A REVIEW OF THE GENERA OF CLEPTOPARASITIC BEES OF THE TRIBE ERICROCINI (HYMENOPTERA: ANTHOPHORIDAE)

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ABSTRACT. The genera comprising the New World bee tribe Ericrocini are reviewed. Each genus is separated by a key, is described, its included species-group names listed, and pertinent morphological features illustrated. Nine genera are recognized: *Mesoplia* (=*Melissa*) and its new subgenus *Eumelissa* (type species, *Melissa decorata* F. Smith), *Hopliphora* (=*Eurytis* = *Oxynedys* = *Cyphomelissa*), *Mesonychium* (=*Epiclopus*), *Ericrocis, Abromelissa* (new genus; type species, *Melissa lendliana* Friese), *Aglaomelissa* (new genus; type species, *Melissa duckei* Friese), *Ctenioschelus* (=*Melissoda*), *Mesocheira,* and *Acanthopus.*

A cladistic analysis of the Ericrocini is included.

Known hosts are listed in a table.

INTRODUCTION

The Ericrocini are a New World tribe of cleptoparasitic bees largely centered in the Amazonian Basin. So far as known, all hosts are within the related tribe Centridini. Despite their attractive appearance, these moderate- to large-sized bees have received scant attention from taxonomists, probably due largely to their rarity in collections.

HISTORICAL RESUME

The first ericrocine genus to be described was *Acanthopus,* proposed by Klug (1807) for a single South American species. Lepeletier and Serville (1825) described *Mesonychium* (monobasic) and *Mesocheira* (three species). *Ctenioschelus* was described by Romand (1840) for a single, bizarre species and in 1841 Lepeletier described *Melissoda* (later shown to be isogenotypic with *Ctenioschelus* through synonymy), *Mesoplia* and *Hopliphora.* Shuckard (1840) named *Ischnocera,* with no included species, but it has long been recognized as an obvious synonym of *Ctenioschelus.*

F. Smith (1854) added two new genera, *Eurytis* (monobasic), and *Melissa* (four species). All these genera were placed in his subfamily Denudatae, together with such genera as *Melecta, Thalestria,* and *Liogaster.* He recognized *Eurytis, Melissa* (=*Mesoplia*), *Mesocheira, Ctenioschelus* (=*Melissoda* = *Ischnocera*) and *Acanthopus.* The one Nearctic genus, *Ericrocis,* was described by Cresson (1887) for a single species.

Ashmead (1899) assigned these bees to the family Nomadidae, recognizing the genera *Ericrocis, Eurytis* (=*Hopliphora*), *Melissa, Mesocheira, Mesonychium,* and *Acanthopus* (=*Ctenioschelus*). A few years later, Schrottky (1902) produced his key to the Brazilian genera of Nomadidae, recognizing *Melissa, Eurytis, Mesocheira, Ctenioschelus,* and *Acanthopus,* to which he added two new genera: *Cyphomelissa* and *Oxynedes.*

For the next 40 years, Schrottky's generic concepts were more or less followed by Cockerell, Ducke, and Friese, the principal describers of Neotropical bees during that time. Generic limits were flexible and considerable confusion existed regarding the application of the names *Melissa, Mesonychium,* and *Mesoplia.* These three names were very inconsistently used, but in general *Melissa* was used to contain most species in preference to *Mesoplia,* and *Mesonychium* fell heir to those species which seemed not to be *Mesoplia.*

The Nearctic genus, *Ericrocis,* was included in the Melectinae by Linsley (1939) who noted, however, its uniqueness and commented that it is "perhaps . . . an offshoot from some group like *Epicharis,* which Grutte considers to be ancestral to *Acanthopus* and *Rathymus.*" As Linsley noted, Cockerell and Atkins (1902) had earlier emphasized the unusual features of *Ericrocis* and related genera, and suggested that a separate subfamily might be appropriate for these bees.

When Michener (1944) reorganized the higher classification of the bees, he placed *Ericrocis,* and such similar genera as *Acanthopus, Mesocheira,* and *Ctenioschelus,* in the tribe Ericrocini, near the Centridini. He clearly set forth the dif-

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ferences between the Ericrocini and such cleptoparasitoid groups as Melectini, Epeolini, and Nomadini.

The last author to deal with the group, more or less as a whole, was Moure (1946). The geographic scope of this work was limited to Brazil, but since nearly all the genera occur there, the treatment was nearly complete. Moure recognized, and separated in a key, *Ctenioschelus, Mesonychium, Mesoplia, Hopliphora, Cyphomelissa, Acanthopus,* and *Oxynedis* (a misspelling of *Oxynedys*). Under Moure's concepts, *Mesoplia* included *Melissa,* and *Epiclopus* fell into *Mesonychium.*

TERMINOLOGY

In general, the morphological terminology follows that established by Michener (1944), Michener and Fraser (1978), and Winston (1979). A few terms used here necessitate explanation. The *interantennal distance* is the shortest distance between the inner margins of the antennal sockets. The *antennal socket diameter* is the maximum transverse distance across the antennal socket, from inner margin to outer margin. The *antennocular distance* is the shortest distance between the outer margin of the antennal socket and the inner eye margin.

As in most bees, the short anterior face of the mesepisternum and the much longer lateral face meet in a curved surface. Sometimes, this juncture is marked by a raised carina, the *anterior mesepisternal carina* (amc, Fig. 70). In most ericrocines that possess this carina, it is thin, translucent, and lamelliform. Ventrally, the anterior mesepisternal carina usually is confluent with a carina that bounds the posterior portion of the procoxal cavity; this is the *acetabular carina* (acc, Fig. 70) (Bohart and Menke, 1976). In a few ericrocines (e.g., *Acanthopus*), there is a low, rounded, shiny ridge which begins in front of the metacoxa and extends for a short distance onto the lateral face of the mesepisternum, the *sternopleural ridge* (spr, Fig. 70). In most genera, the mesepisternum slopes abruptly toward the coxal cavity, but there is no definite shiny ridge. The *supraspiracular ridge* originates dorsolaterally on the propodeum and extends posteriorly, above the propodeal spiracle. The ridge is said to be *strong* if it terminates in a blunt tooth or projection, *weak* if it becomes evanescent apicad.

Male genital structures are somewhat confusing. The gonostylus is, in dorsal view, short, broad and more or less flattened. In some genera the gonostylus is simply a very broad, somewhat flattened structure, bearing diagnostic gonostylar setae, but with little, if any, dorsal lobe. Dorsal lobes are present in such genera as *Mesoplia, Abromelissa,* and *Acanthopus;* they may be present or absent in *Hopliphora.* When present, the dorsal lobe is usually narrow, thin, lightly sclerotized and always setose (Fig. 22). A second, much shorter and broader, lobe may also be present immediately above the base of the longer lobe.

In some genera there is a distinctive, heavily sclerotized plate along the inner, basal portion of the gonostylus. No similar structure is known within the Centridini or Rhathymini. For want of a better term this structure is here called the *inner* apical sclerotization of the gonocoxite.

SYSTEMATICS

Although there are parasitic bee species in other families, the greatest diversity, in numbers of genera and of species, is within the Anthophoridae. One subfamily, the Nomadinae, is exclusively parasitic and includes the majority of the species in such large genera as *Nomada, Hypochrotaenia,* and *Epeolus.* The few remaining parasitoid groups are mostly in the Anthophorinae: Melectini, Rhathymini, and Ericrocini.

The most conspicuous difference between these three tribes, as a group, and the worldwide Nomadinae is that females of Nomadinae, with some exceptions (especially in the Old World), possess a distinct, usually beveled, prepygidial fimbria or brush on the distal portion of the fifth abdominal tergum. Most Nomadinae females, and often the males as well, have a conspicuous, sharply defined, pygidial plate that is commonly about one-half as broad at the base as the width of the sixth tergum. Females of the Nomadinae (except *Hexepeolus*) have only five exposed metasomal sterna (six exposed sterna in cleptoparasitic Anthophorinae) and the legs are commonly spiculate or tuberculate. In both sexes the second abscissa of vein M+Cu of the hind wings is usually at least twice as long as the (usually) transverse cu-v; in those groups in which the second abscissa is not twice as long as cu-v, the labrum is conspicuously longer than broad. The apical portions of the wings are not papillate, as they are in the Ericrocini.

The Melectini are a worldwide group that includes the genera *Melecta* and *Thyreus* and a few smaller genera. *Melecta* is a Holarctic genus that appears to be limited to northern temperate regions and *Thyreus* is an exclusively Old World genus that is primarily southern, reaching South Africa and Australia. The hosts are mostly within the related pollen-gathering tribe Anthophorini, from which the Melectini are presumed to be derived.

Characteristics by which the Melectini differ from the Ericrocini are: the marginal cell barely, or not at all, exceeds the last submarginal cell; the mesotibial spur is not modified; the male gonostyli are slender and elongate; the mesobasitarsus is more or less rounded in cross section and is without a cariniform ridge along the posterior margin, whereas, in the Ericrocini they are laterally flattened, with a cariniform ridge (except *Acanthopus* and *Hopliphora*); the labrum is about as long as broad (except *Zacosmia*) and has a distinct basal bulla on either side; and, the meso- and metatibiae of the females are provided with coarse, spine-like setae.

The Rhathymini are exclusively Neotropical; there are fewer than half a dozen species, all placed in the genus *Rhathymus.* Known hosts are species of Centridini. The Rhathymini are, like the Ericrocini, presumed to be derived from the Centridini and the two groups have many shared character states, e.g., the general pattern of the wing venation, the lack of spine-like setae on the meso- and metatibiae of the females, the configuration of the scutellum and of the face, as well as other features. Rhathymini differ from Ericrocini in the pres-

ence of basal bullae on the labrum, the wings are hairy, the papillae are smaller and have hairs, the mesotibial spur is unmodified, and the body is without appressed, metallic scale-like hairs.

Tribe Ericrocini

Ericrocini Cockerell and Atkins, 1902:46. Michener, 1944: 288; 1954:145.
Ctenioschelini Michener, 1965:10. NEW SYNONYMY.

Medium-sized to large, robust bees, often with distinct patterns of white and iridescent blue, green or purple reflective scales and/or hairs, especially on abdomen.

Head conspicuously narrower than thorax, which is broader than long or deep; labrum broader than long, with transverse preapical ridge or median tubercle; clypeus about twice wider than long, apical margin broadly concave; lateral angle confluent with inner eye margin or nearly so. Malar space virtually absent. Mandible simple or with a single preapical tooth; posterior angle below middle of lower end of eye. Postflabellum present. Maxillary palpus with 1–4 segments. Antenna short, except in male *Ctenioschelus;* scape robust, shorter than combined lengths of first three flagellar segments; first flagellar segment short, little, if any, longer than broad (except male *Ctenioschelus*).

Pronotum short, collar closely appressed to front of mesoscutum; scutellum usually bituberculate. Three submarginal cells present in forewing; marginal cell considerably exceeding third submarginal cell; distal part of wings strongly papillate, basal part sparsely hairy; jugal lobe of hindwing no more than one-third as long as vannal lobe; second abscissa of M+Cu sometimes absent, always shorter than oblique cu-v and less than one-half as long as M. Mesotibial spur bifid or multidentate at apex; tarsal claws with large inner basal lobe or tooth; tarsal arolia absent (except *Ctenioschelus*).

Female pygidial plate often poorly defined; prepygidial fimbria absent; female sternum 6 with longitudinal median carina. Male tergum 7 bilobate or bidentate at apex; gonostylus squamiform in dorsal view.

The tribal name Ericrocini was first proposed by Cockerell and Atkins (1902) to include the Nearctic genus *Ericrocis.* Ctenioschelini was first introduced by Michener (1965). Even though *Ctenioschelus* is an older generic name than *Ericrocis,* the Law of Priority applies to tribal names and Ericrocini thus remains the correct name for this group.

DISCUSSION

The affinities of the Ericrocini have been obscure, though they have been presumed to be derived from the Centridini which are their hosts, perhaps via the same stock from which *Epicharis* is derived.

CLADISTIC ANALYSIS

The proboscis is considered to be directed downward so that it has anterior and posterior surfaces, thus Figures 70 and 72 show the posterior surface of the labiomaxillary complex.

The cladogram was made with aid of the computer program PAUP (Swofford, 1984). *Caenonomada,* which is undoubtedly the centridine genus with the most ancestral traits, was considered as the outgroup using ordered, unweighted character (i.e., 0 = primitive, 1 = derived, 2 or more = more derived characters of a transformation series). Polarity decisions were also decided considering "primitive" anthophorids such as Exomalopsini and in some cases short-tongued bees. Variables which exhibit two or more characters within a taxon were scored as the most primitive character found in that taxon. For example in variable 33 not all species of *Mesonychium* have flattened setae, on their meso- or metadistitarsus, so the absence of these setae, which is a plesiomorphy, was used for *Mesonychium* in the cladistic analysis. The reasoning is that the plesiomorphic, rather than the apomorphic, character will best show the relationships to other taxa. Therefore the characters of the most primitive members would be more useful in elucidating cladogenesis.

Table 1 is a list of 67 variables relevant to the Ericrocini, Rhathymini, and Centridini. Polarities of variables were ascertained by consideration of the Centridini, from which the ericrocine bees were presumably derived. Table 2 gives the raw data. The Centridini are solitary, nest-making bees. Before 1944 the Centridini had often also included exomalopsine bees, but since Michener (1944), the Centridini has included only *Centris* and *Epicharis.* Snelling (1984) elevated *Ptilotopus,* previously a subgenus of *Centris,* to generic standing. For purposes of outgroup comparisons we are including a fourth genus *Caenonomada,* in the Centridini. *Caenonomada* is the most "primitive" centridine bee, having previously been placed in the Exomalopsini (Michener and Moure, 1957). The reasons for this transfer will be given in a subsequent paper. The Centridini may be paraphyletic. *Centris, Epicharis,* and *Ptilotopus* share some apomorphies with the Ericrocini, which are not shared with *Caenonomada,* such as fusion of gonostylus with apex of gonocoxite, loss of arolia, the elongate, narrowed flabellum which has a cobblestone-like posterior surface, profile of the scutellum vertical to overhanging the metanotum, profile of the metanotum more or less vertical, the elongate mesocoxae, the stigma not extending into the marginal cell and not wider than the prestigma (measured to the costal margin of the wing), and alar papillae large and not ending in hairs [except *Epicharis* (*Epicharoides*) and *E.* (*Epicharitides*) which have alar papillae small and ending in hairs]. Therefore *Caenonomada* may be the sister group to the rest of the Centridini and Ericrocini. For purposes of this study we consider Centridini paraphyletic.

The Rhathymini are shown as the sister group to Ericrocini (Fig. 78a) or as the sister group to Ericrocini plus Centridini (Fig. 78b). *Rhathymus* shares with *Caenonomada* and/or *Epicharis* plesiomorphic hairy wings, small alar papillae ending in hairs, a hairy propodeal triangle, presence of arolia, presence of basal bullae on labrum, and unmodified mesotibial spurs, all of which are not shared with Ericrocini. The many common synapomorphies of the Rhathymini and Ericrocini could be convergences somewhat reminiscent of convergences between ericrocine and nomadine or melectine

Table 1. List of variables. Apomorphies are discussed first under each character (plesiomorphies are in brackets; their symbols for Table 2 are 0).

1. Labrum with preapical ridge or tubercle (1). [Labrum simple.] This ridge is not found in Centridini and is an obvious apomorphy of Ericrocini.

2. First flagellar segment of female differentiated, longer than others and shorter to longer than scape (1). [First flagellar segment of female not differentiated, more or less similar in length and shape to following segments.] A non-differentiated first flagellar segment is a plesiomorphy for bees in general and is typical of sphecoid wasps, short-tongued, and exomalopsine bees. Primitive centridine bees possibly had a slightly differentiated first flagellar segment as seen in *Caenonomada.* The highly derived centridines have a very long first flagellar segment. If such Centridini are ancestral to Ericrocini, their undifferentiated first flagellar segment is apomorphic. If Centridini is monophyletic (*sensu* Hennig), i.e., the sister group to Ericrocini, the ericrocine first flagellar segment would be primitive.

3. Inner eye margins divergent above (1). [Inner eye margins more or less parallel.] In nearly all Ericrocini and in all Centridini the inner eye margins are more or less parallel. The divergent eye margins apparently have appeared twice, once in *Ericrocis* and once in the *Mesonychium* group.

4. Male flagellar segments greatly elongated, flagellum longer than body (1). [Male flagellar segments normal, length of a segment about equal to width.] The bizarre greatly elongated flagellum of *Ctenioschelus,* reminiscent of long-horned beetles, is an obvious apomorphy.

5. Mandible of female simple, without subapical tooth (pollex) on upper margin (1). [Mandible of female with subapical tooth on upper margin.] Typically bees have toothed mandibles; loss of this tooth is derived.

6. Paraglossa two-thirds as long as prementum or longer (1). [Paraglossa less than two-thirds as long as prementum.] Short paraglossae are found in short-tongued and exomalopsine bees and are considered ancestral. Centridini as well as ericrocine bees have short paraglossae except the *Hopliphora* group.

7. Stipes without comb (1). [Stipes with comb.] Most non-parasitic long-tongued bees have stipital combs. Almost all parasitic anthophorids have lost the comb but have retained the preapical concavity which housed the comb of bristles. The presence of the comb is a plesiomorphy and its loss an apomorphy associated with parasitic habits.

8. Lower end of anterior conjunctival thickening [=suspensory thickening of Winston (1979)] near basal third of prementum (1). [Lower end of anterior conjunctival thickening near base of prementum.] Colletid and andrenid bees have the lower end of the anterior conjunctival thickening near the basal third of the prementum. This is the primitive character for Apoidea, whereas halictids and nearly all long-tongued bees have the lower end of the anterior conjunctival thickening near the base of the prementum. *Acanthopus* has presumably reverted (for Apoidea) to the ancestral condition which is an apomorphy for Ericrocini.

9. First segment of labial palpus less than twice as long as second (1). [First segment of labial palpus at least twice as long as second.] Short-tongued bees have the first and second labial palpal segments nearly the same length. The evolutionary trend has been toward a shortening of the second segment and/or lengthening of the first segment either of which is derived for Apoidea. In the Ericrocini and Centridini the comparatively short first segment of the labial palpus is found only in *Acanthopus* and is an apomorphy as is the apomorphy of character 8.

10. Mentum appearing Y-shaped because of deep apical emargination (Fig. 73) (1). Mentum appearing U-shaped because of deeper emargination (Fig. 71) (2). [Mentum with little if any apical emargination.] The mentum of most long-tongued bees is long, narrow and apically with little or no emargination. The deep apical emargination of the mentum of the Ericrocini is characteristic for this tribe (Fig. 73) and *Nomada* (Nomadinae) although in *Mesoplia* the emargination is not strong (Fig. 76). *Acanthopus* has the most derived mentum in that it is so deeply divided that it appears U-shaped.

11. Lorum basally divided such that the loral apron is separate sclerites held together by membrane (1). [Lorum V-shaped.] The lorum in Centridini as well as other anthophorids is V- or Y-shaped (Fig. 73). *Acanthopus* has a uniquely apomorphic lorum, basally divided such that the loral apron (Michener, 1985) is two sclerites held mediobasally by membrane and is fused to the cardines (Fig. 71).

12. Postflabellum present (1). [Postflabellum absent.] The postflabellum (Michener and Brooks, 1984) is unique to the ericrocine bees and is an obvious apomorphy.

13. Forewing tips (and sometimes marginal cell) infuscated with rest of wing clear (1). [Forewing tips concolorous with rest of wing, clear or infuscated.] Infuscated wing tips have appeared convergently many times in the Apoidea. The primitive condition of a concolorous wing, whether infuscated or clear, is found in most bees including the Centridini and most Ericrocini. Only the *Ctenioschelus* group and some *Mesoplia* have infuscated wing tips although they are variable in *Ctenioschelus* since the Middle American populations have less distinctive infuscation than the Brazilian ones.

14. Maxillary palpus with three or four segments (1). Maxillary palpus with one or two segments (2). Maxillary palpus absent or represented by a small bump fused to stipes (3). [Maxillary palpus with five or six segments.] The maxillary palpus primitively has six segments as seen in most bees including *Caenonomada.* Other centridines have five segments. The evolutionary direction in the ericrocines has been reduction and sometimes fusion of segments, culminating in complete loss of the palpus in *Acanthopus.*

15. Metasomal integument with metallic reflection (1). [Metasomal integument without metallic reflection.] Note that this statement refers to the color of the *integument,* not the metallic body hairs. The plesiomorphic condition is found in most Centridini [*Centris* s. str., some *C.* (*Paracentris*), and *C.* (*Wagenknechtia*) have metallic terga] and almost all Ericrocini where the integument is black to red-brown with no metallic reflections. Only *Abromelissa* has the apomorphic metasomal integumental color which is metallic blue.

16. Vestiture metallic in color (1). [Vestiture non-metallic.] The primitive condition is found in Centridini and *Ericrocis.* All other ericrocines have metallic vestiture.

17. Profile of scutellum vertical or at least at strong angle to scutum (1). Profile of scutellum overhanging metanotum (2). [Profile of

Table 1. Continued.

scutellum with posterior part more or less horizontal to a 45° angle.] Most of the short-tongued and exomalopsine bees have the primitive type of scutellum as does *Caenonomada.* The ericrocines, like the rest of the centridines, have an apomorphic scutellum whose profile is vertical and additionally overhangs the metanotum in *Mesoplia, Abromelissa,* and the *Ctenioschelus* group.

18. Profile of metanotum vertical (1). [Profile of metanotum slanting, more or less at a 45° angle.] Most short-tongued bees, all exomalopsine bees and *Caenonomada* have the plesiomorphic type of metanotum which slants. All the rest of the centridines and ericrocines have an apomorphic, more or less vertical metanotum.

19. Propodeal triangle hairless (1). [Propodeal triangle hairy.] A propodeal triangle with hair is found in all Centridini. The Ericrocini have a hairless propodeal triangle which is presumably an apomorphy, although many other bee groups possess this character.

20. Propodeum in profile with horizontal basal zone short, less than one-third as long as declivous surface (1). Propodeum in profile entirely declivous (2). [Propodeum in profile with horizontal basal zone long, about two-thirds as long as declivous surface.] Most "primitive" anthophorids and *Caenonomada* have a propodeum with a long horizontal basal zone. The evolutionary trend has been a shortening of this zone.

21. Jugal lobe shortened, one-third to one-half as long as vannal lobe measured from wing base (1). Jugal lobe short, one-fourth to less than one-third as long as vannal lobe (2). Jugal lobe very short, less than one-fourth as long as vannal lobe (3). [Jugal lobe long, apex much nearer vannal incision than wing base.] The evolutionary direction has been a shortening of the jugal lobe from a plesiomorphic long lobe of about three-fourths the length of the vannal lobe (as in *Caenonomada*) to a smaller one.

22. Hindwing with second abscissa of M+Cu almost absent to half the length of the crossvein cu-v (1). [Hindwing with second abscissa of M+Cu about equal in length to crossvein cu-v, second abscissa of M+Cu 0.75 to less than 1.50 times as long as crossvein cu-v.] In the Centridini the second abscissa of the M+Cu is about equal to the length of vein cu-v. The evolutionary trend in the Ericrocini has been toward a shortening of the second abscissa of the M+Cu which has culminated in its near to complete absence.

23. Hindwing with second abscissa of M+Cu considerably shorter than M (1). [Hindwing with second abscissa of M+Cu about as long as vein M.] This character is correlated with the previous character because as the second abscissa of M+Cu shortens (which is primitively almost equal in length to vein M as seen in short-tongued and exomalopsine bees), vein M will obviously be lengthened.

24. Hindwing with crossvein cu-v slanted toward wing base from second abscissa of M+Cu (1). [Hindwing with crossvein cu-v perpendicular to slanted apically to wing tip from second abscissa of M+Cu.] The hindwing of short-tongued bees generally has vein cu-v perpendicular to or slanted apically to wing tip from the second abscissa of vein M+Cu. Generally in the derived anthophorids this crossvein has become slanted toward wing base from the second abscissa of M+Cu.

25. Stigma not or scarcely extending into marginal cell, not wider than prestigma measured to costal margin of wing (1). [Stigma slender, posterior margin angulate at base of vein R, extending into marginal cell but oblique and straight there, not or little wider than prestigma.] *Caenonomada* has a moderately large stigma that extends into the marginal cell. A slendering of the stigma and its decreasing extension into the marginal cell is the derived condition. *Caenonomada* has a stigma intermediate between most exomalopsines and the rest of the centridines.

26. Stigma about as long as prestigma (1). Stigma shorter than prestigma, absent to nearly absent (2). [Stigma longer than prestigma.] The plesiomorphic long stigma as seen in *Caenonomada* has apomorphically decreased in length until it is nearly absent in the other Centridini, but it has decreased in length somewhat less in the Ericrocini.

27. Wings bare or with small patches of hair (1). [Wings hairy throughout or at least over large areas.] Hairy wings are found in the Exomalopsini, Melitomini, Eucerini, *Caenonomada,* and *Epicharis.* The Ericrocini have lost the hair.

28. Alar papillae large, not ending in hairs (1). [Alar papillae small and ending in hairs.] "Primitive" anthophorids, *Caenonomada,* and two subgenera of *Epicharis* (*Epicharoides* and *Epicharitides*) have alar papillae that end in hairs. In the other Centridini and the Ericrocini the papillae have become larger and have lost the small apical hairs.

29. First recurrent vein distad to interstitial, or nearly so with 1st transverse cubital vein (1). [First recurrent vein intersecting distal half of posterior margin of submarginal cell 2.] The first recurrent vein intersects the distal half of the posterior margin of submarginal cell 2 in all Centridini. The interstitial first recurrent and 1st transverse cubital veins in Ericrocini is an apomorphy. The polarity of this character is reversed for the Apoidea since exomalopsine, melitomine, and eucerine bees have the first recurrent and 1st transverse cubital interstitial.

30. First recurrent vein (as well as second) intersecting submarginal cell 3 (1). [First recurrent vein basad to interstitial with 1st transverse cubital vein.] In almost all apoids the first recurrent vein intersects submarginal cell 2 or is interstitial with the vein shared by submarginal cells 2 and 3. It is extremely rare to find the first and second recurrent veins entering submarginal cell 3. This is an obvious apomorphy and unique to *Acanthopus* among the ericrocine-centridine bees.

31. Marginal cell short, length less than 1.2 the distance from apex of marginal cell to wing tip (1). Marginal cell very short, length less than 0.7 the distance from apex of marginal cell to wing tip or marginal cell very long, length 1.8 the distance from apex of marginal cell to wing tip (2). [Marginal cell long, length 1.2–1.45 the distance from apex of marginal cell to wing tip.] Primitively the marginal is long, longer than the distance from the apex of the marginal cell to the wing tip. This plesiomorphy is seen in exomalopsine bees as well as *Epicharis* and *Caenonomada.* This Y-shaped variable consists of an apomorphic shortening in the Ericrocini starting from a long marginal cell, but in *Acanthopus* the evolutionary direction apparently changed to a lengthening of the marginal cell.

32. Mesobasitarsus laterally compressed, posterior margin carinate (1). [Mesobasitarsus somewhat round in cross section to slightly compressed, posterior margin not carinate.] The posterior margin of the mesobasitarsus is commonly compressed and carinate, terminating in a blunt tooth or spur that extends beyond the end of the segment. Its presence, found in most ericrocines, is an apomorphy since the Centridini lack it.

Table 1. Continued.

33. Meso- and/or metadistitarsi with flattened setae (1). [Meso- and/or metadistitarsi normal, without flattened setae.] The dark flattened setae of the meso- and/or metadistitarsi have presumably arisen twice in the Ericrocini. *Ericrocis* and most *Mesonychium* have this apomorphy not found in the Centridini.

34. Metadistitarsus five times longer than wide (1). [Metadistitarsus at most four times longer than wide.] The greatly elongated metadistitarsus of *Acanthopus* is unique in the Ericrocini and Centridini.

35. Arolia absent (1). [Arolia present, small.] The primitive centridine *Caenonomada* has small arolia. Arolia have been lost in all other centridines and ericrocines except in *Aglaomelissa* and *Ctenioschelus* in which they are small. The loss of arolia is certainly an apomorphy since almost all bees and sphecoid wasps have arolia. If the cladogram is correct it is very unlikely that the presence of arolia in *Aglaomelissa* and *Ctenioschelus* is independently derived since the arolium is a complex structure, composed of many parts, all of which are present in these two as in other aroliate bees. Moreover, it would be improbable if their presence requires five independent losses of arolia in the other Ericrocini. We believe that, assuming the accuracy of the cladogram, the origin of arolia in *Aglaomelissa* and *Ctenioschelus* is best explained as a reversion due to reactivation of genes that were suppressed during much of centridine and ericrocine evolution.

36. Mesotibial spur modified with several apical teeth (1). [Mesotibial spur normal, apically simple.] The modified mesotibial spur of the Ericrocini is an obvious apomorphy which the Centridini do not possess.

37. Females with tooth of tarsal claw a flattened basal lobe (1). [Female with tooth of tarsal claw not a flattened basal lobe.] The modified tooth becoming a flattened lobe is an apomorphy of Ericrocini which has convergently appeared at least three times in the Anthophoridae. Almost all non-parasitic bees have the plesiomorphic toothed claw, whereas all Ericrocini, Rhathymini, Melectini, and almost all Nomadinae have the tooth a flattened basal lobe.

38. Strigilar malus without teeth (1). [Strigilar malus with teeth.] Primitively the strigilar malus has teeth as found in many short-tongued bees. The loss of the teeth has occurred twice in the Ericrocini, once in the *Mesonychium* group and again in *Aglaomelissa*. This character may be of little phylogenetic significance since it is so variable throughout the Anthophoridae but it further unites the *Mesonychium* group and may prove valuable for future studies.

39. Scopa absent (1). [Scopa present.] All non-parasitic female bees have scopae [except Hylaeinae (Colletidae)]. The loss of the scopa is an obvious apomorphy seen in the Ericrocini and to varying degrees in all parasitic bees.

40. Anterior mesepisternal carina present (1). [Anterior mesepisternal carina absent.] The junction of the short anterior face and the long lateral face of the mesepisternum is rounded in Centridini. The apomorphic state has apparently appeared twice, once in *Acanthopus* and again in the *Ctenioschelus* group though lacking in *Ctenioschelus*.

41. Sternopleural ridge present (1). [Sternopleural ridge absent.] The presence of the sternopleural ridge is an apomorphy found only in the *Hopliphora* group.

42. Supraspiracular ridge well developed, terminating abruptly in a blunt tooth-like process (1). [Supraspiracular ridge weak to absent.] The supraspiracular ridge is not developed in Centridini and many ericrocines. It is developed in the *Mesonychium* and *Ctenioschelus* groups (except *Aglaomelissa*).

43. Scutellum bilobed (1). Scutellum bilobed and projecting over propodeum (2). [Scutellum not projecting over propodeum, simple.] In Centridini as in most non-parasitic anthophorids the scutellum is not modified. The scutellum is commonly modified in most parasitic anthophorids and all Ericrocini. The modification in ericrocine bees is the presence of two rounded lobes which are further modified in the *Ctenioschelus* group (except *Aglaomelissa*) as dorsoventrally flattened plate-like eminences extending over the vertical metanotum and propodeum.

44. Midcoxal length 1.00–1.35 length of distance from summit of coxa to hind wing base (1). Midcoxal length at least 1.36 length of distance from summit of coxa to hind wing base (2). [Midcoxal length 0.85–0.99 length of distance from summit of coxa to hind wing base.] In many parasitic anthophorine bees the midcoxa has become elongated as well as more exposed and hence is a further derivation as seen in most ericrocines (except the reversion found in the *Mesonychium* group) and centridines (except *Caenonomada*).

45. Hind basitarsus of female with distal process, not provided with a pencillus (1). [Hind basitarsus of female with distal process ending in a pencillus.] Almost all non-parasitic anthophorid bees have a pencillus. The loss of the pencillus in almost all parasitic bees is an apomorphy.

46. Basitibial plate absent or only represented by a carina (1). [Basitibial plate of female present, well developed.] The basitibial plate present in female Centridini has been lost in the Ericrocini as well as most other parasitic bees and is an apomorphy.

47. Basitibial plate of male incomplete, represented by a scale or series of tubercles (1). Basitibial plate absent or only represented by a carina (2). [Basitibial plate of male present, well developed.] Male Centridini have well-developed basitibial plates (except *Centris*). The loss of these plates in male Ericrocini is an apomorphy.

48. Dorsum of metasomal tergum 1 subangulate in profile (Fig. 77) (1). [Dorsum of metasomal tergum 1 rounded in profile (Fig. 76).] Usually, the vertical and horizontal faces of the first metasomal tergum, as viewed in profile, meet in a distinctly rounded angle, the junction, however, may be so narrowly and abruptly rounded as to appear angulate. This is an obvious apomorphy of the *Ctenioschelus* group.

49. Prepygidial and pygidial fimbriae absent (1). [Prepygidial and pygidial fimbriae present.] The Centridini as well as all non-parasitic anthophorine bees have prepygidial and pygidial fimbriae. The loss of these fimbriae in the Ericrocini is derived.

50. Metasomal terga with patches of appressed white hair (1). [Metasomal terga, without patches of appressed white hair.] The Centridini have the metasoma with long, erect to suberect hair and/or entirely covered with appressed hair or virtually all bare. Most ericrocines have patches of white hair either laterally on the terga or in various patterns, but this apparently has been reversed in the *Hopliphora* group and *Abromelissa*. This apomorphy has arisen many times in other parasitic anthophorids.

Table 1. Continued.

51. Metasomal sternum 3 of male with dense lateral patch of white hair (1). [Metasomal sternum 3 of male simple, without dense lateral patch of white hair.] The Centridini lack the dense lateral patch of white hair on metasomal sternum 3. All Ericrocini have this apomorphy except the *Hopliphora* and *Mesonychium* groups.

52. Metasomal sterna 4 and/or 5 of male with dense apical band of long curved hair (1). [Metasomal sterna 4 and 5 of male simple without apical band of long curved hair.] *Caenonomada, Epicharis,* and the Ericrocini (except *Mesoplia* and *Mesonychium*) share the apomorphy of an apical band of long curved hair on metasomal sterna 4 and/or 5. "Primitive" anthophorids such as Exomalopsini, Melitomini, and Eucerini lack bands.

53. Metasomal sternum 5 (and sometimes 4) on basal half of disc with felt-like pad of dense hair (1). [Metasomal sternum 5 and 4 simple, without felt-like pad of dense hair.] The presence of a felt-like pad of short pubescence on metasomal sternum 5 (and sometimes 4) which Centridini lacks is an obvious apomorphy found in all Ericrocini except the *Mesonychium* group.

54. Male metasomal sternum 4 concealed (1). [Male metasomal sternum 4 normal, not concealed.] Because the margins of the fourth metasomal sternum may be broadly incurved, each segment may be largely hidden under the preceding segment. This apomorphy is found scattered throughout the Ericrocini.

55. Male metasomal sternum 5 concealed (1). [Male metasomal sternum 5 normal, not concealed.] See discussion for character 54.

56. Female metasomal sterna 2–5 longitudinally carinate medially (1). [Female metasomal sterna 2–5, not carinate medially.] Female ericrocines usually have metasomal sterna 2–5 uniformly flat as in most bees. *Mesocheira* is the only genus which has the unique apomorphy of sterna 2–5 carinate medially.

57. Female metasomal sternum 6 with longitudinal median carina (1). [Female metasomal sternum 6 longitudinally simple without median carina.] All Ericrocini have this unique apomorphy which the Centridini as well as other non-parasitic anthophorids lack.

58. Sixth metasomal sternum of male medioapically flat, not convex, usually entire or emarginate, rarely pointed (1). [Sixth metasomal sternum of male bluntly pointed medioapically, strongly convex.] The sixth metasomal sternum of male medioapically pointed and convex is seen in all exomalopsine, melitomine, eucerine, and centridine bees.

59. Sternal apodemes of some metasomal sterna without dorsal processes (1). [Sternal apodemes of metasomal sterna with dorsal processes.] Centridini have metasomal sternal apodemes with dorsal processes. This condition is commonly found among the non-parasitic Anthophoridae. All Ericrocini have lost the dorsal processes except *Ericrocis.* This loss is an apomorphy.

60. Eighth metasomal sternum of male without or with greatly reduced spiculum (1). [Eighth metasomal sternum of male with spiculum.] Most anthophorid bees have a spiculum as found in the Centridini. An obvious apomorphy is loss or great reduction of the spiculum as seen in the Ericrocini except *Abromelissa.*

61. Spatha short, weakly developed (1). Spatha absent (2). [Spatha present, well developed.] Centridini except *Epicharis* have a well to weakly developed spatha. The presence of a spatha is presumably a plesiomorphy since it is commonly found among "primitive" anthophorids. Apparently the loss of the spatha in Ericrocini is an apomorphy.

62. Eighth metasomal sternum of male without apical process (1). [Eighth metasomal sternum of male with apical process.] Many short-tongued bees, the "primitive" anthophorid and Centridini have a well-developed apical process which may be variously modified. The reduction of this apical process such that the disc of the eighth sternum is broader than long is an apomorphy typical of Ericrocini.

63. Eighth metasomal sternum of male a broad plate (1). [Eighth metasomal sternum of male short, transverse, sometimes with one or two long apical processes.] For discussion see variable 62.

64. Penis valve without basolateral lobe (1). [Penis valve with basolateral lobe.] The penis valves of centridine bees have basolateral lobes. The presence of these lobes is an apomorphy though a weak one since it has apparently appeared three times, being a character of *Ericrocis, Aglaomelissa,* and the *Hopliphora* group.

65. Gonostylus of male greatly reduced to absent, if present then represented only by a membranous, flat, circular to slit-like area (1). [Gonostylus of male an elongate appendage.] The presence of a gonostylus as an elongate appendage often incurved apically distad of the penis valves is common in the "primitive" anthophorids and the Centridini. Recognition of the gonostylus is often aided by the long setae which all anthophorid bees have on their gonostyli, as well as the reduced sclerotization of the gonostylus. The most primitive condition is articulation to the apex of the gonocoxite as it is in *Caenonomada.* In the other centridines and ericrocines it is fused to the apex of the gonocoxite and is very narrow, round in cross section and more elongate. The reduction or absence of the gonostylus is a weak apomorphy since it has disappeared in three separate ericrocine groups.

66. Mesopleuron with knob-like process (1). [Mesopleuron without knob-like process.] The knob-like process on the mesopleuron of *Rhathymus* is an obvious autoapomorphy.

67. Apical margin of metasomal sternum 5 laterally with notch (1) (Fig. 76). [Apical margin of metasomal sternum 5 laterally simple.] This unique autoapomorphy is found only in *Mesocheira.*

bees. Figure 78b necessitates 11 convergences between the two tribes, which is possible considering there are 12 convergences [characters 7, 17, 18, 20(2), 21(2), 37, 39, 45–47, 49, 58, and 59] between the melectine and the ericrocine-rhathymine bees. Nevertheless, the male terminalia of Ericrocini and Rhathymini are similar and in conjunction with the numerous apparent synapomorphies shared by the two tribes, we prefer Figure 78a. The cladogram of Figure 78a eliminates all 11 convergences of Figure 78b and so is 11 steps shorter.

Unique characters for taxa were obvious apomorphies, whereas other polarity decisions encompassed centridine

Table 2. Matrix of characters listed in Table 1. Variables 1-67 are represented by the columns from left to right. Variables which are not constant are indicated by both characters which appear in the genus, i.e., 0.

CAENONOM	00000000000000000001201100000000000000000000000000100000001000000
RHATHYMU	01001010100003001102301110002000000010100001200100100000100001010
MESOPLIA	11000010010101012112211111112011001110100010112011101010111121100000
HOPLIPHO	11000110010101011112211111112011001110101011112010011000111121110000
MESONYCH	11100010010102011112211111112011001111100110112011000100111121101000
ABROMELI	11100000010101112112311111112011001111100110112010010000111021100000
ERICROCI	11100010010101001112211111112021101110100012112011111000110121111000
AGLAOMEL	01001010010112012112311111112010000011110011112111111000111121110000
CTENIOSC	11011010010112012112311111112010000011010012111211111000111121100000
MESOCHEI	01001010010112012112311111112011001110110121112111111011111121100001
ACANTHOP	11001111121103011112211111112100011110111011112010011010111121110000

outgroup comparisons or centridine-exomalopsine outgroup comparisons or comparisons against short-tongued bees, with the variables of the ericrocine bees. The long first flagellar segment of the Centridini, which is a derived feature for the family Anthophoridae, is considered here as a plesiomorphy, the somewhat non-differentiated first flagellar segment of the ericrocines being the apomorphous character.

Table 1 includes notes on the distribution of characters of the variables and the bases for our judgments of polarity (evolutionary direction). Discussion is frequently abbreviated but is sufficient to suggest reasons for our decisions.

DISCUSSION

Linsley (1939) suggested that *Ericrocis* may have arisen from *Centris* (=*Hemisia*) or *Epicharis.* Michener (1944) stated that Melectini, Ericrocini, and the Rhathymini may have had a common origin with *Anthophora* but later he (Michener, 1974) separated the melectine and rhathymine-ericrocine lineages in his dendrogram, indicating common origins of the Anthophorini with the former and Centridini with the latter. Our work supports Michener's latter hypothesis and is more or less in agreement with Rozen's larval work (1969). Rozen states that the larvae of melectines, ericrocines, and rhathymines share an apomorphy not found in centridine or anthophorine larvae, i.e., they lack galeae. But as he points out, this may not indicate a common origin for these parasitic bees since galeae have been lost in many unrelated groups of bees and loss characters are often convergent. Rozen further states that the Melectini share a plesiomorphy with the Anthophorini not shared with the Ericrocini and Rhathymini; i.e., the maxillary palpus is preapical in position. The Ericrocini and Rhathymini have maxillary palpi which are apical as well as greatly elongated labiomaxillary regions. These apomorphies support the contention that the Ericrocini and Rhathymini are sister groups. On the other hand the strongly denticulate atrial wall and spinous primary tracheal opening of the ericrocines (not found in rhathymines) is similar to the spiracular structure of *Epicharis* and anthophorines and therefore could suggest a separate origin for the Rhathymini. We believe that the rhathymine-ericrocine clade is monophyletic (*sensu* Hennig) since it has 10 adult and two larval synapomorphies. It is unlikely that all of the apomorphies are convergent and have appeared *de novo* in each tribe. We have presented, however, other characters which do not support this hypothesis.

We have recognized several lineages within the Ericrocini: (a) *Ericrocis* group (*Ericrocis*), (b) *Hopliphora* group (*Hopliphora* and *Acanthopus*), (c) *Mesoplia* group (*Mesoplia*), (d) *Mesonychium* group (*Mesonychium* and *Abromelissa*), and (e) *Ctenioschelus* group (*Ctenioschelus, Aglaomelissa,* and *Mesocheira*). Here and below the numbers in parentheses represent variables as numbered in Table 1. The most "primitive" lineage is presumably *Ericrocis* since it lacks metallic setae (16) and integumental coloration (15) and has metasomal sternal apodemes (59) like Centridini. This is not fully convincing since the loss of metallic coloration could be a reversion in *Ericrocis* rather than a plesiomorphy shared with Centridini. Metallic hair has arisen three times at least in the Anthophorinae, in *Amegilla* (Anthophorini), in *Thyreus* (Melectini) as well as in the Ericrocini. Many *Thyreus* have non-metallic white appressed vestiture like *Ericrocis* and a polarity decision of whether that type of vestiture is primitive or derived will probably be similarly uncertain.

Acanthopus has the most derived mouthparts and legs of any ericrocine and two unique apomorphies in the forewing, making its relationship to the rest of the Ericrocini obscure. Nevertheless, it shares three strong apomorphies with *Hopliphora,* i.e., relatively long paraglossae (6), presence of the sternopleural ridge (41) and the absence of tergal patches of white appressed hair (50). *Hopliphora* and *Acanthopus* are the largest ericrocines and both have large centridine hosts. Lack of apomorphies for *Hopliphora* suggests that it is possibly a paraphyletic group from which *Acanthopus* evolved. We have no problem in recognizing paraphyletic taxa since we find it unnecessary that classifications and cladograms be redundant, especially when more than one cladogram is equally plausible (or parsimonious).

The *Mesoplia, Mesonychium,* and *Ctenioschelus* groups have three apomorphies, a well-developed scutellum which overhangs the metanotum (43) (reverted to a less developed state in *Mesonychium*), metasomal sternum 3 of male with

dense lateral patch of white hair (51) (which is reversed in the *Mesonychium* group), and penis valve with basolateral lobe (64) (lost in *Aglaomelissa*). In view of the reversals, one must admit that the three characters are not very convincing.

Mesoplia is quite distinctive, having elongate segments in the maxillary palpus (14), the male has lost the apical bands of long curved hair on metasomal sterna 4 and 5 (52) and has a broadly emarginate sternum 5 such that it is concealed under sternum 4 (55).

The *Mesonychium* and *Ctenioschelus* groups share a reduction of the number of maxillary palpal segments to one or two (14) (reduced to three in *Abromelissa*), a reduction of the length of the jugal lobe to less than one-fourth the distance between the vannal incision and wing base (21) (reduced to between one-third and one-fourth this distance in *Mesonychium*), and presence of the supraspiracular ridge (42).

The *Mesonychium* group is characterized by five strong apomorphies. The inner eye margins are divergent above (3), the strigilar malus lacks teeth (38), the midcoxa is short (44), metasomal sternum 3 lacks a dense lateral patch of white hair (51), and sterna 4 and 5 lack dense felt-like pads of pubescence (53) which ancestrally cover the basal halves of their discs. It is interesting also that *Abromelissa* is the only ericrocine genus with metallic integument (15). The *Mesonychium* group, although it includes Amazonian species, is largely peripheral to the distribution of other ericrocine genera. *Mesonychium* is one of the largest genera in the tribe, with about half a dozen species in Chile and temperate Argentina. Also limited to Chile is its possible derivative, *Abromelissa,* so *Mesonychium* may be paraphyletic.

The *Ctenioschelus* group is distinguished by several derived characters: the subapical mandibular tooth is lost (5), the forewing tips are infuscated (13), and tergum 1 has a relatively sharply angulate profile (48) (Fig. 76). Other noteworthy characters which are found in two of the three genera are the presence of arolia (35) (except *Mesocheira*), the apically simple labrum (1), the presence of an anterior mesepisternal carina (40) (except *Ctenioschelus*), and the projection of the scutellar lobes over the propodeum (43) (except *Aglaomelissa*). There is also a trend toward the development of the occipital margin into a sharp ridge or flange, or a flange-like carina across the entire pronotum, and of strongly developed acetabular carinae with the procoxae deeply recessed. The *Ctenioschelus* group is centered in Amazonia but *Mesocheira* ranges from central Mexico to Paraguay. *Ctenioschelus* and *Aglaomelissa* are primarily South American, but both range north to Costa Rica.

KEY TO GENERA OF ERICROCINI

1a. Second and third submarginal cells of forewing each receiving a recurrent vein; metatarsus without dense fringe of long, dark plumose hairs 2
b. Third submarginal cell large, receiving both recurrent veins; metatarsus very long, with dense brush of long, dark, plumose hairs ..... *Acanthopus*
2a. Juncture of basal and discal surfaces of tergum 1 slightly humped and subangulate in middle (Fig. 77); mesobasitarsus without distal, flattened, spine-like projection on posterior margin (Fig. 49); mandible simple 3
b. Juncture of basal and discal surfaces of tergum 1 evenly rounded, never appearing subangulate (Fig. 76); mesobasitarsus almost always with distal, flattened process on posterior margin, often continued basad as a raised, cariniform ridge (Fig. 1); mandible usually with single preapical tooth 5
3a. Scutellum bituberculate, the processes stout, subconical and suberect; forewing dusky with apex darker 4
b. Scutellum bituberculate, the processes flat and plate-like, directed caudad; forewing dusky, with an apical cloud in marginal cell in addition to that at wing apex ..... *Mesocheira*
4a. Pronotum carinate between collar and lobe; mesepisternum with lamelliform ridge between anterior and lateral surfaces; male antenna normal, not extending much beyond tegula ..... *Aglaomelissa*
b. Pronotum not carinate between collar and lobe, end of collar clearly defined; mesepisternum abruptly rounded between anterior and lateral surfaces; male flagellar segments greatly elongate, flagellum extending well beyond apex of abdomen ..... *Ctenioschelus*
5a. Meso- and metadistitarsi with a cluster of appressed, short flattened setae on each side (Fig. 28) (setae reduced in some *Mesonychium* in which antennocular distance is greater than antennal socket diameter and third submarginal cell is distinctly narrowed anteriorly); inner eye margins divergent above; male gonostylus without dorsal lobe (Figs. 33, 38) 6
b. Meso- and metadistitarsi with normal setae and hairs, without flattened setae (Fig. 2); inner eye margins various, but usually not divergent above; male gonostylus with dorsal lobe (Figs. 7, 22, 43) (except some *Hopliphora*) 7
6a. Abdominal scales contrasting black and white (may be somewhat tawny); labrum with erect preapical median tubercle; scutellum without raised, mammiform tubercles ..... *Ericrocis*
b. Abdominal scales or hairs iridescent blue or green, with or without contrasting whitish hairs; labrum with transverse preapical ridge; scutellum usually with a pair of mammiform tubercles ..... *Mesonychium*
7a. Abdominal integument blackish, usually more or less covered with blue or green-reflective, appressed, scale-like hairs, but if not, mesepisternal hairs are black; tegula rectangular or elliptical but not abruptly narrowed anteriorly (Figs. 61, 63, 64) 8
b. Abdominal integument shiny metallic blue, with sparse erect blackish hairs; hairs of thorax whitish; tegula abruptly narrower in anterior one-third (Fig. 66) ..... *Abromelissa*
8a. Tegula oval, outer margin evenly curved (Fig. 61); abdomen usually appearing black, without patterns of appressed pale pubescence ..... *Hopliphora*
b. Tegula, from above, approximately elliptical, often with outer margin somewhat sinuate in part and with posterior margin oblique or truncate; abdomen bright iri-

descent bluish or greenish, often with conspicuous patches of white or yellowish pubescence ..... *Mesoplia*

Ericrocis Group

Although the body is richly marked with conspicuous patterns of blackish and white to tawny pubescence, the complete lack of metallic-reflective hairs or scales is diagnostic for this group. Other characteristics of the *Ericrocis* group are: inner eye margins divergent above (shared with *Mesonychium* group); meso- and metadistitarsi with flattened setae (shared with some *Mesonychium*); sternal apodemes of some metasomal sterna without dorsal processes (unique within the Ericrocini).

(A) Inner eye margins divergent above. (B) Ocellocular distance greater than diameter of anterior ocellus. (C) Mandible with preapical tooth. (D) Maxillary palpus two-segmented. (E) Hypostomal carina low, uniform. (F) Malus of protibia short, less than half as long as velum, finely serrate on inner margin. (G) Mesobasitarsus usually compressed and more or less sharply carinate along posterior margin; distal process usually present. (H) Meso- and metadistitarsi with lateral patch of short, flattened setae on each side (Fig. 28). (I) Metatarsus without posterior fringe. (J) Marginal cell of forewing about 0.80 times distance from its apex to wing tip. (K) Juncture of basal and discal faces of first tergum rounded. (L) Male seventh tergum bilobate at apex or with two stout teeth. (M) Gonostylus without dorsal lobe.

The one genus included in this group, *Ericrocis,* is restricted to the Nearctic Region.

Genus *Ericrocis* Cresson

Figures 34–38, 60, 72–74

Ericrocis Cresson, 1887:131, 134. Type species: ? *Crocisa lata* Cresson, 1878 (monobasic).

DIAGNOSIS

Abdominal color black, with conspicuous pattern of appressed, plumose white to somewhat tawny hairs; labrum with a median preapical tubercle; dorsal face of scutellum without tubercles.

DESCRIPTION

(1) Head much broader than long; inner eye margins essentially straight, strongly divergent above; occipital margin nearly flat, slightly elevated above ocelli. (2) Maxillary palpus two-segmented, first segment distinctly longer than second. (3) Labrum with median preapical tubercle; apical margin subtruncate. (4) Interantennal distance greater than antennal socket diameter; antennocular distance greater than antennal socket diameter. (5) Ocelloccipital distance slightly greater than diameter of anterior ocellus. (6) Occipital margin subangulate. (7) Antenna short in both sexes; minimum length of first flagellar segment about equal to maximum width and shorter than second segment on same side.

(8) Pronotum not carinate between collar and posterior lobe. (9) Midline of mesoscutum deeply impressed, more weakly so distad; parapsidal lines in broad, shallow impressions. (10) Dorsal face of scutellum broadly impressed along midline, broadly convex on either side. (11) Anterior mesepisternal carina, acetabular carina and sternopleural ridge absent. (12) Supraspiracular ridge evanescent distad.

(13) Tegula (Fig. 65) rectangular, narrowed anteriorly, outer margin somewhat sinuate. (14) Second submarginal cell narrower on M than first or third; 1st m-cu interstitial with 1st r-m; 2nd m-cu a little basad of 2nd r-m.

(15) Mesotibial spur slender, parallel-sided, apex bispinose, outer spine often obsolete, intercalary denticles present. (16) Metatrochanter rounded ventrally; metatibial spurs normal; metadistitarsus about 2.5 times longer than wide.

(17) Female sixth tergum with weakly defined pygidial plate, apex narrowly rounded. (18) Male fourth sternum broadly concave along apical margin, with a distal fringe of long, dark plumose hairs, their apices broadly reflexed. (19) Male fifth sternum broadly and more shallowly concave along apical margin, with or without distal fringe. (20) Male seventh sternum (Fig. 34) transverse, evenly rounded or with short, truncate projection. (21) Male eighth sternum (Fig. 35) short, bilobate at apex. (22) Male gonostylus short, thick, truncate; dorsal lobe absent; inner apical sclerotization of gonocoxite poorly defined. (23) Penis valve abruptly deflected ventrad; basolateral lobe absent (Fig. 38).

DISCUSSION

This Nearctic genus is, in many respects similar to the South American genus *Mesonychium,* with which it shares the presence of a cluster of short, flattened setae on either side of the meso- and metadistitarsi, a feature unique to these two genera. Unlike *Mesonychium* and all other ericrocine genera, *Ericrocis* lacks metallic hairs or scales. Instead, there are richly marked patterns of black and white and (sometimes) tawny pubescence. *Ericrocis* includes two species: *E. lata* (Cresson) and *E. pintada* Snelling and Zavortink. The genus was revised by Snelling and Zavortink (1985).

It should be noted that the figures of the labiomaxillary complex cited by Winston (1979: fig. 44) as those of *Mesocheira bicolor* appear, instead, to be based on *Ericrocis lata.* Michener and Fraser (1978) figure mandibles purported to

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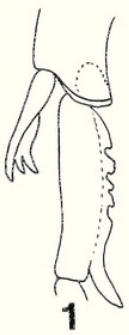
Figures 1-7. *Mesoplia (M.) azurea.* **1,** female mesobasitarsus, pilosity omitted; **2,** metadistitarsus, lateral view; **3,** male sternum 7; **4,** male sternum 8; **5-7,** male genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm (Figs. 3–7 only).



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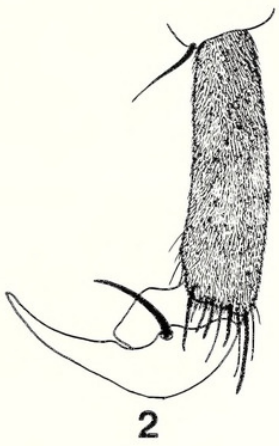

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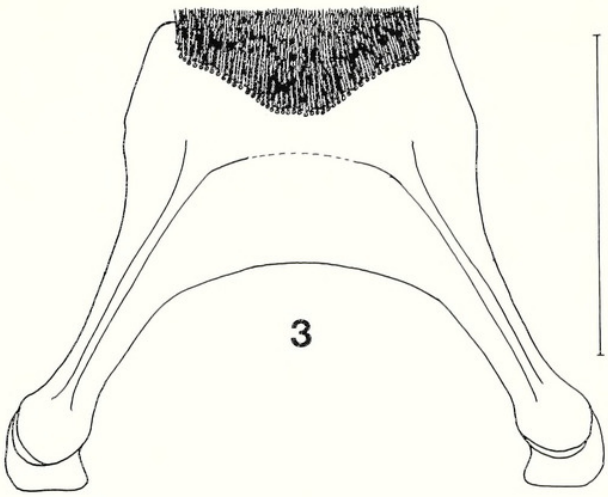

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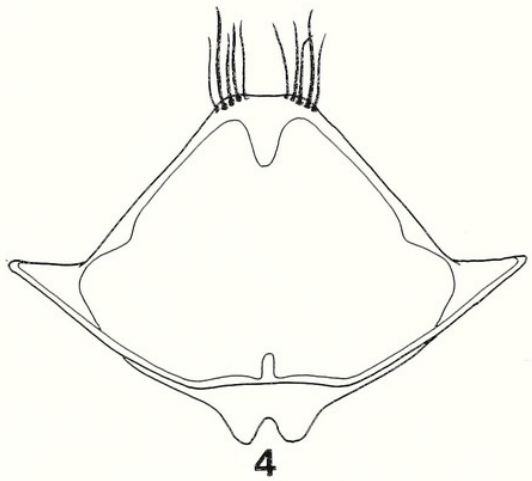

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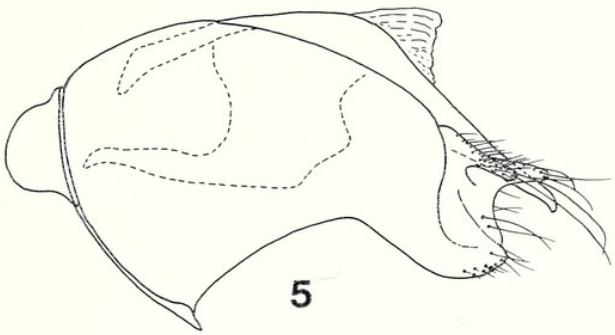

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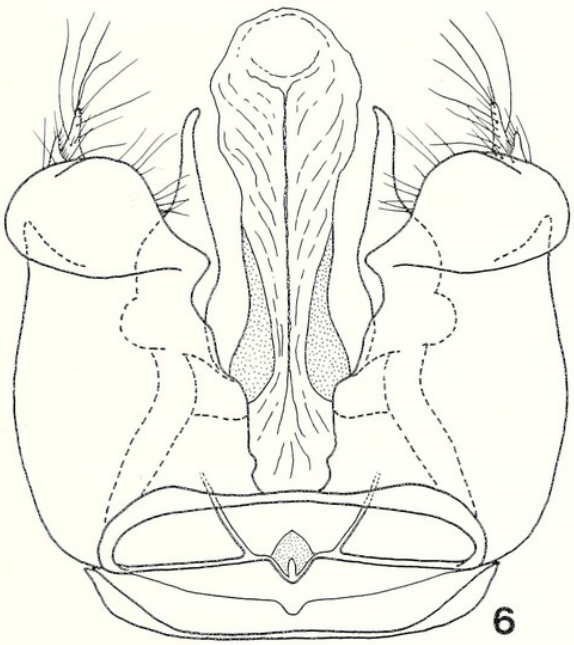

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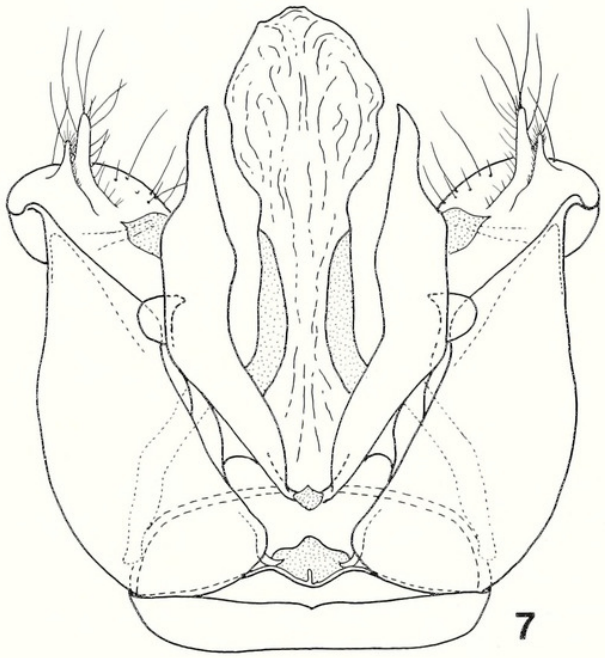

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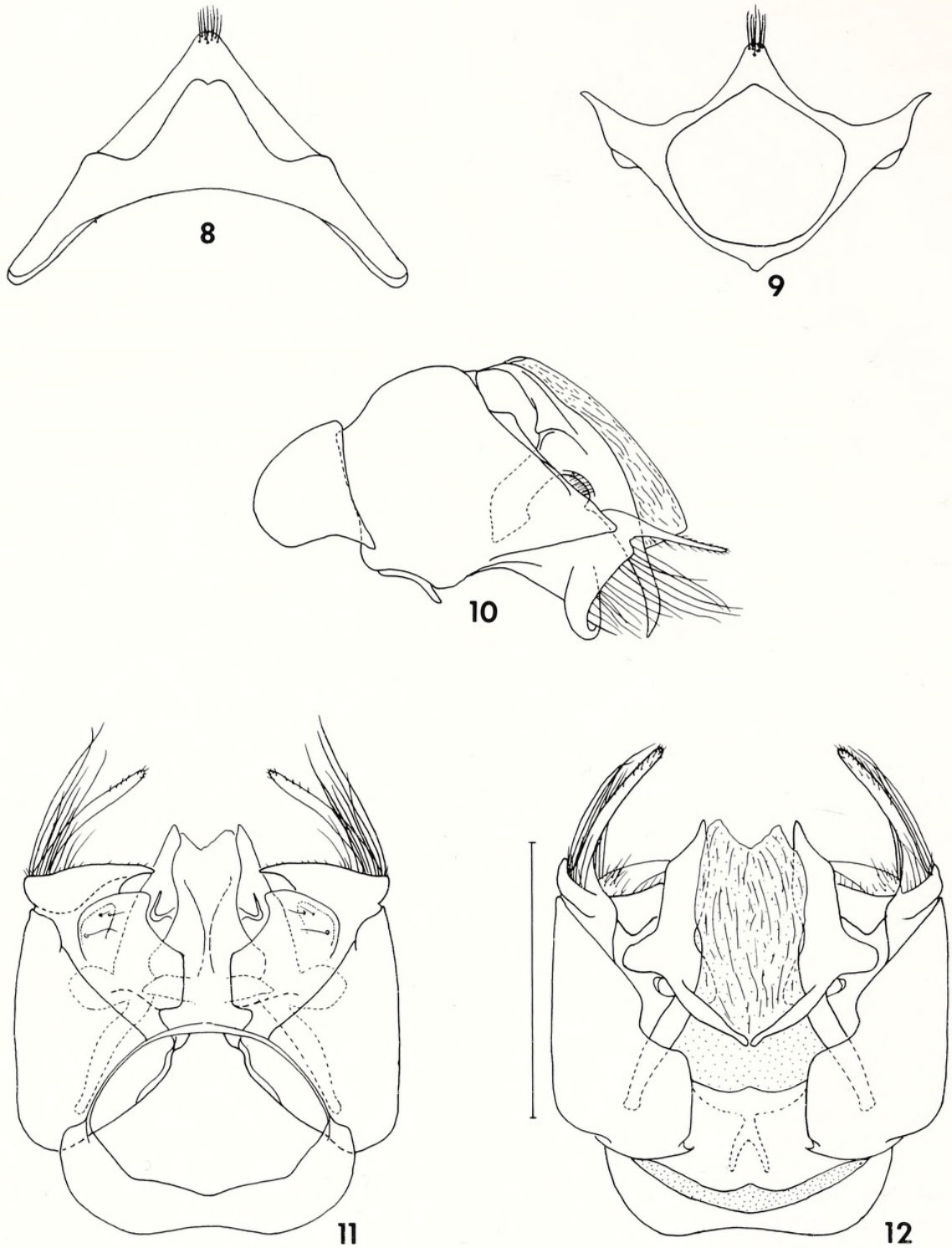


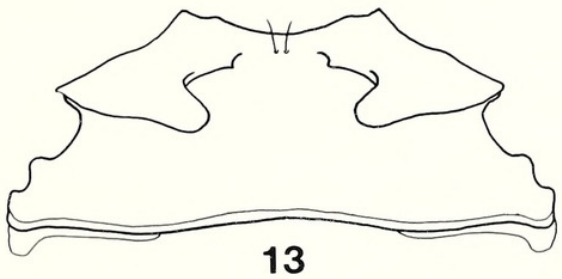
Figures 8-12. *Mesoplia* (*Eumelissa*) *decorata,* male. **8,** sternum 7; **9,** sternum 8; **10-12,** genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.

be those of *E. lata* (Fig. 16); since the mandible of *E. lata* possesses a distinct preapical tooth (wholly lacking in the figure), the mandible figured is not that of *E. lata.* Also, they stated that the tooth of the pollex is absent (p. 477); it is present as the preapical tooth.

Hosts for *Ericrocis* are not known but, based on distribution, will almost certainly prove to be species of *Centris,* subgenus *Paracentris,* and possibly subgenus *Acritocentris.*

INCLUDED NAMES

arizonensis Baker, 1906 (*Ericrocis*)
lata (Cresson, 1878) (? *Crocisa*)



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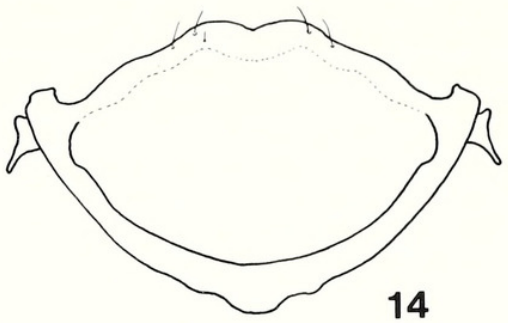

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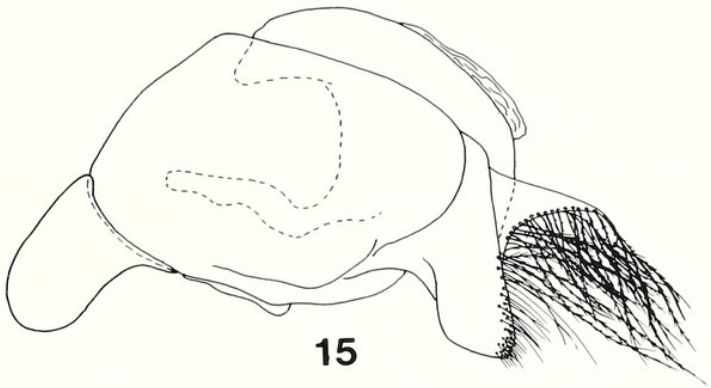

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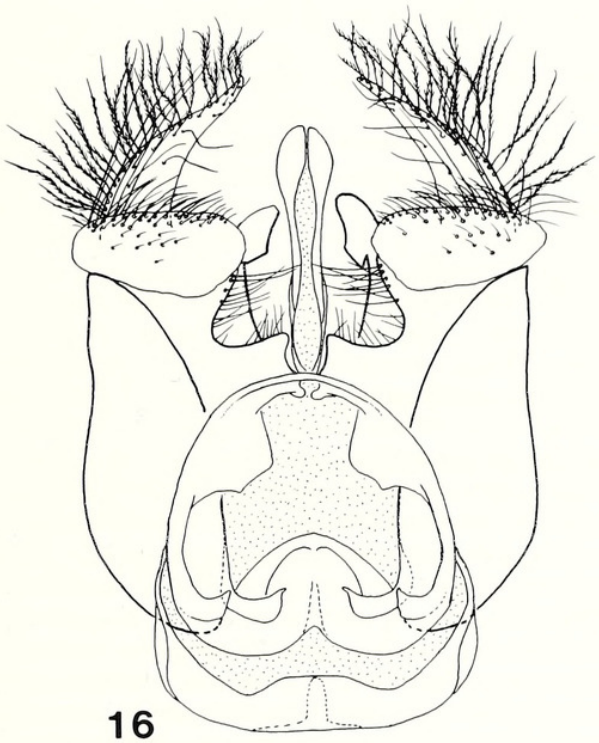

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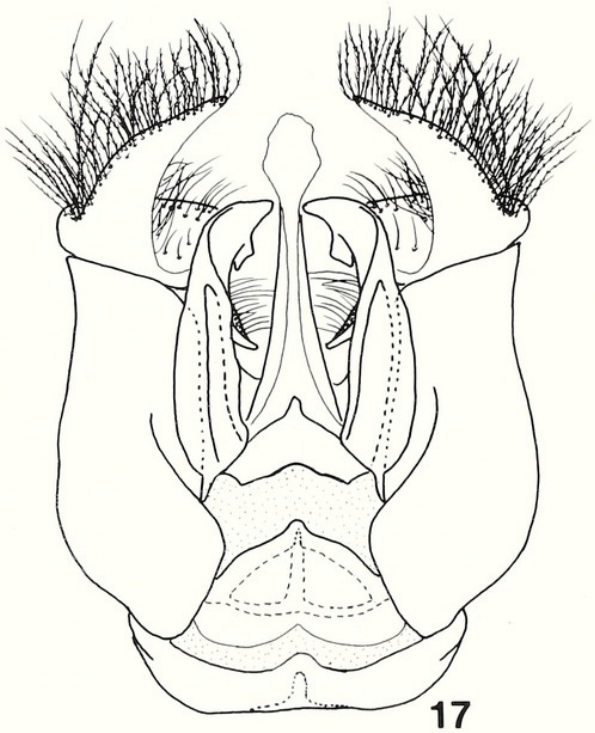

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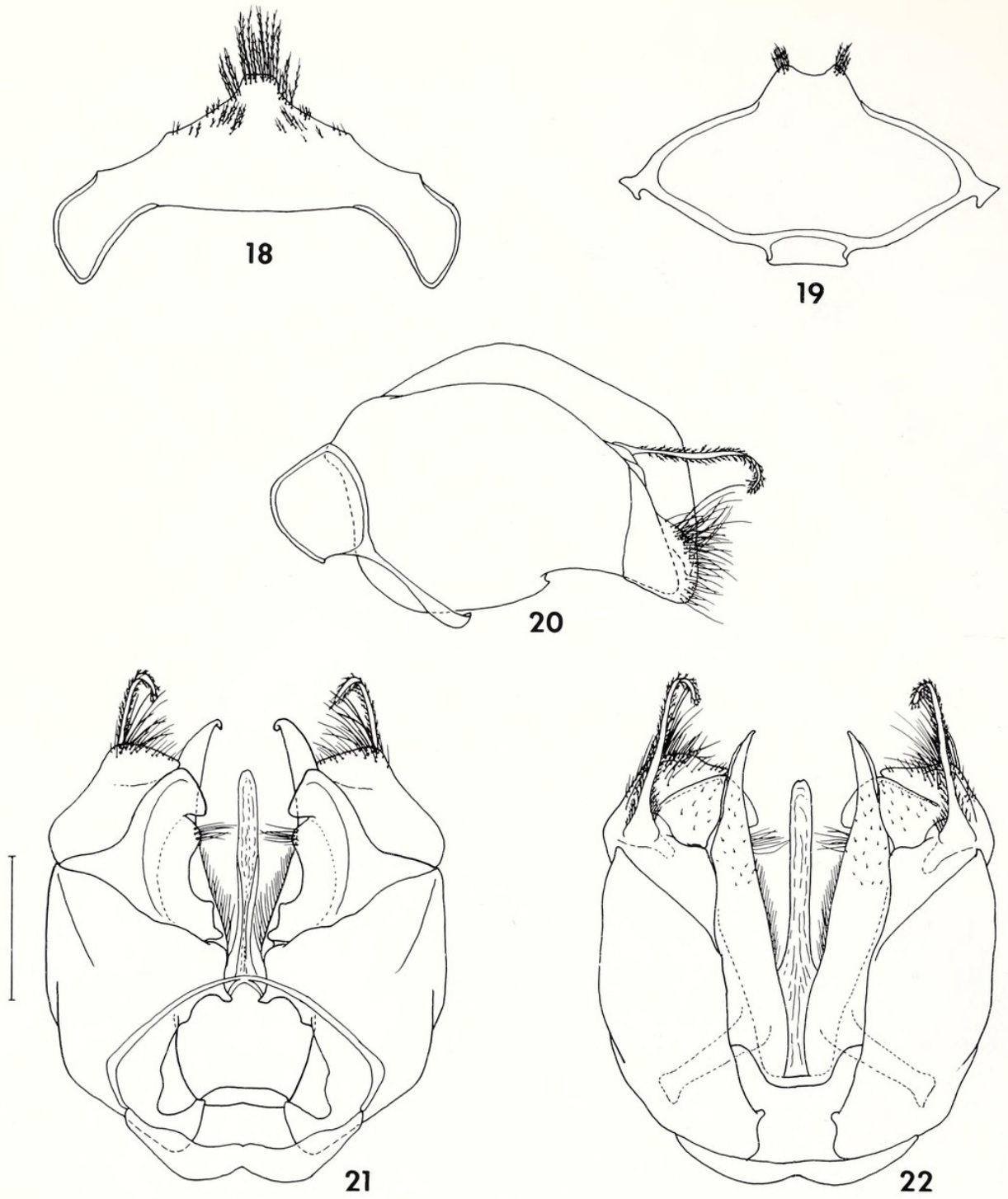
Figures 13-17. *Acanthopus palmatus,* male. **13,** sternum 7; **14,** sternum 8; **15-17,** genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.



Figures 18-22. *Hopliphora velutina,* male. **18,** sternum 7; **19,** sternum 8; **20-22,** genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.

melectoides Baker, 1906 (*Ericrocis*)
pintada Snelling and Zavortink, 1985 (*Ericrocis*)
rossi Linsley, 1939 (*Ericrocis*)
rugosa Fox, 1893 (*Ericrocis*)

Hopliphora Group

The two genera that comprise this group are characterized by the lack of tergal patches or bands of appressed pale hairs, the presence of a sternopleural ridge (weak in some *Hopliphora*), and the relatively long paraglossa (at least two-thirds as long as the prementum).

(A) Inner eye margins slightly convergent above. (B) Ocellocular distance equal to diameter of anterior ocellus. (C) Mandible with or without preapical tooth. (D) Maxillary palpus absent or three-segmented. (E) Hypostomal carina low, uniform. (F) Malus of protibia slender, shorter than velum, without teeth. (G) Mesobasitarsus compressed and carinate along posterior margin; distal process present, or not compressed and without distal process. (H) Meso- and meta-

distitarsi without lateral patches of short, flattened setae. (I) Metatarsus with or without posterior fringe. (J) Marginal cell of forewing about 0.75–1.8 times distance from its apex to wing tip; third submarginal cell usually more or less triangular. (K) Juncture of basal and discal faces of first tergum rounded. (L) Male seventh tergum bidentate at apex. (M) Male gonostylus with or without dorsal lobe.

The group is represented by the two South American genera *Hopliphora* and *Acanthopus.*

Genus *Hopliphora* Lepeletier

Figures 18–27, 61

Hopliphora Lepeletier, 1841:458. Type species: *Mesocheira velutina* Lepeletier and Serville, 1825 (monobasic).

Eurytis F. Smith, 1854:279. Type species: *Eurytis funereus* F. Smith, 1854 (monobasic).

Oxynedys Schrottky, 1902:491. Type species: (*Oxynedys beroni* Schrottky, 1902) = *Mesocheira velutina* Lepeletier and Serville, 1825 (monobasic and original designation).

Cyphomelissa Schrottky, 1902:493. Type species: (*Cyphomelissa pernigra* Schrottky, 1902) = *Melissa diabolica* Friese, 1900 (monobasic and original designation). NEW SYNONYMY.

Oxynedis: Moure, 1946:18, 27, 31 (lapsus).

DIAGNOSIS

Third submarginal cell receiving second recurrent vein only.

DESCRIPTION

(1) Head distinctly broader than long; inner eye margins essentially straight, slightly convergent above; occipital margin distinctly elevated above ocelli. (2) First segment of maxillary palpus distinctly shorter than second or third. (3) Labrum with transverse preapical ridge; apical margin convex to concave. (4) Interantennal distance distinctly greater than antennal socket diameter; antennocular distance distinctly less than antennal socket diameter. (5) Ocelloccipital distance greater than diameter of anterior ocellus. (6) Occipital margin abruptly rounded. (7) Antenna short in both sexes; minimum length of first flagellar segment less than width at apex and less, usually distinctly so, than length of second segment on same side.

(8) Pronotum not carinate between collar and posterior lobe. (9) Midline of mesoscutum broadly and deeply impressed on anterior three-fourths, less strongly so toward posterior margin; parapsidal lines not impressed. (10) Dorsal face of scutellum broadly impressed along midline and with a pair of suberect to erect blunt to subacute tubercles. (11) Anterior mesepisternal carina and acetabular carina absent; sternopleural ridge present, but often weak. (12) Supraspiracular ridge strong, terminating in stout, tooth-like process well above, and slightly behind, spiracle.

(13) Tegula (Fig. 63) oval, outer margin evenly curved. (14) Second submarginal cell, on M, as wide as, or wider than, first; third submarginal cell not at all narrowed, or greatly narrowed, anteriorly; 1st m-cu distinctly basad of 1st r-m; 2nd m-cu at, or a little beyond, middle of third submarginal cell; marginal cell 0.75 times as long as distance from its apex to wing tip.

(15) Mesotibial spur robust and very broad at apex (slender and parallel-sided in one species), outer distal tooth often indistinguishable from prominent intercalary teeth. (16) Metatrochanter rounded beneath; metatibia with two normal spurs; metadistitarsus 2.5–3.5 times longer than wide.

(17) Female sixth tergum with well-defined, sharply marginate pygidial plate, apex acute and reflexed, or narrowly rounded and flat. (18) Male fourth sternum with distal margins straight or broadly emarginate, with distal fringe of more or less prostrate long, dark, plumose hairs. (19) Male fifth sternum either fully exposed and with straight apical margin or hidden and with deeply emarginate margin, with or without distal fringe. (20) Male seventh sternum with margin angularly (Fig. 18) or broadly (Fig. 23) produced. (21) Male eighth sternum variously produced. (22) Male gonostylus short, thick, blunt; dorsal lobe present (Fig. 22) or absent (Fig. 27); inner apical sclerotized portion of gonocoxite distinct. (23) Penis valve evenly curved ventrad; basolateral lobe obsolete (Figs. 22–27).

DISCUSSION

Those species in which the third submarginal cell is triangular, or even petiolate, have traditionally been placed in the separate genus *Cyphomelissa.* However, species assigned to *Hopliphora* have the third submarginal cell so strongly narrowed anteriorly that the difference becomes one of degree only. It is not enough, in our opinion, to place these two groups of species in separate genera.

Superficially, some species of *Mesonychium* look much like small *Hopliphora* and were included in *Cyphomelissa* by Schrottky (1902). The following names are applicable to *Hopliphora* as we understand the genus.

INCLUDED NAMES

beroni (Schrottky, 1902) (*Oxynedys*)
commata (Moure, 1958) (*Cyphomelissa*)
diabolica (Friese, 1900) (*Melissa*)
funereus (F. Smith, 1854) (*Eurytis*)
iheringi (Schrottky, 1902) (*Acanthopus*)
magnifica (Moure, 1958) (*Cyphomelissa*)
pernigra (Schrottky, 1902) (*Cyphomelissa*)
superba (Ducke, 1902) (*Melissa*)
velutina (Lepeletier and Serville, 1825) (*Mesocheira*)

Genus *Acanthopus* Klug

Figures 13–17, 62, 70, 71

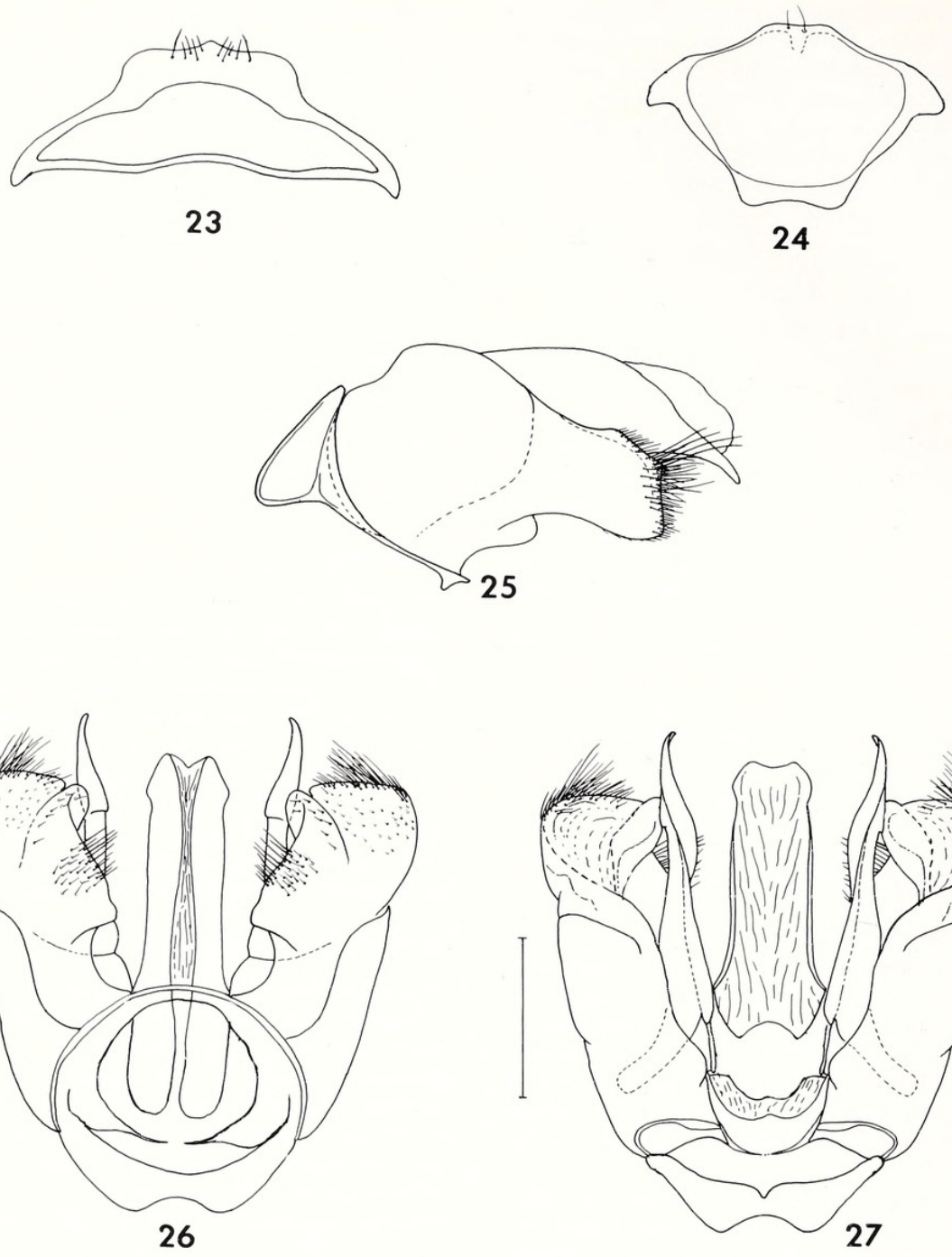
Acanthopus Klug, 1807:199, 226. Type species: (*Apis splendida* Fabricius, 1793) = *Apis palmata* Olivier, 1789 (monobasic).

DIAGNOSIS

Third submarginal cell receiving both recurrent veins.

DESCRIPTION

(1) Head distinctly broader than long; inner eye margins essentially straight, distinctly convergent above; occipital

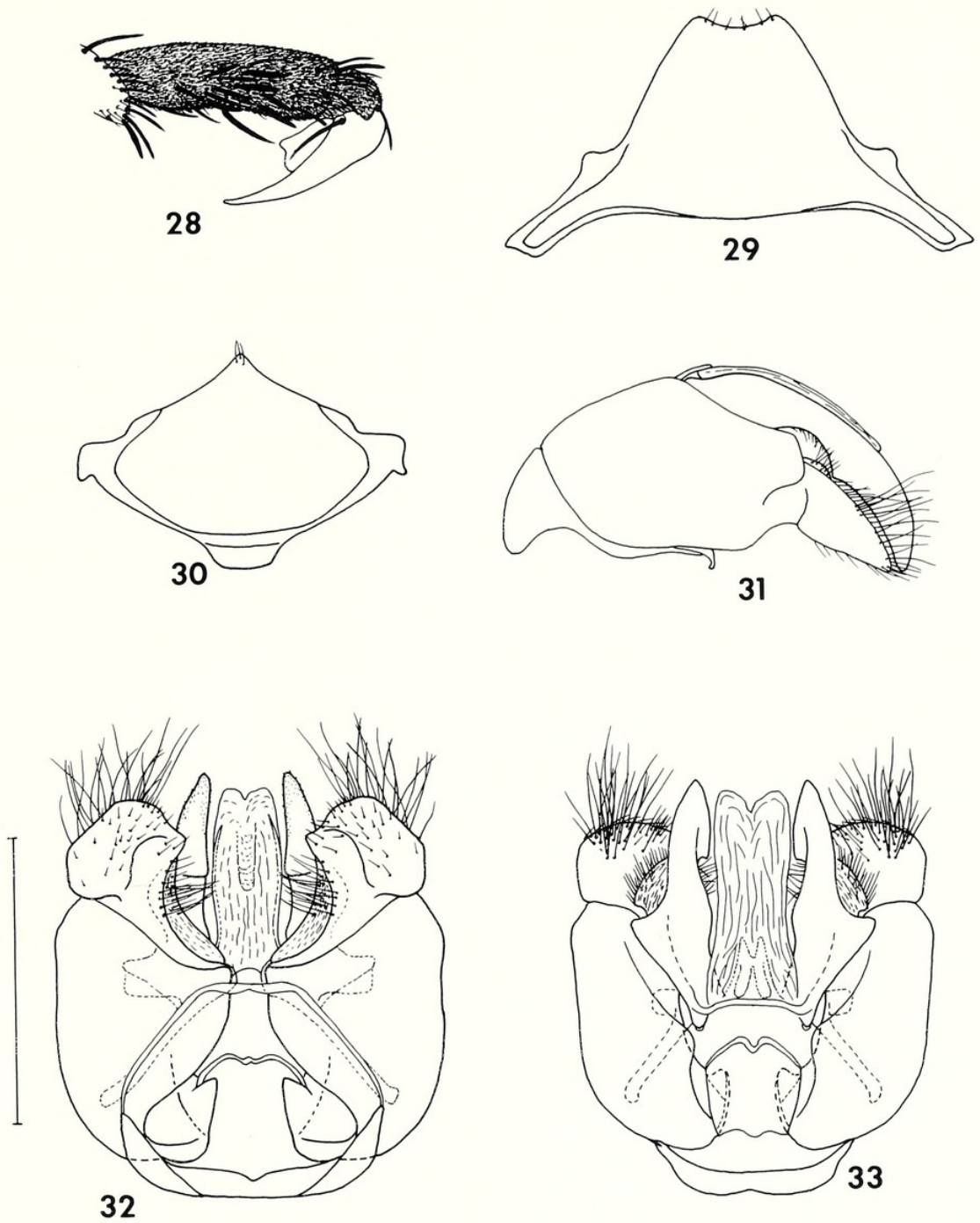


Figures 23-27. *Hopliphora superba,* male. **23,** sternum 7; **24,** sternum 8; **25-27,** genital capsule, lateral, ventral, and dorsal view. Scale line = 1.00 mm.

margin broadly convex and distinctly elevated above ocelli. (2) Maxillary palpus absent. (3) Labrum with narrow, short transverse preapical ridge; distal margin weakly, broadly convex. (4) Interantennal distance less than antennal socket diameter. (5) Ocelloccipital distance about three times diameter of anterior ocellus. (6) Occipital margin abruptly rounded. (7) Antenna short in both sexes; minimum length of first flagellar segment greater than apical width and greater than length of second or third segments on same side.

(8) Pronotum not carinate between collar and posterior lobe. (9) Midline of mesoscutum deeply impressed for entire length; parapsidal lines not impressed. (10) Dorsal face of scutellum deeply impressed in middle, with a pair of erect, conical tubercles. (11) Anterior mesepisternal carina present; acetabular carina obsolete in middle; sternopleural ridge present. (12) Supraspiracular ridge weak, evanescent distad.

(13) Tegula (Fig. 62) elliptical, outer margin evenly curved, posterior margin oblique. (14) Second submarginal cell about

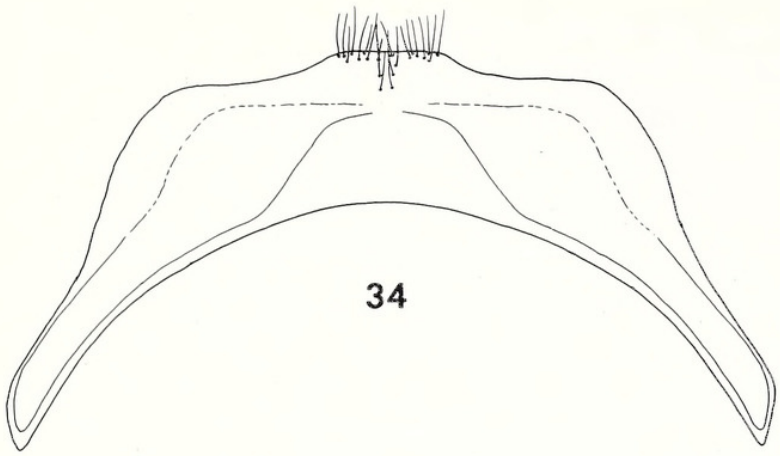


Figures 28-33. *Mesonychium coerulescens.* **28,** metadistitarsus, lateral view; **29,** male sternum 7; **30,** male sternum 8; **31-33,** male genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm (Figs. 29–33 only).

as broad as long; third submarginal cell on M longer than first or second, receiving 1st and 2nd m-cu, latter near mid-length; marginal cell 1.8 times as long as distance from its apex to wing tip.

(15) Mesotibial spur wide, outer spine much longer than inner, surface between strongly oblique and with three long, widely spaced intercalary teeth. (16) Metatrochanter rounded beneath; metatibial spurs normal, outer spur strongly curved at tip; metadistitarsus about six times longer than wide.

(17) Female sixth tergum with short, subtruncate pygidial plate. (18) Male fourth sternum deeply, subangularly incised and with a prostrate fringe of long hairs. (19) Male fifth sternum largely hidden, posterior margin deeply incised and with distal fringe of prostrate hairs. (20) Male seventh sternum (Fig. 13) with posterior margin broadly and somewhat irregularly produced, apically acuminate. (21) Male eighth sternum (Fig. 14) moderately produced, apex weakly emarginate. (22) Male gonostylus short, broad, thickly digitiform



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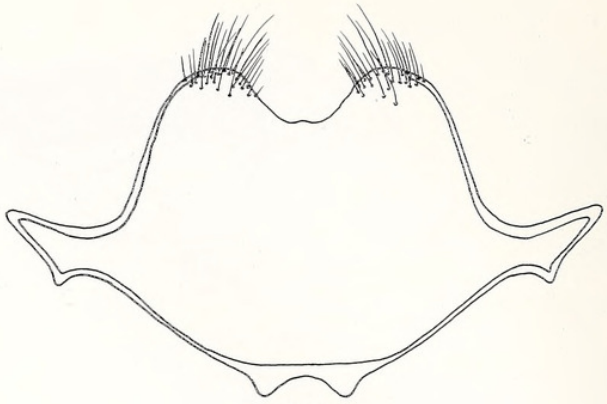

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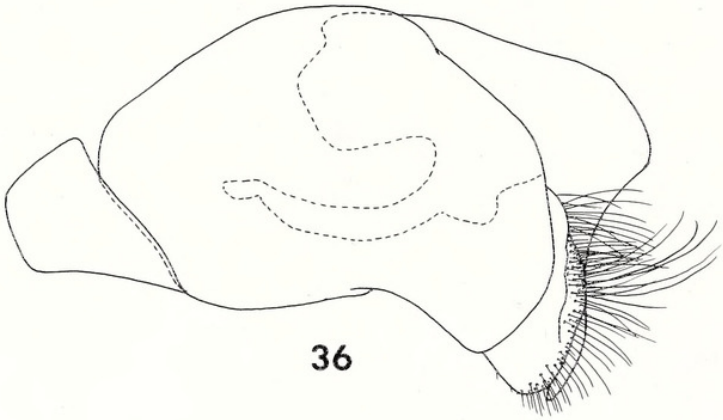

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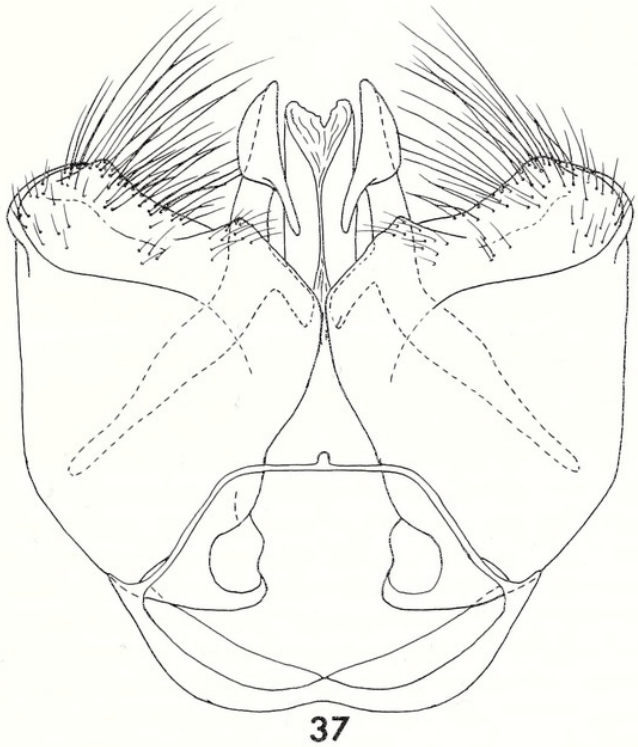

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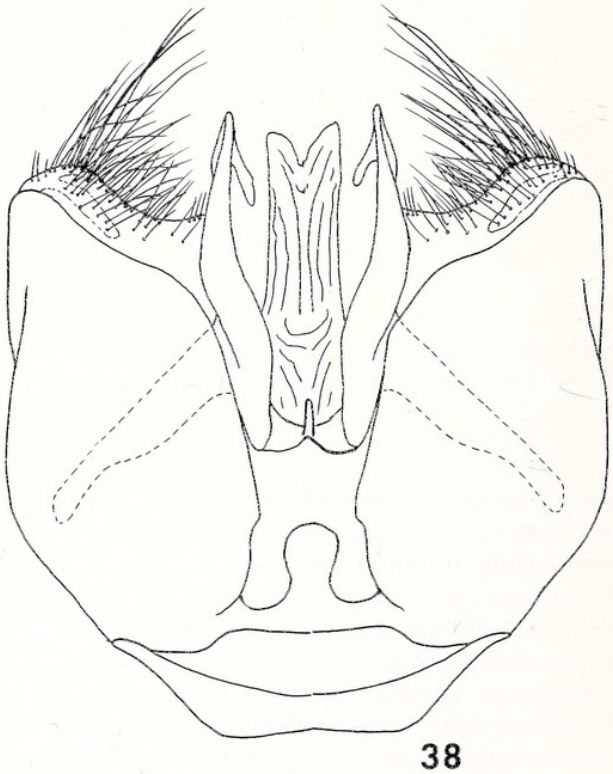

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Table 3. Known or suspected hosts of Ctenioschelini.

Parasitoid	Host	Authority
Mesoplia dugesi	*Centris anomala* Snelling	Snelling, 1984[1]
Mesoplia rufipes	*Centris carrikeri* Cockerell	Rozen, 1969
	Centris inermis Friese (as *C. segregata* Crawford)	Coville et al., 1983
	Epicharis albofasciata F. Smith	Rozen, 1969
Mesonychium gayi	*Centris chilensis* Spinola	Wagenknecht, 1974
	Centris cineraria F. Smith	Wagenknecht, 1974
	Centris nigerrima Spinola	Wagenknecht, 1974
	Centris rhodophthalma Perez	Wagenknecht, 1974
Mesonychium jenseni	*Centris autrani* Vachal	Wagenknecht, 1974
Mesonychium wagenknechti	*Centris chilensis* Spinola	Wagenknecht, 1974
	Centris rhodophthalma Perez	Wagenknecht, 1974
Abromelissa lendliana	*Centris cineraria* F. Smith	Wagenknecht, 1974
	Centris nigerrima Spinola	Wagenknecht, 1974
	Centris orellanai Ruiz	Wagenknecht, 1974
	Centris rhodophthalma Perez	Wagenknecht, 1974
Aglaomelissa duckei	*Centris carrikeri* Cockerell	NEW RECORD[2]
Acanthopus palmatus (as *A. splendidus urichi*)	*Ptilotopus derasus* (Lepeletier)	Rozen, 1969

[1] Suspected host—observed at nest site.

[2] Suspected host—observed at nest site (J.G. Rozen, Jr., personal communication).

in profile; dorsal lobe long, slender; inner apical sclerotization of gonocoxite small but distinct. (23) Penis valve abruptly deflected ventrad; basolateral lobe absent (Fig. 17).

DISCUSSION

The unusual wing venation (elongate marginal cell and second submarginal cell receiving both recurrent veins) and the conspicuous peculiar fringes on the metatarsi will immediately separate *Acanthopus* from other genera of ericrocines.

There is apparently but a single species, ranging from Trinidad and the Guianas to Brazil. The one known host is a species of *Ptilotopus* (Table 3).

INCLUDED NAMES

excellens Schrottky, 1902 (*Acanthopus*)
jheringi Friese, 1904 (*Acanthopus*)
palmata (Olivier, 1789) (*Apis*)
splendida (Fabricius, 1793) (*Apis*)
urichi Cockerell, 1926 (*Acanthopus*)

Mesoplia Group

Diagnostic for this group are the elongate segments of the maxillary palpus, the male lacks felt-like pads of pubescence along the apical margins of metasomal sterna 4 and 5 (shared with the *Mesonychium* group), and male sternum 5 is broadly emarginate and largely concealed under sternum 4. The inner eye margins are approximately parallel, rather than divergent above as in the *Mesonychium* group.

(A) Inner eye margins weakly to distinctly divergent above. (B) Ocellocular distance less than, equal to, or greater than diameter of anterior ocellus. (C) Mandible with adnate preapical tooth. (D) Maxillary palpus three- or four-segmented. (E) Hypostomal carina moderately high, lamelliform. (F) Malus of protibia short to long, usually with one or two teeth along inner margin. (G) Mesobasitarsus compressed and carinate along posterior margin; distal process present. (H) Meso- and metadistitarsi without lateral patches of short, flattened setae. (I) Metatarsus without posterior fringe. (J) Marginal cell of forewing 0.90–0.94 distance from its apex to wing tip. (K) Juncture of basal and discal faces of first tergum rounded. (L) Male seventh tergum bilobate at apex. (M) Male gonostylus with dorsal lobe.

Only the genus *Mesoplia* is included in this group which ranges from the southwestern United States (Arizona) to Argentina.

Genus *Mesoplia* Lepeletier

Figures 1–12, 63, 64, 75

Mesoplia Lepeletier, 1841:457. Type species: *Mesocheira azurea* Lepeletier and Serville, 1825 (monobasic).

←

Figures 34–38. *Ericrocis lata,* male. **34,** sternum 7; **35,** sternum 8; **36–38,** genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.

Melissa F. Smith, 1854:279. Type species: *Mesocheira azurea* Lepeletier and Serville, 1825 (designation of Sandhouse, 1943:570).

DIAGNOSIS

Same as description for *Mesoplia* group.

DESCRIPTION

(1) Head distinctly broader than long; inner eye margins essentially straight, subparallel to divergent above; occipital margin nearly straight to low-convex, slightly, or not at all, elevated above ocelli. (2) Maxillary palpus, except first segment, slender and elongate, segments more or less fused but recognizable. (3) Labrum with transverse preapical ridge; apical margin subtruncate. (4) Interantennal distance greater than antennal socket diameter; antennocular distance less than antennal socket diameter. (5) Ocelloccipital distance equal to, or greater than, diameter of anterior ocellus. (6) Occipital margin rounded. (7) Antenna short in both sexes; minimum length of first flagellar segment less than apical width and distinctly less than length of second segment on same side.

(8) Pronotum with or without carina between collar and front of posterior lobe. (9) Midline of mesoscutum impressed for most of its length; parapsidal lines weakly, or not, impressed. (10) Dorsal face of scutellum impressed along midline, with suberect to erect mammiform tubercle on each side. (11) Anterior mesepisternal carina, acetabular carina and sternopleural ridge absent. (12) Supraspiracular ridge weak, terminating well before spiracle.

(13) Tegula shape as in Figures 60 and 61, narrowed in front, outer margin more or less sinuate. (14) First submarginal cell, on M, as wide as, or wider than, second or third; second and third submarginal cells narrowed anteriorly; 1st m-cu interstitial with 1st r-m; 2nd m-cu at, or a little distad of, middle of third submarginal cell.

(15) Mesotibial spur usually moderately broadened distad and with one or more distinct intercalary teeth, but may be parallel-sided for entire length. (16) Metatrochanter rounded beneath; metatibial spurs of female normal; of male, normal or with two very short, stout spurs or with a single short, stout spur; metadistitarsus two and one-half to three times longer than wide.

(17) Female sixth tergum with well-defined pygidial plate, apex narrowly to broadly rounded. (18) Male fourth sternum weakly to strongly concave along apical margin, with or without distal fringe of long, plumose hairs. (19) Male fifth sternum hidden, distal margin deeply incurved and usually with distal fringe of long, plumose hairs. (20) Male seventh sternum either (a) quadrately produced distad and with dense patch of dark, bristle-like setae (Fig. 3) or (b) with posterior margin more or less triangular, apex acute, truncate or bilobed, and with scattered normal setae (Fig. 8). (21) Male eighth sternum with small apical process which may be acute, truncate or bilobate (Figs. 4, 9). (22) Male gonostylus short, broad, thick and deflected ventrad (Figs. 5–7) or short, broad, thin and curved mesad above the inner apical sclerotization of the gonocoxite (Figs. 10–12). (23) Penis valves evenly curved, or abruptly deflected, ventrad; basolateral lobe distinct.

DISCUSSION

Mesoplia includes a dozen or so species ranging from southern Arizona in the United States southward to northern Argentina. The genus is apparently absent from Chile and most of the species occur in the Amazonian region of South America.

We have herein divided *Mesoplia* into two subgenera. The males of the two subgenera are especially different in details of the genitalia and associated sterna and these segregates may be better regarded as distinct genera. However, the magnitude of differences in the males is not reflected in the females. Until all of the species of *Mesoplia* in the broad sense can be critically examined, we believe that generic separation of the two segregates recognized here would be premature.

Known and suspected hosts are all species of *Centris* and *Epicharis* (Table 3).

Subgenus *Mesoplia*

Figures 1–7, 60

DIAGNOSIS

MALE. With a single metatibial spur or with two very short, stout spurs, the longer not extending beyond basal one-third of metabasitarsus; metafemur often with robust basal tooth-like projection ventrally; metatibia with inner, distal patch of black hairs. Female: pygidium broad, densely covered with appressed iridescent scales; dorsal surface of metacoxa angulate or carinate at juncture with anterior face.

DESCRIPTION

(24) Ocellocular distance equal to, or (usually) greater than, diameter of anterior ocellus. (25) Pronotum with or without low carina from collar to front of posterior lobe. (26) Dorsal face of metacoxa sharply subangulate or carinate where it meets anterior and posterior faces. (27) Metafemur of male with or without stout, tooth-like basoventral projection. (28) Metatibia of male with inner, distal hair patch and with one or two apical spurs; if with two apical spurs, both short and stout, neither extending beyond basal one-third of metabasitarsus. (29) Tegula shape as in Figure 60. (30) Female pygidium broad, apex broadly rounded, disc covered with appressed metallic scales. (31) Male seventh sternum (Fig. 3) quadrately produced and with distal patch of short, dense, stout, black setae. (32) Male gonostylus short, broad, thick, deflected ventrad (Fig. 5); dorsal lobe short, broad. (33) Basolateral process of penis valve relatively stout (Fig. 7).

DISCUSSION

This subgenus, with species ranging from the southwestern United States to Argentina, includes two distinctive species groups. In both sexes of the *M. azurea* group (*sensu* Moure, 1960a, b) there is a low carina extending laterad from the

pronotal collar to the front of the posterior lobe. In the males, the metafemur has a stout, basal projection on the ventral surface and there is a single metatibial spur.

The *M. bifrons* group (*sensu* Moure, 1960a, b) includes species that do not possess a carina between the pronotal collar and the posterior lobe. Males do not have a basoventral projection on the metafemur and there are two short, stout metatibial spurs.

In the following list, names marked by an asterisk (*) belong to the *M. azurea* group and those marked with a dagger (†) belong to the *M. bifrons* group; group placement is uncertain for those names that are unmarked.

INCLUDED NAMES

**azurea* (Lepeletier and Serville, 1825) (*Mesocheira*)
†bifrons (Fabricius, 1804) (*Melecta*)
chalybea (Friese, 1912) (*Melissa*)
chiruana (Holmberg, 1885) (*Melissa*)
**dugesi* (Cockerell, 1917) (*Mesonychium*)
**guatemalensis* Cockerell, 1912 (*Mesoplia*)
**imperialis* (Ashmead, 1900) (*Melissa*)
†imperialis (Friese, 1912) (*Melissa*) PREOCCUPIED
†imperatrix (Friese, 1913) (*Melissa*)
†insignis (F. Smith, 1879) (*Melissa*)
itaitubina (Ducke, 1902) (*Melissa*)
maculata (Friese, 1900) (*Melissa*)
ornata (Spinola, 1841) (*Mesocheira*)
†pilicrus (Friese, 1902) (*Melissa*)
pretiosa (Friese, 1912) (*Melissa*)
†regalis (F. Smith, 1854) (*Melissa*)
**rufipes* (Perty, 1833) (*Crocisa*)
simillima Schrottky, 1920 (*Mesoplia*)

Eumelissa, new subgenus

Figures 8–12, 61

DIAGNOSIS

MALE. Metatibial spurs normal, inner spur extending to, or beyond, midlength of metabasitarsus; metafemur without basal tooth; metatibia without inner, distal seta patch. Female: pygidium narrow, shiny, surface bare; metacoxa rounded above, neither carinate nor angulate at juncture with anterior face.

DESCRIPTION

(24) Ocellocular distance equal to, or less than, diameter of anterior ocellus. (25) Pronotum without carina between collar and front of posterior lobe. (26) Metacoxa abruptly rounded between dorsal and lateral faces, not angulate or subcarinate. (27) Metafemur of male without basal tooth or projection. (28) Metatibia of male without inner, distal patch of setae and with two normal apical spurs, the longer extending to, or beyond, midlength of metabasitarsus. (29) Tegula (Fig. 61) elliptical, narrowed behind. (30) Female pygidium completely marginate, narrow, apex narrowly rounded, disc bare and shiny. (31) Female sixth sternum weakly carinate along midline. (32) Male seventh sternum (Fig. 8) with apical margin somewhat triangularly produced in middle, apex acute, truncate or bilobate, with a few short, simple setae. (33) Gonostylus of male short, broad, curved mesad over inner plate (Fig. 11); dorsal lobe elongate. (34) Basolateral process of penis valve relatively slender (Fig. 12)

TYPE SPECIES

Melissa decorata F. Smith, 1854.

ETYMOLOGY

Greek prefix *eu-* (beautiful) plus *melissa* (bee).

DISCUSSION

Males of this subgenus are easily recognized by the unmodified metafemur and metatibia, as well as by the genitalia and associated structures. Both sexes share the unmodified metacoxa, the dorsal surface of which is distinctly rounded into the anterior and posterior surfaces, rather than carinate or sharply subangulate as in species of *Mesoplia* s. str. Females otherwise are very similar to those of the nominate subgenus but differ in the narrow, shiny pygidial plate which is devoid of the dense covering of metallic scales characteristic of that subgenus.

The included species are all South American, but we have seen both sexes of a possibly undescribed species from Costa Rica. Moure (1960b) included *Melissa duckei* Friese with this group of species, but in our opinion this species is not congeneric and is the type species for the genus *Aglaomelissa,* described below.

INCLUDED NAMES

albogutta (Ducke, 1905) (*Melissa*)
albopunctata Moure, 1967 (*Mesoplia*)
decorata (F. Smith, 1854) (*Melissa*)
friesei (Ducke, 1902) (*Melissa*)
guedesii (Ducke, 1902) (*Mesocheira*)

Mesonychium Group

Diagnostic characteristics of this group are inner eye margins divergent above (shared with *Ericrocis* group); strigilar malus without teeth (shared with *Aglaomelissa* in the *Ctenioschelus* group); the mesocoxa is less than 1.35 times the distance from the summit of the coxa to the base of the hind wing; metasomal sternum 3 of the male is without a dense lateral patch of white hair; and, male sterna 4 and 5 are without felt-like pads of pubescence along the apical margins. Metallic, scale-like hairs are present in *Mesonychium,* but absent in *Abromelissa,* in which the metasomal integument is metallic bluish, a unique apomorphy within the Ericrocini.

(A) Inner eye margins divergent above, often strongly so. (B) Ocellocular distance greater than diameter of anterior ocellus. (C) Mandible with preapical tooth. (D) Maxillary palpus one- or two-segmented. (E) Hypostomal carina low, uniform. (F) Malus of protibia short, one-half or less length of velum, inner margin simple. (G) Mesobasitarsus usually

compressed and more or less sharply carinate along posterior margin; distal process usually present. (H) Meso- and metadistitarsi with lateral patch of short, flattened setae on each side (Fig. 28) (except *Abromelissa* and a few *Mesonychium*). (I) Metatarsus without posterior fringe. (J) Marginal cell of forewing 0.60–0.94 times distance from its apex to wing tip. (K) Juncture of basal and discal faces of first tergum rounded. (L) Male seventh tergum bilobate at apex or with two stout teeth. (M) Gonostylus without dorsal lobe.

The two included genera, *Mesonychium* and *Abromelissa* are confined to South America.

Genus *Mesonychium* Lepeletier and Serville

Figures 28–33, 65

Mesonychium Lepeletier and Serville, 1825:107. Type species: *Mesonychium coerulescens* Lepeletier and Serville, 1825 (monobasic).

Epiclopus Spinola, 1851:183. Type species: *Epiclopus gayi* Spinola, 1851 (monobasic).

DIAGNOSIS

Abdomen with appressed metallic scales or hairs; labrum with transverse preapical ridge which may be divided in middle; scutellum usually bituberculate.

DESCRIPTION

(1) Head much broader than long; inner eye margins straight, moderately to strongly divergent above; occipital margin little, if any, elevated above ocelli. (2) Maxillary palpus consisting of a single short, spindle-shaped segment. (3) Apical margin of labrum subtruncate; preapical transverse ridge (sometimes interrupted in middle) present. (4) Interantennal distance greater than antennal socket diameter; antennocular distance greater than antennal socket diameter. (5) Ocelloccipital distance greater than diameter of anterior ocellus. (6) Occipital margin abruptly rounded to subangulate. (7) Antenna short in both sexes; minimum length of first flagellar segment distinctly less than, to about equal to, apical width and much shorter than, to as long as, length of second segment on same side.

(8) Pronotum not carinate between collar and posterior lobe. (9) Midline of mesoscutum impressed for nearly its entire length; parapsidal lines weakly impressed, if at all. (10) Dorsal face of scutellum broadly, often weakly, impressed along midline; with a pair of erect, mammiform tubercles or (one species) no tubercles. (11) Anterior mesepisternal carina, acetabular carina, and sternopleural ridge absent. (12) Supraspiracular ridge weak to moderately strong, terminating in a stout tooth or projection above spiracle. (13) Tegula (Fig. 64) elliptical, outer margin evenly curved. (14) Second submarginal cell, on M, wider than, or equal to, first and wider than third; third submarginal cell narrowed anteriorly, sometimes triangular or petiolate; 1st m-cu basad of, or interstitial with, 1st r-m; 2nd m-cu distinctly basad of 2nd r-m.

(15) Mesotibial spur long, slender, parallel-sided, outer distal tooth obsolete. (16) Metatrochanter rounded beneath; metatibial spurs normal; metadistitarsus less than three times longer than wide.

(17) Female sixth tergum with short, distinct pygidial plate, apex narrowly rounded to subtruncate. (18) Male fourth sternum usually concealed under third, its apical margin broadly, deeply incurved. (19) Male fifth sternum exposed, apical margin broadly, shallowly incurved or subtruncate. (20) Male seventh sternum (Fig. 29) more or less produced in middle, subtruncate to bilobate at apex. (21) Male eighth sternum (Fig. 30) with apical margin little produced. (22) Male gonostylus short and broad in dorsal view, stoutly digitiform in lateral view; dorsal lobe absent; inner apical sclerotization of gonocoxite usually well defined. (23) Penis valve weakly curved ventrad; basolateral lobe prominent (Fig. 33).

DISCUSSION

Mesonychium has never been adequately distinguished from *Mesoplia* by previous workers. Although species in the two genera are often somewhat similar in appearance, the two are distinct. Most species of *Mesonychium,* for example, possess very distinct patches of flattened setae on the meso- and metadistitarsi, which are lacking in *Mesoplia.* Male gonostyli lack dorsal lobes in species of *Mesonychium* and in both sexes of this genus the inner eye margins are moderately to strongly divergent above. *Mesonychium* is similar to the Nearctic genus *Ericrocis,* from which it is easily separated by the presence of metallic blue or green hairs and/or scales on various areas of the body.

Mesonychium appears to be an exclusively South American genus with species in Peru and Brazil south to Argentina and Chile. Within the genus there are two principal groups. The first of these includes the generotype and a few other species in which the meso- and metadistitarsi bear a cluster of short, flattened setae on each side and the pubescence of the head and body are generally dark. In a few species in this group the pubescence of the thoracic dorsum is very short and sparse. Species assigned to the *M. coerulescens* group include: *M. asteria* (F. Smith), *M. garleppi* (Schrottky), *M. jenseni* (Friese), *M. littoreum* Moure, *M. viridescens* (Friese), and *M. viridis* (Friese).

A second group of species lacks the distitarsal setae and in most the thorax and first two abdominal segments are densely clothed with long, erect white hairs; at least one species is dark haired. The species of this second group include those previously assigned to *Epiclopus,* but this group is so diverse in its morphological features that use of that name, even as a subgenus, would not be appropriate at this time. The following species belong to this group: *M. gayi* (Spinola), *M. wagenknechti* Ruiz, and an undescribed Peruvian species.

Although *M. lendlianum* (Friese) has traditionally been associated with such other Chilean species as *M. gayi,* which it resembles, it is anomalous in *Mesonychium,* and is the sole representative of the new genus *Abromelissa,* described below.

INCLUDED NAMES

albescens (Friese, 1921) (*Melissa*)
andina (Friese, 1925) (*Melissa*)
asteria (F. Smith, 1854) (*Mesocheira*)

coerulescens Lepeletier and Serville, 1825 (*Mesonychium*)
chilensis (F. Smith, 1854) (*Melecta*)
garleppi (Schrottky, 1910) (*Cyphomelissa*)
gayi (Spinola, 1851) (*Epiclopus*)
jenseni (Friese, 1906) (*Melissa*)
littoreum Moure, 1944 (*Mesonychium*)
porteri (Herbst, 1917) (*Melissa*)
violacea (Friese, 1900) (*Melissa*)
viridescens (Friese, 1930) (*Melissa*)
viridis (Friese, 1900) (*Melissa*)
wagenknechti Ruiz, 1938 [*Mesonychium* (*Epiclopus*)]

Abromelissa, new genus

Figures 39–43, 66

DIAGNOSIS

Separable from all other ericrocine genera by the metallic blue integument of the abdominal terga, without appressed metallic-reflective scales or hairs; further separable from *Mesonychium* and *Ericrocis* by the presence of a long cylindrical dorsal lobe on the male gonostylus, and in both sexes by the broader than long abdomen.

DESCRIPTION

(1) Head much broader than long; inner eye margin straight, moderately divergent above; ocelli on top of preocciput. (2) Maxillary palp three-segmented, first segment very short, second more than twice longer than first and about 1.5 times longer than third. (3) Apical margin of labrum subtruncate; preapical transverse ridge present and entire. (4) Interantennal distance greater than antennal socket diameter; antennocular distance greater than antennal socket diameter. (5) Ocelloccipital distance greater than diameter of anterior ocellus. (6) Occipital margin abruptly rounded. (7) Antenna short in both sexes; minimum length of first flagellar segment greater than apical width and greater than length of second segment on same side.

(8) Pronotum not carinate between collar and posterior lobe. (9) Midline of mesoscutum impressed almost to posterior margin; parapsidal lines not impressed. (10) Dorsal face of scutellum barely impressed along midline and without mammiform tubercles, but with a pair of sublateral, short, erect spines at margin of declivity. (11) Anterior mesepisternal carina, acetabular carina and sternopleural ridge absent. (12) Supraspiracular ridge strong, ending in a stout, blunt projection above spiracle.

(13) Tegula pyriform (Fig. 66). (14) Second submarginal cell, on M, wider than either first or third; third submarginal cell narrower on Rs than on M; 1st m-cu interstitial with 1st r-m; 2nd m-cu much basad of 2nd r-m.

(15) Mesotibial spur long, slender, parallel-sided, outer distal tooth obsolete. (16) Metatrochanter rounded beneath; metatibial spurs normal; metadistitarsus less than three times longer than wide and without lateral patch of short, flattened setae.

(17) Female sixth tergum with short, distinct pygidial plate, apex narrowly rounded. (18) Male fourth sternum exposed, its apical margin transverse and with a dense fringe of decumbent, long, dark hairs. (19) Male fifth sternum normally visible only at extreme sides, its apical margin broadly and shallowly incurved and partially concealed under fourth. (20) Male seventh sternum (Fig. 39) with well-developed distal lobe, weakly trilobate. (21) Male eighth sternum (Fig. 40) with apical margin moderately produced. (22) Male gonostylus (Fig. 43) with dorsal, elongate, cylindrical lobe; inner apical sclerotization of gonocoxite short, broad and concave on dorsal face (Fig. 42), stout and subtruncate in lateral view (Fig. 41). (23) Penis valve strongly curved ventrad; basolateral lobe prominent.

TYPE SPECIES

Melissa (*Epiclopus*) *lendliana* Friese, 1910.

ETYMOLOGY

Combines Greek *habros* (graceful or pretty) with *melissa* (bee).

DISCUSSION

This genus includes only the type species, found in Argentina (Provinces of Neuquen and Valdivia) and Chile (Provinces of Aconcagua, Coquimbo, Valparaiso, Santiago, Ñuble, Curico, and Aisen). *Melissa friesei* Herbst, 1918 (not *M. friesei* Ducke, 1902) and *Mesonychium frieseanum* Ruiz, 1938, are synonyms of *A. lendliana* (NEW SYNONYMIES). The one species of *Abromelissa* superficially resembles two Chilean species of *Mesonychium, M. gayi* and *M. wagenknechti,* since the hairs of the thorax and first tergum are long, erect and pale, and there are no short, appressed, metallic-reflective scales on the body. From both of these, however, it differs in the dark metallic blue color of the tergal integument, a feature which appears to be unique within the tribe.

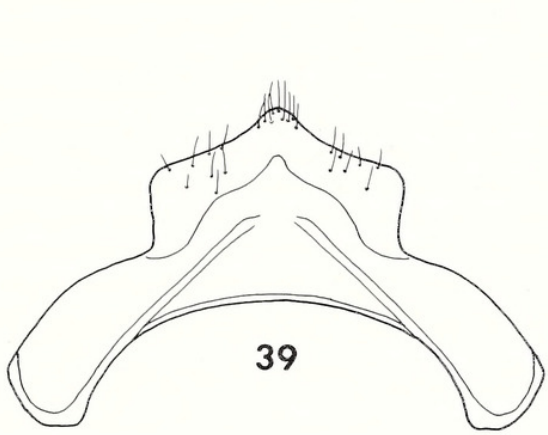
In addition to the characteristics described above, there are a few other features of *Abromelissa* that are distinctive within the *Mesonychium* group. The surface of the mesoscutum is smooth and shiny between subcontiguous coarse punctures and sparse giant punctures, and the scutellum is coarsely rugosopunctate and foveolate on the dorsal face. Although the mesobasitarsus is without a ridge along its posterior margin, an inconspicuous distal process is present. The male pygidial plate is narrowly translucent at its apex and is weakly bilobate.

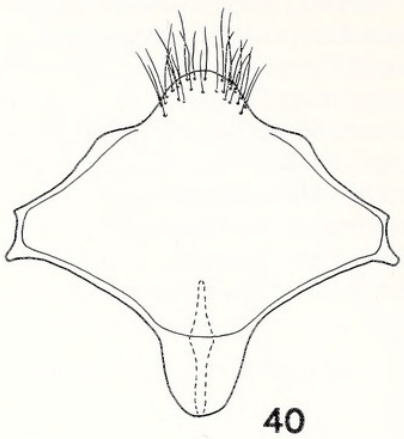
The known hosts are all species of *Centris* in the subgenera *Paracentris* and *Wagenknechtia* (Table 3).

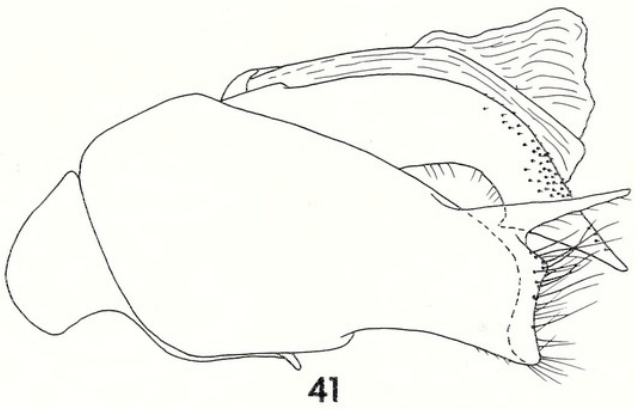
Ctenioschelus Group

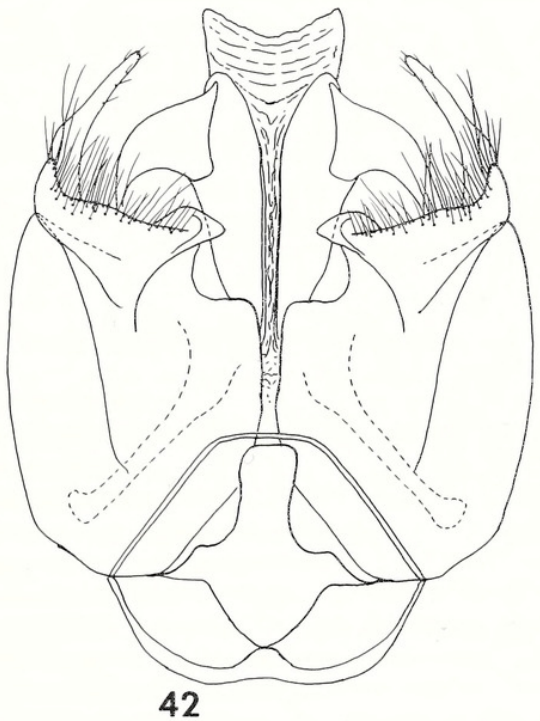
Several unique apomorphies define the *Ctenioschelus* group: the preapical tooth is lost; the forewing tips are infuscated; metasomal tergum 7 is subangulate in profile (Fig. 76). Arolia are present (except in *Mesocheira*) and an anterior mesepisternal carina is present (except in *Ctenioschelus*).

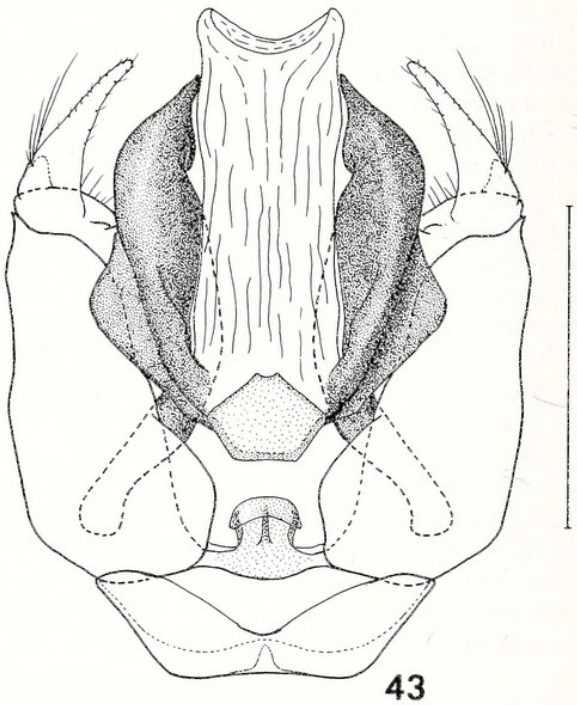
(A) Inner eye margins subparallel or weakly convergent above. (B) Ocellocular distance less than diameter of anterior ocellus. (C) Mandible without preapical tooth, sometimes fused with stipes. (D) Maxillary palpus consisting of one short segment. (E) Hypostomal carina high, lamelliform. (F) Malus











Figures 39-43. *Abromelissa lendlianum,* male. **39,** sternum 7; **40,** sternum 8; **41-43,** genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.

of protibia short (0.25 or less length of velum), stout, simple. (G) Mesobasitarsus neither compressed nor carinate along posterior margin; distal process absent. (H) Meso- and metadistitarsi without lateral patches of short, flattened setae. (I) Metatarsus without posterior fringe. (J) Marginal cell of forewing 1.0–1.2 times distance from its apex to wing tip. (K) Juncture of basal and discal faces of first tergum slightly elevated and subangulate. (L) Male seventh tergum bidentate, teeth well separated. (M) Male gonostylus absent or, if present, without dorsal lobe.

The three genera, *Aglaomelissa, Ctenioschelus,* and *Mesocheira* occur in Central and South America.

Aglaomelissa, new genus

Figures 44–48, 67

DIAGNOSIS

Separable from *Ctenioschelus* and *Mesocheira* by the following combination of characteristics: male antenna short; anterior mesepisternal carina present; scutellar prominences mammiform; marginal cell of forewing without apical cloud.

DESCRIPTION

(1) Head a little broader than long; inner eye margins straight, slightly convergent above; occipital margin elevated above ocelli. (2) Maxillary palpal segment short, broad, lightly sclerotized and fused to stipes. (3) Labrum without preapical tubercle or transverse ridge; apical margin slightly produced and truncate. (4) Interantennal distance slightly greater than antennal socket diameter; antennocular distance about equal to one-half antennal socket diameter. (5) Ocelloccipital distance about two times diameter of anterior ocellus. (6) Occipital margin subcarinate. (7) Antenna short in both sexes; minimum length of first flagellar segment less than greatest width and distinctly less than length of second segment on same side.

(8) Pronotum not carinate between collar and posterior lobe. (9) Midline of mesoscutum impressed almost to posterior margin; parapsidal lines not impressed. (10) Dorsal face of scutellum broadly impressed in middle and with a pair of suberect mammiform tubercles. (11) Anterior mesepisternal carina sharp, lamelliform and confluent with acetabular carina, or nearly so; sternopleural ridge absent. (12) Supraspiracular ridge evanescent where its distal portion turns ventrad.

(13) Tegula (Fig. 67) elliptical, outer margin narrowed anteriorly. (14) Submarginal cells about equally long on M, third much narrowed anteriorly; 1st m-cu interstitial with 1st r-m; 2nd m-cu distinctly basad of 2nd r-m; marginal cell about as long as distance from apex to wing tip.

(15) Mesotibial spur stout, apex broad, with 1–3 elongate intercalary teeth. (16) Metatrochanter compressed and subangular below; outer metatibial spur short, stout, strongly curved at apex; metadistitarsus about twice longer than wide.

(17) Female sixth tergum with well-defined, narrow pygidial plate, apex subacute. (18) Male fourth sternum broadly incurved and with distal fringe of long, plumose, prostrate hairs. (19) Male fifth sternum more shallowly incurved and with shorter distal fringe. (20) Male seventh sternum (Fig. 44) with median lobe on apical margin. (21) Male eighth sternum (Fig. 45) with apical margin produced, emarginate, and narrowly truncate in middle. (22) Male gonostylus absent (Figs. 46, 47) inner apical sclerotization of gonocoxite distinct. (23) Penis valve evenly curved ventrad; basolateral lobe absent.

TYPE SPECIES

Melissa (*Mesocheira*) *duckei* Friese, 1906.

ETYMOLOGY

Greek, *aglaos* (splendid or beautiful) plus *melissa* (bee, also an old generic name in this tribe).

DISCUSSION

Although this genus is related to *Ctenioschelus* and *Mesocheira,* it is easily separated from both. Males of *Ctenioschelus* have extraordinarily long antennae, and both sexes of that genus lack pronotal, anterior mesepisternal, and acetabular carinae. In *Mesocheira* the processes of the dorsal face of the scutellum are flattened and plate-like, extending over the base of the abdomen.

The only species of *Aglaomelissa* is known from a few specimens from Costa Rica, Panama, Trinidad, Colombia, and Venezuela.

Although Moure (1960b) included *A. duckei* in his *Mesoplia decorata* group, this bee is clearly not a *Mesoplia.* Particularly indicative of its relationship to *Ctenioschelus* and *Mesocheira* are the presence of the anterior mesepisternal carina and the subangulate profile of the first metasomal tergum.

The suspected host is a species of *Centris* (Table 3).

Genus *Ctenioschelus* Romand

Figures 49–54, 68

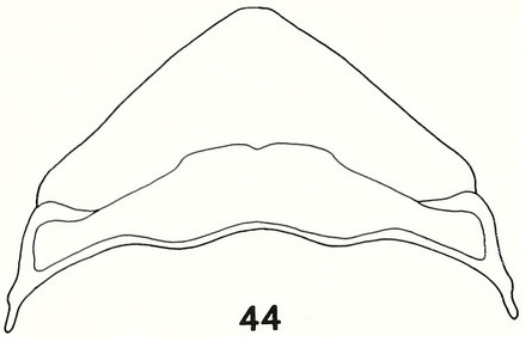
Ctenioschelus Romand, 1840:336. Type species: *Acanthopus goryi* Romand, 1840 (monobasic).

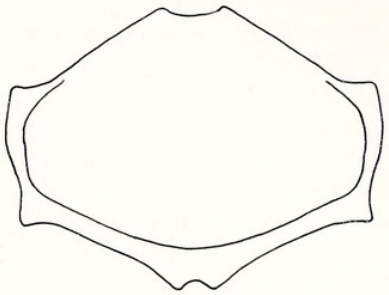
Ischnocera Shuckard, 1840:166. No included species.

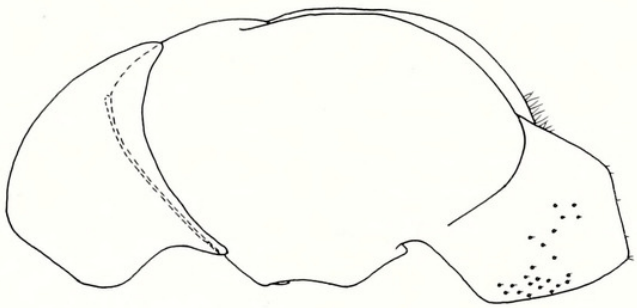
Melissoda Lepeletier, 1841:508. Type species: (*Melissoda latreillei* Lepeletier, 1841) = *Acanthopus goryi* Romand, 1840 (monobasic).

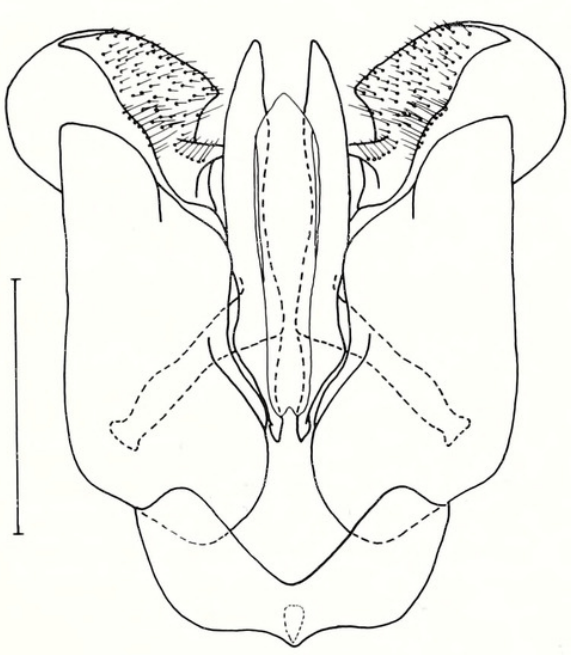
DIAGNOSIS

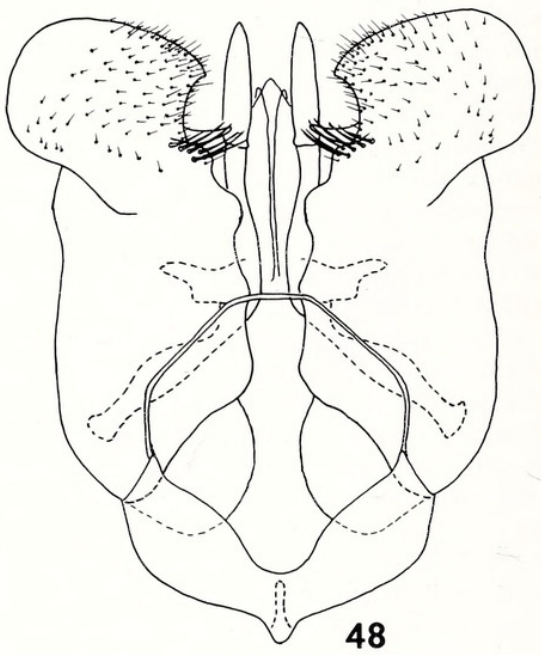
Male immediately separable from all other ericrocine genera by the greatly elongate flagellum reaching beyond apex of abdomen. Additional features characteristic of both sexes: no anterior mesepisternal carina; scutellar tubercles prostrate, mammiform, and extended over propodeum; meso-











Figures 44-48. *Aglaomelissa duckei,* male. **44,** sternum 7; **45,** sternum 8; **46-48,** genital capsule, lateral, dorsal, and ventral views. Scale line = 1.00 mm.

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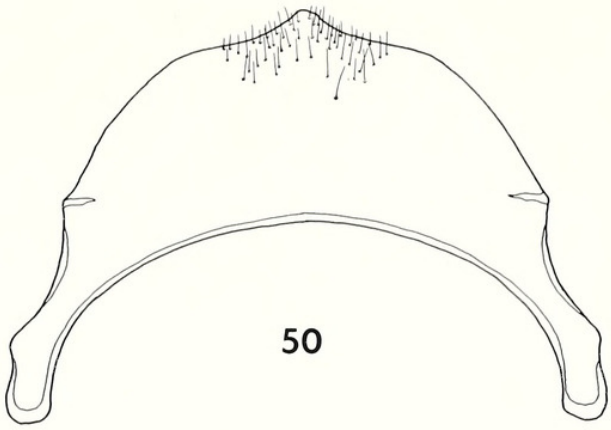

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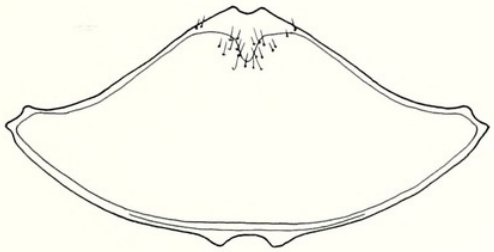

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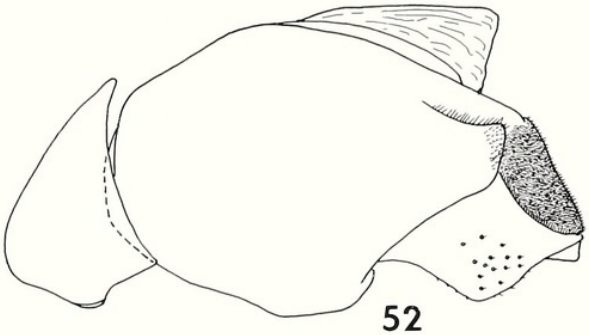
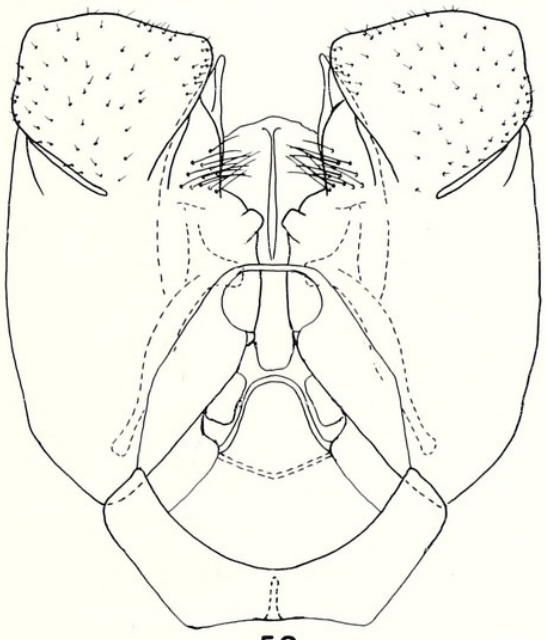


52



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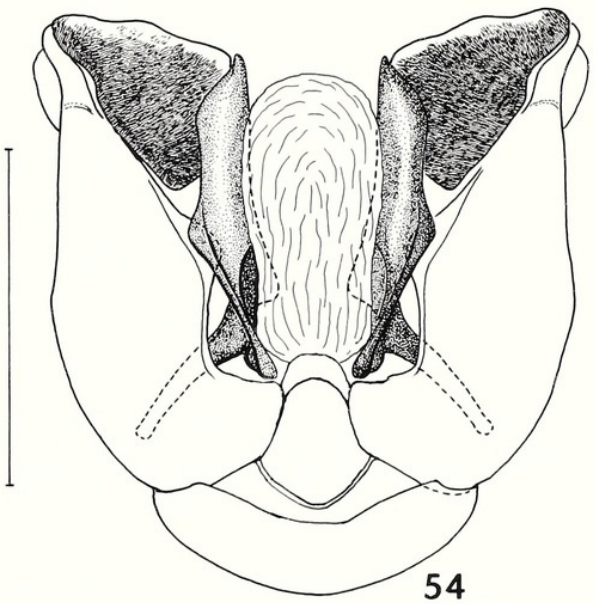

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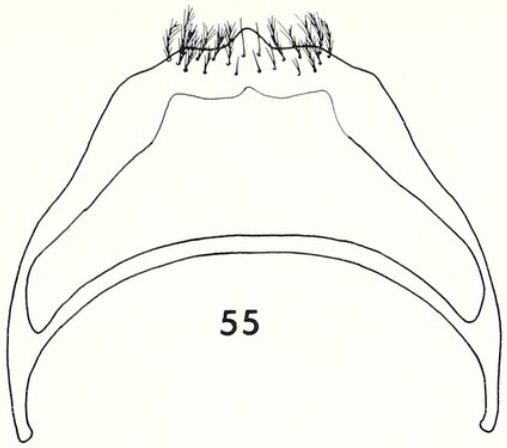
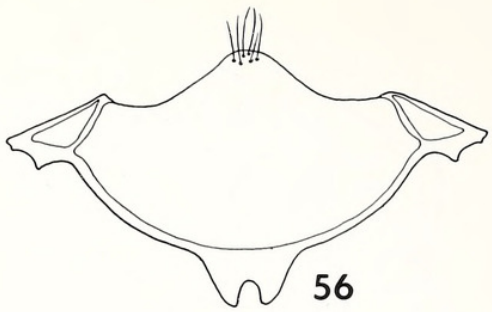
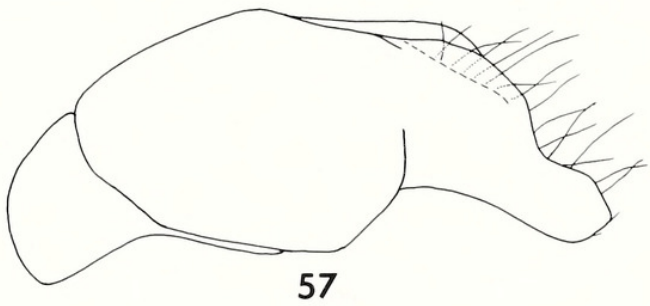
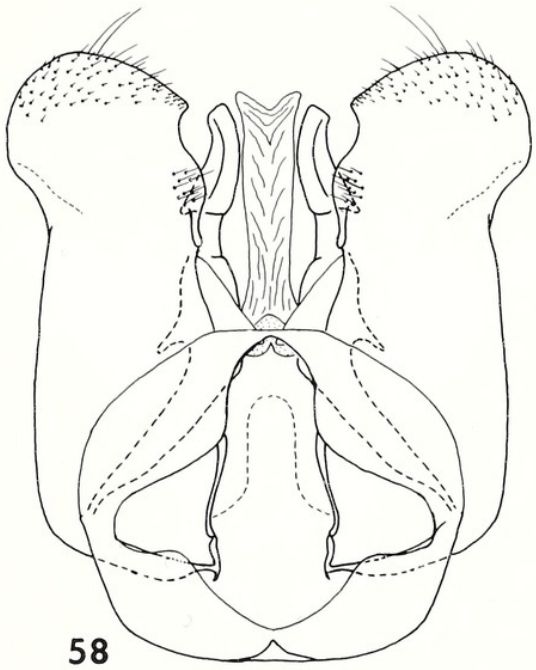
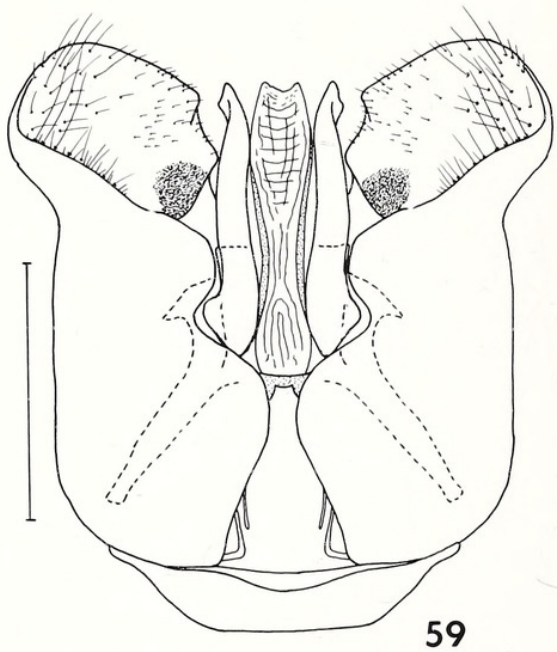
Figures 49-54. *Ctenioschelus goryi.* **49,** female mesobasitarsus, pilosity omitted; **50,** male sternum 7; **51,** male sternum 8; **52-54,** male genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.









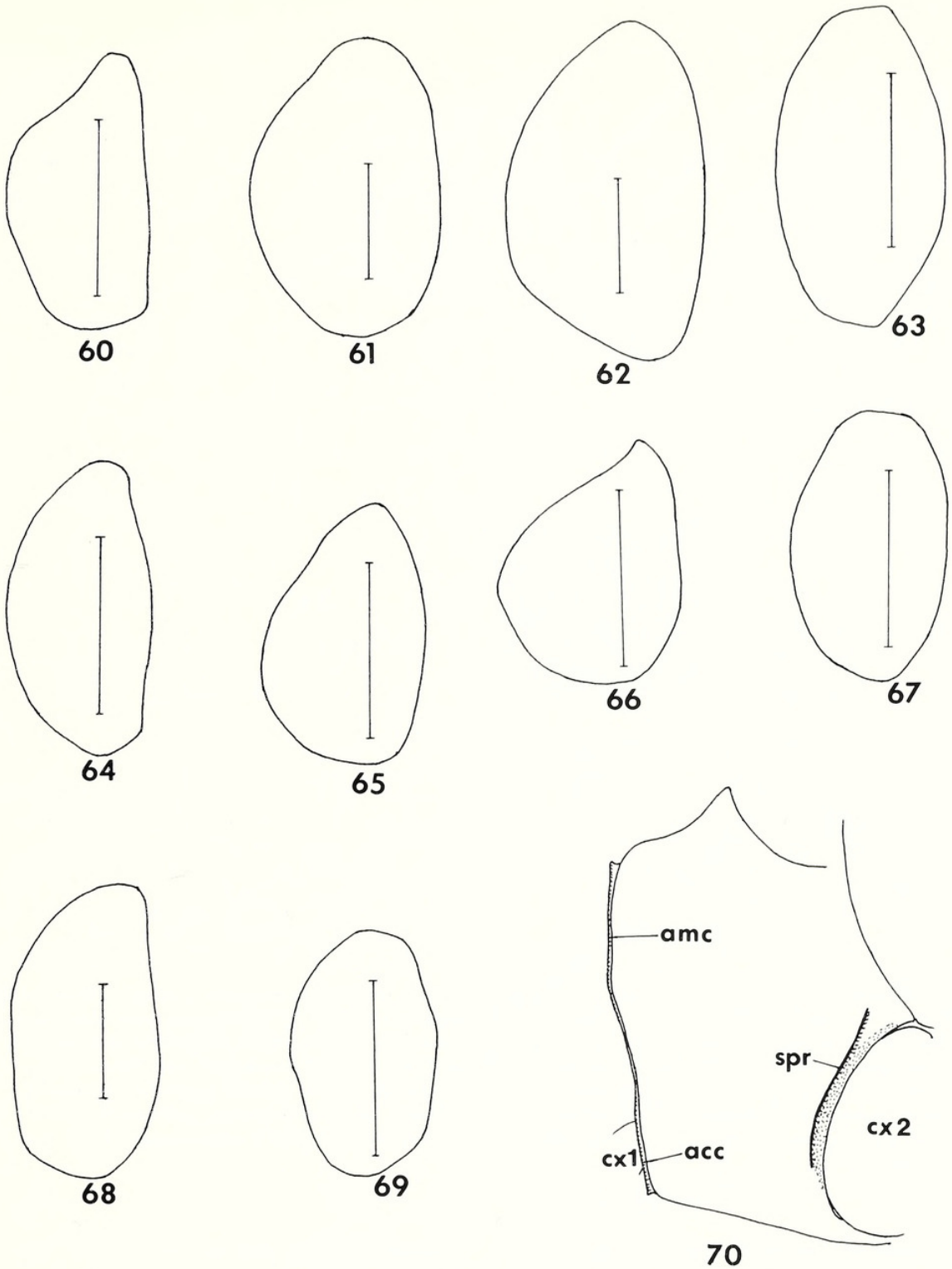


Figures 55-59. *Mesocheira bicolor,* male. **55,** sternum 7; **56,** sternum 8; **57-59,** genital capsule, lateral, ventral, and dorsal views. Scale line = 1.00 mm.

basitarsus without posterior carina or distal process; juncture of basal and discal faces of first tergum elevated and angulate.

DESCRIPTION

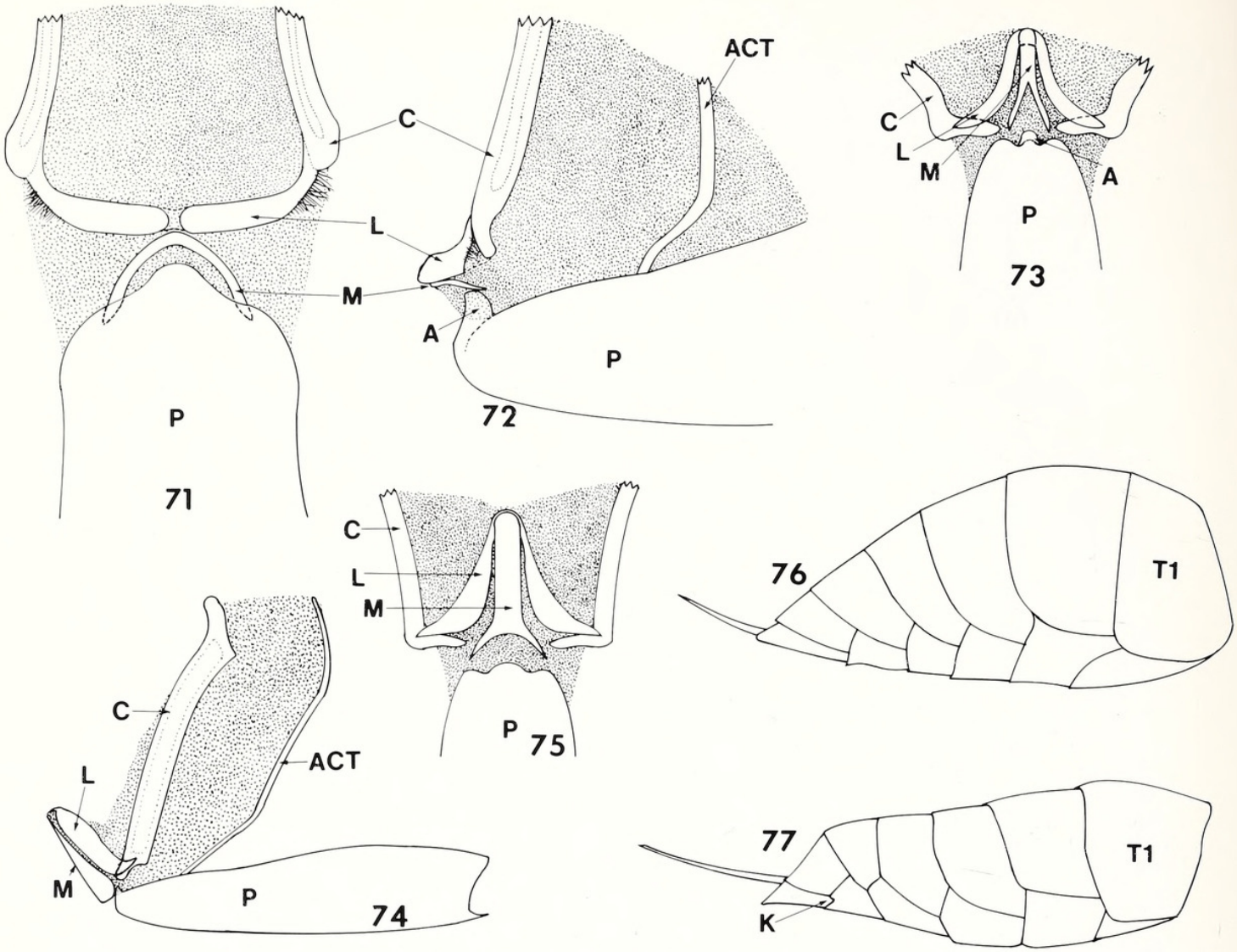
(1) Head a little broader than long; inner eye margins essentially straight, convergent above; occipital margin little elevated above ocelli. (2) Maxillary palpal segment short, flattened. (3) Labrum impressed along midline and with weak transverse preapical ridge; apical margin broadly rounded, subtruncate in middle. (4) Interantennal distance less than antennal socket diameter; antennocular distance less than antennal socket diameter. (5) Ocelloccipital distance more



Figures 60-69. Dorsal view of left tegula of: **60,** *Ericrocis lata;* **61,** *Hopliphora velutina;* **62,** *Acanthopus palmatus;* **63,** *Mesoplia* (*M.*) *rufipes;* **64,** *M.* (*Eumelissa*) *decorata;* **65,** *Mesonychium coerulescens;* **66,** *Abromelissa lendliana;* **67,** *Aglaomelissa duckei;* **68,** *Ctenioschelus goryi;* **69,** *Mesocheira bicolor;* scale line = 1.0 mm. **70,** diagrammatic mesopleuron, illustrating positions of: anterior mesepisternal carina (amc); acetabular carina (acc); mesocoxa (cx 2); procoxa (cx 1); sternopleural ridge (spr). Precoxal depression stippled.

than twice diameter of anterior ocellus. (6) Occipital margin subangulate. (7) Antenna short in female, flagellum longer than body length in male; minimum length of female first flagellar segment less than width and about one-half as long as second segment; minimum length of male first flagellar distinctly greater than width and less than one-third as long as second on same side; middle segments of male flagellum about seven times longer than wide.

(8) Pronotal collar prominent on each side, no carina between collar and posterior lobe. (9) Midline of mesoscutum



Figures 71-77. *Acanthopus palmatus,* female: **71-72,** Posterior and side view of cardines (apices only), lorum, mentum, and basal portion of prementum arranged in a single plane. *Ericrocis lata,* female: **73-74,** posterior and side view of cardines (apices only), lorum, mentum, and basal portion of prementum arranged in a single plane. **75,** side view of metasoma, spiracles omitted. *Mesoplia imperatrix,* male: **76,** posterior view of cardines (apices only), lorum, mentum, and basal portion of prementum arranged in a single plane. *Mesocheira bicolor,* female: **77,** side view of metasoma, spiracles omitted, arrow indicates character 67. Abbreviations are A, basal apodeme of prementum; ACT, anterior conjunctival thickening [=suspensory thickening of Winston (1979)]; C, cardo; K, notch of metasomal sternum 5; L, lorum; M, mentum; P, prementum; T1, first metasomal tergum. Dotted areas represent the membranous surface of the labiomaxillary tube extending toward its attachment to the head.

not impressed; parapsidal lines weakly impressed. (10) Dorsal face of scutellum impressed along midline; lateral processes nearly prostrate, dorsally convex, projecting over concave vertical face, metanotum, and propodeum. (11) Anterior mesepisternal carina, acetabular carina, and sternopleural ridge absent. (12) Supraspiracular ridge prominent, shelf-like, not curved ventrad behind spiracle.

(13) Tegula subrectangular, outer margin sinuate (Fig. 68). (14) First submarginal cell, on M, narrower than second or third; third submarginal cell much narrowed anteriorly; 1st m-cu interstitial with 1st r-m; 2nd m-cu distinctly basad of 2nd r-m; wing tip infuscated.

(15) Mesotibial spur broad at apex, with two or three long intercalary teeth. (16) Metatrochanter compressed and angulate ventrally; metatibial spurs normal; metadistitarsus about three times longer than wide.

(17) Female sixth tergum with short, poorly defined, narrowly truncate pygidial plate. (18) Male fourth sternum broadly emarginate, distal portion bare and transparent, but largely hidden by long brush of hairs arising near midlength. (19) Male fifth sternum similar but transparent margin narrower, more fully concealed by preapical fringe. (20) Male seventh sternum (Fig. 50) rounded distad, subangulate in middle. (21) Male eighth sternum (Fig. 51) produced along apical margin, with small median emargination. (22) Male gonostylus almost absent, situated beneath much enlarged

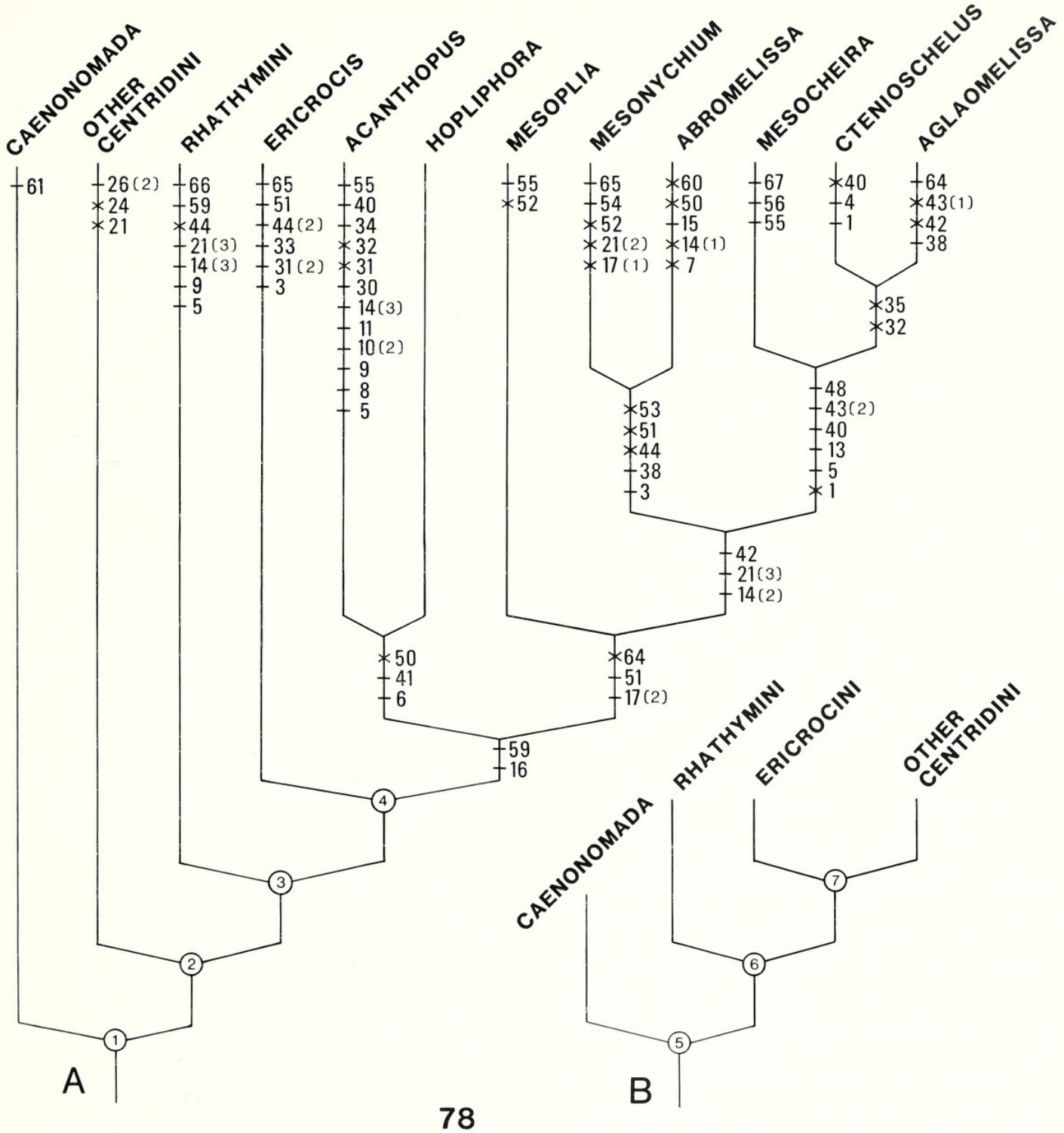


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Figure 78. A. Cladogram showing the generic relationships of the Ericrocini and its sister group the Rhathymini which are shown derived from the Centridini. *Caenonomada* has other apomorphies which have not been given. A bar indicates an apomorphy, an X a reversal. Synapomorphies which root both trees are 20, 23, 24, 52. Synapomorphies of the centridine-rhathymine-ericrocine lineage (internode 1–2) are the derived characters of variables 17, 18, 20(2), 25, 26, 44, 47(2). When there is more than one derived character composing a variable the relevant one is indicated in parentheses. Synapomorphies of the rhathymine-ericrocine lineage (internode 2–3) are 2, 7, 14, 21(2), 29, 37, 39, 46, 49, 64. Synapomorphies of the Ericrocini (internode 3–4) are 1, 10, 12, 19, 22, 27, 28, 31, 32, 35, 36, 45, 50, 53, 57, 58, 60, 61(2), 62. B. Alternative cladogram showing relationships of the tribes. Synapomorphies of rhathymine-centridine-ericrocine bees (internode 5–6) are 17, 18, 20(2), 25, 26, 47(2). Synapomorphies of Rhathymini are 2, 5, 7, 14(3), 21(3), 29, 37, 39, 45 (character is not constant), 46, 49, 58, 59, 64, 66. Synapomorphies of centridine-ericrocine bees (internode 6–7) are 27 (character is not constant), 28, 31 (character is not constant), 44. Synapomorphies for Centridini (excluding *Caenonomada*) are 21 (reversion), 24 (reversion), 26(2). Synapomorphies of the Ericrocini are 1, 2, 7, 10, 12, 14, 19, 21(2), 22, 27–29, 31, 32, 35–37, 39, 43, 45–47, 49, 50, 57–60, 61(2), 62–64.

concave and densely setose inner apical sclerotization of gonocoxite (Fig. 54). (23) Penis valve evenly curved ventrad; basolateral lobe weak (Fig. 54).

DISCUSSION

The bizarrely slender and elongate antennae are immediately distinctive for *Ctenioschelus* males. Females resemble those of *Mesoplia* but are readily separable by the subangulate profile of the first tergum. The one species is apparently not common and ranges from Costa Rica to Brazil. Brazilian specimens have their forewing tips more heavily infuscate than do the Peruvian to Central American populations. Its host is unknown.

INCLUDED NAMES

goryi (Romand, 1840) (*Acanthopus*)
latreillei (Lepeletier, 1841) (*Melissoda*)

Genus *Mesocheira* Lepeletier and Serville

Figures 55–59, 69, 76

Mesocheira Lepeletier and Serville, 1825:106. Type species: (*Mesocheira bicolor* Lepeletier and Serville, 1825) = *Melecta bicolor* Fabricius, 1804 (designation of Taschenberg, 1883).
Mesochira Schulz, 1906:257 (lapsus).

DIAGNOSIS

Scutellar processes prostrate and shelf-like, extending over base of abdomen; anterior mesepisternal carina present; marginal cell of forewing with apical cloud.

DESCRIPTION

(1) Head a little broader than long; inner eye margins essentially straight, weakly convergent above; occipital margin not elevated above ocelli. (2) Maxillary palpal segment short, button-like. (3) Labrum impressed along midline, without preapical ridge or tubercle; apical margin transverse or slightly concave. (4) Interantennal distance about equal to antennal socket diameter; antennocular distance less than antennal socket diameter. (5) Ocelloccipital distance almost twice diameter of anterior ocellus. (6) Occipital margin reflexed and cariniform. (7) Antenna short in both sexes; minimum length of first flagellar segment about one-half maximum width and less than one-half length of second segment on same side.

(8) Side of pronotal collar raised and subcarinate, with high lamelliform carina from collar to front of posterior lobe. (9) Midline and parapsidal lines of mesoscutum weakly impressed. (10) Dorsal face of scutellum narrowly impressed along midline; lateral processes flat, shelf-like, extending over base of abdomen. (11) Anterior mesepisternal carina lamelliform, confluent below with acetabular carina; sternopleural ridge absent. (12) Supraspiracular ridge prominent, curved ventrad for a short distance behind spiracle.

(13) Tegula subrectangular, outer margin sinuate (Fig. 69). (14) First submarginal cell, on M, narrower than second or third; third submarginal cell strongly narrowed anteriorly; 1st m-cu interstitial with 1st r-m; 2nd m-cu virtually interstitial with 2nd r-m; wing clear, with apical infuscation in marginal cell and at wing tip.

(15) Mesotibial spur stout, weakly broadened distad, with one or two long, acute intercalary teeth. (16) Metatrochanter compressed and subangulate beneath; metatibial spurs normal; metadistitarsus less than three times longer than wide.

(17) Female sixth tergum with well-defined, acute pygidial plate. (18) Male fourth sternum with sharp, median, longitudinal carina on basal one-half, distal margin nearly straight. (19) Male fifth sternum hidden under fourth, apical margin deeply concave. (20) Male seventh sternum (Fig. 55) with apical margin strongly produced, subtruncate and with median triangular projection. (21) Male eighth sternum (Fig. 56) with medioapical portion produced, often irregular in shape. (22) Male gonostylus almost absent, reduced to a mere slit only visible from apicodorsal aspect (Fig. 59); inner apical sclerotization of gonocoxite nearly absent. (23) Penis valves evenly curved ventrad; basolateral lobe moderately produced.

DISCUSSION

The plate-like, posteriorly directed mesoscutellar processes will separate both sexes of *Mesocheira* from all other ericrocine genera. There appears to be but a single species that ranges from Mexico to Brazil and Paraguay. Although hosts are unknown, the relatively small size suggests species of the subgenera *Hemisiella* and *Heterocentris* of *Centris*. The senior author has taken females at a nest site of *C.* (*Hemisiella*) *nitida* F. Smith in Mexico.

The figures of the labiomaxillary complex of the mouthparts, illustrated (fig. 44) by Winston (1979) as those of *Mesocheira bicolor,* are not of that bee. They appear to be based on *Ericrocis lata.*

INCLUDED NAMES

bicolor (Fabricius, 1804) (*Melecta*)
bilamellosa (Cockerell, 1949) (*Exaerete*)
elizabethae Cockerell, 1910b (*Mesocheira*)
melanura (Cockerell, 1949) (*Exaerete*)
pulchella Holmberg, 1887 (*Mesocheira*)
sericea Guérin-Méneville, 1846 (*Mesocheira*)

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LITERATURE CITED

Ashmead, W.H. 1899. Classification of the bees, or the Superfamily Apoidea. *American Entomological Society, Transactions* 26:49–100.

———. 1900. Report upon the aculeate Hymenoptera of the islands of St. Vincent and Grenada, with additions to the parasitic Hymenoptera and a list of the described Hymenoptera of the West Indies. *Entomological Society of London, Transactions* 1900:207–367.

Baker, C.F. 1906. American bees related to *Melecta. Invertebrata Pacifica* 1:142–145.

Bohart, R.M., and A.S. Menke. 1976. Sphecid wasps of the World. *University of California Press,* Berkeley. ix + 695 pp.

Cockerell, T.D.A. 1910a. Some Neotropical bees. *Psyche* 17:142–143.

———. 1910b. Some bees from Ecuador. *Psyche* 17:247.

———. 1912. Descriptions and records of bees. XLIV. *Annals and Magazine of Natural History* (8)9:554–568.

———. 1917. Descriptions and records of bees.—LXXV. *Annals and Magazine of Natural History* (8)19:473–481.

———. 1921. Descriptions and records of bees.—XCI. *Annals and Magazine of Natural History* (9)8:359–368.

———. 1926. Descriptions and records of bees. CVIII. *Annals and Magazine of Natural History* (9)17:214–226.

———. 1949. Bees from Central America, principally Honduras. *United States National Museum, Proceedings* 98: 429–490.

Cockerell, T.D.A., and E. Atkins. 1902. On the bees of the family Nomadidae of Ashmead. *Annals and Magazine of Natural History* (7)10:40–46.

Coville, R.E., G.W. Frankie, and S.B. Vinson. 1983. Nests of *Centris segregata* (Hymenoptera: Anthophoridae) with a review of nesting habits of the genus. *Kansas Entomological Society, Journal* 56:109–122.

Cresson, E.T. 1878. Descriptions of new North American Hymenoptera in the collection of the American Entomological Society. *American Entomological Society, Transactions* 7:61–136.

———. 1887. Synopsis of the families and genera of the Hymenoptera of America, north of Mexico. *American Entomological Society, Transactions supplement* 351 pp.

Ducke, A. 1902. Algumas especies novas de abelhas parasiticas. *Museu Paraense, Boletim* 3:577–579.

———. 1905. Zur Abgrenzung der neotropischen Schmarotzerbienen-gattungen aus der nächsten Verwandtschaft von *Melissa* Sm. *Zeitschrift für Hymenopterologie und Dipterologie* 4:227–229.

Fabricius, J.C. 1793. Entomologia systematica emendata et aucta. Copenhagen, viii + 519 pp.

———. 1804. Systema Piezatorum. Braunschweig, 439 + 30 pp.

Fox, W.J. 1893. Report on some Mexican Hymenoptera, principally from Lower California. *California Academy of Sciences, Proceedings* (2)4:1–25.

Friese, H. 1900. Neue exotische Schmarotzerbienen. *Entomologische Nachrichten* 26:65–67.

———. 1902. Beitrag zur Apidenfauna der grossen Antillen. Zeitschrift für Hymenopterologie und Dipterologie 2:196–201.

———. 1904. Zur Synonymie der Apiden. *Zeitschrift für Hymenopterologie und Dipterologie* 4:100.

———. 1906. Neue Schmarotzerbienen aus der Neotropischen Region. *Zeitschrift für Hymenopterologie und Dipterologie* 6:118–121.

———. 1910. Zur Bienenfauna des südlichen Argentinien (Hym.). *Abteilung für Systematik, Geographie und Biologie der Tiere* 6:641–660.

———. 1912. Neue und wenig bekannte Bienenarten der neotropischen Region. *Archiv für Naturgeschichte* 78(A)6: 198–226.

———. 1913. Über einige neue Apiden. *Archiv für Naturgeschichte* 78(A)12:85–89.

———. 1921. Neue Arten der Schmarotzerbienen. *Deutsche Entomologische Zeitschrift* 1921:251–266.

———. 1925. Neue neotropische Bienenarten, zugleich II. Nachtrag zur Bienenfauna von Costa Rica. *Stettiner Entomologische Zeitung* 86:1–41.

———. 1930. Die Schmarotzerbienengattung *Osiris* Sm. (Hym.). *Stettiner Entomologische Zeitung* 91:103–127.

Guérin-Méneville, F.E. 1846. Iconographie du règne animal de G. Cuvier. Vol. 7. Paris, p. 456.

Herbst, P. 1917. Nuevas avispas antófilas de Chile. *Revista Chilena de Historia Natural* 21:105–112.

———. 1918. Nuevas avispas antófilas de Chile. *Revista Chilena de Historia Natural* 22:149–152.

Holmberg, E.L. 1885. Sobre algunos Himenópteros de la República Oriental del Uruguay. *Sociedad Cientifica Argentina, Anales* 18:201–228.

———. 1887. Sobre Ápidos Nomadas de la República Argentina. *Sociedad Cientifica Argentina, Anales* 23:17–33, 67–82.

Klug, J.C.F. 1807. Kritische Revision der Bienengattungen in Fabricius neuem Piezatensysteme mit Berücksichtigung der Kirbyschen Bienenfamilien und Illigers Bemerkungen zu Kirbys Monographie. *Magazin für Insektenkunde* 6:200–228.

Lepeletier de Saint-Fargeau, A. 1841. Histoire naturelle des Insectes, hyménoptères. Vol. 2. Paris, 680 pp.

Lepeletier de Saint-Fargeau, A., and A. Serville. 1825. *In:* P.A. Latreille, Encyclopédie Méthodique, Histoire Naturelle. Entomologie, ou Histoire Naturelle des Crustaces, des Arachnides et des Insectes. vol. 10. Paris, 833 pp.

Linsley, E.G. 1939. A revision of the Nearctic Melectinae (Hymenoptera, Anthophoridae). *Entomological Society of America, Annals* 32:429–468.

Michener, C.D. 1944. Comparative external morphology,

phylogeny and a classification of the bees (Hymenoptera). *American Museum of Natural History, Bulletin* 82:151–326.

———. 1954. Bees of Panamá. *American Museum of Natural History, Bulletin* 104:1–175.

———. 1965. A classification of the bees of the Australian and South Pacific Regions. *American Museum of Natural History, Bulletin* 130:1–362.

———. 1974. The social behavior of the bees. A comparative study. *Harvard University Press,* Cambridge, xii + 404 pp.

———. 1985. A comparative study of the mentum and lorum of bees (Hymenoptera: Apoidea). *Kansas Entomological Society, Journal* 57(4):705–714.

Michener, C.D., and R.W. Brooks. 1984. Comparative study of the glossae of bees (Apoidea). *American Entomological Institute, Contributions* 22:1–73.

Michener, C.D., and A. Fraser. 1978. A comparative anatomical study of mandibular structure in bees. *University of Kansas, Science Bulletin* 51:463–482.

Michener, C.D., and J.S. Moure. 1957. A study of the classification of the more primitive non-parasitic anthophorine bees (Hymenoptera, Apoidea). *American Museum of Natural History, Bulletin* 112(5):395–452.

Moure, J.S. 1944. Apoidea da coleção do Conde Amadeu A. Barbiellini (Hym. Apoidea). *Revista de Entomologia* 15:1–18.

———. 1946. Notas sôbre as Mamangabas. *Boletim Agricola* 4:1–32.

———. 1958. On the bee genus *Cyphomelissa* (Hymen., Apoidea). *Entomological News* 69:191–194.

———. 1960a. Notas sôbre os tipos de abelhas do Brasil descritas por Perty em 1833. *Boletim da Universidade do Paraná, Zoologia* 6:1–23.

———. 1960b. Notes on the types of Neotropical bees described by Fabricius (Hymenoptera: Apoidea). *Studia Entomologia* 3:97–160.

———. 1967. Uma nova espécie de *Mesoplia* da Bolívia (Hymenoptera—Apoidea). *Revista Brasiliera de Entomologia* 12:91–95.

Olivier, A.G. 1789. Encyclopédie Méthodique, Dictionnaire des Insectes. Vol. 4. Paris and Liege, 331 pp.

Perty, J.A.M. 1833. De insectorum in America meridionali habitantium vitae genere, moribus ac distributione geographica observationes nonnullae. Monachii, 44 pp.

Romand, B.E. de. 1840. Sur l'Hyménoptère nommé *Acanthopus Goryi. Revue Zoologie* 3:248, 335–336.

Rozen, J.G. 1969. The larvae of the Anthophoridae (Hymenoptera, Apoidea). Part 3. The Melectini, Ericrocini and Rhathymini. *American Museum Novitates* 2382:1–24.

Ruiz, F. 1938. Nuevas especies de abejas chilenas. *Revista Chilena de Historia Naturale* 42:148–153.

Sandhouse, G.A. 1943. The type species of the genera and subgenera of bees. *United States National Museum, Proceedings* 92:519–619.

Schrottky, C. 1902. Ensaio sôbre as abelhas solitarías do Brasil. *Revista do Museu Paulista* 5:330–613.

———. 1910. Two new Nomadidae (Hymenoptera) from South America. *New York Entomological Society, Journal* 18:208–210.

———. 1920. Himenópteros nuevos o poco conocidos sudamericanos. *Revista do Museu Paulista* 12:1–51.

Shuckard, W.E. 1840. *In:* Swainson and Shuckard, On the history and natural arrangement of insects. London, 406 pp.

Schulz, W.A. 1906. Spolia Hymenopterologia. Paderborn, 356 pp.

Smith, F. 1854. Catalogue of hymenopterous insects in the collection of the British Museum. Part II. Apidae. *British Museum,* London, 465 pp.

———. 1879. Descriptions of new species of Hymenoptera in the collection of the British Museum. *British Museum,* London, 240 pp.

Snelling, R.R. 1984. Studies on the taxonomy and distribution of American Centridine bees (Hymenoptera: Anthophoridae). *Natural History Museum of Los Angeles County, Contributions in Science* 347:1–69.

Snelling, R.R., and T.J. Zavortink. 1985. A revision of the cleptoparasitic bee genus *Ericrocis* (Hymenoptera: Anthophoridae). *Wasmann Journal of Biology* 42:1–26.

Spinola, M. 1841. Hyménoptères recueillis à Cayenne en 1839 par M. Leprieur, Pharmacien de la Marine Royale. *Société Entomologique de France, Annales* 10:85–149.

———. 1851. *In:* Gay, Historia fisica y politica de Chile. Zoologica, Insecta, Hymenoptera. Paris, 6:153–572.

Taschenberg, E.L. 1883. Die Gattungen der Bienen (*Anthophila*). *Entomologische Zeitschrift* 27:37–100.

Wagenknecht, H.R. 1974. Contribución a la biología de los Apoidea chilenos. Parte 1. *Museo de Historia Natural, Anales,* Valparaiso 2:171–176.

Winston, M.L. 1979. The proboscis of the long-tongued bees: a comparative study. *University of Kansas Science Bulletin* 51:631–667.

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