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## Biology and Immature Stages of Some Cuckoo Bees Belonging to Brachynomadini, with Descriptions of Two New Species (Hymenoptera: Apidae: Nomadinae)

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## ABSTRACT

Biological information on the South American *Brachynomada roigi*, new species, *Kelita toroi* Ehrenfeld and Rozen, and *K. tuberculata* Ehrenfeld and Rozen is presented. Hosts are identified, egg depositions are described, and data on ovarioles and oocytes of these species, as well as of *Triopasites penniger* (Cockerell), *Melanomada chica* Snelling and Rozen, and *M. margaretae*, new species, are tabulated.

Mature larvae of known Brachynomadini (*Brachynomada*, *Kelita*, *Melanomada*, *Triopasites*, and *Paranomada*) are characterized and a key is presented for their identification. Mature larvae of *Brachynomada roigi* and *Kelita toroi* are described taxonomically and illustrated, and information on the larva of *K. tuberculata* is offered to augment a

previous description of that species. The pupa of *Brachynomada roigi* is described and compared with those of other members of the Brachynomadini.

Data concerning both biologies and immature stages indicate that the tribe is monophyletic, and these data, though limited, suggest that the tribe is a sister group of the other Nomadinae (exclusive of the Isepeolini, Protepeolini, Osirini, and *Coeioxoides*). Within the tribe, *Kelita* appears to be the sister group of the other genera.

In the appendix, *Brachynomada roigi*, new species, from Argentina and *Melanomada margaretae*, new species, from Mexico are named and described.

## INTRODUCTION

We have long recognized (Rozen, 1977; Snelling and Rozen, 1987) that the cleptoparasitic bees belonging to the genera *Triopasites*, *Melanomada*, and *Paranomada* formed a group quite distinct from *Nomada* in spite of the fact that all had been traditionally placed in the Nomadini (Michener, 1944; Hurd, 1979). Roig-Alsina and Michener (1993) have now assigned these genera as well as the South American *Kelita* and *Brachynomada* to a separate tribe, the Brachynomadini. The present paper provides information about the immature stages and biologies of the South American representatives of this tribe. This information expands our understanding of the tribe, confirms the appropriateness of its recognition, and contributes to an understanding of the relationships within the tribe and its relationships to other Nomadinae.

Specimens of adult and immature cleptoparasites, their hosts, and samples of nest components are preserved in the American Museum of Natural History except where stated otherwise.

## ACKNOWLEDGMENTS

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Argentina and to Luis E. Peña Guzman and Alfredo Ugarté Peña for their participation in the 1991 expedition to Chile and Argentina. Arturo Roig-Alsina and Charles D. Michener permitted me to review their manuscript (1993) on the phylogenetic relationships of the long-tongued bees and thereby made it possible to compare their findings with those reported here.

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Specimens of *Melanomada margaretae*, new species, were collected and preserved as a result of the first expedition sponsored by National Science Foundation grant number BSR 90-24723 to the University of Illinois (W. E. LaBerge, principal investigator) to conduct a faunal study of the bees of Mexico under the aegis of El Programa Cooperativo Sobre la Apifauna Mexicana.

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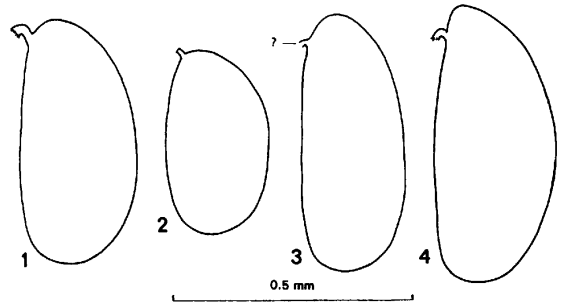
## BIOLOGY

*Brachynomada roigi*, new species

*Brachynomada roigi* was first associated with its host on November 6, 1989, when adult cleptoparasites were found in the nest

of a polychrome (red, yellow, and black) *Psaenythia*, similar but not identical to a specimen identified as *P. thoracica* Gestaecker by J. S. Moure, in the American Museum of Natural History. Precise identification of the host will have to await revision of this large panurgine genus. The nest, in a nearly horizontal, mostly unshaded footpath, appeared to be communal and yielded 86 adults (both sexes), 7 pupae, and 20 larvae of *Psaenythia* and 9 females and 8 males of *Brachynomada* adults. Unquestionably other adults escaped or were not collected. Although several pairs of *Psaenythia* were mating underground, no *Brachynomada* were observed mating in the nest nor were immatures of the cleptoparasite recovered. The nest consisted of both old vacated cells (presumably from one or more previous generations) and cells from the current generation, at depths of 10 to more than 20 cm. As no freshly provisioned cells or feeding larvae were discovered, the nest was studied just as adults of the current generation were starting their emergence.

On a return to the same locality on November 11, 1991, I discovered a cluster of at least five nest entrances (all open) within an area of less than 1 m<sup>2</sup> several hundred meters from the first nest. All were occupied by the same species of *Psaenythia* as the earlier nest, and most (if not all) were communal. *Brachynomada roigi* was associated with several of them. From one of the nests were recovered (all between depths of 10–20 cm) 16 *Psaenythia* females and 2 *Psaenythia* males (mostly teneral), 1 slightly frayed *Brachynomada* female (probably leaving the nest after oviposition), 1 teneral *Brachynomada* female, and 2 fresh *Brachynomada* males (probably newly emerged). In the same nest there were freshly provisioned cells with *Psaenythia* eggs, cells containing mature, slowly moving predefecating *Psaenythia* larvae, 1 *Psaenythia* pupa, and vacated cells. However, no newly hatched, intermediate stage, or postdefecating *Psaenythia* larvae were discovered. One *Brachynomada* egg, 2 quiescent postdefecating *Brachynomada* larvae, and 1 *Brachynomada* pupa were also collected from the nest. These facts indicate 1) that a new nesting season had just started, 2) that, at the same time, some of the im-



Figs. 1–4. Oocytes of members of the Brachynomadini, lateral view. 1. *Brachynomada roigi*. 2. *Kelita toroi*. 3. *Melanomada margaretae*. 4. *Triopasites penniger*. Scale refers to all figures.

matures of the last generation were completing their development, and 3) that *Brachynomada* larvae undergo a postdefecating diapausing period whereas *Psaenythia* larvae remain as slowly moving predefecating larvae until just before they pupate (an unusual but not unique feature of panurgine bees).

The *Brachynomada* egg possessed a shiny, clear chorion and had a maximum diameter of 0.25 mm. Its length could not be measured because it was “toe-nailed” at an oblique angle under a flap of wall in the side of the cell so that only the rounded end could be seen (but see description of oocyte, below). The flap (not unlike that illustrated for *Holcopasites*, Rozen, 1965: fig. 3, and for *Kelita chilensis*, Rozen, 1970: fig. 1) was semicircular, 0.3 mm long, and with a 0.6 mm-long hinge of cell lining which proved that egg deposition took place after the cell lining had been applied by the host bee. The egg insertion hole appeared to be a simple slit, without chinking or cementing of the edges of the opening.

The *Brachynomada* egg hatched on November 15, 1991. The first instar, 0.625 mm long, possessed: a normally rounded (i.e., not dorsoventrally flattened), prognathus, pigmented head capsule; obscure antenna; conspicuous (but not extremely long) paired labral tubercles; apically curved and attenuated, sharp-pointed, pigmented mandible; pronounced maxillary palpus; and mostly membranous labiomaxillary region. These features are consistent with those of some other Nomadinae (Rozen, 1991b). The body lacked lateral projections, and a paired pygopod was

not detected (contrary to the description of the first instars of the Nomadinae, Rozen, 1991b). However, the larva was able to crawl forward by inverting and then everting the apex of its abdomen while it used the venter of abdominal segments 4 and 5 as the fixed point while contracting the abdominal apex. Thus the front of the larva often remained elevated, seeming to search the air space rather than the surface of the substrate. This larva was also able to stand erect on the presumably sticky apex of its abdomen and appeared to search the area around its head for host or rival.

The ovaries and oocytes of one recently emerged female (as evidenced by the lack of wing wear) preserved in Kahle's solution were examined; the statistical information is summarized in table 1. She contained 20 mature oocytes, a remarkably high number compared with many other cleptoparasitic bees. However, until oocyte counts are made on a series of females of various ages, we will be unable to assess to what extent, if any, this high number is age-related. The oocytes (fig. 1), slightly more cream-color than immature ones, were identified as mature (category A of Iwata, 1955) because their chorions had been deposited and a small anterior hook could usually be identified. In contrast to the slender oocytes of most apids, these were unusually short, imparting a "fat" appearance. All oocytes were approximately of the same size, and their anterior ends were more pointed than the broadly rounded posterior ends. Each had a clear, smooth (unsculptured), rather brittle chorion that possessed a distinct hook at the anterior end. At its apex, the hook seemed divided into several short submicroscopic filaments suggestive of the frayed end of a piece of string. The egg index of 0.23 (Iwata and Sakagami, 1966) indicated that these oocytes were shorter relative to mesosomal width than those of any other known cleptoparasitic bee except for *Kelita toroi* (discussed below).

The number of ovarioles could not be accurately counted on the preserved females because of the density of so many follicles and the brittleness of preserved ovarian tissue, but the number was probably much larger than that of most cleptoparasites (see section on Biological Comparisons). As a result,

the number of mature oocytes per ovary is unknown for *Brachynomada*.

*Kelita toroi*  
Ehrenfeld and Rozen

This species of cleptoparasite was moderately common along an infrequently used, unpaved road 6 km south of Vicuña, Elqui Province, Chile. This section of roadway, sloping 20–30° from horizontal, consisted of soil with a clay texture that cracked extensively as it dried. Cracks were used by a number of bee species to gain access to the moist, more easily excavated substrate (see Rozen, 1993, for more complete description and picture of nesting area). Host nests were occasionally encountered during my excavation of nests of other species of bees. On October 20, 1991, after completing my studies of the other species, I investigated the biology of this cleptoparasite and returned about a month later, November 15–20, 1991, to further these observations.

*Kelita toroi* apparently had two host species at this locality, but the identity of one of the hosts remains uncertain. Larvae of *Kelita toroi* were recovered from the nests of *Leioproctus erithrogaster* Toro and Rojas. Females of this host are dimorphic, some possessing a mostly red metasoma and others, an all black metasoma. Host larvae from one nest definitely associated with an adult host possessing a mostly red metasoma (identified by H. Toro) were immediately recognizable because they had very small thoracic spiracles and greatly enlarged abdominal spiracles with long atrial spines. On postdefecating larvae these spiracles were on pigmented tubercles. Numerous postdefecating *Kelita* larvae were recovered in association with postdefecating larvae of *Leioproctus erithrogaster*, identified by their unusual spiracular characteristics. Nests of this species were about 10 cm deep and were occupied by single females (i.e., this species is noncommunal).

Several *Kelita* larvae were also collected in October from nests containing host larvae with small spiracles of uniform size which on postdefecating larvae were not on pigmented tubercles; host females were not associated with these nests. It is virtually impossible that

the two very different types of host larvae are the same species because of the dramatic differences in their spiracles. This second host is presumably also a *Leioproctus* as determined by larval anatomy (described in McGinley, 1981).

Cells of nests of both host species were at similar depths, and no differences in nest architecture were observed. Cell linings adhered to the semismooth cell walls in most places. However, in all cells, linings were separated here and there from irregularities in the cell wall, suggesting that the cell lining was not as closely bonded to the wall as is characteristic of the cells of other families of ground-nesting bees.

Eggs of *Kelita toroi* were deposited in puncture holes in the cell walls. Although no live eggs were discovered in situ, at least nine insertion holes were found, four in one cell fragment (one of these with a dead first instar partly emerged, presumably killed by one of its cell mates), two in another, and one per fragment in three other fragments. The insertions differed from those of *Kelita chilensis* (Friese) (Rozen, 1970) and that of *K. tuberculata* (described below) in that none exhibited a flap of cell lining with soil particles adhering, with the flap connected to the cell surface by the lining. Each appeared as a somewhat irregular tear in the cell lining, usually with the lining and shed chorion somewhat elevated (pulled away) from the wall. Under this elevation in six insertions, there was an amorphous mass of whitish material, probably mold hyphae. Puncture holes in the cell wall were usually partly obscured by the elevated cell lining, cast chorions, and mold hyphae, but two holes in the wall measured 0.25 mm in diameter. In several cases these holes penetrated the wall at an oblique angle. The disturbed area in the cell lining associated with each insertion hole was irregular and elongate, 0.35–0.43 mm in maximum length and 0.18–0.25 mm in maximum width.

Without examining a live egg in situ, it is difficult to interpret these observations in light of the egg depositions reported for *Kelita chilensis* (Rozen, 1970), *K. tuberculata* (described below), and the other members of the Brachynomadini. However, the insertions may be similar but seem to differ because the clay texture of the cell wall (and substrate) at

the *Leioproctus* site did not chip as did the sandier substrate of the other species and because the cell lining of *Leioproctus* is not firmly bonded to the substrate as is the case with other host bees.

Two cast chorions, removed from the insertion holes, were searched for remnants of a hidden earlier instar exoskeleton. None was detected, indicating that the hospicial larva briefly described below is indeed the first instar. In many (and possibly all) of the pollen-collecting, nonsocial apids, the first instar is enclosed in the chorion for the entire stadium, its exoskeleton is shed with the remnants of the chorion, and the second instar crawls away (and is therefore easily mistaken as the first instar) (Rozen, 1991a).

A partly fed first instar, 1.5 mm long and with a head capsule width of 0.2 mm, possessed: a pigmented, prognathous head capsule that was constricted posteriorly; ventral sclerotized postoccipital bridge; troughlike, external hypostomal groove; low antenna; very long, paired labral tubercles; moderately long, curved sharp-pointed mandible; long maxillary palpus; obscure labial palus; mostly membranous labiomaxillary region; and a narrowly tapering, apically trilobed abdominal apex as a result of short pygopod rami and a posteriorly projecting abdominal segment X. Thus, this larva generally agreed with others in the Nomadinae (Rozen, 1991b).

Feces of *Kelita toroi* were deposited as a single lumpy mass appressed to the rear of one of the cells.

Mature quiescent larvae characteristically were coated with a transparent, colorless, brittle, glasslike substance that on preserved specimens cracked and could be removed in large flakes that bore the exact impression of the insects' integument. The source of the substance is unknown, but it presumably is a secretion that is deposited and hardens after the larva has defecated. The coating, insoluble in ethanol or Kahle's solution, appears evenly over the head region, posterior body segments, and dorsal tubercles. However, its thickness or even presence in the region of the spiracles needs to be evaluated on freshly collected specimens before the flakes are loosened and eroded by the sloshing of preservative during transport. It may prevent water loss or shield the hibernating larva from

pathogens or parasites. Hibernating host larvae bear a similar but somewhat more elastic coating. Such coatings may be a phenomenon associated with hibernating larvae of many taxa of bees that do not spin cocoons.

Statistics regarding the ovaries of a female with well worn wings preserved in Kahle's solution are presented in table 1. The oocyte (fig. 2) was nearly identical in shape and color to that of *Brachynomada roigi*. This oocyte also possessed an anterior hook with an apical fibrous texture. Actually smaller than the *Brachynomada* oocyte, its egg index (0.21) was also slightly smaller. *Kelita toroi* has the smallest egg index of any known bee, cleptoparasitic or otherwise (with the possible exception of meliponine trophic eggs). The ovarioles were difficult to count but appeared to number approximately 10 per ovary. Because this was an estimate, the number of oocytes per ovariole was not calculated.

*Kelita tuberculata*  
Ehrenfeld and Rozen

The following brief notes augment the fragmentary life history information presented earlier on this species (Ehrenfeld and Rozen, 1977; Rozen, 1989).

As reported in Ruz and Rozen (1993), two isolated communal nests of *Parasarus atacamensis* Ruz were discovered at 6 km south of Vicuña, the area identified above for *Kelita toroi*. One of the nests, excavated on October 19, 1991, was more than 50 m from the *Leioproctus/Kelita toroi* site and was found in the margin of another unpaved road. The soil here was quite sandy and therefore of a very different texture from that of the *Leioproctus* site. Four host females were collected from the burrow discovered when I observed a female of *Kelita tuberculata* entering it. The nest contained a number of host larvae of various ages, several meloid larvae, and one, probably penultimate larval instar of *K. tuberculata*. One of the cells contained a *Kelita* egg insertion.

The egg, which had hatched, had been placed into a curved slit in the cell wall so that its long axis entered the wall obliquely. A flap (length 0.38 mm long, 0.25 mm wide) of cell lining with adhering soil was raised slightly from the cell wall along the slit, an

egg insertion like that of *Kelita chilensis* (Rozen, 1970).

NOTES ON OTHER BRACHYNOMADINI

The ovaries of representatives of three other species were also examined and the statistics entered into table 1: *Triopasites penniger*, from 5 mi north of Rodeo, Hidalgo Co. N.M., September 1, 1989 (J. G. and B. L. Rozen, R. L. Foster), and *Melanomada chica* Snelling and Rozen and *Melanomada margaretae*, both from Reserva de la Biosfera de Mapimí, near Ceballos, Durango, México, August 23, 1991 (J. G. Rozen).

*Triopasites penniger* is known to be a cleptoparasite of *Exomalopsis compactula* Cockerell which nests communally (Rozen, 1977, 1984). One of its mature oocytes (fig. 4) possessed a smooth transparent chorion with a small hook near the anterior end. As with the other oocytes described here, this hook was fibrous distally. The anterior end of the oocyte was more pointed than the rounded rear and was somewhat flatter in profile in the vicinity of the hook than the other oocytes depicted here. Except for this flatness and its somewhat more elongate shape, this oocyte was similar to those of *Brachynomada roigi* and *Kelita toroi*.

The host of *Melanomada chica* is unknown although Snelling and Rozen (1987) suggested that its host will probably be "one of the smaller species of *Exomalopsis*, such as *rufiventris*, which occurs in the vicinity of the type locality." The *Exomalopsis* fauna at the Mapimí station was diverse, suggesting further that one or more species of *Exomalopsis* host this species. The chorion of its oocyte was fragile (perhaps a function of small size), so that it was impossible to dissect the follicular tissue without injuring the oocyte. However, its measurements were taken through the follicular tissue, and sufficient tissue was removed to reveal that the chorion was smooth and colorless and that the oocyte possessed a hook at the anterior end, identical to that associated with the other species treated here.

It seems likely that *Melanomada margaretae* will be found to parasitize nests of one or more species of *Exomalopsis* because of

TABLE 1  
 Statistical Information on Ovarioles and Oocytes of Four Genera in the Brachynomadini

Taxon	Egg index	Total number mature oocytes	Mature oocytes per ovariole	Number of ovarioles	Oocyte length/diameter (mm)	Specimens examined
<i>Brachynomada roigi</i>	0.23	20	—	—	0.50/0.25	1
<i>Kelita toroi</i>	0.21	15	—	≈10:10	0.40/0.24	1
<i>Triopasites penniger</i>	0.29	8	0.4	10:10	0.58/0.25	1
<i>Melanomada chica</i>	0.39	5	0.3?	9:6?	0.46/0.20	1
<i>Melanomada margaretae</i>	0.40	5	0.3	9:8	0.55/0.23	1

the abundance of *Exomalopsis* species at Mapimí and because all other North American brachynomadines are associated with *Exomalopsis*. As with *M. chica*, the oocyte could not be extracted intact from the follicle. However, more rounded at the posterior end than at the anterior end, its shape (fig. 3) was drawn through the follicular wall, and its dimensions are given in table 1. The chorion was clear and unsculptured, but details of the hook at the anterior end could not be observed.

#### BIOLOGICAL COMPARISONS IN THE BRACHYNOMADINI

The biological information has been published on a number of other members of this complex: *Brachynomada* near *argentina* Holmberg (Rozen, 1977); *Triopasites penniger* (Cockerell) (Rozen, 1977); *Melanomada sidaefloris* (Cockerell) (ibid.; Rozen, 1984); *Melanomada annectens* Snelling and Rozen (Rozen, 1984, misidentified as *Hesperonomada melanantha* Linsley; Rozen and Snelling, 1986, as unnamed *Melanomada*); *Paranomada velutina* Linsley (Rozen, 1977); *Paranomada nitida* Linsley (Rozen, 1984); *Kelita chilensis* (Friese) (Rozen, 1970, 1986); *Kelita tuberculata* Ehrenfeld and Rozen (Ehrenfeld and Rozen, 1977; Rozen, 1989). The following generalizations are based on these accounts and on the data presented in this paper.

Females of *Brachynomada roigi*, *Kelita toroi*, and *K. tuberculata* insert their eggs in the host brood cell, presumably while the host female is away. Females of all known members of the Brachynomadini (Rozen, 1992) typically make an oblique slit in the cell lining

and insert their egg under the flap of loose cell lining with soil attached, made by the slit. Possible (but unlikely) exceptions are *Triopasites penniger* (Rozen, 1977) and *Kelita toroi* (see discussion above). This mode of egg deposition is also characteristic of *Nomada*, *Holcopasitini* (at least *Holcopasites*), and probably other groups of *Nomadinae* as well (Rozen, 1992).

Hosts of members of the Brachynomadini tend to be communal nesters; exceptions are *Leioproctus erithrogaster* (host of *Kelita toroi*), *Psaenythia annulata* (Gerstaecker)<sup>2</sup> (host of *Brachynomada* near *argentina*), and possibly *Liphanthus parvulus* (Friese) (host of *Kelita chilensis*). In the few cases known, species of *Brachynomada* have been associated with only the panurgine genus *Psaenythia*. *Kelita* until now was thought to be a cleptoparasite of only the Panurginae, specifically several species of *Liphanthus*, and *Parasarus* (Friese, 1916; Ehrenfeld and Rozen, 1977; Ruz and Rozen, 1993). Hence, the certain association of *Kelita toroi* with the paracolletine *Leioproctus erithrogaster* is unexpected.

First instars of *Kelita toroi* and *Brachynomada roigi* agree with those of the known members of the *Nomadinae* in being hospitable, with the usual specializations characteristic of nomadine first instars (Rozen, 1991b).

Cleptoparasitic bees tend to have oocytes that are smaller than those of solitary bees of the same body size as was first noted in the pioneer works of Iwata (1955) and Iwata and

<sup>2</sup> Only a single nest of this species was observed (Rozen, 1989); other species of *Psaenythia* nest communally.

Sakagami (1966) and subsequently recorded by others (Alexander and Rozen, 1987; Rozen and Roig-Alsina, 1991; Rozen and McGinley, 1991; Rozen, 1992). The extremely small egg index (size of oocyte compared to mesosomal width) of *Brachynomada roigi*, *Kelita toroi*, and also *Triopasites penniger*, even compared with that of other parasitic bees, is noteworthy and is here regarded as a likely synapomorphy. The egg indices of *Melanomada chica* (0.39) and *M. margaretae* (0.40) are somewhat higher but still low compared with most other nomadines.

Oocytes of all the species listed in table 1 tend to be much shorter in relation to their length compared with all known Nomadinae oocytes (Iwata, 1960; Alexander and Rozen, 1987; Rozen and Roig-Alsina, 1991, Rozen and McGinley, 1991; Rozen, 1992). Hence their length is less than 2.5 times their maximum diameter, whereas with other known Nomadinae, egg length is more (usually much more) than 3.25 the maximum diameter. These "fat" oocytes tend to be pointed at their anterior end and broadly rounded at their posterior end, with their maximum diameter occurring in the posterior half of the oocyte seen in side view. This shape, atypical for apid oocytes and eggs, is probably a synapomorphy. The presence of a hook at the anterior end of the oocyte of the known members of the Brachynomadini reinforces this probability. In other nomadine taxa, this hook when less pronounced is nipplelike. It was reported first (as a nipple) by Iwata (1960) for several species of *Nomada* and has been observed in some other tribes of nomadine bees (Caenoprosopidini, Rozen and Roig-Alsina, 1991; Townsendiellini, Rozen and McGinley, 1991). Hence it is not a synapomorphy of the Brachynomadini alone and may prove useful in sorting out relationships within the Nomadinae. Its function is unknown, but it may be associated with the micropyle.

We can speculate that the very small size of the mature oocytes permits the female to have many eggs ready for release at one time. This might be advantageous for a cleptoparasite of a communal bee such as the hosts of *Brachynomada roigi* and *Triopasites penniger*, because once a host nest is found there

may be a number of open cells being provisioned simultaneously and therefore available for parasite oviposition. However, the number (8) of mature oocytes in *T. penniger* was not especially high. Although *Leioproctus erithrogaster*, the host of *Kelita toroi*, is not communal, it is gregarious, numerous nests occurring close to one another along the roadway. Thus there is an advantage for females of *K. toroi* to have a large number (15) of mature oocytes because the cleptoparasite might encounter numerous opportunities to oviposit in quick succession. Small cleptoparasite eggs also decrease their chances of being detected in the cell wall when reentering host females deposit more provisions or oviposit.

The ovariole counts listed in table 1 are high, and the total number of ovarioles in *Brachynomada roigi*, though impossible to estimate, was perhaps commensurate with these others. Of all the cleptoparasitic bees (excluding the social parasite, *Psithyrus*), only *Hexepeolus rhodogyne* Linsley and Michener, has an equally large number of ovarioles (11:9) (Rozen, 1992).

## MATURE LARVAE

### CHARACTERIZATION OF BRACHYNOMADINI, BASED ON MATURE LARVAE

The mature larvae of representatives of all of the currently recognized brachynomadine genera are now known (but at least one new South American genus has yet to be described). With the exception of *Kelita*, they are quite uniform. The following characterization and key are based on the larvae of *Brachynomada roigi* (described below), *Melanomada sidaefloris* (Rozen, 1977), *M. annectens* (Snelling and Rozen, 1987), *Paranomada velutina* (Rozen, 1977), *Triopasites penniger* (Rozen, 1977), *Kelita toroi* (described below), and *K. tuberculata* (Ehrenfeld and Rozen, 1977).

HEAD: Vertex, except in *Kelita*, swollen above each antenna so that in lateral view top of head curving abruptly from front; raised area more (*Melanomada sidaefloris*, Rozen 1977: figs. 3, 4) or less (*Brachynomada roigi*, fig. 6) wrinkled; in *Kelita* (fig. 13) top and front curving into one another more gradu-



ally, wrinkling not evident. Anterior tentorial pit, when evident, very low on face (fig. 6), near anterior mandibular articulation, except in *Kelita* (fig. 13) where pit is about halfway between articulation and lower edge of antennal disc. Antennal prominence weakly developed (except in *Kelita*, fig. 14, where prominence is small but more elevated than in other taxa). Labral tubercles separated by their basal diameter or less except in *Kelita* (fig. 13) where distance between labral tubercles distinctly greater than basal diameter. Mandible usually elongate, S-shaped in adoral view, with apex pointing downward; in *Triopasites* mandible shorter, straight in adoral view; in *Kelita* mandible short, straight in adoral view, with apex curving upward; in all species, cuspal area not projecting as seen from above or below. Maxillary palpus (fig. 7) small but sharply projecting, longer than basal diameter except in *Kelita* (fig. 14) where palpus is about as long as basal diameter.

**BODY:** Intrasegmental lines not evident. Abdomen with paired, conical (not pronouncedly transverse), apically rounded, dorsolateral tubercles, except these tubercles reduced in *Kelita toroi* (but not in *K. tuberculata*); dorsolateral tubercles of thorax smaller than those of abdominal segments I–V except in *K. toroi* (but not in *K. tuberculata*); venter of abdominal segment IX not produced ventrally or produced slightly (*Melanomada*) apparently because of dorsal attachment of segment X to IX. Spiracular atrial wall with distinct or indistinct spicules or with ridges, sometimes forming reticulate pattern, but without long spines.

**REMARKS:** As indicated above, the mature larvae of *Kelita* do not agree in many respects with larvae of the other taxa and suggest the possibility that the Brachynomadini may not be monophyletic. However, paired, conical dorsolateral tubercles are unknown elsewhere in the Nomadinae (Rozen, 1966; Rozen and McGinley, 1974, 1991; Rozen and Roig-Alsina, 1991) and therefore may be a synapomorphy defining the complex. These tubercles are not well developed in *K. toroi*, but they are pronounced in *K. tuberculata*. Furthermore in *K. tuberculata* and in all of the other genera in the complex, the thoracic tubercles are smaller than the midabdominal tubercles, a peculiar phenomenon that seems

to support their homology from one genus to the next.

The elongate, S-shaped, apically down-curved mandible of many members of the complex is a unique synapomorphy of those taxa that share it; this modification is unknown elsewhere in the Apoidea. The structure of the mandible as exhibited in *Triopasites* (Rozen, 1977: figs. 12–14) may well be a further modification of the synapomorphy since the mandible has its dorsal and adoral surface dentate as is characteristic of all other Brachynomadini except *Kelita*. The mandible of *Kelita toroi* appears to be primitive, since the apex curves normally as is characteristic of most bee larvae. This is consistent with the idea the *Kelita* might be a sister group of the other genera.

KEY TO THE MATURE LARVAE  
OF THE BRACHYNOMADINI

1. Hypopharynx nonspiculate (figs. 13, 14); anterior tentorial pit about halfway between anterior mandibular articulation and antennal disc (fig. 13). *Kelita*. . . . . 2
  - Hypopharynx spiculate (figs. 6, 7); anterior tentorial pit either absent or adjacent to anterior mandibular articulation (fig. 6) . . . . . 3
- 2(1). Middle dorsolateral body tubercles pronounced, larger than tubercles of thorax and abdominal segments VII–X (Ehrenfeld and Rozen, 1977: fig. 10). . . . .
  - Kelita tuberculata* Ehrenfeld and Rozen
  - Middle dorsolateral body tubercles less elevated than those of thorax and abdominal segments VII, VIII (fig. 12). . . . .
    - . . . . . *Kelita toroi* Ehrenfeld and Rozen
- 3(1). Mandible elongate, apically down-curved (figs. 6, 7, 9). . . . . 4
  - Mandible short, apically straight (Rozen, 1977: fig. 13). . . . .
    - . . . . . *Triopasites penniger* (Cockerell)
- 4(3). Labral tubercles separated by less than their basal diameter (fig. 6); prothoracic dorsolateral tubercles larger than those of mesothorax (fig. 5). . . . .
  - . . . . . *Brachynomada roigi*, new species
  - Labral tubercles separated by about their basal diameter (e.g., Rozen, 1977: fig. 16); prothoracic dorsolateral tubercles subequal to or smaller than those of mesothorax (Rozen, 1977: figs. 2, 15; Snelling and Rozen, 1987: fig. 19). . . . . 5
- 5(4). Head capsule very wide as seen in frontal

- view (Rozen, 1977: fig. 16); dorsolateral thoracic tubercles larger (Rozen, 1977: fig. 15). . . . . *Paranomada velutina* Linsley
- Head capsule not abnormally wide (Rozen, 1977: fig. 3; Snelling and Rozen, 1987: fig. 21); dorsolateral thoracic tubercles scarcely noticeable (Rozen, 1977: fig. 2; Snelling and Rozen, 1987: fig. 19). *Melanomada*. . . . . 6
- 6(5). Vertex strongly produced on each side above antenna (Rozen, 1977: figs. 3, 4). . . . .  
 . . . . *Melanomada sidaefloris* (Cockerell)
- Vertex less produced on each side above antenna (Snelling and Rozen, 1987: figs. 20, 21). . . . .  
 . . . *Melanomada annectens* Snelling and Rozen

*Brachynomada roigi*

Figures 5-11

The postdefecating larva of this genus has not been treated before. The first instar of another species was briefly characterized by Rozen (1977).

**DIAGNOSIS:** The mature larva of this species differs from larvae of *Kelita toroi* and *K. tuberculata* in that it has elongate apically down-curved mandibles, labral tubercles that are separated by less than their basal diameter, a spiculated hypopharynx, and anterior tentorial pits that are adjacent to the anterior mandibular articulations. *Brachynomada roigi* shares these characteristics with all other known larvae of the Brachynomadini (except anterior tentorial pits are not evident on some). By contrast, larvae of *Kelita* differ from larvae of *B. roigi* and the others because both species of *Kelita* have short, normally curved mandibles, labral tubercles that are separated by much more than their basal diameter, nonspiculated hypopharynx, and anterior tentorial pits that are situated approximately halfway between the anterior mandibular articulations and the lower edge of the antennal disc. *Kelita* larvae also exhibit an evenly rounded upper part to their head and restricted but evident antennal prominence, both as seen in lateral view (fig. 14), rather than a frons that more or less abruptly angles with the vertex (the result of a wrinkled swelling above each antenna) and a weakly developed antennal prominence (fig. 7).

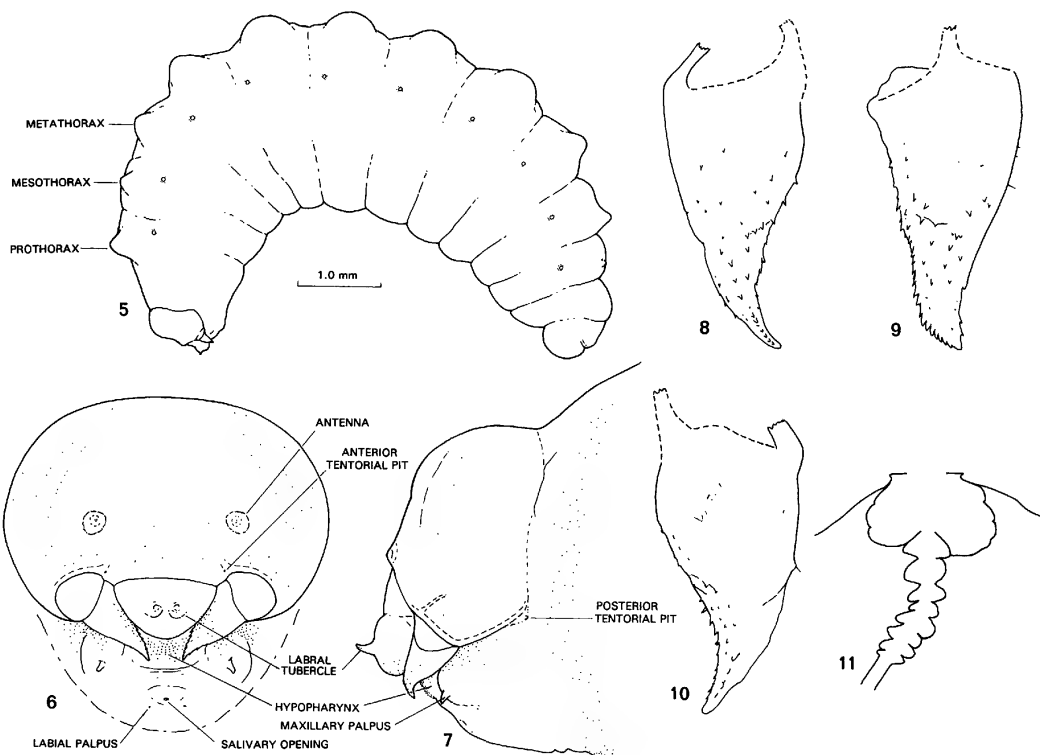
Mature larvae of *Brachynomada roigi*, though similar to larvae of the non-*Kelita*

members of the Brachynomadini, can be distinguished as follows (contrasting characters of others in parentheses): labral tubercles separated by considerably less than their basal diameter (by their diameter); mesothoracic dorsolateral tubercles smaller than prothoracic tubercles (subequal to or larger than prothoracic tubercles); atrial opening of most spiracles vaguely polyhedral or scalloped (circular); atrial wall with nondenticulated ridges that form pronounced, coarse reticulated pattern (with rows of indistinct spicules that sometimes make vaguely reticulate pattern [*Melanomada*]; with rows of distinct sharp spicules but without reticulation [*Triopasites*]; or with distinct short ridges sometimes bearing several spicules, without reticulations [*Paranomada*]).

Characters italicized below appear to be important for distinguishing this tribe from others in the Nomadinae; characters in bold-face (though not necessarily unique to *Brachynomada*) are helpful in separating this genus from one or more others in the tribe.

**HEAD** (figs. 6, 7): Integument faintly pigmented, with scattered, very short sensilla that are not obviously setiform; internal ridges, antennae, apices of mandibles, and maxillary palpi somewhat darker; **following head areas spiculate: hypopharynx**, sides of labrum, and side and top of maxilla.

Head size moderately small compared with body; head capsule wider than long in frontal view; **vertex swollen on each side above antennae as seen in lateral view (fig. 7)**; produced area at most indistinctly wrinkled. *Tentorium including dorsal arms complete, very thin*; **anterior tentorial pit** very small, inconspicuous, **very low on face, just above anterior mandibular articulation**; posterior tentorial pit small, slightly below hypostomal ridge at rear of head; posterior margin of head capsule not marked by internal ridge but more or less evident because head capsule faintly sclerotized and smooth whereas neck membranous and wrinkled; median longitudinal ridge of head capsule absent; hypostomal ridge moderately well developed; pleurostomal ridge evident but weak; epistomal ridge indistinctly developed at anterior tentorial pits and fading completely above them. Parietal bands evident. **Antennal prominence weakly developed**; antennal disk moderate in size;



Figs. 5–11. Mature larva of *Brachynomada roigi*. 5. Postdefecating larva, lateral view. 6, 7. Head, frontal and lateral views. 8–10. Right mandible, dorsal, adoral, and ventral views. 11. Spiracle, side view. Scale refers to figure 5.

antennal papilla also moderate in size, possessing three or four sensilla. Clypeus wide in frontal view; *frontoclypeal area in lateral view normal, not protruding beyond labrum*. **Labrum narrow relative to head width in frontal view**, projecting moderately beyond clypeus in lateral view; labral sclerite not evident; labral tubercles moderately long, sharp-pointed, arising close to one another; epipharynx a simple curved surface.

**Mandible (figs. 8–10) slender and elongate, tapering to bladelike simple apex; dorsal and adoral surface with scattered sharp denticles; outer surface with a few short setae but without conspicuous setiferous tubercles; mandible as seen in adoral or aboral view S-shaped much as in *Melanomada*; cusp and apical concavity not differentiated, i.e., adoral mandibular surface a gently curved surface with scattered sharp denticles; dorsal and ventral apical edges serrate; ventral apical edge with fewer teeth than dorsal edge. Labiomaxillary region recessed and fused. Maxillary apex a**

simple lobe, bearing conspicuous sharp-pointed palpus and no galea; maxillary sclerites not evident. Labium not divided into prementum and postmentum; premental sclerite not evident; labial palpus unpigmented, not projecting, represented by single sensillum below and laterad of salivary opening. Salivary opening a simple hole without lips or other modifications although area around opening wrinkled. *Hypopharynx lobelike, projecting farther in lateral view than labiomaxillary region; hypopharyngeal groove evident.*

**BODY:** Integument without setae, distinctly *spiculate* behind head and on midventer of most abdominal segments but *not on venters of abdominal segments IX and X*; integument without spines or distinctly sclerotized tubercles. Body form (fig. 5) moderately robust; intersegmental lines not deeply incised but evident; intrasegmental lines not evident; *paired low, conical (i.e., not transverse) dorsolateral tubercles present on most body seg-*

*ments*, those of prothorax distinctly larger than those of mesothorax and slightly larger than those of metathorax; tubercles of abdominal segments II–V obtusely rounded; abdominal segment IX not produced ventrally but somewhat bulging dorsally; abdominal segment X bulging ventrally, perhaps attached somewhat dorsally to IX; anus positioned slightly dorsally on segment X; perianal area with smooth transverse lips. Spiracles (fig. 11) moderately large, most appearing on small projecting tubercles because atrium projecting above body surface; spiracles on abdominal segment VIII slightly smaller than others; atrium large relative to both subatrium and diameter of atrial rim, pigmented, with rim; atrial wall with non-denticulate ridges that form coarse reticulate pattern; wall between ridges curving outward so that atrial wall from outside seems to be coarsely, irregularly pebbled; peritreme present, moderately narrow; atrial opening on most spiracles faintly polyhedral or irregularly scalloped (i.e., not circular and smooth as in most bee larvae); primary spiracular opening small in comparison with atrial opening, with well-developed collar; subatrium annulate, with approximately eight chambers. Female with paired cuticular scars associated with imaginal discs on venter of abdominal segments VII, VIII, and IX; male sex characters unknown.

**MATERIAL STUDIED:** Two postdefecating female larvae, one cast larval skin, San Fernando, Catamarca Province, Argentina, November 11, 1991 (J. G. Rozen, A. Ugarté) from nest of *Psaenythia* sp.

*Kelita toroi*

Figures 12–18

**DIAGNOSIS:** The mature larvae of *Kelita toroi* and *K. tuberculata* can immediately be set apart from those of other members of the Brachynomadini by features presented in the diagnosis of *Brachynomada roigi*, above. The very low dorsal body tubercles of *Kelita toroi* (fig. 12) distinguish this species from *K. tuberculata* which has much more pronounced dorsal tubercles (Ehrenfeld and Rozen, 1977: fig. 10).

Head (figs. 13, 14): As described for *Brachynomada roigi*, except for following:

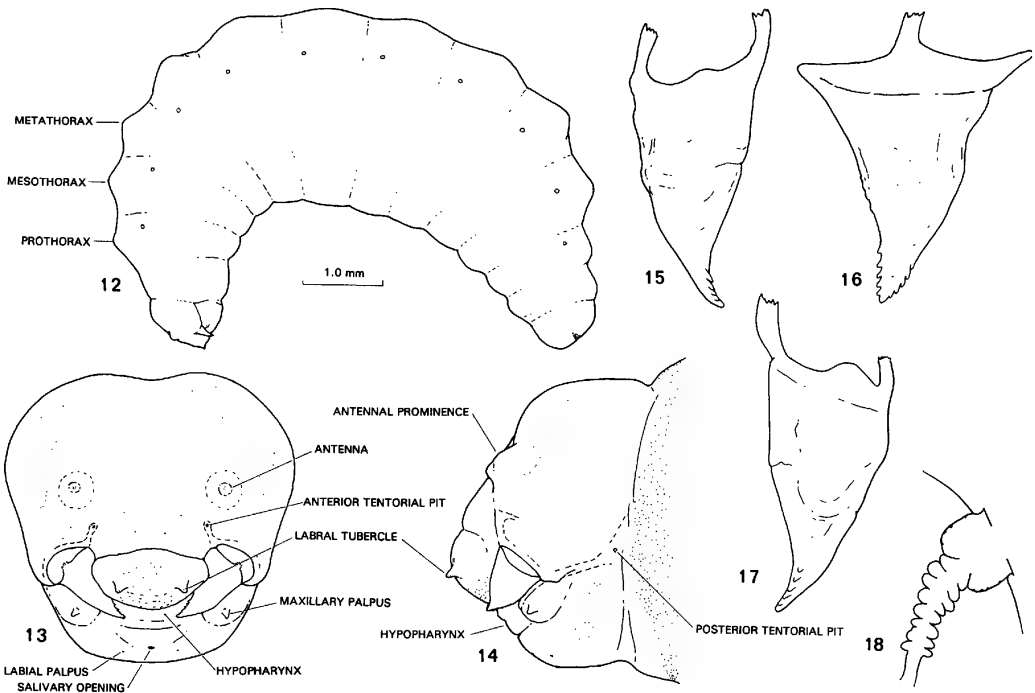
Integument unpigmented except for hypostomal ridge, antennal papillae, labral tubercles, mandibles, maxillary and labial palpi, and salivary opening; distinct spicules found only on sides of labrum, indistinct ones on dorsum and apex of labrum and on sides of labiomaxillary region; hypopharynx nonspiculate.

Head size moderate compared with body, not large as in *Kelita tuberculata* (Ehrenfeld and Rozen, 1977); head capsule wider than long in frontal view but narrower than that of *Brachynomada roigi*; vertex normally produced above antenna as seen in lateral view (fig. 14); this area not swollen nor more wrinkled than rest of integument. Anterior tentorial pit positioned about halfway between anterior mandibular articulation and antennal disc; posterior tentorial pit in weakly sclerotized area at junction of hypostomal ridge and posterior margin of head capsule; hypostomal ridge developed anteriorly, gradually becoming weaker posteriorly so that it is only vaguely evident in vicinity of posterior tentorial pit; epistomal ridge well developed between anterior mandibular articulation and anterior tentorial pit but absent between anterior pits. Antennal prominence small but well elevated as seen in lateral view (fig. 14). Labrum broad relative to head width in frontal view; labral tubercles widely separated from each other; epipharynx a nearly flat surface with low longitudinal median ridge.

Mandible (figs. 15–17) broad at base, short, tapering to bladelike simple apex; dorsal and adoral surfaces without distinct denticles but with some irregularities; outer surface without setiferous tubercles or setae but with scattered sensilla; mandible as seen in adoral or aboral view curving upward, not S-shaped and curving downward; dorsal and ventral apical edges with approximately same number of teeth. Labial palpus pigmented but not projecting, represented by single sensillum. Hypopharyngeal groove deeply incised.

**BODY:** As described for *Brachynomada roigi* except for following:

Integument distinctly spiculate behind head and weakly spiculate on venter of most body segments. Body form as illustrated (fig. 12); on postdefecating larva, very low, paired, conical dorsolateral tubercles present on most



Figs. 12–18. Mature larva of *Kelita toroi*. 12. Postdefecating larva, lateral view. 13, 14. Head, frontal and lateral views. 15–17. Right mandible dorsal, adoral, and ventral views. 18. Spiracle, side view. Scale refers to figure 12.

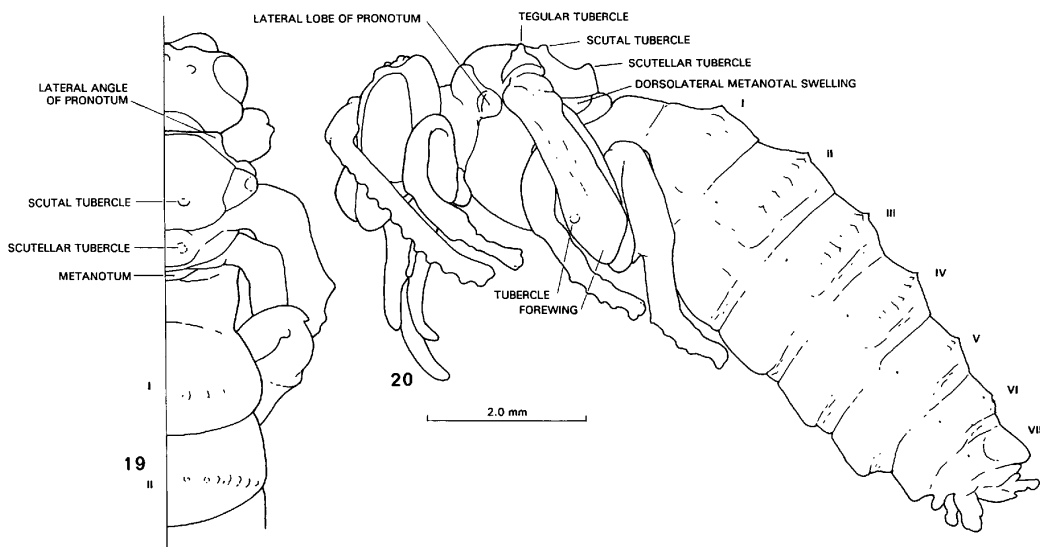
anterior and posterior body segments but on midbody segments tubercles scarcely noticeable (contrasting with conspicuous paired tubercles of most body segments of *Kelita tuberculata* [Ehrenfeld and Rozen, 1977: fig. 10]); mesothoracic dorsolateral tubercles larger than prothoracic tubercles; on predefecating larva, paired dorsal tubercles somewhat more evident but still low; abdominal segment IX not unusually produced dorsally or ventrally; segment X produced slightly more ventrally than dorsally, attached centrally to IX; anus apical in position. Spiracles (fig. 18) moderately small, not on tubercles; those of abdominal segment VIII slightly smaller than others; atrium (fig. 18) of normal size in relation to subatrium and to diameter of atrial rim, with rim; atrial wall with more or less concentric ridges; these ridges in places distinct and in others indistinct or even interrupted to the point of seeming like rows of merged spicules; ridges generally not forming reticulate pattern as in *Brachynomada roigi* (re-examination of the spiracles of *Kelita tuberculata* shows that the atrial wall, though less

ridged than that of *K. toroi*, does have vague ridges, contrary to the finding of Ehrenfeld and Rozen, 1977); peritreme present; atrial opening normally smooth and circular; primary spiracular opening normal, slightly smaller than atrial opening, with well-developed collar; subatrium annulate with approximately 8 chambers. Male with ventral transverse median scar between abdominal segments IX and X; female sex characters unknown.

**MATERIAL STUDIED:** 8 preserved postdefecating larvae, 7 preserved predefecating larvae, 4 live postdefecating larvae, 6 km south of Vicuña, Elqui Province, Chile, October 20, November 15, 16, 1991 (J. G. Rozen, A. Ugarté) from nests of *Leioproctus erithrogaster* Toro and Rojas (determined by H. Toro) and unknown paracolletine.

#### *Kelita tuberculata*

Although the postdefecating larva of this species was described by Ehrenfeld and Rozen (1977), details of its head capsule were



Figs. 19, 20. Pupa of *Brachynomada roigi*, body extended because of postmortem changes. 19. Right side of anterior part, dorsal view. 20. Entire pupa, lateral view.

omitted because the head capsule was lost during preparation. A larva from the Vicuña site, almost certainly belonging to the penultimate instar, suggests that not only it but also the last instar possesses the following features: tentorium thin but complete (including dorsal arms); antenna papilla with three sensilla; mandibular cusp not strongly produced, evenly curved, little, if at all dentate; hypopharynx nonspiculate. These features together with the description of the last instar in Ehrenfeld and Rozen (1977) agree closely with the description of the last instar of *Kelita toroi* (above); the most obvious structural difference in the larvae of these two species is the pronounced dorsal body tubercles of *K. tuberculata* (ibid.: fig. 10) (also pronounced in penultimate instar) in contrast with the much lower ones of *K. toroi* (fig. 12).

#### PUPA OF *Brachynomada roigi* Figures 19, 20

The following is comparative with descriptions of the pupae of *Melanomada sidaefloris* and *Paranomada velutina*, the only *Brachynomadini* whose pupae have been treated (Rozen, 1977). This species readily keys to *Paranomada* in Rozen and McGinley (1974).

DIAGNOSIS: Pupae of *Brachynomada roigi*, like those of *Melanomada sidaefloris* and

*Paranomada velutina*, lack sharp-pointed, small tubercles over much of their body surface, in contrast to all other known *Nomadinae* (see McGinley, 1989, for references). These three species also possess a projecting, rounded tegular tubercle, a feature not associated with other *Nomadinae*. The presence of paired paramedian scutal tubercles in *B. roigi* distinguishes it from the other two species.

HEAD: Scape and frons without distinct tubercles except for low mound on each side between lateral ocellus and antennal socket; vertex without distinct swellings although uneven; ocelli pronounced; each apical lateral angle of clypeus without tubercle; mandible with subapical swelling ventrally.

MESOSOMA: Setae absent. Lateral angles and posterior lobes of pronotum moderately produced. Mesepisternum without tubercles; mesoscutum with paramedian pair of small but distinct tubercles; axillae rounded, not produced; scutellum with pair of paramedian tubercles somewhat more pronounced than those of scutum; dorsolateral metanotal swellings conspicuous; metanotum swollen; propodeum without protuberances. Tegula with conspicuous, dorsally projecting tubercle, similar to that of *Melanomada sidaefloris* and *Paranomada velutina*; anterior wing with small tubercles near anterior margin, be-

tween two-thirds and three-fourths way to apex. All coxae and trochanters without distinct tubercles; fore and hind femora with small apical swellings; forefemur also swollen at base; tibiae without distinct tubercles; for basitarsi (of male) expanded toward apex, very much as in male of *Paranomada velutina*.

**METASOMA:** Terga I–VI each with apical transverse row of small, more or less distinct tubercles that are not apically pigmented and some of which are sharp-pointed. Sterna without such tubercles; terminal spine not present.

**MATERIAL STUDIED:** One male, San Fernando, Catamarca Province, Argentina, November 11, 1991 (J. G. Rozen, A. Ugarté), from nest of *Psaenythia* sp.

#### PHYLOGENETIC CONSIDERATIONS BASED ON BIOLOGIES AND IMMATURE STAGES

Information presented in this paper invites the following thoughts concerning the phylogenetic relationships of the Brachynomadini.

(1) Recent studies (summarized in Roig-Alsina, 1991b) indicate that the Nomadinae as defined by Michener (1974), Rozen et al. (1978), and Alexander (1990) included some taxa that made it polyphyletic. These taxa have now been identified and removed so that the Nomadinae *sensu stricto* appears monophyletic. However, it seems prudent to reconsider the relationships of other elements in the subfamily whenever new information becomes available. The synapomorphies pertaining to biology and immature stages that support inclusion of the Brachynomadini in the Nomadinae are presented in table 2 (italicized ones seem exceptionally strong because such features are unique or uncommon in the Apidae).

(2) The monophyly of the Brachynomadini is supported by the shape of their oocytes/eggs, extremely small egg index, and the conical dorsolateral body tubercles of the mature larvae.

(3) There are some new data that illuminate the phylogenetic relationships of the tribe with other groups in the Nomadinae. All known pupae of the Nomadinae (Nomadini, s.s., Rozen, 1977; Ammobatini, Rozen and

TABLE 2

#### Apomorphies Pertaining to Biologies and Immature Stages Shared by the Brachynomadini with Other Nomadinae

(Those judged to be exceptionally strong in italics.)

1. *Females enter open host cells and embed eggs in cell walls.* The Protepeolini are the only other parasitic apids with this feature.
2. *Numerous features of hospicidal first instars<sup>a</sup>* (see text for listings of features for *Brachynomada roigi* and *Kelita toroi*) as identified and coded in Rozen (1991b).
3. Mature larva<sup>a</sup>:
  - a. Tentorium slender or absent.
  - b. *Posterior tentorial pit weak, absent, or shifted from junction of postoccipital ridge and hypostomal ridge.*
  - c. *Posterior margin of head capsule without a distinct ridge or with very weak one.*
  - d. Longitudinal thickening of head capsule absent.
  - e. *Paired, acute labral tubercles present.*
  - f. Antennal prominence weak or absent.
  - g. *Mandible short* (except in some Brachynomadini).
  - h. Maxillary palpus distinct, acute, while labial palpus virtually absent.
  - i. Labrum not divided into prementum and postmentum.
  - j. Salivary opening without lips.
  - k. *Intrasegmental lines reduced or absent.*
1. *Distinct dorsolateral body tubercles absent, or, if present (Brachynomadini), then conical rather than transverse.*

<sup>a</sup> In analyses, homologous features of first and last stage larvae should be treated as a single character in many cases. For example, the paired labral tubercles of the first instar and those of the last instar are obviously the same structure.

McGinley, 1974; also Biastini, Epeolini, Holcopositini, new information) except those of the brachynomadine genera *Melanomada*, *Paranomada*, and *Brachynomada* (Rozen, 1977 and present paper) have small tubercles with sharp, darkly pigmented apices on many areas of the body (vertex, scutum, scutellum, and/or hind femur) in addition to bands of such tubercles apically on the metasomal terga. Occurrence of these tubercles on the head, mesosoma, and legs appears to be derived because this feature is unknown in the rest of the Apidae except in the Melectini (Torchio and Youssef, 1968). The absence of these tubercles in the Brachynomadini suggests that the tribe may be the sister group of the rest of the Nomadinae. The vertex of the mature

larva of the Brachynomadini, in lateral view, is either normally produced (*Kelita*) or slightly swollen (other genera), whereas in the other Nomadinae the vertex is unusually sloping in lateral profile, a presumed apomorphy. Hence, this character also suggests that the Brachynomadini are a sister group of the other Nomadinae.

Rozen et al. (1978) on the basis of mature larvae, Alexander (1990) using larval and adult characters, and Roig-Alsina and Michener (1993) analyzing larval features hypothesized the Brachynomadini to be the sister group of the other Nomadinae s.s. (present sense). Roig-Alsina's (1991a) analysis of another set of adult characters showed the tribe to be a highly evolved nomadine, a sister group of only the Epeolini. A reanalysis based on an expanded set of adult characters by Roig-Alsina and Michener (1993) supported Roig-Alsina's (1991) conclusions. These two hypotheses have yet to be resolved.

(4) What are the phylogenetic relationships of the genera within the Brachynomadini? The swollen, more or less wrinkled vertices of the mature larvae in all genera but *Kelita* are considered to be derived, and suggest that *Kelita* is the sister group of the other genera. The short mandible of the mature larvae of *Kelita* corresponds to the short mandibles of the other nomadines and appears to be a synapomorphy of the subfamily. The elongate, apically down-curved mandible of the other brachynomadines is unique in the Apidae and is presumably derived from the short mandible. The short, straight condition of the mandible of *Triopasites* can be interpreted as either a transitional step toward the elongate, down-curved mandible or a reversal.

## APPENDIX

Two new species referred to above are described and named here.

### *Brachynomada roigi*, new species

Figures 21–25

**DIAGNOSIS:** The genus *Brachynomada*, like many groups of cleptoparasitic bees, has been poorly collected in the past and is need of revision. Roig-Alsina (in litt.) kindly compared specimens of this species with the type

of *B. argentina* Holmberg and found that they agree closely. *Brachynomada roigi* differs "in having longer hairs on the undersurface of the femora and trochanters." Furthermore, "the apex of the female hind tibia ends in a point," rather than being "rounded as in *argentina*." It is his impression that *B. roigi* is a species "close to but distinct from *argentina*."

In preparing the description, I identified most characters by comparing specimens of this species and six other *Brachynomada* species (all unnamed) in the collection of the American Museum of Natural History. Those features that should be most helpful for species recognition are italicized.

**DESCRIPTION:** *Female.* Head width (maximum distance between outer margins of eyes) approximately 1.2–1.4 times length (vertex to lower margin of clypeus); width 1.78–2.13 mm; length 1.38–1.60 mm; wing length (from apex of costal sclerite to wing apex) 4.5–5.27 mm; total body length 5.5–7.7 mm.

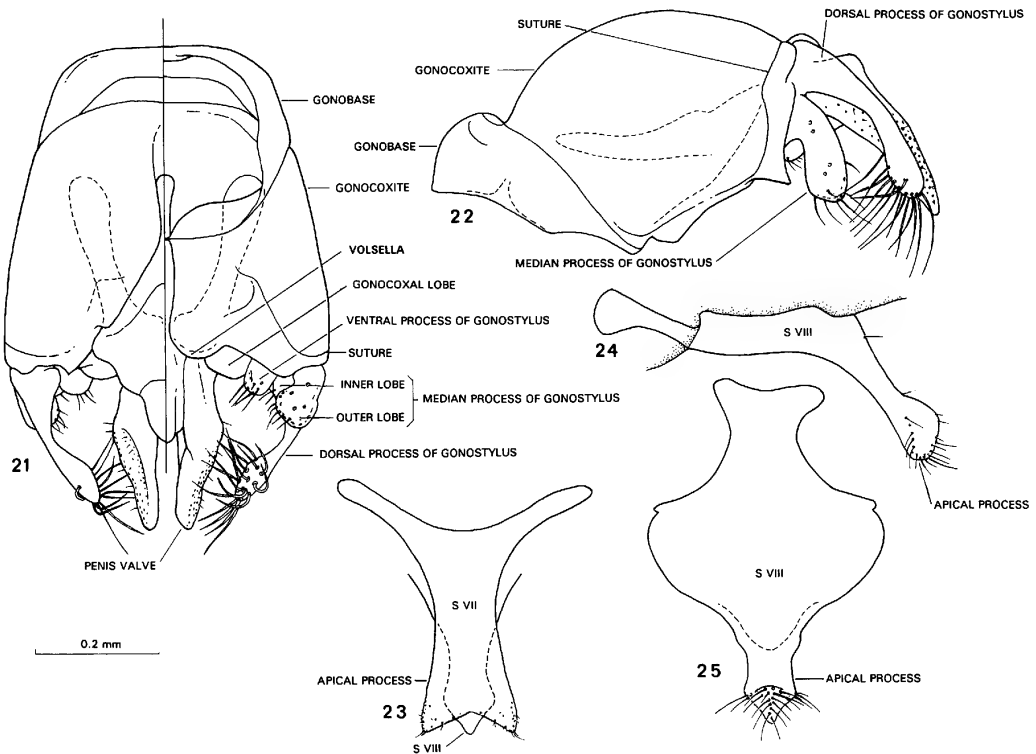
Inner eye margins converging slightly below; eye convergence index (lower interocular distance divided by upper interocular distance) 0.88–0.96. Apical margin of labrum with row of 3 to 5 rounded denticles; *clypeal disc convex, not flat.* *Maxillary palpus five-segmented*, about 1/3 length of galea; segment 2 longest, segment 5 longer than 3 or 4; first segment of labial palpus 2 times longer than second.

Forewing with three submarginal cells.

Mesoscutellum depressed only posteromedially. Apex of hind femur ending in point (that of *Brachynomada argentina* Holmberg rounded, according to Arturo Roig-Alsina, in litt.). Median apical triangle of metasomal sternum I bordered laterally by rounded ridge; surface of triangle with some decumbent plumose setae as well as erect, elongate, only microscopically plumose setae.

*Integument of frons immediately below ocelli smooth, shiny, with sparse, moderate-sized punctures, three to four puncture-widths apart* (on most other species, integument more densely punctate and punctures larger; on one other species, integument with extremely fine punctures and extremely polished); this area with scattered decumbent plumose setae on fresh specimens. *Integument of mesoscutal disc polished, with punctures mostly along in-*





Figs. 21–25. Male genitalia and associated sterna of *Brachynomada roigi*. 21. Genitalia, dorsal (left) and ventral (right) views. 22. Same, lateral view. 23. Sternum VII, showing width of its apical process in relation to that of sternum VIII, ventral view; setae at apex of VIII not illustrated. 24, 25. Sternum VIII, lateral and ventral views. Scale refers to all figures.

*cised midline and near parapsidal lines; between these groups, integument with widely scattered fine to very fine punctures so as to appear almost glabrous (most other species more densely, evenly punctate with punctures larger); setae on scutal disc sparse, fine, decumbent, scarcely noticeable. Mesepisternum with vestiture gradually becoming sparser below so that there is not an abrupt line separating upper and lower parts (as seen from side); setae in lower part moderately plumose, suberect (some other species with mesepisternum appearing nearly white above because of densely plumose, decumbent setae and abruptly dark below because of the sparseness and lack of plumosity of setae below). Middle and hind trochanters and femora with moderately dense, long, strongly curved setae that are white and finely but distinctly plumose (some other species with these setae sparser, shorter, at most weakly curved and scarcely plumose, so as to appear inconspicuous; one other species with setae even dens-*

*er and longer but less plumose). Metasomal tergum II with punctures very fine. Metasomal sterna II–IV with suberect setae long, finely plumose (more conspicuous than very fine, shorter setae of some other species).*

*Head black above, grading to reddish below antennal sockets so that clypeus reddish (with most species, clypeus mostly black or dark brown); undersurface of scape reddish. Mesoscutum reddish with narrow, dark-brown triangle spreading forward along median line from dark mesoscutellum; this triangle not reaching pronotum (with other species, pattern of dark area on scutum not triangular); mesepisternum reddish with brownish area above scrobe and with lower part dominated by large brownish maculation; legs mostly reddish except mid and hind basitarsi and hind tibia dark brown. Forewing with tip darker than rest of wing. Metasoma reddish, with only tergum V on some specimens partly darkish brown (with other species, dark apex*

of metasoma pronounced and extending farther forward).

*Male.* Head width approximately 1.3–1.4 times length (vertex to lower margin of clypeus); width 1.80–2.15 mm; length 1.33–1.63 mm; wing length 4.4–5.2 mm; total body length 5.8–7.7 mm.

Inner eye margins converging only very slightly; eye convergence index 0.90–0.98. Other structural features as described for female except for following: Mesoscutellum slightly depressed medially anteriorly as well as posteriorly. Fore basitarsus with apical one-fourth of inner side faintly sulcate, as seen in silhouette (modification much less pronounced than that found in male of *Paranomada*); this area covered by long curved hairs arranged in linear series forming comb in line with strigilis. Hind femur normal, without ventral projection; hind tibia normally wide apically, with two spurs (see Remarks following description of *Melanomada margaretae*). *Pygidial plate apically rounded* (not emarginate). *Metasomal sternum VII with apical process much broader at apex than that of sternum VIII* (fig. 23) (in another species, these processes subequal in width). *Dorsal processes of gonostylus shorter than penis valve in lateral view* (fig. 22) (in another species, dorsal process longer than penis valve); *setae of dorsal process arising only from apical one-fifth of process and only moderately long* (in another species, setae arising from apical one-half of process and very elongate); *ventral process of gonostylus* (see Remarks below. MDBU/) *relatively large, projecting beyond gonocoxal lobes in ventral view* (fig. 21) (in another species, smaller, surpassed by gonocoxal lobe in ventral view).

Integumental punctation in general denser, larger than that of female and consequently space between punctures not so great (on males of other species, integument may also be more densely punctate and with punctures larger). *Integument of mesoscutal disc polished* (not dull because of minutely tessellate sculpturing), *with punctures grouped along incised midline and near parapsidal lines; between these groupings, integument with scattered, moderately large punctures, two to three puncture-widths apart; setae on scutal disc sparse, fine, decumbent, scarcely noticeable.* Mesepisternum with vestiture gradually be-

coming sparser below so that there is not an abrupt line separating upper and lower parts (as seen from side); *setae in lower part moderately plumose, suberect* (some other species with mesepisternum appear nearly white above because of densely plumose, decumbent setae and abruptly dark below because of the sparseness of setae below). Metasoma with marginal tergal bands narrow, composed of sparse white decumbent setae (on some species these bands broader, more conspicuous, and occasionally of yellowish setae).

Head black except lower part of clypeus grading to reddish; scape brownish. Mesoscutum on most specimens black or black with indefinite reddish or brownish areas along anterior margin, but on several specimens dark reddish except for median blackish maculation extending forward from posterior margin but not reaching anterior margin; mesepisternum blackish except on several specimens indefinite brownish to reddish area near pronotum and midcoxa; coxae tending to be mostly dark with some reddish coloring apically, other leg segments dark reddish except mid and hind basitarsi and hind femur dark brown. Forewing with tip darker than rest of wing. Metasomal tergum I mostly reddish except at base and usually for indefinite median brown mark on disc; tergum II reddish anteriorly on both sides grading to brownish black medially and posteriorly; elsewhere metasoma dark brown to black.

**HOLOTYPE:** Female, ARGENTINA, **Catamarca:** San Fernando, November 11, 1991 (J. G. Rozen, L. Peña, and A. Ugarté) *Psaenythia* nest #2; allotype, same data except November 3–6, 1989 (J. G. Rozen, A. Roig) *Psaenythia* nest #2.<sup>3</sup> The holotype and allotype are in the collection of the American Museum of Natural History.

**PARATYPES:** 2 males, same data as holotype; 1 male, same data as holotype except *Psaenythia* nest #6; 1 female, 29 males, same data as holotype except no nest; 7 females, 5 males, same data as allotype; 1 female, same data as allotype except no nest; 2 males, same

<sup>3</sup> *Psaenythia* nest #2 of November 3–6, 1989, was a different nest of the same species of *Psaenythia* from the nest #2 of November 11, 1991.

data as allotype except November 25, 1989, no nest. 3 males, **San Juan:** Pampa de Tucunuco, S of San José de Jáckal, November 1, 1991 (J. G. Rozen, L. Peña, and A. Ugarté).

**ETYMOLOGY:** It is a pleasure to name this species in honor of Dr. Arturo Roig-Alsina, who assisted in collecting the type series and compared specimens with the type of *Brachynomada argentina*.

**HOST:** *Psaenythia* sp.

**REMARKS:** The male genital capsule and its appendages in the Brachynomadini are incompletely understood. Ehrenfeld and Rozen (1977) attempted to identify the structures in *Kelita*, and the same terminology has been applied in *Melanomada margaretae* (figs. 26, 27) and *Brachynomada roigi* (figs. 21, 22). The volsella is weakly developed in *Kelita*, *Melanomada*, *Brachynomada*, and in other genera in the complex and is identified only by its position. The gonocoxal lobe appears to be a well-defined structure, consistent among the genera in the complex, but its homologies to features in other nomadines are unknown.

*Brachynomada*, *Melanomada*, *Paranomada*, *Triopasites*, and *Kelita* show great diversity in structures that seem to involve their gonostyli. In *Kelita* (Ehrenfeld and Rozen, 1977), the gonostylus was thought to consist of a number of setiferous processes and attempts were made to homologize them from one species to the next. According to that study, the gonostylus in lateral view consisted of a dorsal process (ibid.: fig. 28), a median processes which had an outer and inner lobe in some (but not all) cases (ibid.: fig. 27), and a ventral process. Some of the species seemed to be missing the dorsal processes. The setiferous process of the gonostylus in *Melanomada margaretae* (figs. 26, 27) (as well as in other species in the genus, Snelling and Rozen, 1987) and in *Brachynomada roigi* (figs. 21, 22) apparently can be homologized with those of *Kelita*, as illustrated. In *Brachynomada* and *Melanomada*, the ventral process lies close to the gonoxal lobe and is actually no more ventral than the outer lobe of the median process. The inner lobe of the median process is reduced and hidden between the dorsal process and the ventral process but bears one or more setae which help in its identification. Michener and Roig (1993: figs.

33, 34) illustrated several setiferous processes at the base of the gonostylus of *Hexepeolus* and called one of them the parapenial lobe. It seems likely that they are homologs of the setiferous processes of the gonostylus of the Brachynomadini. Future studies of the male genitalia of the Nomadinae and Apinae are required to establish the true homologies of these processes.

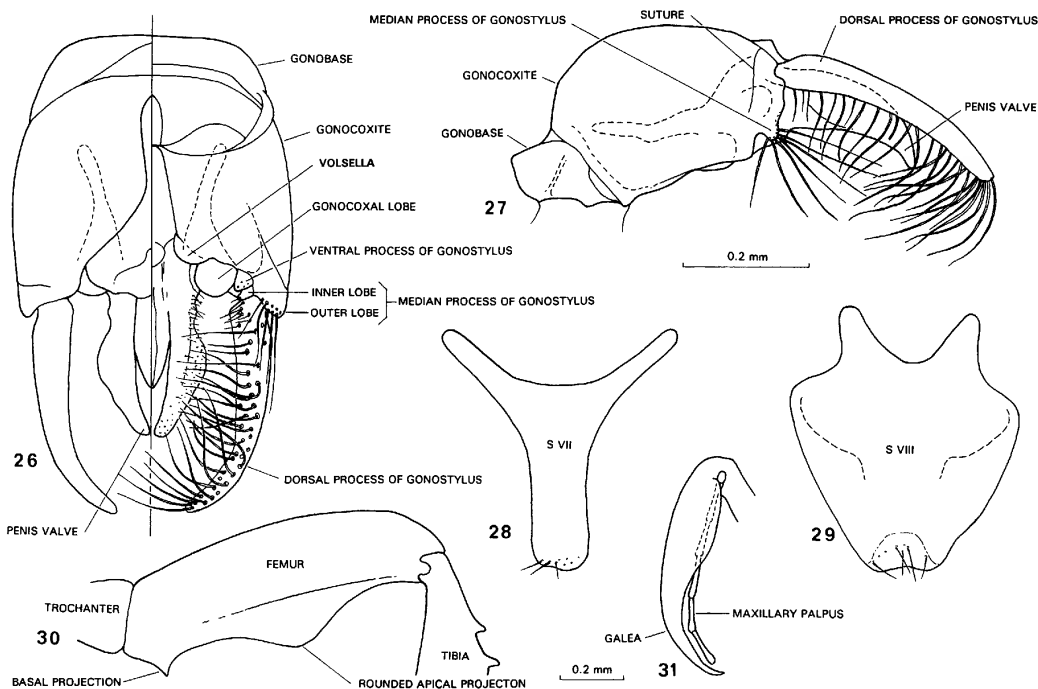
An interesting structure on the distal end of each gonocoxite is a suture that in the case of *Melanomada margaretae* and *Brachynomada roigi* is the external evidence of a conspicuous internal phragma. Michener and Roig-Alsina (1993: fig. 33) termed this suture in *Hexepeolus* the ventrolateral sulcus. In *Kelita* (Ehrenfeld and Rozen, 1977), the suture was suggested to be the demarcation between the gonocoxite and gonostylus, but this identification is by no means certain. The suture (and phragma) in *M. margaretae* and *B. roigi* does not shed additional light on its homologies.

For discussion of other features, see Remarks following the description of *Melanomada margaretae*.

#### *Melanomada margaretae*, new species

Figures 26–31

**DIAGNOSIS:** Both sexes of this species superficially appear black (although leg extremities and tegulae are paler) and consequently can be distinguished from most of the other species of *Melanomada* which usually have partly or even completely reddish metasomata. The maxillary palpi of *M. margaretae* are unusually long, nearly as long as the galeae, and are similar therefore only to the palpi of *M. chica* which, however, are even longer than the galeae. The terminal palpal segment is subequal to the others and is widened only slightly apically, in contrast to the terminal palpal segment of *M. chica*. The smaller body size of *M. chica* and its completely ferruginous metasoma and conspicuous ferruginous areas elsewhere also easily separate the two species. *Melanomada margaretae* is the only known species in the genus to possess both a basal ventral projection and a more distal, rounded ventral projection on the hind leg of the male. Males of all other species have only a single basal ventral pro-



Figs. 26–31. Adult structures of *Melanomada margaretae*. 26. Male genitalia, dorsal (left) and ventral (right) views; setae depicted only in ventral view. 27. Same, lateral view. 28. Male metasomal sternum VII, ventral view. 29. Male metasomal sternum VIII, ventral view. 30. Hind right femur of male, posterior view. 31. Left maxilla, showing galea in relation to maxillary palpus, side view. Scales refer to figures 26–29 and figures 30, 31, respectively.

jection (which appears to be an autapomorphy of the genus).

The format of the following has been modified from Snelling and Rozen (1987). Italicized characters should be especially helpful in distinguishing this species from the others in the genus.

**DESCRIPTION:** *Female*. Head width approximately 1.3 times length (vertex to lower margin of clypeus); width 1.55–1.73 mm; length 1.15–1.25 mm; wing length 3.8–4.2 mm; *total body length* 4.8–5.3 mm, greater than that of *Melanomada chica* but smaller than that of *M. sidaefloris*, *M. melanantha* (Linsley), and *M. annectens* Snelling and Rozen.

Vertex strongly arched above tops of eyes; inner eye margins converging moderately below; eye convergence index (lower interocular distance divided by upper interocular distance) averaging 0.85; posterior ocelli separated from posterior margin of head by their diameters or more, as seen from above.

*Disc of clypeus flat*, not convex as in *Melanomada annectens*, *M. melanantha*, and *M. sidaefloris*. Middle flagellar segments about 1.2 times longer than broad. *Maxillary palpus* (fig. 31) six-segmented, almost equal in length to galea; segments 2–6 subequal in length; segment 6 only slightly expanded apically; first segment of labial palpus more than 2.5 times longer than second.

*Forewing with three submarginal cells.*

Median apical triangle of metasomal sternum I conspicuous, bordered laterally by distinct, rounded (i.e., noncarinate) ridge; surface of triangle hidden by decumbent plumose setae.

Integument smooth and shiny; clypeus with sparse, fine punctures and irregularly distributed minute punctures; supraclypeal area with scattered fine punctures; frons and vertex with moderately sparse, small punctures; front of head below midlength largely obscured by dense, appressed, copiously plumose pubescence on fresh specimens. Mesoscutum and

scutellum shiny between fine punctures that are mostly separated by distances greater than their diameters (not as impunctate as *Melanomada chica*, *M. sidaefloris*, and apparently *M. grindeliae* [Cockerell] but not as densely punctate as *M. nimia* Snelling and Rozen and *M. annectens*). Mesepisternal punctures fine, subcontiguous, its integument largely obscured by copiously plumose, appressed hairs, all as in *M. nimia*. Sides of propodeal triangle (unlike those of *M. grindeliae*) largely obscured by copiously plumose appressed hairs; median, apubescent area of triangle mostly dull, due to fine longitudinal rugulae. Basal metasomal terga shiny between scattered, obscure, minute punctures; succeeding terga with surface increasingly finely punctate, hence duller.

*Head, mesosoma, metasoma, and legs mostly black to very dark brown*; labrum, apical margin of clypeus, pronotal lobe, and tegula dark ferruginous. Underside of flagellum brown to black. Wings transparent brown (as in *Melanomada annectens*); veins and stigma dark brown.

*Male*. Head width approximately 1.4 times length; width 1.63 mm; length 1.18–1.20 mm; wing length 4.0 mm; *total body length 5.8 mm*.

Other features as described for female, except for following: Eye convergence index approximately 0.89. Middle flagellar segments about 1.2 times broader than long. Fore basitarsus little modified (about as in female); setae on apical inner side only slightly longer and thicker than those on rest of inner side, not arranged in linear series to form comb. *Hind femur (fig. 30) with small but distinct ventral projection at base, with more rounded, larger ventral projection about two-thirds way toward apex, and with vague swelling near apex on anterior surface*. As in female, hind tibia normally wide apically, with two spurs (in contrast to males of two undescribed species belonging to the Brachynomadini; see Remarks). Metasomal sterna VII and VIII as illustrated (figs. 28, 29). Genitalia as illustrated (figs. 26, 27).

**HOLOTYPE:** Female, MÉXICO, Durango: Reserva Biosfera Mapimí near Ceballos, August 23, 1991 (J. G. Rozen); allotype, same except on *Malvella leprosa*. These specimens are deposited in the Instituto de Biología,

Universidad Nacional Autónoma de México, México, D.F.

**PARATYPES:** 4 females, same as holotype; 1 male, same except “dunas” (R. Ayala); 1 female, same except “dunes N estac.” August 22, 1991 (T. Griswold); 1 female, MÉXICO, Chihuahua: 26 km NW Camargo, August 27, 1991 (J. L. Neff); 1 male, same except 27 km N Camargo, August 27, 1991 (T. Griswold) on *Dyssodia*.

**ETYMOLOGY:** The name of this species honors Margaret Ann Rozen.

**HOST:** Unknown, but possibly one or more species of *Exomalopsis*, which were abundant in the area. This species was found flying with the smaller *Melanomada chica*.

**REMARKS:** The elongate maxillary palpus of this species as well as that of *Melanomada chica* indicate that palpal length is variable within the genus and is not, therefore, a good criterion for attribution to the Brachynomadini, contrary to Snelling and Rozen (1987).

Some characters, not formerly used, are introduced in this description (and also in that of *Brachynomada roigi*, above): (1) The hind femur of the male in *Melanomada* exhibits a basal ventral projection in all species and has no counterpart in related genera. In the case of *M. margaretae* alone (fig. 30), the femur also has a more apical ventral swelling with the consequence that the intervening area seems to form a groove, perhaps used for clasping the female during copulation. (2) The apex of the hind tibia of the male is normal for bees in that it bears two spurs and it is not greatly broadened with its anterior edge produced as a large fixed hooked spine. Such modifications are known for two undescribed taxa belonging to this complex, one from Argentina and the other from Mexico. In spite of this remarkable similarity between these two taxa, they do not in other ways seem related. (3) Metasomal sternum I in both sexes of *M. margaretae* has a median triangular area extending forward from the apical margin. The sides of the triangle are formed by a raised ridge that is rounded and not carinate. In *Triopasites penniger* the triangle is very pronounced because its sides are carinate, strongly projecting, and there is a sharp, jagged transverse ridge extending between the two sides that is generally more pronounced

in males than in females. In *Brachynomada roigi*, the sides of the triangle are low and rounded in males, low but sometimes finely

carinate in females, and without a transverse ridge in both sexes.

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