

Nest and Immatures of the South American Anthidiine Bee *Notanthidium* (*Allanthidium*) *chilense* (Urban) (Apoidea: Megachilidae)

JEROME G. ROZEN, JR.¹

ABSTRACT

A nest of the leaf-cutter bee *Notanthidium* (*Allanthidium*) *chilense* (Urban) (Anthidiini) is described and illustrated, the second such account for the genus. The nest, presumably constructed from resin, consisted of four cells and was attached to a stem of the plant genus *Baccharis* (Asteraceae) in the high Andes of northern Chile. The cells held two postdefecating larvae, a male pupa, and an emerged adult female, all in cocoons, permitting the first descriptions of the immature stages and cocoon for the genus. To the extent possible the immatures are compared with those of other tribal members.

INTRODUCTION

As Michener (2007) pointed out, the nesting habits of the megachilid tribe Anthidiini are diverse. Thus, it seems worthwhile to document the nesting habits of those anthidiine taxa that have remained little known. Presented here is the description of a single external nest of *Notanthidium* (*Allanthidium*) *chilense* (Urban). The late Luis Peña, a well-known Chilean naturalist and collector, found this nest attached to a plant stem high in the Andes in 1969. Knowing of my interests in bee biology, he presented it to me shortly after finding it. One of the cells produced a female that remained unidentified for many years. At the time of the female's recovery, two mature larvae and a male pupa were collected from the same nest and preserved, allowing their descriptions at this time. The following is believed to be the second account of a nest of

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

this genus and the first account of the mature larva, pupa, and cocoon of any of the 10 species assigned to this South American genus. The only other description of a *Notanthidium* nest was published by Claude-Joseph (1926) (see Discussion), who did not recover larvae or pupae.

MATERIAL, METHODS, AND TERMINOLOGY

Peña's nest was attached to the stem of "*Baccharis santeliceae*" (presumably an error for *Baccharis santelicensis* Phil., considered a synonym of *Baccharis tola* subsp. *santelicensis* (Phil.) Joch. Müll.). The nest is labeled as follows: "Chile: Tarapaca: Murmuntani (entre Zapaphuria y Chapiquiña). Altura-aprox.: 3,800 m. Fecha: 5-V-1969." A single adult female was extracted from the nest in the laboratory on I-22-1970. The nest, cocoons, and immature stages represented by two larvae (one of which apparently had died well before being removed from its cocoon and preserved) and a single male pupa were also preserved. At the same time and from the same site, Peña also collected a single male specimen, which John S. Ascher recently identified as *N. chilense*. Subsequently, Terry Griswold confirmed the identification based on the single adult female taken from the nest. Thus, it is possible to present the following descriptions of the nest, cocoons, and immatures.

The mature larvae were prepared for both stereoscopic and SEM examination with the equipment and procedures presented in Rozen and Hall (2011).

Anthidiine taxa whose larvae are discussed are fully named in table 1 with reference to the original larval descriptions and associated figure numbers in those descriptions. Similarly, table 2 lists the previously published studies of the fully named anthidiine pupae.

DESCRIPTIONS OF NEST AND COCOONS

The nest is an oblong dark gray mass, presumably of resinous material, attached to and surrounding a thin, stem with a diameter of 4–5 mm (figs. 1–3). The mass is 3 cm long and 1–1.5 cm in diameter. It is hard to the touch, fractures brittlely, and has an uneven, irregular surface, covered with fine, nearly microscopic strands of pale mold hyphae (fig. 4), the hardness and hyphae possibly artifacts of 45 years of storage. It had obviously been constructed above ground level and on partial dissection was found to contain four elongate cells, each of which accommodates a cocoon or partial cocoon. Cocoons and their cells are approximately parallel to one another and to the stem, which they surround. All are arranged with their front ends directed downward toward the stem base. The front ends are defined in three cells by the presence of a centrally placed nipple extending beyond the disclike surface of the cocoon. Although the nipple had not survived in the fourth cell after the removal of the contents, the rounded posterior end of the cocoon persists. In the three cells containing nipped cocoons, a large open chamber (fig. 4, fecal chamber) with a diameter of the cocoon extends beyond the front end of the cocoon. In two of the cells, the chamber is about 5 mm long before it reaches the cell closure. The cell closure seems merely a rough blockage of the cell without any special form such as a spiral. In all four cells, the cocoon rear fits closely to the end of the cell where there is no open space. The external surface of the nest mass reveals no evidence of cell closures.

Table 1. Anthidiine taxa, mature larvae of which have been described. References are to original descriptions, and figure references are to illustrations of 5th instars, pre- and/or postdefecating forms, in those references. Figure numbers for **mandibles** are in boldface and *spiracles* are in boldface italics.

TAXON	REFERENCE	FIGURE REFERENCE
<i>Anthidium</i> (<i>Proanthidium</i>) <i>oblongatum</i> (Illiger) (as <i>Anthidium oblongatum</i> Latreille)	Xambeu, 1896 Maneval, 1937	No figs. Figs. 35–39–42–45
<i>Anthidiellum ehrhorni</i> (Cockerell)	Michener, 1953	Figs. 119, 123–124 , 127
<i>Anthidiellum notatum robertsoni</i> (Cockerell)	Michener, 1953	Figs. 121–122 , 128
<i>Dianthidium curvatum sayi</i> Cockerell	Michener, 1953	Figs. 130–131–132 , 133
<i>Dianthidium heterulkei heterulkei</i> Schwarz	Clement, 1976	Fig. 2, A–D–E–G
<i>Hoplostelis</i> (<i>Hoplostelis</i>) <i>bilineolata</i> (Spinola) (as <i>Odontostelis bilineolata</i> (Spinola))	Rozen, 1966	Figs. 1–3–6–8
<i>Notanthidium</i> (<i>Notanthidium</i>) <i>steloides</i> (Spinola) (as <i>Anthidium steloides</i> Spin.)	Claude-Joseph, 1926	No figs.
<i>Pseudoanthidium</i> (<i>Pseudoanthidium</i>) <i>scapulare</i> (Latreille) (as <i>Anthidium lituratum</i> (Panzer))	Enslin, 1923 Micheli, 1934	Figs. 2–3 Fig. 1 (1–8–9)
<i>Rhodanthidium</i> (<i>Asianthidium</i>) <i>caturigense</i> (Giraud) (as <i>Anthidium catugirensis</i> and <i>caturigense</i> Giraud)	Micheli, 1935 Maneval, 1936	Figs. 1–(1–7–8, 10) Figs. 2–3
<i>Rhodanthidium</i> (<i>Rhodanthidium</i>) <i>septemdentatum</i> (Latreille) (as <i>Anthidium 7-dentatum</i> Lep.)	Xambeu, 1896 Grandi, 1961	No figs. Figs 361–362 (2)–(6–7)–363
<i>Stelis</i> (<i>Heterostelis</i>) <i>hurdi</i> (Thorp) (as <i>Heterostelis hurdi</i> Thorp)	Thorp, 1966	Figs. 14–15–16
<i>Stelis</i> (<i>Stelis</i>) <i>ater</i> Mitchell	Rozen and Hall, 2011	Figs. 81–86, 91–94–95–97
<i>Stelis</i> (<i>Stelis</i>) <i>chlorocyanea</i> (Cockerell)	Rust and Thorp, 1973	Figs. 16– 19–20–22–24–25
<i>Stelis</i> (<i>Stelis</i>) <i>elongativentris</i> Parker	Rozen, 1987	Figs. 6– 10–12–13
<i>Stelis</i> (<i>Stelis</i>) <i>lateralis</i> Cresson	Michener, 1953	Figs. 114– 115–116 , 118
<i>Stelis</i> (<i>Stelis</i>) <i>minuta</i> Lepeletier and Audinet-Serville	Enslin, 1925	Figs. 11–12
<i>Stelis</i> (<i>Stelis</i>) <i>ornatula</i> (Klug)	Micheli, 1935	Fig. II. 1–7–9
<i>Stelis</i> (<i>Stelis</i>) <i>phaeoptera</i> (Kirby) (as <i>S. (S.) murina</i> Pèrez)	Rozen and Kamel, 2009	Figs. 9– 10–12–21–22–23–24
<i>Stelis</i> (<i>Stelidomorpha</i>) <i>nasuta</i> (Latreille)	Maneval, 1937	Figs. 47– 48–49
<i>Trachusa</i> (<i>Heteranthidium</i>) <i>larreae</i> (Cockerell)	Rozen and Hall, 2012	Figs. 44– 54–57–58–59–64–65
<i>Trachusa</i> (<i>Trachusomimus</i>) <i>perdita</i> Cockerell	Michener, 1953	Figs. 109– 112–113 , 117

Two cocoons are 12.5 and 13.0 mm long from rear end to apex of nipple, and one cocoon is 6.0 mm at maximum width. The cocoon fabric consists of a single sheet. From a distance, it appears reddish brown externally (figs. 2, 3). Its internal surface is semitransparent and wrinkled with a grayish hue where it is attached to the gray cell wall. When pulled away from the wall and flooded from behind with strong light, it was a bright translucent yellow. The front (lower) end of the cocoon is straw colored both inside and out and concentrically fibrous when viewed in reflective light (fig. 4). The front disc is somewhat concave on the inside and convex on the outside where it bears the central expansion, the so-called “nipple” (fig. 4). In general, the front disc is less concave than the rounded rear of the cocoon.

Examination of the cocoon by SEM revealed that its inner surface (fig. 5) consists of strands of silk over which had been deposited a thin layer of material, almost certainly more silk that

Table 2. Previous descriptions of pupae of anthidiine taxa.

TAXON	REFERENCE
<i>Anthidiellum</i> (<i>Loyolanthidium</i>) <i>perplexum</i> (Smith) (as <i>Anthidiellum perplexum</i> (Smith))	Baker et al., 1985
<i>Hoplostelis</i> (<i>Hoplostelis</i>) <i>bilineolata</i> (Spinola) (as <i>Stelis</i> (<i>Odontostelis</i>) <i>bilineolata</i> (Spinola))	Rozen, 1966
<i>Stelis</i> (<i>Heterostelis</i>) <i>hurdi</i> (Thorp) (as <i>Heterostelis hurdi</i> Thorp)	Thorp, 1966
<i>Stelis</i> (<i>Stelis</i>) <i>chlorocyanea</i> (Cockerell) (as <i>Stelis</i> (<i>Chelynia</i>) <i>chlorocyanea</i> Cockerell)	Rust and Thorp, 1973

provided a thin but moisture-proof, airtight surface, as has been found present on other Megachilidae (Rozen and Hall, 2011; Rozen et al., 2011; Rozen and Mello, 2014). The only place where there is a passageway to the outside of the cocoon is through the nipple, as shown in figures 6–9. Thus, the nipple serves as the filter area, allowing air exchange between the interior of the cocoon and the outside, and simultaneously barring with a network of silk strands (figs. 7, 9) ingress of such hazards as mites and parasitic insects. Interestingly, this implies that the nest matrix at least at cell closures is porous, allowing air exchange. Rust and Clement's (1972) detailed description of the cocoon of the anthidiine *Stelis sexmaculata* Cresson suggests that it functions in a similar manner.

On superficial examination, cells seemed to lack any indication of feces, and fecal pellets were not noticed in any of the cocoons nor found between the cocoon and cell wall. However, on closer inspection, traces of finely granular, grayish-green material was discovered in the walls of the open chamber anterior to the cocoon nipple in three cells. This material was almost certainly feces.² Thus the now open chamber is thought to be remnant of the fecal storage area at the front end of the cell before cocoon spinning. Presumably pellets had been dislodged at the time of collection and/or during the 45 following years. If so, it indicates that defecation is mostly, if not fully, completed before the larva of *Notanthidium chilense* spins its cocoon.

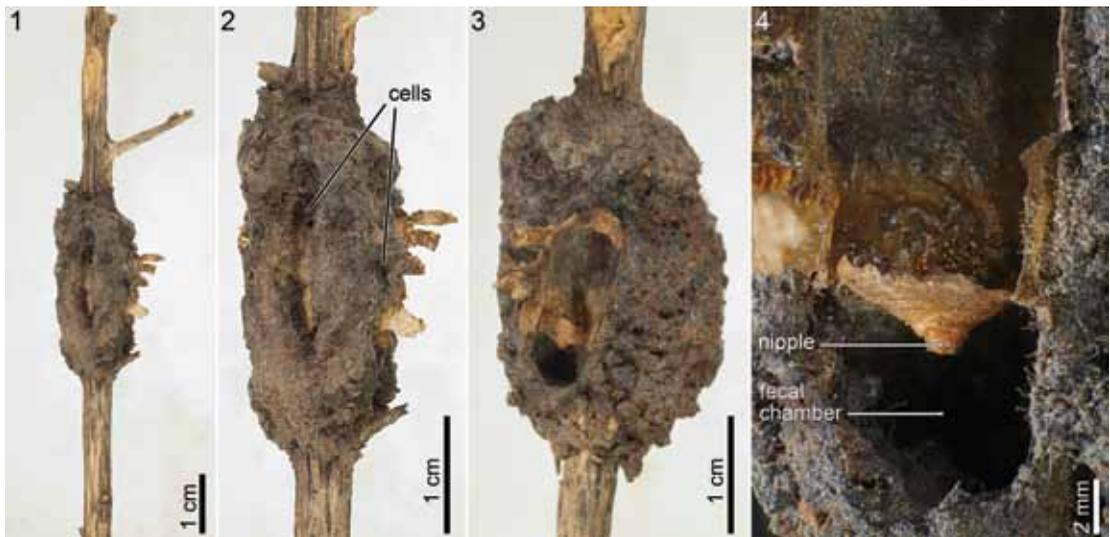
MATERIAL EXAMINED: The nest and some cocoon material are preserved in the collection of the AMNH.

DESCRIPTION OF LAST LARVAL INSTAR

Figures 10, 12–22

Because all the immatures were retrieved from cocoons and cocoons are spun after defecation, the following larva of *Notanthidium chilense* was obviously postdefecating. However, the distended postcephalic region was perplexing because of its resemblance to a typical predefecating form. Furthermore, the tentorial bridge was intact, contrary to expectations for the onset of ecdysis. Nonetheless, when the body was cleared, the alimentary tract was without pollen, and abundant adipose tissue accounted for the distended body.

² Because one of the reviewers suggested that it might well reveal evidence of pollen exines, microscopic examination of this material was attempted. Unfortunately, the material was too fragmented and/or compressed. Positive affirmation must wait discovery of fresh nests.



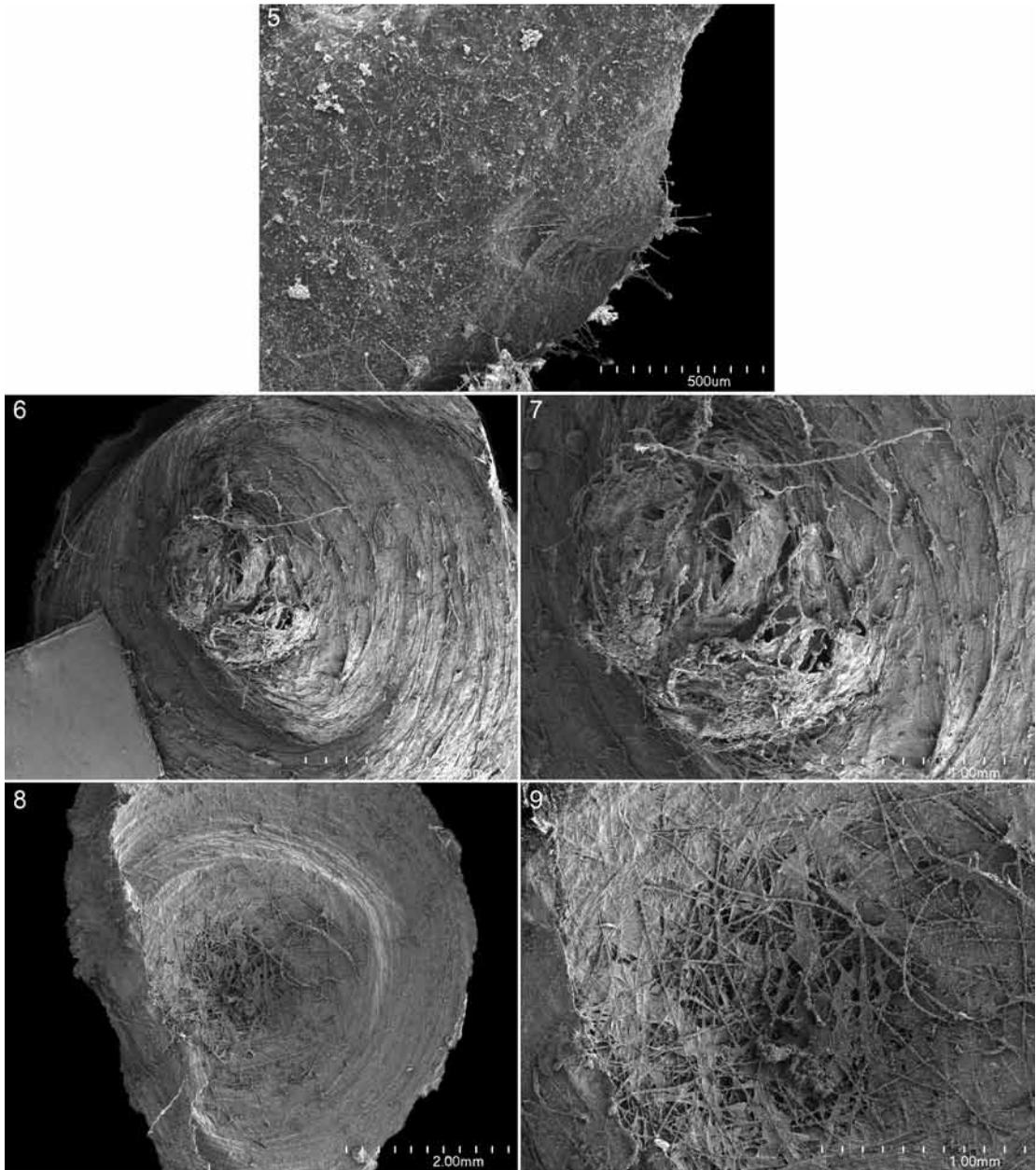
FIGURES 1–4. Partly dissected nest of *Notanthidium chilense*, outer view. **1.** Nest surrounding twig of *Baccharis*. **2.** Closer view of same (note cut shreds of cocoon fabric extending from right side of nest). **3.** Same with stem rotated 90°. **4.** Close-up of cell of same. Although much of the cocoon is removed, the front end remains in place with nipple pointing downward. Open area below cocoon is believed to have held feces. Note rough, dark, texture of nest matrix.

DIAGNOSIS: The postdefecating larva of *Notanthidium chilense* (fig. 10) shares the extremely robust body form with *Trachusa larreae* (Rozen and Hall, 2012: fig. 53) and *T. perdita* (Michener, 1953: fig. 109). However, they can be immediately distinguished by mandible shape: that of *N. chilense* tapers apically to a clearly bidentate apex (fig. 13) whereas those of both *Trachusa* species taper far less and end in a single subtruncate apex (Michener, 1953: fig. 112; Rozen and Hall, 2012: fig. 55).

The mature larva of *Hoplostelis (Hoplostelis) bilineolata* described and illustrated by Rozen (1966: fig. 2) is also robust, and its mandible (Rozen, 1966: figs. 6–7) more closely matches that of *N. chilense* (figs. 12–14). However, larvae can be distinguished because the atrial wall of *H. bilineolata* bears dentate ridges (Rozen, 1966: fig. 3) whereas the concentric ridges on the atrial wall of *N. chilense* (fig. 21) are not dentate. Furthermore, *H. bilineolata* is a cleptoparasite of *Euglossa*, whereas all *Trachusa* are nonparasitic.

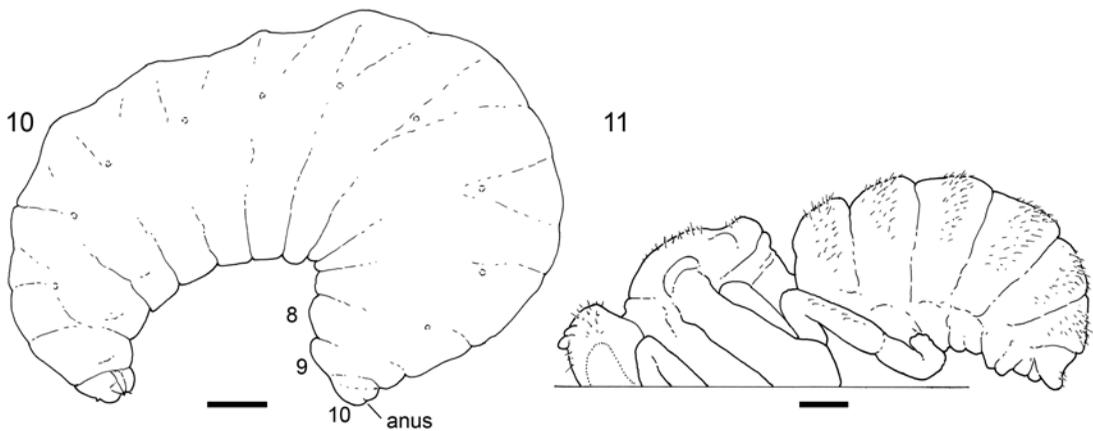
All species of *Stelis* are cleptoparasitic, and mature larvae of most of *Stelis* species studied to date have robust postcephalic bodies and attenuate, apically pointed mandibles, sometimes with a small dorsal tooth positioned subapically, but with other species, this tooth is absent. Thus, the dominant ventral tooth is a tool to kill host larvae that have not yet encountered an earlier cleptoparasitic instar, as explained by Rozen and Hall, 2011. These species include *S. (S.) ater* (Rozen and Hall, 2011: fig. 94), *S. (S.) elongativentris* (Rozen, 1987: figs. 10–12),³ *S. (S.) lateralis* (Michener, 1953:

³ Sclerotized postmental sclerites were not reported for *Stelis elongativentris* (Rozen, 1987: fig. 13), whereas this unusual feature had first been discovered by Rust and Thorp (1973) in *Stelis chlorocyanea*. It was again observed in *S. phaeoptera* (Rozen and Kamel, 2009: figs. 14, 15) and *S. ater* (Rozen and Hall, 2011: figs. 83, 84). I decided to restain the specimen of *S. elongativentris* with Chlorazol Black E and reexamine it. I also stained the specimen of *S. lateralis* studied by Michener for his 1953 paper. Neither species showed a pair of sclerites on its postmentum.



FIGURES 5–9. SEM micrographs of cocoon of *Notanthidium chilense*. 5. Inner surface of cocoon wall showing thin layer of silk covering silk fibers. 6. Outer surface of the disc-shaped anterior end of cocoon showing concentric pattern of silk fibers and central nipple in which can be seen the openings to the passageways to the interior. 7. Close-up of nipple. 8. Inner surface of anterior end of cocoon also showing concentric pattern of silk fibers surrounding filter area of cocoon behind exterior nipple. 9. Close-up of filter area, revealing guarded openings to exterior of cocoon.

figs. 115, 116), *S. (S.) minuta* Enselin, 1925: fig. 12), *S. (S.) ornatula* (Micheli, 1935: fig. 7), and *S. (S.) phaeoptera* (Rozen and Kamel, 2009: figs. 10–12). Because of mandibular shape, often dentate atrial wall, and their parasitic lifestyle, mature larvae of these species can be differentiated from those

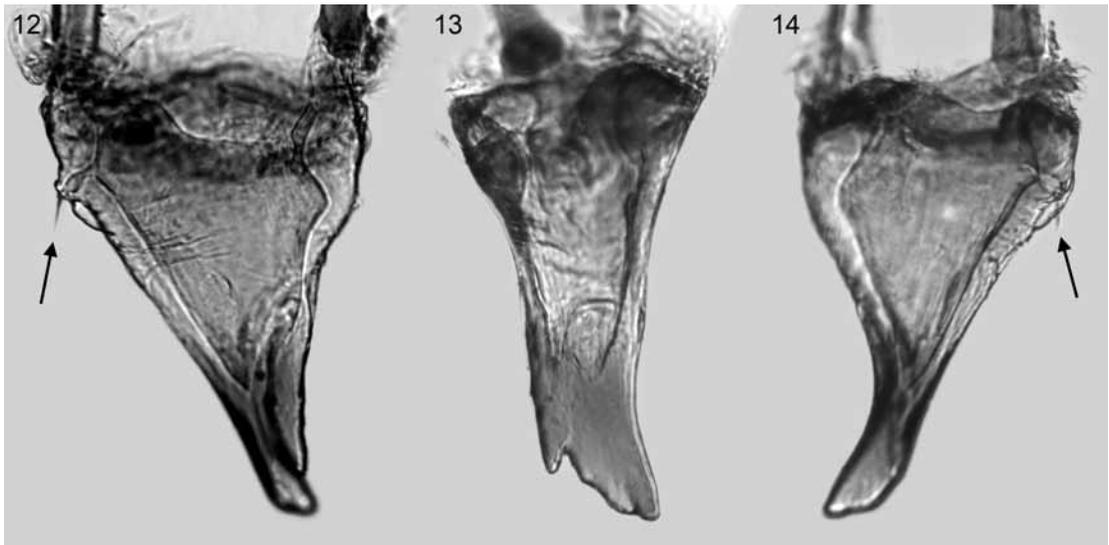


FIGURES 10, 11. Diagrams of postdefecating larva and of dorsal part of pupa of *Notanthidium chilense*, lateral view, respectively, with setae approximated only on pupa.

of *Notanthidium chilense*. Michener (1953) interpreted Maneval's (1937: figs. 46–49) description and illustrations of the larva of *Stelis (Stelidomorpha) nasuta* to have a different body contour from that of *S. lateralis* and noted that unlike *S. lateralis* it had bidentate mandibles. However, Michener's illustration (1953: fig. 114) of the larva of *S. lateralis* depicts its middorsal tubercles to be unusually exaggerated and thus suggests that the specimen may have been a predefecating form in which these tubercles tend to be accentuated (see Rozen and Hall, 2011: cf. figs. 81 and 85).

DESCRIPTION: Head: Setae moderately long, basally stout, tapering, moderately abundant. Following areas moderately to faintly pigmented: labral sclerite; mandibles, especially at apices and points of articulation; most internal head ridges; dorsal surface of premental sclerite; arms of stipites; cardo, all palpi. Fine spiculation restricted to lateral lobes of hypopharynx. Area immediately above hypostomal ridge and just behind posterior mandibular articulation not produced as downward-directed tubercle as present in many *Coelioxys* (Rozen and Kamel, 2007: fig. 47). Coronal ridge absent; postoccipital ridge moderately developed; as seen from above, this ridge gradually curving forward toward median line; hypostomal ridge well developed; dorsal ramus present but fading before reaching postoccipital ridge; center of large anterior tentorial pit about equally distant to anterior mandibular articulation and to basal ring of antenna; epistomal ridge present only laterad of (below) anterior tentorial pits; tentorium moderately robust including dorsal arms. Parietal bands evident. Maximum diameter of basal ring of antenna about equal to distance from ring to center of anterior tentorial pit; antennal papilla slender, tapering apically, somewhat longer than basal diameter, bearing about three sensilla. Lower margin of clypeus strongly angled upward at midline, so that at midpoint margin nearly at level of anterior tentorial pits.

Mandible (figs. 12–14) moderately robust bearing two acutely pointed apical teeth with ventral tooth substantially longer than dorsal one (fig. 13); ventral edge of dorsal tooth uneven; dorsal edge of ventral tooth crenulate; outer surface of mandible with single large seta arising from basal tubercle (arrows, figs. 12, 14). Cardo and stipital rod sclerotized, pigmented; articulating arm of stipes evident; maxillary apex directed mesad far beyond insertion of maxillary palpus, so the palpus subapical in position; maxillary palpus tapering, length about twice basal diameter. Labium clearly divided into prementum and postmentum; apex normally wide; pre-

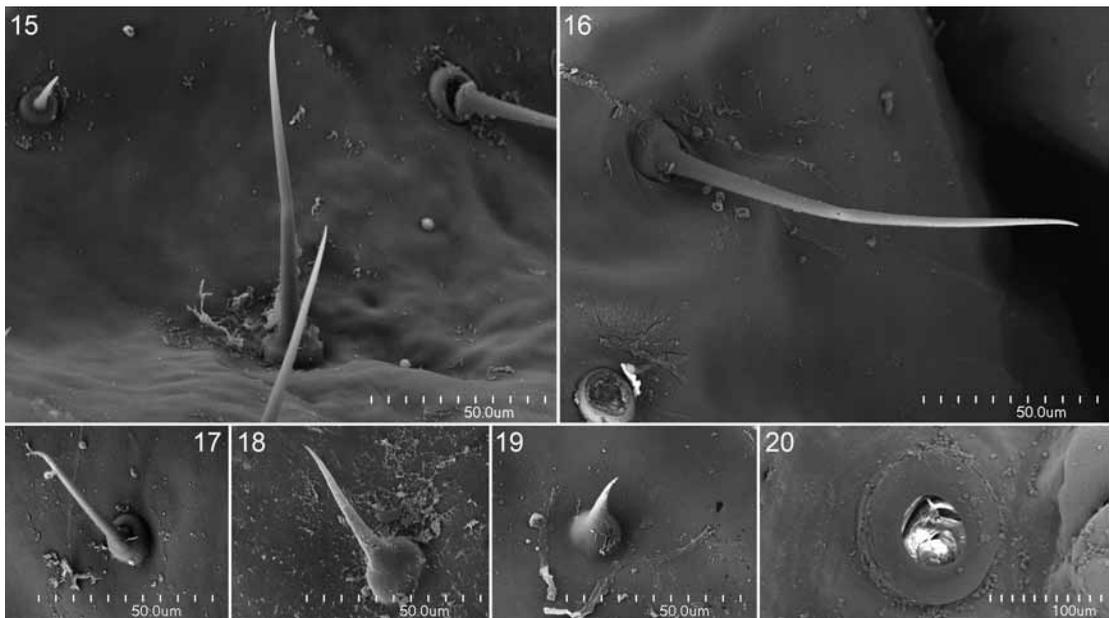


FIGURES 12–14. Photomicrographs of larval right mandible of *Notanthidium chilense* (arrows pointing to single large seta arising from small tubercle on outer base). 12. Dorsal, 13. inner, and 14. ventral views.

mental sclerite sclerotized and pigmented above but fading, becoming absent below; labial palpus tapering, length about three times basal diameter, distinctly longer than maxillary palpus. Salivary lips projecting, transverse, width about equal to distance between bases of labial palpi; inner surface with numerous parallel, raised ridges extending outward. Hypopharynx consisting of two separated lateral lobes that are spiculate.

Body (fig. 10): Body vestiture consisting of moderately short setae to short setae possibly mixed with spicules (figs. 15–19);⁴ lateral swelling of abdominal segment 8 with approximately 10 setae and short setae (or setiform spicules) combined; middorsal tubercles without setae/spicules. Body form strongly robust posteriorly (fig. 10); intersegmental lines not deeply incised dorsally; cephalic and caudal annulets not strongly differentiated in lateral view (fig. 10); intra-segmental lines weakly expressed; paired dorsal body tubercles absent; pleural thoracic swellings not evident; lateral lobes of abdominal segments 1–9 not pronounced; abdominal segment 10 attached to approximate middle of segment 9; anus positioned toward dorsal surface of segment 10. Spiracles (figs. 20–22) well sclerotized, unpigmented, subequal in diameter, though spiracle of abdominal segment 8 noticeably smaller; atrium globular with width about equal to depth, projecting slightly beyond body wall, with rim; diameter of atrial opening about twice radial width of peritreme; atrial inner surface with pronounced ridges lacking spicules (fig. 22) concentric with primary tracheal opening; primary tracheal opening with collar; subatrium with about 20 chambers; externally, subatrium (fig. 21) tapering only slightly from body surface inward and expanding slightly before connection to tracheal system. Sex-specific characters unknown.

⁴ Because the second larva had apparently died and deteriorated before it was extracted from the cocoon and placed in preservative, the SEM micrographs of body vestiture were difficult to interpret; longer setae (figs. 15–17) could be distinguished but small projections might either have been very short setae or spicules (figs. 18, 19). Stereoscopic examination of a cleared specimen did not resolve this issue.



FIGURES 15–19. SEM micrographs of larval vestiture of *Notanthidium chilense*, all to same scale. **15.** Cluster of setae of various lengths **16.** Long, slender seta. **17.** Shorter seta. **18, 19.** Setae or spicules? **FIGURE 20.** Spiracle, external surface.

MATERIAL EXAMINED: Two postdefecating larvae, one of which probably died sometime before collection because of its molding condition.

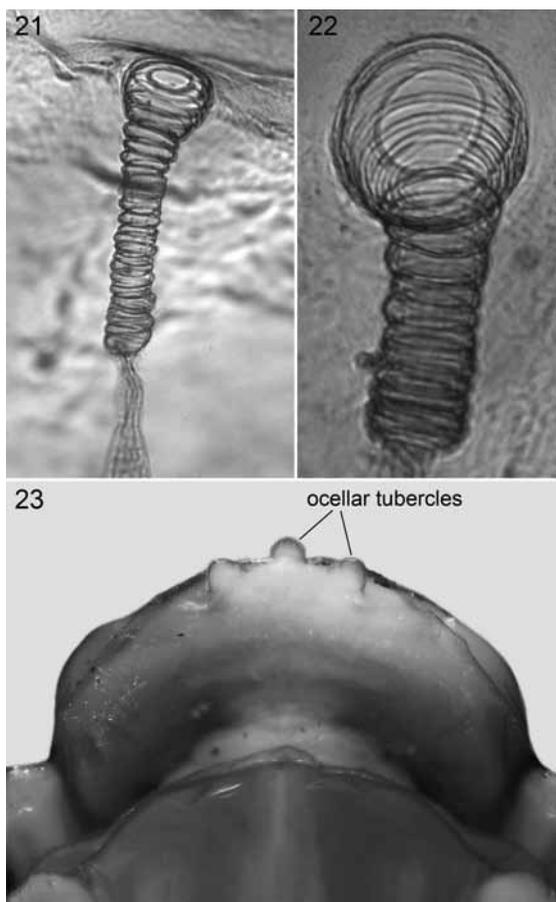
DESCRIPTION OF PUPA

Figures 11, 23

Relatively few pupae of Anthidiini have been described (McGinley, 1989) and are listed in table 2. Two features of the pupa of *Notanthidium chilense* may distinguish it from those of other tribal members. The ocellar tubercles are strongly projecting, extending outward about as far as their maximum diameter (fig. 23). Pupal specimens of *Hoplostelis bilineolata* still available from the 1966 study clearly have ocellar tubercles that are far less projecting. Ocellar tubercles of *Anthidiellum perplexum* depicted by Baker et al., (1985; fig. 1 C, E) appear less projecting than those of *N. chilense* (fig. 23). Only paired lateral ocellar tubercles of *Stelis hurdi* are acknowledged as “short and rounded” while no mention is made of a median ocellar tubercle (Thorp, 1966). The ocellar tubercles of *S. chlorocyanea* are convincingly shown as low (Rust and Thorp, 1973: fig. 15).

The other pupal feature of *Notanthidium chilense* that appears to separate it from other known anthidiines is the abundance of dorsal body setae (fig. 11).⁵ These setae, though pale and therefore difficult to evaluate against an unpigmented background, appear more numerous and extensive than those on other known anthidiine pupae. Furthermore, these setae are clearly present on the

⁵ Figure 11 depicts the relative abundance and distribution of dorsal body setae on the pupa, but the mode of illustration is misleading because of the black ink lines. The setae are thin and pale on the actual specimen, which is unpigmented, so that the setae are far more obscure than in the illustration.



FIGURES 21, 22. Photomicrographs of spiracles. **21.** Long view of atrium and subatrium. **22.** Close-up of atrium showing annulated ridges concentric with primary spiracular opening. **FIGURE 23.** Photomicrograph of pupal head, dorsal view, showing projecting ocellar tubercles.

tubercles of Michener, 1953) may depend somewhat on the growth stage of the specimen examined even in the last larval stadium. Although Michener suggested that body setae might be a primitive feature, Rozen and Hall's (2012) study of the nesting biology of *Trachusa larreae* pointed out that body setae combined with spiculation (i.e., body vestiture) was restricted to the last larval instar and was probably an adaptation providing the larva with traction for moving around the cell to complete feeding and to spin its cocoon. The highly adaptive nature of conspicuous body setae is found again in the allodapines (Apidae) and not elsewhere among bees. This suggests that pronounced body vestiture has evolved *de novo* and independently in each of these two groups.

A feature that deserves further study, not only among larval Anthidiini but throughout the Megachilidae, is a more thorough understanding of the anatomical and functional features of the vestiture. Where on the larva's body does the vestiture occur? The study of the setae and spicules of *Trachusa larreae* (Rozen and Hall, 2012) demonstrated the diversity and patterning

scutellum of *N. chilense*; they are not apparent on the scutellum in the case of *A. perplexum*. No body setae are discussed nor pictured for *S. chlorocyanea*, and *S. hurdi* is said to have no "long setae" on body parts (Thorp, 1966).

Although mesoscutellar shape as defined by its posterior margin is primarily an adult feature, it can serve well for pupae. The posterior scutellar margin is broadly curved with a slight median indentation in pupal *Notanthidium chilense*, as also seems to be the case for *Anthidiellum perplexum* (Baker et al., 1985: fig. 1 C). However, the posterior margin of *Hoplostelis bilineolata* is straight, giving the scutellum a quadrate appearance (Rozen, 1966: fig. 18). The adult scutellar shape of *S. hurdi* predicts that its pupa will have a curved posterior margin.

MATERIAL EXAMINED: One male pupa without ocular or integumental pigmentation, in the collection of AMNH.

DISCUSSION

As Michener (1953) pointed out over 60 years ago, larval characters of Megachilidae are very homogeneous, and this is reinforced by the current study of larval anthidiines. We now think that some of the differences he recorded in the degree of expression of mid-dorsal tubercles and lateral lobes (ventrolateral

of the distribution of these structures and hints at the possibility that variation in them from one taxon to the next might demonstrate phylogenetic relationships if better understood.

Although the current study seems to indicate that the concentric atrial ridges (fig. 22) are helpful in distinguishing larval *Notanthidium chilense* from other anthidiine taxa, comparisons of spiracles of other anthidiine larvae (as identified in table 1) seem to indicate that strong atrial ridges, whether denticulate or not, are a common feature among some groups of Megachilidae.

Mandibular shape appears to be a helpful feature for distinguishing some taxa. For this reason references to mandibular figures in description of articles are identified in table 1. Within *Stelis* there is considerable variability in the presence and size of a dorsal mandibular tooth. Does this relate to mode of parasitism, and if so, how?

The only other account of nesting behavior of a species of *Notanthidium* was published by Claude-Joseph (1926: fig. 93) referring to *N. (N.) steloides* (Spinola) (as *Anthidium steloides* Spin.). He described and illustrated two nests, one in a beetle gallery in a dry branch and the other in a hollow piece of bamboo. The differences between nesting in preformed hollow spaces and constructing an external nest on a bush seem extreme, although cell partitions of resin match the nest matrix material of *N. chilense*. Unfortunately, Claude-Joseph recovered no larvae from the nest.

ACKNOWLEDGMENTS

I thank both John S. Ascher and Terry Griswold for their efforts in identifying the species that constructed the nest based upon the adult bees associated with it. Stephen Thurston, Senior Scientific Assistant, took all of the macrophotographs of the nest and cocoons. In addition, he arranged all illustrative material for publication. Eli Wyman, Curatorial Assistant, prepared specimens and took the SEM micrographs of cocoons and larvae and proofread the manuscript. I express my appreciation to two anonymous reviewers for their suggestions and corrections.

Ronald J. McGinley's (1989) catalogue of immature bees was a valuable resource for tracking down descriptions of bee larvae and pupae.

I acknowledge with great appreciation the long-term loan of larval specimens from the University of Kansas made possible by Charles D. Michener. This was particularly valuable because I was able to reevaluate material that he had used for his pioneering comparative study of bee larvae published in 1953.

REFERENCES

- Baker, J.R., E.D. Kuhn, and S.B. Bambara. 1985. Nests and immature stages of leafcutter bees (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 58: 290–313.
- Claude-Joseph, F. (H. Janvier). 1926. Recherches biologiques sur les hyménoptères du Chili (Mellifères). *Annales des Sciences Naturelles* (10^e Série) 9: 113–268.
- Clement, S.L. 1976. The biology of *Dianthidium heterulkei heterulkei* Schwarz, with a description of the larva (Hymenoptera, Megachilidae). *Wasmann Journal of Biology* 34: 9–22.
- Enslin, E. 1923. Beiträge zur Kenntnis der Hymenopteren, III. *Deutsche Entomologische Zeitschrift* 1923:169–187.
- Enslin, E. 1925. Beiträge zur Kenntnis der Hymenopteren, IV. *Deutsche Entomologische Zeitschrift* 3: 177–210.

- Grandi, G. 1961. Studi di un entomologo sugli imenotteri superiori. Bollettino dell'Istituto di Entomologia della Università di Bologna 25: 1–661.
- Maneval, H. 1936. L'*Anthidium caturigense*, son nid et sa larve (Hym. Apidae). Annales de la Société Entomologique de France 105: 1–5.
- Maneval, H. 1937. Notes sur les hyménoptères (5^e série). Revue Française d'Entomologie 4: 162–181.
- McGinley, R.J. 1989. A catalog and review of immature Apoidea (Hymenoptera). Smithsonian Contributions to Zoology 494: 1–24.
- Micheli, L. 1934. Note biologiche e morfologiche sugli imenotteri (contributo 5). Bollettino della Società Entomologica Italiana 66: 246–252.
- Micheli, L. 1935. Note biologiche e morfologiche sugli imenotteri (VII serie). Bollettino della Società Veneziana di Storia Naturale 1: 126–134.
- Michener, C.D. 1953. Comparative morphology and systematic studies of bee larvae with a key to the families of hymenopterous larvae. University of Kansas Science Bulletin 35: 987–1102.
- Michener, C.D. 2007. Bees of the World. 2nd ed. Baltimore, MD: Johns Hopkins University Press, 953 pp.
- Rozen, Jr., J.G. 1966. Taxonomic descriptions of the immature stages of the parasitic bee, *Stelis (Odonostelis) bilineolata* (Spinola) (Hymenoptera: Apoidea: Megachilidae). Journal of the New York Entomological Society 74: 84–91.
- Rozen, Jr., J.G. 1987. Nesting biology of the bee *Ashmeadiella holtii* and its cleptoparasite, a new species of *Stelis* (Apoidea: Megachilidae). American Museum Novitates 2900: 1–10.
- Rozen, Jr., J.G., 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, Jr., J.G., and H.G. Hall. 2012. Nesting biology and immatures of the oligolectic bee *Trachusa larvaeae* (Apoidea: Megachilidae: Anthidiini). American Museum Novitates 3765: 1–24.
- Rozen, Jr., J.G., and S.M. Kamel. 2009. Last larval instar and mature oocytes of the Old World cleptoparasitic bee *Stelis murina*, including a review of *Stelis* biology. (Apoidea: Megachilidae: Megachilinae: Anthidiini). American Museum Novitates 3666: 1–19.
- Rozen, Jr., J.G., and S.M. Kamel. 2007. Investigations on the biologies and immature stages of the cleptoparasitic bee genera *Radoszkowskiana* and *Coelioxys* and their *Megachile* hosts (Hymenoptera: Apoidea: Megachilidae: Megachilini). American Museum Novitates 3573: 1–43.
- Rozen, Jr., J.G., and M.L.S. Mello. 2014. Polarization microscopy and topochemistry of the cocoon of *Lithurgus chrysurus* (Hymenoptera: Megachilidae). Annals of the Entomological Society of America 107: 625–634.
- Rozen, Jr., J.G., 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.
- Rust, R.W., and S.L. Clement. 1972. The biology of *Osmia glauca* and *Osmia nemoris* (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society 45: 523–528.
- Rust, R.W., and R.W. Thorp. 1973. The biology of *Stelis chlorocyanea*, a parasite of *Osmia nigrifrons* (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society: 46: 548–562.
- Thorp, R.W. 1966. Synopsis of the genus *Heterostelis* Timberlake (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society 39: 131–146.
- Xambeu, V. 1896. Moeurs et métamorphoses des *Anthidium oblongatum* et *7-dentatum*, Hyménoptères du groupe des Apides. Bulletin de la Société Entomologique de France (1896): 328–331.