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Source: American Museum Novitates, 2000(3308) : 1-23

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0082(2000)308<0001:BOTBCA>2.0.CO;2

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3308, 23 pp., 34 figures 13 December, 2000

Biology of the Bee *Canephorula apiformis* and Its Cleptoparasite *Melectoides bellus*: Nesting Habits, Floral Preferences, and Mature Larvae (Hymenoptera, Apidae)

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CONTENTS

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ABSTRACT

Data are presented on the nesting and phenology of *Canephorula apiformis* Friese (Apidae: Eucerini), a monotypic genus of bees endemic to the arid and semi-arid regions of the Argentinian northwest. Aggregations of nests are found in the ground where the surface is horizontal and frequently exposed to the sun. The brood cells, 5–6 cells per nest, are at an approximate depth of 20 cm. Floral hosts include *Prosopis strombulifera* (Fabaceae), *Atamisquea emarginata* (Capparidaceae), *Larrea divaricata* (Zygophyllaceae), and *Tessaria absinthioides* (Asteraceae) and are visited mainly between 10:00 and 14:00 hr. Adults and immature stages of *Melectoides bellus* (Jörgensen) (Apidae: Isepeolini) were found in the nests, the first association for this cleptoparasitic tribe with any host other than the genus *Colletes. Canephorula apiformis* may have two generations per year while the voltinism of its cleptoparasite is uncertain.

The mature larvae of both host and cleptoparasite are described for the first time and compared with known larvae of their respective tribes. Cocoons of the two species are also described, illustrated, and compared to those of related taxa.

INTRODUCTION

Canephorula Friese, a monotypic genus, is restricted to the arid and semi-arid regions of northwestern Argentina (Michener, 1979), with records from the provinces of Mendoza, Tucumán, Salta, and La Rioja (Friese, 1908; Jörgensen, 1912; Schrottky, 1913; Michener et al., 1955). It was first assigned to the apid tribe Eucerini (Michener, 1944) because of its long paraglossa but was later placed in a monotypic tribe due to its large number of autapomorphies (Michener et al., 1955). More recently, Roig-Alsina and Michener (1993) reassigned it to the Eucerini based on their phylogenetic study of long-tongued bees.

In this paper we present data about floral preference of *Canephorula apiformis* Friese, daily and annual phenologies, and some aspects of its nesting habits in San Juan Province. We also provide data on phenology and food sources of its cleptoparasite, *Melectoides bellus* (Jörgensen) (Apidae: Isepeolini), known previously from the provinces of Salta, Santiago del Estero, Catamarca, La Rioja, Mendoza, and Rio Negro. Until now, available data indicated that isepeolines were parasites of only the colletid genus *Colletes* (Roig-Alsina, 1991). This assumption was based primarily on observations of the genus *Isepeolus*; however, *Melectoides triseriatus* (Friese) was recorded as a cleptoparasite of *Colletes araucariae* Friese and *C. laticeps* Friese (Claude-Joseph, 1926, in Roig-Alsina, 1991). Mature larvae of both *Canephorula apiformis* and *M. bellus* are described and illustrated, as are cocoons of both species.

The fieldwork described here was carried out by the first author (ERFM), the last author (JGR) prepared the descriptions of the larvae, and both ERFM and JGR described the cocoons. All authors contributed to the final presentation.

STUDY SITE AND METHODS

The study sites were located in San Juan Province, in habitats that are part of the Monte Biogeographic Province (Cabrera and Willink, 1973). Bee samples were regularly collected at two sites in the Valley of Zonda-Ullum, in the eastern sections of the Andean Pre-Cordillera, at about 800 m elevation, in the counties of Ullum and Zonda. The Valley of Zonda-Ullum is dominated by a shrubby xerophytic vegetation with more mesic areas, mainly along rivers, that include halophytic species, as described by Haumann (1947), Morello (1958), Cabrera (1971), and Cabrera and Willink (1973).

One of the study sites was in the northern part of the valley (68°40′W, 31°29′S), where the *matorrales* are the predominant vegetation, characterized by the abundance of *Larrea* (Zygophyllaceae), *Bulnesia retama* (Gill. ex Hook.) Griseb. (Zygophyllaceae), and *Prosopis chilensis* (Mol.) Stuntz (Fabaceae), as well as lesser quantities of *Cercidium* (Fabaceae) (Caesalpinioideae), *Atamisquea emarginata* Miers ex Hook. and Arn. (Capparidaceae), and *Zuccagnia punctata* Cav. (Caesalpinioideae). The other study site, in

the southern part of the Valley (68°40′W, 31°33′S), had more mesic soil found along a temporary river. Here predominates the *chilcales* (Cabrera and Willink, 1973) on which *Tessaria absinthioides* (Hook. and Arn.) DC. (Asteraceae), *Baccharis salicifolia* (Ruiz and Pavón) (Asteraceae), *Prosopis strombulifera* (Lam.) Benth. (Fabaceae), and *Tamarix gallica* L. (Tamaricaceae) are the more abundant species. This area is locally called Zonda Swamp. *Atriplex lampa* (Moq.) Gillies ex Small (Chenopodiaceae), a characteristic halophytic plant, is also very frequent here. On the mountain slopes and *bajadas*, *matorrales* are the predominant vegetation. (For the list of floral species, see Michelette and Camargo, in press.)

Sporadic collections were made in the Valley of Iglesia (Pismanta, 69°10′W, 30°20′S), located at the Cordillerano Valley proper, between the Pre-Cordillera and the Frontal Cordillera, at 1989 m elevation (fig. 1). In this area the *matorrales* are also the predominant vegetation, although more scattered than at the other sites mentioned above.

The collection periods for phenological and nest samples were from May 1993 to May 1994, from November 1995 to March 1996, and from May 1996 to May 1997; additional observations were made from November 1995 to March 1996. The duration of each phenological sampling period lasted from 12 to 14 hours, depending on the season. The interval between the periods was about 15 days, with a maximum of 30 days. The bees were collected *ad libitum*, near or at flowers.

Nest aggregations were found in two places in the Valley of Zonda. The first aggregation was discovered during routine collecting in November 1993 when we were attracted by a large number of mostly male *Canephorula* hovering 30 cm above the ground in an area approximately 150 m^2. The largest one was next to the dry bed of the intermittent river Zonda Swamp, mentioned above (fig. 2). Later, another aggregation was found about 1 km away, closer to the western slope of the Sierra Chica de Zonda. Here the ground is drier, and the plants include *Prosopis chilensis*, *Atriplex* sp., *Bulnesia retama*, and *Larrea* spp. The physiognomy of this site is quite different from the other one, although, due to their proximity, it could be termed a transition area between *chilcales* and *matorrales* (fig. 3). The soil at both places is light- to medium-brown clay, more moist and compact at the cell level than at the surface. At other sites, such as Ullum and Pismanta, nests were not found, and few adults were collected. The composition of the flora in Pismanta is somewhat different from that of the Valley of Zonda-Ullum, although it includes some important host plants such as *Atamisquea emarginata* (fig. 4).

During collecting periods for phenological samples, bee activity at nests was always observed. Nests were excavated on the following dates: **in 1994:** Feb. 02, Nov. 28; **in 1995:** Feb. 05, Nov. 30, Dec. 03, 10, 17; **in 1996:** Feb. 08, 15; and **in 1997:** Feb. 08, 20.

Bees and plant voucher specimens are deposited at the Faculdade de Filosofia, Ciências and Letras de Ribeirão Preto, Universidade de São Paulo (Camargo Collection).

RESULTS AND DISCUSSION

NESTING

To study nest architecture, we excavated several nests at both sites in the Zonda Valley. The nests were always grouped near one another in horizontal areas that were frequently exposed to the sun. Distances between neighboring nest entrances were 20 cm or less. The nest entrance, a circular hole 5.0–5.2 mm in diameter, remained open and lacked a tumulus. The main tunnel descended more or less obliquely, running to a depth of about 15–20 cm, where 5–6 brood cells were found per nest. Cells were oriented with their long axis titled about 45° to the rear. It was not possible to observe lateral tunnels leading to cells, as they were apparently soil filled.

We collected a total of 137 cells. Of these, 97 contained eggs and larvae in various developmental stages. Twenty-two were filled with soil and likely represented chambers from which the brood had emerged. In the lab we verified that 51 cells contained *Canephorula* larvae and 46 held larvae of *Melectoides.* Only 3 cells contained *Canephorula* imagos (1 female and 2 males). The remaining 15 cells were maintained in a terrarium to follow developmental periodicity.

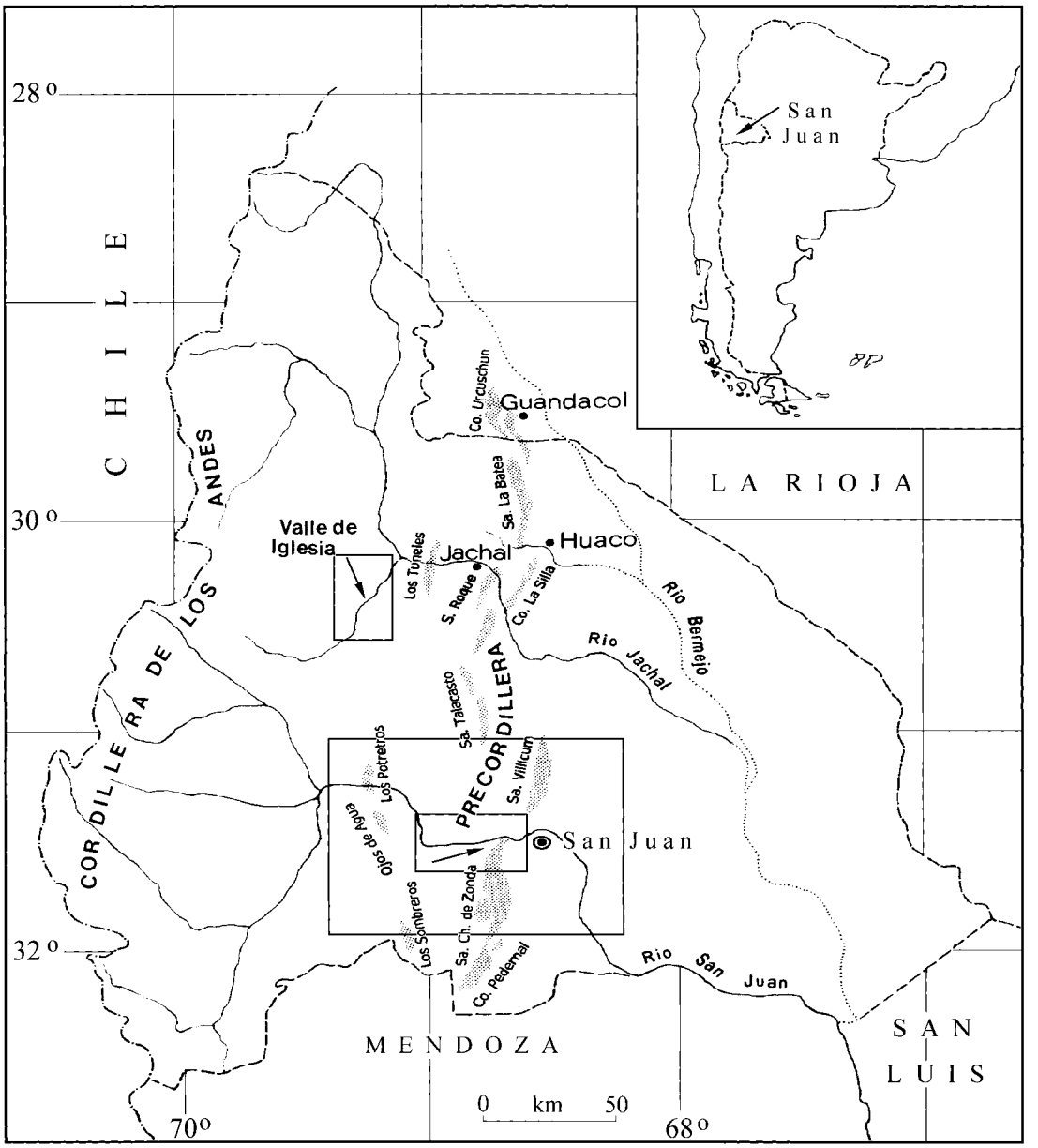
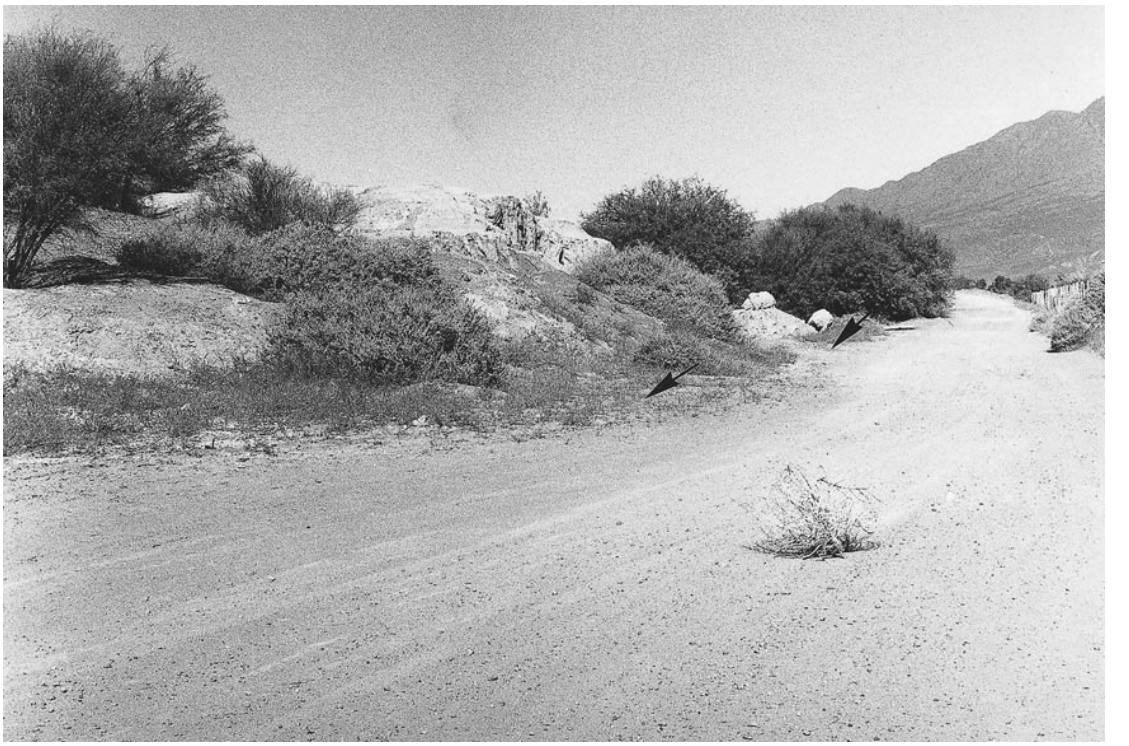


Fig. 1. Position (arrows) of Valley of Zonda-Ullum and Valley of Iglesia, San Juan Province, Argentina.

Cells were oval in shape. Their inside dimensions ranged from 11.0 to 14.0 mm in length and 6.5 to 7.5 mm in maximum diameter (N = 15). Cell walls were 0.6–1.0 mm thick, composed of soil more compact than the substrate, and cemented with a substance of unknown origin (fig. 5). The inner surface of cells, in contrast with the outer layer, was very compact and polished, although the soil particles that composed it were the same as those of the rest of the wall, and lined with a delicate, transparent pellicule (insoluble in ether), detachable from the substrate (fig. 5). In one freshly built cell the



Figs. 2, 3. Nest sites of *Canephorula apiformis* in the Valley of Zonda-Ullum, San Juan Province, Argentina. **2.** (Above) nests located in left side of picture. **3.** (Below) nests at the margin of the road (arrows).

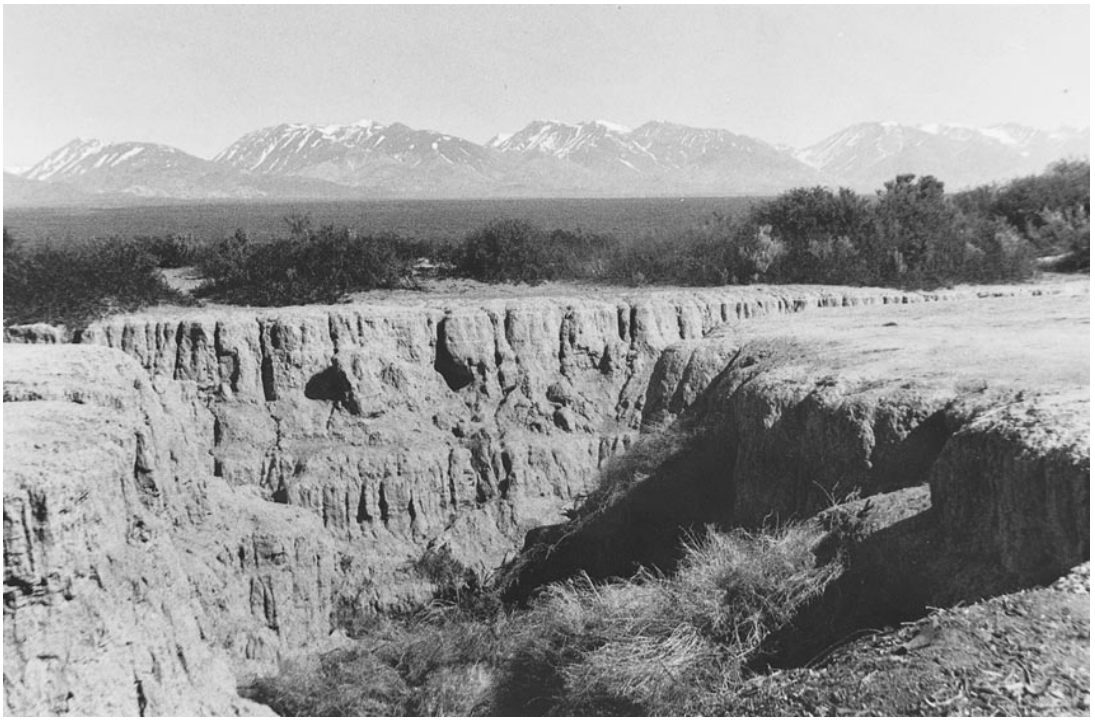


Fig. 4. Landscape at Pismanta (Iglesia), San Juan Province, Argentina.

food consisted of a small orange (gruellike) mass of wet pollen (presumably incomplete), occupying about one-fifth of the cell volume (fig. 5). Eggs were on the top of provisions.

The cocoon of *Canephorula* (fig. 6), except for the closure end, conformed exactly to the shape of the cell, and the clear, colorless lining tended to adhere to specimens removed from the substrate. Except at the closure end, cocoons preserved in ethanol seemed to consist of two transparent layers of amber, cellophane-like material between which were sandwiched an opaque, rather even but thicker layer of feces (fig. 7). (On a dry specimen this layer was about 0.06 mm thick at the cell bottom.) The exterior transparent layer consisted of an outer colorless layer and an inner amber-colored layer that adhered completely to one another (although easily separated with fine forceps) and that, when viewed under high magnification, revealed traces of fibers even though the silk was sheetlike (i.e., without fenestrations). Similarly, the inner transparent layer consisted of two completely distinct adhering layers, the one next to the feces being amber, while the one next to the larva was colorless. Possibly the amber hue was derived from the feces. Fecal material was finely granular. When preserved in ethanol, it was medium

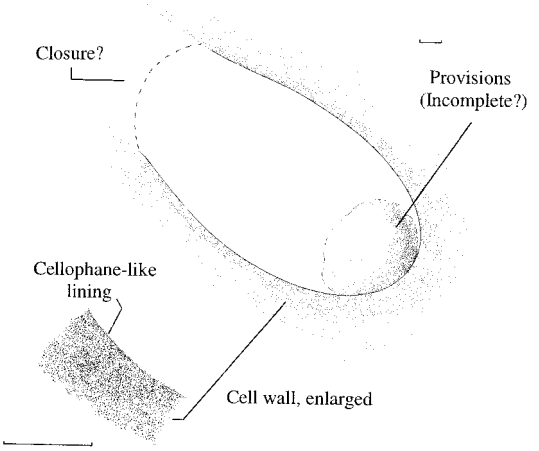
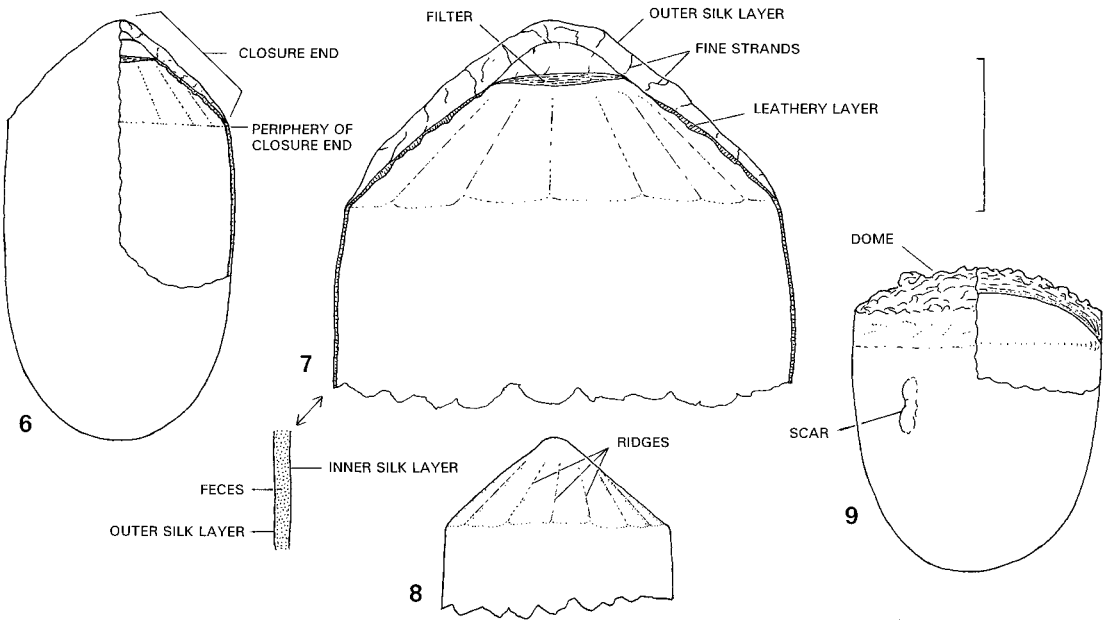


Fig. 5. Cell of *Canephorula apiformis* and provisions, with enlarged section of cell wall. Scale = 1.0 mm.



Figs. 6–9. Diagrams of cocoon of *Canephorula apiformis.* **6.** Entire cocoon showing external shape, side view, with upper right side cut away to show internal structure. **7.** Cross section of the upper end enlarged, showing inner structure, and greatly enlarged section of cocoon wall demonstrating layers of silk and feces. **8.** Upper end with outer silk layer removed to show radiating ridges of leathery layer. **9.** Diagram of cocoon of *Melectoides bellus,* side view, showing external shape, upper right side cut away. Scale (= 5.0 mm) refers to figs. 6, 8, and 9.

brown, but, when dry, mottled dark brown and black when viewed from outside. Under high magnification, some pollen exines could be identified although most were crushed and distorted.

The closure end of the cocoon (figs. 6–8) had a very different appearance from the rest of the cocoon. Instead of being evenly curved like the bottom of the cell, it was more or less conical when seen from the side (fig. 6), angling abruptly where it met the rest of the cocoon. (This angle hereafter is called the periphery of the closure end.) It consisted of several fragile, transparent, cellophanelike amber layers, which were mostly, but not completely, separated from one another except at the periphery and at the apex of the cone (the center of the closure end). These layers showed some threadlike strands connecting them. The layers are almost certainly extensions of the silk sheets from the rest of the cocoon although there may have been additional sheets deposited as well. In addition to these thin sheets there was a much thicker, leathery inner layer (figs. 7, 8) consisting of a number of layers of transparent silk with smears of feces in between. Some places had been left uncoated and therefore remained transparent. The feces in dried cocoons appeared almost black when viewed from inside the cocoon, the inner surface of which was shiny. The dark-brown fecal material was semitransparent (not nearly opaque like elsewhere in the cocoon) and may have consisted mostly of metabolites rather than pollen exines. It is uncertain whether or not the fecal material was sandwiched between double layers of sheetlike silk as found elsewhere in the cocoon. The leathery inner layer had several distinctive features. At its center and at a right angle to the long axis of the cocoon, there was a flat, fibrous disk (figs. 7, 10, 11) (here termed ''filter''), 1.5–2.0 mm in diameter (N = 9), that was pale, nonreflective, yellowish-tan rather than the essentially black, highly reflective surface of the surrounding inner surface of the closure end. In cross section (fig. 11), this disk was com-

posed of numerous threadlike strands of silk and may function as a filter, permitting gas exchange while excluding parasites (Rozen and Buchmann, 1990).

On the outer surface of the leathery layer (fig. 8), a series of approximately 12 wrinkled ridges radiated from the level of the filter toward the periphery of the closure end, thus dividing the closure end into a number of shallowly concave facets. Although it is unclear how the ridges were created, they may be an artifact resulting from the application of the feces to the outside silk layer of the leathery layer. This application might have caused a shrinking and weighing down of the silk layer, which probably would have been domelike when first manufactured. Although the inside silk layer had indistinct facets, the fact that it did not show the fine wrinkles as did the outer layer seems to support this hypothesis. Examination of cocoons while being built would almost certainly elucidate the construction mechanism for this peculiar structure.

Miliczky (1985) and Rozen (1991a) have provided comparative descriptions of the cocoons of other genera of eucerine bees based on original observations and published accounts. The cocoon of *Canephorula apiformis* shows several unusual features when compared with those of other genera. Unlike in other genera, the feces of *C. apiformis* are incorporated in the entire cocoon, whereas in other known genera the feces are placed mostly outside the cocoon, just below the cell closure, so that they form a plug, although they sometimes extend partway down the cell wall, as in *Eucera (Synhalonia)* (called *Tetralonia* by Miliczky, 1985, and references therein). In *Eucera (Synhalonia)* defecation is completed before silk production commences, as indicated by the fecal placement exterior to the cocoon. In *Idiomelissodes* silk is incorporated in feces, although most of the cocoon is produced after defecation (Rozen, 1991a). The sandwiching of feces of *Canephorula* between two layers of silk implies that the larva first spins the outer layer(s), stops spinning, and defecates, and then completes the cocoon by spinning the inner silken layer.

Cocoons of all other eucerines are rather flexible and semitransparent, so that the larva or pupa can be seen vaguely through the cocoon wall. The fecal layer renders the *Canephorula* cocoon rigid and opaque from the outside.

The closure end of the inner, leathery layers of the *Canephorula* cocoon is unique in that radiating ridges extending from the level of the filter to the periphery have no counterpart among other eucerine genera whose cocoons have been studied. The small diameter of the flat fibrous disk of this genus is unusual but not unique; cocoons built by species of *Florilegus* sp., *Idiomelissodes,* and *Eucera (Synhalonia)* have a small disk diameter (compared with periphery of the closure end), while cocoons of *Thygater analis* (Lepeletier), *Eucera sociabilis* (Smith), and *Svastra obliqua obliqua* (Say) have a filter that is the same diameter as the periphery of the closure end (all cocoons preserved in the AMNH).

The cocoon of *Melectoides bellus* was brown and substantially different in shape (fig. 9) from that of the host. It was shorter compared with its maximum diameter, and its closure end consisted of a low, lidlike dome. Externally, the dome (figs. 12, 14) was composed of coarse silk fibers and was roughly 1 mm thick at the periphery. In cross section (fig. 13), the dome was composed of numerous, essentially parallel sheets of woven silk. The intermediate sheets could be pulled apart by forceps to reveal silk fibers finer than those of the external surface. The innermost layer was finely textured, without distinct threads of silk but with fenestrations, particularly around the periphery. Presumably these fenestrations and coarser cocoon fabrics permit gas exchange while excluding parasites.

Fecal material adhered to the external surface of the dome (fig. 14) and was also found between its layers of silk, indicating that the cocoon spinning and defecation overlapped in time. It also suggests that the dome is spun before the rest of the cocoon, since feces are not incorporated into the cocoon wall elsewhere.

The rest of the cocoon conformed to the shape of the lower part of the cell. The cocoon wall was externally smooth, much thinner than the closure end, leathery-tough (difficult to tear with forceps), and, on a dried

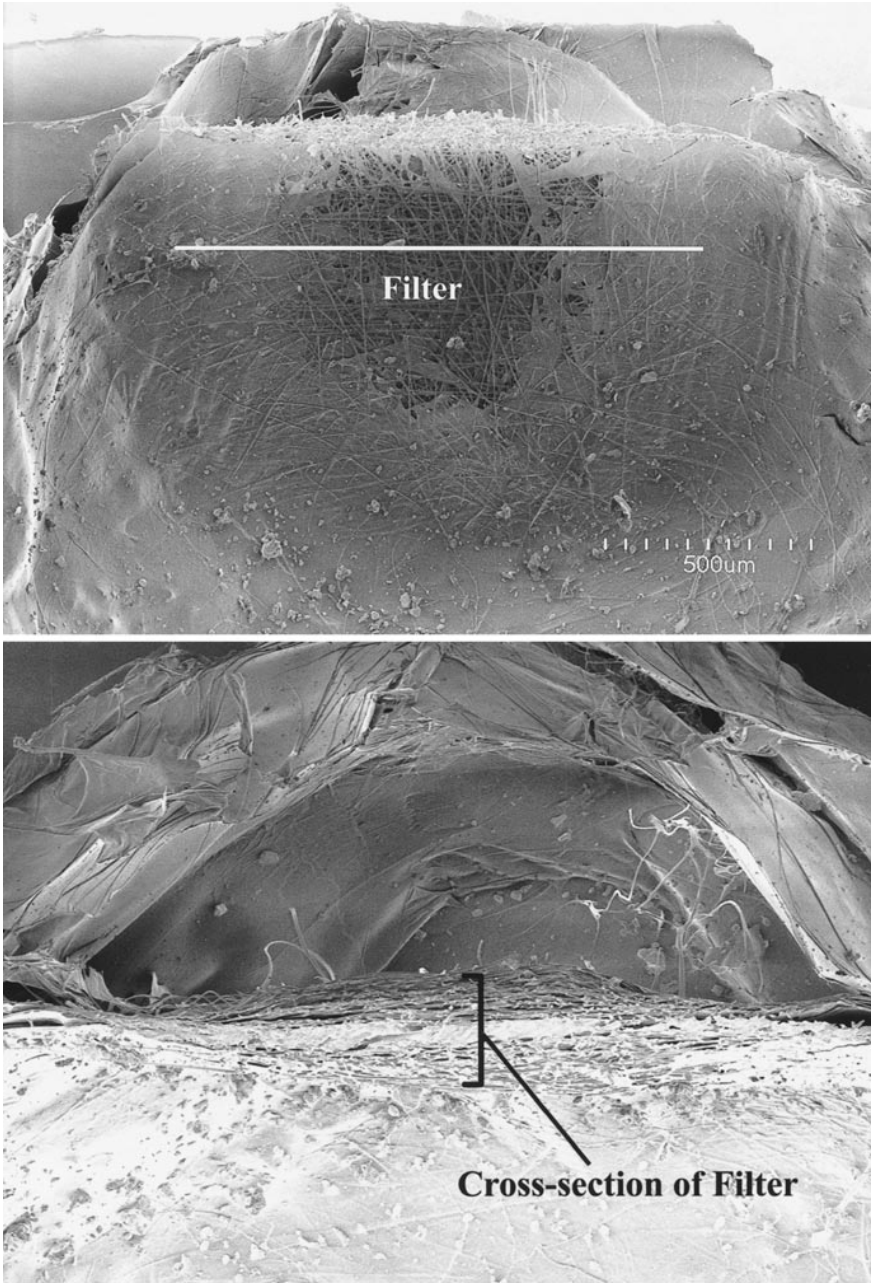
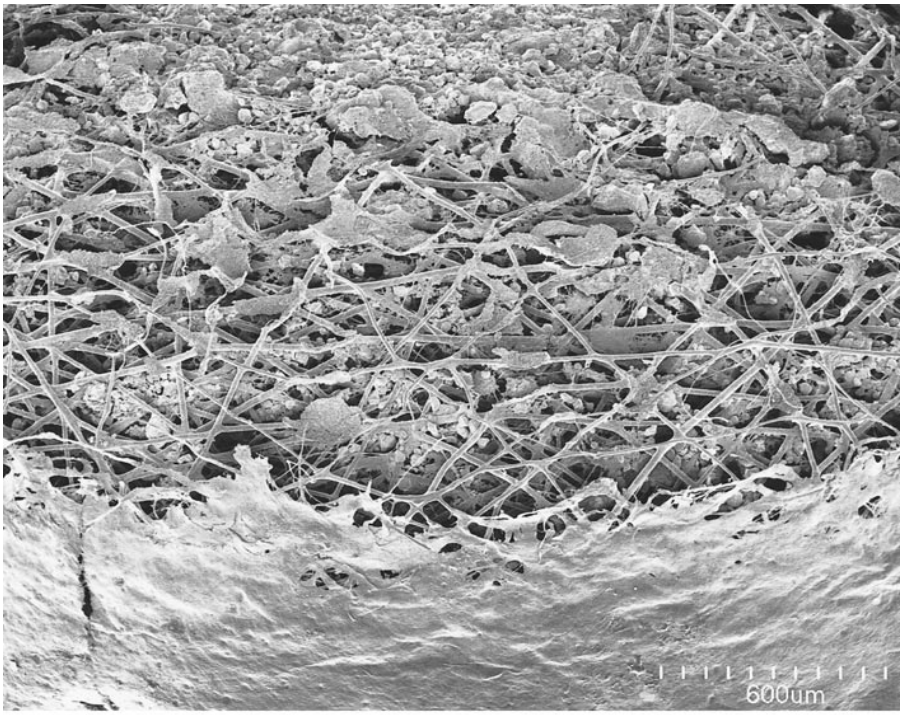


Fig. 10. (Above) SEM micrograph of filter of the cocoon of *Canephorula apiformis*, as seen from inside the cocoon. Upper part of filter cut away.

Fig. 11. (Below) SEM micrograph of apex of closure end of cocoon of *Canephorula apiformis* in cross section.



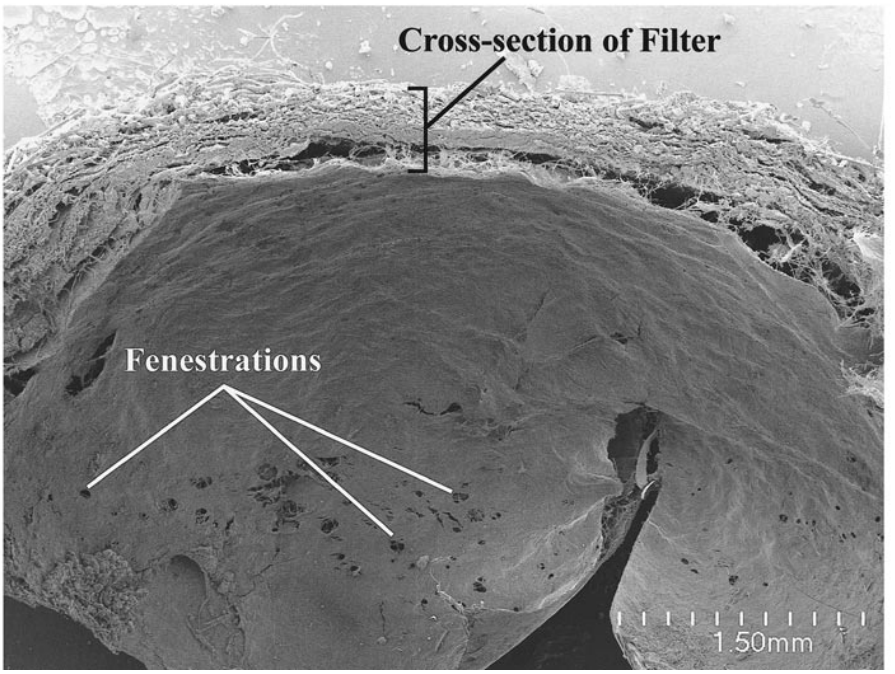


Fig. 12. (Above) SEM micrograph of part of the domelike closure end of cocoon of *Melectoides bellus*, showing coarse silk fibers on external surface. Periphery of closure end toward bottom of micrograph.

Fig. 13. (Below) same specimen, in cross section, showing layers of silk and fenestrations on lower surface.

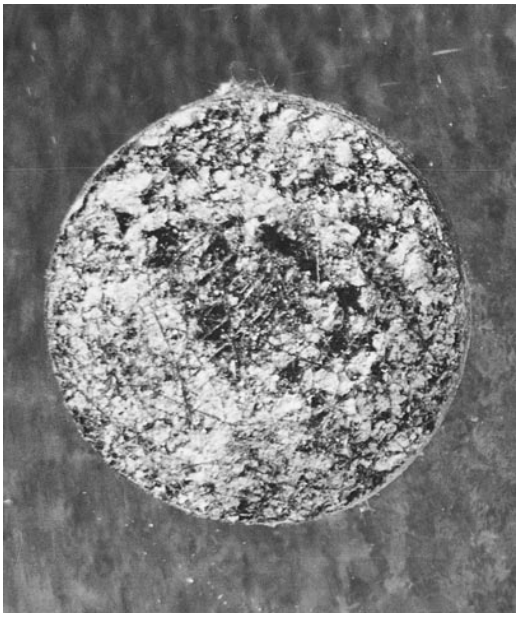


Fig. 14. Top of cocoon of *M. bellus*, external view, showing fecal material in situ.

specimen, single layered. On material examined in alcohol, several layers of nearly clear fabric with identifiable silk threads could be separated from the leathery exterior, suggesting that the cocoon wall was composed of numerous sheets of silk. The exterior layers were fused to one another and lacked silk threads, while the interior layers exhibited silk threads. The lower part of the cocoon was slightly transparent, revealing the vague shape of the larva.

All three cocoons of *Melectoides bellus* available for study displayed an elongate, scarlike deformity, about 1.5 mm long, on the cocoon wall (fig. 9). The scar was raised externally and also internally, and the cocoon fabric in the vicinity of the deformity was somewhat darker and thicker. A cross section of one scar revealed that it consisted of layers of silk. These facts suggest that the larva may have applied an abundance of silk to an elongate pit in the cell wall. This feature was consistent in all three cocoons; we hypothesize that this might be an egg-insertion pit (as found in most Nomadinae) of the cleptoparasite. Further investigation might illuminate why the pit is so thickly sealed from the lumen. At this time, we do not know how females of the Isepeolini introduce their eggs into host cells, nor have any of the eggs been described.

Michener (1957) accurately described, but did not illustrate, the cocoon of *Isepeolus viperinus* (Holmberg), representing the only other genus in the Isepeolini. Because he preserved a specimen, additional details can now be added and comparisons made with the cocoon of *Melectoides bellus.* The cocoon of *I. viperinus* is an oblong ovoid, conforming to the shape of cell of its host (*Colletes*). Hence, its shape is quite different from the truncated hemi-ovoid of the cocoon of *M. bellus.* Another remarkable difference between the two cocoons is in their external structure. The dome of *M. bellus* is constructed with a thick, opaque fabric of partly fused, coarse silk strands, while the remainder of the cocoon is smooth and semitransparent. In contrast, the entire external surface of the cocoon of *I. viperinus* is covered by a thick, opaque fabric of partly fused coarse silk (fig. 15). However, these external fabrics of the two genera appear to be identical when viewed as SEM micrographs (figs. 12, 15). Both (figs. 13, 16) are composed of numerous layers of silk; an external layer is constructed of course fibers, while fine silk is used to spin more internal layers. The innermost layer of *I. viperinus* is shinier than that of *M. bellus.* However, as noted by Michener, the lining at the closure end of the *Isepeolus* cocoon (fig. 16) is more fibrous, supporting the idea that gas exchange may take place in this region. Michener noted fecal material on the outside of the cocoon of *I. viperinus*; as on *M. bellus,* fecal material was also dispersed among the silken sheets of the cocoon of *I. viperinus,* indicating that both bees defecate while cocoon-spinning.

The cocoons of these two related cleptoparasitic genera display great differences in shape and macrostructure, yet share tremendous similarities in microstructure.

Life Cycles

A total of 275 adults of *Canephorula apiformis* were collected: 257 (211 males and 46 females) in flowers and 18 (15 females and 3 males) near nest entrances or in nests. During the first survey period (1993–1994),

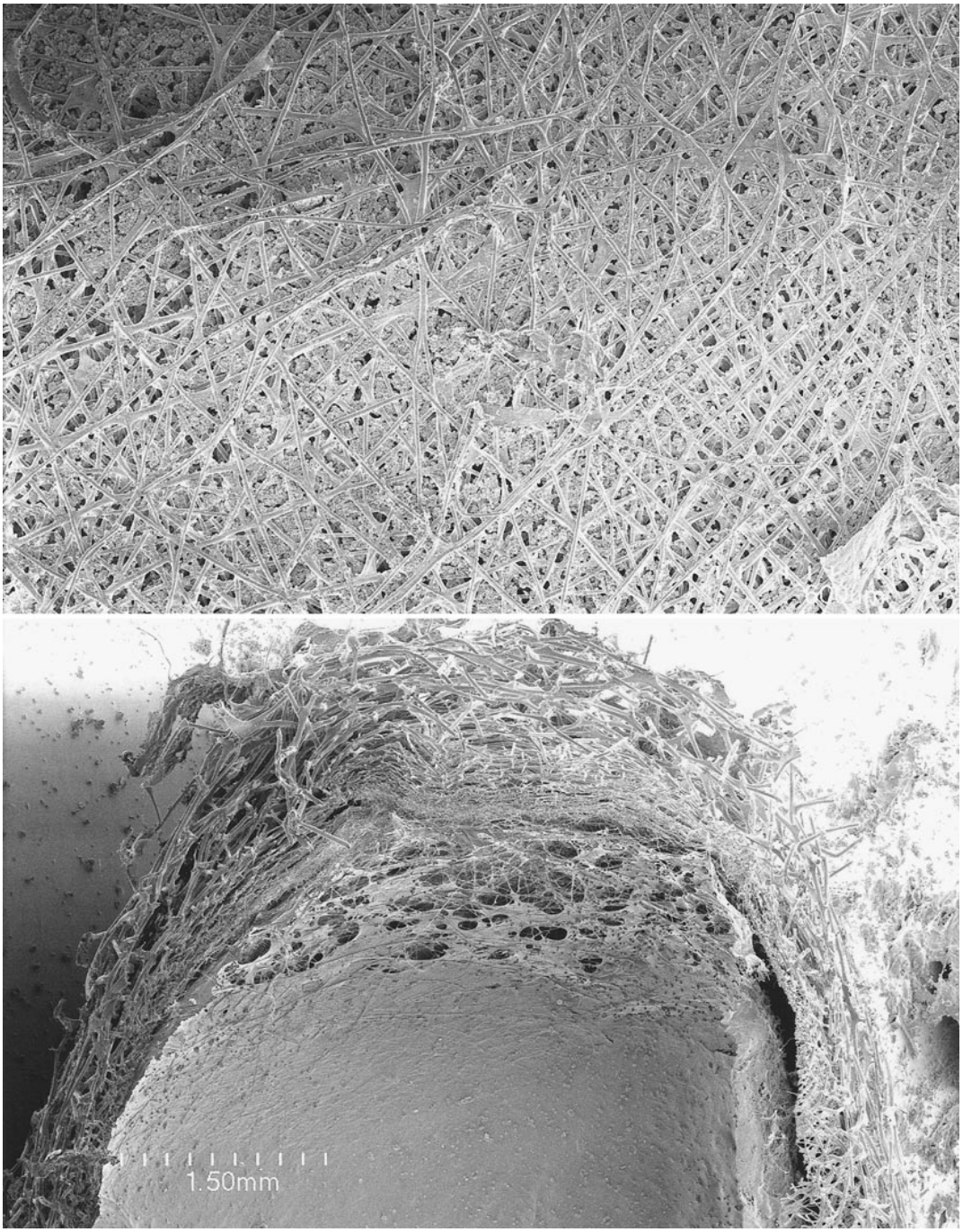


Fig. 15. (Above) SEM micrograph of part of external surface of cocoon of *Isepeolus viperinus*, showing similarity to that of dome of *Melectoides bellus* (fig. 12); both figures to same scale.

Fig. 16. (Below) SEM micrograph of front end of cocoon of *Isepeolus viperinus*, showing coarse outer silk layer, finer intermediate silk layers, and very fine innermost silk layer with fenestrations at closure.

the bees were active from November to February (fig. 17); however, in additional samplings (1996), 1 male and 1 female were recorded in early March. In 1996–1997 the activity of the bees in the study site was restricted to November and December (fig. 17). The absence of activity in January and February (1997) was probably related to disturbance caused by caterpillar tractor activities on the nest aggregations.

The observations made at nest aggregations during 1993–1994, 1995–1996, and 1996–1997 revealed that the bees emerged in mid-November until early December; in December females were seen provisioning the nests. In January the activities practically ceased, with only a few bees flying over the nests. In the beginning of February, activity became intense again, and young adults were seen leaving the nests. In early March, activity completely ceased. This pattern, with two activity peaks, one in November–December and the other in February, with bees newly emerged in the beginning of each, indicates that *Canephorula apiformis* may be a bivoltine species, as the diagram of flower-visit frequencies (fig. 17) also suggests. On the other hand, the stage of development of the immatures obtained from the nest excavations is more indicative of only one generation per cycle. In the excavations at the end of November when many newly emerged bees were seen, only three cells were found that contained pupae from the emerging population. In early December only eggs and small larvae were found. In mid-December there were large larvae. In January, no excavation was made, but only mature larvae were found in excavations made in early to mid-February. The mature larvae observed in February entered diapause, remained in this state during fall, winter, and part of spring, and emerged in November–December. In February 1995, closed cells (N = 15) were collected and maintained in a terrarium. The individuals in these cells remained in diapause until the end of November, when the first adults began to emerge in synchrony with the emergence of adults at the nesting sites. Of the 15 cells, 8 individuals (5 males and 3 females) completed development and emerged.

A total of 180 adults (171 males and 9 females) of *Melectoides bellus* was collected on flowers (fig. 17) and 2 additional females were captured around the nests of *Canephorula*. *Melectoides* was active from November to the beginning of February, overlapping with the entire activity period of its host (fig. 17), and appears to have one generation per year. December was the peak of activity, with 133 cleptoparasites collected.

Floral Preference and Phylogeny

Figure 18 shows the flowering periods and flower visitation frequency of *Canephorula apiformis.* The plant species visited were: *Prosopis strombulifera, Atamisquea emarginata, Tessaria absinthioides, Baccharis salicifolia,* and *Larrea divaricata. Tessaria absinthioides* was visited by the greatest number of individuals, with 83 males and 35 females collected. In descending order of visitation frequency were *A. emarginata,* with 67 males and 9 females; *B. salicifolia,* with 35 males and 2 females; *L. divaricata,* with 23 males; and *P. strombulifera* with 3 males (fig. 18). The individuals of *Canephorula apiformis* were active from 8:00 hr to 20:00 hr, mostly between 10:00 hr and 14:00 hr (fig. 20).

The majority of the females (35 of the 46 collected on flowers) were collected on *Tessaria absinthioides.* However, the pollen load carried by 22 of the 46 females was exclusively composed of pollen from *Atamisquea emarginata.* In 6, the load was a mixture of pollen predominantly from *A. emarginata* and in lesser quantity from *T. absinthioides.* One female had pollen only from *Baccharis salicifolia.* Of all the females that visited *T. absinthioides,* only 4 had a few grains of pollen from this species. Since the amount of pollen from *T. absinthioides* was small, we consider it a contaminant.

Therefore, at least during November and December, our data indicate that the main source of pollen at the study sites was *Atamisquea.* This floral species blooms only until the beginning of January; during January and February another plant should substitute for it. Likely candidates are *Baccharis salicifolia,* which blooms until the end of the season, or *Larrea,* whose flowering season overlaps that of *Baccharis* during February and March

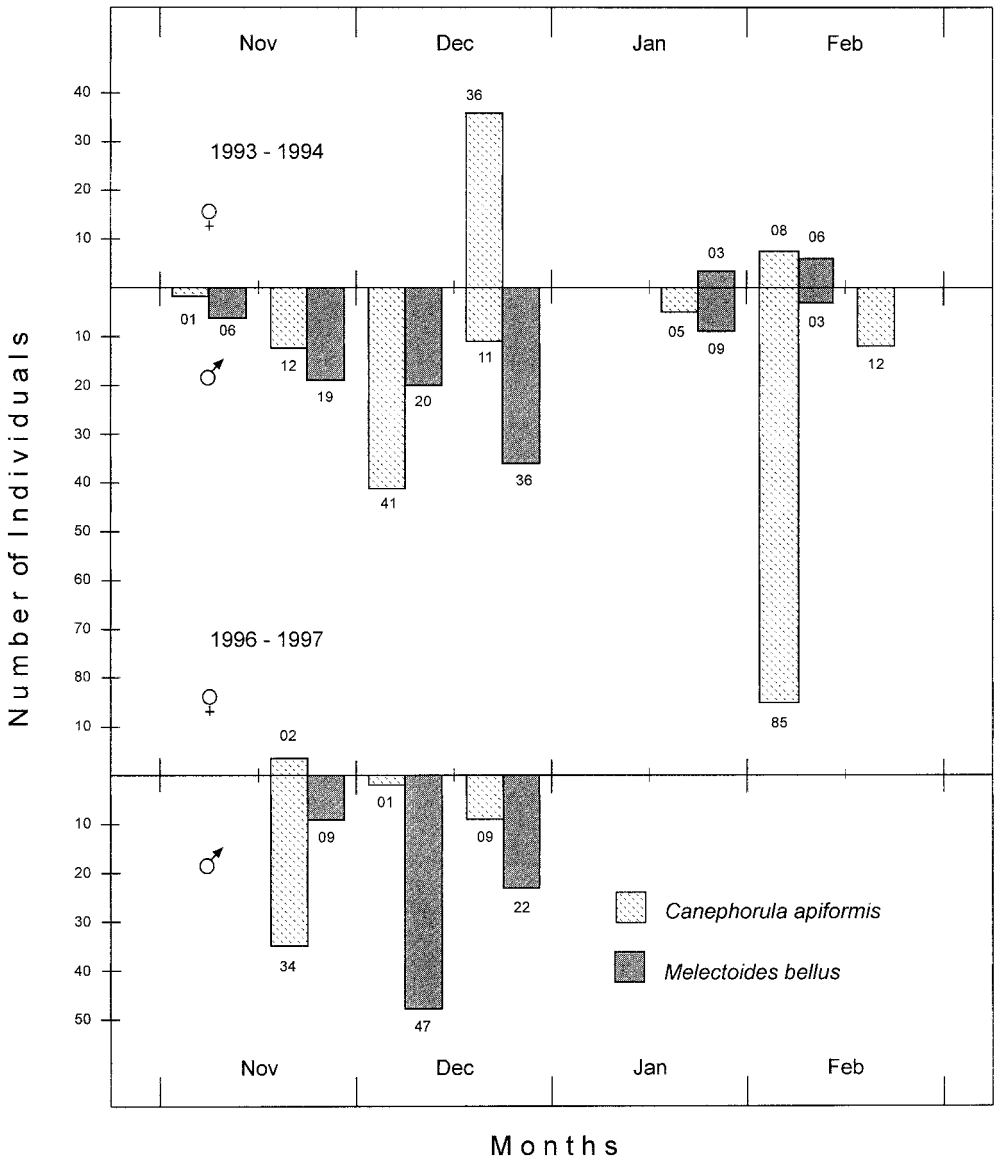
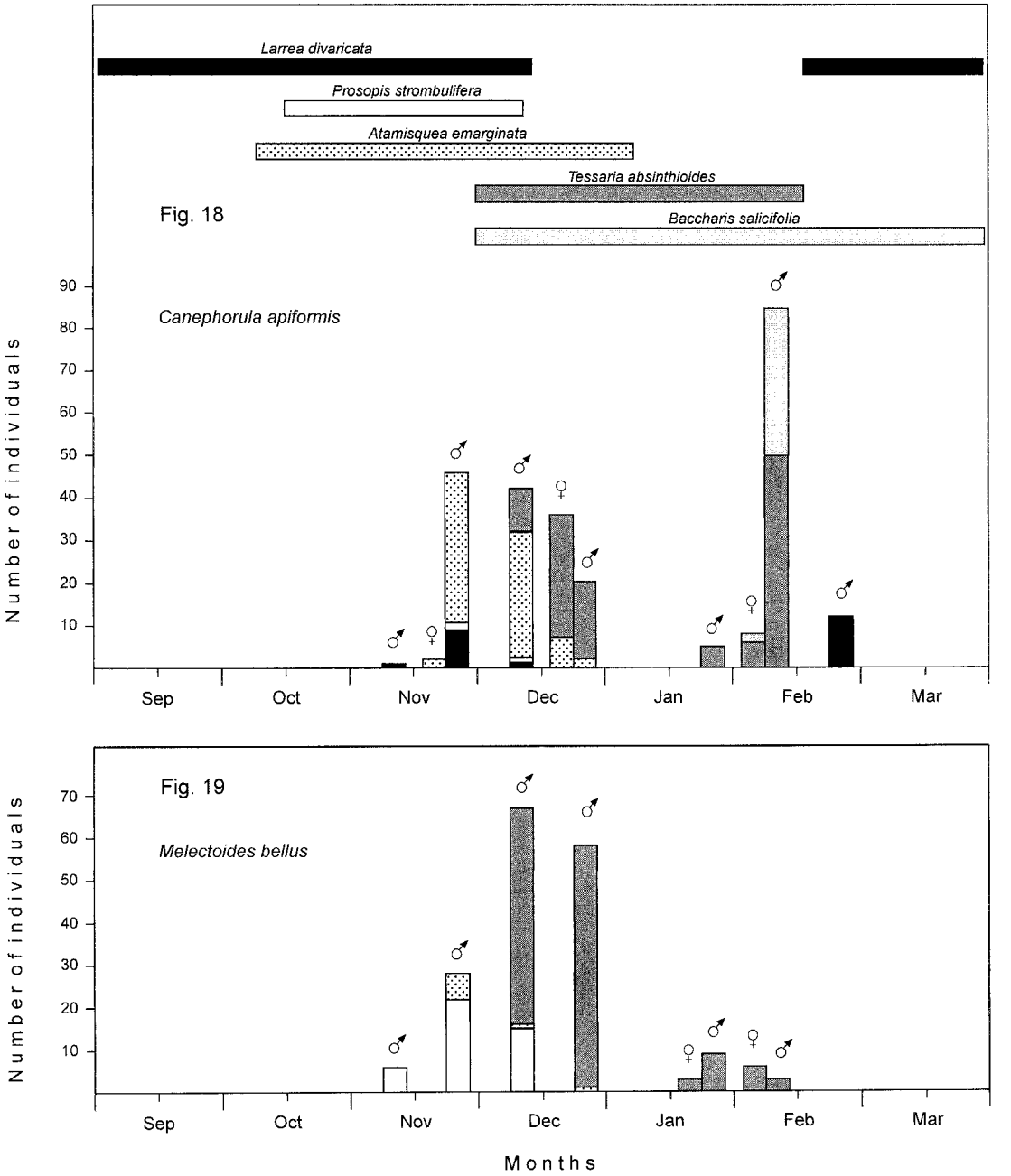


Fig. 17. Frequency of individuals of *Canephorula apiformis* and *Melectoides bellus* on flowers during the months of activity in the Valley of Zonda-Ullum, San Juan Province, Argentina.

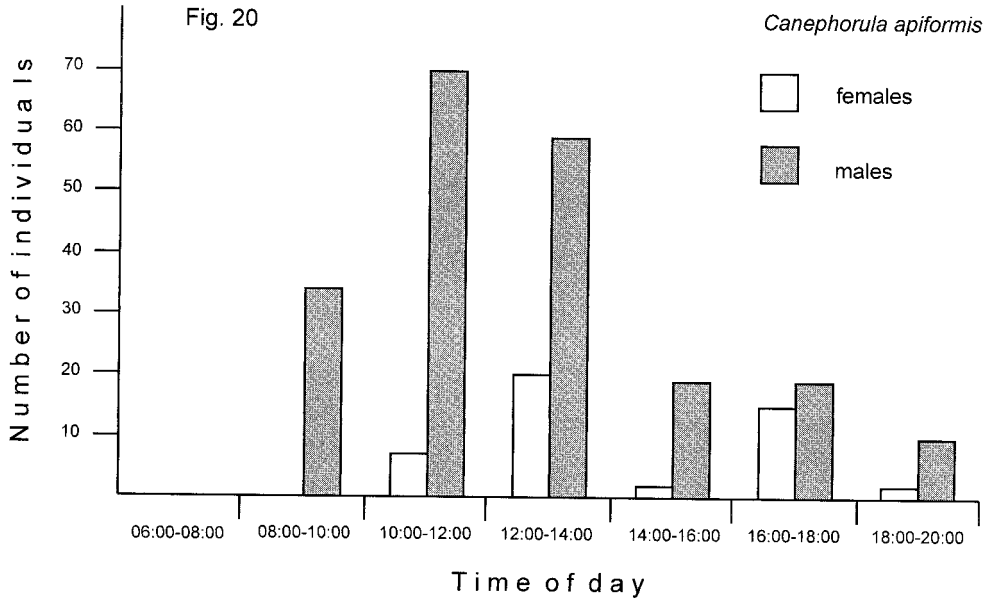
(fig. 18). During this period only 8 females were collected (6 at flowers of *Tessaria* and 2 at flowers of *Baccharis*), but they were not carrying pollen loads except for 1 female with some pollen grains of *Baccharis* and 4 with some pollen grains of *Tessaria.*

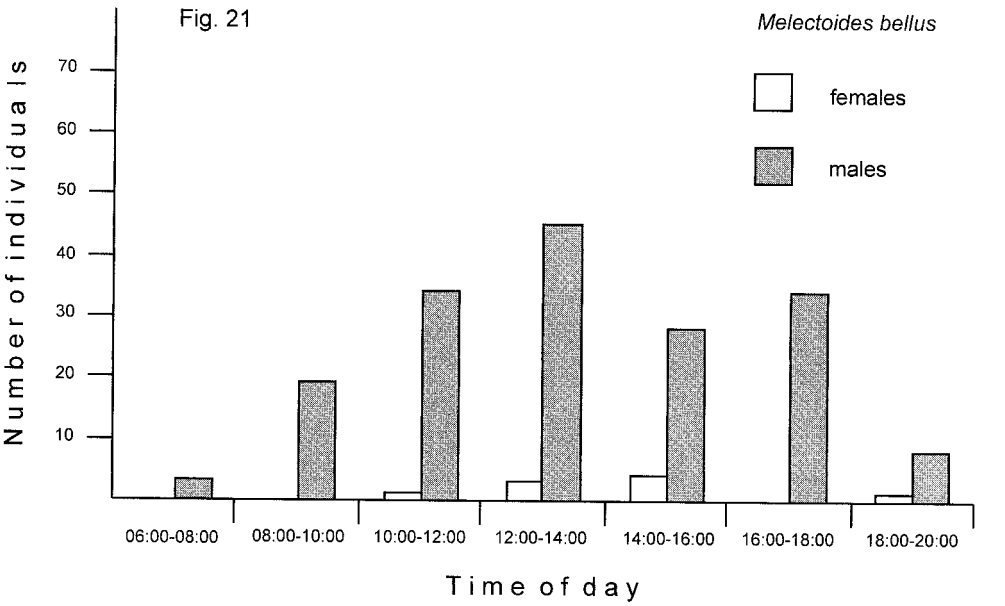
Jensen-Haarup (1908a, 1908b) and Cocucci et al. (1992) provided records of *Canephorula* visiting some caesalps in Argentina. According to Simpson and Neff (1985), *Canephorula* should be restricted to caesalpinoid types of Fabaceae (e.g., *Cercidium, Caesalpinia,* and *Zuccagnia*). Although *Cercidium praecox* (Ruiz and Pav.) Harms and *Zuccagnia punctata* were present in the sampled areas and other species of bees were observed at flowers of *C. praecox* during this study, no males or females of *Canephorula* were found visiting them.

The full pollen load of *Canephorula api-*



Figs. 18, 19. **18.** Above, blooming periods of plant species visited by *Canephorula apiformis* and *Melectoides bellus*, years 1993–1994 and 1996–1997, in the Valley of Zonda-Ullum, San Juan Province, Argentina. Below, frequency of *C. apiformis* collected on different floral species during the months of activity. **19.** Frequency of individuals of *Melectoides bellus* collected on different floral species identified in fig. 18 during the months of activity.





Figs. 20, 21. Daily activity of individuals of *Canephorula apiformis* and *Melectoides bellus* at food plants during 1993–1994 and 1996–1997, in the Valley of Zonda-Ullum, San Juan Province, Argentina. **20.** *Canephorula apiformis.* **21.** *Melectoides bellus.*

formis is typically large, covering the entire anterior surface of the hind tibia and basitarsus.

The flowers most commonly visited by *Melectoides bellus* were *Tessaria absinthioides* (129 individuals), *Prosopis strombulifera* (43 individuals), and *Atamisquea emarginata* (8 individuals) (fig. 19). This bee was active mostly between 8:00 and 18:00 hr (fig. 21).

POSTDEFECATING LARVA OF *CANEPHORULA APIFORMIS* (FRIESE)

Figures 22–28

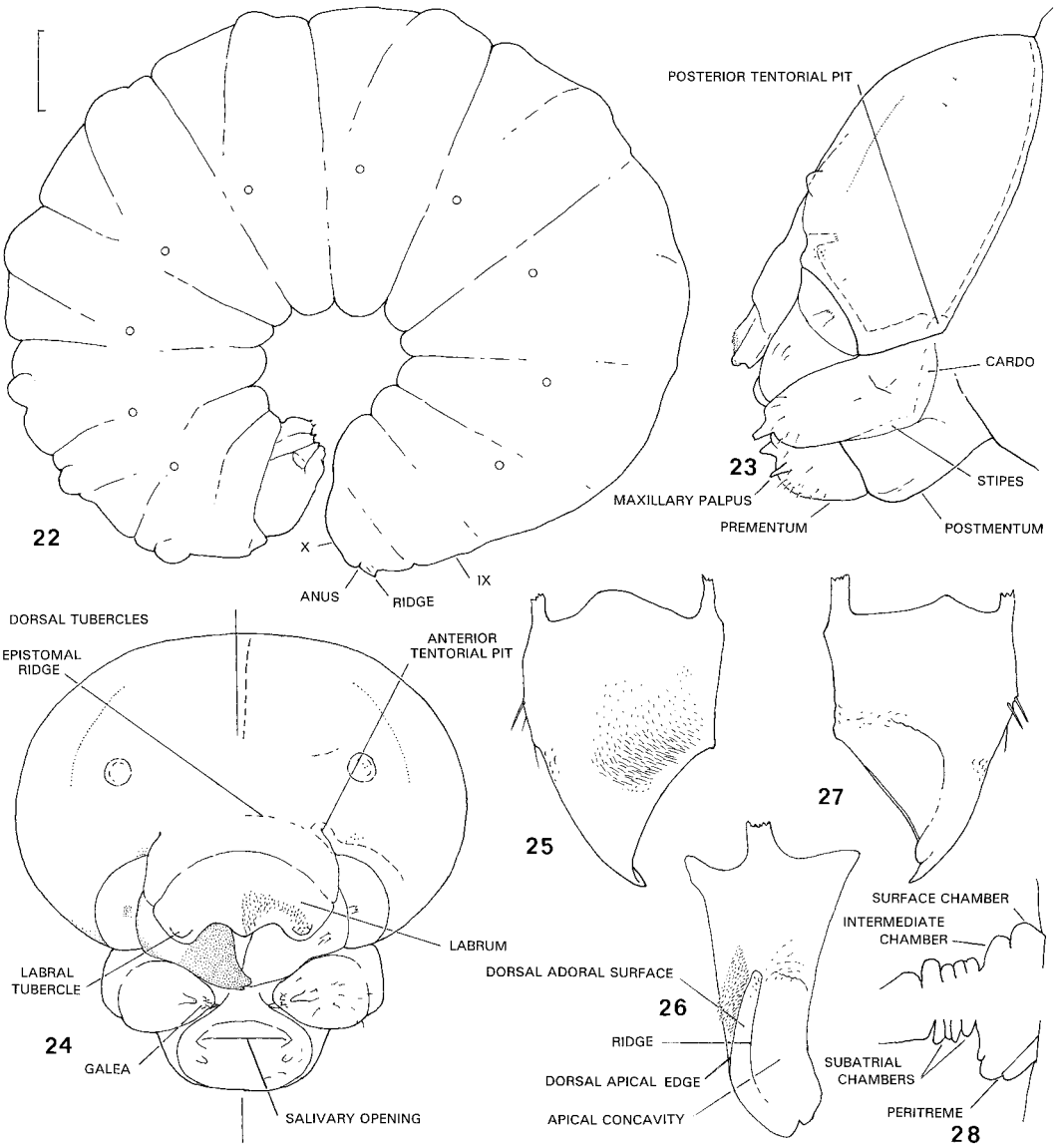
DIAGNOSIS: Mature larvae of Eucerini are quite similar (for references to descriptions, see McGinley, 1989; Rozen, 1991a), and the larva of *Canephorula apiformis* conforms well to the tribal description of larvae presented by Rozen (1965). The significant tribal features are in boldface below. Characters in italics may prove useful for distinguishing the larva of this genus from those of other eucerine genera.

DESCRIPTION: Length (if straight) approximately 20 mm.

Head (figs. 23, 24): Integument unpigmented except for following areas: hypostomal ridges, anterior mandibular articulations, apices and extreme base of mandibles, base of cardines, stipites toward distal ends, and articulating arms of stipes; cranium with widely scattered, small setiform sensilla; labral tubercle, apex of labrum, maxillae (particularly apically), and apex of labrum with larger setiform sensilla; **following areas with conspicuous elongate setiform spicules: surface of labrum between tubercles (fig. 24),** epipharynx on either side of midline (above similar patches on closed mandibles), **dorsal surface of mandibles (fig. 25).**

Head size moderately small compared with body; head capsule wider than long in frontal view. Tentorium complete (including dorsal arms); anterior arms robust; rest of tentorium moderately developed; anterior tentorial pit much closer to anterior mandibular articulation than to antenna; posterior tentorial pit conspicuous, well impressed, and found at junction of hypostomal ridge and postoccipital ridge. Median longitudinal thickening of head capsule well developed to level of antenna. Postoccipital ridge moderately well developed; hypostomal ridge, pleurostomal ridge, and lateral arms of epistomal ridge well developed; *median section of epistomal ridge faintly developed,* far less so than lateral arms. Parietal band evident. Antennal prominence scarcely developed; antennal disk differentiated from papilla; antennal papilla moderately projecting (height less than diameter), with approximately three sensilla. Front of head capsule as seen in lateral view (fig. 23) sloping normally so that labrum extending well beyond clypeus and clypeus beyond frons. **Labrum broad as seen in frontal view, apically trilobed, with pair of low tubercles apicolaterally;** labral sclerite (as found in Megachilidae, McGinley and Rozen, 1987: fig. 27) not evident; epipharynx apparently a simple, slightly curved surface.

Mandible (figs. 25–27) robust, moderately long so that, in repose, mandibular apices meet; outer surface with several elongate setae on small tubercles; **mandibular apex bidentate with dorsal tooth longer and broader; both teeth acutely pointed** ***but their extreme apices rather blunt***; **dorsal adoral surface of mandibles separated from apical concavity by distinct ridge that more or less parallels dorsal apical edge;** *dorsal adoral surface with irregularities toward base but not distinctly denticulate as in* Idiomelissodes duplocincta *(Cockerell)* (Rozen, 1991a), smooth toward apex; cusp and apical concavity well developed with irregular surface near cusp. **Labiomaxillary region strongly projecting.** Maxillary apex distinct, bearing elongate palpus apically, *inner apical surface not strongly produced* and with integument irregular; **galea represented** *by very low mound bearing cluster of approximately three elongate setae* between palpal base and inner apex; cardo and stipes well developed; articulating arm of stipes evident. Labium divided into prementum and postmentum; premental sclerite not developed; apex of labium with surface irregular; labial palpus elongate, nearly as large as maxillary palpus. **Salivary opening** a transverse slit on projecting lips, the opening **as in most other eucerines extremely broad, as wide as distance between labial palpi;** hypopharyngeal groove not incised and therefore not evident. **Hypopharynx a flat**



Figs. 22–28. Postdefecating larva of *Canephorula apiformis.* **22.** Entire larva, lateral view. **23.** Head, lateral view. **24.** Head, frontal view, pigmentation on left, sensilla and spicules on right. **25–27.** Right mandible, dorsal, inner, and ventral views. **28.** Spiracle, side view. Scale (= 1.0 mm) refers to fig. 22.

continuation of dorsum of labrum to buccal cavity.

Body (fig. 22): Integument without setae except for very fine setiform sensilla on abdominal segment X, mostly below anus; integument very finely, evenly spiculate in many areas; integument without spines or sclerotized tubercles. Body form robust; intersegmental lines moderately defined; **intersegmental lines evident on most body segments** although sometimes partly obscured by bending of body; *paired dorsal tubercles present on caudal annulet of each thoracic segment; these tubercles transverse,* only briefly separated dorsally on each segment; abdominal segments without dorsal tubercles (however, indefinite paired dorsal tubercles on anterior abdominal segments appearing on

immature larvae); lateral tubercles (below level of spiracles) absent; abdominal segment X in lateral view (fig. 22) attached dorsally to segment IX; anus dorsal in position on X as seen in lateral view; perianal area with strong transverse ridges above anus. Spiracles (figs. 22, 28) moderately large, subequal in size; *division between atrium and subatrium uncertain* because primary spiracular opening apparently without collar and because of presence of *irregularly formed chamber intermediate in size between surface chamber and subatrium chambers* (this intermediate chamber possibly subdivision of atrium; see Remarks below); atrium projecting slightly beyond body wall, with rim; subatrium short, with approximately 5–6 chambers; *atrial and subatrial walls without denticles.* Female with pair of imaginal disks ventrally on each of segments VII, VIII, and IX, those of IX being contiguous and preceding ones successively farther apart; cuticle associated with each disk slightly impressed. Male sex characters unknown.

MATERIAL STUDIED: Two postdefecating larvae, Zonda, San Juan Province, Argentina, December 17, 1995 (E. Michelette).

REMARKS: Spiracular morphology of mature eucerine larvae does not conform to that of most bee larvae, in which the spiracular apparatus consists of a large atrium subtended by a narrow, multichambered subatrium (Michener, 1953: fig. 15). Instead, larval representatives of *Svastra, Xenoglossa, Melissodes, Peponapis, Thygater,* and apparently *Eucera (Synhalonia)* (Miliczky, 1985; Packer, 1987; Rozen, 1965) appear to have the subatrium divided into two parts, termed (in boldface) by Rozen (1965: fig. 5) as the more transparent and wider **outer subatrium** and the optically denser and narrower **inner subatrium.** Rozen (1991a) considered the subatrium of *Idiomelissodes* to consist of only the three chambers, but reexamination of the specimen reveals a short, optically dense area immediately below the atrium. The spiracle of this genus needs further study to determine if the denser area may be homologous to the inner subatrium of the other genera. The spiracle of *Canephorula* (fig. 28), described above, is clearly a departure from the spiracles of the other genera in that it lacks an optically dense inner subatrium. However, the intermediate chamber between the surface chamber (fig. 28) and the narrower inner subatrium is ambiguous in that it can be interpreted either as a single-chambered outer subatrium (with the inner subatrium being the remaining narrow chambers) or a subdivision of the atrium.

POSTDEFECATING LARVA OF *MELECTOIDES BELLUS* (Jörgensen)

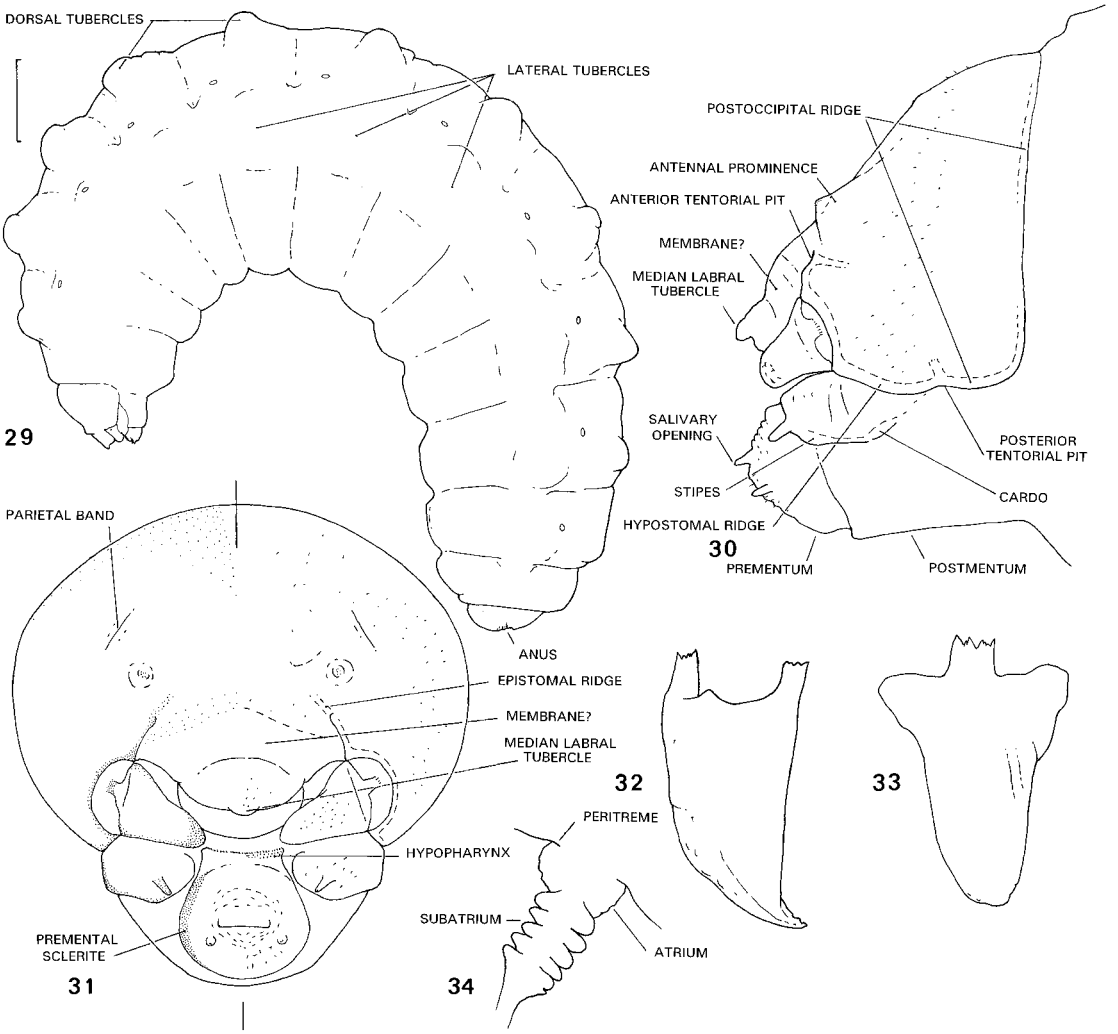
Figures 29–34

The Isepeolini are a small group of South American cleptoparasitic bees comprising two genera (*Isepeolus* and *Melectoides*) and 21 species according to Roig-Alsina (1991). Immatures of only the following two species have been described previously: *Isepeolus luctuosus* (Spinola) (Claude-Joseph, 1926 [mature larva]) and *I. viperinus* (Holmberg) (Michener, 1957 [first instar, pupa]; Lucas de Oliveira, 1966 [first and last larval instars]; Rozen, 1966 [last larval instar]; Rozen, 1991b [first instar]).

DIAGNOSIS: The mature larvae of *Melectoides bellus, Isepeolus luctuosus* and *I. viperinus* can easily be separated from other bee larvae by their labrum bearing a single median tubercle and by their more-or-less evident lateral body tubercles in addition to the paired dorsal tubercles on most body segments. *Melectoides bellus* and *I. viperinus* can be separated from one another by the features presented in italics below. (These features are unknown for *I. luctuosus.*) Characters shared by *M. bellus* and *I. viperinus* are printed in boldface; presumably they are the main diagnostic features of mature larvae of the Isepeolini.

DESCRIPTION: Length approximately 10 mm.

Head (figs. 28, 29): Integument very faintly pigmented except darkly pigmented in following areas: tentorium in vicinity of anterior and posterior tentorial pits, hypostomal, pleurostomal, and lateral segments of epistomal ridges, lateral basal angles of labrum, cardo, stipes, base and apex of mandible, premental sclerite, and apices of salivary lips; in addition, palpi, antennae and dorsomesal streak from each anterior tentorial pit faintly pigmented; cranium, apices of labium and maxillae with fine setiform sensilla; la-



Figs. 29–34. Postdefecating larva of *Melectoides bellus.* **29.** Entire larva, lateral view. **30.** Head, lateral view. **31.** Head, frontal view, pigmentation on left, sensilla and spicules on right. **32, 33.** Right mandible, dorsal and inner views. **34.** Spiracle, side view. Scale (= 1.0 mm) refers to fig. 29.

brum with all surfaces nonspiculate; hypopharynx with spicules.

Head size small compared with body; head capsule wider than long in frontal view. Tentorium complete (including dorsal arms), moderately developed but not robust; anterior tentorial pit moderately small, well separated from anterior mandibular articulation, about midway between it and antenna; **posterior tentorial pit** conspicuous, well impressed, and **found well in front of posterior boundary of head capsule, as seen in lateral view (fig. 29).** Median longitudinal thickening of head capsule scarcely developed. *Postoccipital ridge* weak dorsally, becoming well developed below where it *gradually curves forward to become linear extension of hypostomal ridge at posterior tentorial pit (thus contrasting with lower part of postoccipital ridge of* Isepeolus, *which angles upward immediately behind posterior tentorial pit)*; hypostomal and pleurostomal ridges moderately well developed; lateral arms of epistomal ridge less well developed; median section of epistomal ridge apparently represented by darkly pigmented, slightly

thickened cuticle running dorsomesally from anterior tentorial pit; this thickening ending well laterad of midline of head. Parietal band represented by short oblique line (fig. 28) above antenna. Antennal prominence moderately weakly developed; antennal disk differentiated from papilla; **antennal papilla** moderately projecting (height about one-half diameter) **with approximately six sensilla.** Front of head capsule as seen in lateral view (fig. 31) sloping normally with labrum extending well beyond clypeus and clypeus beyond frons; boundary between clypeus and labrum apparently an elongate membranous area (see Remarks below). **Labrum small with single median tuberclelike projection bearing cluster of sensilla;** labral sclerite (as found in Megachilidae, McGinley and Rozen, 1987: fig. 27) not evident; epipharynx a simple curved surface bulging beneath labrum.

Mandible (figs. 32, 33) moderately robust, *short, curving to a rounded apex as seen in aboral and adoral view; apex with small indistinct point; upper and lower apical edges with a few small indistinct teeth;* outer surface with numerous small sensilla; **cusp not produced, nondentate. Labiomaxillary region strongly projecting, not greatly fused. Maxillary apex distinct, bearing elongate palpus apically;** galea not evident; **cardo and stipes well developed;** articulating arm of stipes evident, connecting with premental sclerite (as in *Paratetrapedia swainsonae* [Cockerell], Rozen and Michener, 1988: fig. 12). **Labium divided into prementum and postmentum; premental sclerite evident and pigmented;** apex of labium finely wrinkled suggesting that labium beyond premental sclerite can be strongly projected during cocoon spinning; **labial palpus elongate, nearly as large as maxillary palpus. Salivary opening a transverse slit on projecting lips;** hypopharyngeal groove not incised and therefore not evident. Hypopharynx recessed well behind labral apex, projecting upward, and flat or nearly so in frontal view (fig. 30).

Body (fig. 29): Integument without obvious setae although that of perianal area with scattered, very fine setiform sensilla; integument appearing nonspiculate under normal stereoscopic examination but under high magnification patches of very fine, evenly spaced spicules visible on dorsal areas of thorax; integument without spines or sclerotized tubercles. Body form moderately robust; intersegmental lines moderately defined; intrasegmental lines not evident; paired dorsal tubercles present on each thoracic segment and on abdominal segments I–VII; these tubercles slightly transverse in that, viewed dorsally, each with anterior-posterior length less than lateral width; those of midbody segments separated dorsally on each segment by distance of approximate width of one tubercle; **lateral conical tubercles (below level of spiracles) present on most body segments,** evident on mesothorax, metathorax, and abdominal segments I–VIII (these tubercles not visible in lateral view, but their position indicated in fig. 27); *these tubercles far less pronounced than those of Isepeolus viperinus* (Rozen, 1966: fig. 2; Lucas de Oliveira, 1966: fig. 2); abdominal segment IX with venter not produce, so that segment X appearing to be attached to approximate middle of IX in lateral view; anus slightly dorsal in position because venter of X somewhat more produced than dorsum; perianal area without transverse ridges but with numerous fine integumental irregularities surrounding anus. Spiracles (figs. 29, 34) moderately small, subequal in size; atrium moderately small compared with subatrium; atrial wall with indistinct concentric ridges; atrium projecting beyond body wall but without rim; narrow peritreme present; primary tracheal opening with collar; **subatrium short, with approximately 5–6 chambers.** Sex characters unknown.

MATERIAL STUDIED: Three postdefecating larvae, Zonda, San Juan Province, Argentina, November 5, 1995 (E. Michelette).

Remarks: An unusual feature of this larva is the apparent elongate membranous area separating the labrum from the clypeus. This area lacks the conspicuous sensilla and smooth, shiny cuticle found on both the clypeus and the labrum; instead the cuticle of this area is finely wrinkled. It appears to allow for a flexible labrum. This possibility is also supported by the presence of a darkly pigmented spot on each side of the base of the labrum that suggests a muscle attachment point. The morphologically similar larva of *Isepeolus vi-*

perinus was examined for homologous structures but was inconclusive in confirming the anatomy of the clypeal/labral boundary.

Previous investigations on the phylogenetic relationships of the Isepeolini to the other cleptoparasitic Apidae have been reviewed by Roig-Alsina (1991), and more recently Roig-Alsina and Michener (1993) have dealt with the phylogeny of all long-tongued bees, including this tribe, through a series of cladistic analyses. While the mature larvae of *Melectoides bellus* and *Isepeolus viperinus* share numerous unusual features that attest to the monophyly of the Isepeolini, the anatomy of *M. bellus* does not further illuminate the relationship of the tribe to other parasitic and nonparasitic groups.

ACKNOWLEDGMENTS

The cocoon of *Isepeolus viperinus* (Holmberg), compared with that of *Melectoides bellus*, below, is on long-term loan to JGR from the Department of Entomology, University of Kansas, with thanks to Charles D. Michener.

Dr. Michael S. Engel is thanked for critically reviewing the manuscript and offering valuable comments on improving it. We also express our appreciation to two anonymous reviewers for their thoughtful suggestions and comments.

The SEM micrographs were prepared by Molly Rightmyer, Division of Invertebrate Zoology, the American Museum of Natural History. She and Eric Quinter are thanked for assistance in editing the manuscript. Silvia Regina de Menezes Pedro is thanked for suggestions, manuscript revision, and preparation of graphics for figures 17–21.

ERFM was supported by a postdoctoral fellowship from Fundação de Amparo à Pesquisa do Estado de São Paulo while at the Department of Biology, Faculdade de Filosofia, Ciências e Letras—Ribeirão Preto—Universidade de São Paulo. ERFM thanks M. Allende, F. Maldonado, and J. Marques of the Instituto y Museo de Ciencias Naturales, Facultad de Ciencias Exactas, Físicas y Naturales de la Universidad Nacional de San Juan, for identification of the plants.

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