AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3281, 10 pp., 12 figures, 1 table December 8, 1999

A New Ground-Nesting Genus of Xeromelissine Bees from Argentina and the Tribal Classification of the Subfamily (Hymenoptera: Colletidae)

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ABSTRACT

A new genus of the bee subfamily Xeromelissinae from Argentina is proposed as *Geodiscelis* (type species, *Geodiscelis megacephala*, new species). *Geodiscelis* possesses a mixture of characters from both of the previously recognized tribes of Xeromelissinae. The tribes Chilicolini and Xeromelissini therefore merge and are no longer recognized, the five genera being united in the subfamily without tribal classification. Prior reports of nests of xeromelissines describe series of cells in burrows in stems or abandoned burrows of beetles in twigs. *Geodiscelis*, however, nests in loose sand, and cells are isolated at the ends of lateral burrows. It is a probable specialist visitor to flowers of *Heliotropium*, and its unusual glossa may be related to use of this floral resource.

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 ISSN 0003-0082 / Price $1.50

INTRODUCTION

The Xeromelissinae, a Western Hemisphere subfamily of the bee family Colletidae, is most speciose in temperate parts of South America. The subfamily contains species of *Chilicola* that nest in pithy stems or abandoned beetle burrows in wooden sticks (Claude-Joseph, 1926; Eickwort, 1967; Herbst, 1922); larvae now known to be those of *Chilimelissa* were taken by JGR from stems and described as Xeromelissinae species A by McGinley (1981). It was therefore a surprise to find a new genus and species in San Juan Province, Argentina, making its nests in sandy soil and visiting flowers of *Heliotropium* (Boraginaceae). Like those of *Colletes*, females of the new genus do not have the usual structures (basitibial and pygidial plates, pygidial and prepygidial fimbriae) of bees that construct cells in the ground.

The new genus exhibits a mixture of characters of the two tribes of Xeromelissinae that were segregated by Michener (1995). As a result we recommend abandonment of the tribal classification of the five genera in the subfamily.

While both authors have dealt with all parts of this paper, the systematic part was written by CDM and the part on biology by JGR who studied the new form in the field. The abbreviations F, S, and T are used for flagellomere, sternum, and tergum respectively; hence T1 refers to the first metasomal tergum, S5 to the fifth metasomal sternum, etc.

ACKNOWLEDGMENTS

JGR thanks Hernán Navarrete for his assistance in the fieldwork involved with this study. The host plant, *Heliotropium curassavicum*, was kindly identified by Dr. Jacquelyn A. Kallunki, New York Botanical Garden.

The field trip to South America that lead to the discovery of this bee was supported by the Robert G. Goelet Field trip Fund of the American Museum of Natural History (AMNH).

We thank Dr. Michael Engel for his careful review of the manuscript and for suggestions on improving it. He prepared the key to genera, which we have modified in minor ways.

SYSTEMATICS

Geodiscelis, new genus

TYPE SPECIES: *Geodiscelis megacephala*, new species.

DIAGNOSIS: This genus contains a small, slender bee with yellow areas on the clypeus, antennae, and legs, and with whitish apical metasomal fasciae. Some of its principal characters are indicated in table 1. It seems most closely related to *Chilimelissa* and is indeed similar to those species of that genus, such as *Chilimelissa nortina* Toro and Moldenke, that have large but not greatly elongated heads. It resembles *Chilimelissa* in the extraordinarily large head (fig. 1), the produced clypeus with anterior tentorial pits extending down as grooves almost to the apex of the clypeus, the short antenna (flagellum of female shorter than compound eye), the unmodified hind legs of the male, and the apical pale integumental tergal fasciae. It differs from *Chilimelissa* in the short, unmodified, six-segmented maxillary palpi, the short labial palpi, the long apical lobes of the glossa, the simple claws of the female, the more elongate mesosoma, the broader stigma, all as indicated in detail below, and in the basal hair bands on T1–4 (fig. 1).

Only one species is presently known; therefore generic and specific characters are not distinguished in the following description.

DESCRIPTION: **Female.** Body length 4 mm. *Head* shorter than mesosoma (fig. 1); inner orbits slightly converging below; closest at lower thirds below which they diverge, without marked emarginations; base of clypeus above lower ocular tangent; antennal bases at level of lower third of eyes; vertex convex as seen from front, upper ocular tangent passing through median ocellus (frontal view); interocellar distance about two ocellar diameters and slightly greater than ocellocular distance; ocelloccipital distance somewhat greater than ocellar diameter; facial foveae not recognizable; genal area narrower than eye (fig. 1); preoccipital carina absent; clypeus strongly produced and protuberant for distance equal to width of eye in side view (fig. 1); anterior tentorial pit extending downward as strong shining groove nearly to clypeal apex (as in *Chilimelissa*); from lower

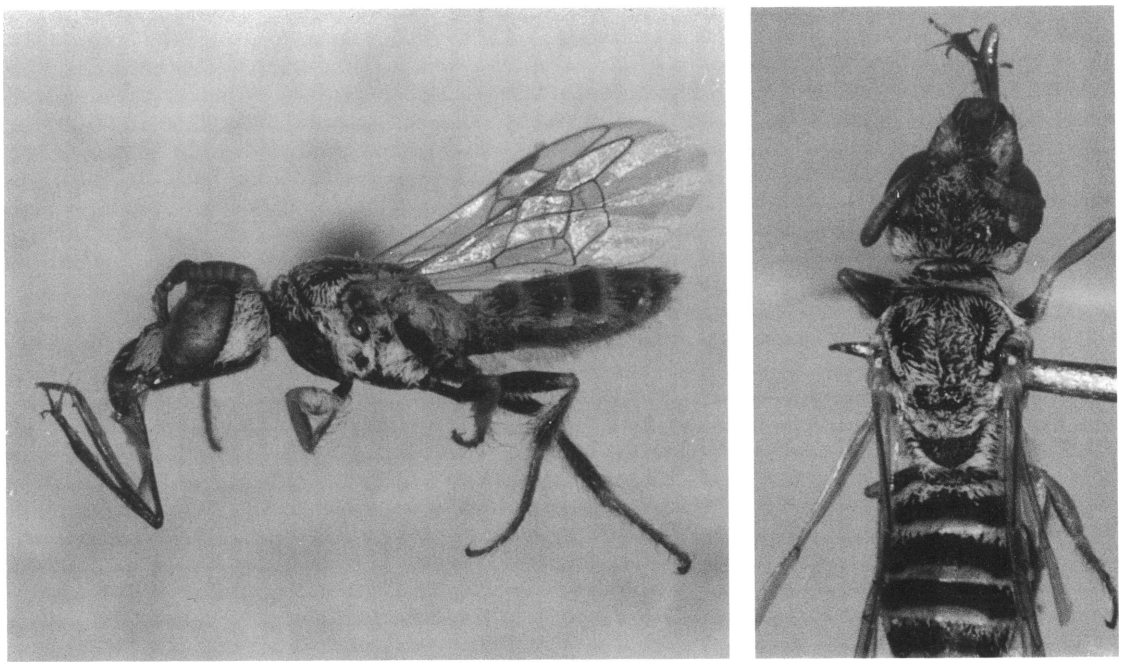


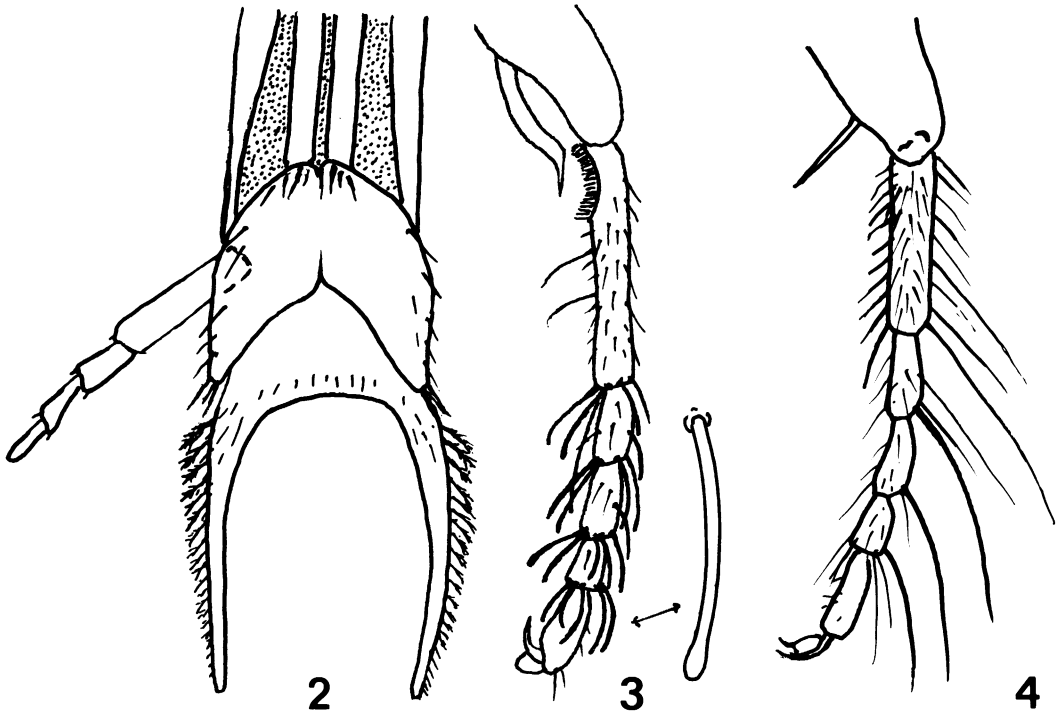
Fig. 1. Lateral and dorsal views of *Geodiscelis megacephala*, female.

end of groove epistomal suture presumably curving back to mandibular articulation leaving long paraocular lobe extending into clypeus, but this structure not clearly evident except in cleared specimen; labrum gently convex, rounded, about as long as broad; mandible with strong preapical tooth. Proboscis long and slender, cardo as long as head (fig. 1), stipes even longer; galeal blade about 2.5 times as long as broad and 0.21 times as long as stipes; maxillary palpus six-segmented, slightly longer than galeal blade, first segment longest, others subequal, segments 1–5 of equal width, segment 6 more slender; labial palpus four-segmented, about as long as galeal blade, segment 1 longer than any other segment; glossa with two slender apicolateral lobes longer than width of prementum (fig. 2), these lobes often directed posteriad rather than apicad. Antenna about as long as head; scape slender, more than twice as long as broad; pedicel as broad as scape, rounded, somewhat broader than long; flagellum somewhat narrower basally, F1 almost as long as apical width, F2–4 each about twice as broad as long, flagellomeres progressively broader and longer, F9 and F10 broadest, all broader than long except F10 which is about 1.5 times as long as broad.

Mesosoma elongate, distance from posterior margin of pronotal lobe to metasomal articulation longer than dorsoventral thickness; propodeum with triangle on subhorizontal dorsal surface which is as long as scutellum, much longer than metanotum. Legs slender, basitibial plate absent, claws simple. Front and middle tarsi with distinctive long hairs (figs. 3, 4). Stigma broader than prestigma (measured to wing margin), margins of stigma basal to vein r distinctly diverging apically, posterior margin distal to vein r (i.e., in marginal cell) straight or very weakly convex; apex of marginal cell briefly obliquely truncate with short appendage; wing venation shown in figure 1.

Metasoma distinctly flattened; T1 with large dorsal surface, same size as T2 and much longer than anterior surface of T1; T6 much narrower than T5, apex rounded, pygidial plate absent.

Coloration black with the following parts dark yellow: labrum, disc of clypeus extending down to apical margin, mandible except dark apex, antennal scape, pedicel (dusky ba-



Figs. 2–4. *Geodiscelis megacephala*, female. **2.** Distal part of labium, palpus omitted on one side. **3.** Front tarsus. **4.** Middle tarsus.

sally), under surfaces of F3 or 4–F10, apices of femora, front and middle tibiae (dusky on inner surfaces), base of hind tibia, and bases of front and middle basitarsi (fading to dark brown on rest of tarsi); upper surface of flagellum brown. Tegula and basal wing sclerites transparent yellowish; wings transparent with veins and stigma brown. T1–5 with apical translucent white band, each band grading to yellow brown basally, anterior margin of each band emarginate laterally.

Pubescence dull whitish to brilliant white. Scattered erect, simple, pale hairs on clypeus, labrum, hypostomal area, legs, metasomal sterna, T5, T6, and extreme sides of other metasomal terga. Scopal hairs particularly long and branched on S2, shorter on S1 and S3; scopal hairs of hind tibia simple, about as long as tibial diameter, a few of them longer; those of hind femur simple and shorter. Tarsi with long unbranched hairs scattered from basitarsi to penultimate tarsomeres; apical hairs of fore tarsomeres elongate, curved, and clavate (fig. 3) (possibly used for pollen collecting or sand manipulation); hairs of middle tarsus longer than those of other tarsi, about three of longest middle tarsal hairs longer than first tarsomere, some of them bristlelike (fig. 4). The following areas with dense, white hairs hiding surface (fig. 1): lower two-thirds of paraocular areas and lower frons immediately above antennal bases, genal area, dorsal posterior band across pronotum between posterior pronotal lobes, lateral margins of scutum, most of lateral surface of mesepisternum, metanotum, upper half of propodeum except triangle, band on posterior surfaces of front and mid femora, basal bands on T1–4 (fig. 1; those on T2–4 can be hidden by preceding terga). Other dorsal surfaces of head and thorax with sparser broad white hairs, individually distinct against black background; well-separated white hairs of scutum forming distinctive pattern with longitudinal median hairless stripe and bare area around parapsidal line (fig. 1). Scutellum largely bare except around margins.

Integument of head and mesosoma shining but minutely granular, smoother on yellow

part of clypeus, propodeal triangle bare (fig. 1), granular. Metasomal terga minutely transversely lineolate, thus silky; sterna shiny with minute, scattered punctures and lineolation coarser than that of terga.

Male. Agrees with description of female except as follows: Body length 3.0 to 3.5 mm. Inner orbits converging nearly to lower ends; interocellar distance about 1.25 times ocellocular distance; mandible with preapical tooth minute, separated from rutellum of mandible by narrow acute notch; antenna slightly longer than head, F1 and F2 broader than long (F2–4 much longer than in male), succeeding flagellomeres about as broad as long and progressively more robust except F11 which is about 1.5 times as long as broad. Claws briefly cleft at apices. T7 rounded apically, without pygidial plate. Under surfaces of F1–11 yellow, front and middle femora with distal halves yellow, tibiae yellow, mid and hind tibiae with dusky median areas; front tarsus yellow; mid and hind basitarsi largely yellow; T1–6 with apical integumental bands, like those of T1–5 of female but anterior emarginations often weak. Scattered erect simple hairs on T5–7 and more basal terga laterally; scopal hairs absent. Tarsi without extraordinarily long hairs, although a few midtarsal hairs are about 1.5 times as long as tarsomere 2. Scopal hairs absent. Basal bands of white hairs on T1–6, except on T1 largely hidden by preceding terga. Genitalia and hidden sterna as shown in figures 5–8; exposed sterna unmodified; apex of S6 rather narrowly rounded; S7 bilobed with disc relatively broad (unlike other Xeromelissinae); S8 elongate (unlike all other Xeromelissinae except certain *Chilicola* [*Hylaeosoma*], which have the apical process bifid); gonostylus distinct, long, weakly sclerotized with small hairy ventral lobe near base. (No other Xeromelissinae have such long gonostyli but *Chilimelissa nortina* Toro and Moldenke and *C. australis* Toro and Moldenke have somewhat elongate gonostyli; see Toro and Moldenke, 1979).

ETYMOLOGY: The genus-group name is derived from *ge* (Greek, earth) plus *Oediscelis*, a genus-group name in Xeromelissinae. The word *oediscelis* (Greek, swollen thighs) is not descriptive of *Geodiscelis*, which has slender legs. The reference is to the ground-nesting behavior.

Geodiscelis megacephala, new species

Figures 1–8

DESCRIPTION: The above genus-species description characterizes this species and validates the name.

TYPE MATERIAL: Holotype female and 14 female and 25 male paratypes: 16 km west of Media Agua, San Juan Province, Argentina, 8, 9 November 1998 (J. G. Rozen, H. Navarrete). The holotype and 33 paraptypes are in the AMNH; a male and a female paratype have been placed in each of the following: the Museo Argentino de Ciencias Naturales, Buenos Aires; the Snow Entomological Division, University of Kansas Natural History Museum, Lawrence, Kansas; the collection of Prof. Haroldo Toro, Universidad Católica de Valparaíso, Valparaíso, Chile. One female paratype at AMNH is cleared and preserved in glycerin; seven female and one male paratypes at AMNH are preserved in Kahle's solution; one female and three male paratypes lack the metasoma.

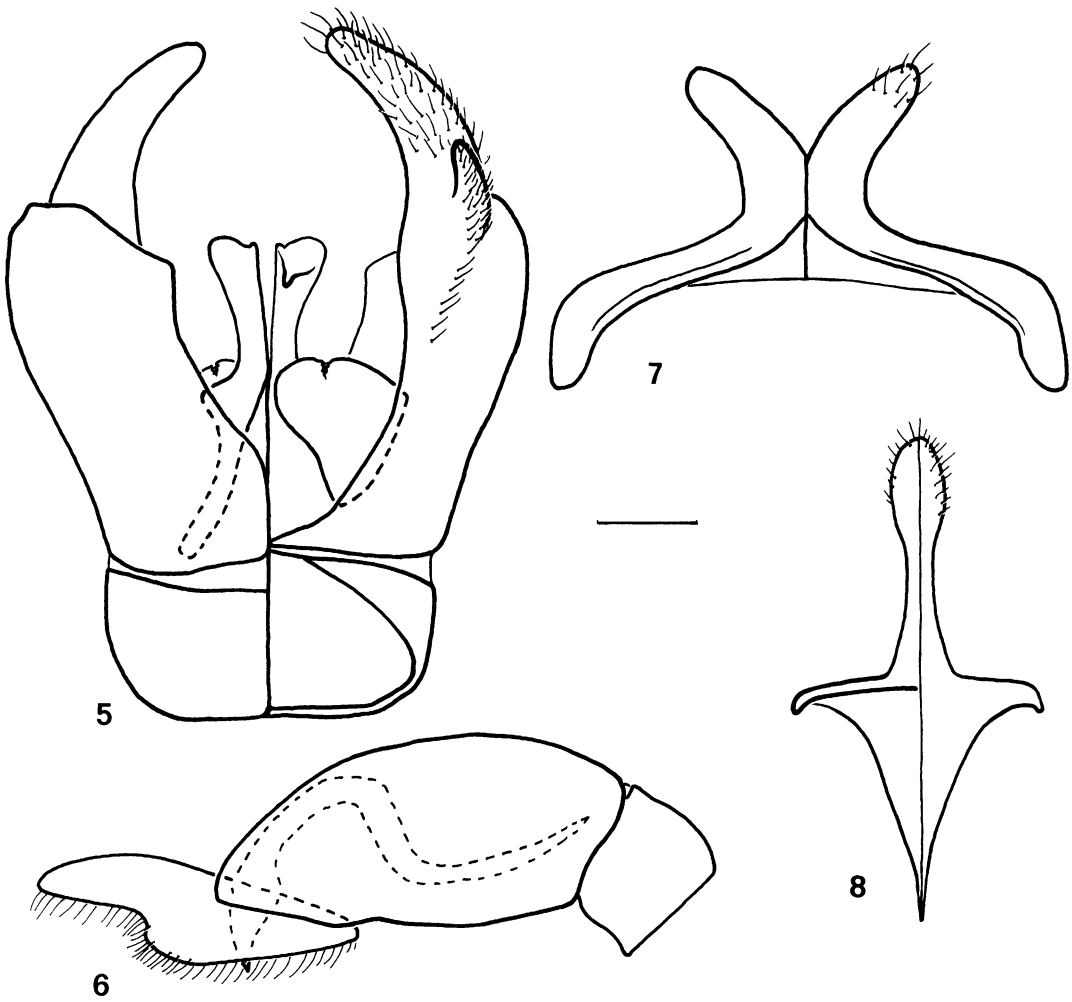
ETYMOLOGY: The specific epithet is derived from the Greek words *megas* (large) plus *kephale* (head).

TRIBES OF XEROMELISSINAE

Michener (1995) recognized two tribes in the subfamily Xeromelissinae, i.e., Xeromelissini and Chilicolini. The new genus described above combines characters of these tribes. Table 1 summarizes the principal tribal characters and shows how *Geodiscelis* agrees with Chilicolini in several features, but in the structures of the lower face, which are the hallmark of the Xeromelissini, it agrees with that tribe. We do not consider that continued recognition of these tribes is appropriate; the classification proposed in 1995 recognizes only four genera, here increased to five, in the subfamily.

Key to Genera of Xeromelissinae

1. Stigma basal to vein r with margins diverging apically, beyond vein r inner margin of stigma in marginal cell frequently convex, sometimes straight; mesosoma elongate (explained in footnote of table 1); maxillary



Figs. 5–8. *Geodiscelis megacephala*, terminalia of male, dorsal on left of divided drawings. **5.** Genitalia. **6.** Lateral view of genitalia. **7.** Seventh metasomal sternum. **8.** Eighth metasomal sternum. Scale = 0.1 mm.

palpus not abruptly more slender at segment 4; paraocular area not invading clypeus as a strong lobe, epistomal sulcus continuing directly, straight or gently curved, from anterior tentorial pit to mandibular base (except in *Geodiscelis*, which has a strong paraocular lobe) 2

– Stigma basal to vein r nearly parallel-sided, beyond vein r margin of stigma in marginal cell straight; mesosoma not elongate; maxillary palpus abruptly more slender at segment 4; paraocular area produced downward as an elongate lobe into clypeus, along mesal border of which the anterior tentorial impression slants down into clypeus; epistomal sulcus (often weak or not recognizable) curving back from lower end of this impression to mandibular base 4

2. Paraocular area produced downward as an elongate lobe into clypeus; glossa of usual short hylaeine or xeromelissine type; metasoma frequently without ivory integumental bands. 3

– Paraocular area not invading clypeus; glossa with slender apicolateral lobes (fig. 2); metasoma with ivory integumental bands .... *Geodiscelis*, new genus

3. Basal sloping part of propodeum about as long as metanotum, less than half as long as declivitous vertical surface (as seen in profile); inner orbits of compound eyes nearly straight, not emarginate .... *Xenochilicola*

TABLE 1

Principal Characters of the Formerly Recognized Tribes of Xeromelissinae and of the New Genus *Geodiscelis*

	Paraocular lobe and recurved epistomal suture	Maxillary palpus abruptly slender at segment 4	Thorax elongate[a]	Margins of stigma basal to vein r diverging	Ivory integumental bands on metasoma	Male gonoforceps with preapical lobe
Chilicolini	−	−	+	+	− (usually)	−
Xeromelissini	+	+	−	−	+	+
Geodiscelis	+	−	+	+	+	−[b]

[a] In an elongate mesosoma, the length from the posterior margin of the pronotal lobe to the metasomal articulation is greater than the dorsoventral thickness.

[b] The preapical lobe of the former tribe Xeromelissini arises from the gonoforceps, or in the cases where the gonostylus and gonocoxite are recognizable, from the distal part of the gonocoxite (see figures of *Chilimelissa nortina* and *C. australis* in Toro and Moldenke, 1979). In *Geodiscelis* a small lobe on the base of the gonostylus is probably not homologous to the preapical lobe of the gonoforceps.

- Basal sloping or subhorizontal part of propodeum longer than metanotum, often as long as scutellum, half as long as vertical surface or frequently longer (as seen in profile); inner orbits of compound eyes emarginate or at least slightly concave at about upper third or fourth (for subgeneric classification, see Michener, 1995) ..... *Chilicola*

4. Anterior tentorial impression slanting down almost to apex of clypeus; labial palpus four-segmented; maxillary palpus consisting of six easily seen segments, the first three markedly broader than the distal three .... *Chilimelissa*
- Anterior tentorial impression not approaching apex of clypeus; labial palpus three-segmented; maxillary palpus consisting of three large segments followed, at least sometimes, by two to five extremely minute segments (these are easily broken off in specimens) ..... *Xeromelissa*

NESTING BIOLOGY

JGR observed numerous individuals of *Geodiscelis megacephala* as they flew low over a sandy area and visited flowers of *Heliotropium curassavicum* Linnaeus (Boraginaceae) 16 km west of Media Agua, San Juan Province, Argentina, on November 8, 1998. The day was clear but extremely windy, resulting in much blowing sand. A search for nests in twigs and pithy stems, the known nest sites of the Xeromelissinae, was unsuccessful. Simultaneously the soil surface was scanned, but blowing sand almost immediately removed traces of possible burrows. The following morning was far less windy, and by midmorning a number of females had been observed digging into the sand.

The nesting area was a nearly flat, disturbed stretch between a road and a fenced agricultural field. The vegetation (fig. 9) was sparse, consisting mostly of low-growing *Heliotropium* plants, between which were barren sandy patches. Blown sand tended to accumulate around these plants, and most of the burrow entrances were in these deposits of loose sand.

Male flight was typically close to the ground, swift, with sudden stops on barren sand, and then equally sudden departures into the air. Males tended to circle as they flew and often alighted on the same spot of sand. They seemed to chase one another when one was encountered at rest. Several brief encounters were observed, but they were difficult to distinguish from male/female encounters because of small body size and the lack of strong sexual dimorphism. Males occasionally flew to the *Heliotropium* flowers, but they were difficult to observe there because of their small size. However, their activity was such that mating presumably occurred on the sand beside the plants and on the flowers themselves.

Nest entrances were scattered over the barren patches of horizontal to sloping sand. An active nest could usually be identified by a tumulus of loose, dry sand to one side of the opening, which was more or less evident (fig. 10). Occasionally females were observed

Fig. 9. Hernán Navarrete examining a section of the nesting site of *Geodiscelis megacephala* in front of low-growing bushes of *Heliotropium curassavicum*, 16 km west of Media Agua, San Juan Province, Argentina.

rapidly flinging fine sand out of the nest entrance with synchronous backward thrusts of their legs. This seemed to be the standard method of entering a nest because of the partial collapse of the soft, sandy entrance material. The long bristles and hairs of the front and middle tarsi (figs. 3, 4) may have a function in sand manipulation; because the bees are so small, accurate observations were impossible. Two delta-shaped tumuli measured about 1.5 cm long from the entrance and 2 cm at greatest width, the approximate dimensions of most of the tumuli (fig. 10). Because of the fine, dry sand, tumuli are probably ephemeral, being blown away during the night or almost instantaneously on windy days. The substrate showed no signs of moisture to the level of the cells.

The elongate, clavate hairs on the foretarsi of females (fig. 3) are a sex-limited character in that males have only normally short setae. Other bees that are oligolectic on *Heliotropium* have, like *Geodiscelis*, special features of their mouthparts presumably adaptive for collecting pollen from this genus of plants; these tarsal setae may also have such a function rather than for sand manipulation. The fact that some of the *Heliotropium* oligoleges possess long, curved, clavate (even capitate) hairs on their mouthparts supports this idea.

NEST STRUCTURE

Seven or eight nests of *Geodiscelis megacephala* were examined and excavated on November 9, 1998. All angled into the ground at about 20° from horizontal and curved downward to descend nearly vertically with a few slight bends. In two cases the open main tunnel then branched at a depth of 4–6 cm, and the two laterals radiated nearly horizontally for about 1 or 2 cm (N = 2) before each ended in a single cell. The branching pattern of the nest and the presence of single cells at the ends of branches, in addition to ground nesting, were unanticipated because in all other known nests of Xeromelissinae, cells are arranged in lin-

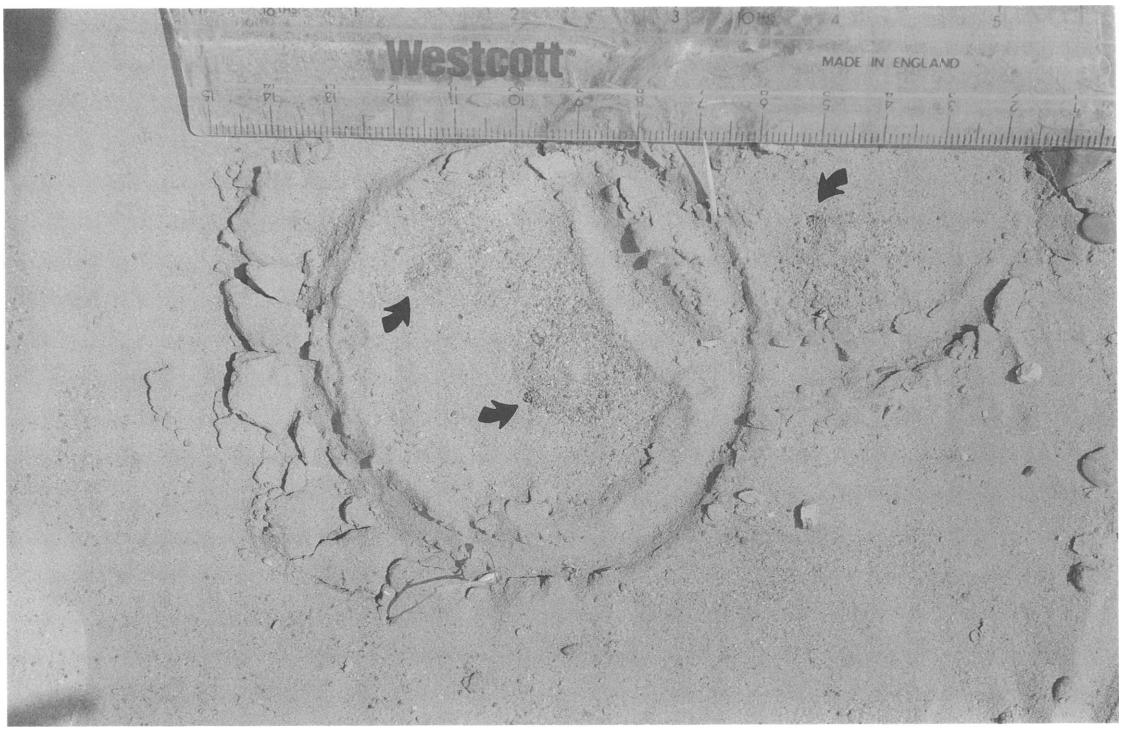
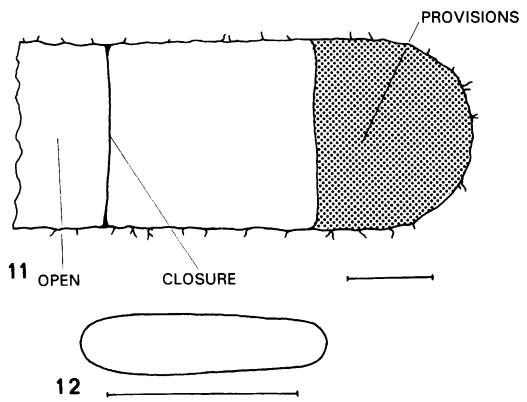


Fig. 10. Nest entrances (arrows) of *Geodiscelis megacephala*. Circles in sandy surface were made by plastic drinking glasses inverted to capture emerging females.

ear series in twigs, stems, or burrows in wood (references in Introduction).

All cells were at about the same depth (5–6 cm) and seemed to represent the same generation; they were nearly horizontal. Cells (total of 7 discovered) were almost or actually parallel-sided, little if any larger in diameter than the burrows, with one (fig. 11) having an entrance diameter of 2.4 mm and a maximum diameter of 2.5 mm. In this respect, they seemed more like cells of ground-nesting *Scrapter* (Rozen and Michener, 1968: figs. 3–8) than those of *Colletes* (see e.g., Malyshev, 1935: figs. 7, 12; Rozen and Favreau, 1968: fig. 1).



Figs. 11–12. Diagram of cell of *Geodiscelis megacephala*, side view. **12.** Egg of same, dorsal (or ventral) view. Scales = 1.0 mm.

Cells had distinct cellophanelike linings, in one case (fig. 11) 6.0 mm long. The lining consisted of a single nonfenestrated layer and, hence, was not two-layered as depicted by Rozen and Favreau (1968) for one species of *Colletes*. (Cells of other species of *Colletes* vary specifically in the thickness of the outer layer, which may sometimes appear to be absent.) The inner surface of the lining was smooth. Its outer surface was loosely attached to the substrate in some places by fibers attached to sand grains and in other places by the lining itself adhering to sand grains. The loose attachment of the cell lining to the substrate appears to be character-

istic of cells of Xeromelissinae, Hylaeinae, and Colletinae (situation unknown for the Euryglossinae), but not of those of the Diphaglossinae (Rozen, 1984).

The cell closure, of the same cellophanelike material, appeared to be a single sheet but may have consisted of more than one layer around the periphery, suggesting that the act of closing may have involved a complicated pattern of folding similar to that mentioned by Malyshev (1935: 257) for *Colletes* and *Hylaeus* (as *Prosopis*) and described by Rozen and Favreau (1968) for one species of *Colletes*. (Subsequent unpublished studies by JGR on other species of *Colletes* suggest that patterns of closure folding vary specifically in that genus.) As shown in figure 1, the closure was recessed 1.25 mm from the cell entrance (as defined by the cellophanelike lining).

Opaque, sticky, semifluid provisions occupied 2.0 mm of the rear of the cell. These provisions were not noticeably different from those of *Colletes*. Egg placement within a cell was not discovered, but two nearly straight white eggs (fig. 12) from separate cells had smooth chorions and were 1.3 mm long. Both were slightly wider at one end with a maximum diameter of 0.3 mm; the narrower end of one egg was slightly less than 0.3 mm. Other immature stages were not found.

No cleptoparasitic bees or other parasites were found associated with these nests.

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