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Phylogenetic Analysis of the Cleptoparasitic Bees Belonging to the Nomadinae Based on Mature Larvae (Apoidea: Apidae)

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ABSTRACT

The phylogenetic relationships of the large cleptoparasitic bee subfamily Nomadinae are investigated through a parsimony analysis of 29 characters of mature larvae. These larvae represent 22 genera of the 10 tribes currently recognized in the subfamily. Characteristics of the hypothetical ancestor are inferred from examination of larvae of 17 other apid taxa and 5 nonapid taxa.

The subfamily, as treated, consists of the various taxa traditionally placed in it, with the exception of the Osirini, *Coelioxoides*, Isepeolini, and Protepeolini. Numerous larval synapomorphies are identified and attest to the monophyly of the subfamily in this restricted sense.

In a series of analyses, the relationships of the Nomadinae based on the larval characters from the current study are compared with relationships determined by cladistic analysis of adult characters, as reported in Alexander (System. Entomol. 15: 121–152, 1990), Roig-Alsina (J. Kansas Entomol. Soc. 64: 13–37, 1991), and Roig-Alsina and Michener (Univ. Kansas Sci. Bull. 55: 123–173, 1993). The studies of adults encompass three more or less distinct sets of characters. In each case, a cladogram calculated from larval characters is compared with that from adult characters, and each is then compared with a cladogram based on a combined matrix of adult and larval characters. Congruence of topologies is interpreted as being supportive of the hypothesized relationships. Trees based on combined larval and adult features are assumed to be more meaningful than trees based on only a single life stage.

In these analyses, two cladograms (Analyses 2

and 3) based on larval characters alone tend to be more congruent with those based on combined matrices than are cladograms based on adult characters. However, for most analyses neither life stage is favored in comparison with the combined matrix. One analysis (Analysis 5) shows a strong congruence of the adult cladogram and the combined one. The latter is based on the most recent study involving adults and therefore should be the most reliable. However, cladistic procedures and the reduced number of taxa treated cloud interpretation of this analysis as well as the others.

In analyses where the genera of polytypic tribes are treated separately (i.e., not fused), the composition of each of these tribes holds up consistently in the combined cladograms with a single exception, suggesting that tribes of the Nomadinae are correctly identified and that the main problem is in understanding the interrelationships of the tribes.

In comparing the cladograms based on combined larval and adult matrices, *Hexepeolus* appears as the basal clade in all but two of the analyses. In all combined cladograms except one, *Hexepeolus* is closely linked to the brachynomadine genera as is also the case in the initial analysis dealing with the entire larval matrix. In all combined cladograms, the Caenoprosopidini and Ammobatini are sister taxa.

To further resolve the phylogenetic relationships of the subfamily, more taxa need to be included in subsequent analyses. To the same end, a number of more or less independent data sets are identified for future investigation.

INTRODUCTION

The discovery of the mature larva of *Hexepeolus rhodogyne* Linsley and Michener (Rozen, 1994b; Rozen, 1996) made available one of the last pieces of the puzzle of the phylogenetic relationships of the tribes of the Nomadinae based on their mature larvae. The central purpose of this paper is to reassess the relationships within the subfamily on the basis of the last-stage larvae. In order to evaluate the significance of the resulting phylogenetic hypothesis, a series of analyses was undertaken combining the data matrix based on larval features with matrices based on adult features presented in three recent studies (Alexander, 1990; Roig-Alsina, 1991; and Roig-Alsina and Michener, 1993). An integral step in achieving this purpose is a re-

evaluation of larval characters used in past studies by me and others so that character-state variation and polarity can be understood with more confidence. The overriding purpose of this study is to develop eventually a better (more convincing) understanding of the phylogeny of the subfamily, presumably one based on all life stages and all other lines of evidence that might reveal phylogeny.

All tables presented here are grouped together at the end of this paper, immediately after References.

Although cleptoparasitism has evolved many times in the Apoidea, the Nomadinae are unquestionably the largest, most varied group of cleptoparasitic bees. Their hosts are a diverse lot of solitary bees belonging to all

recognized bee families except for the Stenotritidae. So far as is known, all nomadine species attack host nests according to a single ground plan, that is, a female searches out and enters a host nest while the host female is away (presumably foraging for nest provisions). The cleptoparasite hides her markedly small egg almost invariably in a small hole or slit that she excavates in the cell wall of the still unsealed host brood cell. The female cleptoparasite then immediately departs, normally before the host female returns and completes the nest. The egg hatches after the host female has provisioned the cell, oviposited, and closed the cell. In all cases the cleptoparasitic first instar is a highly modified, ambulatory larva with a heavily sclerotized head capsule which bears elongate, forward-projecting, sharp-pointed mandibles. So equipped, the first instar seeks out the host egg or young larva, kills it, and then starts feeding on the provisions intended for the host's larva. With each successive molt, the larval cleptoparasite changes form until it reaches the last larval stage, completes feeding, and then defecates. In appearance, the last instar is quite unlike the hospicidal first instar. Most Nomadinae are univoltine. The last instar quickly enters diapause after defecating and remains quiescent until the next year. In the appropriate season, it molts to the pupal stage and soon after transforms into the imago. Shortly thereafter the fresh adult cleptoparasite emerges from the host nest, at about the same time that the new generation of hosts becomes active.

One of the advantages of carrying out parsimony analyses on holometabolous insects, such as bees, is that the researcher can investigate two phenotypes (or even four if eggs and pupae are available) of the same organism. Importantly, these appear to be decoupled evolutionarily, in the sense that the larval and adult stages evolve phyletically at separate rates, adapting in unlike ways to very different ecological niches, as if they were controlled by different genotypes. In fact, of course, they have a single genotype, and significantly both phenotypes undergo cladogenesis simultaneously. This means that branching sequences of a cladogram based on larvae must be congruent with those based on adults, if both cladograms are cor-

rect. Hence, a cladogram of one stage can be a test of the other. This study is based upon that principle. Character matrices of both life stages can be combined, providing the researcher with a greater number of characters for analysis. Topologies of cladograms calculated from these large matrices can then be compared separately with the topologies of cladograms based solely on adult characters and on larval characters. Greater congruence of the cladogram based on both stages with the cladogram based on one stage or the other can be interpreted as a measure of the reliability of the various cladograms. Such analyses are carried out in the current study.

Taxa whose larvae are used in the investigation are listed in table 1. As indicated there, many of these larvae have been described before and used in earlier phylogenetic studies. At the start, I planned to rely on these earlier descriptions as the primary source of data, but I soon learned that specimens needed to be examined for character reinterpretation. A number of additional taxa whose larvae had not been described became available because of donations to the collections of the American Museum of Natural History and because of my own fieldwork. The names of these taxa are also included in table 1.

To establish character polarity, I examined larvae of other apid taxa and of some non-apid taxa as well. These species are listed in table 2, and generic names in the text refer to them.

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I would like to acknowledge my indebtedness to the late Pedro W. Wygodzinsky, who, as a newly appointed curator, introduced cladistic methodology to the staff of the American Museum of Natural History in the mid-1960s. In his quiet way, he encouraged me at that time to apply this new approach to my early investigations on nomadine larvae. This paper is a direct descendent of those earlier studies.

Arturo Roig-Alsina kindly supplied the matrix combining adult characters from his 1991 paper and those used by Roig-Alsina and Michener (1993) in the separate treatment of the Nomadinae in the latter investi-

gation (*ibid.*, p. 157), for Analysis 5 of the current study. Byron Alexander sent me a copy of his manuscript (1996) on the comparative morphology of the female reproductive systems of nomadine bees. The fine cooperation of my colleagues is most appreciated.

Larval bees (like the immature stages of most insects) have not been widely collected, in part because recovering them from nests is time consuming and difficult, in part because they do not preserve particularly well compared to adults, and in part perhaps because some taxonomists assume that larvae are less useful than adults for systematic studies. I owe a special thanks to my colleagues who have made the effort to collect larvae, who have seen the value of maintaining them in collections, and/or who have made specimens available to me for this and previous investigations on nomadine bees. In this regard, I would especially like to acknowledge my appreciation to the following: Frederick D. Bennett, George E. Bohart, the late Mont A. Cazier, E. A. Cross, Bryan N. Danforth, the late Paul D. Hurd, Jr., Marjorie S. Favreau, the late J. W. MacSwain, Ronald J. McGinley, Charles D. Michener, A. R. Moldenke, the late Radclyffe B. Roberts, Arturo Roig-Alsina, Roy R. Snelling, and Philip F. Torchio.

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HISTORICAL BACKGROUND

This section explains what taxa are included in the Nomadinae at this time and why certain recent studies of the relationships of the Nomadinae to other Apidae are selected for comparison and analysis. This section does not discuss the history of the classification of the bees now placed in the Nomadinae. Such a history is long and would serve little purpose here. Persons interested in it are

referred to Grütte (1935), Linsley and Michener (1939), Michener (1944), Roig-Alsina and Michener (1993), and Eardley (1994). These same references also deal to some extent with the history of our concepts of the phylogenetic relationships of the Nomadinae to other Apidae and with interrelationships of the taxa included in the subfamily at one time or another.

Of concern to the present study are works that discuss the monophyly of the subfamily and cladistically derived phylogenies of the component taxa. As recently discussed by Alexander (1994), the first series of studies of the phylogeny of the Nomadinae using cladistic methodology (by cerebration) were in Rozen (1966, 1977) and Rozen et al. (1978). The studies, based on characteristics of mature larvae and on oviposition habits of adults, defined the subfamily to include all the cleptoparasites of the Apidae (*sensu* Michener, 1944) except for the Rhathymini, Ericrocidini, Melectini, and cleptoparasitic Euglossini. Such a definition was only tentative, however, because larvae of many of the included tribes and subfamilies were unknown as were their oviposition characteristics.

Recently, Alexander (1990) undertook a computerized parsimony analysis of the Nomadinae, defined (though provisionally) as in Rozen et al. (1978). Using Hennig86 (Farris, 1988), he confirmed the cladogram of Rozen et al. (1978) as the single most parsimonious one. He also compared the topologies of this cladogram based on larvae with one based on adults of the same 15 genera. He then expanded the number of genera to 34 and analyzed their relationships on the basis of adult characters alone. The adult characters were those used in existing taxonomic literature, especially Linsley and Michener (1939) and Michener (1944). Alexander examined taxa in order to score characters for the data matrix. He also searched for new characters and redefined characters previously used (Alexander, personal commun.). It is this expanded matrix of adult features, modified by removal of several genera, that is combined with the matrix of larval characters (table 4) in Analysis 2 of the present study, below.

Shortly after the publication of Alexan-

der's analyses, Roig-Alsina (1991) studied the cladistic relationships of the Nomadinae from which he had previously removed the Osirini (Roig-Alsina, 1989) and *Coelioxoides* (Roig-Alsina, 1990). He separated the Protepeolini and Isepeolini (treated by Rozen et al. and Alexander as basal clades in the Nomadinae) from the remaining tribes, the Nomadinae sensu stricto, the subject of his analysis. His investigation was based on adult characters alone. His data matrix was added to the matrix of larval characters of the present study and used in Analysis 3, below.

More recently, Roig-Alsina and Michener (1993) completed an ambitious cladistic analysis of long-tongued bees. Their study, using exemplars, treated all major taxa of solitary, cleptoparasitic, and social long-tongued bees, and was based on both adult and larval characters. Their conclusion (p. 158) regarding the monophyly of the Nomadinae was "The position of the Osirini, Protepeolini, and Isepeolini well separated from the Nomadinae support[s] the recent and sometimes tentative removal of these groups from Nomadinae or placement of them as basal branches in analyses of parasitic, *Nomada*-like bees . . ." Their study also upheld the placement of *Coelioxoides* in the Tetrapediini (Apinae), as had been previously determined by Roig-Alsina (1990). Because of these findings, the present study of the Nomadinae excludes the Osirini, Protepeolini, Isepeolini, and *Coelioxoides* from consideration. A study of the mode of parasitism and the anatomy of the first instars of the cleptoparasitic apids (Rozen, 1991) tended to support the exclusion of the Protepeolini and Isepeolini from the Nomadinae. (The mode of parasitism and first instars of *Coelioxoides* and the Osirini, unfortunately, are still unknown.) However, the only way to prove that these cleptoparasites are not close relatives of the Nomadinae is to identify their closest relative as being some other group. Such a proof was not within the scope of that study.

The data matrix of adult characters used by Roig-Alsina and Michener (1993: table 2, taxa of the Nomadinae only) was combined with the matrix of larval characters of the current study in Analysis 4, below. Because the relationships within the Nomadinae as shown in their analysis differed in several

ways from those given in Roig-Alsina (1991), they undertook a reanalysis (op. cit., p. 157) of the Nomadinae alone, using 36 adult characters from that study and 9 adult characters from Roig-Alsina (1991: characters 4–8, 10–13). They repolarized characters as necessary according to the conditions found in the basal node of the subfamily, and coded *Biastes* as plesiomorphic for Roig-Alsina's character 12 because the same condition is found in the near relative *Rhopalolemma*. They did not include in the reanalysis autapomorphies "in the context of cladogram 2a on page 150" (Roig-Alsina, personal commun.). The resulting cladogram was like the one in Roig-Alsina in topology except that the positions of *Hexepeolus* and *Nomada* were reversed. Because this modified matrix represented an attempt to reconcile the two studies based on adults, it was used in a separate study here, as Analysis 5.

Eardley's (1994) careful examination of the phylogeny and systematics of the Ammobatini was more restricted in scope than the works cited above, but he did define and treat cladistically the genera of that tribe with *Caenoprosopis*. He also attempted to employ larval characters as well as adult characters although the larval characters were insufficient "to produced a structured tree." His generic nomenclature has been adopted here. Because larvae of only four ammobatine genera are known, a detailed analysis comparing tree topologies based on his adult characters and larval characters from the present study was not undertaken. However, a tree based on a combined matrix of adult and larval characters was calculated (see Discussion and Conclusions).

METHODOLOGY

The current investigation is based on mature larvae. This stage is the one most often encountered in the field because solitary and cleptoparasitic bees (with some notable exceptions such as many *Andrena*, Halictinae, and Xylocopinae) spend the greatest part of their lives as mature larvae. In the past, the overwintering, postdefecating larva has usually been described for the same reason and because its body shape is often more clearly and uniformly defined due to its more rigid

integument, at least in noncocoon-spinning taxa. However, certain features of the integument, such as spiculation, sclerotization, and normal pigmentation become obscure with integumental thickening, wrinkling, and increase in pigmentation associated with diapause. Therefore, this study often examined mature predefecating larvae as well as postdefecating larvae.

Many characters can be observed on uncleared specimens, but other features of the exoskeleton are visible only on specimens from which the tissue has been removed. For clearing, heads were severed from bodies, and both parts were boiled in an aqueous solution of potassium hydroxide. After being washed in water, they were transferred to wellslides filled with glycerin, in which they are stored indefinitely.

So as not to bias my thinking, I initially ignored the characters and character states of larvae used by Roig-Alsina and Michener (1993) when I assembled larval characters and determined polarity for the current investigation. Subsequently I reviewed their list in detail and attempted to relate their characters with mine as indicated in table 3 and in the following section. **R&M #.** refers to Roig-Alsina and Michener's characters by numbers. The characters of larvae analyzed by them were those listed by McGinley (1981) that varied among long-tongued bees and for which Roig-Alsina and Michener (1993: 138) were able to identify polarity.

Throughout the manuscript I have tried to simplify wording by using such expressions as "larval characters" for characters of the larva, "adult cladograms" for cladograms based on characters of the adults, "combined matrix" for the matrix based on characters of both larvae and adults, "larval tree" for a cladogram calculated from characters of the larvae, and "combined tree" for a cladogram based on larval and adult characters.

Most larval characters used in this study have been illustrated in previous publications, and references to these illustrations are provided. Some characters are new and are illustrated here for the first time. Captions to these diagrams include parenthetical information indicating collection data in the event questions arise concerning identification of specimens used.

EVALUATION OF CHARACTERS

The larval characters that support the monophyly of the Nomadinae are presented in the following section, and a complete listing of larval characters used in phylogenetic analysis is presented in table 3. However, some characters warrant more detailed explanation because their anatomy is now more clearly understood than in earlier studies, because they are newly discovered, or because their polarity can be interpreted in more than one way.

1. The term "hypopharyngeal groove" has commonly been used in descriptions of bee larvae to denote an often-observed line that stretches between the maxillae and appears to separate the hypopharynx from the labium. Its morphology was discussed by Rozen and Michener (1988). It is greatly reduced to virtually absent in the Nomadinae, and its degree of expression depends on whether predefecating or postdefecating larvae are examined. For these reasons it is not dealt with in the current study. Roig-Alsina and Michener (1993) treated it (R&M #55) as absent in the nomadine taxa they considered. The fact that it cannot be seen in some genera in which the hypopharynx is nonspiculate can make defining the position of the salivary opening relative to the hypopharynx problematical.

2. The apparent position of the posterior tentorial pits below the hypostomal ridges and more or less anterior to the postoccipital ridge has been considered a synapomorphy among some nomadine larvae (Rozen, 1966; Rozen et al., 1978). This character is also used in the current study, but it has been redefined to form two separate characters (table 3, characters 2 and 3).

Although these two characters vary independently (as revealed in table 4), they appear to be functionally associated with a suite of interrelated features, some of which show variability within the Nomadinae, including: a) the general weakening of the postoccipital, hypostomal, and other internal ridges of the head capsule (table 3, characters 4 and 5); b) the reduction in the swelling and curvature of the parietals characteristic of most other bee larvae; c) weakening of the tentorium and reduction in the size of the posterior pits;

and d) reduction in the constriction of the foramen magnum at the level of the posterior tentorial pits so that points of connection between the posterior tentorial bridge and the postoccipital ridge are not deeply buried in the inflection of the cuticle on the sides of the head capsule (compare figs. 1 and 2). The short mandibles of many (but not all) nomadine last instars may also belong to this suite of characters, and the musculature and functioning of the mandibles, as yet unstudied, should be investigated in this regard.

3. In Rozen et al. (1978), the Ammobatini and *Nomada* were depicted as forming a clade because they shared two internal ridges (or lines), one in front of the other, along the posterior boundary of the head capsule. At the time, this character seemed reasonably strong, but in light of more nomadine taxa now being available its reliability is uncertain. Hints of double ridges are visible in *Caenoprosopis* and perhaps *Caenoprosopina* and in *Holcopasites eamia* (but not in other species in the genus). In many nomadines the postoccipital ridge is so weak that it cannot be certainly identified. Faint double ridges (lines) appear to be correlated with the general weakening of the posterior margin of the head capsule (also mentioned in 2, above). They may actually be a prolongation of the postoccipital ridge normally found in bee larvae, the anterior line being the front boundary and the posterior one being the rear boundary of the ridge. This is suggested by the fact that muscle scars are associated with the posterior ridge on many cleared specimens. Resolution of these lines may be forthcoming through comparative studies of the musculature of nomadines and non-nomadine larvae. For the present study, this character state has been abandoned as distinct from the extensive weakening of the posterior margin of the head (table 3, character 4, state 2).

4. There appears to be an almost continuous variation in the spiracles from a smooth atrial wall to one that is distinctly denticulate with the denticles forming ridges. Furthermore, both conditions occur in *Nomada*, the atrial wall of *Ammobates* consists of granules arranged in vague rows, and the atrial denticles of *Oreopasites* are scattered or absent. Hence characters R&M #72 and #73 have

been recast as character 30 of the present study.

5. The larval characters analyzed by Roig-Alsina and Michener (1993) in their large treatment of long-tongued bees were those of McGinley (1981). Some characters of larvae used by them did not vary among the more limited taxa treated here, as follows: R&M #1, 12, 14, 16, 18, 21, 22, 25, 26, 28, 30, 33, 36–40, 42, 46–52, 54, 58, 62, 67, and 70.

Other characters they analyzed are here redefined or reinterpreted as indicated in table 3. The extent to which these characters have been changed must be interpreted in each case by comparing their statement with the one given in table 3.

Still others of their larval characters were abandoned, as not useful for this study:

R&M #6. Pigmentation of head. Extensive continuous variation in this character among taxa and between hibernating and nonhibernating larvae make it unusable for coding.

R&M #13. Posterior thickening of head wall. Discussed under 3, above.

R&M #17. Angle of hypostomal ridge to posterior thickening of head wall [postoccipital ridge]. Continuous variation in this character, difficulty in defining the postoccipital ridge, and curvature at the junction of these ridges among taxa combine to make the character unusable.

R&M #19. Epistomal ridge or depression. Roig-Alsina and Michener (1993) coded the epistomal ridge arching upward to or above the level of the antennae as an autapomorphy of the Ammobatini. In this tribe there tends to be an internal ridge (particularly well developed in *Oreopasites*) that projects upward from each anterior tentorial pit just mesad of the antennae. These ridges fade, however, before they join at the median line. A suggestion of such ridges is also evident among other nonammobatines, including *Nomada*, *Tripeolus*, and *Thalestria*. Larvae of most Nomadinae (such as *Kelita*, *Neopasites*, *Neolarra*, *Triopasites*, and *Caenoprosopis*) exhibit no external epistomal depression or any hint of a ridge between the anterior tentorial pits. Hence determination of state (0) is impossible, and the character, there-

fore, is unusable here. Nonetheless, the ridges displayed by the ammobatines and others are noteworthy and deserve further study. Whether they are actually the mid-section of the epistomal ridge is questionable but perhaps could be determined by examining head musculature to define the head regions.

R&M #32. Mandibular cusp. In general the cuspal area of nomadine mandibles is weakly produced. In contrast, the mandible of larval *Triepeolus* strongly projects on its inner surface, almost certainly a secondary derivation rather than a plesiomorphy. Although the cusp of *Nomada* was described as projecting moderately (Rozen, 1966), examination of a number of species clearly indicates that the cuspal area is weakly produced.

R&M #35. Teeth on dorsal apical edge of mandible. Although the mandible of *Triepeolus* had been described as lacking teeth on the dorsal apical edge, a careful examination of a predefecating larva showed very fine, distinct teeth. Examination of other epeolines showed a gradation from moderately large serrations along this edge to vague irregularities, also evident in *Ammobates*. The distinctiveness of the two character states is thus obscured.

R&M #41. Labium. This character, relative length of labium compared with maxilla, is of doubtful meaning in the Nomadinae. The method of determining polarity is unclear, and the polarity given is questionable. The method of measuring length (to the apex of the palpi?, to the base of the palpi?, or to the apex of the structure exclusive of palpi in lateral view?) would have to be explained. In some taxa it is impossible to determine the exact boundary of the labium and hypopharynx, and the hypopharynx often exceeds the apices of the labium and maxilla. Furthermore, if this character is treated as nonadditive, as was done by Roig-Alsina and Michener (1993), its state in *Sphecodopsis* (1) is an autapomorphy in the Nomadinae, of no value in determining relationships within the group.

R&M #44. Maxillary palpus. The robustness versus slenderness of the maxillary palpus in the Nomadinae (in contrast to the

Colletidae, McGinley, 1981) is difficult to interpret because the palpi tend to be small. Hence coding the states becomes too subjective to be meaningful.

R&M #53. Hypopharyngeal size. An enlarged hypopharynx was a synapomorphy of all of the Nomadinae treated by Roig-Alsina and Michener (1993) except for *Neolarra* and *Neopasites*. However, defining the size of the hypopharynx is difficult in larvae in which the entire labiomaxillary region is greatly recessed and fused, the boundaries of the hypopharynx are unclear, and its integument is nonspiculate. For these reasons this character is abandoned here although character 21 (table 3) regarding the projection of the hypopharynx is related to it.

R&M #55. Hypopharyngeal groove. Discussed under 1, above.

R&M #56. Body integument. This character, the presence or absence of "patches or transverse rows of conspicuous spicules or setae," was modified by Roig-Alsina and Michener (1993) from McGinley (1981). It would seem to imply that spicules and setae are homologous structures. This is a doubtful assumption and suggests that they should be treated as separate characters when both are present. The Nomadinae lack setae, but most taxa possess postcephalic patches of spicules. However, the degree of expression of the spicules and the position of the patches vary widely among the taxa so that neither feature can be usefully categorized for resolving relationships. The codings in their matrix (Roig-Alsina and Michener, 1993: table 3) for the Nomadinae do not correspond to the presence of spicules on taxa previously described or treated here.

R&M #57. Body integument. The few minute setae that have been reported on the postcephalic region of some Brachynomadini (Rozen, 1977) are too obscure for the larval integument to be characterized as "seemingly conspicuously setose" (Roig-Alsina and Michener (1993). All mature nomadine larvae are virtually nonsetose.

R&M #59–61. Body length and form. These characters, dealing with body elongation, degree of robustness, and shape, are so subjective as to be useless in the No-

madinae. (Many of the values for R&M #60 were apparently incorrectly transcribed from McGinley, 1981.)

R&M #65. Length of abdominal segment X.

Although relative lengths of segment X seemed valid for distinguishing between *Neopasites* and *Neolarra* (Rozen, 1966), discovery of larvae of other species of *Neolarra* reveals variability in length of segment X. Furthermore, other nomadine taxa display a wide range of intermediate conditions between a very short and very elongate abdominal segment X.

R&M #68. Anus position. Although the position of the anus varies in taxa from being apical to being somewhat dorsal as seen in lateral view, the character is difficult to use. Differences in position are subtle in many cases. Furthermore, the apparent position depends on the shape of the dorsal and ventral parts of the segment (character 25), which also depends in some cases on whether a predefecating or postdefecating larva is examined. There is also a question as to whether the more dorsal positions are homologous from one taxon to the next.

R&M #69. Spiracular sclerites. Pigmented spiracular sclerites, usually associated with spiracular tubercles, are more or less expressed in some but not all postdefecating larvae of the Epeolini. They are apparently not evident on predefecating larvae. They are also vaguely present on postdefecating larvae of *Pasites* and *Brachynomada*. Because of the variability in degree of expression, this character is of doubtful use in the present study.

R&M #71. Spiracular atrium. The production of the atrium above the body wall varies among taxa, but the variation is continuous and impossible to code discretely. Degree of production may also depend on whether the larva is predefecating or postdefecating, and there may be confusion between this feature and the spiracular tubercles discussed under R&M #69, above.

R&M #74. Spiracular atrial rim. Roig-Alsina and Michener (1993) coded the character state for *Neopasites* as absent (1). However, there is a nearly 90° angle between the peritreme and atrium (Rozen, 1966: fig. 73) which is here interpreted as plesiomorphic (0). *Odyneropsis* (Rozen,

1966: fig. 35) is depicted as having no spiracular rim. However, the illustration was based on a caste larval skin which had undergone deformation; a whole larva needs to be examined to confirm this state before this character is analyzed.

R&M #75. Width of spiracular peritreme.

Within the Nomadinae, a wide spiracular peritreme is an apparent autapomorphy of *Sphecodopsis* (Rozen and McGinley, 1974: fig. 9). However, the states of this character in descriptions have been applied subjectively in the past. If they are to be used in the future, they need to be defined, perhaps by relating peritreme width to the diameter of the atrium or of the atrial opening. In *Sphecodopsis* and perhaps some other genera, spiracles on a larva are not uniform in size; relative width of the peritreme may vary with spiracular size.

R&M #76. Primary tracheal collar. Although a spinose tracheal collar has been recorded for some *Triepeolus* species (Michener, 1953: fig. 197; Rozen, 1966: fig. 11), it apparently is not uniform for the genus (Rozen, 1966: fig. 23). A survey of the spiracles of the epeoline genera listed in table 1 reveals variation in spiracular structure and ornamentation that might well prove valuable in analyzing intergeneric relationships within the tribe. Such a study is not attempted at this time because there are too few exemplars available.

R&M #77. Spiracular subatrial length.

This character is of dubious value because most subatria are adapted to lengthen and shorten, because the apparent length of a subatrium may depend on whether the larva is pre- or postdefecating, and because the length of the subatrium varies on a single specimen in some cases. Furthermore, atria vary in size as well as shallowness from one taxon to the next. Hence measuring the length of the subatrium in relation to the size of the atrium could be misleading.

6. As indicated above, some characters used by Roig-Alsina and Michener (1993) and McGinley (1981) have been more or less modified as indicated in table 3. The following characters used here are new: 8, 10, 14, 21, 22, and 23.

MONOPHYLY OF THE NOMADINAE

The monophyly of the Nomadinae is supported by numerous synapomorphies found in mature larvae. Many of the synapomorphies are associated with the fact that these larvae do not spin cocoons. Cocoon spinning is plesiomorphic in the Apoidea and in Hymenoptera in general, as are larval structures enabling this behavior such as projecting labiomaxillary regions, produced salivary lips, elongate palpi, well-sclerotized maxillary sclerites, and labium divided into postmentum and prementum.

- (1) **Labrum with pair of acute tubercles arising from disc.** Paired labral tubercles that arise from the disc are unknown in other Apidae although paired, more or less distinct, rounded tubercles arising from the anterior margin are found in several apid tribes. Because of differences in shape and position on the labrum, the two sets of tubercles are not considered homologous. Paired acute tubercles also arising from the labral disc are characteristic of the Panurginae, a case of parallel evolution. First-stage nomadines have labral tubercles that are even more pronounced than those of last instars, no doubt modifications for finding host immatures and rivals (Rozen, 1991). First-instar panurgines have scarcely noticeable labral tubercles (Rozen, 1958: figs. 2–3).
- (2) **Labiomaxillary region recessed, greatly fused so that only extreme apices of maxillae distinguishable.** In all bees, larvae of taxa that do not spin cocoons exhibit a labiomaxillary region that is fused and recessed compared with labiomaxillary regions of cocoon-spinning, close relatives. However, the degree of fusion in the Nomadinae is far greater than that of Anthophorini and Xylocopinae, no members of which spin cocoons, and of noncocoon-spinning members of the following tribes of noncocoon-spinning and cocoon-spinning taxa: Exomalopsini, Melectini, and Centridini.
- (3) **Labium not divided into prementum and postmentum.** In all other apids (including those that do not spin co-

coons), as well as in all larvae of cocoon-spinning bees, the labium is separated into a structurally distinct postmentum and prementum.

- (4) **Maxillary sclerites (cardo, stipes, and articulating arm of stipes) absent.** These sclerites, typical of cocoon-spinning larvae, vary in degree of expression among the apids, but at least some sclerites (particularly the stipes) are present in all apids except the Nomadinae.
- (5) **Labial palpus not projecting, reduced to single sensillum which may or may not be found on small sclerite.** In all other apids the labial palpus is represented by a short or elongate projection bearing one to many sensilla, as is characteristic of most other groups of bees.
- (6) **Salivary opening a simple hole or narrow slit, without lips (but with rim in some cases).** More or less broad, projecting salivary lips between which silk is extruded are characteristic of cocoon-spinning larvae. Such salivary openings are not normally found in larvae that no longer have the ability to spin cocoons. Such a loss, independently evolved, is also characteristic of other noncocoon-spinning apids (e.g., Anthophorini, *Epicharis*, *Thyreus*).
- (7) **Tentorium thin.** A robust tentorial structure is generally characteristic of other apids and other bee larvae that spin cocoons. This character, however, is difficult to use diagnostically because it is subjective and because degree of robustness varies considerably irrespective of cocoon-spinning abilities.
- (8) **Internal head ridges weak.** The generally reduced to nearly absent internal ridges of the head capsule (especially the postoccipital ridge but also the epistomal, pleurostomal, and hypostomal ridges) of the Nomadinae are not found elsewhere in the Apidae, except for the Isepeolini. This feature is probably functionally related to (7) and (9) but not necessarily to (11).
- (9) **Posterior tentorial pits often removed from junction of weak to nearly absent hypostomal and postoccipital ridges.** The variable position of the

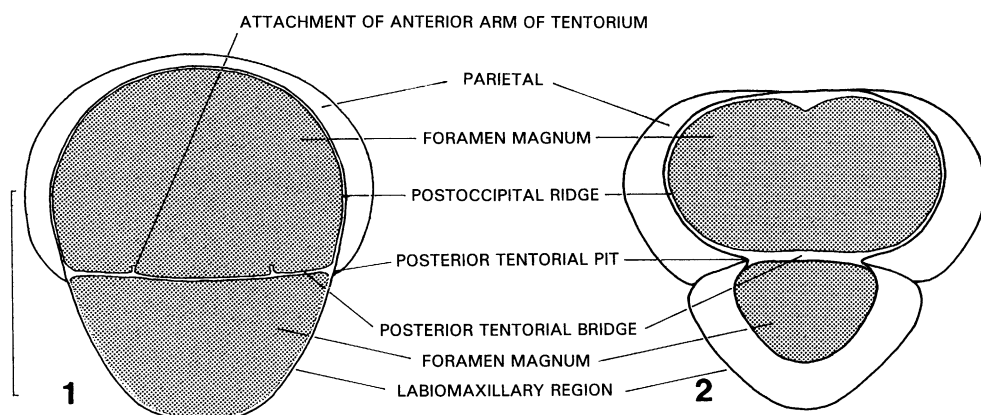


Fig. 1. Head of postdefecating larva of *Melanomada sidaefloris* (Cockerell), posterior view, showing lack of constriction of foramen magnum at posterior tentorial pits (i.e., at junctions of posterior tentorial bridge and postoccipital ridge), characteristic of the Nomadinae. (5 mi north of Willcox, Cochise Co., Arizona, September 3, 1983 [J. G. Rozen, M. Favreau], from nest of *Exomalopsis sidae* Cockerell.)

Fig. 2. Head of postdefecating larva of *Ancyloscelis apiformis* (Fabricius), posterior view, showing pronounced constriction of foramen magnum at posterior tentorial pits, characteristic of most noncleptoparasitic bees. (Maracas Valley, Trinidad, February 24, 1966 [F. D. Bennett, J. G. Rozen].) Scale = 1.0 mm, referring to both figures.

small posterior tentorial pits in relation to the postoccipital and hypostomal ridges found in many (but not all) of the Nomadinae is unknown elsewhere in the Apidae. It has a counterpart (no doubt independently evolved) only in the Oxaeidae. It is discussed in Evaluation of Characters, above.

- (10) **Mandible apically simple, without projecting cusp or scooplike apical concavity.** Mandibles of this description are not found elsewhere in the Apidae (excepting Protepeolini and Isepeolini). Other apids tend to have mandibles that are either apically bidentate with a pronounced, dentate cusp or apically broadly rounded and scoop-shaped. The short, sharply pointed mandibles lacking projecting cusps are probably a specialization of the Nomadinae, and the elongate, sinuate mandible (unique among bees) in the Brachynomadini presumably is derived from the short nomadine mandible.

- (11) **Midsection of epistomal suture missing.** Most nonparasitic apids have a complete epistomal ridge. Most parasitic apids (excepting *Xeromelecta*) agree with the nomadines in this regard. See

discussion under R&M #19 in the previous section.

- (12) **Parietals not expanded and with their posteroventral edge (in vicinity of posterior tentorial pits) not strongly inflexed so that foramen magnum, as seen in rear view (fig. 1), is not constricted at level of posterior tentorial pits.** In most bees (excepting Oxaeidae) the parietals are more expanded and the foramen is strongly constricted at the level of attachment of tentorial bridge (fig. 2). In spite of the fact that it has a projecting labiomaxillary region and pronounced salivary lips, *Isepeolus* agrees with the Nomadinae with respect to this feature.
- (13) **Median coronal ridge virtually absent.** A distinct median coronal ridge that extends from the posterior occipital ridge a short way toward, or all the way to, the epistomal ridge is characteristic of other apids (also absent in Isepeolini and Protepeolini and very short in Rhathymini).

Characters 1–5, 8, 10, and 12 above are especially strong either because they are unique to the Nomadinae within the Apidae

or because of their uncommon occurrence elsewhere in the family. All of the larval characters combined indicate that the Nomadinae form a very distinctive group within the Apidae.

PHYLOGENY OF THE NOMADINAE

The following analyses are based on the larvae of the species listed in table 1. Because the sister group of the subfamily is not apparent, a hypothetical ancestor was constructed using features of cocoon-spinning bee larvae after specimens of the taxa listed in table 2 were examined. The characters and their states are presented in table 3. Table 4 is the data matrix of the Nomadinae and the hypothetical ancestor based on these characters.

All analyses were performed with Hennig86, version 1.5 (Farris, 1988). Unless stated otherwise, trees were calculated using **mh***; **bb***; commands, resulting in most cases in more than one equally parsimonious tree. Where encountered in reduced matrices, autapomorphies were treated as inactive. In cases of more than one tree, matrices were then submitted for recalculation through successive-approximations character weighting as provided by the **xsteps** command with the **w** option of Hennig86.

Because a hypothetical ancestor was used as the outgroup for larval characters, unrooted ingroup analyses were performed in all analyses whether or not they were based on adult, larval, or combined matrices. The resulting trees were then rooted, as recommended by Nixon and Carpenter (1993: 421-422). In each of these cases, the entire matrix was first submitted to cladistic analysis to determine the position of the root. Next, the hypothetical ancestor was deactivated in DADA, version 1.00 (Nixon, 1995) using the **TT** command, and the matrix was submitted to Hennig86 to calculate one (or more) unrooted tree(s) from which the statistics were then recorded. The position of the root was then observed on the tree(s) from the first analysis and placed on the unrooted tree by the **reroot** command (**<SHIFT-F10>** branch/node) of CLADOS, version 1.2 (Nixon, 1992). When rerooting trees with a basal polytomy it was necessary to use the key command **m** (move) to restructure the tree in

cases in which one of the immediate descendants became the outgroup.

In analyses involving larval and adult characters (i.e., all but Analysis 1), congruence between larval and adult data sets was tested statistically using the **Con-test** command in DADA on the basis of 100 iterations (Farris et al., 1994). Also, each separate matrix was fitted to the combined tree in CLADOS to determine which matrix implied more homoplasy. These tests were performed on matrices with the hypothetical ancestors deactivated and without the matrices being submitted to successive-approximations weighting calculations.

Taxa treated in the earlier studies were not exactly the same as the taxa represented by larvae used in this study. For that reason it was necessary to fuse characters of some taxa or to combine larval features of one taxon with adult features of a different but related taxon (e.g., larval characters of *Neopasites* and adult features of *Biastes*). Modification of matrices was greatly aided by use of DADA. When characters were fused, polymorphic features were coded (?) (default mode for DADA) unless otherwise specified. Sequence of presentation of taxa and characters is uniform in all matrices, with larval features given before those of adults in combined matrices.

Cladograms were printed using CLADOS. Hashmark shading is as follows:

black	nonhomoplastic forward changes and nonhomoplastic, nonadditive changes (these changes can be reversed)
open	nonhomoplastic reverse changes
dark gray	homoplastic forward changes and homoplastic, nonadditive changes
light gray	homoplastic reverse changes

The following abbreviations are used in cladogram captions and indices are scaled to 100 throughout:

l	length in steps
ci	consistency index
ri	retention index
A.90	Alexander (1990)
R.91	Roig-Alsina (1991)
R&M.93	Roig-Alsina and Michener (1993)

Analysis 1: Phylogeny of the Nomadinae based on larval features alone (table 4).

With the use of Hennig86, a single minimum-length tree was produced (length 60 steps, consistency index 55; retention index 78) from a matrix consisting of 22 taxa plus the hypothetical ancestor and 29 characters using the procedures described above, with characters 13, 14, and 26 coded nonadditive. When rooted (fig. 3) this tree was completely resolved except for the trichotomy *Brachynomada*–*Melanomada*–*Paranomada*. These three genera and *Triopasites* formed the monophyletic basal clade, but *Kelita*, currently included in the Brachynomadini, was now united with *Hexepeolus* in a separate clade. The Epeolini, Nomadini, and Ammobatini each were shown to be monophyletic, and the Caenoprosopidini appeared paraphyletic. This cladogram, of course, was the most complete larval cladogram of the investigation since it included all the nomadine taxa whose larvae are known.

Analysis 2: Phylogeny of the Nomadinae based on larval characters from current study and adult characters from Alexander (1990: appendix 6) (table 5).

In order to compare the larval analysis with an analysis based on adults (corresponding to Alexander, 1990: analysis 3, fig. 3, appendix 6), it was first necessary to exclude from consideration all taxa that were not in common between the adult and larval matrices, leaving 19 taxa and the ancestor (which was based on actual taxa for adult characters). Characters 29–64 in table 5 are the characters and codings for adults taken directly from Alexander's appendix 6, with taxa reduced to the ones treated in the current study. All uninformative adult characters were excluded from the matrix. Characters 30, 48, and 54–56 in this table were coded nonadditive in accordance with Alexander's work.

When adult characters (table 5, characters 29–64) were analyzed with the hypothetical ancestor deactivated, six equally parsimonious trees resulted. Successive-approximations weighting procedures yielded two equally parsimonious trees (weighted length 426 steps, consistency index 80, retention index 84). These differed only in that one showed *Brachynomada*, *Kelita*, and *Paran-*

omada as a trichotomy whereas the other (fig. 4) showed *Paranomada* to be basal to the other two. These trees differed in many ways from the tree based on adult and larval characters depicted by Alexander (1990: fig. 3) and from the one based on adult characters alone (ibid.: fig. 4).

In order to compare the topology of the tree based on adults (fig. 4) with one based on larval characters, taxa (*Sphecodopsis* and *Caenoprosopina*) not treated by Alexander (1990) were deleted from the larval matrix (table 4) and characters of *Nomada* and *Micronomada* were fused as Nomadini (making character 6 uninformative, coded inactive) by using the fuse taxa command in DADA. An analysis calculated from the reduced matrix (table 5, characters 0–28) with characters 13, 14, and 26 coded nonadditive produced 10 equally parsimonious trees. When submitted to successive weighting procedures, the reduced matrix produced a single tree (weighted length 234 steps, consistency index 78, retention index 89) which, when rooted (fig. 5) appeared completely resolved except for the trichotomy *Brachynomada*–*Melanomada*–*Paranomada*. The topology of this tree was similar to the one based on the full larval matrix except that the interrelationships of the Nomadini, *Holcopasites*, and the epeoline genera shifted, and the ammobatine genera realigned. This tree was substantially incongruent with the one based on adult characters (fig. 4) although the ammobatine genera and the epeoline genera each formed a monophyletic grouping, as was the case with the adult tree.

Table 5 in its entirety is the combined reduced larval matrix from the current study and the modified adult matrix from Alexander (1990: appendix 6). All characters were coded as indicated above. Hennig86 produced 16 equally parsimonious trees with the ancestor deactivated (length 189 steps, consistency index 51, retention index 64). Successive weighting procedures calculated a single tree (weighted length 569 steps, consistency index 79, retention index 87). The rooted tree (fig. 6) had *Hexepeolus* as the basal branch, the brachynomadine genera formed a monophyletic clade, and the Nomadini and epeoline genera grouped as another clade.

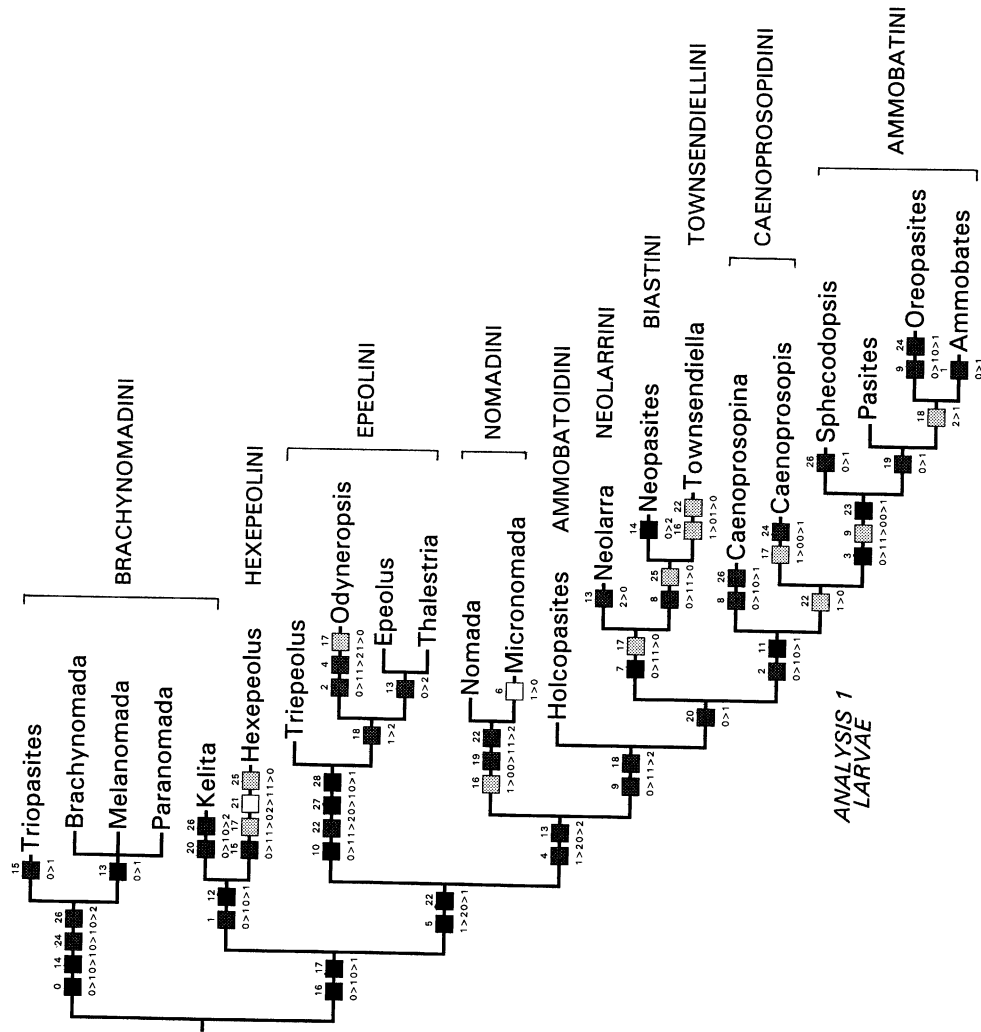
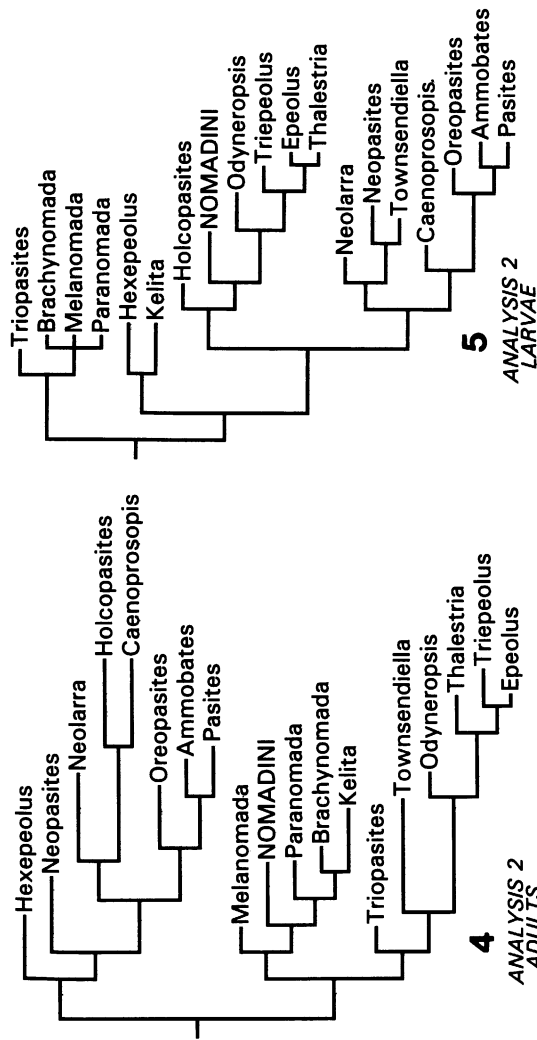


Fig. 3. Analysis 1 (table 4), single most parsimonious tree (l = 60, ci = 55, ri = 78) of the Nomadinae based on characters of the mature larvae.



Figs. 4, 5. Analysis 2 (table 5). 4. One of two minimum-length rooted cladograms calculated by successive weighting procedures, based on adult characters from A.90 (table 5, characters 29–64) (weighted 1 = 426, ci = 80, ri = 84). 5. Rooted minimum-length tree (weighted 1 = 234, ci = 78, ri = 89) based on larval characters from the present study (table 5, characters 0–28), calculated through successive weighting procedures.

The topology of figure 6, based on larval and adult characters, was substantially different from the adult tree (fig. 4). It agreed much more closely with the topology of the larval cladogram (fig. 5) in that (1) the *Neolarra*–*Neopasites*–*Townsendiella*–*Caenoprosopis*–*ammobatine* clade remained constant, (2) as did the *Holcopasites*–*Nomadini*–*epeoline* genera clade, and (3) the brachynomadine genera (except for *Kelita*) grouped as a clade.

The **Con-test** command of DADA produced a value of less than 1%, indicating significant incongruence between adult and larval characters. When the adult and larval matrices were fitted to the combined trees, the larval data produced a consistency index that was at most three percentage points higher than that of the adult matrix, indicating that adult and larval matrices were about equally homoplastic (or nonhomoplastic).

Analysis 3. Phylogeny of the Nomadinae based on larval characters from current study and adult characters from Roig-Alsina (1991) (tables 6 and 7).

This analysis is divided into parts 3A and 3B.

Analysis 3A. Larval taxa fused to correspond to tribes of Roig-Alsina (1991).

The larval analysis from the current study was compared to Roig-Alsina's investigation of the phylogeny of the Nomadinae based on adult characters. The latter analysis was carried out primarily at the tribal level but treated *Rhopalolemma* separately from the rest of the Biastini. Because the larva of *Rhopalolemma* is still unknown, that genus was excluded here. The taxa, characters, and character codings that he used are given in table 6, characters 29–48. With the deletion of *Rhopalolemma*, his characters 9 and 14 became uninformative and were excluded in the present study. When the modified matrix of adult characters was submitted to cladistic analysis using the **ie*** command of Hennig86, three equally parsimonious unrooted trees resulted. Successive-approximations weighting produced a single resolved tree which was then rooted (fig. 7) (weighted length 122 steps, consistency index 89, retention index 92). The topology of this tree was completely congruent with the more fa-

vored cladogram of Roig-Alsina (1991: fig. 15a).

The taxa in the larval matrix from the current study were fused (table 6, characters 0–28) so as to reflect the tribal categories of the Roig-Alsina investigation. Characters 13, 14, and 26 continued to be coded nonadditive (as in Analysis 1), and characters 0, 1, 3, 6, 10, 12, 14, 15, 19, 23, 24, and 26–28 became uninformative and accordingly were coded inactive. Larval features of *Neopasites* and *Holcopasites* alone were used for the Biastini and Ammobatoidini, respectively, although adult characters used for these tribes by Roig-Alsina were based on a larger number of genera. Calculations carried out with the **ie*** command of Hennig86 produced a single most parsimonious tree with the following statistics: length 21 steps, consistency index 76, and retention index 79. When rooted, its topology (fig. 8) was congruent with that based on the complete larval matrix (fig. 3) except that: (1) *Hexepeolus* was the most basal clade; (2) the *Brachynomada* complex (now recognized as the Brachynomadini) became the next most basal clade; (3) the Nomadini and Epeolini were united as a clade; and (4) the Caenoprosopidini became monophyletic.

The only congruence between the trees based on adult and larval characters (figs. 7 and 8) was the sister-group relationship of the Caenoprosopidini and Ammobatini.

The final step in Analysis 3A was to compare the adult and larval trees with the tree calculated from both sets of characters. Table 6 is the combined matrix of adult and larval characters, and the codings used were those employed in the calculations, above. Hennig86 found three minimum-length unrooted trees. Successive-approximations weighting resulted in a single resolved tree which was then rooted (fig. 9) (weighted length 201 steps, consistency index 88, retention index 91). The topology of this tree was identical to the one based on larvae alone (fig. 8) except that *Neolarra* shifted from the Biastini–*Townsendiella* clade to the Ammobatini–*Caenoprosopidini* clade. The only point of similarity between the tree based on the combined matrix (fig. 9) and the one based on adults (fig. 7) was the grouping of *Neolarra*–*Caenoprosopidini*–*Ammobatini*.

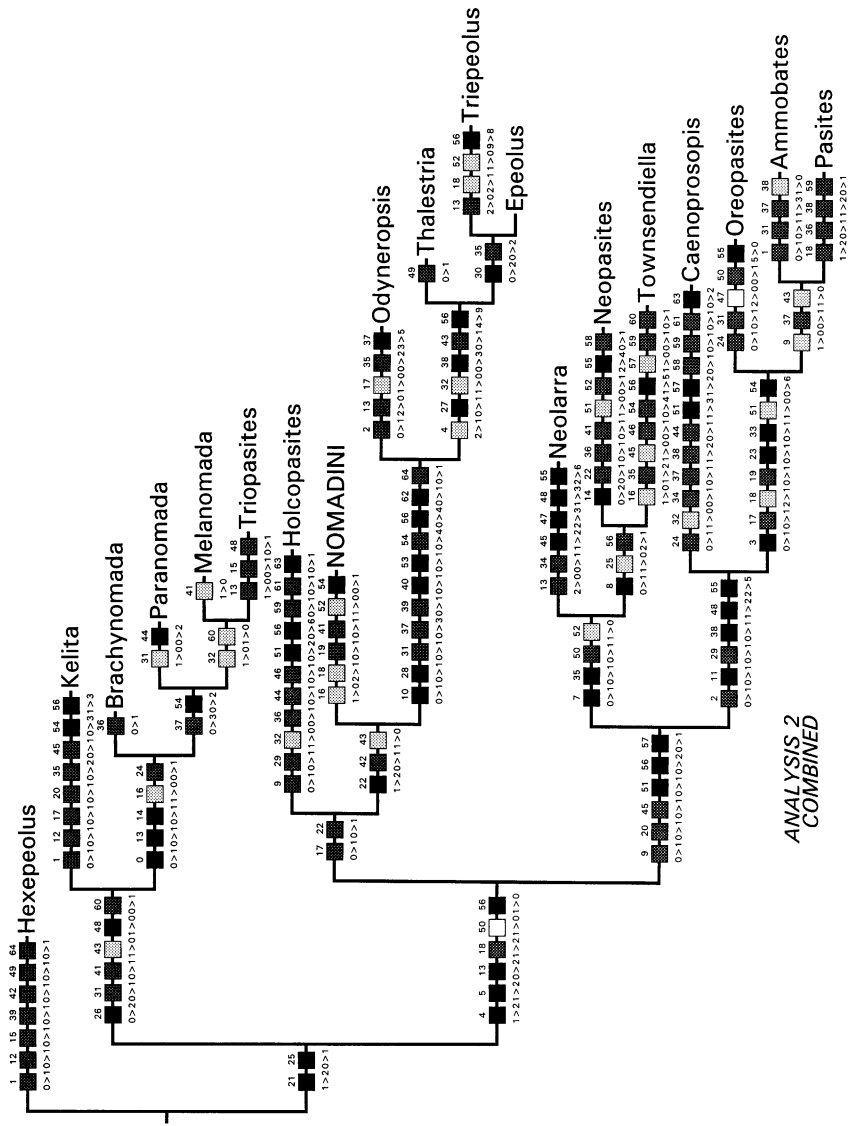
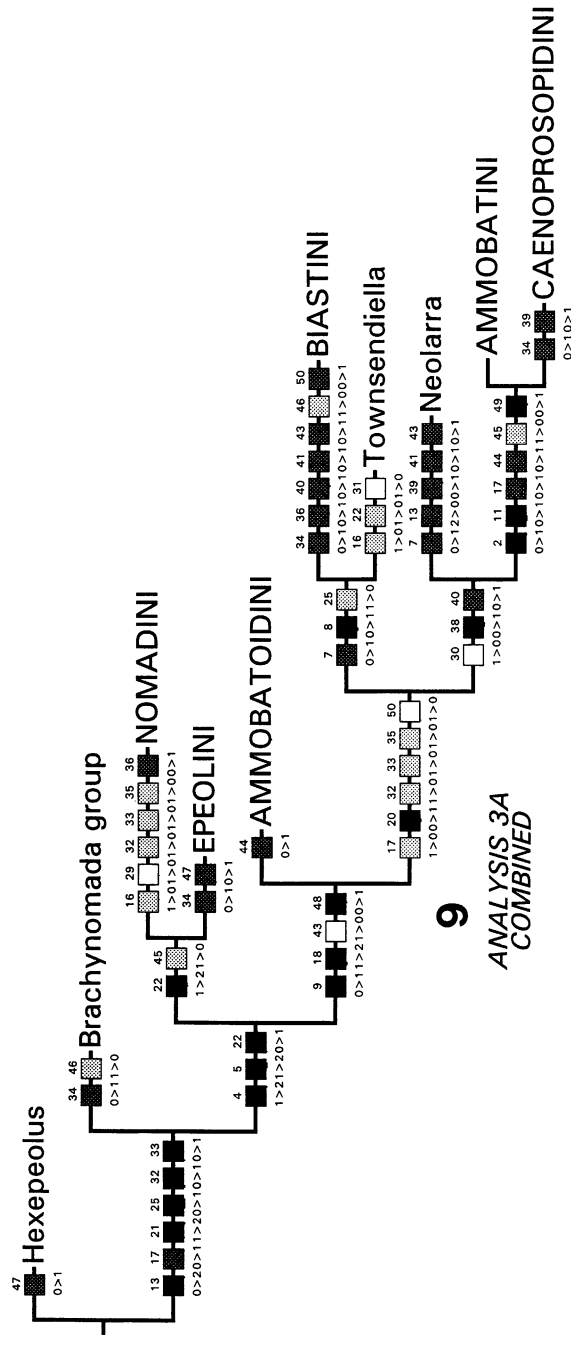
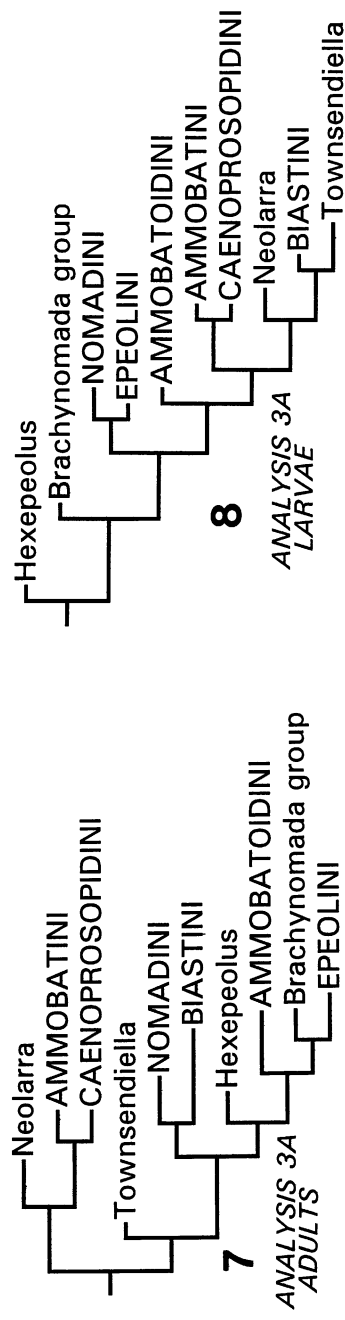


Fig. 6. Analysis 2 (table 5, characters 0–64), rooted minimum-length tree of the Nomadinae (weighted $l = 569$, $ci = 79$, $ri = 87$) based on larval characters from present study and adult characters from A.90: appendix 6, calculated by successive-approximations weighting.



Figs. 7–9. Analysis 3A (table 6). 7. Rooted minimum-length cladogram (weighted $l = 122$, $ci = 89$, $ri = 92$) based on adult characters from R.91 (table 6, characters 29–48), calculated using successive weighting procedures. 8. Rooted single most parsimonious cladogram ($l = 21$, $ci = 76$, $ri = 79$) based on larval characters from current study fused to taxa used by R.91 (table 6, characters 0–28). 9. Rooted minimum-length tree of the Nomadinae based on larval characters from present study and adult characters from R.91 (table 6, characters 0–48), calculated using successive weighting procedures (weighted $l = 201$, $ci = 88$, $ri = 91$).

The **Con-test** command of DADA produced a value of less than 1%, indicating significant incongruence between adult and larval characters. When the single life-stage matrices were fitted to the combined tree, the consistency index of the larval matrix proved to be 3–6 percentage points higher than the adult matrix, indicating that the larval characters were somewhat less homoplastic than the adult characters.

Analysis 3B. Adult taxa expanded to correspond to genera of current study. Yet another approach to compare cladograms based on larvae and adults was to use the taxa from the larval matrix (except for those of the Nomadini) and replicate the adult characters from Roig-Alsina (1991) for each genus in a tribe (as identified in table 7). Again, uninformative characters 9 and 14 from Roig-Alsina (1991) were eliminated from the matrix. When submitted to parsimony analysis, the adult matrix (table 7, characters 29–48) produced six unrooted minimum-length trees. Successive weighting procedures calculated a single minimum-length tree (not shown) (weighted length 158 steps, consistency index 79, retention index 94) which was congruent with figure 7, as expected.

Larval characters (table 7, characters 0–28) were analyzed with character 6 coded inactive and characters 13, 14, and 26 nonadditive. The resulting single minimum-length tree (not shown), when rooted, was identical in topology to the tree (fig. 3) of Analysis 1 (except for the fusion of nomadine genera) (length 59 steps, consistency index 54, retention index 77).

When larval and adult matrices (table 7) were combined using the same codings, seven equally parsimonious cladograms were calculated for the ingroup. Successive weighting procedures produced a single most parsimonious cladogram which was then rooted (fig. 10) (weighted length 347 steps, consistency index 72, retention index 90). The combined tree from Analysis 3A (fig. 9) and this tree were similar in some respects. However, now the epeoline genera aligned themselves with the Brachynomadini rather than the Nomadini and *Neopasites* (Biastini) and *Townsendiella* no longer formed a sister group.

The cladogram based on adult characters (see fig. 7) agreed with that based on the combined matrix in that *Neolarra*, *Ammobatini*, and *Caenoprosopidini* formed a clade, as did the Epeolini and brachynomadine genera. However, in other respects the two trees were dissimilar. The cladogram based on larval characters (see fig. 3) was also substantially different from that based on the combined matrix. In the larval tree the brachynomadine genera (except for *Kelita*) constituted the basal clade, not *Hexepeolus*; *Kelita* and *Hexepeolus* formed the next most basal clade; the epeoline genera were the sister group of the remaining taxa; and the alignment of *Neolarra*, *Holcopasites*, and *Townsendiella* shifted.

The **Con-test** command of DADA produced a value of less than 1%, indicating significant incongruence between adult and larval characters. When the single life-stage matrices were fitted to the combined tree, the consistency index of the larval matrix proved to be 4–7 percentage points higher than the adult matrix, indicating that the larval characters were somewhat less homoplastic than the adult characters, as in Analysis 3A.

Analysis 4. Phylogeny of the Nomadinae based on larval characters from current study and adult characters from Roig-Alsina and Michener (1993) (table 8).

As another analysis, relationships based on larval characters from the present study were compared with those based on adult characters identified by Roig-Alsina and Michener (1993: table 2). Because their table 2 was a matrix that dealt with all of the long-tongued bees as well as the Melittidae, non-nomadine taxa were eliminated from the matrix. *Rhogepeolus* was also eliminated from the matrix since the larva of that genus is unknown. The adult characters of *Pachynomada* and *Centrias* were fused under Nomadini, as were the larval characters of *Nomada* and *Micronomada*. In all, 11 nomadine taxa were considered.

The adult matrix and its codings in Analysis 4 were kindly supplied by Roig-Alsina (personal commun.). Adult characters that did not vary within the Nomadinae had been eliminated by Roig-Alsina and Michener. Because DADA identified their character 131 as also being uninformative, it too was elimi-

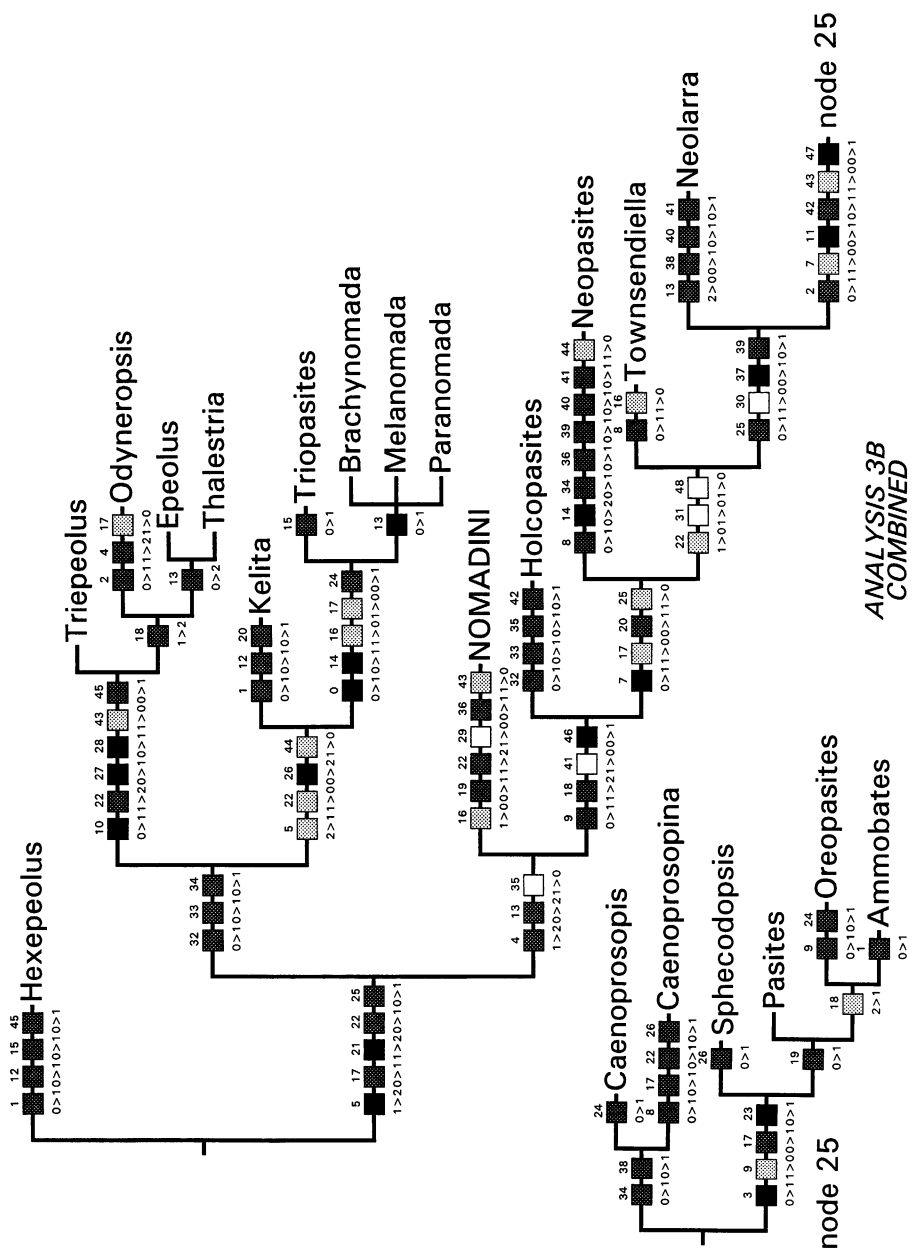


Fig. 10. Analysis 3B (table 7, characters 0–48), rooted minimum-length tree calculated by successive-approximations weighting procedures based on larval characters from present study and adult characters from R.91 (weighted 1 = 347, ci = 72, ri = 90). Generic representation of adult characters in table 7 based on iteration of tribal characters from R.91: table 2. The cladogram beyond node 25 is in the lower left corner.

nated from the matrix (table 8) as well as from Analysis 5, below.

Table 8 shows the characters used for Analysis 4 (characters 0–63) and for Analysis 5 (characters 0–72).

Adult characters in table 8 (characters 29–63) were coded as nonadditive, as treated by Roig-Alsina and Michener (1993), and were polarized as shown. When these characters were submitted to Hennig86 analysis, seven unrooted minimum-length trees were calculated. Successive-approximations weighting procedures yielded a single tree which was then rooted (fig. 11) by the reroot command of DADA (weighted length 213 steps, consistency index 83, retention index 87). This tree was completely resolved. *Oreopasites* and *Caenoprosopis* comprised the basal clade. *Triepeolus* and *Epeolus* formed a clade as did *Brachynomada* and the Nomadini, and *Kelita* and *Brachynomada* were paraphyletic.

This cladogram was incongruent in many respects with the nomadine branch of Cladogram 1b of Roig-Alsina and Michener (1993: 149, beyond node 8). Although the *Oreopasites*–*Caenoprosopis* clade was basal in both trees, the relative positions of the epeoline and *Holcopasites* clades switched, and all of the remaining taxa realigned following the reroot command. The differences in the two trees were due solely to the fact that the in-group analysis was executed first and then rooted in the current study. A simultaneous analysis based on adult characters in table 8 produced a cladogram that was completely congruent with their tree.

In table 8, characters 0–28 are of the larvae from the present study shared by the taxa treated by Roig-Alsina and Michener (1993). Because the mature larva of *Biastes* is unknown, characters of larval *Neopasites* were used to represent the Biastini. Characters 0, 3, 6, 8, 14, 15, and 23 were uninformative and were coded inactive. Characters 13, 14, and 26 were treated as nonadditive. The *ie** command of Hennig86 produced two unrooted minimum-length trees. Successive weighting procedures calculated a single unrooted minimum-length tree which was then rooted (fig. 12) (weighted length 149 steps, consistency index 89, retention index 93). This tree was completely congruent with that based on the entire larval matrix of Analysis 1.

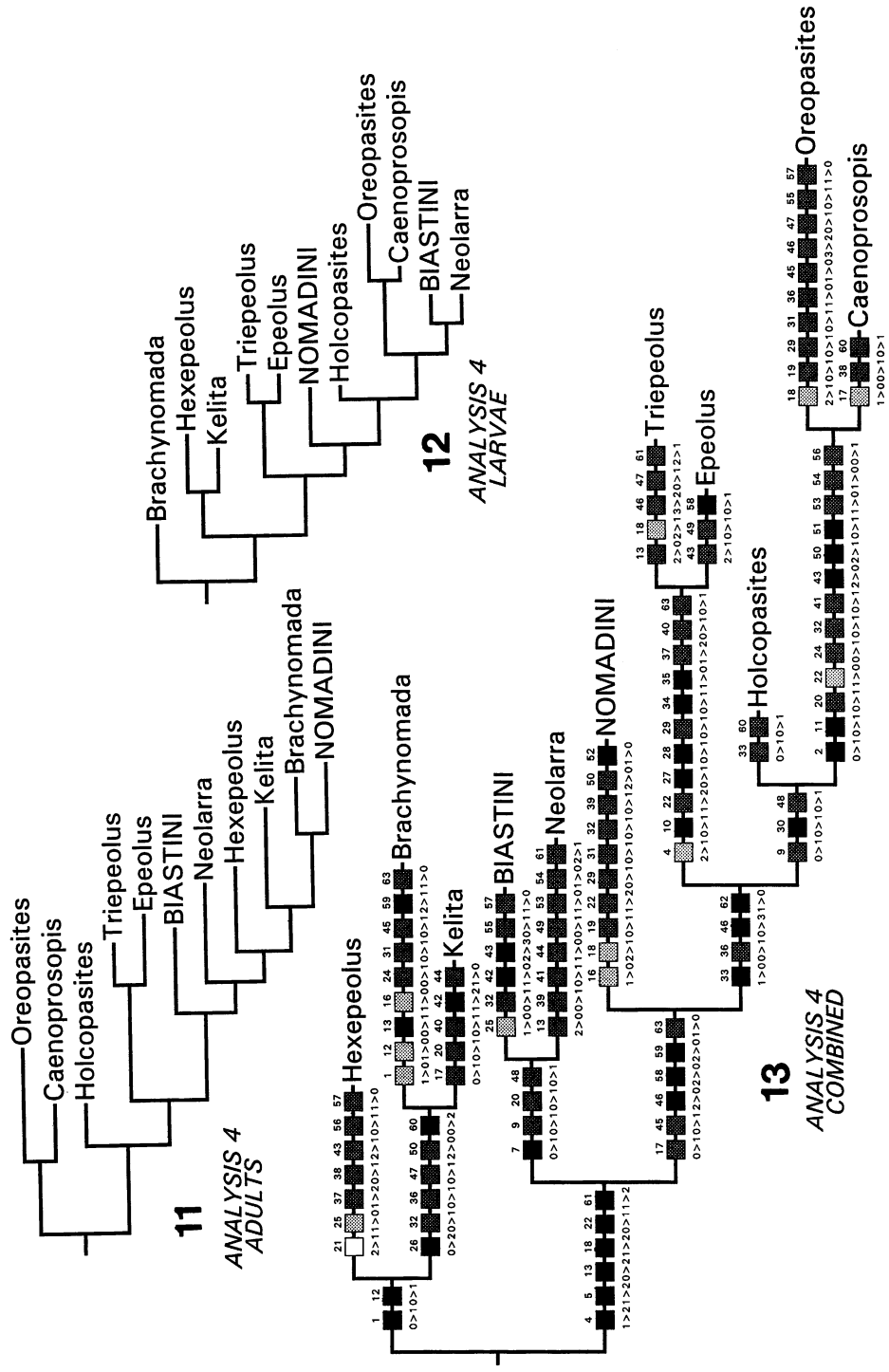
When the combined matrix (table 8, characters 0–63) was submitted to analysis, four unrooted minimum-length trees were calculated. Successive weighting procedures produced a single tree (weighted length 335 steps, consistency index 82, retention index 84). This tree (fig. 13), like the ones (figs. 11 and 12) calculated from the adult and larval matrices, agreed in that *Oreopasites* and *Caenoprosopis* and the epeoline genera each formed a clade. In other respects all three trees were broadly incongruent although the sister-group relationship of the Biastini and *Neolarra* was present in combined and larval trees.

The **Con-test** command of DADA produced a value of less than 1%, indicating significant incongruence between adult and larval characters. When the single life-stage matrices were fitted to the combined tree, the consistency indices of the adult and larval matrices were approximately equal, indicating that larval and adult characters were equally homoplastic.

Analysis 5. Phylogeny of the Nomadinae based on larval characters from current study and adult characters from reanalysis in Roig-Alsina and Michener (1993: 157) based on adult characters from that study and nine adult characters from Roig-Alsina (1991) (tables 8 and 9).

Within Roig-Alsina and Michener's (1993: 157) broad analysis of the long-tongued bees was a separate treatment of just the Nomadinae in which adult characters from their study were augmented by nine characters previously used by Roig-Alsina (1991) (see Historical Background, above, or Roig-Alsina and Michener, 1993: 157, for details). They repolarized the characters to conform with the values found at the basal node of the Nomadinae and treated all of them non-additively. Analysis 5 attempted to evaluate the relations of 11 nomadine taxa (excluding *Rhogepeolus* whose larva is unknown, and fusing characters of *Pachynomada* and *Centrias* into the single taxon Nomadini) on the basis of all adult characters combined with the larval ones from the current study (table 8).

Adult characters in table 8 (characters 29–72) produced seven minimum-length trees. Application of successive-approximations



Figs. 11–13. Analysis 4 (table 8). **11.** Rooted minimum-length tree (weighted $l = 213$, $ci = 83$, $ri = 87$) based on adults of R&M.93 (characters 29–63), calculated by successive-approximations procedures. Characters polarized according to values of basal node of Nomadinae (R&M.93). **12.** Rooted minimum-length tree of same based on larval characters from current study (characters 0–28), taxa reduced to correspond to those treated by R&M.93, using successive weighting procedures (weighted $l = 149$, $ci = 89$, $ri = 93$). **13.** Rooted minimum-length tree of the Nomadinae based on larval characters from present study and adult characters polarized according to values at basal node of Nomadinae from R&M.93 (characters 0–63) (weighted $l = 335$, $ci = 82$, $ri = 84$), calculated using successive weighting procedures.

weighting procedures yielded a single unrooted tree (weighted length 253 steps, consistency index 83, retention index 87), which was then rooted (fig. 14). This tree differed from that described by Roig-Alsina and Michener (1993) in that (1) *Oreopasites*–*Caenoprosopis* became the basal clade because *Neolarra* now connected as the basal branch of the remaining taxa, (2) *Hexepeolus* and the Nomadini exchanged positions, and (3) *Holcopasites* and the brachynomadine genera also exchanged positions. These differences were caused by the elimination of *Rhogepeolus* from the matrix in the current study as determined through analyses of the character matrix of Roig-Alsina and Michener with and without *Rhogepeolus*.

Figure 12 is the larval cladogram for Analysis 5 as well as 4. The adult tree (fig. 14) was broadly incongruent with it, the only coincidences being the sister-group relationships of *Oreopasites*–*Caenoprosopis* and the epeoline genera.

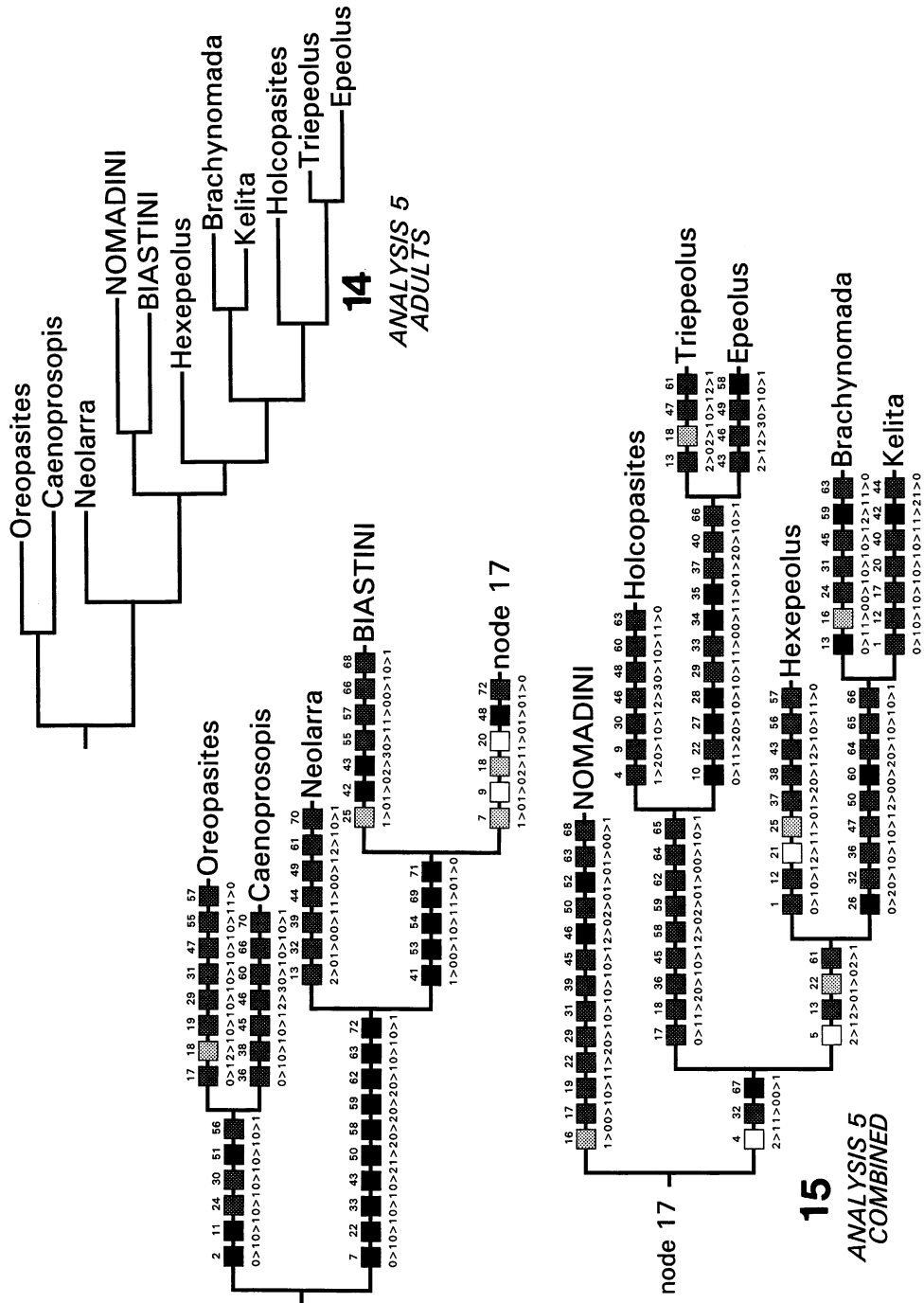
The combined larval and adult matrix produced at first a single unrooted minimum-length tree, length 142 steps, consistency index 53, and retention index 53. When the matrix was submitted to successive weighting procedures, a tree somewhat different in topology was calculated (weighted length 352 steps, consistency index 80, retention index 84). The Nomadini shifted from being the sister group of *Holcopasites* and the epeolines to being the sister group of these and *Hexepeolus* plus the brachynomadines. When rooted this cladogram (fig. 15) agreed with those based on larvae (fig. 12) and adults (fig. 14) with respect to the sister-group relationships of *Oreopasites*–*Caenoprosopis* and of epeoline genera. The adult tree shared the basal position of *Oreopasites*–*Caenoprosopis*, *Neolarra* being the sister of the remaining taxa, as well as the terminal clade of *Holcopasites* and the epeoline genera. However, the placements of the Nomadini and *Hexepeolus* were different. On the other hand, the cladogram based on larvae was totally incongruent with that based on the combined matrices (with the exceptions of the two sister groups shared by all trees). Adult and combined cladograms were obviously more similar than were the larval and combined cladograms.

The **Con-test** command of DADA produced a value of 2%, indicating significant incongruence between adult and larval characters. When the single life-stage matrices were fitted to the combined tree, the consistency indices of the adult and larval matrices were approximately equal, indicating the larval and adult characters were equally homoplastic.

DISCUSSION AND CONCLUSIONS

Analysis 1 fulfills the central purpose of this paper in that it presents a hypothesis of phylogenetic relationships in the Nomadinae based on all 22 genera whose mature larvae have been collected to date. Of all of the larval cladograms in this paper, figure 3 is preferred because it is based on the largest number of taxa and incorporates the maximum number of characters. The analysis followed a reassessment of larval characters used in the past by me and others and includes a number of new characters as well. Subsequent analyses presented here attempt to determine the reliability of the cladogram of Analysis 1. They also address the transcending purpose of the investigation in that they offer various hypotheses regarding the phylogeny of the subfamily based on different sets of adult characters (but always the same larval characters) and different subsets of taxa.

An a priori assumption of this paper was that larval and adult phenotypes evolve independently of one another, and therefore parsimony analysis based on one life stage can be a test of the analysis of the other life stages. If both are correct, the resulting trees will be congruent. If there is a lack of congruence, then the tree that most closely fits a tree based on a matrix of both larval and adult characters should be the more reliable reflection of the true relationships. This is based on another assumption, namely that a study based on both larval and adult characters is more likely to mirror accurately the evolutionary pathways of a group than one based on a single life stage. Whether this assumption is correct cannot be tested by the data contained in this paper, since it requires the analysis of at least one other set of characters independent from those already treat-



Figs. 14, 15. Analysis 5, adult characters polarized as in R&M.93 based on 29 larval characters from current study, 35 adult characters from R&M.93, and nine adult characters from R.91. **14.** Rooted minimum-length tree based on adult characters (table 8, characters 29–72) (weighted $l = 253$, $ci = 83$, $ri = 87$) calculated by successive-approximations weighting procedures. **15.** Rooted single most parsimonious tree based on ycombined larval and adult characters (table 8, characters 0–72) (weighted $l = 352$, $ci = 80$, $ri = 84$). Cladogram beyond node 17 continued below, as indicated.

ed. Nonetheless the assumption appears reasonable on an a priori basis because increases in the number of characters should tend to overcome undetected evolutionary convergences and reversals.

Another premise of the study was that more recent published analyses based on adult characters were more accurate than previous ones. Alexander (1996), in studying the female reproductive system, combined his newly-found characters with the adult matrix of Roig-Alsina (1991) (Roig-Alsina and Michener, 1993, study not yet complete at that time). Alexander (personal commun.) informed me that the 1991 study by Roig-Alsina was based on firsthand research and its characters were probably more reliable than those in Alexander (1990), based in part on literature accounts. The adult characters used in Roig-Alsina and Michener (1993: 157) then would seem to be the most reliable of all since they are a combination of adult characters from Roig-Alsina (1991) and from Roig-Alsina and Michener (1993). That study then is not only more recent but also incorporates two sets of data.

To what extent did the cladograms based on the combined matrix support the larval cladograms versus the adult cladograms? In Analyses 2 and 3A, combined cladograms were more congruent with the larval trees than with adult trees. Analyses 3B and 4 were indeterminant because none of the combined cladograms was appreciably more similar in topology to the larval or adult cladograms. In Analysis 5 the combined cladogram was more similar to the adult cladogram than to the larval one.

Hence, the analyses following Analysis 1 did not clearly support either the larval or adult data sets. The greatest support for the larval cladograms came from the earlier and presumably less reliable studies, whereas support for the adult cladograms appeared only in 5, the last study which should have been the most reliable.

Most of the analyses suffered because too many taxa had to be eliminated from consideration. The effect of reducing the matrices can be observed by comparing larval cladograms. Whereas the larval cladogram of Analysis 4 (fig. 12) is congruent with that of Analysis 1, those of Analyses 2 (fig. 5) and

3A (fig. 8) are not. The differences are due entirely to deleting and/or fusing taxa since the characters are identical. The considerable differences in the adult cladograms are clearly due in part to the fact that they are based on different suites of characters. Nonetheless, there are differences unquestionably caused by deletion of taxa. This is demonstrated by the effect of removing *Rhogepeolus* from the matrix of adult characters in Analysis 5 (compare fig. 11 with that described by Roig-Alsina and Michener, 1993: 157).

No two cladograms based on combined adult and larval characters were congruent. This is not surprising because of incongruence among cladograms based on adult characters alone. However, where the genera of polytypic tribes were treated separately (i.e., not fused), the composition of each of these tribes held up consistently in the combined cladograms although not always in cladograms treating only one life stage. Hence, in figures 6, 10, 13, and 15, the brachynomadine genera and those of the Epeolini each formed a clade, as did the ammobatines in figures 6 and 10. This suggests that the tribes of the Nomadinae are correctly identified and that the main problem in understanding the phylogeny of the subfamily deals with how the tribes are related to one another. However, the cladogram (fig. 3) from Analysis 1 hints that relationship of *Kelita* to the other brachynomadine genera needs to be confirmed as does the monophyly of the Caenoprosopidini.

The following attempts to summarize, to the extent possible, the probable phylogenetic relationships in the Nomadinae on the basis of the analyses undertaken in this paper. In cladograms dealing with combined adult and larval characters (figs. 6, 9, 10, 13, and 15) *Hexepeolus* appears as the basal clade except in Analyses 4 (fig. 13) and 5 (fig. 15). However, in all combined cladograms (including figure 15), *Hexepeolus* is closely linked to the brachynomadine genera as is also the case in Analysis 1 (fig. 3). Also, in all combined cladograms the caenoprosopidine and ammobatine representatives become a terminal sister group. In other respects, there is little congruence among these cladograms.

Eardley (1994) examined the relationships

of the genera of the Ammobatini using *Caenoprosopis* as part of the ingroup and *Neolarra* as the outgroup. Larval characters from the present study were combined with the adult characters of *Caenoprosopis*, *Pasites*, *Sphecodopsis*, *Oreopasites*, and *Ammobates* from his treatment based on generic ground plans (ibid.: 13, table 4, fig. 4). Of the 33 characters that remained informative according to DADA, seven were from the larval matrix. When the combined matrix was submitted to Hennig86, the i.e.* command calculated a single tree, which, when rooted, differed from his figure 4 in that *Sphecodopsis* and *Pasites* exchanged positions: (ancestor (*Caenoprosopis* (*Sphecodopsis* (*Pasites* (*Oreopasites* + *Ammobates*))))). Hence the topology was identical to the same terminal clade of figure 3.

FUTURE STUDIES

To resolve affinities in the subfamily further, several investigatory paths are obvious. First, additional taxa need to be included. The importance of this is exemplified by the *Rhogepeolus* exclusion in Analyses 4 and 5, discussed above. Second, suites of additional characters independent of those used here need to be explored. Molecular systematics immediately comes to mind, but the Nomadinae seem to be replete with opportunities in nonmolecular systematics as well, as follows:

Several recent studies (Alexander and Rozen, 1987; Rozen, 1992a) have summarized information about external egg structure and method of egg deposition in nomadine bees. These two subjects are functionally interrelated, show considerable variability in the subfamily, and need further investigation before their complexities can be fully understood. It seems likely that the relatively unmodified egg chorion associated with the egg being placed obliquely in a slit in the brood cell wall (Rozen, 1992a: category 1) is plesiomorphic. These features are characteristic of all Brachynomadini genera treated here, *Nomada*, *Townsendiella*, and *Holcopasites*. Other egg shapes and types of insertions in the cell wall (ibid.: category 2) are presumably derived. They are characteristic of Ammobatini, Epeolini, Neolarrini,

and *Neopasites*. It seems reasonable to assume that presence of a distinct operculum which is flush with the cell wall and the often U-shaped insertion posture of the eggs of the ammobatine genera are synapomorphies of that tribe. Likewise, the characteristics of the eggs and egg insertions (see Rozen, 1992a: table 1) of epeoline genera are synapomorphies of that tribe. It is likely that such features as presence of an operculum, angle of the long axis of the inserted egg to the cell wall, areas of specialized chorion, and specialized egg shapes can be homologized from one tribe to the next, at least in some cases. These features do vary remarkably in the subfamily (see discussion in Rozen, 1992a). Further gathering of these data should be pursued so that egg structure and oviposition features can be assessed cladistically.

Pupae of bees in general have been little studied in large part due to the fact that this stadium in bees is short. Consequently, pupae are infrequently encountered and preserved. Nonetheless, they do possess characters of taxonomic value that are uniquely pupal adaptations and not adult features (Michener, 1954). Pupae of a number of groups of Nomadinae have been described: Michener, 1954 (*Holcopasites*); Rozen and McGinley, 1974 (*Oreopasites*, *Pasites*); Rozen, 1977 (*Melanomada*, *Paranomada*, *Nomada*), 1992b (*Oreopasites*), 1994a (*Brachynomada*). Pupae of a number of other taxa (*Neolarra*, *Holcopasites*, *Epeolus*, *Odyneropsis*, *Triepeolus*) have been casually examined for this study. Nomadine pupae clearly possess characters useful for cladistic analysis. The most obvious feature is the absence (plesiomorphic) or presence (apomorphic) of small, apically pigmented, acutely pointed tubercles on the vertex, mesoscutum, and mesoscutellum (see Rozen, 1992b: figs. 5, 8) in all genera listed above except for those of the Brachynomadini and *Odyneropsis*. There is every reason to believe that a more thorough comparative study of pupae will yield additional characters, particularly after more taxa are represented in collections.

The newly eclosed larvae of the Nomadinae, like those of the cleptoparasitic bees with hospicidal first instars, are highly modified and appear to be replete with features of taxonomic value (Rozen, 1989, 1991).

Some of these characters are clearly not independent of the last larval instar, as for example the greatly reduced labial palpi of first and last instars. But other features appear to be independent. One example is the heavily sclerotized head capsule of first instars in contrast to the very weak crania of last instars. Another is the greatly elongate mandibles of the first instars, which contrast with the unusually short mandibles of the last instars (except in the *Brachynomadini*). There can be little doubt that, on careful study, first instars will yield characters that are independent of those of last instars and that will therefore help determine relationships among the included taxa.

Almost all systematic studies of the *Nomadinae* have been based on external anatomy. In a pioneering study, Alexander (1996) recently examined the internal anatomy of the female reproductive system of the *Nomadinae*. Among other things, he discovered that female *nomadines* possessed "glandular pouches" attached to the vagina. Variation in these sacs among the representatives

of the subfamily suggests that they may be useful in parsimony analysis once fresh specimens are examined. In the same study, he demonstrated that variation in ovariole number in conjunction with adult characters used by Roig-Alsina (1991) can be analyzed cladistically in order to understand the relationships of the *nomadine* tribes. Thus internal anatomy holds promise in furthering our understanding of the *Nomadinae*.

The relationships of *Protepeolini* and *Isepeolini* (both of whose larvae have been described) to the other apids have not been addressed in the current investigation, which was limited to the *Nomadinae sensu stricto*. However, a preliminary survey of the mature larvae of a large number of apid taxa was carried out at the initiation of this study. Obvious relationships of the two parasitic groups with pollen-carrying apids were not immediately evident. A more thorough study of mature larvae of these two tribes and the nonparasitic apids should be carried out, particularly in light of the affinities identified in Roig-Alsina and Michener (1993).

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TABLE 1
Mature Larvae of the Nomadinae Studied

Included references provide informative descriptions of the larvae. Larvae of other species have been briefly described [see McGinley, 1989] but information about them is too sketchy to be meaningful. Taxa without references are those whose larvae have been examined in connection with this study although descriptions have not been published. Tribal assignments follow Roig-Alsina and Michener, 1993, including the placement of *Holcopasites* in the Ammobatoidini [such placement seems reasonable in light of the adult synapomorphies of the tribe identified in Roig-Alsina, 1991]. Mature larvae of the Protepeolini [Rozen et al., 1978; McGinley, 1981; Roig-Alsina and Rozen, 1994] and Isepeolini [Rozen, 1966; Lucas, 1966], formerly considered in the subfamily, are now excluded.

Species	Reference
HEXEPEOLINI	
<i>Hexepeolus rhodogyne</i> Linsley and Michener	Rozen, 1996
BRACHYNOMADINI	
<i>Brachynomada roigi</i> Rozen	Rozen, 1994a
<i>Kelita toroi</i> Ehrenfeld and Rozen	Rozen, 1994a
<i>K. tuberculata</i> Ehrenfeld and Rozen	Ehrenfeld and Rozen, 1977
<i>Melanomada annectens</i> Snelling and Rozen	Snelling and Rozen, 1987
<i>M. sidaefloris</i> (Cockerell)	Rozen, 1977
<i>Paranomada velutina</i> Linsley	Rozen, 1977
<i>Triopasites penniger</i> (Cockerell)	Rozen, 1977
NOMADINI	
<i>Nomada (Nomada) fowleri</i> Cockerell	Michener, 1953; Rozen, 1966
<i>N. (Micronomada) suavis</i> Cresson	Rozen, 1966
<i>N. (N.) sp. A</i>	Rozen, 1966
<i>N. (N.) sp. C</i>	Rozen, 1966
<i>N. (Micronomada) gutierreziae</i> (Cockerell)	
<i>N. sp. B</i>	Rozen, 1966
EPEOLINI	
<i>Triepeolus grandis</i> (Friese)	Rozen, 1966; McGinley, 1981; both as <i>T. sp. A</i>
<i>T. kathrynae</i> Rozen	Rozen, 1966, as <i>T. sp. B</i>
<i>T. mesillae</i> Cockerell	Rozen, 1966
<i>T. remigatus</i> (Fabricius)	Rozen, 1966
<i>T. sp. C</i>	Michener, 1953, as <i>T. sp.?</i> ; Rozen, 1966
<i>Epeolus pusillus</i> Cresson	Rozen, 1966
<i>E. sp. A</i>	Rozen, 1966
<i>Odyneropsis apicalis</i> Ducke	Rozen, 1966
<i>Thalestria</i> sp.	
AMMOBATINI	
<i>Oreopasites (Oreopasites) favreauae</i> Rozen	Rozen and McGinley, 1974, as <i>O. sp.</i> from cells of <i>Nomadopsis helianthi</i>
<i>O. (O.) vanduzeei</i> Cockerell	Rozen, 1954, 1966; McGinley, 1981
<i>O. (Perditopasites) barbarae</i> Rozen	Rozen and McGinley, 1974, as <i>O. sp.</i> from cells of <i>Perdita</i>
<i>Sphecodopsis fumipennis</i> (Bischoff)	Rozen and McGinley, 1974, as <i>Pseudodichroa fumipennis</i> Bischoff; McGinley, 1981
<i>Ammobates carinatus</i> Morawitz	Rozen and McGinley, 1974; McGinley, 1981
<i>Pasites histrio</i> (Gerstaecker)	Rozen and McGinley, 1974, as <i>Morgania histrio transvaalensis</i> Bischoff; McGinley, 1981
AMMOBATOIDINI	
<i>Holcopasites (Holcopasites) calliopsidis</i> (Linsley)	Rozen, 1966
<i>H. (Holcopasites) eamia</i> (Cockerell)	
<i>H. (Holcopasites) minimus</i> (Linsley)	
<i>H. (Trichopasites) insoletus</i> (Linsley)?	Rozen, 1966; McGinley, 1981
<i>H. (Trichopasites) ruthae</i> Cooper	
<i>H. sp. A</i>	Rozen, 1966

TABLE 1—(Continued)

Species	Reference
BIASTINI	
<i>Neopasites (Micropasites) cressoni</i> Crawford	Rozen, 1966; McGinley, 1981
NEOLARRINI	
<i>Neolarra (Neolarra) californica</i> Michener	Rozen, 1966
<i>N. (N.) pruinosa</i> Ashmead	
<i>N. (N.) verbesinae</i> (Cockerell)	
<i>N. (Phileremulus) vigilans</i> (Cockerell)?	
<i>N. sp.</i>	
CAENOPROSOPIDINI	
<i>Caenoprosopis crabronina</i> Holmberg	Rozen and Roig-Alsina, 1991
<i>Caenoprosopina holmbergi</i> Roig-Alsina	Rozen and Roig-Alsina, 1991
TOWNSENDIELLINI	
<i>Townsendiella (Townsendiella) pulchra</i> Crawford ^a	Rozen and McGinley, 1991

^a Probably not a mature larva.

TABLE 2
Mature Larvae of Non-Nomadine Taxa Studied

Colletidae	Apidae (Continued)
<i>Ptiloglossa arizonensis</i> Timberlake	<i>Ancyloscelis apiformis</i> (Fabricius)
Halictidae	<i>Ptilothrix tricolor</i> (Fries)
<i>Dufourea mulleri</i> (Cockerell)	<i>Svastra obliqua obliqua</i> (Say)
Melittidae	<i>Anthophora occidentalis</i> Cresson
<i>Meganomia gigas</i> Michener	<i>Centris caesalpiniae</i> Cockerell
Megachilidae	<i>Epicharis fasciata</i> Lepeletier and Serville
<i>Pararhophites orobinus</i> (Morawitz)	<i>Bombus steindachneri</i> Handlirsch
<i>Neofidelia profuga</i> Moure and Michener	<i>Ctenoplectra armata</i> Magretti
Apidae	<i>Leiopodus singularis</i> (Linsley and Michener)
<i>Xylocopa virginica</i> (Linnaeus)	<i>Isepeolus viperinus</i> (Holmberg)
<i>Exomalopsis sidae</i> Cockerell	<i>Xeromelecta californica</i> (Cresson)
<i>Teratognatha modesta</i> Ogloblin	<i>Ericrocis lata</i> (Cresson)
<i>Paratetrapedia (Arhysoceble) melampoda</i> (Moure)	<i>Rhathymus trinitatis</i> Cockerell

TABLE 3

**Characters Used in Phylogenetic Analysis of the Tribes and Genera of the Nomadinae,
Based on Mature Larvae**

(0 = plesiomorphy; 1, 2, etc. = derived states. To facilitate comparison, numbers used by Roig-Alsina and Michener, 1993, for larval characters are indicated as follows: R&M #—. Multistate characters are considered additive unless indicated otherwise.)

Head Capsule and Antenna

0. Vertex without wrinkled swelling on each side above antenna and mesad of upper end of parietal band (Rozen, 1994a: fig. 14) (0); with more or less distinct swelling on each side, integument of which tends to be wrinkled (Rozen, 1977: figs. 3, 4, 10, 11, 16, 17) (1). R&M #7, 8. Such swellings (though in some cases subtle) are a unique apomorphy of the Brachynomadini exclusive of *Kelita* (paired low irregular tubercles on face of *Rhathymus* [Rozen, 1969] are not considered homologous because they are positioned lower on face).
1. Anterior tentorial pit normal in position, that is, close to anterior mandibular articulation (Rozen, 1994a: fig. 6) (0); removed from anterior mandibular articulation by at least one-third distance between anterior mandibular articulation and antenna (Rozen, 1994a: fig. 13) (1). R&M #9. The polarity of this character is uncertain because state (0) is found commonly in the Apinae whereas (1) is characteristic of many of the other species listed in table 2. The character state for the ancestor has therefore been coded (?). Because species of *Nomada* exhibit both states, the genus is coded (?) in the matrix.
2. Posterior tentorial pit on hypostomal ridge (Rozen, 1994a: figs. 7, 14) (0); somewhat below hypostomal ridge at rear of head (Rozen, 1966: fig. 34) (1). R&M #10, see Evaluation of Characters. Among all bee larvae, posterior tentorial pits are below the hypostomal ridge only in some nomadines, in the Oxaeidae, and in the andrenine *Euherbstia* (Rozen, 1993).
3. Posterior tentorial pit immediately in front of cervical fold or near it (Rozen, 1994a: fig. 14) (0); well in front of fold (Rozen and McGinley, 1974: figs. 8, 17, 24) (1). R&M #10, see Evaluation of Characters. In almost all bee larvae except those of some Nomadinae and *Isepeolus*, the posterior tentorial pits are close to the cervical fold, the plesiomorphic state. Although the position of the pits is somewhat variable in the Nomadinae, the apomorphic condition, as here used, is restricted to the Ammobatini.
4. Postoccipital ridge present as single internal ridge across entire cranium, in normal position at posterior margin of head capsule (Rozen, 1993: fig. 8) (0); weak and interrupted toward midline (Rozen, 1994a: figs. 7, 14) (1); very weak to virtually absent (Rozen, 1966: figs. 71, 75, 82), sometimes represented by two faint ridges, one in front of the other (Rozen, 1966: fig. 48) (2). R&M #11 and 13 combined, see Evaluation of Characters. The single available specimen of *Sphecodopsis* was predefecating. Because lack of pigmentation made evaluation of the character state difficult, the genus was coded (?) in the matrix. A well-developed postoccipital ridge is characteristic of almost all bee larvae and is therefore plesiomorphic. (The greatly reduced and double postoccipital ridges are also encountered in *Isepeolus* and *Leiopodus*, respectively. It is unknown whether these features are homologous among these three groups.)
5. Hypostomal ridge of postdefecating larva well-developed (Rozen, 1993: fig. 8) (0); weaker (Rozen, 1966: figs. 10, 17, 20) (1); very weak (Rozen, 1966: figs. 40, 48) (2). R&M #15, but note subdivision of their single apomorphic condition into (1) and (2). Because a strong hypostomal ridge is found among almost all bee larvae, this condition is obviously plesiomorphic but is not found in the Nomadinae.
6. Antennal papilla projecting at least as far as its basal diameter (Rozen, 1966: figs. 47, 48) (0); shorter than basal diameter (Rozen, 1994a: figs. 6, 7) (1). R&M #20. Because the elongate condition is found among many sphecids and pollen-collecting apids, it is believed primitive for bees. In the Nomadinae it is characteristic of only *Micronomada* and is perhaps secondarily derived.
7. Frontoclypeal area in lateral view normal, not protruding beyond labrum (Rozen, 1994a: figs. 7, 14) (0); extending beyond labrum (Rozen, 1966: figs. 75, 82) (1). R&M #23. A bulging frontoclypeal area, as seen in lateral view, is unknown elsewhere in the Apidae and is therefore apomorphic.

Mouthparts

8. Labrum of normal length relative to width in frontal view, that is, longer than one-half width (Rozen, 1994a: figs. 6, 13) (0); transverse, about one-half width or less (Rozen, 1966: fig. 74) (1). The small, very short labrum as found in some Nomadinae appears to be unique and is therefore considered apomorphic. Although a short labrum is found among some other apids (e.g., *Svastra*, *Anthophora*, *Rhathymus*, and *Ericrocis*), it is associated with a long clypeus and is therefore believed to have had a different evolutionary origin from that of the nomadine short labrum combined with a very short clypeus, apparently a unique apomorphy.
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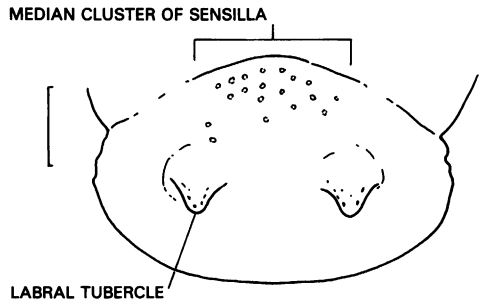


Fig. 16. Labrum of postdefecating larva of *Triepeolus grandis* (Fries), anterior view, showing median cluster of large sensilla on upper part of disc. Scale = 0.1 mm. (Portal, Cochise Co., Arizona, August 31, 1983 [J. G. Rozen], from *Ptiloglossa arizonensis* Timberlake, nest no. 1.)

TABLE 3—(Continued)

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- | | |
|-----|---|
| 9. | Labrum projecting forward beyond lower edge of clypeus in lateral view (Rozen, 1994a: figs. 7, 14) (0); projecting only as far as lower edge of clypeus or more recessed (Rozen, 1966: figs. 75, 82) (1). R&M #24, reinterpreted. Because larvae of most bees exhibit a labrum that projects beyond the clypeus, this condition is considered plesiomorphic. |
| 10. | Labrum with scattered sensilla but without median cluster of five or more large sensilla on disc (Rozen, 1994a: figs. 6, 13) (0); with median cluster of five or more conspicuous sensilla on disc (fig. 16) (1). The latter is an autapomorphy of the Epeolini. |
| 11. | Labrum spiculate on sides (Rozen, 1994a: figs. 7, 14) (0); nonspiculate on sides (Rozen and Roig-Alsina, 1991: figs. 5, 13) (1). Because most bee larvae have spicules on the sides, this state is tentatively coded plesiomorphic. R&M #3. In recent descriptions of bee larvae, the lateral part of the labrum has been considered part of the epipharyngeal surface because it seemed continuous with the ventral (posterior) surface of the labrum. However, the boundary between the labrum and epipharynx is uncertain in the Nomadinae because the labrum is rather bulbous instead of dorsoventrally compressed in some cases. Furthermore, in <i>Nomada</i> and to a lesser extent in the Ammobatini the ventral surface of the labrum bears a conspicuous median lobe immediately in front of the mouth. This lobe, which comes in contact with the dorsal surface of the hypopharynx, might reasonably be considered the epipharynx. To avoid confusion, the spiculated or nonspiculated sides of labrum are not termed the epipharynx here. The area (lobelike or not) immediately in front of the mouth and opposing the hypopharynx is apparently never spiculated in the Nomadinae.
The sides of the labrum are clearly spiculate in <i>Neolarra verbesinae</i> but not certainly so in the other, smaller species of the genus. The character is coded (0) for the genus since it is assumed that spicules in the other species have been lost, perhaps in correlation with their very small size.
The area is also spiculate in <i>Neopasites</i> , as can be observed on newly acquired material, contrary to Rozen (1966) and Roig-Alsina and Michener (1993).
Both <i>Nomada</i> and <i>Epeolus</i> are polymorphic in regard to this character and accordingly are coded (?). |
| 12. | Labral disc without spicules (Rozen, 1994a: fig. 6) (0); bearing fine, sharp spicules (Rozen, 1994a: fig. 13) (1). R&M #2. Spiculated labral discs are uncommon among the Apoidea and are therefore considered apomorphies. Because the disc is spiculate in <i>Nomada</i> species A but not in other known species of <i>Nomada</i> (Rozen, 1966), this character is coded (?) for that genus. |
| 13. | Mandible of normal length (Rozen, 1994a: figs. 15–17) (0); elongate (Rozen, 1994a: figs. 8–10) (1); very short (Rozen and Roig-Alsina, 1991: figs. 4, 7, 8) (2). R&M #31, reinterpreted. NONADDITIVE. |
| 14. | Mandible with apex curving toward head (Rozen, 1994a: figs. 13, 16) (0); curving downward (i.e., mandible sinuate) (Rozen, 1994a: figs. 6, 9) (1); straight (Rozen, 1966: figs. 76–78) (2). NONADDITIVE. The basic mandible type curves toward the larval head. |
| 15. | Mandibular apex acutely pointed (Rozen, 1994a: figs. 9, 16) (0); rounded (Rozen, 1977: fig. 14) (1). R&M #29. Mandibular apices of bee larvae are extremely variable, and the polarities associated with this variability in the superfamily are unclear. However, within the Nomadinae, simple, acutely pointed mandibles are by far the most common type, and the two known cases of apically rounded mandibles probably arose independently from acutely pointed mandibles. |
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TABLE 3—(Continued)

16. Dorsal and adoral mandibular surfaces with distinct, sharp denticles (Rozen, 1977: figs. 7, 13, 19) (0); without sharp denticles although sometimes with irregularities (Rozen, 1994a: 16) (1). R&M #34. The denticles are assumed to correspond to those found on the cusp of larval pollen-collecting bees.
17. Maxilla with at least some spicules (Rozen, 1994a: figs. 6, 7) (0); nonspiculate (ibid.: figs. 13, 14) (1). R&M #5. Spicules occur on the maxillae of most apoid larvae and are therefore tentatively considered primitive. Because the spiculated areas are greatly reduced and restricted to just below the hypostomal ridge in *Neolarra* and *Caenoprosopis*, they are easily overlooked in these two genera (Rozen and Roig-Alsina, 1991: figs. 4, 5).
18. Maxillary palpal length much greater than basal diameter (Rozen, 1966: figs. 4, 5) (0); approximately as long as basal diameter (Rozen, 1994a: figs. 6, 7, 13, 14) (1); much less than basal diameter or palpus not evident (Rozen and Roig-Alsina, 1991; figs. 4, 5, 12, 13) (2). R&M #43, reinterpreted. Rozen et al. (1978) and Alexander (1990) subdivided (1) and (2) into three categories: "moderately short," "short," and "virtually absent." Additional taxa with maxillary palpi of intermediate lengths now suggest that these three states are more conveniently and reasonably assigned to the two states shown here. Because cocoon-spinning larvae are primitive and because they tend to have elongate palpi, this condition is plesiomorphic and is not found in the Nomadinae.
19. Maxillary palpus removed from posterior mandibular articulation (Rozen, 1977: figs. 4, 11, 17) (0); near articulation (Rozen and McGinley, 1974: figs. 17, 24) (1). Perhaps related to R&M #45, but reinterpreted. As a measure of the degree of recession of the maxilla, the palpus near the posterior mandibular articulation must be derived.

Hypopharynx and Salivary Opening

20. Hypopharynx spiculate (Rozen, 1994a: figs. 6, 7) (0); smooth, nonspiculate (Rozen, 1994a: figs. 13, 14) (1). R&M #4. A spiculate hypopharynx is considered primitive because only *Leiopodus* and *Ctenoplectra*, among all the other apid taxa examined (table 2), exhibit nonspiculate hypopharynges. Although the hypopharynx of *Townsendiella* was reported to be nonspiculate (Rozen and McGinley, 1991), reexamination of the immature specimen makes this matter uncertain. The genus is coded (?) for this reason.
21. Hypopharynx not projecting as far as salivary opening (Rozen, 1966: fig. 5) (0); projecting about as far as salivary opening as viewed from the side with hypopharyngeal groove horizontal (Rozen, 1996: fig. 4) (1); projecting farther than salivary opening (Rozen, 1966: figs. 10, 17, 20, 27, 29, 34, 40) (2). Cocoon-spinning bee larvae typically have the salivary opening projecting in front of the hypopharynx, the plesiomorphic condition. The projecting salivary opening of *Neolarra* (Rozen, 1966: fig. 82) (which does not spin a cocoon) is almost certainly secondarily derived and is coded (?).^a
22. Salivary opening well separated from hypopharynx (Rozen, 1994a: figs. 6, 13) (0); close to it (1); adjacent to it (Rozen, 1966: figs. 9, 16, 19, 39) (2). With cocoon-spinning bee larvae (the primitive type), the salivary opening is situated apically on the protruding labium and is therefore removed from the hypopharynx. Hence, on non-cocoon-spinning larvae, separation of the salivary opening from the hypopharynx is considered plesiomorphic. Migration of the opening toward the hypopharynx would then seem to be derived. The interpretation of the two

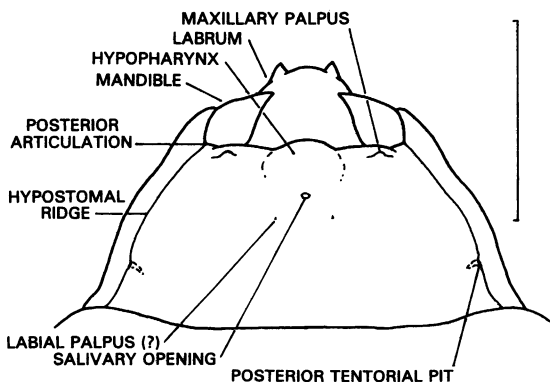


Fig. 17. Head of postdefecating larva of *Pasites histrio* (Gerstaecker), ventral view, showing salivary opening well behind posterior mandibular articulations. Scale = 1.0 mm. (3 mi west Grahamstown, Cape Province, Republic of South Africa, November 28, 1966 [J. G. Rozen], from cell of *Tetraloniella minuta* [Friese] [originally identified as *Tetralonia recisa*].)

TABLE 3—(Continued)

- apomorphic states is sometimes difficult because the boundary (see discussion of the hypopharyngeal groove in Evaluation of Characters) between the labium and hypopharynx is not always clear. Because of this and because of the forward position of the salivary opening in *Neolarra* (Rozen, 1966: figs. 81, 82), this character is coded (?) for that genus. It is also coded (?) for *Pasites* because the lower boundary of the nonspiculate hypopharynx was uncertain on the material examined.
23. Salivary opening in ventral view (i.e., hypostomal ridges at right angle to line of vision) anterior to, or in line with, posterior mandibular articulations (0); posterior to posterior mandibular articulations (fig. 17) (1). The greatly recessed salivary opening of the Ammobatini is clearly apomorphic, with no counterpart elsewhere in the Apidae.

Postcephalic Region

24. Dorsolateral body tubercles absent (Rozen and Roig-Alsina, 1991: figs. 9, 11) (0); paired dorsolateral tubercles present on some segments (Rozen and Roig-Alsina, 1991: figs. 1, 3; Rozen, 1994a: fig. 5) (1). R&M #63, redefined. Cocoon-spinning apid larvae generally lack dorsolateral body tubercles (known exceptions include *Isepeolus*, *Paratetrapedia*, and *Tapinotaspidoides*), a feature that is therefore tentatively considered primitive. Because the tubercles are very low (if evident at all) in some cases, this character is difficult to use. In *Kelita*, one species (Ehrenfeld and Rozen, 1977: fig. 10) has conspicuous tubercles, and another (Rozen, 1994a: fig. 12) almost no tubercles (Rozen, 1994a); therefore the character is coded (?) for the genus. It is also coded (?) in *Odyneropsis* which is known as a larva only from a cast skin.
25. Abdominal segment X attached dorsally to IX as seen in lateral view (Rozen, 1966: fig. 72) (0); attached centrally to IX (Rozen, 1994a: fig. 12) (1). Possibly akin to R&M #64. The polarity of this character is uncertain, and the ancestral state is coded (?). The two character states are often difficult to distinguish and for that reason a number of taxa are coded (?) in the matrix.
26. Abdominal segment X normal, not greatly produced ventrally as seen in lateral view (0); produced posteroventrally (1); bulging posteroventrally (2). R&M #66, but redefined. The unmodified abdominal segment X is found widely among bee larvae and is therefore probably primitive. The two apomorphic conditions are found only among a few taxa and are considered apomorphies. Because *Holcopasites* species A (Rozen, 1966) and perhaps *H. eamia* have the venter of abdominal segment X unmodified whereas the other species have it produced posteroventrally, this feature is coded (?) for the genus. NONADDITIVE.

Spiracles

27. Spiracles of postdefecating larva not on tubercles (0); on projecting sclerotized, pigmented tubercles (1). Spiracular tubercles are uncommon among apids and are therefore considered derived. R&M #69. The slight elevation of the spiracles in *Pasites* (Rozen and McGinley, 1974) is thought not to be the same as the spiracular tubercles found in the Epeolini. This character could not be evaluated on the cast skin of *Odyneropsis* or on the predefecating larvae of *Sphecodopsis* and *Townsendiella*.
28. Atrial wall smooth, with concentric ridges, denticulate ridges, or other ornamentation but without long, setiform denticles (0); with elongate setiform denticles (1). R&M #72 and 73, reevaluated (see Evaluation of Characters). State (1) appears to be an autapomorphy of the Epeolini within the Nomadinae, and no intermediate is known between short denticles of (0) and elongate ones of (1). Because the larva of *Townsendiella* was immature, its atrial wall was not evaluated.

^a At Alexander's suggestion (personal commun.), this character for *Neolarra* was coded (0), and parsimony analysis confirmed that the character state was indeed a reversal.

TABLE 4
Analysis 1. Data Matrix for Analysis of Generic Relationships Within the Nomadinae,
Based on Mature Larvae
(Taxa and their sequence of presentation given in table 1; character codings, in table 3.)

Characters:	0 0123456789	1 0123456789	2 012345678
Ancestor	0700000000	0000000000	000007000
Hexepeolus	0100111000	0010011010	010000000
Brachynomada	1000111000	0001100010	020017200
Kelita	0100111000	0010001110	120071200
Melanomada	1000111000	0001100010	020017200
Paranomada	1000111000	0001100010	020017200
Triopasites	1000111000	0000110010	020017200
Nomada	0700221000	0772000111	022001000
Micronomada	0000220000	0002000111	022001000
Triepeolus	0000121000	1000001110	022001011
Epeolus	0000121000	1702001120	022001011
Odyneropsis	0010221000	1000001020	022077771
Thalestria	0000121000	1002001120	022001011
Oreopasites	0011221001	0102001111	120111000
Sphecodopsis	0011721000	0102001120	120101170
Ammobates	0111221000	0102001111	120101000
Pasites	0011221000	0102001121	127101000
Holcopasites	0000221001	0002001120	021001700
Neopasites	0000221111	0002201027	121000000
Neolarra	0000221101	0000001020	177001000
Caenoprosopis	0010221001	0102001020	120011000
Caenoprosopina	0010221011	0102001127	121001100
Townsendiella	0000221111	0702000020	720000077

TABLE 5

Analysis 2. Data Matrix for Analysis of Generic Relationships Within the Nomadinae, Based on Mature Larval Characters (0–28) and Adult Characters (29–64) from Alexander (1990)
(For further explanation, see text.)

Characters from Alexander (1990): appendix 6:		0 1 2 3 4 5 6					
0	0123456789	0123456789	012345678	9012345678	9012345678	9012345678	9012345678
Characters:							
Ancestor	0?00000000	0000000000	00000?0000	0?000?0000	?00000000?	0100002?00	?00000
<i>Hexepeolus</i>	0100111000	0010011010	0100000000	0001000000	100110?021	1101002100	000001
<i>Brachynomada</i>	1000111000	0001100010	02001?2000	00110001?0	001000?020	0101002100	010000
<i>Keliia</i>	0100111000	0010001110	1200?12000	0011002000	0010001020	0101032300	010000
<i>Melanomada</i>	1000111000	0001100010	02001?2000	00100000?0	000000?020	0101022100	000000
<i>Paranomada</i>	1000111000	0001100010	02001?2000	00010000?0	0010020020	0101022100	010000
<i>Triopasites</i>	1000111000	0000110010	02001?2000	001?000030	0010000021	0101022100	000000
NOMADINI	0?0022?000	0??2000111	0220010000	00?100000?	001100002?	0?00012000	000000
<i>Triepeolus</i>	0000121000	1000001110	0220010111	021000?033	11011000?1	00001?2800	000101
<i>Epeolus</i>	0000121000	1?02001120	0220010111	02100020?3	11011000??	0001142900	000101
<i>Odyneropsis</i>	0010221000	1000001020	0220????1	0011002050	1101000021	0001142400	000101
<i>Thalestria</i>	0000121000	1002001120	0220010111	0010000033	1101100021	1001142900	000101
<i>Oreopasites</i>	0011221001	0102001111	1201110000	1011100001	00000101002	0101060210	000000
<i>Ammobates</i>	0111221000	0102001111	1201010000	1011100030	000?010?2	0? ?106?210	000000
<i>Pasites</i>	0011221000	0102001121	12?1010000	1001100112	0000001022	0001065210	100000
<i>Holcopasites</i>	0000221001	0002001120	021001?000	10000?0100	00001101??	?0210002600	101010
<i>Neopasites</i>	0000221111	000220102?	121000000?	00010011?0	?010101?1	0101004111	000000
<i>Neolarra</i>	0000221101	0000001020	1? ?0010000	00001011000	0000102033	0110?06210	000000
<i>Caenoprotopsis</i>	0010221001	0102001020	1200110000	1?00?10012	?0?0111022	0031005221	101020
<i>Townsendiella</i>	0000221111	0?02000020	?200000??	00010020?0	00001001?1	0110042500	110000

TABLE 6
Analysis 3A. Data Matrix for Analysis of Tribal Relationships Within the Nomadinae, Based on Mature Larval Characters (0–28) and Adult Characters (29–48) Used by Roig-Alsina (1991) (For explanation, see text.)

Characters from Roig-Alsina (1991: table 2):			0	1	2
			1234567801	2356789012	
Characters:	0	1	2	3	4
	0123456789	0123456789	012345678	9012345678	9012345678
Ancestor	0?00000000	0000000000	00000?000	0000000000	0000000000
<i>Hexepeolus</i> ^a	0100111000	0010011010	0100000000	1110001000	0010111001
<i>Brachynomada</i> group ^b	??00111000	00?????710	?200??200	1111111000	0010100001
NOMADINI	0?0022?000	0??2000111	022001000	0110000100	0010010001
EPEOLINI	00?0?21000	1?0?001??0	0220?????1	1111111000	0010011001
AMMOBATINI	0?11?2100?	01020011??	12?1?1?7?0	10????00010	1001010110
AMMOBATOIDINI	0000221001	0002001120	021001?00	1111101000	0001110101
BIASTINI	0000221111	000220102?	121000000	1110010100	1110100101
<i>Neolarra</i> ^a	0000221101	0000001020	1??001000	10????00011	1110110100
CAENOPROSOPIDINI	00102210?1	0102001?2?	12?0?1?00	10????10011	1001010110
<i>Townsendiella</i> ^a	0000221111	0?02000020	?200000??	1100000000	0000110100

^aMonotypic tribe.
^bNow the *Brachynomadini*.

TABLE 7
Analysis 3B. Data Matrix of Larval Characters (0–28) from Current Study and Adult Characters (29–48) from Roig-Alsina (1991) Replicated for Each Tribe (Except Nomadini) (For further explanation, see text.)

Characters from Roig-Alsina (1991):			0	1	2
			1234567801	2356789012	
Characters:	0	1	2	3	4
	0123456789	0123456789	012345678	9012345678	9012345678
Ancestor	0?00000000	0000000000	00000?000	0000000000	0000000000
<i>Hexepeolus</i>	0100111000	0010011010	0100000000	1110001000	0010111001
<i>Brachynomada</i>	1000111000	0001100010	02001?200	1111111000	0010100001
<i>Kelita</i>	0100111000	0010001110	1200?1200	1111111000	0010100001
<i>Melanomada</i>	1000111000	0001100010	02001?200	1111111000	0010100001
<i>Paranomada</i>	1000111000	0001100010	02001?200	1111111000	0010100001
<i>Triopasites</i>	1000111000	0000110010	02001?200	1111111000	0010100001
NOMADINI	0?0022?000	0??2000111	022001000	0110000100	0010010001
<i>Triepeolus</i>	0000121000	1000001110	022001011	1111111000	0010011001
<i>Epeolus</i>	0000121000	1?02001120	022001011	1111111000	0010011001
<i>Odyneropsis</i>	0010221000	1000001020	0220?????1	1111111000	0010011001
<i>Thalestria</i>	0000121000	1002001120	022001011	1111111000	0010011001
<i>Oreopasites</i>	0011221001	0102001111	120111000	10????00010	1001010110
<i>Sphecodopsis</i>	0011?21000	0102001120	1201011?0	10????00010	1001010110
<i>Ammobates</i>	0111221000	0102001111	120101000	10????00010	1001010110
<i>Pasites</i>	0011221000	0102001121	12?101000	10????00010	1001010110
<i>Holcopasites</i>	0000221001	0002001120	021001?00	1111101000	0001110101
<i>Neopasites</i>	0000221111	000220102?	121000000	1110010100	1110100101
<i>Neolarra</i>	0000221101	0000001020	1??001000	10????00011	1110110100
<i>Caenoprosopis</i>	0010221001	0102001020	120011000	10????10011	1001010110
<i>Caenoprosopina</i>	0010221011	010200112?	121001100	10????10011	1001010110
<i>Townsendiella</i>	0000221111	0?02000020	?200000??	1100000000	0000110100

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