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Biologies of the Bee Genera *Ancylandrena* (Andrenidae: Andreninae) and *Hexepeolus* (Apidae: Nomadinae), and Phylogenetic Relationships of *Ancylandrena* Based on Its Mature Larva (Hymenoptera: Apoidea)

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CONTENTS

Introduction, Acknowledgments	2
Biological notes on <i>Ancylandrena larreae</i> , <i>A. rozeni</i> , and comparative information on their nests	2
Biological notes on <i>Hexepeolus</i>	9
Mature larvae of <i>Ancylandrena larreae</i> and <i>A. rozeni</i>	11
Phylogenetic relationships of <i>Ancylandrena</i> based on its mature larva	15
Appendix, <i>Ancylandrena rozeni</i> Zavortink, new species	17

ABSTRACT

Comparative biological information concerning *Ancylandrena larreae* (Timberlake) and *A. rozeni* Zavortink, new species, is presented, adding to our understanding of this ground-nesting genus. Subjects include habitat preference, nest structure,

phenology, number of females in a nest, provisioning, and larval behavior with respect to feeding and defecation. The biology of *Hexepeolus rhodogyne* Linsley and Michener, the cleptoparasite of *A. larreae* and possibly *A. rozeni*, is also treated,

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including such matters as host-nest search behavior, egg deposition, larval eclosion, and larval diapausing posture.

Mature larvae of *Ancylandrena larreae* and *A. rozeni* are described taxonomically, the first such description for the genus. They differ from one another only slightly but can be readily distinguished from larvae of other members of the Andrenidae by characters given. A cladistic analysis based on mature larvae investigates the relationships among the Andreninae (*Ancylandrena*, *Andrena*, *Euherbstia*), the Panurginae, Oxaeidae, and

Stenotritidae. This analysis suggests that *Ancylandrena-Andrena*-Panurginae form a clade separate from *Euherbstia*, Oxaeidae, and Stenotritidae and that *Ancylandrena* is the sister group to *Andrena*-Panurginae, but no classificatory changes are made to reflect the paraphyletic arrangement of the Andreninae as they now stand because of the need for corroborative data.

The taxonomic description of *Ancylandrena rozeni* Zavortink, new species, is appended, based on adults collected visiting flowers of *Marina parryi* (Torr. & Gray) Barneby.

INTRODUCTION

New biological information about *Ancylandrena* and its nomadine cleptoparasite, *Hexepeolus rhodogyne* Linsley and Michener, is presented, augmenting a recent account of their nesting biologies (Rozen, 1992). The data come from a study of nesting sites of *A. larreae* (Timberlake) and *A. rozeni* Zavortink, new species, in Arizona in 1993. These sites yielded mature larvae of *A. larreae* and *A. rozeni*, described herein for the first time, thus making possible an analysis of the phylogenetic relationships of *Ancylandrena* to other members of the Andreninae and to taxa outside the subfamily, on the basis of mature larvae. Andreninae contain a large number of species currently assembled into six genera, with one genus (*Andrena*) containing almost all of the species. To date, larvae of only *Andrena* and the Chilean *Euherbstia* have been described (see Rozen, 1993a, for references).

Larvae of *Hexepeolus rhodogyne* were also collected and will be treated in a separate paper addressing the phylogenetic relationships of the tribes of the Nomadinae on the basis of mature larvae. *Hexepeolus rhodogyne* is the only species assigned to the Hexepeolini.

The taxonomic description of *A. rozeni* Zavortink is appended, validating the name.

Immature stages of all species, nest samples of both species of *Ancylandrena*, and the holotype and allotype of *A. rozeni* are in the collection of the American Museum of Natural History.

ACKNOWLEDGMENTS

I wish to thank Barbara L. Rozen who greatly assisted me in searching for nests of

A. larreae near Wickenburg. Dr. Robert L. Smith, Director, Desert Station, Department of Entomology, University of Arizona, kindly permitted me to excavate the nest of *Ancylandrena rozeni* (as well as nests of a number of other bees) at the Station, on the east side of the Tucson Mountains (Pima County). Specimens of *A. rozeni* were also collected a short distance away at the Arthropod Discovery Center, Steve Prchal, Resident Director, on the west side of the Tucson Mountains. It was there that Axhel Muñoz discovered the foraging species and collected part of the type series. Dr. Thomas J. Zavortink identified the adults of *A. rozeni* as belonging to an unrecognized new species and kindly prepared its description, included herein. The host plant of *A. rozeni* was identified by Rupert Barneby, New York Botanical Garden.

Wallace E. LaBerge and Thomas J. Zavortink kindly reviewed this manuscript. I also wish to thank Dr. Zavortink for preparing the description of the new species of *Ancylandrena* included here.

BIOLOGICAL NOTES ON *ANCYLANDRENA*

Ancylandrena larreae (Timberlake)

The nesting site of *Ancylandrena larreae*, in Yavapai Co., 8 mi northwest of Wickenburg, Maricopa Co., was described in Rozen (1992). A flat, open, creosote bush habitat (fig. 1) with sandy soil, the terrain was strikingly different from that of the nest site of *A. rozeni* in the Tucson Mountains, described below. Five nest entrances stretched in a roughly linear fashion for 21 m when identified on May 5, 1993. Distances between nests ranged



Fig. 1. Nesting site of *Ancylandrena larreae* at 8 mi northwest of Wickenburg, Maricopa Co., Arizona. Arrows mark three nest entrances. The nest from the earlier study occurred just on the other side of the creosote bush in the center of the picture.

from 5 to 10 m except for two that were only 20 cm apart. The closest nest was about 10 m from the nest described in Rozen (1992). *Ancylandrena larreae* nests were difficult to discover because entrances were often partly hidden by sparse grass or windblown debris and lacked obvious tumuli. Furthermore, females were rarely observed departing and returning. No vegetative or topographic features distinguished this terrain from vast areas of adjoining creosote-bush desert. Only the concentration of female *Hexepeolus* indicated the presence of nests, and most entrances were discovered by monitoring spots that seemed to attract the attention of the cleptoparasites. Entrances were fully exposed to the sun or in semishade near creosote bushes.

Three nests were excavated at the time of discovery in May, during the period of adult activity. The open main burrows, 5–7 mm in diameter in all cases, descended more or less vertically in a meandering fashion. Two branched at about the depth of 10 cm, but

the side branches were either soil filled and lost or were actually short blind side tunnels. Further branching occurred at a depth of 15–20 cm, and the main tunnels ceased. These branches were soil filled and could not be traced, but in some cases they seemed to angle downward at first. All cells ($N = 6$) were between 20 and 25 cm below the surface and ranged 8 to 25 cm from the lower end of the main tunnels. The greatest number of cells in a nest was 5 (this nest probably incomplete), and they radiated from the main burrow terminus in an arc of 120° .

The remaining two nests, 20 cm apart, were marked with the hope that they could be rediscovered and studied later when larvae were mature. The site was revisited on August 24 and 25, 1993, and one of the nests was found and excavated. This nest, like the others, consisted of an open, meandering, descending main burrow, extending to a depth of 20 cm where it branched into a number of short tunnels. Although most of these branches were

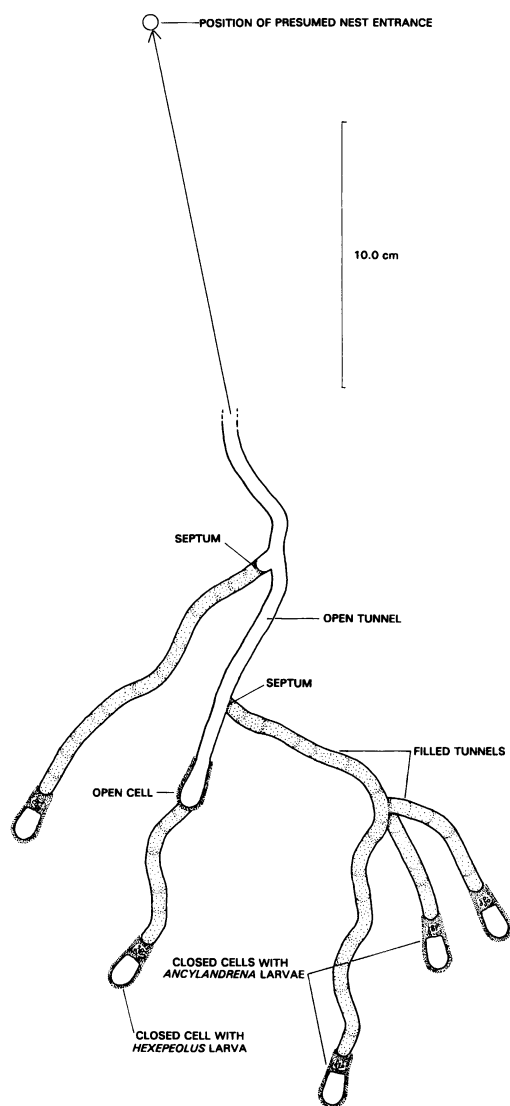


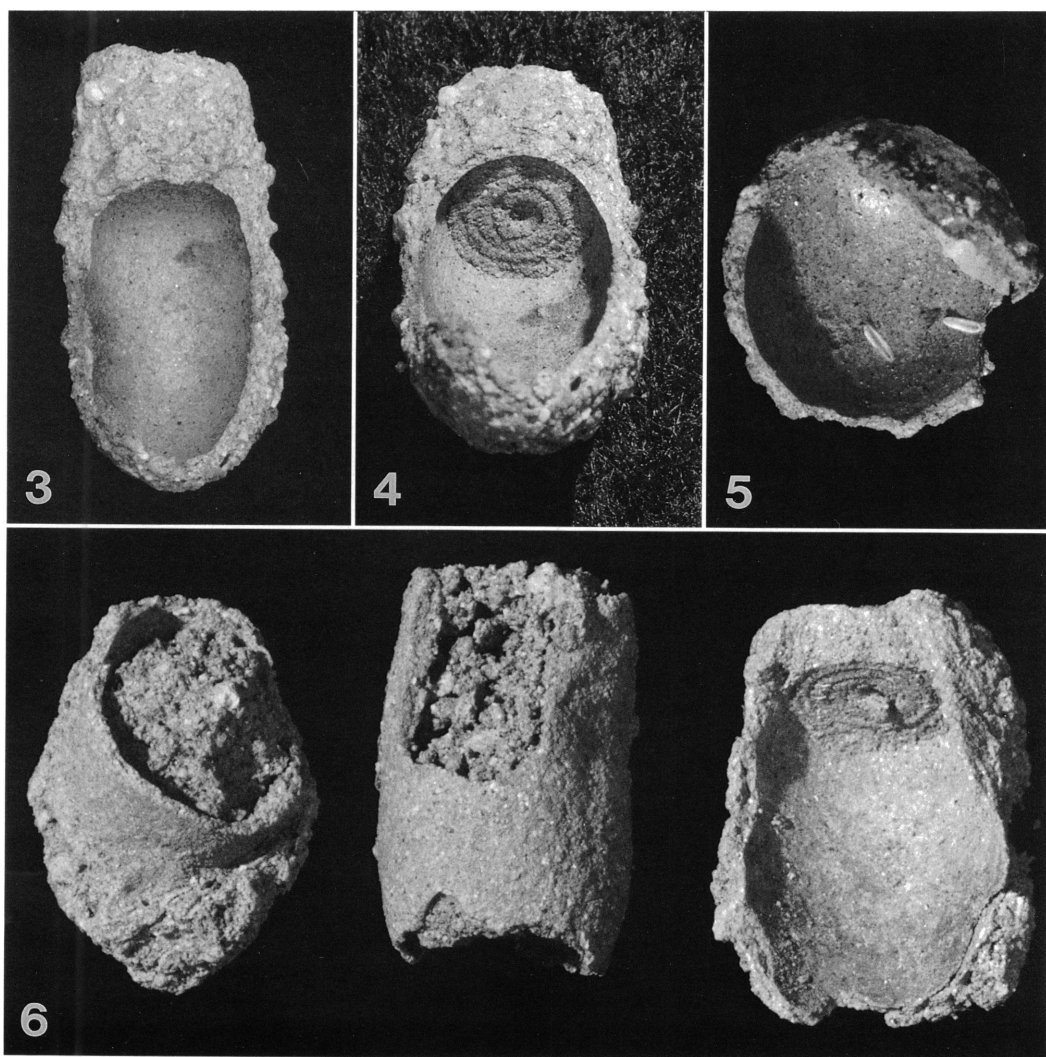
Fig. 2. Diagram of the horizontal southeast lateral of the nest of *Ancylandrena larreae*, viewed from above. All tunnels and cells were between 19 and 24 cm deep. For further explanation, see text.

lost or anastomosed, one extended toward the southwest and was traced for a distance of 32 cm. Although it dipped and rose, it was essentially horizontal. It divided at least twice (in one case a concave septum, smooth on the outside, closed off one ramus). A number of cells, all destroyed presumably by meloids, were clearly associated with this lateral. Other cells (some containing live postdefecating

Ancylandrena larvae, one with a live *Hexepeolus* larva, and others vacated) were found southwest of the entrance but were not clearly associated with the traced lateral. The presence of vacated cells indicated that the site had been used by previous generations, but it could not be determined whether the same burrow (nest) had been used by more than one generation. The fact that some cells were at a depth much greater (maximum 32 cm) than the horizontal lateral (ca. 20 cm) indicates that nest architecture may be more varied than suggested here.

The discovery and tracing of a horizontal lateral system (fig. 2) leading southeast from the entrance of this nest shed additional light on the nest structure. (It seems likely, but not proven, that this lateral actually connected to the descending main burrow.) The southeast lateral, like the southwest one, extended horizontally, rising and descending equal distances over its length. As seen from above (fig. 2), the open lateral extended to an open cell containing a moldy pollen-nectar mass, suggesting that the female had been unable to close the cell and nest. Other laterals branched from the open one but in each case was walled off by a well-formed smooth septum, one of which was concave on the nest-entrance side, while others were flush with the lateral wall and thus not detectable on the nest-entrance side. All filled laterals contained loose soil that was formed into a series of fragile concave septa, far less firm than lateral closures or the outer septum of the cell closure. Behind the open cell (fig. 2), the lateral, now filled with soil, continued to a closed cell containing a postdefecating *Hexepeolus* larva. All other closed cells contained postdefecating *Ancylandrena* larvae. In addition to the six cells diagrammed, two other cells essentially at the same depth were discovered later and almost certainly belonged to the same nest, their laterals having been overlooked.

Walls of both open and closed laterals were nonwaterproof but were lined with fine soil, finer and more consolidated than the surrounding substrate, and firmer than the fill, thus permitting them to be traced. The walls, however, were not as firm as those of the cells and did not have pebbles embedded on the substrate side, as is characteristic of the cells.



Figs. 3–5. Cells of *Ancylandrena larreae*. 3. With top of brood chamber removed but with antechamber not exposed, top view. 4. Same, tipped to show characteristic coil on inner face of closure. 5. Rear of cell showing two white vacated chorions of *Hexepeolus rhodogyne* embedded in the wall.

Fig. 6. Three fragments of vacated cells of *Ancylandrena rozeni* in which the outer layer of cell wall has partly or completely eroded. On the two fragments to the left the smooth even surface is the inner layer; the uneven material within the fragments is backfill created when the adults emerged. In the fragment on the right, the cell closure remains intact; the diagonal crack on the lower right corner marks the boundary between the inner and outer layers.

They were, therefore, substantially different from the cell walls.

Cells (figs. 3, 4) from all nests corresponded closely to the description and illustration in Rozen (1992: fig. 4) in that, when completed, a cell consists of a brood chamber and a pebble-filled antechamber, all surrounded by a

hard wall. The small pebbles of the antechamber were generally uniform in size and in many, if not all, cases were not cemented in place. The cells from the current study differed from those in the earlier report in that the inner surface of the spiral closure (with 4 to 5 coils) (fig. 4) was usually even

flatter in cross section than that previously illustrated and the center of the closure was invariably recessed, as shown in figure 4. Furthermore, the two cells observed by Rozen (1992) seemed to have a straight axis so that the axis of the antechamber and that of the brood chamber were continuous. The large sample of cells collected in 1993 indicated that, in many cases, the axis of the antechamber intersected the plane of the cell closure at right angles, but the axis of the brood chamber angled slightly downward so that its axis was not perpendicular to the plane of the closure. As a consequence, the ceiling of the brood chamber was somewhat longer than its floor. Viewed from the outside in side view, most cells appeared slightly curved, bending downward toward the rear.

Cells were oriented more or less horizontally. Three tipped to the rear about 10°, two 20°, and one 30°.

Hence the general nest pattern for *Ancylandrena larreae* appears to be an open main tunnel meandering downward to an approximate depth of 20 cm. At that point, long to very long, filled, generally horizontal, branching laterals extend to single cells, a pattern seemingly consistent with that reported in Rozen (1992). Each of the three nests excavated in May contained a single female. However, the large nest excavated in August may have been the result of two females (one per long lateral). Rozen (1992) collected two females from a single nest in 1991.

Additional information about the nest of this species and that of *Ancylandrena rozeni* is presented in the section on Comparative Information on Nests of the Two Species.

Ancylandrena rozeni Zavortink

A single active nest containing one female of *Ancylandrena rozeni* was discovered on the grounds of the Desert Station, on the east side of the Tucson Mountains, Pima Co., Arizona, on April 14, 1993. It was located on the southeast side of a rocky ravine descending to the northeast (fig. 7). The surface (fig. 8), partly shaded by bushes, sloped about 45°, and the nest entrance was approximately 1 m (measured vertically) from the bottom of the ravine. The subsurface consisted primarily of fractured rhyolite. The main burrow,

open and 5.0 mm in diameter, penetrated one of the soil- and rock-filled cracks in the rhyolite (fig. 9). Its irregular downward path was determined by the smaller pieces of rhyolite that were wedged into the crack. The crack ranged from approximately 4.5 cm in width near the surface to 2 cm at the level of the cells. In spite of the unlikely appearance of the habitat for bee nesting, *Dufourea australis* (Michener) (and its cleptoparasite *Neopasites cressoni* Crawford), *Perdita* (*Perdita*) sp., *Centris cockerelli* Fox, and *Exomalopsis completa* Cockerell nested within 1 m of the *Ancylandrena* entrance at the time the nest was being studied. Because of immovable rhyolite blocks surrounding the nest, it could not be excavated to reveal nest structure and cell orientation.

Approximately 10 cells were reached and removed with 25 cm forceps. These cells were tightly clustered about 20–22 cm into the crack. Some contained live immatures (post-defecating larvae, feeding larvae, and an egg), and others had recently been vacated. In addition, remnants of cells from one or more previous generations were recovered. The close approximation of the cells in the nest did not conform to the long laterals and widely separated cells found in nests of *Ancylandrena larreae*. Although this difference in nest structure may be genetic, certainly the sharply limited substrate available in the case of *A. rozeni* would not have permitted a more dispersed nest structure.

No cleptoparasitic immatures were found, but a single adult *Hexepeolus rhodogyne* was collected in the vicinity of the site, suggesting that it may attack the nests of *Ancylandrena rozeni* as well as those of *A. larreae*.

Additional comparative information concerning nesting biology of *Ancylandrena rozeni* and *A. larreae* is presented below.

COMPARATIVE INFORMATION ON NESTS OF *ANCYLANDRENA LARREAE* AND *A. ROZENI*

The following data are best understood when compared and contrasted for both species at the same time.

Inner dimensions of cells of the two species differed, reflecting the relative body sizes of the adults. For *Ancylandrena larreae*, maximum cell diameter was 6.5–7.5 mm (N =

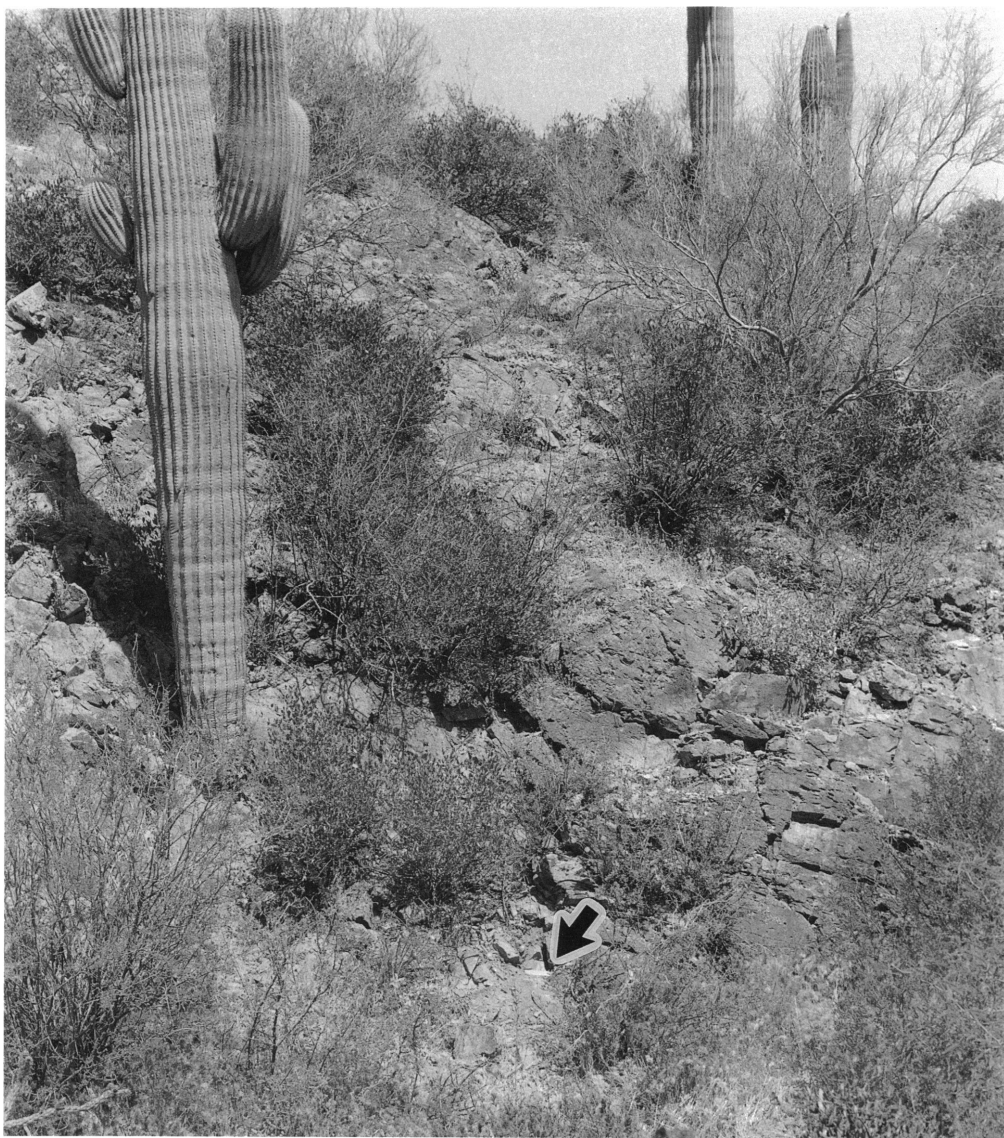
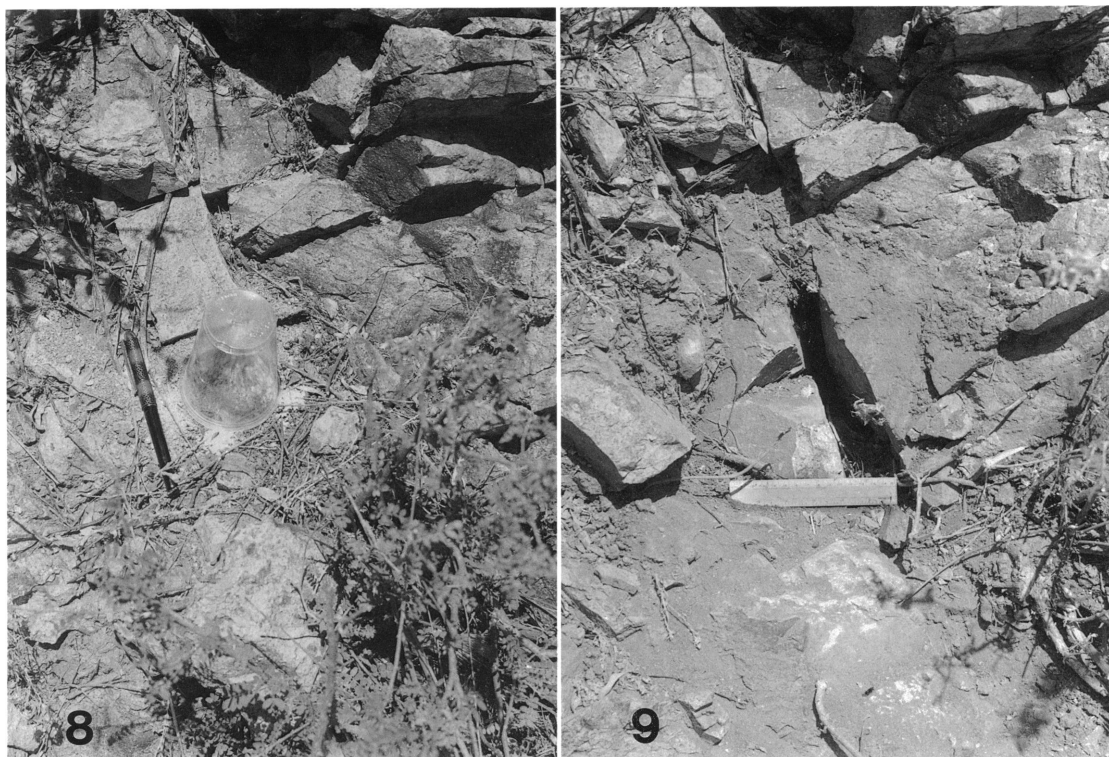


Fig. 7. Nesting habitat of *Ancylandrena rozeni*, in the Tucson Mts., Pima Co. Arizona. Arrow points to nest entrance.

15), cell length was 10.0–11.5 mm ($N = 10$), and diameter of the inner face of the closure was 5.0–5.5 mm ($N = 11$). (The first two statistics agree closely with those in Rozen, 1992.) Corresponding dimensions of samples of *A. rozeni* were: maximum cell diameter 4.0–4.4 mm ($N = 9$), cell length 9.0–10.0 mm ($N = 3$), and diameter of inner face of closure 5.2–5.7 mm ($N = 8$).

There was also an apparent difference in

the cell walls of the two species. For *Ancylandrena larreae*, broken edges of cell walls appeared to consist of larger and small particles on the outside grading to uniformly smaller ones toward the inside (as reported in Rozen, 1992). Only in a few cases was there a distinct boundary between an outer layer and a fine-grain inner one. Broken edges of cell walls of *A. rozeni* revealed an outside layer of irregular thickness composed of less



Figs. 8, 9. Closeup of nest of *Ancylandrena rozeni*. 8. Plastic drinking cup, center, covers the nest entrance before excavation. 9. Same view after excavation showing crack into which the burrow descended and from which all cells were recovered. Ruler is 15 cm long.

consolidated soil distinct from an inner, even, consolidated layer. The boundary between the two was often sharply defined, and joining surfaces did not adhere tightly to one another. The inner layer was 0.13–0.25 mm thick (but thicker near the cell closure). In some cases there was a suggestion that several even inner layers may have been applied, one layer being plastered over the previous one. The lamination of the wall was best seen on cells of past generations where the outer wall had partly deteriorated (fig. 6).

In spite of these differences, females of both species probably first excavate a cell cavity and then smooth (tamp?) and impregnate the wall with a water-soluble hardening substance (nectar or a secretion), thus accounting for the hard outer layers. They then mix fine-grain soil with nectar or a secretion and apply the mixture as a plaster to the wall of the cavity. How they perform this act is unknown, and how to account for the differ-

ences in the cell wall of the two species is also obscure. As a final step, females of both species then cover the cell surface with a thin, semitransparent, somewhat shiny lining, no doubt a secretion.

With both species, the inner cell closure and cell wall just inside the closure were non-waterproof on recently closed cells. Water droplets were immediately absorbed on the outer and inner surfaces of the inner closure and the adjoining cell wall, and, when the front end of a closed cell was submerged in water, the soil disassembled almost immediately. On cells from which postdefecating larvae were removed, these same surfaces were water repellent when tested. The soil in these areas was now glued together with a substance that was insoluble in water. This glue-like substance had completely penetrated the soil of the closure as well as the cell wall next to the closure. (The outer cell closure remained water-absorbent.) The point in the

larval development where this change takes place should be determined, and the source of the material needs to be identified. These observations suggest that seemingly cocoonless bees may have adaptations of a different sort that afford them protection in the form of a rigid, waterproof enclosure. Related observations on changes in cell linings during development of other noncocoon-spinning bee larvae (see Rozen, 1993b: 13–14, for references) suggest that this phenomenon may be widespread but has been largely overlooked by bee biologists.

Provisions of both species were elongate, homogeneously mealy-moist masses shaped as described in Rozen (1992: figs. 4–6). A provision loaf of *Ancylandrena larreae*, measured after it dried, was 6.0 mm long, 5.1 mm wide, and 3.1 mm high. A loaf of *A. rozeni* measured shortly after excavation was 5.3 mm long, 4.6 mm wide, and 3.4 mm high. A shiny, curved, white egg of *A. rozeni* was attached by its posterior end to the middle of the top surface of the provisions, as pictured for *A. larreae* (Rozen, 1992: fig. 4).

A feeding larva of *Ancylandrena rozeni* chewed very rapidly, 80–100 bites per minute. Last-stage feeding larvae had elongate apices to their mandibles as did recently developed postdefecating larvae (as in figs. 14, 15, 19–22). However, two postdefecating larvae of *A. rozeni*, perhaps representing the previous year's generation, and 13 of the 14 postdefecating larvae of *A. larreae* collected in August had the apices of the mandibles greatly worn (figs. 16, 17) and also cuspal denticles somewhat reduced in size, presumably because of wear. Mandibles of the predefecating larva of *A. rozeni* were unworn as was the case for all intermediate-stage larvae and a newly developed postdefecating larva of *A. larreae* from near Wickenburg. These facts argue that after defecation larvae of both species wear down their mandibles quickly, very possibly by chewing the hard cell wall. An early postdefecating larva of *A. larreae* was observed attempting to chew the cell wall, not an uncommon phenomenon for bee larvae that have just completed feeding and often interpreted as a residual feeding behavior.

An explanation of this postfeeding wear of larval mandibles in *Ancylandrena* is yet unknown. However, other kinds of postfeeding

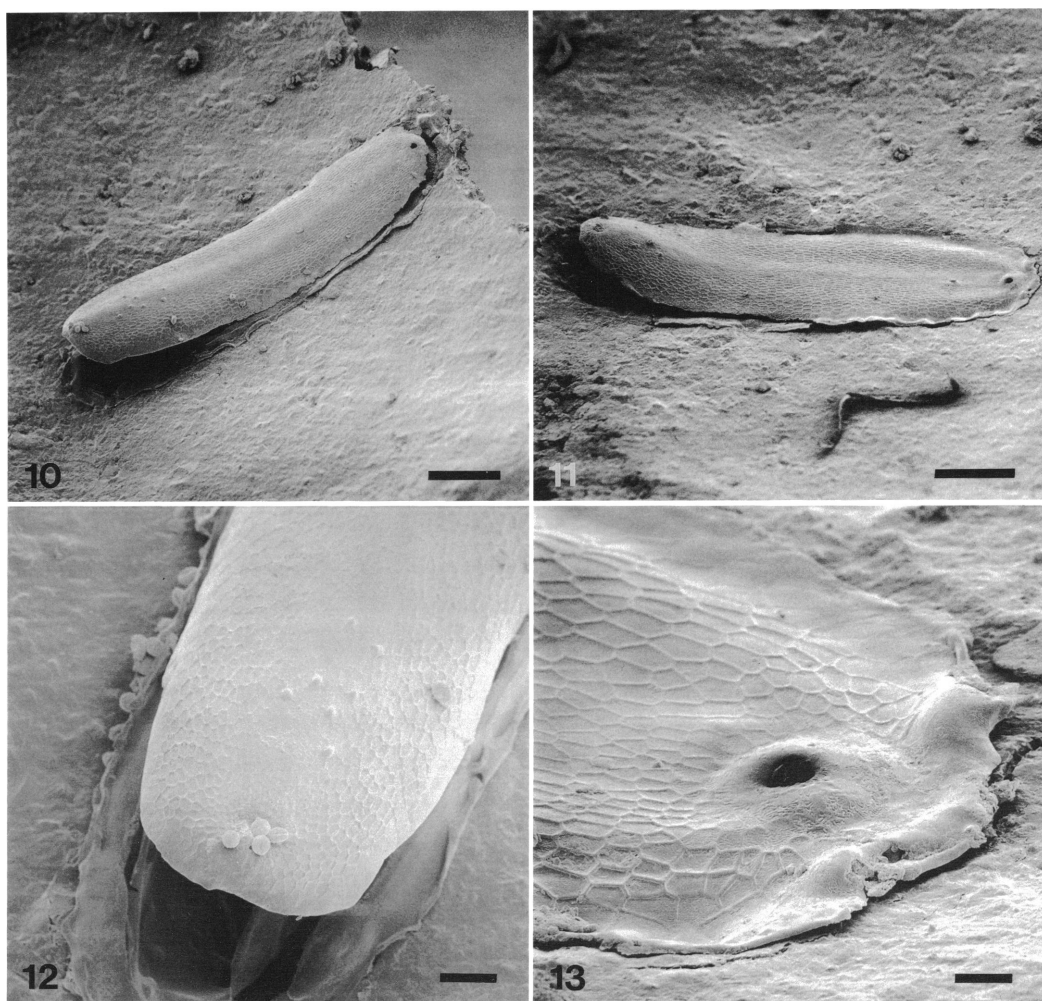
larval behavior involving mandibles are known: In most diphaglossine bees, chewing the cell wall seems to be an attempt to perforate the thick cell lining, thereby allowing fecal liquid to drain into the substrate (Rozen, 1984). In the case of fideliine bees (Rozen, 1977), soil particles (mostly sand) are ingested from the substrate after food consumption and later discharged through the anus, providing a rigid inner layer to the cocoon. Neither of these situations applies to *Ancylandrena* since its cell lining is not particularly thick, the feces are not very moist, and no cocoon is spun (nor soil found in the gut of predefecating or early postdefecating larvae). More observation on the activities of early postdefecating bee larvae may be revealing.

As is the case with all known andrenids, neither species of *Ancylandrena* spins a cocoon. Feces were thinly deposited on all parts of the cell wall as flattened ribbons that radiate forward from the cell rear. In several cases (but perhaps routinely) the fecal smears were also deposited on the cell closure.

Postdefecating larvae were active at first. Although usually remaining quiet and curled, they were able to uncurl and curl their bodies slowly, but they seemed incapable of opening and closing their mandibles. The posterior end of the keeled venter (fig. 14) of the postdefecating larva (see taxonomic description, below) effectively became a terminal spine to the body and may function to permit the larva to rotate in the cell. Postdefecating larvae of *Ancylandrena larreae* recovered in August no longer moved. On the other hand, the two postdefecating larvae of *A. rozeni*, which appeared to come from cells of a previous generation, could still curl and uncurl their bodies.

BIOLOGICAL NOTES ON *HEXEPEOLUS*

Female *Hexepeolus rhodogyne* searched for nests of *Ancylandrena larreae* at 8 mi northwest of Wickenburg in May 1993 as described in Rozen (1992). One female attempted to reach a nest entrance covered with a plastic drinking glass. This suggests that *Hexepeolus* females "trap-line" nests, that is, return to



Figs. 10–13. SEM micrographs of vacated chorions of *Hexepeolus rhodogyne* in cell wall of *Ancylandrena larreae*. 10, 11. Entire dorsal surface of eggs showing raised slit at anterior end through which the larvae had emerged, and small hole at posterior end. Scale = 200 μm . 12. Closeup of anterior end, with micropyle partly obscured by pollen grains. Scale = 50 μm . 13. Closeup of hole at posterior end. For discussion, see text. Scale = 20 μm .

previously discovered nests in attempts to oviposit in new cells as they are constructed.

Two cells contained vacated egg chorions of *Hexepeolus* embedded in the cell walls. One cell contained a single egg; the other, seven eggs. The morphology of the chorions and egg depositions corresponded closely to those reported by Rozen (1992). However, two new features were revealed. 1) The posterior end² of dorsal (exposed) surface of the

chorion bore a small hole, approximately 18 μm in diameter ($N = 2$) (figs. 10, 11, 13), in addition to the micropyle at the anterior end (fig. 12). This hole had not been detected in the earlier study (Rozen, 1992: fig. 10), which was based on unhatched eggs. Hence the hole may become visible only after eclosion. Its function is unknown, although respiration through an otherwise coriaceous dorsal surface comes to mind. 2) The dorsal (exposed) surface of the eggs (figs. 10–12) had fewer papillae than the one shown in Rozen (1992: fig. 10), and far more papillae dotted the anterior end of the surface than the posterior

²The anterior and posterior ends of the eggs were deduced from the fact that emerging larvae must have crawled *forward* out of the narrow slit.

end. Number of papillae appears to be subject to individual variation.

In hatching, the chorion splits along the undersurface of the flange (Rozen, 1992: figs. 8, 9) where it attaches to the transparent part of the chorion that covers the lower (embedded) part of the egg. In most cases this splitting extends around the circumference of the lower part except at a point at the posterior end. Consequently, most of the dorsal surface of the chorion was separated from the lower part, to which it was hinged at the end. In one case, the splitting stopped about a quarter of the way from the end. Although the dorsal surface tended to be flat near the hinge, it became more curved in cross section toward the anterior end, probably because of the natural curvature of the surface when its sides were no longer attached to the cell wall. At eclosion, the anterior end of the dorsal surface lifted away from the lower part only far enough to permit the larva to crawl out of the crack (figs. 10–12). When viewed from above, a hatched egg scarcely looked different from one that had not hatched; the crack was not visible.

The chorion of the dorsal surface was white, semiopaque, and coriaceous (fig. 5). The rest of the chorion, embedded in the cell wall, was thin, transparent, and colorless. Shiny material around the edge of the transparent chorion indicated that the female *Hexepeolus* had applied a secretion that sealed the space between the egg and the cell lining. Dorsal surfaces of eggs were 1.2–1.3 mm long ($N = 6$) and 0.33–0.44 mm at maximum width.

The eggs and egg depositions of *Hexepeolus* and *Neopasites* (Torchio et al., 1967) agree in that, in both genera, eggs are deposited in the host's cell wall so that the entire length of the egg is nearly flat, exposed, and more or less flush with the wall. Furthermore, with both parasites, the exposed surface is thick and opaque or semiopaque, while the rest of the chorion is thin, fragile, and transparent. The crack between the cell wall and the egg is covered, presumably so as to be undetectable by a host female. Eggs of *Neopasites*, however, do not have a flange, and, on hatching, a circular or semicircular emergence hole appears at the front end of the exposed surface. Hence, it is uncertain whether the similarities of these two genera with respect to their eggs are evolutionary convergences or shared apomorphies.

The cell with seven *Hexepeolus* chorions also contained the remains of seven dead first instars of the cleptoparasite (to be described elsewhere) as well as two dead triungulins (representing two very different species). It is unknown why at least one inhabitant of the cell had not survived. The successful hatching of all *Hexepeolus* eggs strongly suggests that the egg stage is not subject to attacks by first-instar conspecifics.

Two postdefecating larvae of *Hexepeolus rhodogyne* were recovered from cells of *Ancylandrena larreae* in August. Both, totally quiescent, were oriented with their heads next to the cell closures, the anterior part of their bodies curved, and the posterior end straight. Parts of head capsules of previous instars were randomly attached to their body surfaces, and, on one larva, parts of head capsules of two first instars attested to there having been more than one *Hexepeolus* egg deposited in the cell.

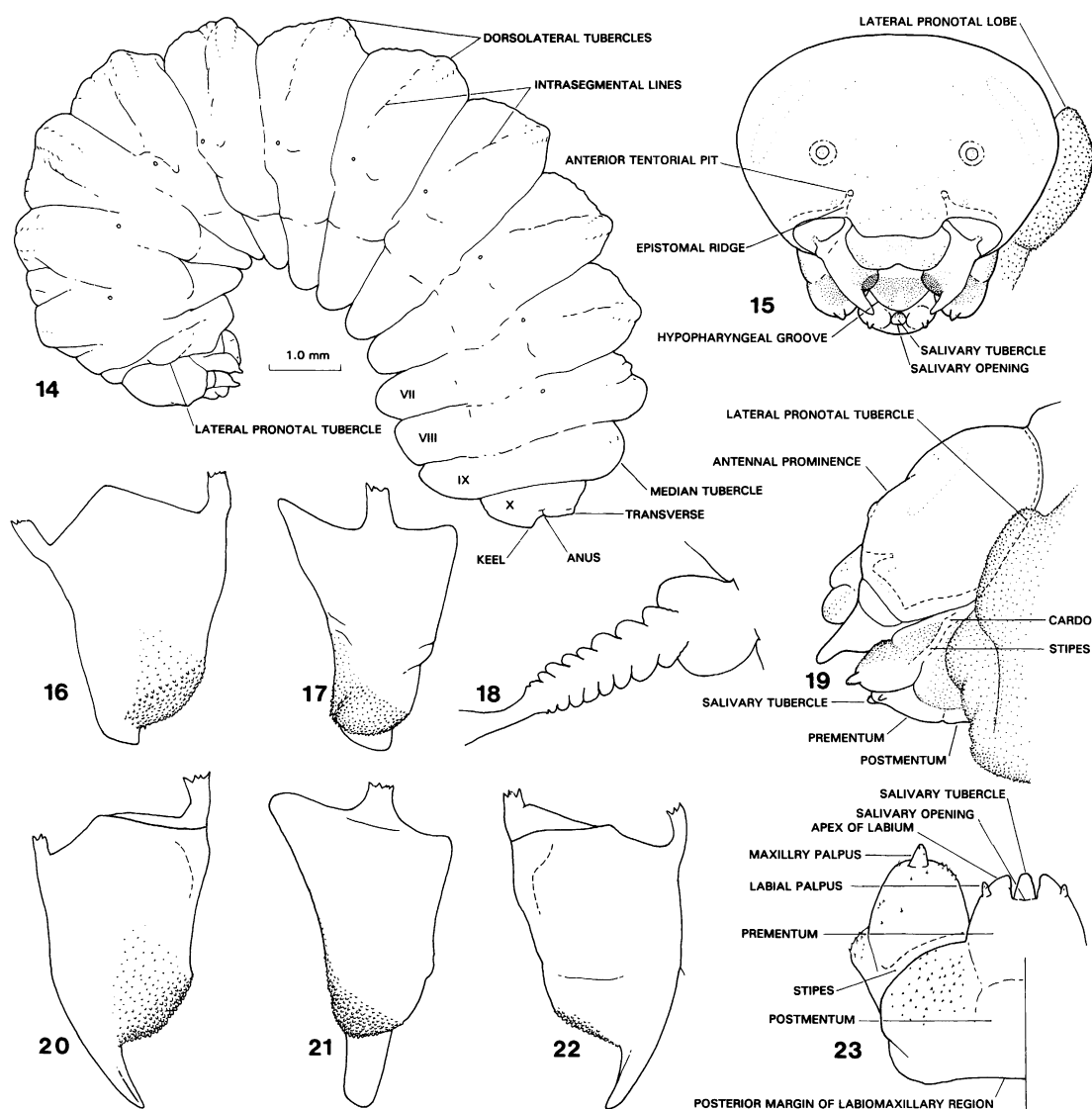
MATURE LARVA OF *ANCYLANDRENA*

Ancylandrena larreae

Figures 14–23

DIAGNOSIS: Mature larvae of *Ancylandrena larreae* and *A. rozeni* are quite distinct from larvae of other andrenids. The presence of transverse rather than conical dorsolateral body tubercles and vague apical labral swellings rather than acutely pointed paired labral tubercles that arise from the labral disc immediately set both apart from larval Panurginae. Larval *Ancylandrena* can be distinguished from the mature larva of *Euherbstia excellens* Friese by many features (Rozen, 1993a): The latter lacks paired lateral spiculated pronotal swellings, and it possesses conspicuous spiracular tubercles (postdefecating larva only), a large tubercle on the outer surface of the mandible, and a distinct epistomal ridge between the anterior tentorial pits, all features at variance with *Ancylandrena*. Although mature larvae of *Andrena* and *Ancylandrena* are similar, *Ancylandrena* lacks the pronounced swelling on the vertex and projecting antennal prominences characteristic of *Andrena*, and its postdefecating larva uniquely possess the posteriorly pointed projection on the venter of abdominal segment X.

See diagnosis of larva of *Ancylandrena rozeni* for comparison of *A. rozeni* and *A. larreae*.



Figs. 14–23. Postdefecating larva of *Ancylandrena larreae*. 14. Entire larva, lateral view. Larva drawn immediately after defecation, hence mandibles unworn. 15. Head of same, frontal view. Only left lateral pronotal tubercle depicted. 16, 17. Worn right mandible of another larva, dorsal and inner views. 18. Spiracle. 19. Head of larva with unworn mandibles, lateral view. 20–22. Unworn right mandible, dorsal, inner, and ventral views. 23. Enlarged view of undersurface of labiomaxillary region (mostly right side), ventral view. Scale refers to figure 14.

In the following description, comparisons are made with larvae of *Euherbstia excellens* (Rozen, 1993a: figs. 4–14) and *Andrena* as represented by *A. accepta* Viereck (Rozen, 1973: figs. 3–10). The format follows Rozen (1993a). The description is based only on the postdefecating larva because the predefecat-

ing larva was not studied in detail. It is probably safe to assume that the predefecating form agrees in most, if not all, respects to that of *Ancylandrena rozeni*, treated below.

LENGTH: Approximately 10 mm.

HEAD (figs. 15, 19): Integument of head capsule with scattered nonsetiform sensilla,

faintly pigmented except mandibles darkly pigmented apically.

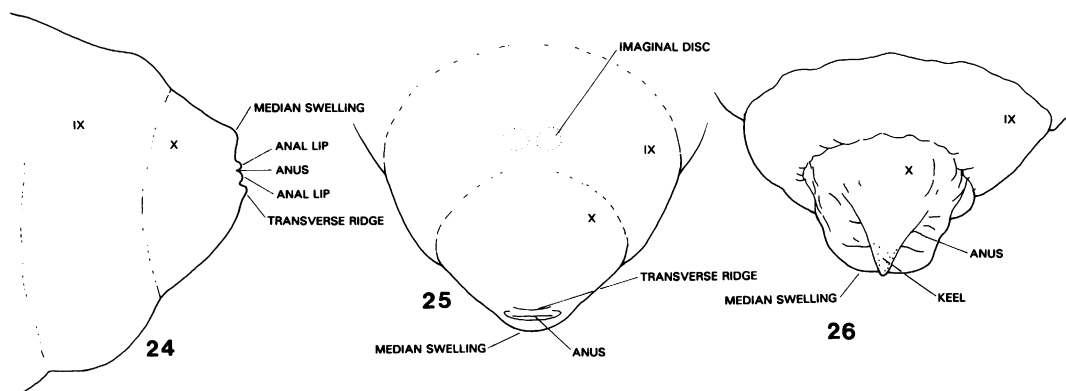
Head size (fig. 14) moderate by comparison with rest of body. Vertex not strongly produced on each side above antenna, so that in profile (fig. 19) top of head rounded, not as flat as in *Euherbstia*, but much less produced than that of *Andrena*. Front-to-back length of head capsule normally short as in most other bee larvae. Tentorium well developed but not robust; anterior tentorial pits normal in position on face; posterior pits normal in position; postoccipital ridge moderately developed; hypostomal and pleurostomal ridges well developed; epistomal ridge below (laterad of) anterior tentorial pits well developed, absent mesad of pits; median longitudinal thickening of head capsule absent except immediately in front of postoccipital ridge. Parietal bands evident. Antennal prominences weakly developed, as in *Euherbstia*, in sharp contrast to those of *Andrena*; antennal papilla not projecting, on one specimen bearing 4 sensilla on one side, 6 on other side, and on another specimen, 3 and 5, respectively; antennal disc moderate in size. Labrum produced apicolaterally on each side, somewhat similar to *Andrena*; labral apex shallowly emarginate medially; median part of labrum bearing very fine, sharp-pointed spicules; epipharyngeal surface with large, sharp, nonseiform spicules; this surface without large preoral lobe.

Mandibular base robust (figs. 16, 17, 20–22); on unworn specimen, apical part slender but tapering only slightly as seen in adoral view (fig. 21) and with apex rounded; hence apical part bladelike, somewhat curved seen in dorsal or ventral views (figs. 20, 22); flat inner surface directed adorally; upper and lower apical edges nonserrate, nearly smooth; on worn specimens, apical part greatly eroded, short (figs. 16, 17); cuspal area produced, broad as seen in adoral view, regularly denticulate, rounded, not produced into toothlike projection as in *Euherbstia*; denticles tending to be fine and even, as in *Euherbstia*; denticles on worn mandibles also partly worn; dorsal surface with some fine spicules; outer surface without swelling, in contrast to pronounced swelling in *Euherbstia*.

Labiomaxillary region moderately recessed, about as in *Andrena*, not greatly re-

cessed as in *Euherbstia*. Maxilla well separated from labium apically, its apex not produced mesially, much of its surface spiculate; galea not evident; palpus moderately large, longer than its basal diameter; cardo and stipes sclerotized but not pigmented; articulating arm of stipes deeply embedded in hypopharyngeal groove. Labium weakly divided into prementum and postmentum; labial palpus shape like maxillary palpus, but about one-half as long; labial apex strongly produced on each side of salivary tubercle as seen in ventral view (fig. 23). Salivary tubercle (termed salivary swelling in Rozen, 1993a) strongly projecting, spiculate dorsally; salivary opening a curved, transverse slit ventrad of salivary tubercle, this arrangement similar to that of *Andrena*. Hypopharynx more or less bilobed on most specimens, spiculate; hypopharyngeal groove deeply separating hypopharynx from base of labium.

BODY: Integument only moderately rigid, much less so than that of *Euherbstia*; integument conspicuously wrinkled; setae absent; sensilla inconspicuous; most segments evenly, extensively spiculate ventrally; some segments with areas of fine spiculation dorsally; spiracular tubercles absent. Prothorax (figs. 14, 15, 19) with pair of strongly spiculate rounded lateral tubercles immediately behind head capsule; most body segments with pair of very low, transverse dorsolateral tubercles on caudal annulet; intersegmental lines deeply incised; intrasegmental lines evident on most body segments; on abdominal segment IX, dorsolateral tubercles coalesced, forming single median raised smooth area; abdominal segment X attached centrally to IX (fig. 14); segment X with transverse apical dorsal median swelling (fig. 14); venter of abdominal segment X laterally compressed forming median posteriorly pointed keel (fig. 14); apex of keel more or less spiculate (degree of spiculation apparently quite variable in both species). Anus a transverse slit; anal area recessed so that dorsal transverse swelling and apex of ventral keel projecting posteriorly beyond anus and anus more or less hidden by wrinkled integument. Spiracles (fig. 18) moderate in size, subequal, not on tubercles; peritreme flat; atrium projecting slightly beyond integument; atrial wall smooth; primary tracheal opening with cir-



Figs. 24–26. *Ancylandrena rozeni*, mature larvae. 24. Apex of abdomen of predefecating form, lateral view. 25. Same, ventral view. 26. Apex of abdomen of postdefecating larva, ventral view.

cular collar; collar with concentric ridges; subatrium with approximately eight chambers. Sex characters unknown.

MATERIAL STUDIED: 1 postdefecating larva, 8 mi northwest of Wickenburg, Maricopa Co., Arizona, collected as predefecating larva May 4, 1993, preserved as postdefecating larva May 17, 1993 (J. G. and B. L. Rozen); 1 feeding larva, same data except collected May 4, 1993, preserved May 8, 1993, trying to molt to last stage; 15 postdefecating larvae, same locality, August 24, 1993 (J. G. Rozen).

Ancylandrena rozeni

Figures 24–26

DIAGNOSIS: Postdefecating larvae of *Ancylandrena rozeni* and *A. larreae* are nearly identical. The few differences expressed below will be of doubtful value for distinguishing between these two species although the relative differences in size are real and are reflected in adult size as well as size of brood cells.

LENGTH: Approximately 8.5 mm.

HEAD: As described for *Ancylandrena larreae* except for following: Each antennal papilla with four sensilla on one specimen. As in *A. larreae*, mandible of predefecating larva with long, bladelike apex; that of postdefecating larva with apex greatly shortened, presumably because of wear. Salivary tubercle only indistinctly spiculated dorsally.

BODY: As described for *Ancylandrena larreae*, including keellike modification of abdominal segment X (fig. 26) on postdefecat-

ing form, except for following: integument of predefecating larva smooth, without wrinkles characteristic of postdefecating form; predefecating larva without spicules on venter or abdominal segment X; dorsolateral tubercles best seen on postdefecating larva because their apices smooth relative to wrinkled integument elsewhere; on predefecating larva these tubercles nearly indiscernible, appearing as smoothly raised caudal annulet; intersegmental lines generally weakly incised on predefecating larva except more pronounced anteriorly; intrasegmental lines evident, more pronounced on postdefecating rather than predefecating larva; on predefecating larva coalesced dorsolateral tubercles of abdominal segment IX obscure; on predefecating larva abdominal segment X attached somewhat dorsally (fig. 24); segment X with dorsal median swelling above anus on predefecating larva (figs. 24, 25); on postdefecating larva dorsal median swelling more transverse (fig. 26) as in *A. larreae*; venter of abdominal segment X (figs. 24, 25) broadly curved with low transverse ridge immediately below anus on predefecating larva; on postdefecating larva venter now laterally compressed forming median posteriorly pointed keel (fig. 26) as in *A. larreae*; on predefecating larva, anus surrounded by low lips (figs. 24, 25); on postdefecating larva (fig. 26), anal area recessed as in *A. larreae*; male ventrally bearing paired imaginal discs in posterior half of abdominal segment IX (fig. 25); corresponding cuticular scar evident; female with paired imaginal discs ventrally in abdominal segments VII,

VIII, and IX, each pair closer together than in preceding segment.

MATERIAL STUDIED: 2 postdefecating larvae, 1 predefecating larva, Desert Station, east side of Tucson Mts., Pima Co., Arizona, April 15, 1993, predefecating larva preserved April 18, 1993 (J. G. Rozen).

RELATIONSHIPS OF *ANCYLANDRENA* BASED ON ITS MATURE LARVA

The phylogenetic relationships of *Ancylandrena* were analyzed using James S. Farris' Hennig86 Version 1.5 program (Farris, 1988). This analysis, based solely on features of mature larvae, compared the genus with *Andrena*, *Euherbstia*, *Protandrena*, Oxaeidae, and Stenotritidae, just as *Euherbstia* had been compared to the other taxa in Rozen (1993a). *Protandrena*, one of the more primitive panurgines, was used to represent the Panurginae.

The characters list in Rozen (1993a: table 1) were used (plesiomorphy = 0; apomorphy = 1, 2) except character 17 was reevaluated and characters 24 and 25 were added, as follows:

17. Area above salivary opening not or scarcely produced, not surrounded by recessed area (0); area above salivary opening produced, surrounded by broad recessed area (1); area above salivary opening sharply produced as a tubercle-like projection, surrounded by distinct, deep, narrow trough ("curved groove" of McGinley, 1981) (2). By interpreting the character this way, the character states for *Andrena* and *Protandrena* are changed to (2) in the matrix (table 1; compared with Rozen, 1993a: table 2). The last state is considered derived because the well-defined salivary tubercle in *Andrena*, *Ancylandrena*, and the primitive panurgines (lost in some of the higher panurgines) does not occur elsewhere among non-cocoon-spinning bee larvae. It is uncertain whether this is a transformation series and whether the conditions exhibited in oxaeids and *Euherbstia* are homologous.
24. Prothorax without pair of lateral, spiculated tubercles immediately behind posterior tentorial pits (0); with pair of

TABLE 1
Data Matrix for Analysis of Relationships of *Euherbstia*, *Ancylandrena*, *Andrena*, Panurginae (*Protandrena*), Oxaeidae, and Stenotritidae, Based on Mature Larvae

(Character codings given in Rozen, 1993a, and herein)

Taxon	Character states							
	01234		56789		01234		56789	
	0	1	0	1	0	1	0	1
Ancestor	00000	00000	0?000	00000	00?00	0		
<i>Euherbstia</i>	00100	00100	01120	21101	01100	0		
<i>Ancylandrena</i>	00000	00101	01010	11200	10001	1		
<i>Andrena</i>	10011	00101	01010	11200	10001	0		
<i>Protandrena</i>	10011	10001	00010	12200	20001	0		
Oxaeidae	01100	11010	10021	22111	00210	0		
Stenotritidae	00000	0000?	0?110	12000	00000	0		

large, well-defined, lateral tubercles (figs. 14, 15, 19) bearing conspicuous spicules, these tubercles near anterior prothoracic margin and tending to project forward over posterior tentorial pits (1). Lateral spiculated prothoracic swellings, though less defined than those of *Andrena*, *Ancylandrena*, and *Protandrena*, also occur in at least some Nomiinae and Rophitinae, but these are doubtfully homologous with the distinct prothoracic swelling of these andrenids. Lateral prothoracic tubercles are lost in some of the higher panurgines.

25. Venter of abdominal segment X on postdefecating larva rounded as in most other bee larvae (0); narrowing posteriorly into a keellike structure that terminates as a ventral median spine (1). The latter is an autapomorphy of *Ancylandrena*.

Table 1 is the character matrix. The analysis was executed with the ie command, with autapomorphies (1, 6, 8, 10, 14, 18, 21, 23, 25) coded inactive. Contrary to Rozen (1993a), character 22 was coded additive, thereby making it possible to be included in figure 27. The result was a single tree (fig. 27) with a length of 39, consistency index of 82, and a retention index of 70. This tree is consistent with that in Rozen (1993a: fig. 15) insofar as they treat the same taxa. The present tree shows that *Ancylandrena* is a sister

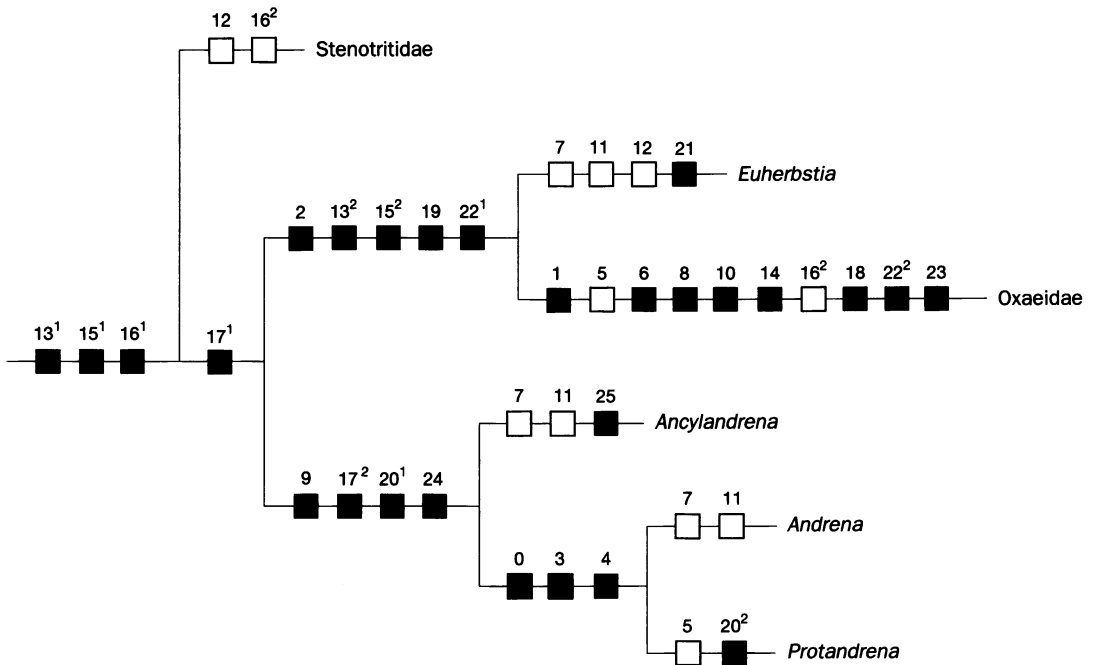


Fig. 27. The single most parsimonious cladogram of *Ancylandrena*, *Euherbstia*, *Andrena*, *Protandrena*, the Oxaeidae, Stenotritidae, and a hypothetical ancestor, based on characters of mature larvae. Solid squares are unique character states; open squares are parallel states. Tree length 39, consistency index 82, and retention index 70. For further explanation see text.

group to *Andrena-Protandrena*, all sharing (9) a reduced mandibular tubercle, (17²) a salivary tubercle surrounded by a deep groove, (20¹) dorsolateral body tubercles, and (24) a pair of distinct spiculated lateral pronotal tubercles. That they should be related is not surprising, because bee specialists have not questioned this relationship on the basis of adult characters.

However, the lack of close relationship of *Euherbstia* to this group, demonstrated in Rozen (1993a), is still noteworthy.³ Furthermore, the closer agreement of *Andrena* to *Protandrena* rather than to *Ancylandrena* is unexpected, and, if supported by additional studies, would create a paraphyletic group of the Andreninae, as currently constituted. Larval synapomorphies of *Andrena-Protandrena* distinguishing them from *Ancylandrena* are: (0) their strongly angulate vertex

as seen in lateral profile, (3) missing midsection of the epistomal ridge, and (4) strongly produced antennal prominences. On the other hand, Michener (1986) listed two (or perhaps three) adult characters that seem to indicate that the Andreninae are holophyletic. Hence, further judgment of the holophyly-paraphyly of the Andreninae awaits additional evidence, perhaps in the form of newly discovered synapomorphies or from examination of larvae of other andrenine genera (*Megandrena*, *Orphana*, and *Alocandrena*). Surely the discovery of mature larvae of these genera will be of great interest in that it will permit evaluation of phylogenetic relationships for the entire subfamily based on larval features, which can then be compared with Michener's (1986) study of the adults of the subfamily.

From the present analysis it must be assumed that the appearance of (7) a finely spiculated labrum and (11) loss of subapical mandibular tooth in each of *Andrena*, *Ancylandrena*, and *Euherbstia* were separate evolutionary events.

³Earlier, Moure (1950) also questioned the placement of *Euherbstia* in the Andreninae on the basis of adult features and placed it in its own subfamily, the Euherbstiinae.

APPENDIX

Description of
Ancylandrena rozeni, new species

by Thomas J. Zavortink

Ancylandrena rozeni is described at this time to provide a Linnaean name for the description of its nesting biology and immatures by Jerome G. Rozen, Jr. When I revised *Ancylandrena* (Zavortink, 1974), I saw one male of this species and, almost certainly, two females, but I failed to associate the sexes with each other and failed to recognize either of them as representing an undescribed species.

To simplify comparison of *A. rozeni* with other species in the genus, the following description is patterned after those in my revision of *Ancylandrena*.

DIAGNOSIS: Diagnostic comparisons of this species with others are incorporated in the Discussion.

BOTH SEXES: Head. Greatest width 1.18–1.27 times length from top of vertex to apex of clypeus. Ocelli normal. Clypeus strongly protuberant, moderately long; preapical transverse groove strong, conspicuously angled or curved away from apex laterally. Punctuation very fine and very close in center of face, becoming coarser dorsad. Integument roughened. Mouthparts. Apex of labrum gently convex. Mandible with abductor swelling at base of outer surface blisterlike.

Mesosoma. Pubescence of mesoscutum relatively sparse. Punctuation predominantly moderately fine and moderately close in anterior portion of mesoscutum. Integument smooth or nearly so on anterior portion of mesoscutum and disc of scutellum.

Metasoma. Integument of disc of terga II–IV roughened.

MALE: Length, exclusive of antennae, 8.5–9.5 mm. Length of fore wing 6.0–6.5 mm. Width of head 2.8–2.9 mm.

Head. Width of face at level of clypeal base 0.83–0.88 length from lower edge of median ocellus to apex of clypeus. Eyes convergent ventrally. Pale mark of lower paraocular area cream colored to yellowish, slightly to conspicuously broadened below, more or less narrowly to broadly triangular or L-shaped; its inner margin concave to nearly straight; clypeus black. Pubescence of clypeus dense, long. Hair on upper part of face and vertex dark brown to blackish. Antenna. Flagellum short; segment 1 slightly longer than segment 3; segment 2 broader than long; segments 3–10 1.26–1.54 times as long as broad. Mouthparts. Mandible black with reddened apex; blisterlike abductor swelling yellowish brown.

Mesosoma. Propodeum long, basal portion moderately declivous. Most dorsal mesosomal hair

white, some light to dark brown or black on posterior half of mesoscutum and disc of scutellum; if most hair on disc of scutellum deeply pigmented, then additional light brown or grayish hair on axilla and edge of scutellum. Legs. Fore femur with long hair on posterior and lower surfaces. Wings. Fore wing sparsely pubescent basally.

Metasoma. Concavity of first tergum weakly to moderately developed, relatively inconspicuous. Pygidial plate deltoid; length 1.3–1.5 times basal width; lateral margin straight or concave; median keel moderately developed. Pubescence of terga relatively short and sparse, whitish; terga II–V without apical fascia or fringe, but II–IV with band of short, brown, suberect hair along apical margin medially; hair of sternum II as long as hair of sternum I; sterna III, IV with complete, concave, apical fringe of long (laterally) to moderately long (medially) plumose hair; pubescence of proximal sterna white or some elongate hair tinged with tan. Punctuation of terga fine, moderately close. Distal sterna and genitalia. Sternum VI with gradulus curved toward antecosta medially, but not reaching it. Sternum VII with emargination between arms of caudal process U-shaped; basal portion of emargination densely pubescent; strongly pigmented distal portion of arms of caudal process broad, nearly circular; membranous flap of process narrow, with dense pubescence, the proximal hair short, simple, spiniform, the distal hair long, densely plumose. Sternum VIII with caudal process moderately broad, conspicuously expanded at truncate apex; dorsolateral edge of process without flange; pubescence of side and apex of process dense. Gonoforceps slightly curved ventrad distally; apex pointed in ventral aspect; subapical angle directed ventrolaterally. Volsella with cuspis and digitus separated by deep notch with sensilla basiconica on its walls. Aedeagus strongly bent, the distal portion directed ventroposteriorly; distal lobe of aedeagus not expanded.

FEMALE: Length, exclusive of antenna, 9.4–11.0 mm. Length of fore wing 6.2–6.7 mm. Width of head 3.0–3.2 mm.

Head. Width of face at level of clypeal base 0.93–0.97 length from lower edge of median ocellus to apex of clypeus. Eyes slightly convergent ventrally. Preapical transverse groove of clypeus densely setaceous medially. Integument uniformly black. Hair on upper part of face and vertex dark brown to black. Antenna. Flagellum moderately long, segment 3 broader than long, segments 4–9 as broad as long to slightly longer than broad. Mouthparts. Mandible black with reddened apex; blisterlike abductor swelling yellowish to yellowish brown or brown.

Mesosoma. Propodeum long, the basal portion

moderately declivous. Dark brown to blackish hair on posterior half of mesoscutum and disc of scutellum; dirty white to grayish or brownish hair on edge of mesoscutum, edge of scutellum, metanotum, and axilla. Legs. Pubescence of coxae, trochanters, and femora predominantly white; pubescence of outer surface of fore and mid tibiae and basitarsi light brown to brown; scopal hair on outer surface of hind tibia dirty white anteriorly, grayish brown to brown basally and, to a lesser degree, to apex posteriorly; scopal hair on hind basitarsus light grayish brown to brown basally, becoming darker brown distally.

Metasoma. Concavity of first tergum moderately conspicuous. Long hair of tergum I white; short outstanding hair of terga II–IV predominantly dark brown to blackish; apical fascia of terga II–IV complete or very narrowly interrupted medially on segment II; hair of apical fasciae closely appressed to integument; prepygidial and pygidial fimbriae chocolate brown to blackish-brown medially, becoming lighter or white laterally; scopa poorly developed, present on sterna I, II; sterna III, IV with hair short and fine, more similar to hair of sternum V than to that of sternum II; pubescence of proximal sterna white or tinged with tan or gray; hair of sternum VI brown. Punctuation of terga very fine, close, inconspicuous.

TYPE MATERIAL: Holotype male, allotype female, and 2 male paratypes from W. side Tucson Mts., Pima Co., Arizona, IV-16-93, on *Marina parryi* (J. G. Rozen; American Museum of Natural History). Additional paratypes: 1 male, 1 female, Arthropod Study Center, W. side Tucson Mts., Pima Co., Arizona, IV-16-93, on *Marina parryi* (J. G. Rozen; AMNH); 1 female, Desert Station, E. side Tucson Mts., Pima Co., Arizona, IV-14-93, *Ancylandrena* nest #1 (J. G. Rozen; AMNH); 1 female, Desert Station, U. of A., Tucson, Pima Co., AZ, 13 Apr 93 (A. A. Muñoz; University of Arizona); 2 females, SASI, Tucson Mts., Tucson, Pima Co., AZ, 16 Apr 93, (A. A. Muñoz; UA).

ETYMOLOGY: This species is named in honor of Jerome G. Rozen, Jr., in recognition of his contributions to the knowledge of bees.

DISCUSSION: Males of *Ancylandrena rozeni* are very similar to those of *A. larreae*, whereas females are almost indistinguishable from those of *A. timberlakei* Zavortink. Males of *A. rozeni* resemble those of *A. larreae* most significantly as follows: by having the abductor swelling at the base of the outer surface of the mandible somewhat enlarged, yellowish to tan or brown in color, and translucent, so that it is blisterlike; by lacking any indication of an apical fascia on metasomal terga II–IV; by having a concave apical fringe of moderately long to long hair on metasomal sterna III and IV; and by having the caudal process of metasomal ster-

num VIII moderately broad and conspicuously expanded at its apex. Males of *A. rozeni* differ from those of *A. larreae* by the following, often subtle, characteristics: (1) the smaller size, (2) the shorter clypeus, (3) the shorter flagellum of the antenna, (4) the smaller pale-colored face mark in the lower paraocular area, (5) the more widely spaced punctures and sparser pubescence on the anterior portion of the mesoscutum, (6) the greater extent of entirely dark brown to blackish hair on the upper part of the face, and (7) the broad, nearly circular, strongly pigmented distal portion of the arms of the Y-shaped caudal process of metasomal sternum VII. Females of *A. rozeni* resemble those of *A. timberlakei* in most respects, including the following important taxonomic characteristics: their small size; in having a relatively short clypeus; in having some scopal hair on the outer surface of the hind tibia grayish brown to brown; and in lacking a scopa on metasomal sterna III and IV. They differ slightly from those of *A. timberlakei* in: (1) the blisterlike development of the abductor swelling of the mandible, as described above for the male, (2) the greater extent of entirely dark brown to black hair on the upper part of the face, (3) the greater extent of light pubescence on the anterior part of the mesoscutum, all hair in front of the level of the middle of the tegulae being white, and (4) the greater extent of light-colored scopal hair on the outer surface of the hind tibia. All these differences, including the development of the abductor swelling of the mandible, are subtle, making separation of the females of these species very difficult. In *A. timberlakei*, the abductor swelling of the mandible of the female is not enlarged, but it is sometimes brown, rather than black, and somewhat translucent, so that it is not much different from its development in *A. rozeni*.

When I revised *Ancylandrena* (Zavortink, 1974), I studied one male and two females from the Santa Catalina Mountains, Pima County, Arizona. I considered the male to be *A. larreae* although I noted that it was smaller than average and had reduced face marks and shortened antennae. Even though I have not reexamined this specimen, it is undoubtedly *A. rozeni*. I considered the two females to be *A. timberlakei*. Although I have not reexamined them either, they are almost certainly *A. rozeni* also. If this is the case, then *A. timberlakei* is not known to occur east of western Arizona, and *A. timberlakei* and *A. rozeni* are allopatric.

Four males and two females of the type series were collected from the flowers of *Marina parryi* and two additional females without floral data bear appreciable amounts of the characteristic long, slender, cylindrical, white pollen of this species in their scopae. The male of *A. rozeni* that I misidentified as *A. larreae* in 1974 was collected at

the flowers of a related plant, *Dalea greggii* A. Gray.

Ancylandrena rozeni is presently known from only the Tucson Mountains and Santa Catalina Mountains in Pima County, Arizona. These are among the easternmost localities from which the genus has been recorded in the United States.

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