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Biology of the Bee *Ancylandrena larreae* (Andrenidae: Andreninae) and its Cleptoparasite *Hexepeolus rhodogyne* (Anthophoridae: Nomadinae) with a Review of Egg Deposition in the Nomadinae (Hymenoptera: Apoidea)

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ABSTRACT

A nest of the solitary communal ground-nesting bee *Ancylandrena larreae* Timberlake is described, the first such account for any genus in the Andreninae except for *Andrena*. Included are nest architecture, brood-cell structure and closure, provisioning, and egg deposition. These features are compared with those of other andrenids. In most respects the nesting biology of *Ancylandrena* is similar to that of *Andrena*.

Eggs of the cleptoparasitic bee *Hexepeolus rhodogyne* Linsley and Michener were recovered from the *Ancylandrena* nest, confirming the suspected association of host and parasite. A dissected *Hexepeolus* female contained a total of 20 ovarioles and 9 mature oocytes and had an egg index of 0.48. The *Hexepeolus* eggs and dissected oocytes are described. The method of oviposition in the wall of the *Ancylandrena* cell is explained and discussed in a review of egg deposition in the Nomadinae.

INTRODUCTION

The large bee family Andrenidae, found on all continents except Australia and Antarctica, currently consists of two subfamilies, the Andreninae and Panurginae. The Andreninae contains only 6 genera (Michener, 1986). *Andrena* is speciose with perhaps 1200 species confined mostly to the Holarctic region (LaBerge, 1986). The other 5 genera are represented by 10 species known from the southwestern United States, Peru, and Chile (Michener, 1986). In contrast, the Panurginae, with somewhat fewer species, conser-

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vatively consists of 35 genera, 11 of which are Old World; 23 New World; and 1 both Old and New World (Ruz, 1987). The nesting biology and other aspects of the behavior and ecology of the Panurginae have received considerable attention in recent years (see Rozen, 1989b, for references). The Andreninae are relatively poorly investigated in that data have been published on the nesting biology of only one genus, *Andrena* (Batra, 1990; Miliczky, 1988; and references therein). Information on the nesting activities of *Ancylandrena larreae* Timberlake is presented here to contribute to our understanding of the biology of the Andreninae.

Hexepeolus has long been suspected of parasitizing nests of *Ancylandrena* (Michener, 1944), and the discovery of its eggs in the nest of *A. larreae* confirms this association. *Hexepeolus rhodogyne* Linsley and Michener is the only species recognized in the genus (Gingras, 1983), and its tribal assignment within the Nomadinae remains unsettled, as discussed below. We can hope that the eventual discovery of its immature stages will shed light on its phylogenetic relationships and tribal placement. The discovery and description of the egg of *H. rhodogyne* have led to a review of the eggs and oviposition habits of nomadine bees, presented below. Although our knowledge about these matters is still fragmentary, some generalizations are drawn, and we hope this review will encourage others to gather additional and more complete data.

ACKNOWLEDGMENTS

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BIOLOGY OF *ANCYLANDRENA LARREAE*

The single nest of *Ancylandrena larreae* was discovered and studied in Yavapai Co., Arizona, at 8 mi northwest of Wickenburg, Maricopa Co., on May 9, 1991. The site had first been identified in the spring of 1990 when Rozen and McGinley (1991) investigated the biology of *Hesperapis larreae* Cockerell and its cleptoparsite, *Townsendiella pulchra* Crawford, and found *Hexepeolus* females searching the ground for host nests. I returned on April 24, 1991, and again on April 30, at which times neither *Ancylandrena* nor its cleptoparasite were evident, in spite of the fact that *Larrea tridentata,* the pollen source of *A. larreae,* was blooming. When I visited the site on May 8 and 9 (warm and clear days), the creosote bushes were still in abundant bloom with many flower buds yet to open and no more than 10 percent of the blossoms having gone to seed, and adults of *Hexepeolus* were fairly common. The previous visits to this site had apparently preceded the active nesting period of *Ancylandrena.*

Description of Site: Creosote bushes (*Larrea tridentata*) dominated the area that extended over many kilometers, and *Acacia greggii* and *Prosopis* occurred along draws. Grasses and other low-growing herbs sparsely dotted openings between the creosote bushes (fig. 1), and occasional small clumps of *Sphaeralcea* were also present. Because only a single nest was found, the dimensions of the potential nesting area can only be estimated by the occurrence of *Hexepeolus* females searching for host nests. Almost all were observed on a gently sloping (approximately 10° from horizontal) surface at one end of a more grassy horizontal savanna with sparsely spaced creosote bushes. *Hexepeolus* females were most abundant in an area approximately 100 m long and 20 m wide, although only the horizontal savanna offered a clear boundary on one side. Because of the extensive distribution of creosote bushes, other concentrations of *Hexepeolus* and its hosts might well have existed in adjoining areas.

Other bees present were *Hesperapis larreae* and its cleptoparasite *Townsendiella pulchra*; *Trachusa* (*Heteranthidium*) *larreae* (Cockerell); *Epeolus mesillae* (Cockerell) (identified by R. W. Rust) (but its presumed host *Colletes* was not collected); *Triepeolus* sp. and a confirmed host, *Melissodes lutulenta* LaBerge (identified by W. E. LaBerge); *Anthidium* sp.; and *Dioxys productus subruber* (Cockerell). No *Ancylandrena larreae* adults were seen on the creosote bush flowers although little time was spent looking for them. The only two specimens seen and collected came from the nest itself.

The nest entrance was near the center of an open space between creosote bushes where the unshaded ground was sparsely covered with scattered low-growing herbs (fig. 1). The soil surface was fine-textured with scattered small pebbles, and the subsurface soil was moderately fine and easily excavated.

The *Ancylandrena* nest was identified because it was one of several potential nest entrances that arrested the wandering flight of *Hexepeolus* females. All such openings were covered with inverted plastic drinking glasses.

Description of Nest: The entrance (fig. 2), in the open and unshaded, was not surrounded by tumulus. Approximately 4.5 mm in diameter, it was irregular and appeared to be an emergence hole because it lacked a smooth, worn edge, typical of an entrance actively being used by foraging bees. Because there had been no precipitation to create a surface crust, the irregularity of the entrance is unexplained. The tunnel beneath penetrated the surface obliquely for less than 2 cm where it widened to about 10 mm in diameter (fig. 3). It ran to a depth of about 4 cm at which point a short vestibule about 2 cm long extended obliquely downward. Below the vestibule the tunnel, still open, narrowed to approximately 5 mm in diameter and twisted and curved downward to a depth of approximately 18 cm at which point it curved outward and downward to its lowest point, about 26 cm. I encountered a short tunnel (not shown in fig. 3) just before the burrow reached the lowest level. This tunnel was questionably connected with the main tunnel, and, because it seemed slightly flattened in cross-section, it may have been a termite gallery. At the lowest level, the *Ancylandrena* tunnel branched, with one branch seeming to end blindly after extending briefly downward 5 cm. This short branch may have ended because of an obstruction, but could possibly have been a mostly filled tunnel leading to a cell which would have been destroyed by my excavation. (When I found it, I was unaware of the extensive length of the tunnel leading to the two discovered cells.) The second branch, completely open and still 5 mm in diameter, curved horizontally under the upper part of the nest and then began to ascend gradually. Its direction was more or less straight for 20 cm from the lowest point; it then angled (not visible in fig. 3) and continued its ascent in a somewhat different direction. Shortly thereafter it forked with one ascending branch ending in a closed cell about 33 cm from the nest's lowest point and the second branch ending in an open cell 41 cm from the lowest point. The closed cell was at a depth of 23 cm, and the open cell at 18 cm. The unusual features of the nest architecture were the long ascending open tunnel leading to cells and the lateral extent of the nest compared with its shallowness.

Tunnel walls were unconsolidated (except immediately before the cells), rather smooth, and unlined. Although not tested with a water droplet, they were almost certainly water absorbent.

The two burrows leading to cells started to widen approximately 1 cm in front of the narrowest part of the cell openings to maximum diameters of 6.0 and 7.0 mm, then narrowed again to 5.0 mm at the cell entrances. The widened portion of each burrow formed an antechamber whose consolidated walls were extensions of the cell walls. The hardened walls of the antechambers and cells were 1–2 mm thick. Their outer surface consisted of fine soil as well as larger pebbles 2–3 mm in diameter. The inner surface, lacking pebbles, was composed solely of fine soil. This even-grained texture indicates that the *Ancylandrena* female separates fine and coarse soil particles during cell construction. The inner surfaces of the antechamber and cell were identically smooth—smoother than the tunnel walls leading to the antechamber. However, they differed in that the antechamber of at least the open cell was immediately absorbent to water droplets, whereas the cell wall was waterproof except for the first several millimeters, inside the entrance. The inner surface of the cell was also faintly shiny (visible under high magnification), indicating a transparent lining that was almost certainly responsible for the waterproofing.

The closed cell (fig. 4) demonstrated that the antechamber became part of the 1 cm-long cell closure after egg deposition. A spiral septum closed the narrowest part of the cell entrance. Its inner surface, slightly concave, consisted of a distinct spiral of four coils made from uniformly fine-grained soil containing

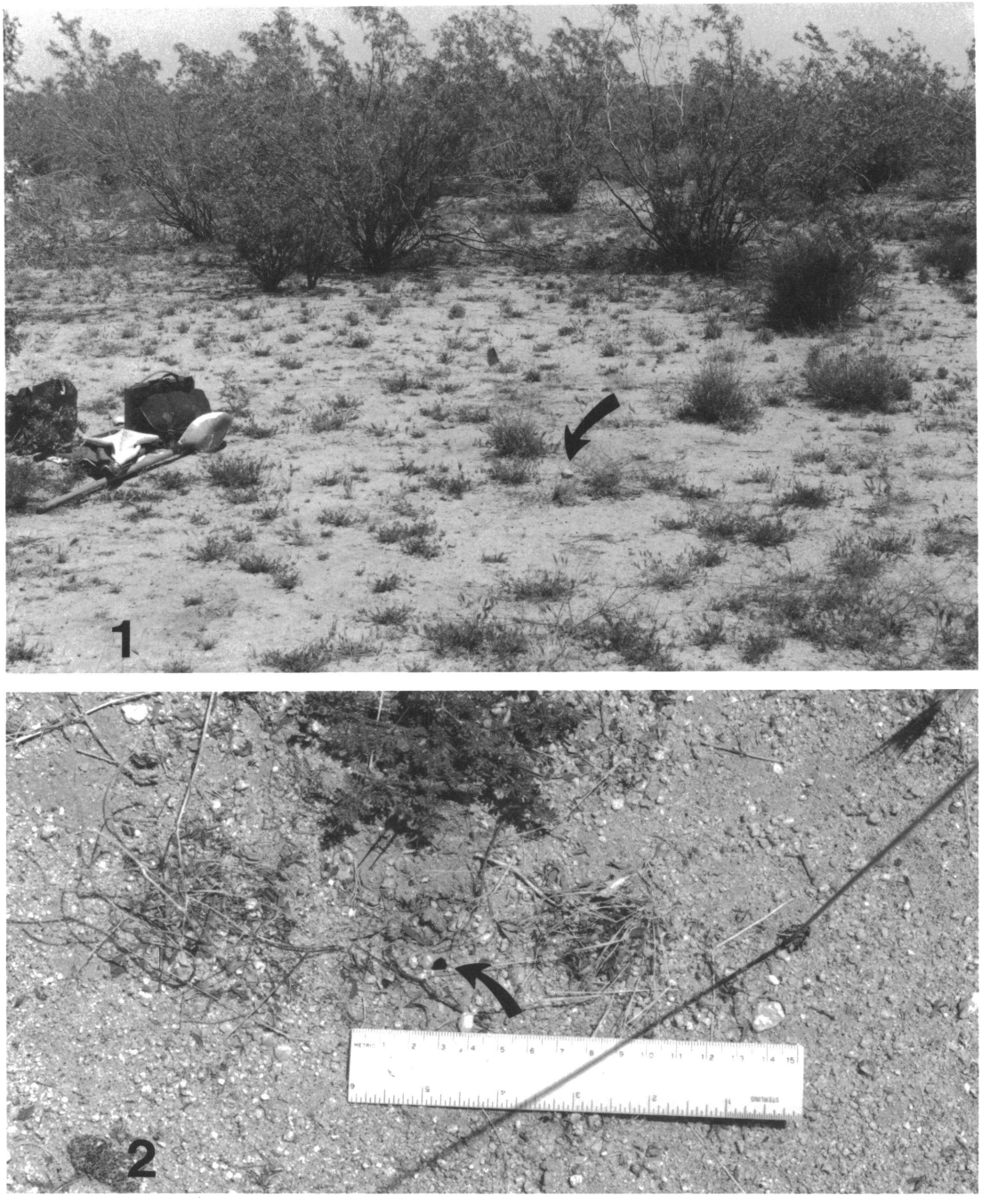
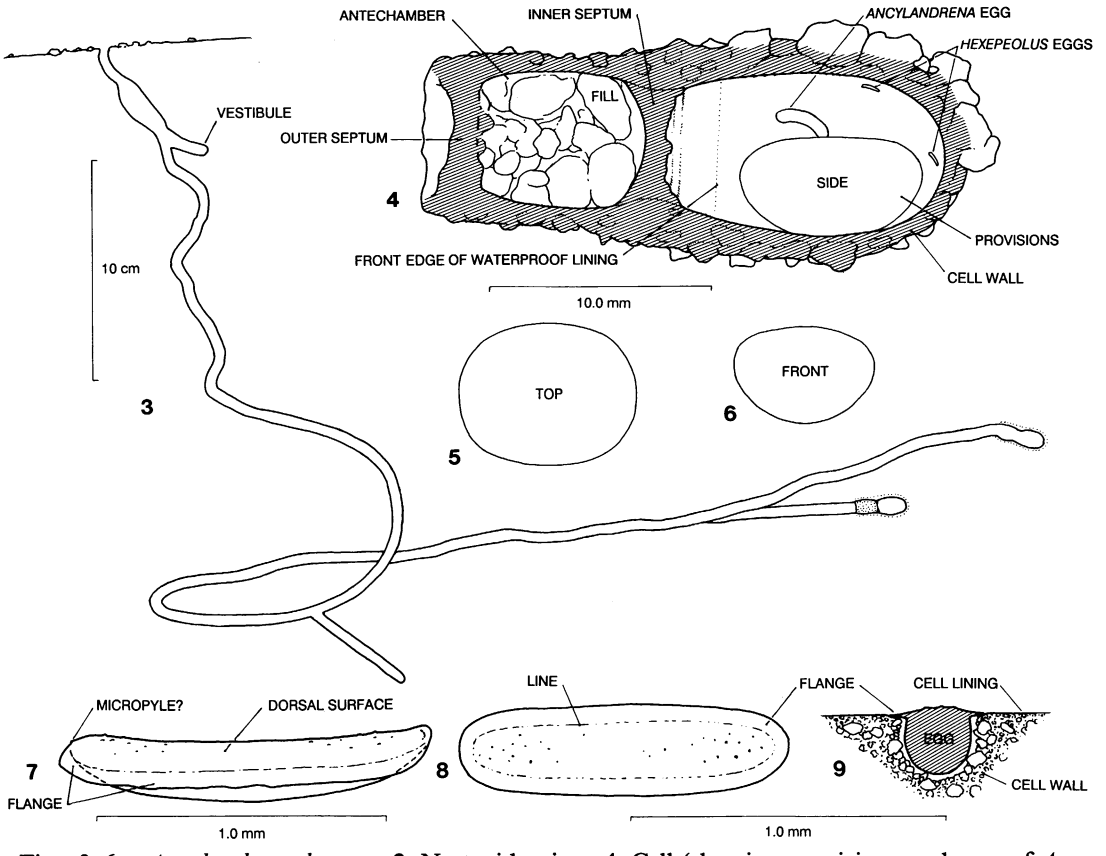


Fig. 1. Nesting area of *Ancylandrena larreae,* 8 mi northwest of Wickenburg, Maricopa Co., Arizona. Nest entrance location identified by arrow. Fig. 2. Nest entrance of *Ancylandrena larreae.* Note lack of tumulus.

no pebbles. Its outer surface was concave and smooth. The septum was about 1 mm thick at the middle but wider at the periphery. After making this seal, the female packed the antechamber with larger pebbles and some fine-grained soil, resulting in an antechamber



Figs. 3–6. *Ancylandrena larreae.* **3.** Nest, side view. **4.** Cell (showing provisions and eggs of *Ancylandrena* and *Hexepeolus rhodogyne*) and cell closure, side view. **5, 6.** Provisions, top and front views. Figs. 7–9. *Hexepeolus rhodogyne.* **7.** Oocyte, lateral view. **8, 9.** Diagrams of egg, dorsal and cross-sectional views. Scale lines refer to figures 3, 4–6, 7, and 8 and 9, respectively.

filled with material that was less consolidated than the walls of the cell and antechamber. Lastly, the female constructed an outer septum, concave and rough on the outside, that had an inner surface seemingly cemented to the pebbles filling the chamber. The outer septum was water absorbent.

The closed cell was more or less horizontal, its exact orientation obscured because I excavated it intact with surrounding soil. The open cell, also nearly horizontal, tilted to the rear about 20°. The inner dimensions of the closed cell were 12.0 mm long and 7.5 mm in maximum diameter. The open cell was 11.5 mm long from its rear to the narrow part of the entrance; its diameter was approximately the same as that of the other cell. Both cells seemed to be symmetrical around their long axes, and, when brought into the laboratory and dried, the walls became extremely hard, an indication that the *Ancylandrena* female had added a hardening substance when making the walls.

Provisioning and Egg Deposition: Whereas the open cell contained no provisions, the closed cell held a large, orange, oblong food mass (figs. 4–6) consisting of mealy, moistened pollen. The mass was 8.2 mm long, 6.5 mm wide and had a maximum height of 4.5 mm. Its top surface was nearly flat except at the edges, whereas the bottom surface was more evenly rounded as seen in lateral view (fig. 4). It was moderately dull, and not coated with a waterproof secretion or with a layer of nectar. It rested on the cell floor, and, where it touched the floor, there was no liquid.

The white curved egg (fig. 4) with a clear, shiny, nonreticulated chorion was attached

by its posterior end to this food mass in the sagittal plane of the cell at a point slightly anterior to the midpoint of the top surface of the mass. Its free anterior end was directed toward the cell entrance. The anterior and posterior ends were identical in shape. It measured 2.5 mm long and 0.6 mm in maximum diameter.

Phenology: Both Zavortink (1974) and Hurd and Linsley (1975) demonstrated that *Ancylandrena larreae* is a vernal species that flies primarily in the morning. Emergence of the two females from the nest at 10:30 a.m. is consistent with the previous observations. The data provided by these authors suggest there is but one generation a year.

The low numbers of *Ancylandrena larreae* specimens (only one nest found in two days of searching in an area where *Hexepeolus* was not uncommon), the relative freshness of the two captured females, and the small numbers of brood cells in the nest may indicate that the flight season was still early. The relative abundance of *Hexepeolus rhodogyne,* in contrast with the discovery of but a single nest, might indicate that the cleptoparasite and host populations were not fully synchronized. However, other cleptoparasites (*Triepeolus* sp. on *Melissodes lutulenta*; *Townsendiella pulchra* on *Hesperapis larreae*) also appeared to be more abundant than their hosts.

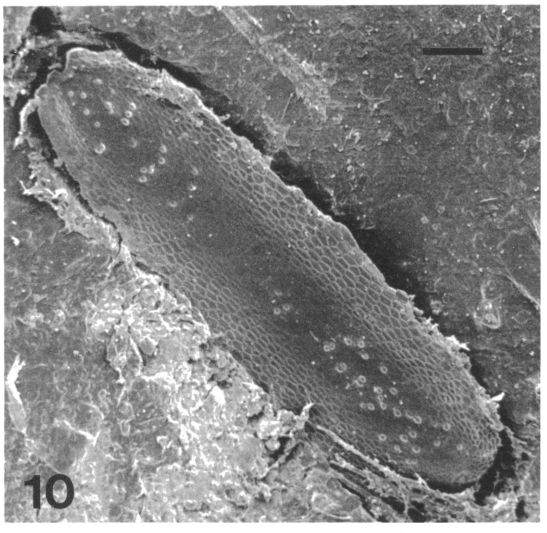
COMPARISON OF NESTING BIOLOGY OF *ANCYLANDRENA* WITH THAT OF OTHER ANDRENIDAE

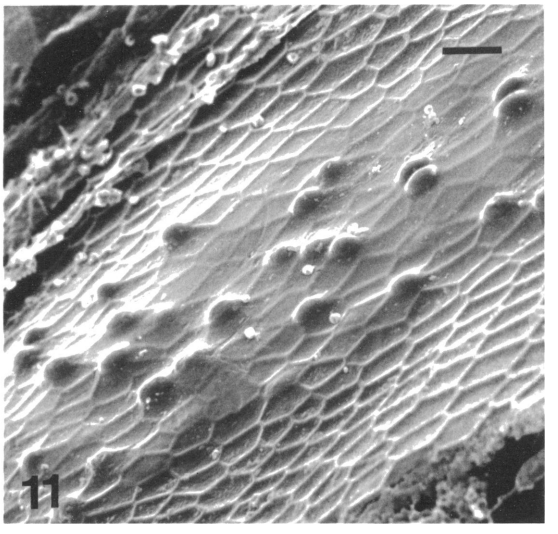
Ancylandrena, like all other members of the family, is ground nesting. Most of the fragmentary information presented above falls within the parameters of the known nesting biology of the family (e.g., Hirashima, 1962; Youssef and Bohart, 1968; Matsumura, 1970; Miliczky, 1988; Osgood, 1989; Rozen, 1989b; Batra, 1990; and references therein).[2]

Two features, however, stand out as not having been reported heretofore. The long, double cell closure appears to be unique for the family, and the open, elongate ascending tunnels leading to cells apparently have no known counterpart in other andrenids. The nest was in the early stages of construction and possibly the long ascending burrows might have become a linear series of cells as has been reported for some Japanese *Andrena* (Hirashima, 1962; Matsumura, 1970). Although such a hypothesis would not explain the ascending nature of the tunnels, it would account for their length and openness. It could even account for the long closure in that the outer septum might have been the beginning point for the construction of the next cell in the series; thus the filled antechamber might actually be the filled tunnel between two cells in a series (as diagrammed by Hirashima, 1962: figs. 4, 8, 11). The ascending direction of the tunnels may be the random directions of burrows often found in communal nests, or they may indeed be constant characteristics of *Ancylandrena.* Discovery and examination of more complete nests will certainly test these explanations.

Other nesting features, though interesting, are probably not unique for the Andreninae. Communal nests have been reported for a number of European and North American species of *Andrena* (Osgood, 1989), and entrances of communally nesting bees generally lack tumuli. No andrenid has been reported to have provisions that are somewhat longer than their horizontal width and at the same time to have a top surface somewhat flatter than the bottom part that rests on the cell floor. However, food masses of *Andrena* have usually been described rather briefly (e.g., as flattened spheres, or as nearly spherical). When more precise observations are made, provisions of some species of *Andrena* and *Ancylandrena* will probably prove to be sim-

[2] Although within the Andreninae only the nests of *Andrena* have been described in the literature, nests of *Euherbstia excellens* Friese were found in an old road by Elizabeth Chiappa in early October 1987 near Vicuña, Chile (Haroldo Toro, in litt.). One tunnel descended about 35 cm where a cell was uncovered, a fragment of which was sent to me and is now preserved in the American Museum of Natural History. The cell was large, at least 8 mm in maximum diameter, possessed a very smooth cell wall with a conspicuous clear shiny lining, and contained a moist but firm pollen mass that was not coated by a waterproof secretion. These features are characteristic of many bees and are probably plesiomorphic in the Andrenidae. The site was left undisturbed so that I could investigate it later. When I finally visited the site in October 1989, the weather had been excessively dry for several years, and no *Euherbstia* were found.





Figs. 10, 11. SEM micrographs of egg of *Hexepeolus rhodogyne*. **10.** Egg embedded in cell wall, dorsal view, showing reticulations and papillae on exposed surface. **11.** Closeup of exposed surface, oblique view, showing same features. Scale lines = 100 μm and 20 μm, respectively.

ilar. The moist, firm consistency of the provisions of *Ancylandrena* is well within the known range of most andrenids. The information presented here does not drastically expand our concept of the nesting biology of the Andreninae, and we cannot as yet identify features pertaining to the nests, provisions, or eggs that set the Andreninae and Panurginae apart.

BIOLOGY OF *HEXEPEOLUS RHODOGYNE*

Searching Behavior: Females of *Hexepeolus rhodogyne* searched for host nests by slowly flying low over the ground, zigzagging as they traveled from one potential nest to another. They hesitated at small clumps of grass or other herbs where nest entrances presumably may have been hidden and at holes not surrounded by tumulus in the unvegetated ground. This suggests that nests of *Ancylandrena* might occur in either of these two situations and not just in the open where the single nest was discovered. *Hexepeolus* females were not attracted to the abundant nest entrances of *Ammophila* and *Trachusa larreae* which were both surrounded by conspicuous tumuli. Although the *Hexepeolus* flight changed direction from one suspected nest entrance to another, females tended to fly in one general direction, thoroughly exploring a wide path. When finished with the zigzag traverse of an open area, a female would often fly swiftly upward and return to near where she had started the previous traverse. She would then start another slow passage, rarely visiting the same potential nest entrances again. Thus an open area tended to be thoroughly and systematically searched.

The female *Hexepeolus* that pointed out the *Ancylandrena* nest described above landed at the nest entrance, briefly inserted the anterior part of her body into the passageway, withdrew it, and then flew about the entrance for a minute or more but did not enter again before she flew away. I placed a plastic drinking glass over this entrance hole from which two female *Ancylandrena* emerged nearly simultaneously more than half an hour later, at 10:30 a.m., Rocky Mountain Standard Time. No *Hexepeolus* matings were observed, and males were uncommon in the search area. Of 18 adults collected, only one was a male. While this sex ratio seems greatly biased in favor of females, mating may normally take place somewhere else where males may be more abundant.

Females were seen most often in midmorning and were rarely found in the afternoon.

Egg Deposition and Description: Only the closed *Ancylandrena* cell had been parasitized. It contained two *Hexepeolus* eggs, one of which was embedded in the upper cell wall toward the rear and the other in the rear cell wall behind the food mass (fig. 4). These eggs had almost certainly been deposited before cell closure while the cell was being provisioned, as is characteristic of all known Nomadinae. It would have been impossible for the female *Hexepeolus* to deposit her egg behind the egg and pollen mass of *Ancylandrena* to say nothing of entering the complicated double closure of the cell.

Both cleptoparasite eggs (figs. 8–11), nearly identical, were embedded in the cell wall so that their entire lengths were exposed to the cell lumen. With each, the exposed chorion was nearly flat and flush with the cell wall. The exposed surfaces measured 1.13 and 1.20 mm long and 0.28 and 0.34 mm in maximum width. They were slightly wider and more rounded at one end (presumably the anterior) and more tapering and pointed at the other end. As discussed below, each egg possessed a thin flange[3] around the entire circumference of the exposed surface. This flange made the surface essentially continuous with the cell wall, perhaps an important hiding technique preventing the *Ancylandrena* female from tactually detecting the egg in the totally dark cell. A partial crack (fig. 10) appeared between the flange and the cell wall after the sample dried and was cleaned prior to SEM photographing. This crack probably resulted from shrinking of the egg and/or cell wall.

When first discovered, the *Hexepeolus* eggs were slightly yellowish and there appeared to be an incised line (fig. 8, "line") bordering their exposed surfaces. This line disappeared and the chorion became white after the eggs dried, and no trace of the line could be found on the palladium-coated specimen in the SEM micrographs. Only when the dried eggs were submerged in alcohol and the opaque palladium coating removed after photographing did it become apparent that the line was actually the edge of the sides of the egg showing through the semitransparent surface of the exposed chorion. The surface between the line and the edge of the exposed surface was the flange mentioned above. The flange is an integral part of and continuous with the rest of the exposed chorion; it is not set off by an incised line as seemed to be the case with the live eggs. This apparent line was also observed in the dissected oocytes discussed below.

The nearly flat exposed chorion (figs. 10, 11) was microscopically reticulate with the greatest length of the polygons running parallel to the long axis of the egg. The reticulations faded toward the middle of the egg so that a nearly smooth, shiny band ran from one end of the egg to the other. However, as can be seen in figure 11, even this band had slight reticulations. Scattered papillae, conspicuous on the micrographs (figs. 10, 11), were more or less grouped at the two ends of

[3] P. F. Torchio (in litt.) on reviewing this manuscript thought that the term *flange* should be reserved for the thin, outward extension of the chorion only where the flange surrounds the nomadine operculum. Implied in his reasoning is that this kind of flange is a specialized structure which is an integral part of the operculum, "a higher ordered characteristic that may be unique to the nomadines" (Torchio, in litt.). The term was first introduced with reference to *Pseudodichroa* (Rozen and Michener, 1968), where the flange does indeed surround the nearly circular operculum. However, those authors regarded the flange as a connecting barrier that prevents liquids from entering or leaving the parasitized nest cell. They did not imply that the flange defined the operculum, and subsequent studies (e.g., Rozen and Favreau, 1968; Torchio et al., 1967) have shown that some nomadine eggs with opercula lack a flange that bounds the operculum (which is presumably also true for *Hexepeolus* if it does have an operculum). Hence I use "flange" in the descriptive sense, referring to a sheetlike extension of the chorion that connects an egg to the cell wall and/or lining. The term, as used here, does not necessarily imply homology or denote function (which seems variable).

The term *operculum* refers to the nearly circular anterior part of the chorion that splits (or is cut) open when the first instar emerges, as exemplified by certain groups of the Nomadinae. The chorion surrounding the operculum may have a distinct flange, may have only a slight rim, may be only slightly thicker than the chorion of the operculum, or may be unmodified. In the Nomadinae it seems to be fundamentally defined by the attachment of the vitelline membrane to the periphery of the operculum (Torchio, 1986, in litt.). It would be interesting to learn if the operculum of *Protepeolus,* now thought not to belong to the Nomadinae (Roig-Alsina, 1991; Rozen, 1991), can be defined the same way.

the egg. Perhaps these papillae help hide the egg from the host female by simulating the cell surface. The exposed surface of the chorion was rigid in that it did not collapse when the eggs dried. However, the other surfaces of the chorion collapsed as was revealed after its removal from the cell wall.

The rest of the live egg, hidden under the exposed surface, was sausage-shaped, round in cross section (except for the exposed surface) (fig. 9), and about 0.2 mm in diameter (excluding the flange). The cell wall cavity into which the egg was inserted corresponded in shape and size to the lower surface of the embedded egg. The walls of this cavity showed no special lining, the sharp edges of some soil particles apparently coming in direct contact with the chorion. However, around the rim of the cavity there may have been traces of some substance, perhaps filling the gap between the cell wall and flange or gluing these surfaces together.

Ovaries and Oocytes of *Hexepeolus rhodogyne*: The ovaries of a specimen collected at 11 mi southwest of Congress, Yavapai Co., Arizona, on May 9, 1990 (a short distance from the study site), and preserved in Kahle's solution were examined. They contained 11 and 9 ovarioles (i.e., 11:9), by far the largest number of ovarioles reported for any cleptoparasitic bee (Alexander and Rozen, 1987; Rozen and Roig-Alsina, 1991; Rozen and McGinley, 1991) (excluding the social parasite *Psithyrus,* some species of which have even greater numbers of ovarioles). These figures reaffirm that the number of ovarioles per ovary, a very consistent character in nonparasitic bees, is highly variable in the Nomadinae and tends to be higher than the plesiomorphic state of 4:4 in the Anthophoridae and Apidae (Alexander and Rozen, 1987). One ovary had 5 mature oocytes[4] and the other 4, so that the mature oocyte per ovariole index was 0.45. Egg index (length of largest mature oocyte divided by the distance between the outer margins of the tegulae) (1.3/2.7 mm) was 0.48. This figure is consistent with the relatively small-sized, mature oocytes (and eggs) of other cleptoparasitic bees (Alexander and Rozen, 1987).

The nearly identical mature oocytes measured 1.275–1.30 mm long (N = 3), were 0.23 mm in maximum thickness in side view, and possessed a clear unpigmented chorion throughout. The contents of the preserved specimens were opaque creamy white. The surface that later becomes the exposed flat surface of the deposited egg (presumably the dorsal surface) was gently concavely curved longitudinally (fig. 7) and convexly curved in cross section (fig. 9). While in the follicle this surface, including the flange, acquires the reticulations and papillae later found on the egg. The flange was thin, colorless, transparent, and completely formed. It curved downward from the body of the oocyte as a skirt (fig. 7) rather than extending outward in a nearly flat plane as occurs after its deposition in the host cell (fig. 9).

REVIEW OF EGG DEPOSITION IN THE NOMADINAE

When Bohart (1970) wrote his survey on parasitism among bees, he recognized that the genera (total 6) of the Nomadinae[5] whose biologies were then known enter open host cells and insert their eggs into the cell walls. Biologies of representatives of many more genera (total 18) are now at least partly known (table 1), and his observation remains valid with the single exception of *Neolarra.* In the case of *Neolarra,* the extremely small egg merely rests with its long axis parallel to the cell wall between the sand grains (new information, referring to *N. vigilans* [Cockerell] found in the nest of *Perdita lenis* Timberlake at 19 mi southwest of Apache, Cochise Co., Arizona, August 28, September 1, 1986; also see Shanks, 1977).

It seems plausible that embedding helps

[4] The mature oocytes, corresponding to Iwata's (1955) Category A oocytes, could be immediately differentiated in their follicles from other large oocytes because the flange of the chorion appeared as a distinct ridge on either side of the follicle and its junction with the rest of the oocyte formed a line that was visible through the follicular wall. Before the chorion is deposited, a follicle is externally sausage shaped.

[5] Nomadinae as used here is as defined by Roig-Alsina (1991) and Rozen (1991); that is, it refers to all those taxa normally placed in the subfamily with the exception of the Protepeolini, Isepeolini, *Coelioxoides* (Roig-Alsina, 1990), and Osirini sensu Roig-Alsina (1989).

TABLE 1

Methods of Ovipositing in the Nomadinae

(Information is also presented on oocyte morphology because of the correlation between egg shape and method of oviposition. For full explanation of methods, see text.)

Taxon	Method of egg deposition
NOMADINI	
Nomada sp.	Inserted in cell wall (MacSwain, 1954).
N. (*Holonomada*) sp.	Inserted in cell wall (MacSwain, 1954).
N. opacella Timberlake	Angled part way under hinged flap; fluid material coating egg cavity in wall (Linsley and MacSwain, 1955).
N. edwardsii Cresson	Angled part way under hinged flap; egg cavity with membranous lining (Linsley and MacSwain, 1955).
Nomada sp.	Inserted about halfway into hole, not cemented (i.e., crack around egg obvious) (Rozen, 1971).
Nomada spp.	Oocytes of 4 spp. without specialized opercula (Alexander and Rozen, 1987).
Nomada spp.	Oocytes of 3 spp. without specialized opercula (Iwata, 1955).
Nomada spp.	"in a manner similar to that of *Nomada opacella* (Linsley and MacSwain, 1955)" (Miliczky et al., 1990).
BRACHYNOMADA GROUP[a]	
Melanomada sidaefloris (Cockerell)	In oblique slit with hinged flap (Rozen, 1977, 1984b).
M. annectans Snelling and Rozen (as *M.* sp.)	In deep elongate puncture with raised cell lining on one side and in hole under hinged flap (Rozen and Snelling, 1986).
Kelita chilensis (Friese)	Angled part way under hinged flap (Rozen, 1970b).
Triopasites penniger (Cockerell)	In hole, probably under hinged flap (Rozen, 1977).
Paranomada velutina Linsley	In hole, sometimes with hinged flap (Rozen, 1977).
P. nitida Linsley and Michener	In hole with irregular hinged flap (Rozen, 1984b).
Brachynomada near *argentina* Holmberg	In hole, under hinged flap (Rozen, 1977).
AMMOBATINI/PASITINI	
Pseudodichroa capensis (Friese)	Fitted tightly through hole in cell lining; flanged operculum flush with cell wall (Rozen and Michener, 1968).
P. fumipennis Bischoff	Fitted tightly through hole in cell wall; flanged operculum flush with cell wall (Rozen and Michener, 1968).
Ammobates carinatus Morawitz	Oocyte with specialized operculum (Alexander and Rozen, 1987).
Pasites maculatus Jurine	Fitted tightly into hole; flanged operculum flush with cell wall (Rozen, 1986b).
Morgania histrio transvaalensis Bischoff	In hole in cell wall (Rozen, 1969).[b]
Oreopasites sp.	In cell wall (Rozen, in Bohart, 1970).
O. sp. (species associated with *Perdita biguttata* Timb.	Fitted tightly, perhaps cemented; flanged operculum flush with wall (new information).
O. vanduzeei Cockerell	Oocyte with flanged operculum (Rozen, 1986a).
O. arizonicus Linsley (as *O.* sp.)	In cell wall (Rozen, 1970a).
CAENOPROSOPIDINI	
Caenoprosopis crabronina Holmberg	Cemented (chinked) in hole; no specialized operculum on oocyte (Rozen and Roig-Alsina, 1991).
Caenoprosopina holmbergi Roig-Alsina	No specialized operculum on oocyte (Rozen and Roig-Alsina, 1991).

TABLE 1—(*Continued*)

Taxon	Method of egg deposition
TOWNSENDIELLINI	
Townsendiella pulchra Crawford	Hole in cell wall; oocyte without specialized operculum (Rozen and McGinley, 1991).
NEOLARRINI	
Neolarra sp.	Glued to cell wall (Shanks, 1977).
N. vigilans (Cockerell)	Resting on cell wall between sand grains (present paper).
BIASTINI	
Neopasites cressoni Crawford	Inserted parallel to and more or less flush with wall, cemented; without flange; operculum not evident before hatching (Torchio et al., 1967).[c]
HOLCOPASITINI	
Holcopasites insoletus (Linsley) or *arizonicus* (Linsley)	Angled part way under hinged flap; without specialized operculum (Rozen, 1965).
H. tegularis Hurd and Linsley	Under hinged flap (Rozen, 1989b).
H. eamia (Cockerell)	Part way in hole, no flap, no cement (Rozen, 1989b).
HEXEPEOLUS GROUP[d]	
Hexepeolus rhodogyne Linsley and Michener	Inserted parallel to and flush with wall, possibly cemented, with flange (present paper).
EPEOLINI	
Epeolus pusillus Cresson	Fitted tightly into cell lining, with unflanged operculum flush with lining (Rozen and Favreau, 1968).
E. compactus Cresson	Fitted tightly into cell lining, with flanged operculum flush with lining (Torchio and Burdick, 1988).
Triepeolus remigatus (Fabricius)	Fitted tightly to and at right angle with wall; flanged operculum flush with wall (Bohart, 1966).
T. dacotensis (Steven)	Fitted tightly and at right angle to wall; flanged operculum nearly flush with wall (Bohart, 1970; Torchio, 1986).
T. loomisorum Rozen	Fitted tightly and at right angle to wall; flanged operculum flush (Rozen, 1989a).
T. grandis (Friese)	Fitted tightly and at right angle to wall; flanged operculum flush (Rozen, 1984a).
T. pectoralis (Robertson)	Oocyte with operculum at anterior end (Alexander and Rozen, 1987).

[a] The taxa identified in this group have traditionally been assigned to the Nomadini. However, studies of mature larvae (Rozen et al., 1978), mature larvae and adults (Alexander, 1990), and adults only (Alexander, 1990; Roig-Alsina, 1991) show that these taxa are not close relatives of *Nomada*.

[b] I reexamined the cells of the host, *Tetraloniella minuta* (Friese). *Morgania* oviposition holes were simple, nearly perpendicular, without a hinged flap of cell wall, but, since the chorions were missing, I could not determine whether the eggs had been cemented into the wall.

[c] Although there was no indication of an operculum before hatching, *Neopasites* eggs developed a circular slit at the anterior end at eclosion so that, when the first instar crawled away, a circular opening with a circular piece of chorion (operculum) partly attached was left behind.

[d] In separate cladistic analyses of adult characters, both Alexander (1990) and Roig-Alsina (1991) have shown *Hexepeolus*, formerly placed in the Nomadini (e.g., Michener, 1944), to be not closely related to either *Nomada* or the *Brachynomada* group. This genus is thus treated separately here.

hide Nomadinae eggs from host females, an important phenomenon because host females appear to chew discovered eggs from cell walls (e.g., Rozen, 1970a; Rozen, 1986b; Rozen and Snelling, 1986; Rozen and Roig-Alsina, 1991). Also, in some bee nests, fresh cells are occasionally completely filled with soil (e.g., Rozen, 1977; Rozen and Snelling, 1986). Such cells suggest that a host bee, detecting that the cell may have been parasitized when she

was foraging, completely packs the cell with soil, thereby entombing the parasite's egg.

It is tempting to speculate that the small size of nomadine eggs is another form of detection-avoidance. However, Alexander and Rozen (1987) demonstrated that the oocytes (and therefore, the eggs) of small cleptoparasitic bees other than nomadines tend to be smaller than those of small solitary bees. Presumably, but not certainly (available information is inconclusive), some of these other small cleptoparasitic bees oviposit in cells that have already been closed and therefore would not be inspected by returning host females. However, the oocytes of Ericrocidini and Melectini (large cleptoparasites) are relatively large (Alexander and Rozen, 1987), and these two cleptoparasitic anthophorids are known definitely to oviposit in closed host cells (see Rozen, 1991, for references). Hence the possible adaptive significance of small egg size among cleptoparasites is moot and worthy of future examination.

Considerable information has accumulated about how, where, and when eggs of Nomadinae are deposited in host cells (table 1) and about peculiarities of the chorions of these eggs (and oocytes) that, at least in some cases, seem to be involved with their deposition (see references in table 1; Rozen, 1986a; Alexander and Rozen, 1987). Excluding egg depositions of *Neolarra* (presumably dictated by the very small size of the eggs), those of the other Nomadinae seem to fall into two categories:

Category 1. The female parasite, after entering the open cell, makes a slit in the cell wall (no doubt with her apical abdominal sterna) and places her egg in the slit at an oblique angle so that one end projects into the cell lumen. The hole is rough and does not fit tightly around the egg, so that a distinct, irregular crack is usually evident between the egg and the cell wall. Furthermore, there is often a flap of cell lining with soil attached that is hinged by the flexible cell lining to one side of the slit. It is unclear whether this flap is normally always present and is merely broken off during investigation, or whether with some species it is normally not present (as possibly suggested by *Holcopasites eamia,* Rozen, 1989b, and *Paranomada velutina,* Rozen, 1977).

With this type of oviposition, the eggs (and oocytes) are either normal in shape (like a curved sausage) and the texture of the chorion is homogeneous throughout, or the eggs possess a small nipple or hook at the anterior end but are otherwise unremarkable. Information referred to in table 1, though incomplete, suggests that this type of oviposition is found in the following genera: *Nomada, Melanomada, Kelita, Triopasites, Paranomada, Brachynomada, Townsendiella,* and *Holcopasites.*

Category 2. In this category, the female cleptoparasite also inserts her egg into the cell wall (or lining), but instead of a jagged hole, the cell lining appears to fit tightly around the egg so there is no obvious crack. The egg does not project into the cell lumen; the surface of the chorion that is exposed to the lumen is flat or in other ways modified. The exposed surface is usually (but not invariably) surrounded by a flange (as in the case of *Hexepeolus*) that either provides a smooth continuation of the flat surface of the egg with the cell wall (a detection-avoidance mechanism as suggested above) and/or perhaps helps seal the insertion hole and thereby prevents moisture imbalance between the surrounding soil and the cell lumen. These eggs (and oocytes) are very different from normally shaped bee eggs because of the flat surfaces and flanges, and the chorion of the exposed surfaces is often very differently textured and pigmented from that of the rest of the egg. These eggs seem to be deposited in taxon-specific ways: Those of the Epeolini are straight, and their long axis is nearly at right angles to the cell wall. Their anterior end is often surrounded by a flange, and opens as an operculum on hatching. Similarly, eggs of ammobatines also have a modified anterior end that is flanged and opens as an operculum, but during deposition the egg is bent on itself except in *Pseudodichroa.* In *Neopasites* and *Hexepeolus* the entire length of the egg is exposed to the cell lumen, and the exposed chorion is more (*Hexepeolus*) or less (*Neopasites*) flat, much more coriaceous than the rest of the chorion, and is either surrounded by a flange (*Hexepeolus*) or without a flange (*Neopasites*). The few similarities in the egg depositions shared by these two genera, however, seem insufficient by themselves to suggest a

sister-group relationship. In some cases (see, for example, Torchio et al., 1967; Torchio, 1986) there is an indication that category 2 eggs are glued or cemented into place by some activity of the parasite female during oviposition. This is also suggested by the tight fit between the eggs and the cell lining.

Caenoprosopis (and presumably the Caenoprosopidini) does not fall precisely in either category because it appears to "chink" the crack around the egg with soil mixed with a hydrofuge secretion and at the same time it has a sausagelike egg with a small hook, that is, a category 1 type egg (Rozen and Roig-Alsina, 1991). Observation of a live egg in situ, rather than just a vacated chorion, might explain this situation.

A scattering of other observations suggests that the oviposition process in both category 1 and category 2 is more complex and diverse than these categorizations imply. In most cases, no mention has been made as to whether the egg insertion hole is lined with a secretion or other material, and I have not noticed this phenomenon with any species that I have studied. However, Linsley and MacSwain (1955) mentioned a membranous lining of the hole created by *Nomada edwardsii* and a fluid coating the basal portion of the cavity used by *Nomada opacella.* Torchio (in litt.) stated ". . . the posterior tip of a *Nomada* sp. (on *Andrena miserabilis*) egg is quite strongly bent, and a yellowish material deposited in the excavated hole firmly binds the *Nomada* egg to the host's cell wall (northern Utah). A cementing material has also been found on the posterior tip as well as the dorsal surface (where v-bend occurs) of *Oreopasites scituli* eggs inserted in the cell walls of *Nomadopsis scitula* in northern Utah . . ." Torchio and Burdick (1988) indicated that *Epeolus compactus* females deposit a small quantity of liquid that, on hardening, seals the anterior end of the egg to the cell lining. The soil surrounding the egg of *Caenoprosopis crabronina* was more hydrofuge than the cell wall, suggesting the female had used a secretion to moisten the soil to fill the crack (Rozen and Roig-Alsina, 1991). *Neopasites cressoni* seems to seal the crack between the egg and cell wall with a cementlike material (Torchio et al., 1967). Possibly the close fit between cell wall and operculum flange may be accompanied by a fluid or cementlike material in the case of other or all category 2 depositions. These observations indicate the need for further investigations of both categories 1 and 2 types of oviposition. Ehrenfeld and Rozen (1977) hypothesized that category 1 depositions were plesiomorphic and category 2 apomorphic because the egg type of the former is more like that of nonparasitic bees and because the presumed plesiomorphic condition is found in nomadines that, on other grounds, do not appear closely related. Furthermore, a slit in the cell wall would seem to be a simpler task than the manipulations required for gluing or cementing an egg into the cell wall so that the exposed surface of the egg seems a continuum with the wall. This hypothesis may be valid, but available information is still inconclusive. Even if this hypothesis is correct, we cannot assume that depositions of category 2 are all homologous. Egg opercula and flanges are also found in the Protepeolini (Rozen et al., 1978; Roig-Alsina and Rozen, in prep.), a tribe now believed to have had a separate evolutionary origin from that of the Nomadinae (Rozen, 1991). Hence these features could also have arisen more than once in the Nomadinae. Nonetheless, variations in egg deposition and features of the eggs associated with this process are data available for phylogenetic analysis.

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