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Immatures of Exomalopsine Bees with Notes on Nesting Biology and a Tribal Key to Mature Larvae of Noncorbiculate, Nonparasitic Apinae (Hymenoptera: Apidae)

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ABSTRACT

This paper describes the eggs/mature oocytes (including ovarian statistics), mature larvae, and pupae of bees belonging to the Exomalopsini, furthering our understanding of the anatomical and behavioral diversity of included taxa. The mature larva is the life stage best represented with the following treated: *Anthophorula* (*Anthophorula*) *completa* (Cockerell), *Anthophorula* (*Anthophorisca*) *chionura* (Cockerell), *Anthophorula* (*Anthophorisca*) *consobrina* (Timberlake), *Anthophorula* (*Anthophorisca*) *nitens* (Cockerell)*, *Anthophorula* (*Anthophorisca*) *sidae* (Cockerell)*, *Anthophorula* (*Isomalopsis*) *uncicornis* González-Vaquero & Roig-Alsina, *Eremapis parvula* Ogloblin, *Exomalopsis* (*Exomalopsis*) *auropilosa* Spinola, *Exomalopsis* (*Exomalopsis*) *bruesi* Cockerell*, *Exomalopsis* (*Stilbomalopsis*) *solani* Cockerell*, *Exomalopsis* (*Stilbomalopsis*) *solidaginis* Cockerell, *Chilimalopsis parvula* Toro*, and *Teratognatha modesta* Ogloblin*. Pupae of those species bearing an asterisk (*) are also described. Most specimens were collected in association with studies of nesting biologies. Although some biologies were reported in earlier papers, those of the following species are included as the terminal section herein: *Anthophorula* (*Anthophorula*) *completa* (Cockerell), *Anthophorula* (*Isomalopsis*) *uncicornis* González-Vaquero and Roig-Alsina, *Eremapis parvula* Ogloblin, *Chilimalopsis parvula* Toro, and *Teratognatha modesta* Ogloblin. A preliminary key to mature larvae of the nonparasitic apine tribes (exclusive of the corbiculate tribes) is appended.

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INTRODUCTION

Over 35 years of fieldwork I have gathered the immature stages of bees belonging to the apine tribe Exomalopsini. Although I have published the bionomics of many of these bees (Rozen, 1984), I have left an investigation of the anatomy of their life stages until now. Present here are descriptions of eggs, mature larvae, and pupae of these bees. Because additional biological data have come to light following the 1984 study, this information is also included. As an addendum, I have attached a preliminary tribal key to mature larvae of the nonparastic Apinae exclusive of corbiculate tribes with the hope that a more complete key will evolve in the future. The key does not include the Ancylaini, the immature stages of which will be the last to be discovered.

Following Michener (2007), I retained *Chilimalopsis* and *Teratognatha* in the Exomalopsini rather than placing them in a separate tribe, Teratognathini (Silveira, 1995), in order to assess whether biology and/or anatomy of immatures would illuminate relationships (see Discussions of Immature Stages).

SPECIMEN PREPARATION AND TERMINOLOGY

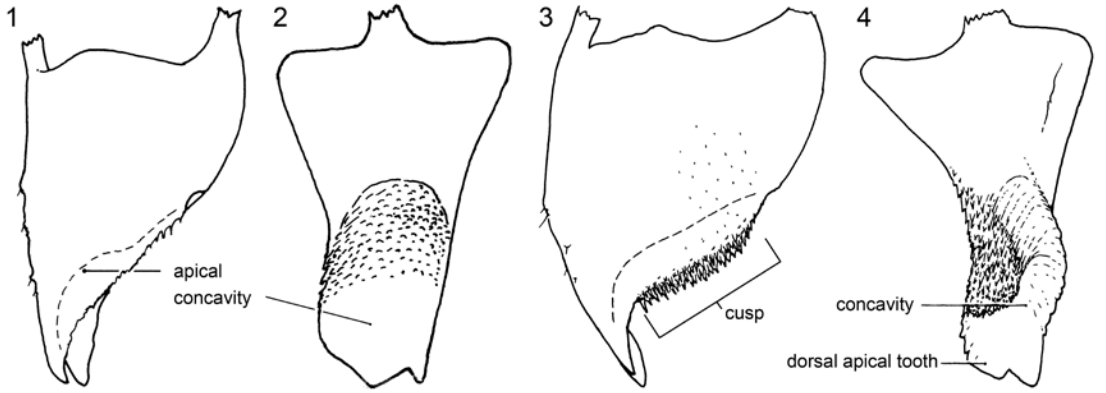
Larval specimens (pre- and postdefecating forms) are best examined before preparation at which time illustrations, if required, can be drawn. The head is then separated from the thorax, and both sections are cleared in an aqueous solution of sodium hydroxide. After being washed in water they are transferred to 70%–75% ethanol, stained with Chlorazol Black E, washed in ethanol, and submerged in glycerin on a well slide for study, illustration verification and augmentation, and storage.

To determine the foramen-to-head width index of mature larvae, the maximum transverse width of the foramen is divided by the maximum transverse head width. This is a measure of the degree of constriction of the posterior edge of the head capsule relative to the lateral expansion of the parietals.

Specimens (eggs, larvae) to be examined with a Hitachi S-4700 scanning electron microscope (SEM) were critical-point dried and then coated with gold/palladium. Cocoons did not require drying and were simply mounted on stubs and coated. Larval mandibles from cleared specimens were removed from glycerin, washed in ethanol, and air dried before being mounted on stubs. Microphotographs of other mandibles were taken with a Cannon PowerShot SD880 IS handheld to the ocular of a Zeiss compound microscope. Figure 9 showing the mandibular dentition of *Exomalopsis solidaginis* Cockerell was taken with as Carl Zeiss LSM 710 confocal microscope. Nesting soil textures were classified according to the USDA, NRCS, Soil Texture Calculator.

MANDIBULAR MORPHOLOGY

This study revealed that the larval mandible of the Exomalopsini and the other apine tribes treated in the appendix is a complex structure showing considerable anatomical variation of



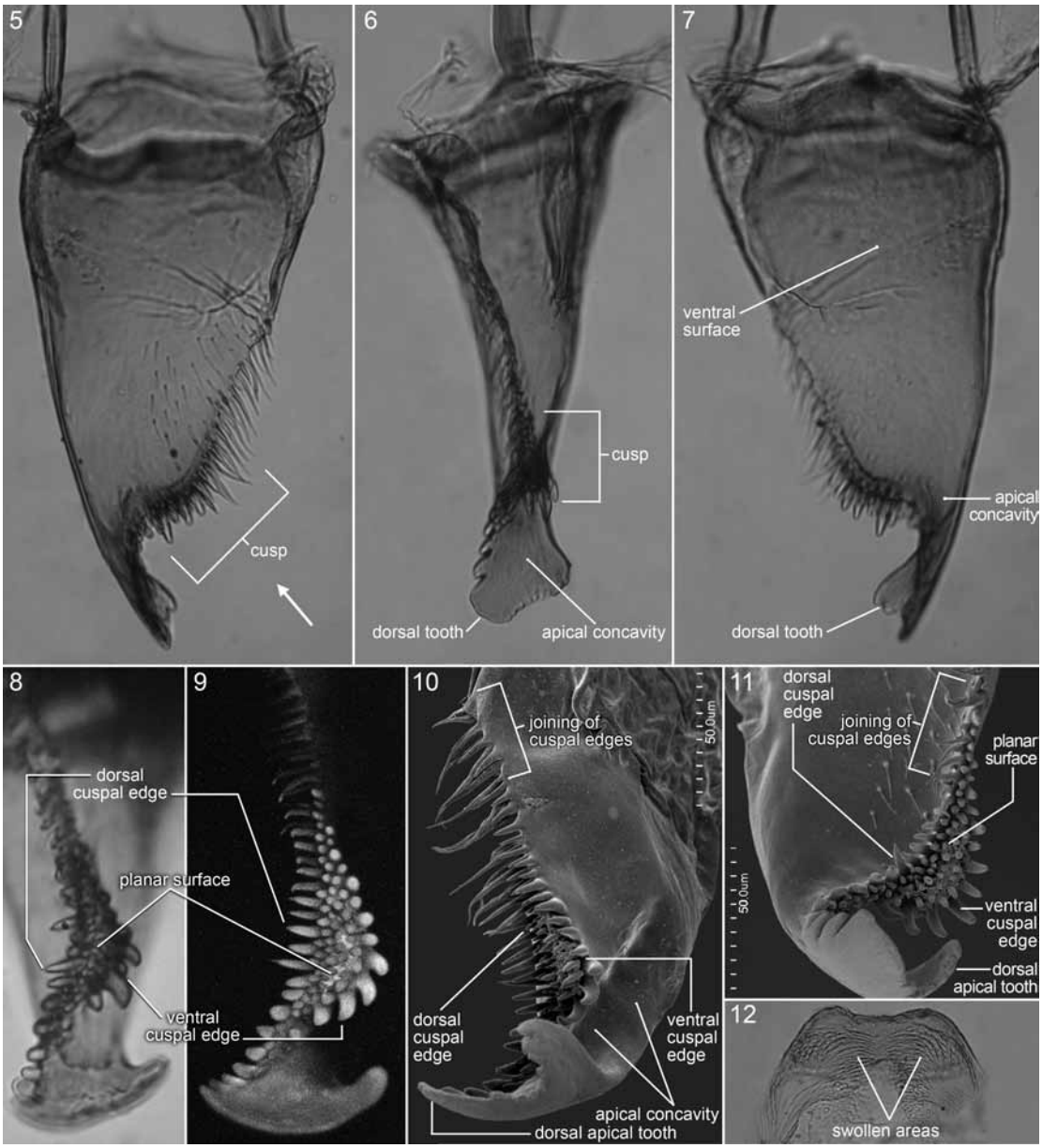
FIGURES 1–4. Diagram of right mandibles of mature larvae of Tapinotaspini. **1, 2.** *Monoeca haemorrhoidalis* (Smith), dorsal and inner views, respectively (modified from Rozen et al., 2006). **3, 4.** *Paratetrapedia swainsonae* (Cockerell), dorsal and inner views, respectively (from Michener and Rozen, 1988).

diagnostic value. In descriptions, the long axis of the mandible is assumed to be horizontal, so that the upper (or top) surface is dorsal and the lower surface is ventral. Descriptions of most larval mandibles refer to the right mandible, which often can be removed without distorting the left side of the head capsule.

In attempting to understand the anatomy of the exomalopsine larval mandible, it helps to consider the simple, broad mandible of such Tapinotaspidini as that of *Monoeca haemorrhoidalis* (Smith) (figs. 1, 2), which has two apical teeth and a well-defined, adorally directed apical concavity, and a serrate dorsal apical edge. In the same tribe, *Paratetrapedia swainsonae* (Cockerell) (figs. 3, 4) has a narrower mandible with two apical teeth, an apical concavity, and a serrated dorsal apical edge, but the more basal part of the dorsal apical edge is greatly broadened and covered with numerous spines. The broadened part of the dorsal edge is termed the cusp (Rozen et al., 2006: figs. 72, 73). Broadening of the dorsal edge combined with the projection of the dorsal edge beyond the ventral edge directs the concavity in a more ventral direction in *Paratetrapedia.*

In *Exomalopsis solidaginis* and other exomalopsines the larval mandible narrows even more subapically (figs. 6, 32–40) than in *Paratetrapedia,* and the cuspal area projects apically more sharply as seen in dorsal (fig. 5) or ventral (fig. 7) outline. Beyond the subapical constriction, the mandibular apex tends to expand more or less before terminating (figs. 6, 32–40). The number (two or three) and shape of the terminal teeth are good diagnostic features, as are the size and arrangements of the cuspal spines.

For purposes of description, the cusp when viewed as indicated by the arrow in figure 5 is considered to be a planar surface (figs. 8, 9, 11). This surface has a series of long spines that are a continuation of the teeth along the dorsal apical edge, which in this area is referred to as the *dorsal cuspal edge,* and a series of stouter spines along the ventral cuspal edge (figs. 8, 9, 10, 11). The dorsal and ventral cuspal edges join toward the base of the mandible where the spines of both edges become long and seem to intertwine (figs. 10, 11). The planar surface itself



FIGURES 5–9. Mature larva of *Exomalopsis solidaginis*. **5–7.** Microphotographs of cleared right mandible, dorsal, inner, and ventral views, respectively. **8.** Microphotograph close-up of cusp taken from direction of arrow in figure 5. **9.** Same except of different specimen taken with confocal microscope. FIGURES 10, 11. SEM micrographs of right mandible of same, showing apex and cusp. **10.** Mostly ventral view. **11.** Mostly dorsal view. FIGURE 12. Microphotograph of epipharyngeal area of cleared labrum showing direction of spiculation on paired swellings.

(figs. 8, 9, 11) is set with numerous smaller spines. These spines are depicted in various ways in figures 8, 9, and 11. The dorsal surface (figs. 5, 11) of the mandible is beset with widely spaced, fine, hairlike spines (or spicules; function considered below). The area along the inner edge of the dorsal mandibular surface is also shallowly concave. The mandibular apical concavity is clearly the inner surface of the mandibular apex, but its basal and ventral boundaries are not defined by ridges; its surface gradually grades into the ventral surface of the mandible (fig. 10).

When one visualizes how the moving mandible positions itself between the epipharyngeal surface of the labrum above and the dorsal maxillary surface and hypopharyngeal surface below, one realizes that the mandible functions in concert with the surfaces that it passes while closing and opening. All of these structures are coadapted and intricately perform the task of transporting provision into the pharynx. During the feeding motions of larval *Exomalopsis solidaginis,* the row of spines of the dorsal cuspal edge (figs. 8, 9) presumably acts like a comb as it sweeps through the matt of curved long spicules (fig. 12) of the epipharyngeal surface, thus loosening the food mass so that the planar cuspal surface can push food toward the mouth opening. The shallowly concave area on the upper surface of the mandible accommodates the slightly swollen spiculate area on each side of the epipharyngeal surface (fig. 12). One also assumes that the broad curved surface of the mandibular apex, which is the apex of the apical concavity, must be instrumental in pushing the bolus toward the pharynx. However, more needs to be learned about the function of the hypopharynx relative to mandibular movement and ingestions. For example, although the scoop-shaped mandibular apex of such larvae as those of *Monoeca* (figs. 1, 2) and *Centris* (fig. 82) face the pharynx, the apical scoop in each fits exactly over the hypopharyngeal lobe when the mandible is closed (also see Rozen, 2010b).

Mandibles of fifth instars show considerable wear, which alters the appearance of their apices. This was especially noticeable in the case of *Chilimalopsis parvula* (figs. 37, 38). However, although the apices of mandibles are subjected to this abrasion, the cuspal spines seem unaffected. To the extent possible, descriptions are based on unworn mandibles, i.e., last instars that have not finished food consumption

OVARIAN STATISTICS OF EXOMALOPSINI

Table 1 gives the ovarian and egg/oocytes statistics based on specimens and field notes. The species listed are ones for which eggs or mature oocytes were currently available. The egg index is calculated by dividing the length of the largest mature oocyte (E) by the distance between the outer rims of the tegulae (M) (as a measure of body size) of the female carrying the oocyte (Iwata and Sakagami, 1966). However, if adults were not preserved in Kahle's solution, but preserved eggs were available, then the length of the egg was divided by the averaged length of the intertegular distance of five females collected at the same time from where the egg was recovered. Either way, the resulting index value provides a means of assessing egg/oocyte length relative to the size of a female's body. Iwata and Sakagami (1966: table 2) devised a classification of bee egg indices as follows: ***dwarf,* E/M < 0.50; *small,* 0.50 < E/M ≤ 0.75; *medium,* 0.75 < E/M ≤ 1.00; *large,* 1.00 < E/M ≤ 1.10; and *giant,* 1.10 < E/M.** The column

TABLE 1. Ovaries and Eggs of Exomalopsini. Statistics of ovaries, eggs, and mature oocytes; shaded cells refer to oocytes. Egg index calculated by dividing egg length with average intertegular distance from five females from same locality as egg. Ovariole formula for all taxa assumed to be 4:4.

Taxon	Egg index	No. oocytes or eggs	Mature oocytes/ ovariole	Egg/oocyte length (mm)	Max. diameter (mm)	Reference
Anthophorula (*Anthophorisca*) *nitens*	0.86	1 egg		2.0	0.50	Current study
	0.83	1 oocyte	0.125	2.03	0.20	
A. (*Anthophorisca*) *sidae*	1.07[a]	1 egg		2.2–2.3	0.45	Rozen, 1984
A. (*Isomalopsis*) *uncicornis*	0.75	1 egg		1.61	0.40	Current study
Eremapis parvula	0.94	1 egg		1.5–1.8	0.40–0.45	Current study
Exomalopsis (*Stilbomalopsis*) *solani*	0.86	1 oocyte	0.125	2.6	0.25	Current study
Exo. (*Stilbomalopsis*) *solidaginis*	0.99	1 oocyte 1 egg	0.125	2.48–2.75	0.50–0.58	Current study
Chilimalopsis parvula	0.76	2 oocytes	0.125	1.38–1.5	0.35–0.38	Current study
Teratognatha modesta	0.73	2 eggs		1.25–1.5	0.33–0.35	Current study

[a] Intertegular distance based on a sample of 10 females.

"Mature oocytes/ovariole" indicates the four species whose oocytes were examined. Each had only one mature oocyte among her eight ovarioles.

Because knowledge of mature oocytes comes from preserved females that had not been dissected at time of capture, the oocytes were misshapen[2] (note variation in *Chilimalopsis parvula* oocytes, figs. 19, 20). A comparison of ovarian and egg statistics of *Anthophorula nitens* in table 1 shows little difference in the egg indices calculated using an egg rather than a mature oocytes, suggesting the use of both procedures for calculating egg indices may be appropriate. However, also note that maximum egg diameters of *A. nitens* are not in agreement, and the oocyte shape of *C. parvula* gives further evidence of the unreliability of using mature oocytes dissected from previously preserved females.

The egg indices shown in table 1 show a considerable range in values. At the low end of values, both *Anthophorula uncicornis* and *Teratognatha modesta* fall in the upper end of the *small* category, and *Chilimalopsis parvula* stands close to the bottom of *medium*. Perhaps not surprisingly, the most prevalent category is *medium* with five representatives, although *Exomalopsis solidaginis* at 0.99 is close to *large*, a category reached only by *A. sidae*. These limited data do not seem to correlate with taxonomic classification or with body size of adults.

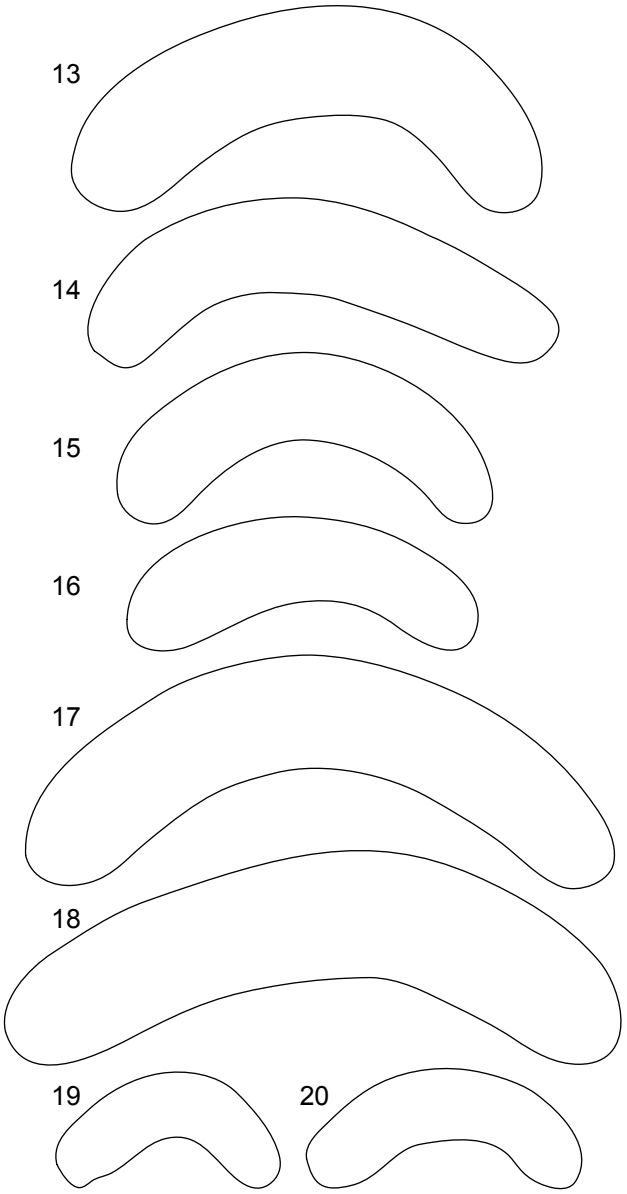
[2] Subsequent to the time these specimens were collected I learned that preliminary dissection of the ovaries of the female could be easily preformed immediately after capture by rupturing the intersegmental membrane between the third and fourth (or fourth and fifth) metasomal segments and by gently pulling apart the two body parts with forceps. The ovaries were usually attached with the posteror part and both parts could be stored in Kahle's solution. Mature oocytes with shape intact can later be removed from ovarioles tissue in the laboratory.

EGGS OF EXOMALOPSINI

Statistics regarding egg and mature oocyte dimensions are given in table 1, and camera lucida diagrams (figs. 13–20) depict them in lateral view, all to the same scale.

Although eggs of the tribe vary in size as might be expected from ranges of adult body size, they are fairly uniform in shape: elongate, nearly parallel sided when viewed laterally but always with the anterior half slightly wider than posterior half; note that *Exomalopsis solani* (fig. 18) would seem not to be in agreement, but, as mentioned in the previous section, compare the two diagrams of *Anthophorula nitens* based on egg (fig. 13) and oocyte (fig. 14). A diagram of an oocyte dissected long after the female is preserved is unreliable. Known eggs of the tribe have a normally rounded anterior end and a posterior end that is slightly more narrowly rounded. All are white and possess a smooth chorion when viewed with a stereomicroscope. The micropyle is too obscure to be seen at similar magnification. SEM micrographs reveal the micropyles of two species, *A. nitens* (Cockerell) (figs. 21, 22) and *A. uncicornis* (fig. 23). Both appear as a dense closure of pits with faint radiated ridge extending outward before disappearing. Elsewhere chorions appear featureless beyond having a smooth texture.

All eggs and mature oocytes observed are distinctly curved, and, when viewed in situ on the food mass, eggs are always found touching the



FIGURES 13–20. Camera lucida outline illustrations of eggs and mature oocytes of Exomalopsini, lateral view, all to same scale, anterior end toward left. **13.** Egg, *Anthophorula nitens.* **14.** Oocyte, same. **15.** Egg, *Anthophorula uncicornis.* **16.** Egg, *Eremapis parvula.* **17.** Oocyte, *Exomalopsis solidaginis.* **18.** Oocyte, *Exomalopsis solani.* **19, 20.** Two oocytes, *Chilimalopsis parvula.*

FIGURES 21–23. SEM micrographs of anterior pole of eggs of: **21.** *Anthophorula nitens* from a distance; **22.** close-up of rectangle in figure 21; and **23.** *A. uncicornis,* close-up of micropyle.

provision with both ends while the middle part does not touch the surface. Very early instars retain this arched posture for a while. I suspect the marked egg curvature relates to their method of eclosion and urge that this be investigated, as is being done in a current study of a *Centris* (Rozen et al., 2011).

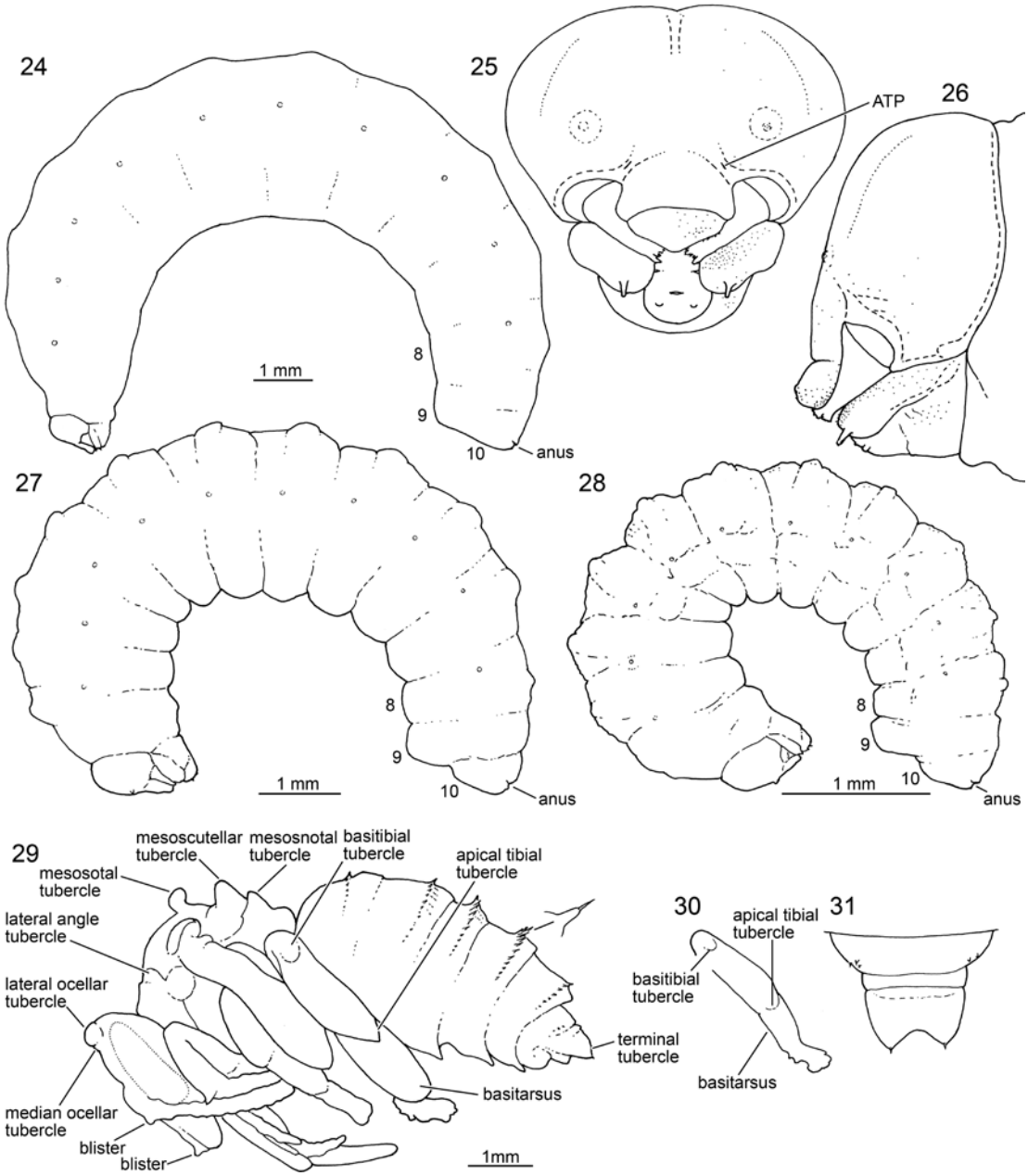
MATURE LARVAE OF EXOMALOPSINI

Tribal Description of Mature Larvae of Exomalopsini

Diagnosis: The combination of characters in boldface below best distinguishes mature larvae of Exomalopsini from those of other tribes of Apinae.

Head: Integument of head capsule with scattered, minute sensilla, so small as not appearing setiform under stereomicroscope; epipharyngeal surface sparsely to densely beset with short to long spicules; mandibular corium usually finely spiculate, but apparently not so in smallest species (*Eremapis parvula* and *Chilimalopsis parvula*). Integument unpigmented except for mandibular apices and mandibular points of articulation with head capsule; palpi occasionally faintly pigmented.

Head moderately small compared to elongate body (figs. 24, 27, 28); width of foramen magnum compared to head width ranging from 0.85 (*Anthophorula consobrina*) to 0.68 (*Exomalopsis auropilosa*); tentorial bridge between posterior tentorial pits well developed, but rest of tentorium perhaps less robust. Center of anterior tentorial pit much closer to anterior mandibular articulation than to outer ring of antenna in frontal view (fig. 25), so that lateral segment of epistomal ridge short; posterior tentorial pit (i.e., junction point of postoccipital ridge, hypostomal ridge, and tentorial bridge) in normal position but deeply recessed; all internal head ridges strongly developed except sometimes coronal ridge fading out at variable distance from vertex to epistomal ridge in frontal view; median section of epistomal ridge often thinner than lateral sections and pleurostomal ridges; dorsomedial portion of postoccipital ridge straight or nearly so (not bending forward) as viewed from above; hypostomal ridge generally without distinct dorsal ramus except in *Teratognatha modesta* and *Chilimalopsis parvula* but faintly developed in some other species, such as *Exomalopsis auropilosa.* Parietal bands



FIGURES 24–26. Predefecating larva of *Exomalopsis solidaginis.* **24.** Entire larva, lateral view. **25, 26.** Head, frontal and lateral views, respectively, with sensilla and spicules illustrated on left side. FIGURES 27, 28. Post-defecating larvae, lateral view: *Anthophorula completa,* drawn from preserved specimen and *Chilimalopsis parvula,* drawn from live specimen, respectively. FIGURES 29–31. Pupal *Exomalopsis bruesi:* **29.** Female, entire pupa, lateral view, and enlarged metasomal tubercle. **30.** Male hind leg, lateral view. **31.** Paired metasomal terminal tubercles, dorsal view.

evident or not, as integumental scars. Antennal prominence nonextant; antennal papilla varying from low mound to conical projection longer than basal diameter. **Apex of labrum (fig. 26) evenly rounded or sometimes shallowly emarginated in frontal view;** front surface of labrum usually with pair of large but low, forward-projecting, sensilla-bearing lobes; transverse labral sclerite absent.

Mandible as seen from above or below (figs. 5, 7) robust at base, gradually tapering to cusp where inner edge abruptly turns so that cuspal area strongly projecting relative to mandibular apex; **mandible as seen in inner or outer view with subapical constriction (figs. 6, 32–40)** (though mandible of *Eremapis parvula* atypical, figs. 41–44); **mandibular apex expanding distally from subapical constriction before terminating in two main teeth, each variably serrate with long to short teeth; in several species, dorsal tooth divided, so that apex appearing to end with three terminal teeth (fig. 35); maximum width of apex variable, but always greater than subapical constriction of mandible as seen in inner or outer views; cuspal surface with numerous spines; apical concavity usually directed obliquely downward because of projecting dorsal apical edge of mandible (although sometimes mandibular apex twisted, e.g., Eremapis parvula); cuspal surface elongate and without ridge or serrations defining basal and ventral boundary basad of mandibular apex (fig. 10);** dorsal mandibular surface often with a few small elongate hairlike projections near inner edge thought to be spicules or spines rather than setae (fig. 11); outer mandibular surface usually without setae. Labiomaxillary region moderately projecting in lateral view. Maxilla with apex turned adorally, bearing palpus subapically; galea not evident; cardo and stipes sclerotized but unpigmented; articulating arm of stipital sclerite evident, sometimes faintly pigmented; maxillary palpus well developed, usually about twice as long as labial palpus (except for *Eremapis parvula*) and, except for *Er. parvula,* much longer than antennal papilla. Labium weakly but clearly divided into prementum and postmentum; premental sclerite not evident to faintly evident; labial palpus less than one-half as long as maxillary palpus to nearly as long as maxillary palpus. Salivary opening on apex of prementum, with or without projecting lips, but always transverse. Hypopharynx paired spiculate low lobes well behind apices of articulating arms of stipes, sometimes so low as to be recognized only by spiculate surfaces; hypopharyngeal groove present, distinct.

Body: Integument without general body setae and with usually weakly spiculate areas on anterior part of body and on ventral surfaced to abdominal segments except for segment 10, although dorsal surface of abdominal segment 10 of *Exomalopsis* and *Eremapis* with sublateral spiculate patch on each side of anus. Body form of predefecating larva (fig. 24) elongate, linear; extent of expression of inter- and intrasegmental lines as well as of paired dorsal tubercles determined by amount of food ingested so that on fully fed larva these features not visible (fig. 24); on many available postdefecating larva (*Anthophorula completa:* fig. 27; *A. chionura, A. sidae, Exomalopsis solani, Chilimalopsis parvula:* fig. 28) cephalic and caudal annulations evident; paired dorsal tubercles more or less evident but always low; **abdominal segment 9 on pre- and postdefecating forms strongly produced ventrally as seen in lateral view (figs. 27, 28); abdominal segment 10 positioned dorsally on 9 in lateral view (figs. 24, 27, 28); anus positioned close to dorsal surface on segment 10 (figs. 24, 27, 28); on postdefecating larvae,**

dorsal surface of segment 10 traversed by groove extending from one side of anus to other and forming strong transverse ridge posteriad to it that surrounds anus dorsally. Spiracles (figs. 24, 27, 28) small, inconspicuous, subequal in size throughout, not surrounded by sclerites, and not on tubercles; peritreme present; atrium projecting beyond body wall, with distinct rim, globose; atrial wall smooth, without ridges or spines, moderately thick; primary tracheal opening with collar; subatrium varying from normal in length, consisting of about 12 chambers, to short, consisting of about 6 chambers depending on species; subatrial chambers decreasing in outside diameter from body surface inward. Males to extent known with single median scar on apex of ventral protuberance of abdominal segment 9; females presumably lacking scars.

Key to Species of Exomalopsini Based on Mature Larvae

Although there are slight differences among species of the subgenus *Anthophorisca* as reflected in their descriptions, these features are of questionable value and are not incorporated in the key. Salivary lips of *Teratognatha modesta* are projecting but not as markedly so as in other cocoon spinning exomalopsines; for that reason, this species will run both ways at couplet 1.

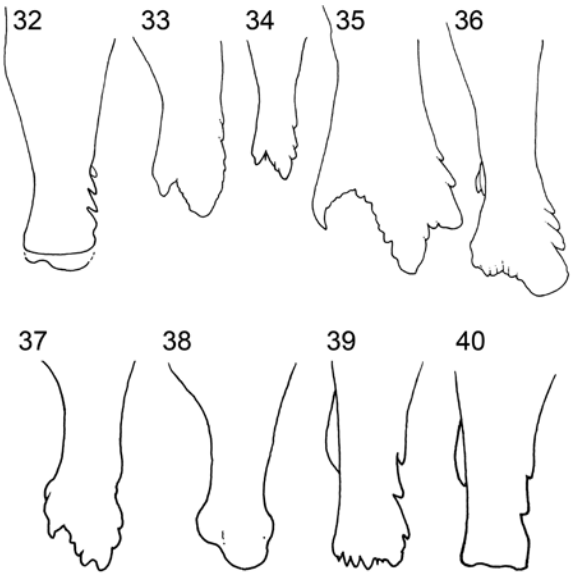
1. Head capsule with salivary lips not projecting or at most only slightly so (non–cocoon spinning) 2
– Head capsule with strongly projecting salivary lips (larval stage possibly cocoon spinning some time in annual life cycle) 5

2(1). Antennal papilla large, somewhat longer than basal diameter, and clearly longer than maxillary palpus; mandibular apex subtruncate with declivity between apical teeth shallow; lower edge of cusp bearing 5–6 very large spines . . *Teratognatha modesta*
– Antennal papilla small, always shorter than basal diameter and shorter than maxillary palpus; mandibular apex terminating in two or three teeth separated by distinct declivities; spines of lower cuspal edge smaller, less conspicuous 3

3(2). Mandibular apex nearly parallel sided in outer or inner view (fig. 31), ending in two acutely pointed teeth; abdominal segment 10 without dorsolateral patch of spicules on each side . . . . . *Anthophorula* (*Isomalopsis*) *uncicornis*
– Sides of mandibular apex broadly expanded in inner or outer view (figs. 32, 33), terminating in two or three teeth; if ending in two, these teeth obtusely rounded (figs. 6, 33); abdominal segment 10 with dorsolateral patch of spicules on each side . . . 4

4(3). Mandibular apex trifid (when unworn) (fig. 35); spiracular subatrium short, consisting of approximately 6 chambers. . . . . *Exo.* (*Exomalopsis*) *auropilosa* and *bruesi*
– Mandibular apex bifid; spiracular subatrium longer, consisting of approximately 12 chambers . . . . . *Exo.* (*Stilbomalopsis*) *solani* and *solidaginis*

5(1). Antennal papilla elongate, conical, about as long as basal diameter, and about as long as, or longer than, maxillary palpus; small-bodied species 6



FIGURES 32–36. Apices of right mandibles of mature larvae of Exomalopsini outer surface, figures 32–36 to same scale, apical end toward bottom, showing variation in shape, as follows: **32.** *Anthophorula completa,* **33.** *A. chionura,* **34.** *A. uncicornis,* **35.** *Exomalopsis auropilosa,* and **36.** *Exo. solidaginis.* FIGURES 37–40. Outer apical surface of right mandibles of mature larvae of *Chilimalopsis parvula* and *Teratognatha modesta,* demonstrating both differences between the two taxa, and differences between predefecating and postdefecating stages of the same taxon resulting from wear. **37, 38.** *Chilimalopsis parvula,* pre- and postdefecating larva, respectively. **39, 40.** *Teratognatha modesta,* pre- and postdefecating larva, respectively. Figures 37–40 to approximately same scale.

– Antennal papilla short, apically rounded, much shorter than basal diameter except in *A. nitens* in which maxillary palpus clearly longer than antennal papilla; larger-bodied species 8

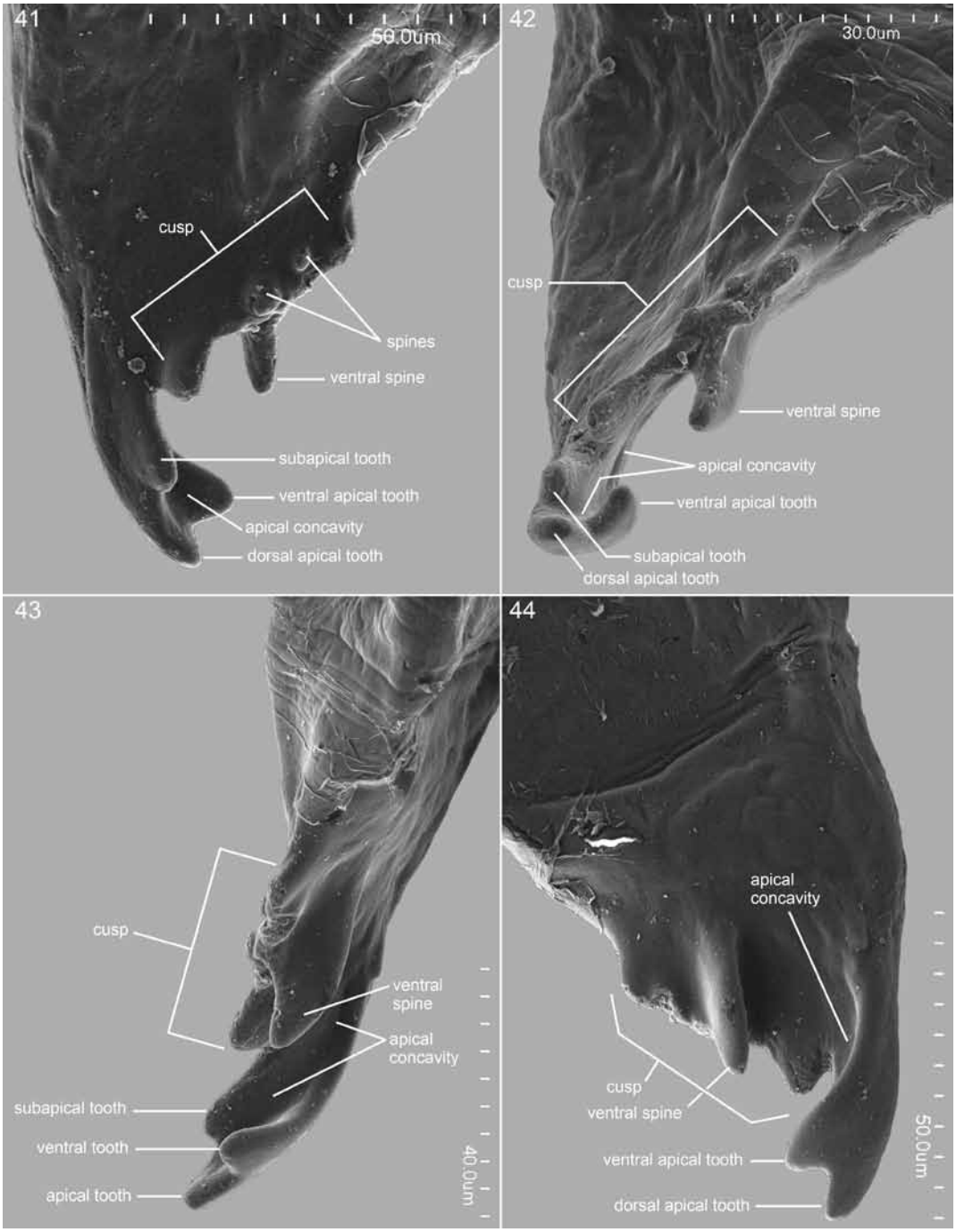
6(5). Mandibular cusp (figs. 41–44) narrow (i.e., lamellate) without planar surface, projecting basad of dorsal subapical tooth, its edge irregular except for large, thumblike spine rising from ventral side (figs. 41–44); mandibular apex slender in outer or inner view (fig. 42), its maximum subapical width only slightly greater than more basil width . . . . . *Eremapis parvula*

– Mandibular cusp broader (not lamellate) with planar surface having numerous spines basal to subapical tooth; mandibular apex broadening subapically in outer or inner view, its maximum subapical width broader than more basal width (figs. 38, 40) 7

7(6). Mandibular apex rounded on postdefecating larva (fig. 38), not truncated; on predefecating larva (fig. 37), dorsal apical tooth large, extending well beyond smaller ventral tooth; salivary lips projecting more, faintly pigmented, wider; spines along ventral cuspal edge smaller, less sharply pointed; distribution Chile[3] . . . . . *Chilimalopsis parvula*

– Mandible apex truncated, with dorsal apical angle not, or scarcely, exceeding ventral apical angle (figs. 39, 40); salivary lips less projecting, unpigmented, narrower; spines along ventral cuspal edge of mandible more robust and sharply pointed; distribution Argentina . . . . . *Teratognatha modesta*

[3] Another species of *Chilimalopsis* is found in Argentina.



FIGURES 41–44. SEM micrographs of right mandible of *Eremapis parvula* showing presumed homologies of structures compared with those of *Exomalopsis solidaginis* and other exomalopsines. **41.** Mandibular apex, ventral view. **42.** Entire mandible, inner view from direction of arrow in figure 5 slightly from above. **43.** Same, except viewed slightly from below, showing thinness of cuspal lamella and mandibular apex, as well as upturned apical concavity at apex. **44.** Entire mandible ventral view.

8(5). Mandibular apex with dorsal tooth obtusely rounded, with notch separating it from rounded ventral tooth weak (fig. 32); both teeth subequal in length; when worn, apex becoming subtruncate and notch disappearing . . . . . *A.* (*Anthophorula*) *completa*

– Mandibular apex with both teeth acutely pointed (fig. 33); ventral tooth much shorter than dorsal tooth with notch between them well identified . . . . . *A.* (*Anthophorisca*) *chionura, consobrina, nitens, sidae*

Anthophorula (*Anthophorula*) *completa* (Cockerell)

Figures 27, 32

Diagnosis: This species can be distinguished from others with projecting salivary lips by the shape of the mandibular apex, both teeth of which are obtusely rounded (unworn) or, when worn, fused as an oblique truncation. The antennal papilla is shorter than its basal diameter, unlike the elongate papilla of *Eremapis parvula,* and not sharply pointed as in *Chilimalopsis parvula* and *Teratognatha modesta.*

Head: Antennal papilla apically rounded, slightly shorter than basal diameter, much shorter than maxillary palpus. Labrum with apical edge weakly bilobed in frontal view; epipharyngeal surface bearing dense patch of long spicules on each side; mandibular corium finely spiculate.

Mandibular apex with dorsal and ventral teeth obtusely rounded; notch separating them shallow; on worn specimen mandibular apex becoming subtruncate, notch becoming even shallower; dorsal apical edge of mandible with moderately small teeth; spines of upper edge of cusp abundant, becoming elongate toward mandibular base; lower edge of cusp with row of approximately 5–7 stout spines, with largest one at leading edge of cusp, smaller spines decreasing in size extending basad and meeting upper edge. Labial palpus nearly twice as long as basal diameter. Salivary lips strongly projecting, their apex much wider than one-half distance between bases of labial palpi in frontal view.

Body: Spiracular atrium consisting of about 12 chambers. Male with transverse median scar on apex of ventral protuberance of abdominal segment 9.

Material Studied: Four postdefecating and two predefecating larvae: AZ: Pima Co., Desert Station E side of Tucson Mts. IV-28-1994 (J.G. Rozen).

Remarks: Nesting biology of this species is described below.

Anthophorula (*Anthophorisca*) *chionura* (Cockerell)

Figure 33

Rozen (1957) originally described the mature larva of this species as *Exomalopsis chionura.*

Diagnosis: Mature larvae of this species and others of the subgenus *Anthophorisca* can be distinguished from those of other exomalopsine treated here because they possess projecting salivary lips and their mandibles bear two acutely pointed terminal teeth. Unfortunately, the species of this subgenus cannot be certainly distinguished from one another. A helpful distin-

guishing character of the subgenus is the apically rounded antennal papilla that is shorter than its basal diameter in combination with projecting salivary lips.

Head: Antennal papilla about as long as basal diameter, much shorter than maxillary palpus. Labrum with apical edge broadly curved in frontal view; epipharyngeal surface bearing dense patch of long spicules on each side; mandibular corium with fine spicules.

Mandibular apex bifid, with dorsal tooth longer; both teeth acutely pointed; notch separating apical teeth sharply defined; dorsal apical edge of mandible with small teeth; ventral apical edge with one or two small teeth near apex of ventral apical tooth; spines of upper edge of cusp abundant, becoming elongate toward mandibular base; lower edge of cusp with row of approximately 5–6 stout spines, with largest ones at leading edge of cusp, smaller spines decreasing in size extending basad until meeting upper edge. Labial palpus about twice as long as basal diameter. Apex of salivary lips wider than one-half distance between bases of labial palpi in frontal view.

Body: Spiracular atrium consisting of approximately 10–12 chambers. Male with small but well-defined transverse median scar on apex of ventral protuberance of abdominal segment 9.

Material Studied: Numerous (10+) pre- and postdefecating larvae: CA: Marin Co.: Alpine Lake, VIII-12-1955 (C.D. MacNeill, J.G. Rozen). This was the collection studied by Rozen (1957).

Remarks: Rozen and MacNeill (1957) studied the nesting biology of this species.

Anthophorula (*Anthophorisca*) *consobrina* (Timberlake)

Diagnosis: Mature larvae of *Anthophorisca consobrina* are nearly indistinguishable from those of *A. chionura,* above. On several specimens the antennal papilla seemed to be shorter, its length about one half its basal diameter, but after preparation, the difference was less distinct. The dorsal tooth of the mandibular apex of *A. consobrina* was slightly more acute with the side straighter than the slightly curved edges of that of *A. chionura.*

The spiracular atrium consists of about 12 chambers. Males have a transverse median scar on the apex of the ventral protuberance of abdominal segment 9.

Material Studied: One postdefecating, five predefecating larvae: NM: Hidalgo Co.: 26 mi S Animas, IX-12, 13-1976 (J.G. Rozen), N #E2.

Remarks: Nesting biology was described by Rozen (1977) under the name "*Exomalopsis* near *chlorina* Cockerell."

Anthophorula (*Anthophorisca*) *nitens* (Cockerell)

Diagnosis: The larva of this species is also nearly identical to that of *Anthophorula chionura,* but the spines on the planar cuspal surface are smaller and less pronounced than those of *A. chionura* and *A. consobrina,* and the large spines on the ventral edge are more pronounced.

Material Studied: Four predefecating larvae: CA: Riverside Co., 12 mi S of Corona, V-25-1985 (J.G. Rozen, R. Snelling).

Remarks: Nesting biology was described by Rozen and Snelling (1986).

Anthophorula (*Anthophorisca*) *sidae* (Cockerell)

Diagnosis: Postdefecating larvae of *Anthophorula sidae* appeared to be unusual for the subgenus because the apex of the apical tooth was rounded and the lateral serrations were rounded crenulations. However, the predefecating larva had an acutely pointed apical tooth with more pointed lateral serrations, strongly suggesting the mandibles of last instars wear over time. The dorsal cuspal edge bears numerous spines as seen in all other species, but the planar surface bears only short spines. The spines of the ventral cuspal edge are extremely large and seem to range from four to six in number.

The spiracular atrium consists of approximately 8 chambers. Males have a transverse median scar on the apex of the ventral protuberance of abdominal segment 9.

Material Studied: Fifteen postdefecating and six predefecating larvae: AZ: Cochise Co.: 5 mi N Willcox, IX-3-1983 (J.G. Rozen, M.S. Favreau), postdefecating larvae removed from cocoons.

Remarks: Nesting biology was reported by Rozen (1984).

Anthophorula (*Isomalopsis*) *uncicornis* González-Vaquero and Roig-Alsina

Figure 33

The single available specimen was damaged in that its labrum was mostly missing.

Diagnosis: This is the only species of the genus *Anthophorula* that is not known to spin a cocoon; the salivary lips of the mature larva do not project. It can be separated from other exomalopsines without projecting salivary lips by the characters presented in the key.

Head: Antennal papilla slightly shorter than basal diameter, much shorter than maxillary palpus. Labrum with apical edge missing; epipharyngeal surface mostly missing but with spicules at lateral edge; mandibular corium spiculate with sharply pointed spicules.

Mandibular apex (fig. 33) bifid, with dorsal tooth longer; both teeth acutely pointed; notch separating apical teeth sharply defined; dorsal apical edge of mandible with moderately small teeth; spines of upper edge of cusp abundant, becoming elongate toward mandibular base; lower edge of cusp with row of approximately 5–7 stout spines, with largest at leading edge of cusp, smaller spines decreasing in size, extending basad until meeting upper edge; planar surface of cusp unusually narrow. Maxillary palpus much longer than antennal papilla. Labial palpus twice as long as basal diameter. Salivary lips transverse, nonprojecting; width about one-half distance between bases of labial palpi in frontal view.

Body: Spiracular subatrium consisting of 6–7 chambers.

Material Studied: One predefecating larva: Argentina: San Juan Prov.: Basilio Nievas, XI-19-1998 (J.G. Rozen).

Remarks: Nesting biology of this species is described below.

Eremapis parvula Ogloblin

Figures 41–44

Diagnosis: This is the smallest species treated here, and its mature larva can be distinguished from the others by the unique lamellate conditions of the mandibular cusp and by the presumed reduction of the ventral cuspal edge to a single large thumblike spine (figs. 41–44). The homologies of the various mandibular features identified in SEM micrographs with those of other exomalopsines seem logical but need verification.

Head: Integument with spicules on dorsal surface of maxilla and hypopharynx; epipharyngeal surface uneven, questionably with spicules, but if present fine and very short. Mandibular corium without spicules.

Antennal papilla conical, elongate, longer than basal diameter and nearly as long as maxillary palpus. Apex of labrum shallowly emarginated in frontal view; front surface of labrum with paired lobes scarcely evident.

Mandible as seen in inner view with upper and lower silhouettes tapering apically to slender, nearly parallel sided, heavily sclerotized apex terminating in acutely rounded dorsal tooth and somewhat shorter but similar ventral apical tooth; mandibular apex strongly rotated so that inner surface of apical concavity surface directed dorsally at apex (figs. 43, 44) basad to which it becomes ventral; dorsal apical edge of mandibular apex with large subapical tooth so close to terminal teeth that mandible appearing tridentate (figs. 41–43); basad of subapical tooth apical mandibular edge with another large tooth presumably indicating distal end of cusp (figs 41–44) of which dorsal edge strongly produced as heavily sclerotized thin edge (referred to as *lamellate* in key and elsewhere), irregular in silhouette, bearing several low rounded projections (possibly modified spines), basad to which it fuses with mandible; planar surface of other exomalopsines apparently so narrow as to become cuspal edge; single large, apically rounded spine arising from ventral side (figs. 43, 44) of cuspal edge presumably homolog of spines on lower cuspal edge of other exomalopsines, as suggested by its position and slight dorsal curve; outer mandibular surface without setae although possibly with alveoli. Labial palpus slightly shorter than maxillary palpus but thinner, about twice length of its basal diameter. Salivary opening with strongly projecting lips, its width wide but clearly less than distance between labial palpi. Hypopharynx spiculate lobes but configuration uncertain.

Body: Abdominal segment 10 with dorsolateral patch of very fine spicules and with fine setae or setiform sensilla below anus suggestive of similar setae in Emphorini. Intersegmental lines clearly evident on postdefecating larva; intrasegmental lines at most weakly apparent because of association with leading edge of dorsal tubercles; abdominal segment 9 produced ventrally far less on postdefecating larvae compare with predefecating form, as seen in lateral view. Spiracular subatrium consisting of about 12 chambers. Male with single median short transverse scar on apex of ventral protrusion of abdominal segment 9; sex characters of female unknown.

Material Studied: Numerous (10+) pre- and postdefecating larvae: Argentina: La Rioja Province: Guandacol, 42 km SW Unión, XI-29-93 (J.G. Rozen, P. Hazeldine).

Remarks: Nesting biology of this species was first described by Neff (1984), and additional life history information is found below.

The presence of fine setae below the anus is a unique feature of *Eremapis parvula* compared with other Exomalopsini, but a similar arrangement of seta is found in the Emphorini; this matter is considered further in Discussion of Immature Stages.

Exomalopsis (*Exomalopsis*) *auropilosa* Spinola

Diagnosis: Only *Anthophorula* (*Isomalopsis*) *uncicornis* and the species of *Exomalopsis* treated here lack projecting salivary lips. The former species has paired apical mandibular teeth that are acutely pointed, whereas those *Exomalopsis* that are bifid (in contrast to trifid) have obtusely rounded teeth. Although all species of *Exomalopsis* dealt with are non–cocoon spinners and therefore lack projecting salivary lips, other species are reported to produce cocoons (Raw, 1977).

Head: Antennal papilla about as long as basal diameter, shorter than maxillary palpus. Labrum with apical edge broadly curved in frontal view although forward directed paired tubercles moderately large; epipharyngeal surface bearing dense patch of long spicules on each side; mandibular corium with extremely fine, scarcely visible spicules.

Unworn mandibular apex (see Mandibular Morphology) appearing trifid because dorsal mandibular tooth subdivided into to two large teeth; ventral most tooth angling away from two dorsal teeth, so that mandibular apex clawlike in inner or outer views; apical edge of mandible with small apically directed teeth; dorsal edge of cusp with moderately long, evenly arranged row of teeth; ventral edge with row of somewhat larger teeth; spines of planar area smaller than those of dorsal and ventral edges but well developed, abundant. Labial palpus small, about one-half as long as maxillary palpus. Salivary opening without distinct projecting lips, but opening transverse, width about one-third distance between bases of labial palpi.

Body: Abdominal segment 10 with patch of strong spicules above and laterad of anus on each side. Spiracular subatrium short, consisting of about six chambers.

Material Studied: Four predefecating larvae: Brazil: São Paulo: Ribeirão Prêto, V-10-1968 (R. Zucchi).

Remarks: Nesting biology of this species was treated by Zucchi (1973).

Exomalopsis (*Exomalopsis*) *bruesi* Cockerell

Diagnosis: This species agrees almost completely with the description of *Exomalopsis auropilosa* above, including the short subatrium. The only apparent differences are in the length of the antennal papilla, which is about half that of its diameter and in the cuspal teeth that are slightly longer and more sharply pointed. As in *Exo. auropilosa* the mandibular apex is distinctly trifid.

Material Studied: One postdefecating larva and two predefecating larva: Peru: Lima Province: 8 km E Chosica, VI-23-95 (J.G. Rozen, A. Ugarté).

Remarks: Nesting biology was treated by Rozen (1997).

Exomalopsis (*Stilbomalopsis*) *solani* Cockerell

Diagnosis: Postdefecating larva of this species is similar to that of *Exomalopsis auropilosa* except the antennal papilla is very low, the width of the salivary opening is about one-half the distance between the bases of the labial palpi, and spines along the lower edge of the cusp are about the same stoutness as the teeth along the top edge. The mandible of the postdefecating larva is apically bidentate on all specimens; predefecating larvae are unknown. Its spiracular subatrium consists of about 12 chambers, as in *Exo. solidaginis.* The patch of spicules on each side of abdominal segment 10 is less conspicuous in this subgenus compared with *Exomalopsis* s.s.

Material Studied: Two postdefecating larvae: NM: Hidalgo Co.: 1 mi N Rodeo, VII-15-1974 (K.C. Rozen); four postdefecating larvae: AZ: Cochise Co., Apache, VIII-30, 31-1988 (B.B. Norden).

Remarks: Nesting biology was described by Norden et al. (1994).

Exomalopsis (*Stilbomalopsis*) *solidaginis* Cockerell

Figures 5–12, 24–26, 36

This description is based on only predefecating last larval instars.

Diagnosis: Similar to that of *Exomalopsis auropilosa,* the mandibular apex of this species ends in two broad apical teeth, each with scalloped edges (fig. 36). Salivary opening is transverse, short (width about one-half distance between labial palpi), and without projecting lips. Hypopharynx is a pair of spiculate lobes well behind apices of articulating arms of stipes. The moderately long spiracular subatrium consists of about 12 chambers. Sex characters are unknown. As in *Exomalopsis solani,* the spicules lateral to and above the anus are smaller than those found in *Exomalopsis* s.s.

Material Studied: Numerous (10+) predefecating larvae: New Mexico: Hidalgo Co., 20 mi S Animas, IX-14-1977 (J.G., B.L. Rozen).

Remarks: Rozen (1984) described the nesting biology of *Exomalopsis solidaginis* from several nests excavated in southern Arizona and New Mexico including the one from which this material was taken.

Chilimalopsis parvula Toro

Figures 28, 37, 38

Diagnosis: The mature larva of this species is similar to that of *Teratognatha modesta,* below. Both are characterized by their sharply pointed, elongate antennal papilla. Although the antennal papilla of *Eremapis parvula* is equally elongate, its apex is rounded, thereby different from those of *Chilimalopsis parvula* and *T. modesta.* They can be distinguished on the basis of

characters in the key. Mandibular apices, particularly of *C. parvula* and *T. modesta,* are subject to considerable wear, so that those of younger fifth instars tend to differ from older ones (figs. 37–40).

Head: Integument with spicules on dorsal surface of maxilla, hypopharynx, and with pair of patches of curved, mesad directed spicules on epipharynx; mandibular corium without spicules.

Antennal disc large, its diameter about three-fourths of distance between anterior tentorial pit and disc; antennal papilla cone shaped, sharply pointed, projecting, about as high as basal diameter, and about as long as maxillary palpus.

Mandible as seen in aboral view with upper and lower surfaces from base with narrowest width in vicinity of cusp and then expanding outward before terminating; in predefecating larva (fig. 37) mandible ending in two main teeth, i.e., (1) large dorsal tooth accompanied on each side by several slightly smaller teeth and (2) a smaller, more ventral tooth with several points; teeth 1 and 2 obviously representing general exomalopsines plan of large, longer dorsal tooth and smaller ventral tooth; in postdefecating larva (fig. 38) mandibular apex apparently greatly worn; mandible now ending as rounded apex, sometimes with irregularly scalloped edged, with ventral lobe representing ventral exomalopsine tooth; dorsal apical mandibular edge with regularly spaced, moderate-size teeth that in cuspal area border upper edge of cusp; lower edge of cusp bordered by similar teeth; planar surface of cusp covered with smaller teeth; outer mandibular surface with single seta. Maxillary palpus well developed, about twice as long as basal diameter. Labium clearly divided into prementum and postmentum; labial palpus about half as long as maxillary palpus, its length greater than its basal diameter. Salivary opening with projecting lips, transverse, width about one-half distance between labial palpi. Hypopharynx spiculate but configuration of surface uncertain; hypopharyngeal groove present, distinct.

Body: As illustrated (fig. 28). Subatrium normal in length, consisting of about 12 chambers, decreasing at most only very slightly in outside diameter from body surface inward. Sex characters unknown.

Material Studied: Four postdefecating and many (10+) predefecating larvae: Chile: Elqui Province, 26 km S Vicuña, X-31–XI-10-1992 (J.G. Rozen, E. Chiappa).

Remarks: Nesting biology of this species is described below.

Teratognatha modesta Ogloblin

Figures 39, 40

Diagnosis: See Diagnosis of *Chilimalopsis parvula,* above.

Head: Epipharynx with pair of dense patches of elongate, mesally directed spicules; mandibular corium with fine spicules. Antennal papilla large, projecting, cone shaped, sharply pointed, slightly longer than basal diameter, and slightly longer than maxillary palpus. Mandible as seen in aboral view with upper and lower silhouettes tapering rapidly to narrowest area in vicinity of multispined cusp and then expanding outward before ending in two apical teeth; these teeth with coarsely serrated edges; serrations so long between apical teeth that they

appear to make single truncated mandibular apex on unworn mandible; on worn mandible mandibular apex appearing subtruncate with crenulated or scalloped edges; dorsal apical mandibular edge with several large teeth but in cuspal area dorsal edge forming row of approximately 10 moderately long, regularly spaced teeth; lower edge of cusp bordered by approximately 5–6 very large teeth and one or more smaller teeth; planar surface of cusp pebbled with smaller teeth; outer mandibular surface with single seta toward base. Salivary opening with weakly projecting transverse lips, width less than one-half distance between labial palpi. Hypopharynx faintly curved medially with entire surface spiculate, with pair of lobes; hypopharyngeal groove present, distinct.

Body: Subatrium moderately short, consisting of only about seven chambers, clearly decreasing in outside diameter from body surface inward. Male with small transverse scar on apex of protuberance of abdominal segment 9; female characters unknown.

Material Studied: Two predefecating larvae: Argentina: Salta Province: 6 km SW of Pichanal, XI-11-1993 (J.G. Rozen, A. Roig).

Remarks: Nesting biology of this species is described below.

PUPAE OF EXOMALOPSINI

Exomalopsis (*Exomalopsis*) *bruesi* Cockerell

Figures 29–31

Following are the first exomalopsine pupae to be described and illustrated. Because the longest series of males and females are those of *Exomalopsis bruesi,* its pupae are described first; comparative pupal descriptions of other species follow.

Female Description: **Head:** Integument without setae; most areas microscopically papillate giving integument slight milky, pale appearance. Vertex with pronounced tubercle associated with each lateral ocellus and smaller, but still large, tubercle over median ocellus; following cephalic areas with small blisterlike swellings that sometimes develop small, dark (almost black) spots, these swellings associated with points of contact with surrounding surface (spots possibly resulting from contact): pair on labral apex, one each on anterior apex of scape, on lateral ocellar tubercle; upper surface of compound eye with faint verrucae that may develop one or more dark spots.

Mesosoma: Integument in some areas papillate, without setae. Lateral angle of pronotum sharply projecting; posterior lobe of pronotum with small tubercle. Mesepisternum with linear swelling (accommodating dense adult setae) extending ventrally in front of midleg; mesoscutum with paramedian pair of conspicuous balloonlike (i.e., basally constricted) tubercles; axilla faintly swollen; mesoscutellum with conspicuous pair of paramedian, conical tubercles; metanotum pair of small paramedian tubercles. Tegula with faint varicosities, without tubercle; wings without tubercles but with a few irregular swellings. All coxae each with apical tubercle; all trochanters each with apical tubercle; fore- and midfemora each with basal tubercle; hind tibia (fig. 29) with large basitibial tubercle, tibia and basitarsus swollen, and apical tubercle

(accommodating adult scopa) on outer surface elongate.

Metasoma: Integument covered in most areas with minute papillae that become minute spicules on subapical spines. T1–T5 each with subapical row of erect sharp-pointed tubercles, those of T1 moderately small but those of T3–T4 longer; those of T5 smaller; sublateral tubercles of each row tending to be most strongly developed; T6 with only a few fine sharp-pointed spines; metasomal apex with paramedian pair of large terminal tubercles (figs. 29, 31), each with darkly pigmented apical point. Sterna without tubercles; S2–S4 each extending posteriorly as flat lamella.

Male Description: As described for female except for following: Dark contact spots on head tubercles far less common. Rear hind leg (fig. 30) more slender; apical tibial tubercles shorter. T1 with subapical spines fewer and smaller; spines on T2–T6 fewer than in female; T7 with subapical row of spines. Most of genital appendages exposed.

Material Studied: Twenty-one female and 10 male pupae: Peru: Lima Prov.: 8 km E Chosica, VI-23-95, VII-03-95 (J.G. Rozen, A. Ugarté).

Exomalopsis (*Stilbomalopsis*) *solani* Cockerell

The pupa, known from a single female, was preserved when close to molting, so that some of the pupal integument was missing, including much of the leg segments and metasomal venter. It closely agrees with the description of *Exomalopsis bruesi* Cockerell except the vertical tubercles are much smaller, at most similar in size to those of *Anthophorula sidae,* although the paramedian mesoscutal, mesoscutellar, metanotal tubercles are essentially that same as those of *Exo. bruesi* (though without black spots). T6 appears to lack a subapical row of sharp tubercles, and the tubercles on the subapical rows of preceding segments may be less elongate.

Material Studied: One female pupa: NM: Hidalgo Co.: 1 mi N. Rodeo, VIII-15-1974 (K.C. Rozen).

Anthophorula (*Anthophorisca*) *nitens* (Cockerell)

Although not described before, the pupa of this species was compared with that of *Paratetrapedia swainsonae* (Cockerell) by Rozen and Michener (1988). Female pupae are unknown, but since the males are indistinguishable from those of *Anthophorula sidae,* female pupae of these two species are probably similar.

Material Studied: Two male pupae: CA: Riverside Co.: 12 mi S Corona, V-26-85 (J.G. Rozen, R.R. Snelling), preserved V-31-1985; one male pupa: same except: V-5-85, preserved VI-10-1985.

Anthophorula (*Anthophorisca*) *sidae* (Cockerell)

Female Description: **Head:** As described for female pupa of *Exomalopsis bruesi* except for following: Vertex with tubercle positioned as in *Exo. bruesi* but much smaller; blisterlike swelling present but none with small dark spots.

Mesosoma: As described for female pupa of *Exomalopsis bruesi* except for following: Mesoscutum with paramedian pair of small tubercles that are not balloonlike; metanotal pair of paramedian tubercles that, though small, are substantially larger than those of *Exo. bruesi.* Leg tubercles not examined, assumed to be like those of *Exo. bruesi,* except: as in *Exo. bruesi,* basitibial tubercle, tibia, and basitarsus swollen, and apical tubercle (accommodating adult scopa) on outer surface elongate.

Metasoma: As described for female pupa of *Exomalopsis bruesi* except subapical row of sharp-pointed spines somewhat smaller and spines of T6 found on pair of sublateral elevations.

Male Description: As described for female except with exception of hind legs and metasomal features like those of male *Exomalopsis bruesi.*

Material Studied: Three female and 4 male pupae: AZ: Cochise Co.: 5 mi N. Willcox, VIII-29-1983 (J.G. Rozen), nest #4.

Chilimalopsis parvula Toro

Female Description: **Head:** Integument without setae or special microscopic texture. Vertex without tubercles; other cephalic areas without large or small tubercles or varicosities.

Mesosoma: Integument without setae or special microscopic texture. Lateral angle of pronotum somewhat swollen; posterior lobe of pronotum enlarged. Mesepisternum without swelling or tubercles; mesoscutum nearly smooth, with only faint paramedian varicosities; axilla not produced; mesoscutellum with paramedian pair of erect, small, apically rounded tubercles; metanotum with pair of paramedian tubercles that are so small that they might be overlooked. Tegula apparently without varicosities; wings without tubercles. Because of limited study material, basal leg segments not examined; hind tibia without basitibial swelling; apical tibial tubercle on outer surface moderately large; basitarsus large, expanding apically before ending.

Metasoma: Integument in some areas with microscopic granular texture. T1 apparently without tubercles, or if present too small to be certainly detected; T2–T5 each with subapical row of erect, sharp-pointed tubercles; sublateral tubercles of each row tending to be most strongly developed; those of T2 very small and those of T2–T5 longer; T6 without tubercles or spines; metasomal apex ending in nonspined, broadly acute, single point. Sterna unremarkable.

Male Description: Unknown.

Material Studied: One female pupa: Chile: Elqui Province: 26 km S Vicuña XI-01-1992 (J.G. Rozen).

Teratognatha modesta Ogloblin

The single available pupa of this species, a female, is almost indistinguishable from that of *Chilimalopsis parvula.* The basitibial plates appear to have a more uneven (varicose) surface than those of *C. parvula,* and, although the metanotum is produced near the midline, it appears to be a single central swelling. Furthermore, the subapical rows of tergal spines appear to rise from somewhat more pronounced and elevated tubercles.

Male Description: Unknown.

Material Studied: One female pupa: Argentina: Salta Province, 6 km SW Pichanal, XI-11-1993 (J.G. Rozen, A. Roig).

DISCUSSION OF IMMATURE STAGES

The close agreement in mature larval anatomy, in pupal anatomy, and small body size support the studies of Silveira (1995) and Michener (2007) that *Chilimalopsis* and *Teratognathus* are closely related, despite the fact that larval *C. parvula* spins a cocoon, whereas *T. modesta* is not known to do so. As is evidenced in the following section, cocoon production among the Exomalopsini is not a consistent behavior: most *Anthophorula* spine cocoons, whereas *A.* (*Isomalopsis*) *uncicornis* does not. Similarly, in *Exomalopsis* some species spin whereas others are known not to do so.

However, small body size alone is not a reliable feature as evidenced by *Eremapis parvula,* the smallest species studied. Its larval mandible is remarkably different from those of any other species treated, seemingly far more different than are the mandibles of *Chilimalopsis* and *Teratognatha* from those of the other genera examined here. Another remarkable feature of *E. parvula* is the integumental ornamentation of abdominal segment 10. The finely spiculate patch laterad of and dorsal to the anus on each side may or may not be homologous to those of *Exomalopsis.* However, the setae below the anus are unique in this study but closely resemble the distribution of setae on abdominal segment 10 in larval Emphorini, *Ctenoplectra* (New Information), and Tetrapediini (New Information), although in the latter two cases, setae are smaller, far less pronounced. The significance of this feature deserves further study.

One is left with the impression that immature stages (eggs, mature larvae, and pupa) of the Exomalopsini, so far as known, provide few features that help explain interrelationships of the included taxa, and indeed offer few features by which they can be distinguished from larvae of related tribes.

NESTING BIOLOGY OF EXOMALOPSINI

Nesting biology of the tribe was reviewed by Rozen (1984), although subsequently *Ancyloscelis* was placed in the Emphorini and *Paratetrapedia, Lanthanomelissa, Tapinotaspis,* and *Monoeca* are now assigned to the Tapinotaspidini. Dimensions of cells of species dealt with here as well as those of exomalopsine species treated in earlier studies are presented in tabular form for ease of comparison (table 2).

Anthophorula (*Anthophorula*) *completa* (Cockerell)

Table 2

I discovered a single nest of *Anthophorula completa* at Desert Station on the east side of the Tucson Mountains in Pima Co., Arizona, and excavated it on April 28, 1993. A year later

to the day I found two more close by. The entrance to one of these was at the overhanging edge of a piece of rhyolite on the side of the sloping surface of a small ravine.

Nest Architecture: One of the nests discovered in 1994 had its main open burrow descending at about 45° following an irregularly curved path. First cells were encountered about 15 cm from the entrance and all others, about 20 total, were found from there to 22 cm beyond the entrance. The burrow branched many times and all cells were clumped side by side and apparently end to end, presumably because of limited space created by rock inclusions. Cell inclination seemed variable. Although the cells appeared fresh, most were vacated, but at least one contained fresh provisions, two or three held feeding larvae, and several more had postdefecating larvae. Two other cells contained feeding larvae of *Triopasites penniger* (Cockerell) (Nomadinae: Brachynomadini). The second nest was similar but had fewer cells.

Cells preserved in the collection show that cell walls, up to 0.5 mm thick, are more consolidated than the substrate and have a shiny lining that is highly water repellent when tested with a water droplet. Obviously coated with a smooth semitransparent material, walls show a faint longitudinal ripple pattern. Cells are elongate ovals, with their top surface more curved than the slightly flatter lower surface holding the provisions. Their anterior end is more elongate than the rear, so that the maximum diameter is about 2 mm from the rear end. Cell closures have a nearly flat inner surface showing a well-defined spiral of soil in some samples consisting barely of three coils to the radius, although others have four coils; the outer surface of the closure is concave and smooth, but not shiny. The closure thickness at the center on one specimen is somewhat less the 0.5 mm. When tested with water, the inner surface of closures is relatively water retardant, and the outside surface slowly absorbs a droplet.

Provisioning and Development: Provisions of *Anthophorula completa* (figs. 45, 46) were loaflike with an unusually flat upper surface, and a backward slanting, flattened front that ended below in a ventral projection, a "foot" (as illustrated in Rozen and MacNeill, 1957: figs. 1, 2). The rear of the provisions is apparently attached to the lower curved rear of the cell, and the foot apex either just nearly reach the cell floor at the front. Eggs were deposited on the top surface, somewhat toward the front, as judged from exuviae found on provisions stored in the museum (fig. 46). The widest part of the loaf was in the posterior part, when viewed dorsally or laterally (figs. 45, 46).

Almost all feces are deposited against the closure and the front wall of the cell for about one mm behind the closure. When torn apart the feces seem to incorporate fibers of silk, suggesting cocoons are initially started during defecation, although the walls of the cocoon elsewhere contain no feces, an indication that the body of the cocoon is spun after defecation is complete. Most of the cocoon fabric is a semitransparent, extremely thin parchmentlike sheet of silk closely applied to the cell surface, so that one can see the position of the feces through the cocoon from inside the cell. However, the cocoon incorporating the feces at the cell closure is thicker and its texture of the inner surface is more fibrous.

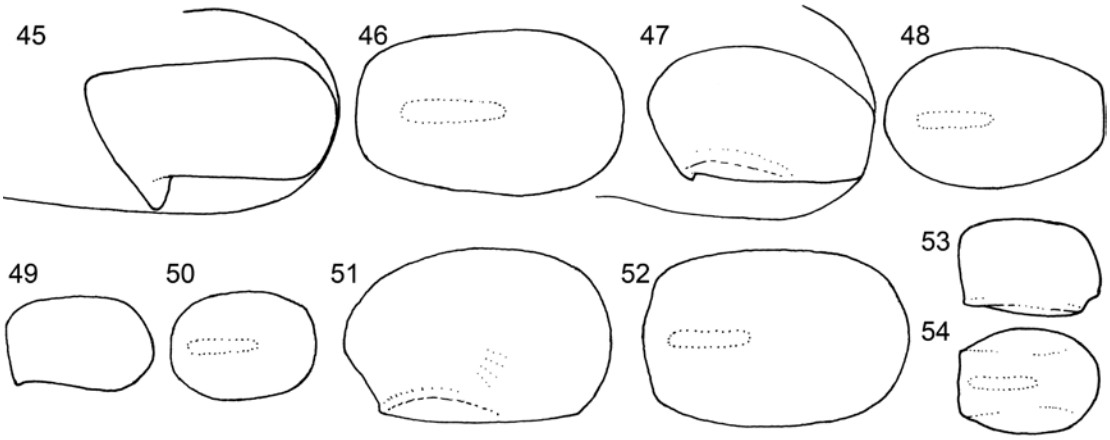
When examined with an SEM, a cocoon wall was a single sheet partly imbedding silk strands with other free strands partly covering the inner surface. Whether the sheet was composed solely of fused silk or of another secretion that was deposited during silk spinning is

TABLE 2. Nest Statistics of Exomalopsines Treated in Nesting Biology. H = horizontal nester, F = fissure nester (see text). Length and height of provisions measured in side view (figs. 45, 47, 49, 51, 53); width measured in top or bottom view (figs. 46, 48, 50, 52, 54). Shaded cells contain data from earlier publications as indicated under References. In cases where sample size is not offered in literature accounts, *N* = 1 is substituted, and when a range is given *N*+ = 2. Cell tilt is from horizontal.

Taxon	Nester type	Burrow diameter, mm (*N*)	Cell length, mm (*N*)	Max. cell diameter, mm (*N*)	No. cells in series	Cell tilt	Provisions					Reference
							Length, mm	Height, mm	Width, mm	*N*	Foot?	
Anthophorula (*Anthophorula*) *compactula*	H	4.0 (1)	6.2–7.2 (3)	3.5 (2)	1–2?	10–30°						Rozen, 1984
A. (*Anthophorula*) *completa*	H	4.0 (1)	6.0–6.5 (3)	3.8–4.2 (3)	1–2?	Various	4.5–4.9	2.0	3.0	3	Yes	Current study
A. (*Anthophorula*) *crenulata*	H	3.5 (1)	5.7–6.3 (20)	3.5–3.9 (20)	1						Yes	Parker, 1984
A. (*Anthophorisca*) *chionura*	F	2.5 (1)	6.0 (5)	3.6 (7)	1–5	Various	3.5	2.2	2.4	???	Yes	Rozen & MacNeill, 1957; Rozen, 1984
A. (*Anthophorisca*) *consobrina*	H	3.0 (1)	7.5 (1)	4.5 (1)		45°	4.0	3.0		1	Yes	Rozen, 1977
A. (*Anthophorisca*) *nitens*	F	3.3–3.5 (4)	7.0–8.0 (5)	4.8–5.0 (7)	1–2	0–45°[a]	5.0[a]	3.0[a]	3.0[a]	1[a]	Yes	Rozen & Snelling, 1986
A. (*Anthophorisca*) *sidae*	H	3.5 (1)	7.8–8.5 (6)	4.2–4.6 (8)	1		4.3–5.2	2.4–5.2	3.3–3.8[b]	7	Yes	Rozen, 1984

A. (*Isomalopsis*) *uncicornis*	H	2.8–3.5 (1)	7.0–7.5 (2)	3.8–4.0 (3)	1	45–75°	3.5–4.0	2.2–2.5	2.4–2.7	5	Yes	Current study
Eremapis parvula	H	1.75–3.0 (4)	4.0–5.0 (8)	2.5–2.9 (10)	1–2	0–30°	2.3–2.6	1.7–1.8	1.8–2.0	5	No	Current study
Chilimalopsis parvula	F	1.5–2.0 (2)	3.8–4.2 (10)	2.4–2.8 (11)	1–3	0–80°	2.0–2.2	1.0–1.9	1.6[c]	2	No	Current study
Teratognatha modesta	F	2.0–2.2 (4)	4.0–4.6 (10)	2.6–2.8 (12)	1–3		2.0–2.3	1.4–1.7	1.8[c]	3	No[d]	Current study
Exo. (*Exomalopsis*) *auropilosa*	H	4.0 (2)	10.0 (1)	5.0 (1)	1	90°					No	Zucchi, 1973
Exo. (*Exomalopsis*) *bruesi*	H	4.0–4.5 (2)	7.0-8.0 (?)	5.0 (?)	1	20–80°	4.4–4.7	3.1–3.2	3.0–3.2	3	No	Rozen, 1997
Exo. (*Exomalopsis*) *pulchella*	H			8.8	1	40°					No	Raw, 1977
E. (*Exomalopsis*) *similis*	H & F			8.8	1	≈0°					No	Raw, 1977
Exo. (*Stilbomalopsis*) *solani*	H		8.0–9.5 (31)	5.0–5.6 (35)	1		5.0	3.3	3.2	1	No	Rozen, 1984; Norden et al., 1994
Exo. (*Stilbomalopsis*) *solidaginis*	H	4.5 (1)	7.5–8.5(8)	5.0–5.5 (8)	1	35–80°	5.0–6.1	2.9–3.5	3.2–4.0	8	Yes	Rozen, 1984

[a] New data, from single food mass store in AMNH or from notes.
[b] 3 data.
[c] Single datum.
[d] See text for explanation.



FIGURES 45–54. Camera lucida illustrations of provision loaves of Exomalopsini with position of eggs indicated in top views, front end at right, all to same scale. All provision loaves oriented artificially as if cells were horizontal. **45, 46.** *Anthophorula completa,* side view in a cell and top view, respectively. **47, 48.** *Anthophorula uncicornis,* side view and top view, respectively. **49, 50.** *Eremapis parvula,* side view and top view, respectively. **51, 52.** *Exomalopsis bruesi,* side view and top view, respectively. **53, 54.** *Teratognatha modesta,* side view and top view, respectively.

unknown. It was, however, extremely thin (somewhat less than 5 μm, fig. 62) on the sides of the cocoon wall and had no openings or fenestrations, except at the anterior pole (fig. 58). There a large, more or less circular hole (diameter < 1 mm) occurred, screened by an open but dense webbing of silk strands (figs. 59, 60). This feature presumably allows gas exchange between inside and outside of the cocoon, which is necessary because the immature bee must survive until the next blooming of its food plants, perhaps 10 months away. It seems likely that the thin cocoon fabric elsewhere protects the bee from desiccation while the screening at the opening helps prevent parasite/predator invasion. Although no external protrusion is noticeable on the outside of the cocoon, this structure corresponds to the nippled end of megachilid cocoons that serves similar functions (Rozen and Hall, 2011).

The cocoon of *Anthophorula completa* is similar to that described for *Anthophorula sidae* (Rozen, 1984) in that most of the feces of *A. sidae* are applied to the front end of the cell, and elsewhere the cocoon fabric is semitransparent. With *A. completa* all the feces are applied only to the front end, but *A. sidae* also applies a thin layer of feces to the entire cell wall where it is loosely held in place by fine open strands of silk spun before the semitransparent layer. The cocoons *A. chionura* and *A. nitens* are opaque, matte, and dense with feces applied to all surfaces during cocoon construction (Rozen and MacNeill, 1957; Rozen and Snelling, 1986). Hence, their cocoons have a very different appearance from the semitransparent, thin, seemingly delicate cocoon of *A. completa.*

Parasitism: As indicated above, the cleptoparasite *Triopasites penniger* successfully attacked these nests; its larval feces were broadly smeared against much of the cell wall, not unlike the habits of its tribal partner *Brachynomada sidaefloris* (Cockerell), which attacks

Anthophorula sidae (Cockerell) (Rozen, 1984: figs. 31, 32). *Triopasites penniger* also parasitizes nest of *Anthophorula compactula* (Rozen, 1977).

Anthophorula (*Isomalopsis*) *uncicornis* Vaquero and Roig

Table 2

I found four nests of *Anthophorula uncicornis* with their entrances grouped near one another (two were 13 cm apart) on the horizontal ground surface at Basilio Nievas, San Juan Prov., Argentina, on November 10, 1998, where *Eremapis parvula* and also an unknown eucerine (probably *Canophorula*) also actively nested in the fine soil, which was dry on the surface but moist below. The area was partly surrounded by *Prosopis* trees. *Anthophorula uncicornis* appeared to be in the early stages of nesting activity since numerous eggs and small larvae were observed, but almost no late-stage larvae were detected. Since vacated cells from early populations were uncovered, the site obviously had been used previously.

Nest Architecture: Three nests of *Anthophorula uncicornis* contained 5, 8, and 14 females, respectively. Two excavated nests revealed in each an open main tunnel descending vertically, one to a depth of 25 cm and the other to 17 cm at which points they gave rise to numerous side tunnels. One of five (or six) cells associated with the first nest was uncovered at a depth of 35 cm. Main burrows tended to be wider (i.e., 3.5 mm in diameter) near the surface and narrower (2.8 mm in diameter) where the soil was moist.

Cells were oriented with their rear end much lower than the front (see table 2). Ovoid in general shape, their upper surface was longer and more curved while their lower surface was flatter when viewed from the side, and the region of greatest diameter was approximately one-third of the cell length from the posterior end. The inside closure diameter of 2.7 mm ($N = 2$). At the posterior end the cell surface was very smooth and reflective where the provision loaf was attached and, when tested with a water droplet, highly nonabsorbent. (In four cells preserved in the collection, the point of provisions attachment is marked by a small spot of provisions in the middle of the reflective surface, proof of regular attachment of provisions to the cell's rear end.) The reflective area is restricted just to this area. Where the surface dulls it becomes somewhat more water absorbent when tested,[4] and the surface itself is not as smooth. At the front end of the cell, the surface becomes even more uneven, though not as much as the wall of the lateral. All cells, old or fresh, were found singly, far from one another. Cell closures were deeply concave spirals of four distinct coils to the radius, and laterals were soil filled.[5]

[4] For testing the waterproof qualities of cell walls, I have found that a small-bore hypodermic syringe is an excellent tool for delivering a small droplet to the surface of small cells. Because different parts of cell walls may repel droplets differentially, small drops can be applied to different parts of the same wall to detect variability.

[5] A single cell of *Anthophorula* (*Isomalopsis*) *macrodonata* Vaquero and Roig (Argentina: Tucaman Prov., 11 km N Cadillal, 12-03-1989 (A. Roig)) preserved in the AMNH collection had smooth walls and a closure similar to those of *A. uncicornis* except the closure was not as deeply concave; the rear end of the cell had not been preserved.

Provisioning and Development: Females of *Anthophorula uncicornis* shape mealy-moist provisions into a loaflike mass described below. When viewed from the side or from above (figs. 47, 48), the front end is broadly rounded while the rear tapers to a terminal truncation where it attaches to the rear surface of the cell. As in *A. chionura* (Rozen and MacNeill, 1957: figs. 1, 2), the front lower edge bears a ventral projection, i.e., a "foot," and its top surface is curved in side view, as in *A. chionura,* unlike the flattop provisions of *A. completa* (fig. 45). The entire lower surface of the provisions including the foot is elevated (fig. 47) and does not touch the wall. The attachment of the provisions to the most nonabsorbent surface of the cell may function to prevent moisture loss without the female bee devoting effort or waterproofing agent to the entire cell surface. The female places her elongate, curved, white egg with a smooth chorion on the top surface of the provisions in the sagittal plane of the cell, no doubt with the egg's anterior end pointing toward the closure. Because of its strong curvature, the egg touches the surface of the provisions only by its front and posterior ends, while the midsection arches upward.

Young larvae crawl over the provisions as they feed, but no observations were made that might reveal how larger larvae hold provisions as they feed. Last larval instars do not spin cocoons, as evidenced by their absence in cells of a previous generation and the lack of strongly projecting salivary lips on mature larvae. Fecal material in these cells is plastered against the wall mostly toward the rear.

Parasitism: No cleptoparasites were associated with these nests.

Eremapis parvula Ogloblin

Table 2

Neff (1984) provided extensive information on nesting habits of this species. The following observations supplement his original account.

I investigated two nesting sites of *Eremapis parvula.* One at Pampa Vieja near San José de Jáchal, San Juan Province, Argentina, I discovered on November 2, 1991, and took brief notes on one active nest and vacated cocoons. I visited it again on November 28, 1993, when I carried out a more thorough observation. Although females were carrying pollen loads into nests, no new cells were encountered, but numerous cells whether vacated or with mature larvae gave insight into cocoon construction and phenology. The other site, at Guandacol, 42 km southwest of Unión, La Rioja Province, Argentina, I discovered and examined on November 29, 1993, and the following day. Almost no vacated cells were encountered, suggesting that the site was newly established, but numerous cells containing feeding larvae were recovered, giving insight into provisioning and larval development. Both sites were densely populated.

The Pampa Vieja site was restricted to a nearly barren horizontal area 2–3 m wide and 8–10 m long, on the east side of a row of trees and bushes that bordered an irrigation ditch. Fully exposed to the sun during the morning, at midday the site was partly shaded by the trees, some of which were *Prosopis,* the known pollen source of *Eremapis parvula.* Although at first they were presumed to be the sole source, a low-growing species of *Prosopis* also occurred some

distance away. The fact that males were collected there suggests that females may have foraged from that species as well.

Soil at both sites was fine grained with few inclusions. Analysis of soil from Pampa Vieja indicated a composition of 50% sand, 42% silt, 8% clay, 0.5% coarse fragments, with a texture of sandy loam/loam. There the soil was dry even at the cell level; moisture at Guandacol resulting from recent irrigation was evident.

Nest Architecture: Nests at both sites were shallow, with cells occurring 5–10 cm below the surface.[6] At both, burrow entrances were open as were main tunnels, but laterals leading to cells were soil filled. Small concentric tumuli were also evident at Guandacol and at Pampa Vieja in 1991 but not in 1993, perhaps because there were fewer active nests. I suspected in 1991 that nests seemed to contain single females, as had already been reported by Neff (1984).

Main tunnels tended to descend vertically but then turned and meandered at the cell level, where many branched and perhaps anastomozed. Burrow walls were unlined and obviously (though not tested) water absorbent. Many cells were arranged singly but some were in linear series of 2. All were horizontal or tilted as much as 30°; diameter of entrance was 1.5 mm (N = 2). In lateral outline, cell shape was an elongate oval, somewhat more elongate than the one diagrammed by Neff (1986: figs. 2, 3), and cell closures were deeply concave spirals of about 3 coils to the radius, deeper than depicted by Neff (ibid.). Cell walls appeared unlined (unlike those of any other exomalopsine taxon described in this paper), as was also reported by Neff. They were tested with a water droplet, which was absorbed immediately.[7] See table 2 for other nest statistics.

Provisioning and Development: So far as known, the pollen sources of *Eremapis parvula* are several species of *Prosopis* (Fabaceae). The reader is referred to the paper by Neff (1984), who offers considerable information concerning floral preferences and discusses the bands of conspicuous specialized setae on adult female metasomal sterna 2–5, which he refers to collectively as a "metasomal scopa." These setae are uniformly arranged and directed, and each is apically curved and points posteriad. One wonders whether they serve as a comb to manipulate dry pollen found in the curved, long and long-branch, scopal setae of the hind basitarsus and tibia.

Provisions are shaped in the form of a loaf (figs. 49, 50) with a curved top on which the female deposits an egg in the sagittal plane of the cell. The loaf is positioned on the floor (i.e., lower cell wall) of the cell, but whether it touches the floor with only its front and back edges (as depicted by Neff (ibid.: fig. 2) or rests its full length on the floor (as indicated by notes taken in 1993) needs to be confirmed. Although a distinct "foot" on the lower front edge of the provisions was not evident, on some preserved masses that edge was faintly produced. Young larvae crawl over the food mass while they eat making visible grooves on the surface of the provisions.

[6] A nesting aggregation of *Eremapis parvula* subsequently encountered but not studied at Basilio Nievas, San Juan Province, on November 10, 1998, contained cells with larvae and old cocoons at a depth of ca. 8 cm.

[7] This test was performed on a sample that had been stored in the museum for 17 years. Although one might question whether the waterproof substance would not deteriorate over such a long period, other cells in this study, stored equally as long, had retained their hydrophobic nature when tested.

Intermediate-stage larvae have dorsal paired tubercles on most body segments, but these tubercles all but disappear later. Older larvae were encountered encircling the provisions so that the provisions no longer touched any part of the cell wall. These larvae had positioned themselves approximately in the equatorial plane of the cell (i.e., at right angle to the cell's long axis) so that they touched the cell wall with most of their dorsal surface while they circled the provisions. At this stage a larva starts defecating while still feeding, excreting greenish-brown elongate fecal pellets. Because the larva crawls (presumably with remnants of its dorsal tubercles) in the equatorial plane of the cell, almost all of the feces are applied as a broad band circling the cell wall. This band when complete forms a dark grayish-green belt up to 2 mm wide composed of more or less parallel fecal pellets that circles the cell. Larvae subsequently applies a pale, thin cocoon (fig. 63) the like of which, because of fecal placement, has not been reported for any other known bee, as pointed out by Neff (1984). The cocoon fabric adheres tightly both to the inner surface of the fecal band and to the rear and front of the cell and inner surface of the closure. The soil is glued to and hides the silk from the outside, but the inner surface of the cocoon glistens, and with SEM examination is seen to be composed of one or more thin sheets of material with embedded strands of silk, as in *Anthophorula completa*.

Future studies of this bee should consider the possibility that its larval behavior functions to remove the stored provision as soon as possible from contact with the cell wall that has no waterproof lining. See commentary on this matter in Discussion of Exomalopsine Nesting Biology, below.

Adult Activity: Although males of this species were encountered at both nesting sites, matings were not seen to take place there, an observation paralleling Neff's (1984). Males and females were observed at Pampa Vieja during the heat of the day. Late in the day at the Guandacol site, numerous males and females were seen over a section of the nesting site, which was judged to be about a meter square. The following morning a *Larrea* bush densely shaded the same area, and little or no activity was observed to take place in the shade, although elsewhere in sunny portions males and females were observed.

Parasitism: Cleptoparasitic bees were not found at nesting sites.

Chilimalopsis parvula Toro

Table 2

Chilimalopsis parvula and *Chalepogenus rozeni* Roig (Tapinotaspidini) nested in cracks in the ground at 26 km S of Vicuña, Elqui Province, Chile on October 30, 1992, and the site was studied on October 31 and November 1, 1992, and again on November 8 and 10, 1992. Both species were actively foraging and nested in the same cracks. Freshly constructed cells as well as those from previous generations of both were intermixed in the soil next to the cracks. The ground surface, unshaded except for scattered low-growing plants, sloped to the west generally 20° to 30° from horizontal, and at least some *Chilimalopsis* entered cracks where the surface sloped about 45°. The pollen source of *C. parvula* was the low-growing *Pleurophora polyandra* Hook. and Arn. (Lythraceae), which matted the adjacent ground surface. The cracks, created

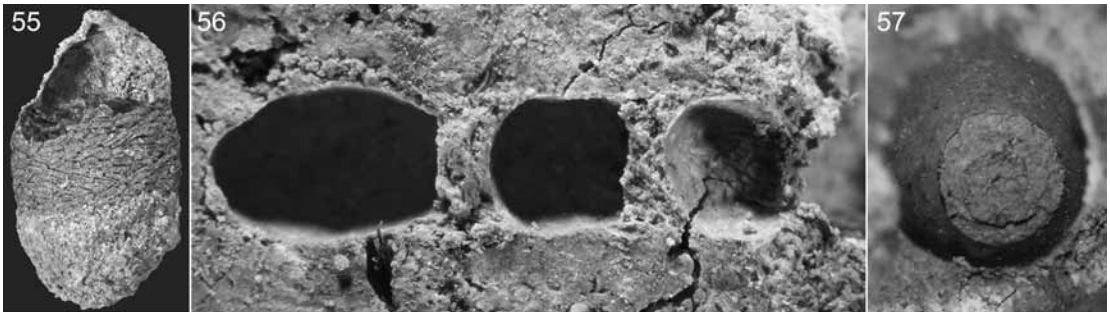


FIGURE 55. Macrophotographs of cocoon of *Eremapis parvula*, showing adult emergence hole (upper left) and fecal pellets extruded by larva before spinning. FIGURES 56, 57. Macrophotographs of nest components of *Chilimalopsis parvula.* **56.** Cell showing double closure and cell asymmetry, side view. **57.** Spiral closure of cell viewed from inside cell.

by drying, were generally vertical and most abundant near the surface where the soil was the least moist. Soil consisted of 48% sand, 17% silt and 35% clay and classified as sandy clay/sandy clay loam. Larger cracks descended to approximately 40 cm, well below the lowest cell depth. Bees avoided excavating through the extremely hard, dry surface soil by descending through the cracks to the moist lower soil, which could be more easily dug with their mandibles. Although a few vespids also nested in these cracks, no other bees were observed using them.

Nest Architecture: Nest entrances of *Chilimalopsis parvula* were scattered as circular, open holes on the vertical or nearly vertical faces of cracks, mostly 12–18 cm below the surface.

Small pellets of excavated soil, uniform in size, adhered to the crack faces below the entrances. Main tunnels penetrated the soil in variable directions, ascending, descending and/or twisting for up to, but no more than, 2 cm into the surface. The largest nests appeared to consist of only three cells, and some obviously were of single or two cells. Cells in a single nest were often arranged in linear series of two or the tunnel branched with a short, soil-filled lateral leading to another cell. Because cells in a nest were so few in number, nests were probably constructed by single females, and almost certainly females normally constructed more than one nest. Because of the fine soil texture, burrow walls bore distinct impressions of having been tapped repeatedly by the female's pygidial plate.

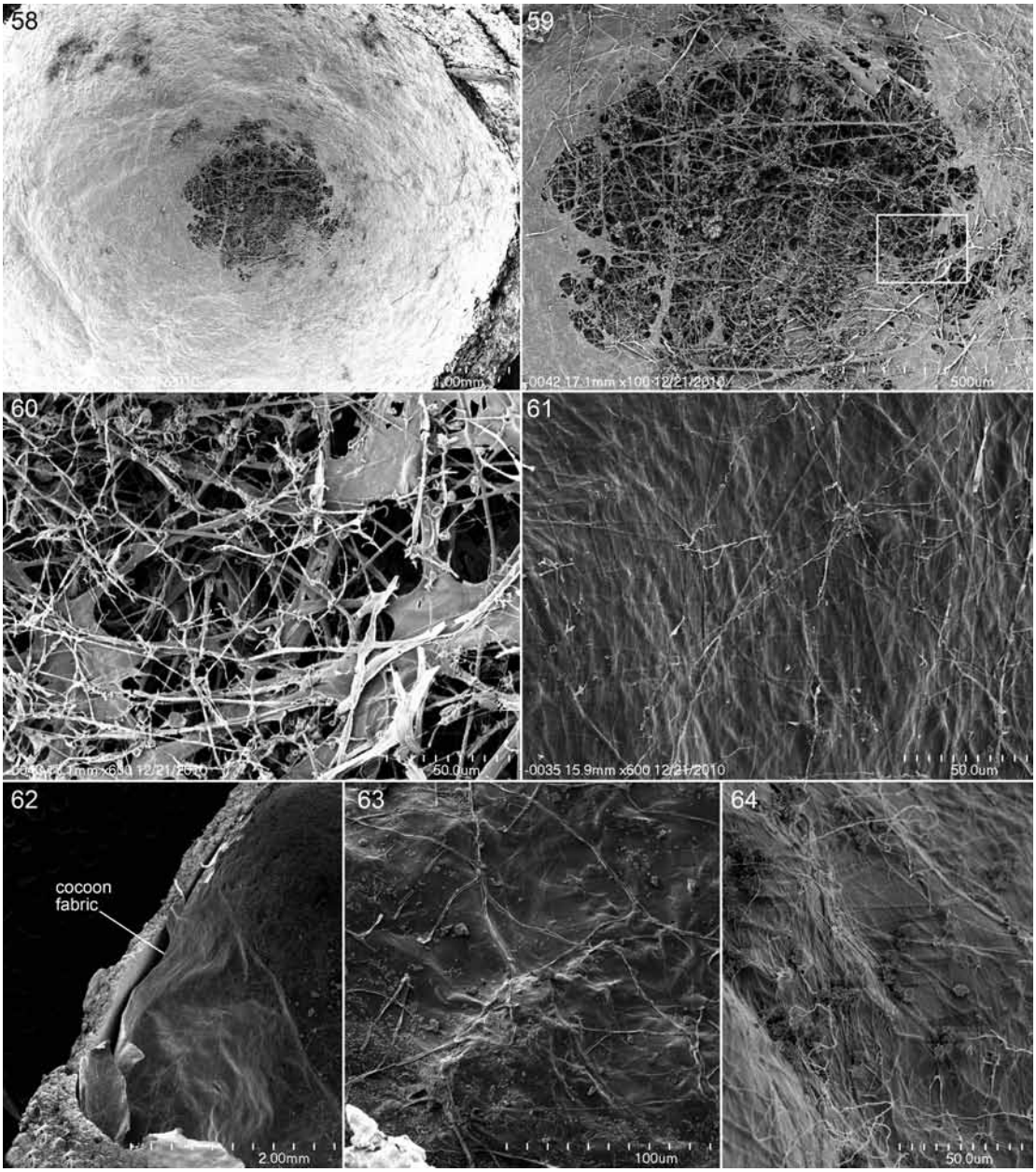
Whether nests are normally closed by main tunnels being filled with soil after nest completion remains questionable. Certainly many main tunnels leading to closed cells appeared open. Several nests were discovered where an intercalary cell somewhat smaller than a brood cell appeared in front of the brood cell (fig. 56), and in one of these cases the tunnel in front of the intercalary cell was filled with loose soil particles. A septum forming the front of an intercalary cell was concave and smoothed on the outside, like the cell closure itself; the inside surface was a spiral but rougher than the inner face of brood cell closures. Intercalary cells may simply be a nest closure consisting of two cell closure, the last one being spaced a short distance in front of a cell closure. More completed nests need to be examined to resolve our understanding nest closures.

Cells ranged in depth from 12 to 30 cm, but most seemed to be concentrated between the depths of 13–18 cm. Cell orientation was variable with the long axis ranging from being nearly horizontal to tilting toward the rear as much as 80° as indicated in table 2. Cell entrances were generally somewhat smaller than the burrow diameter. When first observed cells seemed to be symmetrical around their long axis, but on close examination one was clearly slightly flatter on one side (fig. 56); I suspect that all are probably flattened to a similar extent. Several cells were discovered partly penetrating vacated cells that had been packed with fill either by the nesting female or by emerging adults. Cell walls were smooth and lined with a shiny waterproof material from the rear of the cell all of way through the cell entrance. The smooth outer surface of the closure was also waterproof when tested with a droplet, but shortly in front of the closure the lining to the tunnel lost its smooth texture and became water absorbent.

Inner surfaces of cell closures were 1.5–1.8 mm ($N = 5$) in diameter, uniformly flat, and consisted of a spiral of 3–4 coils to the radius (fig. 57). When tested with a droplet, the surface absorbed water in several seconds, suggesting that soil compactness rather than a waterproof secretion was responsible for slowness of absorption. Closures were uniformly thick, about 0.7–0.8 mm in the middle. The coil was constructed first, and then soil of the outer surface was deposited, smoothed, and waterproofed by the female. Septa separating cells in series were also uniform in thickness, about 0.5–0.8 mm thick in the middle, and the inner surface of the closure of the rear cell was also a coil identical to that of the first cell.

Provisioning and Development: In provisioning, female *Chilimalopsis parvula* first deposit the reddish-purple pollen of *Pleurophora polyandra* as irregular masses on the cell floor. After importing the total allotment for a cell, she shapes it into a freestanding, loaflike mass that varied considerably in contour and degree of surface smoothness; internally it was mealy-moist. In all cases it was longer than wide or high, and its top surface was somewhat flattened. Its undersurface conformed to the curvature of the cell floor. Dimensions are given in table 2.

Eggs (table 1), curved, white, and with shiny, smooth chorions, rested with their anterior and posterior ends touching the top surface of the provisions, their long axis in the sagittal plane of the cell, and their more rounded anterior end directed toward the cell closure. On hatching, young larvae were elongate and moved over the surface of the provisions, making shallow channels roughly the width of their body as they progressed. As the larvae grew, the provisions became smaller and more ovoid. Older larvae cradled ovoid provisions holding them away from the cell surface in that only the dorsal surface of the larva touched the cell wall. When the provisions were reduced to a small semitransparent irregular mass, the larva discharged the contents of its Malpighian tubules, which up to that time were yellow, clearly visible through the transparent body wall because of the dark reddish color of the filling mid intestine. The discharge, an opaque yellow material, was applied by the anus onto the cell wall as a series of blotches. Afterward the vacated Malpighian tubules were transparent, no longer visible. Defecation commenced immediately thereafter, before the food mass was entirely consumed. Because the tubule discharge was so limited, the discharge obviously was not instrumental in modifying the absorption quality of the cell wall, as has been suggested for some bees (Rozen, 1987).



FIGURES 58–64. SEM micrographs of cocoons of Exomalopsini. **58.** *Anthophorula completa*: Front end of cocoon showing gas exchange aperture; **59.** close view of aperture; **60.** close-up of rectangle in figure 59; **61. c**ocoon fabric elsewhere; **62.** cut end of fabric showing thinness. **63.** *Eremapis parvula*: cocoon fabric. **64.** *Chilimalopsis parvula*: cocoon fabric.

Feces were deposited first as elongate reddish pellets applied to the cell wall. They eventually covered all surfaces of the cell including the closure as an even layer before cocoon construction started; they were not embedded in cocoons as characteristic of *Anthophorula nitens* and *A. chionura.* Cocoons were a distinct white or slightly tan, soft, tissuelike, semiopaque sheet of silk strands that covered the entire cell surface and fecal layer. In some cases they were light brown, not much darker than the surrounding soil. Although the fabric appeared to be a single layer, when it was pulled away from the fecal lining to the cell, a layer of silk strands remained glued to the fecal material although the part pulled away maintained its integrity. Under a light microscope, the front end of the cocoon was of the same consistency and structure as the rest of the cocoon.

From the appearance of vacated cocoons, emerging adults chew away the front end of the cocoon at egress. Those emerging from the rear cell in a series chew not only a hole in the front of their cells but also obviously a hole in the rear of the cell in front. Vacated cocoons were loosely packed with soil no doubt from the cell closure and perhaps from the closure of intercalary cells and burrow fill if present. Cocoons from the present as well as from previous generations appear uniform in texture indicating that all individuals still spin cocoons (in some multivoltine bees, nondiapausing generations do not always make cocoons or the cocoon produced by the earlier generation is different in construction from that of the overwintering generation (Rozen, 1984)). Although the gas exchange aperture was not found on the remnants of any cocoons, there is no reason to think that it is absent. Cocoon fabric (fig. 64) is similar to that of other exomalopsines treated here viewed with an SEM.

Adult Activity: Adults were on the flowers and flying over the ground in considerable abundance. Mating was not studied, but numerous small masses of adults (as many as 5 or 6) tumbling on the ground suggested that groups of males aggressively attempt to mate with a female, with some individuals departing and others joining the mass. Males were also noted gathered around cracks, entering and departing, suggesting that they may have been searching for emerging females in the cracks. Adults were most active during midday, both with respect to mate searching and foraging.

There appears to be only one generation a year. Only one pupa was encountered, presumably an individual that was slow in emerging in the spring. All larvae became quiescent after cocoon spinning.

Parasitism: No parasitic bees of appropriate small size were discovered at this site, and no cells contained cleptoparasitic bee larvae. Bombyliids and meloids, either as adults or immatures, were not detected at the site.

Teratognatha modesta Ogloblin

Table 2

I studied nests of this species at 6 km SW of Pichanal, Salta Province, Argentina, on November 11, 1993, along the border of a large field previously cultivated but in which numerous plants, especially *Sphaeralcea* and *Heliotropium* (the food source of *Teratognatha modesta*),

now grew. Although these plants were widely dispersed throughout this field (perhaps 1 km long and nearly 0.5 km wide), I observed nests only along one edge of the field. Time limitations prevented a broad survey of the field where other nesting aggregations may have existed, though clearly nests were not ubiquitous. The absence of nests from previous generations indicated that this nesting area had not been used by this species previously.

Nest entrances where first identified in barren stretches between clumps of weedy vegetation when females (both with and without pollen) were seen flying close to the ground, stopping, and entering cracks in the surface soil that existed throughout the nesting area. These cracks, caused by drying soil and mostly filled with loose soil, penetrated deeply into the substrate (perhaps as much as 10 cm). Soil on analysis consisted of 22% sand, 40% silt, 38% clay and was classified as clay loam. It was quite homogeneous, containing few stones. Occasionally females entered single surface holes, but on excavation these holes merely led to cracks below surface crust. Consequently, main burrows could not be followed from the surface to cell level, and cells were excavated only by blindly digging areas beneath holes and around cracks into which females had disappeared. Because main nest burrows could not be traced nor their entrances identified, numbers of females to a nest is unknown. However, so many females entered the same crack it seems likely that nests were composite.

Nest Architecture: Tunnels of nests, about 2.0 mm in diameter, could be recognized only in the vicinity of cells where tunnels were not soil filled. Their surface was not waterproof and was finally roughened, almost certainly a result of being tamped by the female's pygidial plate.

The precise number of nests encountered is unknown because we were unable to determine nest boundaries. However, at least four separate clusterings of cells and cell series were found. Centers of these aggregations were at depths of 16, 21, 26, and 28 cm. Most cells were in a straight linear series of three, and certainly in some nests at least two such series were evident. In one case a series of two was found, and some apparent series of three might actually have consisted of two cells in front of which was a celllike chamber without a closure (suggesting an interruption to nest construction). The length of the lateral between the leading cell in a series and the main burrow was 4.0 cm in two cases and 7.0 cm in another. The short laterals were completely soil filled in the first two cases, but a 3 cm gap remained open immediately in front of the cell in the 7.0 cm lateral.

Many cells (and cell series) (dimension in 2) were oriented 45° from horizontal (rear end lower than the front), but more observations on cell orientation are needed. Cells appeared symmetrical around their long axes even after repeated careful examination. Cell walls could not be differentiated from the substrate by color or hardness when dry. They were lined with a transparent, slightly reflective material that was mostly waterproof toward the rear of the cell but permitted water to be absorbed more or less rapidly near the cell closure. The inner surface was darker than the substrate when first excavated but upon drying matched the substrate. The inner surface of the cell was unusually smooth toward the rear, moderately shiny, but in most cells was slightly more irregular toward the cell closure. Septa between cells were very thin, less than 0.5 mm in thickness at the periphery. The front surface of the septum formed the smooth, lined, concave

rear of the preceding cell. The opposite surface of the septum was the essentially flat inner face of the cell closure in the form of a spiral of approximately 3–4 four coils to the radius.

Provisioning and Development: Female *Teratognatha modesta* transport pollen as moist masses on their hind tibiae and basitarsi. In cells, each female forms the mealy-moist, yellowish provisions into a loaf (figs. 53, 54) that rests its entire length on the cell floor without touching the rear of the cell. These masses varied somewhat in shape and in general had the dimensions given in table 2. They were elongate, rounded at the rear, and had a curved upper surface. As viewed from the side (fig. 53), their highest point was approximately ⅔ toward the rear. From the highest point the top surface curved gently to the nearly flat front. At its base on the cell floor, the front end bore a more or less distinct transverse ridge, questionably corresponding to the "foot" on provisions of *Anthophorula chionura* (Rozen and MacNeill, 1957: fig. 2). A reexamination of a preserved food loaf of *Exomalopsis bruesi* Cockerell (figs. 14, 15) during the current study showed that it too bore this transverse low ridge where the front surface met the cell wall.

The curved white egg rested by its front and rear ends on the gently curved top of the provisions in the sagittal plane of the cell while its midsection curved upward, not touching the surface. The chorion was smooth, shiny, transparent, and lacked reticulations or other sculpturing when viewed stereoscopically. Egg dimensions are given in table 1. Larvae crawled as they fed, leaving a shallow groove on the surface of the provision. The elongate form of the intermediate stage larva appeared characteristic of exomalopsines; the protruding venter of abdominal segment 9 apparently assisted in crawling. The dorsal attachment of abdominal segment 10 to 9 permits the larva to appress its feces against the cell wall, a process that begins before the provisions are completely consumed. Feces are applied to the entire cell wall including the inner surface of the closure.

No cocoons were spun by these larvae, all of which pupated or would have done so if permitted to develop. Interesting is the fact that the salivary lips of the last instar are clearly projecting, though perhaps not as much as those of some other exomalopsines, although the width of the opening is narrow. It is uncertain, therefore, whether a late summer generation might spin cocoons, as suggested by Rozen (1984) and Rozen and Snelling (1986) for certain other exomalopsines. No cocoons from a previous generation occurred at the site, and the absence of empty vacated cells with or without cocoons indicated that the site had not been used before. This species has more than one generation per year; all larvae remained active after feeding and developed pupal tissue internally.

Adult Activity: Mating was not observed at the nesting site; hence, it probably occurs at the flowers. Females were most active in the morning, 10 a.m. to 12 noon. Their host plant is *Heliotropium,* and there can be little doubt that the peculiar modifications of the female's distal maxillary and labial palpal segments are adaptations for extracting pollen from the flowers of this plant, as was first suggested by Michener and Moure (1957) although the host plant was not known at that time. Other, distantly related bees, such as *Calliopsis hesperia* (Swenk and Cockerell), several unnamed South American *Calliopsis,* and a species each of *Callonychium* s.l. and *Paranychium* (all Andrenidae: Panurginae), harvest pollen from this

plant genus and have unusual mouthpart modifications, presumably adaptive for that purpose (New Information).

Parasitism: No parasites were associated with this site.

Discussion of Nesting Biology

This section is intended to provide an overview of the nesting biology of the Exomalopsini. The reader is also directed to an earlier attempt (Rozen, 1984), which discusses additional information on cocoon spinning, defecation, and voltinism that is not repeated here.

Based on the observations above and literature accounts (see references below), all species are ground nesting, and nest entrances are always without turrets. Many species (hereinafter termed horizontal nesters and identified in table 2 by "H") tunnel into more or less horizontal surfaces that are exposed to open sunlight, but some species (including several of the subgenus *Anthophorisca,* at least one species of *Chilimalopsis,* and *Teratognatha modesta*) (termed fissure nesters and identified in table 2 by "F") utilize cracks in the ground resulting from soil drying and shrinking. Raw (1977) reported that *Exomalopsis* (*E.*) *pulchella* Cresson (as *Exo. globosa* (F.)) is the only known species to both nest in cracks and on horizontal surfaces. The fissures allow females easy access to moist soil that can be excavated with mandibles, thereby conserving energy and avoiding mandibular wear. Nests of horizontal nesters normally are occupied by more the one female, as was first recognized by Hicks (1936) for *Anthophorula* (*Anthophorula*) *torticornis* (Cockerell), when he observed four females entering a single nest. So far as currently known, the numbers of females per nest are comparatively few, such as 5–14 for *Anthophorula sidae* or 12–35 for *Exomalopsis solidaginis.* However, Hurd and Linsley (1975) claimed that nests of *Exo. solani* Cockerell may contain colonies of several hundred individuals, and Zucchi (1973) reported 884 females in one nest of *Exo. auropilosa* Spinola.

Nests of fissure nesters have been impossible to monitor because the entrance to the nest is deep in the crack. By excavating one side of a crack, one immediately upsets the comings and goings of inhabitants. No one has yet removed one side of a crack at night when nest inhabitants are asleep and then collected adults the next day as they emerged from nests on the preserved side. Furthermore, there is a possibility that a crack serves as a counterpart of a main tunnel of horizontal nesters. If that is the case, then nest tunnels opening along the face of a fissure may be the counterparts of the more or less horizontal branches attached to the main tunnel of the horizontal nester. In several cases where nests consisting of only two or three cells (*Anthophorula nitens* (Cockerell) and *Chilimalopsis parvula*) were found near the fissure, I have proposed that they might have been constructed by a single female, which might be interpreted to support the assumption that the small group of interconnected cells are indeed the counterpart of horizontal side tunnels of a horizontal nest. However, the situation is unresolved because at this time we do not understand the interactions of adults inside nests with multiple females. For example, does a single female in such a nest work a single branch by herself, or does she place her cells wherever she finds herself? Or does she work coopera-

tively with other females in building and provision cells as has been suggested by Michener (1966) and others? Such matters are not insoluble and need to be addressed.

Depths of exomalopsine nests as measured by the deepest cells uncovered tend to fall in the first half meter below the surface. The shallowest nests are those of *Eremapis parvula,* in which cells ranged 5–7 cm deep. By far the deepest exomalopsine nests recorded are those of *Exomalopsis auropilosa,* two of which were 4.6 and 5.3 m deep (Zucchi, 1973).

Main burrows tend not to be soil filled, as are side tunnels where they branch from the main tunnel though they seem filled closer to cells. Laterals immediately in front of closed cells are usually filled, except the situation is uncertain for *Chilimalopsis parvula,* q.v.

Table 2 lists dimensions of nest components and of provisions of those Exomalopsini that have been studied to date. The dimensions in table 2 seem unremarkable in light of the small sizes of many of the bees. Of some interest is that burrow diameters of many species tend to be slightly wider than the burrow opening at the surface (data not supplied); intuitively one would think that nest entrances would tend to wear and widen with passages of adults.

Column titled "Cell tilt" in table 2 gives the approximate range of the tilt of the long axis of the cells from a horizontal position. The anterior end of the cell is always equal to or above the posterior end. Hence, if the long axis is horizontal it would be 0°, and if perpendicular to the horizontal position, it is, of course, at 90°. Because these ranges are based on only a few measurements, they should be considered rough estimates. With most taxa, cell orientation is probably rather variable within a species.

As shown in table 2, many exomalopsine nests have cells in linear series consisting of two cells end-to-end mixed with single cells. However, both in *Chilimalopsis parvula* and *Teratognatha modesta* series consist of three cells, and in *Anthophorula chionura* series can consist of as many as five cells. However, singles and series of two are also encountered in all of them. Only single cells have been reported for *A. crenulata* (Timberlake), *A. sidae, A. uncicornis,* and for all species of *Exomalopsis.*

A feature that seemed distinctive at first was the presence of a cell wall that was more consolidated than the substrate such as those found with *Anthophorula compactula, A. completa,* and *Exomalopsis solidaginis.* On further examination, I realized that the distinction of this feature is obvious only when cells are built into a soft substrate. Those found in consolidated substrates did not have walls that could be differentiated from the matrix. None of the material examined by me appeared to have a wall composed of any material other than that of the surrounding substrate. However, with all species the cell wall has been modified in that it has been manipulated by the female and except for *Eremapis parvula* (and possibly *A. crenulata*) been made hydrophobic, presumably being impregnated with a glandular secretion that apparently also helps consolidate the inner cell surface. The clear, reflective surface of the wall is evidence of this presumed secretion. The cell wall of *Er. parvula* is dull and water absorptive. Although the cell wall of *A. crenulata* was reported "polished and shiny," water droplets were "quickly absorbed" (Parker, 1984). I have noted that different parts of a cell wall have differential absorption rates as, for example, in *A. uncicornis* (above), and wonder whether that might explain Parker's observation.

Cells are normally constructed with one side more elongate and curved than the other side,

so that for an inclined cell the upper surface is longer and more curved than the bottom side, the latter straighter and shorter than the upper. This is usually obvious, as illustrated in figure 56. In cells of *Eremapis parvula* and *Chilimalopsis parvula,* this asymmetry is difficult to detect because of their small size and because the plane of their closure is closer to being at a right angle to the long axis of the cell in side view.[8] If they are opened in strict lateral view, it becomes apparent (fig. 56). However, I have been unable to detect asymmetry in cells of *Teratognatha modesta,* and Zucchi (1973: figs. 5b, 5C) illustrated the cells of *Exomalopsis auropilosa* as symmetrical as well as perpendicular.

With the exception of *Eremapis parvula,* cell surfaces of exomalopsine bees are lined with a clear material that affords a hydrophobic barrier, presumably safeguarding the occupant from desiccation. However, in the Exomalopsini there is a strong suggestion that this barrier also serves to protect the provisions from coming in contact with the cell wall. For example, in *Anthophorula uncicornis* this lining is most developed at the very rear of the cell where the provisions are attached. As noted in the case of *Chilimalopsis parvula,* older larvae cradle food masses so they do not come in contact with cell surfaces, as also shown to be the case for *Exomalopsis solidaginis* (Rozen 1984: figs. 23, 24). In *Eremapis parvula* the peculiar pattern of fecal deposition can be interpreted to be an outgrowth of holding the provision away from cell wall. Although one assumes that this is to prevent wicking of moisture from the provisions by the cell wall, one must also consider safeguarding the provisions from microbial agents.

In all cases cell closures are a spiral on the inside, usually of 3–4 coils to the radius on the inside surface, but for larger species (*Exomalopsis bruesi* and *Exo. solani*) the number increases to 4–6 coils (Norden et al., 1994: fig. 2A). In all known cases, the outside surface is concave, smooth, and variably water retardant to a droplet, but the form of the inside surface ranges from flat (or even weakly convex) to deeply concave, with those of *Anthophorula sidae, A. uncicornis,* and *Eremapis parvula* being deeply concave and those of *A. completa, A. crenulata, A. consobrina* (Timberlake), *Chilimalopsis parvula,* and *Teratognatha modesta* being remarkably flat. Others are weakly concave or indeterminate at this time.

Larval provisions of all species are formed into a loaflike mass consisting of mealy-moist pollen with the moisture presumably derived from nectar. In cells that are inclined the loaf rests on the lower, somewhat flatter side of the brood chamber, as in *Anthophorula sidae* (Rozen, 1984: fig. 28) or against the rear of the cell, as in *A. nitens* (Rozen and Snelling, 1986: fig. 5), *Exomalopsis solidaginis* (Rozen, 1984: fig: 20), and *Exo. solani* (Norden et al., 1994). In *A. uncicornis* the loaf is actually attached to the rear of the cell, and in the perpendicular cell of *Exomalopsis auropilosa* the loaf is in contact only with the rear of the cell.

In table 2 is the column "Foot?" meaning "is there a pointed projection on the lower front edge of the provision mass?" as original intended by Rozen and MacNeill (1957). Although Zucchi (1973) stated the *Exomalopsis auropilosa* had such a structure, he identified it as the

[8] As noted by Rozen (1984: fig. 17) with respect to *Exomalopsis solidaginis* the plane of the closure (line e–f) is quite different from the line c–d that is perpendicular to the long axis of the cell, thus accounting for the top surface of the cell being conspicuously longer than the lower surface.

structure at the rear of the provisions where the food mass contacts the rear of the cell rather than at the front end (his fig. 5D). Although the shape of the mass otherwise is convincingly that of an exomalopsine, the structure at the rear of the mass seems to be a novelty because of its position, and accordingly *Exo. auropilosa* is scored "No." Although I have scored *Eremapis parvula, Teratognatha modesta,* and *Exomalopsis bruesi* as "No," some of the preserved specimens of each have a suggestion of this projection. Raw stated that provisions of neither *Exo. puchella* nor *Exo. similis* bore a "foot." To be noted: the food mass of *Anthophorula uncicornis* (fig. 47) is affixed to the cell's rear wall and still has a foot that never contacts any part of the wall, as also is the case for *Exo. solidaginis* (Rozen, 1984: fig. 20).

Eggs of all species that I have studied are deposited on the top surface of the provisions somewhat toward the front end (as in figs. 46, 48, 50, 52, 54) in the sagittal plane of the cell. In all cases the egg contacts the surface of the provisions only with its anterior and posterior ends. Young and intermediate stage larvae slowly crawl over the provisions as they feed, thereby channeling the surface.

Most Exomalopsini spin cocoons including *Anthophorula compactula, A. completa, A. crenulata, A. chionura, A. consobrina, A. nitens, A. sidae, Eremapis parvula, Chilimalopsis parvula, Exomalopsis puchella,* and *Exo. similis.* However, of these, *A. chionura, A. nitens,* and *A. sidae* have an early generation in the year that transforms to the pupal stage without spinning a cocoon; these species do not spin cocoons until they reach the overwintering generation. On the other hand, cocoons of the following species are unknown: *A. uncicornis, Teratognatha modesta, Exo. auropilosa, Exo. bruesi, Exo. solani,* and *Exo. solidaginis.*

It is assumed that cocoon spinning is a plesiomorphic condition among bees, if not among all Hymenoptera. The apparent multiple loss of the ability (or need for) cocoon spinning among various taxa within the small tribe Exomalopsini is worthy of consideration. There is also a strong suggestion in the case of such multivoltine species as *Anthophorula chionura* and *A. consobrina,* cocoon spinning can be suspended in summer generations and be initiated again for the overwintering generation. However, the anatomy of the larva of the summer generation is still that of the overwintering one, i.e., salivary lips continue to be projecting. In those exomalopsine taxa that never spin cocoons, the salivary lips are nonprojecting (or project only slightly). Oddly, while strongly projecting lips are no longer present, the salivary opening in all cases is transverse, unlike in larvae of any other non–cocoon spinning bee taxon where the opening tends to be a simple round opening to the salivary duct. The meaning of this is not clear. It could be interpreted that the original assumption that cocoon spinning once lost might indeed evolve again. Or perhaps we do not understand the phylogenetic relationships among the taxa. In any event, it points to the fact that we still have an ongoing puzzle worthy of exploring.

Information presented here does not refer to social interactions of adults bees in communal nests, as has been mentioned by others (Michener, 1966; Zucchi, 1973; Raw, 1977; Parker, 1984). These are interesting matters that deserve further investigations. This study also does not consider how colonies occupying single nests are established nor does it reveal information about the duration of such assemblages. There is more work to be done.

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APPENDIX

Preliminary Tribal Key to Mature Larvae of Nonparasitic Apinae Exclusive of the Corbiculate Tribes

Now that mature larvae of exemplars of almost all nonparasitic, noncorbiculate tribes of the Apinae are known, the following tentative key is presented based upon characters that distinguish the tribes to the extent larvae have been collected. Of nine tribes in the subfamily, larvae of only Ancylaini have yet to be collected and characterized. The various cleptoparasitic taxa are excluded because presumably convergent hospicidal features would make the key impractical; the reader is referred to the key to mature larvae of cleptoparasitic bees (Rozen, 2001). Table 3 lists the taxa upon which the key is based and gives references to published larval descriptions.

TABLE 3. Taxa upon which the Tribal Key to Mature Larvae of Nonparasitic Apinae Exclusive of Corbiculate Tribes Was Based, with References to Published Descriptions or Specimens in Collection: AMNH = American Museum of Natural History; KU = University of Kansas; UC(B) = University of California (Berkeley)

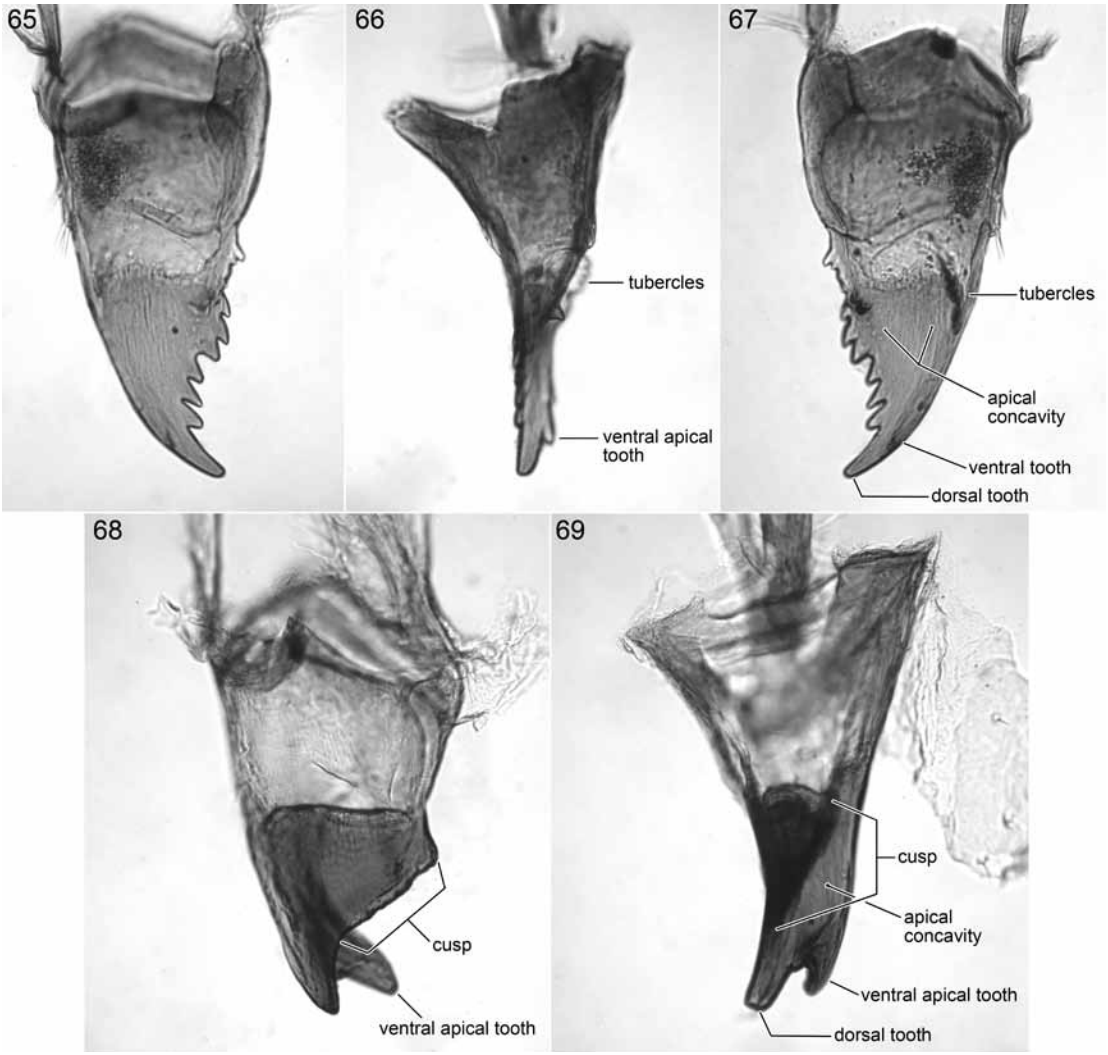
Taxon	Reference
Exomalopsini	
As listed in current paper	As listed in current paper
Tapinotaspidini	
Arhysocebele picta (Friese)	AMNH collection
Lanthanomelissa betinae Urban	Rozen et al., 2006
Monoeca haemorrhoidalis (Smith)	Rozen et al., 2006
M. lanei (Moure)	AMNH collection
Paratetrapedia swainsonae (Cockerell)	Rozen & Michener, 1988
Trigonopedia glaberrima (Friese)	KU collection
Tapinotaspoides tucumana (Vachal)	AMNH collection
Tetrapediini	
Tetrapedia diversipes Klug	Alves-dos-Santos et al., 2002
Ctenoplectrini	
Ctenoplectra armata Magretti	Rozen, 1978
C. cornuta Gribodo	Rozen, 2010
Emphorini	
Ancyloscelis apiformis (Fabricius)	KU and AMNH collections
Diadasia enevata (Cresson)	Michener, 1953
D. rinconis Cockerell	AMNH collection
Diadasina sp.	AMNH collection
Melitoma segmentaria (Fabricius)	AMNH collection
Ptilothrix bombiformis (Cresson)	AMNH collection
Toromelissa nemoglassa (Toro & Ruz)	AMNH collection
Eucerini	
Canephorula apiformis (Friese)	Michelette et al., 2000
Eucera hamata (Bradley)	Miliczky, 1985
Eucera lanuginosa Klug	Mohamed, 1974
Florilegus condignus Cresson)	LaBerge & Ribble, 1966
Melissodes sp.	Michener, 1953
M. pallidisignata Cockerell	Rozen, 1965
M. robustior Cockerell	Rozen, 1965
M. rustica (Say)	Clement, 1973
Peponapis fervans (Smith)	Rozen, 1965
Svastra duplocincta (Cockerell)	Rozen, 1991
S. oblique oblique (Smith)	Rozen, 1964
Tetralonia malvae (Rossi)	Grandi, 1961
Tetraloniella minuta (Friese)	AMNH collection
Thygater sp.	Packer, 1987
Xenoglossa angustior Cockerell	Rozen, 1965
X. fulva Smith	Rozen, 1965
X. strenua (Cresson)	Rozen, 1965

TABLE 3. *Continued*

Taxon	Reference
Anthophorini	
Anthophora abrupta Say	Michener, 1953
A. edwardsii Cresson	Michener, 1953
A. furcata syringae (Cockerell)	Michener, 1953
A. linsleyi imberlake	Michener, 1953
A. occidentalis Cresson	AMNH collections
A. stanfordiana Cockerell	Michener, 1953
A. urbana Cresson	Michener, 1953
Centridini	
Centris aenea Lepeletier	Rozen, 1965
C. caesalpiniae Cockerell	Rozen & Buchmann, 1990
C. derasa Lepeletier	Rozen, 1965
C. lanipes (Fabricius)	Rozen, 1965
C. pallida Fox	Rozen & Buchmann, 1990
C. rufosuffusa Cockerell	Rozen, 1965
Epicharis fasciata Lepeletier & Serville	Rozen, 1965
E. rustica (Olivier)	Rozen, 1965

Comparing exomalopsine mature larvae with those of other Apinae, mature larvae of the Xylocopinae[9] can be recognized because the opening of the salivary gland duct is on the hypopharynx immediately in front of the pharyngeal opening (Rozen, 2010b) rather than at the apex of the prelabium as in larvae treated in this key as well as in all other known bee larvae. From larval Nomadinae, which are all cleptoparasitic, mature larval mandibles of Exomalopsini are basically bidentate (though occasionally with the two teeth partially fused) or tridentate and the labium is clearly divided into an apical prementum and postmentum. The salivary opening is transverse, whether or not it has projecting lips, and a basal postmentum. Furthermore, the labral tubercles are rounded apical swellings. In contrast larval nomadine mandibles taper to a single pointed apex, the salivary opening is a small circular hole, the labium is a single lobe not subdivided into a postmentum/prementum, and the paired labral tubercles are sharply pointed and arise from the middle of the labrum. Although it is currently impossible to list characters by which mature larvae treated here can be distinguished with certainty from those of Megachilidae, a feature reliable in most cases pertains to the two principal apical mandibular teeth. In Megachilidae, the lower apical tooth is somewhat longer and larger than the dorsal tooth, whereas in nonparasitic Apinae, the dorsal tooth more often dominates, though there are many exceptions. A very useful feature for recognizing mature larvae of some megachilids and distinguishing them not only from those of the Exomalopsini but also all other bee larvae is abundant body setae. Indeed of all known bees, conspicuous body setae are found only on fifth instars of Osmiini, Dioxyini, Anthidiini, and Megachilini, and not on younger

[9] Larvae of *Macrogalea* (Xylocopinae: Allodapini) may be a single exception; see Rozen (2010).



FIGURES 65–69. Microphotographs of cleared right mandibles of Emphorini. **65–67.** *Ancyloscelis apiformis.* Dorsal, adoral, and ventral surfaces, respectively. **68, 69.** *Melitoma segmentaria,* Dorsal and adoral views, respectively.

instars of these tribes and not on larvae of any other megachilids (Lithurgini and Fideliinae, including *Pararhophites*) (New Information).

1. Labrum apically trilobed in frontal view (fig. 70); dorsal mandibular surface with strong pattern of long, decumbent, setalike spicules (fig. 71); mandibular cusp present, with long planar surface lacking teeth or denticles (fig. 72) . . . . . Eucerini
– Labrum apically truncate, bilobed (figs. 3, 4), or curved (fig. 24), never trilobed in frontal view; dorsal mandibular surface usually without setalike spines or spicules,

rarely with weak pattern of hairlike spicules; mandibular cusp usually present, with minutely irregular surface, teeth, and/or denticles 2

2(1). Abdominal segment 10 with fine scattered seta best seen on cleared specimen with compound microscope; mandible with 7 or more setae on outer surface except for Chilean *Toromelissa.* Emphorini 3

– Abdominal segment 10 without setae except in Argentine *Eremapis parvula,* which has 3 setae or fewer on outer mandibular surface 4

3(2). Entire mandibular apex rotated and flattened, bladelike so that dorsal edge directed adorally, forming very broad, ventrally directed apical concavity (fig. 67); dorsal apical tooth elongate, gradually narrowing to acute point directed adorally (mandible appearing rapacious) (figs. 65, 67); ventral apical tooth greatly reduced (figs. 66, 67). . . . . Emphorini, subtribe Ancyloscelina

– Mandibular apex rotated less or not at all, not bladelike (figs. 68, 69); dorsal tooth not sharply pointed, not appearing rapacious (fig. 69); ventral apical tooth not greatly reduced[10]. . . . . Emphorini, subtribe Emphorina

4(2). Labral apex strongly bilobed in frontal view (figs. 74, 77); labrum with distinct (though not necessarily pigmented) basal sclerite (figs. 74, 77); ventral apical mandibular tooth at least slightly longer than dorsal tooth (fig. 75). 5

– Labral apex usually simple curve, rarely faintly bilobed; labrum without basal sclerite; relative lengths of apical mandibular teeth variable. 6

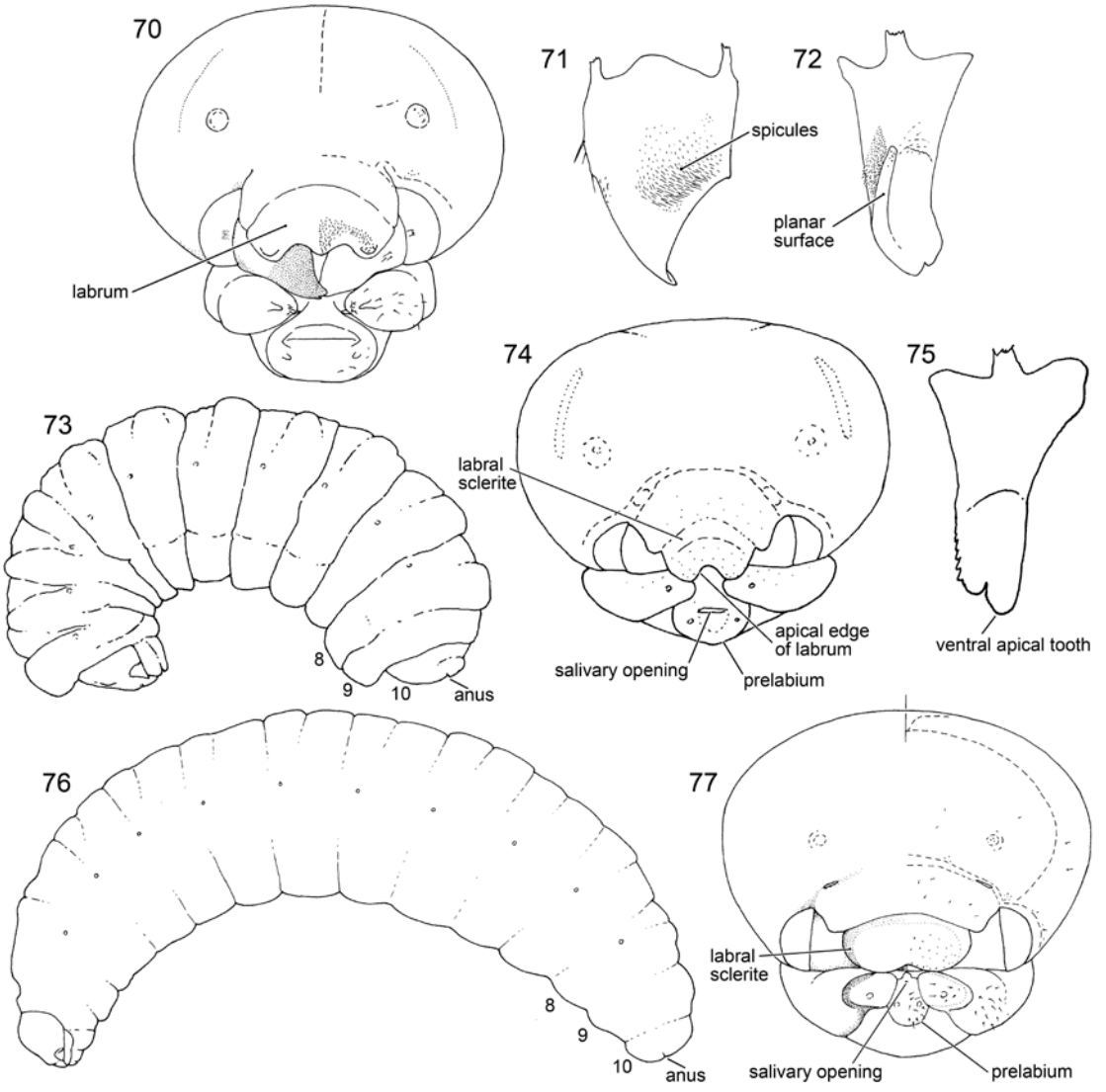
5(4). Anus terminal on abdominal segment 10 (fig. 76); prelabium unusually small (fig. 77); salivary opening a simple hole, not transverse or on projecting lips (fig. 77); labrum less strongly emarginated (fig. 77). . . . . Tetrapediini

– Anus more or less dorsally situated on abdominal segment 10 (fig. 73); prelabium normal in size (fig. 74); salivary opening transverse, on projecting lips (fig. 74); labrum more strongly emarginated (fig. 74) . . . . . Ctenoplectrini

6(4). Mandible subapically constricted and usually expanding apical to constriction before terminating in inner or outer views (figs. 6, 29, 30, 32, 33, 42), but if only slightly expanding (*Anthophorula uncicornis,* fig. 31) then entire apex very narrow; ventral edge of oblique apical mandibular concavity not defined by ridge (figs. 7, 12). . . . . Exomalopsini

– Mandible ending in single tooth or in two teeth, neither constricted subapically nor widening before terminating, as seen in outer or inner views; apical cavity usually broad, well defined ventrally by sharp, often serrate edge. 7

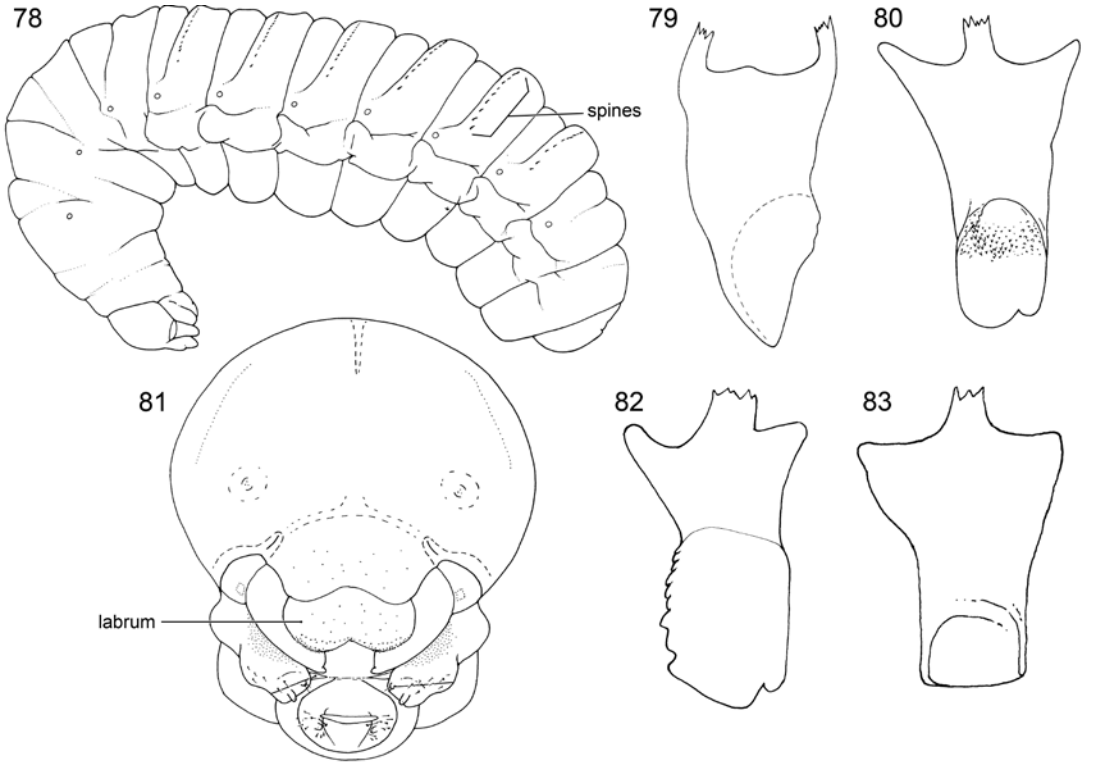
[10] In *Diadasia enevata* (Cresson) (and perhaps in some other species in that genus) the ventral apical tooth appears missing (Michener, 1953: figs. 209, 210). Examination of a predefecating larva shows that it is clearly present, but in postdefecating forms it is worn away leaving the mandibular apex obliquely truncate, bearing a large, adorally directed apical concavity.



FIGURES 70–77. Diagrams of exemplars of mature larvae of tribes of Apinae. **70–73.** Eucerini (*Canephorula apiformis* Friese) head (frontal view), right mandible (dorsal and adoral surfaces), respectively, from Michelette et al. (2000). **74, 75.** Ctenoplectrini (*Ctenoplectra cornuta* Gribodo) entire larva (lateral view) and head (frontal view), respectively, from Rozen (2010a). **76, 77.** Tetrapediini (*Tetrapedia diversipes* Klug) entire larva (lateral view), head (frontal view), respectively, from Alves-dos-Santos et al. (2002).

7(6). Non–cocoon spinning larvae; salivary lips not projecting strongly or at all; labial and maxillary palpi short, no longer than basal diameter. 8

– Cocoon spinning larvae; salivary lips strongly projecting, labial and maxillary palpi elongate, much longer than basal diameter 9



FIGURES 78–83. Diagrams of exemplars of mature larvae of Centridini and Anthophorini. **78–80.** Centridini (*Epicharis fasciata* Lepeletier and Serville) entire larva (lateral view) and right mandible (dorsal and adoral surfaces), respectively, from Rozen (1965). **81, 82.** Centridini (*Centris caesalpiniae* Cockerell), head (frontal view) and right mandible (adoral surface), respectively, from Rozen and Buchmann (1990). **83.** Anthophorini (*Anthophora occidentalis* Cresson) right mandible (adoral surface).

8(7). Caudal annulets of most body segments with single transverse row of posteriorly directed, pigmented spines (fig. 78); mandible terminating with two distinct apical teeth (fig. 80) . . . . . Centridini, *Epicharis*

– Caudal annulets of all body segments without pigmented spines; mandibles terminating in single broad apex (fig. 83) . . . . . Anthophorini

9(7). Labrum normally narrow; mandible normally with broad, multispined cusp (fig. 4) but in *Monoeca* (fig. 2) cusp narrow at first glance, appearing composed of single row of spines but on closer inspection possibly consisting of two or more rows of spines . . . . . Tapinotaspidini

– Labrum unusually wide (fig. 81); cusps absent, dorsal apical edge of mandible (fig. 82) coarsely to finely serrate . . . . . Centridini, *Centris*

REFERENCES

Alves-dos-Santos, I., G.A.R. Melo, and J.G. Rozen, Jr. 2002. Biology and immature stages of the bee tribe Tetrapediini (Hymenoptera: Apidae). American Museum Novitates 3377: 1–45.

Clement, S.L. 1973. The nesting biology of *Melissodes* (*Eumelissodes*) *rustica* (Say), with a description of the larva (Hymenoptera: Anthophoridae). Journal of the Kansas Entomogical Society 46: 516–525.

Gandi, G. 1961. Studi di un entomologo sugli imenotteri superiori. Edizioni Calderini Bologna. 661 pp.

Hicks, C.H. 1936. Nesting habits of certain western bees. The Canadian Entomologist 68: 47–52.

Hurd, P.D., Jr., and E.G. Linsley. 1975. The principal *Larrea* bees of the Southwestern United States (Hymenoptera: Apoidea). Smithsonian Contributions to Zoolo 193: 1–74.

Iwata, K., and S.F. Sakagami. 1966. Gigantism and dwarfism in bee eggs in relation to the mode of life, with notes on the number of ovarioles. Japanese Journal of Ecology 16: 4–16.

LaBerge, W.W., and D.D. Ribble. 1966. Biology of *Florilegus condignus* (Hymenoptera: Anthophoridae). With a description of its larva, and remarks on its importance in alfalfa pollination. Annals of the Entomological Society of America 59: 944–950.

Michelette, E., J.M.F. Camargo, and J.G. Rozen, Jr. 2000. Biology of *Canephorula apiformis* and its cleptoparasite *Melectoides bellus* (Hymenoptera, Apoidea): nesting habits, floral preferences, and immature stages. American Museum Novitates 3308: 1–23.

Michener, C.D. 1966. Evidence of cooperative provisioning of cells in *Exomalopsis* (Hymenoptera: Anthophoridae). Journal of the Kansas Entomological Society 39: 315–317.

Michener, C.D. 2007. Bees of the World, Second Edition. Baltimore, MD: Johns Hopkins University Press. 953 pp.

Michener, C.D. and J.S. Moure. 1957. A study of the classification of the more primitive non-parasitic anthophorine bees. Bulletin of the American Museum of Natural History 112: 395–452.

Miliczky, E.R. 1985. Observations on the nesting biology of *Tetralonia hamata* Bradley with a description of its mature larvae (Hymenoptera: Anthophoridae). Journal of the Kansas Entomological Society 58: 686–700.

Mohamed, M.I. 1974. Seasonal distribution of *Tetralonia lanuginosa* Klug with a taxonomic description of different stages. Deutsche Entomolgische Zeitschrift 21: 167–178.

Neff, J.L. 1984. Observations on the biology of *Eremapis parvula* Ogloblin an anthophorid bee with a metasomal scopa (Hymenoptera: Anthophoridae). Pan-Pacific Entomologist 60: 155–162.

Norden, B.B., K.V. Krombein, and S.W.T. Batra. 1994. Nests and enemies of *Exomalopsis* (*Phanomalopsis*) *solani* Cockerell (Hymenoptera: Apoidea, Mutillidae; Diptera: Asilidae). Proceedings of the Entomological Society of Washington 96: 350–356.

Packer, L. 1987. Description of the mature larva and cocoon of the bee *Thygater* Hymenoptera: Anthophoridae). Journal of the New York Entomological Society 95: 23–27.

Parker, F.D. 1984. Biological notes on the bee *Exomalopsis crenulata* Timberlake (Hymenoptera: Anthophoridae). Pan-Pacific Entomologist 60: 188–192.

Raw, A. 1977. The biology of two *Exomalopsis* species (Hymenoptera: Anthophoridae) with remarks on sociality of bees. Revista de Biologia Tropical 25: 1–11.

Rozen, J.G., Jr. 1957. External morphological description of the larva of *Exomalopsis chionura* Cockerell, including a comparison with other anthophorids (Hymenoptera: Apoidea). Annals of the Entomological Society of America 50: 469–475.

Rozen, J.G., Jr. 1964. The biology of *Svastra obliqua obliqua* (Say), with a taxonomic description of its larvae (Apoidea, Anthophoridae). American Museum Novitates 2170: 1–13.

Rozen, J.G., Jr. 1965. The larvae of the Anthophoridae (Hymenoptera, Apoidea). Part 1. Introduction, Eucerini, and Centridini (Anthophorinae). American Museum Novitates 2233: 1–27.

Rozen, J.G., Jr. 1977. Immature stages of and ethological observations on the cleptoparasitic bee tribe Nomadini (Apoidea, Anthophoridae). American Museum Novitates 2638: 1–16.

Rozen, J.G., Jr. 1978. The relationships of the bee subfamily Ctenoplectrinae as revealed by its biology and mature larva (Apoidea: Melittidae). Journal of the Kansas Entomological Society 51: 637–652.

Rozen, J.G., Jr. 1984. Comparative nesting biology of the bee tribe Exomalopsini (Apoidea: Anthophoridae). American Museum Novitates 2798: 1–37.

Rozen, J.G., Jr. 1987. Nesting biology and immature stages of a new species in the bee genus *Hesperapis* (Hymenoptera: Apoidea: Melittidae: Dasypodinae). American Museum Novitates 2887: 1–13.

Rozen, J.G., Jr. 1991. Nesting biology and mature larva of the bee *Idiomelissodes duplocincta* (Hymenoptera: Anthophoridae: Eucerini). American Museum Novitates 3012: 1–11.

Rozen, J.G., Jr. 1997. New taxa of brachynomadine bees (Apidae: Nomadinae). American Museum Novitates 3200: 1–26.

Rozen, J.G., Jr. 2001. Taxonomic key to mature larvae of cleptoparasitic bees (Apoidea). American Museum Novitates 3309: 1–27.

Rozen, J.G., Jr. 2010a. Immatures of the Old World oil-collecting bee *Ctenoplectra cornuta* (Apoidea: Apidae: Apinae: Ctenoplectrini). American Museum Novitates. American Museum Novitates 3699: 1–14.

Rozen, J.G., Jr. 2010b. Anatomy of the labiomaxillary region of mature larval xylocopine bees (Hymenoptera: Apidae: Xylocopinae). Journal of the Kansas Entomological Society 83: 332–339.

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 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. MacNeill. 1957. Biological observations on *Exomalopsis* (*Anthophorula*) *chionura* Cockerell, including a comparison of the biology of *Exomalopsis* with that of other anthophorid groups. Annals of the Entomological Society of America 50: 522–529.

Rozen, J.G., Jr., and R.J. McGinley. 1974. Phylogeny and systematics of Melittidae based on the mature larvae (Insecta, Hymenoptera, Apoidea). American Museum Novitates 2545: 1–31.

Rozen, J.G., Jr., and C.D. Michener. 1988. Nests and immature stages of the bee *Paratetrapedia swainsonae* (Hymenoptera: Anthophoridae). American Museum Novitates 2909: 1–13.

Rozen, J.G., Jr., and R.R. Snelling. 1986. Ethology of the bee *Exomalopsis nitens* and its cleptoparasite (Hymenoptera: Anthophoridae). Journal of the New York Entomological. Society 94: 480–488.

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). Appendix: Taxonomic notes on *Monoeca* and description of a new species of *Protosiri*s, by Gabriel A.R. Melo. American Museum Novitates 3501: 1–60.

Rozen, J.G., Jr., S.B. Vinson, R. Coville, G. Frankie. 2011. Biology of the cleptoparasitic bee *Mesoplia sapphirina* (Ericrocidini) and its host *Centris flavofasciata* (Centridini) (Apidae: Apinae). American Museum Novitates 3723: 1–36.

Silveira, F.A. 1995. Phylogenetic relationships of the Exomalopsini with a new tribe Teratognathini. University of Kansas Science Bulletin 55: 425–454.

Zucchi, R. 1973. Aspectos bionômicos de *Exomalopsis aureopilosa* [sic] e *Bombus atratus* incluindo considerações sobre a evolução do comportamento social. 172 pp. Ribeirão Preto, Brazil: thesis, Faculdade de Filosofia, Ciências e Letras.

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