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Biology, Larvae, and Oocytes of the Parasitic Bee Tribe Caenoprosopidini (Hymenoptera: Anthophoridae: Nomadinae)

JEROME G. ROZEN, JR.¹ AND ARTURO ROIG-ALSINA²

ABSTRACT

As a result of field studies in Argentina, *Caenoprosopis crabronina* Holmberg is reported to be a nest cleptoparasite of *Arhysosage* (Andrenidae: Panurginae) and *Caenoprosopina holmbergi* Roig-Alsina, of *Callonychium* (Andrenidae: Panurginae). The egg of *Caenoprosopis* (and almost certainly of *Caenoprosopina*) is deposited in the cell wall of the host, as is characteristic of other nomadines. Oocytes of both species are elongate, and in each case the rounded anterior end bears a small

hook. What are believed to be first instars are hospicidal with sharp mandibles, somewhat prognathous head capsules, and elongate labral tubercles. Postdefecating larvae of both species are described, compared with those of other Nomadinae, and found to be similar to those of the related Ammobatini. Besides strong similarities of uncertain polarity, Caenoprosopidini and Ammobatini share at least one larval synapomorphy that supports the hypothesis that they are sister groups.

RESUMEN

Como resultado de estudios de campo en Argentina, se registran *Caenoprosopis crabronina* Holmberg como cleptoparásito de *Arhysosage* (Andrenidae: Panurginae) y *Caenoprosopina holmbergi* Roig-Alsina, de *Callonychium* (Andrenidae: Panurginae). El huevo de *Caenoprosopis* (y casi con certeza el de *Caenoprosopina*) es de-

positado en la pared de la celda del huésped, como es característico de otros nomadinos. Los oocitos de ambas especies son alargados y en cada caso el extremo redondeado anterior lleva un pequeño gancho. Los que se consideran como primeros estadios son hospicidas, con mandíbulas agudas, cabeza algo prognata y tubérculos del labro alarga-

¹ Curator, Department of Entomology, American Museum of Natural History.

² Museo Argentina de Ciencias Naturales "Bernardino Rivadavia," Av. Angel Gallardo 470, 1405 Buenos Aires, Argentina. Present address: Snow Entomological Museum, Snow Hall, University of Kansas, Lawrence, Kansas 66045-2119.

dos. Se describen las larvas postdefecantes de ambas especies, se las compara con las de otros Nomadinae, y se las encuentra similares a las de la tribu relacionada Ammobatini. Además de no-

tables similitudes, de polaridad incierta, Caenoprosopidini y Ammobatini comparten al menos una sinapomorfía larval que apoya la hipótesis de que son grupos hermanos.

INTRODUCTION

At the time that Roig-Alsina (1987) reported on the systematics of the South American cleptoparasitic bee tribe Caenoprosopidini, nothing had been recorded concerning the biology and host associations of its two monotypic genera, *Caenoprosopis* and *Caenoprosopina*, and their immature stages were unknown. As a result of two field trips (October–December 1989 and March 1990) to northern Argentina to study its rich fauna of panurgine bees, we encountered both *Caenoprosopis crabronina* Holmberg and *Caenoprosopina holmbergi* Roig-Alsina in association with the calliopsidine bee genera *Arhysosage* and *Callonychium* (Andrenidae: Panurginae), respectively. The purposes of this paper are to report on these associations, relate information about the mode of parasitism, and to provide descriptions of the oocytes and mature larvae of both species.

The discovery of the mature larvae of this tribe is propitious because a number of studies are appearing (Alexander, 1990; Roig-Alsina, 1987, in press) that test the cladistic relationships within the Nomadinae that were proposed earlier through studies of larvae (Rozen, 1966, 1977; Rozen et al., 1978). The early studies were limited because immatures of some of the included tribes were unknown. Larvae of *Caenoprosopis* and *Caenoprosopina* can now be incorporated into analyses of the Nomadinae.

The Nomadinae are here considered to consist of those taxa normally ascribed to it exclusive of the Protepeolini, Isepeolini, Osirini, and *Coelioxoides*. Roig-Alsina (in press, and references therein) through studies of adult features concluded that Osirini and *Coelioxoides* have affinities elsewhere. Further, he was unable to identify synapomorphies uniting the Protepeolini and Isepeolini with the Nomadinae. Rozen (in prep.), examining first instars of known parasitic anthophorids, concluded independently that the Protepeolini and Isepeolini (larvae of Osirini and *Coelioxoides* are still unknown) did not

share a common cleptoparasitic ancestor with one another or with the Nomadinae.

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Dr. Frank Koch, Museum für Naturkunde der Humboldt–Universität zu Berlin, DDR, kindly loaned types and specimens of *Callonychium minutum* (Fries) permitting the identification of one of the host species of *Caenoprosopina*.

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BIOLOGY OF CAENOPROSOPIS

We observed adults of *Caenoprosopis crabronina* near nests of two species of *Arhysosage* in northwestern Argentina. On November 7, 1989, a female briefly investigated the nest entrance of *Arhysosage* species near *ochracea* (Fries)³ at El Desmonte, Catamar-

³ Females from this population possess extensive black integumental coloration, in contrast to typical pale females of *ochracea*. Collections from other localities also showed remarkable population variation in female color patterns correlated in some cases with distinctive mandibular shapes in males. These facts suggest that collections of associated males and females (especially copulating pairs) may reveal the existence of more than one species similar to *ochracea*. Moure (1958) already commented on the extensive range of color pattern of this nominal species.

ca Province. The nest was in a seldom-used, unpaved, and unimproved roadway bordered on one side by a fence row of *Opuntia*, a food source of *Arhysosage*. In the early stages of construction, the nest consisted of only the upper part of the main burrow. When we returned on November 23, we found a number of *Arhysosage* nests along the same short section of roadway, observed several adult *Caenoprosopis* flying over the nesting area, and captured a female *Caenoprosopis* seen entering and emerging from a nest. Neither this nest nor five others contained immatures of *Caenoprosopis*. The nests, each consisting of either one or two cells, were obviously in the early stages of construction. Hence the absence of immature *Caenoprosopis* cannot be interpreted to mean that the cuckoo bee is not a parasite of this species of *Arhysosage*. *Liopoeum argentina* (Joergensen) and *L. mendocinum* Joergensen, also nesting in the roadway in sparse numbers, might also have hosted *Caenoprosopis*.

We definitely associated *Caenoprosopis crabronina* with *Arhysosage flava* Moure at Cruz Quemada about 40 km south of Güemes, Salta Province. Here we observed a male of *Caenoprosopis* sitting on the tumulus of *Arhysosage flava* on November 10, 1989, when the *Arhysosage* were starting to nest. We marked a number of nests for later excavation, and, on our return on November 20, 1989, we studied four nests. In one we discovered two early last instars of the cleptoparasite and one very small, probably first instar. The two last instars completed feeding in an artificial container, defecated, and, by December 3, 1989, were postdefecating. One soon became quiescent and obviously had started to overwinter. The other continued to move slowly but died and was preserved on December 26, 1989. When it was dissected, the pupal integument was clearly visible indicating that the specimen had not entered diapause and had continued to develop before dying.

Six cells from the site had small to large irregular holes "chewed" into their walls suggesting that *Arhysosage* females had excised and destroyed eggs of *Caenoprosopis* (similar defense measures have been reported against other nomadines; see Rozen, 1986b). Other cells had puncture marks in the walls that

may have been egg insertion holes. Only one cell, containing a *Caenoprosopis* larvae, had a small hole in the ceiling into which was embedded a shriveled chorion of *Caenoprosopis crabronina*. The chorion (length 0.65 mm) was approximately the same size as that of the oocyte described below. It had an oval opening 0.19 mm in maximum diameter at the anterior end that was flush with the cell wall. The soil surrounding the hole was somewhat more water-retardant than the cell wall elsewhere, presumably as a result of the female parasite using a hydrofuge secretion to moisten soil to chink the hole around the embedded egg. The chorion was clear, cellophanelike, lacked microscopic sculpturing, and possessed a small hooklike projection (also found on the oocyte) attached next to the opening.

A female preserved in Kahle's solution from El Desmonte, Catamarca Province, had six ovarioles per ovary, and each contained a mature oocyte. The specimen had an egg index (ratio of length of largest oocytes to distance between the outer margins of the tegulae; Alexander and Rozen, 1987, modified from Iwata, 1955) of 0.40 mm. The oocytes (fig. 15) (length 0.78 mm, maximum diameter 0.24 mm, $N = 1$) were white. Each possessed a shiny unpigmented chorion, lacked both an operculum and corrugations found on the oocytes of some Nomadinae, and bore a single small hooked projection ("nipple" of Alexander and Rozen, 1987) at the more-rounded anterior end. (Eggs of bees are deposited posterior end first; the anterior ends of oocytes develop anteriorly in the ovarioles.) This oocyte was similar to that of *Caenoprosopina holmbergi* (fig. 14) described below and nearly identical to the oocytes of some species of *Nomada* (illustrated for *Nomada vicina* Cresson, Alexander and Rozen, 1987: fig. 3).

The small larva had already ingested a considerable amount of food, so that the body was distended. It appeared to be a first instar and agreed closely with the first instar of *Caenoprosopina* discussed below. However, without knowledge of the anatomy of subsequent instars, we cannot determine its stage with certainty, particularly because some of its features are not as highly modified as those of *Oreopasites* (Rozen, 1954) and certain oth-

er Nomadinae (e.g., Epeolini, Rozen, 1989). Its head capsule was unpigmented, and the mandibles were very sharp-pointed and only moderately long, not as elongate as those of *Oreopasites*. The head, although somewhat prognathous, was constricted at the rear. Labral tubercles were elongate and forward directing, and the antennae, inconspicuous. The abdominal apex bore a pair of terminal, low, posteroventrally directed protrusions (the pygopod). This obviously hospicidal larva will be described in detail (with that of *Caenoprosopina*) in a comparative study planned by Rozen on first instars of the Nomadinae.

BIOLOGY OF *CAENOPROSOPINA*

Tentative associations of *Caenoprosopina holmbergi* with species of *Callonychium* were made a number of times. The first hint of this association was at El Desmonte on November 7, 1989, where we found several individuals of *Caenoprosopina*. The only potential hosts in an appropriate size range were an undescribed species of *Callonychium* sensu stricto and one of the *Callonychium* subgenus *Paranychium*. We again encountered *Caenoprosopina holmbergi* at a small nesting site of another unnamed species of *Callonychium* s.s. at 6 km east of Embarcación, Salta Province, on November 16, 1989, but the nests were so few that no immatures were discovered. We saw many *Caenoprosopina holmbergi* adults examining nest tumuli of *Callonychium* (*Paranychium*) *minutum* (Fries)⁴ and of still another new species of *Callonychium* s.s. at Copacabana near Tinogasta, Catamarca Province, on November 28, 1989. Although our excavations yielded no larvae, so many adult cuckoo bees were seen to penetrate tumuli, at least of *C. minutum*, that

this association was nearly certain. A definite association of *Caenoprosopina holmbergi* and *Callonychium minutum* was made at Belén, Catamarca Province, on November 30, 1989, when we excavated a first instar of *Caenoprosopina* attacking the young host larva. Unfortunately no egg insertion holes, vacated chorions, or other larval instars were discovered here.

Three postdefecating parasitic bee larvae described below were excavated while we studied the nests of a large *Callonychium* s.s. and of *Callonychium* (*Paranychium*) *minutum* at Amaicha del Valle, Tucumán Province, on March 6 and 12, 1990. For reasons related below, these three larvae were almost certainly associated with *C. minutum*. The wall of the cell from which one larva was removed displayed small, irregular-size fecal pellets over much of its surface.

From the above information we believe that *Caenoprosopina* attacks the cells of more than one species of the genus *Callonychium*. However, we did not encounter *Caenoprosopina holmbergi* at all nesting sites of the various species of *Callonychium*. An extensive nesting site of another unnamed *Paranychium* near Tumbaya, Jujuy Province, on November 19, 1989, lacked cuckoo bees of any sort.

A female of *Caenoprosopina holmbergi* from 6 km east of Embarcación, Salta Province, preserved in Kahle's solution had 6 ovarioles per ovary, each ovariole containing a mature oocyte. The egg index was 0.48. The grayish white oocytes (fig. 14) (length 0.49 mm, maximum diameter 0.11 mm, N = 1) were relatively more slender than those of *Caenoprosopis crabronina*. They possessed a clear, somewhat shiny, unpigmented chorion

⁴ Fries (1906) described *Callonychium* (*Paranychium*) *minutum* as *Camptopoeum minutum* from a single female "von Salta 2500 mtr.; Steinbach leg. N. Argentina." In order to correctly identify specimens of this species, JGR borrowed six specimens identified by Fries in the Museum für Naturkunde der Humboldt-Universität zu Berlin. The borrowed specimens included one male bearing a purple "Type" label and a female and male with orange "Typus" labels. None of these specimens were from Salta, although the data on the male "Type" matched those recorded by Fries (1908) in the subsequent description of the supposed male of *minu-*

tum. The two "Typus" specimens were collected in 1910, after the publication of the name. Among the other three borrowed specimens was a single female with the following data: "Argentina, Salta, 3. 1905, Steinbach." Although it lacks a type label and was identified as *minutum* by Fries in 1909, the collection data substantiate that it is the holotype. This specimen agrees with the females referred to as *minutum* in this study. However, males from this study (some collected *in copula* with females) are not conspecific with Fries's purple "Type" specimen, an indication that Fries had misidentified the male of another species of *Paranychium*.

that might have been denticulate. The anterior end exhibited a small, hook-shaped projection, similar to that of *Caenoprosopis crabronina*.

The first instar of this species was similar to that of *Caenoprosopis*, described above, and will be treated in detail in a comparative study of nomadine first instars.

MATURE LARVAE OF THE CAENOPROSOPIDINI

DIAGNOSIS: Not surprisingly, the mature larvae of *Caenoprosopis crabronina* and *Caenoprosopina holmbergi* possess most of the larval synapomorphies of the Nomadinae including paired labral tubercles, greatly fused and reduced labiomaxillary region, weak internal ridges of the head capsule, weak tentorium, and posterior tentorial pits not arising from the junction of the posterior thickening of the head and the hypostomal ridges. Unlike members of the *Brachynomada* group (Roig-Alsina, in press, i.e., the *Melanomada* complex of Rozen et al., 1978) but like most of the other Nomadinae, the Caenoprosopidini exhibit a sloping vertex (in lateral view), unusually short mandibles, a weakly defined posterior margin of the head capsule, and two transverse lines seeming to represent the posterior margin. The tribe can be distinguished from the Holcopasitini (*Holcopasites*) because it lacks a spiculated hypopharynx and spiculated patch on the venter of abdominal segment X (Rozen, 1966). Unlike the Caenoprosopidini, the Epeolini have a spiculated hypopharynx and their spiracular atria exhibit elongate spines. *Nomada* has a labrum that is strongly projecting and a spiculated, dorsoventrally long hypopharynx, in contrast to those of the Caenoprosopidini. The frontoclypeal region of *Caenoprosopis* does not overhang a small labrum as is characteristic of both the Biastini (*Neopasites*) and Neolarrini (*Neolarra*), but this feature is difficult to interpret for *Caenoprosopina* because of the indistinct labral-clypeal boundary. In contrast to the situation in these two tribes, the hypopharynx of larval caenoprosopidines protrudes beyond the labium in lateral view. Caenoprosopidini seem most similar to the known Ammobatini, which can also be differentiated from the taxa

listed above by the same features (Rozen and McGinley, 1974). Indeed, there is no single feature or set of features that will distinguish the Caenoprosopidini from all Ammobatini. In the key to the Ammobatini genera (Rozen and McGinley, 1974), *Caenoprosopis* runs to couplet 3(2) and most easily to *Oreopasites*. However, *Caenoprosopis* has more widely set labral tubercles than does *Oreopasites* (Rozen, 1954). *Caenoprosopina* does not readily run in the key.

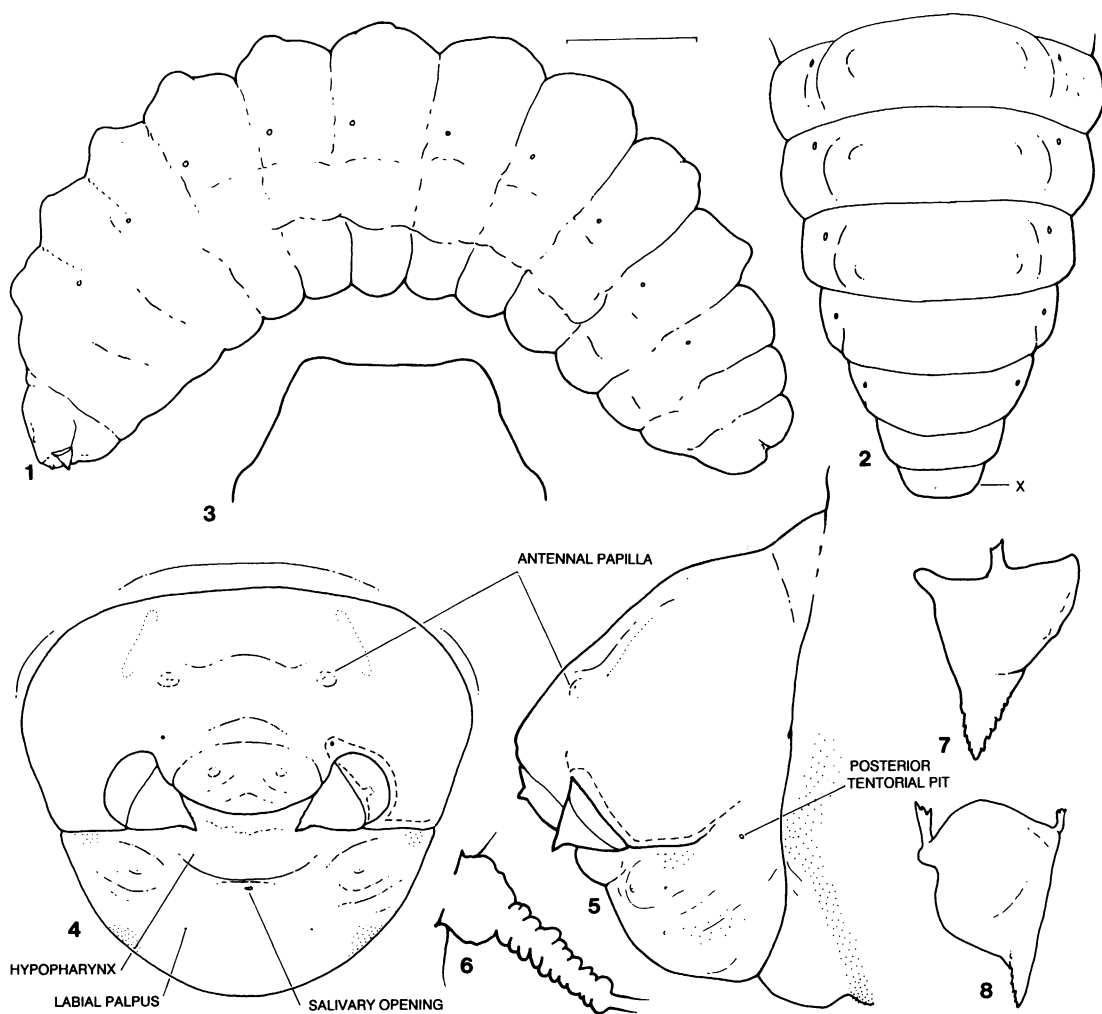
Caenoprosopis crabronina Figures 1–8

DIAGNOSIS: Although the mature larvae of *Caenoprosopis crabronina* and *Caenoprosopina holmbergi* show many similarities, as indicated above, they are also quite distinct from one another. *Caenoprosopis* possesses obscure antennal papillae (figs. 4, 5), spicules on the labiomaxillary region (fig. 5), produced dorsolateral swellings on most body segments (figs. 1–3), deeply incised intersegmental lines on the lateral body swellings (fig. 2), and a normally protruding venter of abdominal segment X (fig. 1). Not only is the larva of *Caenoprosopina* much smaller, but it has: large, projecting antennal papillae (figs. 12, 13), a nonspiculate labiomaxillary region (fig. 13), a smooth lateral body outline as viewed from above (fig. 10) because the intersegmental lines do not invade the lateral body swellings, and an elongate venter of abdominal segment X (fig. 9). Further, it lacks dorsolateral swellings on its body segments (fig. 11).

TOTAL LENGTH: Approximately 6.5 mm.

HEAD (figs. 4, 5): Integument of head capsule with widely scattered minute nonsetiform sensilla, nonspiculate except for a few spicules on maxilla immediately below hypostomal ridge and for a few on sides of labiomaxillary region; epipharynx and hypopharynx nonspiculate. Integument weakly pigmented, except apices of mandibles darkly pigmented and hypostomal and pleurostomal ridges moderately pigmented.

Head size normal in relation to rest of body; maximum head capsule width much greater than length from top of vertex to level of hypostomal ridges in frontal view. Tentorium extremely thin, but apparently com-



Figs. 1–8. *Caenoprosopis crabronina*, mature larva. 1. Entire larva, live, lateral view. 2. Abdominal segments IV–X, dorsal view. 3. Dorsum of abdominal segment II at maximum elevation, anterior view. 4, 5. Head, frontal and lateral views. 6. Spiracle, side view. 7, 8. Right mandible, inner and ventral views. Scale (=1 mm) refers to figures 1, 2.

plete; anterior tentorial pit very small, low on face, close to mandibular precoila; posterior tentorial pit small, in line with hypostomal ridge but posterior part of ridge curving upward and fading so that pit seems below ridge and not associated with it; pit anterior to posterior margin of head; posterior margin of head capsule bearing two faint transverse lines, much as in *Nomada* and in most Ammobatini (Rozen and McGinley, 1974); posterior thickening of head capsule not developed; median longitudinal thickening of head capsule at most only vaguely visible dorsally;

hypostomal ridge moderately developed anteriorly but becoming obscured posteriorly, without dorsal ramus; pleurostomal ridge moderately developed; moderately developed epistomal ridge evident only below and laterad of anterior tentorial pits, absent between pits; external epistomal depression not evident between anterior pits. Parietal band scarcely evident. Antennal prominence undeveloped; antennal disc moderate in size; papilla scarcely projecting, bearing two sensilla. Vertex sloping as seen from side and grading into frontal area, without unusual

projections or tubercles; clypeus short as seen in frontal and lateral views, with lower margin at about level of anterior tentorial pits; frontoclypeal area normal in lateral view, not produced as a bulge beyond base of labrum as is characteristic of *Neopasites* and *Neolarra* (Rozen, 1966). Labrum in lateral view not strongly projecting, somewhat small, and recessed so as not to project beyond clypeus; labral sclerite not evident; paired labral tubercles arising from labral disc and not from lower (anterior) margin, small but distinct, moderately widely separated; labrum not emarginate apically; epipharynx not produced ventrally as in *Nomada* (Rozen, 1966).

Mandible (figs. 7, 8) small, short, robust at base, tapering apically, without spiculation; mandibular apex finely serrate on both dorsal and ventral edges; adoral ventral surfaces massively produced as in *Ammobates carinatus* Morawitz (Rozen and McGinley, 1974). Labiomaxillary region recessed and greatly fused, so that maxillae only vaguely distinct from labium; maxilla a vague swelling on side of head; maxillary sclerites not discernible; maxillary palpus small, shorter than basal diameter, but evident; galea absent. Labium not divided into prementum and postmentum; premental sclerite not defined; labial palpus not produced, apparently represented by single sensilla. Salivary opening small, oval, without lips; hypopharynx projecting beyond labium, rounded in lateral view and not bilobed.

BODY: Integument without setae, distinctly spiculate laterally and ventrally on prothorax and ventrally on other body segments except for abdominal segments VIII to X; spicules on anterior part of body tending to be well developed, sharp-pointed; integument of postdefecating form wrinkled. Body without spines or sclerotized tubercles. Body form moderately slender, tapering somewhat both anteriorly and posteriorly, nearly identical to that of *Oreopasites* (Rozen, 1954) and *Morgania histrio transvaalensis* Bischoff (Rozen and McGinley, 1974); intersegmental lines deeply incised; these lines also defined laterally so that, when viewed from above, profile (fig. 2) of body scalloped (as in *Morgania histrio transvaalensis*, Rozen and McGinley, 1974: fig. 19) rather than nearly smooth as in *Caenoprosopina holmbergi* (fig. 10) and

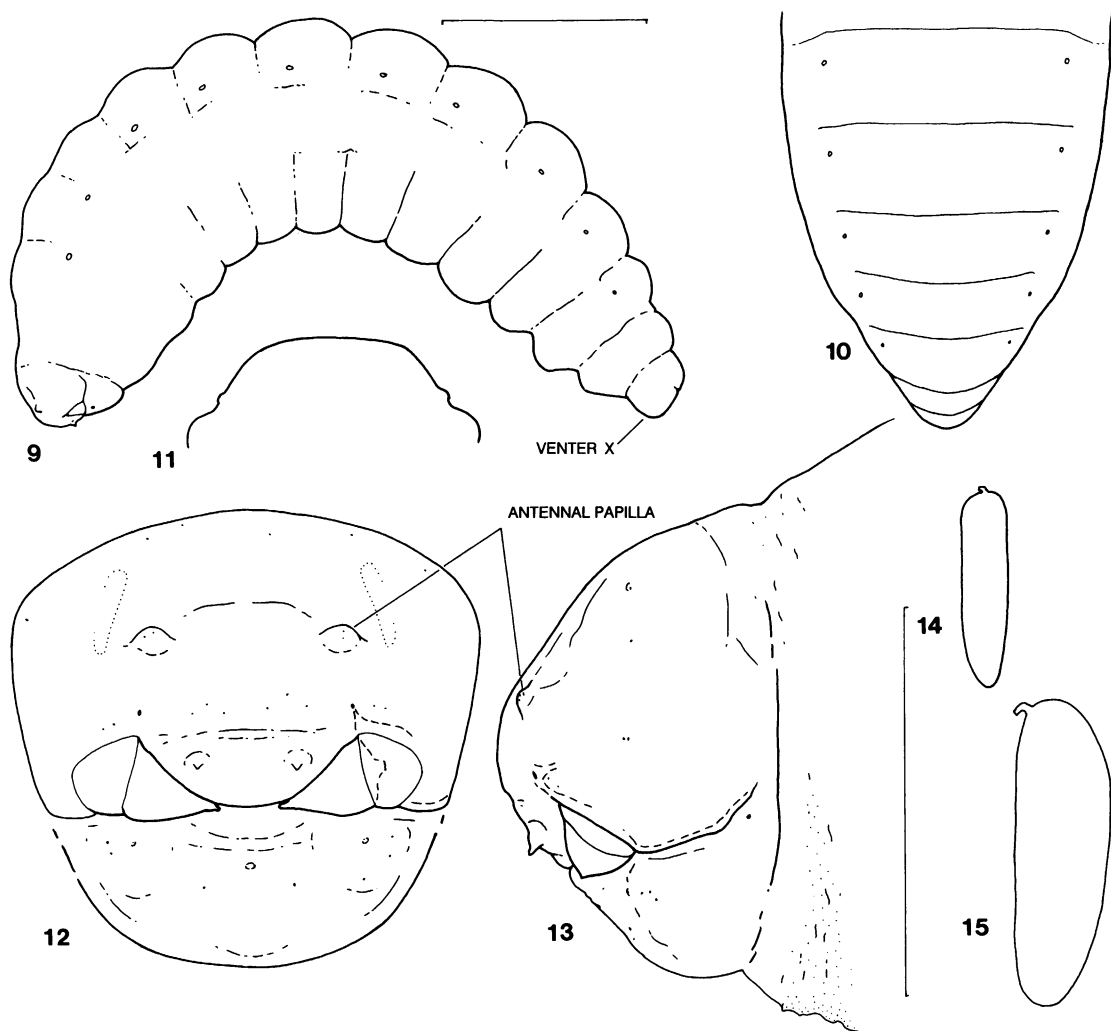
Ammobates carinatus (Rozen and McGinley, 1974: fig. 11); intrasegmental lines not evident; most body segments with dorsolateral elevations that are neither sufficiently high nor well defined to be considered true tubercles; swellings below spiracles present (as in most Ammobatini); venter of abdominal segments IX and X not produced; abdominal segment X moderate in length and in lateral view attached to middle of preceding segment; dorsal surface of segment X rounded, without ridges; anus apical. Spiracle (fig. 6) moderate in size, without spiracular sclerite; thoracic spiracles somewhat smaller in diameter than anterior abdominal spiracles, but posterior abdominal spiracles decreasing in diameter; peritreme flat; atrium projecting above body wall, globose, bearing irregular annulations but no spines or other ornamentation; primary tracheal opening apparently with low collar; subatrium moderate in length, containing approximately 10 chambers that are irregular in size. Sexual characteristics unknown.

MATERIAL STUDIED: Two postdefecating larvae, Cruz Quemada, Salta Province, Argentina, collected as early last instars on November 20, 1989; preserved as postdefecating larvae December 1989 (J. G. Rozen, A. Roig-Alsina) from nests of *Arhysosage flava*.

Caenoprosopina holmbergi

Figures 9–13

The identification of two of the larvae described below was at first uncertain because they were not collected in association with adults of *Caenoprosopina* or even with host larvae. However, tentative identification was based on the facts that: (1) the larvae possess many nomadine features, (2) there are no other known nomadine parasitic bees in Argentina of such small size, (3) the small cell from which one was taken lacks a cell lining as is characteristic of *Callonychium*, and (4) these larvae are similar (but not identical) to those of *Caenoprosopis*. On a subsequent visit, we recovered a few *Caenoprosopina* adults and a third postdefecating larva from where *Callonychium* (*Paranychium*) *minutum* was actively nesting and from the same shallow depth as *Callonychium* cells. These facts further support the identification of these larvae and the association of host and parasite.



Figs. 9–13. *Caenoprosopina holmbergi*, mature larva. 9. Entire larva, live, lateral view. 10. Abdominal segment IV–X, dorsal view. 11. Abdominal segment II at maximum elevation, anterior view. 12, 13. Head, frontal and lateral views.

Figs. 14, 15. Oocytes of the *Caenoprosopidini*, side view. 14. *Caenoprosopina holmbergi*. 15. *Caenoprosopis crabronina*.

Scales (=1 mm) refer to figures 9–11 and to figures 14, 15, respectively.

DIAGNOSIS: See diagnosis of *Caenoprosopis crabronina*.

TOTAL LENGTH: Approximately 3.5 mm.

HEAD (figs. 12, 13): As described for *Caenoprosopis crabronina* except for the following: Some sensilla slightly elongate and therefore minutely setiform; integument completely nonspiculate.

Tentorium extremely thin but definitely complete except for dorsal arms; median lon-

gitudinal thickening of head capsule absent; hypostomal ridge moderately pronounced, more distinct than other internal ridges of head capsule, angling upward just before posterior tentorial pit; pleurostomal ridge weakly developed; epistomal ridge weakly developed below and laterad of anterior tentorial pits, absent between pits; antennal disc apparently enlarged compared with that of *Caenoprosopis* and papilla enlarged, occupying much

of disc, and protruding, in contrast to antennal papilla of *Caenoprosopis*. Clypeus perhaps somewhat short but labral-clypeal boundary indistinct and therefore feature difficult to evaluate; frontoclypeal area (fig. 13) in lateral view perhaps slightly produced beyond base of labrum but indistinct labral-clypeal boundary making this feature difficult to interpret.

Mandibles apparently with basal adoral surface less produced than that of *Caenoprosopis*. Labiomaxillary region even more fused than in *Caenoprosopis*; hypopharynx projecting only slightly beyond labium and hypopharyngeal groove poorly defined.

BODY: As described for *Caenoprosopis crabronina* except for following: Intersegmental lines only moderately incised and not extending laterally on most body segments so that, when viewed from above, profile of body smooth much as in *Ammobates carinatus* (Rozen and McGinley, 1974: fig. 11); in contrast to *Caenoprosopis*, body segments without dorsolateral elevations (fig. 11); venter of abdominal segment IX not produced (also true in *Caenoprosopis*) but venter of abdominal segment X produced posteriorly though nonspiculate. Spiracular atrium smooth, without annulations; subatrial chambers more uniform in size than those of *Caenoprosopis*.

MATERIAL STUDIED: Three postdefecating larvae, Amaicha del Valle, Tucumán Province, Argentina, March 6, 12, 1990 (J. G. Rozen and A. Roig-Alsina).

DISCUSSION

The information presented here confirms that the *Caenoprosopidini* are *Nomadinae* (as defined above). This is revealed by the facts that their eggs (at least of *Caenoprosopis*) are embedded in the cell walls, their hospicidal first instars exhibit the major features of known first instars of *Nomadinae*, and the mature larvae of *Caenoprosopis* and *Caenoprosopina* possess numerous apomorphic features of larval *Nomadinae*.

The close similarity of the mature larvae of *Caenoprosopis* and *Caenoprosopina* to the larvae of the *Ammobatini* and the synapomorphy of the nonspiculated hypopharynx (in the context of the cladogram presented by Rozen et al., 1978, and also Alexander, 1990:

figs. 1 and 2) support the hypothesis that the *Caenoprosopidini* and *Ammobatini* are sister groups (Roig-Alsina, 1987). So similar are the larvae of these two groups that larval characters alone do not seem to justify separating them. For example, the larvae of *Oreopasites* and *Caenoprosopis* are nearly identical. *Oreopasites* can be recognized only because the maxillary palpi are slightly larger (as long as or longer than their basal diameters) and the labral tubercles less widely separated. By contrast, larvae in each of the two tribes reveal considerable generic variability. Our knowledge of ammobatine larvae is restricted to four genera (*Oreopasites*, *Morgania*, *Ammobates*, and *Pseudodichroa*), and the systematics of the large, mostly Old-World tribe need revision. The descriptions of the larvae of the *Caenoprosopidini* presented here should be viewed as grist for future analysis perhaps when the *Ammobatini* are revised and the relationships of the *Ammobatini* and *Caenoprosopidini* are reconsidered.

Roig-Alsina (1987), Roig-Alsina (in press), and Alexander (1990) have pointed out several apparent incongruencies between the cladistic analysis of the *Nomadinae* based on known mature larvae (most recently Rozen et al., 1978) and their own investigations using various suites of adult features. Studies of the larvae of the *Caenoprosopidini*, so similar to immature ammobatines, unfortunately do not address these incongruencies.

The single hooked projection on the egg and oocyte of the *Caenoprosopidini* is somewhat surprising considering the close agreement (based on larvae and adults) of the tribe to the *Ammobatini*, which have eggs and oocytes possessing anterior opercula rather than single hooks (Rozen and Michener, 1968; Rozen, 1986a, 1986b; Alexander and Rozen, 1987). In addition to some *Nomada* and the *Caenoprosopidini*, *Holcopasites eamia* Cockerell and *Brachynomada* species near *argentina* Holmberg possess single small, hooked projections on the anterior ends of their eggs (new information). The wide distribution of this feature in the *Nomadinae* suggests that it may be the plesiomorphic state and the conditions found in the *Ammobatini*, *Neopasites* (Torchio et al., 1967), and *Epeolini* (Bohart, 1966; Rozen and Favreau, 1968; Torchio, 1986) may represent derived states.

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