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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 54, No. 1, pp. 1–23 November 15, 1989

The Tribe Osirini, its Scope, Classification, and Revisions of the Genera *Parepeolus* and *Osirinus* (Hymenoptera, Apoidea, Anthophoridae)[1]

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ABSTRACT

The limits of the hitherto monotypic tribe Osirini are expanded to include *Epeoloides*, *Parepeolus* and three new genera: *Ecclitodes*, *Osirinus* and *Protosiris*. It is suggested that the tribe does not belong in the subfamily Nomadinae, but represents a group of parasites independently derived from pollen-collecting ancestors. A cladistic analysis, a key and descriptions are presented for the genera. For *Parepeolus* and *Osirinus* keys to the species, synonymies and descriptions are provided; four new species are described.

INTRODUCTION

The present paper has three objectives. First, to argue that the monotypic tribes Osirini and Epeoloidini, the hitherto unplaced genus *Parepeolus* Ducke and the new genera *Ecclitodes*, *Osirinus* and *Protosiris* constitute a monophyletic group, the Osirini. Second, to suggest that the tribe so constituted does not belong in the subfamily Nomadinae, but is better understood as an independently derived group of parasitic bees within the Anthophorinae. Third, to present an analysis of the relations among the genera of Osirini and revisions of certain genera.

This study was triggered by the discovery of some bees, particularly the new species *Osirinus lemniscatus*, that were obviously related to *Osiris* Smith by characters of wing venation and genitalia but had a very different aspect. The build of the body resembled that of *Parepeolus* and *Ecclitodes*. Indeed, at first sight *O. lemniscatus* looks much like the

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[1] Contribution number 2082 from the Department of Entomology, University of Kansas, Lawrence.

Chilean *E. stuardi* (Ruiz). Some of those bees have dark integument but others are definitely pale. Such annectant forms, several previously described as *Osiris*, are grouped here in two new genera. The Holarctic genus *Epeoloides* Giraud should also be included in the group. Warncke (1982) has already suggested a close relation of *Epeoloides* to the South American *Parepeolus*, based on overall similarity.

Previous treatments of the group are restricted to *Osiris* and *Epeoloides*, and *Parepeolus* has seldom been mentioned in the literature since its description by Ducke (1912). Important accounts of *Osiris* are those by Friese (1930), Grütte (1935), Popov (1939), Michener (1944, 1954) and the recent generic revision by Shanks (1986). Important accounts of *Epeoloides* are those by Linsley and Michener (1939) and Popov (1958). Both genera have long been considered as isolated elements, each forming a tribe. The tribal name for all the groups mentioned above should be Osirini according to Michener (1986).

The Osirini occur in the Holarctic and Neotropical regions. *Epeoloides* (3 species) is found in the eastern half of North America and in Europe, with the easternmost record at 58° East longitude in the Soviet Union. *Osiris* (over 20 species) ranges from Mexico to northern Argentina. *Parepeolus* (4 species) and *Osirinus* (3 species) range from northern Brazil to central Argentina. *Protosiris* (4 species) occurs from Panama to southern Brazil and Bolivia, and *Ecclitodes* (2 species) is restricted to Chile and southern Argentina. The two genera showing the most plesiomorphies, *Epeoloides* and *Ecclitodes*, occur at the extremes of the distribution.

Most arguments presented below for excluding the Osirini from the Nomadinae also hold for *Coelioxoides*, a genus that has been considered many times as a relative of *Osiris* due to the peculiar modification of the sixth sternum of the female. *Coelioxoides* does not possess the apomorphies of Osirini, and the shape of the sternum is clearly convergent, as indicated by the terminal position of *Osiris* in the cladogram. The relations of *Coelioxoides* will be treated elsewhere.

ACKNOWLEDGEMENTS

I express sincere thanks to Charles D. Michener for his advice and support during the preparation of this paper; to Byron Alexander, James S. Ashe, George W. Byers, Jerome G. Rozen, Jr., and Haroldo Toro, for their comments and suggestions on an earlier draft. I am also grateful to the Consejo Nacional de Investigaciones Científicas y Técnicas, República Argentina, that made possible my stay at Lawrence.

MATERIAL AND METHODS

Material studied, including types, was obtained from several collections. I am indebted to the following: American Museum of Natural History, New York, J.G. Rozen, Jr. (AMNH); R.B. Brooks, Lawrence, Kansas; Cornell University, Ithaca, G.C. Eickwort and B. Alexander; Florida State Collection of Arthropods, Gainesville, L.A. Stange (FSCA); M. Fritz, Rosario de Lerma, Salta; Instituto Miguel Lillo, Tucumán, A. Willink; Los Angeles County Museum, Los Angeles, R.R. Snelling; Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Museo de La Plata, La Plata, R. Ronderos (MLP); R.B. Roberts collection, Rutgers University, New Brunswick (RBR); Snow Entomological Museum, University of Kansas, Lawrence, C.D. Michener (SEM); Universidade Federal do Paraná, Curitiba, J.S. Moure (UFPR); Zoologisches Museum, Humboldt-Universität, Berlin, F. Koch. The acronyms are used below to indicate depositories of specimens.

Morphological terminology of Michener (1944, 1965) has been followed, except that metapostnotum is used instead of propodeal triangle (Brothers, 1976). In the descriptions the metasomal terga (T) and sterna (S) are identified with Arabic numerals. For easy comparison characters are numbered in the generic descriptions. Diagnostic characters are italicized.

RELATIONSHIPS OF THE OSIRINI

The monophyly of the tribe Osirini is supported by two synapomorphies: the ventral sclerite in the cervical membrane and the carina along the inner and basal ventral margins of the forecoxa. The presence of a ventral sclerite in the cervical membrane is unique among bees. It is independent and united by membrane to the postgenal bridge that closes the foramen magnum ventrally (fig. 4). In other bees there may be a faint sclerotization of the membrane (as in many long-tongued bees). The ventral cervical sclerite is round, usually with a posterior carina. A similar sclerite is present in sphecoid wasps of the subfamily Philanthinae. The forecoxal ventral carina is always complete along the inner margin, but the basal sector varies in extent. A similar carina is found in the subgenera *Heterocentris* and *Hemisiella* of *Centris* (Snelling, 1984), obviously independently derived. The tribe Osirini may be further characterized by the epistomal suture faded laterally so that there is no separation between clypeus and paraocular area near the eye, by the vestiture of the thorax usually consisting of long, plumose hairs, and by the presence of an extruded, upcurved sting visible in some pinned specimens. The last character is seen only sporadically; I have observed it in specimens of *Parepeolus*, *Ecclitodes* and *Osiris*, but not in *Epeoloides*, *Osirinus* or *Protosiris*. I have failed to find a satisfactory explanation for such exserted stings. The sting is impressive in *Osiris* (Friese, 1930, fig. 3; Shanks, 1986, fig. 42), but in other genera it is not much different from that of pollen-collecting bees, except for the proportionally longer rami and furcula. Many nomadines (e.g., Epeolini) also have stout stings with long rami and furculae, but they are never so extruded. The depressed metasoma of most osirines may be the concurrent factor that leads to such upcurved stings; in this case *Epeoloides*, with a moderately depressed metasoma, is not expected to have an upcurved sting.

The genera of Osirini have been placed previously in the Nomadinae. The apomorphies that best indicate the monophyly of the subfamily Nomadinae are those presented by Rozen (1966) and Rozen et al. (1978) based on morphology of the larvae and adult behavior (oviposition pattern). Those characters, however, are not known for the Osirini. There are some characters of adult morphology unique for the Nomadinae and useful in defining the group, even though exceptions occur in one or more tribes for each character. These are: 1) Retraction and concealment of the sixth metasomal sternum of the female (partial in Protepeolini). 2) Sixth metasomal sternum of the female apically emarginate, ending in two points (exceptions are Protepeolini, Isepeolini and *Nomada*). 3) Sixth metasomal sternum of the female bearing spine-like setae (exceptions are Protepeolini, Neolarrini, Ammobatini and Caenoprosopidini; variable within Isepeolini). 4) Fifth metasomal tergum of the female with a specialized apical area of hairs, the pseudopygidial area (exceptions are Towsendiellini, Neolarrini, Ammobatini and Caenoprosopidini; a hairy apical flap in the Isepeolini is probably not homologous with the pseudopygidial area.) The tribes Isepeolini and Protepeolini are the most problematic groups in the above characterization of the Nomadinae.

Osirini do not share any of the features just mentioned. The sixth metasomal sternum of the female does not differ much from the condition seen in pollen-collecting bees (figs. 37, 39), with the exception of *Osiris*,which shows a trend in elongation of the segment different from any trend seen in the Nomadinae. A pseudopygidial area is absent. Furthermore, nomadines lack a stipital comb, or it is weak (as in *Biastes*, Winston, 1979), a feature considered characteristic of the parasitic syndrome in long-tongued bees (Michener, 1944). In Osirini, on the contrary, the stipital comb is developed and frequently occupies a concavity much as in many pollen-collecting bees.

In all the above comparisons it is possible to argue that the condition in Osirini is plesiomorphic. Hence the group could not have arisen from within the nomadines, but it may still constitute the most primitive representative of that lineage.

Further features in which Osirini differ from nomadines suggest possible connections to other anthophorid groups: 1) The Exomalopsini have along the outer surface of the stipes a sclerotized ridge (Winston, 1979); the length and position of the ridge is identical in Osirini (figs. 5, 14, 24, 30, 34, 45, 52); the ridge is absent in Nomadinae. 2) The sternal region behind the third apophyseal pit is produced into a triangular lamella, which in Osirini is translucent, not punctate, and arched. A similar condition is found in *Melecta*, Emphorini and many Exomalopsini. In most Nomadinae the triangular projection is thick (not translucent), flat and punctate (exceptions are some *Brachynomada*, *Nomada* and *Paranomada* with extensively impunctate integument and *Isepeolus* with the triangular projection thick and punctate, but arched). 3) The fifth metasomal tergum of the female in Osirini has a wide, polished apical margin bordered by long hairs. A similar condition is present in the Melectini. 4) The marginal cell in Osirini is separated from the wing margin for its entire length, so that there is a membranous costal rim as wide as the radial vein; the rim even continues along the pterostigma. This is not the condition in the Nomadinae; in the Anthophorinae various degrees of separation are present, the Tetrapediini have a well developed rim (Michener and Moure, 1957). This list does not represent an exhaustive comparison of the Osirini with the many tribes of the Anthophorinae (such a task is outside the scope of the present paper) but is suggestive of possible relationships.

Since biological information indicates that at least some of the Osirini are parasites of Exomalopsini, and in consideration of the morphological affinities between the two tribes mentioned above, it is tempting to think of a close relationship between these two tribes. However, characters of osirine male genitalia that may be considered plesiomorphic among anthophorid bees (gonobasal ring complete, not fused ventrally to the gonocoxites, volsellae present, well developed dorsal ramus of the gonostylus) preclude the derivation of Osirini from any extant Exomalopsini.

From the above discussion it appears that there is no support for including the tribe Osirini in the Nomadinae and that they may represent a group of parasites independently derived from pollen-collecting ancestors, as do the melectines, rhathymines and ericrocines. Regarding the position of the Osirini in the current classification, I suggest considering them as a tribe in the subfamily Anthophorinae, pending a comprehensive revision of the members of this subfamily.

GENERIC ANALYSIS OF THE OSIRINI

The cladogram in figure 1 was constructed by hand, taking as outgroups the other tribes of Anthophorinae, paying particular attention to those mentioned above as sharing some features with the Osirini. Since relations of Osirini are not certain, all tribes were considered to form a polytomy for outgroup comparison. Only those characters for which the polarity was clear were used in constructing the tree. Many more characters discussed below may become cladistically relevant when the relations of Osirini are better understood.

The branch that leads to *Epeoloides*, *Osirinus*, *Protosiris* and *Osiris* is supported by two genitalic characters (10, 11): the unusual curvature of the apodeme of the penis valve (figs. 26, 41, also figures in Michener, 1954, and Shanks, 1986) and the shape of the dorsal gonocoxal bridge. The common condition in anthophorids is that the dorsal basal union of the gonocoxites projects into the capsule as a prong or a plate. Such a projection is recurved and apically truncate in the genera on the right branch of the tree (figs. 26-27, GCX, 40-41). In *Parepeolus* and *Ecclitodes*, even if smaller, it is pointed, the plesiomorphic condition.

The two main branches of the tree are further characterized phenetically. *Epeoloides*, *Osirinus*, *Protosiris* and *Osiris* share an elongate jugal lobe, lateral margin of clypeus continued upward by a carina, basal vein of forewing arising apical to vein cu-v (both veins meeting in *Osirinus fritzi* and females of *Epeoloides coecutiens*) and basal sector of forecoxal carina extended all the way across the coxa. *Parepeolus* and *Ecclitodes* have a small, round jugal lobe, no carina continuing the margin of the clypeus, basal vein arising basal to vein cu-v (both veins meeting in two species of *Parepeolus*) and basal sector of forecoxal carina short (fig. 4).

The position of *Epeoloides* in the cladogram is interesting in view of its Holarctic distribution and host relationship to the Melittidae; all other genera are Neotropical and probably associated with Exomalopsini.

Besides representing the taxa with more profuse plumose hairs, *Epeoloides* and *Ecclitodes* each show for some characters the most plesiomorphic state within the tribe. In *Epeoloides* the jugal lobe is long, between 1/3 and 2/5 as long as the vannal lobe measured from the wing base (fig. 23); the claws of the male are bifid, much as in most pollen-collecting bees. In *Ecclitodes* the seventh sternum of the male has apicolateral projections (fig. 9) suggestive of the lobed sternum of many pollen-collecting bees; the eigth sternum has a conspicuous spiculum; the genitalia are fairly complex and certainly plesiomorphic.

The *Parepeolus-Ecclitodes* branch is supported by the unique gonostylus (characters 8, 9). The recognition of both groups as genera is based on their clear sister-group relationship and their distinctiveness. *Parepeolus* has two apomorphies, the suprategular carina directed anteriorly and the enlarged dorsal branch of the gonostylus, but has retained plesiomorphic features such as the concavity on the stipes (fig. 14). *Ecclitodes* has a weaker stipital comb and no stipital concavity; the microstriated sculpture of the metapostnotum is unique. The two genera are further distinguished from each other by differences in the number of segments of the maxillary palpus, pattern of the vestiture and wing venation.

Osiris, *Osirinus* and *Protosiris* have the marginal cell pointed close to the wing margin, the disc of the labrum flat with several preapical denticles and the first submarginal cell with a bowed posterior margin. The three groups have dark and pale species, but in *Protosiris* and *Osiris* even the darkest species (e.g., *P. caligneus*, some specimens of *O. variegatus*) have translucent integument. In all species of *Osiris* and at least in one species each of *Osirinus* and *Protosiris*, the sixth tergum of the female has a conspicuous spot (figs. 38, 50, 51, and Shanks, 1986, figs. 38-39). The spot represents the contour of a sector of the duplication that is in intimate contact with the inner surface of the disc. Such a sector becomes evident in species with translucent integument but is equally present in the remaining species.

Osiris is restricted here to a group of species that presents a large number of apomorphies (table 1), including the striking apical abdominal segment of the female (characters 17, 18). Such specialization, surely related to the parasitic way of life, leads to the suspicion that *Osiris* may also be a behaviorally distinctive genus. Other Osirini have the sixth sternum of the female not forming an elongate, tubular structure. Their sternum, even though narrower and more pointed, is not much different from that of pollen-collecting bees. The lateral

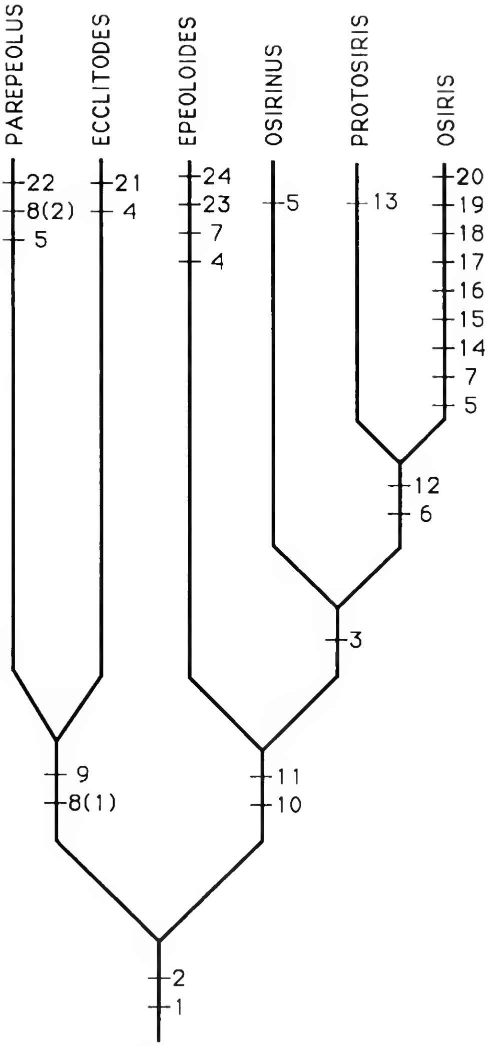


Fig. 1. Cladogram showing the relationships of the genera of Osirini. Characters are numbered as in table 1.

and ventral views of the sixth sternum of an *Exomalopsis* (fig. 39) are illustrated for comparison. Besides the apomorphies shown in the tree, *Osiris* has the inner margin of the eye gently emarginate in the upper third, a sharp preoccipital ridge behind the ocelli and the hypostomal carina forming a right angle when it reaches the mandibular socket.

Table 1. List of apomorphous characters. Outgroups are other tribes of Anthophorinae. Apomorphous characters were coded (1), or if further derived as (2).

1. Cervical membrane with ventral sclerite present (fig. 4) (1). Outgroups with sclerotization faint or absent. (The sclerite is small in *Epeoloides coecutiens* but well developed in *E. pilosula*).

2. Forecoxa with ventral carina (fig. 4) (1). Carina absent in outgroups. (A similar carina has arisen independently in two subgenera of *Centris*).

3. Apex of marginal cell pointed, close to costal wing margin (fig. 28) (1). Marginal cell sometimes pointed in outgroups, but apex bent away from wing margin. (Apex of the marginal cell close to the costal margin is the usual condition in short-tongued bees but is rare in anthophorids; it is also found in several Nomadini, to which *Osiris* was thought to be related).

4. Stipital comb-bearing concavity reduced (figs. 5, 24) (1). Stipital comb-bearing concavity present in most outgroups (except Melectini); presence of such concavity plesiomorphic for long-tongued bees in general (Winston, 1979; Michener and Greenberg, 1980).

5. Maxillary palpus with 4 or 5 segments (1). Plesiomorphic condition is 6 segments. (Species of *Parepeolus* have 4 or 5 segments.)

6. Legs elongate, scarcely hairy; hairs mostly simple (1). Legs stout, with abundant plumose hairs in pollen-collecting anthophorids. (Elongate legs with few hairs also occur in one other parasitic group, the Rhathymini. Since both states of the character occur in the Osirini, the polarity was based on the assumption that a reversal is unlikely).

7. Dorsal branch of gonostylus absent (1). Gonostylus with 2 branches plesiomorphic for anthophorid bees in general. (Most tribes of Anthophorinae, except Eucerini, have at least a few taxa with 2-branched gonostylus. Reduction of the gonostylus, or fusion to the gonocoxite in such a way that it is not distinguishable, is a common trend usually associated with overall simplification of the genitalia, and evidently derived).

8. Dorsal branch of gonostylus flattened (fig. 7) (1). Dorsal branch of gonostylus flattened and enlarged (figs. 17, 19, 21) (2). Dorsal branch not flattened and smaller than ventral branch in outgroups.

9. Ventral branch of gonostylus bifid (figs. 7, 17, 19, 21) (1). No such bifid gonostylus in outgroups.

10. Internal projection of dorsal bridge of gonocoxite truncate (figs. 7, 40, 48) (1). Internal projection of dorsal bridge pointed or lamellate in outgroups.

11. Penis valve with apodeme curved dorsally (figs. 26, 41) (1). Apodeme not so curved in outgroups.

12. Pterostigma strikingly large, more than 7 times length of prestigma (1). Pterostigma in outgroups variable, usually less than 4 times length of prestigma (exception is *Paratetrapedia* within Exomalopsini).

13. Mandible long, sickle shaped (figs. 44, 47) (1). Mandible in outgroups not strongly curved.

14. Mandible with 2 subapical teeth (1). Plesiomorphic condition for anthophorid bees in general is one subapical tooth (Michener and Fraser, 1978). (Presence of two subapical teeth is a rare feature among parasitic anthophorids; besides *Osiris*, it is also found in some Isepeolini).

15. Dorsolateral lobes of pronotum bulging (1). Lobes not bulging in outgroups.

16. Anterior dorsal margin of pronotum broadly recurved (1). Anterior dorsal margin of pronotum straight or slightly recurved in outgroups.

17. S6 of female elongate, distally tubular, forming a sheath for the sting (fig. 55) (1). Sternum not so in outgroups. (*Coelioxoides* has an elongate S6, independently derived).

18. T6 of female with rim apical to pygidial plate (fig. 51) (1). Unique feature of *Osiris* (Grütte, 1935).

19. Pygidial plate of male absent (1). Pygidial plate present is plesiomorphic for bees in general. (Absence of the pygidial plate occurs in some of the outgroups, but in every case it is interpreted as the derived condition).

20. Posterior lateral margin of pronotum deeply emarginate below pronotal lobe (fig. 54) (1). No such deep emargination in outgroups (probably related to character 15).

21. Metapostnotum microstriated (1). Unique feature of *Ecclitodes*, not present in outgroups.

22. Suprategular carina directed anteriorly, diverging from tegular margin (fig. 11) (1). Unique feature of *Parepeolus*, not present in outgroups.

23. Eyes of male strongly convergent above (1). Similar convergence found in a few other bees, but not in outgroups.

24. Pygidial plate of male spatulate (1). Pygidial plate with sides parallel or converging apically in outgroups.

The species excluded from *Osiris*, together with new ones described below, are recognized as belonging to two new genera. *Protosiris* shares with *Osiris* the slender habitus, long legs, sparse vestiture and elongate pterostigma. Shanks (1986) recognized the group as a species-group within *Osiris*. She characterized it by the short head, the parallel inner margins of the eyes, the mandible with one subapical tooth, the pygidial plate present in both sexes (that of the female rounded apically), and the gonostylus articulated. All those characters, with the probable exception of the parallel inner margins of eyes, are symplesiomorphies, their alternatives being apomorphies for *Osiris*. The recognition of *Protosiris* as a natural group is supported by the long, curved, sickle shaped mandible, unique among osirines. The parallel margins of the eyes also represent an apomorphy for the group in the context of the cladogram in figure 1.

The three species of *Osirinus* are small and have a similar habitus. They are differentiated from *Osiris* and *Protosiris* by the stouter build of the body, short legs, inner margin of eyes almost straight and convergent below, mandible short with one subapical tooth, and plumose vestiture dense at least on the mesopleuron, scutellum and tibiae. The type species is strikingly hairy, with wide bands of plumose hairs on the metasomal terga. Most of these characters represent plesiomorphies; undoubtedly *Osirinus* is close to the ancestral stock that gave rise to the *Osirinus-Protosiris-Osiris* branch. The short legs, shorter than in any other osirines, may represent a synapomorphy. There are some characters that seem to have arisen independently in the three genera: reduction of the maxillary palpus and loss of the volsella. *Osirinus* and *Osiris* are characterized by a maxillary palpus with 5 segments, *Protosiris* has species with 4 to 6 segments. Species of *Osiris* and the only species of *Osirinus* with known males do not have volsellae; in *Protosiris* there are species with and without volsellae.

BIOLOGY

Knowledge of the biology of the Osirini is quite fragmentary and limited to a few host associations. *Epeoloides* is known to be parasitic in the nests of the melittid genus *Macropis*. The European *E. coecutiens* has been associated with *M. labiata* and *M. fulvipes* (Popov, 1958, and references therein). All other hosts are in the Exomalopsini. Rozen (1984) reported *Parepeolus niger* (mentioned as *Parepeolus sp.*) flying in association with *Tapinotaspis (Tapinotaspoides) tucumana* in southern Brazil; he found a female of the parasite inside a nest of *T. tucumana*. I collected a series of *Ecclitodes stuardi* in Chile (Cabrería, Malleco Province, 22-XII-1985) that were flying back and forth along a low, sunny slope occupied by *Tapinotaspis (Tapinorhina) caerulea*. From time to time the parasites perched on nearby herbs or more frequently stayed still on the ground. I did not observe actual entrance of the parasites into the nests. H. Toro (personal communication) also found *Ecclitodes* in association with *Tapinotaspis caerulea* in the province of Malleco, Chile (Nahuelbuta, 9-I-1979). The host relationships of *Osiris* are not known, but indirect evidence suggests *Paratetrapedia* and *Monoeca* as possible hosts (summarized in Shanks, 1986).

It is interesting to note that all recorded hosts of the osirines are known or suspected to be oil-collecting bees.

TRIBE OSIRINI

Length 5.5-18 mm, with slender habitus when over 13 mm. Integument moderately punctate to almost impunctate, polished between punctures. Vestiture abundant and plumose to sparse and mostly simple. Labrum transverse with sides sharply bent backwards. Maxillary palpus with 4 to 6 segments. *Stipes with longitudinal ridge on outer surface.* Stipital comb developed, usually on edge of distinct concavity. *Epistomal suture faded laterally near eye.* Preoccipital carina absent, except present behind ocelli in *Osiris*. *Cervical membrane with rounded ventral sclerite.* Axilla not projecting. *Forecoxa with ventral carina along inner and basal margins*, sometimes basal sector of carina short. Middle coxa slightly longer than distance from its summit to hind wing base. Claws usually with flat, square inner tooth. Forewing with 3 submarginal cells. Pterostigma moderate to large, 3-8 times as long as prestigma. Jugal lobe of hindwing 0.2-0.4 times as long as vannal lobe measured from wing base. Abdomen depressed, moderately so in *Epeoloides*. *T5 of female without pseudopygidial area, instead with wide, polished apical margin.* S6 of female without spine-like setae, more or less boat-shaped and pointed posteriorly; elongate in *Osiris*. *Sting sometimes upcurved over metasoma.* Pygidial plate usually present in both sexes. Male genitalia with gonobasal ring complete; gonostylus usually articulated, with a dorsal and a ventral branch; midapical lobe of gonocoxite present in *Ecclitodes* and *Parepeolus*, complex; spatha present, small.

KEY TO THE GENERA OF OSIRINI

1. Jugal lobe of hindwing rounded (fig. 10). Basal vein of forewing arising basal to cu-v or sometimes meeting it. Lateral margin of clypeus not continued above level of anterior mandibular articulation by paraocular carina (figs. 3, 12). Labrum with pair of preapical tubercles or 2-4 teeth near middle of disc (figs. 3, 12, 15). Genitalia of male with ventral ramus of gonostylus bifid, dorsal ramus flattened (figs. 7, 17, 19, 21) 2

—. Jugal lobe of hindwing elongate (fig. 23). Basal vein of forewing arising apical to cu-v or sometimes meeting it. Lateral margin of clypeus continued by paraocular carina above level of anterior mandibular articulation (figs. 25, 29, 33, 43, 53). Labrum with single preapical tubercle or several small preapical denticles (figs. 25, 33, 43, 53). Ventral ramus of gonostylus simple; dorsal ramus small, cylindrical or absent (figs. 40, 48) 3

2. Metapostnotum microstriate. Posterior margin of first submarginal cell more than twice as long as apical margin (fig. 10). Maxillary palpus with 6 segments. Metasomal terga with apical bands of pale hairs. Suprategular carina curved cephalad of tegula, following tegular margin, reaching mesoscutum-pronotal lobe boundary close to tegula . . . . *Ecclitodes*

—. Metapostnotum polished, smooth or with few scattered punctures. Posterior margin of first submarginal cell less than 1.5 times as long as apical margin (fig. 13). Maxillary palpus with 4-5 segments. Metasomal terga black or variously patterned with pale hairs; apical band, when present, only on T1. Suprategular carina slightly curved, directed anteriorly, diverging from tegular margin and reaching mesoscutum-pronotal lobe boundary near middle (fig. 11) . . . . *Parepeolus*

3. Apex of marginal cell curved away from wing margin (fig. 23). Paraocular carina almost reaching top of eye. Eyes of male strongly converging above, those of female slightly so. Labrum with strong preapical tubercle. Pterostigma moderate, 2.8-3.2 times as long as prestigma. Claws of male with rami similar and adjacent . . . . *Epeoloides*

—. Apex of marginal cell terminating close to wing margin (fig. 28). Paraocular carina fading as soon as it reaches lower margin of eye. Eyes of both sexes parallel or diverging above. Labrum with several small denticles. Pterostigma long, more than 5.5 times as long as prestigma. Inner ramus of male claws shorter than outer, flattened 4

4. Collar of pronotum dorsally bulging, with distinct subhorizontal portion connecting rounded dorsolateral lobes. Inner margin of eye not straight, with shallow emargination near upper third (fig. 53). Mandible with two subapical teeth. S6 of female usually exceeding T6. Apex of pygidial plate of female not reaching margin of tergum; wide rim apical to plate present (fig. 51). Pygidial plate of male reduced to sclerotization on tergal margin . . . . *Osiris*

—. Tranverse dorsal sector of pronotal collar short or absent medially, so that dorsolateral lobes are nearly connected. Inner margin of eye almost straight (figs. 29, 33, 43). Mandible with one subapical tooth or simple (an inner angle may be present). S6 of female not exceeding T6. Apex of pygidial plate of female constituting apex of tergum (figs. 36, 38, 50). Pygidial plate of male present 5

5. Inner margins of eyes almost parallel; proportion of lower to upper interocular distance 0.97-1.03:1. Mandible long, strongly curved (fig. 44, 47); outer basal width 0.33-0.35

times length of mandible (measured along dashed line shown in figure 44). Mesopleuron with hairs simple or at most with one or two basal barbs. Legs slender; strigilar concavity 0.26-0.27 times length of forebasitarsus (fig. 46). Scutum as long as intertegular span . . . . *Protosiris*

—. Inner margin of eyes convergent below; proportion of lower to upper interocular distance 0.82-0.90:1. Mandible short (fig. 33); outer basal width 0.4-0.45 times length of mandible. At least anterior part of mesopleuron with plumose hairs. Legs short, stout; strigilar concavity shallow, 0.38-0.41 times length of forebasitarsus (fig. 32). Scutum shorter than intertegular span . . . . *Osirinus*

Ecclitodes, new genus

(figs. 2-10)

Type species: *Epeolus stuardi* Ruiz, 1935.

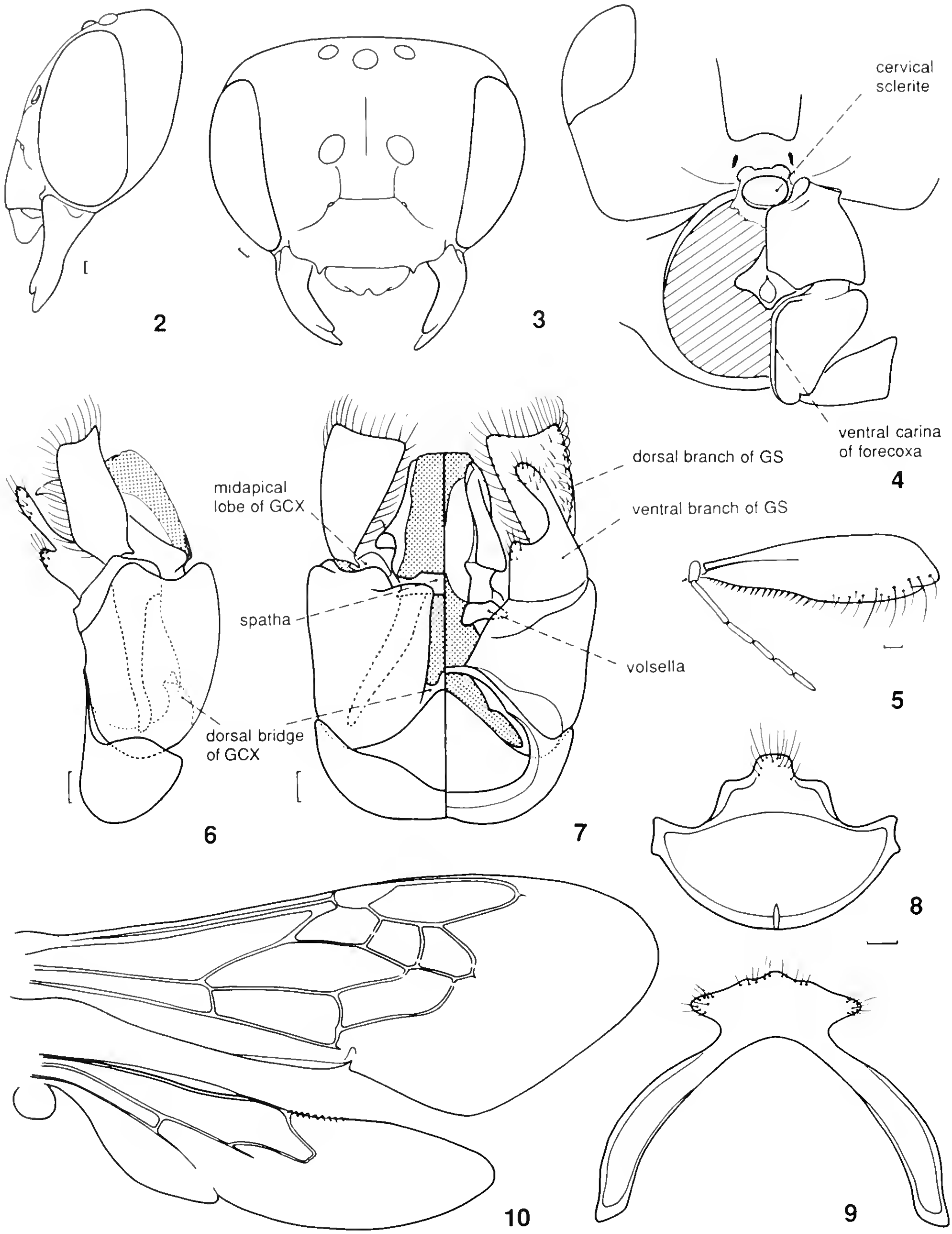
Ecclitodes includes bees with black and pale, silvery hairs, head robust with a wide gena, and depressed metasoma. It is distinguished from the closely related *Parepeolus* by the *metapostnotum with microstriae*, the *metasoma with apical bands of pale hairs on T1-T5*, the *disc of the labrum with two blunt preapical tubercles*, and the apex of the marginal cell slightly truncate, usually briefly appendiculate.

Description. 1. Length 8.5-10.5 mm. 2. Integument black; flagellum, mandible and tarsi sometimes red. 3. Mesopleura with dense, small punctures, those on scutum extremely fine; metapostnotum microstriated, striae running parallel to metanotum at sides, curving medially and then running parallel to longitudinal sulcus; parts of metapostnotum not striated with fine, close punctures. 4. Vestiture long and plumose on head, mesosoma and legs; metasoma with apical tergal fasciae of appressed plumose hairs. 5. Eyes convergent below, proportion of lower to upper interocular distance 0.75:1; inner margin of eye almost straight. 6. Lateral ocellus separated from posterior margin of head by 1.5 ocellar diameters. 7. Maximum width of gena 0.75 times maximum width of eye seen from side; gena slanting toward base of mandible. 8. Preoccipital and paraocular carinae absent. 9. Short malar space present, 0.15 times as long as basal width of mandible. 10. Disc of labrum with two close, blunt, preapical tubercles. 11. Mandible with one subapical tooth. 12. Stipital comb-bearing concavity absent. 13. Maxillary palpus with 6 segments. 14. Hypostomal carina forming rounded angle near mandibular socket. 15. Proportion of first to second flagellomere 0.8-1.0:1. 16. Pronotum not forming raised collar; anterior dorsal margin not recurved. 17. Scutum shorter than intertegular span (approximately 0.8). 18. Suprategular carina curving anteriorly close to tegula. 19. Apex of marginal cell curved away from wing margin, sometimes briefly appendiculate. 20. Prestigma approximately 1.5 times as long as wide; pterostigma 3 times as long as prestigma. 21. First submarginal cell with posterior margin straight, 2.2-2.8 times as long as apical margin. 22. Basal vein of forewing arising basal to vein cu-v. 23. Jugal lobe of hindwing rounded, 0.2 times as long as vannal lobe. 24. Forecoxa with basal sector of ventral carina short, restricted to third. 25. Legs short, stout; external surface of hindtibia densely hairy; strigilar concavity of forebasitarsus 0.38 times as long as segment. 26. Metapostnotum usually with basal subhorizontal zone, but some specimens with metapostnotum declivous, more or less convex. 27. Pygidial plate present in both sexes. 28. Genitalia as in figures 6, 7; ventral branch of gonostylus bifid, dorsal branch flattened, not larger than ventral branch; apodeme of penis valve more or less straight; volsella present.

Comments. This genus has been recognized by various authors in the past, but has never been described. I have seen names on labels by Brèthes, Moure and Moldenke; I have chosen the oldest one, written on labels by Brèthes. The root *ekklites* means "the one who doesn't like to work," a name quite appropiate for a parasitic bee.

Two series of specimens from nearby areas in the province of Malleco (Chile) each contain specimens that are easily separated into two forms by the features mentioned below. These two forms may represent a single dimorphic species or else two sympatric ones. I am inclined toward the second alternative, since the differences are clear and hold in the few specimens that I have examined from other areas. On the other hand, there is only one suspected host for the two putative species. Both host and parasites need to be studied in more detail to solve this problem.

Specimens that I have identified as *stuardi* agree better with the color pattern described by Ruiz: antenna brownish, mesothorax with patches of black and silvery hairs, last metasomal segment of female black. The second species has light red antennae, mesothorax mostly covered with pale hairs and sixth tergum of female with pale hairs, too. Since there is some variation in the extent of the pale hairs, the identification is tentative. Other features mentioned by Ruiz fit both forms. Study of the types or material from the type locality (Termas de Chillán, Ñuble) will allow clarification of this point. Females that I regard as



Figs. 2-10. *Ecclitodes stuardi*: 2-5 and 10, female; 6-9, male. 2, head, lateral. 3, face. 4, ventral view of head and prothorax; right half of prosternum and right coxa removed. 5, stipes. 6, genitalia, lateral. 7, genitalia, dorsal and ventral. 8, sternum 8. 9, sternum 7. 10, wings. Scale lines 0.1 mm. GCX = gonocoxite; GS = gonostylus.

stuardi have a triangular pygidial plate with sides converging at an angle of 30 degrees and males have the dorsal branch of the gonostylus with the inner apex not lobed. The other species presents a strikingly narrowed pygidial plate in the female and the male gonostylus has a lobed dorsal branch. There is variation in the shape of the metapostnotum. It usually has a basal subhorizontal zone, but in some specimens it is more or less declivous. There is no correlation between this variation and the set of characters mentioned above.

I have studied material from the provinces of Malleco, Cautín and Valdivia in Chile and from the province of Rio Negro in Argentina.

Parepeolus Ducke

Parepeolus Ducke, 1912: 71, 102. Type species: *Leiopodus lecointei* Ducke, 1907 (= *Epeolus aterrima* Friese, 1906), by designation of Sandhouse, 1943: 585.

Parepeolus is distinguished by the *polished metapostnotum*; the *suprategular carina directed anteriorly*, slightly curved; the metasoma depressed, variously patterned, but with an apical band of pale hairs only on T1; the apex of the marginal cell usually broadly rounded; and the *dorsal branch of the male gonostylus flat, strikingly large*.

Description. Agreeing with *Ecclitodes*, except as follows: 1. Length 6-13 mm. 2. Integument black to dark reddish brown. 3. Punctures of mesopleura from small and dense to extremely fine; metapostnotum always impunctate and shiny. 4. Vestiture of metasoma short, appressed, variously patterned with black and pale hairs. 5. Proportion of lower to upper interocular distance 0.67-0.79:1. 6. Lateral ocellus separated from posterior margin of head by 1-2.3 ocellar diameters. 9. No malar space. 10. Labrum with transverse carina near middle, bearing at least two teeth, usually four. 12. Stipital comb-bearing concavity present, or concavity reduced. 13. Maxillary palpus with 4 to 5 segments. 15. Proportion of first to second flagellomere 0.75-1.75:1. 18. Suprategular carina slightly curved, directed anteriorly, reaching boundary of scutum with pronotal lobe near middle. 19. Apex of marginal cell rounded, away from wing margin. 20. Prestigma 1-1.4 times as long as wide; pterostigma 3-4 times as long as prestigma. 21. Posterior margin of first submarginal cell 0.95-1.5 times as long as apical margin. 22. Basal vein arising basal to vein cu-v or meeting it. 26. Metapostnotum entirely declivous. 28. Genitalia as in figures 17, 19, 21; dorsal branch of gonostylus flattened, larger than ventral branch.

Comments. Four species are recognized in *Parepeolus*, two of them known from only one sex. Since there is little sexual dimorphism in the punctation and structure of *aterrimus* and *niger*, I expect that the unknown sexes of *minutus* and *laticeps* will be easily associated when discovered.

KEY TO THE SPECIES OF PAREPEOLUS

Females

1. Patches of pale hairs yellowish to light brown. Scutellum at each side of median line with tuft of erect, plumose, brownish hairs, longer than third flagellomere. Labrum with two teeth near middle of disc (fig. 12). Mesepisternum polished, with scattered small punctures barely twice diameter of hairs arising from them. Forewing hyaline with apex dark. Length 6mm . . . . *minutus*

—. Patches of pale hairs white, or hairs wholly black. Scutellum with plumose hairs mostly appressed, shorter than third flagellomere. Disc of labrum with carina bearing 4 teeth (fig. 15). Mesepisternum with punctures distinct. Forewing usually black, partly hyaline in specimens of *aterrimus* from northern Brazil. Length 7.5-13 mm 2

2. Face and body in general with dense hairs hiding integument. Mesepisternum with dense punctures, below scrobe less than a diameter apart. Propodeal spiracle surrounded by punctures, those behind spiracle as large as those on mesepisternum. Proportion of first to second flagellomere 0.75-1:1. Pygidial plate with distinct punctures bearing short setae . . . . *aterrimus*

—. Face and body in general with sparse hairs not hiding shiny integument. Punctures on mesepisternum more than one diameter apart. Integument around propodeal spiracle mostly smooth and shiny; if fine punctures behind, then much smaller than those of mesepisternum. Proportion of first to second flagellomere 1.25-1.5:1. Pygidial plate finely sculptured, without punctures or short setae . . . . *niger*

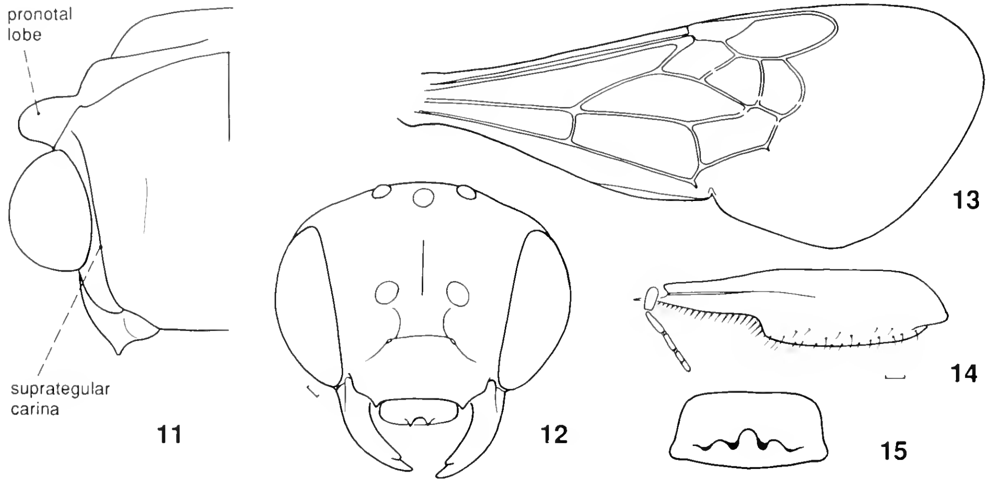
Males

1. S6 with apical, central patch of short hairs and lateral brushes of long, dense hairs separated from margin of segment by polished area, together forming sinuous fringe, arched at sides. Genitalia, fig. 19 . . . . *aterrimus*

—. S6 without lateral brushes of long, dense hairs 2

2. Lateral ocellus separated from posterior margin of head by 2.3 ocellar diameters. Scutellum slightly bigibbous. Flagellomeres 3-6 each with small subapical tubercle on polished underside; these tubercles of equal size. Genitalia, fig. 21 . . . . *laticeps*

—. Lateral ocellus separated from posterior margin of head by 1.15-1.40 ocellar diameters. Scutellum evenly convex. Flagellomeres 4-6 each with small subapical tubercle on underside, that on flagellomere 4 more conspicuous. Genitalia, fig. 17 . . . . *niger*



Figs. 11-15. *Parepeolus*, females. 11, *P. aterrimus*, left half of pronotum and scutum. 12, *P. minutus*, holotype, face. 13, *P. niger*, holotype, forewing. 14, *P. aterrimus*, stipes. 15, *P. aterrimus*, labrum. Scale lines 0.1 mm.

***Parepeolus aterrimus* (Friese), new combination**

(figs. 11, 14-16, 19-20)

Epeolus aterrima Friese, 1906: 101. Type male from Mendoza, Argentina, Jensen-Haarup coll. (not examined); Friese, 1908: 81, 82; Jörgensen, 1909: 219, 225.

Epeolus aterrima fuscipennis Friese, 1906: 101. Male and female types from Tucumán, Argentina, 2000 m, Steinbach coll. (not examined). **New synonymy**.

Leiopodus lecointei Ducke, 1907: 88. Lectotype female, by present designation, from Lago Grande de Vilafranca, Pará, Brazil, Lecointe coll. (Mus. Berlin, examined); Ducke, 1908a: 103-104; Ducke, 1908b: 79. **New synonymy**.

Leiopodus gigas Friese, 1908: 91. Holotype male from Jundiahy, São Paulo, Brazil, 17 November (Mus. Berlin, examined). **New synonymy**.

Epeolus lecointei: Ducke, 1910: 104.

Isepeolus aterrimus: Jörgensen, 1912a: 142; 1912b: 316.

Parepeolus lecointei: Ducke, 1912: 102; Sandhouse, 1943: 585.

Parepeolus gigas: Ducke, 1912: 102.

P. aterrimus can be distinguished from the other species of *Parepeolus* by the dense punctures of similar size on the mesepisternum and the propodeum, the first flagellomere usually shorter than the second (proportion of the first to the second flagellomere 0.75-1.10:1), the maxillary palpus with 5 segments, the disc of the pygidial plate in the female with distinct punctures bearing short setae, the disc of the pygidial plate in the male covered with hairs, and the distinctive lateral brushes on S6 of the male.

This species shows considerable variation in the pattern of pale hairs and the color of the wings. Specimens from northern Brazil have extensive white maculations; specimens from central and western Argentina are wholly black (fig. 16). The lectotype of *lecointei*, at one extreme of this variation, has the following areas with white hairs: frons, labrum, gena, pronotal band including the pronotal lobes, two anterior patches on scutum, most of scutellum, metanotum, upper half of the mesepisternum, propodeum, outer sides of legs, most of T1 except two subapical black spots, lateral spots on T2, T5 and T6, lateral and central spots on T3 and T4 and small latero-apical spots on S2-S5. These patches may be reduced or absent in specimens from other areas. The lectotype of *lecointei*, as well as specimens from the states of Ceará and Bahia in Brazil, have at least the basal half of the forewing hyaline; specimens from elsewhere have the forewing entirely black. I have not found any morphological characters, including the genitalia, suggesting that this is not a single species.

Fig. 16. Distribution of *Parepeolus aterrimus*. Open circles represent specimens with patches of white pubescence; dots represent specimens with pubescence wholly black.

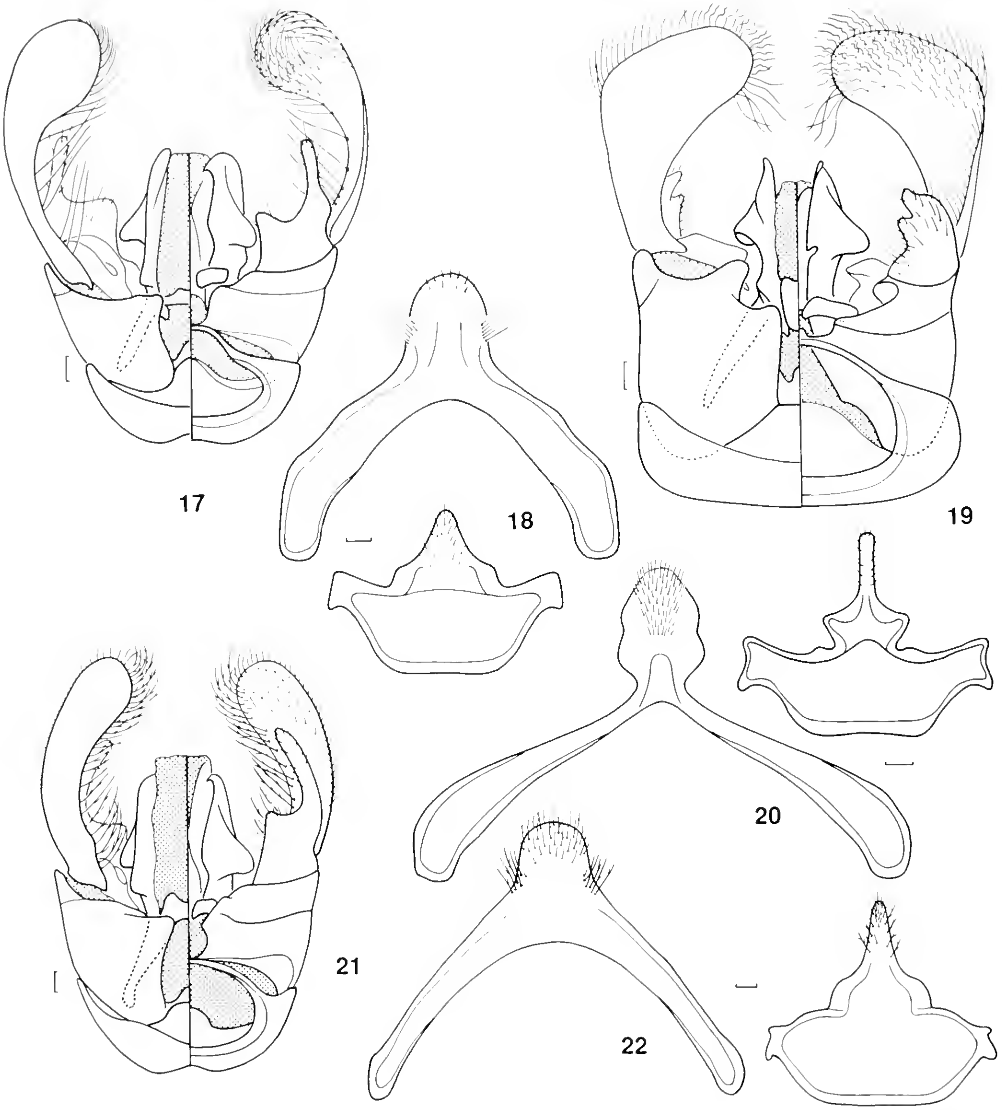
I have not seen the types of *aterrimus* or *fuscipennis*, but Friese's original descriptions do not leave doubt about their identity. He mentions for *aterrimus* the shape of the fringe of hairs of S6 of the male, diagnostic for the species; *fuscipennis* is described as a color variant of the former. *P. lecointei* was described from both sexes in a key, the intended original description, more detailed, appeared one year later (Ducke, 1908a). The selected lectotype is the only specimen that I have studied from the original series. *Leiopodus gigas* Friese is a further synonym. The size of the holotype falls within the range of the species (8-12.5 mm long); it does not differ from males of *aterrimus* in any significant respect.

I have studied material from the states of Pará, Ceará, Bahia, Mato Grosso, São Paulo, Paraná and Rio Grande do Sul in Brazil, from Montevideo in Uruguay and from the provinces of Formosa, Corrientes, Santa Fe, Córdoba, Tucumán, Salta, Catamarca, La Rioja, Mendoza, San Luis, La Pampa and Buenos Aires in Argentina (fig. 16). Collection dates in northern Brazil are June, July and February; in southeastern Brazil, December and January; in Uruguay and Argentina, November to March.

Parepeolus niger, new species
(figs. 13, 17-18)

This species can be distinguished by the punctation of the mesepisternum, coarser than that of the propodeum; the first flagellomere 1.25-1.7 times longer than the second; the forewing with basal vein and cu-v meeting; the pygidial plate in both sexes without distinct punctures; and flagellomeres 4-6 in the male each with a small subapical tubercle, that on flagellomere 4 larger than the other two.

Female. Length 8-11 mm (holotype 8.8); length of forewing 6-7.2 mm (holotype 6.6). Integument black; apex of mandible reddish; flagellum on underside brownish; pronotal lobe, tegula, legs and metasoma dark reddish brown to black. Forewing deeply infuscated; hindwing infuscated on apical half, base hyaline. *Vestiture.* Pubescence of head, thorax and propodeum black, some specimens, including holotype, with white hairs on supraclypeal area and upper half of clypeus; few specimens with hairs on propodeum white. Hairs of mesepisternum and propodeum long, plumose; those of scutellum mostly appressed, but some stiff, erect hairs present. Pubescence of legs black, except apical white spot on hindcoxa; external surface of hindtibia with dense, plumose white hairs on apical two thirds (holotype) (some specimes with legs wholly black). Pubescence of metasoma black with following pattern of white hairs: T1 with apical band notched medially and expanded laterally; T2-T4 with lateroapical spots (holotype), some specimens with lateroapical spots on T5 too, others with T2-T5 wholly black. *Sculpture.* Face shining, punctures on clypeus and paraocular areas minute; mesepisternum with distinct punctures, below scrobe clearly more than one diameter apart, leaving shiny interspaces; densest punctures close to anterior border of mesepisternum, nearly one diameter apart; lower third of metapleura polished, above with minute punctures; propodeum shiny, around spiracle without punctures or with punctures behind spiracle much smaller than those of mesepisternum; metapostnotum polished, impunctate; pygidial plate finely sculptured, without punctures or setae. *Morphology.* Proportion of lower to upper interocular distances 0.78-0.80:1. Lateral ocellus separated from posterior margin of head by 1.1-1.3 ocellar diameters. Labrum 0.43-0.48 times as long as wide, with transverse, arched carina on apical third that bears 4 teeth, the central ones stronger. Maxillary palpus with 4 segments. Proportion of first to second flagellomere 1.25-1.50:1; of second to third 0.9-1.0:1. Scutellum evenly convex. Basal vein of forewing meeting cu-v; in one specimen briefly basad. Pterostigma 2.75-3.5 times as long as prestigma; second submarginal cell longer than first or third; proportion of lengths on posterior margin 0.7-0.95:1:0.55-0.75. Posterior margin of first submarginal cell 0.9-1.3 times as long as apical margin.



Figs. 17-22. *Parepeolus*, males. *P. niger*: 17, genitalia, dorsal and ventral; 18, sterna 7 and 8. *P. aterrimus*: 19, genitalia, dorsal and ventral; 20, sterna 7 and 8. *P. laticeps*, holotype: 21, genitalia, dorsal and ventral; 22, sterna 7 and 8. Scale lines 0.1 mm.

Male. Length 7.5-10 mm; length of forewing 6.5-7.5 mm. Color, vestiture and punctation similar to those of female, but some specimens with white appressed hairs on face from above antennal sockets to apex of clypeus and white hairs on external surface of mid and hindtarsi; metasomal sterna sometimes with poorly defined subapical bands of white hairs and fringes on S3-S5 white; other specimens with sterna entirely black. *Morphology*. Proportion of lower to upper interocular distance 0.73-0.80:1. Lateral ocellus separated from posterior margin of head by 1.15-1.40 ocellar diameters. Proportion of first to second flagellomere 1.3-1.7:1, second and third of same length. Flagellomeres 4-6 each with small subapical tubercle on underside; tubercle on flagellomere 4 more conspicuous. Disc of pygidial plate polished, without hairs or punctures. Apex of S6 with central patch of short hairs bordered by polished lateral areas. Genitalia, figure 17.

Comments. This species was recognized and named on labels by J. S. Moure; I am using the name that he proposed. Specimens from Argentina have more extensive areas of white hairs;

most specimens from Brazil are entirely black except for the apical band on T1. This distribution of pale and dark forms is the converse of the geographic variation seen in *P. aterrimus*.

Material studied. Holotype female from El Sauce, Dpto. Calamuchita, Prov. Córdoba, Argentina, XII-1938, M. J. Viana (MACN). Paratypes: *ARGENTINA*: *Jujuy*: 1 male, Jujuy, Spegazzini coll. (MACN). *Tucumán*: 1 female, San Pedro de Colalao, II-1949, Arnau (SEM); 1 male, San Pedro de Colalao (UFPR). *Córdoba*: Agua de Oro, I-1940, J. A. de Carlo (SEM). *PARAGUAY*: 1 male, SW Saltos del Guayra, Paraná, 8-XII-1971, L. Peña (AMNH). *BRAZIL*: *Paraná*: 3 females, 4 males, Villa Velha, 20-I-5-II-1974, J. G. Rozen, F. C. Thompson and J. S. Moure (1 female, 1-II-1974, with indication "nest", specimen referred to by Rozen, 1984) (AMNH); 2 females, 1 male, Rio Negro, 7-II-1974, J. G. Rozen and F. C. Thompson (AMNH). *São Paulo*: 1 female, Mogi-Guacu, 23-I-1974, J. G. Rozen, F. C. Thompson and J. S. Moure (AMNH).

Parepeolus laticeps, **new species**

(figs. 21, 22)

This species is allied to *niger*, from which it is distinguished by the broader vertex (hence the specific name), the slightly bigibbous scutellum, the finer punctation of the mesepisternum, the number and size of the flagellar tubercles and the shape of the gonostylus.

Male. Length 13 mm; length of forewing 10.3 mm. Integument black; apex of mandible reddish. Wings deeply infuscated except pale basal third of hindwing and pale longitudinal line crossing submarginal cells. *Vestiture*. Pubescence of head black; a few pale hairs above antennal sockets. Thorax with black hairs, those on mesepisternum long, plumose; those on scutellum mostly appressed, some scattered, erect, stiff. Propodeum with long, plumose, white hairs. Legs mostly with black hairs, but white hairs as follows: foredistitarsus above; external surfaces of mid and hindtarsi; apical third of midtibia; most of hindtibia and apical spot on mid and hindcoxae. Hairs on hindtibia strikingly dense. Pubescence of metasoma black including apical fringes of S4-S5; with following pattern of white hairs: T1 with apical band expanded medially and laterally, forming two dark preapical spots, T2 with large lateral spot, T3-T6 with apicolateral spots, small on T3 and T6, moderate on T4-T5. *Sculpture*. Integument of head and thorax shiny, with fine, fairly dense punctures; mesepisternum with small punctures, more than one diameter apart below scrobe; metapleura with minute punctures, except lower fourth; propodeum shiny, before spiracle without punctures, behind spiracle with fine punctures similar to those of mesepisternum. Metapostnotum polished, impunctate. *Morphology*. Proportion of lower to upper interocular distances 0.84:1. Lateral ocellus separated from posterior margin of head by 2.3 ocellar diameters. Labrum 0.43 times as long as wide; with transverse carina near middle bearing 4 teeth, central ones stronger. Maxillary palpus with 4 segments. Proportion of first to second flagellomere 1.75:1, of second to third 0.9:1. Flagellomeres 3-6 each with small subapical tubercle on underside; tubercles equal in size. Scutellum slightly bigibbous. Basal vein of forewing meeting vein cu-v. Pterostigma 3 times as long as prestigma. Proportion of lengths of submarginal cells along posterior margin 0.8:1:0.63. Posterior margin of first submarginal cell 0.97 times as long as apical margin. Disc of pygidial plate polished, without punctures or hairs. Apex of S6 with central patch of short hairs bordered by polished lateral areas. Genitalia, fig. 21; dorsal branch of gonostylus slightly swollen distally; long hairs plumose.

Material studied. Holotype male from Itá Ibaité (Alto Paraná), Prov. Corrientes, Argentina, March 1962 (MACN).

Parepeolus minutus, **new species**

(fig. 12)

This species is the smallest in the genus. It can be distinguished by the yellowish brown color of the maculations, the fine punctation, the labrum with only two teeth, and the two tufts of erect hairs on the scutellum. The specific name refers to the small size.

Female. Length 6 mm; length of forewing 4.8 mm. Integument black; mandibles reddish except base; legs dark reddish brown. Wings slightly infuscated with apex dark beyond closed cells; marginal cell dark along anterior half. *Vestiture*. Pubescence of head sparse, black; face above and around antennal sockets with whitish, plumose hairs intermixed with black, stiff, almost simple hairs. Pubescence of thorax black with following pattern of yellowish brown hairs: posterior margin of pronotum with band not reaching pronotal lobes; anterior margin of scutum with lateral patches and small notaular spots; posterior margin of scutum with lateral patches joining band of scutellum; scutellum including axilla and metanotum with golden brown hairs, those on scutellum at each side of median line long, erect, plumose, darker at tips, forming distinct tuft. Propodeum with whitish, plumose hairs. Pubescence of legs black, except white spot on apical third of hindtibia. Pubescence of metasoma black with following areas yellowish brown: T1 with apical band, T2-T4 with short latero-apical bands expanded basally at sides, T5 with roundish paramedian patch that leaves central black eyespot. Posterior margins of S2-S5 with small lateral whitish spots. *Sculpture*. Integument of head and thorax shiny, with fine, sparse punctures; mesepisternum with widely separated punctures as small as those on clypeus and propodeum; metapleura with minute punctures; metapostnotum shiny, impunctate; propodeum shiny, around spiracle with scattered punctures. *Morphology.* Proportion of lower to upper interocular distance 0.70:1. Lateral ocellus separated from posterior margin of head by 1.3 ocellar diameters. Labrum 0.5 times as long as wide, with 2 teeth near middle; beyond teeth longitudinal depression reaches apical margin. Maxillary palpus with 4 segments. Proportion of first to second flagellomere 1.08:1, of second to third 1:1. Scutellum evenly convex, although tufts of hairs give impression of bigibbousness. Basal vein of forewing arising basal to vein cu-v by distance equal to 3 times thickness of basal vein. Pterostigma 3.8 times as long as prestigma. Proportion of lengths of submarginal cells along posterior margin 0.83:1:0.83. Posterior margin of first submarginal cell 1.3 times as long as apical margin. Pygidial plate finely sculptured, without punctures or setae.

Material studied. Holotype female, 17 km E Magdalena, Prov. Buenos Aires, Argentina, 16-XI-1985, L. Moffatt (MACN).

Genus *Epeoloides* Giraud

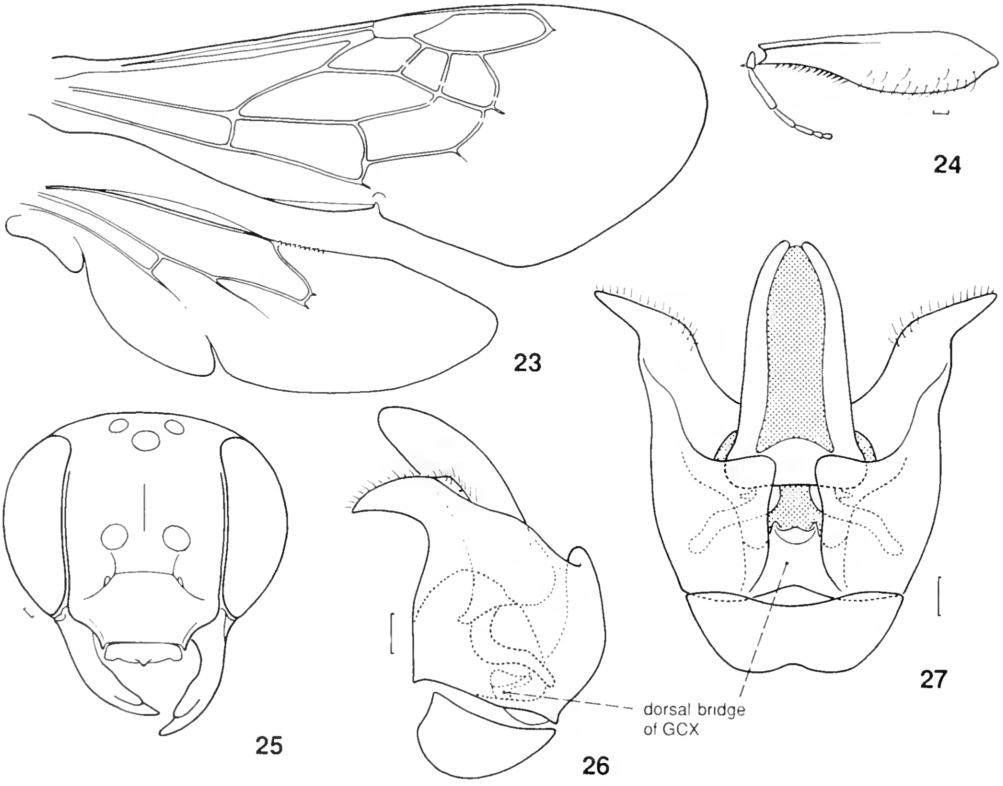
(figs. 23-27)

Epeoloides Giraud, 1863:45. Type species: *Epeoloides ambiguus* Giraud, 1863 (=*Apis coecutiens* Fab., 1775), by monotypy.

Viereckella Swenk, 1907: 298. Type species *Viereckella obscura* Swenk, 1907, by original designation.

Epeoloides is distinguished by the long and plumose vestiture, the *eyes of the male strongly converging above*, the *paraocular carina almost reaching the top of the eyes*, the *labrum with a single preapical tubercle*, the shiny metapostnotum with scattered plumose hairs, the *claws of the male with the rami adjacent and similar*, and the *spatulate pygidial plate of the male*.

Linsley and Michener (1939) presented a detailed generic description. The statements below are included to complement that description and to facilitate comparison with the other genera described here.



Figs. 23-27. *Epeoloides coecutiens*, female: 23, wings; 24, stipes. *Epeoloides pilosula*, female: 25, face. *Epeoloides pilosula*, male: 26, genitalia, lateral; 27, genitalia, dorsal. Scale lines 0.1 mm.

Description. 1. Length 7-9.5 mm. 5. Eyes of female slightly converging above; proportion of lower to upper interocular distance 1.04-1.1:1; inner margin of eye slightly concave. Eyes of male strongly converging above; proportion of lower to upper interocular distance 1.25-1.54:1. 11. Mandible with one subapical tooth, inner angle may be present. 12. Stipital comb-bearing concavity absent. 13. Maxillary palpus with 6 (*coecutiens*) or 4 segments (*obscura*, *pilosula*). 14. Hypostomal carina forming rounded angle near mandibular socket. 15. Proportion of first to second flagellomere dimorphic, in females 0.5-0.8:1, in males 1.0-1.25:1. 17. Scutum shorter than intertegular span (0.8-0.9). 18. Suprategular carina anteriorly curving close to tegula. 20. Prestigma twice as long as wide; pterostigma 2.8-3.2 times as long as prestigma. 23. Jugal lobe of hindwing elongate, 0.3-0.4 times as long as vannal lobe. 24. Forecoxa with basal sector of ventral carina running completely across the coxa. 28. Genitalia, figures 26, 27.

***Osirinus*, new genus**

Type species: *Osirinus lemniscatus*, new species.

Osirinus shares with *Osiris* and *Protosiris* the shiny integument, pointed marginal cell, flat labrum with small preapical denticles, and the bowed posterior margin of the first submarginal cell. It is distinguished by the *plumose vestiture*, the *stout, short legs*, and the *eyes diverging above with the inner margins almost straight*.

Description. 1. Length 5.5-10 mm. 2. Integument black, patterned with red, to entirely testaceous. 3. Integument shiny; metapostnotum shiny, with or without hairs laterally. 4. Vestiture of head, mesosoma and legs consisting of long, plumose hairs; metasomal terga basally fasciate to almost bare. 5. Eyes convergent below, proportion of lower to upper interocular distance 0.82-0.90:1; inner margins of eyes almost straight. 6. Lateral ocellus separated from posterior margin of head by 1.1-1.6 ocellar diameters. 7. Maximum width of gena 0.5-0.7 times as wide as maximum width of eye seen from side. 8. Preoccipital carina absent; paraocular carina short, continuing lateral margin of clypeus. 9. Malar space absent. 10. Labrum with 2 or more small preapical denticles. 11. Mandible with one subapical tooth; inner angle may be present. 12. Stipital comb-bearing concavity present. 13. Maxillary palpus with 5 segments. 14. Hypostomal carina forming rounded angle near mandibular socket. 15. Proportion of first to second flagellomere 0.55-1.2:1. 16. Pronotum not forming raised collar; dorsolateral lobes may be globose, but without median subhorizontal portion connecting them; anterior dorsal margin not recurved; posterolateral margin not emarginate below pronotal lobe. 17. Scutum shorter than intertegular span (0.78-0.9). 18. Suprategular carina curving anteriorly close to tegula. 19. Marginal cell pointed, apex close to wing margin. 20. Prestigma as long as or slightly longer than wide; pterostigma 5.6-6.0 times as long as prestigma. 21. First submarginal cell with posterior margin arched, 1.1-1.6 times as long as apical margin. 22. Basal vein of forewing meeting or arising apical to vein cu-v. 23. Jugal lobe of hindwing elongate, 0.22-0.25 times as long as vannal lobe. 24. Forecoxa with basal sector of ventral carina complete, running all across the coxa. 25. Legs short, stout; hindtibia usually with stiff, broad setae intermixed with slender ones; strigilar concavity of forebasitarsus 0.38-0.41 times as long as segment. 26. Metapostnotum with differentiated basal sector or entirely declivous. 27. Pygidial plate present in both sexes. 28. Genitalia as in figures 40, 41 (male known only for *O. lemniscatus*). Ventral branch of gonostylus not articulated, dorsal branch cylindrical, articulated; apodeme of penis valve strongly curved; volsella absent.

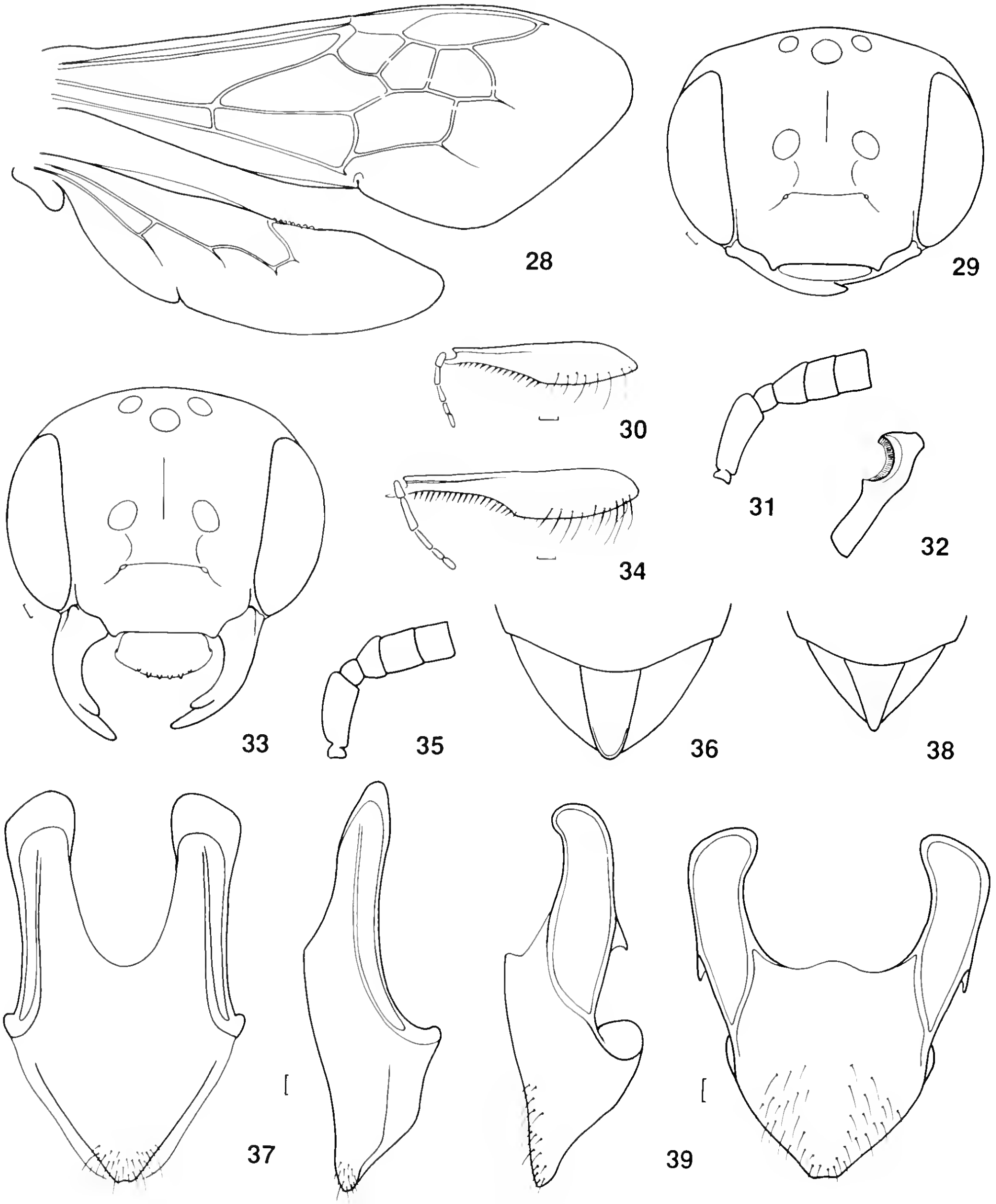
KEY TO FEMALES OF OSIRINUS

1\. T2-T4 with broad basal bands of plumose, appressed, yellowish hairs. Scutellum with tuft of erect hairs at each side of median line. Integument mostly dark. Forewing infuscate, with conspicuous subapical hyaline spot; pterostigma yellowish. Proportion of first to second flagellomere 0.86-1:1 (fig. 31). Metapostnotum with basal, central depression and lateral patches of appressed hairs . . . . *lemniscatus*

—. T2-T4 almost bare. Scutellum with erect hairs not forming tufts. Integument mostly reddish to pale yellowish brown. Forewing evenly infuscate; pterostigma dark. Proportion of first to second flagellomere 0.55-0.6:1 (fig. 35). Metapostnotum bare, entirely declivous 2

2\. Apex of pygidial plate acute, spot on disc evident (fig. 38). Hindtibia without differentiated, stiff setae. Labrum with two preapical denticles separated by short longitudinal depression. Posterior margin of first submarginal cell 1.6 times as long as apical margin . . . . *rutilans*

—. Apex of pygidial plate rounded, no spot evident on disc (fig. 36). Hindtibia with stiff, basally broad and apically curved setae along dorsal margin. Labrum with row of 6 preapical denticles. Posterior margin of first submarginal cell 1.25 times as long as apical margin . . . . *fritzi*



Figs. 28-39. *Osirinus lemniscatus*, female: 28, wings; 29, face; 30, stipes; 31, basal segments of antenna; 32, forebasitarsus. *Osirinus fritzi*, female holotype: 33, face; 34, stipes; 35, basal segments of antenna; 36, T6 showing pygidial plate; 37, S6, ventral and lateral. *Osirinus rutilans*, female: 38, T6 showing pygidial plate. *Exomalopsis* sp., female: 39, S6, ventral and lateral. Scale lines 0.1 mm.

Osirinus lemniscatus, new species

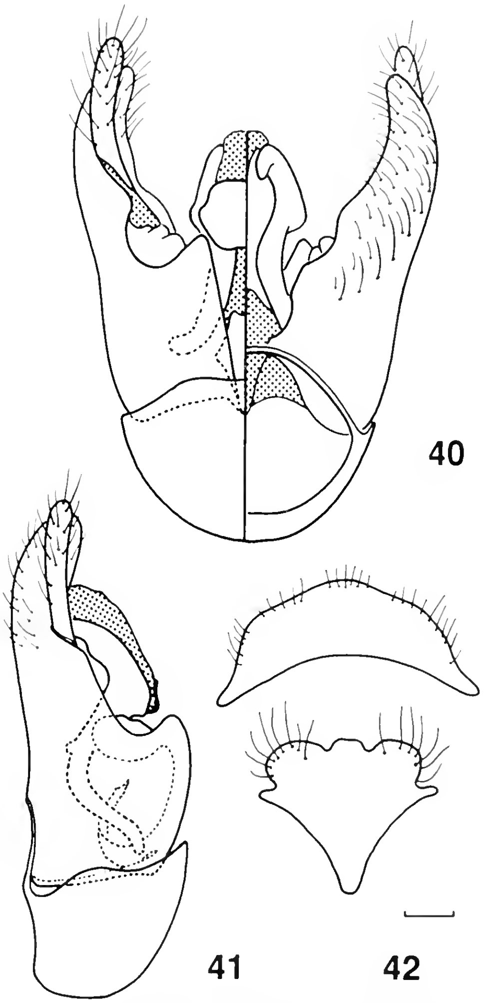
(figs. 28-32, 40-42)

This species is easily distinguished by its abundant plumose vestiture and dark integument, the basal bands of appressed hairs on the metasomal terga (unique in the tribe), the hyaline subapical spot on the forewing and the subequal first and second flagellomeres.

Female. Length 5.5-10 mm (holotype 6.0); length of forewing 4.8-7.4 mm (holotype 5.0). Head black with reddish, elongate spot between lateral ocellus and eye, reddish spot on gena near upper corner of eye, and some specimens with apex of clypeus and labrum reddish; mandible reddish except base. Scape dark with base brownish; pedicel and flagellum light brown, sometimes with longitudinal dark band. Thorax black to dark reddish brown, with following parts yellowish brown to reddish brown: pronotal lobes, antero-lateral angles and posterior margin of scutum, scutellum including axilla, middle of metanotum, and upper part of mesepisternum excluding hypoepimeral area (some specimens with mesepisternum entirely black). Propodeum black. Legs dark reddish brown; apices of femora, usually apices and bases of tibiae, and most tarsomeres light brown (hindtibia sometimes entirely so). Metasoma dark reddish brown to black; pygidial plate light brown. Forewing infuscate, with irregular hyaline spot surrounding third intercubitus and second recurrent vein, feebly connected with smaller hyaline spot behind second submarginal cell; in some specimens cells paler medially; pterostigma yellowish, veins brown. Hindwing hyaline with apex infuscate. *Vestiture.* Hairs plumose. Hairs on head mostly brown, whitish around antennal socket and on vertex behind ocelli. Thorax with intermixed whitish and brown hairs, short, appressed on scutum, long, erect and conspicuously plumose on mesepisternum, dense on upper half, scattered on lower half; scutellum with tuft of erect hairs with tips dark brown to black at each side of median line. Metapostnotum with lateral patch of short, appressed, white hairs. Propodeum with white hairs, denser along posterolateral angles. Legs with intermixed white and brown hairs; hindtibia with hairs strikingly dense on outer surface, black on basal third and white apically. Metasomal T2-T4 with broad basal bands of dense, appressed, yellowish hairs, behind such bands short, grayish hairs, posterior margins polished; T5 with grayish hairs that leave wide polished apex and longitudinal, median, polished band. *Sculpture.* Integument shiny with punctures minute, more or less dense corresponding to hairy areas; impunctate are: lower half of metepisternum, most of metapostnotum except lateral patches, propodeum below spiracle and around metapostnotum, and upper surface of T1. Metapostnotum with median basal depression and short longitudinal striae. *Morphology.* Proportion of lower to upper interocular distance 0.82-0.88:1. Head with vertex flat (fig. 29). Labrum with 3-5 small preapical denticles difficult to see due to dense pilosity; anterior margin slightly convex. Proportion of first to second flagellomere 0.86-1:1. Basal vein of forewing arising apical to vein cu-v. Proportion of lengths of submarginal cells on posterior margin 1.04-1.2:1:1.35-1.65. Posterior margin of first submarginal cell 1.1-1.25 times as long as apical margin. Hindtibia with stiff setae almost hidden by plumose hairs. Pygidial plate with apex narrowly rounded; in some specimens subapical spot on disc visible, similar to that of *O. rutilans.*

Male. Length 5.5-8.5 mm; length of forewing 4.5-7.5 mm. Color, vestiture and punctation similar to those of female, but scape pilose; T5 with basal band usually hidden by preceding tergum; S4 with latero-apical tuft of hairs; S5 with apical fringe of hairs. Proportion of lower to upper interocular distance 0.85-0.9:1. Proportion of first to second flagellomere 1-1.22:1. Genitalia, figures 40, 41.

Comments. The variation in size of this species is striking. Specimens of a series collected in the same place, the same day (Dique Cadillal, 18-XI-1983, R.B. Roberts) vary from 5.5 to 10 mm in length. This poses an interesting question about the host relations of *O. lemniscatus.* The specimens from Córdoba are paler, with the tufts on the scutellum almost completely light brown.



Figs. 40-42. *Osirinus lemniscatus*, male: 40, genitalia, dorsal and ventral; 41, genitalia, lateral; 42, sterna 7 and 8. Scale lines 0.1 mm.

Etymology. The specific name, beribboned in Latin, refers to the metasomal bands.

Material studied. Holotype female from Tafí Viejo, Prov. Tucumán, Argentina, December 1913, Curard (MACN). Following paratypes: *ARGENTINA*: *Tucumán*: 2 females, 1 male, same as holotype (MACN); 1 male, San Pedro de Colalao, Trancas, XII-1949, Foerster (SEM); 6 females, 1 male, 11 km N Dique Cadillal, 750 m, 11 and 18-XI-1983, R.B. Roberts (RBR); 1 female, Tacanas, 10-XII-1977, L. Stange (FSCA); 1 male, La Quebradita, near Tafí del Valle, 2030 m, 27-XII-1979, L. Stange (FSCA). *Córdoba*: 3 males, Jesus María, 14-XI-1940 (MLP).

Osirinus rutilans (Friese), new combination

(fig. 38)

Osiris rutilans Friese, 1930: 123. Type female from Bahia, Brazil (not examined). Shanks, 1986: 44-45.

I have not seen the type of *rutilans*, but its redescription by Shanks leaves no doubt about its placement in *Osirinus*. I have studied one specimen from São Paulo in the collection of the University of Kansas that Shanks attributed to *rutilans* with reservations, due to its black head and infuscate wings, but that was said to be morphologically identical. The diagnostic characters used for *rutilans* in the key above are based on that specimen.

Osirinus fritzi, new species

(figs. 33-37)

This species is easily recognized by its integument patterned with bright reddish and black. It is allied to *rutilans*; both species share the same shape of head, the short first flagellomere, reduced vestiture and impunctate metapostnotum. *O. fritzi* is distinguished from *rutilans* by the spiculate hindtibia, the shape of the pygidial plate and the denticles of the labrum.

Holotype female. Length 8 mm; length of forewing 6.5 mm. Integument bright reddish with following parts black: head, antenna, lower half of pronotum, prosternum, forecoxa, mid and hindtarsi, tegula and propodeum; brownish are: mandible, foretarsus, mid and hindcoxae and trochanters, metasternum and narrow apical bands on T1-T5. Wings infuscate with pterostigma and veins dark (both right wings are missing). *Vestiture* consisting of intermixed plumose and simple white hairs; hairs long and abundant around antennal sockets, side and lower third of clypeus, labrum, episterna, posterolateral angle of propodeum and legs; short, appressed on gena; rest of body with hairs sparse, scattered on polished scutum and scutellum; short and inconspicuous on discs of T2-T4. *Sculpture.* Integument shiny with minute punctures; following areas impunctate: lower half of metepisternum, propodeum below stigma, metapostnotum, disc of T1 and apices of T2-T5. *Morphology.* Proportion of lower to upper interocular distance 0.9:1. Labrum with row of 6 small preapical denticles, the outermost smaller; anterior margin convex. Proportion of first to second flagellomere 0.6:1. Head in front view with vertex rounded (fig. 33). Basal vein of forewing meeting vein cu-v. Proportion of lengths of submarginal cells on posterior margin 0.9:1:1. Posterior margin of first submarginal cell 1.25 times as long as apical margin. Hindtibia along dorsal margin with stiff, basally broad and apically curved setae. Pygidial plate with apex rounded, no spot evident on disc.

Etymology. This species is named after Manfredo Fritz, who collected the holotype, as well as so many other interesting parasitic bees.

Material studied. Holotype female from Palmar de Colón, Prov. Entre Rios, Argentina (no date), M. Fritz (MACN).

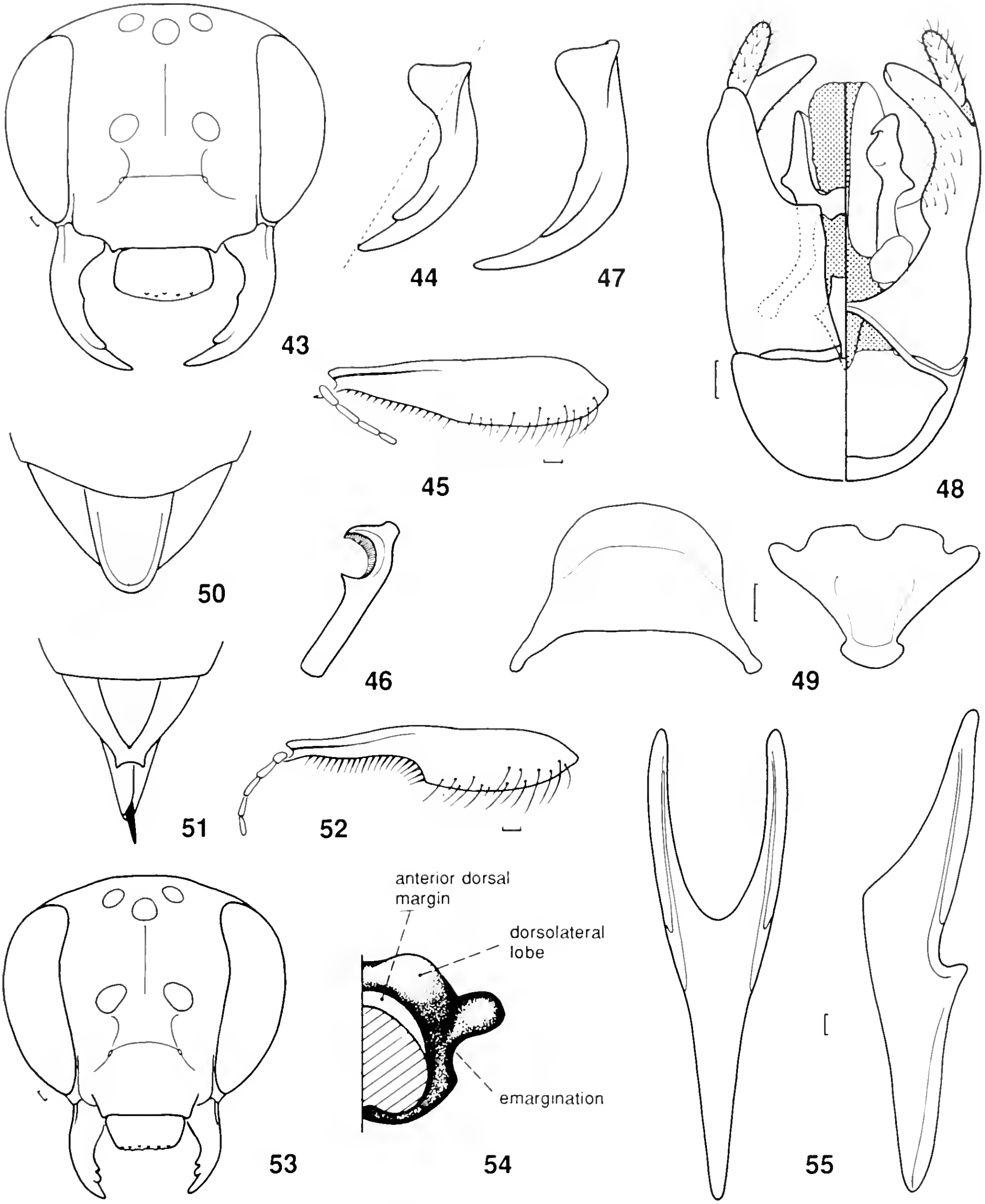
Protosiris, new genus

(figs 43-50)

Type species: *Osiris obtusus* Michener, 1954.

Protosiris recalls *Osiris* by its polished integument, the vestiture sparse, mostly simple, and the long, slender legs. It is distinguished by the *integument having sparse, minute punctures*; the *inner margins of the eyes parallel or nearly so*; the *mandible long, sickle shaped*, usually with one subapical tooth; and the apex of the female pygidial plate constituting the apex of the tergum. The male genitalia are as in *Osirinus*, with an articulated dorsal branch on the gonostylus.

Description. 1. Length 9.5-17 mm. 2. Integument dark reddish brown to entirely yellowish. 3. Integument highly polished; metapostnotum shiny, sometimes sculptured at base. 4. Vestiture short and dense on scutum; sparse, long and almost simple on rest of mesosoma, head and legs; metapostnotum always bare; metasoma with fine, short hairs to almost bare. 5. Eyes with inner margins parallel, proportion of lower to upper interocular distance 0.97-1.03:1; inner margin of eye almost straight. 6. Lateral ocellus separated from posterior margin of head by 0.7-1.2 times ocellar diameter. 7. Maximum width of gena 0.43-0.48 times maximum width of eye seen from side. 8. Preoccipital carina absent; paraocular carina short, continuing lateral margin of clypeus. 9. Malar space absent or only about 0.1 as long as width of base of mandible (*caligneus*). 10. Disc of labrum flat, with small preapical denticles. 11. Mandible long, strongly curved, with one subapical tooth or simple (*caligneus*); inner angle sometimes present. 12. Stipital comb-bearing concavity present (*mcginleyi*), or concavity reduced. 13. Maxillary palpus with 6 (*mcginleyi*) to 4 segments. 14. Hypostomal carina forming rounded angle near mandibular socket. 15. Proportion of first to second flagellomere 0.25-0.6:1. 16. Collar of pronotum with dorsolateral lobes



Figs. 43-55. *Protosiris obtusus*, female: 43, face; 44, mandible; 45, stipes; 46, forebasitarsus. *Protosiris caligneus*, female: 47, mandible. *Protosiris obtusus*, male: 48, genitalia, dorsal and ventral; 49, sterna 7 and 8. *Protosiris mcginleyi*, female: 50, T6 showing pygidial plate. *Osiris variegatus*, female: 51, apex of metasoma, dorsal aspect; 52, stipes; 53, face; 54, anterior view of pronotum, left half; 55, S6, ventral and lateral. Scale lines 0.1 mm.

globose, without median subhorizontal portion, or dorsolateral lobes flat connected by extremely short subhorizontal portion (*obtusus*). Anterior dorsal margin of pronotum not recurved; posterolateral margin not emarginate below pronotal lobe. 17. Scutum as long as intertegular span. 18. Suprategular carina curving anteriorly close to tegula. 19. Apex of marginal cell pointed, close to wing margin. 20. Prestigma as long as wide; pterostigma 7.0-8.3 times a long as prestigma. 21. First submarginal cell with posterior margin bowed, 1.7-2.3 times as long as apical margin. 22. Basal vein of forewing arising distal to vein cu-v. 23. Jugal lobe of hind wing elongate, 0.2 as long as vannal lobe. 24. Forecoxa with basal sector of ventral carina complete, running completely across coxa. 25. Legs slender; dorsal margin of hindtibia with stiff, basally broad and apically curved setae, intermixed with slender ones; strigilar concavity of forebasitarsus 0.26-0.27 times as long as segment. 26. Metapostnotum with anterior and posterior slanting sectors, posterior one steeper. 27. Pygidial plate present in both sexes. 28. Genitalia as in *Osirinus*, but volsella present or absent.

Comments. The group has been treated as a species group by Shanks (1986); the reader is referred to that paper for descriptions and a key to the species. Besides *P. obtusus* (Michener) the following taxa are included: *P. caligneus* (Shanks), new combination, *P. mcginleyi* (Shanks), new combination, and *P. tricosus* (Shanks), new combination.

Genus *Osiris* Smith

(figs. 51-55)

Osiris Smith, 1854: 288. Type species: *Osiris pallidus* Smith, 1854, by designation of Sandhouse, 1943: 580. Friese, 1930: 103-127. Shanks, 1986: 1-56.

Euthyglossa Radoszkowsky, 1884: 21. Type species: *Euthyglossa fasciata* Radoszkowsky, 1884, by monotypy.

This is the largest and most specialized of osirine genera. *Osiris* has numerous characters unique in the tribe, those shown in the cladogram and table 1 (11, 14-20) and characters 5, 8a, 9 and 14 below. The latter group of characters were not included in the cladistic analysis because it was not possible to establish their polarity by outgroup comparison, but they also represent autapomorphies for *Osiris* in the context of the cladogram in figure 1.

Shanks (1986) redescribed the genus and presented an excellent revision of its species. The statements below are intended to complement that description with some new characters and to restrict the extent of others, due to the exclusion of several species that now belong in *Osirinus* and *Protosiris*.

Description. 5. Inner margin of eye with shallow emargination near upper third. 8a. Preoccipital carina present behind ocelli. 8b. Paraocular carina short, continuing lateral margin of clypeus, sometimes reaching lower third of eye (*pallidus*, *mourei*). 9. Malar space present, 0.2-0.5 times as long as basal width of mandible. 10. Labrum with row of small preapical denticles. 11. Mandible short, with two subapical teeth. 12. Stipital comb-bearing concavity present. 13. Maxillary palpus with 5 segments. 14. Hypostomal carina high, forming sharp angle near mandibular socket. 16. Pronotum with anterior dorsal margin widely recurved; posterolateral margin below pronotal lobe emarginate. 17. Scutum slightly shorter than or as long as intertegular span (0.9-1). 18. Suprategular carina curving anteriorly close to tegula. 20. Prestigma as long as wide; pterostigma 7-8 times as long as prestigma. 21. First submarginal cell with posterior margin bowed. 22. Basal vein of forewing arising distal to vein cu-v. 23. Jugal lobe of hindwing elongate, 0.17-0.25 times as long as vannal lobe. 24. Forecoxa with basal sector of ventral carina complete or fading near middle of coxa. 25. Hindtibia with sparse, slender hairs; strigilar concavity of forebasitarsus 0.25-0.3 times as long as segment. 27. T6 of female with wide rim apical to pygidial plate; spot on plate always present, subcircular. 28. Genitalia without dorsal branch of gonostylus.

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The International Standard Serial Number of this publication is US ISSN 0022-8850.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 54, No. 2, pp. 25–34 December 20, 1989

The Nannochoristidae of South America (Mecoptera)[1]

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ABSTRACT

The family Nannochoristidae is briefly characterized. *Nannochorista andina*, new species, is described and illustrated. The other South American species, *N. neotropica* Navás and *N. edwardsi* Kimmins, are briefly characterized and illustrated; and all are included in a taxonomic key. Biogeography of the family is discussed.

INTRODUCTION

Among the Mecoptera, the Nannochoristidae are unusual or unique in several respects. They have elongate, aquatic larvae (Pilgrim, 1972), while those of other Mecoptera are eruciform or somewhat scarabaeiform and terrestrial. The mandibles of adults are relatively broad, subtriangular and acutely tipped, yet they do not reach the end of the rostrum, so that their function in feeding is not easy to hypothesize and remains unknown. In labial structure, particularly the expanded apical segments of the labial palps, nannochoristids are remarkably like some nematocerous Diptera and unlike other Mecoptera. At the base of the aedeagus are two large, somewhat ovoid capsules, close together or partially fused medially depending on the species (Figs. 5, 12, 13). I have not determined the function of these parts, which are unique to Nannochoristidae. The males also have no distinct sperm pump (Willmann, 1981), a characteristic they share with male Boreidae but in which they differ from other Mecoptera and from Antliophora generally. Broad fusion of the basistyles both dorsally and ventrally gives the genital segment of male nannochoristids a characteristic appearance (Figs. 6, 15, 17). Dorsal fusion of the basistyles exceeds ventral fusion in most families, but the reverse is true in Bittacidae, and there is essentially no fusion in Boreidae or Meropeidae. Mickoleit (1975) has described the terminal abdominal structure of females of *Nannochorista*, point-

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[1] Contribution no. 2080 from the Department of Entomology, University of Kansas, Lawrence.

ing out the unique median separation of sternal sclerites ("gonocoxosternites") on both the eighth and ninth segments (Fig. 10). Two large setae near the bases of veins A_1 and A_2 on the front wing (Fig. 9) are of unknown function, though probably sensory, and I have not seen equivalent setae in other families.

The family includes the only mecopteran genus, *Nannochorista*, that occurs both in Australia (where there are half a dozen endemic genera in other families) and South America; therefore, Nannochoristidae are of particular interest to biogeographers.

Only two South American species of *Nannochorista* have been named: *N. neotropica* Navás (1929) and *N. edwardsi* Kimmins (1929). In recent years, Dr. Oliver S. Flint, Jr., of the National Museum of Natural History, Washington, D.C., has collected numerous individuals of a third species, described below. I am indebted to Dr. Flint for his persistent efforts to collect Mecoptera in connection with his own field work on the neotropical Trichoptera.

In the lists of specimens examined of each species, the sequence of data is as follows: country, province (in alphabetical order), locality or localities (in the language of the specimen label), elevation in meters if recorded, date, collector(s), number of males and females (m, f, in parentheses), and name of collection (in parentheses; see acknowledgments for abbreviations).

KEY TO SOUTH AMERICAN SPECIES OF NANNOCHORISTA

1. Front wings 8.8-12.2 mm long (males smaller than females), darkly tinged with yellowish brown; in male, abdominal tergum 11 terminating well before posterodorsal margin of fused basistyles (Fig. 11), dorsal and ventral projections from posteromesal edges of approximately equal length (Figs. 11, 15) . . . . *neotropica* Navás

—. Front wings 6.2-9.2 mm. long, only faintly tinged with yellowish brown; in male, abdominal tergum 11 terminating at or beyond posterodorsal margin of fused basistyles (Figs. 12, 13), dorsal projections from basistyles twice as long as ventral projections, or longer (Figs. 1, 3) 2

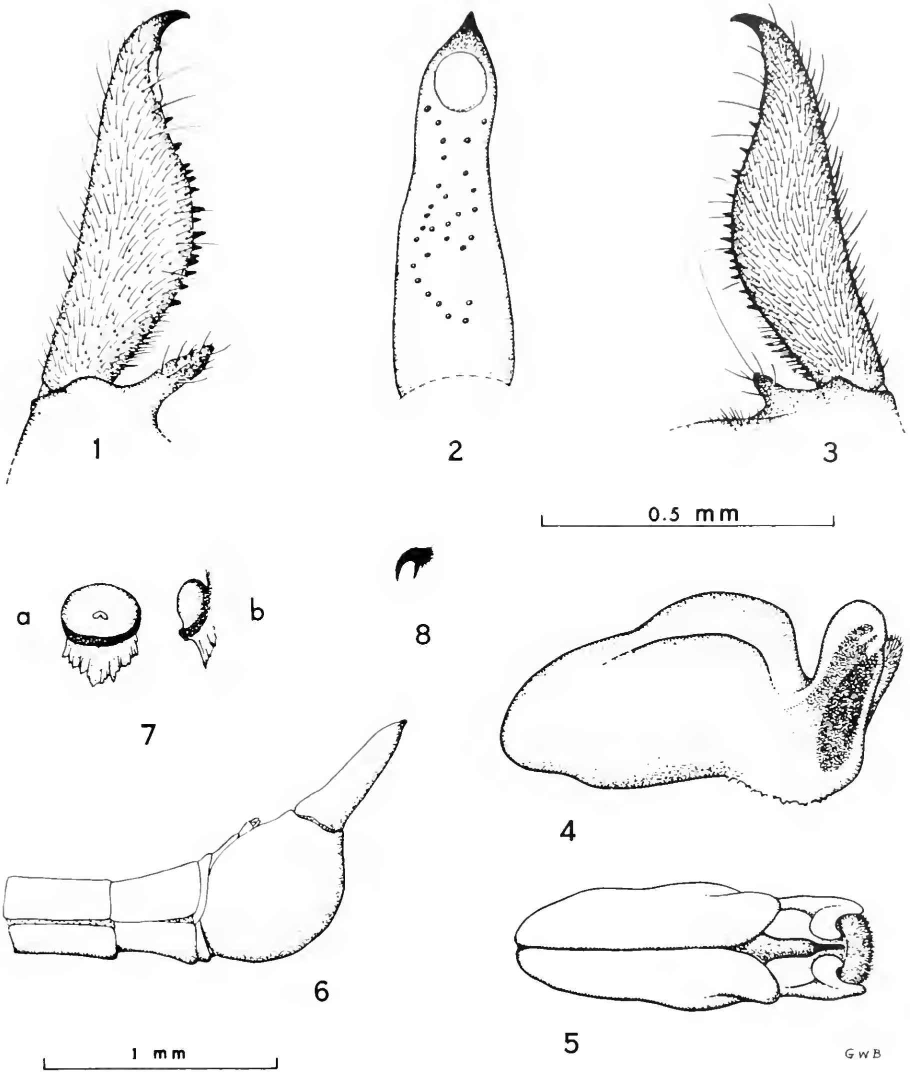
2. Dark spots or borders often present along cross-veins in basal half of wing; in male, dorsal apical notch between basistyles broadly U-shaped, with only tips of capsules of aedeagal base visible (Fig. 12); in female, sclerites of abdominal sternum 8 twice as wide subapically as at mid-length, and sclerites of sternum 9 continguous . . . . *edwardsi* Kimmins

—. No dark spots or borders along cross-veins; in male, dorsal apical notch between basistyles broadly V-shaped, with paired capsules of aedeagal base conspicuously exposed (Fig. 13); in female, sclerites of abdominal sternum 8 only slightly wider subapically than at mid-length, and sclerites of sternum 9 distinctly separated (Fig. 10) . . . . *andina*, new species

Nannochorista andina, new species

Description based on 44 males, 12 females, pinned.

Head: Vertex, occiput and upper frons dark gray, with fine, short pilosity, slightly paler brown adjacent to eyes. Lower frons and clypeus dull dark yellowish brown to grayish brown. Eyes dull dark red (holotype) to blackish brown. Ocelli amber, on low, blackish brown prominence. Rostrum slightly shorter than diameter of eye in frontal aspect, abruptly narrowed near mid-length, darkened, slender and sharp at apex. Maxillary palps brown; labial palps blackish. Anterior tentorial pit at each side of rostral base deep, circular. Antennal scape wider than long, dull yellowish brown; pedicel ovoid, dark yellowish brown to gray; basal flagellomere less than half diameter of pedicel, nearly three times length of second flagellomere; 23-26 flagellomeres in male (holotype 25), 24-25 in female. Flagellum dull yellowish brown in basal one-fifth to one-fourth, grading into dark gray apically; most flagellomeres four times as long as their diame-



Figs. 1-8. *Nannochorista andina*, n. sp. 1. Right dististyle, male paratype, dorsal aspect. 2. Right dististyle, mesal aspect, showing distribution of denticles. 3. Right dististyle, ventral aspect. 4. Aedeagus, left lateral aspect. 5. Aedeagus, dorsal aspect. 6. Terminal abdominal segments, male paratype, left lateral aspect. 7. Genital plate of female paratype, ventral (a) and right lateral (b) aspects. 8. Pretarsal claw. Upper scale: figs. 1-5, 7; lower scale: fig. 6.

ters, with hairs about as long as diameter of respective flagellomeres. Length of antennae about 4.5 mm. in male, 3.9 mm. in female.

Thorax: Pronotum short, transverse, dark grayish brown except narrowly sordid yellowish brown at sides and on slightly raised posterior margin; no conspicuous setae. Mesoscutum brown with short, yellowish setae and fine grayish pubescence; irregular, shiny spot adjacent to wing base and short, longitudinal spot nearer mid-line, both resulting from absence of pubescence. Scutellum with few setae on each side curved toward mid-line. Metathoracic dorsum generally like mesothoracic. Pleural surfaces and coxae unevenly dull brown to grayish brown with fine, light gray pilosity; hairs longer on anterior surfaces of coxae. Legs and tarsi dark yellowish brown with short, pale hairs and larger, black setae. Two tibial spurs at ventral apex of tibia, with comb of dark amber setae extending from one spur over dorsal curvature of tibia to other spur; length of spurs approximately equal to diameter of slightly expanded apex of tibia. Tibiae slightly longer than femora. Basitarsi longer than other tarsomeres together (proportions of hind tarsomeres, holotype, 60:20:12:10:7). Pretarsal claws each with one large basal tooth about as long as claw (Fig. 8).

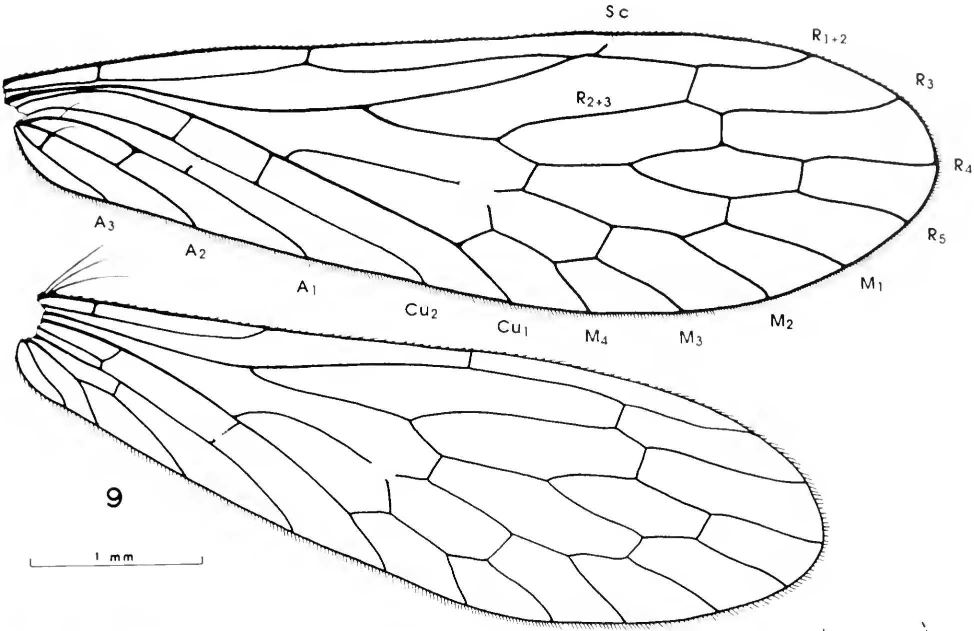
Wings (Fig. 9) lightly tinged with grayish brown in male, more darkly tinged in female, without spots or darkening along veins; membrane iridescent; stigmal area scarcely darker than rest of membrane. Veins brown, with pale thyridia at first fork of M, on cross-vein between Cu$_2$ and A$_1$ in front wing and on cross-vein between Cu$_1$ and Cu$_2$ near origin of M in hind wing. Vein Cu$_2$ paler and more slender than other veins, very weak in hind wings. In front wing, R$_1$ arched toward C, nearly touching Sc or fused with Sc for short distance before latter turns diagonally toward costal margin. Sc bent slightly toward C at costal cross-vein a little before level of origin of Rs. Cell 1st R$_4$ relatively shorter than in other species; basal section of R$_4$ equal to or shorter than adjoining section of R$_{4+5}$. Wing length, male, 6.2-7.2 mm. (holotype 6.5 mm.); female, 7.6-9.2 mm. (allotype 8.1 mm.)

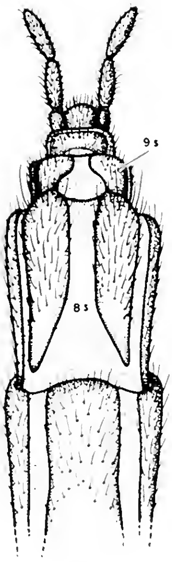
Abdomen of male: Terga and sterna of segments 1-8 dark blackish brown, glossy, with sparse short, pale hairs. Terga 9 and 10 brown, 11 dark yellowish brown. Segment 8 very short. Basistyles and dististyles of abruptly enlarged ninth (genital) segment contrastingly colored yellowish brown. Tenth tergum less than half as wide as ninth, truncate to slightly emarginate apically. Cerci short, barely projecting at each side of tergum 11. Basistyles only shallowly separated dorsally, almost totally fused ventrally (Fig. 13), with short projection near inner base of each dististyle both dorsally and ventrally. Dististyles (Figs. 1, 2, 3) somewhat expanded near mid- length, with densely sclerotized, hook-like apex and approximately 30 blackened denticles on mesal surface; a circular, membranous stylar organ also on mesal surface slightly before apex. Aedeagus (Figs. 4, 5) arising from pair of contiguous, sclerotized but pale yellowish brown capsules, projecting backward between posterior extensions from these capsules, then turning dorsad in anterodorsal channel in finely pubescent median lobe. Proctiger (segments 10-11) extending to mid- dorsal margin of fused basistyles.

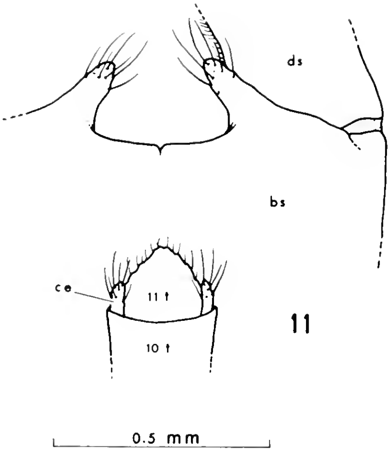
Abdomen of female: Segments 2-8 slightly compressed, tapering evenly toward apex; segments 9-11 abruptly smaller than 8, with 10 and 11 mostly recessed into ninth segment in dried specimens. Terga and sterna 1-7 unevenly dark brown to blackish brown, glossy, with sparse, short pale hairs. Pleural membrane paler brown. Terga 8-10 nearly black; segment 11 and cerci brown. Sterna narrow, four to five times as long as wide; sternum 6 with medial anterior notch. Eighth sternum (subgenital plate; Gonocoxit 8 of Mickoleit) completely divided by membranous zone along mid-line (Fig. 10), extending backward beyond end of tergum 8 and beneath ninth segment. Sclerites of ninth sternum also wholly separated by membrane. Tenth sternum short, undivided. Segment 11 lightly sclerotized. Cerci three-segmented, basal segments immovably fused to sides of segment 11. Genital plate (medigynium) an oval, sclerotized pad surrounding opening of spermathecal duct (Fig. 7).

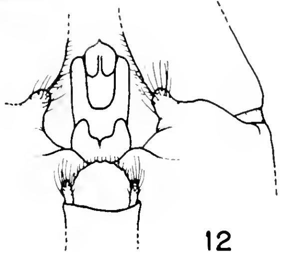
Body length, male, about 5.2-7.0 mm. (holotype 5.7 mm.); female, about 7.5-8.2 mm. (allotype 7.5 mm.).

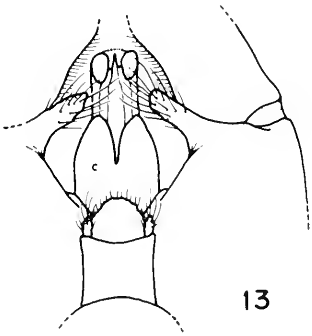
Types: Holotype, male, Argentina, Neuquén, Río Totoral, 24 km. NW of Villa La Angostura, 20 February 1978, C. M. and O. S. Flint, Jr. Allotype, Argentina, Neuquén, Río Nonthue, Estacion Forestal, Pucará, 24 February 1978, C. M. and O. S. Flint, Jr. Paratypes: ARGENTINA, NEUQUÉN: Arroyo Rosales, near San Martin de los Andes, 22 Jan. 1974, O. S. Flint, Jr. (10 m.); Arroyo Culebra, 20 km. S of San Martin de los Andes (40°18'S, 71°23'W), 2 Feb. 1974, O. S. Flint, Jr. (7 m., 1 f.); Canal, Estacion Forestal, Pucará (40°09'S, 71°39'W), 28-29 Jan. 1974, O. S. Flint, Jr. (2 f.); 5 km. SE of Lago Huechulafquen (39°46'S, 71°28'W), 26 Jan. 1974, O. S. Flint, Jr. (1 m.); Lago Nonthue, 12 Sept. 1951, "Schovskoy" (probably L. Schajovskoi) (1 f.); Los Totoros, 23 km. NW of Villa La Angostura, 20 Feb. 1978, C. M. and O. S. Flint, Jr. (1 m.); Río Totoral, 23 km. NW of Villa La Angostura, 31 Jan. 1987, C. M. and O. S. Flint, Jr. (1 m.); Río Bonito, SE of Villa La Angostura, 21 Feb. 1978, C. M. and O. S. Flint, Jr. (1 m.); Río Nonthue, Estacion Forestal, Pucará, (40°09'S, 71°39'W), 24 Feb. 1978, C. M. and O. S. Flint, Jr. (3 m.); Yuco, W of San Martin de los Andes, 23 Feb. 1978, C. M. and O. S. Flint, Jr. (1 m.). RÍO NEGRO : 5 km. S of Río Villegas (41°34'S, 71°32'W), 7 Feb. 1974, O. S. Flint, Jr. (1 m., 1 f.). CHILE . ARAUCO: Elicura, Contulmo, 28 Dec. 1985, L. E. Peña (1 m., 1 f.); CHILOE: Isla Chiloe, Ahoni Alto, SE of Chonchi, 22-23 Feb. 1988, L. E. Peña (4 m.); Dalcahue, 21-23 Oct. 1969, O. S. Flint and G. Barria (1 m.); Pio-Pio, 15 km. NW of Queilén, 10-11 March 1987, L. E. Peña (1 m.); Piruquina (near Castro), 15 March 1987, L. E. Peña (2 f.); Río Butalcura, 21 Oct. 1969, O. S. Flint and G. Barria (1 m.); PALENA: Termas Amarillo, about 30 km. SE of Chaitén, 250 m., 22 Jan. 1987, C. M. and O. S. Flint, Jr. (6 m., 1 f.); ÑUBLE: Las Trancas, 21 km. E of Recinto, 1300 m., near high waterfall, 17 Jan. 1979, M. and D. Davis and B. Akerbergs (1 m.; 1 f.); MALLECO: Contulmo National Park, 19 Oct. 1969, O. S. Flint and G. Barria (1 f.); Nahuelbuta National Park, near Los Gringos Camp, 29 Jan.-5 Feb. 1979, M. and











Figs. 9-13. *Nannochorista* spp. 9. *N. andina*, n. sp., right wings; venation according to Comstock-Needham system. 10. *N. andina*, n. sp., terminal abdominal segments of female paratype; s - sternum. 11. *N. neotropica*, diagram of portion of genital bulb of male, to show tergum 11 ending well before margin of fused basistyles; bs - basistyle, ce - cercus, ds - dististyle, t - tergum. 12. *N. edwardsi*, diagram of portion of genital bulb of male, showing tergum 11 ending at margin of fused basistyles. 13. *N. andina*, n. sp., diagram of portion of genital bulb of male, showing tergum 11 extending slightly beyond margin of fused basistyles; c - capsule at base of aedeagus. Upper scale: fig. 9; lower scale: figs. 10-13.

D. Davis and B. Akerbergs (1 m.).

Holotype, allotype and most paratypes are in the National Museum of Natural History, Washington, D.C.; 3 male and 1 female paratypes in Snow Entomological Museum, University of Kansas, Lawrence.

Nannochorista andina closely resembles *N. edwardsi* in both size and color, and the two species have rather broadly overlapping ranges. The smoky-gray maculations along certain cross-veins in *edwardsi*, as described by Kimmins (1929), would appear to make differentiation of these species easy, but these spots are absent in many individuals of *edwardsi* identified on the basis of external genital structures. Males are readily recognized by the aedeagal structure: in *andina* the basal capsules are broadly exposed in the relatively deep notch between the basistyles (Fig. 13), while in *edwardsi* only the tips of the capsules are exposed, the basistyles being more completely fused (Fig. 12). Females may be differentiated by the shapes of the sternal sclerites of abdominal segments 8 and 9 (see key).

Nannochorista edwardsi Kimmins, 1929

Clearly, this species and *N. andina* comprise a distinct group within *Nannochorista*. The length of abdominal segments 10 and 11 in relation to the posterodorsal margin of the fused basistyles (Figs. 12, 13) is unlike the condition seen in males of all other species in the family. In such a small genus, however, subgeneric recognition of this difference seems unnecessary. *N. edwardsi* and *N. andina* are very similar in size, color of body and wings, number of antennal flagellomeres and various other details.

Males of these species are easily differentiated by the shape of the space between the posterodorsal projections from the basistyles. As indicated in the key, this space, or notch, is broadly U-shaped in *edwardsi*. Only the apical one-third to one-half of the basal capsules of the aedeagus projects from beneath the median margin of the fused basistyles (Fig. 12). These basal capsules have somewhat pointed posterior apices in the male holotype but are usually more rounded apically, as illustrated here. The dorsal projections from the basistyles are only about as long as their basal width, while the ventral ones are much smaller in all dimensions.

Kimmins (1929:191) illustrated the wing of a female paratype, showing all cross-veins distinctly bordered by "blackish" pigmentation, as well as spots at the origin of Rs and M. This is a highly variable character, and if one may rely on the described differences in genitalia (as above and in the key), there are numerous individuals of this species with no wing maculations whatsoever. The male holotype shows no pigmentation along most cross-veins in the apical half of the wing (Fig. 16).

The male holotype and female paratype were examined at the British Museum (Natural History). The holotype is intact in every respect. Its locality-date label reads "L. Gutierrez, 3-14-xi-1926." This lake is just south of large Lake Nahuel Huapi and west of San Carlos de Bariloche (see Map 1).

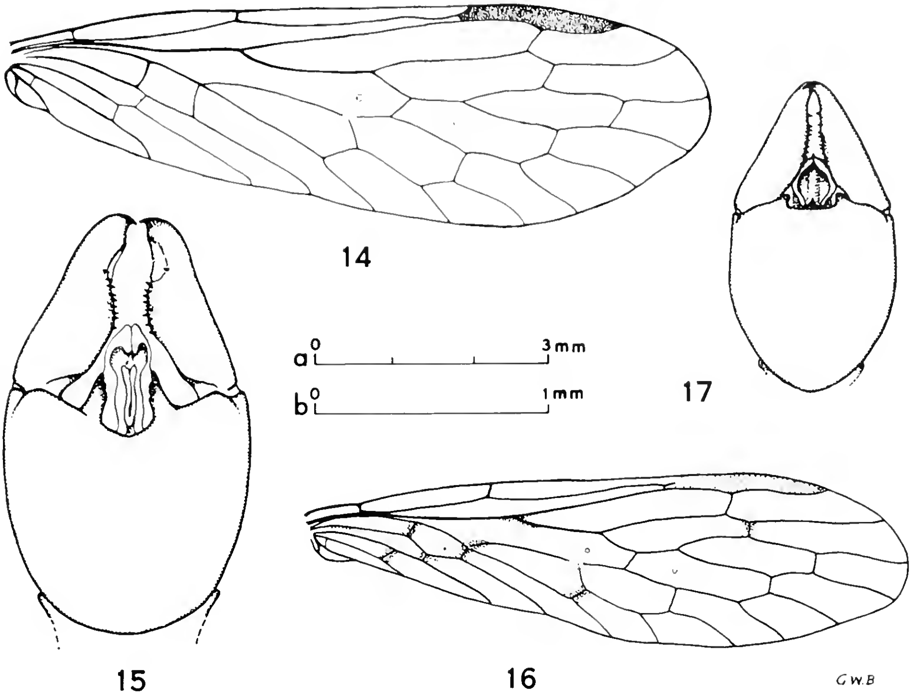
Specimens examined. ARGENTINA . NEUQUÉN: Pucará, Parque Nacional Lanín, - Dec. 1952, L. Schajovskoi (1 m.) (FMC); Lake Correntoso, 18-25 Nov. 1926, F. & M. Edwards (2 m.) (BMNH). RÍO NEGRO: Bariloche (San Carlos de Bariloche), 3 Nov. 1926 (1 m.) and 28 Nov. 1926 (1 f.), F. & M. Edwards (BMNH); Lake Gutierrez, 3-14 Nov. 1926, F. W. Edwards (1 m., holotype) (BMNH). CHILE . ARAUCO: San Alfonso above Caramávida, 16-17 Oct. 1969, O. S. Flint & G. Barria (7 m.) (USNM). AYSEN: Puerto Cisnes, - Feb. 1961, Luis Peña (1 f.) (KU). CHILOE: Isla Chiloe, Castro, 20-22 Nov. 1926, F. & M. Edwards (1 m.) (BMNH); Isla Chiloe, Dalcahue, 21-23 Oct. 1969, Flint & Barria (1 m., 3 f., 1 without abdomen) (USNM). OSORNO: Puyehue National Park, Paso Puyehue, 1360 m., 13 Feb. 1978, C. M. & O. S. Flint (1 m.) (USNM); Río Golgol, Cordillera Osorno, 300-400 m., 13-19 Mar. 1955, Luis E. Peña (1 f.) (KU); Río Chanlelfu, Puyehue, 250 m., 21 Nov. 1963, G. F. Edmunds no. 22 (1 f.) (Edmunds collection).

Nannochorista neotropica Navás, 1929

This is a relatively large *Nannochorista* (fore wing about 9-12 mm. long, compared to 6-9 mm. in other regional species). In fact, it is the largest known member of its family. It is readily recognized also by the amber or dark yellowish brown color of the wings. There is a conspicuous whitish thyridium at the first fork of the media (Fig. 14), and two easily noticeable nygmata (small, clear, circular thin spots in the wing membrane) occur in cells R and first R_5, with a less conspicuous one in cell second Cu_1 near the base of the wing.

In the male, abdominal segments 10 and 11 are relatively short and the dorsal notch between the basistyles quite shallow, so that the apex of tergum 11 is far short of the margins of the basistyles (Fig. 11). This is the condition in all the Australian Nannochoristas, as well, and in the single species of *Microchorista* in New Zealand. It differs strikingly, however, from the condition in *N. edwardsi* and *N. andina*.

Also in the male, there is a finger-like projection from the posterior margin of each basistyle,



Figs. 14-17. *Nannochorista* spp. 14. *N. neotropica*, right front wing, male holotype. 15. *N. neotropica*, genital bulb, male holotype, ventral aspect. 16. *N. edwardsi*, right front wing, male holotype. 17. *N. edwardsi*, genital bulb, male holotype, ventral aspect. Scales: a - figs. 14, 16, b - figs. 15, 17.

near the mid-line. In a corresponding position on the posteroventral margin of the basistyle there is an equally long, more densely sclerotized projection (Fig. 15). The ventral projections are somewhat flattened and blade-like, with the inner (mesal) edge more ventral than the outer edge. A tongue-like appendage of the aedeagus is usually visible between the two ventral projections.

The holotype, in the Museum National d'Histoire Naturelle, Paris, is a male that is generally intact and clean. It lacks the left front and left middle tarsi and parts of the left hind and right front tarsi and the right antenna beyond the 16th flagellomere. The type specimen is labelled "Perales (Chile)," which is probably Los Perales, about 40 km. southeast of Valparaíso. The locality is the headwaters of Río Marga, which is probably why Navás gave the type locality as "Marga-Marga."

Specimens examined. ARGENTINA. NEUQUÉN: Río Nonthue, Est. For. Pucará, 24 Feb. 1978, C. M. & O. S. Flint (8 m., 3 f.) (USNM); Pucará, Parque Nacional Lanín, - Nov. 1951 (1 f.), - Dec. 1951 (1 f.), 15 Feb. 1953 (1 m.), L. Schajovskoi (FMC). CHILE . ARAUCO: Caramávida, 17-19 Oct. 1969, O. S. Flint & G. Barria (1 m.); San Alfonso, above Caramávida, 16-17 Oct. 1969, Flint & Barria (1 f.) (both USNM). CAUTÍN: Fundo el Coigue, 500 m., about 29 km. NE of Villarica, 28 Feb. - 3 Mar. 1979, M. & D. Davis & B. Akerbergs (1 m., 1 f.) (USNM). CHILOE: Isla Chiloe, Dalcahue, 21-23 Oct. 1969, Flint & Barria (1 m., 1 f.) (USNM). LLANQUIHUE: Hornohuinco, 300 m., 11 km. SW of Lago Chapo, 29-31 Dec. 1981, D. R. Davis (1 m.) (USNM). MAGELLANES: Tierra del Fuego, Rusfin, 17-20 Nov. 1960, Luis E. Peña (1 m.) (KU). MAULE: Tregualemu, 600 m., 27 Jan. 1979, Luis E. Peña (1 f.) (USNM). ÑUBLE: Recinto, 4-6 Mar. 1968, O. Flint & L.

Peña (4 m., 1 f.); Las Trancas, 1300 m., 21 km. E of Recinto, near high waterfall, 17 Jan. 1979, M. & D. Davis & B. Akerbergs (1 m.); Las Trancas, 2 Mar. 1968, O. Flint & L. Peña (1 m., 2 f.); Las Trancas, Cordillera Chillan, 21-30 Nov. 1964, L. E. Peña (2 f.); Shangri-la, SW side of Volcán Chillan, 1600 m., 19- 21 Jan. 1979, D. & M. Davis & B. Akerbergs (1 f.) (all USNM); Las Cabras, S. of Volcán Chillan, 1480 m., 10-23 Dec. 1954, L. E. Peña (3 m., 1 f.); same but 19-23 Dec. (1 f.); same but 8-15 Feb. 1959 (1 m.); Recinto, Cordillera Ñuble, - Feb. 1953, L. E. Peña (1 m.); Las Trancas, Cordillera Chillan, 1200 m., 23-28 Feb. 1956, L. E. Peña (1 f.) (all KU). OSORNO: Puyehue National Park, 600 m., Ag. Calientes vic., D. & M. Davis & B. Akerbergs (1 f.) (USNM). TALCA: Alto de Vilches, 17-24 Oct. 1964, L. E. Peña (1 m.) (USNM). VALDIVIA: Rincon de Piedra, 30 m., about 20 km. SE of Valdivia, 24-25 Feb. 1979, D. & M. Davis & B. Akerbergs (1 m.) (USNM). VALPARAÍSO: Los Perales (=Perales) (headwaters of Río Marga), - Feb. 1921, Jaffuel & Pirion (1m., holotype) (Paris).

BIOGEOGRAPHY OF NANNOCHORISTIDAE

At present, four species of *Nannochorista* are known from southeastern Australia and three in southern South America. A single species of the closely related *Microchorista* (formerly *Choristella*) occurs on the South Island of New Zealand. This geographic distribution of the Nannochoristidae is in accord with the concept of an ancient Gondwanaland, the widespread fauna of which was fragmented as present-day land areas broke away by the process of continental drift. New Zealand having been isolated the longest, its nannochoristid species is expected to show the greatest phenetic divergence, which is the case (maculate fore wings, cell R_4 much shorter than in *Nannochorista* and not divided by a cross-vein, etc.).

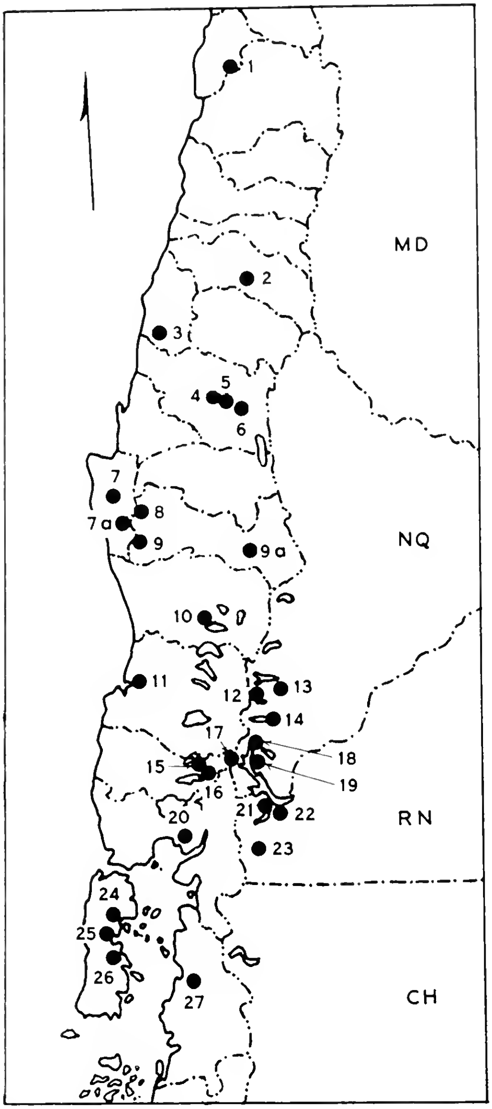
Toward the close of the Triassic Period, about 180 million years ago, Australia-Antarctica is supposed to have begun to separate from South America-Africa. Since the larvae of *Nannochorista* are confined to fresh-water streams and the adults have low vagility, it is reasonable to assume that the South American and Australian ancestors of living Nannochoristas became isolated from each other at that time.

When one invokes continental drift to explain present-day distributions, it is necessary to have reason to believe that the taxa involved are old enough to have participated in the geologic events described. Although there are no fossil species of *Nannochorista*, there are some similar genera known from the upper Permian strata of eastern Australia (Riek, 1953). Wings of *Nannochoristella reducta* Riek and *Neochoristella optata* Riek, both Nannochoristidae, are among many remains of Mecoptera of various families found in sediments perhaps 260 million years old, between Belmont and Warner's Bay, New South Wales.

The known ranges of the three extant South American species (or, as well, the four in Australia) do not suggest where or how these species arose. All three ranges overlap broadly, that of *Nannochorista neotropica* being the most extensive. It is probable, however, that the *andina-edwardsi* group (characterized by relatively prolonged terminal abdominal segments in the male) evolved in South America during or after the Cretaceous Period.

ACKNOWLEDGMENTS

I am grateful to Dr. Oliver S. Flint, Jr., for collecting and making available to me most of the specimens upon which this report is based; these are in the National Museum of Natural History, Washington, D.C. (USNM). My research has been supported by the National Science Foundation, most recently through grant DEB-80-22342. I also thank Dr. Luis E. Peña of Santiago, Chile, for collecting several specimens of *Nannochorista* now in the Snow Entomological Museum, University of Kansas (KU), and Dr. F. M. Carpenter, Museum of Comparative Zoology, Harvard University, for the loan of specimens from his collection (FMC). Dr. Edgar Riek and Dr. Courtenay Smithers kindly sent specimens of Australian species of *Nannochorista*, permitting useful comparisons. Finally, my appreciation is expressed to the curatorial staffs of the British Museum (Natural History), London (BMNH), and the Museum National d'Histoire Naturelle, Paris, for facilitating my study of type specimens and others in their care.



Map 1. Portion of Chile and adjacent Argentina from approximately 32°30'S to 44°00'S. Localities where *Nannochorista* has been found are numbered from north to south. For each, the province is named first, then the locality. Abbreviations (provinces of Argentina): CH - Chubut; MD - Mendoza; NQ - Neuquén; RN - Río Negro. Localities are given in the language of respective specimen labels, with geographic coordinates added for some.

1. Valparaíso, Los Perales, headwaters of Río Marga ("Marga Marga" in Navás, 1929).
2. Talca, Alto de Vilches.
3. Maule, Tregualemu (35°59'S, 72°48'W).
4. Ñuble, Recinto (36°48'S, 71°44'W)
5. Ñuble, Las Trancas, 21 km. E of Recinto, Cordillera Chillan.
6. Ñuble, Las Cabras, south of Volcán Chillan (36°54'S, 71°18'W); also "Shangri-la" on the southwest side of Volcán Chillan.
7. Arauco, Caramávida (37°41'S, 73°21'W); also San Alfonso, above Caramávida.

7a. Arauco, Elicura, Contulmo.

8. Malleco, Nahuelbuta National Park (37°48'S, 73°04'W).
9. Malleco, Contulmo National Park (38°00'S, 73°14'W).

9a. Malleco, Lonquimay, Icalma (38°49'S, 71°17'W).

10. Cautín, Fundo el Coigue, approx. 29 km. NE of Villarica.
11. Valdivia, Rincon de Piedra, approx. 20 km. SE of Valdivia.
12. Neuquén, Pucará Forestry Station (Estacion Forestal), Lanín National Park; also Río Nonthue, Estacion Forestal Pucará; also Lago Nonthue.
13. Neuquén, 5 km. SE of Lago Huechulafquén (lake is at 39°46'S, 71°28'W).
14. Neuquén, San Martin de los Andes (town, 40°18'S, 71°23'W); also Arroyo Culebra, 20 km. S of San Martin; Arroyo Rosales, near San Martin; Yuco, west of San Martin.
15. Osorno, Río Golgol, Cordillera Osorno (40°39'S, 72°21'W).
16. Osorno, Puyehue National Park.
17. Osorno, Paso Puyehue, Puyehue National Park.
18. Neuquén, Lake Correntoso.
19. Neuquén, Villa La Angostura (40°47'S, 71°40'W) vicinity, including Los Totoros and Río Totoral, 23 and 24 km. NW of Villa La Angostura, and Río Bonito, SE of town.
20. Llanquihue, Hornohuinco, 11 km. SW of Lago Chapo.
21. Río Negro, Lago Gutierrez (41°15'S, 71°24'W).
22. Río Negro, San Carlos de Bariloche (Bariloche in Kimmins, 1929).
23. Río Negro, 5 km. S of Río Villegas (41°34'S, 71°32'W).
24. Chiloe, Isla Chiloe, Dalcahue; also Río Butalcura, northwest of Dalcahue.
25. Chiloe, Isla Chiloe, Castro; also Piruquina (42°24'S, 73°48'W).
26. Chiloe, Isla Chiloe, Ahoni Alto, SE of Conchi; also Pio-Pio, 15 km. NW of Queilén.
27. Palena (formerly Chiloe), Termas Amarillo, about 30 km. SE of Chaitén.
28. Aysen (Aisen), Puerto Cisnes (44°45'S, 72°42'W) (not on map).
29. Magellanes, Tierra del Fuego, Rusfin (Russfin) (53°32'S, 68°54'W) (not on map).

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The International Standard Serial Number of this publication is US ISSN 0022-8850.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 54, No. 3, pp. 35-73 May 3, 1990

Bombus of México and Central America (Hymenoptera, Apidae)[1]

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Contents

ABSTRACT

This study consists of a taxonomic analysis and geographic account of the species of the genus *Bombus* in México and Central America. Keys are included to identify specimens to the specific level. Seven subgenera are recognized: *Fervidobombus,* the most diversified, with 11 taxa included in 10 different species; *Pyrobombus,* with three species; *Crotchiibombus* with two species; *Cullumanobombus, Brachycephalibombus, Dasybombus,* and *Robustobombus,* each with one species.

For each taxon, synonyms are listed and a description is given, as well as the following additional information: area of distribution, season of activity, localities where the specimens were collected, comments of taxonomic importance, and the museum where the type specimen is deposited. Also, for each taxon a map of the distribution, as well as drawings of the male genitalia and female sting capsule are provided.

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[1] Contribution number 1919 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66045-2119, U.S.A.

RESUMEN

Este estudio es un análisis taxonómico y de la distribución geográfica del género *Bombus,* en México y Centroamérica. El trabajo incluye claves para separar 20 diferentes taxones. En el área se encuentran siete subgéneros: a) *Fervidobombus,* el más diversificado con 11 taxones incluidos en 10 distintas especies, b) *Pyrobombus,* con tres especies entre las cuales se incluye la de más amplia distribución en el área, *B. ephippiatus;* c) *Crotchiibombus* con dos especies de distribución muy restringida; d) *Cullumanobombus, Brachycephalibombus, Dasybombus* y *Robustobombus* cada uno con una especie y cuyos ejemplares son colectados muy ocasionalmente.

Para cada taxón se incluye una descripción de reinas, obreras y machos, una lista de las sinonimias más importantes, el area de distribución, actividad estacional, localidad donde los ejemplares fueron colectados, comentarios de importancia taxonómica o geográfica y el museo donde los tipos se encuentran depositados. Para cada especie se proporciona un mapa del área de distribución, dibujos de los genitales del macho y del aguijón de la hembra. Por último, se sugieren estudios que son necesarios realizar para cada especie.

INTRODUCTION

The bumble bees are a group of social insects, most diversified and abundant in the temperate and cold regions of the Northern Hemisphere. The species of *Bombus,* together with those of *Psithyrus,* constitute the subfamily Bombinae of the family Apidae.

The genus *Bombus* contains approximately 200 species, all large robust, hairy bees. Diagnostic characters are: 1) malar space large, 2) jugal lobe of hind wing absent, 3) female with wide and shiny corbicular area (pollen basket) on hind tibia, 4) distal margin of hind tibia with a transverse row of stout spines and two antero-distal spurs, 5) males with gonocoxite and squama (upper gonostylus) sclerotized, 6) females without lateral carina on S-6, 7) females with two castes, 8) dense pile of black or brightly colored hair, especially on thorax and metasoma.

In the Western Hemisphere *Bombus* is found from almost as far north as there is land, on Ellesmere Island, to Tierra del Fuego, in the Antarctic Ocean. In the Old World these bees are found only north of the Sahara desert and west of Wallace's line. They are not present in the lowlands of southern Asia nor on the Australian continent, but have been introduced in New Zealand (Michener, 1974).

Bumble bees are much more common and diverse in temperate than in subtropical and tropical regions. South of the United States these bees are usually found in the south temperate zone or in highlands, although a few species occur in the lowland tropics.

In temperate regions bumble bees are seasonal; their colonies break up during the autumn, and the winter is passed by the inseminated gynes buried in the soil. Colonies are reestablished by single gynes next spring and broods of workers appear during summer. In late summer or autumn, depending on the species, the colony production shifts to reproductives; the young gynes after fecundation disperse (except in a few cases) and burrow in the soil to hibernate (Alford, 1975; Michener, 1974). In tropical regions, however, some species are active all year long, and the establishment of new colonies does not follow the synchronized pattern of temperate areas (Zucchi, 1973). In some cases the colonies can contain more than one egg-laying queen, and may survive for several years. Because México contains both temperate and tropical habitats, México and Central America are particularly interesting areas in which to study seasonal and associated behavioral ramifications of *Bombus* biology.

Few studies have been made on bumble bees in areas south of the United States. The most important and comprehensive is that by Franklin (1913) which, although excellent for its time and the material then available, contains many taxonomic errors and insufficient distributional data. In 1925 Frison published a contribution to the classification of the bumble bees of Central and South America; his work solved some taxonomic questions left by Franklin and added new species and distributional data for the already known taxa. Moure and Sakagami (1962) published an excellent work on the bumble bees of Brazil; they recognized six species of *Bombus* for that region and solved the problem of the polymorphic *B. atratus*, which varies from completely black to yellow banded. They gave an excellent account of the geographic distribution, habitats and variation of each Brazilian species. In 1973 Milliron initiated his controversial monograph of the Western Hemisphere bumble bees, which included the species found south of the U.S.A. However, his work was left incomplete and many taxa were never discussed. Some other papers dealing with mostly taxonomic aspects of the bumble bees of México and Central America are: Cockerell (1899, 1912, 1949), Fox (1893), Franklin (1907, 1915, 1954), Friese (1903, 1916, 1921), Frison (1928), Peters (1968), and Schwarz (1943).

The most complete studies of the nest structure, behavior and life cycle of a neotropical *Bombus* are those by Dias (1958), Sakagami et al. (1967) and Zucchi (1973) for *B. transversalis* and *B. atratus;* neither of these taxa is found in México or Central America. Besides these papers, few other data have been accumulated on the nesting behavior of neotropical bumble bees. Rau (1941) published some observations on *B. medius* in México. Michener and LaBerge (1954) discovered a huge colony of the same species in San Luis Potosí, which up to now is the largest colony of bumble bees ever found. Janzen (1971) studied an arboreal nest of *B. pullatus* in Costa Rica and discussed its ecological significance. Laverty and Plowright (1985) compared *B. ephippiatus* with temperate bumble bees.

The purposes of this work are to review the taxonomic status and distribution of bumble bee species in México and Central America, and to make them easily identifiable. The area of study (Mesoamérica) is in many ways unnatural, since several taxa of *Bombus* found on the Altiplano Mexicano are also present in the U.S.A. and Canada. Likewise, some species found in southern Central America also exist in the Andes of South America. However, the region is important for the diversification of flora and fauna (Halffter, 1964, 1976, 1987). In fact, almost three-fourths of the bumble bee species studied are restricted to Mesoamérica, and some taxa found to the north or south quite probably have evolved in and dispersed from this region (Franklin, 1954; Rzedowski, 1978).

LIST OF INCLUDED SPECIES

The species studied are listed below with page numbers of the accounts of each. Asterisks (*) indicate taxa restricted to México and Central America and the number sign (#), those that possibly evolved in the area but which now have a wider distribution. The remaining species are either Nearctic or Andean, and probably have recently penetrated México or Central America.

Subgenus Fervidobombus

*Bombus fervidus sonomae**, p. 48
*Bombus weisi**, p. 49
*Bombus trinominatus**, p. 51
Bombus pennsylvanicus sonorus#, p. 52
Bombus pennsylvanicus pennsylvanicus#, p. 52
*Bombus diligens**, p. 54
*Bombus steindachneri**, p. 55
*Bombus medius**, p. 56
*Bombus mexicanus**, p. 57
Bombus pullatus#, p. 58
*Bombus digressus**, p. 59

Subgenus Pyrobombus

Bombus huntii, p. 59
*Bombus ephippiatus**, p. 60
*Bombus wilmattae**, p. 62

Subgenus Cullumanobombus

B. rufocinctus, p. 64

Subgenus Crotchiibombus

Bombus crotchii, p. 64
*Bombus haueri**, p. 65

Subgenus Brachycephalibombus

*Bombus brachycephalus**, p. 65

Subgenus Robustobombus

Bombus volucelloides, p. 69

Subgenus Dasybombus

*Bombus macgregori**, p. 71

ACKNOWLEDGMENTS

I would like to thank the museum curators who kindly provided the specimens of *Bombus* for this study. I especially recognize the support and advice of C. D. Michener who helped me in different ways to finish and improve this work, thanks in part to National Science Foundation grant B5R87-16817. Many of Prof. Michener's ideas and comments are included in this study; also Dr. M. Ito's and Dr. P. Williams' insights in the group helped me to wrap up my knowledge on bumble bees.

I also wish to acknowledge a scholarship of the Universidad Nacional Autonoma de México (UNAM); in particular I thank Dr. José Sarukhan for his support in obtaining it. Finally, I dedicate this work to the memory of Dr. Raul MacGregor L., who extended his friendly hand when I needed it most.

MATERIAL AND METHODS

Bumble bee specimens were received for study from the following persons and institutions: Academy of Natural Sciences of Philadelphia; American Museum of Natural History; University of Arizona; University of California, Berkeley; California Academy of Sciences; Cornell University; University of California, Davis; Illinois Natural History Survey; Snow Entomological Museum, University of Kansas; Los Angeles County Museum of Natural History; Musum of Zoology, University of Michigan; Museum of Comparative Zoology, Harvard University; National Museum of Natural History (U.S.A.); University of California, Riverside; D. Roubik, Smithsonian Tropical Research Institute, Balboa, Panamá; Instituto de Biología and Facultad de Ciencias, Museo de Historia Natural de la Ciudad de México; M. Sousa, personal collection, México City; Instituto Nacional de Investigaciones Agrícolas (INIA), Chapingo, Edo. de México; Centro de Investigaciones Agrícolas de Oaxaca; Museum National d'Histoire Naturelle, Paris.

Several hundred specimens were also studied in the Canadian National Collection, Biosystematic Research Institute, Ottawa and in the National Museum of Natural History in Washington, D.C. Many data were also obtained from specimens in Los Angeles County Museum, University of California at Berkeley and at Davis, and the California Academy of Sciences during visits made in 1981.

The anatomical terminology used in this work follows Michener (1944, 1965). The list of abbreviations utilized throughout the work is as follows:

OOD—Ocellocular distance
IOD—Interocellar distance
UID—Upper Interocular distance
LID—Lower Interocular distance
T-n—Metasomal tergum number n
S-n—Metasomal sternum number n
Notum—Thoracic dorsum

A term not mentioned by Michener is the ocellar area (Moure and Sakagami, 1962; Richards, 1968), which refers to the unpunctured area around the ocelli (Figs. 3, 4). For the measurements of hair length given in the species descriptions, hairs were taken from the queen scutellum.

The male genitalia and female sting capsules were dissected and placed for 24 hours in KOH (10%), soaked in water for a few minutes and then placed in glycerin or dry mounted on cardboard points. Terms used for genitalic parts are indicated in the left hand column of Table 1. The other column shows an alternative nomenclature sometimes used. Sterna VII and VIII are illustrated in dorsal view (Figs. 10, 11); the male genital capsule dorsal views are on the left sides of the drawings and ventral views are on the right (Figs. 7-9). The illustrations of sting capsules are dorsal views of the rami; this is commonly referred to by bumble bee taxonomists as the anterior face of the sting (see Fig. 6).

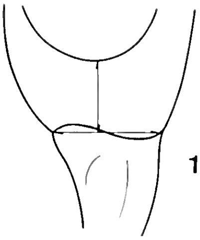
Table 1. Male genitalic terms used in bumble bee taxonomy.

Michener, 1944, and this paper	Richards, 1968
Gonobase	Cardo
Gonocoxite	Stipes
Squama	Squama
Gonostylus	Lacinia
Spatha	Spatha
Penis valve	Sagitta

Any distances given in the Imperial system (British) were transformed to metric units: e.g., altitudes given in feet, to meters. In the preparation of the maps, I found that many collecting localities were very close; consequently, one spot can sometimes cover more than one locality.

A frequent problem found with the Mexican locality data is erroneous state names. In most of these cases, the locality name was placed among those in the correct state. However, in some dubious situations a special notation is used, e.g., Durango: Potrerillos, "Sinaloa". This means that the Potrerillos mentioned is probably the one in Durango; however, a homonymous name exists in Sinaloa. This situation is very common in México, where the same name is used for places in different states. For example, Tuxpan is a name for cities in the states of Veracruz, Michoacán and Nayarit; Tlapa is a locality in Guerrero as well as Tabasco.

A different problem frequently found is incompletely recorded names of localities; in these cases the complete name is the one cited in this work. For example: I. de Matamores is a town in the state of Puebla whose complete name is Izucar de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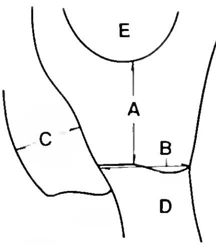

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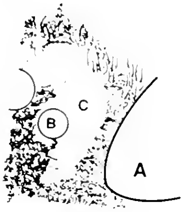

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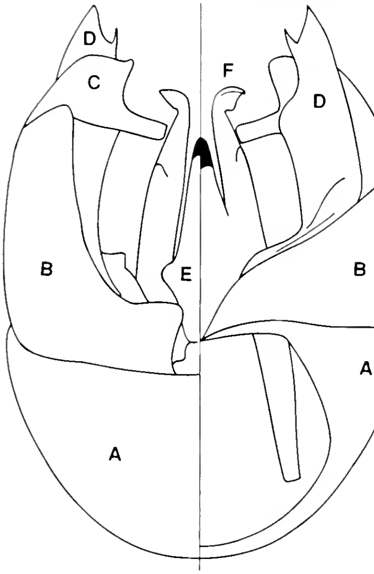

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Fig. 1. Lateral view of *B. brachycephalus* female head, front to the left. **Fig. 2.** Lateral view of *B. diligens* female head: A, malar space length; B, malar space width; C, clypeal protuberance width; D, mandible; E, lower part of the eye. *B. brachycephalus* is a *Bombus* with a short malar space; *B. diligens* is a species with a long malar space. **Fig. 3.** Ocellar area of *B. diligens*. **Fig. 4.** Ocellar area of *B. brachycephalus:* A, eye; B, lateral ocellus; C, ocellar area. *B. diligens* is a *Bombus* with poorly defined ocellar area; *B. brachycephalus* is a species with a well-defined ocellar area. **Fig. 5.** Diagrams of dorsal (left) and ventral (right) views of the male genitalia of a bumble bee: A, gonobase; B, gonocoxite; C, squama; D, gonostylus; E, spatha; F, penis valve head.

Matamoros. The correct name for San Cristóbal in Chiapas is San Cristóbal de las Casas.

For the topographic features and vegetation types the Spanish names have been used, with the corresponding names in English listed in Tables 2 and 3.

The lists of synonyms are for those relevant to the area of study; more complete lists can be found in Franklin (1912, 1913) and Milliron (1971, 1973a, b).

KEY TO THE SPECIES OF *BOMBUS* OF MÉXICO AND CENTRAL AMERICA

—Antennae with 10 flagellomeres; hind tibia with corbicula (pollen basket) well developed; metasomal apex pointed . . . . Females

—Antennae with 11 flagellomeres; hind tibia without corbicula; metasomal apex rounded . . . . Males

Females

1. Thorax with at least some yellow pile 2

—Thorax all black haired or with some white on pronotum 16

2. Sides of thorax pale haired 3

—Sides of thorax black haired, sometimes yellow on upper part of mesepisternum 9

3. Scutellum black haired or largely red in some queens 4

—Scutellum yellow or white haired, at least along posterior margin 6

4. Last two metasomal terga with a row of yellow hairs along posterior margin of each, especially evident on T-5; T-2 and T-3 laterally black haired . . . . *B. weisi*

—Last two metasomal terga all black or largely red, T-6 sometimes with a few pale hairs on posterior margin, never enough to make a row; T-2 and T-3 laterally reddish, black or yellow haired 5

5. T-1 yellow haired; T-2 mediobasally yellow, red or black laterally. Frequently collected . . . . *B. ephippiatus*

—T-1 and T-2 mediobasally black and laterally yellow. Known only from Guatemala and Costa Rica, rarely collected . . . . *B. digressus*

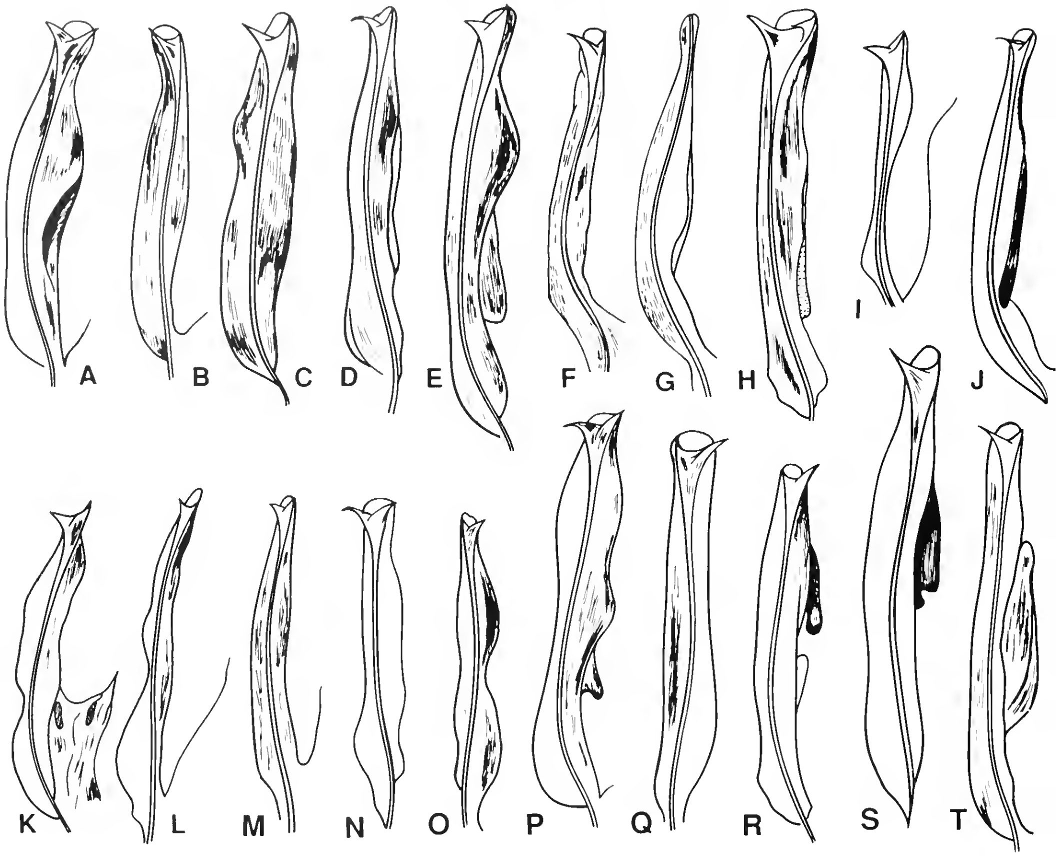


Fig. 6. Dorsal views of the rami of the sting (= anterior face of the sting, lateral to the left): A, *B. fervidus sonomae;* B, *B. weisi;* C, *B. trinominatus;* D, *B. pennsylvanicus;* E, *B. diligens;* F, *B. mexicanus;* G, *B. medius;* H, *B. steindachneri;* I, *B. digressus*; J, *B. pullatus;* K, *B. huntii;* L, *B. ephippiatus;* M, *B. wilmattae* (yellow form); N, *B. rufocinctus;* O, *B. wilmattae* (white form); P, *B. haueri;* Q, *B. brachycephalus* (red form); R, *B. volucelloides;* S, *B. crotchii;* T, *B. macgregori.*

6. Metasomal terga without reddish pile 7

—Metasoma with reddish pile covering at least one whole tergum (Altiplano Mexicano) 8

7. Anterior part of scutum with yellow pile; T-1 to T-4 with yellow pile. Rarely collected. Altiplano Mexicano . . . . *B. fervidus sonomae*

—Scutum with pile black; T-1 to T-3 mediobasally yellow or white and laterally yellow or black, T-4 black. Chiapas and Guatemala . . . *B. wilmattae*

8. Pile around antennal bases black, at most some pale hairs mixed with black ones; malar space wider than long (usually 50 wider). Rarely collected . . . . *B. rufocinctus*

—Pile around antennal bases yellow; malar space as long as wide or longer. More commonly collected *B. huntii*

9. T-2 black haired, sometimes with some pale hairs. 10

—T-2 yellow haired 12

10. Thorax with a black interalar band on posterior portion of scutum; scutellum yellow haired. (Gulf side of México and Atlantic side of Central America) . . . . *B. medius*

—Scutum without a black interalar band, posterior portion of scutum and scutellum concolorous. 11

11. Scutum and scutellum all yellow haired, metasoma black except T-3 yellow haired. Pacific side of México; frequently collected . . . . . .

. . . . *B. steindachneri*

—Anterior portion of scutum yellow, posterior part and scutellum black haired, metasoma black except T-3 and T-4 yellow haired. Altos de Oaxaca; rarely collected . . . . *B. trinominatus*

12. Scutellum and T-1 black or mainly black haired, no well defined black interalar band on scutum 13

—Scutellum and T-1 yellow haired, well defined interalar band 14

13. T-2 and T-3 yellow haired, T-4 black, scutellum and T-1 sometimes with an even mixture of black and yellow hairs. Altiplano Mexicano, frequently collected . . . . *B. pennsylvanicus pennsylvanicus*

—T-2 yellow, T-3 black and T-4 a variable mixture of black and yellow pile, scutellum and T-1 all black. Northern portion of Baja California Norte, not frequently collected . . . . *B. crotchii*

14. Last two metasomal terga and T-3 reddish haired. (Sierra Madre Occidental, not frequently collected) . . . . *B. haueri*

—Last two metasomal terga black, T-3 yellow 15

15. T-1 to T-4 yellow haired; mesobasitarsus almost four to four times as long as wide. Sierra Madre Occidental, not frequently collected. *B. fervidus sonomae*

—T-1 to T-3 yellow haired, T-4 black haired; mesobasitarsus three times as long as wide. Dry areas of the Altiplano Mexicano and Altos de Chiapas . . . . . . *B. pennsylvanicus sonorus*

16. Last two metasomal terga all black, at most with a few yellow hairs. 17

—Last two metasomal terga white or reddish haired 19

17. T-3 all yellow haired, rest of body black . . . . *B. mexicanus*

—Metasoma all black or T-3 with yellow laterally but never mediobasally and T-2 largely yellow haired 18

18. Body all black haired; ocellar area poorly defined; malar space as long as wide or longer. . . . . *B. pullatus*

—Body mainly black; queens with some yellow hairs on last metasomal terga, workers with conspicuous yellow pile laterally on T-2 and sometimes also with few yellow hairs laterally on T-3; ocellar area well defined; malar space as long as wide or wider. . . . . *B. brachycephalus*

19. Last three metasomal terga reddish

Table 2. Main topographic features of Mexico and Central America.

Sistema Montañoso de Baja California	Mountain System of Baja California
Desierto Sonorense	Sonoran Desert
Sierra Madre Occidental	Main Western Mountain Chain (Chihuahua to Jalisco)
Altiplano Mexicano	Mexican Plateau
Sierra Madre Oriental	Main Eastern Mountain Chain (Nuevo León to Puebla)
Eje Volcánico Transversal	Mexican Volcanic Belt (Nayarit to Veracruz)
Sierra Madre del Sur	Main Southern Mountain Chain (Jalisco to Oaxaca)
Sistema Montañosa del Norte de Oaxaca (Altos de Oaxaca)	Highlands of Oaxaca
Sierra del Norte de Centroamérica (Altos de Chiapas and Guatemala)	Highlands of Chiapas and Guatemala
Sierras y Mesetas Volcánicas de Centroamérica	Volcanic Chain and Highlands of Central America (North of Nicaraguan Lowland)
Cadena Volcánica del Pacifico y Depresion Nicaraguense	Pacific Volcanic Chain and Basin of Nicaragua
Sistema Montañoso del Sur de Centroamérica	Mountain System of Southern Central America (South of Nicaraguan Lowland)

haired 20

—Last four metasomal terga white haired 21

20. Ocellar area poorly defined (Fig. 3) and at most one ocellar diameter in width; malar space as long as wide or longer; apical metasomal pile bright reddish . . . . *B. diligens*

—Ocellar area defined (Fig. 4) and more than one ocellar diameter in width; malar space as long as wide or wider: apical metasomal pile orange-reddish . . . . *B. brachycephalus*

21. Known only from Guerrero, México. Inner thickening of sting with one sclerotized area (Fig. 6T). Not frequently collected . . . . . . *B. macgregori*

—Costa Rica to South America (Andean region). Inner thickening of sting with two sclerotized areas (Fig. 6R). Frequently collected . . . . *B. volucelloides*

MALES

1. Scutum black haired; if pronotum covered with pale hairs then metasomal apex reddish haired 2

—Scutum anteriorly, pronotum and usually scutellum pale haired 10

2. Sides of thorax black or dusky haired; metasomal T-1 and T-2 all black haired 3

—Sides of thorax yellow haired; metasomal T-1 and T-2 with at least some conspicuous yellow pile. 7

3. Last two metasomal terga all black . . 4

—Last two metasomal terga white or reddish haired, sometimes black pile mixed with white or reddish hairs. . . . 5

4. T-3 covered with yellow pile, rest of body black haired; squama wider than long, gonostylus projected beyond squama more than one squamal width, distal margin of gonostylus U-shaped (Fig. 8E). Central México to South America. . . . . *B. mexicanus*

—Body all black haired; squama as wide as long, gonostylus projected beyond squama less than one squamal width, distal margin of gonostylus J-shaped, outer corner more distal than inner one (Fig. 7D). Central America. . . . . . *B. pullatus*

5. Metasomal apex white haired; squama one and a half times as long as wide, gonostylus extending beyond squama more than one squamal width. Gonostylus with distal portion finger shaped, penis valves with basal portions parallel and distal portions convergent, penis valve head downward directed with a sharp lateral inward projection (Fig. 9A). Guerrero, México . . . . *B. macgregori*

—Metasomal apex reddish haired; squama as wide as long, gonostylus projecting beyond squama less than one squamal width. Central México to Central America 6

6. Ocellar area well defined (Fig. 4), ocelli more than one diameter below supraorbital line; malar space wider than long; squamal projection pointed downward and never reach-

Table 3. Types of vegetation in Mexico and equivalent names used by other authors, or equivalent types of vegetation in other areas.

Bosque Tropical Perennifolio	Tropical Rain Forest; Tropical Evergreen Forest; Lower Montane Rain Forest
Bosque Tropical Caducifolio	Deciduous Seasonal Forest; Dry Deciduous Forest; Short Tree Forest
Pastizal	Grassland; Short-Grass Prairie
Matorral Xerófito	Desert; Mesquite-Grassland (part); Arid Tropical Scrub (part)
Bosque de Encino	Oak Forest
Bosque de Pino	Pine Forest
Bosque Mesofilo de Montana	Cloud Forest

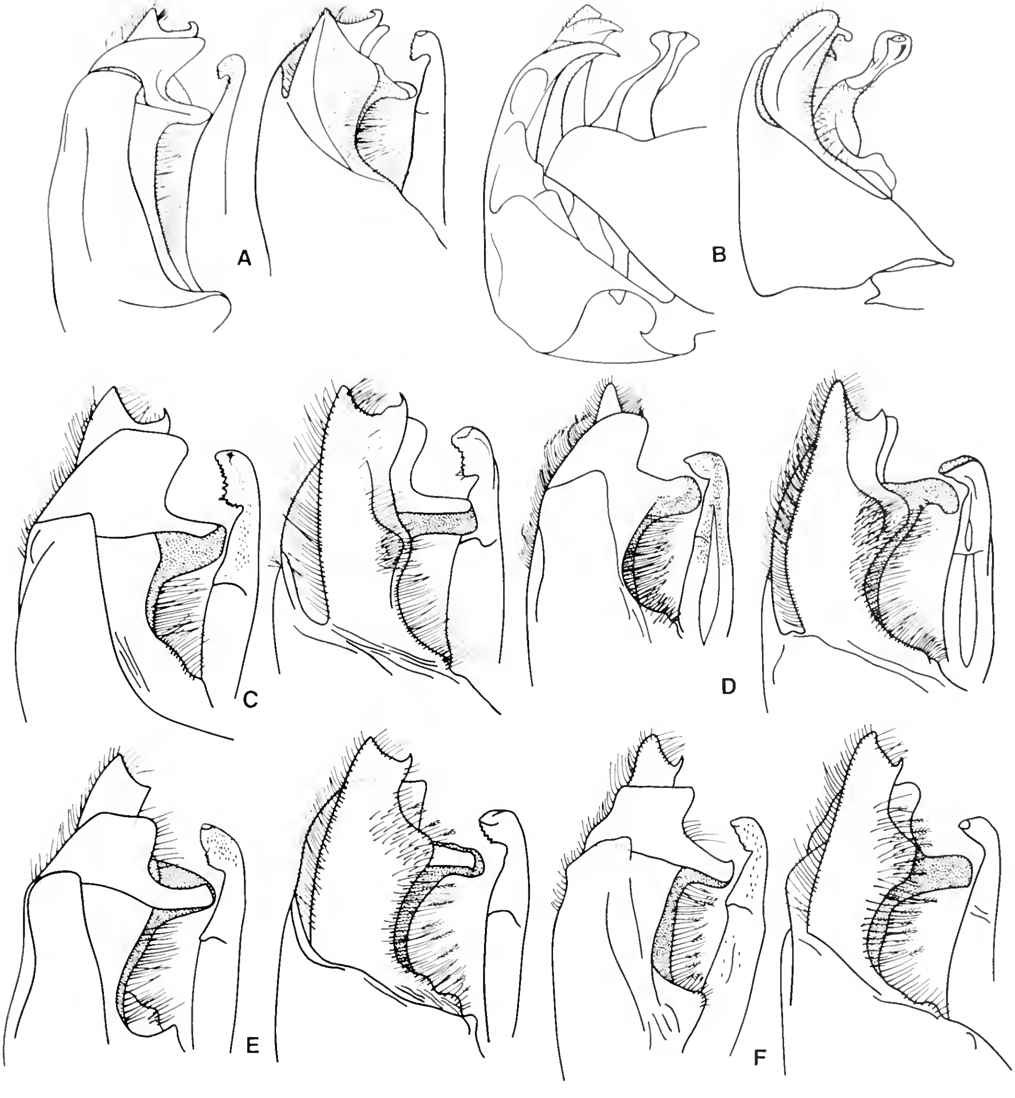


Fig. 7. Dorsal (left) and ventral (right) views of the male genitalia: A, *B. fervidus sonomae;* B, *B. digressus;* C, *B. diligens;* D, *B. pullatus;* E, *B. medius;* F, *B. steindachneri.*

ing outer margin of penis valve; distal margin of gonostylus truncated with outer corner more distal than inner one; penis valves convergent, penis valve head downward directed with a sharp lateral inward projection; gonostylus covered with hairs (Fig. 9C) . . . . *B. brachycephalus* (red form)

—Ocellar area poorly defined (Fig. 3), ocelli at most one diameter below supraorbital line; malar space longer than wide; squamal projection horizontal and beyond outer margin of penis valve; distal margin of gonostylus U-shaped; penis valves parallel, penis valve head outward directed without projections; gonostylus with outer-basal portion almost hairless (Fig. 7C) . . . . . *B. diligens*

7\. Last two metasomal terga black, each with a row of pale hairs on posterior margin. 8

—Last two metasomal terga all black haired 9

8. T-1 and T-2 yellow haired and posterior margins of T-6 and T-7 each with a row of yellow hairs; squama wider than long, with an outer-distal rounded prominence and an inner-distal sharp projection; gonostylus with inner margin straight; penis valves parallel, penis valve head directed outward (Fig. 8B). México to Central America. . . . . *B. weisi*

—T-1 and T-2 mediobasally black with latero-distal corners yellow haired; posterior margins of T-6 and T-7 each with a row of orange hairs; squama longer than wide, projecting inward as a broad hook; gonostylus inner margin with a subapical process directed inward and parallel to squama; penis valves strongly convergent, penis valve head directed slightly downward (Fig. 7B). Guatemala and Costa Rica. . . . . . *B. digressus*

9. Pronotum all black haired or with some yellow laterally. México to Panamá. . . . . *B. ephippiatus*

—Pronotum with a variable and conspicuous number of pale hairs on the center. Chiapas and Guatemala . . . . *B. wilmattae*

10. Sides of thorax black haired; T-1 black or black mixed with yellow pile 11

—Sides of thorax at least partially pale haired; T-1 mediobasally yellow, reddish or dusky haired 15

11. Scutellum and T-1 black or with a mixture of black and yellow hairs, T-3 and T-4 yellow haired 12

—Scutellum and T-3 yellow, T-1 and T-4 black haired. 14

12. T-2 black haired; squama wider than long, squamal projection not reaching outer margin of penis valve; gonostylus projecting beyond squama more than one squamal width; penis valve head without teeth; gonostylus inner prominence with a few and short (never beyond squamal projection) hairs (Fig. 8D). (Altos de Oaxaca, México) . . . . *B. trinominatus*

—T-2 yellow haired; squama as wide as long, squamal projection reaching outer margin of penis valve; gonostylus projecting beyond squama; penis valve head with teeth on outer margin; gonostylus inner prominence with abundant and long (as long as squamal projection) hairs (Fig. 8A, C) 13

13. Scutellum and T-1 yellow, at most with some black hairs on scutellum; clypeus moderately punctuate. Dry areas of the Altiplano Mexicano and Altos de Chiapas . . . . *B. pennsylvanicus sonorus*

—Scutellum and T-1 black or with an even mixture of black and yellow pile; clypeus strongly punctuate. Wet areas of the Altiplano Mexicano and Altos de Chiapas. . . . . *B. pennsylvanicus pennsylvanicus*

14. Scutum yellow haired; gonostylus distal margin with truncated outer corner more distal than inner one; gonostylus with a subapical spine-like process directed distally, gonostylus distal portion with a longitudinal subdivision; penis valve head elongated (Fig. 7F). Pacific coast of México . . . . *B. steindachneri*

—Scutum with a band of black hairs, rest of scutum yellow haired; gonostylus without any process and with distal margin U-shaped, distal portion not subdivided; penis valve head rounded (Fig. 7E). Gulf coast of México and Atlantic side of Central America . . . . *B. medius*

15. Sides of thorax entirely yellow haired; T-2 and T-3 reddish, whitish or ferrugineous; if T-3 black then T-2 mediobasally yellow and laterally black haired 16

—Sides of thorax bicolored, pale haired anteriorly, black haired posteriorly; T-2 and T-3 yellow or mediobasally bare or black haired and laterally yellow haired; if black pile on thoracic sides reduced to area below wing bases, then T-2 yellow and T-3 largely black. 19

16. T-2 and T-3 same color, T-4 concolorous or yellow haired 17

—T-2 mediobasally yellow and laterally black, T-3 black or at most with a yellow spot mediobasally, T-4 with black, at most a few yellow hairs mediobasally. [Squama longer than wide with two lobe-like protuberances on inner margin, gonostylus extending beyond squama by at most half squamal width (Fig. 9G).] Chiapas and Guatemala . . . .

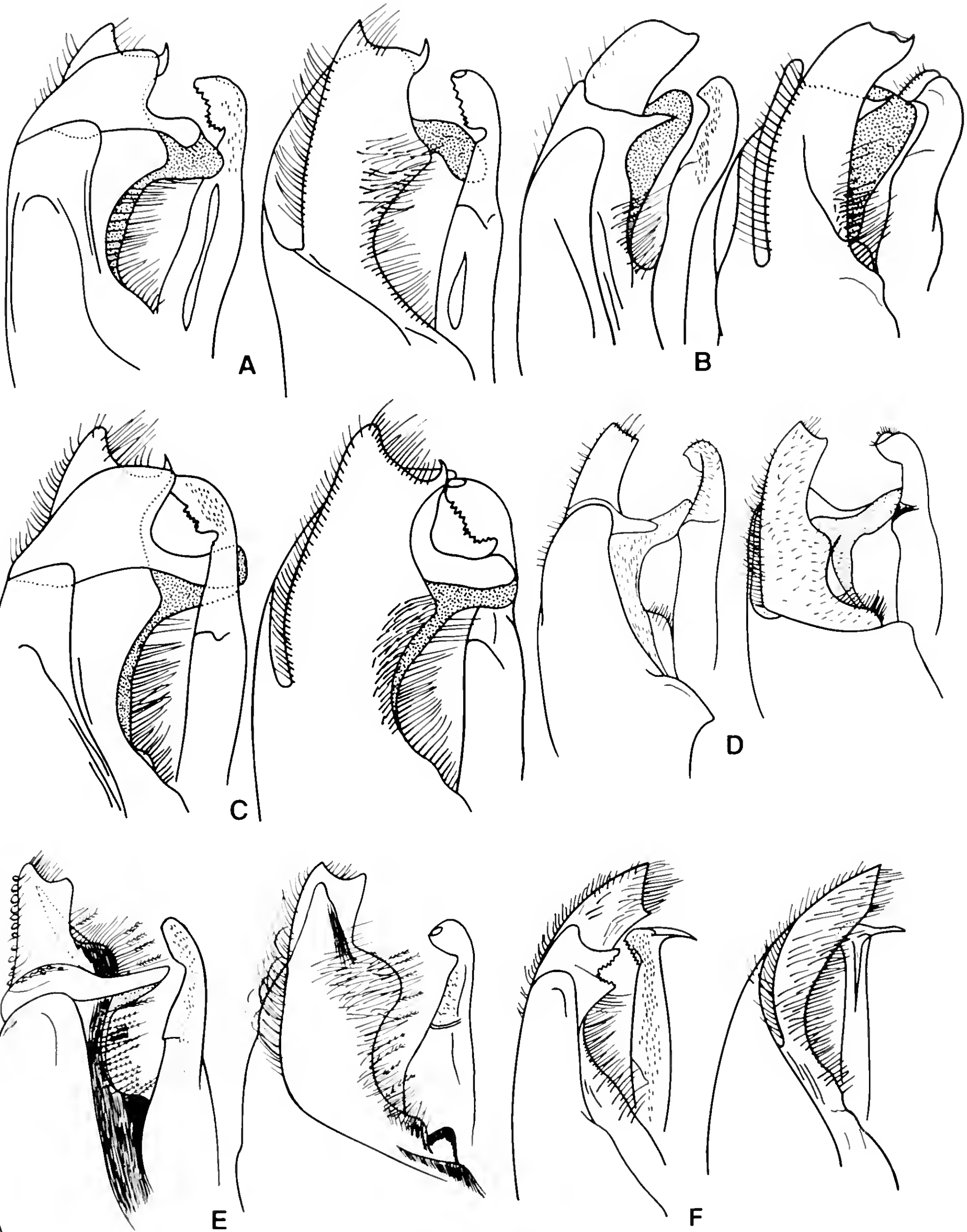


Fig. 8. Dorsal (left) and ventral (right) views of the male genitalia: A, *B. p. pennsylvanicus;* B, *B. weisi,* C, *B. pennsylvanicus sonorus;* D, *B. trinominatus;* E, *B. mexicanus;* F, *B. rufocinctus.*

. . . . *B. wilmattae* (yellow form)

17. T-2 and T-3 white haired. [Male genitalia as above.] Chiapas and Guatemala . . . *B. wilmattae* (white form)

—T-2 and T-3 reddish or ferrugineous haired 18

18. Scutum with a well defined interalar black band; T-1 yellow haired, T-2 and T-3 reddish, rest of metasoma black haired; squama longer than wide with one lobe-like prominence on inner margin, sometimes slightly subdivided; gonostylus projecting beyond squama by half squamal width; penis valves parallel, penis valve head pointed inward (Fig. 9E) . . . . *B. huntii*

—Scutum with a poorly defined interalar black band (black hairs around tegula mixed with yellow pile); T-1 to T-5 ferrugineous, rest of metasoma concolorous or a mixture of black and ferrugineous pile; squama wider than long with two sharp projections on inner margin, gonocoxite projecting beyond squama by more than one squamal width; penis valves slightly divergent, penis valve directed ventrally with sharp inward projection (Fig. 8F). . . . . . . *B. rufocinctus*

19. Metasoma except for last tergum yellow haired, sometimes black and yellow pile on T-3 and T-4 20

—Metasoma with last tergum and at least one more black haired 21

20. Ocelli two diameters below supraorbital line; eyes large and about twice as long as wide, almost covering genal area (genal width less than half eye width); S-7 distal portion covered with hairs (Fig. 10B); squama inner margin relatively straight, gonostylus distal margin truncate; penis valves slightly divergent, penis valve head ventrally directed with sharp inward projection; gonostylus with a subapical palm-like process, gonostylus distal portion not subdivided (Fig. 9D). Northern Baja California Norte, México . . . . *B. crotchii*

—Ocelli at most one diameter below supraorbital line; eyes normal, more than two times as long as wide, genal area normal (genal width approximately same as eye width); metasomal S-7 distal portion with a small lateral patch of hairs (Fig. 10D); squama projecting inward; gonostylus distal margin U-shaped; penis valves distal portions convergent, penis valve head projecting outward; gonostylus distal portion subdivided (Fig. 7A). Sierra Madre Occidental and Eje Volcánico Transversal of México . . . . *B. fervidus sonomae*

21. T-2 [also T-1] yellow haired, rest of metasoma black; squama longer than wide, squamal projection horizontally directed; gonostylus with a subapical palm-like process. [Penis valves divergent, penis valve head pointed inward (Fig. 9F).] (Costa Rica and Panamá to the Andean region) . . . . *B. volucelloides*

—T-2 mediobasally yellow and laterally black haired, or mediobasally hairless (appearing black) and laterally yellow haired; squama as wide as long; gonostylus without any process 22

22. T-1 all yellow, T-2 mediobasally yellow and laterally black, rest of metasoma black; squama with two lobe-like protuberances on inner margin; gonostylus projected beyond squama by half squamal width; penis valves basally parallel and distally convergent, penis valve head pointed inward (Fig. 9G). Chiapas and Guatemala . . . . . *B. wilmattae*

—T-1 dusky haired, T-2, T-3 and T-6 mediobasally bare or black haired, laterally yellow haired, T-4 and T-5 black haired; squama with a downward pointing projection; gonostylus beyond squama by one squamal width, penis valves basally divergent and distally convergent, penis valve head directed ventrally with sharp inward projection (Fig. 9C). Central México to Nicaragua . . . . *B. brachycephalus* (black form)

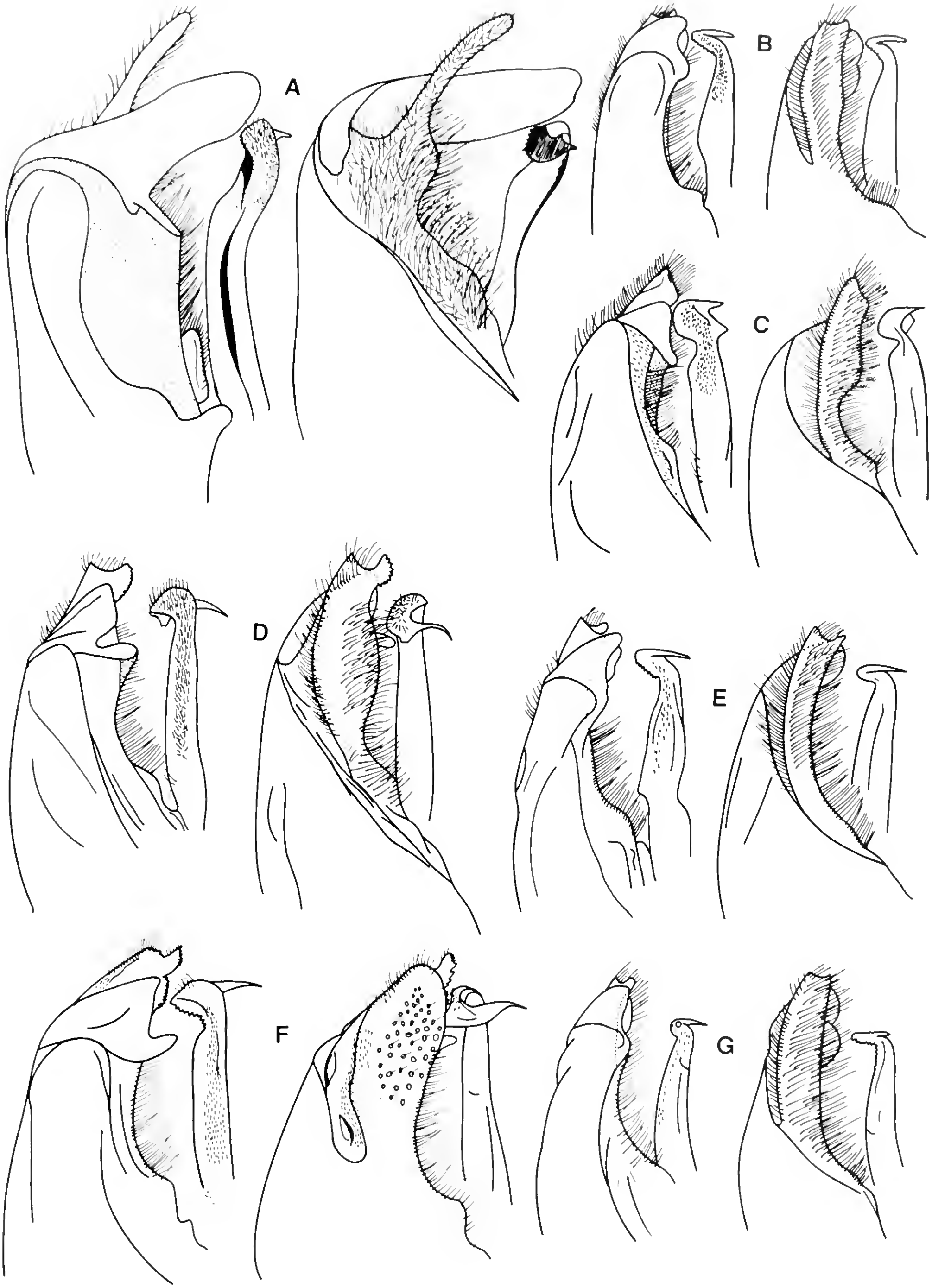


Fig. 9. Dorsal (left) and ventral (right) views of the male genitalia: A, *B. macgregori;* B, *B. ephippiatus;* C, *B. brachycephalus;* D, *B. crotchii,* E, *B. huntii;* F, *B. volucelloides;* G, *B. wilmattae.*

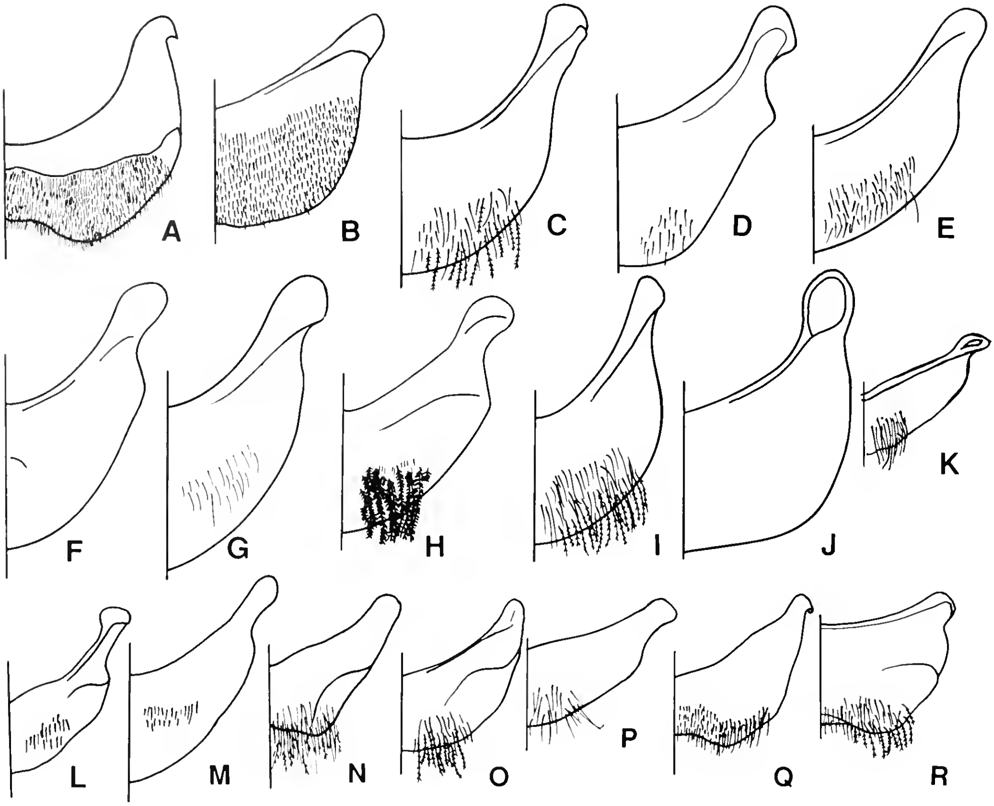


Fig. 10. Dorsal view of seventh metasomal sternum: A, *B. macgregori;* B, *B. crotchii;* C, *B. mexicanus;* D, *B. fervidus sonomae;* E, *B. pullatus;* F, *B. pennsylvanicus;* G, *B. diligens;* H, *B. medius;* I, *B. steindachneri;* J, *B. volucelloides;* K, *B. digressus* (redrawn from Laverty et al., 1984); L, *B. weisi;* M, *B. trinominatus;* N, *B. ephippiatus;* O, *B. wilmattae;* P, *B. huntii;* Q, *B. rufocinctus;* R, *B. brachycephalus.*

SPECIES ACCOUNTS

Bombus (Fervidobombus) fervidus sonomae Howard

(Figs. 6, 7, 10, 11; Map 7)

Bombus sonomae Howard, 1901: pl. 2, fig. 7.
Bombus (Bombus) sonomae; Franklin, 1913: 133.
Fervidobombus (Fervidobombus) sonomae; Skorikov, 1922: 154.
Bremus sonomae; Frison, 1925: 160.
Megabombus (Megabombus) fervidus sonomae; Milliron, 1973a: 160.

PILE: Dense, longest hairs 1.5 times length of tegula. Queen with body black except yellow on pronotum, anterior portion of scutum, scutellum and upper portion of mesepisternum, hence with a black interalar band; T-l to T-4 yellow. Workers with side of thorax predominantly yellow. Male almost completely yellow except black on head, interalar band (usually narrow), and T-7.

QUEEN: Length 22 mm. UID 2.9 mm, LID 3.3 mm. Ocelli just below supraorbital line. OOD 2.5 times lateral-ocellar diameter. IOD approximately the same as OOD. Clypeus moderately punctate, upper margin and sides with more dense and coarse punctations; middle disk with sparse and fine ones, especially near lower margin. Clypeus in profile protuberant for distance at most width of malar space. Malar space 15 to 20 longer than wide. Thoracic width between wing bases 6.5 mm. Mesobasitarsus four times as long as wide. T-2 width 10 mm.

WORKER: Similar to queen except as follows: Length 12 mm, lateral ocelli touching supraorbital line. Clypeus less densely punctate. Other parts proportionally reduced in size.

MALE: Similar to queen except as follows: Length 17 to 19 mm. UID 2.3 mm, LID 2.5 mm. Malar space 50 longer than wide.

DISTRIBUTION: This taxon is restricted to the Sierra Madre Occidental and central portion of the Eje Volcánico Transversal. Its distribution and altitudinal range correspond with *Pinus* forest. I have only seen specimens collected during July and August. However, Milliron (1973a) comments that they are found until October.

They might fly during September and October, and also in June, but they must be rare. The vertical distribution is from 2300 to 2700 m.

LOCALITIES: Chihuahua: San José Babicora, Madera, Santa Clara, Meadow Valley (Río Piedras Verdes, 6 km S Colonia García). Durango: Coyotes, El Salto, Otinapa. Distrito Federal: Ciudad de México. Puebla: Canadá Morelos (7 km SE).

COMPARATIVE COMMENTS: This form is related to *B. fervidus fervidus* and *B. fervidus californicus,* from which it is isolated by the dry area along the northern border of Chihuahua. The subspecies *B. f. californicus* is found mainly in the coastal valleys from California (U.S.A.) to British Columbia (Canada) (Stephen, 1957). *B. f. fervidus* is found almost throughout the U.S.A. and southern portions of Canada (Mitchell, 1962). Milliron (1973a) considers these two subspecies to intergrade in the western U.S.A.; however, Thorp et al. (1983), based on Hobbs (1966) observations, separates them as different species. The pile coloration of *B. f. sonomae* is sometimes similar to that of *B. f. fervidus;* in fact Frison in 1924 recorded one specimen from Delaware as *sonomae,* an assignment that was clearly wrong (Milliron, 1973a). The status of *sonomae* as a subspecies of *fervidus* or as a distinct species cannot readily be decided since the known ranges do not meet. For the present, because of the similarity to *fervidus,* I follow previous authors in considering them subspecies.

This taxon can sometimes be mistaken for *B. p. sonorus.* They can be separated by the male genitalia and because the females have the pile of T-4 always yellow in *B. f. sonomae* but black in *B. p. sonorus.* This form was described by Franklin in 1913, but had been named by Howard in an illustration years before.

TYPE: In the National Museum of Natural History, Washington. Type locality: Meadow Valley, Chihuahua, México.

Bombus (Fervidobombus) weisi Friese
(Figs. 6, 8, 10, 11; Map 1)

Bombus laboriosus Smith, 1861: 153.
Bombus weisi Friese, 1903: 254 (female only).
Bombus nigrodorsalis Franklin, 1907: 90.
Bombus ephippiatus var. *laboriosus;* Franklin, 1907: 91.
Bombus nigrodorsalis var. *laticollis* Franklin, 1907: 91.

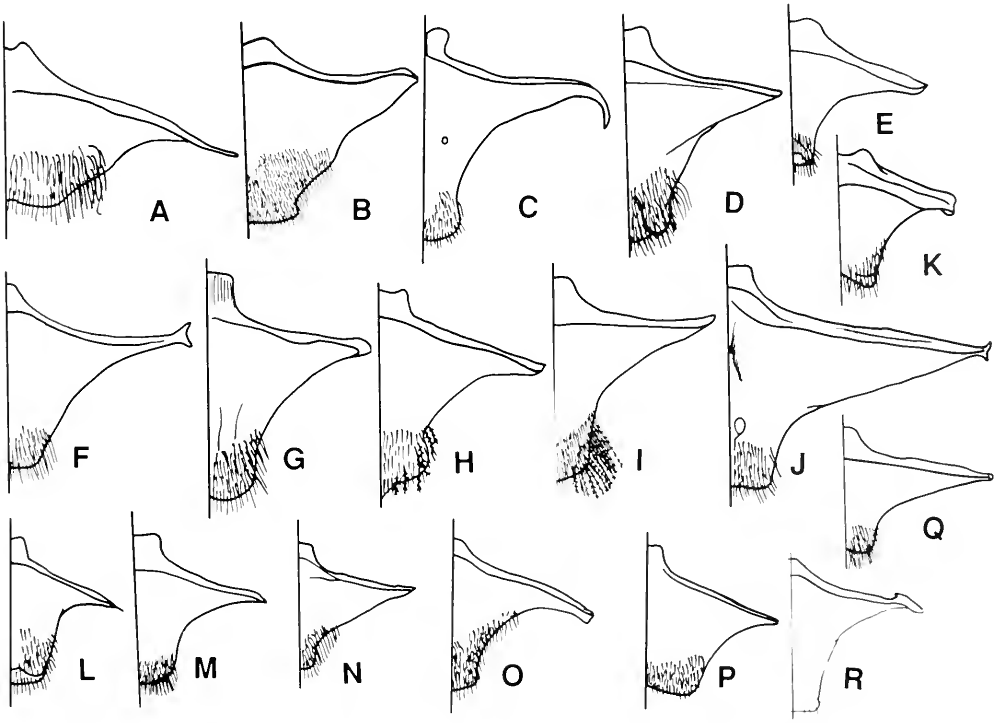


Figure 11. Dorsal view of eighth metasomal sternum: A, *B. volucelloides;* B, *B. macgregori;* C, *B. fervidus sonomae;* D, *B. pullatus;* E, *B. wilmattae;* F, *B. diligens;* G, *B. mexicanus;* H, *B. medius;* I, *B. steindachneri;* J, *B. pennsylvanicus;* K, *B. ephippiatus;* L, *B. weisi;* M, *B. trinominatus;* N, *B. rufocinctus;* O, *B. crotchii;* P, *B. brachycephalus;* Q, *B. huntii;* R, *B. digressus* (redrawn from Laverty et al., 1984).

Bombus ephippiatus var. *montezumae* Cockerell, 1908: 344 (nomen novo for *B. laboriosus* Smith, 1861, nec Fabricius, 1805, nec Say, 1837).
Bombus (Bombus) nigrodorsalis; Franklin, 1913: 98.
Bombus (Bombias) weisi; Franklin, 1913: 148 (female only).
Bombus (Bombus) montezumae; Franklin, 1913: 95.
Fervidobombus (Fervidobombus) nigrodorsalis; Skorikov, 1922: 154.
Fervidobombus (Fervidobombus) montezumae; Skorikov, 1922: 153.
Bremus nigrodorsalis; Frison, 1925: 150.
Bombus mateonis Cockerell, 1949: 487.
Megabombus nigrodorsalis; Milliron, 1962: 731.
Megabombus (Megabombus) nigrodorsalis nigrodorsalis; Milliron, 1973a: 212.
Megabombus (Megabombus) nigrodorsalis montezumae; Milliron, 1973a: 216.

PILE: Dense, longest hairs 2.5 times length of tegula. Both sexes yellow but black on head, posterior margin of pronotum, scutum, middle of scutellum and T-4 to T-6; sometimes also black on sides of scutellum and T-3; yellow hairs on pronotum varying from few in center of anterior margin to a line along margin; also yellow hairs on posterior margins of T-5 and T-6. Queen with mixture of long black hairs and short whitish plumose ones above antennae, and with yellow hairs on vertex; sometimes hairs on T-1 to T-3 reddish. Some workers with whitish hairs on clypeus, intermixed with longer black ones. Male with whitish hairs longer, usually as long as black ones, also present below antennae and along inner margin of eye; in few cases whitish hairs on upper portion of clypeus; hairs of T-7 usually reddish; some specimens with T-4 completely yellow, sides of T-3 black as in some queens.

QUEEN: Length 17 to 18 mm. UID 2.7 mm, LID 3.1 mm. Ocelli just below supraorbital line. OOD two times lateral ocellar diameter. IOD approximately the same as OOD. Clypeus strongly punctate on upper margin and sides; middle disc weakly punctate to smooth. Clypeus in profile protuberant for distance at most width of malar space. Malar space as wide as long. Thoracic width between wing bases 7.0 mm. Mesobasitarsus little more than three times as long as wide. Width of T-2 10 mm.

WORKER: Similar to queen except as follows: Length 12 to 15 mm; clypeus with smooth clypeal disc larger than in queen to absent (i.e., completely punctuate); malar space as wide as long to 20 wider. Other parts proportionally reduced in size.

MALE: Similar to queen except as follows: Length 12 mm. UID 2.0 mm, LID 2.3 mm. Ocelli on supraorbital line. OOD almost three times lateral ocellar diameter. Malar space 10 to 20 wider than long. Mesobasitarsus four times as long as wide.

DISTRIBUTION: This species is found in the Pacific Coast mountains of México (Sierra Madre Occidental, Sierra Madre del Sur, Sierra Madre de Chiapas), Eje Volcánico Transversal, southern portion of the Altiplano Mexicano, and Sierra Madre Oriental; also in mountains of Guatemala, Honduras and Costa Rica. This distribution corresponds to various vegetational zones: Matorral Xerófito, Bosque Espinoso, Pastizal, Bosque Tropical Caducifolio and Bosque de Pino y Encino (Rzedowski, 1978). I believe this species is more frequently found in the last two types of vegetation, especially pine forest. However, it can also be found even in very dry areas like the Sierra de Juárez in Oaxaca (collected during the wet season, July to August).

I have studied specimens collected from January to November in the Sierra Madre Occidental and the Eje Volcánico Transversal. For the Sierra Madre del Sur, Altos of Chiapas and Guatemala, Honduras and Costa Rica, I have records from February to December. For the Eastern portion of the Altiplano Mexicano and Sierra Madre Oriental (San Luis Potosí and Hidalgo), I have seen few specimens, all collected in August and September. Even though flying almost all year long, this species is not frequently collected.

The altitudinal distribution is from 2000 to 3000 m in the Sierra Madre Occidental and the Eje Volcánico Transversal. For the Sierra Madre del Sur, Chiapas and Guatemala I have records from 1800 to 2500 m; for San Luis Potosí and Hidalgo, 1300 and 1400 m.

LOCALITIES: CHIHUAHUA: Meadow Valley (Río Piedras Verdes, 9 km S Colonia García). SINALOA: Los Reyes. DURANGO: El Salto, Huichichilas, Navios. JALISCO: Mazamitla. MICHOACÁN: Zacapu, Patzcuaro. ESTADO DE MÉXICO: 39 km W Toluca, W slope of Popocatépetl, San Juan Tezontla. MORELOS: Cuautla, Zempoala, La Pera (km 55 hwy México-Cuernavaca), Huitzilac, Tres Cumbres, Coahuila. DISTRITO FEDERAL: Atzcapotzalco, Desierto de los Leones, Pedregal de San Angel. SAN LUIS POTOSÍ: Xilitla. HIDALGO: Zimapan, Jacala. TLAXCALA: Tlaxcala. VERACRUZ: E slope Volcán Citlaltépetl (Pico de Orizaba). PUEBLA: Canadá Morelos. OAXACA: Nochixtlán, San José del Pacifico, Sierra de Miahuatlán, Ixtlán de Juarez, San Juan Teziutlán. CHIAPAS: Motozintla, La Unión, Las Margaritas, Chanal, Comitán, San Cristóbal de las Casas, Tenejapa, Sibaktejel. GUATEMALA: Monte Pacaya, San Cristóbal. HONDURAS: Monte Uyacu. COSTA RICA: Tres Ríos (Cartago).

COMPARATIVE COMMENTS: Franklin in 1913 considered *B. weisi* (= *nigrodorsalis*) and *B. montezumae* to be two different species, and the most primitive of all New World *Bombus.* Milliron (1973a) regarded them as two different subspecies of *Megabombus nigrodorsalis,* which together with *M. digressus* and *M. trinominatus* formed his group nigrodorsalis.

I have not found any characters that justify the specific or subspecific separation of *weisi* from *montezumae,* except for the yellow band across the anterior portion of the thorax (pronotum and anterior margin of scutum). On the contrary, I have seen a range of color variation from completely black (*weisi*) to specimens with a wide yellow band on the pronotum and anterior portion of scutum (*montezumae*). Some of these individuals even fit the extreme yellow color variant called *laticollis* by Franklin (1907). Therefore, I am considering *weisi* and *montezumae* the same taxon, a viewpoint which agrees with the final opinion of Franklin (1915).

TYPES: The type of *B. weisi* is a female; moreover, the female was described first by Friese. The type, from San Carlos, Costa Rica, is in the Zoologisches Museum der Humboldt Universität, Berlin (Milliron, 1960). The types of *nigrodorsalis, laticollis* and *mateonis* are in the National Museum of Natural History, Washington. The type of *laboriosus* (= *montezumae*) is in the British Museum (Natural History), according to Milliron (1973a). The type locality of *nigrodorsalis* is Headwaters Río Piedras Verdes, Chihuahua; the type locality of *montezumae* is Oaxaca, México.

Bombus (Fervidobombus) trinominatus Dalla Torre

(Figs. 6, 8, 10, 11; Map 1)

Bombus modestus Smith, 1861: 153 (nec Eversmann, 1852).
Bombus trinominatus Dalla Torre, 1890: 139.
Bombus (Bombus) trinominatus; Franklin, 1913: 83.
Pratobombus trinominatus; Skorikov, 1922: 158.
Megabombus (Megabombus) trinominatus; Milliron, 1973a: 220.

PILE: Dense, longest hairs three times length of tegula. Black except yellow on posterior margin of vertex, pronotum, anterior part of scutum, T-4 and posterior margin of T-3; queen head above antennae with mixture of short, whitish, plumose hairs and long, black, simple ones; some queens with whitish hairs on middle of mesepisternum. Scutellum and upper portion of mesepisternum with mixture of yellow and black hairs; sometimes yellow predominant on scutellum, hence with a black interalar band on scutum. T-5 with a line of yellow hairs along posterior margin; T-6 almost all reddish, a few reddish hairs also on posterior margin of corbicula and metabasitarsus. Worker similar to queen, but without whitish hairs on face or body. Male head with whitish hairs more evident. Pronotum and scutum yellow haired, scutellum and sides of thorax mainly black. T-l, T-2 and basal portion of T-3 black, T-4 to T-6 mainly yellow.

QUEEN: Length 18 to 20 mm. UID 2.9 mm, LID 3.0 mm. Ocelli just below supraorbital line. OOD two times lateral ocellar diameter. IOD approximately the same as OOD. Clypeus sparsely punctate, punctation mainly near upper margin, sides, and lower corners. Clypeus in profile protuberant for distance at most two-thirds width of malar space. Malar space 10 wider than long. Thoracic width between wing bases 7.0 mm. Mesobasitarsus little more than three times as long as wide. T-2 width 10 mm.

WORKER: Similar to queen except as follows: Length 10 mm. Ocelli on supraorbital line, malar space 25 wider than long. Other parts proportionally reduced in size.

MALE: Length 12 mm. UID 2.2 mm, LID 2.3 mm. Ocelli on supraorbital line. OOD one and a half times lateral ocellar diameter. IOD approximately the same as OOD. Clypeus uniformly punctate. Clypeus in profile protuberant for approximately malar space width. Malar space as long as wide. Thoracic width between wing bases 4.5 mm. Mesobasitarsus four times as long as wide. T-2 width 7.0 mm.

DISTRIBUTION: This species is restricted to the Altos de Oaxaca, where it is probably associated with the Bosque de Pino (Rzendowski, 1978).

All the specimens I have seen were collected from July to September, which is the wet season in the area. The altitudinal distribution is 2700 to 2850 m.

LOCALITIES: OAXACA: 20 km NE Ixtlán de Juarez, 30 km NE Guelatao, 30 km N Puerta del Sol.

COMPARATIVE COMMENTS: Franklin in 1913 considered *B. trinominatus* to be a member of the pratorum group, which today corresponds to the subgenus *Pyrobombus*. Milliron (1973a) placed this species in the subgenus *Megabombus;* together with *B. nigrodorsalis* (=*weisi*) and *B. digressus,* it formed his nigrodorsalis group. I place this species in the subgenus *Fervidobombus* because of the male genitalia, sting capsule and the external morphology of males and females.

Milliron's separation of the nigrodorsalis group from other species of *Fervidobombus* was made without specifying any characters. The male genitalia of *B. weisi* are the smallest of the *Fervidobombus* species found in México and Central America, followed by those of *B. trinominatus*. Some other features distinguish these two taxa from the other species, particularly the morphology of the gonostylus. However, I think these differences are not important enough to justify a group by themselves for these taxa. A cladistic analysis made by Williams (1985), based on the male genitalia, retains *nigrodorsalis* (=*B. weisi*) in the subgenus *Fervidobombus*.

On biological characters other than morphology, *B. trinominatus* and *B. weisi* are also closely related. Both are high altitude taxa presumably found in pine vegetation. The coloration of males and females is similar, and queens of both are the smallest of the Mexican *Fervidobombus*. They are sympatric in Oaxaca, the area where *B. trinominatus* is endemic. I consider *B. trinominatus* as an offshoot of *B. weisi*.

On the other hand, *B. digressus* is very different from the two taxa mentioned above (see comments under *B. digressus*). Milliron probably placed this species together with the above mentioned taxa because he did not have a male.

B. trinominatus can be confounded with *B. pennsylvanicus pennsylvanicus* from which it is separable by the following characters: the hairs of T-2 and the anterior margin of T-3 are all black in *B. trinominatus* but yellow in *B. p. pennsylvanicus*. Moreover, the queens of *B. trinominatus* are always smaller than those of *B. p. pennsylvanicus*, under 20 mm in contrast to over 20 mm, usually about 25 mm for the latter species.

TYPE: The type of *B. modestus* is in the British Museum (Natural History) according to Milliron (1973a). Type locality: Oaxaca, México. This probably means the state of Oaxaca, not the city, since other records are at higher altitude and further north than the city of Oaxaca.

Bombus (Fervidobombus) pennsylvanicus sonorus Say
(Figs. 6, 8, 10, 11; Map 4)

Bombus sonorus Say, 1837: 413.
Bombus (Bombus) sonorus; Franklin, 1912: 407.
Bombus (Fervidobombus) sonorus; Skorikov, 1922: 154.
Megabombus (Megabombus) pennsylvanicus sonorus; Milliron, 1973a: 196.

PILE: Dense, longest hairs as long as tegula. Both sexes black except hairs yellow on pronotum, anterior portion of scutum, and scutellum; hence with a black interalar band; T-1 to T-3 also yellow. Males with whitish plumose hairs on clypeus, above and below antennae and on anterior portion of vertex; also with yellow hairs on upper portion of mesepisternum and T-4; usually reddish ones on sides and posterior margins of T-6 and T-7.

QUEEN: Length 20 to 25 mm. UID 3.2 mm, LID 3.5 mm. Lateral ocelli on supraorbital line, middle ocellus just below. OOD 2.0 to 2.5 times lateral ocellar diameter. IOD approximately same as OOD. Clypeus moderately punctate. Clypeus in profile protuberant for distance at most half width of malar space. Malar space 10 to 15 wider than long. Thoracic width between wing bases 8.0 mm. Mesobasitarsus little more than three times as long as wide. T-2 width 12 mm.

WORKER: Similar to queen but smaller, length 11 to 18 mm. Parts proportionally reduced in size.

MALE: Similar to queen except as follows: Length 13 to 22 mm. UID 2.0 to 2.4 mm, LID 2.4 to 2.7 mm. Clypeus protuberant for two-thirds to three-fourths width of malar space. Thoracic width between wing bases 6.0 mm. Mesobasitarsus almost four to 4.5 times as long as wide. T-2 width 6.0 to 8.0 mm.

DISTRIBUTION AND COMPARATIVE COMMENTS: See *Bombus pennsylvanicus pennsylvanicus*.

LOCALITIES: BAJA CALIFORNIA NORTE: Ensenada, Bahía de Todos los Santos. BAJA CALIFORNIA SUR: La Paz, Mulege, San Marcos, Comondu, Boca de la Sierra, San Antonio, Rancho el Coyote, Bahía de Concepción, La Burrera, Las Animas (Sierra Laguna), San Ignacio, Las Cruces (near La Paz), Los Frailes. SONORA: Pitiquito, Guaymas, Isla Tiburón. CHIHUAHUA: Pedernales, Parral, Chihuahua, Meoquí, Maderas, Delicias, Terrero, Santa Barbara, Catarinas, Ciudad Juárez, Ojo de Laguna. DURANGO: Nombre de Dios, Yerbanis, San Juan del Río, Ciudad de Durango, Palos Colorados, El Tascate, El Palmito, El Salto, Navios, Tlahuilo. COAHUILA: Monclova, San Pedro de las Colonias, Saltillo, Cabos, Cuesta, La Muralla, Zaragoza. ZACATECAS: Sain Alto, Fresnillo. NUEVO LEÓN: Galeana, Villa Santiago, Monterrey, Iturbide, Arroyo, Juanito, La Soledad. TAMAULIPAS: Ciudad Victoria. SAN LUIS POTOSÍ: Cedral, Ciudad del Maíz, San Luis Potosí. HIDALGO: Actopan, Jacala, Huesca, Dolores, Venados. QUERETARO: Peña Miller, Vizarron, Peña Blanca, Higuerillas. AGUASCALIENTES: Aguascalientes (10 km E). JALISCO: Villa Hidalgo, Guadalajara, Encarnacion de Díaz, Mazamitla, Pegueros, Ajijic. MICHOACÁN: Tuxpan, Quiroga, Uruapan, Pátzcuaro, Zamora, Morelia, La Huerta, La Picada, Río San Lorenzo. ESTADO DE MÉXICO: Chapingo, San Miguel Texmelucan, Ecatepec, Toluca, Texcoco. DISTRITO FEDERAL: Pedregal San Angel, Tacubaya, Xochimilco, Coyoacan, Chapultepec. MORELOS: Cuernavaca. PUEBLA: Puebla. VERACRUZ: Jalapa (Punta Clavijero). CHIAPAS: Tuxtla Gutiérrez. GUATEMALA: Ruinas de Quirigua.

TYPE: Lost, as is true of nearly all the rest of Say's insect material. The type locality is "Mexico". Possibly the type was from the vicinity of México City; in any case it probably did not come from Sonora as the name might suggest, since little collecting had been done in northwestern México before 1837. It could have been named *sonorus* because someone said it made a loud noise (buzz); "*sonorus*" in Latin means loud, noisy.

Bombus (Fervidobombus) pennsylvanicus pennsylvanicus (Degeer)
(Figs. 6, 8, 10, 11; Map 4)

Apis pennsylvanica Degeer, 1773: 575.
Bombus americanorum Fabricius, 1805: 346.
Bombus pennsylvanicus; Handlirsch, 1888: 238.
Bombus (Bombus) pennsylvanicus; Franklin, 1912: 399.
Megabombus (Megabombus) pennsylvanicus pennsylvanicus; Milliron, 1973a: 190.

PILE: Dense, longest hairs 1.5 times length of tegula. Black except yellow on pronotum, anterior part of scutum, T-2, T-3, and usually posterior portion of T-1. Males with plumose and whitish hairs on clypeus, above and below antennae and anterior portion of vertex; also yellow hairs on upper part of mesepisternum and T-4.

QUEEN: Length 20 to 25 mm. UID 3.0 to 3.2 mm, LID 3.3 to 3.5 mm. Ocelli just below supraorbital line. OOD 2.0 to 2.5 times lateral ocellar diameter. IOD approximately same as

OOD. Clypeus strongly punctate, in profile protuberant for distance at most half width of malar space. Malar space 20 wider than long. Thoracic width between wing bases 6.0 to 7.0 mm. Mesobasitarsus little more than three times as long as wide. T-2 width 10 to 11 mm.

WORKER: Similar to queen but smaller, length 14 to 18 mm. Parts proportionally reduced in size.

MALE: Similar to queen except as follows: Length 14 mm. UID 2.3 mm. LID 2.4 mm. Clypeus protuberant for three-fourths width of malar space. Thoracic width between wing bases 4.0 to 4.5 mm. Mesobasitarsus 4.5 times as long as wide. T-2 width 6.0 mm.

DISTRIBUTION: In México the sonorus-type coloration is more frequently found in the drier areas of the Altiplano Mexicano, Desierto Sonorense and Baja California; in the United States *sonorus* occurs in the southwestern states (western Texas to southern California). The pennsylvanicus-type coloration tends to occur near the mountain chains and more humid areas of the Altiplano Mexicano and the Altos of Oaxaca; in the United States it is found east of the hundredth meridian, as far south as Florida and northward to Canada (Quebec and Ontario). However, in México typical *pennsylvanicus pennsylvanicus* queens are also found in the west (Sierra Madre Occidental, Chihuahua), associated with grassland and near *Pinus* forests, while typical *pennsylvanicus sonorus* also occurs in the northeast in Nuevo León and Tamaulipas, associated with Matorral Xerófito. Both forms are present in the Altos de Chiapas and Guatemala, which have in general a temperate vegetation. Thus the forms are geographically intermixed in México, and chromatically intermediate specimens occur, mainly in northeastern México and southwestern Texas.

The distribution of *B. p. pennsylvanicus* and *B. p. sonorus* includes the following types of vegetation: Matorral Xerófito, Pastizal, and Bosque Espinoso, constituting the Region Xerófita Mexicana, which has a largely Neotropical origin (Rzedowski, 1978). These bees, however, also occur in the Bosque de Pino and Encino (Nearctic) and in some places like Michoacán and Nayarit in the Bosque Tropical Caducifolio (Neotropical).

The seasonal distribution of *B. p. sonorus* in central México is from February to December; the altitudinal distribution is 1000 to 2400 m. It probably flies at lower altitudes but not at sea level. In the Desierto Sonorense and Baja California this form is found from March to October, and the altitudinal distribution is sea level to 1800 m. I have only one specimen from Chiapas collected in May, another one from Guatemala in August. Both lack altitudinal data but the Mexican one is from Tuxtla Gutiérrez, a middle altitude locality (above 1000 m).

The seasonal distribution of *B. p. pennsylvanicus* in the western part of the Altiplano Mexicano (Chihuahua, Durango) is May to September. This form is found up to 2500 m in the Sierra Madre Occidental. In the central and eastern portions of México it is found from May to December, flying as low as 300 m. In Southern México (Oaxaca) it can be found from January to August, between 1800 and 2000 m. Milliron (1973a) reported 26 workers from Comitán, Chiapas, in the Canadian National Collection; they are now in the Academy of Natural Sciences of Philadelphia.

LOCALITIES: Sonora: Imuris. Chihuahua: Encinillas, Barranca del Cobre, San José Babicora, Maderas, Juárez (239 km S), Delicias, Matachic. Durango: Palos Colorados, Durango, Canutillo. Coahuila: Sabinas. Nuevo León: Linares, General Teran, El Cercado, China. Tamaulipas: Sisal, Ciudad Victoria, Villagrán, Soto La Marina, El Limón, Llera, Padilla. San Luis Potosí: Ciudad del Maíz, El Salto. Hidalgo: Pachuca, Ixmiquilpan, Tulancingo, Zimapan. Queretaro: San Juan del Río. Jalisco: Lagos de Moreno, Villa Guadalupe. Nayarit: Singayta, Ahuacatlán. Michoacán: Hidalgo, Jacona, Zitácuaro. Estado de México: Texcoco, Toluca, Ixtapan de la Sal (40 km S), Jalapa, Naolinco. Oaxaca: Oaxaca, Puerto Angel, Huajuapan, Monte Albán, La Esperanza, San Pedro Guegorene, Huitzo, Nochixtlán, Chula.

COMPARATIVE COMMENTS: *Bombus sonorus* and *Bombus pennsylvanicus* were considered different species by Franklin (1912). However, Milliron in 1962 regarded them as only subspecifically different. Both authors recognized the similarity in external morphology and male genitalia, observations which are corroborated in my study. In fact, it is sometimes difficult to place a Mexican specimen in either subspecies because there are specimens with the coloration of the scutellum and the punctation of the clypeus intermediate between the two taxa. Average differences of certain proportions are found (see above description of malar space and mesobasitarsus) but do not differentiate all specimens. Peters (1968) reported a male of *sonorus* in a nest of *pennsylvanicus*.

The subspecific differentiation is useful in the U.S.A. and Canada where these two forms are allopatric, although meeting in a few areas, for example, West Texas. However, in México where these forms are partially sympatric, separation may not make much sense. Field studies may show them to be ecologically segregated subspecies; they might even be sibling species. I have followed Milliron (1973a) and have retained them as different subspecies for this work.

TYPE: In the Degeer Collection, Naturhistoriske Riksmuseet, Stockholm, according to Milliron (1960). Type locality: Pennsylvania, U.S.A.

Bombus (Fervidobombus) diligens Smith
(Figs. 1, 3, 6, 7, 10, 11; Map 6)

Bombus diligens Smith, 1861: 154.
Bombus dolichocephalus Handlirsch, 1888: 244.
Bombus (Bombus) dolichocephalus; Franklin, 1913: 108.
Fervidobombus (Fervidobombus) dolichocephalus; Skorikov, 1922: 130.
Bremus dolichocephalus; Frison, 1925: 159.
Megabombus (Megabombus) diligens; Milliron, 1973a: 166.

PILE: Dense, longest hairs 1.5 times length of tegula. Both sexes black except reddish on T-4 to T-6. Male with T-7 also reddish, sometimes with anterior portion of T-4 black; face covered with mixture of long, simple, black hairs and short, plumose, whitish ones. Both sexes and female castes with a smooth and almost bare area at center of posterior portion of scutum.

QUEEN: Length 18 to 23 mm. UID 2.7 mm, LID 3.2 mm. Ocelli below supraorbital line. OOD at least twice lateral ocellar diameter, in some specimens 2.5 diameters. IOD approximately the same as OOD. Clypeus with upper margin and sides strongly and densely punctate, middle and lower margin with more sparse punctation. Clypeus in profile protuberant for distance at most four-fifths width of malar space. Malar space 20 longer than wide. Thoracic width between wing bases 8.0 mm. Mesobasitarsus 3.5 times as long as wide. T-2 width 11 to 12 mm.

WORKER: Similar to queen except as follows: Length 14 to 18 mm. OOD 2.5 times lateral ocellar diameter. Clypeus less densely punctate, but following same pattern as queen. Mesobasitarsus three times as long as wide. Other parts proportionally reduced in size.

MALE: Similar to queen except as follows: Length 18 mm. UID 2.3 mm, LID 2.6 mm. Clypeus evenly punctate but a small smooth area on lower middle portion. Clypeus protuberant for almost width of malar space. Length of malar space variable, 25 to 40 longer than wide. Thoracic width between wing bases 7.0 mm. Mesobasitarus more than four times as long as wide. T-2 width 10 mm.

DISTRIBUTION: This species is found from Northern México to Oaxaca. It occurs along the Sierra Madre Occidental (Sinaloa and Nayarit), the Eje Volcánico Transversal, the Sierra Madre Oriental (Veracruz, San Luis Potosí, Puebla, Hidalgo), and the Sierra Madre del Sur (Guerrero and Oaxaca). This distributional pattern corresponds in part to that of the Bosque Tropical Caducifolio and the Bosque de Pino y Encino of Rzedowski (1978). This species is probably more frequently found in the *Pinus* and *Quercus* forests, since its altitudinal range is similar to that of these kinds of vegetation. *B. diligens,* however, is not known to follow the vegetation types beyond its distributional area. I have seen one specimen labeled Guatemala (San José Pinula); but this species' southern limit may be the Isthmus of Tehuantepec. If present in the Altos of Chiapas and Guatemala, it must be rare and more collections are needed to corroborate the Guatemalan record.

I have studied specimens collected mainly during the second and last thirds of the year. For the Pacific and central portions of México (Sinaloa to Morelos) specimens were taken from June to December, more frequently between July and October. The altitudinal distribution is 1400 to 2500 m. For the Gulf side (Puebla, Veracruz, San Luis Potosí) I have seen specimens captured in March, and from June to November. The altitudinal distribution is 1300 to 2000 m. For the Sierra Madre del Sur (Guerrero and Oaxaca) specimens were taken from July to November, more commonly in July and August. The altitudinal distribution was 1800 to 2400 m.

LOCALITIES: SINALOA: El Palmito, Santa Lucía. NAYARIT: Compostela, Tepic, Ahuacatlán, Jésus María. JALISCO: Guadalajara, Mascota, Mazamitla, Cojumatlán, Tequila, Ajijic, La Quemada. MICHOACÁN: Morelia, Pátzcuaro, Tancitaro, San Lorenzo, Quiroga, Tuxpan, Zacapu. ESTADO DE MÉXICO: Necaxa, Valle de Bravo, Salvatierra, Ixtapan de la Sal, Iztapantongo, Malinalco. MORELOS: Yautepec, Cuautla, Xochicalco, Cuernavaca, Oaxtepec. GUERRERO: Chilpancingo, Almolongo, Taxco, Omilteme, Xochipala. OAXACA: Huajuapan de Léon, Ixtlan de Juárez, Guelatao, Oaxaca, Sierra de Miahuatlán. PUEBLA: Huauchinango, Atlixco, Puebla, Matamoros. VERACRUZ: Acutzingo, Jamapa (Río), Orizaba, Jalapa, Coscomatepec, Jilotepec, Río Blanco. SAN LUIS POTOSÍ: Xilitla. HIDALGO: Istula. GUATEMALA: San José Pinula.

COMPARATIVE COMMENTS: This species can be separated from almost all other *Bombus* in México and Central America by its black body and red apical metasomal segments. However, *B. brachycephalus,* a species of *Brachycephalibombus,* is chromatically almost identical. These two species can be separated not only by the male genitalia but also by the characters listed in Table 4. In general, characters 2 to 5 are excellent to separate both female and male specimens of these taxa. However, they have to be used together since both species show a wide range of morphological variation and frequently overlap in these external characters.

B. diligens and *B. brachycephalus* appear to be parts of a mimetic complex in central México. One species of Anthophorini, *Deltoptila aurolentocaudata* (Dours), has the same coloration and is partially sympatric (Morelia, Amecameca, Tepoztlán, Huauchinango, Jalapa), and is found at the right altitude (1650 to 2280 m) from June to

August. Furthermore, the size of this species is within the range of size of the *Bombus* workers.

TYPE: The lectotype of *B. diligens* established by Milliron is in the British Museum (Natural History). The type of *B. dolichocephalus* is in the Naturhistorisches Museum in Vienna, according to Franklin (1913). The type locality of the former name is Oaxaca, México.

Bombus (Fervidobombus) steindachneri Handlirsch

(Figs. 6, 7, 10, 11; Map 2)

Bombus steindachneri Handlirsch, 1888: 239.
Bombus (Bombus) steindachneri; Franklin, 1913: 105.
Fervidobombus (Fervidobombus) steindachneri; Skorikov, 1922: 154.
Megabombus (Megabombus) steindachneri; Milliron, 1973a: 205.

PILE: Dense, longest hairs as long as tegula. Both sexes black except yellow on dorsum of thorax and T-3, usually a transverse line of yellow hairs (sometimes few) on anterior part of T-2. Male also with yellow on clypeus, subantennal area, vertex, and anterior part of T-4, sometimes on upper part of mesepisternum. Both sexes usually with bare area on middle of mesoscutum small.

QUEEN: Length 20 to 25 mm. UID 3.0 mm, LID 3.5 mm. Ocelli just below supraorbital line. OOD at least twice lateral ocellar diameter. IOD approximately the same as OOD. Clypeus sparsely punctate. Clypeus in profile protuberant for distance at most half width of malar space. Malar space 1.75 to 2.0 times as wide as long. Thoracic width between wing bases 8.0 mm. Mesobasitarsus almost four times as long as wide. T-2 width 12 mm.

WORKER: Similar to queen but smaller, length 10 to 18 mm. Parts proportionally reduced in size.

MALE: Similar to queen except as follows: Length 16 to 18 mm. UID 2.0 to 2.5 mm, LID 2.0 to 3.1 mm. Malar space little wider than long. Thoracic width between wing bases 6.0 mm. T-2 width 6.0 to 8.0 mm.

DISTRIBUTION: This species is restricted to the Eje Volcánico Transversal, Sierra Madre Occidental, and the Sierra Madre del Sur of México. This distribution corresponds in part to that of the Bosque Tropical Caducifolio (Rzedowski, 1978) which, however, is also found near the Gulf Coast and in southern México. This species can also be found in Rzedowski's Bosque de Encino y Pino and Bosque Espinoso.

I have studied specimens of both sexes and both female castes taken in almost every month of the year. On the Pacific Coast (Jalisco, Nayarit, Sinaloa, Sonora) specimens were taken from February to December. The altitudinal distribution in this area is from near sea level (50 m) to 2500 m. For the central part of México I have records from January to December, with an altitudinal distribution from 1000 m to 1900 m. Probably they also fly at lower altitudes in the Río Balsas valley.

LOCALITIES: SONORA: Río Mayo, Los Álamos. CHIHUAHUA: Barranca del Cobre, Bakachaca, Guirocoba. DURANGO: El Palmito, "Sinaloa." SINALOA: Villa Unión, Pericos, San Ignacio, Concordia, Santa Lucía, Chupaderos (46 km E). NAYARIT: Jalcocotán, Venustiano Carranza, Ixtlán del Río, Tepic, Compostela, La Yerba, Ahuacatlán, Xalisco, Jumatán. JALISCO: Mazamitla, Yelapa, Volcán Tequila, Volcán Colima, Guadalajara, Puente Grande, Sayula, Plan de Barrancas, Jojutla, Puerto los Mazos, Jocotepec, Ajijic, Puerto Vallarta (8 km SE). MICHOACÁN: Jungapeo, Zamora, Jacona, Tumbiscatio. ESTADO DE MÉXICO: Temascaltepec, Tonatico, Ixtapan de la Sal. MORELOS: Cuautla,

Table 4. Comparison of *Bombus diligens* and *B. brachycephalus*.

Character	*B. diligens*	*B. brachycephalus*
1. Length of queen body	20-24 mm	17-19 mm
Length of male body	16-18 mm	12-14 mm
2. Ocellocular distance	2.0 to 2.5 × lateral ocellar diameter	At most, 2.0 × lateral ocellar diameter
3. Ocellar area	Poorly defined (Fig. 3)	Well defined (Fig. 4)
4. Malar space	As long as wide, usually longer in queens (Fig. 2)	Wider than long (Fig. 1)
5. Punctation along margin of eye	Coarse, not evenly distributed	Fine, evenly distributed
6. Posterior distal angle of mesobasitarsus	Acute to nearly right angle	Rounded
7. Pubescence of hind basitarsus	Short, hairs numerous	Long, hairs very sparse
8. Color of metasomal apex	Deep red	Orange (central México) Black (southern México)

Cuernavaca, Yautepec, Tepoztlán, El Rodeo, Alpuyeca, Las Granadas, Teocelo. PUEBLA: Tehuitzingo, Atlixco, Izucar de Matamoros, Acatlán. GUERRERO: Chilpancingo, Petlaca, Los Limones (Km 35 Hwy 95), Acuitlapan, Pololcingo, Iguala, Acahuizotla, Taxco. OAXACA: Candelaria-Loxicha.

COMPARATIVE COMMENTS: The closest relatives of *Bombus steindachneri* are *B. medius, B. pennsylvanicus pennsylvanicus* and *B. pennsylvanicus sonorus.* It is easy to separate this species from its relatives; *B. medius* and *B. p. sonorus* have a black interalar band on the scutum, *B. p. pennsylvanicus* has the scutellum and posterior part of scutum black. *B. steindachneri* has all the notum yellow, except for a hairless spot in the middle.

Although the chromatic differences between *B. medius* and *steindachneri* are conspicuous, the male genitalia are extremely similar. The head of the penis valve of *B. steindachneri* is less rounded and lacks lateral serrations (50×), the preapical tooth of the gonostylus is more slender and sharper, and the genital capsule is smaller. The two forms are allopatric, *B. medius* being eastern and *B. steindachneri* western (Map 2). In both taxa, males, queens and workers are in flight all year long. The lack of chromatic and morphological intermediates supports the idea of two different species. If hybridization occurs, Oaxaca (southeastern) will be a possible place for it; also the states of Veracruz (central), Hidalgo and Estado de México (northeastern) should be potential areas for hybridization.

TYPE: In the Naturhistorisches Museum, Vienna, according to Milliron (1960). Type locality: Cuernavaca, Morelos, México.

Bombus (Fervidobombus) medius Cresson
(Figs. 6, 7, 10, 11; Map 2)

Bombus medius Cresson, 1863: 97.
Bombus (Bombus) medius; Franklin, 1913: 123.
Fervidobombus (Fervidobombus) medius; Skorikov, 1922: 154. *Megabombus (Megabombus) medius;* Milliron, 1973a: 172.

PILE: Dense, longest hairs as long as tegula. Both sexes black except yellow on pronotum, anterior part of scutum, scutellum and metasoma T-3; hence with a black interalar band on scutum. Male also with whitish hairs on clypeus and subantennal area and yellow on vertex and upper portions of thoracic sides.

QUEEN: Length 20 to 25 mm. UID 3.0 mm, LID 3.5 mm. Ocelli just below supraorbital line. OOD at least twice lateral ocellar diameter, usually 2.5 times. IOD approximately the same as OOD. Clypeus moderately punctate. Clypeus in profile protuberant for distance between two-thirds to four-fifths width of malar space. Malar space as long as wide. Thoracic width between wing bases 7.5 mm. Mesobasitarsus almost four times as long as wide. T-2 width 12 mm.

WORKER: Similar to queen but smaller, length 8 to 18 mm. Parts proportionally reduced in size.

MALE: Similar to queen except as follows: Length 16 to 18 mm. UID 2.5 mm, LID 2.9 m. Clypeus protuberant for two-thirds to three-fourths width of malar space. Malar space little longer than wide. Thoracic width between wing bases 6.0 mm. Mesobasitarsus more than four times as long as wide. T-2 width 6.0 to 8.0 mm.

DISTRIBUTION: This species occurs on the Gulf side and southern México south to Honduras (including the Yucatán Peninsula). The distributional pattern in México corresponds with the Bosque Tropical Caducifolio and the Bosque Tropical Perennifolio of Rzedowski (1978).

Throughout the year, males and both female castes can be found. I have seen specimens taken in Southern México (Chiapas, Tabasco, Oaxaca, Yucatán Peninsula) and Central America from March to December, more frequently from June to September. The altitudinal distribution is from sea level to 1100 m. In Veracruz (Central) and Puebla I have records from January to December with an altitudinal distribution from sea level to 1600 m. From the Huasteca (northern Veracruz and Hidalgo, eastern San Luis Potosí, and southern Tamaulipas) I have records from May to December, with an altitudinal distribution from sea level to 800 m.

LOCALITIES: TAMAULIPAS: Altamira, Ciudad Mante. VERACRUZ: Coatepec, Veracruz, Fortin de las Flores, Catemaco, Papantla, Cuichapa, San Rafael, Jalapa, Coatzacoalcos, Jésus Carranza, Huatusco, Cordoba, Minatitlan, Suchil, Pajaritos, Cotaxtla, Orizaba, Atoyac, Zongolica, Coscomatepec, Las Lajas, Xico, Los Tuxtlas, Teoceolo, Hueyapan, Chicontepec, Las Choapas, Tajin, Tempoal, Río Jamapa, Panuco, Totola, Naranjos, Ixhuatlán, Tecolutla, Atoyac, Naolinco, Macaya, Nanchital, Barranca de Metlac. SAN LUIS POTOSÍ: Tamazunchale, Ciudad Valles, Xilitla, Huichihuayan, El Salto, El Bonito. HIDALGO: Chapulhuacán. PUEBLA: Xicotepec de Juárez, Teziutlán, La Ceiba, Atzalán. OAXACA: Tolosa, Oaxaca. TABASCO: Cardenas, Teapa. CHIAPAS: San Carlos, Ocozocuautla, Cintalapa, Simojovel, La Revancha, Yaxoquintela, Las Margaritas, Comitán, Berriozabal. CAMPECHE: San Dimas. YUCATÁN: Chichen Itzá, Piste. QUINTANA ROO: Carrillo Puerto, X-can. GUATEMALA: Petén, San Cristóbal. EL SALVADOR: San Salvador. HONDURAS: Tegucigalpa, Zamorano, Sigualtepeque, Agua Amarillo, Subirana Yoro, Portilla Grande, El Progreso.

COMPARATIVE COMMENTS: This taxon has frequently been confounded with *B. atratus,* a South American species highly variable in coloration, because one of the color variants of *B. atratus* is similar to *B. medius.* Franklin (1913) mixed these species and indicated the distribution of *B.*

medius as México to Paraguay. This species actually extends south at most to Panamá; my data indicate a distribution only to Honduras but Milliron (1973a) reported two males from Chiriqui, Panamá, in the National Museum of Natural History (U.S.A.). I could not find these specimens, however.

The similarities between *B. medius* and *B. atratus* may extend beyond the coloration and morphology. The colonies of *Bombus atratus* are well known as perennial (Zucchi, 1973), having several reproductive phases during the year. This could also be the case with *B. medius* as noted by Michener and LaBerge (1954), who found a nest of *B. medius* in San Luis Potosí (Tamazunchale) with a queen that had produced at least 2183 worker offspring. The size of this colony and the presence of both sexes in flight all year long are important arguments to support the idea of perennial colonies.

TYPE: Probably lost according to Milliron (1973a). The type locality given by Cresson (Utah, U.S.A.) is incorrect; probably the type was from México.

Bombus (Fervidobombus) mexicanus **Cresson**

(Figs. 6, 8, 10, 11; Map 6)

Bombus mexicanus Cresson, 1878: 187.
Bombus unifasciatus Smith, 1879: 133.
Bombus cayennensis var. *mexicanus;* Handlirsch, 1888: 241.
Bombus (Bombus) mexicanus; Franklin, 1913: 128.
Fervidobombus (Fervidobombus) mexicanus; Skorikov, 1922: 153.
Bombus mexicanus var. *adani* Cockerell, 1949: 488.
Megabombus (Megabombus) mexicanus; Milliron, 1973a: 227.

PILE: Dense, longest hairs two-thirds length of tegula. Both sexes black except yellow on T-3. Males with face and vertex covered with mixture of black simple hairs and whitish plumose ones, which are usually even in length on clypeus; T-4 varying from having few yellow hairs on anterior margin to covered with yellow pile. Some individuals (particularly bigger ones) with short and plumose yellow hairs on sides of thorax and scutum, especially evident above coxal bases and in front of tegula; also with last segment and sides of T-6 covered with reddish hairs. Both sexes with a large smooth bare area on middle of posterior portion of scutum.

QUEEN: Length 20 to 25 mm. UID 3.7 mm, LID 4.0 mm. Ocelli just below supraorbital line, lateral ones on the line. OOD three times lateral ocellar diameter. IOD approximately same as OOD. Clypeus evenly punctate with mixture of coarse and fine punctures. Clypeus protuberant in profile for distance at most half width of malar space. Malar space 20 to 25 wider than long. Thoracic width between wing bases 8.0 mm. Mesobasitarsus four times as long as wide. T-2 width 12.0 mm.

WORKER: Similar to queen except as follows: Length 12 to 16 mm. Clypeus less densely punctate, some smooth areas on middle. Malar space 20 wider than long. Other parts proportionally reduced in size.

MALE: Similar to queen except as follows: Length 12 to 18 mm. UID 2.5 mm, LID 2.6 mm. Malar space as wide as long.

DISTRIBUTION: This species is found from the Eje Volcánico Transversal south to Panamá. Franklin (1913) said it was also present in Colombia and Ecuador, but I have not seen specimens from those countries. The distributional pattern in México corresponds in part to the Bosque Tropical Caducifolio and Bosque de Pino y Encino of Rzedowski (1978). Milliron (1973a) recorded one worker from El Destierro, San Luis Potosí, well north of the area from which I have seen specimens. In the Eje Volcánico Transversal all specimens were taken in July. No altitudinal data are given, but the localities indicate they were found above 1000 m and perhaps to 1800 m. This species is rare in Central México. In southern México (Chiapas and Oaxaca) and northern Central America (Guatemala, El Salvador, Honduras and Northwestern Nicaragua) specimens have been taken from January to December except in May. The altitudinal distribution is 150 to 1800 m, more frequently 400 to 1000 m.

From southern Central America (Costa Rica, Panamá, southeastern Nicaragua), I have seen specimens collected in January, February, April to August and in November. They probably fly throughout the year. The altitudinal distribution is 800 to 1400 m. Quite probably they fly at lower altitudes; I have seen one specimen labeled Balboa, Panamá, which must have been captured near sea level if the locality is correct. Moreover, among many specimens from Costa Rica, a well surveyed area, a few were captured at sea level.

LOCALITIES: JALISCO: Chapala. MICHOACÁN: Patzcuaro, Carapán. PUEBLA: South of Puebla. VERACRUZ: Orizaba. OAXACA: Tapanatepec. CHIAPAS: San Jeronimo Tacana, Navenchauc, Guadalupe Atodia, Soyalo, El Zapote near Tuxtla Gutiérrez, El Sumidero near Tuxtla Gutiérrez, Tuxtla Gutiérrez, Angel Albino, La Trinitaria, Chiapa de Corzo, Motozintla, San Cristóbal de las Casas, Arriaga, Jitotal, Ocozocoautla, Izapa, Suchiapa, Comitán. GUATEMALA: Guatemala, San Cristóbal, Variedades, Chicacao, Antigua, Amatitlán, Lago de Atitlán, Coatepeque, Nahualate, Retalhuleu, Monte Pacaya, Santa Emilia Pochula, Yepocapa, Panamá, La Providencia Obispo, Moca Guatalon. HONDURAS: San Marcos de Colón (Choluteca), Suyapa (Morazan), Tegucigalpa, Zamorano. EL SALVADOR: Monte San Salvador, Cerro Verde, San Salvador, Quezaltepeque, San Juan Tepezontepec (La Paz), S. de los Planes. NICARAGUA: Las Nubes (Managua), Jinotega, Piriamba. COSTA RICA: Monteverde, San José, Liberia (Guanacaste), Orotina, Pacayas, Playas del Coco (Guanacaste), Vara Blanca (Heredia), Las Cruces, San Vito, San Mateo, Comelec near Bagaces (Guanacaste), Santa Clara, Tres Ríos (Cartago), Orosí, La Carpentera. Panamá: Boquete, Potrerillos, Balboa, Volcán Chiriquí, Niño.

COMPARATIVE COMMENTS: This species can be separated from other *Bombus* by the yellow band on T-3, and the otherwise black body. However, *B. brachycephalus* in southern Mexico and Central America is chromatically similar to *B. mexicanus*. These two species can be distinguished because the yellow hairs of *B. brachycephalus* are on T- 2, with only a few such hairs on the anterior margin of T-3.

Furthermore the yellow band on *B. brachycephalus* is always incomplete in the middle. On the other hand, the yellow band of *B. mexicanus* is always complete and mainly on the middle and posterior part of T-3.

Franklin (1913) considered *B. medius* as the closest relative of *B. mexicanus*. Milliron (1973a) placed this species together with *B. transversalis* and *B. brevivillus* in a separate group of *Megabombus*, his Mexicanus group. However, Ito (1985) indicates that *B. brevivillus* is a unique species quite apart from other *Fervidobombus*. I believe the closest relative of *B. mexicanus* is *B. diligens;* less close are *B. medius* and *B. steindachneri*.

TYPE: Cresson's type is in the Academy of Natural Sciences of Philadelphia, according to Franklin (1913). Type locality: México. Type of *adani* in the National Museum of Natural History, Washington. Type of *B. unifasciatus* in the British Museum (Natural History).

Bombus (Fervidobombus) pullatus Franklin

(Figs. 6, 7, 10, 11; Map 8)

Bombus (Bombus) pullatus Franklin, 1913: 122.
Bombus (Bombus) niger Franklin, 1913: 120.
Fervidobombus (Fervidobombus) niger; Skorikov, 1922: 153.
Megabombus (Megabombus) pullatus; Milliron, 1973a: 201.

PILE: Dense, longest hairs as long as tegula. Both female castes completely black. Males usually with a mixture of long black hairs and short gray ones on vertex and face, rest of body black.

QUEEN: Length 20 to 25 mm. UID 3.4 mm, LID 3.8 mm. Lateral ocelli on supraorbital line, middle ocellus just below. OOD 2.0 to 2.5 times lateral ocellar diameter. IOD approximately the same as OOD. Clypeus sparsely puncatate. Clypeus in profile protuberant for distance at most half width of malar space. Malar space as wide as long. Thoracic width between wing bases 7.0 mm. Mesobasitarsus more than three times as long as wide. T-2 width 12 mm.

WORKER: Similar to queen but smaller, length 12 to 14 mm. Parts proportionally reduced in size.

MALE: Similar to queen except as follows: Length 12 to 20 mm. UID 2.6 mm, LID 2.7 mm. Clypeus protuberant for width of malar space. Thoracic width between wing bases 4.0 to 6.0 mm.

DISTRIBUTION: This species is found from Honduras to Panamá, and in the Andes. In Central America it is probably found in the Bosque de Niebla, and in equivalent vegetation in South America; in the lowlands it should be found in Bosque Tropical Perennifolio (Rzedowski, 1978). The seasonal distribution is probably all year long. I have seen specimens from southern Central America collected from January to August, and November (Nicaragua). The altitudinal distribution is from sea level to 1800 m but the species is more frequently collected above 1000 m (Janzen, 1971).

This species has been recorded from México, and in Central America from Guatemala to Panamá (Franklin, 1913; Milliron, 1973a). I have not seen any true *Bombus pullatus*, however, from México, Guatemala, Belize, or El Salvador. Several specimens from Chiapas and Guatemala, although chromatically identical to *B. pullatus,* are *B. brachycephalus*. In 1973 Milliron recorded this species from Brazil. However, Moure and Sakagami (1962) did not record it from there. All the specimens similar to *B. pullatus* that I have seen from that country belong to the black form of *B. atratus*.

LOCALITIES: Honduras: Lago Yojoa (Cortes), Lago Yojoa (Peña Blanca). Nicaragua: Musawas-Huaspuc River. Costa Rica: San José, San Isidro de El General, Rincón, Golfito, Palmas, San Vito de Java, Chilaria, Volcán Poas, San Miguel, San Antonio, La Fuente, Quebradas, Paraíso, Turrialba, Potrero Grande, Puerto Quepos, Santiago de Puriscal, Guapiles, Puerto Viejo de Sarapiquí. Panamá: Cerro Campana, Volcán de Chiriquí, Bocas del Toro, El Valle de Antón, Potrerillos, Fort Clayton.

COMPARATIVE COMMENTS: This species is chromatically similar to *B. diligens, B. brachycephalus* and *B. mexicanus,* from which it can be separated as follows. The last species has a band of yellow hairs on T-3, and *B. diligens* has T-4 and T-5 covered with reddish hairs, as does one form of *B. brachycephalus*. A second form of *B. brachycephalus* has yellow hairs on the sides of T-2 and T-3. A third form of *B. brachycephalus* is completely black like *B. pullatus,* but has the ocelli closer to the eyes than does that species (see Table 4).

TYPE: *B. pullatus* and *B. niger* types are in the National Museum of Natural History, Washington, according to Franklin (1913) and Milliron (1973a). Type localities: Ecuador.

Bombus (Fervidobombus) digressus (Milliron)

(Fig. 6, 7, 10, 11; Map 4)

Bombus lateralis Smith var., 1879: 134 (misident.).
Megabombus (Megabombus) digressus Milliron, 1962: 730.
Bombus digressus; Laverty, Plowright & Williams, 1984: 1051.

PILE: Dense, longest hairs two times length of tegula, worker with body black except yellow on sides of thorax, T-1 and T-2; some yellow hairs behind tegula and on sides of T-3. Male like worker but pale plumose hairs mixed with black simple pile around antennal bases and clypeus.

QUEEN: Unknown.

WORKER: Length 12.0 mm. UID 2.3 mm, LID 2.4 mm. Ocelli on supraorbital line. OOD two times lateral ocellar diameter. IOD one and one-fourth OOD. Clypeus uniformly but sparsely punctured with a mixture of coarse and fine punctures. Clypeus in profile protuberant for almost one-third more than malar space width. Malar space as long as wide to 25 longer. Thoracic width between wing bases 5.0 mm. Mesobasitarsus three times as long as wide. T-2 width 6.0 mm.

MALE: Similar to worker except as follows: Length 16.0 mm. OOD one and a half times lateral ocellar diameter. Mesobasitarsus four and a half times as long as wide.

DISTRIBUTION: This species has been collected only in Guatemala and Costa Rica. All specimens preserved with dates were taken in June. The only altitude record is from Villa Mills (Costa Rica) at 3300 m.

LOCALITIES: Guatemala: Volcán de Fuego, Dept. of Escuintla. Costa Rica: Río Sucio, Prov. de Limón; Villa Mills, Prov. de Cartago.

COMPARATIVE COMMENTS: Franklin (1913) placed *B. lateralis* sensu Smith as a synonym of *B. (Pyrobombus) ephippiatus,* but he never examined the specimens of Smith's "variety." Milliron (1962) recognized this "variety" as a distinct species, *B. digressus,* and placed it in the genus and subgenus *Megabombus.* Laverty et al. (1984), on the basis of the male genitalia, established the new subgenus *Digressobombus* for this species, but Williams (1985) in a cladistic analysis of male genitalia, returned *B. digressus* to *Fervidobombus.*

This species can be confounded with *B. ephippiatus* in Central America. However, the coloration of T-1 and T-2 is black mediobasally with yellow pile laterally in *B. digressus.* In contrast, *B. ephippiatus* is predominantly yellow on T-1 and mediobasally on T-2, with black pile laterally.

TYPE: The type of *B. digressus* is in the British Museum (Natural History). Type locality: Volcán de Fuego, Guatemala.

Bombus (Pyrobombus) huntii Greene
(Figs. 6, 9, 10, 11; Map 7)

Bombus huntii Greene, 1860: 172.
Bombus ternarius; Cresson, 1863: 104 (misident.).
Bombus rufosuffusus Cockerell, 1905: 271.
Bombus (Bombus) huntii; Franklin, 1912: 319
Bombus (Bombus) laticinctus Franklin, 1913; 85.
Bremus huntii var. *laticinctus;* Frison, 1925: 149.
Pyrobombus (Pyrobombus) huntii; Milliron, 1971: 42.

PILE: Dense, longest hairs twice length of tegula. Queen with mixture of yellow and black on head, yellow especially abundant above and below antennae; thorax yellow except for a wide black interalar band on scutum; T-1 yellow, T-2 to T-4 reddish or T-4 yellow; T-5 to T-6 black. Legs and sterna black. Some specimens with T-4 yellowish. Worker with head almost completely yellow and T-4 yellow. Male with head yellow; T-2 and T-3 reddish-ferrugineous, T-4 yellow; interalar band narrower than in females. Legs predominantly yellow, especially on basal portions.

QUEEN: Length 15.0 mm. UID 2.8 mm, LID 3.0 mm. Lateral ocelli on supraorbital line, middle ocellus just below. OOD twice lateral ocellar diameter. IOD approximately the same as OOD. Clypeus sparsely and coarsely punctate, upper margin and sides more densely punctate. Clypeus in profile protuberant for distance at most width of malar space. Malar space as wide as long. Thoracic width between wing bases 6.0 mm. Mesobasitarus little more than three times as long as wide. T-2 width 9.0 mm.

WORKER: Similar to queen except as follows: Length 10 to 14.0 mm. Ocelli on the supraorbital line. Parts proportionaly reduced in size.

MALE: Similar to queen except: Length 12.0 mm. Ocelli on supraorbital line. OOD almost three times lateral ocellar diameter. Thoracic width between wing bases 4.5 mm. Mesobasitarsus almost five times as long as wide; T-2 width 5.0 mm.

DISTRIBUTION: This species is abundant in the western U.S.A. and Canada (Stephen, 1957), from British Columbia to Arizona. In México it is less common and restricted to the Altiplano Mexicano. Its distribution in México corresponds with pine vegetation (Rzedowski, 1978). I have seen specimens taken during July and August. They probably fly also in June and September, and the queens even as early as April; they follow this pattern in U.S.A. The vertical distribution is 3000 to 4300 m. This species and *B. rufocinctus* are the only ones found above 4000 m in México and Central America.

LOCALITIES: Chihuahua: Meadow Valley (Río Piedras Verdes, 6 km S Colonia García). Jalisco: Volcán de Colima. Michoacán: Cerro Tancitaro. Estado de México: Toluca, Volcán de Toluca, Paso de Cortez (Popocatépetl), Volcán Popocatépetl, Llano Grande, Tequesquinahuac (Cerro Tlaloc). Nuevo León: Cerro Potosí. Coahuila: El Túnel. Veracruz: Volcán Citlaltépetl (Pico de Orizaba).

COMPARATIVE COMMENTS: This species was placed by Franklin (1912, 1913) in the Pratorum group, and by Stephen (1957) in the subgenus *Pratobombus.* Milliron (1971) placed it in

Pyrobombus (Pyrobombus), where the New World species of *Pratobombus* are now placed. I think this is correct.

Only a few males of this species have been collected in México, mainly in Nuevo León. Franklin (1913) recorded one male from Meadow Valley, Chihuahua; I have not seen this specimen. I have used several males from Arizona (U.S.A.) for comparison with the Mexican material.

TYPE: Greens's type probably lost, according to Stephen (1957). The types of *B. rufosuffusus* and *B. laticinctus* are in the National Museum of Natural History, Washington.

Bombus (Pyrobombus) ephippiatus **Say**

(Figs. 6, 9, 10, 11; Map 5)

Bombus ephippiatus Say, 1837: 414.
Bombus formosus Smith, 1854: 403.
Bombus pulcher Cresson, 1863: 108.
Bombus lateralis Smith, 1879: 134.
Bombus schneideri Friese, 1903: 253.
Bombus (Bombus) ephippiatus; Franklin, 1913: 86.
Bombus (Bombus) pulcher; Franklin, 1913: 91.
Bremus folsomi Frison, 1923: 322.
Bremus ephippiatus var. *variegatus* Frison, 1925: 139.
Bombus vau-flavus Cockerell, 1949: 486.

PILE: Dense, longest hairs two times length of tegula. This species is extremely variable in coloration. In general, head and notum are black with side of thorax yellow; T-l and mediobasal portion of T-2 (sometimes T-3) yellow, contrasting in color with T-4 to T-6 (T-7 males) which are black, and with sides of T-2 and T-3, which are reddish or black.

Queens in México and northern Central America with head and notum black; sides of thorax and T-l yellow; T-2 varying from yellow with some reddish hairs on posterior corners to a line of yellow hairs mediobasally and rest of tergum reddish; other specimens mediobasally covered with yellow and reddish hairs and sides with reddish and black ones. T-3 varying from mediobasally yellow and sides reddish, to mediobasally reddish and sides black; T-4 usually black but sometimes reddish ferrugineous. T-5 and T-6 always black. Some queens with yellow pile on axillae from few hairs to a patch, also with yellow hairs on center of pronotum. Workers in Mexico from Chihuahua to Oaxaca similar to queen, few specimens more yellowish, even with some yellow hairs on scutum.

Males from Chihuahua to Oaxaca with face and vertex black to mixture of long, simple, black and short, plumose, whitish hairs; some specimens with whitish predominant; several specimens with long yellow hairs on outer margin of mandible; notum black or with some yellow hairs on pronotum. T-l yellow, a few specimens with reddish hairs on sides; T-2 varying from yellow with few reddish hairs, to mediobasally yellow and sides reddish. T-3 varying from yellow to mediobasally yellow and sides black; many specimens with reddish hairs on sides; T- 4 black, few individuals with anterior margin yellow or with whole tergum yellow. T-5 to T-7 black. Sterna black posterior margin of S- 6 with several yellow hairs; some specimens with sterna all yellow. Legs black with yellow hairs on posterior margins of tibiae, especially on distal corners; specimens with sterna yellow have legs yellow-haired.

Queens in southern Central America (Costa Rica and Panamá) with head black to mixed black and reddish, reddish hairs more abundant on labrum (anterior margin); genal area mainly black; notum reddish ferrugineous, sides of thorax yellow. T-l yellow; T-2 reddish but some yellow hairs in middle; T-3 to T-5 reddish, T-6 black. Legs black except on posterior margin of corbicula, to black and reddish; reddish hairs on posterior margin from coxa to tibia and around corbicula. Metasomal sterna yellow along posterior margins. Workers from Chiapas to Panamá black except yellow on anterior margin of labrum, sides of thorax, axillae, T-l, and middle of T-2. Some specimens with several yellow hairs on vertex and pronotum.

Males from Chiapas to Panamá, with mixture of long, black, simple and short, yellowish, plumose hairs on vertex and face; outer margin of mandible with long reddish hairs; genal area with long yellow hairs; notum with mixture of black and reddish, red ones mainly on pronotum; side of thorax and T-l yellow; T-2 mainly yellow but sides black; T-3 mediobasally reddish, rest of tergum black; T-4 to T-7 black. Legs reddish, especially on posterior margins and tibiae; some specimens with face, vertex and notum yellow; T-2 yellow but a few black hairs on sides, T-3 black but some yellow hairs on center. Few specimens with mixture of black and reddish hairs on legs.

QUEEN: Length 16 to 20 mm. UID 3.0 to 3.3 mm, LID 3.3 to 3.5 mm. Ocelli just below supraorbital line. OOD little more than 2.0 times lateral ocellar diameter. IOD approximately the same as OOD. Clypeus coarsely and moderately punctate, middle disc sparsely and finely punctate and hairless. Clypeus in profile protuberant for distance at most two-thirds width of malar space. Malar space 0.2 to 0.3 wider than long. Thoracic width between wing bases 6.5 mm. Mesobasitarsus 3.0 times as long as wide. T-2 width 10 mm.

WORKER: Similar to queen except as follows: malar space 1.5 times wider than long. Clypeus more evenly punctate and less prominent, usually protuberant for 0.5 times malar space width. Other parts proportionally reduced in size.

MALE: Similar to queen except as follows: length 15 mm. UID 2.3 mm, LID 2.5 mm. Ocelli on supraorbital line. OOD almost three times lateral ocellar diameter. Clypeus finely and evenly punctate. Mesobasitarsus 4.0 times as wide as long. Genital capsule highly variable in morphology, especially inner margin of squama and apical portion of gonostylus.

DISTRIBUTION: This species is found from Chihuahua to Panamá. Franklin (1913) recorded

B. ephippiatus from Colombia, Ecuador, and (as *B. pulcher*) from Venezuela. The species may be there, but I have not seen material from South America. The distributional pattern and altitude correspond with the Bosque de Pino y Encino, and the Bosque Tropical Caducifolio in México (Rzedowski, 1978). However, *B. ephippiatus* can be found in drier habitats such as the Matorral Xerófito in the Altiplano Mexicano. It can fly at low altitudes in southern México and Central America; rarely specimens have been taken at sea level where they may be in Bosque Tropical Perennifolio (Rzedowski, 1978). One record from La Venta, Tabasco, is probably from such vegetation (locality not indicated in the map).

The seasonal distribution of this species is all year long. In northwestern México (Chihuahua, Sinaloa, Durango, Nayarit) it has been found in January and April to November. The altitudinal distribution is 1600 to 2600 m. In the Eje Volcánico Transversal (Jalisco, Michoacán, Estado de México, Morelos, Distrito Federal, Puebla) and the Altiplano Mexicano (Hidalgo, Queretaro, Guanajuato, Zacatecas), I have seen specimens taken from January to December except March. The altitudinal distribution is 1200 to 3400 m. I have seen specimens taken on the Gulf side (Nuevo León, San Luis Potosí, Veracruz, Tabasco) in January, March, and May to December. The altitudinal distribution is 1000 to 2400 m; the lower altitude corresponds with the upper limit of the Bosque Tropical Perennifolio. I have seen specimens taken in the Sierra Madre del Sur (Guerrero, Oaxaca) from May to October and December: they may not be active from January to May since these months correspond with the drier period. The altitudinal distribution is 1900 to 2800 m. The lower limit could be related to the lack of collections or to the drier conditions and change in vegetation. I have records throughout the year for southern México (Chiapas) and northern Central America (Guatemala, Honduras, El Salvador). The altitudinal distribution is 1200 to 3900 m. The lower altitude corresponds with the upper limit of the Bosque Tropical Perennifolio for the zone (Rzedowski, 1978). I also have records throughout the year for Southern Central America (Costa Rica and Panamá). The altitudinal distribution is 200 to 3400 m; they are more commonly found above 1000 m (Laverty and Plowright, 1985) but they can be collected near sea level (Janzen, 1971).

LOCALITIES: Chihuahua: Gaborachic, Creel, Río Urique (between Creel and La Bufa), Madera. Durango: La Campana (3 km W El Salto), Paraíso, Las Adjuntas, La Ciudad, Tepalcates, El Palmito, El Palmito ''Sinaloa'', Potrerillos ''Sinaloa''. Sinaloa: Villa Unión, Copala, Mazatlán (75 km E). Nayarit: Ahuacatlán, Cerro del Sanganguey (near Tepic). Zacatecas: Zacatecas. Guanajuato: Guanajuato (5 km N). Jalisco: Volcán Tequila, Mazamitla (10 km S), Nevado de Colima, Atenquiqui, Jiquilpan. Michoacán: Hidalgo, Zitacuaro, Morelia, Pino Gordo, Patzcuaro, Tuxpan, Quiroga, San Juan de la Vina, Zacapu, Tancitaro, Macho de Agua. Estado de México: Tequesquinahuac (Cerro Tlaloc), Toluca, Chapingo, Temascaltepec (Real de Arriba), Río Frio, Valle de Bravo, Atlapulco, Tenancingo, Necaxa, Lengua de Vaca. Morelos: Cuernavaca, Tepoztlán, Laguna de Zempoala, Derrame Volcán Chichinautzin (near Cuernavaca), Coahuila, Huitzilac. Distrito Federal: Popocatépetl (N slope), Tacubaya, Contreras, Ajusco, Xochimilco, Desierto de los Leones. Queretaro: Vizarron. Hidalgo: Jacala, El Chico (near Pachuca), Chalpulhuacan, Real del Monte. San Luis Potosí: Tamazunchale, Xilitla. Nuevo León: Iturbide (10 km W), Galeana, San Juanito (20 km N), Los Altares. Puebla: Villa Juárez, Camino Taitic, Chapulco, Huauchinango, Teziutlán. Veracruz: Acatenango, Naolinco, Nacimiento Río Atojac, Fortin de las Flores, Santa Rosa (Teocelo), Ciudad Mendoza, La Joyita, Jalapa, Monte Pío (Los Tuxtlas), Calcahualco, Coscomatepec, Tecolutla, Misantla, Naolinco, Huatusco, Las Vigas, Orizaba, Coatepec, Volcán Citlaltépetl (Pico de Orizaba). Guerrero: Omilteme, Chilpancingo (6 km W). Oaxaca: La Esperanza (60 km NE), Oaxaca, El Tejocote (50 km N), Nochixtlan (10 km SE), Puerta del Sol (250 km N), Guelatao (30 km NE), Ixtlán de Juárez (18 km NE), Monte Alban. Tabasco: La Venta. Chiapas: San Cristóbal de las Casas, Chilil (Chanal), Sibaktejal (Tenejapa), Pueblo Nuevo, Simojovel, Notozintla, Tzontehuitz (Mitontik), El Porvenir, Cerro Male (El Porvenir), Villa Las Rosas, Las Margaritas, Teopisca, Tuxtla Gutiérrez, Soyalo, Comitán, Lagos de Montebello (40 km E La Trinitaria), Navenchauc (Zinacanton), San Carlomino, Rizo de Oro (near Oaxaca border), Dos Lagos (La Trinitaria), Laguna Chamula (Comitán), Volcán Takana (La Unión), Achjulum (Tenejapa), Jitotal, El Chorreadero, Ocosingo, Lomatán, Izapa, Chiapa de Corzo, Santuario Quetzal (Montebello), Arriaga. Guatemala: San Cristóbal, Cobán, Guatemala, Monte Pacaya, Cunen, Volcán Tajumulco (San Marcos), San Miguel Duenas, Yepocapa, El Rancho, Nebaj. El Salvador: Cerro Verde, Monte Cristo, Monte San Salvador, Puerto La Libertad, Chauchapa. Honduras: Sigualtepeque (16 km N), Monte Uyacu. Costa Rica: Monteverde, La Palma, Villa Mills, San José, Boruca, Volcán Irazú, Vara Blanca, Volcán Poas, Cerro de la Muerte, San Mateo, Pacayas, Tilarán, La Trinidad, Colombiana Farm, El Empalme, La Holanda, Puerto Viejo, Potrero Grande, San Isidro de El General, Volcán Barba, Concordia. Panamá: Volcán Chiriquí, Osra Clara, Balboa, Potrero Verde, Volcán Boquete, Río Candela, Bombito, Alto Lino.

COMPARATIVE COMMENTS: This species is the most commonly collected bumble bee in México and Central America. It has a wide latitudinal and altitudinal distribution. It is also highly variable in color and morphology, and therefore has been the source of many taxonomic problems. Franklin (1913) recognized two different species: *B. ephippiatus* and *B. pulcher* (= *B. formosus,* see below). Franklin's description of the former taxon I think was based on specimens from southern Central America (Costa Rica and Panamá); that of *B. pulcher* on specimens collected in central México and northern Central America. Franklin recognized that his two taxa were much alike except for the coloration of queens and some differences in the male genitalia. Milliron (1962), on the contrary, divided this group into two species, *B. schneideri* (see below) from Central America, and *B. ephippiatus.* This last was then subdivided into three subspecies: *B. ephippiatus ephippiatus, B. ephippiatus formosus,* and *B. ephippiatus pretiosus.* The first two correspond to Franklin's two species and may have different altitudinal preferences. The last subspecies was from southern México and Central America (northern), and in the words of Milliron is the "southernmost population . . . tending toward *B. e. ephippiatus."* However, in his list of 1973b, Milliron does not mention *B. e. pretiosus* but instead lists *B. ephippiatus vauflavus* which in 1962 he placed as a synonym of *B. ephippiatus ephippiatus.* In none of his works does Milliron give reasons for the separation or fusion of the different taxa, or for the change of some synonyms to full species status. For example, *B. schneideri* was placed by Franklin as a synonym of *B. ephippiatus;* however, Milliron recognized it as a distinct species. I think the two species (Franklin's sense) or two species and three subspecies (Milliron's sense) are a single species, as shown by the intergradation of color and male genital morphology.

The chromatic variation is particularly interesting since it is different for queens than for workers and males. From Chihuahua (México) south to Honduras queens are of the black and yellow form, with the sides of T-2 and T-3 and sometimes T-4 reddish. However, in Costa Rica and Panamá they are abruptly different, largely reddish (see description of pile above). On the other hand, workers and in a similar fashion males show a gradual change in coloration. From Chihuahua to Oaxaca (México) they are similar to the queens; however, in Oaxaca there is a shift in the color of the sides of T-2 and T-3 from red to almost black. This yellow and black form is predominant from Chiapas (México) to Panamá. Hence workers and males look very different from the queens in all of Central America.

The genital capsule of the male varies in a gradual way. The gonostylus, the inner margin of squama, and the basal portion of gonocoxite show a gradient from Chihuahua to Panamá. These changes, even when gradual, are sometimes difficult to understand, since an altitudinal factor also appears to affect these characters.

Some other characters besides the above mentioned, which could be important in a study of variation in this species are the following: the ocellar area in some queens is large and clearly defined, while in others from different areas it is small and poorly delimited. The punctation of the clypeus, the shape of the middle and hind basitarsus of both sexes, and the hind tibia (corbicular area) of males also vary. A statistical study of the morphological and color variation of this species is needed, to show the correlation between morphology and latitudinal and altitudinal distribution. Too many of the available museum specimens lack altitudinal data, and in a topographically rough country one cannot be sure from stated localities that specimens were taken at the altitude of the places indicated on the labels.

The names *B. pulcher* and *B. formosus* were for some years the subject of argument. Since Smith's type of *formosus* could not be found and the name suggested an oriental origin to Franklin (1913), he considered *B. pulcher* the correct name for the species. However, Meade-Waldo in 1916 found Smith's type, and demonstrated that it was from Oaxaca, México; see also Frison (1925).

TYPES: Say's type of *B. ephippiatus* is lost. Franklin's males of *B. ephippiatus* ("Cotypes") are in the National Museum of Natural History, Washington, but of course are not genuine types. Smith's types of *B. formosus* and *B. lateralis* are in the British Museum (Natural History), according to Meade-Waldo (1916). The type of *B. pulcher* is in the Naturhistorische Hofmuseum, Vienna. The type of *B. schneideri* is in the Zoologisches Museum der Humboldt-Universität, Berlin. The type of *B. folsomi* is in the Academy of Natural Sciences of Philadelphia. It supposedly came from Borneo but must have been mislabeled (Starr, 1989). The type of *B. e. variegatus* is in the Museum of Zoology, Univ. of Michigan, Ann Arbor. The type of *B. vau-flavus* is in the National Museum of Natural History, Washington.

Bombus (Pyrobombus) wilmattae Cockerell

(Figs. 6, 9, 10, 11; Map 3)

Bombus ephippiatus var. d. Handlirsch, 1888: 233.
Bombus lateralis wilmattae Cockerell, 1912: 21.
Bombus guatemalensis Franklin, 1912: 196, nomen nudum.
Bombus wilmattae; Franklin, 1913: 100.
Bombus (Bombus) alboniger Franklin, 1915: 409 (new synonym).
Pyrobombus wilmattae; Milliron, 1962: 732.
Pyrobombus alboniger; Milliron, 1962: 732.

PILE: Dense, longest hairs as long as tegula. Queen with pile on vertex and face black, or with mixture of black and yellowish hairs; some specimens with head all black. Anterior margin of labrum with a row of reddish hairs; thorax black haired, with pronotum, side of thorax and scutellum yellow or white haired. T-1 yellow or white; T-2 yellow or white mediobasally, and sides black; T-3 with yellow or white hairs on center and rest of tergum black, some specimens with tergum all black; T-4 to T-6 black. Legs black, some specimens with yellowish hairs on anterior margins of trochanters and basal corners of femora; others with reddish hairs on distal parts of tibiae. Worker darker, without yellow or whitish hairs below antennae and few on legs. Male with yellow or whitish hairs on clypeus and gena; mandible with long reddish hairs. Sternal pile sometimes yellowish- reddish, mainly on S-6. Some specimens with legs reddish.

QUEEN: Length 20 mm. UID 3.1 mm, LID 3.5 mm. Ocelli below supraorbital line. OOD two to three times lateral ocellar diameter. IOD approximately the same as OOD. Clypeus sparsely and coarsely punctate on sides and upper margin. Clypeus in profile protuberant for distance at most width of malar space. Malar space 25 to 50 wider than long. Thoracic width between wing bases 6.0 mm. Mesobasitarsus two to almost three times as long as wide. T-2 width 9.0 mm.

WORKER: Similar to queen except length varies from 10 to 16 mm. Parts proportionally reduced in size.

MALE: Length 12 mm. UID 2.3 mm, LID 2.3 mm. Ocelli on supraorbital line. OOD two times lateral ocellar diameter. Clypeus finely and evenly punctate. Clypeus protuberant 1.5 times width of malar space. Malar space as wide as long. Thoracic width between wing bases 4.0 to 5.0 mm. Mesobasitarsus four times as long as wide. T-2 width 5.0 to 7.0 mm.

DISTRIBUTION: This species is restricted to the Altos de Chiapas y Guatemala. Its distribution corresponds to that of the Bosque de Pino y Encino and the Bosque Tropical Caducifolio of Rzedowski (1978).

The species is probably in flight all year long. I have seen specimens taken throughout the year except January, May, June, and September. The altitudinal distribution is 600 to 2200 m.

LOCALITIES: Chiapas: El Chorreadero, Motozintla, El Porvenir, Mitontik, Navenchauc, La Unión (Volcán Takana), Chiapa de Corzo, San Cristóbal de las Casas. Guatemala: Chimaltenango, Ciudad de Guatemala, Monte Pacaya, Puerta Parada, San Miguel Duenas, Acatenango, Santa Rita (Nahuala), Huehuetenango, Panajachel (Solola), Chichicastenango, Cunén, Antigua, San José Pinula, Cerro Zunil.

COMPARATIVE COMMENTS: This species was originally described as two different taxa (Cockerell, 1912; Franklin, 1915). In 1962 Milliron commented on the morphological similarities of *B. alboniger* and *B. wilmattae*. However, in his list of 1973 he still separated them as two different species. Morphologically these two forms are identical. The male genitalia show a gradient of variation. The pile coloration was always an important point to differentiate these two, *B. wilmattae* having a yellow-black pattern and *B. alboniger* a white- black one. However, I have seen several specimens from Chiapas with a mixture of yellow and white pile; other specimens have whitish on the metasomal and thoracic sides and yellowish on the pronotum and middle portions of the metasomal terga. Consequently I think these two forms are the same species.

Moreover, the separation of *B. wilmattae* from *B. ephippiatus* is in doubt. Franklin in 1915 thought *B. alboniger* was close to *B. pulcher* (= *B. formosus* = *B. ephippiatus*). I have not found any clear differences between *B. wilmattae* and *B. ephippiatus,* as they occur in the same area. In fact, *B. wilmattae* was originally described by Cockerell as a subspecies of *B. lateralis,* a synonym of *B. ephippiatus.* The male genitalia appear slightly different, but when one considers the range of morphological variation within *B. ephippiatus,* the possibility that these forms intergrade is evident (see Figs. 9B, 9G). The only constant character that I have found to separate *B. wilmattae* is the coloration of the pronotum, which is always black in *B. ephippiatus,* yellow or white in *B. wilmattae.* Some specimens from Chiapas, however, have the sides of pronotum black and only a patch of yellow or white hairs on the middle. They thus closely approach *B. ephippiatus.* I have also studied one paratype of *B. alboniger* from Cerro Zunil, Guatemala, in which the sides of the pronotum have a mixture of yellow and black hairs (see above comments on *B. nigrodorsalis* for a similar problem).

A more detailed study in Chiapas and Guatemala is needed to demonstrate the true relationship of the two taxa. Cockerell (1912) after his description of *B. wilmattae* makes the following comments: "The original *B. lateralis* Sm. was described from the mountains of Guatemala, at a higher altitude than the localities of *wilmattae.* I think it is probable that the difference is only racial, the form from the higher altitudes being more melanic."

The so called "queen type" of Franklin (1913) of *B. wilmattae* was recorded as from Ecuador. I doubt this species reaches that country. The description does not fit very well with the specimens I have seen.

TYPES: Cockerell's type is in the Academy of Natural Sciences of Philadelphia, according to Cockerell, 1912. Franklin's type of *B. alboniger* is in the British Museum (Natural History). The type localities for both are in Guatemala.

Bombus (Cullumanobombus) rufocinctus **Cresson**
(Figs. 6, 8, 10, 11; Map 7)

Bombus rufocinctus Cresson, 1863: 106.
Bombias rufocinctus; Swenk, 1907: 295.
Bombus (Bombias) rufocinctus; Franklin, 1912: 438.
Bombus (Bombias) mexicensis Franklin, 1913: 138.
Bombus rufocinctus; Stephen, 1957: 62.
Pyrobombus (Cullumanobombus) rufocinctus; Milliron, 1973b: 317.

NOTE: The description given below is based on Mexican specimens only.

PILE: Dense, longest hairs as long as tegula. Queen head black with few yellow hairs around antennae and on vertex; pronotum, scutellum and side of thorax yellow; scutum black. T-l yellow; T-2 to T-4 reddish with some yellow hairs intermixed, especially mediobasally on T-2; T-5 to T-6 black. Sterna and legs black. Worker head black; T-2 almost all yellow.

QUEEN: Length 14.0 to 16.0 mm. UID 2.6 mm. LID 2.8 mm. Ocelli just below supraorbital line. OOD two times lateral ocellar diameter. IOD 10 shorter than OOD. Clypeus sparsely and finely punctate. Clypeus in profile protuberant for distance at most three-fourths width of malar space. Malar space 50 wider than long. Thoracic width between wing bases 7.0 mm. Mesobasitarsus 3.0 times as long as wide. T-2 width 9.0 mm.

WORKER: Similar to queen but smaller, length 9.0 to 10.0 mm. Parts proportionally reduced in size.

MALE: See below under comments.

DISTRIBUTION: This species has a broad distribution in the U.S.A. and Canada (Stephen, 1957; Milliron, 1973b; Thorp et al., 1983). In México, all the specimens seen are from the Eje Volcánico Transversal. Its pattern of distribution and altitude corresponds with the Bosque de Pino of Rzedowski (1978).

I have seen specimens collected in June, July and October. The altitudinal distribution is 2000 to 4000 m.

LOCALITIES: ESTADO DE MÉXICO: Toluca, Santa Elena (Toluca). DISTRITO FEDERAL: Volcán Popocatépetl, Desierto de los Leónes.

COMPARATIVE COMMENTS: This species shows great color variation in North America. For many years it was separated into various different species, or as distinct color variants each one with a particular name. However, Stephen (1957) demonstrated that all these color variants are part of a continuum in variation, and recognized *B. rufocinctus* as a polymorphic taxon. Later, Milliron (1973b) considered that *B. mexicensis* was a color variant of this species, although possibly isolated by a long distance from the rest of the species' range.

This species is rarely collected in México. The few females I have seen are similar in morphology and coloration. Franklin described B. mexicensis based in four queens. I have studied both female castes but no male from México. Milliron (1973b) recorded two males from Ixtlahuaca (Estado de México?), in the Instituto Nacional de Investigaciones Agrícolas (Chapingo, México); I could not find these specimens, however. The coloration of North American *B. rufocinctus,* according to Stephen (1957) and Thorp et al. (1983), varies without correlation with known biogeographic factors.

The male genitalia are characteristic; particularly important is the shape of squama (Fig 8F). I have studied the male genitalia of specimens found in U.S.A. and Canada; they do not show much variation despite the differences in altitude and latitude.

TYPES: Cresson's type is in the Academy of Natural Sciences of Philadelphia. Type locality: Colorado (Pike's Peak), U.S.A. Franklin's type of *B. mexicensis* in the National Museum of Natural History, Washington.

Bombus (Crotchiibombus) crotchii **Cresson**
(Figs. 6, 9, 10, 11; Map 3)

Bombus crotchii Cresson, 1878: 184.
Bombus nigrocinctus Provancher, 1888: 342.
Bombus improbus Howard, 1901: pl. 2, fig. 13 (nec Cresson, 1878).
Bombus (Bombias) crotchii; Franklin, 1912: 434.
Bremus crotchii var. *nigricaudata* Frison, 1927: 375.
Bombus (Crotchiibombus) crotchii; Franklin, 1954: 51.
Bombus crotchii crotchii; Stephen, 1957: 57.
Pyrobombus (Cullumanobombus) crotchii; Milliron, 1973b: 256.

PILE: Dense, longest hairs two-thirds as long as tegula. Queen head and thorax black, notum in front of tegula yellow. T-l black, T- 2 yellow but mediobasally black; T-3 to T-6 black; some specimens with T-5 and T-6 yellow-reddish, others even with T-4 reddish; legs and metasomal sterna black. Workers similar to queen but metasomal terga more variable; T-5 and T-6 yellow, posterior margin of T-4 sometimes also yellow. Male head and thorax yellow, but a narrow black interalar band on scutum; mesepisternum with yellow pile extending from lateral lobe of pronotum to coxal bases; some specimens with lower portion of mesepisternum mixed with black hairs, other specimens with yellow only on upper middle; T-l and T-2 yellow, basal portion of T-l usually black; T-3 to T-7 black or in some specimens T-3 black, T- 4 to T-7 mediobasally black and sides yellow; or metasomal terga all yellow.

QUEEN: Length 20 to 28 mm. UID 2.8 mm, LID 3.5 mm. Ocelli below supraorbital line. OOD 1.3 times lateral ocellar diameter. IOD 0.25 more than OOD. Clypeal punctation moderately coarse, especially punctate on sides and upper margin; middle disc almost smooth. Clypeus in profile protuberant for a distance at most width of malar space. Malar space 30 wider than long. Thoracic width between wing bases 6.5 mm. Mesobasitarsus four times as long as wide. T-2 width 8.0 mm.

WORKER: Similar to queen but smaller,

length 12.0 mm. Parts proportionally reduced in size.

MALE: Length 16.0 mm. UID 1.6 mm, LID 2.2 mm. Ocelli well below supraorbital line. OOD half lateral ocellar diameter. IOD 3.5 times OOD. Clypeus densely and finely punctate. Clypeus protuberant for width of malar space. Malar space 1.5 times wider than long. Thoracic width between wing bases 5.5 mm. Mesobasitarsus almost six times as long as wide. T-2 width 7.0 mm.

DISTRIBUTION: This species is restricted to California (U.S.A.) and northern Baja California Norte (México).

I have seen Californian specimens collected from June to September; Milliron (1973b) commented that this species flies as early as March. The altitudinal distribution in California is from sea level to 2500 m.

LOCALITIES: Baja California Norte: El Progreso (Sierra de Juárez).

COMPARATIVE COMMENTS: I have seen only one specimen from Mexico (queen); it fits the description of Frison's variety *nigricaudata*. However, I have also studied several typical specimens of *B. crotchii* from California. This species is one of the largest and most distinctive bumble bees.

This species was placed by Franklin (1912) in the fraternus group; later Stephen (1957) put it in the subgenus *Separatobombus* and Milliron (1973b) in *Pyrobombus (Cullumanobombus)*. However, Franklin (1954) erected the subgenus *Crotchiibombus* especially for it, an idea that was accepted by Richards (1968) and Ito (1983). I think this species is quite different from other bumble bees except *B. haueri*.

TYPES: The type of *B. crotchii* is in the Academy of Natural Sciences of Philadelphia (Cresson, 1916, lectotype). Type locality: California (U.S.A.). The type of *nigricaudata* is in the California Academy of Sciences, San Francisco.

Bombus (Crotchiibombus) haueri Handlirsch

(Fig. 6; Map 3)

Bombus haueri Handlirsch, 1888: 234.
Bombus haueri; Franklin, 1907: 91.
Bombus (Bombias) haueri; Franklin, 1913: 141.
Alpigenobombus haueri; Skorikov, 1922: 156.
Megabombus (Bombias) haueri; Milliron, 1961: 56.
Pyrobombus (Cullumanobombus) haueri; Milliron, 1973b: 305.

PILE: Dense, longest hairs three-fourths length of tegula. Queen head and thorax black, but yellow on notum in front of tegula and scutellum, hence with a black interalar band on posterior portion of scutum; T-l and T-2 yellow, T-3 to T-6 reddish; legs and sterna black. Workers with T-3 basally yellow, and reddish coloration less intense.

QUEENS: Length 18.0 to 22.0 mm. UID 3.0 mm, LID 3.5 mm. Ocelli below supraorbital line. OOD 2.0 times lateral ocellar diameter. IOD 0.15 more than OOD. Clypeus coarsely and densely punctate, especially on sides and upper margin. Clypeus in profile protuberant for distance at most width of malar space. Malar space 30 to 40 wider than long. Thoracic width between wing bases 8.0 mm. Mesobasitarsus almost 4.0 times as long as wide. T-2 width 12.0 mm.

WORKER: Similar to queen except as follows: Length 14 to 16 mm. Malar space one-fourth wider than long. Other parts proportionally reduced in size.

DISTRIBUTION: This species is restricted to the Altiplano Mexicano and adjacent mountains. The pattern of distribution corresponds with the grassland and pine forest vegetation (Rzedowski, 1978).

I have seen specimens captured from June to October. The altitudinal distribution is 1700 to 2500 m.

LOCALITIES: Chihuahua: Catarinas. Durango: Coyotes, Palos Colorados, El Salto. Coahuila: Lirios. Jalisco: San Juan de Los Lagos. Michoacán: Zitacuaro, Zacapu, Ciudad Hidalgo. Estado de México: Atlacomulco, Chapingo, Toluca. Distrito Federal: Cuajimalpa, Tlalpan, Guadalupe (Villa de ?), Teotihuacán, km 16 hwy México-Toluca. Morelos: Cuernavaca. Nuevo León: Providencia.

COMPARATIVE COMMENTS: This is a rare species, but very characteristic in morphology and coloration. I have not seen much variation except in the color of pile on T-3.

This species was placed by Franklin (1913) in the fraternus group. Milliron first placed it in *Megabombus* (1961), and later in *Pyrobombus (Cullumanobombus)* in a group called dentatus (1973b). The external morphology of the females is similar to that of *B. crotchii;* moreover the dentatus group is Southeast Asian (Milliron, 1973b). Franklin also (1913) considered that the closest relative of this species was *B. crotchii*.

Only one male of this taxon has ever been found, captured in Eslava, D.F. (Franklin, 1907). I have not found this specimen, however. The queens are the most frequently collected form, a fact that may suggest social parasitism.

TYPE: In the Naturhistorisches Hofmuseum, Vienna. Type locality: Tacubaya, D.F., México.

Bombus (Brachycephalibombus) brachycephalus Handlirsch

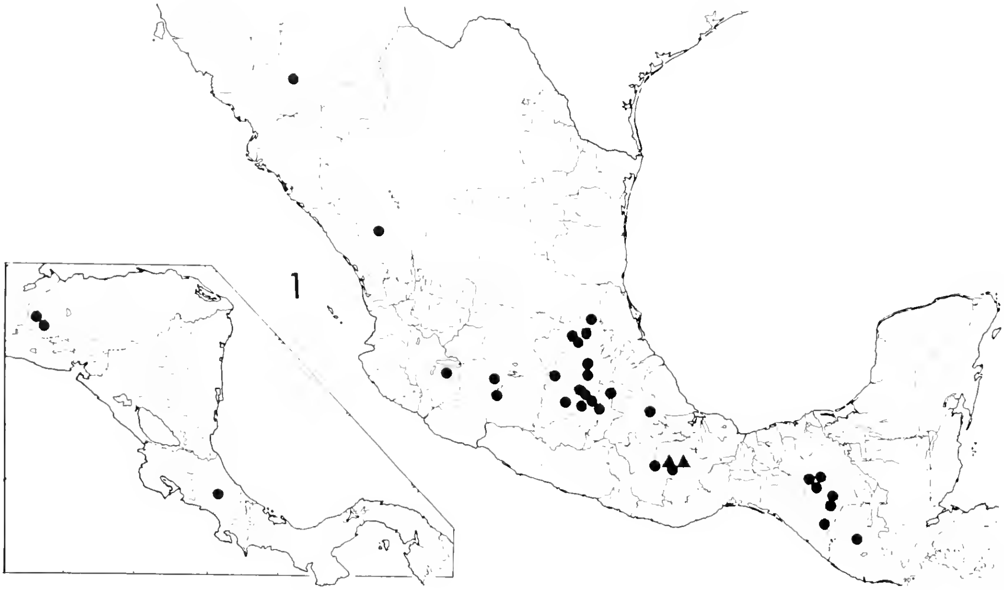
(Figs. 2, 4, 6, 9, 10, 11; Map 9)

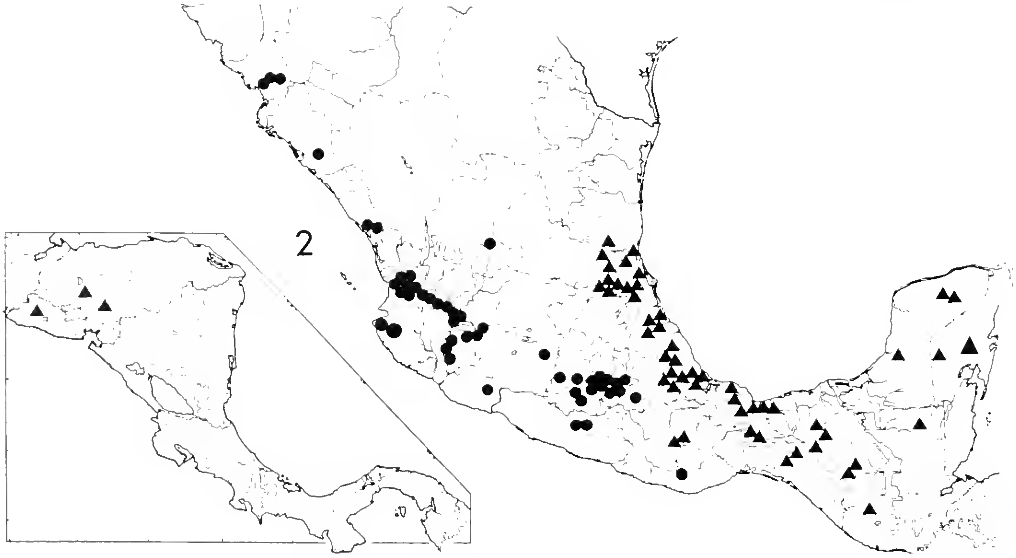
Bombus diligens Smith, 1861: 154 (part).
Bombus brachycephalus Handlirsch, 1888: 244.
Bombus (Bombias) brachycephalus; Franklin, 1913: 143.
Alpinobombus brachycephalus; Skorikov, 1922: 156.
Bremus neotropicus Frison, 1928: 151.
Pyrobombus (Cullumanobombus) brachycephalus; Milliron, 1973b: 259.

PILE: Moderately dense, longest hairs one-half length of tegula. A geographically variable species, in general terms black with some reddish or yellow hairs on metasoma. One morph found in Central México has females all black except for orange-reddish pile on T-4 to T-6 and grayish hairs on vertex and notum in front of tegula. Males of this form are similar to females but vertex and thoracic hairs with a more yellowish hue; T-7 also orange-reddish.

In southern México and Central America queens are always black. Workers can be either all black or black with T-2 yellow on sides; the latter form sometimes has T-5 also covered with yellow pile. Hence, there are two different morphs of workers in this area. Males are highly variable; some are all black except yellow on last two or three segments at sides, others with yellow on notum, sides of thorax and each metasomal segment.

QUEEN: Length 16.0 to 18.0 mm. UID 2.8 mm, LID 3.4 mm. Ocelli below supraorbital line. OOD 1.5 times lateral ocellar diameter. IOD 0.25 more than OOD. Clypeus densely and



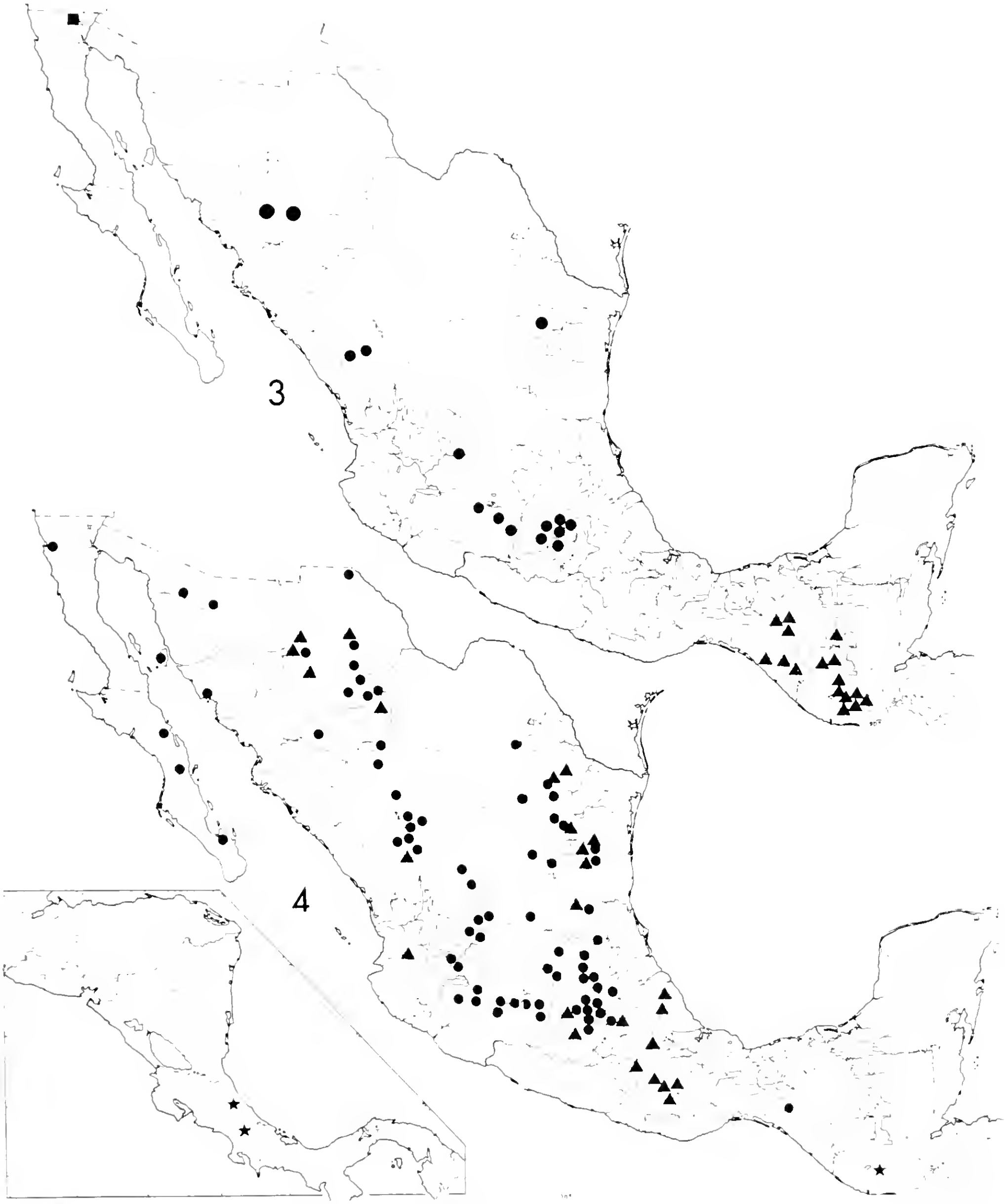


Map 1. Distribution of bumble bees in México and Central America: circles, *B. weisi;* triangles, *B. trinominatus.* **Map 2.** Distribution of bumble bees in México and Central America: circles, *B. steindachneri;* triangles, *B. medius.*

coarsely punctate. Clypeus in profile protuberant for distance at most width of malar space. Malar space 0.3 wider than long. Thoracic width between wing bases 7.0 mm. Mesobasitarsus three to three and a half times as long as wide. T-2 width 12.0 mm.

WORKER: Similar to queen except as follows: Length 14.0 mm. Malar space variable, from quadrate to 25 wider than long. Other parts proportionally reduced in size.

MALE: Length 16.0 mm. UID 1.7 mm, LID 2.3 mm. Ocelli well below supraorbital line. OOD half lateral ocellar diameter. IOD almost 3.0 times OOD. Clypeus elongate, finely and densely punctate, protuberant for width of malar space. Malar space 30 longer than wide. Thoracic



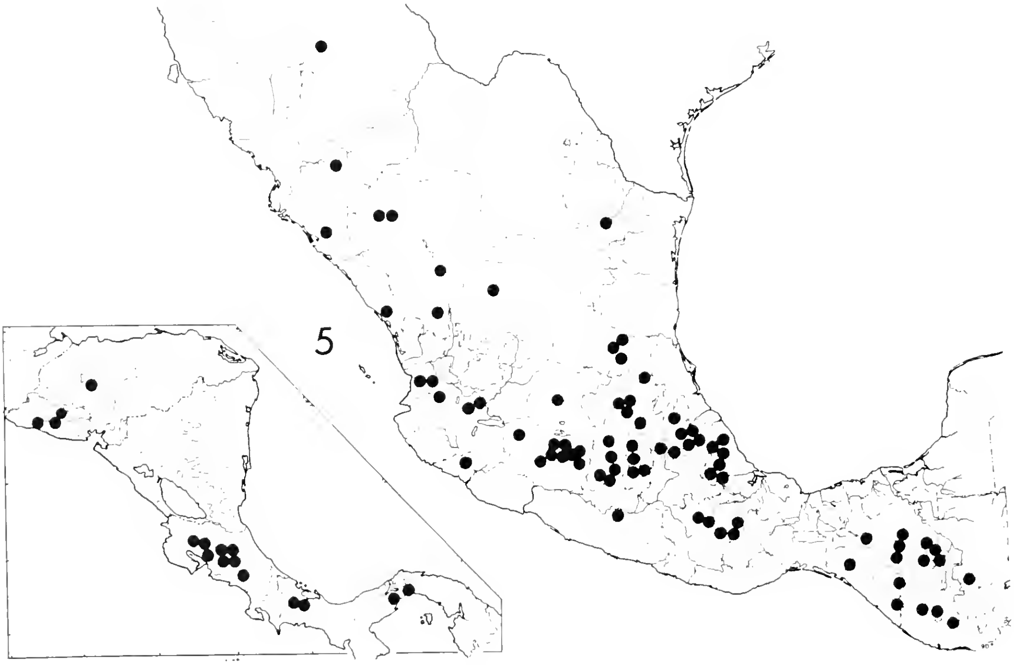
Map 3. Distribution of bumble bees in México and Central America: circles, *B. haueri;* triangles, *B. wilmattae;* square, *B. crotchii.* **Map 4.** Distribution of bumble bees in México and Central America: circles, *B. pennsylvanicus sonorus;* triangles, *B. pennsylvanicus pennsylvanicus;* stars, *B. digressus.*

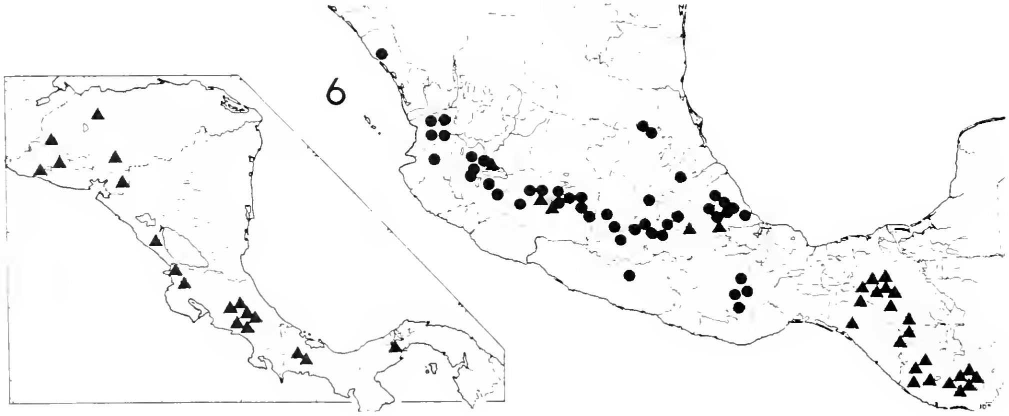
width between wing bases 5.0 mm. Mesobasitarsus little more than four times as long as wide. T-2 width 7.0 mm.

DISTRIBUTION: This species is found in mountainous areas of central México, and the highlands of Chiapas, Guatemala and Honduras. This distribution pattern corresponds to that of the Bosque Tropical Caducifolio and the Bosque de Pino y Encino (Rzedowski, 1978). However, in Chiapas it might be found in the Bosque Tropical Perennifolio, since the altitudinal data correspond to such vegetation.

From Central México, north of the Isthmus of Tehuantepec, I have seen specimens taken from July to December. The altitudinal distribution is 1000 to 2700 m. Specimens from southern México (Chiapas), Guatemala and Honduras were taken in January, February, and July to December, which suggests they are found throughout the year. The altitudinal distribution is 700 to 2700 m.

LOCALITIES: Nayarit: Tepic. Jalisco: Mazamitla, Mascota. Michoacán: Patzcuaro, Morelia, Carapán, Quiroga, Tuxpan, Tancitaro.





Map 5. Distribution of *B. ephippiatus* in México and Central America. **Map 6.** Distribution of bumble bees in México and Central America: circles, *B. diligens;* triangles, *B. mexicanus.*

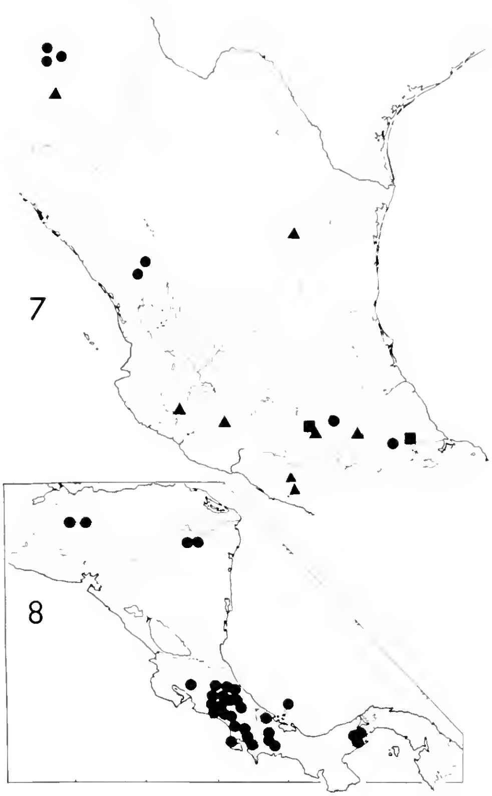
Puebla: Huauchinango, Xicotepec de Juárez. Veracruz: Acutzingo, Coscomatepec, Naolinco, Orizaba, Huatusco. San Luis Potosí: Xilitla. Guerrero: Chilpancingo. Oaxaca: Oaxaca, Juchatenango. Chiapas: Motozintla, Chiapa de Corzo, Tuxtla Gutiérrez, La Trinitaria, San Cristóbal de las Casas, Lagunas de Montebello, Yerba Buena, El Bosque. Guatemala: Monte Pacaya, Los Amates, San Cristóbal, Yepocapa. Honduras: Monte Uyacu.

COMPARATIVE COMMENTS: This species is frequently confounded with *B. diligens,* from which it can be separated using the characters given in Table 4. In Chiapas and northern Central America the two worker morphs of *B. brachycephalus* are similar to *B. mexicanus* and *B. pullatus.* The characters given under the comments on *B. mexicanus* help to differentiate workers from *B. brachycephalus.* The queens of *B. brachycephalus* in this area are similar to those of *B. pullatus;* to separate queens and workers, the ocellar area, 00D, and malar space are useful (see details in the descriptions of both species). The specimens of *B. brachycephalus* frequently have a few yellow hairs on the metasoma, especially on the last segments, whereas queens of *B. pullatus* are always completely black. Differences in distribution also exist (see comments under *B. pullatus*).

The chromatic and geographic separation of the populations found north and south of the Isthmus of Tehuantepec sugest subspecific status for the populations at either side of the Isthmus. However, I have seen a few specimens (all females, of both castes) similar to the red-tailed form of Central México, in Chiapas. For this reason, I retain this species as a unit, until more collections are made in southern México.

Despite the color variation, this species is morphologically stable. The ocellar area is always large and clearly defined, an easy character to separate this species from any taxon of Mexican and Central America *Fervidobombus.* The eyes of males are extremely swollen, with the inner margins almost touching the lateral ocelli, which are well below the supraorbital line. On the other hand, females have the eyes normal in size and the ocelli nearer to the supraorbital line. This combination of characters is characteristic of this taxon and of *B. crotchii.* But the male genitalia of *B. brachycephalus* are characteristic, with the head of the penis valve globular and bent downward and the tip hooked inward (Fig. 9C). For this reason the species has been separated subgenerically from *B. crotchii* (Williams, 1985).

TYPES: Handlirsch's type is in the Naturhistorisches Museum of Vienna, according to Milliron (1973b). Type locality: México. I think it probably was collected in central México. Smith's type of *B. diligens* is in the British Museum (Natural History). The type of *B. neotropicus* is in the Museum of Zoology, Univ. of Michigan, Ann Arbor.



Map 7. Distribution of bumble bees in México and Central America: circles, *B. fervidus sonomae;* triangles, *B. huntii* except that two southmost triangles represent *B. macgregori;* squares, *B. rufocinctus.* **Map 8.** Distribution of *B. pullatus* in Central America.

***Bombus (Robustobombus) volucelloides* Gribodo**
(Figs. 6, 9, 10, 11; Map 9)

Bombus volucelloides Gribodo, 1891: 119.
Bombus weisi Friese, 1903: 254 (male only).
B. vogti Friese, 1903: 254 (part).
Bombus leucomelas Crawford and Swenk, 1903: 268.
Bombus (Bombias) volucelloides; Franklin, 1913: 155.
Bombus (Bombias) weisi; Franklin, 1913: 148 (male only).
Bombus (Bombias) funebris; Franklin, 1913: 157 (nec Smith 1854).
Volucellobombus volucelloides; Skorikov, 1922: 149.
Bremus volucelloides; Frison, 1925: 152.
Bremus weisi; Frison, 1925: 151.
Pyrobombus (Cullumanobombus) volucelloides; Milliron, 1973b: 263.
Pyrobombus (Cullumanobombus) melaleucus; Milliron, 1973b: 267.

PILE: Dense, longest hairs as long as tegula. Queen black except for patch of whitish hairs on notum in front of tegula and T-3 to T-6 which are white. Worker similar to queen but anterior portion of T-3 black haired. Males with head yellow except vertex; thorax yellow except poorly defined interalar band and some hairs below tegula black; T-1 yellow, T-2 mainly yellow, T-3 to T-7 black; anterior surfaces of legs yellow; sterna black.

QUEEN: Length 20.0 mm. UID 3.0 mm, LID 3.8 mm. Ocelli below supraorbital line. OOD 1.5 times lateral ocellar diameter. IOD 10 wider than OOD. Clypeus finely and sparsely punctate, middle disc almost smooth. Clypeus in profile protuberant for distance at most width of malar space. Malar space 20 to 25 wider than long. Thoracic width between wing bases 9.0 mm. Mesobasitarsus little more than three times as long as wide. T-2 width 12.0 mm.

WORKER: Similar to queen except as follows: Length 12.0 to 16.0 mm. Malar space 30 wider than long. Other parts proportionally reduced in size.

MALE: Length 15.0 mm. UID 1.6 mm, LID 2.3 mm. Ocelli below supraorbital line. OOD half lateral ocellar diameter. IOD 2.5 times OOD. Clypeus densely and finely punctate, protuberant for width of malar space. Malar space 50 wider than long. Thoracic width between wing bases 6.0 mm. Mesobasitarsus five times as long as wide. T-2 width 8.0 mm.

DISTRIBUTION: This species is found in the mountainous areas of southern Central America (Costa Rica, Panamá), and South America (Venezuela, Colombia, Ecuador, Perú). In this zone it is probably found in vegetation similar to the Bosque Tropical Caducifolio of Rzedowski (1978). In Central America it may be found in Bosque de Niebla (Bosque Mesofilo de Montana, Rzedowski, 1978).

This species is probably active throughout the year. I have seen specimens collected from January to September, and in December. Its altitudinal distribution is 1400 m to 2000 m.

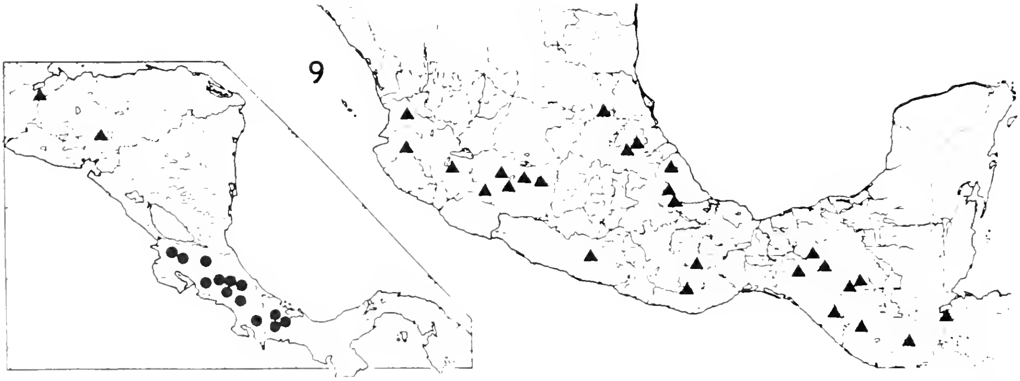
LOCALITIES: COSTA RICA: Tres Ríos, Monteverde, Turrialba, San José, San Vito, El Angel (Puerto Viejo), Cerro de la Muerte, San Mateo, Pacayas, La Suiza. PANAMÁ: Boquete, Cocte, Río Candela, Potrero Verde (Volcán), Osra Clara, Volcán Chiriquí, Río Palo Alto (Boquete).

COMPARATIVE COMMENTS: This species was placed by Franklin (1913) in the fraternus group, and by Milliron (1973b) in the subgenus *Cullumanobombus* (Volucelloides group). I think the characters of the male genitalia and external morphology of both sexes correspond better with the subgenus *Robustobombus,* as described by Richards (1968).

Until 1962 this species was known only from the female castes; Milliron (1962), however, considering the distribution and external morphology, regarded the male that was associated with *B. weisi* as the male of *B. volucelloides.* However, it is chromatically very different from *B. volucelloides* (see description above). I have no field evidence to support Milliron's opinion, which I nonetheless accept, in part because males chromatically similar to female *B. volucelloides* are unknown.

Milliron in 1962 recognized two similar taxa, *B. volucelloides* and *B. melaleucus* Handlirsch. In 1973 he gave the distribution for *B. melaleucus* as Costa Rica to Bolivia. I think this species is strictly Andean and probably not present in Central America. Milliron based his record on nine workers, which can be very similar to those of *B. volucelloides.* I have not seen specimens from Costa Rica or Panamá that can be separated from *B. volucelloides* and placed in *melaleucus.*

TYPES: The type of *B. volucelloides* is In the Museo Civico di Storia Naturale, Genoa. Type locality: Chiriquí, Panamá (Milliron, 1973b). The type of *B. vogti* is in the Zoologisches Museum der Humboldt-Universität, Berlin.



Map 9. Distribution of bumble bees in México and Central America: circles, *B. volucelloides;* triangles, *B. brachycephalus.*

Bombus (Dasybombus) macgregori Labougle and Ayala
(Fig. 6, 9, 10, 11; Map 7)

Bombus (Dasybombus) macgregori Labougle and Ayala, 1985: 47.

PILE: Dense, longest hairs two times length of tegula. Queen head all black to black with a few white hairs on vertex and around antennal bases; thorax, T-1 and anterior margin of T-2 black haired, rest of metasoma white haired. Worker similar to queen but T-2 and anterior margin of T-3 black haired, rest of metasoma white haired. Male head with a mixture of black and white pile, especially on vertex, gena and around antennal bases; thorax black haired but several gray hairs mainly on sides of thorax; metasoma as in worker.

QUEEN: Length 20.0 mm. UID 2.7 mm, LID 3.6 mm. Ocelli just below supraorbital line. OOD one and a half times lateral ocellar diameter. IOD one and one-fourth OOD. Clypeus densely and coarsely punctured, especially on upper margin and sides; middle disk less punctured, some specimens with disk almost smooth. Clypeus in profile protuberant for distance approximately same as malar space width. Malar space 25 to 50 wider than long. Thoracic width between wing bases 7.5 to 8.0 mm. Mesobasitarsus three to almost four times as long as wide. T-2 width 12.0 mm.

WORKER: Similar to queen except as follows: Length 11.0 mm. Ocelli on supraorbital line. Malar space as wide as long. Other parts proportionally reduced in size.

MALE: Length 14.0 mm. UID 1.7 mm, LID 2.2 mm. Ocelli below supraorbital line. OOD half lateral ocellar diameter. IOD three times OOD. Clypeus densely and uniformly covered with fine punctures. Clypeus in profile protuberant for distance at most width of malar space. Malar space at most 25 wider than long. Thoracic width between wing bases 5.0 mm. Mesobasitarsus six times as long as wide. T-2 width 8.0 mm.

DISTRIBUTION: This species is known only from the Sierra Madre del Sur in Guerrero. It has been collected in *Abies* forest, sometimes mixed with *Pinus* and deciduous forest elements. It probably flies all year long; specimens have been collected in January, May, July, October and November but it is not common. The only altitudinal record is 2450 m; this species is probably a high altitude taxon found above 2000 m, which corresponds with Abies forest in central México.

LOCALITIES: GUERRERO: Puerto del Gallo (Mpo. de Tlacotepec), Toro Muerto, Puerto de la Galera (Mpo. de San Miguel Totolapan).

COMPARATIVE COMMENTS: This species is morphologically very different from the other bumble bees; it has been placed in a separate subgenus (Labougle and Ayala, 1985). Its closest relatives may be *B. brachycephalus* and *B. volucelloides* but more studies are needed to establish its relationships.

Chromatically both sexes and castes are almost identical to *B. volucelloides* females. However, they are morphologically very different, smaller in size and geographically separated from the latter species. The pattern of coloration of *B. macregori* is also similar to that of *B. diligens* and the Central Mexican form of *B. brachycephalus*. Consequently, *B. macgregori* may be a member of a mimetic complex in Central México.

TYPE: In the Instituto de Biología (UNAM), México City. Type Locality: Puerto del Gallo, Guerrero, México.

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The International Standard Serial Number of this publication is US ISSN 0022-8850.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 54, No. 4, pp. 75–164 Sept. 21, 1990

Classification of the Apidae[1] (Hymenoptera)

BY CHARLES D. MICHENER[2]

Appendix: *Trigona genalis* Friese, a Hitherto Unplaced New Guinea Species

BY CHARLES D. MICHENER AND SHÔICHI F. SAKAGAMI[3]

CONTENTS

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ABSTRACT

This is a review of the classification of the family Apidae. Alternative phylogenies for the subfamilies are presented. The Meliponinae is considered in greatest detail; 21 genera are recognized. Keys are provided for genera and subgenera. Male genitalic characters, worker sting rudiments, and worker palpal characters have been little used in the past and are incorporated in this work. An African group of genera that has been regarded as ancestral in the past is here considered to be derived from an American group of genera. A new subgenus, *Papuatrigona* Michener and Sakagami, is described for *Trigona genalis* Friese from New Guinea. The subfamilies Euglossinae, Bombinae, and Apinae are treated in less detail, but with keys to genera and synonymies.

INTRODUCTION

This is an account of the classification of the family Apidae in the sense of Michener (1974), Sakagami and Michener (1987) and many others. So understood, the Apidae includes four taxa here considered subfamilies: the Meliponinae (stingless honey bees), Euglossinae (orchid bees), Bombinae (bumble bees), and Apinae (honey bees). As explained by Sakagami and Michener (1987), the Apidae appears to be the sister group of the Xylocopinae, which is currently usually included in the Anthophoridae. This arrangement probably will be changed when studies of the higher categories of bees are finished. If the Anthophoridae is then united with the Apidae, the Apidae in the present sense will probably become the subfamily Apinae, and the four current subfamilies will be tribes. The classification would then be that of Michener (1944). But for the time being it is sufficient to note that the Apidae in the present sense appears to be a holophyletic clade unless its complex pollen-manipulating behavior and associated structures arose independently in two or more subfamilies. This possibility seems unlikely because of other synapomorphies.

The following character states are well known synapomorphies of the Apidae, although they have been lost in parasitic genera and in queens of highly social forms (Meliponinae and Apinae): Corbicula present on outer surface of hind tibia in females. Rastellum (comb of setae across inner surface of apex of hind tibia) present in females (weak in some Meliponinae). Hind basitarsus of female articulated near anterior end of apex of tibia. These character states are, of course, associated with the pollen-carrying and manipulation behaviors which are distinctive for Apidae (Michener, Winston and Jander, 1978). Other synapomorphies of the family are: Basitibial plate completely absent. Pygidial plate completely absent. Maxillary palpus reduced, one or two segmented. Nests usually constructed in large or irregular cavities, cells built up rather than excavated in the substrate. (In most other bees although not in many Megachilidae cells and burrows are excavated into a substrate. Sakagami [1966] has pointed out that the ability to excavate in substrates, so obvious in Anthophoridae, is virtually absent in Apidae. This is presumably a synapomorphy, although Bombinae and Meliponinae often enlarge subterranean cavities and young queens of the former excavate hibernacula in the soil.)

Listed below are other character states that show that the four subfamilies of Apidae are related to one another, i.e., that no one of them is an anthophorid group that has convergently evolved the external features of Apidae. These characters suffer from not having been examined in many species; yet they have been examined in various species of each subfamily and appear to be family characteristics.

Cephalic salivary glands present and formed of many alveoli. In other families these glands are tubular (sometimes locally expanded) or absent (Cruz-Landim, 1967).

Hypopharyngeal glands attenuate, usually pedunculate, each discharging through a single duct. In other families these glands are usually shorter, sessile, crowded against the hypopharyngeal plate or rods, the single duct at each side absent or hidden among the acini (Cruz-Landim, 1967).

Thoracic salivary glands made up of short, simple tubes, quite distinct from collecting ducts; cells cubical and secretory tubes formed by cuboid cells. In other families the tubes are of diverse types but not as in the Apidae (Cruz-Landim, 1967, 1973).

Larva (except in *Apis*) with small, conical dorsolateral tubercles on at least the thoracic segments (Michener, 1953).

In this paper the largest subfamily, Meliponinae, is treated in some detail because of new findings as to relationships within this group. The other subfamilies are treated in a more cursory way.

TERMINOLOGY AND MATERIALS

The terminology used is that of Michener (1944) with some modifications. The word *thorax* is used for the thorax plus the propodeum, while segments 2-9 of the abdomen are referred to as segments 1-8 of the *metasoma*, so that segment numbers will conform to those used in almost all taxonomic work on bees. It would be logical to use the word mesosoma for the thorax plus the propodeum, but no confusion results from use of the shorter and more familiar word, thorax. Confusion as to segment numbering would result if the word abdomen were to be used instead of metasoma, because the propodeum is the first abdominal segment. The abbreviations T1, etc., and S1, etc., refer to metasomal terga and sterna by number. The term *basal area of propodeum* is continued, as a convenience, even though the triangular area (which comprises most of the basal area in Apidae) is apparently the metapostnotum (Brothers, 1976). (The triangular area is vaguely defined if recognizable at all in Apidae; loss of the lines demarking the triangle also occurs in certain other bees.)

The word *keirotrichia* (introduced by Michener, 1981: 4) is used for the small hairs of uniform length, blunt or (in other families of bees) briefly bifid or spatulate, occupying part of the inner surface of the hind tibia. The area occupied, the *keirotrichiate area,* is of great importance in the classification of Meliponinae. Unfortunately nothing is known about the function of these hairs.

Several special terms are associated with the pollen carrying and manipulating structures of Apidae. All are unique to females of the family (see Introduction, above) or to parts of the family. They are absent in most parasitic or robber taxa, and in queens of highly social bees. The *corbicula* is the smooth, concave or sometimes flat area, surrounded by long hairs, on the outer surface of the hind tibia. The *rastellum* is the comb of strong, usually blunt tipped bristles across the inner surface of the apex of the hind tibia (Fig. 184). It is reduced to ordinary hairs in some Meliponinae; I have described it in such cases as a rastellum made up of hairs, or tapering (pointed) hairs. I could have said "rastellum absent" but since there are all degrees of reduction, it is hard to say at what point such a comment would be appropriate. The *auricle* is the posterior expansion of the base of the hind basitarsus for pushing pollen up into the corbicula. It is absent in Meliponinae. The *penicillum* is a compact tuft of strong bristles arising near the front of the apical margin of the hind tibia, usually directed posteriorly, sometimes almost parallel to the apical tibial margin (Fig. 184). It is found only in Meliponinae. The *anterior* and *posterior parapenicilla* are groups of bristles arising at the anterior and posterior apical angles, respectively, of the hind tibia of some Meliponinae. There are always hairs in these positions; how coarse they must be to be called parapenicilla is a matter of judgment. The posterior parapenicillum is developed only in the genus *Meliponula.* The anterior parapenicillum is more widespread. Since these terms are difficult to define, I have used them only sparingly.

I have described positions of structures on the legs in the traditional way. Some authors advocate standardization by considering all legs to project laterally from the body. The following tabulation shows equivalent terms for the hind tibia and basitarsus; I use those in the first column:

outer surface	anterior surface
inner surface	posterior surface
posterior margin	upper margin
anterior margin	lower margin

Following Plant and Paulus (1987), I use the term *lorum* in place of submentum as used by Michener (1944, 1985).

The lengths of the *jugal* and *vannal lobes* of the hind wing are both measured from the wing base to the most distal part of the lobe. The *gonostyli* (third valvulae or sting sheaths) of workers in Meliponinae commonly have strong *setae* arising from distinct bases. In some genera there are also, or instead of such setae, *minute hairs.* These are consistently much smaller than the setae and distinctive setal bases are invisible at a magnification of 160×.

The male genitalia of Meliponinae sometimes have the gonocoxites opening basad, in a more or less straight line across the base of the genital capsule, as in most other bees. However, in some genera and in some preparations of others the capsule is split longitudinally from the base by a V-shaped incision and the gonocoxites open mesad along the arms of the V. To avoid repeated wordy descriptions, I call the former *rectigonal,* the latter, *schizogonal,* and forms believed able to exhibit both conformations are called *amphigonal.* The matter is discussed in greater detail under the subfamily Meliponinae.

The uses of certain other descriptive terms are indicated in the accounts of characters in Tables 1 and 2.

Except as otherwise indicated in the text, and except for some "subgenera" of *Bombus* and *Psithyrus,* specimens of the type species of each named supraspecific taxon (whether or not recognized as distinct) were examined. In the Meliponinae, the worker sting apparatus provides useful characters. The sting and associated structures were removed, usually with part of the metasoma, from relaxed specimens and placed for a few hours in a 10% solution of KOH at room temperature. Meliponines are weakly sclerotized; prolonged treatment and high temperature are not desirable. After passage through acidulated (with acetic acid) water and dissection as needed to reveal the structures, the material was placed in glycerin for study and eventually for preservation, like male genitalia, in microvials with the specimens from which they were taken. Mouthparts were similarly treated, sometimes without KOH, and sometimes were preserved in glycerin jelly on slides.

In my sketches of meliponine stings, the lateral parts of the sting apparatus give only a general impression of the first valvifer, base of the second valvifer, and their connections. These parts are weakly sclerotized, often difficult to see, and are often curved away from the observer. A new study, perhaps with uncleared material examined at right angles to the plane in which the structures lie, might reveal additional interesting characters.

By no means all species of each meliponine taxon were dissected, but divergent species of each were dissected where possible. Males are unknown for many species and three genera. It is often possible to verify major features of worker gonostyli and sting stylets, and of lancets if they are long, by opening the apex of the metasoma of a relaxed specimen, without dissection and clearing. This was done for various species to determine the consistency of character states found in dissected material of related species.

ANALYSIS OF RELATIONSHIPS AMONG APID SUBFAMILIES

Relationships among the four subfamilies, Apinae (A), Bombinae (B), Euglossinae (E), and Meliponinae (M), have been considered for many years and are discussed in several recent papers (Winston and Michener, 1977; Kimsey, 1984; Plant and Paulus, 1987; A. Weller, unpublished).

Unlike previous authors, I have ignored autapomorphies in this analysis. Although autapomorphies are important in showing monophyly of the subfamilies, inclusion of autapomorphies in a statistical analysis of relationships among subfamilies allows one to maximize the consistency index and thus improve the apparent strength of the analysis without really adding information on relationships among taxa. Each subfamily is quite distinctive and numerous autapomorphies could be listed, fewer for B than for the other three. Partly because the subfamilies are so different from one another, largely because of autapomorphies, structure in the relationships among them has been hard to establish.

Table 1 is a list of actual or potential synapomorphies that vary among subfamilies of Apidae. The apomorphous condition (1) was recognized by comparison with plesiomorphies (0) found in *Manuelia* (the base group of Xylocopinae, probable sister group of the Apidae, Sakagami and Michener, 1987) and other Anthophoridae, specifically *Exomalopsis* and *Anthophora*. Condition (2), when present, is presumably derived from (1), so that the codes for the states are ordered.

A few supposed synapomorphies that have seemed useful previously were omitted from Table 1. The stipital sclerite of the maxilla (Winston, 1979; called the subgaleal sclerite by Winston and Michener, 1977) was found to be strong with an anteriorly projecting angle at each end in M (as in *Xylocopa*), but relatively delicate in A B E. Because of similarity to *Xylocopa*, the strong sclerite was considered plesiomorphic, the delicate sclerite, synapomorphic for A B E. But *Xylocopa* was the wrong outgroup; *Manuelia* and other small Xylocopinae, and most other long-tongued bees, have a delicate sclerite and the strong sclerite in *Xylocopa* is probably related to the strength of the proboscis in that genus. The strong sclerite in M is therefore an autapomorphy, not a plesiomorphy.

Kimsey (1984) correctly points out that the loss of the basistipital process, as a synapomorphy of A B E as stated by Winston and Michener (1977), is an error because the process is present in B E, as in M. The loss is therefore an autapomorphy of A.

Kimsey (1984) described the sclerotic bridge below the foramen magnum (her postgenal lobes) as showing similarity between B and E. It is true that in these two groups the bridge is over half as wide as the foramen magnum whereas it is narrower in A; in M it is also usually narrow but is variable, so that I have chosen to ignore this feature for present purposes. In all four subfamilies the bridge includes a lightly sclerotized invagination, well illustrated for M by Camargo, Kerr, and Lopes (1967, pl. B). When the bridge is broad the invagination is large, especially so in E, but in no species that I have seen is the lower part of the bridge incomplete as illustrated by Kimsey for E. Plant and Paulus (1987) also did not consider this character state as a synapomorphy.

The slender base of the hind basitarsus of workers of Meliponinae (Figs. 184-187), i.e., the lack of an auricle in contrast to the other three subfamilies of Apidae (Figs. 188, 189), seems at first to be a plesiomorphy because other families of bees also lack an auricle and have a relatively slender basitarsal base. However, in all pollen collecting Apidae the basitarsus arises from near the anterior distal angle of the tibia, i.e., from near the anterior end of the apical tibial margin. In other families of bees the basitarsus arises nearer the median axis of the tibia. After discussion with Michael Prentice of the University of California, I believe it likely that the family characteristic of Apidae, anterior position of the hind tibiotarsal articulation, permitted development of the auricle by providing space for it. The auricle was later lost in ancestors of the Meliponinae when a different pollen manuipulating device (involving the penicillum) evolved, although the position of the tibiotarsal articulation was retained. Loss of the auricle is therefore an autapomorphy at the subfamily level and is not included in the cladistic analysis. Of course if this interpretation is incorrect, the meliponine condition probably would be plesiomorphic relative to other Apidae and a strong indication that M is the sister group of A B E.

Larval apids are not particularly similar to those of the outgroup, Xylocopinae, presumably because the latter have lost cocoon spinning behavior and correlated structures. The larval mandibles of A M are weakly sclerotized, the apices simple or with fine denticles. The larval mandibles of B E are robust, with considerable sclerotization, without denticles but with a strong tooth on the upper margins (Michener, 1953). Neither type of mandible occurs in the Xylocopinae but mandibles similar in general form to those of B E occur in various Anthophorinae. Nonetheless a decision as to which apid type is apomorphic is not clear, and I have chosen not to use this character in the cladistic analysis. The weak larval mandibles of A and M are quite different from one another and their weakness could be convergent, not synapomorphic.

For cladistic analysis the synapomorphies listed in Table 1 were plotted upon all possible topologically different dendrograms for the four subfamilies. Five of the results are shown in Figures 1-5. The character states of the four subfamilies are indicated in the same table by the initials (A, B, E, and M) indicated above.

The total number of character state changes, i.e., dendrogram length, as well as corresponding consistency indices, are indicated in Figures 1-5. The calculations were made by the computer program McClade version 2.1 (Maddison and Maddison, 1987) using a hypothetical outgroup consisting of all the plesiomorphies. The most parsimonious tree is Figure 1, which corresponds to the traditional view of apid classification (Michener, 1974).

Subsequently Michael Prentice and Howell V. Daly of the University of California kindly sent me their as yet unpublished analysis of subfamilial relationships of Apidae. They have found other subfamilial characters, the details of which they will describe and illustrate. Of their characters I found eight to be particularly useful and polarizable with some confidence, using the same outgroups that I used previously. These are four characters of the prosternum, which are particularly strong, one of the internal ridge in front of the middle coxa, two of the maxilla, and one of the pharyngeal plate.

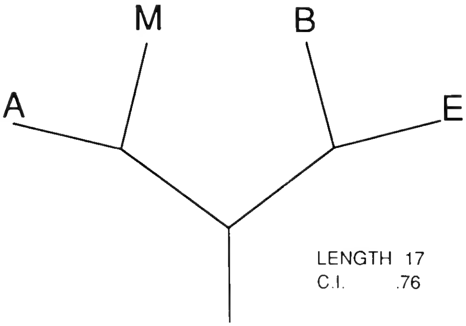

Figure 1. Dendrogram showing possible cladistic relationships among subfamilies of Apidae. A = Apinae, B = Bombinae, E = Euglossinae, and M = Meliponinae. Length = total number of character state changes in 12 characters. CI = consistency index.

Analysis using the parsimony computer program PAUP version 2.4 (Swofford, 1985) (hypothetical ancestor, all plesiomorphies) yielded (for my original 12 characters) dichotomous trees like Figure 1. However, for all 20 characters, the result was like Figure 3. PAUP version 3.0 gave two equally short trees for all 20 characters; one was dichotomous like Figure 1, the other had a branching pattern like Figure 3 (tree length 28, consistency index .786, retention index .714).

I believe that the evidence is strong that the A and M are sister groups, as indicated by Figures 1 and 3. This is not in agreement with the recent views of Winston and Michener (1977) and Kimsey (1984), who regarded M as the sister group to the clade of A B E, as in Figures 4 and 5. Some common character states for A and M, i.e., states that support the sister group relationship of these subfamilies, are losses. However striking, they might be independently evolved in A and M. Examples are: reduction of man-

TABLE 1. Characters used in cladistic analysis of subfamilies of Apidae. Distribution of character states is indicated thus: A = Apinae; B = Bombinae; E = Euglossinae; M = Meliponinae. (0) = the plesiomorphous character state; (1) = the apomorphous alternative.

Character 1. Body size. (0) Small to middle-sized and often rather slender (A M). (1) Large and robust (B E). Polarization is based on the small size of *Manuelia* but since some anthophorids are large, it may be incorrect.

Character 2. Papillae on distal parts of wings. (0) Absent (A M). (1) Present (B E). In various groups of bees, large sized taxa have evolved, and they often (although not always) have papillate wings. There is no certainty that these character states are homologous in the large Apidae (B E). Moreover, since large body size and wing papillae are often associated, this character suffers from the same problems as character 1; neither is a strong character.

Character 3. Grooves and ridges on outer surface of mandible. (0) Present (Figs. 173, 174) (B E). (1) Absent (Fig. 175), or in M with a single groove (Fig. 172) apparently not homologous to grooves of other bees (A M). A M are almost the only bees with greatly reduced mandibular grooves (Michener and Fraser, 1978). Therefore loss of grooves is likely to be homologous. However, as in all loss characters, convergence is possible and seems more likely because the highly social bees (A M) are the ones in which extensive nest structures of wax are made. Possibly relatively weak and more or less grooveless mandibles are adequate for such work, especially since these bees do not excavate burrows and cells.

Character 4. Mentum and "lorum" (= submentum). (0) United (E). (1) Separated (A B M). Plant and Paulus (1987) showed that these sclerites which have been regarded as primitively separate but united in most bees (Michener, 1985) actually evolved in the opposite direction and are separated only in A B M. It appears to be a strong character.

Character 5. Arolia. (0) Present (A M). (1) Greatly reduced (B). (2) Absent (E). This reduction and loss could have occurred independently, since arolia are lost in diverse groups of bees. The character states are ordered.

Character 6. Upper margin of main axis (basal part of malus) of strigilis. (0) Not expanded and without an apical prong (Fig. 176) (M). (1) Expanded (anterior velum of Schönitzer, 1986) and ending in a short prong or lamella above the pointed apex of the malus (Fig. 177) (A B E). The expansion is weakly developed in some Exomalopsini, Centridini, etc., but otherwise appears to be a synapomorphy for A B E. A distinct possibility, however, is that the expansion was lost in M, and the polarity therefore reversed.

Character 7. Hind tibial spurs. (0) Present (B E). (1) Absent (A M). Since the apomorphy is a loss, it might have arisen twice rather than once. Loss of tibial spurs is exceedingly rare in other bees, however.

Character 8. Stigma. (0) Large, several times as long as prestigma (Figs. 162-171) (M). (1) Small, shorter than prestigma (Figs. 178-182) (A B E). Stigmal reduction occurs in such a wide variety of bees that there is no strong evidence of its homology in A B and E. Alternatively, enlargement of the stigma occurs in minute Hymenoptera (Danforth, 1989), perhaps including minute meliponines, so that the polarization shown here may be wrong.

Character 9. First recurrent vein. (0) Longer, more oblique, not angulate or in B moderately so (Figs. 178-181) (B E). (1) Short and angulate (Figs. 162-171, 182), sometimes absent in M (A M). This character seems strong but may be in part related to size. As Danforth (1989) has shown, oblique veins tend to be more transverse (hence shorter) in small forms and more longitudinal (hence longer) in large forms. The angulation seems to remain as an indication that the condition is homologous in A and M. The states could have been considered as a developmental series from E → B → A M but evidence for the origin of the short, angulate vein of A M from the longer and somewhat angulate vein in B is lacking; I have therefore recognized only two states for this character.

Character 10. Jugal lobe of hind wing. (0) Present (Figs. 162-171, 182) (A M). (1) Absent (Figs. 178-181) (B E). This loss could have occurred independently in B and E. However, it did not occur in other bees. Plant and Paulus (1987) depreciate the loss as a synapomorphy, noting that in E the jugal lobe is replaced by a row of bristles. This is true, but the presence of bristles does not show that the lobe was not first lost.

Character 11. Gonobase of male. (0) Well developed (Figs. 189, 190) (B E). (1) Absent or nearly so (Figs. 138-161, 183) (A M).

Character 12. S7 and 8 of male. (0) Well developed (B E). (1) Much reduced or S8 almost absent (A M). Characters 11 and 12 involve reductions and losses that could have occurred independently, especially considering the great morphological differences between A and M in these features. However, loss of the gonobase is rare among bees and is therefore possibly homologous in the Apidae.

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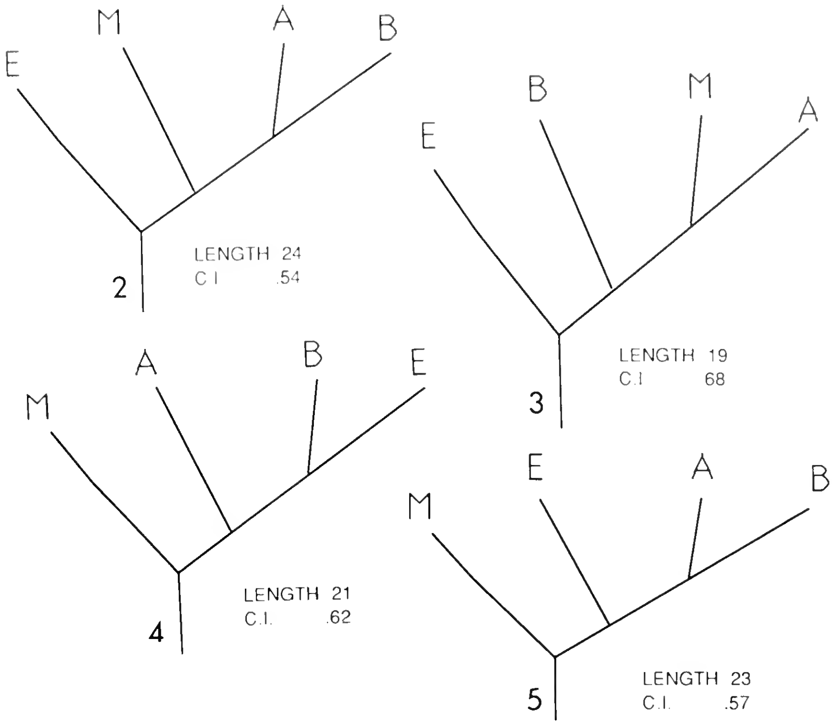
dibular grooves (3, Table 1), loss of hind tibial spurs (7, Table 1), and reduction of hidden sterna and most male genitalic parts (11, 12, Table 1). Some prosternal synapomorphies, however, such as its slender body, large anterior region and anterolateral processes, elongate groove instead of round apophyseal pit, etc., are not loss features and seem unlikely to have evolved convergently. Another such synapomorphy of A and M is the broad pharyngeal plate with transverse (rather than longitudinal) fields of sensilla (to be illustrated by Prentice and Daly).

The choice between a cladistic pattern like Figure 1 and a pattern like Figure 3 is not clear. To support the latter, one needs strong synapomorphies for the clade A B M. The articulation of the lorum and mentum (4), unique among bees, is the only strong, convincing character state of this sort, although one prosternal character state and states of the mesepisternum (in front of coxa 2) and pharyngeal plate also support A B M as a clade; these and others will be described and illustrated by Prentice and Daly. In support of the alternative, the dichotomous pattern of Figure 1, are apparent synapomorphies of B E. Body size and papillate wings (1, 2) perhaps are not polarized correctly, and the presumed derived conditions appear repeatedly among other bees, so might have arisen independently in B and E. Large size and papillate wings are often correlated among bees. The great reduction or loss of the jugal lobe of the hind wing (10) is unique among bees and thus strongly supports the sister group relationship of B and E, although the actual condition is rather different in the two subfamilies. Likewise, the great reduction in B and loss in E of the arolium and associated structures (5) supports the sister group relationship of these taxa. Both of these are losses and of course could have evolved independently.

Some apparent plesiomorphies appear in M, their corresponding apomorphies characterizing A B E. These are responsible for the trees such as Figures 4 and 5, showing M as the sister group for A B E, as advocated by Winston and Michener (1979) and Kimsey (1984). One such character is (6), the simple main axis of the malus of the strigilis in M, contrasted with the expanded lamella or prong (anterior velum of Schönitzer, 1986) found on the velum of A B E. An approach to such a structure occurs in some anthophorids such as *Epicharis*, although in most bees including *Manuelia* it is simple. If Figures 1 and 3 represent the most probable cladistic patterns, the strigilis of M probably represents a reversion. Likewise the large stigma of M (8) seems to be plesiomorphic relative to the reduced stigma of A B E, since large stigmata generally characterize the more primitive bees, including *Manuelia*, etc. As is well known, however, relative stigmal size is negatively correlated with body size in aculeate Hymenoptera (Danforth, 1989). The reduced wing venation of M suggests that this group originated as minute bees, which may therefore have had an enlarged stigma as a reversion that has been retained along with reduced venation even in larger meliponines. Finally, the slender base of the hind basitarsus of workers, i.e., the lack of an auricle, long seemed to me an important plesiomorphy contrasting with the unique synapomorphy, presence of an auricle, in A B E. For reasons discussed above I now regard loss of the auricle in M to be an autapomorphy or reversion. These same comments apply to the Plant and Paulus (1987) diagram of relationships (Fig. 2), except that in place of A B E, one should read A B.

A cladogram with M as the lowest branch (sister group to A B E) seems reasonable because we know that M is old (Cretaceous; Michener and Grimaldi, 1988a, b). M is also the most widely distributed; in appropriate climatic zones it occurs worldwide. The other three subfamilies are all geographically limited—A to Eurasia and Africa before being dispersed by man, B to the Holarctic, Oriental (montane) and Neotropical regions, and E to the Neotropics. Such distributions might indicate groups less old than M.

It will probably be possible to greatly increase the number of characters showing the similarities of large, robust taxa (B E) as opposed to the small bodied taxa (A M). For example, the lateral promotor of the mid coxa in B E is V-shaped and the lower branch extends forward behind the second and third pleuroaxillary muscles. In A M this muscle is much smaller, not or scarcely V-shaped, and does not extend so far for-



Figures 2-5. Dendrograms showing possible relationships among subfamilies of Apidae. Explanation as for Figure 1.

ward (Wille, 1956). Likewise the dilator of the salivary syringe has its origin below the posterior lateral margin of the prementum in B E, on the anterior lateral margin in A M (Wille, 1971); the latter condition is considered derived by Wille. These internal characters and characters 2, 8, and possibly 9, Table 1, are likely to be related to size and robustness rather than phylogeny.

The number of plesiomorphies that unite B and E could be augmented, but the corresponding presumed apomorphies of A and M are not necessarily homologous. Besides characters 3, 7, 9, 11, and 12, such plesiomorphies include (a) the form of the penis valves, which are very divergently modified in A and M; and (b) the presence of volsellae in the male (see discussion of Bombinae), which are absent in A and M. Characters 11 and 12 are actually divisible into several such states that may have evolved independently.

While Figures 1 and 3 appear to represent the best cladograms, it is difficult to choose between the two. It is therefore premature to decide on a classification that indicates structure among the four taxa. For this reason and because of their phenetic distinctness, I term them all subfamilies. Even if one of the cladograms were known to represent the truth, I see no reason to unite two or three of the taxa in a single subfamily since all four are so different from one another.

There is, of course, considerable interest in the question of whether the highly social behavior of A and M is homologous or convergent. If either of the hypotheses indicated by Figures 1 or 3 is correct, as is likely, such behavior probably arose once. The other three cladograms (Figs. 2, 4, 5) suggest independent origin of highly social behavior in the two subfamilies, a view supported by Sakagami (1971), Winston and Michener (1977) and Kimsey (1984).

Unfortunately fossil Apidae as now known do not help in the solution of the problems discussed above. For most of them, anatomical details are not sufficiently well preserved or described. The fossil Apidae have been reviewed by Zeuner and Manning (1976) and in part by Wille (1977). Those with clear relations to existing subfamilies are discussed under the subfamilies, below. Taxa of greater interest, because they appear to represent extinct types that might shed light on the relationships of the subfamilies, are *Chalcobombus, Sophrobombus* (placed in Meliponinae by Zeuner and Manning) and *Electrapis* (with subgenera *Protobombus* and *Roussyana,* placed in the Apinae by Zeuner and Manning). All these are from the Eocene Baltic amber and none is so well preserved or studied that definitive placement is possible.

KEY TO THE SUBFAMILIES OF APIDAE

1. Posterior tibial spurs absent; arolia present; jugal lobe of posterior wing present; labrum three to four times as broad as long; marginal cell open or with veins narrow or evanescent distally or, if completely delimited by strong veins, reaching to within one-third or less of its length from wing tip 2

—Posterior tibial spurs present; arolia greatly reduced or absent; jugal lobe of posterior wing absent or much reduced; labrum at most twice as broad as long; apex of marginal cell completely delimited by strong veins, separated from wing tip by a distance equal to at least half length of cell. 3

2. Marginal cell open (or its veins weak) distally (Figs. 162-171), tapering from broad base; second recurrent vein absent; stigma of moderate to large size, extending well beyond base of vein r; claws of female simple; sting reduced, not exsertable. . . . . Meliponinae

—Marginal cell complete, parallel-sided for a large part of its length; second recurrent vein present; stigma minute, not tapering beyond base of vein r; claws cleft; sting well developed . . . . Apinae

3. Proboscis reaching at least to base of metasoma in repose; scutellum produced posteriorly to a margin overhanging metanotum and propodeum; posterior tibiae of male usually swollen, always with a deep hairy fossa on apical half of posterior margin . . . . Euglossinae

—Proboscis usually not reaching behind middle coxae; scutellum rounded posteriorly, overhanging metanotum but not propodeum; posterior tibiae of male neither swollen nor fossate . . . . Bombinae

SUBFAMILY MELIPONINAE

These are the stingless honey bees found in tropical and southern subtropical areas throughout the world (Roubik, 1989). They are the only highly social bees except the true honey bees, subfamily Apinae. There are several hundred species, an approximation to the real number being impossible because of the abundance of cryptic species, differing from their relatives only on the bases of seemingly trivial characters. Most genera in most areas have not been adequately analyzed for recognition of such forms; a good start for part of one genus *(Partamona)* is the fine work by Camargo (1980).

Description: Minute (1.8 mm long) to moderate sized (13.5 mm long), sparsely hairy or short haired to moderately hairy bees. Eyes usually bare. *Claws of female simple; arolia present; hind tibial spurs absent;* strigilis without prong on anterior side; hind basitarsus rather slender at base, without auricle; hind tibia of worker with penicillum. *Forewing with venation reduced* (Figs. 162-171); marginal cell often open apically, at least distal parts of its veins much narrower than veins of basal part near stigma; *stigma large to moderate sized,* vein r arising near middle; in *Melipona* stigma slender but in other genera stigma rather broad and margin within marginal cell convex; prestigma short, often almost absent; second recurrent vein absent; first recurrent vein, when present, short and strongly angled near anterior end; first and second submarginal cells, at most, weakly defined, third not defined, because of weakness or absence of transverse cubital veins. Hind wing with well developed jugal lobe one half to one third as long as vannal lobe. Clypeus flat, not protuberant. Maxillary palpus minute, one-segmented, sometimes less than twice as long as wide and extremely inconspicuous. Male S8 absent except for laterally compressed remnant of spiculum (largest in Fig. 145); S7 flat, weakly sclerotized and usually without large apodemes; S6 transverse, with lateral apodemes and usually with median apical process. Male gonobase absent or represented by narrow ribbon or weak lateral sclerites; gonostylus long, usually slender, simple (presumably this is the upper gonostylus, the lower one being absent); penis valve large with heavily sclerotized, slender, curved, tapering apex; spatha usually present; volsella absent. *Female with sting and associated structures greatly reduced* (Figs. 9-48).

A hitherto unrecorded apomorphy of Meliponinae, called to my attention by Ricardo Ayala, is the demarcation of the preaxilla. In most bees, including other subfamilies of Apidae and numerous groups of anthophorids, the preaxilla is separated from the dorsal surface of the mesoscutum by a strong supra-alar carina, immediately mesad to which is a groove that joins the scuto-scutellar suture posteriorly (Michener, 1944). In Meliponinae the supra-alar carina and adjacent groove are absent. The dorsal surface of the mesoscutum is either separated from the preaxilla by an angle (it could be called a weak carina but is not raised) or it rounds onto the preaxilla with only a change in sculpturing to indicate the upper margin of the preaxilla.

Camargo, Kerr, and Lopes (1967) give an excellent morphological account of *Melipona marginata* Lepeletier. Sakagami (1982), Wille (1983), and Roubik (1989) review biology of Meliponinae.

Larva: Without strong tubercles, but with small, conical, dark dorsolateral tubercles on first three to ten body segments. Mandible attenuate, apex blunt, concave on inner surface, margins and often apex denticulate but without large teeth.

Larvae are described and illustrated by Michener (1953) and Oliveira (1965).

Nest: The nests of most species occupy cavities that the bees find, and may limit by walling off unused areas, but the bees usually do little or no excavating. Some excavating is probably done by certain of the species that nest in the ground, and is done by some species that regularly establish their nests in nests of *Nasutitermes.* The cavities used vary from small, e.g., an abandoned cerambycid burrow, to large hollows in a tree trunk or cavity in the soil. Other species, however, do not occupy cavities but make exposed nests on tree branches or on cliff faces.

Nests are made of mixtures of wax secreted from the metasomal terga and resins and gums collected by the bees. A few species add mud, feces, or other materials to certain parts of the construct.

Cells are mass provisioned and either clustered or arranged in combs which are usually horizontal. The cells open upward (rarely horizontally) and are closed after an egg is laid on the provisions. Food is stored in pots, quite different from and larger than brood cells. Details of nest architecture are dealt with by Schwarz (1948); Michener (1961); Wille and Michener (1973); Fletcher and Crewe (1981); Sakagami, Yamane, and Hambali (1983); Sakagami, Inoue, Yamane, and Salmah (1983); Roubik (1979, 1983); and works cited therein. Reviews are by Sakagami (1982), Wille (1983), and Michener (1974).

Social behavior: This is one of the two groups of highly social bees, with "permanent" colonies and morphologically very different female castes (queens and workers). In contrast to the Apini, new nests are begun by workers going back and forth from an existing colony, carrying building materials and food. Ultimately a young queen goes to the new site, workers stay there, and independence from the old colony is gradually attained. Long distance dispersal by individual reproductives or by swarms is therefore impossible. Colony size ranges from a few dozen workers to thousands.

Distinctive aspects of meliponine social behavior include oviposition rituals and communication concerning resources. These are discussed further in the next section, on relationships among meliponine genera.

Distribution: This subfamily is found in the tropics of the world (except not east of the Solomon Islands in the Pacific). To the south it extends into temperate regions (about 35°S in Australia and South America, 28°S in Africa). To the north it extends little beyond the Tropic of Cancer (23.5°N).

Relationships among Meliponine Genera

History: The classification of stingless honey bees has been presented very differently by different authors (see review by Sakagami, 1982). Schwarz (1948) and Michener (1944) recognized only two principal genera, *Melipona* and *Trigona. Lestrimelitta* was often recognized as a distinct robber genus, lacking pollen collecting and carrying structures (e.g., by Schwarz, 1948) and *Meliponula* and *Dactylurina* often received generic status (e.g., by Wille and Michener, 1973). Wille (1979b) likewise recognized *Trigona* (with numerous subgenera) and *Melipona,* but in addition five small genera: *Cleptotrigona, Dactylurina, Lestrimelitta, Meliplebeia,* and *Meliponula.*

Moure (1951, 1961), however, elevated many of the subgenera to the genus level and described additional genera so that in 1961 he recognized 23 genera (no subgenera) from the Old World and 10 from the New World. In the New World, however, he recognized 27 supraspecific taxa (genera and subgenera). Moure (1971) elevated some of the subgenera (and by inference others) to the genus level, making his classification of New World Meliponinae more nearly comparable to that of the Old World. An additional genus was added subsequently (Camargo and Moure, 1983).

Sakagami (1975, 1982) presented an intermediate system, in some ways similar to that developed in the present study.

Many of Moure's genera (based on external characters of workers) seemed to me so similar that I saw no need to recognize them at the genus level, especially since some were justified largely on the basis of a single character. Nonetheless, the male genitalia of two of his externally similar genera, *Liotrigona* and *Hypotrigona,* turned out to be so different that I could not consider them congeneric (Brooks and Michener, 1988). Some details could not even be homologized. The sixth and seventh sterna were also very different, as were the gonostyli of the workers. These are all characters that can only be revealed by dissection. On the basis of external characters of workers, Brooks and Michener (1988) could not place certain species as to genus.

Analysis: In view of the situation described above, I reviewed all the supraspecific taxa, examining the worker gonostyli and sting, worker labial palpi (see Michener and Roubik, in press), as well as the male genitalia and hidden sterna when males were available. Originally the taxa had been based on external characters of workers.

Table 2 is a list of characters with synapomorphic character states. Autapomorphies were not included in the computer analysis and most of them are not listed in Table 2. They are often numerous, however, and contribute to the recognition of taxa but not to an understanding of their relationships.

Using a character matrix based on the characters 1-16 listed in Table 2 and the PAUP 2.4 computer program (Swofford, 1985), a preliminary cladistic analysis of supraspecific taxa was made. Six of the characters had either three or four states. PAUP options were as follows: Root = ancestor; addseg. = closest; swap = global. Some of the characters were polarized, as indicated within Table 2; others were not polarized for reasons stated in that Table. *Bombus* and *Manuelia* were used as outgroups, but the "ancestor" in the PAUP computer analysis was artificial, consisting of all the character states coded 0, i.e., plesiomorphic for the polarized characters.

Usually because of similarity to other taxa, but sometimes because of lack of material (males not known), certain taxa were omitted from the computer analysis. Of 52 supraspecific taxa recognized by one or more authors, 26 were included in the preliminary

TABLE 2. Characters used or considered in cladistic analyses of genera and subgenera of Meliponinae. Characters marked with asterisks were used in the generic analysis, after generic limits had been determined. (0) = the plesiomorphous character state; (1), (2), etc., indicate apomorphous alternatives in sequence such that (1) is thought to be derived from (0), (2) from (1), etc.

Character 1. Apical margin of mandible of worker (Fig. 172). (0) Most or at least lower half of mandibular margin edentate, usually one or two small teeth at upper end (or in the upper half) of margin. (1) With four or five teeth occupying entire margin. In other subfamilies of the Apidae the mandibular margin (at least of females) is partly edentate (Michener and Fraser, 1978) but in other bees with a broad mandibular margin (Xylocopinae, Megachilidae), it is usually dentate. This condition therefore could be plesiomorphic for the Meliponinae. This interpretation is supported by the fully toothed mandibular margin of the Cretaceous *Trigona prisca* Michener and Grimaldi (1988a, b). However, a toothed mandibular margin is found in only two recent taxa, *Trigona (Trigona)* and *Paratrigona,* quite unrelated groups neither of which is near the base of the dendrogram derived later. This distribution suggests that a fully dentate mandibular margin may be a derived feature. Moreover, the presence in Meliponinae of the oblique mandibular groove, not homologizable with grooves of other bees, suggests that such mandibular features are basic for Meliponinae, with teeth developed later, as apomorphies not homologous to teeth of xylocopine or other bees. In summary, the polarity of this character is in doubt but probably multiple teeth are a derived feature. This character was not used in the generic analysis (a) because of doubtful polarity; (b) because within *Trigona* multiple teeth characterize only one, derived subgenus (for cladistic analysis involving a variable feature, one should use the plesiomorphic condition since the objective is to clarify basal connections, not evolution within the taxon); and (c) because as a generic character state, multiple teeth characterize only *Paratrigona* and are thus in effect an autapomorphy.

Character 2. Mandible of male. (0) With apical acute point and preapical tooth on upper margin (Fig. 135), i.e., the apex of the pollex (see Michener and Fraser, 1978). This is the mandibular form of many bees, including *Manuelia* and *Anthophora.* (1) With apical point rounded, little exceeding pollex, the two separated by only a shallow emargination, or apex of mandible truncate, rounded, or rarely pointed (Fig. 136, 137). The supposedly plesiomorphic condition described above (0) is found among Meliponinae in *Hypotrigona.* Ths character was not used in the generic analysis since character state (1) is either a uniquely retained plesiomorphy or an autapomorphy of *Hypotrigona.*

**Character 3.* Scutellar fovea of worker. (0) Shining transverse depression on scutoscutellar line simple. (1) Depression on scutoscutellar line extending posteriorly into scutellum on midline, forming a V-shaped or U-shaped fovea in scutellum (Fig. 190). Character state (1) is not found outside of the Meliponinae and is therefore no doubt a derived feature. It characterizes *Nannotrigona* and *Scaptotrigona.*

**Character 4.* Keirotrichia of worker. (0) Keirotrichia uniformly distributed (as in other subfamilies of Apidae) over wide area from premedian longitudinal ridge of tibia nearly to posterior margin of tibia, leaving at most a narrow bare margin (as in *Plebeia* s. str., Fig. 184). (1) Keirotrichia leaving broad bare tibial margin (as in *Hypotrigona*). (2) Keirotrichia restricted to median longitudinal band on tibia (as in *Trigona,* Fig. 185). There is more or less a continuum between (0) and (2) but in nearly all cases there was no problem in assigning a species to one category or another, using the exemplars listed above. All other Apidae show state (0). Xylocopinae have a very different sort of tibia but lack bare zones comparable to those for states (1-2). The polarity indicated above can be questioned on the basis that the oldest fossil bee, the late Cretaceous *Trigona prisca* Michener and Grimaldi, has state (2). Moreover the Oligocene *Proplebeia dominicana* (Wille and Chandler) has state (1). These findings are hardly decisive, however.

**Character 5.* Hind tibial cross-section of worker. (0) Inner surface of hind tibia flat from premedian longitudinal ridge (most elevated part of inner surface) to posterior margin (with or without hairless margin) as in other Apidae. (Anthophoridae have no bare margin.) (1) Inner surface of hind tibia with narrow depressed zone along posterior margin (as in *Plebeia* s. str., Fig. 184). (2) Inner surface of hind tibia with broad depressed posterior zone (as in *Hypotrigona*). (3) Inner surface of hind tibia with broad raised median longitudinal zone with keirotrichia, behind which the depressed smooth zone is often as broad as the median ridge (as in *Trigona,* Fig. 185). This character is related to character 4 but provides additional information. For example there are forms having character state (0) of character 4 but state (1) of character 5. The polarity indicated above can be questioned on the basis of fossils as for character 4. There is evidence that state (1) has arisen more than once or has reverted to (0). Thus in *Plebeia (Scaura) timida* (Silvestri) the condition is intermediate between (0) and (1), although its relatives have state (1) and in the distantly related genus *Meliponula* intermediate conditions also exist.

Character 6. Fringe along posterior margin of hind tibia of worker. (0) Composed entirely of simple hairs (Figs. 184, 186, 187). (1) Including plumose hairs (Fig. 185). Polarization of this character remains uncertain, since plumose hairs are found in some other Apidae *(Bombus)* and on the equivalent tibial area of many Xylocopinae. However, the groups with such plumose hairs (*Dactylurina* and most *Trigona*) are not basal in the dendrograms developed later, a finding that supports the polarization indicated. (A few branched hairs are also found in *Plebeina* and some species of *Meliponula,* and in two species of *Plebeia.*) This character was not used in generic analysis because a plumose fringe is a generic character state only for *Dactylurina* and thus would appear as an autapomorphy. Although plumose hairs are prevalent in *Trigona,* the presumably plesiomorphic alternative also exists in that genus and would be used in analysis at the genus level. (See explanation for character 1.) (See also character 28.)

Character 7. Hairs on posterior apical angle (or curve) of hind tibia of worker. (0) Slender, often very long but similar in form and color to nearby hairs. (1) Robust bristles, thicker than nearby hairs and amber to blackish in color, forming the "posterior parapenicillum" of Wille (1979b). This character was not used in the generic analysis because all forms having state (1) are considered congeneric; the character state is therefore an autapomorphy of *Meliponula* at the genus level.

**Character 8.* Rastellum. (0) Of strong bristles, mostly ending somewhat bluntly. (1) Of soft hairs, with slender, tapering apices, suggesting tapering hairs of other bees. In *Dactylurina* and some others the bristles are strong but taper to slender points; they were coded as (1). Since the rastellum is absent in other families of bees, one would assume that in the Apidae a rastellum of ordinary hairs should be plesiomorphic relative to a rastellum of strong bristles. However, all subfamilies of Apidae other than Meliponinae have the rastellum strong in all nonparasitic, non-queen females. If, within the Meliponinae, the rastellum evolved from weak to strong, the same must have happened elsewhere in the Apidae, i.e., there must have been at least two origins of the strong rastellum. I prefer the view that it originated once, in primitive Apidae, and is reduced in some Meliponinae, such as *Meliponula.* The potential for reduction and loss is indicated by its loss in parasitic genera of Euglossinae and Bombinae, robber genera of Meliponinae, and in queens of all highly social forms. The polarity indicated above is in accordance with this view.

**Character 9.* Submarginal cells of forewing. (0) At least first submarginal cell defined by line representing first transverse cubital vein (Figs. 162-164). (1) Not defined because transverse cubital veins are entirely absent (Fig. 168). Generally associated with states (0) and (1) are all the differences in forewing venation enumerated in couplet 1 of the key to genera. Venational reduction evidently occurred independently in various taxa of minute Meliponinae; even in some relatively large ones, e.g., *Trigona (Papuatrigona),* the transverse cubital veins are essentially absent, being indicated by denser setae than on the adjacent wing membrane.

Character 10. Basal area of propodeum. (0) Bare, as in Xylocopinae and many other bees. (1) Hairy, as in other subfamilies of Apidae. Polarization of this character is in doubt on the basis of outgroups. Hairs crop up on the basal area of the propodeum of species widely scattered through the Meliponinae. At the genus level such hairs characterize four genera, *Cephalotrigona, Melipona, Meliponula,* and *Partamona,* but they occur also in *Plebeia (Schwarziana), P. (Plebeia) caerulea* (Friese), *Trigona (Tetragona) lurida* Smith, the *Trigona (Heterotrigona) planifrons* Smith group (part of *Platytrigona*), and *T. (H.) canifrons* Smith. Since polarity is not certain and hairs appear to have evolved sporadically (Figs. 82-129) even though they might be plesiomorphic in other cases, this character is omitted from the generic analysis.

**Character 11.* Gonostyli of worker. (0) Well separated at bases, usually parallel or converging apically (Figs. 9-33). (1) Adjacent or close together at bases, usually diverging apically (Figs. 40-48). In functional stings the bases of the gonostyli are well separated and the gonostyli converge to sheath the sting. It is therefore probable that even in the greatly reduced meliponine sting, separation of the stylar bases is the plesiomorphic condition. The bases are adjacent or nearly so in certain genera, and also in various species of diverse genera as an infrageneric apomorphy.

**Character 12.* Setae or bristles on gonostylus of worker. (0) abundant (unless gonostylus is reduced in size) and dispersed over nearly all parts of gonostylus (Figs. 9-39) (as in other bees). (1) Few and restricted to one edge or thickening on one side of gonostylus (Figs. 41-46). (2) Absent (Fig. 48). Characters 12 and 13 vary concordantly, states (1) and (2) of character 12 being correlated with state (1) of character 13. In theory a meliponine worker gonostylus with abundant setae as well as minute hairs should be possible. I know of no such gonostylus; possibly there is a developmental or physiological factor that prohibits such a combination.

**Character 13.* Minute, dense hairs on gonostylus of worker, usually much smaller than the smallest setae (Figs. 37-48). (0) Absent (Figs. 9-36). (1) Abundant. Minute hairs are scarce or absent in most related bees (other subfamilies of Apidae; Xylocopinae); *Apis* has an area of such hairs and numerous but small setae.

**Character 14.* Sting stylet of worker (Figs. 9-48). All Meliponinae have the entire sting apparatus greatly reduced. This character concerns the fused second valvulae or stylet. (0) Stylet distinct, sharp (thus most nearly like a functional sting) (Figs. 9, 41, 43-45). (1) Stylet with apex about right angular or with apex rounded, more often obtuse, broadly rounded, or reduced to a transverse band.

Character 15. Apical process of S6 of male. (0) Strongly sclerotized, directed posteriorly or downward. (1) Strongly sclerotized, reflexed and apex directed forward. Characters states (0) and (1) intergrade and in some cases coding was arbitrary. Outgroups lack the process. Polarity is based only on the belief that such a structure is more likely to have evolved flat, then become reflexed.

In scattered unrelated meliponine taxa, S6 is a broad, simple plate (Fig. 148) more or less like the preceding sterna and without or with only a small apical process. Such groups are *Lestrimelitta,* certain species of *Paratrigona, Trigona (Homotrigona), T. (Lepidotrigona)* and a subgroup of *T. (Heterotrigona),* i.e., the subgroup called *Odontotrigona = Tetrigona.* It is tempting to consider this the plesiomorphic (0) condition, because in many other groups of bees S6 is a simple plate. However, the appearance of this state in groups that show no other special signs of plesiomorphy suggests independent reversions from the usual meliponine condition. All bees must possess genes for producing ordinary sterna (S2-5); a developmental shift could no doubt cause such genes to function for S6. (Further discussions under several of the taxa listed above.)

Taxa lacking the apical process of S6 were coded 9 for the preliminary PAUP analysis, the hypothesis being that the process in some cases has been lost. Because of the dubious basis for polarity and because the states intergrade, this character was not used in the generic analysis.

**Character 16.* Gonobase. (0) Recognizable as separate band on each side. (1) A thin ribbon, or fused to gonocoxite, or absent.

**Character 17.* Base of male genital capsule. (0) Not curved ventrad and apicad. (1) Strongly produced ventrad and apicad (*Liotrigona* and *Cleptotrigona,* Figs. 153, 154). *Meliponula* s. str. has a slightly down-curved base of the genital capsule.

**Character 18.* Male genitalia (Figs. 130-161). (0) Rectigonal or amphigonal. (1) Seemingly permanently schizogonal. In most bees, including the Euglossinae and Bombinae, the genitalia are rectigonal. In most Meliponinae considered to exhibit state (0), the genitalia can probably take up the schizogonal conformation during the life of the individual, hence are termed amphigonal. *Lestrimelitta* and *Hypotrigona*, however, are probably permanently rectigonal and others may be. Character state (1), not found in other bees and hence clearly apomorphic, is found in *Melipona* and most of the African genera.

**Character 19.* Gonostylus of male. (0) Slender, not much flattened. (1) Broadly flattened beyond slender base (Fig. 161). (This character state varies between the two species of *Dactylurina*.)

Character 20. Attachment of gonostylus to gonocoxite of male. (0) At apex of gonocoxite, as in most Hymenoptera. (1) Preapical on gonocoxite. (2) Near middle of gonocoxite. (3) Near base of gonocoxite. The above coding of this character seemed appropriate for forms with elongate gonocoxites, but "apex" means something quite different for rectigonal and schizogonal gonocoxites. Moreover, in forms with short, transverse gonocoxites, the differences between the four states are negligible. (In *Trigona iridipennis* Smith and its close relations the gonostylus arises from the dorsum of the gonocoxite rather than from the side.) The character was ultimately abandoned for all cladistic analysis and was not used in the generic cladogram.

Character 21. Gonostylus of worker (Figs. 9-48). (0) Cylindrical or tuberculiform. (1) Flattened. Character state (0) most nearly resembles the form found in other bees. All degrees of flattening exist, and flattening is sometimes difficult to detect for these minute structures. There are already three characters (11-13) based on worker gonostyli. Moreover, flattening is largely concordant with minute, dense hairs (character 13, state 1). Character 21 was therefore abandoned as difficult to quantify and unlikely to provide additional information. It is listed here largely for historical reasons, because it was emphasized by Wille (1959a, 1979b).

**Character 22.* Sting lancet (first valvula) of worker (Figs. 9-48). (0) Long, free, apex more or less longitudinal and attaining at least bases of gonostyli. (1) Shorter, largely transverse, but apex free. (2) Short to absent, included in membrane. As for character 14, polarity is based on the degree of divergence from the structure found in functional stings. The three states intergrade so that some coding decisions were arbitrary.

**Character 23.* Scutellum. (0) Rounded and rather thick in lateral view. (1) Projecting as a thin shelf over metanotum and base of propodeum as seen in lateral view (*Nannotrigona, Paratrigona, Scaptotrigona*, Figs. 90-92). Character state (0) is suggestive of the condition in Bombinae, Apinae, and many other bees, and is therefore regarded as plesiomorphic.

**Character 24.* Vein M of forewing. (0) Bent at point where it meets (or would meet) first recurrent vein (Figs. 164, etc.). (1) Ending without such a bend (Figs. 168, 169). In other bees including the outgroups the vein bends and continues beyond the first recurrent vein. As is suggested by the first couplet of the key to genera, this character is highly correlated with character 9. It does provide some additional information, however, and is therefore included in the study.

**Character 25.* Submarginal angle in forewing. (0) Strongly acute (60°-70°). (1) Slightly acute to obtuse. A strongly acute angle is characteristic of most other bees, including the outgroups, and is therefore considered plesiomorphic.

Character 26. Setae on posterior surfaces of worker labial palpal segments one and two (Figs. 49-81). (0) Short, not or little longer than width of segments, and nearly straight. (1) Certain median (i.e., not marginal) setae much enlarged ("giants"), much longer than palpal width, straight or curved (hooked in terminology of Michener and Roubik, in press). (2) As in (1) but some or all giant setae sinuous (wavy). Character state (0) is plesiomorphic to judge by its occurrence in all other subfamilies of Apidae, and in other bees. States (1) and (2) are found in many Meliponinae. The problem with this character is that reversals occur, as in robber genera, necrophagous species, etc., that do not collect pollen from flowers (Michener and Roubik, in press). It is therefore impossible to know whether, in a given case, short setae are plesiomorphic or derived. If they are all plesiomorphic except for the robbers, necrophages, etc., then giant and sinuous setae arose repeatedly. For these reasons I have not used this character in the phylogenetic analysis.

Character 27. Hairs of outer surface and posterior margin of hind tibia of male. (0) All simple or some long hairs near posterior margin with short branches along one side. (1) With plumose hairs among longer simple hairs along posterior margin and sometimes also on outer surface. This is similar to character 6 (the equivalent character for workers) and is not used in analysis for the same reason. However, the distribution of the states is not the same as for workers. State (0) is found in all genera except *Dactylurina* and some subgenera of *Trigona*. This is true also for workers. Within the genus *Trigona*, state (0) is found in the subgenera *Tetragona, Tetragonisca, Lepidotrigona* and some *Heterotrigona* (some species but not all of the *Tetragonula* group, the *Platytrigona* group). Other *Heterotrigona* species and subgenera such as *Geotrigona, Frieseomelitta* and *Trigona* s. str. have state (1). Of the subgenera listed, only *Lepidotrigona* lacks equivalent plumose hairs in the worker. Illustrations of hind tibiae of some male melipones and discussion of assimilation of worker characteristics by males are given by Sakagami and Ito (1981). The outer surface of the hind tibia is usually convex but is concave and corbicula-like in some species having state (0) and in some with state (1).

computer analysis, as follows: *Apotrigona*, *Austroplebeia*, *Axestotrigona*, *Cephalotrigona*, *Cleptotrigona*, *Dactylurina*, *Hypotrigona*, *Lepidotrigona*, *Lestrimelitta*, *Liotrigona*, *Meliplebeia*, *Melipona*, *Meliponula*, *Nannotrigona*, *Nogueirapis*, *Oxytrigona*, *Paratrigona*, *Partamona*, *Plebeia*, *Plebeina*, *Scaptotrigona*, *Scaura*, *Schwarziana*, *Tetragona*, *Trigona* s. str., and *Trigonisca*. Except for *Trichotrigona*, *Lisotrigona*, and *Pariotrigona*, whose males are unknown, there is no confusion as to the relationships of the omitted taxa. Dissections were made and the omitted taxa were excluded from the cladistic analysis because of similarity to included taxa. That is, each omitted taxon (except for the three listed above) is similar to an included taxon, either being a sister group to the included taxon or to be incorporated into the included taxon. Most omitted taxa did not differ from corresponding included taxa in any of the characters used in this analysis and clearly, the included taxa cover the range of structural diversity in Meliponinae.

PAUP analyses were made using all 16 characters. Characters with three or four states were coded as ordered, but were also tried unordered. Analyses yielded numerous (>100) trees of which every tenth was printed. Consistency indices of shortest trees ranged from 0.41 to 0.47. Of course complete resolution was not achieved with so few characters. Inclusion of autapomorphies would have distinguished all taxa but would not have changed the topology of the cladogram as determined by the synapomorphies.

Informal (i.e., non-numerical) phenetic observations along with examination of these preliminary PAUP results led to my decisions as to 21 genera to be recognized and thus relegation of various taxa to subgeneric or synonym status. Study of character state distributions using McClade 2.1 (Maddison and Maddison, 1987) was useful in this process.

PAUP produces only the most parsimonious cladograms without regard to one's views as to the probability of reversals of particular characters. Some reversals that appeared in PAUP-generated cladograms were eliminated because they seem unlikely, e.g., reacquisition of lost wing veins as in 9(1) to 9(0) and redevelopment of an acute sting stylet as in 14(1) to 14(0). Such reversals were from state 1 to 0 for characters 9, 14, and 16.

For what is here called the "generic study" (as opposed to the "preliminary analysis"), characters 17 to 27 of Table 2 were considered for the analysis. They had not been recognized, or had not been appropriately coded, for the preliminary analysis. Several, however, cannot be reliably polarized, or are weak for various reasons, but are discussed in the table because others have used them. None of them led to changes in the taxa that were considered as genera. A new PAUP analysis, and a Hennig 86 analysis (the results were the same) was based on the 17 characters listed in Table 3 (marked by asterisks in Table 2) and the 21 taxa recognized as genera. The reasons for excluding the other characters are indicated below and in Table 2. The three genera whose males are not known were now included, male character states being recorded as unknown. Table 3 shows the states for the 17 characters, the characters and states being numbered as in Table 2. Certain genera are identical in the character states recorded in Table 3, as follows: genera 3 and 4; genera 6, 7, and 8; and genera 13 and 14. That is, complete resolution was impossible because some genera (recognizable by autapomorphies at the genus level) did not differ in strong, polarizable synapomorphies.

Some characters used in the preliminary analysis of 26 taxa were omitted in the generic study because they could not be polarized with any degree of confidence. Others were eliminated because they were not synapomorphic at the genus level. Character state 1(1), for example, occurs only in one (derived) subgenus of *Trigona* and in the distantly related genus *Paratrigona*. Thus at the genus level it does not characterize *Trigona* and becomes an autapomorphy for *Paratrigona*. Character state 7(1) became an autapomorphy at the genus level when the taxa possessing it fell together in the genus *Meliponula*. Other such cases are explained in Table 2.

As in the study of 26 taxa, numerous trees resulted from the PAUP analysis. Also as in that study, rather than developing a consen-

TABLE 3. Characters of the 21 genera of Meliponinae used in the generic analysis. All characters are polarized, with 0 as plesiomorphic, and the character states are ordered. The numbers of the characters correspond to those in Table 2.

Characters	3	4	5	8	9	11	12	13	14	16	17	18	19	22	23	24	25
1. Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2. *Melipona*	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
3. *Hypotrigona*	0	1	1	1	1	0	0	0	1	1	0	0	0	2	0	1	1
4. *Pariotrigona*	0	1	1	1	1	0	0	0	1	?	?	?	?	2	0	1	1
5. *Lestrimelitta*	0	0	0	1	0	0	0	0	1	1	0	0	0	2	0	0	1
6. *Oxytrigona*	0	2	2	0	0	0	0	0	1	1	0	0	0	2	0	0	1
7. *Cephalotrigona*	0	2	2	0	0	0	0	0	1	1	0	0	0	2	0	0	1
8. *Trigona*	0	2	2	0	0	0	0	0	1	1	0	0	0	2	0	0	1
9. *Trichotrigona*	0	2	2	1	0	0	0	0	1	?	?	?	?	?	0	0	1
10. *Nannotrigona*	1	0	0	0	0	0	0	0	1	1	0	1	0	2	1	0	1
11. *Scaptotrigona*	1	0	0	0	0	0	0	0	1	1	0	0	0	2	1	0	1
12. *Paratrigona*	0	0	0	0	0	0	0	0	1	1	0	0	0	2	1	0	1
13. *Plebeia*	0	0	0	0	0	0	0	0	1	1	0	0	0	2	0	0	1
14. *Partamona*	0	0	0	0	0	0	0	0	1	1	0	0	0	2	0	0	1
15. *Trigonisca*	0	1	1	1	1	0	1	1	1	1	0	0	0	2	0	1	1
16. *Lisotrigona*	0	1	1	1	1	0	1	1	1	?	?	?	?	1	0	1	1
17. *Austroplebeia*	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1
18. *Cleptotrigona*	0	0	0	1	1	1	1	1	0	1	1	1	0	0	0	1	1
19. *Liotrigona*	0	1	1	1	1	1	1	2	1	1	1	1	0	1	0	1	1
20. *Dactylurina*	0	2	2	1	1	1	1	2	1	1	0	1	1	2	0	0	1
21. *Plebeina*	0	1	1	1	1	1	1	2	1	0	0	1	1	1	0	0	1
22. *Meliponula*	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1

sus tree, I have eliminated those that involve the most improbable reversals. The remaining trees resembled in topology Figures 6 and 7, differing only in trivial ways. For Figure 6, I modified the PAUP results only by rearranging character state 8(1). This state, the reduction of coarse, often blunt bristles of the rastellum to slender, tapering bristles or hairs, occurs not only in the genera above point A, but also in the robber or possibly parasitic genera *Lestrimelitta* and *Trichotrigona.* No doubt it evolved independently in these genera in connection with their loss of pollen manipulating behavior. I have therefore moved branches for those genera to show this character state as an independent apomorphy for each of these genera as well as on stem A. The fossil genus *Proplebeia* was added to Figure 6 by hand on the basis of features of the worker sting apparatus, some of them only vaguely seen.

For the part of the cladogram above point A, I have shown in Figure 7 an unmodified representation of the PAUP output. This parsimonious cladogram (26 character changes, not including autapomorphies) is improbable. The minute forms, *Pariotrigona* to *Liotrigona* on the tree (also *Cleptotrigona* and some *Austroplebeia*), constitute a group with greatly reduced wing venation, from which the African genera *Meliponula, Dactylurina,* and *Plebeina,* larger bees with fuller (ancestral) wing venation 9(0), 24(0), appear to have evolved. I believe that once lost, a vein is unlikely to reappear. Tinkering by differential weighting of characters is just as subjective as adjustments made, as in Figure 8, on the basis that the minute genera had independent origins and the larger African forms did not evolve from minute ones with reduced venation. I believe that parsimony programs are important aids in thinking about phylogeny but do not necessarily give the most probable cladistic hypotheses.

Figure 8 also is not without some improbable features. For example the sting stylet is shown as reverting to its acute pointed condition 14(0) in *Cleptotrigona* and *Meliponula.* The gonobase of the male is larger 16(0) in *Meliponula* and *Plebeina* than in

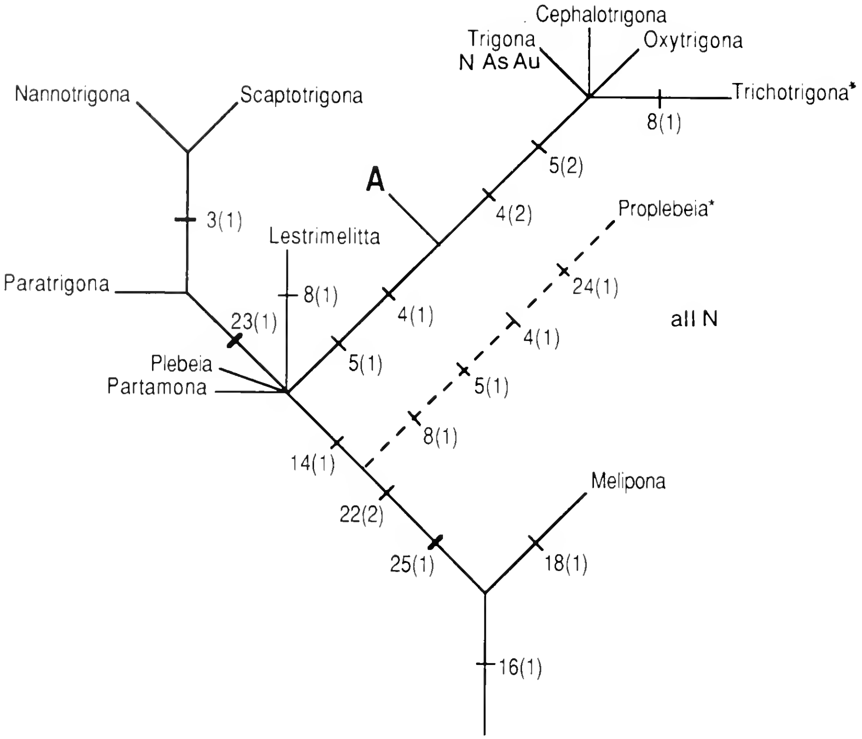


Figure 6. Dendrogram based on generic analysis of Meliponinae. A indicates continuation in Figures 7 and 8. The fossil *Proplebeia* was inserted by hand on the basis of few characters. Character numbers (and states in parentheses) are those used in Tables 2 and 3. Those marked with heavy cross lines are particularly strong. Males of genera marked by asterisks are unknown. All these genera are Neotropical (N); *Trigona* is also found from Asia (As) to Australia (Au).

any other Meliponinae. These would seem to be plesiomorphic features, but are reversals according to Figures 7 and 8.

Trigonisca is geographically isolated (in America) from other minute genera (all African or Asiatic). The relation with *Lisotrigona* shown in Figures 7 and 8 may be entirely wrong; when males of *Lisotrigona* are known they may indicate different relationships. The number of synapomorphies is so low that a few added characters could greatly change the cladogram. In the preliminary analysis (26 taxa) a sister-group relation was shown between *Austroplebeia* (Australia) and *Trigonisca*. Such a relationship is supported from an unexpected source. *Trigonisca* (along with *Hypotrigona*) and *Austroplebeia* have the last two metasomal ganglia completely fused, unlike other Meliponinae studied by Wille (1961). Thus the *Plebeia*-like *Austroplebeia* may indeed be the sister group of *Trigonisca*; alternatively, the fusion may be convergent.

The isolation of *Melipona* at the base of the cladogram (Fig. 6) is contrary to one of the relationships suggested previously, namely derivation of *Melipona* from *Plebeia*-like ancestors (Wille, 1979b). The acute sting (Fig. 9; character 14) and acute submarginal angle in the forewing (Fig. 162; character 25) are plesiomorphic features not shared by *Plebeia*, showing that *Melipona* could not have evolved from *Plebeia*. However, *Plebeia* and *Melipona* are in fact reasonably closely related; only four character changes separate them in Figure 6.

Wille (1979b) considered the flattened worker gonostyli of various African genera

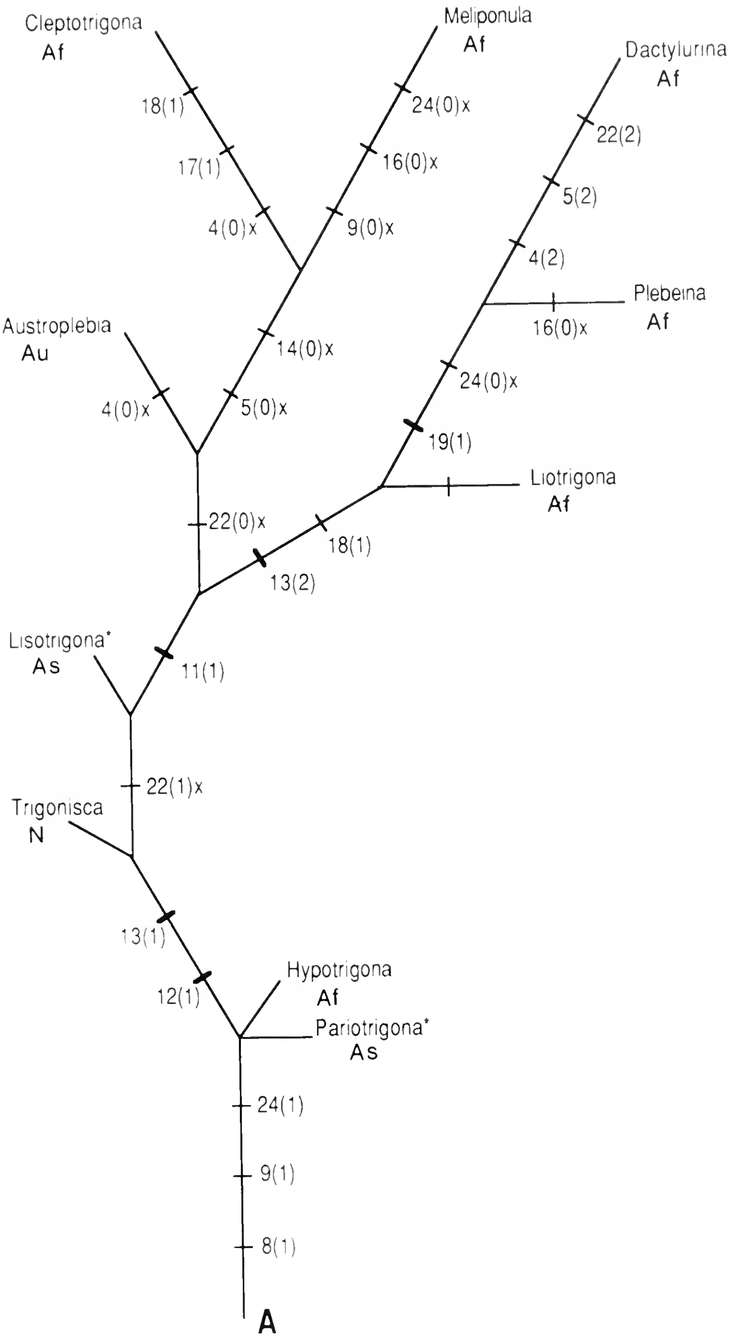


Figure 7. Continuation of Figure 6, showing results of PAUP analysis with character states of equal weight. Explanation as for Figure 6. Characters marked X represent reversals. N = Neotropical, Af = Africa, As = Asia, Au = Australia. Autapomorphies are omitted but provide additional characters for taxa without indication of characters or with reversals only.

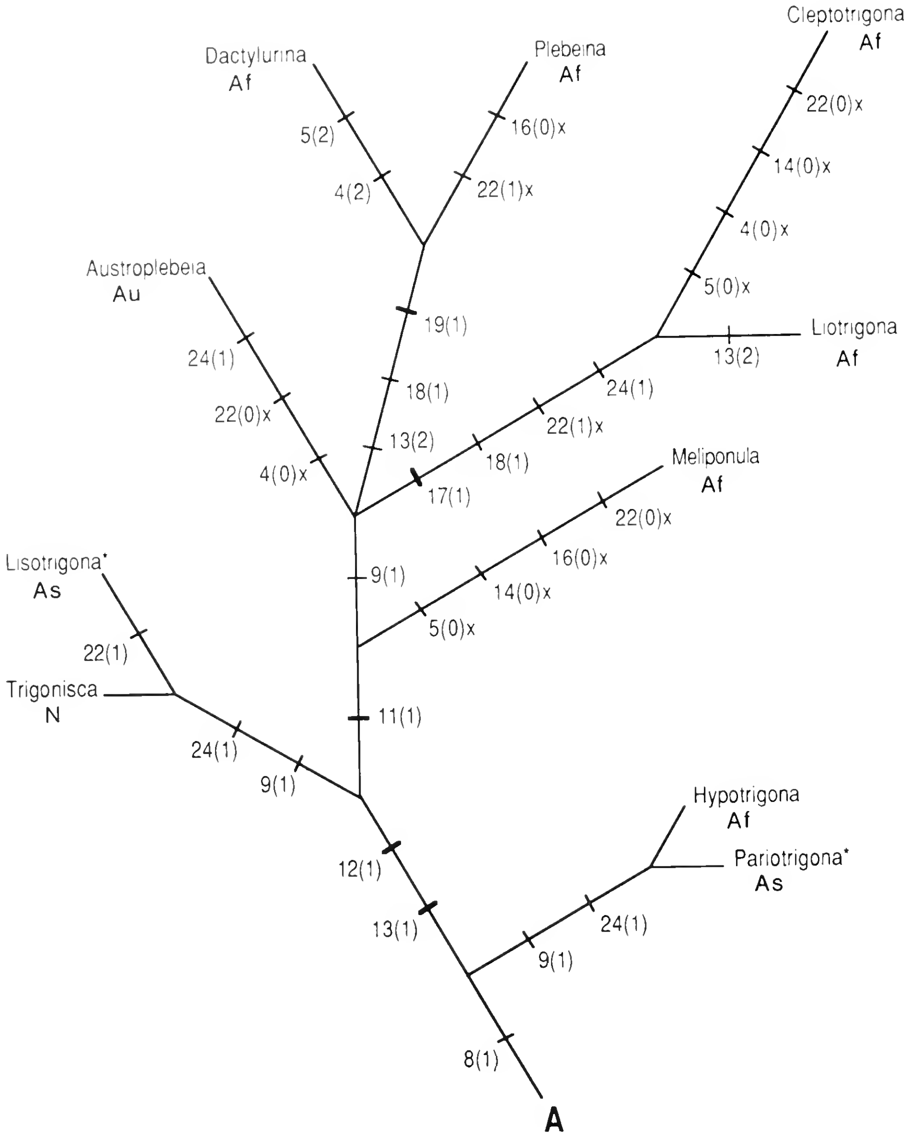
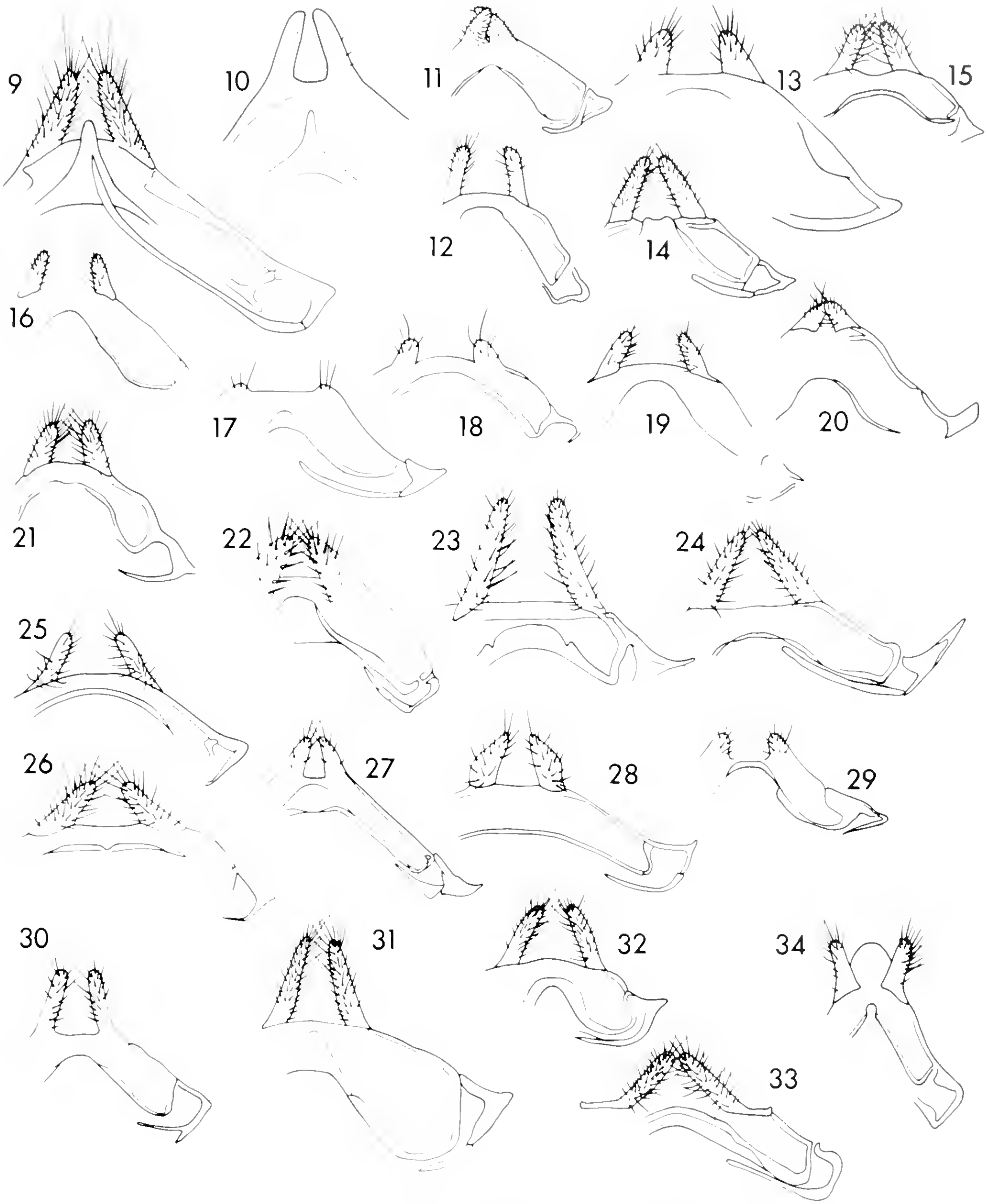


Figure 8. Continuation of Figure 6, showing modification of PAUP analysis. See text. Explanation as for Figures 6 and 7.

as ancestral, probably because in two of the genera (*Cleptotrigona* and *Meliponula*) this character state is associated with a pointed sting stylet. I consider the flattened gonostyli (Figs. 40-48; character 21, Table 2), presence of minute hairs on them (character 13), reduction of setae on them (character 12), and tendency of the gonostyli to diverge from proximate bases (character 11), to be derived character states, since they do not appear in other subfamilies of Apidae. I therefore do not follow Wille in regarding the African genera as an ancestral group from which other Meliponinae arose. Instead, the African, etc., group (Figs. 7, 8) appears to have evolved from a cluster of American genera (Fig. 6).

The genera appearing in Figure 6 have a distinctive combination of plesiomorphic and apomorphic character states. The for-



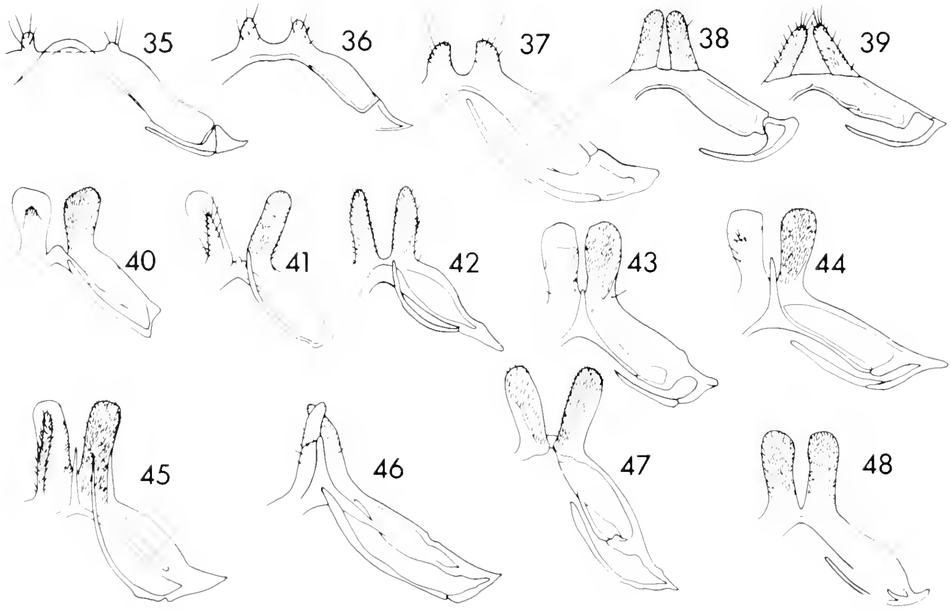
Figures 9-34. Sting rudiments of workers of Meliponinae. 9, *Melipona rufiventris* Lepeletier. 10, Fossil, *Proplebeia dominicana* (Wille and Chandler). 11, *Plebeia (Plebeia) frontalis* (Friese). 12, *Plebeia (Plebeia) caerulea* (Friese). 13, *Plebeia (Plebeia) schrottkyi* (Friese). 14, *Plebeia (Schwarziana) quadripunctata* (Lepeletier). 15, *Plebeia (Scaura) latitarsis* (Friese). 16, *Plebeia (Nogueirapis) mirandula* (Cockerell). 17, *Partamona* near *cupira* (Smith). 18, *Partamona zonata* (Smith). 19, *Paratrigona opaca* (Cockerell). 20, *Nannotrigona testaceicornis* (Lepeletier). 21, *Scaptotrigona mexicana* (Guérin). 22, *Lestrimelitta limao* (Smith). 23, *Oxytrigona mellicolor* (Packard). 24, *Cephalotrigona capitata* (Smith). 25, *Trigona (Lepidotrigona) terminata* Smith. 26, *Trigona (Papuatrigona) genalis* Friese. 27, *Trigona (Frieseomelitta) nigra* Cresson. 28, *Trigona (Geotrigona) mombuca* Smith. 29, *Trigona (Heterotrigona) carbonaria* Smith. 30, *Trigona (Tetragonisca) angustula* Latreille. 31, *Trigona (Tetragona) lurida* Smith. 32, *Trigona (Heterotrigona) apicalis* Smith. 33, *Trigona (Trigona) amalthea* (Olivier). 34, *Trigona (Trigona) cilipes* (Fabricius).

mer include cylindrical or papilliform, setose worker gonostyli (Figs. 9-34), commonly converging apically, with well separated bases and without minute hairs; the strong, usually blunt setae of the rastellum (Figs. 184, 185); and the posterior or downward directed midapical process of S6 of the male. Apomorphies include the obtuse or rounded sting remnant (except for *Melipona*) and reduced gonobase remnants.

The situation is in fact more complex. *Hypotrigona,* which agrees in various features with the genera in Figure 6, is restricted to Africa. In *Melipona,* a Neotropical genus, the sting is right angular to acute, in some species (e.g., *M. fulva* Lepeletier) as strong as in any African genus; the male gonocoxites are elongate and the genitalia schizogonal; and the gonobase is represented by a slender strip. Except that the gonobase remnant is quite different from the remnants in the African group, these character states are suggestive of that group. *Trigonisca,* a Neotropical genus, and *Austroplebeia,* an Australian genus, have worker gonostyli with minute hairs like those of the African group but in the other characters listed above they agree with the genera that appear in Figure 6.

The genera indicated by stars in Figures 6 to 8 are known only in the worker caste. Male genitalic characters are therefore unknown. *Trichotrigona* is possibly a robber or parasitic group derived from *Trigona (Frieseomelitta),* as suggested by the narrow ridge with keirotrichia on the inner surface of the hind tibia. *Lisotrigona* and *Pariotrigona* are minute forms superficially similar to *Hypotrigona, Liotrigona,* and *Trigonisca.* Their relationships remain uncertain until males are found (but see generic descriptions).

Biogeography: While cladograms, especially if based on relatively few characters, provide only hypotheses of relationships, they are strengthened if they make sense geographically or in terms of characters not used in



Figures 35-48. Sting rudiments of workers of Meliponinae. 35, *Hypotrigona braunsi* (Kohl). 36, *Pariotrigona pendleburyi* (Schwarz). 37, *Lisotrigona scintillans* (Cockerell). 38, *Trigonisca buyssoni* (Friese). 39, *Trigonisca longicornis* (Friese). 40, *Liotrigona mahafalya* Brooks and Michener. 41, *Cleptotrigona cubiceps* (Friese). 42, *Austroplebeia cassiae* (Cockerell). 43, *Meliponula (Meliplebeia) beccarii* (Gribodo). 44, *Meliponula (Axestotrigona) erythra* (Schletterer). 45, *Meliponula (Meliponula) bocandei* (Spinola). 46, *Meliponula (Meliplebeia) lendliana* (Friese). 47, *Plebeina denoiti* (Vachal). 48, *Dactylurina schmidti* (Stadelmann).

cladogram construction. Figures 6 and 8 do make reasonable geographic sense.

As indicated above, there is an African group of genera (Figs. 7, 8) with outliers, sharing some of its derived features, in Australia *(Austroplebeia)* and the Neotropics *(Trigonisca),* and a primarily Neotropical (also Indoaustralian because of *Trigona*) group (Fig. 6) with an outlier (or third group?), *Hypotrigona,* in Africa. *Melipona* (Neotropical) could be a member of this group but the evidence is weak. A biogeographical puzzle is how *Trigona* came to occur abundantly in the Neotropics and the Indoaustralian area while being absent from Africa. If male character states show *Lisotrigona* to be related to *Trigonisca,* they could constitute together a second genus having a distribution similar to that of *Trigona.*

No genus occurs both in Africa and South America. Therefore the meliponine faunas of these continents probably date from after the origin of the South Atlantic ocean in the late Cretaceous. The cladogram suggests that the Meliponinae arose in tropical America (which at that time extended far into North America). We know nothing of when the group moved between the American continents, but, as noted below, there is a late Cretaceous *Trigona* from New Jersey (Michener and Grimaldi, 1988a, b). The dissimilarity of the Neotropical and African faunas could suggest that meliponines reached South America from North America later, after considerable separation of South America from Africa.

Following the idea of Kerr and Maule (1964), the meliponines (including *Trigona*) may have spread through what is now the Holarctic region when it was warmer. The Eocene *Kelneriapis* from Baltic amber (see below) is evidence of meliponines in the Holarctic region. With climatic deterioration during the Tertiary, *Trigona* is now limited to southern Asia (south to Australia) and the Neotropical region.

The African fauna must have evolved when Africa was substantially isolated from American and Eurasian invasions (Michener, 1990).

Behavior: In view of the diverse types of recruitment to food sources found in Meliponinae (Kerr, 1969; Michener, 1974), it would seem that attributes of this system should be of phylogenetic significance. *Melipona* is quite different from the rest, in agreement with the cladogram. Otherwise, this system does not seem closely related to the branches shown in Figures 6 to 8. Rather, it seems that small forms (probably with small flight ranges) exhibit little recruitment ability while larger species have better recruitment. Scent trails, i.e., series of odor spots for recruiting, are known in *Cephalotrigona, Lestrimelitta, Oxytrigona, Scaptotrigona,* and *Trigona* (*Geotrigona* and *Trigona* s. str.). Kerr and Esch (1965, fig. 10) provide some details and exceptions [especially *Trigona (Duckeola) ghilianii* (Spinola), a large species not known to have scent trails].

Nest architecture, likewise, neither supports nor refutes the cladogram. The most striking variation in nest architecture is in brood cell arrangement. This feature has been emphasized by authors who wish to demonstrate that the subgenus *Frieseomelitta* is archaic or ancestral, having brood cells in clusters rather than combs.

It is not unreasonable to suppose that cells in a disorganized cluster is a plesiomorphy relative to cells arranged in combs. Most Meliponinae arrange cells in horizontal (sometimes spiral) combs. Cells in clusters, however, characterize not only all *Trigona (Frieseomelitta)* but also *T. (Heterotrigona) canifrons* Smith and most species of the *Tetragonula* group of *T. (Heterotrigona).* Moreover, cells are placed in clusters by all species of *Austroplebeia* [although layered, approaching combs, in *A. cincta* (Mocsary); Michener, 1961], *Cleptotrigona, Hypotrigona, Liotrigona, Trichotrigona,* and *Trigonisca,* and by some species of both *Plebeia (Plebeia)* and *Plebeia (Scaura).*

As suggested by Michener (1961), clustering may be the ancestral cell arrangement for Meliponinae (perhaps retained by *Austroplebeia*) while being derived for others. In particular, it is probably derived for species like *Trigona (Heterotrigona) fuscobalteata* Cameron that nest in small, irregular cavities where combs would be impractical. Indeed, most cluster-makers are small to minute bees. Michener (1961) contended that nearly spherical cells in clusters (as in *Austroplebeia*) are probably ancestral, that elongate cells resulted from packing cells into combs, and that therefore species that make elongate cells in clusters are derived from species that made combs. Unfortunately for this theory, spherical cells are almost unknown in other families of bees, so there is no good evidence for polarity of this character.

Dactylurina is unique among Meliponinae in that its combs, instead of being horizontal or nearly so with cells opening upward, are vertical with cells on both sides opening laterally, as in the combs of *Apis*.

Interesting aspects of social behavior of Meliponinae are the oviposition rituals and associated activities, much studied and described in a series of papers by Sakagami and others (reviewed by Sakagami, 1982; see also Sakagami, Yamane and Inoue, 1983, and Sakagami and Yamane, 1987). These rituals are often group-specific and often accompanied by laying of trophic eggs (usually queen food) by workers. The behavior of queens and workers during laying might produce characters of phylogenetic significance; some of the behavioral character states are indicated below in the comments on various genera and subgenera. It must be remembered, however, that these comments are based on few species and that sometimes closely related forms differ considerably in behavior. Therefore, generalizations as to a taxon's behavior may not always be applicable to all species. Polarization of most of these behaviors is dubious since there are no counterparts in outgroups. The following are some examples, selected from many possible characters.

New brood cell construction in most cases is unsynchronized (called successive), so that new cells at the advancing front (Michener, 1961) are in various stages of construction. This apparently unorganized construction of new cells is likely to be plesiomorphic. In a few taxa, while cell contruction starts successively, it becomes synchronized by the time that a number of cells are completed. Such taxa are *Trigona (Duckeola), T. (Lepidotrigona), Plebeia (Plebeia) minima* (Friese) and *schrottkyi* (Friese), and two groups of *Trigonisca,* namely *T. muelleri* (Friese) and *longicornis* (Friese), i.e., *Leurotrigona* and *Celetrigona,* respectively. Finally, in some taxa, a number of cells are constructed synchronously. Such taxa are *Plebeia (Plebeia)* except as indicated above, *Nannotrigona, Paratrigona, Trigona (Frieseomelitta) flavicornis* (Fabricius), and *T. (Heterotrigona) moorei* Schwarz. It should be noted that, in the successive group, there are the following close relatives of taxa listed above as partially or fully synchronous: *Plebeia (Schwarziana* and *Scaura), Trigona (Frieseomelitta)* of other species, *T. (Trigona* s. str., *Tetragona, Tetragonisca, Geotrigona,* and the *Tetragonula* group of *Heterotrigona),* and *Trigonisca* of other species. One can only conclude that if successive cell construction is plesiomorphic, synchronization has evolved independently in various groups.

Cell provisioning is in general parallel to cell construction, i.e., successive if cells are finished successively, synchronous if cells are constructed or finished synchronously.

Oviposition proper by the queen is less subject to brief summary than the features mentioned above, but egg laying by workers (in queenright colonies) is of interest. It is not confirmed in *Trigonisca muelleri* (Friese), *Trigona (Frieseomelitta)* and probably *T. (Duckeola).* Oviposition by workers occurs in queenright colonies of all other forms studied. In *Plebeia (Plebeia)* except *P. minima* Friese, in *Hypotrigona,* and in *Lestrimelitta,* the eggs are not laid in connection with the queen's oviposition process and are eaten by workers or the queen. In other taxa, worker laying is associated with queen oviposition, on or near a cell being provisioned, before provisioning starts in the case of *Trigona (Geotrigona),* but afterwards in all others. Such eggs are usually eaten by the queen. Usually the trophic egg is laid on the cell margin. [*Plebeia (Plebeia) minima* Friese is in this group.] It is much larger than the queen's egg in *Scaptotrigona* and *Plebeia (Schwarziana).* In certain taxa, however, it is laid on the food mass like the queen's egg. Such taxa are *Plebeia (Scaura), Paratrigona, Trigonisca longicornis* (Friese) *(Celetrigona), Melipona* and *Meliponula (Meliponula).* If, as seems likely, the last (laying on the food mass like the queen) is plesiomorphic, then modifications of that behavior must have occurred repeatedly and are not indicative of recognizable clades.

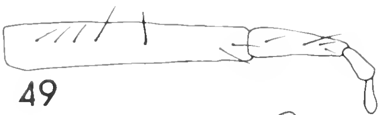
It is of interest that in all the characters listed above relevant to oviposition, *Melipona* has the presumably plesiomorphic behavior. This reinforces its position near the base of the cladogram rather than as a specialized derivitive group.

Labial palpi: The hairs of the posterior surfaces of the labial palpi of workers, character 26, provide character states that are of interest in connection with the cladograms (Figs. 49-81). Other subfamilies of Apidae, and various groups of Meliponinae, have these hairs short (little if any longer than palpal width) and straight. This is probably the plesiomorphic condition seen in *Melipona* and may also be plesiomorphic in such other taxa as *Cephalotrigona*, *Hypotrigona*, *Plebeia (Schwarziana* and *Scaura)*, *Trigona (Geotrigona* and *Tetragona)* and even in *Meliponula (Meliplebeia)*. If so, then giant curved and often wavy setae must have arisen repeatedly if Figures 6 to 8 mean anything. As indicated by Michener and Roubik (in press), the giant setae probably have to do with extracting pollen from anthers, minute flowers, etc. They appear to have been lost, i.e., replaced by short, straight setae, in bees that do not collect pollen from flowers, e.g., the robber genera *Lestrimelitta* and *Cleptotrigona,* the possibly parasitic *Trichotrigona,* and the species of the carrion-feeding group of *Trigona (Trigona) hypogea* Silvestri. When giant setae are lost, the condition is not visibly different from the plesiomorphic condition. These setae are therefore of little value in reinforcing or weakening the cladogram although their diversity as shown in Figures 49 to 81 suggests that they are important characters.

Wing venation: Characters 9, 24, and 25, Table 2, involve wing venation, but several additional features of wing venation vary widely among meliponine bees. In general they neither support nor refute the cladograms, but I deal with them at some length because they are conspicuous and have been used by others in the past. While of obvious interest, they sometimes vary within taxa, and some of them appear to vary with body size irrespective of phylogenetic relationship, along the lines indicated by Danforth (1989) for other groups of bees. For example, the basal vein is more transverse in small species, more longitudinal in large ones. The basal angle of the first submarginal cell (between first abscissa of Rs and Rs+M), i.e., the submarginal angle (character 25, Table 2), is acute in non-meliponine bees. It is also acute (60°-70°), no doubt plesiomorphic, in *Melipona* (Fig. 162). It is slightly acute in *Cleptotrigona, Plebeina,* most *Plebeia,* and some *Paratrigona.* It is right angular or approximately so (i.e., the first abscissa of Rs is more transverse) in most Meliponinae, grading to slightly obtuse in several groups such as *Scaptotrigona,* some *Partamona,* some *Paratrigona,* and *Meliponula (Axestotrigona).* It is very strongly obtuse, correlated with a short first abscissa of Rs (often only about one tenth as long as the basal vein (= first abscissa of M), in *Cephalotrigona, Dactylurina, Oxytrigona, Trichotrigona,* and some species of each of the following subgenera of *Trigona*: *Frieseomelitta, Tetragona, Trigona* s. str. (Figs. 166, 167). Other species of these subgenera as well as the subgenera *Geotrigona, Heterotrigona, Homotrigona, Lepidotrigona,* and *Tetragonisca,* have the angle weakly obtuse or right angular. Thus a strongly obtuse angle is found only in taxa with a narrow keirotrichiate ridge on the inner surface of the hind tibia, but has no doubt evolved independently in some such taxa (at least *Dactylurina* vs. the others). It is not clear whether the subgenera of *Trigona* like *Tetragonisca* retain an ancestral submarginal angle or have developed to a right angle along with their small body size. There are, however, rather large species of *Homotrigona* and *Heterotrigona* with the angle right angular.

The first abscissa of Rs is relatively long in related subfamilies and families of bees. Among Meliponinae it is about one fourth as long as the basal vein in *Melipona* as well as in *Lestrimelitta, Nannotrigona, Paratrigona,* and *Plebeina.* It is similarly rather long, one third to rarely one fifth (in *Cleptotrigona*) as long as the basal vein, in all the minute genera segregated in couplet 1 of the generic key, and in the minute *Plebeia (Plebeia) schrottkyi* (Friese). In *Cephalotrigona* and some species of *Trigona (Trigona* and *Tetragona)* it is only about one tenth as long as the basal vein, an obviously derived condition. All other Meliponinae have an intermediate Rs (first abscissa) length, one fifth to one eighth as long as the basal vein.

When the basal vein is relatively long, it is



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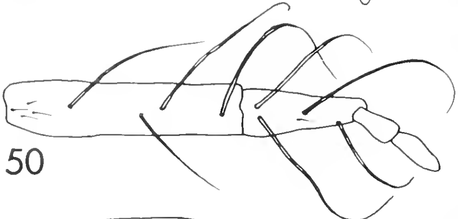

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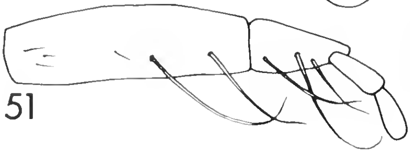

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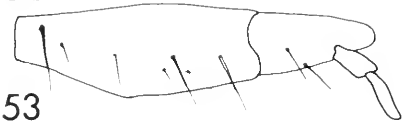

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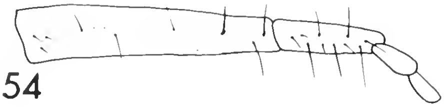

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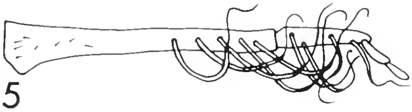

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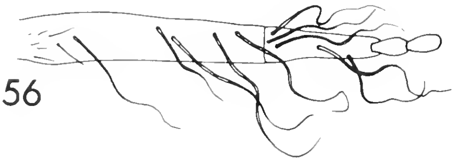

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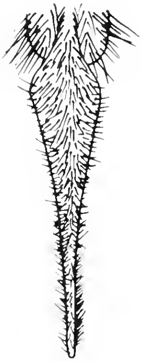

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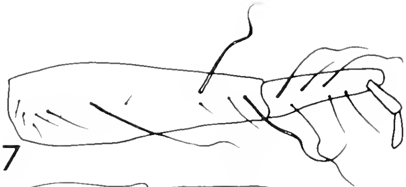

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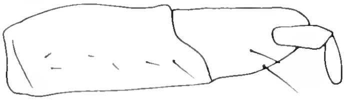

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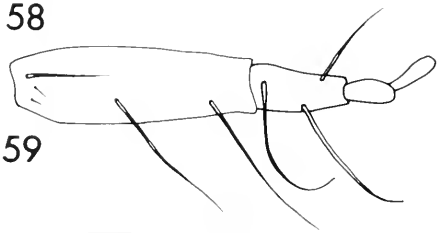

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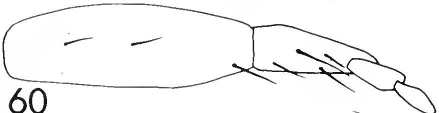

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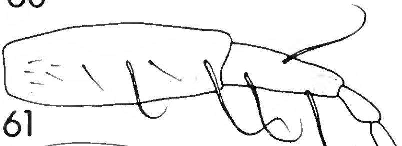

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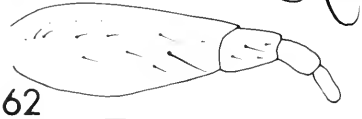

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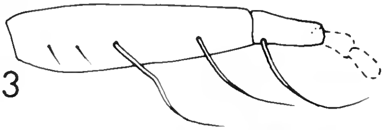

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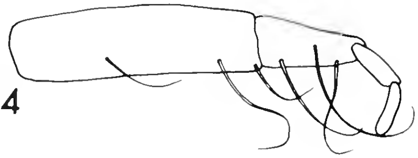

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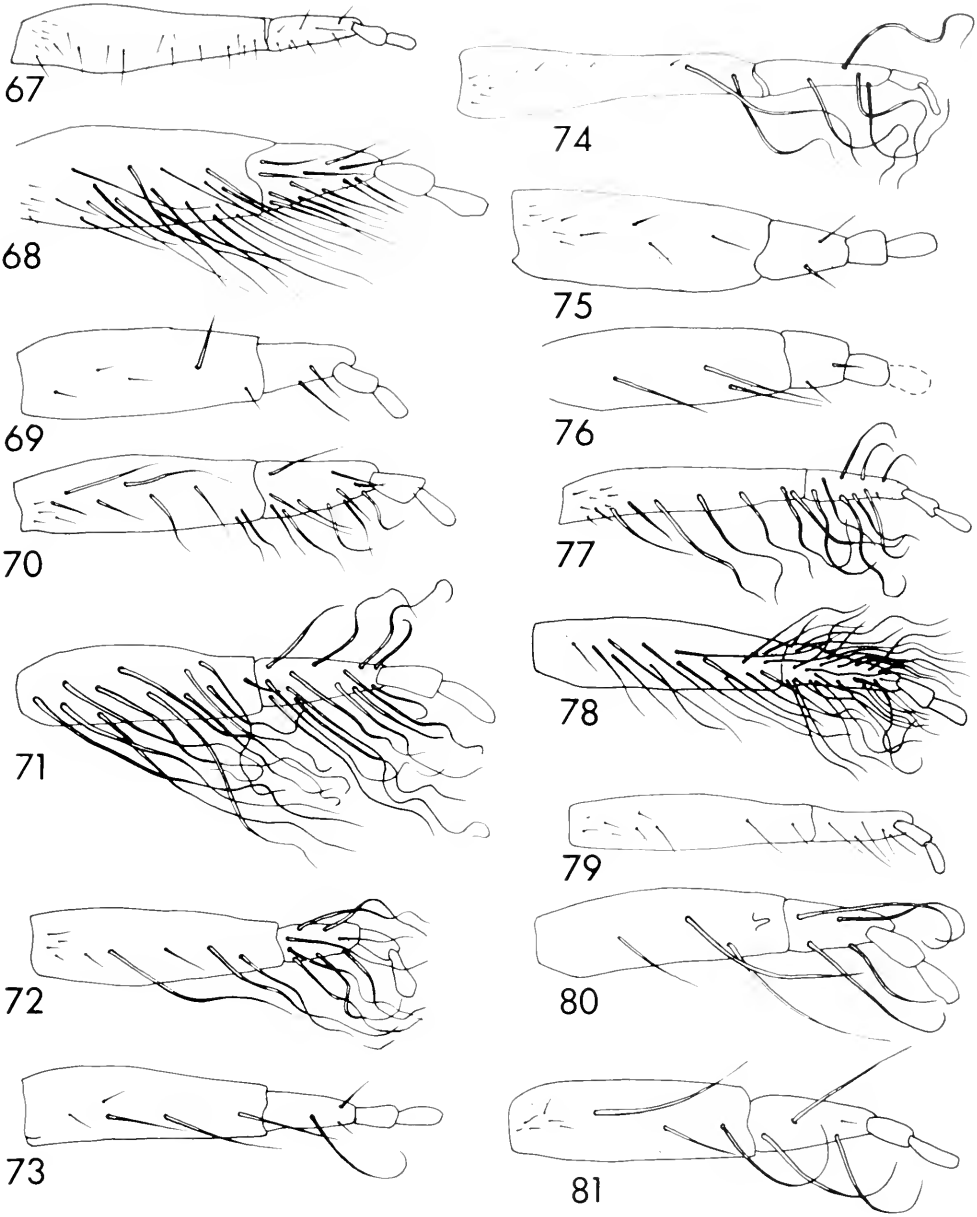
Figures 49-64 (modified from Michener and Roubik, in press). Posterior surfaces of labial palpi of workers. Marginal hairs and small hairs are omitted. Mesal margins are uppermost. The first and to some degree the second segments are sheath-like so that breadth varies with compression and should not be considered a useful character. 49, *Melipona fasciata* Latreille. 50, *Plebeia (Plebeia) frontalis* (Friese). 51, *Plebeia (Plebeia) schrottkyi* (Friese). 52, *Plebeia (Schwarziana) quadripunctata* (Lepeletier). 53, *Plebeia (Scaura) latitarsis* (Friese). 54, *Scaptotrigona pachysoma* (Cockerell). 55, *Paratrigona impunctata* (Ducke). 56, *Nannotrigona testaceicornis* (Lepeletier). 57, *Partamona* near *cupira* (Smith). 58, *Lestrimelitta limao* (Smith). 59, *Trigonisca buyssoni* (Friese). 60, *Hypotrigona braunsi* (Kohl). 61, *Liotrigona mahafalya* Brooks and Michener. 62, *Cleptotrigona cubiceps* (Friese). 63, *Pariotrigona pendleburyi* (Schwarz). 64, *Lisotrigona scintillans* (Cockerell).

Figures 65, 66. Flabellum of workers. 65, *Cephalotrigona capitata* (Smith). 66, *Trigona fulviventris* Guérin.



Figures 67-81 (modified from Michener and Roubik, in press). Posterior surfaces of labial palpi of workers. Explanation as for Figures 49-64. 67, *Cephalotrigona capitata* (Smith). 68, *Oxytrigona obscura* (Friese). 69, *Trigona (Tetragona) clavipes* (Fabricius). 70, *T. (Duckeola) ghilianii* Spinola. 71, *T. (Frieseomelitta) savannensis* Roubik. 72, *T. (Tetragonisca) angustula* Latreille. 73, *T. (Heterotrigona) carbonaria* Smith. 74, *T. (Trigona) pallens* (Fabricius). 75, *T. (Trigona)* species near *hypogea* Silvestri from Panama. 76, *Trichotrigona extranea* Camargo and Moure. 77, *Meliponula (Meliponula) bocandei* (Spinola). 78, *M. (Axestotrigona) erythra* (Schletterer). 79, *M. (Meliplebeia) beccarii* (Gribodo). 80, *Dactylurina staudingeri* (Gribodo). 81, *Austroplebeia cassiae* (Cockerell).

usually straight except near its basal end. This is the condition in most species of *Trigona* and its relatives with keirotrichia on a ridge *(Cephalotrigona, Trichotrigona, Oxytrigona)* as well as in *Dactylurina,* most *Meliponula, Plebeia (Schwarziana), Plebeina,* and *Scaptotrigona.* The basal vein is gently curved in all the other genera, although there are intermediates with very weak curvature such as *Partamona, Lestrimelitta,* some species of *Plebeia,* and some species of *Trigona (Heterotrigona).*

The basal vein is basal to cu-v in most species of *Trigona* and its relatives with a similar inner surface of the hind tibia *(Cephalotrigona, Dactylurina, Oxytrigona, Trichotrigona).* The same is true of *Scaptotrigona, Plebeina,* and some species of *Plebeia* and *Paratrigona.* The basal vein is distal to cu-v in the minute genera segregated in couplet 1 of the key to genera, and in the minute *Plebeia (Plebeia) schrottkyi* (Friese), also in *Lestrimelitta, Meliponula,* and some other species of *Plebeia.* The intermediate condition, the basal vein meeting cu v or nearly so, is found in the remaining groups including some species of *Plebeia* and *Trigona.*

Male genitalia: In the Meliponinae characters of males have been infrequently used hitherto for genus or subgenus recognition because of the scarcity of males in collections. It is risky to use male characters, as I have repeatedly done in keys and descriptions, when males remain unknown for many species. For various genera and subgenera for which males of only one species are known, I have indicated the male characters of the taxon on the basis of that one species. I hope that males of related species agree with my characterization, but they may not. As males of more species become known, any errors that I have introduced in this way will become evident.

A comment on schizogonal, rectigonal, and amphigonal genital capsules is appropriate here (see section on Terminology and Materials for explanation of these terms). I originally thought that these terms represented phylogenetically significant conditions, rectigonal being the plesiomorphic state and schizogonal derived. However, at least in various genera, this is clearly not the case, for specimens of the same species can be either rectigonal or schizogonal [see Fig. 134, based on two males of *Partamona* near *cupira* (Smith) from Costa Rica]. The genital capsule is so loosely put together that the gonocoxites are hinged on the median points where they meet and can fold basad to take the schizogonal position, so that sometimes the originally basal margins almost meet one another.

Commonly associated with this movement, the heavily sclerotized prong-like penis valves rotate and at the same time flex laterad. Note that in Figure 134, the shape of the prong of the penis valve in lateral view is the same as that shown in the dorsoventral drawing of a schizogonal specimen. Thus one has the same view of the penis valve in both cases because of its rotation.

Males often die with the penis valves directed laterally. It is not practical to return them to a more or less longitudinal position. Some illustrations show them directed laterad. Perhaps this is the position in copulation, with the penis valves hooking into the body of the queen so that the genitalia are pulled out of the male. Unfortunately lateral views of genitalia in this condition are not worth much and dorsoventral views look very different from those of the same species with the penis valves directed apicad.

Some of the conspicuous differences among genitalic preparations result from mobility of parts. Apparently the mobility varies; it is great in most meliponines, those that are amphigonal, but can apparently be slight in the permanently rectigonal and the permanently schizogonal forms.

Either by comparisons of different male specimens or of published drawings with specimens, it is clear that genitalia can appear either rectigonal or schizogonal (often with accompanying rotation of the penis valves) in the following species: *Austroplebeia essingtoni* (Cockerell), *Partamona cupira* (Smith), *Plebeia schrottkyi* (Friese), *Trigona amalthea* (Olivier), and *T. pallens* (Fabricius). There are numerous other taxa in which gonocoxal shape (about as long as broad) probably permits such change in genital appearance. These are *Austroplebeia, Nannotrigona, Oxytrigona, Paratrigona, Partamona, Plebeia, Scaptotrigona, Trigonisca,* and most subgenera of *Trigona.* Such forms are informally called amphigonal, to save explanatory space.

Nonetheless there are groups in which the genitalia appear to be permanently schizogonal, and in which this feature is therefore an apomorphic character state. These are the groups in which the gonocoxites are sufficiently elongate that they could hardly adopt a rectigonal conformation; in some such groups (especially *Melipona*) males of numerous species have been examined by me or illustrated by previous authors; all are schizogonal. Such taxa are *Cleptotrigona, Dactylurina, Liotrigona, Melipona, Meliponula, Plebeina,* and *Trigona (Geotrigona, Tetragonisca).* In at least some of these taxa the penis valves can flex laterad without great effect on gonocoxal positions. Figure 161 shows this for *Dactylurina.* In *Liotrigona* and *Cleptotrigona* the flexion is entirely different in that each penis valve flexes contralaterally, the penis valves crossing near their bases (Figs. 153, 154).

Finally there are taxa in which the genitalia are probably rigidly rectagonal: *Lestrimelitta* (Figs. 141-143) and probably *Hypotrigona* (Fig. 151). This condition should be ancestral to judge by Bombinae, Euglossinae, and other families of bees. Figures 6-8 do not support this view.

Poison glands: Kerr and Lello (1962) investigated remnants of the poison gland (and storage sacs) in meliponine workers. They found large sacs in *Meliponula bocandei* (Spinola) and in *Trigona (Frieseomelitta) freiremaiai* (Moure) and apparently assumed them to be plesiomorphic. In fact, they are much larger than in stinging bees *(Apis, Bombus)* and the large size must be a derived condition. In *Nannotrigona, Plebeia* [*schrottkyi* (Friese) and *droryana* (Friese)] and *Dactylurina* the glands are not large but are well developed; I suspect that this is the plesiomorphic condition. *Melipona* and *Trigona (Tetragonisca) angustula* (Latreille) have vestigial but recognizable sacs. In other genera examined the glands are vestigial or absent; such taxa are *Partamona, Trigona (Trigona), Cephalotrigona, Oxytrigona, Lestrimelitta,* and *Scaptotrigona.*

Chromosome numbers: Haploid chromosome numbers have been reported for numerous meliponine bees as well as other Apidae, etc., mostly by W. E. Kerr and his associates (see Mello and Kerr, 1984, and Kerr 1987, for summaries). Table 4 presents the data derived from these sources. These authors regard the ancestral chromosome number as 8, but since outgroups (other subfamilies of Apidea, Xylocopini) have 15 to 25 chromosomes, it seems likely that *Trigonisca muelleri* (Friese) (the *Leurotrigona* group of *Trigonisca*), with 8 chromosomes and *Melipona* with 9 or 10 chromosomes achieved these numbers by fusion rather than retention of ancestral numbers.

Unfortunately, bee chromosomes are minute and details that might clarify these matters are little known. Using numbers alone, no sensible pattern of phylogenetic importance is evident for the Meliponinae.

TABLE 4. Haploid chromosome numbers (largely based on Mello and Kerr, 1984, and Kerr, 1987).

Xylocopa	16
Melipona	9, 10, 18[1]
Plebeia	
Plebeia s. str. (including *"Friesella"*)	18
Schwarziana	16
Partamona	17
Paratrigona	18
Nannotrigona	17
Scaptotrigona	17
Lestrimelitta	14
Oxytrigona	17
Cephalotrigona	17
Trigona	
Geotrigona	17
Frieseomelitta	15
Duckeola	15
Trigona s. str.	14, 17
Hypotrigona	14[2]
Trigonisca	
"Leurotrigona"	8
"Celetrigona"	15
Cleptotrigona	18
Meliponula	
Axestotrigona	18
Meliplebeia	17
"Plebeiella"	18
Meliponula s. str.	18
Dactylurina	17
Euplusia	15
Eulaema	15
Bombus	18, 20
Psithyrus	25
Apis	16

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[1] Based on Kerr (1972).

[2] Kerr (in litt.) indicated that this number is doubtful because of poor slides.

Convergence: Unless there has been convergence in such characters as worker gonostyli, there has been remarkable convergence in external features of workers of various meliponine bees. Wille (1979b) deals with this in some detail. The following paragraphs summarize the main points:

Melipona (Neotropical) and *Meliponula* s. str. (Africa). Robust, thorax and head densely hairy, integument dull, basal propodeal area hairy, dorsal vessel arched between longitudinal indirect muscles of flight. The arch of the dorsal vessel, characteristic of many large, fast-flying bees, may be related to the robust body and fast flight of *Melipona* and *Meliponula* s. str.; the form of the dorsal vessel is documented for various taxa by Wille (1958, 1963, 1979b).

Hypotrigona (Africa), *Liotrigona* (Africa), *Lisotrigona* (Asia), *Pariotrigona* (Asia) and *Trigonisca* (Neotropical). Minute, sparsely haired, pterostigma relatively large, wing venational characters as listed in first alternative of key to genera, below. All except possibly the two rare Asiatic taxa are attracted to perspiration. At least *Hypotrigona, Liotrigona, and Trigonisca* are quite unrelated to one another (Fig. 6) to judge by the sting and male genitalic character states, although superficially almost indistinguishable. *Cleptotrigona* (Africa) also falls in this group but has the special features of robbers.

Dactylurina (Africa), *Trigona* (Neotropical; Asia to Australia). Typically rather elongate and long-legged, although some American forms (like the subgenus *Geotrigona* and some species of *Trigona* s. str.) have the metasoma short and broad. Inner surface of hind tibia of worker with longitudinal band of keirotrichia on elevated ridge usually little if any wider than depressed, shining posterior zone of tibia. Posterior fringe of hind tibia of worker including plumose hairs except in some small subgenera of *Trigona.*

Austroplebeia (Australia), *Meliponula* (except s. str.) (Africa), *Nannotrigona, Paratrigona,* and *Plebeia* (Neotropical), *Plebeina* (Africa). Mostly small, robust bees of superficially similar aspect, often with restricted dull yellowish markings on head and thorax. Posterior margin of inner surface of hind tibia commonly shiny, often depressed, but sometimes with keirotrichia reaching margin.

Cleptotrigona (Africa), *Lestrimelitta* (Neotropical). Robber bees with shiny, sparsely haired bodies; vertex and genal areas broad; proboscidial fossa greatly narrowed posteriorly; eyes small; clypeus small; labrum concave between lateral prominences; corbicula absent, penicillum and rastellum reduced to tapering hairs. Wille (1979b) correctly showed that in spite of their similarities, these genera are not closely related.

Partamona, Scaptotrigona, and *Trigona* s. str. (*spinipes* group), *T. (Geotrigona)* (all Neotropical). Robust, often black bees with short metasomas, superficially similar in form and color.

Classificatory questions: Regardless of one's methods, decisions as to classificatory levels are subjective. There will be some reasonable disagreements with my decisions. Some would regard all genus-group names as genera. I believe that this obscures relationships that are useful to show in the classification. However, even if one accepts in a general way the classification presented below, there are decisions that I had to make arbitrarily and that could equally well have been different. Chief among these are the following:

Scaura could have been given generic status with *Schwarzula* as a monotypic subgenus if desired, instead of placement of *Scaura* as a subgenus of *Plebeia.*

Scaptotrigona could have been placed as a subgenus of *Nannotrigona.* They are sister groups whose relationship might well be indicated by the classification, but they are different in appearance, easily distinguished, and I hesitantly gave both generic status.

Cephalotrigona could have been considered a subgenus of *Trigona.*

Ptilotrigona could have been given subgeneric status in *Trigona*, instead of synonymizing it with the subgenus *Tetragona.*

Five groups of the subgenus *Heterotrigona* of *Trigona* could have been given subgeneric status, as suggested in the discussion of *Heterotrigona.* Subjectively these groups seem less distinct than the subgenera here recognized. No cladistic study of *Trigona* subgenera has been made.

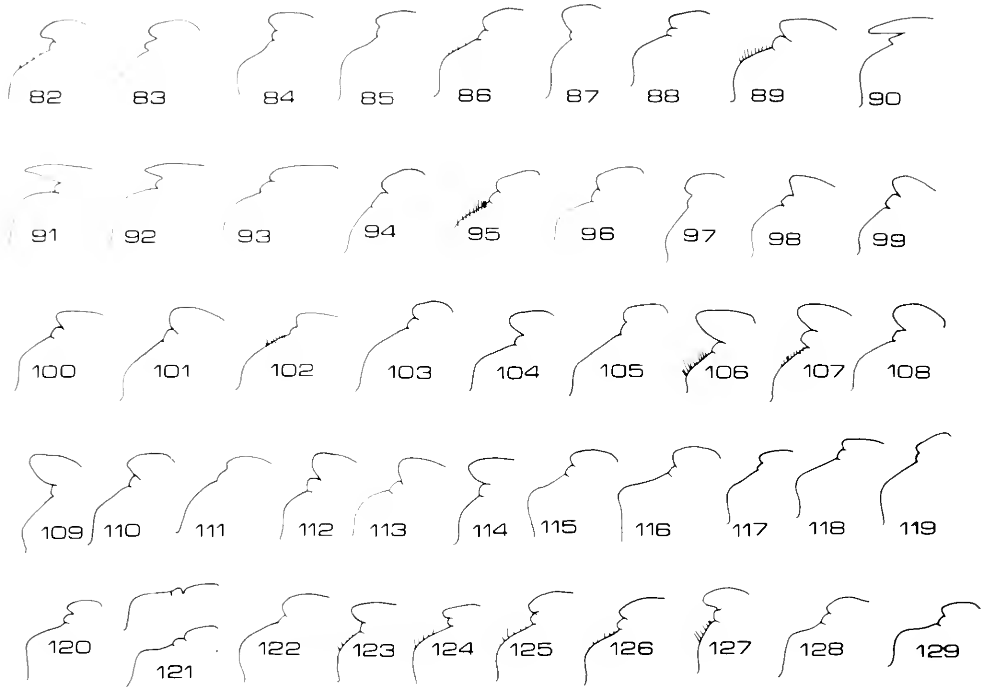
The four named groups of *Trigonisca* could have been given subgeneric status.

The three named groups of *Meliponula*

subgenus *Meliplebeia* could have been given subgeneric status.

Fossil Meliponinae

The best described fossil Meliponinae are *Plebeia (Nogueirapis) silacea* (Wille, 1959b) from the Miocene of southern Mexico, *Proplebeia dominicana* (Wille and Chandler, 1964) from the Oligocene of the Dominican Republic (see also Michener, 1982), and *Trigona prisca* Michener and Grimaldi (1988a, b) from the late Cretaceous of New Jersey.



Figures 82-129. Profile (head to the right) of posterior part of thorax and propodeum of workers (except as otherwise indicated) of Meliponinae. When hairs are present at or near the middle of the basal area of the propodeum, they are indicated. Otherwise hairs are omitted. 82, *Melipona favosa* (Fabricius). 83, *Proplebeia dominicana* (Wille and Chandler). 84, *Plebeia (Plebeia) frontalis* (Friese). 85, *Plebeia (Plebeia) caerulea* (Friese). 86, *Plebeia (Schwarziana) quadripunctata* (Lepeletier). 87, *Plebeia (Scaura) latitarsis* (Friese). 88, *Plebeia (Nogueirapis) mirandula* (Cockerell). 89, *Partamona* near *cupira* (Smith). 90, *Paratrigona opaca* (Cockerell). 91, *Nannotrigona testaceicornis* (Lepeletier). 92, *Scaptotrigona mexicana* (Guérin). 93, *Lestimelitta limao* (Smith). 94, *Oxytrigona mellicolor* (Packard). 95, *Cephalotrigona capitata* (Smith). 96, *Trigona (Lepidotrigona) terminata* Smith. 97, *Trigona (Papuatrigona) genalis* Friese. 98, *Trigona (Geotrigona) acapulconis* Strand. 99, *Trigona (Frieseomelitta) nigra paupera* Provancher. 100, *Trigona (Tetragonisca) angustula* Latreille. 101, *Trigona (Tetragona) clavipes* (Fabricius). 102, *Trigona (Tetragona) lurida* Smith. 103, *Trigona (Duckeola) ghilianii* Spinola. 104, *Trigona (Heterotrigona) apicalis* Smith. 105, *Trigona (Heterotrigona) itama* Cockerell. 106, *Trigona (Heterotrigona) canifrons* Smith. 107, *Trigona (Heterotrigona) planifrons* Smith. 108, *Trigona (Heterotrigona) fuscobalteata* Cresson. 109, *Trigona (Heterotrigona) atripes* Smith. 110, *Trigona (Homotrigona) fimbriata* Smith. 111, *Trigona (Heterotrigona) thoracica* Smith. 112, *Trigona (Trigona) cilipes* (Fabricius). 113, *Trigona (Trigona) fulviventris* Guérin. 114, *Trichotrigona extranaea* Camargo and Moure. 115, *Hypotrigona braunsi* (Kohl). 116, *Pariotrigona pendleburyi* (Schwarz). 117, *Lisotrigona scintillans* (Cockerell). 118, *Trigonisca buyssoni* (Friese). 119, *Trigonisca longicornis* (Friese). 120, *Liotrigona mahafalya* Brooks and Michener. 121, *Cleptotrigona cubiceps* (Friese), male below. 122, *Austroplebeia cassiae* (Cockerell). 123, *Meliponula (Meliplebeia) nebulata* (Smith). 124, *Meliponula (Meliplebeia) lendliana* (Friese). 125, *Meliponula (Meliplebeia) beccarii* (Gribodo). 126, *Meliponula (Axestotrigona) erythra* (Schletterer). 127, *Meliponula (Meliponula) bocandei* (Spinola). 128, *Plebeina denoiti* (Vachal). 129, *Dactylurina schmidti* (Stadelmann).

Information on less fully studied fossil stingless bees is summarized by Wille (1977) and Zeuner and Manning (1976).

P. silacea is no doubt correctly placed, since it is close at the species level to Recent species of *Plebeia (Nogueirapis).* The other fossils are placed with little certainty because we now know that convergence in external features is rampant in Meliponinae. The gonostyli of workers are visible in at least one fossil of the Antillean *Proplebeia,* which is best regarded as a separate genus.

The true position of *T. prisca* must be viewed as dubious, even though it was originally described as a species of *Trigona* s. str. with which it agrees in toothed mandibles and other external characteristics except the probably simple hairs of the posterior margin of the hind tibia. In the latter feature it resembles the subgenus *Lepidotrigona* and perhaps *Papuatrigona.* There may have been a very few branched hairs, as in some *Trigona (Geotrigona).* Thus there is nothing in its external characters to exclude it from the genus *Trigona* in spite of its great antiquity. The problem is that the same can be said of the African *Dactylurina,* yet the worker gonostyli and male genitalia show that *Dactylurina* is only distantly related to *Trigona.* The problem is accentuated by the realization that in the Cretaceous when *T. prisca* was living, its location (New Jersey) was not far from Africa, where *Dactylurina* now lives.

Three genus-group names have been based on fossils. The current status of our knowledge of each is indicated below.

Genus *Meliponorytes* Tosi

Meliponorytes Tosi, 1896:352. Type species: *Meliponorytes succini* Tosi, 1896, by designation of Sandhouse, 1943:570.

Two species were placed in this genus by Tosi (1896). Both were in Miocene Sicilian amber. The specimens have been destroyed (Wille, 1977). Schwarz (1948), Kerr and Maule (1964), and Zeuner and Manning (1976) give detailed interpretations of Tosi's descriptions and figures. Schwarz believed that Tosi's figures showed the inner surface of the hind tibia to be like that of *Melipona* while Zeuner and Manning interpreted the same figures to show a structure like that of *Trigona (Tetragona).* Biogeographic considerations suggest a possible relationship to the African group, e.g., *Meliponula.* The relation to *Meliponula* was rejected by Wille (1977) but seems more reasonable in the context of the broad interpretation of that genus adopted here. More material will be necessary to place this genus.

Genus *Kelneriapis* Sakagami

Kelneriapis Sakagami, 1978 (June):232. Type species: *Trigona (Hypotrigona) eocenica* Kelner-Pillault, 1970, by monotypy.

Kelnermelia Moure and Camargo, 1978 (November 17):565. Type species: *Trigona (Hypotrigona) eocenica* Kelner-Pillault, 1970, by original designation.

This generic name is based on a species from the late Eocene Baltic amber. Many details of its structure are indicated by Kelner-Pillault (1970) and reworded by Moure and Camargo (1978). Unfortunately the inner surface of the hind tibia was not visible and the description and illustration do not even verify the existence of a corbicula on the outer surface. Lack of a corbicula (and apparently of a penicillum) suggests that the specimens were males. The antenna is illustrated and described as 13-segmented, further supporting the sex assignment. Nothing in the descriptions by Kelner-Pillault or by Moure and Camargo suggest realization that they may have been comparing male characters with the worker characters known for other genera.

The bee was minute (3 mm long) with wing venation more or less like that of modern minute species (couplet 1 of key to genera). Its relationships to modern genera remain unknown. Re-examination of the type might partially clarify the situation. At the Institute of Geology and Paleontology, University of Göttingen, however, the type, which should have been there according to the original description, could not be found (inquiry in 1976); the late Dr. S. Kelner-Pillault wrote that she no longer had it in Paris at that time.

Genus *Proplebeia* Michener

Trigona (Proplebeia) Michener, 1982:44: Type species: *Trigona (Liotrigona) dominicana* Wille and Chandler, 1964, by original designation.

This species, from presumably Oligocene amber from the Dominican Republic, was illustrated and described in considerable detail by Wille and Chandler (1964), with additional characters described and illustrated by Michener (1982). It is a common fossil and hundreds of specimens are known, all workers. In the Snow Entomological Museum, University of Kansas, is one specimen (in an amber block containing many specimens) with the apex of the metasoma open, clearly showing the gonostyli and somewhat less clearly, the sting stylet (Fig. 10).

The gonostyli are separated by about 1.5 stylar widths at the bases and converge apically. They clearly have a few setae, visible along the outer margin of one gonostylus. Probable setal bases are visible on all parts of the gonostyli but against the pale background the setae themselves are not visible. There is no evidence of hairlike spicules but they would probably be invisible. It seems almost certain that the gonostyli are like those of most American genera; very clearly they are not like those of *Liotrigona* to which the species was originally attributed.

The sting stylet in some views is convincingly visible, dark in color, slender and acute. If this interpretation is correct, the sting stylet and gonostyli considered together resemble those of *Melipona*, but no other genus.

The placement of *Proplebeia* near *Plebeia* by Michener (1982) still seems reasonable. As noted at that time, the smooth posterior margin of the inner surface of the hind tibia is broader than in *Plebeia (Plebeia)*, about as in *Hypotrigona* (illustrated by Michener, 1982). Moreover, the bristles of the rastellum, while strong, are pointed at the apices, not blunt as usual in *Plebeia*. The profile of the propodeum (Fig. 83) is more declivous, with less of a subhorizontal basal area, than in *Plebeia* and most other Meliponinae. If *Proplebeia* were Recent, there would be problems with couplet 1 of the key to genera, below. The first transverse cubital vein is indicated by a strong spur at the posterior (or basal) end, tapering to a weak line that completes the definition of the first submarginal cell. The veins outlining cell second Cu distally are weak but recognizable (see illustration by Wille and Chandler, 1964). But as in the genera of minute meliponines, vein M of the forewing ends abruptly without a bend (misstated as curved by Michener, 1982), and *Proplebeia* is minute. It must be noted that veins seem weaker in wings preserved in amber (or balsam) than in wings in the air. Except for the problem with vein M, *Proplebeia* runs reasonably well to *Plebeia* in the key to genera.

The principal differences of *Proplebeia* from *Plebeia* are the acute sting stylet and the broad smooth margin of the inner surface of the hind tibia, supplemented by the pointed rastellar bristles and the straight apex of vein M. *Proplebeia* seems best regarded as a distinct genus.

Taxonomic Account of Recent Genera of Meliponinae

The supraspecific taxa of Meliponinae have been described in detail and included in keys by Moure (1951, 1961) as well as by Wille (1959a). For this reason, although the classification is quite changed, no full descriptions are necessary here. Comments on each taxon are limited to interesting problems and character states, and structures not described by previous authors. Included species are listed for each genus and subgenus. Except for the smallest taxa, these lists are limited to a few well-known or for some reason important species, and will serve principally to facilitate the work of users of this paper whose collections were identified when most species of the subfamily were placed in the genus *Trigona*. More comprehensive lists of included species are found in the works cited, or in some cases are not available. Useful regional keys to supraspecific taxa and to species are included in the following works: Schwarz (1934), Panamá; Schwarz (1937), Borneo; Schwarz (1938), Guyana; Schwarz (1939a), Indomalayan region; Schwarz (1948), Neotropical region; Schwarz (1949), Mexico; Sakagami, Inoue, and Salmah (1985), Sumatra.

The following key will be most useful if attention is given to the geographical information provided. In certain cases *(Pariotrigona* and *Lisotrigona)* generic status is tentative, pending discovery of males, and geographic information is essential.

The key is based primarily on workers. Male characters have been added in various couplets. When "workers" are not specified, the character states given apply to males also but are often less well developed in males, so that identification of a male, not accompanied by workers, will often be difficult. Fortunately males are almost always found with workers. Queens have been available for only a few taxa and their characters have not been incorporated into the key or the descriptions.

Key to the Recent Genera of Meliponinae

1. Hind wing without closed cells, veins closing cells R and Cu, if visible at all, clear and unpigmented; forewing with transverse cubital veins almost always completely absent so that there are no indications of submarginal cells; at least distal part of cell second Cu of forewing undefined or defined by completely unpigmented vein traces; vein M of forewing

terminating without bend at about position of anterior end of first recurrent vein (1st m-cu) which, however, is absent (Fig. 168); minute, forewing length less, usually much less, than 4 mm (See comment at end of key.) 2

—Hind wing commonly with cells R and Cu closed by at least weakly brownish veins; forewing with one or two transverse cubital veins usually weakly indicated, first submarginal cell usually recognizable; cell second Cu of forewing completely indicated at least by faint veins; vein M of forewing except in some minute species of *Plebeia, Trigona (Heterotrigona),* etc. extending at least slightly beyond position of anterior end of first recurrent vein and angulate at end of that vein, which is usually at least faintly visible; forewing length commonly (but not always) over 4 mm (See comment at end of key.) 9

2. Outer surface of hind tibia of worker convex, corbicula and penicillum absent; clypeus much more than twice as wide as long (Africa) . . . . *Cleptotrigona*

—Distal part of outer surface of hind tibia of worker flat or concave, forming corbicula; penicillum present; clypeus twice as wide as long or less 3

3. Posterior apical part of hind tibia of worker forming distinct angle; gonostyli of worker adjacent or separated by one or two gonostylar widths 4

—Posterior apical part of hind tibia of worker rounded; gonostyli of worker minute, tuberculiform, separated by several diameters (Africa) . . . . *Hypotrigona*

4. Australia or New Guinea; scutellum and usually scutum and face with well developed yellow markings . . . . *Austroplebeia* (part)

—From other continents; scutellum, scutum, and face in some Neotropical species with white or yellow markings, otherwise without markings or scutellum and edges of scutum sometimes with straw-colored streaks 5

5. Southeast Asiã (males unknown) 6

—Africa, Madagascar, and Neotropics. 7

6. Malar space almost one fifth as long as eye, much longer than flagellar diameter; gonostylus of worker with setae but without minute hairs . . . . *Pariotrigona*

—Malar space shorter than flagellar diameter; gonostylus of worker with many minute hairs (in addition to setae along outer and distal margins) . . . . *Lisotrigona*

7. Base of marginal cell broad, its basal angle (between stigmal margin and vein r, within marginal cell) slightly acute (about 68°) to nearly right angular; gonostylus of worker with a few setae in addition to minute hairs (Neotropical region). . . . . *Trigonisca*

—Base of marginal cell of usual shape, its basal angle strongly acute, not over 50°; gonostylus of worker with setae or minute hairs but not both 8

8. Gonostylus of worker with minute hairs but no setae (Africa and Madagascar). . . . . *Liotrigona*

—Gonostylus of worker with setae but no minute hairs (Neotropics). . . . . . *Plebeia* (part)

9. Inner surface of hind tibia with strongly depressed, shining, posterior marginal area which at least apically is usually about as broad as longitudinal median keirotrichiate ridge, and midway of tibial length is at least half as wide as keirotrichiate ridge (Fig. 185) 10

—Inner surface of hind tibia with depressed posterior marginal area narrow (much less than half as wide as area with keirotrichia) or absent, keirotrichia extending to or close to margin (Fig. 184). 14

10. Eyes hairy; rastellum reduced to tapering hairs (South America) . . . . . . *Trichotrigona*

—Eyes bare; rastellum strongly developed. 11

11. First metasomal segment longer than broad; gonostyli (third valvulae) of worker adjacent basally, flattened, with minute hairs but without setae; rastellum consisting of tapering bristles (Africa). . . . . *Dactylurina*

—First metasomal segment broader than long; gonostyli of worker usually separated at bases by at least width of a gonostylus, not flattened, with strong setae but no minute hairs;

rastellum with at least some bristles blunt (Neotropical and Indoaustralian regions). 12

12. Face short and broad, minimum distance between eyes much greater than length of eye; clypeus less than twice as broad as long; malar space almost twice as long as flagellar diameter; keirotrichiate zone on inner side of worker hind tibia nearly twice as wide as depressed marginal zone at midlength of tibia (Neotropical region) . . . . *Oxytrigona*

—Face of ordinary shape, minimum distance between eyes little more than to less than length of eye; clypeus usually more than twice as broad as long; malar space usually little over 1.5 times as long as flagellar diameter or usually much less; keirotrichiate zone on inner surface of worker hind tibia usually narrower, rarely over 1.5 times as wide as depressed marginal zone at midlength of tibia (Neotropical and Indoaustralian regions) 13

13. Preoccipital carina strong and shining across full width behind vertex; lower face and genal area shining and coarsely punctate in contrast to dull, densely, minutely punctate upper face, genal area and scutum . . . . *Cephalotrigona*

—Preoccipital carina absent; lower face and genal area finely sculptured like upper part of head and scutum . . . . *Trigona*

14. First flagellar segment of worker nearly as long as second plus third, of male nearly as long as second; outer surface of hind tibia convex, without corbicula, anterior margin convex like posterior margin; penicillum absent; rastellum consisting of tapering hairs (Neotropical region) . . . . *Lestrimelitta*

—First flagellar segment of worker shorter than second plus third together, of male much shorter than second; outer surface of hind tibia of worker (and some males) flat or concave at least distally, anterior margin gently convex to concave, unlike largely or wholly convex posterior margin; penicillum present; rastellum variable 15

15. Gonostylus of worker with setae having strong bases, without minute hairs; rastellum consisting of strong bristles, usually some of them with blunt apices (Neotropical region) 16

—Gonostylus of worker without or with few setae, with numerous minute hairs; rastellum usually consisting of weaker, flexible looking bristles or hairs that taper to attenuated apices and are sometimes plumose (Africa, Australia, New Guinea) 21

16. Hamuli 9-14 (rarely 8); wings extending little if any beyond apex of metasoma; stigma with margin within marginal cell straight or weakly concave (Fig. 162). (Body robust; basal propodeal area dull, hairy). . . . . *Melipona*

—Hamuli 5-7, rarely up to 9 or even 10; wings long, extending well beyond apex of metasoma; stigma with margin within marginal cell slightly convex (Figs. 163-171). 17

17. Anterior part of scutellum with longitudinal V- or U-shaped median shining depression opening anteriorly into scutoscutellar fossa (Fig. 190); preoccipital carina present, extending far down laterally on each side of foramen magnum 18

—Anterior part of scutellum without such a median, shining depression (Fig. 191); preoccipital carina absent or with transverse part only, behind vertex and weakly indicated 19

18. Head and thorax, or at least scutellum, with extremely coarse, cribriform punctation; posterior margin of scutellum notched or emarginate medially as seen from above; anterior margin of pronotal lobe with strong, transverse carina . . . . *Nannotrigona*

—Head and thorax with fine punctation; posterior margin of scutellum entire; anterior margin of pronotal lobe rounded . . . . *Scaptotrigona*

19. Mandible of worker with four apical teeth (lower two sometimes united by translucent septum but teeth still recognizable); scutellum seen in lateral view projecting posteriorly as thin shelf over median part of metanotum . . . . *Paratrigona*

—Mandible of worker with (rarely without) one or two denticles at upper end of apical margin, otherwise without teeth; scutellum in lateral view rather thick and rounded, not projecting as thin shelf over metanotum. 20

20. Hind tibia of worker greatly broadened, spoon-shaped, about three times as wide as femur, outer surface largely occupied by corbicula (Fig. 187); basal area of propodeum densely hairy . . . . *Partamona*

—Hind tibia of worker triangular, not greatly broadened, much less than three times as wide as femur, corbicula extending but little if at all basad of middle of tibia (Fig. 184); basal area of propodeum usually hairless . . . . *Plebeia* (part)

21. Male genital capsule rectigonal, gonocoxite transverse, much wider than long; gonobase completely absent (Australia, New Guinea). . . . . *Austroplebeia* (part)

—Male genital capsule schizogonal, gonocoxite longer than broad; gonobase represented by fragment on each side (Africa). 22

22. Hind tibia of worker rather spoon-shaped, posterior apical angle rounded but with coarse, amber colored to blackish bristles (posterior parapenicillum); sting stylet of worker distinct, acute . . . . *Meliponula*

—Hind tibia of worker slender, triangular with distinct posterior apical angle which supports long hairs that are neither especially coarse nor amber colored; sting stylet of worker a mere rounded convexity. . . . . *Plebeina*

Note on Couplet 1. This couplet conveniently separates some groups of minute species from the rest of the Meliponinae. Unfortunately, no one of the characters listed is completely reliable. For this reason *Plebeia* and *Austroplebeia* can be run both ways. Minute species exist among other genera [e.g., *Trigona (Heteroterigona) fuscobalteata* Cameron] and various such minute or merely small species possess some of the character states listed in the first alternative of couplet 1, yet should be run with the second alternative. Species such as *T. fuscobalteata* Cameron would run to 2 although cell second Cu is better defined than in most minute forms; it can easily be distinguished from all of the forms that should go to 2 by the characteristic *Trigona*-like inner surface and marginal fringe of the hind tibia. Many specimens of *Plebeia (Plebeia) schrottkyi* (Friese) lack the bend at the end of vein M shown in Figure 164, and would easily run to 2; this is why *Plebeia* can be run through either alternative. *P. schrottkyi* also lacks closed cells in the hind wing. The narrow depressed shining possterior margin of the inner surface of the hind tibia easily places this species in *Plebeia*. In *Austroplebeia cincta* (Mocsary) traces of a transverse cubital vein and of cell second Cu are evident, yet vein M ends without a bend. Some other species of the genus lack such traces and run easily to 2. I have placed this genus in the key twice to take care of this problem.

The following character states exclude small species from the first alternative and send them to 9 in the key:

(1) Hind tibia with plumose hairs among simple ones along posterior margin *(Trigona)*.

(2) Shining posterior margin of inner side of hind tibia absent or less than one third as wide as keirotrichiate zone at midlength of the tibia, except for *Cleptotrigona* and *Pariotrigona*. The forms that should go to 2 have the shining, marginal zone at least one third as wide as the keirotrichiate zone except for *Pariotrigona* (southeast Asia) and the African robber bee, *Cleptotrigona,* which lacks corbicula and penicillum.

(3) Rastellum consisting of strong, usually amber bristles, usually some of them blunt. In forms that should be run to 2 (except *Plebeia*), the rastellum consists of pallid, flexible, tapering hairs; such rastella also occur in some groups that run to 9, such as *Meliponula*.

Genus *Melipona* Illiger

(Figs. 9, 49, 82, 130, 162, 172, 176)

Melipona Illiger, 1806: 157. Type species: *Apis favosa* Fabricius, 1798, by designation of Latreille, 1810: 439.

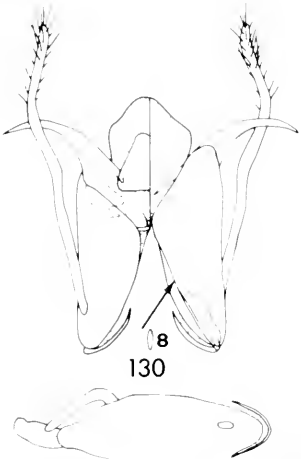
Melipona (Micheneria) Kerr, Pisani and Aily, 1967: 139 (not Orfila and Rossi, 1956). Type species: *Melipona scutellaris* Latreille, 1811, by original designation.

Melipona (Michmelia) Moure, 1975: 621. New name for *Micheneria* Kerr, Pisani and Aily. Type species: *Melipona scutellaris* Latreille, 1811 (autotypic) (new synonym).

This is the most distinctive meliponine genus although it was not reliably distinguished from the others until well into the present century (see Schwarz, 1932). It consists of rather large (8-15 mm long) species, mostly somewhat more robust than workers of *Apis*. Wille (1979b) and Moure (1951, 1961) tabulated the most distinctive features (as the tribe Meliponini), which include wings that extend little if any beyond the apex of the metasoma, slender stigma that is not convex within the marginal cell, and 9 to 14 hamuli. The setae of the labial palpus are short and straight. The sting stylet of the worker is right angular or acute, sometimes (as in *M. fulva* Lepeletier, Fig. 9) as strong as in the African genus *Meliponula*, and the male genital capsule is schizogonal, the gonocoxites elongate, not transverse. Illustrations of male genitalia and hidden sterna can be found in Schwarz (1932), Snodgrass (1941), Camargo, Kerr and Lopes (1967), and Camargo, Moure and Roubik (1988). In the sting stylet and genital characters *Melipona* resembles the African group of genera. Unlike that group, however, the rastellum is strongly developed with many of the bristles blunt or abruptly narrowed at apices and the worker gonostyli are widely separated, setose and without minute hairs. It is the only Recent genus with such gonostyli and at the same time with an acute sting and long male gonocoxites. All three of these character states are plesiomorphies, as is the indication of a gonobase in males in the form of a slender sclerotic strip.

Melipona also differs from all other Meliponinae in having the third abdominal ganglion of workers and males (it innervates metasomal segment 2) in the thorax, the next one in the petiolar region and the last in metasomal segment 3 (Wille, 1961; Cruz-Landim et al., 1972). This cephalization is an apomorphy of the genus. Also, the digestive tract is relatively long (Cruz-Landim and Rodrigues, 1967).

In nesting biology, *Melipona* is unique among Meliponinae in rearing numerous small queens in cells that are identical to worker cells. In all other genera only a few large queens are pro-



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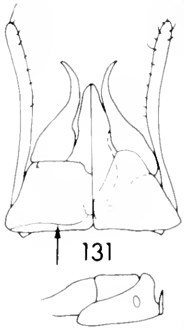
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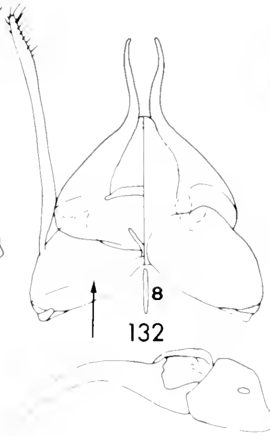

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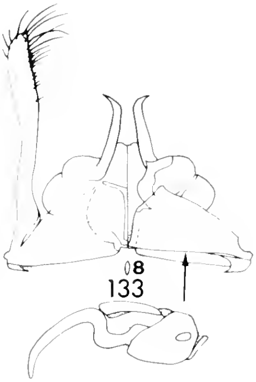

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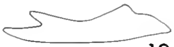
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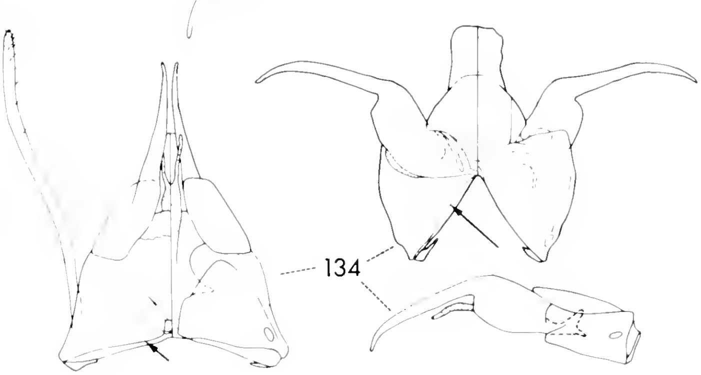
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Figures 130-134. Male genitalia of Meliponinae, dorso-ventral views (dorsal at left) and lateral views with gonostylus and (for 130, 131) penis valve omitted or apex omitted. In this and other sets of figures of male genitalia, arrows indicate the basal opening of the gonocoxites into the metasomal cavity; 8 = probable relictual spiculum of S8. 130, *Melipona fulva* Lepeletier. 131, *Plebeia (Plebeia) frontalis* (Friese). 132, *Plebeia (Plebeia) schrottkyi* (Friese). 133, *Plebeia (Plebeia) caerulea* (Friese). 134, *Partamona* near *cupira* (Smith) rectigonal conformation at left, schizogonal conformation with gonostyli omitted at right.

Figures 135-137. Mandibles of male Meliponinae, apices at left. 135, *Hypotrigona braunsi* (Kohl). 136, *Liotrigona mahafalya* Brooks and Michener. 137, *Trigona (Trigona) fulviventris* Guérin.

duced in special large cells. Caste determination of *Melipona* is apparently partly genetic. The method of recruitment to resources is also different from that of other Meliponinae. See review by Michener (1974).

In view of its many autapomorphies, the recognition of a tribe Meliponini for *Melipona* can be justified on phenetic bases. Cladistic analysis does not strongly reinforce this tribal arrangement (Fig. 6) and tribal rank does not seem necessary for a single genus.

The division of the genus into two groups by Kerr, Pisani and Aily (1967) does not seem to me to necessitate subgeneric names. I have therefore included *Michmelia* as a synonym, but this is a matter of judgement.

Melipona ranges from Mexico to Argentina and contains about 40 species. The species were revised by Schwarz (1932) with an important review of the classification by Moure and Kerr (1950). Some well known species are *M. beecheii* Bennett, *fasciata* Latreille, *favosa* (Fabricius), *fulva* Lepeletier, *marginata* Lepeletier, *rufiventris* Lepeletier, and *seminigra* Friese.

Genus *Plebeia* Schwarz

This genus has shiny cephalic and thoracic integument with minute [somewhat larger in *P. (P.) caerulea* (Friese)], well separated punctures, varying to dull, densely and minutely punctate, in the subgenus *Schwarziana* and in *P. (P.) schrottkyi* (Friese). The scutellum is rounded in lateral view, not shelf-like, and often but not always overhangs and hides the median part of the metanotum as seen from above. The scutellum lacks a median depression in the anterior margin like that of *Nannotrigona* and *Scaptotrigona,* but in some species there is a weak indication of such a depression. The preoccipital carina is weak but present dorsally in the subgenus *Schwarziana* and some species of *Plebeia* s. str. but the lateral parts extending down toward the mandibles are always absent. The broad area with keirotrichia on the inner side of the hind tibia extends nearly to the posterior margin of the tibia but the margin is shiny, largely bare (Fig. 184), and abruptly depressed [except not depressed on distal third of tibia of *P. (Scaura) timida* (Silvestri) and not at all depressed in the subgenus *Nogueirapis*]; the area with keirotrichia may or may not reach the rastellum. The explanation of the inclusion of *Nogueirapis* as a subgenus in the genus *Plebeia* is given under the discussion of the subgenus.

A widely used character in Meliponinae is the presence or absence of plumose hairs on the posterior margin of the hind tibia of workers (character 6, Table 2). In *Plebeia* s. str. there are often one or two hairs with a branch or two near the apex of the posterior margin, and in *P. (Plebeia) caerulea* (Friese) and *P. (Schwarziana) quadripunctata* (Lepeletier) numerous hairs have short branches on one side. In *Plebeia* it is the long hairs that have such branches; in *Trigona* the long hairs are simple and intercalated shorter hairs are usually plumose.

The worker gonostyli are adjacent to widely separated, converging apically, overlapping apically when adjacent at bases, setose. The sting stylet is broad, rounded or irregular. The lancet is short; it is free at the apex only in the subgenus *Schwarziana.*

The male genitalia of *Plebeia* s. str. (Figs. 131-133 and Camargo and Moure, 1988) and *Schwarziana* (illustrated by Schwarz, 1948) are rather similar, rectigonal [in reality amphigonal at least in *P. (Plebeia) schrottkyi* (Friese), for which both rectigonal and schizogonal preparations are at hand (probably all species are amphigonal)]. Unlike most such forms, the gonocoxites are nearly as long as broad or longer. In *Scaura* (see Schwarz, 1948) the gonocoxites are short and transverse as in most rectigonal (amphigonal) Meliponinae and the same is probably true of *Nogueirapis* in view of Wille's (1964) comparison of the male genitalia of *P. (N.) mirandula* (Cockerell) with those of species of *Trigona* s. str. I have not seen males of the subgenus *Nogueirapis;* apparently males are not present in the collection at the Universidad de Costa Rica where Wille's material is preserved.

The forms listed above with dull cephalic and thoracic integument are not closely related to one another as judged by tibial and other characters. In *Trigona,* also, there is a subgenus with fine, dull thoracic integument *(Lepidotrigona),* a subgenus with a somewhat more shining and less closely punctate thoracic integument *(Papuatrigona),* in addition to the majority, which are shiny with well separated, minute punctures. Also in *Partamona* there are dull as well as shiny species. The idea that this is necessarily a generic or subgeneric character should be abandoned.

Brood cell construction is particularly variable in this genus. It is successive in the subgenera *Schwarziana* and *Scaura,* synchronous in most *Plebeia* s. str., and intermediate (starting successively but becoming synchronous) in *Plebeia (Plebeia) schrottkyi* (Friese) and *minima* (Friese).

Key to the Subgenera of *Plebeia*

1. Hind basitarsus thickened, nearly as broad as or broader than tibia. (Face without yellow markings.) . . . . *Scaura*

—Hind basitarsus flat, much narrower than tibia 2

2. Body (including metasomal terga) dull, minutely and closely punctured; forewing length about 6 mm; S3 of male with enormous procurved band of erect hooked hairs, behind which is a concave membranous area with erect hairs . . . . *Schwarziana*

—Body or at least metasoma shining; forewing length less than 5 mm, usually 4 mm or less; S3 of male unmodified 3

3. Hind tibia with posterior margin of inner surface narrowly depressed, shining, in sharp contrast to keirotrichiate area (Fig. 185) . . . . *Plebeia* s. str.

—Hind tibia with posterior margin of inner surface narrowly shining but not or scarcely depressed . . . . *Nogueirapis*

Subgenus *Plebeia* Schwarz, s. str.

(Figs. 11-13, 50, 51, 84, 85, 131-133, 163, 164, 184)

Trigona (Plebeia) Schwarz, 1938: 480. Type species: *Trigona mosquito* Smith, 1863, by original designation.
Mourella Schwarz, *in* Moure, 1946a: 442. Type species: *Melipona caerulea* Friese, 1900, by original designation.
Friesella Moure, 1946a: 441; 1946b: 611. Type species: *Melipona schrottkyi* Friese, 1900, by original designation.

This is a subgenus of small bees, mostly with whitish or yellow markings on the face and thorax. Unlike *Scaura,* which commonly has a more slender metasoma, that of *Plebeia* s. str. is as broad as the thorax. Except in *P. (P.) caerulea* (Friese), the labial palpi have five to nine large setae. At least one [in *P. (P.) franki* (Friese)] is curved and usually most are curved; in some species those on segment two are slightly sinuous.

Two unusual species have received genus-group names. *Mourella* was proposed for a rather large, robust species with the head and thorax dark blue-green (the only metallic meliponine), *P. caerulea* (Friese), with the mesoscutum a little more coarsely punctate than in other species, and with hairs on the basal area of the propodeum except medially. Unlike other *Plebeia* s. str., the scape of the worker is long, reaching to within one ocellar diameter of the median ocellus, and large setae are absent on the labial palpi, the hairs being short and straight. *Friesella* was proposed for a tiny species, *P. schrottkyi* (Friese). It has the mesoscutum dull with small close punctures and lacks yellow marks on the face; such marks on the thorax are absent in males, in workers there is commonly a weak pale line next to the tegula and sometimes a spot on the axilla. The wing venation is much reduced (see note after key to genera). While these two species are clearly quite different from ordinary species of *Plebeia,* I doubt if subgeneric names are needed for them. *Mourella* was described and illustrated by Schwarz (1948). Descriptions of *Plebeia* s. str. (and of the monotypic *Friesella* and *Mourella,* here synonymized) were given by Moure (1951).

Wille (1960) emphasized the intermediacy of *P. intermedia* (Wille) between *Plebeia* s. str. and *Schwarziana.* This species is large for a *Plebeia* s. str., with a rather closely punctured thoracic dorsum and with the scutellum not extending over the metanotum, features suggesting *Schwarziana.* However, the generally shiny surface, the shiny basal area of the propodeum, etc., are as in *Plebeia* s. str. and I suspect that when the male is found, it will not have the characteristics of *Schwarziana*.

Plebeia s. str. ranges from Mexico to Argentina. There are about 30 species; several occur in most areas. The unusual species, *P. (P.) schrottkyi* (Friese) and *caerulea* (Friese), occur in southern Brazil and adjacent countries; *P. (P.) intermedia* (Wille) is from Bolivia.

Familiar names are *Plebeia (Plebeia) caerulea* (Friese), *droryana* (Friese), *emerina* (Friese), *franki* (Friese), *frontalis* (Friese), *jatiformis* (Cockerell), *minima* (Friese), *mosquito* (Smith), *remota* (Holmberg), *schrottkyi* (Friese), and *tica* (Wille).

Subgenus *Schwarziana* Moure

(Figs. 14, 52, 86)

Trigona (Schwarziana) Moure, 1943: 147. Type species: *Melipona quadripunctata* Lepeletier, 1836, by original designation.

I have retained this name for a large species (body length 7 mm) that suggests in body form and pale markings a large *Plebeia* s. str. with a minutely punctate, dull body (including the metasomal terga). The dorsal propodeal area has a few hairs. The most remarkable features are those of the male sterna, which are highly modified as illustrated by Schwarz (1948); see also above key to the subgenera. The base of the propodeum is hairy, unlike other subgenera except for *P. (Plebeia) caerulea* (Friese). The scape is long, reaching nearly to the median ocellus, as in *P. (P.) caerulea.* The male genitalia are similar to those of *Plebeia* s. str. (see Schwarz, 1948; Camargo, 1974). The lack of large setae on the labial palpi (numerous short straight setae present) might be a plesiomorphic feature. Thus this could be the sister group to the subgenus *Plebeia* as here understood. Full descriptions were given by Moure (1951) and Camargo (1974).

The single species, *Plebeia (Schwarziana) quadripunctata* (Lepeletier), is found in Brazil (Goiaz and Minas Gerais southward), Paraguay, and northern Argentina.

Subgenus *Nogueirapis* Moure
(Figs. 16, 88)

Partamona (Nogueirapis) Moure, 1953: 247. Type species: *Trigona butteli* Friese, 1900, by original designation.

Nogueirapis has hitherto been placed either as a subgenus of *Partamona* (Moure, 1953, 1982) or as an independent genus. The association with *Partamona* is an error. It differs from that genus in the ordinary (not enlarged and spoon-shaped) hind tibia of the worker as well as small size, abundant yellow markings, the few and mostly curved (none sinuous) large setae of the labial palpi (as in various species of *Plebeia* s. str.), and the shining and hairless basal propodeal area as was indicated by Wille (1964). The detailed descriptions of *Plebeia* and *Nogueirapis* by Wille (1959) agree in all details except as follows: (1) *Nogueirapis* is said to have the posterior apical angle of the worker hind tibia rounded, *Plebeia* s. str., angular. Actually it is angular in both and some species of *Plebeia* s. str. have the tibia almost exactly as in *Nogueirapis*. (2) The inner surface of the hind tibia of *Nogueirapis* has a narrow, bare, shiny, but not depressed posterior margin whereas it is depressed in *Plebeia* s. str. This last character state has been the hallmark of *Plebeia* and would exclude *Nogueirapis* from *Plebeia*. No one character, however, should alone determine the classification, especially in a group so noted for convergence as the Meliponinae. Moreover, *P. (Scaura) timida* (Silvestri) is intermediate in this character, which is also variable within the genus *Meliponula*. In view of the many similarities between *Plebeia* s. str. and *Nogueirapis*, I regard them as congeneric.

Inclusion of *Nogueirapis* in the genus *Plebeia* results in a genus *(Plebeia)* with no known diagnostic apomorphies. The depressed posterior hind tibial margin is a probable synapomorphy for the rest of the genus. However, this character state is probably subject to reversals. A partial reversal is likely for *P. (Scaura) timida* (Silvestri) and polarization of this character is not at all convincing in the genus *Meliponula*. Thus the condition in *Nogueirapis* could be derived from that in other groups of *Plebeia* instead of the reverse. It is therefore best to place *Nogueirapis* on the basis of its close phenetic resemblance to *Plebeia* s. str., while hoping for the discovery of relevant synapomorphies.

This subgenus contains three species, *Plebeia (Nogueirapis) butteli* (Friese), *minor* (Moure and Camargo), and *mirandula* (Cockerell), and ranges from Costa Rica to Bolivia. In addition, it includes the Miocene fossil species *Plebeia (Nogueirapis) silacea* (Wille, 1959b) from southern Mexico.

Subgenus *Scaura* Schwarz
(Figs. 15, 53, 87)

Trigona (Scaura) Schwarz, 1938: 479. Type species: *Trigona latitarsis* Friese, 1900, by original designation.
Schwarzula Moure, 1946a: 439. Type species: *Trigona timida* Silvestri, 1902, by original designation.

This subgenus differs from other Meliponinae in the hind basitarsi which are nearly as broad as to broader than the tibia and convex on the outer surfaces, at least apically, as illustrated along with other character states (including those of male genitalia and sterna) of the *latitarsis* group by Schwarz (1948). These are small bees; *P. timida* (Silvestri) has the form of a *Plebeia* s. str., the others have variably more slender metasomas, very slender in *P. tenuis* (Ducke) and *longula* (Lepeletier). An interesting feature, best developed in *P. (S.) latitarsis* (Friese), is the series of flat, curved bristles on the posterior margins of S4 and S5 of the worker. The head and thorax are black, without the yellow markings characteristic of nearly all species of *Plebeia* s. str. The body surface is shining with small, scattered punctures like those of most *Plebeia* s. str. Unlike nearly all species of *Plebeia* s. str., the labial palpi lack large setae; the setae are rather short and straight. A full description of *Scaura* was given (as a genus) by Moure (1951).

The subgenus consists of two units that differ considerably. *P. (S.) timida* (Silvestri) has more plesiomorphies, as shown by the two denticles on the upper part of the apical mandibular margin and the less broad hind basitarsi which are only weakly convex on the outer surface. Unlike other species of the genus *Plebeia* (except *Nogueirapis*), the posterior margin of the inner surface of the hind tibia is not depressed in the apical third or fourth of the tibia. *P. timida* has been placed in a monotypic genus or subgenus *Schwarzula*. The other species of *Scaura* have untoothed mandibles (or the two denticles near the upper end of the apical margin are barely perceptible), broader and more convex hind basitarsi, and a fully depressed inner posterior margin of the hind tibia as in *Plebeia* s. str. *P. timida* appears to be the sister to all other species of *Scaura*, and I have elected to include it in *Scaura*, thus synonymizing *Schwarzula*.

Scaura ranges from southern Mexico to Brazil and Bolivia; there are four species, *Plebeia (Scaura) latitarsis* (Friese), *longula* (Lepeletier), *tenuis* (Ducke), and *timida* (Silvestri).

Genus *Partamona* Schwarz

(Figs. 17, 18, 57, 89, 134, 187, 191)

Trigona (Patera) Schwarz, 1938: 475 (not Lesson, 1837; not Albers, 1850). Type species: *Melipona testacea* Klug, 1807, by original designation.

Trigona (Partamona) Schwarz, 1939b: 23. Type species: *Melipona testacea* Klug, 1807 (autobasic and original designation). Replacement for *Patera* Schwarz, which is preoccupied.

Trigona (Parapartamona) Schwarz, 1948: 428. Type species: *Trigona zonata* Smith, 1854, by original designation.

This genus is composed of relatively robust forms superficially suggestive of *Scaptotrigona*, some species of *Trigona* s. str., etc. *Partamona* differs from such forms by having yellowish face marks (often restricted), by the rather dense covering of erect hair on the basal propodeal area, and by the hind tibial structure of workers. This tibia is greatly broadened, about three times as wide as the femur, spoon-shaped, the outer surface mostly occupied by the enormous corbicula (Fig. 187). There are two hairs, often about as long as the tibial width and often apically wavy, arising from the posterior part of the corbicula. The inner surface of the tibia has the broad keirotrichiate area extending nearly to the posterior margin, which is shining but not depressed. The worker gonostyli are mere rounded tubercles with a few setae or in *P. zonata* (Smith) about 1.5 times as long as broad. The sting stylet is rounded, the lancet is moderately long and the distal part free of the membrane, or almost absent in *P. zonata*. The male genital capsule is amphigonal [both conformations seen in *P. cupira* (Smith), Fig. 134]. It is illustrated here as well as by Snodgrass (1941). The large setae of the labial palpus are about 11 to 13 in number, mostly sinuous but some only curved.

In most species the cuticle is shining with minute, widely separated punctures. In *P. zonata*, the type species of *Parapartamona*, however, the cuticle is dull and exceedingly minutely punctate or roughened. Other species that have the extremely long wings of *Parapartamona* have intermediate cuticular structure, or even as in *P. grandipennis* (Schwarz), cuticle like that of typical *Partamona*. For these reasons I do not think that *Parapartamona* should be recognized as a subgenus. A full description of *Partamona* was given by Moure (1951) and of *Parapartamona* by Moure (1953).

Partamona has not been revised as a whole but the *Parapartamona* group was dealt with by Schwarz (1948) and the species with testaceous bodies by Camargo (1980).

The genus, with about 16 species, ranges from Mexico to central Brazil and Peru, but appears to be absent from southern Brazil and adjacent countries. Familiar species are *Partamona bilineata* (Say), *cupira* (Smith), *helleri* (Friese), *peckholti* (Friese), *testacea* (Klug), and *zonata* (Smith). Except as otherwise indicated, the references to and illustrations of "*Partamona* near *cupira*" are based on Mexican specimens that are probably *P. bilineata*.

Genus *Paratrigona* Schwarz

(Figs. 19, 55, 90)

Trigona (Paratrigona) Schwarz, 1938: 487. Type species: *Melipona prosopiformis* Gribodo, 1893.

Paratrigona (Aparatrigona) Moure, 1951: 60. Type species: *Melipona impunctata* Ducke, 1916.

This genus contains small species with the head and thorax (often also the abdomen) dull with extremely minute punctation and with conspicuous yellow to white markings on the thorax and usually on the face. As in *Nannotrigona* and *Scaptotrigona*, the scutellum is produced posteriorly as a thin shelf hiding the median part of the metanotum as seen from above. The scutellum, however, lacks the anteromedian depression characteristic of those genera. The proboscis is unusually long, the first segment of the labial palpus being about three times as long as the second which is about six times as long as wide. The eight or nine large setae of the labial palpi are strongly curved. The preoccipital carina is completely absent. The inner surface of the hind tibia has the broad keirotrichial area extending nearly to the posterior margin which is not depressed. There are two unusually long hairs (about as long as tibial width) arising from the posterior part of the corbicula; this is suggestive of *Partamona* but less conspicuous than in that genus because the tibia is narrower. The four-toothed mandibles of workers distinguish this genus from all Meliponinae except *Trigona (Trigona)*; the two lower teeth may be united by a thin septum, however, so that the mandibular profile looks like that of an ordinary meliponine with the two denticles on the upper part of the apical margin unusually large. Full descriptions are given by Schwarz (1948) and Moure (1951), and Schwarz gives an illustrated account of the species, including figures of male genitalia and hidden sterna.

The worker gonostyli are widely separated, setose, convergent apically. The sting stylet is broad, rounded and the lancet, if present, is a mere strip in the membrane. The male genital capsule is rectigonal, but may well be really amphigonal. No specimens with the schizogonal conformation have been seen, however.

Moure (1951) separated two unusually robust species as a subgenus *Aparatrigona*. There is no doubt that they constitute a monophyletic unit that is the sister group to the rest of the genus.

They possess plesiomorphies relative to other species such as a partly smooth metasoma and relatively abundant hair (other species are nearly nude). I doubt that *Aparatrigona* is sufficiently different from *Paratrigona* s. str. to necessitate recognition of the subgenus for only two species.

It is noteworthy that in *P. opaca* (Cockerell) S6 of the male is a plate entirely without the apical process usual in meliponines and found in other species of *Paratrigona*. A somewhat intermediate condition exists in *P. prosopiformis* (Gribodo), in that S6 is broader than usual and the apical process triangular (see illustrations of Schwarz, 1948). These character states are not associated with other distinctive features and additional supraspecific taxa do not seem to be desirable for these species. In *Trigona (Heterotrigona)* also there is a species, *T. (H.) apicalis* Smith, with S6 similar to more anterior sterna; see also *Trigona (Homotrigona)*.

Paratrigona ranges from Mexico to Argentina. There are about a dozen species; see the revision by Schwarz (1948). Familiar names are *Paratrigona impunctata* (Ducke), *lineata* (Lepeletier), *opaca* (Cockerell), and *peltata* (Spinola).

Genus *Nannotrigona* Cockerell

(Figs. 20, 56, 91, 138)

Nannotrigona Cockerell, 1922: 9. Type species: *Melipona testaceicornis* Lepeletier, 1836.

This genus is characterized by the very strong, usually cribriform punctation of the head and thorax or at least the scutellum; the scutellum produced posteriorly as a thin shelf (side view) hiding the median part of the metanotum in dorsal view; the notched or emarginate apex of the scutellum (dorsal view); the presence of a shining, depressed V- or U-shaped median depression in the anterior margin of the scutellum (as in Fig. 190); the straight lateral clypeal margins (concave in most other Meliponinae); the distinct preoccipital carina, laterally extending down toward the mandibles, although weak dorsolaterally; the strong transverse carina across the anterior margin of the pronotal lobe; the distinct (although not carinate) angle between the anterior and lateral surfaces of the mesepisternum; and the broad area of keirotrichia on the inner side of the hind tibia, extending to or nearly to the posterior margin of the tibia which is not abruptly depressed, and extending apically to the bases of the rastellar bristles. The worker gonostyli are short, separated at the bases by less than a stylar width, strongly convergent and overlapping distally. The sting stylet is broad and rounded, the lancet absent. The male genital capsules examined are schizogonal, very thick, with the spatha nearly vertical; the schizogonal conformation may be permanent. The genitalia are strangely similar to those of *Trigona (Tetragonisca)*. The large setae of the worker labial palpi are few, about 10, sinuous. Full descriptions of the genus are given by Moure (1951) under his genus and subgenus *Nannotrigona*.

Nannotrigona looks like a deeply punctate, pitted *Plebeia* s. str. Thus it is quite different in appearance from the larger, robust *Scaptotrigona*. As emphasized by Schwarz (1938:483) and Wille (1959a, 1979b), however, *Nannotrigona* and *Scaptotrigona* share numerous character states and I do not doubt their close relationship.

Nannotrigona is so distinctive that Cockerell (1922), who was generally conservative in such matters, named it as a distinct genus while leaving other Meliponinae except *Melipona* in the genus *Trigona*. About nine species range from Mexico to southern Brazil and Paraguay. The most familiar is *Nannotrigona testaceicornis* Lepeletier.

Genus *Scaptotrigona* Moure

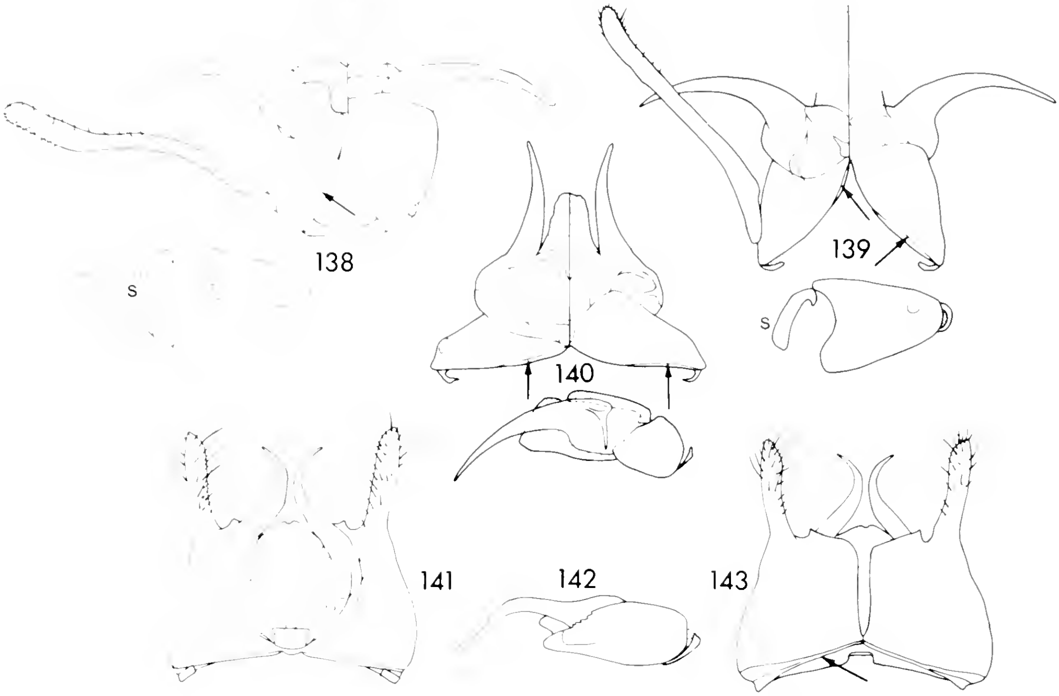
(Figs. 21, 54, 92, 139, 140, 190)

Trigona (Scaptotrigona) Moure, 1942: 315. Type species: *Trigona postica* Latreille, 1807, by original designation.

These are among the most robust of the Meliponinae. The head and thorax are rather strongly punctate, more coarsely so than in *Plebeia* and its relatives (although approached in coarseness by *Plebeia caerulea* Friese) and with shining ground between the punctures. As in *Nannotrigona* the scutellum is produced as a thin shelf (side view) hiding the median part of the metanotum from above. Also as in *Nannotrigona* there is a shining depressed V or U-shaped median depression on the anterior margin of the scutellum (Fig. 190) and the preoccipital carina and hind tibia are also as described for *Nannotrigona*. *Scaptotrigona* differs from *Nannotrigona* not only in form and punctation but also in the rounded apex of the scutellum (seen from above) and the rounded anterior margin of the pronotal lobe. A full description of the genus is given by Moure (1951) as a subgenus of *Nannotrigona*.

The worker gonostyli are setose, convergent apically. The sting stylet is broad and irregularly rounded and the lancet, if present at all, is short and fades into the membrane. The male genital capsule is schizogonal in specimens of *S. pectoralis* (Dalla Torre) and rectigonal in *S. mexicana* (Guérin). Probably it is really amphigonal in both. The setae of the labial palpus are short and straight.

Most character states of *Scaptotrigona* are plesiomorphic relative to *Nannotrigona* although the larger size and robust form may be derived



Figures 138-143. Male genitalia of Meliponinae, dorso-ventral views (dorsal at left), or separate dorsal and ventral views for *Lestrimelitta*, and lateral views with gonostyli omitted, penis valves also omitted in Figures 138 and 139. Arrows are explained with Figures 130-134; s = spatha. 138, *Nannotrigona testaceicornis* (Lepeletier), gonostylus omitted on ventral view. 139, *Scaptotrigona barrocoloradensis* (Schwarz), gonostylus omitted on ventral view, schizogonal conformation. 140, *Scaptotrigona mexicana* (Guérin), right gonostylus omitted, rectigonal conformation. 141-143. *Lestrimelitta limao* (Smith), dorsal, lateral (gonostylus omitted, attachment indicated by jagged line), and ventral views.

features. The genus is so distinct from the highly derived *Nannotrigona* that it is reasonable to recognize it at the genus level. Moreover, the worker-laid trophic eggs of *Scaptotrigona* are much larger than eggs of the queen, while in *Nannotrigona* they are not so large. This is no doubt an apomorphy of *Scaptotrigona*, supporting the view that the two are sister groups.

Scaptotrigona contains about two dozen species and ranges from Mexico to Argentina. Familiar species are *Scaptotrigona hellwegeri* (Friese), *mexicana* (Guérin), *pectoralis* (Dalla Torre), *postica* (Latreille), and *tubiba* (Smith).

Genus *Lestrimelitta* Friese

(Figs. 22, 58, 93, 141-143, 165)

Trigona (Lestrimelitta) Friese, 1903: 361. Type species: *Trigona limao* Smith, 1863 (monobasic).

Like *Cleptotrigona*, this is a robber genus. The workers do not forage except in nests of other Meliponinae, especially species of the genera *Plebeia* and *Nannotrigona*, more rarely *Melipona*, *Scaptotrigona* and *Trigona;* they even attack weak colonies of *Apis*. As in other forms that do not forage from flowers, there are only short, straight setae on the labial palpus.

Unlike nearly all other Meliponinae, S6 of the male lacks a median apical process and has instead a small notch. S7 has a broad, squarish body. Both S6 and S7 have long basolateral apodemes (see illustrations by Schwarz, 1948). These features seem ancestral (i.e., more like more basal sterna) relative to the specialized or reduced aspects of these sterna in other Meliponinae. However, it seems unlikely that a robber genus would preserve archaic structure, for its habits and the related features such as loss of the corbicula and rastellum are obviously derived. Another explanation is that since genes for ordinary sterna are obviously present, a developmental change could lead to their control of the more apical sterna as well as the preceding ones. The external generic character states were listed by Schwarz (1948), Moure (1951) and Wille (1979b).

The male genital capsule is probably permanently rectigonal; unlike other rectigonal and amphigonal Meliponinae except some *Plebeia,* the gonocoxites are about as long as broad, thus not strongly transverse. The male gonostyli are shorter than in most Meliponinae and broadly fused to the gonocoxites (Fig. 141 and Schwarz, 1948). The worker gonostyli are a little longer than broad, separated basally by a little more than a gonostylar width, convergent distally, and with setae (without minute hairs). The sting stylet is broad and blunt and the lancet, although short, has the apex free of membrane.

The hind tibia of the worker, on the inner surface, has only a narrow, slightly depressed, marginal zone without keirotrichia, suggesting *Plebeia (Plebeia).* This may be because the tibia is not flattened and expanded posteriorly as in forms with a corbicula. However the keirotrichiate area is broad; this combined with the narrowness of the marginal zone may indicate derivation from an ancestor of *Plebeia (Plebeia).* The rastellum is reduced to tapering hairs.

Lestrimelitta consists of possibly ten species (mostly unnamed), of which *L. limao* (Smith) is best known. The genus is widespread in the Neotropical region—Mexico to Argentina. Included species were described and illustrated by Schwarz (1948), Moure (1951), Wille (1979b), and Roubik (1980).

Genus *Oxytrigona* Cockerell
(Figs. 23, 68, 94)

Trigona (Oxytrigona) Cockerell, 1917a: 124. Type species: *Trigona flaveola mediorufa* Cockerell, 1913, by original designation.

This genus is closely related to *Trigona* and could be considered a subgenus of that genus. *Oxytrigona* has several striking character states of its own, however, and *Trigona* has at least one probable synapomorphy (the narrower, better defined keirotrichiate band) that usually distinguishes it from *Oxytrigona* and suggests that *Oxytrigona* is the sister genus of *Trigona* plus *Cephalotrigona.* When this character state fails in *Trigona,* the marginal depressed zone is nonetheless quite broad. In *Oxytrigona* it is narrower, suggestive of that of *Plebeia* although not so narrow as in that genus.

Noteworthy features of *Oxytrigona* include the following: the short, wide face (see key to genera); the small clypeus, widely separated from the eyes; the shining but distinctly punctate clypeus and lower paraocular areas; the long malar space of the worker (about one third as long as the eye); the convex genal area of the worker, providing space for the posterior ramus of the deeply bifid mandibular gland (Michener, 1974); the abundant, large, straight setae on the labial palpus of the worker, a feature unique in the Meliponinae; the simple hairs of the posterior margin of the hind tibia; the largely vertical propodeal profile (quite different from that of *Trigona*); and the worker gonostyli which are four or five times as long as wide, converging distad, separated at their bases by three or more stylar diameters, and bearing numerous setae. Unique among Meliponinae is the short second valvifer, shorter than the gonostylus (Fig. 23). The lancet of the sting is almost invisible, and may not be realistically illustrated in Fig. 23. As in many species of *Trigona,* the genital capsule is rectigonal but probably in reality amphigonal; the gonocoxites are strongly transverse. Schwarz (1948) listed the included species (as varieties) and provided detailed descriptions and illustrations of *Oxytrigona;* Camargo (1984) added species and raised some varieties to the species level. Moure (1951) described the genus comparatively.

An attribute of interest is the secretion of the mandibular glands which contain formic acid (Roubik, Smith and Carlson, 1987). Workers, in nest defense, bite this liquid into the skin of an intruder, causing painful and long-lasting lesions in human skin (Michener, 1974). The name "fire bee" is therefore in wide use for this insect.

Oxytrigona contains about eight closely related species ranging from Mexico to Bolivia and southern Brazil. *O. tataira* (Smith) is the best known of these species.

Genus *Cephalotrigona* Schwarz
(Figs. 24, 65, 67, 95, 166, 172)

Trigona (Cephalotrigona) Schwarz, 1940: 10. Type species: *Trigona capitata* Smith, 1854, by original designation.

This genus is closely related to *Trigona* and could be considered a subgenus of that genus. The body seems more strongly sclerotized than in *Trigona.* Unique features include (1) the strongly, coarsely punctate and shining clypeus, lower supraclypeal area, lower paraocular area, and lower genal area contrasting with the dull, reticulate frons, the dull, closely punctate vertex and scutum, and the extremely dull and minutely punctate upper genal area; (2) the distal margin of the mandible of the worker which has a single large tooth at the upper extremity, separated by a broad, shallow concavity from the rest of the margin which is edentate; and (3) the strong, shining preoccipital carina across the interocular width of the head. The large, broad mandibular tooth is more like the upper tooth of the mandible of *Trigona (Trigona)* than the one or two small or sharp teeth (denticles) on the mandibles of most Meliponinae. It may not be homologous to such denticles. Additional interesting features are the following: The keirotrichiate, median, elevated zone of the inner surface of the hind tibia is about as wide as the shining marginal zone and separated from it by a gentle slope, not an abrupt one; this slope fades away in the basal fifth of the tibia rather than continuing as a channel nearly to the tibial base. The propodeal triangle has conspicuous hair bases and, like the rest of the propodeum, abundant plumose hairs. S6 of the male has a short median process and lateral processes about as long as the median one (see illustrations in Schwarz, 1948). The male genitalia are rectigonal (probably amphigonal) with extremely short, broad gonocoxites. The labial palpus of workers and males has abundant short, straight setae and lacks large setae.

Cephalotrigona could be merely a specialized derivative of *Trigona,* in which case it probably should not receive generic status. However, the better defined keirotrichiate band of *Trigona* is probably an apomorphy suggesting that *Cephalotrigona* is the sister group of *Trigona.* S. F. Sakagami (in litt.) regards *Cephalotrigona* as a subgenus of *Trigona* because he considers its differences from *Trigona* to be no greater than differences among some subgenera of that genus. This was my opinion also early in the development of this work, but rather arbitrarily and for the reasons indicated above, I have decided to recognize it at the generic level. Sakagami notes that the oviposition behavior, with frequent "body insertions" by workers alternating with inspections by the queen of the cell in which she will oviposit, is similar in *Cephalotrigona* and *Trigona (Tetragona, Frieseomelitta* part, *Duckeola* and *Trigona* s. str.).

The characters of the genus are well illustrated by Schwarz (1940, 1948) and described comparatively by Moure (1951). The genus contains about three species (listed as varieties by Schwarz, 1948) and is found from Mexico to Argentina. *Cephalotrigona capitata* (Smith) is the best known species.

Genus *Trigona* Jurine

This is the largest and most widely distributed genus of Meliponinae. It is distinguished from all other genera except *Oxytrigona, Cephalotrigona,* and the superficially similar *Dactylurina* by the inner surface of the hind tibia of the worker which has a longitudinal elevation covered with keirotrichia, behind which is a depressed shining marginal zone without keirotrichia, usually about as wide as the elevated zone, at least toward the apex of the tibia (Fig. 185). In *Trigona* the slope separating the keirotrichiate ridge from the smooth zone behind it is abrupt (except in the subgenera *Lepidotrigona* and *Papuatrigona*) and extends basad as a shining channel nearly to the base of the tibia. The male genitalia and hidden sterna are similar in many members of the genus to those of *Oxytrigona,* as shown by illustrations of Schwarz (1939, 1948) and Figures 144 to 150; they are known to be amphigonal in some species and probably are in others. However, in the subgenera *Geotrigona, Tetragonisca,* and *Homotrigona* the genital capsule is probably permanently schizogonal and the gonocoxites about as long as broad or longer than broad (Figs. 145, 146). The gonostyli of the workers are setose, without minute hairs. They vary from about 1.5 to 6 or 7 times as long as broad. They vary even within species groups. Thus within the *iridipennis (Tetragonula)* group of the subgenus *Heterotrigona,* in *T. carbonaria* Smith they are less than 1.5 times as long as broad and separated by little more than one stylar length while in *T. fuscobalteata* Cameron they are about twice as long as broad and separated by about two stylar lengths. The gonostyli are typically separated by two or more stylar diameters basally and converge apically. In *T. (Frieseomelitta) nigra* Cresson and *T. (Trigona) cilipes* (Fabricius), however, the gonostyli are separated by one basal stylar diameter or less (Figs. 27, 34). In *T. cilipes* [but not in other species of *Trigona (Trigona),* e.g., *amalthea* (Olivier), *chanchamayoensis* Schwarz, and *fulviventris* Guérin], the gonostyli diverge apically (Figs. 33, 34).

The sting stylet is ordinarily a mere convexity but in *T. (Tetragona) lurida* Smith (Fig. 31) its lateral margins are at an acute angle to one another although the apex is broadly rounded and in *T. (Trigona) cilipes* (Fabricius) (Fig. 34) the sting stylet is only narrowly rounded at the apex. The stronger, longer stylet in the last two species and the diverging gonostyli in *T. cilipes* may be related to the elongate metasomas of these species, laterally compressed in *T. cilipes.*

The lancets of the sting are ordinarily much reduced and lie in the membrane, sometimes being transparent and almost invisible. In *T. (T.) amalthea* (Olivier) but not in *T. (T.) cilipes* (Fabricius), etc., the apices of the lancets are free of the membrane.

Trigona is found in the Neotropics from Mexico to Argentina and in the Indoaustralian region from India and Sri Lanka to Taiwan, east to the Caroline Islands (introduced?), the Solomon Islands, and south throughout Indonesia and New Guinea to about latitude 34°S in Australia.

In several subgenera of *Trigona* there is a well-defined sericeous area of short, dense, easily lost hairs (Fig. 184) on the base of the inner surface of the hind basitarsus. Such an area is present in workers, and in some subgenera, in males also. It is not a generic characteristic since it is altogether absent, the surface being uniformly setose, in some subgenera. Any bee with the sericeous area, however, belongs to the genus *Trigona*. Interestingly, the worker of *Dactylurina staudingeri* (Gribodo) but not *D. schmidti* (Stadelmann) has a weakly differentiated approach to such a sericeous area.

In the great majority of species of *Trigona* and in all those in the Americas, some of the hairs along the rear margin of the hind tibia are plumose (Fig. 184). No other Meliponinae except for the African genus *Dactylurina* have such hairs. (There are a few on the distal part of the margin in some species of *Meliponula* and *Plebeia*.) This characteristic is therefore useful in generic recognition of most species of the genus.

The subgenus with the hairs on the posterior margin of the hind tibia all simple, *Lepidotrigona*, has sometimes been given generic status. Because it is basically similar to the other subgenera, and because *Papuatrigona* has plumose hairs only on the apical sixth of the posterior tibial margin and is thus intermediate, I have chosen not to do so. As noted below, *Papuatrigona* is also intermediate between *Lepidotrigona* and the other subgenera in scutal sculpturing. *Lepidotrigona* and *Papuatrigona* differ from the remaining subgenera (and agree with the genus *Cephalotrigona*) in the less sharp distinction between the elevated keirotrichiate zone on the inner surface of the hind tibia and the shiny margin. In *Lepidotrigona* and *Papuatrigona* the area with keirotrichia is not *abruptly* elevated. In the genus *Cephalotrigona* the same is true. In the genus *Oxytrigona* it is more abruptly elevated but is unusually wide, so that at the middle of the tibia it is much wider than the depressed, shiny, marginal zone. A broad keirotrichiate zone is also found in some forms clearly placed in *Trigona* such as *T. (Heterotrigona) carbonaria* Smith and *planifrons* Smith, but in such species the zone is more elevated and its delimitation extends almost to the base of the tibia (see couplet 1, key to subgenera).

Workers of the genus *Oxytrigona* and of *Trigona (Lepidotrigona)* have unusually broad hind basitarsi, convex on the outer surfaces, thus suggesting *Plebeia (Scaura)*. In *Oxytrigona* and in species of *Lepidotrigona* without greatly broadened tibiae, such as *T. (Lepidotrigona) terminata* Smith, the basitarsal width is about equal to the width of the tibia at midlength. In view of the dissimilarity of *Oxytrigona, Lepidotrigona,* and *Scaura,* I regard their large hind basitarsi as convergent rather than as a synapomorphy.

In most species of *Trigona* the scutum is shining with minute, widely separated punctures. In the subgenus *Lepidotrigona* it is dull with minute, dense punctures, as in the genus *Cephalotrigona*. *Papuatrigona* is intermediate with minute punctures separated by about a puncture width of shiny ground.

The two teeth of the upper part of the apical margin of the worker mandible are large and occupy about half of the mandibular margin in *T. (Homotrigona) fimbriata* Smith, but they are nearly as large in the *Heterotrigona* groups of *T. apicalis* Smith, *reepeni* Friese (the only member of the *Tetragonula* group with large teeth), and *canifrons* Smith. *T. (Tetragona) lurida (Ptilotrigona)* from the Neotropical region has similarly large teeth. There seem to be no other characters that associate these large-toothed species. *T. (Heterotrigona) itama* Cockerell and *erythrogastra* Cameron in southeast Asia have only one such tooth. As is well known, the species of *Trigona (Trigona)* have four or usually five mandibular teeth.

T. (Tetragona) lurida (Ptilotrigona) in the Neotropics and *T. (Heterotrigona) planifrons* Smith, *flaviventris* Friese, *keyensis* Friese *(Platytrigona)* and *canifrons* Smith *(Lophotrigona)* in southeast Asia are unusual in the hairy basal area of the propodeum, a feature that crops up several times in unrelated Meliponinae and does not even characterize all species of the *planifrons* group (i.e., *Platytrigona*). The American and Asiatic species show no other significant similarities and probably evolved the hairs independently; the Asiatic groups may also have evolved such hairs independently.

An architectural character that has received attention in classification of the genus *Trigona* is arrangement of the brood cells. Various species arrange the cells in combs. In the *iridipennis* group *(Tetragonula)*, however, most species arrange cells in clusters although some (e.g., *T. carbonaria* Smith) make combs and others are intermediate (*T. hockingsi* Cockerell) (see Michener, 1961). *T. canifrons* Smith and the subgenus *Frieseomelitta* also arrange their cells in clusters. Probably the cluster arrangement within the genus *Trigona* is derived, presumably independently in the Indoaustralian and American taxa, the ancestral pattern being horizontal combs.

In most subgenera of *Trigona* brood cell construction is successive (Sakagami, 1982), a presumed plesiomorphic state, but in the subgenus *Lepidotrigona* and in *T. (Frieseomelitta) flavicornis* (Fabricius) but not other species of its subgenus, it is synchronous. It is intermediate, initially successive but becoming synchronous, in the subgenus *Duckeola*.

Key to the Subgenera of *Trigona*

1. Hairs along posterior margin of hind tibia of workers and males all simple or some plumose only on apical fifth or sixth of margin; elevated, keirotrichiate median zone of inner surface of hind tibia separated from shining posterior marginal zone by gentle slope 2

—Hairs along posterior margin of hind tibia of workers and some males partly plumose (in some species of *Geotrigona* the few branched hairs may have only two or three branches so that plumosity is inconspicuous); elevated, keirotrichiate median zone of inner surface of hind tibia separated from shining marginal zone by abrupt slope. 3

2. Head and thorax dull with minute close punctures; propodeal dorsum finely reticulate; posterior margin of hind tibia of worker without plumose hairs; scutum margined with whitish, densely plumose ("scalelike") hairs (Southeast Asia) . . . . *Lepidotrigona*

—Head and thorax shining although with minute, rather close punctures; propodeal dorsum smooth, shining; posterior margin of hind tibia of worker with plumose hairs among bristles on apical fifth or sixth of margin; scutum without conspicuous plumose hairs (New Guinea) . . . . *Papuatrigona*

3. Mandible of worker with 4 or 5 teeth along distal margin; inner surface of hind basitarsus of males and workers with basal sericeous area (Neotropical region). . . . . *Trigona* s. str.

—Mandible of worker with lower half or two thirds of distal margin edentate, upper part of margin with one or usually two teeth; inner surface of hind basitarsus of male without basal sericeous area, of worker variable (Neotropical region; Asia to Australia). 4

4. Metasoma short, dorsoventrally flattened, about as wide as thorax; posterior margin of hind tibia of worker usually with few plumose hairs, most of them with only two to six scattered branches not concentrated toward apices; yellow markings absent; vein M of forewing dark almost to wing margin (Neotropical region). . . . . *Geotrigona*

—Metasoma usually narrower than thorax, often noticeably elongate; posterior margin of hind tibia of worker with numerous strongly plumose hairs, usually with abundant branches toward apices; yellowish or reddish markings present on face of some Neotropical species; vein M of forewing usually fading away near widest part of wing (Neotropical region; Asia to Australia). 5

5. Inner surface of hind basitarsus of worker with basal sericeous area covered with minute setae or sometimes lacking setae (Fig. 184) 6

—Inner surface of basitarsus of worker rather uniformly setose, without basal sericeous area 7

6. S6 of male with median apical process very broad and long so sternum is much longer than broad (Neotropical region) . . . . *Tetragonisca*

—S6 of male much broader than long (Indoaustralian region) . . . . *Heterotrigona*

7. S6 of male a broad sternum without apical process (Southeast Asia) . . . . *Homotrigona*

—S6 of male with median apical process of the usual slender, heavily sclerotized form (male of *Duckeola* unknown) (Neotropical region) 8

8. Posterior margin of vertex elevated as strong, hairy ridge between summits of eyes; posterior distal angle of hind tibia of worker acute. . . . . *Duckeola*

—Posterior margin of vertex not elevated; posterior distal angle of hind tibia of worker broadly rounded 9

9. Labial palpi with large, sinuous setae on first two segments . . . . *Frieseomelitta*

—Labial palpi with setae no longer than palpal width and straight or nearly so. . . . . *Tetragona*

Subgenus *Lepidotrigona* Schwarz

(Figs. 25, 96)

Trigona (Lepidotrigona) Schwarz, 1939a: 132. Type species: *Trigona nitidiventris* Smith, 1857, by original designation.

Schwarz (1939a) described and illustrated the main features of this subgenus; Moure (1961) described it comparatively and listed included species. These are delicate bees similar to many species of the subgenus *Heterotrigona*, but differing not only in the character states listed in the key but also in the mostly dull, minutely roughened integument and, in males, in the pair of long spines on S5 [but see *T. (Heterotrigona) itama* Cockerell]. S6 is more like an ordinary sternum than in most other males, having a moderately large disc with the median process short and triangular, as illustrated by both Schwarz (1939a) and Sakagami (1975). The genital capsule is rectigonal, probably actually amphigonal. The labial palpus of the worker has about 18 large, sinuous setae (or some merely curved); this is within the range of variation found in *Heterotrigona.* The hind tibia of the worker especially of *T. nitidiventris* Smith and *trochanterica* Cockerell, is slender, expanded apically, thus "racket-shaped," a convergence with some species of the New World subgenus *Frieseomelitta.*

This subgenus of about four species (plus color variants) occurs from India to the Philippines and Taiwan, south to Sumatra, Borneo and Java. Included species are *Trigona (Lepidotrigona) nitidiventris* Smith, *terminata* Smith, *trochanterica* Cockerell and *ventralis* Smith (list provided by S. F. Sakagami, in litt.).

Subgenus *Papuatrigona* Michener and Sakagami

(Figs. 26, 97, 195, 196, 198, 199, 201-205, 207, 208-210, 212-219)

Papuatrigona Michener and Sakagami, see Appendix. Type species: *Trigona genalis* Friese, 1908, by original designation.

This subgenus (which is fully described in the Appendix) at first seems to lack plumose hairs on the posterior margin of the hind tibia, but such hairs are present among simple hairs on the distal fifth or sixth of the tibial margin. The keirotrichiate ridge on the inner surface of the hind tibia is nearly twice as wide as the depressed marginal zone, and the slope from the ridge to the marginal zone is gentle, the ridge not being high; distally there is almost no slope, the ridge being undefined and scarcely higher than the zone behind it; proximally the slope is more distinct and extends well into the basal fourth of the tibia. The outer surface of the hind basitarsus has a posterior basal concavity behind a longitudinal, curved, hairy ridge (Figs 207, 210) as in *Lepidotrigona* and many species of *Heterotrigona,* suggesting a relationship with those subgenera, and also with *Homotrigona* which also has such a concavity. Such a basitarsal concavity also occurs in the American genus *Oxytrigona* which *Papuatrigona* resembles in certain features. The broad face, long malar space, and broad clypeocular space, so unusual and distinctive of *Oxytrigona,* are all approached in *Papuatrigona.* I presume this resemblance is a result of convergence; all these characteristics are apparently results of a single tendency in facial development. The unique vestiture of the labial palpus of *Oxytrigona* (abundant long, straight setae) is not shared by *Papuatrigona,* which has about eleven large, sinuous setae, thus falling within the range of variation of *Heterotrigona.* The worker gonostyli are setose, well separated, convergent; the second valvifer is not unusually short as it is in *Oxytrigona.* While the keirotrichiate ridge is similar in breadth in *Oxytrigona* and *Papuatrigona,* it is abruptly defined in the former, not in the latter.

Features distinguishing *Papuatrigona* from *Heterotrigona* and *Homotrigona* include the tibial character states listed above and also, for *Heterotrigona,* the lack of a sericeous area on the inner surface of the hind basitarsus. *Papuatrigona* is most similar to *Lepidotrigona,* which also lacks the sericeous basitarsal area. *Lepidotrigona* has the head and thorax dull with minute, dense punctation. The surface is less dull and the punctation less dense in *Papuatrigona,* which also lacks the areas of dense, highly plumose ("scalelike") hairs found in *Lepidotrigona. Lepidotrigona* has plumose hairs among simple hairs on the posterior apical angle of the hind tibia but not extending along the posterior margin. The inner surface of the hind tibia is alike, however, in the two subgenera. The longer malar area, wider face and interalveolar space, smaller mandibular teeth, smooth basal propodeal area, smaller corbicula, etc., as detailed in the Appendix, all differentiate *Papuatrigona* from *Lepidotrigona.*

This subgenus includes only one species, *Trigona (Papuatrigona) genalis* Friese. It is known only from New Guinea. Details of its character states are given in the Appendix.

Subgenus *Geotrigona* Moure

(Figs. 28, 98, 145)

Trigona (Geotrigona) Moure, 1943: 146. Type species: *Trigona mombuca* Smith, 1863.

This subgenus consists of robust black species, superficially resembling because of the short, broad metasoma some of the black species of *Partamona, Scaptotrigona,* and *Trigona (Trigona).* The *Geotrigona* group was included in *Tetragona* by Wille (1979b) and others and it is closely related to that subgenus. In both, the hairs of the labial palpi are short and straight. *Geotrigona* differs, however, not only in the body form but in the relatively short legs (hind tibia much shorter than cell R of forewing) and the sparseness of branched hairs, and of the branches themselves, on the posterior margin of the hind tibia. The branches are scattered along the hairs, not concentrated toward the apices. These hairs are especially sparse and with few branches in *T. (G.) acapulconis* Strand, and are thus intermediate between the simple hairs of the preceding subgenera and the strongly plumose hairs of *Heterotrigona, Homotrigona, Tetragonisca, Tetrigona,* and *Trigona* s. str. The male genital capsule is schizogonal, probably permanently so, the gonocoxites being at least as long as broad (*T. mombuca* Smith examined). Moure (1951) described the external features of the subgenus comparatively.

This subgenus contains a few similar species and ranges from Mexico to Argentina (Santiago del Estero). Well known names in this subgenus include *Trigona (Geotrigona) acapulconis* Strand, *leucogastra* Cockerell, and *mombuca* (Smith).

Subgenus *Tetragonisca* Moure
(Figs. 30, 72, 100, 146)

Tetragonisca Moure, 1946: 438. Type species: *Trigona jaty* Smith, 1863 (= *Trigona angustula* Latreille, 1811).

This is one of a group of subgenera separated from *Tetragona* with some hesitation. It consists of small, slender species, and is the only Neotropical group other than *Trigona* s. str. with a sericeous area on the base of the inner side of the hind basitarsus of the worker (but not the male). The labial palpus differs from that of the subgenus *Tetragona* in having 12 to 15 large, sinuous setae; there are no large setae in *Tetragona.* In this respect *Tetragonisca* resembles *Frieseomelitta.* Males at least of *T. (Tetragonisca) angustula* Latreille differ from *Tetragona* in the probably permanently schizogonal genital capsule and from all other Meliponinae in the enormous (broad and long), not especially sclerotized, median apical process of S6, making the sternum much longer than broad, and in the elongate S7, reaching beyond the apex of S6. The male genitalia are unusual for *Trigona* (but interestingly similar to the very different genus *Nannotrigona*) in the great thickness of the genital capsule with the spatha almost vertical (Fig. 146). External characteristics are listed by Moure (1951).

The male metasomal character states are apomorphies that suggest that *Tetragonisca* is derived from *Tetragona,* leaving the latter paraphyletic. However, given the widespread occurrence of the sericeous area on the hind basitarsus *(Heterotrigona, Trigona* s. str., and *Tetragonisca),* it seems quite possible that it is lost in *Tetragona,* so that *Tetragonisca* and *Tetragona* could be sister groups. S. F. Sakagami (in litt.) notes that the oviposition behavior of *Tetragonisca* is very different from that of *Cephalotrigona* and *Trigona* [*Duckeola, Frieseomelitta* (part), *Tetragona* and *Trigona* s. str.]. Without knowledge as to the polarity of these characters, it is difficult to use them in classification.

Tetragonisca ranges from Mexico to Argentina and contains about four species, of which *Trigona (Tetragonisca) angustula* Latreille, *buchwaldi* Friese, and *pfeifferi* Friese are well known.

A characteristic of workers of *Tetragonisca* is the extremely small corbicula, the concavity being limited to the apical fifth of the tibia and not occupying the full tibial width. The same feature characterizes the subgenus *Frieseomelitta* which, however, lacks the sericeous area on the inner surface of the hind basitarsus. Species included in these two groups are listed by Wille (1962). The African genus *Dactylurina* has equally reduced corbiculae. This must be an independently derived feature in *Trigona* and *Dactylurina,* probably also independent in the *Trigona* subgenera *Tetragonisca* and *Frieseomelitta.* Intermediates between such small corbiculae and large ones occur in various groups of the subgenera *Tetragona* and *Heterotrigona.*

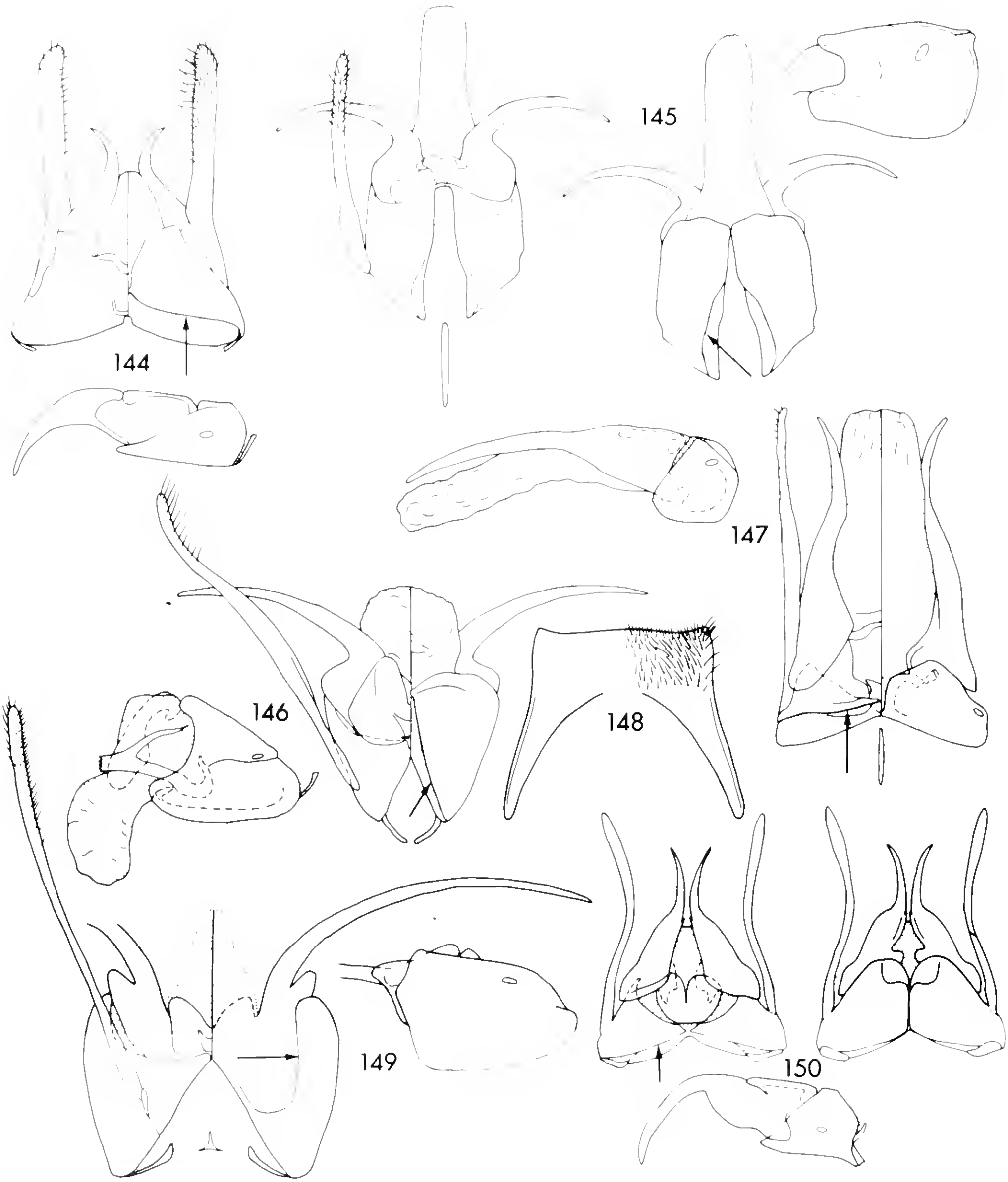
Subgenus *Tetragona* Lepeletier and Serville
(Figs. 31, 69, 101, 102, 147, 149)

Trigona (Tetragona) Lepeletier and Serville, 1828: 710. Type species: *Trigona elongata* Lepeletier and Serville, 1828 (= *Centris clavipes* Fabricius, 1804) by original designation.

Trigona (Ptilotrigona) Moure, 1951: 47. Type species: *Trigona heideri* Friese, 1900 (= *Trigona lurida* Smith, 1854) by original designation.

This subgenus as here limited consists of long-legged bees, similar in form to *Tetragonisca* and *Frieseomelitta* but somewhat less delicate. The hind tibia is nearly as long as cell R of the forewing. *Ptilotrigona* is based on a distinctive species, differing from the rest of the subgenus in its large size, large mandibular teeth (two, on upper part of apical margin), and hairy propodeal triangle. The amount of difference is probably not enough to justify subgeneric rank for a single divergent species, but J. M. F. Camargo (in litt.) tells me of two undescribed species of *Ptilotrigona.* One could easily justify recognizing it as a subgenus. Comparative descriptions are provided by Moure (1951).

Tetragona differs from the Indoaustralian *Heterotrigona* in the uniformly setose inner surface of the hind basitarsus of the worker, and in lack of large setae on the labial palpi (palpal setae are short and straight). See also the discussion of *Heterotrigona.* Given the similarity of *Tetragona* and *Heterotrigona* it is necessary to compare the species groups of both of these subgenera, along with *Duckeola, Frieseomelitta, Geotrigona, Tetragonisca,* and *Homotrigona,* to see if some other classification makes more sense. The variation among the species groups is kaleidoscopic, each character seemingly distributed differently from the others. Moure's (1961) tabulation of character states of the Indoaustralian groups shows the lack of con-



Figures 144-150. Male genitalia of Meliponinae, dorso-ventral views (dorsal at left, dorsal and ventral for 145 and 150), gonostylus usually omitted from ventral views, lateral views with gonostyli omitted, apex of penis valve omitted in lateral 145, 146, 149. Arrows are explained with Figures 130-134. 144, *Trigona (Frieseomelitta) nigra paupera* Provancher. 145, *Trigona (Geotrigona) mombuca* Smith, gonostyli omitted from ventral view. 146, *Trigona (Tetragonisca) angustula* Latreille. 147, *Trigona (Tetragona) clavipes* (Fabricius). 148. S6 of *Trigona (Heterotrigona) apicalis melanoleuca* Cockerell. 149. *Trigona (Tetragona) lurida* Smith. 150. *Trigona (Trigona) fulviventris* Guérin.

cordance among characters. The same is observable with the American groups.

Male genitalia are rectigonal in *T. (Tetragona) clavipes* (Fabricius) and schizogonal in a male of *T. (T.) lurida* Smith; probably they are really amphigonal.

About 13 species of *Tetragona* are found from Mexico to Brazil. Well known species are *Trigona (Tetragona) clavipes* (Fabricius), *dorsalis* Smith, *lurida* Smith, and *perangulata* Cockerell.

Subgenus *Frieseomelitta* von Ihering
(Figs. 27, 71, 99, 144)

Frieseomelitta von Ihering, 1912: 5. Type species: *Trigona silvestrii* Friese, 1902 (monobasic).

This subgenus consists of slender, delicate-looking species that agree with *Tetragona* in subgeneric attributes except that the labial palpus of the worker possesses many (19-23 in species examined) large, sinuous setae. Such setae are absent in *Tetragona*, although present in *Tetragonisca*.

Frieseomelitta is further distinguished from all other American groups of the genus *Trigona* in the arrangement of the brood cells—in clusters rather than in combs. This architectural character does not separate subgenera among the Indoaustralian *Trigona* and in the genus *Plebeia*, but appears to do so in American *Trigona*. Another architectural character state of *Frieseomelitta* is the elongate storage pots. Elongate storage pots are also found in the genus *Trigonisca* and in some species of *Trigona (Heterotrigona)*.

The male genitalia are rectigonal in *T. (F.) nigra* Cresson and *silvestrii* Friese (see Camargo and Moure, 1988); probably in reality they are amphigonal.

Frieseomelitta contains about ten species and ranges from Mexico to Brazil. Well known species are *Trigona (Frieseomelitta) nigra* Cresson, *silvestrii* Friese, and *varia* Lepeletier.

Subgenus *Duckeola* Moure
(Figs. 70, 103)

Duckeola Moure, 1944a: 72. Type species: *Trigona huberi* Friese, 1901 (= *Trigona ghilianii* Spinola, 1853) by original designation.

This subgenus consists of a large, rather robust species, so different from other *Tetragona*-like bees that it must be placed in its own subgenus. It resembles *Tetragona* in lacking a sericeous area on the inner surface of the hind basitarsus of the worker. It differs from *Tetragona* and all other subgenera in the strong, hairy ridge on the posterior margin of the vertex between the summits of the eyes (this is different from the shiny, hairless carina in a similar position in the genus *Cephalotrigona*), in the rather slender hind tibia of the worker with the posterior apical angle strongly produced apicad and acute, and in the about 20 large setae of the labial palpi which are at most only about 1.5 times as long as the palpal width, yet are mostly curved or slightly sinuous. In other meliponines with curved or sinuous setae, these setae are much longer.

Two species, *Trigona (Duckeola) ghilianii* Spinola and *pavani* Moure, are found in Brazil. Males are unknown.

Subgenus *Homotrigona* Moure
(Fig. 110)

Homotrigona Moure, 1961: 200. Type species: *Trigona fimbriata* Smith, 1857, by original designation.

Like *Duckeola, Frieseomelitta, Geotrigona, Heterotrigona,* and *Tetragonisca,* this subgenus is separated from *Tetragona* with some hesitation. The male shows plesiomorphic features (especially S6) that suggest this as a possible outgroup for the rest of *Trigona*. It therefore seems reasonable to give it subgeneric status. Other phenetically distinctive groups, such as the group of *T. (Heterotrigona) itama* Cockerell, are distinguished by clearly derived, autapomorphic features and are not recognized here at the subgenus level.

Homotrigona consists of rather large, robust species with the metasoma short. The two mandibular teeth are large, occupying the upper half of the distal mandibular margin, and are along the mandibular axis so that a line between their apices is almost parallel to the long axis of the mandible. *Homotrigona* is the only Indoaustralian subgenus of *Trigona* except *Lepidotrigona* and *Papuatrigona* that lacks the sericeous area on the base of the inner side of the hind basitarsus; in this respect it resembles the American subgenera *Duckeola, Frieseomelitta,* and *Tetragona*. The most unusual feature is S6 of the male, which is a rather ordinary looking sternum, without traces of the heavily sclerotized median apical process usual in Meliponinae. *Lestrimelitta, Paratrigona opaca* Cockerell but not other species of the genus, *Trigona (Heterotrigona) apicalis* Smith and its relatives (i.e., the *Odontotrigona* = *Tetrigona* group of *Heterotrigona*) but not other species of that subgenus, and *Trigona (Lepidotrigona)* also have S6 broad although in the last it has a short, triangular median process. These forms do not seem closely related to one another. The shape and setal pattern of S6 are so similar, however, in males of *Homotrigona* and *T. (Heterotrigona) apicalis* Smith (Fig. 148) that they must indicate a common origin. To judge by bees in general, this condition should be plesiomorphic, but see comment on this character under *Lestrimelitta*. Prof. S. F. Sakagami has called my attention to the complete absence of a spatha in the male genitalia of

Homotrigona, a character state shared with the genus *Dactylurina* and with the *Tetragonula* and *Platytrigona* groups of *Heterotrigona.* The labial palpus of the worker has the large setae long and straight; in nearly all other Asiatic species of *Trigona* at least one or two are curved, and frequently they are sinuous.

The external character states of *Homotrigona* are given by Moure (1961) and those of the male by Sakagami (1963). Moure listed the included taxa, probably representing a single species, *Trigona (Homotrigona) fimbriata* Smith, that ranges from west Malaysia to Vietnam and south to Sumatra and Borneo.

Subgenus *Heterotrigona* Schwarz

(Figs. 29, 32, 73, 104-109, 111, 148, 184, 197, 200, 206, 209)

Trigona (Heterotrigona) Schwarz, 1939a: 96. Type species: *Trigona itama* Cockerell, 1918, by original designation.

Platytrigona Moure, 1961: 203. Type species: *Trigona planifrons* Smith, 1864, by original designation.

Lophotrigona Moure, 1961: 205. Type species: *Trigona canifrons* Smith, 1857, by original designation.

Tetragonula Moure, 1961: 206. Type species: *Trigona iridipennis* Smith, 1854, by original designation.

Tetragonilla Moure, 1961: 210. Type species: *Trigona atripes* Smith, 1857, by original designation.

Geniotrigona Moure, 1961: 212. Type species: *Trigona thoracica* Smith, 1857, by original designation.

Odontotrigona Moure, 1961: 213. Type species: *Trigona haematoptera* Cockerell, 1919, by original designation.

Tetrigona Moure, 1961: 215. Type species: *Trigona apicalis* Smith, 1857, by original designation.

Trigonella Sakagami and Moure, *in* Sakagami, 1975: 57. Type species: *Trigona moorei* Schwarz, 1939, by monotypy.

This subgenus contains minute to moderate-sized Indoaustralian bees with a sericeous area on the base of the inner side of the hind basitarsus of workers but not in males. The unity of *Heterotrigona* and *Homotrigona* is indicated, however, by the frequently concave surface of the posterobasal part of the hind basitarsus, this area being delimited anteriorly by a low ridge bearing a row of hairs (the "additional" row of hairs of the pollen press, Wille, 1979a; Figs. 206, 207, 209, 210). This structure is weakly developed or unrecognizable in small species. Contrary to Wille, I do not find it in any American species of *Trigona,* but it is present in *Oxytrigona.* Another character that is useful although not decisive in separating the Indoaustralian species from *Tetragona* is the setae of the labial palpus. In *Tetragona* there are no large setae. In *Heterotrigona* and *Homotrigona* there are large setae and at least one or two are curved; frequently most are curved or sinuous. All intergradations occur from about six with only one or two curved to about 35, mostly sinuous. Only in *T. (H.) canifrons* among Indoaustralian species are the setae straight and only moderately long. Except for these hind basitarsal and palpal characters, there are no other known group attributes that differentiate *Heterotrigona* from *Tetragona.* I hesitantly decided to recognize *Heterotrigona* because of these character states (only the first is entirely reliable) and because it occurs on the other side of the world from the neotropical *Tetragona.*

The genitalia are rectigonal in *T. (Heterotrigona) itama* Cockerell, *apicalis* Smith (*Tetrigona*), *atripes* Smith (*Tetragonilla*), *moorei* Schwarz (*Trigonella*), and various representatives of the *iridipennis* group (*Tetragonula*), varying to schizogonal among other species of the group (Sakagami, 1978; Sakagami and Inoue, 1985, 1987). Among all the above, the appearance of the genitalia suggests that each species is amphigonal, i.e., capable of either the rectigonal or schizogonal conformation.

Unfortunately the type species of *Heterotrigona, T. (H.) itama* Cockerell, is aberrant relative to nearly all of the rest of the species. Workers have only one denticle instead of two on the upper part of the apical mandibular margin. Males have a greatly enlarged and apically pointed hind tibia; much shortened small segments of the hind tarsus; long, thickened, and only briefly cleft hind claws; and long, fingerlike lateroapical processes on S5 (Schwarz, 1939a). These character states were the basis for *Heterotrigona,* a name which heretofore has been used only for *T. (H.) itama* and *erythrogastra* Cameron, along with various probable synonyms (Moure, 1961). Males of the group of *T. (H.) moorei* Schwarz (*Trigonella*) have hind legs and other features somewhat modified in the direction of *T. (H.) itama* as shown by Sakagami and Inoue (1987). The same is true for *T. thoracica* Smith (*Geniotrigona*), at least insofar as the hind tarsi are concerned (Sakagami and Inoue, 1989). These findings support the placement of other groups in the same subgenus as *T. itama.* Sakagami and Inoue (1989) have shown in greater detail the close relationship of what I call the *itama, moorei,* and *thoracica* species groups.

The males of *T. (H.) apicalis* Smith and *melanoleuca* Cockerell (*Tetrigona*), differ from other species of *Heterotrigona* in S6, which is an ordinary looking sternum with a large distal area of coarse hairs (Fig. 148); it is not short and heavily sclerotized with a median apical process as in other *Heterotrigona* and most other Meliponinae. In this respect they resemble *Homotrigona;* see comments on this character under that subgenus.

The name *Heterotrigona* is used here in a broad sense, as the oldest name for the various species groups listed in the above synonymy. Of these, several are monotypic or probably so; only the *iridipennis* group (*Tetragonula*) contains more than two or three species. The named taxa in the synonymy appear to represent natural groups or single distinctive species but do not seem different enough to recognize at the subgenus level. I have not seen males of all of them, however, and male characters might indicate recognition (at the subgenus level) of more of Moure's genera. Sakagami and Khoo (1987) have already united *Tetragonula* and *Tetragonilla*. Detailed descriptions of external features are provided by Moure (1961) and illustrations of genitalia and other structures by Schwarz (1939a), Sakagami (1978), and Sakagami and Inoue (1985, 1989).

Prof. S. F. Sakagami (in litt.) has kindly given me his opinions about the classification of the species of *Trigona* that I have placed in *Heterotrigona*. While I am not in full agreement with his view that five subgenera should be recognized instead of one, I recognize his groups and present his conclusions as follows:

Group 1. *Heterotrigona* (*T. itama* Cockerell, *erythrogaster* Cameron), *Trigonella* (*T. moorei* Schwarz, *lieftincki* Sakagami and Inoue), *Geniotrigona* (*T. thoracica* Smith). Similarity of these three subgroups are indicated in a paragraph above and by Sakagami and Inoue (1989).

Group 2. *Odontotrigona* and *Tetrigona* (*T. apicalis* Smith, *haematoptera* Cockerell, *melanoleuca* Cockerell and *peninsularis* Cockerell). There are no major differences among these species to justify two subgroups. See the comments above about S6 of the male.

Group 3. *Lophotrigona* (*T. canifrons* Smith). Like most species of *Tetragonula*, this species places its brood cells in clusters rather than combs.

Group 4. *Tetragonula* (numerous species) and *Tetragonilla* (four species). See Sakagami and Khoo, 1987. This group differs from others except number 3 by the exaggerated posterior displacement of the scutellum (Figs. 108, 109). Sakagami recognizes seven subgroups in *Tetragonula*.

Group 5. *Platytrigona*. Recognized by Moure (1961) on the basis of the medially hairy propodeal triangle but this character is variable. Sakagami recognizes three subgroups: a, *Platytrigona* sensu Moure (*T. planifrons* Smith, *flaviventris* Friese, *keyensis* Friese), recognized by the hairy propodeal triangle; b, *T. hobbyi* Schwarz with the middle of the propodeal triangle glabrous and without strong bristles on the vertex and scutellum; and c, *T. atricornis* Smith with a propodeum like that of *Papuatrigona*, i.e., hairless dorsally except for small lateral patches. Placement of *T. atricornis* is based on the male genitalia, which have a long neck joining the midbasal part of the penis valves with the median articulation of the gonocoxites. This is as in the *planifrons* subgroup (as well as *Lepidotrigona*, see Sakagami, 1975). Females of *T. atricornis* cannot be placed in *Platytrigona* with certainty; they could be in the *Trigonella* subgroup of *Heterotrigona*.

There are some 36 species in this subgenus. They were listed by Moure (1961) and Sakagami (1978). They are abundant in southeast Asia including Borneo and Sumatra. The number of species diminishes westward to only three in India, one of which reaches Sri Lanka; few species are found east and south to the Philippines, Solomon Islands, and Australia (south to about 34°S). The subgenus also occurs in the Caroline Islands, where it is likely to have been introduced. It apparently does not reach Taiwan. The species in marginal regions such as Sri Lanka, most of India, and Australia are all in the *iridipennis* group (*Tetragonula*). Familiar species of *Heterotrigona* are those listed above as type species of *Heterotrigona* and its synonyms, and those listed in the above account of five subgroups. To this list may be added *Trigona (Heterotrigona) carbonaria* Smith and *fuscobalteata* Cameron.

Species not included by Moure (1961) are *T. (Heterotrigona) keyensis* Friese, 1901, from Kai and New Guinea and *atricornis* Smith, 1864, from New Guinea. They are largely red, with coloration like that of *T. (Papuatrigona) genalis* Friese, but are members of the *planifrons* group of *Heterotrigona*. *T. keyensis* differs from members of that group listed by Moure and from his characterization of the group ("genus *Platytrigona*") in the wider interalveolar space; much shorter malar space (about two thirds of flagellar diameter); ocelloccipital distance about equal to ocellar diameter; scutellum not surpassing metanotum; bifurcation of veins M and Cu well beyond cu-v; etc. Thus it reduces the distinctness of *Platytrigona*. For identification of *T. keyensis* I am indebted to Prof. S. F. Sakagami. For information on *T. atricornis*, see Appendix.

Subgenus *Trigona* Jurine s. str.

(Figs. 33, 34, 66, 74, 75, 112, 113, 137, 150, 167, 172, 185)

Trigona Jurine, 1807: 245. Type species: *Apis amalthea* Olivier, 1789, by designation of Latreille, 1810: 439.
Amalthea Rafinesque, 1815: 123. Unnecessary replacement name for *Trigona* Jurine. Type species: *Apis amalthea* Olivier, 1789, autobasic.

The principal characteristics of this subgenus and the included species were well illustrated by Schwarz (1948) and Camargo and Moure (1988) and were listed comparatively by Moure (1951). The male genitalia and associated sterna of *T. cilipes* (Fabricius) were illustrated (as *T. compressa* Latreille) by Snodgrass (1941) and of this and other species by Schwarz (1948). The genitalia were shown in most cases as rectigonal, but for others as schizogonal. As noted above, both conformations are known for *T. (T.) amalthea* (Olivier) and *pallens* (Fabricius), and doubtless all species are in reality amphigonal. There are only two taxa of Meliponinae with the distal margin of the mandible of the worker toothed in its lower part (Fig. 172) and often for its full length—*Trigona* s. str. and *Paratrigona*. The teeth are best developed in the former, and are either four or five in number. Sometimes in *T. (T.) cilipes* (Fabricius) the distal teeth are united by a thin septum, but the dentate margin is still distinct from the convex margin with at most two denticles near its upper end, as in most Meliponinae (Fig. 172). The labrum differs from other Meliponinae in that the apex is produced to a distinct angle. Males and workers of *Trigona* s. str. have a basal sericeous area on the inner side of the hind basitarsus. Such an area occurs elsewhere only in workers of the subgenera *Tetragonisca*, *Tetrigona*, and *Heterotrigona*. The labial palpi of workers have six to about 38 large, mostly sinuous setae, except that in *T. hypogea* and its relatives there are only short, straight setae.

Trigona s. str. is found from Mexico to Argentina. It contains about 30 species, or more as sibling species are recognized. Well known species are *Trigona (Trigona) amalthea* (Olivier), *cilipes* (Fabricius), *corvina* Cockerell, *fulviventris* Guérin, *fuscipennis* Friese, *hyalinata* Lepeletier, *hypogea* Silvestri, *nigerrima* Cresson, *pallens* (Fabricius), *silvestriana* Vachal, and *williana* Friese. The subgenus was revised by Schwarz (1948).

Various species of this subgenus are attracted to carrion (Baumgartner and Roubik, 1989) and probably use it as a supplementary protein source as well as for nest construction. The group of *T. (T.) hypogea* Silvestri does not collect pollen, uses carrion as its protein source, lacks large palpal setae, has reduced corbiculae, and has relatively narrow hind tibiae (Schwarz, 1948; Roubik, 1982).

As noted previously, *Trigona prisca* Michener and Grimaldi (1988a, b) from the New Jersey Upper Cretaceous was placed in *Trigona* s. str. on the basis of the single known worker specimen. It has toothed mandibles similar to those of ordinary specimens of *T. (Trigona) cilipes* (Fabricius). The hairs on the posterior margin of the hind tibia are probably simple, unlike most *Trigona*, but there may be a few, sparsely plumose ones as in *Trigona (Geotrigona) acapulconis* Strand. The gonostyli are invisible in the fossil. In view of the impressive convergence of external characteristics in some Meliponinae, it could be that *T. prisca* is convergent with rather than closely related to *Trigona* s. str.

Genus *Trichotrigona* Camargo and Moure
(Figs. 76, 114)

Trichotrigona Camargo and Moure, 1983: 421. Type species: *Trichotrigona extranea* Camargo and Moure, 1983, by original designation.

This genus, known from a single nest collection in Amazonas, Brazil, was well described and illustrated by Camargo and Moure (1983). It has many features of *Trigona (Frieseomelitta)* including cluster rather than comb arrangement of its brood cells. The keirotrichiate ridge on the inner surface of the hind tibia is as in *Frieseomelitta* and most other subgenera of *Trigona*, with the shiny concave channel marking its posterior margin extending onto the basal fourth of the tibia. J. M. F. Camargo has kindly sent me a sketch of the sting rudiments and associated structures of *Trichotrigona*. The structure is similar to that illustrated here for *Trigona (Heterotrigona) carbonaria* Smith (Fig. 29) but with the gonostyli longer, as in *T. (Frieseomelitta) nigra* Cresson (Fig. 27).

Extraordinary features of *Trichotrigona* are (1) the hairy eyes and unusually hairy body and wings, with most of the hairs of the body coarse, almost bristle-like, not plumose; (2) the short, broad second segment of the labial palpus, about as broad as long and only somewhat over one fourth as long as the first segment [large setae on these segments few (about 5) and straight]; (3) the rudimentary penicillum and the replacement of the rastellar bristles with slender, tapering hairs; (4) the slender, parallel-sided, hind basitarsus of the worker (nearly four times as long as broad) with all its hairs directed apicad (i.e., without the posteriorly directed hairs and associated ridges near the base that contribute to the pollen press function in most Meliponinae; Wille, 1979a); (5) the lack of plumose hairs on the posterior margin of the hind tibia except at its apex where it rounds onto the convex apical margin of the tibia, which has numerous plumose hairs; (6) the presence of numerous, scattered, rather short hairs on the surface of the corbicula in addition to a few longer hairs; (7) the robust front tibia covered on the outer surface with coarse, weakly spatulate hairs; and (8) the flattened, pointed, bare projection suggestive of a pygidial plate on T6. Males of *Trichotrigona* are unknown.

The reduced rastellum and penicillum and lack of pollen press structures of the hind basitarsus, the presence of rather numerous hairs on the surface of the corbicula, and perhaps also the labial palpus as described above suggest that the only species, *Trichotrigona extranea* Camargo and Moure, is a robber bee like *Lestrimelitta* and *Cleptotrigona* or possibly the only known meliponine social parasite. The single known colony was found in the Amazon valley as a nest of *Trigona (Frieseomelitta) paranigra* Schwarz was being opened; the relation if any to the *paranigra* colony is unknown; no connection was observed. Three of the workers from the nest of *T. extranea* had pollen on the corbiculae and hind basitarsi according to J. M. F. Camargo (in litt.). Given the hind tibiotarsal structure, it is not clear how they would get pollen onto the corbicula using the usual apid movements (Michener, Winston and Jander, 1978). One could imagine, however, placement of sticky pollen from the host nest on the hind legs in the same way that meliponines manipulate and carry resin.

Probably *Trichotrigona* is a derivative of *Trigona (Frieseomelitta).* If so, its existence makes the latter and the genus *Trigona* paraphyletic taxa. *Trichotrigona* is so distinctive, however, that generic status for it is justified. Even those who do not tolerate paraphyletic taxa should hesitate until males of *Trichotrigona* are known and its cladistic position is clearly ascertained. J. M. F. Camargo (in litt.) is strongly of the opinion that *Trichotrigona* is a relictual type not closely related to *Frieseomelitta* in spite of common character states.

Genus *Hypotrigona* Cockerell

(Figs. 35, 60, 115, 135, 151)

Trigona (Hypotrigona) Cockerell, 1934: 47. Type species: *Trigona gribodoi* Magretti, 1884, by original designation.

This is one of the genera of minute stingless bees that exhibit (convergently) the character states listed in couplet 1 of the above key to genera. It is, however, a distinct and isolated genus (with the possible exception that *Pariotrigona,* unknown in the male, may be related). Character states unique within the Meliponinae include the apical process of S5 of the male (considered to be S6 by Brooks and Michener, 1988) which is not especially heavily sclerotized and lies horizontally in the concavity of S6 (S7 in 1988); the U-shaped S6 with strong basolateral apodemes like those of more anterior sterna; and the form of S7 (S8 in 1988) which is a transverse bar with a small, median, basal angle. The sternal characteristics were illustrated by Brooks and Michener (1988), who interpreted what I believe is the apical process of S5 as S6 fused to S5. The male genital capsule is illustrated by the same authors, and in Figure 151. It is rectigonal but unique among Meliponinae in the completely dorsal basal opening of the gonocoxites and the largely membranous basal bulb of the penis valves. The male gonostyli are freely articulated but do not break off easily. The gonostyli of workers are minute to papilliform, not flattened, separated by several times their lengths, with several setae (Fig. 35) but without minute hairs; those of all other African Meliponinae have minute hairs. The sting stylet is a mere convexity. The lancet is insignificant, in the membrane. A remarkable feature is the fusion of the second valvifer with the eighth hemitergite. The strongly bidentate male mandible (Fig. 135) is like that of many other families of bees but unlike that of other Meliponinae. The setae of the labial palpus are short and straight. The external generic character states were listed in detail by Moure (1961).

The mandibular and sternal characteristics of male *Hypotrigona* could be plesiomorphous. If so, then the alternative characters of other Meliponinae would be apomorphies showing that *Hypotrigona* is the sister group to all the other genera. However, the short, transverse male gonocoxites, the reduced wing venation, etc., are apomorphies shared by only part of the other meliponine genera. It therefore seems premature to place *Hypotrigona* as the first branch of the meliponine cladogram.

The mesoscutum is typically dull; in the worker the posterior apical angle of the hind tibia is absent, i.e., broadly rounded; and the scutellum is wholly dark. These are character states that usually distinguish *Hypotrigona* from other minute Meliponinae. Brooks and Michener (1988), however, were unable to distinguish certain workers from *Liotrigona* on the basis of these and other characters. Dissection of the workers shows that their Sp. 2 is a *Hypotrigona;* the gonostylar characteristics were not known to these authors in 1988.

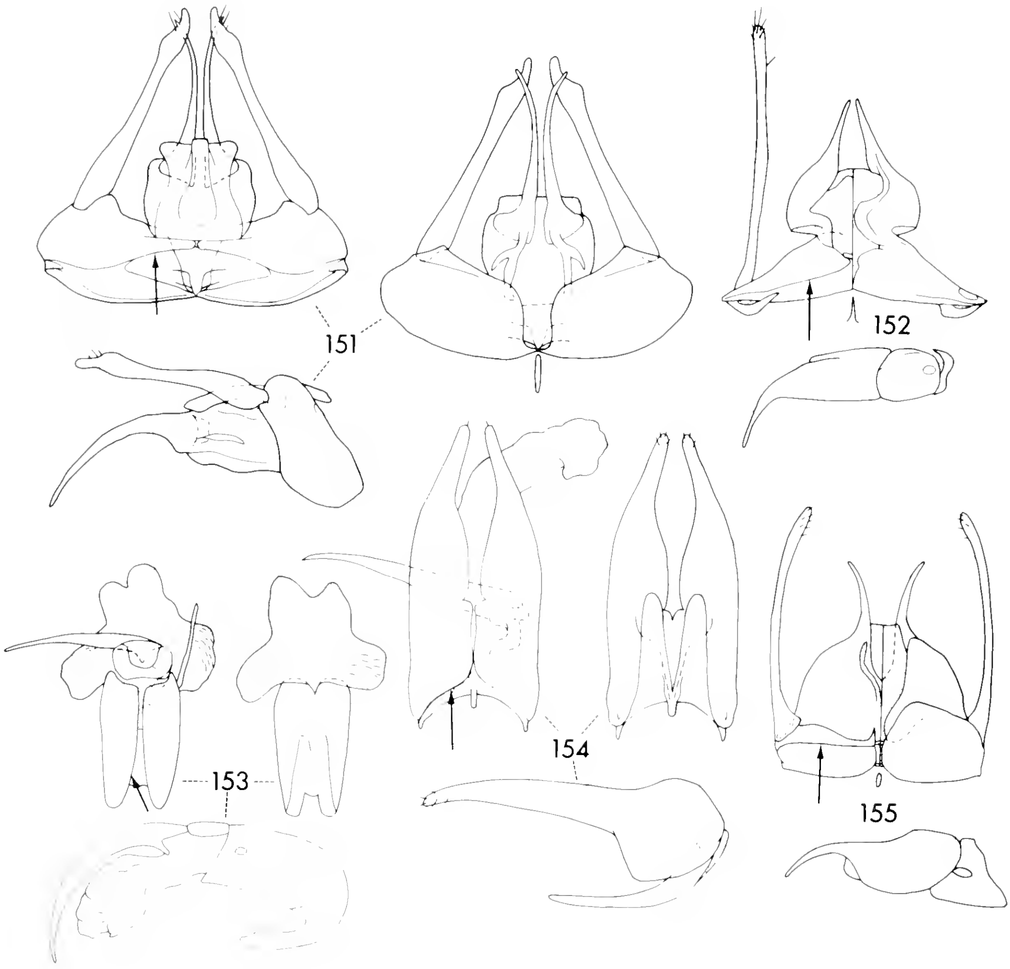
Hypotrigona is widespread and abundant in tropical Africa—Ghana to Kenya, south to Angola and Natal—although represented by only a few species. It does not occur in Madagascar. Included species were listed by Moure (1961), who, however, had not seen and did not place *Hypotrigona magrettii* (Friese, 1900) new combination. It is the smallest *Hypotrigona,* about 2 mm in body length. The type specimen (from Accra, Ghana) has a dull, closely punctate scutum, like that of typical *Hypotrigona;* the posterior apical angle of the hind tibia is rounded; there are no pale streaks on the scutellum; and I have not examined the worker gonostyli. Well known species are *Hypotrigona araujoi* (Michener), *braunsi* (Kohl) and *gribodoi* (Magretti).

Genus *Pariotrigona* Moure

(Figs. 36, 63, 116)

Pariotrigona Moure, 1961: 192. Type species: *Trigona pendleburyi* Schwarz, 1939, by original designation.

This is another genus of minute Meliponinae, sharing the character states listed in couplet 1 of the above key to genera. As it is known only from workers, its generic status and its position relative



Figures 151-155. Male genitalia of Meliponinae, dorsal (at left), ventral, and lateral views (dorsoventral for Figs. 152 and 155). Arrows are explained with Figures 130-134. 151, *Hypotrigona braunsi* (Kohl). 152, *Trigonisca buyssoni* (Friese), gonostylus on dorsal view only. 153, *Liotrigona mahafalya* Brooks and Michener, gonostylus only at right side of dorsal view, penis valve at right of dorsal view and on lateral view. 154, *Cleptotrigona cubiceps* (Friese), penis valve on right side of dorsal view only. 155, *Austroplebeia essingtoni* (Cockerell).

to other genera remain in doubt. The large setae of the worker labial palpus are few (two on segment 1, one on segment 2) and curved, as in *Lisotrigona*. The gonostyli of workers bear setae and lack minute hairs (Fig. 36). The only other minute genus with such gonostyli is *Hypotrigona*. However, those of *Pariotrigona* are quite different, being broadened at the bases and separated by little more than a stylar width. The sting lancet is absent, the stylet a broad convexity. The hind tibia has a distinct although rounded posterior apical angle in *Pariotrigona*, lacking in *Hypotrigona*. The long malar space of *Pariotrigona* suggests some species of the Neotropical genus *Trigonisca*, a similarity strengthened by the nearly right angular basal angle of the marginal cell and the transverse rows of hairs on the inner surface of the hind basitarsus. *Trigonisca*, however, has quite different worker gonostyli. The external generic characteristics were listed by Moure (1961).

Pariotrigona is known from two uncommon species found from the Malay Peninsula to Indo-china, Borneo and Sumatra. I have dissected only *P. pendleburyi* (Schwarz) but *P. klossi* (Schwarz) appears certainly congeneric.

Genus *Lisotrigona* Moure

(Figs. 37, 64, 117)

Lisotrigona Moure, 1961: 194. Type species: *Melipona cacciae* Nurse, 1907, by original designation.

This genus of minute bees shares the character states listed in couplet 1 of the above key to genera. It is known only from workers; hence its position relative to other genera is in doubt. The gonostyli of workers are flat, separated by a median concavity about as wide as a gonostylus, and are covered with abundant minute hairs; on the outer and distal margin of each there are several long, delicate setae. Thus the gonostylar vestiture is similar to that of *Trigonisca*. The sting stylet is merely convex. The lancet, however, is long and free. The hind tibia has a much rounded posterior apical angle, the hairs on the inner side of the hind basitarsus are not in noticeable rows, and the base of the marginal cell is acute; in these features *Lisotrigona* differs from *Trigonisca*. It differs from the other minute Asiatic Meliponinae [ignoring small species of *Trigona* such as *T. (Heterotrigona) fuscobalteata* Cameron], i.e., the genus *Pariotrigona,* not only by the character states indicated in the key but by the acute base of the marginal cell and other features listed by Moure (1961) who described both groups in detail. The large hairs of the labial palpi, however, are essentially as in *Pariotrigona* and within the range of variation found in *Trigonisca*.

Lisotrigona contains two perhaps distinct, uncommon species known from Sri Lanka and Madhya Pradesh in India to Vietnam, Borneo and Sumatra. I have seen only *L. scintillans* (Cockerell) but Moure (1961) indicates its close similarity to *L. cacciae* (Nurse).

Genus *Trigonisca* Moure

(Figs. 38, 39, 59, 118, 119, 152, 168, 186)

Hypotrigona (Trigonisca) Moure, 1950a: 249. Type species: *Trigona duckei* Friese, 1900, by original designation.

Hypotrigona (Leurotrigona) Moure, 1950a: 244. Type species: *Trigona muelleri* Friese, 1900, by original designation.

Hypotrigona (Celetrigona) Moure, 1950a: 246. Type species: *Trigona longicornis* Friese, 1903, by original designation.

Hypotrigona (Dolichotrigona) Moure, 1950a: 248. Type species: *Trigona longitarsis* Ducke, 1916, by original designation.

Of the four simultaneously published names listed above, Wille (1979b) selected *Trigonisca* for the inclusive taxon (here recognized as a genus); several species resemble *T. duckei* and were included in *Trigonisca* by Moure while each of the other genus-group names was proposed for a single divergent species. A second species related to *Trigonisca muelleri* (Friese), i.e., of the *Leurotrigona* group, has recently been described, however (Moure, Camargo, and Garcia, 1988). (Unfortunately due to a lapsus the description is headed with the name *muelleri,* but the intended new name *pusilla* Moure and Camargo appears in the abstract, figure captions, etc., and is thus validated.) In the present classification it would be *Trigonisca pusilla* (Moure and Camargo) new combination.

Trigonisca is one of the minute, *Hypotrigona*-like genera segregated in couplet 1 of the key to genera. It is the only such genus found in the Western Hemisphere although a few minute American species exist in other genera, e.g., *Plebeia (Plebeia) schrottkyi* (Friese) and *P. (Nogueirapis) minor* (Moure and Camargo).

Trigonisca differs from all other American Meliponinae in the minute hairs which are widespread on the worker gonostyli. In addition there are setae, mostly or all along the outer margin of each gonostylus. The gonostyli are adjacent or separated by somewhat over one gonostylar width, and converge so that when adjacent at the bases, they overlap distally. The worker gonostyli of the Asiatic *Lisotrigona* are somewhat similar but are short, do not converge, and are separated by an emargination. The sting stylet of the worker is broadly rounded or very obtusely angulate. The lancet of the worker sting is short but its apex is free of the membrane. The male genital capsule is rectigonal in specimens that I have studied and as illustrated by Moure, Camargo, and Garcia (1988), although I categorize it as amphigonal because it can probably assume the schizogonal conformation, the gonocoxites being transverse, much broader than long or about as long as broad. The large setae of the worker labial palpus are few (5-7), straight or curved.

An unusual feature is the vestiture on the inner surface of the hind basitarsus of the worker; the hairs are in transverse rows, suggesting *Apis* and the Asiatic genus *Pariotrigona.* Also, some of the large hairs on the posterior margin of the hind tibia arise from tubercles (Fig. 186) which are particularly conspicuous in the species with the tibia slender. Thus the posterior edge of the tibia appears weakly nodulose to strongly tuberculate, instead of smooth as in other Meliponinae. The right angular or weakly obtuse basal angle of the marginal cell, associated with a broad base of this cell, as indicated in couplet 7 of the key to genera, is variable and requires some explanation. In *T. muelleri* (Friese) the marginal cell is much more as in other Meliponinae than is that of other *Trigonisca.* Nonetheless, in *T. muelleri* the basal angle of the cell (between the stigmal margin and vein r) is about 68° and the width of the marginal cell at the apex of the stigma is greater than the distance across the submarginal cell area from vein Rs to vein M. In other genera the basal angle is less than 50° and the width of the marginal cell at the apex of the stigma is not greater than the distance across the submarginal cell area. These characters, among others, show the relationship of the four groups listed in the generic synonymy.

The external character states of the genus are listed in detail by Moure (1951) and those of each group within the genus by Moure (1950); see also the above key to genera. Unlike most species which have two small denticles at the upper end of the apical mandibular margin, *T. longitarsis* (Ducke) and *schulthessi* (Friese) have only one. The former has a bituberculate labrum, suggesting *Lestrimelitta*. If more species of these groups are found, it will be reasonable to recognize the names in the above synonymy as subgenera. I think it is important, however, to indicate their close relationship (shown by the worker gonostyli, the broad base of the marginal cell, the tuberculate hind tibiae, etc.) to the rest of *Trigonisca*.

Within the genus there is considerable variation in brood cell construction and worker oviposition. In *Trigonisca* s. str. construction is successive but in *T. muelleri* (Friese) and *longicornis* (Friese) it starts successively but becomes synchronized by the time a number of cells are completed. Worker-laid eggs are unknown in *T. muelleri* but are deposited on the food mass like those of the queen in *T. longicornis* (Sakagami, 1982). The observations are fragmentary for these tiny bees but may support subgeneric status for the four names listed in the above synonymy.

These minute bees are attracted to perspiration and are sometimes pests from Mexico to Paraguay. There are about 17 species; familiar ones are *Trigonisca buyssoni* (Friese), *duckei* (Friese), *longicornis* (Friese), *longitarsis* (Ducke), and *muelleri* (Friese).

Genus *Liotrigona* Moure

(Figs. 40, 61, 120, 136, 153)

Liotrigona Moure, 1961: 223. Type species: *Trigona bottegoi* Magretti, 1895 (=? *Trigona madecassa* Saussure, 1891), by original designation.

This is one of the genera of minute bees segregated in couplet 1 of the above key to genera. Unlike the superficially similar *Hypotrigona, Liotrigona* is a member of the African group with flattened worker gonostyli bearing numerous minute hairs. The gonostylar bases are separated by less than the width of a gonostylus, and setae are absent. The gonostyli do not diverge as in most African Meliponinae. Each has a dorsal thickening, suggesting that of *Cleptotrigona,* but it bears minute hairs rather than coarse setae. The sting stylet is unsclerotized, blunt. The lancet is moderately long, free of the membrane.

The male genital capsule is elongate, permanently schizogonal, the gonocoxites much longer than broad and broadly fused ventrally, the bases (plus possibly the gonobase) curled under and directed apicad, fused to one another except distally. The gonostyli are slender, arising near the apices of the gonocoxites, easily detached from the gonocoxites during dissection. As in *Cleptotrigona,* the flexion of the penis valves is contralateral so that they cross one another when flexed. The genitalia and hidden sterna are illustrated by Brooks and Michener (1988). The sterna differ greatly from those of *Hypotrigona;* T6 has a midapical reflexed process that is much broader than in most Meliponinae. The large hairs of the labial palpus of the worker are few (5-6), mostly curved, unlike *Hypotrigona* which lacks such hairs. The external generic characteristics are listed in detail by Moure (1961).

Workers of *Liotrigona* can usually be distinguished without dissection from *Hypotrigona* by the shiny mesoscutum with only minute well separated punctures; the distinct posterior apical angle of the hind tibia, and the presence of pale or yellowish streaks on the preaxilla and posterior margin of the scutellum. As noted above in the discussion of *Hypotrigona,* these character states occasionally fail, and Brooks and Michener (1988) were unable to place certain undescribed species. Dissection of the worker gonostyli shows that their Sp. 1 is a *Liotrigona.*

Liotrigona is widespread but not very common in Africa—Ethiopia to Natal, Ghana to Angola—and is common in Madagascar. There are six or more species (Brooks and Michener, 1988; Michener, 1989) of which the most familiar names are *L. bottegoi* (Magretti), *madecassa* (Saussure), and *mahafalya* Brooks and Michener.

Genus *Cleptotrigona* Moure

(Figs. 41, 62, 121, 154)

Lestrimelitta (Cleptotrigona) Moure, 1961: 219. Type species: *Lestrimelitta cubiceps* Friese, 1912, by original designation.

Cleptotrigona forages in nests of *Hypotrigona* and probably *Liotrigona.* It is not known to visit flowers. This African robber genus is strongly convergent with the American robber, *Lestrimelitta,* so that Moure (1961) regarded them as congeneric. Wille (1979b), however, emphasized their distinctness and recognized their resemblances as convergent, although extending beyond loss of the pollen carrying and manipulating structures. Both authors listed many characters.

In *Cleptotrigona* workers the gonostyli are flat, divergent, the bases separate by about half a gonostylar width; they bear many minute hairs in addition to several setae along the edges of a dorsal thickening. The sting stylet is slender, acute, and little sclerotized, especially basally. The lancet is long and largely free of membrane. The male gonocoxites are longer than broad, broadly fused apically to gonostyli that are broad and flattened at the bases and tapering apically. Such gonostyli are unique in the Meliponinae and strikingly different from the extremely slender, easily deciduous gonostyli of *Liotrigona*. The genitalia appear to be permanently schizogonal although the base of the genital capsule is perhaps secondarily rectigonal, curled under the rest of the genitalia and extends apicad as far as the bases of the gonostyli as two slender lobes. This suggests the structure of *Liotrigona* in which, however, the lobes are fused to one another except apically. The sixth and seventh sterna are quite ordinary for Meliponinae, not platelike as in *Lestrimelitta,* the sixth with a midapical reflexed process.

Cleptotrigona is one of the genera of minute Meliponinae segregated in couplet 1 of the above key. The short, straight setae of the worker labial palpus suggest *Hypotrigona* but probably reflect loss of large setae associated with the robbing way of life (Michener and Roubik, in press). *Cleptotrigona* appears to be the sister group of *Liotrigona,* as indicated especially by the curled-under base of the genital capsule. Moreover, in both genera the penis valves, when extended laterad, cross at their bases, so that the left hand penis valve is directed to the right, and the right hand one to the left (Fig. 153). This is unlike other Meliponinae and is a probable synapomorphy supporting the relationship shown in Figure 8. *Liotrigona* has apomorphies not shared by *Cleptotrigona* (smaller, less slender sting stylet of workers; fused ventral lobes of the genital capsule of males), indicating that *Cleptotrigona* was not derived from *Liotrigona.* Both have the rastellum reduced to tapering hairs.

The rather flat scutellum, not at all overhanging the metanotum and elevated but little above the level of the dorsal surface of the propodeum (Fig. 121) is unique in the Apidae. Among bees as a whole this feature is a plesiomorphy but within the Apidae it must be an apomorphy, i.e., a reversion to the condition found in many non-apid bees.

Cleptotrigona consists of two species, *C. cubiceps* (Friese) and *curriei* (Cockerell) known from Liberia to Tanzania, Angola and South Africa. The species are listed by Moure (1961). *Trigona magrettii* Friese (1900), considered as a possible *Cleptotrigona* by Moure, is a *Hypotrigona.*

Genus *Austroplebeia* Moure

(Figs. 42, 81, 122, 155, 169)

Austroplebeia Moure, 1961: 195. Type species: *Trigona cassiae* Cockerell, 1910, by original designation.

This genus includes bees that superficially closely resemble species of the Neotropical group *Plebeia (Plebeia)* as well as the African *Plebeina. Austroplebeia* species are rather robust with distinct yellow areas on the scutellum and axillae, usually also on the lateral margins of the scutum and on the face. It differs from *Plebeia* in the abundant, minute hairs and few small setae on the worker gonostyli and the slender and pointed bristles of the rastellum. The worker gonostyli are slightly divergent, separated at the bases by about a gonostylar width. The sting stylet is rounded. The lancet is quite long, mostly free of the membrane. The five to about seven large setae of the labial palpus are curved to weakly sinuous. *Austroplebeia* differs from the *Plebeia*-like African genera *Plebeina* and *Meliponula* by the well separated worker gonostyli which are not noticeably flattened; the not or scarcely depressed posterior margin of the inner surface of the hind tibia (variable in *Meliponula*); the short, transverse, amphigonal male gonocoxites [both conformations seen in *A. essingtoni* (Cockerell)]; and lack of the male spatha and gonobase.

In the reduced wing venation, especially the lack of a bend near the end of vein M of the forewing and lack [except in *A. cincta* (Mocsary)] of vestiges of the first transverse cubital vein, *Austroplebeia* resembles the minute genera segregated in the first couplet of the key to genera (see Note after that key). Although small, *Austroplebeia*'s robust form does not resemble that of the other minute genera. Unlike those genera, the inner side of the hind tibia has the keirotrichiate area closely approaching the posterior margin of the tibia, leaving a narrow shiny margin as in *Plebeia* s. str. but less depressed or even not depressed.

Because of its male genitalic character states this genus does not appear related to African genera, but rather to American ones. The hair-like spicules of the worker gonostyli are shared only with *Trigonisca* in America, *Lisotrigona* in Asia, and most African genera. Discovery of males of *Lisotrigona* might expose a relationship between it and *Austroplebeia.* External features of *Austroplebeia* were described by Moure (1961).

This genus contains several species found in the northern half of Australia and in New Guinea. The specific names involved were listed by Michener (1965, as *Plebeia*) and by Moure (1961). Well known specific names are *Austroplebeia australis* (Friese), *cassiae* (Cockerell), *cincta* (Mocsary) and *essingtoni* (Cockerell).

Genus *Meliponula* Cockerell

This generic name is used in a new sense to include not only the type species, *M. bocandei* (Spinola), but also a series of smaller African forms placed in other genera (see subgenera, below) by Moure (1961) and Wille (1979b). Some of the latter, such as *M. beccarii* (Gribodo) and *erythra* (Schletterer), are almost as robust and *Melipona*-like as *M. bocandei*. *Meliponula* shares with most other African Meliponinae the flattened worker gonostyli with many minute hairs (sometimes also with a few setae), the presence of a conspicuous remnant of the gonobase attached to the male gonocoxite lateroventrally, the schizogonal (presumably permanently) male genital capsule with the gonocoxites longer than broad, at least in ventral view, and the strongly reflexed median apical process of S6 of the male.

Meliponula resembles *Cleptotrigona* and the American genus *Melipona* in having the sting stylet of workers distinct and acute. *Meliponula* differs from *Plebeina* in the reduction of the rastellum to slender hairs, no coarser than those of similar length on adjacent parts of the tibial apex; the rounded or very obtuse posterior apical angle of the worker hind tibia so that the tibia is rather spoon-shaped; the presence of coarse, amber or blackish bristles arising from or near this angle forming what Wille (1979b) calls the posterior parapenicillum in *M. bocandei* (Spinola); the presence of hairs, at least laterally, on the basal area of the propodeum, and the acute worker sting stylet. Like *Plebeina* and unlike other African genera, *Meliponula* has a broad area of keirotrichia on the inner surface of the worker hind tibia; the posterior margin may be depressed and shining, almost as in *Plebeia* s. str., only slightly depressed (e.g., in *Meliponula* s. str.), or poorly defined and not at all depressed (subgenus *Axestotrigona*). The smaller species of *Meliponula* resemble the larger species of *Plebeia* s. str. superficially, but differ from most *Plebeia* not only in character states indicated in the above discussion but in the dense punctation at least of the mesoscutum.

The reduction of the rastellum to slender hairs is not found among other moderate-sized, pollen-collecting Meliponinae, although it is seen in some minute genera. Given the function of the comblike rastellum in other Apidae (Michener, Winston, and Jander, 1978), a study of the pollen manipulating movements in *Meliponula* would be interesting.

Key to the Subgenera of *Meliponula*

1. Propodeal profile largely vertical; corbicula occupying less than distal half of hind tibia; apical reflexed process of S6 of male short and rounded; metasomal terga dull, minutely sculptured . . . . *Meliponula* s. str.

—Propodeal profile with slanting dorsal portion rounding onto vertical portion; corbicula occupying more than distal half of hind tibia; apical reflexed process of S6 of male longer than body of sternum; metasomal terga at least partly shining 2

2. Head and thorax without yellow markings; inner surface of worker hind tibia without well defined shining, depressed posterior margin, although keirotrichiate area does not reach margin at least distally . . . . *Axestotrigona*

—Head and thorax with yellow markings; inner surface of worker hind tibia with shining posterior margin at least slightly depressed . . . . *Meliplebeia*

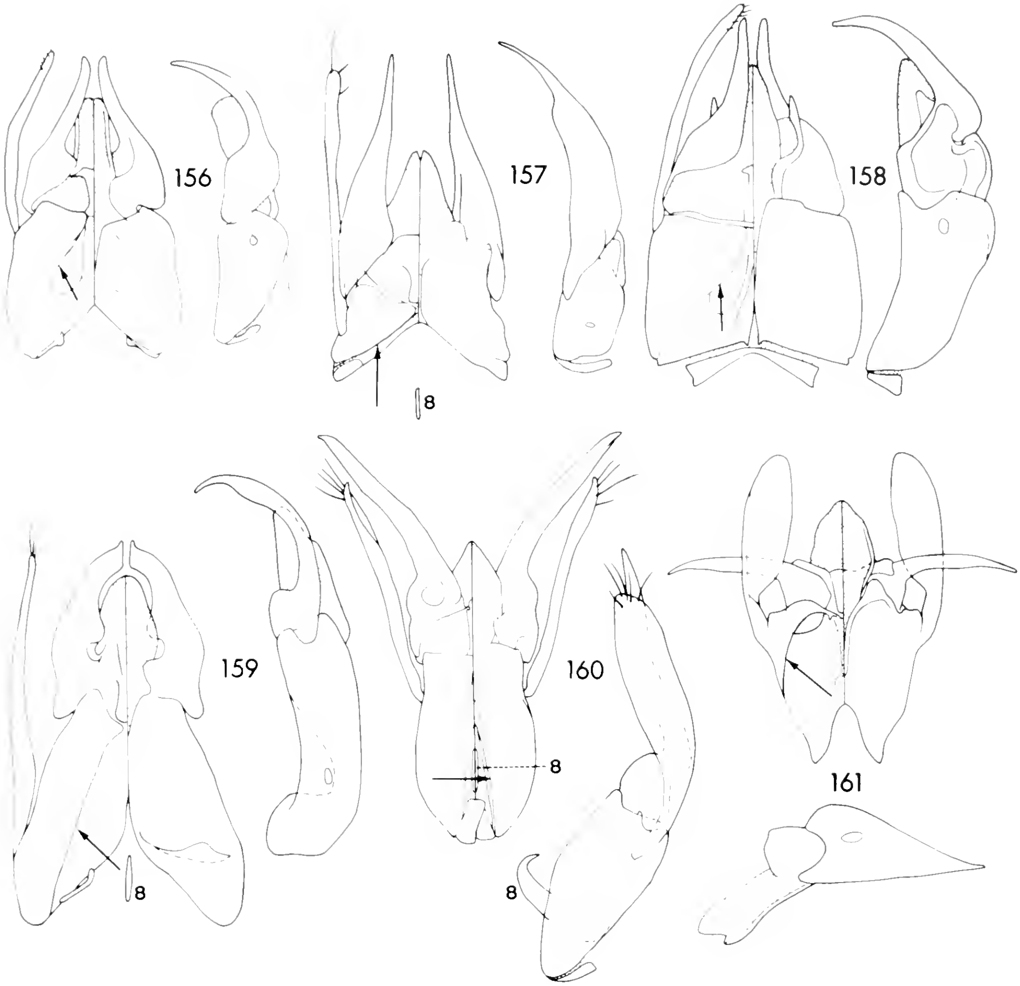
Subgenus *Axestotrigona* Moure

(Figs. 44, 78, 126, 158)

Axestotrigona Moure, 1961: 237. Type species: *Melipona ferruginea* Lepeletier, 1836, by original designation.

This subgenus contains moderate-sized robust species. There are delicate plumed hairs among the marginal bristles at the posterior apical angle of the worker hind tibia and across the apex of the tibia. The sting stylet of the worker is long and slender, almost as in *Meliponula* s. str., but the lancet is weak and in the membrane. The about 24 large hairs of the worker labial palpus are mostly curved on segment one, sinuous on segment two. The male gonostylus arises near the apex of the gonocoxite. I regard the genitalia (Fig. 158) as permanently schizogonal, as in the other subgenera. However, this is only evident in dorsal view, for ventrally the gonocoxites are broadly expanded so that they are secondarily rectigonal. The principal characteristics are indicated in the above key and in the description by Moure (1961).

There are several species; their names are indicated by Moure (1961). The most common species is *Meliponula (Axestotrigona) erythra* (Schlet-



Figures 156-161. Male genitalia of Meliponinae, dorso-ventral views (dorsal at left) and lateral views, gonostyli omitted from most lateral and ventral views. Arrows and "8" are explained with Figures 130-134. 156, *Meliponula (Meliplebeia) beccarii* (Gribodo). 157, *Meliponula (Meliplebeia) lendliana* (Friese). 158, *Meliponula (Axestotrigona) erythra* (Schletterer). 159, *Meliponula (Meliponula) bocandei* (Spinola). 160, *Plebeina denoiti* (Vachal). 161, *Dactylurina schmidti* (Stadelmann).

terer) which may be a form of *ferruginea* (Lepeletier). The subgenus ranges from Gambia to Kenya, south to Angola and the Transvaal.

Subgenus *Meliplebeia* Moure

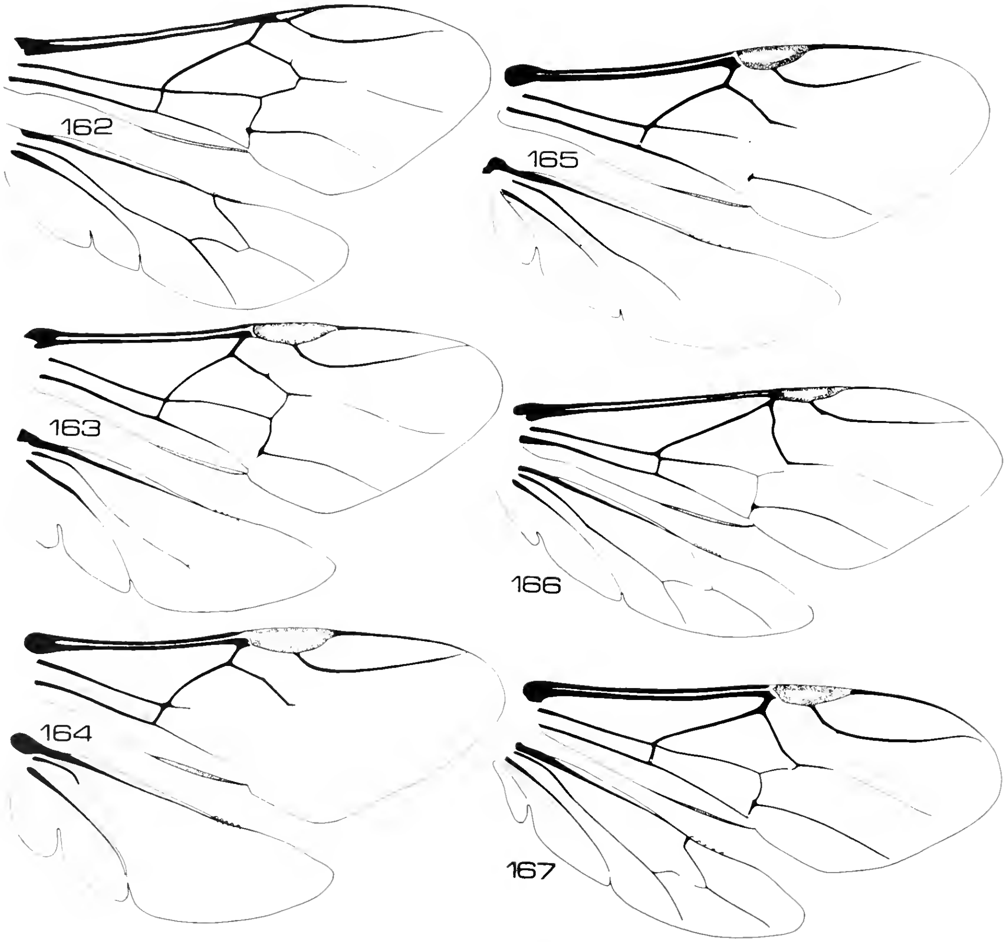
(Figs. 43, 46, 79, 123-125, 156, 157)

Meliplebeia Moure, 1961: 229. Type species: *Trigona beccarii* Gribodo, 1879, by original designation.
Plebeiella Moure, 1961: 226. Type species: *Trigona lendliana* Friese, 1900, by original designation.
Apotrigona Moure, 1961: 233. Type species: *Trigona nebulata* Smith, 1854, by original designation.

Wille (1979b) selected the name *Meliplebeia* for this group, rather than either of the other names proposed at the same time. The three groups named by Moure are distinctly different from one another. The subgenus contains moderate-sized [e.g., *M. beccarii* (Gribodo)] to small [*M. lendliana* (Friese)] species. In *Meliponula (Meliplebeia) beccarii* there are delicate plumed hairs among the bristles near the posterior apical angle of the worker hind tibia, as in the subgenus *Axestotrigona*. Such hairs are absent in the other groups of *Meliplebeia*. The lancet of the worker sting is weak and in membrane in *M. (M.) beccarii* but quite long and apically free, although transparent, in *M. (M.) lendliana* (Friese) and *nebulata* (Smith). The hairs of the first two segments of the labial palpus of workers in *M. (M.) beccarii* are short and straight, while in both *M. nebulata* and *lendliana* there are large setae, hooked and slightly sinuous.

In view of the characters listed above, it is tempting to recognize two subgenera *Meliplebeia* and *Plebeiella*, with *Apotrigona* as a synonym of *Plebeiella*. The differences between the groups of *Meliplebeia* are accentuated by S6 of males. In *M. (M.) beccarii* (Gribodo) S6 is a transverse band not greatly different from that of *Axestotrigona*, and the reflexed median apical process, although long, ends in a rounded apex. In *M. (M.) lendliana* (Friese) S6 is enlarged, dorsoventrally thickened laterally, and the reflexed apical process is bifid near the base, one prong above the other, both long and slender, the upper one extending toward the base of the metasoma (broken off in the one available specimen). Unfortunately the male of *M. (M.) nebulata* (Smith) is unknown to me. Until its character states are known, I have decided that the best classification is one that shows the close relationship of the three groups given generic names by Moure, especially in view of the small number of species involved.

Meliplebeia contains several species (representatives listed above) and ranges from Senegal to Ethiopia, south to Namibia and Natal. The species names and external character states are listed by Moure (1961) under his three generic names (see above synonymy). The emphasis that Moure places on mesoscutal sculpturing (punctate in *Apotrigona*, tessellate in the others) seems to me misplaced. It is dull, finely and closely punctate, finest in *M. lendliana* (Friese).



Figures 162-167. Wings of Meliponinae. 162, *Melipona fasciata* Latreille. 163, *Plebeia (Plebeia) frontalis* (Friese). 164, *Plebeia (Plebeia) schrottkyi* (Friese). 165, *Lestrimelitta limao* (Smith). 166, *Cephalotrigona capitata* (Smith). 167, *Trigona (Trigona) chanchamayoensis* Schwarz.

Subgenus *Meliponula* Cockerell s. str.

(Figs. 45, 77, 127, 159, 170, 172)

Trigona (Meliponula) Cockerell, 1934: 47. Type species: *Melipona bocandei* Spinola, 1851, by original designation.

This subgenus contains the largest and most *Melipona*-like species of the genus. It is robust, compact in form, and lacks yellow markings although it has yellowish brown areas, for example, the scutellum and axillae. On the posterior and distal margins of the hind tibia there are bristles, no plumose hairs. The inner surface of the worker hind tibia has a well defined but rather dull, slightly depressed posterior margin. The worker sting stylet is unusually long and slender and the lancet is long and largely free. The about 15 large setae of the worker labial palpus are curved to slightly sinuous. The male gonostylus arises near the base of the gonocoxite. Other character states are indicated in the above key and in Moure's (1961) comparative description, and especially in Wille (1963). An interesting feature emphasized by Wille is the arch of the aorta between the longitudinal muscles of the thorax. This is as in *Melipona*, but unlike other stingless bees [including *Meliponula (Meliplebeia) beccarii* (Gribodo), see Wille, 1958]. It is, however, a feature of many moderate-sized and large, fast flying bees and is doubtless a convergence in *Melipona* and *Meliponula* s. str., not an indication of close relationship.

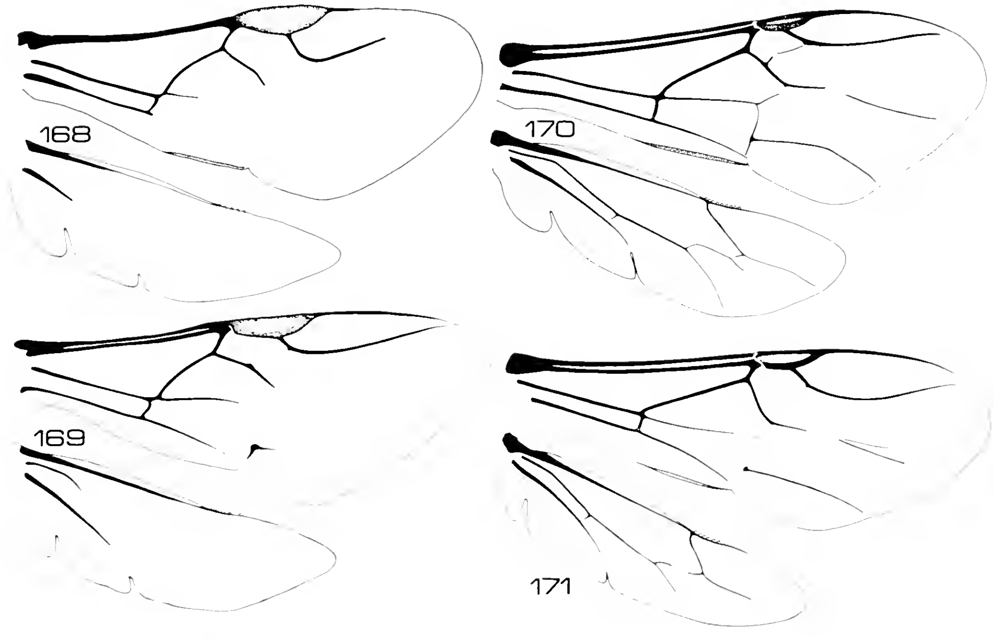
The single species, *Meliponula (Meliponula) bocandei* (Spinola), ranges from Liberia, the Central African Republic, and Uganda south to Angola.

Genus *Plebeina* Moure

(Figs. 47, 128, 160)

Plebeina Moure, 1961: 228. Type species: *Melipona (Trigona) denoiti* Vachal, 1903, by original designation.

This African genus is similar to the Neotropical *Plebeia (Plebeia)* in body form, presence of limited yellowish marks at least on the face, and the narrow, depressed, shining posterior margin of the inner surface of the worker hind tibia. It differs in having the worker gonostyli diverging apically, flattened, without setae and with numerous minute hairs; the sting lancet moderately long and largely free of membrane, the male gonocoxites schizogonal (probably permanently) and much longer than wide; and the gonobase remnants rather large. These features are as in most African Meliponinae. In spite of its appearance, this genus is evidently not closely related to *Plebeia*. Another character state that distinguishes it from most *Plebeia* is the presence of branched hairs at the posterior distal angle of the worker hind tibia and a few on the distal fourth of the



Figures 168-171. Wings of Meliponinae. 168, *Trigonisca buyssoni* (Friese). 169, *Austroplebeia australis* (Friese). 170, *Meliponula (Meliponula) bocandei* (Spinola). 171, *Dactylurina schmidti* (Stadelmann).

posterior margin of the tibia. This is as in some species of *Meliponula*, a genus to which *Plebeina* is closely related. In two species of *Plebeia*, *P. (Plebeia) caerulea* (Friese) and *P. (Schwarziana) quadrimaculata* (Lepeletier), there are branches on one side of numerous hairs. *Plebeina* differs from *Meliponula* in the about right angular posterior apical angle of the worker hind tibia, this angle bearing long, slender whitish hairs; in the strong although pointed bristles of the rastellum; in the hairless basal area of the propodeum; and especially in the sting stylet of the worker which is merely a rounded, membranous prominence. The about 15 large setae on the worker labial palpus are curved to weakly sinuous. A full description of external characteristics is given by Moure (1961).

This genus contains one variable species, *Plebeina denoiti* (Vachal), or a few closely related species. Moure (1961) omitted presumably inadvertently the name of a form considered in the last paragraph of his discussion of the genus. It was *Plebeina denoiti katangensis* (Cockerell). The genus ranges from Kenya and Uganda to eastern Zaire, Botswana, northern Transval and Natal. It may be absent from West Africa.

Genus *Dactylurina* Cockerell

(Figs. 48, 80, 129, 161, 171)

Dactylurina Cockerell, 1934: 47. Type species: *Trigona staudingeri* Gribodo, 1893, by original designation.

This is the only African group that has the long legs, slender body, plumose hairs on the posterior margin of the hind tibia, and narrow keirotrichiate ridge on the inner surface of the hind tibia, as in *Trigona;* the resemblance is closest to some species of the subgenera *Heterotrigona* and *Frieseomelitta*. A further similarity to some *Trigona* is found on the inner surface of the hind basitarsus of workers of *D. staudingeri* (Gribodo), but not *D. schmidti* (Stadelmann). In the former, in the basal area where many *Trigona* species have a well-defined sericeous area covered with short, dense, fine and sometimes deciduous hairs, there is an ill-defined somewhat sericeous area where the bristle-like setae are sparse. In *D. schmidti* the bristle-like setae are uniformly distributed as in most Meliponinae.

Dactylurina has sometimes been given generic status in the past because of its nest architecture (see introductory section on this topic). Its male genitalia and worker gonostyli show that it is only distantly related to *Trigona* in spite of its resemblance to species of that genus. Unusual features include the slender, fingerlike metasoma and the presence of only one denticle on the upper part of the apical mandibular margin.

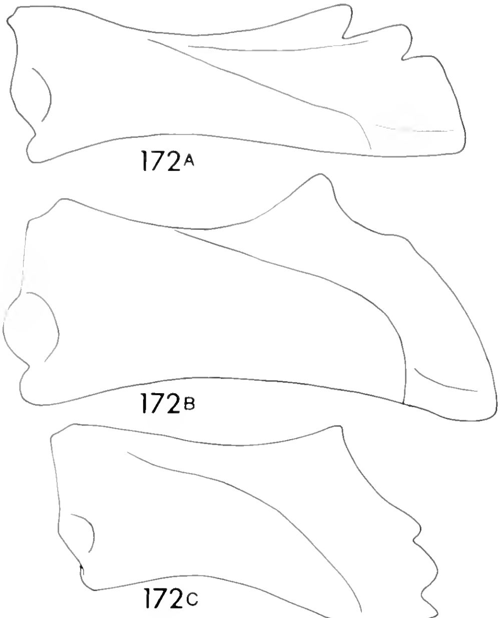
The worker gonostyli are adjacent to one another basally, slightly divergent apically, covered with minute hairs, and without setae. The sting stylet is a mere convexity. The lancet is short and in the membrane, unlike that of most African Meliponinae. The male genital capsule is schizogonal (probably permanently), the gonocoxites longer than broad. The gonobase appears to be absent. The male gonostyli are hairless, firmly attached to the gonocoxites and, although slender in *D. staudingeri* (Gribodo), are broad and flattened in *D. schmidti* (Stadelmann). The gonocoxites are wide open on the ventral side. The labial palpi of the worker have about six large, curved setae; an unusual feature is that segments three and four together are much longer than segment two. The worker gonostyli and male gonocoxites show the relationship of this genus to other African genera. As shown in Figure 6 it appears to be the much modified sister group of *Plebeina*.

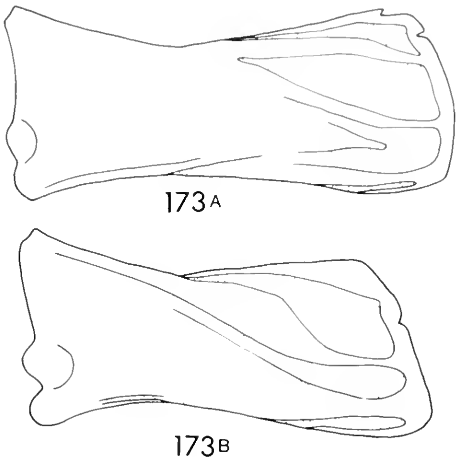
There are two species, *Dactylurina staudingeri* (Gribodo) from west Africa and *schmidti* (Stadelmann) from east Africa. Considered together they are widespread in tropical Africa—Kenya and Tanzania to Zaire and Liberia.

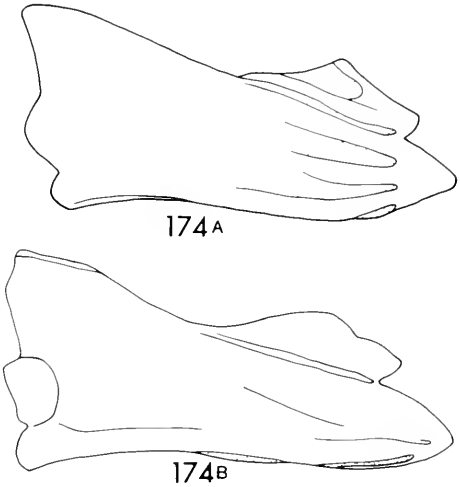
SUBFAMILY APINAE

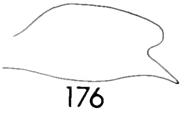
These are the true honey bees. More has been written about *Apis mellifera* Linnaeus than any other insect. Probably because of the familiarity and importance of that species, there has been considerable proliferation of names, considering that *Apis* is a small and morphologically and behaviorally unified group. Maa (1953) made a careful revision of the subfamily, recognizing four genus-group names and many species. His work has often been ignored because of the widespread belief that there are only four species. While he clearly split more than necessary at both the genus-group and species levels, more and more of his conclusions are turning out to be correct. His work is the basic one for a study of apine systematics. Many more recent papers have been reviewed by Ruttner (1987), whose morphometric studies are important at the infraspecific level. A phylogenetic treatment is provided by Alexander (in press).

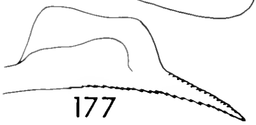
Description: Small (7 mm long) to large (19 mm long), moderately hairy, rather elongate bees. *Eyes hairy.* Claws of female cleft; arolia present; *hind tibial spurs absent;* strigilis with prong on anterior side; hind basitarsus of worker almost as broad at base as at middle, with posterior basal projection or auricle; hind tibia without penicillum. Forewing with complete, strong vena-











Figures 172-175. Mandibles of females (workers in social species) of Apidae. 172, Meliponinae; a, *Meliponula bocandei* (Spinola), b, *Cephalotrigona capitata* (Smith), c, *Trigona (Trigona) cilipes* (Fabricius). 173, Bombinae; a, *Bombus pennsylvanicua* (Degeer), b, *Psithyrus variabilis* (Cresson). 174, Euglossinae; a, *Eufriesea violacea* (Blanchard), b, *Exaerete smaragdina* (Guérin). 175, Apinae; *Apis mellifera* Linnaeus.

Figures 176-177. Strigilis of worker, inner surface. 176, *Melipona rufiventris* Lepeletier. 177, *Bombus pennsylvanicus* (Degeer).

tion, marginal cell about four times as long as distance from its apex to wing tip; stigma small and slender, scarcely recognizable in large species, vein r arising near middle, margin within marginal cell straight to concave; prestigma almost as long as stigma; second and third transverse cubital veins directed posterodistad and forming acute angles with vein M. Hind wing with jugal lobe little more than half to nearly two thirds as long as vannal lobe (measured from wing base); *jugal and vannal incisions shallow* (Fig. 182). Clypeus gently convex but scarcely protuberant. Maxillary palpus minute, two segmented. Male S8 reduced to a transverse bar, without a spiculum; S7 hidden by S6, transverse, sometimes attenuate medially, with strong lateral apodeme. *Male genitalia of other Hymenoptera largely replaced by huge and elaborate endophallus;* gonobase absent; gonocoxite represented by plate bearing a minute, hairy, apical projection, broader than long, presumably the gonostylus; gonocoxites sometimes widely separated by membrane; penis valves thick, blunt, hairy (incorrectly identified as gonostyli by Smith, 1970); spatha and volsella absent (Fig. 183).

Larva: Without small conical tubercles but with transverse dorsolateral elevations on segments 1 to 4, strongest on 1 and progressively weaker to the rear. Mandible scarcely sclerotized, bluntly pointed, edentate or with fringe of small teeth at apex, without concavity on inner surface.

Larvae are described and illustrated by Michener (1953), Torchio and Torchio (1975), and others.

Nest: Nests are exposed or in cavities such as hives or hollow trees, sometimes in cavities in the ground. The nests are made primarily of wax secreted by the sternal wax glands of workers.

Cells are subhorizontal, forming vertical combs of two layers of cells opening in opposite directions, their bases constituting a median vertical wax sheet. Food for larvae is provided progressively; cells are not closed until the larva has finished feeding. A nest may consist of a single exposed comb or of multiple combs, usually in a cavity. Brood cells for workers and storage cells for honey or pollen are hexagonal, similar in diameter; brood cells for males are similar but larger. Queen-producing cells are not in combs and tend to hang from brood combs of worker cells.

Social behavior: This is the only group of highly social bees (i.e., bees with "permanent" colonies and morphologically very different castes) other than the Meliponinae. New colonies are formed by fission, the old queen and a swarm of workers leaving to find a new site. Colony sizes range from a few thousand to 60,000 or more workers. Accounts of behavior can be found in Michener (1974) and Ruttner (1987), and in innumerable books on the honey bee (*Apis mellifera* Linnaeus); an excellent recent one with numerous references to others is by Winston (1987).

There are no parasitic or obligate robber species.

Distribution: This subfamily is primarily tropical, and was restricted to the Old World until *Apis mellifera* was introduced worldwide. Unlike the Meliponinae, the Apinae spread primarily northward from the tropics, *Apis mellifera* probably being native as far north as southern Norway and *A. cerana* as far as northern China and the Pacific maritime provinces of the U.S.S.R. Only in Africa does the original range of *Apis* extend into the south temperate zone, to the southernmost part of the continent. In the tropical asiatic islands, *Apis* ranges south to Java and east to Timor and the Philippines, but did not reach New Guinea, Australia, etc., before *A. mellifera* was introduced.

Taxonomic Account of Apinae

There is only one genus, *Apis,* in the subfamily Apinae. The relatively few species are so impressively similar that there is no need to recognize multiple genera; it is important instead to emphasize the similarity among the species.

Ruttner (1987) followed tradition in recognizing only four "or at most five" modern species of *Apis* although Maa (1953) had recognized many more. Recent work has demonstrated that a few more of Maa's species are valid, but the total number is small. The two genus-group names based on fossils both have the highly characteristic *Apis* wing venation and have no character states that separate them at a genus level from *Apis*. *Synapis* is from the Oligocene, *Hauffapis* from the upper Miocene, both from Germany.

Genus *Apis* Linnaeus

(Figs. 175, 182, 183)

Apis Linnaeus, 1758: 343, 574. Type species: *Apis mellifica* Linnaeus, 1761 = *A. mellifera* Linnaeus, 1758, designation of Latreille, 1810: 439.

Apicula Rafinesque, 1814: 29 (unnecessary replacement for *Apis* Linnaeus; type automatically the same as for *Apis*).

Apiarus Rafinesque, 1815: 123 (unnecessary replacement for *Apis* Linnaeus; type automatically the same as for *Apis*).

Megapis Ashmead, 1904: 120. Type species: *Apis dorsata* Fabricius, 1793, by original designation.

Micrapis Ashmead, 1904: 122. Type species: *Apis florea* Fabricius, 1787, by original designation.

Apis (Synapis) Cockerell, 1907: 229. Type species: *Apis (Synapis) henshawi* Cockerell, 1907 (fossil), by monotypy.

Hauffapis Armbruster, 1938: 37. Type species: *Hauffapis scheuthlei* Armbruster, 1938 = *Apis armbrusteri* Zeuner, 1931 (fossil), designation of Zeuner and Manning, 1976: 243. *Hauffapis* is not a valid name. It was proposed to include several species. No type species was designated by Armbruster; original type designation is required for genus-group names proposed after 1930 (Internat. Code Zool. Nomen., article 13c). The subsequent type designation by Zeuner and Manning was in the synonymy of *Apis* and thus does not validate the name as *Hauffapis* Zeuner and Manning (I.C.Z.N., art. 11c).

Apis (Sigmatapis) Maa, 1953: 556. Type species: *Apis cerana* Fabricius, 1793, by original designation.

As noted by Ruttner (1987), various authors have regarded *A. florea* Fabricius (or its group) as the first branch of a dendrogram of *Apis* species. Information from various sources has led to this conclusion, but one of the formerly most convincing works concerns geotaxis (Jander and Jander, 1970), which is similar (progeotactic) in diverse families of bees (Colletidae to *Apis florea*) but is different (metageotactic) in *Apis dorsata* Fabricius, *cerana* Fabricius, and *mellifera* Linnaeus. (The Janders' study, in Malaysia, was doubtless based on *A. andreniformis* Smith, not on *florea,* which is rare or absent there.) Horn (1975), however, has shown that the progeotaxis of *A. florea* is different from that of *Bombus* and presumably other bees, so that the Janders' conclusion may not have the phylogenetic significance originally attributed to it. But it has been widely overlooked that morphological data on males of the sort regularly used by systematists, published by Snodgrass (1941), show that in certain characters *A. florea* is plesiomorphic relative to *A. cerana* and *mellifera*.

Some plesiomorphies of the *A. florea* group (recognized because they are more like other bees, e.g., anthophorids, as well as other apids such as *Bombus*) are listed below, followed by the corresponding apomorphies of *A. cerana* and *mellifera* in parenthesis:

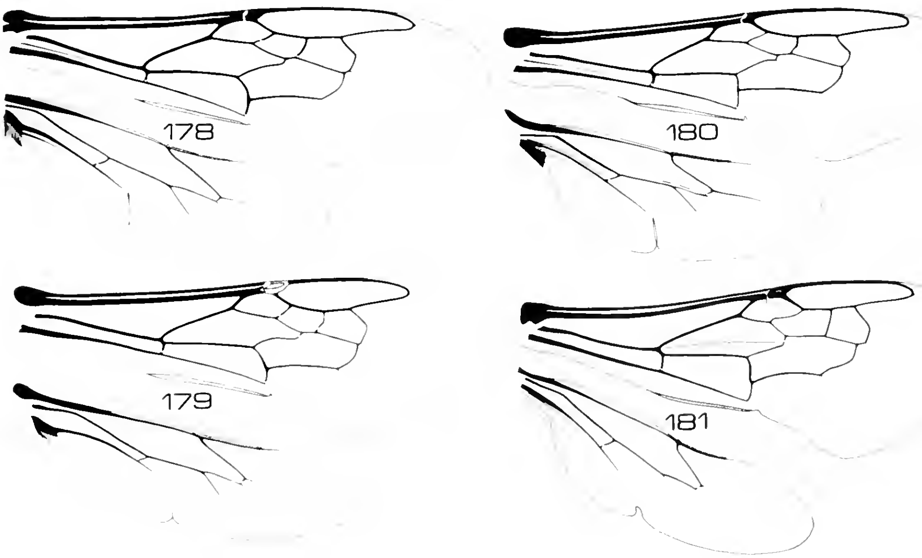
Gonocoxites large and almost meeting (small and widely separated).
S7 and S8 separated by suture (fused medially).
Area behind S8 membranous (a sclerotized, sternum-like region).

Of the remaining species (i.e., other than the *florea* group), *A. cerana* and *mellifera* are obviously close relatives, so that the *dorsata* group must constitute the second branch of a phylogenetic tree, after divergence of *florea*. This viewpoint is supported by the male sternal and genitalic characteristics of *A. dorsata,* which, according to Alexander (in press), are similar to those of *A. mellifera,* but with some features such as gonocoxite size differing in the direction of *A. florea.*

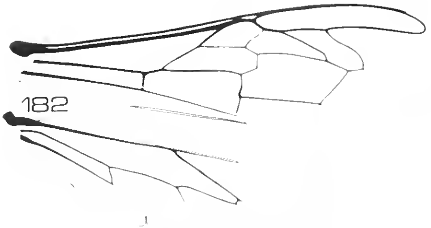
The following is a list of the species that are probably distinct, annotated to explain or give references to accounts justifying specific rank for forms not considered specifically distinct by Ruttner (1987):

florea Fabricius, 1787.
andreniformis Smith, 1858. Sympatric with *florea* in southern China and parts of southeast Asia (Wu and Kuang, 1986, 1987).
dorsata Fabricius, 1793.
binghami Cockerell, 1906. (This is an allopatric insular form from Sulawesi (Celebes). It seems distinctive enough to justify specific separation from *dorsata,* but this is a subjective decision.)
breviligula Maa, 1953. (A Philippine form; comments the same as for *B. binghami.*)
laboriosa Smith, 1871. A Himalayan species probably parapatric with *dorsata* although the two are sometimes found at the same place (Sakagami, Matsumura, and Ito, 1980; Roubik, Sakagami and Kudo, 1985; McEvoy and Underwood, 1988).
cerana Fabricius, 1793.
koschevnikovi Buttel-Reepen, 1906. (This = *vechti* Maa, 1953, and is sympatric with its closest relative, *A. cerana,* in Borneo; Tingek et al., 1988.)
mellifera Linnaeus, 1758.

Additional species of the *cerana* and *mellifera* groups may eventually be recognized.



Figures 178-181. Wings of Euglossinae and Bombinae. 178, *Exaerete smaragdina* (Guérin). 179, *Eufriesea violacea* (Blanchard). 180, *Eulaema cingulata* (Fabricius). 181, *Bombus pennsylvanicus* (Degeer).



Figures 182, 183. 182, Wings of *Apis mellifera* Linnaeus. 183, Genitalia of male of *Apis mellifera* Linnaeus, endophallus omitted; dorsal view at left, ventral at right. P = penis valve, PA = penis valve apodeme, S = gonostylus (#), C = gonocoxite.

SUBFAMILY EUGLOSSINAE

These are the orchid bees of the American tropics, so called because the males are pollinators of the larger orchids of that region. The name is also appropriate because of the large size and gaudy coloration of many of the bees themselves.

Males are attracted to various aromatic compounds (Dodson et al., 1969; Dressler, 1982a). For this reason they have been much collected in recent years. A list of species was given by Kimsey and Dressler (1986).

Description: Moderate-sized (8.5 mm long) to very large (29 mm long), moderately to densely hairy, usually robust bees. Claws of female with basal tooth, of male similar or cleft; *arolia absent;* hind tibial spurs present; strigilis with prong on anterior side; hind basitarsus of nonparasitic females broadest at base, with posterior basal angle or auricle; hind tibia of nonparasitic females greatly expanded with immense corbicula, without penicillum; *hind tibia of males with large hairy slit on upper margin distally,* male hind tibia greatly swollen in nonparasitic genera. Forewing with complete, strong venation, marginal cell less than twice as long as distance from apex to wing tip; stigma minute, vein r arising near middle, margin within marginal cell straight or concave; prestigma shorter than to longer than stigma. *Hind wing without jugal lobe, with comb of bristles in its place* (Figs. 178-180). Clypeus strongly protuberant; labrum much less than twice as wide as long, thus longer than in other apids, sometimes longer than broad. Maxillary palpus two-segmented. Male S8 large, strongly sclerotic, longer than broad, with strong, usually pointed apical process and short, posterolaterally directed apodemes; S7 with apically hairy, sometimes bifid disc and long lateral apodemes (see illustrations in Sakagami and Michener, 1987). Male genitalia strongly sclerotized with distinct gonobase (narrow but almost continuous ventrally); large gonocoxite; small to moderate-sized, sometimes bifid, hairy upper gonostylus; minute to large, hairy, lower gonostylus; and rather small, minutely hairy volsella (Fig. 192).

Larva: With small, pointed dorsolateral tubercles on thoracic segments and at least sometimes on first abdominal segment and a pair of similar tubercles on vertex. Mandible heavily sclerotized, blunt, with large apical concavity on inner surface.

Larvae of *Eufriesea* were described by Michener (1953), of *Euglossa* by Roberts and Dodson (1967).

Nest: Nests are exposed (some species of *Euglossa*) or in cavities in banks, tree trunks, logs, old buildings, etc. Aside from the outside covering of exposed nests, the construction consists principally of brood cells, which are mass provisioned. There are no storage pots or storage cells as in other apid subfamilies. Construction materials are resin *(Euglossa),* resin often mixed with bark fragments *(Eufriesea),* and mud or feces perhaps with resin *(Eulaema).*

Social behavior: Some species are solitary *(Euglossa, Eufriesea).* Some species of *Eufriesea* often produce aggregations of cells in protected places. Some species of *Euglossa* and perhaps all *Eulaema* regularly have several females per nest. The nature of the interactions among them are diverse and little known, but the colonies are seemingly not eusocial.

The genus *Aglae* is cleptoparasitic in the nests of *Eulaema; Exaerete* is cleptoparasitic in nests of *Eulaema* and *Eufriesea.*

These and other aspects of euglossine biology are summarized by Dressler (1982a).

Distribution: Except for *Aglae,* which is known from eastern Panamá to Bolivia, each genus ranges from Mexico to Argentina, mostly in the moist forests.

Relationships among Euglossine Genera

History: The genera of this subfamily, although rather diverse in appearance, are remarkably uniform in many features, and all the nonparasitic species were included in *Euglossa* early in this century by most authors. The opposite extreme was achieved by Moure (1944b) who placed the five genera here recognized in five monogeneric tribes and two subfamilies. Moure himself (1950b) retreated from this extreme, however, recognizing only two tribes, Exaeretini for the cleptoparasites, Euglossini for the others, replacing his two subfamilies of 1944. Since the two cleptoparasitic genera seem to be independently derived from nonparasitic ancestors, there is no justification for these tribes.

Females of the parasitic forms lack corbiculae and other pollen carrying and manipulating structures. The hind tibiae are therefore slender, not excessively broadened as in females of nest-making genera. Interestingly, males of the parasitic genera also have slender hind tibiae, not swollen like those of the non-parasites. Since the hind tibiae of males receive the aromatic compounds collected by males, and this function is probably related somehow to mating behavior, one wonders why males of parasitic genera would not have hind tibiae as enlarged as those of other genera. Perhaps the slender hind tibiae of males are plesiomorphic features preserved in parasitic forms, as occurs in various other groups of parasitic bees.

Analysis: Kimsey (1982, 1987) presented two different cladograms for the genera of Euglossinae. Unfortunately, in presenting the second one, she did not discuss the first cladogram or the reasons for changes. The difference between the two is that in 1982 she placed *Aglae* as the sister group to all other genera, while in 1987 she placed it as the sister to *Eulaema* only. The reason for this change is a change in polarization of a single character, the thickness of S8 in profile.

The following comments refer only to the 1987 cladogram. It is based on 25 characters, 16 of which consist of a character state of a single genus, contrasting with all the rest; these states are presumably autapomorphies. Character states of single genera of course could be plesiomorphic (the other genera being united by the alternative synapomorphies) but Kimsey's interpretations (that they are derived) seem reasonable in all cases. The remaining 9 characters involve synapomorphies and are therefore potentially useful in cladogram construction. These are her characters 1, 3, 4, 5, 9, 14, 16, 19, and 25. Kimsey correctly emphasizes that, because most euglossine characters have no homologues in other subfamilies or families of bees, polarization based on out-group comparisons is often impossible. For example, on the outer surface of the mid tibia of males there are velvety areas whose number, size, and shape provide generic character states (Kimsey's characters 6 and 7). And on the hind tibia of males there is a hairy slit (Kimsey's characters 13-15) into which the aromatic compounds collected by males are placed. No homologues of these structures are found in other bees. If polarization is to be done, it must be by methods other than out-group comparisons. Kimsey uses the notion that a widespread character state is plesiomorphic relative to a less widespread alternative, but as is well known, this is often unreliable. I can see no logical basis for concluding that two adjacent midtibial velvety areas, one large and one small, is ancestral to other arrangements, or that a large, long hind tibial slit is ancestral to a short one. On bases such as these, I consider that polarization of Kimsey's characters 3, 5, 9, and 14 is in doubt.

The single supposed synapomorphy uniting *Euglossa* and *Exaerete* in Kimsey's cladogram is 14, curvature of the hind tibial slit of the male. Since both its polarity and the homology of the rather different looking curvature is in doubt, the reasonable course is to consider that *Euglossa, Exaerete,* and the remaining genera are connected at a trifurcation rather than showing the weakly justified additional cladistic structure. Synapomorphies 19 and 25, as well as 16 with a reversion for *Aglae,* seem to unite the three remaining genera, but the four synapomorphies used by Kimsey to unite *Aglae* and *Eulaema* as the sister group to *Eufriesea* turn out to be dubious. Numbers 3, 5, and 9 are not reliably polarizable, and 1 is not a unique synapomorphy for it is a loss (of two palpal segments) that occurs also in some species of *Exaerete;* it could have arisen independently in *Aglae* and *Eulaema.* The conservative course, showing only what is not too speculative, is to unite *Aglae, Eufriesea,* and *Eulaema* at an unresolved trifurcation. Thus the best cladogram now possible can be summarized thus: *(Euglossa, Exaerete, (Eufriesea, Eulaema, Aglae)).* This is not as satisfying as a fully dichotomous cladogram but better demonstrates our current ignorance.

Taxonomic Account of Euglossinae

This subfamily contains five genera that are separable by the key given below. For the most part they are easily separable in general appearance also: *Exaerete* species are large, all green, not conspicuously hairy; *Aglae* is slender, blue; and *Euglossa* is small and usually brilliantly metallic (but there are a few dull colored species). *Eufriesea* and *Eulaema* are similar superficially, large and conspicuously hairy, except that some species of *Eufriesea* are less hairy and brilliantly metallic, resembling *Euglossa*. There are cases of probable Müllerian mimicry involving *Eufriesea* and *Eulaema* (Dressler, 1979) so that close examination may be needed to recognize the usually rarer *Eufriesea*.

Key to the Genera of Euglossinae
(modified from Kimsey, 1987)

1. Hind tibia three or more times as long as broad in both sexes; female hind tibia somewhat inflated, without corbicula; cleptoparasitic species 2

—Hind tibia twice as long as broad or less in both sexes; female hind tibia flat and shield-like with enormous corbicula (Fig. 188); nonparasitic species 3

2. Hind femur swollen and usually denticulate ventrally; hind tibia curved and expanded apically; scutellum dorsally convex, with sublateral tubercle or welt . . . . *Exaerete*

—Hind femur slender and unmodified; hind tibia straight and apically narrowed; scutellum flat. . . . . *Aglae*

3. Labrum whitish with two large, dark oval spots; male hind tibial slit short, not reaching apical margin of tibia, and basally curved; male midtibia with two, or less commonly 1 or 3, small felty patches in basal end of large patch; female with median, black scutellar tuft . . . . *Euglossa*

—Labrum dark in color; male hind tibial slit long, reaching apical margin, broad and not curved basally; male midtibia with one relatively large basal felty patch adjacent to large patch; female with *(Eulaema)* or without *(Eufriesea)* scutellar tuft. 4

4. Labial palpus 4-segmented; face metallic without white markings; clypeal ridging various, usually without single medial ridge. . . . . *Eufriesea*

—Labial palpus 2-segmented; face black or brown, often with white markings; clypeus with single strong medial ridge . . . . *Eulaema*

Genus *Eufriesea* Cockerell
(Figs. 174, 179, 192)

Plusia Hoffmannsegg 1817: 52 (not Hübner, 1806). Type species: *Plusia superba* Hoffmannsegg, 1817 (monobasic).

Eumorpha Friese 1899: 126 (not Hübner, 1807). Type species: *Euglossa pulchra* Smith, 1854, by designation of Cockerell, 1908: 41.

Eufriesea Cockerell 1908: 41 (new name for *Eumorpha* Friese, 1899). Type species: *Euglossa pulchra* Smith, 1854 (autobasic).

Euplusia Moure 1943: 189 (new name for *Plusia* Hoffmannsegg, 1817). Type species: *Plusia superba* Hoffmannsegg, 1817 (autobasic).

This genus, most species of which were placed in *Euplusia* from 1943 to about 1980, was revised by Kimsey (1982). She showed (1979b) that the broad, flat scutellum formerly thought to separate *Eufriesea* from *Euplusia* cuts across natural groups and is not a useful generic or subgeneric character state. There are about 52 species, many of them brilliantly metallic but others with colorful yellow and black hairs and superficially resembling *Eulaema* except for weak metallic reflections at least on the face.

Nests consist of linear or branched series of cylindrical cells of resin often mixed with bark fragments. They are located in protected crevices or cavities, under overhangs of rocky banks, under buildings, in pre-existing burrows in wood, in termite nests, etc. Although such nests are sometimes aggregated, there is no evidence of social organization. Kimsey (1982) summarizes what is known about the nests.

Genus *Aglae* Lepeletier and Serville

Aglae Lepeletier and Serville, 1825: 105. Type species: *Aglae caerulea* Lepeletier and Serville, 1825 (monobasic).

This is a monotypic genus of relatively slender, steel blue bees reported to be cleptoparasites of *Eulaema*. It is the most distinctive euglossine genus, as indicated by Kimsey (1982) who considered it the sister group of all the other genera, and Kimsey (1987) who documents its many autapomorphies. In the latter work she regards it as the sister group of *Eulaema*, but see my comments above on relationships among the genera.

Genus *Euglossa* Latreille

(Fig. 188)

Euglossa Latreille, 1802a: 436. Type species: *Apis cordata* Linnaeus, 1758, by designation of Blanchard, 1849: 219.

Cnemidium Perty 1833: 148, not Goldfuss, 1826. Type species: *Cnemidium viride* Perty, 1833 (monobasic).

Euglossa (Glossura) Cockerell 1917b: 144. Type species: *Euglossa piliventris* Guérin, 1845, by original designation.

Euglossa (Euglossella) Moure 1967: 401. Replacement for *Cnemidium* Perty, 1833. Type species: *Cnemidium viride* Perty, 1833 (autobasic).

Euglossa (Dasystilbe) Dressler, 1978: 193. Type species: *Euglossa villosa* Moure, 1968, by original designation.

Euglossa (Glossurella) Dressler, 1982b: 131. Type species: *Euglossa bursigera* Moure, 1970, by original designation.

This genus consists of moderate-sized (the smallest of Euglossinae) to rather large, usually brilliantly metallic species. With 103 species described, it is the largest genus of the subfamily. Dressler (1978) provided a classification of the species, placing them in 12 species groups organized into four subgenera (*Dasystilbe* Dressler, *Glossura* Cockerell, *Euglossa* Latreille, s. str., and *Euglossella* Moure). The subgenera are seemingly natural groups but there is some intergradation among them. Later Dressler (1982b) elevated another group to subgeneric status under the name *Glossurella*. As I have nothing to dd to Dressler's classification, further comment seems unnecessary.

Nests of some species are constructed of resin and located on stems or twigs in the open. The cells are packed into the interior of a more or less spherical resinous envelope. Other species construct cells, isolated or in small clumps, in small cavities in tree branches or trunks, earthen banks, or in buildings. Some nests are built and occupied by lone females while others contain several females seemingly living more or less cooperatively (Roberts and Dodson, 1967).

Genus *Exaerete* Hoffmannsegg

(Figs. 174, 178)

Exaerete Hoffmannsegg, 1817: 53. Type species: *Apis dentata* Linnaeus, 1758 (monobasic).

Chrysantheda Perty, 1833: 147. Type species: *Chrysantheda nitida* Perty, 1833 (=*Apis dentata* Linnaeus, 1758) (monobasic).

Caliendra Gistel 1848: viii. Type species: *Chrysantheda nitida* Perty, 1833 (=*Apis dentata* Linnaeus, 1758) (autobasic) (unnecessary replacement for *Chrysantheda* Perty).

This is a genus of large, brilliant green, cleptoparasites of *Eufriesea* and *Eulaema*. The six species were revised by Kimsey (1979a). Its closest relative remains undetermined, although Kimsey (1987) places it as a sister group of *Euglossa*.

Genus *Eulaema* Lepeletier

(Fig. 180)

Eulaema Lepeletier, 1841: 11. Type species: *Apis dimidiata* Fabricius, 1793 (=*Apis meriana* Olivier, 1789) by designation of Taschenberg, 1833: 85.

Eulaema (Apeulaema) Moure 1950b: 184. Type species: *Eulaema fasciata* Lepeletier, 1841 (=*Centris cingulata* Fabricius, 1804), by original designation.

This genus was at one time called by the name *Centris* Fabricius (1804) (Sandhouse, 1943; Michener, 1944) because of an early and usually ignored type designation for *Centris*. However, the usual meanings of the names *Centris* and *Eulaema* have been preserved, thanks to Opinion 567 of the International Commission on Zoological Nomenclature. Sandhouse (1943) lists two unjustified emendations of the name *Eulaema*.

This genus consists of about 13 species of large bees, all black or with conspicuous patterns of yellow or orange hair, sometimes with limited metallic tints, usually on the metasoma.

Nests consist of clusters of oval cells made of mud, feces, and probably resin, located in cavities in soil, banks, tree trunks, etc. Often more than one female works simultaneously in a single nest, but details of interactions among individuals remain little known (Michener, 1974).

The genus was revised by Moure (1950b) and Dressler (1979). Moure (1950b) gives the distinctions in detail between the subgenera *Eulaema* s. str. and *Apeulaema*. R. L. Dressler (in litt.) indicates that there are four species groups; it is not clear whether any of them justify subgeneric status.

SUBFAMILY BOMBINAE

This subfamily consists of the bumble bees. Except for the parasitic species, all are primitively eusocial. The approximately 250 species are morphologically monotonous compared to the Euglossinae and especially to the Meliponinae. Nonetheless there is interesting diversity in a few structures—the male genitalia, stings, mandibles, etc. Most of the classification of the group is based on the male genitalia.

Description: Middle sized (9 mm long) to very large (22 mm long), robust, hairy bees. Claws of female cleft; arolia small but present; hind tibial spurs present. Strigilis with prong or strong elevation on inner margin. Hind tibia and basitarsus of female as in Apinae except in social parasites *(Psithyrus)*. Forewing with complete strong venation; marginal cell somewhat longer than distance from its apex to wing tip; stigma

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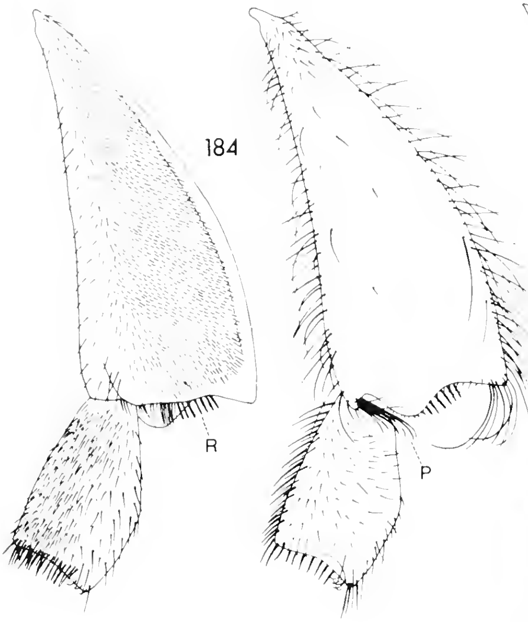
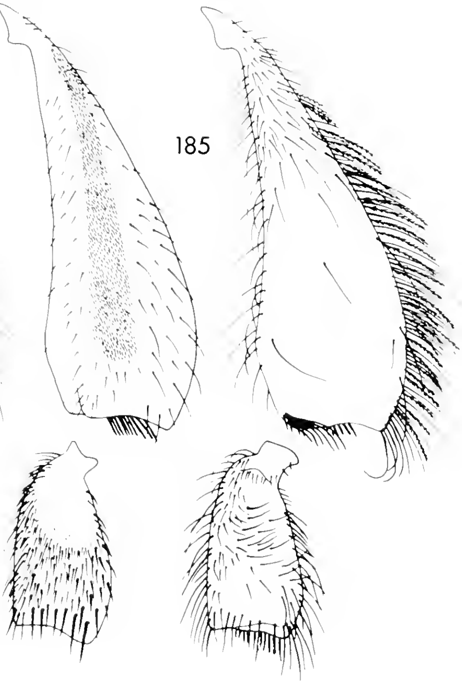


185



Figures 184-185. Hind tibiae and basitarsi of meliponine workers, inner surface (without marginal hairs) at left. 184, *Plebeia (Plebeia) frontalis* (Friese). 185, *Trigona (Trigona) amalthea* (Olivier). R = rastellum, P = penicillum.

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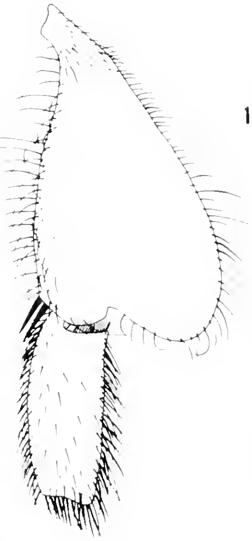

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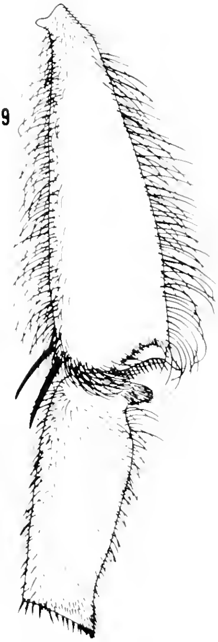

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Figures 186-189. Hind tibiae and basitarsi of female Apidae (workers of social species), outer surfaces. 186, *Trigonisca longitarsis* (Ducke). 187, *Partamona* near *cupira* (Smith). 188, *Euglossa imperialis* Cockerell. 189, *Bombus pennsylvanicus* (Degeer).

Figures 190, 191. Dorsal views of scutellum of meliponine workers. 190, *Scaptotrigona mexicana* (Guérin). 191, *Partamona* near *cupira* (Smith).

small, little if any longer than prestigma, vein r arising near or beyond middle, margin within marginal cell straight or usually concave. *Hind wing without jugal lobe* (Fig. 181). Clypeus slightly convex, weakly to moderately protuberant. Maxillary palpus two segmented. Male S8 well developed, sclerotized, with median apical, truncate or emarginate, hairy process, body of sternum not thickened and excavated as in most Euglossinae, apodemes distinct, directed laterally or posterolaterally. S7 with disc rather broad, like preceding sterna but smaller, apical margin rounded or slightly bilobed (for this and associated structures, see series of illustrations by Ito, 1983, 1985). Male genitalia well sclerotized with distinct gonobase broadly interrupted midventrally; large gonocoxite; short and broad, often variously angulate, gonostylus (squama); and broad, hairy volsella attaining the apex of the gonostylus or exceeding it and also extending far toward the base of the gonocoxite on the lower surface.

The homologies and terminologies for the male genitalic parts have been confusing in Bombinae and are the subject of a separate section below.

Larva: With small pointed dorsolateral tubercles on thoracic segments. Mandible heavily sclerotized, apex bluntly rounded or minutely denticulate, acute in *Psithyrus,* with small preapical tooth on upper margin, with large apical concavity on inner surface.

Larvae have been described and illustrated in detail by Ritcher (1933), Cumber (1949), Michener (1953), Stephen and Koontz (1973), and others. There is significant variability among them that may clarify relationships among groups of *Bombus.*

Nest: A summary of nest architecture is given by Michener (1974). Nests are commonly in rodent nests, bird nests, cavities under bunch grass or other vegetation, etc. There may or may not be a thin wax (and pollen) covering over the nest. The cells are totally different from those of all other bees, for they are closed (sometimes incompletely) but grow with the growing larvae, commonly contain several eggs and later larvae, develop a separate bulge for each larva, and may even become divided into several cells as the larvae mature. Katayama (1989) has discussed such cells and their possible evolutionary origin in detail. Larvae are fed progressively, either by food introduced through the tops of the cells or by food pressed in through pockets at the bases of the cells and forming the cell floors. Both methods may occur in the same species, usually at different seasons. Both honey and pollen are stored in pots separate from brood cells; they are often made of old cocoons but may be wholly constructed by the bees. In *B. mendax* Gerstacker, unlike most species, the cocoons are wholly destroyed and honey storage is in a series of crowded (therefore sometimes hexagonal) pots separate from the pollen pots (Haas, 1976).

Social behavior: Except for the social parasites, the Bombinae are all eusocial. Their colonies are usually annual. Each is started by a single queen; in temperate and arctic climates this is in the spring. Her early progeny are all workers, usually much smaller than the queen but morphologically similar. Males and young queens are produced later; they mate, the colony fades away, and the young queens hibernate until the following spring. In the tropics this sort of cycle is sometimes modified, but it never attains the major features of highly social bees whose queens never live alone and are morphologically very different from workers. Other features of *Bombus* behavior are described by Michener (1974), Free and Butler (1959), Morse (1982) and others.

A few species of Bombinae are workerless social parasites in nests of species of *Bombus.* Most of the parasites are in the genus *Psithyrus;* females of this genus lack the pollen gathering and manipulating structures characteristic of *Bombus* and the apex of the metasoma is more pointed than in *Bombus* and curled downward, housing a powerful sting. The female social parasite dominates or kills the host queen and may become, in essence, the queen of a colony consisting of herself and workers of the host species. Fisher (1987) gives a recent study of one species with references to older works.

Distribution: Bumble bees are for the most part adapted to cool climates and thus are uncommon in places where Euglossinae are common. They are most abundant in the cool temperate parts of the holarctic region, with many more species and subgenera in Eurasia than in North America. Williams (1985) indicates that there are 199 species in Asia, 58 in Europe, 41 in North America, and 43 in Mexico, Central and South America. Northward, they range in small numbers as far as there is land. Southward they occur in North Africa but not in subsaharan Africa. There is one specimen of what appears to be a South American species reported from Cameroon (Tkalců, 1966); it was no doubt mislabeled or introduced. To the east they are numerous in the Himalayas but absent below 1000 m altitude in India (Williams, 1985); to the southeast a few species occur in the mountains of Southeast Asia, as far as Java and the Philippines, but they are absent from the lowlands. In the Western Hemisphere there is a rather small *Bombus* fauna all the way to Tierra del Fuego, mostly in montane areas or temperate latitudes, but unlike the situation in Africa and Asia, a few species occur in the lowland moist tropics.

It is curious that close to the center of diversity [and the area where the most plesiomorphic species occur, according to Williams (1985)], i.e., the Palearctic region, the lowland tropics seem to have been an absolute barrier to Bombinae. Moreover, in spite of widespread mesic Pleistocene conditions in what is now the Sahara, they did not reach the mountains and highlands of East Africa, as have other mesic northern groups like *Andrena*. On the other hand, in the Western Hemisphere, with poorer northern bombine diversity, they range almost as far south as there is land, and occur in the lowland tropics, e.g., the Amazon Valley.

Relationships among Bombine Genera and Subgenera

History: Traditionally two genera of Bombinae have been recognized, *Bombus* and *Psithyrus,* the latter consisting of social parasites of the former. Indeed, because of their divergent habits and the structures relating to pollen collecting, or lack of them in *Psithyrus,* some older authors (Ashmead, 1899; Friese, 1923) placed *Psithyrus* in a different subfamily or family from *Bombus.*

As to *Bombus,* although various subgeneric names had been proposed earlier (starting with Dalla Torre, 1880), and Robertson (1903) had proposed *Bombias* as a genus, it was Skorikov (1922) who divided *Bombus* into numerous genera. Most authors did not follow him, for the genera were hard to tell apart. Milliron (1961) divided *Bombus* into three genera and Tkalců (1972) recognized eight genera. These genera, likewise, are hard to distinguish, intergrade, and have little usefulness. The smaller supraspecific units, subgenera or species groups, however, based primarily on male genitalic character states, are more stable and for a *Bombus* specialist are useful. There are about 35 such units in the genus *Bombus,* all with subgeneric names. Some of them such as *Fervidobombus* are still quite diversified and may not represent unified recognizable groups. Ito (1983, 1985) gives a detailed and useful historical account, while a briefer one is provided by Richards (1968). Given the morphological homogeneity of *Bombus,* most authors have continued to use it in the traditional broad sense. Efforts to find a few recognizable units have failed because of intergradation and discordance in character state distributions, a problem that plagues even some of the finer divisions (subgenera or species groups). Moreover, the species of *Bombus* s.l., as noted above, are very much alike, not superficially separable into genera or subgenera, and have many distinctive behavioral attributes. Richards (1968) described the 35 subgenera that he recognized, gave keys, and thus for the first time provided a worldwide classification for subgenera of *Bombus.*

Many authors have speculated on the relation of *Psithyrus* to *Bombus.* Because of the superficial similarity of some Palearctic *Psithyrus* to their hosts, the suggestion that *Psithyrus* species arose polyphyletically from different groups of *Bombus* was made, for example by Richards (1927). The similarities of *Psithyrus* species would thus have to be a result of convergence. Recent studies by Ito (1983, 1985), Ito and Sakagami (1985), and Williams (1985) placing emphasis on male genitalia and hidden sterna, which are unlikely to evolve convergently, show decisively that *Psithyrus* is a monophyletic unit related to certain groups of *Bombus.* Electrophoretic studies of genetic relationships support the cohesiveness among *Psithyrus* species (Pamilo, Pekkarinen and Varvio, 1987; Obrecht and Scholl, 1981).

Recent studies by Ito (1983, 1985) and Williams (1985) provide a wealth of information as well as interpretations. Ito gives excellent illustrations of male sterna and genitalia of nearly all groups. His analyses (based on genital character states of males) are phenetic; they show six groups of *Psithyrus* together but in the midst of *Bombus* groups, and closest to groups called *Mucidobombus, Eversmannibombus,* and *Orientalibombus.* A cladistic study of the problem by Ito and Sakagami (1985) indicates a relationship of *Psithyrus* to *Orientalibombus* and some species of *Fervidobombus,* especially *Bombus dahlbomii* Guérin.

Williams (1985) developed a cladogram for all groups of Bombinae, based on male genitalic character states. He utilized 14 characters, with 2 to 33 states per character. Polarities were judged by comparison with Euglossinae, although the characters with 24, 27, and 33 states were not ordered; they are branching characters.

Although a different method of coding, with more characters and fewer states per character, would seem desirable and would probably permit better polarization, Williams' study is interesting and valuable and his major phylogenetic conclusions are probably correct. *Mendacibombus* appears in his study as the sister group of all other Bombinae; *Psithyrus* is the next branch, the sister group of all but *Mendacibombus.* On this basis, following the practice of those who base classifications on cladograms only, Williams recognized three genera, *Mendacibombus, Psithyrus,* and *Bombus.* Ito (1983, 1985) also recognized *Mendacibombus* as a distinctive group, but in all but one of his phenograms it was closely associated with other groups of *Bombus.* Richards (1968) did not consider *Mendacibombus* unusual.

I regard Williams' cladogram as important but, as his title and introduction indicated, preliminary. His classificatory response seems to me premature. First, *Mendacibombus* is recognized on his cladogram by a single synapomorphy plus three plesiomorphies that distinguish it from the rest of the subfamily. Furthermore, about two thirds of all the other segments of the tree are also defined by single synapomorphies. Thus while the tree is in general convincing because some of the major groups of subgenera recognized by other authors tend to come out together, it is no doubt subject to change when other characters and taxa are added to the study. One objective of classification is stability; to base a classification on such fragile evidence is a mistake. Williams indicates (in litt., 1989), however, that the male genitalia of numerous species not available to him in 1985 have modified his cladogram in detail but the general form of the tree remains about the same.

Second, Williams (in litt.) reports that with other species now available, he finds *Mendacibombus* to represent more than one clade; it is therefore paraphyletic. If it were to be subdivided, one would have genera scarcely distinguishable from one another.

Third, Williams' cladogram is based exclusively on character states of male genitalia. A cladogram to be used as a basis for classification should be based on all available synapomorphies, or at least not on one single set of characters that in theory might exhibit convergences. Williams defends his limited character set on the basis that the genitalic character states selected are those likely to be more conservative than those involving other structures that do not fit the female securely to prevent interruption of copulation. In short, he argues that his characters are unlikely to exhibit convergence; he is probably right.

Fourth, lack of characters is illustrated by branches *(Mucidobombus, Rhodobombus)* that lack synapomorphies. From the viewpoint of Williams' cladogram, these groups should be regarded as paraphyletic. It should be noted, however, that Williams' cladogram was based on certain species, and that the traditional subgeneric names were then added; he is not responsible for these "subgenera."

Fifth, the genitalic characters themselves often involve minor changes whose polarity is subject to judgement. *Bombus (Mendacibombus) mendax* Gerstaecker not only looks like a *Bombus* but its genitalia are similar to those of other *Bombus.* Polarization of characters by outgroup comparison using Euglossinae is not only difficult, but may be deceptive since most similarities of Euglossinae and Bombinae are due to plesiomorphies, and the Euglossinae have many more autapomorphies (at the subfamily level) than do the Bombinae. Thus comparison of the states of a character is likely to be between a plesiomorphic state in Bombinae and a derived homologue in the Euglossinae.

Finally, I do not believe that the unified and homogeneous group *Bombus,* which has an enormous number of common character states and for which predictions concerning characteristics of little-studied species can be made, is any less useful because it can be shown to have given rise to another genus. In short, paraphyletic taxa are sometimes useful. One needs to know that they are paraphyletic, but the classification should often reflect other things than the cladistic pattern.

Given the problems described above, and noting that very intensive studies of Bombinae have been made and that additional useful characters are hard to find, I believe that those who rigidly wish classifications to be redundant, i.e., to duplicate information in cladograms, have no choice but to incorporate *Psithyrus* into *Bombus.* This would mean that many statements about *Bombus* must contain alternatives—either with a corbicula or without, with a rastellum or without, etc.

The alternative which I follow is to recognize a paraphyletic genus *Bombus.* I think this solution is correct not only currently, until a cladogram with more characters is devised, but also in the long term, because a classification that simply duplicates the cladistic pattern is redundant. The classification should be as useful as possible, and thus reflect information beyond that in the cladogram, in this case the phenetic distinctness of *Bombus* s.l. from *Psithyrus.*

Genitalia of the Bombinae

Partly because the Bombinae were among the first bees whose male genitalia were investigated, and partly because of problems in recognizing the homologies of certain parts, special terminologies often have been used in describing bombine genitalia. The greatest problems concern the identity of the volsella.

At one stage I believed that the structure called the volsella by Williams (1985) was in fact the lower branch or lamina of the gonostylus. In Bombinae it extends apicad and is hairy like a gonostylus, and its base is not very different from the base of the lower gonostylus of halictids like *Nomia melanderi* Cockerell. The presence of two gonostyli (really upper and lower and largely separate gonostylar structures) is widespread and presumably plesiomorphic in anthophorid bees, and seemed to explain the two apical processes from the bombine gonocoxite. Two gonostyli are well developed and distinct, for example, in *Tapinotaspis* (Exomalopsini), *Epicharis* (Centrini), *Diadasia* (Emphorini) in the Anthophorinae; in *Nomada* and other Nomadinae; and in *Manuelia postica* (Spinola) but not other *Manuelia,* in the Xylocopinae. As indicated by Sakagami and Michener (1987), *Manuelia* is close to the ancestor of the Apidae. It therefore would not be surprising to find the same structures in the apids that have most plesiomorphies, i.e., the Bombinae and Euglossinae.

Euglossinae (e.g., *Eufriesea pulchra* Smith, Fig. 192) clearly have the two gonostyli. In addition, however, they have a minutely hairy sclerite more basad along the lower inner margin of the gonocoxite; it appears to represent the volsella. In *Epicharis elegans* Smith (Anthophoridae) the two gonostyli are also clearly present, and in addition the volsella, as a separate small sclerite with a long, minutely hairy, apical process. The volsellae of *Eufriesea* and *Epicharis* cannot represent the lower gonostyli, which are easily recognizable; these volsellae are clearly homologous to the volsella of Bombinae (Fig. 193) as recognized by Williams. There are not two distinct gonostyli in Bombinae, but the gonostylus often appears bilobed, with a mesal and an apical projection, which may represent the two gonostyli of some other bees. The volsella was correctly identified by some earlier authors, e.g., Boulangé (1924, as voselle) and Smith (1970) who considers the structure in Bombinae to be the cuspis of the primitive chelate volsella.

I here accept the terminology of Williams (1985); its relation to certain other terminologies of bombine genitalia is indicated in Table 5.

TABLE 5. Terminology of bombine male genitalia.

Snodgrass (1941)	Michener (1944)	Richards (1968)	Ito (1985)	Williams (1985)
Basal ring	Gonobase	Cardo	Gonobase	Gonobase
Lamina parameralis	Gonocoxite	Stipes	Gonocoxite	Gonocoxite
Paramere	Gonostylus	Squama	Squama	Gonostylus
Paramere	Gonostylus	Lacinia	Gonostylus	Volsella
Dorsal plate of penis	Spatha	Spatha	Spatha	Spatha
Sagitta	Penis valve	Sagitta	Penis valve	Penis valve

Fossil Bombinae

None of the fossils that have been attributed to Bombinae can be reliably placed there except probably the Oligocene and Miocene species placed in *Bombus* (Zeuner and Manning, 1976).

Taxonomic Account of Bombinae

As indicated above, I recognize two bombine genera, with the clear understanding that one of them, *Bombus*, is paraphyletic.

Key to the Genera of Bombinae

1. Female hind tibia with corbicula and rastellum; hind basitarsus with strong auricle; apex of metasoma of female not curved downward, S6 without carinae; hind tibia of male often bare and shiny; gonostylus and volsella usually hardened, volsella often not greatly exceeding gonostylus, usually variously angulate . . . . *Bombus*

—Female hind tibia convex, hairy on outer surface, so that corbicula is absent; rastellum absent; hind basitarsus without auricle; apex of metasoma of female curved downward, S6 with lateral carina; hind tibia of male with abundant short dark hair; gonostylus and volsella more membranous, volsella extending well beyond gonostylus, simple, flat, without angles or teeth . . . . *Psithyrus*

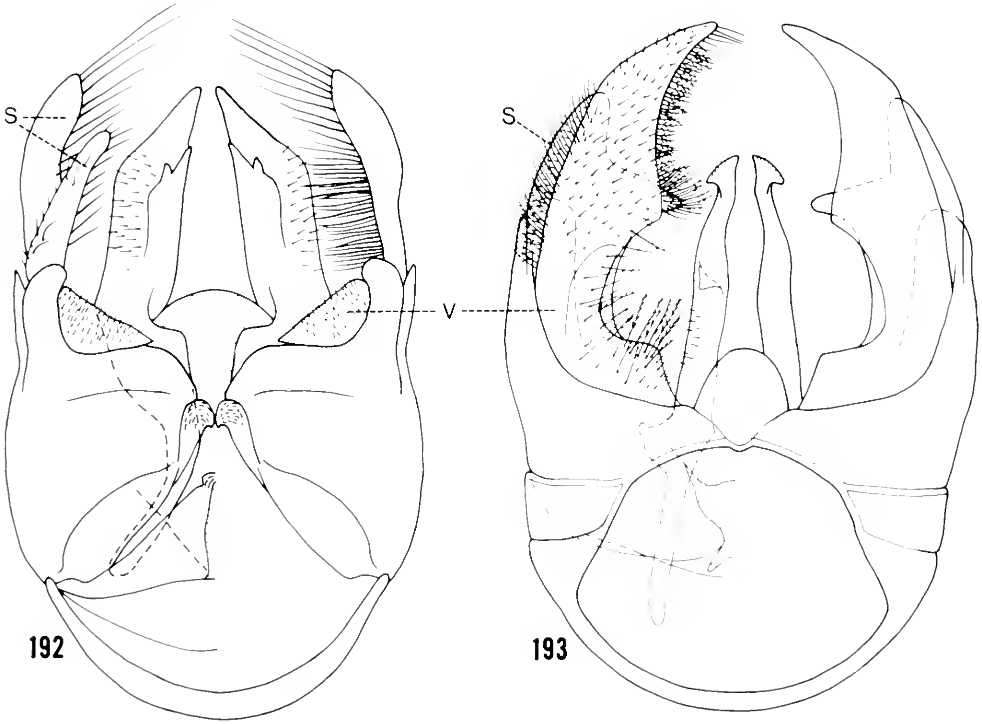
Genus *Bombus* Latreille

(Figs. 173, 177, 181, 189)

Bombus Latreille, 1902b: 385. Type species: *Apis terrestris* Linnaeus, 1758 (monobasic).

The enormous list of synonymous or subgeneric names has been given elsewhere (Richards, 1968; Ito, 1983, 1985; Williams, 1985). It seems unnecessary to repeat here these lists, type species, etc. The following are names proposed since Richards' paper:

Pyrobombus (Festivobombus) Tkalců, 1972: 27. Type species: *Bombus festivus* Smith, 1861, by original designation.



Figures 192, 193. Ventral views of male genitalia. 192, *Eufriesea pulchra* (Smith), lower gonostylus omitted on right side. 193, *Psithyrus variabilis* (Cresson). S = gonostylus, V = volsella.

Bombus (Digressobombus) Laverty, Plowright and Williams, 1984: 1051. Type species: *Megabombus digressus* Milliron, 1962, by original designation.

Bombus (Brachycephalibombus) Williams, 1985: 247. Type species: *Bombus brachycephalus* Handlirsch, 1888, by original designation.

Bombus (Dasybombus) Labougle and Ayala, 1985: 49. Type species: *Bombus macgregori* Labougle and Ayala, 1985, by original designation.

The scope of this genus is indicated above in the section on relationships among bombine genera and subgenera. Its distribution is that of the subfamily. It contains all the nonparasitic species of the subfamily, and in addition a very few parasitic species (Richards, 1973; Yarrow, 1970).

The named subgenera are less different from one another than are subgenera in most groups of bees. In fact, the homogeneity of the species in the genus is outstanding. These bees have been carefully studied to find group character states by diverse specialists (Richards, 1968; Sakagami and Ito, 1981; Ito, 1983, 1985; Williams, 1985). I do not consider recognition of the subgenera essential. The only key (except regional ones) is that of Richards (1968).

Further studies of behavioral characters like those of Hobbs (1964), Sakagami (1976) and Katayama (1989) may help in the delineation of more useful units. Such studies are needed for many more groups. Katayama (1989) recorded in admirable detail the often subgenus-specific behaviors in cell construction and egg laying, but the sampling of species was necessarily limited. Particularly, more data are needed on the earliest stages of colony development, when some of the most important characters are manifest.

As biochemical methods of determining genetic relatedness have evolved, various authors have used such methods to indicate relationships among species of *Bombus*. Such studies usually reinforce the groups or subgenera based on morphological differences, showing that most of these groups are useful monophyletic or paraphyletic units (Pamilo, Pekkarinen and Varvio, 1987).

Important regional treatments of species are by Franklin (1912, 1913), Krueger (1917), Burks (1951), Moure and Sakagami (1962), Thorp, Horning and Dunning (1983), Labougle (1990) and many others.

Genus *Psithyrus* Lepeletier
(Figs. 173, 193)

Psithyrus Lepeletier, 1832: 373. Type species: *Apis rupestris* Fabricius, 1793, by designation of Curtis, 1833: pl. 468.

As for *Bombus*, the subgeneric (really synonymous) names seem not worth listing as they have been listed by Ito (1983, 1985) and Williams (1985). The following is a recent addition to the list:

Citrinopsithyrus Thorp, in Thorp, Horning and Dunning, 1983: 50. Type species: *Apathus citrinus* Smith, 1854, by original designation. (Replacement for *Laboriopsithyrus*, the type species of which turns out to be an anthophorid bee of the genus *Habropoda*.)

As shown by both Ito and Williams, the subgenera in *Psithyrus* are even more similar than those of *Bombus;* I consider them synonyms of *Psithyrus*. They were treated in detail by Popov (1931).

As indicated earlier, *Psithyrus* consists of social parasites in the nests of *Bombus,* and lacks a worker caste.

Psithyrus is a holarctic genus found in the areas where *Bombus* is most abundant, but not ranging into the high arctic or into the mountains of southeast Asia and nearby islands, and in the New World, probably not ranging south of Guatemala.

Regional treatments of *Psithyrus* species are usually included in the regional accounts of *Bombus* cited above; see also Popov (1931).

ACKNOWLEDGMENTS

For the loan of type material important for this study, I am indebted to Frank Koch, Museum für Naturkunde der Humboldt Universität, Berlin. David W. Roubik of the Smithsonian Tropical Research Institute sent preparations of meliponine mouthparts as well as males of various species not otherwise available to me.

Michael Prentice and Howell V. Daly of the University of California sent me copies of their as yet incomplete manuscript (and illustrations) on the relationships of the subfamilies of Apidae. This work was of great value in modifying my ideas on this subject.

S. F. Sakagami of the University of Hokkaido, J. M. F. Camargo of the Faculdade de Filosofia, Ciencias e Letras, Universidade de São Paulo, and Ricardo Ayala of the Estacion Chamela, Universidad Nacional Autonoma de México, reviewed the section on Meliponinae, made many useful suggestions, and called my attention to characters than I had not previously recognized.

Byron Alexander of the University of Kansas reviewed the section on Apinae and made useful suggestions.

Robert L. Dressler of the University of Florida provided helpful information for my treatment of Euglossinae; Paul Williams of the Natural History Museum London reviewed the section on Bombinae and has been most helpful in providing unpublished materials on this subfamily, in patiently correcting my misinterpretation of homologies of bombine male genitalia, and in explaining his classification of this group.

Analyses using Hennig 86 were by James Pakaluk; those using PAUP were in collaboration with Stephen Reyes and Arturo Roig-Alsina; the use of PAUP 3.0 was through J. S. Ashe.

Joetta Weaver and Virginia Ashlock have done excellent secretarial and editing work, which I much appreciate.

This study is a product of National Science Foundation Grant BSR 87-16817.

APPENDIX: *TRIGONA GENALIS* FRIESE, A HITHERTO UNPLACED NEW GUINEA SPECIES

by Charles C. Michener and Shôichi F. Sakagami

In his seminal work on the classification of Old World stingless bees (Meliponinae), Moure (1961) did not include certain species from New Guinea. Two of these (*T. genalis* Friese and *atricornis* Smith) are the principal subject of this Appendix. Although these two species are deceptively similar, the first is so unusual that each of us independently described it in manuscript as a new subgenus of *Trigona,* here named *Papuatrigona* Michener and Sakagami. *T. atricornis* also is unusual within its group. In the body of the text it is included by CDM in the subgenus *Heterotrigona,* but as indicated there, SFS places it as an unusual species of *Platytrigona.* It does not agree with Moure's characterization of *Platytrigona,* the definition of which must be broadened to include *T. atricornis.*

Most of the descriptive material on the subgenus *Papuatrigona* is the work of CDM; the discussion and comparative material is by both of us, and the specific descriptions and illustrations (Figs. 194 to 219) are by SFS. The subgenus is incorporated into the body of this work; the Appendix provides added details including descriptive material comparable to that of Moure (1961).

A third species, *T. keyensis* Friese, described from the Kepulavan Kai but also found in New Guinea, is a member of the group of *Platytrigona* defined by Moure (1961), i.e., a relative of *T. planifrons* Smith and *flaviventris* Friese with the basal area of the propodeum hairy throughout. It differs from the species known to Moure by certain characters listed in the body of the text, under *Heterotrigona.* Although *T. keyensis* also has the reddish yellow body coloration like *T. genalis* and *atricornis,* it is not discussed further here except to give the following New Guinea collection data: Northeast New Guinea: Wagu/Black River, Western Highlands, Oct. 3, 1972 (Hohmann).

Papuatrigona Michener and Sakagami, new subgenus

Type species: *Trigona genalis* Friese, 1908.

To facilitate comparison with other taxa, the lettering system of Moure (1961) is utilized.

a) Integument rather shiny but head and thorax minutely punctured throughout, punctures separated by about a puncture width in most areas, clypeus and lower paraocular area not more coarsely punctured than rest of face. Integument largely testaceous, yellow marks absent.

b) Head as broad as thorax. Interocular distance greater than eye length; inner orbits converging upward in upper thirds, gently converging downward in lower third so that upper and lower interorbital distances are about equal (Table 6). Upper alveolar tangent well below middle of face; interalveolar distance scarcely greater than half alveolorbital distance. Frontal line a fine groove; frons gently convex.

c) Clypeus gently convex, slightly more than twice as broad as long; lateral parts of epistomal suture incurved below.

d) Mandible with two small denticles in upper fourth of apical margin, the lower one smaller than upper and almost evanescent. Labrum simple. Malar area as long as about 1.5 flagellar diameters; clypeocular distance two flagellar diameters. Gena rounded, almost as wide as eye in side view. Labial palpus with about five large, sinuous setae on first segment, six on second; second segment more than half length of first, less than three times as long as wide, extending slightly beyond base of third segment; segments three plus four about as long as two. Galea with numerous straight or weakly hooked setae.

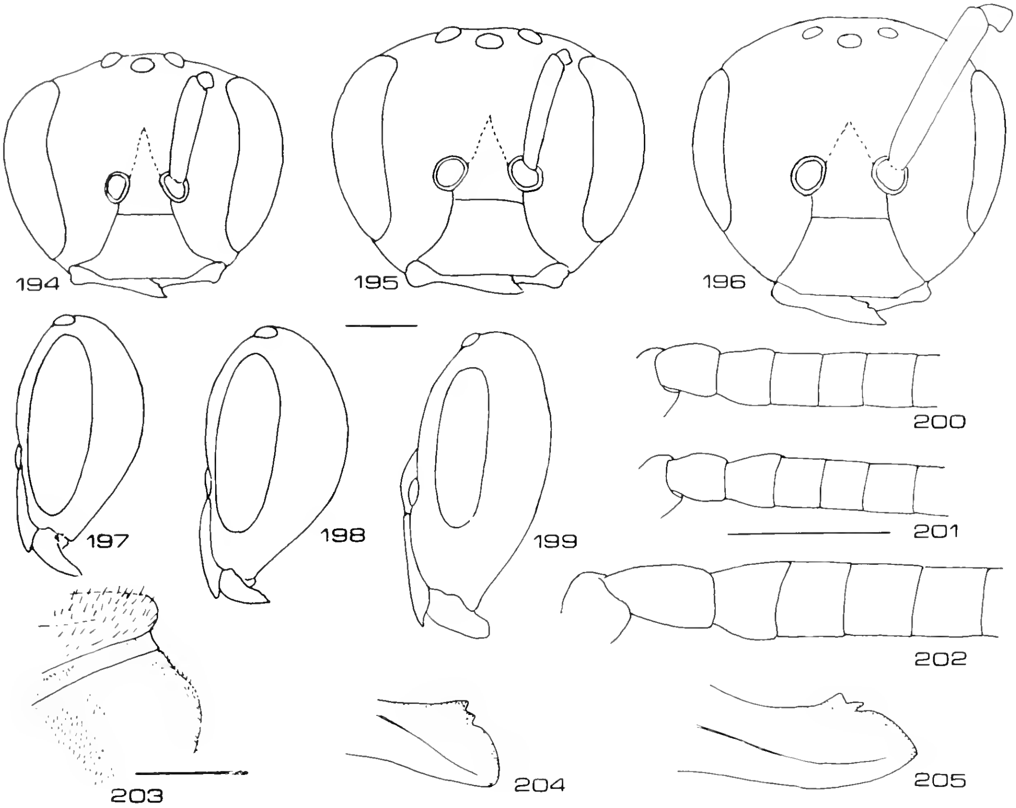
e) Vertex weakly procurved behind ocelli, not produced or ridged; ocelloccipital distance about equal to ocellar diameter and half of ocellocular distance, orbitoccipital distance and interocellar distance, which are about equal to one another.

f) Scape shorter than alveolocellar distance, not reaching median ocellus. Flagellar segments mostly slightly longer than broad, second slightly longer than first which is about as long as wide.

g) Notaulus and median line visible but not impressed; parapsidal line small. Scutellum short, rounded, slightly overhanging steeply sloping metanotum.

h) Forewing extending well beyond apex of metasoma; stigma moderate sized, prestigma shorter than width of stigma. Marginal cell over four times as long as broad, acute at base, only narrowly open at apex where Rs bends apicad almost parallel to wing margin. M-Cu bifurcation coincident with or rarely slightly basal or apical to m-cu; Cu strong; transverse cubitals almost unrecognizable so that submarginal cells are almost confluent; submarginal angle (between Rs and M at base of first submarginal cell) very slightly obtuse; M bent at first recurrent vein and continuing almost to wing margin. Hamuli seven per wing; jugal lobe one-third as long as vannal lobe, half as long as cubital cell.

i) Hind tibia more than 2.5 times as long as wide, posterior margin convex (almost straight in basal half), posterior distal angle obtuse and somewhat rounded; hair on posterior margin mostly simple and of moderate length but plumose hairs intermixed in distal fifth or sixth of margin; corbicula occupying distal half. Inner surface with keirotrichiate zone at widest point



Figures 194-205. *Trigona atricornis* Smith and *T. genalis* Friese. 194, Face of worker, *T. atricornis.* 195, 196, Faces of worker and queen, *T. genalis.* 197-199, Lateral views of heads of *T. atricornis* and *genalis,* workers, and *T. genalis,* queen. 200-202, Apex of scape, pedicel, and base of flagellum, *T. atricornis* worker and *T. genalis* worker and queen. 203, Posterolateral view of propodeum of worker of *T. genalis.* 204, 205, Mandibles of worker and queen, *T. genalis.* (Drawings by S. F. Sakagami.) Scale line = 0.5 mm; one applies to all heads, another to antennae and mandibles, and the third to the propodeum.

(about two-thirds of length of tibia from base) nearly twice as wide as shiny posterior marginal zone, not reaching apex of tibia, on distal part of tibia sloping gradually to marginal zone, the latter more depressed in middle of tibia so that there is slope at edge of keirotrichiate zone, this slope extending onto basal fourth of tibia. Penicillum and rastellum strong; bristles of rastellum robust, mostly blunt tipped.

j) Hind basitarsus about two times as long as wide, about two thirds as wide as tibia, inner surface uniformly setose.

k) Propodeum rather short, basal area steeply inclined, medially smooth, shiny, and glabrous but with small, isolated patch of hairs sublaterally, above. Metasoma narrower than thorax, not particularly elongate, first four terga smooth, shiny.

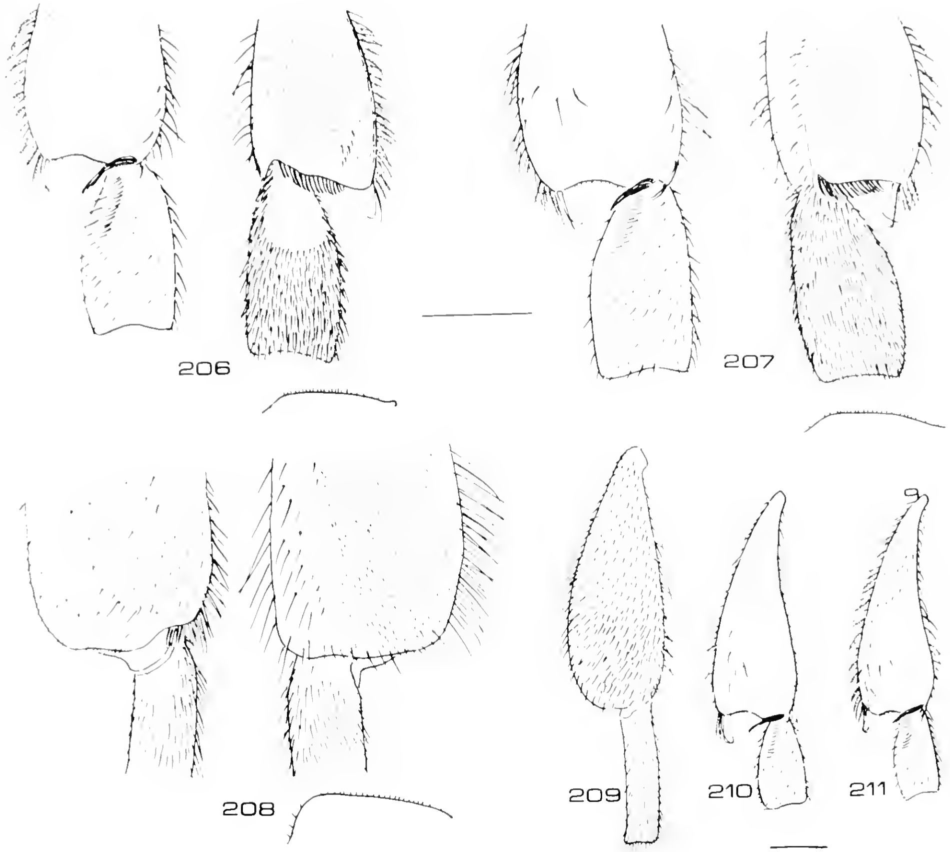
The name of this subgenus is based on Papua, a part of New Guinea, plus *Trigona.*

Trigona (Papuatrigona) genalis Friese

Because neither *T. genalis* nor *T. atricornis* has been fully described, we present a description, including metric information for both species (Table 6). The description is for *T. genalis,* with comparative information for *T. atricornis* added in parentheses; subgeneric characters listed above are mostly not repeated.

WORKER: *Color.* Pale honey brown, apical terga and apex of mandible darker. Pedicel except base, first flagellomere (often except apex), and rest of flagellum dusky, paler beneath. Middle and hind basitarsi and posterior margin of hind tibia often dusky or blackish (*T. atricornis* pale form nearly identical, dark form chestnut brown, mesoscutum dark brown, epistomal suture black; malar space, hind tibia and basitarsus, and apical terga sometimes blackish).

Pilosity. Occiput and vertex with moderately



Figures 206-211. *Trigona atricornis* Smith and *T. genalis* Friese. 206, 207, Outer views and inner views of basitarsus and apex of tibia and cross-section of inner tibial surface of workers of *T. atricornis* and *genalis*. 208, Same, queen of *T. genalis*. 209-211, Outer views of tibia and basitarsus, *T. genalis* queen and worker, *T. atricornis* worker. (Drawings by S. F. Sakagami.)

dense, pale brown bristles, up to about 200 μ long. (In *T. atricornis* brown, up to about 150 μ long.) Ocellocular area with similar but shorter and sparser hairs. Short appressed pale brown hairs on upper face; more conspicuous on lower face, some plumose, silvery in some positions; on apex of clypeus some erect hairs. Mesoscutum with sparse, erect hairs, 50-75 μ long (in *atricornis* denser and 125-150 μ) and denser fine semiappressed hairs ± 25 μ long (in *atricornis* ± 50 μ). Scutellar bristles up to 175 μ long (in *atricornis* to 250 μ), rather sparse. Pleura with fine, dense hairs 25-30 μ and sparser, semierect, plumose white hairs over 50 μ long above to 300 μ below. Propodeum above broadly glabrous medially, laterally with small patch of sparse hairs (Fig. 203) (this patch also present in *T. atricornis* as well as in *T. moorei* Schwarz). T1 and T2 discs virtually glabrous with few fine pale brown hairs up to 20 μ long; T3 similar but apical fimbria more distinct and laterally with sparse pale brown bristles to 50 μ; T4 and 5 similar but hairs on discs slightly denser. T6 with pale brown bristles to 150 μ. Sterna with simple hairs, some slightly curved apically, to 175 μ.

Structure. See measurements, Table 6, and subgeneric description. Lateral ocellus less protuberant than in *T. atricornis* (Figs. 194, 195). Sculpture coarser and less shining than in *atricornis* (see subgeneric description). Basal vein usually meeting cu-v of forewing, rarely basal or distal to cu-v (in *atricornis*, usually basal). Hind tibial and basitarsal character states illustrated for *genalis* and *atricornis*.

QUEEN: Entirely honey brown, with caste differences from worker common to many if not all known stingless bees: longer head, smaller ocelli, longer malar space, smaller eye, longer supraorbital part of head, longer scape, wider mesosoma, larger metasoma (cf. Figs. 195, 196), less reduced sting (Figs. 218, 219), more reduced mouthparts (Figs. 214-217), and hind tibia and basitarsus (Figs. 207-210).

SPECIMENS EXAMINED: CDM examined three specimens kindly lent by Dr. F. Koch of the Museum für Naturkunde, Berlin. Two bear Friese's orange "Typus" labels. The other has the red label, "Type," and we designate it as the lectotype. It (as well as the other two specimens) is labeled "Manikion 16.28.II.03" [Feb. 16-28, 1903] "*Trigona genalis* 1904 Friese det. m" [mihi]. Manikion was evidently on the north coast of Indonesian New Guinea; one of the specimens, in addition to the labels listed above, is labeled "N. Guinea, Holland. 03", presumably with reference to Hollandia (= Kotabaru = Sukarnapura = Djajapura).

Other specimens are as follows (all workers except one queen from Marua River): *Papua New Guinea:* 50 from nest 9, Marua River near Kerema, 6 May 1959 (C.D. Michener). *Northeast New Guinea:* One, Dreikikir, Sepik District, 350 m altitude, June, 1969 (J.L. and M. Gressitt). *Indonesian New Guinea:* 22, Bodem, 10-17 July 1959 (T.C. Maa); 22, Bodem, 11 km SE of Oefberfaren, 100 m altitude, 7-17 July 1959 (T.C. Maa); one, Bodem, Sarmi area, 10 July 1959 (T.C. Maa); two, Waris, south of Hollandia, 450-500 m altitude, 1-2 August 1959 (T.C. Maa); Klamono Oil Fields, 14-18 August 1948 (M.A. Lieftinck). The last specimens are in the Leiden Museum. All others are in the Bishop Museum, Honolulu; duplicates are in the Snow Entomological Museum, Lawrence, Kansas; the Universidade Federal do Paraná, Curitiba; and the S. F. Sakagami Collection, Hokkaido University, Sapporo.

Fragmentary information on the nest on the Marua River is given by Michener (1961).

TABLE 6. Measurements of *Trigona genalis* (G) and *T. atricornis* (A) workers (n = 10 for each species).

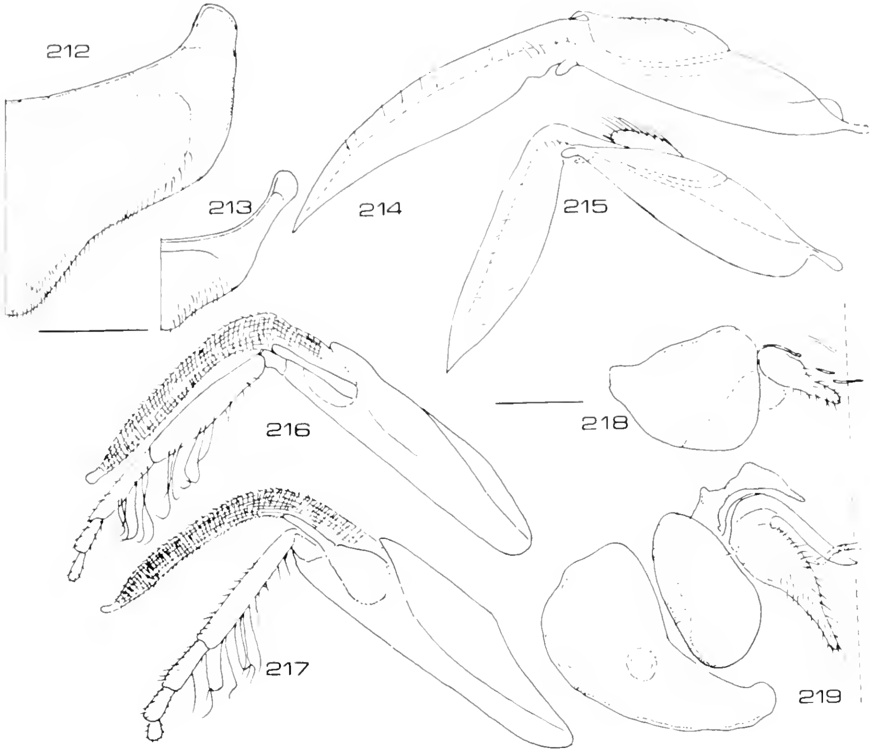
Feature	$\bar{X}$		SD		Range		Scale
	G	A	G	A	G	A	
Body length	51.50	46.70	3.01	3.74	45–56	40–55	10 = 1mm
Wing length with tegula	54.62	52.55	2.02	2.41	52–57	50–56	10 = 1mm
Mesoscutal width[a]	44.40	37.10	3.04	1.22	36–43	35–39	25 = 1mm
Mesoscutal length	31.21	29.45	0.83	1.31	29–32	27–31	25 = 1mm
Scutellar length	10.24	10.05	0.90	0.65	9–12	9–11	25 = 1mm
Metasomal width	44.40	41.36	3.04	2.10	37–48	38–45	25 = 1mm
Head width	54.27	50.18	1.69	1.64	53–56	47–52	25 = 1mm
Head length	43.60	41.05	1.20	1.01	41–45	40–43	25 = 1mm
Upper interorbital dist.	33.25	29.35	0.93	0.89	31–35	28–31	25 = 1mm
Max. interorbital dist.	37.65	34.60	1.23	1.18	35–39	32–36	25 = 1mm
Lower interorbital dist.	35.06	28.55	1.30	0.91	32–36	27–30	25 = 1mm
Eye length	31.65	32.25	0.87	1.01	30–33	31–34	25 = 1mm
Scape length	20.75	19.40	0.64	0.49	20–22	19–20	25 = 1mm
Interalveolar dist.[b]	7.70	7.25	0.46	0.40	7–8	7–8	40 = 1mm
Alveolorbital dist.	15.71	12.94	0.93	0.33	14–17	12–14	40 = 1mm
Interocellar dist.[c]	15.05	13.05	0.35	0.47	14–16	12–14	40 = 1mm
Ocellocular dist.[d]	12.60	10.77	0.66	0.58	11–13	10–12	40 = 1mm
Genal width	18.40	14.60	0.66	0.49	17–19	14–15	40 = 1mm
Malar length	9.10	4.45	0.66	0.52	8–10	3.5–5.0	40 = 1mm
Flagellomere 1 length	4.85	4.40	0.32	0.30	4.5–5.5	4–5	40 = 1mm
Flagellomere 2 length	5.25	4.80	0.28	0.24	5–6	4.5–5.0	40 = 1mm
Flagellomere 3 length	5.45	5.15	0.22	0.23	5.0–5.5	5.0–5.5	40 = 1mm
Flagellomere 2 width	6.05	5.43	0.35	0.11	5.5–7.0	5.0–5.5	40 = 1mm

[a] Greatest width in front of tegulae.

[b] Distance between antennal alveoli.

[c] Distance between posterior ocelli.

[d] Margin of lateral ocellus to nearest eye margin.



Figures 212-219. *Trigona genalis* Friese. 212, 213, S6 of queen and worker. 214, 215, Maxilla, worker and queen. 216, 217, Labium, worker and queen. 218, 219, Sting and associated structures, worker and queen. (Drawings by S. F. Sakagami.) Scale line for S6, 0.5 mm; for other structures, 0.25 mm.

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The International Standard Serial Number of this publication is US ISSN 0022-8850.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 54, No. 5, pp. 165–177 Dec. 12, 1990

Tenebrionoid-Basidiomycete Relationships with Comments on Feeding Ecology and the Evolution of Fungal Monophagy (Coleoptera/Hymenomycetes)[1]

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ABSTRACT

Fungal host patterns and life history notes are discussed for eastern U.S. species of tenebrionoids (Mycetophagidae, Tetratomidae, Melandryidae [Eustrophinae], Tenebrionidae, Mordellidae, and Colydiidae). Adults and larvae are found most commonly on Polyporaceae, and most species are polyphagous. Although many groups of mycophagous Coleoptera seem to be polyphagous, a substantial proportion of beetle taxa are monophagous or occur on a limited set of fungal taxa. Previous hypotheses suggest that natural selection favors polyphagy within insect-basidiomycete systems; in contrast, monophagy may either represent an evolutionary novelty or if stable among related beetle taxa, may represent phylogenetic constraint.

INTRODUCTION

The purpose of this paper is to provide new and additional basidiomycete host records for eastern North American tenebrionoid beetles exclusive of Ciidae (Mycetophagidae, Tetratomidae, Melandryidae [Eustrophinae], Tenebrionidae [Diaperine group], Mordellidae, and Colydiidae) and to discuss patterns of host use. Although the phylogenetic history of most taxa is poorly understood, some comments are provided about the evolution of host relationships.

The data presented in this paper are the result of a survey of mycophagous tenebrionoids made in Arkansas. Field collections consisted of bimonthly forays, usually on weekends, during 1986–1988. Additional visits were made to localities in Oklahoma, Georgia, Louisiana, and Tennessee. All basidiomycetes seen were examined for beetles. Survey results are given in the Appendix. Each family is treated separately in discussions combining survey data and previously published results. Comments attributed to K. Stephan refer exclusively to Oklahoma populations.

Biases associated with fungal host data are

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discussed in Ashe (1984), Newton (1984), Hanski (1989), and Skelley et al. (in prep.). Additional information on methodology and a listing of fungus author names are cited in Leschen (1988a) and Skelley et al. (op. cit.).

The Tenebrionoidea includes 28 families (Lawrence 1982), of which members of 11 families are known to be mycophagous. Eight of these have some members that use basidiomycete food sources. Basidiomycete hosts have been recorded for many Tenebrionoidea in scattered references, but detailed analyses have been limited to the European and North American Ciidae (Pavior-Smith 1960; Lawrence 1973). Ciid fungal hosts determined during this survey are consistent with Lawrence's observations and are excluded from the present report.

Mushrooms (order Basidiomycetes) are the most commonly used foods of mycophagous tenebrionoids. The mushrooms are composed mainly of two large groups within the Hymenomycetes, the Polyporaceae (Aphyllophorales), which form spores within tubes and rarely on teeth, and the Agaricales, which form spores on gills or in tubes (for more information see Webster 1980). Most polypores are lignicolous and most agarics are terrestrial. Other hymenomycete groups may also serve as hosts for tenebrionoids. The order Ascomycetes is also known to be a food source for some tenebrionoids (Lawrence 1977b; Crowson 1984). However, the overwhelming majority of hosts are found among the Basidiomycetes.

Lawrence (1973) organized many North American polypore species into groups that were delimited on textural and other physical features, and were not necessarily intended to reflect phylogenetic relationships. Three of Lawrence's groups commonly used by tenebrionoids and discussed in this paper are as follows: 1) *Trametes* group (= *Coriolus*): *Trametes, Lenzites;* 2) *Phellinus* group: *Inonotus, Phaeolus, Phellinus;* 3) *Ganoderma* group: *Bjerkandra, Daedaleopsis, Fomes, Ganoderma, Laetiporus,* and *Piptoporus.* For information on polypore growth habits see Lawrence (1973) and Overholts (1953).

The biology of mycophagous tenebrionoids is poorly known. Many larvae and adults are capable of burrowing into the tissue of fungal hosts. Bodies of larvae that burrow are generally weakly sclerotized (Lawrence 1989). Adult mouthpart structure is generally conservative; in contrast, larval mouthparts reveal a variety of adaptations associated with diverse feeding habits (Lawrence 1989). Larval mandibles are generally asymmetrical and may or may not have molae. Some, such as some members of the tenebrionid genus *Platydema* (Lawrence 1989; Leschen pers. obs.), have a molar region but lack the usual "grinding" microsculpture.

Duration of larval development is often longer for mycophagous tenebrionoids than for mycophagous members of other families such as Staphylinidae, some Erotylidae, and some Nitidulidae. Pupation of many species occurs within the host tissue, particularly if the host is relatively hard and persists over time.

PHYLOGENETIC CONSIDERATIONS

Crowson (1955) suggested that the primitive tenebrionoids may have evolved from an erotylidlike ancestor that fed on relatively hard fungi, much like some members of the recent erotylid subfamilies Dacninae and Triplacinae. There are data that indicate that the possibly related families within the Tenebrionoidea (Mycetophagidae, Tetratomidae, Ciidae, Pterogeniidae, Archeocrypticidae, and eustrophine Melandryidae) have some members that feed on Basidiomycetes. Some groups are similar to the extent that distinctions between the Mycetophagidae and Tetratomidae (Crowson 1955; Miyataki 1960) or Tetratomidae and Eustrophinae (Hyashi 1975; Crowson 1966; Viedma 1971) are unclear (see Lawrence 1977a), suggesting that the present taxa may be grouped by plesiomorphies. Lawrence and Newton (1982) hypothesized that there are six separate lineages within the Tenebrionoidea. Two of Lawrence and Newton's lineages are pertinent to this paper: 1) Archeocrypticidae, Pterogeniidae, and Ciidae; and 2) Tetratomidae, Melandryidae, Mordellidae, and Rhipiphoridae. The Colydiidae appear to be closely related to the Monommidae, Zopheridae, and other families (Doyen and Lawrence 1979; Lawrence and Newton 1982).

Relationships within the family Tenebrionidae are also poorly understood. Upon reviewing Watt's (1974) classification, Doyen and Lawrence (1979) noted that the tribes Diaperini, Rhipidandrini, and Bolitophagini should be grouped together. The diaperine group, as understood presently, is well defined by a number of synapomorphies and contains members of these tribes (Doyen and Tschinkle 1982). The affinities of the Bolitophagini, however, remain enigmatic and it could be considered either as a primitive member of the diaperine group, or as a member of the Toxicinae (Doyen and Tschinkle 1982). Doyen and Tschinkle (1982) mention that mycophagy may have evolved more than once within the diaperines and that the similarities of Bolitophagini to the diaperines could be the result of convergent feeding habits.

Phylogenies are only available for the Tenebrionidae. Phylogenetic information, cladograms, and phenograms for Tenebrionidae are given in Doyen and Tschinkel (1982). Although they do not include an exhaustive sampling of taxa, the hypotheses they propose are critical to understanding the relationships among the tenebrionids. Additional phylogenetic analyses must be done in order to address questions of evolutionary biology among Tenebrionoidea.

MYCETOPHAGIDAE

The Mycetophagidae are distributed worldwide and include relatively few genera, with the highest diversity occurring in temperate regions (Lawrence 1982). There are five genera with 26 species currently recognized in the United States (Parsons 1975), 10 of which were collected during this survey. In Oklahoma, two additional species of *Mycetophagus* are found commonly on soft polypores on willows (*M. melsheimeri* LeConte) and on pines (*M. pini* Zeigler) (K. Stephan pers. com.).

Most of the tenebrionoids covered in this study feed on the context tissue of the host fungus; however, among the Mycetophagidae there are exceptions. *Thrimolus minutus* Casey is rare on sporocarps, but one collection from the resupinate polypore *Schizopora paradoxa* yielded adults and larvae. Gut contents of a dissected larva revealed a saccular gut filled entirely with spores. Fungal sporophagy also occurs in some *Litargus*, and in at least one species of *Mycetophagus* (Hingley 1971; Lawrence 1977b).

Based on current data, members of the Mycetophagidae do not appear to be host specific. Species of *Mycetophagus* prefer the tissues of softer polypores and wood rotting Agaricales (Wiess 1919, 1924; Wiess and West 1920, 1921b; Park 1931; Chagnon 1935; Moennich 1944; Benick 1952; Minch 1952; Graves 1960; Pielou and Verma 1968; Mathewman and Pielou 1971; Shepard 1976). One species of *Mycetophagus* was collected from the ascomycete *Xylaria* (Xylariacaeae) in Costa Rica (Leschen pers. obs.).

Mycetophagus flexuosus, M. obsoletus, and *M. pluripunctatus* were generally found during the cooler times of the year. Seasonality of hosts may limit host ranges of these species.

Litargus was found commonly during the summer, and is especially abundant on sporocarps of Agaricales that become dry during the decay process (for additional hosts of *Litargus* see Wiess and West 1920, 1921a; and Moennich 1939). Lawrence (1977b) reared specimens of *L. sexpunctatus (Say)* from *Hypoxylon* (Ascomycetes; Xylariacea) spore fields, and at least one other species of *Litargus* has been collected from an ascomycete (Xylariaceae) in Peru (Leschen pers. obs.).

Larvae of *M. serrulatus* and *M. punctatus* were found feeding on the powdery residue of *Inonotus* that had accumulated in pockets between the separated cork and cambium layers of a dead oak tree. In the laboratory, larvae burrowed in the residue and were not seen at the surface. After a week, dried sporocarps of *Armillariella* and *Pleurotus* (Agaricales) were added to the observation chamber. Larvae aggregated below these new provisions. Larvae appeared to prefer intact fungi to the powdery matrix in which they were collected. All other larval *Mycetophagus* collected fed within the host tissue. These observations suggest that these *Mycetophagus* prefer compact foods although smaller food particles may be consumed under some circumstances.

TETRATOMIDAE

The tetratomids are a relatively small family distributed mainly in the Holarctic region with six genera and 10 species in the United States. Six species were collected in Arkansas. Specimens of *Abstrulia tesselata* were collected only once from a polypore sporocarp; adults are more commonly associated with subcortical hyphae (K. Stephan pers. com.). Most species are cool season adapted, and all species were collected from September to May. Cool season abundance has been documented also for other *Tetratoma* species (Crowson 1963; Pavior-Smith 1964a,b; Leschen 1988b).

There is no well-defined host pattern for tetratomids based upon previous data and that given in the Appendix. Larvae and adults have been collected from polypores and other lignicolous basidiomycetes (Minch 1952; Park 1931; Graves 1960; Miyatake 1960; Lawrence 1982). In the present study adults (except for *Abstrulia* and *Penthe*) fed on the context tissue of polypores. Adults of *Penthe* were not observed feeding.

Adults of *Pisenus* were common on terrestrial Hydnaceae (tooth fungi) and Polyporaceae in September, and larvae were reared to adults from lignicolous polypores in February and April. It is possible that adults emerge from summer aestivation, congregate on terrestrial basidiomycetes, and later reproduce on lignicolous fungi.

MELANDRYIDAE

Mycophagy is limited to the subfamilies Eustrophinae (four genera, 10 species in the United States; cosmopolitan) and Hallomeninae (*Hallomenus,* six spp. in the United States; mainly Holarctic) and the tribe Orchesiini (three genera, eight species in the United States; mainly north temperate) (Arnett 1965; Lawrence 1982). Seven species of these groups were collected in this survey.

Larvae of all genera that were collected fed upon the tissues of basidiomycetes. My observations agree with previous records that indicate these taxa are primarily associated with softer polypores (Wiess 1919; Wiess and West 1920, 1921b; Chagnon 1935; Donisthorpe 1935; Benick 1952; Minch 1952; Rehfous 1955; Dajoz 1966; Mathewman and Pielou 1971; Lawrence 1973). Larval *Holostrophus* (Eustrophinae) were not collected during this study, but larvae of a Japanese form were described from specimens collected from "tree fungi" (Hyashi 1975).

Orchesia species appear to have restricted host ranges. Lawrence (1973) reported that *O. castanea* and *O. gracilis* are associated with the *Trametes* group and the *Phellinus* group, respectively. In this survey *O. castanea* and *O. cultriformis* were associated with *Phellinus*. However, early winter collections of *O. castanea* from *Trametes* contradict the local pattern and support Lawrence's data. Mating adults of this species were observed during one winter collection.

Eustrophinus bicolor is a generalist that has been reared from from a variety of polypores. Its pattern of host use does not corerespond to Lawrence's (1973) fungal groups.

Hallomenus scapularis reproduces on both *Sparassis crispa* (Clavariaceae), a coral fungus, and *Tyromyces* (Polyporaceae). On both hosts larvae were very abundant. *Tyromyces* is a relatively soft polypore and the single collection record was from a specimen growing high above the ground on an oak. *Sparassis* is found growing at the base of trees where it produces large coral-like sporocarps that have a soft pliable texture.

MORDELLIDAE

Mordellids are most common on flowers as adults and are generally mycophagous and xylophagous as larvae (Lawrence 1982). Distribution of the family is worldwide. The United States fauna consists of four genera.

There are few host records in the literature, those primarily from polypores (Wiess 1920a; Wiess and West 1920; Scheerpeltz and Höfler 1948; Benick 1952). *Mordella marginota,* the only species collected during this survey, has been reared from *Lenzites* by Wiess and West (1920) and, in this study, from *Daedeleopsis confragosa,* which suggests that oviposition and larval development of this species may be limited to polypores.

COLYDIIDAE

Many colydiids are associated with fungal growth in wood and are uncommon on fruiting bodies (K. Stephan pers. com.). The family is worldwide in distribution; there are about 23 genera with 76 species in the United States (Stephan 1989). Only four species of colydiids were collected from basidiomycetes in this survey.

Adults of some species feed on the spores of Ascomycetes (Lawrence 1977b; Crowson 1984). Only two species collected during this study may be mycophagous, *Namunaria guttulata* and *Paha laticollis*. Specimens of *Namunaria* were reared once from the polypore *Spongipellis unicolor*, and adults were maintained and observed to feed on provisions of dry *Pleurotus* sporocarps. Adults of *Paha* were frequently encountered in low numbers on basidiomycetes encrusting the bottoms of rotting fallen limbs.

TENEBRIONIDAE

The Bolitophagini *(Bolitophagus, Bolitotherus),* Rhipidandrini *(Rhipidandrus),* and Diaperini *(Diaperis, Neomida, Platydema)* are the primary mycophagous lineages within the Tenebrionidae (Doyen and Lawrence 1979; Doyen and Tschinkel 1982). For numbers of tenebrionid species and genera in the United States, see Arnett (1965).

Larvae of most genera collected in this study fed within the host tissue. In contrast, adults are usually found in or on the fungus or under bark near the fungal host. Previous fungal host data for diaperines and bolitophagines indicate that these groups are consistently collected from polypores (Scheerpeltz and Höfler 1948; Benick 1952; Rehfous 1955; Lawrence 1973; Klimaszewski and Peck 1987).

The bolitophagines in Arkansas are *Bolitotherus cornutus* Panzer and *Bolitophagus corticola* Say. The host relationships and biology of *B. cornutus* are well known (Heatwole and Heatwole 1968). *Bolitotherus cornutus* is found on the *Phellinus* group (Lawrence 1973) with a few individuals occurring rarely on other fungi (Heatwole and Heatwole 1968; Leschen pers. data). Based upon my collections, the only known host for *B. corticola* is *Perreniporia fraxinea*.

There are three described species of *Rhipidandrus* in the eastern United States; *R. flabellicornis* is the only species that was collected from fungi in Arkansas. Previous fungal host records for *Rhipidandrus* are the *Ganoderma* group and other polypores (Wiess 1920a; Wiess and West 1920, 1921a; Lawrence 1973). Large numbers of adults and larvae of *R. flabellicornis* were collected from the polypore *Spongipellis pachydon*.

Only *D. maculata* was commonly collected in Arkansas. Most host records are from a variety of polypores, with few collections from Agaricales (Wiess 1920a, 1924; Wiess and West 1920, 1921a; Park 1931; Chagnon 1931; Minch 1952; Graves 1960; Ackerman and Shenefelt 1973; Lawrence 1973). These data indicate that northern populations of *D. maculata* are associated with the northern fungus *Piptoporus betulinus*. In contrast, my data indicate that southern populations occur on a variety of fungi. Adults often occur in large numbers on fresh fungal hosts perhaps suggesting that host odors or intraspecific pheromones may be attractive to individual beetles.

Neomida bicornis is most often collected on polypores in the *Trametes* group (Wiess 1920b; Weiss and West 1920, 1921b; Park 1931; Graves 1960; Ackerman and Shenefelt 1973; Lawrence 1973).

Nine species of *Platydema* were collected in this survey. Most were associated with Polyporaceae, but at least one species in Peru feeds and reproduces in the sporocarps of *Xylaria* (Ascomycetes; Xylariaceae) (Leschen pers. data.).

Polyphagous *Platydema* species include *P. americanum* (Park 1931; Pielou and Verma 1968; Lawrence 1973), *P. erythrocerum*, and *P. ruficorne* (Wiess and West 1920, 1923; Lawrence 1973). These species are distributed widely, and fungal hosts may vary geographically. The following species, on the other hand, appear to be monophagous (hosts in parentheses): *P. ellipticum* (*Phellinus* spp.; Weiss and West 1920, 1921a; Lawrence 1973); the predominantly northwestern species *P. oregonense* and *P. neglectum* (*Cryptoporus volvatus*, Hubbard 1892; Borden and McClaren 1972; Lawrence 1973), *P. excavatum (Schizophyllum)*, *P. subcostatum (Stereum)*, and possibly *P. ruficolle* (*Ganoderma lucidum,* K. Stephan pers. com.).

Some of the host patterns of *Platydema* may be obscured by collecting bias. I collected larval and adult specimens almost exclusively from sporocarps without searching adjacent regions beneath bark. K. Stephan (pers. com.) collected many adult specimens from under the bark of rotting logs. He has found *Platydema excavatum* and *P. teleops* Triplehorn associated with subcortical hyphae of *Trametes versicolor,* and *Platydema flavipes* (Fabricius) and *P. picilabrum* Melsheimer under the bark of fungus-infected logs.

Platydema micans was found at the bases of trees in leaf litter by K. Stephan (pers. obs.) and was collected by me from polypores adjacent to the forest floor. W. Steiner and C. Triplehorn (pers. com.) state that this species is not a member of *Platydema* and should be reassigned to an existing neotropical genus.

DISCUSSION

Most mycophagous tenebrionoids feed on polypores. The majority of taxa included in this survey feed on the context tissue of basidiomycetes, while fungal sporophagy is rare, only occurring in some species of mycetophagids. Based upon phylogenetic information, feeding on macroscopic basidiomycetes may be an ancestral condition for the Tenebrionoidea. However, until the phylogeny of the groups is better resolved, distribution of feeding types cannot be cogently discussed.

Fungal host relationships are incompletely known for the majority of taxa discussed. Records are few and according to Hanski (1989), this lack of data might falsely indicate monophagy. Well-defined or monophagous host patterns typify some members of the genera *Orchesia* (Melandryidae) and possibly *Platydema* (Tenebrionidae). Polyphagy is widespread especially within the Mycetophagidae and Tetratomidae.

In her study of European ciids, Paviour-Smith (1960) suggested that these beetles choose hosts based upon texture differences, while Lawrence (1973) adds that fungal chemistry may have a more significant role in host selection. The range of textural types used by the other North American tenebrionoids seems to be limited to softer polypores, with the notable exception of *Platydema ellipticum* and *Orchesia* species that feed upon hard *Phellinus* sporocarps. Also, *Platydema ruficorne* and *Bolitotherus cornutus* both use *Ganoderma* species which also have relatively hard sporocarp tissues. If distinct host textures are preferred by members of individual species (taxa) of beetles and these textural types are found in a variety of unrelated polypore taxa, then polyphagy would be a predictable consequence. Such is the case for the majority of North American ciids (Lawrence 1973).

Strong et al. (1984) noted that many insect/host plant ecologists define monophagy and polyphagy differently. For purposes of this paper and the discussion that follows, I consider that monophagy relates to the relationship that is exhibited when a beetle taxon is associated with a single mushroom taxon, independent of categorical rank. For example, a genus of beetles that feeds upon a single host species is obviously monophagous; if limited to a single genus of mushroom, it would be considered to show generic monophagy. The term monophagy would be modified by an adjective corresponding to the category of fungus taxon. Polyphagy would include any relationships between a single beetle taxon and a polyphyletic assemblage of hosts. These definitions imply that ecological relationships are independant of taxonomic level. Broad patterns of host use may be based upon ecology and/or the monophyly of the group of hosts and of the beetles. It is also important to note that adults may be polyphagous, while oviposition may be limited to a narrow range of hosts (Ashe 1984). This pattern might also be considered monophagy; for hosts of a single genus, larval generic monophagy.

In the above context there are numerous monophagous groups of fungus beetles. Within the family Erotylidae, the North American genus *Triplax* is separated into two species groups which appear to be host specific (species group monophagy). Members of the *Triplax thoracica* group are most commonly associated with the genus *Pleurotus;* and those of the *Triplax macra* group are found predominately on *Inonotus* (Skelley et al. in prep.). The following species are associated commonly with the agaric family Russulaceae (comprised of two genera): *Tritoma angulata* Say and *Pseudischyrus extricatus* (Crotch) (Erotylidae; Skelley et al. in prep.) and *Gyrophaena egena* Casey (Aleocharinae; Ashe 1984). Similarly, some *Platydema* species appear to be associated with either one species or one genus of fungal host. Other Coleoptera families that may include some monophagous species are: Scaphidiidae (Leschen 1988c); Staphylinidae (possibly Oxyporinae; Leschen and Allen 1988); Derodontidae (Leschen pers. obs.); Nitidulidae (Lawrence 1990); and Ciidae (Lawrence 1973).

Hanski (1989) provided much discussion of the ecology of mycophagy. His major conclusion was that polyphagy, rather than monophagy, is selected for among mycophagous insects. His assertion is based upon two hypotheses. The quality hypothesis assumes that all fungi can serve as potential hosts and are equally edible. Any mushrooms that are temporally co-occurring are therefore equally likely to become a food source for a mycophagous species. The quantity hypothesis was adopted from Jaenike (1978a) by Hanski and states that since fungal species are geographically patchy and ephemeral over time, natural selection would favor species that would have broad host patterns. Hanski (1989) offers a large quantity of data that supports his arguments. Hanski did not define his use of monophagy, but it appears that he was concerned with a species/species interaction. Nevertheless, I agree with the premises and the importance of some of the factors concerning Hanski's arguments. I ask, however, if selection favors polyphagy, why are there many monophagous taxa?

To answer this question I address two types of monophagy within mycophagous Coleoptera. Type I monophagy occurs when more than one closely related species of beetle use a single fungal taxon as a food source, indicating that host patterns remained unchanged after prior speciation events. This is probably the case for *Triplax* species groups, indicating that a phylogenetic constraint may limit fungal host shifts (for a current review on the definitions for constraint, see Gould [1989]). In contrast, Type II monophagy occurs when there is a distribution of monophagy and polyphagy within a clade, such that fungal host taxa do not correlate with phylogenetic pattern. Type II monophagy may indicate that host shifts, or monophagy, are not limited by phylogenetic constraints. New patterns of host relationships may represent evolutionary novelties within some clades. Evolutionary novelties in the form of host shifts are only recognizable if they are derived conditions and some decision regarding the polarity or direction of evolution of the new behavior has been made. Monophagy may be a local phenomenon (see Bernays and Graham 1988) and can be tested by thorough collecting in disparate or adjacent geographical regions.

According to Hanski's (1989) hypotheses natural selection should produce derived species that are polyphagous. In this scenario monophagy would be ancestral. Support for the predicted outcome would require phylogenetic analysis in beetle groups that exhibit mixtures of both monophagous and polyphagous species. In the genus *Platydema*, monophagous species would be predicted to be ancestral relative to the remaining species in a phylogenetic tree. Another possible set of circumstances consistent with Hanski's argument would be if natural selection on host range is a population effect, not necessarily expected to be observable as branching patterns in phylogeny. Then, monophagous species would be relatively young species and would become polyphagous in time. The fact that such groups as *Triplax* have entire species groups limited to one host (Type I monophagy) would either falsify Hanski's hypothesis or would be deemed irrelevant to the scenario. Another and more attractive possibility is that Type I monophagy is a phenomenon that represents a behavioral or phylogenetic constraint that is maintained in a lineage in spite of the expected patterns of natural selection.

It may be that the only general unifying feature of host pattern evolution is that beetles and their hosts both have phylogenetic histories so that each lineage has its own unique past and concomitant suites of phylogenetic constraints. Thus far, no species level cladogram has been proposed for mycophagous (on Basidiomycetes) beetles.

These cladograms would be required in order to plot host patterns on terminal taxa (for an example, see Ashe 1984). Once phylogeny is reconstructed, processes or factors controlling ecological relationships can be discussed (Coddington 1988) and the phylogeny can serve as a guide for further study of population genetics and other microevolutionary interactions.

For at least some mycophagous taxa, there are phylogenetic constraints that limit host shifts. This would be indicated by the redundancy of hosts among monophyletic groups. This phenomena has been briefly alluded to in insect-plant interactions for which more data are available (Bernays and Graham 1988). Although monophagy is predominant in insect-plant systems, polyphagy is more predominant in insect-mushroom systems (Hanski 1989). Natural selection is favored by a majority of workers to be the dominant process that affects host patterns in both systems. I have illustrated that at least one pattern (Type I monophagy) may result from phylogenetic constraint.

Factors other than geography or host texture that have been postulated to affect mushroom host patterns are host seasonality, ephemerality, seasonal abundance, persistance, and chemistry (Scheerpeltz and Höfler 1948; Benick 1952; Rehfous 1955; Dajoz 1966; Lacy 1984; Hanski 1989). An understanding of the evolution of mycophagous insects must be based on a variety of perspectives since there may be no single unifying process or underlying factor affecting the evolution of host patterns.

More research is necessary to test hypotheses and make predictions about phylogenetic constraints that affect the evolution of mycophagous beetles and their patterns of host relationships. The tenebrionoid taxa mentioned in this paper are ideal study groups. Particularly interesting is the genus *Platydema*, whose members show a wide variation of host patterns and life history adaptations that may be the result of a combination of phylogenetic constraints and evolutionary novelties.

ACKNOWLEDGMENTS

I am grateful to the following mycologists who identified Coleoptera host fungi for this study and my masters thesis: J. Justice, M. Blackwell, and R. Gilbertson. For information and insights regarding tenebrionoid mycophagy, and the identification of *Thrimolus minutus* larva, I thank J. F. Lawrence. I especially appreciate the kindness of Karl Stephan, who has taught me a great deal about North American Coleoptera. I also thank him for comments and observations included in this paper. This study is part of a masters thesis presented at the University of Arkansas, Fayetteville. I thank the members of my advising committee, R. T. Allen, E. Dale, and J. Phillips, for their guidance during this study. I also thank C. E. Carlton and other members of the faculty at UA for their moral support. R. T. Tommy Cox (homemaker) assisted in the development of the data formula (used in the Appendix). Portions of this manuscript were reviewed by S. J. Ashe, J. Danoff-Burg, J. F. Lawrence, C. D. Michener, and K. Stephan. Lastly, I thank S. J. Ashe for his encouragement of ongoing studies of beetle mycophagy.

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APPENDIX

Basidiomycete host fungi for the Tenebrionoidea obtained in the survey of Arkansas and neighboring states (see Introduction) are given below. Previously known host data are excluded from the list but are cited in the family discussions in the body of this paper.

Data below take the following form:

Beetle name

Fungus name (A) B-C/D(E)*, where:

A = acronym for higher fungal taxon (see below); **B** = number of adults collected; **C** = number of larvae (associated or reared); **D** = number of times collected in the month; and **E** = month (e.g., 2 = February). The number of asterisks (*) indicates the number of times beetles were reared from immature stages in that species of fungus.

Fungal taxa acronyms are as follows:

Hymenomycetes
AGA - Agaricales
TRE - Tremellales
Aphyllophorales
CAN - Cantharalleacea
CLA - Clavariaceae
COR - Corticiaceae
HYD - Hydnaceae
POL - Polyporaceae
SCH - Schizophyllaceae
STE - Stereaceae

MYCETOPHAGIDAE

Litargus balteatus **LeConte**
Meripilus giganteus (POL) 1-0/1(7)
Perreniporia fraxinea (POL) 2-0/2(10)
Litargus didesmus **Say**
Amanita (AGA) 16-0/4(8), 1-0/1(11)
A. rubescens (AGA) 2-0/1(8)
Armillariella mellea (AGA) 1-0/1(8)
A. tabescens (AGA) 10-0/4(9)
Boletaceae (AGA) 10-0/4(9)
Boletinellus meruliodes (AGA) 49-44/1(7), 22-0/1(8)*
Boletus spp. (AGA) 4-0/2(6), 3-0/2(7), 26-0/4(8)*
Boletus spadiceus group (AGA) 17-4/1(6), 1-0/1(8)
Cantharellus cibarius (CAN) 3-0/1(7),
Collybia sp. (AGA) 1-0/1(5)
Daedeleopsis confragosa (POL) with undetermined mold 5-0/2(5)
Gerronema strombodes (AGA) 3-0/(7)
Gymnopilus sp. (AGA) 5-0/1(8)
Inonotus sp. (POL) 1-0/1(5)
Inonotus dryadeus (POL) 3-0/1(8)
Lactarius spp. (AGA) 9-0/2(6), 3-0/1(7), 2-0/1(8)
L. argillaceifolius (AGA) 11-0/1(6)
L. subvellereus (AGA) 6-0/1(6)
Lepiota sp. (AGA) 3-0/1(8)
Leptocybe sp. (AGA) 4-0/1(5)
Meripilus giganteus (POL) 6-0/1(7)
Omphalotus oleolaris (AGA) 1-0/1(5), 2-0/1(9)
Oudemansiella radicata (AGA) 1-0/1(5)
Panus rudis (AGA) 1-0/1(6)
Phylloporus rhodoxanthus (AGA) 4-0/1(6), 2-0/1(7)
Pleurotus ostreatus (AGA) 2-0/1(5), 1-0/1(6), 5-0/2(8)
Polyporaceae (undetermined) 1-0/1(5), 3-0/1(7), 5-0/1(8), 3-0/2(9)
Ramaria sp. (CLA) 1-0/1(6), 1-0/1(9)
Russula spp. (AGA) 1-0/1(6), 3-0/2(8), 1-0/1(11)
Sparassis crispa (CLA) 12-0/1(9)
Strobilomyces floccopus (AGA) 2-0/1(6), 1-0/1(7)
Trichaptum biformis (POL) 1-0/1(6)
Trichalomopsis platyphylla (AGA) 3-0/2(5)
Tylopilus spp. (AGA) 1-0/1(6), 10-0/1(7)
Litargus nebulosus **LeConte**
Armillariella mellea (AGA) 2-0/1(11)
Boletinellus meruliodes (AGA) 37-0/1(7)
Meripilus giganteus (POL) 3-0/1(8)
Mycetophagus flexuosus **Say**
Bjerkandera adusta (POL) 1-0/1(5)
Inonotus sp. (POL) 3-0/1(3)
Laetiporus sulphureus (POL) 1-0/1(9)
Meripilus giganteus (POL) 2-0/1(7), 5-0/1(8)
Naematoloma fasciculare (AGA) 2-0/1(8)
Perreniporia fraxinea (POL) 1-0/1(10)
Pleurotus ostreatus (AGA) 1-1/1(8), 16-0/1(9)
Trichalomopsis platyphylla (AGA) 1-0/1(5)
Mycetophagus obsoletus **(Melsheimer)**
Inonotus sp. (POL) 4-0/1(5)
Hericium sp. (HYD) 2-0/1(4), 13-0/1(11)*
Schizopora paradoxa (POL) 9-9/1(5)*
Spongipellis pachydon (POL) 155-0/2(8)**
Mycetophagus pluripunctatus **LeConte**
Amanita sp. (AGA) 1-0/1(10)
Armillariella mellea (AGA) 13-0/1(11)
Bjerkandera adusta (POL) 9-7/1(11)*
Hericium sp. (HYD) 9-0/1(4), 3-0/1(11)*
Omphalotus oleolaris (AGA) 5-0/1(11)
Pleurotus ostreatus (AGA) 12-0/2(2), 8-0/1(3), 1-0/(3), 1-0/1(5), 24-0/1(10)
Spongipellus unicolor (POL) 54-27/2(4)**, 1-0/1(11)
Mycetophagus punctatus **Say**
Boletinellus meruliodes (AGA) 1-0/1(7)
Inonotus sp. (POL) 2-0/1(10)
Meripilus giganteus (POL) 1-1/1(8)
Pluerotus ostreatus (AGA) 1-0/1(5), 16-3/2(6), 2-2/1(7), 1-0/1(9)
Mycetophagus serrulatus **(Casey)**
Armillariella tabescens (AGA) 1-0/1(9)
Hericium sp. (HYD) 3-0/1(4)
Inonotus sp. (POL) 5-0/1(5)*, 40-0/1(10)*, 10-0/1(11)
Meripilus giganteus (POL) 50-2/1(7)*
Pleurotus ostreatus (AGA) 3-0/2(5), 3-0/1(6), 1-2/1(8)*
Spongipellis unicolor (POL) 3-0/1(4)
Thrimolus minutus **Casey**
Marasmius siccus (AGA) 1-0/1(6)
Polyporus alveolaris (POL) 2-0/1(10)
Schizopora paradoxa (POL) 4-10/1(6)
Spongipellis pachydon (POL) 1-0/1(8)
Typhaea stercorea **(Linnaeus)**
Amanita sp. (AGA) 1-0/1(8)
Boletinellus meruliodes (AGA) 4-0/1(7)
Lactarius argillaceifolius (AGA) 1-0/1(6)

TETRATOMIDAE

Abstrulia tessellata **(Melsheimer)**
Trametes versicolor (POL) 2-0/1(5)
Penthe obliquata **(Fabricius)**
Bjerkandera adusta (POL) 2-0/1(5)
Schizopora paradoxa (POL) 1-0/1(4)
Tyromyces sp. (POL) 3-2/1(6)*
Penthe pimelia **(Fabricius)**
Inonotus sp. (POL) 3-0/1(4)
I. dryadeus (POL) 5-4/1(10)*
Meripilus giganteus (POL) 1-0/1(7)
Perreniporia fraxinea (POL) 1-0/1(10)
Pleurotus ostreatus (AGA) 2-0/1(5)
Pisenus humeralis **(Kirby)**
Albatrellus sp. (POL) 24-0/2(10)
Bjerkandera adusta (POL) 1-0/1(11)
Dentinum sp. (HYD) 13-0/2(9)
Hericium erinaceus (HYD) 1-0/1(3)
Inonotus dryadeus (POL) 1-0/1(1)

Ischnoderma resinosum (POL) 2-6/1(1)*
Pleurotus ostreatus (AGA) 1-0/1(11)
Spongipellis unicolor (POL) 50-3/1(4)*, 17-0/1(11)
Pisenus pubescens Casey
Albatrellus sp. (POL) 1-0/1(10)
Tetratoma truncorum LeConte
Bjerkandera adusta (POL) 2-0/1(10), 2-0/2(11)
Spongipellis unicolor (POL) 14-21/1(4)*, 0-40/1(11)
Trametes versicolor (POL) 1-3/1(3)

MELANDRYIDAE

Hallomenus scapularis Melsheimer
Perreniporia fraxinea (POL) 1-0/1(10)
Polyporaceae 2-11/1(9)
Sparassis crispa (CLA) 4-9/2(9)*, 2-37/1(10)*
Tyromyces sp. (POL) 76-11/1(11)*
Eustrophinus bicolor (Fabricius)
Armillariella tabescens (AGA) 3-0/2(9), 1-0/1(10)
Inonotus sp. (POL) 8-0/1(4)
I. dryadeus (POL) 14-30/1(8)*
Laetiporus sulphureus (POL) 11-6/1(9)*
Meripilus giganteus (POL) 5-15/1(7)*
Omphalotus olearius (AGA) 1-0/1(10)
Perreniporia fraxinea (POL) 4-0/1(3), 3-0/2(10)
Phaeolus schweinitzii (POL) 2-0/1(9)
Pleurotus ostreatus (AGA) 6-0/1(5), 1-0/1(6), 1-0/1(8), 3-0/1(9)
Trametes versicolor (POL) 2-0/1(5)
Tyromyces sp. (POL) 2-0/1(7)
Eustrophus tomentosus (Say)
Armillariella tabescens (AGA) 1-0/1(9)
Inonotus sp. (POL) 1-0/1(10)
I. dryadeus (POL) 2-0/1(5)
Spongipellis pachydon (POL) 1-2/1(8)
Trametes versicolor (POL) 1-0/1(5)
Holostrophus bifasciatus Say
Laetiporus sulphureus (POL) 2-0/1(3)
Schizopora paradoxa (POL) 1-0/1(4)
Trametes versicolor (POL) 1-0/1(4)
Orchesia castanea Melsheimer
Inonotus sp. (POL) 13-0/1(5)*
I. dryadeus (POL) 55-0/1(8)*
I. hispidus (POL) 6-0/1(4)*
Phellinus gilvus (POL) 1-0/1(7)*
Orchesia cultriformis Lilibert
Inonotus hispidus (POL) 3-0/1(4)*
Phellinus gilvus (POL) 1-0/1(4)
Russulaceae (AGA) 1-0/1(5)
Synstrophus repandus (Horn)
Meripilus giganteus (POL) 2-4/1(8)

MORDELLIDAE

Mordella marginota (Melsheimer)
Daedeleopsis confragosa (POL) 12-3/1(7)*

COLYDIIDAE

Bitoma quadriguttata (Say)
Bjerkandera adusta (POL) 1-0/1(10)
Inonotus sp. (POL) 1-0/1(4)
Pleurotus ostreatus (AGA) 1-0/1(5)
Namunaria guttulata (LeConte)
Irpex lacteus (POL) 1-0/1(8)
Spongipellis unicolor (POL) 4-1/1(4)*
Paha laticollis (LeConte)
Irpex lacteus (POL) 1-0/1(3), 1-0/1(5), 1-0/1(8)
Meripilus giganteus (POL) 1-0/1(9)
Phanerocaete chrysorhizon (POL) 9-0/1(6)
Polyporus alveolaris (POL) 1-0/1(5)
P. elegans (POL) 1-0/1(8)
Schizophyllum commune (SCH) 1-0/1(5)
Schizopora paradoxa (POL) 1-0/1(9)
Stereum sp. (STE) 1-0/1(9)

TENEBRIONIDAE

Bolitophagus corticola Say
Perenniporia fraxinea (POL) 10-5/1(3), 3-0/1(5), 26-1/2(10)
Diaperinus maculata Olivier
Cerriporia sp. (POL) 11-6/1(8)
Fistulina hepatica (POL) 4-2/1(8)
Inonotus sp. (POL) 27-91/1(5)
I. dryadeus (POL) 1-1/1(8)
I. querqustris (POL) 3-0/1(8)
Irpex lacteus (POL) 4-0/1(5)
Laetiporus sulphureus (POL) 1-0/1(3), 4-0/1(9)
Meripilus giganteus (POL) 35-1/1(7)*, 12-12/5(8)*, 3-0/1(9)
Perenniporia fraxinea (POL) 1-0/1(5)
Phellinus sp. (POL) 1-0/1(5)
Pleurotus ostreatus (AGA) 8-0/1(5), 2-0/1(7), 1-0/1(9)
Schizopora paradoxa (POL) 1-0/1(5)
Tyromyces sp. (POL) 3-1/1(6), 1-0/1(8)
Diaperis nigronota Pic
Inonotus querqustris (POL) 2-0/1(8)
Neomida bicornis (Fabricius)
Daedeleopsis confragosa (POL) 1-0/1(4), 3-0/1(5)
Ganoderma sp. (POL) 6-0/1(7)*
G. lucidum (POL) 1-0/1(3)
Lenzites betulina (POL) 15-0/1(3), 20/-0/3(5), 2-0/1(9)
Pleurotus ostreatus (AGA) 1-0/1(10)
Polyporus alveolaris (POL) 10-0/3(5), 2-0/1(6)
P. arcularius (POL) 1-0/1(5)
P. brasiliensis (POL) 2-0/1(8)
Spongipellis unicolor (POL) 1-0/1(7)
Trametes bicornus (POL) 2-1/1(12)*
T. hirsuta (POL) 11-0/1(5)
T. versicolor (POL) 11-0/1(2), 16-0/1(3)*, 24-1/4(4)*, 38-0/3(5), 1-5/1(8), 8-0/1(11)
Platydema americanum Laporte and Brullé
Inonotus sp. (POL) 1-0/1(10)
Meripilus giganteus (POL) 3-0/1(8), 2-0/1(9)
Merulius incarnatus (COR) 1-0/1(7)
Platydema ellipticum (Fabricius)
Hericium sp. (HYD) 1-0/1(4)
Phellinus gilvus (POL) 0-3/1(3), 8-0/2(5)*, 3-0/1(6), 15- 35/1(7)*
Platydema erythrocerum Laporte and Brullé
Bjerkandera adusta (POL) 4-6/2(5)*, 2-0/1(8), 1-0/1(10)
Irpex lacteus (POL) 1-0/1(5)
Meripilus giganteus (POL) 71-8/1(7)*, 5-5/2(8), 3-0/1(9)
Perenniporia fraxinea (POL) 2-0/1(5)

Pleurotus ostreatus (AGA) 4-0/1(5), 1-0/1(7), 5-0/1(8), 4- 0/2(9), 1-0/1(10)

Polyporus brasiliensis (POL) 2-0/1(8)

Schizopora paradoxa (POL) 12-2/1(5), 1-0/1(6), 12-23/1(8)*

Sparassis crispa (CLA) 1-0/1(9)

Trametes cervinus (POL) 3-0/2(5)

Tyromyces sp. (POL) 1-0/1(7)*, 1-0/1(9)

Platydema excavatum **(Say)**

Auricularia auricula (TRE) 3-0/1(4)

Schizophyllum commune (SCH) 48-2/3(5)*, 2-0/1(7), 2-0/2(8)

Platydema flavipes **(Fabricius)**

Irpex lacteus (POL) 1-0/1(5)

Platydema laevipes **Haldeman**

Spongipellis unicolor (POL) 1-0/1(4)

Platydema micans (Sturm)

Polyporus alveolaris (POL) 10-0/2(6)

Platydema ruficolle **Laporte and Brullé**

Boletinellus meruliodes (AGA) 1-0/1(7)

Lactarius sordidus (AGA) 1-0/1(6)

Platydema ruficorne **(Sturm)**

Bjerkandera adusta (POL) 8-0/2(5), 1-0/1(8), 10-0/2(10)

Cerrena unicolor (POL) 3-0/1(3)

Ganoderma sp. (POL) 4-2/2(8)

G. lucidum (POL) 8-3/1(8)*

Inonotus sp. (POL) 2-0/1(4)

Irpex lacteus (POL) 3-0/1(5), 2-0/1(7)

Perenniporia fraxinea (POL) 4-41/1(7)*, 3-0/1(10)

Polyporus brasiliensis (POL) 2-0/1(8)

Trametes versicolor (POL) 2-0/1(3), 4-0/1(8)*

Platydema subcostatum **Laporte and Brullé**

Stereum complicatum (STE) 2-15/1(10)

S. osteum (STE) 5-15/1(3)*, 1-4/1(10)*

Rhipidandrus paradoxus **Beauvois**

Bjerkandera adusta (POL) 6-0/1(8)

Meripilus giganteus (POL) 2-0/1(7)

Pleurotus ostreatus (AGA) 1-0/1(5), 2-0/1(6)

Schizopora paradoxa (POL) 6-0/1(5)

Spongipellis pachydon (POL) 113-11/3(8)***

S. unicolor (POL) 2-0/1(4)

ANNOUNCEMENT

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The International Standard Serial Number of this publication is US ISSN 0022-8850.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 54, No. 6, pp. 179–207 May 3, 1991

Revision of the Bee Genus *Braunsapis* in the Oriental Region (Apoidea: Xylocopinae: Allodapini)[1]

BY STEPHEN G. REYES

CONTENTS

ABSTRACT

The genus *Braunsapis* from the oriental region is revised; 19 species are treated. Eight species are described as new, namely: *B. flaviventris, B. malliki, B. clarihirta, B. apicalis, B. lateralis, B. signata, B. aurantipes* and *B. indica. Allodape marginata* Smith, *A. parvula* Smith and *A. pumilio* Cockerell are synonymized under *B. mixta* (Smith). *Allodape sauteriella* Cockerell is synonymized under *B. hewitti* (Cameron). *Allodape iwatai* Sakagami is synonymized under *B. puangensis* (Cockerell). *Allodape cupulifera bakeri* Cockerell and *A. hewitti sandacanensis* Cockerell are synonymized under *B. cupulifera* (Vachal). Likewise, *Allodape mindanaonis*

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[1] CONTRIBUTION NUMBER 3011 FROM THE DEPARTMENT OF ENTOMOLOGY, UNIVERSITY OF KANSAS, LAWRENCE, KANSAS 66045.

Cockerell is placed under *B. philippinensis* (Ashmead). *Allodape mindanaonis reducta* Cockerell is elevated to specific level as *B. reducta* (Cockerell). Important characters used in discriminating the oriental species are discussed. Keys and illustrations are provided.

INTRODUCTION

This paper is a preliminary revision of the genus *Braunsapis* of the oriental region. This area includes India and Pakistan, the Indo-China region, southern China, Taiwan, the Philippines, Malaysia, and most of Indonesia including the smaller Sunda Islands. New Guinea and the Solomon Islands have been excluded and their species are treated in an account of Australian species (Reyes, in press).

Braunsapis is the largest and most widespread genus of Allodapini, ranging from Africa, where it is abundant and diversified, across southern Asia as far as Taiwan and the Solomon Islands, and south to the northern half of Australia. These are small, slender, black bees that nest in dead pithy stems, with immature stages free in the burrow and not in individual cells.

In a series of papers, Michener (1966b, 1969, 1970, 1975a, b, 1976, 1977a, b; Michener and Scheiring, 1976) revised the tribe Allodapini at the generic level, as well as the species of Africa, using characters of both adults and immature stages. At present, there are 13 genera recognized in the tribe Allodapini; the genus *Braunsapis* is believed to be closely related to *Effractapis, Allodape* and *Nasutapis*. Smith described the first oriental species as *Prosopis mixtus* in 1852, and other early authors assigned oriental species either to the genus *Allodape* or *Prosopis*. *Prosopis* is a wholly unrelated colletid bee that superficially resembles *Braunsapis*. Asian species were placed in the genus *Allodapula* for a time (Michener, 1966a); Michener (1969, 1975a) recognized *Allodapula* as a strictly African group and proposed the name *Braunsapis*. The only allodapine bees found in the oriental region are in the genus *Braunsapis*.

Prior to the present study, 18 trivial names had been proposed for species in the genus *Braunsapis* from the oriental region as here defined. There have been a few biological papers on some species (Maeta et al., 1984, 1985; Sakagami, 1960; Shiokawa and Michener, 1977), but nothing has been done to treat the group from the oriental region in a more comprehensive manner. There is difficulty in studying the group if one is limited to comparing adults. At least in Africa, larval characters are more evident than adult characters (Michener, 1975b, 1976). In some instances, adults are mainly separated by size (as indicated by head width) and clypeal markings, as in the case of *B. picitarsis* and *B. philippinensis* (see below). Others such as *B. cupulifera* and *B. hewitti* have the females sometimes barely distinguishable, but in the males the trochanter is lobed distally and excised medially in the former and simple in the latter. While it would be ideal to have clear-cut characters to distinguish the closely related species of oriental *Braunsapis,* this is not the case for the adults, especially the females. It is best, therefore, to take these distinctions among closely related species as hypotheses until other characters, particularly larval characters, can be incorporated into the study to provide evidence for or against the conclusions presented below. The purpose of this paper is to provide a taxonomic framework for the scarce and widely scattered information on oriental *Braunsapis*. Other studies, especially on biological and behavioral aspects of this particularly interesting group of bees, should be encouraged.

Braunsapis (along with other genera of allodapine bees on other continents) is of special interest because of the abundance of pairs of extremely similar species (Michener 1975a), the strong larval characters (Michener, 1975b, 1976), and the primitively social behavior in which a minority of the nests contain two or more adult females, one of which is queen-like (Sakagami, 1960; Wilson, 1971; Michener, 1971, 1974, 1990).

MATERIALS AND METHODS

In the descriptions, measurements in parentheses are those of the type specimens. Characters are numbered to facilitate comparison among species. The numbering system is similar to the one developed for a study of Australian species (Reyes, in press). Various characters that are the same for all oriental species are omitted, so that the numbers are not consecutive. Only the first species within each species group is fully described; characters of other species that are similar to the first species are omitted in the following descriptions. Characters similar to those described for the females are omitted in the description of males, e.g., the color of the pronotal lobe, tegula and axillary sclerites and the length of malar space, because they fall within the range described for the females. Characters denoted by asterisks in the descriptions further help in distinguishing the species but alternatives are not specified for all the species. Thus the notation "legs orange" for one species is not countered by "legs wholly or largely dark" for all other species. Some characters are abbreviated as follows: fourth to sixth metasomal terga as T4–6, seventh and eighth metasomal sterna as S7 and S8. HW refers to head width and HW/HL refers to the head width/length ratio.

Genitalia and mouthparts were examined in glycerin after clearing with KOH at room temperature and normalization with acetic acid. Illustrations of genitalia and mouthparts were made from such preparations, using an ocular grid. Scanning electron photomicrographs were obtained using a Philips 500 electron microscope. Bright reflections on the facial photographs were dulled by applying a diluted solution of India ink.

Abbreviations or acronyms used for the different museums or collections are given below. I thank the following individuals and institutions for the loan of specimens:

AEI—American Entomological Institute, Gainesville, Florida (H. K. Townes).
Bangalore—Department of Entomology, University of Agricultural Sciences, Bangalore, India (B. Mallik).
Berlin—Humboldt University Museum, Berlin, Germany (F. Koch).
Bishop—Bernice P. Bishop Museum, Honolulu, Hawaii (G. M. Nishida).
BMNH—The Natural History Museum, London (G. R. Else).
Budapest—Hungarian Natural History Museum, Budapest, Hungary (J. Papp).
CAS—California Academy of Sciences, San Francisco (N. D. Penny).
CMNH—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (C. W. Young).
CN—Canadian National Museum, Ottawa, Canada.
CU—Cornell University, Ithaca, New York (G. C. Eickwort).
Delhi—Indian Agricultural Research Institute, New Delhi, India (S. Ghai).
Genoa—Museo Civico di Storia Naturale, Genova, Italy (V. Raineri).
FSAG—Faculté des Sciences Agronomiques de l' Etat, Zoologie Générale et Appliquée, Gembloux, Belgium (A. Pauly).
Hokkaido—Entomological Institute, Hokkaido University, Sapporo, Japan (S. F. Sakagami).
IZAS—Institute of Zoology, Academy of Sciences, Beijing, China (Y. Wu).
LNHM—Natural History Museum of Los Angeles County, California (R. R. Snelling).
Leiden—Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands (C. van Achterberg).
MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts (J. M. Carpenter).
NMNH—National Museum of Natural History, Smithsonian Institution, Washington, D.C. (R. J. McGinley).
Osaka—Osaka City University, Osaka, Japan.
Oxford—Hope Department of Entomology, Oxford University Museum, Oxford, England (C. O'Toole).
Paris—Muséum d'Histoire Naturelle, Paris, France.
SMUK—Snow Entomological Museum, University of Kansas, Lawrence, Kansas (C. D. Michener).
UPLB—Museum of Natural History, University of the Philippines at Los Baños, College, Laguna, Philippines (C. R. Baltazar).
USUL—Systematics and Bee Biology Laboratory, Utah State University, Logan, Utah (T. Griswold).
ZM—Zoologisk Museum, Copenhagen, Denmark (B. Petersen).

CHARACTERS

Comments on the characters used in distinguishing the species are given so that the reader may have an idea of the limitations of these characters. Furthermore, comments are also included on some characters that differ in importance in different areas and species groups. The terminology is that of Michener (1975) except as otherwise indicated for the male genitalia.

a) Body length. Measured with ocular micrometer with the body in lateral view. This is only a rough approximation because of the variations in the position of the head and metasoma and the telescoping of the latter.

b) Color of labrum and mandible. Yellow labrum and mandibles are common in males but not in females. Males with lobed and excised hind trochanters have yellow mandibles and labrum while those with simple trochanters have a yellow labrum and black mandibles. A few females have yellowish mandibles, e.g., *B. reducta*, *B. reversa*, *B. signata*, *B. palavanica*, *B. aurantipes* and *B. clarihirta*.

c) Clypeal mark. This character is quite useful in the females, especially when used in combination with other characters such as head width and type and color of hairs on T4–6. The clypeus is either entirely yellow (Figs. 73, 80) or partly black below with the clypeal mark narrowing toward the apex (Figs. 67, 69), or the clypeus is largely black with a T-shaped clypeal mark (Figs. 71, 90, 98). In the males, clypeal markings are more extensive, and the yellow on the lower half of the clypeus is seldom reduced.

d) Paraocular mark. Paraocular marks are more common in males than in females. Females of *B. palavanica, B. clarihirta, B. lateralis* and *B. apicalis* have paraocular marks, a character useful in separating females of these four species from those of other oriental species. The utility of this character in males is suspect since there is a tendency for reduction or loss as in *B. palavanica* and *B. hewitti.*

e) Color of pronotal lobe. Unlike the species from Australia, the pronotal lobes are yellow in all oriental *Braunsapis*. This is character 5 in the descriptive format for the Australian species (Reyes, in press), but it is not useful here and therefore is omitted in the descriptions of the oriental species.

f) Color of tegula and axillary sclerites. All the sclerites of the wing bases are referred to as axillary sclerites. Tegular color is relatively consistent in most species and ranges from transparent to slightly infuscated mesally; in a few species it ranges from translucent fuscous to fuscous. Axillary sclerites are yellow in species with transparent tegulae and yellow, mixed or fuscous in those with translucent fuscous or dark tegulae. Most oriental species have transparent tegulae and yellowish axillary sclerites.

g) Head width. This character is especially useful in separating closely related species such as *B. mixta, B. picitarsis, B. philippinensis, B. reversa* and *B. signata.* Measurements in parentheses are those of holotypes.

h) Head width/head length ratio. The heads of oriental species of *Braunsapis* are usually broader than long; only *B. aurantipes* and *B. indica* of the *cupulifera* species group have the head as long as or longer than broad.

i) Malar space. Shorter than width of scape in all oriental species. This is character 9 in the descriptive format for Australian species (Reyes, in press), but it does not have any utility in the discrimination of oriental species and is therefore omitted from the descriptions.

j) Middle of the epistomal suture. Slightly raised in most oriental species and not as useful for separating the oriental species as for those from the Australian region.

k) Length of scape. Larger specimens with head width over 1.53 mm have the scape reaching the front ocellus or sometimes the posterior ocelli, especially in the largest individuals. Smaller individuals with the head width 1.53 mm or less have the scape not reaching the front ocellus.

l) Basitibial plate. This plate is defined posteriorly by a carina that is sometimes indistinct. In contrast to larger individuals from Australia, which usually have a distinctly raised or acute carina ending in a conical protuberance, oriental species have at most a distinct carina while in the majority of species it is indistinct.

m) Hairs on T4–6. The hairs concerned are on the middorsal parts of the fourth to sixth metasomal terga. Lateral parts of the terga have simple hairs over twice as long as the width of scape. The middorsal hairs may be long or short; the former are usually suberect, curved or slanting, while the latter are usually subprostrate or prostrate. The longer hairs may be spiculate (about as long as width of scape) as in *B. mixta* (Fig. 107), blunt as in *B. hewitti* (Fig. 106) or simple as in *B. puangensis* (Fig. 105). Blunt or simple hairs are usually longer than the width of scape. Simple means slender and tapering to a point. The color varies from transparent to light fuscous or fuscous to black. Hair form, length and color are sometimes useful in separating species. Hair colors and forms in males are quite similar to those of females, but may differ slightly, e.g., if the hairs are spiculate and transparent in the female, they may be spiculate or blunt and light fuscous in the male.

n) Male hind trochanter. Either notched midventrally and lobed apically (Fig. 100) or simple (Fig. 99). Hind femora of the males from the oriental region are not modified except for *B. puangensis,* in which they are swollen basally and excised medially on the undersurface (Figs. 101, 102).

o) Male genitalia. Some parts are variable among individuals of the same species and some quite similar in general among the different species. Some parts, however, provide useful specific characters. The form of the dorsal part of the penis valve is a useful character in separating the species, and some terminology is introduced and illustrations are provided to explain the different forms of the penis valve (Figs. 26, 27). The mid-lateral flange of the penis valve (MLF) is a lateral expansion (measured at its greatest width) between the anterior projection (AP) and the posterior projection (PP). The dorso-lateral gap (DLG) is the space between the base of the mid-lateral flange and the apex of the posterior projection of the penis valve. The width of the gap is useful in differentiating some species and appears to be consistent within species. The mid-lateral flange of the penis valve may be broad in some species as in Figures 52, 55 and 60 or entirely absent as in *B. breviceps* (Fig. 7). The ventro-apical plate of the gonocoxite has a number of teeth or peglike projections. The ventro-apical plates (VAP) can be symmetrical or asymmetrical; that is, both the right and left plates have the same number of peglike processes or one plate has fewer peglike processes than the other. The number of peglike processes is quite variable even in individuals found in the same nest, i.e., *B. hewitti* (see below). As in the Australian species, the roof of the genital chamber is wrinkled in all the specimens examined; no oriental species were found having a smooth surface as do some African species (Michener, 1975a). Because examination of genitalia requires dissection, they have not been examined for every male specimen; the number of genitalic dissections is indicated in the descriptions, e.g. (n = 4).

KEY TO FEMALES OF ORIENTAL *BRAUNSAPIS*

1\. T6 scoop-shaped (Fig. 103); mouthparts reduced (Figs. 3, 4); scopa reduced (Fig. 5). 2

— T6 rounded (Fig. 104); mouthparts normal (Figs. 1, 2); scopa developed (Fig. 6) 3

2\. Pronotal collar with yellow mark; tarsi yellow; India . . . . *kaliago*

— Pronotal collar without yellow mark; tarsi dark; Indonesia, Malaysia . . . . . *breviceps*

3\. Head as long as broad 4

— Head broader than long 5

4\. Clypeus largely black, clypeal mark T-shaped (Fig. 98); scopa with patch of dark hairs distally on outer surface of tibia; legs black; head width 1.61 mm; India . . . . *indica*

— Clypeus partly black below, clypeal mark narrowed toward apex (Fig. 96); scopa with silvery hairs; legs orange; head width 1.23 mm; Vietnam . . . . *aurantipes*

5\. Paraocular mark present. 6

— Paraocular mark absent (or a scarcely noticeable fleck) 9

6\. Clypeus partly black below, clypeal mark narrowed toward apex (Figs. 88, 89) 7

— Clypeus entirely yellow (Figs. 77, 86) 8

7\. Clypeus partly black on upper half, clypeal mark slender on lower half, T-shaped, central yellow area smaller than black lateral areas; head width 1.70–1.87 mm; Malaysia, Indonesia . . . . *lateralis*

— Clypeus mostly yellow on upper half, clypeal mark broader on lower half, central yellow area larger than black lateral areas; head width 1.47–1.67 mm; Malaysia, Indonesia . . . . *apicalis*

8\. Scape black underneath; head width 1.63–1.70 mm; longer hairs on T4–6 light brown to fuscous; Malaysia, Indonesia, Philippines . . . . *palavanica*

— Scape yellow underneath; head width 1.32–1.50 mm; longer hairs on T4–6 transparent; Thailand, Malaysia, Singapore, Indonesia, Philippines . . . . . *clarihirta*

9\. Metasomal terga mostly yellow; Sri Lanka, Thailand, Burma, Malaysia *flaviventris*

— Metasomal terga black or nearly so 10

10\. Clypeus entirely yellow; labrum yellow to fusco-ferrugineous 11

— Clypeus partly black below, clypeal mark narrowed toward apex; labrum fusco-ferrugineous to black 13

11\. Tibia and tarsus orange; India . . . . *malliki*

— Tibia and tarsus reddish brown to black. 12

12\. Longer hairs on T4–6 simple, tapering as in Figure 105; head width/length ratio 1.05–1.09; Vietnam, Burma, Thailand, Malaysia, Singapore, Indonesia, Philippines . . . . *cupulifera*

— Longer hairs on T4–6 blunt to spiculate as in Figures 106, 107; head width/length ratio 1.09–1.16; Taiwan, Vietnam, Laos, Thailand, Malaysia, Indonesia, Philippines. . . . . *hewitti*

13\. Mandible yellow or with large yellow mark 14

— Mandible fusco-ferrugineous to black. 16

14\. Clypeus largely black, clypeal mark T-shaped (Fig. 90); longer hairs on T4–6 transparent; Malaysia, Indonesia, Philippines. . . . . *reducta*

— Clypeus partly black below, clypeal mark narrowed toward apex (Figs. 92, 94); longer hairs on T4–6 light brown to fuscous 15

15\. Head width 1.47–1.70 mm; outer surface of scopa with patch of golden hairs; Philippines . . . . *reversa*

— Head width 1.69–1.91 mm; outer surface of scopa with patch of dark brown hairs; Philippines. . . . . *signata*

16\. Head width 1.83–2.00 mm; hairs on T4–6 light brown to fuscous; Vietnam, Laos, Thailand, Malaysia, Singapore, Indonesia, Philippines . . . . *philippinensis*

— Head width 1.73 mm or less; hairs on T4–6 transparent to partly fuscous 17
17. Head width 1.20–1.57 mm 18
— Head width 1.60–173 mm; Pakistan, India, Sri Lanka, Laccadive Arch. . . *picitarsis*
18. Clypeus largely black below, clypeal mark strongly narrowed to a point (Fig. 81); head width/length ratio 1.06–1.11; India, Nepal, Vietnam, Laos, Thailand, Malaysia, Hong Kong, Indonesia . . . . *puangensis*
— Clypeus partly black below, clypeal mark narrowed toward apex (Fig. 65); head width/length ratio 1.14–1.18; Pakistan, India, Sri Lanka . . . . *mixta*

KEY TO MALES OF ORIENTAL *BRAUNSAPIS*

(Males are unknown for *B. flaviventris*, *B. malliki*, *B. apicalis*, *B. lateralis* and *B. indica*)

1. Head broad, 1.24–1.29 times broader than long; mouthparts reduced (as in Figs. 3, 4) 2
— Head less broad, 1.24 times or less broader than long; mouthparts normal (as in Figs. 1, 2) 3
2. Paraocular mark reduced or absent; S8 without upturned spiculum (Fig. 9); penis valve without mid-lateral flange (Fig. 8); gonostylus with single long seta (Fig. 8); Indonesia, Malaysia . . . . *breviceps*
— Paraocular mark present; S8 with short upturned spiculum as in Figure 16; penis valve with reduced mid-lateral flange (Fig. 12); gonostylus with three setae (Fig. 13); India . . . . *kaliago*
3. Hind femur swollen basally, emarginate medially (Figs. 101, 102); India, Nepal, Vietnam, Laos, Thailand, Malaysia, Hong Kong, Indonesia . . . . *puangensis*
— Hind femur at most slightly swollen basally, not emarginate medially (Fig. 99). . . 4
4. Hind trochanter lobed distally and excised medially (Fig. 100); mandible yellow 5
— Hind trochanter simple (Fig. 99); mandible black 10
5. Head width 1.21–1.43 mm; head width/length ratio 1.04–1.09 6
— Head width 1.47–1.91 mm; head width length ratio 1.11–1.19 7
6. Legs orange; Vietnam . . . . *aurantipes*
— Legs fusco-ferrugineous to black except tarsi yellow; Vietnam, Burma, Thailand, Malaysia, Singapore, Indonesia, Philippines . . . . *cupulifera*
7. Paraocular mark present 8
— Paraocular mark absent 9
8. Ventro-apical plate of gonocoxite with sunken peglike processes (Fig. 50); head width/length ratio 1.16–1.22; Malaysia, Indonesia, Philippines . . . . *reducta*
— Ventro-apical plate of gonocoxite with peglike processes not sunken (Fig. 42); head width/length ratio 1.12–1.16; Thailand, Malaysia, Singapore, Indonesia, Philippines . . . . *clarihirta*
9. Head width 1.47–1.57 mm; head width/length ratio 1.20–1.24; Philippines . . . . *reversa*
— Head width 1.60 mm; head width/length ratio 1.15; Philippines . . . . *signata*
10. Paraocular mark absent; head width 1.80–1.97 mm; Vietnam, Laos, Thailand, Malaysia, Singapore, Indonesia, Philippines . . . . *philippinensis*
— Paraocular mark present; head width less than 1.80 mm 11
11. Longer hairs on T4–6 fuscous; Malaysia, Indonesia, Philippines . . . . . . *palavanica*
— Longer hairs on T4–6 transparent to light brown 12
12. Mandible black, sometimes with yellow spot; head width 1.23–1.67 mm; head width/length ratio 1.12–1.19 13
— Mandible yellow; head width 1.60–1.73 mm; head width/length ratio 1.12–1.14; Pakistan, India, Sri Lanka, Laccadive Arch. . . . . *picitarsis*
13. Longer hairs on T4–6 blunt to spiculate; head width 1.23–1.47 mm; Pakistan, India, Sri Lanka . . . . *mixta*

— Longer hairs on T4–6 simple to blunt; head width 1.27–1.67 mm; Taiwan, Vietnam, Laos, Thailand, Malaysia, Indonesia, Philippines. . . . . *hewitti*

THE *BREVICEPS* SPECIES GROUP

The species of this group are social parasites in the nests of other species of *Braunsapis* (Michener, 1966, 1970; Reyes and Michener, 1990). No other oriental species are parasitic so far as known.

The members of this species group are recognized largely by the characters associated with parasitism. This includes reduction of the scopa (Fig. 5) and the mouthparts (Figs. 3, 4), also the short head and the glossy or at most very finely punctured face and the scoop-shaped T6 (Fig. 103). The first two characters are convergent among parasitic species in other areas and therefore not good indicators of close phylogenetic relationships. The mouthparts of *B. breviceps* and *B. kaliago* (Figs. 3, 4) differ from those of non-parasitic species as follows: the maxillary palpus is 4-segmented (6-segmented in non-parasitic species), the second segment of the labial palpus is about as long as the third and fourth segments combined (sometimes over twice as long as the third and fourth combined in non-parasitic species), the galea is shorter than the stipes (about 1.5 times as long as stipes in non-parasitic species), and the glossa is about as long as the stipes (about twice as long as the stipes in non-parasitic species). The recognition of this species group could seem arbitrary, but the two species resemble one another in nearly all other characters and are no doubt close relatives. Furthermore, the males have the mid-lateral flange of the penis valve either reduced as in *B. kaliago* (Fig. 12) or absent as in *B. breviceps* (Fig. 7).

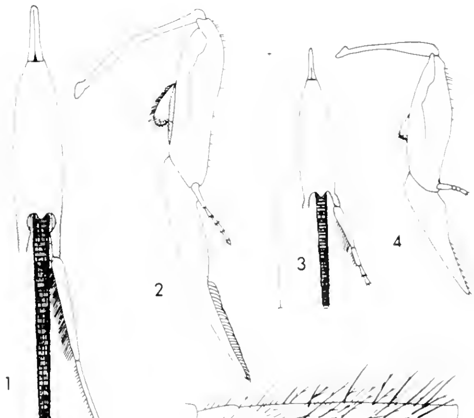
The species group is most closely related to the *mixta* species group and shares with it the following characters: the females have relatively broad heads (broader than in other non-parasitic species) and the males have simple trochanters and femora as in Figure 98.

Braunsapis breviceps (Cockerell)

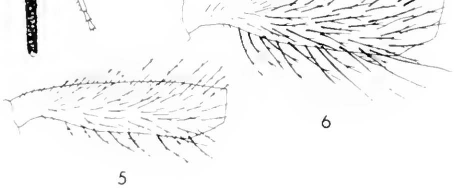
Allodape breviceps Cockerell, 1920b: 623. Type: female, Penang Is., Malaysia (NMNH).
Allodapula breviceps: Michener, 1966a: 705; 1970.
Braunsapis breviceps: Reyes and Michener, 1990.

Female. Face as in Figure 61. (1) Length 5.1–5.7 mm. (2) Labrum ferrugino-testaceous, mandible fusco-ferrugineous. (3) Clypeus entirely yellow, color sometimes reduced near apex. (4) Paraocular mark absent. (*) Scape yellow underneath. (6) Tegula transparent, axillary sclerites yellow or mixed. (7) HW 1.27–1.43 mm (1.43 mm). (8) HW/HL ratio 1.21–1.24 (1.23). (10) Middle of epistomal suture slightly raised. (11) Scape reaching front ocellus. (12) Basitibial plate with carina indistinct. (13) Hairs on T4–5 transparent; longer hairs suberect, blunt, longer than width of scape; shorter hairs subprostrate, spiculate. (*) T6 scoop-shaped, lateral margin produced into slightly elevated shoulder, tip blunt and short, slightly curved upward (Fig. 102).

Male. Face as in Figure 62. (14) Length 4.2–4.5 mm. (15) Labrum yellow, mandible fusco-ferrugineous. (16) Clypeus entirely yellow. (17) Paraocular mark reduced, sometimes just a small spot. (*) Scape yellow underneath. (18) HW 1.33–1.40 mm. (19) HW/HL ratio 1.24–1.27. (20) Hind trochanter simple. (21) Hairs on T4–6 transparent to light brown; longer hairs suberect, blunt, longer than width of scape; shorter hairs subprostrate to slanting, simple. (22) Genitalia (n = 4) as in Figures 7–11; gonostylus rounded apically, with one long seta (Fig. 8); ventro-apical plate of gonocoxite either symmetrical or asymmetrical; right ventro-apical plate with 2 peglike processes and left with 3 peglike processes or both plates with 2 peglike processes (Fig. 10); penis valve with the mid-lateral flange absent (Fig. 8); S8 without upturned spiculum (Fig. 9); roof of genital chamber wrinkled (Fig. 11).



Figures 1–4. Mouthparts: labium and maxilla of female *Braunsapis* from Central Java, Indonesia. Figs. 1, 2. *B. hewitti.* Figs. 3, 4. *B. breviceps.*



Figures 5, 6. Scopa of female *Braunsapis* (redrawn from Michener, 1966). Fig. 5. *B. breviceps.* Fig. 6. *B. simillima* (Smith).

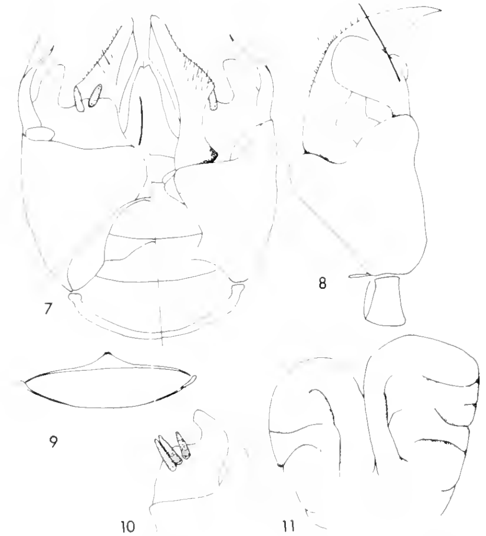
Specimens examined. **Indonesia.** 9 females and 7 males, Boyolali, Central Java, 10-23.v.1973, C.D. Michener (SMUK); 1 male, Bogor, West Java, 15.v.73, C.D. Michener (SMUK); 1 female, Flores, 10-16.vi.27, S.G. Rensch (Berlin). **Malaysia.** 2 females, 1 male, Georgetown, Penang Is., 4.vi.73, C.D. Michener (SMUK); 3 females, 2 males, Ampang, E. of Kuala Lumpur, 3.vi.73, C.D. Michener (SMUK); 1 female (holotype), Penang Is., Baker (NMNH).

Remarks. This is the only Asiatic species that was recognized by Michener (1966a) as parasitic on the basis of adult morphology. This species is quite similar to *B. kaliago.* They are separated by the following characters: the females of *B. breviceps* do not have a yellow mark on the pronotal collar and the tarsi are reddish brown to black; the males lack the mid-lateral flange of the penis valve (Fig. 7), the gonostylus has a single long seta (Fig. 8), S8 does not have an upturned spiculum (Fig. 9), and the paraocular marks are either reduced or absent (Fig. 62).

Biological observations on this species are reported by Reyes and Michener (1990). All specimens taken by Michener were from nests of *B. hewitti* and *B. puangensis.* No specimens of *B. breviceps* were taken on flowers.

Braunsapis kaliago Reyes and Sakagami

Braunsapis kaliago Reyes and Sakagami, 1990: 458. Type: male, Mehruli near Delhi, India (SMUK).



Figures 7-11. Male genitalia of *B. breviceps,* Boyolali, Central Java, Indonesia. Fig. 7. Dorsal (right) and ventral (left) view of male genitalia. Fig. 8. Same, lateral view. Fig. 9. S7 and S8. Fig. 10. Right ventro-apical plate of gonocoxite. Fig. 11. Roof of genital chamber, dorsal view.

Female. Face as in Figure 63. (1) Length 5.3-6.0 mm (5.3 mm). (2) Labrum ferrugino-testaceous, mandible black. (3) Clypeus partly black below, clypeal mark narrowed toward apex. (*) Scape with yellowish mark underneath. (6) Tegula transparent with yellow spot mesally, axillary sclerites yellow. (7) HW 1.33-1.37 mm (1.37 mm). (8) HW/HL ratio 1.28. (11) Scape not reaching front ocellus. (13) Hairs on T4-5 transparent; longer hairs suberect, slightly spiculate at tips, three times longer than width of scape; shorter hairs subprostrate, weakly spiculate. (*) T6 scoop-shaped as in *B. breviceps.*

Male. Face as in Figure 64. (14) Length 5.0 mm. (15) LabrumT (Tyellow, mandible yellow at tip. (17) Paraocular mark present. (18) HW 1.33 mm. (19) HW/HL ratio 1.29. (21) Hairs on T4-6 transparent; longer hairs suberect, slightly spiculate at tips, one and a half times longer than width of scape, shorter hairs subprostrate, weakly spiculate. (22) Genitalia as in Figures 12, 13; ventro-apical plate of gonocoxite with pair of peglike projections (Fig. 12); penis valve with mid-lateral flange reduced, small (Fig. 12); gonostylus slightly narrowing toward apex, with three setae (Fig. 13); S8 with strong upturned spiculum as in Figure 16.

Specimens examined. **India.** 1 female, 1 male (holotype), Mehruli, Delhi, 6-8.iii.88, L.R. Batra and S.W.T. Batra (SMUK); 1 female, same data except (Hokkaido); 1 female, Hissar (Bee Shelter), 4.iv.84, F.B. Parker (USUL).

Remarks. B. kaliago is quite similar to *B. breviceps,* but differs from it by the following characters: the females have a pair of yellowish spots on the pronotum and the tarsi are entirely yellow; the males have a yellow paraocular mark, S8 has an upturned spiculum, the penis valve has reduced mid-lateral flange (Fig. 12) and the gonostylus has three setae (Fig. 13).

THE *MIXTA* SPECIES GROUP

The males of this species group have simple hind trochanters and femora (Fig. 99) and the females have more or less broad heads. The mid-dorsal part of the penis valve of the males appears quadrate when viewed from above and the mid-lateral flange is usually rounded on its posterior margin (Figs. 22, 26, 31). The ventro-apical plate of the gonocoxite has the mesal process less developed (Figs. 18-20) in contrast to that of the *puangensis* species group. The simple trochanter and the genitalic features above may represent an ancestral state compared to those of the *cupulifera* species group (see below).

The females of *B. mixta, B. picitarsis* and *B. philippinensis* have the clypeus partly black below with the clypeal mark narrowed toward the apex (Figs. 67, 69, 71). The females of *B. hewitti, B. flaviventris* and *B. malliki,* on the other hand, have the clypeus entirely yellow (Figs. 73, 76, 80). In addition to the yellow clypeus, the females of *B. palavanica* have paraocular marks (Fig. 77).

Braunsapis mixta (Smith)

Prosopis mixtus Smith, 1852: 50. Type: female, India (BMNH); Meade-Waldo, 1923: 24 (placed under *Allodape*).

Allodape marginata Smith, 1854: 230. Type: female, "East Indies?" (BMNH) (**New synonymy**).

Allodape parvula Smith, 1879: 98. Type: female, Bombay, India (BMNH) (**New synonymy**).

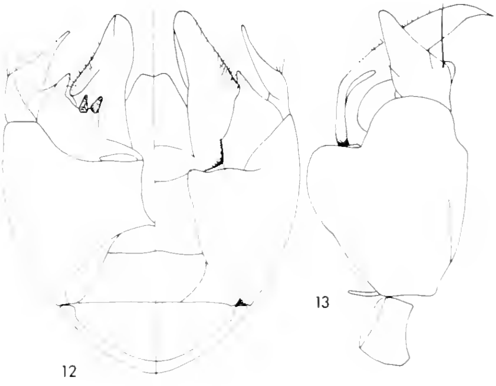
Prosopis leucotarsis Cameron, 1897. Type: female, Ceylon; Cockerell, 1921: 363 (placed under *Allodape*); Meade-Waldo, 1923: 24 (placed as synonym of *A. mixta*).

Allodape pumilio Cockerell, 1911: 182. Type: female, Karachi, N.W. India (= Pakistan) (BMNH) (**New synonymy**).

Female. Face as in Figure 65. (1) Length 3.8-6.1 mm. (2) Labrum black, sometimes with small yellow spot, mandible black. (3) Clypeus partly black below, sometimes mostly yellow. (4) Paraocular mark absent. (*) Scape with small yellow mark underneath, sometimes absent. (6) Tegula transparent, axillary sclerites yellow. (7) HW 1.23-1.57 mm (1.43 mm). (8) HW/HL ratio 1.14-1.18 (1.14). (10) Middle of epistomal suture slightly raised. (11) Scape not or barely reaching front ocellus. (12) Basitibial plate with carina indistinct. (13) Hairs on T4-6 transparent, longer hairs slanting, spiculate; shorter hairs subprostrate, spiculate (Fig. 107).

Male. Face as in Figure 66. (14) Length 3.6-4.9 mm. (15) Labrum yellow to fusco-ferrugineous, mandible black. (16) Clypeus entirely yellow. (17) Paraocular mark present, sometimes reduced. (*) Scape with yellow mark underneath, sometimes reduced. (18) HW 1.23-1.47 mm. (19) HW/HL ratio 1.14-1.19. (20) Hind trochanter simple. (21) Hairs on T4-6 transparent; longer hairs slanting to suberect, blunt to spiculate; shorter hairs prostrate, spiculate. (22) Genitalia (n = 5) as in Figures 14-20; gonostylus tapering toward apex, with one short seta (Fig. 15); ventro-apical plate of gonocoxite asymmetrical, right plate with 2 or 3 peglike processes, left plate with 3 or 4 peglike processes (Figs. 18-20); penis valve with mid-lateral flange narrowed and with rounded posterior margin, dorso-lateral gap narrow, gap about twice as long as the mid-lateral flange (Fig. 14); S7 and S8 as in Figure 16; roof of genital chamber wrinkled (Fig. 17).

Specimens examined. **Pakistan.** 2 females (including holotype of *A. pumilio*), Karachi (BMNH); 5 females, 1 male, Karachi, 22.vi.71, M.T (TShadab (AMNH); 27 females, 4 males, Sind, Karachi, 26.vii-25.viii.72, M. Shadab (AMNH); 3 females, 1 male, same data except (SMUK); 2 females, Hyderabad, 5.viii.72, M. Shadab (AMNH); 3 females, Lasbella Prov., 8 km S. of Bella, 27.iii.65, J.W. Neal (NMNH); 2 females, Lahore (= West Punjab), 19.iv.08, G.R. Dutt (Delhi). **India.** 2 females (including lectotype) (BMNH); 9 females, Bankipur, Bengal, 25.x.11, T.B.F. (Delhi); 1 female, 1 male, Pusa, Bengal (= Bihar), 21.v-x.07, G.R. Dutt (Delhi); 1 male, Pusa, Bengal (= Bihar), 11.ix.08, T.N.T. (Delhi); 1 female, Vengurla, Maharashtra, 25.viii.83, B. Mallik (Bangalore); 3 females, V.C. Farm, Madya, 10.viii.82, B. Mallik (Bangalore); 17 females, 3 males, Poona (= Pune), W. India, 3.ix.66-1975 (Oxford); 1 male, Poona, xi.67, F.L. Wain (SMUK); 18 females, 1 male, Lonaula, W. Ghats, W. India, 7.xi.61-28.v.76 (Oxford); 22 females, 1 male, Lonaula, W. Ghats, 17-18.v.63, F.L. Wain (Hokkaido); 2 females, Kakay, W. Ghats, 14.ii.63, F.L. Wain (Hokkaido); 1 female, Keukau Matteirau, W. India, 22.xii.65 (Oxford); 2 females, Kerala Alwaye, S. India, 11.iii.70 (Oxford); 1 female, Punjab Agri. College, Ludhiana Campus, Punjab, 28.ix.64, S.W.T. Batra (SMUK); 12 females, Cholasahib Vill., Amritsar Dist., Punjab, 5.x.64-27.iv.65, S.W.T. Batra (SMUK); 1 female, Hissar, Punjab, 28.ii.65, S.W.T. Batra (SMUK); 7 females, Chandigarh, Punjab, 17.iv.65, S.W.T. Batra (SMUK); 1 female, Kakanakote Forest Sta., Mysore, 8.i.65, S.W.T. Batra (SMUK); 2 females, Chandigarh, Punjab, 17.iv.65, S.W.T. Batra (MCZ); 1 male, Tanjore, 28.x, P.S. Nathan (MCZ); 1 female, Karakal, Tanjore, ix.51, P.S. Nathan (NMNH); 2 females (including holotype of *A. parvula*), Bombay (NMNH); 1 female, Lonavia, 2000 ft., Bombay, 16.v.59, F.L. Wain (SMUK); 2 females, Delhi, 25.xii.64 (SMUK); 1 female, 1 male, Coimbatore, Madras (= Tamil Nadu), 30.iii.78 (Hokkaido); 1 female, Coimbatore, Madras (= Tamil Nadu), ix.64, P.S. Nathan (SMUK); 1 female, Coimbatore, Madras (= Tamil Nadu), 11.vii.49, P.S. Nathan (NMNH); 5 females, 2 males, 10-15 km N.W. of Udagamandalam (= Ooty), 1500-2000 m,

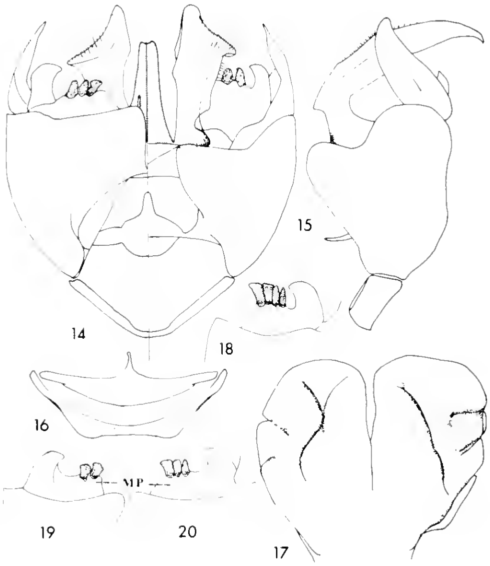


Figures 12, 13. Male genitalia of *B. kaliago* (holotype), Mehruli, Delhi, India. Fig. 12. Dorsal (right) and ventral (left) view of male genitalia. Fig. 13. Same, lateral view.

Tamil Nadu State, 17.viii.90, C.D. Michener (SMUK); 37 females, 3 males, Mudumalai Wildlife Sanctuary, 1000–1200 m, 30 km N.W. of Udagamandalam (=Ooty), Tamil Nadu State, 13–16.viii.90, C.D. Michener (SMUK); 2 females, Mudumalai Preserve, 1100 m, 30 km N.W. of Udagamandalam (=Ooty), Tamil Nadu State, 16.viii.90, C.D. Michener (SMUK); 2 females, Mudumalai Preserve, 5 km S. of Theppakadu, Tamil Nadu State, 13.viii.90, W.T. Wcislo (SMUK); 35 females, 1 male, Madras, x.73, I. Kudo (Hokkaido); 10 females, 1 male, same except (SMUK); 3 females, Adyar, Madras (=Tamil Nadu), 12.viii.73, I. Kudo (Hokkaido); 5 females, City Park, Madras, 19.viii.73, I. Kudo (Hokkaido); 1 female, Calcutta, 14.iv.72, T. Matsumura (Hokkaido); 1 female, Calcutta, 24.i.78 (Hokkaido); 1 female, 4 males, Calcutta and Rungtong, 28.i–1.ii.1897 (CN); 1 female, Lampoon, 25.ii.58 (Hokkaido); 2 females, 3 males, Mehruli, Delhi, 6–8.iii.88, L.R. Batra and S.W.T. Batra (Hokkaido); 1 female, Delhi, x.58, N.L.H. Krauss (NMNH); 1 female, Mormugao, Goa, vi.25, J.C. Bridwell (NMNH); 2 females, Goa, 26–27.xi.27, H. Schmidt (Berlin); 1 female, Bulandshahr, 15.iii.07, Bingham (Berlin); 4 females, Deesa (NMNH); 14 females, 2 males, Deesa (BMNH); 1 female, Dacca, 22.viii.45, D. Leston (BMNH); 2 males, Dohnavur, Tinnevelly District, 10.x.38 (BMNH); 1 female, Burrakpore, 31.i.78 (Hokkaido); 1 female, 1 male, Belgaum, Bombay Prov. (=Karnataka), 2500 ft., 10.viii.10, T.B.F. (Delhi); 10 females, 3 males, Ullal, Cashew Res. Stn., Mangalore, Karnataka State, 18–28.viii.83, B. Mallik (Bangalore); 7 females, 1 male, 12 km N. of Yelburga, Karnataka State, 23–27.xi.80, K.D. Ghorpade (ZM); 3 females, Bangalore, Karnataka State, 2.i.65, S.W.T. Batra (SMUK); 6 females, Bangalore, 1000 m, Karnataka State, 10–19.viii.90, C.D. Michener (SMUK); 5 females, 2 males, Bangalore, Karnataka State, 18.ii.77–30.iii.80, K.D. Ghorpade (ZM); 1 female, 1 male, Bangalore, Karnataka State, 25.iv.78–7–23.v.80 (ZM); 2 females, Bannerghatta, Bangalore, Karnataka State, 27–31.x.77, Zool. Mus. Copenhagen Exp. (ZM). **Sri Lanka.** 28 females, 12 males, Colombo, iii.57, Perera (SMUK); 11 females, 4 males, Yakkala Estate, 20 mi. N.E. of Colombo, Western Province, 5–10.viii.59, R.L.A. Perera (SMUK); 4 females, 1 male, Mediriginya, North Central Province, 21–27.iii.58, R.L.A. Perera (SMUK); 2 females, Hiniduma, Southern Province, 20–28.ii.58, R.L.A. Perera (SMUK); 6 females, 3 males, Gampaha Botanic Garden, Colombo Dist., 28.i.79, K.V. Krombein, P.B. Karunaratne, T. Wiijesinhe, S. Siriwardane, T. Gunawardane (NMNH).

Remarks. The type of *Allodape leucotarsis* from Sri Lanka could not be located. Based on the description of Cameron (1897), it appears similar to *B. mixta* in size, clypeal marking and color of scopa. Meade-Waldo (1923) first proposed the synonymy and is followed in this paper. The type of *Allodape marginata* is similar to *B. mixta* in having the same clypeal marking, transparent tegula, yellow axillary sclerites, transparent and weakly spiculate longer hairs on T4–6. The type of *Allodape parvula* is headless but every preserved character such as the form and color of metasomal hairs on T4–6, color of tegula, basitibial carina and scopa is the same as *B. mixta*. The type of *Allodape pumilio* has a smaller head width (1.30 mm) compared to the type of *B. mixta* (1.43 mm) but is otherwise similar to the latter. The cotype (=paratype) of *A. pumilio* is headless but also similar in other body characters to *B. mixta*. All are within the range of variation found in other specimens that I attribute to *B. mixta*.

Sympatric populations of *B. mixta* and *B. picitarsis* occur in India, Pakistan and Sri Lanka. *B. mixta* is distinguished from *B. picitarsis* by its relatively small size; the head is broader (HW/HL ratio 1.14–1.18 in females) compared to most oriental species and the hairs on T4–6 are slanting and spiculate. The male is separated from



Figures 14–20. Male genitalia of *B. mixta,* Mehruli, Delhi, India. Fig. 14. Dorsal (right) and ventral (left) view of male genitalia. Fig. 15. Same, lateral view. Fig. 16. S7 and S8. Fig. 17. Roof of genital chamber, dorsal view. Fig. 18. Left ventro-apical plate of gonocoxite, male from Mehruli, India. Figs. 19, 20. Ventro-apical plates of the gonocoxites, left and right plates, respectively, from Colombo, Sri Lanka. MP, mesal process of ventro-apical plate.

B. picitarsis by its broader head (HW/HL ratio 1.14–1.19) and smaller size as indicated by the head width (1.23–1.43 mm). Eleven females from Madras have the clypeus mostly yellow. Six females from Sind, Pakistan, three from Lonaula, W. Ghats and eight from Sri Lanka have the scape yellow underneath.

Braunsapis picitarsis (Cameron)

Allodape picitarsis Cameron, 1902: 60. Type: female, Minikoi Is., Laccadive Arch. (BMNH).

Female. Face as in Figure 67. (1) Length 5.8–7.7 mm. (2) Labrum and mandible black. (*) Scape yellow underneath. (7) HW 1.53–1.80 mm (1.67 mm). (8) HW/HL ratio 1.09–1.14 (1.09). (10) Middle of epistomal suture raised. (11) Scape reaching front ocellus. (12) Basitibial plate indicated by weak carina. (13) Hairs on T4–6 transparent to light brown; longer hairs slanting to suberect, simple to weakly spiculate; shorter hairs subprostrate, simple.

Male. Face as in Figure 68. (14) Length 5.2–5.8 mm. (15) Labrum yellow, mandible black. (17) Paraocular mark present, sometimes reduced or absent. (*) Scape yellow underneath. (18) HW 1.60–1.77 mm. (19) HW/HL ratio 1.12–1.14. (21) Hairs on T4–6 transparent to light brown; longer hairs suberect, simple; shorter hairs subprostrate, simple. (22) Genitalia (n = 3) as in Figures 21–23, ventro-apical plate of gonocoxite with 3 peglike processes (Fig. 21); penis valve with mid-lateral flange broad, posterior margin quadrate as seen dorsally, dorso-lateral gap about as wide as mid-lateral flange (Fig. 22); gonostylus longer than broad, with one small seta (Fig. 23).

Specimens examined. **Pakistan.** 3 females, Lasbella Prov., 8 km S. of Bella, 27.iii.65, J.W. Neal (NMNH). **India.** 4 females, Karikal, Pondicherry State, ii.64, P.S. Nathan (SMUK); 2 females, Chandigarh, Punjab, 17.iv.65, S.W.T. Batra (SMUK); 1 female, Saproon, 5000 ft., Punjab, 16.iv.65, S.W.T. Batra, (SMUK); 2 females, Mussoorie Kemty Falls, 4000 ft., Uttar Pradesh, 16.x.64–25.vi.65, S.W.T. Batra (SMUK); 1 female, Bombay, Maharashtra, 11–15.iii.17, G.R. Dutt (Delhi); 1 female, Pusa, Bengal (= Bihar), 18.ix.08, R.D.D. (Delhi); 1 female, Pusa, Bihar, 28.iv.15, Boy Coll. (Delhi); 1 male, Palnis, Kodaikanal, Tamil Nadu, x.21, Fletcher Coll. (Delhi); 41 females, 2 males, Coimbatore, 1400 ft., Tamil Nadu, ix.64–xi.65, P.S. Nathan (SMUK); 1 female, Mudumalai Wildlife Sanctuary, 1200 m, 30 km N.W. of Udagamandalam (= Ooty), Tamil Nadu State, 16.viii.90, C.D. Michener (SMUK); 1 female, Mudumalai Preserve, Center for Ecological Studies, 4.viii.90, C.D. Michener (SMUK); 1 female, Coimbatore, 1400 ft., Tamil Nadu, xi.65, P.S. Nathan (NMNH); 1 female, Poonmudi Range, 3000 ft., Trivandrum District, Kerala State, v.72, T.R.S. Nathan (SMUK); 1 female, City Park, Madras, 19.viii.73, I. Kudo (Hokkaido); 1 female, 1 male, Belgaum, Bombay Prov. (= Karnataka), 10.viii.10, T.B.F (Delhi); 4 females, Ullal, Cashew Res. Stn., Mangalore, Karnataka, 18–28.vii.83, B. Mallik (Bangalore); 1 female, Nagarhole, Mysore, Karnataka, 4.ix.82, B. Mallik (Bangalore); 2 females, Bangalore, Karnataka State, 2.i.65, S.W.T. Batra (SMUK); 1 female, Bangalore, Karnataka State, 26.i.78, I. Kudo (Hokkaido); 1 female, Bangalore, 1000 m, Karnataka State, 18-19.viii.90, C.D. Michener (SMUK); 4 females, 1 male, Nedungadw, Tanjore, 1–2.vi, P.S. Nathan (MCZ); 4 females, 1 male, Poona (= Pune), 16.viii.66–21.X.74 (Oxford); 1 female, Ranchi, iv.57, G. Pingalet (NMNH); 2 females, Calcutta, 1.ii.1897 (CN); 1 female, Bandra, Jayakar (BMNH). **Sri Lanka.** 9 females, Colombo, iii.57, R.L.A. Perera (SMUK); 4 females, 1 male, Medirigaya, North Central Province, 21–27.iii.58, R.L.A. Perera (SMUK); 1 female, 1 male, Yakkala Estate 20 mi. N.E. of Colombo, Western Province, 5–10.viii.59, R.L.A. Perera (SMUK); 1 male, Galkissa 7 mi. S. of Colombo, Western Province, 4.v.59, R.L.A. Perera (SMUK); 1 female, Kullupitiya, Colombo District, 6.xi.78, G. Ratynaweera (NMNH); 1 female, Colombo, 22.viii.58 (Oxford). **Laccadive Arch.** 8 females (including lectotype), 2 males, Minikoi Is., 20.vi.00, J.S. Gardiner (BMNH); 1 female, 1 male, Feridhu Is., 4°3′N 72°42′W, Maldive Is., 5.x.88, P.S. Kevan (SMUK); 2 females, Aridhu Is., 3°30′N 72°51′W, 30.ix.88, P. Kevan (SMUK); 1 female, North Male Atoll, Maldive Is., 26.i.57, W.W.A. Phillips (BMNH).

Remarks. The female of *B. picitarsis* is quite similar to that of *B. mixta*, especially in the facial marking (Figs. 65, 67). However, the head of the former (HW/HL ratio 1.09–1.14) is narrower than that of *B. mixta* and also larger (at least in those populations found in Sri Lanka and India, head width 1.60–1.73 mm). The males are quite similar to those of *B. mixta* and *B. hewitti* but differ from these two species by their larger size (Fig. 68) and yellow mandibles.

Braunsapis philippinensis (Ashmead)

Prosopis philippinensis Ashmead, 1904: 5. Type, female, Manila, Luzon, Philippines (NMNH); Cockerell, 1916: 302 (placed under *Allodape*); 1919: 191.

Allodape mindanaonis (Cockerell), 1915: 109. Type: female, Dapitan, Zamboanga, Mindanao, Philippines (NMNH) (**New synonymy**).

Allodape marginata picitarsis Cameron: Cockerell, 1916: 302 (distr. Philippines) (misidentification).

Female. Face as in Figures 69, 71. (1) Length 6.1–8.2 mm. (2) Labrum and mandible black. (3) Clypeus partly black, sometimes clypeal mark T-shaped. (6) Tegula transparent, sometimes slightly infuscated, axillary sclerites yellow or mixed. (7) HW 1.73–200 mm (1.97 mm). (8) HW/HL ratio 1.11–1.14 (1.14). (10) Middle of epistomal suture raised. (11) Scape reaching front ocellus. (13) Hairs on T4-6 light brown to fuscous; longer hairs slanting, blunt to spiculate; shorter hairs subprostrate, spiculate.

Male. Face as in Figures 70, 72. (14) Length 5.6-7.3 mm. (15) Labrum yellow, sometimes reduced, mandible black. (16) Clypeus partly black, clypeal mark sometimes reduced to longitudinal mark. (17) Paraocular mark present, reduced or absent. (18) HW 1.77-1.97 mm. (19) HW/HL ratio 1.11-1.15. (*) Tarsi dark. (21) Hairs on T4-6 fuscous; longer hairs slanting to suberect, blunt; shorter hairs subprostrate, weakly spiculate. (22) Genitalia (n=8) as in Figures 24-28; ventro-apical plates of gonocoxite asymmetrical, right plate with 3-4 peglike processes and left plate with 4-6 peglike processes (Figs. 24, 25); penis valve with mid-lateral flange wider than in *B. mixta* with posterior margin rounded, dorso-lateral gap narrow, slightly less than the width of mid-lateral flange (Figs. 26, 27); gonostylus longer than broad, with one to two setae (Fig. 28).

Specimens examined. **Vietnam.** 7 females, Dai Lanh N. of Nha Trang, 30.xi-5.xii.60, C.M. Yoshimoto (Bishop). **Laos.** 2 females, 1 male, Wapi, Wapikhamthong Prov., 15.x.67 (Bishop); 1 female, Tha Ngone, Vientiane Prov., 6.ix.65 (Bishop); 2 females, Ban Van Eue, Vientiane Prov., 13.iv.65, J.L. Gressitt (Bishop); 1 female, Phou-kow-kuei, 800 m, N. of Vientiane, 17.iv.65, J.L. Gressitt (Bishop); 1 female, Dong Dok, 30.ix.65 (Bishop); 1 female, Nongtevada, 4.xi.65 (Bishop); 1 female, Gi. Sion Vill., de Tha Ngone, Vientiane, 24-31.x.66 (Bishop); 1 female, Pakse, Sedone Prov., 31.v.67 (Bishop); 1 female, Savannakhet, Savannakhet Prov., 15.iii.67 (Bishop); 1 female, Paksane, Borihane Prov., 15.xi.65 (Bishop). **Thailand.** 1 female, Bangkok, 14.ix.35, C. Tongyai (CU); 3 females, Koh Tao, 17.ix.28, H.M. Smith (NMNH); 3 females, Phet Chanburi, 3.ix.79, A. Pauly (FSAG); 1 female, Yala, 3.viii.76, A. Pauly (FSAG); 1 female, Kanchana Buri, 7.ix.76, A. Pauly (FSAG); 3 females, Bangkok, 3.vii.61, K. Iwata (Hokkaido); 1 female, Banna, 5-10.v.58, T.C. Maa (Bishop). **Malaysia.** 3 females, near Gombak, 12 mi. N.E. of Kuala Lumpur, 1.vi.73, C.D. Michener (SMUK); 3 females, Fraser's Hill, 12-16.ix.68, R. Jander (Hokkaido); 1 female, Fraser's Hill, 25.xii.64, R. Oghgushi (Hokkaido). **Singapore.** 1 male, vi.29, R.H.V. van Zwaluwenburg (Bishop). **Indonesia.** 2 females, Krakatau, v.08, E. Jacobson (Paris); 1 female, Petapan, Kangean Is., iii.36, K.M. Walsh (BMNH); 1 female, Tenggarong, Loa Teback, Borneo, 5.vii.37, K.M. Walsh (BMNH); 9 females, 10 males, Sumbawa, S.G. Rensch (Berlin); 1 female, Endeh, Flores, 4.vi.29, I.M. Mackerras (NMNH); 1 female, Endeh, Flores, 15.ii.27 (Berlin); 1 female, 2 males, Flores, S.G. Rensch (Berlin); 1 female, Medan, L. Fumek (Berlin); 10 females, 2 males, Waai, Ambon Is., 27.xi.64-15.i.66, A.M.R Wegener (Bishop). **Philippines.** 6 females, 5 males, Abatan, Bugias, 600 km S. of Bontoc, 1800-2000 m, 19-20.v.64, H.M. Torrevillas (Bishop); 1 male, Mayoyao, Ifugao, Mt. Province, 1200-1500 m, 2-3.viii.66, H.M. Torrevillas (Bishop); 2 males, Wa-wa Dam, 150-200 m, Mt. Montalban, Rizal, 1.iii.65, H.M. Torrevillas (Bishop); 1 female, 1 male, Baguio, Benguet, C.F. Baker (NMNH); 1 female, Wackwack, Rizal Prov., 12.ix.45, R.P. Dow (MCZ); 4 females, Biliran Is., C.F. Baker (NMNH); 1 female, Batbatan Is., 18.vi, R.C. McGregor (NMNH); 1 female, Lamao, Luzon (Leiden); 2 females, 2 males, Manila, 18.ii.74, I. Kudo (Hokkaido); 1 female (holotype of *P. philippinensis*), Manila, W.A. Stanton (NMNH); 1 female, Bureau of Agriculture, Manila, C.R. Jones (NMNH); 19 females, 3 males, 24.vii.19-xi.25, Manila, R.C. McGregor (NMNH); 1 female, 12.ii.19, Manila (NMNH); 13 females, 6 males, Mt. Makiling (=Maquiling), Laguna, C.F. Baker (NMNH); 11 females, 6 males, Mt. Maquiling, 50 m, Laguna, x.45-27.vii.48, L.B. Uichanco (UPLB); 2 females, 1 male, Mt. Maquiling, Laguna, 7.i.51-1.vii.59, C.R. Baltazar (UPLB); 3 females, Los Baños, Laguna, C.F. Baker (BMNH); 1 female, Los Baños, Laguna, E.M. Ledyard (NMNH); 17 females, 1 male, Los Baños, Laguna, C.F. Baker (NMNH); 2 females, Los Baños, vii.16, F.X. Williams (Bishop); 1 female, Los Baños, x-xi.15, F. Muir (Bishop); 4 females, 1 male, San Pablo, Laguna, 25.ii.74, I. Kudo (Hokkaido); 1 male, Mt. Banahaw, Quezon, C.F. Baker (NMNH); 1 female, 1 male, Guinobatan, Albay, 7.ix.54, L.B. Uichanco (UPLB); 2 females, 1 male, Cagusos, Libon, 200 m, Albay, 18-19.v.65, H.M. Torrevillas (Bishop); 1 female, Mt. Isarog, Pili, 800-900 m, Camarines Sur, 22.iv.65, H.M. Torrevillas (Bishop); 10 females, Lian area, Batangas, 19-27.vii.86, C.K. Starr (LNHM); 1 female, 8 males, San Antonio, Sto. Tomas, Batangas 14.xii.85, C.K. Starr (LNHM); 1 female, 2 males, Nasugbu, Batangas, 28.ii.58, H. Townes (AEI); 1 female, Rosario, La Union, 30.xi.53, H. Townes (AEI); 1 female, Hagonoy, Abulalas, Bulacan, 1.xi.86, C.K. Starr (LNHM); 1 female, Paggudpud, Balao, Ilocos Norte, 24-25.v.87, C.K. Starr (LNHM); 2 females, 1 male, Kalaukalau, Negros Occ., 20.ix (Bishop); 1 female, Culasi, Panay Is., vi.18, R.C. McGregor (AMNH); 1 female, Culasi, Panay, vi.18, McGregor (NMNH); 1 female, Palo, Leyte, 27.v.57 (Bishop); 1 female, Mindoro, xii.21, F.X. Williams (Bishop); 1 female, Puerto Princesa, Palawan, C.F. Baker (NMNH); 1 female, Puerto Princesa, R.C. McGregor (NMNH); 2 females, Ursula Island at South Palawan, 2.x.61, Noona Dan Exp. 61-62 (ZM); 1 female, Dalwan Bay, Balabac, 11.x.61, Noona Dan Exp. 61-62 (ZM); 3 females, 1 male, Cuernos Mts., Negros, C.F. Baker (NMNH); 1 female, Tacloban, Leyte, C.F. Baker (NMNH); 1 female, San Jose, Dadiangas, Cotabato, 3.viii.50, G.B. Viado (UPLB); 55 females (including holotype of *A. mindanaonis*), 14 males, Dapitan, Mindanao, C.F. Baker (NMNH), 5 females, 3 males, same data except (SMUK).

Remarks. The female type of *B. mindanaonis* has the clypeus mainly black with the clypeal mark T-shaped (Fig. 71), while in *B. philippinensis* the clypeus is partly black below and the clypeal mark narrows toward the apex (Fig. 69). Furthermore, the male from Mt. Makiling, Luzon has only 4 peglike processes on its left ventro-apical plate while the one from Mindanao has 5 processes. The number of processes on the ventro-apical plate, however, is quite variable within the species, ranging from 3 to 4 on the left plate and from 4 to 6 on the right plate. The gonostylus has two small hairs (Fig. 28); or the one near the apex is sometime absent. In most characters the nominal species are alike; for example both have light brown to dark and blunt to spiculate longer hairs on T4–6; therefore *B. mindanaonis* is synonymized under *B. philippinensis.* Cockerell (1916) identified two females from Baguio, Benguet, Philippines as *A. marginata picitarsis*, but based on the morphology and distribution of the specimens, these fit the desciption for *B. philippinensis.* This species is easily distinguished from other species of *Braunsapis* by its large size and light brown to dark longer hairs on T4–6.

Eight females from Thailand have the clypeus mostly yellow (quite similar to *hewitti*) and the longer hairs on T4–6 light brown. Unfortunately there are no associated males. It is quite possible that these females represent a different species. However, the females and male from Laos fit the description for *B. philippinensis,* and probably the population in Thailand is a variant among other mainland populations. Males usually have dark longer hairs on T4–6 and dark tarsi, but 2 males from Manila, 5 males from Mt. Makiling, Laguna, 10 males from Waai, Ambon and 10 males from Sumbawa, Indonesia have yellow tarsi and light brown to brownish hairs on T4–6.

***Braunsapis hewitti* (Cameron)**

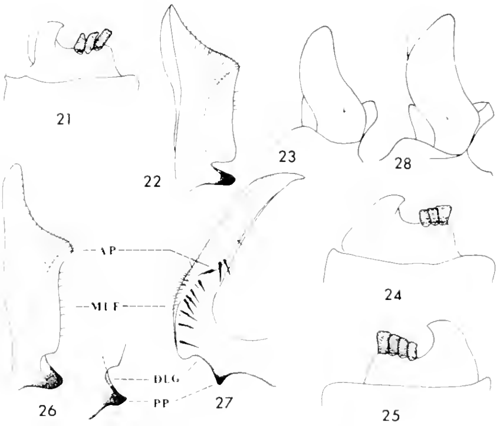
Prosopis hewitti Cameron, 1908: 565. Type: female, Kuching, Sarawak, Borneo, Malaysia (BMNH); Meade-Waldo and Morley, 1914: 403 (placed under *Allodape*).

Allodape sauteriella Cockerell, 1916: 303. Type: female, Formosa (= Taiwan) (NMNH); Cockerell, 1929: 149 (distr. Thailand) (**New synonymy**).

Female. Face as in Figure 73. (1) Length 4.0–6.5 mm. (2) Labrum yellow to fusco-ferrugineous; mandible black, sometimes with yellow mark. (3) Clypeus entirely yellow, sometimes lower half partly black with clypeal mark narrowing toward apex. (*) Scape sometimes with yellow mark underneath. (7) HW 1.27–1.73 mm (1.40 mm). (8) HW/HL ratio 1.09–1.16 (1.10). (11) Scape either not reaching or reaching front ocellus. (13) Hairs on T4–6 transparent to light brown; longer hairs slanting to suberect, blunt to spiculate; shorter hairs subprostrate, simple to blunt (Fig. 106).

Male. Face as in Figures 74, 75. (14) Length 4.0–5.3 mm. (15) Labrum yellow, mandible black. (17) Paraocular mark present or absent. (*) Scape yellow underneath. (18) HW 1.27–1.67 mm. (19) HW/HL ratio 1.12–1.19. (21) Hairs on T4–6 transparent to light brown; longer hairs suberect, simple to blunt; shorter hairs subprostrate, weakly spiculate. (22) Genitalia (n = 12) as in Figures 29–34; ventro-apical plate of gonocoxite either symmetrical or asymetrical with 1–4 peglike processes (Figs. 32–34); penis valve with mid-lateral flange narrow with rounded posterior margin and dorso-lateral gap narrow, less than width of mid-lateral flange (Fig. 31); gonostylus longer than broad, slightly more tapered apically (Fig. 30) compared to *B. palavanica* (Fig. 35).

Specimens examined. **China.** 2 females, Hainan Is., 6.iv.60, Li Chang-xing (IZAS). **Taiwan.** 3 females (including holotype of *A. sauteriella*), Takao, 11.x–21.xi.07, H. Sauter (NMNH); 2 females, Takao, 15.x.07–xi.17, H. Sauter (BMNH); 3 females, Pilam, v–viii.12, H. Sauter (BMNH); 53 females, 2 males, Takao, 1907, Sauter (Budapest); 1 female, Taihanroku, 1908,



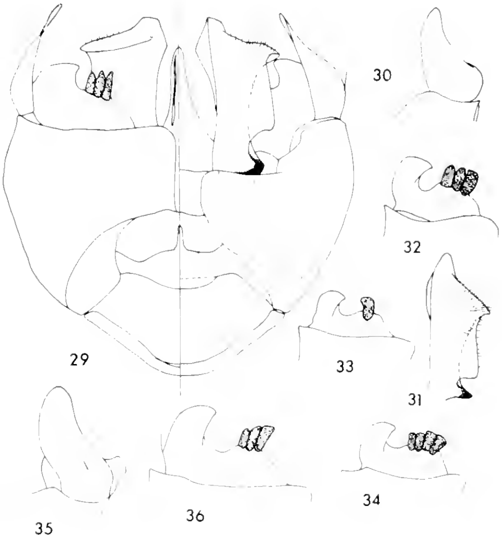
Figures 21–23. Male genitalia of *B. picitarsis,* Columbo, Sri Lanka. Fig. 21. Ventro-apical plate of the gonocoxite. Fig. 22. Penis valve, dorso-apical view. Fig. 23. Gonostylus, lateral view.

Figures 24–28. Male genitalia of *B. philippinensis,* Mt. Makiling, Luzon, Philippines. Figs. 24, 25. Ventro-apical plates of the gonocoxite, left and right plates, respectively. Fig. 26. Penis valve, dorso-apical view. Fig. 27. Same, lateral view. Fig. 28. Gonostylus, lateral view. AP, anterior projection; MLF, mid-lateral flange; DLG, dorso-lateral gap; PP, posterior projection.

Sauter (Budapest); 1 male, Ins. Lambeh, 1908, Sauter (Budapest); 3 females, 3 males, Kengting Park, 3.v.80, Y. Maeta (SMUK); 2 females, Szuchunhsi, 5.v.80, Y. Maeta (SMUK); 7 females, 1 male, Pingilin, 27.iv-4.v.74, M. Shiokawa (Hokkaido); 4 females, Wushe, 1150 m, 2.v.83, H. Townes (AEI); 1 female, Taitung Hsein, i-ii.64, T.C. Maa (Bishop); 2 females, Kwantau Shih, Nantou, 18.iv.73, S. Yamane (Hokkaido); 1 female, Juisui, Hualien County, 2.v.80, Sk. Yamane (Hokkaido); 2 females, 1 male, Oluanpi, 6.v.76, M.A. Lieftinck (Leiden); 1 female, Shihmen nr Hengchuen, 7.v.76, M.A. Lieftinck (Leiden). **Thailand.** 1 female, Sam Ngao at Bhumipol Dam, 6-8.xi.79, Zool. Museum Exp. Copenhagen (ZM); 1 female, Konthathan waterfall area, 600 m, Doi Suthep-Pui National Park, 20-27.x.79, Zool. Museum Exp. Copenhagen (ZM); 1 female, Hua Hin, W. Coast of Siam Gulf, 8.viii.79, B. Petersen (ZM); 2 males, Paklua, N. of Pathaya, E. coast of Siam Gulf, 11-13.xi.79, Zool. Museum Copenhagen Exp. (ZM); 1 female, Doi Intanom, 8.vi.58, K. Yoshikawa (Hokkaido); 1 female, Chieng Dao, 4.xii.62, S. Nakao (Hokkaido); 4 females, Kanchana Buri, 7-9.ix.76, A. Pauly (FSAG); 1 female, 1 male, Surat-Thani, 27.viii.76, A. Pauly (FSAG); 1 female, Nong Kai, 25.xii.62, S. Nakao (Hokkaido); 1 female, Doi Suthep, 18.-xi.62, S. Nakao (Hokkaido); 1 female, Chieng Mai (=Chiang Mai), 300 m, Chieng Mai Prov., 2.x.81, Zool. Museum Copenhagen Exp. (ZM); 2 males, Chiengmai (=Chiang Mai), 12.iii.61, K. Iwata (Hokkaido); 3 males, Chiangmai (=Chiang Mai), Fang, 5-19.iv.58, T.C. Maa (Bishop); 2 females, Banna, 108 m, 5-10.v.58, T.C. Maa (Bishop). **Laos.** 2 males, Paksong, Sedone Prov., 17.v.65, P.D. Ashlock (Bishop); 1 female, Muong SingT (TN.W. of Luang Prabang, 650 m, 6-10.vi.60, S. and L. Quate (Bishop); 1 female, Luang Prabang, 300 m, 4-5.vi.60, L.W. Quate (Bishop); 1 female, Nongtevada, 4.xi.65 (Bishop); 1 female, Wapi, Wapikhamthong Prov., 31.v.67, (Bishop); 3 females, Gi Sion Vill. of Nha Ngone, Vientiane, 721.ii.65-24-31.x.66 (Bishop); 2 females, Sayaboury, Sayaboury Prov., 25.viii.66 (Bishop). **Vietnam.** 19 females, 1 male, Ninh Hoa N. of Nha Trang, 28.xi.60, C.M. Yoshimoto (Bishop); 24 females, Dai Lanh, N. of Phan Rang, 30.xi-5.xii.60, C.M. Yoshimoto (Bishop); 1 female, 15-35 km N.W. of Phan Rang, 8-16.xi.60, C.M. Yoshimoto (Bishop); 1 female, Ban Me Thuot, 500 m, 16-18.v.60, L.W. Quate (Bishop); 1 female, Di Linh (Djiring), 22-28.iv.60, L.W. Quate (Bishop); 1 female, Karyu, Danar, 200 m, 13-28.ii.61, N.R. Spencer (Bishop). **Hong Kong.** 1 female, v.58, N.L.H. Krauss (Bishop). **Malaysia.** 46 females, 8 males, George Town, Penang Is., 4.vi.73, C.D. Michener (SMUK); 1 female, Penang Is., C.F. Baker (NMNH); 3 females, 1 male, Penang Is., 12.vi-12.vii.55, H.T. Pagden (BMNH); 5 females, 5 males, Kuala Lumpur, 4.viii-7.xi.29, H.T. Pagden (BMNH); 24 females, 10 males, Kuala Lumpur, 2.iv-10.xii.35 (BMNH); 10 females, 1 male, Kuala Tahan, Malaya, 26-31.viii.70, R. Jander (Hokkaido); 4 females, 1 male, Kuala Tembeling, Malaya, 30.ix.68, R. Jander (Hokkaido); 1 male, Penan, Malaya, 3-4.x.68, R. Jander (Hokkaido); 2 females, Selangor, 15.ix.21-15.iv.26 (BMNH); 1 female, Kota Kinabalu, Sabah, 24.v.85, P.J. and J.O. Schmidt (SMUK); 5 females, Kota Kinabalu, Sabah, 24.v.85, J.O. Schmidt and C.K. Starr (LNHM); 1 female, Forest Camp, 19 km. N. of Kalabakan, 30.xi.62, K.J. Kuncheria (Bishop); 1 female, Ranau, 30.ix-5.x.58, L.W. Quate (Bishop); 2 males, Pangkalan Tabang, Bau District, Sarawak, Borneo, 300-400 m, 5-8.-ix.58, T.C. Maa (Bishop); 1 female (holotype of *A. hewitti*), Kuching, Borneo (BMNH); 1 female, Kuching, Sarawak, 8.ix.66, Ocusea (Hokkaido); 16 females, 2 males, Sandakan, Borneo (NMNH); 1 female, Tawau, Tawau Residency, 19.xi.58, T.C. Maa (Bishop). **Indonesia.** 1 female, Lang Eiland, Krakatau, v.08, E. Jacobson (Paris); 4 females, 2 males, Semarang, Java, 1906, E. Jacobson (Paris); 2 males, Batavia (=Jakarta), Java, ii-xi.08, E. Jacobson (Paris); 7 females, Oedjoeugkoelon, Bantain, Java, 12-13.ix.42, M.A. Lieftinck (Leiden); 5 females, Genteng Bay, Java, 1-2.vii.39, M.A. Lieftinck (Leiden); 2 females, 1 male, Baai, Batavia (=Jakarta), 15.x.38, M.A. Lieftinck (Leiden); 36 females, 10 males, Boyolali, 450 m, Central Java, 10-23.v.73, C.D. Michener (SMUK); 4 females, 1 male, 15 km W. of Boyolali, 1500 m, 10.v.73, C.D. Michener (SMUK); 3 females, 1 male, Bogor, West Java, 15.v.73, C.D. Michener (SMUK); 1 male, Buitenzorg (=Bogor), 8.xi.53, M.A. Lieftinck (Leiden); 2 females, Djasinga, Java, 2.viii.52, M.A. Lieftinck (Leiden); 3 females, Sumatra, ii.38, L.E. Cheesman (BMNH); 2 females, Tekuk Kabung Road, Padang Painan, Sumatra, 16.x.80, R. Ohgushi, S.F. Sakagami and T. Inoue (Hokkaido); 1 female, Bengen River, Tabang, 125 m, Borneo, 29.viii.56, A.M.R. Wegner (Leiden); 1 female, Kangean, 19.viii.54, A. Hoogerwerf (Leiden); 1 female, Komodo Is., vi.53, A. Hoogerwerf (Leiden); 2 females, Toraut, 211 m, Dumoga-Bone N. Pk., 47 km W.S.W. of Kotamobagu, Sulawesi, iv-v.85, G.R. Else (BMNH); 14 females, Ranu River, Tengah, Sulawesi, 11-19.v.80, P. Kevan (SMUK); 1 female, Petapan, Kangean Is., iii.36, K.M. Walsh (BMNH); 11 females, Kampung Pasir Puti, Jalilolo Dist., Halmahera Is., ii.81-1-4.vi.81, A.C. Messer and P.M. Taylor (NMNH); 16 females, 12 male, Sumbawa, S.G. Rensch (Berlin); 12 females, 6 males, Flores, S.G. Rensch (Berlin); 1 female, S. Batjan, Moluccas, vi-vii.53, A.M.R. Wegner (Leiden). **Philippines.** 3 females, 4 males, Uring Uring, Brookes Point, Palawan, 16-26.viii.61, Noona Dan Exp. 61-62 (ZM); 4 females, Dalawan Bay, Balabac, 5-12.x.61, Noona Dan Exp. 61-62 (ZM); 1 male, Ursula Island at South Palawan, 2.x.61, Noona Dan Exp. 61-62 (ZM); 1 female, 92 males, Aborlan, Isla Sombero, Palawan, 20.ii.87, C.K. Starr (LNHM); 1 female, San Antonio, Sto. Tomas, Batangas, 14.xii.85, C.K. Starr (LNMH); 1 female, Lian area, Batangas, 19–27.vii.86, C.K. Starr (LNMH); 1 female, Balaoi, Pagudpud, Ilocos Norte, 24–25.v.87, C.K. Starr (LNHM); 1 female, 2 males, nr. Kias, Mt. Prov., 31.x.53, Townes Family (AEI); 1 female, Arayat Natl. Park, Arayat, Pampanga, 11.v.77, C.R. Baltazar (UPLB); 3 males, Labrador, Pangasinan, 16.iii.67, M.A. Alviar (UPLB); 1 female, Hagonoy, Bulacan, 1.xi.86, C.K. Starr (LNHM); 1 female, Rees Road, Rizal Prov., 14.x.45, R.P. Dow (MCZ); 1 female, Dinalupihan Municipality, 5.5 mi. W. of Culo, Bataan Prov., 16.ix.45 (MCZ); 1 female, R. Brown, no locality (NMNH); 8 females, 10.xi.19–xi.25, Manila, R. C. McGregor (NMNH); 1 male, Manila, R. C. McGregor (CU); 1 female, Manila, R. Brown (NMNH); 2 females, Mt. Makiling (=Maquiling), Laguna, C.F. Baker (NMNH); 7 females, 5 males, Mt. Maquiling, 50 m, Laguna, 22.vi.48–24.v.50, L.B. Uichanco (UPLB); 1 female, Los Baños, Laguna, C.F. Baker (NMNH); 1 female, Los Baños, Laguna, C.F. Baker (AMNH); 2 females, Los Baños, Laguna, 2.vii.–5.xii.47, L.B. Uichanco (UPLB); 1 female, Los Baños, vii.16, F.X. Williams (Bishop); 1 female, Batangas, 30.i.60, B.P. Gabriel (UPLB); 1 female, Biliran Is., Baker (NMNH); 1 female, Guinobatan, Albay, 7.ix.54, L.B. Uichanco (UPLB); 4 females, 2 males, Sibuyan Is., C.F. Baker (NMNH); 1 male, Sulat, San Francisco, Samar, 24.iv.87, C.K. Starr (LNHM); 1 female, Negros Occ., 20.ix (Bishop).

Remarks. The type of *B. hewitti* (HW 1.40 mm) is similar to that of *B. sauteriella* (HW 1.60 mm) except that it is smaller. Earlier, the population found in Taiwan was treated under the name *sauteriella*. Five females from Pingilin, Taiwan are smaller (HW 1.37–1.50 mm) and six females from the type locality (Takao, Taiwan) are also relatively small (HW 1.43–1.50 mm), compared to the type of *B. sauteriella* (HW 1.60 mm). All the females have the clypeus entirely yellow, the longer hairs on T4–6 transparent and simple to blunt, the labrum yellow and the mandibles black. The same is true for the males. The ventro-apcal plate of the gonocoxite has 1 (n = 1) or 3 (n = 4 individuals from the same nest) peglike processes in the Indonesian population (Figs. 32, 33), 2 to 4 (n = 3 individuals from the same nest) in the Malaysian population and 2 to 4 (n = 4) peglike processes in the Taiwan population (Fig. 34). The number of peglike processes on the ventro-apical plate therefore varies among individuals found in the same nest as well as those found in the same locality. The size differences between the types as well as the differences in the number of the peglike processes on the ventro-apical plate of the gonocoxite of the males led me, at first, to think that these two are different species. However, variability in the number of peglike processes among the oriental and Australian species is quite common. Furthermore, the size differences do not show a bimodal distribution as would be expected if two species were involved. *Allodape sauteriella* is therefore synonymized under *B. hewitti*.

Females of *B. cupulifera* cannot be readily separated from those of *B. hewitti* except for the hairs on T4–6, which are simple in the former and blunt to spiculate in the latter. Furthermore, the head of *B. hewitti* (HW/HL ratio 1.09–1.16) is slightly broader than that of *B. cupulifera* (HW/HL ratio 1.05–1.09). The relatively large females of *B. hewitti* from Java and Malaysia (HW 1.53–1.63 mm) have their antennal scape reaching the front ocellus, while the smaller ones (HW 1.27–1.50 mm) have the scape not or barely reaching the front ocellus; this variation is known in other species that vary in size. The males of *B. mixta* are also not easily distinguished from *B.*



Figures 29–34. Male genitalia of *B. hewitti*, Boyolali, Central Java, Indonesia. Fig. 29. Dorsal (right) and ventral (left) view of male genitalia. Fig. 30. Gonostylus, lateral view. Fig. 31. Penis valve, dorso-apical view. Figs. 32, 33. Ventro-apical plates of gonocoxite, individuals from the same nest from Boyolali, Central Java. Fig. 34. Ventro-apical plate of gonocoxite, individual from Pingilin, Taiwan.

Figures 35, 36. Male genitalia of *B. palavanica*, Puerto Princesa, Palawan, Philippines. Fig. 35. Gonostylus, lateral view. Fig. 36. Ventro-apical plate of gonocoxite.

hewitti except for the longer hairs on T4-6, which are blunt to spiculate in the former and simple to blunt in the latter. In addition, *B. hewitti* is limited to the Southeast Asian region while *B. mixta* is found only in India, Pakistan and Sri Lanka.

Ten females from Sulawesi, Indonesia, and four from Wushe, Taiwan, have yellow mandibles and yellow marks under the scape. Forty females from Vietnam, ten from Sumbawa, seven from Java and Sumatra, five from Halmahera, five from Sulawesi, nine from Laguna, and three from Manila and Bataan have the lower half of the clypeus partly black with the clypeal mark narrowing toward the apex. Three males from Taiwan, one from Thailand, two from the Philippines and three from Indonesia have the paraocular mark either reduced or absent.

The life cycle, nesting biology and social behavior of this species (under the name *Braunsapis sauteriella*) from Taiwan were studied by Maeta et al. (1984, 1985), Sakagami (1960) and Shiokawa and Michener (1977).

Braunsapis flaviventris, n. sp.

Holotype: female, Nabon, Thailand, 15.vii.61, K. Iwata (SMUK). *Paratypes:* 2 females, same data as holotype except (Hokkaido).

Female. Face as in Figure 76. (1) Length 4.6-5.2 mm. (2) Labrum yellow, mandible black. (3) Clypeus entirely yellow. (7) HW 1.37-1.40 mm (1.37 mm). (8) HW/HL ratio 1.14-1.19 (1.14). (11) Scape barely reaching front ocellus. (13) Hairs on T4-6 transparent; longer hairs slanting, weakly spiculate, longer than width of scape; shorter hairs prostrate, weakly spiculate. (*) Metasomal terga largely yellow.

Additional specimens examined. **Sri Lanka.** 1 female, no locality (BMNH). **Burma.** 1 female, Mandalay, 15.ix.00, Bingham (Berlin). **Malaysia.** 1 female, Relau, Penang, 12.xi.56, H.T. Pagden (BMNH).

Remarks. The female has a yellowish clypeus (Fig. 76), its head (HW/HL ratio 1.14-1.19) relatively broader than that of *B. cupulifera* and the longer hairs on T4-6 transparent and weakly spiculate. This species is almost identical to *B. hewitti* and it is possible that these females may be just atypical specimens of *B. hewitti.* Collection of the males and the nest of this species will clarify whether this is really a good species. It is quite remarkable, however, in having yellowish metasomal terga; this character also separates it from all other oriental species of *Braunsapis.*

The name *flaviventris* is derived from the Latin *flavus,* meaning yellow, plus the Latin *venter,* meaning abdomen, referring to the largely yellow metasomal terga of the species.

Braunsapis palavanica (Cockerell)

Allodape palavanica Cockerell, 1916: 303. Type: female, Puerto Princesa, Palawan, Philippines (NMNH).

Female. Face as in Figure 77. (1) Length 5.5-7.3 mm. (2) Labrum yellow, mandible sometimes with yellow mark. (3) Clypeus entirely yellow. (4) Paraocular mark present. (*) Scape yellow underneath, sometimes absent. (7) HW 1.63-1.77 mm (1.70 mm). (8) HW/HL ratio 1.07-1.11 (1.11). (10) Middle of epistomal suture raised. (11) Scape reaching front ocellus. (13) Hairs on T4-6 light brown to fuscous; longer hairs suberect, simple to blunt; shorter hairs prostrate, simple.

Male. Face as in Figures 78, 79. (14) Length 5.5-6.4 mm. (15) Labrum yellow, mandible black. (*) Scape yellow underneath, sometimes absent. (18) HW 1.63-1.73 mm. (19) HW/HL ratio 1.11-1.14. (21) Hairs on T4-6 fuscous; longer hairs suberect, simple to blunt; shorter hairs prostrate, simple. (22) Genitalia (n = 5) as in Figures 35, 36; ventro-apical plate of gonocoxite with 3 peglike processes (Fig. 36); gonostylus longer than broad, with one seta (Fig. 35); penis valve as in *B. hewitti.*

Specimens examined. **Malaysia.** 1 female, Fraser Hill, 25.xii.64, R. Ohgushi (Hokkaido); 1 female, Ranau, 8 mi. N. of Paring Hot Spring, 500 m, W. Coast Residency, N. Borneo, 8-11.-x.58, L.W. Quate (Bishop); 1 female, Ranau, 500 m, W. Coast Residency, N. Borneo, 7.x.58, T.C. Maa (Bishop). **Indonesia.** 1 female, Sungai Dareh, Sumatera Barat, 5.i.81, S. Yamane (Hokkaido); 1 female, Ranu River, Tengah, Sulawesi, 11.ii.80, P. Kevan (SMUK). **Philippines.** 10 females (including holotype), 3 males, Puerto Princesa, Palawan, C.F. Baker (NMNH); 14 males, Aborlan, Isla Sombrero, Palawan, 20.-ii.87, C.K. Starr (LNHM); 1 female, Macagua, 75 m, Brooke's Point, Palawan, 1-4.iv.62, M. Thompson (Bishop); 2 females, Uring Uring, Brookes Point, Palawan, 16-26.vii.61, Noona Dan Exp., 61-62 (ZM); 7 females, Pinigisan, 600 m, Mantalingajan, Palawan, 2-22.ix.61, Noona Dan Exp. 61-62 (ZM).

Remarks. The female of this species is readily distinguished by having paraocular facial marks (Fig. 77) and fuscous hairs on T4-6. The presence of the paraocular marks is shared with *B. clarihirta, B. apicalis* and *B. lateralis. B. clarihirta* is relatively smaller (HW 1.32-1.60 mm), the scape has a yellow mark underneath and the longer hairs on T4-6 are transparent. *B. apicalis* and *B. lateralis* have the lower half of the clypeus partly black and the longer hairs on T4-6 light brown. Two females from Borneo and three females from Palawan have small yellow spots on their mandibles. The males of *B. palavanica* have simple trochanters and the longer hairs on T4-6 fuscous. They are quite similar to males of *B. philippinensis* and *B. picitarsis* but can be separated from the first by their smaller size (HW 1.63–1.73 mm) and the yellow clypeus (Figs. 78, 79) with the clypeal mark not reduced as in *B. philippinensis* (Figs. 70, 72) and from *B. picitarsis* (Fig. 68) by having the paraocular mark either reduced or absent (Figs. 78, 79).

Braunsapis malliki, n. sp.

Holotype: female, Cashew Research Station, Ullal, Mangalore, India, B. Mallik (BMNH). *Paratypes:* 2 females, same data as holotype except (Bangalore); 2 females, same except (Delhi); 2 females, same except (SMUK); 1 female, same except (BMNH).

Female. Face as in Figure 80. (1) Length 4.8–5.6 mm. (2) Labrum yellow, mandible fusco-ferrugineous to black. (3) Clypeus entirely yellow. (*) Scape yellow underneath. (7) HW 1.48–1.67 mm (1.53 mm). (8) HW/HL ratio 1.13–1.18 times broader than long. (11) Scape barely reaching or reaching front ocellus. (13) Hairs on T4–6 light brown; longer hairs slanting, spiculate, longer than width of scape; shorter hairs prostrate, spiculate. (*) Tibia and tarsus orange.

Remarks. This species is easily separated from other species occurring in India by the yellow clypeus and the orange tibiae and tarsi. It is also similar to *B. hewitti* (which does not occur in India) in having a yellow clypeus, but differs from it by having light brown hairs on T4–6 and the legs partly orange. Furthermore, the face is slightly more convex and glossy compared to females of *B. hewitti*.

This species is named for Dr. B. Mallik of the University of Agricultural Sciences, Bangalore, India, for his contribution to the knowledge of parasitic Hymenoptera, and for his interest in bees.

THE *PUANGENSIS* SPECIES GROUP

This species group includes only one species. However, the males are quite distinctive in having the hind femur swollen basally and emarginate on the undersurface (Figs. 101, 102), the penis valve with a hairy lobe on the posterior margin of the mid-lateral flange (Figs. 39, 40) and the ventro-apical plate of the gonocoxite reduced medially (Figs. 37, 38, 40). The females are quite similar to those of *B. mixta* except that the lower half of the clypeus is mostly black, the clypeal mark narrower toward the apex and the head less broad than in *B. mixta*. It is possible that this species is a derived member of the *mixta* species group, as is suggested by the number of uniquely derived features found in the males described below.

Braunsapis puangensis (Cockerell)

Allodape puangensis Cockerell, 1929: 149. Type: female, Kum Perang Creek, Thailand (NMNH).

Allodape iwatai Sakagami, 1961: 424. Type: female, Cheng Mai (=Chiang Mai), Thailand (Osaka) (**New synonymy**) Holotype lost; **neotype,** female, Cheng Mai (=Chiang Mai), Thailand (SMUK).

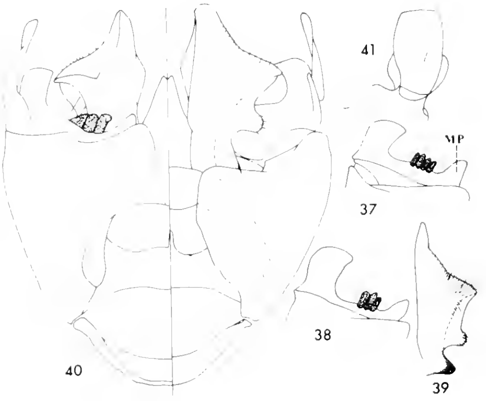
Female. Face as in Figure 81. (1) Length 4.2–6.7 mm. (2) Labrum fusco-ferrugineous, mandible black. (3) Clypeus partly black below with clypeal mark narrowing to a point toward apex. (4) Paraocular mark absent. (*) Scape sometimes yellow underneath. (6) Tegula transparent, axillary sclerites yellow. (7) HW 1.20–1.60 mm (1.34 mm). (8) HW/HL ratio 1.06–1.11 (1.11). (10) Middle of epistomal suture slightly raised. (11) Scape not reaching front ocellus. (12) Basitibial plate with carina indistinct. (13) Hairs on T4–6 transparent to partly fuscous; longer hairs slanting to suberect, simple to spiculate; shorter hairs prostrate, simple to weakly spiculate (Fig. 105).

Male. Face as in Figure 82. (14) Length 4.0–5.2 mm. (15) Labrum yellow, mandible black. (16) Clypeus entirely yellow. (17) Paraocular mark absent. (18) HW 1.13–1.43 mm. (19) HW/HL ratio 1.10–1.13. (20) Hind trochanter simple. (*) Hind femur emarginate medially, swollen basally (Figs. 100, 101). (*) Tarsi dark. (21) Hairs on T4–6 fuscous; longer hairs suberect, simple; shorter hairs prostrate, simple. (22) Genitalia (n=5) as in Figures 37–41; ventro-apical plate of gonocoxite reduced medially, with 3 to 4 peglike processes (Figs. 37, 38, 40); penis valve with mid-lateral flange expanded and posterior margin lobed and hairy, dorso-lateral gap less than width of mid-lateral flange (Fig. 39, 40); gonostylus truncate at apex, with one small seta (Fig. 41); S8 with upturned spiculum as in Figure 16; roof of genital chamber wrinkled.

Specimens examined. **India.** 1 male, Chandigan, Punjab, India, 17.iv.65, S.W.T. Batra (SMUK); 3 females, 3 males, Punjab Agri. Univ., Ludhiana Campus, Punjab, India, 17.v.65, S.W.T. Batra (SMUK); 1 female, same except ix.64 (SMUK); 2 females, Abbottabad, Uttar Pradesh, 10.vi.16, Fletcher Coll. (Delhi); 1 female, Coimbatore, 1400 ft., Madras (=Tamil Nadu), S. India, ix.64, P.S. Nathan (SMUK); 1 female, Walayar, Kerala, 29.i.78 (Hokkaido); 5 females, Poona (=Pune), W. India, 29.x.66–21.iv.67 (Oxford); 1 female, same except (NMNH); 1 female, Katra, Ghats, W. India, x.58 (Oxford); 5 females, 1 male, Lonaola, W. Ghats, W. India, 9.iv.66–29.iv.67 (Oxford); 1 female, same except (BMNH); 1 female, Deesa (NMNH); 1 female, Deesa (BMNH); 2 females, Goa, 23.xi.27–22.viii.31, H. Schmidt (Berlin); 3 females, Kengeri, near Bangalore, Karnataka, 1.v.82, B. Mallik (Bangalore); 1 female, 916 m, Bangalore, Karnataka, 25.iv.78 (ZM); 1 female, Jeolikote, 21 km N.W. of Kathgodam, Kumaon, 1800 m, 7.x.78, M.A. Lieftinck (Leiden). **Nepal.** 1 female, 2 males, Katmandu, 23-26.iii.68, T. Matsumura (Hokkaido); 1 male, Godavari, Napal Valley, 26.iii.68, T. Matsumura (Hokkaido); 2 females, Bonuwa, 28.v.68, T. Matsumura (Hokkaido); 1 female, Dana, Palpla, 3.v.68, T. Matsumura (Hokkaido); 1 female, Pokhara, 25.v.68, T. Matsumura (Hokkaido). **China.** 3 females, Hainan Is., 10-340 m, Li Chang-xing and Zhang Xue-zhong (IZAS); 1 female, Xishuangbana, 650 m, Yunnan Prov., 14.vii.58, Zhang Eh-ren (IZAS). **Thailand.** 1 female (holotype of *A. puangensis*), Kum Perang Creek (BMNH); 4 females, Chanta Buri, 17-18.vi.61, K. Iwata (Hokkaido); 1 female, Chienglow, 14.iv.61, K. Iwata (Hokkaido); 1 female, Saraburi, 8.ii.61, K. Iwata (Hokkaido); 1 female, Fang, 29.xi.62, S. Nakao (Hokkaido); 3 females, Cheng Mai (=Chiang Mai), 23-29.i.58, K. Yoshikawa (Hokkaido); 3 females (including neotype of *A. iwatai*), same except (SMUK); 2 females, Chiengmai (=Chiang Mai), F.G. Kerr (BMNH); 1 female, same except (NMNH); 5 females, Kanchana Buri, 7.ix.76, A. Pauly (FSAG); 1 female, Yala, 3.viii.76, A. Pauly (FSAG); 1 female, Surat-Thani, 27.viii.76, A. Pauly (FSAG); 4 females, 12.vii.76, A. Pauly (FSAG); 1 female, Songkla, 16.viii.76, A. Pauly (FSAG); 3 females, 3 males, Nakhon, 108 m, S. Banna, 5-10.v.58, T.C. Maa (Bishop); 1 female, Chawang nr. Nabon, 70 m, 4.ix.58, J.L. Gressitt (Bishop); 1 female, Ban Muak Lek Nat. Park, Saraburi Prov., 5.vi.65 (Bishop). LAOS. 1 female, 1 male, Paksong, Sedone Prov., 17-18.-v.65, P.D. Ashlock (Bishop); 5 females, 3 males, Gi Sion Vill., de Tha Ngone, Vientiane Prov., 9-30.i.66 (Bishop); 1 male, Ban Van Eue, 31.xii.68 (Bishop); 1 male, Paksane, Borikhane Prov., 14.ii.66 (Bishop). **Vietnam.** 3 females, 2 males, Fyan, 900-1,200 m, 11.vii-9.viii.61, N.R. Spencer (Bishop); 7 females, 6 males, Mt. Liang Bian, 1500-2000 m, 19.v-8.vi.61, N.R. Spencer (Bishop); 14 females, 6 males, Dalat 6 km S., 1400-1500 m, 9.iv-7.vii.61, N.R. Spencer (Bishop); 1 female, Dalat, 1500 m, 29.iv-4.v.61, N.R. Spencer (Bishop); 1 km W. of Dalat, 1500 m, 19.ix.60, R.E. Leech (Bishop); 1 female, Karyu Danar, 200 m, 13-28.ii.61, N.R. Spencer (Bishop); 1 female, Ninh Hoa N. of Nha Trang, 28.xi.60, C.M. Yoshimoto (Bishop); 1 female, Ban Me Thuot, 500 m, 16-18.v.60, S. Quate (Bishop); 2 males, Di Linh (Djiring), 900 m, 22-28.iv.60, S. and L.W. Quate (Bishop); 1 male, Di Linh (Djiring), 27.ix-14.x.60, C.M. Yoshimoto (Bishop). **Malaysia.** 27 females, 9 males, Ampang, E. of Kuala Lumpur, 3.vi.73, C.D. Michener (SMUK); 14 females, 6 males, Ampang, nr. Kuala Lumpur, 30.ix.73, P.O. Wah (SMUK); 1 female, 7 males, Kuala Lumpur, 4.viii-22.ix.29, H.T. Pagden (BMNH); 11 females, 7 males, Kuala Lumpur, 15.i.22-5.xii.35 (BMNH); 1 female, 1 male, Kuala Lumpur, xi.35-28.vi.36, H.M. Pendlebury (BMNH); 4 females, 2 males, George Town, Penang Is., 4.vi.73, C.D. Michener (SMUK); 1 female, Sungei, Pinang Hills, Penang Is., 4.vi.73, C.D. Michener (SMUK); 3 females, Penang Is., 12.viii.76, A. Pauly (FSAG); 1 female, Gombak Valley, Selangor, 25.i.31, (BMNH); 1 female, Batang Padang, Perak, 7.iii.24, H.M. Pendlebury (BMNH); 1 female, W. Coast Residency, Ranau, 8 mi. N. of Paring Hot Spring, 500 m, 9-18.x.58, T.C. Maa and L.W. Quate (Bishop); 1 female, Forest Camp, 19 km N. of Kalabakan, 600 m, 21.xi.62, K.J. Kuncheria (Bishop). **Hong Kong.** 1 female, 600 ft., 24.ix.37, Hurford (BMNH).

Remarks. The type and paratype of *Allodape iwatai* could not be located and are presumed lost. Dr. Sakagami kindly searched for the type and the rest of the series that he studied from Thailand but could not find these in the Osaka collection. I, therefore, designate a neotype for *A. iwatai* from the other specimens collected from that same study; the neotype is in SMUK. The female of *A. iwatai* is similar to the female type of *B. puangensis* and the species is therefore judged to be a synonym of *puangensis*.

Aside from the character of the femur, the penis valve of the male is quite distinct in having an expanded mid-lateral flange with a lobed and hairy posterior margin (Fig. 39). The males from Georgetown, Malaysia have 3 peglike processes on the ventro-apical plate (Fig. 38) while a male from Ampang (E. of Kuala Lumpur) has 4 peglike processes (Fig. 37). Females have the clypeal mark narrowing toward the apex, the longer hairs on T4-6 light brown to partly



Figures 37-41. Male genitalia of *B. puangensis,* Malaysia. Figs. 37, 38. Ventro-apical plates of the gonocoxite, from Georgetown (Penang) and Ampang, Malaysia, respectively. Fig. 39. Penis valve, dorso-apical view. Fig. 40. Dorsal (right) and ventral (left) view of genitalia, male from Punjab, India. Fig. 41. Gonostylus, lateral view. MP, mesal process of ventro-apical plate.

fuscous and the head relatively broad (HW/HL ratio 1.08–1.11). Females are somewhat similar in facial markings to some females of *B. cupulifera* from Sumatra, which have a slightly reduced clypeal mark (Fig. 84), but the latter usually have yellow mandibles and scape, the longer hairs on T4–6 are transparent to light brown and simple and the head is less broad (HW/HL ratio 1.05–1.09) than in *B. puangensis*.

Specimens from India are smaller in size as shown by head width (female HW 1.20–1.47 mm; male HW 1.13–1.14 mm) and the longer hairs on T4–6 shorter, transparent and weakly spiculate. The females are sometimes not easily separated from *B. mixta*, which occurs sympatrically in India. The clypeal mark of some females of *B. mixta* approaches that of *B. puangensis* but *B. mixta* differs from the latter by having a relatively broader head (HW/HL ratio 1.14–1.18).

THE *CUPULIFERA* SPECIES GROUP

This species group is readily distinguished by the males having the trochanter excised medially and lobed distally (Fig. 100). Furthermore, the mandibles of both males and females are yellow or with yellow markings. The male genitalia of this species group are variously modified, and at least three subgroups can be distinguished. *B. reducta* has the ventro-apical plate of the gonocoxite notched medially along the apical margin, the peglike processes situated in this concavity (Fig. 50), and the mid-lateral flange of the penis valve with the posterior margin broadly rounded. *B. cupulifera* has the mid-lateral flange acutely angled posteriorly (Fig. 49). *B. reversa* and *B. signata* have the mid-dorsal part of the penis valve subtriangular when viewed from above (Fig. 55) and the mid-lateral flange relatively expanded compared to other species. *B. clarihirta* and *B. aurantipes* have the penis valve relatively more slender compared to other species (Figs. 44, 60). I consider the lobed and excised hind trochanter derived compared to the simple form found in the other species groups, and the different modifications of the genitalia of this species group seem to support that idea. There may be, however, two or more monophyletic groups lumped together in the *cupulifera* species group if the trochanteral modifications have arisen more than once. This problem will be clarified when other characters, especially those of the immatures, are considered in the future.

Females of *B. cupulifera* and *B. clarihirta* have the clypeus entirely yellow and the latter has paraocular marks. Females of *B. reducta, B. reversa* and *B. signata* have the clypeus partly black below; in addition to the latter character, *B. apicalis* and *B. lateralis* have paraocular marks. Females of *B. aurantipes* and *B. indica* have the head as long as or longer than broad.

Braunsapis cupulifera (Vachal)

Allodape cupulifera Vachal, 1894: 447. Type: male, Carin Cheba, 900–1100 m, Birminia (= Burma) (Genoa).
Allodape cupulifera bakeri Cockerell, 1916: 302. Type: male, Los Baños, Laguna, Luzon, Philippines (NMNH) (**New synonymy**).
Allodape hewitti var. *sandacanensis* Cockerell, 1920a: 226. Type: female, Sandakan, Borneo, Malaysia (NMNH) (**New synonymy**).

Female. Face as in Figures 83, 84. (1) Length 4.2-5.9 mm. (2) Labrum yellow to fuscoferrugineous, mandible black, sometimes with yellow mark. (3) Clypeus entirely yellow, sometimes slightly reduced apically. (4) Paraocular mark absent. (*) Scape sometimes yellow underneath. (6) Tegula transparent, axillary sclerites yellow. (7) HW 1.20-1.47 mm. (8) HW/HL ratio 1.05-1.09. (10) Middle of epistomal suture slightly raised. (11) Scape not reaching front ocellus. (12) Basitibial plate indicated by indistinct carina. (13) Hairs on T4-6 transparent to light brown; longer hairs slanting, simple; shorter hairs prostrate, simple.

Male. Face as in Figure 85. (14) Length 3.8-4.6 mm. (15) Labrum and mandible yellow. (16) Clypeus entirely yellow. (17) Paraocular mark present, sometimes slightly reduced. (*) Scape yellow underneath, sometimes black. (18) HW 1.15-1.37 mm (1.37 mm). (19) HW/HL ratio 1.08-1.09 (1.08). (20) Hind trochanter excised medially and lobed distally. (21) Hairs on T4-6 light brown; longer hairs slanting, simple; shorter hairs prostrate, simple. (22) Genitalia (n 10) as in Figures 45-49, ventro-apical plate of gonocoxite with 3-5 peglike processes (Figs. 45-47); penis valve with mid-lateral flange expanded with angulate posterior margin and dorso-lateral gap wider than mid-lateral flange (Fig. 49); gonostylus longer than broad, slightly expanded apically, with one short seta; S8 with an upturned spiculum as in Figure 16; roof of genital chamber wrinkled.

Specimens examined. **Thailand.** 2 females, Ratburi, 15.viii.66, T.C. Maa (Bishop). **Vietnam.** 3 females, Fyan, 1200 m, 11.vii-9.viii.61, N.R. Spencer (Bishop); 1 female, Blao (Balao), 500 m, 14-21.x.60, C.M. Yoshimoto (Bishop); 1 female, Di Linh (Djiring), 1200 m, 22-28.iv.60, L.W. Quate (Bishop); 3 females, Di Linh (Djiring) 27.ix-14.x.60, C.M. Yoshimoto (Bishop); 3 females, Kontum N. of Pleiko, 550 m, S. Quate (Bishop). **Burma.** 1 male (holotype of *A. cupulifera*), Carin Cheba, 900-1100 m (Genoa). **Malaysia.** 1 male, George Town, Penang Is., 4.vi.73, C.D. Michener (SMUK); 1 female, Sungei, Pinang Hills, Penang Is., 30.xi.55, H.T. Pagden (BMNH); 4 females, Pasoh Forest Res., Negri S., 29.x.79-11.v.80, P. and M. Becker (AEI); 1 female, Kuala Lumpur, 27.ix.29, H.T. Pagden (BMNH); 7 females, 1 male, Kuala

Lumpur, 6.vii.26-ix.40 (BMNH); 2 females, 1 male, Kuala Lumpur, 4.i.36-30.iv.39, H.M. Pendlebury (BMNH); 1 female, Sungei Pomsom, Ubu Hangat, 9.ix.28, H.T. Pagden (BMNH); 1 female, Santubong, 797-1500 m, Kuching, Sarawak, Borneo, 26.vi.58, T.C. Maa (Bishop); 1 female, Lake area, Bau, Sarawak, Borneo, 29.viii.58, T.C. Maa (Bishop); 1 female, Sarawak, 19.vi.61, M. Wan (BMNH); 1 male, Ranau, N. Borneo, 30.ix-5.x.58, L.W. Quate (Bishop); 1 female, Sandakan, Borneo, C.F. Baker (AMNH); 13 females (including holotype of *A. hewitti sandacanensis*), 2 males, Sandakan, Borneo, C.F. Baker (NMNH); 1 female, Mt. Kinabalu, 5000 ft., Sabah, 1-5.v.73, K.M. Guichard (BMNH). **Singapore.** 1 female, 1905, H.N. Ridley (BMNH); 2 females, vi.29, R.H.V. van Zwaluwenburg (Bishop); 2 females, 5 males, C.F. Baker (NMNH); 10 females, Bukit Tinak, 12.x.86, J. W. Wenzel (SMUK). **Indonesia.** 20 females, 13 males, Boyolali, 450 m, Central Java, 10.v.73, C.D. Michener (SMUK); 8 females, 15 km W. of Boyolali, 1500 m, Central Java, 10.v.73, C.D. Michener (SMUK); 5 females, Genting Bay, Java, 1.vii.39, M.A. Lieftinck (Leiden); 3 females, Depok, Java, 25.xii.38-18.v.39, M.A. Lieftinck (Leiden); 3 females, Batavia (=Jakarta), Java, 1908, E. Jacobson (Paris); 5 females, Baai, Batavia (=Jakarta), Java, 15.x.38, M.A. Lieftinck (Leiden); 9 females, 1 male, Batavia (=Jakarta), Java, x.07-v.09, E. Jacobson (Leiden); 1 female, Tapos, 800 m, Gedeh, Java, 16.x.32, M.A. Lieftinck (Leiden); 3 females, Tjisaroea, Gedeh, Java, 22.i-14.v.39, M.A. Lieftinck (Leiden); 2 females, Tjisaroea, Mt. Panggerango, 1000 m, Java, 11.i.42-6.vi.48, M.A. Lieftinck (Leiden); 1 female, Panggerango, Mt. Gede, 1450 m, Java, 2.viii.52, Lieftinck (Leiden); 10 females, 1 male, Bogor, West Java, 15.v.73, C.D. Michener (SMUK); 1 female, Buitenzorg (=Bogor), Java (AMNH); 2 females, Buitenzorg (=Bogor), Java 1.i.39-6.iv.53, M.A. Lieftinck (Leiden); 1 female, Oedjoengkoelon, Bantam, Java, 12.ix.42, M.A. Lieftinck (Leiden); 1 female, Djamnangs, Bodjonglopang, Java, 1.i.41, M.A. Lieftinck (Leiden); 1 female, Djampang, Java, xii.39 (Leiden); 1 female, 3 males, Djasinga, Java, 26.xi.39-8.xii.40, M.A. Lieftinck (Leiden); 1 female, Semarang, Java, 1906, E. Jacobson (Paris); 1 female, Java (no locality), v.29, R.H.V. van Zwaluwenburg (Bishop); 4 females, Sibolangit, 450 m, Sumatra, 16-17.xi.50, M.A. Lieftinck (Leiden); 2 females, Mt. Tanggamoes, 600 m, Sumatra, 19-31.iii.40, M.A. Lieftinck (Leiden); 7 females, 1 male, S.W. Lampong Dist., Mt. Tanggamoes, 600 m, Sumatra, xii.39, M.A. Lieftinck (Leiden); 2 females, 4 males, Kampung Pasir Putih, Jailolo Dist., Halmahera Is., 15-31.v.81, A.C. Messer and P.M. Taylor (NMNH); 3 females, Petapan, Kangean Is., iii.36, K.M. Walsh (BMNH); 1 female, Sangkoeling Bay, Borneo, 30.iv.37, K.M. Walsh (BMNH); 1 female, Pelewan Mt., Borneo, vi.37, K.M. Walsh (BMNH); 1 female, Sangeang Is., Lesser Sunda Is., 23.viii.65, J. Winkler (Bishop); 1 female, Flores, S.G. Rensch (Berlin); 1 female, Endeh, Flores, S.G. Rensch (Berlin); 3 females, 2 males, Sumbawa, S.G. Rensch (Berlin). **Philippines.** 1 female, Imugin, Viscaya, C.F. Baker (NMNH); 3 males, Pangasinan, C.F. Baker (NMNH); 12 males, Wa-wa Dam, 150-200 m, Mt. Montalban, Rizal, 27.ii-29. iii.65, L.M. Torrevillas (Bishop); 2 females, 3 males, Palawan, 3 km N.E. of Tinabog, 7-15.v.62, H. Holtmann (Bishop); 3 females, 2 males, Uring Uring, Brookes Point, Palawan, 25.viii.61, Noona Dan Exp. 61-62 (ZM); 1 female, Tarawakan, N. of Batu Batu, Tawi Tawi, 27.x.61, Noona Dan Exp. 61-62 (ZM); 2 males, Pinigisan, 600 m, Mantalingajan, Palawan, 11-22.ix.61, Noona Dan Exp. 61-62 (ZM); 3 females, 1 male, Aborlan, Isla Sombrero, Palawan, 20.ii.87, C.K. Starr (LNHM); 8 males, Canaualan, Pangasinan, 18.iii.36, Roman Abalos (SMUK); 11 females, 1 male, Subic Bay, Grand Is., Luzon, 7.x.-15.xi.67, C.E. Goodpasture (LNHM); 6 females, 1 male, Manila, vi.19.vii.20, R.C. McGregor (SMUK); 12 females, Manila, 19.-xi.25, R.C. McGregor (AMNH); 57 females, 5 males, Manila, 11.ii.19-xi.25, R.C. McGregor (NMNH); 3 females, 1 male, same except (SMUK); 1 female, Manila, 19.xi.25, R.C. McGregor (BMNH); 4 females, Manila, R. Brown (NMNH); 1 female, 1 male, Manila, W.A. Stanton (NMNH); 1 female, Bur. Agr., Manila, C.R. Jones (NMNH); 3 females, 1 male, Manila, R. Brown (NMNH); 1 female, 2 males, Manila, iv-v.24, R.C. McGregor (CU); 1 female, Luzon, V. Rolle (Berlin); 1 female, 11.vi.31, C.S. Banks (MCZ); 1 female, Laguna de Bay nr Tatay, 16.ix.45, H.E. Milliron (Bishop); 2 females, Los Baños, ix.17, F.X. Williams (Bishop); 1 female, 1 male, Mt. Makiling (=Maquiling), 50 m, 20.vii.48-22.ix.49, L.B. Uichanco (UPLB); 1 female, Mt. Maquiling, 50 m, 7.i.51, C.R. Baltazar (UPLB); 10 females, 2 males, Mt. Makiling (=Maquiling), Laguna, C.F. Baker (NMNH); 1 female, 1 male (holotype *A. cupulifera bakeri*) Los Baños, Laguna, C.F. Baker (NMNH); 2 females, 2 males, Los Baños, Laguna, C.F. Baker (BMNH); 1 female, Paete, Laguna, 1927, C.F. Baker (NMNH); 6 females, 1 male, San Pablo, Laguna, 21-25.x.74, I. Kudo (Hokkaido); 1 female, Atimonan, Quezon, C.F. Baker (NMNH); 1 female, Batbatan Is., 18.iv, R.C. McGregor (NMNH); 1 female, Mt. Mayon, Albay, 9.xii.53, H. Townes (AEI); 1 male, Nasugbu, Batangas, 28.ii.54, H. Townes (AEI); 1 female, Cebu, iv.17, F.X. Williams (Bishop); 1 female, Saravia, Negros Occ. (NMNH); 1 female, Momungan, Mindanao (Leiden).

Remarks. Cockerell (1916) gave the name *Allodape cupulifera bakeri* to the Philippine population of *B. cupulifera* because the male specimen he examined had the scape black underneath. However, several males that I have examined from

Manila and Los Baños, which I recognize as *B. cupulifera* on the basis of genitalic characters, have the scape either yellow or black underneath. I therefore synonymize *A. cupulifera bakeri* under *B. cupulifera*.

The femaile type of *Allodape hewitti sandacanensis* is quite similar to the female type of *B. hewitti* in having a yellow clypeus and being small in size as indicated by head width (1.20 mm), but it differs from *B. hewitti* by having a narrower head (HW/HL ratio 1.06) and the longer hairs on T4-6 simple. The close similarity in general appearance between the females of the two species presumably led Cockerell (1920a) to describe the female *B. cupulifera* as a variety of *B. hewitti*. Nests collected from Java containing both sexes helped separate the similar females of the two species; the male *B. cupulifera* can be easily distinguished from *B. hewitti* because of its lobed and medially excised hind trochanter.

The females are small and distinguished from other species by the slightly narrower head (HW/HL ratio 1.05-1.09), the entirely yellow clypeus (though yellow mark may be slightly reduced apically) and the longer hairs on T4-6 light brown, slanting and simple. The preceding set of characters separates this species from the similar females of *B. hewitti*. Those females with the clypeal mark reduced on the lower half of clypeus are quite similar to *B. reversa* (HW 1.47-173 mm) but separated from it by the relatively smaller head width (HW 1.15-1.47 mm) and the transparent to light brown longer hairs on T4-6. The males are quite similar to those of *B. reducta*, *B. reversa* and *B. signata* but are smaller.

Some variability in the male genitalia is apparent; males from West and Central Java have 4 to 5 peglike processes on the ventro-apical plate (Figs. 45, 46), while a male from Georgetown, Penang Island, Malaysia has only 3 peglike processes (Fig. 47). Twelve males from Mt. Montalban, Rizal, Philippines have dark tarsi. Most females from Java and Sumatra have yellow mandibles, but four females from Java and one from Sumatra (Leiden) have black mandibles. Five females from Sumatra, two from Java, two from Halmahera, 15 from Sandakan, Borneo and 65 from Manila, Mt. Maquiling and Los Baños, Philippines have the lower half of the clypeus partly black, the clypeal mark narrowing toward the apex (Fig. 84). Thirty-nine females from Manila with reduced clypeal mark have the mandibles and the scape black. Two females from Di Lingh, Vietnam and four females from Pasoh Forest Park, Malaysia have the tibiae and tarsi reddish brown. Two females from Fyan, Vietnam have orange legs and yellow mandibles and labrum.

Braunsapis clarihirta, n. sp.

Holotype: Male, Waai, Ambon, Indonesia, 9.x.65, A.M.R. Wegner (Bishop). *Paratypes:* 2 females, same data as holotype except 1 female deposited in SMUK; 1 female, Ambon, S. Moluccas, x.49, M.A. Lieftinck (SMUK); 1 female, Ambon, 27.vii.40, M.A. Lieftinck (Leiden).

Female. Face as in Figure 86. (1) Length 4.6-7.0 mm. (2) Labrum and mandible yellow, rarely mandible black. (3) Clypeus entirely yellow. (4) Paraocular mark present, sometimes slightly reduced. (*) Scape yellow underneath. (7) HW 1.20-1.73 mm. (8) HW/HL ratio 1.08-1.12. (11) Scape at most barely reaching front ocellus. (*) Legs orange. (13) Hairs on T4-6 transparent to light brown, slanting, simple to blunt, slightly longer than width of scape; shorter hairs subprostrate, weakly spiculate.

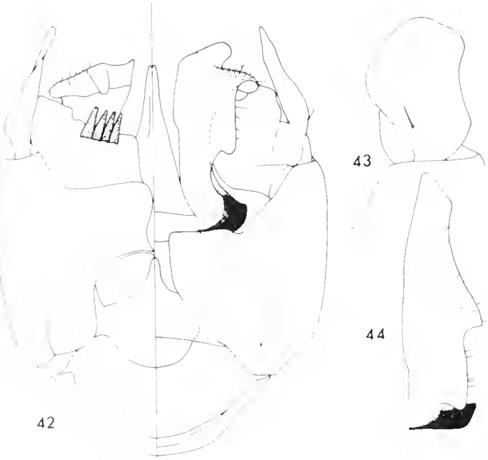
Male. Face as in Figure 87. (14) Length 5.5 mm. (*) Scape with yellow mark underneath. (18) HW 1.43-1.70 mm. (19) HW/HL ratio 1.12-1.16. (*) Legs orange. (21) Hairs on T4-6 light brown; longer hairs suberect, longer than width of scape, simple; shorter hairs subprostrate, weakly simple. (22) Genitalia as in Figures 42-44; gonostylus longer than broad, slightly expanded at apex, with one seta (Fig. 43); ventro-apical plate of gonocoxite with 4 peglike processes (Fig. 42); penis valve with mid-lateral flange with rounded posterior margin and dorso-lateral gap about as wide as mid-lateral flange (Fig. 44).

Specimens examined. In addition to type material, the following specimens are probably this species. **Thailand.** 1 female, Chantaburi, 18.vi.61, K. Iwata (Hokkaido); 1 female, Khaophanppha Khaochang, 200 m, Trang Prov., 11-12.i.64, G.A. Samuelson (Bishop); 1 female, Banna, 108 m, 5-10.v.58, T.C. Maa (SMUK). **Indonesia.** 1 female, Sibolangit, 450 m, N.E. Sumatra, 17.ix.50, M.A. Leiftinck (Leiden); 1 female, same except (SMUK); 2 females, Depok, Buitenzorg (=Bogor), 100 m, W. Java, 18.x.-42, M.A. Leiftinck (Leiden); 1 female, same except (SMUK). **Malaysia.** 3 females, Kuala Lumpur, 18.viii-17.xi.29, H.T. Pagden (BMNH); 6 females, 2 males, Kuala Lumpur, 4.iv.26-6.ix.31 (BMNH); 3 females, 2 males, Gombak Valley, Selangor, 26.xii.30-25.i.31 (BMNH); 1 female, Pasoh Forest Res., Negri s., 7.ix.78, P. and M. Becker (AEI); 1 female, Bukit Kutu, Selangor, 9.vi.29, H.M. Peddlebury (BMNH); 1 male, Gumo Mulu N.P., Sarawak, Borneo, ix-xi.77, D. Hollis et al. (BMNH); 1 female, Ranau, 8 mi. N. of Paring Hot Spring, 500 m, W. Coast Residency, N. Borneo, 9-18.x.58, T.C. Maa (Bishop). **Singapore.** 1 female, vi.29, R.H.V. van Zwaluwenburg (Bishop). **Philippines.** 1 male, Los Baños, Laguna, 18.ix.53, Townes family (AEI).

Remarks. The male type and the female paratypes from Ambon, Indonesia have orange legs, yellow labrum and mandible, the longer hairs on T4-6 light brown and simple. The other females from W. Java, Sumatra, Borneo, Thailand and Malaysia have dark legs. Also the females from Sibolangit, Sumatra and Negri s., Malaysia (HW 1.20-1.32 mm) are quite small compared to the females from Ambon (HW 1.54-1.60 mm). Two females from W. Java have slightly reduced paraocular marks and two females from Thailand have the mandibles black. Two males from Los Baños, Laguna, Philippines have broader heads (HW 1.70 mm) and dark legs except for the mid and hind basitarsi and the rest of the tarsomeres yellow. The species recognized here may be a complex of species, but too few specimens are available to resolve the matter.

The presence of yellow clypeus and paraocular marks in females is shared with *B. palavanica*. Such convergence of facial markings is probably common and quite similar to the case of the females of *B. cupulifera* and *B. hewitti*. The females of *B. clarihirta* can be distinguished from *B. palavanica* by having transparent to light brown hairs on T4-6, scape with a yellow mark underneath, mandibles with large yellow mark and some females are smaller, especially those from Java, Sumatra, Malaysia and Thailand (HW 1.20-1.50 mm).

The name *clarihirta* is derived from the Latin *clarus*, meaning clear, plus the Latin *hirtus*, meaning hairy, referring to the transparent hairs on T4-6.



Figures 42-44. Male genitalia of *B. clarihirta* (holotype), Ambon, Indonesia. Fig. 42. Dorsal (right) and ventral (left) view of genitalia. Fig. 43. Gonostylus, lateral view. Fig. 44. Penis valve, dorso-apical view.

Braunsapis apicalis, n. sp.

Holotype: female, Sandakan, Borneo, Malaysia, C.F. Baker (NMNH). *Paratypes:* 1 female, Mt. Semeroe, 800 m, S.E. Java, 6-13.vi.41, M.A. Lieftinck (Leiden); 1 female, Fraser's Hill, Malaya, 25.xii.64, R. Ohgushi (Hokkaido).

Female. Face as in Figure 88. (1) Length 5.9-6.2 mm. (2) Labrum fusco-ferrugineous, mandible with yellow spot. (3) Clypeus partly black below with clypeal mark narrowed toward apex. (4) Paraocular mark present. (*) Scape sometimes with small yellow spot underneath. (*) Small yellow spot on lower posterior orbit of compound eyes. (7) HW 1.47-1.67 mm (1.53 mm). (8) HW/HL ratio 1.10-1.15 (1.15). (10) Middle of epistomal suture slightly raised. (11) Scape barely reaching front ocellus. (*) Scopa light fuscous. (13) Hairs on T4-6 light brown; longer hairs slanting, simple, longer than width of scape; shorter hairs prostrate, weakly spiculate.

Additional specimens examined. **Malaysia.** 1 female, Fraser's Hill, 25.xii.64, R. Ohgushi (Hokkaido). **Indonesia.** 1 female, Mt. Semeroe, 800 m, S.E. Java, 6-13.vi.41, M.A. Lieftinck (SMUK).

Remarks. This species is remarkable in having the clypeal mark narrowing toward the apex but the paraocular marks present. The female of *B. apicalis* is quite similar to that of *B. lateralis* but differs from it by being smaller as shown by the head width (HW 1.47-1.67 mm) and in having the longer hairs on T4-6 light brown and simple. It is comparable in size to *B. clarihirta* but the lower half of the clypeus is partly black and the mandibles dark.

The type has a small yellow spot underneath the scape and a small spot on the mandible and both it and the two paratypes have a yellow mark on the lower posterior orbit of the compound eye. A second female from S.E. Java has no yellow on the posterior orbit but yellow marks on the outer surfaces of the fore and hind femora; its scopa is transparent, the hind femur orange and the tarsi are reddish orange. Except for this variation, it is quite similar to one of the paratypes from the same locality and is, therefore, included under this species.

The name *apicalis* is derived from the Latin *apiculus*, meaning apex, referring to the yellow clypeal mark narrowing strongly toward the apex of the clypeus.

Braunsapis lateralis, n. sp.

Holotype: female, Ranu River, Tengah, Sulawesi, Indonesia, 11.ii.80, P. Kevan (SMUK). *Paratypes:* 6 females, same data except dates 2-16.ii.80 (SMUK); 2 females, same except (NMNH); 2 females, same except (BMNH).

Female. Face as in Figure 89. (1) Length 5.6–7.1 mm. (2) Labrum sometimes with small yellow spot, mandible with yellow mark. (3) Clypeus largely black with a T-shaped clypeal marking. (4) Paraocular mark present. (6) Tegula translucent fuscous, axillary sclerites mixed. (7) HW 1.70–2.00 mm (2.00 mm). (8) HW/HL ratio 1.14–1.20 (1.20). (11) Scape reaching front ocellus. (12) Apex of basitibial plate represented by small conical protuberance. (13) Hairs on T4–6 fuscous; longer hairs suberect, about as long as width of scape, blunt; shorter hairs subprostrate, simple.

Additional specimens examined. **Malaysia.** 1 female, Sandakan, Borneo, Baker (NMNH). **Indonesia.** 2 females, Ranu River, Tengah, Sulawesi, 11.ii.80, P. Kevan (SMUK).

Remarks. This species is closely allied to *B. apicalis* from Java and Borneo and *B. boharti* from the Solomon Islands. The female of *B. boharti* differs from *B. lateralis* by having the middle of the epistomal suture elevated, the wings translucent fuscous (hyaline in *B. lateralis*), the clypeal and paraocular yellow areas more reduced and the labrum and mandible black (with yellow marks in *B. lateralis*). Two females were not included among the paratypes. One has the clypeal mark slightly broader on the lower half of the clypeus compared to the rest of the series. The other from the same locality does not have the paraocular marks but otherwise fits the description of the species and therefore is included here.

The name *lateralis* is Latin, meaning of the side, referring to the yellow marks on the paraocular area.

Braunsapis reducta (Cockerell), new status

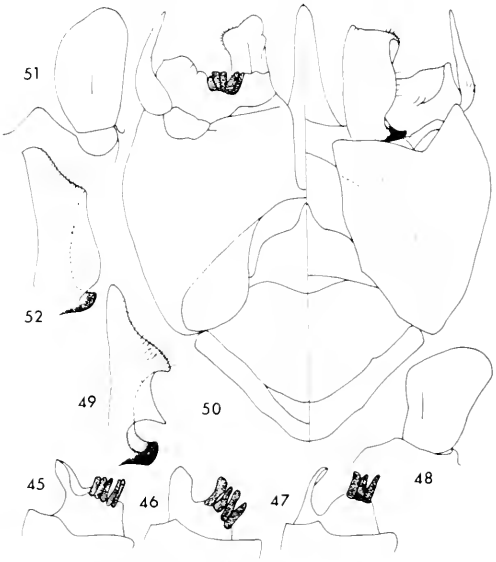
Allodape mindanaonis reducta Cockerell, 1916: 302. Type: male, Dapitan, Mindanao, Philippines (NMNH).

Female. Face as in Figure 90. (1) Length 6.0–6.7 mm. (2) Labrum and mandible yellow. (3) Clypeus largely black with clypeal mark T-shaped. (*) Scape yellow underneath. (7) HW 1.57–1.91 mm. (8) HW/HL 1.16–1.19. (10) Middle of epistomal suture not raised. (11) Scape reaching front ocellus. (*) Mesepisternum with shallow oblong punctures containing finer punctures. (12) Basitibial plate carina weak. (13) Hairs on T4–6 transparent; longer hairs slanting, spiculate; shorter hairs subprostrate, spiculate.

Male. Face as in Figure 91. (14) Length 5.2–5.6 mm. (18) HW 1.60–1.77 mm (1.60 mm). (19) HW/HL ratio 1.16–1.22 (1.18). (21) Hairs on T4–6 transparent; longer hairs suberect, blunt to spiculate; shorter hairs subprostrate, spiculate. (22) Genitalia (n = 3) as in Figures 50–52; ventro-apical plate of gonocoxite with 4–5 sunken peglike processes (Fig. 50); gonostylus longer than broad, with one seta (Fig. 51); penis valve with mid-lateral flange narrowed, flange with posterior margin rounded and dorso-lateral gap less than the width of mid-lateral flange (Fig. 52).

Specimens examined. **Malaysia.** 3 males, Tenompok, Borneo, 10–14.ii.59, T.C. Maa (Bishop). **Indonesia.** 1 female, Sungai Dareh, Sumatera Barat, 11.x.83, T. Inoue (Hokkaido); 1 female, Sulawesi, 8.viii.85, C. Young (CMNH); 2 females, Flores, S.G. Rensch (Berlin). **Philippines.** 39 (including holotype of *A. mindanaonis reducta*) females, 2 males, Dapitan, Mindanao, C.F. Baker (NMNH); 5 females, 1 male, same except (SMUK); 8 females, Tacloban, Leyte, C.F. Baker (NMNH), 1 female, Samar, C.F. Baker (NMNH); 1 female, Horns of Negros, Dumaguete, Negros Is., J.W. Chapman (MCZ); 1 female, Mt. Iriga, 500–600 m, Camarines Sur, 27.iv.62, H.M. Torrevillas (Bishop); 1 female, Mt. Makiling (= Maquiling), Laguna, C.F. Baker (NMNH); 1 female, Bangui, Luzon, xi.23, R.C. McGregor (NMNH); 1 female, Subic Bay, Grand Is., Luzon, 7.x–15.xi.67, C.E. Goodpasture (LNHM).

Remarks. This form is sufficiently distinct that it is elevated to species rank. The females are distinguished by the T-shaped clypeal mark (Fig. 90), the labrum and mandible yellow and the hairs on T4–6 transparent. It is quite similar to *B. reversa* and *B signata* except in those species the



Figures 45–49. Male genitalia of *B. cupulifera*, Java and Malaysia. Figs. 45–47. Ventro-apical plates of the gonocoxite, from Boyolali, Central Java; Bogor, West Java; and Georgetown, Penang, Malaysia, respectively. Fig. 48. Gonostylus, lateral view. Fig. 49. Penis valve, dorso-apical view.

Figures 50–52. Male genitalia of *B. reducta*, Dapitan, Mindanao, Philippines. Fig. 50. Dorsal (right) and ventral (left) view of male genitalia. Fig. 51. Gonostylus, lateral view. Fig. 52. Penis valve, dorso-apical view.

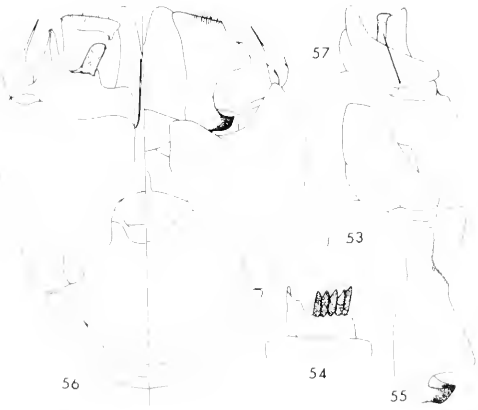
clypeal mark is not T-shaped and the longer hairs on T4-6 are light brown to fuscous. The males are also similar to *B. clarihirta*, *B. reversa* and *B. signata* except for the presence of paraocular marks and the ventro-apical plate of the gonocoxite having 4 to 5 sunken peglike processes in *B. reducta* (Fig. 50).

The scape of two females from Flores is ferrugineous in part, the labrum black, and the mark on the lower part of clypeus is broader than in those from Mindanao. Also, a female from Sumatra has a broader yellow mark on the lower half of the clypeus. Males from Borneo have the scape black underneath and the paraocular marks relatively reduced compared to those from the type locality.

Braunsapis reversa (Cockerell)

Allodape reversa Cockerell, 1916: 303. Type: male, Puerto Princesa, Palawan, Philippines (NMNH).

Female. Face as in Figure 92. (1) Length 5.0-6.4 mm. (2) Labrum fusco-ferrugineous, mandible with yellow mark, sometimes reduced to small spot. (3) Clypeus partly black below with clypeal mark narrowing toward apex. (7) HW 1.47-1.73 mm. (8) HW/HL ratio 1.14-1.18. (10) Middle of epistomal suture not raised. (11) Scape reaching front ocellus. (12) Basitibial plate carina weak. (*) Scopa with dark goldenbrown patch on distal half of outer surface. (13) Hairs on T4-6 fuscous; longer hairs slanting, simple; shorter hairs subprostrate, simple.



Figures 53-55. Male genitalia of *B. reversa*, Puerto Princesa, Palawan, Philippines. Fig. 53. Gonostylus, lateral view. Fig. 54. Ventro-apical plate of gonocoxite. Fig. 55. Penis valve, dorso-apical view.

Figures 56, 57. Male genitalia of *B. signata* (paratype), Surigao, Mindanao, Philippines. Fig. 56. Dorsal (right) and ventral (left) view of male genitalia. Fig. 57. Gonostylus, lateral view.

Male. Face as in Figure 93. (14) Length 4.4-5.0 mm. (17) Paraocular mark absent. (18) HW 1.47-1.57 mm (1.47 mm). (19) HW/HL ratio 1.20-1.24 (1.22). (21) Hairs on T4-6 fuscous; longer hairs suberect, simple; shorter hairs subprostrate, simple. (22) Genitalia (n = 4) as in Figures 53-55; ventro-apical plate of gonocoxite with 5 peglike processes (Fig. 54); gonostylus longer than broad, slightly expanded apically (Fig. 53); penis valve with mid-lateral flange expanded with angulate posterior margin and dorso-lateral gap wider than the mid-lateral flange (Fig. 55).

Specimens examined. **Philippines.** 38 females, 9 males (including holotype), Puerto Princesa, Palawan, C.F. Baker (NMNH); 24 females, Pinigisan, 600 m, Mantalingajan, Palawan, 2-22.ix.61, Noona Dan Exp. 61-62 (ZM); 1 female, Uring Uring, Brooke's Point, Palawan, 25.viii.61, Noona Dan Exp. (ZM).

Remarks. This species is closely allied to *B. signata* and the females of both can be distinguished from those of *B. philippinensis* and *B. picitarsis* by the presence of a yellow mark on the mandible, the light brown to fuscous hairs on T4-6 and the clypeal marking more narrowed toward the apex (Fig. 92). The females of *B. reversa* can be separated from *B. signata* by having the outer surface of the scopa with golden-brown patch of hairs on its distal half. The male of *B. reversa* has a broader head (HW/HL ratio 1.20-1.24) but is smaller in size (HW 1.47-1.57 mm) than *B. signata*. It can be separated easily from the male of *B. reducta* by the absence of paraocular marks, the fuscous longer hairs on T4-6, and its smaller size.

Braunsapis signata, n. sp.

Holotype: female, Surigao, Mindanao, Philippines, C.F. Baker (NMNH). *Paratypes:* 2 females, 1 male, same data as holotype (NMNH); 2 females same data as holotype except (SMUK); 5 females, Davao, Mindanao, Philippines, C.F. Baker (NMNH); 2 females, same except (SMUK); 2 females, Billiran, Philippine Islands, 1927, C.F. Baker (NMNH); 1 male, Mt. Mayon, Albay, Philippines, 9.xii.53, H. Townes (AEI).

Female. Face as in Figure 94. (1) Length 6.0-7.0 mm. (2) Labrum ferrugino-testaceous to fusco-ferrugineous, mandible with large yellow mark. (3) Clypeus partly black below with clypeal mark narrowing toward apex. (6) Tegula transparent, axillary sclerites yellow, primary sclerite with dark spot medially. (7) HW 1.69-1.91 mm (1.80 mm). (8) HW/HL ratio 1.11-1.16 (1.15). (10) Middle of epistomal suture not raised. (11) Scape reaching front ocellus. (12) Basitibial plate carina weak. (*) Outer surface of scopa with dark patch of hairs on distal half of hind tibia. (13) Hairs on T4-6 light brown to fuscous; longer hairs slanting, simple; shorter hairs subprostrate, simple.

Male. Face as in Figure 95. (14) Length 5.0 mm. (17) Paraocular mark absent. (18) HW 1.60 mm. (19) HW/HL ratio 1.15. (21) Hairs on T4–6 light brown; longer hairs suberect, simple; shorter hairs slanting, simple. (22) Genitalia as in Figures 56, 57; ventro-apical plate of gonocoxite with one peglike process (Fig. 56); gonostylus longer than broad, slightly tapering toward the apex, with one seta (Fig.57); penis valve similar to that of *B. reversa* (Fig. 55).

Remarks. The outer surface of the female scopa has a patch of dark hairs on the distal half and the males have the ventro-apical plate with only one peg (Fig. 56) and the gonostylus slightly tapering toward the apex (Fig. 57).

The name *signata* is derived from the Latin *signatus*, meaning mark, referring to the distinctive patch of dark hairs marking the outer surface of the scopa.

Braunsapis aurantipes, n. sp.

Holotype: male, Fyan, 1200 m, Vietnam, 11.vii-9.viii.61, N.R. Spencer (Bishop). *Paratypes:* 1 female, 1 male, same data as holotype except male deposited in SMUK.

Female. Face as in Figure 96. (1) Length 4.8–6.2 mm. (2) Labrum and mandible yellow, mandibular mark sometimes reduced. (3) Clypeus partly black below with clypeal mark narrowing toward apex. (4) Paraocular mark reduced to very small yellow spot. (*) Scape yellow underneath. (6) Tegula transparent, axillary sclerites yellow. (7) HW 1.23 mm. (8) Head as long as broad. (10) Middle of epistomal suture raised. (11) Scape not reaching front ocellus. (12) Basitibial plate carina indistinct. (*) Legs orange. (13) Hairs on T4–6 transparent; longer hairs suberect, simple, longer than width of scape; shorter hairs subprostrate to slanting, simple.

Male. Face as in Figure 97. (14) Length 3.8–4.5 mm. (15) Labrum and mandible yellow. (16) Clypeus entirely yellow. (17) Paraocular mark present. (*) Scape yellow underneath. (18) HW 1.20 mm. (19) HW/HL ratio 1.04–1.06 (1.04). (20) Hind trochanter excised medially and lobed distally. (*) Legs orange. (21) Hairs on T4–6 light brown; longer hairs suberect, simple, longer than width of scape; shorter hairs subprostrate, simple. (22) Genitalia as in Figures 58–60; ventro-apical plate of gonocoxite with 2 peglike processes (Fig. 58); gonostylus longer than broad with one seta; penis valve with mid-lateral flange broad with slightly angulate posterior margin (Fig. 60).

Remarks. The female is unique in having the following combination of characters: head about as long as wide, legs orange, clypeal marking narrowing toward the apex, small paraocular marks and face glossy. The male antennal sockets are less sunken and the face is slightly convex and glossy compared to males of *B. cupulifera* and *B. clarihirta*.

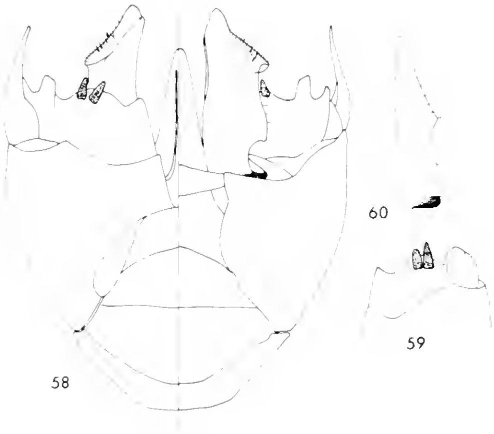
The name *aurantipes* is derived from the Latin *aurantus*, meaning orange, plus the Latin *pes*, meaning foot, referring to the orange colored legs.

Braunsapis indica, n. sp.

Holotype: female, 10 km N.W. of Udagamandalam (=Ooty), 2000 m, Tamil Nadu State, 17.viii.90, C.D. Michener (SMUK). *Paratype:* female, Kodaikanal, 6500 ft., Pulney Hills, S. India, iv–v.53, P.S. Nathan (NMNH).

Female. Face as in Figure 98. (1) Length 7.3 mm. (2) Labrum and mandible black. (3) Clypeus largely black with clypeal mark T-shaped. (4) Paraocular mark absent. (6) Tegula translucently fuscous, axillary sclerites yellow, primary sclerite with large dark medial spot. (7) HW 1.61 mm. (8) HW/HL ratio 1.01. (10) Middle of epistomal suture slightly raised. (11) Scape reaching front ocellus. (12) Basitibial plate carina weak. (*) Outer surface of scopa with patch of golden hairs on distal half. (13) Hairs on T4–6 transparent; longer hairs slanting, weakly spiculate; shorter hairs prostrate, weakly spiculate.

Remarks. This species can easily be distinguished by the T-shaped clypeal mark and the head longer than broad. A species from Madagascar, *B. madecassa* (Benoist), is quite similar in appearance as well as having the head as long as broad. However, *B. indica* differs from *B. madecassa* by having the clypeus mainly black with



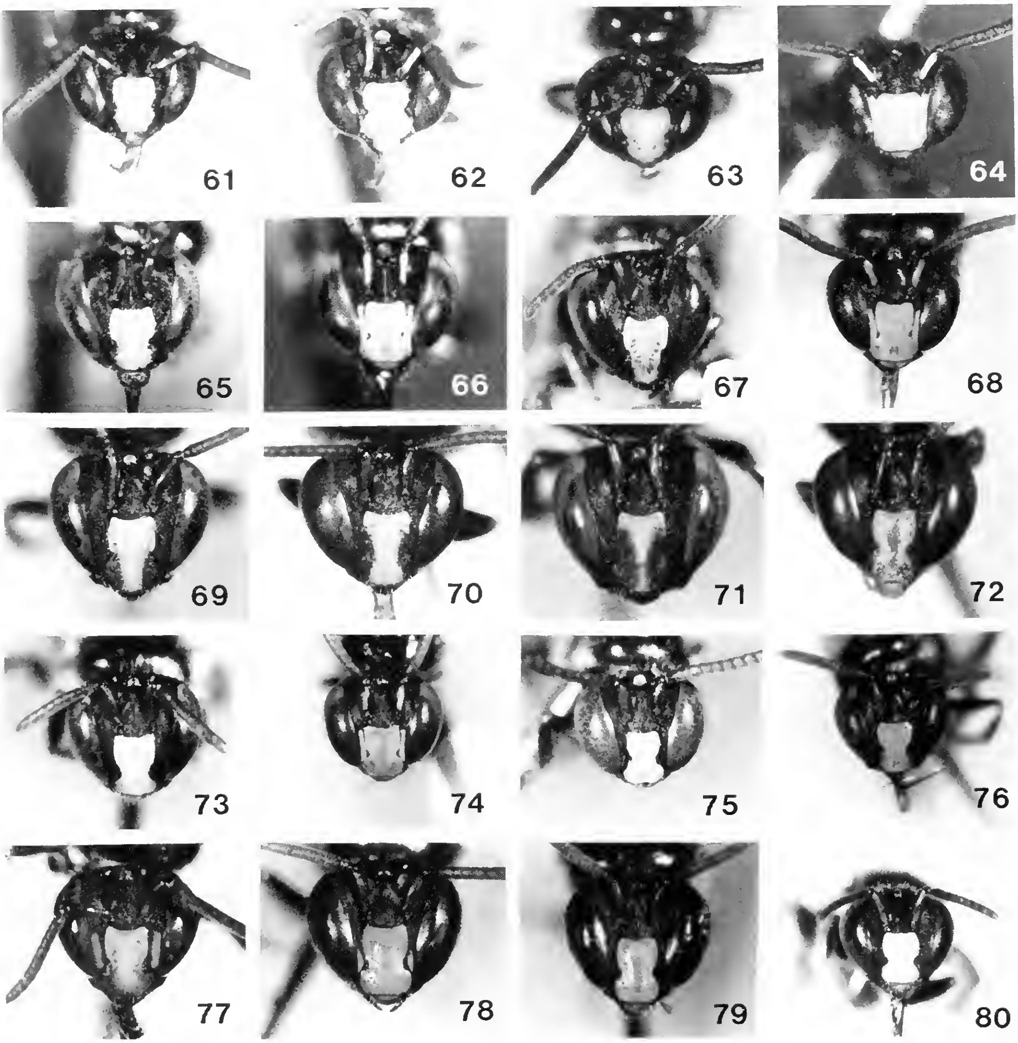
Figures 58–60. Male genitalia of *B. aurantipes* (paratype), Fyan, Vietnam. Fig. 58. Dorsal (right) and ventral (left) view of male genitalia. Fig. 59. Ventro-apical plate of gonocoxite. Fig. 60. Penis valve, dorso-apical view.

a slender T-shaped yellow mark, the scopa with a patch of golden hairs on the outer surface and larger size as indicated by the head width (1.61 mm).

The name *indica* is derived from the Latin *indicus,* meaning Indian, referring to the country where this species is found.

ACKNOWLEDGMENTS

I am most grateful to Charles D. Michener, Byron Alexander and George W. Byers for carefully reading the manuscript and their helpful suggestions. I thank Bruce Cutler of the Division of Biological Sciences, University of Kansas, for his help in the preparation of the SEM photo-



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graphs. This study was made possible thanks to the National Science Foundation Grant BSR 87-16817 (C. D. Michener, principal investigator).

To the institutions and persons listed under Materials and Methods, I am indebted for the loan of specimens. I am especially grateful to Prof. S. F. Sakagami for searching for the type of *B. iwatai* and for permission to place some type materials in the Snow Entomological Museum, University of Kansas.

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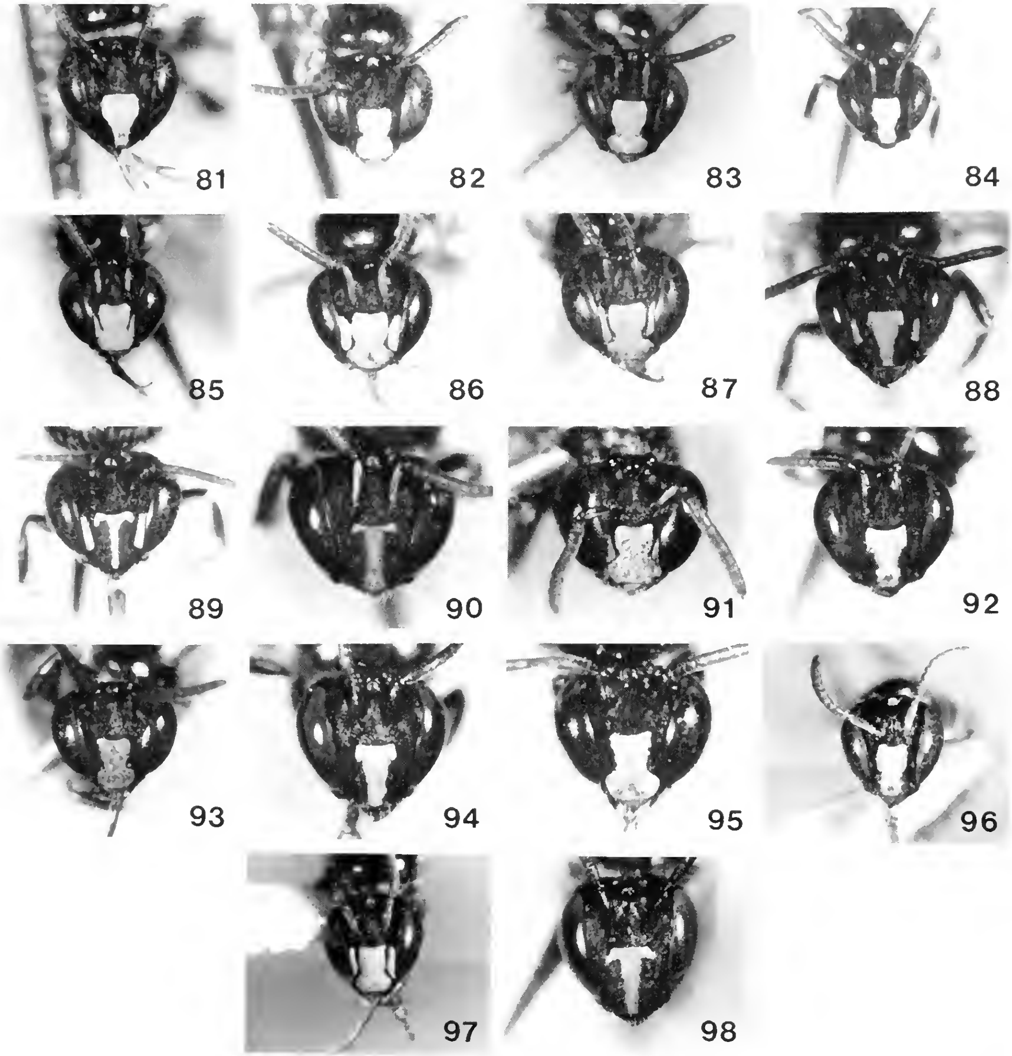

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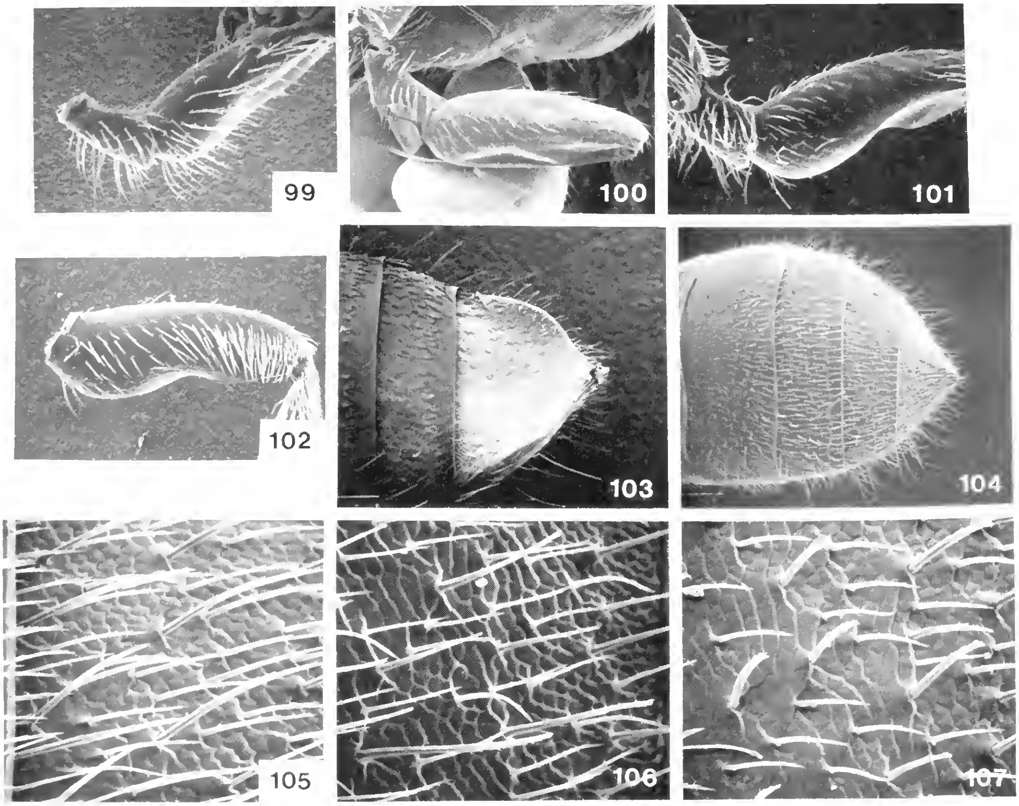

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The International Standard Serial Number of this publication is US ISSN 0022-8850.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 54, No. 7, pp. 209–256 May 31, 1991

Classification and Phylogenetic Relationships of the Panurgine Bees: The Calliopsini and Allies (Hymenoptera: Andrenidae)[1]

By Luisa Ruz[2]

CONTENTS

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ABSTRACT

This is part of a taxonomic study of the genera and subgenera of the andrenid subfamily Panurginae. Three tribes are recognized and described here: Calliopsini (with two new subgenera and one new species), Protomeliturgini *(Protomeliturga)* and Perditini *(Perdita)*. The Calliopsini includes *Acamptopoeum, Calliopsis* (*Calliopsis* s. str.), *C. (Perissander), C. (Calliopsima), C. (Verbenapis), C. (Liopoeum), C. (Hypomacrotera), C.* (*Liopoeodes,* n. subg.), *C.* (*Ceroliopoeum,* n. subg.), *C. (Nomadopsis), C. (Macronomadopsis), C. (Micronomadopsis), Arhysosage, Spinoliella,* and *Callonychium.* Extensive generic descriptions provide much more information than has been available in the past on the features of the taxa under study. Keys to all genera and subgenera of these tribes are included.

A cladistic analysis has been made in order to understand the relationships among the genera and subgenera of the Calliopsini and closely related taxa. At least some clarification of lines between genera has been attained. A broad interpretation of the genus *Calliopsis* is proposed. Illustrations for each genus-group taxon are provided.

INTRODUCTION

The family Andrenidae contains two subfamilies: Andreninae and Panurginae. A study of the Panurginae at generic and subgeneric levels, with a classification and phylogeny of the included taxa, was presented by Ruz (1986). That study shows that the Panurginae is a monophyletic group and that several tribes can be recognized.

The Panurginae contains numerous genera and, like the Andreninae, is found in all continents except Australia. Its diversity and abundance, however, are greatest in the Western Hemisphere.

The present paper is part of the subfamilial study mentioned above and treats a strongly derived group, the Calliopsini, along with its closest relatives, *Protomeliturga* (Protomeliturgini) and *Perdita* (Perditini). The three tribes are restricted to the Western Hemisphere.

Robertson (1922) recognized Calliopsinae as one of the subfamilies of his Panurgidae but otherwise authors have not recognized a higher taxon based on *Calliopsis.* The Calliopsini, as here understood, contains five genera: *Acamptopoeum, Calliopsis* (11 subgenera, two of them new), *Arhysosage, Spinoliella* (2 subgenera) and *Callonychium* (2 subgenera). The genus *Calliopsis* is treated here in a wider sense than in the past.

MATERIALS AND METHODS

About 20,000 panurgine bees have been the study material for this and previous investigations (Ruz, 1986). At least three species (3 individuals each, or more if required) of each polytypic genus and subgenus have been carefully examined and dissected. Structures like male genitalia and associated sterna, sting apparatus of female, mouthparts, last tergum and sterna 5 and 6, were cleared in a cold solution of KOH (10%) for 12 hours or less, depending on the degree of sclerotization of the structures, then washed with water for several minutes and preserved in glycerol for later examination.

The morphological analysis of the species selected as representatives of each genus (type species plus at least two additional species when possible) was made using a stereomicroscope and, for details, a compound microscope. The names of the species studied in detail are preceded with an asterisk (*) in lists of species under each taxon.

Illustrations were made using a camera lucida, comparable structures being drawn at about the same size regardless of differences in size of the bees. Sternum 6 of females was drawn with the latero-distal margin in its ordinary, curved position in order to avoid breaking it; therefore the distal part of the sternum appears somewhat narrower than in a flattened sternum. Figures of certain structures are omitted if similar structures are illustrated for related taxa or if other sources with good drawings are available.

In the descriptions, each character (or groups of morphologically associated characters) is numbered. For purposes of comparison these numbers have been maintained within taxa of the same level. Certain characters (and numbers) are omitted if they are similar in related taxa. Subfamilial characters are omitted in the tribal, generic and subgeneric descriptions, unless they represent an exception for the group; in this case those distinctive characters are kept in the description. The number of a given character used in the descriptions is not coincident with that used for Tables 1 and 2 and the cladogram (Fig. 30).

In order to facilitate comparisons, the number of each apomorphy as it appears in Table 1 and in Ruz (1986) has been maintained for the whole revision of the subfamily. The numbers of the characters not used in the Calliopsini and their close relatives are skipped in the present work. In order to maintain the sequence of numbered apomorphies, certain autapomorphies have been inserted with a number already used plus a letter.

The morphological terms in the descriptions are mainly based on those used by Snodgrass (1935, 1956), Michener (1944, 1965, 1981), Rozen (1951), Winston (1979), and Michener and Brooks (1984). Some characters whose interpretations may be difficult are explained below.

20. Basal area and apex of labrum: As indicated in Figure 1F.
33. Tentorial pit: Small, rounded, the most dorsal part of the external depression associated with the anterior tentorial arms (Fig. 6A, D).
39. Orbits: Inner ocular orbits, as seen in facial view (Fig. 6A–D).
46. Pterostigma and prestigma lengths (Fig. 2E) were measured on vein Rs; their breadths (maximum) were measured perpendicular to the lengths. Prestigmal width was not measured to the wing margin but is only the width of the prestigma proper.
48. Submarginal cells (SM): For length comparison, SM cell 2 (if only two SM cells present) has been called SM cell 2 + 3 assuming that vein 1st r-m (2nd transverse cubital vein) has disappeared. When three SM cells are present, cells 2 and 3 are indicated as SM 2 and 3.

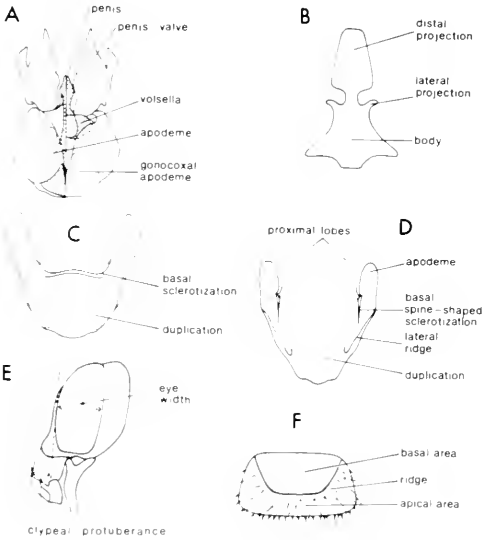

Figure 1. Diagram to show terminology for *Calliopsis* (A, B, D–F) and *Perdita* (C). A, Male genitalia, dorsal and ventral views; B, S8 of male; C, D, S6 of females; E, Head, lateral view; F, Labrum.

50. Cell 2nd M of forewings: 3rd discoidal cell.
69. Male terga: Postgradular depression width measured along the longitudinal axis of the body.
70. Pygidial plate: Glabrous plate on distal part of T7 of male and T6 of female (the latter not considered here), laterally delimited by carinae. The same area delimited only by hairs or only a projection of last tergum has not been considered as a real plate in this study.
71. T7 of female: Hemitergite of Michener, 1944.

In describing margins of a leg segment, the leg has been considered as extended laterally; the antenna has been considered extended forward. The word vertex has been used to mean the posterior margin of the vertex rather than the whole top of the head.

In order to save space, terga and sterna are abbreviated as T or S plus arabic numbers of the metasomal segments (i.e., not counting the propodeum). Thus T1 is the first metasomal (second abdominal) tergum.

ACKNOWLEDGMENTS

Acknowledgments for the study material used in the whole revision of the subfamily are given here. They may be omitted in subsequent papers of this series. Abbreviations in parentheses are used for institutions or collections through the rest of the work.

This study would not have been possible without the encouragement and assistance of numerous people. I am particularly grateful to Charles D. Michener of the Department of Entomology, University of Kansas (KU), Lawrence, Kansas, for his generosity, advice, interest and help in the preparation of the manuscript and for the use of material in the Snow Entomological Museum (KU). I also thank the following persons: George W. Byers and the late Peter D. Ashlock (KU) for their suggestions in editing the manuscript; Edward O. Wiley (KU) for his advice and willingness to discuss aspects of this investigation; Frank Koch of the Museum für Naturkunde der Humboldt-Universität, Berlin, for lending Friese's types and other valuable specimens, as well as generously permitting study of material from the collection under his care when I visited the Museum; George R. Else of the British Museum (Natural History), London, England; Till Osten of Staatliches Museum für Naturkunde, Stuttgart, Germany; and Mario Zunino of the Museo ed Istituto di Zoologia Sistematica della Università di Torino, Italy, also kindly lent type specimens. The late Radclyffe B. Roberts of Rutgers University, New Brunswick, New Jersey and John L. Neff of the Central Texas Melittological Institute, Austin (CTMI), lent and donated important specimens. Professors Salvador Peris and Elvira Mingo of the Instituto Español de Entomología of Madrid, Spain, permitted my study of that collection. Yu. A. Pesenko of the Zoological Institute, Academy of Sciences, Leningrad; Klaus Warncke of Ruckteschellweg, Germany; George C. Eickwort of the Department of Entomology, Cornell University, Ithaca, New York; the late Robert O. Schuster of the University of California, Davis, California (UCD); Paul H. Arnaud of the California Academy of Science, San Francisco, California; Wallace E. LaBerge, Illinois Natural History Survey, Champaign, Illinois; and William L. Overal of the Museu Paraense Emilio Goeldi, Belém, Pará, Brazil, lent important study material. Ronald J. McGinley of the Smithsonian Institution, Washington, provided material from the Reed Collection then under his care at Harvard University, Cambridge, Massachusetts (MCZ). Robert W. Brooks of the Snow Entomological Museum, University of Kansas, Lawrence, Kansas (KU), helped in the preparation of diagrams, made some preliminary photographs and provided certain specimens for study. Terry Griswold of the U.S. Department of Agriculture, ARS-Bee Laboratory, Utah State University, Logan, Utah (USDA), lent study material, made available the panurgine collection of the Bee Laboratory and kindly provided housing on my visits to Logan. Jerome G. Rozen Jr. of the American Museum of Natural History, New York (AMNH), contributed valuable ideas, lent many specimens for study, permitted the use of the bee collection of the Museum, and very kindly provided housing and help when I visited the Museum. Zine Ajmal de Toledo of the Instituto de Zoologia Miguel Lillo, Tucumán, Argentina (IZML), lent an important panurgine collection under her care. Haroldo Toro of the Universidad Católica de Valparaíso, Chile (UCV), made valuable suggestions and provided numerous specimens. Dr. James S. Ashe (KU) and Francisco Saiz (UCV) provided help and let me use photographic equipment under their care; Carlos González (UCV), Chile, and Stephen Reyes (KU) did some photographic work.

I am also indebted to Rudolf Jander, Hans-Peter Schultze and Arturo Roig-Alsina (all from KU) for their help in translating materials from German to English.

The drawings were mostly inked by Donna Stevens (KU); some of them were also prepared by Carmen Tobar (UCV).

The typing of the manuscript and editorial assistance was by Joetta Weaver (KU). Many thanks also to Virginia Ashlock (KU) for her help in typing and editorial work.

This study was possible thanks to the financial aid of the Dirección General de Investigaciones, Universidad Católica de Valparaíso, Chile, and especially the National Science Foundation grants DEB82-12223 and BSR87-16817 (C. D. Michener, principal investigator).

SUBFAMILY PANURGINAE

Diagnosis. Short-tongued bees usually with nonmetallic integument, 2–11 mm long; first segment of labial palp usually flattened; labrum (proximally) without lateral process to articulate with clypeus as in Andreninae; paraglossa elongate and somewhat tapered distally, usually as long as suspensorium or longer (in Andreninae wider distally and shorter than suspensorium); scrobal suture usually absent; marginal cell distally truncate (often obliquely); middle femur of female with ventral margin a ridge, with a comb basally and sparce plumose hairs distally; scopa present, mainly on tibia and basitarsus, moderately abundant to sparse; T2 with lateral fovea or at least a dark spot; gonobase absent (except 3 genera with a "gonobase" that may not be homologous with the real gonobase).

The three panurgine tribes considered in the present paper, Perditini, Protomeliturgini and Calliopsini, share the following principal characters: 47. Submarginal cells two (exceptionally three in Perditini). 66. Tibial scopa of female usually (at least partially) of minutely branched hairs. 82. Gonocoxal apodeme not inflexed. 88. Sting short to extremely short, with first valvula slightly sclerotized, without valve (except a possible rudiment in *Calliopsis (Ceroliopoeum)*.

KEY TO TRIBES CALLIOPSINI, PROTOMELITURGINI AND PERDITINI

1\. Marginal cell (nearly always) about half as long as distance between its apex and wing tip (Fig. 2B); if longer, then lower part of face, in profile, not or scarcely divergent from eye. S6 of male 3 or more times as broad as long (length measured medially); distal margin medially almost straight or with very wide and rather shallow V-shaped emargination. Usually with metallic color . . . . Perditini

—Marginal cell more than half as long as distance between its apex and wing tip. Lower part of face, in profile, distinctly divergent from eye. S6 of male usually less than 3 times wider than long; if wider, then distal margin with tapered projections and rather deeply emarginate medially; or if otherwise, of different shape than above. Almost never metallic 2

2\. Tentorial pit at intersection of outer subantennal and epistomal sutures. Pre-episternal groove extending below scrobal level. Middle femur of female with hairs of ventral margin not well organized in a comb . . . . Protomeliturgini

—Tentorial pit in outer subantennal suture (Fig. 6A–D). Pre-episternal groove short, absent below scrobal level. Middle femur of female with a distinct, well-defined comb basally on ventral margin (Fig. 10D). . . . . Calliopsini

TRIBE PERDITINI

This tribe contains a single enormous genus, restricted to North America. It has not been reclassified in the present work; it is diverse but monophyletic. In the current classification it contains only the genus *Perdita*, which is subdivided into 21 subgenera.

The following features characterize this tribe: 2. Integument usually metallic and with yellow markings. 33. Tentorial pit usually at intersection of outer subantennal and epistomal sutures. 45. Pre-episternal groove curved, meeting scrobe. 46. Pterostigma large, with sides divergent; margin within marginal cell clearly convex. 47. Marginal cell usually half as long as distance between its apex and wing tip or less. 61. Hind tibia of male with dorsal border usually untoothed. 69. T2–5 of male with posterior marginal areas glabrous or nearly so. 72. T8 of male usually tapered distally and hairy. 76. S5 of female with distal margin broadly concave. 77. S6 of male about three times as broad as long (length measured on midline). 82. Gonocoxal apodeme not inflexed. 83. Gonocoxites fused ventrally. 85. Volsellae weakly attached to each other medially, with denticles. 88. Sting extremely short, rudimentary, second valvifer elongate, first valvula slightly sclerotized, without valve.

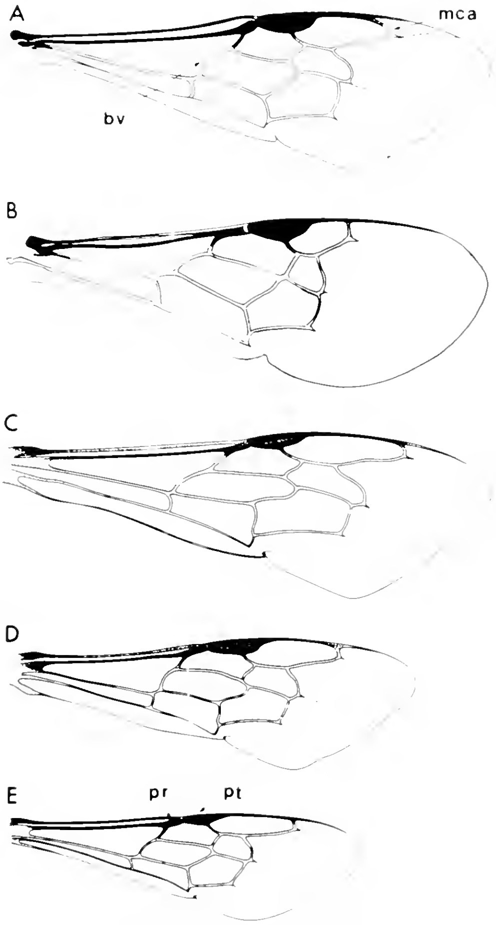

Figure 2, A–E. Forewings of males. A, *Protomeliturga turnerae* (Ducke); B, *Perdita halictoides* Smith; C, *Acamptopoeum submetallicum* (Spinola); D, *Calliopsis (Ceroliopoeum) laetum* (Vachal); E, *Calliopsis (Hypomacrotera) callops* (Cockerell and Porter). pt = pterostigma; pr = prestigma; mca = marginal cell apex; bv = basal vein.

Genus *Perdita* Smith

(Figs. 2, 3, 30)

Perdita Smith, 1853: 128. Type species: *Perdita halictoides* Smith (monobasic).

The list of subgenera and synonymy for each can be found in Hurd (1979), with another subgenus in Timberlake (1954).

I have not attempted to study the subgenera (or genera?) encompassed under the name *Perdita*. In the following description, however, I have attempted to indicate the variation within *Perdita* in characters useful elsewhere at the generic level. To shorten the description I use mostly subgeneric names to identify variants; in reality, however, I have examined primarily the species listed below and the use of a subgeneric name does not indicate that all species of that subgenus have the specified characters: *Perdita* s. str. (*halictoides* Smith); *Pentaperdita* (*albovittata* Cockerell); *Perditella* (*larreae* Cockerell); *Hexaperdita* (*ignota crawfordi* Cockerell); *Pygoperdita* (*interrupta* Cresson); *Heteroperdita* (*trifasciata* Timberlake, female); *Glossoperdita* [*pelargoides* (Cockerell)]; *Hesperoperdita* (*trisignata* Cockerell); *Alloperdita* (*novaeangliae* Viereck, female); *Macrotera* [*texana* (Cresson), *bicolor* Smith]; *Macroterella* (*mortuaria* Timberlake, male); *Macroteropsis* (*latior* Cockerell); *Pseudomacrotera* (*turgiceps* Timberlake); *Allomacrotera* (*stephanomeriae* Timberlake, male); *Epimacrotera* (*ainsliei* Crawford); *Callomacrotera* (*maritima* Timberlake, *acapulcona* Timberlake); *Cockerellia* (*albipennis* Cresson); *Cockerellula* (*opuntiae* Cockerell); *Procockerellia* (*albonotata* Timberlake); *Xerophasma* (*bequaertiana* Cockerell). Additional information on characters and their variability among and within subgenera of *Perdita* is given by Ruz (1986) and Danforth (1991).

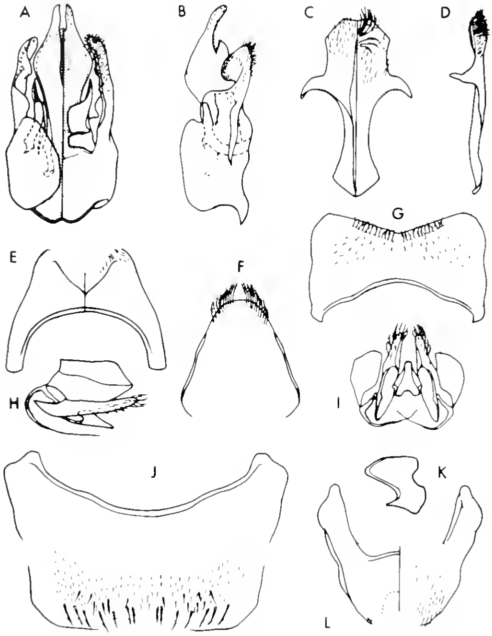

Figure 3. *Perdita halictoides* Smith. *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, D, S8, dorsal, ventral and lateral views; E, S7, dorsal and ventral views; F, T8; G, S6, ventral view. *Female:* H, Sting; I, Sting, ventral view; J, S5, ventral view; K, T7; L, S6, dorsal and ventral views.

Description. 1. Length 2–11 mm. 2. Integument metallic (at least partially), except in species of the subgenera *Macrotera, Macroterella, Xerophasma, Perditella, Cockerellula.* 5. Pubescence in general short, usually minute on most of metasoma, especially on terga. 8. Head narrower to wider than thorax. 11. Glossa much shorter to longer than prementum; usually with flabellum. 17. Galeal comb of 0–15 setae. 20. Labrum less than twice as broad as long to more than twice as long; basal area usually glabrous, sometimes almost fully pilose; distal margin of basal area a ridge; labrum somewhat protuberant, with apex inflexed or not. 25. Mandible of male simple to bidentate, or with prebasal tooth-like projection. 30. Inner subantennal suture usually curved, sometimes almost straight. 33. Tentorial pit usually at intersection of outer subantennal and epistomal sutures (sometimes in outer suture though close to the epistomal suture). 34. Antennal sockets below middle of face [e.g., *P. (P.) halictoides* Smith] to slightly above as in *Xerophasma.* 36. Antennal flagellum of male unmodified, shorter to longer than head. 37. Lower mesal paraocular area rather flattened or slightly convex as in *P. (P.) halictoides* (sometimes somewhat protuberant). 39. Orbits usually subparallel, sometimes convergent below as in *Callomacrotera,* or divergent below as in male of *Macrotera.* 45. Pre-episternal groove usually curved, reaching scrobe, sometimes absent (e.g., *Macrotera, Macroteropsis, Cockerellia, Pentaperdita*). 46. Pterostigma longer than and twice as broad (or more) as prestigma; margin basal to vein r clearly diverging from costa (slightly so in *Macrotera* and *Macroteropsis*); margin within marginal cell usually convex [except in *Macrotera* and in *P. (Macroteropsis) latior*]. 47. Marginal cell broadly truncate, very short, usually nearly half as long as distance from apex to wing tip (Fig. 2B) (not as short in *Xerophasma* and *Macrotera*). 48. Submarginal cells two except in *Xerophasma* and *Alloperdita,* which have three, but second small and petiolate anteriorly. 50. Cell second M sometimes absent or weak. 51. First recurrent vein usually close to first transverse cubital, sometimes meeting it. 55. Propodeal triangle with no visible hairs (sometimes with sparse, minute hairs [e.g., *P. (Allomacrotera) stephanomeriae, Epimacrotera ainsliei,* and *P. (Glossoperdita) pelargoides*]. 57. Basitarsus 1 (both sexes) from six to nine times longer than broad; tarsomeres 2–4 unmodified. 58. Femur 2 of female with comb on ventral margin basally not well defined (not easily differentiated from other hairs). 59. Middle tibial spurs finely toothed, slightly curved (or almost straight), somewhat shorter than basitarsus 2; strongly curved at apex in *Macrotera.* 61. Tibia 3 of female somewhat less than twice as long as basitarsus 3, with keirotrichia on most of inner surface, sometimes very sparse toward the middle, only at ends, or apparently absent; male with dorsal margin of tibia 3 usually untoothed, with keirotrichia usually on most of surface, sometimes sparse. 62. Tibial scopa usually of rather short hairs (long in some species); in most cases apparently simple but with minute branches, with rather long alternate branches in *P. (Callomacrotera) maritima* Timberlake; scopal hairs usually sparse or moderately abundant, dense in *Macrotera* and *Callomacrotera.* 63. Hind tibial spurs usually slightly curved, strongly curved at apices as in *Macrotera;* outer spur usually shorter than inner. 64. Basitibial plate of male well defined. 66. Claws bifurcate. 67. Metasoma in male usually wider than to sometimes narrower than thorax. 70. Pygidial plate of male absent, though T7 at apex usually with median projection (projecting area truncate, bifurcate, or tapered). 71. T7 of female as in Figure 3K. 72. T8 of male generally somewhat tapered at apex, distinctly hairy (Fig. 3F). 74. S4 of male with distal margin broadly and gently concave or almost straight. 75. S5 of male with distal margin widely and gently concave (sometimes almost straight). 76. S5 of female with no median sclerotized area proximally and no gradulus; distal margin broadly and shallowly concave (Fig. 3J). 77. S6 of male three or more times wider than long (length measured medially), distally with a very wide V-shaped emargination or margin almost straight (Fig. 3G). 78. S6 of female with no proximal laminar lobes, basal sclerotization fully fused to sternum and not spine-shaped (similar to that of *Protomeliturga*), lateral margin with ridge almost straight or curved, longitudinal basal carina absent, duplication membranous (sclerotized area below it), distal margin distinctly concave or narrowly emarginate medially, S6 with small sparse hairs proximally, forming dense patch at both sides of midline distally (Figs. 1C, 3L). 79. S7 of male with two distal lateral lobes and with shallow to deep V-shaped or concave apical emargination (Fig. 3E). 80. S8 of male cross-like with distal part wide to narrow, truncate, rounded or tapered; basal part wider to narrower than distal projection (Fig. 3C, D), bilobed, or bifurcate in some species. 82. Gonocoxal apodeme well or usually strongly developed (laterally or medially in ventral view), not inflexed (Fig. 3A, B). 83. Gonocoxites elongate, connected by slightly sclerotized cuticle to fully fused ventrally. 84. Gonostylus fused to gonocoxite, well developed, elongate. 85. Volsellae attached to each other by small membranous area; with denticles. 86. Penis valves elongate, simple, usually tapered apically, fused to each other generally rather extensively (sometimes free only at apices). 87. Penis membranous, usually almost as long as and wider than valve, fused to valves in great part. 88. Sting short (sometimes truncate, e.g., *P. halictoides*), not reaching stylus, first valvifer (triangular plate) rather elongated (not triangular), first valvula little sclerotized, valve absent (Fig. 3H, I).

Comments. This is the largest genus of the subfamily, containing approximately 500 species, grouped in 21 subgenera and several species groups.

Discussion. The genus *Perdita,* in spite of all the diversity that it presents, has several apomorphies that make it a distinctive group. According to the cladogram (Fig. 30) this genus is the sister group of the Calliopsini and *Protomeliturga* together. Rozen (1966) has found that *Perdita* has distinct larval characters different from those of any other Panurginae.

The pollen balls in the cells of several species of *Perdita* are coated with a secreted, cellophane-like layer, a synapomorphy shared with the Calliopsini (Rozen, 1967, and personal communication). If *Protomeliturga* does not cover the pollen ball, this fact may mean that *Perdita,* not *Protomeliturga,* is the sister group of Calliopsini. This was the result that I obtained in a preliminary cladistic analysis using a smaller set of characters.

Distribution. This genus occurs in southern Canada, the United States, México and Guatemala (Hurd, 1979).

TRIBE PROTOMELITURGINI

The main characters of this monotypic tribe are the following: 20. Labrum of female with basal area hairy laterally. 33. Tentorial pit at intersection of outer subantennal and epistomal sutures. 45. Pre-episternal groove extending below scrobal level. 46. Pterostigma with sides diverging; margin within marginal cell convex. 61. Hind tibia of male with dorsal border a carina. 69. T2–5 of male with posterior marginal areas pilose laterally forming a hair band. 70. T7 of male with a strong lateral projection. 76. S5 of female with distal margin almost straight. 82. Gonocoxal apodeme not inflexed. 83. Gonocoxites short, fused ventrally. 85. Volsellae well separate from each other, without denticles. 87. Penis extremely wide and completely fused to penis valves. 88. Sting very short, first valvula little sclerotized, without valve.

Genus *Protomeliturga* Ducke
(Figs. 2A, 4, 5, 30)

Protomeliturga Ducke, 1912: 63, 90. Type species: *Calliopsis turnerae* Ducke, 1907 (monobasic).

Diagnosis. Segments 3 and 4 of labial palp at right angle to segment 2. Basal vein (forewing) strongly curved. Terga with distal hair bands laterally. *Male.* Antennal flagellum much shorter than length of head. Tibia 3 with dorsal margin a sharp carina. T7 at apex strongly bent down and forward, with a conspicuous projection laterally.

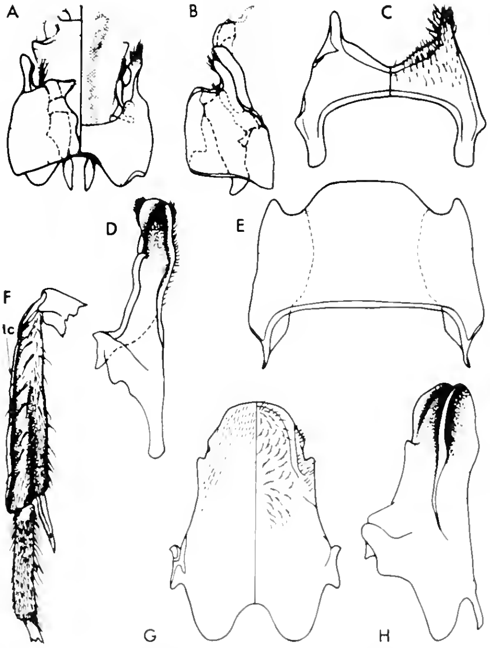

Figure 4. *Protomeliturga turnerae* (Ducke). *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, S7, dorsal and ventral views; D, S8, lateral view; E, T7; F, Leg 3, outer view; G, S8, dorsal and ventral views; H, S8, ventrolateral view. tc = tibial carina.

Female. Middle tibial spur finely and densely toothed. Tibia 3 more than twice as long as basitarsus 3, with scopa mostly of long, minutely branched hairs. Inner hind tibial spur conspicuously curved.

Description. 1. Length 5–8 mm. 3. Lower part of face (clypeus of male, small spot in lower paraocular of female) and areas of thorax and legs yellow. 4. Metasoma with no yellow marks. 5. Pubescence in general short, mostly appressed, rather abundant, inconspicuous in most of dorsum of thorax. 6. Integument microareolate, dull on most of head and thorax, shiny on metasoma. 7. Punctures fine, mostly dense. 8. Head wider than long and narrower than thorax (sometimes as broad as thorax). 11. Glossa somewhat longer than prementum. 13. Segment 1 of labial palp longer than 2–4 together. 14. Segment 2 of labial palp about three times longer than 3. 15. Segment 3 of labial palp articulated at angle to segment 2 so that 3 and 4 project at angle to 1 and 2 (as in long-tongued bees). 16. Maxillary blade more than twice as long as prepalpal part of galea. 17. Galeal comb of about 11 bristles. 20. Labrum somewhat wider than long; basal area densely hairy and with distal margin a strongly projecting ridge; labral apex strongly inflexed as in *Pseudopanurgus* (Fig. 5B, C). 27. Clypeus slightly more than twice as wide as long in male, a little less than three times in female; moderately protuberant (about 1/3 width of eye in lateral view); distal margin with rounded projection near lateral margin of labrum (Fig. 5I, K, L). 30. Inner subantennal suture almost straight. 31. Subantennal area wider than half length of inner suture and as wide as socket. 33. Tentorial pit at intersection of epistomal and outer subantennal sutures (Fig. 5I). 34. Antennal sockets in middle of face. 36. Flagellum of male slightly clavate (Fig. 5J), much shorter than head; flagellomere 1 about twice as long as 2, longer than broad. 37. Lower mesal paraocular area slightly convex. 38. Facial fovea narrow and shallow in male, wider and well-marked in female. 39. Orbits convergent below in male, subparallel in female. 40. Ocelli mostly above orbital tangent. 41. Vertex convex. 42. Gena of male (lateral view) narrower than eye, of rather uniform width. 43. Pronotum with dorsolateral preapical lamella, without dorsal ridge medially. 44. Mesepisternum with almost no flat area facing anteriorly. 45. Pre-episternal groove rather shallow, punctate, extending below scrobe, more clearly marked above. 46. Pterostigma longer and wider than prestigma; side basal to vein r clearly diverging from costa, that within marginal cell convex. 47. Marginal cell rather pointed at apex (obliquely truncate, Fig. 2A); length little shorter to somewhat longer than distance from its apex to wing tip. 48. Submarginal cells two. 49. Submarginal cell 1 about as long as cell 2 + 3. 50a. Basal vein strongly curved. 51. First recurrent vein distant from first transverse cubital. 52. Forewing with cu-v longer than second abscissa of M + Cu. 53. Hind wing with cu-v 1/4 to 1/5 as long as second abscissa of M + Cu. 54. Dorsal surface of propodeum about as long as metanotum. 55. Propodeal triangle densely pilose, especially on lateral areas, with no striae. 57. Basitarsus 1 about six times longer than broad in male and more than three times longer in female; tarsomeres 2–4 unmodified. 58. Femur 2 of female on ventral margin basally with comb not well developed and not clearly defined. 59. Middle tibial spur of both sexes slightly more than half as long as basitarsus 2 with fine, minute and dense teeth. 60. Basitarsus 2 of both sexes about as long as 1 and shorter than 3. 61. Tibia 3 of female more than twice as long as basitarsus 3 (Fig. 5H), with keirotrichia on most of inner surface except close to dorsal and ventral margins; male tibia 3 with dorsal margin a strong, sharp carina (as in *Pseudopanurgus*) (Fig. 4F), with keirotrichia as in female. 62. Tibial scopa mostly of long, branched hairs (some with branches only distally, a few on dorsal margin simple). 63. Hind tibial spurs with minute, fine teeth; outer somewhat shorter than inner and slightly curved at

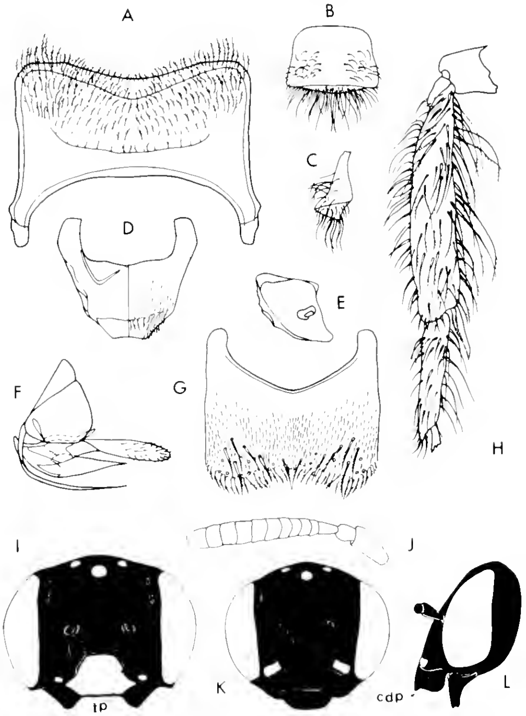

Figure 5. *Protomeliturga turnerae* (Ducke). *Male:* A, S6, ventral view. *Female:* B, Labrum; C, Labrum, lateral view; D, S6, dorsal and ventral views; E, T7; F, Sting; G, S5, ventral view; H, Leg 3, outer view; I, Head, frontal view (hairs and labrum omitted). Male: J, Antenna; K, L, Head, frontal and lateral views (hairs omitted, labrum only in K). tp = tentorial pit; cdp = distal clypeal projection.

apex; inner more conspicuously curved, especially in female. 64. Basitibial plate of male well defined, margins carinate. 65. Tarsus 3 with no modifications except basitarsus of female with small apical projection. 66. Claws deeply cleft; rami subequal in male, inner shorter than outer in female. 67. Metasoma in male somewhat broader than thorax. 69. T2-5 of male with gradulus posterolaterally absent and with postgradular depression rather shallow; posterior marginal areas of T1-5 in male and T1-4 in female pilose, forming bands laterally (band less distinct on T5 of male and T4 of female); lateral fovea of T2 (both sexes) rather narrow, gently depressed. 70. Pygidial plate of male absent; T7 at apex strongly curved down and forward, with a conspicuous projection laterally (Fig. 4E). 71. T7 of female as in Figure 5E. 72. T8 of male trapezoidal. 73. Metasomal sterna of male mostly with hairs straight, short, appressed, except on S6 obliquely directed toward midline. 73a. S1-5 of female with hairs as in male but longer and branched on premarginal areas. 74. S4 of male with distal margin slightly and broadly convex. 75. S5 of male with margin straight medially. 76. S5 of female with neither median proximal sclerotized area nor gradulus; distal margin broadly and gently concave (Fig. 5G). 77. S6 of male broadly and gently concave medially (Fig. 5A). 78. S6 of female similar to that of *Pseudopanurgus* except longitudinal basal carina absent; duplication well sclerotized; distal margin slightly concave medially; premarginal area fully hairy but sparsely so medially; rest of sternum with hairs minute (Fig. 5D). 79. S7 of male wide, distally with a V-shaped emargination and a lateral, short projection; proximal arms forming a U (Fig. 4C). 80. S8 of male wide, large, strongly carinate laterally and much exposed distally (surpassing T7) (Fig. 4D, G, H). 82. Gonocoxal apodeme well developed (dorsal view), rather wide, not inflexed (suture almost invisible) (Fig. 4A, B). 83. Gonocoxites much shorter than penis valve, fused medially. 84. Gonostylus fused to gonocoxite, slightly shorter than half length of gonocoxite. 85. Volsella strongly lateral in position, free mesally, fused to gonocoxite proximally, without denticles. 86. Penis valves wide, completely fused to each other and to penis. 87. Penis long (slightly surpassing penis valve), extremely wide, with two mesal longitudinal sclerotized areas. 88. Sting short, not reaching stylus, first valvula little sclerotized, valve absent (Fig. 5F).

Comments. This genus is known only from one species, *Protomeliturga turnerae* (Ducke).

The material available for this study was: the type of *P. turnerae* (lectotype female and lectoallotype male) from the Museu Paraense Emilio Goeldi (Belém, Pará, Brazil) (not dissected) and two specimens (one male and one female) from the Berlin Museum which, although labeled "Typus," are not the real types. The specimens from the two museums are certainly conspecific.

Discussion. The cladistic analysis shows this species to be the sister group of the Calliopsini. It presents a series of derived features, although at first sight the genus suggests a rather primitive panurgine. Probably because of its lateral hair bands on the metasomal terga, Ducke (1907) erroneously placed it in *Calliopsis*.

Distribution. Protomeliturga is known only from São Luiz de Maranhão, Brazil.

TRIBE CALLIOPSINI

This tribe, found only in the western hemisphere, is the most derived group of the Panurginae. I list below a series of its characters, using the same series of character numbers as in the generic descriptions, in order to avoid repetition in the descriptions of the genera as well as to emphasize the unity of the tribe.

30. Inner subantennal suture about as long as antennal socket diameter or shorter. 33. Tentorial pit in outer subantennal suture. 45. Pre-episternal groove rather short, absent below scrobal level. 46. Pterostigma basally nearly as wide as distally or little narrower; side within marginal cell usually straight. 48. Submarginal cells two. 55. Propodeal triangle glabrous. 58. Middle femur of female, on ventral margin, with a distinct, well-defined comb. 61. Tibia 3 of female, on inner surface, with keirotrichia present toward dorsal border and at base and apex, sometimes only at the two ends; male tibia 3 with dorsal border untoothed. 62. Tibial scopa, on outer surface, of sparse to extremely sparse, mostly minutely branched and simple hairs. 69. T1-5 of male and T1-4 of female with posterior marginal area usually completely or partially hairy (short hairs). 70. Pygidial plate of male usually present. 72. Tergum (T)8 of male usually about as wide as long and roughly hexagonal but with lateral angles rather rounded. 73. S1-5 of male with hairs mostly directed straight backward. 76. S5 of female with a median sclerotized area between proximal margin and gradulus except in *Callonychium* (Fig. 10E); gradulus usually short except in *Callonychium* long and recurved; distal margin broadly convex medially. 78. S6 of female with proximal laminar lobes; with basal spine-like sclerotization except of different shape in some *Calliopsis (Nomadopsis)* and absent in *Callonychium;* basal sclerotization free from disc of sternum distally (except fused on *Arhysosage*); lateral margin with a strong, usually almost straight ridge; longitudinal basal carina absent; duplication usually at least somewhat sclerotized except thin in some *Calliopsis* s. l.; most of surface with minute sparse hairs except apically with well-defined rows of dense hairs forming a lateral patch or a continuous, usually curved, band of hairs. 80. S8 of male with distal projection well developed;

basal body with a lateral acute projection except in *Acamptopoeum* and *Calliopsis (Verbenapis)*, which have no projection or only a small convexity, respectively. 82. Gonocoxal apodeme (ventral view) conspicuous, not inflexed. 83. Gonocoxites globose, connected with one another by weakly sclerotized cuticle to completely fused and highly sclerotized. 84. Gonostylus inconspicuous or absent. 85. Volsella usually well developed and without denticles [except with denticles in *C. (Nomadopsis)*]; volsella sometimes apparently absent or rudimentary (completely fused to gonocoxite?) as in *Arhysosage*, *Spinoliella* and *Callonychium*. 86. Penis valves dorsally fused through a small, narrow bridge. 88. Sting usually short or greatly reduced (except surpassing stylus in *Acamptopoeum*); second valvifer (triangular plate) usually unmodified; first valvula only slightly sclerotized, valve absent [except a rudiment of valve in *Calliopsis (Ceroliopoeum)*].

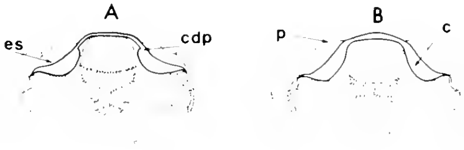

Figure 7, A, B. Heads of males, ventral views. A, *Spinoliella (Peniella) maculata* (Spinola); B, *Callonychium (Callonychium) mandibulare* Brèthes. cdp = distal clypeal projection; es = epistomal suture; c = clypeus, lateral area; p = paraocular area.

KEY TO THE GENERA OF THE TRIBE CALLIOPSINI

1. Male 2
—Female 6
2. Orbits convergent below. Tentorial pit clearly below median point of outer subantennal suture (Fig. 6A, B) 3

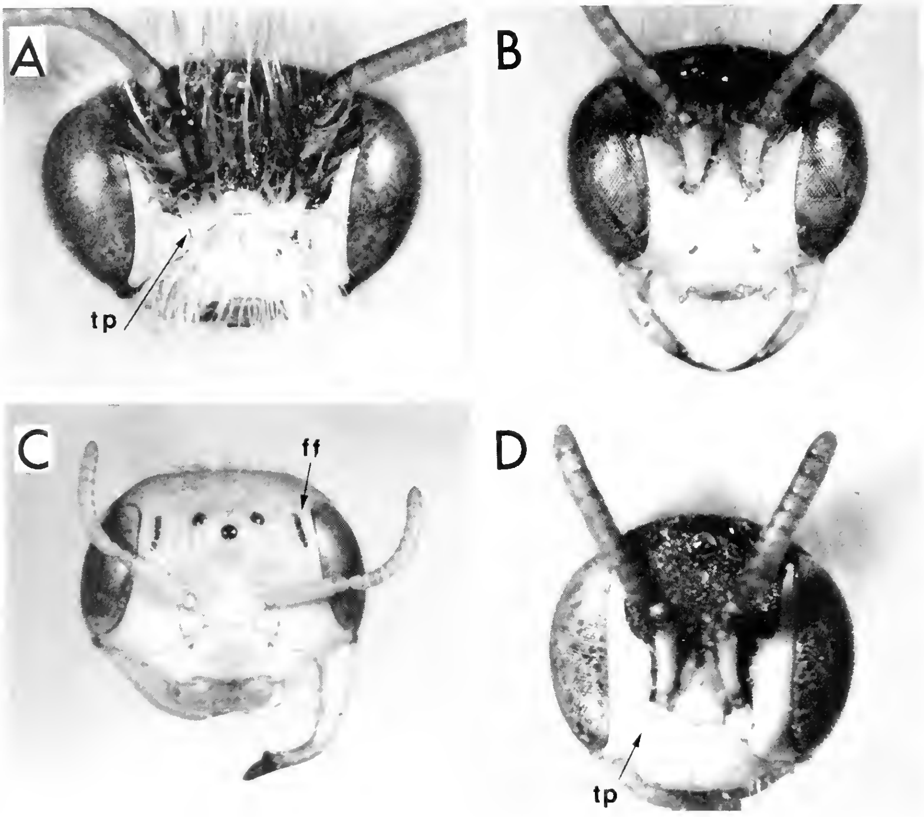

Figure 6, A–D. Heads of males, frontal views. A, *Acamptopoeum submetallicum* (Spinola); B, *Calliopsis (Calliopsis) andreniformis* Smith; C, *Arhysosage ochracea* Brèthes; D, *Callonychium (Paranychium) chilense* (Friese). tp = tentorial pit; ff = facial fovea.

—Orbits subparallel or divergent below. Tentorial pit at median point of outer subantennal suture or nearly so (Fig. 6C, D) 4

3. T7 distally with a median smooth area, delimited by hairs, tapered at apex. S4 with distal margin straight medially. S5 on distal margin without median projection or any other modification . . . . *Acamptopoeum*

—T7 with pygidial plate rounded or truncate at apex (sometimes poorly delimited by ridge or carina laterally). S4 with distal margin usually produced in middle, broadly concave mesally (Fig. 11G). S5 with well-developed median projection on distal margin, though sometimes inconspicuous (Figs. 11C, 18E, 20H) . . . . *Calliopsis*

4. Orbits strongly divergent below. Lower paraocular area flat. Most of body yellow. Hind tibial spurs strongly curved (similar to those of female in Fig. 26C). Metasoma much wider than head. Total length about 1 cm or nearly so . . . . *Arhysosage*

—Orbits usually subparallel, if not so, lower paraocular area very swollen on inner area. Body with yellow markings but usually predominantly black. Inner hind tibial spur almost straight, outer straight or somewhat curved (similar to those of female in Fig. 27G). Metasoma as broad as head. Total length 4–7 mm 5

5. Metasoma at apex slightly curved or straight. Paraocular area yellow only on lower part. Clypeus (ventral view) distally with projection beside lateral part of labrum; epistomal suture laterally sinuous (Fig. 7A). Antennal socket usually at lower 1/3 of face . . . . *Spinoliella*

—Metasoma at apex strongly curved downward and foreward. Paraocular area with yellow surpassing antennal socket level, usually narrowly following orbit. Clypeus (ventral view) with margins of lateral areas usually almost straight (Fig. 7B). Antennal socket (lower margins) usually at lower 1/4 of face . . . . *Callonychium*

6. Labrum with basal area well excavated, distal part convex, protuberant in lateral view. Orbits generally convergent below or if not, lower paraocular area not swollen on inner corner 7

—Labrum flat or with smooth, rounded, nearly transverse ridge, distal area flat, not inflexed. Orbits subparallel or divergent below 8

7. Labrum with basal area at least laterally pilose (Fig. 9F, G). Hind tibia with keirotrichia widespread on most of inner surface (Fig. 10F) . . . . *Acamptopoeum*

—Labrum with basal area usually glabrous; if pilose, also flat (without ridge). Hind tibia with keirotrichia widespread but absent toward ventral margin to completely absent between dense patch at each end . . . . *Calliopsis*

8. Orbits divergent below. Metasoma wider than thorax. Middle and hind tibial spurs strongly curved at apices (Fig. 26C). Lower paraocular area convex . . . . *Arhysosage*

—Orbits subparallel. Metasoma about as wide as thorax or narrower. Middle and hind tibial spurs slightly curved (Fig. 27G). Lower paraocular area strongly convex only on inner corner (Fig. 7A, B) 9

9. Gena black. Paraocular area on lower part with yellow spot not narrowed along orbit. Antennal sockets at lower 1/3 of face. Claws bifurcate. Facial fovea not linear . . . . *Spinoliella*

—Gena with longitudinal yellow band to completely yellow (Fig. 8D). Paraocular area with lower yellow spot narrowed along orbit (Fig. 6D). Antennal sockets (lower margins) usually at lower 1/4 of face. Claws simple. Facial fovea linear . . . . *Callonychium*

Genus *Acamptopoeum* Cockerell
(Figs. 2C, 6A, 9, 10, 30)

Friesea Schrottky, 1902: 418 (preoccupied). Type species: *Friesea brasiliensis* Schrottky, 1902 = *Acamptopoeum prinii* (Holmberg, 1884) (monobasic).

Acamptopoeum Cockerell, 1905: 320. Type species: *Camptopoeum trifasciatum* Spinola, 1851, sensu Cockerell, 1905 = *Acamptopoeum submetallicum* (Spinola, 1851) (monobasic and original designation).

Parafriesea Schrottky, 1906: 118 (new name for *Friesea* Schrottky). Type species: *Friesea brasiliensis* Schrottky, 1902 = *Acamptopoeum prinii* (Holmberg, 1884) (autobasic).

Diagnosis. Close to *Calliopsis;* distinguishing characters are as follows: Pubescence of thorax similar in length and density to that of *Colletes.* Orbits convergent below. Labrum with strong transverse salient. Hair bands (sometimes absent in male) on premarginal areas of metasomal terga. *Male.* S4 and S5 with distal margins almost straight. *Female.* Middle tibial spur coarsely toothed. Sting surpassing stylus, truncate at apex.

Description. 1. Length 8–11 mm. 2. Integument dull or metallic. 3. Lower half of face (extending up beside orbit), pronotum (sometimes) and legs yellow (spots reduced in female). 4. Metasoma

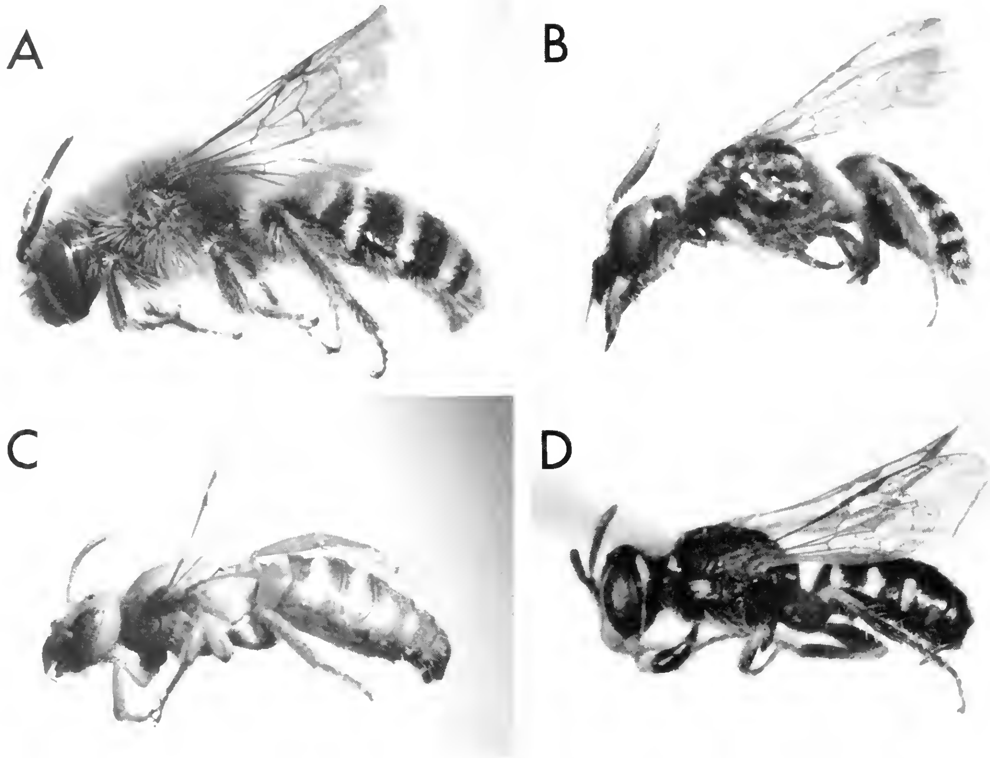

Figure 8, A–D. Calliopsine males, lateral views. A, *Acamptopoeum submetallicum* (Spinola); B, *Calliopsis (Calliopsis) andreniformis* Smith; C, *Arhysosage ochracea* Brèthes; D, *Callonychium (Paranychium) chilense* (Friese).

with no yellow marks. 5. Pubescence relatively long on head and thorax, denser on thorax (similar to that of *Colletes*), much shorter on metasoma. 7. Punctures in general fine, usually dense on thorax and metasoma, sparser on sterna of male. 8. Head distinctly broader than long and broader than thorax. 11. Glossa less than half as long as prementum, slender. 13. Segment 1 of labial palp almost twice as long as 2–4 together or somewhat longer. 16. Maxillary blade less than twice as long as prepalpal part of galea. 17. Galeal comb of 18–24 bristles. 20. Labrum less than twice as broad as long; basal part partially or almost completely pilose; distal margin of basal area strongly salient, hiding inflexed apical part of labrum (Fig. 9F, G). 25. Mandible with upper margin rather conspicuously medially produced. 27. Clypeus somewhat less than three times broader than long and somewhat protuberant (about 1/3 width of eye in lateral view); distal margin with a usually conspicuous acute or rounded projection near lateral margin of labrum. 30. Inner subantennal suture angulate. 31. Subantennal area wider than inner suture length and than socket. 33. Tentorial pit in outer subantennal suture, but close to epistomal suture. 34. Antennal sockets approximately at middle of face. 36. Antennal flagellum of male unmodified, somewhat longer than head; flagellomere 1 about as long as 2 and about as long as broad. 37. Lower mesal paraocular area rather flattened or slightly convex. 38. Facial fovea oval, shallow. 39. Orbits strongly convergent below. 40. Ocelli above dorsal orbital tangent. 41. Vertex convex. 42. Gena of male (lateral view) somewhat variable (usually narrower than eye but sometimes wider; wider dorsally than ventrally. 43. Pronotum with dorsal preapical ridge rounded. 44. Mesepisternum with anterior surface sometimes reduced, slightly convex. 45. Pre-episternal groove curved, reaching scrobal level, not extending below. 46. Pterostigma somewhat longer and somewhat wider than prestigma; margin basal to vein r subparallel to costa; that within marginal cell straight (or slightly convex). 47. Marginal cell obliquely and rather broadly truncate at apex, much longer than distance from its apex to wing tip. 49. Submarginal cell 1 shorter (at least slightly) than cell 2 + 3. 51. First recurrent vein far from first transverse cubital. 52. Forewing with cu-v two or three times longer than second abscissa M + Cu. 53. Hind wing with cu-v 1/4 to 1/5 as long as M + Cu. 54. Dorsal surface of propodeum about as long as metanotum. 55. Propodeal triangle very smooth, depressed medially. 57. Basitarsus 1 five to seven times longer than broad in male, about four times longer than broad in female; tarsomeres 2–4 unmodified. 59. Middle tibial spur of female about as long as basitarsus 2 or somewhat shorter, with coarse teeth (Fig. 10G); in male rather longer than half basitarsal length and with fine, dense teeth. 60. Basitarsus 2 of male longer than 1 or 3 (2 and 3 somewhat variable in female); tarsomeres 2–4 unmodified. 61. Tibia 3 of female somewhat less than twice as long as basitarsus 3, with keirotrichia on inner surface except toward ventral and dorsal margins (Fig. 10F); male tibia 3 with keirotrichia as in female. 62. Tibial scopa rather sparse, though dense on dorsal margin; outer surface with branched and simple hairs. 63. Hind tibial spurs (both sexes) with fine and dense teeth (appearing untoothed), slightly curved toward apices, outer somewhat shorter than inner. 64. Basitibial plate of male well defined. 65. Tarsus 3 with no modifications except basitarsus of female with apical process. 66. Claws bifurcate; rami subequal in male, inner much shorter than outer in female. 67. Metasoma in male somewhat wider than thorax. 69. T2–5 of male with gradulus posterolaterally not surpassing anterior half of tergum, not carinate, with postgradular depression on T2 and T3 well marked and narrow, shallower on posterior terga; posterior marginal areas of T1–5 in male and T1–4 in female pilose, forming hair bands (sometimes weak in male); lateral fovea of T2 (both sexes) oval, weak (borders difficult to see). 70. Pygidial plate of male absent, represented only by an apically acute, smooth and bare area. 71. T7 of female squared (Fig. 10C). 72. T8 of male as in Figure 9H. 73. Metasomal sterna of male with hairs directed caudad, mostly on premarginal areas and not appressed, sparse or absent on midline. 73a. S1–5 of female with hairs short, dense and appressed, mixed with hairs somewhat longer, sparser, and not appressed (Fig. 10E). 74, 75. S4 and 5 of male with distal margins almost straight medially. 77. S6 of male with small apical emargination (Fig. 9E). 78. S6 of female with basal sclerotization long and very acute, duplication fully and strongly sclerotized, distal margin concave medially, S6 with patch of dense hairs on premarginal area, interrupted medially (Fig. 10H). 79. S7 of male with distal median projections short, proximal arms widely open (Fig. 9C). 80. S8 of male with median distal projection long, clavate, abruptly separated from a transversely rectangular body (Fig. 9D). 83. Gonocoxites globose, ventrally completely fused to each other. 84. Gonostylus fused to gonocoxite, short (almost 1/3 length of gonocoxite in ventral view). 85. Volsellae well developed, fused to each other forming a highly sclerotized plate, without denticles. 86. Penis valves with folds, somewhat intricate, rather rounded at apices; dorsally fused to each other by small and narrow bridge; laterally with a long row of hairs (Fig. 9A, B). 87. Penis usually reaching apex of penis valve or nearly so, narrower than valve, largely sclerotized, clearly separated from penis valve. 88. Sting elongate, truncate at apex, surpassing stylus (Fig. 10A, B).

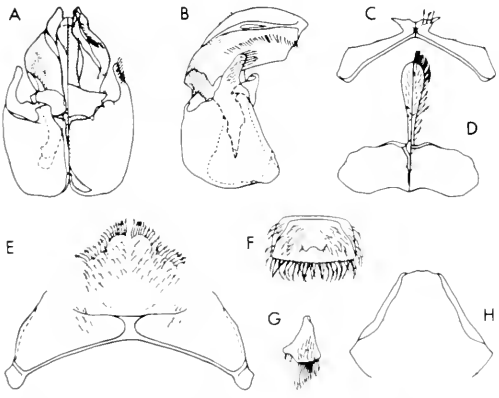

Figure 9. *Acamptopoeum submetallicum* (Spinola). *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, D, S7 and 8, dorsal and ventral views; E, S6, ventral view; F, Labrum; G, Labrum, lateral view; H, T8.

Comments. Cockerell indicated that the type species of this genus is *Camptopoeum trifasciatum* Spinola, 1851 (now in *Liopoeum*). His description, however, corresponds to *Camptopoeum submetallicum* Spinola, 1851. Because of this misidentification the latter species has been considered for many years as the type species of *Acamptopoeum.* According to the International Code of Zoological Nomenclature, Article 70c, cases of misidentified type species have to be referred to the International Commission on Zoological Nomenclature for resolution. I will therefore request the International Commission to designate *Camptopoeum submetallicum* Spinola (= *C. trifasciatum* of Cockerell, not Spinola, 1851) as the type species of *Acamptopoeum.*

If the request is denied, then the *name* used by Cockerell in designating the type species must be

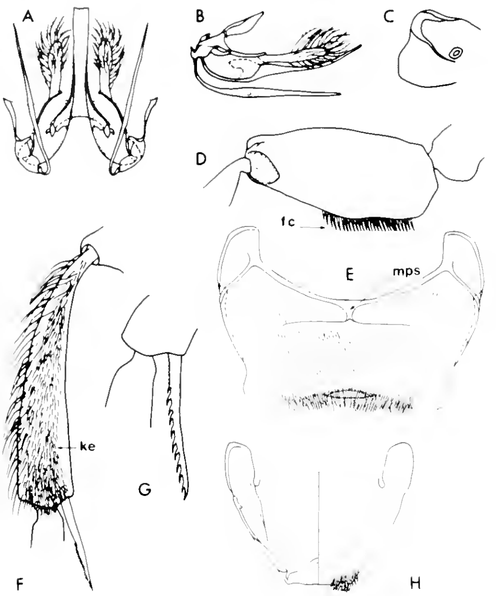

Figure 10. *Acamptopoeum submetallicum* (Spinola). *Female:* A, B, Sting, ventral and lateral views; C, T7; D, Femur 2 (hairs on inner surface omitted); E, S5, ventral view; F, Tibia 3, inner view; G, Spur, leg 2; H, S6, dorsal and ventral views. fc = femoral comb; ke = keirotrichia; mps = median proximal sclerotization.

maintained. In that case *Acamptopoeum* would contain the species here placed in *Calliopsis (Liopoeum); Liopoeum* would be a junior synonym. *Parafriesea* would stand as the generic name for the species now placed in *Acamptopoeum.*

The South American genus *Acamptopoeum* is represented by the following species: **A. argentinum* (Friese, 1906a), **A. prinii* (Holmberg, 1884), *A. inauratum* (Cockerell, 1926), *A. colombiensis* Shinn, 1965, *A. nigritarse* (Vachal, 1909), *A. vagans* (Cockerell, 1926), *A. maculatum* (Smith, 1853) (see Shinn, 1965), and **A. submetallicum* (Spinola, 1851).

The type locality (east Florida) given for *A. maculatum* is not within the otherwise known range of the genus. It seems very unlikely that Florida is its real habitat (Shinn, 1967; Mitchell, 1960, under *Calliopsis*).

Discussion. Acamptopoeum is a distinctive genus although in the past its position has been confused. At first its species were considered as *Camptopoeum,* together with European and other South American species (Spinola, 1851); later it was treated as synonym of *Liopoeum* (Michener, 1944; Rozen, 1951, 1958).

Shinn (1967) noted that according to Moure (1956, personal communication to Shinn) *Acamptopoeum* constitutes "a clearcut group of closely related species." On the other hand, Shinn (1967) agrees with Michener (1944: 246) in considering the possibility that "*Parafriesea* = *Acamptopoeum* . . . is probably a mere subgenus of *Calliopsis.*"

My study, however, does not support the idea of including *Acamptopoeum* in any other genus. The cladistic analysis indicates it to be the sister group of *Calliopsis* s. l. The cladogram (Fig. 30) shows that *Acamptopoeum,* in spite of the superficial similarity to some subgenera of *Calliopsis,* presents a series of apomorphies which support it as a good genus (see discussion in Cladistic Analysis section).

Distribution. This genus occurs in Argentina, Perú, Paraguay, Uruguay, Brazil, Colombia, and Chile (Moure, in litt.; Schrottky, 1903, 1913; Friese, 1906a, b; Holmberg, 1844, Shinn, 1965).

Genus *Calliopsis* Smith

Diagnosis. Superficially similar to *Acamptopoeum* but differing as follows: Pubescence of thorax usually shorter and less dense than in *Colletes.* Labrum usually with transverse ridge but not strongly salient. *Male.* S4 with distal margin produced medially (sometimes inconspicuously). S5 usually with well-developed median projection distally. *Female.* Sting not reaching stylus, tapered at apex.

Description. 3. Head, thorax, and legs usually with yellow marks. 8. Head broader than long (sometimes as broad as long in female). 20. Labrum with basal area glabrous. 33. Tentorial pit in outer subantennal suture, close to epistomal suture. 39. Orbits at least slightly convergent below, usually more strongly so in male; or in female sometimes subparallel. 41. Vertex at least slightly convex. 45. Pre-episternal groove not reaching scrobal level. 74. S4 of male with distal margin produced in the middle, sometimes inconspicuously so. 75. S5 of male with distal median projection, usually well developed (inconspicuous in *C. (Verbenapis).* 80. S8 of male with two short, lateral projections between body and distal projection, sometimes very small. 84. Gonostylus absent.

Discussion. The genus *Calliopsis* is treated here in a new broad sense to include not only the subgenera *Calliopsis* s. str., *Perissander, Calliopsima* and *Verbenapis,* traditionally included in the genus, but also *Nomadopsis* s. str., *Macronomadopsis, Micronomadopsis, Hypomacrotera, Liopoeum* and two new subgenera *Liopoeodes* and *Ceroliopoeum.* This new concept of the genus *Calliopsis* is based on the following facts:

1. The similarity between some complex genitalic structures of *Nomadopsis* (in the former sense, as a genus) and those of some species of *Calliopsis* (in the usual sense) suggests that some species of *Nomadopsis* are more closely related to some *Calliopsis* than to other *Nomadopsis*. The cladogram (Fig. 30), however, still shows *Nomadopsis* (usual sense) as a monophyletic group, although the synapomorphies are not strong. Small ridges on the lateral part of the penis valve of males occur in *Micronomadopsis, Hypomacrotera, Calliopsis* s. str., *Perissander, Liopoeodes* and *Ceroliopoeum*. This fact may indicate a close relationship among these six taxa.
2. Chemosystematic studies indicate that, looking at the Dufour's gland lipids, the *Calliopsis–Nomadopsis–Hypomacrotera* group (''paraffin bees'') appears to be monophyletic (Cane, 1983). The cladogram of this analysis shows one species of *Calliopsis* (usual sense) as being more closely related to one species of *Nomadopsis* than to two other species of *Calliopsis*.
3. Lack of strong characters to diagnose the traditional genera. *Calliopsis* and *Nomadopsis* (in the old sense) have been characterized mainly by the presence of hair bands and of yellow integumental marks on the metasomal terga respectively. Both characters appear independently in other Panurginae. Larval characters also do not differentiate these groups (Rozen, 1966).
4. Existence of *C. (Liopoeodes) xenopous* n. sp., a species that does not fit within taxa already established. Maintaining generic rank for *Calliopsis, Nomadopsis* and *Hypomacrotera* leads to proliferation of genera difficult to separate from one another.
5. There is little morphological differentiation among the subgenera except for *Liopoeodes* and *Verbenapis*, which appear in the cladogram as having more apomorphies than the rest of the subgenera. There is no constant apomorphy for *C. (Micronomadopsis)*, which therefore may be paraphyletic.
6. The cladistic analysis indicates that *Calliopsis* s. l. is a natural group. The cladogram shows six synapomorphies (62, 81, 84, 85, 111, 115) that make this group monophyletic. The strongest characters are: 62, 81, 84, and 115.

KEY TO THE SUBGENERA OF THE GENUS *Calliopsis*

1\. Males 2
—Females 12
2\. Pubescence of basitarsus 3 on dorsal margin (at least in part) about as long as basitarsus or longer (Fig. 16A). Apical area of labrum clearly convex, almost glabrous except margin; labrum with no defined ridge separating basal and apical areas (Fig. 15H) . . . . *Liopoeum*
—Pubescence of basitarsus 3 on dorsal margin about half as long as basitarsus or shorter. Apical area of labrum hairy, rather flattened; labrum with ridge or carina separating basal and apical areas (Fig. 1F) [except entire labrum flat and pilose in *C. (H.) subalpina*] 3
3\. T2-5 at least laterally with premarginal hair bands. 4
—T2-5 without premarginal hair bands 7
4\. Subantennal area black. Metanotum laterally without velvet area. Propodeal triangle basally smooth, concave medially . . . . *Verbenapis*
—Subantennal area yellow. Metanotum laterally with area (sometimes reduced to a small and narrow strip) of dense velvety hairs. Propodeal triangle basally rugose or at least slightly roughened. 5
5\. Clypeus (lateral view) clearly protuberant (Figs. 1E, 8B). Metanotum laterally with conspicuous patch of velvet-brown hairs . . . . *Calliopsis* s. str.
—Clypeus (lateral view) almost flat. Metanotum laterally with small patch of velvet-white hairs 6
6\. Labrum with basal area delimited by strong carinate ridge. Basitarsus 2 somewhat shorter than 3. Propodeal triangle basally with strong striae; striated basal part delimited by strong transverse ridge . . . . *Calliopsima*
—Labrum with basal area delimited by weak ridge. Basitarsus 2 much longer than 3. Propodeal triangle basally with weak striae, posteriorly not delimited by strong transverse ridge . . . . *Perissander*
7\. Metasoma without yellow marks. 8
—Metasomal terga usually with interrupted or complete yellow bands 10
8\. Antennal scape robust (Fig. 24F). Pterostigma (maximum width between costa and Rs) more than twice as broad as prestigma, side within marginal cell clearly convex (Fig. 2D) . . . . *Ceroliopoeum*

—Antennal scape normal. Pterostigma less than twice as broad as prestigma, side within marginal cell straight or nearly so (Fig. 2E) 9

9. Inner orbits subparallel. Marginal cell about twice as long as submarginal cell 2 + 3 or longer. Tarsus 3 with tarsomeres 2–5 unmodified . . . . *Hypomacrotera*

—Inner orbits convergent below (Fig. 22H). Marginal cell less than twice as long as submarginal cell 2 + 3. Tarsus 3 with basitarsus and tarsomeres 2–4 asymmetrical; distitarsus widened medially (Fig. 22K) . . . . *Liopoeodes*

10. Tarsi 1, 2 with tarsomeres slender. Tarsus 3 often with tarsomeres 2–4 broadened laterally, asymmetrical (Fig. 21I) . . . . *Micronomadopsis*

—Tarsi 1–3 with tarsomeres broadened distally, symmetrical 11

11. Tibia 3 about twice as long as basitarsus 3. S4 clearly produced in middle of distal margin. S5 with well-developed median projection on distal margin (Fig. 18E). . . . . *Nomadopsis*

—Tibia 3 somewhat longer than basitarsus 3. S4 inconspicuously produced in middle of distal margin. S5 distally with short median projection (Fig. 20H). . . . . *Macronomadopsis*

12. Pterostigma (maximum width between costa and Rs) more than twice as broad as prestigma, margin within marginal cell clearly convex. Middle femur with ventral comb less than half length of femur. . . . . *Ceroliopoeum*

—Pterostigma less than twice as broad as prestigma, margin within marginal cell straight or nearly so. Middle femur with ventral comb about half length of femur 13

13. T2–4 with premarginal hair bands at least laterally 14

—T2–4 without premarginal hair bands 19

14. Integument black (with some slight blue but no yellow). Wing venation mostly dark. Inner orbits subparallel (Fig. 23B). T1–2 polished, scarcely punctate . . . . *Liopoeodes*

—Integument with at least some yellow marks. Wing venation mostly yellowish. Orbits convergent below. Terga with rather abundant punctation. 15

15. Middle tibial spur with coarse teeth distally (Fig. 16F). Tibia 3 with keirotrichia on inner surface at base and at apex only (Fig. 16D). S6 distally with oblique patch of hairs beside midline (Fig. 16G). . . . . *Liopoeum* (part)

—Middle tibial spur with teeth somewhat coarse distally (Fig. 14K). Tibia 3 with keirotrichia on most of inner surface or absent toward ventral border. S6 distally with hairs forming a curved fringe 16

16. Tarsus 1 on inner surface with hairs sparse, mostly stiff, curved and not tapered at apices (Fig. 14H). Metanotum laterally without patch of white, velvety hairs . . . . *Verbenapis*

—Tarsus 1 on inner surface with hairs dense, unmodified. Metanotum laterally with small (sometimes inconspicuous) patch of white, velvety hairs 17

17. Clypeus (lateral view) protuberant 1/3 width of eye or more. Paraocular area with lowest part noticeably wider than at level of antennal sockets, usually swollen on lower inner corner . . . . *Calliopsis* s. str.

—Clypeus (lateral view) protuberant about 1/4 to 1/9 width of eye. Paraocular area with lowest part almost as wide as at level of antennal sockets, slightly convex 18

18. Propodeum mostly punctate, at base conspicuously rugose and triangle delimited by strong ridge or carina. Metanotum laterally with patch of white velvety hairs clearly visible *Calliopsima*

—Propodeum posteriorly with extensive impunctate area, at base usually little or not very strongly rugose, triangle delimited by rather rounded ridge. Metanotum laterally with inconspicuous (difficult to see) patch of white, velvety hairs . . . . *Perissander*

19. Middle tibial spur with most teeth much longer than those of hind tibial spurs (Fig. 16F). S6 distally with oblique patch of hairs beside midline (Fig. 16G) . . . . *Liopoeum* (part)

—Middle tibial spur with most teeth only slightly longer than those of hind tibial spurs, fine or somewhat coarse (Fig. 17I). S6 distally with hairs forming a curved fringe (Fig. 17H). 20

20. Propodeal triangle polished. Metasoma with no yellow markings. . . . . *Hypomacrotera*

— Propodeal triangle at least slightly rugose basally. Metasoma usually with complete or interrupted yellow integumental bands 21

21. Body length less than 10 mm. Middle tibial spur with 4 teeth on distal half (Fig. 21H) . . . . *Micronomadopsis*

—Body length 10 mm or longer. Middle tibial spurs with more than four (coarse or fine) teeth on distal half (Figs. 19D, 20J) . . . . *Macronomadopsis* and *Nomadopsis*

Subgenus *Calliopsis* Smith s. str.

(Figs. 1A, B, D–F; 6B, 8B, 11, 12, 30)

Calliopsis Smith, 1853: 128. Type species: *Calliopsis andreniformis* Smith, 1853 (by designation of Ashmead, 1899: 85).

Diagnosis. Glossa somewhat shorter than prementum. Metasomal terga black, withdistal hair bands. Axilla and metanotum laterally with dense patches of velvety hairs. *Male.* Basitarsus 2 somewhat longer than 1 and 3.

Description. 1. Length 5–8 mm. 3. Lower half of face, some spots on thorax (pronotum dorsally, pronotal lobe, tegula) and legs yellow in male, yellow much reduced in female. 4. Metasoma black. 5. Pubescence short, especially short and appressed on metasoma, forming premarginal bands on terga. 7. Punctures fine, well marked, dense on thorax. 8. Head broader than long and broader than thorax. 11. Glossa somewhat shorter than prementum. 13. Segment 1 of labial palp longer than 2–4 together. 16. Maxillary blade longer than prepalpal part of galea. 17. Galeal comb of 17–26 bristles. 20. Labrum slightly protuberant, about twice as broad as long; basal area depressed, its distal margin a rounded ridge; labral apex somewhat inflexed. 27. Clypeus more than twice as broad as long, protuberant (about 1/3 width of eye in lateral view); distal margin with a rather small, pointed projection near lateral margin of labrum in male, rounded and bigger in female. 30. Inner subantennal suture curved. 31. Subantennal area wider than inner suture length and than antennal socket. 34. Antennal socket below middle of face. 36. Antennal flagellum of male unmodified (Fig. 12G); length variable (shorter than head as in *C. andreniformis* or longer); flagellomere 1 longer than 2 (almost twice as long or less) and about as long as broad. 37. Lower mesal paraocular area slightly convex to strongly swollen. 38. Facial fovea clearly visible, very narrow (almost linear). 40. Ocelli just above dorsal orbital tangent. 42. Gena of male (lateral view) narrower than eye, broader dorsally than ventrally. 43. Pronotum dorsally with preapical ridge rounded, developed only laterally, not strong. 43a. Axilla of male (lateral to scutellum) with patch of velvety, brown hairs. 43b. Metanotum laterally with velvety hairs forming a conspicuous brown patch in males, and small white patch in females. 44. Mesepisternum with anterior flat area reduced. 45. Pre-episternal groove deep, narrow, punctate. 46. Pterostigma somewhat longer than and about as wide as prestigma; side basal to vein r subparallel to costa, that within marginal cell straight. 47. Marginal cell narrowly truncate at apex, little longer than distance from its apex to wing tip. 49. Submarginal cell 1 about as long as cell 2 + 3 (or inconspicuously longer). 51. First recurrent vein not meeting first transverse cubital but sometimes very close to it. 52. Forewing with cu-v about three times longer than second abscissa M + Cu. 53. Hind wing with cu-v 1/4 to 1/5 as long as second abscissa M + Cu. 54. Dorsal surface of propodeum shorter than metanotum. 55. Propodeal triangle striate basally, not delimited by ridge or carina posteriorly. 57. Basitarsus 1 about seven to eight times longer than broad in male and about four to five times in female; tarsomeres 2–4 unmodified. 59. Middle tibial spur with minute and fine teeth, almost straight and longer than half length of basitarsus in female, slightly curved at apex and about 1/3 as long in male. 60. Basitarsus 2 of male somewhat longer than 1 and 3; in female basitarsus 1 as long as 2 and 3, tarsomeres 2–4 unmodified. 61. Tibia 3 of female about twice as long as basitarsus 3, inner surface with keirotrichia except along ventral half; male tibia 3 with keirotrichia on most of inner surface. 62. Tibial scopa of medium-sized, sparse, and mostly simple hairs. 63. Hind tibial spurs toothed similarly to middle one, somewhat curved, outer shorter than inner. 64. Basitibial plate of male well defined. 65. Basitarsus 3 of female with moderate apical projection; tarsomeres 2–4 unmodified. 66. Claws deeply cleft with rami subequal in male, inner ramus much shorter than outer in female. 67. Metasoma in male wider than thorax. 69. T2–5 of male with

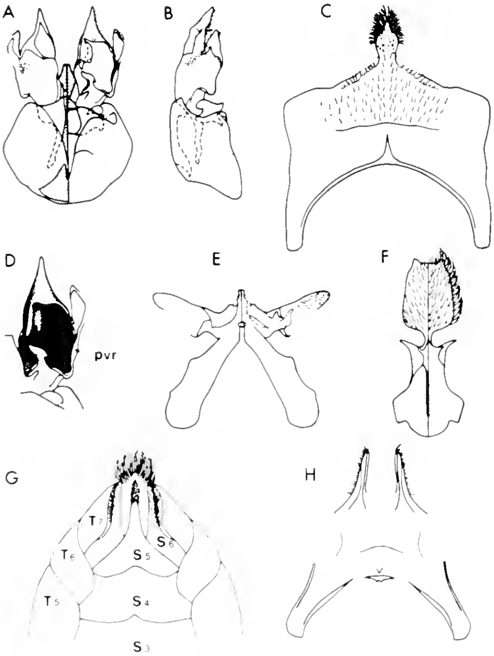

Figure 11. *Calliopsis (Calliopsis) andreniformis* Smith. *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, S5, ventral view; D, Penis valve; E, F, S7 and 8, dorsal and ventral views; G, Metasomal tip, ventral view; H, S6, ventral view. pvr = penis valve ridges.

gradulus posterolaterally reaching to middle of postgradular area at most, not strongly carinate and with postgradular depression rather shallow, narrow; posterior marginal areas of T1–5 in male and T1–4 in female each with hair band; lateral fovea of T2 (both sexes) slightly or well depressed, small and narrow in male, larger and wider in female. 70. Pygidial plate of male present. 71. T7 of female rather square, with no large dorsal, proximal expansion (Fig. 12B). 72. T8 of male similar to that of *Calliopsima*. 73. S1–5 of male with hairs mostly directed posteriorly; S6 pilose only on distal projections, mostly directed outward. 73a. S1–5 of female with hairs short, simple, appressed proximally; longer, branched, not appressed on premarginal and marginal areas medially. 75. S5 of male with a long and acute median apical projection, densely pilose at apex (Fig. 11C). 77. S6 of male distally with deep median emargination between two tapered projections (Fig. 11H). 78. S6 of female with basal sclerotization almost completely free from sternum; duplication thin, attached to a distal hardened area of sternum; distal margin produced in middle; S6 with distal hairs forming dense, somewhat curved band (Fig. 12C). 79. S7 of male with two distal (almost transverse), elongate projections (complex at base); proximal arms forming a V (Fig. 11E). 80. S8 of male with distal projection almost rectangular, with two small laterodistal lobes; body robust with two lateral curved and acute projections distally and with a weak median longitudinal ridge dorsally (Fig. 11F). 83. Gonocoxites globose, distally (ventral view) connected to one another by weakly sclerotized cuticle. 85. Volsellae attached to one another by slightly sclerotized cuticle, with no denticles. 86. Penis valves complex (with projections, folds, etc.), tapered distally, with minute ridges laterally (ventral view) (Fig. 11A, D), fused dorsally by a narrow bridge. 87. Penis much shorter and narrower than valve, clearly separated from penis valve, somewhat sclerotized. 88. Sting not reaching stylus apex (Fig. 12D).

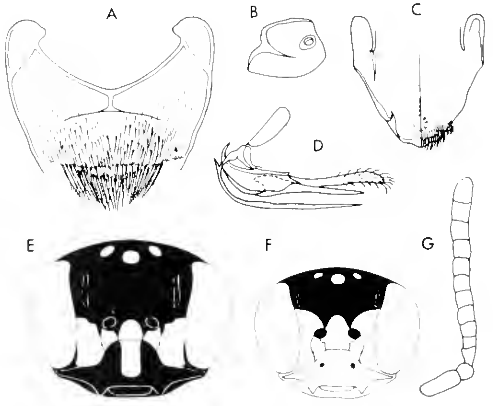

Figure 12. *Calliopsis (Calliopsis) andreniformis* Smith. *Female:* A, S5, ventral view; B, T7; C, S6, dorsal and ventral views; D, Sting; E, Head, frontal view. Male: F, Head, frontal view; G, Antenna.

Comments. *Calliopsis* s. str. contains 12 described species (Shinn, 1967). The species that I studied in detail were: *C. (C.) andreniformis* Smith and *C. (C.) hondurasica* Cockerell.

Discussion. Shinn (1967) indicated that *Calliopsis* s. str. is most closely related to *Perissander*. This has been confirmed by the cladistic analyses presented here.

Distribution. This subgenus occurs from Panamá to Canada, and from the eastern United States to Utah, Nevada, California, and Baja California Sur.

Subgenus *Perissander* Michener

(Figs. similar to 11, 12; 30)

Perissander Michener, 1942: 275. Type species: *Calliopsis anomoptera* Michener, 1942 (monobasic and original designation).

Diagnosis. Similar to *Calliopsis* s. str. but differing as follows: Glossa much shorter than prementum. Only metanotum with narrow patch of dense hairs laterally. Propodeal triangle delimited by rounded ridge posteriorly. *Male.* Forewing sometimes brown at apex. Basitarsus 2 much longer than 1 or 3.

Description. As in *Calliopsis* s. str. except: 3. Wing tip of male sometimes brown as in male of *Hypomacrotera*. 4. Metasoma sometimes fully or partially reddish. 7. Punctures of metasoma of male somewhat denser than those of *Calliopsis* s. str. 11. Glossa much shorter than prementum. 13. Segment 1 of labial palp about as long as 2–4 together. 16. Maxillary blade tapered abruptly at apex, slightly shorter than prepalpal part of galea. 17. Galeal comb of 11 bristles. 20. Labrum of male sometimes almost flat [e.g., in *C. (P.) anomoptera*] with basal area narrow and with distal margin a weak ridge. 27. Clypeus about three times broader than long, little protuberant (about 1/5 or 1/6 width of eye in lateral view); distal margin with a rounded projection near lateral margin of labrum, little developed in male. 30. Inner subantennal suture angulate. 31. Subantennal area about as wide as antennal socket. 36. Antennal flagellum of male as long as or slightly shorter than head; flagellomere 1 about as long as 2. 37. Lower mesal paraocular area somewhat convex. 38. Facial fovea of variable shape. 43b. Metanotum with narrow patch of dense hairs laterally (usually hidden by base of hind wing). 45. Pre-episternal groove shallow. 46. Pterostigma about as long as prestigma. 47. Marginal cell about as long as to much longer than distance from its apex to wing tip. 51. First recurrent vein not as close to first transverse cubital as in *C.*

andreniformis Smith. 52. Forewing with cu-v about half to twice as long as M + Cu. 54. Dorsal surface of propodeum longer than metanotum. 55. Propodeal triangle basally with weak striae, in middle delimited by ridge posteriorly. 59. Middle tibial spur with few and sparse teeth in female and about 1/5 as long as basitarsus 2 in male. 60. Basitarsus 2 of male much longer than 1 and 3. 61. Tibia 3 of female less than twice as long as basitarsus 3. 63. Hind tibial spurs generally with fine teeth (sometimes somewhat coarse). 66. Claws in male with rami short, subequal on legs 1 and 3, inner shorter than outer on leg 2. 75. S5 of male with distal, median projection sometimes somewhat rounded at apex. 78. S6 of female with distal margin concave in the middle. 80. S8 of male with only one small median lobe at apex. 85. Volsellae fully fused to each other distally, connected proximally by weakly sclerotized cuticle.

Comments. There are seven described species in this subgenus (Shinn, 1967). I studied in detail: *C. (P.) anomoptera* Michener, *C. (P.) gilva* Shinn and *C. (P.) rogeri* Shinn.

Discussion. The subgenus *Perissander,* as noted above and in Figure 30, is closely related to *Calliopsis* s. str. and both together are the sister group of the subgenera *Liopoeum, Hypomacrotera, Micronomadopsis, Macronomadopsis, Nomadopsis* s. str., *Ceroliopoeum,* and *Liopoeodes.* The metanotal velvet area of males, so well developed in *Calliopsis* s. str., is small, less dense, and rather difficult to see, although still present, at least in the species that I studied. This is in disagreement with Shinn (1967) who has stated that this pilose area is absent in this subgenus.

Distribution. Perissander is found in the southwestern United States and northwestern México, including Baja California (Shinn, 1967).

Subgenus *Calliopsima* Shinn
(Figs. 13, 30)

Calliopsima Shinn, 1967: 834. Type species: *Calliopsis rozeni* Shinn, 1967 (original designation).

Diagnosis. Differs from *Calliopsis* s. str. as follows: Glossa longer than prementum. Clypeus flattened. Labrum with distal margin of basal area a strong carina. Metanotum basilaterally with narrow patch of dense hairs. Basitarsus 2 shorter than 3. *Male.* Labral apex short.

Description. Agrees with description of *Calliopsis* s. str. except: 1. Length 7-8 mm. 5. Pubescence denser on metasoma. 7. Punctures dense on metasoma of both sexes. 11. Glossa longer than prementum. 13. Segment 1 of labial palp about twice as long as 2-4 together. 16. Maxillary blade longer than prepalpal part of galea. 17. Galeal comb of 13 bristles. 20. Labrum of male with basal area large and slightly depressed; distal margin of basal area (both sexes) usually a strong carina; apex of labrum very narrow in male, wider in female. 27. Clypeus flattened (about 1/9 width of eye in lateral view); distal margin with projection near lateral margin of labrum rounded, similar to that of *Perissander.* 31. Subantennal area about twice as wide as inner suture length and slightly wider than antennal socket. 36. Antennal flagellum of male somewhat shorter than head; flagellomere 1 somewhat longer than 2 and slightly wider than long. 37. Lower mesal paraocular area rather flat or slightly convex. 45. Pre-episternal groove rather wide and shallow. 46. Pterostigma less than twice as broad as prestigma. 47. Marginal cell longer than in *Calliopsis* s. str. 49. Submarginal cell 1 somewhat longer to shorter than cell 2 + 3. 51. First recurrent vein clearly distant from first transverse cubital. 52. Forewing with cu-v longer than second abscissa M + Cu. 54. Dorsal surface of propodeum longer than metanotum. 55. Propodeal triangle striate laterally, rugose medially, posteriorly delimited by carina. 57. Basitarsus 1 about six to seven times longer than broad in male and about four times in female. 59. Middle tibial spur about half as long as basitarsus 2. 60. Basitarsus 2 in both sexes longer than 1 and shorter than 3. 61. Tibia 3 of female less than

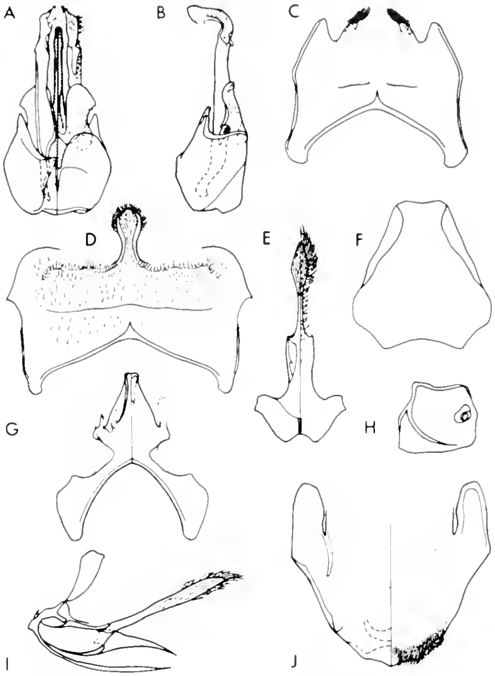

Figure 13. *Calliopsis (Calliopsima) rozeni* Shinn. *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, D, S6 and 5, ventral views; E, S8, dorsal and ventral views; F, T8; G, S7, dorsal and ventral views. *Female:* H, T7; I, Sting; J, S6, dorsal and ventral views.

twice as long as basitarsus. 62. Tibial scopa of medium-sized, dense, branched hairs. 69. T2–5 of male with gradulus long and distinctly carinate; postgradular depression rather deep on T2–3; fovea of T2 clearly visible, in female only slightly bigger and not much wider than that of male. 71. T7 of female rather squared (Fig. 13H). 75. S5 of male with median apical projection, rather short and clavate (Fig. 13D). 77. S6 of male with distal margin broadly produced medially; with two short distal mesal lobes (Fig. 13C). 79. S7 of male with distal area trianglar, laterally with a weakly sclerotized elongate projection; proximal arms forming a V (Fig. 13G). 80. S8 of male with distal projection long and narrow except arrowhead-shaped at apex; body of S8 with latero-distal projections acute but very small (Fig. 13E). 85. Volsellae strongly developed (of different shape and much larger than in *Calliopsis* s. str. and *Perissander*), fused to each other proximally, free distally, with no denticles. 86. Penis valves long, rather simple, angulate at apex, attached to each other dorsally by reduced membranous area. 87. Penis long, narrower than valve. 88. Sting even shorter than in *Calliopsis* s. str. (much shorter than stylus) (Fig. 13I).

Comments. The subgenus *Calliopsima* contains 15 species (Shinn, 1967). *C. (C.) rozeni* Shinn and *C. (C.) coloradensis* Cresson were examined in detail.

Discussion. The cladogram (Fig. 30) shows that the subgenus *Calliopsima* is the sister group of the other subgenera of *Calliopsis* s. l. (based on male characters only) but is more closely related to *Verbenapis* than to *Calliopsis* s. str. and *Perissander* together. The relationships among these subgenera agree with those stated by Shinn (1967).

Distribution. According to Shinn (1967) *Calliopsima* occurs from Canada to southern México.

Subgenus *Verbenapis* Cockerell and Atkins
(Figs. 14, 30)

Verbenapis Cockerell and Atkins, 1902: 44. Type species: *Calliopsis verbenae* Cockerell and Porter, 1899 (monobasic).

Diagnosis. Genitalic and associated sterna more similar to those of *Calliopsima* than to those of *Calliopsis* and *Perissander.* It differs from these subgenera as follows: Metanotum laterally without velvety hairs. Subantennal and supraclypeal areas black. Glossa as in *Calliopsima. Male.* Basitarsus 2 shorter than 3 (as in *Calliopsima*). S6 with median projection with minute median distal emargination. *Female.* Tarsus 1 on inner surface with rigid hairs, curved at blunt apices.

Description. Agrees with that of *Calliopsis* s. str. except: 1. Length 7–8 mm. 3. Face with yellow marks restricted to clypeus and lower paraocular area; thorax black; legs with yellow reduced, although extensive in male. 5. Tergal hair bands less dense in male. 7. Punctures sparser on thorax and metasoma. 11. Glossa longer than prementum as in *Calliopsima.* 13. Segment 1 of labial palp more than three times longer than 2–4 together. 16. Maxillary blade more than twice as long as prepalpal part of galea. 17. Galeal comb of 18 bristles. 20. Labrum of male similar to that of *Calliopsima;* in female, basal area well depressed and with weaker distal ridge. 27. Clypeus somewhat protuberant (about 1/4 width of eye in lateral view); distal margin with a small rounded projection near lateral margin of labrum as in *Perissander.* 36. Antennal flagellum of male similar to that of *Calliopsima.* 37. Lower mesal paraocular area somewhat convex as in *Perissander.* 38, 45, 46, 47. Facial fovea, pre-episternal groove, pterostigma, and marginal cell as in *Calliopsima.* 49. Submarginal cell 1 somewhat longer than cell 2 + 3. 51. First recurrent vein somewhat distant from first transverse cubital. 52. Forewing with cu-v longer (about twice) than second abscissa M + Cu. 55. Propodeal triangle polished, shiny, with deep median concavity. 57. Basitarsus 1 about eight times longer than broad in male and about seven times in female, inner surface with

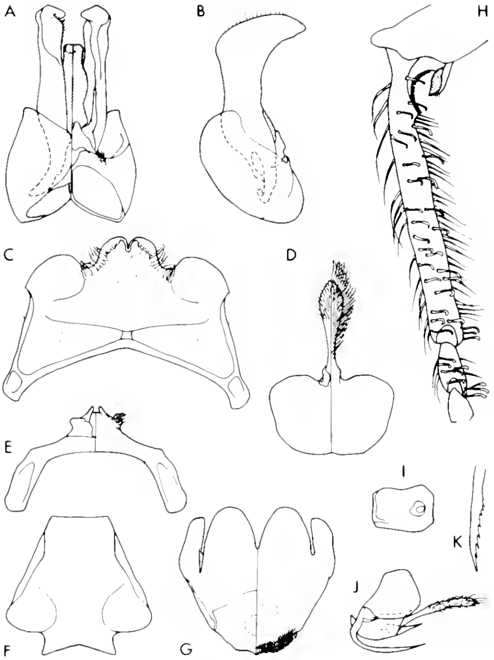

Figure 14. *Calliopsis (Verbenapis) verbenae* Cockerell and Porter. *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, S6, ventral view; D, E, S8 and 7, dorsal and ventral views; F, T8. *Female:* G, S6, dorsal and ventral views; H, Tarsus 1, inner view; I, T7; J, Sting; K, Spur, leg 2.

curved hairs in female; tarsomeres of female (inner surface) with hairs as on basitarsus. 58. Femur of female with comb of hairs shorter than in *Calliopsis* s. str. 59. Middle tibial spur with teeth serrate (Fig. 14K), sparser than in *Calliopsis* s. str., similar to that of *Perissander*. 60. Basitarsus 2 of male as in *Calliopsima;* female with basitarsus 2 as long as 1 and 3. 61, 62. Tibia 3 of female and tibial scopa similar to those of *Calliopsima* but scopa of sparser hairs with shorter branches. 67. Metasoma in male similar to that of *Calliopsis* s. str. but only slightly wider than thorax. 69. T2-5 of male with gradulus short; that of T2 (both sexes) indistinct, difficult to see. 70. Pygidial plate of male present. 71. T7 of female as in Figure 14I. 72. T8 of male as in Figure 14F. 74. S4 of male with distal margin inconspicuously produced in middle (difficult to see). 75. S5 of male with distal margin little produced medially, with no projection as in the other subgenera of *Calliopsis*. 77. S6 of male with a small median emargination (Fig. 14C). 78. S6 of female similar to *Calliopsis* but duplication somewhat sclerotized (Fig. 14G). 79. S7 of male similar to that of *Calliopsima* but distal area shorter and with no lateral elongated projection (Fig. 14E). 80. S8 of male with distal projection elongate, clavate; proximal area almost rectangular with no projections but small bumps (Fig. 14D). 85. Volsellae almost fully fused, well sclerotized medially, with no denticles. 86. Penis valves similar to those of *Calliopsima* but wider (especially in lateral view), dorsally fused to each other through a narrow sclerotized bridge. 87. Penis long, but somewhat wider than in *Calliopsima*, narrower than valve. 88. Sting extremely short (Fig. 14J).

Comments. The subgenus *Verbenapis* comprises four species (Shinn, 1967; Hurd, 1979). *C. (V.) verbenae* Cockerell and Porter, *C. (V.) nebraskensis* Crawford and *C. (V.) micheneri* Shinn were available for this study.

Discussion. Verbenapis is, according to the cladogram (Fig. 30), the sister group of the remaining subgenera of *Calliopsis*. On one hand it is the most closely related to *Calliopsima;* on the other hand it is the closest relative of *Acamptopoeum*. This is in disagreement with Shinn (1967), who stated that *Calliopsima* has a mixture of the characters found in *Calliopsis* s. str. and *Acamptopoeum*.

Verbenapis, however, is the subgenus that possesses the most characters agreeing with those of *Acamptopoeum*. *Verbenapis* has the propodeal triangle smooth, concave medially, and lacks the metanotal pad of hairs, as in *Acamptopoeum*. At the same time other characters seem transitional in *Verbenapis*. For example, S6 in *Acamptopoeum* has a very small distal, median emargination; in *Verbenapis* the same area is slightly sclerotized, with two small, weakly differentiated lobes laterally (Fig. 14C), while in *Calliopsima* the lateral lobes of S6 are well developed and the apical margin clearly concave. Finally, in the subgenera *Calliopsis, Perissander, Liopoeum, Hypomacrotera, Micronomadopsis, Ceroliopoeum* and *Liopoeodes,* S6 has elongate, acute lateral projections and a strongly concave margin medially. A similar gradual progression is shown by S8.

Distribution. United States (except southeast and west) and México (Shinn, 1967).

Subgenus *Liopoeum* Friese
(Figs. 15, 16, 30)

Liopoeum Friese, 1906b: 176. Type species: *Camptopoeum hirsutulum* Spinola, 1851 (by designation of Sandhouse, 1943: 564).

Diagnosis. Close to *Hypomacrotera* but differing as follows: Pubescence long, especially on legs. *Male.* Tarsus 3 with tarsomeres 2-4 expanded laterally. Terga with or without yellow marks. S5 with distal median projection long, truncate or tapered at apex. *Female.* Middle tibial spur with sparse and usually coarse teeth. Tibia 3 on inner

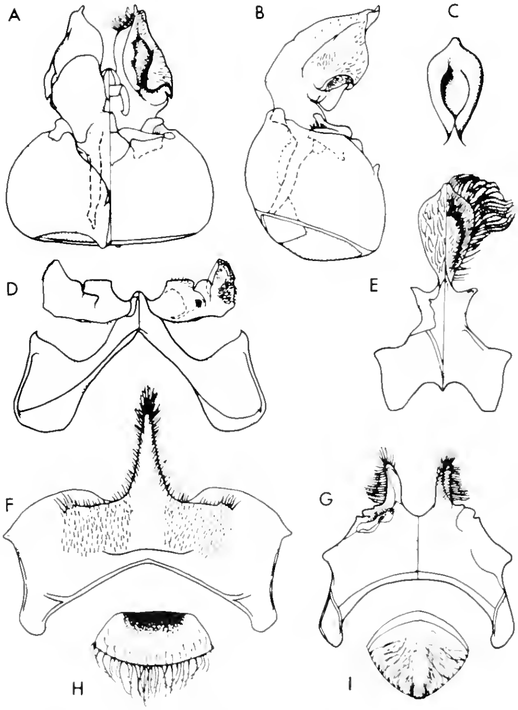

Figure 15. *Calliopsis (Liopoeum) hirsutulum* (Spinola). *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, S8, apex, ventral view (hairs omitted); D, E, S7 and 8, dorsal and ventral views; F, S5, ventral view; G, S6, dorsal and ventral views; H, Labrum; I, T7 apex.

surface with keirotrichia dense at proximal and distal ends, sometimes present toward dorsal margin but sparse. S6 with distal patch of oblique hairs (in well-organized rows) at each side of produced median area.

Description. 1. Length 5–8 mm. 3. Lower half of face, pronotum (sometimes) and legs with yellow marks; spot on paraocular area (both sexes) extending up beside orbit as in *Acamptopoeum* (male); spots of female usually more reduced on face than in male, absent on thorax. 4. Metasoma with or without yellow marks on terga. 5. Pubescence usually long on head and thorax and especially so on legs; usually shorter on metasoma. 7. Punctures fine, usually much sparser on metasomal terga. 8. Head wider than thorax (about as wide as thorax in female of *C. (L). trifasciata* (Spinola) and an undescribed Chilean species from Bio-Bio area). 11. Glossa longer than half length of prementum. 13. Segment 1 of labial palp usually slightly longer than 2–4 together. 14. Segment 2 of labial palp less than twice as long as 3. 16. As in *Calliopsis* s. str. 17. Galeal comb of 16–19 bristles. 20. Labrum similar to that of *Calliopsis* s. str. but with no well-defined ridge (Fig. 15H). 27. Clypeus more than twice as broad as long and somewhat to slightly protuberant (1/3 to 1/6 width of eye in lateral view); distal margin with an acute or rounded projection near lateral margin of labrum. 30. Inner subantennal suture angulate or strongly curved. 31. As in *Calliopsis* s. str. 34. Antennal socket about middle of face in female, below middle in male. 36. Antennal flagellum of male unmodified, longer than head; flagellomere 1 about as long as 2 and about as long as broad (slightly longer in an undescribed Chilean species). 37. Lower paraocular area similar to that of *Acamptopoeum*. 38. Facial fovea variable (oval with borders not well delimited or narrow and well defined in an undescribed Chilean species). 40. Ocelli above dorsal orbital tangent except tangent crossing the middle ocellus in undescribed Chilean species. 42. Gena of male (lateral view) about as broad as, or broader than eye, dorsally wider than ventrally. 43, 44. As in *Calliopsis* s. str. 45. Pre-episternal groove weak (sometimes seen only as a smooth strip). 46. Pterostigma longer than and slightly less than twice as broad as prestigma; otherwise as in *Calliopsis* s. str. 47. Marginal cell somewhat obliquely truncate at apex, much longer than distance from apex to wing tip. 49. Submarginal cell 1 longer than cell 2+3. 51. As in *Calliopsis* s. str. 52. Forewing with cu-v longer than second abscissa M+Cu. 53. Hind wing with cu-v about 1/3 as long as second abscissa M+Cu. 54. Dorsal surface of propodeum about as long as metanotum. 55. Propodeal triangle basally smooth, microareolate, or with striae (sometimes depressed medially). 57. Basitarsus 1 five to six times longer than broad in male and about four times in female; tarsomeres 2–4 unmodified. 59. Middle tibial spur of female with sparse and usually coarse teeth (Fig. 16F) (not very coarse in undescribed Chilean species), about as long as basitarsus 2 or slightly shorter; in male with very fine and dense teeth, about 1/2 basitarsal length. 60. Basitarsus 2 of both sexes about as long as 1 and somewhat shorter than or as long as 3; tarsomeres 2–4 unmodified. 61. Tibia 3 of female less than twice as long as basitarsus 3, inner surface with keirotrichia at proximal and distal ends (almost absent medially); male tibia 3 with keirotrichia on most of inner surface. 62. Similar to that of *Calliopsis* s. str. 63. Hind tibial spurs (both sexes) with fine teeth (denser in male), almost straight or clearly curved toward apex, outer slightly shorter than inner. 64. Basitibial plate of male distinguishable, though margins not strongly developed (weaker in undescribed Chilean species). 65. Basitarsus 3 unmodified; tarsomeres 2–4 in male expanded laterally (at least slightly), in female unmodified. 66, 67. Similar to those of *Calliopsis* s. str. 69. T2–5 of male with gradulus posterolaterally short and weak (or almost absent) and postgradular depression narrow, rather shallow; posterior marginal areas of T1–5 in male and T1–4 in female usually scarcely pilose; terga of female sometimes with distal hair bands; lateral fovea of T2 (both sexes) narrow, slightly depressed. 70. Pygidial plate of male recognizable, short, not well delimited laterally, truncate or rounded at apex (Fig. 15I). 71. T7 of female as in Figure 16C. 72. T8 of male similar to that of *Hypomacrotera*. 73. S1–5 of male with hairs directed posteriorly, very short (except longer distally), present mostly on lateral areas; on S6 mostly directed obliquely outward, on distal projections only. 73a. S1–5 of female with hairs as in *Acamptopoeum*. 75. S5 of male, on distal margin, with long median projection; projection truncate or tapered and densely pilose apically (Fig. 15F). 77. Similar to that of *Calliopsis* s. str. 78. S6 of female as in *Calliopsis* s. str. but with distal hairs forming a dense oblique patch (several well-organized rows), absent on midline (Fig. 16G). 79. S7 of male with distal lateral projections intricate, with minute, dense hairs at apex and small brush of longer hairs medially; proximal arms forming a V (Fig. 15D). 80. S8 of male with distal projection with apical long hairs, deeply concave ventrally (Fig. 15C, E). 83. Gonocoxites globose, in ventral view fused to each other proximally, connected by membrane distally; in dorsal view, proximally with a well-developed mesal projection. 85. Volsellae well developed, fused to each other by a narrow firm bridge distally, by membrane proximally, with few denticles. 86. Penis valves complex (intricate, with folds), tapered toward apices; dorsally fused to each other by small and narrow bridge. 87. Similar to that of *Calliopsis* s. str. 88. Sting elongate, reaching but not surpassing apex of stylus (Fig. 16B).

Comments. The subgenus *Liopoeum* contains a few described species, most of which have been

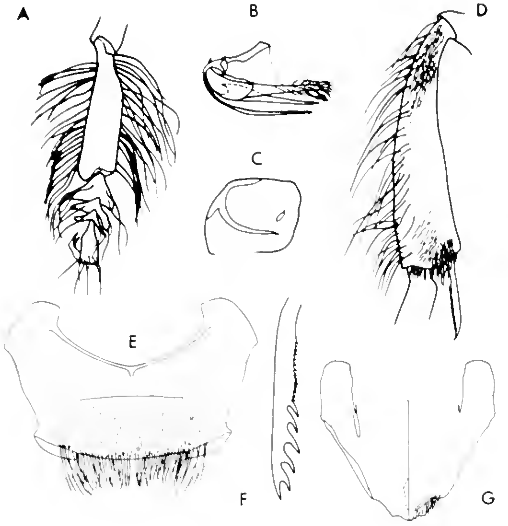

Figure 16. *Calliopsis (Liopoeum) hirsutulum* (Spinola). *Male:* A, Tarsus 3. *Female:* B, Sting; C, T7; D, Tibia 3, inner view; E, S5, ventral view; F, Spur, leg 2; G, S6, dorsal and ventral views.

placed erroneously in *Camptopoeum* (see Spinola, 1851). (*Camptopoeum* is palearctic and not in the Calliopsini.) Friese (1908) segregated *Liopoeum* as a subgenus of *Camptopoeum* for some South American species. However, they were still mixed with species of other genera.

The described species now recognized as belonging to the subgenus *Liopoeum* are: **C. (Liopoeum) argentina* (Jörgensen), **hirsutula* (Spinola), **mendocina* (Jörgensen), and **trifasciata* (Spinola) (all new combinations).

Discussion. Among the subgenera of *Calliopsis, Liopoeum* is one of the most distinctive. Some species in this subgenus have hair bands on the metasomal terga of females, while others have tergal yellow marks, and no hair bands. This fact indicates that the presence or absence of these characters may not be useful or diagnostic at the subgeneric level.

Distribution. C. (Liopoeum) occurs in Argentina and Chile.

Subgenus *Hypomacrotera* Cockerell and Porter
(Figs. 2E, 17, 30)

Hypomacrotera Cockerell and Porter, 1899: 418. Type species: *Hypomacrotera callops* Cockerell and Porter, 1899 (original designation).

Diagnosis. Metasoma without yellow marks [red in *C. (H.) subalpina* (Cockerell)]. Pilosity short. Marginal cell narrowly truncate and much longer than distance from its apex to wing tip. Pterostigma with sides parallel. *Male.* Tarsus 3 unmodified. Forewing tip dark brown. S5 distally with median elongate tapered projection. *Female.* Middle tibial spur with fine and dense teeth. S6 distally with rounded fascia of dense hairs.

Description. Agrees with description of subgenus *Liopoeum* except: 1. Length 5–8 mm. 3. Lower part of face (approximately 1/3) yellow (or whitish); apex of forewing in male brown. 4. Metasoma without yellow marks [red in *C. (H.) subalpina*[. 5. Pubescence in general short; much shorter on metasoma than on rest of body. 7. Punctures rather dense on metasomal terga. 13. Segment 1 of labial palp somewhat longer than 2–4 together. 17. Galeal comb of 10–16 bristles. 20. Labrum less than twice as broad as long; male with basal area and ridge in *C. (H.) callops* (Cockerell and Porter), similar to that of *Liopoeum* but flat, in *C. (H.) subalpina* more extensively pilose; female with well-developed ridge. 27. Clypeus width more than three to five times broader than long, rather flattened (lateral view). 30. Inner subantennal suture angulate. 31. Subantennal area broader than inner suture length and about as wide as (or slightly wider than)

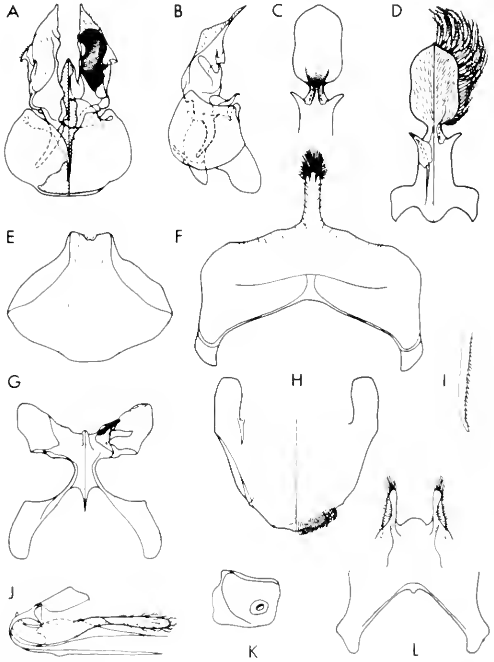

Figure 17. *Calliopsis (Hypomacrotera) callops* (Cockerell and Porter). *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, S8, tip (hairs omitted); D, S8, dorsal and ventral views; E, T8; F, S5, ventral view; G, S7, dorsal and ventral views; L, S6, ventral view. *Female:* H, S6, dorsal and ventral views; I, Spur, leg 2; J, Sting; K, T7.

socket. 34. Antennal socket approximately at middle of face. 36. Flagellomere 1 slightly longer than broad (or about as wide as long). 37. Lower paraocular area similar to that of *Acamptopoeum*. 38. Facial fovea oval, weakly differentiated. 39. Orbits convergent below, slightly so in *C. (H). subalpina*. 40. Ocelli just above dorsal orbital tangent. 42. Gena of male (lateral view) nearly as wide as eye; somewhat wider dorsally than ventrally. 45. Pre-episternal groove weak, short, not reaching scrobal level. 46. Pterostigma longer than and about as wide as prestigma (or somewhat less than twice as broad as prestigma). 47. Marginal cell narrowly and transversely truncate at apex, longer than distance from its apex to wing tip. 51. First recurrent vein rather close to first transverse cubital. 53. Hind wing with cu-v 1/4 to 1/5 as long as second abscissa M + Cu. 54. Dorsal surface of propodeum similar to that of *Liopoeum* but somewhat variable. 55. Propodeal triangle basally smooth, depressed medially, glabrous. 57. Basitarsus 1 three times longer than broad in female. 59. Middle tibial spur of female slightly more than half length of basitarsus 2, with fine and dense teeth (Fig 17I); of male toothed as in female but less than half basitarsal length. 60. Basitarsus 2 of male longer than 1 and somewhat shorter than 3; of female as in male but sometimes basitarsus 2 about as long as 3. 61. Tibia 3 of female on inner surface with keirotrichia except toward ventral margin. 62. Tibial scopa of sparse, rather short and apparently simple hairs on outer surface, inconspicuously branched and somewhat longer on margins. 63. Hind tibial spurs (both sexes) almost straight. 65. Tarsus 3 with no modifications. 69. Male with postgradular depression deep on T2, shallow on T3–5; posterior marginal areas of T1–5 in male and T1–4 in female pilose; terga (both sexes) with no hair bands; lateral fovea of T2 (both sexes) weakly depressed, somewhat wider in female. 70. Pygidial plate of male well developed in *C (H.) subalpina,* in *C (H.) callops* only distinguishable at apex. 71. T7 of female rather squared, with dorsal, proximal area not greatly expanded (Fig. 17K). 75. S5 of male with median elongate projection tapered (Fig. 17F). 78. S6 of female with distal hairs longer than in *Liopoeum* and arranged in well-defined, curved band of dense hairs (Fig. 17H). 79. S7 of male with no patch of hairs forming a distal brush and with median small spine-like projection between proximal long arms (Fig. 17G) [absent in *C. (H). subalpina*]. 80. S8 of male with distal part ventrally concave only at base, with hairs shorter than in *Liopoeum* (Fig. 17C, D). 83. Gonocoxite dorsally, on proximal area, with no mesal projection in *C. (H.) callops* [but present in *C. (H). subalpina*]. 86. Penis valves with ridges medially on outer margin (ventral view) (Fig. 17A).

Comments. Only two species of this subgenus are recognized: **C. (H.) callops* (Cockerell and Porter) and **C. (H.) subalpina* (Cockerell) (new combinations), each with two subspecies (Hurd, 1979). Because of size and metasomal color, the two species are superficially very different. Nonetheless, they are closely related.

Until now *Hypomacrotera* has been poorly characterized, the major diagnostic character having been the infuscated area at the apex of the forewing in males. This character is not strong, since a brown spot on the apex of the forewing also appears in males of some species of *Calliopsis* s. str., *C. (Perissander),* and in *C. (Liopoeodes) xenopous,* n. sp. The latter species has characters that are a mixture of those of *Hypomacrotera, Liopoeum,* and *Calliopsis* s. str.

The cladogram (Fig. 30) shows that the subgenus *Hypomacrotera* is more closely related to *Liopoeum* than to other subgenera of *Calliopsis.* Rozen (1970) indicates that *Hypomacrotera* coats pollen masses with a waterproof substance as do other *Calliopsis.*

Distribution. C. (Hypomacrotera) occurs in the southwestern United States (Colorado, New Mexico, Arizona, California) and México (Baja California and Sonora) (Hurd, 1979).

Subgenus *Nomadopsis* Ashmead
(Figs. 18, 19, 30)

Nomadopsis Ashmead, 1898: 285. Type species: *"Perdita" zonalis* Cresson, 1879 (monobasic and original designation), *lapsus* for *Calliopsis zonalis* Cresson, 1879.

Spinoliella subg. *Claremontiella* Cockerell, 1933: 25. Type species: *Spinoliella euxantha* Cockerell, 1933 = *Calliopsis zonalis* Cresson, 1879 (monobasic and original designation).

Diagnosis. Metasomal terga with yellow bands. Sterna with hairs mostly short, straight, appressed. Differs from *Macronomadopsis* as follows: *Male.* Tarsus 1 and 2 with tarsomeres 2–4 widened distally. Tarsus 3 similar to 1 and 2, symmetrical. S4 and S5 with distal produced area well developed.

Description. 1. Length 7–12 mm. 3. Lower part of face, some areas of thorax (pronotum, tegula), and legs with yellow marks, reduced in female. 4. Metasoma with complete or interrupted yellow bands. 5. Pubescence in general short; dense, mostly very short and appressed on sterna. 7. Punctures mostly fine, well marked, smaller and usually dense on metasoma. 8. Head nearly as broad as thorax, sometimes narrower in female. 11. Glossa longer than prementum (flabellum present in several species). 13. Segment 1 of labial palp more than two to five times longer than 2–4 together. 16. Maxillary blade more than twice as long as prepalpal part of galea. 17. Galeal comb of 18–23 bristles. 20. Labrum broader than long; basal area depressed; distal margin of basal area a rounded ridge; labral apex convex, inflexed. 27.

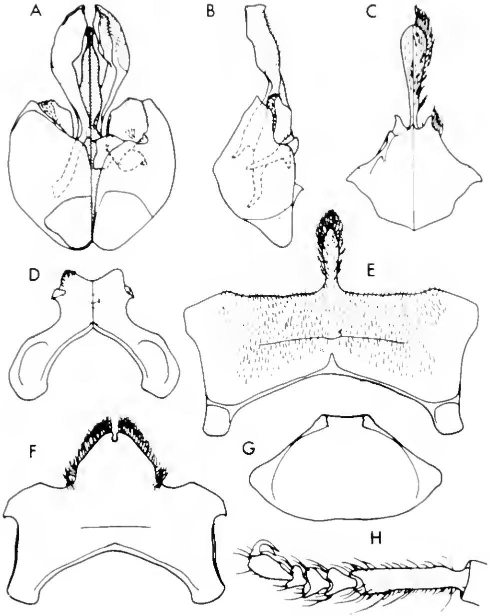

Figure 18. *Calliopsis (Nomadopsis) zonalis* Cresson. *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, D, S8 and 7, dorsal and ventral views; E, F, S5 and 6, ventral view; G, T8; H, Tarsus 3.

Clypeus more than twice as broad as long, protuberant (usually 1/2 width of eye in lateral view in male and usually 1/3 in female, except almost flat in both sexes of *C. (N.) edwardsii* Cresson; distal margin with a rounded projection beside lateral margin of labrum. 30. Inner subantennal suture curved or somewhat angulate. 31. Subantennal area about as wide as inner suture length and at least slightly wider than antennal socket. 34. Antennal socket somewhat below middle of face. 36. As in *Calliopsis* s. str. but flagellomere 1 longer than 2, about as long as broad or little longer. 37. Lower mesal paraocular area somewhat swollen to almost flat. 38. Facial fovea rather deep, narrow. 39. Orbits sometimes subparallel in female. 40. Ocelli fully or mostly above dorsal orbital tangent. 42. Gena of male (lateral view) little wider to little narrower than eye; somewhat widened dorsally. 43. As in *Calliopsis* s. str. 44. Mesepisternum with area facing anteriorly rather reduced and slightly convex. 45. Preepisternal groove narrow, shallow, punctate, not reaching scrobal level or at least not extending below it. 46. Pterostigma about as long as or longer than and about twice as wide as prestigma (sometimes less than twice); otherwise as in *Calliopsis* s. str. 47. Marginal cell obliquely and broadly truncate, clearly longer than distance from its apex to wing tip. 49. Submarginal cell 1 at least slightly longer than cell 2+3. 51. As in *Calliopsis* s. str. 52. Forewing with cu-v somewhat longer to three times longer than second abscissa M+Cu. 53. Hind wing with cu-v about 1/4 as long as second abscissa M+Cu. 54. As in *Calliopsis* s. str. 55. Propodeal triangle finely striate basally. 57. Basitarsus 1 five to nine times longer than broad in male, two to five times in female; tarsomeres moderately widened distally in male. 59. Middle tibial spur with fine, rather sparse teeth; straight and about half as long as (or longer than) basitarsus 2 in female; slightly curved at apex, usually less than half as long as basitarsus 3, in male. 60. Basitarsus 2 of male longer than 1 and about as long as 3; shorter than 1 and 3 in female; male tarsomeres 2–4 widened distally. 61. Tibia 3 of female less than twice as long as basitarsus 3, inner surface with keirotrichia scarce dorsally between patches near ends, absent ventrally; male tibia 3 with keirotrichia on most of inner surface of tibia. 62. As in *Calliopsis* s. str. 63. Hind tibial spurs with fine teeth, inner spur longer than outer; slightly curved at apices. 64. As in *Calliopsis* s. str. 65. Basitarsus 3 unmodified, that of female gradually and slightly tapered toward apex; tarsomeres 2–4 similar to those of tarsi 1 and 2 (although shorter) in male (Fig. 18H), narrower in female. 66, 67, 68. As in *Calliopsis* s. str. 69. T2–5 of male with gradulus posterolaterally short, usually not strongly carinate and postgradular depression shallow, very narrow; posterior marginal areas of T1–5 in male and T1–4 in female pilose; terga (both sexes) with no hair bands; lateral fovea of T2 (both sexes) slightly depressed, narrow in male, much wider in female. 70. Pygidial plate of male long, with well-defined margins. 71. T7 of female with dorsal, proximal area not greatly expanded (Fig. 19B). 72. T8 of male as in Figure 18G. 73. S1–5 of male with hairs dense, mostly directed backward and appressed, usually longer on distal area; S6 with hairs only on distal projections. 73a. S1–5 of female with hairs similar to those of male. 75. S5 of male with a median, narrow, medium-sized projection on distal margin; projection densely pilose at apex (Fig. 18E). 77. S6 of male with distal margin greatly projected medially; projection with small distal emargination (Fig. 18F). 78. S6 of female with proximal laminar lobes sometimes with very shallow emargination between them; basal sclerotization usually spine-shaped [widened at apex in *C. (N.) zonalis* Cresson, tapered in other species], mostly free from sternum; duplication somewhat sclerotized, attached to a distal hardened area of sternum; distal margin produced medially; S6 with distal hairs curved, forming a dense curved band (Fig. 19A). 79. S7 of male distally rectangular, usually distally emarginate and with two short lateral lobes; proximal arms forming a V (Fig. 18D). 80. S8 of male with distal projection elongate, clavate; body of sternum widened medially, with a small, tapered projection at each side of the distal projection (Fig. 18C). 83. Gonocoxites globose,

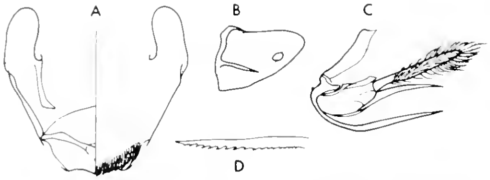

Figure 19. *Calliopsis (Nomadopsis) zonalis* Cresson. *Female:* A, S6, dorsal and ventral views; B, T7; C, Sting; D, Spur, leg 2.

ventrally connected by membranous area. 85. Volsellae large, connected by slightly sclerotized cuticle, with numerous denticles. 86. Penis valves with some folds, tapered distally, fused dorsally through a rather narrow sclerotized bridge. 87. Penis completely sclerotized except at apex (unlike any other *Calliopsis,* J. Rozen, personal communication), shorter and narrower than valve, clearly separated from valves. 88. See *Calliopsis* s. str. and Figure 19C.

Comments. This subgenus contains eight described species (Rozen, 1958). I studied *C. (N.) linsleyi* (Rozen), *puellae* (Cockerell), and *zonalis* Cresson (the first two are new combinations). The females of this subgenus do not present features that distinguish them as a group from *Macronomadopsis* and *Micronomadopsis* (Rozen, 1958).

Discussion. Although *Nomadopsis* (usual sense) was confused with *Spinoliella* for a long time, there is no doubt that they belong to two different lineages among the Calliopsini. A similar statement was also made by Shinn (1967). Rozen (1951, 1958) and Shinn (1967) agree about the close relationship among the traditional *Nomadopsis, Calliopsis, Hypomacrotera, Liopoeum* and *Acamptopoeum,* the latter being, in my analyses, a distinct genus, the sister group of *Calliopsis.*

The cladogram (Fig. 30) shows that *Micronomadopsis* is the sister group of *Nomadopsis* s. str. and *Macronomadopsis.* According to Rozen (1958), however, based on male genitalia and S7-8, *Nomadopsis* s. str. " . . . is quite distinct from *Macronomadopsis* and *Micronomadopsis* and can not be affiliated more closely with one or the other." The male genitalia of *Nomadopsis* resemble those of *Macronomadopsis* (especially in shape of penis valve and volsella), more than those of *Micronomadopsis.* The first two share some apomorphies that indicate that they are more closely related to one another than to *Micronomadopsis.* Furthermore, the shape of the sterna of some *Nomadopsis* s. str. and *Macronomadopsis* is transitional between the two subgenera.

Distribution. Western United States, southern British Columbia, and northern México.

Subgenus *Macronomadopsis* Rozen
(Figs. 20, 30)

Macronomadopsis Rozen, 1958: 93. Type species: *Nomadopsis micheneri* Rozen, 1958 (original designation).

Diagnosis. Differs from *Nomadopsis* as follows: *Male.* Tarsus 1 and 2 with tarsomeres 2-4 conspicuously widened distally. S4 with distal median projection inconspicuous. S5 with median projection on distal margin small, slightly sclerotized.

Description. Agrees with description of *Nomadopsis* except: 1. Length 8-12 mm. 3. Pronotum sometimes with no yellow marks. 13. Segment 1 of labial palp somewhat longer than to twice as long as 2-4 together. 16. Maxillary blade longer than prepalpal part of galea. 17. Galeal comb of about 30 bristles. 20. Labrum usually broader than long [about twice as broad as long in *C. (M.) zebrata* Cresson]. 27. Clypeus usually more than twice as broad as long [little less than twice as broad in *C. (M.) anthidia* Fowler]; in lateral view protuberant 1/3 to 1/5 width of eye. 31. Subantennal area slightly wider than inner suture length. 34. Antennal socket about middle of face. 37. Lower mesal paraocular area swollen to slightly convex. 38. Facial fovea shallow. 42. Gena of male (lateral view) somewhat narrower than eye, slightly widened dorsally. 45. Pre-

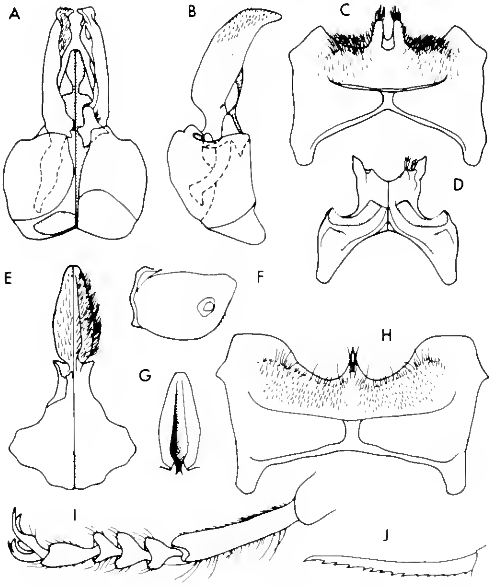

Figure 20. *Calliopsis (Macronomadopsis) zebrata* Cresson. *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, S6, ventral view; D, E, S7 and 8, dorsal and ventral views; G, S8, distal projection, ventral view (hairs omitted); H, S5, ventral view; I, Tarsus 3. *Female:* F, T7; J, Spur, leg 2.

episternal groove very short and weak, difficult to see. 46. Pterostigma less than twice as broad as prestigma. 51. First recurrent vein never very close to first transverse cubital. 53. Hind wing with cu-v about 1/3 or 1/4 as long as second abscissa M + Cu. 54. Dorsal surface of propodeum about as long as metanotum. 57. Basitarsus 1 six to seven times longer than broad in male and about four times in female; tarsomeres 2–4 of all tarsi distinctly expanded distally in male, slightly so in female. 59. Middle tibial spur with fine teeth as in *Nomadopsis* but clearly longer than half length of basitarsus 2 in female, about half as long in male. 60. Basitarsus 2 of male shorter than 1 and 3; about as long as 1 and shorter than 3 in female; tarsomeres 2–4 widened distally, more conspicuously so in male than in female. 61. Tibia 3 of female about twice as long as basitarsus 3. 65. Tarsus 3 with tarsomeres 2–4 somewhat expanded distally (Fig. 20I). 71. T7 of female rather square (Fig. 20F). 74. S4 of male inconspicuously produced on distal margin medially. 75. S5 of male with median projection on distal margin small, rather tapered at apex, slightly sclerotized (Fig. 20H). 77. S6 of male with a narrow, median distal emargination and 2 short, mesal projections (Fig. 20C). 78. S6 of female similar to that of *Nomadopsis* but with deep V-shaped emargination between proximal laminar lobes, basal sclerotization spine-like. 79. S7 of male similar to that of *Nomadopsis* but distal margin more deeply emarginated and lateral lobes better defined (Fig. 20D). 80. S8 of male with distal projection narrowed toward apex (Fig. 20E, G). 85. Volsellae connected by slightly sclerotized cuticle, with no denticles. 86. Penis valves strongly curved at apices (Fig. 20A). 87. Penis partially sclerotized, about as wide as valve.

Comments. This subgenus contains five species (Rozen, 1958; Hurd, 1979). I studied *C. (Macronomadopsis) micheneri* (Rozen) and *zebrata* Cresson (only *C. zebrata* illustrated) (new combinations).

Distribution. United States west of South Dakota, Colorado, and New Mexico (Hurd, 1979).

Subgenus *Micronomadopsis* Rozen
(Figs. 21, 30)

Micronomadopsis Rozen, 1958: 107. Type species: *Nomadopsis fracta* Rozen, 1958 (original designation).

Diagnosis. Similar to but usually smaller than *Nomadopsis* and *Macronomadopsis,* from which it differs as follows: *Male.* Tarsus 1 with tarsomeres 2–4 very thin. Tarsus 3, in several species, with tarsomeres 2–4 widened laterally, asymmetrical. Penis valve (in most species) as in Figure 21A. S4 and S5 as in *Nomadopsis. Female.* Middle tibial spur with only 4 teeth on distal half.

Description. Agrees with description of *Nomadopsis* except: 1. Length 5–10 mm. 8. Head broader than thorax in male, about as broad in female. 11. Glossa somewhat longer than prementum to much shorter. 13. Segment 1 of labial palp slightly shorter to about three times longer than 2–4 together. 16. Maxillary blade length as in *Macronomadopsis.* 17. Galeal comb of about 14 bristles. 27. Clypeus sometimes twice as broad as long, protuberant almost 1/3 to 1/7 width of eye. 31. Subantennal area wider than inner suture length, about as wide as socket (sometimes wider). 34. Antennal sockets about middle of face as in *Macronomadopsis.* 36. Antennal flagellum of male as long as head or longer. 42. Gena of male (lateral view) narrower than eye, broadest in the middle. 43. Pronotum similar to that of *Nomadopsis,* although ridge laterally less developed. 45. Pre-episternal groove short, sometimes indistinct. 46. Pterostigma longer than prestigma. 51. First recurrent vein as in *Macronomadopsis.* 52. Forewing with cu-v usually slightly longer than second abscissa M + Cu. 53. Hind wing with cu-v as in *Macronomadopsis.* 54. Dorsal surface of propodeum usually somewhat longer than metanotum, shorter in *C. (Micronomadopsis) helianthi* (Swenk and Cockerell). 55. Propodeal triangle weakly striate, sometimes smooth. 57. Basitarsus 1 six to seven times longer than broad in male, three to four times longer in female; tarsomeres 2–4 unmodified. 59. Middle tibial spur about 1/2 to 1/4 as long as basitarsus 2 in male. 60. Basitarsus 2 of male at least slightly longer than 1, somewhat variable in relation to 3; of female as in *Macronomadopsis.* 61. Tibia of female similar to that of *Nomadopsis* except with keirotrichia of inner surface denser dorsally in *C. (M.) helianthi.* 62. Tibial scopa sometimes of hairs with very short branches. 65. Basitarsus 3 unmodified, sometimes very short; tarsomeres 2–4 from un-

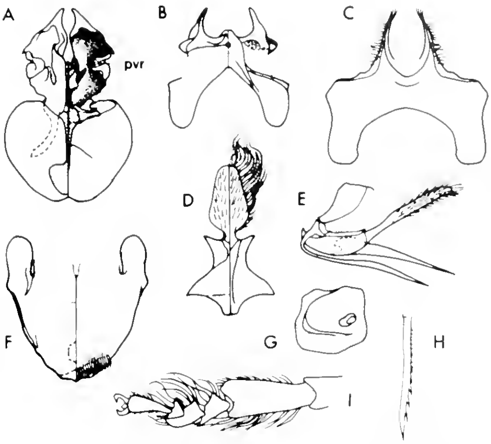

Figure 21. *Calliopsis (Micronomadopsis) scutellaris* Fowler. *Male:* A, Genitalia, dorsal and ventral views; B, S7, dorsal and ventral views; C, S6, ventral view; D, S8, dorsal and ventral views; I, Tarsus 3. *Female:* E, Sting; F, S6, dorsal and ventral views; G, T7; H, Spur, leg 2. pvr = penis valve ridges.

modified to widened and asymmetrical in male of several species (Fig. 21I), slender, unmodified in female. 67. Metasoma narrower to slightly wider than thorax. 70. Pygidial plate of male sometimes shorter and wider than in *Nomadopsis* [e.g., in *C. (M.) helianthi*]. 71. T7 of female square (Fig. 21G). 75. S5 of male with distal median projection longer than in *Nomadopsis* (tapered or truncate at apex). 77. S6 of male with distal margin deeply emarginate medially, with two elongate, tapered projections (Fig. 21C). 78. S6 of female similar to that of *Macronomadopsis*. 79. S7 of male with distal area usually with lateral, almost horizontal expansions (Fig. 21B); sometimes with short, median, spine-shaped projection on proximal margin. 80. S8 of male somewhat similar to that of *Macronomadopsis* (Fig. 21D). 85. Volsella similar to that of *Macronomadopsis*. 86. Penis valve complex, similar to that of *Liopoeum, Hypomacrotera, Calliopsis, Perissander, Liopoeodes* and *Ceroliopoeum*, with fine, minute ridges laterally (ventral view) as in *Hypomacrotera, Calliopsis, Perissander, Liopoeodes* and *Ceroliopoeum* (Fig. 21A). 87. Penis very short, partially sclerotized, much narrower than valve. 88. Sting as in Figure 21E.

Comments. Micronomadopsis contains 20 species (Rozen, 1958; Hurd, 1979). I studied *C. (Micronomadopsis) helianthi* (Swenk and Cockerell) [=*euphorbiae* (Cockerell)], *fracta* (Rozen) (new combinations), and *scutellaris* Fowler.

Rozen's (1958) species of uncertain position, *C. boharti* (Rozen), *smithi* (Rozen) and *xenus* (Rozen), were not assigned to any subgenus. Some of their characters fit with *Macronomadopsis* and others with *Micronomadopsis*.

Distribution. This subgenus is widespread in the western part of the United States.

Liopoeodes, new subgenus
(Figs. 22, 30)

Type species: *Calliopsis (Liopoeodes) xenopous,* new species (see Appendix).

Diagnosis. Similar to *Liopoeum* except: Integument mostly dark. Hairs of head and thorax rather brownish and erect. *Male.* Forewing tip dark as in *Hypomactrotera.* Hind tarsus with all segments modified. *Female.* Black, metasomal terga with apical white hair bands.

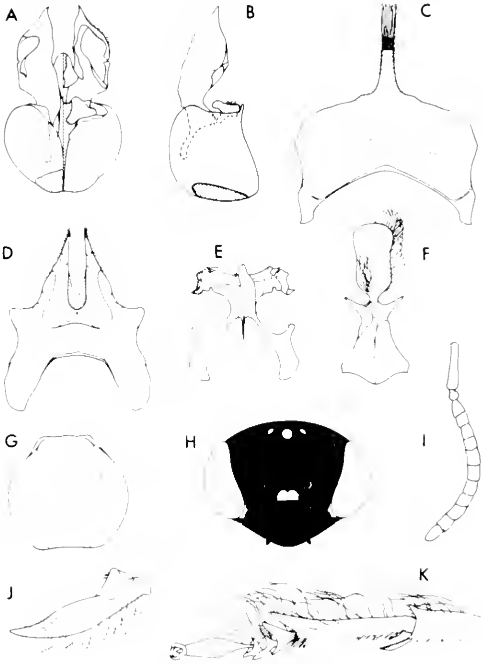

Figure 22. *Calliopsis (Liopoeodes) xenopous* n. sp. *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, S5; D, S6; E, F, S7 and 8, dorsal and ventral views; G, T8; H, Head, frontal view (hairs omitted); I, Antenna; J, Mandible; K, Tarsus 3.

Description. As in *Liopoeum* except: 1. Length 6-8 mm. 3. Lower half of face (reduced spots) and forelegs of male with yellow marks; female without yellow. 4. Metasoma without yellow areas. 5. Pubescence darkened; on head and thorax mostly erect and clearly longer than that of metasoma. 7. Punctures especially fine and dense on metasomal terga. 14. Segment 2 of labial palp slightly longer than 3. 17. Galeal comb of 23 bristles. 20. Labrum less than twice as broad as long; basal area with distal margin a well marked ridge. 27. Clypeus somewhat protuberant (1/2 to 1/3 width of eye in lateral view); distal margin with well-developed projection near lateral margin of labrum. 34. Antennal socket somewhat below middle of face in both sexes. 36. Antennal flagellum of male with flagellomere 1 slightly longer than broad. 37. Lower paraocular area slightly convex. 38. Facial fovea well defined, longer and broader in female than in male. 42. Gena of male (lateral view) narrower than eye. 46. Pterostigma with margin within marginal cell slightly convex. 49. Submarginal cell 1 somewhat shorter than cell 2+3. 51. First recurrent vein rather close to transverse cubital vein. 53. Hind wing with cu-v about 1/5 as long as second abscissa M+Cu. 55. Propodeal triangle basally microareolate, depressed medially, with fine and weak striae. 57. Basitarsus 1 about seven times longer than broad in male and almost six times in female. 59. Middle tibial spur of female with several well-defined and clearly separated teeth, slightly shorter than basitarsus 2; in male about 1/3 basitarsal length. 60. Basitarsus 2 of male less than twice as long as 1 and 3; basitarsus 2 of female slightly longer than 1 and 3. 61. Tibia 3 of female about twice as long as basitarsus 3, inner surface with keirotrichia at proximal and distal ends and toward upper margin. 63. Hind tibial spurs with fine teeth, almost straight in male, outer one somewhat curved at apex in female. 64. Basitibial plate of male clearly distinguishable. 65. Basitarsus 3 of male modified distally; tarsomeres 2–4 asymmetrical; distitarsus modified (Fig. 22K). 66. Claws with rather short rami in male, especially on tarsus 3. 69. T1–5 of male and T1–4 of female with posterior marginal areas apparently glabrous; terga of female with distal hair bands; lateral fovea of T2 widened and slightly depressed, almost indistinguishable and ventral in position rather than lateral in male. 70. Pygidial plate of male apparently absent. 71. T7 of female as in Figure 23D. 72. T8 of male as in Figure 22G. 73. S1–5 of male with hairs sparse, mostly on middle line. 75. S5 of male with median projection shorter than in *Liopoeum;* apical hairs of projection longer than in *Liopoeum* (Fig. 22C). 79. S7 of male with tapered projection between proximal arms as in *Hypomacrotera* (Fig. 22E). 80. S8 of male with distal projection somewhat convex ventrally (Fig. 22F). 83. Gonocoxites, in dorsal view, without mesal proximal projection. 85. Volsellae with no denticles. 88. Sting rather short, not reaching stylus apex (Fig. 23C).

Comments. The subgenus *Liopoeodes* contains a single species from Argentina. The subgeneric name is slightly modified from one used by J. S. Moure on some 30-year-old identification labels found in the collection of the Snow Entomological Museum (KU).

Discussion. The mosaic of features exhibited by this new subgenus (some of them also present in other calliopsine genera) is one more evidence that it and its close relatives should be treated as species of the genus *Calliopsis.*

The presence of a darkened area at the apex of the forewing of the male suggests *C. (Hypomacrotera)* and some species of *C. (Perissander).* On the other hand, because of other characters indicated above, *Liopoeodes* appears to be more like *C. (Liopoeum).*

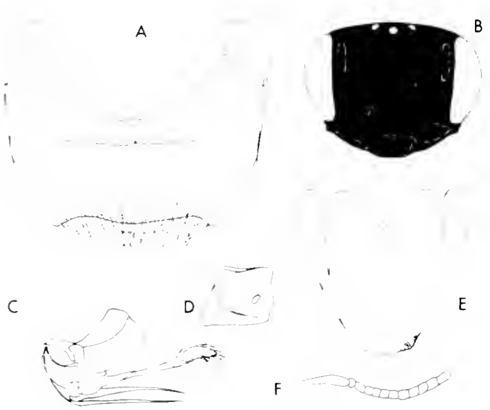

Figure 23. *Calliopsis (Liopoeodes) xenopous* n. sp. *Female:* A, S5, ventral view; B, Head, frontal view (hairs omitted); C, Sting; D, T7; E, S6, dorsal and ventral views; F, Antenna.

Etymology. The name of this subgenus is based on *Liopoeum* plus the Greek suffix *-odes,* indicating similarity to *Liopoeum.*

***Ceroliopoeum,* new subgenus**

(Figs. 2D, 24, 30)

Type species: *Camptopoeum laetum* Vachal, 1909.

Diagnosis. Appearance similar to that of *Liopoeum* but clypeus convex medially and with marginal projection (beside labrum) broadly rounded; labrum with distal margin of basal part a strong ridge, almost a carina; pubescence short and rather sparse. *Male.* Antennal scape stout. Basitarsus 2 very narrow, longer than basitarsus 3 (at least slightly). Tarsus 3 with tarsomeres 2–4 narrow, apices not expanded laterally. *Female.* Tibial spur 2 as long as basitarsus 2, sinuate, with small, well-separated teeth.

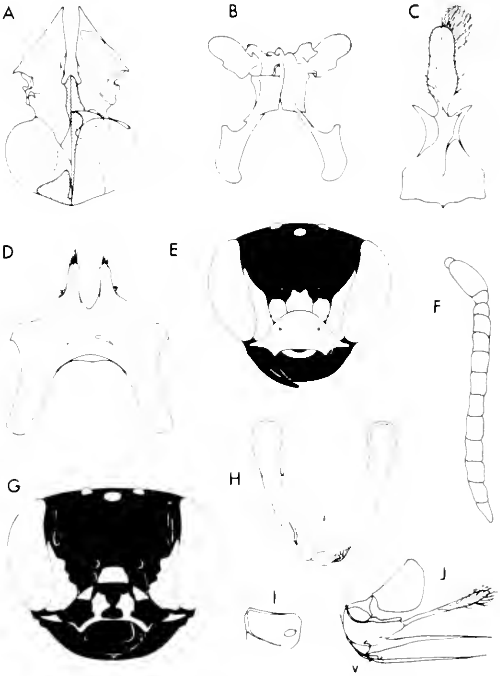

Figure 24. *Calliopsis (Ceroliopoeum) laeta* (Vachal). *Male:* A, Genitalia, dorsal and ventral views; B, C, S7 and 8, dorsal and ventral views; D, S6, ventral view; E, Head, frontal view; F, Antenna. *Female:* G, Head, frontal view; H, S6, dorsal and ventral views; I, T7; J, Sting. v = valve-like structure.

Description. Agrees with that of *Liopoeum* except: 1. Length 5–6 mm. 3. Male with legs mostly yellow; female with yellow spots on pronotum (as in male), tibiae and tarsi. 5. Pubescence rather short, mostly very short and appressed on metasoma. 8. Head about as wide as thorax. 17. Galeal comb of 12 bristles. 20. Labrum with distal margin of basal part a strong ridge, almost a carina; apical area flattened. 27. Clypeus somewhat protuberant (1/3 width of eye in lateral view), with distal margin (frontal view beside labrum) broadly rounded; central area convex. 34. Male with flagellomere 1 about half as long as 2. 35. Antennal scape robust. 38. Facial fovea narrow, well delimited. 42. Gena of male (lateral view) about 1/2 as wide as eye. 46. Pterostigma somewhat more than twice as broad as prestigma; margin within marginal cell slightly convex. 52. Forewing with cu-v about as long as second abscissa of M + Cu. 55. Propodeal triangle microareolate, depressed medially and with very fine longitudinal striae. 57. Basitarsus 1 almost eight times longer than broad in male, about six times in female. 59. Middle tibial spur of female as long as basitarsus 2, sinuose, with fine, well-separated teeth. 60. Basitarsus 2 about as long as 1 and slightly longer than 3 in male, and about as long as 1 and 3 in female. 61. Tibia 3 of female on inner surface with keirotrichia dense at proximal and distal ends, sparser toward dorsal margin. 62. Tibial scopa of sparse and minutely branched hairs. 65. Tarsus 3 unmodified. 67. Metasoma in male narrower than thorax. 69. T1–5 of male and T1–4 of female with posterior marginal area scarcely pilose; hairs somewhat denser on T4 of female; lateral fovea of T2 (both sexes) indistinguishable. 70. Pygidial plate of male clearly delimited laterally, rather truncate at apex. 71. T7 of female as in Figure 24I. 73a. S1–5 of female with hairs sparser than in *Liopoeum* and *Acamptopoeum* and mostly not appressed. 75. S5 of male with median projection tapered apically (as in Fig. 11G). 79. S7 of male with patch of small, sparse hairs medially on latero-distal projections (Fig. 24B). 80. S8 of male with distal projection convex ventrally (Fig. 24C). 83. Gonocoxites, in dorsal view, without proximal mesal projection. 85. Volsella without denticles. 88. First valvula of sting with a minute expanded area, perhaps a rudiment of valve, and a very short, curved hair behind this structure (Fig. 24J).

Comments. C. (Ceroliopoeum) laeta (Vachal) is the only known species of this subgenus.

Discussion. In the cladogram (Fig. 30), *Ceroliopoeum* is the sister group of *Hypomacrotera, Liopoeum, Nomadopsis, Macronomadopsis* and *Micronomadopsis* together.

Distribution. Argentina.

Etymology. The name of the subgenus refers to the distinctive antennal flagellum and the likeness to *Liopoeum.* It is from the Greek *keraos,* horned, plus *Liopoeum.*

Genus *Arhysosage* Brèthes
(Figs. 6C, 8C, 25, 26, 30)

Arhysosage Brèthes, 1922: 121. Type species: *Arhysosage johnsoni* Brèthes, 1922 = *Camptopoeum ochraceum* Friese, 1908 (monobasic).

Ruiziella Timberlake, 1952: 105 (preoccupied). Type species: *Camptopoeum ochraceum* Friese, 1908.

Ruziapis Timberlake, 1952: 528 (*lapsus* for *Ruizapis,* and replacement for *Ruiziella*).

Ruizapis Timberlake, 1953: 598 (emendation of *Ruziapis*).

Diagnosis. Related to *Spinoliella* and *Callonychium,* sharing with them the low position of the antennal sockets. It can be differentiated by the following characters: Orbits distinctly divergent below. Hind tibial spurs distinctly curved toward apices. *Male.* Body almost completely yellow. Mandible strongly curved and elongate, with preapical tooth and projection on upper margin.

Description. 1. Length about 10 mm. 3. Most of head and thorax of male yellow; size of yellow areas of female variable. 4. Metasoma with yellow bands very extensive to largely incomplete. 5. Pubescence in general short; appressed hairs on most of dorsum of thorax and metasoma. 7. Punctures very fine and dense. 8. Head broader than long and broader than thorax. 11. Glossa longer than prementum, slender. 12. Paraglossa shorter than suspensorium. 13. Segment 1 of

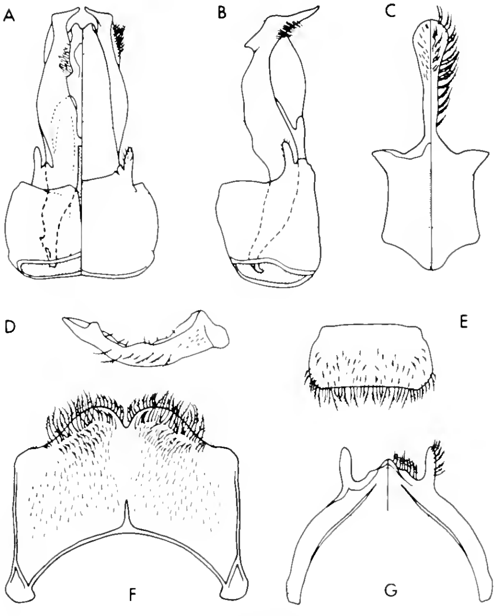

Figure 25. *Arhysosage ochracea* Brèthes. *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, S8, dorsal and ventral views; D, Mandible; E, Labrum; F, S6, ventral view; G, S7, dorsal and ventral views.

labial palp less than twice as long as 2–4 together. 16. Maxillary blade longer than prepalpal part of galea. 17. Galeal comb absent. 20. Labrum less than twice as broad as long, partially or fully pilose; flat in male, with slight transverse ridge (almost flat) in female. 25. Mandible of male strongly arcuate, upper margin with prebasal projection and also with preapical tooth (sometimes very conspicuous) (Figs. 6C, 25D). 27. Clypeus more than four times broader than long and somewhat protuberant (1/3 width of eye, lateral view) in male; about three times broader than long and distinctly protuberant (about 1/2 width of eye, lateral view) in female; distal margin with distinct projection (variable in size) near lateral margin of labrum. 30. Inner subantennal suture angulate. 31. Subantennal area wider than length of inner suture and than antennal socket. 33. Tentorial pit almost at middle of outer subantennal suture. 34. Antennal socket far below middle of face (on lower third in male, somewhat higher in female). 36. Antennal flagellum of male unmodified, much shorter than head; flagellomere 1 about as long as 2 or little longer and about as long as broad. 37. Lower mesal paraocular area slightly convex. 38. Facial fovea deep, narrow. 39. Orbits strongly divergent below in male, slightly so in female. 40. Middle ocellus below dorsal orbital tangent, lateral ocelli above. 41. Vertex convex. 42. Gena of male (lateral view) wider than eye, slightly wider dorsally than ventrally. 43. Pronotum with dorsal preapical ridge rounded, strong in male, weak in female. 44. Mesepisternum with flattened area facing anteriorly rather reduced. 45. Pre-episternal groove only distinguishable above scrobal level, continued downward as black line (difficult to see on dark integument). 46. Pterostigma longer than and slightly wider than prestigma; side basal to vein r subparallel to costa, that within marginal cell straight. 47. Marginal cell obliquely and broadly truncate at apex, longer than distance from apex to wing tip (slightly so in female). 49. Submarginal cell 1 about as long as cell 2 + 3 or longer. 51. First recurrent vein clearly distant from first transverse cubital. 52. Forewing with cu-v as long as or longer than second abscissa M + Cu. 53. Hind wing with cu-v little less than 1/2 to 1/3 as long as second abscissa M + Cu. 54. Dorsal surface of propodeum slightly longer than metanotum. 55. Propodeal triangle basally with fine striae, depressed medially. 57. Basitarsus 1 about five times longer than broad in male and four times longer in female; tarsomeres 2–4 unmodified. 59. Middle tibial spur about half as long as basitarsus 2 or somewhat longer, distinctly curved apically, finally serrate (apical teeth larger than those at base). 60. Basitarsus 2 about as long as 1 and shorter than 3, tarsomeres 2–4 unmodified. 61. Hind tibia of female somewhat longer than basitarsus 3; inner surface with keirotrichia in patch at base and apex, sparse or absent toward dorsal margin, absent ventrally (Fig. 26C); male tibia 3 with keirotrichia on most of inner surface but sparser ventrally. 62. Tibial scopa of moderately dense and apparently simple, but minutely branched hairs. 63. Hind tibial spurs strongly curved toward apices, outer about as long as inner or somewhat longer; teeth small. 64. Basitibial plate of male with margins well defined. 65. Tarsus 3 unmodified. 66. Claws deeply cleft, rami subequal in male, inner ramus much shorter than outer in female. 67. Metasoma in male wider than thorax. 69. T2–5 of male with gradulus posterolaterally long (surpassing middle of each tergum), strongly carinate (especially on T2–4) and with postgradular depression narrow, rather shallow; posterior marginal areas of T1–5 in male and T1–4 in female pilose (minute hairs); terga (both sexes) with no hair bands; lateral fovea of T2 (both sexes) slightly depressed, small in male, larger in female. 70. Pygidial plate of male well developed, abruptly elevated and carinate laterally on distal part, apex slightly emarginate. 71. T7 of female not expanded dorsally but with a strong ventral proximal projection (Fig. 26D). 72. T8 of male hexagonal (Fig. 26F). 73. S1–6 of male with most of hairs minute, dense, appressed, and directed posteriorly, longer distally. 73a. S1–5 of female pilose as in male but hairs somewhat longer and denser. 74, 75. S4 and 5 of male with distal margins slightly and broadly concave medially. 77. S6 of male distally bilobed, with small median V-shaped emargination (Fig. 25F). 78. S6 of female with basal spine-like sclerotization fused to sternum; lateral margin with strong curved ridge; duplication thin, attached to distal hardened area of sternum; distal margin concave medially; S6 apically with a well-defined, curved and dense band of curved hairs (Fig. 26B). 79. S7 of male distally with 2 rather short, finger-like lateral projections; proximal arms long and forming a U (Fig. 25G). 80. S8 of male with a median long distal projection clavate at apex, abruptly separated from basal part which has weak median ridge dorsally (Fig. 25C). 83. Gonocoxite short, squared, completely fused both dorsally and ventrally (Fig. 25A, B). 84. Gonostylus short, finger-like, fused to gonocoxite. 85. Volsella apparently absent? (or completely fused to gonocoxite). 86. Penis valves long, with some folds, distally bent downward at right angle, tapered toward apex, dorsally fused to each other by small, narrow bridge. 87. Penis almost reaching apices of penis valves, proximally wider and fused to valve; distal half well sclerotized ventrally. 88. Sting very short (not attaining stylus apex) (Fig. 26E).

Comments. This genus contains three known species: *A.* **flava* Moure, **germana* Moure, **ochracea* (Friese).

Discussion. Arhysosage is, according to the cladogram (Fig. 30), the sister group of *Spinoliella* and *Callonychium.*

Distribution. Argentina.

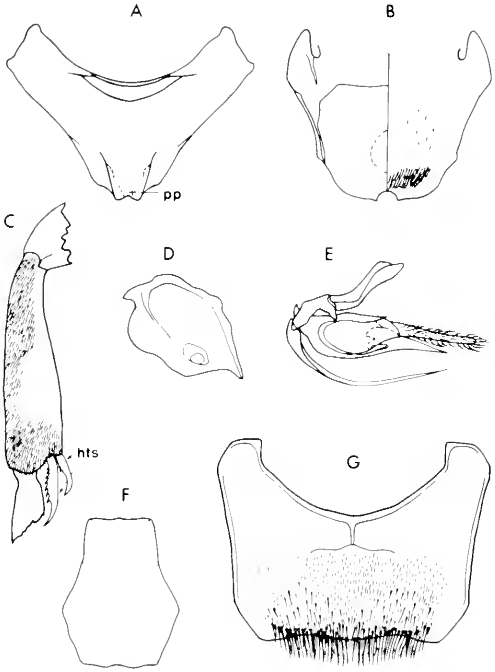

Figure 26. *Arhysosage ochracea* Brèthes. *Male:* A, T7, dorsal view; F, T8. *Female:* B, S6, dorsal and ventral views; C, Tibia 3, inner view; D, T7; E, Sting; G, S5, ventral view. hts = hind tibial spurs; pp = pygidial plate.

Genus *Spinoliella* Ashmead

(Figs. 7A, 27, 28, 30)

Diagnosis. Closer to *Callonychium* than to *Arhysosage.* It can be differentiated from *Callonychium* as follows: Gena black. Antennal sockets on lower third of face or nearly so. Clypeus with lateral part (beside mandibular articulation) rather horizontal. *Male.* Basitibial plate a swollen and shiny area, not delimited by carina. *Female.* S6 narrowed and with patch of hairs distally. Sting short, not reaching stylus.

Description. 1. Length 4–9 mm. 3. Lower part of face (below antennal socket) and some areas of legs with yellow marks. Thorax black (sometimes with small yellow spots). 4. Metasomal terga with yellow laterally or forming bands. 5. Pubescence short, especially short and appressed on metasoma. 7. Punctures in general fine. 8. Head broader than long and as broad as thorax or nearly so. 11. Glossa approximately as long as prementum or longer. 13. Segment 1 of labial palp about twice as long as 2–4 together, or somewhat longer. 16. Maxillary blade about twice as long as prepalpal part of galea. 17. Galeal comb of about 14–17 bristles. 20. Labrum less than twice as broad as long; basal part glabrous; distal margin of basal area a weak transverse ridge; labral apex flattened (Fig. 27D). 25. Mandible with well-developed, pointed, basal projection on upper margin [mandible strongly curved in male of *S. nomadoides* (Spinola)] (Fig. 27F). 27. Clypeus variable in width (in males more than three to five times broader than long, in females less than three to four times broader); distinctly protuberant (lateral view); distal margin with strong projection near lateral margin of labrum. 30. Inner subantennal suture angulate or strongly curved. 31. Subantennal area slightly wider than inner suture length and than antennal socket. 33. Tentorial pit approximately at midpoint of outer subantennal suture. 34. Antennal socket on lower third of face or nearly so. 36. Antennal flagellum of male unmodified, much shorter than head; flagellomere 1 about as long as 2 or little longer, and slightly longer than broad. 37. Lower paraocular area strongly swollen mesally. 38. Facial fovea narrow, well marked. 39. Orbits subparallel or slightly divergent below. 40. Middle ocellus below dorsal orbital tangent. 41. Vertex convex. 42. Gena of male (lateral view) generally wider than eye (about as wide as eye in *S. psamita* Toro and Ruz), of uniform width or somewhat wider in the middle. 43. Pronotum with dorsal preapical ridge usually more prominent laterally than medially. 44. Mesepisternum with surface facing anteriorly extremely reduced and slightly convex. 45. Pre-episternal groove weak, almost reaching

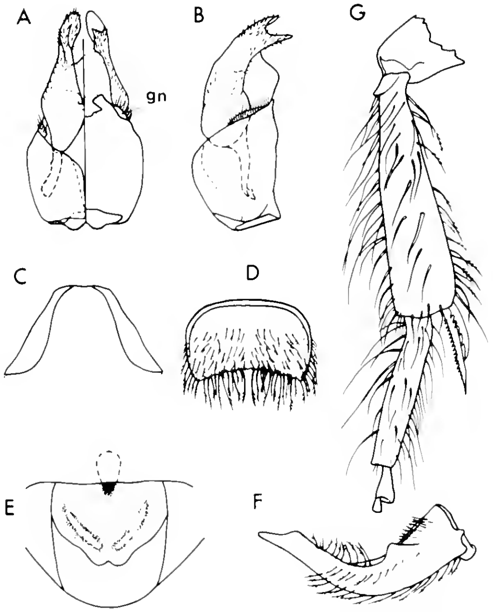

Figure 27. *Spinoliella nomadoides* (Spinola). *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, T8; D, Labrum; E, Metasomal tip showing S6; F, Mandible. *Female:* G, Leg 3, outer view. gn = gonostylus.

scrobal level. 46. Pterostigma longer than (at least slightly) and somewhat less than twice as wide as prestigma; side basal to vein r subparallel to costa, that within marginal cell straight or nearly so. 47. Marginal cell rather widely and somewhat obliquely truncate at apex, variable in length. 49. Submarginal cell 1 longer than cell 2 + 3. 51. First recurrent vein distant from first transverse cubital. 52. Forewing with cu-v longer than second abscissa M + Cu. 53. Hind wing with cu-v less than 1/2 as long as second abscissa M + Cu. 54. Dorsal surface of propodeum at least twice as long as metanotum. 55. Propodeal triangle basally depressed medially, microareolate, with no striae, glabrous. 57. Basitarsus 1 about seven times longer than broad in male, five times longer in female; tarsomeres 2–4 unmodified. 59. Middle tibial spur almost straight, finally serrate; usually about half as long as basitarsus 2 (sometimes somewhat longer). 60. Basitarsus 2 usually as long as 1 (sometimes somewhat longer) and shorter than 3, tarsomeres 2–4 unmodified. 61. Tibia 3 of female (Figs. 27G, 28D) almost twice as long as basitarsus 3; keirotrichia on inner surface forming patches at both ends (sometimes with few hairs between patches); male tibia 3 with keirotrichia rather dense but absent medially. 62. Tibial scopa of medium-sized, simple, sparse hairs (especially on outer surface). 63. Inner hind tibial spur with fine and dense teeth, almost straight; outer with teeth sparser than on inner. 64. Basitibial plate of male a swollen shiny area without defined margins; in female, rounded with margin a weak ridge. 65. Basitarsus 3 of female and tarsomeres unmodified. 66. Claws (in both sexes) bifurcate as in *Arhysosage.* 67. Metasoma in male usually slightly narrower than thorax. 69. T2–5 of male with gradulus posterolaterally short, not strongly carinate and with postgradular depression narrow (about 1/10 length of tergum) and shallow except somewhat deeper on T2; posterior marginal areas of T1–5 in male and T1–4 in female pilose; terga (both sexes) with no hair bands; lateral fovea of T2 (both sexes) slightly depressed, usually oval, somewhat variable in size. 70. Pygidial plate of male well developed with margins carinate. 71. T7 of female trapezoidal (Fig. 28C) or squared. 72. T8 of male as in Figure 27C. 73. Metasomal sterna of male with hairs mostly very short, more abundant laterally, sparse or absent on midline, directed posteriorly (some directed obliquely on S6). 73a. Metasomal sterna of female with hairs short, dense, directed caudad, not appressed, longer only on distal sternal margins. 74, 75. Similar to *Arhysosage.* 77. S6 of male with distal margin produced medially (Fig. 27E). 78. S6 of female with proximal laminar lobes surpassing the apodemes; duplication thin (attached to hardened area of sternum distally); S6 with distal margin medially produced or concave; with premarginal fringe or patch of hairs at apex (Fig. 28E). 79. S7 of male distally with two small projections; proximal arms forming a V (Fig. 28B). 80. S8 of male with body gradually separated from median distal projection; projection tapered toward apex and short-pilose (Fig. 28A). 83. Gonocoxites rather elongate, though somewhat wider in middle except *S. psamita,* rather squared (seen from ventral side); ventrally completely fused on midline. 84. Gonostylus vestigial (about 1/8 length of gonocoxite in ventral view) and fused to gonocoxite (Fig. 27A, B). 85. Volsellae indistinct, apparently absent (perhaps represented only by sclerotized area fused to gonocoxite and gonostylus). 86. Penis valve apically bilobed (simple in undescribed Argentine species not placed as to subgenus). 87. Penis completely membranous, somewhat shorter and wider than valve, and fused to valves basally. 88. Sting short (not reaching stylus apex) (Fig. 28F).

Discussion. In the cladogram (Fig. 30) *Spinoliella* is the sister of *Callonychium;* it has few unique apomorphies.

The subgenera *Spinoliella* s. str. and *Peniella* Toro and Ruz are not redescribed here. A key to these two subgenera, however, is given mainly to note some additional characters that separate them and to correct a mistake in the key by Toro and Ruz (1972).

Key to the Subgenera of *Spinoliella*

1. Males 2
—Females 3
2. Basitarsus 3 on outer surface with hairs short, dense. Facial fovea at least as

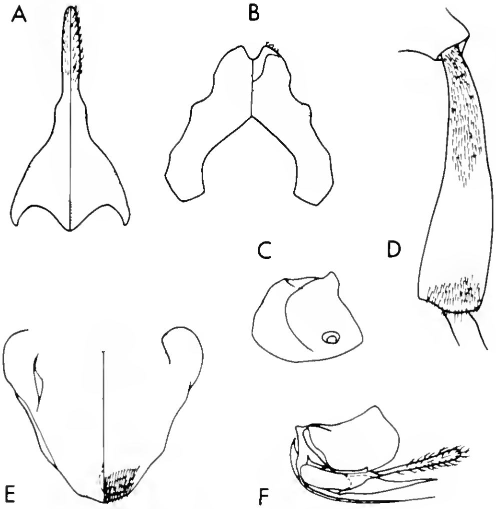

Figure 28. *Spinoliella nomadoides* (Spinola). *Male:* A, B, S8 and 7, dorsal and ventral views. *Female:* C, T7; D, Tibia 3, inner view; E, S6, dorsal and ventral views; F, Sting.

broad as one-third minimum width of scape. S6 with distal projection gradually separated from rest of sternum and noticeably surpassing lateral areas . . . . *Spinoliella* s. str.

—Basitarsus 3 on outer surface with hairs long, sparse. Facial fovea approximately as broad as one-fifth minimum width of scape. S6 with distal projection rather abruptly separated from rest of sternum and slightly surpassing lateral areas . . . . *Peniella*

3. Outer hind tibial spur about half length of inner, distinctly curved at apex (Fig. 27G). S6 distally much narrower than proximally; hairs at apex dense, forming a patch at each side of midline . . . . *Spinoliella* s. str.

—Outer hind tibial spur about 2/3 length of inner, almost straight. S6 with distal area slightly narrower than proximally; hairs at apex ordered in 3 well-defined rounded rows . . . . *Peniella*

Subgenus *Spinoliella* Ashmead s. str.

Spinoliella Ashmead, 1899: 84. Type species: *Camptopoeum nomioides* (sic) Spinola = *Camptopoeum nomadoides* Spinola, 1851 (monobasic and original designation).

This subgenus is easily distinguished by the characters given in the above key and in Toro and Ruz (1972).

Comments. Spinoliella s. str. contains two species: **S. (S.) nomadoides* (Spinola) and **psamita* Toro and Ruz.

Distribution. Chile.

Subgenus *Peniella* Toro and Ruz

Peniella Toro and Ruz, 1972: 146. Type species: *Camptopoeum maculatum* Spinola, 1851 (original designation).

This subgenus is distinguished by the characters given in the above key and by Toro and Ruz (1972).

Comments. Peniella includes four species: *S. (P.)* **maculata* (Spinola), **herbsti* (Friese), **rozeni* Toro and Ruz and **rufiventris* Toro and Ruz.

Distribution. Chile.

Genus *Callonychium* Brèthes
(Figs. 6D, 7B, 8D, 29, 30)

Diagnosis. Close to *Spinoliella,* distinguished as follows: Gena with yellow. Antennal sockets (lower margins) usually at lower fourth of face. Lateral part of clypeus strongly bent posteriorly. *Male.* Basitibial plate flattened, delimited by carina. Metasomal apex strongly bent down and forward. Sterna with modifications (ridges, projections, carinae). *Female.* S6 distally almost as broad as basally, distal margin slightly concave with curved distal band of curved and dense hairs.

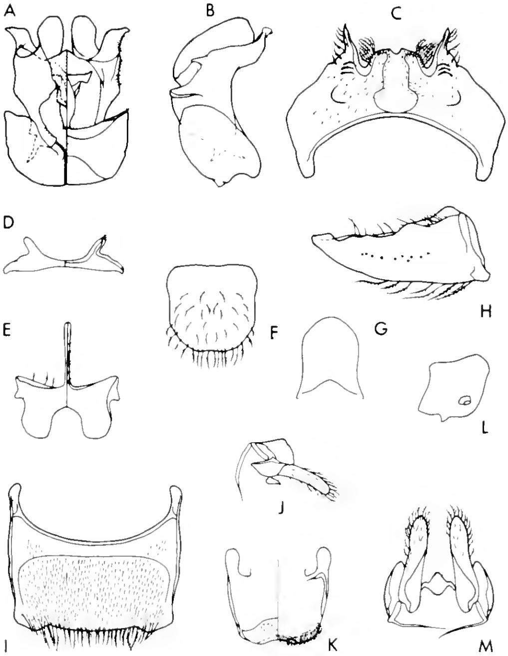

Figure 29. *Callonychium mandibulare* Brèthes. *Male:* A, B, Genitalia, dorsal, ventral and lateral views; C, S6, ventral view; D, E, S7 and 8, dorsal and ventral views; F, Labrum; G, T8; H, Mandible. *Female:* I, S5, ventral view; J, Sting, lateral view; K, S6, dorsal and ventral views; L, T7; M, Sting, ventral view.

Description. 1. Length 3–7 mm. 3. Head and thorax with several to extensive yellow areas, more abundant in male than in female. Yellow area of lower part of face generally prolonged onto dorsal part along orbit, yellow also on gena. Thorax with yellow at least on pronotum, metanotum and legs. 4. Metasoma with yellow marks laterally only or forming complete or fragmented bands. 5. Pubescence short and sparse on head and thorax, shorter and appressed on metasoma. 6. Integument in general distinctly microareolate, especially on head and thorax, slightly so on metasoma. 7. Punctures mostly fine, sparse on head and thorax, smaller on metasoma except on sterna of male, dense on sterna of female. 8. Head somewhat broader than long and usually about as broad as thorax. 11. Glossa about as long as prementum or longer. 13. Segment 1 of labial palp almost three times longer than 2–4 together or longer. 16. Maxillary blade about twice as long as prepalpal part of galea. 17. Galeal comb absent. 20. Labrum about as long as broad or broader; basal area glabrous; distal margin of basal area in male usually appearing flattened or with weak ridge, of female with ridge stronger than in male; labral apex not inflexed in either sex. 25. Mandible of male with moderate to strong process on upper margin. 27. Clypeal width variable (almost three to five times broader than long), usually distinctly protuberant (about 1/3 of eye width in lateral view), lateral part strongly bent posteriorly, distal margin usually with no projection near lateral margin of labrum. 28. Epistomal suture, below intersection of outer subantennal suture, usually almost straight. 30. Inner subantennal suture angulate just below antennal socket (Fig. 6D). 31. Subantennal area wider than inner suture length and wider (or much wider) than socket. 33. Tentorial pit at midpoint of outer subantennal suture or nearly so. 34. Antennal sockets (lower margins) usually at lower fourth of face (sometimes at lower third). 36. Antennal flagellum of male unmodified, much shorter than head; flagellomere 1 as long as 2 or longer, about as long as broad. 37. Lower mesal paraocular area often conspicuously protuberant; lateral part of lower paraocular area strongly bent posteriorly. 38. Facial fovea well marked, narrow (almost linear). 39. Orbits generally subparallel, sometimes slightly convergent below in male. 40. Ocelli variable in position (middle ocellus above or below dorsal orbital tangent). 41. Vertex convex. 42. Gena of male (lateral view) somewhat variable in width, of uniform width from above to below or somewhat wider medially. 43. Pronotum with dorsal preapical ridge prominent only laterally (weak or absent medially). 44. Mesepisternum with area facing anteriorly usually reduced and slightly convex. 45. Pre-episternal groove shallow, appearing only as a line (as in *Arhysosage*) if extending below scrobal level. 46. Pterostigma longer than and about twice as wide as prestigma; side basal to vein r subparallel to costa [except clearly divergent in *C. mandibulare* (Friese)], that within marginal cell straight. 47. Marginal cell obliquely and widely truncate at apex, shorter than distance from its apex to wing tip. 48. Submarginal cells two. 49. Submarginal cell 1 longer than cell 2 + 3. 51. First recurrent vein entering 2nd submarginal cell but variable in position, not meeting first transverse cubital. 52. Vein cu-v shorter than second abscissa M + Cu. 53. Hind wing with vein cu-v 1/4 to 1/6 as long as second abscissa M + Cu. 54. Dorsal surface of propodeum usually about twice as long as metanotum or longer. 55. Propodeal triangle basally with no special modifications, glabrous. 57. Basitarsus 1 five to seven times longer than broad in male and four to seven in female; tarsomeres 2–4 unmodified. 59. Middle tibial spur somewhat curved, finely toothed and about half as long as basitarsus 2 or nearly so. 60. Basitarsus 2 longer than basitarsus 1 (at least slightly) and shorter than 3. 61. Tibia 3 of female about twice as long as basitarsus 3 or nearly so; inner surface with keirotrichia limited to patch at each end; male tibia 3 with keirotrichia forming narrow band of sparse hairs on inner surface between patches at ends. 62. Tibial scopa of medium or small, scattered and inconspicuously branched hairs on outer surface; longer and denser on dorsal margin. 63. Hind tibial spurs appearing untoothed but with minute teeth difficult to see; outer shorter than inner, slightly curved or almost straight, inner straight. 64. Basitibial plate of male well defined, sometimes with smooth borders. 65. Tarsus 3 unmodified. 66. Claws deeply cleft with rami subequal in male, simple in female. 67. Metasoma in male narrower than thorax (except about as broad as thorax in *C. mandibulare* Friese). 69. T2–5 of male with gradulus posterolaterally short (weak) or absent and postgradular depression narrow, shallow, except deep on T2 of *C. mandibulare;* posterior marginal areas of T1–5 in male and T1–4 in female pilose; terga (both sexes) without hair bands; lateral fovea of T2 (both sexes) with shape, length and depth variable. 70. Pygidial plate of male well developed, rounded or bifurcate at apex. 71. T7 of female rather squared, with dorsal and proximal area not greatly expanded (Fig. 29L). 72. T8 of male somewhat variable but usually similar to an elongated trapezoid (Fig. 29G). 73. S1–5 of male with hairs mostly directed posteriorly, variable in length and density, mostly short, somewhat oblique on S6; sternal surface with modifications such as protuberances, projections, ridges or carinate areas; metasoma strongly curved down and forward at apex. 73a. S1–5 of female with hairs mostly short, dense, appressed. 74. S4 of male with distal margin almost straight, somewhat concave or emarginate (except widely convex in *C. mandibulare*). 75. S5 of male with distal margin almost straight medially (except widely convex in *C. mandibulare*). 76. S5 of female with long and recurved gradulus and no median sclerotized area between gradulus and proximal margin (Fig. 29I). 77. S6 of male distally with emargination (deep or shallow) between lateral and median areas (Fig. 29C). 78. S6 of female with proximal laminar lobes widely separated from lateral apodemes; basal sclerotization absent; lateral margin with strong, somewhat curved ridge; duplication heavily sclerotized; distal margin concave medially with dense curved hairs (Fig. 29K). 79. S7 of male transverse, bar-like, with a short laterodistal projection (Fig. 29D). 80. S8 of male with elongate, slender, median projection abruptly separated from a proximally emarginate rectangular body (Fig. 29E). 83. Gonocoxites short, rather square, ventral and dorsal sides completely fused. 84. Gonostylus rudimentary, fused to gonocoxite (recognizable only by the few, small hairs). 85. Volsellae indistinct, apparently absent (or represented only by a sclerotized transverse area completely fused to each other and to gonocoxite). 86.

Penis valves usually complex; dorsally, not attached to each other by bridge but attached basally to penis by membrane. 87. Penis membranous (variable in shape), shorter and wider than valve, with special internal sclerotization. 88. Sting rudimentary (reduced to a small sclerotized area), triangular plate modified, elongate (Fig. 29J, M).

Comments. The subgenera *Callonychium* Brèthes and *Paranychium* Toro recognized by Toro (1989) have not been redescribed in this study, although a key for subgenera by Toro and Herrera (1980) is here provided. The type species of this genus, *C. argentinum,* was not available for study.

Discussion. Callonychium is clearly differentiated by its apomorphies and is more closely related to *Spinoliella* than to *Arhysosage.* The relationship among these three genera has been also noted by Toro and Herrera (1980).

Rozen (personal communication) has studied the larvae of *Spinoliella herbsti* and a new species of *Callonychium.* His preliminary observations indicate that both species present "peculiar thoracic tubercles . . ." that "may represent a synapomorphy." He has also found that the low antennal papillae of most panurgines are somewhat or strongly projecting in these species; they are presumably synapomorphic. On the other hand he stated that "the recessed labial maxillary region of *Callonychium* and the projecting one of *Spinoliella* seem incongruous with the idea of the close relationship."

In my opinion the first two characters indicated by Rozen are likely to be good synapomorphies, which would reinforce the close cladistic relationship indicated by adult characters between *Spinoliella* and *Callonychium.* The third character, however, may not be useful to establish relationships.

The similarity between the flabellum of *Callonychium* and that of *Perdita* that Michener and Brooks (1984) observed does not lead to the conclusion that these two genera are closely related, and as those authors concluded, must result from convergence.

KEY TO THE SUBGENERA OF *CALLONYCHIUM*

1. Axilla yellow, acute. First metasomal sternum of male without premarginal process . . . . *Callonychium* s. str.
—Axilla black, depressed. First metasomal sternum of male with premarginal process . . . . *Paranychium*

Subgenus *Callonychium* Brèthes s. str.

Callonychium Brèthes, 1922: 120. Type species: *Callonychium argentinum* Brèthes, 1922 (monobasic).

This subgenus is distinguished by the characters given in Toro and Herrera (1980).

Comments. The subgenus *Callonychium* s. str. contains six species: *C. argentinum* Brèthes, *brasiliense* (Ducke), **flaviventre* (Friese), *luteimaculatum* (Strand), **mandibulare* (Friese) and *petuniae* Cure and Wittmann and others (undescribed) from eastern South America.

Distribution. Argentina, Paraguay, Brazil.

Subgenus *Paranychium* Toro

Paranychium Toro and Herrera, 1980: 213 (not valid because no type species was designated).
Paranychium Toro, 1989: 231. Type species: *Camptopoeum chilense* Friese, 1906 (original designation).

This subgenus is distinguished by the characters given by Toro and Herrera (1980) and by Toro (1989).

Comments. The subgenus *Paranychium* contains five species: *C. (P.)* **chilense* (Friese), **aricense* Toro and Herrera, **atacamense* Toro and Herrera, **coquimbense* Toro and Herrera and *minutum* (Friese) as well as undescribed species from Argentina.

Distribution. Argentina, Chile.

CLADISTIC ANALYSIS

This is part of a larger study of the subfamily Panurginae. A preliminary hypothesis of relationships among genera of Panurginae was used to identify the close relatives of the three tribes Perditini, Protomeliturgini, and Calliopsini (Ruz, 1986). The tribe Meliturgini was regarded as the sister to the three tribes mentioned above, and these four were in turn related to the tribe Panurgini. This outgroup information was used to construct a hypothetical ancestor using the Maddison, Donoghue and Maddison algorithm (1984). This ancestor is characterized in the matrix (Table 2) and its characters were coded according to codes for the entire subfamily. Thus "1" may be apomorphic at the subfamily level, but plesiomorphic at the present level of analysis. This was done so that the several studies I plan (including Ruz, 1986) can be examined together.

When a character is variable within a taxon, the code for the plesiomorphic state (0) was used in the analysis. An exception was character 72 (Fig. 30) for which the derived state in *C. (Micronomadopsis)* was used to demonstrate an apparent convergence with *C. (Liopoeodes).* Omission of character 72 did not change the topology of the cladogram.

Table 1. List of characters for genera and subgenera of panurgine tribes Calliopsini, Protomeliturgini and Perditini. (For the Panurginae as a whole, (0) is considered plesiomorphic but for the groups treated here it is in a few cases apomorphic.)

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3. *Metasoma with yellow markings* (1). Although the presence of yellow on the metasoma is widespread among bees, including some genera of Panurginae, it is lacking almost completely in the outgroups, which indicates that its presence should be considered as apomorphic. Lack of yellow was coded (0).

5. *Metasomal terga with distal hair bands* (1). Several groups of bees exhibit this feature, which apparently has arisen independently in different lineages. Among the Panurginae, however, it is present only in *Protomeliturga, Acamptopoeum, Calliopsis* s. str., *C. (Perissander), C. (Calliopsima),* and *C. (Verbenapis).* Since this character is also present in various Andreninae and colletid bees (both outgroups) it is possible that the lack of these hair bands (coded 0) is not plesiomorphic but is apomorphic. The genera of Panurginae mentioned above, however, because of other sets of characters, are considered among the most derived genera. Therefore the presence of these hair bands is likely to be apomorphic.

6. *Glossa more or less as long as prementum* (1). This condition was considered as apomorphic for the subfamily, since a shorter glossa (0) is present in most genera of the Andreninae and Colletinae. This study, however, shows that this condition (1) may be present in the ancestor of Calliopsini and is widespread among the Calliopsini and other Panurgini; it therefore is considered as a plesiomorphy for Calliopsini.

Glossa shorter than prementum (coded as 0 in Table 2) is an apomorphy for the present analysis and appears as a reversal in the cladogram (Fig. 30) for *C. (Perissander)* and *Perdita* (although the glossa is long in some groups of *Perdita*).

8. *Paraglossa shorter than suspensorium* (1). An autapomorphy for *Arhysosage,* a highly derived genus. Although the paraglossa is short in Andreninae (outgroup), this feature seems to be autapomorphic for *Arhysosage,* a genus with many derived characters. In other Panurginae the paraglossa is longer than or about as long as the suspensorium (0), and for this subfamily this condition is presumably plesiomorphic. Both shortness of the paraglossa in *Arhysosage* and its strong elongation among the long-tongued bees seem to be apomorphic.

9. *Segment 2 of labial palpus about three times longer than 3* (1). Autapomorphic, unique for *Protomeliturga.* Segment 2 of the labial palpus in other Panurginae and in the outgroups is usually about as long as 3, or if longer, less than two times longer than segment 3 (0).

11. *Segments 3–4 of labial palpus articulating preapically and projecting at about 90° to the axis of 1–2* (1). An autapomorphy for *Protomeliturga,* unique among the short-tongued bees, in almost all of which the articulation of the labial palpal segments 2–4 is apical (0). The preapical articulation between labial palpal segments 2 and 3 is present in long-tongued bees and is certainly derived.

12. *Mentum about 1/5 length of prementum* (1). A few Panurginae present the apomorphic condition: *Callonychium* and two Old World genera, *Camptopoeum* and *Melitturga.* Short-tongued bees usually have a mentum shorter to much shorter than 1/5 the length of the prementum, a condition which is plesiomorphic and coded (0).

13. *Galeal comb absent* (1). Many Panurginae and the outgroups have a well-developed galeal comb (0). This comb is absent in *Arhysosage, Callonychium* (also in some *Perdita*) and in several Old World panurgines. The evolutionary trend goes from comb well developed, reduced, to absent; the latter condition is clearly derived.

15. *Labrum of male with weak transverse ridge* (1). *Labrum of male flat* (2). One or the other of the derived states of this character appears occasionally among Panurginae. A weak ridge is present in *Spinoliella* and *Callonychium,* while a flat labrum characterizes some Old World and North American genera, and *Arhysosage.* A labral ridge (sometimes strong) or carina (delimiting the basal area) (0) is widespread among bees including the outgroups except in *Megandrena* (Andreninae) in which the labrum is flat, without a ridge.

16. *Labrum of male with basal area pilose* (1). Generally when a labral ridge or carina exists, hairs appear lateral and distal to the ridge or carina. This is also the case among many Panurginae and in the outgroups. The genera that present the derived feature are indicated in the cladogram, except for *Perdita* in which only some species have developed the derived condition. Lack of such hairs is coded (0).

17. *Labrum of female with apex not inflexed* (1). Among females of Panurginae and the outgroups, this feature is present only in *Arhysosage, Spinoliella,* and *Callonychium.* Otherwise the female labrum usually

shows the plesiomorphic condition, that is, with the apex at least slightly inflexed (0).

18. *Mandible of male simple* (1). This is an apomorphic character for the Panurginae since nearly all colletids and most Andreninae have bidentate mandibles. Among the Calliopsini, a *preapical tooth* is present only in *Arhysosage*. This condition (coded as 0 in Table 2) also appears in many Perditini and should be considered as apomorphic for the tribes here considered. The cladogram shows this as a reversal in *Perdita* and *Arhysosage*.

22. *Tentorial pit of male at intersection of outer subantennal and epistomal sutures* (1). *Tentorial pit of male in outer subantennal suture (close to epistomal suture)* (2). *Tentorial pit of male near middle of outer subantennal suture* (3). In colletids (second outgroup for Panurginae), even though they possess only the inner subantennal suture, the tentorial pit is in the epistomal suture sometimes considerably below the subantennal suture (0). In Andreninae (first outgroup for Panurginae) this pit is sometimes in the intersection between the epistomal and the outer subantennal suture, as in (1). The migration of the tentorial pit into the outer subantennal suture is unique to Panurginae and obviously apomorphic. Condition (1) should be considered plesiomorphic in this study, while (2) and (3) are sequential apomorphic states and uniquely derived characters in the Calliopsini.

23. *Antennal sockets of male (lower margins) on lower 1/3 or 1/4 of face* (1). In most Panurginae and outgroups the antennal sockets are placed more or less in the middle of the face (0).

24. *Antennal scape of male robust* (1). Apomorphy for some Old World genera and *Calliopsis (Ceroliopoeum)*. A derived feature among Panurginae, absent in the outgroups. A slender scape is coded (0).

28. *Lower paraocular area strongly swollen mesally* (1). This character is rarely present among bees. The only Panurginae with this feature are *Spinoliella* and *Callonychium*, although it is approached in some *Calliopsis* and *Perdita*. The rest of the genera have the lower paraocular area flattened or slightly convex (0). In the outgroups this area is usually completely flat.

37. *Pronotal carina or lamella of male present* (1). This structure is present only in three genera of Panurginae, one of which is *Protomeliturga*, although it seems that it appears independently in several other groups of bees. Many bees, including the panurgine outgroups, show the plesiomorphic condition, i.e., the lack of a carina or lamella on the dorsal part of pronotum (0); instead, at least laterally, a rounded ridge is developed.

39. *Pre-episternal groove short, not extending below scrobal level* (1). A short pre-episternal groove is present in all the tribe Calliopsini, in some other panurgine genera and some Andreninae. The Colletinae (second outgroup), however, show a very long groove that always extends below the scrobe (0). This fact indicates that a long groove is plesiomorphic and a short one apomorphic.

40. *Pre-episternal groove curved, meeting scrobe* (1). Some Andreninae and *Perdita* and *Acamptopoeum* among the Panurginae present this feature, which is clearly apomorphic. In Colletinae the pre-episternal groove is straight and does not meet the scrobe (0), which indicates that this is the primitive condition. In Andrenidae as a whole the scrobal suture is absent in front of the scrobe. Therefore it is unlikely that the lower part of the curved groove noted above is derived from the scrobal suture, although this is the usual interpretation.

41. *Axilla of male with patch of velvety hairs* (1). The presence of this feature is a unique apomorphy for *Calliopsis* s. str.; it is unknown in other bees. Lack of such hairs is coded (0).

42. *Metanotum with lateral patch of short velvety hairs* (1). This character, known only in *Calliopsis* s. str., *C. (Perissander)* and *C. (Calliopsima)*, must be an apomorphy. Hairs in this area usually are not different than on the rest of the thoracic dorsum (0). In *Calliopsis* s. str. the patch is conspicuous and brown in males, small and white in females; the latter condition is also present in both sexes of *C. (Perissander)* and *C. (Calliopsima)*.

44. *Pterostigma with sides parallel or subparallel* (1). Among Panurginae this character appears in the whole tribe Calliopsini and independently in a few other genera. Although this character is also present in some genera of the outgroups, it should be considered an apomorphic, since in Panurginae, the Calliopsini are the most derived bees. Pterostigma with margin basal to vein r divergent from costa so that the stigma is relatively broad is the plesiomorphy (0).

45. *Pterostigma with margin within marginal cell straight or nearly so* (1). All the Calliopsini present this apomorphy, although it has also appeared independently in two unrelated genera. Most genera of the outgroups show the plesiomorphy, that is, pterostigma with margin within marginal cell clearly convex (0).

46. *Marginal cell shorter than distance between its apex and wing tip* (1). *Marginal cell much shorter than distance between its apex and wing tip* (2). Most Panurginae and also the outgroups have a marginal cell about as

long as or usually longer than the distance between its apex and the wing tip (0); this is the plesiomorphic condition.

49. *Basal vein (fore wing) strongly curved toward wing base* (1). A unique character for *Protomeliturga;* among Panurginae and the outgroups this vein is usually straight or slightly curved (0).

52. *Propodeal triangle smooth* (1). Only a few genera of Panurginae (all of them Calliopsini) possess this derived character. These are: *Acamptopoeum, C. (Verbenapis), C. (Hypomacrotera)* and some *C. (Micronomadopsis).* Usually the propodeal triangle is striate or rugose, or at least minutely areolate (0). This plesiomorphy occurs in Andreninae and in many Colletinae.

55. *Tarsus 1 of female on inner surface mainly with hairs rigid, curved at apices* (Fig. 14H) (1). A strong, unique character of *Calliopsis (Verbenapis).* Hairs on this part of the tarsus 1 are rigid but straight (0) in other genera and in the outgroups.

56. *Femur 2 of female with well-defined basal comb on ventral margin* (Fig. 10D) (1). A uniform comb clearly differentiated from the hairs of the surrounding parts of the femur is present in all Calliopsini and, although appearing independently, in a few other genera of Panurginae. The comb of femur 2 of the female in the outgroups consists of stiff, short, dense, but irregularly organized hairs not very different from those of the surrounding areas (0); this must be the primitive condition.

58. *Basitarsus 2 of male longer than 3* (1). This feature is present only in the Calliopsini [*Acamptopoeum, Calliopsis* s. str., *C. (Perissander), C. (Liopoeodes), C. (Ceroliopoeum),* and several *C. (Micronomadopsis)* and in the Old World genus *Plesiopanurgus*]. In the rest of the Panurginae and in the outgroups basitarsus 2 of the male is equal to or shorter than 3 (0).

60. *Tarsus 2 of male with tarsomeres 2–4 widened distally* (1). This feature is found in a few genera of Panurginae and in *Euherbstia* and *Orphana* (slightly so in the latter) among Andreninae. Rather narrow tarsomeres (0) are plesiomorphic.

62. *Tibia 3 of female on inner surface with keirotrichia forming a longitudinal dorsal or medial strip* (1). *Tibia 3 of female with keirotrichia only at both ends of inner surface* (Fig. 28D) (2). This sequence seems to represent an evolutionary trend. The lack of keirotrichia should be the most derived condition. Presence of keirotrichia on most of the inner surface of tibia 3 (0) as in the outgroups is the primitive condition.

63. *Tibia 3 of male with keirotrichia forming a longitudinal strip* (1). The keirotrichia in many bees are present on most of the inner surface of tibia 3 (0) and (1) should be considered an apomorphy. Reduction to a strip of keirotrichia occurs only in *Spinolella, Callonychium,* and one Old World genus.

64. *Tibia 3 of male with dorsal margin evenly carinate* (Fig. 4F) *or the carina fragmented, forming a series of teeth* (1). This character appears in several members of the Panurginae but not in its outgroups. For this reason the presence of a tibial carina or of teeth may be apomorphic for the subfamily while its absence (0) is plesiomorphic. In this study, however, the ancestor probably had this feature; therefore the lack of teeth on the tibia 3 of the male in all Calliopsini should be interpreted as apomorphy. State (1) is present in *Protomeliturga* and exceptionally in *Perdita.*

67. *Tibial scopa of moderately abundant hairs* (1). *Tibial scopa of extremely sparse hairs* (2). The scopa is dense (0) in most Andreninae and Colletinae and for that reason at the subfamily level this feature is a plesiomorphy. Among the Calliopsini, however, condition (1) is the most widespread and may have been present in their ancestor; in this analysis, therefore, it is considered a plesiomorphy for Calliopsini. In this tribe only *Spinoliella* and *Callonychium* have the tibial scopa of sparse hairs (2), a derived state. A dense scopa (coded as 0 in Table 2) appears in the cladogram as a reversal for *Perdita, Calliopsima,* and *Verbenapis* and should be considered as apomorphic for the tribes here studied.

69. *Basitibial plate of male represented only by a swollen area, laterally not delimited by a ridge or carina* (1). This feature is known only in *Spinoliella* and some *Perdita;* in other panurgines and in most members of the outgroups the plate is delimited (0).

70. *Apex of basitarsus 3 of female with upper distal projection reduced so that apex is oblique* (1). *Apex of basitarsus of female transverse* (2). A well-developed upper distal projection on basitarsus 3 (0) is widespread among bees. Both well-developed and reduced projections are also present in the outgroups of Panurginae. Thus it is difficult to determine the polarity. However, a truncated basitarsus occurs only in some of the otherwise most derived Panurginae, such as *Spinoliella, Arhysosage, Callonychium* and some *Perdita.* Therefore for Panurginae the direction of evolution is indicated.

70a. *Basitarsus 3 of male expanded laterally at apex on ventral margin* (1), an autapomorphy for *C. (Liopoeodes)* (Fig. 22K). Lack of such expansion was coded (0).

71. *Tarsus 3 of male with tarsomeres 2–4 widened* (1). This character has appeared in three different lineages among the Panurginae and is obviously apomorphic. Unmodified tarsomeres (0) are commonly found in many groups of bees including most genera of the outgroups.

72. *Tarsus 3 of male with tarsomeres 2–4 asymmetrical* (1). Tarsomeres are usually symmetrical (0), a condition widespread in bees and wasps. Among panurgines, asymmetry, a unique and strong character, has been found only in some *Calliopsis (Micronomadopsis)*, in *C. (Liopoeodes)* and slightly so in some *C. (Liopoeum)*.

72a. *Distitarsus 3 of male widened medially,* (1), a unique character known only for *C. (Liopoeodes)*. In others the distitarsus is widest apically (0).

73. *Claws of female simple* (1). Among Panurginae this character is present only in a few Old World genera and in *Callonychium*. Bifurcate claws (0) are widespread among bees and are obviously plesiomorphic.

76. *T1–5 of male with posterior marginal areas (at least partially) pilose* (1). This feature appears several times among Panurginae and other bees, and may be apomorphic. Since the metasomal terga in the outgroups present either condition, it is difficult to determine the direction of evolution of this character. However, the majority of the presumably more primitive Panurginae have terga with bare posterior marginal areas (0), a condition that may well be plesiomorphic. All genera with metasomal hair bands (character 5) have densely pilose posterior marginal areas.

79. *Pygidial plate of male well defined* (1). A pygidial plate clearly delimited by a ridge or carina is present in most Calliopsini and independently also in a few Old World Panurginae, all of them quite derived genera as shown by other characters. This structure in males is widespread among bees and wasps and is plesiomorphic for the whole group. In Panurginae, however, it seems to be apomorphic, the plate having been largely lost in ancestors of Panurginae. In most genera of the outgroups the plate is represented only by a bare, shiny, triangular area or by an expansion of tergum 7 (0) similar to that of the the most primitive Panurginae. This last condition is considered plesiomorphic for Panurginae. Reacquisition of the defined plate should be no great evolutionary problem since the plate is defined in females; appropriate genes only need to be turned on in males.

80. *T8 of male at apex rather densely pilose* (1). Usually T8 has sparse hairs or is glabrous (0). However, in some Panurginae, like *Perdita,* T8 is clearly pilose, a condition not found in the outgroups.

81. *S4 of male with distal margin slightly produced medially* (1), as in *C. (Macronomadopsis)* and *C. (Verbenapis),* although barely distinct in the latter. *S4 of male with distal margin clearly produced medially* (2). This character is evidently apomorphic, for it is known only in *Calliopsis* and the Old World genus *Plesiopanurgus,* in which it must have arisen independently. S4 in other groups, including the outgroups, usually has the distal margin concave or almost straight medially (0).

84. *S5 of male with distal margin slightly produced medially* (1). *S5 of male on distal margin with a rather small median projection* (2). *S5 of male distally with an elongate median projection* (3). This feature is present only in the genus *Calliopsis*. The margin of S5 is concave or almost straight medially (0) in most bees and wasps; this condition is plesiomorphic.

85. *S1–5 of female with hairs mostly appressed* (1). Several Calliopsini and also *Protomeliturga* and and one Old World genus exhibit this character. Although this feature arose independently several times in bees, including the outgroups, it is likely to be an apomorphy in Panurginae since it is present only in otherwise derived genera. Sterna with hairs mostly not appressed (0) seems to be the plesiomorphy.

87. *S5 of female with distal margin convex medially* (1). This is a unique and strong synapomorphy of Calliopsini. The rest of Panurginae and outgroups present the plesiomorphic condition, that is, S5 with distal margin concave or almost straight medially (0). This condition is also widespread in other bees and wasps.

88. *S5 of female with median sclerotized area between gradulus and proximal margin of sternum* (Fig. 12A) (1). This derived character is present in Calliopsini and it has also appeared independently in one Old World genus. (In *Callonychium* it is absent, presumably secondarily lost.) The lack of this sclerotization (0) is widespread in bees.

89. *S6 of male with distal, elongate, tapered projection on each side of deep emargination* (Fig. 11H) (1). This structure has arisen only in some Calliopsini. The lack of such projections on S6 (0) is widespread in bees and plesiomorphic.

90. *S6 of male about three or more times broader than long* (1). This strong, derived character is present only in *Perdita*. Usually S6 of the male is about as wide as or somewhat wider than long (0). The outgroups of Panurginae and many other bees possess this plesiomorphic condition.

93. *S6 of female with two proximal laminar lobes* (Fig. 17H) (1). This character is found only in Calliopsini. Without doubt an excellent apomorphy, this structure is unknown in other bees or wasps which have the proximal margin of S6 in females straight (0).

94. *S6 of female without basal sclerotization* (1). This is an autapomorphic character of *Callonychium*. The

presence of basal sclerotization (0) is characteristic of the rest of Panurginae and outgroups.

95. *S6 of female with basal spine-shaped longitudinal sclerotization* (Fig. 1D) (1). This feature is present in most Calliopsini except *Callonychium.* It has also arisen, no doubt independently, in a few other genera of the subfamily. A basal sclerotization of S6 (females) is not spine-shaped (0) in panurgine outgroups; therefore the acquisition of this shape is clearly derived.

96. *S6 of female with basal sclerotization free at least at apex* (1). A basal sclerotization on S6 is usually fused to the sternum (0). Therefore, when the sclerotization has a free apex, it seems clear that this condition is apomorphic.

97. *S6 of female with strong, almost straight ridge on lateral margin* (Fig. 1D) (1). The Calliopsini (except *Arhysosage*), *Perdita,* and some Old World genera possess this character, which is lacking in the outgroups. A lateral ridge on S6, if present, is usually curved (0), a condition which is here considered plesiomorphic.

99. *S6 of female with premarginal hairs in well-organized rows forming a continuous or medially interrupted patch or band* (Figs. 10H, 12C) (1). This unique, strong character appears only in all Calliopsini. Premarginal hairs on S6 are usually organized in a dense patch (0). This primitive condition is present in Andreninae and Colletinae.

102. *S7 of male reduced to a transverse bar with two small latero-distal projections* (Fig. 29D) (1). This unique apomorphy is known only in *Callonychium.* Usually S7 is more conspicuous and of a different shape, commonly v-shaped (0).

103. *S7 of male with small brush of hairs near middle of each lateral projection* (Fig. 15D) (1). This sternal brush is only found in *Calliopsis (Liopoeum);* its absence is coded (0).

105. *S8 of male with a small lateral projection between body and distal projection* (Fig. 11F) (1). This strong character appears only in *Calliopsis* except for *C. (Verbenapis)* in which it exists only as two weak lateral bumps. It is absent (0) in other bees.

108. *S8 of male robust, strongly concave laterally* (Fig. 4G, H) (1). This is a unique, strong feature, present only in *Protomeliturga.* A thin structure with unmodified lateral margins is the plesiomorphy (0).

111. *Gonocoxites (ventral view) connected by membrane* (Fig. 18A) (1). *Gonocoxites partially or fully fused to each other* (Fig. 25A) (2). The gonocoxites are completely separated (except at the very bases) (0) in the presumably most primitive Panurginae and in the outgroups as well. Therefore this feature must be a plesiomorphy. The evolution of this character seems to be toward a full fusion of the gonocoxites.

113. *Gonocoxite (dorsal view) proximally with well-developed, mesal, usually lobe-like process* (Fig. 15A) (1). This strong character is present in *Calliopsis (Liopoeum)* and in one species of *C. (Hypomacrotera).* This structure is always lacking (0) in the outgroups.

115. *Gonostylus about 1/2 to 1/3 length of gonocoxite (ventral view)* (1). *Gonostylus vestigial, about 1/8 length of gonocoxite* (2). *Gonostylus rudimentary (recognizable only by the presence of few, short hairs at apex of gonocoxite)* (3). *Gonostylus absent* (4). Reduction in gonostylar length occurs in a few Old World Panurginae as well as in *Protomeliturga* and Calliopsini (almost lost in *Callonychium*). This strong character is rather rare in other groups of bees and lacking in the outgroups. Gonostylus longer than gonocoxite (0) is the ancestral condition.

118. *Volsella rudimentary or absent* (?) (1). Most Panurginae, all Andreninae and Colletinae have well-developed volsellae (0). *Arhysosage, Spinoliella,* and *Callonychium* are the only Panurginae that have apparently lost them.

119. *Volsellae connected to one another by basal, narrow and weak, membranous bridge* (1). *Volsellae connected to one another by widened membranous area or by slightly sclerotized cuticle* (2). *Volsellae partially fused to one another* (3). *Volsellae fully fused to one another but line of fusion visible* (4). *Volsellae absent or completely fused forming a highly sclerotized plate,* coded as missing (9) for *Arhysosage, Spinoliella* and *Callonychium.* In the outgroups and many other bees the volsellae are free from one another (0). They may be attached to the gonocoxites or penis valves but not to each other. Volsellae mesally free is certainly a plesiomorphy.

120. *Volsellae without denticles* (1). Denticles are usually present (0) on the volsellae. In *Protomeliturga* and some Calliopsini, however, the teeth are lost.

122. *Penis valve (lateral view) with longitudinal row of hairs* (1). This autapomorphy for *Acamptopoeum* is absent in the outgroups, which lack such hairs (0).

123. *Penis valve complex* (1). The presence of complex folds in the penis valve is found only in some subgenera of *Calliopsis.* Most primitive Panurginae and the outgroups possess simple penis valve (0).

125. *Penis completely separated from penis valve* (1). Most Panurginae and outgroups possess a penis partially or fully fused to the penis valve (0). In *Acamptopoeum* and *Calliopsis,* however, these structures are completely separated.

126. *Penis with internal sclerotization* (1). An internal sclerotization of the penis is a rare feature in other bees and is totally absent (0) in the outgroups. It is found only in *Spinoliella* and *Callonychium.*

127. *Sting short to very short, not reaching (or at least not surpassing) stylus* (1). *Sting rudimentary* (2). Females of many bees and wasps have a long sting which is commonly exposed. This is true in colletids and some Andreninae. In Panurginae, only the most primitive ones have an elongate sting (0), which may be seen from outside but less frequently than that of Colletinae. A short sting is present in most Calliopsini (except *Acamptopoeum*), *Protomeliturga, Perdita,* and in a few Old World genera. It is rudimentary, no doubt the most derived condition, in *Callonychium.*

128. *Sting truncate at apex* (1). This strong feature is present only in *Acamptopoeum* and some *Perdita* (e.g., *P. halictoides*). Commonly the sting is acute at the apex (0). An apically truncate sting must mean that, even if it is elongate, it cannot be used for introducing venom.

129. *First valvifer elongate* (1). The first valvifer (triangular plate) is usually more or less triangular (0). In *Perdita* and independently in *Callonychium,* however, the first valvifer is elongate, a modification probably related to reduction of the sting. This clearly derived condition is not found in Colletinae and is rare in Andreninae.

130. *Valve of first valvula rudimentary* (Fig. 24J) (1). *Valve absent* (Fig. 16B) (2). A well-developed valve of the first valvula (0) is present when there is a long sting, as in Colletinae and some Andreninae. The tendency in evolution is toward the loss of the valve, which is correlated with the weak sclerotization of the first valvula. In *Protomeliturga, Perdita,* a few Old World genera, and most Calliopsini there is no valve. A tiny projection that may be a valve rudiment is present in *C. (Ceroliopoeum)* and some Old World genera. In this study the absence of a valve in the three tribes involved should be interpreted as a plesiomorphic character and the presence of a valve-like structure in *Ceroliopoeum,* as an autapomorphy.

Seventeen taxa (15 taxa used by Ruz, 1986, and 2 additional taxa, *Liopoeodes* and *Ceroliopoeum*) and a total of 52 characters have been used in this study (Tables 1 and 2). Of the 130 derived characters previously considered (Ruz, 1986) for the whole subfamily, 53 were eliminated for being invariant among, or not applying to, the taxa here involved. Besides, 17 autapomorphies plus characters 70a and 72a added later, five convergences (see Table 1), and three characters with consistency indices (C.I.) 0.250 or below, were not used in this cladistic analysis. The three characters eliminated were the following: 26, Flagellomere 1 of male about twice as long as 2 or less. Even though this feature is diagnostic for some genera, it appears independently several times among Panurginae. 100, S6 of female with curved band of hairs on premarginal area. This character is known only in Calliopsini and seems to be derived, but it appears to arise independently and to reverse several times within the tribe. 116, Gonostylus partially or fully fused to gonocoxite. The gonostylus is lacking in several genera and subgenera of Calliopsini. Therefore this character was not informative in this study.

The presence of hair bands on the metasomal terga (character 5) was only considered as a character for males. In several taxa among the Calliopsini these hair bands are present in both sexes. In *Calliopsis (Liopoeodes),* however, they are present only in females. The C.I. of this character of females was too low to be considered in the analysis.

The polarity of variables (sequence of character states within each variable) has been determined using outgroup comparison. The outgroups considered for the entire subfamily are: Andreninae (the other subfamily of Andrenidae) and Colletinae (the subfamily considered the most primitive among Colletidae).

The data (Table 2) were analyzed using a computer program (Swofford, 1985, PAUP version 2.4) based on parsimony. The options selected were the following: 1. MULPARS. 2. Rooting. 3. Global branch-swapping. 4. Delayed transformation optimization. Only three most parsimonious trees were found, which showed almost no topological differences. Therefore only one tree (Fig. 30) is illustrated. Statistics of the tree: length = 115; C.I. = 0.6.

The cladistic analysis of the data in Table 2 indicated that Calliopsini is a strong monophyletic group, some of its synapomorphies being unique among all bees. It also shows that this tribe is subdivided into two clearly differentiated lineages, and that the sister group of *Acamptopoeum* is also well supported.

The relationships among the nine taxa at the top of the tree, however, do not seem to be very stable due to homoplasies. Moreover, some taxa or groups of taxa are differentiated by reversals only. *Calliopsis* s. str. and *Perissander,* the sister group of the remaining seven taxa, may appear in a trichotomy depending on the distribution of character 42. This character may arise earlier in the cladogram (as a synapomorphy for all the nine taxa plus *Calliopsima*) and be reversed later

Table 2. Data matrix of 52 synapomorphic characters for 17 taxa of the panurgine tribes Calliopsini, Protomeliturgini and Perditini. Coding is the same as for the whole subfamily Panurginae (Ruz, 1986). Therefore plesiomorphies at the level of the present study may be (1) instead of (0).

Taxon	Character																																																			
	3	5	6	13	15	16	17	18	22	23	28	39	40	42	44	45	46	52	56	58	60	62	63	64	67	70	71	72	76	79	81	84	85	87	88	89	93	95	96	97	99	105	111	115	118	119	120	123	125	126	127	129
Ancestor	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Protomeliturga	0	1	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	2	1	0	0	1	0	0	0	1	0
Perdita	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1
Acamptopoeum	0	1	1	0	0	1	0	1	2	0	0	1	1	0	1	1	0	1	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	1	1	0	1	1	1	1	1	0	2	1	0	4	1	0	1	0	0	0
Calliopsis	0	1	1	0	0	0	0	1	2	0	0	1	0	1	1	1	0	0	1	1	0	1	0	0	1	0	0	0	1	1	2	3	0	1	1	1	1	1	1	1	1	1	1	4	0	2	1	1	1	0	1	0
Perissander	0	1	0	0	0	0	0	1	2	0	0	1	0	1	1	1	0	0	1	1	0	1	0	0	1	0	0	0	1	1	2	3	0	1	1	1	1	1	1	1	1	1	1	4	0	2	1	1	1	0	1	0
Calliopsima	0	1	1	0	0	0	0	1	2	0	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	2	3	0	1	1	0	1	1	1	1	1	1	1	4	0	3	1	0	1	0	1	0
Verbenapis	0	1	1	0	0	0	0	1	2	0	0	1	0	0	1	1	0	1	1	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	1	0	1	1	1	1	1	0	1	4	0	4	1	0	1	0	1	0
Nomadopsis	1	0	1	0	0	0	0	1	2	0	0	1	0	0	1	1	0	0	1	0	1	1	0	0	1	1	1	0	1	1	2	3	1	1	1	0	1	1	1	1	1	1	1	4	0	2	0	0	1	0	1	0
Macronomadopsis	1	0	1	0	0	0	0	1	2	0	0	1	0	0	1	1	0	0	1	0	1	1	0	0	1	1	1	0	1	1	1	2	1	1	1	0	1	1	1	1	1	1	1	4	0	2	1	0	1	0	1	0
Micronomadopsis	1	0	1	0	0	0	0	1	2	0	0	1	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	1	2	3	1	1	1	1	1	1	1	1	1	1	1	4	0	2	1	1	1	0	1	0
Hypomacrotera	0	0	1	0	0	0	0	1	2	0	0	1	0	0	1	1	0	1	1	0	0	1	0	0	1	0	0	0	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	4	0	2	0	1	1	0	1	0
Liopoeum	0	0	1	0	0	0	0	1	2	0	0	1	0	0	1	1	0	0	1	0	0	2	0	0	1	0	1	0	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	4	0	2	0	1	1	0	1	0
Liopoeodes	0	0	1	0	0	0	0	1	2	0	0	1	0	0	1	1	0	0	1	1	0	1	0	0	1	0	1	1	1	0	2	3	1	1	1	1	1	1	1	1	1	1	1	4	0	2	1	1	1	0	1	0
Ceroliopoeum	0	0	1	0	0	0	0	1	2	0	0	1	0	0	1	1	0	0	1	1	0	1	0	0	1	0	0	0	1	1	2	3	0	1	1	1	1	1	1	1	1	1	1	4	0	2	1	1	1	0	1	0
Arhysosage	1	0	1	1	2	0	1	0	2	1	0	1	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0	0	1	1	0	0	1	1	1	0	1	1	0	0	1	0	2	1	1	9	9	0	0	0	1	0
Spinoliella	1	0	1	0	1	0	1	1	3	1	1	1	0	0	1	1	0	0	1	0	0	2	1	0	2	2	0	0	1	1	0	0	1	1	1	0	1	1	1	1	1	0	2	2	1	9	9	0	0	1	1	0
Callonychium	1	0	1	1	1	0	1	1	3	1	1	1	0	0	1	1	1	0	1	0	0	2	1	0	2	2	0	0	1	1	0	0	1	1	0	0	1	0	0	1	1	0	2	3	1	9	9	0	0	1	2	1

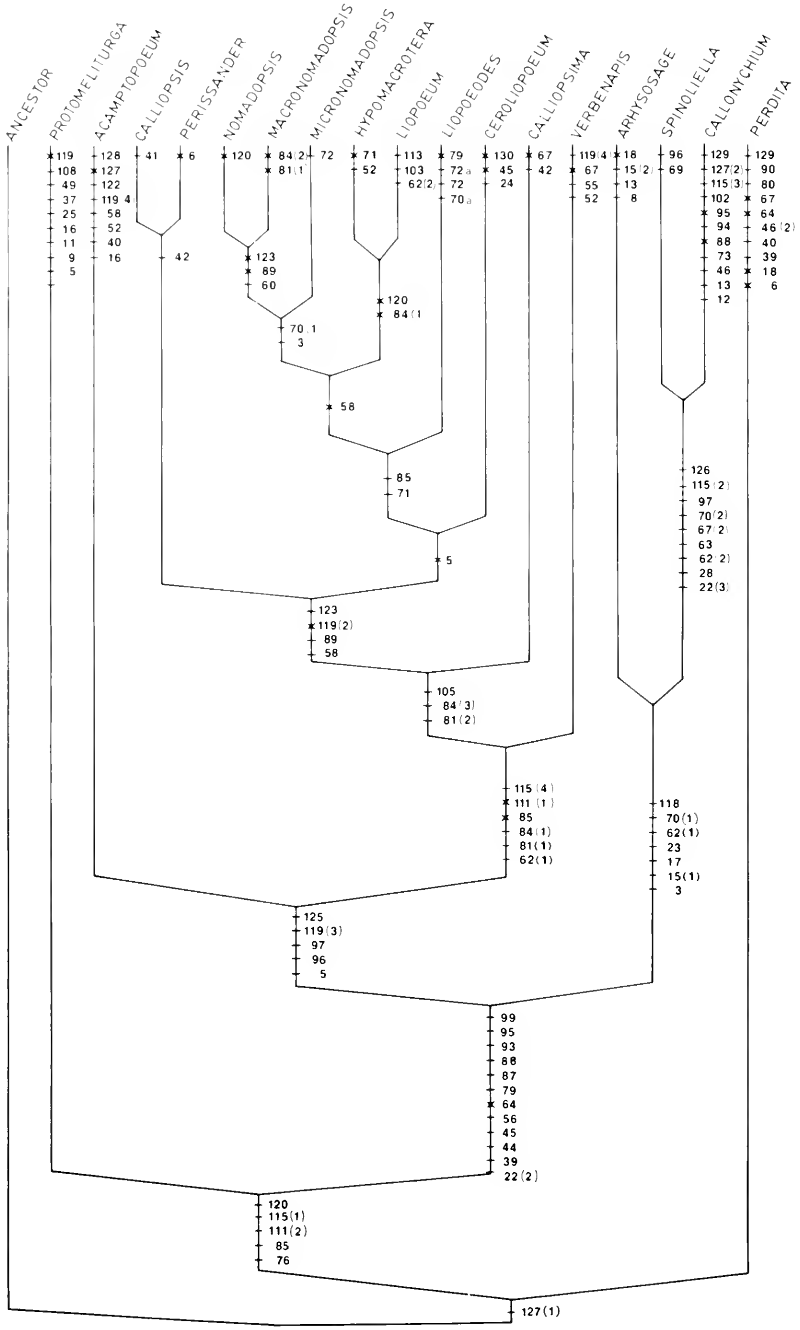

Figure 30. Cladogram showing the phylogenetic relationships of the genera and subgenera of the tribes Perditini, Protomeliturgini and Calliopsini. Autapomorphies and convergences (see Table 1) are also included here but only data in Table 2 were used in cladogram construction.

for the seven taxa mentioned above. On the other hand, if the characters eliminated (see above: 26, 100, 116) are maintained, some of the trees show *Acamptopoeum* as the sister group of the whole tribe, although there are only two characters that would support this arrangement.

The subgenera of *Spinoliella* and *Callonychium* agree in all characters shown in Table 2 and therefore were not segregated in the cladistic analysis.

The two outgroups of the Calliopsini, *Protomeliturga* and *Perdita,* were considered here to show how they relate to the tribe Calliopsini. A preliminary study that did not include *Protomeliturga* because it was not then available, indicated that *Perdita* was the sister group of the taxa now included in Calliopsini.

APPENDIX. A NEW SPECIES OF CALLIOPSINI FROM ARGENTINA

Calliopsis (Liopoeodes) xenopous, new species

Diagnosis. This is the only species of *Liopoeodes* and can be recognized by the subgeneric characters. Its general appearance is like *Liopoeum* but it is mostly black and not so hairy. *Male.* With apices of forewings brown as in *C. (Hypomacrotera)* and some species of *C. (Perissander);* tarsus 3 modified. *Female.* With hair bands on metasomal terga.

Male. Length 6–8 mm. Forewing length 5.5 mm. *Coloration.* Head and thorax black; face very slightly blue metallic and the following parts yellow: clypeus (lateral area), lower paraocular area beside inner orbit (usually L-shaped spot), supraclypeal area, underside of antennal flagellum (upper side brownish black), foreleg (on tarsus, outer surface of tibia and apex of femur), sometimes also with tiny spot at apex of femur 2 and at base of tibia 2. Tegula brown. Wings slightly yellowish; veins, pterostigma and forewing at apex brown. Terga brown-black, slightly metallic blue; sterna brown. *Punctation.* Labrum with basal area smooth, shining, impunctate. Clypeus shining with punctures fine and rather abundant. Rest of face with integument slightly microareolate, punctures mostly smaller than on clypeus. Gena with punctures even smaller. Rather sparse and fine on thorax, denser and very fine on upper half of metapleura. Propodeal triangle basally with fine and weak striae; shining, smooth posteriorly. Metasomal terga shiny with punctures small, but abundant, intermixed with sparser and coarser punctures; punctation coarser and deeper on T7. Metasomal sterna with punctures sparser and somewhat larger than on terga, mostly present distally toward middle line, except very fine distally on S5 but absent on middle line. *Pubescence.* Relatively sparse, fine, mostly brownish or black (whitish on venter of thorax and metasoma); hairs medium-sized (nearly as long as or longer than antennal scape), similar to those of *Liopoeum* on head and thorax, somewhat abundant on clypeus and between antennal sockets; short on labrum, forming a median tuft below labral ridge. Metasomal terga with hairs mostly very short, appressed, rather dense (similar to those of *Hypomacrotera*); not appressed, somewhat longer, sparse, and dark on latero-distal parts of terga, denser on T6 and T7; short, not appressed, and sparse (mostly absent on middle line) on sterna. *Structure. Head* about twice as broad as long (8.3:4.2). Inner orbits sinuose, convergent below. Clypeus more than twice as broad as long (4.5:1.9); distal projection (beside labrum) slightly rounded at apex. Interalveolar distance almost as broad as alveoloorbital distance 1.1:1.3). Inner subantennal suture angulate, less than half as long as outer and slightly shorter than width of subantennal area. Frontal line with upper part in a shallow groove, lower part (little more than half of total length) a well-marked carina reaching interalveolar area. Facial fovea five times longer than broad and 1/4 length of eye (1.0:0.2:4.0). Alveolo-ocellar distance about four times longer than distance between alveolus and epistomal suture and about as long as antennal scape (2.1:0.5:2.2). Ocellorbital distance about four times greater than that from lateral ocellus to vertex (1.9:0.5). Alveolus diameter similar to that of median ocellus (0.6:0.6). Antennal flagellum slightly shorter than head, flagellomeres longer than broad except second about as long as broad; two first flagellomeres somewhat shorter than remaining ones. Gena (lateral view) slightly broader than half of eye width (laterally) (1.3:2.1). Pterostigma slightly more than twice as long as broad (1.2:0.5). Prestigma about 1/2 of pterostigmal length and 1/2 pterostigma width (0.7:1.2:0.25:0.5). Marginal cell more than four times longer than broad and longer than distance from its apex to wing tip (4.5:1.0:3.1). *Thorax* narrower than head (7.0:8.3). Mesoscutum more than twice as long as scutellum and almost five times longer than metanotum (3.7:1.6:0.7). Propodeum with basal part almost horizontal. Leg 1 without modifications. Leg 2 with tarsal segments much more elongate than those of forelegs; basitarsus more than ten times longer than broad. Leg 3 with tarsus clearly modified; basitarsus much shorter than middle one, and wider and with strong outer projection at apex; tarsomeres 2–4 much shorter and much wider than those of middle legs, with projection similar to that of basitarsus, 3 and 4 widened toward inner side; distitarsus longer than those of fore and middle legs and widest medially instead of at distal end (Fig. 22K). *Metasoma* (maximum width) narrower than head and slightly broader than thorax

(8.3:7.0:7.3). Fovea of T2 almost invisible and in ventral position. T8 as in Figure 22G. S5 with rather short median distal projection; apical hairs dense and somewhat longer than projection (Fig. 22C). Genitalia and associated sterna as in Figure 22A, B, E, F.

Female. Length 8.5 mm. Forewing length 6.2 mm. *Coloration.* Black, except mandible with small basal spot yellow, apically mostly mahogany; antennal flagellum (extended forward) with upper side brown-yellowish, underside dark brown; tegula, legs, pterostigma, and wing venation brown. Wings slightly brownish, infuscated on tip of forewing. *Punctation.* Mostly fine as in male but much denser on metasomal sterna. *Pubescence.* Similar to that of male but not as dark; mostly shorter than antennal scape on face. White hair bands distally on T2–5 (interrupted medially on T2). *Structure. Head* less than twice as broad as long (8.4:5.6). Inner orbits slightly sinuose, slightly convergent below. Clypeus about three times broader than long (5.5:1.8); marginal projection as in male. Interalveolar distance narrower than alveolo-orbital distance (1.1:1.6). Inner subantennal suture curved toward middle line, little less than half length of outer subantennal suture and slightly shorter than width of subantennal area (0.5:1.1:0.8). Frontal line with distal carina shorter than in male. Facial fovea about four times longer than broad and about half as long as eye (2.2:0.5:4.2). Alveolo-ocellar distance about five times longer than distance between alveolus and epistomal suture and slightly shorter than antennal scape (2.1:0.4:2.5). Ocello-orbital distance about nine times greater than that from lateral ocellus to vertex (2.9:0.2). Alveolar diameter similar to that of median ocellus (0.5:0.5). Antennal flagellum shorter than head. Flagellomeres of similar length about as long as broad except first and last two somehwat longer. Gena (lateral view) narrower than eye laterally (1.3:1.8). Pterostigma slightly more than twice as long as broad (1.4:0.6). Prestigma somewhat longer than half of pterostigmal length and 1/2 of pterostigma width (0.9:1.4:0.3:0.6). Marginal cell five times longer than broad and longer than distance from its apex to wing tip. *Thorax* narrower than head (7.3:8.4). Mesoscutum slightly more than twice as long as scutellum and about four times longer than metanotum (3.5:1.6:0.8). Propodeum similar to that of male. Legs with no modifications. Middle femur, on ventral margin, with well-defined brush on basal half. Middle tibial spur somewhat shorter than basitarsus 2, almost straight, with small teeth. *Metasoma* about as broad as head and broader than thorax (8.5:8.4:7.3). T2 with lateral fovea weakly marked, narrowed at ends. S6 and sting apparatus as in Figure 23C, E.

Type material (all from Argentina). PROV. JUJUY: Holotype male and allotype female, Huacalera, 17 km N Tilcara, 2800 m, I-6-1972 (D. J. Brothers) (KU). *Paratypes.* 35 males and 83 females, same data as holotype; 3 males, Huacalera, XI-3-5-1968 (C. C. Porter); 2 males, same locality, X-10-1975 (G. M. Bohart); 1 female, Posta Lozano, XII-15-17-1967 (C. C. Porter); 10 females, end of Garganta del Diablo, Infiernillo, Tilcara (no date indicated) (Solbrig); 3 males and 1 female, 10 km S Humahuaca, 2900 m, 1-6-1972 (D. J. Brothers); 24 males and 16 females, 9 km S Humahuaca, XII-10-1975 (G. M. Bohart). *Additional paratypes.* PROV. TUCUMÁN: 2 males, San Pedro de Colalao, Dpto. Las Trancas, XI-1951 (no collector indicated); 1 male, Horco Molle, XII-10-23-1967 (C. C. Porter); 1 male and 1 female, Las Lenguas, XII-27-1972 (J. L. Neff); 1 female, same locality and collector, XII-5-1973. PROV. SALTA: 1 female, Payogasta, I-23-1966 (C. C. Porter); 1 female, Rosario de Lerma, XI-17-18-1983, Malaise trap (M. Wasbauer). Paratypes have been deposited in the following collections: KU; MCZ; USDA; UCD; CTMI; AMNH; IZML and UCV.

Comments. A gynandromorph from Jujuy, Argentina, was found among the specimens from the MCZ. It has the head and legs 1 and 2 (right side) like the female; the rest of the body like a male.

Etymology. The specific name is from Greek *xeno* meaning "strange" and *pous,* foot, referring to the modified hind tarsus. It is a noun in apposition and does not change with the gender of the genus name.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 54, No. 8, pp. 257-288 October 11, 1991

Revision of the Cleptoparasitic Bee Tribe Isepeolini (Hymenoptera: Anthophoridae)[1]

By A. Roig-Alsina

CONTENTS

ABSTRACT

The tribe Isepeolini is interpreted to comprise the revalidated genus *Melectoides* Taschenberg, with 10 species, and *Isepeolus* Cockerell, with 11 species. The tribe is South American, with maximal diversity in Argentina and Chile. Three species are described as new and several synonyms and new combinations are proposed. A cladistic analysis, keys to the genera and species, descriptions and illustrations are provided.

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[1] Contribution number 3060 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66045.

INTRODUCTION

Bees of the tribe Isepeolini are cleptoparasites of bees of the genus *Colletes* Latreille, but they may have a wider host range, as suggested below. The first instar larva has large, sharp mandibles, which it uses to kill the host larva (Michener, 1957) before consuming the provisions stored in the nest. The tribe is endemic to South America. Its maximal diversity is in Argentina and Chile, but one species reaches as far north as Colombia. The purpose of the present paper is to clarify the generic composition of the tribe and to review the species of the two recognized genera.

The tribe is interpreted to comprise *Melectoides* Taschenberg and *Isepeolus* Cockerell. The genus *Melectoides* was properly recognized by Holmberg (1887), Brèthes (1909) and Ducke (1912), but later it disappeared from the literature. Schrottky (1902) mistakenly identified and diagnosed specimens of *Leiopodus lacertinus* Smith as *Melectoides senex* Taschenberg, creating a lasting confusion on the identity of *Melectoides*. Sandhouse (1943) listed *Melectoides* as a junior synonym of *Leiopodus* Smith. Taschenberg's genus is revalidated here and its scope broadened to include several species previously treated as *Isepeolus*.

The genus *Isepeolus* has been considered a close relative of *Leiopodus* (Protepeolini). Moreover, the two genera have been confused in the past. Ducke (1907) treated the *Isepeolus* species known to him as *Leiopodus*, and Jörgensen (1909) described two species of *Leiopodus* as *Isepeolus*. Ducke (1912) clarified the limits of both genera. Linsley and Michener (1939) included *Isepeolus* in their new tribe Protepeolini. The unusually large arolium of the pretarsus is the most conspicuous feature that supports such a relationship. Later Michener (1944), even though including *Protepeolus*, *Leiopodus* and *Isepeolus* in that tribe, suggested that *Isepeolus* might belong in a separate tribe, in consideration of its largely bare, papillate wings, long first flagellomere and articulated male gonostylus. Rozen et al. (1978) remarked on the striking divergence of *Protepeolus* and *Isepeolus* in larval morphology, dismissed a close relationship between them, and proposed the monotypic tribe Isepeolini. It should be noted that the females of both tribes have modified apical segments of the metasoma, probably related to the process of oviposition, but they are modified in completely different fashions. The Isepeolini have the sixth sternum specialized, bearing a single sclerotized apical point, sometimes bordered by spinelike setae. It is the sixth tergum which is modified in the Protepeolini, with spinelike setae at each side of the spatulate apex, the sixth sternum being unspecialized.

The distinctiveness of the Isepeolini is well supported by both larval and adult morphology, but its phylogenetic relationships remain elusive. Isepeolines have been customarily considered as members of the Nomadinae. Rozen (1966), in his study of Nomadinae larvae, found that *Isepeolus* was in many respects plesiomorphic and in others quite divergent from nomadines, and suggested that it might represent a basal branch to that group, or even an independent lineage from nonparasitic ancestors. Bohart (1970) also suggested a separate origin. Nevertheless the Isepeolini have been included in the Nomadinae in recent studies (Rozen et al., 1978; Alexander, 1990). Roig-Alsina (1989, 1990) excluded several genera from the Nomadinae, suggesting later in a tribal analysis of the group (1991) that the subfamily is monophyletic in such a restricted sense. He could not find any synapomorphy uniting the Isepeolini (or the Protepeolini) to the re-defined Nomadinae. The tribe was left in an uncertain position, since it may still be the sister group of the Nomadinae, or belong elsewhere in the Anthophoridae. J. G. Rozen, Jr. (in press) is advancing a new hypothesis, based on the analysis of first instar larvae, that suggests a close relationship to the cleptoparasitic tribe Ericrocidini.

Systematic accounts of the Isepeolini consist mainly of species descriptions. Exceptions are the contributions of Grütte (1935), who separated and diagnosed as species groups of *Isepeolus* the two genera here recognized, and of Toro and Rojas (1968), who published a useful key to the Chilean species. The present contribution is the first revision of the group.

ACKNOWLEDGMENTS

I express sincere thanks to Charles D. Michener for his advice and support during the preparation of this paper. I thank also Byron Alexander and Jerome G. Rozen, Jr., for their useful comments on the manuscript. Several persons kindly made available material for study; they are acknowledged in Material and Methods. I am also grateful to the Consejo Nacional de Investigaciones Científicas y Técnicas, República Argentina, that made possible my stay at Lawrence. This paper was prepared with the aid of National Science Foundation grant BSR 87-16817 (C. D. Michener, principal investigator).

MATERIALS AND METHODS

Material studied, including types, was obtained from several collections. I am indebted to the following: American Museum of Natural History, New York, J. G. Rozen, Jr. (AMNH); California Academy of Sciences, San Francisco, W. J. Pulawski (CAS); Central Texas Melittological Institute, Austin, J. L. Neff (CTMI); Florida State Collection of Arthropods, Gainesville, L. A. Stange (FSCA); M. Fritz, Rosario de Lerma, Salta (MF); Instituto Miguel Lillo, Tucumán, A. Willink (IML); Martin Luther Universität, Halle, M. Dorn; Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Museo de La Plata, La Plata, R. Ronderos (MLP); Natural History Museum, London, G. R. Else; National Museum of Natural History, Washington, R. J. McGinley (USNM); Naturhistorisches Museum, Bern, H. D. Volkart; Snow Entomological Museum, University of Kansas, Lawrence, C. D. Michener (SEM); Universidad Católica de Valparaíso, H. Toro (UCV); Universidade Federal do Paraná, Curitiba, J. S. Moure (UFPR); University of California, Davis, L. S. Kimsey; Utah State University, Logan, T. L. Griswold; Zoologisches Museum, Humboldt-Universität, Berlin, F. Koch; Zoologisk Museum, Copenhagen, B. Petersen. The acronyms are used below to indicate depositories of specimens.

Morphological terminology of Michener (1944, 1965) has been followed, except that metapostnotum is used instead of propodeal triangle (Brothers, 1976). The metasomal terga (T) and sterna (S) are identified with Arabic numerals. Abbreviations used are upper interocular distance (UID), lower interocular distance (LID), ocello-ocular distance (OOL) and distance between posterior ocelli (POL). UID has been measured along the lower tangent of the anterior ocellus. The malar space has been measured at the level of the abductor swelling of the mandible. For easy comparison characters are numbered in the descriptions and are applicable to both genera. The cladograms were obtained with the help of the computer program Hennig86, version 1.5 (Farris, 1988).

BIOLOGY

Most of the published information indicates that isepeolines are parasitic in the nests of the genus *Colletes*. Host relationships are known for four species, and each one has been associated with more than one *Colletes*, indicating a low host specificity. Claude-Joseph (1926) associated *Isepeolus luctuosus* (Spinola) with *C. cyanescens* Haliday, *C. araucariae* Friese and *C. laticeps* Friese; *Melectoides triseriatus* (Friese) with the same three hosts; and *I. septemnotatus* (Spinola) with *C. musculus*. Michener (1957) reared *I. viperinus* (Holmberg) from nests of *C. kerri* Moure and from other unidentified *Colletes;* later Oliveira (1966) obtained the same species from nests of *C. petropolitanus* Dalla Torre. Two specimens of *I. septemnotatus* collected by P. Herbst in Cautín, Chile (CAS) bear the following labels: "raised from cell of *Colletes seminitidus* Spinola" and "raised from cell of *Colletes musculus*," respectively. Other records are those of Janvier (1933) and of Gazulla and Ruiz (1928), who reported a dense aggregation of *C. laticeps* heavily parasitized by *I. luctuosus*. Claude-Joseph (1926) mentioned *Lonchopria zonalis* (Reed) as the host of *I. viperinus* (Holmberg); since *viperinus* does not occur in Chile, it is uncertain what species he referred to.

The host relationships of isepeolines may be more varied than is suggested by the available data. The large *Melectoides senex* Taschenberg and *M. tucumanus* (Friese) (up to 16 mm long) need a similarly large host, and there is no species of *Colletes* of such a size in Argentina. Indirect evidence suggests *Caupolicana* as the possible host (J. Genise, personal communication).

There is a single record on the parasitic behavior of the adults. Claude-Joseph (1926) stated for *I. luctuosus*, "As soon as the *Colletes* provision the cells, they [*Isepeolus*] frequently visit the colonies and, in the absence of the owners, they lay an egg on the provisions." Claude-Joseph's observations should be taken cautiously, and new field studies are needed. Morphological specialization of female isepeolines suggests that they might hide their eggs in some way in the host cells. Females have a modified sixth sternum which ends in a sharp point and, depending on the group, may bear short or long spinelike setae. The possession of a modified abdominal apex is convergent with nonhomologous modifications in the Protepeolini and the Nomadinae (Roig-Alsina, 1991, and references therein), which are known to hide their eggs, embedding them in the cell walls (Rozen et al., 1978, and references therein). An analogous behavior can be expected for the Isepeolini. Another trend of specialization is seen in the mandibles of both sexes. Mandibles are elongate and sharp in the *Melectoides senex* group and tridentate in most *Isepeolus*. The functional meaning of such mandibles is not known; they may well be related to the female parasitic behavior.

Immatures of *I. viperinus* (Holmberg) are known in detail. Michener (1957) discovered and described the first stage larva, as well as the pupa. Oliveira (1966) and Rozen (1966) described the mature larva. A detailed comparison of isepeoline larvae to other parasitic anthophorids is to be found in Rozen et al. (1978) and Rozen (in press). The mature larva spins a cocoon before overwintering.

CLADISTIC ANALYSIS

The monophyly of the Isepeolini is supported by the broad, apically fimbriate T6 of the female, which lacks any trace of a pygidial plate (character 5, Figs. 15, 16), by the apically sclerotized, pointed S6 of the female (character 6, Figs. 9–14 and 50–61), and by the large spatha of the male genitalia covering almost all the dorsum of the penis (character 11, Figs. 20, 71). The two first features are unique, but an enlarged spatha is present in other groups, although not to the extent seen in the Isepeolini. The Melectini and some Anthophorini have spathae with poorly defined apical margins, covering up to two-thirds of the dorsum of the penis.

Striking features of the known larvae also support the distinctiveness of the Isepeolini. The first instar larva has a strongly depressed, prognathous head, with maxillae, labrum and hypopharynx forming a single sclerotized ventral plate (Michener, 1957; Rozen, in press). The presence of lateral body tubercles, the elongate labial and maxillary palpi and the single median labral tubercle of the mature larva are considered apomorphies of the tribe (Rozen, 1966; Rozen et al., 1978).

Primary analysis. A first analysis of the 21 species of Isepeolini was performed using as outgroups other tribes of Anthophoridae. As mentioned above, relationships of Isepeolini are not certain; hence all the tribes were considered to form a polytomy for outgroup comparison. This procedure has the drawback that only a reduced set of available characters, those invariant in the outgroups, can be polarized (characters 1–13 in Table 1). Until a general analysis of the anthophorid tribes is available, this is the alternative of choice. Characters with more than one apomorphic state were coded as nonadditive; all characters were given equal weight. Fourteen most parsimonious trees were obtained (tree length = 18 steps, CI = 88, RI = 95). Ten trees resulted from the uncertainty in the position of *M. fumipennis* due to the lack of information on its male characters, and the apparent sister group relationships suggested are dismissed as artifacts. The four remaining topologies depend on the interpretation of the reduction of the male gonostylus (character 13); one of them is shown in Fig. 1a. Alternatively *M. rozeni* may be the sister group to all other *Melectoides*, and *M. bellus* and *kiefferi* may be united to the terminal polytomy or may be the sister group to it. The interpretation of character 13 is discussed below.

The analysis suggests that *Melectoides* and *Isepeolus* are monophyletic groups, and supports their recognition as distinct genera. Apomorphies of *Melectoides* are related to specializations of the terminal segments of the female metasoma. The fifth tergum is prolonged apically by a membranous rim bearing upcurved setae (character 4, Figs. 15, 16). The sixth sternum has a series of long spinelike setae bordering the apical point, and the lateral apical margin of the sternum is expanded, membranous, folded and clothed with short hairs (characters 7 and 8, Figs. 9–14). The lateral apical margin of S6 is variable in the outgroups; it can be more or less sclerotized or membranous, but the condition seen in *Melectoides* is unique. *Isepeolus* is supported by the presence of a subapical tubercle on the male sixth sternum

TABLE 1. List of apomorphous characters. In the primary analysis (characters coded with numbers) outgroups are other tribes of Anthophoridae; in the secondary analysis (characters coded with letters) each of the two major clades obtained in the primary analysis is used as the outgroup for the other.

1. Mandible with two subapical teeth (Fig. 43) (1). Mandible with one subapical tooth is the plesiomorphic condition in Anthophoridae (Michener and Fraser, 1978).

2. Labrum with arched transverse carina and two lower preapical tubercles (Fig. 44) (1). Tubercles and carinae are common features on the labra of cleptoparasitic bees, but such a labrum is unique for a group of species of *Melectoides*.

3. Claws of all legs of female and of middle and hind legs of male with inner ramus flattened and truncate apically (Figs. 47, 49) (1). An inner flattened ramus occurs in several cleptoparasitic bee groups (Michener, 1944), but in every case it is interpreted as the derived condition.

4. Apical margin of T5 of female prolonged by membranous, usually hyaline rim bordered by upcurved hairs (Figs. 15, 16) (1). No such rim in outgroups.

5. T6 of female without pygidial plate, apex broad and bordered with a fringe of hairs (Figs. 15, 16) (1). Unique feature of Isepeolini. A tapering tip of metasoma is the usual condition in Anthophoridae, and considered plesiomorphic.

6. S6 of female ending in sclerotized apical point (Figs. 9–14, 50–61) (1). Unique feature of Isepeolini.

7. S6 of female with short spinelike setae at each side of sclerotized apical point (Figs. 56–61) (1); spinelike setae long and curved (Figs. 9–14) (2). Absence of spinelike setae is the plesiomorphic condition. Females of several groups of Nomadinae have spinelike setae on S6, but on lateral lobes of the sternum, suggesting that the structures are not homologous.

8. S6 of female with lateral apical margin membranous, much expanded and folded (Figs. 9–14) (1). A simpler margin as in Figures 50–61 approaches the condition in outgroups.

9. S6 of male with subapical tubercle (Figs. 77–79) (1). Sternum without tubercle in outgroups.

10. Gonocoxite of male genital capsule with sub-basal constriction (Figs. 71, 73 and 75) (1). No such constricted capsule in outgroups.

11. Spatha of male genitalia large, extended dorsally as strong sclerotization almost to tip of penis (Figs. 20, 71) (1). Spatha continued by dorsal sclerotization of penis in some other anthophorids (Melectini, some Anthophorini) but never to the extent seen in Isepeolini.

12. Volsella of male genitalia absent (1). Volsella present is plesiomorphic condition for bees in general.

13. Gonostylus of male genitalia short, one-third to one-fourth as long as gonocoxite (1). Gonostylus reduced to small triangular pilose lobe, not fused (Figs. 30, 32) (2). Gonostylus a small lobe fused dorsally to gonocoxite (Fig. 20) (3). (This lobe may not be homologous to the gonostylus of other Isepeolini; if not, then a gonostylus would be absent.) Gonostylus variable in outgroups, but articulate, pilose and well developed is considered plesiomorphic for anthophorids. Gonostyli of most *Isepeolus* (Figs. 71, 73) and *M. rozeni* (Fig. 22) are interpreted as plesiomorphic.

a. Bees over 12.5 mm long (1). All *Isepeolus* and the *triseriatus* group of *Melectoides* range between 6 and 11 mm long.

b. Lateral ocellus separated from posterior margin of head by 1.2 ocellar diameters, or more (1). Vertex narrow, lateral ocellus separated from posterior margin of head by 0.6–1.1 ocellar diameters in *Isepeolus*.

c. Mandible narrow and elongate, approximately 3 times as long as basal width (Fig. 39) (1). Mandible at most 2.5 times as long as basal width in *Isepeolus*.

d. Hypoepimeral area with lower polished band (1). Hypoepimeral area thoroughly punctate or with small polished round spot above scrobe in *Isepeolus*.

e. S5 of female with broad, round apical notch; margin of notch with row of close hairs, basal to which are plumose hairs, longest medially, and at each side a group of stout setae (1). Notch basal to marginal row of hairs with bare, hyaline area that forms a band separating apical row from basal plumose hairs (2). Apex of S5 with notch V-shaped; margins of notch densely hairy and with no further specializations in *Isepeolus*.

f. S6 of female with sclerotized apical point sharp (Figs. 52–61) (1). Apical point spatulate, concave below, in all species of *Melectoides*.

g. S6 of female basal to spinelike setae with "pocket" (Fig. 14, p) (1). No such pocket in *Isepeolus*.

h. Apex of female metasoma extraordinarily broad, T6 more than half of maximum width of T2 (Fig. 68) (1). T6 approximately one-third as broad as maximum width of T2 in *Melectoides* and most *Isepeolus*.

i. S3 of male without fringe of hairs (1). S3 with well developed fringe of hairs in *Melectoides*.

j. T7 of male with broad bare basal band (basal one-third to one-half bare) (1). Hairs arising nearby to tergal base, as on other terga, in *Melectoides* and most *Isepeolus*.

k. Gonocoxite of male genitalia without digitiform ventral lobe (1). Gonocoxite with digitiform ventral lobe in all *Isepeolus* (Fig. 71).

(character 9, Figs. 77–79) and by the basal constriction of the gonocoxite (character 10, Figs. 71, 73, 75). The two genera are further characterized phenetically. The most conspicuous differences (shape of the head and sexual dimorphism of the first flagellomere) are given in the key to the genera; a more detailed list is given under each genus heading.

Both genera have species with spinelike setae bordering the sclerotized apical point of the female sixth sternum. The size and position of such setae are constant in each group: all species of *Melectoides* have setae long, curved, and directed upward; species of the *viperinus* group of *Isepeolus* have setae short, straight, and directed laterally. Since no intermediate cases are known that link the two types, the homology of the spinelike setae can be seen as problematic. Besides the nature of the setae, the shape of the sclerotized point is different, being spatulate and concave below in *Melectoides*, and usually conical in the *viperinus* group (*I. lativalvis* has a secondarily reduced apical point). In the analysis the two types were treated as derived states of the same character (homology assumed), but coded to evolve independently (nonadditively) from the plesiomorphic state. The cladogram obtained suggests that the acquisition of stout setae has occurred independently.

Secondary analysis. A second approach was attempted in order to resolve the polytomies seen in Fig. 1a. Characters that show variation in one of the two genera but are constant in the other can therefore be polarized. An additional 11 characters were found (characters a–k in Table 1). Two types of characters are included here, those that vary in the outgroups and therefore could not be polarized in the primary analysis (a, b, c, d, i, j), and those that are exclusive to the Isepeolini, so the observed variation could not be rationalized a priori (e, f, g, h, k). Again multistate characters were coded nonadditively. Two most parsimonious topologies were obtained (tree length = 33 steps, CI = 84, RI = 92), differing in the interpretation of character g (female S6) in *Melectoides*. The new trees show a better resolution (Fig. 1b).

The basal position of *I. octopunctatus* within *Isepeolus* is reinforced, suggesting that the pointed inner tooth of the claws of both sexes of *I. septemnotatus* represents a reversed condition (character 3). The claws of the latter species look like those of the pollen-collecting outgroups, and before the analysis *I. septemnotatus* was a likely candidate as the sister species of all other *Isepeolus*. It is interesting to note that the fore claws of the males are always bifid, pointed, in the Isepeolini; since this condition has not completely disappeared it is possible to think that the reappearance of pointed claws in the mid and hind legs is due to some developmental rearrangement. Within the *I. viperinus* group two additional clades are distinguished. *I. lativalvis* and *smithi* are united by the broad apex of the female metasoma, and *I. vachali* and *wagenknechti* are united by the bare base of the male T7.

The basal ambiguity in *Melectoides* is resolved, further distinguishing the pair *M. senex* and *tucumanus*, and placing it as the sister group to all other *Melectoides* species. As mentioned above, the two topologies obtained in the secondary analysis differ in the interpretation of character g (basal pocket of female S6). If a reversal is allowed, a loss supports the clade *M. niveiventris* plus *fumipennis;* if g arises in parallel, the clade above *M. rozeni* becomes a trichotomy. The interpretation of characters e and g in Fig. 1b seems problematic. Character e in particular (S5 of female) is a complex feature with a peculiar arrangement of different types of setae, unlikely to have appeared twice *de novo*. A more satisfying topology would be with *M. rozeni* as sister taxon of the polytomy that includes *M. triseriatus*, etc. (Fig. 1c). Characters e and g would arise only once, *M. rozeni* would have lost the transverse carina of the labrum, and characters 13 and k (reduction of gonostylus, and reduction of ventral lobe of gonocoxite respectively) would arise convergently. This suggested topology is two steps longer, but in it new structures appear once and losses add to the homoplasy. It should be noted that a reduction of the gonostylus also occurs independently in a group of *Isepeolus*, and reduction of the genitalia in general is a common trend in many groups of bees.

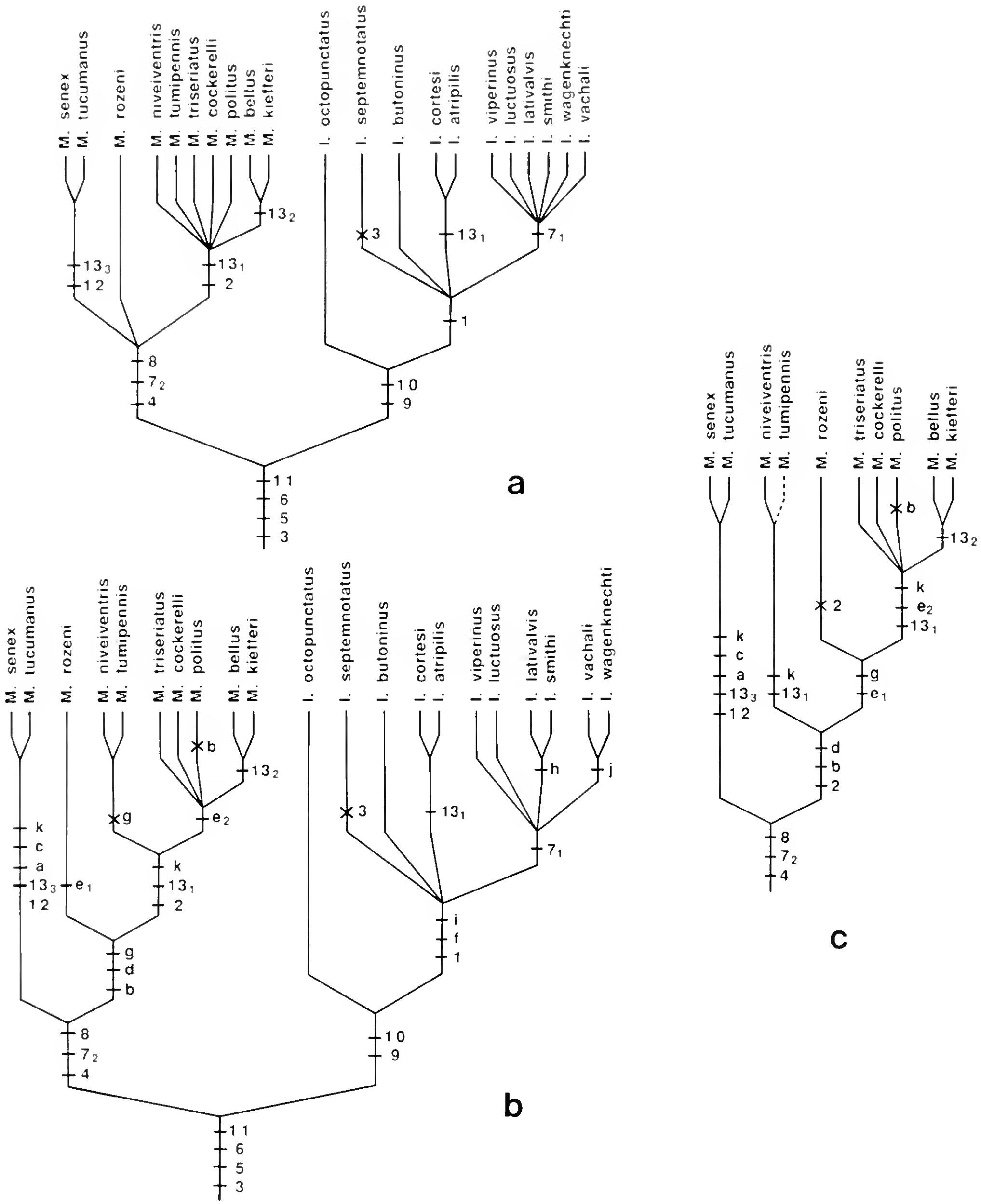


Figure 1. Cladograms showing relationships of species of Isepeolini. a. Primary analysis. b. Secondary analysis. c, alternative interpretation of b; dashed line indicates tentative position for species known only from female, node being supported only by male characters. Bars indicate apomorphies, crosses indicate reversals. Characters numbered according to Table 1.

KEY TO THE PARASITIC GROUPS OF SOUTH AMERICAN ANTHOPHORIDAE

A key is provided below to facilitate the recognition of the isepeolines among other groups of parasitic Anthophoridae in South America. The key will not work for other areas, since the Melectini and several tribes within the Nomadinae, which add to the variability of the subfamily, are not included. Current knowledge suggests that parasitism may have arisen independently in the seven groups presented below.

1. Metapleura strikingly narrow, meso-metapleural and metapleural-propodeal sutures close together, appearing as only one suture. Gena bordered posteriorly by strong carina, which reaches top of eye . . . . *Coelioxoides* Cresson
—Metapleura broad, meso-metapleural and metapleural-propodeal sutures distinct and well separated. Never with carina reaching top of eye 2
2. Forecoxa with ventral carina along inner margin and sometimes also along basal margin. Neck with round ventral sclerite on cervical membrane. T5 of female with wide polished apical margin, bordered by long hairs . . . . Osirini
—Forecoxa without carina, ventral inner margin rounded. Cervical membrane at most with faint ventral sclerotization. T5 of female usually hairy to apex of tergum 3
3. S6 of female apically emarginate forming two projecting lobes or points, or sometimes truncate; usually bearing spinelike setae. S6 of female concealed, usually only tip of apical points or margin of truncate apex visible beyond apex of S5. T7 of male with distinct pygidial plate; lateral margins of plate well defined. Exception is T7 of male Caenoprosopidini with square apico-lateral angles and raised into central, apically bilobed area; in this case labrum longer than wide . . . . Nomadinae
—S6 of female apically rounded or pointed; when spinelike setae present, S6 with conspicuous apical sclerotized point. S6 of female visible beyond apex of S5. T7 of male with apex usually bilobate or bidentate, sometimes apex more or less carinate, but never with pygidial plate defined basal to it. Labrum usually wider than long, at most as long as wide 4
4. Basal vein of forewing arising from base of second cubital cell. First flagellomere longer than second 5
—Basal vein of forewing arising from apex of first cubital cell. First flagellomere shorter than to as long as second 6
5. T6 of female with apex broad, medially emarginate and margin with fringe of hairs longer at sides. Mandible of male with sparse, long hairs on outer surface . . . . Isepeolini
—T6 of female with narrow spatulate apex, bordered by spinelike setae. Mandible of male with dense brush of hairs on outer surface. . . . . Protepeolini
6. Midtibial spur with apex bifid or multidentate. Foretibial spur with no prong coming out from main axis . . . . Ericrocidini
—Midtibial spur with apex pointed. Main axis of foretibial spur with strong prong at 90 degrees to velum . . . . Rhathymini

TRIBE ISEPEOLINI

Diagnosis. Length 6 to 16 mm. Vestiture on head, thorax and propodeum usually long, erect; on metasoma short, appressed, usually forming distinctive patterns of pale and dark maculations. First flagellomere elongate, 1.8 to 5 times as long as second, broadened apically in females (apex twice as broad as base), variable in males. Mandible with one or two subapical teeth. Labrum transverse, with sides bent backward. Maxillary palpus with three to four flattened segments. Stipes with longitudinal ridge on outer surface; stipital comb absent. Gena frequently depressed behind eye. Preoccipital and paraocular carinae absent. Axilla rounded. Metanotum and propodeum steeply slanting to vertical. Claws usually with flat, truncate inner tooth in both sexes, but fore claws of males always bifid. Wings basally largely bare, beyond closed cells papillate. Forewing with three submarginal cells, pterostigma moderate, 2.3–3.4 times as long as wide. Marginal cell shorter than distance from its apex to wing tip (0.65–0.80 : 1); apex separated from wing margin, truncate to pointed. Jugal lobe of hindwing one-third as long as vannal lobe measured from wing base. T5 of female without pseudopygidial area. T6 of female without pygidial plate; apex broad, medially emarginate and margin with fringe of hairs longer at sides. S6 of female with apex sclerotized, forming a point; in some groups such a point bordered by spinelike setae. T7 of male without pygidial plate, but apical margin sclerotized. Male genitalia with gonostylus simple, articulate; volsella present, setose; spatha large, covering almost all dorsum of penis.

Most Isepeolini, with the single exception of

M. tucumanus, have distinctive pale and dark color patterns on the metasoma due to short, dense, appressed hairs that form definite maculae. The pattern of maculation is not described in detail for each species in the present contribution (except for the new ones), since many of the original descriptions include illustrations of the patterns, or they can be easily recognized from the literature. The patterns are quite constant for most species. The extent and shape of the maculae in *I. viperinus* look alike over its entire range of distribution, from Colombia to southern Argentina. Other species that show constancy in pattern over large areas are *M. bellus* (from Salta to Río Negro in Argentina), *M. triseriatus* (from Atacama to Cautín in Chile), *I. septemnotatus* (from Coquimbo in Chile to Río Negro in Argentina) and *I. luctuosus* (from Copiapó in Chile to Chubut in Argentina). In some species the extent of the maculae is variable, mainly geographycally. Four such species are *I. vachali* (Fig. 67), *I. octopunctatus, I. atripilis* and *I. bufoninus;* the last one has wide white maculae on the metasoma of specimens from Buenos Aires, Argentina, but specimens from Paraná, Brasil, have the metasoma almost black. *I. cortesi* also presents latitudinal variation in the color pattern (Toro and Rojas, 1968).

KEY TO THE GENERA OF ISEPEOLINI

1. Vertex of head between lateral ocellus and eye slightly rounded to flat in frontal view (Figs. 2-6, 8), at most with shallow depression (Fig. 7). First flagellomere of male conspicuously widened apically, as much as that of female (Figs. 33-35). Female S6 with sclerotized apex bordered by long spinelike setae, and lateral apical margin folded down, partially covering such setae (Figs. 9-14). Apex of female T5 prolonged by membranous rim bordered by upcurved hairs (Figs. 15, 16). Male S6 without subapical tubercle . . . . *Melectoides* Taschenberg

—Vertex of head with conspicuous depression near eye (Figs. 62-65). First flagellomere of male slightly widened apically, contrasting with conspicuously apically widened female first flagellomere (Figs. 36-38). Sclerotized apex of female S6 with spinelike setae absent or short, barely visible at low magnification; lateral apical margin not expanded, not folded down (Figs. 50-61). Apex of female T5 without membranous rim. Male S6 with conspicuous subapical tubercle (Figs. 77-79) . . . . *Isepeolus* Cockerell

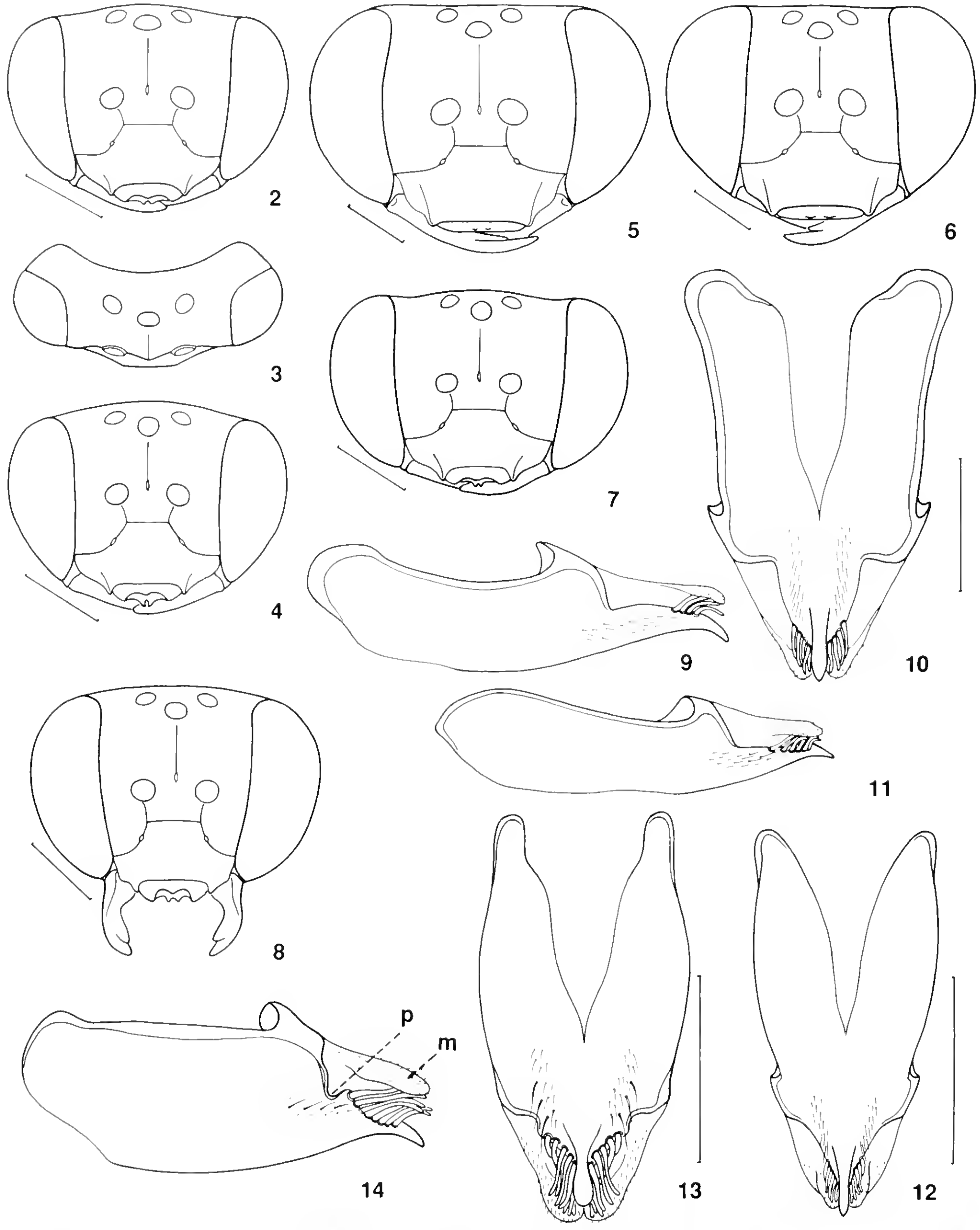
Genus *Melectoides* Taschenberg

Melectoides Taschenberg, 1883: 75. Type species: *Melectoides senex* Taschenberg, 1883, by original designation and monotypy.

Diagnosis. Length 7.5-16.0 mm. Head with vertex flat to slightly rounded. Gena behind eye depressed to rounded. Lateral ocellus surrounded by polished area, not wider than ocellar diameter. Inner orbit of eye in females concave to almost straight, of males almost straight to convex. Distance from lateral ocellus to posterior margin of head 0.74-1.40 times ocellar diameter. First flagellomere equally widened apically in males and females. Mandible with one subapical tooth. Hind coxa with upper external margin strongly keeled to carinate. Marginal cell with apex rounded or pointed, not truncate. T5 of female with subapical band of dense hairs and apex of tergum prolonged by membranous rim with upcurved hairs. S6 of female with sclerotized apical point curved, spatulate, concave below; apical point bordered by 4-8 long spinelike setae at each side; lateral apical margin of sternum membranous, enlarged and folded. S3-5 of male with dense apical fringes of hairs. S6 of male densely hairy, without subapical tubercle. S7 and S8 of male with disc reduced. Gonocoxite of male genitalia rounded basally.

The genus *Melectoides* includes two distinctive groups of species. *M. senex* and *tucumanus* are robust bees with extensive metallic pubescence that much resemble some ericrocidines, in particular those of the genus *Mesonychium* Lepeletier and Serville. They have several unique features (characters 12, 14, a, c, in Table 1 and Fig. 1). The group can be further distinguished by the eyes of the female slightly converging below (proportion of LID to UID, 0.95-0.98 : 1), the eyes of the male diverging below (proportion of LID to UID, 1.15 : 1), the lateral ocellus of the female separated from the occipital margin by 0.7-0.8 times the diameter of the ocellus, the long first flagellomere of both sexes subequal to sum of flagellomeres 2-4 in the female (1 : 0.93-1.02), longer in the male (1 : 0.78) and the hind coxa with the upper external margin sharply keeled.

A second, more numerous group, formed of smaller species of predominantly dark and white pubescence, has been treated in the literature as *Isepeolus*. Despite the similarity to *Isepeolus* in size and color, they share derived structural characters with the *senex* group and should be placed in *Melectoides*. Most species, with the exception of *M. rozeni*, are easily recognized by the arched labral carina. The group is distinguished by the eyes converging below in both sexes (proportion of LID to UID, females 0.75-0.85 : 1, males 0.83-0.95 : 1), the lateral ocellus of the female separated from the occipital margin by 1.1–1.4 times the diameter of the ocellus, the first flagellomere of the female shorter than the sum of flagellomeres 2–4 (1 : 1.5–1.8), subequal to shorter in males (1 : 0.95–1.65) and the hind coxa with the upper external margin mostly rounded, at most with a weak carina. Three subgroups can be recognized, one including *niveiventris* and *fumipennis*, another with *rozeni*, and a third with the remaining species. Their relationships and the supporting characters are discussed in the cladistic analysis.



Figures 2–14. 2–8, heads of *Melectoides* species. 2, 3, *M. politus,* female; 4, *M. politus,* male; 5, *M. senex,* female; 6, *M. senex,* male; 7, *M. niveiventris,* female; 8, *M. fumipennis,* female holotype. 9–14, S6 of *Melectoides* species, lateral and ventral views. 9, 10, *M. tucumanus;* 11, 12, *M. fumipennis;* 13, 14, *M. kiefferi;* p, pocket; m, membranous lateral apical margin. Scale lines 1 mm.

Key to the Species of *Melectoides*

1. Large species, 12.5–16.0 mm long. Pubescence of metasoma metallic, bluish or greenish. Mandible elongate, 2.85 (males) to 3.25–3.30 (females, Fig. 39) times as long as basal width 2

—Medium-sized species, 7.5–11.0 mm long. Pubescence of metasoma not metallic, brown to black with white maculation. Mandible of both sexes 2.0–2.3 times as long as basal width (Figs. 40, 41) 3

2. Pubescence of metasoma greenish with white maculation; female T1–4 with apical bands, those on T1–3 narrow, on T4 widest medially, T2–4 with bands also widened on sides of terga; male with similar pattern, but band on T1 absent, on T5–6 widest medially. Both sexes with white hairs on face, vertex, scape, pronotal lobe and scutum above tegula 1. *senex* Taschenberg

—Pubescence of metasoma bluish with no maculations. White hairs absent or restricted to face around antennal sockets and spot above tegula . . . . 2. *tucumanus* (Friese)

3. Labrum at most with two rounded elevations in center of disc separated by median longitudinal depression. Gonostylus of male genitalia as long as gonocoxite. . . . . 5. *rozeni* (Toro)

—Labrum with strong arched carina and two preapical tubercles (sometimes fused into single one); usually lateral parts of carina nearly parallel to sides of labrum (Fig. 44). Gonostylus of male genitalia one-third or less as long as gonocoxite 4

4. Integument of scutellum and metanotum red. Hairs of mesopleuron below hypoepimeral area appressed, short, as long as or shorter than diameter of pedicel. 5

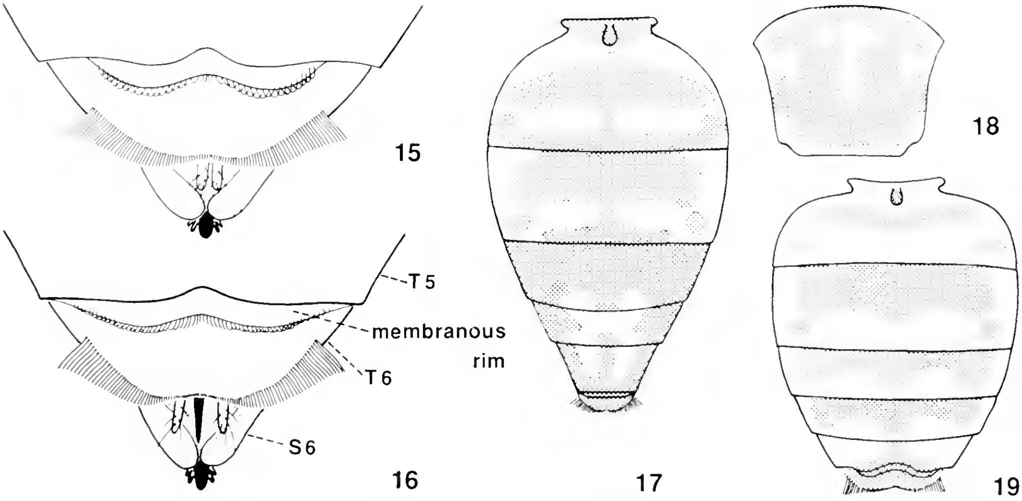
—Integument of thorax black. Hairs of mesopleuron below hypoepimeral area usually erect, longer than diameter of pedicel 7

5. Wings infuscated. Membranous apical rim of female T5 almost reaching sides of tergum in dorsal view (Fig. 17); apex of T5 approximately one-fourth as wide as apex of T2. Maxillary palpus with second segment longer than wide. (Only female known.) . . . . . . 4. *fumipennis* n. sp.

—Wings hyaline. Membranous apical rim of female T5 restricted to central part of tergum in dorsal view (Figs. 15, 19); apex of T5 over one-third as wide as apex of T2. Maxillary palpus with second segment flattened, about as long as wide 6

6. T1 with continuous apical band of white hairs, T2 with extended white pubescence on sides and apical margin, leaving central dark area and 2 small black spots; T5–7 of male white; T5 of female mostly white, leaving distinctive apical anchor-shaped dark area. T7 of male with apex rounded. . . . . 9. *bellus* (Jörgensen)

—T1–2 with lateral white maculae prolonged mesally by narrow, fingerlike lobe separated from



Figures 15–19. 15, *Melectoides kiefferi,* apex of female metasoma, dorsal view. 16, *M. cockerelli,* apex of female metasoma, dorsal view. 17, *M. fumipennis,* female, pattern of metasomal pubescence, dorsal view. 18, *M. fumipennis,* female, pattern of pubescence of scutum. 19, *M. politus,* female, pattern of metasomal pubescence, dorsal view.

apical margin; T5–7 of male with white spots; T5 of female dark or at most with 2 white spots. T7 of male with apex emarginate . . . . 10. *kiefferi* (Jörgensen)

7. T1–3 with white hairs covering almost all dorsum, laterally black; T4–5 black . . . . 3. *niveiventris* (Friese)

—T1–3 with pale maculation on a dark background; T4–5 usually also maculated 8

8. Pubescence on pleura, sternal region and face below antennae, white. Parapsidal furrow on elevated ridge. Metapostnotum, at least at sides, dull, minutely rugose (Chile) 6. *triseriatus* (Friese)

—Pubescence on lower part of mesopleuron, sternal region and face below antennae, black. Parapsidal furrow not elevated. Metapostnotum shiny, although with minute roughening in *cockerelli* (Argentina). 9

9. Scutellum evenly rounded, sometimes with median longitudinal furrow indicated on posterior half; hairs on scutellum sparse, polished integument visible. Hypoepimeral area polished on lower half. Female T5 with apical hyaline rim laterally not reaching the bending side of tergum (Fig. 19) . . . . 8. *politus* n. sp.

—Scutellum bigibbous, with median longitudinal furrow conspicuous; hairs on scutellum dense, hiding integument at least posteriorly. Hypoepimeral area polished on lower third. Female T5 with apical hyaline rim laterally reaching the bending side of tergum (Fig. 16) 7. *cockerelli* (Jörgensen)

1. *Melectoides senex* Taschenberg

(Figs. 5, 6, 20, 21, 33, 39)

Melectoides senex Taschenberg, 1883: 75. Lectotype female, by present designation, from Paraná (Prov. Entre Ríos, Argentina, March) (Halle, examined). Holmberg, 1887: 18. Dalla Torre, 1896: 318. Schrottky, 1903: 183. Ducke, 1912: 101. Schrottky, 1913: 264.

Melissa senex: Friese, 1912a: 201.

The size, elongate mandible, keeled hind coxa, metallic pubescence of the metasoma, elongate first flagellomere in both sexes and the eyes of the male converging above, distinguish *M. senex* from most *Melectoides* except *tucumanus*. It can be separated from *tucumanus* by the green metallic pubescence of the metasoma with whitish maculae, and the more extended white hairs on the head and thorax, as detailed in the key to species. The sexual dimorphism in the shape of the head is distinctive. The female has a broad face with eyes slightly converging below and a narrow vertex, the lateral ocellus being closer to the posterior margin of the head than in any other *Melectoides*. The male has eyes converging above and a broad vertex behind the ocelli.

Female lectotype. Length 15 mm; length of forewing 13 mm. (1) Vertex flat in frontal view. (2) Gena depressed behind eye. (3) Eyes slightly converging below, proportion of LID to UID 0.98 : 1; inner orbits concave. (4) Proportion of OOL to POL 1.17 : 1. (5) Lateral ocellus separated from posterior margin of head by 0.77 ocellar diameter. (7) Labrum with short transverse carina on upper third, below slightly concave, preapical tubercles absent, apical margin denticulate. (8) Malar space absent at level of abductor swelling, but anterior articulation of mandible separated from margin of eye by 0.25 times mandibular width. (9) Maxillary palpus with 4 segments, second and third longer than wide. (10) First flagellomere subequal to sum of flagellomeres 2–4, proportion 1 : 0.98. (11) Hairs of mesopleuron black with greenish tinge, erect; hypoepimeral area nearly all punctate, small polished area above scrobe present. (12) Scutellum convex, evenly rounded. (13) Metapostnotum tessellate. (14) Hind coxa with keeled carina on apical three-quarters of upper external margin. (15) Vein cu-v of hindwing as long as second abscissa of M + Cu. (16) Membranous apical rim of T5 dark, laterally not reaching the bending sides of tergum.

Male. Length 14 mm; length of forewing 12 mm. (18) Eyes converging above, proportion of LID to UID 1.14–1.15 : 1; inner orbits slightly concave on upper third, convex below. (19) Proportion of OOL to POL 0.70–0.83 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.78. (21) Hind femur not swollen. (22) Apex of T7 rounded. (25) Genitalia as in Figure 20, volsella and gonostylus absent.

Material studied. Besides lectopype, 1 male paralectotype, same locality and date (Mus. Halle) and 1 male, Paraná, Entre Ríos, Argentina, 1919, J. Brèthes (MACN).

2. *Melectoides tucumanus* (Friese)

(Figs. 9, 10)

Melissa tucumana Friese, 1906a: 102. Holotype female, Tucumán, Argentina, Steinbach leg. (not examined). Friese, 1912a: 210, fig. 9. Schrottky, 1913: 265.

Melectoides tucumanus: Ducke, 1912: 101.

This species is closely related to *senex*. It is distinguished by the blue metallic pubescence of the metasoma without white maculations, and the areas of white hairs reduced on head and thorax. The color pattern is quite constant over its distribution range. *M. tucumanus* is considered as different from *senex*, in spite of the close similarity in morphological features, until the variability of *senex* is known and males of *tucumanus* are collected.

Female. Length 12.5–16.0 mm; length of forewing 10–12 mm. (1, 2, 7, 9, 12–16) As in *M. senex*. (3) Proportion of LID to UID 0.98–1.0 : 1. (4) Proportion of OOL to POL 1.21–1.28 : 1. (5) Lateral ocellus separated from posterior margin of head by 0.75–0.80 ocellar diameter. (8) Malar space 0.05 times as long as mandibular width; anterior articulation of mandible separated from margin of eye by 0.25 times mandibular width. (10) First flagellomere subequal to sum of flagellomeres 2–4, proportion 1 : 0.93–1.02. (11) Hairs of mesopleuron blue, erect.

Male. Unknown.

Material studied. ARGENTINA. **Salta:** 1 female, Tastil, 3200 m, I-1988, M. Fritz (MF). **Catamarca:** 2 females, Andalgalá, 17-III-1973 and 12-III-1974, J. L. Neff (CTMI). **San Luis:** 1 female, Merlo, Duret col. (MF).

3. *Melectoides niveiventris* (Friese) n. comb.

(Figs. 7, 24)

Epeolus niveiventris Friese, 1925: 35–36. Holotype female, Baños de Cauquenes, 1900, Herbst leg. (Cauquenes, Maule, Chile) (ZMB, examined).
Isepeolus niveiventris: Grütte, 1935: 501. Toro and Rojas, 1968: 60.

This species is easily recognized by the color pattern: the scutum, scutellum, metanotum and T1–3 are dorsally wholly covered by white pubescence; the face, pleura, legs and T4–6 have black hairs. A similar pattern is seen in *Isepeolus wagenknechti* Toro and Rojas, *Mesonychium gayi* (Spinola), and many other Chilean bees. *M. niveiventris* and *fumipennis* differ from other small *Melectoides* in the *Isepeolus*-like shape of the female S5, medially compressed and densely hairy apically, without round apical notch.

Female. Length 9.8 mm; length of forewing 7 mm. (1) Vertex slightly depressed between lateral ocellus and eye in frontal view. (2) Gena slightly depressed behind eye. (3) Eyes converging below, proportion of LID to UID 0.79–0.82 : 1; inner orbits concave. (4) Proportion of OOL to POL 1.04–1.24 : 1. (5) Lateral ocellus separated from posterior margin of head by 1.4 ocellar diameters. (7) Labrum with arched transverse carina and two subapical, central tubercles; apical margin not denticulate. (8) Malar space 0.15 times as long as mandibular width; anterior and posterior mandibular articulations equidistant from margin of eye. (9) Maxillary palpus with three segments, second as long as wide, third minute. (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.59–1.64. (11) Hairs of mesopleuron black, erect; hypoepimeral area polished on lower half. (12) Scutellum evenly rounded with weak median longitudinal furrow. (13) Metapostnotum polished. (14) Hind coxa with weak carina on apical 0.4 of upper external margin. (15) Vein cu-v of hindwing 0.65 times as long as second abscissa of M+Cu. (16) Membranous apical rim of T5 hyaline, laterally not reaching the bending sides of tergum, but wide, 0.8 times as wide as T5 apically.

Male. Length 8–9 mm; length of forewing 6.5–7.2 mm. (18) Proportion of LID to UID 0.84–0.91 : 1; inner orbits almost straight, convex below. (19) Proportion of OOL to POL 0.93–1.0 : 1. (20) First flagellomere subequal to sum of flagellomeres 2–4, proportion 1 : 0.95–1.10. (21) Hind femur not swollen. (22) Apex of T7 emarginate. (25) Genitalia, Figure 24.

Material studied. CHILE. **Coquimbo:** 1 male, Embalse Laguna, 10-I-1940, Wagenknecht (SEM); 1 male, Laguna Dam, 5-XII-1950, Ross and Michelbacher (CAS); 1 male, Elqui (SEM). **Santiago:** 1 female, Farellones, 17-II-1980, M. Arroyo (UCV). **Maule:** 1 female holotype, see data above.

4. *Melectoides fumipennis* n. sp.

(Figs. 8, 11, 12, 17, 18)

This species is known from the female sex only. It is distinguished by the infuscated wings and the extended reddish coloration of the integument. The metasoma is more elongate and narrowed apically than in any other *Melectoides;* the apex of T5 is approximately one-fourth of the apical width of T2. Measurements of the paratype are indicated in parentheses below.

Female. Length 9.5 mm (8.5–11.0); length of forewing 7.3 mm (6.3–7.1). Integument of head black, with apex of clypeus, labrum, mandible and antenna reddish; propodeum black; thorax, legs and metasoma dark reddish, but tegula, pronotal lobe, hypoepimeral area and tarsi light red. Wings infuscated, darkest beyond closed cells. *Vestiture.* Pubescence of head white, hairs appressed on face and gena, erect on vertex, occipital region and around proboscidial fossa; scape with hairs white on basal half, brown on apex. Thorax, legs and metasoma with short, appressed hairs forming design of brown and white maculae; hairs of mesopleuron shorter than diameter of pedicel. Propodeum laterally with short, appressed brown hairs, along lateral angles and posteriorly with long, erect, white hairs. Hairs white on most of pronotum, except on anterior surface of pronotal lobe, laterally and a transverse band near anterior margin of scutum brown. Scutum with maculae as in Figure 18. Axilla with brown erect hairs that give appearance of elevated axilla; posterior margin with hairs white. Scutellum with hairs white leaving round brown spot on top of each gibbosity. Metanotum and upper half of pleura with hairs white; lower half of mesopleuron and ventral region of thorax with mixed brown and white hairs, except anterior surface of mesopleuron brown and two well-delimited brown spots at level of upper end of midcoxa; in holotype anterior spot connected to anterior surface of mesopleuron and posterior spot continued with lower half of metapleuron, in paratype both spots surrounded by white hairs. Hairs white on anterior surface of coxae, lower surface of fore femur and apex of mid and hind femora and tarsi. Tibiae with irregular pattern of brown and white hairs. Maculae on metasomal terga as in Figure 17. Sterna with intermixed brown and white hairs not forming definite pattern, except lateral apical white spot on S3 and S4. *Sculpture.* Punctation dense and even; punctures on scutum leaving interspaces a third to a half as wide as diameter of punctures. *Morphology.* (1) Vertex rounded between lateral ocellus and eye in frontal view. (2) Gena rounded behind eye. (3) Eyes converging below, proportion of LID to UID 0.80(0.72–0.87) : 1; inner orbits concave. (4) Proportion of OOL to POL 0.95(0.93) : 1. (5) Lateral ocellus separated from posterior margin of head by 1.4 ocellar diameters. (7) Labrum with arched carina and two preapical tubercles; lateral parts of carina parallel to sides of labrum. (8) Malar space 0.05 times as long as mandibular width; anterior and posterior mandibular articulations equidistant from margin of eye. (9) Maxillary palpus with four segments, second and third little longer than wide, fourth minute. (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.56(1.60–1.61). (11) Mesopleuron with appressed hairs, shorter than length of pedicel; hypoepimeral area polished on lower half. (12) Scutellum bigibbous, median longitudinal furrow broad posteriorly. (13) Metapostnotum tessellate at sides and above, polished below. (14) Hind coxa with weak carina on apical 0.4 of upper external margin. (15) Vein cu-v of hindwing 0.86 (0.75–0.94) times as long as second abscissa of M + Cu. (16) Membranous apical rim of T5 hyaline, laterally reaching the bending sides of tergum; T5 narrow, 0.28 times as wide as T2 apically.

Male. Unknown.

Material studied. Holotype female, Cebollar, La Rioja, Argentina, 14-XI-1944 (MLP). Paratype female, Los Tigres, Santiago del Estero, Argentina, 11–16-I-1970, R. Golbach (IML); paratype female, between El Cadillal and Ticucho, Tucumán, Argentina, 27-X-1989, J.G. Rozen and A. Roig-A. (AMNH).

5. *Melectoides rozeni* (Toro) n. comb.
(Figs. 22, 23)

Isepeolus rozeni Toro, 1971: 262–265, fig. 4. Holotype female, 41.5 km S Copiapó, Atacama (Chile), 19 Oct. 1969, Rozen and Peña leg. (AMNH, examined).

This species resembles *niveiventris* in the slightly depressed lateral areas of the vertex and the continuous bands of white pubescence on the metasoma, but those bands do not cover the entire terga and are also present on T5 (Toro, 1971, fig. 4); the face above the clypeus has white hairs. It can be distinguished from *niveiventris* and all other *Melectoides* of similar size by the labrum without transverse carina but with two rounded elevations at each side of a central longitudinal depression. The female S5 has a round apical notch with specialized setae, relating *rozeni* to *triseriatus* and close species, but the male genitalia have plesiomorphic features that render the placement of this species in the analyses conflicting. The gonostylus is long, well developed, and the gonocoxite has a digitiform lobe much as in all *Isepeolus.* Also the T7 of the male has the disc less reduced than in other *Melectoides.*

Female. Length 10 mm; length of forewing 6.3 mm. (1) Vertex between lateral ocellus and eye slightly depressed in frontal view. (2) Gena slightly depressed behind eye. (3) Eyes converging below, proportion of LID to UID 0.78 : 1; inner orbits almost straight. (4) Proportion of OOL to POL 1.04 : 1. (5) Lateral ocellus separated from posterior margin of head by 1.3 ocellar diameters. (7) Labrum medially elevated at each side of central longitudinal depression; apical margin not denticulate. (8) As in *niveiventris.* (9) Maxillary palpus with 3 segments, second longer than wide, third as long as wide, apically emarginate. (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.57. (11) Hairs of mesopleuron erect, white on upper half; hypoepimeral area polished on lower fourth. (12) Scutellum evenly rounded, with weak median longitudinal furrow. (13) Metapostnotum minutely rugose. (14) Hind coxa with weak carina on apical third of upper external margin. (15) Vein cu-v of hindwing 0.65 times as long as second abscissa of M + Cu. (16) Membranous apical rim of T5 hyaline, laterally not reaching the bending sides of tergum.

Male. Length 8 mm; length of forewing 7.2 mm. (18) Proportion of LID to UID 0.83 : 1; inner orbits convex. (19) Proportion of OOL to POL 0.88 : 1. (20) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.64. (21) Hind femur not swollen. (22) Apex of T7 rounded. (25) Genitalia, Figure 22.

Material studied. Besides holotype, 1 male, Coquimbana, 25 km from Freirina, Atacama, Chile, 19-20-X-1957, L. Peña (SEM).

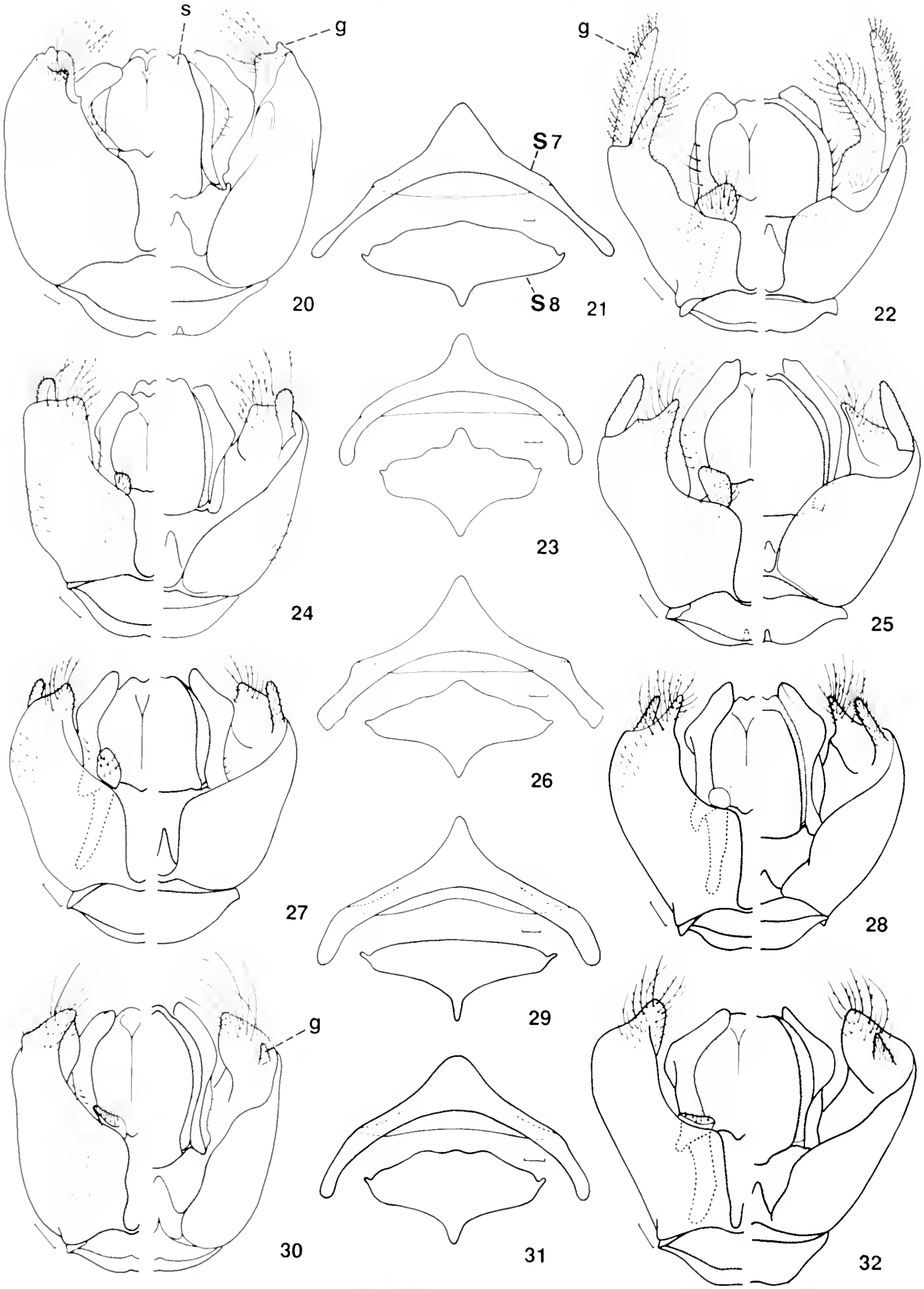
6. *Melectoides triseriatus* (Friese)
(Figs. 25, 26, 34, 41, 44)

Epeolus triseriatus Friese, 1908: 82–83. Lectotype female, by present designation, from Concepción, Chile, XII-1903, Herbst leg. (Berlin, examined). Schrottky, 1913: 265.

Isepeolus triseriatus: Claude-Joseph, 1926: 268. Gazulla and Ruiz, 1928: 302. Janvier, 1933: 325. Grütte, 1935: 501. Toro and Rojas, 1968: 60.

Melectoides triseriatus: Alexander, 1990: 144.

The name *triseriatus* has been consistently applied to a Chilean species by several authors, as shown in the synonymy, and is fixed in this sense in the present revision. To my knowledge this species does not occur in Argentina and the



Figures 20–32. Genitalia of males of *Melectoides;* ventral left, dorsal right; g, gonostylus; s, spatha; sparser stippling indicates partially sclerotized ventral surface of penis. 20, *M. senex;* 22, *M. rozeni;* 24, *M. niveiventris;* 25, *M. triseriatus;* 27, *M. cockerelli;* 28, *M. politus;* 30, *M. bellus;* 32, *M. kiefferi.* S7 and S8 of males of *Melectoides.* 21, *M. senex;* 23, *M. rozeni;* 26, *M. triseriatus;* 29, *M. politus;* 31, *M. bellus.* Scale lines 0.1 mm.

specimen from Tucumán included by Friese in the original description was probably *M. bellus* (Jörgensen) or *M. kiefferi* (Jörgensen).

This species is recognized by its dense punctation, the punctures with almost no interspaces; the pubescence is correspondingly dense. The parapsidal furrow is situated on an elevated ridge, the metapostnotum is usually rugose with polished areas reduced or absent and the hypoepimeral area is also sculptured, tessellate.

Female. Length 9.0–10.2 mm; length of forewing 6.5-7.0 mm. (1) Vertex rounded between lateral ocellus and eye in frontal view. (2) Gena rounded behind eye. (3) Eyes convergent below, proportion of LID to UID 0.73–0.79 : 1; inner orbits slightly concave. (4) Proportion of OOL to POL 1.09–1.21 : 1. (5) Lateral ocellus separated from posterior margin of head by 1.4 ocellar diameters. (7) Labrum with strong, arched carina and two middle, close preapical tubercles, lateral parts of carina nearly parallel to sides of labrum; apical margin not denticulate. (8) Malar space 0.1 times as long as mandibular width; anterior and posterior articulations of mandible equidistant from margin of eye. (9) Maxillary palpus with 4 segments, second and third longer than wide, fourth minute. (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.54–1.76. (11) Mesopleuron with dense, erect hairs, white on upper two-thirds, below with variable pattern of white and dark hairs; hypoepimeral area without hairs on lower half, but integument tessellate. (12) Scutellum slightly bigibbous, with median longitudinal furrow forming behind a wide triangular depression. (13) Metapostnotum minutely rugose, sometimes polished below. (14) Hind coxa with carina on apical half of upper external margin. (15) Vein cu-v of hindwing 0.75 times as long as second abscissa of M+Cu. (16) Membranous apical rim of T5 hyaline, laterally not reaching the bending sides of tergum. (17) S6 of female basal to spinelike setae with pocket (as in Fig. 14, p).

Male. Length 7.8–10.0 mm; length of forewing 6.5-7.5 mm. (18) Proportion of LID to UID 0.84–0.91 : 1; inner orbits slightly convex. (19) Proportion of OOL to POL 0.93–1.0 : 1. (20) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.21–1.32. (21) Hind femur usually swollen. (22) Apex of T7 truncate, with lateral angles sometimes curved up; usually short median carina present ending at moderate apical projection. (25) Genitalia, Figure 25.

Material studied. Chile. **Atacama:** 1 male, 20 km N Vallenar, 29-IX-1957, L. Peña (SEM). **Coquimbo:** 1 male, Portezuelo Tres Cruces, 30-31-X-1957, L. Peña (SEM); 1 female and 4 males, Fray Jorge, 15 km SW Pachingo, 20-X-1966, Schlinger and Irwin (CAS). **Valparaíso:** 1 male, Rio Marga-Marga, Los Perales, 13-X-1966, Irwin and Schlinger (CAS); 1 female, Lilenes, 7-XI-1965, De la Hoz (Logan). **Santiago:** 1 male, El Canelo (SEM); 2 females, El Canelo, 14-XI, Ramírez (MLP); 1 male, Cajón del Maipo, 21-XI-1965, Dazarola (Logan); 2 males, Pérez Caldera, XII-1988, M. Fritz (MF). **Cautín:** 1 female, Temuco, P. Herbst (CAS).

7. *Melectoides cockerelli* (Jörgensen) n. comb.
(Figs. 16, 27)

Isepeolus cockerelli Jörgensen, 1912a: 144–145, fig. C. Lectotype male, by present designation, from Chacras de Coria (Prov. Mendoza, Argentina), 21-X-1908, Jörgensen leg. (MLP, examined). Jörgensen, 1912b: 316.

Isepeolus bruneri Cockerell, 1917: 479–480. Holotype female, Carcarana (Carcarañá, Prov. Santa Fe, Argentina) (USNM, type number 23159, examined). **New synonym.**

This species is similar to *kiefferi* in pattern of maculation, but the integument is black. It differs from *kiefferi* and all other species in the group that have the S5 of the female with a large, round apical notch, by the wide apical rim of T5, that reaches the sides of the tergum.

Female. Length 8.5–9.5 mm; length of forewing 6.2-6.8 mm. (1) Vertex between lateral ocellus and eye flat in frontal view. (2) Gena slightly depressed behind eye. (3) Eyes converging below, proportion of LID to UID 0.79-0.83 : 1; inner orbits slightly concave. (4) Proportion of OOL to POL 1.0–1.08 : 1. (5) Lateral ocellus separated from posterior margin of head by 1.2 ocellar diameters. (7, 8) As in *triseriatus.* (9) Maxillary palpus with at least 3 segments, second and third as long as wide, in some specimens a fourth minute segment distinguishable. (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.55–1.79. (11) Hairs of mesopleuron black, erect; hypoepimeral area polished on lower third to lower half. (12) Scutellum bigibbous. (13) Metapostnotum polished. (14) Hind coxa with weak carina on apical 0.4 of upper external margin. (15) Vein cu-v of hindwing 0.75 times as long as second abscissa of M+Cu. (16) Membranous apical rim of T5 hyaline, laterally reaching the bending sides of tergum. (17) As in *triseriatus.*

Male. Length 8.0–9.5 mm; length of forewing 7.0-7.3 mm. (18) Proportion of LID to UID 0.89-0.9 : 1; inner orbits almost straight. (19) Proportion of OOL to POL 0.81–0.93 : 1. (20) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.16–1.28. (21) Hind femur swollen. (22) Apex of T7 emarginate. (25) Genitalia, Figure 27.

Material studied. Argentina. **Santa Fe:** 1 female, holotype of *I. bruneri* Cockerell, data above. **Mendoza:** 1 male, lectotype of *I. cockerelli* Jörgensen, data above; 3 females paralectotypes, Mendoza, 17-X-1908 and 1-XI-1908, P. Jörgensen (MLP); 1 male, Mendoza, C.S. Reed (MACN). **Neuquén:** 1 male, Confluencia Traful, 20-XII-1964, A.J. Giai (SEM); 1 male, Aluminé, Rinconada, XI-1965, M. Gentili (MF).

8. *Melectoides politus* n. sp.

(Figs. 2–4, 19, 28, 29, 40)

This species is recognized by the sparse punctation and polished integument, the punctures being particularly sparse on the scutum, scutellum, metanotum and lower half of mesopleuron. Also characteristic are the low, evenly rounded scutellum and the sinuous apex and membranous rim of the female T5. Measurements of the female paratypes are indicated in parentheses.

Female. Length 8.5 mm (8.0–8.5); length of forewing 6.5 mm (6.3–6.6). Integument black; mandible, pedicel, pronotal lobe, tegula and tarsi dark reddish brown. Wings hyaline, weakly infuscated, with pterostigma and veins dark brown. *Vestiture.* Hairs long, erect, on head, thorax and propodeum, those on mesopleuron over 1.5 as long as diameter of pedicel. With black and white intermixed hairs on face below antennal sockets, around proboscidial fossa, occipital region, sides of pronotum, ventral half of pleura, ventral region of thorax and coxae. Hairs white on upper half of face, gena, vertex, pronotal lobe, upper half of mesopleuron, propodeum, below fore femur and apex of mid and hind femora and basitarsi. Fore and mid tibiae with irregular pattern of black and white hairs; hind tibia mostly black; tarsi with intermixed black and white hairs. Metasoma with short, appressed hairs forming white and black maculae as in Figure 19. Sterna mostly black, except S1 with some intermixed white hairs and S2 with narrow white apical band. *Sculpture.* Integument polished and punctation sparse; punctures on scutum leaving interspaces 2–5 times as wide as diameter of punctures. *Morphology.* (1, 2, 7, 15–17) As in *triseriatus.* (3) Eyes converging below, proportion of LID to UID 0.85 : 1 (0.79–0.87 : 1); inner orbits slightly concave. (4) Proportion of OOL to POL 0.91 : 1 (0.82–1.0 : 1). (5) Lateral ocellus separated from posterior margin of head by 1.1 ocellar diameters. (8) Malar space 0.15 times as long as mandibular width; anterior and posterior articulations of mandible equidistant from margin of eye. (9) Maxillary palpus with 3 segments, second flattened, roundish, third not always clearly distinguishable. (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.79 (1.70–1.89). (11) Hairs of mesopleuron erect, white on upper half; hypoepimeral area polished on lower two-thirds. (12) Scutellum flat, evenly rounded, median longitudinal furrow inconspicuous. (13) Metapostnotum polished. (14) Hind coxa angulose on upper external margin, but no carina.

Male. Length 8.0–9.5 mm; length of forewing 7.0–7.5 mm. Color and vestiture similar to female, but hairs black on lower half of face, most of pleura and propodeum; T3–6 with apical white spots, T7 black. (18) Proportion of LID to UID 0.90–0.95 : 1; inner orbits almost straight. (19) Proportion of OOL to POL 0.79–0.94 : 1. (20) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.05–1.19. (21) Hind femur swollen. (22) Apex of T7 rounded. (25) Genitalia, Figure 28.

Material studied. Holotype female from Quebrada Horcones, 2900 m, Departamento Las Heras, Mendoza, Argentina, 10-I-1985, A. Roig-Alsina (MACN); 5 females and 4 males, paratypes, same data as holotype (MACN, SEM).

9. *Melectoides bellus* (Jörgensen) n. comb.

(Figs. 30, 31)

Epeolus triseriatus. Jörgensen, 1909: 225 (misidentification).

Isepeolus bellus Jörgensen, 1912a: 149–150, fig. G. Holotype female, Chacras de Coria (Prov. Mendoza, Argentina), 5-XII-1907, Jörgensen leg. (MLP, examined). Jörgensen, 1912b: 316.

This species can be distinguished by the extensive short, appressed, white pubescence and red scutellum and metanotum. The female T5 has a characteristic median anchor-shaped dark spot. This species is related to *kiefferi,* as indicated by the reduced male gonostylus and the rounded second segment of the maxillary palpus.

Female. Length 8.2–10.5 mm; length of forewing 5.8–7.5 mm. (1, 2, 7, 9, 13–17) As in *politus.* (3) Eyes convergent below, proportion of LID to UID 0.73–0.78 : 1; inner orbits slightly concave. (4) Proportion of OOL to POL 0.83–0.95 : 1. (5) Lateral ocellus separated from posterior margin of head by 1.1–1.3 ocellar diameters. (8) Malar space almost absent; anterior and posterior articulations of mandible equidistant from margin of eye. (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.50–1.71. (11) Mesopleuron with appressed hairs, as long as diameter of pedicel, hairs white on upper half. (12) Scutellum bigibbous.

Male. Length 9.5–10.5 mm; length of forewing 7.8–8.3 mm. (18) Proportion of LID to UID 0.84–0.86 : 1; inner orbits slightly convex. (19) Proportion of OOL to POL 0.76–0.77 : 1. (20) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.32–1.59. (21) Hind femur swollen. (22) Apex of T7 rounded. (25) Genitalia, Figure 30.

Material studied. ARGENTINA. **Salta:** 1 male, Cafayate, I-1983, M. Fritz (MF); 1 female, Río Las Conchas, 35 km Cafayate, 3-III-1978, A. Willink (IML). **Santiago del Estero:** 1 female, 37–47 km SE Añatuya, 20-XI-1979, C. and M. Vardy (London). **Catamarca:** 1 female, Joyango-Coipes, on flowers of *Verbesina encelioides,* 2-XII-1972, J.L. Neff (CTMI). **La Rioja:** 1 male and 1 female, Cebollar, 14-XI-1944, A. Ogloblin (MLP); 1 female, Chepes, 24-XI-1944, A. Ogloblin (MLP); 1 male, La Rioja (MACN). **Mendoza:** 1 female, holotype, see data above. **Río Negro:** 6 females, Río Colorado, 1321-II-1946, Hayward and Willink (MLP, SEM); 1 female, Choele Choel, 15-XII-1989, M. Fritz (MF).

10. *Melectoides kiefferi* (Jörgensen) n. comb.
(Figs. 13-15, 32, 35)

Isepeolus kiefferi Jörgensen, 1912a: 148-149, fig. F. Lectotype female, by present designation, from Mendoza (Argentina), 26-X-1908, Jörgensen leg. (MLP, examined). Jörgensen, 1912b: 316.

M. kiefferi can be recognized by its short, appressed pubescence and by its red, bigibbous scutellum and red metanotum. These characters are shared with *bellus*, from which it is distinguished by the reduced white vestiture and the emarginate apex of the male T7.

Female. Length 9.5-10.5 mm; length of forewing 7.2-7.5 mm. (1, 2, 7, 9, 13, 15-17) As in *politus*. (3) Eyes convergent below, proportion of LID to UID 0.75-0.78 : 1; inner orbits slightly concave. (4) Proportion of OOL to POL 0.95-1.09 : 1. (5) Lateral ocellus separated from posterior margin of head by 1.3 ocellar diameters. (8) As in *bellus*. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1 : 1.50-1.59. (11) Mesopleuron with appressed, short hairs, as long as diameter of pedicel; usually with a white band below hypoepimeral area, which is polished on lower third. (12) Scutellum bigibbous. (14) Hind coxa with weak carina on apical 0.4 of upper external margin.

Male. Length 10.0-10.7 mm; length of forewing 7.3-9.0 mm. (18) Proportion of LID to UID 0.90-0.91 : 1; inner orbits slightly convex. (19) Proportion of OOL to POL 0.8 : 1. (20) First flagellomere shorter to longer than sum of flagellomeres 2-4, proportion 1 : 0.95-1.13. (21) Hind femur swollen. (22) Apex of T7 emarginate. (25) Genitalia, Figure 32.

Material studied. ARGENTINA. **Catamarca:** 2 females, Punta Balasto, 30 km Santa María, 24-XI-1966, A. Willink (IML). **La Rioja:** 1 male, Patquía, IX-1945, A. Breyer (MACN). **Mendoza:** 1 female lectotype, see data above. **Neuquén:** 1 male, 16 km E Picún Leufú, 5-XII-1987, A. Willink (IML). **Río Negro:** 1 female, Choele Choel, 22-23-XI-1946 (MLP). **Chubut:** 1 male, San Jorge (MACN).

GENUS *ISEPEOLUS* COCKERELL

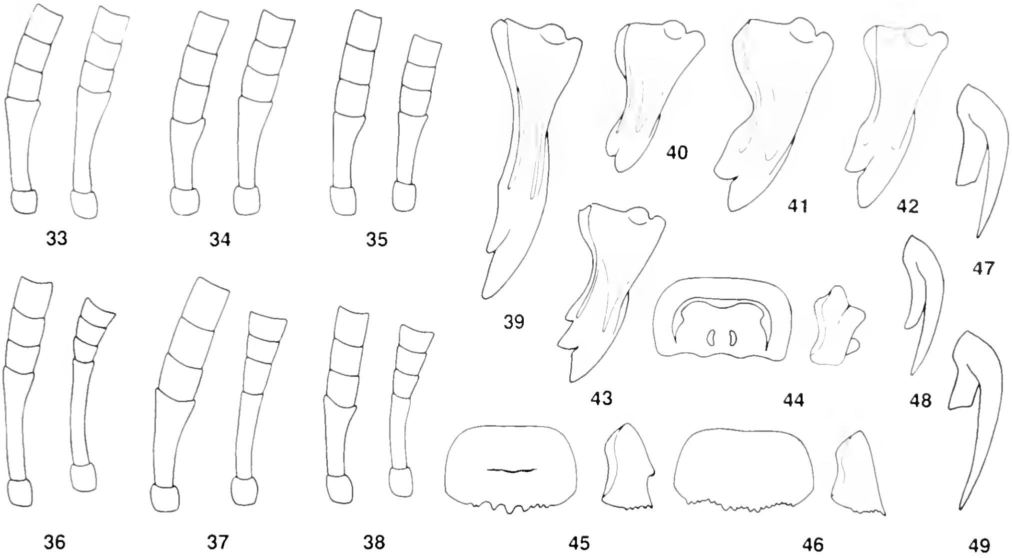
Isepeolus Cockerell, 1907: 64. Type species: *Isepeolus albopictus* Cockerell, 1907 (= *Epeolus viperinus* Holmberg, 1886), by monotypy.

Palinepeolus Holmberg, 1909: 77. Type species: *Epeolus viperinus* Holmberg, 1886, by original designation. **New synonym.**

Calospiloma Brèthes, 1909: 68. Type species: *Epeolus viperinus* Holmberg, 1886, by original designation. Synonymy with *Isepeolus* by Jörgensen, 1912a: 142.

Diagnosis. Length, 6.0-10.5 mm. Head with vertex raised behind ocelli and depressed between lateral ocellus and eye. Gena depressed behind eye. Punctation of vertex variable, dense to sparse with large polished areas. Inner orbit of eye in females concave, converging below, that of males usually sinuous, viz. concave on upper half and convex below. Distance from lateral ocellus to posterior margin of head usually 0.7-1.0 times ocellar diameter. First flagellomere of male slightly widened apically, that of female broadly widened apically. Mandible usually with two subapical teeth (one in *octopunctatus*). Hindcoxa with upper external margin angulate to carinate on apical one-third to one-half. Marginal cell with apex truncate. T5 of female with narrow apical band of dense dark hairs that usually leaves middle triangular area of pale, silky hairs; no membranous rim continuing apex of tergum. Apex of S5 of female densely hairy, medially compressed, with V-shaped notch whose sides frequently are close together forming vertical slit in upturned apical zone. S6 of female with sclerotized apical point sharp, frequently keeled ventrally; lateral apical margin of sternum not folded. S3-4 of male without apical fringes of hairs, or if present, fringes conspicuously weaker than that on S5. S6 of male with subapical tubercle. Gonocoxite of male genitalia with basal constriction.

Three groups of species can be recognized in *Isepeolus*. One of the groups is not supported by synapomorphies; the similarity among its species is most probably due to plesiomorphy. This group includes *I. octopunctatus, septemnotatus* and *bufoninus*. The three species have long black vestiture with a bluish tinge on the head and the thorax; their integument has dense punctation, leaving almost no polished areas around ocelli; the males have eyes with nearly parallel inner orbits, and the subapical tubercle of the male S6 is conical or compressed longitudinally. A second group is formed by *I. cortesi* and *atripilis*. In this group the vein cu-v of the hindwing is 0.7-1.0 times as long as the second abscissa of vein M + Cu, the subapical tubercle of the male S6 is transverse, bilobed, and the males have genitalia with reduced gonostyli. The head of the male is narrow, as wide as the pronotal width (measured at the pronotal lobes); species of the other two groups usually have the head wider than the pronotum. The group comes out from a polytomy in the cladograms (Figs. 1a, b), but if a conical subapical tubercle on the male S6 is taken as plesiomorphic for *Isepeolus* in the context of those topologies, then the transverse tubercle of *cortesi* and *atripilis* would unite them to the next group. The *viperinus* group includes the remaining six species. It is characterized by the presence of short spinelike setae on the female S6 and the transverse, pointed or rounded subapical tubercle of the male S6. Most species in the group have wide polished areas on the vertex and the anterior margin of the scutum.



Figures 33–49. 33–38, pedicel and flagellomeres 1–4 of Isepeolini; female left, male right. 33, *Melectoides senex;* 34, *M. triseriatus;* 35, *M. kiefferi;* 36, *Isepeolus octopunctatus;* 37, *I. bufoninus;* 38, *I viperinus.* 39–43, mandibles of females. 39, *M. senex;* 40, *M. politus;* 41, *M. triseriatus;* 42, *I. octopunctatus;* 43, *I. viperinus.* 44–46, labra of females, front and lateral views. 44, *M. triseriatus;* 45, *I. vachali;* 46, *I. octopunctatus.* 47–49, outer claw of female hind leg. 47, *I. atripilis;* 48, *I. septemnotatus;* 49, *I. octopunctatus.*

Key to the Species of *Isepeolus*

Females

1. Metasoma with white maculation as follows: T1 with apical central band, T2 almost wholly covered except at sides, T3–4 with central white spots and black laterally . . . . 10. *wagenknechti* Toro and Rojas

—Pattern of white maculation on metasoma different, disc of T2 never wholly covered, and maculation on all terga more expanded laterally than mesally, leaving central dark areas 2

2. T5 broad (Fig. 68), its apical width more than half (0.55–0.65) of apical width of T2 3

—T5 (Figs. 67, 69) with apical width less than half (0.3–0.4) of apical width of T2 4

3. Apex of S6 rounded (Fig. 56). First flagellomere shorter than the sum of flagellomeres 2–4 (1 : 1.24–1.30). T4 with white maculae confluent, usually forming continuous band; T5 dorsally with white spots . . . . 8. *lativalvis* (Friese)

—Apex of S6 pointed (as in Fig. 58). First flagellomere subequal to the sum of flagellomeres 2–4 (1 : 1.00–1.04). T4 with white maculation forming 4 separate spots (sometimes only 2); T5 dorsally dark . . . . 9. *smithi* Jörgensen

4. Pleura with hairs black, sometimes with a bluish tinge, at most with a tuft of white hairs covering spiracular entrance 5

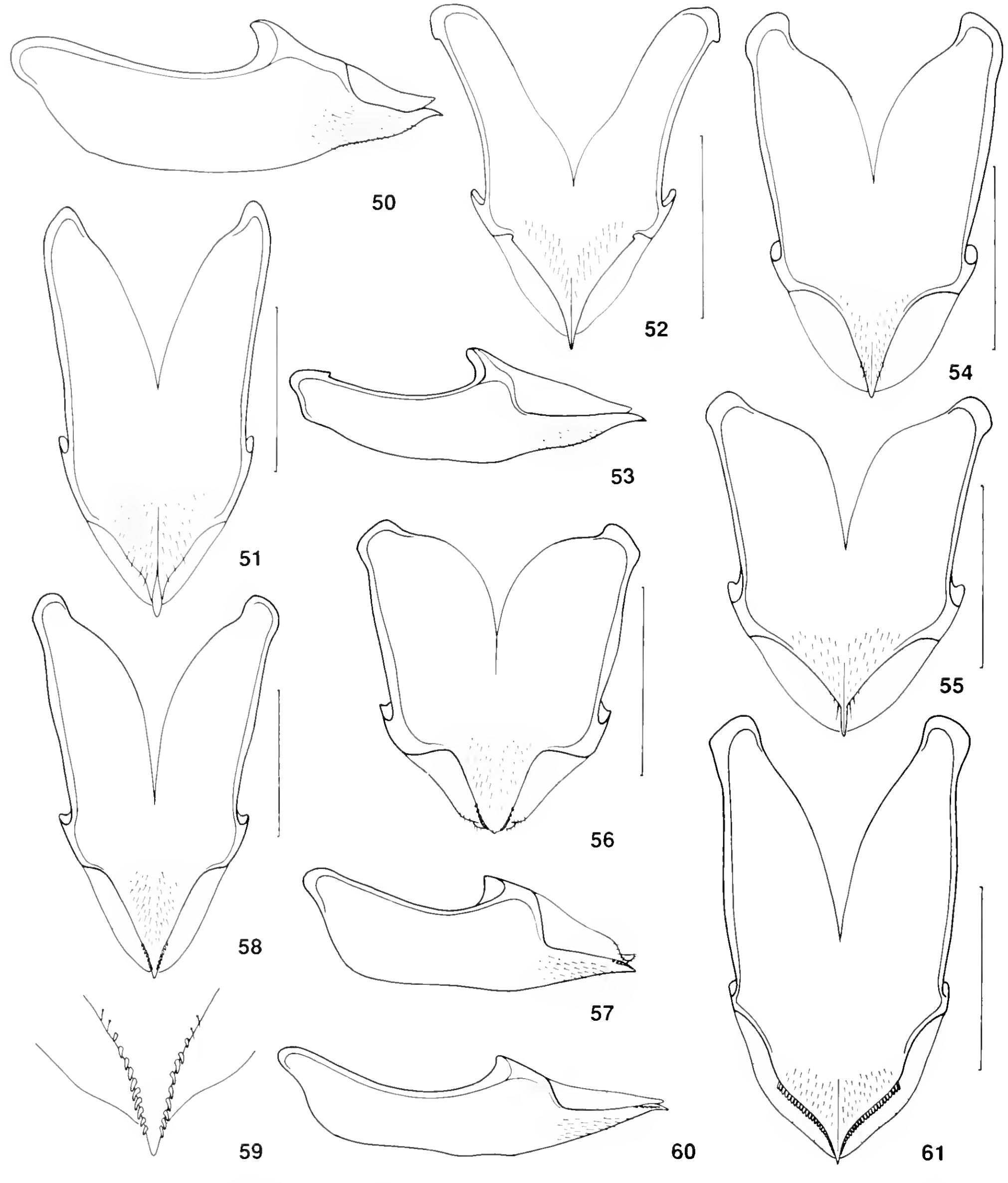
—Pleura with hairs white at least on upper half, no conspicuous bluish tinge 9

5. Punctation on vertex leaving wide polished areas, those between lateral ocellus and eye wider than ocellar diameter. Scutellum bigibbous. S6 with short spinelike setae bordering apical point (seen as serration at low magnification) . . . . 11. *vachali* Jörgensen (part)

—Punctation between and around ocelli dense, almost no polished areas, or such areas less than three-fourths diameter of lateral ocellus. Scutellum usually evenly rounded, sometimes median longitudinal furrow distinct on posterior half. S6 without spinelike setae 6

6. Flagellum black. T2 with white spot at each side and T4 with two apical central spots that can be confluent. Inner tooth of claws narrowly rounded apically (Fig. 48) . . . . 3. *septemnotatus* (Spinola)

—Flagellum reddish. Pattern of white maculation on metasoma different. Inner tooth of claws truncate apically (Figs. 47, 49). 7



Figures 50–61. S6 of *Isepeolus* females, lateral and ventral views. 50, 51, *I. octopunctatus;* 52, 53, *I. septemnotatus;* 54, *I. atripilis;* 55, *I. cortesi;* 56, 57, *I. lativalvis;* 58–60, *I. viperinus,* with detail of apical point of sternum; 61, *I. wagenknechti.* Scale lines 1 mm.

7. Outer ramus of claws elongate, more than twice as long as truncate inner ramus (Fig. 49). Mandible bidentate (Fig. 42). . . . . 1. *octopunctatus* (Jörgensen)
—Outer ramus of claws less than twice as long as inner ramus. Mandible tridentate (Fig. 43) . . . 8
8. Hind wing with vein cu-v and second abscissa of vein M + Cu of similar length. Labrum with blunt transverse elevation on apical third. First flagellomere subequal to sum of flagellomeres 2–4 (1 : 0.93–1.04). S3–4 thoroughly dark . . . . 5. *atripilis* n. sp.
—Hind wing with vein cu-v nearly half as long as second abscissa of vein M + Cu. Labrum flat to slightly concave. First flagellomere shorter than sum of flagellomeres 2–4 (1 : 1.29–1.35). Apex of S3–4 laterally with white hairs . . . . 2. *bufoninus* (Holmberg)

9. Integument of scutellum and metanotum red. Pubescence on terga, other than pale maculations, usually reddish brown. . . . . 6. *viperinus* (Holmberg)

—Integument of scutellum and metanotum black. Pubescence on terga, other than pale maculations, dark brown to black 10

10. Scutum with even, dense punctation. Hind wing with vein cu-v 0.70–0.85 times as long as second abscissa of vein M + Cu. S6 without short spinelike setae bordering apical point (Fig. 55) . . . . 4. *cortesi* Toro and Rojas

—Scutum along anterior margin and along anteromedian lines with polished areas. Hind wing with vein cu-v approximately half (0.46–0.57) as long as second abscissa of vein M + Cu. S6 with short spinelike setae bordering apical point (seen as serration at low magnification) (as in Figs. 58, 59) 11

11. T1 with basal white band and lateral white crescentic or horseshoe-shaped macula at each side, which encloses marginal semicircular black spot; each side of T2 with white macula bearing central black spot (Chile and southern Argentina) . . . . 7. *luctuosus* (Spinola)

—T1 usually with 4 apical white maculae, median ones rectangular, lateral ones sometimes connected to basal white band; T2 with white macula at each side not encircling black spot, even though a notch present (Specimens from northern Argentina may have vaguely formed black spots on T2, but in areas of sympatry with *luctuosus* maculation is distinctive; specimens from southern Argentina run to couplet 5.) . . . . 11. *vachali* Jörgensen (part)

Males

1. Integument of scutellum and metanotum red. Pubescence on terga, other than pale maculation, usually reddish brown . . . . 6. *viperinus* (Holmberg)

—Integument of scutellum and metanotum black. Pubescence on terga, other than pale maculation, dark brown to black 2

2. Hairs of mesopleuron black, with conspicuous bluish tinge. Subapical tubercle of S6 cone-shaped or somewhat compressed longitudinally; hairs dense 3

—Hairs of mesopleuron usually white on upper half, sometimes black, but no bluish tinge. Subapical tubercle of S6 transverse, posteriorly devoid of hairs or at most with hairs sparse (Figs. 77–79) 5

3. Claws of all legs bifid. S4 with apical fringe of hairs restricted to sides. Subapical tubercle of S6 somewhat keeled posteriorly and hairs directed caudally . . . . 3. *septemnotatus* (Spinola)

—Claws of middle and hind legs with inner flattened, apically truncate tooth. S4 with apical fringe of hairs complete. Subapical tubercle of S6 conical, hairs directed downward, parallel to axis of tubercle. 4

4. Outer ramus of claws elongate, more than twice as long as truncate inner ramus (Fig. 49). Mandible bidentate. First flagellomere much longer than sum of flagellomeres 2–4 (1 : 0.57–0.61). . . . . 1. *octopunctatus* (Jörgensen)

—Outer ramus of claws less than twice as long as inner ramus. Mandible tridentate. First flagellomere longer than sum of flagellomeres 2–4 (1 : 0.69–0.86) . . . . . 2. *bufoninus* (Holmberg)

5. Subapical tubercle of S6 in caudal view bilobed (Fig. 77), without posterior longitudinal carina. Triangular polished area contiguous with lateral ocellus at most three-fourths of ocellar diameter 6

—Subapical tubercle of S6 pointed, rounded, or sometimes briefly truncate, usually with posterior longitudinal carina. Triangular polished area contiguous with lateral ocellus extended laterally, as wide as ocellar diameter or wider 7

6. Mesopleuron with hairs black, at most a tuft of white hairs covering entrance of spiracle. T4–6 black. . . . . 5. *atripilis* n. sp.

—Mesopleuron with white hairs on upper half. T4–6 usually with white spots . . . . 4. *cortesi* Toro and Rojas

7. Face below antennal sockets and pleura with hairs black. Metasoma with white maculation usually restricted to T1–2, if present on T3–5, then white hairs on T1–2 forming complete bands across those terga . . . . 10. *wagenknechti* Toro and Rojas

—Face with white hairs below antennal sockets; pleura at least with white hairs above. T1–5 with white maculae, those of T1–2 never forming complete transverse bands 8

8. T2 at each side with white macula bearing central black, round spot, sometimes small; mesal margin of macula without notch. 9

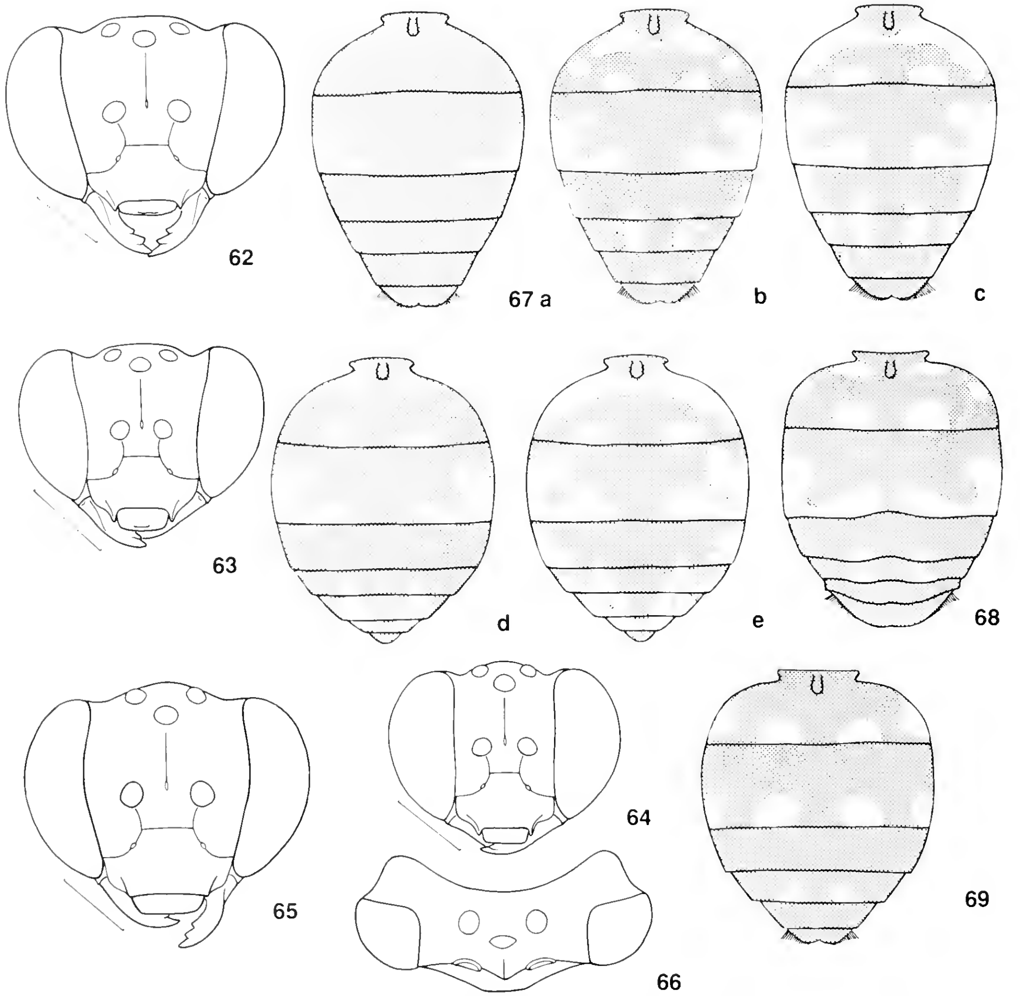
—T2 at each side with white macula that, although having a notch, does not enclose a black spot 10

9. Subapical tubercle of S6 a strong transverse elevation almost reaching sides of sternum (Fig. 79). T7 thoroughly covered by hairs, without bare basal band (Chile and southern Argentina) . . . . 7. *luctuosus* (Spinola)

—Subapical tubercle of S6 smaller (Fig. 78), separated from sides of sternum. T7 with wide bare basal band (tergum needs to be pulled off to observe this band) (central and northern Argentina to Peru; specimens from southern Argentina run to couplet 11) . . . . 11. *vachali* Jörgensen (part)

10. First flagellomere broadened on apical fifth, second flagellomere shorter than its basal width. Apical fringe of S4 with dense, short hairs barely surpassing margin of sternum. T7 usually with hairs white. Subapical tubercle of S6 with some scattered long hairs on posterior surface . . . . 8. *lativalvis* (Friese)

—First flagellomere broadened at very tip, second flagellomere as long as or longer than its basal width. Apical fringe of S4 with long hairs, surpassing margin of sternum. T7 with hairs brown. Subapical tubercle of S6 usually glabrous posteriorly 11



Figures 62–69. 62–66, heads of *Isepeolus* species. 62, *I. atripilis,* female; 63, *I. atripilis,* male; 64, *I. bufoninus,* male; 65, 66, *I. bufoninus,* female. 67–69, pattern of metasomal pubescence of *Isepeolus* species, dorsal view. 67, *I. vachali,* a, female from Río Negro, Argentina, b, female from Catamarca, Argentina, c, female from Moquegua, Perú, d, male from Río Negro, Argentina, e, male from Catamarca, Argentina; 68, *I. smithi,* female; 69, *I. atripilis,* female. Scale lines 1 mm.

11. Lateral border of clypeus weakly lamellated and such lamella not continued above level of anterior mandibular articulation. Outer surface of mandible with basal patch of hairs white with brown spot, dense. T7 thoroughly covered by hairs, without bare basal band . . . . 9. *smithi* Jörgensen

—Lateral border of clypeus conspicuously lamellated, lamella continued above level of anterior mandibular articulation. Outer surface of mandible with basal patch of hairs whitish, thin. T7 with broad bare basal band (tergum needs to be pulled off to observe band) . . . . 11. *vachali* Jörgensen (part)

1. *Isepeolus octopunctatus* (Jörgensen)

(Figs. 37, 42, 46, 49, 50, 51)

Epeolus octopunctatus Jörgensen, 1909: 226. Holotype female, from Chacras de Coria (Prov. Mendoza, Argentina), 11 Nov., Jörgensen leg. (location of type?). Schrottky, 1913: 265.

Isepeolus octopunctatus: Cockerell, 1910: 144. Jörgensen, 1912a: 142-143. Jörgensen, 1912b: 316.

It was not possible to locate the holotype of this species. Jörgensen's original description fits equally well the species described below as *I. atripilis*, but his redescription (1912a) includes an additional character that narrows the possibilities to the present interpretation. The strong blue shine of the body hairs, mentioned by Jörgensen (1912a), readily distinguishes *octopunctatus* from *atripilis*. The present treatment of the species is also supported by a specimen identified by Jörgensen as *octopunctatus* in the Museo de La Plata. The pattern of maculation of the metasoma varies in both species and overlaps to a large extent; I have studied specimens of both species with eight spots on T1-2. The bidentate mandible and the long outer rami of the claws differentiate *octopunctatus* from *atripilis* and all other species of *Isepeolus*.

Female. Length 7.5-10.0 mm; length of forewing 6-8 mm. (3) Proportion of LID to UID 0.81-0.84 : 1. (4) Proportion of OOL to POL 0.85-0.95 : 1. (5) Lateral ocellus separated from posterior margin of head by 0.65-0.70 ocellar diameter. (6) Punctures between and around ocelli dense, leaving no interspaces; narrow polished area around lateral ocellus less than one-quarter of ocellar diameter. (7) Labrum flat to medially weakly elevated on each side of median line; apex denticulate. (8) Malar space 0.1 times as long as mandibular width; anterior articulation of mandible slightly further from eye margin than posterior articulation. (9) Maxillary palpus with three segments, second as long as wide. (10) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.83-0.97. (11) Mesopleuron with hairs erect, black with blue tinge, sometimes with white tuft covering spiracular entrance; hypoepimeral area thoroughly punctate. (12) Scutellum evenly rounded, median longitudinal furrow inconspicuous. (13) Metapostnotum rugose, with upper areolate band narrow, less than one-quarter of width of metanotum. (15) Vein cu-v of hindwing 0.52-0.57 times as long as second abscissa of M+Cu. (17) S6 with apex briefly concave ventrally, keeled basal to concavity; spinelike setae absent.

Male. Length 7-10 mm; length of forewing 7-8 mm. (18) Eyes nearly parallel, proportion of LID to UID 0.9 : 1. (19) Proportion of OOL to POL 0.65-0.69 : 1. (20) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.57-0.61. (22) Apex of T7 triangular, narrowly rounded. (23) S3 with fringe of hairs present, weaker than that of S4. (24) S6 with subapical tubercle conical. (25) Genitalia similar to those of *septemnotatus*.

Material studied. ARGENTINA. **Salta:** 4 males, Cafayate, 19-X-1948, J. Núñez (MLP). **Tucumán:** 3 females, Amaicha, 19-XI-1966, L. Stange (IML); 1 female, Amaicha del Valle, 28-X-1973, J.L. Neff, on flowers of *Prosopis chilensis* (CTMI). **Catamarca:** 3 females, Santa María, 19-X-1948, J. Núñez (MLP). **San Juan:** 1 male, Carpintería, A. Martínez (MF). **Mendoza:** 1 female, Mendoza, 14-III-1908, P. Jörgensen (MLP). **Buenos Aires:** 2 females, Felipe Sola, XI-1942, A. Martínez (MLP). **Río Negro:** 1 female, Lamarque, X-1957, M. Fritz (UFPR). **Santa Cruz:** 1 female, 5.6 km E Los Antiguos, 360 m, 23-XI-1966, Schlinger and Irwin (CAS).

2. *Isepeolus bufoninus* (Holmberg)

(Figs. 37, 64-66)

Epeolus bufoninus Holmberg, 1886b: 283-284. Syntypes, females from Las Conchas, Buenos Aires (Argentina), Feb. 1879, M.O. Cesar and E.L. Holmberg (lost). Dalla Torre, 1896: 328. Schrottky, 1903: 183.

Palinepeolus bufoninus: Holmberg, 1909: 78.

Isepeolus bufoninus: Schrottky, 1913: 264.

Holmberg's detailed description permits recognition of this species in spite of the loss of the types. This species resembles *octopunctatus* in the strong punctation of the head and thorax and the conical subapical tubercle of the male S6, but the scape is shorter in both sexes (see proportions below), the mandible is tridentate, the outer ramus of the claws is less than twice as long as the inner ramus and the apices of S3-4 are clothed laterally with white hairs. Specimens from Argentina have broad white maculae on the metasoma, the lateral macula of the male T2 enclosing a black spot; specimens from Brazil have reduced white areas, the lateral macula of the male T2 being notched, not enclosing a black spot, and the lateral maculae of the female terga being reduced to narrow apical stripes.

Female. Length 8.0–9.5 mm; length of forewing 6.2–7.0 mm. (3) Proportion of LID to UID 0.81–0.83 : 1. (4) Proportion of OOL to POL 0.89–0.9 : 1. (6) As in *octopunctatus.* (7) Labrum with disc flat, apex denticulate. (8) Malar space 0.13 times as long as mandibular width; anterior and posterior articulations of mandible equidistant from margin of eye. (9) Maxillary palpus with 3 segments, second as long as wide. (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.29–1.35. (11, 12) As in *octopunctatus,* but median longitudinal furrow of scutellum distinct on posterior half. (13) Metapostnotum rugose, with strongly areolate upper band one-third as wide as metanotum. (15) Vein cu-v of hindwing 0.52–0.58 times as long as second abscissa of M + Cu. (17) S6 with apex pointed and ventrally keeled; spinelike setae absent.

Male. Length 7.5–9.5 mm; length of forewing 7–8 mm. (18) Eyes nearly parallel, proportion of LID to UID 0.95–1.0 : 1. (19) Proportion of OOL to POL 0.62–0.71 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.69–0.86. (22) Apex of T7 rounded. (23) S3 without fringe of hairs. (24) S6 with subapical tubercle conical. (25) Genitalia similar to those of *septemnotatus,* but gonostylus short, 0.35 times as long as gonocoxite.

Material studied. Argentina. **Buenos Aires:** 1 female, Tigre, 3-XI-1937, A. Ogloblin (MLP); 1 male, Pacheco, 22-X-1925, Muhn (MACN). **Entre Rios:** 1 male, Pronunciamiento, I-1964, J. Foerster (UFPR). Brazil. **Paraná:** 2 females and 2 males, Curitiba, XII-1951, V-1953 and XI-1953, J.S. Moure (UFPR, SEM); 1 male Guarapuava, 1120 m, 8-IX-1955, C.D. Michener (SEM); 1 female, Guarapuava, 7-IX-1955, Michener and Moure (UFPR); 1 male, S. José dos Pinhais, 14-IX-1955, R. Lange (UFPR).

3. *Isepeolus septemnotatus* (Spinola)

(Figs. 48, 52, 53, 71, 72)

Melecta septemnotata Spinola, 1851: 186–187. Type male from Araucanía, Illapel, Chile (not examined). Reed, 1892: 228. Dalla Torre, 1896: 318. Ducke, 1912: 102.

Epeoloides septemnotatus: Friese, 1906b: 172. Friese, 1908: 88–89. Friese, 1912b: 364. Herbst, 1917: 269. Claude-Joseph, 1926: 268. Janvier, 1933: 326.

Isepeolus septemnotatus Grütte, 1935: 501. Toro and Rojas, 1968: 60.

I have not seen type material of this species, but its identity is clear. The pattern of maculation of the metasoma described by Spinola is diagnostic for the species. He also mentioned that the claws are bifid, *I. septemnotatus* being the only species in the tribe with such claws. The subapical tubercle of the male S6 is also characteristic for the species (see 24 below).

Female. Length 8.0–9.5 mm; length of forewing 6.2–7.0 mm. (3) Proportion of LID to UID 0.85–0.88 : 1. (4) Proportion of OOL to POL 0.76–0.9.0 : 1. (6) As in *octopunctatus.* (7) Labrum with median transverse carina somewhat arched down at sides, surface below carina concave; apex feebly denticulate. (8) As in *octopunctatus.* (9) Maxillary palpus with 4 segments, second three times as long as wide. (10) First flagellomere subequal to sum of flagellomeres 2–4, proportion 1 : 0.97–1.0. (11) Mesopleuron with hairs erect, black with blue tinge; hypoepimeral area thoroughly punctate. (12) Scutellum evenly rounded, median longitudinal furrow distinct on posterior half. (13) Metapostnotum rugose, with upper band strongly areolate, half as wide as metanotum. (15) Vein cu-v of hindwing 0.53–0.55 times as long as second abscissa of M + Cu. (17) S6 with apex pointed, ventrally with longitudinal keel; spinelike setae absent.

Male. Length 7.5–9.5 mm; length of forewing 6.5–7.5 mm. (18) Eyes nearly parallel, proportion of LID to UID 0.94–1.0 : 1. (19) Proportion of OOL to POL 0.63–0.67 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.61–0.67. (22) Apex of T7 rounded. (23) S3–4 without fringes of hairs. (24) S6 with subapical tubercle compressed longitudinally, posteriorly carinate; hairs dense, those surrounding carina directed caudally. (25) Genitalia, Figure 71.

Material studied. Chile. **Coquimbo:** 3 females, Hacienda Illapel, 600–900 m, 19-X-1966, Schlinger, Irwin and Peña (CAS). **Valparaíso:** 1 male, Marga Marga, 21-IX-1923, P. Herbst (CAS); 1 female and 2 males, Valparaíso, 18-IX-1914, P. Herbst (CAS). **Aconcagua:** 1 male, Río Blanco, Piscicultura, XI-1963, Peña (UFPR). **Santiago:** 1 female, El Manzano, 23-XII-1968, J. Valencia (MF). **Talca:** 3 females, El Radal, 1100 m, 23-30-X-1957, L. Peña (SEM). **Linares:** 4 females and 2 males, Romehual, Cord. Parral, XI-1960, L. Peña (UFPR). **Valdivia:** 1 female, Santo Domingo, 18-XI-1984, E. Krahmer (MF). **Cautín:** 1 female, Lago Budi, 1923, P. Herbst, "aus Zelle von *Colletes musculus* Friese gezüchtet" (CAS); 1 male, Temuco, 1923, P. Herbst, "aus Zelle von *Colletes seminitidus* Spin. gezüchtet" (CAS). Argentina. **Río Negro:** 1 female, Isla Victoria, 19-XII-1944, on flowers of *Fragaria* (MLP); 1 male, El Bolsón, 20-I-1964, A. Kovacs (UCV); 1 male, Bariloche, XI-1975, R.M. Bohart (Davis).

4. *Isepeolus cortesi* Toro and Rojas

(Fig. 55)

Isepeolus cortesi Toro and Rojas, 1968: 58–60, figs. 1–5. Holotype male from El Salto, Valparaíso, Chile, Oct. 1967, H. Toro and E. de la Hoz (H. Toro collection, not examined).

This species is closely related to *atripilis,* from which it is readily differentiated by the more extended white pubescence on the scutum, the pleura and the metasomal terga. Females of *cortesi* can be distinguished by the lack of spinelike setae on the apex of S6 and the white hairs on the upper half of the mesopleuron. The males are characterized by the bilobate subapical tubercle of S6 and the reduced gonostylus. This is the smallest species in the genus; some males are scarcely 6 mm long.

Female. Length 6.5–7.5 mm; length of forewing 5.2–5.7 mm. (3) Proportion of LID to UID 0.72–0.75 : 1. (4) Proportion of OOL to POL 0.85–0.95 : 1. (6) Punctures between and around ocelli dense, leaving no interspaces to interspaces one-quarter as wide as diameter of punctures; polished triangular area between lateral ocellus and eye less than ocellar diameter. (7) Labrum transversely elevated on apical third, but without carina; apex feebly denticulate. (8) As in *octopunctatus*. (9) Maxillary palpus with 3 segments, second as long as wide. (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.08–1.12. (11) Mesopleuron with hairs white on upper half; hypoepimeral area punctate, with small polished area above scrobe. (12) Scutellum evenly rounded, median longitudinal furrow inconspicuous, sometimes hairs give it bigibbous appearance. (13) Metapostnotum tessellate, sometimes polished on lower fourth. (15) Vein cu-v of hindwing 0.70–0.82 times as long as second abscissa of M+Cu. (17) S6 with apex pointed, ventrally keeled; spinelike setae absent, but some stiff setae present.

Male. Length 6–8 mm; length of forewing 5.8–6.5 mm. (18) Eyes convergent below, proportion of LID to UID 0.83–0.84 : 1. (19) Proportion of OOL to POL 0.71–0.73 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.58–0.61. (22) Apex of T7 rounded. (23) S3 without fringe of hairs. (24) S6 with subapical tubercle bilobed. (25) Genitalia, figure 4 in Toro and Rojas (1968).

Material studied. CHILE. **Coquimbo:** 1 male, Fray Jorge, 10-X-1977, De la Hoz (UCV). **Valparaíso:** 1 female paratype, El Salto, 17-X-1967, De la Hoz (UCV); 1 female, Peñuelas, 7-XII-1967, H. Toro (UCV). **Curicó:** 1 female, 6 km E Los Queñes, 4-I-1967, M.E. Irwin (CAS). ARGENTINA. **Neuquén:** 1 male, Paso Coihue, 5-I-1964, A. Giai (SEM); 1 female, Laguna Blanca, 23-XII-1965, A. Giai (SEM). **Río Negro:** 1 female, 30 km E Bariloche, 16-XI-1964, A. Giai (SEM).

5. *Isepeolus atripilis* n. sp.

(Figs. 47, 54, 62, 63, 69, 75–77)

This species is related to *cortesi* as indicated by the reduced male gonostylus, the hindwing with a short second abscissa of vein M+Cu and the bilobate subapical tubercle of the male S6. The female may be confused with dark specimens of *vachali,* from which it is distinguished by the evenly rounded scutellum and the hindwing venation. It may also be confused with *octopunctatus,* as noted under the latter species. Measurements in parentheses below correspond to the holotype; for other variable characters the holotype condition is indicated by italics.

Female. Length 7–10 (8.7) mm; length of forewing 5.5–7.5 (7) mm. Integument black, apex of mandible, distotarsi and sometimes tegula reddish brown; pedicel and flagellum reddish. Wings hyaline, weakly infuscated beyond closed cells; veins and pterostigma dark brown to black. *Vestiture* black, some specimens completely so, but others with the following parts white: some hairs above antennal sockets, vertex, pronotal lobes, *scutum on* anterior and *posterior margins and above tegula, scutellum along median line,* metanotum at sides, *spot on tegula,* a tuft on mesopleuron covering spiracular entrance, *4 apical spots on T1 and T2,* central ones sometimes missing, sometimes 2 apical median spots on T4 (Fig. 69), and apices of femora and tibiae. *Sculpture.* Punctation dense and even, on mesopleuron leaving no interspaces, on scutum leaving interspaces half as wide as to as wide as diameter of punctures. *Morphology.* (3) Proportion of LID to UID 0.71–0.76(0.76) : 1. (4) Proportion of OOL to POL 0.83–0.93(0.88) : 1. (6) Punctation between and around ocelli dense, almost no interspaces among punctures; polished triangular area between lateral ocellus and eye narrower than ocellar diameter. (7) Labrum with weak transverse elevation on apical third; apex feebly denticulate. (8) Malar space 0.13 times as long as mandibular width; anterior articulation of mandible slightly further from eye margin than posterior articulation. (9) Maxillary palpus with 3 or sometimes a fourth minute segment, second as long as wide. (10) First flagellomere subequal to sum of flagellomeres 2–4, proportion 1 : 0.93–1.04(1.04). (11) *Mesopleuron with hairs black,* sometimes white hairs covering spiracular entrance; hypoepimeral area punctate, with small polished area above scrobe. (12) Scutellum evenly rounded, median longitudinal furrow inconspicuous. (13) Metapostnotum tessellate, polished on lower fourth. (15) Vein cu-v of hindwing 0.75–1.00 times as long as second abscissa of M+Cu. (17) S6 with apex pointed, ventrally keeled; spinelike setae absent, but a few stiff setae bordering point.

Male. Length 7.5–8.5 mm; length of forewing 6.5–7.5 mm. (18) Eyes converging below, proportion of LID to UID 0.85–0.87 : 1. (19) Proportion of OOL to POL 0.70–0.72 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.64–0.67. (22) Apex of T7 rounded. (23) S3 without fringe of hairs. (24) S6 with subapical tubercle bilobed. (25) Genitalia, Figure 75.

Material studied. Holotype female, Paso Córdoba, Río Negro, Argentina, 24-I-1975, A. Willink and G. Claps (IML). Paratypes. ARGENTINA. **Tucumán:** 1 male, road Tafí-Amaicha km 90, 17-XII-1973, L. Stange, on flowers of *Adesmia inflexa* (IML). **Catamarca:** 2 females, La Ciénaga, 26-XI-1975, R.M. Bohart (Davis); 1 female, Cuesta Mina Capillitas, 2300 m, 17-XI-1972, J.L. Neff, on flowers of *Glandularia microphylla* (CTMI); 1 female, El Desmonte, 7-XI-1989, J.G. Rozen and A. Roig A. (AMNH). **Mendoza:** 1 female, Punta de Vacas, 9-I-1980, E. Domínguez (IML); 1 female, Puente del Inca, 2700 m, 26-I-1973, A. Willink (IML); 1 male, Quebrada Horcones, 2900 m, 10-I-1985, A. Roig A. (MACN). **Buenos Aires:** 1 male, Patagones, J.M. Viana (MACN). **Neuquén:** 2 females, Confluencia Traful, 20-XII-1964, A. Giai (SEM). **Río Negro:** 1 female and 1 male, same data as holotype (IML); 3 males, Río Colorado, 13-21-II-1946, Hayward and Willink (MLP); 1 female and 1 male, Luis Beltrán, XI-1987, M. Fritz (MF). **Santa Cruz:** 1 female, Lago Argentino, 13-I-1953, A. Willink (IML). CHILE. **Magallanes:** 1 female, 4 km W Laguna Amarga, 8-XII-1966, Irwin and Schlinger (CAS).

6. *Iseopeolus viperinus* (Holmberg)
(Figs. 38, 43, 58-60, 70, 73, 74)

Epeolus viperinus Holmberg, 1886a: 155-156. Holotype female, from Tandil (Prov. Buenos Aires, Argentina), I-29-1883 (MACN, examined). Holmberg, 1886b: 282-283. Dalla Torre, 1896: 333. Schrottky, 1903: 183.

Leiopodus depressiventris Ducke, 1907: 88. Lectotype female, by present designation, from Barbacena, Minas Gerais (Brazil), 23-XI-1905, A. Ducke (Bern, examined). Ducke, 1908a: 102-103. Ducke, 1908c: 79. **New synonym.**

Isepeolus albopictus Cockerell, 1907: 65. Holotype male from Carcarañá, Argentina (USNM, type number 55258, examined). **New synonym.**

Calospiloma viperinum: Brèthes, 1909: 68.

Palinepeolus viperinus: Holmberg, 1909: 78.

Epeolus depressiventris: Ducke, 1910: 104.

Isepeolus depressiventris: Ducke, 1912: 100. Grütte, 1935: 501.

Isepeolus viperinus: Jörgensen, 1912b: 316. Schrottky, 1913: 264. Grütte, 1935: 501. Michener, 1957: 141-146. Rozen, 1966: 10-12. Oliveira, 1966: 163-176. Rozen et al., 1978: 10-16. Alexander, 1990: 144.

The holotype of *I. viperinus* lacks the abdomen and bears the following two labels: "I-29" and "*Epeolus viperinus*, Tandil."

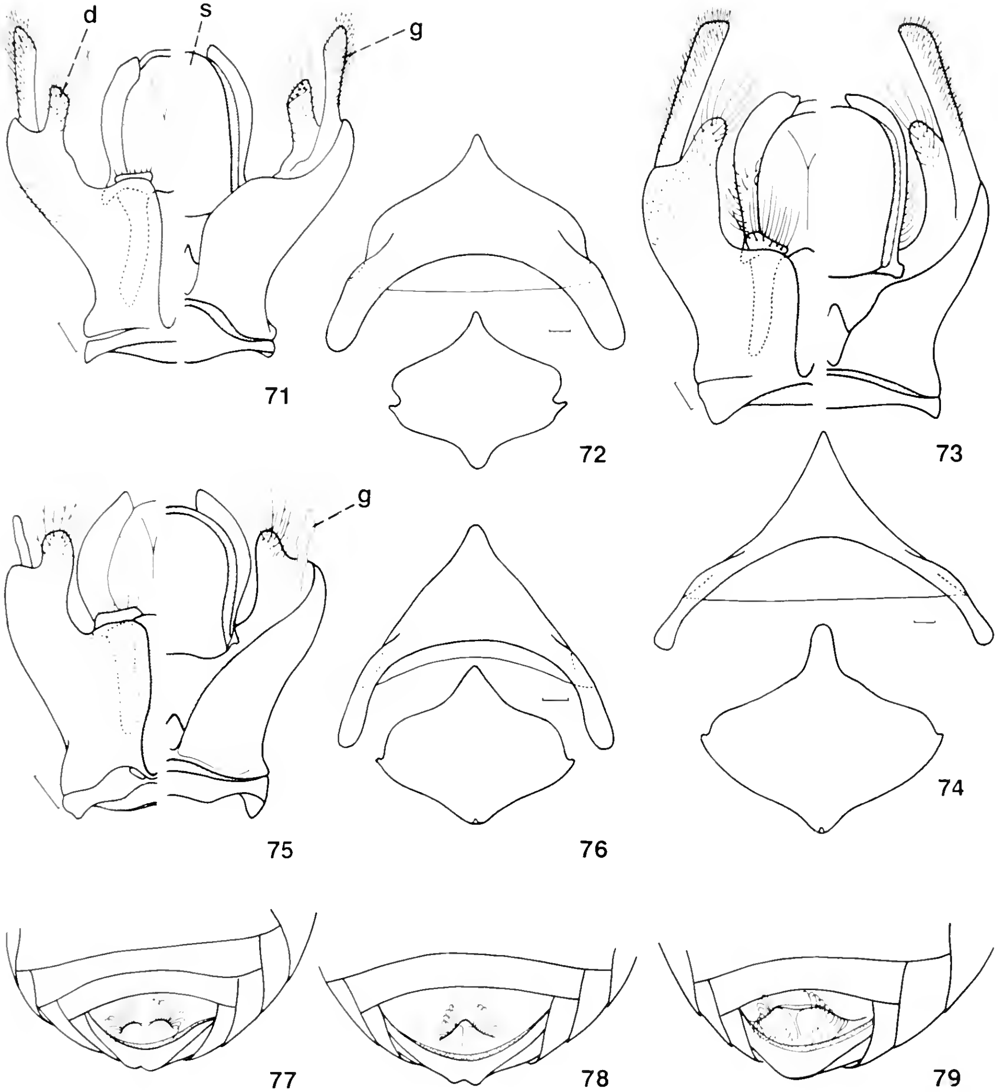
This is the only *Isepeolus* species that has the integument of the scutellum and the metanotum red. Some specimens may also have the pronotum, the scutum and the pleura red in a variable extent. The pattern of maculation is fairly constant; specimens from Colombia look almost identical to specimens from the type locality in Argentina. The subapical tubercle of the male S6 is usually transverse and glabrous posteriorly, but specimens from southern Argentina (Río Negro and Chubut) have the tubercle conical and thoroughly hairy, much as in *octopunctatus*. The hind femur of the male seems to follow an allometric pattern, being conspicuously swollen in large specimens.

Female. Length 6.5-10.0 mm; length of forewing 5.0-7.5 mm. (3) Proportion of LID to UID 0.80-0.85 : 1. (4) Proportion of OOL to POL 0.87-0.89 : 1. (6) Punctures sparse, between and around ocelli mostly polished; sometimes between front ocellus and vertex with longitudinal rugose area with no definite punctures; polished triangular area between lateral ocellus and eye wider than ocellar diameter. (7) Labrum medially elevated, with 2 conspicuous denticles, below denticles concave; apical margin denticulate. (8) Malar space 0.1 times as long as mandibular width; anterior articulation of mandible twice as far from eye margin as posterior articulation. (9) Maxillary palpus with 3 poorly defined segments, second and third forming an ovoid structure. (10) First flagellomere shorter than sum of flagellomeres 2-4, proportion 1 : 1.24-1.30. (11) Mesopleuron with hairs white on upper half, but in front of hypoepimeral area a distinctive brown spot; hypoepimeral area with small polished area above scrobe. (12) Scutellum bigibbous. (13) Metapostnotum rugose, sometimes polished on lower fourth or less. (15) Vein cu-v of hindwing 0.48-0.58 times as long as second abscissa of M + Cu. (17) S6 with apex pointed, no ventral keel; with short spinelike setae bordering point.

Figure 70. Distribution of *Isepeolus viperinus.*

Male. Length 6.5-10.0 mm; length of forewing 5.5-8.0 mm. (18) Eyes converging below, proportion of LID to UID 0.87-0.89 : 1. (19) Proportion of OOL to POL 0.81-1.13 : 1. (20) First flagellomere longer than sum of flagellomeres 2-4, proportion 1 : 0.66-0.73. (22) Apex of T7 emarginate. (23) S3 without fringe of hairs. (24) S6 with subapical tubercle transverse, triangular to almost conical. (25) Genitalia, Figure 73.

Material studied (Fig. 70). Colombia. **Valle:** 1 female, Cali, 8-I-1972, C.D. Michener (SEM); 1 female, Mun. Candelaria, 1010 m, Lago San Luis, 4-6-IV-1975, R. Wilkerson (Gainesville). Brazil. 38 specimens from the states of Ceará, Bahia, Minas Gerais, São Paulo, Paraná and Santa Catarina (collection dates August to March). Argentina. 304 specimens from the provinces of Jujuy, Salta, Tucumán, Catamarca, La Rioja, Santiago del Estero, Córdoba, San Juan, Mendoza, San Luis, Entre Ríos, Santa Fe, Buenos Aires, La Pampa, Río Negro, Neuquén and Chubut (collection dates September to April).



Figures 71–79. 71–76, Genitalia (ventral left, dorsal right), S7 and S8 of *Isepeolus* males; g, gonostylus; s, spatha; d, digitiform ventral lobe; sparser stippling indicates partially sclerotized ventral surface of penis. 71, 72, *I. septemnotatus;* 73, 74, *I. viperinus;* 75, 76, *I. atripilis.* 77–79, Apex of male metasoma, ventral view showing subapical tubercle of S6. 77, *I. atripilis;* 78, *I. vachali;* 79, *I. luctuosus.* Scale lines 0.1 mm.

7. *Isepeolus luctuosus* (Spinola)
(Figs. 79, 80)

Epeolus luctuosus Spinola, 1851: 189–190. Types: male and female, from Provincias del Norte, Coquimbo, Chile (not examined). Smith, 1854: 258. Reed, 1892: 229. Dalla Torre, 1896: 329. Herbst, 1917: 269. Gazulla and Ruiz, 1928: 301, 302. Ruiz, 1936: 168.

Leiopodus luctuosus: Ducke, 1908b: 39.

Calospiloma luctuosum: Brèthes, 1909: 68.

Isepeolus luctuosus: Cockerell, 1910: 144. Ducke, 1912: 100. Schrottky, 1913: 264. Claude-Joseph, 1926: 267. Janvier, 1933: 325. Grütte, 1935: 501. Toro and Rojas, 1968: 60. Alexander, 1990: 139, 144, fig. 9a, b.

I have not seen types of *I. luctuosus,* but Spinola's original description leaves no doubt about its identity. He describes in detail the pattern of coloration, which cannot be confused with that of any other Chilean species. The lateral white maculae on T1–2 encircling central black spots are particularly distinctive.

Female. Length 7.5–10.0 mm; length of forewing 6.0–7.5 mm. (3) Proportion of LID to UID 0.70–0.76 : 1. (4) Proportion of OOL to POL 1.05–1.17 : 1. (6) Punctation between and around ocelli variable, from extensively polished to moderately punctate; triangular polished area between lateral ocellus and eye as wide as or wider than ocellar diameter. (7–9) As in *viperinus.* (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.31–1.39. (11) Mesopleuron with hairs white on upper half; hypoepimeral area with small polished area above scrobe. (12) Scutellum bigibbous. (13) Metapostnotum as in *viperinus,* but with upper areolate band one-third as wide as metanotum. (15) Vein cu-v of hindwing 0.53–0.56 times as long as second abscissa of M+Cu. (17) As in *viperinus.*

Male. Length 6.2–9.5 mm; length of forewing 5.4–8.0 mm. (18) Eyes converging below, proportion of LID to UID 0.83–0.90 : 1. (19) Proportion of OOL to POL 0.79–0.84 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.71–0.87. (22) Apex of T7 rounded. (23) S3 without fringe of hairs, fringe on S4 weak. (24) S6 with subapical tubercle as strong transverse elevation almost reaching margin of sternum; tubercle posteriorly usually carinate. (25) As in *viperinus.*

Material studied (Fig. 80). Chile. 93 specimens from the provinces of Copiapó, Coquimbo, Valparaíso, Santiago, Ñuble, Curicó, Malleco, Concepción and Llanquihue (collection dates October to February). Argentina. 22 specimens from the provinces of Neuquén, Río Negro and Chubut (collection dates January to April).

8. *Isepeolus lativalvis* (Friese)
(Figs. 56, 57)

Epeolus lativalvis Friese, 1908: 83. Lectotype female, by present designation, from Concepción, Chile, 27-XII-1907, Herbst leg. (Berlin, examined). Schrottky, 1913: 264.

Isepeolus lativalvis: Grütte, 1935: 501. Toro and Rojas, 1968: 60.

Friese based *lativalvis* on specimens from Tucumán (Argentina) and Concepción (Chile). A female from the latter locality is selected as the lectotype, following current usage of the name. A syntype specimen from Tucumán (the printed label is overwritten "Mendoza") in the Berlin collection, labeled *lativalvis* by Friese, corresponds to *Melectoides cockerelli* (Jörgensen). *I. lativalvis* as presently delimited occurs in Chile and southern Argentina.

This species together with *smithi* is easily recognized by the broad, rounded apex of the female abdomen. It is distinguished from *smithi* and all other *Isepeolus* by the female S6 which is apically rounded, with a blunt median point.

Female. Length 7.5–8.5 mm; length of forewing 5.5–6.0 mm. (3) Proportion of LID to UID 0.75–0.77 : 1. (4) Proportion of OOL to POL 0.94–0.95 : 1. (6, 7) As in *luctuosus,* but median denticles of labrum usually weak. (8) Malar space 0.1 times as long as mandibular width; anterior articulation of mandible slightly further from eye margin than posterior articulation. (9) As in *luctuosus.* (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.24–1.30. (11, 12) As in *luctuosus.* (13) As in *luctuosus,* but upper areolate band narrow. (15) Vein cu-v of hindwing 0.5–0.6 times as long as second abscissa of M+Cu. (16) Apical width of T5 more than half of apical width of T2. (17) S6 with apex rounded, no ventral keel; short spinelike setae bordering apex present.

Male. Length 6.8–8.0 mm; length of forewing 5.5–6.3 mm. (18) Eyes converging below, proportion of LID to UID 0.87 : 1. (19) Proportion of OOL to POL 0.72–0.75 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.62–0.69. (22) Apex of T7 emarginate. (23) S3 and S4 without fringes of hairs. (24) S6 with subapical tubercle triangular, transverse, usually posteriorly carinate. (25) As in *viperinus.*

Material studied. Chile. **Santiago:** 2 males, Santiago, F. Ruiz (ZMC). **Ñuble:** 1 female and 1 male, 5.6 km N Cobequecura, 29-I-1976, L. Stange (IML). **Curicó:** 1 female, 15-I-1924, P. Herbst (CAS). **Malleco:** 1 female, Vegas Blancas, 21-XII-1985, A. Roig-A. (MACN). **Bio Bio:** 1 female, Los Angeles, I-1953, M. Fritz (MLP). **Cautín:** 1 female and 3 males, 20 km E Temuco, 7-I-1951, Ross and Michelbacher (CAS). **Llanquihue:** 1 female, Lepihue, 21-I-1951, Ross and Michelbacher (CAS). Argentina. **Neuquén:** 1 male, Hua Hum, Parque Nac. Lanín, 12-1-1950, Schajovskoi (MLP); 1 male, San Martín de Los Andes, 5-XII-1980, M. Gentili (MACN); 4 males, Catán Lil, 15-I-1954, M. Senkute (SEM). **Río Negro:** 1 male, Bariloche, M. Fritz (MF); 1 male, El Bolsón, II-1955, J. Foerster (SEM).

9. *Isepeolus smithi* Jörgensen

(Fig. 68)

Isepeolus smithi Jörgensen, 1912a: 146–147, fig. D. Lectotype male, by present designation, from Mendoza (Argentina), 28-X-1908, Jörgensen leg. (MLP, examined). Jörgensen, 1912b: 316.

This species is closely allied to *lativalvis*, from which it is distinguished by the sharp pointed apex of the female S6. The male is distinguished by the margin of the clypeus not continuing as a carina above the level of the anterior mandibular articulation, and the mandible with a dense basal patch of hairs, which is white with a characteristic brown spot.

Female. Length 7.5–8.5 mm; length of forewing 6.0–6.5 mm. (3) Proportion of LID to UID 0.74–0.75 : 1. (4) Proportion of OOL to POL 1.06–1.12 : 1. (6) Punctures sparse, area between and around ocelli mostly polished; polished triangular area between lateral ocellus and eye subequal to ocellar diameter. (7–9) As in *lativalvis*. (10) First flagellomere subequal to sum of flagellomeres 2–4, proportion 1 : 1.00–1.04. (11) Mesopleuron with variable amount of white hairs, wholly black to white on upper half leaving a dark spot anterior to hypoepimeral area; hypoepimeral area with small polished area above scrobe. (12) Scutellum slightly bigibbous, median longitudinal furrow weak. (13) As in *lativalvis*. (15) Vein cu-v of hindwing 0.50–0.62 times as long as second abscissa of M + Cu. (16) T6 distinctively wide, as in *lativalvis*. (17) S6 with apex pointed, sharp, ventral keel present; spinelike setae present.

Male. Length 6.8–7.5 mm; length of forewing 5.8–6.3 mm. (18) Eyes converging below, proportion of LID to UID 0.84–0.88 : 1. (19) Proportion of OOL to POL 0.91–0.97 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.68–0.69. (22) Apex of T7 emarginate. (23) S3 without fringe of hairs, present on S4. (24) As in *lativalvis*. (25) As in *viperinus*.

Material studied. Argentina. **Tucumán:** 1 female, Alto del Tío, Tafí-Amaicha road, 2700 m, 6-III-1968, A. Willink (IML). **Catamarca:** 1 female, Cuesta Mina Capillitas, 17-XII-1972, J.L. Neff (CTMI). **Mendoza:** 1 female, Villavicencio, 20-XI-1941 (MLP); 3 males, Uspallata, 6-XII-1979, A. Roig-A. (MACN); 3 males, Uspallata, 6-XII-1979, C. and M. Vardy (London). **Buenos Aires:** 1 female and 6 males, Patagones, M.J. Viana (MACN, SEM). **Neuquén:** 1 female, Mariano Moreno, 750 m, 16-XII-1966, Irwin and Schlinger (CAS). **Río Negro:** 1 male, Río Colorado, 13-21-II-1946, Hayward and Willink (MLP); 1 female, Luis Beltrán, XI-1987, M. Fritz (MF). **Chubut:** 3 males, 13 km N Puerto Madryn, 14-XII-1966, Irwin and Schlinger (CAS).

10. *Isepeolus wagenknechti* Toro and Rojas

(Fig. 61)

Isepeolus wagenknechti Toro and Rojas, 1968: 55–58. Holotype female from Quebrada Honda, Coquimbo, Chile, 10 Nov. 1957, R. Wagenknecht (H. Toro collection, not examined). Toro, 1971: 261–262, figs. 1–3.

This species has a color pattern that makes it easily distinguishable from related forms in which the female S6 bears short spinelike setae and the male S6 has a transverse subapical tubercle. The color pattern of *I wagenknechti* much resembles that of *Melectoides niveiventris*. The vestiture is deep black, except for most of the dorsum of the body, which has white hairs; the metasomal T1–2 have broad white uninterrupted bands and T3–4 have median white spots.

Female. Length 9–10 mm; length of forewing 6.8–7.2 mm. (3) Proportion of LID to UID 0.74–0.76 : 1. (4) Proportion of OOL to POL 0.80–0.81 : 1. (6) Punctures between and around ocelli dense; polished triangular area between lateral ocellus and eye subequal to ocellar diameter. (7) As in *viperinus*. (9) Maxillary palpus with second segment longer than wide, distinct from third; a fourth minute segment may be present in some specimens. (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.11–1.18. (11) Mesopleuron with hairs black; hypoepimeral area punctate. (12) Scutellum bigibbous. (13) Metapostnotum rugose, with upper areolate band as wide as half of metanotum. (15) Vein cu-v of hindwing 0.45–0.52 times as long as second abscissa of M + Cu. (17) S6 with apex pointed, ventral keel present; short spinelike setae present.

Male. Length 7.5–8.0 mm; length of forewing 6.0–6.6 mm. (18) Eyes converging below, proportion of LID to UID 0.84–0.87 : 1. (19) Proportion of OOL to POL 0.68–0.71 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.74–0.80. (22) T7 with bare basal band present, apex rounded. (23) S3 without fringe of hairs. (24) S6 with subapical tubercle transverse, low, medially elevated and with longitudinal carina posteriorly. (25) Genitalia, figure 3 in Toro (1971).

Material studied. Chile. **Atacama:** 4 males, 20 km SE Caldera, 16-X-1957, L. Peña (SEM). **Coquimbo:** 1 female, Quebrada Los Choros, 12-X-1977, L. Ruz (UCV); 1 female, Loros Bajos, La Serena, 9-XI-1961, R. Wagenknecht (UCV).

11. *Isepeolus vachali* Jörgensen

(Figs. 45, 67, 78, 80)

Isepeolus vachali Jörgensen, 1912a: 143–144, fig. B. Lectotype female, by present designation, from Chacras de Coria, Mendoza (Argentina), 17-X-1908, Jörgensen leg. (MLP, examined). Jörgensen, 1912b: 316.

Isepeolus viecki Jörgensen, 1912a: 147–148, fig. E. Lectotype female, by present designation, from Mendoza (Argentina), 17-X-1908, Jörgensen leg. (MLP, examined). Jörgensen, 1912b: 316. **New synonym.**

Isepeolus vierecki Cockerell, 1917: 479 (emendation).

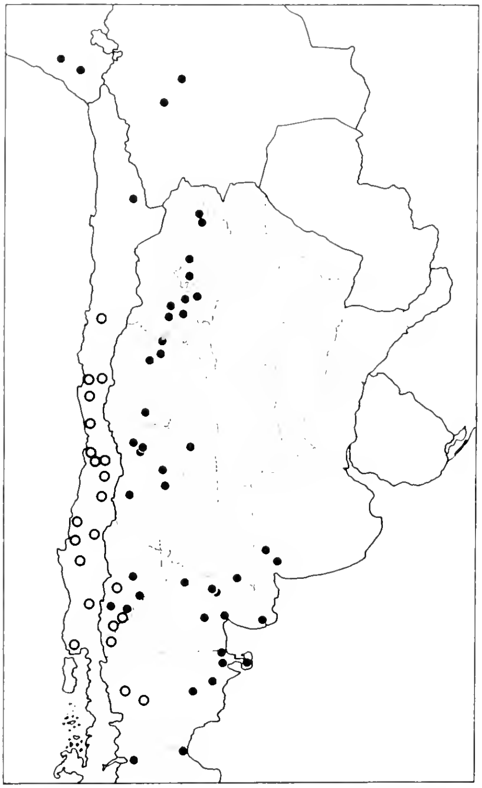


Figure 80. Distributions of *Isepeolus luctuosus* (open circles) and *I. vachali* (dots).

This species shows considerable variation in the color pattern. The vestiture is extensively white in specimens from Perú to central Argentina, while specimens from southern Argentina (Neuquén, Río Negro and Chubut) have white vestiture reduced. Southern specimens are less variable in size, averaging 8–10 mm in length; elsewhere the size range is broader, probably due to exploitation of more than one host. Small pale specimens, common in northern Argentina, look quite different from the mostly black, large specimens from the south. I have not found any morphological features suggesting that this is not a single species. Populations from Mendoza are particularly variable, and most intermediates in color and size can be found. This species is related to *wagenknechti* by the male T7 which has a broad bare basal band.

Female. Length 6.5–10.5 mm; length of forewing 5–8 mm. (3) Proportion of LID to UID 0.71–0.81 : 1. (4) Proportion of OOL to POL 1.03–1.21 : 1. (6, 7–9) As in *viperinus,* but sometimes median denticles of labrum forming single strong projection. (10) First flagellomere shorter than sum of flagellomeres 2–4, proportion 1 : 1.18–1.35. (11) Mesopleuron with variable amount of white hairs; hypoepimeral area as in *viperinus.* (12, 13) As in *viperinus,* but upper areolate band one-third as wide as metanotum. (15) Vein cu-v of hindwing 0.46–0.57 times as long as second abscissa of M+Cu. (17) As in *viperinus.*

Male. Length 6.5–10.0 mm; length of forewing 6.0–8.7 mm. (18) Eyes converging below, proportion of LID to UID 0.84–0.9 : 1. (19) Proportion of OOL to POL 0.71–0.79 : 1. (20) First flagellomere longer than sum of flagellomeres 2–4, proportion 1 : 0.63–0.71. (22) T7 with basal bare band present, apex emarginate. (23) S3 without fringe of hairs. (24) S6 with subapical tubercle transverse, triangular, usually with posterior longitudinal carina. (25) As in *viperinus.*

Material studied (Fig. 80). PERU. **Arequipa:** 1 female, Yura, 12-X-1983, A. Roig-A. (MACN). **Moquegua:** 2 females, Carumas, IV-1961, Zevallos (IML). CHILE. **Antofagasta:** 1 female, Chiu Chiu, 24-I-1972, Sielfeld (SEM). BOLIVIA. **Cochabamba:** 1 female, Cochabamba, 26-IX-1972, G. E. Bohart (Logan). **Oruro:** 1 male, Poopo, 15-IX-1965, J.C. Ballard (Logan). ARGENTINA. 319 specimens from the provinces of Jujuy, Salta, Tucumán, Catamarca, La Rioja, Mendoza, La Pampa, Buenos Aires, Neuquén, Río Negro, Chubut and Santa Cruz (collection dates October to April).

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 54, No. 9, pp. 289-333 January 24, 1992

Laboratory Studies on the Behavior and Colony Structure of *Braunsapis hewitti,* a Xylocopine Bee from Taiwan (Hymenoptera: Anthophoridae)

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ABSTRACT

Braunsapis hewitti, an allodapine bee (earlier studied under the name *B. sauteriella*) that nests in dead pithy or hollow stems, was kept in cages in a greenhouse, nesting in numerous tubular glass observation nests, for 15 months. An ethometric study was made both in the solitary nests (inhabited by a single female and her immature progeny) and in eusocial and semisocial colonies consisting of two or three adult females plus immatures. Most self-maintenance behaviors were those to be expected of any solitary bee. Moving of pith dust and of pollen from place to place within the nest and storing of pollen on the walls of the nest, however, are unusual behaviors for solitary bees, perhaps important in permitting social evolution. A series of ''nest-maintenance'' behaviors includes many features rare or unknown among bees except for the Allodapini. These include grooming and moving immatures (like ants), extending the nest while rearing immatures, progressive feeding of larvae, and storage of honey on the bodies of larvae. These behaviors occur in solitary nests but are probably important in permitting colonial life in the same population. Interadult behaviors in colonies include feeding of young adults and food exchange among others. Agonism is not or rarely evident but dominance-subordinance patterns can be demonstrated statistically, the principal reproductive (queen) dominating the forager (worker). In the frequencies and durations of many behaviors, solitary females are intermediate between the two castes found in colonies; each caste thus appears to have deviated more or less equally from the ancestral solitary condition.

INTRODUCTION

Previous papers on the Taiwanese facultatively social xylocopine bee, *Braunsapis hewitti* (Cameron), formerly known as *B. sauteriella* (Cockerell) (see Reyes, 1991), included field studies on nesting biology (Iwata, 1938; Shiokawa and Michener, 1977). More recently, we have made more detailed field studies (Maeta et al., 1984) and laboratory studies on the life cycle and nesting biology (Maeta et al., 1985). This third and final paper of the series reports behavior and colony structure in artificial nests in cages in a greenhouse. It is the first comprehensive, long-term study of behavior of an allodapine confirmed directly through glass walls of observation nests. Our purpose is not detailed ethological analysis, but to distinguish the various behavior patterns and use them to clarify the life cycle and social structure. Thus, assumptions as to stimuli releasing or directing each behavior are usually not made.

Aspects of behavior of other allodapine bees have been observed directly by Rayment (1951), Skaife (1953), Michener (1962, 1968, 1972a, b), Mason (1987, 1988), and Schwarz (1986). Most of what has been known about allodapine behavior, however, was learned from censuses, dissections and measurements of numerous nest populations at various times of the year. Aspects of the life cycle and social structure can often be surmised from such data, as indicated in works by Iwata (1938), Michener (1962, 1965, 1968, 1971, 1974), Houston (1977), and Maeta et al. (1984, 1985). Such information was summarized for Allodapini and compared with that on other tribes of Xylocopinae by Sakagami (1960) and Michener (1974, 1985, 1990). It is good to have such surmises corrected or verified by direct observation.

Most allodapine nests are simple burrows in hollow or pithy, dry stems. Although most bees construct a cell for each egg, closing it after it is mass provisioned and the egg laid, allodapines rear young in a common cavity, i.e., they construct no cells. Most allodapines, and all that have been directly observed in their nests, provision their larvae progressively.

In *Braunsapis* (and most other Allodapini) each nest is started by a foundress that ordinarily rears the first brood alone. *Colonies* (meaning two or more adult females living and working in the same nest) are therefore rare in recently founded nests. In fact, the majority of *Braunsapis* nests contain only one adult female each, forming with her young a *subsocial* group. For simplicity of expression we often call such nests *solitary nests.* At least a few nests in all species, and many of the older nests of most species, contain colonies of two to several adult females. These are *multifemale nests.* Such colonies probably usually arise when (a) two or more bees, commonly sisters or a mother and daughter(s), pass through a prereproductive break in activities (e.g., winter), and remain together in an old nest after others disperse or die, or (b) one or more daughters remain with their mother without a prereproductive break in activity. Mother-daughter combinations are considered *eusocial* while bees of the same generation form *semisocial* colonies. Occasional colonies are produced when one or more bees join a lone nest initiator, as occurred in certain nests in our cages, but Michener (1968) showed that *Braunsapis* in Africa do not readily join others, even under pressure. For convenience, we often use the expressions *solitary phase, eusocial phase* and *semisocial phase* with reference to the status of nest inhabitants.

The adult females in a colony ordinarily differ in reproductive condition. One (or in larger colonies, more than one) has enlarged ovaries and is inseminated. One or more others have more slender ovaries and are commonly not inseminated. The former, a queen, is usually larger, is the principal egg-layer, the principal guard, and the minimal forager. The latter, workers, are usually smaller, often lay few or no eggs, and some of them are usually active foragers. In the following pages, the words *queen, mother,* and *guard* are synonymous except when otherwise indicated. Likewise, the words *worker* and *forager* are synonymous, as is *daughter* if young females that will soon disperse are excluded. We show that queens are in general dominant, workers submissive. Therefore the expressions *dominant female* and *submissive female* are also available for the weakly differentiated female castes. The queen may be the same age as and probably the sister of the worker(s), forming a semisocial colony, or older than and probably the mother of the workers, forming a eusocial colony. Details of these relationships are summarized by Michener (1990), the work from which the above comments are drawn.

Because the castes are so similar, some would prefer the words mother and daughter for the castes in eusocial colonies and large and small for the castes in semisocial colonies. Because the castes are similar in the two types of colonies, we find it useful to use the same names—queen and worker—in both cases.

In our studies the caste problem is minimized because most of our colonies consisted of only two adult females, a queen and a worker. In the field, however, larger (older?) colonies often arise, with intermediates between castes or with two or three individuals that have enlarged ovaries. Application of terms like queen and worker are less clear in such nests, although one worn (old) individual with enlarged ovaries and sperm cells in the spermatheca can usually be recognized as the queen.

MATERIALS AND METHODS

Except as otherwise stated, all observations concern adult females of *Braunsapis hewitti.* Bees were collected from flowers and from nests at Kenting in southern Taiwan (sites described by Maeta et al., 1984), May 3 to 8, 1980, and reared in a greenhouse in Morioka, Japan. Two cages in the greenhouse were described by Maeta et al. (1985). Each cage was provided with artificial nest substrates and with flowers as explained in detail by Maeta et al. (1985). We used two of the nest types described by those authors: type 3 and type 1v. Most observations were made with nest type 3, a pithy core from stems of *Kerria japonica* with a guide furrow along one side, inserted snugly into a glass tube. A bee excavated its burrow in the pith along the furrow next to the glass, so that the nest burrow and contents were visible to us when an opaque covering was removed for observations; the bee was free to fly to flowers in the cage for food. For some observations, nest type 1v was used; this is a type 3 nest with the entrance opening into a transparent plastic vial containing supplies of honey water (1:1 mixture) and *Typha* pollen mixed with soybean flour; thus such bees could not fly freely in the cage.

Observations continued from May 14, 1980, when bees were liberated in the cages, to August 21, 1981 (162 observation days, 313 observation hours). Each behavior was described until a definite pattern was recognized by repeated checking and redescription; thereafter recognized behaviors were recorded by abbreviations. In multifemale nests (the maximum number per nest in our cages was only three), each bee could be distinguished by body size, wing wear, and color; individual marking was not necessary.

Physical as well as behavioral characteristics of adult females were useful to clarify the social structure. Adult females from both artificial nests and natural nests collected in Taiwan were examined to determine (1) whether or not bees in a nest were of the same generation (wing wear, cuticular color); (2) body size as represented by head width; (3) ovarian state including indications of previous laying (white and gray bodies, Michener, 1971); and (4) whether inseminated (sperm cells in spermatheca). Techniques used for these examinations were those of Kurihara et al. (1981) and Goûkon et al. (1987).

Although the observation nests were nearly horizontal (about 8° from horizontal) as illustrated by Maeta et al. (1985), nests in the field are often vertical although very variable in orientation. We refer to the entrance as being at the *top* of the nest; the other end is the *bottom;* corresponding directions are *upward* and *downward.* The direction toward the ventral surface of a bee is termed *ventrad,* not downward.

The word *juvenile* is used for young adults, normally found in nests with mature adults. At first they are paler in color than mature adults. After they make trips out of the nest it seems reasonable to consider them adults, no longer juveniles. Unless juveniles are specified, references to bees or to *adults* concern mature adult females.

Narrowing the nest opening is the *entrance collar* (Fig. 1), constructed by the bees. At the bottom of the nest is a concave layer of pith particles tamped into position and constituting the *basal plug* (Fig. 1).

Since the bees in a single nest may pass through a series of social stages, subsocial (from the standpoint of adults present, solitary) to eusocial or semisocial, and with death of the queen, back again, we record events as being in the solitary, eusocial, or semisocial phases. Such terms are not applicable to species in *Braunsapis,* but to inhabitants of a given nest at a given time, as has been repeatedly stated (e.g., Michener, 1990).

The two adults required for interadult behaviors are termed the *actor* (active partner) and *actee* (passive partner); they may encounter one another either face to face or face to tail.

Details of methods for analysis of frequencies and durations of behaviors are explained in Section 4.1.

While all the authors did some work on all aspects of this paper, YM made observations throughout the study and SFS made most of the one-hour detailed observations. CDM's observations of the nests were limited to one week. YM assembled the data and prepared a preliminary manuscript in Japanese; SFS did much of the statistical work and prepared a draft in English; and CDM reworked much of this and added various sections, especially comparative material and discussion.

RESULTS

Observed behaviors were classified in three functional (often interconnected or overlapping) groups: self-maintenance behaviors, nest-maintenance behaviors including immature-adult interactions, and interadult behaviors (Table 1).

While some simple functions are achieved by unit behaviors (each a single action), others require an obvious succession of several behavior units. Such a sequence is called a behavior chain. We are not in a position to claim that succeeding units in a behavior chain are each mediated by the prior unit, although this is probably often true. Again, the categories of unit and chain behaviors are interconnecting and overlapping. No behavior that we recognize is so simple that it cannot be subdivided. Thus the distinction is relative and subjective. Nonetheless we have found it convenient to use the terms from time to time. In behavior chains a given sequence may be briefly interrupted

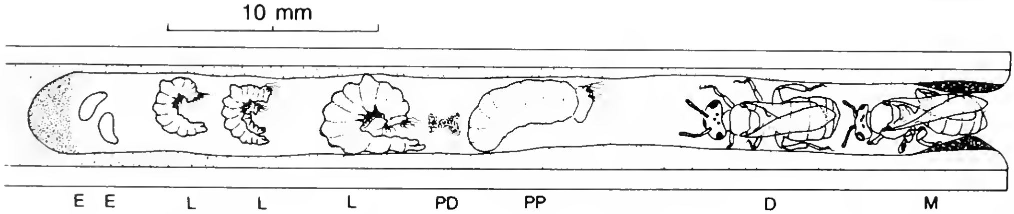

Fig. 1. Longitudinal sectional view seen from above of type 3 laboratory nest of *Braunsapis hewitti* inhabited by a eusocial colony. Outer unstippled, glass tube; lightly stippled, pith of *Kerria japonica;* darkly stippled, entrance collar and basal plug; E, eggs; L, larvae; PD, pollen deposit; PP, prepupa; D, daughter (worker); M, mother (queen and guard). A rather small larva is out of the usual sequence from youngest to oldest, perhaps because it is stuck to a larger larva.

Table 1. List of unit behaviors and behavior chains recognized in females of *Braunsapis hewitti*, and page on which each is explained.

	Behavior	Page
	1. Self-Maintenance Behaviors	
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2.1.1	Guarding	296
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2.3	Enlargement of the nest burrow[1,2]	300
2.4	Preparation of the basal plug[1]	301
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2.9.1	Feeding honey to larvae[2]	309
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3.3	Thrusting	310
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3.5	Pushing away	312
3.6	Feeding of adults[1]	312
3.7	Face brushing	312
3.8	Inhibiting juvenile's approach to the nest entrance	313
3.9	Oophagy	313

[1] Behavior chains; all others are called unit behaviors.

[2] Characteristic of *Braunsapis;* all others shared with *Ceratina* (Maeta and Sakagami, unpublished), although sometimes differing in behavior patterns.

by such unit behaviors as walking, turning, checking, and resting. These interruptions are not reported as parts of sequences.

Weather can have a major influence on activity. Unlike most solitary bees, *Braunsapis* does not always forage even in fine weather, nor always rest at night. In general, females forage between 08:00 and 19:00 with two peaks (ca. 09:00 and 15:00–17:00). Unlike *Ceratina* reared in the same greenhouse, *Braunsapis* foraged more on rainy and cloudy days than on warm days. The lower liminal temperature for foraging was 22°C. The lower liminal light intensity for homing was 280 lux (rainy day, 25°C) and for departure, 680 lux (rainy day, 24.2°C). Intranidal activities continued down to 22°C or less. Our observations were, of course, constrained by these temporal, light, and temperature limits. Although the bees were usually resting when observed about midnight, they are often temporarily active at night. Most of our observations were made between 08:00 and 19:00, supplemented by sporadic earlier, later, and night observations.

1. SELF-MAINTENANCE BEHAVIORS

Most self-maintenance behaviors resemble those of other bees and wasps (Baerends, 1941; Sakagami and Yamane, 1990). Each self-maintenance behavior can occur independently, but some also become components of nest-maintenance behaviors (e.g., grooming as a component of pollen foraging or the walking and turning that link other behaviors). The important self-maintenance behaviors that we recognized are described below:

1.1 Resting.—Resting is a background behavior, that is, it often occurs within or as linkage between other behaviors; it is often interchangeable with grooming in behavioral sequences. It can be completely akinetic or can include slight movements; these types of resting were not distinguished in this study, but more time appears to be spent in the former than in the latter. Resting happens by default if the bee is not doing something else. Guarding (2.1.1) is actually mostly resting at the nest entrance. Long periods of resting within the nest burrow away from the entrance are rare in solitary nests, but in multifemale nests, one female is commonly found at the entrance while others rest in the burrow. No matter where in the nest a bee may be, in prolonged resting the head is usually directed downward. A resting bee keeps the outsides, not the insides of the fore and middle tarsi in contact with the burrow walls. (The fore and middle legs of *Braunsapis* are not extended as illustrated by Wilson, 1971: 84, figs. 5–7.) The antennae of akinetic resting bees are usually directed ventrad, not forward. Resting also occurs outside the nest, on flowers or leaves and stems.

1.2 Alerting/Inspecting.—These behaviors appear in response to unusual stimuli. In alerting, the head and antennae are moved toward the source of stimulus; sometimes the forelegs are raised. Alerting becomes inspecting when another behavior is started; usually the head and antennae are then more definitely directed toward the stimulus and antennating is frequent. No precise records of these behaviors were made except that a bee facing outward at the nest entrance was considered to be inspecting (see sections 4 and 5, also see Checking, 2.1.2).

1.3 Walking.—Walking links various other behaviors, but the sequence rest-walk-rest is frequent (frequencies for various behaviors are given in Table 6). In walking, the antennae are stretched out to the front, forming an angle of about 30° with each other, never directed ventrad; thus the apices are well above the substrate. Inside the burrow, bees walk both forward and backward with equal skill, changing speed according to the situation. Walking is seen also extranidally, on flowers for example, but is not prolonged.

1.4 Turning around.—Turning means reversing direction, i.e., turning around, in the nest. Turning involves first curling the body, then twisting with the legs stretched against the burrow wall so as to reverse direction of movement. The ability to turn in the burrow is indispensable for development of social behavior in Aculeata living in narrow tubes. *Braunsapis* has no turning chamber near the extrance as does *Ceratina* but can turn anywhere in the burrow. (Turning in front of another adult may serve a social function; see 5.2.)

1.5 Stinging.—Stinging was observed (experienced) neither in the laboratory nor the field, but it may happen under circumstances that did not occur during this study, for females have a well-developed sting. CDM has been stung by larger allodapines held in the fingers, but small *Braunsapis* are rarely able to penetrate the skin (see 2.1.1). Mason (1988) reports C-posturing (the fighting posture with both sting and mandibles directed toward an enemy, Bell and Hawkins, 1974), which may involve use of the sting, as one of the interactions seen among colony members of African allodapines.

1.6 Flight.—Flight, usually to food resources, is a behavior chain that consists of departure-orientation flight-flying-landing-flying-homing. Departure is preceded by inspecting at the nest entrance. Contrary to many bees, *B. hewitti* inspects the outside by turning its head with the antennae extended.

If the bee continues the behavior chain, it turns venter up and departs with the head directed upward. This description does not apply to departures from vertical nests, opening upward, which are common in the field; the laboratory nests were nearly horizontal. Each departure is followed by an orientation flight, perhaps because of the low number (commonly one, see 2.8) of flights per day (a characteristic shared with *Ceratina*). The orientation flight is a zig-zag, progressively broader as the distance from the nest gradually grows, up to but not exceeding 1 m. In flight, the legs are not in contact with the sides of the body and the antennae are directed forward. Nest memory is very precise and appears to involve details of the entrance or outside of the nest and/or nest-specific odors. If, while a bee was away, a nest was moved (up to about 20 cm) from the nest stand to the table or held in front of the observer, the homing bee never returned to the original site, but to the nest in its new location. Other behaviors often associated with flight are self-feeding, mating, and defecating.

Four cases of extranidal overnighting, probably involving flight and long-term resting somewhere in the cage, were recorded: a 1-night absence in July, two 4-night absences in August, and a 3-night absence in September.

1.7 Self-grooming.—Self-grooming is for cleaning the body surface. The sequences of self-grooming in *Braunsapis* are similar to those of *Ceratina*, and are as follows: (1) The head, antennae, and mouthparts are cleaned with the forelegs. (2) Dust gathered with the forelegs is transferred via the middle legs onto the hind tibial scopa; then the hind legs are rubbed together, brushing off accumulated dust. (3) The dorsum of the metasoma is cleaned with the hind legs. (4) The wing surfaces are cleaned with the hind legs. (5) The thorax is cleaned with the middle legs and dust transferred to the hind legs (see Jander, 1976). Self-grooming is very frequent. It alternates with resting, and occurs after foraging and before and after pollen unloading. (Interadult allogrooming was never observed.)

The same movement sequences are used in pith dust and pollen transfer, except that sweeping material off from the hind legs is delayed so that dust or pollen is transferred to a new site in the nest or to the nest entrance. Thus burrow excavation, enlargement and cleaning (1.12, 2.2, 2.3) and pollen handling (1.14, 2.8.8) use movements apparently derived from self-grooming.

Extension and retraction of the proboscis is frequent and can be regarded as functionally part of grooming. Sometimes the tongue is repeatedly scraped with the forelegs.

1.8 Mandibulating.—This is opening and closing of the mandibles; its function is unknown. Mandibulating may be associated with grooming, eating, burrowing, or feeding, and may even occur at defecating.

1.9 Pollen intake.—Pollen eating is associated with mandibular movement, usually without extension of the proboscis. Pollen is eaten on flowers and, in the burrow, from a pollen heap on the nest wall or occasionally from the body surface of a larva being groomed (see 2.8).

1.10 Nectar (honey) intake.—In the absence of data on nectar processing (except in 1.11) in Allodapini, we use the words nectar and honey synonymously. Liquid food is secured by the extended tongue from flowers or from honey deposited on immature stages, usually larvae. This behavior is also used in interadult food transfer (see 2.8.2, 3.6).

1.11 Nectar (honey) ripening.—This behavior has been observed both inside and outside of the nest, and is similar to that seen in other bees. Water evaporation from a nectar droplet held with the glossa is presumably promoted by alternate extending and retracting of the bent glossa. Nectar ripening is rarer in *Braunsapis* than in many bees. Honey droplets left on body surfaces of larvae would also evaporate water (see 2.8.1).

1.12 Defecating.—Defecating by adults usually occurs outside the nest. Sometimes the female in guarding posture defecates just outside the nest entrance, rubbing the metasomal apex on the entrance. The excrement dries and later falls off. Defecating at the entrance was seen less frequently than in

Ceratina, but feces were seen at the entrances of many nests. Extranidal defecating was observed on flower petals, leaves, the covers of nest tubes, etc.

Defecation by adults inside the burrow was never seen in nests containing a single adult. When juvenile daughters cohabit with their mothers, they (daughters) defecate inside the burrow. These feces are sooner or later cleared out by an adult.

1.13 Transfer of pith dust.—Pith dust results from burrow excavation or enlargement. The dust is transferred from place to place in the nest, or to the nest entrance. This behavior chain ensues when the forelegs of a female contact a heap of pith dust in the burrow. She gathers dust with the forelegs and, via the middle legs, transfers it to the hind legs; then, after turning (1.4), she dumps the dust at another place in the burrow or at the nest entrance (1.7). This chain is often repeated continuously, sometimes for more than 10 minutes.

1.14 Transfer of pollen.—This behavior chain, which is like that for transfer of pith dust (1.13), relates to pollen heaps in the nest. It is especially frequent before, during, and after a feeding behavior chain that follows foraging (2.9.2). Both pith and pollen transfer are probably modified grooming behavior patterns. These behaviors differ from grooming in that materials are picked up from substrates rather than from the body surface, and "sweeping off" is often delayed to provide for transport of materials, in this case pollen.

2. NEST-MAINTENANCE BEHAVIORS

Nest maintenance is interpreted broadly to include not only construction and defense of the nest but also care of the immature stages, foraging, and the like. Transfer of pith dust and pollen (1.13, 1.14) could be included under nest maintenance, although these activities also include cleaning of the bodies of bees. Some other self-maintenance behaviors are incorporated into nest-maintenance behaviors, either as independent behaviors or as components, i.e., linking behaviors. Some nest-maintenance behaviors are unit behaviors, but many constitute behavior chains.

2.1 Simple nest-maintenance behaviors.—Although they do not form a functional category, it is convenient to discuss the simple behaviors first.

2.1.1 Guarding.—Guarding is seen in both solitary and social phases in *Braunsapis.* In solitary nests, the female nearly always rests at the entrance and is functionally a guard except when she is foraging or working in the nest. In multifemale nests, guarding is more continuous and is done primarily by the queen while other bees rest within the burrow, forage, and perform most other tasks. When the queen is not at the entrance, however, other females will guard; the entrance is not left open. When challenged with a fine stick, workers or juveniles guarded less persistently than queens.

While guarding, the bee occupies the mouth of the burrow and faces into the nest. Fourteen censuses of the nests showed that of 133 bees observed at the entrances, only 6 were facing outward. The occasional bee that was facing out was probably about to depart and we have classified such behavior as inspecting (1.2) rather than guarding. Such inspecting behavior was never seen after dark, an observation that supports its exclusion from guarding, since it is only during the day that departures occur. A guard inserts the metasoma in the entrance collar, completely closing the orifice with the apical three segments, which are dorsally somewhat flattened and have special short vestiture (Fig. 2). Such guarding is similar to that observed in nearly all studied species of Allodapini. The guarding posture in *B. hewitti* may be slightly different in daytime and at night. In daytime, the apical metasomal dorsum is always in contact with the upper margin of the collar; at night, the body is often a little farther into the nest.

The guard is usually indifferent to gentle stimuli such as the landing of a still drifting (foreign) bee on the entrance. Nudging an inspecting bee (facing outward) with a fine stick or needle ($N = 37$) produced the following responses: some promptly turned and plugged the entrance with the metasoma (2 cases); most performed the following chain: backed into the burrow (more than its own body length)-turned-ascended-guarded with

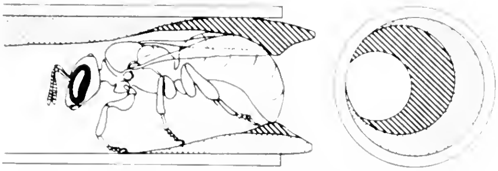


Fig. 2. Nest entrance (type 3 laboratory nest) and guard of *Braunsapis hewitti* showing (at left) the guard's position (seen from side) and (at right) a frontal view of the nest entrance. Outer white layer, glass tube; stippled, pith of *Kerria japonica;* lined, entrance collar constructed by the bee.

the metasoma plugging the entrance (35 cases). When the metasoma of a guard (facing into the nest) was nudged, it either descended and ascended quite quickly, taking up its original position, or it firmed up its position by extending its legs (each response more than 20 cases). Turning and facing the entrance, as in *Ceratina,* was not observed.

When a *Trogium pulsatorium* (Psocoptera) invaded a nest through a narrow space between the entrance collar and the guard's metasoma, the guard killed this invader with its mandibles and threw it out from the nest entrance. Situations in which the sting might be used never occurred in our nests, nor were they induced artificially, although some guards thrust the metasoma out beyond the entrance as though to use the sting. Perhaps in the field there are occasions when the sting is used in nest defense but it probably serves primarily for individual defense.

In nest type 1v, the queen guarded most frequently, but she often moved away from the entrance, and sometimes a male instead of a worker replaced her at the entrance.

2.1.2 Checking.—Before starting any nest-maintenance behavior, a bee patrols the burrow wall, the basal plug, the immatures, and pollen masses, checking with the antennae. The flagella are directed down and slowly and alternately tap on each object. Eggs are especially carefully checked. Possibly checking is to be regarded as a form of inspecting (see 1.2), done while walking; it may be comparable to patrolling as seen in *Apis* (Lindauer, 1971).

2.1.3 Cleaning the burrow wall.—This behavior is associated with others such as carrying dust and sweeping dust away from the nest entrance. It is a behavior chain, although simpler than other chains described later. The forelegs are flexed inward and the wall is brushed by the outer surfaces of the tarsi, which are rapidly moved back and forth. This behavior seems to remove a small amount of dust (including pollen). Sometimes the particles are then transferred via the middle legs to the scopa on the hind legs and swept off onto the wall again by self-grooming behavior. Larger amounts of dust are swept off at the nest entrance (see 1.7, 1.13). Pollen piled on the wall is swept away when it becomes old and is replaced by fresh pollen (see 1.14). While gathering pollen from the burrow wall, a bee may face in either direction, but a bee sweeping off pollen always faces the entrance (as it also does in unloading pollen after foraging).

The removal and dumping at the entrance of larval feces and exuviae, of feces of juveniles, and of dead (or possible still alive) immatures is included here; such behavior was postulated by Michener (1971) and others.

2.1.4 Grooming immatures.—Grooming of immatures is often associated with the transport and sweeping away of pith dust as well as transport and feeding of immatures, but it also occurs independently.

An egg, lightly adhering near the bottom of the nest, is checked with ventrad-directed antennae. The mandibles touch the egg and rhythmically open and close. Probably a small amount of dust is removed. Then the egg is brushed with the hairs of the inner surfaces of the fore tarsi and dust is transferred via the middle legs to the scopae on the hind legs. Sometimes eggs are brushed with the folded glossa.

Larvae are also brushed to remove dust, as are eggs. Exuviae and feces attached to larvae are held with the mandibles and then detached by brushing with the dorsal surfaces of both fore tarsi. Afterward the detached material is pushed backward with the metasomal apex to the entrance and dumped like other debris. An old or solidified pollen mass is detached from a larva by rhythmical movements of the mandibles and likewise dumped at the entrance. A curled larva can be caused to straighten by insertion of the mandibles within the curl; then the pollen inside the curl is removed and dumped or occasionally eaten by the bee. Often the mandibles touch a larva's head (near the mouthparts), as if giving a physical stimulus, and the larva responds by gently shaking its head; such touching is often followed by cleaning.

Pupae are brushed in the same manner as larvae, although less frequently.

In the course of feeding larvae (2.9), some grooming behaviors used with larvae (brushing with fore tarsi, removal of pollen, and touching with the mandibles) occasionally occur, but their low frequencies (Table 4) suggest the independence of the grooming-immatures behavior from feeding larvae.

When the grooming-immatures behavior appears independently, it is usually confined to one or a few immatures near the nest entrance. It is only rarely applied to those near the nest bottom. A particular immature, however, may be persistently groomed and moved. For example, in one nest (eusocial, with mother, daughter, and seven immatures) in the course of an 84-minute observation, the daughter repeatedly transported and returned piled pollen (7 times), cleaned the burrow (18 times), groomed one (but not other) fourth instar larva (16 times), and moved this larva (not others) (24 times). After that, the daughter transferred the piled pollen to the entrance, where it was swept away by the mother, who was on guard.

2.1.5 Moving immatures.—Moving of immature individuals by adults, unknown in cell-making bees except for movement within cells by some *Ceratina* (Sakagami and Maeta, 1977, 1986, 1987b), is antlike. It has been described previously, e.g., by Michener (1968, 1972b). It occurs either independently or with any of three other chains: extension of burrow (2.2), feeding larvae (2.9), or grooming immatures (2.1.4). It also appeared when the black paper sheath of the observation nest was suddenly slid aside and the nest interior exposed to light.

The types of moving of immatures were classified as follows:

I. Relative positions of adult and immature unchanged.

I-1. Pushing with head.

I-2. Moving small immature (egg or first instar larva) forward or backward stuck to the face of the adult. Eggs and young larvae are sticky enough to be carried on the face, and to stick to one another; once we saw two eggs moved together on the face of a bee. When pushed against the basal plug or nearby burrow wall, an egg sticks there (2.7.2). [Rarely larger larvae or even pupae (1 record) are moved two or more at a time.]

I-3. Advancing with immature held with mandibles.

I-4. Pushing immature with fore tarsi, sometimes with outer surfaces of the tarsi.

I-5. Backing with immature held by or pulled with the mandibles, and often also lightly held by forelegs.

I-6. As in I-5, followed by pushing with middle legs.

I-7. Backing, pulling immature with the fore tarsi, with intermittent use of middle legs.

II. Relative positions of adult and immature exchanged.

II-1. First, pulling or raking immature with fore tarsi, then climbing over it using middle and hind legs.

II-2. Getting over the immature with slight pushing.

The relative frequencies of the variants of moving behavior are shown in Table 2, in which mass moving of immatures by females is included, but moving by males is excluded. Eggs or small larvae stuck together in a tight mass are often moved together. Mass moving of pupae was observed once.

Immatures are often moved in the course of other activities. Examples are listed below. All are included in Table 2 except three cases explained in (4).

(1) Guard moved an immature to the bottom of the burrow, then returned to guard (5 cases).

(2) Moving immatures during passing of an immature (13 cases, 4 by males).

(3) Moving immatures during the following other behaviors: cleaning burrow wall (2 cases); touching larva (1 case); honey withdrawal from larva (2 cases); grooming pupa (2 cases); touching larva—cleaning burrow wall (1 case); touching larva—pollen manipulation (1 case); touching larva—self grooming—pollen manipulation (1 case); touching larva—cleaning burrow wall—self grooming (1 case).

(4) Extended movement of immatures: three cases (A, B, C) are detailed. CASE A: June 16, 1980: A female moved a large larva using moving type II-1, then pushed it backward with the middle and hind legs; then she turned and held a small larva with her mandibles and pressed it onto the basal plug (moving type I-3). CASE B: August 14, 1980: A worker held a small larva with her mandibles and moved backward (moving type I-5) into the newly excavated part of the burrow. CASE C: August 14, 1980: Immatures

Table 2. Number of observed movings of immature stages by females of *Braunsapis hewitti.* (A, adult facing nest bottom; B, adult facing entrance; C, direction not recorded. Types of moving are explained under 2.1.5 in text.)

		Type of Moving								Grand Total
	I-1	I-2	I-3	I-4	I-5	I-6	I-7	II-1	II-2	
Egg										
A	9	3	—	—	—	—	—	2	—	14
B	1	—	—	—	—	—	—	4	—	5
C	2	—	2	—	5	—	—	—	—	9
Total	12	3	2	—	5	—	—	6	—	28
Young larva										
A	14	1	—	1	—	—	—	1	—	17
B	1	—	—	—	—	—	—	3	—	4
C	1	—	1	—	4	—	1	1	—	8
Total	16	1	1	1	4	—	1	5	—	29
Medium larva										
A	17	—	—	1	—	—	1	10	—	29
B	—	—	—	—	—	—	—	9	—	9
Total	17	—	—	1	—	—	1	19	—	38
Old larva										
A	18	—	—	2	—	—	5	40	—	65
B	—	—	—	—	—	—	1	51	—	52
C	2	—	—	—	2	—	—	1	—	5
Total	20	—	—	2	2	—	6	92	—	122
Unknown larva										
(C)	—	—	—	—	5	1	6	1	—	13
Prepupa, pupa										
A	3	—	—	—	—	—	—	—	—	3
B	—	—	—	—	—	—	—	—	3	3
C	8	—	—	—	1	—	6	3	—	18
Total	11	—	—	—	1	—	6	3	3	24
Grand Total	76	4	3	4	17	1	20	126	3	254

(eggs to mature larvae) were transported to the newly extended part of a burrow using three different methods (I-2, I-3, and I-5) in succession. Such transport into the new part of a burrow is illustrated in Figure 3.

Iwata (1938) and Michener (1962) wrote that the sequence in which immatures of species now placed in *Braunsapis* are arranged in the burrow, from oldest nearest the entrance to youngest at the bottom, is restored if it is artificially disturbed. Such large scale adjustments probably occur only after a traumatic disturbance. As mentioned above, we have observed immatures often being moved about during passing or other tasks. Since eggs are laid at the nest bottom, the sequence can be maintained by repeated small scale movements of older immatures toward the entrance.

2.2 Burrowing.—Burrowing in pith is especially obvious in the prelaying period of the solitary phase, when nests are established by lone females. After selecting a nest substrate (in our case, including a small-diameter furrow in pith), the female constructs the burrow or extends both its length and diameter by the series of behaviors outlined below, interrupted by periods of rest. In single-female nests, the pith dust (particles of pith loosened by scraping) is swept out of the burrow entrance only once per burrowing episode, not continuously carried to the entrance and swept out there. After completion of the burrow and preparation of the basal plug and egg-laying in type 3 artificial nests, the burrow lengths ranged from 20.7 mm to 72.3 mm ($\bar{x} = 47.2 \pm 11.8$ mm, $N = 27$)

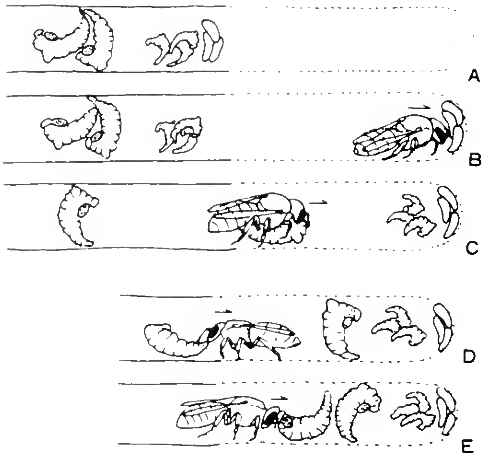


Fig. 3. Moving immatures of *Braunsapis hewitti* into a newly constructed extension (dotted) of the nest burrow (immatures as seen from above, adults as seen from side). A, before immatures were moved, but pith dust resulting from the work has been carried past them and dumped (to the left); B, pushing eggs to new position with head (moving type I-1); C, moving large larva held with front legs (I-4); D, pulling large larva with mandibles (I-5); E, pushing large larva with head (I-1). All this (B to E) occurred in about three minutes (from Sakagami and Maeta, 1986).

(Maeta et al., 1985). Later, if nests are occupied by multiple females, they are usually extended (see 2.3).

2.2.1 Scraping pith.—This is done with the mandibles and serves to initiate, extend, or enlarge a burrow until it has the diameter and length for a nest. The antennae are directed down and moved in various directions to explore the surface being excavated, as in checking (2.1.2). The fore tibiae and tarsi are bent backward and thus do not interfere with the action of the mandibles.

2.2.2 Gathering pith dust.—Pith dust is gathered with the fore tarsi and transferred to the scopa as described in 1.13. The sequence is the same as that in pollen gathering and is like self-grooming behavior (1.7; Jander, 1976), except of course that the dust is picked up from the substrate and not brushed off until the bee moves to a new place. Presumably both dust gathering and pollen gathering are derived from self-grooming movements (1.7) (Beecken, 1934; Schremmer, 1972).

2.2.3 Carrying pith dust.—When the scopa is fully loaded, the dust is carried to a place of deposition (1.13). Sometimes, when the amount of dust exceeds the capacity of the scopa, some is kept under the venter, being carried by the fore and middle legs as in *Ceratina.* Sometimes a pile of dust is pushed backward by the metasomal apex toward the nest entrance. Dropped dust is picked up with the middle and hind legs and pushed to the entrance by backward movement. Dust dropped previously is collected again with the forelegs, transferred to middle and hind legs and incorporated in the dust mass on the scopa.

2.2.4 Depositing pith dust within the burrow.—The load of pith dust is commonly deposited on the burrow wall near the nest entrance (1.13). The depositing behavior is exactly like that seen in unloading fresh pollen in the burrow (2.8.8). Such sweeping off, either of pith or pollen, is always followed by intense self-grooming.

2.2.5 Sweeping pith dust from the nest entrance.—Pith dust deposited on the burrow wall near the entrance is pushed backward, usually by the queen in multifemale nests, using the metasomal apex bent under. At the entrance it is swept off with the hind legs.

2.3 Enlargement of the nest burrow.—In one nest, although there was still ample space, a mother, before laying an egg on the basal plug, scraped the nearby wall and swept the dust out of the entrance (2.2). In this case the basal plug remained untouched; there was no burrow extension. After the initial reproductive activity, however, the burrow is frequently enlarged in diameter and is commonly extended in length. Such enlargement is rare in nonallodapine tube nesters but has been repeatedly reported for allodapine bees as a result of comparative nest measurements and observations of pith dust ejected from intact nests (Iwata, 1938; Michener, 1965, 1968, 1971). In *B. hewitti* the behaviors and their sequence are exactly like those observed in initial burrowing (2.2) except that the sequence is followed by grooming and carrying of immatures into the newly made part of the nest (Fig. 3). Observations of five nests showed that before oviposition began again, following the eclosion of workers, enlargement of the burrow continued for several days. Preparation of a new basal plug (2.4) followed, suggesting a linkage between the two chains.

In these five nests, burrow extension and enlargement was done in two cases by mothers and in three cases by daughters. In nests with two daughters, one worked more actively and persistently than the other. We observed parts of two episodes of burrow extension and preparation of the basal plug in detail in one nest. Both times (July 31, Case A; August 1, Case B), a daughter performed most of the task. We present the activities in some detail to give a clearer idea of the behavior.

CASE A: The nest contained the mother (queen), two daughters (D1 10 days after eclosion and D2, 6 days), a large larva, and an egg. July 31 was day 3 of enlargement work. A new basal plug was already prepared (probably on day 2). The burrow had been enlarged but not lengthened, and on day 3 was being further enlarged near the bottom.

From 8:42 to 9:45 D1, near and facing the bottom of the nest, scraped the wall at least five times. Carrying away the resultant dust seemed confused; possibly light in the nest, suddenly admitted for our observations, resulted in repetitious behavior. In any case, pith dust was carried by D1 five times to a site about one-fourth of the distance from the bottom to the entrance, and deposited there. At intervals she carried dust 13 times from that deposit to near the bottom of the nest and back again. (Such sisyphean work sequences were frequently seen in gathering/unloading of both pollen and pith dust, and will be noted below.) Once the mother (queen, guard) gathered dust near the middle of the nest, backed to the entrance, and threw it out. D1 once pushed dust backward to near D2, who did not respond. At 9:26 D1 exchanged positions (venter to venter) with D2, who soon pushed dust to D1, who relayed it to a site near the mother. D1 soon turned and pushed dust toward the bottom of the nest, then again toward the mother, who this time received it and swept it out of the nest. D2 now at least three times scraped the wall where D1 had been scraping, and moved dust to near D1. D1 several times moved dust to near the mother, then three times pushed it toward the bottom of the nest and each time back toward the mother, finally very near the mother, who then gathered it and swept it out of the nest. D1 was seen scraping and smoothing the wall and depositing dust near the mother twice later in the day; observations were not continuous after 9:45.

As shown above, most tasks on day 3 were done by D1 while D2 did some work. Possibly the presence of a large larva halfway down the burrow interfered with the carrying of dust and caused a loop in behavior, the sisyphean work. The mother (guard) usually did not sweep out dust unless it was piled close to her head.

CASE B (same nest as Case A): On day 4, when observations began (8:17), the basal plug presumably made on day 2 had been removed. The egg had been moved to the glass part of the burrow wall, no doubt before or during destruction of the basal plug. The burrow had been deepened 12 mm, attaining a length of 61 mm. This activity had occurred after 16:20 on day 3, when the nest was last observed.

From 8:17 to 9:34 (day 4) the following observations involving completion of the burrow and construction of the basal plug were made: D1 scraped the bottom of the burrow and D2 relayed pith dust deposited in front of her by D1 to the mother near the entrance. At 8:24 D1 turned, deposited pith dust in the bottom of the nest, and tamped it with the apex of the metasoma. This scrape-deposit-tamp sequence was repeated at least 16 times by D1 and clearly represented construction of the basal plug, which seemed completed by 9:31. This activity was interrupted once by transfer of dust to D2.

Throughout the observations described above the larva and egg were often enveloped with dust, and were as frequently cleaned, mostly by D2. D2 removed dust from the larva and egg and sometimes from the burrow wall and transferred it to the mother 13 times. The mother swept dust from the nest entrance six times. The relay system in Case B was from D1 to D2 to the mother.

2.4 Preparation of the basal plug.—The basal plug consists of pith dust compacted into a concave layer at the bottom of the nest. The chain for its preparation can be seen in the prelaying period of single-female nests. In type 3 artificial nests, the basal plug was always prepared before the beginning of oviposition; it was not always prepared first in nests in natural substrates (see Maeta et al., 1985, nest types 4, 5). (Indeed, in some allodapine bees a basal plug is not evident in nests excavated into intact pith where the bottom is merely a rounded end to the burrow; Michener, 1971.) In *B. hewitti* basal plug construction is similar to burrowing sequences (2.2.1 to 2.2.4) except for the place of pith dust deposition and the addition of tamping and compacting.

Even in the eusocial phase, this chain is performed by one bee only (see observations made on day 4 in 2.3). In one eusocial nest, the basal plug was prepared by the mother (queen), in another by a daughter (worker).

Pith dust for the plug is gathered mainly near the bottom of the burrow.

Compaction by tamping is done as follows: pith dust in the scopa is deposited by rubbing the hind legs together. The metasoma is slightly down-curved, the apex put on the dust, and then moved up and down to compact the dust by tamping. The forelegs and middle legs extend to the wall to support the body, but the hind legs are held free from the wall. The antennae are stretched forward. The body is rotated about the axis of the nest so that pith is evenly tamped. At first scraping, gathering, unloading, and tamping are in regular sequence, or tamping is occasionally omitted. Later when the plug becomes thicker, the amount of scraping decreases and more time is spent in tamping. Sometimes a scrape-tamp-scrape sequence also occurs.

Although this same chain appears in preparation of the entrance collar (2.5), the tamping behavior is not the same.

2.5 Preparation and repair of the entrance collar.—This chain appears only in the prelaying period or when a collar has been damaged or removed. The sequence is like that of preparation of the bottom plug except for differences in tamping. Moreover, scraping and depositing sometimes appear synchronously, carrying being omitted. Photographs of *Braunsapis* collars are given by Michener (1962, 1971).

When hollow stems are used for nesting, the entrance collar is prepared soon after cleaning of the hollow cavity. In excavated type 3 nests, some females build the basal plug before the collar, while others build the collar first (Maeta et al., 1985).

To investigate entrance collar construction, collars of two nests were removed with a needle at 9:00 on October 3 (day 1); dust was removed with an aspirator. In CASE A no repair occurred until the evening of day 3 and the new collar was found completed in the early morning of day 4. In CASE B, collar construction began on the afternoon of day 1 and the details of construction were recorded. (The nest contained a mother, daughter, and several immatures, as shown in Fig. 1.) The entrance collar and the guard's normal position are shown in Figure 2.

Upon removal of the collar in CASE B, the mother flew away, but was returned by force a few minutes later. Thereafter she guarded in an exaggerated posture, supporting the body with her fore and middle legs raised high and stretched and her metasoma conspicuously bent (Fig. 4).

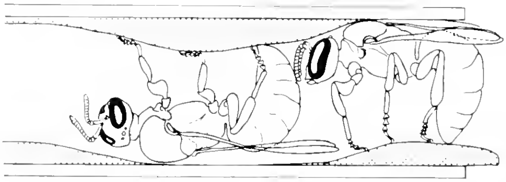


Fig. 4. Nest entrance in sectional view from side, type 3 nest, after removal of collar. The guard (queen) at right has taken up an exaggerated posture blocking the wide-open entrance. Clear walls are glass; pith is dotted.

The mother began to construct a new entrance collar at 13:19 of day 1. Facing inward, her mandibles scraped pith from the burrow walls near the entrance; the posture and location are indicated in Figure 5. Pith was transferred to the hind legs via the middle legs and then deposited (carrying was unnecessary). She put the metasomal apex on the point where the burrow had previously been narrowest, deposited pith dust there and tamped it with the metasomal apex. Later she proceeded a centimeter or two from the entrance, scraped pith there, and carried dust to the collar site. Before or after carrying pith to the site, the inner or outer side of the collar was tamped and consolidated; the sides were tamped in no particular sequence, sometimes the inner and sometimes the outer. Tamping of the inner side and edge of the collar was by the metasomal apex but that of the outer side was by the apical terga (Fig. 6).

Although the first pith loads were deposited with little tamping, tamping gradually increased in frequency and was observed not only before and after but also during deposition of later pith loads. The pith dust included an admixture of pollen, etc. By 13:39, the mother had deposited seven pith loads. Then the daughter began scraping and carrying pith dust to a point in front of the mother, who then used pith gathered both by herself and by the daughter. Both mother and daughter scraped pith while facing toward the nest bottom. Part of the entrance intersected the glass wall of the nest, and the collar was not

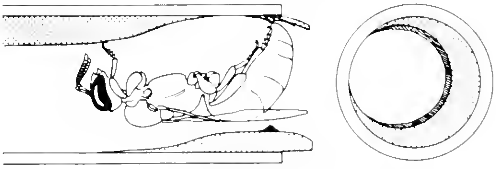


Fig. 5. Nest entrance and frontal view of entrance, as in Figure 4 but new pith dust being added and compacted to start the new collar in the same position as the one that was removed. New construction is shown as lined.

prepared there (no pith was placed there). The two bees continued to work until 14:45. While the mother was at the entrance most of the time, their positions and activities were reversed for one period of six minutes. In all, the mother carried and tamped pith dust 21 times and the daughter three times; the mother scraped and transferred pith dust twice while the daughter did so nine times. The mother turned around and checked the growing collar with her antennae five times, in each case reversing and tamping again. Occasionally the collar-constructing activities of the daughter were interrupted when she tamped the burrow walls (Fig. 7, 2.6) near where she was scraping. In consolidating the collar, the mother rotated her body, alternately depositing pith from her body and tamping.

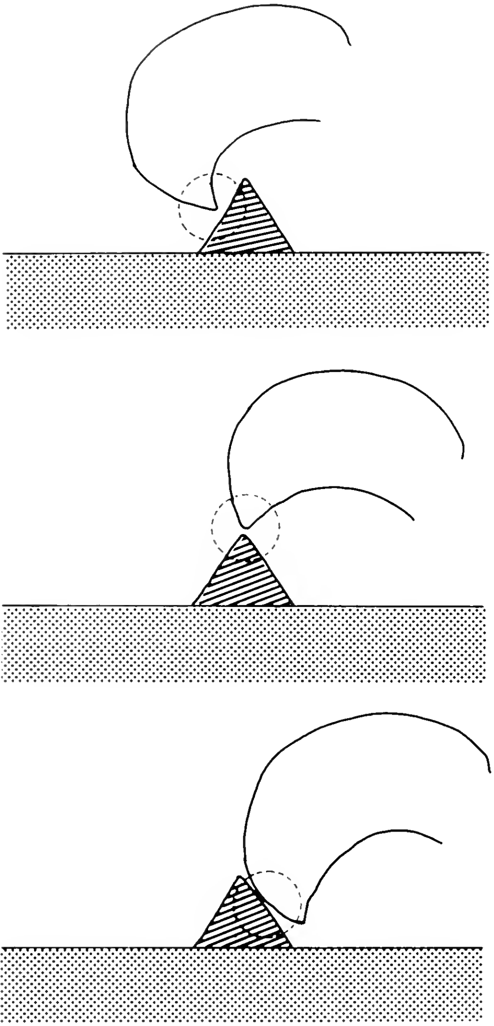


Fig. 6. Diagrammatic views (nest entrance to left) showing how the tamping of collar material is done with the metasomal apex for the outer surface and edge of the collar (upper and middle figures), with the apical terga for the inner surface of the collar (below).

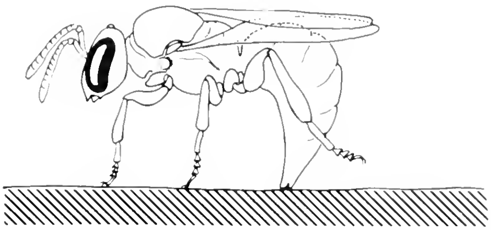
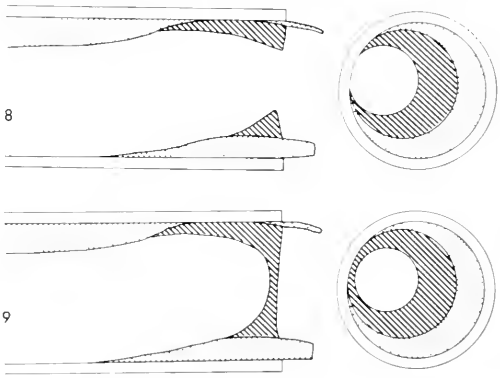


Fig. 7. Diagrammatic view of a worker of *Braunsapis hewitti* tamping the burrow wall.

At 15:49, the daughter was resting but the mother again added pith to the entrance collar. No further change took place until 17:50, the collar having attained the state shown in Figure 8. On day 2 at 08:45, the entrance collar had become generally thicker, and on day 4 the new collar had been built across the glass part of the nest wall (Fig. 9).

In summary, the entrance collar was completed over three days, but most of the work was done during a 2.5-hour period. Our two cases show that collar replacement may start either relatively soon after collar destruction or after a few days and may occur by day or during the night. The collar is about as hard as cell partitions of *Xylocopa*. Consolidation may well require not only tamping but also addition of some secretion, but no such addition was observed. Michener (1971)



Figs. 8, 9. Nest entrance, sectional and frontal views, shading as for Figures 4 and 5. **Fig. 8,** showing the collar not extending across the glass wall at the burrow entrance. **Fig. 9,** two days later, showing the entrance further narrowed by the collar, which now extends across the glass wall.

postulated "bits of pith or fibers from inside the burrow stuck together with an invisible material" for collar construction. In *Xylocopa pubescens* secretion from yellow glands in the metasoma hardens the partition (Gerling et al., 1979).

2.6 Smoothing and consolidating the burrow wall.—This chain was observed for five days in the nest in which rebuilding of the entrance collar (2.5, Case B) was also observed. Otherwise, it was seen rarely, during the ovipositing behavior (2.7) involving adjustment of the basal plug. Although not confirmed, it may also occur during preparation of the basal plug (2.4) and is also seen, rarely and sporadically, in the usual cleaning of the burrow wall (2.1.3).

To consolidate pith of the burrow walls, bees tamp the surface. All legs are stretched and extended to keep the body as high as possible. The metasoma is strongly bent downward (Fig. 7); the apex then tamps to solidify the burrow wall. This behavior appears synchronously with cleaning the burrow wall (2.1.3). Tamping appeared during gathering of pith and other trash and during and after the deposition of pith carried on the scopa. Tamping can be done upside down, i.e., with the dorsum on the burrow floor and the forelegs stretched to the ceiling. Sometimes a bee walks with the metasoma curved ventrad, possibly exploring for parts to be repaired using sensory hairs on the metasomal apex. During this activity, immatures are moved and cleaned if necessary.

Consolidation of the burrow wall was seen best after artificial removal of an entrance collar (2.5). On October 3, the day the collar was removed, the daughter consolidated for 33 minutes; on October 9 the mother did so for 58 minutes; and on October 11, the mother did so for 52 minutes. These consolidation sequences were mostly continuous, not interrupted with resting, but on October 9, cleaning and moving of immatures were inserted into the activity. On October 9 and 11, the mother received honey from a daughter by regurgitation slightly before the end of the sequence, and after the sequence, rested for more than an hour. As part of smoothing burrow walls, junctions of pith and glass walls in nest type 3 were thoroughly cleaned; pith dust and other debris were consolidated by tamping with the metasomal tip to produce a circular cross-section for the burrow.

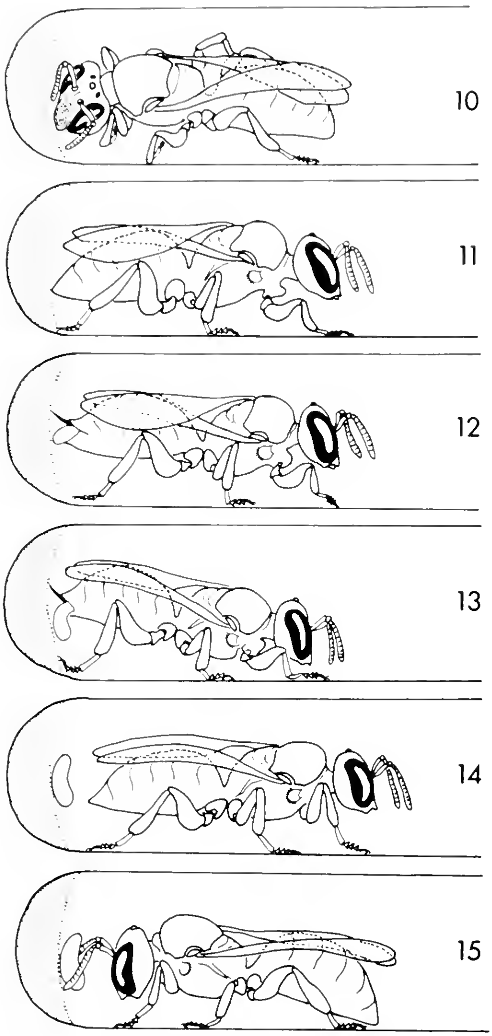
2.7 Oviposition behavior.—Unlike oviposition in cell-building Aculeata, this behavior in *Braunsapis* is not preceded by any "predictive" behaviors such as preparation of food provisions to receive an egg as in most mass provisioners. The sequence starts rather abruptly and ceases quickly. Only three cases were observed.

2.7.1 Adjustment of the basal plug.—Before oviposition, burrow walls adjacent to the basal plug are cleaned (2.1.3). Fine pith dust and admixed trash are consolidated onto the plug with the metasomal apex. This adjustment can also appear independent of oviposition, or at least not soon followed by oviposition. Sometimes admixed pollen particles make the plug yellowish. Adjustment of the basal plug was observed in detail only once (Case C, below). It was followed by checking with the antennae and pressing with the mandibles (Fig. 10).

2.7.2 Oviposition and subsequent activities.—Discovery of new eggs at our first morning survey suggests that laying is often (not always) at night. Laying is on the surface of the basal plug, the convex side of the egg commonly fitting the concave surface of the plug. The female puts the metasomal apex on the plug. The antennae are directed ventrad and occasionally moved up and down slowly. After keeping this position for a while (Fig. 11), the female raises her metasoma slightly from the plug. The tip opens. Soon the sting appears; it twitches slightly, less so after appearance of the end of the egg. The female puts the end of the egg on the plug (Fig. 12). The metasoma is raised (Fig. 13) as the egg is gradually discharged. At separation of the egg from the body, the egg is pressed by the metasomal apex and the dorsal surface of the egg is put on the approximate center of the basal plug (Fig. 14).

The time from appearance of the sting to separation of the egg from the body was 50 to 63 seconds ($x = 58$ sec., $N = 3$), distinctly less than in *Ceratina* (84–328 sec. in *C. japonica*), probably reflecting the relatively smaller egg of *Braunsapis* (Sakagami and Maeta, 1985).

After oviposition, the female advances slightly and turns around. Before or after turning, or both, she takes a short rest (up to 3 min.), accompanied by self-grooming. Then she pinches the egg with her antennae



Figs. 10–15. Egg deposition in a type 3 nest of *Braunsapis hewitti*. The plug is stippled. **Fig. 10.** Queen checking basal plug. **Fig. 11.** Apex of metasoma touching basal plug. **Fig. 12.** Egg being laid, sting being shaken. **Fig. 13.** Egg mostly exposed. **Fig. 14.** Egg deposited on basal plug. **Fig. 15.** Pinching egg with antennae.

(Fig. 15) and gently cleans it with the mandibles for 20 seconds. The brushing with the inner hairs of the fore tarsi seen with older eggs was not observed.

When older eggs are dropped on the burrow floor, which happens often, they are groomed like new eggs. Pith and other dust are removed by the forelegs (and transferred to the hind legs) and the egg is pressed onto the basal plug with the face (2.1.5). Apparently eggs are always put on the basal plug when noticed.

Oviposition rates are remarkably low. The mean number of eggs laid per nest during five months was only 3.6 in solitary nests and 9.5 in eusocial colonies, with a mean per nest oviposition interval of 12.9 and 9.7 days, respectively.

Some details of the three observed layings are given here to show how this behavior is integrated with other activities.

CASE A (July 13): This nest was in the solitary phase, with a single female and a few immatures. Before 15:37, the female guarded at the entrance. At 15:37 she walked toward the bottom of the nest, manipulated and pressed a larva, passed the pupa, reached the bottom, and turned around there. The egg was laid as described above. Soon she returned to the entrance and resumed guarding.

CASE B (August 28): This colony was in a semisocial phase, with a larger (queen) and a smaller (worker) female as well as immatures. Shortly before oviposition, the queen was on the basal plug. At 16:18–16:27, the queen laid an egg and pinched it with her antennae (Fig. 15) as described above. At 16:28 she groomed herself, turned, pinched the egg with her antennae again, and touched it with the mandibles again, and then groomed again. She then walked toward the entrance, turned around, returned to the nest bottom, pushed one egg against the basal plug, and rearranged two other eggs as she pushed two larvae to the plug. She rested, then again pushed a larva against the plug. From 16:33 to 17:33 she drank honey from a larva (the honey was absent when observation began and had probably been deposited on the larva by the worker during the observation period), manipulated pollen dust on the floor, groomed the two larvae near the middle of the nest and pushed them toward the bottom, and repeated such acts alternately.

CASE C (October 9): This colony was in the eusocial phase with a mother (queen), daughter (worker), and immatures. From 08:46 to 10:08 the mother guarded. At 10:08 the mother and daughter exchanged positions, the daughter now guarding. After a brief rest near a larva, the mother walked to the basal plug, turned, gnawed the burrow wall and pressed the dust into the plug with her metasomal apex, turned again and continued tamping dust. Then she touched the plug with her closed mandibles, possibly smoothing the surface. At 10:25 the queen laid an egg as described above. The time from appearance of the sting to deposition of the egg was 63 seconds. Then the mother rested, walked a little, and turned around, turned again, walked a little holding an old egg with her forelegs, put it on the basal plug beside the new egg, pinched it with her antennae and touched it with the mandibles, then brushed it with the forelegs. The new egg was pinched but not groomed. The mother turned around, walked, groomed herself, and turned around again. From 10:32 to 11:06 the queen entered into a series of activities in the nest, i.e., walking, moving and grooming four larvae, regurgitating honey on two larvae, and retrieving it from one. At 11:06 the daughter and queen exchanged places and the queen resumed guarding.

2.8 Foraging and associated activities.—This chain occurs in all phases, solitary, semisocial, or eusocial. For this reason and because of the presence of exposed immatures to be cared for and fed, the foraging chain in *Braunsapis* is more complicated than in solitary, mass-provisioning bees; moreover, the foraging chain is closely connected with feeding larvae (2.9). The queen does not participate in foraging. A foraging bee may return with both pollen and nectar or with nectar alone. (Returns without pollen or nectar are included in the latter category as they cannot always be distinguished from nectar-carrying trips and may be merely feeding flights, 1.6.)

The number of pollen foraging trips per day for a nest is usually one (maximum, four). On many days, foraging does not occur, even in colonies with immatures and during favorable weather. The duration of pollen foraging trips was 1-16 minutes ($\bar{x} = 5.3 \pm 4.1$, $N = 22$) and of nectar trips 2-22 minutes ($\bar{x} = 8.8 \pm 6.4$, $N = 8$). Flowers were always present less than a meter from the nests.

Pollen loads are deposited on the nest floor, usually in one heap (maximum, three). Such pollen stores are to be seen in the prelaying period of the solitary phase (confirmed May 17, only three days after bees were liberated in the cage). When the amount of stored pollen per nest was checked once a day, it became clear that pollen storage occurs irrespective of social phase and the presence or absence of immatures. Pollen storage on burrow walls is well known in other allodapine bees (Michener, 1968, 1971, 1990); in *Allodapula acutigera* it rarely occurs in the absence of growing larvae but other *Braunsapis* species resemble *B. hewitti* in this respect (Michener, 1971). Stored pollen in the prelaying period of the solitary phase is occasionally eaten by the female (and by other females who drift into the nest), but it is seemingly not stored for the coming brood rearing. In some nests, particularly those in which drifting was frequent, more than one female brought pollen loads several times; their traffic spread pollen over the nest walls, staining them yellow. This dry pollen when old is occasionally swept out of the nest (2.1.3) and renewed. Pollen foraged during the brood rearing period is moist and in clumps—probably it is mixed with nectar—and it is evidently eaten by both larvae and adults.

From liberation on May 14 to October 27, the observed number of pollen renewals (when pollen stored in a nest disappeared [swept out] amd then was replaced by fresh pollen) was 0-12 ($\bar{x} = 4.7$, $N = 20$) per nest in solitary nests, 1-13 ($\bar{x} = 7.6$, $N = 6$) in semisocial nests, and 2-10 ($\bar{x} = 6.3$, $N = 4$) in eusocial nests. This indicates frequent renewal of the pollen stores irrespective of social phase, and corresponds with field observations (Michener, 1968, 1971) that most of the time most *Braunsapis* larvae have no food. Of course small increments of pollen would have gone unnoticed in our observations of sizes of pollen stores.

2.8.1 Honey deposition on immatures.—Before departure for foraging, a female commonly regurgitates honey onto the curved venter of the large larva located nearest the entrance (Fig. 16). The same larva may receive as many as four honey droplets in succession. Occasionally pollen is admixed in the regurgitant. Smaller larvae are used in the absence of larger ones and eggs in the absence of larvae. Once a drop was found on the head of a pupa. Honey drops are of course bigger on larger larvae. Honey may also be deposited on a larva that is holding a pollen lump or on two larvae lying side by side.

Because honey so deposited was usually retrieved by the same bee soon after homing, the deposition cannot be regarded as feeding, although partial intake by the larva is not precluded and was sometimes observed.

As shown in Table 3 honey deposition was also observed toward the end of the day without departure of female bees. In such cases, as when the bee made a trip, the honey was retrieved sooner or later; one honey drop remained on a larva for four days. On August 22 (21:00) a larva in three out of 30 nests held a honey drop. On August 28, such larvae were found in six of the 30 nests. Perhaps departure after deposition was forestalled by decreased light intensity, or perhaps deposition was for evaporation of water from the honey. One female deposited honey on a larva, looked out at the entrance but did not depart, and then retrieved the honey from the larva. Sometimes bees other than the depositor ingested honey from larvae (see 2.9.1).

2.8.2 Honey delivery to adults.—Both honey delivery to and withdrawal from adults (2.8.6) are interadult behaviors but are described under 2.8 because of their intimate linkage with foraging. Delivery of honey to another adult by a forager before departure is behaviorally identical with feeding by regurgitation (Fig. 17), but can be distinguished by the retrieval that takes place after the forager's return. (Food regurgitation after solicitation was regarded as feeding nest mates, 3.6.)

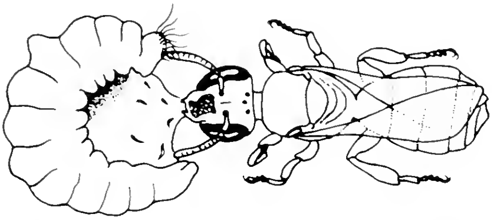


Fig. 16. Departing forager of *Braunsapis hewitti* depositing honey on larva.

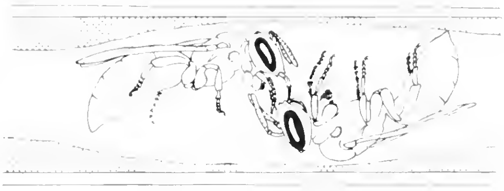


Fig. 17. Departing forager of *Braunsapis hewitti* (right) delivering honey to queen.

Deposition on immatures and delivery to other adults before departure, both followed by withdrawal on return, must decrease body weight of foragers for flight. Deposition on the burrow wall is probably avoided because honey soaking into the burrow wall would be lost and might lead to the growth of fungus. Table 3 shows that immatures were more frequently used for temporary honey storage than adults.

Returned foragers often gave the impression that they "knew" where "their" honey had been deposited before departure, and came back to reclaim it either from larvae

Table 3. Honey storage. Numbers and castes of departing *Braunsapis hewitti* observed and relationship between their departures and honey deliveries onto immatures or to adult (mostly guard) bees. Delivery of small drops of honey to immatures was considered to be probable feeding and was excluded from this table (Q, queen; W, worker).

Honey delivery	Phase					Total
	Solitary[1]	Semisocial		Eusocial		
		Q	W	Q	W	
No delivery	4	6	6	2	3	21
Onto immatures[2]	45	1	11	1	18	76
To adults	—	—	2	1	1	4
Onto immatures and to adults[3]	—	—	6	1	6	13
Onto immatures without departure[4]	14	—	2	—	1	17

[1] Only nests containing immatures.

[2] Time from delivery to departure: 2-28 min. ($\bar{x} = 6.7 \pm 7.7$, $N = 10$).

[3] Time from delivery to departure: 4-18 min. ($\bar{x} = 9.5 \pm 5.6$, $N = 11$).

[4] Observed only between 15:00 and 21:00 hrs.

(2.8.1) or from adults. Because of our small nest populations, however, there was commonly only one adult or larva in the appropriate place from which the forager could retrieve honey.

2.8.3 Pollen collecting.—This sequence is like that seen in various other taxa of bees. Pollen is collected from anthers with the forelegs, transferred via the middle legs to the hind legs (tibial scopa), and accumulated there as pollen loads, which are not swept off until the bee is back in its nest (2.8.8).

2.8.4 Knocking and raking.—Like 2.8.2, 2.8.5, and 2.8.6, this behavior belongs among the interadult behaviors described subsequently. However, these behaviors also form part of the foraging behavior chain in multifemale nests.

In multifemale nests, the returned forager knocks on the metasoma of the guard rhythmically with the mandibles to release turning around by the guard and subsequent exchange of positions. When highly motivated, the forager also rakes with a quickly moved foreleg on the guard's metasoma. Raking also appears within the burrow, when one bee solicits exchange of position from behind another (3.4).

2.8.5 Buccal contact.—In response to knocking (and raking), the guard turns and faces the returned forager. Before exchanging positions, these bees lightly touch each other's closed mandibles. This buccal contact at exchange of positions also occurs within the burrow. Occasionally it is repeated violently, but it is often omitted in smooth exchanges of positions (see 3.4).

2.8.6 Honey withdrawal from adults.—At buccal contact, the forager may retrieve honey from the bee to whom honey was delivered before departure, usually the guard. Such withdrawal occurs all at once or in several acts interrupted by brief rests. Occasionally withdrawal does not occur. Sometimes instead the forager feeds the other bee by regurgitation (3.6).

2.8.7 Honey withdrawal from immatures.—The returned forager commonly withdraws (=retrieves) honey deposited on immature(s) (Fig. 18). This may follow retrieval of honey from an adult (usually the guard). Retrieval from a larva is often repeated several times (maximum of eight) interspersed with episodes of resting, grooming, walking, guarding, and pollen depositing on immatures. Retrieval is often incomplete. In an extreme case, honey deposited on a large larva was left for four days before retrieval, and then was taken all at once.

Sometimes a female other than the depositor drinks honey from an immature, probably as food. Withdrawal time varies with amount deposited, but the longest continuous withdrawal lasted for 136 seconds, and discontinuous withdrawals ofted lasted for several minutes with pauses every few seconds. After honey retrieval from a larva—and during deposit of pollen—a pollen lump on the larva is sometimes lightly kneaded or its position changed.

Occasionally after incomplete honey retrieval, pollen is deposited on the larva, forming a pollen paste. Moreover, deposition of pollen on a larva with a large drop of honey often occurs in the evening when honey deposition has not been followed by departure.

2.8.8 Pollen unloading.—In unloading pollen, the bee uses a portion of the self-grooming routine (1.7); the middle legs sweep pollen from the scopa, the hind legs being held close to the body. Afterward, the hind legs are rubbed together, removing the remaining pollen. The bee always faces toward the entrance when unloading, as in *Ceratina*.

2.9 Feeding larvae.—Seen in the brood-rearing period of solitary, semisocial, and eusocial nests, this behavior chain occurs (1) after the foraging chain, (2) after oviposition when the mother is returning to the entrance to guard (honey only), (3) independently (although this seems exceptional), and (4)

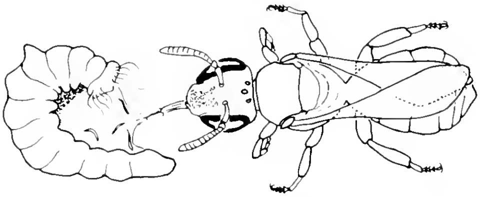


Fig. 18. A returned forager retrieving honey that she had deposited on the larva.

during grooming of larvae. The sequence includes grooming a larva, feeding the larva honey, and then picking up pollen and depositing it on the larva. The last two are repeated.

There were numerous combinations and sequences of behavior by foragers returning with pollen and/or honey. In 30.6% of 111 cases studied, the returning forager that had deposited honey on a larva before leaving retrieved honey from the surface of a larva, then unloaded pollen on the nest wall. In another 21.7% the forager retrieved honey from a larva but did not have a pollen load to deposit. No other combination of behaviors exceeded 7.2% of the observed sequences. There was no significant difference in these behaviors among social phases. Cases in which the foraging and feeding chains occurred synchronously (homing with pollen load—pollen unloading—pollen deposition on larva) constituted 29% of all observed cases. Only in three cases (8%) did bees that homed without pollen then pick up pollen from the burrow floor to deposit on a larva. Deposits were often made on larvae that already held pollen on their venters.

From these facts, it seems that the feeding chain is not merely a continuation of the foraging chain. Feeding is synchronized with grooming of larvae so rarely as to suggest that these two behaviors are also independent (Table 4).

2.9.1 Feeding honey to larvae.—We have already described the large amounts of honey that are deposited on immatures by foragers before they fly away (2.8.1), perhaps to decrease body weight. This honey is commonly retrieved when the foragers return. Small amounts of honey, however, are occasionally put on the larval venter near the mouthparts during grooming (Table 4), when a mother returns to the entrance to guard after oviposition, or as burrow walls are being cleaned. These deposits are not usually retrieved. Sometimes, a small fraction of a large deposit is left on an immature. Such small amounts of honey must serve as food for the larvae. Occasionally small amounts of honey are deposited, usually on small larvae, during walking in the burrow; these are occasionally followed by deposition of a bit of pollen. As Table 4 shows, grooming larvae and deposition of honey only are more prevalent in the eusocial phase than in the others, while deposition of pollen only seems to show the reverse relationship. It should be noted that in this table comparisons up and down the columns are appropriate but comparisons between the three phases depend on the numbers of nests in those phases and are therefore of little biological significance.

2.9.2 Feeding pollen stores to larvae.—Pollen in the nest burrow creates a situation in which larvae are fed progressively but from a mass of stored pollen. Dry pollen stored on the burrow walls is scraped up with the mandibles and usually moistened beneath the folded glossa before it is deposited on the venter of a larva. Michener (1972b) described the process in greater detail. Honey on a larva may also serve to moisten deposited pollen.

Pollen is deposited on the larval venter in the same position as honey (2.8.1). Placement of pollen on a larva usually takes place before, during, or promptly after retrieval of previously deposited honey; usually pollen is deposited once but sometimes several times on the same larva (maximum, four times) with intervening travel to and from the pollen storage place or interruption by feeding honey. Sometimes a pollen lump is kneaded and shaped before deposition; the maximum time for such kneading is one minute. When two larvae of similar size lie side by side, a communal pollen lump may be placed between them, but this seems rather accidental—an "occasional event" according to Michener (1971), writing about other *Braunsapis* and *Allodape* species.

3. INTERADULT BEHAVIORS

Of course interadult behaviors occur only in multiple female nests. One group of interadult behaviors has already been described because their association with the foraging chain in multifemale nests seemed important. These behaviors are included under nest maintenance (2.8.2, 2.8.4 to 2.8.7).

The same interadult behaviors were seen in semisocial and eusocial colonies. The few

Table 4. Number of observations showing the relationship between grooming and feeding of larvae in *Braunsapis hewitti*.

	Phase					Total
	Solitary	Semisocial		Eusocial		
		Q	W	Q	W	
Depositing pollen only	31(2)[1]	1	23	3	20(3)[1]	78(5)[1]
Depositing pollen soon after grooming larva	1	—	2	—	—	3
Grooming larva only	6	5	18	6	89	124
Depositing honey only[2]	4	—	7	3	12(2)[1]	26(2)[1]
Depositing honey immediately after grooming larva[2]	1(1)[3]	—	1	2	8(4)[3]	12(5)[3]

[1] Cases associated with kneading and shaping of pollen mass are indicated in parentheses. When honey only is deposited, it is mixed with pollen already on the larva for kneading.

[2] Only cases with deposition of a small amount, excluding cases soon followed by complete retrieval of the honey. A large amount of honey deposition was not regarded as feeding.

[3] Cases with partial retrieval after deposition are shown in parentheses.

male behaviors observed are described in Section 6; mating and related behaviors were not observed. Frequencies of interadult behaviors are low (lower part of Table 6). In multifemale nests, the queen usually spends most of her time guarding (2.1.1) while other females (workers) stay in the burrow or forage. Encounters occur either at the nest entrance, where departing or returning worker foraging bees meet the guard (queen) or, within the burrow, where workers meet other workers or the queen when she moves down into the nest. The interactions include thrusting and pushing away (3.3, 3.5), actions that may involve agonism, but no clearly aggressive or agonistic behaviors were observed.

Most interadult behaviors are brief; they are linked by resting and walking, which are not mentioned below unless necessary. Except for inhibiting the approach of a juvenile to the entrance (3.8), most interadult behaviors appear to be connected with other behaviors; they include self- and nest-maintenance behaviors as primordia, but the relationships are difficult to clarify.

3.1 Avoidance.—Interadult avoidance includes alerting, checking, and turning around, all discussed as self-maintenance or nest-maintenance behaviors, and antennation, which is a part of checking behavior. An actor (see Materials and Methods) approaching an actee, face to face or face to tail, either checks the actee with the antennae or stops without contact. Then the actor may (1) rest at the stopping point (actee also rests or walks forward), (2) retreat backward (actee either rests or walks forward or backward), or (3) turn around and walk away, leaving the actee.

Avoidance may reflect submissiveness, as is likely in *Lasioglossum zephyrum* (Buckle, 1982), but in *Braunsapis* it is performed by both queens and workers; queens avoid less frequently, probably because they usually guard at the entrance and so move less.

3.2 Antennation.—Antennation is checking with the antennae. All interadult behaviors except some avoidance interactions are prefaced by antennation, usually mutual, although it is not mentioned below in each case.

3.3 Thrusting.—After a face to face encounter and antennation, the actor may thrust at the actee. A thrust is a short, sharp forward movement by the actor; the head of the actor touches or nearly touches the actee. It is approximately the movement called a nudge in the literature on the halictine, *Lasioglossum zephyrum* (e.g., Brothers and Michener, 1974). Thrusting is usually done only once in a given encounter. In only one of 22 cases did an actor thrust twice in succession. Thrusting occurred between all combinations of nest mates: sisters of the same generation, mother and daughter, mother and son, and males of the same generation. These 22 cases were analyzed as follows:

In meetings involving thrusting between the guard (queen) and another individual, the guard thrust 15 times out of 22 cases, both thrust simultaneously in one, and the other bee thrust in six. In the six cases of thrusting between mother (queen) and daughter, the mother thrust in five; between same generation females, the queen thrust in seven out of 10 cases; and between mother and son, the son thrust in three of the four cases.

Before or after thrusting, the actor solicited position exchange (see 3.4) in seven of 16 cases. (Encounters between a male and a female are excluded, for males do not solicit position exchange.) After thrusting, position exchange occurred in 14 of 22 cases, whether or not it was solicited. After thrusting, the actee turned or retreated without position exchange in 5 of 18 cases.

Although not quantitatively documented, thrusting occurred irrespective of whether the actor faced toward the entrance or the nest bottom. Between queens and workers, the queen usually thrust and position exchange followed. Thus, thrusting may be part of solicitation for position exchange (3.4). Retreat or turning by the actee may serve as avoidance of position exchange.

3.4 Position exchange.—Smooth exchange of position by nest mates is essential in species that have multiple-female nests in narrow burrows or tubes. Position exchange consists of unit behaviors: solicitation by knocking and raking (2.8.4) and the exchange itself (a simple application of walking, 1.3). A smooth exchange requires only a few seconds. It is well developed in *Braunsapis* and is usually performed face to face (84 of 95 instances), and the passing is usually venter to venter as noted by Michener (1972b), although we observed several variants (Fig. 19). In a face to face position exchange, which is usually preceded by raking (see 2.8.4), the actor either crawls over or creeps beneath the actee. Although not separately counted, passing over was commoner than passing beneath. (Passing beneath large immatures was also uncommon.) In face to tail situations, raking usually released turning around by the actee, and the actual exchange was made face to face. This was true of all 44 censused interactions at the nest entrances (worker leaving or returning past a guard) and of all 41 face to face position exchanges monitored in the nest burrows.

3.4.1 Solicitation of exchange.—When the actor and actee are in face to tail positions, as when a homing bee (actor) wishes to pass the guard (actee), the actor solicits exchange by knocking and raking, and position exchange occurs immediately. (Raking is less frequent in *Braunsapis* than in *Ceratina*.) When the actee turns around in response to the knocking and raking, or when the encounter is initially face to face, the actor appears to solicit exchange by "head-rotating" about one body length

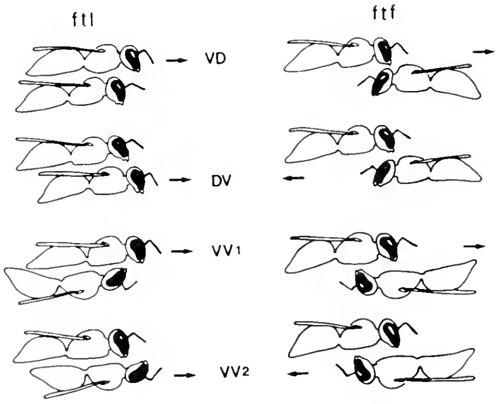


Fig. 19. Diagrams showing different types of position exchange in nests of *Braunsapis hewitti;* ftl, meeting face to tail; ftf, face to face; V, ventral; D, dorsal. The actor (initiator of the exchange) is indicated in each case by an arrow (in front of its head) showing its direction of movement.

away from the actee. The head is rotated several times more than 180° fairly quickly. (In *Ceratina okinawana* but not in *C. japonica* or *C. flavipes,* the actor slowly turns her head, Maeta and Sakagami, unpublished.) It is not clear how such a movement could be perceived in a dark natural burrow; possibly a vibration or odor is associated with rotation. In smooth exchanges, this act is often omitted. Buccal contact (2.8.5) frequently appears between the homing bee and the guard, but is less frequent in exchanges within the burrow.

3.4.2 Exchange.—Before position exchange, one of the pair ordinarily turns upside down and exchange is made venter to venter, as noted above (3.4). The actee presses the dorsum of the body, particularly of the head and metasoma, against the burrow wall, stretches out the antennae, and keeps the legs tightly in contact with the body, thus preparing an ample space between itself and the other burrow wall to facilitate passage (Fig. 20).

3.5 Pushing away.—After exchanging positions with the guard, a departing worker inspects the outside, extending her antennae. If this hesitation is prolonged, the queen, still facing outward, pushes the worker away with the mandibles. If the forager is still there after the guard has turned to face the bottom of the nest, the guard pushes her away with the metasoma. Pushing away may be an aggressive modification of thrusting.

3.6 Feeding of adults.—This chain consists of food solicitation by the actor, regurgitation by the actee, and food intake by the actor. The sequence includes frequent antennation. Standing face to face, the actor extends her glossa to touch the base of the folded glossa of the actee (solicitation), and the actee relaxes the glossal base and regurgitates honey, which is withdrawn by the actor. Occasionally both bees take the same dorsal-up position as in honey bees, but usually one partner, either the actor or actee, takes the upside down position as illustrated by Michener (1972a), and as in *Ceratina.* This position may facilitate food transfer within the narrow nest cavity. Sometimes the glossa is inserted between the relaxed mandibles of the actee. Rarely, the actee rejects solicitation.

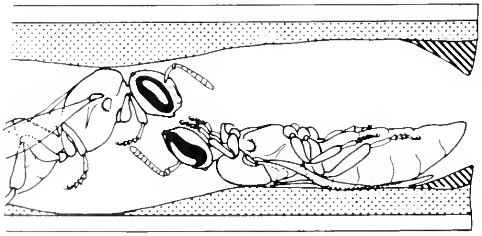


Fig. 20. Common position of actee (at right) of *Braunsapis hewitti* in position exchange, leaving space above its body for passage of actor.

At the end of the solitary phase, a newly emerged daughter is fed by the mother. Newly emerged adults are presumably fed in all nests. After daughters make flights from the nest at 4 to 6 days of age, they are not again fed. However, a mother may be fed by a daughter. Michener's (1972a) observations of *Braunsapis foveata* were of older adult females feeding younger bees of both sexes.

Newly emerged adults of *Braunsapis hewitti* eat pollen from the floor of the burrow. When one newly emerged daughter found no pollen store, she performed face brushing (3.7) with the mother for a long time. The mother departed and on her return swept pollen off in front of the daughter, who ate it as in *Ceratina.*

3.7 Face brushing.—Face brushing occurs in face to face encounters when the actor, who may face either the entrance or the nest bottom, brushes the eyes or paraocular areas of an actee with the hairs of the fore tarsi by moving her forelegs quickly up and down. The actee withdraws the antennae and keeps them in tight contact with her face (Fig. 21).

Face brushing was observed in both eusocial and semisocial colonies between

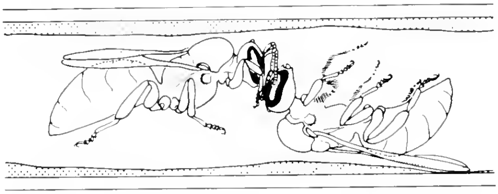


Fig. 21. Face brushing by *Braunsapis hewitti;* individual at left is actor, at right, actee.

queens and workers. Of 26 observed cases, three were followed by no obvious response; activities associated with the other 23 were as follows: in 17 cases there was simultaneous honey solicitation by the actor who was then fed; in one case solicitation and feeding followed immediately after brushing, and in five cases, the bee whose face was being brushed solicited position exchange.

Face brushing is commonly associated with food solicitation, appearing irrespective of caste. As honey feeding usually occurs only in response to solicitation, face brushing may represent an indirect type of food solicitation.

3.8 Inhibiting juvenile's approach to the nest entrance.—When a newly emerged juvenile walks toward the nest entrance and confronts the queen, the latter inhibits further advance by pushing the juvenile back with her head, which is moved up and down slowly but distinctly. The queen's mandibles may be open or closed. The juvenile either backs up or turns around and walks away. This behavior was not seen with young adults more than two days old.

3.9 Oophagy.—This behavior was not observed directly, but it is included here because it often appears in social contexts in other social Aculeata. The rate of egg disappearance is somewhat higher in solitary nests of *Braunsapis* than in colonies (Table 13), which suggests that socially motivated oophagy is not common in this species.

4. Ethometry

Parts 1 to 3 describe numerous recognized behaviors but give minimal and often only qualitative information on their frequencies and durations. Some such behaviors are common, others rare; some take a long time, others are brief. In this section the relative frequencies and durations of behaviors are examined.

4.1 Methods.—For the frequency scores, the number of times a behavior occurred per one-hour observation period was counted and analyzed (Table 5, left side; Table 6). For the duration scores, the amount of time spent in each behavior (rounded to the nearest minute) was calculated. Behaviors completed within a minute were counted as taking one minute. If two or three behaviors occurred in the same minute, the duration of each was counted as one-half or one-third minute, respectively. More than three behaviors never occurred within one minute. After the time spent in each behavior was calculated (Table 5, right side; Table 7), the sum was subtracted from 60 minutes to obtain the approximate duration of guarding, the most time-consuming behavior. Sometimes two or three relatively inactive nests were observed at the same time, resulting in two or three of the one-hour observation periods. Some nests, probably with more active colonies, were chosen more frequently than others for observations. Therefore the data are biased toward activity; time spent resting and guarding must be even more predominant than indicated by our statistics.

Not all self-maintenance, nest-maintenance and interadult behaviors described in Parts 1–3 are cited in the ethometric tables because many were so rare as not to occur in the hours of intensive observation. Guarding (2.1.1), inspecting at the nest entrance (1.2) and self-grooming (1.7) are cited in the time scores but not in the frequency scores because their durations are great, while turning around within the nest (1.4) is cited in the frequency scores alone because it only takes a few seconds. Some of the behavior names as given in Parts 1–3 are simplified for Part 4, and functionally related behaviors are combined. The behavior names used here are listed below with the equivalents for Parts 1–3 in parentheses. This list provides for easy reference from the brief titles of behaviors cited in Tables 5 to 7, to the sections where those behaviors are described.

Walking (1.3, Walking).
Turning (1.4, Turning around).
Grooming immatures (2.1.4, Grooming immatures).
Pollen handling (1.14, Transfer of pollen; 2.9.2, Feeding pollen stores to larvae).
Pollen unloading (2.8.8, Pollen unloading).
Burrow cleaning (2.1.3, Cleaning the burrow wall; 2.2.5, Sweeping pith dust from the nest entrance).
Flight (1.6, Flight; 1.9, Pollen intake; 1.10, Nectar [honey] intake; 2.8.3, Pollen collecting; 1.7 [part], Self-grooming). This category includes all extranidal activities. The distinction between mere flight and foraging was sometimes impossible to make, and so they are lumped. The self-grooming (1.7) that occurs immediately before and after Pollen unloading is included here.
Honey withdrawal (2.8.7, Honey withdrawal from immatures).
Feeding larvae (2.9.1, Feeding honey to larvae). Feeding pollen stores to larvae (2.9.2) is included in Pollen handling.
Moving immatures (2.1.5, Moving immatures).
Oviposition (2.7.2, Oviposition and subsequent activities).
Guarding (2.1.1 [part], Guarding).

Inspecting (1.2, Alerting/Inspecting). Included here is only inspecting at the nest entrance, i.e., guarding facing outward.
Resting (1.1, Resting; head directed toward the nest bottom).
Self-grooming (1.7, Self-grooming).
Compacting pith dust (2.5, Preparation and repair of the entrance collar; 2.6, Smoothing and consolidating the burrow wall).
Buccal contact (2.8.5, Buccal contact).
Position exchange (3.4.1, Solicitation of exchange; 3.4.2, Exchange).
Pushing away (3.5, Pushing away).
Feeding adults (3.6, Feeding of adults).

We suspect that bees imprisoned in nests and attached vials (1v nests) may behave less like free individuals than those able to forage in a greenhouse cage. The sometimes distinctive behavior of bees in 1v nests may be due to imprisonment, or to presence of males, which were absent in all other nests. References in the following sections to semisocial nests exclude type 1v nests unless we write "all semisocial nests."

4.2 Behaviors in solitary nests.—The results of 81 nest-hours of observations are presented in Table 5. It shows (right half) that most of the bee's daily life is spent guarding at the entrance, facing into the nest. This behavior, combined with inspecting outward at the entrance, occupies 90.9% of daily life. As noted in 1.1, guarding is actually resting at the entrance; resting in the interior occurs only occasionally in solitary nests (Table 5).

Except for guarding and inspecting, walking was the behavior most frequently observed in solitary nests. The value given in Table 5 is an underrepresentation because when walking was associated with other behaviors, it was not counted. Nevertheless, the duration of walking is relatively short. The same can be said of turning around, for the duration of each turn was so short that it could not be reliably measured. These two behaviors are often interspersed among other behaviors, thus leading to rather high scores in Table 5.

Grooming immatures was the most frequent nest-maintenance behavior (Table 5), partly because mere touching of immatures with the forelegs or tongue was counted.

Table 5. Frequencies and durations of behaviors in 29 solitary nests of *Braunsapis hewitti* (81 observation hours).

	Frequencies		Durations	
	No.	Percent of Total	Minutes	Percent of Total
Walking	160	37.7	18.0	0.4
Turning[1]	108	25.3	—	—
Grooming immatures	71	16.6	56.2	1.2
Pollen handling	27	6.3	17.0	0.3
Pollen unloading	19	4.4	16.0	0.3
Burrow cleaning	16	3.7	9.5	0.2
Flight	10	2.3	220.2	4.5
Honey withdrawal	7	1.6	7.0	0.1
Feeding larvae	5	1.2	1.5	0.0
Moving immatures	3	0.7	4.5	0.1
Oviposition	1	0.2	0.5	0.0
Guarding[2]	—	—	3974.0	81.8
Inspecting[2]	—	—	440.5	9.1
Resting[2]	—	—	57.4	1.2
Self-grooming[2]	—	—	37.5	0.8
Totals	427	100	4860.0	100

[1] Not scored for duration because it happens too quickly for meaningful measurement.

[2] Not scored for frequency (see text).

Table 5 shows that the time spent in grooming immatures is longer than that spent in self-grooming.

Pollen unloading (2.8.8) is seen in two different situations: after pollen foraging and quite apart from foraging, in combination with pollen handling. At least in artificial nests, pollen often accumulates on the burrow floor. Females frequently gather this pollen on their hind legs and then unload it, as if "trapped" by this meaningless sisyphean task.

Oviposition was observed only once during the 81 nest-hours of observation, indicat-

Table 6. Frequencies of behaviors in colonies of *Braunsapis hewitti*.[1]

	5 Eusocial Colonies (45 hrs.)				2 Semisocial Colonies (15 hrs.)				2 Semisocial Colonies in 1v nests (14 hrs.)					
	Queens		Workers		Queens		Workers		Queens		Workers		Males	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
Walking	**48**	30.0	**142**	25.9	**39**	43.5	**93**	25.4	40	47.6	45	31.0	15	27.9
Turning	**64**	40.0	**112**	19.9	**28**	31.1	**98**	26.2	24	29.3	22	15.2	12	22.2
Grooming immatures	**9**	5.6	**64**	11.4	**6**	6.7	**32**	8.6	**3**	4.9	**10**	6.9	0	0.0
Pollen handling	**0**	0.0	**17**	3.0	**2**	2.2	**51**	13.6	1	1.2	2	1.4	1	1.8
Pollen unloading	**1**	0.6	**32**	5.7	**5**	5.5	**29**	7.8	**0**	0.0	**7**	4.8	0	0.0
Burrow cleaning	**7**	4.4	**83**	14.8	*4*	4.4	*12*	3.2	**1**	1.2	**24**	16.6	0	0.0
Flight	4	2.5	19	3.4	*2*	2.2	*9*	2.4	1	1.2	1	0.7	3	5.6
Honey withdrawal	0	0.0	11	1.9	**0**	0.0	**11**	2.9	0	0.0	0	0.0	3	5.6
Feeding larvae	1	0.6	13	2.3	1	1.1	5	1.3	0	0.0	0	0.0	2	3.7
Moving immatures	**3**	1.9	**21**	3.7	1	1.1	6	1.6	*4*	4.9	*12*	8.3	3	5.6
Oviposition	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	—	0.0
Compacting pith dust	4	2.5	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Buccal contact	11	6.8	10	1.8	2	2.2	6	1.6	*7*	8.5	*6*	4.1	5	9.2
Position exchange	**6**	3.8	**31**	5.5	**0**	0.0	**21**	5.6	*1*	1.2	*15*	10.3	8	14.8
Pushing away	2	1.2	0	0.0	0	0.0	1	0.3	0	0.0	0	0.0	0	0.0
Feeding adults	0	0.0	5	0.5	0	0.0	0	0.0	0	0.0	1	0.7	2	3.6
Total	160	100	561	100	90	100	374	100	82	100	145	100	54	100

[1] The number of nests observed is indicated before, and the number of hours of observation in parentheses after, each nest phase type. The semisocial colonies in 1v nests contained males; none of the others contained males. *N* = the number of times each behavior was observed, with the total observed behaviors at the foot of the column. The next column in each case shows the percentage of the total for each behavior. Comparison of the activity of the castes (and sexes) within each type of colony can be obtained by comparing the columns headed "*N*." A number in bold face for one caste differs from that for the other caste of the same colony type at $p < 0.01$ by chi-square test; numbers in italics differ likewise at $0.01 < p < 0.05$.

ing a very low laying rate (see 2.7.2).

4.3 Behaviors in colonies.—Records were made separately for mothers (queens) and daughters (workers) in five eusocial colonies (45 hours of observation), large (queen) and small (worker) females in two semisocial colonies (15 hours of observation), and large (queen) and small (worker) females and males in two other semisocial colonies in 1v nests, each of the last with one male (14 hours of observation). Several behaviors not listed in Table 5 are reported; nearly all are interadult behaviors (Part 3). For frequencies, interadult behaviors were recorded only for the actors, not the actees. For durations, times for both actors and actees were tallied. Tables 6 and 7 summarize the results of these studies.

To shed light on possible clustering of behaviors, we examined the number of hours in which each behavior occurred for each class of nest. Of course in general the number of hours in which a behavior was seen is highly correlated with the frequency and total duration of that behavior. But if a behavior was seen in numerous hours, probably that behavior was well scattered through the observation time. The exceptions, in which behaviors are limited to a few hours, are in those series of observations based on few or only two nests (Tables 6 and 7, especially all the semisocial nests). We conclude that these exceptions are results of sparse data, and thus do not indicate biologically meaningful clumping of behaviors. None of the behaviors were observed principally in June or principally in August, etc.; seasonal influence on behavior evidently was not great.

Two linking behaviors, walking and turning, are most frequent in both multifemale and solitary nests. Of course, as shown in Tables 5 and 7, certain other activities like Guarding take far more time, but are not reported as frequencies. Most behaviors are more frequent in colonies (averaging queens and workers), especially semisocial colonies, than in solitary nests; i.e., the bees in colonies are more active. For most behavioral frequencies, females in solitary nests are intermediate between queens and workers (in colonies).

4.4 Task allocation to castes and sexes.—Virtually all behaviors (doubtless including egg laying, although we lack data on this) are performed at least occasionally by both queens and workers. The differences between castes are matters of frequencies and durations.

Caste differences show up prominently in Tables 6 and 7 for nearly all the behaviors listed, with the workers having higher frequencies than the queens. Even walking turns out to be a more common activity of workers than of queens. This, of course, is largely or entirely because of the large amount of time spent guarding by the queen. For the same behaviors, the same caste differences are evident in Table 7, which, however, also shows the behaviors in which queens exceed workers—guarding, inspecting, and compacting pith dust.

Guarding is clearly a key queen behavior. Obviously oviposition is also a key queen behavior but occurs so rarely that it was not seen in the multifemale nests during the periods of detailed observations; it was seen only three times in the entire study. Key worker behaviors are resting, flight (i.e., foraging), pollen unloading, and pollen handling.

In most social insects, foraging for the larval food is the most characteristic worker task. When homing flights of *Braunsapis* with or without pollen were analyzed, only once in 27 trips did the mother (queen) in a eusocial colony come home with pollen. This was soon after the emergence of her daughter and the colony may not yet have been functionally eusocial. Daughters (workers) in eusocial nests homed with pollen in 11 of 24 trips. In 17 trips, no large females (queens) in semisocial colonies homed with pollen, but smaller females (workers) did so in 13 of 36 trips. *Braunsapis* appears to follow the general rule in social insects, even though many females of the species are not in colonies.

The absence of honey withdrawal from larvae or other adults by queens reflects the fact that this behavior usually appears in workers returned from foraging flights; queens make few such flights. The low incidence of queens feeding larvae probably depends on this same fact. The somewhat

Table 7. Summed durations of behaviors of queens and workers (and males) in colonies of *Braunsapis hewitti* and percentages of total durations.[1]

	5 Eusocial (2700 mins.)				2 Semisocial (900 mins.)				2 Semisocial in 1v Nests (840 mins.)					
	Queens		Workers		Queens		Workers		Queens		Workers		Males	
	Min.	%	Min.	%	Min.	%	Min.	%	Min.	%	Min.	%	Min.	%
Walking	16.3	0.60	59.4	2.20	13.0	1.4	21.0	2.3	14.0	1.7	8.0	1.0	32.0	3.8
Grooming immatures	6.5	0.24	83.3	3.08	5.2	0.6	20.3	2.2	2.5	0.3	7.5	0.9	0.0	0.0
Pollen handling	0.0	0.00	14.8	0.55	1.7	0.2	38.3	4.2	0.0	0.0	0.3	0.1	0.0	0.0
Pollen unloading	1.0	0.04	50.2	1.86	4.7	0.5	30.5	3.4	0.0	0.0	3.5	0.4	0.0	0.0
Burrow cleaning	9.0	0.33	53.7	1.99	3.5	0.4	49.0	5.4	2.5	0.3	13.5	1.6	1.0	0.1
Flight	6.0	0.22	207.5	7.68	1.0	0.1	91.5	10.2	0.0	0.0	56.5	6.7	54.0	5.1
Honey withdrawal	0.0	0.00	5.3	0.20	0.0	0.0	8.0	0.9	0.0	0.0	4.0	0.5	0.0	0.0
Feeding larvae	0.3	0.01	9.6	0.36	0.0	0.0	5.3	0.6	0.0	0.0	0.5	0.1	0.0	0.0
Moving immatures	2.5	0.09	14.6	0.54	1.0	0.1	11.5	1.3	1.0	0.1	5.3	0.6	5.0	0.6
Oviposition	0.0	0.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—
Guarding	2538.4	94.01	0.0	0.0	842.5	93.1	0.0	0.0	675.5	80.4	19.0	2.3	0.0	0.0
Inspecting	5.0	0.18	3.0	0.11	5.0	0.6	3.5	0.4	9.0	1.1	0.0	0.0	0.0	0.0
Resting	29.0	1.07	2087.4	77.17	4.5	0.5	577.4	64.2	115.0	13.7	684.1	81.3	703.5	88.3
Self-grooming	9.3	0.34	84.5	3.13	1.0	0.1	26.3	2.9	0.5	0.1	20.8	2.5	6.5	0.8
Compacting pith dust	51.0	1.89	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Buccal contact	7.7	0.28	7.7	0.28	3.2	0.4	3.2	0.4	2.0	0.2	1.0	0.1	1.0	0.1
Position exchange	19.0	0.70	19.0	0.70	14.2	1.6	14.2	1.6	18.2	2.1	16.0	1.9	10.0	1.2
Pushing away	0.0	0.00	0.0	0.0	0.5	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

[1] The number of nests observed is indicated before, and the total number of minutes of observation in parentheses after, each phase type (2700 mins. = 45 hrs., 900 mins. = 15 hrs., 840 mins. = 14 hrs.; see Table 6). Only the semisocial colonies in 1v nests contained males. Min., number of minutes for each behavior. The next column in each case shows the percentage of the total number of minutes of observation of that phase type. Comparison of the activity of the castes (and sexes) within each type of colony can be obtained by comparing columns headed "Min."

more common pollen unloading among queens in semisocial colonies reflects the fact that the performers appeared trapped in a sisyphean cycle of "gathering pollen in the burrow—pollen unloading."

Table 6 shows that for all groups of females, walking and turning are the major behaviors whose frequencies were tabulated. These self-maintenance behaviors, however, are relatively more frequent compared to nest-maintenance behaviors in queens than in workers. Solitary females are intermediate

(Table 5). Thus ratios of different kinds of behavior also distinguish castes.

Except for position exchange and buccal contact, most interadult behaviors are so rare that they did not occur during the intensive observations used for calculation of the frequency scores. Position exchange is quite frequent and usually initiated by a worker (Table 6). Buccal contact counts in Table 7 do not include such occurrences immediately before position exchange, and could therefore be higher.

Data on durations of activities (Table 7) show that the majority of time is spent by queens guarding at the entrance and by workers and males resting within the nest. Thus for both castes, the time for inactivity far exceeds that for all activities together. (The inactivity is actually higher than represented, for many nest-maintenance and interadult behaviors lasted less than the minute used for statistical purposes, the remainder of such minutes commonly being devoted to guarding or resting.)

Percent duration of inactivity was greater for queens and less for workers compared to the figure for solitary females (except for workers in type 1v nests with males). Walking was greater for females in colonies compared to solitary females and queens walked less than workers (again, except in type 1v nests). Flight was distinctly less for queens and greater for workers compared to solitary females. Thus for various durations, as for frequencies, solitary females are intermediate between queens and workers.

In addition to the observations recorded in Tables 6 and 7, we have many records made during the entire observation period. In general they support the conclusions on caste differences indicated above and in the tables. Significant differences exist for Flight. Returning home without pollen was less common for queens than for workers, but not overwhelmingly so as is shown in Table 6. Frequencies were Queens 11, Workers 13, in eusocial colonies; 13 and 23 respectively in semisocial colonies. Honey delivery to adults (withdrawals from guards on returning home not counted) was relatively more frequent than indicated in Table 6. If feeding of daughters during the first days after their eclosion is excluded, it is almost exclusively a worker activity; for workers in eusocial nests it amounted to about 5% of all recorded behaviors (0.5% in Table 6).

Table 8, also based on observations over the entire period of study, shows the age in days after eclosion at which performance of various tasks was first recorded. Some suspiciously delayed first appearances (Nest 57) are certainly caused in part by our overlooking the first real date. Others show that various tasks are started fairly quickly after emergence. Two of the daughters dispersed at 12 and 15 days. Although they were not long-term workers, they performed some workerlike tasks before leaving.

As shown in Tables 6 and 7, males sporadically perform some nest maintenance behaviors: pollen handling, honey withdrawal, feeding larvae, moving immatures, and feeding adults. For more information on the diversity of male behavior see section 6.

5. SOCIAL STRUCTURE

Parts 4.3 and 4.4 provide data on caste differences in *Braunsapis.* Section 5 examines some aspects of caste interactions and social structure.

5.1 Transfer of honey.—Nectar or honey flow among adult colony members differs widely from that found in other bees because of two unusual routes, intake from larvae on the surface of which honey had been deposited by females and honey withdrawal from guards that received honey from departing nest mates. Table 9, based on the whole study period, shows rather frequent honey flow from queens to workers, which is rare in other social insects. However, most of these cases are accounted for either as those that appear soon after the emergence of a daughter or as withdrawal of honey from a guarding queen by a foraging worker at homing. Other instances of the queen to worker flow are rare, as in other social insects. In Table 9, delivery (to adults or immatures) and retrieval of honey by foragers is omitted (2.8.1, 2.8.2, 2.8.6, 2.8.7); likewise feeding small quantities to larvae is omitted (2.9.1).

5.2 Position exchange and domi-

Table 8. Age of beginning tasks. Age in days after eclosion of six daughters when they were first seen (last seen for first row) performing various tasks in eusocial nests of *Braunsapis hewitti* (D1, first and usually only daughter; D2, second daughter).

	Nest Code, Daughter Sequence, and Date of Emergence					
	57 D1 Jl 30	65 D1 Ag 28	69 D1 Ag 13	76 D1 Jl 21	76 D2 Jl 25	81 D2 Sp 21
Final honey solicitation[1]	—	4	—	4	2	12
Burrow cleaning	61	4	54	4	2	2
Grooming immatures	24	4	54	3	6	6
Departure from nest	61	4	9	6	23	—
Pollen foraging	61	4	13	6	23	—
Pollen deposit on larva	61	4	13	7	25	—
Feeding larva with honey	24	4	9	4	23	—
Feeding adult with honey	69	4	9	6	2	—
Survived until	Oc 27	Oc 27	Oc 27	—	Oc 27	—
Dispersed at day	—	—	—	15	—	12

[1] Refers to the feeding of young adults by the queen.

nance.—Buckle (1982) showed that in *Lasioglossum zephyrum*, the frequency of passing at encounter relates to social rank among nest mates, workers seeming to avoid queens. In studying this situation in *Braunsapis*, which seldom exhibits intracolonial aggressiveness, encounters between bees in the guard position and other nest mates were excluded because guards usually do not give way to nonforaging nest mates but always give way to departing and returning foragers. In other words, our study was based on encounters that occurred within the nest burrow. The following three sequences were observed: A. Actors approached actees and passed them. B. Actors approached actees

Table 9. Honey flow among nest mates of *Braunsapis hewitti*, and number of times that each type was recorded (L, larva with honey deposit; Q, queen; W, worker; M, male). (For exclusions, see text, 5.1.)

Social Phase	Flow Route	No Flight Activity	At Departure	At Homing		Total (excl. withdrawal)
				Withdrawal	Feeding	
Eusocial	W → Q	3	15	1	2	21 (20)
	Q → W	8[1]	3[1]	3	2[1]	3 + 13[1] (13[1])
	L → Q	2	—	—	—	2 (2)
	L → W	3	—	—	—	3 (3)
	W → W	1	4	4	—	9 (5)
Semisocial	W → Q	6	13	—	2	21 (21)
	W → M	10	—	—	2	12 (12)
	Q → W	1	—	7	—	8 (1)
	Q → M	—	—	—	—	0 (0)
	L → Q	6	—	—	—	6 (6)
	L → W	3	—	—	—	3 (3)
	L → M	2	—	—	—	2 (2)
	W → W	2	7	3	1	13 (10)

[1] Observed only with juvenile daughters (here called workers).

and actees retreated. C. Actors approached actees but retreated without passing them. A and B were regarded as dominance behaviors by actors and C as a submissive behavior by actors. A number of other behaviors occasionally performed by actors were ignored in this analysis: buccal contact, face brushing, head rotating, thrusting, honey feeding and being fed, and turning. Passing was mostly face to face but included some face to tail encounters.

In eusocial colonies, queens as actors were very significantly more dominant than workers as actors ($p < .001$, Chi squared; $N = 122$). The same situation and probability are seen in semisocial colonies ($N = 40$). Among workers in the same colony, the larger workers as actors ($N = 29$) were more often dominant than the smaller ones ($N = 22$), but the difference was not highly significant ($0.01 < p < 0.05$).

Combining eusocial and semisocial colonies, queen-worker difference was highly significant ($p < .001$, $N = 162$) while the larger-smaller worker difference was less highly significant ($0.01 < p < 0.02$, $N = 51$). Clearly, caste difference is correlated with the dominance order in *Braunsapis hewitti,* even though this species seldom exhibits the overt intracolonial aggressiveness found in many other primitively social insects. This fact, together with the largely unidirectional honey flow from workers to queens within the colony (when withdrawal from larvae and guards is excluded), demonstrates the presence in *Braunsapis* of social interactions common to many primitively social insects. That the dominant behavior characteristic of queens is restrained while they are guarding should not cloud the issue.

5.3 Colony composition and productivity in natural nests.—Colonies of *Braunsapis* collected in spring (May, 1980) and autumn (November, 1985) in southern Taiwan showed the following characteristics (Table 10):

(a) In spring, all colonies were eusocial; in autumn most were eusocial but a few were semisocial. (Most nests were inhabited by single adults, not by colonies; Maeta et al., 1984).

(b) In spring, the mean number of adult females per colony was 3.7 ± 2.0 ($N = 10$). In autumn, the number of adult females per colony was essentially the same, 3.6 ± 2.3 ($N = 12$), with a maximum of 10 females. The number of egg layers (including the mother) per colony increased in larger colonies, so that decisions as to caste are less obvious than in our small laboratory colonies.

(c) Nonlaying daughters are either workers or juveniles that presumably have the potential to become workers or layers in their natal nest, or to establish new nests. Hence, the productivity of a colony per female (= number of immatures + number of adult males/number of adult females) was calculated using only the number of laying females (C/A, Table 10) rather than the total number of adult females (C/B). This value was approximately 6.0 in both spring and autumn, irrespective of colony size. In solitary nests containing immatures, the corresponding productivity value was 2.5 ± 2.5 ($N = 31$, range 1–11) in spring and 3.3 ± 2.3 ($N = 6$, range 2–8) in autumn. Unlike most Hymenoptera (Michener, 1964), the productivity per individual in *B. hewitti* did not decrease with the increase in number of laying females. On the other hand, because of the long lives of *Braunsapis* and the probable departure of some adults before our censuses, our measure of productivity is extremely imprecise and does not at all represent life productivity of the mothers. Moreover, because we did not include workers, our figures are not comparable to productivity per female as calculated by others (e.g., Michener, 1964). The problems are the difficulty of recognizing castes in field-collected colonies, the probability that any or most females can function either as queens or as workers depending on the circumstances, and the probability of many caste intermediates. More work is needed to provide meaningful results on productivity per female (layers plus workers) in the field.

(d) The sex ratio (= F / F + M) of pupae was 0.69 (19/26) in spring nests and essentially the same, 0.70 (16/28) in autumn nests; it was 0.79 (527/671) in adults collected on flowers in spring.

5.4 Productivity of colonies in the

Table 10. Social structure of natural colonies of *Braunsapis hewitti* collected in Taiwan [A, number of egg layers (queen or other females with enlarged ovaries[1]); B, total number of adult females; C, number of immatures (egg to pupa) plus adult males in nest; D, daughter; E, egg; L, larva; M, mother; m, male; P, pupa (in column P, f, female, m, male pupae)].

No. of Layers (A)[1]	Nest Code	No. of Females (B)	No. of Immatures and Adult Males (C)					No. of Inseminated Daughters	Ratio	
			E	L	P	m	Tot.		C/A	C/B
May 5–8, 1980 (Kenting and Szechungchi)										
1	C-8	M + D	0	1	1	0	2	—	2.0	1.0
1	A-39	M + D	0	5	0	0	5	—	5.0	2.5
1	B-58	M + D	1	2	0	0	3	—	3.0	1.5
Means (A = 1)		2.0					3.3	—	3.3	1.7
2	A-19	M + D	5	3	1	0	9	—	4.5	4.5
2	D-19	M + D	2	1	1	0	4	—	2.0	2.0
2	K-14	M + 3D	6	17	9	0	32	—	16.0	8.0
2	K-27	M + 3D	1	3	1	1	6	—	3.0	1.5
2	B-12	M + 6D	2	4	1	1	8	—	4.0	1.1
Means (A = 2)		3.8					11.8	—	5.9	3.4
3	B-45	M + 4D	5	2	3	1	11	—	3.7	2.2
3	A-5	M + 6D	5	12	6	2	15	—	8.3	3.6
Means (A = 3)		6.0					13.0	—	6.0	2.9
November 16, 1985 (Kenting)										
1	25	2D	1	4	0	0	5	0	5.0	2.5
1	6	M + D	0	3	0	0	3	0	3.0	1.5
1	12	M + D	0	1	1f	0	2	0	2.0	1.0
1	18	M + D	0	1	0	0	1	0	1.0	0.5
1	4	M + 2D	0	11	2f	1	14	0	14.0	4.7
Means (A = 1)		2.2					5.0		5.0	2.0
2	14	2D	2	1	0	0	3	2	1.5	1.5
2	21	M + D	4	9	4m1f	0	18	0	9.0	9.0
2	11	M + 3D	2	10	1m1f	0	14	0	7.0	3.5
Means (A = 2)		2.7					11.7		5.8	4.7
3	39	M + 2D	1	6	1m1f	0	9	0	3.0	3.0
3	7	M + 4D	4	8	0	0	12	0	4.0	2.4
3	30	M + 5D	2	11	4m2f	0	19	0	6.3	3.2
Means (A = 3)		4.7					13.3		4.4	2.9
4	34	M + 9D	2	13	3m2f	3	23	0	5.8	2.3

[1] Determined by the method used by Kurihara et al. (1981) and Goûkon et al. (1987).

greenhouse.—These notes and Tables 11 and 12 supplement those provided by Maeta et al. (1985). The number of eggs laid in multifemale nests was naturally larger than in solitary nests; the number laid per female did not differ much between solitary and semisocial nests. It was slightly larger in eusocial nests (Table 11). In multifemale nests, the interval between ovipositions was clearly shorter than in solitary nests (2.7.2); the shortening may have been caused either by a decrease in interval of laying by the queen or by participation of workers in laying.

Table 11. Numbers of eggs laid per female in solitary and multifemale nests of *Braunsapis hewitti* (types 1, 1v, 3; cf. Maeta et al., 1985), the foundresses of which survived until Oct. 27, 1980.

Phase (no. of females per nest)	No. of Eggs Laid Per Nest			No. of Eggs Laid Per Female	No. of Nests Examined
	Max.	Mean + SD	Min.		
Solitary (1)	6	3.6 ± 1.1	2	3.6	20
Multifemale					
Semisocial (2)	13	8.4 ± 4.6	1	4.2	5
Semisocial (3)		12		4.0	1
Eusocial (2)[1]	11	9.5 ± 1.3	8	4.8	4

[1] Colonies whose daughters remained in their natal nests for more than 15 days after eclosion were regarded as eusocial.

In nests that did not attain eusociality, the mortality of immatures, especially of eggs and last instar larvae, was high (Table 12). Such high mortality of immatures must retard the appearance of eusociality, but is probably partly a result of our greenhouse nest conditions. In greenhouse nests established in stems of *Rubus* and *Miscanthes*, immature survival was higher than in glass nest substrates. As pointed out by Maeta et al. (1985), this indicates that our observation nests were not good for the bees. Inadequacy of our rearing conditions is also suggested by the fact that females reared in the greenhouse averaged smaller than their mothers (brought from Taiwan) while workers obtained in the field in Taiwan were not smaller than the queens.

Table 12. Mortalities of immatures in solitary and multifemale nests (types 1, 1v, 3, cf. Maeta et al., 1985) of *Braunsapis hewitti* whose foundresses survived until Oct. 27, 1980 (D, daughter; E, egg; L + number, larval stages; F, females; M, mother; pp, prepupa; P, pupa).

Social Type	Percent Mortality								$\bar{x}$ Survived Per Nest[1]	Number Examined[2]	
	E	L1	L2	L3	L4	pp	P	Total		Nests	Imma.
Solitary (M)	29.6	0	7.0	5.6	23.9	1.4	0	67.6	1.2	20	71
Multifemale											
Semisocial (2F)	14.3	0	4.8	7.1	26.2	0	0	52.4	4.0	5	42
Semisocial (3F)	25.0	0	0	0	25.0	0	0	50.0	6.0	1	12
Eusocial (M + D)	—	—	—	—	—	—	—	—	—	4	38
Solitary phase (M)[3]	—	0	0	0	0	0	0	0	3.5		
Eusocial phase (2F)	2.6	0	0	10.5	10.5	2.6	0	26.3	7.0		

[1] Individuals that developed into adults, May until October, plus surviving immatures on October 27, 1980.

[2] Immatures ejected from nests by bees were regarded as dead.

[3] Initially these were not different from solitary nests recorded in line 1 of this table. However, when daughters remained in the nests, they presumably influenced their nest mates, including those that lived parts of their lives under solitary conditions.

5.5 Probable sequence of social phases in nature.—The following speculations on the sequence of social phases in *Braunsapis hewitti* in a subtropical climate are based on information in sections 5.3 and 5.4 as well as on Maeta et al. (1984, 1985: fig. 2).

In southern Taiwan, at the northern margin of the normal range of allodapine bees, seasonal activities of *B. hewitti* are interrupted by overwintering. During the active period, any of the three social phases, solitary, semisocial, and eusocial, is possible. Overwintered nests contain both immatures and adult females (Table 10). If such adults are a mother-daughter combination, eusociality may continue into the spring if the mother survives (with one or more workers) and resumes laying. Reversion to the solitary phase occurs either when the mother is succeeded by a single daughter or by one of several sibling daughters, the rest having left the natal nest to found new solitary nests. Such new nests may appear at any time during the active period judging from the presence of many solitary nests in both spring and autumn and at all seasons in other species of *Braunsapis* (Michener, 1971). Semisociality develops after the death of the mother in nests retaining more than one daughter.

Semisociality produced by joining, not by failure of daughters to disperse, appears to be rare (2 out of 43 nests started in the greenhouse, 1980). In Cameroon, Michener (1968) forced a shortage of nest substrates on 50 nests of *Braunsapis,* but did not succeed in producing semisociality by joining. On the other hand, Schwarz (1986) in Australia reported frequent formation of semisocial colonies (1–6 females, $\bar{x} = 2.6$) in *Exoneura bicolor* by natural joining in spring (November).

Larvae orphaned by the death of a mother are sometimes reared by an older sister, even in the very nearly solitary *Allodape macronata* (= *angulata)* and *Allodapula (Dalloapula) acutigera* (= *halictoides)* (Skaife, 1953). In our greenhouse, the mother in Nest 58 died on October 1, leaving two fourth-stage larvae. The second daughter of Nest 81, who dispersed from her parental nest on October 5, visited Nest 58 from October 5 to 8, dumped out the dead female, and fed the larvae with pollen. She did not stay; yet the observation suggests that young adult females are likely to care for even unrelated immatures.

6. MALE BEHAVIORS

Females in closed nests (type 1v) produced only males; females in other types of nests did not produce any males during our experiments, so male intranidal behaviors were observed only in five type 1v nests, from which bees could escape only into the vial at the entrance.

Adult males were fed by both mother and "aunts," but also took honey from the feeder in the vial attached to the nest. When males departed from the nest, they were readily readmitted by the guards. It is unknown whether males stay in or return to nests in nature. Position exchanges between males and between a male and a female were as smooth as between females, although solicitation behavior by males (3.4.1) was not observed.

Males exhibit most self-maintenance behaviors observed in females. However, nectar ripening, transfer of pith dust, and of course stinging, were not observed.

The only nest-maintenance behaviors observed in males were occasional guarding, checking, moving of immatures, honey delivery to adults, and honey withdrawal from immatures.

Among interadult behaviors, the males performed avoidance, antennation, food solicitation, being fed, face brushing, knocking and raking, and, rarely, feeding of adults (see below). Males born in semisocial colonies brushed the faces of both mothers and "aunts." Allowance of exchange and inhibiting juvenile's approach to the nest entrance were not observed.

One young male was twice observed to feed a female of the previous generation with honey. On October 4, he faced her in the burrow and before his departure (11:05), he fed her honey. She was guarding on his return (11:13), and fed him honey. On October 9, he faced the same female, who was again on guard, and fed her honey before his departure. He did not receive honey from her on his return, but did not solicit it. These are exactly like the honey delivery and honey withdrawal behaviors between adult females (2.8.2, 2.8.6).

DISCUSSION AND CONCLUSIONS

Braunsapis is a member of the tribe Allodapini of the subfamily Xylocopinae. The relations of the Allodapini to other tribes of Xylocopinae, Ceratinini and Xylocopini are indicated by Sakagami and Michener (1987); there is no doubt that each of these taxa is holophyletic (i.e., monophyletic in the strict sense). Sakagami and Michener indicated, furthermore, that the Xylocopinae is the sister group to the Apidae. This relationship is disputable, but probable.

Michener (1990) presented a long list that shows similarities in behavior and life history between Allodapini and its sister tribe, Ceratinini, at the same time explaining relevant differences between these tribes and the Xylocopini. The present more detailed study of one allodapine species does not counter any of the items on Michener's list, but provides additional items for it.

The behavior of other allodapines differs from that of *Braunsapis hewitti* in frequently unknown ways. Comparable investigations of other allodapine genera and species will be needed to determine the generality of some of the comparisons made below. However, much is known or reliably inferred about the societies of some other allodapines. The following paragraphs concern items that extend Michener's list or that provide useful comparisons with other Allodapini and with Ceratinini. The data on *Ceratina* are from Sakagami and Maeta (1982, 1984, 1987a, b, 1989), summarized by Michener (1985, 1990).

Comparisons with certain apid and halictid bees are also included. Social behavior in these groups (most certainly in the halictids) must have arisen independently from that in the Xylocopinae, so that similarities in such behavior are convergent rather than homologous.

Life cycle, longevity and size. The life cycle is summarized in the Introduction and in section 5.3. Climatic data from Kenting, Taiwan (Maeta et al., 1985), where our *Braunsapis* were collected, show that December and January correspond to an inactive season, although mean air temperatures during this period do not drop below 20°C. Table 10 suggests the presence of immatures in most overwintering nests, and large larvae of other *Braunsapis* species are known to overwinter in warm temperate parts of southern Africa (Michener, 1971). Probably as in some *Ceratina* in warm temperate southern Brazil (Sakagami and Laroca, 1971), foraging and feeding of larvae do not completely cease in the winter.

Sakagami and Maeta (1989) confirmed the compatibility of solitary life with the various social types in the same population of *Ceratina okinawana*. *Braunsapis* exhibits a similar compatibility, but with two important differences from *C. okinawana*. (1) Overwintering nests contain both adults and immatures, and brood rearing does not seem to cease entirely. Activities in the nest as well as ovarian development are slowed or arrested by low temperature. In *C. okinawana,* however, overwintering nests do not contain immatures; overwintering young adults are apparently in reproductive diapause, although this species is multivoltine and its diapause seems to be optional, not obligatory as in such univoltine species as *C. japonica* and *C. flavipes*. (The life cycles of truly tropical species of *Ceratina* are still unknown.) (2) The principal life modes of *B. hewitti* may be eusociality and semisociality if the nest survives long enough; it probably usually does not, even in durable nest substrates like bamboo, as indicated by the relatively small number of colonies found in the field compared to the number of solitary nests (see Maeta et al., 1984). In *C. okinawana,* the principal life mode is solitary.

Allodapine bees have long active adult lives (normal maximum durations unknown); one female *Braunsapis* was killed when at least 16 months old (Maeta et al., 1985). A *Ceratina* survived into a third summer of activity (summary: Michener, 1990). It is easy to imagine selection for longevity in a social bee when the oldest female in any colony ordinarily becomes the queen and when the queen (presumably) has fitness advantages.

In view of the long active adult life, long intervals between ovipositions are not unexpected (see 2.7.2 and Maeta et al., 1985); mean intervals per female vary from 9.7 to 25.7 days depending on the period, nest groups and social phase involved. By contrast, means for various species of *Ceratina* in the greenhouse ranged from 1.7 to 2.6 days (Maeta, unpublished) and for most bees the period is much less if weather is good, 0.6 days for the megachilid *Osmia cornifrons* (Sugiura and Maeta, 1989). *Braunsapis*, *Ceratina*, and *Osmia* have moderately large to very large eggs (Iwata and Sakagami, 1966). Some other Allodapini, especially *Allodapula*, lay much smaller eggs, apparently at much shorter intervals (Michener, 1971).

The duration of immature stages also appears to be long in all allodapines. In *Braunsapis hewitti*, in summer (May-August), duration of immature stages ranged from little over one month to over four months; in the same nest at the same time, 60 and 107 days (Maeta et al., 1985). Immatures going into winter of course often continue much longer as larvae, particularly as large larvae.

It is likely that the slow development of larvae, long intervals between ovipositions, long life of adults, and small number of foraging flights per day are all interrelated; these extraordinary features probably evolved together. It is not clear that some one of them drove the others.

In highly social bees like Meliponinae and *Apis*, there is a long period after eclosion of a worker before it starts foraging. In its short preforaging period, as little as four days after eclosion (Table 8), *Braunsapis* is unlike such highly eusocial bees, but resembles *Lasioglossum*, *Ceratina*, etc. In this respect, *Braunsapis* resembles the solitary and other primitively social bees more than the highly social Apidae.

While in many allodapines and colonial *Ceratina*, mean queen size averages slightly larger than that of workers (Michener, 1990), this was not verified in field-collected nests of *Braunsapis hewitti*. In greenhouse nests, however, the head widths of daughters were always less than those of their mothers, and those of later daughters averaged less (and their immature stages of longer duration) than those of the first daughters (Maeta et al., 1985). Some of the daughters in field colonies may have been reared in eusocial colonies while all of those in the greenhouse were reared in solitary nests, i.e., by a mother without workers. This or inferior conditions for *Braunsapis* in the greenhouse could account for the findings.

Individual behaviors. Most solitary bees spend some time at the nest entrance, facing outward, as though inspecting or checking the environment before flying out. They thus look like temporary guards and may delay parasites and predators trying to enter the nest. Colonies of Halictinae and Apidae are guarded by bees that face outward at the nest entrance. In many halictines, however, when a guard is disturbed, it turns and plugs the nest entrance with the apical metasomal terga. *Ceratina* usually guards in this position, but if disturbed, often turns and faces the intruder. *Braunsapis* and most other allodapines guard facing inward, with the nest entrance blocked by the flattened apical metasomal terga. If disturbed by an intruder, a *Braunsapis* guard firms up its position rather than turning to face the intruder. After turning and facing the "enemy," *Ceratina* secretes an odoriferous substance from its mouth area. The same response is probably also found in *Exoneura*, an Australian allodapine (Michener, 1965; Cane and Michener, 1983). In *Braunsapis* such secretion was not observed.

In *Braunsapis hewitti*, the allocation of guarding to queens was almost complete in our nests. Mason (1988) also found queens to be major participants in guarding in the species of *Braunsapis* and *Allodape* that she observed. Guarding by a worker in *B. hewitti* reflects occasional brief relief of the queen while she is in the nest, sometimes feeding a larva. Most such queen activity is possible because of progressive feeding of larvae in *Braunsapis*, which permits occasional feeding by the queen using pollen accumulated on the nest walls and honey from her own crop. In general, however, the system is similar to that found in the occasional colonies of mass-provisioning *Ceratina*. In such colonies queens also participate to a limited degree in such tasks as preparation of the larval provisions. But Sakagami and Maeta (1987a, b) found guarding at the nest entrance to be a key task of *Ceratina* queens.

An unusual feature of the nesting biology of *Braunsapis* and some other allodapine bees is that they can extend or enlarge the nest while rearing brood. This is impossible for other tube-nesters because closed cells are in the way. In *Braunsapis,* the pith dust that results from nest extension is carried up the nest, past eggs, larvae, and pupae if they are present, and dumped out the nest entrance. Immature stages may become enveloped in pith dust, but are later cleaned and groomed by the adults. *Braunsapis* and its relatives are unique among tube-nesting bees in keeping the immatures in the sequence eggs (at the bottom of the nest) to pupae (nearer the entrance). Ancestral allodapines presumably kept their young in normal sequence (youngest near the nest entrance) and could not extend the nest during brood rearing because the provisions stored for larval consumption prevented access to the bottom of the nest. The genus *Halterapis* exhibits these behavioral features today (Michener, 1971). Hence the reverse arrangement of immatures and the ability to extend the nest while rearing young must have evolved within the history of Allodapini, not before the group arose.

Like all nonparasitic bees, *Braunsapis hewitti* forages from flowers (2.8). In multifemale phases, queens do not participate in foraging. This agrees with Mason's (1988) observations on *Braunsapis foveata,* but in some of her colonies of *Allodape exoloma* the principal forager was the queen.

Braunsapis is unusual in that, whether solitary or in colonies, the bees deposit pollen on the nest walls. Michener (1968) showed that adults of two African species of *Braunsapis* eat and feed larvae pollen taken from the burrow wall instead of using pollen directly from the scopas of foraging bees. In nests in black, charred pith, guts of both larvae and adults and pollen masses on larvae (i.e., food for larvae) contained many particles of black pith scraped from the burrow walls along with the pollen.

Pollen may be stored by *Braunsapis hewitti* on nest walls whether or not there are larvae to eat it; it is clearly for adult food in such cases. This is most evident in new nests inhabited by a single adult, without eggs or larvae. In *Ceratina japonica, flavipes, okinawana* and *iwatai,* one female forages more than enough nectar and pollen for all her nest mates in the mother-juvenile cohabiting period. Although the behavior appears in different phases of the life cycle in *Ceratina* and *Braunsapis,* it is noteworthy that pollen is stored in both genera for adult consumption. Such behavior is unknown in bees other than the Xylocopinae and the Apidae.

To get pollen into brood cells, cell-making bees face the nest entrance while brushing pollen off the scopa after foraging flights (Batra, 1964, *Lasioglossum zephyrum;* Maeta, 1978, *Osmia*). It is interesting that although *Braunsapis* performs many activities facing in either direction and the nest arrangement is such that sweeping off pollen could be performed equally well facing the bottom of the nest, it is always done facing the nest entrance (2.1.3, 2.8.8), even if only an episode between other behaviors. This is true whether the bee is unloading after foraging or after picking up pollen from a pile in the nest. Turning toward the entrance before brushing off pollen must be a functionless heritage from an ancestor that constructed cells.

The walls of a nest excavated in pith absorb nectar or honey if it is placed on them, and fungal development is likely on an area so treated. Ignoring honey held in bees' crops, the Allodapini are the only bees other than Apidae that store honey; they do it by placing drops on the bodies of immature stages, especially large larvae (2.8.1), as we observed for *Braunsapis hewitti.* Honey deposition on immatures has also been observed in *Allodape exoloma* and *B. foveata* (Mason, 1987, 1988) and honey drops have been found on allodapine larvae in nests in the field, e.g., by Michener (1971).

Grooming and moving of immatures (2.1.4, 2.1.5) are activities characteristic of most allodapines. They suggest behavior of ants. Indeed *Braunsapis* (and most other allodapines) show interesting resemblances to ants in lack of brood cells and in resultant behaviors, also in longevity of larvae and adults. Even the use of immatures for the temporary nectar storage reminds one of the more elaborated use of the larvae for preparing nests in *Oecophylla* ants. The diversity of methods of moving immatures suggests the lower ants *(Myrmecia),* not the more stereotypical methods of higher ants (Wilson, 1971). Moving of larvae is not known in other bees except *Ceratina* of the subgenus *Ceratinidia* which move and clean immatures in cells (Sakagami and Maeta, 1977, 1986, 1987b). Such behavior probably arose within the Allodapini, for some members of this tribe (*Halterapis;* see Michener, 1971) probably do not exhibit this behavior.

The large amount of time spent by *Braunsapis* adult females grooming and otherwise caring for immatures (Table 5) is noteworthy. Such thoroughgoing care of immatures is not seen in non-allodapine social bees except *Apis.*

In most Aculeata larval defecation is delayed until feeding is complete. In most Megachilidae and Xylocopinae, however, larval defecation begins during the last larval stage while it is still feeding. This is true of *Braunsapis* (Maeta et al., 1985; Michener, 1971) and many other Allodapini. In *Braunsapis* adults remove feces of larvae quite promptly. In *Halterapis* feces are not removed promptly because adults cannot get past food masses and growing larvae to the lower part of the nest. The same is true of *Allodapula* but in this case larvae have reverted to the typical aculeate pattern of defecating only after feeding is completed (Michener, 1971).

Most social bees and some solitary ones that have small nest entrances make special constructs that narrow the entrance or otherwise modify it. The Allodapini are unique in making an entrance collar of nest-wall particles, similar in content to the cell partitions of their closest relatives, the Ceratinini (2.5). Collar construction behavior is similar to that for cell partitions in *Ceratina,* suggesting that the technique as applied to construction of the collar (also the bottom plug) survives from among the mass-provisioning and closed-cell antecedents of the Allodapini.

There are, however, some differences: direction of the body in preparation of the entrance collar, facing the bottom, is opposite to that seen in preparation of cell partitions by *Ceratina,* facing the entrance. However, this difference is not invariable. In *Ceratina* subgenus *Ceratinidia,* when the female opens a closed brood cell to clean the interior, she faces the bottom as she rebuilds the partition, like *Braunsapis,* although the rebuilding is completed in less than 30 seconds.

In *Ceratina* the scraped mass of pith is formed into a ring by insertion of the metasoma in the mass, rotation of the body, and consolidation of the mass with the dorsa of the hind tarsi (Maeta and Sakagami, unpublished). *Braunsapis* never uses its legs for consolidation. Moreover, *Ceratina* does not consolidate the inner surface of the partition (corresponding to the inner side of the entrance collar in *Braunsapis*) with the apical metasomal terga, as does *Braunsapis.*

Time spent in consolidation by *Braunsapis* was long, relative to the amount of pith used. In *Ceratina,* even in subgenera that do not reenter cells, cell partitions are less hard than the entrance collar of *Braunsapis.*

Oophagy is known in so many social Hymenoptera that it may well be universal (Crespi, in press). While it sometimes occurs in a social context, solitary allodapines sometimes eat their own eggs, as is probable for *Braunsapis hewitti* (3.9). Skaife (1953) found oophagy frequent in *Allodapula acutigera* (=Skaife's *Allodape halictoides*), in which a solitary female ate her own eggs and replaced them later. Mason (1988) presents more data (for African allodapines) on oophagy than we were able to obtain.

Males of *Braunsapis* display a wider variety of nest-maintenance and social behaviors than any other male bees (see 4.4, 6, and Tables 6, 7). Males of some other social Hymenoptera are known to perform some social or maintenance behaviors, many for *Polistes* wasps, but the number of such behaviors known for any one bee species is small (Cameron, 1985, *Bombus* and *Polistes*).

Interadult behaviors. It is clear that many behaviors—honey delivery to and withdrawal from adults, knocking and raking, buccal contact, solicitation and allowance of position exchange, face brushing, inhibiting juvenile's approach to the nest entrance, oophagy—all involve elements developed since the appearance of adult cohabitation. Such behaviors must have been absent or represented only by antecedents in the solitary, mass-provisioning ancestor. The thrusting and pushing away behaviors may derive from those used in defending against enemies, which were not observed in our study.

Almost no clearly aggressive or agonistic behaviors were observed in our study of *Braunsapis hewitti.* In this respect, *Braunsapis* resembles *Ceratina* (Sakagami and Maeta, 1984, 1986) and is unlike most other social insects. Mason (1988), however, reports for other allodapines more agonism than we recognized. As indicated in section 5.2, we were able, with some difficulty, to recognize dominance of queens.

The most obvious dominance is shown by queens (guards) that inhibit exit of young adults (< 2 days after eclosion) from the nest (3.8). Such behavior is far more frequent and violent in *Ceratina (Ceratinidia)* than in *Braunsapis* (Maeta and Sakagami, unpublished).

As noted earlier (3.4) position exchange is necessary for cohabiting adults in narrow burrows. It happens remarkably rapidly and smoothly, usually venter to venter, in *Braunsapis.* Position exchange is also well developed in the mother-juvenile cohabiting phase of *Ceratina,* a basically solitary bee (Sakagami and Maeta, 1977, 1985, 1986, 1987a, b). Such exchange, carried out similarly, is also common in nests of halictid bees, a group in which it must have evolved independently. In colonies of both *Braunsapis* and *Ceratina,* position exchange is most often seen at the nest entrance when a departing forager exchanges positions with the guard (queen), inspects the outside, and flies away. The guard, of course, promptly resumes her position in the nest entrance.

Feeding of adults by other adults is an important behavior for many Xylocopinae, including *Braunsapis.* A single observation on *Braunsapis* (3.6) suggests that juveniles may be able to stimulate adults to forage for pollen. This apparent phenomenon is more conspicuous in *Ceratina.* In *C. flavipes, japonica,* and *okinawana,* juvenile adults "beg" pollen from the mother or an elder forager by a characteristic behavior. They thrust while violently jerking their heads upward, with the mandibles wide open. Seemingly in response, the mother leaves the nest. After homing, she sweeps off pollen in front of the offspring (Maeta and Sakagami, unpublished). Such behavior is never seen in *Braunsapis.*

A noteworthy behavior in our nests was deposition of nectar by foragers on larvae or in crops of adults before departure, usually followed by retrieving the nectar after returning. Because of small colony size there was often only one appropriate larva or female from which nectar could be retrieved, and therefore foragers usually retrieved their own previously deposited nectar. Mason (1988), however, working with larger colonies of *Braunsapis foveata* and *Allodape exoloma,* found that other bees were more active than the returned foragers in removing honey from larvae, and that many individuals both donated and received honey, indicating a circulation of food among colony members.

Division of labor between castes is characteristic of most social forms. While reproduction and foraging are principal behaviors for which castes are specialized, many other behaviors differ between the castes in frequencies and durations, even in species with castes that do not differ morphologically; see Tables 6 and 7 and section 4.4 for *Braunsapis hewitti* and Brothers and Michener (1974) for *Lasioglossum zephyrum,* a primitively social halictine bee.

Obviously bees in the solitary phase must take care of all their own needs and those of their young. On the other hand, bees in colonies can specialize, each caste having its own principal activities. In *Braunsapis,* most nests of which are solitary, all females are probably able to perform all activities. The worker and queen castes, however, differ in the frequencies and durations of nearly all their activities, not merely the key tasks that characterize each caste, like guarding and egg laying for queens and foraging for workers. For nearly all tasks, solitary females are intermediate in frequency and duration between queens and workers in colonies. Thus the differential behavior of the castes appears to have evolved by the specialization of each caste starting from the solitary condition.

In our colonies of *Braunsapis hewitti* foraging was almost exclusively a function of workers and guarding, of queens. Frequencies of these and other behaviors appear in Table 6. Related species sometimes show quite different task allocations. Thus in two African allodapines, *Allodape exoloma* and *Braunsapis foveata*, there were one or two primary foragers per nest, the mother (queen) and first daughter (a worker) in *A. exoloma* and the first daughter only in *B. foveata* (Mason, 1987, 1988). Guarding was done primarily by the mother in *A. exoloma* but by all females in *B. foveata*. As to other behaviors, honey solicitation and honey feeding were observed reciprocally in 93% of all females, but for honey regurgitation, solicitation was most frequent by primary foragers. All females participated in feeding larvae and in "tonguing" larvae (possibly the same as grooming in our study), but primary foragers participated more in feeding larvae than in tonguing and other females, more in tonguing. The caste differentiation of these species seems less sharp than that of *B. hewitti*. It should be remembered, however, that our colonies mostly contained only two bees, while Mason's were larger. Larger colonies of *B. hewitti*, such as occur in nature (5.3), probably also exhibit less clear-cut caste differences. For example, additional egg layers (i.e., in a eusocial colony, egg-laying daughters/workers) tend to reduce the difference between queens and workers in this key behavior of queens.

A major need for the future is ethometric studies of larger colonies of *Braunsapis* in order to learn the influence of more individuals on caste differences. With somewhat better conditions than we were able to provide, many colonies in captivity should develop and grow to consist of several adult females. (We do not know how to improve conditions, but small size of progeny, failure to produce males, etc., show that our observation nests were not ideal.)

Comparisons of time allocations with those of other bees. Comparisons of time allocation in different bee species are difficult because of different classificatory methods, lack of comparability of behaviors, and lack of data. Table 13 presents a synopsis of relative use of time by workers of a highly eusocial bee, *Apis mellifera*, a solitary bee, *Osmia cornifrons*, and the solitary phase of the frequently semisocial or primitively eusocial bee, *Braunsapis hewitti*. Although methods were not the same and behaviors were classified differently in the three studies on which the table is based, functionally related behaviors are grouped in an attempt to permit comparison. The following paragraphs explain some of the classes of work listed in Table 13.

"Idle" in *Apis* includes both resting and self-grooming. As mentioned before (2.1.1), guarding in solitary *Braunsapis* nests is resting at the nest entrance. Although the honeybee is much lazier than is popularly believed, it is about twice as active as *Braunsapis*.

Apis spends much more time walking (patrolling) than either *Osmia* or solitary *Braunsapis*. This fact is probably related to the function of patrolling in determining a bee's subsequent task allocation (Sekiguchi and Sakagami, 1966; Lindauer, 1952, 1971).

The relatively short time allocation to flight in *Apis* was due to storm-caused death; flight is most prominent in late worker life. Time allocations for flight in *Osmia* and *Braunsapis* may also be low, because flowers were provided in the cages close to the nests. In nature greater distances and more search time would usually be required. The large allocation by *Osmia* reflects its frequent foraging trips, consistent with its oviposition rate, which is far higher than in *Braunsapis*.

Guarding in *Apis* is difficult to evaluate because of individual variation; many workers skip this task (Butler and Free, 1952; Sekiguchi and Sakagami, 1966). The presence of many potential guards must assure effective defence. In *Braunsapis*, checking outward at the nest entrance was regarded as comparable to guarding in the other genera, but a considerable part of this behavior must represent resting due to suppression of departure.

Building (cell capping, etc.) may not be useful as represented in Table 13. For *Apis* no cell construction was observed; for *Osmia* nests in some sites would require more con-

Table 13. Use of time (percentages) in three bee species, *Apis mellifera, Osmia cornifrons,* and *Braunsapis hewitti.*

Apis (worker)[1] (highly social)		*Osmia*[2] (solitary)		*Braunsapis*[3] (solitary phase)	
Idle	44.2	Resting and self-grooming	64.8	Guarding, resting, self-grooming	83.8
Patrolling	31.9	Checking	1.2	Walking	0.4
Flights	6.4	Flights	22.4	Flights	4.5
Guarding	0.3	Entrance guarding	3.5	Inspecting at entrance	9.1
Cell capping	7.5	Partition building	2.8		
Feeding larvae	3.8	Preparing larval food	5.2	Feeding, grooming, and moving immatures	1.3
Following dancers, packing and eating pollen	3.2			Honey and pollen handling, burrow cleaning	1.0

[1] Continuous observation of one worker for 176 hours 45 minutes (Lindauer, 1952).

[2] 24-hour observations of 3 females (Maeta, unpublished).

[3] Table 5. For equivalent data on colonies, see Table 7.

struction activity; for *Braunsapis* burrow initiation and construction was not included in the observation period reported in Table 13.

The large amount of time spent preparing the larval food mass by *Osmia* is probably characteristic of mass-provisioning bees (except those that provide liquid food like most Meliponinae and many Colletidae).

It is obviously premature to make precise comparisons based on such weak data as those presented in Table 13. We hope that our presentation may lead to comparative studies that will result in a better understanding of the evolution of apoid ergonomics.

Origin of eusocial and semisocial behavior. The relative frequencies of both eusocial and semisocial colonies of *Braunsapis* suggest that what has evolved was initially a tolerance of conspecifics (perhaps most often daughters or sisters) and thereby a tendency to live in small colonies, not a predilection for establishment of either eusocial or semisocial colonies. Schwarz (1988, 1990) found that new nests of the Australian allodapine, *Exoneura bicolor* Smith, are commonly occupied by more than one female, and that these females are commonly related. Presumably one female starts the nest and is joined by others, and the others are preferentially kin. The same may explain some *Braunsapis* colonies although others result from daughters remaining with their mothers or sisters remaining together. Associated with life in colonies is a strong tendency toward division of labor, so that a queen and a worker are usually recognizable even in a colony of two bees.

From Darwin's time to the present, biologists have been concerned with the problem of establishment of a nepotistic ("altruistic") worker caste in social insects because workers produce few or no offspring and therefore have reduced individual fitness. There must be some compensatory increments of fitness that promote evolution of a caste of reduced productivity; a recent review of the problem is by Strassmann and Queller (1989). Consider a colony such as is common in *Braunsapis* of one queen and one worker (either eusocial or semisocial). Of course mutual defence against predators or parasites could add to the fitness of each, but would not necessarily explain the division of labor. Most studies of social insects have involved larger colonies, such that if a queen dies, the chance of any given worker to replace her is small. The result has been consideration of diverse factors that alone or in combination could make it worthwhile for a worker (with the potential to be a queen) to stay with her mother or sister, i.e., to remain a worker. But in a eusocial colony of two, because the queen is older than the worker, she is very likely to die before the worker. The same may be true even in a semisocial colony. Thus the worker has a high probability of replacing the queen, using the nest, inheriting immatures in it, and acquiring her own worker or workers. The initiation of eusocial behavior is easier to visualize under such circumstances, with colonies of two to a few bees, than when one is thinking of larger colonies like those of *Polistes*.

Unfortunately data on a number of topics are still needed for further elaboration of such ideas. For example, do workers of *Braunsapis* have about the same potential longevity as queens, or are workers much shorter-lived than queens as in most social insects (including halictid bees, whose colonies are often as small as those of *Braunsapis*)? Is foraging (a major worker activity) significantly more dangerous than nest guarding (a major queen activity)? Is it true that any worker can become a queen or a solitary reproductive, even late in adult life, as in the principally solitary but socially predisposed *Ceratina* species? Since workers are often unmated, it is reasonable to ask if mating plays any role in determining which bees are queens, as appears to be the case in some halictid bees (Yanega, 1989).

Data on the genetic population structure are needed in order to evaluate the significance, if any, of kinship in the origin and maintenance of the potential for a worker caste. Such data are available for only one allodapine bee, *Exoneura bicolor* (Schwarz, 1986, 1988, 1990; Blows and Schwarz, 1991), and its population structure appears to be quite different from that of *Braunsapis hewitti*.

In *Xylocopa* eusocial behavior is not verified but in numerous species colonies consist of a mother and one or more daughters who remain in and guard the nest (Michener, 1990). Daughters may leave to start new nests or may inherit the parental nest when the mother dies. No individual is permanently a worker. The question therefore arises, how sure are we that some of the workers of *Braunsapis hewitti* are permanent or long-term workers? (In various allodapines workers average smaller than queens and become worn while unmated and with slender ovaries [Michener, 1971]; such observations strongly suggest that some are long-term workers even though they might become replacement queens or solitary individuals under certain circumstances.)

Questions like those in the preceding paragraphs can be investigated with patient field and laboratory studies. Unfortunately our data do not answer these questions but we commend them to others.

ACKNOWLEDGMENTS

In particular we thank Professor Yau-I Chu of the National Taiwan University (Taipei, Taiwan) and Mr. M. Shiokawa of the Engaru-Kasei High School (Engaru, Hokkaido) for their kind help in collecting materials in Taiwan, and Mr. K. Goûkon for the preparation of most of the figures.

Preparation of the manuscript was made possible in part by a Grant-in-Aid (Bio-Cosmos Program) from the Japan Ministry of Agriculture and Fisheries (BCP91-I-B-5). Michener's participation is possible as a byproduct of National Science Foundation (USA) Grant BSR 87-16817. The editorial assistance of Virginia Ashlock is greatly appreciated.

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The International Standard Serial Number of this publication is US ISSN 0022-8850.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 54, No. 10, pp. 335-406 May 22, 1992

Phylogeny and revision of genera of the subtribe Bolitocharina (Coleoptera: Staphylinidae: Aleocharinae)[1]

By James S. Ashe[2]

CONTENTS

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ABSTRACT

A revision of the genus-level classification of the aleocharine subtribe Bolitocharina is provided. The revision is based on a phylogenetic analysis of 26 species representing all currently recognized described bolitocharine genus-level taxa as well as undescribed taxa. These were chosen from among 52 bolitocharine species examined to encompass the range of variation among them. Species-level taxa were used as terminal taxa in the phylogenetic analysis to represent the full range of structural diversity in the subtribe without making *a priori* decisions about generic assignments or taxonomic composition of genera. A character matrix of 26 taxa + outgroup by 78 derived character states (in 34 characters) was analyzed using the phylogenetic tree generating program HENNIG86. Several alternative phylogenies under different assumptions are provided. All lead to similar conclusions about generic limits. Conclusions are: (1) The subtribe Bolitocharina is shown to be monophyletic by shared possession of (a) large patch of densely arranged denticles in ventral molar area of mandibles, (b) medial setae of prementum staggered one behind the other, (c) narrow medial pseudopore field of prementum without pseudopores. (2) The genus *Ditropalia* Casey, with which many described bolitocharine genera have been synonymized, is based on plesiomorphic features and includes taxa which are not closely related. (3) The genera *Pleurotobia* Casey, *Stictalia* Casey, and *Venusa* Casey, which had been synonymized with *Bolitochara* Mannerheim, are not members of that latter genus. (4) The genus *Phymaturosilusa* Roubal is a junior synonym of *Pleurotobia*. (5) The genus *Venusa* Casey is a junior synonym of *Phymatura* Sahlberg. (6) Two new genera based on undescribed species are described. These are: *Hongophila* new genus (type species *Hongophila arizonica* new species, known from the southwestern United States) and *Neotobia* new genus (type species *Neotobia alberta* new species, known from northern North America from the Rockies eastward). (7) The species *Sternotropa zealandica* Cameron is doubtfully included in the Bolitocharina. It is shown not to be a member of *Sternotropa*, which is a valid genus in the subtribe Gyrophaenina. A new genus, *Austrasilida* n. gen., is described to include it. (8) Nine monophyletic genera, including three newly described, can be recognized in a monophyletic Bolitocharina. These are *Bolitochara* Mannerheim (new synonym *Ditropalia* Casey), *Phymatura* Sahlberg (new synonym *Venusa* Casey), *Pleurotobia* Casey (new synonym *Phymaturosilusa* Roubal), *Pseudatheta* Cameron, *Silusida* Casey, *Stictalia* Casey, *Hongophila* n. gen., *Neotobia* n. gen., and *Austrasilida* n. gen.

INTRODUCTION

The Bolitocharina is a subtribe of beetles in the very incompletely known staphylinid subfamily Aleocharinae. As recognized in this revision, the subtribe is composed of nine genera, in which about 70 species have been described. None of these genera has received comprehensive review, and the taxonomic status of many genera and species is uncertain. Some authors have placed numerous genera and species in synonymy (for example see Fenyes, 1920; Moore and Legner, 1975; Bernhauer and Scheerpeltz, 1926; and others), especially for the North American taxa. Additionally, the subtribe has been variously treated in a broader (e.g., Bernhauer and Scheerpeltz, 1926; and Scheerpeltz and Höfler, 1948) or narrower (e.g., Fenyes, 1918) sense, further resulting in considerable instability in generic composition.

The subtribe Bolitocharina, as a higher taxon within the tribe Bolitocharini, has not been clearly delimited or described in detail. For this reason the genera which have been assigned to the subtribe comprise a very heterogeneous assemblage. Few genera have been adequately described and illustrations of structural features are usually not available. These factors have resulted in confusion about generic limits and assignments.

Categorical rankings of less inclusive groups of genera (subtribes) within the taxon formed by those aleocharines with 4,4,5 tarsal formula [tribe Bolitocharini—hereafter referred to as the Homalotini[1] (see Newton and Thayer, in press)] have not been stable. Various authors have raised one or more of these groups to tribal rank based on their opinion about how distinctive the included genera are in relation to other members. For example, Lohse (1974) recognized five tribes in the European fauna to include those aleocharines with a 4,4,5 tarsal formula. The lack of detailed and comprehensive studies of the higher taxa of aleocharines has contributed substantially to this instability.

I will provide evidence below that many of the taxa included in the tribe Homalotini in a traditional sense share several uniquely derived features which probably indicate that they form a monophyletic group within the Aleocharinae. I will therefore treat these less inclusive higher taxa as subtribes within the more inclusive tribe Homalotini.

This study grew out of my attempts to understand the generic composition and phylogenetic relationships among North American members of the subtribe Bolitocharina. It soon became clear that the question about phylogenetic limits of the subtribe could not be addressed in a regional context. Therefore the study was enlarged to address the question of whether the subtribe Bolitocharina could be shown to be monophyletic based on shared derived characteristics. If so, what would be the generic composition of such a group, and what would be the phylogenetic relationships among these genera? These questions cannot be effectively addressed outside the context of the monophyly of the tribe Bolitocharini as a whole. The goal of this study is to provide a phylogenetic framework within which additional research on bolitocharines can be addressed. Though I have attempted to make it as broad based as possible (see Appendices 1, 2), its completeness is clearly limited. There are a number of probably valid bolitocharine species that I have not examined (see Taxonomic Treatment). Furthermore, the tribe Homalotini is a large, heterogeneous assemblage comprised of hundreds of described genera worldwide, some of which may be correctly placed in the subtribe Bolitocharina as here defined. A complete survey of all such taxa would be prohibitive and is outside the bounds of this study. I hope that this study will stimulate additional research on the subtribe Bolitocharina that will untimately lead to its revision.

MATERIALS AND METHODS

The study of the phylogeny of aleocharine staphylinids has been limited by the lack of detailed comparative structural studies. The small size of most aleocharines, the large number of valid taxa, and the superficial similarity among many of these taxa, have led many workers to suggest that the group as a whole is unsuitable for serious phylogenetic study (Ashe, 1984). The error of this opinion is clear when aleocharines are examined using techniques suitable for observing the great variety of minute, but phylogenetically informative, structural features exhibited by these insects.

The basis for comparative study of microscopic structural features in the mouthparts of the Aleocharinae was laid by Sawada (1970, 1972) and was used effectively in his studies of the athetine complex of genera and species (Sawada, 1974, 1977; Yosii and Sawada, 1976). Later these character systems were used effectively and expanded upon in the study of the phylogenetic relationships and evolution of the subtribe Gyrophaenina (Ashe, 1984) and in elucidating the relationships of the aberrant genus *Tachiona* (Ashe and Wheeler, 1988). The techniques used in this

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[1] Newton and Thayer (in press) have recently convincingly shown that the correct name for the tribe "Bolitocharini" should be the "Homalotini" based on priority. Consequently, the group of aleocharines characterized by 4,4,5 tarsal segmentation usually referred to as the "Bolitocharini" will be referred to as the "Homalotini," except in historical references.

study were designed to maximize the information that could be gained from microscopic characteristics.

Suitable preparation and examination of specimens are essential. Male and female specimens of species for which adequate material was available were cleared in cold, concentrated KOH, and mouthparts, aedeagi and spermathecae were dissected using techniques described in Ashe (1984). The cuticle of darkly sclerotized specimens was bleached using commercially available hydrogen peroxide to facilitate microscopic examination of the entire beetle using transmitted light. Whenever practical, the dissected parts and the body were permanently mounted under cover glasses on microscope slides using Hoyer's mounting medium. Microscope slides were then dried in a drying oven and ringed with Glyptol®. Full dissections of some taxa could not be done because of the paucity of material. In these instances, dissected parts were examined in glycerin and stored in clear glass genitalia vials pinned through the cork onto the same pin as the specimens.

Specimens were examined for general external features at magnifications up to 128× using a dissecting microscope. More detailed examination of microscopic structural features was done with a compound microscope equipped with Nomarski differential interference contrast devices. This optical system is highly recommended for study of the microstructure of small beetles. The detailed structure of many small features (especially sensory pores and similar structures), which are virtually invisible under normal light microscopy, are extremely clear under differential interference contrast optics. Drawings were made with a drawing tube.

Ashe (1984) pointed out that a broad-based comparative study of characters useful for systematic research within the Aleocharinae is not available. The variation in characters and their usefulness for taxonomic and phylogenetic analysis are unknown or at most poorly understood for most groups. This lack of knowledge cannot be remedied easily. Such a comparative base can only be developed slowly as additional detailed studies of a diversity of groups are completed. The comparative base for interpretation of characters for phylogenetic analysis in this study was a microscope slide collection of dissected aleocharines, made specifically for this and related projects, representing over 200 genera and 600 species in all major tribes and subtribes of the Aleocharinae. This breadth of coverage allows for more confident statements about the distribution of character states within the in-group and also among aleocharines as a whole. The main source of material for this slide collection was the excellent staphylinid collection of the Field Museum of Natural History in Chicago. In developing this microslide collection special attention was paid to members of the tribe Homalotini and the subtribe Bolitocharina. Members of these taxa examined are listed in Appendices 1 and 2, respectively.

As noted above, the comparative base for this study was made possible by the excellent collection of the Field Museum of Natural History. Substantial amounts of microslide mounted and pinned material were loaned to me from this collection thanks to the generosity of Dr. Alfred Newton, Jr. This and other public and private collections that contributed material to this project and the curators responsible for the loans are:

American Museum of Natural History (AMNH), Lee H. Herman; Canadian National Collection (CNC), J. M. Campbell, A. Smetana; California Academy of Sciences (CAS), D. Kavanaugh, N. Penny; Field Museum of Natural History (FMNH), A. F. Newton, Jr.; Smithsonian Institution (USNM), T. Erwin; Snow Entomological Museum (SEM); Mr. Karl Stephan, Oklahoma (KSC); Mr. Richard Leschen, University of Kansas (RLC).

Unfortunately, repeated attempts to obtain loan of critically important bolitocharine taxa from the Natural History Museum, London, were not successful.

HISTORY OF THE SUBTRIBE BOLITOCHARINA

Erichson (1839-1840) laid the foundation on which most subsequent taxonomic work on the subfamily Aleocharinae has been built. He established the tradition of character systems centering on the numbers of articles in the maxillary palpi, labial palpi, antennae and tarsi for recognizing higher taxa within this subfamily. Using these characters, Ganglbauer (1895) recognized 10 tribes of aleocharines. These 10 tribes, with additions and emendations, have formed the basic structure of the classification of the Aleocharinae for almost 100 years. One of these tribes, including all those genera which have the front and middle tarsi 4-segmented and the hind tarsi 5-segmented, was the Bolitocharini. Ganglbauer included 17 genera in this tribe. In spite of the similarity in tarsal structure of its members, the composition of Ganglbauer's tribe included a structurally heterogeneous assemblage of genera. The heterogeneity became more acute with discovery of additional genera with a 4,4,5 tarsal formula. By the time that Casey began his studies of the North American Staphylinidae at the turn of the twentieth century, it was clear that there were a number of distinctive subgroups within the tribe Bolitocharini. He recognized five distinctive groups which he called subtribes (Casey, 1906). Later Fenyes (1918), in summarizing knowledge of the Aleocharinae to that date, recognized 14 "Groups" within the tribe Bolitocharini which are essentially equivalent to subtribes as recognized by Casey. Though usefulness of these divisions of the Bolitocharini has not been recognized in all subsequent studies (e.g., Cameron, 1939a, b), they have formed the basis for organizing the heterogeneity among those aleocharines with a 4,4,5 tarsal formula in most later classifications.

The first person explicitly to recognize the subtribe Bolitocharina (as the Bolitocharae) was Casey (1906). He included the described genera *Bolitochara* Mannerheim, *Phymatura* Sahlberg, *Silusa* Kraatz, *Sipalia* Mulsant and Rey, and *Leptusa* Kraatz. In addition he described five new genera: *Ditropalia, Stictalia, Silusida, Venusa,* and *Pleurotobia.* He recognized that these could be conveniently separated into two groups: those with an acute metasternal process and short basal segments of hind tarsi *(Silusa, Sipalia,* and *Leptusa);* and those with broader mesosternal processes and elongate basal segments of hind tarsi (all others). Fenyes (1918) separated the group along these lines and recognized in his group Bolitocharae (= subtribe Bolitocharina) only those taxa with broad mesosternal processes and elongate basal segments of hind tarsi. He placed *Leptusa* and *Sipalia,* along with other genera, in a new "group" the Leptusae, and *Silusa* in the Silusae. Fenyes' group Bolitocharae was similar to Casey's tribe Bolitocharae, but he synonymized several of Casey's genera with *Bolitochara* and added *Caloderina* Ganglbauer and *Gastrophaena* Fauvel. Fenyes gave no reason for synonymizing the genera *Stictalia* Casey, *Venusa* Casey, and *Pleurotobia* Casey with the European *Ditropalia* Casey. However, these synonymies have been perpetuated in all subsequent studies of the Bolitocharina.

Bernhauer and Scheerpeltz (1926) and Scheerpeltz (1934) returned to a broader concept of the subtribe. In effect, they combined Fenyes' groups Bolitocharae and Leptusae and added additional genera for a total of 19 genera in the subtribe. They also followed Fenyes' treatment of Casey's genera except they placed *Ditropalia* Casey as a subgenus of the European *Bolitochara.* Blackwelder (1944) essentially repeated this arrangement with genera found in Mexico, Central America, and South America.

This concept of the subtribe has been generally followed by most subsequent authors. Lohse (1974) treated most of the "subtribes" of the Bolitocharini as tribes. Thus his Bolitocharini is essentially the same as the subtribe Bolitocharina of previous authors. His characterization of the "tribe" Bolitocharini underscores many of the problems with this concept of the taxon. It essentially includes those taxa with 4,4,5 tarsal formula that do not have the derived features that characterize any one of the other tribal level taxa with this tarsal formula.

Seevers' (1978) revision of the North American Aleocharinae treats the subtribe Bolitocharina much as did Casey (1906), except that Seevers made no attempt to resolve the problems associated with the synonymies of Casey's genera proposed by Fenyes (1920). He accepted Fenyes' genus-level classification but admitted that some of Casey's genera may be valid. He noted that this complex of genera badly needs revision, but generic groupings could not be considered until the male genitalia had been comparatively studied. Until such a time, he chose to recognize broader genera.

PHYLOGENETIC ANALYSIS

SYSTEMATIC POSITION OF THE SUBTRIBE BOLITOCHARINA

When defined by 4,4,5 tarsal segmentation, the tribe Homalotini includes a large and diverse array of genera. Surprisingly, detailed examination of representatives of many of these genera (Appendix 2) has revealed several derived features which, in addition to similarity in tarsal segmentation, indicate that many of the included genera represent a monophyletic group within the Aleocharinae. These apomorphic features are (1) presence of more or less well-developed denticles in the molar region of the ventral (condylar) side of the mandible; (2) narrowing of the distance between the medial setae of the prementum so that the insertions of the setae are close or contiguous; and (3) narrowing of the medial pseudopore field so that the medial pseudopores, if present, are compressed into an irregular longitudinal row. In spite of dramatic differences in other mouthpart features (compare, for example, the maxillary and labial structures of *Silusa* and related genera with those of *Bolitochara*) and diversity of external forms, these three derived features are distributed in virtually perfect concordance with each other and 4,4,5 tarsal segmentation among most genera typically placed in the tribe Homalotini. The states of these apomorphic conditions, especially number and arrangement of molar denticles on the mandibles, vary considerably among taxa within the Homalotini. For example, molar denticles vary from large and prominent among members of *Bolitochara* to very small and indistinct in *Heterota,* or arranged in a large dense patch in *Bolitochara,* to arranged in well-separated transverse rows in *Diestota,* to arranged in more or less longitudinal rows in many *Gyrophaena.* Similar variation is exhibited to a lesser extent in other apomorphic characters. Nonetheless, considering the concordance among these features and their uniqueness within the

Aleocharinae, it seems most parsimonious to treat these variations as modifications of more basic synapomorphic conditions.

Among genera examined which have been previously placed in the Homalotini, some do not share these derived features. Of particular note in this regard are the genera *Placusa* (usually placed in the subtribe Homalotina) and *Euvira* [usually placed either in the subtribe Autaliina (e.g., Fenyes, 1918) or in its own group (e.g., Seevers, 1978, the Euvirae)]. The features that distinguish these two genera have been briefly discussed by Ashe and Kistner (1989) and in more detail by Ashe (1991). Seevers' (1978) statement that members of *Philotermes* have molar denticles appears to be incorrect; the molar regions of the specimens of this genus that I have examined are without denticles. Members of *Philotermes* also lack the other shared derived features mentioned above. Among the intertidal Phytosina, the genera *Liparocephalus, Diaulota,* and *Actocharis* do not have these derived features, while *Phytosus, Bryobiota,* and *Thinusa* do (molar denticles only very faintly present).

Naturally, many genera have not been examined in the detail necessary to evaluate fully the distribution and concordance of these characters. Nonetheless, they offer a robust first hypothesis about the monophyletic limits of the tribe Homalotini, which can be evaluated with additional study and subsequently modified if necessary.

The monophyletic nature of most of the 11 to 14 subtribes of the Homalotini, and their appropriate generic composition, has not been examined and cannot be addressed here. However, the subtribes Gyrophaenina (treated by Ashe, 1984) and the Bolitocharina (treated here) clearly represent monophyletic assemblages within this larger group. In addition, several other subtribes appear to have apomorphic features which would suggest that at least some genera assigned to them represent monophyletic groups. These include the Silusina (based on the derived condition of the maxillae and labial palpi, see Ashe and Wheeler, 1988) and the Autaliina (based on the derived structure of the ligula of the labium, see Hoebeke, 1988).

It seems most appropriate to treat each of these groups as a "subtribe" within the more inclusive "tribe" Homalotini, rather than raising each of these relatively autapomorphic subgroups to independent tribal rank as done by Lohse (1974). The latter approach is certainly legitimate in that there is no objective way to assign coordinate taxa to categories in the Linnean hierarchy; however, if these monophyletic subgroups are treated as tribes, then there is no standard category for the more inclusive monophyletic taxon. Either one would loose that level of information in the classification or one would have to create a new supertribal category. Because the subfamily Aleocharinae is presently so poorly understood phylogenetically, and substantial modification of its classification can be expected with subsequent study, I prefer a conservative approach to its classification. Since tribal rank has been often used for the more inclusive "Bolitocharini" (= Homalotini), I will continue this approach to classification which seems to provide the greatest stability in the classification while still allowing the appropriate categorical recognition of monophyletic taxa.

CHOICE OF TERMINAL TAXA

Study of the higher-level phylogeny of the Bolitocharina is seriously hampered by the instability of genus-level taxa as outlined above (see historical section). It is difficult to choose representatives of monophyletic groups as terminal taxa, since there is no evidence that any of the higher taxa are monophyletic. I therefore used species as terminal taxa for cladistic analysis without any *a priori* expectations about the limits of the genus-level taxa. The expectation was that monophyletic groups which could be recognized as genus-level taxa would become evident as a result of cladistic analysis. Terminal taxa were chosen to represent as much of the range of character variation within each traditional higher taxon as possible within the constraint of the material available for detailed study. Taxa included in the analysis share a suite of apomorphic features believed to define a monophyletic lineage. These features included: (1) mandibles with large patch of densely arranged denticles in ventral molar area; (2) medial setae of prementum arranged one behind the other; and (3) medial pseudopore field of prementum narrow and without pseudopores. To avoid *a priori* decisions about the composition of genera, I have treated each described genus-level taxon whose members meet the synapomorphic criteria as outlined above as valid. I have included the type species of each of these genera except *Stictalia* (because of inadequate material for dissection) in the analysis. This helps assure that pertinent variation will not be overlooked by *a priori* decisions about generic synonymies.

Taxa included in the analysis are listed in Appendix 2. Other potential bolitocharine genera examined and found not to be part of the monophyletic Bolitocharina are listed in Appendix 1. Decisions about the possible inclusion in, or exclusion from, this analysis of the subtribe Bolitocharina of several taxa require discussion.

Sternotropa zealandica Cameron from New Zealand is included in the Bolitocharina in spite of lack of several synapomorphies that unite the remaining members of the subtribe. Structure of the labium is particularly problematic. The ligula, rather than being elongate, parallel-sided, and apically bifid as in other Bolitocharina, is short and bifid to the base (Fig. 153). More important, the medial setae of the prementum are not arranged one behind the other, but rather are on the same transverse plane. Also, the setal bases are fairly distant from one another in comparison to most other members of the tribe Bolitocharini. In conjunction with this feature, the medial pseudopore field is not greatly narrowed and retains a few pseudopores. Inclusion in the Bolitocharina is indicated by the large, well-developed patch of denticles on the ventral molar area of the mandible, which is similar to that of other Bolitocharina. In addition, the structure of the maxillae, secondary sexual characteristics, and aedeagus are all very similar to those of other Bolitocharina. Because of these similarities, I have included *Sternotropa zealandica* in the subtribe Bolitocharina for cladistic analysis, but with considerable reservation.

A second problematic genus is *Caloderina*, known only from the Palearctic *C. hierosolymitana* Saulcy. This genus was included in the "Group Bolitocharae" by Fenyes (1918-1921). This genus has a perplexing array of characteristics in comparison to the Bolitocharina. The mandibles have only a few, very tiny scattered denticles in the ventral molar area, unlike other Bolitocharina. The ligula of the labium is similar to that of the Bolitocharina and the bases of the medial setae of the prementum are close and slightly staggered one behind the other. However, the medial pseudopore field retains a few small pseudopores. The maxillae are also very similar to members of the Bolitocharina. In contrast, the terga of the abdomen of males lack the secondary sexual characteristics found in most Bolitocharina. Perhaps the most enigmatic feature of *Caloderina* is that males have a concentration of glandular and setose pores baso-medially on abdominal sternum VII. This is remarkably similar to the structure on sternum VII of *Pleurotobia* and *Bolitochara* and is not known to occur in any taxon outside of the Bolitocharina. However, males of *Caloderina* also have a broad band of pores on the base of sternum VII. Also, the apical margin of sternum VI is not modified into a projecting flap which covers this porose concentration as it is in all Bolitocharina which have such a porose structure on sternum VII.

The enigmatic distribution of synapomorphies between members of *Caloderina* and some Bolitocharina does not provide the basis for an unambiguous decision about whether *Caloderina* should be included in the subtribe Bolitocharina. I have very tentatively, and with considerable reservation, elected not to include *Caloderina* in the Bolitocharina in this study.

It is clear that either or both of the decisions to include *Sternotropa zealandica* in, and exclude *Caloderina* from, the subtribe Bolitocharina may be in error and require additional study. I have attempted to provide the basis for evaluating my decisions, and the starting point for more detailed study of the systematic positions of these two taxa, in the preceding discussion.

I have not had opportunity to examine

representatives of *Gastrophaena* Fauvel which was first included in the Bolitocharina by Fenyes (1918-1921). However, the description of this genus, as well as its occurrence with ants, leads me to believe that it is not a bolitocharine, but this proposition requires verification.

Bierig (1937) described the new subgenus *Bolitochara (Agaribiota)* in the genus *Bolitochara* based on the new species *B. (Agaribiota) cinctigastra* Bierig. He states that the holotype and paratypes were placed in his collection which was ultimately deposited in the Field Museum of Natural History, Chicago. I was unable to locate specimens of this taxon among the bolitocharines in the Field Museum. However, based on the description and figures provided by Bierig (1937), it seems very unlikely that *Agaribiota* is correctly placed in the Bolitocharina. I have not included it in this analysis.

Two undescribed bolitocharine taxa included in the analysis were of uncertain generic placement. Consequently, these were tentatively assigned to *"Bolitochara"* for analysis and discussion and were subsequently appropriately assigned based on the results of the phylogenetic analysis. These are *"Bolitochara"* n. sp. A and *"Bolitochara"* n. sp. B.

CHARACTER VARIATION AND CHARACTER ANALYSIS

The most critical process in reconstruction of phylogenetic relationships among taxa is analysis of characters. This process involves two major procedures: (1) recognition and description of homologous character states, and (2) recognition of transformation series and development of hypotheses about their polarity. I agree with numerous authors (e.g., Eldredge and Cracraft, 1980; Wheeler, 1986) that *ad hoc* character weighting is highly subjective and should be used only under special circumstances. Therefore, *ad hoc* character weighting is avoided in this analysis (but see Alternative Phylogeny III), though *post hoc* character weighting in the form of "successive approximation" (Farris, 1969) is applied to the data.

Watrous and Wheeler (1981) and Maddison et al. (1984) have effectively argued that the appropriate method for determination of polarity of transformation series is out-group comparison. This method requires that the distribution of character states be compared both among taxa in the group under analysis (in-group comparisons) and among closely and more distantly related taxa (out-group comparisons). If two states of a character occur in the in-group and only one of these states occurs in the out-group, then the state with a more restricted distribution in the in-group is the apomorphic condition. This simple instance is often not reflected in analysis, however, because of character state evolution within the out-group subsequent to the separation of in-group and out-group lineages. Out-groups may be relatively apomorphic in the characters under consideration in relation to the in-group, or some or all taxa in the out-group may have evolved relatively apomorphic states independently of, and in parallel with, members of the in-group. A single out-group is not sufficient to resolve polarity in these and similar situations, and character state comparisons across more distantly related out-groups are required to establish polarity (Maddison et al., 1984). The problems of complex character state distributions among in-group and out-group taxa is especially pertinent to this study.

Choice of appropriate out-groups for polarization of character states within the subtribe Bolitocharina is complicated by the highly autapomorphic conditions of other subtribes within the tribe Homalotini. Ashe (1984, 1986) hypothesized that the most closely related taxon to the Bolitocharina is the subtribe Gyrophaenina. Ashe (1984, 1986) discusses shared derived characters that support this relationship. Additional shared adult characters not mentioned previously that support this relationship include: (1) bases of the two medial setae of the labium modified from side-by-side to one behind the other (among gyrophaenines this is only seen in members of *Probrachida;* other gyrophaenines have lost one of the setae); (2) loss of the medial pseudopore field on the labium. Other larval characters which support this sister group relationship include: (1) reduction of the four anal hooks of the abdomen (lost in gyrophaenines), (2) the similar derived chaetotaxy of the 8th abdominal segment, and (3) similarities in the tergal gland reservoir and associated gland ducts of the 8th abdominal segment (see Ashe, 1986, 1990, for details). Association of all members of both the Bolitocharina and Gyrophaenina with fresh mushrooms is possibly an additional apomorphy linking these two groups, and is in full concordance with the structural features mentioned above. However, the nature of the association with mushrooms is quite different within the two groups (Ashe, 1984, 1986, 1990; Topp, 1973).

The usefulness of the Gyrophaenina as an out-group for polarizing character states found among the Bolitocharina is seriously limited by the highly autapomorphic condition of the Gyrophaenina. The array of characters which exhibit uniquely derived states within the Gyrophaenina is extremely large (see Ashe, 1984, 1986). Polarization of these characters, as well as those for which gyrophaenines and bolitocharines share two or more states, requires comparisons across one or several more distantly related out-groups.

As noted above, *Leptusa* and related genera (Group Leptusae as recognized by Fenyes, 1918-1921) should not be included in a monophyletic Bolitocharina. They are, however, similar in many structural features. However, *Leptusa* and related genera are characterized by a number of apomorphic features in comparison to the Bolitocharina. These include: (1) reduction of eyes, loss of flight wings (and associated thoracic modifications) and reduction of the elytra by many deep-litter and soil inhabiting taxa; (2) reduction or loss of secondary sexual characteristics of males; and (3) two-segmented labial palpi. More generalized leptusines share many features with the Bolitocharina as well as other taxa within the tribe Homalotini, suggesting that they are suitable for polarizing the states of these characteristics.

As a still more distant out-group within the Homalotini, the subtribe Silusina must be considered. Silusines are highly apomorphic in mouthpart structure in relation to other bolitocharines (see Ashe and Wheeler, 1988), but some (especially *Silusa*) are very similar in male secondary sexual characteristics to some members of the Bolitocharina as well as to some less specialized leptusines. This suggests that these character states, as well as others that are similarly distributed, may be relatively plesiotypic within the Bolitocharini as a whole.

Other homalotine subtribes (Homolotina, Autaliina, Phytosina, etc.) are highly derived in most pertinent structural features and offer little information useful for character analysis within the subtribe Bolitocharina.

Some members of the subtribe Bolitocharina have states of some characters that are not found among other members of the tribe Homalotini, but are widely distributed among other aleocharines. These include three-segmented labial palpi and numerous setose projections on the flabellum of the wing. In addition, some states found among members of the Bolitocharina and also scattered among taxa in related tribes are broadly distributed among other aleocharines. This distribution of character states suggests that members of the subtribe Bolitocharina retain the primitive states of these characters for which apomorphic states have been derived either uniquely or in parallel in all other members of the tribe Homalotini. Therefore, polarization of these characters must be done by using the Aleocharinae as a whole as an outgroup.

In spite of the preceding discussion, problems in polarity of characters resulting from lack of a uniquely and clearly defined out-group only become apparent in a few transformation systems (Characters 1, 5, 10). These problems and my tentative resolutions are discussed under the appropriate characters.

Use of such a hierarchy of out-groups to polarize characters within the subtribe Bolitocharina is not very satisfying. However, a more concisely delimited out-group cannot be recognized at the present time. This highlights the fact that a careful character analysis within almost any large group of aleocharines is limited by our superficial understanding of characters, character states, and their distribution within this diverse assemblage of organisms. I hope that the character analysis presented below and the phylogenetic diagram based on it will stimulate additional studies to test it as well as provide a base on which other studies in the Aleocharinae can be built. A summary of characters and states analyzed here is presented in Appendix 3.

Character 1. Head: Shape.—States of this character among bolitocharines form a more or less continuous series which can be arbitrarily divided into five states: (0) head distinctly broader than long (width : length ratio 1.1 or greater); (1) head more or less oval, slightly broader than long (width : length ratio >1.0<1.1) (Fig. 28); (2) head more or less quadrate or round (width : length ratio about 1.0) (Fig. 132); (3) head slightly elongate (width : length ratio <1.0>0.9) (Fig. 96); (4) head distinctly elongate (width : length ratio 0.9 or less) (Fig. 7). Relatively broad heads (width : length ratio 1.1 or greater) are widely distributed among the Gyrophaenina, more generalized Leptusina and some Silusina as well as other Aleocharinae. Based on this, condition 0 above is considered the plesiotypic condition and the transformation series is arranged in a linear series of decreasing head width (0⇒1⇒2⇒3⇒4). It is reasonable to assume that this transformation has occurred many times independently.

Alternative hypotheses about polarity of this character would focus on the relatively quadrate heads of many *Leptusa* and some gyrophaenines as well as many other bolitocharines. This condition could be considered to be plesiomorphic. If so, the transformation series would be bidirectional, head width increasing in one direction and decreasing in the other. However, a relatively broad head appears to be the more generally distributed condition. Also, a quadrate head appears to be associated with other derived body proportions in *Leptusa* and others. Therefore, this latter hypothesis is less parsimonious than the former.

Character 2. Head: Infraorbital Carina.—Only two states of this character are recognized among bolitocharines: (0) infraorbital carina moderate to strong, complete; and (1) infraorbital carina absent, except faintly evident near maxilla. A well-developed infraorbital carina is widely distributed among all outgroups. Therefore state 0 is considered the plesiotypic condition. A single transformation series from presence of an intraorbital carina to loss is indicated (0⇒1).

Character 3. Head: Neck.—Three states of this character are recognized among bolitocharines: (0) neck absent (Fig. 81); (1) neck present but slightly developed (neck wider than 2/3 head width) (Fig. 22); and (2) neck present, distinct to very distinct (neck 2/3 to 1/2 head width) (Fig. 7). Head without a neck is the condition found among most gyrophaenines, most leptusines, and silusines as well as many other aleocharines. Therefore, state 0 is considered to be the plesiotypic condition. A transformation series reflecting progressive constriction of the base of the head into a neck is indicated (0⇒1⇒2).

Character 4. Head: Setation.—Three states of this character can be recognized among bolitocharines: (0) setae directed medially in postero-lateral areas and anteriorly in midline and anterior portions of head; (1) most to all setae directed anteriorly; and (2) most to all setae directed medially. State 0 is found among many gyrophaenines, leptusines, and silusines as well as many other aleocharines. However, within each of these groups, one can also find members which exhibit the other states. The general distribution of state 0 suggests that this is the plesiotypic condition. However, polarity of this character is not strongly supported. A bidirectional transformation series is indicated, one direction of modification leading to all setae directed anteriorly and an independent modification leading to all setae directed medially (1⇐0⇒2).

Character 5. Pronotum: Width : Length Ratio.—Although the states of this character form a more or less continuous series within the Bolitocharina, gaps in the distribution of relative widths of the pronota among members suggest that the character distribution can be conveniently divided into three states: (0) width : length ratio = 1.4 or greater (Fig. 80); (1) ratio = >1.2<1.4 (Fig. 110); and (2) ratio = 1.2 or less (Fig. 6). Relatively wide pronota (width : length ratio greater than 1.4) are widely distributed within the Gyrophaenina and Silusina, and are found among some Leptusina. This is also a widely distributed feature among other aleocharines, where it is usually associated with other pronotal features generally considered to be relatively plesiotypic. Given this distribution, state 0 is hypothesized to be plesiotypic. A transformation series of decreasing width : length ratio is indicated (0⇒1⇒2).

Character 6. Pronotum: Width of Pronotum Relative to Width of Base of Elytra.—The range of this character within the Bolitocharina can be conveniently divided into two states: (0) pronotal base as wide or virtually as wide as base of elytra (Fig. 80); and (1) pronotal base distinctly narrower than base of elytra (Fig. 6). State 0 is the condition found among most members of all of the out-groups, and is hypothesized to be the plesiotypic condition. A transformation series involving narrowing of the pronotum in relation to the elytra is indicated (0⇒1).

Character 7. Pronotum: Microsculpture.—Three states of this character are recognized: (0) integument with slight to moderate reticulate microsculpture; (1) integument with obsolete microsculpture; and (2) integument smooth and shining, without a trace of microsculpture. Most members of the out-groups (especially leptusines) and many other aleocharines have reticulate integumental microsculpture. Therefore state 0 is hypothesized to be plesiotypic. A transformation series involving progressive loss of microsculpture is indicated (0⇒1⇒2).

Character 8. Wing: Average Number of Setose Projections on Flabellum.—The number of setose projections on the flabellum of the wing varies from 0 to 13 within the Bolitocharina, yet is relatively constant within a given taxon. This character varies more or less continuously when the Bolitocharina are considered as a unit. The total range can be divided more or less arbitrarily into five states: (0) 10–13 setose projections on flabellum (Fig. 57); (1) $>4 \leqslant 8$ (Fig. 140); (2) $\geqslant 3 \leqslant 4$ (Fig. 124); (3) $>1<3$ (Fig. 89); (4) 1 or less (Fig. 104).

This character represents one of the most enigmatic in terms of polarity of any in the Bolitocharina. The flabellum of the wing is a small lobe at the base from which arise elongate setose projections. Reduction in number of such projections is associated with general reduction in size of the flabellum. Within the tribe Homalotini the presence of a flabellum with setose projections is extremely rare outside of the subtribe Bolitocharina. Notably they are absent from the wings of all gyrophaenines, leptusines, and most silusines. Among the Homalotini that I have examined, I have found them to be present only in some members of the genus *Silusa* (3–5 projections per flabellum). If out-group comparison were made only among subtribes within the Homalotini then the polarity would have to be hypothesized to be from absence of a setose flabellum to origin and enlargement of the flabellum. However, presence of a well-developed flabellum with 10–15 setose projections per wing is widely, if erratically, distributed among other aleocharines. For example, Sawada (1977) noted the occurrence of these structures and the variation in number of setose projections among some athetine aleocharines. This suggests that members of the Bolitocharina may retain the primitive condition of presence of a well-developed flabellum, as they appear to do in the instance of three-articled labial palpi. The alternative hypothesis, that presence of a flabellum among the Bolitocharina represents a reversal from absence to presence with subsequent enlargement, is also possible, and is more consistent with the condition in more closely related out-groups. However, I tentatively accept the hypothesis that the presence of a well-developed flabellum (state 0) among bolitocharines is the plesiotypic condition, with subsequent reduction of the flabellum within the lineage ($0 \Rightarrow 1 \Rightarrow 2 \Rightarrow 3 \Rightarrow 4$). This implies that other lineages within the Homalotini have independently lost the flabellum.

Character 9. First Visible Abdominal Tergum: Direction of Setae.—Two conditions are recognized among the Bolitocharina: (0) all setae directed posteriorly; and (1) some setae directed obliquely or transversely toward the midline. State 0 is the condition found among most members of all outgroup taxa and most other aleocharines. Therefore state 0 is hypothesized to be plesiomorphic and a unidirectional transformation is indicated ($0 \Rightarrow 1$).

Character 10. Mesosternum: Medial Carina.—Three states may be recognized among the Bolitocharina: (0) medial carina strong, complete to apex of mesosternal process (Fig. 14); (1) medial carina strong but fading in apical 0.5–0.2 of mesosternum (Fig. 56); (2) medial carina present only on basal 0.2–0.3 of mesosternum (Figs. 88, 123). A strong, complete mesosternal carina is widely distributed among taxa in all out-groups and most other aleocharines. Therefore, state 0 is hypothesized to be the plesiotypic condition with progressive reduction of the carina apically as the more derived condition ($0 \Rightarrow 1 \Rightarrow 2$).

Character 11. Intercoxal Processes: Degree of Separation of Middle Coxae.—This character can be divided into three relatively arbitrary states: (0) coxae narrowly separated, by less than 0.15 times total length of meso- and metasternal processes (Fig. 103); (1) coxae moderately separated, by more than 0.15 times and less than 0.35 times combined length of meso- and metasternal processes (Fig. 35); (2) coxae widely separated, by more than 0.35 times combined length of meso- and metasternal processes (Fig. 56). Polarization of this transformation series is not clear. Gyrophaenines and some silusines (e.g., *Diestota*) have broadly separated mesocoxal cavities. However, leptusines, most silusines, and most other aleocharines have narrowly separated mesocoxae. I tentatively accept the hypothesis that narrowly separated mesocoxae are plesiotypic among bolitocharines. This implies the assumption that the wide separation of mesocoxae of gyrophaenines is derived independently from that condition in bolitocharines. This hypothesis about polarization of this character should be applied with considerable caution; however, it implies a transformation series of enlargement of the meso- and metasternal processes and subsequent widening of the distance between the mesocoxae ($0 \Rightarrow 1 \Rightarrow 2$).

Character 12. Intercoxal Processes: Isthmus Present or Absent.— Three states in relative length of the isthmus between the meso- and metasternal processes can be conveniently recognized: (0) isthmus distinctly present (length greater than 0.1 times combined length of meso- and metasternal processes plus isthmus) (Fig. 103); (1) isthmus slight (visible isthmus length between 0.1 and 0.02 times combined length of processes plus isthmus (Fig. 75); and (2) visible isthmus virtually to completely absent (meso- and metasternal processes in contact or separated by no more than 0.02 times their combined length) (Fig. 56). Problems with unambiguous polarization of this series of character states directly parallel those discussed under Character 11. A very few gyrophaenines have a very slight isthmus (Ashe, 1984) but most have contiguous meso- and metasternal processes. Most other out-group taxa have distinctly visible isthmuses. I tentatively accept the hypothesis that state 0 is the plesiotypic condition for the same reasons as noted for Character 11. Likewise, the same caution in application of this polarity hypothesis is implied. A transformation direction of increasing approximation of the meso- and metasternal processes is indicated ($0 \Rightarrow 1 \Rightarrow 2$) by this polarity.

Character 13. Antenna: Antennomere 4.—Three states are recognized: (0) antennomere 4 similar in setation, microsculpture and general shape to antennomeres 5-10; (1) antennomere 4 transitional in setation, microsculpture and general shape between antennomeres 1-3 and 5-10; and (2) antennomere 4 similar in setation, microsculpture and general shape to antennomeres 1-3. State 0 is widely distributed among all outgroup taxa except gyrophaenines, among which it is the condition exhibited only by a few relatively plesiotypic taxa (see Ashe, 1984). State 0 is therefore hypothesized to be plesiotypic. Ashe (1984) previously discussed the distribution of this character among gyrophaenines, which do not exhibit intermediate conditions of antennomere 4, and were relatively easy to assign to one or the other of the extreme states. However, some bolitocharines exhibit an intermediate condition which requires an additional state (state 1) in this analysis. The transformation series indicated is toward progressive modification of antennomere 4 to be more similar to antennomeres 1-3 (0 ⇒ 1 ⇒ 2).

Character 14. Antenna: Relative Lengths of Articles 5-10.— Three states of this character can be recognized among bolitocharines: (0) articles 5-10 progressively decreasing in relative lengths apically; (1) articles 5-10 more or less the same in relative lengths; and (2) articles 5-10 distinctly increasing in relative lengths toward the apex. State 0 is the condition found among leptusines, silusines and all but a very few more highly derived groups of gyrophaenines. It is also a condition which is widely distributed among other aleocharines. State 0 is therefore hypothesized to be the plesiotypic condition. A transformation series toward increasing lengths of the apical antennomeres is indicated (0 ⇒ 1 ⇒ 2).

Character 15. Mandibles: Molar Denticles.—Only a single state of this character is found among members of the subtribe Bolitocharina. Comparison of this character among bolitocharines and out-groups reveals two recognizable states at this level of analysis: (0) denticles in molar region few to numerous, scattered, not densely arranged; and (1) denticles very numerous, arranged densely in a large patch (Figs. 10, 31, 52). State 0 is found in all members of the tribe Homalotini except the subtribe Bolitocharina (but the exact arrangement of the denticles varies among higher taxa). State 0 is considered to be plesiotypic, and state 1 is synapotypic for the subtribe Bolitocharina (0 ⇒ 1).

Character 16. Maxillary Lacinia: Inner Apical Teeth.—Four states of this character can be recognized among the bolitocharines: (0) one row of teeth on inner face of the lacinia in apical 0.25-0.35 (Fig. 53); (1) inner face of apical 0.25 of lacinia with one row of teeth more basally and two irregular rows more apically (Fig. 137); (2) inner face of lacinia with 3-6 rows of teeth in apical 0.25, with a noticeably denser concentration of teeth near apex (Figs. 12, 54); and, (3) 3-6 rows of teeth in apical 0.25 with a very dense and large concentration of teeth near apex (Fig. 151). Members of the Leptusina, Silusina, and most other aleocharines have a single inner row of teeth in the apical 0.25-0.35. Gyrophaenines have highly autapomorphic lacinial apices, which have been modified into dense patches of spines which function as spore brushes (see Ashe, 1984). Comparisons with gyrophaenines are not appropriate for resolution of the polarity of this character. However, the very general distribution of state 0 among other out-groups indicates that this is the plesiomorphic condition. If this hypothesis of polarity is accepted, then a transformation series of increasing number of teeth on the inner face of the lacinia, especially near the tip is indicated (0 ⇒ 1 ⇒ 2 ⇒ 3).

Character 17. Labium, Ligula: Pair of Sensory Spines.—Three states of this character can be recognized: (0) pair of large, prominent sensory spines on ligula (Fig. 55); (1) pair of sensory spines on ligula minute to small (Fig. 138); and (2) sensory spines absent from ligula (Fig. 102). Some gyrophaenines, most leptusines, and many silusines have a prominent pair of sensory spines on the ligula. These have been reduced or are absent among many gyrophaenines. Nonetheless, the hypothesis that state 0 is plesiotypic is most parsimonious. A transformation series involving increasing reduction of this pair of spines is suggested (0 ⇒ 1 ⇒ 2).

Character 18. Labium: Medial Setae.—Five states of this character can be recognized among members of the subtribe Bolitocharina and related bolitocharines: (0) medial setae side by side, bases close to contiguous; (1) medial setae side by side anterior to medial pseudopore field, bases distant (Fig. 153); (2) medial setae arranged one laterally behind the other in medial pseudopore field, bases close to contiguous (Fig. 74); (3) medial setae arranged one directly behind the other, bases close (Fig. 122); and (4) medial setae arranged one directly behind the other, bases distant (Fig. 102). Virtually all members of the tribe Homalotini except the subtribes Bolitocharina and Gyrophaenina have state 0. Most other aleocharines have state 1. In addition, within the subtribe Bolitocharina, *Sternotropa zealandica* exhibits state 1. This latter species shares so many other features with members of the subtribe Bolitocharina that it seems most parsimonious to hypothesize that this relatively plesiotypic condition for aleocharines as a whole is secondarily derived in this lineage. Members of the subtribes Bolitocharina and Gyrophaenina are unique among aleocharines as far as is known in sharing the condition that the bases of the medial setae are placed one behind the other. Most gyrophaenines have in addition lost one of the setae. Since state 0 is widespread within the tribe Homalotini, it is hypothesized to be the primitive condition for this analysis. State 1 is treated as an independent evolution of a relatively plesiotypic condition. States 2, 3, and 4 are hypothesized to represent a transformation series involving increasing displacement of one medial seta behind the other. A bidirectional transformation series is indicated (1 ⇐ 0 ⇒ 2 ⇒ 3 ⇒ 4).

Character 19. Labium: Medial Pseudopore Field.—Three states may be recognized among members of the Bolitocharina and closely related outgroups: (0) medial pseudopore field narrow, pseudopores present in a linear array; (1) medial pseudopore field more or less broad, pseudopores present in a more or less rectangular array (Fig. 153); and (2) medial pseudopore field narrow, pseudopores absent (Figs. 74, 122). State 0 is widely distributed among all members of the tribe Homalotini except the subtribes Bolitocharina and Gyrophaenina. As in Character 18, only *Sternotropa zealandica* shares character 1 with most aleocharines outside of the Homalotini. For the same reasons as noted under Character 18, I hypothesize that this condition in *S. zealandica* represents secondary evolution to a more plesiotypic condition. Members of the subtribes Bolitocharina and Gyrophaenina share state 2, though the medial pseudopore field is wider among gyrophaenines than among bolitocharines. State 0 is hypothesized to be the plesiotypic condition in relation to the condition found among the Bolitocharina (state 2) as well as in relation to the secondary derivation of a more plesiotypic condition in *S. zealandica* (state 1). A bidirectional transformation series is indicated (1 ⇐ 0 ⇒ 2).

Character 20. Male Secondary Sexual Characteristics: Elytra, Sutural Carinae.—Three conditions are recognized among the Bolitocharina: (0) elytral suture not modified; (1) each elytron with a small knob or tubercle near the suture in posterior 0.5; (2) each elytron with a distinct and strong carina near the suture in posterior 0.5. The condition among most numbers of all out-groups is state 0. Based on this distribution, state 0 is hypothesized to be the plesiotypic condition. The presence of a small sutural knob in a very few members of North American *Leptusa* does not seem sufficient to hypothesize that state 1 is the plesiotypic condition. State 2 is found only among some members of the subtribe Bolitocharina. A unidirectional transformation series is indicated (0 ⇒ 1 ⇒ 2).

Character 21. Male Secondary Sexual Characteristics: Tergum VII.—A great variety of male secondary sexual characters can be found on abdominal tergum VII of bolitocharines. These can be divided into six states: (0) small to moderate medial tubercle, without lateral scattered asperities (Fig. 39); (1) small to very small medial tubercle, with small to very small lateral asperities (Fig. 105); (2) without medial tubercle, with very faint scattered asperities (Fig. 111); (3) with short distinct medial carina (Fig. 144); (4) with very long, prominent medial carina (Fig. 45); (5) with two to three oblique carinae on each side of midline (Fig. 60). State 0 is found among many gyrophaenines, leptusines which retain secondary sexual characteristics, and many silusines. None of the other conditions are widely distributed among the out-groups. Therefore state 0 is hypothesized to be the plesiotypic condition. The diversity of states suggests a complex character state tree within the transformation series. I hypothesize two independent directions of modification. One direction is characterized by increase in lateral asperities followed by reduction of the medial tubercle, and ultimately loss of secondary sexual characteristics except for very faint scattered asperities (0 ⇒ 1 ⇒ 2). The alternative direction of modification is characterized by enlargement of the medial tubercle to a carina and subsequent enlargement of this carina (0 ⇒ 3 ⇒ 5). Origin of state 4 (two to three oblique carinae on each side) within this transformation series is uncertain. I tentatively hypothesize that it is a modification of state 3 by progressive division of the medial carina, but there is little direct evidence for this. This is the only resolution of the origin of this state that is concordant with the more confident resolution of Character 22. While this is a weak justification, it is more parsimonious than creating a known discordant character state distribution. The following transformation series is indicated.

$$\begin{tikzcd}
2 & 1 \arrow[l, Rightarrow] & 0 \arrow[l, Rightarrow] \arrow[r, Rightarrow] & 3 \arrow[r, Rightarrow] \arrow[d, Rightarrow] & 4 \\
 & & & 5.
\end{tikzcd}$$

Character 22. Male Secondary Sexual Characteristics: Tergum VIII.—The diversity of male secondary sexual characteristics on abdominal tergum VIII parallels that of abdominal tergum VII. Six states can be recognized: (0) small to very faint medial tubercle (Fig. 39); (1) a few minute, scattered asperities (Fig. 105); (2) no modifications (Fig. 111); (3) short medial carina (Fig. 144); (4) prominent long medial carina (Fig. 45); (5) moderate to prominent medial carina with shorter flanking carinae or tubercles (Fig. 60). Resolution of the polarity of states of this character is directly analogous to that of Character 21. State 0 is the only one of the states found among bolitocharines that is generally distributed among the out-groups. Therefore, state 0 is hypothesized to be plesiotypic. Two independent directions of modification are indicated. One direction of transformation involves loss of secondary sexual features (0 ⇒ 1 ⇒ 2). The other direction involves enlargement of the medial tubercle to form a carina which becomes more prominent and develops secondary carinae on each side, as indicated thus.

$$\begin{tikzcd}
0 \arrow[r, Rightarrow] & 3 \arrow[r, Rightarrow] \arrow[d, Rightarrow] & 5 \\
 & 4
\end{tikzcd}$$

State 5 is hypothesized to be derived from state 3 rather than state 4 because of the greater similarity of the carina in state 5 to that of state 3 than to that of state 4.

Character 23. Male Secondary Sexual Characteristics: Tergum VIII, Denticles in Apical Emargination.—The posterior margin of the eighth tergum is broadly emarginate in most bolitocharines. The depth of the emargination and the development of the denticles in the emargination vary among taxa. Three states can be recognized: (0) emargination broad and deep, denticles moderate to robust (Fig. 60); (1) emargination broad and shallow, denticles very small to faint (Fig. 39); and (2) emargination very shallow to indistinct, denticles virtually absent to absent (Fig. 111). Polarization of the states of this character is not immediately evident. Gyrophaenines have a great diversity of modifications of the apical margin of tergum VIII of males, but none of these seem directly homologous with the modifications found among bolitocharines. All three states can be found among leptusines. Among silusines, *Silusa* has state 0. The presence of state 0 in a very few *Leptusa* and *Silusa* provides the basis for the hypothesis that this is the plesiotypic condition. If correct, then the presence of states 1 and 2 among both bolitocharines and leptusines would indicate independent reduction of male secondary characteristics in these two groups. An unidirectional transformation series is indicated within the Bolitocharina (0 ⇒ 1 ⇒ 2).

Character 24. Male Secondary Sexual Characteristics: Sternum VI, Lobate Projection Apicomedially.—Males of some taxa of Bolitocharina have a small, lobate projection medially on the apical border. This projection may be glabrous or setose. Three states are recognized: (0) lobate projection absent (Figs. 38, 76, 90); (1) lobate projection present, glabrous (Figs. 16, 17, 125, 126); (2) lobate projection present, setose (figs. 58, 59). This lobate projection is not found in any taxa outside of the Bolitocharina. Therefore state 0 is the plesiotypic condition. The setae in state 2 are clearly highly modified. Their presence is hypothesized to be derived in comparison with a glabrous lobe. A unidirectional transformation series is indicated (0 ⇒ 1 ⇒ 2).

Character 25. Male Secondary Sexual Characteristics: Sternum VII, Medial Setose Glandular Area.—Males of the Bolitocharina and most males of other subtribes in the Homalotini have a band of many hundreds of asetose sensory pores extended around the basal margin of sternum VII. These are clearly evident under compound microscope examination, especially with differential interference optics. Males of some bolitocharines have in addition to this band of pores, a medial concentration of sensory pores from which arise modified setae. Some also have rugose surrounding areas which appear to be evaporative surfaces. Three states of this character can be recognized: (0) uniform broad band of asetose sensory pores present around base of sternum VII, medial setose glandular concentration absent (Figs. 37, 76, 90, 106); (1) band of asetose sensory pores around base of sternum VII broad, medial setose glandular concentration present but small (Fig. 125); and (2) band of asetose sensory pores around base of sternum VII reduced, medial setose glandular concentration present, large (Figs. 16, 59). As noted above most males of the tribe Homalotini (including many Bolitocharina) have a band of asetose pores at the base of sternum VII. This band may be quite broad and contain hundreds of pores. Males of some species also have such a band on the bases of other sterna. States 1 and 2 only occur in some groups of Bolitocharina (except for *Caloderina,* see discussion under subtribe Bolitocharina above). State 0 is hypothesized to be plesiotypic. A single unidirectional transformation series is indicated (0 ⇒ 1 ⇒ 2).

Character 26. Male Secondary Sexual Characteristic: Sternum VIII, Apical Triangular Lobe.—Two states of this character are recognized: (0) margin of lobe setose to edge (Figs. 16, 58, 125); and (1) lobe with distinct asetose margin (Figs. 38, 90, 106, 141). Males of many Homalotini have the posterior margin of sternum VIII modified into a prominent triangular projection. This projection is also present in some females, but it is always much broader and far less prominent in females. Some males of the subtribe Bolitocharina have an asetose margin on the triangular lobe. Since state 0 occurs in all out-groups (except the Gyrophaenini, in which this triangular lobe occurs in greatly reduced state in only a few taxa) and also in some members of the Bolitocharina, state 0 is hypothesized to be plesiotypic. A single transformation is indicated (0 ⇒ 1).

Character 27. Male Genitalia: Apical Lobe of Aedeagus.—Shape of the apical lobe of the aedeagus varies considerably among members of the Bolitocharina, but five distinctive forms can be recognized: (0) apical lobe large, tentlike (Figs. 21, 62, 66, 93); (1) apical lobe slender and elongate (Figs. 41, 46, 79); (2) apical lobe slender, rather footshaped in lateral aspect (Figs. 107, 114); (3) apical lobe slender, recurved (Fig. 112); and (4) apical lobe bifid (Fig. 146). A large, rather tentlike apical lobe is the condition found among some gyrophaenines and most leptusines and silusines, though within each of these taxa the apical lobe has been variously modified independently. Two basic directions of modification are indicated. In one the apical lobe is modified into a slender, elongate structure (0 ⇒ 1). In the other the apical lobe is modified into a slender, footlike structure with subsequent modification of the footlike apex into a recurved structure (0 ⇒ 2 ⇒ 3). The position of state 4 in this transformation series is uncertain. I am taking a conservative position and hypothesizing that it arose independently from state 0 (0 ⇒ 4), but it may be an intermediate form between states 0 and 2. Alternatively, it may have been independently derived from state 2, though this hypothesis would be highly discordant with other characters. A tridirectional transformation series is indicated.

$$\begin{tikzcd}
1 & 0 \arrow[l, Rightarrow] \arrow[r, Rightarrow] \arrow[d, Rightarrow] & 2 \arrow[r, Rightarrow] & 3 \\
 & 4 & &
\end{tikzcd}$$

Character 28. Male Genitalia: Aedeagus, Internal Plates.—Three states can be recognized among the Bolitocharina: (0) internal plates present, plates large, flattened (Figs. 21, 62, 66); (1) internal plates present, plates spinose and recurved (Fig. 128); (2) internal plates absent (Figs. 41, 46, 79, 93). All leptusines and silusines have a pair of large, flattened plates within the median lobe. These are absent from all gyrophaenine median lobes; however, this condition is most parsimoniously hypothesized to be derived independently from the similar condition in Bolitocharina. Based on this distribution, state 0 is hypothesized to be plesiotypic. Two independent directions of modification are likely. In one direction the plates are modified into spinose structures. Alternatively, the plates may be lost. A bidirectional transformation series is indicated (1⇐0⇒2).

Character 29. Male Genitalia: Median Lobe, Flagellum.—The length and shape of the flagellum of the aedeagus varies considerably among the Bolitocharina. Four states of the flagellum can be recognized: (0) moderate length, tubular (Figs. 21, 62); (1) short tubular (Fig. 112); (2) very long, tubular (Figs. 107, 114); (3) moderate length, tapering to sharp apex (Figs. 41, 46, 128). State 0 is found among many gyrophaenines, leptusines, and silusines and this is hypothesized to be the plesiotypic state. No clear morphocline is evident that would link any of the other states together into a transformation series. Therefore, each apotypic state is hypothesized to have originated independently from the plesiotypic condition.

$$\begin{tikzcd}1 & 0 \arrow[l, Rightarrow] \arrow[r, Rightarrow] \arrow[d, Rightarrow] & 2 \\ & 3 &\end{tikzcd}$$

Character 30. Female Spermatheca: Basal Bulb Shape.—Three conditions of the basal bulb are here recognized: (0) basal bulb simple, base rounded (Figs. 19, 24); (1) basal bulb elongate, rounded at base (Fig. 131); and (2) basal bulb simple, with small knob at base (Fig. 109). State 0 is found among most members of all out-group taxa, and is therefore hypothesized to be the plesiotypic condition. States 1 and 2 do not appear to be parts of a single transformation series, and are here hypothesized to have arisen independently from the plesiotypic condition (1⇐0⇒2).

Character 31. Female Spermatheca: Neck Shape.—Three conditions of the deflection of the spermathecal neck can be recognized among the Bolitocharina: (0) neck straight to very slightly bent (Fig. 94); (1) neck bent at more than a 30° angle and less than a 90° angle (Figs. 24, 63); and, (2) neck bent at more than a 90° angle (Fig. 109). State 0 is widespread among gyrophaenines, leptusines and silusines and is hypothesized to be plesiotypic. States 1 and 2 can be most parsimoniously arranged in a transformation series of increasing deflection of the spermathecal neck (0⇒1⇒2).

Character 32. Female Spermatheca: Tube Structure.—Two states can be recognized: (0) tube membranous (Figs. 24, 42); (1) spermathecal tube sclerotized (Fig. 109). State 0 is the condition in most bolitocharines and all members of the out-group, and is hypothesized to be the plesiotypic condition. State 1 is limited to a few members of the Bolitocharina. A transformation from unsclerotized to sclerotized spermathecal tube is indicated (0⇒1).

Character 33. Female Spermatheca: Tube Shape.—Three states can be recognized among the Bolitocharina: (0) spermathecal tube of moderate length, more or less straight (Fig. 24); (1) spermathecal tube very long and irregularly convoluted (Figs. 43, 130); and (2) spermathecal tube twisted into 1 to 3 distinct loops (Fig. 109). State 0 is found among most members of the Bolitocharina as well as being widely distributed among the out-groups. State 0 is therefore hypothesized to be the plesiotypic condition. States 1 and 2 do not appear to be parts of a single transformation series, and are here hypothesized to have arisen independently from the plesiotypic condition (1⇐0⇒2).

Character 34. Female Sexual Characteristics: Vaginal Sclerotization.—Many members of the Bolitocharina have a circular sclerotized area in the vagina. The spermathecal duct opens into the membranous areas near the center of this sclerotized area. The sclerotized ring may be complete and very distinct, or only partially complete and slightly sclerotized. Three states can be recognized among the Bolitocharina: (0) vaginal sclerotization very lightly sclerotized, absent or present as an inconspicuous arc (Fig. 43); (1) vaginal sclerotization moderately to slightly sclerotized, evident as approximately 0.5 circle of sclerotized area (Fig. 24); and (2) vaginal sclerotization moderately to well sclerotized, sclerotized ring complete or at least 0.75 complete (Figs. 63, 94, 143). A sclerotized vaginal ring, either partial or complete, is not found among the out-groups. Therefore, state 0 is hypothesized to be the plesiotypic condition. States 1 and 2 can be most parsimonously arranged in a transformation series of increasing sclerotization of the vaginal ring (0⇒1⇒2).

Cladistic Analysis

Additive binary coding of character states was used for the states of each character. This coding method was required for two reasons: (1) many character transformation series included more than one derived state; and (2) complex character state trees involving transformations in two or more directions from the plesiotypic condition are indicated for some characters. Additive binary coding allows for accurate representation of such multidirectional transformations within a character state matrix. The additive binary code for each character state is shown in Appendix 3. This produces a matrix of 78 potentially derived character states representing 34 separate characters. All character states are coded for 26 bolitocharine taxa. In addition, a hypothetical out-group is constructed in which all character states are set to the plesiomorphic condition, and this group is inserted into the matrix. Missing data for some characters and some taxa resulted from the fact that both sexes were not available for dissection for all taxa and/or the particular characters were not observable on the specimens available for a variety of reasons. These missing data are coded in the matrix as a "?". The resulting character state matrix of 27 taxa (including out-group) by 78 characters is shown in Table 1.

Character state data were analyzed using the phylogenetic tree generating program HENNIG86 version 1.5 (Farris, 1988). Analysis options provided for generation of several initial trees produced by addition of terminal taxa in different sequences, followed by branch-swapping on each of these trees (option "hennig*"), and extended branch swapping with retention of all shortest possible trees (option "bb*"). Additional phylogenetic patterns were examined by successive approximation (Farris, 1969), a technique which relies on *post hoc* character weighting according to the fit of each character to the available shortest trees. This procedure is provided for in the HENNIG86 program by the options "xs w, cc" which will calculate the weights of the characters and list their weights. This option was used successively on each set of generated shortest trees until character weights no longer changed, indicating stability in the trees. Farris (1969) has shown that this technique will clarify phylogenetic pattern even in data sets which exhibit considerable homoplasy. Shortest trees were combined into their most general mutually consistent branching pattern by generation of a Nelson consensus tree.

Initial unweighted analysis of the data yielded 58 shortest trees with a length of 189, a consistency index of 0.38, and a retention index of 0.72. A Nelson consensus tree of these shortest trees revealed that phylogenetic pattern was poorly resolved for many taxa (Fig. 1). The phylogeny resulting from unweighted analysis is characterized by a large basal multichotomy. Three monophyletic groups are resolved [*Pleurotobia* + *Phymaturosilusa*, *Bolitochara* (including *Ditropalia*), and *Stictalia*]. However, species of *Silusida*, *Venusa*, all *Phymatura*, *Pseudatheta*, "*Bolitochara*" n. sp. A, "*Bolitochara*" n. sp. B, and "*Sternotropa*" *zealandica* are all parts of the single basal multichotomy.

Successive approximation required five iterations to reach stability in character weights. This resulted in nine shortest trees, each with a consistency index of 0.69 and a retention index of 0.90. A Nelson consensus of these nine shortest trees showed excellent resolution of branching pattern with unresolved nodes appearing only in a few terminal taxa (Fig. 2). Decisions about generic limits are based primarily on this tree, although alternatives will be presented later. Therefore, I will discuss the structure of this tree in some detail.

The Major Lineages.—The subtribe Bolitocharina is shown to be monophyletic by two apomorphic features by which inclusion in the subtribe was determined (see above) (characters 15-1, mandibles with dense patch of molar denticles, and 18-2-4, medial labial setae with bases arranged one behind the other). In addition, four other apomorphic features are concordant with these: characters 8-1, wings with $>4\leqslant 8$ setose projections on flabellum; 10-1, mesosternum with strong carina that fades in apical 0.5-0.3; 12-1, intercoxal process with slight isthmus; and, 31-1, female spermatheca with neck bent $>30^\circ<90^\circ$. Character states 8-1 and 10-1 at this level in the analysis require reversals of these characters to the plesiotypic condition at other levels on the tree. The analysis, and the consensus tree, require that the states of several characters be treated as though they are ambiguous at this level on the tree (13-2,1; 13-1,0; 17-1,0; 31-1,0).

The phylogenetic tree of bolitocharine rela-

Table 1. Primitive (0) and derived (1) states of 34 character systems for an outgroup and 26 taxa of the subtribe Bolitocharina.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
	----	-	--	--	--	-	--	----	-	--	--	--	--	--	--	---	--	----	--	--	-----	-----	--	--	--	-	----	--	---	--	--	-	--	--
State	4321	1	21	12	21	1	21	4321	1	21	21	21	21	21	1	321	21	1432	12	21	45321	54312	21	21	21	1	4321	12	321	21	21	1	12	21
Outgroup	0000	0	00	00	00	0	00	0000	0	00	00	00	00	00	0	000	00	0000	00	00	00000	00000	00	00	00	0	0000	00	000	00	00	0	00	00
Pleurotobia																																		
sp. A	0000	0	00	00	00	0	00	0000	0	00	11	11	11	00	1	011	00	0111	01	11	01100	10100	00	11	11	0	0000	00	000	00	00	0	00	11
trimaculata	0000	0	00	01	00	0	00	0000	0	01	11	11	00	00	1	011	00	0111	01	11	01100	10100	00	11	11	0	0000	00	000	00	00	0	00	11
Phymaturosilusa																																		
magnifica	0000	0	00	00	00	0	00	????	0	01	11	11	00	00	1	011	00	0111	01	11	01100	10100	00	11	11	0	0000	00	000	00	00	0	00	11
Silusida																																		
marginella	0000	0	00	00	00	0	00	0111	0	11	00	01	01	00	1	001	01	0111	01	00	00000	00000	00	00	00	1	0000	01	001	00	00	0	00	11
"Bolitochara"																																		
n. sp. B	0000	0	00	00	00	0	00	0001	0	11	01	01	11	01	1	000	00	0111	01	00	00000	00000	00	00	00	1	1000	01	010	00	01	0	00	11
n. sp. A	0000	0	00	00	00	0	00	0001	0	01	00	01	11	00	1	000	01	0111	01	01	00001	00001	00	01	01	0	0001	10	100	01	01	0	10	00
Venusa																																		
blanchardi	0000	0	00	00	00	0	00	0001	0	11	01	11	11	11	1	000	11	0011	01	00	10100	01100	00	00	00	1	0001	01	100	00	01	0	10	01
Phymatura																																		
brevicollis	0000	0	00	00	00	0	00	0011	0	01	01	11	11	11	1	000	01	0111	01	00	00100	00000	00	00	00	1	0001	01	100	00	00	0	00	01
picta	0000	0	00	00	00	0	00	????	0	00	01	11	11	11	1	???	??	????	01	00	00100	00000	00	00	00	?	0001	01	100	??	??	?	??	??
jucunda	0000	0	00	00	00	0	00	????	0	00	01	11	10	11	1	???	??	????	01	01	00100	00100	00	00	00	?	0001	01	100	??	??	?	??	??
Stictalia																																		
brevicornis	0011	0	00	00	01	0	00	1111	0	01	00	01	11	00	1	011	11	0111	01	00	00011	00011	01	00	00	1	0110	01	001	10	11	1	01	01
nigrina	0001	0	00	00	01	0	00	????	1	01	00	01	11	00	1	011	11	0111	01	00	00001	00001	01	00	00	1	0110	01	001	10	11	1	01	01
minor	0011	0	00	00	01	0	00	1111	1	01	00	01	11	00	1	011	11	0111	01	00	00001	00011	11	00	00	1	0110	01	001	10	11	1	01	00
californica	0011	0	00	10	01	1	01	1111	0	01	00	01	11	00	1	011	11	0111	01	00	00001	00001	01	00	00	1	0010	01	010	10	11	1	01	00
rugipennis	0111	0	00	10	01	1	11	1111	0	01	00	01	11	00	1	011	11	0111	01	00	00001	00001	01	00	00	1	0010	01	010	10	11	1	01	00
sp. 3	0111	0	00	10	01	1	11	????	0	01	00	01	11	00	1	011	11	0111	01	00	00001	00001	01	00	00	1	0010	01	010	10	11	1	01	00
unicolor	0111	0	00	10	11	1	11	????	0	00	00	01	11	00	1	011	11	0111	01	00	00011	00011	11	00	00	1	0010	01	010	10	11	1	01	00
sp. 6	0111	0	00	10	01	1	01	1111	1	00	00	01	11	00	1	011	11	0111	01	00	00001	00001	11	00	00	1	0010	01	010	10	11	1	01	00
bakeri	0011	0	00	10	01	1	00	0111	0	00	00	01	11	00	1	011	11	0111	01	00	00001	00011	01	00	00	1	0010	01	010	10	11	1	01	00
Bolitochara																																		
(D.) bella	1111	0	00	00	11	1	11	0001	0	00	01	11	00	00	1	000	00	0001	01	11	10100	00011	00	01	11	0	0000	00	010	00	11	0	00	01
(s.s.) lucida	0011	1	11	01	11	1	11	0001	0	00	11	11	01	00	1	111	01	0111	01	11	10100	01100	01	01	11	0	0000	00	001	00	11	0	00	01
(s.s.) lunulata	0111	1	11	01	11	1	11	0011	0	00	01	11	01	00	1	111	00	0111	01	11	10100	01100	01	01	11	0	0000	00	001	00	11	0	00	01
(D.) mulsanti	0111	0	11	00	11	1	11	0001	0	00	01	01	00	00	1	011	00	0011	01	11	10100	00001	00	01	11	0	0000	00	001	00	??	?	??	??
(D.) obliqua	0111	0	01	01	11	1	11	0001	0	00	01	11	00	00	1	011	01	0111	01	00	00011	00011	11	01	11	0	0000	00	001	00	01	0	00	01
Pseudatheta																																		
elegans	0011	0	00	01	00	0	11	1111	0	11	00	11	00	01	1	000	01	0001	01	11	?????	00000	00	00	00	0	0001	01	100	??	??	?	??	??
"Sternotropa"																																		
zealandica	0001	0	00	10	00	0	11	1111	1	00	11	11	11	00	1	111	11	1000	10	00	?????	00011	00	00	00	0	0000	01	010	00	01	1	00	11

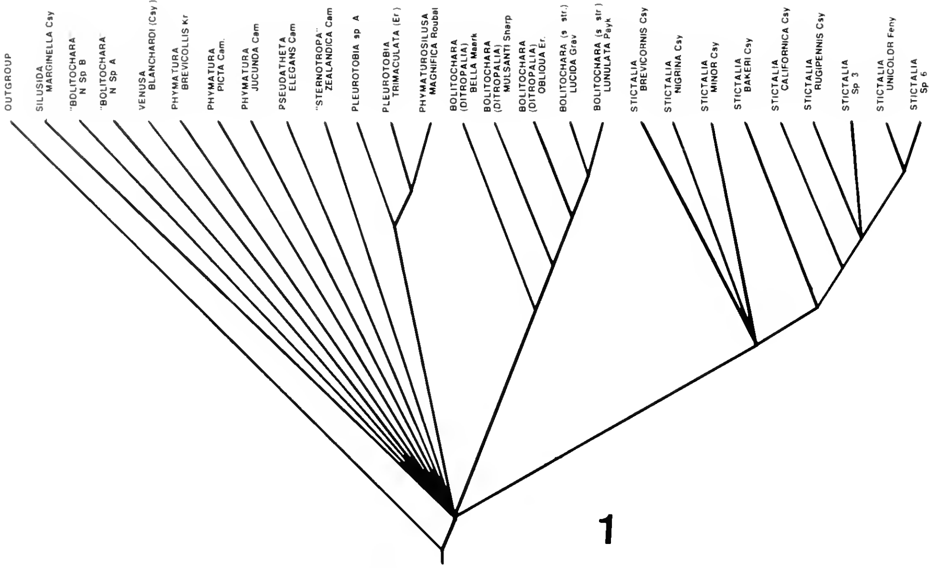

Fig. 1. Phylogeny of bolitocharine taxa. All taxa included; without successive approximation. Nelson consensus tree of 58 shortest trees. Length = 189; C.I. = 0.38; R.I. = 0.72.

tionships splits basally into two main lineages. For convenience of discussion I provide informal names for these lineages. The "*Bolitochara* lineage" includes species that have at various times been placed in the following four genera: *Phymaturosilusa, Pleurotobia, Bolitochara, Ditropalia,* and an undescribed species designated as "*Bolitochara*" n. sp. A. The "*Stictalia* lineage" includes species which have been variously placed in five genera: *Phymatura, Venusa, Silusida, Pseudatheta, Stictalia,* as well as the aberrant *Sternotropa zealandica* and an undescribed species here designated "*Bolitochara*" n. sp. B for analysis.

The "*Bolitochara* lineage" is hypothesized to represent a monophyletic lineage based on three shared derived conditions in the male secondary sexual characteristics: 20–1, male elytra with a small knob or carina near suture in posterior 0.5; 24–1, male sternum VI with medial lobate projection; and; 25–1, male sternum VII with baso-medial concentration of setose glandular pores and corresponding reduction of broad band of asetose pores around base of sternum. These three features, especially 24–1 and 25–1, offer robust evidence of the monophyly of this lineage. These features are unique to the Aleocharinae as far as is known (but see discussion about *Caloderina* above). There can be no reasonable doubt about the derived condition of these character states. Additionally, the complex nature of these structures and their similarity among all taxa provide strong evidence for homology. Since characters 24–1 and 25–1 are consistently found together in all bolitocharines in which they occur, it could be argued that they form a functional complex which evolved together. Consequently, they might be treated as a single character. However, the structures are located on different areas of adjacent sterna, and at this point functional correlation is only presumed, not demonstrated. Most important, treating these two characters as a single character would not alter their robust support for the monophyly of the "*Bolitochara* lineage."

The most basally derived lineage, and the sister group to all other taxa in the "Bolitochara lineage," is the species designated "*Bolitochara*" n. sp. A. Members of this species (and presumably other members of this lineage) differ from other members of the "Bolitochara lineage" by derived features of the aedeagus, male secondary sexual characteristics, and spermatheca (see descriptive section for details). In addition, it lacks many of the derived features which characterize other members of the "Bolito-

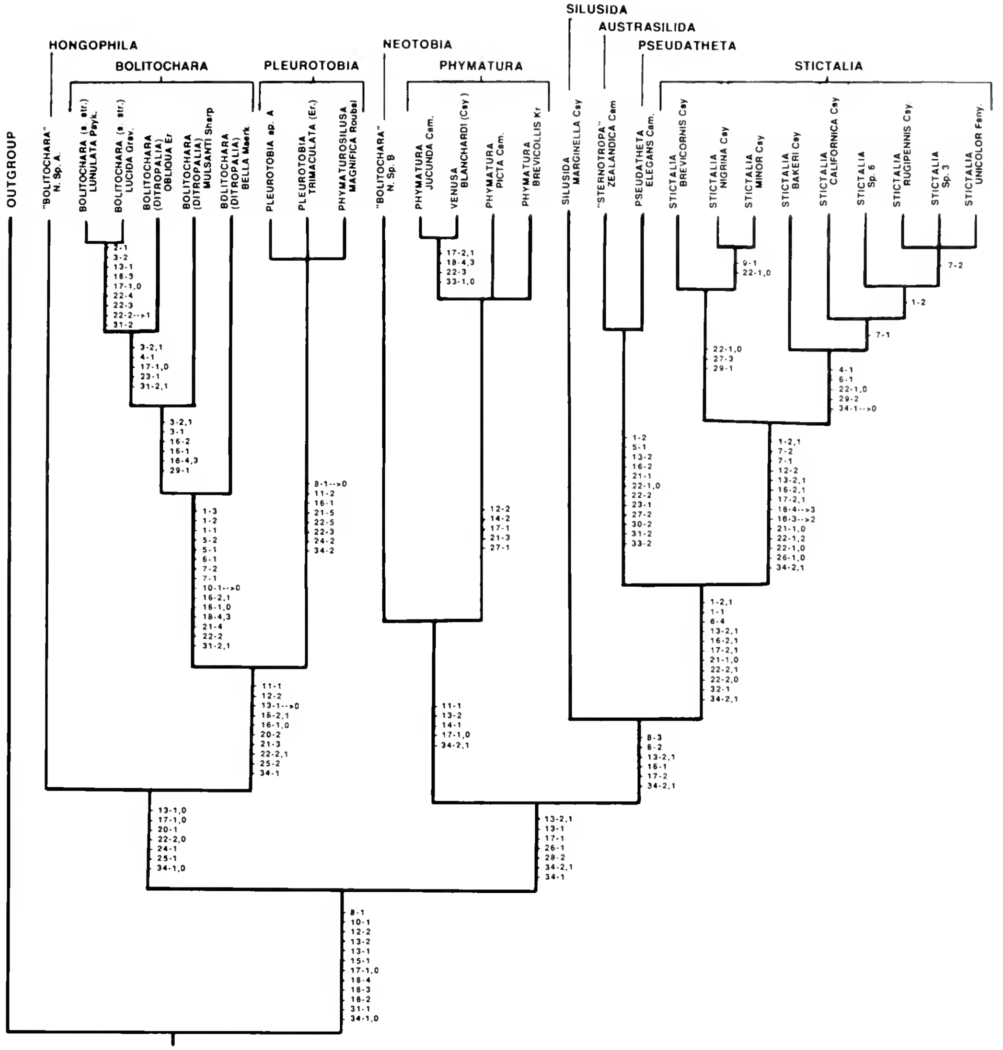

Fig. 2. Phylogeny of bolitocharine taxa. All taxa included; after successive approximation. Nelson consensus tree of nine shortest trees. Length = 473; C.I. = 0.69, R.I. = 0.90. Names at the top indicate genera as recognized in this study. The genera *Hongophila*, *Neotobia*, and *Austrasilida* are newly described. Numbers on branches of the tree indicate the character states that are hypothesized to be synapomorphic at that level.

chara lineage'' (see below).

The sister group to ''*Bolitochara*'' n. sp. A is the lineage which includes *Phymaturosilusa*, *Pleurotobia*, *Ditropalia* and *Bolitochara*. This lineage is hypothesized to be monophyletic based on four shared derived features and one derived reversal: 11-1, intercoxal processes moderately broad, separating coxae >0.15<0.35 times combined length of processes; 12-2, isthmus of intercoxal processes virtually to completely absent; 20-2, male elytra with strong carina near the suture in posterior 0.5; 21-3, male tergum VII with short distinct medial carina; and 13-0 (reversal 13-1 ⇒ 13-0), antennomere 4 similar to 5 through 10.

The next more terminally derived lineage includes the species *Phymaturosilusa magnifica*, *Pleurotobia trimaculata*, and an undescribed species, *Pleurotobia*, n. sp. A. The monophyly of this lineage is robustly supported by eight synapomorphies, one of which is a derived reversal: 11-2, intercoxal processes wide, separating coxae greater than 0.35 times the combined width of the coxae; 16-1, maxillary lacinia with one row of inner apical teeth more basally and two or more irregular rows apically; 21-5, male tergum VII, with two to three oblique carinae on each side of midline; 22A-5, male tergum VIII with moderate to prominent medial carina flanked by shorter carinae or tubercles (includes state 22-3, male tergum VIII with short medial carina); 24-2, male sternum VI with lobate projection setose; 34-2, female vaginal sclerotization moderate to distinct (0.75-1.00 complete ring of sclerotized tissue); and 8-0 (reversal 8-1⇒8-0), wing with 10 to 13 setose projections on flabellum. The relationships among the three taxa combined by these synapomorphies cannot be resolved by characters used in the analysis. They are very similar in general habitus, male secondary sexual features, aedeagus, and spermatheca. A further derived similarity among these taxa which is not included in the analysis is that males of all three taxa have relatively longer antennal articles than females. Specimens of *Phymaturosilusa* differ from those of *Pleurotobia* primarily in that the lateral carinae on terga VII and VIII of male *Phymaturosilusa* are greatly reduced; the most lateral ones are absent to virtually absent in many instances.

The sister lineage to the *Pleurotobia-Phymaturosilusa* lineage is one which includes members of the genera *Ditropalia* (usually treated as a subgenus of *Bolitochara*) and *Bolitochara*. This lineage is hypothesized to be monophyletic based on six synapomorphies and one reversal: 1-3, head shape slightly elongate (width : length ratio$<1.0<0.9$); 5-2, pronotum relatively narrow, width : length ratio 1.2 or less; 6-1, pronotum distinctly narrower than elytra; 7-2, pronotum without microsculpture, integument smooth and shining; 21-4, male tergum VII with very large medial carina; 22-2, male tergum VIII with no secondary sexual features; and 10-0 (reversal 10-1⇒10-0) medial carina of mesosternum strong, complete to apex of process. Although none of these characters is particularly striking and none offers robust confirmation of the monophyly of this lineage, the number of concordant derived characteristics shared by all of the taxa on this lineage is strong evidence of monophyly.

An important feature of the *Ditropalia-Bolitochara* lineage is that the three species of *Ditropalia* (usually treated as a subgenus of *Bolitochara*), *D. bella*, *D. obliqua* and *D. mulsanti,* do not appear to represent a monophyletic group. In fact, *D. mulsanti* shares a number of derived features with members of *Bolitochara* (s. str.) and *D. obliqua* (3-1, neck present, slightly developed, neck width greater than 2/3 head width; 16-2, inner face of maxillary lacinia with 3 to 6 rows of teeth in apical 0.25 with noticeably denser concentration of teeth near apex; and, 29-1, median lobe of aedeagus with short, tubular flagellum). No evidence exists for the monophyly of *Ditropalia.* This will be discussed more fully in a later section of this paper.

Ditropalia obliqua and the two species of *Bolitochara* are hypothesized to form a monophyletic group based primarily on two unambiguous shared derived characteristics: 4-1, almost all head setae directed anteriorly (a condition derived independently in some *Stictalia*), and 23-1, male tergum VIII with broad shallow apical emargination with denticles very small to faint. The monophyly of these three species in relation to *Ditropalia mulsanti* is not strongly supported by these characters. However, the lineage which includes all examined species of *Bolitochara* (s. str.) *(B. lunulata* and *B. lucida)* forms a monophyletic group based on eight shared derived features. Most important among these are: 2-1, infraorbital carina absent except faintly present near maxillary insertion; 3-2, neck present, narrow, width 2/3 to 1/2 head width; 16-3, inner apical teeth of maxillary lacinia with 3 to 6 rows of teeth in apical 0.25 and very dense and large concentration of teeth near apex; 22-4, male tergum VIII with very long prominent medial carina; 31-2, neck of spermatheca bent at greater than a 90° angle. These characters show that these taxa of *Bolitochara* are highly derived in relation to the taxa of *Ditropalia* examined. However, as noted above, *Ditropalia* does not appear to represent a monophyletic group in relation to *Bolitochara.*

Sister lineage to the ''Bolitochara lineage'' is the ''Stictalia lineage.'' The ''Stictalia lineage'' is hypothesized to represent a monophyletic group based on five shared derived features at this level of the cladogram: 13-1, antennomere 4 transitional in setation between 1-3 and 5-10; 17-1, sensory spines of ligula minute to small; 26-1, apical triangular lobe of male sternum VIII with a distinct asetose margin; 28-2, median lobe of aedeagus without internal plates; and 34-1, sclerotization of female vagina moderate to slight, present as approximately 0.5 circle of sclerotized cuticle. Of these synapomorphies, characters 26-1 and 28-2 provide the strongest evidence of monophyly. Character 26-1 is unique as far as I know within the Aleocharinae. Character 28-2 represents a loss; however, the concordance of this character with 26-1 and others suggests that the loss of internal plates in the median lobe of the aedeagus is probably homologous among all members of this lineage.

The most basally derived lineage of the ''Stictalia lineage'' unites all examined species of *Phymatura, Venusa* and *''Bolitochara''* n. sp. B into a monophyletic group. These taxa share three unambiguous shared, derived traits: 11-1, middle coxae moderately separated, intercoxal processes width >0.15<0.35 times combined width of coxae; 13-2, antennomere 4 similar to 1-3; and 14-1, antennomeres 5 to 10 more or less similar in relative lengths (relative lengths of antennomeres neither increasing or decreasing). These are not particularly strong characters, and they are made weaker by the fact that all of them are derived independently in other parts of the *''Stictalia''* lineage. The monophyly of this lineage cannot be considered strongly supported. However, the alternative placement of *''Bolitochara''* n. sp. B on the sister lineage near *Silusida* is also unsatisfactory.

The species designated *''Bolitochara''* n. sp. B is an aberrant taxon. It is clearly not a member of any monophyletic and previously recognized genus-level taxon. In addition to lacking the synapomorphies which define the lineage that includes all *Phymatura* and *Venusa* as a monophyletic group (see below), it exhibits uniquely derived characteristics in the aedeagus, and a derived reversal in the large number of setose projections on the flabellum of the wing (6-8).

The genera *Phymatura* and *Venusa* are shown to be a monophyletic unit based on five shared derived characteristics; 12-2, isthmus of intercoxal processes virtually to completely absent, (shared with some members of the *''Bolitochara''* lineage as well as being homoplasous within the *''Stictalia''* lineage); 14-2, relative lengths of antennomeres 5 to 10 distinctly increasing in relative lengths toward the apex of the antenna; 17-1, pair of sensory spines on ligula minute to small; 21-3, male tergum VII with short distinct medial carina; and 21-1, apical lobe of aedeagus slender and elongate. It is not possible to show that *Venusa* is monophyletic in relation to *Phymatura* with available data. Instead, *Venusa* appears to be a member of the monophyletic genus *Phymatura*.

The sister lineage to the *Phymatura-Venusa-''Bolitochara''* n. sp. B lineage includes all members of the genera *Silusida, Pseudatheta, ''Sternotropa'' zealandica,* and *Stictalia.* This lineage is hypothesized to be monophyletic based on three synapomorphies: 8-3, >1<3 setose projections on flabellum of wings; 16-1, maxillary lacinia with one row of teeth more basally and two or more irregular rows more apically; and 17-2, pair of sensory spines absent from ligula of labium. The most basally derived taxon in this lineage is *Silusida.* The genus *Silusida* is unique in the structure of the aedeagus and the very short, incrassate antenna with strongly transverse antennomeres.

The sister lineage to the *Silusida* includes *''Sternotropa'' zealandica, Pseudatheta,* and *Stictalia.* Eleven derived conditions are shared by members of these three taxa. However all but three of these are ambiguous (resolved as at least two possible states) at this level on the consensus tree. The three unambiguous synapomorphies are: 1-1, head shape oval (width : length = >1.0<1.1); 8-4, one or less setose projections on the flabellum of the wing; and 32-1, tube of female spermatheca sclerotized (reversed in *Pseudatheta* and *''Sternotropa''*). Evidence for the monophyly of this lineage, and probably the entire *''Stictalia''* lineage, is complicated by the presence of *''Sternotropa'' zealandica* within this lineage. While this is undoubtedly the most parsimonious position for *"Sternotropa" zealandica,* it is so aberrant within the Bolitocharina (see discussion under "Choice of Taxa" above) that its presence seriously complicates character state distributions throughout the tree (see Alternative Phylogenies).

The lineages *"Sternotropa" zealandica + Pseudatheta* and all *Stictalia* are hypothesized to be sister lineages. The lineage *"Sternotropa" + Pseudatheta* is the most enigmatic on the tree. As noted above, the character state distributions on this lineage are seriously confused by the aberrant nature of *"Sternotropa" zealandica.* Of the 12 character states which form the basis for recognition of this lineage, eight are represented by ambiguous states of the characters and two represent reversals to plesiotypic conditions. The two remaining unambiguous derived character states which imply monophyly for this lineage are: 7-2, pronotum microsculpture absent, integument smooth and shining; and 12-2, intercoxal processes with isthmus virtually to completely absent. Both of these are derived in parallel in other parts of the tree. Therefore, the evidence for a sister group relationship between *"Sternotropa" zealandica* and *Pseudatheta* is highly suspect. This doubt is only enhanced by the dramatic differences between members of these two taxa. In spite of this most parsimonious resolution of relationships, I seriously doubt if they are closely related. The problem seems to be with the position of *"Sternotropa."* It appears that this taxon is placed with *Pseudatheta* simply because it will not fit anywhere else on the tree with any parsimony. The evidence of the sister group relationship is primarily negative rather than the positive possession of shared derived characters.

All species of *Stictalia* included in the analysis group into a single lineage which is hypothesized to be monophyletic based on 11 shared derived character states: 1-2, head shape more or less quadrate (width : length = about 1.0); 5-1, pronotum width : length ratio >1.2<1.4; 13-2, antennomere 4 similar to 1-3; 15-2, inner face of maxillary lacinia with 3 to 6 rows of teeth in apical 0.25 and noticeably denser concentration of teeth near apex; 21-1, male tergum VII with small to very small medial tubercle and small to very small lateral asperities; 22-2, male tergum VIII with no modifications; 23-1, denticles in apical emargination of male tergum VIII very small to faint; 27-2, median lobe of aedeagus with apical lobe slender, foot-shaped in lateral aspect; 30-2, basal bulb of spermatheca with small knob at base; 31-2, neck of female spermatheca bent at >90° angle; and 33-2, tube of spermatheca twisted into 1 to 3 regular loops. Many of these character states are unique to this group of species within the Bolitocharina. These shared derived conditions provide strong evidence that the species of *Stictalia* represent a monophyletic group.

Two monophyletic lineages within *Stictalia* can be recognized. These are recognized most readily by the dramatic differences in their aedeagal structure. These correspond to the groups that I tentatively recognized as *Stictalia* type I and *Stictalia* type II. Interestingly, these groups were shown to be monophyletic in this analysis. *Stictalia* type I (characterized by *Stictalia brevicornis* Casey), including three species *(S. brevicornis, S. nigrina, S. minor)* in this analysis, is hypothesized to be monophyletic based on: 27-3, medial lobe of aedeagus with apical lobe slender, recurved; and 29-1, flagellum of median lobe short, tubular. *Stictalia* type II (characterized by *Stictalia californica* Casey and including *S. notata,* the type species of *Stictalia*), including six species *(S. californica, S. rugipennis, S. bakeri, S. unicolor, S.* sp. 3, *S.* sp. 6) in this analysis, is hypothesized to be monophyletic based on three shared derived states and one derived reversal: 4-1, most or all head setae directed anteriorly; 6-1, pronotum distinctly narrower than elytra; 29-2, flagellum of aedeagus very long, tubular; and 34-0 (reversal 34-1 ⇒ 0) female vaginal sclerotization very slight, sclerotized portion absent or present only as an inconspicuous arc. In addition to the apomorphies indicated by this analysis, these two different groups of *Stictalia* can be easily recognized externally by differences in color pattern, punctation and male secondary sexual characteristics.

ALTERNATIVE PHYLOGENIES

Because of the uncertainties about inclusion of *"Sternotropa" zealandica* in the Bolitocharina (see discussion under "Choice of Taxa"). "*S.*" *zealandica* was removed from the data matrix and a series of alternative phylogenies computed. The same algorithm and options were used as in the previous computations.

Alternative Phylogeny I.—The first phylogeny is based on computation of all shortest trees without weighting and without successive approximation. Two shortest trees were produced with a length of 181, a consistency index of 0.41 and a retention index of 0.75. A Nelson consensus of these two trees (Fig. 3) has a number of features which are different from the previous preferred tree (Fig. 2). "*Bolitochara*" n. sp. A is shown to be sister to all other Bolitocharina in the analysis. All other Bolitocharina are divided into two lineages: a *Stictalia-Silusida* lineage and a lineage which includes all others. One very dramatic difference is that "*Bolitochara*" n. sp. B and all species of *Phymatura, Venusa,* and *Pseudatheta* are on a lineage with *Pleurotobia* and *Bolitochara* rather than with *Stictalia.* Another difference is that the members of *Phymatura* do not group into a single monophyletic group. This seems unlikely to be a correct representation of phylogeny because all members of *Phymatura* + *Venusa* share unique derived features in the aedeagus. This cladogram is similar to that in Figure 2 in that *Phymaturosilusa* is a member of *Pleurotobia,* and *Pleurotobia* and *Bolitochara* (+ *Ditropalia)* are each shown to be monophyletic and sister groups to each other.

Alternative Phylogeny II.—The second phylogeny produced without "*S.*" *zealandica* involved successive approximation on the two trees produced in Alternative Phylogeny I. Five consecutive runs were required before character weights reached stability. Six shortest trees were produced with a length of 479, a consistency index of 0.67 and a retention index of 0.89. A Nelson consensus of these six trees (Fig. 4) produced only a single major difference from Alternative Phylogeny I. That is, all members of *Phymatura* + *Venusa* united into a single monophyletic group. This is similar to the preferred phylogeny (with "*Sternotropa*" *zealandica,* Fig. 2). The overall structure of the consensus tree is similar to that of Alternative Phylogeny I: "*Bolitochara*" n. sp. A is sister to all other bolitocharines; there are two main lineages—a *Silusida-Stictalia* lineage, and a "*Bolitochara*" n. sp. B-*Phymatura* (+ *Venusa*) - *Pseudatheta* - *Pleurotobia* (+ *Phymaturosilusa*)-*Bolitochara* (+ *Ditropalia*) lineage. The most dramatic difference between Alternative Phylogeny II and the preferred phylogeny (Fig. 2) is the inclusion of "*Bolitochara*" n. sp. B, *Phymatura, Venusa,* and *Pseudatheta* on a lineage with *Pleurotobia* and *Bolitochara* rather than *Stictalia.*

Alternative Phylogeny III.—If the states of Characters 24 (male sternum VI with lobate projection medially) and 25 (male sternum VII with medial setose glandular area) are each given an ad hoc weight of 3, then 38 shortest trees are produced with a length of 191, a consistency index of 0.43 and a retention index of 0.78. A Nelson consensus of these 38 trees (Fig. 5) is very similar to that of the preferred tree (Fig. 2). It differs only in that *Pseudatheta* is placed as a part of a basal trichotomy rather than as a member of the lineage which includes *Stictalia.* This *ad hoc* weight does not seem unreasonable because the derived states of these characters are virtually unique within the Aleocharinae.

In summary, it is clear that the presence of "*Sternotropa*" *zealandica* within the Bolitocharina has a dramatic effect on the phylogenetic analysis. This effect is reflected primarily in modifications of the composition of major lineages when "*S.*" *zealandica* is eliminated from the analysis. In spite of the differences between the alternative phylogenies (Figs. 3, 4, 5) and the preferred phylogeny (Fig. 2), it is striking that the compositions of monophyletic lineages above the basal branches remain the same throughout. For example, in all analyses, members of *Pleurotobia* + *Phymaturosilusa, Phymatura* + *Venusa, Bolitochara* (including *Ditropalia*) and *Stictalia,* are united as monophyletic lineages. In addition, *Silusida, Pseudatheta,* "*Bolitochara*" n. sp. A and "*B.*" n. sp. B are consistently treated as monophyletic lineages rather than as members of other genus-level taxa. New characters and additional analyses will be required to resolve conflicts in the composition of basal lineages. However, the present analyses provide a solid base for delimiting monophyletic

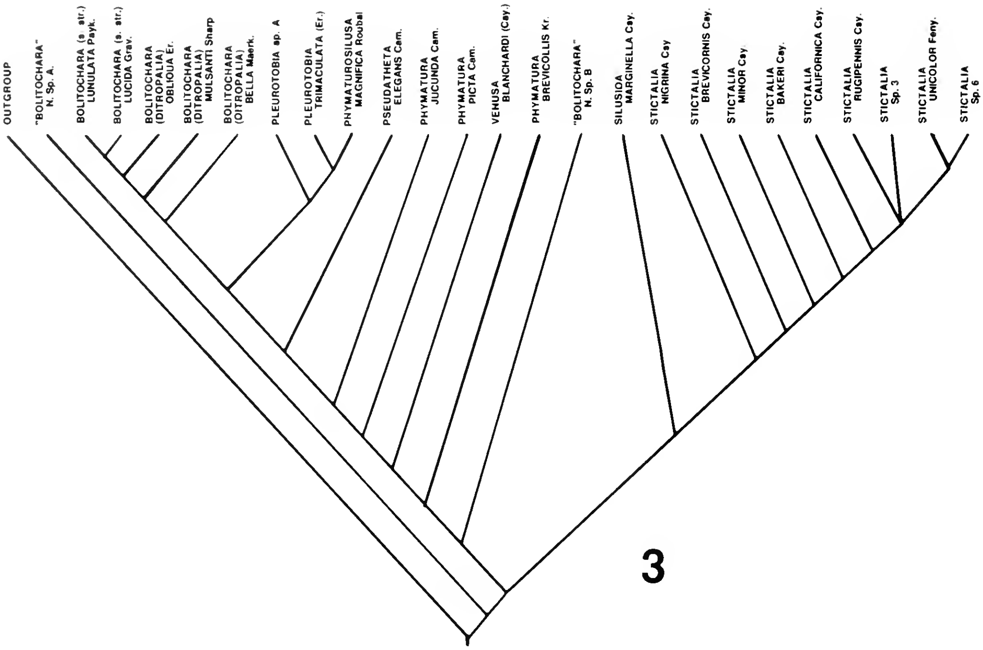

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Fig. 3. Alternative phylogeny I of bolitocharine taxa. "*Sternotropa*" *zealandica* Cam. excluded; without successive approximation. Nelson consensus tree of two shortest trees. Length = 181; C.I. = 0.41; R.I. = 0.75.

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Fig. 4. Alternative phylogeny II of bolitocharine taxa. "*Sternotropa*" *zealandica* Cam. excluded; with successive approximation. Nelson consensus tree of six shortest trees. Length = 479; C.I. = 0.67; R.I. = 0.89.

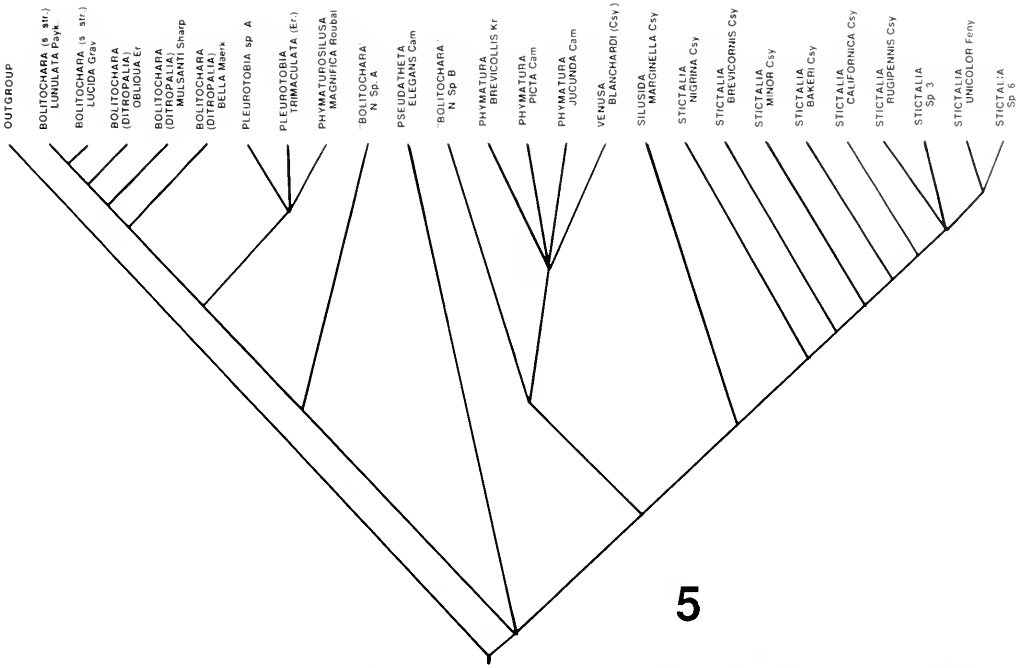


Fig. 5. Alternative phylogeny III of bolitocharine taxa. "*Sternotropa*" *zealandica* Cam. excluded; without successive approximation; with characters 24 and 25 each given an *ad hoc* weight of "3." Nelson consensus tree of 38 shortest trees. Length = 191; C.I. = 0.43; R.I. = 0.78.

genus-group taxa within the Bolitocharina.

TAXONOMIC CONCLUSIONS BASED ON CLADISTIC ANALYSIS

Since there is good evidence that the members of the subtribe Bolitocharina as here recognized form a monophyletic group, there are two possible approaches to categorical ranking. Firstly, since many of the included taxa have previously been synonymized with the genus *Bolitochara*, one could consider the entire subtribe to represent one genus. The correct name of this genus would be *Bolitochara*. Monophyletic groups within this genus could be treated as subgenera. Alternatively, one could continue to assign the entire monophyletic lineage to the subtribal category, as presently done, and treat each of the monophyletic subunits as a genus. Within the context of the cladistic analysis these alternative treatments of categorical assignment are equivalent in that each conveys the same cladistic information. There are no completely objective criteria which would allow one to choose between them. Under these circumstances, one must choose between the two ranking systems based on other criteria, such as historical precedent, nomenclatorial stability and efficient storage and retrieval of information, as long as application of these criteria does not obscure or violate the cladistic information about monophyletic lineages.

I have elected to follow the second of the rankings systems. In effect, this results in the entire lineage being assigned to the subtribal category and each demonstrably monophyletic lineage which has previously had a generic name assigned to one or more of its members being assigned to the genus category. This requires that three taxa be assigned to newly described monotypic genera. Two of these include only previously undescribed species, and one represents a new assignment (see below).

I have chosen this alternative for ranking of taxa for the following reasons: (1) most of the monophyletic lineages include one or more taxa which have previously been placed in described genera. Therefore, there are valid genus-group names available for most monophyletic lineages. (2) The structural diversity within the subtribe is substantial. (3) Genera previously synonymized with *Bolitochara* were synonymized and placed in the subgenus *Ditropalia* based on plesiotypic characteristics and do not represent a monophyletic group. (4) Several distinctive lineages (e.g., *Phymatura, Silusida*) have never been synonymized with *Bolitochara.* (5) If coordinate sister groups should be given equal categorical rank, then the monophyletic "Bolitocharina" must be given the same rank as its sister group, the subtribe Gyrophaenina. While there are also valid reasons for assigning the entire monophyletic lineage to the genus *Bolitochara* (the alternative ranking method), I believe that these are no more compelling than those supporting the rankings that I have chosen.

The fate of described genus-level taxa and other appropriate monophyletic groups as a result of the cladistic analysis and the ranking criteria chosen are discussed below.

Bolitochara Mannerheim.—The International Commission of Zoological Nomenclature (1961, Opinion 599) conserved the name *Bolitochara* (as separate from the genus *Zyras* Stephens) by fixing the type species as *Bolitochara lunulata* (Paykull). In the analysis, *B. lunulata* forms a monophyletic group with *B. lucida, B. (=Ditropalia) obliqua, B. (= Ditropalia) mulsanti,* and *B. (=Ditropalia) bella.* The lineage including these five taxa is robustly indicated to be monophyletic (see discussion above) and cannot be divided into less comprehensive monophyletic genus-level taxa. Under this interpretation, *Bolitochara* includes the type species of the genus *Ditropalia* Casey.

Ditropalia Casey.—Casey (1906) proposed the name *Ditropalia* to include those European "*Bolitochara*" which have the head more strongly narrowed behind than North American species (but neck greater than 1/2 as wide as head), and have a complete infraorbital carina. He included in this genus *Bolitochara bella* Maerkel (fixed as type species of *Ditropalia* by Fenyes 1918), *B. mulsanti* and *B. obliqua* as well as other undesignated European "*Bolitochara*" with similar features. Later Fenyes (1920), Moore, and Legner (1975) and others (see history above) assigned North American bolitocharines to this genus. The analysis shows that those features on which *Ditropalia* was based are plesiotypic within the genus *Bolitochara* and the subtribe as a whole (see also discussion under *Bolitochara*). Even within *Bolitochara* the taxa assigned to *Ditropalia* do not form a monophyletic lineage. North American taxa previously assigned to *Ditropalia* do not form parts of monophyletic lineages which include the type species of *Ditropalia.* The conclusion that *Ditropalia* is a taxon based solely on plesiotypic features, and that other taxa have been assigned to it because of shared possession of plesiotypic features, cannot be avoided. For this reason I am placing the name *Ditropalia* Casey in junior synonymy with *Bolitochara* Mannerheim and recommending that it no longer be treated as a useful subgenus of *Bolitochara.*

Phymatura J. Sahlberg.—The genus *Phymatura* was originally described by J. Sahlberg (1876) to include the single European species *Bolitochara brevicollis* Kraatz. Casey (1906) subsequently designated the type of *Phymatura* to be *P. brevicollis* (Kraatz). It was originally distinguished from European *Bolitochara* because its members possess a much broader pronotum and head and shorter antenna with transverse antennomeres. Later Cameron (1939a) assigned a number of Oriental and Indian species to this *Phymatura.* In the cladistic analysis, *Phymatura brevicollis* forms a well-supported monophyletic group with two other representative species of *Phymatura* as well as the North American *Venusa blanchardi* (Casey). This group occurs on a different branch in the cladogram from *Bolitochara* and can be treated as a separate genus without ambiguity.

Phymaturosilusa Roubal.—The genus *Phymaturosilusa* was described by Roubal (1932) to include the single eastern European species *Phymaturosilusa magnifica* Roubal. It was characterized by relatively large size, very broad head and pronotum, and distinctive secondary sexual characteristics, including longer antennomeres of males in comparison to those of females. *Phymaturosilusa magnifica* appears on the cladogram in an unresolved trichotomy with two species of the North American taxon *Pleurotobia* Casey. *P. magnifica* is extremely similar to North American

Pleurotobia in external form and appearance, and differs primarily in having much smaller (virtually absent) lateral carinae on the male tergum VII and VIII. The monophyly of *Phymaturosilusa* and *Pleurotobia* is robustly supported by synapomorphic features and there can be no reasonable doubt that they should be combined into one genus-level taxon. For this reason I am placing *Phymaturosilusa* Roubal in junior synonymy with *Pleurotobia* Casey.

Pleurotobia Casey.—*Pleurotobia* was originally described by Casey (1906) to include three North American species. Fenyes (1918) subsequently designated *Pleurotobia suturalis* Casey as the type. Fenyes (1920) synonymized *Pleurotobia* with *Ditropalia* because of the possession of an intraorbital carina by members of both groups. This synonymy was perpetuated by Blackwelder (1952), Moore and Legner (1975) and other studies of the Bolitocharina. I have shown above that *Ditropalia* is based on plesiotypic characteristics and should not be used. In addition, the sampled members of *Pleurotobia* (+*Phymaturosilusa)* form a well-supported monophyletic group which is the sister group to the European *Bolitochara*. None of the members of *Pleurotobia* unite with members of *Bolitochara*. Therefore, *Pleurotobia* is a valid genus-level taxon separate from *Bolitochara*. I will treat it as a genus. An alternative ranking would be to enlarge the concept of *Bolitochara* to include both monophyletic groups. *Bolitochara* would then still be monophyletic with two valid subgenera, *Bolitochara* (s. str.) and *Bolitochara (Pleurotobia)*. However, members of *Pleurotobia* and *Bolitochara* are substantially different from each other in a variety of external structural features, as well as general appearance. Therefore, I can see little advantage in combining them into a single genus, and have chosen to treat them separately.

Pseudatheta Cameron.—*Pseudatheta* was described by Cameron (1920) to include the single species *Pseudatheta elegans* Cameron from Southeast Asia. Though he included the genus in the tribe Bolitocharini, he did not specifically assign it to the subtribe Bolitocharina. He subsequently described other species in this genus (1932, 1939a). The genus has not received subsequent study and has always been treated as separate from *Bolitochara*. The ranking of *Pseudatheta* is problematic. The single species studied forms a monophyletic group with "*Sternotropa*" *zealandica* (see discussion below). However, the two taxa are dramatically different in external appearance as well as in apomorphic features. Furthermore, the apomorphies which unite them are not convincing (see analysis above). I, therefore, have elected to treat each as representing a valid genus-level taxon.

Silusida Casey.—*Silusida* was described by Casey (1906) to include two species of North American bolitocharines characterized by weakly rounded sides of the prothorax and short and strongly incrassate antennae with very transverse antennomeres IV–X. Fenyes (1918) later designated the type to be *Silusida marginella* (Casey). In contrast to the fate of most North American bolitocharine taxa [i.e., to be synonymized with *Bolitochara (Dipropalia)*], *Silusida* has most often been treated as a separate genus. However, Blackwelder (1952) indicated that it should be treated as a *Bolitochara*, and Seevers (1978) synonymized all North American bolitocharines with *Bolitochara*. However, the cladistic analysis indicates that *Silusida* is not closely related to *Bolitochara*. Furthermore, it does not combine into a monophyletic group with any other taxa examined in the analysis. Members of *Silusida* exhibit numerous apomorphic features which separate them from other bolitocharines. In spite of the low diversity of *Silusida* (a single valid known species—see taxonomic treatment), there is no phylogenetic justification for treating *Silusida* as a member of any other genus-level taxon. Therefore, I have chosen to maintain *Silusida* as a separate genus.

Stictalia Casey.—*Stictalia* was described by Casey (1906) to include a variety of North American bolitocharines which have the prothorax distinctly narrower than the elytra, the head slightly narrowed behind the eyes, and the mesocoxal cavities more narrowly separated by the meso- and metasternal processes than in other North American bolitocharines. This is the most diverse group of North American bolitocharines, with 17 species limited to the west coast of North America. Fenyes (1920) synonymized

Stictalia with *Ditropalia*, apparently because all members of *Stictalia* have a prominent and complete infraorbital carina. The cladistic analysis provides no evidence that the members of *Stictalia* are closely related to those of *Bolitochara*. The nine examined members of *Stictalia* combine into a monophyletic group, on a different branch of the cladogram than *Bolitochara* and substantially separated from it. Under the ranking criteria applied in this paper, the genus *Stictalia* clearly forms a valid genus-level taxon.

Venusa Casey.—The genus *Venusa* was described by Casey (1906) to include those North American bolitocharines which have a broad head, very broad and transverse prothorax, antennomeres which are elongate and do not gradually increase in width apically, and different secondary sexual characteristics. Fenyes (1918) subsequently fixed the type to be *Venusa picta* Casey (= *Bolitochara blanchardi* Casey). Fenyes (1920) synonymized *Venusa* with *Ditropalia*, apparently because members of *Venusa* possess a prominent and complete infraorbital ridge. This treatment has been followed by all subsequent workers. However, in the cladistic analysis, the single valid species of *Venusa* examined combines as a part of a monophyletic group with all members of *Phymatura* represented in the analysis. This combination is robustly supported by numerous synapomorphies (see cladistic analysis). The similarity of the aedeagus of members of *Venusa* and *Phymatura* is especially striking and quite different from the form of the aedeagus of any other group of bolitocharines. The primary difference between members of *Venusa* and *Phymatura* is found in the elongate antennomeres and non-incrassate antenna of members of *Venusa* (transverse antennomeres and incrassate antenna for most members of *Phymatura*) and the more prominent carina on tergum VII of males of *Venusa*. These differences are overshadowed by the synapomorphies that the two groups share. The phylogenetic evidence provides strong support for the conclusion that *Phymatura* and *Venusa* represent a single genus-level taxon. I therefore am placing *Venusa* Casey in junior synonymy with *Phymatura* Sahlberg.

"Bolitochara" n. sp. A (= *Hongophila* new genus).—This taxon was designated as a *"Bolitochara"* solely to provide a name for discussion. *Bolitochara* n. sp. A is known only from the mountain systems of the southwestern United States; however, I have seen specimens of several closely related species from Mexico. In the cladistic analysis this taxon is shown to be the basal member of the branch which includes *Pleurotobia* and *Bolitochara*. However, it shares few synapomorphies with either of these taxa. In addition, the aedeagus, spermathecae and secondary sexual characteristics of members of *"Bolitochara"* n. sp. A are built on dramatically different, and highly derived patterns. If *Bolitochara* and *Pleurotobia* are treated as separate genera then there is no choice but to treat *"Bolitochara"* n. sp. A as a new genus level taxon. Because members of *"Bolitochara"* n. sp. A are relatively plesiotypic in external features, the genus is relatively difficult to characterize and recognize, based on apomorphic features, without examination of sexual characteristics. *"Bolitochara"* n. sp. A could only be incorporated into a previously described genus by expanding the concept of *Bolitochara* to include all members of the "Bolitochara" lineage (*Bolitochara* + *Pleurotobia* + *"Bolitochara"* n. sp. A). While this would reduce the number of genera, it would have the effect of making *Bolitochara* a structurally very diverse taxon and subsequently, it would be very difficult to characterize or distinguish from genus-level taxa on the *"Stictalia"* lineage. Such a ranking decision would also have the effect of requiring that all taxa on the *"Stictalia"* lineage also be treated as a single genus-level taxon (since the *"Bolitochara"* and *"Stictalia"* lineages are sister taxa and therefore coordinate taxa). This, in my opinion, would result in more taxonomic problems and difficult to define taxa than would the alternative ranking which requires a new genus-level taxon for *"Bolitochara"* n. sp. A. I, therefore, have chosen to treat *"Bolitochara"* n. sp. A as a new genus-level taxon (see Taxonomic Treatment, *Hongophila* new genus).

"Bolitochara" n. sp. B (= *Neotobia* new genus).—As above, the name *"Bolitochara"* n. sp. B was chosen only to provide a label for discussion. Only a single undescribed species of this taxon is known from widely

scattered localities across the northern part of North America from the Canadian Rockies to the northeastern United States. "*Bolitochara*" n. sp. B forms a weakly supported monophyletic lineage with members of *Phymatura* and *Venusa* in some analyses (Figs. 2, 5). However, "*Bolitochara*" n. sp. B is sister group to a diversity of taxa in other analyses (Figs. 3, 4). Two alternative rankings of "*Bolitochara*" n. sp. B are possible. One could enlarge *Phymatura* to encompass "*Bolitochara*" n. sp. B. This would result in a broad genus *Phymatura* which would be difficult to characterize or recognize, and it would destroy the striking uniformity within *Phymatura* of highly distinctive and apomorphic aedeagal structures exhibited by members of *Phymatura* and *Venusa*. The alternative is to treat "*Bolitochara*" n. sp. B as a new genus-level taxon (see Taxonomic Treatment, *Neotobia* new genus). This latter choice seems to me to be the better one since then each taxon can be recognized and characterized based on apomorphic features. Also, "*Bolitochara*" n. sp. B does not group as part of a monophyletic group with *Phymatura* in two of the alternative phylogenies (see Figs. 3, 4). This results in some doubt about the correct placement of the two lineages as sister groups. Therefore including them together in one genus is questionable.

"*Sternotropa*" *zealandica* Cameron (=*Austrasilida* new genus).—The name *Sternotropa zealandica* was applied by Cameron (1947) to a small "bolitocharine" found in New Zealand. However, it is not closely related to other members of *Sternotropa*, a genus in the subtribe Gyrophaenina (Ashe, 1984), and is clearly not a gyrophaenine. However, though externally similar to many Bolitocharina, its inclusion in the subtribe is problematic. For reasons discussed elsewhere I have tentatively accepted it as a bolitocharine (see discussion under "Choice of Taxa"). In the cladistic analysis "*Sternotropa*" *zealandica* appears as sister group to *Pseudatheta elegans* (see discussion under *Pseudatheta* above). However, the monophyly of the lineage that includes these two taxa is very weakly supported (see "Cladistic Analysis" section for discussion). The problem seems to center on the unusual combination of characteristics exhibited by "*Sternotropa*" *zealandica*. Many of these are aberrant for the Bolitocharina as a whole. This makes "*S.*" *zealandica* difficult to fit on the tree, and results in a considerable increase in homoplasy when it is included in the analysis. The position of "*S.*" *zealandica* (as sister group to *Pseudatheta*) is too weakly supported to base any taxonomic decisions on such a placement. Changes in character coding, addition of only a small number of characters, or addition of other taxa could very easily alter such a tentative placement. With these considerations it seems that the only reasonable action is to treat "*Sternotropa*" *zealandica* as a new genus-level taxon. Under any circumstances, the taxon needs a new generic assignment, since it is clearly not a member of *Sternotropa* (see Taxonomic Treatment, *Austrasilida* new genus).

TAXONOMIC TREATMENT

SUBTRIBE BOLITOCHARINA

Diagnosis.—Adults of the Subtribe Bolitocharina can be recognized by the combination of 4,4,5 tarsal segmentation; 3-articled, nonstyliform labial palpi (Figs. 5, 13, 34, 55); mandibles with large patch of densely arranged denticles in molar area of ventral (abcondylar) side (Figs. 10, 31, 52); ligula of labium elongate and bifid at apex; medial setae of prementum either one laterally behind the other or one directly behind the other (Fig. 34); medial pseudopore field of prementum very narrow and without pseudopores (Fig. 13); lacinia of maxilla with numerous spines and setae on apical 0.75 of inner face (Figs. 11, 32); many with mesocoxae moderately broadly separated by broad meso- and metasternal processes; and many with male secondary sexual characters consisting of medial or lateral carinae or knob on terga VII and VIII, and broadly emarginate margin of tergum VIII with 3 to 5 small to moderate-sized denticles in each half of emargination.

Description.—Body length 1.2–4.2 mm. Body form various (Figs. 6, 27, 48, 80, 95), most elongate and more or less parallel-sided. Body color various, most with contrasting light and dark colors, especially on elytra.

Head.—Distinctly broader than long to distinctly elongate. Infraorbital carina strongly developed and complete to reduced and present only faintly near mandibular insertion. Neck absent (Fig. 81) to slightly developed (Fig. 22) or well developed (Fig. 7), prominent, less than 1/2 width of head. Eye size relatively large, length greater than 1.5 times length of tempora, to small, length less than 1.0 times length of tempora. Head setation directed medially and anteriorly or all setae directed anteriorly or all directed medially.

Mouthparts.—Labrum (Figs. 8, 29, 50) with major setae well developed, without accessory setae; medial sensilla well developed; lateral sensillum row with 3 to 5 sensilla, sensilla more or less distant from lateral margin. Maxillary palpus 4-articled. Lacinia (Figs. 12, 33, 54) with single to multiple rows of teeth in apical 0.25, with numerous spines and setae on apical 0.75 of inner face. Galea with numerous close rows of setae apically. Mandibles (Figs. 10, 31, 52) more or less robust, apices simple; right with well-developed preapical tooth; ventral molar area with large patch of densely arranged and well-developed denticles; prostheca well developed, with flattened and apically bifid structures in basal 0.5. Labial palpus distinctly 3-articled, not styliform. Ligula (Figs. 13, 34, 55) of labium elongate, bifid apically. Medial setae of labium two, bases arranged one behind the other, setal bases either laterally behind each other or in same anteroposterior line. Medial pseudopore field very narrow, without pseudopores; lateral pore field with one spinose pore, two real pores and most with numerous pseudopores.

Thorax.—Pronotum transverse to more or less quadrate; posterior margin moderately bisinuate to broadly rounded. Pronotum almost as wide as base of elytra to distinctly narrower than base of elytra. Hypomera broadly visible in lateral aspect. Elytral apical angles markedly to moderately sinuate. Msosternum with medial carina markedly developed (Fig. 154) and complete to apex of mesosternal process or well developed only basally (Fig. 123). Mesosternal process broad or narrow, extended between coxae 0.5 or greater length of coxae to contact or virtually contact rounded metasternal process, isthmus very short or absent; mesocoxae moderately to narrowly separated. Tarsal segmentation 4,4,5.

Abdomen.—Abdominal terga III–V or III–VI more or less deeply transversely impressed. Tergum VII with abdominal gland openings on anterior margin.

Male Secondary Sexual Characteristics.—Most with moderately developed to strong carina or knob medially on terga VII and VIII (Fig. 18), or two or three oblique carinae on each side (Fig. 60), greatly reduced to small knob and scattered asperities in some (Fig. 105) to absent in a few. Some with small knob or distinct carina at sutural margin of elytra. Most with apical margin of tergum VIII broadly emarginate with row of small to moderate-sized denticles in emargination (Figs. 18, 39), emargination and denticles greatly reduced in some (Fig. 111). Sternum VIII triangularly produced into a distinct lobe posteriorly.

Aedeagus.—Median lobe and parameres varied. Flagellum long or short, tubular, moderately sclerotized. Median lobe with internal structure of pair of sclerotized plates (Figs. 21, 62, 128) or such plates absent (Figs. 41, 93, 107, 146). Apical process simple and tentlike (Figs. 21, 62) or spinose (Figs. 41, 46) or recurved structures (Figs. 107, 112, 114). Paramere with apical lobe very long, length greater than 0.5 times length of basal portion in most (Fig. 61), shorter in some (Fig. 145).

Female Genitalia.—Spermathecal tube membranous to slightly sclerotized, short to very long and convoluted or complexly looped, without lateral flangelike plate (except in *Austrasilida* new genus). Spermatheca simple, basal bulb elongate (Fig. 131), rounded (Fig. 24), or slightly knobbed basally (Fig. 109); neck more or less straight (Fig. 94) to bent 90° or more (Figs. 109, 131).

Discussion and Reclassification.—The subtribe Bolitocharina as here defined is comprised of a number of genera that share several apomorphic features as listed above (see Choice of Taxa and Cladistic Analysis). Treated in this way, the subtribe Bolitocharina is more narrow than its treatment in such works as Lohse (1974) and Seevers (1978) in that it does not include *Leptusa* and its relatives. *Leptusa* and similar genera [essentially the "Group Leptusae" of Fenyes (1918)] lack these apomorphies. In addition, this latter group of genera has 2-articled labial palpi (3-articled in the Bolitocharina), an undivided, elongate ligula of the labium (divided in the Bolitocharina), and a very different lacinia of the maxilla. These genera should be placed in a separate subtribe centered on *Leptusa,* though the generic composition of this subtribe is not yet clear and requires additional study.

Restricting the subtribe Bolitocharina to be comprised of those genera sharing the synapomorphies listed above serves to make the group much more homogeneous in both external features and in biology. Both larvae and adults of all taxa are associated with macroscopic fruiting bodies of fungi, especially members of the Polyporaceae and some ligniferous Agaricales. This uniformity of habitat preferences may be an additional synapomorphy linking members of the Bolitocharina. The concordance among the three synapomorphies listed and the habitat preference provides relatively robust evidence that the subtribe so defined is monophyletic.

In this revision I recognize nine genera in the subtribe. These are:

- *Bolitochara* Mannerheim
    - *Ditropalia* Casey
- *Phymatura* J. Sahlberg
    - *Venusa* Casey
- *Pleurotobia* Casey
    - *Phymaturosilusa* Roubal
- *Pseudatheta* Cameron
- *Silusida* Casey
- *Stictalia* Casey
- *Hongophila* new genus (for "*Bolitochara*" n. sp. A)
- *Neotobia* new genus (for "*Bolitochara*" n. sp. B)
- *Austrasilida* new genus (for *Sternotropa zealandica* Cameron)

Justification for dividing available taxa into these genera is provided in the phylogenetic section of this paper.

IDENTIFICATION

One of the consequences of the classification philosophy adopted in this study is that, while many bolitocharine genus-level taxa are easily distinguished, others are difficult to identify based on easily observable external characteristics. Some can only be identified with certainty by examination of microscopic features of the mouthparts, or by examination of male secondary sexual or aedeagal characteristics. This problem is illustrated by problems with separating specimens of *Hongophila* and *Neotobia*. Because of retention of many primitive features in members of both of these taxa, they are surprisingly similar in external appearance. However, they are not closely related within the Bolitocharina. Differences in male secondary sexual features provide the most readily accessible means for distinguishing them. But they can also be distinguished by other features which can only be observed with compound optics.

A similar problem results from considering the taxa from a worldwide perspective. Many taxa which are distinct when faunas are considered locally have broader variation in the world fauna such that taxa that are not very closely related have some members which are similar in many external features. This is illustrated by the example of *Phymatura*. When only Old World *Phymatura* are considered, the genus can be easily characterized based on readily observable external features. However, when the North American *Phymatura (= Venusa) blanchardi* (Casey) is included in the genus, many of the previously useful key characteristics, especially in the antennae, are no longer distinctive for the group. However, there can be no doubt that they represent a monophyletic genus-level taxon based on the highly derived and unique aedeagal structure.

Many of the problems associated with identification of genera among bolitocharines, and the Aleocharinae as a whole, are a result of the fact that specimens of these taxa are small, often minute. As a result many very useful identification characteristics can only be observed by examination of properly prepared and dissected specimens using compound optics. This is unfortunate, but is probably unavoidable in this group. Reluctance to study specimens of the Aleocharinae in this way has been one of the reasons for the present taxonomic difficulty of the group.

With the above considerations in mind, I have tried to provide a key to the genera of the Bolitocharina using characteristics that are as readily observable as possible. I have placed more easily observable characteristics at the beginning of each couplet, and those which are more difficult to observe, require special preparation and handling, or are limited to one sex, toward the end of the couplet. This arrangement does not necessarily reflect the reliability of the characters. Often those which are most difficult to observe are the most reliable for correct identification.

The key below will provide correct identification of specimens of all the taxa that I have had opportunity to examine. I have been unable to obtain specimens of some taxa (see descriptive section). Examination of these, as well as bolitocharine taxa that are likely to be discovered in the future, may require modification of the key. Nonetheless, I hope that this key will provide access to the bolitocharine fauna of the world, and will lead to studies which will result in its subsequent revision.

KEY TO KNOWN GENERA OF THE SUBTRIBE *BOLITOCHARINA* OF THE WORLD

1. Pronotum broadly transverse, 1.35–1.50 (most 1.4–1.5) times as wide as long (Figs. 27, 48, 80, 115). Pronotal base of most slightly to moderately bisinuate (not bisinuate on specimens of *Neotobia* but then base of pronotum as wide as elytra). Base of pronotum as wide as, or virtually as wide as, base of elytra, not appearing noticeably narrower than elytra. Eyes large, length of most greater than 1.2 times length of temple (Figs. 28, 49, 68, 81, 132, 147) [eye length of *Hongophila* 1.1–1.2 times length of temples (Fig. 116) but then pronotum 1.4 times as wide as long and base of pronotum as wide as base of elytra] 3

—. Pronotum less broadly transverse, 1.1–1.3 times as wide as long (Figs. 5, 95, 110). Pronotal base broadly rounded, not bisinuate. Base of pronotum slightly to moderately narrower than base of elytra. Eyes small, length of most less than 1.1 times length of temple (Figs. 7, 22, 95) (eyes of *Stictalia nigrina* and *Bolitochara obliqua* 1.1–1.2 times length of temple, but other features apply) 2

2. Head moderately to strongly narrowed behind eyes to form distinct neck (Figs. 7, 22). Mesocoxal cavities moderately broadly separated by intercoxal processes, apex of mesosternal process rounded to more or less truncate (Fig. 14). Male sternum VI with small asetose medial lobe on posterior margin (Figs. 16, 17), sternum VII with concentration of setose glandular pores medially in addition to broad band of sensory pores basally (Figs. 16, 17). Posterior angular projection of male sternum VIII without asetose posterior margin (Fig. 17). Median lobe of aedeagus with pair of distinct sclerotized internal plates (Figs. 21, 26). Spermathecal duct not sclerotized and complexly looped (Figs. 19, 24). Most taxa known from Old World . . . . *Bolitochara*

—. Head at most only slightly narrowed behind eyes to indistinct neck (Fig. 96). Mesocoxal cavities narrowly to very narrowly separated by intercoxal processes, apex of mesosternal process sharply pointed (Fig. 103). Male sternum VI without small medial lobe on posterior margin, sternum VII with broad band of sensory pores basally, without concentration of setose glandular pores medially (Fig. 106). Posterior angular projection of male sternum VIII with asetose posterior margin (Fig. 106). Median lobe of aedeagus without distinct pair of internal sclerotized plates (Figs. 107, 112, 114). Spermathecal duct sclerotized and complexly looped (Fig. 109). Known only from west coast of North America . . . . *Stictalia*

3. Pronotal hypomeron strongly horizontally inflexed throughout, only narrowly visible, or not visible, in lateral aspect 4

—. Pronotal hypomeron inflexed basally in some but deflexed toward vertical anteriorly, at least anterior half broadly visible in lateral aspect 7

4. Size larger, length 2.1–4.0 mm. Abdominal terga III–V with moderate transverse basal impressions. Wings with 2 to 5 setose projections on flabellum (Figs. 36, 89). Triangular projection of male sternum VIII with distinct asetose posterior margin occupying at least 50 percent of width of posterior margin (Figs. 38, 90) 5

—. Size smaller, length 1.5–2.0 mm. Abdominal terga III–IV with at most moderate to slight basal impressions. Wings without setose projections on flabellum. Triangular projection of male sternum VIII without asetose margin or asetose area very small, indistinct and limited only to apex of projection (Figs. 86, 155) 6

5. Postero-lateral angles of pronotum moderately to sharply angulate (Fig. 27). Mesocoxal cavities moderately broadly separated by intercoxal processes, mesosternal process broader, apex not acutely pointed (Fig. 35). Median lobe of aedeagus distinctive, apical process elongate, slender; flagellum moderately elongate, slender and acutely pointed (Figs. 41, 46). Known from Europe, India, Asia, Southeast Asia, Japan, and eastern North America *Phymatura*

—. Postero-lateral angles of pronotum broadly rounded (Fig. 80). Mesocoxal cavities narrowly separated by intercoxal processes, mesosternal process narrow, apex acutely pointed (Fig. 88). Median lobe of aedeagus distinctive, apical process large, tentlike; flagellum short, tubular and obliquely truncate apically (Fig. 93). Known only from eastern North America . . . . *Silusida*

6. Mesocoxal cavities narrowly separated by intercoxal processes; mesosternal process narrow, pointed apically (Fig. 75). Mesosternum without medial longitudinal carina (Fig. 75). Head setae mostly directed medially. Lacinia of maxilla with single row of teeth on apical third (Figs. 71, 72). Ligula of labium long, bifid only in apical third (Fig. 74). Known from India, Southeast Asia, Nepal, Africa. . . . . *Pseudatheta*

—. Mesocoxal cavities widely separated by intercoxal processes; mesosternal process broad, broadly rounded apically (Fig. 154). Mesosternum with strong medial longitudinal carina (Fig. 154). Head setae mostly directed anteriorly. Lacinia of maxilla with patch of numerous spines forming a dense "brush" on apical third (Figs. 150, 151). Ligula of labium short, split to the base into two widely separated lobes (Fig. 153). Known only from New Zealand . . . . *Austrasilida zealandica*

7. Eyes very large, eye length 1.3–1.5 times length of temple (Fig. 149). Mesocoxal cavities very widely separated by intercoxal cavities; mesosternal process broad, broadly rounded apically (Fig. 56). Mesosternal medial carina extended 0.60–0.75 times combined length of mesosternum and mesosternal process (Fig. 56). Wing with 10 to 13 setose projections on flabellum (Fig. 57). Lacinia of maxilla with 3 to 4 irregular rows of teeth on apical quarter (Fig. 54). Male tergum VII with oblique to posteriorly directed carinae on each side of midline (variously developed on different males, reduced or absent on some) (Figs. 60, 64); male tergum VIII with large medial carina and 1 to 2 smaller lateral carinae on each side (Figs. 60, 64). Median lobe of aedeagus with large, tentlike apical process, and internal sac with pair of large sclerotized platelike structures (Figs. 62, 66). Known from eastern North America and central Europe . . . . *Pleurotobia*

—. Eyes moderately large, eye length 1.1–1.3 times length of temple (Figs. 116, 132). Mesocoxal cavities moderately to narrowly separated by intercoxal processes, mesosternal process narrow, slightly to sharply pointed apically (Figs. 123, 139). Mesosternal medial carina extended only 0.2–0.4 times combined length of mesosternum and mesosternal process (Figs. 123, 139). Wings with 3 to 8 setose projections on flabellum (Figs. 124, 140). Lacinia of maxilla with 1 row of teeth on apical quarter (Figs. 121, 137). Male tergum VII either with small medial tubercle and larger lateral tubercles (Fig. 127) or moderate medial tubercle (Fig.

144); male tergum VIII either with numerous small asperities (Fig. 127) or small medial tubercle (Fig. 144). Medial lobe of aedeagus with elongate slender (Fig. 128) or bifid (Fig. 146) apical lobe, and internal sac either without sclerotized plates or sclerotized structures spinose rather than platelike 8

8. Antenna with at least some of articles 5 to 10 distinctly elongate. Wings with 6 to 8 setose lobes on flabellum (Fig. 140). Male sternum VI without medial projecting lobe on posterior margin. Male sternum VII with broad band of numerous sensory pores basally, without medial concentration of setose sensory pores (Fig. 141). Posterior triangular projection of male sternum VIII with distinct asetose posterior margin (Fig. 141). Known only from the northern half of North America . . . . *Neotobia*

—. Antenna with articles 5 to 10 either quadrate or transverse. Wings with 3 to 5 (a few specimens with 6) setose lobes on flabellum (Fig. 124). Male sternum VI with small medial projecting lobe on posterior margin (Figs. 125, 126). Male sternum VII with medial concentration of setose sensory pores as well as broad band of sensory pores basally (Figs. 125, 126). Posterior projection of male sternum VIII without distinct asetose posterior margin (Fig. 125). Known only from the southwestern United States and Mexico . . . . *Hongophila*

Genus *Bolitochara* Mannerheim
(Figs. 6–26)

Bolitochara Mannerheim 1831, p. 489. Type species *Bolitochara lunulata* (Paykull). Fixed by International Commission of Zoological Nomenclature (1961, Opinion 599); not *Bolitochara collaris* (Paykull) as proposed by Blackwelder 1952.—Mannerheim 1831: 489.—Stephens 1832: 431.—Erichson 1837: 296.—Kraatz 1858: 36.—Thomson 1860: 272.—Mulsant and Rey 1871: 194.—Ganglbauer 1895: 262.—Casey 1906: 263.—Fenyes 1920: 111-112.—Lohse 1974: 62.—Scheerpeltz and Höfler 1948: 178.—Seevers 1978: 164.

Ditropalia Casey 1906, p. 263. Type species *Ditropalia bella* (Maerkel). Fixed by Fenyes 1918, p. 22.—Casey 1906: 263.—Fenyes 1920: 114.—Seevers 1978: 164.

Diagnosis.—Among bolitocharine genera specimens of *Bolitochara* can be easily recognized by the combination of: relatively large size, adults 3.0–5.0 mm in length; relatively small eyes, 1.1–0.8 times length of temple; head slightly to moderately narrowed behind the eyes to form a slight to very distinct neck (Figs. 7, 22); relatively narrow pronotum (Fig. 6), 1.1–1.2 times as wide as long with fully exposed hypomeron in lateral aspect; pronotum distinctly narrower than base of elytra, not bisinuate basally; moderately widely separated mesocoxal cavities, apex of mesosternal process rounded to more or less truncate (Fig. 14); terga III–V or III–VI with moderate to deep transverse basal impressions; sterna III–V with moderate transverse basal impressions; male sternum VI with medial lobate asetose projection on posterior margin (Fig. 17); male sternum VII with concentration of setose pores medially, as well as band of numerous sensory pores basally (Fig. 16); triangular projection of male sternum VIII without asetose posterior margin (Fig. 16); median lobe of aedeagus with large, tentlike apical process, two platelike structures on internal sac, and tubelike flagellum (Fig. 21). This is the only bolitocharine genus which includes some members which lack a complete infraorbital carina on the head.

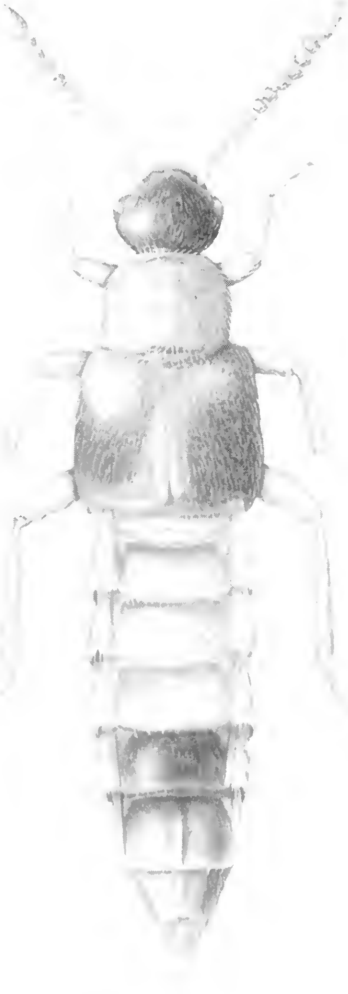
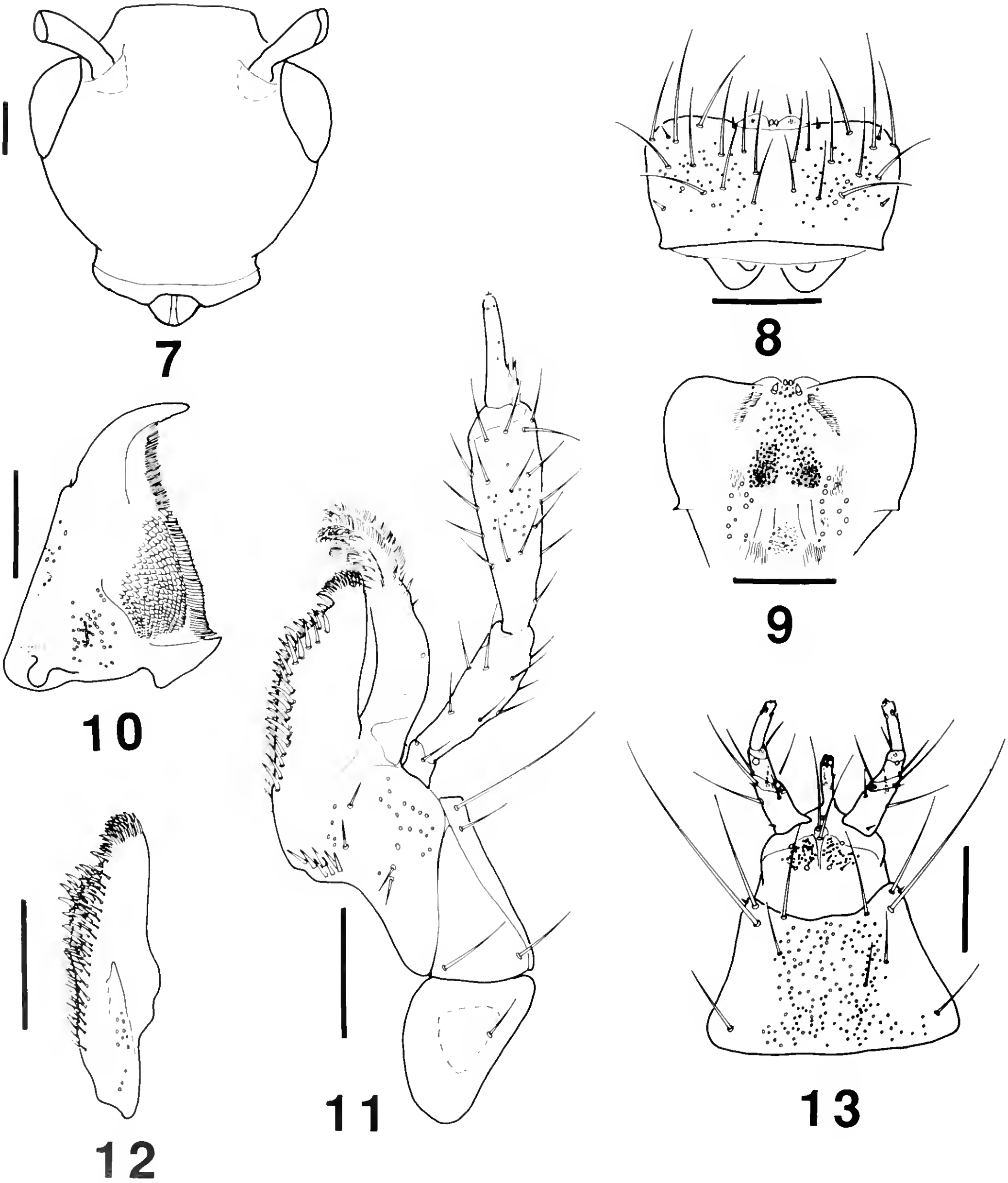


Fig. 6. *Bolitochara lunulata* Payk. Habitus. Total length = 4.2 mm.

Description (Fig. 6).—Lengths of adults 3.0–5.0 mm. Body elongate, more or less parallel-sided and convex in cross section. Surface sculpture faint to absent, surface shiny. Body slightly to moderately pubescent; microsetae stiff, moderately dense to widely dispersed; punctures small and inconspicuous to large and prominent, asperite or not. Macrosetae inconspicuous.

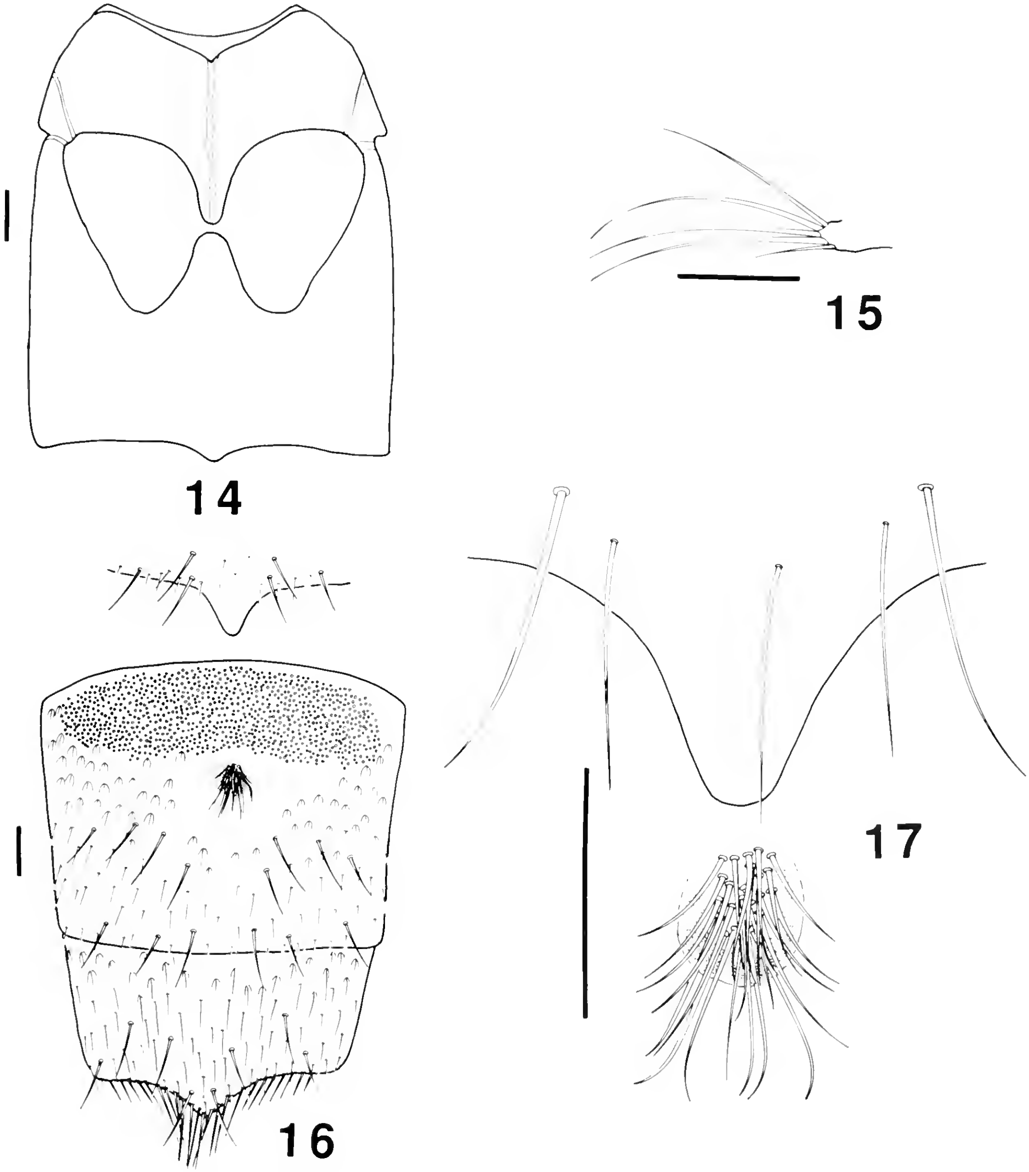
Head (Fig. 7).—More or less oval to slightly elongate, rounded and narrowed behind the eyes to form conspicuous neck less than 0.5 times width of head, to inconspicuously narrowed behind to form, at most, a slight neck (Fig. 22). Sculpture absent, integument shiny. Punctures moderately large, shallow, distant to small and inconspicuous; setae fine to moderately stiff, di-



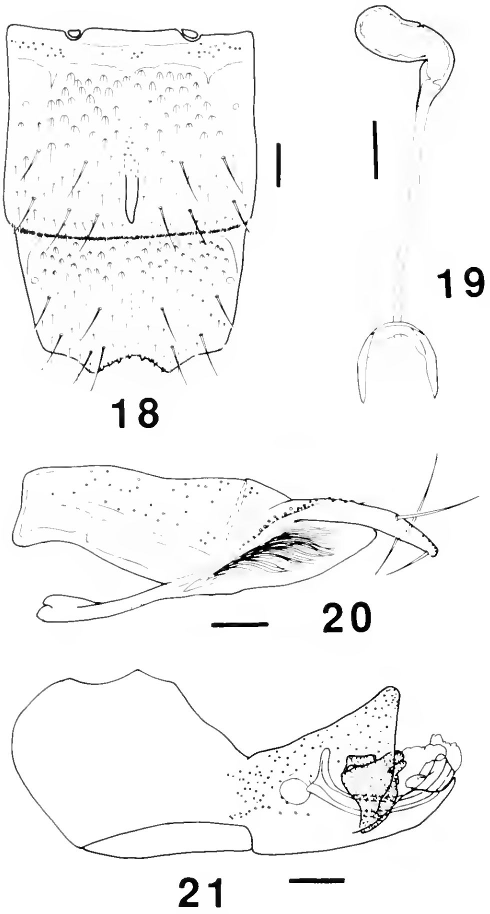
Figs. 7–13. *Bolitochara lunulata* Payk. **7**, Head, dorsal aspect. **8**, Labrum, dorsal aspect. **9**, Labrum, epipharyngeal aspect. **10**, Mandible, ventral aspect. **11**, Maxilla, ventral aspect. **12**, Lacina of maxilla, dorsal aspect. **13**, Labium, ventral aspect. (Scale line = 0.1 mm.)

rected medially and anteriorly or only medially. Eyes moderate sized to small, 1.1–0.8 times length of temple. Infraorbital carina moderately developed and complete, or absent except faintly near maxillary insertion. Antenna moderately long to elongate, not incrassate toward apex; article 4 quadrate to elongate, similar to 5 to 10 in setation and sculpture; article 5 transverse to elongate; article 10 transverse to quadrate, antennal articles 5 to 10 decreasing in relative lengths apically.

Mouthparts.—Labrum (Figs. 8, 9) with epipharyngeal area with medial pores moderately large to large, numerous, in a well-delimited longitudinal field. Mandibles with abcondylar molar patch of denticles large, denticles numerous and close (Fig. 10). Maxilla with teeth on apical 0.25 of lacinia various, from numerous, in



Figs. 14–17. *Bolitochara lunulata* Payk. **14,** Meso-metasternum, ventral aspect. **15,** Flabellum of wing. **16,** Male sternal features, posterior margin of sternum VI, and sterna VII and VIII. **17,** Male, detail of asetose lobe of sternum VI and concentration of setose pores on sternum VII. (Scale line = 0.1 mm.)

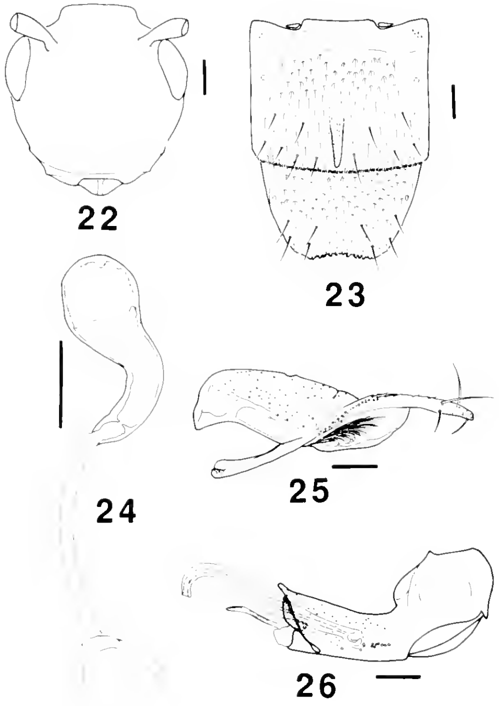


Figs. 18–21. *Bolitochara lunulata* Payk. **18,** Male terga VII and VIII. **19,** Female, spermatheca. **20,** Male, paramere of aedeagus, external aspect. **21,** Male, median lobe of aedeagus, lateral aspect. (Scale line = 0.1 mm.)

several irregular rows forming a dense patch of teeth (Fig. 12), to fewer, in only a single row; galeal apex with 8 to 10 rows of unmodified (setose) setae or modified subspatulate or flattened setae (Fig. 11). Labium (Fig. 13) typical of subtribe, with pair of sensory setae on ligula, sensory setae moderate sized or small; two medial setae of labium present, bases arranged one laterally behind the other or one directly behind the other, setal insertions close to distant; medial pseudopore field narrow, without pseudopores.

Thorax.—Pronotum relatively narrow, 1.1–1.2 times as wide as long, slightly to moderately convex in dorsal outline; distinctly narrower at base than base of elytra; postero-lateral angles slightly to strongly angulate; base not bisinuate; punctures large to small, numerous, dense, microsetae fine, moderately dense; integument strongly shiny, without microsculpture. Elytra with postero-lateral angles moderately sinuate; punctures large, lunulate (open behind), very close to moderately so; microsetae fine, moderately dense. Wings with 3 to 8 (most with 5 to 8) setose lobes on moderately developed flabellum (Fig. 15). Hypomeron broadly visible in lateral aspect, deflexed to near vertical throughout, anterior margin of hypomeron contacting lateral line of pronotum distinctly posterior to antero-lateral angles. Mesosternal carina present, complete to apex of process or fading medially. Mesocoxal cavities moderately to broadly separated by meso- and metasternal processes (Fig. 14); relative lengths mesosternal : isthmus : metsternal process varies from 4 : 0 : 3 to 7 : 1 : 5; apex of mesosternal process rounded, apex of metasternal process subtruncate to broadly rounded. Hind tarsomere I almost to fully as long as II and III together (0.7–1.0 times as long as II and III).

Abdomen.—More or less parallel-sided; terga III–V or III–VI with deep transverse basal impressions; punctures moderately large, lunulate, distant to close; microsetae fine and distant to moderately dense, all microsetae on basal terga directed posteriorly; macrosetae inconspicuous.



Figs. 22–26. *Bolitochara bella* (Maerkel). **22,** Head, dorsal aspect. **23,** Male, terga VII–VIII. **24,** Female, spermatheca. **25,** Male, paramere, external aspect. **26,** Male, median lobe of aedeagus, lateral aspect. (Scale line = 0.1 mm.)

Sterna III–V with moderate transverse basal impressions.

Secondary Sexual Characteristics.—Males: each elytron with moderate to small carina near suture in posterior 0.5–0.2 (most species) to elytra without carinae (a few species); tergum VII of most (Figs. 18, 23) with moderate to strong medial carina 0.5–0.6 times length of tergum, some with additional carinate asperities on each side of carina, or medial carina absent from tergum VII and surface with small scattered asperities; tergum VIII (Figs. 18, 23) broadly emarginate posteriorly, with 4 to 6 denticles in emargination on each side of midline, denticles moderate in size to minute and faint, virtually absent in some; tergum VIII with long medial carina or carina absent and a few faint scattered asperities present or without asperities; sternum VI (Figs. 16, 17) with small medial lobe on posterior margin, medial lobe asetose; sternum VII with concentration of setose glandular pores medially, porose area large, as well as broad band of sensory pores basally (Figs. 16, 17); sternum VIII with posterior triangular projection, projection without asetose posterior margin (Fig. 16).

Aedeagus.—Paramere (Figs. 20, 25) with apical lobe of paramerite relatively short (<0.5 times length of paramerite) to long (0.8–1.0 times length of paramerite); setae 1 to 4 of apical lobe of paramerite long, not clustered near tip. Aedeagus (Figs. 21, 26) with apical lobe large, tentlike; internal sac with pair of large sclerotized platelike structures; flagellum short, tubular.

Spermatheca (Figs. 19, 24).—Basal bulb simple, apex rounded; spermathecal tube membranous, more or less straight; neck bent ≤90° angle. Vaginal sclerotization moderate, about 0.5–0.7 of complete circle of sclerotized cuticle.

Discussion.—About 30 species have been described in either *Ditropalia* or *Bolitochara* (not including those transferred to *Ditropalia* but more correctly placed in other genera). A complete study of all taxa is outside the range of this study. However, in addition to the five Palearctic taxa included in the phylogenetic analysis (Appendix 2), I have examined the following five other Palearctic taxa: *Bolitochara humeralis* (Lucas) (from *Ditropalia*); *B. lauferi* Bernhauer (from *Ditropalia*); *B. reyi* Sharp; *B. schusteri* Bernhauer (from *Ditropalia*); and *B. varia* Erichson (from *Ditropalia*). All of these are correctly placed in *Bolitochara* as here defined.

Other species, that I have not examined, have been described from southeast Asia [*Ditropalia strigosa* Cameron, *D. granulata* Cameron, *D. nigra* Cameron, *Bolitochara (Ditropalia) smetanai* Pace], and Japan (*B. varipes* Sharp, *B. iridescens* Sawada, *Ditropalia lobata* Sawada) as well as others from the Palearctic. In addition, there are a number of species of doubtful placement described from Chili, Columbia, Australia, New Guinea, and Argentina (see Fenyes, 1918–1921 for list). It is interesting that no species which can be placed in *Bolitochara* as here defined has been found in North America.

Genus *Phymatura* J. Sahlberg

(Figs. 27–47)

Phymatura J. Sahlberg 1876, p. 85. Type species *Phymatura brevicollis* (Kraatz.). Fixed by Casey 1906, p. 264.—J. Sahlberg 1876: 85.—Ganglbauer 1895: 266.—Casey 1906: 264.—Fenyes 1920: 116.—Cameron 1939a: 217.—Lohse 1974: 61.

Venusa Casey 1906, p. 272. Type species *Venusa picta* Casey. Fixed by Fenyes 1920, p. 26.—Casey 1906: 272.—Fenyes 1920: 114 (as a synonym of *Ditropalia* Casey).—Seevers 1978: 164 (as a synonym of *Bolitochara* Mannerheim).

Diagnosis.—Members of *Phymatura* can be recognized by the following combination of characteristics: eyes large, about 1.2–2.0 times as long as temples; head not noticeably narrowed behind

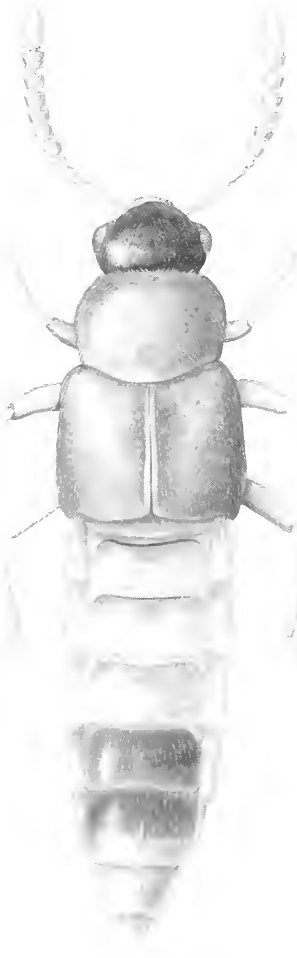
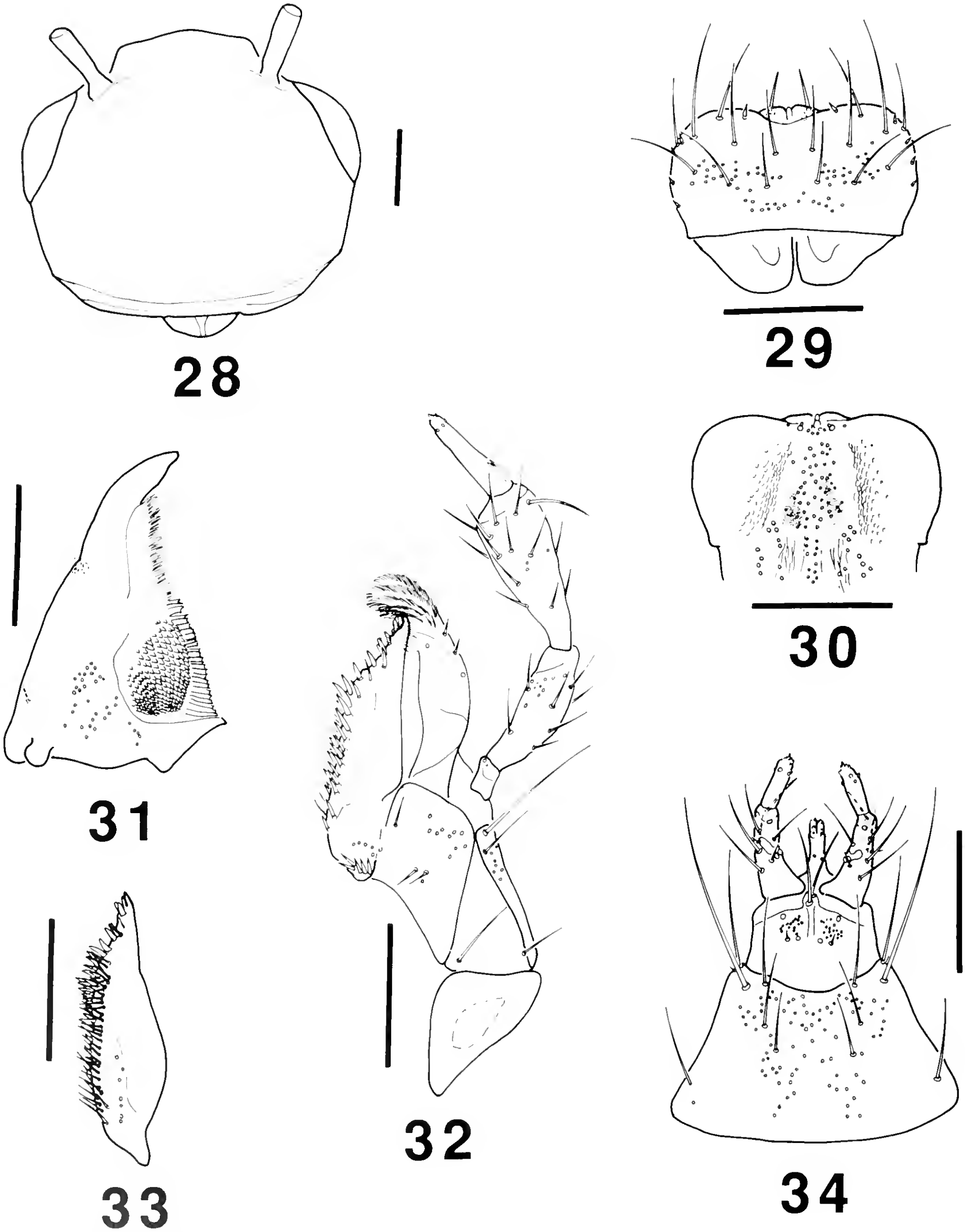


Fig. 27. *Phymatura* (=*Venusa*) *blanchardi* (Casey). Habitus. Length = 3.1 mm.

eyes to form a neck; pronotum strongly transverse, 1.4–1.5 times as wide as long; pronotum as wide as, or virtually as wide as, base of elytra, not noticeably narrower than the elytra; pronotum slightly bisinuate basally; hypomeron strongly inflexed into more or less horizontal plane throughout, only narrowly visible or not visible in lateral aspect; abdominal terga III–V with moderate to deep transverse basal impressions (some III–VI); male sternum VI without lobate projection on posterior margin; male sternum VII with broad band of numerous sensory pores basally,



Figs. 28–34. *Phymatura brevicollis* (Kraatz). **28**, Head, dorsal aspect. **29**, Labrum, dorsal aspect. **30**, Labrum, epipharyngeal region. **31**, Mandible, ventral aspect. **32**, Maxilla, ventral aspect. **33**, Lacinia of maxilla, dorsal aspect. **34**, Labium, ventral aspect. (Scale line = 0.1 mm.)

without concentration of setose sensory pores basally (Fig. 37); posterior triangular projection of male sternum VIII with asetose posterior margin (Fig. 38); median lobe of aedeagus with slender, spinose apical process and slender and pointed flagellum, without pair of sclerotized structures on internal sac (Figs. 41, 46).

Description (Fig. 27).—Lengths of adults 2.3–4.0 mm. Body relatively broad in dorsal outline, slightly depressed, slightly narrowed anteriorly and posteriorly. Surface sculpture reticulate to virtually absent, surface shiny or not. Body microsetae fine, moderately dense, more or less uniformly distributed, punctures moderate in size, dense, uniformly distributed, not asperite. Macrosetae inconspicuous.

Head (Fig. 28).—Broad, transverse, noticeably narrower than apex of pronotum to virtually as wide as apex of pronotum. Head not narrowed behind eyes, neck absent. Integumental sculpture slightly reticulate to virtually absent. Punctures moderate sized, round. Setation moderately dense, directed medially and anteriorly. Eyes very large to moderate in size, 2.0–1.2 times length of temple. Infraorbital carina markedly developed, complete. Antenna elongate to short, slightly incrassate toward apex or parallel-sided; article 4 transverse to elongate, similar to articles 1 to 3 in examined representatives, article 5 transverse to elongate; article 10 slightly elongate to transverse; antennal articles 5 to 10 increasing in relative lengths more apically in examined representatives.

Mouthparts.—Labrum (Figs. 29, 30) with epipharyngeal area with medial pores small to very small, numerous, evenly dispersed in longitudinal sensory field. Mandibles with abcondylar molar patch of denticles large, denticles moderate-sized to very small, dense (Fig. 31). Maxilla (Figs. 32, 33) with teeth in apical 0.25 of lacinia arranged in a single row of widely dispersed teeth; apex of galea with 7 to 8 rows of unmodified (setose) setae. Labium (Fig. 34) typical of subtribe; ligula with pair of sensory setae small or absent; two medial setae of prementum present, arranged one directly behind the other; medial setal insertions close to moderately distant; medial pseudopore field narrow, without pseudopores.

Thorax.—Pronotum broad, transverse, 1.4–1.5 times as wide as long, slightly convex in dorsal outline; about as wide at base as base of elytra; postero-lateral angles moderately to sharply angulate; base slightly to moderately bisinuate; punctures small, round, numerous, setation fine, moderate to densely distributed; integument slightly reticulate. Elytra with postero-lateral angles moderately sinuate; punctures moderate in size, dense, lunulate (open behind); microsetae dense, moderately fine. Wings with setose lobe on flabellum various, 3-6 (Fig. 36). Hypomeron strongly inflexed throughout, not, or only narrowly, visible in lateral aspect; hypomeron contacting lateral border of pronotum at or very near antero-lateral angles of pronotum. Mesosternal medial carina strong, present in anterior 0.2–0.5 of mesosternum. Mesocoxal cavities moderately separated by meso- and metasternal processes (Fig. 35); relative lengths mesosternal : isthmus : metasternal processes about 4.0–4.5 : 0.5 : 3; apex of mesosternal process narrow, obtusely pointed, apex of metasternal process acutely to broadly rounded. Hind tarsomere I moderately long, about as long as II and III together.

Abdomen.—Slightly tapered apically to broadly pointed apex; terga IV–V (VI slightly in some) with moderate transverse basal impressions; punctures moderately large, lunulate, dense; microsetae fine, densely distributed; microsetae on basal terga directed posteriorly; macrosetae inconspicuous. Sterna III–V with slight transverse basal impressions.

Secondary Sexual Characteristics.—Males: elytron without carina near suture or small knob at sutures about 0.4 length of elytron from posterior edge; tergum VII (Figs. 39, 45) with long prominent medial carina to short prominent medial carina; tergum VIII (Figs. 39, 45) broadly emarginate posteriorly, with 4 to 5 denticles in emargination on each side of midline, denticles moderate to large in size; dorsum of tergum VIII with moderately long medial carina, short, but distinct, medial carina, or small medial tubercle; sternum VI without small medial lobe on posterior margin; sternum VII (Fig. 37) with broad band of sensory pores basally (visible in microslide preparations), without concentration of setose glandulai pores medially, sternum VIII (Fig. 38) with posterior triangular projection, projection with asetose posterior margin.

Aedeagus.—Paramere (Figs. 40, 47) with apical lobe of paramerite relatively short (<0.5 times length of paramerite) to long (0.8 times length of paramerite), setae 1 to 4 of apical lobe of paramerite long or short, not clustered near tip. Aedeagus (Figs. 41, 46) with apical lobe elongate, slender; internal sac without sclerotized internal plates; flagellum moderately long, tapering to an acute apex.

Spermatheca (Figs. 42, 43, 44).—Basal bulb simple, apex rounded; neck bent <90° to more or less straight; spermathecal tube membraneous, more or less straight (Fig. 42) or very long and convoluted (Fig. 44). Vaginal sclerotization slight, less than to about 0.5 complete circle of sclerotized cuticle.

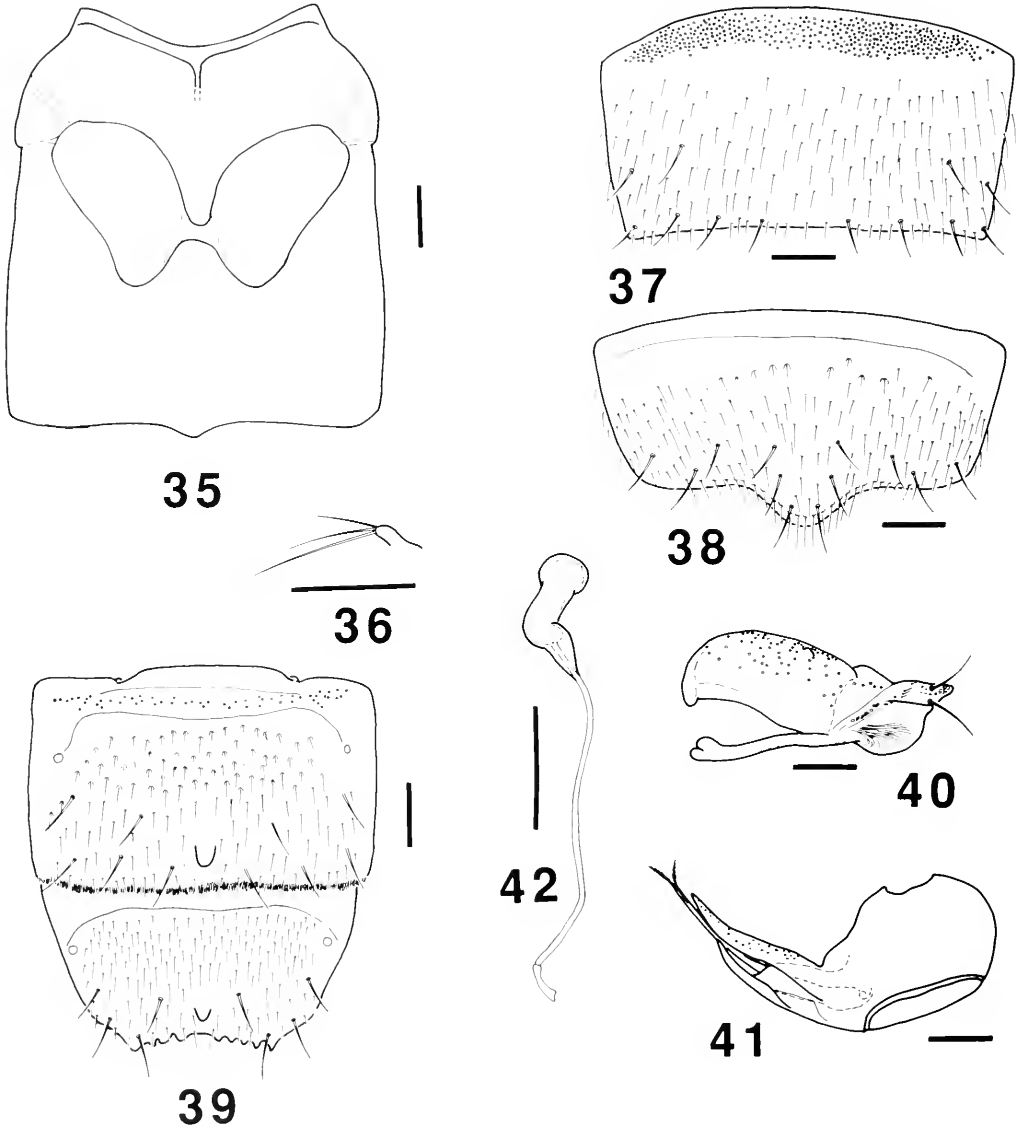
Discussion.—About 15 species have been described in either *Phymatura* or *Venusa*. Among *Phymatura* I have examined five species (*Phymatura brevicollis* Kraatz from Europe and *P. picta* Cameron, *P. intermedia* Cameron, *P. juncunda* Cameron and *P. aspericeps* Cameron from India) that are correctly placed in this genus. Other *Phymatura* that I have not examined, have been described from southeast Asia (*P. orientalis* Cameron, *P. malaisei* Scheerpeltz), Japan (*P. japonica* Cameron), Nepal (*P. suturalis* Pace), and South America (*P. dubiosa* Bernhauer, *P. barbiellinii* Bernhauer, and *P. brasiliana* Bernhauer). Casey (1906) described two new species of *Venusa* from eastern North America (*Venusa picta* and *V. laetula*) and transferred *Bolitochara blanchardi* Casey to *Venusa*. There appears to be only a single valid species, *Venusa picta* Casey (= *Bolitochara blanchardi* Casey).

The species of *Phymatura* and *Venusa* included in the phylogenetic analysis were shown to form a monophyletic group in all but one of the analyses. The derived features in the aedeagus of all examined members of these taxa provide strong evidence of their monophyly (see phylogenetic analysis).

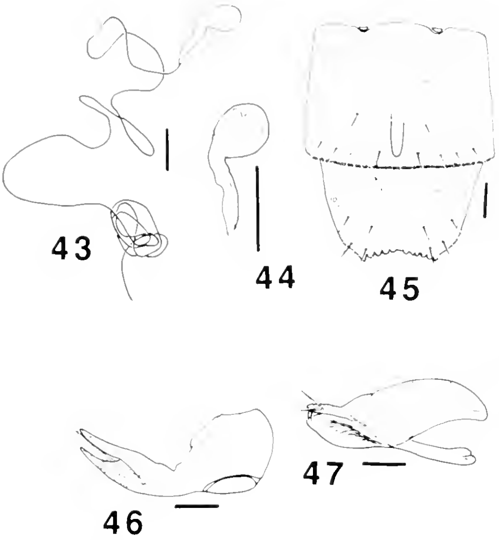
Phymatura is the sister group to *Neotobia* new genus in some of the phylogenetic analyses (figs. 2, 5) but not in others (Figs. 3, 4).

Genus *Pleurotobia* Casey
(Figs. 48–67)

Pleurotobia Casey 1906, p. 273. Type species *Pleurotobia suturalis* Casey. Fixed by Fenyes 1918, p. 24.—Casey



Figs. 35–42. *Phymatura brevicollis* (Kraatz). **35**, Meso-metasternum, ventral aspect. **36**, Flabellum of wing. **37**, Male, sternum VII. **38**, Male, sternum VIII. **39**, Male, terga VII–VIII. **40**, Male, paramere, external aspect. **41**, Male, median lobe of aedeagus, lateral aspect. **42**, Female, spermatheca. (Scale line = 0.1 mm.)



Figs. 43–47. *Phymatura* (= *Venusa*) *blanchardi* (Casey). **43,** Female, spermatheca, outline showing long, convoluted spermathecal duct. **44,** Female, spermathecal bulb, detail. **45,** Male, terga VII–VIII. **46,** Male, median lobe of aedeagus, lateral aspect. **47,** Male, paramere, external aspect. (Scale line = 0.1 mm.)

1906: 273.—Fenyes 1920: 114 (as a synonym of *Ditropalia* Casey).—Seevers 1978: 164 (as a synonym of *Bolitochara* Mannerheim).

Phymaturosilusa Roubal 1932, p. 178. Type species *Phymaturosilusa magnifica* Roubal 1932, p. 178, by monotypy.—Roubal 1932: 178.—Smetana 1957: 322.—Lohse 1974: 61.

Pleurotobia can be easily recognized by the combination of: head broad with very large eyes, eyes 1.3–1.5 times as long as length of temples; head not at all narrowed behind the eyes to form a neck; moderately long antenna with antennomeres 5 to 10 transverse to elongate, longer in males than in females; pronotum broad, transverse, 1.4–1.5 times as wide as long; hypomeron inflexed into near horizontal plane basally but deflexed to near vertical in apical half, at least apical half broadly visible in lateral aspect; pronotum not noticeably narrower than elytra, slightly bisinuate basally; mesocoxal cavities broadly separated by intercoxal processes (Fig. 56), apex of mesosternal process broadly rounded; terga III–V with moderate transverse basal impressions; sterna III–V with slight transverse basal impressions; male sternum VI (Figs. 58, 59) with medial setose lobate projection on posterior margin; male sternum VII (Figs. 58, 59) with concentration of setose pores medially, as well as band of numerous sensory pores basally; triangular projection of male sternum VIII (Fig. 58) without asetose posterior margin; most with tergum VII (Figs. 60, 64) with 2 to 3 oblique to posteriorly directed carinae on each side of midline (reduced in some); tergum VIII (Figs. 60, 64) with medial carina and 1 to 2 lateral carinae on each side; median lobe of aedeagus (Figs. 62, 66), with large, tentlike apical process, two platelike structures on internal sac, and tubelike flagellum.

Description (Fig. 48).—Lengths of adults 3.0–5.0 mm. Body relatively broad and elongate in dorsal outline, more or less parallel-sided and convex in cross section. Surface sculpture faintly reticulate, body more or less shiny. Body moderately densely pubescent with fine microsetae. Body moderately densely punctured, punctures coarse to fine, asperite or not. Macrosetae inconspicuous.

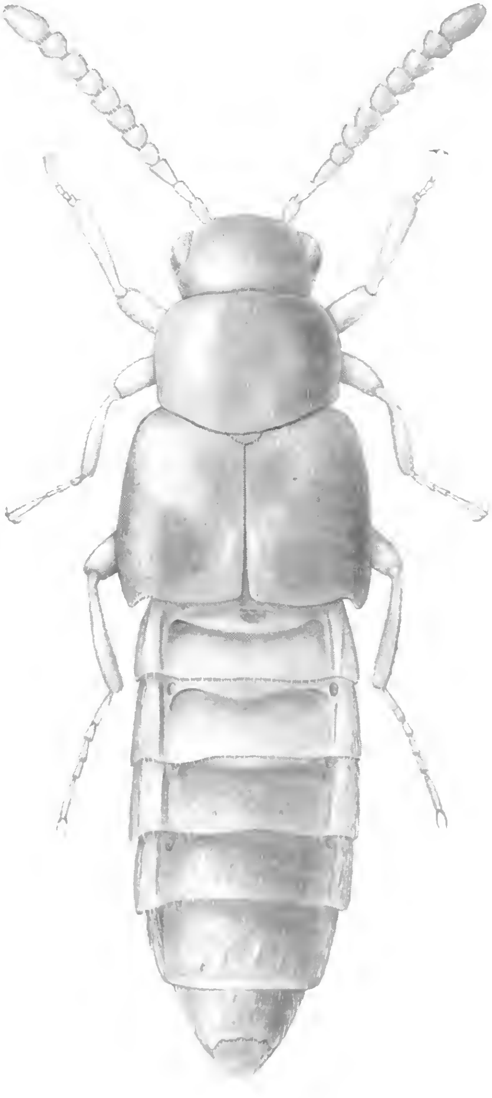
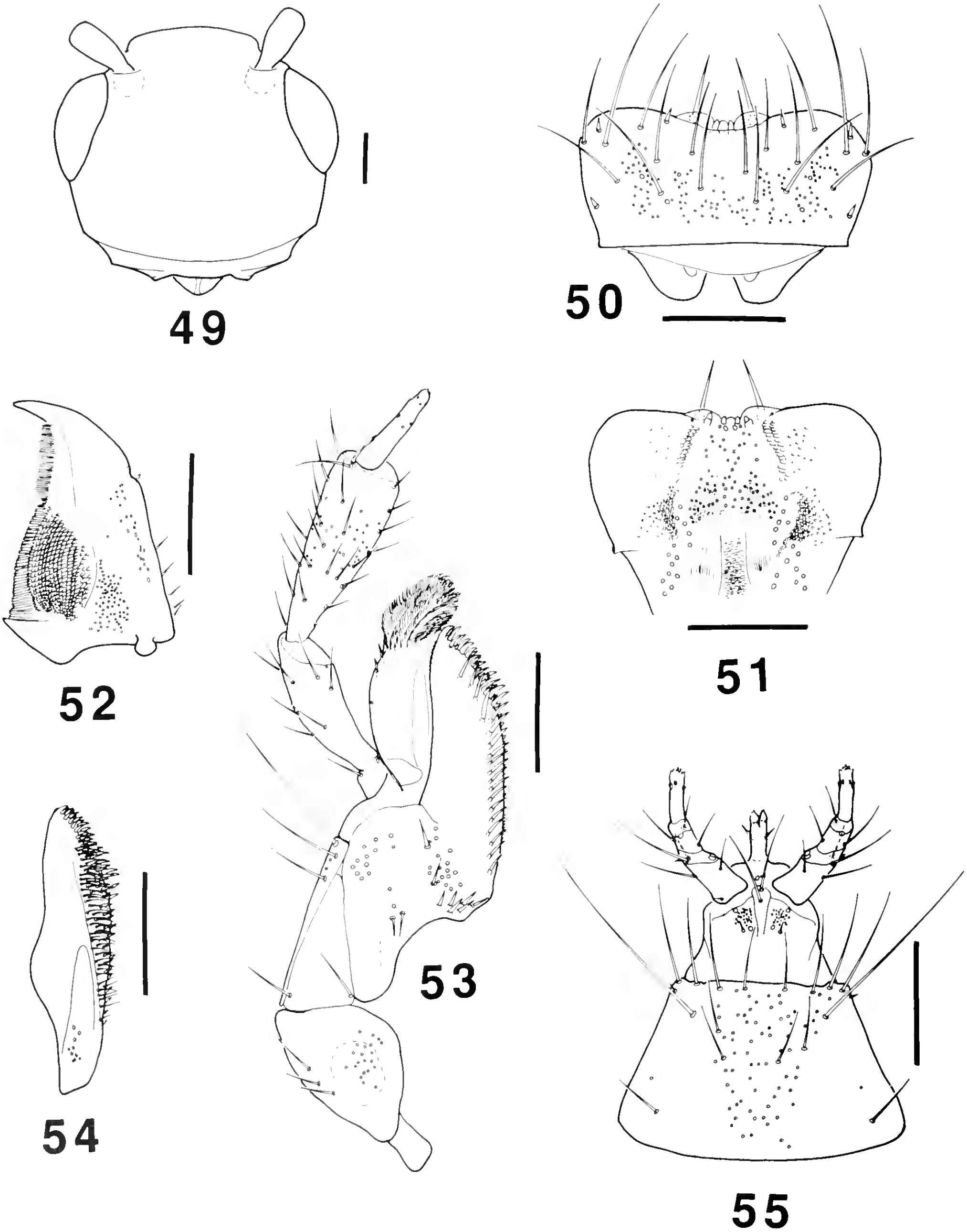


Fig. 48. *Pleurotobia trimaculata* (Erichson). Habitus. Length = 4.5 mm.

Head (Fig. 49).—Broad, almost as wide as apex of pronotum. Head not narrowed behind eyes, neck absent. Integumental sculpture faint to absent, surface shiny. Punctures large to small, densely distributed, round; setae directed medially and anteriorly or virtually all directed medially. Eyes large to moderately large, eye length 1.5–1.3 times length of temple. Infraorbital carina complete, markedly developed. Antenna moderately elongate, more or less parallel-sided

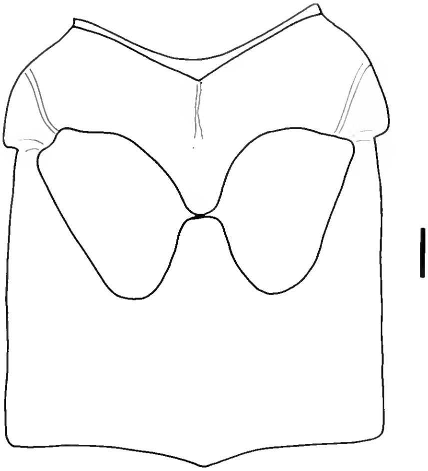


Figs. 49–55. *Pleurotobia trimaculata* (Erichson). **49**, Head, dorsal aspect. **50**, Labrum, dorsal aspect. **51**, Labrum, epipharyngeal region. **52**, Mandible, ventral aspect. **53**, Maxilla, ventral aspect. **54**, Lacinia of maxilla, dorsal aspect. **55**, Labium, ventral aspect. (Scale line = 0.1 mm.)

from article 5 to 10, not noticeably incrassate; antennal structure different in males and females (see secondary sexual characteristics below); article 4 elongate to quadrate, similar in setation and sculpture to articles 1 to 3 or 5 to 10; article 5 elongate to transverse; article 10 transverse to quadrate; antennal articles 5 to 10 decreasing in relative lengths more apically.

Mouthparts.—Labrum (Figs. 50, 51) with epipharyngeal area similar to that of *Bolitochara*. Mandibles with abcondylar molar patch of denticles large, denticles moderate sized to small, very numerous, densely arranged (Fig. 52). Maxilla (Fig. 53) with teeth on apical 0.25 of lacinia arranged into 3 to 4 irregular rows and densely arranged near apex (Fig. 54); apex of galea with 10 to 12 rows of unmodified (setose) setae (Fig. 53). Labium (Fig. 55) typical of subtribe; ligula with pair of sensory setae large; two medial setae present on prementum, bases arranged one directly behind the other, setal insertions moderately separated; medial pseudopore field of prementum narrow, without pseudopores.

Thorax.—Pronotum broad, transverse, 1.4–1.5 times as wide as long, slightly convex in dorsal outline; almost as wide at base as base of elytra; postero-lateral angles sharply angulate; base slightly to moderately bisinuate; punctures small to large, round, numerous; microsetae fine, moderately dense; microsculpture slightly to moderately reticulate. Elytra with postero-lateral angles moderately to strongly sinuate; punctures large, numerous, lunulate; setae fine, moderately dense. Wings with large flabellum with 11 to 13 setose



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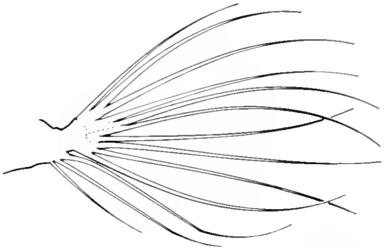

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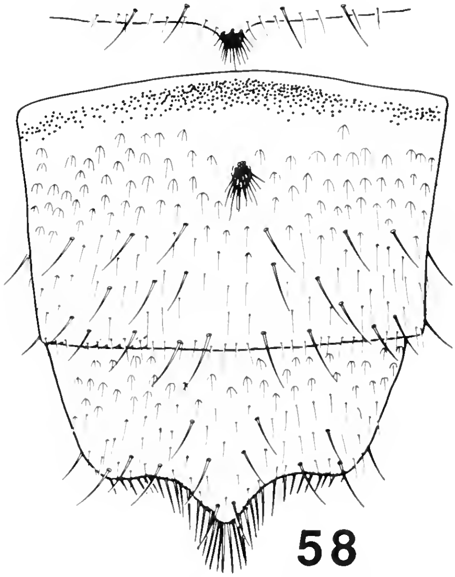

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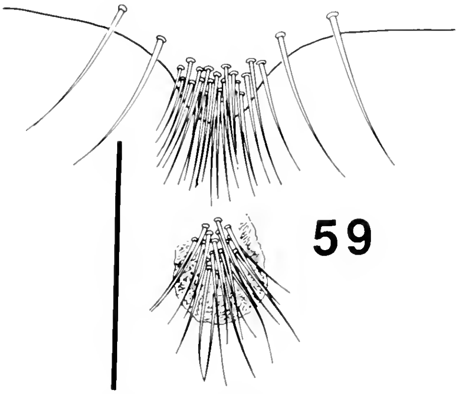

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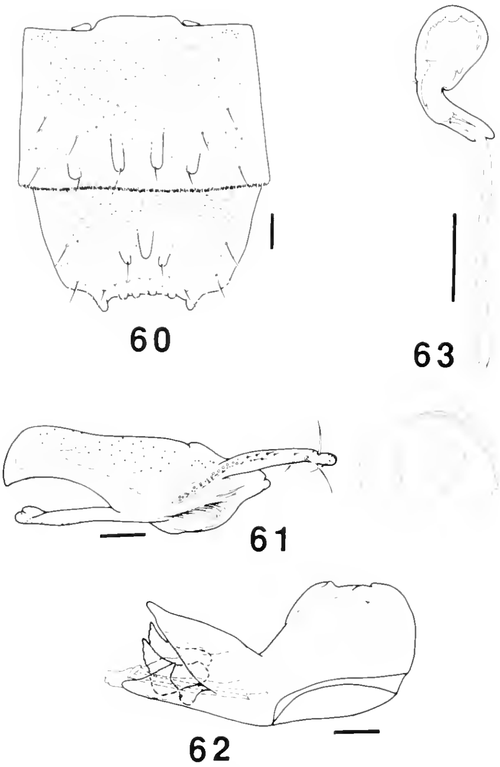
Figs. 56–59. *Pleurotobia trimaculata* (Erichson). **56,** Meso-metasternum. **57,** Flabellum of wing. **58,** Male sternal features, posterior margin of sternum VI, sterna VII and VIII. **59,** Male, detail of setose lobe of sternum VI and concentration of setose pores on sternum VII. (Scale line = 0.1 mm.)



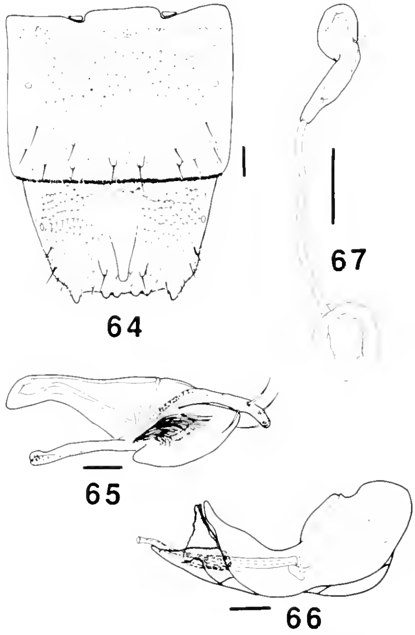
Figs. 60–63. *Pleurotobia trimaculata* (Erichson). **60,** Male, terga VII–VIII. **61,** Male, paramere, external aspect. **62,** Male, median lobe of aedeagus, lateral aspect. **63,** Female, spermatheca and vaginal sclerotization. (Scale line = 0.1 mm.)

lobes (Fig. 57). Hypomeron broadly visible in lateral aspect, inflexed posteriorly and deflexed almost vertically anteriorly, hypomeron contacting lateral line of pronotum slightly posteriorly to anterolateral angles. Mesosternal medial carina (Fig. 56) markedly developed, spreading to lateral angles of mesosternal process near apex of process or fading in apical 0.25 of process. Mesocoxal cavities widely separated by meso- and metasternal processes (Fig. 56); relative lengths mesosternal : isthmus : metsternal processes 5.5 : 0–5 : 4.5; apex of mesosternal process slightly rounded, apex of metasternal process truncate. Hind tarsomere I long, about as long as II and III together.

Abdomen.—Robust, more or less parallel-sided; terga III–V (VI slightly) with deep basal transverse impressions; punctures numerous, large to moderately large, lunuate; microsetae fine, numerous, more or less densely arranged, macrosetae inconspicuous. Sterna III–V with slight transverse basal impressions.

Secondary Sexual Characteristics.—Males: each elytron with markedly to moderately developed carina near suture, variously developed in different males, up to 0.5 times length of suture; tergum VII (Figs. 60, 64) with 2 to 3 oblique to posteriorly directed carinae on each side of midline, variously developed in different males, some with most lateral carinae reduced to small asperity or completely absent; tergum VIII (Figs. 60, 64) broadly and distinctly emarginate posteriorly, with 2 to 3 moderate-sized to robust denticles in emargination on each side of midline; dorsum of tergum VIII with medial carina and 1 to 2 smaller lateral carinae on each side; sternum VI (Figs. 58, 59) with small medial lobe on posterior margin, medial lobe setose; sternum VII (Figs. 58, 59) with concentration of setose glandular pores medially, porose area large, as well as broad band of sensory pores basally, with concentration of setose glandular pores medially, porose area large; sternum VIII (Fig. 58) with posterior triangular projection, projection without asetose posterior margin. Antennal articles of males relatively longer than comparable articles of females.

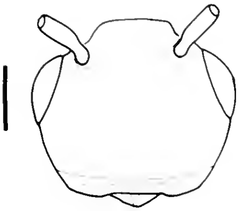
Aedeagus.—Paramere (Figs. 61, 65) with apical lobe of paramerite moderately long, 0.8–0.5 times length of paramerite; setae 1 to 4 of apical lobes moderate length to long, not clustered near tip. Aedeagus (Figs. 62, 66) with apical lobe large, tentlike; internal sac with pair of large sclerotized platelike structures; flagellum of moderate length, tubular.



Figs. 64–67. *Pleurotobia* (= *Phymaturosilusa*) *magnifica* Roubal. **64,** Male, terga VII–VIII. **65,** Male, paramere of aedeagus, external aspect. **66,** Male, median lobe of aedeagus, lateral aspect. **67,** Female, spermatheca and vaginal sclerotization. (Scale line = 0.1 mm.)

Spermatheca (Figs. 63, 67).—Basal bulb simple, apex rounded; neck only slightly bent to bent about 60° from straight. Spermathecal tube membranous, more or less straight. Vaginal sclerotization markedly developed; about 0.75 to almost complete circle of sclerotized tissue.

Discussion.—Casey (1906) described three species in his new genus *Pleurotobia* from eastern North America (*P. suturalis* Casey, *P. tristigma* Casey, and *P. texana* Casey). I have examined the types of all three of these species and cannot find any significant difference among them. They all appear to be synonymous with *Bolitochara trimaculata* Erichson. *Pleurotobia tristigmata* (Erichson) reported by Ashe (1990) is an error for *Pleurotobia tristigma* Casey. There is an undescribed species of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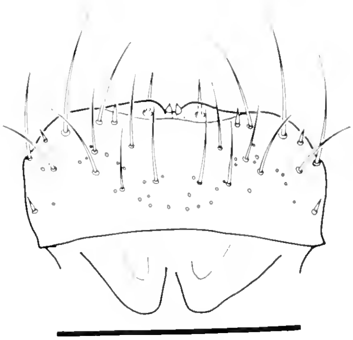
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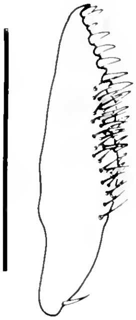
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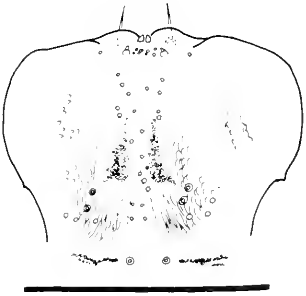
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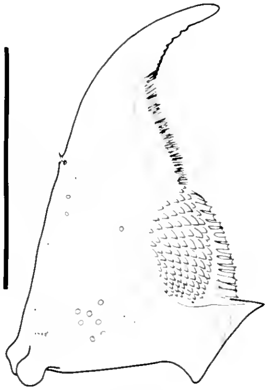
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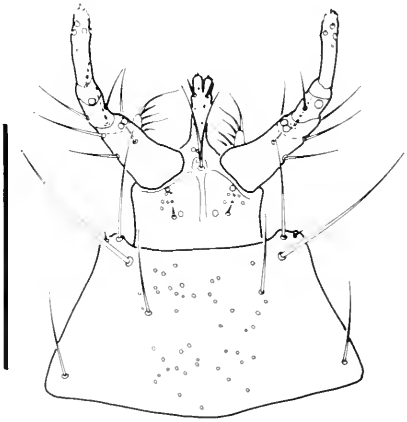
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Figs. 68–74. *Pseudatheta elegans* Cameron. **68**, Head, dorsal aspect. **69**, Labrum, dorsal aspect. **70**, Labrum, epipharyngeal aspect. **71**, Maxilla, ventral aspect. **72**, Lacinia of maxilla, dorsal aspect. **73**, Mandible, ventral aspect. **74**, Labium, ventral aspect. (Scale line = 0.1 mm.)

Pleurotobia (here reported as "*P.* sp. A") from Oklahoma.

The single known species of *Phymaturosilusa*, *P. magnifica* Roubal, is only known from central Europe. As noted above (see Phylogeny), there is good evidence that *Pleurotobia* and *Phymaturosilusa* are synonyms.

Members of the genus are only known to occur in the eastern half of North America and central Europe.

Genus *Pseudatheta* Cameron
(Figs. 68-79)

Pseudatheta Cameron 1920, p. 224. Type species *Pseudatheta elegans* Cameron 1920, p. 224, by monotypy.—Cameron 1920: 224.—Cameron 1932: 141.—Cameron 1939a: 224.

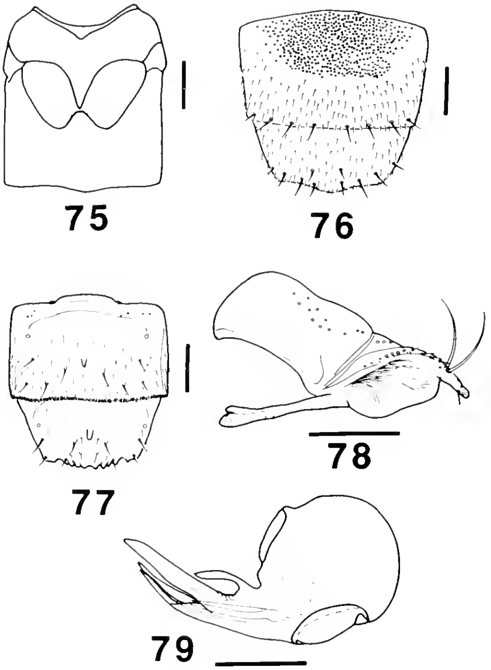
Diagnosis.—Members of *Pseudatheta* can be recognized by: small size, length 1.5-2.0 mm, eyes large, as long as length of temples; head not narrowed behind eyes to form a neck (Fig. 68); antenna slightly incrassate, pronotum very broad, 1.5 times as wide as long, not noticeably narrower than elytra; hypomeron inflexed into horizontal plane throughout, not visible in lateral aspect; mesosternum without medial longitudinal carina; mesocoxal cavities narrowly separated by intercoxal processes, mesosternal process slender and acutely pointed (Fig. 75); hind tarsomere I not significantly longer than II; only abdominal tergal III-IV moderately impressed at base; sterna not basally impressed; male sternum VI without medial lobate projection on posterior margin; male sternum VII (Fig. 76) with broad band of sensory pores basally, without medial concentration of setose sensory pores; triangular projection of posterior margin of male sternum VIII (fig. 76) without asetose posterior margin; median lobe of aedeagus (Fig. 79) with slender, pointed apical process, flagellum tapered to an acute apex, without sclerotized plates on internal sac.

Description.—Lengths of adults 1.5-2.0 mm. Body relatively broad and somewhat flattened, more or less parallel-sided and slightly narrowed behind, to slightly robust. Surface sculpture absent to slight, surface shiny or not. Body finely and moderately pubescent. Punctures of moderate size, densely distributed. Macrosetae inconspicuous.

Head (Fig. 68).—More or less oval, slightly less broad than apex of prothorax; not narrowed behind, without neck. Sculpture absent to slight, surface shiny or not. Punctures large, round. Microsetae directed medially. Eyes moderately large, length about equal to length of temple. Infraorbital carina markedly developed, complete. Antenna moderately short, incrassate toward apex; article 4 transverse, similar in setation and sculpture to 1 to 5; article 5 transverse; article 10 transverse; articles 5 to 10 about equal in relative length.

Mouthparts.—Labrum (Figs. 69, 70) with epipharyngeal area with medial pores small, distant in medial longitudinal sensory field. Mandibles with abcondylar molar patch of denticles large, denticles small, densely arranged (Fig. 73). Maxilla (Figs. 71, 72) with teeth in apical 0.25 arranged in single row of distantly spaced teeth; apex of galea typical of subtribe, setae unmodified. Labium (Fig. 74) typical of subtribe; ligula with pair of sensory setae very small; prementum with two medial setae, medial setae arranged one directly behind the other, setal insertions close, medial pseudopore field narrow, without pseudopores.

Thorax.—Pronotum broad, transverse, about 1.5 times as wide as long, rather flat in dorsal outline; about as wide at base as base of elytra; postero-lateral angles rounded; base broadly rounded, not bisinuate; punctures moderate sized, round, numerous, dense; integument without microsculpture or slightly reticulate. Elytra with postero-lateral angles moderately sinuate; punctures large, densely arranged, lunulate; microsetae fine, moderately dense. Wings without flabellum, without setose lobes. Hypomeron strongly inflexed throughout, not visible in lateral view. Mesosternum without medial carina. Mesocoxal cavities narrowly separated by meso- and metasternal processes (Fig. 75); relative



Figs. 75-79. *Pseudatheta elegans* Cameron. **75,** Meso-metasternum. **76,** Male, sterna VII-VIII. **77,** Male, terga VII-VIII. **78,** Male, paramere of aedeagus, external aspect. **79,** Male, median lobe of aedeagus, lateral aspect. (Scale line = 0.1 mm.)

lengths mesosternal : isthmus : metasternal processes about 5 : 0 : 2; apex of mesosternal process pointed, apex of metasternal process rounded. Hind tarsomere I short, only slightly longer than II.

Abdomen.—Slightly narrowed apically to broadly pointed apex; terga III–IV with transverse basal impressions. Punctures moderate in size, round, not lunulate; microsetae numerous, more or less dense. Sterna without noticeable transverse basal impressions.

Sexual Characteristics.—Males: each elytron with small to minute tubercle near suture; tergum VII (Fig. 77) with transverse rows of small tubercles or with short medial carina; tergum VIII (Fig. 77) truncate, not incised, with four denticles on each side of midline on apical margin, lateral denticle separated from others by slight gap; dorsal surface of tergum VIII with small medial tubercle and scattered lateral asperities; sternum VI without small medial lobe in posterior margin, sternum VI and VII (Fig. 76) with very broad band of numerous sensory pores which takes up most of ventral surface of tergum; sternum VIII (Fig. 76) with very slight posterior triangular projection, projection without asetose posterior margin.

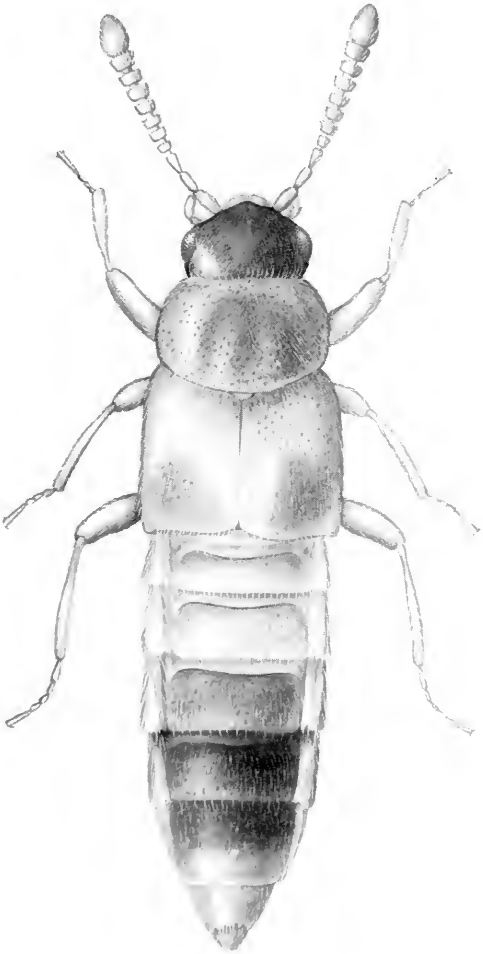


Fig. 80. *Silusida marginella* Casey. Habitus. Length = 2.5 mm.

Aedeagus.—Paramere (Fig. 78) with apical lobe of paramerite short, length less than 0.5 times length of paramerite; setae 1 to 4 of apical lobe moderate in length, not clustered near the tip. Aedeagus (Fig. 79) with slender pointed apical process; internal sac without sclerotized internal plates; flagellum moderately long, tapered to an acute apex.

Spermatheca.—Not examined.

Discussion.—The genus *Pseudatheta* is known from six species from southeast Asia (*P. elegans* Cameron, *P. indica* Cameron), Africa (*P. africana* Cameron) and Nepal (*P. smetanai* Pace, *P. mendica* Pace and *P. ghoropanesis* Pace). Pace (1989) recently described the three species from Nepal. His illustrations indicate that the aedeagi of these species are somewhat similar to that of *P. elegans*. This suggests that they may be correctly placed in *Pseudatheta*. However, they differ somewhat in external appearance from the generic description provided here. Most notably, *P. ghoropanesis* is larger (3.7 mm in length), and has smaller eyes, longer temples and a head which is slightly narrowed behind. If, after examination, these species prove to be correctly placed in *Pseudatheta*, then the generic description provided here will require modification.

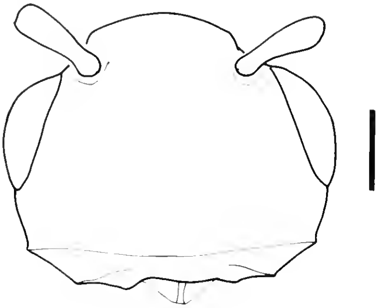
Only the type species of *Pseudatheta (P. elegans)* is included in the phylogenetic analysis. Its phylogenetic position is uncertain. Various analyses either place it as the sister group to *Austrasilida* new genus (Fig. 2), sister group to *Pleurotobia* + *Bolitochara* (Fig. 4) or the most basal lineage in the subtribe (Fig. 5).

Genus *Silusida* Casey
(Figs. 80–94)

Silusida Casey 1906, p. 270. Type species *Silusida marginella* Casey. Fixed by Fenyes 1918, p. 25.—Casey 1906: 270.—Fenyes 1920: 116.—Notman 1920: 713.—Seevers 1978: 164 (as a synonym of *Bolitochara* Mannerheim).

Diagnosis.—Members of *Silusida* can be recognized by the combination of: head (Fig. 81) broad, with moderately large eyes, eye size 1.3–1.5 times as long as temple; head not at all narrowed behind the eyes to form a neck; pronotum broadly transverse, 1.5 times as wide as long; short incrassate antenna with antennomeres 5 to 10 transverse; basal angles of pronotum broadly rounded, not angulate; pronotum not noticeably narrower than elytra; hypomeron inflexed into horizontal plane throughout, only narrowly visible in lateral aspect; abdominal terga III–VI with moderate transverse basal impressions; sterna not noticeably impressed basally; male sternum VI without medial lobate projection on posterior margin; male sternum VII (Fig. 90) with broad band of numerous sensory pores basally, without concentration of setose pores medially; triangular projection of male sternum VIII (Fig. 90) with asetose posterior border; median lobe of aedeagus (Fig. 93) with apical process large, tentlike, without obvious sclerotized plates on internal sac, and short, tubular flagellum.

Description (Fig. 80).—Lengths of adults 2.1 to 3.0 mm. Body relatively broad, more or less parallel-sided, somewhat depressed in cross section. Surface sculpture faintly reticulate, body not strongly shiny. Body moderately densely pubes-



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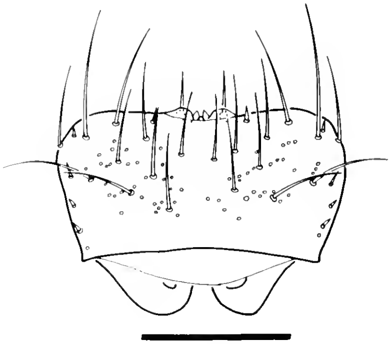

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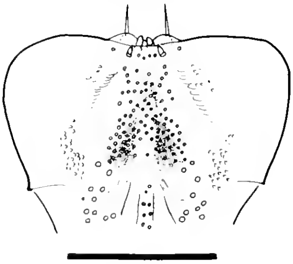

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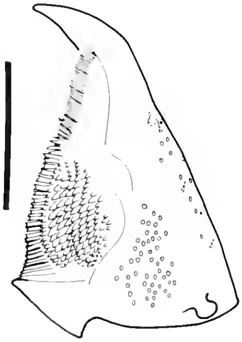

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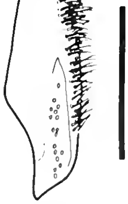

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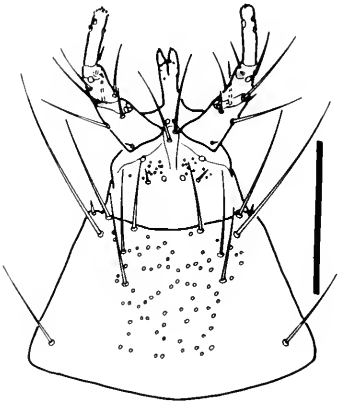

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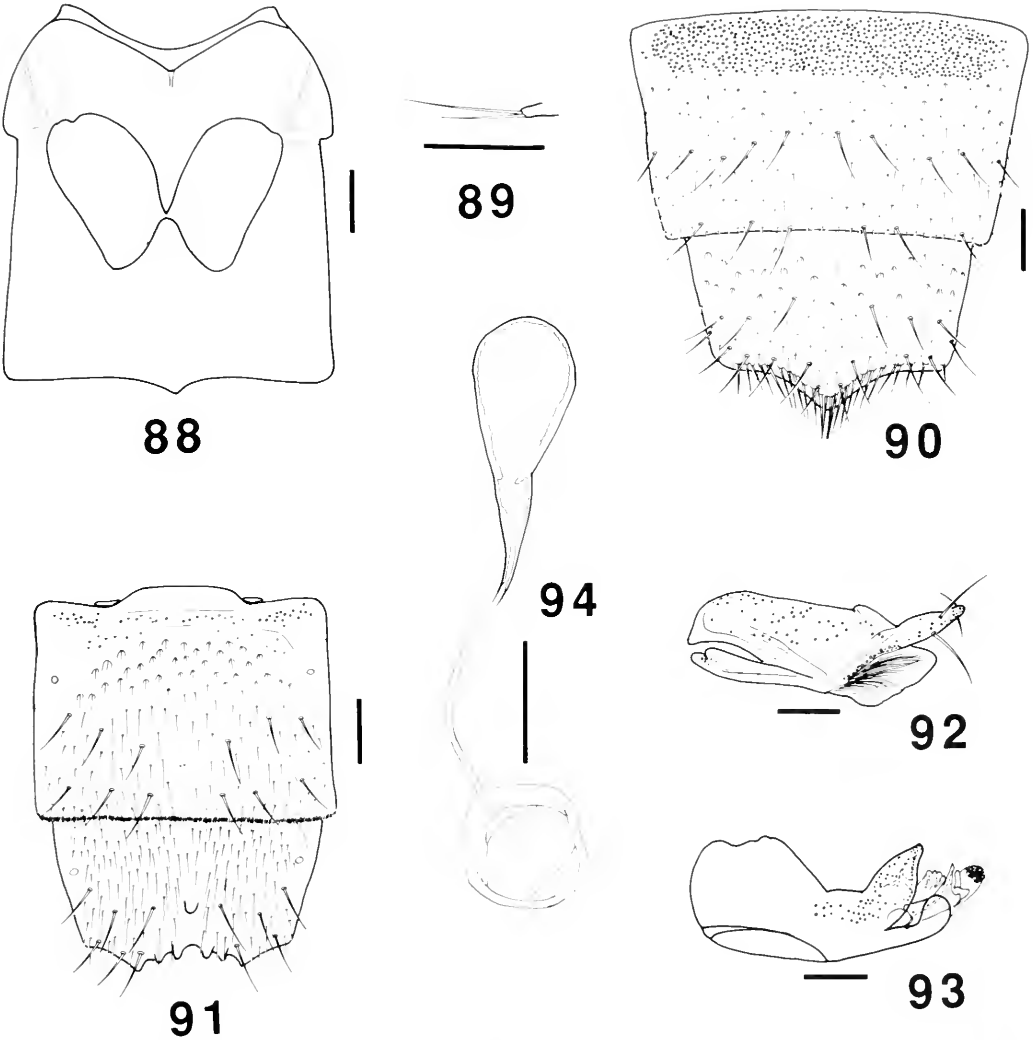
Figs. 81–87. *Silusida marginella* Casey. **81**, Head, dorsal aspect. **82**, Labrum, dorsal aspect. **83**, Labrum, epipharyngeal aspect. **84**, Mandible, ventral aspect. **85**, Maxilla, ventral aspect. **86**, Lacinia of maxilla, dorsal aspect. **87**, Labium, ventral aspect. (Scale line = 0.1 mm.)

cent, punctures small, densely and uniformly distributed. Macrosetae inconspicuous.

Head (Fig. 81).—Broad, about as wide as apex of pronotum. Head not narrowed behind the eyes, neck absent. Integumental sculpture slightly reticulate. Punctures small, round, densely distributed; microsetae directed medially and anteriorly. Eyes moderately large, length 1.3–1.5 times length of temples. Infraorbital carina complete, markedly developed. Antenna short, incrassate toward apex from article 4 to 11; article 4 quadrate to slightly transverse, intermediate in sculpture and shape between articles 1 to 3 and 5 to 10; article 5 transverse; article 10 strongly transverse; antennal articles 5 to 10 decreasing in relative lengths apically.

Mouthparts.—Labrum (Figs. 82, 83) with epipharyngeal area with larger, more distinct pores in longitudinal medial sensory field. Mandibles (Fig. 84) with abcondylar molar patch of denticles large, denticles small, very numerous, densely arranged. Maxilla (Figs. 85, 86) with teeth on apical 0.25 of lacinia arranged in 1 to 2 irregular rows (Fig. 86); apex of galea with 8 to 9 rows of unmodified (setose) setae (Fig. 85). Labium typical of subtribe (Fig. 87); ligula with pair of sensory setae very minute; prementum with two pair of sensory setae, arranged one directly be-



Figs. 88–94. *Silusida marginella* Casey. **88**, Meso-metasternum. **89**, Flabellum of wing. **90**, Male, sterna VII–VIII. **91**, Male, terga VII–VIII. **92**, Male, paramere of aedeagus, external aspect. **93**, Male, median lobe of aedeagus, lateral aspect. **94**, Female, spermatheca and vaginal sclerotization. (Scale line = 0.1 mm.)

hind the other, insertions moderately distant; medial pseudopore field narrow, without pseudopores.

Thorax.—Pronotum broad, transverse, about 1.5 times as wide as long, relatively flattened in dorsal outline; almost as wide as base of elytra; postero-lateral angles more or less rounded; base very slightly bisinuate or not noticeably bisinuate; punctures small, numerous, round, setation fine; moderately dense, uniformly distributed; integumental microsculpture slightly reticulate, surface not noticeably shiny. Elytra with postero-lateral angles moderately sinuate; punctures small, numerous, lunulate; microsetae fine, densely and uniformly distributed. Wings with very small flabellum (Fig. 89) with two (a few specimens with three) setose lobes on each. Hypomeron strongly inflexed throughout, only narrowly visible in lateral aspect; anterior margin of hypomeron contacting pronotal lateral line very near antero-lateral angle of pronotum. Mesosternal medial carina (Fig. 88) slightly present in anterior 0.25 to virtually absent in some specimens. Mesocoxal cavities narrowly separated by meso- and metasternal processes (Fig. 88); relative length mesosternal : isthmus : metasternal processes 7 : 1 : 3; apex of mesosternal process acutely pointed, apex of metasternal process broadly rounded. Hind tarsomere I almost as long as II and III together.

Abdomen.—Somewhat broad and flattened, slightly tapered to obtusely pointed apex, terga III–V moderately transversely impressed basally; punctures small, numerous, lunulate; microsetae fine, numerous, moderately densely arranged. Sterna III–V without noticeable transverse basal impressions.

Secondary Sexual Characteristics.—Males: elytra without sutural carina or tubercle; tergum VII (Fig. 91) with faint to small median tubercle or knob; tergum VIII (Fig. 91) broadly and distinctly emarginate posteriorly, with 4 to 5 moderate-sized to small denticles on each side of midline in emargination; dorsum of tergum VIII (Fig. 91) with small to very faint medial knob or tubercle in most, a few specimens without knob or tubercle; sternum VI without small medial lobe on posterior margin; sternum VII (Fig. 90) with broad basal band of numerous sensory pores, without medial concentration of setose sensory pores; sternum VIII (Fig. 90) with moderately developed posterior triangular projection, with asetose posterior margin.

Aedeagus.—Paramere (Fig. 92) with apical lobe of paramerite short, length less than 0.5 times length of paramerite; setae 1 to 4 of apical lobe long, not clustered near apex of lobe. Aedeagus (Fig. 93) with apical process large, tentlike; internal sac without obvious sclerotized plates; flagellum short, tubular.

Spermatheca (Fig. 94).—Basal bulb simple, apex rounded, neck very slightly bent; spermathecal tube membranous, more or less straight; vaginal sclerotization large, with complete circle of sclerotized cuticle.

Discussion.—Casey (1906) described two species of *Silusida* from eastern North America (*S. marginella* Casey and *S. nanella* Casey). I was not able to locate any specimens of the type series of *S. nanella* in the Casey collection. In addition, *Silusida tenuicornis* Notman from Florida is not a bolitocharine. Therefore, only a single species of *Silusida* can be confirmed for eastern North America.

Silusida is shown to be the sister taxon to *Stictalia* in all phylogenetic analyses. Members of the two taxa differ substantially from each other in numerous derived features of external morphology, secondary sexual characteristics, spermatheca, and aedeagus. Members of the two genera are easily distinguished on the basis of external structure alone. There is no justification for combining them into a single genus.

Genus *Stictalia* Casey
(Figs. 95–114)

Stictalia Casey 1906, p. 234. Type species *Stictalia notata* (Mäklin). Fixed by Fenyes 1918, p. 25.—Casey 1906: 234.—Fenyes 1920: 114 (as a synonym of *Ditropalia* Casey).—Seevers 1978: 164 (as a synonym of *Bolitochara* Mannerheim).

Diagnosis.—Members of *Stictalia* can be recognized by the combination of: eyes moderate sized to small, 1.2–0.5 times length of temples; head slightly narrowed behind eyes to form an inconspicuous neck (Fig. 96) or not obviously narrowed; pronotum only slightly transverse, 1.2–1.3 times as wide as long; pronotum not bisinuate basally; pronotum noticeably to very distinctly narrower than base of elytra; hypomeron moderately to broadly visible in lateral aspect; mesocoxal cavities narrowly to very narrowly separated by intercoxal processes, mesosternal process narrow, acutely pointed apically (Fig. 103); terga III–V or III–VI with moderate to deep transverse basal impressions; sterna III–V with moderate basal impressions or impressions indistinct; many with male secondary sexual characteristics of tergum VII and VIII (Figs. 105, 111) greatly reduced; male sternum VI without VI without medial lobate projection on posterior margin; male sternum VII (Fig. 106) with band of numerous sensory pores basally, without concentration of setose pores medially; triangular projection of male sternum VIII (Fig. 106) with asetose posterior margin; median lobe of aedeagus (Figs. 107, 112, 114) with apical process slender, recurved or foot-shaped, internal sac without obvious sclerotized platelike structures, flagellum tubular; spermatheca distinctive, spermathecal tube sclerotized and distinctively looped (Fig. 109). Known distribution of members of this genus is limited to the west coast of North America, and it is the only genus of the Bolitocharina currently known to occur in that region.

Description (Figs. 95, 110).—Lengths of adults

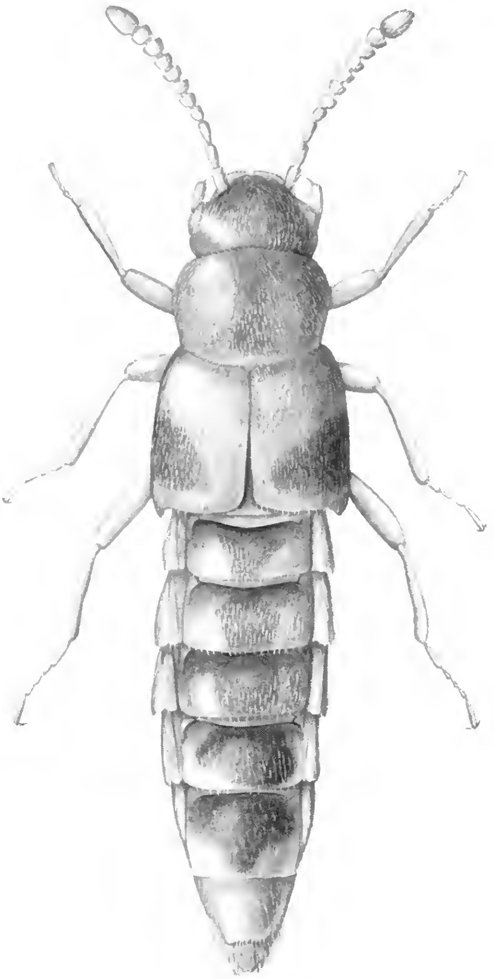


Fig. 95. *Stictalia californica* Casey. Habitus. Length = 3.8 mm.

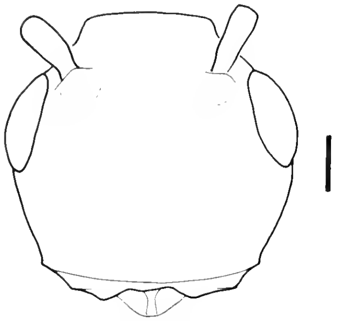
2.0–4.0 mm. Body form more or less elongate, slender, parallel-sided, somewhat convex in cross section. Surface sculpture various, from moderately reticulate to sculpture absent, surface shiny or not. Body moderately to densely pubescent with fine microsetae; punctation various on different body regions and among species, punctures large and dense to small and more distantly distributed, punctures asperite or not. Macrosetae inconspicuous.

Head (Fig. 96).—More or less oval, quadrate or slightly longer than wide, at most slightly narrowed behind the eyes to produce very broad and inconspicuous neck. Sculpture absent to moderately reticulate, surface shiny or not. Punctures small to moderate sized, numerous, densely distributed, round; microsetae directed medially and anteriorly or all directed anteriorly. Eyes moderate sized to small, length 1.1–1.2 times length of temples to about 0.5 times length of temples. Infraorbital carina complete, markedly developed. Antenna various, not noticeably incrassate toward apex; article 4 quadrate to elongate, similar in setation and sculpture to articles 1 to 3; article 5 slightly transverse to slightly elongate; article 10 transverse; antennal articles 5 to 10 decreasing in relative lengths toward apex.

Mouthparts.—Labrum (Figs. 97, 98) with epipharyngeal area with medial pores very small, few, not close, in well-delimited longitudinal sensory field. Mandibles (Fig. 101) with abcondylar molar patch of denticles large, denticles numerous and closely arranged. Maxilla (Figs. 99, 100) with teeth on apical 0.25 of lacinia in 3 to 5 irregular rows, teeth arranged in dense concentration especially near apex (Fig. 100); galeal setae in 6 to 7 rows of unmodified (setose) setae. Labium (Fig. 102) typical of subtribe, ligula without pair of sensory setae; two medial setae present on prementum, bases arranged one directly behind the other, setal insertions moderately distant from each other; medial pseudopore field of prementum narrow, without pseudopores.

Thorax.—Pronotum only slightly transverse, 1.2–1.3 times as wide as long, slightly to markedly convex in dorsal outline; base slightly to distinctly narrower than base of elytra; postero-lateral angles slightly to markedly angulate; base broadly rounded, not bisinuate; punctures large to small, numerous, densely arranged; microsetae fine to relatively stiff, more or less dense; microsculpture various, reticulate to microsculpture absent. Elytra with postero-lateral angles moderately sinuate; punctures moderate to very large, numerous, densely arranged, lunulate; microsetae fine, dense. Wings with very small flabellum (Fig. 104) with 1 (specimens of most species) to 3 (specimens of a few species) setose projections. Hypomeron somewhat inflexed posteriorly to broadly deflexed throughout, moderately to broadly visible in lateral aspect; anterior margin of hypomeron contacting lateral border of pronotum slightly to distinctly posterior to anterior angles of pronotum. Mesosternal medial carina (Fig. 103) various, strong anteriorly and fading in posterior 0.3–0.4 or complete to apex of process. Mesocoxal cavities narrowly to very narrowly separated by meso- and metasternal processes (Fig. 103); relative lengths mesosternal : isthmus : metasternal processes various, from 2.5 : 1 : 1.5 to 6.5 : 1 : 3.5; apex of mesosternal process narrow, acutely pointed; apex of metasternal process acutely rounded. Hind tarsomere 1 long, as long as II and III together.

Abdomen.—Slender, more or less parallel-sided; terga III–V or III–VI with moderate to deep transverse basal impressions, punctures small to large, numerous, densely arranged, lunulate; setae fine, densely arranged to sparse, most taxa with all setae directed posteriorly, some with setae



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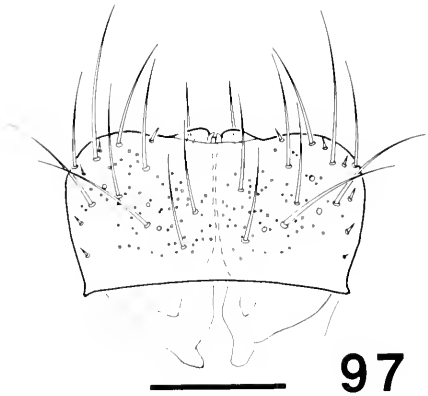

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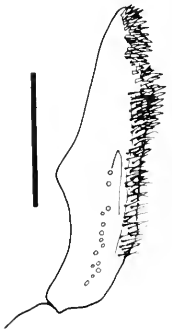

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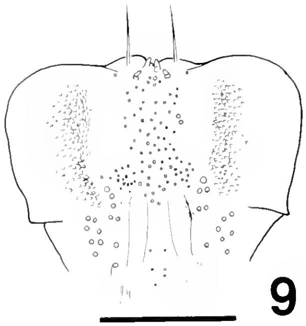

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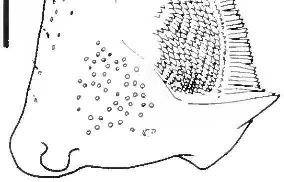

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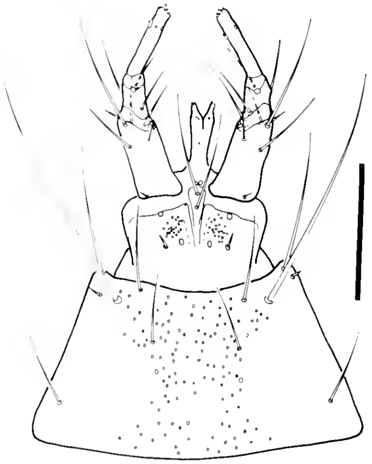

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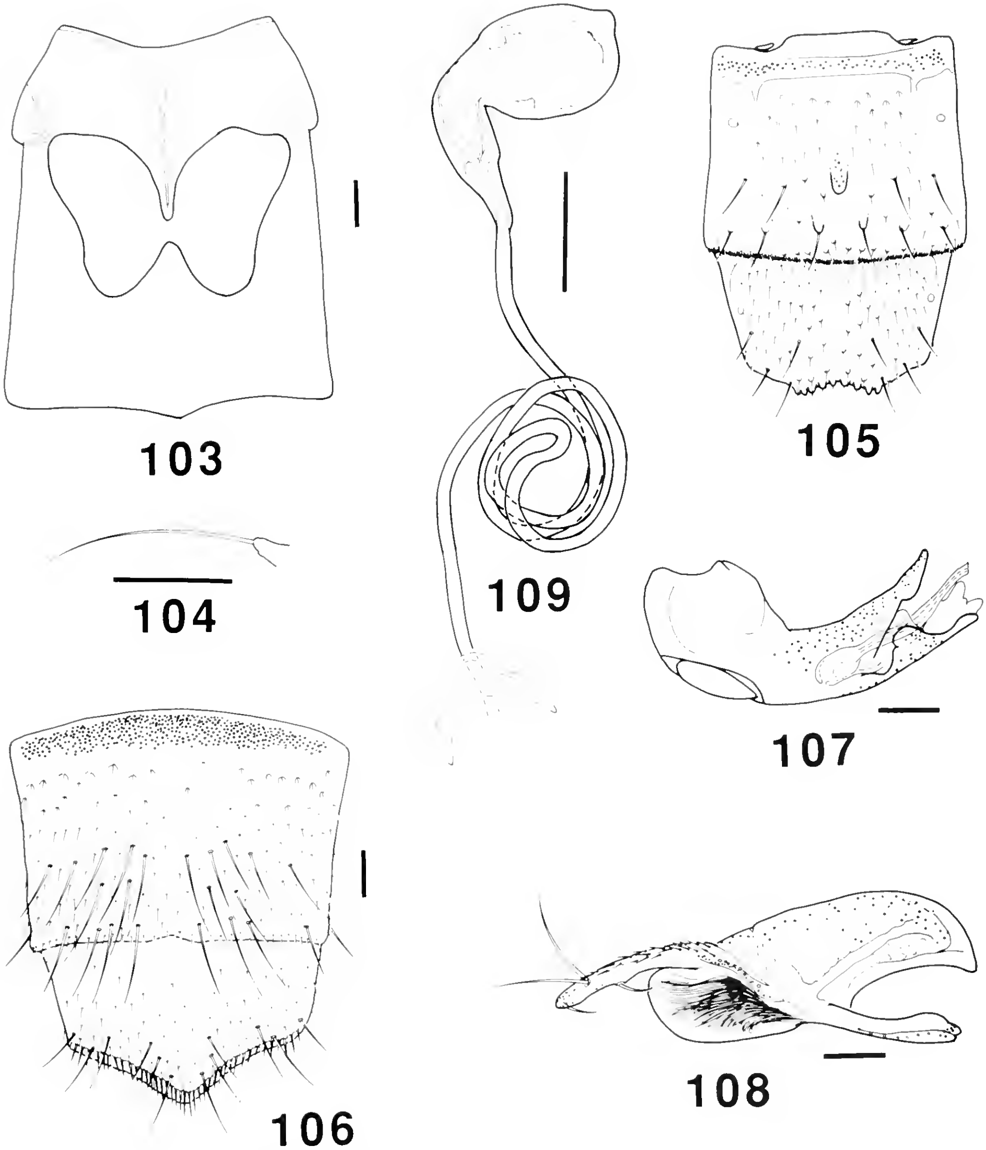
Figs. 96–102. *Stictalia californica* Casey. **96**, Head, dorsal aspect. **97**, Labrum, dorsal aspect. **98**, Labrum, epipharyngeal aspect. **99**, Maxilla, ventral aspect. **100**, Lacinia of maxilla, dorsal aspect. **101**, Mandible, ventral aspect. **102**, Labium, ventral aspect. (Scale line = 0.1 mm.)

on basal abdominal terga directed obliquely toward midline; integumental microsculpture various, reticulate, obsolete, slightly wavy, or absent. Many with sterna III–V with moderate basal impressions or such impressions indistinct.

Secondary Sexual Characteristics.—Males: elytra without sutural carina or tubercle; tergum VII (Figs. 105, 111) of most with small to moderate medial knob or tubercle with scattered lateral moderate to minute asperities, some without medial knob and/or asperities; tergum VIII (Figs. 105, 111) with very shallow emargination posteriorly, some with emargination indistinct to absent, with 3 to 4 small to minute denticles on each side of midline in emargination, some with denticles virtually to completely absent, dorsum



Figs. 103–109. *Stictalia californica* Casey. **103,** Meso-metasternum. **104,** Flabellum of wing. **105,** Male, terga VII–VIII. **106,** Male, sterna VII–VIII. **107,** Male, median lobe of aedeagus, lateral aspect. **108,** Male, paramere of aedeagus, external aspect. **109,** Female, spermatheca and vaginal sclerotization. (Scale line = 0.1 mm.)

of tergum VIII without modification or with very small medial knob or carina and/or scattered asperities; sternum VI without small medial lobe on posterior margin; sternum VII (Fig. 106) with broad basal band of numerous sensory pores, without medial concentration of setose sensory pores; sternum VIII (Fig. 106) with moderately developed posterior triangular projection, with asetose posterior margin.

Aedeagus.—Paramere (Figs. 108, 113) with apical lobe of paramerite very long, length 0.8–1.0 times as long as paramerite; setae 1 to 4 of apical lobe long, not clustered near apex. Aedeagus (Figs. 107, 112, 114) with apical process slender, recurved or footlike; internal sac without distinct pair of platelike sclerotizations but with faint sclerotized areas; flagellum tubular, short or long.

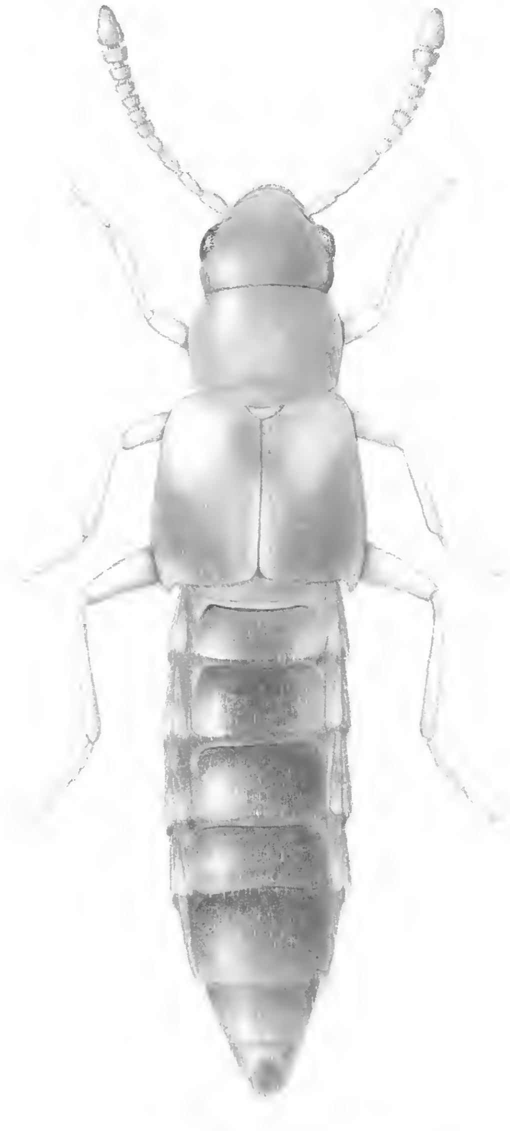


Fig. 110. *Stictalia brevicornis* Casey. Habitus. Length = 3.1 mm.

Spermatheca (Fig. 109).—Basal bulb simple, apex with small knob; most with neck bent into angle greater than 90°, a few with neck bent into 30–60° angle; spermathecal tube lightly to moderately sclerotized, arranged in a distinctive pattern of 2 to 3 loops; vaginal sclerotization very small, present as inconspicuous arc of sclerotized cuticle or not visible.

Discussion.—Casey (1906) proposed the genus name *Stictalia* to include 12 new species of bolitocharines from the west coast of North America and included *Bolitochara notata* Mäklin within the group. I have examined all described taxa as well as several undescribed species of *Stictalia,* including specimens of *S. notata* from Alaska and the Queen Charlotte Islands. The species of *Stictalia* included in the analysis form a monophyletic group in all phylogenetic analyses. The type species of *Stictalia, S. notata* (Mäklin), was not included in the phylogenetic analysis because of lack of specimens for dissection. However, it is clearly a member of this genus and is very closely related to *S. californica* Casey.

There are two distinct groups of species within *Stictalia,* one exemplified by *S. brevicornis* (provisionally called Type I) (Figs. 110, 111, 112) and one exemplified by *S. notata* (Fig. 114) and *S. californica* (Figs. 95, 105, 107) (provisionally called Type II). These differ in body shape, color pattern, setation, secondary sexual features, and aedeagal features.

Members of *Stictalia* are found on the west coast of North America from Alaska to southern California with one species occurring as far east as Banff, Alberta, in the Canadian Rockies.

***Hongophila* Ashe, new genus**

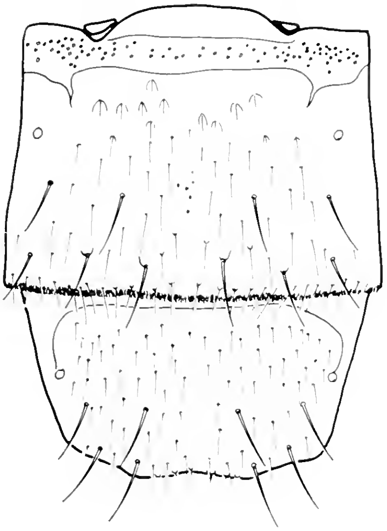
(Figs. 115–131)

Type species *Hongophila arizonica* Ashe.

Diagnosis.—Members of *Hongophila* may be recognized by the combination of: eyes moderately large, 1.1–1.2 times as long as length of tempora; head not at all narrowed behind eyes, neck absent; antennomeres 5 to 10 quadrate to transverse; pronotum moderately transverse, 1.4 times as wide as long, not noticeably narrower at base than base of elytra; hypomeron inflexed to near horizontal plane basally and deflexed more vertically anteriorly, anterior half moderately visible in lateral aspect; mesocoxal cavities narrowly separated by intercoxal processes, mesosternal process narrow, pointed apically (Fig. 123); terga III–V with moderate transverse basal impressions; sterna III–V with very slight transverse basal impressions; male sternum VI (Figs. 125, 126) with medial lobate projection on posterior margin, lobate projection asetose; male sternum VII (Figs. 125, 126) without band of numerous sensory pores basally, with small concentration of setose pores medially; triangular projection of male sternum VIII (Fig. 125) without asetose posterior margin; median lobe of aedeagus (Fig. 128) with apical process elongate, slender, internal sac with pair of spinose and recurved sclerotized plates, flagellum long and tapered to an acute apex. Members of this genus are very difficult to distinguish from those of *Neotobia*. Examination of secondary sexual and aedeagal features are necessary for confident identification of these taxa.

Description. (Fig. 115).—Length of adults 2.8–3.5 mm. Body more or less narrow and elongate. Surface sculpture distinct, reticulate throughout in known species, body not shiny; punctures very small, numerous, densely and uniformly distributed, microsetae fine, uniformly and densely distributed. Macrosetae inconspicuous.

Head (Fig. 116).—Broad, almost as broad as apex of pronotum, not noticeably narrowed behind, neck absent. Surface distinctly reticulate in known species; punctures very small, round, densely distributed. Microsetae directed medially and anteriorly. Eyes moderately large, length 1.1–1.2 times length of temples. Infraorbital ca-



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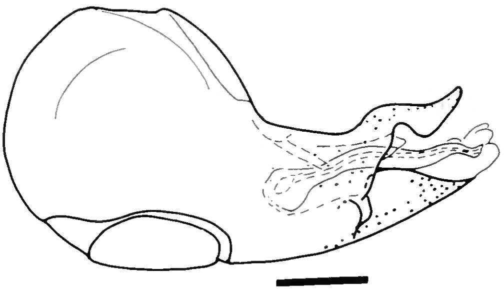

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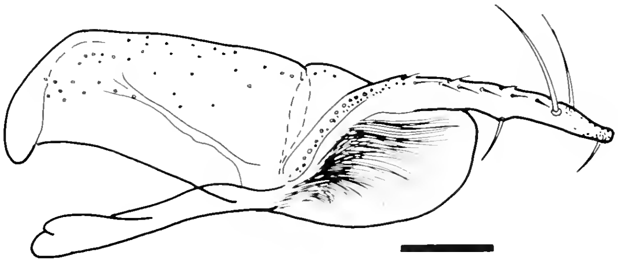

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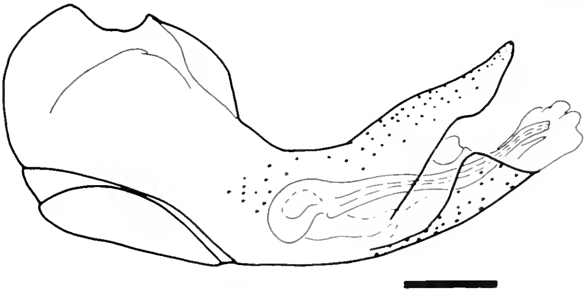

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Figs. 111–113. *Stictalia brevicornis* Casey. **111**, Male, terga VII–VIII. **112**, Male, median lobe of aedeagus, lateral aspect. **113**, Male, paramere of aedeagus, external aspect. (Scale line = 0.1 mm.)

Fig. 114. *Stictalia notata* (Mäklin), male, median lobe of aedeagus, lateral aspect. (Scale line 0.1 mm.)

rina markedly developed, complete. Antenna moderately elongate, slightly incrassate toward apex; article 4 slightly elongate, similar to articles 1 to 3 in setation and sculpture; article 5 more or less quadrate, article 10 transverse; articles 5 to 10 decreasing in relative lengths apically.

Mouthparts.—Labrum (Figs. 117, 118) with epipharyngeal area with medial pores very small, rather distantly separated in medial longitudinal sensory field. Mandibles (Fig. 119) with abcondylar molar patch of denticles moderate sized, molar denticles relatively more dispersed than other Bolitocharina. Maxilla (Figs. 120, 121) with teeth on apical 0.25 of lacinia arranged in a single row of rather widely dispersed teeth (Fig. 121); apex of galea with 6 to 7 rows of unmodified (setose) setae. Labium (Fig. 122) typical of subtribe; ligula with pair of sensory setae very minute; two medial setae present on prementum, bases arranged one directly behind the other, setal insertions close; medial pseudopore field narrow, without pseudopores.

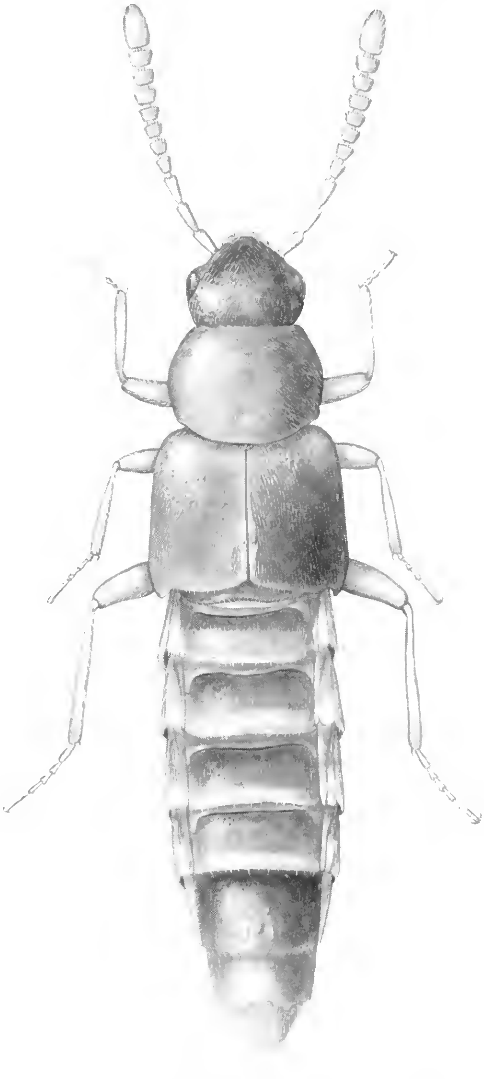


Fig. 115. *Hongophila arizonica* n. sp. Habitus. Length = 3.2 mm.

Thorax.—Pronotum broad, transverse, 1.4 times as wide as long in known species, very slightly convex in dorsal outline; about as wide at base as base of elytra; postero-lateral angles slightly angulate but not sharply pointed; base broadly rounded, only very slightly bisinuate basally; punctures small, round, numerous, densely and uniformly distributed; microsetae dense, fine; microsculpture reticulate. Elytra with postero-lateral angles slightly sinuate; punctures small, densely distributed, round, setation fine, densely distributed. Wings with moderate-sized flabellum with 3 to 6 (most with 4) setose lobes (Fig. 124). Hypomeron inflexed posteriorly and deflexed more vertically anteriorly, broadly visible anteriorly; anterior line of hypomeron contacting lateral marginal line of pronotum very near antero-lateral angles of pronotum. Mesosternal medial carina (Fig. 123) present only in anterior 0.2-0.3 of mesosternum. Mesocoxal cavities narrowly separated by meso- and metacoxal processes (Fig. 123); relative lengths mesosternal : isthmus : metasternal processes 5.5 : 0.5 : 3.5 in known species; apex of mesosternal process narrow, broadly pointed; apex of metasternal process acutely rounded. Hind tarsomere I about as long as II and III together.

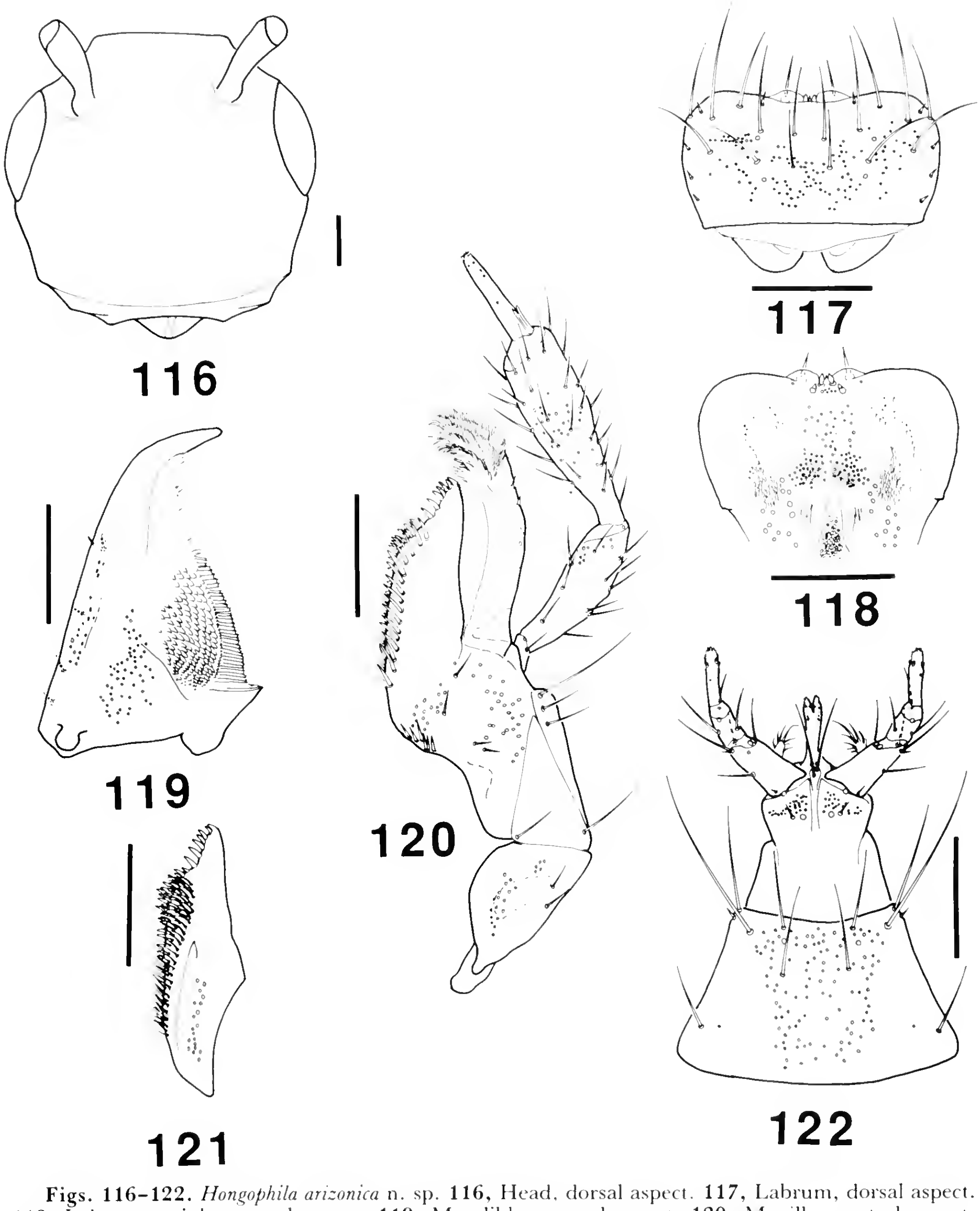
Abdomen.—Elongate, slender, more or less parallel-sided; terga III-V with moderately deep transverse basal impressions; punctures small, densely distributed, most round, a few broadly lunulate in known species; microsetae numerous, densely distributed, all directed posteriorly; macrosetae inconspicuous. Sterna III-V with very slight transverse basal impressions.

Secondary Sexual Characteristics.—Males: each elytron with small knob near suture and posterior suture slightly flexed dorsally; tergum VII (Fig. 127) with small medial tubercle and larger lateral tubercles; tergum VIII (Fig. 127) broadly and distinctly emarginate, with 5 to 6 moderate to small denticles on each side of midline in emargination; dorsum of tergum VIII with numerous small asperities in known species; sternum VI (Figs. 125, 126) with small medial lobe on posterior margin, lobe without setae; sternum VII (Fig. 125, 126) with concentration of setose glandular pores medially, porose area small, as well as broad band of sensory pores basally; sternum VIII (Fig. 125) with moderate posterior triangular projection, projection without asetose posterior margin.

Aedeagus.—Paramere (Fig. 129) with apical lobe of paramerite moderate in length, length about 0.7-0.8 times length of paramerite; setae 1 to 4 of apical lobe long, not clustered near apex. Aedeagus (Fig. 128) with apical process elongate, slender; internal sac with prominent pair of spinose and recurved sclerotized plates; flagellum moderately long, tapered to an acute apex.

Spermatheca (Figs. 130, 131).—Basal bulb elongate, apex rounded; neck bent at angle of about 30° (Fig. 131); spermathecal tube membranous, very long and convoluted (Fig. 130). Vaginal sclerotization very slight, only present as inconspicuous arc of sclerotized cuticle.

Discussion.—The genus *Hongophila* is known from only a single species (*H. arizonica* n. sp., see below) which occurs in the mountain systems of Arizona and New Mexico. I have seen specimens of at least two undescribed species which should



Figs. 116–122. *Hongophila arizonica* n. sp. **116,** Head, dorsal aspect. **117,** Labrum, dorsal aspect. **118,** Labrum, epipharyngeal aspect. **119,** Mandible, ventral aspect. **120,** Maxilla, ventral aspect. **121,** Lacinia of maxilla, dorsal aspect. **122,** Labium, ventral aspect. (Scale line = 0.1 mm.)

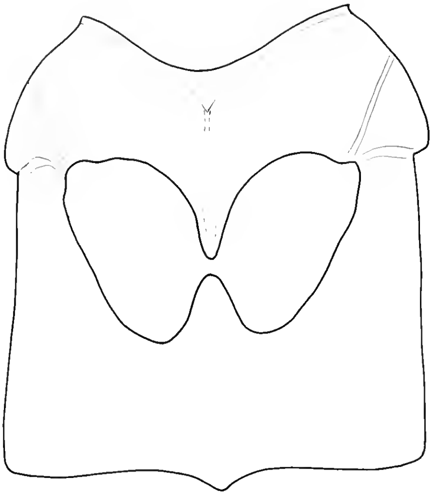
be placed in this genus from the State of Oaxaca in Mexico.

The phylogenetic position of *Hongophila* is somewhat problematic. Those analyses that weight sternal secondary sexual features heavily (Figs. 2, 5) place *Hongophila* as the primitive sister group to *Pleurotobia* + *Bolitochara*. However, unweighted analyses either fail to resolve the position of *Hongophila* (Figs. 1, 3) or place it as an independent basal lineage of bolitocharines (Fig. 4).

Members of *Hongophilia* are superficially similar to those of *Neotobia* new genus, but these two genera are not closely related.

Hongophila arizonica Ashe, new species
(Figs. 115–131)

Description (Fig. 115).—Length 2.8–3.5 mm. Body color reddish brown to brown with head slightly darker brown in some specimens, and external basal angles of elytra and posterior margins of abdominal segments III–VI lighter, antenna reddish brown with apical article lighter; legs light brown. Body covered with moderately dense pile of short, fine hairs; punctation very fine, moderately dense. Head, pronotum, and elytra with moderately developed reticulate



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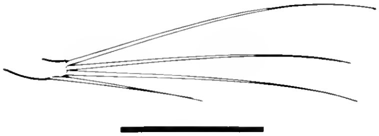

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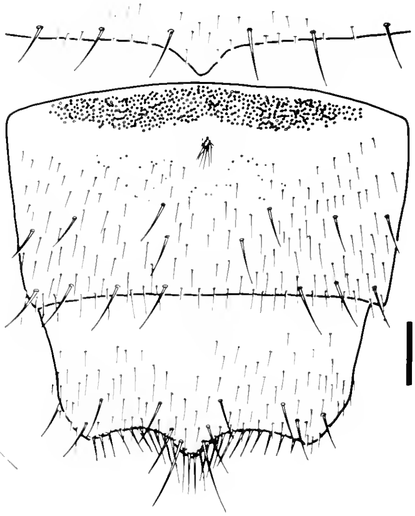

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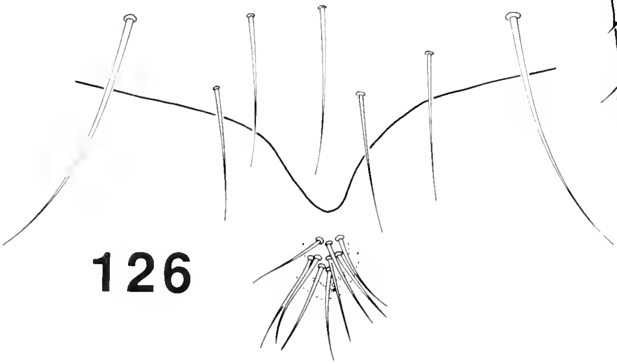

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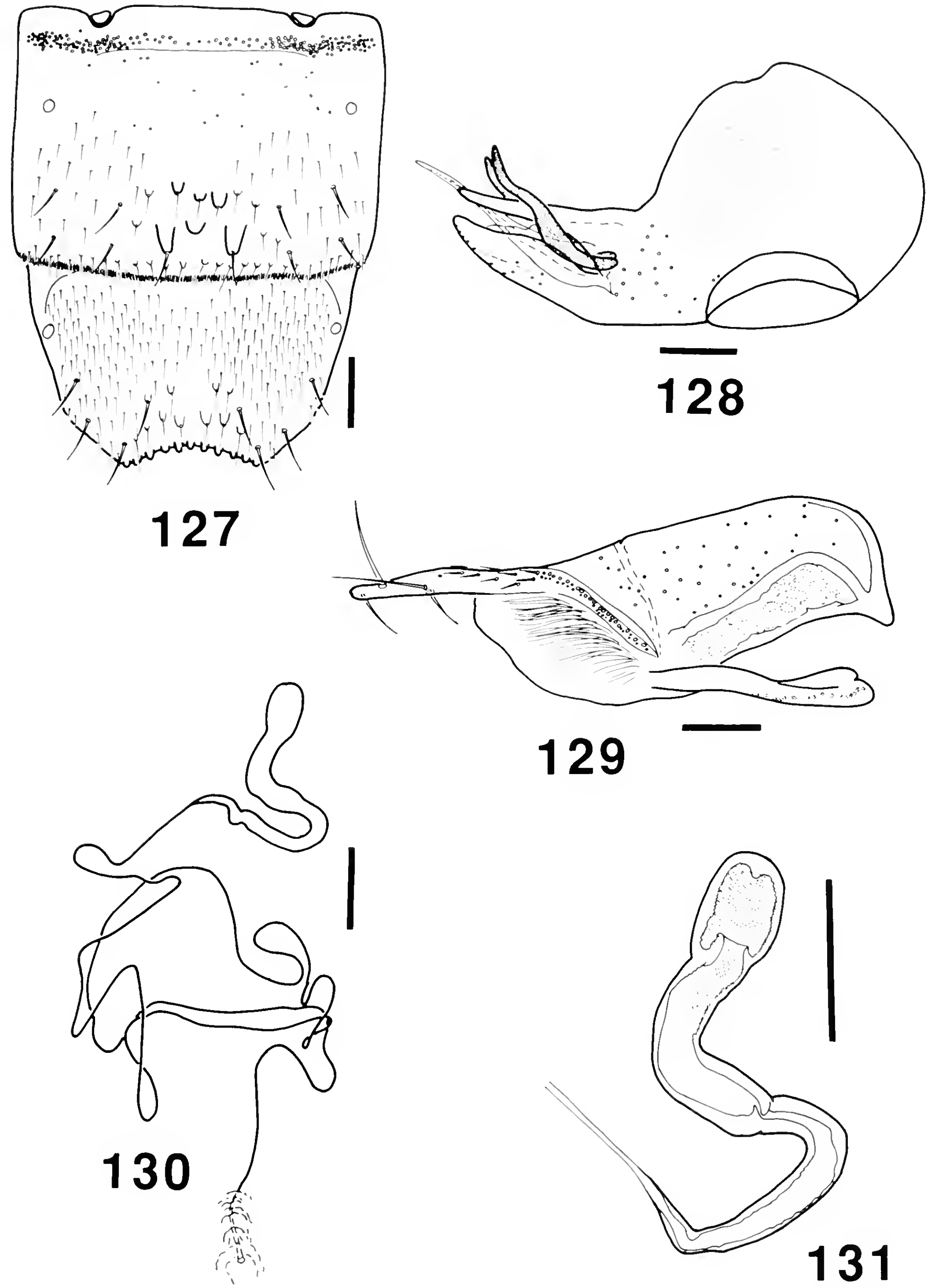
Figs. 123–126. *Hongophila arizonica* n. sp. **123**, Meso-metasternum. **124**, Flabellum of wing. **125**, Male sternal features, posterior margin of sternum VI and sterna VII–VIII. **126**, Male, detail of asetose lobe on posterior margin of sternum VI and concentration of setose pores on sternum VII. (Scale line = 0.1 mm.)



Figs. 127–131. *Hongophila arizonica* n. sp. **127,** Male, terga VII–VIII. **128,** Male, median lobe of aedeagus, lateral aspect. **129,** Paramere of aedeagus, external aspect. **130,** Spermatheca, outline showing long, convoluted spermetheecal duct. **131,** Spermatheca, detail of basal bulb. (Scale line = 0.1 mm.)

microsculpture; reticulate microsculpture moderately developed to obsolete on abdomen, abdomen slightly shining, with characteristics of the genus.

Male Secondary Sexual Characteristics.—As in Figures 125, 126, 127.

Aedeagus.—As in Figures 128, 129.

Spermatheca.—As in Figures 130, 131.

Type.—Holotype, male, with labels as follows: "USA: Arizona, Coronado National Forest, Chiricahua Mountains, Rustler Park, 16 July 1976, J. S. Ashe, ex polypore, coll. no. 245," "HOLOTYPE, *Hongophila arizonica* Ashe, desig. J. S. Ashe, 1991." Deposited in the Snow Entomological Museum, University of Kansas, Lawrence, Kansas.

Paratypes.—97. ARIZONA: 2 (on microslides), Apache Co., Apache National Forest, Big Lake, 3-VIII-1976, J. S. Ashe, ex polypore on conifer log (SEM); 17, type locality, 27-VII-1983, J. S. Ashe, ex *Hirchioporus abietinus* (1 pinned, 3 on microslides), ex *Fomitopsis pinicola* (2), ex *Armillariella* sp. on conifer stumps (1), ex *Xeromphalina campinella* (1) (FMNH, SEM); 2, Huachuca Mountains, Carr Canyon, 2150 m, 23-VII-1976, J. M. Campbell (CNC); 1, Huachua Mountains, Miller Canyon, 2190-2380 m, 4-VIII-1979, A. Smetana (CNC); 2, Coconino Co., Flagstaff, no date or collector (CAS); 4, Navajo Co., Sitgraves National Forest, 47.8 mi. E. Payson, hwy. 260, 6-VIII-1983, ex Cortinariaceae, J. S. Ashe (SEM, FMNH); 16 (4 on microslides), Pima Co., Coronado National Forest, Santa Catalina Mountains, Mt. Lemmon Ski Area, 2590 m, 21-VII-1983, ex *Fomitopsis pinicola* (FMNH, SEM); 1, same, ex *Fomitopsis cajanderi* (FMNH); 4, same, ex *Hirchioporus abietinus* (FMNH, SEM), 4 (2 on microslides), same, ex *Flammulina velutipes* (FMNH); 16 (3 on microslides), same locality, 22-VII-1983, ex *Fomitopsis pinicola* (FMNH, SEM); 1, same localilty and date, ex *Fomes fomentarius* (FMNH); 5, same locality, 24-VII-1983, ex *Fomitopsis pinicola* (FMNH, SEM); 9, same locality and date, ex *Hirchioporus abietinus* (FMNH, SEM); 3, same localilty and date, ex *Pleurotus* sp. (FMNH); 2, same locality and date, ex leathery polypore on aspen log (FMNH); 1, same locality, 25-VII-1983, ex crustose polypore on aspen log (FMNH). NEW MEXICO: 1, state label only (CAS); 2, Lincoln Co., Cibola National Forest, S. slope Gallinas Peak, Red Cloud Campground, 3-VIII-1983, J. S. Ashe, ex *Sparassis radicata* (FMNH); 15 (6 on microslides), Lincoln Co., Lincoln National Forest, White Mountains, 3.2 mi. W. Alta, rd. 532, 2-VIII-1983, J. S. Ashe, ex *Ganoderma tsugae* (FMNH, SEM); 1, same except ex rotting *Paxillus* (?) (FMNH); 1, Otero Co., Cloudcroft, 8-VII-1903, Knaus (CAS); 1, San Miguel Co., Povenis, no date or collector (CAS); 3 (1 on microslide), Socorro Co., Cibola National Forest, San Mateo Mountains, 15.1 mi. S. hwy. 60 on 62, 1-VIII-1983, J. S. Ashe, ex *Clavaria* sp. (FMNH, SEM).

Distribution.—Mountain systems of the southwestern United States. Known from the Chiricahua, Huachuca, Santa Catalina Mountains, as well as the Flagstaff area, in Arizona, and the Gallinas Peak, White, San Mateo and Sacramento Mountains in New Mexico.

Bionomics.—Adults are primarily associated with polypores of the genera *Formitopsis, Fomes, Ganoderma,* and *Hirchioporus.* However, they have also been collected on ligniferous gilled mushrooms of the genera *Pleurotus, Flammulina, Xeromphalina,* and *Armillariella,* and the coral mushroom *Clavaria.* Adults have been collected only in July and August. Larvae have not been collected.

Discussion.—*Hongophila arizonica* is the only bolitocharine known to occur in the southwestern United States. This unique range as well as the distinctive color pattern and sexual features of adults are sufficient to distinguish this from all other North American species. However, two undescribed species of *Hongophila* from Mexico can be distinguished from *H. arizonica* primarily by aedeagal features.

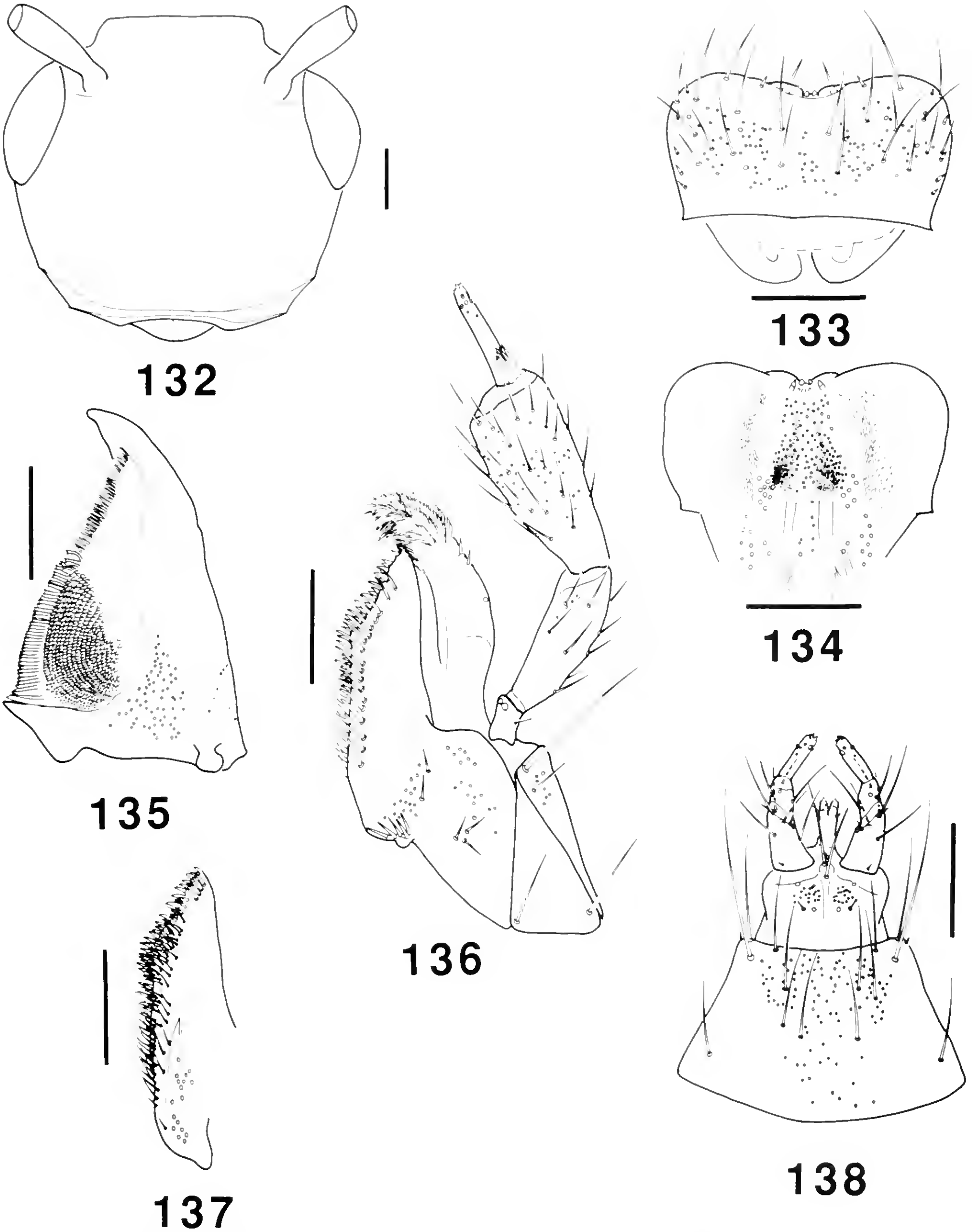
Neotobia Ashe, new genus
(Figs. 132-146)

Type species *Neotobia alberta* Ashe.

Diagnosis.—Member of *Neotobia* may be recognized by the combination of: eyes moderately large, length 1.2-1.3 times length of temples; head not at all narrowed behind the eyes, neck absent (Figs. 132); at least some antennomeres 5 to 10 elongate; pronotum moderately transverse, 1.35-1.4 times as wide as long, not noticeably narrower at base than base of elytra; hypomeron inflexed to near horizontal plane basally and deflexed more vertically anteriorly, anterior half moderately visible in lateral aspect; mesocoxal cavities moderately separated by intercoxal processes (Fig. 139), mesosternal processes moderately broad, acutely rounded apically; terga III-V (VI slightly) with moderately deep transverse basal impressions; sterna III-V with very faint transverse basal impressions; male sternum VI without medial lobate projection on posterior margin; male sternum VII (Fig. 141) with broad band of numerous sensory pores basally, without concentration of setose pores medially; triangular projection of male sternum VIII (Fig. 141) with asetose posterior margin; median lobe of aedeagus (Fig. 146) with apical process bifid, slender, without sclerotized plates on internal sac, flagellum tubular. As above (see diagnosis of *Hongophila*), members of *Neotobia* are difficult to confidently separate from *Hongophila* without examination of male secondary sexual and aedeagal characteristics.

Description.—Lengths of adults of known species 3.0-4.2 mm. Body somewhat robust, linear, parallel-sided, rather convex in cross section. Surface sculpture markedly reticulate throughout, surface not shiny. Body microsetae fine, dense, more or less uniformly distributed; punctures small, dense, uniformly distributed. Macrosetae inconspicuous.

Head (Fig. 132).—Broad, transverse, slightly less broad than apex of pronotum. Head not narrowed behind eyes, neck absent. Integumental microsculpture markedly reticulate. Punctures very small, round, densely distributed. Microsetae directed medially and anteriorly. Eyes mod-



Figs. 132–138. *Neotobia alberta* n. sp. **132,** Head, dorsal aspect. **133,** Labrum, dorsal aspect. **134,** Labrum, epipharyngeal aspect. **135,** Mandible, ventral aspect. **136,** Maxilla, ventral aspect. **137,** Lacinia of maxilla, dorsal aspect. **138,** Labium, ventral aspect. (Scale line = 0.1 mm.)

erately large, length 1.2–1.3 times as long as temples. Infraorbital carina markedly developed, complete. Antenna elongate, very slightly incrassate toward apex; article 4 slightly elongate, similar to 1 to 3 in sculpture and setation; article 5 elongate; article 10 slightly elongate or more or less quadrate; antennal articles 5 to 10 about equal in relative lengths in known species.

Mouthparts.—Labrum (Figs. 133, 134) with epipharyngeal region with medial pores small, scattered, not numerous, evenly dispersed in longitudinal sensory field. Mandibles (Fig. 135) with abcondylar molar patch of denticles large, denticles very small, densely arranged. Maxilla (Figs. 136, 137) with teeth in apical 0.25 of lacinia arranged in a single row (Fig. 137); apex of galea with 10 to 12 rows of small, unmodified (setose) setae. Labium (Fig. 138) typical of subtribe; ligula with pair of sensory setae large; 2 medial setae of prementum present, arranged one directly behind the other, insertions moderately separated; medial pseudopore field narrow, without pseudopores.

Thorax.—Pronotum moderately broad, transverse, 1.35–1.4 times as wide as long, convex in dorsal outline, almost as wide at base as base of elytra; postero-lateral angles slightly angulate but not acutely pointed; base not bisinuate; punctures small, round, numerous; microsetae fine, densely and uniformly distributed; integumental microsculpture markedly reticulate. Elytra with postero-lateral angles moderately sinuate; punctures small, densely distributed, broadly lunulate in form; microsetae fine, densely and uniformly distributed. Wings each with moderately large flabellum with 6 to 8 setose lobes (Fig. 140). Hypomeron inflexed posteriorly and deflexed more vertically anteriorly, broadly visible in lateral aspect anteriorly; anterior line of hypomeron contacting marginal line of pronotum very near antero-lateral angles of pronotum. Mesosternal medial carina distinct, present only in anterior 0.2–0.25 of mesosternum (Fig. 139). Mesocoxal cavities moderately separated by meso- and metasternal processes (Fig. 139); relative lengths of mesosternal : isthmus : metasternal processes of known species 6 : 1 : 3; apex of mesosternal process obtusely pointed; apex of metasternal process broadly rounded. Hind tarsomere I about as long as II and III together.

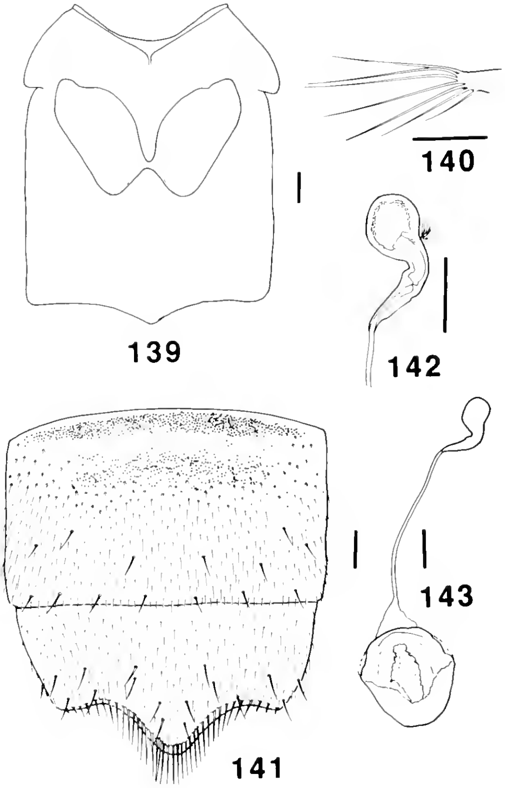
Abdomen.—More or less robust and parallel-sided. Terga III–V (VI slightly) with moderately deep transverse basal impressions; punctures very small, numerous, densely distributed; microsetae on basal terga directed posteriorly; macrosetae inconspicuous. Sterna III–V with very faint transverse basal impressions.

Secondary Sexual Characteristics.—Males: elytra without knob, tubercle or carina near suture, posterior 0.3 of sutural area of each slightly deflexed dorsally in some; tergum VII (Fig. 144) with large median tubercle; tergum VIII (Fig. 144) broadly and distinctly emarginate posteriorly, with 4 to 5 moderately developed denticles on each side of midline in emargination; dorsum of tergum VIII with small median tubercle; sternum VI without small medial lobe on posterior margin; sternum VII (Fig. 141) with broad band of sensory pores basally (visible in microslide preparations), without medial concentration of setose glandular pores, sternum VIII (Fig. 141) with prominent posterior triangular projection, projection with asetose posterior margin.

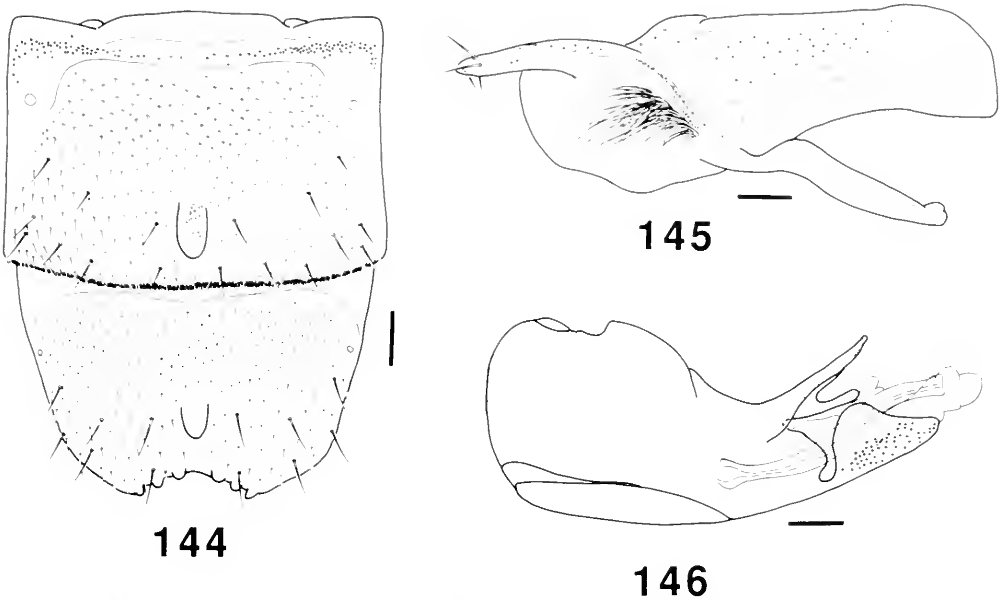
Aedeagus —Paramere (Fig. 145) with apical lobe of paramerite moderate in length, length about 0.5–0.6 times as long as paramerite; setae 1–4 of apical lobe short, clustered near apex of lobe. Aedeagus (Fig. 146) with apical lobe bifid; internal sac without sclerotized internal plates; flagellum long, tubular.

Spermatheca (Fig. 143).—Basal bulb simple, apex rounded; neck bent at angle of about 30°; spermathecal tube membranous, straight. Vaginal sclerotization well developed, present as complete circle of sclerotized cuticle.

Discussion.—The genus *Neotobia* is known from



Figs. 139–143. *Neotobia alberta* n. sp. **139,** Meso-metasternum. **140,** Flabellum of wing. **141,** Male, sterna VII–VIII; **142.** Female, spermatheca, detail of basal bulb. **143,** Female, spermatheca outline showing spermathecal duct and vaginal sclerotization. (Scale line = 0.1 mm.)



Figs. 144–146. *Neotobia alberta* n. sp. **144,** Male, terga VII–VIII. **145,** Male, paramere of aedeagus, external aspect. **146,** Male, median lobe of aedeagus, lateral aspect. (Scale line = 0.1 mm.)

only a single newly described species (*N. alberta* n. sp., see below) which occurs in the northern regions of North America from the Canadian Rockies eastward.

Phylogenetically, *Neotobia* appears to be most closely related to *Phymatura,* though members of *Neotobia* are quite different from those of *Phymatura* in general body form and aedeagal structures.

Members of *Neotobia* are superficially similar to those of *Hongophila.* This similarity is primarily due to retention of a similar array of plesiotypic characters in both genera. They share few derived features and do not appear to be closely related.

Neotobia alberta Ashe, new species

(Figs. 132–146)

Description.—Length 3.0–4.2 mm. Body color light reddish brown with head, pronotum, mesometasternum and abdominal segments VI–VII darker, black, piceus or dark brown. Elytra uniformly light reddish brown. Legs, antennae and mouthparts light brown. Body covered with moderately dense pile of fine hairs; punctation very fine, moderately dense; with moderate to distinct reticulate microsculpture throughout, integuments not markedly shining. With characteristics of the genus.

Male Secondary Sexual Characteristics.—As in Figures 141, 144.

Aedeagus.—As in Figures 145, 146.

Spermatheca.—As in Figure 143.

Type.—Holotype, male, with labels as follows: "CANADA: Alberta, George Lake, 53°57′N 114°06′W, 1 June 1980, J. S. Ashe, ex *Polystictus,*" "HOLOTYPE, *Neotobia alberta* Ashe, desig. J. S. Ashe, 1991." Deposited in the Snow Entomological Museum, University of Kansas, Lawrence, Kansas.

Paratypes.—26. 1, same data as holotype (SEM); 5, CANADA, Alberta, George Lake, 53°57′N 114°06′W, 22 August, 1979, J. S. Ashe (SEM, dissected on microslides); 2, same except 9 August 1980 (SEM, on microslides); 5, Alberta, Edmonton, south bank North Saskatchewan River, 12 July 1981, J. S. Ashe, ex *Polyporus picipes* (SEM, 1 pinned, 4 on microslides); 1, Alberta, Elk Island National Park, 7-IX-1980, J. S. Ashe, ex polypore mushroom (SEM, on microslide); 2, E. Ontario, 1887 (CNC); 1, Manitoba, Winnipeg, Hanham (CAS); 1, Montreal (CAS). USA. 1, New Hampshire, Grafton Co., Franconia Notch, 6-VIII-1951, mushrooms, C. Seevers (FMNH); 1, "ME" (=Maine?), Frost (CAS); 7, Wisconsin, Ashland Co., Chequamegon National Forest, 15 mi. W. Mellen, 19-26-VII 1947, C. F. Seevers, ex mushrooms (FMNH, SEM).

Distribution.—Northern North America from the Rockies eastward. Known from Alberta, Manitoba, Ontario and Quebec in Canada, and Maine (?), New Hampshire, and Wisconsin in the United States.

Bionomics.—Adults are primarily found on polypore mushrooms, especially members of the genera *Polyporus* and *Coriolus* (Ashe, unpubl. data) from July through September. Larvae have been found in association with adults on *Polyporus picipes* in July (Ashe, unpubl. data).

Discussion.—As the only known species in the genus *Neotobia*, *N. alberta* can be identified by use of the generic key. In addition, among North American bolitocharines, specimens of *N. alberta* are very easily recognized by their relatively large size, northern distribution, distinctive color pattern (see above), and unique aedeagus and spermatheca.

Austrasilida Ashe, new genus
(Figs. 147–159)

Type species *Austrasilida zealandica* (Cameron) (from *Sternotropa zealandica* Cameron, 1947, p. 726–727).

Diagnosis.—Members of *Austrasilida* can be recognized by: small size, adult length 1.5–2.0 mm; eye length about equal to length of temples; head not at all narrowed behind eyes, neck absent (Fig. 147); antenna short, incrassate, with antennomeres 5 to 10 moderately to strongly transverse; maxillary lacinia with large patch of spines forming a large brush apically (Figs. 150, 151); ligula of labium short and bifid to base (Fig. 153); pronotum strongly transverse, 1.5 times as wide as long, as wide at base as base of elytra; hypomeron inflexed into horizontal plane throughout, only very narrowly visible in lateral aspect; mesosternum with medial longitudinal carina complete to apex of mesosternal process; mesocoxal cavities broadly separated by intercoxal processes (Fig. 154), mesosternal process broad and broadly rounded apically; hind tarsomere I only slightly longer than II; abdominal terga III–IV with at most only slight transverse basal impressions; sterna not basally impressed; male sternum VI without medial lobate projection on posterior margin; male sternum VII (Fig. 155) with broad band of sensory pores basally, without medial concentration of setose sensory pores; triangular projection of posterior margin of sternum VIII (Fig. 155) with very slight asetose margin at apex; median lobe of aedeagus (Fig. 158) with apical process large, tentlike, internal sac without sclerotized plates, flagellum tapered to a point apically. Known only from New Zealand.

Description.—Length of adults 1.5–2.0 mm. Body relatively broad, somewhat robust in build, slightly narrowed anteriorly and posteriorly. Surface sculpture absent, integument strongly shiny. Body microsetae fine, rather stiff, moderately densely and uniformly distributed. Macrosetae inconspicuous.

Head (Fig. 147).—Broad, transverse, almost as wide as apex of pronotum. Head not narrowed behind eyes, neck absent. Integumental sculpture absent, surface shiny. Punctures moderate sized, round; microsetae rather stiff, directed mostly anteriorly. Eye length about equal to length of temple. Infraorbital carina markedly developed, complete. Antenna short, distinctly incrassate toward apex; article 4 transverse, similar to articles 1 to 3 in sculpture and setation; article 5 transverse; article 10 very transverse; articles 5 to 10 decreasing in relative lengths apically.

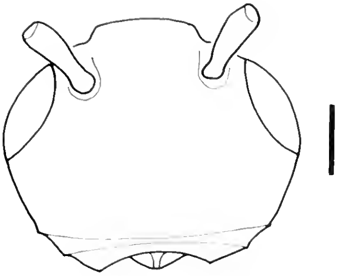
Mouthparts.—Labrum (Figs. 148, 149) with epipharyngeal area with medial pores very minute antero-medially and mostly absent elsewhere in median longitudinal sensory field. Mandibles (Fig. 152) with abcondylar molar patch of denticles large, denticles large, numerous, dense. Maxilla (Figs. 150, 151) with teeth on apical 0.25 arranged into a dense, compact patch of numerous teeth (Fig. 151); apex of galea with 5 to 6 rows of unmodified (setose) setae. Labium (Fig. 153) different from those of other members of subtribe; ligula short, divided almost to base, without pair of sensory spines; two medial setae present, arranged transversely (one beside the other), bases widely separated; medial pseudopore field broad, with 5 to 6 pseudopores.

Thorax.—Pronotum broad, transverse, about 1.5 times as wide as long, moderately convex in dorsal outline; almost as wide at base as base of elytra; postero-lateral angles moderately angulate, not sharply pointed; slightly bisinuate basally; punctures moderately large, close, densely arranged; microsetae dense, stiff; integument without microsculpture. Elytra with postero-lateral angles moderately sinuate; punctures moderately large, round, densely distributed; microsetae dense, stiff. Wings without apparent flabellum, without setose lobes. Hypomeron inflexed into horizontal plane, only very narrowly visible in lateral aspect. Mesosternal medial carina very prominent (Fig. 154), complete to apex of process. Mesocoxal cavities widely separated by meso- and metasternal processes (Fig. 154); relative lengths mesosternal : isthmus : metasternal processes 3.5 : 0 : 2 in known species; apex of mesosternal process rounded; apex of metasternal process broadly rounded. Tarsomere I of hind tarsus short, only about 1.1 times as long as II.

Abdomen.—Slightly tapered from base to obtusely pointed apex; terga III–IV with very slight transverse basal impressions; punctures small, densely distributed; microsetae very fine, densely distributed, oriented obliquely toward midline on first visible tergum; macrosetae present but not large. Sterna III–V without transverse basal impressions.

Secondary Sexual Characteristics.—Males: elytra without carina, knob or tubercle near suture; tergum VII (Fig. 156) with conspicuous spine on each side of midline or spines inconspicuous or absent; tergum VIII (Fig. 156) deeply emarginate posteriorly, with markedly developed spinose processes at each lateral edge of emargination, with 3 to 4 moderately strong spinose processes on each side of midline in emargination; dorsum of tergum VIII without modifications; sternum VI without medial lobe on posterior margin; sternum VII (Fig. 155) with broad band of sensory pores basally (visible in microslide preparations), without concentration of setose gladular pores medially; sternum VIII (Fig. 155) with very slight and broad triangular projection, with asetose posterior margin only at apex of projection.

Aedeagus.—Paramere (Fig. 157) with apical



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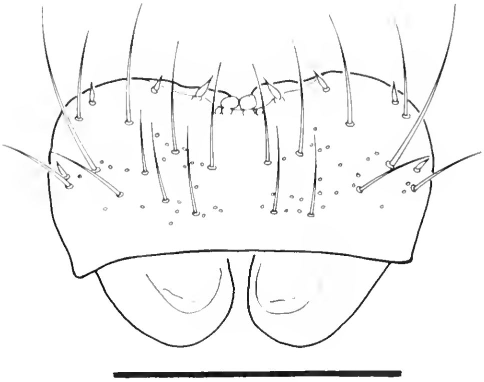

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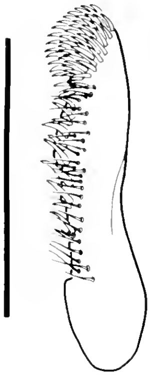

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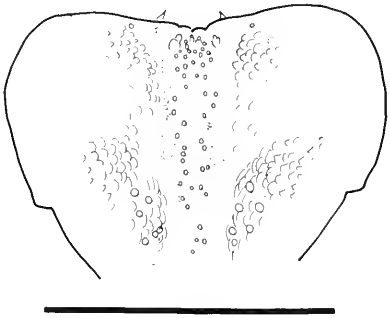

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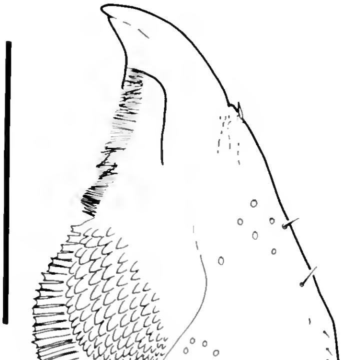

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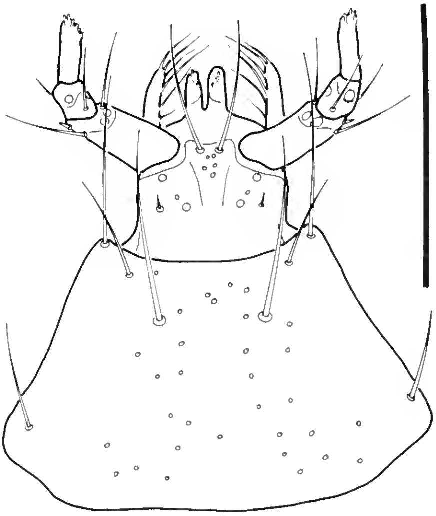

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Figs. 147–153. *Austrasilida zealandica* (Cameron). **147,** Head, dorsal aspect. **148,** Labrum, dorsal aspect. **149,** Labrum, epipharyngeal aspect. **150,** Maxilla, ventral aspect. **151,** Lacinia of maxilla, dorsal aspect. **152,** Mandible, ventral aspect. **153,** Labium, ventral aspect. (Scale line = 0.1 mm.)

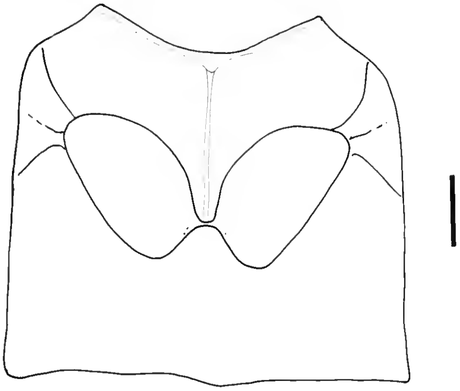
lobe of paramerite moderately long, about 0.5 times as long as paramerite; setae 1 to 4 of apical process long, clustered near apex. Aedeagus (Fig. 158) with apical lobe large, tentlike; internal sac without internal sclerotized plates; flagellum long, tubular but tapered to point apically.

Spermatheca (Fig. 159).—Basal bulb simple, globular, apex rounded; neck bent about 60° from straight; spermathecal tube membranous, straight, very long; vaginal sclerotization very slight to absent.

Discussion.—Cameron (1947) described *Sternotropa zealandica* without providing any explanation about why he placed it in *Sternotropa*. It is clearly not a member of *Sternotropa*, a genus in the subtribe Gyrophaenina. Furthermore, it is not a member of any other monophyletic bolitocharine genus. Therefore, *S. zealandica* requires a new generic assignment.

As noted elsewhere (see "Choice of Taxa") inclusion of *Austrasilida zealandica* in the subtribe Bolitocharina is problematic. If included, it appears to be most closely related to *Pseudatheta* (Fig. 2). However, its position is not strongly supported by synapomorphies (see "Phylogenetic Analysis"). Also, the phylogenetic structure of the cladogram is substantially affected if *Austrasilida* is not included in the analysis.

Austrasilida could be a very basal member of the subtribe Gyrophaenina. The structure of the



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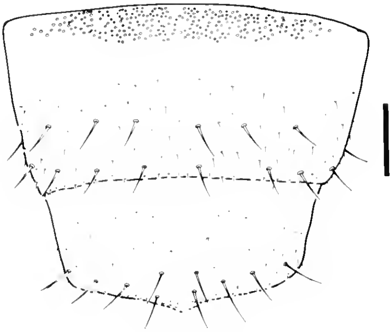

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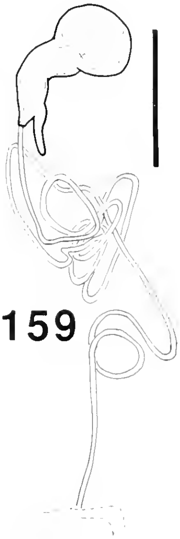

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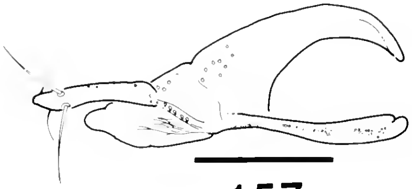

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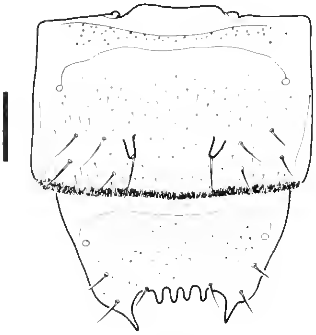

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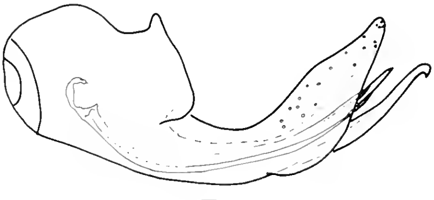

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Figs. 154–159. *Austrasilida zealandica* (Cameron). **154,** Meso-metasternum. **155,** Male, sterna VII–VIII. **156,** Male, terga VII–VIII. **157,** Male, paramere of aedeagus, external aspect. **158,** Male, median lobe of aedeagus, lateral aspect. **159,** Female, spermatheca. (Scale line = 0.1 mm.)

"spore brush" on the lacinia of the maxilla and the lateral flange on the spermatheca are apomorphies shared with all gyrophaenines. However, structure of the ligula of the labium and the presence of two medial setae on the prementum are inconsistent with this interpretation. Further resolution of the phylogenetic position of *Austrasilida* must await additional study.

ACKNOWLEDGMENTS

I thank the following institutions and individuals for their contributions to this project. Numerous museums and individuals, as listed in the Methods section of the paper, loaned specimens which were critical to this study. Alfred F. Newton, Jr. and Margaret Thayer generously made available to me, and allowed me to cite, their excellent manuscript on family-group names in the Staphyliniformia. They have also provided me with numerous courtesies and a place to stay during my return visits to the Field Museum. At various times during this project Thomas Mooney and Philip Parrillo provided outstanding technical support. The habitus illustrations were drawn by Marlene H. Werner while I was an employee of the Field Museum. Joetta Weaver typed the numerous drafts of the manuscript. This research was supported by National Science Foundation Research Grant BSR-8415660.

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APPENDIX 1. TAXA OF THE TRIBE HOMALOTINI (=BOLITOCHARINI) AND "RELATED" GROUPS EXAMINED

This list includes homalotine and related taxa which were examined to determine character distributions for outgroup analysis, and were critical in evaluating the monophyly of the subtribe Bolitocharina as presented here. Taxa included here are either traditionally included in the Homalotini or have at one time or another been included in the Homalotini or subtribe Bolitocharina. The monophyly and correct placement of these higher taxa and their included genera and species are outside the range of this study and have not been examined in any comprehensive way. Therefore, the arrangement of taxa in this list should not be taken to be an adequate classification scheme. Representatives of all taxa on this list have been fully dissected, mounted on microscope slides and examined using compound optics.

The letters following each species name indicate whether primary type material (T, holotype or syntype) or other identified specimens (S) were examined. A brief summary of the distribution of each species is given.

TRIBE HOMALOTINI

Subtribe Bolitocharina
  (see Appendix 2)
Subtribe Gyrophaenina
  (see Ashe, 1984)
Subtribe Homalotina
  Anomognathus cribrum Fauv., S, New Guinea
  A. cuspidatus Er., S, Europe
  Homalota borgeoni Bernh., S, Africa
  H. flavomaculata Bernh., S, Africa
  H. fuscipennis Cam., S, S.E. Asia
  H. intrusa Er., S, South America
  H. plana Gyll., S, Europe
  H. variventris Kr., S, Ceylon
  Thecturota sp., S, North America
Subtribe Leptusina
  Euryusa brachelytra Kiesenw., S, Europe
  E. castanoptera Kr., S, Europe
  E. optabilis Heer, S, Europe
  Leptusa alpicola Brancsik, S, Europe
  L. angusta Aubé, S, Europe
  L. carpathica Weise, S, Europe
  L. eximia Kr., S, Europe
  L. flavicornis Brancsik, S, Europe
  L. granulicauda Eppels., S, Europe
  L. hopffgarteni Eppels., S, Europe
  L. lombarda Bernh., S, Europe
  L. piceata Muls. & Rey, S, Europe
  L. oreophila Penecke, S, Europe
  L. reitteri Eppels., S, Europe
  L. ruficollis Er., S, Europe
  L. secreta Bernh., S, Europe
  L. tricolor Scriba, S, Europe
  Leptusa sp. 1, S, North America
  Leptusa sp. 2, S, North America
  Leptusa sp. 3, S, North America
  Leptusa sp. 4, S, North America
  Paraleptusa graeca Bernh., S, Europe
Subtribe Silusina
  Diestota angustula Casey, S, USA
  D. brasiliana Bernh., S, Brazil
  D. laticornis Sharp, S, Central America
  D. luederweldti Bernh., S, Brazil
  D. obsoleta Er., S, Central America
  D. rufipennis Casey, S, North America
  D. testacea Kr., S, S.E. Asia
  Elachistarthron ambiguum Notman, S, North America
  Neosilusa ceylonica Kr., S, S.E. Asia
  Silusa californica Casey, S, W. North America
  S. opaca Fenyes, S, W. North America
  S. rubra Er., S, Europe
  Silusa sp., S, USA
  Tachiona deplanata Sharp, T,S, Mexico
  T. monteverdensis Ashe, T,S, Costa Rica
  T. latipennis Ashe, T,S, Panama
  Toxoxelia parvipennis Bernh.
Unplaced Homalotini
  Calodera hierosolymitana Saulcy, S, Europe
  Coenonica puncticollis Kr., S, Ceylon
  Gansia varicornis Sharp, S, South America
  Heterota plumbea Waterhouse, S, Europe
  Ophioglossa araucana Fauv., S, South America
  O. cava Sharp, S, South America
  Paracyphea asperata Bernh., S, Seychelles
  Pseudoplacusa rufiventris Cam., S, S.E. Asia
  Trichiusa sp., S, North America
Tribe Autaliini
  Autalia impressa Oliv., S, Europe
  A. rivularis Grav., S, USA, Europe
  A. puncticollis Sharp, S, Europe
  Autalia n. sp., S, Costa Rica
Tribe Philotermini
  Philotermes pilosus Kr., S, North America
Tribe Phytosini
  Actocharis marina Fauv., S, Europe
  Bryobiota bicolor Casey, S, W. North America
  Diaulota densissima Casey, S, W. North America
  D. fulviventris Casey, S, W. North America
  Liparocephalus brevipennis Mäklin, S, W. North America
  Phytosus balticus Kr., S, Europe
  P. spinifer Curtis, S, Europe
  Thinusa maritima Casey, S, W. North America
Tribe Placusini (see Ashe, 1991)
  Placusa atrata Sahlb., S, Europe
  P. complanata Er., S, Europe
  P. despecta Er., S, USA
  P. spinigera Kr., S, Ceylon
  P. tachyporoides Waltl, S, Europe
  P. tacomae Casey, S, W. USA
  P. trispinosa Bernh., S, Africa
  Euvira cubana Bierig, T,S, Cuba
  E. debilis Sharp, S, Central America
  E. diazbatresi Ashe & Kistner, T,S, Mexico
  E. godmani Sharp, S, Central America
  E. nigra Sharp, S, Central America

APPENDIX 2. TAXA OF THE SUBTRIBE BOLITOCHARINA EXAMINED

Taxa included in the phylogenetic analysis are indicated by an asterisk (*) following the name. Taxa examined which represent synonyms are indicated by placing them in parenthesis below the valid name for the taxon. Specimens of most taxa included on this list were fully dissected and examined on microslides. At least genitalia of all were examined with compound optics.

The letters following each species name indicate whether primary type material (T, holotype or syntype) or other identified specimens (S) respectively were examined. A brief summary of the distribution of each species is given. In this table, genera are listed in the sequence of the descriptive section, and species are ordered alphabetically under each genus.

Bolitochara Mannerheim
  (*Ditropalia* Casey)
    B. bella Maerk.* (from *Ditropalia*), S, Europe
    B. humeralis (Lucas) (from *Ditropalia*), S, N. Africa, Europe
    B. lauferi Bernh. (from *Ditropalia*), S, N. Africa
    B. lucida Grav.*, S, Europe, N. Africa
    B. lunulata Payk.*, S, Europe
    B. mulsanti Sharp* (from *Ditropalia*), S, Europe
    B. obliqua Er.* (from *Ditropalia*), S, Europe
    B. reyi Sharp, S, Europe
    B. schusteri Bernh. (from *Ditropalia*), S, Tunis
    B. varia Erichson (from *Ditropalia*), S, S. Europe, N. Africa
Phymatura Sahlberg
  (*Venusa* Casey)
    P. aspericeps Cam., S, India
    P. blanchardi (Csy.)* (from *Venusa*), T,S, E. North America
      (*Bolitochara blanchardi* Casey), T,S, E. North America
      (*Venusa laetula* Casey), T, E. North America
      (*Venusa picta* Casey), T, E. North America
    P. brevicollis Kr.*, S, Europe
    P. intermedia Cam., S, India
    P. juncunda Cam.*, S, India
    P. picta Cam.*, S, India
Pleurotobia Casey
  (*Phymaturosilusa* Roubal)
    P. magnifica (Roubal)* (from *Phymaturosilusa*), S, Central Europe
    P. trimaculata (Er.)* (from *Bolitochara*), S, E. North America
      (*P. suturalis* Casey), T, E. North America
      (*P. texana* Casey), T, E. North America
      (*P. tristigma* Casey), T, E. North America
    P. n. sp. A*, S, Central North America
    Pseudatheta Cameron
    P. elegans Cam.*, S, S.E. Asia
Silusida Casey
    S. marginella Casey*, T,S, E. North America
      (*S. nanella* Casey ?), specimens not found
Stictalia Casey
    S. arcuata Casey, T, W. North America
    S. aspera Casey, T, W. North America
    S. bakeri Casey*, T,S, W. North America
    S. brevicornis Casey*, T,S, W. North America
    S. carlottae Casey, T,S, W. North America
    S. californica Casey*, T,S, W. North America
    S. collaris Casey, T, W. North America
    S. densicollis Casey, T, W. North America
    S. laxicornis Casey, T, W. North America
    S. minor Casey*, T,S, W. North America
    S. nigrina Casey*, T,S, W. North America
    S. notata (Mäklin) (from *Bolitochara*), S, W. North America
    S. obsolescens Casey, T,S, W. North America
    S. rugipennis Casey*, T,S, W. North America
    S. unicolor (Fenyes) (from *Bolitochara*), T,S, W. North America
    S. n. sp. 1, S, W. North America
    S. n. sp. 2, S, W. North America
    S. n. sp. 3*, S, W. North America
    S. n. sp. 4, S, W. North America
    S. n. sp. 5, S, W. North America
    S. n. sp. 6*, S, W. North America
Hongophila Ashe (new genus)
    H. arizonica Ashe* (new species), T,S, S.W. USA
Neotobia Ashe (new genus)
    N. alberta Ashe* (new species), T,S, N. North America
Austrasilida Ashe (new genus)
    A. zealandica (Cam.)* (from *Sternotropa*), S, New Zealand

APPENDIX 3. STATES AND ADDITIVE BINARY CODING OF CHARACTERS USED IN CLADISTIC ANALYSIS OF TAXA OF SUBTRIBE BOLITOCHARINA

Character	States	Binary Coding
1. Head: shape		
	0. distinctly broader than long (width: length 1.1 or greater)	0000
	1. more or less oval, slightly broader than long (width:length ratio >1.0<1.1)	0001
	2. more or less quadrate (width:length ratio about 1.0)	0011
	3. slightly elongate (width:length ratio <1.0>0.9)	0111
	4. distinctly elongate (width:length ratio 0.9 or less)	1111
2. Head: infraorbital carina		
	0. infraorbital carina strong to moderate, complete	0
	1. infraorbital carina absent except faintly near maxillary insertion	1
3. Head: neck		
	0. absent	00
	1. present, slightly developed (neck wider than 2/3 head width)	01
	2. present, distinct to very distinct (neck 2/3 to 1/2 head width)	11
4. Head: setation		
	0. setae directed medially in postero-lateral areas and anteriorly in midline and anterior portions of head	00
	1. most to all head setae directed anteriorly	10
	2. most to all head setae directed medially	01
5. Pronotum: width:length ratio		
	0. width:length ratio 1.4 or greater	00
	1. width:length ratio >1.2<1.4	01
	2. width:length ratio 1.2 or less	11
6. Pronotum: width relative to elytra width		
	0. almost as wide as base of elytra	0
	1. distinctly narrower than elytra	1
7. Pronotum: microsculpture		
	0. slightly to moderately reticulate	00
	1. obsoletely reticulate	01
	2. smooth and shiny, without microsculpture	11
8. Wing: number of setose projections on flabellum		
	0. 10-13	0000
	1. >4⩽8	0001
	2. ⩾3⩽4	0011

   3. >1<3 0111
   4. 1 or less 1111

9. First visible abdominal tergum: direction of setae
   0. all directed posteriorly 0
   1. some setae oblique or transverse 1
10. Mesosternum: medial carina
   0. medial carina strong, complete to apex of mesosternal process 00
   1. medial carina strong, but fading in apical 0.5-0.3 of mesosternum 01
   2. medial carina strong but present only on basal 0.2-0.3 of mesosternum 11
11. Intercoxal processes: degree of separation of middle coxae
   0. coxae narrowly separated (separation less than 0.15 total length meso- and metasternal processes) 00
   1. coxae moderately separated (separation >0.15<0.35 times combined length of processes) 01
   2. coxae widely separated (separation greater than 0.35 times combined length of processes) 11
12. Intercoxal processes: isthmus present or absent
   0. isthmus distinctly present (isthmus length greater than 0.1 times combined length of processes) 00
   1. isthmus slight (isthmus length 0.1 to 0.02 times combined length of processes) 01
   2. isthmus virtually to completely absent (processes in contact or separation not greater than 0.02 times combined length of processes) 11
13. Antenna: antennomere 4
   0. similar to antennomeres 5-10 00
   1. transitional in setation, microsculpture and general shape between antennomeres 1-3 and 5-10 01
   2. similar to antennomeres 1-3 11
14. Antenna: relative lengths of antennomeres 5-10
   0. antennomeres 5-10 distinctly decreasing in relative lengths apically 00
   1. antennomeres 5-10 more or less the same in relative lengths 01
   2. antennomeres 5-10 distinctly increasing in relative lengths apically 11
15. Mandibles: molar denticles
   0. denticles in molar region few to numerous, scattered, not densely arranged 0
   1. denticles in molar region very numerous, arranged densely in large patch 1
16. Maxillary lacinia: inner apical teeth
   0. one row of teeth on inner face of lacinia in apical 0.25-0.35 000
   1. inner face of apical 0.25 of lacinia with one row of teeth more basally and two irregular rows more apically 001
   2. inner face of lacinia with 3-6 rows of teeth in apical 0.25 with noticeably denser concentration of teeth near apex 011
   3. lacinia with 3-6 rows of teeth in apical 0.25 with very dense and large concentration of teeth near apex 111
17. Labium, ligula: pair of sensory spines
   0. pair of large sensory spines on ligula 00
   1. pair of sensory spines on ligula minute to small 01
   2. sensory spines absent from ligula 11
18. Labium: medial setae
   0. medial setae side by side, bases close to contiguous 0000
   1. medial setae side by side anterior to medial pseudopore field, bases distant 1000
   2. medial setae arranged one laterally behind the other 0001
   3. medial setae arranged one directly behind the other, bases close 0011
   4. medial setae arranged one directly behind the other, bases distant 0111
19. Labium: medial pseudopore field
   0. medial pseudopore field narrow, pseudopores present in linear array 00
   1. medial pseudopore field broad, pseudopores present in more or less rectangular array 10
   2. medial pseudopore field narrow, pseudopores absent 01
20. Male secondary sexual char.: elytra, sutural carina
   0. elytra suture not modified 00
   1. each elytron with small knob or tubercle near suture in posterior 0.5 01
   2. each elytron with distinct and strong carina near suture in posterior 0.5 11
21. Male secondary sexual char.: tergum VII
   0. small to moderate medial tubercle, without lateral scattered asperities 00000
   1. small to very small medial tubercle, with small to very small lateral asperities 00001
   2. without medial tubercle, with very faint scattered asperities 00011
   3. with short distinct medial carina 00100
   4. with very long prominent medial carina 10100
   5. with two to three oblique carinae on each side 01100
22. Male secondary sexual char.: tergum VIII
   0. small to very faint medial tubercle 00000
   1. a few minute, scattered asperities 00011
   2. no modifications 00001
   3. short, medial carina 00100
   4. prominent long medial carina 01100
   5. moderate to prominent medial carina with shorter flanking carinae or tubercles 10100
23. Male secondary sexual char.: tergum VIII, denticles in apical emargination
   0. emargination broad and deep, denticles moderate to robust 00
   1. emargination broad and shallow, denticles very small to faint 01
   2. emargination very shallow to indistinct, denticles virtually absent to absent 11
24. Male secondary sexual char.: sternum VI, lobate projection apico-medially
   0. small lobate projection absent 00
   1. lobate projection present, glabrous 01
   2. lobate projection present, setose 11
25. Male secondary sexual char.: sternum VII
   0. uniform broad band of asetose sensory pores present around base of sternum

VII, medial setose glandular concentration absent	00
1. band of asetose sensory pores around base of sternum VII broad, medial setose glandular concentration present but small	01
2. band of asetose sensory pores around base of sternum VII reduced, medial setose glandular concentration present, large	11
26. Male secondary sexual char.: sternum VIII, apical triangular lobe	
0. margin of lobe setose to edge	0
1. lobe with distinct asetose margin	1
27. Male genitalia: apical lobe of aedeagus	
0. apical lobe large, tentlike	0000
1. apical lobe slender and elongate	0001
2. apical lobe slender, rather foot-shaped in lateral aspect	0010
3. apical lobe slender, recurved	0110
4. apical lobe bifid	1000
28. Male genitalia: aedeagus, internal plates	
0. internal plates present, plates large, flattened	00
1. internal plates present, plates spinose and recurved	10
2. internal plates absent	01
29. Male genitalia: median lobe, flagellum	
0. moderate length, tubular	000
1. short, tubular	001
2. very long, tubular	010
3. moderate length, tapering to sharp apex	100
30. Female spermatheca: basal bulb shape	
0. basal bulb simple, base rounded	00
1. basal bulb elongate, base rounded	01
2. basal bulb simple, with a small knob at base	10
31. Female spermatheca: neck shape	
0. neck straight to very slightly bent	00
1. neck bent at >30° and <90°	01
2. neck bent at >90° angle	11
32. Female spermatheca: tube structure	
0. tube membranous	0
1. tube sclerotized	1
33. Female spermatheca: tube shape	
0. tube of moderate length, more or less straight	00
1. tube very long and irregularly convoluted	10
2. tube twisted into 1-3 regular loops	01
34. Female sexual char.: vaginal sclerotization	
0. vaginal sclerotization very light, absent or present as an inconspicuous arc	00
1. vaginal sclerotization moderate to slight, evident as approximately 0.5 circle of sclerotized area	01
2. vaginal sclerotization moderate to distinct, sclerotized ring complete or at least 0.75 complete	11

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The International Standard Serial Number of this publication is US ISSN 0022-8850.

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