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Immature Stages of and Ethological Observations on the Cleptoparasitic Bee Tribe Nomadini (Apoidea, Anthophoridae)

JEROME G. ROZEN, JR.¹

ABSTRACT

The mature larvae of the North American cleptoparasitic bees *Melanomada sidaefloris* (Cockerell), *Triopasites penniger* (Cockerell), and *Paranomada velutina* Linsley, and the pupae of *M. sidaefloris*, *P. velutina*, and *Nomada* species are described taxonomically. Cladistic analysis of the characteristics of these mature larvae demonstrates that *Melanomada*, *Triopasites*, *Paranomada*, and probably the South American *Kelita* are monophyletic and a sister group of the Ammobatini, *Nomada* Epeolini, *Holcopasites*, *Neopasites*, and *Neolarra*. Hitherto unreported host associations of various species of nomadine parasitic bees are as follows (host in parenthe-

ses): *M. sidaefloris* (*Exomalopsis* near *chlorina* Cockerell), *T. penniger* (*Exomalopsis compactula* Cockerell), *P. velutina* (*Exomalopsis solani* Cockerell), the South American *Brachynomada* near *argentina* Holmberg (*Psaenythia annulata* (Gerstaecker)). Biological data concerning egg deposition, larval habits, search behavior of adults, and other features are given concerning these parasitic taxa. In general the biological information conforms to what is known of other Nomadinae.

Triopasites pasitura (Cockerell, 1935) is synonymized with *T. penniger* (Cockerell, 1894).

INTRODUCTION

This paper provides comparative descriptions of the mature larvae of the rare North American cuckoo bee genera *Melanomada*, *Paranomada*, and *Triopasites* and also includes an account of the pupae of *Nomada*, *Melanomada*, and *Paranomada*. In addition, ethological notes on these genera and on the South American genus *Brachynomada* are given. An expanded interpretation of the phylogeny of the tribe and its relation to others of the subfamily based on the larvae described here, those treated in Rozen (1966), and

Ehrenfeld and Rozen (1977) concludes the paper.

The Nomadini, consisting of approximately 10 genera, most of which contain only a few species, have a limited distribution. *Nomada*, an exception, contains hundreds of species and is abundantly distributed in the Holarctic Region, but sparsely in the Southern Hemisphere.

My research for this paper spanned many years and was centered at the Southwestern Research Station of the American Museum of

¹Deputy Director for Research and Curator of Hymenoptera, the American Museum of Natural History.

Natural History in the southeast corner of Arizona. While visiting the Station in 1966, my wife and I excavated a nest of *Exomalopsis compactula* that had been invaded by several adult *Triopasites penniger*. We recovered two larvae of the parasitic bee from it. The following year, ably assisted by Ms. Gisela Krueger, I recovered a number of larvae similar to those of *Triopasites* from a nest of *Exomalopsis solani* several miles from the *Triopasites* site. We reared these and they turned out to be *Paranomada velutina*. So similar were the larvae of these two parasitic bees that I decided that the *Triopasites-Exomalopsis* association of the previous year may have been spurious, and that possibly I had obtained *Paranomada* from both sites. In 1976 I associated *Melanomada sidaefloris* with *Exomalopsis* near *chlorina* and discovered that the mature larva of *Melanomada* was remarkably similar to the other two lots collected 10 years earlier. This led to a careful re-examination of the anatomical differences among all three lots. As a result I now conclude that each lot does contain a distinct and separate taxon.

In addition to the two persons mentioned above who assisted in the field work, I thank Mr. Ronald J. McGinley for his efforts in finding and excavating the nest containing the *Melanomada*. A number of people contributed to the illustrations presented here: Mrs. Marjorie Favreau, Mr. Ronald J. McGinley, and Mrs. Barbara Rozen. The importance of the Southwestern Research Station for long-term ethological research on natural populations cannot be overemphasized. Without such a base of operation our knowledge of many groups of North American bees would be far less than it is now. I thank Mr. Vincent Roth, Resident Director of that Station, for his hospitality on my numerous visits there.

A major problem has been the proper identification of parasites and host bees. The following people have contributed either by lending specimens or by providing identifications: Dr. Paul H. Arnaud, California Academy of Sciences, San Francisco; Dr. Paul D. Hurd, Jr., Smithsonian Institution, Washington, D.C.; Dr. Charles D. Michener, The University of Kansas, Lawrence; Dr. Daniel Otte, The Academy of Natural Sciences of Philadelphia, Pennsylvania; Professor P.

H. Timberlake, Division of Biological Control, University of California, Riverside.

Larvae and adults of hosts and cleptoparasites, as well as cells and cocoons of host, are in the American Museum of Natural History.

The research was supported by National Science Foundation Grant no. GB32193.

ETHOLOGICAL OBSERVATIONS

Most of this section of the paper records information on *Melanomada sidaefloris*. In subsequent subsections, however, fragments of information are included on *Paranomada*, *Triopasites*, and *Brachynomada*. Biological information on *Kelita*, a related Chilean genus, is given by Rozen (1970) and Ehrenfeld and Rozen (1977). Little other information is available concerning the ethology of the Nomadini, except for *Nomada*, biological data of which have been published in many places and summarized by Bohart (1970).

Melanomada sidaefloris (Cockerell)

The type of *M. sidaefloris* is a male; only females were collected during the course of this study. These females agree with the type in every possible respect (including dense, decumbent plumose setae on the venter of mesosoma) although certain identification will require comparisons of the same sexes. Further, the type was collected at Mesilla, New Mexico, only 130 miles from the nesting site, on the flowers of *Sida*, which also grow at the nesting site. These geographic and ecological factors seem to support this identification. Females from the nesting site are not conspecific with the female of *M. heleniella* (Cockerell) or the male type and female specimens identified by Cockerell of *M. grindeliae* (Cockerell), the other two named species in the genus.

Adult females of this species were first observed flying over the barren, slightly sloping shoulder of a dirt roadway 26 miles south of Animas, Hidalgo County, New Mexico, on September 11, 1976. Adults of *Zacosmia maculata* (Cresson), *Holcopasites apacheorum* Hurd and Linsley, *Nomada* species, *Triepeolus* (two species), and *Sphecodes* species were often seen in the same area.

In addition to *Exomalopsis* near *chlorina*

Cockerell, the host of *M. sidaefloris*, *E. sidae* Cockerell also nested alongside the roadway¹; two nests of *E. sidae* were found within 2 meters of the nest entrance of *E. near chlorina*. The burrow entrances of both species were briefly investigated by females of *M. sidaefloris*. I excavated the single nest *E. chlorina*, and recovered the mature larvae of *M. sidaefloris* described below. McGinley carefully dissected both nests of *E. sidae*, one of which contained only four or five cells with *Exomalopsis* larvae; the other nest had no larvae. On the basis of this information, I cannot determine whether *M. sidaefloris* is restricted to *E. near chlorina* or whether it is a parasite of both species of *Exomalopsis*.

Nesting Biology of Host. The nest entrance and main tunnel of *E. near chlorina* were open and no tumulus was present. About 3 mm. in diameter, the main burrow descended vertically with some irregular turns. At a depth of 4 cm. and again at 10 cm. it branched, each case giving rise to a short (3 and 5 cm.) obliquely descending burrow that ended blindly. The first cell, 27 cm. deep and connected to a 7 cm. lateral, was open and partially filled with soil. All other cells were clumped from about 32 to 56 cm. and extended outward within a radius of about 9 cm. from the imaginary vertical continuation of the main burrow. All laterals were filled with soil except for those leading to open cells; open laterals meandered considerably.

Cells (fig. 1) were approximately 7.5 mm. long and 4.5 mm. in maximum diameter. Tilted approximately 45 degrees and with the closure end higher than the rear, the cell had a floor somewhat flatter than the curving ceiling. Smooth and shiny, the cell surface was obviously waterproofed with a thin layer of transparent material, but there was no clear evidence of a "built-in" cell-lining as reported for *Exomalopsis chionura* Cockerell (Rozen and MacNeill, 1957). The closure was an unusually flat spiral being only slightly concave on the inside; it exhibited a depression in the middle, perhaps where the tongue of the bee was last removed while forming the closure.

¹ Both species of *Exomalopsis* were identified by P. H. Timberlake.

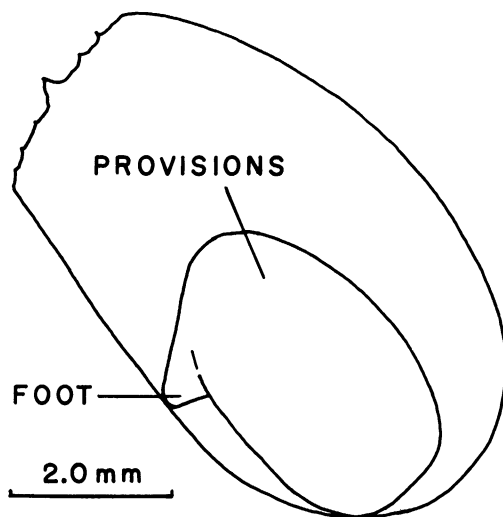


FIG. 1. Cell and provisions of *Exomalopsis near chlorina*, side view.

Over 24 hours, five females were collected emerging from the burrow and probably represent the entire adult population of the nest. No males were found within the nest.

Provisions (fig. 1) were shaped in the characteristic form of those of *E. chionura* (Rozen and MacNeill, 1957, figs. 1-4) and were approximately 4.0 mm. long and 3.0 mm. wide. A semi-solid, the food mass rested with the rounded end affixed to the lower rear of the cell by moisture, with the "foot" touching the cell floor. It should be noted that the diagram presented by Stephen, Bohart, and Torchio (1969, fig. 293) has the food erroneously oriented; *Exomalopsis chionura* like *E. near chlorina* had the food mass positioned as shown in figure 1.

The young *Exomalopsis* larva, as it fed, circled the food mass and left a channel behind it. The "foot" of the mass was quickly consumed so that even small larvae were found circling a pillar of food attached only at the rear of the cell.

Before finishing feeding, the last instar started defecating. Cocoon spinning apparently commences after food is consumed, but while the larva is still defecating, because, in addition to smears of fecal materials pressed to the cell wall enclosure feces were incorporated somewhat un-

evenly in the cocoon fabric. The cocoon was translucent whitish where no feces occurred, but the cocoon appeared yellow elsewhere because of the feces. The cocoon fabric was thin, one-layered, fragile, but not obviously fenestrated; it occupied the entire lumen of the cell.

Ethology of Melanomada. In searching for host nests, female *M. sidaefloris* flew moderately swiftly close to the ground. They tended to investigate one area by flying in a meandering fashion over it. They would then dart swiftly, in a nearly straight line, without slowing or stopping, to a new area which they would explore with a meandering flight. Although essentially the same size and color pattern as *Holcopasites apacheorum*, females of *M. sidaefloris* could be distinguished in flight by their more rapid flight with swift passage to a new area for exploration. *Holcopasites apacheorum* females flew slower, meandered more or less continuously, often retraced just-explored areas, and rarely departed to a new section in a straight-line flight. Both species stopped briefly at burrow entrances, which presumably had the attributes of the entrances of the appropriate hosts.

A female of *M. sidaefloris* entered a burrow of *E. near chlorina* and another, the burrow of *E. sidae*, although in neither case did she remain in the nest sufficiently long to oviposit.

Although no eggs of *Melanomada* were found, two parasitized cells exhibited an oblique slit in the cell wall, similar to egg-deposition slits made by *Nomada*, *Kelita* (Rozen, 1970), and especially *Holcopasites* (Rozen, 1965, fig. 3). Both slits were less than 0.5 mm. from the cell closure and possessed an elongate flap of earth and cell lining about 0.5 mm. long attached along one side. In each case the hinge or the flap was the part closest to the cell closure. There is little doubt that *Melanomada* deposits its eggs as do the other genera mentioned above.

The first larval instar, although not discovered, is presumed to possess elongate mandibles as is characteristic of other Nomadini (and indeed most members of the subfamily). However, no data are available on the activities of the feeding larvae. Mature, predefecating larvae and one intermediate-size larva of *Melanomada* possessed bright yellow Malpighian tubules, a characteristic of the subfamily and also of at least

predefecating larvae of known Exomalopsini and Melitomini.

The nest of *E. near chlorina* contained 53 cells with contents as follows:

Cells with <i>Exomalopsis</i> near <i>chlorina</i>	
Occupied cocoons	20
Vacated cocoons	2
Feeding larvae	7
Total	<u>29</u>
Cells with <i>Melanomada sidaefloris</i>	
Postdefecating larvae	3
Defecating larva	1
Mature, predefecating larvae	5
Feeding larva	<u>1</u>
Total	10
Other Cells	
Open cells	4
Moldy cells	7
Meloid larva	1
Other	<u>2</u>
Total	14

Because most feces of exomalopsines are deposited before or during cocoon spinning, the occupied cocoons (20) contained postdefecating larvae or at least larvae that were nearly in that condition. At first glance the distributions of developmental stages of host and parasite seem to be at variance. Specifically, the ratio of 20 quiescent, postdefecating larvae to seven feeding larvae of *E. near chlorina* seems markedly different from three postdefecating larvae (one of which was still active) to six defecating or predefecating larvae to one feeding larva of *M. sidaefloris*. That is to say, a large portion of parasites were still active compared with hosts. This might lead one to conclude that the parasite adult attacks host nests for only part of the season that the host is provisioning. Such conclusions, however, are tenuous because nothing is known concerning the comparative rates of development of host and cuckoo bees.

Melanomada sidaefloris larvae did not start voiding feces until all food had been consumed, in contrast to the hosts that started defecating during the last stadium while they continued to feed. In all cases where the orientation of the mature larva of the cleptoparasite was observed,

its head was closest to the cell closure. In two cells, the feces were plastered as elongate, semi-moist pellets to the rear and top of the cell, whereas the rest of the cell lining was free of such material. In contrast the host applied feces as elongate, moist pellets to the entire cell wall including the cell closure; as indicated above its feces are also incorporated in the cocoon fabric.

Melanomada sidaefloris, like all other known Nomadinae (except for *Protepeolus* and *Isepeolus*—condition for *Leiopodus* not known), does not spin a cocoon as reflected in the recessed labiomaxillary region of the mature larva. *Melanomada sidaefloris* overwinters as a totally quiescent, white larva. Several live larvae held in the laboratory pupated in May 1977.

Triopasites penniger (Cockerell)

Males of the *Triopasites* collected in the vicinity of the nest site of the host bee appear conspecific with the male type of *T. penniger* in the collection of The Academy of Natural Sciences of Philadelphia.

Two nests of *Exomalopsis compactula* Cockerell (kindly identified by P. H. Timberlake) were visited by *Triopasites penniger* at 5 miles north of Rodeo, Hidalgo County, New Mexico, between August 30, 1966 and September 3, 1966. These nests yielded two cells containing the larvae described in the present paper. Although this is the first definite host association of *Triopasites*, Cockerell had tentatively associated *Triopasites pasitura* (Cockerell), a junior synonym of *penniger*, New Synonymy, with *E. compactula* in 1935.

One cell had a thick covering of fecal material plastered over the cell wall, rear, and closure. In neither cell was there a cocoon. In another *Exomalopsis* cell was found an oval oviposition incision, 0.5 mm. long by 0.3 mm. wide, in the cell wall, about two-thirds the distance from the closure to the rear. A shriveled, somewhat moldy chorion, attached to what might have been a flap of cell lining affixed to the feces, was pulled away from the incision, a fact suggesting that the egg insertion had been similar to that of other Nomadini. It is not clear whether the cell had been inhabited by a postdefecating *Triopasites* larva or whether the egg had died and the *Exomalopsis* had matured.

Paranomada velutina Linsley

Both *P. velutina* and *P. nitida* Linsley and Michener are known from the vicinity of the Southwestern Research Station. *Paranomada velutina* is the far more commonly encountered species. Its males and females can be recognized by their dark integumental coloring and uninterrupted metasomal hair bands. A female reared from the nest is unquestionably *P. velutina* even though the type specimen is a male.

More than a dozen larvae, including all instars of this species, were excavated from a single large nest of *Exomalopsis solani* Cockerell, 1 mile north of Rodeo, Hidalgo County, New Mexico, on August 28, 1967 by the author and Gisela Krueger. Oviposition incisions were found in the cell walls of six cells: two midway to the rear of the cell, two just before the wall curved at the rear, one two-thirds of the way to the rear of the cell, and one just inside the cell closure. In most, the vacated chorion was still inserted in the incision. Only one of the six had a flap of cell lining and soil, 0.5 mm. long and 0.3 mm. wide, attached along one side to the cell wall as is characteristic of *Nomada* and *Melanomada*. As these incisions were examined in cells that had been preserved in the American Museum of Natural History for nine years, I cannot determine whether the flaps had accidentally broken off after excavation or whether the cleptoparasite does not normally leave a flap when ovipositing.

First instars possessed a pigmented, prognathous head capsule and elongate, sickle-shaped mandibles (as is characteristic of *Nomada*, *Oreopasites*, and indeed most Nomadinae) with which the host egg or early larval instar is killed. One *Paranomada* first instar was found in a cell containing a host egg and another was found in a cell with a dead, early instar host larva. Three mature larvae were kept alive: one pupated on June 29, 1968, and the adult emerged July 11, 1968; another died while trying to pupate and was preserved on May 23, 1969; and the last pupated on July 8, 1968, and was preserved with pigmented eyes on July 15, 1968.

This is believed to be the first definite host association of any species of *Paranomada*. However, Linsley (1945) recorded that P. H. Timberlake suggested that *Exomalopsis verbesinae*

Cockerell may be the host of *Paranomada californica* Linsley.

The adaptive significance of the dorsoventrally flattened body, especially of adult females of *Paranomada*, has been a mystery. I suggest that this body shape may enable adult cleptoparasites to appress themselves against burrow walls and thereby permit host adults, which nest communally, to pass without detecting the *Paranomada*. The highly polished integument of the vertex, scutum, and other areas as well as the posteriorly directed setae on the venter of the parasite would further assist passage. Although this is probably true, a question remains as to why *Melanomada* and *Triopasites* have normally convex bodies, as both of these genera are also associated with communally nesting *Exomalopsis*.

Brachynomada near *argentina* Holmberg

These specimens were identified by comparison with specimens in the collection at the Universidad do Paraná, Brazil, with the kind assistance of Padre J. S. Moure. They are similar to *B. argentina* but are darker and somewhat more densely punctate.

Three females of this species were collected flying near several nests of *Psaenythia annulata* (Gerstaecker) (identified by the author by comparisons with specimens in the collection of the Universidad do Paraná) at Furnas, Vila Velha, Paraná, Brazil, on February 9, 1974. One was trying to enter an open main nest burrow even though a plastic drinking glass had been inverted over the entrance. A first instar larva, almost certainly of this species, was found attacking an egg of the host in one cell of that nest, and another completed cell possessed an egg inserted in the cell wall. The egg, 0.9 mm. long and 0.3 mm. at the widest part near one end (presumably the anterior end) tapered gradually to the other end which was narrowly rounded. Unfortunately the egg, which was white and had a smooth chorion, was dislodged with a flap of earth and cell lining at the time of excavation and was still attached by its tapered end to the flap. The flap had come from a notch in the cell wall just inside the closure. In all likelihood the egg had been inserted in the cell wall very much as are the eggs of *Nomada* or *Holcopasites* (Rozen, 1965). The first instar, like that of other nomadines, possessed a

pigmented, sclerotized, prognathous head capsule, long slender curved mandibles and elongate labral tubercles.

The first cell in the nest had been filled with soil, suggesting that this behavior pattern may be a method by which the host destroys eggs of cleptoparasites; similarly filled cells have been found in the host nests of other Nomadinae. The fact that at least two and very possibly three cells had already been completed and provisioned and that the *Brachynomada* female was collected as it was trying to enter the nest opening covered with a drinking glass strongly indicates that a parasite female learns the location of a nest and returns to it time and again to parasitize successive cells as they are being provisioned.

Conclusions Concerning Ethology of the Nomadini

The biological information presented above, although previously unrecorded, yields few surprises because it is similar to what is known of *Nomada* and of other tribes in the subfamily.

All genera about which there is information (*Nomada*, *Melanomada*, *Triopasites*, *Paranomada*, *Kelita*, and *Brachynomada*) insert their eggs into a notch in the cell wall of the host. This incision is probably made by the terminalia of the female. Some, and perhaps all, place the egg under a flap composed of cell lining and soil which is attached on one side to the cell wall. The position of the egg in the cell seems variable in the few cases where sufficient samples are available (*Nomada* and *Paranomada*). In none of the cases presented here was more than one cleptoparasite egg found in a cell. However, Linsley and MacSwain (1955), who made a careful study of *Nomada opacella* Timberlake, indicated that a female normally deposited two eggs to a cell and that the eggs were characteristically placed one at the base (rear) of the cell and the other near the middle, although there was some variability in position.

The first instars of most and probably all Nomadini have prognathous, pigmented, sclerotized head capsules, with elongate sickle-shaped mandibles with which they kill the young host. Almost certainly all first instars are able to crawl; after hatching they move from the cell wall onto the food mass where they destroy the host. After feeding on the provisions, they overwinter as a

mature, quiescent larva (not known for *Brachynomada* and for many *Nomada*). No species is known to have more than one generation a year although this feature might well be species-specific as seems to be the case with some genera in other nomadine tribes. No species spins a cocoon (not known for *Brachynomada*).

Host associations are variable. *Melanomada*, *Paranomada*, and *Triopasites* attack different species of *Exomalopsis*. *Brachynomada* and *Kelita* are only associated with panurgine bees. *Nomada* is often thought to be a parasite of *Andrena*, but various species have also been associated with *Panurgus* (Rozen, 1971), *Dasy-poda*, *Nomia*, *Halictus*, and *Eucera* (Bohart, 1970) and probably other *Nomada* will be associated with still other hosts. The hosts of *Melanomada*, *Triopasites*, *Brachynomada*, and some *Nomada* (*Panurgus* and *Halictus*) nest communally, whereas the host of *Kelita*, *Brachynomada*, and other *Nomada* are solitary so far as we now know. Because females of nomadines probably always enter and oviposit in cells that are in the process of being provisioned, numerous host females coming and going in a communal nest might require special adaptations on the part of the female cleptoparasite to avoid attacks by host adults. With the exception of the flattened body of the female *Paranomada*, we are not yet able to recognize these adaptations.

DESCRIPTIONS OF MATURE LARVAE

This section treats mature larvae of available Nomadini. Because of their small size, first instars are better studied with a scanning electron microscope and are therefore reserved for a further investigation that will deal with first stage forms, not only of Nomadini, but of all the Nomadinae. Mature larvae of *Nomada* have been described by Rozen (1966) and those of *Kelita* by Ehrenfeld and Rozen (1977), and therefore are not included here.

Melanomada sidaefloris (Cockerell)

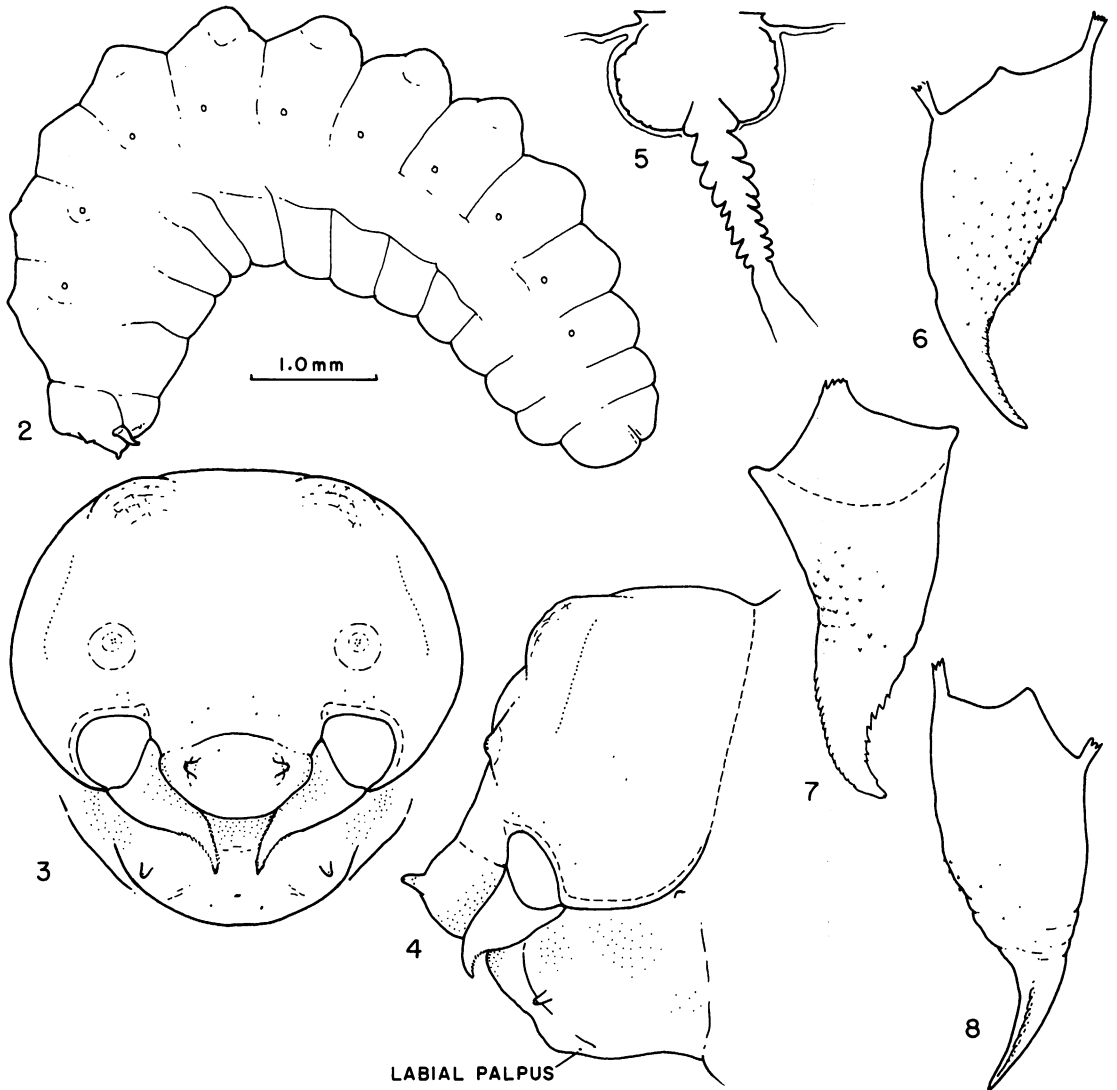
Figures 2-8

Diagnosis. See diagnosis of *Paranomada velutina* and *Triopasites pasitura*.

Head (figs. 3, 4). Integument very faintly pigmented; internal ridges and mandibular tips more darkly pigmented; epipharynx, hypopharynx,

and lateral portions of maxillae spiculate. Head capsule not especially elongate as seen in lateral view but definitely not so wide as that of *P. velutina*; vertex as seen in lateral view produced on each side above antenna; produced area appearing as a wrinkled mound; this production considerably more pronounced than in *Kelita tuberculata* Ehrenfeld and Rozen (1977). Tentorium complete but very thin; anterior tentorial pits very small, best identified by position of anterior tentorial arms; these pits very close to anterior mandibular articulation; posterior pits small but evident, situated just behind hypostomal ridge and posterior thickening of head capsule; posterior thickening of head capsule not evident except in vicinity of posterior tentorial pits where thickening is curved continuation of hypostomal ridge; hypostomal ridge itself thin but evident. Parietal bands weak. Antennal papilla a rather pronounced convexity with four, and in one case five, sensilla; antennal protuberances moderately developed. Labrum projecting moderately strongly as seen in lateral view and bearing two sharp-pointed tubercles directed anteriorly. Mandibles (figs. 6-8) slender and elongate, tapering to bladelike apex; mandible seen in adoral or aboral view somewhat S-shaped with apex curving strongly downward; dorsal apical edge finely and evenly serrate; ventral apical edge somewhat more coarsely serrate; cusp not produced; dorsal and dorsal adoral surfaces dentate; mandibular adductor apodeme present. Maxillae recessed, broadly fused with labrum; maxillary palpus moderately well developed; galea absent. Hypopharynx large and well defined, projecting farther than either maxillae or rest of labium as seen in lateral view (fig. 4). Labial palpus not defined but apparently represented by a single sensilla. Salivary opening a small simple orifice without lips.

Body. Integument spiculate ventrally especially behind the head; apices of most if not all dorsal tubercles with a few minute setae; abdominal segment X with scattered, very minute setae. Form (fig. 2) moderately robust, with head of postdefecating larva notably large compared with body, as is also the case with *Kelita tuberculata*; body shape similar to that of *K. tuberculata* (Ehrenfeld and Rozen, 1977), that is, not tapering posteriorly as seen in lateral view; intersegmental lines moderately deeply incised; paired



FIGS. 2-8. Mature larva of *Melanomada sidaefloris*. 2. Entire larva, lateral view. 3. Head, frontal view. 4. Head, lateral view. 5. Spiracle, side view. 6-8. Right mandible, dorsal, inner, and ventral views, respectively. Scale refers to figure 2.

conical, rounding dorsal tubercles present on most body segments; tubercles low on predefecating larva but moderately pronounced on postdefecating larva; dorsal intrasegmental lines scarcely evident; abdominal segment X not produced ventrally, somewhat dorsal in attachment to segment IX; segment X moderately large and rounded ventrally; anus transverse, somewhat dorsal in position; perianal area appearing as

transverse, smooth lips. Spiracles (fig. 5) moderately large, not on distinct elevations; atrium subglobular, projecting above body surface, with rim; atrial wall with rows of indistinct spicules; these rows in some cases vaguely reticulate; peritreme present, moderately narrow; primary tracheal opening with well-developed collar; subatrium annulate, moderately short and thin, consisting of seven to eight chambers. Imaginal

discs of genitalia not visible, in spite of number of mature larvae available for study.

Material Studied. Four postdefecating larvae, four predefecating larvae, 26 miles south of Animas, Hidalgo Co., New Mexico, September 12-13, 1976, from cells of *Exomalopsis* near *chlorina* (J. G. Rozen).

Triopasites penniger (Cockerell)

Figures 9-14

This description is based on two specimens recovered from the nest of *Exomalopsis compactula* in 1966. The illustrations of the live larva in lateral view and of the head capsule were prepared in general outline at that time. An attempt was then made to rear the specimens with the idea of using cast skins to fill in details, particularly of the head capsule and spiracles. Unfortunately, both specimens died as they were preparing to pupate. Many anatomical features have now been recorded from the preserved but distorted specimens, but the following description and illustrations lack some information that would have been available if well preserved, unmodified specimens were compared and contrasted with those of *Paranomada velutina* and *Melanomada sidaefloris*.

Diagnosis. *Triopasites penniger* seems to agree even more closely with *M. sidaefloris* than does *P. velutina*. Like *M. sidaefloris*, it can be distinguished from *P. velutina* by its distinctly narrower head capsule and the more pronounced produced areas on the vertex. *Triopasites penniger* differs from *M. sidaefloris* also by the different shape of the mandible and the distinct rows of spicules on the atrial wall.

Head (figs. 10, 11). As described for *M. sidaefloris* except for following: Vertex as seen in lateral view apparently not produced strongly as is case with *M. sidaefloris*; wrinkling of integument on produced areas apparently somewhat less than that of *M. sidaefloris*. Condition of tentorium not known but almost certainly complete and very thin, in keeping with similarities between it and *M. sidaefloris* and with respect to internal ridges of head capsule. Parietal bands weak, but perhaps slightly more evident than those of *M. sidaefloris*. Antennal papilla quite pronounced, more so than in either *M. sidaefloris* or *P. velutina*, with four sensilla. Mandibles (figs.

12-14) slender but not so elongate as in *M. sidaefloris*; apex as seen in ventral and dorsal view not so thin as that of *M. sidaefloris*; in aboral or adoral view mandible not S-shaped; both dorsal and ventral apical edges bearing slender teeth; apex narrowly rounded. Maxillary palpus larger than that of either *M. sidaefloris* or *P. velutina*. Labial palpus, though poorly defined, apparently slightly more differentiated than is case with other two species.

Body (fig. 9). As described for *M. sidaefloris* except for following: Although dorsal tubercles with a few minute setae, presence of setae on abdominal segment X not known. Spiracles with atrial wall having rows of distinct spicules, but without reticulations; subatrium with approximately nine chambers and in general somewhat longer and wider than that of *M. sidaefloris*, more similar to that of *P. velutina*.

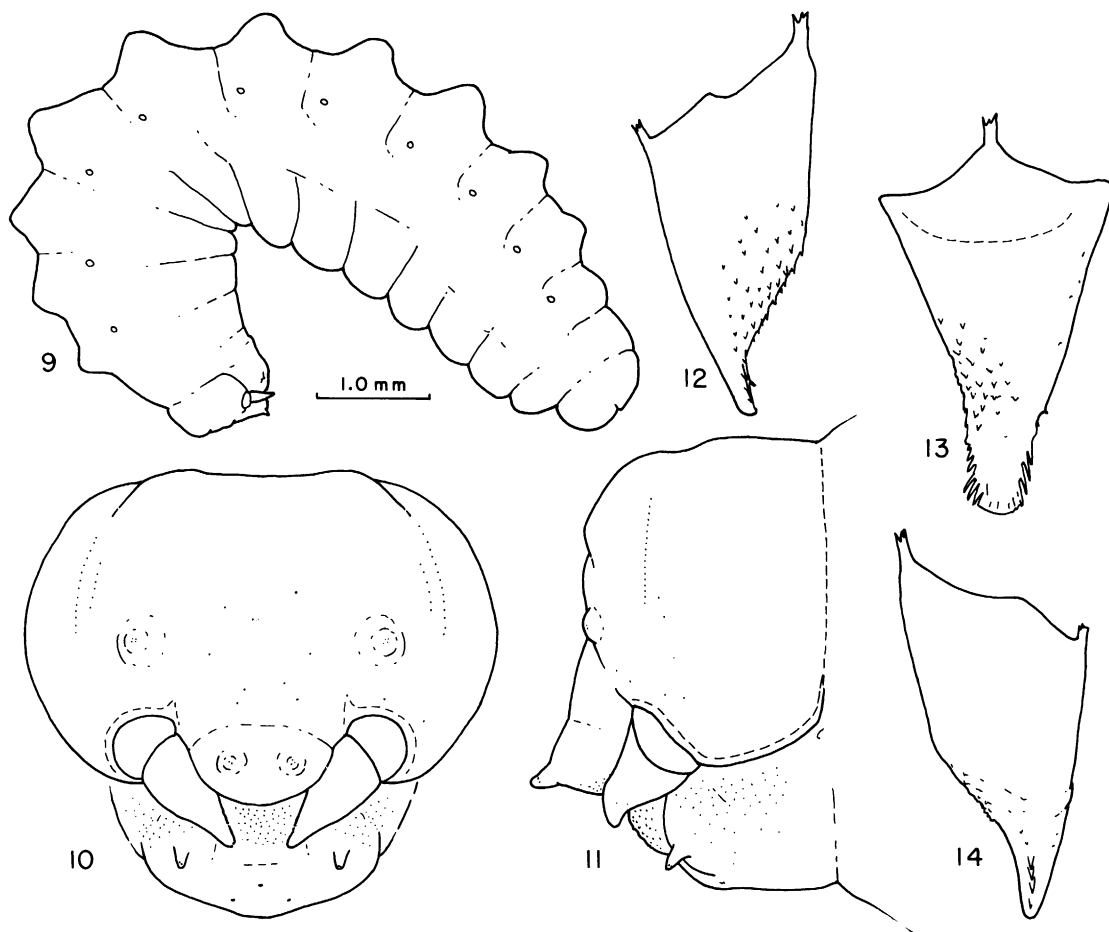
Material Studied. Two postdefecating larvae, 5 miles north of Rodeo, Hidalgo Co., New Mexico, August 30, 1966, from cells of *Exomalopsis compactula* (J. G. and B. L. Rozen).

Paranomada velutina Linsley

Figures 15-20

Diagnosis. The larva of this species closely resembles that of *Melanomada sidaefloris*. It differs in subtle ways as indicated in the following account. The most easily observable diagnostic feature concerns the width of the head capsule, that of *P. velutina* being considerably greater than that of *M. sidaefloris*. Further, the produced areas on each side of the vertex are less pronounced in *P. velutina*.

Head (figs. 16-17). As described for *M. sidaefloris* except for following: Integument slightly more pigmented; spiculations on hypopharynx, and lateral portions of maxillae more extensive. Head capsule as seen from front (fig. 16) much broader than that of *M. sidaefloris*; produced areas on vertex less pronounced than in *M. sidaefloris*, but more evident than in *Kelita tuberculata*. Posterior thickening of head capsule faint, but somewhat more pronounced than in *M. sidaefloris*. Parietal bands scarcely evident. Antennal papilla with four sensilla; antennal protuberances poorly developed. Labrum on most specimens projecting somewhat less than in *M. sidaefloris* with two sharp-pointed tubercles



FIGS. 9-14. Mature larva of *Triopasites penniger*. 9. Entire larva, lateral view. 10. Head, frontal view. 11. Head, lateral view. 12-14. Right mandible, dorsal, inner, and ventral views, respectively. Scale refers to figure 9.

directed somewhat more downward than in *M. sidaefloris*. Mandible (figs. 18-20) with bladeliike apex somewhat broader and mandible in general less tapering than in *M. sidaefloris*; ventral apical edge with serrations apparently less distinct than in *M. sidaefloris*.

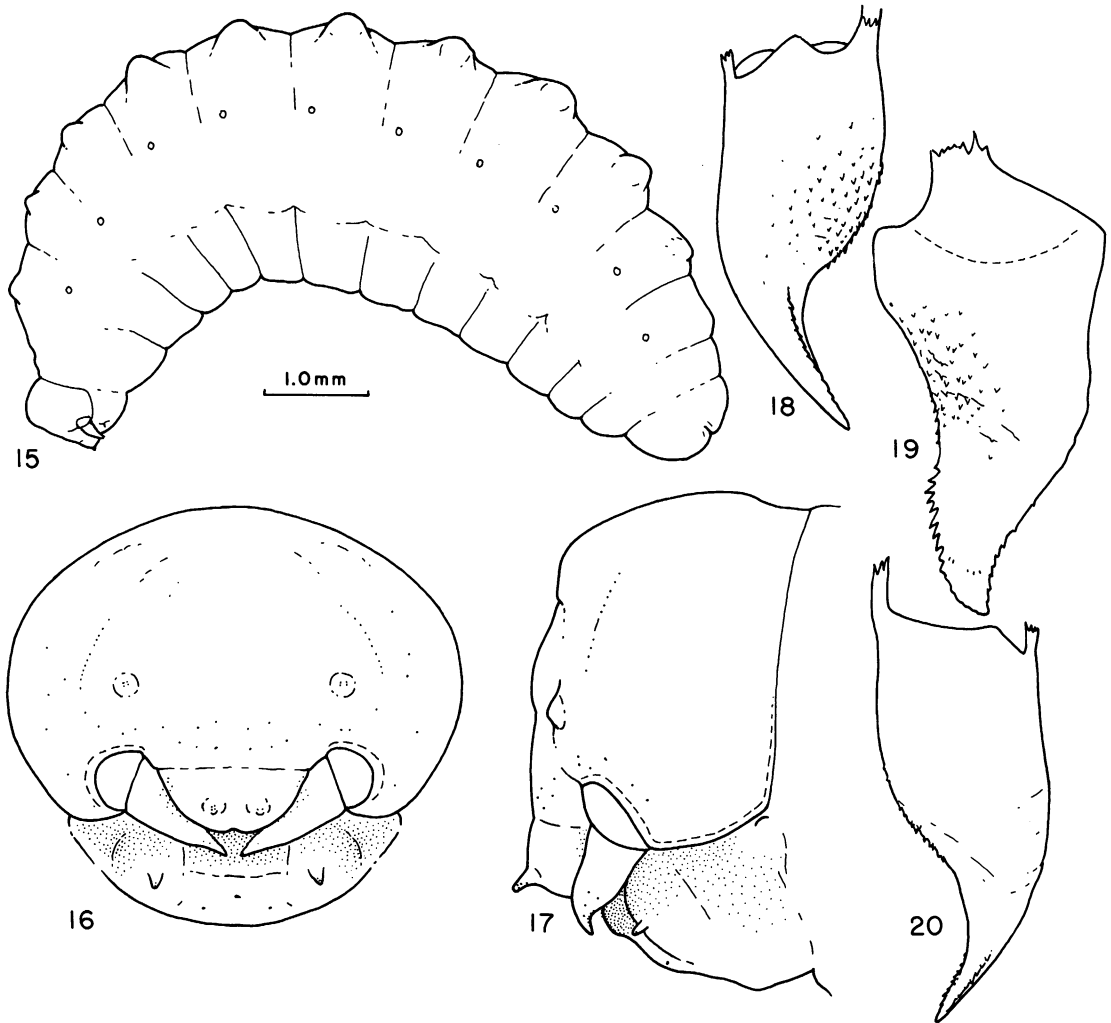
Body (fig. 15). As described for *M. sidaefloris* except for following: Head of postdefecating larva not especially large compared with body; paired dorsal tubercles somewhat more differentiated from dorsum than is case with *M. sidaefloris*. Spiracles having atrial wall with short ridges bearing a number of spicules; reticulations of

atrial wall not evident; subatrium longer than in *M. sidaefloris*, usually consisting of 10 to 20 chambers; subatrium tending to be somewhat wider than that of *M. sidaefloris*.

Material Studied. Three postdefecating, eight predefecating larvae, 1 mile north of Rodeo, Hidalgo Co., New Mexico, August 28, 1967, from nest of *Exomalopsis solani*—nest No. 2 (J. G. Rozen and G. Krueger).

DESCRIPTION OF PUPAE

Pupae of *Nomada* species, *Paranomada velu-*



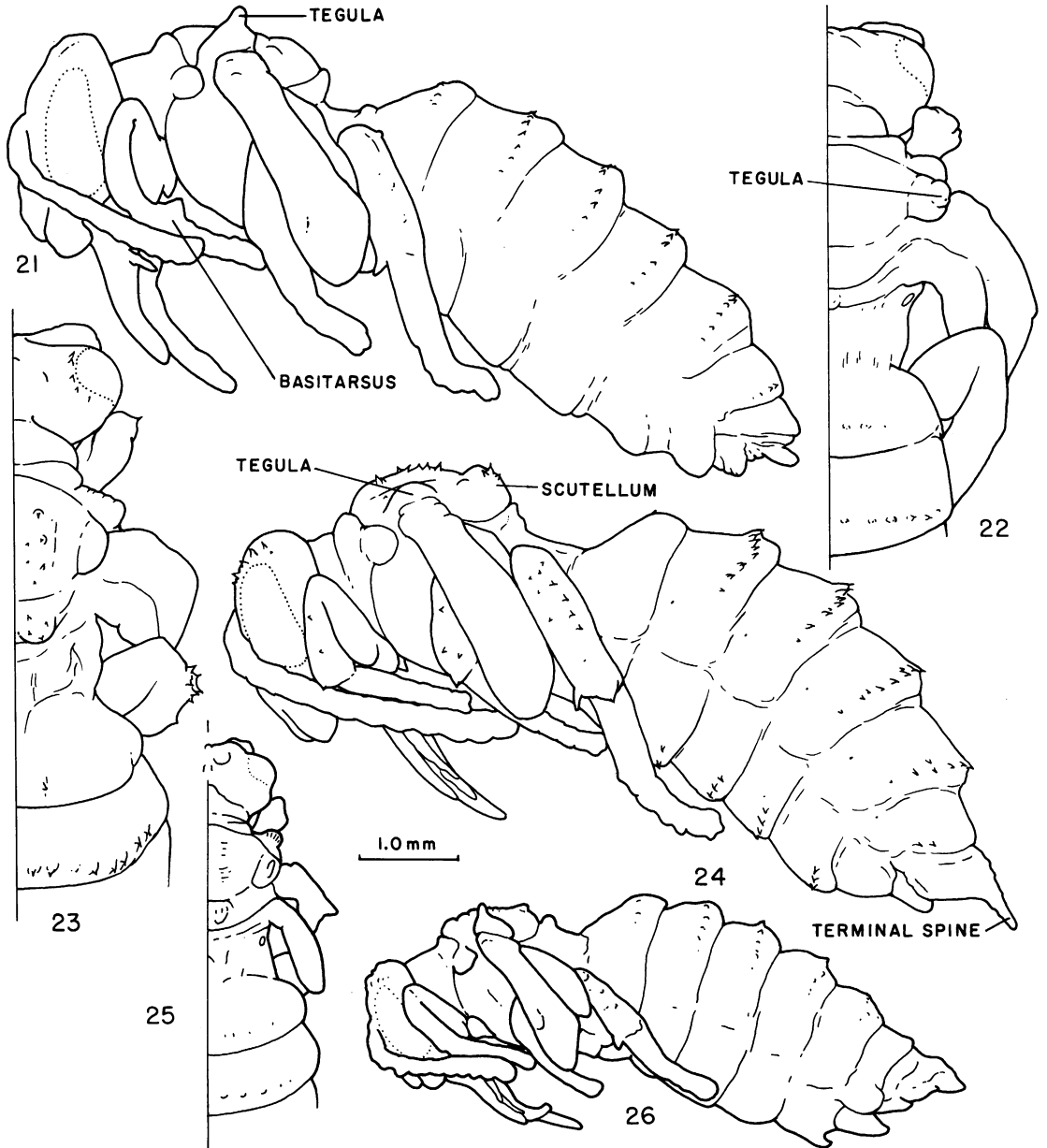
FIGS. 15-20. Mature larva of *Paranomada velutina*. 15. Entire larva, lateral view. 16. Head, frontal view. 17. Head, lateral view. 18-20. Right mandible, dorsal, inner, and ventral views, respectively. Scale refers to figure 15.

tina and *Melanomada sidaefloris* are described here. A preliminary key to the pupae of the Nomadinae was presented in Rozen and McGinley (1974) which separates the pupae of *Nomada* and *Paranomada* in couplet 4. *Melanomada* also runs to couplet 4. Among all known pupae of Nomadinae only *Melanomada* and *Paranomada* have a strongly projecting tubercle on each tegula. As is pointed out in the descriptions the pronounced wing tubercle of *Melanomada* and some-

what more pronounced tubercles on the vertex are especially useful in distinguishing its pupa from that of *Paranomada*.

Melanomada sidaefloris (Cockerell)
Figures 25-26

Head. Scape and frons without distinct tubercles, although integument appearing somewhat lumpy; vertex with large and small low



FIGS. 21-26. Pupae of Nomadini. 21. *Paranomada velutina*, male, lateral view. 22. Same, dorsal view. 23. *Nomada* species, female, dorsal view. 24. Same, lateral view. 25. *Melanomada sidaefloris*, female, dorsal view. 26. Same, lateral view. Scale refers to all figures.

protuberances, all of which are rounded; genal tubercle apparently absent; each apical, lateral angle of clypeus without tubercle; mandible with only indistinct, somewhat irregular swelling on

ventral surface; dorsal surface without distinct tubercle.

Mesosoma. Setae absent. Lateral angles of pronotum moderately produced, perhaps some-

what more pronounced than those of *P. velutina*; posterior lobes of pronotum strongly produced. Mesepisternum without tubercles although with some vague swellings; mesoscutum without distinct tubercles, but with row of irregular, somewhat raised striations extending longitudinally on either side of median line; axilla rounded, not produced; scutellum with low swelling just laterad of median line; propodeum without protuberances. Tegula with conspicuous, dorsally projecting tubercle, similar to that of *P. velutina*; anterior wing with distinct, acutely rounded tubercle along anterior margin, approximately two-thirds of way to apex. Fore-coxa with apical tubercle; mid- and hind coxae each with vague apical swelling; all trochanters each with small, rounded apical tubercle which is somewhat more conspicuous than that of *P. velutina*; fore- and mid-tibiae each with small, vague, indistinct swellings; hind tibia with moderate sized, low, rounded tubercle at base, with somewhat less distinct one apically, and with number of variable-sized, small, rounded tubercles along outer surface; basitarsi without tubercles.

Metasoma. Unlike in *Nomada* and *Paranomada*, metasoma very large in comparison with head and mesasoma so that pupa appearing physogastric. Tergum I with vague, apical row of indistinct tubercles; terga II-V with apical row of small tubercles, most of which are sharp-pointed; sterna without tubercles; terminal spine not present.

Material Studied. One female, 26 mi. south of Animas, Hidalgo Co., New Mexico, collected as larva, Sept. 2, 1976, pupated May 1977 (J. G. Rozen); this specimen was drawn and described while it was still alive.

Paranomada velutina Linsley
Figures 21-22

Head. Scape and frons without tubercles; vertex in vicinity of lateral ocellus with vague mound; genal tubercles absent; each apicolateral angle of clypeus without tubercle; mandible with large tubercle on ventral surface; dorsal surface evenly curved, without tubercles or swellings.

Mesosoma. Setae absent. Lateral angles of pronotum moderately produced; posterior lobe of pronotum not greatly produced. Mesepister-

num without tubercles; mesoscutum without either large or small tubercles; axilla rounded, faintly produced; scutellum without tubercles; metanotum without tubercles; propodeum without protuberances. Tegula with conspicuous, dorsally projecting tubercle; wings without distinct tubercle although anterior wing with vague swelling along anterior margin approximately two-thirds of way to apex. All coxae without tubercles; trochanters, each with small rounded apical tubercle; tibiae without tubercles and with only vague swellings, mostly at apex; fore-basitarsus with conspicuous, rounded tubercle halfway along segment (probably a sex-limited feature, corresponding to special brush found only in male).

Metasoma. Terga I-VI with apical row of small tubercles most of which are sharp-pointed and slightly pigmented at apex; sternal tubercles absent; terminal spine not present.

Material Studied. One male, 1 mile north of Rodeo, Hidalgo Co., New Mexico, collected as larva, August 28, 1967, pupated July 8, 1968, preserved July 15, 1968 (J. G. Rozen and G. Krueger).

NOMADA SPECIES
Figures 23-24

Head. Scape and frons without tubercles; vertex just mesiad of compound eye with approximately five sharp-pointed, apically pigmented tubercles; genal tubercles absent; each apicolateral angle of clypeus without tubercle; mandible without tubercles or swellings.

Mesosoma. Setae absent. Lateral angles of pronotum moderately produced; posterior lobe of pronotum moderately produced; mesepisternum without tubercles; mesoscutum with series of sharp-pointed, apically pigmented tubercles on each side of midline; axilla rounded, scarcely produced; scutellum produced on each side and bearing approximately four or five sharp-pointed, apically pigmented tubercles on each side; neither metanotum nor propodeum produced. Tegula without tubercles; wings without tubercles or swelling. Each coxa with small nonpigmented apical tubercle; trochanters without distinct tubercles; each tibia with dorsal, apical, small, sharp-pointed, apically pigmented tubercle;

fore- and mid-tibiae with several small, apically pigmented tubercles; hind tibia with more than five tubercles; fore basitarsus without tubercle.

Metasoma. Tergum I with a single, small, sharp-pointed, pigmented tubercle; terga II-V with apical row of sharp-pointed, apically pigmented tubercles; tergum VI with several apically pigmented, sharp-pointed tubercles toward apex; sterna II-IV with apical row of small, sharp-pointed, apically pigmented tubercles best developed on each side of midline; terminal spine moderately elongate.

Material Studied. One pupa, Closter, Bergen Co., New Jersey, June 15, 1971, from burrow of *Andrena morrisonella* Vierick (J. G. Rozen).

CONCLUSIONS

Phylogeny of the Nomadini Based on Mature Larvae

Until recently the mature larva of only *Nomada* among all the genera of Nomadini was known. The phylogenetic significance of the *Nomada* larva was interpreted by Rozen (1966) in light of other known larvae of the Nomadinae. Now, both in the present paper and in a study of *Kelita* (Ehrenfeld and Rozen, 1977), larvae of other Nomadini are described, permitting a broader interpretation of interrelationships within the tribe and within the subfamily. Of course, such interpretations are tentative as they are based upon a limited number of characters whose plesiomorphic-apomorphic states can be judged with some degree of reliability. In Rozen (1966, p. 6) the polarity (i.e., plesiomorphic-apomorphic conditions) of a series of characters was given. To that series I now add the following, listing the plesiomorphic condition first:

(1) *Normally long mandible* of *Isepeolus* and *Melanomada* complex (*Melanomada*, *Paranomada* and *Triopasites*) in contrast to *short mandibles* found in all other known larval Nomadinae; (2) *well-developed dorsal tubercles* as found in *Isepeolus* and *Melanomada* complex (including *Kelita*) as opposed to *no dorsal body tubercles*; (3) *minute, widely scattered body setae* of *Isepeolus* and *Melanomada* complex, including *Kelita*, as opposed to *lack of body setae* of all other Nomadinae; and (4) *vertex recessed* as in all Nomadinae except for the *Melanomada* complex in contrast to *vertex with protrusions*. The polarity

of characters (1) and (3) has been determined by out-group comparisons with other families of bees; that of (2) and (4) by correlation with other characters.

Figure 27 is an expanded interpretation of figure 1 in Rozen (1966). The hypothetical ancestral Nomadinae (fig. 27, 1) possessed the plesiomorphic character states listed above and also those listed in Rozen (1966, p. 6). (The synapomorphies defining the Nomadinae will be listed in a forthcoming paper by Rozen, Eickwort, and Eickwort, 1978.) The lineage (fig.

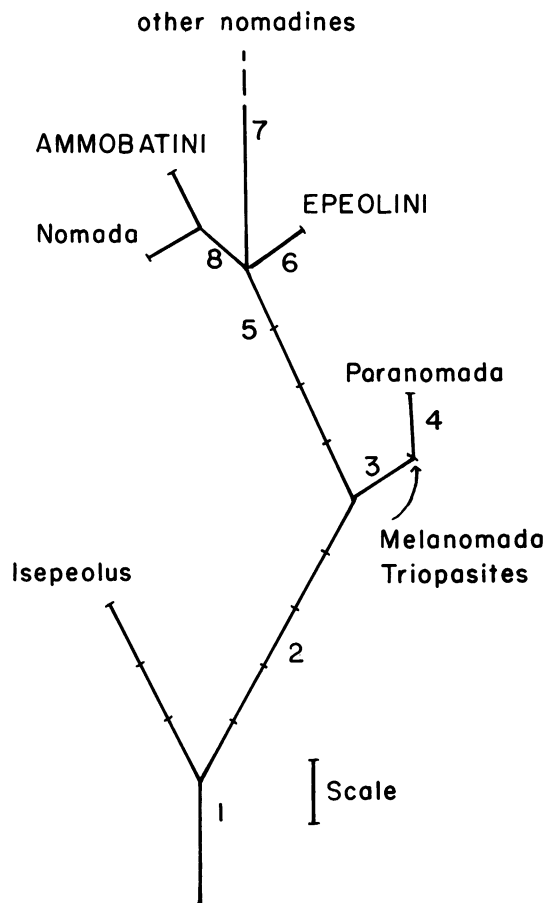


FIG. 27. Phylogenetic interpretation of the Nomadinae based on mature larvae. Numbers refer to text discussion. Sequence of branching has been determined by cladistic analysis. Length of line approximates relative amount of anatomical change. Direction of line and size of angle have no meaning. Scale refers to change in one character state.

27, 2) that gave rise to all the nomadines after *Isepeolus* branched off exhibited the following apomorphic changes: tentorium reduced, maxillary palpi short, labium recessed, not divided into prementum and postmentum, labial palpi lost or almost so, and hypopharynx exceeding labium.

This lineage then split, one branch (fig. 27, 3) giving rise to the *Melanomada* complex (i.e., *Melanomada*, *Triopasites*, and *Paranomada*) with the development of protrusions on the vertex. Unfortunately, this feature is indeterminate in *Kelita*, and other characters of its head capsule, especially the shape of the mandible, cannot be reviewed because the head capsule was accidentally destroyed before such features were studied. *Melanomada*, *Triopasites*, and *Paranomada* are quite similar to one another, and among the differences that they exhibit in the larvae, only the abnormally wide capsule (fig. 27, 4) of *Paranomada* can be identified as apomorphic.

The other branch (fig. 27, 5) underwent considerable change. The hypostomal ridge became weak, mandibles became short, body setae were lost, and the body tubercles were greatly reduced or lost. This branch then split twice, giving rise to three lines, as described by Rozen (1966). One (fig. 27, 6) produced the Epeolini, another (fig. 27, 7) the other Nomadinae (*Holcopasites*, *Neopasites* and *Neolarra*), and the third (fig. 27, 8) *Nomada* and the Ammobatini (*Pseudodichroa*, *Ammobates*, *Morgania*, and *Oreopasites*) (Rozen and McGinley, 1974). Evidence is not on hand to indicate which branching occurred first so that they are presented as being simultaneous in figure 27.

The synapomorphic feature shared by *Nomada* and the Ammobatini (fig. 27, 8) that is, the double transverse line at the posterior margin of the head, is unique among bee larvae and therefore is fairly convincing evidence that *Nomada* and the ammobatines are sister groups. This and the fact that the *Melanomada* complex (probably including *Kelita* and for that matter also *Brachynomada*) is a monophyletic group within the Nomadinae, as shown here, would require the reworking of the tribal classification of the subfamily if the classifier adheres to strict cladistic classification. Even if strict cladistic classification is not followed a re-examination of features of adults and immatures may lead us to conclude

that *Nomada* is in many ways different from the *Melanomada* complex and therefore that the *Melanomada* complex, *Brachynomada*, *Hesperonomada*, and perhaps *Kelita* should be grouped as a separate tribe. In this respect Ehrenfeld and Rozen (1977) have already pointed out, using characteristics of adults, that *Nomada* and *Hypochrotaenia* lineage is a sister group to the rest of the Nomadini lineage (i.e., the lineage that gave rise to *Kelita*, *Brachynomada*, *Hesperonomada*, *Melanomada*, *Triopasites*, and *Paranomada*). Their diagram (Ehrenfeld and Rozen, 1977, fig. 26), though appearing very different from figure 27 in the present paper, is consistent with it in terms of sequence of branching. Their paper did not incorporate an analysis of the adult features of the Ammobatini in relationship to those of the Nomadini. This analysis is now crucial as a test of the hypothesized relationships presented here.

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