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The Cleptoparasitic Bee Genus *Rhopalolemma*, with Reference to Other Nomadinae (Apidae), and Biology of its Host *Protodufourea* (Halictidae: Rophitinae)

JEROME G. ROZEN, JR.,[1] ARTURO ROIG-ALSINA,[2]
AND BYRON A. ALEXANDER[3]

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

[2] Research Associate, Department of Entomology, American Museum of Natural History. Investigador de CONICET. Address: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Av. A. Gallardo 470, 1405 Buenos Aires, Argentina.

[3] Associate Professor, Department of Entomology, University of Kansas, Lawrence, Kansas 66045; deceased November 30, 1996.

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ABSTRACT

A new species, *Rhopalolemma rotundiceps* Roig-Alsina (holotype female), is described from southern Arizona and compared with the only other species in this cleptoparasitic genus, *R. robertsi* Roig-Alsina. The male of the new species is also described, providing the first account of the male of the genus. *R. rotundiceps* attacks nests of *Protodufourea eickworti* Bohart and Griswold, and the biologies of host and parasite are described. Comparisons are made regarding the eggs, oocytes, and ovaries of *Rhopalolemma*, *Neopasites*, and *Townsendiella*, and the comparative morphology of the female reproductive tract is presented. The mature larva of *R. rotundiceps* is also described, the first such description for the genus. Last, the phylogenetic relationships of *Rhopalolemma* are considered based upon adult and larval characters and information regarding eggs and oocytes. Cladistic analysis indicates that *Rhopalolemma* is correctly placed in the Biastini.

INTRODUCTION

In this paper we describe a new species of *Rhopalolemma*, expand our knowledge of the biology of this cleptoparasite genus, and define more accurately its phylogenetic relationships to the other taxa in the Nomadinae. In addition to adults of the new species, *R. rotundiceps*, we describe its egg (and oocyte), mature larva, certain aspects of the female reproductive system, and biology. These are the first such accounts for this genus. Because the biology of its host, *Protodufourea eickworti* Bohart and Griswold (1996), is intertwined with that of the cleptoparasite, notes on the nesting habits of *P. eickworti* resulting from this investigation are included.

Rhopalolemma was named and described in 1991 based on a new species, *R. robertsi* (Roig-Alsina, 1991). It was the first new North American genus of Nomadinae to be recognized in more than 50 years. Its description was based on a single female collected in May 1973 by the late Radclyffe B. Roberts near 29 Palms, San Bernardino Co., California. A year after the genus was described, the late George C. Eickwort discovered a number of specimens, presumed at the time to be *R. robertsi*, flying around the nest entrances of *Protodufourea eickworti* at the Desert Research Station, east side of the Tucson Mtns., Pima Co., Arizona. He concluded correctly from these observations that the cleptoparasite attacked the nests of that rophitine genus. Eickwort showed the first author (JGR) the site in late April of that year, by which time cleptoparasite activity had abruptly ceased although a few *Protodufourea* were still in flight. Because of Eickwort's intention to study the site, he had collected only a few females, and, by the time he attempted to collect males, they had disappeared.

On the basis of Eickwort's discovery of the host, JGR suspected that the late Paul D. Hurd, Jr., might have collected specimens earlier (1966) because of a reference in Moure and Hurd (1987: 26–27) regarding an "unidentified *Neopasites*" associated with nests of an "undescribed *Protodufourea*" 9.1 mi south of Quartzsite, Arizona. Through the kind efforts of Ronald J. McGinley, Smithsonian Institution, and Howell V. Daly, University of California (Berkeley), Hurd's specimens were found. They proved to be the same species of *Rhopalolemma* as the one discovered by Eickwort. Hurd, then, was the first person to collect males as well as females of this seemingly rare genus.

On subsequent midspring trips to the Southwest, JGR revisited Eickwort's locality twice but collected only a single tattered *Rhopalolemma* female in mid-April 1993. *Protodufourea* and *Rhopalolemma* thus appeared to be early spring bees. To be found, they would have to be sought in March, at least in the low deserts, when *Phacelia*, the host plant of *Protodufourea*, was in maximum bloom. In 1995, JGR and his wife, Barbara L. Rozen, searched for the host and cleptoparasite in southern Arizona during the second half of March. They found *Protodufourea eickworti* at a number of localities, including Hurd's site, although no cleptoparasites were seen there. At the suggestion of Jim Cane, the Rozens also visited Organ Pipe Cactus National Monument (Organ Pipe).

There and at the Desert Research Station in the Tucson Mtns., they found the host bees and their cleptoparasites, recovered immature stages of both, and made the observations presented below. When specimens were sent to the second author (AR-A) so that he could describe the male of the presumed *R. robertsi*, he determined that all of the recently collected material as well as Hurd's specimens represented a new species. *Rhopalolemma robertsi* is still known from only the single female specimen upon which the genus was based.

In manuscript preparation, AR-A was responsible for the description of *R. rotundiceps*. JGR described the biology of *Protodufourea* and *Rhopalolemma* as well as eggs, oocytes, and larvae of *Rhopalolemma* and related bees. The third author (BAA) described the female reproductive tract. All authors contributed to the phylogenetic analysis.

The following abbreviations are used: T = tergum; S = sternum.

ACKNOWLEDGMENTS

This study was made possible because of the helpful assistance of the bee specialists mentioned above. Barbara L. Rozen provided valuable field support for the 1995 trip to the Southwest. Dr. Terry L. Griswold, USDA Bee Biology and Systematics Laboratory, Utah State University, kindly identified the *Conanthalictus* associated with this study, and Dr. Tom Zanoni, New York Botanical Garden, identified the *Phacelia*. We thank Mr. John S. Ascher, Cornell University, for the loan of a specimen of *Rhopalolemma rotundiceps* from the Rosekruge Mtns., Arizona. We are indebted to Dr. Wojciech J. Pulawski, California Academy of Sciences, for the loan of the type of *R. robertsi*.

JGR thanks Dr. Robert L. Smith, Department of Entomology, University of Arizona, for permission to study this species and its host at the Desert Research Station. JGR also extends his appreciation to Mr. Timothy Tibbitts and the other officials of the Organ Pipe Cactus National Monument, United States Department of the Interior, National Park Service, Western Region, for allowing investigation of these species at the Monument, south of Ajo, Arizona.

Dr. David A. Grimaldi kindly took the light micrographs of the *Rhopalolemma* eggs (figs. 9, 10). The expertise of Peling Fong-Melville is much appreciated for the SEM micrographs and for the critical point preparation of oocytes.

We express our appreciation to Drs. Robert L. Minckley and Charles D. Michener who have reviewed this manuscript and offered valuable suggestions for improving it.

GENERIC CHARACTERS

Both sexes of *Rhopalolemma rotundiceps* have a brush of setae on the inner apex of the asymmetrical second segment of the foretarsus. When the holotype of *R. robertsi* was re-examined, a similar but less compact brush was found on the asymmetrical second segment of the foretarsus. Hence, the presence in the female of the brush and asymmetry of the segment appear to be diagnostic for the genus. Modified foretarsi with brushes are present in the males of other Nomadinae (e.g., *Nomada*, Brachynomadini, and other Biastini) but not in the females. Another trait that is usual in males of several Nomadinae but not present in any females except those of *Rhopalolemma* is the carinate lateral margin of the clypeus and the shiny groove lateral to it.

The specimens studied show variation in the number of submarginal cells, the position of the first recurrent vein, and the length of the marginal cell. Two males from Organ Pipe, have three submarginal cells on one wing (fig. 6) and two on the other. Usually both recurrent veins meet the second submarginal cell, but in the males from Quartzsite, the first recurrent vein meets the first transverse cubital vein. The length of the marginal cell varies from as long as to 1.2 times longer than the distance from the apex of the cell to the apex of the wing. The presence of three submarginal cells in some specimens suggests that the two-celled condition in the Biastini may have arisen independently from a similar reduction found in other tribes of Nomadinae; reaquisition of a cell is probably more unlikely than independent loss.

Males of *Rhopalolemma* can be separated from the other males of Biastini by the sim-

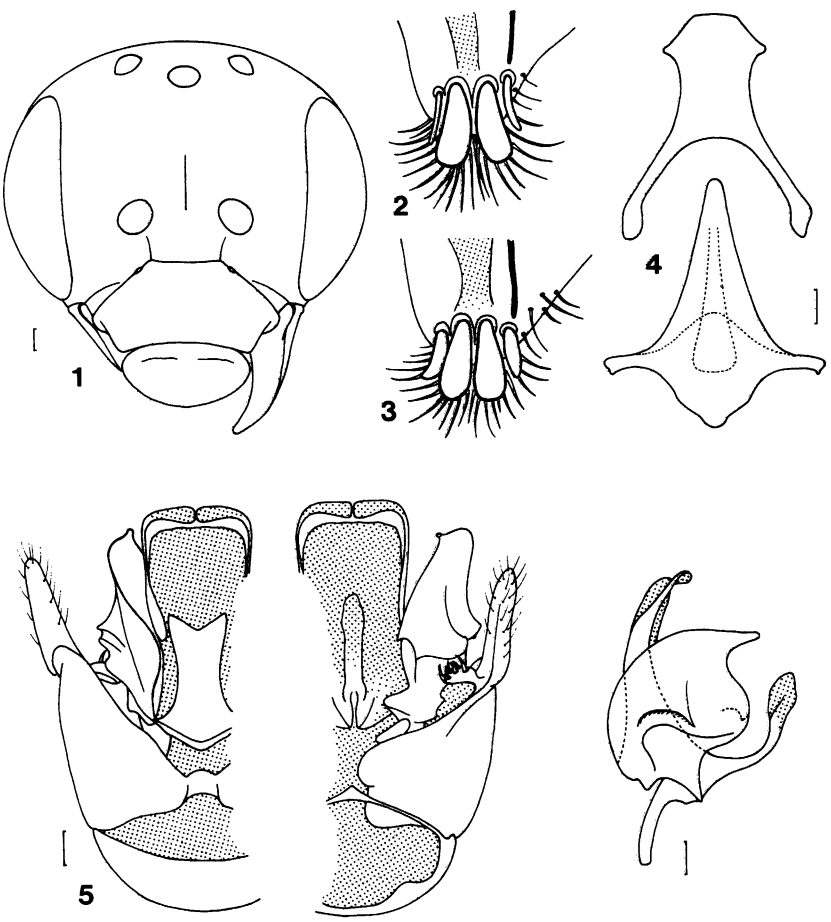
ple mandible and the longer scape. They can be separated from males of other Nomadinae by the following suite of characters: pygidial plate with carinate margins, covering all the exposed dorsal surface of T7; labrum broader than long; marginal cell with rounded apex separated from wing margin; and penis with strong basiventral projection (fig. 5). In the key to genera of bees of North and Central America (Michener et al., 1994) males of *R. rotundiceps* run correctly to *Rhopalolemma*, as long as they are keyed as having two submarginal cells.

ADULTS OF *RHOPALOLEMMA ROTUNDICEPS* ROIG-ALSINA, NEW SPECIES

Figures 1–6

DIAGNOSIS: *Rhopalolemma rotundiceps* differs from *R. robertsi* in its smaller body size, the more rounded, elevated vertex of the head, the median ocellus positioned above the upper tangent of the eyes, the broader frons (proportion of greatest head width to middle interocular distance 1.50 in *R. rotundiceps*, 1.65 in *R. robertsi*), the antennal sockets closer to each other (proportion of antennocular to interantennal distance 0.85 in *R. rotundiceps*, 0.72 in *R. robertsi*), the flatter, less protuberant clypeus, the shorter labrum transversely ridged near the base, the weaker lateral spinelike setae of the lateral lobes of the female S6, and the much more extensive patches of white decumbent setae on the sides of the female T5.

DESCRIPTION: **Female holotype.** Length 5.3 mm; length of forewing 3.4 mm (variation in paratypes: length 5.3–6.0 mm; length of forewing 3.4–4.0 mm). **Coloration.** Integument of head black, except apical rim of clypeus and most of mandible reddish; underside of flagellum dark brown, but first two flagellomeres lighter. Thorax and propodeum black, except pronotal lobe and tegula light reddish. Legs black with apices of femora, bases and apices of tibiae, and foretarsus reddish brown; all tibial spurs light reddish. Metasoma reddish with base of T1 and disk of T2 medially brown, disks of T3–5 almost black; disks of S1–4 with brownish spot laterally. Wings hyaline, with infuscated apices; veins and pterostigma black. **Vestiture.** With short, appressed, plumose white hairs dense on clypeus and supraclypeal area, around antennal socket, on gena and around proboscideal fossa, on upper margin of pronotum and pronotal lobe, on upper half of mesopleura, with lateral band on scutum and elongate patch along notaulus, on lateral parts of scutellum and metanotum, on venter of thorax and coxae, on underside of fore and mid femur and external surface of mid tibia, and on posterolateral angle of propodeum. Vertex of head, disk of scutum, and center of scutellum and metanotum with short plumose brownish hairs. Metapostnotum bare. Other parts of head and thorax with sparse white hairs. Metasomal terga with short, appressed, plumose white hairs surrounding on T1 a transverse discal reddish spot, on T2 a large discal reddish area trilobed apically, on T3 a blackish discal area strongly trilobed apically, and on T4 three round black spots; these hairs on T5 leaving a central band and a narrow area surrounding pseudopygidial area (in some paratypes median lobe of dark area of T3 and median dark spot of T4 reaching apical margin of tergum). Metasomal sterna with appressed white hairs denser medially and apically. **Sculpture.** Frons, scutum, scutellum, and mesopleurae with even punctures separated half to one puncture diameter. Clypeus with shiny, unpunctate apical rim narrow medially, laterally as broad as one-third of flagellum diameter. Labrum closely punctured, transversely ridged near basal fifth. Metapostnotum rugose, areolate close to metanotum. **Morphology.** Vertex convex, in frontal view median ocellus above upper level of eyes. Proportion of lower to upper interocular distance 0.90; greatest head width to middle interocular distance 1.50; distance between posterior ocelli to ocellocular distance 0.82; antennocular distance to interantennal distance 0.85. Labrum 1.8 times as wide as long. Scape 1.8 times as long as apical width, flagellomeres subequal in length. Mandible simple. Foreleg with second tarsomere strongly asymmetrical, bearing apical brush on expanded mesal lobe; third tarsomere slightly asymmetrical. Pygidial plate indicated by lateral carinae, truncate apex swollen, mamillated, bearing minute, erect setae. Pseudopygidial area narrow, bordering apical round emargination of T5. Emargina-



Figs. 1, 2. *Rhopalolemma rotundiceps*, female. **1.** Head, frontal view. **2.** Apex of left lateral lobe of S6, ventral view. Fig. 3. *Rhopalolemma robertsi*, female. Apex of left lateral lobe of S6, ventral view. Figs. 4–5. *Rhopalolemma rotundiceps*, male. **4.** Seventh (above) and eighth (below) metasomal sterna. **5.** Entire genital capsule, dorsal view (left), ventral view (middle), and penis valve and penis, lateral view (right). Scale lines = 0.1 mm.

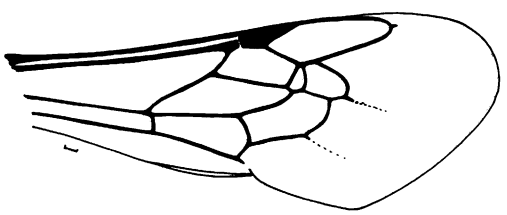


Fig. 6. *Rhopalolemma robertsi*, male, forewing with three submarginal cells. Scale line = 0.1 mm.

tion between strong apical tubercles of S5 bearing dense row of long setae. Lateral lobe of S6 with four principal spinelike setae, central two much larger than lateral ones (fig. 2). Shape of S6 and sting apparatus as in *R. robertsi*.

Male. Length 4.8–6.0 mm; length of forewing 3.4–3.8 mm. **Coloration.** Black, except apex of mandible, pronotal lobe, and tegula reddish. Some specimens with legs all black, except pale tibial spurs; other specimens with legs partly reddish, as in female. Metasoma black, but in some specimens T1–2 with reddish apices, and sterna also partly reddish. **Vestiture** and **sculpture** similar to that of

female. T1–6 with white, appressed pubescence surrounding dark central areas trilobed posteriorly; in some specimens dark areas of T3–5 medially reaching posterior margins of terga. Vestiture of sterna short, appressed, not forming apical fringes. **Morphology**. Proportion of lower to upper interocular distance 0.90; greatest head width to middle interocular distance 1.54; antennocular distance to interantennal distance 0.90. Labrum 1.85 times as wide as long. Antenna with 11 flagellomeres. Scape 1.8 times as long as apical width; first flagellomere as long as its apical width, 1.2 times as long as second flagellomere. Mandible simple. Clypeus with lateral margin carinate and with shiny groove above carina. Foretarsus with second tarsomere asymmetrical, mesally bearing brush of hairs. Claws of foreleg with inner tooth pointed, close to outer tooth; claws of mid and hind legs with inner tooth flattened, separated from outer tooth, apically truncate. Pygidial plate occupying complete exposed dorsal surface of T7, carinate margins converging apically, apex rounded; surface of plate with dense punctures; short base of tergum, basad to pygidial plate, abruptly elevated. Hidden sterna and genital capsule as figured (figs. 4, 5). Penis with long basiventral projection and large dorsal sclerotization continuing spatha; volsellar rudiments present; gonocoxite ventrally at base of gonostylus with short parapenial lobe bearing short, broad-based, pointed setae.

MATERIAL STUDIED: Holotype female from Organ Pipe Cactus National Monument, Pima Co., Arizona, March 23–27, 1995, J. G. and B. L. Rozen (American Museum of Natural History, New York). Paratypes: 1 female and 5 males, same data as holotype (AMNH); 1 female and 3 males, 9.1 miles S Quartzsite, Yuma Co., Arizona, March 21, 1966, on *Phacelia crenulata*, P. D. Hurd (University of California, Berkeley); 4 females and 2 males, Desert Research Station, East side Tucson Mts., Pima Co., Arizona, March 29, 1995, J. G. and B. L. Rozen (AMNH, New York); 1 female, same locality, April 14, 1993, J. G. Rozen (AMNH, New York); 1 female Cocoraque Butte, Pima Co., Arizona, March 19, 1995, on *Phacelia* sp., M. E. McIntosh (in collection of J. S. Ascher). These localities are mapped in figure 7.

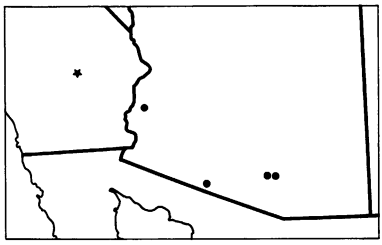


Fig. 7. Localities where *Rhopalolemma robertsi* (star) and *R. rotundiceps* (dots) have been collected in southern California and Arizona.

BIOLOGY OF *PROTODUFOUREA* AND *RHOPALOLEMMA*

A single nest of *Protodufourea eickworti* was found and excavated on March 27, 1995, at Organ Pipe. The nest was near a shallow wash in a predominantly creosote-bush desert (fig. 8), and the pollen plant, *Phacelia distans*, was in full bloom along the wash. Species of both *Conanthalictus* and *Dufourea* were commonly encountered, the *Dufourea* usually on *Phacelia* flowers and *Conanthalictus* apparently primarily on *Nama hispidum*. Whereas adults of *Rhopalolemma* were encountered daily in low numbers, only a single specimen of *Neopasites cressoni* Crawford, known cleptoparasite of *Dufourea*, was identified during five days of investigating the area. Many *Townsendiella rufiventris* Linsley were observed, and one female was seen entering a nest of *Conanthalictus bakeri* Crawford, no doubt one of its hosts. (*Conanthalictus deserticola* Timberlake was also collected at this locality and might also host this *Townsendiella*.)

The open nest entrance had dry, loose tumulus to one side, was on gently sloping ground under a rock, and was unshaded by surrounding vegetation most of the day. It was first noticed because of the searching activity of a female *Rhopalolemma* in the vicinity. After this female entered the nest, she was captured with a plastic drinking glass placed over the hole as she emerged several minutes later. The returning host female was later captured as she tried to enter the nest which was blocked by the replaced glass.

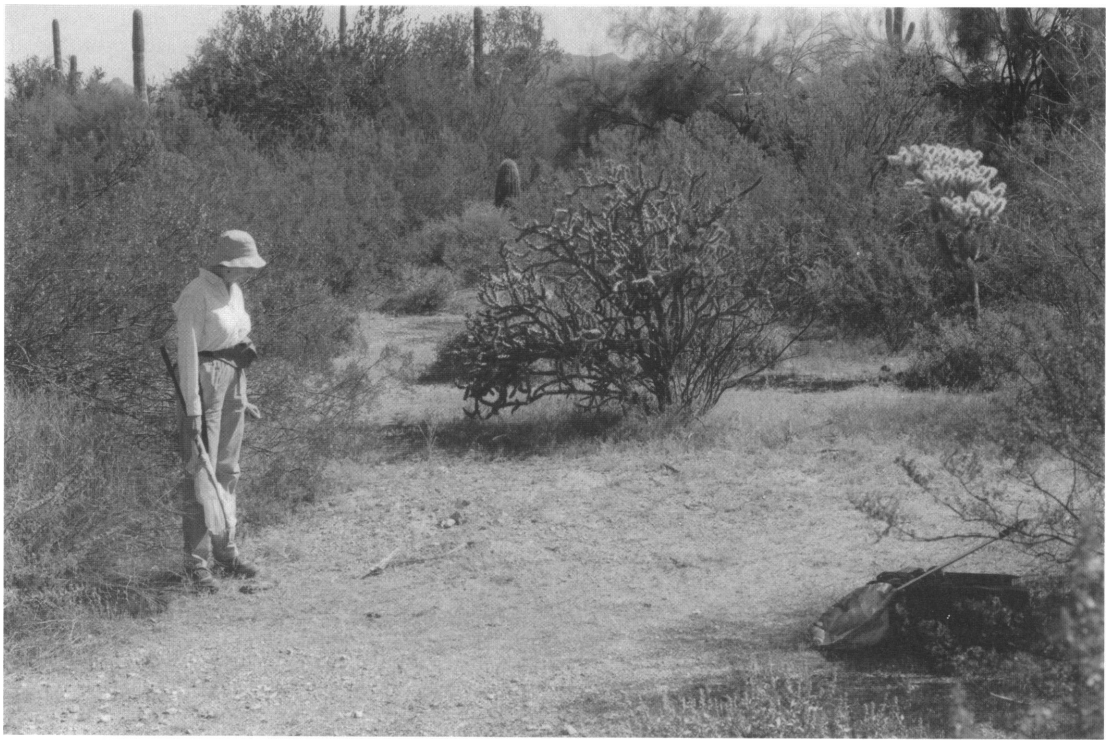


Fig. 8. Habitat view, Organ Pipe Cactus National Monument. Nest of *Protodufourea eickworti* was 1 m in front of person in photo.

Open its entire length, the main burrow was approximately 3.5 mm in diameter and had dull, unlined walls. As seems characteristic of nests of other members of the Rophitinae (Rozen, 1993), it meandered downward through the rocky soil at about a 45° angle and connected to a single open cell at a depth of 12 cm. The cell was still empty of provisions (the returning female had not been carrying pollen) but contained two eggs of *Rhopalolemma* embedded in the wall. This indicates that the cleptoparasite, like all other known Nomadinae, enters the cell before it is closed, while the host female is away.

Two more nests of *Protodufourea eickworti* were discovered at the Desert Research Station almost exactly where George Eickwort had first found *Rhopalolemma*. This site was a rocky ravine, pictured in Rozen (1994: fig. 7). Both nests, about 20 m apart, were on the lower sides of the ravine where the surface sloped at about 45°, very different from the nearly horizontal nest site at Organ Pipe. *Dufourea australis* (Michener), which collected the bright yellow pollen of *Encelia*, also nested in this ravine at the time of these observations. Its cleptoparasite, *Neopasites cressoni*, which has about the same body size and general appearance as *R. rotundiceps*, was often confused in flight with the latter species. Population size of both species of cleptoparasites appeared about the same during the study period. Because the seasonal flight period of *Protodufourea* and *Rhopalolemma* is probably somewhat earlier than that of *Dufourea australis* and *Neopasites*, the relative abundance of the adults of the two parasites would shift with time. When searching for host nests, female *R. rotundiceps* flew back and forth rather slowly, very close to the ground, momentarily slowing even more, or stopping, at suspected nest entrances. This behavior seemed identical to that of female *N. cressoni* (Torchio et al. 1967).

The first nest, found on March 29, consisted of an open main burrow and two recent cells close to one another, the deeper being 17 cm from the surface. One cell contained a cocoon-spinning *Protodufourea* lar-

va, and the other was occupied by an uncoated, lavender-gray pollen mass, 2.2 mm in diameter, presumably incomplete, and without a *Protodufourea* egg or larva. The presence of this food mass indicated that foraging females of this species, like those of other known rophitines, shape the early loads of provisions each time they return from a foraging trip. A single *Rhopalolemma* egg was embedded in the wall of the second cell, a further indication that the cleptoparasite enters the open host cell while the host female is away.

The second nest was discovered and excavated on March 30. Its main burrow twisted through extremely rocky soil and led to ten cells between 15 and 25 cm in depth, some and perhaps all of which were arranged in linear series of two cells per series. These cells were horizontal, or approximately so, and were close to the main burrow. Five contained quiescent, postdefecating *Protodufourea* larvae in cocoons, two contained quiescent postdefecating *Rhopalolemma* larvae, and three held feeding or predefecating *Rhopalolemma* larvae. None of the *Rhopalolemma* larvae were in cocoons.

Cells were ovoid and possibly symmetrical around their long axis (although one cell had the plane of the closure not at right angles to the longitudinal cell axis). Three measured 5.6–6.0 mm long and 4.0–4.5 mm in maximum diameter. At the entrance, they were 2.5–2.8 mm in diameter. As seems to be characteristic for all Rophitinae, the cell wall was smooth, porous, nonreflective, and apparently unlined (but see discussion in Rozen, 1993). Slightly more compact than the substrate, the cell wall also seemed more fine-grained, suggesting that the female somehow sifted the soil during cell construction. Its surface was nonwaterproof when tested with a water droplet. Cell closure, 0.5 mm thick at the center, was a shallowly concave spiral of five coils on the inside and a smooth concave surface with a faint central convexity on the outside.

Protodufourea cocoons were composed of a single tan sheet of very thin but tough silk. The fabric at the cell-closure end of the cocoon was no different from that of the cell wall, that is, there was no special filter as in *Sphecodosoma dicksoni* (Timberlake) (Rozen, 1993). The fabric appeared continuous and cellophanelike under high magnification although fine strands of silk partly embedded in it were visible. Moderately shiny on the inside, the cocoon adhered closely to the cell surface so that the contour of the walls and closure was revealed though it. It could be peeled from the cell surface only with difficulty. The black feces plastered at the rear one-third to one-half of the cell were visible through the cocoon because of its semitransparent nature. Defecation occurred before cocoon construction, and larvae entered diapause soon afterward. In diapause, the larva was curled about as much as that of *Dufourea novaeangliae* (Robertson) (Eickwort et al., 1986) but not to the extent that the terminal abdominal segment came in contact with the venter of the head or prothorax as in *Sphecodosoma dicksoni* (Rozen, 1993: fig. 20) and *Dufourea australis* (Michener) (new information).

In contrast to the feces of *Protodufourea*, those of *Rhopalolemma* larvae were smeared as irregular, pale, grayish-green masses over the entire cell wall and closure. As is characteristic of other Nomadinae, defecation did not begin until after provisions were entirely consumed; cocoons were not spun. After defecation, larval integument hardened and became more opaque, and larvae ceased all movement, signalling entry into diapause. This species, then, is univoltine, as is its host.

A postdefecating larva and a predefecating larva of *Rhopalolemma* were preserved in the same vial of Kahle's solution on the day of capture and examined a week later. A uniformly thin plastic but rigid film that was colorless and clear flaked from the surface of the postdefecating larva but not from the predefecating one. The coating had fit exactly to the integument, reflecting its every wrinkle. The same type of film was seen on the live postdefecating larva of *Neopasites cressoni* when it was illustrated here (fig. 32). JGR has observed similar coatings on larvae of other noncocoon-spinning bees not necessarily closely related to the Nomadinae. The film is suspected to be a secretion, produced after defecation, that solidifies after being discharged. Possibly of salivary- or dermal-gland origin, it may protect the larva from parasites or desiccation. This is one of many

Figs. 9, 10. *Rhopalolemma rotundiceps*, light micrographs of eggs from **9.** Organ Pipe Cactus National Monument and **10.** Desert Research Station. Eggs 0.65–0.68 mm long.

aspects of bee biology deserving more detailed investigation.

Females of *Protodufourea* transport pollen on their hind legs (especially tibia and basitarsus) and on the undersurface of their metasomas.

So far, *Rhopalolemma rotundiceps* is known from only four localities (fig. 7) in Arizona. It has been associated with nests of *Protodufourea eickworti* at three sites. The type locality of *R. robertsi* in California (fig. 7) is in the range of *P. eickworti* as well (T. Griswold, personal commun.), but the larger body size of *R. robertsi* seems to exceed that of *P. eickworti*. Hence, the host of *R. robertsi* is unknown although it may well be some other rophitine since, to date, Biastini are known to be cleptoparasites of only Rophitinae, as follows (host genera in parentheses): *R. rotundiceps (Protodufourea); Neopasites (Dufourea);* and *Biastes (Systropha, Rophites,* and *Dufourea).*

EGGS, OOCYTES, AND OVARIES OF *RHOPALOLEMMA, NEOPASITES,* AND *TOWNSENDIELLA*

The eggs, oocytes, and certain aspects of the female reproductive tract of *Rhopalolemma* are described here. For comparative purposes and also because fine structure of egg and oocyte chorions of *Neopasites* have not been recorded, this related genus is also treated. Because of the suggested relationship of *Townsendiella* with these two genera, the microstructure of its oocyte was also examined. Other aspects of oocytes, eggs, and egg index of *Townsendiella* were treated earlier (Rozen and McGinley, 1991).

Rhopalolemma: Three eggs of *R. rotundiceps* were discovered, two in a single cell at the Organ Pipe site (fig. 9), and one in the first nest excavated at the Desert Research Station (fig. 10). Two of the eggs were embedded in the cell wall so that their longitudinal axes were parallel to the wall and their

top surfaces were rather flat and flush with the wall. These two eggs measured 0.65 and 0.68 mm long and their exposed surface about 0.1 mm wide, giving them a long, narrow appearance.

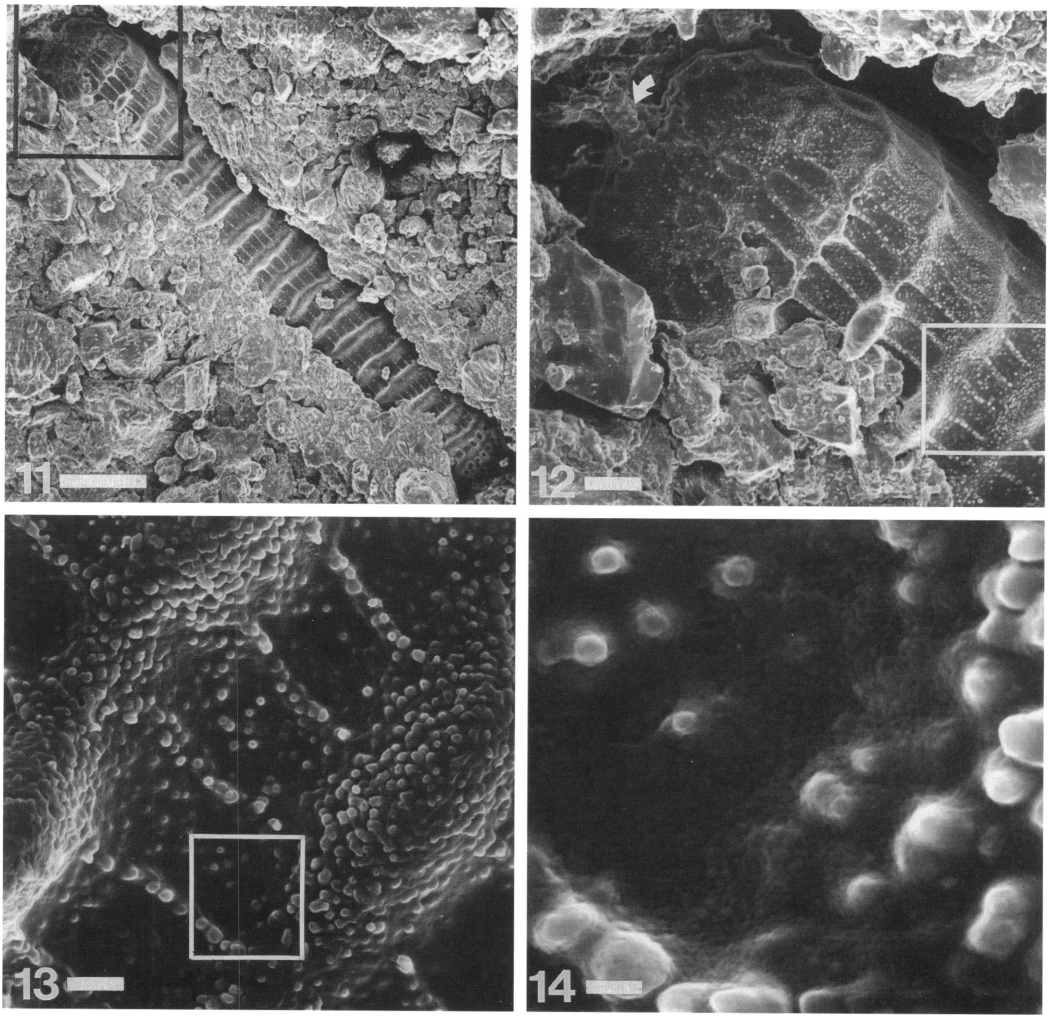
Examined by stereoscopic microscope (figs. 9, 10), the exposed chorion in each egg was nearly opaque white and possessed approximately 18 to 20 transverse, evenly spaced ridges. Near the anterior and posterior ends of the egg, the ridges were less pronounced than in the middle of the egg. These ridges did not extend onto the sides of the egg, which were normally embedded in the cell wall. Some of the ridges near the anterior end of the egg were drawn upward into rounded tubercles, as described below for oocytes. The grooves separating the ridges appeared somewhat shinier than the summits of the ridges. Examined under a scanning electron microscope (figs. 11–14), the exposed chorion revealed more detail. Fine longitudinal ridges extended between the transverse ridges, dividing the surface into rectangles; at the posterior end of the eggs, however, the rectangles were smaller and deeper and became circular. The ridges as well as cells were distinctly pebbled with tiny rounded knobs that were most abundant on the ridges (figs. 12, 13). Between the knobs, particularly in the rectangles, the chorion was pitted so as to appear porous (fig. 14).

The brood cell wall was feathered onto the egg in most places so that there was no space between the egg and wall in these places. (The crack that appears around the SEM micrographs of the egg on the right, fig. 9, resulted from desiccation after collection, SEM preparation, or both.) This means that after depositing the egg, the *Rhopalolemma* female must cement the egg into place by moistening the substrate and drawing the substrate material up to the egg.

The third egg (from Organ Pipe) had a similar appearance, but the anterior end protruded more from the cell surface (fig. 9, right). As the specimen dried after excavation, the egg protruded even more, suggesting that one end of the egg had been partly dislodged from its original placement, perhaps by the host female or the mother of the other *Rhopalolemma* egg. Only the exposed surface of this egg was opaque, as was also noted for the egg of *Neopasites cressoni* (Torchio et al., 1967). Although the embryo had died within, the chorion on the sides of the egg that protruded from the cell wall was obviously more flexible and less opaque than the thick, white chorion of the exposed surface. This flexible, less opaque chorion on all but the exposed surfce is believed to be the normal condition of this species, confirmed by the clear chorion on the sides and bottom of the dissected oocytes, described below. None of the eggs hatched even though JGR attempted to maintain them alive for more than a week.

The female reproductive tract of one specimen (Organ Pipe, Pima Co., Arizona, March 26, 1995, J. G. and B. L. Rozen) preserved in Kahle's solution was dissected to gain a better understanding of egg morphology from the mature oocytes. Four such oocytes, dissected from ovarioles, ranged in length from 0.69 to 0.73 mm and all were 0.15 mm in maximum diameter. They were elongate and slightly curved lengthwise, with their incurved surface bearing the transverse ridges. Their posterior end was slightly tapered compared with the blunter anterior end. The corrugated surface was somewhat flattened transversely and obviously corresponded to the exposed surface of the egg after oviposition. With most bee eggs that are curved, the inside curve is ventral at the time of eclosion, the first instar emerging dorsal surface up. We suspect that the curve of the *Rhopalolemma* oocyte is a special feature, not corresponding to the curve in the eggs of these other bees, otherwise the egg would be deposited upside down and the larva presumably would emerge with its ventral surface away from the cell wall. An alternative explanation, that *Rhopalolemma* embryos do not rotate 180° before emergence, seems less likely since such rotations have been observed in the nomadine genera *Triepeolus* (Torchio, 1986) and *Epeolus* by Torchio and Burdick (1988).

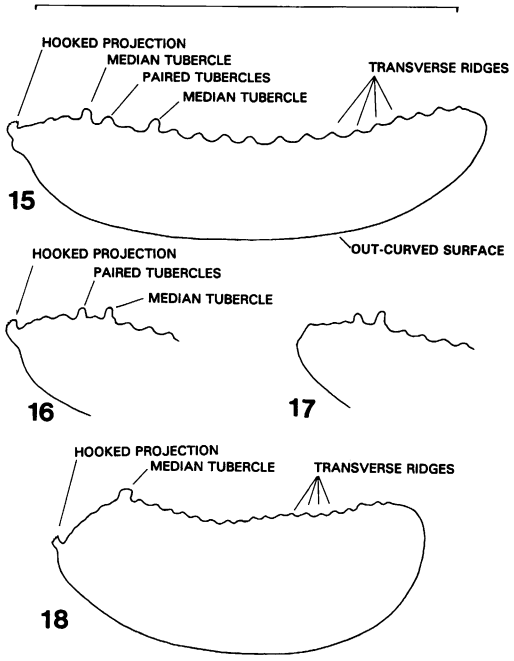
All oocytes (figs. 15–17) possessed a median, apically rounded, somewhat transverse tubercle rising from a transverse ridge near but not at the anterior end, as seen in the egg. Most also had a pair of distinct but less prominent rounded tubercles rising from another ridge in front of the median tubercle



Figs. 11–14. *Rhopalolemma rotundiceps*, SEM micrographs of egg embedded in cell wall of nest of *Protodufourea eickworti*. **11.** Entire egg, top view; scale = 100 μm. **12.** Close-up of anterior part of egg outlined in fig. 11; scale = 20 μm. Arrow points to hooklike projection on anterior end. **13.** Section of chorion outlined in fig. 12; scale = 5 μm. **14.** Extreme close-up of chorion outlined in fig. 13; scale = 1 μm.

(figs. 16, 17, 20). One oocyte (fig. 15) also had yet another median tubercle on another transverse ridge farther back but still before the middle of the oocyte. Still another exhibited only the single median round tubercle. These tubercles, composed of the chorion material, appeared clear (glassy and refractive) even though the chorion from which they arose was somewhat milky. Their exact arrangement on the surface of the chorion was obviously variable from one oocyte to the next. As expected, the sides and ventral surface of the oocyte were smooth and transparent.

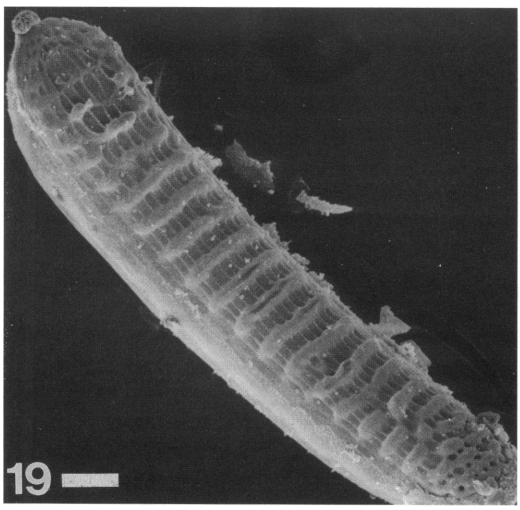
In addition to these round tubercles, four of the oocytes (figs. 15, 16, 19) each bore a small median hooklike projection at the most anterior end, presumably corresponding to the nipplelike or hooklike projections reported for certain other nomadine oocytes (see for example Alexander and Rozen, 1987: figs. 3, 7). Because of the difficulty in removing the follicular tissue from the oocyte, this structure was either damaged or some-

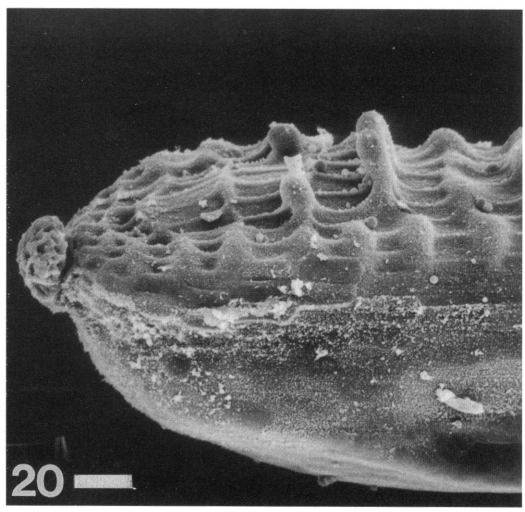


Figs. 15–17. *Rhopalolemma rotundiceps*, silhouette of oocytes, lateral view, showing variation in rounded tubercles. Fig. 18. *Neopasites cressoni*, silhouette of oocyte, lateral view. Scale = 0.5 mm.

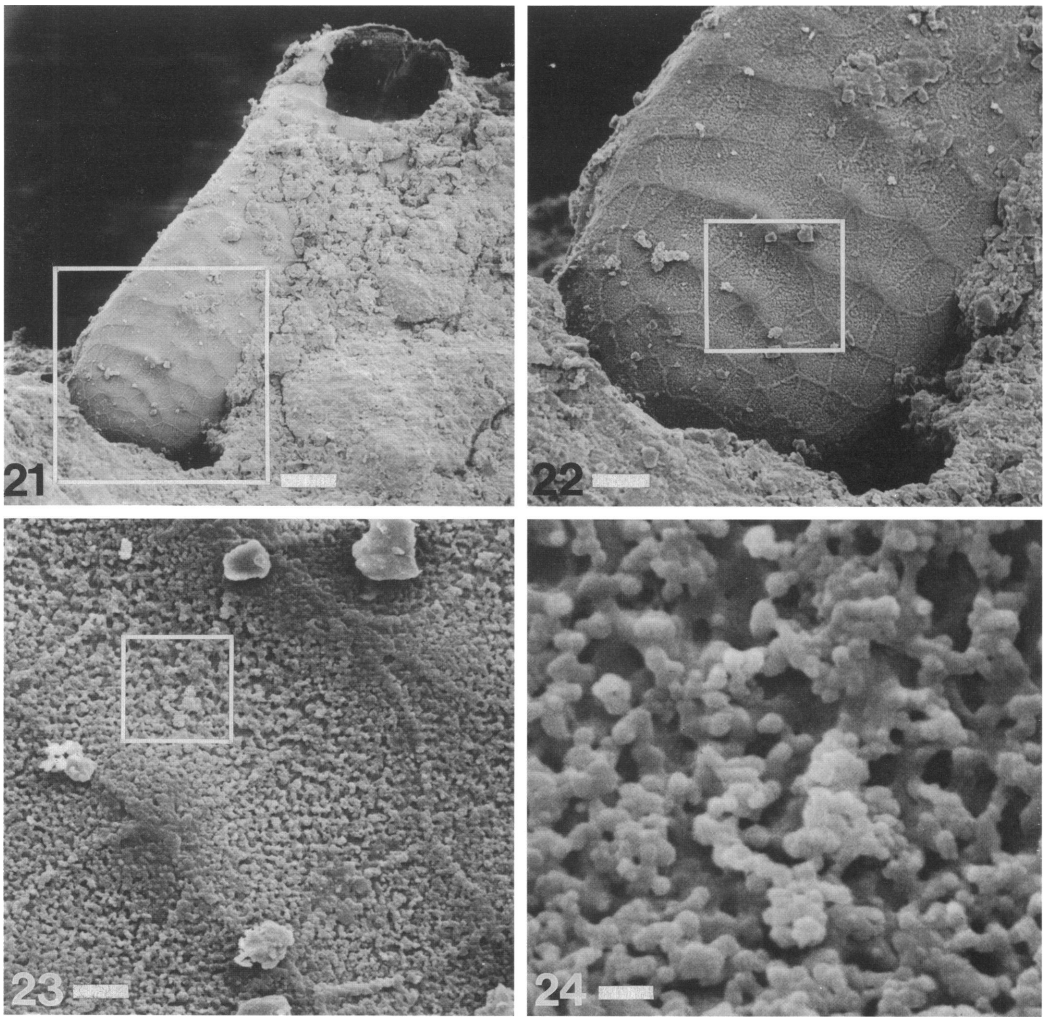
how obscured on another oocyte (fig. 17). This structure was not observed on two of the deposited eggs because of the limitations of light microscopes but was observed partly hidden on the SEM micrograph (fig. 12) subsequent to being identified on the oocyte. In SEM micrographs (figs. 19, 20) it is seen to be deeply pitted. It is likely a constant feature on all oocytes and eggs of this species and probably bears the micropyle.

NEOPASITES: The eggs of *N. cressoni* were described and illustrated by Torchio et al. (1967), and Alexander (1996) has reported in detail on the anatomy of the reproductive system of the same species. Now with the aid of SEM, further information was added to the description of the egg, and comparisons were made with the egg of *Rhopalolemma*. One of the *Neopasites* eggs examined (fig. 21) (3 mi south of Rodeo, New Mexico, May 1, 1965, J. G. Rozen) had been used for the earlier description. Another (same locality, April 27, 1966, J. G. Rozen) was also examined under the SEM because of variation in chorion sculpturing. The eggs and oocytes of *N. cressoni* were slightly shorter than those of *Rhopalolemma* and wider proportional to their length as seen from above (fig. 21; Torchio et al., 1967: fig. 9) or, in the case of oocytes, laterally (fig. 18). The chorion of each genus was opaque white on the





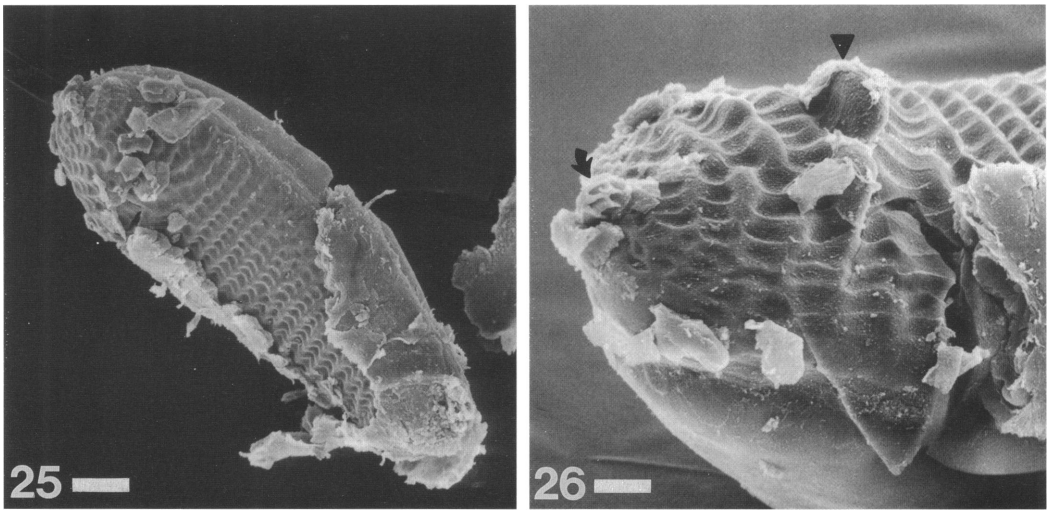
Figs. 19, 20. Micrograph of oocyte of *Rhopalolemma rotundiceps*. **19.** Entire oocyte, dorsolateral view; scale = 50 μm. **20.** Anterior end of oocyte showing detail of deeply pitted, hooklike projection at apex and distribution of rounded tubercles, more lateral view; scale = 20 μm.



Figs. 21–24. *Neopasites cressoni*, SEM micrographs of hatched egg embedded in cell wall of *Dufourea mulleri* (Cockerell). **21.** Entire egg, top view; scale = 100 μm. **22.** Close-up of posterior part of egg outlined in fig. 21; scale = 20 μm. **23.** Section of chorion outlined in fig. 22; scale = 5 μm. **24.** Extreme closeup of chorion outlined in fig. 23; scale = 1 μm.

exposed surface and transparent elsewhere. The transverse ridges (figs. 21, 22) on *Neopasites* eggs are almost certainly homologous with the pronounced transverse ridges of *Rhopalolemma* because of their position on the egg and because they appeared to be about equal in number. These ridges varied considerably in elevation from one egg to another. On the egg shown (fig. 21), they were very low, but on others they matched the pronounced ridges seen on the oocyte (figs. 25, 26). Since all of the oocytes examined were strongly sculptured and came from a single female (2 mi east of Apache, Cochise Co., Arizona, April 30, 1993, J. G. Rozen), variation in chorion sculpturing would seem to vary from female to female.

Neopasites eggs and oocytes (figs. 25, 26) possessed a single, median, rounded tubercle near their anterior end, similar to that of *Rhopalolemma*, but apparently lacked the other rounded tubercles visible on the eggs and oocytes of *Rhopalolemma*. The median tubercle was overlooked in the 1967 study of the egg of *Neopasites* but was clearly evident on the oocytes examined here. When the embedded

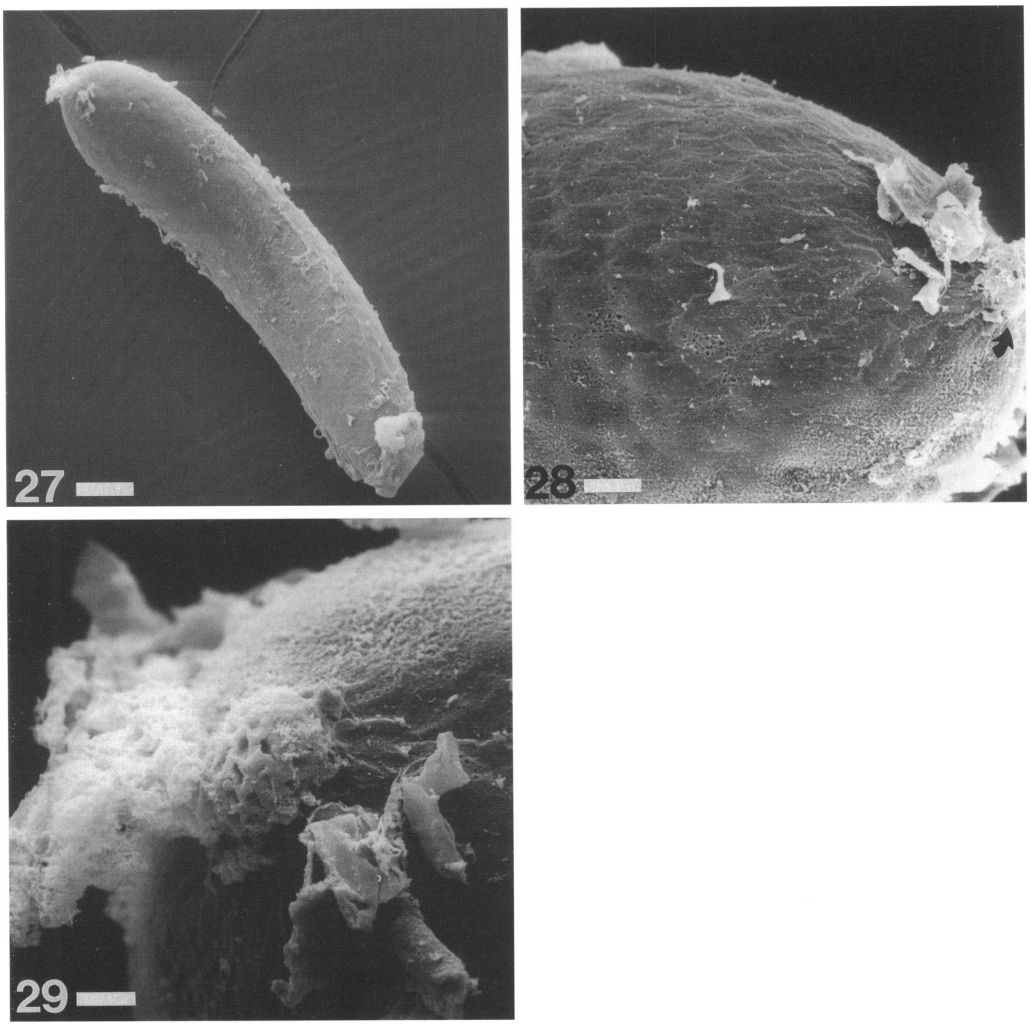


Figs. 25, 26. *Neopasites cressoni*, SEM micrographs of partly dissected oocyte. **25.** Entire oocyte, top view; scale = 50 μm. **26.** Anterior end of oocyte showing deeply pitted hooklike projection; scale = 20 μm. Arrow points to hooklike projection; triangle points to median rounded tubercle.

Neopasites eggs were again examined for the present study, this tubercle was only vaguely evident on an unhatched egg and on the opercula of eggs after eclosion (not shown). *Neopasites* oocytes, like those of *Rhopalolemma*, also possessed an anterior hooklike projection (figs. 25, 26). The microstructure of the eggs of the two species differed considerably (compare figs. 22–24 of *Neopasites* with figs. 12–14 of *Rhopalolemma*; comparable micrographs of both species magnified to same scales). While both appeared porous under very high magnification, the pronouncedly pebbled surface of the egg of *Rhopalolemma* (fig. 13) was lacking in the *Neopasites* egg (fig. 23).

Townsendiella: An oocyte of Townsendiella pulchra Crawford (8 mi northwest of Wickenburg, Maricopa Co., Arizona, May 7, 1990, J. G. and B. L. Rozen) was examined with the SEM. Figure 27 confirmed the generally smooth texture of its chorion, although a closeup micrograph (fig. 28) revealed a faint reticulate pattern in some areas. The oocyte possessed no tubercles, in contrast to the biastine genera, nor was its incurved surface somewhat flattened. The nipplelike projection (fig. 28, arrow) at the anterior end, noticed by Rozen and McGinley (1991), revealed the deep pitting characteristic of these other two genera, but the overall shape was not hooklike.

Discussion: So far as we know, only three genera of cleptoparasitic bees deposit their eggs in shallow grooves so that their long axis is parallel to the cell wall and their exposed surface is more or less flush with the wall: *Rhopalolemma*, *Neopasites* (Torchio et al., 1967), and *Hexepeolus* (Rozen, 1992, 1994). This feature, shared by the first two genera, would seem to be a synapomorphy, supported by the ridges on the exposed chorion (faint in *Neopasites*, Torchio et al., 1967), the white coriaceous nature of the exposed chorion, and the lack of a flange around the edge of the exposed surface (a feature unique to *Hexepeolus*). These three genera also agree in that their oocytes are slightly curved with the incurved surface forming the exposed surface on the embedded egg. The presence of rounded tubercles on the exposed chorion of both *Rhopalolemma* and *Neopasites* was somewhat suggestive of the "papillae" on the same surface of the *Hexepeolus* egg. However, these small projections in *Hexepeolus* are not associated with transverse ridges on either eggs or oocytes, and such projections might be explained as having evolved de novo, providing the large exposed egg surface with a tex-



Figs. 27–29. *Townsendiella pulchra*, SEM micrographs of oocyte. **27.** Entire oocyte, mostly dorsal view; scale = 100 μm. **28.** Anterior end, showing faint sculpturing and partly hidden nipplelike projection (arrow) to the right, mostly side view; scale = 20 μm. **29.** Closeup view of nipplelike projection with deeply pitted surface, top view; scale = 10 μm.

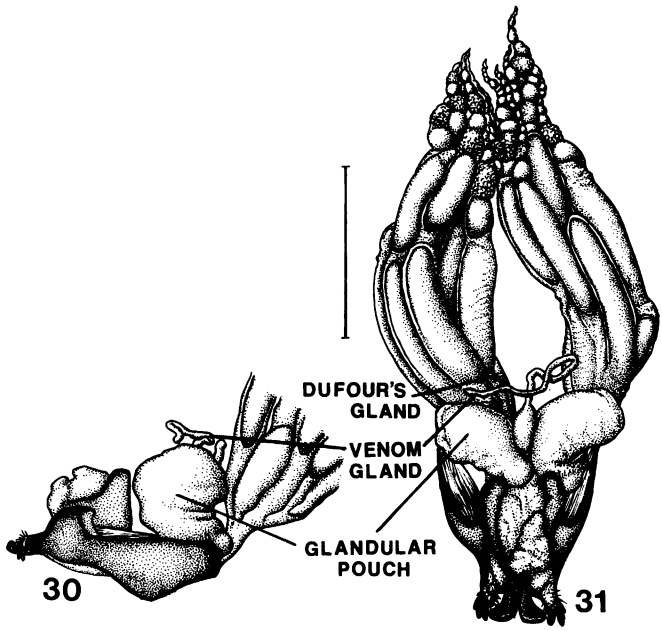
ture similar to the cell wall surface so that returning hosts do not detect and eliminate cuckoo bee eggs. It remains questionable whether the orientation and embedding of the *Hexepeolus* egg are homologous with those of the biastine genera.

The phylogenetic implications (or lack thereof) of the similarity between and among *Rhopalolemma, Neopasites*, and *Townsendiella* with respect to eggs and oocytes are discussed in the final section of this paper.

COMPARATIVE MORPHOLOGY OF FEMALE REPRODUCTIVE TRACT

Figures 30, 31

Three adult females collected at Organ Pipe and preserved in Kahle's solution in March of 1995 were later dissected in order to examine the morphology of the female reproductive system, which varies in interesting ways among nomadine genera (Alexander and Rozen, 1987; Alexander, 1996). Ma-



Figs. 30, 31. *Rhopalolemma rotundiceps*, female reproductive tract, including S6; scale = 1 mm. **30.** Lateral view, distal portion of ovaries not shown. **31.** Dorsal view.

ture oocytes from one of these specimens were also examined in detail, as explained in the previous section.

Because specimens preserved in Kahle's solution are considerably more brittle than fresh material, individual ovarioles cannot be teased apart without breaking, and it is extremely difficult to dissect a specimen without damaging or removing the venom and Dufour's glands (Alexander, 1996). Consequently, counts of the number of ovarioles and mature oocytes were imprecise for *Rhopalolemma rotundiceps*, although it is clear that this species has more ovarioles than most nomadines so far studied. The most accurate count came from the specimen dissected by JGR in order to obtain mature oocytes for detailed study because the individual ovarioles were separately removed from each ovary as this specimen was dissected. There were 17 ovarioles in one ovary and 14+ ovarioles in the other. The ovaries were left intact on the other specimens, dissected by BAA, but at least 10 ovarioles could be seen on each ovary of both specimens. The mean number of mature oocytes (that is, oocytes that were full-sized and possessed a distinct, smooth, shiny chorion on the outcurved surface, fig. 15) was 20.7 (range: 18 to 23). On the one specimen for which we obtained a complete count of ovarioles, there were 0.58 mature oocytes per ovariole. The mean egg index (oocyte length divided by distance between the outer margin of the tegulae) for the three specimens was 0.38 (range: 0.36 to 0.39).

The *Neopasites* female from which the oocytes were removed (see previous section) had an egg index of 0.31, identical to that reported by Alexander (1996). However, compared with Alexander's study, it had 17 mature oocytes (cf. 14), 1.54 mature oocytes per ovariole (cf. 1.08), and an ovarian formula of 5:6 (cf. 6:6 or 6:7). Variation in number of mature oocytes is not surprising, given that a cleptoparasitic bee is likely to be maturing and laying eggs throughout her adult life, but opportunities for oviposition are presumably unpredictable and fleeting. Variation in number of ovarioles is perhaps more surprising, although it has been reported in some other nomadine species (Alexander and Rozen, 1987; Alexander, 1996).

Like other genera of Nomadinae sensu Roig-Alsina (1991 et seq.), *Rhopalolemma rotundiceps* had a pair of glandular pouches,

one near the base of each ovary (Alexander, 1996). The glandular pouches in this species were relatively large, readily visible in lateral (fig. 30) or dorsal (fig. 31) view. Between them lay a smaller sac that was interpreted as the venom reservoir for the venom gland (fig. 31). On one of the three dissected specimens, there appeared to be a single tubular gland attached to this sac, although it was intertwined with Malpighian tubules and fat body, so that its length could not be accurately determined (the structure depicted in fig. 31 is the illustrator's estimate of the size of this gland, with fat body and Malpighian tubules removed). To the left of the venom sac on this specimen was a short tube of slightly greater diameter than that of the Malpighian tubules and venom gland. Unfortunately, this tube was broken off before the dissection was completed. On the basis of its position and of the form of the gland in other nomadine genera (Alexander, 1996), this structure was tentatively identified as the Dufour's gland. Neither of these structures was seen on the other two specimens, but, in view of the special care that was necessary to recover even fragments of the structures on the one specimen on which they were seen, we suggest that they may have been destroyed during dissection of the other specimens.

The glandular pouches of *Rhopalolemma rotundiceps* are similar to those of most other nomadine bees, including the only other species in the tribe Biastini that has been examined, *Neopasites cressoni*. The limited information about the Dufour's and venom glands suggests that those of *R. rotundiceps* may also be similar to those of most other members of Nomadinae. The latter conclusion, although necessarily tentative because of the circular reason involved in supporting it, is of interest because *N. cressoni* has a very unusual and conspicuous accessory gland associated with the female reproductive system (Alexander, 1996: fig. 5). Alexander provisionally identified this bizarre structure as the venom gland. The *Neopasites* specimens examined by Alexander had also been preserved in Kahle's solution, so the observed differences between *Neopasites* and *Rhopalolemma* are apparently real structural differences and not a result of differences in methods of specimen preparation or artifacts of dissection. Both *Neopasites* and *Rhopalolemma* have a reduced sting apparatus and similar modes of oviposition, so the reason for the striking difference in the accessory glands of their female reproductive systems is unclear.

MATURE LARVAE OF *RHOPALOLEMMA*

Figures 33–38

DIAGNOSIS: Of the two other genera of the Biastini, the mature larva of only *Neopasites cressoni* has been described (Rozen, 1966; McGinley, 1981). Although the earlier descriptions were based on the same single specimen, other specimens have now been collected and examined. Figure 32 is a lateral view of an entire larva, not illustrated before. The mature larvae of both *Rhopalolemma rotundiceps* and *N. cressoni* shared numerous features, such as the forward-bulging crania (also shared with *Neolarra*), greatly reduced internal cranial ridges, short labrum, greatly reduced maxillary palpi, virtually lost labial palpi, and dorsally positioned abdominal segment X. In spite of these similarities the larvae of the two species are easily separated. *Rhopalolemma*: with low but evident dorsolateral body tubercles (as postdefecating larva); body very pale cream color (as live postdefecating larva); hypopharynx spiculate; clypeus not projecting farther than labrum in lateral view; and mandible normally curving toward mouth. *Neopasites*: without dorsolateral body tubercles (fig. 32); body darker yellow; hypopharynx nonspiculate; clypeus projecting farther than labrum; mandible straight, almost styliform, not curving toward mouth.

In addition to the mature larva of *Neopasites cressoni*, an intermediate-stage larva of *Biastes emarginatus* (Schenk) has been briefly characterized (Rozen, 1993). It shared with *Rhopalolemma* and *Neopasites* a very short, recessed labrum; paired labral tubercles; short, apically thin and sharp-pointed mandibles; greatly recessed and fused labiomaxillary region, ventrally produced abdominal segment IX; and segment X somewhat dorsally attached to IX. No feature enabled it to be distinguished with certainty from either of the other two genera, although

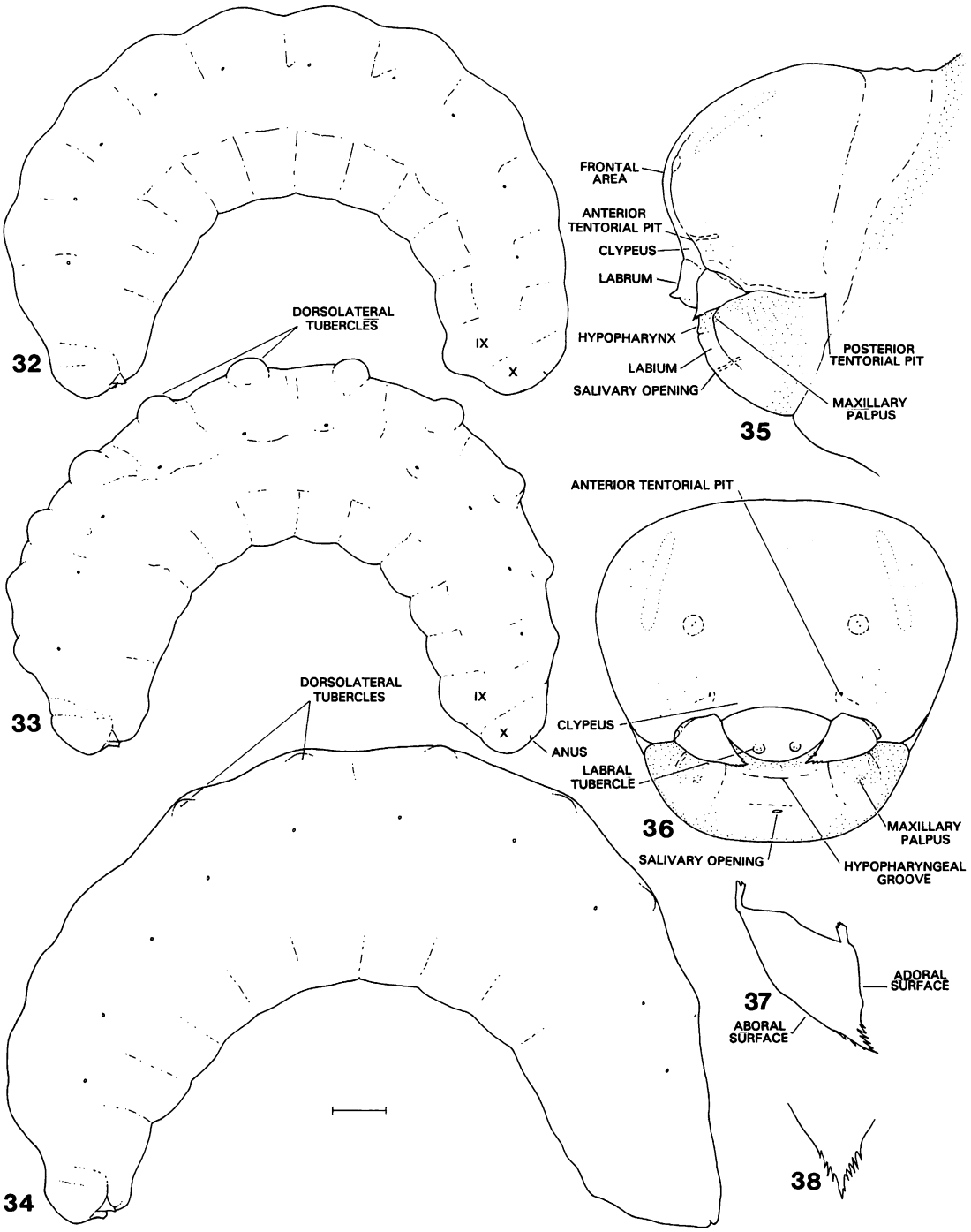


Fig. 32. *Neopasites cressoni*, live postdefecating larva, lateral view (Desert Research Station, east side Tucson Mtns., Pima Co., Arizona, collected May 1, 1993, by J. G. Rozen, from nest of *Dufourea australis*). Figs. 33–38. *Rhopalolemma rotundiceps*, mature larvae. **33.** Live postdefecating larva, lateral view. **34.** Recently preserved predefecating larva, lateral view. **35.** Head, postdefecating larva, lateral view. **36.** Same, frontal view. **37.** Right mandible, same, dorsal view. **38.** Apex of right mandible, same, outer view, maximum profile. Scale (= 1.0 mm) refers to figures 32–34.

it was unusually elongate and possessed low, rounded, dorsolateral body tubercles.

DESCRIPTION: Length approximately 5.0 mm. **Head** (figs. 35, 36): Integument, except for mandibular apices, unpigmented, with only inconspicuous sensilla, none of which are setiform; following head areas spiculate: hypopharynx, sides and top of maxillae, sides of labrum (sometimes referred to as epipharynx), and parts of labium; spicules of hypopharynx irregularly scattered; those of sides of labrum few in number and widely spaced; labral disc without spicules.

Head size small compared with body; head capsule wider than long in frontal view; as seen in lateral view, vertex not swollen on each side above antennae, as is characteristic of most Brachynomadini. Tentorium including dorsal arms complete but extremely thin; anterior tentorial pit very small, low on face, about one-fifth distance between anterior mandibular articulation and lower edge of antennal disc; posterior tentorial pit small, on hypostomal ridge slightly in front of cervical fold. Posterior margin of head capsule uncertain because postoccipital ridge not identifiable and rear of head capsule with two faint lines, one posterior to other; integument in front of first line slightly shiny (sclerotized); integument behind it less shiny, nonspiculate; integument behind second line spiculate like that of rest of body. Median longitudinal thickening of head capsule absent; hypostomal ridge narrow (weak) but evident; pleurostomal ridge nearly absent; epistomal ridge not evident between anterior tentorial pits and virtually absent between pit and anterior mandibular articulation. Parietal band evident but weak. Antennal prominence absent; antennal disc not differentiated from papilla, moderately small, weakly projecting, with two sensilla. Clypeus broad in frontal view; entire front of head capsule at level of antennae produced so that frontal area protruding beyond labrum in lateral view but, unlike in *Neopasites*, clypeus more recessed so that labrum projecting beyond lower boundary of clypeus in lateral view. Labrum narrow relative to head width in frontal view, short (length equaling one-half width in frontal view); labral disc without median cluster of sensilla as is characteristic of Epeolini; labral sclerite not evident; labral tubercles small, acute; epipharynx a simple curved surface.

Mandible (figs. 37, 38) robust at base (more so than in *Neopasites*), tapering rapidly to sharp-pointed apex, very short so that when in repose, apices far apart in frontal view (fig. 36); mandibles as seen in adoral or aboral view with apices not curved downward as in most Brachynomadini; as seen in dorsal or ventral view, apices curving normally toward mouth, not nearly straight as in *Neopasites*; apices twisted so that serrated dorsal apical edge closer to mouth than ventral apical edge; cusp and apical concavity not differentiated; dorsal and adoral surface without denticles; outer surface without setae but with scattered setiform sensilla, without conspicuous setiferous tubercles; dorsal and ventral apical edges with conspicuous sharp teeth; adoral surface much shorter than aboral surface, as in *Neopasites* and *Neolarra*. Labiomaxillary region recessed and fused. Maxillary apex a vague lobe, bearing greatly reduced, scarcely evident palpus although sensilla visible; as seen in lateral view, palpus not near posterior mandibular articulation, as is characteristic of *Nomada* and some Ammobatini; galea and maxillary sclerites not evident. Labium not divided into prementum and postmentum; premental sclerite absent; labial palpus not identifiable. Salivary opening a simple small slit without lips, well separated from hypopharyngeal groove. Hypopharynx projecting only slightly farther than labium in lateral view, its surface forming continuous curve with labium; hypopharyngeal groove weak but visible as integumental fold on postdefecating larva, not evident on predefecating larva.

Body (figs. 33, 34): Integument without obvious setae although with widely scattered, microscopic, setiform sensilla; integument microscopically spiculate in most areas but spicules very fine and mostly evident only on venter of most body segments and on sides and venter of pronotum behind head; integument without spines or sclerotized tubercles. Body form (figs. 33, 34) moderately slender; intersegmental lines weakly defined on both post- and predefecating larvae; intrasegmental lines not evident; on postdefecating larva (fig. 33), paired, very low, conical (i.e., not transverse), dorsolateral tuber-

cles present on thorax and abdominal segments I–IX; those on thorax subequal in size to one another, not as distinct as those of midabdominal segments; those of abdominal segment IX very small; on predefecating larva (fig. 34), dorsolateral tubercles less pronounced, so that only midbody tubercles vaguely evident; abdominal segment IX appearing produced ventrally because of dorsal position of X to IX but not as protuberant as that of *Neopasites* (fig. 32); abdominal segment X not bulging ventrally; anus strongly dorsal in position on predefecating larva (fig. 34) but less so on postdefecating larva (fig. 33); perianal area without lips. Spiracles very small, subequal in size, projecting slightly beyond body surface, similar to those of *Neopasites* (Rozen, 1966: fig. 73); spiracles of postdefecating larvae not on sclerotized, pigmented tubercles; atrium moderately small compared with subatrium, with rim; atrial wall smooth or nearly so; peritreme present, moderately narrow; primary spiracular opening with collar; subatrium with approximately seven chambers. Male with small, median, transverse cuticular scar on venter near posterior margin of abdominal segment IX; sex characters of female unknown.

MATERIAL STUDIED: Four postdefecating larvae and one predefecating larva, Desert Research Station, east side of Tucson Mtns., Pima Co., Arizona, March 30, 1995 (J. G. and B. L. Rozen) all from same nest of *Protodufourea eickworti*.

PHYLOGENETIC ANALYSIS

How does the information presented herein affect our understanding of the phylogenetic relationship of *Rhopalolemma* to the other Nomadinae?

TRIBAL LEVEL ANALYSIS

To address this question, we undertook a parsimony analysis of the subfamily. As a point of departure we used two recent studies: Roig-Alsina (1991), because it is the only treatment of the subfamily that includes *Rhopalolemma* (adult female characters only), and Rozen (1996), because it is the most recent and complete analysis of the subfamily based on larval characters. By means of Hennig86, version 1.5 (Farris, 1988), trees were calculated using **mh*; bb*;** commands. In cases where more than one tree was obtained, matrices were then submitted for recalculation through successive-approximations character weighting as provided by the **xsteps** command with the **w** option of Hennig86. Manipulation of the matrix was greatly aided by use of DADA, version 1.00 (Nixon, 1995).

Cladograms were restructured and printed using CLADOS, version 1.2 (Nixon, 1992). In cladograms, hashmark shading is as follows:

black	nonhomoplastic forward changes and nonhomoplastic, nonadditive changes
open	nonhomoplastic reverse changes
dark gray	homoplastic forward changes and homoplastic nonadditive changes
light gray	homoplastic reverse changes

Table 1 is a data matrix of character states of the tribes of the Nomadinae and *Rhopalolemma*. The characters of mature larvae (0–28) were those identified in Rozen (1996: table 3) and all of those states were based on that study; those of *Rhopalolemma* were added from the current investigation (no new characters were discovered). As in Rozen (1996), the larval characters for Biastini were based on only *Neopasites*. Characters of adults (29–50) were from Roig-Alsina (1991); the missing values for his characters 15, 17, and 21 were inserted from the current investigation. We added to these character another (51) from Alexander (1996: character 23), an analysis of a number of nomadine genera also based on Roig-Alsina (1991). This character pertains to the number of ovarioles per ovary.

The taxa in table 1 were from Roig-Alsina (1991), that is, the tribes of the Nomadinae sensu stricto with *Rhopalolemma* treated as distinct from the rest of the Biastini. The *Brachynomada* group and *Hexepeolus* from that study have recently each been given tribal status (Roig-Alsina and Michener, 1993). Operationally, the data from table 1 were simply combined with those in Rozen (1996: table 6), and characters 9 and 14 of Roig-Alsina (1991) (autapomorphies, in Rozen, 1996) were reinserted in the matrix.

Uninformative larval characters were cod-

TABLE 1

Data Matrix for Analysis of Relationships of *Rhopalolemma* with the Tribes of the Nomadinae

(New character codings for *Rhopalolemma* in boldface. See text for further explanation.)

From Roig-Alsina (1991,table 2) and Alexander (1996,table 4):				0 1	2		
				1234567890	1234567890	12	3
From Rozen(1996, table 6):	0	1	2	3	4		
	0123456789	0123456789	012345678	90123456/7	890/123456	78	/
	0	1	2	3	4	5	
Characters:	0123456789	0123456789	012345678	9012345678	9012345678	90	1
Ancestor	0?00000000	0000000000	00000?000	0000000000	0000000000	00	0
HEXEPEOLINI	0100111000	0010011010	010000000	1110001000	0000101110	01	4
BRACHYNOMADINI	??00111000	00??????10	?200??200	1111111000	0000101000	01	?
NOMADINI	0?0022?000	0??2000111	022001000	0110000100	0000100100	01	1
EPEOLINI	00?0?21000	1?0?001??0	0220????1	1111111000	0000100110	01	?
AMMOBATINI	0?11?2100?	010200112?	12?1?1??0	10???00001	0100010101	10	?
AMMOBATOIDINI	0000221001	0002001120	021001?00	1111101000	0000011101	01	1
BIASTINI	0000221111	000220102?	121000000	1110010110	0111101001	01	?
Rhopalolemma	**0000221110**	**0002001020**	**020010000**	1110010110	0011**10**1001	**0**1	4
NEOLARRINI	0000221101	0000001020	1??001000	10???00001	1110101101	00	1
CAENOPROSOPIDINI	0010221021	0102001?2?	12?0?1?00	10???10001	1100010101	10	?
TOWNSENDIELLINI	0000221111	0?02000020	?200000??	1100000000	0000001101	00	3

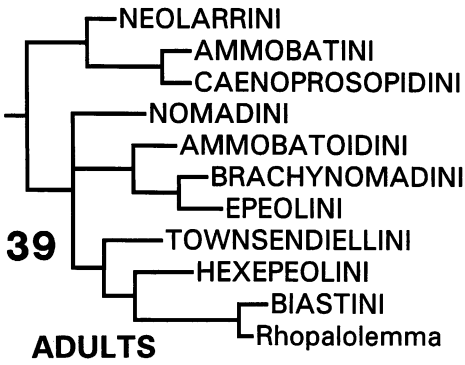
ed inactive, and statistics presented below were calculated after these characters were excluded. Characters 2, 4, 5, 7, 8, 9, 11, 13, 16, 17, 18, 20, 21, 22, and 25 remained active and are described in table 2. Character 13, multistate in Rozen (1996), was now two-state. Characters 4, 5, 18, 21, and 22 were multistate. Each appeared to be a simple linear evolution from a plesiomorphic character state to the most advanced state and consequently were coded additive, as had been done in Rozen (1996).

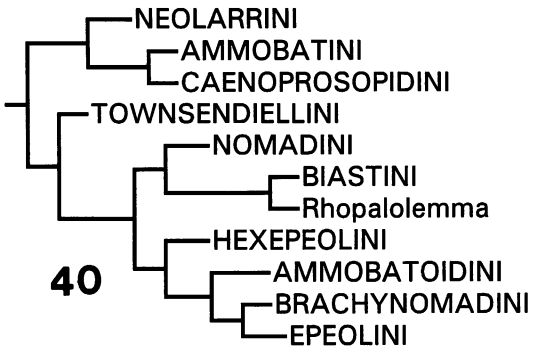
TABLE 2

Explanation of Phylogenetically Informative Larval Characters

(Taken from Rozen, 1996. See that work for more detailed explanation.)

2. Posterior tentorial pit on hypostomal ridge at rear of head (**0**); somewhat below ridge (**1**).
4. Postoccipital ridge present as single internal ridge across entire cranium, in normal position at posterior margin of head capsule (**0**); weak and interrupted toward midline (**1**); very weak to virtually absent (**2**).
5. Hypostomal ridge of postdefecating larva well-developed (**0**); weaker (**1**); very weak (**2**).
7. Frontoclypeal area in lateral view normal, not protruding beyond labrum (**0**); extending beyond labrum (**1**).
8. Labrum of normal length relative to width in frontal view, that is, longer than one-half width (**0**); transverse, about one-half width or less (**1**).
9. Labrum projecting forward beyond lower edge of clypeus in lateral view (**0**); projecting only as far as lower edge of clypeus or more recessed (**1**).
11. Labrum spiculate on sides (**0**); nonspiculate on sides (**1**).
13. Mandible of normal length (**0**); elongate (**1**); very short (**2**).
16. Dorsal and adoral mandibular surfaces with distinct, sharp denticles (**0**); without sharp denticles although sometimes with irregularities (**1**).
17. Maxilla with at least some spicules (**0**); nonspiculate (**1**).
18. Maxillary palpal length much greater than basal diameter (**0**); approximately as long as basal diameter (**1**); much less than basal diameter or palpus not evident (**2**).
20. Hypopharynx spiculate (**0**); smooth, nonspiculate (**1**).
21. Hypopharynx not projecting as far as salivary opening, as seen in lateral view with hypopharyngeal groove horizontal (**0**); projecting about as far as salivary opening (**1**); projecting farther than salivary opening (**2**).
22. Salivary opening well separated from hypopharynx (**0**); close to it (**1**); adjacent to it (**2**).
25. Abdominal segment X attached dorsally to IX as seen in lateral view (**0**); attached centrally to IX (**1**).





Figs. 39, 40. Strict consensus tree of the tribes of the Nomadinae and *Rhopalolemma* summarizing two minimum-length trees based on adult characters (table 1, characters 28–51). **39.** Character 51 coded additive. For details, see text. **40.** Character 51 coded nonadditive.

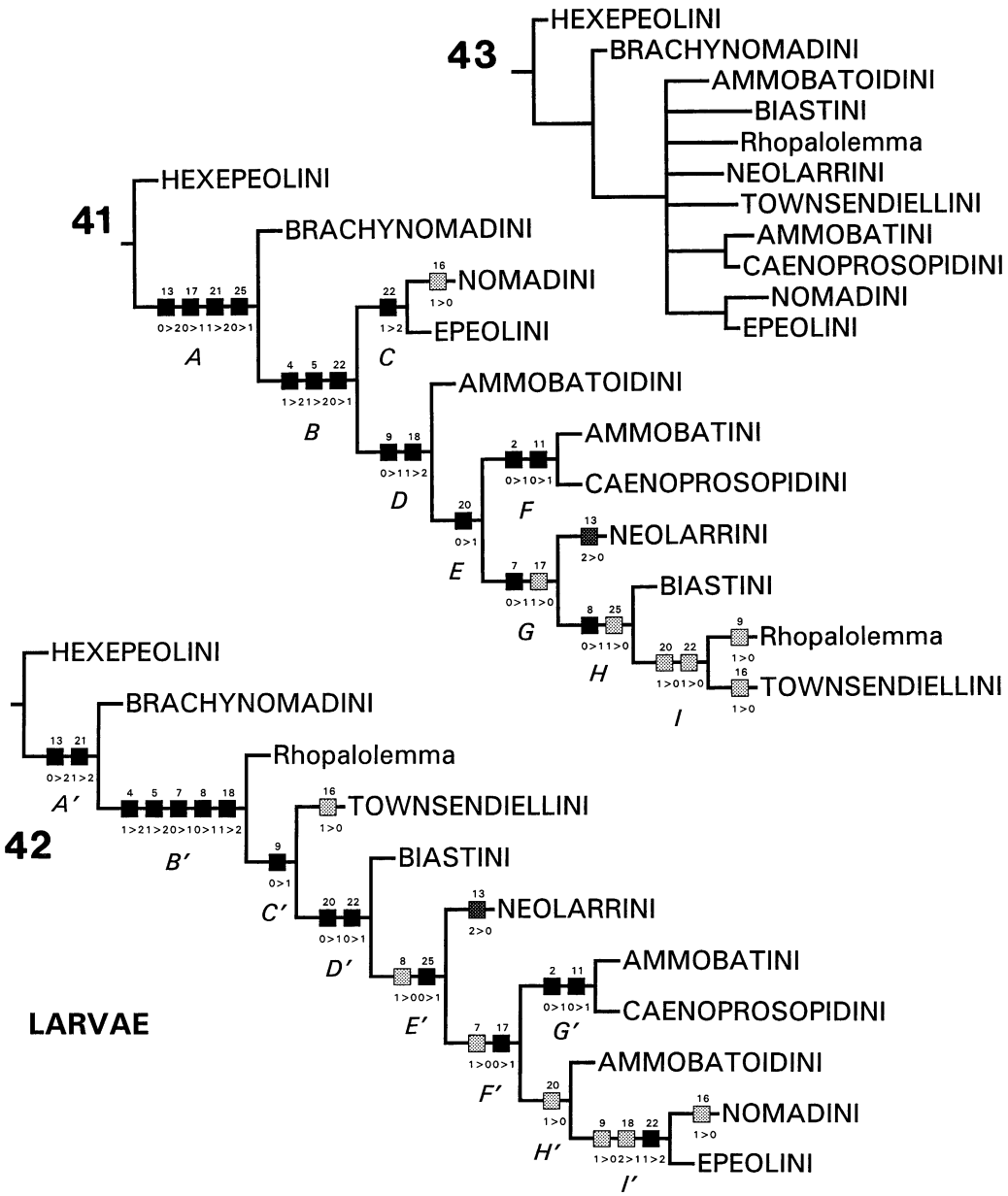
All adult characters were two-state except for character 51. Because Alexander's (1996) matrix was at the generic level, all polymorphic tribes were coded (?) for this character in table 1. The codings that he used (his table 4) were adopted here. He "performed two analyses, to examine the effects of treating ovariole number . . . as an ordered or unordered character," that is, as additive or nonadditive; we too calculated trees based on adult characters both ways.

Following the procedure outlined by Nixon and Carpenter (1993) for dealing with hypothetical ancestor outgroups, all analyses were first carried out with the hypothetical ancestor in the matrix active. Then the matrix was reanalyzed with the hypothetical ancestor deactivated. Resulting trees were rooted using the reroot command of CLADOS according to the position of the hypothetical ancestor on the first tree.

As in Rozen (1996), the analysis was partitioned into three subanalyses. First, the adult characters (table 1: characters 29–51) alone were used, and character 51 was coded additive. With the hypothetical ancestor active, the root of the cladogram was determined, and Neolarrini–Ammobatini–Caenoprosopidini became the basal clade. With the hypothetical ancestor deactivated, three minimum-length trees were calculated (length 42 steps, consistency index 59, retention index 64) that could not be reduced through application of successive-weighting procedures. The topology of these three trees was identical except for the position of the Nomadini. In one tree, it was sister to all except the basal clade. In another, it was the sister of the Ammobatoidini—Brachynomadini–Epeolini clade. In the third tree, it formed a trichotomy with the Ammobatoidini–Brachynomadini–Epeolini and Townsendiellini–Hexepeolini—Biastini–*Rhopalolemma* clades. A rooted strict consensus tree (fig. 39) had a topology identical to the last.

Alternatively, with character 51 coded nonadditive, adult characters produced two trees that yielded a single tree through application of successive-approximations weighting (weighted length 150 steps, consistency index 88, retention index 91). When rooted (fig. 40), the tree topology was identical to the favored tree of Roig-Alsina (1991: fig. 1A).

Second, larval characters alone (table 1: characters 0–28) were analyzed cladistically, resulting in two equally parsimonious trees that could not be reduced through successive-approximations weighting. These trees had the following statistics: length 23 steps, consistency index 69, retention index 74. When rooted, they were dissimilar in topology (figs. 41, 42). A strict consensus tree (fig. 43) summarizing them showed Hexepeolini to be the basal clade and Brachynomadini to be the next most basal clade, followed by a seven-branched polytomy which bore the two sister-groups Ammobatini–Caenoprosopidini and Nomadini—Epeolini. Often a polytomy on a strict consensus tree indicates that the data provide equal support for a number of different sister-group rela-



Figs. 41–43. Rooted cladograms of the tribes of the Nomadinae and *Rhopalolemma* based on characters of the mature larvae (table 1, characters 0–28). See text for explanation of hashmarks. **41, 42.** The two minimum-length trees that were calculated. **43.** Strict consensus tree summarizing the two minimum-length trees.

tionships among the terminal taxa in the polytomy. For example, if one were simply shown figure 43 and told it was a strict consensus tree, one might conclude that *Rhopalolemma* is the sister group of Biastini on one tree, of Ammobatoidini on another, of Neolarrini on another, and so on, and that all of these trees are of equal length. However, figure 43 is a strict consensus between only two conflicting hypotheses—those shown in figures 41 and 42. The principal difference between these two trees is in the rooting of

TABLE 3

Summary of Interpretations of Larval Character Evolution in Analyses on Informative Larval Characters Alone

(Explanation of informative characters given in table 2. Characters are indicated by character number followed by character state number, e.g., 10-1 designates state 1 of character 10. Hypothetical ancestors are designated by *A–I* on fig. 41, *A′–I′* on fig. 42.)

Characters with the same interpretation on both trees

2-1, 11-1: Synapomorphy of Ammobatini + Caenoprosopidini
4-2, 5-2: Synapomorphy of all tribes except Hexepeolini and Brachynomadini
21-2: Synapomorphy of all tribes except Hexepeolini
22-2: Synapomorphy of Nomadini + Epeolini
13: State 2 arises in common ancestor of all tribes except Hexepeolini, reverses to state 0 in Neolarrini
16: State 1 is plesiomorphic, state 0 is independently derived in Nomadini and Townsendiellini

Characters with a different interpretation on each tree

7: Fig. 41, state 1 arises in ancestor *G*
Fig. 42, state 1 arises in ancestor *B′*, reverses to 0 in ancestor *F′*
8: Fig. 41, state 1 arises in ancestor *H*
Fig. 42, state 1 arises in ancestor *B′*, reverses to 0 in ancestor *E′*
9: Fig. 41, state 1 arises in ancestor *D*, reverses to 0 in *Rhopalolemma*[a]
Fig. 42, state 1 arises in ancestor *C′*, reverses to 0 in ancestor *I′*
17: Fig. 41, state 1 arises in ancestor *A*, reverses to 0 in ancestor *G*
Fig. 42, state 1 arises in ancestor *F′*
18: Fig. 41, state 2 arises in ancestor *D*
Fig. 42, state 2 arises in ancestor *B′*, reverses to 1 in ancestor *I′*
20: Fig. 41, state 1 arises in ancestor *E*, reverses to 0 in ancestor *I*
Fig. 42, state 1 arises in ancestor *D′*, reverses to 0 in ancestor *H′*
22: Fig. 41, state 1 arises in ancestor *B*, reverses to 0 in ancestor *I*
Fig. 42, state 1 arises in ancestor *D′*
25: Fig. 41, state 1 arises in ancestor *A*, reverses to 0 in ancestor *H*
Fig. 42, state 1 arises in ancestor *E′*

Characters with unique and unreversed changes

Fig. 41: 7, 8, 18
Fig. 42: 17, 22, 25
Neither: 9, 20

[a] Note that in an analysis that excludes *Rhopalolemma*, this change is unnecessary on figure 41, whereas two steps are required for character 9 on figure 42 with or without *Rhopalolemma*. This is why adding *Rhopalolemma* to the analysis makes figures 41 and 42 equally parsimonious, whereas an analysis without *Rhopalolemma* finds figure 41 most parsimonious.

taxa distal to Brachynomadini. If one imagines a "pruning and regrafting" operation in which figure 41 is cut at branch *B* and reattached at the base of the *Rhopalolemma* branch, the result is figure 42.

Although one of the original trees in this analysis (fig. 41) was congruent with the single, completely resolved, minimum-length tree based on larval characters in Analysis 3A of Rozen (1996: fig. 8), the other (fig. 42) was quite different. The essential difference between the two larval studies was the addition of the characters of *Rhopalolemma*. Comparing the distribution of character states on figure 41 and figure 42, one finds an exact balance between characters that are unique and unreversed on one tree but undergo a single reversal on the other, as summarized in table 3. Adding *Rhopalolemma* to the analysis calls attention to conflicting interpretations of half of the potentially informative larval characters.

As the final step in the tribal level analysis, the entire matrix of combined larval and adult characters (table 1) was analyzed. With character 51 coded additive, Hennig86 calculated nine equally parsimonious unrooted trees (length 72 steps, consistency index 56, retention index 59), which were then reduced to a single tree with successive-approximations weighting (weighted length 246 steps, consistency index 80, retention index 82). When rooted, this tree was identical in topology to the single tree (fig. 44) derived

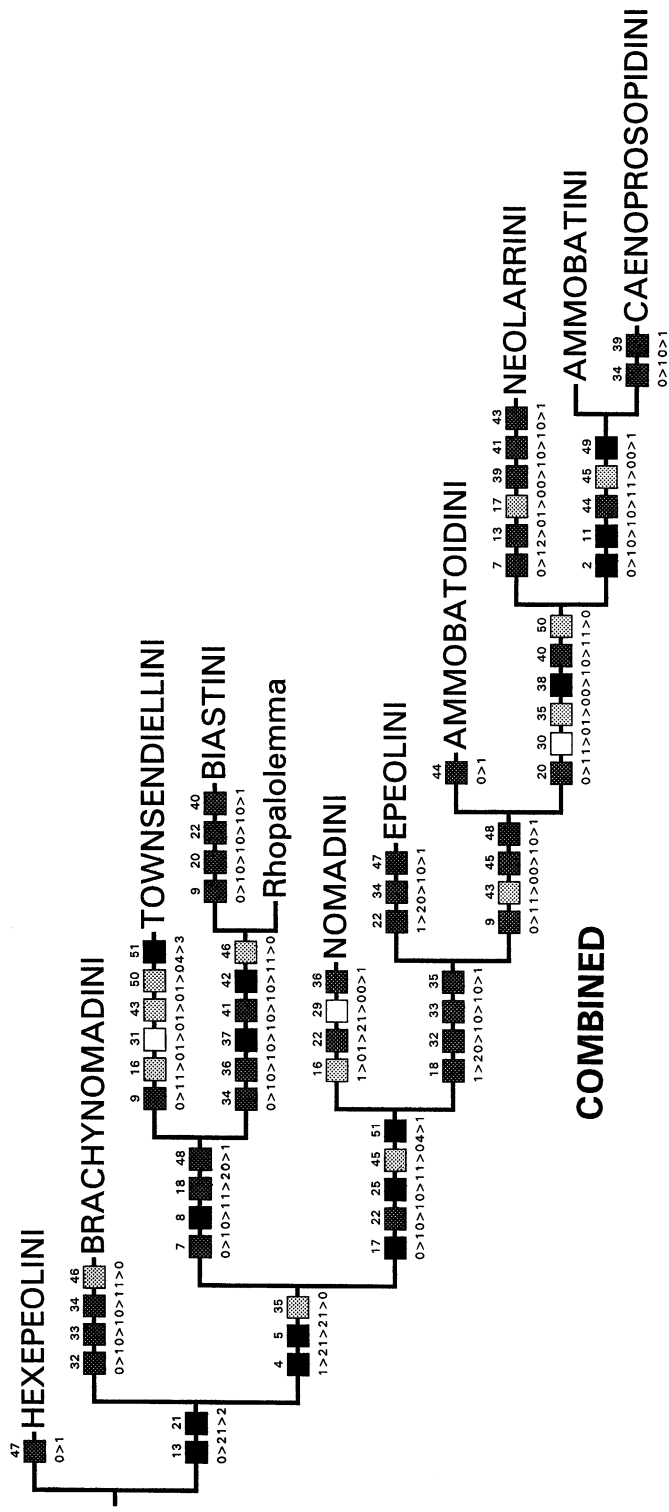


Fig. 44. Rooted cladogram of the tribes of the Nomadinae and *Rhopalolemma* based on the combined larval and adult characters (table 1, characters 0–51), with character 51 coded nonadditive.

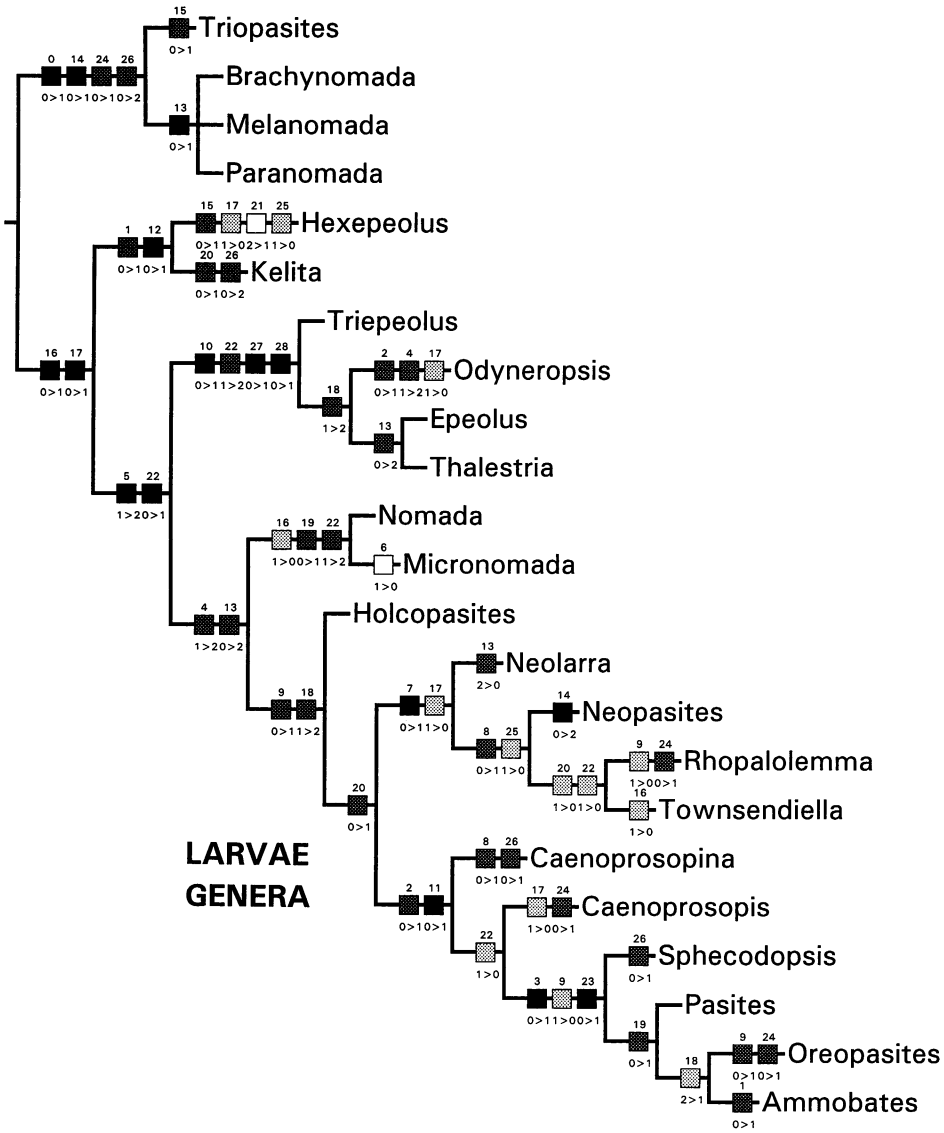


Fig. 45. Rooted cladogram of genera of the Nomadinae based on characters of the mature larvae. For descriptions of characters and their states, see Rozen (1996: tables 3, 4).

from 10 minimum-length trees (length 70 steps, consistency index 57, retention index 58) through successive-weighting procedures with character 51 coded nonadditive (weighted length 242 steps, consistency index 82, retention index 83). Hence, whether character 51 was coded as additive or nonadditive, *Rhopalolemma* appeared as the sister taxon to the Biastini. Because the tree is based on the greatest number of characters, it presumably reflects most accurately the phylogeny of the tribes of the Nomadinae.

As can be seen in figure 44, the monophyly of the Biastini including *Rhopalolemma* is based on derived adult characters only (characters 34, 36, 41, and 42, and character 46, which was a reversal). These have been identified, described, and discussed by Roig-Alsina (1991). All of the derived larval characters of the Biastini including *Rhopalolem-*

ma (characters 7, 8, and 18, and also 9 according to one of two equally parsimonious interpretations of its history) are shared with Townsendiellini.

The adult and larval matrices were each fitted to the combined tree to determine which exhibited the most homoplasy. With character 51 coded additive, the consistency index of the fitted adult matrix was 2 percentage points greater than that of the fitted larval matrix, an indication that adult characters were slightly less homoplastic than larval characters. However, with character 51 nonadditive, the consistency indices were equal.

Generic Level Analysis with Larval Characters Alone

In addition to performing the analysis on larval features at the tribal level, we inserted the larval character values of *Rhopalolemma* into the generic matrix used by Rozen (1996: table 4). We wished to determine what effect the new data would have on tree configuration and where *Rhopalolemma* would appear in an analysis based solely on larval characters. All characters were coded active, and characters 13, 14, and 26 were nonadditive. With the hypothetical ancestor in the matrix active, a single tree was calculated. When the matrix was re-analyzed with the hypothetical ancestor deactivated, it also yielded one tree (length 63 steps, consistency index 52, and retention index 77). When rooted (fig. 45), this tree was completely congruent with the generic tree in Rozen (1996: fig. 3). As in the tribal level analysis, *Rhopalolemma* and *Townsendiella* appeared as sister taxa, supported by the reversal of character 22. Although character 20 seems to support the relationship as well in figure 45, *Townsendiella* was coded (?) for this feature. *Neopasites* was a sister to them.

Discussion: Although analysis of larval characters suggested that *Rhopalolemma* and *Townsendiella* might be sister genera, egg and oocyte morphology and microstructure do not support this hypothesisd. Most bee oocytes and eggs are elongate, rounded at both ends, and circular in cross section. Their chorions are usually smooth, or finely reticulated, and lack ridges and tubercles. These characters then are plesiomorphic, and they are possessed by *Townsendiella*. The specialized features of shape and chorion structure shared by *Neopasites* and *Rhopalolemma* support their sister-group affiliation and corroborate the conclusion based on adult morphology alone or a combined analysis of adult and larval characters. The deeply pitted, sievelike, anterior projections shared by all three genera may well be characteristic of many or all other nomadine eggs and oocytes since these projections have been reported for many, but not all, nomadine taxa. Egg and oocyte microstructure of most taxa has yet to be examined.

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