, *Pseudopanurgus*, *Metapsaenythia*, and almost certainly *Pterosarus*. However, all but one other *Holcopasites* attack the *Calliopsis* subgenera *Calliopsis*, *Calliopsima*, *Verbena-*
pis, but none of the subgenera assigned to *Nomadopsis* even though Ruz's (1987) analysis suggests that *Nomadopsis*, *Calliopsis*, and *Hypomacrotera* should be combined into a single genus. A single species, *Holcopasites illinoiensis minimus* (Linsley), is associated with *Hypomacrotera callops* Cockerell and Porter. On the other hand, all subgenera of *Nomadopsis* host *Oreopasites*, as does *Hypomacrotera subalpinus* (Cockerell) and several species of *Perdita*. No *Oreopasites* has been associated with *Calliopsis* as formerly identified or any of the "primitive" panurgines even though they are sympatric. More data may help.

BIOLOGICAL PROFILE OF THE ANDRENIDAE

The format of this summary follows previous accounts of the biologies of higher bee taxa: Fideliinae (Rozen, 1977a), Diphaglossinae (Rozen, 1984a), and Exomalopsini (Rozen, 1984b). Preliminary in nature, it is based on literature cited above, data presented above, and unpublished fieldnotes.

NESTING: Family distributed worldwide (except for Australia); ground nesting species, abundant in temperate and in warm-arid regions. Body size minute to moderately large, but mostly small. All species nonsocial, non-cleptoparasitic; most species noncommunal but some in composite nests and many others nesting in irregular aggregations. Nesting surfaces usually horizontal or nearly so, but sometimes sloping, rarely vertical; usually in sunny areas. Substrate generally moderately firm, with or without stones and roots, but extremely variable from soft sand to sandstone. Nests shallow to moderately deep (ca. 1 m), apparently mostly progressive but at least one regressive. Nest pattern (of noncommunal species) consisting of main tunnel and radiating short and long laterals leading to cells, usually at various depths. Entrances of noncomposite nests usually with tumuli of loose soil, rarely with conical turrets embed-

ded in tumuli; entrances of composite nests normally without tumuli; entrances either open during foraging or, in some taxa, hidden by tumuli (or completely obscured by loose surface soil). Main burrow almost always circular in cross section, with walls nonwaterproof, generally rougher than cell walls, rarely with special wall; main burrow nearly straight to strongly meandering, shallow or deep; burrow mostly open or soil-filled during provisioning depending on taxon; burrows of some taxa with thin septa of soil at various depths. Laterals leading to closed cells soil-filled except for those of *Psaenythia interrupta*. Nests usually but not invariably with a number of cells, in most species arranged singly, but in some arranged in short linear series; cells of most species nearly horizontal but inclined slightly, usually toward rear; some species with cells variable in inclination (but rear end always lower than front) from nearly horizontal to inclined 45°; others with cells more or less consistently inclined 45°; still others with cells vertical. Cells elongate-oval with maximum diameter greater than diameter of lateral, rounded at the rear, apparently usually nearly symmetrical around longitudinal axis, but in some large species cell ceiling more vaulted than cell floor. Cell walls (i.e., ceiling, sides, floor, and rear, but not closure; the cell lining, a secreted film that the female applies to the walls, is considered a separate structure, described below) usually smooth, though pygidial embossings visible in some species; walls of some taxa thick and harder than substrate, of other taxa thin and only slightly harder than substrate, of still others smooth on the inside but otherwise undifferentiated from substrate; except for hardness, cell walls indistinguishable and not sharply defined from substrate. Cell linings of some taxa shiny, waterproof, transparent, covering all of cell surfaces except closures; linings of other taxa less conspicuous, often reduced, and on some species detectable only as a waterproof area restricted to cell floor where food mass rests (contrary to earlier accounts [Rozen, 1967], at least the lower rear of *Perdita* cells are waterproof even though a lining is not visible); lining material presumably glandular. Cell closures invariably concave spiral on the inner surface with three to seven coils; outer surface usually not detectable, but

concave smooth surface in a few cases; inner surface not lined with waterproofing secretion.

PROVISIONING: Foraging females either depositing early pollen or pollen/nectar loads from hind legs as unshaped masses on floor of cell until entire provisions of cell are gathered, or shaping early loads into small moist spheres, depending on taxon. Completed provisions shaped into flattened sphere, flattened sphere with depression on top, complete sphere, flattened radially symmetrical mass with the top half not symmetrical with bottom half, or somewhat elongate spheroid; provisions often mealy, firm, and homogeneous, sometimes very moist on outside and nearly dry and fluffy on inside, other times very moist (almost semiliquid), depending on taxon; provisions of some taxa (always those that have spherical food masses) coated with shiny transparent waterproof substance perhaps of same material as cell lining. Food mass normally placed on cell floor toward rear, sometimes near middle of floor, and rarely at very rear of cell; mass resting unattached to cell floor, sometimes attached to floor by small amount of liquid (nectar?), sometimes droplets of liquid (nectar?) visible on cell wall, and rarely (in some *Andrena*) mass surrounded by liquid reported to be nectar. Food masses of most species not undergoing extensive liquefaction before being consumed, but liquefaction reported in some *Andrena*.

DEVELOPMENT: Slender, curved, white, shiny egg without reticulated chorion, one to a cell, often placed on top of provisions, either attached by posterior end or by both ends, in sagittal plane of cell; in some taxa eggs placed somewhat behind food masses, in others somewhat toward or on front. Young larvae of all panurgines except some *Panurginus* remaining stationary on top of food masses while they feed until reaching last instar; on reaching last stadium, larvae (with possible exception of *Cephalurgus*) reorienting and then, while resting on dorsal tubercles, feeding on remaining food held on their venters; young *Panurginus* larvae capable of crawling around food mass as they feed. Feeding activities of andrenines unknown. Defecation taking place only after all food consumed. Feces applied to upper rear wall of cell (all

panurgines except *Perdita* and one *Andrena*), to lower rear of cell (reported for a few *Andrena*), or held on venter (most *Perdita*). Cocoons not constructed in any species. Species overwintering as mature diapausing, totally quiescent, postdefecating larvae (most panurgines), as mature semidiapausing postdefecating larvae (in *Protandrena*, *Metapsaenythia*, *Pseudopanurgus*, and *Meliturgula*), as predefecating mature larvae (in *Pseudopanurgus*), or as adults (most if not all *Andrena*).

ADULT ACTIVITY: Bees primarily diurnal, mostly active in late morning and early afternoon; few species (some larger forms) early matinal, active in late afternoon, or vespertine (crepuscular). Bees usually univoltine, but some species with more than one brood per year; adult activity very early spring to mid-fall, depending on taxon. Species monolectic, oligolectic, or narrowly polylectic. Mating behaviors extremely variable.

CLEPTOPARASITIC BEES: Nests of many taxa attacked by many groups of species-specific or genus-specific Nomadinae (Neolarrini, Holcopasitini, Ammobatini, Ammobatoidini, and Nomadini) and infrequently by *Sphecodes* (Halictidae), but not by other cleptoparasitic bees, so far as is known.

REFERENCES

- Chandler, L.
1962. Notes on the species of *Psaenythia* (Hymenoptera: Andrenidae) in the eastern United States. J. Kansas Entomol. Soc. 35: 313-314.
- Claude-Joseph, F.
1926. Recherches biologiques sur les hyménoptères du Chili (Mellifères). Ann. Sci. Nat., Zool., ser. 10, 9: 113-268.
- Danforth, B. N., and C. D. Michener
1988. Wing folding in the Hymenoptera. Ann. Entomol. Soc. Am. 81: 342-349.
- Davis, L. R., Jr., and W. E. LaBerge
1975. The nest biology of the bee *Andrena* (*Ptilandrena*) *erigeniae* Robertson (Hymenoptera: Andrenidae). Illinois Nat. Hist. Surv., Biol. Notes 95: 16 pp.
- Ehrenfeld, J., and J. G. Rozen, Jr.
1977. The cuckoo bee genus *Kelita*, its systematics, biology, and larvae. Am. Mus. Novitates 2631: 24 pp.
- Eickwort, G. C.
1977. Aspects of the nesting biology and descriptions of immature stages of *Perdita octomaculata* and *P. halictoides* (Hymenoptera: Andrenidae). J. Kansas Entomol. Soc. 50: 577-599.
- Fries, H.
1916. Neue Bienen-Arten aus Chile und Südamerika. Stettiner Entomol. Ztg. 77: 163-174.
- Hicks, C. H.
1931. Notes on certain bees, with a consideration of the use of the abdomen in nest construction. Canadian Entomol. 63: 173-178.
1936. Nesting habits of certain western bees. Canadian Entomol. 68: 47-52.
- Hirashima, Y.
1962. Systematic and biological studies of the family Andrenidae of Japan (Hymenoptera, Apoidea). Part I. Biology. J. Fac. Agric., Kyushu Univ. 12: 22 pp.
- Hurd, P. D., Jr., and E. G. Linsley
1972. Parasitic bees of the genus *Holcopasites* Ashmead (Hymenoptera: Apoidea). Smithsonian Contrib. Zool. 114: 41 pp.
- Janvier, H.
1933. Etude biologique de quelques hyménoptères du Chili. Ann. Sci. Nat., Zool., ser. 10, 16: 209-356.
- Linsley, E. G.
1937. The occurrence of double broods in North American andrenid bees (Hymenoptera). Bull. Brooklyn Entomol. Soc. 32: 125-127.
- Linsley, E. G., and J. W. MacSwain
1956. Further notes on the taxonomy and biology of the andrenine bees associated with *Oenothera* (Hymenoptera: Andrenidae). Pan-Pac. Entomol. 32: 111-121.
1959. Ethology of some *Ranunculus* insects with emphasis on competition for pollen. Univ. Calif. Publ. Entomol. 16: 46 pp.
- Linsley, E. G., J. W. MacSwain, P. H. Raven, and R. W. Thorp
1973. Comparative behavior of bees and Onagraceae. V. *Camissonia* and *Oenothera* bees of cismontane California and Baja California. Univ. Calif. Publ. Entomol. 71: 68 pp.
- Malyshev, S.
1926. The nesting habits of *Andrena* F. (Hym., Apoidea). Trudy Leningradskogo Obshchestva Ectestvoispytatelei 56(2): 25-78.
1935. The nesting habits of solitary bees. A comparative study. Eos, Rev. Españ. Entomol. 11: 201-309.

- Michener, C. D.
1986. New Peruvian genus and a generic review of Andreninae (Hymenoptera: Apoidea: Andrenidae). *Ann. Entomol. Soc. Am.* 79: 62–72.
- Michener, C. D., and C. W. Rettenmeyer
1956. The ethology of *Andrena erythronii* with comparative data on other species (Hymenoptera, Andrenidae). *Univ. Kansas Sci. Bull.* 37: 645–684.
- Mitchell, T. B.
1960. Bees of the eastern United States. *North Carolina Agric. Exp. Stn., vol. 1, Tech. Bull.* 141: 538 pp.
- Packard, A. S.
1889. Guide to the study of insects and a treatise on those injurious and beneficial to crops for the use of colleges, farm-schools, and agriculturists. New York: Henry Holt, xii + 715 pp.
- Parker, J. B., and A. G. Böving
1925. The blister beetle *Tricrania sanguinipennis* — biology, descriptions of different stages, and systematic relationship. *Proc. U.S. Natl. Mus.* 64(2513), art. 23: 1–40.
- Pierce, W. D.
1904. Some hypermetamorphic beetles and their hymenopterous hosts. *Univ. Nebraska Stud.* 4: 150–190.
- Rozen, J. G., Jr.
1958. Monographic study of the genus *Nomadopsis* Ashmead (Hymenoptera: Andrenidae). *Univ. Calif. Publ. Entomol.* 15: 202 pp.
- 1965a. Biological notes on the cuckoo bee genera *Holcopasites* and *Neolarra* (Hymenoptera: Apoidea). *J. New York Entomol. Soc.* 73: 87–91.
- 1965b. The biology and immature stages of *Melitturga clavicornis* (Latreille) and of *Sphecodes albilabris* (Kirby) and the recognition of the Oxaeidae at the family level (Hymenoptera, Apoidea). *Am. Mus. Novitates* 2224: 18 pp.
1967. Review of the biology of panurgine bees, with observations on North American forms (Hymenoptera, Andrenidae). *Am. Mus. Novitates* 2297: 44 pp.
1968. Biology and immature stages of the aberrant bee genus *Melitturgula* (Hymenoptera, Andrenidae). *Am. Mus. Novitates* 2331: 18 pp.
- 1970a. Biology and immature stages of the panurgine bee genera *Hypomacrotera* and *Psaenythia* (Hymenoptera, Apoidea). *Am. Mus. Novitates* 2416: 16 pp.
- 1970b. Biological observations on the parasitic bee *Kelita* (Hymenoptera: Apoidea). *J. New York Entomol. Soc.* 78: 146–147.
- 1971a. Biology and immature stages of Moroccan panurgine bees (Hymenoptera, Apoidea). *Am. Mus. Novitates* 2457: 37 pp.
- 1971b. Systematics of the South American bee genus *Orphana* (Hymenoptera, Apoidea). *Am. Mus. Novitates* 2462: 15 pp.
1973. Biology notes on the bee *Andrena accepta* Viereck (Hymenoptera, Andrenidae). *J. New York Entomol. Soc.* 81: 54–61.
- 1977a. The ethology and systematic relationships of fideliine bees, including a description of the mature larva of *Parafieldia*. *Am. Mus. Novitates* 2637: 15 pp.
- 1977b. Immature stages of and ethological observations on the cleptoparasitic bee tribe Nomadini (Apoidea, Anthophoridae). *Am. Mus. Novitates* 2638: 16 pp.
- 1984a. Nesting biology of diphaglossine bees (Hymenoptera, Colletidae). *Am. Mus. Novitates* 2786: 33 pp.
- 1984b. Comparative nesting biology of the bee tribe Exomalopsini (Apoidea, Anthophoridae). *Am. Mus. Novitates* 2798: 37 pp.
1988. Ecology, behavior, and mature larva of a new species of the Old World bee genus *Camptopoeum* (Andrenidae: Panurginae). *Am. Mus. Novitates* 2925: 12 pp.
- Rust, R. W.
1976. Notes on the biology of North American species of *Panurginus* (Hymenoptera: Andrenidae). *Pan-Pac. Entomol.* 52: 159–166.
1988. Biology of *Nomadopsis larreae* (Hymenoptera: Andrenidae), with an analysis of yearly appearance. *Ann. Entomol. Soc. Am.* 81: 99–104.
- Ruz, L.
1987. Classification and phylogenetic relationships of panurgine bees (Hymenoptera—Andrenidae). Ph.D. thesis, Univ. Kansas.
- Ruz, L., and H. Toro
1983. Revision of the bee genus *Liphanthus* (Hymenoptera: Andrenidae). *Univ. Kansas Sci. Bull.* 52: 235–299.
- Schrader, M. N., and W. E. LaBerge
1978. The nest biology of the bees *Andrena (Melandrena) regularis* Malloch and *Andrena (Melandrena) carlini* Cockerell (Hymenoptera: Andrenidae). *Illinois Nat. Hist. Surv., Biol. Notes* 108: 3–24.

- Shinn, A. F.
1967. A revision of the bee genus *Calliopsis* and the biology and ecology of *C. andreniformis* (Hymenoptera, Andrenidae). Univ. Kansas Sci. Bull. 46: 753–936.
- Stephen, W. P.
1966. *Andrena* (*Cryptandrena*) *viburnella*. I. Bionomics. J. Kansas Entomol. Soc. 39: 42–51.
- Thorp, R. W.
1969. Systematics and ecology of bees of the subgenus *Diandrena* (Hymenoptera: Andrenidae). Univ. Calif. Publ. Entomol. 52: 146 pp.
- Thorp, R. W., and G. I. Stage
1968. Ecology of *Andrena placida* with descriptions of the larva and pupa. Ann. Entomol. Soc. Am. 61: 1580–1586.
- Timberlake, P. H.
1969. *Metapsaenythia*, a new panurgine bee genus (Hymenoptera, Andrenidae). Entomol. News 80: 89–92.
- Torchio, P. F.
1975. The biology of *Perdita nuda* and descriptions of its immature forms and those of its *Sphecodes* parasite (Hymenoptera: Apoidea). J. Kansas Entomol. Soc. 48: 257–279.
- Warncke, K.
1985. Beiträge zur Bienenfauna des Iran 19.–20. Die Gattungen *Panurgus* Pz. und *Meliturgula* Fr. (Hymenoptera, Apidae). Boll. Mus. Civ. Stor. Nat. Venezia 34(1983): 221–235.
- Youssef, N. N., and G. E. Bohart
1968. The nesting habits and immature stages of *Andrena* (*Thysandrena*) *candida* Smith (Hymenoptera, Apoidea). J. Kansas Entomol. Soc. 41: 442–455.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates*, *Bulletin*, and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.