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The Chilean Bees *Xeromelissa nortina* and *X. sielfeldi*: Their Nesting Biologies and Immature Stages,
Including Biological Notes on *X. rozeni*(Colletidae: Xeromelissinae)

JEROME G. ROZEN, JR., AND ELI S. WYMAN¹

ABSTRACT

Herein are described the nests and their contents of *Xeromelissa nortina* (Toro and Moldenke) and of *X. sielfeldi* (Toro and Moldenke), found in the dry, high Atacama Desert of northern Chile. Nests of the former, discovered in 2014, contained linear cell series in the central pith channels of dead, broken twigs of *Baccharis*, revealing clear, cellophanelike cell linings that presumably control cell humidity. From the cells, postdefecating larvae were obtained, permitting their description and comparison with our meager understanding of other larval xeromelissines. Nests of *X. sielfeldi*, also found in broken dead twigs, were discovered and first studied in 1971 before the species was described and named, thereby delaying publication until now. Although similar in most respects to nests of *X. nortina*, they occupied abandoned beetle burrows. Toro and Moldenke provided information on eggs, predefecating larvae, and pupae, described herein. At the time of that discovery, adults of *X. rozeni* (Toro and Moldenke), a bee with an exceedingly long proboscis, were also active, permitting observation on their feeding habits, which are included herein.

INTRODUCTION

On a recent field trip to Chile, E.S.W. and Laurence Packer found adults of the bee *Xeromelissa nortina* (Toro and Moldenke) (body length 3.5–4.5 mm) visiting its presumed food plant,

¹ Division of Invertebrate Zoology, American Museum of Natural History.

Acantholippia tarapacana Botta (Verbenaceae), at Aguas Blancas, in El Loa Prov., Region II, elevation 2540 m. At the same site they discovered 12–15 nests of the same bee in broken twigs of *Baccharis* (Asteraceae) lying on the ground, often in the vicinity of live bushes. From nests they recovered and preserved a number of diapausing larvae, making possible the first description of the postdefecating larva of this species and only the third modern account of a larva of any taxon of the Xeromelissinae, although Claude-Joseph (1926) early on had illustrated larvae and nests of *Chilicola inermis* (Friese) and *C. friesei* (Ducke) (McGinley, 1989).

In 1971 J.G.R., accompanied by Luis Peña, found two species of *Xeromelissa* visiting flowers of *Nolana*² (Solanaceae) at Puquios, Atacama Province, Chile, and found nests of the smaller of the two. He made extensive notes on its nest and preserved an egg, several predefecating larvae, and pupae with adults in the collections of the American Museum of Natural History (AMNH). At the time of discovery, both species were unnamed, and therefore the project was suspended. However, Michener (1995: 333) commented on nesting habits of the smaller species by referring to it as an unknown species of *Chilimelissa* (now *Xeromelissa* according to Packer, 2008) collected from Puquios, Chile, by J.G.R. Toro and Moldenke (1979) revised the Chilean Xeromelissinae, describing and naming a number of new species. Now Packer has been able to identify adults of the species that made the nest collected by J.G.R. and Peña as *X. sielfeldi* (Toro and Moldenke). This makes possible a further account of its nesting biology and the first description of the egg, predefecating larva, and pupa of any Xeromelissinae. The larger species flying at the site was identified by Packer as *X. rozeni* (Toro and Moldenke).

Although these two field investigations occurred far apart in time, they both treat members of the same genus and together they provide a more complete understanding of the nesting biology and immature stages of this mostly South American subfamily. Specimens described herein are deposited in the AMNH.

BIOLOGY

NESTING BIOLOGY OF XEROMELISSA NORTINA (TORO AND MOLDENKE)

All nests were in dead, dried stems of *Baccharis*, and most were recovered from stems 6–11 mm in diameter, although the largest was 16 mm in diameter (fig. 2). It is unknown whether nests were also constructed in broken dead branches on living bushes. All nests occupied the central internal pithy channel, from which females removed the soft pith at the start of nest construction. No nests were recovered from burrows that had been created by beetle larvae, as evidenced by the lack of beetle feces in any of the channels, contrasting with the nest of *X. sielfeldi*, described below (fig. 19, arrows). Nest channels were approximately 3 mm in diameter and were filled with brood cells in linear series of 2–8 cells. Each cell was approximately 6 mm in length, and most in each series were arranged end to end.

² Although the species of *Nolana* was not identified at the time, it was almost certainly *Nolana villosa* I.M. Johnst. since J.G.R. again collected *Xeromelissa rozeni* at the same locality while it visited that plant species in 1999.

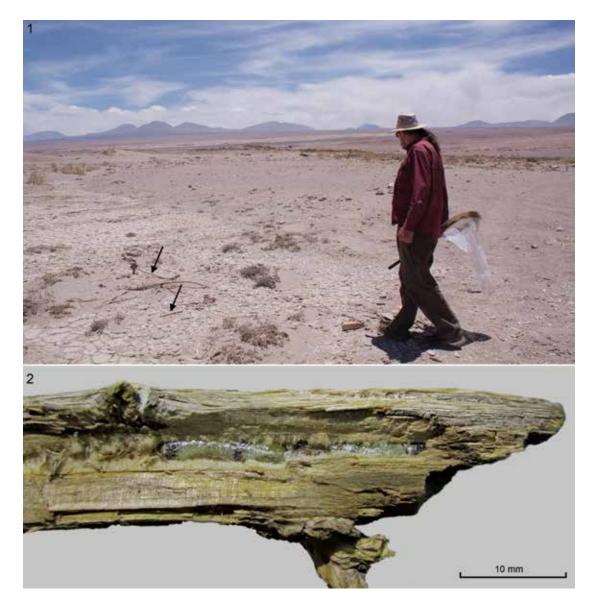
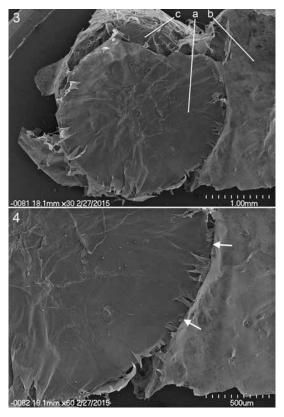


FIGURE 1. Laurence Packer at nesting area of *Xeromelissa nortina* at Region II: El Loa Prov.: Aguas Blancas, -23.2670 -67.9830, Chile, elevation: 2540 m. All nests were recovered from dead dry twigs and stems on the ground, such as those on the foreground, left side (arrows). The food source, locally termed *rica-rica*, can be seen growing behind Packer in the midbackground. FIGURE 2. Nest consisting of a cell series of *X. nortina* in the central pith channel of a large twig (diameter 16 mm) of *Baccharis* from that nesting area.

Cells were lined by a double layer of transparent, cellophanelike material. The outside layer was extremely thin³ while the inside layer, perhaps 0.1–0.2 mm distant from the outer

³ Rozen in Michener and Rozen (1999) was unable to identified an outer layer of the cocoon of the xeromelissine *Geodiscelis megacephala* Michener and Rozen but identified and illustrated the filaments that separate the inner layer from the substrate. This may suggest that in colletids the outer cocoon layer serves as a base to maintain the functional integrity of the inner layer.



FIGURES 3, 4. SEM micrographs of the cell lining of *Xeromelissa nortina*. **3.** Circular closure end (a) with piece of lining wall, right (b), and second layer of folded closure (c) behind, all showing smooth, nonporous texture of surfaces. **4.** Close-up of lining identified in figure 3 showing overlapping surfaces through which air exchange (arrows) may take place.

layer, was somewhat more substantial. Thin strands of silklike material connected the two layers, as has been noted for *Colletes* (Torchio, 1965; Rozen and Favreau, 1968). It seems likely that all known cases of double-layered cell linings in the Colletidae will be found to be similar to those described by Torchio (1984) for *Hylaeus leptocephalus* (Morawitz) (as *H. bisinuatus* Forster).⁴ The lining at the rear of the cell appeared as a curved continuation of the wall lining. At the front end (figs. 3, 4), cell linings were folded to cover the entrance after provisioning and egg deposition. Folds were presumably held in place with additional secretions, presumably as described for *Colletes c. compactus* Cresson (Rozen and Favreau, 1968). Thus, the front end tended to be flat, consisting of a number of transparent layers (fig. 3). The addition of Malpighian tubule secretions as described by Torchio (1965) was not detected, but obviously should be searched for on future studies. A thick wafer of black and brownish fecal material was present at one end of cells containing mature larvae or dead

⁴ Torchio (1984) used a different terminology for cell linings from that used here. The outer layer of the cell lining he termed "the lower cell wall" and he called the inner layer "the upper cell wall." His "cell base layer" is the lining at the rear (or posterior end) of the cell.

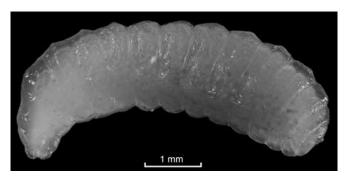
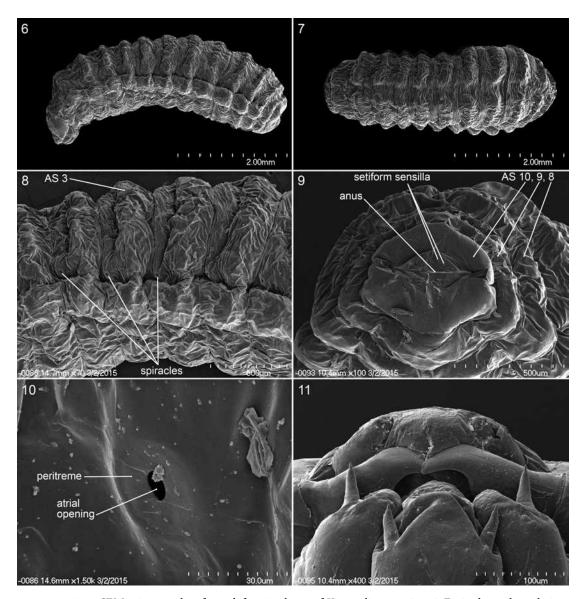


FIGURE 5. Macrophotograph of postdefecating larva of Xeromelissa nortina, lateral view, head to left.

pupae and adults. Cells were never separated by partitions made of soil or other opaque construction material, as is characteristic of many Megachilidae.

The similarity in appearance of the cell lining of this bee to that of the cocoons of many bees is noteworthy considering that they are not homologous structures. Cocoons are created by the last-stage larva whereas cell linings of all colletids are made by the nesting female in preparation for provisioning and egg deposition (although larval Diphaglossinae also spin cocoons). However, both probably serve the same general functions: moisture control within the cell and exclusion of parasites and predators. Provisions of many colletids are liquids or semiliquids, and cell linings probably prevent loss of liquids into substrates. After feeding, these same linings almost certainly maintain cell humidity. This may be especially important in the case of small-bodied *Xeromelissa* during the long hot dry periods in the Atacama Desert where water loss must be a major threat. Cocoons of cocoon-spinning bees are spun only after the larval feeding period and therefore do not provide provision maintenance; they protect only mature larvae or adults from water loss and invasion by parasites/predators.

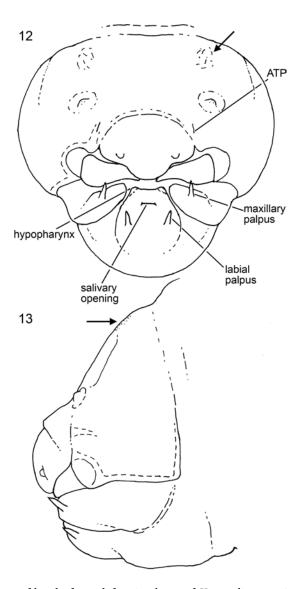
A number of recent papers have demonstrated that cocoons of megachilids (Rozen and Hall, 2011; Rozen et al., 2011; Rozen, 2013; Gotlieb et al., 2014) provide a watertight barrier that regulates water loss. This barrier is the smooth inner surface of the cocoon, which has (usually at its front end) a cluster of small holes, termed the air portal; this portal allows air exchange between the inside of the cocoon and the exterior, necessary for the many months wherein the live animal estivates and then hibernates. Similar air portals on a broad spectrum of apid cocoons are interpreted to indicate a similar function (e.g., Michelette et al., 2000; Rozen and Buchmann, 1990; Rozen et al., 2006). This has also been the case for the fenestrated cocoon "opercula" of Diphaglossinae (Colletidae) (Rozen, 1984) and the "filter areas" on the cocoons of some Rophitinae (Halictidae) (Rozen, 1993). No tests of the porosity of the *Xeromelissa* or any other colletid cell lining has been performed to date. However, the inner surface of the *Xeromelissa* cell also displays a smooth surface (fig. 3), convincingly similar to that of a cocoon, strongly suggesting that it too is a barrier to air exchange between the inside of the cell and the exterior. However, there is no obvious air portal. We here suggest that the air exchange route may be between the folds of the front end of the cell lining (fig. 4, arrows).



FIGURES 6–11. SEM micrographs of postdefecating larva of *Xeromelissa nortina*. **6.** Entire larva, lateral view. **7.** Same, dorsal view. **8.** Close-up of midbody segments showing transverse and lateral tubercles and position of spiracles, lateral view. **9.** Rear of larva, posterior view. **10.** Spiracle of abdominal segment 7 showing lack of atrial rim. **11.** Undersurface of front part of head, ventral view. Abbreviation: **AS**, abdominal segment(s).

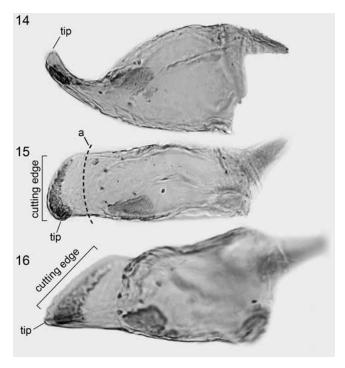
Nesting Biology of *Xeromelissa sielfeldi* (Toro and Moldenke) with Notes on Biology of *X. rozeni*

The following account of the nesting biology of *X. sielfeldi* with additional biological information on *X. rozeni* was extracted from a preliminary manuscript drafted immediately following J.G.R.'s trip to Chile in 1971 on which he was accompanied and assisted by the late Luis



FIGURES 12, 13. Diagrams of head of postdefecating larva of *Xeromelissa nortina*, front and lateral views, respectively. In frontal view internal head ridges depicted on left side by dashed lines. Abbreviation: **ATP**, anterior tentorial pit. Arrows indicate tubercles (see text).

Peña, the well-known Chilean naturalist (fig. 17). Their field site was in and around Puquios (elev. ca. 1600 m) along the extremely dry drainage systems called Quebrada San Andreas extending east-northeast into the Andean foothills. Because of extreme xeric conditions, vegetation was restricted to the nearly flat floor of the drainage system (fig. 17). It consisted almost exclusively of low-growing, scattered bushes representing perhaps four plant species. Due to extreme aridity, the area around Puquios is subject to considerable ranges in diurnal and seasonal temperatures, as well as wind conditions resulting in loss of fine soil, leaving the ground with a gravelly surface.

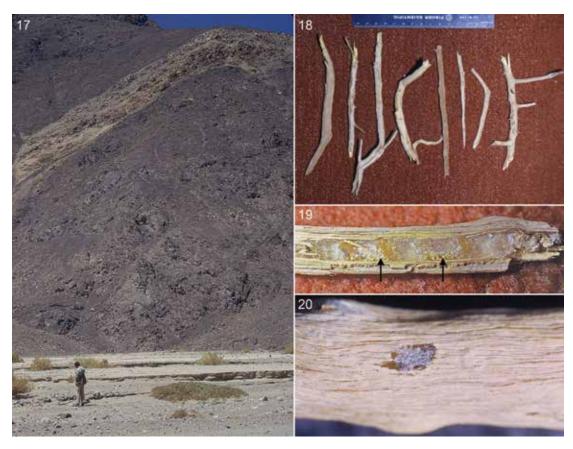


FIGURES 14–16. Microphotographs of right mandible of *Xeromelissa nortina*. **14.** Ventral view, showing strong apical curvature. **15.** Entire mandible with base of mandible in maximum profile, approximate inner view. Mandibular apex is thin and strongly scoop shaped (apicad of line a). **16.** Curved apex in maximum profile, approximate inner view.

The bee fauna of the region seemed impoverished, possibly because of lack of flowering plants. Although several species of *Centris* and a *Megachile* were collected, the most common bees were two species of xeromelissine bees: the smaller one, *Xeromelissa sielfeldi*, and the larger one, *X. rozeni*, characterized by its extremely long mouthparts (fig. 21). Both collected provisions from a then unknown species of *Nolana*³ (figs. 17, 26–31), which was in bloom on October 10, 1971, and also in October 1969 when first discovered by J.G.R. and Peña on a previous field trip. The information below refers to *X. sielfeldi*; nests of *X. rozeni* were not found, suggesting their nest-site requirements are different from those of *X. sielfeldi*. Certain identification of nests was possible because of pupae and dead adults in some, which were then compared with nests lacking them.

Approximately 15–20 nests of *X. sielfeldi* were found, six of which contained live larvae or pupae. Some of the others were from previous generations. All were in dead, dry twigs 5–10 mm in diameter, lacking bark, from unknown plants. Most twigs (fig. 18) were lying on the ground. The immature stages of this species must be able to withstand high temperatures, for the surface temperature on the ground where sticks were found is normally high during the heat of the day in summer. The conspicuous cell lining described below almost certainly plays an important role with respect to water conservation, in regard to the provisions and to the insect's body.

All nests were constructed in abandoned larval burrows of *Acmaeodera* (Buprestidae) (fig. 19), the exit hole of the beetle later becoming the entrance to the bee nest. Somewhat irregular in their diameters, burrows, including entrances, ranged from 1.5 to 3.0 mm. Not infrequently

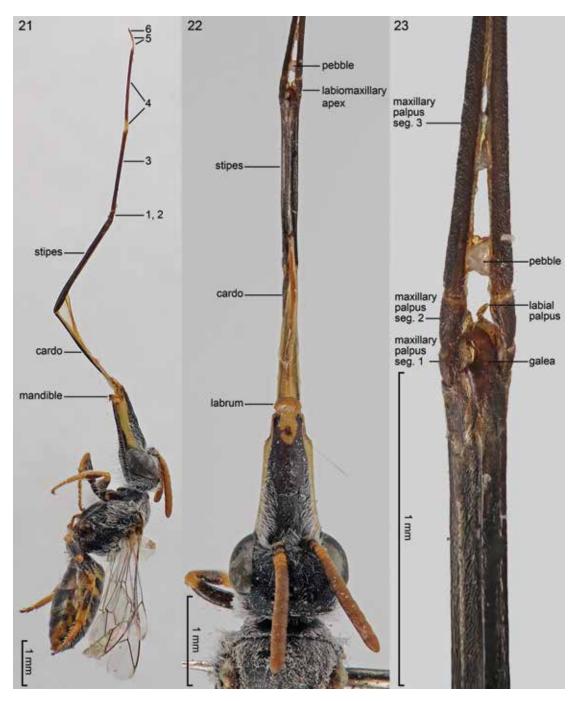


FIGURES 17–20. At Quebrada San Andreas at Puquios, Atacama Province, Chile, in 1971, at the time when *Xeromelissa sielfeldi* and *X. rozeni* were flying there and nests of the former were collected. **17.** View of habitat with Luis Peña standing, lower left, and large patch of blooming *Nolana*, lower right, behind Peña. **18.** Pieces of twigs containing nests of *X. sielfeldi*. **19.** Twig split open to reveal lined cells containing live immatures of *X. sielfeldi*, with remnants of *Acmaeodera* frass on outer surface of linings (arrows). **20.** Entrance to nest opening in twig revealing netlike closure.

live larval *Acmaeodera* were found in twigs occupied by bees. Female bees did not ordinarily modify the burrow walls, for in most cases the chewing ridges created by the beetle larva could be seen on burrow walls. However, beetle burrows are normally filled with frass, and in most nests only traces of beetle feces were detected (fig. 19, arrows), an indication that the female bees had removed most of the frass.

Cells were lined with a colorless, transparent, cellophanelike, double sheet of material (fig. 19) as described for X. nortina, above. Cells, defined by their lining, were 4.0–4.6 mm in length and 1.5 –2.5 mm in diameter, although their circumference was generally not circular because that feature is determined by burrow shape. Rounded at the posterior end, the lining at the front end was flat and consisted of three layers of silk, possibly but not certainly folded as described for X. nortina.

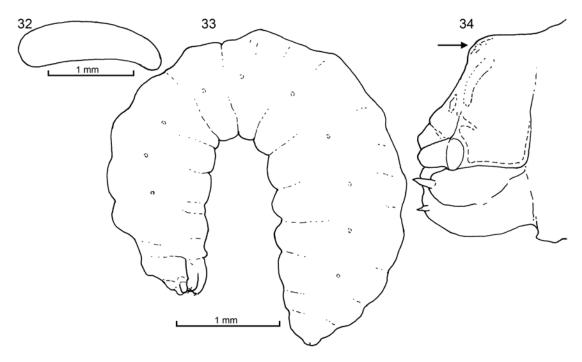
All nests were found by splitting the stems. Of five complete nests uncovered, the smallest contained five cells and the largest eight cells. Cells in a nest were arranged end to end in a



FIGURES 21–23. Macrophotographs of adult of *Xeromelissa rozeni*, showing projecting lower part of head with elongate labium, maxilla, and maxillary palpus. **21.** Entire body, lateral view, demonstrating extreme length of labiomaxillary region relative to body length. **22.** Head and labiomaxillary region, close-up, dorsal view. Note pebble accidentally trapped near base of paired maxillary palpi. **23.** Labiomaxillary apex, close-up, dorsal view, with right galea covering glossa.



FIGURE 24. Close-up of three terminal segments of maxillary palpus of *Xeromelissa rozeni*. FIGURE 25. Close-up of maxillary palpus of *Xeromelissa sielfeldi*. FIGURES 26–31. **26.** Blossom of *Nolana*, lateral view, showing deep corolla. **27.** Blossom of *Nolana* containing foraging adult presumably of *X. rozeni* in corolla. **28.** Same, but with male *X. rozeni*, covered with pollen about to depart. **29.** Blossom of *Nolana* with part of corolla showing recently killed female of *X. sielfeldi* with head at darkly bruised attachment (arrow) at base of filament. **30.** Same, another example (arrow). **31.** Male of *X. sielfeldi* in blossom of *Nolana*.



FIGURES 32–34. Diagrams of immatures of *Xeromelissa sielfeldi*. **32.** Egg, side view, anterior end up. **33.** Predefecating larva, lateral view. **34.** Head of same, lateral view.

linear series and oriented uniformly with front ends directed toward the nest entrance, though rarely an eclosed adult was found facing the wrong direction.

Females of both species of *Xeromelissa* transported pollen dry. The scopal areas of both are poorly defined, for pollen grains adhered to the bases of fore- and midlegs and to the ventral regions of the metathorax. Most of the pollen, however, was found on the hind coxa, tibia, and femur. The scopa was also well developed on the venter of the metasoma, especially the entire area of the second metasomal sternum and the posterior areas of the third and fourth sterna. The scopal setae were sparse, not obviously plumose, and moderate in length.

A partly provisioned cell of *X. sielfeldi* contained a semiliquid, buff-colored mixture of pollen and nectar, identical to that found in a completed cell. No odor was detected from either recently provisioned cells or cells containing mostly grown larvae. Food consistency did not change with time, and in all cases the pollen-nectar mixture was restricted to the rear of the cell. Because a cell must be constructed, provisioned, oviposited in, and enclosed before the next one can be started, the older cell in the series is always the one farthest from the nest entrance. Obviously the oldest immature bee is the farthest from the entrance.

In none of the cell series were cells found all the way to the nest entrance. The length of the tunnel between the last cell constructed and the entrance in one case was 8 mm long; in another case it might have been slightly shorter. The tunnel was filled with strands of silk, sometimes sufficiently dense to be cottonlike, to which adhered frass pellets from *Acmaeodera*. Near the entrance some of these strands become attached to the cell wall, so that the last 1.5

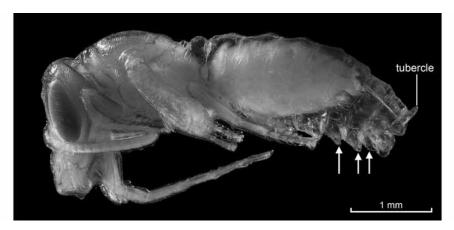


FIGURE 35. Macrophotograph of pupa of *Xeromelissa sielfeldi*, lateral view. Arrows point to downward-directed posterior margins of the metasomal sterna.

mm of the tunnel to the outer edge of the hole becomes a barrier of fine silklike webbing across the entrance (fig. 20) that the female constructs before departing. This netting obviously helps to barricade nest contents from parasites and predators.

Two eggs, described below (fig. 32) were recovered. Each appeared to float lengthwise on the exposed semiliquid surface of the provisions, so that more than half of one side of the chorion was submerged. However, at the time of oviposition, the eggs may have been differently positioned since the twigs had been picked from the ground, split open, and transported to the hotel before the eggs were found.

Small and intermediate-sized larvae were curled, floating on the exposed surface of the provisions, as has been described for *Scrapter* (Colletidae: Scrapterini) (Rozen and Michener, 1968) with part or perhaps most of one side of the body submerged in the liquidlike provisions. Older larvae obviously reorient, but their position is unknown. Provisions were completely consumed, as evidenced by cells containing pupae and no provisions. Development is reasonably rapid as indicated by cell series containing both first and last larval instars. Feces were applied presumably as moist pellets to the rear of the cell. Pellets hardened after adhering to one another, so that they formed a concave, hard, dark brown meconial mass against the rear of the cell with individual pellets discernable. Two pupae, described below (fig. 35), were found with heads directed toward the cell closure. How newly eclosed adults work their way through the hard meconial mass of the cell in front is not understood.

Adults of *X. sielfeldi* and *X. rozeni* were found on the same bushes of *Nolana* at the same time. There is a possibility, however, that bushes with smaller flowers were more attractive to the smaller species and bushes with larger flowers to the larger species. Flight behaviors were difficult, if not impossible, to observe because of strong winds at the time of observation. The fact that males and females of each species were found on the flowers suggested that mating takes place there, but no cases of copulation were noted.

Flowers of *Nolana* are deeply tubular (figs. 26–28), a fact that suggests that long mouthparts and greatly extended lower part of the face of both species are adaptive for feeding from

these flowers. In order to understand the anatomy of the mouthparts and how xeromelissines use them, a survey was undertaken of theses structure among various species of *Xeromelissa*, focused primarily on *X. sielfeldi* (fig. 25) and *X. rozeni* (figs. 21–24) but including other species as well. With most, the cardo and stipes are extremely elongate (fig. 21) and fold to rest in the elongate proboscidial fossa on the undersurface of the head. Approximately at the apex of the stipes is found a small, in some cases minute galea (fig. 23), to which the elongate maxillary palpus is attached.

With X. rozeni there appears to be a short segment 1 on its maxillary palpus followed by nearly as short segment 2 (fig. 23). Segments 3 and 4 (fig. 21), subequal in length, are greatly elongate, together longer than the stipes (fig. 21). They are separate from one another by an unpigmented membranous basal part of segment 4, which presumably allows the two segments to bend relative to one another. These two segments are heavily sclerotized and pigmented. They appear sulcate lengthwise along their medial side, which abuts the two segments on the opposing maxillary palpus, which are similarly sulcate. Thus is formed an elongate tube, presumably functioning as a channel for nectar. Miklasevskaja and Packer (in press) independently also reach this conclusion. The terminal two segments (fig. 24) are slender and short, together much less than half the length of segment 4, and appear incapable of connecting to opposite segments; they probably have a sensory function. The base of segment 5 displays a membranous unpigmented region even longer than this region on segment 4. Although the elongate membranous base of segment 5 obviously allows the maxillary apex flexibility, it may also provide an opening for nectar to be imbibed into the nectar channel formed by the basal segments. Perhaps the membranous connection between segments 3 and 4 also assists in some way in passing along the nectar.

The anatomy of the labiomaxillary region of *X. sielfeldi* (fig. 25) differs as follows. Although the cardo and stipes are extremely long and segment 1 of the maxillary palpus short, segment 2 is approximately twice as long as 1. Segment 3 is somewhat longer than 1 and 2 combined. Segment 4 has a long, membranous basal part that is as long as its distal sclerotized section, together almost as long as segment 3. Maxillary segments 5 and 6 are subequal in length, each only slightly shorter than segment 3. Segment 3 is the most heavily sclerotized segment and may form the nectar channel. Thus the entrance of the nectar channel might be between the long, membranous bases of segment 4.

To explore how mouthparts might be used during feeding in the case of females of *X. sielfeldi*, flowers containing a foraging bee were pulled from the bush and immediately placed in a killing tube so that the bee died in situ (a technique attempted unsuccessfully with *X. rozeni* because individuals of that species were able to extract themselves before succumbing). Afterward the calyx and part of the corolla were stripped away (figs. 29, 31), the adult bee (male or female) could be observed with its head halfway down the corolla tube and with its maxillary palpi extended so that the palpal tips might contact the flower's ovaries at the bottom of the tube (fig. 29), a situation observed five or six different times by J.G.R. Another interesting observation, possibly significant: filaments are often discolored as if bruised (figs. 29, 30, arrows) at about where they attach to the corolla, suggesting

that a foraging bee may clasp onto the anther attachment with one or both mandibles while feeding or food gathering. Similar bruising by the solitary bee *Nolanomelissa toroi* Rozen (Andrenidae) has been documented on flowers of *Nolana rostrata* (Lindley) Dunal in the Atacama Desert (Rozen, 2003).

IMMATURE STAGES

POSTDEFECATING LARVA OF XEROMELISSA NORTINA (TORO AND MOLDENKE)

Figures 5-16

DIAGNOSIS: Although agreeing in many respects, the postdefecating larva of Xeromelissa nortina can immediately be distinguished from those described as Chilicola ashmeadi (Crawford) (Eickwort, 1967: fig. 20) and X. sielfeldi (as "Xeromelissinae species A," McGinley, 1981: figs. 80, 81, fide Packer, 2006, personal commun. with J.G.R.) by the lack of paired tubercles above the antennae on the upper part of the head capsule. The tubercles are low and longitudinally wrinkled in X. sielfeldi (fig. 33, arrow). Although these tubercles are missing in X. nortina, the integument is faintly wrinkled in the same homologous position (figs. 12, 13, arrows). Larvae of these three taxa, however, share the following suite of characters: body form in lateral silhouette prolonged, with dorsal and ventral outlines more or less parallel except at extreme ends (i.e., not gradually tapering at either end); paired dorsal body tubercles distinctly transverse; antennal papilla domelike, with length less than basal diameter; labrum short, with pair of small tubercles, well recessed compared to ventrally projecting apex; mandibular apex sharply turning adorally at nearly right angle; labial and maxillary palpi elongate, tapering to points, directed somewhat dorsally; postoccipital ridge rapidly weakening shortly above posterior tentorial pit to becoming nearly absent along top of parietals; abdominal segment 10 short in lateral view with length much shorter than diameter, with anus terminally positioned, not distinctly closer to dorsal surface than ventral surface. Although some of these features are shared with other colletid taxa, this combination is not known to be shared with others.

DESCRIPTION: Total body length: 4.8-6.2 mm (n = 12).

Head (figs. 11–13): Sensilla on parietals minute, scarce; spiculation possibly present on hypopharynx and epipharynx. Cuticular pigmentation limited to mandibular apex and apices of labral tubercle and apices of palpi. Coronal ridge absent; postoccipital ridge gradually diminishing shortly above posterior tentorial pits and absent from top of head capsule; hypostomal ridge moderately developed, without dorsal ramus; pleurostomal ridge weakly developed; epistomal ridge evident but weakly developed laterad (below) anterior tentorial pit, absent between anterior tentorial pits; tentorium weakly developed. Parietal band evident as narrow depression. Integument on front of parietal above each antenna with patch of integumental wrinkles. Maximum diameter of basal ring of antenna somewhat greater than distance from ring to center of anterior tentorial pit; antennal papilla (fig. 13) domelike, so that length less than basal diameter, bearing about three sensilla. Lower margin of clypeus projecting in lateral view (fig. 13), strongly curving upward at midline, so that at midpoint margin at or above level of anterior

tentorial pits (fig. 12). Labrum with paired tubercles small, widely separated, and with apex strongly developed ventrally (fig. 12); labral sclerite absent.

Mandible, as seen in dorsal or ventral (fig. 14) view, moderately broad basally, narrowing rapidly and evenly to strongly curved apex; as seen in inner (fig. 15) or outer view, mandible tapering only slightly to broad apex because of strong curvature of distal part of mandible; in inner view (figs. 15, 16), mandibular apex (i.e., cutting edge of mandible) appearing as narrow, clear band with curved, crenulate distal edge apical to darkly pigmented, crescentshaped band; when apical part viewed in maximum profile in inner view (fig. 16), crenulate distal edge extending diagonally from dorsal surface of mandible to meet ventral surface, forming elongate, acute mandibular tip; pigmentation possibly evidence of integumental strengthening of cutting edge of mandible; outer surface of mandibular apex distinctly convex corresponding to concave curvature of inner surface, so that mandibular apex is thin and strongly scoop shaped (apicad of line a, fig. 15), no doubt functioning in some way for food ingestion. Cardo and stipital rod sclerotized, unpigmented; articulating arm of stipes small but evident; maxillary palpus arising subapically on maxillary lobe, large, tapering to point. Labium divided into small prementum and larger postmentum but their articulation uncertain; premental sclerite weakly defined; tentorial bridge absent; labial palpus (fig. 11) large, with length about three times basal diameter, tapering to pointed apex. Salivary opening (fig. 12) transverse, slightly downcurved, slightly projecting lips with width about one-half distance between bases of labial palpi. Hypopharynx apparently consisting of two widely separated lateral triangular lobes as seen from in front (fig. 12), with lateral and frontal surface of each rough, perhaps spiculate; these lobes appearing compressed from above to be in line with dorsal surface of base of labial base.

Body (figs. 5-9): Body integument extensively wrinkled and with wrinkling exacerbated by SEM preparation. Body vestiture essentially absent except for short setiform sensilla on integument around anal opening (fig. 9). General body form tending to be cylindrical except for slight expansion toward posterior end; most body segments except for abdominal segments 9 and 10 with paired transverse tubercles; paired tubercles on each segment distinctly separated at dorsal median line; intersegmental lines well defined; dorsal intrasegmental lines faintly defined but anterior edge of dorsal transverse tubercles corresponding to border between cephalic and caudal annulets of other taxa (e.g., in Megachilidae); lateral lobes of most body segments well defined. Abdominal segment 9 not produced ventrally; abdominal segment 10 in lateral view short, attached centrally to 9; anal opening transverse, approximately centrally positioned on segment 10, bearing small setiform sensilla around opening. Spiracles (figs. 8, 10) subequal in size except those of abdominal segments 6-9 sequentially decreasing in size; atrium globular; peritreme without rim (fig. 10); atrial wall smooth except for faint lines concentric with well-defined primary tracheal opening; subatria variable in length; atrial chambers decreasing is size inward. Sex-specific characters unknown.

MATERIAL STUDIED: Twelve postdefecating larvae: Region II: El Loa Prov.: Aguas Blancas, -23.2670 -67.9830, 2540 m, XII-04-2014 (L. Packer, E.S. Wyman), ex twigs.

DISCUSSION: An unusual feature of this larva is its enlarged, downward-directed labral apex and the mandibular apices that curve adorally around the lower surface of the labral lobe. Perhaps future observation of live, feeding larvae will demonstrate how the mandibles interact with the labrum during feeding.

PREDEFECATING LARVA OF XEROMELISSA SIELFELDI (TORO AND MOLDENKE)

Figures 33, 34

DIAGNOSIS: As indicated by the brevity of the following description, the anatomies of the mature larvae of *X. sielfeldi* and *X. nortina* are similar in many ways. This similarity is expressed even in the single character that can be used to differentiate them. While only *X. sielfeldi* exhibits paired tubercles (fig. 32, arrow) on its head capsule, the wrinkled surface where the tubercles would be is also found on the head of *X. nortina* (figs. 12, 13, arrows).

Although most other head features seem shared (e.g., large palpi, similar mandibles, transverse salivary opening, small, well-separated labral tubercles), body features are another matter. Likely, the straight body of *X. nortina* is merely a postdefecating form of the strongly curled body of the still-feeding larva of *X. sielfeldi*. However, the distinct transverse dorsal body tubercles and pronounced lateral body tubercles of *X. nortina* seem remarkably different from the relatively even body surface of *X. sielfeldi*. The eventual discovery of both growth forms of one or the other of the two taxa will resolve this uncertainty.

DESCRIPTION: **Head** (fig. 34): As described for postdefecating larva of *X. nortina* except for following: Spiculation apparently completely absent. Cuticular pigmentation nearly absent. Tentorium complete, moderately developed. Integument on front of parietal above each antenna with low but distinct tubercle bearing integumental wrinkles (fig. 34). Antennal papilla (fig. 34) scarcely elevated.

Mandible, as in *X. nortina* except lacking pigmentation and possibly crenulations along apical edge. Other mouthparts as described for *X. nortina* except articulating arm of stipes not observed and, in frontal view, entire lobe above salivary opening only questionably revealing distinct hypopharynx and lacking spicules. Salivary opening as described for *X. nortina*. Hypopharynx not defined.

Body (fig. 33): Body integument not wrinkled but thin, suggesting potential wrinkling after defecation. Body vestiture essentially absent. General body form (fig. 33) elongate, strongly curved, with midbody thinner than front end, and with posterior end strongly swollen; body segments without tubercles but anterior ones tending to have dorsal outline more swollen at midsegment than at either end (fig. 33); intersegmental lines moderately well defined; dorsal intrasegmental lines not evident; lateral lobes scarcely defined. Abdominal segment 9 not produced ventrally; abdominal segment 10 in lateral view moderately elongate (fig. 33) (not short as in postdefecating larva of *X. nortina*, fig. 5), attached centrally to 9; anal opening transverse, approximately centrally positioned on segment 10, presumably without small setiform sensilla around opening. Spiracles as described for *X. nortina*.

MATERIAL STUDIED: Two predefecating larvae: Chile: Atacama Prov.: Puquios, X-10-1971 (J.G. Rozen, L. Peña), nest D.

EGG OF XEROMELISSA SIELFELDI (TORO AND MOLDENKE)

Figure 32

EGG DIMENSIONS: Length 1.5, 1.6 mm long; maximum diameter 0.35, 0.4 mm (n = 2). Shape (fig. 32) elongate, slightly curved; broadly round at front end, more narrowly rounded at rear. Color creamy white, semitransparent, with smooth but not shiny chorion. Micropyle not visible with stereomicroscope while submerged in Kahle's solution, but faintly visible after critical-point drying before coating as a circular, somewhat shiny area, on the anterior end; SEM examination failed because of poor preservation.

MATERIAL STUDIED: Two eggs: Chile: Atacama Prov.: Puquios, X-10-1971 (J.G. Rozen, L. Peña).

Pupa of Xeromelissa sielfeldi (Toro and Moldenke)

Figure 35

DIAGNOSIS: Bee pupae are rarely described and none of any Xeromelssinae has been so treated. However, Torchio and Burwell (1987) provided information on those available for the Colletidae, and noted that the pupa of *Hylaeus leptocephalus* (Morawitz) (as *H. bisinuatus*) alone among the representatives of other colletid subfamilies bore a "terminal spine," possibly a homolog of the median tubercle on tergum 7 of *X. sielfeldi*. However, the leg "spines" reported for pupal *H. leptocephalus* appear to be lacking in *X. sielfeldi*.

DESCRIPTION: Head shape corresponding closely to that of adult, integument without special tubercles, spines, or setae. Mouthparts with cardo contained in proboscidial fossa, stipes, slightly exserted, and remaining distal elements bending sharply posteriad (fig. 35).

Mesosoma shape also corresponding to that of adult; leg segments without spines or tubercles accommodating developing adult setae.

Metasomal terga without spines or spicules, but more distal ones each with subapical band of vague protuberances (fig. 35) and metasomal tergum 8 with pronounced median tubercle at posterior margin, presumably corresponding to "terminal spine" of *Hylaeus* (Torchio and Burwell, 1987). Metasomal sterna each with posterior margin produced downward as transverse ridge (fig. 35, arrows).

MATERIAL STUDIED: Two male pupae: Chile: Atacama Prov.: Puquios, X-10-1971 (J.G. Rozen, L. Peña).

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REFERENCES

- Claude-Joseph, F. (H. Janvier). 1926. Recherches biologiques sur les hyménoptères du Chili (mellifères). Annales des Sciences Naturelles, 10ème Série, Zoologie 9: 113–268.
- Eickwort, G.C. 1967. Aspects of the biology of *Chilicola ashmeadi* in Costa Rica (Hymenoptera: Colletidae). Journal of the Kansas Entomological Society 40: 42–73.
- Gotlieb, A., et al. 2014. Nests, floral preferences, and immatures of the bee *Haetosmia vechti* (Hymenoptera: Megachilidae: Osmiini). American Museum Novitates 3808: 1–20.
- McGinley, R.J. 1981. Systematics of the Colletidae based on mature larvae with phenetic analysis of apoid larvae (Hymenoptera: Apoidea). University of California Publications 91: 1–307.
- McGinley, R.J. 1989. A catalog and review of immature Apoidea (Hymenoptera). Smithsonian Contributions to Zoology 494: 1–24.
- Michelette, E.R.F., J.M.F. Camargo, and J.G. Rozen, Jr. 2000. Biology of the bee *Canephorula apiformis* and its cleptoparasite *Melectoides bellus*: nesting habits, floral preferences, and mature larvae (Hymenoptera, Apidae). American Museum Novitates 3308: 1–23.
- Michener, C.D. 1995. A classification of the bees of the subfamily Xeromelissinae (Hymenoptera: Colletidae). Journal of the Kansas Entomological Society 68: 332–345.
- Michener, C.D., and J.G. Rozen, Jr. 1999. A new ground-nesting genus of xeromelissine bees from Argentina and the tribal classification of the subfamily (Hymenoptera: Colletidae). American Museum Novitates 3281: 1–10.
- Miklasevskaja, M., and L. Packer. In press. Fluctuating asymmetry in an extreme morphological adaptation in *Xeromelissa rozeni* (Toro & Moldenke) (Hymenoptera: Colletidae). Canadian Entomologist.
- Packer, L. 2008. Phylogeny and classification of the Xeromelissinae (Hymenoptera: Apoidea, Colletidae) with special emphasis on the genus *Chilicoa*. Systematic Entomology 33: 72–96.
- Rozen, J.G., Jr. 1984. Nesting biology of diphaglossine bees (Hymenoptera, Colletidae). American Museum Novitates 2786: 1–33.
- Rozen, J.G., Jr. 1993. Nesting biologies and immature stages of the rophitine bees (Halictidae) with notes on the cleptoparasite *Biastes* (Anthophoridae) (Hymenoptera: Apoidea). American Museum Novitates 3066: 1–28.
- Rozen, J.G., Jr. 2003. A new tribe, genus, and species of South American panurgine bee (Andrenidae: Panurginae), oligolectic on *Nolana* (Nolanaceae). Appendix: evidence for the phylogenetic position of *Nolanomelissa* from nuclear EF-1α sequence data, by John S. Ascher. *In* G.A.R. Melo and I. Alves-dos-Santos (editors), Apoidea neotropica: homenagem aos 90 anos de Jesus Santiago Moure: 93–108. Circiúma, Brazil: Editora UNESC.
- Rozen, J.G., Jr. 2013. Larval development and nesting biology of the adventive wood-nesting bee *Lithurgus* (*L.*) *chrysurus* Fonscolombe (Hymenoptera: Megachilidae: Lithurgini). American Museum Novitates 3774: 1–20.
- Rozen, J.G., Jr., and S.L. Buchmann. 1990. Nesting biology and immature stages of the bees *Centris caesalpiniae*, *C. pallida*, and the cleptoparasite *Ericrocis lata* (Hymenoptera: Apoidea: Anthophoridae). American Museum Novitates 2985: 1–30.

- Rozen, J.G., Jr., and M.S. Favreau. 1968. Biological notes on *Colletes compactus compactus* and its cuckoo bee, *Epeolus pusillus* (Hymenoptera: Colletidae and Anthophoridae). Journal of the New York Entomological Society 76: 106–111.
- Rozen, J.G., Jr., and H.G. Hall. 2011. Nesting and developmental biology of the cleptoparasitic bee *Stelis ater* (Anthidiini) and its host, *Osmia chalybea* (Osmiini) (Hymenoptera: Megachilidae). American Museum Novitates 3707: 1–38.
- Rozen, J.G., Jr., and C.D. Michener. 1968. The biology of *Scrapter* and its cuckoo bee, *Pseudodichroa* (Hymenoptera: Colletidae and Anthophoridae). American Museum Novitates 2335: 1–13.
- Rozen, J.G., Jr., G.A.R. Melo, A.J.C. Aguiar, I. Alves-dos-Santos. 2006. Nesting biologies and immature stages of the tapinotaspidine bee genera *Monoeca* and *Lanthanomelissa* and of their osirine cleptoparasites *Protosiris* and *Parepeolus* (Hymenoptera: Apidae: Apinae). Appendix: taxonomic notes on *Monoeca* and description of a new species of *Protosiris*, by Gabriel A.R. Melo. American Museum Novitates 3501: 1–60.
- Rozen, J.G., Jr., J.R. Rozen, and H.G. Hall. 2011. Gas diffusion rates through cocoon walls of two bee species (Hymenoptera: Apoidea). Annals of the Entomological Society of America 104: 1349–1354.
- Torchio, P.F. 1965. Observations on the biology of *Colletes ciliatoides* (Hymenoptera: Apoidea, Colletidae). Journal of the Kansas Entomological Society 38: 182–187.
- Torchio, P.F. 1984. The nesting biology of *Hylaeus bisinuatus* Forster and development of its immature forms (Hymenoptera: Colletidae). Journal of the Kansas Entomological Society 57: 276–297.
- Torchio, P.F., and B. Burwell. 1987. Notes on the biology of *Cadegualla occidentalis* (Hymenoptera: Colletidae), and a review of colletid pupae. Annals of the Entomological Society of America 80: 781–789.
- Toro, H. and A. Moldenke. 1979. Revisión de los Xeromelissinae Chilenos. (Hymenoptera-Colletidae). Annales del Museo de Historia Natural de Valparaiso 12: 95–182.

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