

33. Key to the Families, Based on Adults

The key to families below is intended to work for the great majority of bees, but exceptions to some of the characters of some couplets exist, usually in rare or geographically limited taxa. These problems are addressed in the notes in Section 34, each note keyed to the pertinent couplet number.

Some general attributes of the families are discussed in Section 21, and the bases for the recognition of families are discussed in Sections 18 to 21, as well as in the main systematic text, Sections 36 to 121. Many of the diagnostic familial characters are in the proboscis, which must be extended for study. Moreover, most of the characters that can be seen without extending the proboscis or dissecting the male genitalia and hidden sterna are variable within families and so not valuable in identifying families. Paradoxically, then, it is often easier to identify the subfamily or tribe, or even the genus, of a bee than to identify its family. The regional keys to genera found in the works listed in Table 32-1, above, often facilitate identification. Section 35, which deals with the practical problems of identification of female bees, should also be helpful.

Key to the Families of Bees, Based on Adults

- 1. Labial palpus with first two segments elongate (Fig. 33-1a), flattened, the last two segments small, usually diverging laterally from axis of first two, not flattened, rarely absent; galeal comb absent or rarely weakly indicated; stipital comb and concavity commonly present (Figs. 19-1a, 33-1b); galeal blade elongate, commonly as long as or longer than stipes (Fig. 33-1b); volsella frequently absent or difficult to recognize, rarely with distinct digitus and cuspis [L-T (long-tongued) bees] 2
- Labial palpus with the four segments similar to one another (Fig. 33-1c), or first or rarely first two elongate but not much flattened; galeal comb commonly present; stipital comb and concavity absent (Fig. 33-1d); galeal blade usually shorter than stipes (Fig. 33-1d); volsella commonly well developed, usually with recognizable digitus and cuspis [S-T (short-tongued) bees] 3

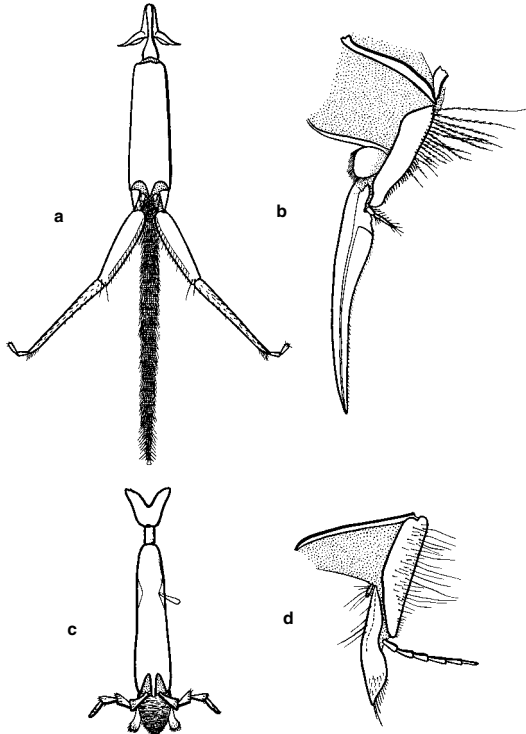


Figure 33-1. Proboscides. **a, b,** Labium and maxilla of *Anthidium atripes* Cresson (Megachilidae); **c, d,** Labium and maxilla of *Andrena mimetica* Cockerell (Andrenidae). From Michener, 1944.

- 2(1). Labrum with basolateral angles enlarged, base forming broad articulation with clypeus, labrum thus widest at base (Fig. 33-2a); labrum at least 0.8 times as long as broad and usually as long as broad or longer; forewing with two submarginal cells, usually about equal in length (except with three in Fideliini); scopa, when present, restricted to metasomal sterna Megachilidae (Sec. 75)
- Labrum with basolateral angles little developed, articu-

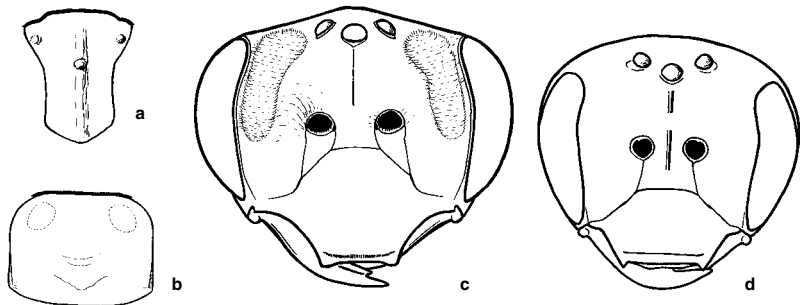


Figure 33-2. Labra and faces. **a,** Labrum of *Heriades apriculus* Griswold, female (Megachilidae); **b,** Labrum of *Anthophora edwardsii* Cresson, male (Apidae); **c,** Face of *Andrena mimetica* Cockerell, female (Andrenidae); **d,** Face of *Halictus farinosus*

Smith, female (Halictidae). (The heavy lines across the tops of a and b represent diagrammatically the clypeal articulations. b, c, from Michener 1944.

- lation with clypeus thus narrower than full width of labrum (Fig. 33-2b); labrum usually broader than long, but in some parasitic forms (where scopa is absent) labrum elongate; forewing with two or three submarginal cells, rarely only one; scopa, when present, on hind leg, particularly the tibia, and usually absent on metasomal sterna Apidae (Sec. 85)
- 3(1). Glossa pointed at apex, sometimes with flabellum..... 4
- Glossa bluntly rounded, truncate, or bilobed at apex (except pointed in males of three hylaeine genera from Australia-New Guinea area); flabellum absent 7
- 4(3). Lacinia represented by scalelike lobe with hairs near base of galea (Fig. 33-1b, d); mentum and lorum forming proboscival lobe (Figs. 33-3b-f, 33-4b), both at least partly sclerotized; lorum not flat 5
- Lacinia inconspicuous or displaced, not a scalelike lobe at base of galea (Fig. 21-2a, b); mentum and lorum not forming proboscival lobe (Figs. 33-3h, i, 34-4a), mentum sometimes membranous; lorum membranous or nearly flat sclerotized membrane (apron) between cardines (Figs. 33-3h, 33-4a) 6
- 5(4). Lorum more or less platelike but produced in middle for attachment to base of mentum; facial fovea present in females (Fig. 33-2c) and some males, fovea sometimes a groove rather than broad as in figure; subantennal area almost always defined by two subantennal sutures below each antennal socket (Fig. 33-2c).....
- Andreninae and Panurginae (Andrenidae) (Sec. 49)
- Lorum slender, V-shaped or Y-shaped, as in L-T bees (Fig. 33-1a); facial fovea absent; a single subantennal suture below each antennal socket (as in Fig. 33-2d) Melittidae (Sec. 68)
- 6(4). Lacinia a small, hairless sclerite hidden between expanded stipites; subantennal area defined by two subantennal sutures below each antennal socket (as in Fig. 33-2c); stigma nearly absent; first flagellar segment as long as scape or longer Oxaeinae (Andrenidae) (Sec. 60)
- Lacinia represented by small, hairy lobe on anterior surface of labiomaxillary tube above rest of maxilla (Fig. 21-2a); a single subantennal suture below each antennal socket (Fig. 33-2d); stigma well developed; first flagellar segment much shorter than scape Halictidae (Sec. 61)
- 7(3). Apex of glossa bluntly rounded, without preapical fringe or apical glossal lobes; episternal groove absent below scrobal groove; scopa present on hind tibia, but absent on femur Stenotritidae (Sec. 36)
- Apex of glossa truncate to bilobed (except pointed in males of three genera in Australia-New Guinea region); episternal groove usually present below scrobal groove; scopa, when present, well developed on hind femur as well as tibia Colletidae (Sec. 37)

35. Practical Key to Family-Group Taxa, Based on Females

Because the key to families (Sec. 33) depends heavily on characters that are difficult to see in dry specimens with the mouthparts in repose, a key based on more readily observable characters seems worthwhile. This key does not usually lead to families, but rather directs the user to tribes or subfamilies. It is based on females; for males, it is best to make the necessary examinations of mouthparts and use the key to families, Section 33.

The tibial hairs of *Pararhophites* (Megachilidae) look like a scopa but may not function for pollen carrying. For the purposes of this key, they are considered to be a scopa (see couplet 1).

Users of the key will find that both Xylocopinae and Apinae run to Apidae, couplet 11. See Section 85 for distinctions between the two.

Ancyla (Ancylini) and the Ctenoplectrini are apids that would run to Melittidae (couplet 11) on the basis of the palpal character. *Ancyla*, from xeric palearctic areas, is a genus of nondescript small anthophoriform bees hard to characterize without examination of the mouthparts. The Ctenoplectrini, from paleotropical and oriental areas, are easily recognized in the female by the broad, finely comblike inner hind tibial spur and the long oil-collecting hairs on the metasomal sterna, the hairs reduced but nonetheless evident in the parasitic genus *Ctenoplectrina*.

The specification "cleptoparasites and social parasites within Apinae" in couplet 23 means the tribes Ericroidini, Isepolini, Melectini, Osirini, Protepeolini, Rhythimini, and parts of Tetrapiidiini, Euglossini, and Bombini. See the key in Section 85.

Key to the Family-Group Taxa of Bees, Based on Adult Females

1. Scopa, consisting of hairs for carrying pollen, present (Figs. 6-4, 8-5b, 8-7b, 10-11a) 2
- Scopa absent (Figs. 8-5a, 8-7a, 8-8a) 18
- 2(1). Scopa consisting of erect branched hairs, longest on S2, shorter on S1 and S3 (Fig. 46-1b), scopal hairs often present also on hind legs [body hylaeiform; submarginal cells two, second much smaller than first (Fig. 46-1)] neotropics) Xeromelissinae (Colletidae) (Sec. 46)
- Scopa variable, but hairs not erect, not longest, and branched on S2 3
- 3(2). Scopa well developed on metasomal sterna (Fig. 8-7b) but absent on hind legs [submarginal cells two, usually about equal in length (Figs. 76-1a, 80-1, 81-1, 82-1, 83-2, 84-1), except three in Fideliini, which have long hairs on hind legs that are not used in carrying pollen] Megachilidae (Sec. 75)
- Scopa on hind legs (Figs. 6-4, 8-5b, 10-11a), sometimes also on sterna 4
- 4(3). Scopa (sometimes as a tibial corbicula) on hind tibia and usually basitarsus, elsewhere not well developed, tibial scopa thus looking considerably larger than that of femur (Figs. 6-4, 10-11a) 5
- Scopa on hind femur (Fig. 8-5b), where a ventral cor-

- bicula is usually evident, scopal hairs usually also present on trochanter, tibia, and basitarsus and sometimes on metasomal sterna 12
- 5(4). Facial fovea rather small but well defined (Fig. 59-1); two subantennal sutures well separated on clypeal margin below each antenna (Fig. 33-2c) [apex of marginal cell truncate or sometimes obliquely cut off (Figs. 50-1f, 53-1, 53-2, 54-1, 56-1, 58-1, 58-2, 59-2) and thus pointed, but apex well separated from wing margin] 6
 - Facial fovea absent or vaguely defined; one subantennal suture below each antenna (Fig. 33-2d) or *if* two, then the two nearly meeting on clypeal margin 7
 - 6(5). Facial fovea deep, with conspicuous hairs (Fig. 50-1a, b) (Peru) Alocandreninae (Andrenidae) (Sec. 50)
 - Facial fovea shallow, hairless, shining Panurginae (Andrenidae) (Sec. 52)
 - 7(5). Two subantennal sutures below each antenna, the two nearly meeting at clypeal margin (Chile) Andreninae (Andrenidae) (Sec. 51)
 - One subantennal suture below each antenna (Fig. 33-2d) 8
 - 8(7). Body largely yellow; labrum with basolateral angles strongly developed, thus broadest at extreme base where articulated to clypeus (as in Fig. 33-2a); subantennal suture short, directed toward outer margin of antennal socket (pygidial and prepygidial fimbriae absent) (Palearctic deserts) Pararhophitini (Megachilidae) (Sec. 77)
 - Body usually exhibiting little or no yellow; labrum with basolateral angles little developed, thus not broadest at extreme base and articulation with clypeus shorter (as in Fig. 33-2b); subantennal suture usually directed toward middle or inner margins of antennal socket 9
 - 9(8). Episternal groove extending below scrobal groove (as in Fig. 20-5b) although frequently shallow (antennae arising below middle of face) Rophitinae (Halictidae) (Sec. 62)
 - Episternal groove not extending below scrobal groove (Fig. 20-5a, c) 10
 - 10(9). Glossa short, apex broadly rounded (inner hind tibial spur pectinate) (Australia) Stenotritidae (Sec. 36)
 - Glossa pointed, often with flabellum 11
 - 11(10). L-T bees, first two segments of labial palpus elongate, flattened (Figs. 10-4a, 19-1b); episternal groove commonly present down to or curving into and joining scrobal groove (Fig. 20-5c) Apidae (Sec. 85)
 - S-T bees, first two segments of labial palpus similar in form to subsequent segments (Figs. 10-4c, 19-5b); episternal groove almost completely absent Melittidae (Sec. 68)
 - 12(4). Facial fovea well developed, covered with short hairs (two subantennal sutures below each antenna, often difficult to see) (Fig. 33-2c) Andreninae (Andrenidae) (Sec. 51)
 - Facial fovea absent or not well defined, not bearing distinctive short hairs, but *if* defined, then bare 13

- 13(12). Stigma absent (Fig. 60-2a); two subantennal sutures below each antenna (as in Fig. 51-1a) (Western Hemisphere) Oxaeinae (Andrenidae) (Sec. 60)
- Stigma present, although sometimes no wider than prestigma as measured to wing margin; ordinarily only one subantennal suture below each antenna (Fig. 33-2d) 14
- 14(13). Stigma almost always shorter than prestigma, vein arising almost at its apex, margin of stigma in marginal cell concave or straight and not much longer than width of stigma (Fig. 43-1); large, robust, euceriform, hairy bees (Western Hemisphere) 14
- Diphaglossinae (Colletidae) (Sec. 42)
- Stigma longer than prestigma, vein arising near its middle or at least well before its apex, margin of stigma in marginal cell straight or convex, much longer than width of stigma; andreniform bees, much more slender than those of above alternative 15
- 15(14). Episternal groove extending little below scrobal groove Nomiinae (Halictidae) (Sec. 63)
- Episternal groove extending far below scrobal groove (Fig. 20-5b), commonly onto venter of thorax 16
- 16(15). Basal vein only feebly arcuate (Fig. 39-5); glossa bilobed (Fig. 19-2a, b) Colletinae (Colletidae) (Sec. 39)
- Basal vein strongly curved (Fig. 65-5); glossa acutely pointed (Figs. 19-2c, d, 28-1a-c) 17
- 17(16). T5 with prepygidial fimbria divided by medial longitudinal zone or triangle of short, dense hairs (Fig. 65-1j) and minute, dense punctations (the hairs sometimes absent) Halictinae (Halictidae) (Sec. 65)
- T5 with prepygidial fimbria weak but continuous (Eastern Hemisphere) Nomiodinae (Halictidae) (Sec. 64)
- 18(1). Episternal groove extending far below scrobal groove (Fig. 20-5b) toward ventral surface of thorax (S6 exposed, not bifurcate) 19
- Episternal groove absent or curving into scrobal groove (Fig. 20-5a, c), extending below scrobal groove only in Caenoprosopidini (in which S6 is retracted, only its bifurcate apex exposed) 21
- 19(18). Glossa pointed (Fig. 19-2c, d); basal vein strongly curved (Fig. 65-5); submarginal cells usually three 21
- Cleptoparasites in Halictinae, both tribes (Halictidae) (Sec. 65)
- Glossa bilobed or broadly truncate (Fig. 19-2a, b); basal vein gently arcuate (Fig. 39-5); submarginal cells two, second usually much smaller than first (Figs. 47-2, 48-2, 48-3) 20
- 20(19). Supraclypeal area elevated abruptly above level of antennal sockets (Fig. 47-3a); pygidial plate usually absent, but *if* present, then broad, its margins converging posteriorly; anterior surface of T1 usually lacking longitudinal median groove Hylaeinae (Colletidae) (Sec. 47)
- Supraclypeal area sloping up from level of antennal sockets; pygidial plate present, the apical part slender, parallel-sided or spatulate; anterior surface of T1 with longitudinal median groove 20
- Euryglossinae (Colletidae) (Sec. 48)
- 21(18). S6 retracted under S5 except for apex, metasomal venter thus appearing to be five-segmented; apex of S6 bilobed, bifurcate, or produced to median spine, frequently bearing rows or clumps of stiff setae (Fig. 91-2) Nomadinae (Apidae) (Sec. 91)
- S6 more fully exposed, the metasomal venter thus recognizably six-segmented; apex of S6 not modified as above 22
- 22(21). Labrum with basolateral angles strongly developed, labrum thus broad at extreme base, where articulated to clypeus (Fig. 33-2a); labral shape more or less rectangular and usually longer than broad (forewing with two submarginal cells) 22
- Cleptoparasites in Megachilinae, all tribes (Megachilidae) (Sec. 79)
- Labrum with basolateral angles weakly developed, labrum thus not broadest at extreme base, articulation with clypeus not extending full width of labrum (Fig. 33-2b); labral shape often less rectangular, often rounded apically, usually broader than long 23
- 23(22). Epistomal suture between lateral extremity and subantennal suture arcuate, upper part of clypeus thus almost parallel-sided (Fig. 90-2); submarginal cells two (Eastern Hemisphere) 23
- Social parasites within Allodapini (Apidae) (Sec. 90)
- Epistomal suture not arcuate upward in such a way that upper part of clypeus is almost parallel-sided; submarginal cells usually three 23
- Cleptoparasites and social parasites within Apinae (Apidae) (Sec. 102)

ters that are responsible for the similarity of Stenotritidae to the Caupolicanini, and for the relationship between Stenotritidae and Oxaeinae indicated in some of the phylogenetic analyses of Alexander and Michener (1995).

The two genera of Stenotritidae are similar to one another in most characters, although strikingly different in the form of S7 and S8 of the males.

Key to the Genera of the Stenotritidae

1. T7 of male usually with well-developed pygidial plate; S7 of male a transverse band sometimes broadened and produced apically at each side, leaving large median emargination (Fig. 36-1c), with hairs on apical margin or projections; basal elevation of labrum of female undivided; inner hind tibial spur of female thickest at basal one-fourth to one-half, with long, coarse teeth..... *Ctenocolletes*
- T7 of male with bare area representing pygidial plate but not defined by carinae; S7 of male with disc greatly reduced, connecting long laterobasal apodemes and a pair of hairy apical lobes (Fig. 36-1f); basal elevated area of labrum of female binodulose; inner hind tibial spur of female tapering from base, with moderate-sized to coarse teeth *Stenotritus*

Genus *Ctenocolletes* Cockerell

Stenotritus (*Ctenocolletes*) Cockerell, 1929c: 358. Type species: *Stenotritus nicholsoni* Cockerell, 1929, monobasic.

Ctenocolletes is composed of large (14.0-20.5 mm long), euceriform, hairy, fast-flying bees (Fig. 36-2). They differ not only from *Stenotritus* but also from most other bees in (1) the broad, platelike or bandlike disc of S7 of the male, bearing short lateral apodemes and an entire to bilobed apical margin (Fig. 36-1c), and (2) the large S8 of the male, which has a short or slender apical process (Fig. 36-1d) and hairs on the apical one-third to one-half of the sternum, which is often exposed. On the basis of these sternal characters, *Ctenocolletes* could be regarded as the most primitive of bees, since S7 and S8 are more like the other sterna than like the totally different S7 and S8 found in most other bees. Supporting this view are the simple, articulated, hairy male gonostyli (Fig. 36-1e) and the well-formed male pygidial plate (except in *C. fulvescens* Houston). But *Ctenocolletes* is closely related to *Stenotritus*, which shares none of these features. It seems likely that regulatory factors lead S7 and S8 to develop more like ordinary sterna in *Ctenocolletes*. Clearly, bees



Figure 36-2. *Ctenocolletes nicholsoni* (Cockerell), female. From Goulet and Huber, 1993.

laeinae and Australian Euryglossinae have no scopa and carry pollen internally, in the crop, instead of externally, on the scopa.

The phylogeny of 20 adult exemplars representing all colletid subfamilies was investigated by Alexander and Michener (1995) as part of a study of S-T bees. The Colletinae consistently appeared as paraphyletic, although the groups derived from within this subfamily varied. An analysis including many more colletid taxa is needed to settle on the most likely relationships. One group that was often derived from within the Colletinae in the analyses was the Diphaglossinae. I do not believe, however, that this is the correct position for Diphaglossinae, for the larvae of that subfamily spin cocoons. This behavior and the projecting labial region of the larva on which the salivary (silk) opening lies are ancestral features shared with sphecoid wasps. No other colletid spins cocoons or has such a projecting labium. It is unlikely that the Diphaglossinae arose from a group that does not spin cocoons, like the Colletinae, and re-evolved cocoon spinning and the structures necessary to do so. One of Alexander and Michener's consensus trees (their fig. 13) shows the Diphaglossinae as the sister group of all other colletids, a position supported by these larval and spinning characters. Nonetheless, the phylogenetic position of the Diphaglossinae is not firmly established. The restriction of the Diphaglossinae to the Western Hemisphere is not what one would expect of the basal colletid clade. The disjunct panaustral distribution of the Colletinae (ignoring the widespread *Colletes*) is much more suggestive of an ancient type.

Alexander and Michener's (1995) analyses usually showed the Hylaeinae and Xeromelissinae as sister groups, closely associated sometimes with the Euryglossinae and sometimes with the tribe *Scraptrini* of the Colletinae. In some analyses the Euryglossinae were part of this same clade. I tend to accept this relationship as likely, although in other analyses the Euryglossinae fell at the base of the Colletidae or the base of all bees. The analyses seem to establish the relation of Xeromelissinae to Hylaeinae, although the former has a small scopa and the latter lacks a scopa. They do not establish the position of Euryglossinae, but as noted in Section 21, the large, crescentic galeal comb on a curved sclerite in both Euryglossinae and Hylaeinae seems to be a unique synapomorphy indicating common ancestry.

The idea that the Euryglossinae might be the sister group to all other bees is supported by such observations as their restriction to Australia, the lack of a scopa, the unusually short proboscis, and, as has been emphasized by John Plant (manuscript, 1991), the lack of a galeal velum in most genera. Except for the association with Australia, these items are wasplike and therefore can be interpreted to support a basal position in bee phylogeny. I interpret these matters differently, however. The scopal loss I consider a probable synapomorphy in common with Hylaeinae, as is the crescentic sclerite bearing the fused bases of the bristles of the galeal comb, among other characters. In the euryglossine genus *Pachyprosopis* the galeal velum is present, just as it is in the Hylaeinae and most other bees. Its loss in several other genera could be a derived condition. The reverse hypothesis, that the galeal velum

evolved in *Pachyprosopis* and in other bees, almost certainly would require it to arise twice, for *Pachyprosopis* is clearly a euryglossine, very different from other bees. The euryglossine galeal blade is not at all similar to that of sphecoid wasps, in spite of the lack of the velum in most genera of both taxa. Features of wasp galeal blades that differ from those of bees, including euryglossines, are the sclerotic plates on the inner galeal surface and the comb, which is not homologous to that of bees. The short proboscis of the Euryglossinae may be a special Australian development. Most native nectar sources in Australia are in the Myrtaceae, whose flowers are wide open like cups of nectar (Michener, 1965b). Long proboscides are thus not needed.

A recent catalog of neotropical species of Colletidae, published in five parts, will greatly facilitate studies, especially on *Colletes* and *Hylaeus* in South America. The parts are: 1, Paracolletini, Moure, Graf, and Urban, 1999; 2, Diphaglossinae, Urban and Moure, 2001; 3, Colletini, Moure and Urban, 2002a; 4, Hylaeinae, Urban and Moure, 2002; 5, Xeromelissinae, Moure and Urban, 2002b.

The subfamilies can be distinguished by reference to the following key.

Key to the Subfamilies of the Colletidae

1. Body usually hairy, female with well-formed scopa enclosing corbicula on underside of hind femur; prepygidial fimbria (apical hair band of T5) of female much stronger (hairs longer and denser) than hair bands (if any) of preceding terga, and T6 with abundant hair (pygidial fimbria) lateral to pygidial plate (except in genera that lack both fimbriae and pygidial plate); pygidial plate of female, if present, usually broad and tapering posteriorly; forewing with three submarginal cells or, *if* two, then second at least two-thirds as long as first, as though second submarginal crossvein is lost; distal submarginal crossvein sinuate, at acute angle to distal part of radial sector forming free part of marginal cell (Fig. 38-17) 2
- Body with hairs short and relatively sparse, female lacking scopa or with a sparse or short scopa forming corbicula on underside of hind femur; prepygidial and pygidial fimbriae of female nearly always absent; pygidial plate of female absent or, *if* present, then usually narrow and parallel-sided posteriorly, or spinelike; forewing with two submarginal cells, second usually much shorter than first, as though first submarginal crossvein is lost; second submarginal crossvein usually not sinuate, usually at right or obtuse angle to distal part of radial sector (Fig. 47-2) 3
- 2(1). Stigma small, shorter than prestigma, as wide as prestigma measured to costal wing margin (Figs. 43-1, 44-1, 45-1); glossa deeply bifid with apical lobes commonly directed strongly apicolaterally (Western Hemisphere) Diphaglossinae (Sec. 42)
- Stigma usually large, at least longer than prestigma, usually wider than prestigma measured to wing margin (Figs. 39-2a, 39-5, 39-11, 41-1); glossa weakly bilobed to deeply bifid but, *if* the latter, then lobes commonly directed more apical than laterally (except apicolaterally in *Leioproctus tomentosus* Houston from Western Australia) Colletinae (Sec. 38)
- 3(1). Facial fovea absent or broad, at least one-third as wide

- as long; female with sparse scopa on S1 to S3 and outlining ventral corbicula on hind femur (Fig. 43-1); longitudinal part of hypostomal carina usually longer than clypeus but, *if* not, then clypeus protuberant and its lower lateral extremities bent back around ends of labrum (neotropical) Xeromelissinae (Sec. 46)
- . Facial fovea usually a narrow groove, sometimes a broader area, wider than diameter of scape, absent in a few females and some males (Figs. 47-4, 47-6, 47-7); scopa absent; longitudinal part of hypostomal carina usually not longer than clypeus; clypeus usually not protuberant, not much bent back around ends of labrum 4
- 4(3). Supraclypeal area elevated abruptly above level of antennal socket (Fig 47-3a); pygidial and basitibial plates usually absent but, *if* present (as in a few Australian and New Guinea species), then pygidial plate of female broad, its margins converging posteriorly; anterior surface of T1 usually without longitudinal median groove; posterior (lower) surface of prementum with longitudinal, usually spiculate depression or fovea (Fig. 41-3a) (weak in a few males) margined by ridges that diverge on basal half of prementum and meet near base of subligular process Hylaeinae (Sec. 47)
- . Supraclypeal area sloping up from level of antennal socket; apical part of pygidial plate of female slender, sometimes a spine, its margins parallel or converging slightly toward apex or spatulate; basitibial plate usually indicated in female, sometimes only by one or more tubercles; anterior surface of T1 with longitudinal median groove; posterior (lower) surface of prementum lacking longitudinal medial fovea but with comparable spiculate area (Australia) Euryglossinae (Sec. 48)

Key to the Tribes of the Colletinae

1. Basitibial and pygidial plates absent; prepygidial and pygidial fimbriae lacking, in both sexes vestiture of T5 and T6 thus similar to that of preceding terga (Fig. 40-1); S7 of male with apicolateral lobes greatly enlarged, disc of sternum and apodemes reduced, slender and delicate, the lobes thus constituting the major part of S7 (Fig. 40-2b) *Colletini* (Sec. 40)
- Basitibial and pygidial plates present, at least in females (pygidial plate absent in most males; basitibial plate absent in both sexes of a few Australian taxa); prepygidial and pygidial fimbriae of female present; S7 of male with apicolateral lobes of moderate size (Figs. 13-2a; 39-1, -3, -7, -9, -10, etc.) (sometimes greatly reduced or absent), disc of sternum and apodemes thus constituting the major part of S7 2
- 2(1). Posterior (lower) surface of prementum with a broad longitudinal depression or fovea margined by shiny ridges (Fig. 41-3b) that diverge on basal part of prementum and converge near base of subligular process; galeal comb reduced to three or four small bristles (Fig. 41-2b) (Africa) *Scraptrini* (Sec. 41)
- Posterior (lower) surface of prementum lacking a fovea or with only a narrow medial groove; galeal comb usually well developed *Paracolletini* (Sec. 39)

39. Tribe Paracolletini

The Paracolletini, in a superficial way, replaces the holarctic genus *Andrena* in the Australian region and in temperate South America. It contains numerous andreniform bees, some of them with special features relevant to the flowers where they collect pollen. As noted in Section 20, these bees exhibit a series of characters listed as probably ancestral for bees in an old work (Michener, 1944) because of similarity to characters of wasps. Yet the paracolletines are not at all wasplike in appearance and, as indicated in Section 20, colletids are probably a derived group of S-T bees, not a basal group.

This is the most diverse of the tribes of Colletinae. Michener (2000) did not segregate it from the tribe Colletini, but the distinctive features of the latter now seem to justify tribal segregation. The distinctive features of the Paracolletini, however, are probable plesiomorphies and the tribe is likely to be paraphyletic. As suggested above, a phylogenetic study using numerous taxa is needed. *Cal-lomelitta* is a very unusual genus and should perhaps be removed from the Paracolletini.

Paracolletini differ from Colletini in the presence of a pygidial plate and pygidial and prepygidial fimbriae, and almost always basitibial plates in females, present also in some males. S7 of the male has a disc to which apodemes and usually the two or four apicolateral lobes, often much reduced, are attached. The posterior surface of the prementum is smooth, convex, sometimes with a longitudinal median groove.

These bees are abundant in Australia and temperate southern South America, ranging north to Misoöl in Indonesia, to New Guinea, and in the Western Hemisphere, to Arizona, USA.

Stenocolletes Schrottky (1909c), which was originally placed among the colletids and would have to be a paracolletine, may be a protandrenine panurgine (see Sec. 53).

Key to the Genera of Paracolletini of the Western Hemisphere

1. Preoccipital carina strong, often lamella-like; pronotum dorsolaterally with strong transverse carina or lamella extending onto pronotal lobe; hind tibial hairs of female shorter than tibial diameter (neotropical to Arizona) *Eulonchopria*
- . Preoccipital and pronotal carinae (or lamellae) absent; many hind tibial hairs of female as long as or longer than tibial diameter 2
- 2(1). Malar space nearly as long as or longer than eye; S8 of male weakly sclerotized, lacking apical process (Fig. 39-13c) (Ecuador) *Lonchorhyncha*
- . Malar space little if any longer than flagellar width, usually virtually absent; S8 of male with strong median apical process 3
- 3(2). Labial palpi enormous, 8-9 mm long, in repose reaching S3 or S4; claws of both sexes deeply cleft, the two rami similar in shape and of almost equal length (Brazil) *Niltonia*

- . Labial palpi unremarkable; claws with inner rami shorter than outer and differently shaped, at least in female, or, rarely, claws simple 4
- 4(3). Forewing with three submarginal cells, second usually about as long as third on posterior margin (but see subgenus *Lonchopria* s. str.); apical process of S8 of male lacking flat apical region resembling a pygidial plate; inner hind tibial spur of female coarsely palmate-pectinate, bases of teeth close together and diverging from thick part of spur (Fig. 39-8e); tibial scopa (except in subgenus *Lonchoprella*) extremely dense, hiding tibial surface; hind basitarsus of female weakly concave on outer surface near upper margin, this surface unlike that of tibia in appearance, the surface easily visible among hairs that are usually shorter than those of inner surface (South America) *Lonchopria*
- . Forewing with two or three submarginal cells, if with three, then second much shorter than third on posterior margin (except in *Leioproctus* subgenus *Cephalocolletes* and most specimens of subgenus *Reedapis*); apical process of S8 of male with flat, bare apical region on upper side, superficially resembling a pygidial plate and usually exposed at apex of metasoma; inner hind tibial spur of female ciliate to coarsely pectinate, not at all palmate and not thickened medially; scopa not hiding tibial surface; hind basitarsus of female flat or convex on outer surface, this surface superficially similar to that of tibia, its hairs longer than those of inner surface (ignoring hairs of upper margin) 5
- 5(4). Stigma small, vein r arising well beyond middle; costal margin of marginal cell 2.5-3.0 times as long as stigma; propodeum almost wholly declivous in profile; volsella of male large, vertically expanded, reaching dorsum of genital capsule, bifid (Fig. 39-1a); mandible of male tridentate (Fig. 39-1e) [middle and both hind tibial spurs strongly curved and coarsely pectinate (Fig. 39-8d) or outer hind spur of male sometimes dentate or almost simple; forewing with two submarginal cells] (South America) *Brachyglossula*
- . Stigma elongate, vein r arising at or slightly beyond middle (Fig. 39-5d-l); costal margin of marginal cell 1.5-2.0 times as long as stigma; propodeum usually with subhorizontal or sloping basal part curving onto steeply declivous posterior surface; volsella of male more or less horizontal, ventral, not attaining dorsum of genital capsule; mandible of male simple or bidentate (tibial spurs not curved and coarsely pectinate, or, if so, as in some species of subgenus *Reedapis*, then forewing with three submarginal cells) (South America) *Leioproctus* (in part)

Key to the Genera of Paracolletini of the Australian Region

1. Marginal cell with apex on wing margin (Fig. 39-2a); facial fovea linear or nearly so (often very short or absent in male); mandible of female two to three times as long as basal width, ending in three equally conspicuous teeth; pygidial plate of female with lateral margins concave, the

- apex very slender and parallel-sided (Australia)..... *Callomelitta*
- Marginal cell bent away from wing margin at apex (Figs. 39-5, 39-11), sometimes, as in *Leioproctus* (*Euryglossidia*), only slightly so; facial fovea broad or absent; mandible of female usually four or more times as long as basal width, bidentate, lower tooth much longer than upper (upper tooth bilobed, giving a tridentate appearance, in *Paracolletes*); pygidial plate of female with lateral margins not strongly concave, apex neither slender nor parallel-sided (except in a few *Leioproctus*) 2
- 2(1). Stigma small, parallel-sided, truncated (in some cases obliquely) at base of vein r or rarely shortly beyond that point, not or scarcely tapering to apex within marginal cell; marginal cell on costal edge of wing 2.75 to 5.0 times as long as stigma; bare part of labrum uniformly convex, one to five times as broad as long 3
- Stigma usually larger (Fig. 39-5) and usually not parallel-sided, apex usually tapering to a point on costal edge of marginal cell, vein r thus arising near middle of stigma; marginal cell on costal edge of wing 1.3 to 2.5 times as long as stigma; bare part of labrum usually with transverse ridge or otherwise not uniformly convex, usually more than five times as broad as long 4
- 3(2). Inner hind tibial spur of female finely serrate, rarely finely pectinate with slender teeth of approximately uniform length arising from a shaft that tapers rather uniformly toward apex (as in Fig. 39-8c); basitibial plate of female and sometimes of male fully defined, in some cases visible without removal of hairs, apex of plate rounded or blunt (angulate in *Paracolletes montanus* Rayment); mandible slender near base, usually expanded apically, female with upper apical tooth bidentate in unworn mandibles, mandibular apex of female thus tridentate; eyes parallel or converging below (Australia) *Paracolletes*
- Inner hind tibial spur of female coarsely pectinate, shaft thick near base and narrowing in region where most of teeth arise (Fig. 39-8f); basitibial plate of female defined only along posterior margin, or, at least apex not defined, plate never visible without removal of hairs; basitibial plate of male variable, acutely pointed if defined; mandible approximately parallel-sided, apex bidentate; eyes often diverging below (Australia) *Trichocolletes*
- 4(2). Metasoma with transverse, pale-yellow, integumental bands, broken or narrowed sublaterally, on subapical parts of terga; clypeus yellow in both sexes; scape of male greatly broadened (Australia) *Neopasiphae*
- Metasoma without yellow integumental bands, yellowish-brown bands occasionally present but not emarginate or broken sublaterally; clypeus dark in female, rarely yellow in male; scape of male usually unmodified, sometimes thickened but not flat 5
- 5(4). Basal vein basal to cu-v of forewing; maxillary palpus about as long as width of galea, four-segmented; first recurrent vein received near basal one-third or one-fourth of second submarginal cell (Fig. 39-5b) (Australia) *Phenacolletes*
- Basal vein meeting or distal to cu-v of forewing (Fig. 39-5); maxillary palpus much longer than width of galea, six-segmented; first recurrent vein received beyond basal one-third of second submarginal cell (Fig. 39-5a, c-f).... 15
- 6(5). S8 of male with two flat, delicate, apical processes, longer than body of sternum (Fig. 39-4b); supraclypeal area with longitudinal, strongly elevated, impunctate, shining carina or broad ridge extending from frontal carina down to upper margin of clypeus; distal three antennal segments of male modified (Fig. 39-4d) (Australia) *Glossurocolletes*
- S8 of male ending in the usual single, commonly heavily sclerotized, apical process; supraclypeal area broadly convex, median part sometimes impunctate; apical antennal segments of male unmodified or rarely crenulate, or last one rarely broadened and flattened 7
- 7(6). Claws (at least of male, those of female unknown) each with broad, flat inner ramus arising near base (Fig. 39-4g); episternal groove below scrobal groove represented only by weak, short depression; strong carina just behind posterior orbit (Australia)..... *Hesperocolletes*
- Claws cleft apically in male and usually in female, inner ramus pointed like outer ramus or sometimes in female reduced to a tooth or absent (in one undescribed species of *Leioproctus* somewhat like those of *Hesperocolletes*); episternal groove distinct below scrobal groove; no strong carina behind posterior orbit 8
- 8(7). S8 of male with median apical process slender and hairy at apex, pale, not exposed (Fig. 39-3b); volsella large, produced posteriorly, reaching beyond apex of articulated gonostylus (Fig. 39-3a); stigma less than one-half as long as marginal cell, measured on wing margin (Fig. 39-5a); apex of marginal cell bent gradually from wing margin for about one-sixth length of cell and bearing long appendage; profile of propodeum nearly vertical (Australia)..... *Chrysocolletes*
- S8 of male with median apical process robust, heavily sclerotized (Fig. 39-6c, g), its apex suggesting a pygidial plate and commonly exposed in repose, or (in some species of subgenus *Goniocolletes*) process broadened and appearing as extension of elongated disc (Fig. 39-7e); volsella not reaching gonostylus or reaching only its basal part, gonostylus fused to gonocoxite; stigma usually larger; apex of marginal cell only minutely bent away from wing margin; profile of propodeum usually with sloping or subhorizontal basal zone (Australian area) *Leioproctus*

Genus *Brachyglossula* Hedicke

Brachyglossa Friese, 1922a: 577, not Boisduval, 1829. Type species: *Brachyglossa rufocaeerulea* Friese, 1922, monobasic. *Brachyglossula* Hedicke, 1922: 427, replacement for *Brachyglossa* Friese, 1922. Type species: *Brachyglossa rufocaeerulea* Friese, 1922, autobasic.

This genus of large (body length 12–16 mm), dark-haired, unbanded bees is distinctive in appearance, except for the superficially similar *Leioproctus* (*Cephalocolletes*) *laticeps* (Friese). In some major features, such as the vestiture and form of the hind basitarsus of the female and the shape of the process of S8 of the male, *Brachyglossula* resembles *Leioproctus*. The other characters are sufficiently marked and unique, however, to support recognition at

colletes (e.g., the crenulate flagellum of the male) are probably convergent. *Leioproctus crenulatus* is transferred to the subgenus *Leioproctus* s. str., at least until that group is properly revised.

Genus *Eulonchopria* Brèthes

This is a genus of coarsely sculptured, nonmetallic bees 8 to 11 mm long with yellow apical integumental bands on at least some of the metasomal terga, but without hair fasciae on the terga, and often with plaited (longitudinally folded) forewings with darkened costal margins (Danforth and Michener, 1988), the whole thus yielding a superficial resemblance to eumenine wasps. The pubescence is short; in *Eulonchopria* s. str., at the anterior and posterior scutal angles and often elsewhere, the hairs are so short that each fits inside a puncture and is broadly plumose. Facial foveae are absent or deeply impressed and well defined in both sexes; when present, they are elongate and low on the face, that is, not reaching the summits of the eyes. The propodeal triangle has large, deep pits; some of the ridges margining the pits are produced, lamella-like or toothlike. The horizontal and vertical surfaces of the propodeum are separated by a sharp angle or lamella. The front basitarsus of the female in *Eulonchopria* s. str. ends with an outer apical process from which a comb extends basad on the outer edge of the basitarsus; in *Ethalonchopria* the comb is present but the apical process is absent. The inner hind tibial spur of the female is coarsely pectinate (three to five teeth); that of the male is coarsely toothed or ciliate, or the hind tibial spurs are completely absent. The hairs of the outer surface of the hind tibia of the female are short and not scopalike, especially on the distal half of the tibia. The basitibial plate of the male ends in a carina extending to the apex of the tibia. The stigma is nearly parallel-sided, vein r arising near the apex, and the margin within the marginal cell is oblique, not convex. There are three submarginal cells; the apex of the marginal cell is obliquely bent away from the wing margin or obliquely truncate. The genitalia and hidden sterna of males were illustrated by Michener (1963a), the wing venation by Danforth and Michener (1988).

Typical members of this genus possess various probable apomorphies that are unusual among bees and not shared by related groups (*Leioproctus* and other Colletinae). The deep, rather slender, bare, well-defined facial foveae (of one subgenus), however, are shared with the Australian genus *Callomelitta* and with some species of the African genus *Scapter*, as well as with the Euryglossinae and Hylaeinae. This character is probably a plesiomorphy. Likewise, the distinct, slender male gonostyli of some species, unique for the Colletidae, are a possible plesiomorphy. The apparently disjunct distribution of *Eulonchopria* (Americas but absent in wet tropics), combined with its unusual characters and the morphological diversity of its species, suggests that *Eulonchopria* is an archaic group possessing many derived features.

Leioproctus simplicicrus Michener (1989) from Peru, originally incorrectly placed as an unusual species of *L. (Nomiocolletes)*, to which it runs in the keys to genera and subgenera, seems to connect *Eulonchopria* and *Leioproctus*, suggesting that *Eulonchopria* is a specialized deriva-

tive of the large paraphyletic genus *Leioproctus*. G. Melo pointed out to me that *L. simplicicrus* resembles *Eulonchopria* in its short pubescence, the obliquely truncate apex of the marginal cell, the apical yellow tergal bands, the carina along the hind tibia of the male, and (especially) its genitalia and hidden sterna (compare Michener, 1963a and 1989). (The female is unknown, and the characters of the scopa cannot be determined.) On the other hand, *L. simplicicrus* differs from *Eulonchopria* and resembles *Leioproctus* in the absence of a preoccipital carina, the absence of a lamella from the posterior pronotal lobe to the dorsum of the pronotum, and the relatively large stigma, which is broadest at the base of vein r and convex within the marginal cell. The propodeal triangle has a few weak rugae basally but lacks the sharp carinae or lamellae characteristic of *Eulonchopria* s. str. When both sexes are known, *L. simplicicrus* may well be placed as a distinct genus or subgenus; females of an unnamed species from Brazil may fall in the same group.

Key to the Subgenera of *Eulonchopria*

1. Facial fovea absent; omaulus not carinate
..... *E. (Ethalonchopria)*
- Facial fovea distinct; omaulus carinate
..... *E. (Eulonchopria s. str.)*

Eulonchopria / Subgenus *Ethalonchopria* Michener

Eulonchopria (Ethalonchopria) Michener, 1989: 670. Type species: *Apista gaullei* Vachal, 1909, by original designation.

This subgenus differs in many features from the other subgenus. In nearly all of the subgeneric characters it is less strange than *Eulonchopria* s. str., that is, more like other colletines. Noteworthy are the punctate and only slightly concave foveal areas on the face, such that distinct foveae are absent; the simple axillae; and the jugal lobe of the hind wing, which extends little more than halfway from the wing base to the level of vein cu-v. Although most of the subgeneric characters are plesiomorphic relative to *Eulonchopria* s. str., the small jugal lobe and the small second submarginal cell are apomorphic. This subgenus is probably the sister group to *Eulonchopria* s. str. ■ The subgenus is known from Bolivia, southern Brazil, and eastern Colombia. The two species names, both dating from Vachal (1909), may represent only one species.

Eulonchopria / Subgenus *Eulonchopria* Brèthes s. str.

Eulonchopria Brèthes, 1909a: 247. Type species: *Eulonchopria psathyroides* Brèthes, 1909, monobasic.

This subgenus contains the more ornate and extraordinary members of the genus. The carinate omaulus and produced, angulate axillae are especially unusual. The preoccipital ridge is expanded as a strong lamella. The carina on the upper margin of the hind tibia of the male is toothed. The jugal lobe of the hind wing nearly attains the level of cu-v. The apex of T7 of the male is bilobed or bidentate.

■ This subgenus ranges from Paraguay, Argentina (Salta province), and Brazil (Santa Catarina to Minas Gerais)

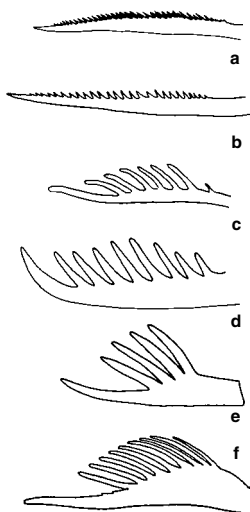


Figure 39-8. Variation in inner hind tibial spurs of females of Colletinae. **a**, *Leioproctus* (*Spinolapis*) *caerulescens* (Spinola); **b**, *L.* (*Perditomorpha*) *bruneri* (Ashmead); **c**, *L.* (*P.*) *inconspicuus* Michener; **d**, *Brachyglossula* *bouvieri* (Vachal); **e**, *Lonchopria* (*Lonchoprella*) *annectens* Michener; **f**, *Trichocolletes* *venustus* (Smith). Both **a** and **b** are considered ciliate, the others pectinate. **a-e**, from Michener, 1989; **f**, from Michner, 1965b.

tributable to any other subgenus. It is almost certainly paraphyletic. The lone South American species included in the subgenus by Michener (2000) and now placed in *Actenosigynes* shows no special affinity at the subgenus level with the Australian members of the genus.

Table 39-1. Subgenera of *Leioproctus* Segregated by Geographical Area.

South America	Australian Region
<i>Actenosigynes</i>	<i>Andrenopsis</i>
<i>Albinapis</i>	<i>Baeocolletes</i>
<i>Cephalocolletes</i>	<i>Ceratocolletes</i>
<i>Chilicolletes</i>	<i>Cladocerapis</i>
<i>Glossopasiphae</i>	<i>Colletellus</i>
<i>Halictanthrena</i>	<i>Colletopsis</i>
<i>Hexanthea</i>	<i>Euryglossidia</i>
<i>Holmbergeria</i>	<i>Excolletes</i>
<i>Hoplocolletes</i>	<i>Filiglossa</i>
<i>Kylopasiphae</i>	<i>Goniocolletes</i>
<i>Nomiocolletes</i>	<i>Lamprocolletes</i>
<i>Perditomorpha</i>	<i>Leioproctus</i> s. str.
<i>Protodiscelis</i>	<i>Nesocolletes</i>
<i>Pygopasiphae</i>	<i>Odontocolletes</i>
<i>Reedapis</i>	<i>Protomorpha</i>
<i>Sarocolletes</i>	<i>Urocolletes</i>
<i>Spinolapis</i>	
<i>Tetraglossula</i>	

- Key to the Subgenera of *Leioproctus* of South America
1. T1-T4 in female and T1-T5 or T6 in male with enamel-like apical marginal zones of yellowish, green, bluish, or whitish, these zones usually at least partly impunctate and hairless *L.* (*Nomiocolletes*)
 - Terga without enamel-like apical marginal zones, with hairs and punctures near apical margins that are concolorous with other parts of terga, or translucent or brownish, or, rarely [in *L.* (*Perditomorpha*) *eulonchopriodes* Michener], with apical yellow bands, but the band of T2 absent 2
 - 2(1). Submarginal cells three 3
 - Submarginal cells two 14
 - 3(2). Dorsolateral angle of pronotum produced as small tooth projecting upward and outward (smallest in male); basitibial plate of female not easily seen because its hairs are erect, similar to those of adjacent parts of tibia, largely hiding marginal carinae *L.* (*Halictanthrena*)
 - Dorsolateral angle of pronotum low, rounded, scarcely evident; basitibial plate of female distinct, its hairs short, appressed, different from those of adjacent areas, its marginal carinae clearly exposed 4
 - 4(3). Second submarginal cell on posterior margin usually at least three-fourths as long as third; second submarginal crossvein usually curved in a manner parallel to third, anterior margin of third submarginal cell thus at least two-thirds as long as posterior margin 5
 - Second submarginal cell on posterior margin much shorter than third (as in Fig. 39-5d, f); second submarginal crossvein usually straight, at least not curved parallel to third, anterior margin of third submarginal cell usually less than two-thirds as long as posterior margin 6
 - 5(4). Mandible of male with preapical tooth; outer hind tibial spur of female pectinate, although more finely so than inner spur; metasoma with at least weak blue reflections *L.* (*Reedapis*)
 - Mandible of male simple; outer hind tibial spur of female coarsely ciliate; metasoma black *L.* (*Cephalocolletes*)
 - 6(4). Thorax dull, minutely roughened, almost lacking punctures; malar area as long as minimum diameter of flagellum; clypeus protuberant in lateral view by fully eye width *L.* (*Torocolletes*)
 - Thorax with at least some areas of shining integument between strong punctures; malar area linear; clypeus not or little protuberant 7
 - 7(6). Males (unknown in *Hoplocolletes*) 8
 - Females (unknown in *Holmbergeria*) 11
 - 8(7). Subantennal suture little over half as long as diameter of antennal socket; supraclypeal and subantennal areas impunctate, shining, hairless, in conspicuous contrast to adjacent areas *L.* (*Holmbergeria*)
 - Subantennal suture as long as diameter of antennal socket; supraclypeal and subantennal areas punctate, with hairs 9
 - 9(8). Gonoforceps hairy to base; gonobase one-half as long as gonoforceps; apex of S6 with broad, shallow emargination; metasoma with pubescence all blackish *L.* (*Leioproctus* s. str.)
 - Gonocoxite (or coxal part of gonoforceps) hairless;

- gonobase one-third as long as gonoforceps or less; apex of S6 with the usual small, V-shaped (sometimes shallow) median emargination; metasoma with some or all hair pale, usually forming apical tergal bands 10
- 10(9). Labrum three times as wide as long, apical margin broadly emarginate *L. (Chilicolletes)*
- Labrum little over twice as wide as long, apical margin convex or with small median emargination *L. (Sarocolletes)* (in part)
- 11(7). Inner hind tibial spur finely pectinate (almost ciliate) with over 25 teeth *L. (Actenosigynes)*
- Inner hind tibial spur strongly pectinate with less than ten teeth 12
- 12(11). S2-S4 with apical bands of sparse, simple hairs not hiding surfaces of sterna *L. (Chilicolletes)*
- S2-S4 with apical bands of long, dense hairs forming a ventral scopa that partially hides surfaces of sterna 13
- 13(12). Tibial and sternal scopal hairs with numerous short, fine branches projecting laterally from rachis (as in Fig. 13-1d) *L. (Sarocolletes)* (in part)
- Tibial scopal hairs dividing to form few major branches; the sternal scopal hairs simple *L. (Hoplocolletes)*
- 14(2). Mandible of male simple; labrum about six times as wide as long, in female with apicolateral lobe bearing part of marginal fringe of bristles (Fig. 39-9a, b) 15
- Mandible of male with preapical tooth on upper margin, as in female; labrum two to five times as wide as long, without apicolateral lobe (Fig. 39-9c) 16
- 15(14). Glossal lobes not much longer than basal width; scopal hairs of tibia and sterna with numerous short, fine branches (Fig. 13-1e); clypeal margin of male unmodified, truncate *L. (Protodiscelis)*
- Glossa deeply divided, the lobes elongate, seven to ten times as long as basal width (as in Fig. 39-12); scopal hairs of tibia and sterna simple, or those of tibia with a few major branches; clypeal margin of male with short median lobe overhanging base of labrum *L. (Tetraglossula)*
- 16(14). Glossa deeply bifid, lobes about five times as long as basal width (Fig. 39-12a) *L. (Glossopasiphae)*
- Glossal lobes short, not much if any longer than basal width 17
- 17(16). Labial palpus five- to nine-segmented, longer than maxillary palpus; hind tibia of male with strong carina from apex of basitibial plate to apex of tibia 27
- Labial palpus four-segmented, usually shorter than maxillary palpus; hind tibia of male without longitudinal carina or, rarely, with weak carina arising behind apex of basitibial plate 18
- 18(17). S2-S5 of female covered with short, unbranched, erect hairs enlarged and curved posteriorly at tips and of uniform length except longer on S2; pygidial plate of male defined, at least posterior end limited by carina; hind tarsus of male elongate, segment 2 well over three times as long as broad *L. (Pygopasiphae)*
- S2-S5 of female with broad apical bands of relatively long, simple or branched hairs; T7 of male with pygidial area indicated only by lack of hairs (but large and somewhat defined in *Kylopasiphae*); hind tarsus of male not especially elongate, segment 2 less than three times as long as greatest breadth 19
- 19(18). Females 20
- Males 24
- 20(19). Tibial and sternal scopal hairs with numerous short, fine side branches projecting at right angles to rachis or curled basad (as in Fig. 13-1d) *L. (Sarocolletes)* (in part)
- Tibial scopal hairs with long branches directed distad (Fig. 13-1a, b); sternum with hairs simple or their branches directed distad 21
- 21(20). Inner hind tibial spur coarsely pectinate with ten teeth or less 22
- Inner hind tibial spur ciliate or finely pectinate with over a dozen teeth 23
- 22(21). Scopa of hind tibia formed around tibia without long, loose hairs extending above and below; basitibial plate with carinate margins not hidden by hair *L. (Perditomorpha)* (in part)
- Hind tibia with a few long, loose hairs fully half as long as tibia on upper and lower margins; basitibial plate hidden by hair except sometimes at base *L. (Kylopasiphae)*
- 23(21). Claws simple or with inner rami reduced to small teeth, shorter than basal diameters of outer rami; body metallic blue or greenish *L. (Spinolapis)*
- Inner rami of claws strong, longer than basal diameters of outer rami, claws thus bifid; body lacking metallic coloration *L. (Perditomorpha)* (in part)
- 24(19). T7 with shiny, hairless, irregularly rough pygidial area, not narrowed posteriorly, defined across posterior border by weak carina, this area occupying much of dorsum of tergum; S7 with apical lobes much reduced, all in a single plane *L. (Kylopasiphae)*
- T7 with dull or shiny, usually ill-defined pygidial area, sometimes a longitudinal strip, sometimes a broader area narrowed posteriorly; S7 with well-developed apical lobes, two to four on each side, usually at two levels 25
- 25(24). Body metallic bluish or greenish; margin of S6 produced midapically as rounded hairy lobe about one-third as wide as sternum, notched medially *L. (Spinolapis)*
- Body almost always nonmetallic; margin of S6 broadly rounded, not produced midapically, with median notch, often broad and shallow 26
- 26(25). Metasoma rather broad and flattened, resembling that of female in shape *L. (Sarocolletes)* (in part)
- Metasoma commonly rather slender, not flattened, usually distinctly different in shape from that of female *L. (Perditomorpha)*
- 27(17). Labial palpus 5-segmented; apicolateral lobes of S7 of male small, rounded *L. (Albinapis)*
- Labial palpus 6- to 9-segmented; apicolateral lobes of S7 of male well-developed *L. (Hexanthea)*

Key to the Subgenera of *Leioproctus* of the Australian Region

1. Submarginal cells two 2
- Submarginal cells three [except in some specimens of *L. (Leioproctus) abnormis* (Cockerell)] 6
- 2(1). First recurrent vein basal to first submarginal crossvein (Fig. 39-5h); clypeus and supraclypeal area usually flat, depressed, shining, largely impunctate; hind tibial spurs robust, curved apically, outer one nearly as coarsely toothed as inner *L. (Baeocolletes)*
- First recurrent vein distal to or rarely meeting first sub-

- marginal crossvein; clypeus and supraclypeal area convex, the latter elevated above level of antennal sockets; hind tibial spurs slender, not strongly curved apically, outer one not coarsely toothed 3
- 3(2). Propodeum almost wholly vertical in profile; stigma small, nearly parallel-sided, little more than half as long as marginal cell on costal margin of wing (Fig. 39-5g) *L. (Andrenopsis)*
- Propodeum with broad basal subhorizontal or horizontal zone, curving onto vertical posterior surface; stigma large, not parallel-sided, at least two-thirds as long as marginal cell on costal margin of wing (Fig. 39-5e) 4
- 4(3). Jugal lobe of hind wing extending well beyond level of cu-v; inner hind tibial spur of female ciliate *L. (Colletellus)*
- Jugal lobe of hind wing short, not attaining level of cu-v (Fig. 39-5e); inner hind tibial spur of female usually pectinate 5
- 5(4). Galea with several very long apical hairs and labial palpus filamentose, about as long as face (Fig. 19-6) *L. (Filiglossa)*
- Mouthparts unmodified *L. (Euryglossidia)*
- 6(1). Arolia absent *L. (Urocolletes)*
- Arolia present 7
- 7(6). Basitibial plate of female and some males absent; pygidial plate of female with apical part slender, parallel-sided or slightly narrowed preapically; basal vein more or less transverse, slanting about 30° to costal margin of wing, and little if any longer than first abscissa of Rs (Fig. 39-5l) *L. (Excolletes)*
- Basitibial plate present (but anterior side not defined in one species of *Lamprocolletes*); pygidial plate of female broad, sides converging posteriorly [except in *L. (Protomorpha) fallax* (Cockerell)]; basal vein slanting 45° or more to costal margin of wing, and much longer than first abscissa of Rs (Fig. 39-5d-f) 8
- 8(7). Clypeus and supraclypeal area flat, depressed, shining, at least partly impunctate, sometimes longitudinally striate, suture separating them weak; anterior basitarsus of female with long coarse bristles on outer surface *L. (Cladocerapis)*
- Clypeus and supraclypeal area not flat, usually punctate, suture separating them distinct [weak or absent but whole area uniformly punctate in *L. (Protomorpha) tarsalis* Rayment]; anterior basitarsus of female with ordinary vestiture 9
- 9(8). Dorsolateral angles of pronotum much elevated above adjacent scutal surface so that dorsal pronotal margin between them is concave *L. (Colletopsis)*
- Dorsolateral angle of pronotum weak or absent, dorsal pronotal margin not concave 10
- 10(9). Malar area more than half as long as broad; S7 of male with apical lobes reduced (New Zealand) *L. (Nesocolletes)*
- Malar area very short; S7 of male usually with two large apical lobes 11
- 11(10). Females 12
- Males 17
- 12(11). Scape not attaining anterior ocellus (small to middle-sized, robust, nonmetallic, commonly strongly punctate species; wings not reaching beyond apex of metasoma; flagellum short, middle segments mostly broader than long or scarcely longer than broad; propodeum, as seen in profile, with horizontal area, if present, usually shorter than metanotum) 13
- Scape usually attaining anterior ocellus, but if shorter, then not agreeing with characters listed in parentheses above 14
- 13(12). Terga usually red, without apical hair bands; forewing length usually over 6 mm *L. (Odontocolletes)*
- Terga usually black, usually with pale apical hair bands; forewing length commonly 5 mm or less *L. (Protomorpha)*
- 14(12). Metanotum with median tubercle (in some cases weak), projection, spine, or bifid process; propodeum as seen in profile vertical or nearly so, without subhorizontal basal area (nearly always metallic species) *L. (Lamprocolletes)*
- Metanotum without median elevation or, if with small median tubercle, then propodeum with distinct horizontal basal area 15
- 15(14). Metasoma, including apical marginal zones of terga, densely punctate; clypeus with longitudinal, median, shining convexity, thus protuberant; claws simple *L. (Ceratocolletes)*
- Metasoma not densely punctate or, if so, then marginal zones of terga not similarly punctate; clypeus not usually protuberant; claws usually cleft 16
- 16(15). Facial fovea commonly impressed; stigma small, slender, parallel-sided, little (if any) more than one-half as long as that part of marginal cell on wing margin (as in Fig. 39-5g); metasomal terga often with basal hair bands and often with very broad, translucent marginal zones *L. (Goniocolletes)*
- Facial fovea not impressed; stigma usually not parallel-sided, more than one-half as long as that part of marginal cell on wing margin (Fig. 39-5k) [except in *L. subpunctatus* (Rayment)]; metasomal terga without basal hair bands, apical marginal zones rarely broadly translucent *L. (Leioproctus s. str.)*
- 17(11). Hind tibial spur one, minute, sometimes apparently absent 18
- Hind tibial spurs two, of ordinary size 19
- 18(17). Hind tibia expanded, a row of coarse bristles on distal part of lower margin; hind basitarsus with broad, flat, median or basal projection from lower margin; mandible simple, sharply pointed, without preapical tooth *L. (Protomorpha)* (in part)
- Hind tibia and basitarsus slightly modified but slender; mandible with preapical tooth *L. (Goniocolletes)* (in part)
- 19(17). Species small to middle-sized, robust, nonmetallic, commonly strongly punctate; wings not reaching beyond apex of metasoma; flagellum short, its middle segments mostly broader than long or scarcely longer than broad; propodeum, as seen in profile, with horizontal area, if present, usually shorter than metanotum 20
- Species not agreeing with combination of characters listed above 21
- 20(19). S7 with apical lobes small, broadly attached to body of sternum; terga without apical hair bands *L. (Odontocolletes)*

- S7 with two large apical lobes; terga often with apical hair bands *L. (Protomorpha)* (in part)
- 21(19). Metanotum with median tubercle (in some cases weak), projection, spine, or bifid process; propodeum as seen in profile vertical or nearly so, without subhorizontal basal area (nearly always metallic species).....
..... *L. (Lamprocolletes)*
- Metanotum without median elevation or, if with small median tubercle, then propodeum with distinct horizontal basal area 22
- 22(21). Metasoma, including apical marginal zones of terga, densely punctate; last antennal segment sometimes enlarged and flattened *L. (Ceratocolletes)*
- Metasoma not densely punctate or, if so, then marginal zones of terga not similarly punctate; last antennal segment unmodified 23
- 23(22). Facial fovea commonly impressed; stigma small, slender, parallel-sided, little (if any) more than one-half as long as that part of marginal cell on wing margin (as in Fig. 39-5g); metasomal terga often with basal hair bands and often with very broad translucent apical marginal zones; S7 produced posteriorly as slender neck to which apical lobes are attached (Fig. 39-7f)
..... *L. (Goniocolletes)* (in part)
- Facial fovea not impressed; stigma usually not parallel-sided, more than one-half as long as that part of marginal cell on wing margin (Fig. 39-5k) [except in *L. subpunctatus* (Rayment)]; metasomal terga without basal hair bands, apical marginal zones rarely broadly translucent; S7 with median portion not so slender and elongate
..... *L. (Leioproctus s. str.)*

***Leioproctus* / Subgenus *Actenosigynes* Moure, Graf, and Urban, new status.**

Actenosigynes Moure, Graf, and Urban, 1999: 2. Type species: *Leioproctus fulvoniger* Michener, 1989, by original designation.

This name was proposed as a genus for the only American species left in *Leioproctus* s. str. by Michener (1989, 2000). Moure, Graf, and Urban (1999) had both sexes and its separation from the Australian *Leioproctus* s. str. is appropriate, but like other similar forms, it is considered a subgenus of *Leioproctus*. It is not particularly similar to any one Australian species or species group. It differs from the great majority of Australian species in having four instead of two apicolateral lobes on S7 of the male. In this respect, however, it resembles the Australian *L. advena* (Smith) and its relatives, which Michener (1965b) noted might well be separated subgenerically from *Leioproctus* s. str. In other features, however, *L. fulvoniger* is quite different from *L. advena*. The presence of only two lobes on S7 is likely to be an apomorphic state, since four is a widespread condition in other colletid subfamilies.

■ The single species, *Leioproctus (Actenosigynes) fulvoniger* Michener, is found in southern Brazil.

***Leioproctus* / Subgenus *Albinapis* Urban and Graf, new status.**

Albinapis Urban and Graf, 2000: 595. Type species: *Albinapis gracilis* Urban and Graf, 2000, by original designation.

Albinapis is a close relative of *Leioproctus (Hexanthes)*. *Leioproctus (Albinapis) gracilis* (Urban and Graf) **new combination** differs from *Hexanthes* in the 5-segmented labial palpi and especially in the small rounded apicolateral lobes of S7 of the male, as illustrated by Urban and Graf (2000a). For additional characters, see the subgenus *Hexanthes*.

■ The single species *Leioproctus (Albinapis) gracilis* (Urban and Graf) occurs in Rio Grande do Sul, Brazil.

***Leioproctus* / Subgenus *Andrenopsis* Cockerell**

Andrenopsis Cockerell, 1905a: 363. Type species: *Andrenopsis flavorufus* Cockerell, 1905, monobasic.

This Australian subgenus contains rather robust, non-metallic species, 7 to 8 mm long, the males nearly as robust as the females. The clypeus of the male is yellow in most species. The facial fovea of the female is broad; it is distinct because of its dull surface and sparser punctation than that on adjacent areas, but it is only slightly depressed. The metanotum is not tuberculate but broadly elevated to the level of the scutellum medially, and with a distinct, more or less vertical posterior declivity. The inner hind tibial spur is finely pectinate in the female; the inner teeth of the claws of the female are present but reduced. The inner hind tibial spur of the male is enlarged and curved in *Leioproctus (Andrenopsis) flavorufus* (Cockerell) but not in other species. The metasoma lacks hair bands but in some cases has orange-brown integumental bands. S7, S8 and the male genitalia were illustrated by Michener (1962b). In *L. (A.) douglasiellus* Michener and perhaps *L. (A.) nigrifrons* Michener there are a few very short hairs on the eyes.

■ *Andrenopsis* is known from Western Australia to Victoria and southern Queensland. The four species were listed by Michener (1965b) and Cardale (1993).

***Leioproctus* / Subgenus *Baeocolletes* Michener**

Leioproctus (Baeocolletes) Michener, 1965b: 70. Type species: *Leioproctus calcaratus* Michener, 1965, by original designation.

This Australian subgenus consists of small (4.5-7.0 mm long), nonmetallic species; the red or partly red metasoma lacks hair bands. The species are more robust than those of the subgenus *Euryglossidia*, having much the form of *Andrenopsis*. The short scape and the form of the facial foveae suggest the subgenus *Protomorpha*. The tibial spurs and the position of the first recurrent vein are unique in the genus (see the key to subgenera). The flat, polished face of two of the species is suggestive of the subgenus *Cladocerapis*, but there is clearly no close affinity with that subgenus. The facial fovea is distinct in the female. The stigma is much more than one-half the length of the margin of the marginal cell on the costa (Fig. 28-8h). The propodeum has a distinct, roughened, subhorizontal basal zone, shorter than the metanotum,

near the base. There are always three submarginal cells. The stigma is slender, not or little broader than the prestigma (measured to the wing margin), somewhat broader in the subgenus *Porterapis*. Vein r arises near the middle of the stigma (Fig. 39-11); the margin of the stigma within the marginal cell is convex, usually somewhat angulate. Male S7, S8, and genitalia were illustrated by Michener (1989) and by papers cited therein; see also Figure 39-10.

Key to the Subgenera of *Lonchopria*

1. Mandible of male with large tooth or process on lower-margin; clypeus of female without or with weakly differentiated, closely punctate, upper median area; the lateral and apical clypeal areas, if differentiated, then merely less closely punctate than upper median area 2
- Mandible of male often with obtuse preapical angle on lower margin but without large tooth or process; clypeus of female with flat or depressed, relatively closely punctate, upper median area contrasting with impunctate or sparsely punctate, convex, U-shaped lateral and apical region 3
- 2(1). Preapical tooth of male mandible enormous, separated from apical part of mandible (rutellum) by curved emargination (Fig. 39-9g); S8 of male with apical process downcurved, apex expanded and quadrangular; mandible of female unusually slender, preapical (pollex) tooth weakly developed (Fig. 39-9f) *L. (Ctenosibyne)*
- Preapical tooth of male mandible absent; S8 of male with apical process short, pointed, scarcely downcurved; mandible of female more robust with well-developed preapical tooth *L. (Lonchopria s. str.)*
- 3(1). Glossa deeply bifid (Fig. 39-12b), each lobe longer than prementum; apex of mandible scoop-shaped, the preapical (pollex) tooth reduced in female, absent in male *L. (Porterapis)*

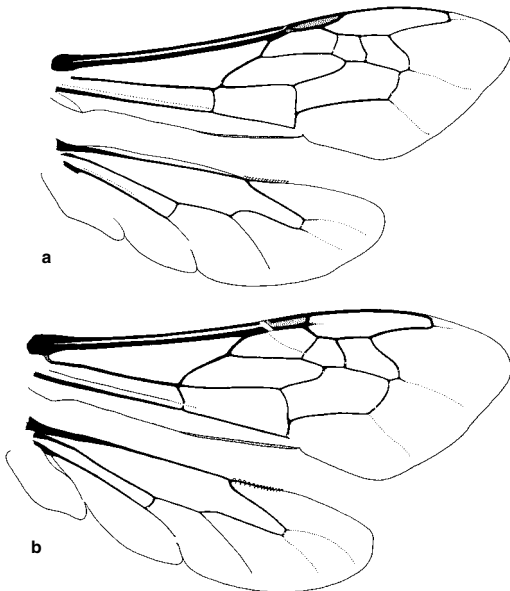


Figure 39-11. Wings of Paracolletini. **a**, *Lonchopria zonalis* (Reed); **b**, *Trichocolletes venustus* (Smith).

- Glossa of the usual bilobed form (sometimes rather deeply so), each lobe less than one-third length of prementum; apex of mandible pointed, preapical tooth (which is sometimes double) usually strong 4
- 4(3). Tibial scopal hairs sparse (as in *Leioproctus*), not hiding tibial surface, which is therefore not greatly different from that of basitarsus; body length 7.5-9.0 mm; jugal lobe of hind wing reaching or surpassing vein cu-v, over two-thirds as long as vannal lobe measured from wing base *L. (Lonchoprella)*
- Tibial scopal hairs extremely dense, hiding tibial surface, which therefore contrasts strongly with more sparsely haired basitarsus; body length variable but in most species over 9 mm; jugal lobe of hind wing usually not reaching vein cu-v and usually less than two-thirds as long as vannal lobe *L. (Biglossa)*

Lonchopria / Subgenus *Biglossa* Friese

Biglossa Friese, 1906c: 374. Type species: *Biglossa thoracica*

Friese, 1906, by designation of Cockerell, 1914: 328.

Biglossidia Moure, 1948: 313. Type species: *Biglossa chalybæa* Friese, 1906, by original designation.

Aeganopria Moure, 1949a: 442. Type species: *Lonchopria nivosa* Vachal, 1909, by original designation.

This is the largest subgenus of *Lonchopria*. The metasoma is slightly blue or green to black, with or without pale hair bands, sometimes uniformly covered with pale hair or with broad mid-dorsal areas of pale hair. The body length is 8 to 14 mm. There is a flat or depressed, closely punctate upper median clypeal area (at least in females) surrounded laterally and below by large, convex, shining, and often hairless and impunctate areas. This feature is shared with certain other subgenera, but the ordinary bilobed glossa, distinct preapical tooth of the mandible, dense tibial scopal hairs, and strong, downcurved, hairy, and often ornate process of T8 of the male distinguish *Biglossa*. The mandible of the female is usually not expanded ventrad preapically, the lower mandibular margin therefore being uniformly curved (Fig. 39-9d). The lower mandibular margin of the male, preapically, is usually expanded ventrad, forming a preapical convexity (Fig. 39-9e). S8 of the male usually has a downcurved apical process, broadened and hairy distally, often with lateral or lateroapical projections from the enlarged apex. S7, S8, and the male genitalia were illustrated by Michener (1989); see also Figure 39-10.

■ *Biglossa* occurs in western Argentina (Mendoza to Jujuy) and north in the Andean uplift through Bolivia and Peru to Colombia. Some species occur in xeric lowlands while others occur at least as high as 3,874 m in the Peruvian Andes. There are nine named species, and others yet to be described. Moure (1949a) gave a key to the species that he placed in *Biglossidia*, and Michener (1989) listed the species.

Most of the species could be placed in a subgenus *Biglossidia* Moure, but if this were done, then *Biglossa* would stand as a monotypic subgenus for *L. thoracica* (Friese), derived from *Biglossidia* and differing from it in a few striking apomorphies. The terminalia of *L. thoracica* fall well within the range of variation among species placed in *Biglossidia*. It therefore does not seem that *L.*

The extremely long labial palpi are the outstanding feature of this genus, but this is by no means a *Leioproctus* with long palpi, as shown by a series of other unique features. *Niltonia* is not obviously allied to any group of *Leioproctus*. The integument is black and nonmetallic. Body length is 10.0 to 12.5 mm. Metasomal hair bands are completely absent. Although the proboscis is short, the labial palpus is enormous, 8 to 9 mm long, its fourth segment much longer than the first three together, tapering, and often extended beyond the apex of the metasoma (fig. 1 of Moure, 1964c; fig. 3 of Laroca and Almeida, 1985). The scopal hairs on the hind leg and on S2-S5 are branched. There are two submarginal cells; the stigma is rather small, vein r arising well beyond its middle and the margin within the marginal cell convex. T7 of the male has a triangular pygidial plate, sharply pointed apically, margined by carinae laterally. S7, S8, and the genitalia of the male were illustrated by Laroca and Almeida (1985) and by Michener (1989).

■ This genus is found in Brazil from Santa Catarina to Rio de Janeiro. The only species, *Niltonia virgilii* Moure, visits flowers of *Jacaranda*. For details of mouthparts and floral behavior, see Laroca, Michener, and Hofmeister (1989).

In certain features *Niltonia* resembles *Brachyglossula*. The large and dorsally expanded volsellae and the distal origin of vein r on the stigma are the most apparent such characters. Possibly both genera arose from a common ancestor within the *Leioproctus* group.

Genus *Paracolletes* Smith

This Australian genus embraces bees larger than the average *Leioproctus*; body length is 10 to 17 mm. The body is nonmetallic and black, or (in the male) the metasoma is partly or wholly red. The inner hind tibial spur of the female is usually finely serrate or ciliate, but in *P. plumatus* (Smith) the teeth are elongated, the spur thus finely pectinate, and in *P. cygni* (Cockerell) there are fewer and even longer teeth. Such pectinate spurs, however, differ strikingly from the almost palmate spurs of *Trichocolletes*. The propodeum is declivous, without differentiated horizontal and vertical (posterior) surfaces. In males the clypeus is sometimes yellow or partly so. The male antennae are often quite long, for which reason some species were described in *Tetralonia* (Eucerini). Genitalia and hidden sterna of both subgenera were illustrated by Michener (1965b).

It is possible to recognize a homogeneous *crassipes* group (*Paracolletes* proper) and a more diversified assembly of other species tentatively called the subgenus *Anthoglossa*. When males of more species become known, the situation should be clearer.

Key to the Subgenera of *Paracolletes*

1. Metasoma with apical tergal hair bands [except in *P. cygni* (Cockerell) and *montanus* Rayment]; basitibial plate of male completely defined, of female usually exposed, rounded apically (angulate in *montanus*), one-fifth as long as tibia or less (but one-fourth in *montanus*); jugal lobe of hind wing little more than half as long as vannal lobe (but nearly two-thirds in *cygni* and *montanus*); first flagellar segment of male longer than broad; apical lobes of S7 of male broad *P. (Anthoglossa)*

- Metasoma without hair bands; basitibial plate of male not or scarcely defined anteriorly, of female hidden by hairs, bluntly rounded apically, nearly one-fourth as long as tibia; jugal lobe of hind wing about two-thirds as long as vannal lobe; first flagellar segment of male broader than long; apical lobes of S7 of male linear *P. (Paracolletes s. str.)*

Paracolletes / Subgenus *Anthoglossa* Smith

Anthoglossa Smith, 1853: 16. Type species: *Anthoglossa plumata* Smith, 1853, monobasic.

The distinctive characters are indicated in the above key and discussion. Unfortunately, because the male of the type species, *Paracolletes plumatus* (Smith), is unknown, there may be instability in the application of the subgeneric name.

■ The species of *Anthoglossa* are mostly from Western Australia, but one is from Victoria. The eight species were listed by Michener (1965b) and Cardale (1993).

Paracolletes / Subgenus *Paracolletes* Smith s. str.

Paracolletes Smith, 1853: 6. Type species: *Paracolletes crassipes* Smith, 1853, monobasic.

The distinctive characters are indicated in the key to subgenera above.

■ This subgenus is found in southern Australia north at least to the latitude of central Queensland. The eight known species were listed by Michener (1965b) and Cardale (1993).

Genus *Phenacolletes* Cockerell

Phenacolletes Cockerell, 1905b: 301. Type species: *Phenacolletes mimus* Cockerell, 1905, monobasic.

Phenacolletes consists of large bees (body length 14 mm); the pubescence is short and appressed, not forming tergal bands, giving the bee the appearance of a larrine wasp such as *Tachysphex*. The antennae of the male are short, suggesting those of a female. There are three submarginal cells; the stigma is little more than one-half as long as the costal part of the marginal cell, this cell being strongly and gradually bent away from the costa and strongly appendiculate apically (Fig. 39-5b). The propodeum is vertical seen in profile. The keirotrichia of the female's hind tibia are short, forming a distinct band on the inner surface. This is a common feature of bees and wasps and probably plesiomorphic. Long keirotrichia, more like ordinary hairs, may be an apomorphy of *Leioproctus* and its derivatives. Thus *Phenacolletes* and *Leioproctus* could be sister groups. The apex of S7 of the male is bidentate, completely lacking the usual apical lobes (Fig. 39-3e). For S7, S8, and the male genitalia, see Figure 39-3d-f and Michener (1965b).

■ This genus is known from Western Australia and South Australia. The single species is *Phenacolletes mimus* Cockerell.

Genus *Trichocolletes* Cockerell

This Australian genus includes moderate-sized to large bees with body lengths 10 to 18 mm. Those that I have

seen in the field differ from *Paracolletes* and *Leioproctus* in their exceedingly fast flight and frequent hovering. *Paracolletes* and *Leioproctus*, by contrast, fly like most species of *Andrena*. Whether the metasoma is red or black, the terga of most species have broad, translucent, testaceous to golden apical margins. In all species the terga have a sericeous texture, owing to very fine sculpturing and short, appressed pubescence. The inner hind tibial spurs of the female are pectinate, thickest basally or medially, the bases of the teeth crowded together (Fig. 39-8f), thus resembling the South American genus *Lonchopria* in this respect. The tarsal claws are fully cleft or the inner tooth is reduced or absent. The eyes of both sexes are commonly divergent below but sometimes parallel; in some species the eyes are hairy. The clypeus is usually protuberant. The second submarginal cell is usually rather large and quadrate but sometimes is small and narrowed toward the costal margin (Fig. 39-11b), as is usual in *Leioproctus*. Male genitalic and other structures were illustrated by Michener (1965b) and Houston (1990).

In view of the many combinations of the characters among species of the genus, clear-cut species groups separated by numerous characters are not apparent. It therefore seems best to divide the genus only as indicated below in spite of the morphological diversity of its extreme species. Noteworthy characters of single species are the greatly shortened labial palpi (second and third segments much broader than long) of *Trichocolletes hackeri* (Cockerell) and the swollen hind legs, lacking tibial spurs, in the male of *T. pulcherrimus* Michener.

Key to the Subgenera of *Trichocolletes*

1. Hind tibial spurs of male present; basitibial plate of female defined only posteriorly, apex not evident *T. (Trichocolletes s. str.)*
- . Hind tibial spurs of male absent; basitibial plate of female complete except for indefinite apex *T. (Callocolletes)*

Trichocolletes / Subgenus *Callocolletes* Michener

Trichocolletes (Callocolletes) Michener, 1965b: 80. Type

species: *Trichocolletes pulcherrimus* Michener, 1965, by original designation.

Callocolletes consists of a single extraordinary species: in the male the legs are incrassate with a large tooth on the anterior trochanter and there are no hind tibial spurs. The basitibial plate of the female is complete except for the indefinite apex; the basitibial plate of the male is well defined. The stigma is more than 1.5 times as long as the prestigma.

■ *Callocolletes* is from Western Australia. The single species is *Trichocolletes pulcherrimus* Michener.

Callocolletes may well be merely the most elaborately modified of the species of *Trichocolletes*. I have not synonymized *Callocolletes*, however, because it has a character that appears to be plesiomorphic relative to other *Trichocolletes*—the retention of a carina on each side of the basitibial plate of the female. In other *Trichocolletes* the female has lost the carina along the anterior margin of the basitibial plate. This variable thus suggests that *Callocolletes* may be the sister group to all other *Trichocolletes*. In this case it is a matter of judgment whether *Callocolletes* should be synonymized; I have chosen to let the current classification stand.

Trichocolletes / Subgenus *Trichocolletes* Cockerell s. str.

Trichocolletes Cockerell, 1912: 176. Type species: *Lamprocolletes venustus* Smith, 1862, by original designation.

The basitibial plate of the female is defined only posteriorly, the apex not being evident; that of the male is variable, but when present is smaller than that of *Callocolletes*. The stigma is less than or about 1.5 times as long as the prestigma (Fig. 39-11b).

■ This subgenus is widespread in the temperate parts of Australia. Cardale (1993) lists 22 named species; see also Michener (1965b).

40. Tribe Colletini

The Colletini is best known for the genus *Colletes*, found in all continents except Australia, almost always recognizable by the sigmoid second recurrent vein and the eyes convergent below, so that the head, seen from the front, is heart shaped. The tribe also includes the genus *Mourecotelles* of temperate South America. Distinctive features are the greatly reduced disc of S7 of the male (Fig. 40-2b) and the enormous apical lobes that constitute most of the sternum. Further information on tribal characters is found in Section 38.

Although the genus *Colletes* is widespread and common in much of the world and is well known as a ground-nesting bee, this tribe and genus may have originated in South America, nesting in pithy stems. Long ago the lack of pygidial and basitibial plates in *Colletes* was noted; these lacks are unusual in ground-nesting bees, most of which use these structures in moving about in their burrows and in constructing cells in the soil. In the South American Andes, however, species of *Colletes* that nest in pithy stems are known (Benoist, 1942). It seems possible that *Colletes* arose as a stem-nesting bee, lost the pygidial and basitibial plates in a life style in which these structures are not useful, and then reverted to ground-nesting and spread over the world (except Australia) despite the lack of usual structures of ground-nesting bees. A South American origin of *Colletes* is supported by the great diversity among the South American species and by the presence, there, of the only closely related genus, *Mourecotelles*. The nesting habits of species of that genus are unknown, but they may also use pithy stems.

Key to the Genera of the Tribe Colletini

- 1. T1 with anterior surface not broadly concave, often with a longitudinal median concavity; dorsal surface of T1 about as long as exposed part of T2 and at least two-thirds as long as anterior surface of T1, as seen in profile; second recurrent vein usually sigmoid with posterior half arcuate distad (Fig. 40-3), rarely angulate distad at alar fenestra on flexion line; base of propodeum with short, subhorizontal to vertical basal zone usually defined posteriorly by a carina (Fig. 37-3) or exhibiting a sharp change in slope or sculpture and divided by longitudinal carinae that may delimit strong pits (worldwide except Indo-Australian region) *Colletes*
- T1 with anterior surface broadly concave; dorsal surface of T1 much shorter than exposed part of T2 and less than two-thirds as long as anterior surface of T1, as seen in profile; second recurrent vein with posterior half straight or gently arcuate (as in Fig. 39-5), its anterior part not curved in the reverse direction, vein thus not sigmoid; base of propodeum with sloping basal zone nearly smooth, not traversed by longitudinal carinae (South America) *Mourecotelles*

Genus *Colletes* Latreille

Colletes Latreille, 1802a: 423. Type species: *Apis succincta* Linnaeus, 1758, monobasic. [For a later type designation, see Michener, 1997b.]

Evodia Panzer, 1806: 207. Type species: *Apis calendarum* Panzer, 1802 = *Apis succincta* Linnaeus, 1758, monobasic.
Monia Westwood, 1875: 221 (not Gray, 1850). Type species: *Monia grisea* Westwood, 1875, monobasic.
Monidia Cockerell, 1905c: 9, replacement for *Monia* Westwood, 1875. Type species: *Monia grisea* Westwood, 1875, autobasic.
Colletes (*Rhinocolletes*) Cockerell, 1910a: 242. Type species: *Colletes nasutus* Smith, 1853, monobasic.
Colletes (*Psilopoda*) Friese, 1921b: 83. Type species: *Colletes maculipennis* Friese, 1921 = *Colletes spiloptera* Cockerell, 1917, monobasic.
Colletes (*Denticolletes*) Noskiewicz, 1936: 25, 486. Type species: *Colletes graeffei* Alfken, 1900, monobasic.
Colletes (*Puncticolletes*) Noskiewicz, 1936: 26, 490. [Not valid under the Code, ed. 3, art. 13(b), because no type species was designated. Warncke (1978) considered *Puncticolletes* a synonym of *Rhinocolletes*.]
Rhynchocolletes Moure, 1943b: 447. Type species: *Rhynchocolletes albicinctus* Moure, 1943, by original designation.
Colletes (*Pachycolletes*) Bischoff, 1954, in Stoeckhert, 1954: 73. Type species: *Apis cunicularia* Linnaeus, 1758, by original designation.
Colletes (*Albocolletes*) Warncke, 1978: 353. Type species: *Halictus albomaculatus* Lucas, 1849, by original designation.
Colletes (*Elecolletes*) Warncke, 1978: 330. Type species: *Colletes elegans* Noskiewicz, 1936, by original designation.
Colletes (*Nanocolletes*) Warncke, 1978: 341. Type species: *Colletes nanus* Friese, 1898, by original designation.
Colletes (*Simcolletes*) Warncke, 1978: 348. Type species: *Colletes similis* Schenck, 1853, by original designation.

A unique feature of *Colletes*, not found in any other bee (only weakly developed in a few species), is the outwardly arcuate posterior part of the second recurrent vein (Fig. 40-3). An unusual feature of females—shared, however, with *Mourecotelles*—is the lack of pygidial and prepigidal fimbriae (Fig. 40-1). In general form (Fig. 40-1) *Colletes* resembles *Andrena* and *Halictus*, from which it differs in the characters just listed and usually in the strongly convergent eyes (Fig. 40-2a). The body length is 7 to 16 mm. In the holarctic region, *Colletes* is the only common genus of hairy colletids. Male genitalia of many species were illustrated by Morice (1904); Swenk (1908); Metz (1910); Noskiewicz (1936); Stephen (1954); and Mitchell (1960); see also Figure 40-2.

The long synonymy above results from two tendencies. The first is the assigning of genus-group names to each unusual species. Thus *Monidia* contains a Mexican species in which the last antennal segment of the male is expanded and the hind tibiae of the male bear long hairs. *Denticolletes* contains a palearctic species in which the axilla is produced and angulate. *Rhinocolletes* (palearctic) and *Rhynchocolletes* (Brazilian) each contain a species in which the malar area is unusually long and the clypeus is produced (in *Rhynchocolletes*, the legs of the male are modified). *Psilopoda* contains two species (Texas to Panama) with spotted wings and, in the male, somewhat

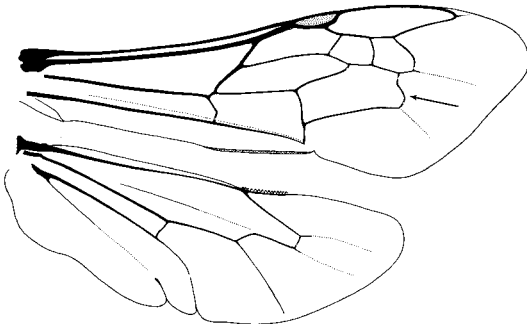


Figure 40-3. Wings of *Colletes* sp. The arrow indicates the sigmoid second recurrent vein characteristic of the genus.

region. *Colletes* has reached various islands, such as the Canary Islands and Cuba, but is not known from Madagascar in spite of its reaching southern Africa. The sub-Saharan fauna, however, is sparse, numbering about 15 species. The *Colletes* species of America north of Mexico were revised by Stephen (1954), those of Colorado were reviewed by Timberlake (1943b), those of the palearctic region by Noskiewicz (1936), of Britain by Richards (1937), of the western palearctic region by Warncke (1978), of the Ukraine by Osychnyuk (1970), and of Japan by Ikudome (1989).

The nesting biology of several species has been studied, for example, by Malyshev (1923b, 1927b), Michener and Lange (1957), Torchio (1965), Rozen and Favreau (1968), Scheloske (1974), and Torchio, Trostle, and Burdick (1988). A noteworthy feature of the burrow architecture of some species is that, instead of shaping each cell more or less identically, as do most other ground-nesting bees, they divide a burrow with transverse partitions made of the transparent cell-lining material. The result is a series of cells (Pl. 15) not identical in shape, the distal one rounded at one end, conforming with the rounded end of the burrow, the others truncate at both ends. In other *Colletes* species each lateral burrow ends in a single cell that is sometimes larger in diameter than the burrow; in this case, all cells are essentially alike in shape. The provisions of *Colletes* are liquid, as in *Hylaeus*, not at all like the firm ball of provisions characteristic of *Leioproctus* and *Lonchopria* as well as Andrenidae, Halictidae, etc. Unlike the eggs of most bees, those of *Colletes* are attached by one end to the upper wall of the cell, rather than being placed on the provisions. Even in *Hylaeus*, which makes similar cells containing liquid provisions, the egg floats on the surface of the provisions. Cell closure in *Colletes* is by a cellophane-like membrane, again as in *Hylaeus*, not by an earthen plug. Aspects of cell construction by various *Colletes* species were reviewed by Rozen and Michener (1968).

Colletes daviesanus Smith, which ordinarily nests in south-facing earth or sandstone banks, has become synanthropic in parts of Germany, boring into and damaging sandstone and mortar buildings (Scheloske, 1974). The cause of the damage is easily determined by the se-

ries of cellophane-like cells in holes in the deteriorating structures. The distribution of nests of this species in outcrops of certain sandstone strata was described in detail by Mader (1992). Mader (1999) gave a detailed compendium of literature on *Colletes* biology (with information also on other bank-nesting bees). Emphasis is on *C. daviesanus* Smith.

Although *Colletes* is ordinarily a ground-nesting genus, in the South American Andes species such as *C. rubicola* Benoist construct series of cells in dead, pithy stems (Benoist, 1942).

Genus *Mourecotelles* Toro and Cabezas

This genus, found only in temperate South America, appears to be the sister group to *Colletes*. Its apomorphies relative to *Colletes* include the shape of T1 (perhaps two independent characters) and the short, almost globose metasoma, T6 of the female being scarcely exerted. The apomorphies of *Colletes* include all the characters listed in the key to genera except those of T1. *Mourecotelles* has more characters like those of *Leioproctus* than does *Colletes*.

There are three subgenera of *Mourecotelles*. *Hemicotelles* and *Xanthocotelles* have simple claws in the female, an apomorphic character relative to Colletinae in general. The same two subgenera have what Toro and Cabezas (1977, 1978) regarded as a rudimentary pygidial plate, a character absent in *Mourecotelles* s. str. This plate, only a small, bare, elevated area at the apex of T6, may well be an apomorphic feature rather than a remnant of a pygidial plate, for it is narrowed to a point anteriorly, instead of broadened anteriorly like a typical pygidial plate. Even in *Mourecotelles* s. str. the same region is broadly elevated, quite unlike that of *Colletes*, although it is not clearly defined or bare as it is in the subgenus *Xanthocotelles*. Male genitalia and hidden sterna were illustrated by Toro and Cabezas (1977, 1978).

Key to the Subgenera of *Mourecotelles*

1. Basal zone of propodeum margined posteriorly by weak carina; middle flagellar segments of male about twice as long as wide (claws of female simple)..... *M. (Hemicotelles)*
- Basal zone of propodeum not margined posteriorly by carina; middle flagellar segments of male less than twice as long as wide..... 2
- 2(1). Claws of female simple; tibiae and tarsi reddish yellow *M. (Xanthocotelles)*
- Claws of female cleft; tibiae and tarsi largely blackish *M. (Mourecotelles* s. str.)

Mourecotelles / Subgenus *Hemicotelles* Toro and Cabezas

Hemicotelles Toro and Cabezas, 1977: 46. Type species: *Lonchopria ruizii* Herbst, 1923, by original designation.

Hemicotelles, recognizable by the characters in the key to subgenera, includes species 12 to 14 mm long.

■ This subgenus ranges from Coquimbo to Aisén, Chile, and to Santa Cruz province, Argentina. The two species were revised by Toro and Cabezas (1977).

42. Subfamily Diphaglossinae

Most members of this American subfamily are large, robust, densely hairy, and euceriform, but some look like middle-sized andreniform Colletinae. The glossa is bifid, the two lobes usually pointed and extending apicolaterad; the preapical fringe is present in the female, absent or weakly developed in the male. The glossal brush is well developed. The prementum lacks a spiculate depression. The facial fovea is suggested by a broad, slightly depressed, impunctate area that extends up into the ocellular region. The episternal groove is variable. The scopa is large and dense on the hind leg, forming a corbicula on the underside of the femur. The basitibial area of the female is covered with short, appressed hair but the basitibial plate is not indicated or only the posterior marginal carina is evident, except that the anterior carina also is evident in *Mydrosomella*; the basitibial plate of the male is absent. There are three submarginal cells. The stigma is shorter than the prestigma (Fig. 43-1), slender or almost absent, the sides parallel or converging toward vein r, which arises from the apex of the stigma. The margin of the stigma within the marginal cell is about as short as possible, that is, transverse to the long axis of the stigma, and straight or concave. The pygidial and prepygidial fimbriae of the female are strong; the pygidial plate is present in the female.

Larval characters are presented by McGinley (1981). The larvae can be distinguished from all other bee larvae by the elongate, spoutlike projection of the salivary lips, forming a circular or short transverse salivary opening. The Diphaglossinae are the only colletids that retain cocoon-spinning behavior and associated larval structures. Pupal characters were described by Torchio and Burwell (1987).

Nests consist of more or less vertical burrows with deep branches, each of which at its distal end usually bends up slightly, then curves sharply down to form a single vertical cell lined with a secreted film and holding the largely liquid provisions on which the egg floats. In various species, but not in *Crawfordapis*, the mature larva scrapes and breaks down the cell lining in the bottom end of the cell, then spins a cocoon that separates this end of the cell from the rest, forming in the bottom of the cell a fecal chamber from which liquid can escape. At the other end the cocoon consists of a strong operculum perforated by numerous round holes. A comparative study of cocoons and nest structures was made by Rozen (1984b). His treatment is so excellent and complete that references to older works on nesting biology cited by him are unnecessary here.

The most distinctive adult character is the reduction of the stigma. The other adult characters are within the range of variation found in the Colletinae. For this reason I long ago suspected that the Diphaglossinae were derived from the Colletinae, making the latter paraphyletic, a conclusion supported by most of the phylogenetic analyses by Alexander and Michener (1995). As noted in Section 37 on the Colletidae, however, the spoutlike salivary opening of diphaglossine larvae, on the one hand, and the reduced salivary lips and loss of cocoon spinning in all other colletids, on the other hand, are both synapo-

morphies relative to ancestral bees and wasps. Thus on the basis of these and associated larval characters, Diphaglossinae appears to be the sister group to all other Colletidae, as shown in a cladistic treatment of larvae by McGinley (1981) and as also indicated by Rozen (1984b) and by Michener (1986b) working with adult characters. (Larvae and cocoons are known for two tribes of Diphaglossinae, the Diphaglossini and Caupolicanini; nests of Dissoglottini have never been found.)

The Caupolicanini differ from other Diphaglossinae in such striking characters (the complete episternal groove, the long and petiolate first flagellar segment, the coarsely papillate distal parts of wings) that Michener (1944) separated Caupolicanini from other Diphaglossinae, placing the former in the Colletinae, the latter in its own subfamily. Moure (1945a) and later Michener (1954b, 1966a), however, placed the Caupolicanini within the Diphaglossinae, a view strongly supported by Alexander and Michener's (1995) phylogenetic study of adults and by the larval characters cited above.

The resemblance of members of this subfamily, and especially the Caupolicanini, to the Australian Stenotritidae and the American Oxaeinae is striking, and includes not only appearance but the reduced stigma, the papillate wings, and the long, petiolate first flagellar segment. Stenotritid and oxaeine larvae, however, show none of the synapomorphies of the Diphaglossinae, and the resemblance of the adults is almost certainly convergent.

Urban and Moure (2001) published a catalog of the species of Diphaglossinae.

Key to the Tribes of the Diphaglossinae (Modified from Michener, 1986b)

- 1. Episternal groove complete; first flagellar segment nearly as long as, to longer than, scape, much longer than subsequent segments, petiolate (Fig. 42-1a) Caupolicanini (Sec. 43)
- Episternal groove absent below scrobal groove; first flagellar segment much shorter than scape, less than twice as long as middle flagellar segments, not or only moderately petiolate (Fig. 42-1b) 2
- 2(1). Notaulus represented by deep groove in anterior part of mesoscutum; malar space nearly one-third as long as eye or longer Diphaglossini (Sec. 44)
- Notaulus weak or absent; malar space short or absent Dissoglottini (Sec. 45)

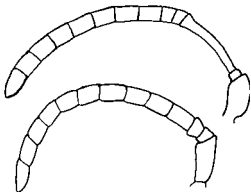


Figure 42-1. Antennae of males of Diphaglossinae. a, *Caupolicana yarrowi* (Cresson); b, *Mydrosoma brooksi* Michener.

43. Tribe Caupolicanini

In this tropical and subtropical American tribe of large, euceriform bees the lower part of the face is short, the malar space being short or absent. The notauli are strong. The jugal lobe of the hind wing is over three-fourths as long as the vannal lobe and extends beyond cu-v (Fig. 43-1). The second submarginal cell is much shorter than the first or third, and the first recurrent vein approximately meets the first submarginal crossvein (Fig. 43-1). The second recurrent vein more or less continues in the same direction as vein Cu₁ (Fig. 43-1). The distal parts of the wings are hairless but strongly papillate, the papillae often ending in slender hairlike points.

The Caupolicanini are divisible into two large genera and one small one, *Craufordapis*, as shown below. Relationships among these genera are shown in a cladogram by Michener (1986b); *Caupolicana* appears there as the sister group to the other two genera together.

Key to the Genera of the Caupolicanini

- 1. Outer hind tibial spur of male immovably fused to tibia (Fig. 43-2a); hind basitarsus of female less than twice as long as broad, second hind tarsal segment broader than long; metasomal terga usually weakly metallic bluish or greenish *Priloglossa*
— Outer hind tibial spur of male articulated at base; hind basitarsus of female more than twice as long as broad (Fig. 43-2c), second hind tarsal segment longer than broad; metasomal terga usually nonmetallic 2
- 2(1). S7 of male with no paired apical lobes; base of marginal cell prolonged as narrow sinus to apex of stigma (as in Fig. 43-1b) (Mesoamerica) *Craufordapis*
— S7 of male with paired apical lobes; base of marginal cell not prolonged as narrow sinus (Fig. 40-1a) *Caupolicana*

Genus *Caupolicana* Spinola

This genus is interpreted broadly to include *Zikanapis* and *Willinkapis*, taxa that could be given generic status. The principal characters are indicated in the key to genera (above).

The subgenera were reviewed by Michener (1966a), as were the species of North America and the West Indies.

Key to the Subgenera of *Caupolicana*

- 1. Metasomal terga rather distinctly metallic bluish; ventral apical lobe of S7 of male probably represented by broad, apically rounded, laterally directed, heavily sclerotized lateral apical projection that is hairless except mesally (South America) *C. (Willinkapis)*
— Metasoma nonmetallic; ventral apical lobe of S7 not heavily sclerotized, not hairless, variable in size and shape but not as above, sometimes absent 2
- 2(1). S6 of male with apex rounded, apex rarely with broad, median, V-shaped notch but no produced region; ventrolateral extremities of T2-T4 lacking specialized regions; clypeus of male not over 0.76 times as long as wide 3
— S6 of male with weak median apical projection that has a broad, median, V-shaped notch; ventrolateral extremi-

- ties of T2-T4 of male with large areas of dense short hair of uniform length; clypeus of male about 0.85 times as long as wide *C. (Zikanapis)*
- 3(2). Inner orbits of male strongly converging above; ocellular distance one-fourth of an ocellar diameter or less (Greater Antilles) *C. (Alayoapis)*
— Inner orbits of male not or weakly converging above; ocellular distance over one-third of an ocellar diameter and usually nearly equal to an ocellar diameter *C. (Caupolicana s. str.)*

Caupolicana / Subgenus *Alayoapis* Michener

Caupolicana (Alayoapis) Michener, 1966a: 728. Type species: *Megacilissa nigrescens* Cresson, 1869, by original designation.

In addition to the characters given in the key, this subgenus is distinctive in having a median area on S6 of the male that is nearly hairless or bears only short hairs, the posterior margin of S6 being rounded, the margin proper being a thin, hairless, translucent flange. The body length is about 15 mm. The male genitalia and hidden sterna were illustrated by Michener (1966a).

■ This subgenus is known from Cuba and Hispaniola. The three species were revised by Michener (1966a).

Caupolicana / Subgenus *Caupolicana* Spinola s. str.

Caupolicana Spinola, 1851: 212. Type species: *Caupolicana gayi* Spinola, 1851, designated by Sandhouse, 1943: 534.

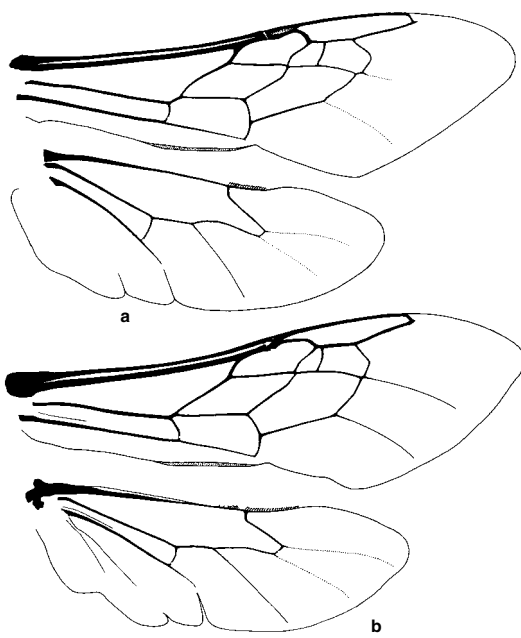


Figure 43-1. Wings of Caupolicanini. a, *Caupolicana hirsuta* (Spinola); b, *Ptiloglossa guinnae* Roberts.

44. Tribe Diphaglossini

In this South American tribe the body of the larger species is euceriform whereas smaller species seem andreniform. The lower part of the face is elongate (see key to tribes). The first flagellar segment is not greatly longer than the others, not as long as the scape, and not petiolate. The notauli are strong. The jugal lobe of the hind wing is less than half as long as the vannal lobe and does not reach the level of cu-v. The submarginal cells decrease in length from first to third, or, rarely, the second and third are equal (Fig. 44-1). The first recurrent vein enters the second submarginal cell more or less medially, and the second recurrent vein is at a distinct angle to Cu₁. The distal parts of the wings are hairy, not strongly papillate. The male genitalia and hidden sterna of all genera were illustrated by Michener (1986b); see also Figures 44-2 and 13-2b.

The relationships among the genera are indicated in a cladogram by Michener (1986b); *Cadeguala* appears to be the sister to the other two genera. The same work provides a revision of the species of this tribe.

Key to the Genera of the Diphaglossini

1. Malar space about two-thirds as long as eye in female, three-fourths in male; S3 of male with broad, median, apical projection bearing stiff, basally directed setae (Chile) *Diphaglossa*
- Malar space about one-third as long as eye; S3 of male simple 2
- 2(1). Third submarginal cell much smaller than second; apex of marginal cell obliquely, and conspicuously, truncate; S7 of male with a small lobe broadly attached on each side at apex (Fig. 44-2a) *Cadegualina*
- Third submarginal cell about as large as second (Fig. 44-

- 1a, b); apex of marginal cell narrow, the truncation inconspicuous or absent; S7 of male with three lobes, two of them large, on each side at apex (Fig. 44-2b, c) *Cadeguala*

Genus *Cadeguala* Reed

Cadeguala Reed, 1892: 234. Type species: *Colletes chilensis* Spinola, 1851 = *Colletes occidentalis* Haliday, 1836, by designation of Sandhouse, 1943: 532.

Policana Friese, 1910a: 651. Type species: *Colletes herbsti* Friese, 1910 = *Colletes albopilosus* Spinola, 1851, by designation of Sandhouse, 1943: 589.

Policana was long given generic status, but is so similar in adult morphology, although smaller in size, that it cannot be separated at the genus level. McGinley (1981) remarks that the differences between the larvae of *Cadeguala* and *Policana* do not support the recognition of separate genera.

Beyond the characters indicated in the key, *Cadeguala* differs from both of the other genera of Diphaglossini in the sparse and relatively short hairs of the sides of the female propodeum, beneath the longer, denser hairs of the upper lateral areas. The body length is 12 to 17 mm. The male genitalia and hidden sterna were illustrated by Michener (1986b).

■ This genus occurs from the Coquimbo region, Chile, and Bolivia south to Valdivia, Chile, and Río Negro, Argentina. It is particularly common in central Chile and Neuquén, Argentina. The two species were revised by Michener (1986b).

The nesting biology of *Cadeguala occidentalis* (Haliday) was described and illustrated by Claude Joseph (1926) and Torchio and Burwell (1987).

Genus *Cadegualina* Michener

Cadegualina Michener, 1986b: 187. Type species: *Bicornelia andina* Friese, 1925, by original designation.

Specimens of this genus (see key to genera) resemble fulvous-haired individuals of the common *Cadeguala occidentalis* (Haliday) but are probably more closely related to *Diphaglossa* (Michener, 1986b). The body length is 10 to 11 mm.

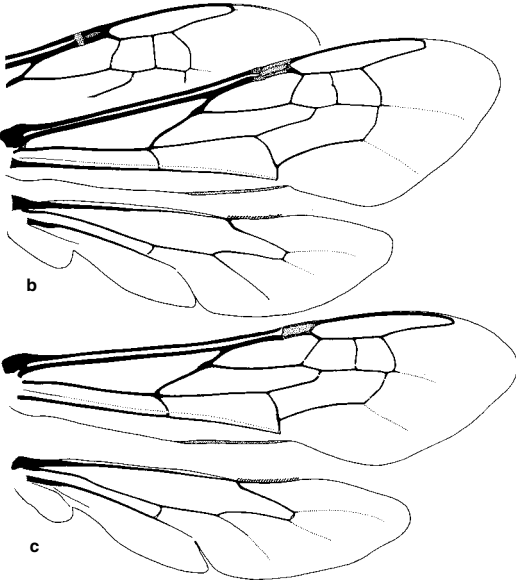


Figure 44-1. Wings of Diphaglossini. **a**, *Cadeguala occidentalis* (Haliday); **b**, *C. albopilosa* (Spinola); **c**, *Diphaglossa gayi* Spinola.

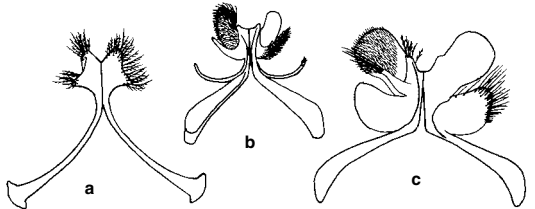


Figure 44-2. S7 of males of Diphaglossini. **a**, *Cadegualina andina* (Friese); **b**, *Cadeguala albopilosa* (Spinola); **c**, *Cadeguala occidentalis* (Haliday). (Dorsal views are at the left.) From Michener, 1986b.

45. Tribe Dissoglottini

Although *Priloglossidia* and larger species of *Mydrosoma* are euceriform, the smaller species are best called andreniform. The lower part of the face is short, as in the Caupolicanini. The first flagellar segment is about as long as the apical one, and less than one-half as long as the scape (female) or much shorter than any others and less than one-fourth as long as the scape (male), not petiolate. The jugal lobe of the hind wing is about one-half as long as the vannal lobe and does not reach the level of cu-v. Submarginal cells and recurrent veins are as described for the Diphaglossini, except that the first recurrent vein enters the second submarginal cell at the base or in the basal one-third (Fig. 45-1). The distal parts of the wing are hairy, not strongly papillate. The male genitalia and hidden sterna of all genera were illustrated by Michener (1986b).

This tribe was formerly called the Mydrosomini; the name Dissoglottini has priority, however, even though the genus *Dissoglotta* is considered a junior synonym of *Mydrosoma* (Michener, 1986b). The tribal name Pitloglossidiini is also a synonym of Dissoglottini.

Key to the Genera of the Dissoglottini

1. Arolia absent; glossa moderately bifid, its apicolateral lobes longer than wide but not attenuate or pointed (Argentina) *Priloglossidia*
- Arolia present; glossa strongly bifid, its apicolateral lobes attenuate, pointed 2
- 2(1). Second submarginal cell smaller than third; basitibial plate of female complete, margined (although hidden by hairs) (Argentina) *Mydrosomella*
- Second submarginal cell larger than or rarely the same size as third (Fig. 45-1); basitibial plate of female at most a slightly elevated area with an elevated posterior margin *Mydrosoma*

Genus *Mydrosoma* Smith

Apista Smith, 1861: 148 (not Hübner, 1816). Type species: *Apista opalina* Smith, 1861, monobasic.

Mydrosoma Smith, 1879: 5. Type species: *Mydrosoma metallicum* Smith, 1879 = *Apista opalina* Smith, 1861, monobasic.

Bicornelia Friese, 1899a: 239. Type species: *Bicornelia serrata* Friese, 1899, monobasic.

Madosoma Ashmead, 1899a: 94, lapsus for *Mydrosoma* Smith, 1879.

Egapista Cockerell, 1904a: 357, replacement for *Apista* Smith, 1861. Type species: *Apista opalina* Smith, 1861, autobasic.

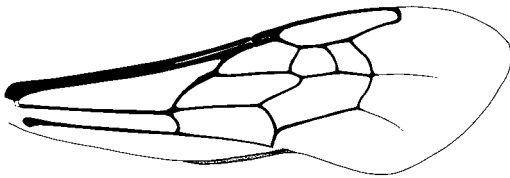


Figure 45-1. Forewing of *Mydrosoma bohartorum* Michener. From Michener, McGinley, and Danforth, 1994.

Dissoglotta Moure, 1945a: 144. Type species: *Dissoglotta stenoceratina* Moure, 1945, by original designation.

This genus of moderate-sized to large bees (body length 12-17 mm) is distinguished from its relatives by the small third submarginal cell (nearly always shorter than second, Fig. 45-1) and the reduced basitibial plate of the female (at most slightly elevated with a ridge along the posterior side, not around the apex). The hind legs of the male, especially the tibiae, are often enlarged and variously modified. Male genitalia and hidden sterna as well as hind legs were illustrated by Michener (1986b).

■ The genus ranges from Santa Catarina in southern Brazil through the tropics to Sinaloa, Mexico. The nine species are all rare in collections; the only one with known foraging habits visits flowers of *Triumfetta* (Tiliaceae) in Jalisco, Mexico, late in the afternoon (1730-1800 hrs). This genus was revised by Michener (1986b).

Genus *Mydrosomella* Michener

Mydrosomella Michener, 1986b: 194. Type species: *Diphaglossa* (?) *gaullei* Vachal, 1904, by original designation.

This genus contains a single species, one that looks superficially like a *Leioproctus* (Colletinae) because of its small size, 10.5 to 12.5 mm in length. (A few species of *Mydrosoma* are almost equally *Leioproctus*-like in appearance.) Some characters, such as that the third submarginal cell is longer than the second, and the almost complete marginal carina of the basitibial plate of the female, are as in many Colletinae and therefore must be plesiomorphic within the Diphaglossinae. Derived characters include a deep fossa for the scuto-scutellar suture. The genus was described and illustrated by Michener (1986b).

■ *Mydrosomella* is known from the provinces of Buenos Aires and Tucumán, Argentina. The only known species is *M. gaullei* (Vachal).

In view of the colletine-like features of *Mydrosomella*, it would be important to know whether the larva has the characteristics of the larvae of other Diphaglossinae.

Genus *Ptiloglossidia* Moure

Ptiloglossidia Moure, 1953a: 73. Type species: *Ptiloglossidia fallax* Moure, 1953, by original designation.

This genus, too, contains a single species, one easily distinguished from all other Diphaglossinae by its lack of arolia, but differing also in numerous other features, including the only moderately bifid glossa, which is thus intermediate between that of most Colletinae and the deeply bifid and attenuately produced glossa of other Diphaglossinae. The body length is 10.5 to 12.5 mm. I have not seen the female; hence all the information on the female is based on Moure's (1953a) description. A remarkable feature is that the head integument of the male is straw yellow, whereas the female has yellow on the labrum, mandible, and genal area only. Michener (1986b) described and illustrated the genus.

■ *Ptiloglossidia* is known only from the province of Salta, Argentina; it contains a single species, *P. fallax* Moure.

46. Subfamily Xeromelissinae

The bees of this Neotropical subfamily are small to minute, mostly slender, and hylaeiform. They are non-metallic black, but sometimes show extensive white integumental bands on the terga and often white to yellow areas on the face, the metasoma rarely red. The first flagellar segment is much shorter than the scape or, in some males, nearly as long as the scape, cylindrical or tapering toward the base, not petiolate. The glossa of both sexes is broader than long, the apex emarginate. Females have a preapical glossal fringe; the annuli and annular hairs form a dense band basal to the preapical fringe, and basal to this band is an exceedingly fine pattern perhaps representing annuli. The annuli do not extend onto the posterior surface of the glossa, which in both sexes has numerous long hairs, grading into the large, long, branched hairs of the apical glossal brush. The male glossa lacks a recognizable preapical fringe; on its anterior surface it has well-separated annuli and pointed annular hairs. The prementum has an elongate, often narrow, depression or fovea on its posterior surface, margined by distinct raised lines. The lacinia, almost hairless and not easily recognized, stretches along the upper edge of the base of the galea or along the stipes. The galeal comb is represented by only a few to about ten rather weak bristles, thus differing markedly from that of the Hylaeinae. The stipes, prementum, and cardo are unusually long (as in the Halictinae). The facial fovea is not recognizable or is represented by a shining groove or depression above the middle of the eye, not extending up between the ocelli and the summit of the eye as is the case in most Hylaeinae. The ocular margin of the paraocular area in the vicinity of the upper one-fourth of the orbit is elevated, especially in those species having an emargination at this point. The episternal groove extends well below the scrobal suture, except in *Chilicola* subgenus *Chilioediscelis*. The basitibial plate is absent. There are two submarginal cells, the second much shorter than the first. The stigma is much longer than the prestigma, usually broad, but rather slender and parallel-sided basal to vein *r* in the Xeromelissini. The scopa on the hind legs is often not recognizable except by the presence of pollen. The hairs are relatively short and sparse (Fig. 46-1a), and on the femur are so arranged as to indicate the femoral corbicula of Colletinae and many other bees. The sternal scopa is recognizable on S1 to S3, the longest hairs being on S2 (Fig. 46-1b). The pygidial plate and prepygidial fimbria are absent. Male genitalia, sterna, and other structures were illustrated by Toro and Moldenke (1979) for all genera; see also Figure 46-4.

Larvae of *Chilicola* were illustrated and described by Eickwort (1967), and those of *Chilimelissa* were characterized (as *Chilicola*) by McGinley (1981); the identity of the latter was clarified by J. G. Rozen (in litt., 1995).

The Xeromelissinae occur in temperate and subtropical regions of southern South America (especially abundant in Chile) north mostly in arid zones or the Andean uplift to northeastern Brazil and to Colombia and Venezuela. They are present but rare in wet forest areas like Belém, Brazil, occurring also on the island of St. Vin-

cent in the Lesser Antilles, in Central America (Panama to Guatemala), and northward to central Mexico (where, at the northern limit of the subfamily's range, species attain an altitude of 3,000 m).

Nests are in holes in hollow stems or beetle burrows in wood and consist of series of cells made with a cellophane-like membrane (Herbst, 1922; Claude-Joseph, 1926; Eickwort, 1967), or alternatively they may be in sandy soil where nests of *Geodiscelis* and *Chilimelissa* have been found (Michener and Rozen, 1999; Packer, 2004b). They do not differ conspicuously from those of *Hylaeus*.

The classification of the subfamily was reviewed by Michener (1995b), who recognized two tribes, Xeromelissini and Chilicolini; but Michener and Rozen (1999), on the basis of the genus *Geodiscelis*, concluded that the two tribes of Xeromelissinae merge and should not be recognized. Lawrence Packer has made a phylogenetic study of the Xeromelissinae, recognizing 18 genus-group taxa. Unfortunately this work is not yet published. The five genera of the subfamily here recognized can be distinguished by the following revision of Michener and Rozen's key:

Key to Genera of Xeromelissinae (modified from Michener and Rozen, 1999)

1. Stigma basal to vein *r* with margins diverging apically; beyond vein *r*, inner margin of stigma in marginal cell frequently convex, sometimes straight; thorax elongate; maxillary palpus not abruptly more slender at and beyond segment 4; paraocular area not invading clypeus as a strong lobe, epistomal sulcus continuing directly, straight or gently curved, from anterior tentorial pit to mandibular base (except in *Geodiscelis*, which has a strong paraocular lobe)2

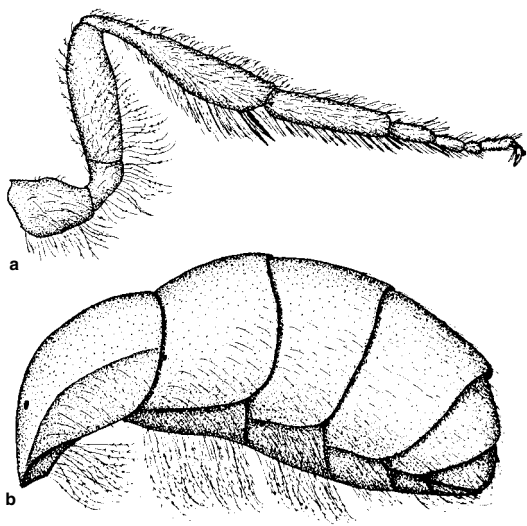


Figure 46-1. Female of *Chilicola ashmeadi* (Crawford) (Xeromelissinae). **a**, Hind leg; **b**, Lateral view of metasoma, showing the sternal scopa. From Eickwort, 1967.

- Stigma basal to vein r nearly parallel-sided; beyond vein r margin of stigma in marginal cell straight; thorax not elongate; maxillary palpus abruptly more slender at and beyond segment 4; paraocular area produced downward into clypeus as an elongate lobe along mesal border of which anterior tentorial impression slants down into clypeus; epistomal sulcus (often weak or not recognizable) curving back from lower end of this impression to mandibular base 4
- 2(1). Paraocular area produced down as lobe (along with groove representing tentorial pit) invading clypeus; glossa with slender apicolateral lobes; metasoma with ivory integumental bands *Geodiscelis*
- Paraocular area not produced downward as lobe into clypeus; glossa of usual short hylaeine or xeromelissine type; metasoma usually without ivory integumental bands 3
- 3(2). Basal sloping part of propodeum about as long as metanotum, less than half as long as declivitous vertical surface (as seen in profile); inner orbits of eyes nearly straight, not emarginate *Xenochilicola*
- Basal sloping or subhorizontal part of propodeum longer than metanotum, often as long as scutellum, half as long as vertical surface or frequently longer (as seen in profile); inner orbits of eyes emarginate or at least slightly concave at about upper third or fourth *Chilicola*
- 4(1). Anterior tentorial impression slanting down almost to apex of clypeus (Fig. 46-5a, b); labial palpus 4-segmented; maxillary palpus consisting of 6 easily seen segments, the first three markedly broader than the distal three *Chilimelissa*
- Anterior tentorial impression not approaching apex of clypeus (Fig. 46-1c, d); labial palpus three-segmented; maxillary palpus consisting of three large segments followed, at least sometimes, by two to five extremely minute segments (these are easily broken off) *Xeromelissa*

Genus *Chilicola* Spinola

Chilicola is a rather large genus with considerable morphological diversity. Species range in length from 3 to 8 mm. The body is elongate; the propodeal upper surface is longer than that of *Xenochilicola* and the pronotum is usually longer than that of *Xenochilicola*, with a distinct dorsal surface on the same level as the scutum. The stigma is large and wide, the margin within the marginal cell distinctly convex (Fig. 46-2). S5 and S6 of the male are simple; the apical process of S8 is usually broad apically, truncate or bifid.

Toro and Moldenke (1979) revised the Chilean fauna; their work is the basis for subsequent taxonomic investigation of *Chilicola* and its relatives. Michener (2002b) showed that there is also a rich fauna of *Chilicola* in the Andes from Venezuela to Peru, consisting of species of the subgenera *Anoediscelis*, *Hylaeosoma*, and *Oroediscelis*. The *Chilicola* of Mexico and Central America were revised by Michener (1994) and the subgeneric classification of the genus was reviewed by Michener (1995b).

The subgenus *Anoediscelis* is quite possibly a paraphyletic group from which *Oediscelis* as well as *Chilicola* s. str. and *Chilioediscelis* were derived. The slender male hind leg and the proportions of its segments in *Anoediscelis* are like those of outgroups such as the Hylaeinae and

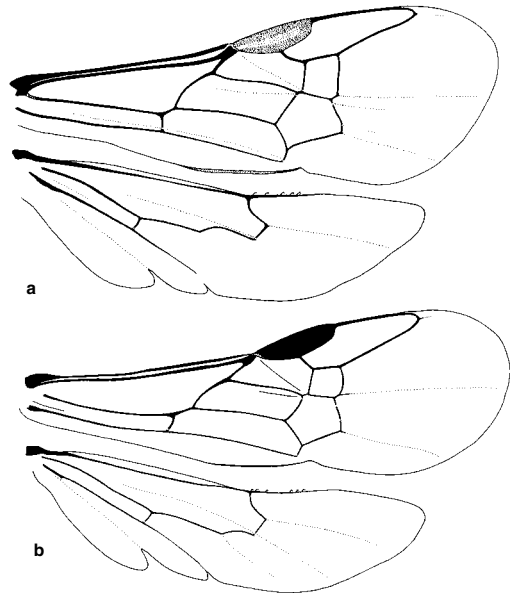


Figure 46-2. Wings of *Chilicola*. a, *C. (Anoediscelis) ashmeadi* (Crawford); b, *C. (Hylaeosoma) mexicana* Toro and Michener.

some *Chilimelissa*; *Anoediscelis* has no known apomorphies. On the other hand, present knowledge does not indicate any particular section of *Anoediscelis* from which the other subgenera may have arisen. The hind leg modifications of males that characterize *Chilicola* s. str., *Chilioediscelis*, and *Oediscelis* could have been reversed with a change in the mating system. That they could also arise more than once is suggested by the presence of similar hind legs in males of *Xeromelissa* (Toro, 1981).

The subgenera *Hylaeosoma*, *Prosopoides*, and *Pseudiscelis*, which have not proliferated in temperate or montane environments as have the other four subgenera, are not easily placed relative to *Anoediscelis*. *Prosopoides* and *Pseudiscelis* have common synapomorphies, such as the prolongation of the tentorial pits, and are presumably sister groups.

Key to the Subgenera of *Chilicola*

1. Hind tibial spurs strong and curved; clypeus and supra-clypeal area rather flat and depressed, face thus seemingly slightly concave 2
- Hind tibial spurs slender and almost straight; clypeus and supra-clypeal area convex 3
- 2(1). Episternal groove extending down to lower part of thorax; claws cleft; hind tibia of male usually showing a transverse or slanting preapical cleft or depression on inner margin *C. (Chilicola s. str.)*
- Episternal groove not extending below level of scrobe; claws of female simple; hind tibia of male somewhat thickened but ordinary in shape *C. (Chilioediscelis)*
- 3(1). Face with depression extending from antennal base toward area between ocelli and upper end of eye (Fig. 46-3d); second submarginal cell usually not extending beyond apex of stigma (Fig. 46-2b) *C. (Hylaeosoma)*
- Face without depression slanting upward from antennal

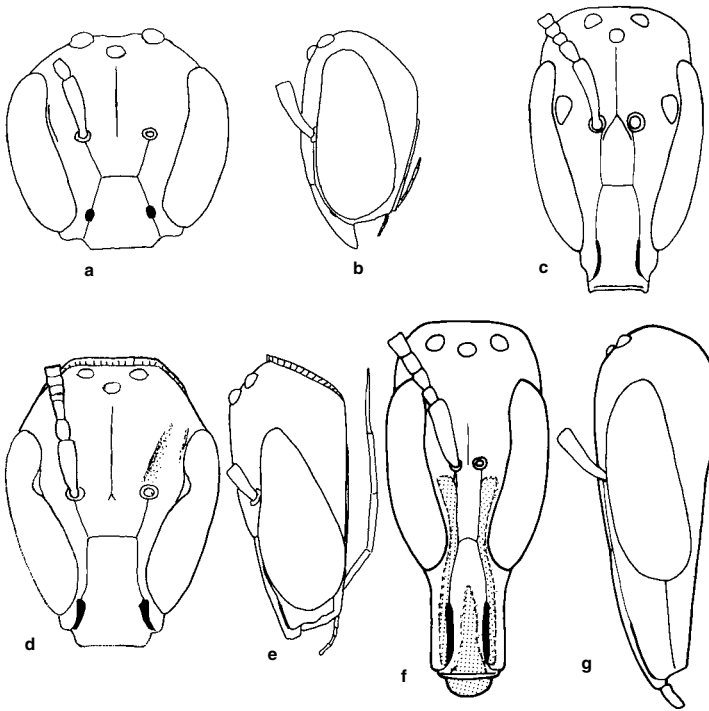


Figure 46-3. Facial and lateral views of heads of *Chilicola*, mandibles omitted. **a, b, C.** (*Anoediscelis*) *ashmeadi* (Crawford); **c, C.** (*Prosopoides*) *prosopoides* (Ducke); **d, e, C.** (*Hylaeosoma*) *polita* Michener; **f, g, C.** (*Pseudiscelis*) *rostrata* (Friese). (Females except f and g, which are male; stippled areas are yellowish.) In part from Michener, 1995b.

- base; second submarginal cell ending distal to apex of stigma (Fig. 46-2a) 4
- 4(3). Anterior tentorial pit extended apicad as deep, shining groove along epistomal suture to area near clypeal apex, where suture bends laterad toward mandibular base (Fig. 46-3c, f); head over 1.5 times as long as wide 5
- Anterior tentorial pit not greatly extended along epistomal suture; head wider than long to about 1.2 times as long as wide 6
- 5(4). A conspicuous, smooth, shining, well-defined facial fovea (less than three times as long as wide) near emargination in inner orbit (Fig. 46-3c); malar space broader than long *C. (Prosopoides)*
- No clearly recognizable facial fovea (Fig. 46-3f); malar space about 1.5 to 3.0 times as long as broad (Fig. 46-3g) *C. (Pseudiscelis)*
- 6(4). Malar space 0.4 to 1.2 times as long as broad; line perpendicular to costal forewing margin at apex of stigma crossing submarginal cells near first transverse submarginal vein; S4 of male with two strong tubercles or projections. (hind femur of male not greatly enlarged) *C. (Oroediscelis)*
- Malar space linear, nearly absent; line perpendicular to costal forewing margin at apex of stigma usually crossing submarginal cells at or beyond middle of second submarginal cell; S4 of male without tubercles or projections 7
- 7(6). Hind femur of male greatly swollen, as long as or longer than tibia, which is enlarged and modified distally *C. (Oediscelis)*
- Hind femur of male not greatly swollen, shorter than tibia, which is also not or little modified *C. (Anoediscelis)*

Chilicola / Subgenus *Anoediscelis* Toro and Moldenke

Anoediscelis Toro and Moldenke, 1979: 131. Type species:

Oediscelis herbsti Friese, 1906, by original designation.

Stenoediscelis Toro and Moldenke, 1979: 135. Type species:

Oediscelis inermis Friese, 1908, by original designation.

This is one of the two large subgenera of *Chilicola*. The species are mostly small (3-7 mm long). Even though some species are quite slender, the dorsal surface of the propodeum is equal to or shorter than the scutellum and usually shorter than the declivous posterior surface. S1 of the male is unmodified, as is the apex of the antenna, segment 13 being as long, or nearly as long, as 12. Male genitalic and other structures were illustrated by Toro and Moldenke (1979) and Michener (1994); see also Figure 46-4e-g. I know of no characters that reliably distinguish females from those of the subgenus *Oediscelis*.

■ *Anoediscelis* occurs from the provinces of Malleco, Chile, and Mendoza, Argentina, north in the Andean countries to Colombia; one species, *Chilicola ashmeadi* (Crawford), is found from Colombia to Mexico as far north as Nayarit and Puebla. The eight species found in Chile were reviewed by Toro and Moldenke (1979). One, as just mentioned, occurs in Mesoamerica. Ten Andean species were revised by Michener (2002b). Three of the Chilean species [*C. olmue* Toro and Moldenke, *orophila* Toro and Moldenke, and *minor* (Philippi)] were included by Toro and Moldenke (1979) in the subgenus *Heteroediscelis*.

the posterior surface. Thus *Amphylaeus*, while retaining to some degree the pointed and perhaps plesiomorphic male glossal shape, lacks most of the other *Andrena*-like features of the posterior surface of the glossa. As in most other colletids, the annulate surface of the male glossa is quite different from that of the female. In *Amphylaeus* s. str. the preapical fringe of the glossa, a well-known female feature, may be indicated in the male by a row of coarse, spatulate hairs on the anterior side of the glossa basal to the midapical protuberance.

In the remaining genera of Hylaeinae the glossa is broader than long, similar in shape in the two sexes, and the apex is slightly rounded, truncate, or emarginate (deeply so in *Hyleoides*). The only exception is *Hylaeus* (*Hylaeorhiza*), in which the male has a small median point arising from the otherwise broadly subtruncate glossal apex. In vestiture, however, male hylaeine glossae are like those of *Amphylaeus*, described above; that is, they differ from those of females in lacking a preapical fringe and clearly demarked glossal lobes and glossal brush, and in the nature of the annuli and annular hairs (Michener, 1992c).

No one has yet made a cladistic study of the Hylaeinae. Of the four Hylaeinae included in Alexander and Michener's (1995) phylogenetic study, which was based on adult characters of S-T (short-tongued) bees, one can say only that no consistent pattern was found. The only genus in that study with an *Andrena*-like glossa in the male, *Meroglossa*, did not appear as the basal hylaeine branch. As explained in Section 20, the Perkins-McGinley hypothesis was not supported by that study.

McGinley (1981) characterized the larvae of Hylaeinae, on the basis of *Amphylaeus*, *Hylaeus*, *Hyleoides*, and *Meroglossa*. He found numerous characters supporting the position of *Hylaeus* as sister group to the other three genera combined, but, obviously, larvae of many more genera should be studied before a reliable cladogram can be produced.

Most users of this work can ignore the key below because *Hylaeus* is the only genus found in most continents. A single rare species found on the mountains of central Africa is placed in the genus *Calloprosois*. Otherwise, all genera other than *Hylaeus* are restricted to Australia, New Zealand, New Guinea, and nearby islands.

Key to the Genera of the Hylaeinae

(Based in part on Houston, 1975a, and Michener, 1965b)

1. Anterior tibial spine prolonged into long curved process, at least as long as basitarsal diameter (Fig. 47-3p); stigma with edge within marginal cell straight (Fig. 47-5a); posterior margin of T1 angulate near apex of lateral carina; apex of S1 transverse; S2 strongly produced downward at base (Fig. 47-3i) (Australian region) *Hyleoides*
- Anterior tibial spine small or absent; stigma with edge within marginal cell usually convex (Figs. 47-2; 47-5b); posterior margin of T1 straight or with broadly rounded posterior lateral angle; apex of S1 with median cleft or slit; S2 not produced downward at base 2
- 2(1). T1-T3 enormous, enclosing apical segments (Fig. 47-3b); basal vein meeting cu-v or nearly so; second recurrent vein beyond second submarginal crossvein; gradu-

- lus of T2 absent, faintly indicated laterally, pregradular area densely hairy, especially laterodorsally (preoccipital carina present) (Australia, New Guinea) *Pharohylaeus*
- T1-T3 of ordinary size, not hiding apical segments; basal vein distal to cu-v; second recurrent vein often meeting or basal to (although in some cases beyond) second submarginal crossvein (Figs. 47-2; 47-5); gradulus of T2 present, pregradular area not densely hairy 3
- 3(2). Males 4
- Females 10
- 4(3). Glossa usually broader than long, gently rounded-truncate to weakly bilobed at apex (a small median point on otherwise subtruncate apex in *Hylaeus*, subgenus *Hylaeorhiza*, Fig. 47-1g) 5
- Glossa usually longer than broad, apex acute (Fig. 47-1h-j) or, at least with preapical margins meeting to form obtuse apical angle (in *Amphylaeus* s. str., Fig. 47-1e, f) 7
- 5(4). Bees brilliant metallic blue or green (with yellow markings); both recurrent veins outside limits of second submarginal cell or meeting submarginal crossveins; propodeal triangle largely dorsal, with strong carina separating dorsal from posterior surface (New Guinea) *Xenorhiza*
- Bees nonmetallic or less brilliant blue or green; second recurrent vein and usually first received by second submarginal cell (except when submarginal and second medial cells are confluent, Fig. 47-5b); propodeal triangle with dorsal and posterior surfaces not separated by a carina, or, if so, then dorsal surface usually only a short zone 6
- 6(5). Gonobase reduced to narrow ring (metallic blue-green) (Africa) *Calloprosois*
- Gonobase large, forming a cuplike base to genital capsule *Hylaeus*
- 7(4). Fovea of T2 linear 8
- Fovea of T2 punctiform or absent 9
- 8(7). Gena and scutum with yellow maculations; first metasomal segment appearing constricted in lateral view (Fig. 47-3j) (Australia) *Hemirhiza*
- Gena and scutum without pale maculations; first metasomal segment not appearing constricted in lateral view (Australia) *Amphylaeus*
- 9(7). Face with large lateral depressions from sides of clypeus to above antennal sockets (Fig. 47-4i); gradulus of T2 exposed and arcuate posteriorly (i.e., recurved) medially; preoccipital carina absent; hind tibia with one or two spines on outer apical margin (Fig. 47-3o) (Australia) *Meroglossa*
- Face without large lateral depressions; gradulus of T2 normally concealed and transverse; preoccipital carina usually present; hind tibia lacking spines on apical margin (New Guinea and nearby islands, Australia) *Palaeorhiza*
- 10(3). Outer apical margin of hind tibia with a pair of spines (Fig. 47-3m-o), the spines sometimes small or only one 11
- Outer apical margin of hind tibia without spines (Fig. 47-3l) 12
- 11(10). Gradulus of T2 usually exposed and arcuate posteriorly (i.e., recurved) medially; fovea of T2 absent or punctiform (Australia) *Meroglossa*

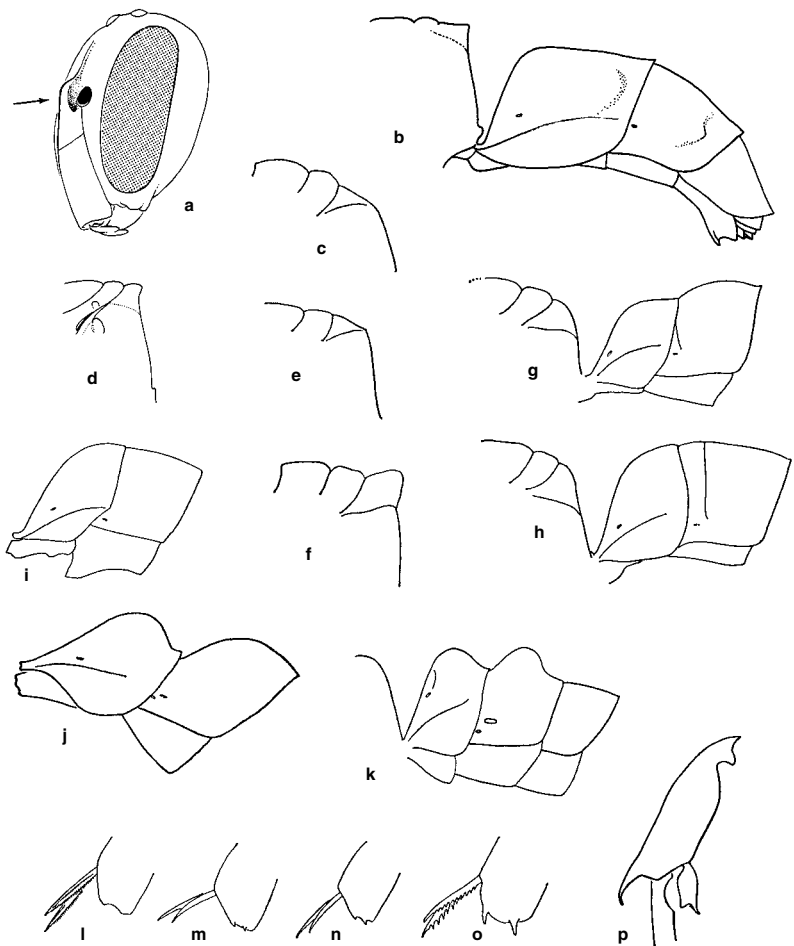


Figure 47-3. Structures of Hylaeinae. **a**, Elevated upper supra-clypeal area, marked by arrow in laterofrontal view of head of *Hylaeus ellipticus* (Kirby); **b**, Propodeal profile and side view of metasoma of *Pharo-hylaeus lactiferus* (Cockerell); **c**, Propodeal profile of *Hylaeus* (*Macrohylaeus*) *alcyoneus* (Erichson); **d**, Same, of *Palaeorhiza* (*Callorhiza*) *stygica* Michener; **e**, Same, of *P. (Anchorhiza) mandibularis* Michener; **f**, Same, of *P. (Ceratorhiza) conica* Michener; **g**, Propodeal profile and base of metasoma of *Hylaeus* (*Analastoroides*) *foveatus* (Rayment), female; **h**, Same, of *Hylaeus* (*Hylaeorhiza*) *nubilosus* (Smith); **i**, Base of metasoma of *Hyleoides*

concinna (Fabricius), showing projection of S2; **j**, Base of metasoma of *Hemirhiza melliceps* (Cockerell); **k**, Same, of *Hylaeus* (*Euprosopellus*) *dromedarius* (Cockerell); **l-o**, Apices of hind tibiae of females of *Hylaeus* (*Hylaeorhiza*) *nubilosus* (Smith), *Amphylaeus* (*Agogenohylaeus*) *nubilosellus* (Cockerell), *A. (Amphylaeus) morosus* (Smith), and *Meroglossa canaliculata* Smith; **p**, Front tibia of *Hyleoides concinna* (Fabricius). **a**, from Michener, McGinley, and Danforth, 1994; **b**, from Houston, 1975a; **c**, from Houston, 1981a; **d-p**, from Michener, 1965b.

- Gradulus of T2 usually hidden and procurved medially; fovea of T2 linear (Australia) *Amphylaeus*
- 12(10). Preoccipital carina present (absent in the only known specimen of *Palaeorhiza bicolor* Hirashima and Liefstinck).....13
- Preoccipital carina absent15
- 13(12). Both recurrent veins outside limits of second submarginal cell or meeting submarginal crossveins; mesepisternum in front of middle coxa sometimes with strong spine or projection (New Guinea) *Xenorhiza*
- Second recurrent vein and usually first received by second submarginal cell; mesepisternum in front of middle coxa simple or with ridge14

- 14(13). Propodeal triangle nearly all on dorsal surface of propodeum except in species with protuberance on dorsum of propodeum; body usually bright metallic blue or green or with abundant white to yellow maculations on gena and mesothorax; vertical ridge in front of middle coxa usually strongly developed (New Guinea area, Australia) *Palaeorhiza*
- Propodeal triangle having less than three-quarters of its length on dorsal surface of propodeum; body rarely brilliant metallic, gena and mesothorax usually without extensive white to yellow maculations; ridge in front of middle coxa weak or absent.....*Hylaeus* (in part)
- 15(12). Gena and scutum with yellow maculations; pro-

- podal triangle smooth, shiny, and evenly rounded in profile; T6 with a distinct pygidial plate; first metasomal segment slightly constricted in lateral view (Australia) *Hemirhiza*
- Gena and scutum without yellow maculations or, if with them, then propodeal enclosure neither smooth, nor shiny, nor evenly rounded; pygidial plate usually absent; first metasomal segment not appearing constricted in lateral view 16
- 16(15). Base of hind tibia with elongate, glabrous ridge on outer side probably representing basitibial plate; propodeal triangle nearly all on dorsal surface (Africa) *Calloprosopis*
- Base of hind tibia without glabrous ridge; propodeal triangle partly on declivous surface of propodeum *Hylaeus* (in part)

Genus *Amphylaeus* Michener

The species of this genus are moderate-sized to rather large, black, marked with yellow or white on the face, scutellum, metanotum, and legs; in general appearance they thus resemble some of the large species of Australian *Hylaeus*. The glossa of the male is bluntly to acutely pointed; the posterior surface lacks coarse seriate hairs, but has abundant slender hairs. The hind tibia of the female has two small spines on the outer apical margin. Among other Hylaeinae, only *Meroglossa* has similar, but usually larger, tibial spines. The lateral fovea of T2 is linear. Male genitalia and other structures were illustrated by Michener (1965b) and Houston (1975a); see also Figure 47-8a.

Key to the Subgenera of *Amphylaeus*

1. Male with clypeus and supraclypeal area indistinguishably fused, subantennal suture and upper lateral part of epistomal suture united as one strongly arcuate suture from tentorial pit to antennal base (Fig. 47-4a); interantennal distance of female equal to minimum clypeocular distance (Fig. 47-4b) *A. (Amphylaeus s. str.)*
- Male with complete epistomal suture of ordinary form joining subantennal sutures in usual way (Fig. 47-4c); female with interantennal distance nearly twice minimum clypeocular distance *A. (Agogenohylaeus)*

Amphylaeus / Subgenus *Agogenohylaeus* Michener

Amphylaeus (Agogenohylaeus) Michener, 1965b: 148. Type species: *Prosopis nubilosellus* Cockerell, 1910, by original designation.

Agogenohylaeus contains moderate-sized species (body length 6.5–7.5 mm) that look like *Hylaeus*.

This subgenus occurs from Victoria to southern Queensland, Australia, in the dividing range and east of it. The three species were revised by Houston (1975a) and listed by Cardale (1993).

Amphylaeus / Subgenus *Amphylaeus* Michener s. str.

Amphylaeus Michener, 1965b: 147, 149. Type species: *Prosopis morosa* Smith, 1879, by original designation.

This subgenus consists of a single large species (body length 11–12 mm) having the remarkable male facial characters indicated in the key to subgenera above (Fig. 47-4a).

■ *Amphylaeus* s. str., which has the same distribution as *Agogenohylaeus*, includes only one species, *A. morosus* (Smith).

The nests, which are similar to those of *Hylaeus*, were described (under the name *Meroglossa sculptifrons* Cockerell) by Michener (1960). Spessa, Schwarz, and Adams (2000) reported that about 23% of the nests of *Amphylaeus morosus* (Smith) contain two or three females, probably living communally.

Genus *Calloprosopis* Snelling

Calloprosopis Snelling, 1985: 27. Type species: *Hylaeus magnificus* Cockerell, 1942, by original designation.

This genus contains a single, rather large (8 mm long), dark-blue species—the only African hylaeine with metallic coloration. Since it may well be derived from *Hylaeus*, I have accepted its generic status with hesitation. In both sexes a ridge on the base of the hind tibia appears to represent the anterior side of the basitibial plate, the ridge ending abruptly in just the position where one would expect the basitibial plate to end. If this is a plesiomorphy, then *Hylaeus* exhibits the apomorphic condition (basitibial plate absent), and the two might be sister groups. A much more obvious difference from all other Hylaeinae, and no doubt an apomorphy, is the reduction of the male gonobase to a narrow ring around the genital foramen. Other characters of the male include the elongate volsellae and reduced S7 having a short body and two small apical lobes, each with a lateral and a posterior projection. Snelling (1985) has described and illustrated this genus.

■ *Calloprosopis* is known only from rather high altitudes in Kenya. The single species is *C. magnifica* (Cockerell).

Genus *Hemirhiza* Michener

Hemirhiza Michener, 1965b: 147. Type species: *Palaeorhiza melliceps* Cockerell, 1918, by original designation.

This genus consists of one rather small (about 6 mm long) species, richly marked with yellow, including yellow on the gena and scutum (also on the face, Fig. 47-4e, f). The glossa of the male is pointed, nearly twice as long as wide, bearing strong seriate hairs on its posterior surface (Fig. 47-1j). The lack of a preoccipital carina distinguishes the species from nearly all *Palaeorhiza*; another distinguishing feature is the linear fovea on the side of T2. The male genitalia and hidden sterna were illustrated by Michener (1965b) and Houston (1975a). The apical lobes of S7, four in number, are rather broad (Fig. 47-8j), as in most species of *Hylaeus (Prosopistemon)*, and unlike those of the species of *Palaeorhiza* whose terminalia are known.

■ *Hemirhiza* is found in southern Queensland and in New South Wales, Australia, in coastal and montane regions of high rainfall. The single species is *H. melliceps* (Cockerell).



pollen of Rosaceae. The view that most *Hylaeus* are polylectic may have arisen from the fact that pollen collecting is not visible because pollen is carried internally. Examination of pollen in nests is needed to determine the prevalence of pollen specialization in *Hylaeus*.

The keys to subgenera below are divided geographically, as follows: Australian region, sub-Saharan Africa, palearctic region, and Western Hemisphere. Because of the relationship of its *Hylaeus* fauna, Hawaii is included for this purpose with the palearctic fauna; if the Oriental fauna were better known, the Hawaiian connection might be just as close with the Oriental region. The subgenera of the Oriental region (meaning tropical Asia and nearby islands) are so little known that no key is provided; and, indeed, most species in that area are not placed in subgenera. The subgenera that are recorded from the Oriental region include *Lambdopsis*, *Nesoprosopis*, *Paraprosopis* (included among palearctic subgenera); *Gephyrohylaeus*, placed under the Australian region; and *Gnathylaeus*, *Hoploprosopis*, and *Nesylaeus*, which may be restricted to tropical Asia and associated islands. Snelling (1980) treated nine species from Sri Lanka and south and central India, providing descriptions and illustrations. Only one could be placed in a subgenus (*Paraprosopis*). Appropriate placement of Oriental species will require much larger collections and association of sexes; most

Figure 47-6. Faces of Australian *Hylaeus*, in each case male and female. **a, b,** *H. (Euprosopellus) chrysaspis* (Cockerell); **c, d,** *H. (Gephyrohylaeus) sculptus* (Cockerell); **e, f,** *H. (Gnathoprosopis) euxanthus* (Cockerell); **g, h,** *H. (Heterapoides) delicatus* (Cockerell); **i, j,** *H. (Hylaeateron) semirufus* (Cockerell); **k, l,** *H. (Hylaeorhiza) nubilosus* (Smith). From Houston, 1981.

species are known from one sex only. Table 47-1 shows the faunal areas in which the subgenera occur.

Since, in the holarctic and neotropical areas, there is only moderate size variation, that is, body length 3.5 to 9.0 mm, measurements are omitted for most subgenera from these areas.

Key to the Subgenera of *Hylaeus* of the Australia-New Guinea Area
(Modified from Houston, 1981a)

- 1. Second submarginal and second medial cells of forewing confluent (Fig. 47-5b); minute, slender bees with T1, at least in male, much longer than broad, as seen from above 2
- Second submarginal and second medial cells of forewing separated, as in other bees (Fig. 47-2); size and form variable, but rarely so slender-bodied, or with T1 so slender 3

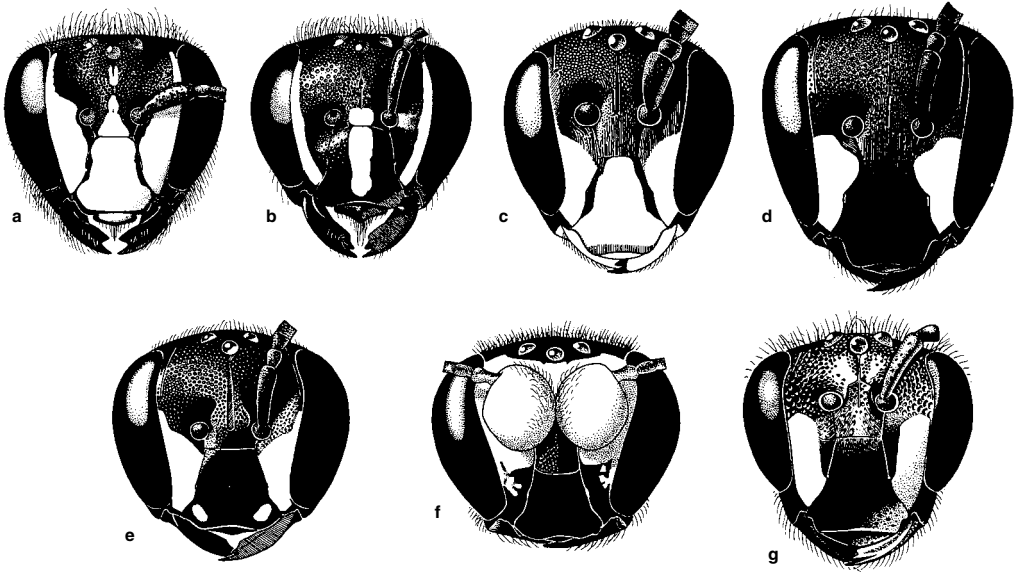


Fig. 47-7. Faces of Australian *Hylaeus*. **a, b**, *H. (Macrohylaeus) alcyconeus* (Erichson), male, female; **c, d**, *H. (Planihylaeus) daviesiae* Houston, male, female; **e**, *H. (Sphaerhylaeus) bicolorellus* Michener, female; **f**, *H. (S.) globuliferus* (Cockerell), male; **g**, *H. (Meghy-laeus) fijiensis* (Cockerell), female. From Houston, 1981.

- 2(1). Mesepisternum broadly attaining or closely approaching propodeum, thus nearly eliminating metepisternum above coxa; preoccipital carina present; facial fovea of female short, not attaining summit of eye (Australia to Borneo and Philippines)..... *H. (Gephyrohylaeus)*
- Mesepisternum separated from propodeum by metepisternum; preoccipital carina absent; facial fovea of female a long groove attaining summit of eye, as in most *Hylaeus* (Australia) *H. (Heterapoides)*
- 3(1). T1 of male, viewed laterally, constricted apically, and T2 strongly humped (Fig. 47-3k); T2 of female moderately humped (Fig. 47-3g) 4
- T1 of male, viewed laterally, not constricted apically, and T2 not strongly humped; T2 of female not at all humped (Fig. 47-3h) 5
- 4(3). Metasoma with bands of dense orange tomentum across apical margins of T1 and T3; terga with even, dense, fine pitting *H. (Analastoroides)*
- Metasoma without bands of orange tomentum; terga with irregular pitting, the pits of two sizes and partially confluent *H. (Euprosopellus)*
- 5(3). Clypeus of female with fine longitudinal median carina (strongest apically); lower face longitudinally striate; face of male with very large depression on each side, from clypeus to well above antennal sockets; scape of male greatly expanded and flattened; subapical metasomal segments of male with large, expanded, pubescent, pregradular areas *H. (Xenohylaeus)*
- Clypeus of female without median carina; lower face striate or not; face of male lacking depressions; scape of male not greatly expanded and flattened [except in *H. (Prosopistemon) semipersonatus* Cockerell, which lacks expanded, pubescent, pregradular areas] 6
- 6(5). Propodeum almost wholly vertical, dorsal surface shorter than metanotum and bearing a single row of regular pits bounded posteriorly by a carina 7
- Propodeum variable, but dorsal surface never very short

- or bearing such a row of pits bounded posteriorly by a carina 9
- 7(6). Upper end of raised interantennal area about as wide as an antennal socket and merging with frons; posterior surface of scape of male without pits; female with distinct mesosternal brush-hairs, and outer apical spines of fore and middle tibiae unmodified *H. (Euprosopis)*
- Upper end of raised interantennal area much narrower than an antennal socket and usually distinct from frons; posterior surface of scape of male with one or two distinct pits; female without mesosternal brush-hairs, but outer apical spines of fore and middle tibiae modified into longitudinal carinae 8
- 8(7). Scutellum and metanotum usually with yellow areas; malar area of male no longer than one-fourth width; S8 of male with apex deeply bifid, hairy (Fig. 47-9g) *H. (Euprosopoides)*
- Scutellum and metanotum without pale areas; malar area of male about one-half as long as width; S8 of male with apex simple, usually hairless *H. (Laccobylaeus)*
- 9(6). Precoxal ridge of mesosternum distinct (propodeum almost entirely vertical, triangle smooth and shiny; scutellum and metanotum bright yellow) *H. (Hylaeorhiza)*
- Precoxal ridge of mesosternum indistinct or absent 10
- 10(9). Preoccipital carina present, at least medially; mandible sometimes broadest at blunt, edentate apex; scape of male sometimes globular 11
- Preoccipital carina absent; mandible never broadest apically; scape of male never globular 14
- 11(10). Dorsal surface of propodeum as long as scutellum,

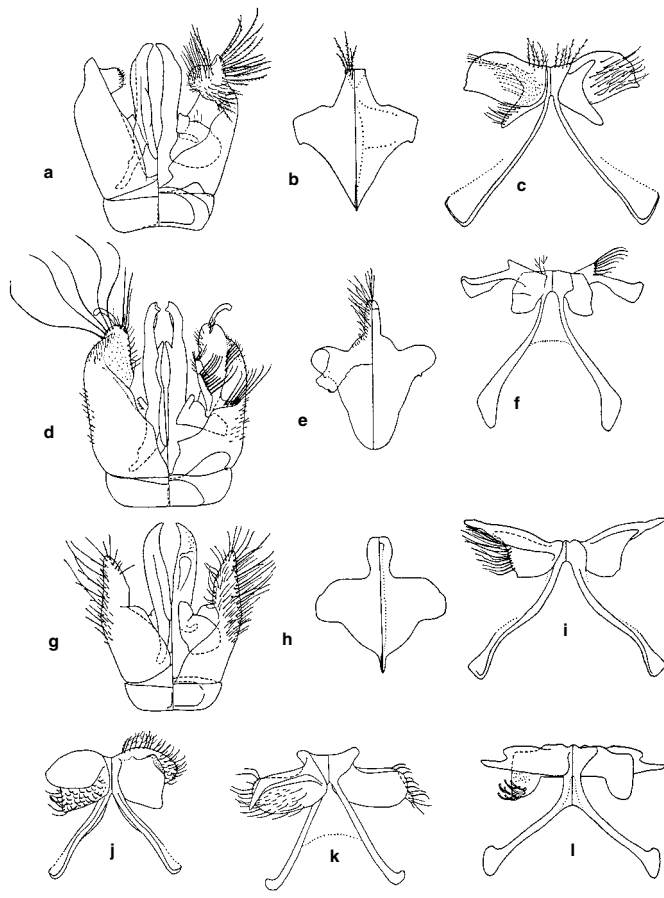


Figure 47-8. Male terminalia of Australian Hylaeinae. a-i, genitalia, S8, and S7 of the following: **a-c**, *Amphylaeus morosus* (Smith); **d-f**, *Meroglossa canaliculata* Smith; **g-i**, *Palaeorhiza stygica* Michener. j-l, S7 of the following: **j**, *Hemirhiza melliceps* (Cockerell); **k**, *Hyleoides concinna* (Fabricius); **l**, *Pharaohylaeus lactiferus* (Cockerell). (Dorsal views are at the left.) From Michener, 1965b.

- triangle nearly all subhorizontal, smooth and shining to microtesellate and somewhat dull; maxillary palpus as long as thorax or longer (New Guinea)..... *H. (Prosopistroides)*
- Dorsal surface of propodeum much shorter than scutellum, triangle thus with extensive area on posterior surface of propodeum, surface of triangle areolate, pitted, partly dull; maxillary palpus normal 12
- 12(11). Mandibles elongate, pollex forming the usual upper mandibular tooth; mandible broadest basally; scape of male almost hemispherical (Fig. 47-7f); frons of male with cavity above each antennal socket..... *H. (Sphaerhylaues)*
- Mandible short, pollex much broadened and rounded or subtruncate, not exceeded by mandibular apex, which is a small tooth; apical width of mandible equal to or greater than basal width [except in male of *H. (Gnathoprosopoides) philoleucus* (Cockerell), in which upper tooth (pollex) is broad and rounded]; scape of male slender to moderately swollen, seldom globular; frons of male without cavity above antennal socket 13
- 13(12). Dorsal surface of propodeal triangle entirely areolate and usually delimited laterally and posteriorly by carina [carina absent in *H. amicus* (Smith)]; S7 of male with single pair of apical lobes *H. (Gnathoprosopis)*
- Dorsal surface of propodeal triangle largely smooth and not at all delimited by carina; S7 of male with two pairs

- of apical lobes *H. (Gnathoprosopoides)*
- 14(10). Propodeum with short subhorizontal dorsal surface separated from long vertical posterior surface by distinct angle (Fig. 47-3c); body length 8.5-15.0 mm; metasoma metallic blue 15
- Propodeum variable, its short subhorizontal dorsal surface not usually separated from vertical posterior surface by distinct line or angle; body length usually under 8 mm; metasoma rarely metallic blue 16
- 15(14). Prestigma about as long as stigma from its base to vein r; interantennal area strongly elevated and separated from frons by distinct edge (Fig. 47-7g); propodeum without a median prominence; mesosternum of female without brush-hairs *H. (Meghylaues)*
- Prestigma much shorter than stigma from its base to vein r; interantennal area convex but not delimited from frons (Fig. 47-7a, b); propodeal triangle with shiny median prominence; mesosternum of female without brush-hairs *H. (Macrohylaues)*
- 16(14). Propodeal triangle areolate or coarsely roughened and delimited laterally and posteriorly by a carina; pronotal collar almost as high as scutum, contiguous laterally with the pronotal lobe through a carinate ridge; body at least partly yellow-brown to red-brown *H. (Rhodohylaues)*
- Propodeal triangle variable, not delimited by a carina or, if so, then pronotal collar much lower than scutum and

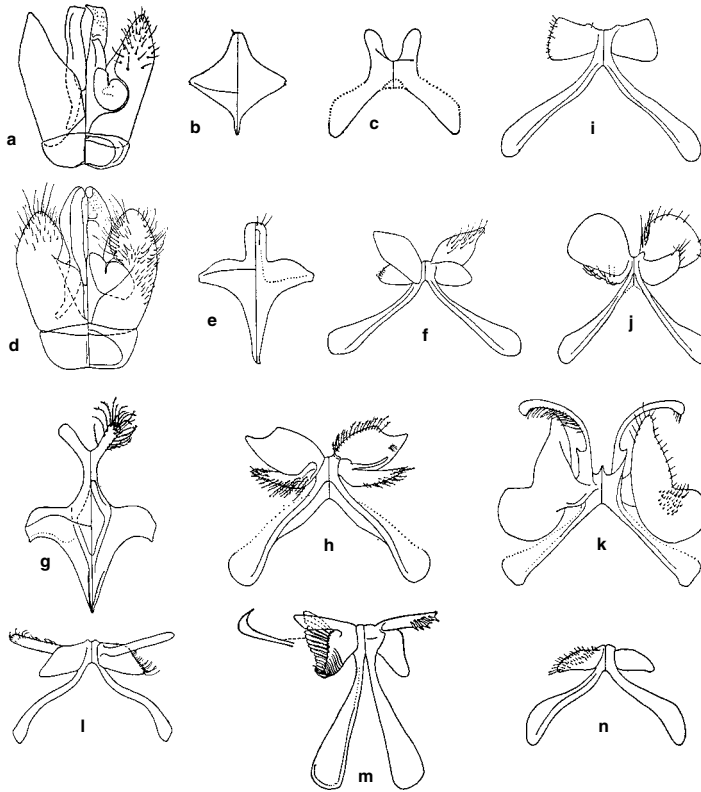


Figure 47-9. Male terminalia of Australian *Hylaeus*. a-f, genitalia, S8, and S7. a-c, *Hylaeus* (*Edriohylaeus*) *ofarrelli* Michener; d-f, *H. (Prosopisteron)* *perhumilis* (Cockerell). g, h, S8 and S7 of *H. (Euprosopoides)* *perconvergens* Michener. i-n, S7 of the following: i, *H. (Euprosopellus)* *dromedarius* (Cockerell); j, *H. (Prosopisteron)* *serotinellus* (Cockerell); k, *H. (Euprosopis)* *elegans* (Smith); l, *H. (Hylaeorhiza)* *nubilosus* (Smith); m, *H. (Xenohylaeus)* *riekei* Michener; n, *H. (Rhodohylaeus)* *ceniberus* (Cockerell). (Dorsal views of all are at the left.)

From Michener, 1965b.

- not contiguous with pronotal lobe through a carinate ridge; color variable 17
- 17(16). Mandible with outer ridge strong or carinate 18
- Mandible with outer ridge inconspicuous 19
- 18(17). Mandible bidentate, the lower tooth usually longest by far; interantennal area not delimited from frons; hind margins of metasomal terga usually translucent and with laterally directed setae; outer margin of fore tarsus with long setae; apex of S8 of male bifid, dorso-apical lobes of S7 with acute apices *H. (Pseudhylaeus)*
- Mandible of female tridentate, of male acutely bidentate; interantennal area elevated and delimited from frons by distinct edges; hind margins of metasomal terga rarely translucent and with laterally directed setae; outer margin of fore tarsus without long setae; apex of S8 of male not bifid, dorso-apical lobes of S7 rounded *H. (Hylaeateron)*
- 19(17). Lower face flat, longitudinally striate; propodeum with steeply sloping dorsal surface, triangle usually areolate anteriorly; lateral fovea of T2 large and rounded; subapical metasomal segments of male with large expanded pubescent pregradular areas; apex of S8 of male bifid and apex of dorso-apical lobes of S7 of male acute *H. (Planihylaeus)*
- Without the combination of characters indicated above: lower face seldom both flat and striate; propodeum variable; lateral fovea of T2 rarely large and rounded; subapical metasomal segments of male with or without expanded pubescent pregradular areas; apex of S8 and dorso-apical lobes of S7 of male variable 20

- 20(19). Body very slender; T1 of male 1.5 times longer than broad, of female nearly as long as broad; propodeum with long, smooth, horizontal dorsal surface rounding evenly onto vertical posterior surface; S7 of male with only one pair of apical lobes broadly fused to broad body of sternum (Fig. 47-9c) *H. (Edriohylaeus)*
- Body seldom very slender; T1 of male usually not longer than broad, of female usually much broader than long; propodeum variable, dorsal surface sometimes roughened anteriorly; S7 of male with two pairs of apical lobes narrowly connected to narrow body of sternum (Fig. 47-9f, j) *H. (Prosopisteron)*

Key to the Subgenera of *Hylaeus* of the Western Hemisphere (Males) (See account of *Orohylaeus*) (By R. R. Snelling)

For illustrations of male genitalia and hidden sterna of North American forms, see Metz (1911), Mitchell (1960), and the more specialized papers referred to under the subgenera.

1. Frons largely covered with conspicuous mat of short, dense, highly plumose pilosity, partly hidden behind swollen scape (neotropics) *H. (Gongyloprosopis)*
- Frons without dense mat of short, plumose pilosity; scape swollen or not 2
- 2(1). **Omaulus**, at least below level of lower end of episternal groove, carinate 3
- **Omaulus** rounded 5
- 3(2). Apical process of S8 flattened and broadly spatuliform, always visible in ventral view; side of propodeum never

Table 47-1. Distribution of the Subgenera of *Hylaeus*

i indicates introduction.

Subgenus	Neotropical	Nearctic	Palaearctic	Oriental	Sub-Saharan	Australian
<i>Abrupta</i>	—	—	x	—	—	—
<i>Alfkenylaus</i>	—	—	—	—	x	—
<i>Analasteroides</i>	—	—	—	—	—	x
<i>Cephalylaues</i>	—	x	—	—	—	—
<i>Cephylaues</i>	x	—	—	—	—	—
<i>Cornylaues</i>	—	—	—	—	x	—
<i>Dentigera</i>	—	—	x	—	—	—
<i>Deranchylaues</i>	—	—	—	—	x	—
<i>Edriohylaues</i>	—	—	—	—	—	x
<i>Euprosopellus</i>	—	—	—	—	—	x
<i>Euprosopis</i>	—	—	—	—	—	x
<i>Euprosopoides</i>	—	—	—	x	—	x
<i>Gephyrohylaues</i>	—	—	—	x	—	x
<i>Gnathoprosopis</i>	—	—	—	—	—	x
<i>Gnathoprosopoides</i>	—	—	—	—	—	x
<i>Gnathylaues</i>	—	—	—	x	—	—
<i>Gongyloprosopis</i>	x	—	—	—	—	—
<i>Heterapoides</i>	—	—	—	—	—	x
<i>Hoploprosopis</i>	—	—	—	x	—	—
<i>Hylaeana</i>	x	x	—	—	—	—
<i>Hylaeopsis</i>	x	—	—	—	—	—
<i>Hylaeorhiza</i>	—	—	—	—	—	x
<i>Hylacteron</i>	—	—	—	—	—	x
<i>Hylaeus</i> s. str.	—	x	x	—	—	—
<i>Koptogaster</i>	—	—	x	—	—	—
<i>Laccohylaues</i>	—	—	—	—	—	x
<i>Lambdopsis</i>	—	—	x	x	—	—
<i>Macrohylaues</i>	—	—	—	—	—	x
<i>Meghylaues</i>	—	—	—	—	—	x
<i>Mebelyana</i>	—	—	x	—	—	—
<i>Metylaues</i>	—	—	—	—	x	—
<i>Metziella</i>	—	x	—	—	—	—
<i>Nesoprosopis</i>	—	—	x	x	—	—
<i>Nesylaues</i>	—	—	—	x	—	—
<i>Nothylaues</i>	—	—	—	—	x	—
<i>Orohylaues</i>	x	—	—	—	—	—
<i>Paraprosopis</i>	—	x	x	x	—	—
<i>Planihylaues</i>	—	—	—	—	—	x
<i>Prosopella</i>	—	x	—	—	—	—
<i>Prosopis</i>	—	x	x	—	—	—
<i>Prosopisteroides</i>	—	—	—	—	—	x
<i>Prosopisteron</i>	—	—	—	—	i	x
<i>Pseudhylaues</i>	—	—	—	—	—	x
<i>Rhodohylaues</i>	—	—	—	—	—	x
<i>Spatulariella</i>	i	i	x	—	—	—
<i>Sphaerhylaues</i>	—	—	—	—	—	x
<i>Xenohylaues</i>	—	—	—	—	—	x

pruinose (introduced from Eurasia to southern California, central Chile)..... *H. (Spatulariella)*
— . Apical process of S8 not flattened and spatuliform; side of propodeum often densely pruinose 4
4(3). Spiracular area of propodeum enclosed by carina; propodeal triangle with coarse, more or less longitudinal rugae; thorax and/or metasoma usually coarsely punctate; omaulus with carina extending above lower end of

episternal groove to pronotal lobe (neotropics).....
..... *H. (Hylaeopsis)*
— . Spiracular area open or, if enclosed, then propodeal triangle lacking coarse longitudinal rugae and thorax finely punctate; omaulus without carina above lower end of episternal groove (neotropics to southwestern USA).....
..... *H. (Hylaeana)*
5(2). Antennal scape much broader than long; S6 elevated

- along midline; pronotum black (nearctic) *H. (Cephalylaeus)*
- Antennal scape usually about twice as long as broad or, if nearly as broad as long, then S6 flat and pronotal collar marked with yellow 6
- 6(5). Dorsolateral angle of pronotum in dorsal view slightly protuberant and sharply truncate; distal process of S8 bent downward at about 45° angle (southwestern USA, Mexico) *H. (Prosopella)*
- Dorsolateral angle of pronotum in dorsal view obtuse or rounded; distal process of S8 straight or nearly so 7
- 7(6). Margins of interantennal elevation nearly parallel between antennal sockets, terminating on frons well above level of upper margins of antennal sockets; apical lobes of S7 laterally pectinate (Fig. 47-10g) (holarctic) *H. (Hylaeus s. str.)*
- Margins of interantennal elevation sharply convergent between antennal sockets and ending little, if any, above level of upper margins of antennal sockets; apical lobes of S7 not pectinate 8
- 8(7). Outer margin of front coxa with sharp laterobasal angle or tooth; apical process of S8 short, triangular, broad at base and tapering to blunt apex (first flagellar segment shorter than second) (nearctic) *H. (Metziella)*
- Outer margin of front coxa without sharp laterobasal angle or tooth; apical process of S8 slender at least basally, usually parallel-sided for most of its length or bifid at apex 9
- 9(8). S7 with apical lobes rather small, flat, broadly attached to and on same plane as body of sternum; process of S8 with basal half slender, distal half robust and expanded distally to shallowly emarginate apex (Brazil) *H. (Cephalylaeus)*
- S7 with apical lobes variable, large and elaborate or, if small, narrowly and flexibly attached to and on different plane from body of sternum; process of S8 slender, parallel-sided, but apex usually enlarged or deeply bifid 10
- 10(9). Apical process of S8 entire, more or less parallel-sided for most of its length and usually subapically broadened, apex rounded or truncate; first flagellar segment about as long as second (holarctic) *H. (Prosopis)*
- Apical process of S8 deeply bifid at apex; first flagellar segment distinctly shorter than second (holarctic) *H. (Paraprosopis)*
- Labrum with paired submedian longitudinal tubercles; pronotal collar with transverse carina or crest or, if rounded, metasomal terga microlineolate, satiny, without obvious punctures 3
- 3(2). Omaular carina absent above lower end of episternal groove; spiracular area of propodeum open or, if enclosed by carina, then basal area of propodeum not rugulose and metasomal terga without obvious punctures; pronotal collar not carinate or with weak anterior carina; thoracic punctures fine to moderate in size (neotropics to southwestern USA) *H. (Hylaeana)*
- Omaular carina extending up to pronotal lobe; spiracular area of propodeum enclosed by carina and basal area of propodeum usually coarsely rugose; pronotal collar usually anteriorly carinate or crested; thoracic (and often metasomal) punctures moderate to coarse (neotropics) *H. (Hylaeopsis)*
- 4(1). Dorsolateral angle of pronotum, in dorsal view, distinctly angulate or protuberant; anterior margin of pronotal collar sometimes with short, low, sublateral carina 5
- Dorsolateral angle of pronotum rounded in dorsal view; anterior margin of pronotal collar rounded 6
- 5(4). Dorsolateral angle of pronotum slightly protuberant; propodeal triangle with transverse subbasal ridge, behind which surface is largely without rugulae; lateral carina of propodeum prominent along spiracular area (neotropics) *H. (Gongyloprosopis)*
- Dorsolateral angle of pronotum abruptly angulate (truncate) but not protuberant; entire propodeal triangle rugulose, rugulae primarily transverse; lateral carina of propodeum absent along spiracular area (southwestern USA, Mexico) *H. (Prosopella)*
- 6(4). Gena as wide as eye or wider in lateral view, and mesepisternal punctures distinct; lateral propodeal carina absent or present only posteriorly; metasomal terga with only scattered, minute punctures 7
- Gena usually conspicuously narrower than eye, but if as wide, then mesepisternum roughened and punctures weak and indistinct; lateral propodeal carina usually extending forward to spiracular area; metasomal terga variable, but often with conspicuous sparse to dense punctures 8
- 7(6). Front coxa with large, triangular lateral process or stout spine; upper end of facial fovea much nearer to inner eye margin than to lateral ocellus; side of face and pronotal lobe with pale markings (nearctic) *H. (Metziella)*
- Front coxa without lateral process; facial fovea ending about midway between eye and lateral ocellus; side of face and pronotal lobe immaculate (nearctic) *H. (Cephalylaeus)*
- 8(6). Outer margin of front coxa more or less distinctly angulate 9
- Outer margin of front coxa evenly curved (not verified for *Cephalylaeus*) 10
- 9(8). Facial fovea ending nearer to lateral ocellus than to inner eye margin; spiracular area of propodeum enclosed by carina (holarctic) *H. (Paraprosopis)* (in part)
- Facial fovea ending nearer to inner eye margin than to lateral ocellus; spiracular area of propodeum open (holarctic) *H. (Hylaeus s. str.)* (in part)

Key to the Subgenera of *Hylaeus* of the Western Hemisphere (Females) (See account of *Orohyllaeus*) (By R. R. Snelling)

1. Omaulus, at least below lower end of episternal groove, carinate; spiracular area of propodeum usually enclosed by carina; anterior margin of pronotal collar often carinate or with distinct crest; metasomal sterna often very finely microstriate and weakly iridescent 2
- Omaulus without carina; spiracular area of propodeum open or enclosed; anterior margin of pronotal collar rounded; metasomal sterna never finely microstriate and never iridescent 4
- 2(1). Labrum with single median tubercle; pronotal collar rounded in front; metasomal terga more or less polished and with sparse, fine, sharply defined punctures (introduced from Eurasia to southern California and Chile) *H. (Spatulariella)*

- 10(8). T1 without apicolateral patch of appressed, pale pubescence, but terga sometimes with narrow apical bands of white hairs laterally, and punctures on T1 and T2 usually fine, scattered, never dense(Brazil) *H. (Cephylaeus)*;
(holarctic) *H. (Hylaeus s. str.)* (in part)
- T1 with apicolateral patch of appressed, highly plumose white pubescence and/or punctures on T1 and T2 conspicuous, well-defined 11
- 11(10). T1 (and often T2) densely punctate, T1 almost always lacking apicolateral pubescent patch; spiracular area of propodeum often enclosed by carina, and mesepisternum finely punctate; facial fovea often ending at or mesal to midpoint between inner eye margin and lateral ocellus (Fig. 47-11l) (holarctic) *H. (Paraprosopis)* (in part)
- T1 sparsely to densely punctate, in latter case apicolateral pubescent patch present; if spiracular area of propodeum enclosed, then mesepisternum coarsely punctate; facial fovea always ending nearer to inner eye margin than to lateral ocellus (as in Fig. 47-11m) (holarctic) *H. (Prosopis)*

Key to Palearctic Subgenera of *Hylaeus* (Males)

(By H. H. Dathe)

For additional illustrations of male genitalia and other structures, see Méhely (1935), Dathe (1980a), and other papers referred to under the subgenera. Illustrations accompanying this key (Figs. 47-10 and 47-11) are by H. Dathe.

1. Face entirely black, and frons broadly concave and shining between ocelli and antennal bases; middle basitarsus dilated at base; gonostylus truncate, the long, stiff bristles on lateral part of transverse margin nearly as long as gonoforceps (Fig. 47-10a) (scape conically swollen, white; S7 with apical lobes well developed, truncate at hairless tips; S8 with long spiculum and apical process, the latter bifurcate, hairy) *H. (Abrupta)*
- Face with white or yellow areas, or, if entirely black, then frons convex and densely punctured medially; middle basitarsus normal; gonostylus apically rounded or pointed, its bristles shorter than gonoforceps 2
- 2(1). Gonostylus and gonocoxite distinctly separated by oblique constriction; outer margin of gonostylus convex, protruding; apical hair tufts of gonostylus dense and feathered (Fig. 47-10b), in normal position projecting from metasomal apex (genital capsule extraordinarily large; S7 with apical lobes finely pectinate; S8 with apical process short, both margins with hairs) *H. (Mehelyana)*
- Gonostylus and gonocoxite not separated, their outline throughout convex or only weakly transversely constricted; apical hair tufts of genitalia not exposed in normal position 3
- 3(2). Gonoforceps conspicuously elongate, slender, distal third or thereabouts surpassing penis valves (Fig. 47-10c); apical process of S8 long, hairless, spoon-shaped, exposed at apex of metasoma (S7 with apical lobes small and simple, triangular, without hairs) *H. (Spatulariella)*
- Gonoforceps of normal length and thickness, about as long as penis valves; S8 in normal position, concealed in metasoma 4
- 4(3). Penis valve with flat, rectangular membrane laterally, basally edge of membrane acutely angulate (Fig. 47-10d); gonostylus and gonocoxite separated by weak constriction (head in frontal view conspicuously longer than broad; pronotum thickened, dorsolateral angle square; propodeum steeply truncate; body robust, with coarse punctures; S7 with apical lobes consisting of two pairs of large membranes without hairs; S8 with apical process elongate, bilobate, with short hairs) *H. (Koptogaster)*
- Penis valves and gonostylus/gonocoxite variable, but not as above 5
- 5(4). Dorsal carinae of the two penis valves in dorsal view parallel and in close contact to their apices (Fig. 47-10e), or, if separated, then only narrowly so, the inner ventral structures thus hidden from above (outline of the two penis valves together cuneiform to spindle-shaped) 6
- Dorsal carinae of penis valves in dorsal view in contact basally but clearly diverging near bases or medially, often abruptly bent laterad, inner ventral structures clearly visible from above between separated penis valves 7
- 6(5). Apical lobes of S7 simple (four in number) with smooth margins (Fig. 47-10f), hairs absent or sparse and confined to lateral part of proximal lobe; scape usually slender; labrum and mandible frequently with yellow spots *H. (Paraprosopis)*
- Apical lobes of S7 pectinate (Fig. 47-10g); scape commonly conically dilated or flattened, but if slender, then sternal callosity or lateral fringe of T1 absent; labrum and mandible black *H. (Hylaeus s. str.)*
- 7(5). S8 with prolonged basal part and apical process (Fig. 47-10i, j), the latter with short hairs or hairless and hooked downward; hook and incision in S6 reduced in some Japanese species, but the hook usually projecting from V-shaped incision in S6; scape broadened, shield-like [except in *H. melba* (Warncke) of northwestern Africa]; paraocular area lacking transverse flat impressions (S7 with apical lobes reduced, of various shapes, compact, with some short hairs; Fig. 47-10k) *H. (Lambdopsis)*
- S8 more or less rhombiform, with short basal and apical parts (Fig. 47-11d, e, g), or apical process, if elongated, then with hairs and not hooked; S6 rounded or emarginate; scape slender or conically enlarged, or, if scutiform, then face with flat transverse impressions on paraocular area and below antennal sockets 8
- 8(7). Penis valves in dorsal view gently bent so that between them can be seen a pair of acute or truncate spines (Fig. 47-11a, b), these being ventral projections of penis valves (S7 with apical lobes reduced, triangular, with or without sparse hairs; S8 strongly reduced, rhombiform, hairless, apical process rarely somewhat elongate and filiform) *H. (Dentigera)*
- Penis valves in dorsal view largely approximate, no spines thus visible from above between penis valves, ventral projections usually short and broad, not spinelike (Fig. 47-11c) 9
- 9(8). S8 with extremely elongated, curved, slender apical process, its apex with pair of hair tufts (Fig. 47-11d, e); S6 emarginate in middle; thorax, particularly mesepisterna, strikingly coarsely and strongly punctate; S7 with apical lobes reduced, slender, pointed, with sparse hairs (Fig. 47-11f) *H. (Nesoprosopis)*
- S8 rhombic, with short, rounded or truncate, hairless apical process; S6 not emarginate; thorax usually finely

punctate; S7 with apical lobes reduced, compact, with hairs (Fig. 47-11h) that may be short and sparse.....
..... *H. (Prosopis)*

Key to the Palearctic Subgenera of *Hylaeus* (Females)
(By H. H. Dathe)

1. Mandible tridentate, inner tooth sometimes short (Fig. 47-11i) 2
- Mandible with two teeth or apex bilobate (Fig. 47-11j) 5
- 2(1). Clypeus with broad, transverse, saddle-like depression below transverse supraclypeal projection and above two lower lateral clypeal projections; epistomal suture largely unrecognizable; face entirely black..... *H. (Abrupta)*
- Clypeus slightly convex, without projections or teeth; supraclypeal projection absent; epistomal suture complete; face usually with yellow on paraocular area 3
- 3(2). Anterior coxa with obtuse process (Fig. 47-11k); clypeus rather rectangular, the middle evenly domed as seen from side *H. (Mehelyana)*
- Anterior coxa without process; clypeal outline trapezoidal; clypeus flat or asymmetrically domed as seen from side 4
- 4(3). Paraocular spots often elongate, contiguous with inner orbits, or, if face entirely black, then T1 transversely obsoletely reticulated; T1 with lateral fringes, partly indistinct *H. (Dentigera) (brevicornis group)*
- Paraocular spots usually rounded, contiguous with clypeal margin or, if face entirely black, then T1 integument smooth; T1 without lateral fringes
..... *H. (Lambdopsis) (in part)*
- 5(1). Vertex swollen, in frontal view surpassing upper ocu-

- lar margins by ocular width; head in frontal view nearly circular; inner margins of eyes not or only slightly convergent below; genal area broad, or, if head conspicuously rectangular and gena narrow, then thorax red (small species) *H. (Dentigera) (brachycephalus group and Hylaeus rubicola Saunders)*
- Vertex convex as usual; head in frontal view rounded or trapezoidal, never rectangular; inner margins of eyes markedly convergent below; genal area narrow; thorax black, with red marks in only a few large species..... 6
- 6(5). Omaulus carinate or lamellate; malar area at least as long as basal flagellar diameter; thorax and clypeus mostly strongly punctate; propodeal triangle with coarse wrinkles *H. (Spatulariella)*
- Omaulus rounded or merely angular; malar area shorter than basal flagellar diameter, rarely longer, in which case another character given above does not agree 7
- 7(6). Head conspicuously longer than broad in frontal view; pronotum thickened, dorsolateral angle square-truncate; mesoscutum coarsely and strongly wrinkled-punctate *H. (Koptogaster)*
- Head shorter, circular or trapezoidal in frontal view; pronotum short, dorsolateral angle rounded or pointed; if mesoscutum coarsely punctate, then head always short 8
- 8(7). Facial fovea elongate, somewhat surpassing upper ocular margin, converging strongly toward ocelli, terminating closer to ocelli than to compound eye (Fig. 47-11l)..... *H. (Paraprosopis)*
- Facial fovea short and straight, barely reaching upper ocular margin and terminating closer to compound eye than to ocelli (Fig. 47-11m)..... 9

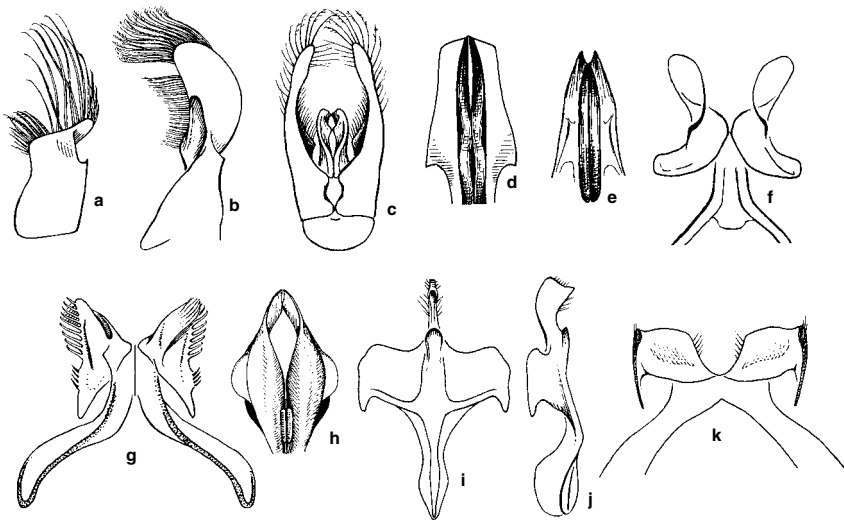


Figure 47-10. Structures of palearctic *Hylaeus*, males, dorsal views except g (dorsal at left, ventral at right) and i and j (which are ventral and lateral). **a**, *Hylaeus (Abrupta) cornutus* Curtis, left gonoforceps; **b**, *H. (Mehelyana) friesei* (Alfken), left gonoforceps; **c**, *H. (Spatulariella) hyalinatus* Smith, genital capsule; **d**, *H. (Koptogaster) punctulatus* Smith, penis valves; **e**, *H. (Hylaeus) an-*

gustatus (Schenck), penis valves; **f**, *H. (Paraprosopis) ater* (Saunders), apical lobes of S7; **g**, *H. (Hylaeus) paulus* Bridwell, apical lobes of S7; **h**, *H. (Lambdopsis) annularis* (Kirby), penis valves; **i**, **j**, *H. (Lambdopsis) annularis* (Kirby), S8; **k**, *H. (Lambdopsis) annularis* (Kirby), S7. **a-e**, from Dathe, 1980a; **f**, from Dathe 1993; others are original by H. Dathe.

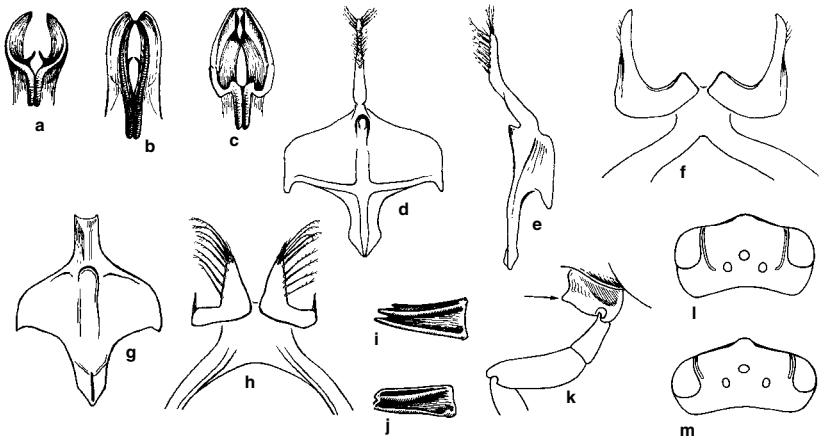


Figure 47-11. Structures of palearctic *Hylaeus*, a-h, males; i-m, females. **a**, *Hylaeus* (*Dentigera*) *brevicornis* Nylander, penis valves, dorsal view; **b**, *H. (Dentigera)* *pilosulus* (Pérez), penis valves, dorsal view; **c**, *H. (Prosopis)* *confusus* Nylander, penis valves, dorsal view; **d, e**, *H. (Nesoprosopis)* *pectoralis* Förster, S8, ventral and lateral views; **f**, *H. (Nesoprosopis)* *pectoralis* Förster, S7, dorsal view; **g**, *H. (Prosopis)* *hyrcanius* Dathe, S8, ventral view; **h**, *H. (Prosopis)* *hyrcanius* Dathe, S7, dorsal view; **i**, *H. (Lampdopsis)* *annularis*

(Kirby), left mandible; **j**, *H. (Hylaeus)* *leptocephalus* (Morawitz), left mandible; **k**, *H. (Mehelyana)* *friesei* (Alfken), left anterior leg, coxal process marked by arrow; **l**, *H. (Paraprosopis)* *sinuatus* (Schenck), dorsal view of vertex with elongate facial foveae; **m**, *H. (Hylaeus)* *communis* Nylander, vertex with short facial foveae. From Dathe, 1980a, except g and h, from Dathe, 1980b, and d-f, original by H. Dathe.

- 9(8). Mesepisternum with strikingly coarse and strong but regular pitlike punctures; T1 without lateral fringe (T1 and T2 polished) *H. (Nesoprosopis)*
- Mesepisternum with fine punctures or, if coarse and strong, then not regular and metasomal terga densely punctate; T1 often with lateral fringe..... 10
- 10(9). Larger species (body length 5-9 mm) usually with short head; facial fovea usually with upper end well separated from eye; propodeum short, at least lateral and posterior surfaces mostly rounded, not delimited by carinae, with fine sculpture and covered with white feltlike hairs; T1 often with lateral fringe of white hairs, but if fringe absent, then metasomal base sometimes red
..... *H. (Prosopis)*
- Smaller species (body length 3.5-8.0 mm) with elongated head; facial fovea shorter, upper end close to eye margin; propodeum usually sharp-edged or with carina around posterior surface; metasoma black, usually without lateral fringe on T1, but if T1 has fringe, then mesepisternum densely, finely punctate and propodeum rounded, with fine sculpture11
- 11(10). T1 usually without lateral fringe and propodeum usually sharp-edged or carinate; if fringe on T1 present, then following terga without hair bands and propodeum rounded, with fine sculpture *H. (Hylaeus s. str.)*
- T1 and T2 with lateral fringe, margins of T3 and T4 with bands of white hairs; propodeum rounded, partially with weak radial carinae.....
..... *H. (Lampdopsis)* (in part, East Asian species)

Key to the Sub-Saharan Subgenera of *Hylaeus*
(Partly modified from Snelling, 1985)

The *Prosopisteron* species in the Australian region do not all agree with the characterization in couplet 1. The

African species was introduced and is known only from the south coast of Cape Province.

- 1. Supraclypeal area gently sloping from midline to antennal sockets, not laterally margined; propodeum smooth, densely tessellate, without defined basal area; entire body densely tessellate, with conspicuous punctures; S7 of male with four similar, hairy apical lobes
..... *H. (Prosopisteron)*
- Supraclypeal area elevated between antennal sockets and laterally margined; propodeum with defined basal area, usually coarsely rugose or roughened or sharply punctate, at least in part; S7 of male with two apical lobes or four that are dissimilar, at least one pair hairless 2
- 2(1). Apex of mandible acute, without distinct teeth; mandible elongate, slender, without grooves and ridges on outer surface*H. (Nothylaeus)*
- Apex of mandible transverse or oblique, two- or three-toothed; mandible short and broad, with the usual grooves and ridges on outer surface 3
- 3(2). Integument very coarsely punctate; scutellum and metanotum each usually with a pair of spines (Fig. 47-12b); occipital carina present, sharp; omaulus sharply carinate.....
..... *H. (Metylaeus)*
- Integument variously punctate; scutellum and metanotum without lateral spines; occipital carina often absent; omaulus not sharply carinate but sometimes with an obscure ridge..... 4
- 4(3). S7 with two apical lobes, these small, directed laterally or basolaterally, with only small setae; gonoforceps of male with distal one-fifth or more narrowed, attenuate, much exceeding apex of penis valve *H. (Alfkenylaeus)*
- S7 with four apical lobes, proximal ones usually with coarse to very coarse setae; gonoforceps of male termi-

- minating bluntly at about level of apex of penis valve (attenuate in some species of *Deranchylaeus*) 5
- 5(4). T1-T3 with abundant erect hairs on discs; proximal apical lobe of S7 of male without setae or with a median row of rather small, thickened setae *H. (Cornylaeus)*
- T1-T3 with or without a few erect hairs on discs; proximal apical lobe of S7 of male with marginal row of large, very coarse setae *H. (Deranchylaeus)*

Hylaeus / Subgenus *Abrupta* Méhely

Prosopis (Abrupta) Méhely, 1935: 32, 137. Type species: *Hylaeus cornutus* Curtis, 1831, monobasic. [For date and authorship of this subgenus, see Michener, 1997b.]

The facial modifications as well as the male genitalia (Fig. 47-10a), as indicated in the key, are distinctive. The gonostylus of the male is perhaps distinctly separated from the gonocoxite (Fig. 47-10a), as in the subgenus *Mehelyana*, but is short, broad, and truncate. The male genitalia and other structures were illustrated by Méhely (1935) and Dathe (1980a). This subgenus does not seem to be closely related to any other.

■ *Abrupta* occurs from Portugal and Morocco east through Europe, northern Africa, and southwestern Asia to Iran and Turkmenistan, north to 55°N in Denmark. The only species is *Hylaeus cornutus* Curtis.

Hylaeus / Subgenus *Alfkenylaeus* Snelling

Hylaeus (Alfkenylaeus) Snelling, 1985: 13. Type species: *Hylaeus namaquensis* Cockerell, 1942, by original designation.

Of the African subgenera with attenuate apices of the male gonoforceps (Fig. 47-13a), this is the one most similar to ordinary *Hylaeus*. Females are not separable by subgeneric characters from the subgenus *Deranchylaeus*. The body is coarsely punctate. The disc of S7 of the male is rather broad, with two small, hairless or nearly hairless lateroapical lobes directed laterobasally. The apical process of S8 of the male is slender, apically enlarged. The body length is 6 to 8 mm. Male genitalia and other structures were illustrated by Snelling (1985).

■ *Alfkenylaeus* occurs in Africa from Kenya, Upper Volta, and Senegal to the Transvaal in South Africa. The four species were revised by Snelling (1985). A fifth species, *Hylaeus arnoldi* (Friese), agrees with *Alfkenylaeus* in most features but the male has a less prolonged attenuation of the gonoforceps and S8 is of a totally different form, having two long, broad apical lobes instead of a median apical process.

Hylaeus / Subgenus *Analastoroides* Rayment

Analastoroides Rayment, 1950: 20. Type species: *Analastoroides foveata* Rayment, 1950, by original designation.

This subgenus (originally called a genus, but see Houston, 1981a) is unique among Hylaeinae in the bands of dense orange tomentum on T1 and T3; this feature, along with size (body length 8.0-12.5 mm) results in a remark-

able superficial resemblance to some species of the genus *Hyleoides* and to some wasps of the genus *Alastor*. The strongly humped T2, especially in the male (Fig. 47-3g shows the female), and the constricted apex of T1 suggest the subgenus *Euprosopellus*, but these characters probably arose independently. In *Analastoroides* the male S7 has two pairs of hairy apical lobes, shaped and attached much as in *Prosopistemon* (Fig. 47-9f), whereas in *Euprosopellus* there is only one pair of lobes, directed laterally but broadly fused to the body of the sternum (Fig. 47-9i). Male genitalia and hidden sterna were illustrated by Houston (1981a).

■ *Analastoroides* is from the coastal zone of Victoria and New South Wales, Australia. The only known species is *Hylaeus foveatus* (Rayment).

Hylaeus / Subgenus *Cephalyaeus* Michener

Michener, 1942a: 273. Type species: *Prosopis basalis* Smith, 1853, by original designation.

Rather large (7-8 mm long) in comparison to other Nearctic *Hylaeus*, the female lacks pale markings and the male has a greatly enlarged scape. The two apical lobes of S7 of the male are broadly fused to an unusually wide sternal body. The apical process of S8 is reduced to a small, hairless point only about as long as its basal width. The male gonoforceps are widest apically, and are provided with an apical crescentic zone of long hairs and a preapical rounded mesal projection on the ventral side. Metz (1911), Mitchell (1960), and Snelling (1968) illustrated the male genitalia and hidden sterna.

■ *Cephalyaeus* ranges across Canada (British Columbia to Newfoundland) and the northern USA, southward to California and in mountain ranges to Colorado. The two species were reviewed by Snelling (1968).

Hylaeus / Subgenus *Cephylaeus* Moure

Hylaeus (Cephylaeus) Moure, 1972: 280. Type species: *Hylaeus larocai* Moure, 1972, by original designation.

This subgenus consists of a small (length 5 mm) Brazilian species that lacks strong carinae. It may be related to the subgenus *Hylaeana*; specimens have not been available and should be reexamined. They might have an ommatidial carina below the lower end of the episternal groove, as does *Hylaeana*; this carina was not observed when *Hylaeana* was originally described and could have been missed when *Cephylaeus* was described. Male genitalia and other structures were illustrated by Moure (1972).

■ *Cephylaeus* is known from Paraná, Brazil. The only species is *Hylaeus larocai* Moure.

Hylaeus / Subgenus *Cornylaeus* Snelling

Hylaeus (Cornylaeus) Snelling, 1985: 8. Type species: *Prosopis aterrima* Friese, 1911, by original designation.

Cornylaeus seems closely related to another African subgenus, *Deranchylaeus*. Its main characters are its larger size (6.0-8.5 mm long), especially of the metasoma of the

orbiza (*Ceratorhiza*) *conica* Michener with a modified propodeum (Fig. 47-3f). The vertical ridge in front of the mesocoxa is usually sharp. The apex of the hind tibia lacks spines on the outer margins. The male genitalia and hidden sterna of certain species were illustrated by Michener (1965b); see also Figure 47-8g.

The majority of species of *Palaeorhiza* occur in New Guinea, and all subgenera are represented there; this is the only bee group that has undergone major diversification on that island. The genus extends into other moist forested areas, west to the Moluccas and as far as Flores in the Lesser Sundas, south as far as southern Queensland in Australia, and east to the Bismarck Archipelago, the Solomon Islands, the Santa Cruz Islands, and the New Hebrides. An Australian species, *P. (Heterorhiza) flavomellea* Cockerell, or a close relative, occurs in New Caledonia. About 150 species have been described, many of them from single individuals; the total number of species must be much greater. The 25 Australian species were listed by Cardale (1993).

The species of *Palaeorhiza* are mostly easily distinguishable. Probably for this reason, it has not been the custom to examine or illustrate the male genitalia and hidden sterna, as is routinely done for other Hylaeinae and indeed for most bees. The subgeneric classification is therefore in a particularly primitive state. Although many of the subgenera differ sharply from one another, Hirashima and Liefstinck (1983) reported 19 species (16 of them new) that they could not assign to subgenus, and Hirashima (1988) did not place 12 new species in subgenera. In 1989, however, he named the subgenus *Calorhiza* to contain the unplaced species. The whole genus needs study in the light of genitalic and other characters that might permit better analysis. The following are some of the unusual characters of certain species or subgenera.

Palaeorhiza (Michenerapis) bicolor Hirashima and Liefstinck, known from a single male specimen, lacks a preoccipital carina. Hirashima and Liefstinck (1982) suggest that it may be generically distinct, but lack of a preoccipital carina by itself does not establish generic distinctness. *Hylaeus* and *Pharohylaeus* are other hylaeine genera in which this carina can be either present or absent.

Unlike those of most other Hylaeinae, females of the subgenus *Cercorhiza* have a well-developed pygidial plate, pygidial and prepygidial fimbriae, and a well-developed basitibial plate (Hirashima, 1975b, 1982b). Presumably these are ancestral features associated with nesting in the ground. At least two species of *Cercorhiza* are known to nest in burrows in the ground, unlike most Hylaeinae. The subgenus *Cnemidorhiza* also has a pygidial plate and fimbria in the female, but there is no basitibial plate. Instead, the basal part of the outer surface of the female hind tibia, where the basitibial plate should be, is broadened and coarsely roughened. This area probably functions as does a basitibial plate, or it may actually be a basitibial plate without marginal carinae. The only species of *Cnemidorhiza* whose nests are known makes burrows in the ground, like those of the subgenus *Cercorhiza* (Hirashima, 1981a). It is likely that *Cnemidorhiza* (with *Cercorhiza*) should form a genus separate

from *Palaeorhiza*, but until further studies are made, particularly of males, such a change would be premature. This is written on the assumption that except for the two subgenera mentioned above, *Palaeorhiza* species, like most Hylaeinae, nest in holes in wood, stems, galls, etc. Unfortunately, *Palaeorhiza* nests are unknown, except for the two ground-nesting subgenera.

The genus *Xenorhiza* consists of a group of species that would easily fall within the range of variability found in *Palaeorhiza*, except that the male glossa is similar to that of the female, as in *Hylaeus* and most other colletids. One can easily imagine that this is a derived group of *Palaeorhiza* in which the female-type glossa was transferred to the male. On the other hand, it might be a relictual basal group from which forms with a pointed male glossa with seriate hairs arose. Pending further study, I am not modifying the current classification.

Key to the Subgenera of *Palaeorhiza*

(Modified from Hirashima and Liefstinck, 1982, with certain subgenera added on the basis of literature only)

1. Preoccipital carina absent; space between clypeus and compound eye narrower than width of middle ocellus; inner hind tibial spur of male strongly modified *P. (Michenerapis)*
- Preoccipital carina present; space between clypeus and compound eye at least about as broad as middle ocellus; inner hind tibial spur of male slender and simple as usual 2
- 2(1). Surface of propodeal triangle strongly convex in middle, or with a conical projection 3
- Surface of propodeal triangle not convex in the middle 4
- 3(2). Propodeal triangle convex in middle; T1 small, its basal portion distinctly constricted and subpetiolate; large, more or less slender and nonmetallic species *P. (Eusphecogastra)*
- Propodeal triangle with rounded conical projection; T1 not constricted; large and robust species, with head and thorax black (with yellow markings) and metasoma blue-green *P. (Ceratorhiza)*
- 4(2). Propodeal triangle densely fluted longitudinally 5
- Propodeal triangle not fluted 7
- 5(4). T2 and T3 each with band of short, dense, appressed white hair across base; anterior surface of T1 covered with dense, scale-like white hairs *P. (Gressittapis)*
- T1 to T3 without short, dense pubescence as described above 6
- 6(5). Integument of head and thorax strongly sclerotized, with dense, usually strong punctures on the latter; inner hind tibial spur of female distinctly serrate; male T7 with a pair of long spines at apex, the spines broadly separated from each other; male mandible simple at apex *P. (Heterorhiza)*
- Integument of head and thorax appearing softer; inner hind tibial spur of female simple; male T7 with or without a pair of projections, these not broadly separated when present; male mandible bidentate *P. (Paraheterorhiza)*
- 7(4). Posterior surface of propodeum hexagonal, surrounded by strong carina connected to longitudinal cari-

- nae separating dorsal, dorsolateral, and lateral areas, dorsal area divided by longitudinal median carina; upper portion of mesepisternum flat, depressed *P. (Noonadania)*
- Propodeum not so divided by strong carinae; upper part of mesepisternum convex 8
- 8(7). Anterior basitarsus slender, slightly or usually considerably longer than tarsal segments 2 to 5 taken together; clypeus and supraclypeal area flat (usually longitudinally rugoso-punctate) *P. (Cheesmania)*
- Anterior basitarsus little if any longer than segments 2 to 5 taken together; clypeus and supraclypeal area convex 9
- 9(8). Thorax, especially mesepisternum, and propodeum extremely coarsely foveolate-punctate; propodeal triangle irregularly coarsely rugose, carinate on lateral margins *P. (Trachyrhiza)*
- Thorax rather finely punctate; propodeal triangle not carinate on lateral margins 10
- 10(9). Female mandible large and edentate; scutellum, metanotum, and most of propodeal enclosure flat; second flagellar segment of male (in *Palaeorhiza mandibularis* Michener) distinctly longer than broad *P. (Anchirhiza)*
- Female mandible as usual; scutellum, metanotum, and most of propodeal enclosure convex as usual; second flagellar segment of male at most as long as broad 11
- 11(10). Dorsal surface of propodeum with pair of small swellings apically, close to propodeal triangle, either depressed apically or densely and finely shagreened and dull 12
- Propodeum without such swellings dorso-apically 13
- 12(11). Propodeal triangle longitudinally depressed in middle apically, smooth, shining; upper portion of supraclypeal area and median portion of frons longitudinally elevated, a broad longitudinal yellow stripe on this portion of face; inner hind tibial spur of female serrate *P. (Palaeorhiza s. str.)*
- Propodeal triangle densely and finely shagreened and dull, transversely slightly concave; swelling of upper portion of supraclypeal area sharply defined from flat frons, no yellow stripe on frons; inner hind tibial spur of female normal *P. (Zarhiopalea)*
- 13(11). Glossa of male longer than head; male S5 concealed by S4; nonmetallic species, the posterior part of thorax, basal part of metasoma, and legs honey-colored (male S6 strongly convex in middle; propodeal triangle somewhat coarsely sculptured in middle) *P. (Eupalaeorhiza)*
- Glossa of male much shorter; male S5 exposed as usual; species usually metallic, not honey-colored 14
- 14(13). Propodeal triangle punctate-roughened at least on apical portion, usually distinctly convex basally; inner hind tibial spur of female finely serrate (large, robust, strongly metallic species) *P. (Hadrorthiza)*
- Propodeal triangle not punctate-roughened; inner hind tibial spur of female simple 15
- 15(14). Basal part of hind tibia of female without basitibial plate and not thickened; T6 of female lacking both fimbria and pygidial plate *P. (Callorhiza)*
- Basal part of hind tibia of female either with basitibial plate or thickened and coarsely sculptured; T6 of female

- with fimbria of hairs differing from those of other terga and sometimes having pygidial plate 16
- 16(15). Female hind tibia thick basally, its dorsal surface usually broad and punctate-roughened or coarsely sculptured basally but without margined basitibial plate; female T6 with a pygidial fimbria of dense downy hairs in middle or a partly formed pygidial plate (female hind femur with apical tuft of black hairs, sometimes obscure) *P. (Cnemidorhiza)*
- Basitibial plate present in female; female T6 with pygidial plate in middle, lateral to which is pygidial fimbria *P. (Cercorhiza)*

Palaeorhiza / Subgenus *Anchirhiza* Michener

Palaeorhiza (Anchirhiza) Michener, 1965b: 147. Type species: *Palaeorhiza mandibularis* Michener, 1965, by original designation.

In this subgenus the body is black, the metasoma is slightly metallic, and the head and thorax have yellow markings. The edentate mandible of the female and the small clypeus, broadly separated from the eye, are distinctive.

■ *Anchirhiza* occurs in Queensland, Australia, and in New Guinea. There are two species. Hirashima (1978a) characterized the subgenus.

Palaeorhiza / Subgenus *Callorhiza* Hirashima

Palaeorhiza (Callorhiza) Hirashima, 1989: 2. Type species: *Prosopis apicatus* Smith, 1863, by original designation.

This subgenus contains a diverse lot of species, that is, all the species that do not fall in any other subgenus. Some are fulvous, some black, some metallic, some have white or yellow markings, in some the metasoma is red; the malar space can be long or short, etc. Their common characters are largely or entirely plesiomorphic relative to related subgenera. Proper study will be possible only when both sexes are known for diverse species.

■ *Callorhiza* is known from Queensland, Australia, and from Misoöl in Indonesia, New Guinea, and the Solomon Islands. Hirashima (1989) listed 40 species.

Palaeorhiza / Subgenus *Ceratorhiza* Hirashima

Palaeorhiza (Ceratorhiza) Hirashima, 1978a: 81. Type species: *Palaeorhiza conica* Michener, 1965, by original designation.

Ceratorhiza consists of large black species with a greenish or purplish metallic metasoma and yellow markings on the head and thorax. The large projection of the propodeal triangle is unique.

■ This subgenus is found in New Guinea. The two species were revised by Hirashima (1978a).

Palaeorhiza / Subgenus *Cercorhiza* Hirashima

Palaeorhiza (Cercorhiza) Hirashima, 1982b: 88. Type species: *Palaeorhiza gressittorum* Hirashima, 1975, by original designation.

This is a subgenus of black, red, or metallic species having yellow marks limited to the faces of the males. As in

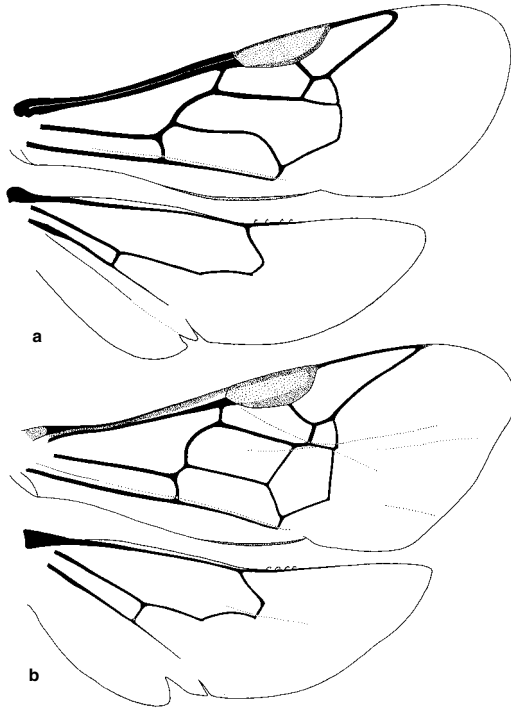


Figure 48-4. Wings of Euryglossinae, Group A. **a**, *Brachyhesma (Microhesma) incompleta* Michener; **b**, *Euryglossula chalcosoma* (Cockerell).

less on a line with the median axis of the eye, instead of on a line with the inner ocular orbit. This character occurs in females of *Pachyprosopis*, *Euryglossina*, *Euryglossula* (weakly), and *Hyphesma*, and in *Eubhesma hyphesmoides* (Michener). It also occurs in males, but not females, of *Brachyhesma*.

The subantennal sutures of Euryglossinae are mostly ordinary. In *Brachyhesma*, *Hyphesma*, and *Xanthesma*, however, the subantennal sutures are absent and the clypeus broadly abuts against the antennal sclerites; in the last two genera the upper lateral parts of the clypeus are commonly drawn up to the antennal sclerites, well above the level of the arcuate median part of the epistomal suture. This is not necessarily very different from the condition in some *Eubhesma*, e.g., in *E. wahlenbergiae* (Michener). In *Callohesma*, however, if Exley's (1974b) interpretation is correct, the apparent subantennal suture is double, with a slender clypeal ribbon extending up between two sutures from each upper clypeal angle to the antennal sclerite. This would be an elaboration of the condition found in *Hyphesma* and *Xanthesma*.

Key to the Genera of the Euryglossinae
(Modified from Michener, 1965b)

1. First abscissa of vein Rs transverse (Fig. 48-4b), so that posterior basal angle of first submarginal cell (often also apex of cell R1) is about 90°; lower end of eye of female protruding mesad above mandibular base [only slightly in *Euryglossula* and *Euryglossina (Microdontura)*], so that anterior mandibular articulation is usually on a line with

median axis of eye; posterior margin of first submarginal cell straight (Fig. 48-4) (lateral fovea of T2 well defined, linear, rarely punctiform or absent in minute species; first recurrent vein joining first submarginal cell or rarely meeting first submarginal crossvein) 2

— First abscissa of vein Rs oblique (Figs. 48-2, 48-3, 48-4a), so that posterior basal angle of first submarginal cell and apex of cell R1 are nearly always acute; lower end of eye (except in females of *Hyphesma* and *Tumidibhesma* and males of *Brachyhesma*) not protruding mesad above mandible, anterior mandibular articulation therefore usually in line with inner orbit; posterior margin of first submarginal cell sinuate (Figs. 48-2, 48-3) [except in *Brachyhesma* (Fig. 48-4a) and *Eubhesma hemixantha* (Cockerell)] 4

2(1). Second submarginal crossvein about one-third longer than first (as in Fig. 48-3b); costal margin of second submarginal cell sloping apically toward costa (as in Fig. 48-3b); labrum of female nearly always with strong apical spine (mandible of female bidentate, rarely simple) *Pachyprosopis*

— Second submarginal crossvein usually little longer than first or absent; costal margin of second submarginal cell subparallel to costal margin of stigma; labrum usually without apical spine (minute species) 3

3(2). Basitibial plate of female defined (though in some cases very indistinctly and incompletely), one-fourth to one-sixth of length of tibia; eye of female protruding but little mesad over mandibular base; clypeus of female not strongly sloping inward but forming continuous arc with supraclypeal area, as seen in profile (Fig. 48-5a); marginal cell pointed on costa (Fig. 48-4b) *Euryglossula*

— Basitibial plate of female not clearly defined, but margin indicated (often vaguely) by tubercles and ending near middle of tibia; eye of female strongly protruding mesad over mandibular base (except in subgenus *Microdontura*); clypeus of female sloping inward, at least below, usually at distinct angle to supraclypeal area (Fig. 48-5b); apex of marginal cell separated from costa, sometimes by less than width of a vein *Euryglossina*

4(1). Clypeus more than 3.5 times as broad as long, as seen from front; scape at least two-thirds as long as eye (Fig. 48-5c, d); antennal bases more than three times as far from median ocellus as from lower edge of clypeus; eye of male usually produced mesad above anterior mandibular articulation (minute, largely yellow forms, antennal sockets immediately above epistomal suture and subantennal sutures thus absent) *Brachyhesma*

— Clypeus usually less than 3.5 times as broad as long; scape usually not much more than one-half as long as eye; antennal bases not much more than twice as far from median ocellus as from lower edge of clypeus; eye of male not produced mesad above anterior mandibular articulation 5

5(4). Costal margin of second submarginal cell distinctly sloping apically toward costa (Fig. 48-3b), the cell having more or less the same shape as that of *Pachyprosopis*; facial fovea of female with lower end curved mesad toward antennal base; eye of female strongly protruding mesad above anterior mandibular articulation (body black, without yellow markings) *Hyphesma*

— Costal margin of second submarginal cell usually sub-

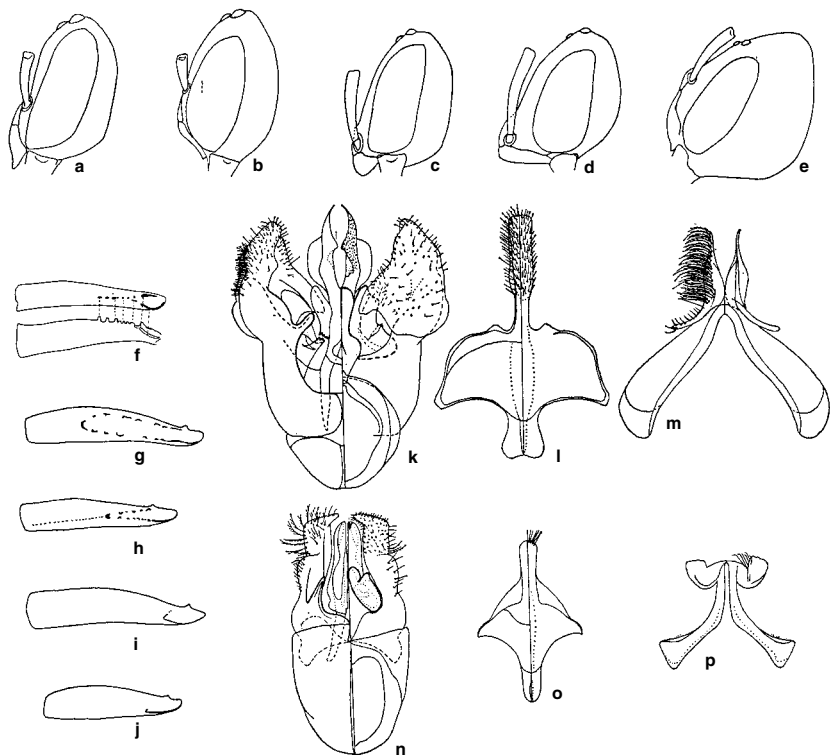


Figure 48-5. Structures of Euryglossinae. **a-e**, Side views of heads. **a**, *Euryglossula chalcosoma* (Cockerell), female; **b**, *Euryglossina* (*Euryglossina*) *hypochroma* Cockerell, female; **c**, *Brachyhesma* (*Microhesma*) *incompleta* Michener, male; **d**, *B. (Brachyhesma)* *sulphurella* (Cockerell), male; **e**, *Sericogaster fasciatus* Westwood, female.

f-j, Posterior views of hind tibiae of females, showing basitibial plates, mostly margined by tubercles as shown in outer view of **f**.

f, *Melittosmithia carinata* (Smith); **g**, *Sericogaster fasciata* Westwood; **h**, *Euryglossa laevigata* (Smith); **i**, *Xanthesma furcifera* (Cockerell); **j**, *Callohesma calliopsiformis* (Cockerell).

k-m, Male genitalia, S8, and S7 of *Callohesma calliopsiformis* (Cockerell); **n-p**, Same, of *Brachyhesma (Microhesma) incompleta* Michener. (Dorsal views are at the left.)

From Michener, 1965b.

parallel to costal margin of stigma (Fig. 48-2); facial fovea of female not curved mesad toward antennal base; eye of female not protruding mesad above anterior mandibular articulation [except in *Tumidihesma* and *Euhesma hyphesmoides* (Michener)] 6

6(5). T1 about as broad as long, as seen from above; body wholly black; distal part of pygidial plate of female narrower than last tarsal segment, apex upturned; inner hind tibial spur finely ciliate *Heterohesma*

— T1 much broader than long *or* body largely yellow; if distal part of pygidial plate of female narrower than last tarsal segment, then inner hind tibial spur pectinate 7

7(6). Second submarginal cell strongly narrowed toward costa, about half as long on anterior side as on posterior side (Fig. 48-2d); second submarginal crossvein strongly curved or sinuate and at an angle of about 45° to first; head and thorax strongly and closely punctate, metasoma dull with dense, minute punctures *Dasyhesma*

— Second submarginal cell little shorter on anterior side than on posterior side, second submarginal crossvein only gently curved and subparallel to first or at an angle of less than 40° to first (Fig. 48-2a-c); head and thorax with punctures fine or well separated, metasoma not dull

with minute, dense punctures, although sometimes dulled by other sculpturing 8

8(7). Basitibial plate in both sexes indicated by two rows of large tubercles, the rows nearly meeting and terminating the “plate” well beyond middle of tibia (Fig. 48-5g); median ocellus closer to antennae than to posterior edge of vertex in female (Fig. 48-5e), and midway between these points in male *Sericogaster*

— Basitibial plate not extending beyond middle of tibia, although a single row of tubercles may extend beyond middle; vertex less produced posteriorly so that median ocellus is at or behind midpoint between antennae and posterior edge of vertex in female and behind midpoint in male 9

9(8). Body slender, T1 seen from above little broader than long (extensive yellow pattern on body; mandible simple in both sexes) *Stenohesma*

— Body of ordinary form, T1 seen from above much broader than long 10

10(9). Clypeus with strong longitudinal median carina (mandible simple) (male unknown) *Melittosmithia*

— Clypeus without longitudinal carina 11

11(10). Anterior end of scutum, especially in female, nearly

- as broad as scutal width at anterior ends of tegulae; front of scutum curved down rather sharply and usually differently sculptured than rest of scutum; scutum coarsely punctured, in female with large, shining interspaces or smooth impunctate areas; basitibial area of female defined by large tubercles or basally by carinae, a particularly strong tubercle at apex (Fig. 48-5h) (inner hind tibial spur of female strongly pectinate; body usually without yellow markings) *Euryglossa*
- Anterior end of scutum much narrower than width at anterior ends of tegulae; front of scutum curved down rather uniformly and usually not sculptured differently than rest of scutum; scutum shining and almost impunctate, as in *Tumidibesma*, or usually dull, minutely lineate or roughened, its punctation variable; basitibial area of female variable, usually without particularly strong tubercle at apex 12
- 12(11). Apex of marginal cell rounded or somewhat pointed, bent well away from wing margin; outer surface of hind tibia of female covered with simple bristles (integument yellow or with yellow markings) *Callobesma*
- Apex of marginal cell pointed on or almost on wing margin; outer surface of hind tibia of female usually with some plumose hairs in addition to simple bristles 13
- 13(12). Mandible of female (male unknown) tridentate; facial fovea linear, not bent toward ocelli; lower end of eye protruding mesad above anterior mandibular articulation *Tumidibesma*
- Mandible simple or bidentate; facial fovea broader, or, if narrowly linear, then upper end bent toward ocelli; lower end of eye not protruding above anterior mandibular articulation (except in *Eubesma hyphesmoides* Michener) 14
- 14(13). Facial fovea of female slender, linear, upper fourth or more bent mesad toward ocelli (Fig. 48-2e); apical lobes of S7 of male usually directed laterad, not extending more than half a lobe width behind median apical margin of S7; mandible of female simple (with small preapical tooth in subgenus *Chaetohesma*); subantennal suture absent, upper lateral part of clypeus usually produced upward to antenna; claws of female simple (except with tooth in a few species of subgenus *Chaetohesma*); body commonly with extensive yellow markings *Xanthesma*
- Facial fovea of female broad or broadly linear, upper end commonly not bent mesad; apical lobes of S7 of male commonly elongate, extending far behind median apical margin of S7; mandible of female with preapical tooth on upper margin; subantennal suture usually present, but upper lateral angle of clypeus sometimes attaining antennal base, eliminating subantennal suture; claws of female cleft or with inner tooth, rarely simple; body usually without extensive yellow markings *Eubesma*

Genus *Brachyhesma* Michener

This is a genus of minute (body length 2.7-4.0 mm), largely yellow-bodied bees. In spite of their small body size, the base of the first submarginal cell is acute (Fig. 48-4a), a plesiomorphy relative to *Euryglossina* and its relatives (see first couplet of the key to genera). As in those *Euryglossina* with more extensive wing venation, the second submarginal cell is complete, but less than half as long as

the first, and the first recurrent vein (when present) ends near the apex of the first submarginal cell. The clypeus, when seen from the front, is 3.5 to 10 times as wide as long, and the antennae arise far down on the face, next to the clypeus, so that subantennal sutures do not exist (Fig. 48-5c, d). Thus the frons is large compared to that of other bees. The labrum of the female lacks the midapical spine found in most *Pachyprosopis* and some *Euryglossina*, but often has several coarse, spinelike apical setae. The facial foveae of females are linear, long, the upper ends curved mesad, usually almost to the lateral ocelli. In males they are long and slender but not curved toward the ocelli. The eyes of the male (not females as in *Euryglossina*, *Hyphesma*, and *Pachyprosopis*) protrude mesad over the mandibular bases, except in the subgenus *Henicohesma*. In males the hind tibial spurs appear to be absent, but are replaced by one to several large bristles, these sometimes curiously shaped. Unlike many other Euryglossinae, *Brachyhesma* has a small basitibial plate, about one-fifth as long as the tibia, weakly defined only on the posterior margin, or unrecognizable in some males. The claws of females are simple. Illustrations of various structures, including male genitalia, were given by Michener (1965b) and Exley (1968e, 1974c, 1975a, 1977); see also Figure 48-5n.

Brachyhesma, a rather large Australian genus, was revised by Exley (1968e, 1977) with keys to species in Exley (1968f, 1975a). On the basis of fragmentary evidence (Exley, 1968f) and excavation of a single nest (Houston, 1969), one can suppose that nests are regularly or always in the ground. All species visit flowers of Myrtaceae.

There are two major subgenera, *Brachyhesma* s. str. and *Microhesma*, and two small or monotypic subgenera, *Henicohesma* and *Anomalohesma*. The latter are not specialized derivatives of the large subgenera, for each has plesiomorphies not shared by the large subgenera. Presumably, the small subgenera are basal branches, each a sister group to one or both of the large subgenera. Subgeneric characters are largely unknown in females.

Key to the Subgenera of *Brachyhesma*, Based on Males

(Modified from Exley, 1977)

1. Supraclypeal area and upper part of clypeus protruding strongly forward between antennal bases (Fig. 48-5d); clypeus, in frontal view, a mere strip across lower end of face, its major area reflexed and exposed ventrally..... 2
- Supraclypeal area and upper part of clypeus not protruding strongly forward between antennal bases (Fig. 48-5c); clypeus rather broadly exposed in frontal view, neither reflexed nor broadly exposed ventrally 3
- 2(1). Reflexed part of clypeus forming a flattened or concave triangular plate; scape nearly as long as to longer than eye (Fig. 48-5d) *B. (Brachyhesma* s. str.)
- Reflexed part of clypeus convex, not forming triangular plate; scape much shorter than eye *B. (Anomalohesma)*
- 3(1). Metasoma yellow with transverse brown tergal bands; profile of clypeus strongly convex (Fig. 48-5c); gonobase almost one-half length of genitalia (Fig. 48-5n) *B. (Microhesma)*
- Metasoma completely yellow; profile of clypeus nearly flat; gonobase about one-third length of genitalia *B. (Henicohesma)*

known, and should contribute to our understanding of these bees.

Key to the Subgenera of *Euhesma*

1. Basitibial area of female margined by large tubercles and reaching middle of tibia, apex of area marked by strong tubercle; disc of scutum almost impunctate, smooth and shiny, in female; inner hind tibial spur of female coarsely pectinate as in *Callohesma* and *Euryglossa* (male unknown) *E. (Parahesma)*
- Basitibial area of female shorter, apex usually not marked by large tubercle, margins usually indicated by carinae that are sometimes mostly absent, sometimes broken into large tubercles; disc of scutum punctate and usually minutely roughened and dull; inner hind tibial spur of female ciliate, serrate, or weakly pectinate, that is, with teeth short *E. (Euhesma s. str.)*

Euhesma / Subgenus *Euhesma* Michener s. str.

Euryglossa (Euhesma) Michener, 1965b: 88. Type species: *Euryglossa wahlenbergiae* Michener, 1965, by original designation.

The principal characters of this subgenus are indicated in the key. The wide variability among species is discussed under the genus *Euhesma*. The present classification is one of convenience. We need to know both sexes of many more species, after which a rational classification of the genus should be possible. Illustrations of male genitalia, sterna, and other characters were given by Michener (1965b) and Houston (1992b).

■ *Euhesma* s. str. is widespread in Australia, including Tasmania, but is not abundant in the north of the continent. Forty-five species were listed by Cardale (1993), and many new species remain to be described; E. Exley has described 20 new species taken on flowers of *Eremophila* (Myoporaceae). E. Exley has started a revisional study of *Euhesma* and revised the *walkeriana* species group (Exley, 2001) and the *crabronica* group (Exley, 2002).

Although some species are associated with Myrtaceae, this subgenus includes many species probably oligolectic on other flowers, such as *Euhesma wahlenbergiae* (Michener) on *Wahlenbergia* (Michener, 1965b), *E. tubulifera* (Houston) on *Calothamnus* (Houston, 1983c), and many species on *Eremophila*. Probably all the species with unusual mouthparts listed in the discussion of the genus are oligolectic on flowers other than Myrtaceae. Nests in the ground were described by Rayment (references in Michener, 1965b: 87).

Euhesma / Subgenus *Parahesma* Michener

Euryglossa (Parahesma) Michener, 1965b: 92. Type species: *Euryglossa tuberculipes* Michener, 1965, by original designation.

This subgenus is known from a single female specimen. It might have been left within the diverse subgenus *Euhesma*, although it deviates from all members of that subgenus in several characters; the principal ones are noted in the key. I list it here purely provisionally, because it has and may deserve a subgeneric name.

■ *Parahesma* is from the state of Victoria, Australia. *Euhesma tuberculipes* (Michener) is the only species.

Genus *Euryglossa* Smith

Euryglossa Smith, 1853: 17. Type species: *Euryglossa cupreochalybea* Smith, 1853, by designation of Meade-Waldo, 1923: 6.

Stilpnosoma Smith, 1879: 16. Type species: *Stilpnosoma laevigatum* Smith, 1879, monobasic.

Euryglossa (Euryglossimorpha) Strand, 1910: 40. Type species: *Euryglossa nigra* Smith, 1879, monobasic.

The name *Euryglossa* is used here in a different than usual sense, to include the subgenus *Euryglossa* s. str. of Michener (1965b) plus the genus *Stilpnosoma*. The latter is based on a single species, *Euryglossa laevigata* (Smith), that differs from the rest of the genus primarily in characters that can be seen as tendencies elsewhere in the genus. Thus *E. laevigata* is bright metallic green; some other species are metallic but less brightly so. *E. laevigata* has broad genal and vertex areas, so that the median ocellus of the female is about midway between the antennal bases and the posterior margin of the vertex; this condition is approached in some other species.

Euryglossa differs from nearly all other moderate-sized to large Euryglossinae in the rather cylindrical, hopliform appearance of the head and thorax, which results from the tendency toward a large and quadrate head and especially from the swollen anterior part of the scutum, which is parallel-sided in front of the tegulae rather than narrowing anteriorly (see the key to the genera). This feature is not well developed in males, many of which can be recognized immediately by their long antennae, sometimes with a flattened distal segment. The body length ranges from 5 to 15 mm, the males usually being much smaller than the females. Although some species are black, others have dark metallic blue or green coloration on the metasoma and thorax, or rather bright green on the whole body; some have a red metasoma or even much of the body may be red. One species, *E. limata* Exley, has extensive yellow markings suggesting species of *Callohesma*. Male genitalia and other structures were illustrated by Michener (1965b) and Exley (1976b).

■ *Euryglossa* is widespread in Australia, including Tasmania, but is not particularly common in xeric areas. The 36 described species were revised by Exley (1976b) and listed by Cardale (1993).

So far as is known, species of this genus make nests in the ground; references to relevant papers were given by Michener (1965b: 87). They visit flowers of Myrtaceae.

Genus *Euryglossina* Cockerell

This is a genus of minute bees (1.8–5.0 mm long) in which the first abscissa of Rs of the forewing is transverse, as described in the first couplet of the key to genera (Figs. 48–4b, 48–6). The body is nonmetallic black, and the clypeus, paracocular areas, supraclipeal area, parts of legs, and pronotal lobes are often yellow; the metasoma is often brownish, yellowish beneath; rarely, as in *Euryglossina (Euryglossina) aurantia* Exley and *E. (Microdontura) mellea* (Cockerell), the body is largely yellow. Usually, the whole clypeus of females slopes inward, at a distinct an-

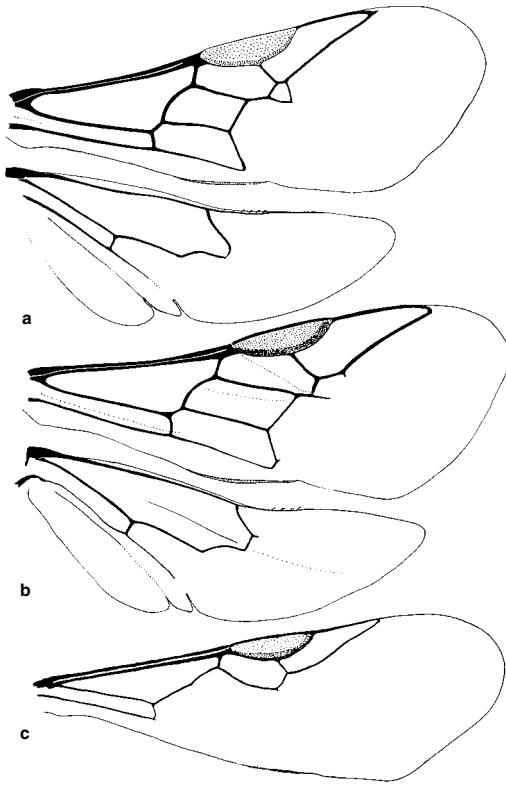


Figure 48-6. Wings of Euryglossinae, Group A. **a**, *Euryglossina* (*Microdontura*) *mellea* (Cockerell); **b**, *Euryglossina* (*Euryglossina*) *nothula* (Cockerell), a species having the “Turnerella” type wing venation; **c**, *Euryglossina* (*Quasihesma*) *moonbiensis* (Exley), diagram showing the most reduced wing venation known among bees.

gle to the supraclypeal area (Fig. 48-5b), thus distinguishing the genus from *Euryglossula*. Sometimes, however, only the apical part of the clypeus curves strongly inward, as seen in profile. The facial foveae are linear but extremely variable in length. The reduced wing venation was illustrated for several species by Michener (1965b); see also Figure 48-6.

I here interpret this genus more broadly than did Exley (1968d), to include two groups to which she gave generic status, i.e., *Euryglossella* and *Quasihesma*, as well as a species placed in *Pachyprosopis* by Michener (1965b), i.e., *Euryglossina* (*Pachyprosopina*) *paupercula* Cockerell, new combination. Various degrees of reduction of wing venation occur independently in different groups. For example, one species of the subgenus *Euryglossella* [*E. (Euryglossella) incompleta* (Exley)] lacks the first recurrent vein, thus having wing venation as in most *Quasihesma*. Likewise, reduction in the number of antennal segments to 12 in males (and to 11 in females of some species of *Quasihesma*) occurs in different groups, i.e., in most *Quasihesma* and some species of different species groups of *Euryglossina* s. str. Thus some characters once thought to have generic importance turn out to be variable. Even the

labral spine of females, a principal character of *Euryglossella*, is shared by at least some *Quasihesma* (Exley, 1974a) and by *Pachyprosopina*; even in the related genus *Pachyprosopis*, which supposedly has such a spine, it is evidently missing (lost?) in one species, *P. (Pachyprosopis) cornuta* Exley (Exley, 1972).

Euryglossina is found throughout Australia, including Tasmania, but is especially abundant in the north and in xeric areas. So far as is known, all species visit principally flowers of Myrtaceae.

Key to the Subgenera of *Euryglossina*

1. Hind tibia (both sexes) with row of suberect, scalelike and spinelike setae on outer surface from near base to apex; apex of pygidial plate of female elongate, upturned *E. (Microdontura)*
- Hind tibiae without such setae, usually with scattered small tubercles, largest one (near middle of tibia in females, slightly basal to middle in males) probably representing apex of otherwise undefined basitibial plate; apex of pygidial plate of female not upturned 2
- 2(1). Costal edge of marginal cell distinctly shorter than stigma (as in Fig. 48-6a); first recurrent vein, if present, entering first submarginal cell near middle; vein M+Cu between basal vein (M) and vein m-cu of forewing longer than basal vein; claws of female with small preapical tooth 3
- Costal edge of marginal cell equal to or slightly longer than stigma; first recurrent vein, if present, entering first submarginal cell near apex or in distal one-fifth; vein M+Cu between basal vein (M) and vein m-cu of forewing about one-third as long as basal vein; claws of female simple 4
- 3(2). S7 of male with small to moderate-sized, laterally directed, apical lobes and broadly expanded, triangular basolateral apodemes; face of male with minute pit (“glandular opening”) above and lateral to antennal base *E. (Quasihesma)*
- S7 of males almost without small posteriorly directed apical lobes or with small ones, basolateral apodemes normal, almost straplike form; face of male lacking pit above and lateral to antennal base *E. (Euryglossella)*
- 4(2). Labrum of female without median apical spine; second submarginal cell usually not shaped as in *Pachyprosopis* *E. (Euryglossina* s. str.)
- Labrum of female with median apical spine; second submarginal cell shaped like that of *Pachyprosopis* (as in Fig. 48-3b) *E. (Pachyprosopina)*

Euryglossina / Subgenus *Euryglossella* Cockerell

Euryglossella Cockerell, 1910c: 263. Type species: *Euryglossella minima* Cockerell, 1910, monobasic.

Zalygus Cockerell, 1929b: 321. Type species: *Zalygus cornutus* Cockerell, 1929, monobasic.

This taxon was given generic rank separate from *Euryglossina* by Exley (1968b) largely because of the strong spine on the labrum of females. The presence of such a spine in a bee that appears to be very like *Euryglossina* s. str., i.e., the subgenus *Pachyprosopina*, suggests that this character appears in rather different groups and may be independently lost or gained. Moreover, a species of the

ple. Michener (1965b) and Exley (1975b) provided illustrations of male genitalia and hidden sterna.

■ *Hyphesma* occurs in all Australian states, including Tasmania. The seven known species were revised by Exley (1975b) and listed by Cardale (1993).

Most of the floral records are for Myrtaceae. Exley (1975b) described a nest in the soil.

Genus *Melittosmithia* Schulz

Smithia Vachal, 1897: 63 (not Milne-Edwards, 1851). Type species: *Scapter carinata* Smith, 1862, by designation of Cockerell, 1910b: 358.

Melittosmithia Schulz, 1906: 244, replacement for *Smithia* Vachal, 1897. Type species: *Scapter carinata* Smith, 1862, by designation of Cockerell, 1910b: 358.

The bees tentatively segregated from *Euhesma* and placed in *Melittosmithia* differ from *Euhesma* in lacking a subapical tooth on the upper mandibular margin of the female, the mandible thus simple (male unknown), and in having a thin, sharp, longitudinal, median clypeal carina. The inner hind tibial spur is ciliate or finely pectinate, an unusual feature in those *Euhesma* having the rather large size of *Melittosmithia*. Body length varies from 6.5 to 9.0 mm. The body is black without yellow markings, with the metasoma partly to wholly red. *Euhesma* could reasonably be synonymized into *Melittosmithia*, but until males are known, it seems best to retain *Melittosmithia* and *Euhesma* as genera. The type species of the two are very different.

■ *Melittosmithia* is found in New South Wales, Victoria, and South Australia. Four specific names, as listed by Cardale (1993), have been applied in this genus. Cockerell (1926b) gave a key to the species.

Genus *Pachyprosopis* Perkins

This genus is usually easily recognized by the venational characters indicated in the first two couplets of the key to genera. Exceptions exist, however, and are discussed below. The body is nonmetallic except for the females of *Pachyprosopis haematostoma* Cockerell, which are blue. The metasoma is sometimes red, and the head and body sometimes have yellow markings or are largely yellow. The head and thorax are finely roughened between small and often sparse punctures. The labrum has a strong apical spine except for *P. (Pachyprosopis) cornuta* Exley. The facial foveae are linear, short, and inconspicuous in some males. The flagellum is short, the middle segments being broader than long. Male genitalia and other structures were illustrated by Michener (1965b) and Exley (1972, 1976a).

Even in the unusual shape of the second submarginal cell, a character also found in *Hyphesma*, there are problems. In *Euryglossula fulroni* (Cockerell) the cell is sometimes shaped a little like that of *Pachyprosopis*, as it is in some specimens of *Euryglossina*. More specifically, in *Euryglossina narifera* (Cockerell) the second submarginal cell is as in *Pachyprosopis*. The same is true of some specimens of *E. hypochroma* Cockerell (see illustration in Exley, 1968d). Because they lack a labral spine, have very short antennae, and have eyes more sharply produced mesad above the mandibles in females, as well as because of their general

form and maculation, such species are included in *Euryglossina*. Presumably, their *Pachyprosopis*-like feature is a result of convergence. The relationship of *Pachyprosopis* to *Euryglossina*, however, is close, as shown, for example, by the head shape. In both *Pachyprosopis* and *Euryglossina* (Fig. 48-5b) the clypeus (or at least the lower part of it, as seen in profile), is bent posteriorly, so that the face is strongly convex. A discussion of variability in *Pachyprosopis* and its relations to other genera was given by Michener (1965b).

Pachyprosopis visits primarily the flowers of Myrtaceae. Nests have been found in abandoned beetle burrows in wood [*P. (Pachyprosopis) haematostoma* Cockerell] and in "termite soil" at the bases of, or in, hollow trees [*P. (Parapachyprosopis) angophorae* Cockerell and *indicans* Cockerell] (Houston, 1969; Exley, 1972).

Pachyprosopis was revised by Exley (1972), with additions to the keys by Exley (1976a).

Key to the Subgenera of *Pachyprosopis* (Females)

1. Facial fovea with upper end on level of, or below, upper end of eye, nearer eye margin than to lateral ocellus, not curved mesad; margin of basitibial plate represented by tubercles that extend beyond middle of tibia; clypeus more than three times as wide as median length *P. (Pachyprosopis) s. str.*
- Facial fovea with upper end above level of upper end of eye [except in *Pachyprosopis (Pachyprosopula) xanthodonta* (Cockerell)], nearer to lateral ocellus than to eye margin and curved mesad toward ocellus; margin of basitibial plate variable but not reaching middle of tibia; clypeus commonly less than three times as wide as median length 2
- 2(1). Thorax and metasoma lacking yellow areas; basitibial plate demarcated by tubercles in addition to carinae *P. (Parapachyprosopis)*
- Thorax and metasoma with yellow areas; basitibial plate usually demarcated by carinae (with one tubercle in *Pachyprosopis flavicauda* Cockerell) *P. (Pachyprosopula)*

Key to the Subgenera of *Pachyprosopis* (Males)

1. Facial fovea adjacent to concavity in inner orbit of eye, thus low on face and far from summit of eye *P. (Pachyprosopis) s. str.*
- Facial fovea adjacent to upper one-third of eye, above concavity of inner orbit, and commonly approaching summit of eye 2
- 2(1). S8 with small, hairy apical lobe on each side of median apical process; S7 with long hairs on mesodistal margin of lateral apical lobe; scutellum not yellow *P. (Parapachyprosopis)*
- S8 without lateroapical lobe; S7 usually without long hairs; scutellum yellow *P. (Pachyprosopula)*

Pachyprosopis / Subgenus *Pachyprosopis* Perkins s. str.

Pachyprosopis Perkins, 1908: 29. Type species: *Pachyprosopis mirabilis* Perkins, 1908, monobasic.

This subgenus is interpreted more narrowly here than by Michener (1965b), who included under *Pachyprosopis* s. str. the species here placed in *Parapachyprosopis*. Al-

ear and nearly parallel with the eye margin, neither end being bent mesad.

■ This genus occurs in dry areas in South Australia, Northern Territory, and Western Australia. The two species were revised by Exley (1996). They visit flowers of Myrtaceae.

Genus *Xanthesma* Michener

Two names, *Xanthesma* and *Xenohesma*, were published simultaneously for elements now included in this genus. Michener (2000), as first revisor, selected *Xanthesma* as the generic name.

This is a genus of minute to moderate-sized (2.9–7.8 mm body length), often largely yellow bees. Michener (1965b) included some of the species in his then more restricted genus *Xanthesma*, while placing others in *Euryglossa sensu lato*. It now seems that the relationships are best shown by broadening the application of the name *Xanthesma* as indicated below. Of the characters listed in the key to genera, the reduced or absent preapical mandibular tooth, the lack of subantennal sutures, the usually simple female claws, and perhaps the others are probable synapomorphies that distinguish *Xanthesma* from *Eubhesma*, the only part of the old (Michener, 1965b) genus *Euryglossa* to which *Xanthesma* may be closely related.

Xanthesma has been found in all Australian states except Tasmania, and is especially abundant in arid areas. So far as is known, all species visit flowers of Myrtaceae.

The subgenera listed below have not hitherto been assigned to a single genus. They are not always easy to separate, however, and one sometimes cannot place a species in its subgenus without having both sexes, as will become obvious with attempts to use the key.

Key to the Subgenera of *Xanthesma*

1. First recurrent vein entering apex of first submarginal cell; stigma as long as or longer than costal edge of marginal cell *X. (Argohesma)*
- First recurrent vein entering base of second submarginal cell or meeting first submarginal crossvein; stigma shorter than costal edge of marginal cell 2
- 2(1). Eyes of male strongly converging above, upper end of eye less than ocellar diameter from lateral ocellus *X. (Xenohesma)*
- Eyes of male subparallel or converging below, upper end of eye more than ocellar diameter from lateral ocellus 3
- 3(2). Mandible of female with weak preapical tooth; male without vertical groove in paraocular area; front coxa of female with several distinctive bristles on apex mesal to base of trochanter *X. (Chaetohesma)*
- Mandible of female simple; many males with vertical groove in paraocular area midway between antennal base and eye, and tuft of hair at lower end of groove (Fig. 47-2e); front coxa of female without such bristles *X. (Xanthesma s. str.)*

Xanthesma / Subgenus *Argohesma* Exley

Argohesma Exley, 1969c: 528. Type species: *Argohesma eremica* Exley, 1969, by original designation.

Except for the weak characters of wing venation listed in the first couplet of the key to subgenera, this subgenus agrees in most features with *Xanthesma* s. str. An additional character is that the claws of males are simple, whereas those of *Xanthesma* s. str. are cleft. (Claws of females are simple in both subgenera.) The body is largely yellow to largely black; its length ranges from 2.4 to 3.7 mm. Illustrations of male genitalia and other structures were provided by Exley (1969c, 1974c).

■ The subgenus is recorded from all Australian states except New South Wales and Tasmania, but is abundant chiefly in Western Australia. The eight known species were listed by Cardale (1993). Exley (1969c) described and revised the genus; Exley (1974c) gave a new key.

Xanthesma / Subgenus *Chaetohesma* Exley

Chaetohesma Exley, 1978a: 373. Type species: *Chaetohesma tuberculata* Exley, 1978, by original designation.

In addition to the key characters, the following are of interest: The fore basitarsus of the female has a brush of dense setae, the setae short in *Xanthesma isae* (Exley). The claws are usually simple in females, cleft in males, but in *X. infuscata* (Exley) they are simple in both sexes, whereas in females of *X. baringa* (Exley), *foveolata* (Exley), *levis* (Exley), and *striolata* (Exley), the claws are toothed, as in many *Eubhesma*. The size is small (body length 3.5–5.3 mm). Male genitalia and other structures were illustrated by Exley (1978a).

■ This subgenus is widespread in the xeric areas of Australia, mostly in the northern half of the continent; it has not been found in Victoria or South Australia. The ten described species were named and revised by Exley (1978a) and listed by Cardale (1993).

Xanthesma / Subgenus *Xanthesma* Michener s. str.

Xanthesma Michener, 1965b: 97. Type species: *Euryglossa furcifera* Cockerell, 1913, by original designation.

This is a subgenus of minute (body length 2.9–5.0 mm), largely yellow bees. Its characters are indicated in the key to subgenera. Its similarity to *Argohesma* is discussed under that subgenus. A relationship to *Xenohesma* is indicated by the presence in males of most species of a vertical groove in the space between the eye and the antenna, the lower end of the groove bearing a tuft of hairs (Fig. 48-2e). Illustrations of male genitalia and hidden sterna were published by Michener (1965b) and Exley (1969d, 1974c). Comments on the subgeneric characters were included in Exley (1978b).

■ Although known from all Australian states except Tasmania and Victoria, this subgenus seems to be particularly abundant in the north and west. The 13 named species were revised by Exley (1969d); a new key was provided by Exley (1974c). The species were listed by Cardale (1993).

Nests of the type species, *X. furcifera* (Cockerell), have been found in the ground (Exley, 1969d; Houston, 1969) and were illustrated by both authors.

fine or velvety hairs, or, in the Chilean genera *Euherbstia* and *Orphana*, the fovea is absent. In female Panurginae the fovea is nearly always present (absent in *Melitturga*) and nearly hairless, as in colletids such as the Euryglossinae and Hylaeinae. This is presumed to be the plesiomorphic condition.

In most Panurginae as well as most other aculeate Hymenoptera of both sexes, on an area of the inner surface of the hind tibia there are many, usually short hairs of uniform length with blunt, capitate or bifid apices. These are the keirotichia (Michener, 1981a); presumably their function is cleaning the wings. They are replaced in females of Alocandreninae and Andreninae by long hairs similar in aspect and, probably, function to the scopal hairs on the outer side of the hind tibia. In *Andrena* (*Melittoides*) (Andreninae) they are long but still have minutely bifid apices. Reanalysis of andrenid phylogeny with more taxa and appropriate outgroups might show the loss of short keirotichia as a synapomorphy of Andreninae (together with Alocandreninae).

A character that supports the similarity of *Euherbstia* and *Orphana* to the Oxaeinae is the unmodified S7 of the male, its form in *Euherbstia* not very different from that of S6 (Fig. 51-6d, h). This could be a plesiomorphy, a significant synapomorphy, or convergence perhaps resulting from transfer of developmental control from more anterior sterna to S7.

Andrenidae occur on all continents except Australia. They are also almost absent from the tropical Asian region. In the north temperate areas, the genus *Andrena* is ubiquitous. In sub-Saharan Africa there are only a few genera and species. In the Western Hemisphere, however, especially in the temperate and xeric parts of both North and South America, there are many andrenid genera and species; in the moist tropics the numbers are small.

All species of Andrenidae nest in the soil, making their own burrows and cells, one or a short series at the end of each lateral burrow. Except in some Panurginae whose cells are unlined, the cells are lined with a shiny secretion. In the Oxaeinae the provisions are viscous and fill the

lower ends of vertical cells. In other Andrenidae the provisions are firm and have the form of a sphere or flattened sphere in each cell. The lower surface of the usually horizontal cell (but slanting to nearly vertical in *Euherbstia*, Rozen, 1993b) is flatter than the upper surface in the Andreninae, the cell thus bilaterally symmetrical around a vertical plane, like the cells of Halictidae and Colletinae such as *Leioproctus*. In Panurginae and Oxaeinae this is not so, the cell being similarly shaped on all surfaces; or in some Panurginae the lower surface may be slightly flatter than the upper. The egg is laid on top of the food mass. No andrenid spins a cocoon. (Nests of Alocandreninae are unknown.)

Key to the Subfamilies of the Andrenidae

1. Stigma essentially absent; marginal cell over seven times as long as broad and only half as wide as widest submarginal cell (Fig. 60-2a); mentum absent or fused to flat lorum; proboscoidal lobe absent; first flagellar segment as long as scape (Western Hemisphere) Oxaeinae (Sec. 60)
- Stigma present; marginal cell shorter and broader, about as wide as widest submarginal cell; mentum and lorum both present, forming proboscoidal lobe; first flagellar segment usually shorter than scape 2
- 2(1). Apex of marginal cell pointed or narrowly rounded on or near wing margin (Fig. 51-2) (facial fovea not or weakly evident in male, in female, when present, slightly depressed, covered with short hairs; gonobase of male distinct and large, reduced to narrow ring or almost absent in *Megandrena*) Andreninae (Sec. 51)
- Apex of marginal cell truncate, sometimes obliquely so, cell thus pointed well away from wing margin (Figs. 50-1f, 53-1) 3
- 3(2). Facial fovea of both sexes a distinct deep pocket with short hairs (Fig. 50-1a, b); gonobase of male distinct and large (Fig. 50-1c-e) (Peru) Alocandreninae (Sec. 50)
- Facial fovea hairless and shining, often absent in males, rarely also in females (*Melitturga*); gonobase of male absent or nearly so Panurginae (Sec. 52)

51. Subfamily Andreninae

Some of the features of this subfamily are explained above in the discussion of the family Andrenidae. Andrenines are small to rather large, somewhat more hairy than most Panurginae (Fig. 49-1), and when yellow integumental markings are present, they are limited to the faces of males and, uncommonly, of females. Most have three submarginal cells (Fig. 51-2), but some species and even certain subgenera of *Andrena* have two, the second rather long, indicating that the second transverse submarginal vein has been lost.

The subfamily Andreninae could reasonably be divided into two tribes, thus: (1) The Andrenini for the genera *Andrena*, *Ancylandrena*, and *Megandrena*, characterized by the broad, velvety facial foveae of the females and found in the holarctic region, ranging south to South Africa and to Panama. (2) The Euerbstiini for the genera *Euerbstia* and *Orphana*, characterized by lack of facial foveae, and found in Chile. I have decided not to formalize these tribes for this work.

As indicated above, the Andreninae are primarily holarctic, but occur also in eastern and southern Africa, in mountains in the oriental region south as far as the Malay peninsula and southern India, and, in the Western Hemisphere, south to Panama, with disjunct forms in Chile. In most parts of the world the keys to genera are unnecessary because only one genus of the subfamily, *Andrena*, is found there. The other genera are found in xeric regions of the southwestern USA, northwestern Mexico, and Chile.

Key to the Genera of the Andreninae (Females)

- 1. Facial fovea depressed, velvety (Fig. 51-1a) 2
 - Facial fovea absent (or vaguely indicated by color or texture of cuticle) 4
- 2(1). Hairs of hind trochanter rather dense, short, the longer ones simple, not much curved; anterior surface of T1 broadly concave, much longer than dorsal surface of T1 (Fig. 51-1c, d) (southwestern North America) *Ancylandrena*
 - Some hairs of hind trochanter long, curved distad, plumose, forming a floccus (Fig. 51-1b) closing basal end of femoral corbicula; anterior surface of T1 with smaller concavity or groove, surface shorter than to slightly longer than dorsal surface of T1 (Fig. 51-1e, f)..... 3
- 3(2). Hind basitarsus more than half as long as hind tibia; stigma often broader than prestigma (measured to wing margin), margins usually converging basad from vein r (Fig. 51-2a, b) *Andrena*
 - Hind basitarsus about half as long as hind tibia; stigma about as wide as prestigma (measured to wing margin), margins parallel or nearly so from vein r to base of stigma (Fig. 51-2c) (southwestern USA) *Megandrena*
- 4(1). Claws each with the usual large inner tooth; inner subantennal suture much shorter than diameter of antennal socket and apparently not converging below toward outer suture (Chile) *Orphana*
 - Claws each with minute inner tooth; inner subantennal suture about as long as diameter of antennal socket and

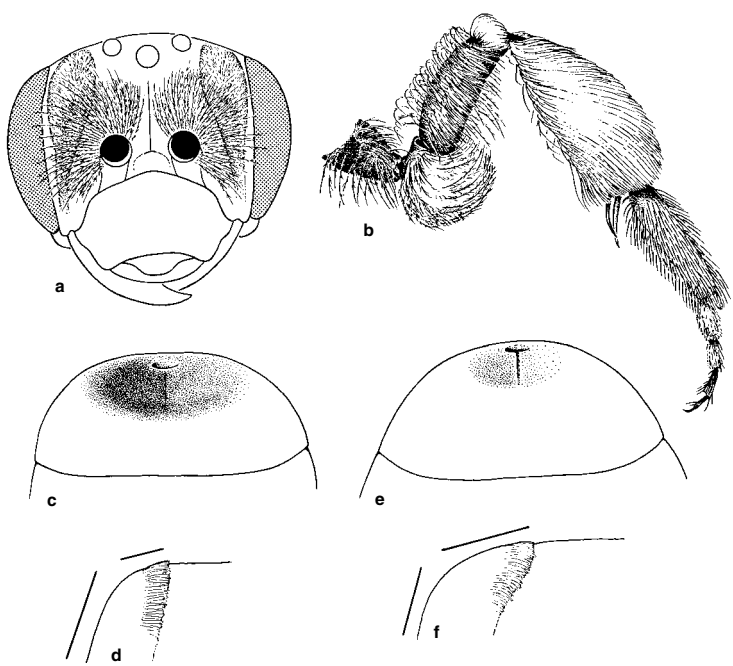


Figure 51-1. Andreninae. **a**, Face of *Andrena mariae* Robertson, female; **b**, Hind leg of *Andrena* sp., female, showing large floccus on trochanter and other scopal hairs on femur and tibia; **c**, **d**, T1 of *Ancylandrena larreae* Timberlake in dorsal and lateral views, with lines showing lengths of dorsal and anterior surfaces; **e**, **f**, Same, of *Megandrena enceliae* (Cockerell). From Michener, McGinley, and Danforth, 1994.

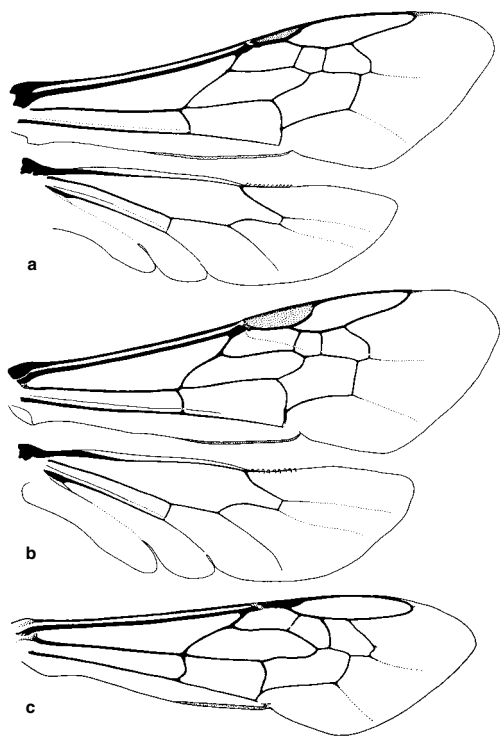


Figure 51-2. Wings of Andreninae. **a**, *Andrena (Callandrena) accepta* Viereck; **b**, *Andrena illinoensis* Robertson; **c**, *Megandrena enceliae* (Cockerell). **c**, from Michener, McGinley, and Danforth, 1994.

converging below toward outer suture, subantennal area thus having only short margin on epistomal suture (Chile) *Euherbstia*

Key to the Genera of the Andreninae (Males)

- 1. Gonobase a narrow ring or essentially absent (Fig. 51-7a, b); mandible simple or with weak preapical shoulder on upper margin (southwestern USA) *Megandrena*
— Gonobase with broad dorsal surface; mandible with preapical tooth on upper margin (except in *Euherbstia* from Chile) 2
- 2(1). Anterior surface of T1 largely convex, the concavity a median, longitudinal groove or depression, this surface shorter than to slightly longer than distance from its upper end to apex of T1; hind basitarsus five or more times as long as wide *Andrena*
— Anterior surface of T1 largely flat (in *Euherbstia*) or concave, the concavity a median, longitudinal line or groove, this surface usually longer than distance from its upper end to apex of T1; hind basitarsus less than five times as long as wide 3
- 3(2). Mandible simple; inner subantennal suture converging below toward outer suture, so that subantennal area has only short margin on epistomal suture (Chile) *Euherbstia*
— Mandible with preapical tooth on upper margin; inner subantennal suture not converging strongly below toward outer suture 4

- 4(3). S7 a broad plate with large median apical process (anterolateral processes partly hairy, not comparable to anterolateral apodemes, Fig. 51-6h); epistomal suture separated from antennal socket by much less than diameter of socket (Chile) *Orphana*
— S7 with a relatively small body, large anterolateral apodemes, and two small apical lobes (Fig. 51-3d); epistomal suture separated from antennal socket by about diameter of socket (Fig. 51-3e) (southwestern North America) *Ancylandrena*

Genus *Ancylandrena* Cockerell

Andrena (Ancylandrena) Cockerell, 1930d: 5. Type species: *Andrena heterodoxa* Cockerell, 1930 (preoccupied) = *A. atoposoma* Cockerell, 1934, monobasic.

This genus consists of hairy, fast-flying *Andrena*-like bees 8 to 15 mm long. The integument is largely black, usually including the male clypeus, but the lower paraocular area of males is partly yellow (Fig. 51-3e). In both this genus and *Megandrena* the tibial and basitarsal scopa includes long hairs and therefore seems less compact than that of *Andrena*; the center of the basitibial plate of the female in both genera is covered by a patch of dense, short, erect black hairs. Male genitalia and other structures were illustrated by Zavortink (1974); see Figure 51-3.

■ *Ancylandrena* occurs in xeric parts of California, Nevada, and Arizona, USA, and in Baja California Norte and Sonora, Mexico. Four species were revised by Zavortink (1974); one additional species has been described.

The nest resembles that of *Andrena* with extremely long horizontal lateral burrows each leading to one cell. The cell wall is extremely thinly covered with a secreted film (Rozen, 1992a).

Genus *Andrena* Fabricius

This well-known genus (Fig. 49-1, Pl. 3) is characterized by the large, velvety facial foveae of the females (in which it resembles *Ancylandrena* and *Megandrena*; the strong femoral scopa, that of the trochanter long, curved distad (Fig. 51-1b), and closing the base of the femoral corbicula (thus resembling *Megandrena*); and the characters of T1 and the hind basitarsus listed in the key to genera. The male genitalia are usually recognizable by the dorsal preapical lobe of the gonocoxite emphasized in Figure 51-4a but see also Figure 51-5a, a lobe that is not found in similar form in other genera. S7 of the male is a simple, rather short plate with a short, bilobed apical process or with no apical process (Fig. 51-5e). The stigma is typically broader than that of the other genera of the subfamily (Fig. 51-2b), although it is slender in some groups of *Andrena* such as the subgenus *Callandrena* and especially *Melittoides* (Fig. 51-2a). Illustrations of many structures, including male genitalia and hidden sterna, were published by Pittioni (1948a, b), Popov (1949c, 1958b), Mitchell (1960), Hirashima (1962-1966a), Warncke (1965), Thorp (1969a), Hirashima and Tadauchi (1975), Svensson and Tengö (1976), Donovan (1977); Wu (1982b, d), Tadauchi and Hirashima (1983, 1984a, b, 1988), Tadauchi (1985), Dylewska (1987), and Tadauchi, Hirashima, and Matsumura (1987), and in numerous papers by LaBerge and Ribble and coauthors.

(perhaps a dozen) but have never received careful, comparative study. They look much like palearctic species and subgenera, and there may be no distinctive sub-Saharan subgenera; at least none is now recognized.

All *Andrena* species nest in the ground. A few are communal, but most make individual nests, sometimes in large aggregations. Probably all communal species are sometimes also solitary, but it seems that most nests of such species are inhabited by several to many females. Most reports are of less than 40 females working in a nest, but Paxton and Tengö (1996) reported nests of *A. jacobae* Perkins in which up to 594 females shared a single nest entrance. Moreover, such nests may be perennial, that is, used for several years; Osgood (1989) reports one nest of *A. crataegi* Robertson with four entrances, its burrows probably enlarged by use, although most nests have only one entrance.

The cells are usually at the ends of lateral burrows radiating from the main burrow, but sometimes two or more cells are in series in a single lateral, as in the case of *A. labialis* (Kirby); see Radchenko (1981). The cells are lined with waxlike material and the pollen mass is smooth and more or less spherical (see photographs in Radchenko, 1981); an apparent exception is *A. viburnella* Graenicher, which, according to Stephen (1966), fills the bottom of a cell with pollen and places the egg in a large depression in the mass. These observations need to be verified, since they differ greatly from the usual *Andrena* behavior. Most species produce only one generation per year; they mature and then hibernate as adults in the cells, the two sexes emerging at more or less the same time the following year. It may be that autumnal species overwinter as prepupae. Such behavior has been observed for two species of the largely autumnal subgenus *Callandrena*, and *A. (C.) rudbeckiae* Robertson in Texas has a mixed strategy, some overwintering as adults, others as prepupae, according to Neff and Simpson (1997). A few species produce two generations per year. Michener and Rettenmeyer (1956), Youssef and Bohart (1968), and Schönitzer and Klinskik (1990) listed and summarized papers on the nesting biology of *Andrena*, but there are numerous other accounts of individual species, for example, Malyshev (1926), Hirashima (1962), Matsumura (1970), Davis and LaBerge (1975), Schrader and LaBerge (1978), Radchenko (1981), Gebhardt and Röhr (1987), Neff and Simpson (1997), and Maeta, Fujiwara, and Kitamura (2004).

Although many species of *Andrena* are polylectic, many others are strictly oligolectic. Some, such as *A. (Iomelissa) violae* Robertson, seem to be morphologically adapted to particular flowers, in this case employing a long glossa for the flowers of *Viola*. Others show little obvious morphological adaptation, but are nonetheless restricted in pollen collecting. An example is the whole subgenus *Onagrاندrena* (see Linsley et al., 1973), which collects pollen from Onagraceae.

Some of the subgenera listed below are similar, and their validity is not evaluated here; the keys provided are essentially as constructed by others. Keys to subgenera have been provided by Hedicke (1933), Hirashima (1952), and Warncke (1968) for palearctic subgenera and by Lanham (1949) and LaBerge (1964, 1986) for nearctic subgenera.

Some special terminology used in *Andrena* is as follows:

The **facial quadrangle** is measured by the width between the eyes at the level of the lower margins of the antennal sockets, and by the length from the apex of the clypeus to the lower margin of the median ocellus. This term is used in the key to American subgenera.

The **basal area of the labrum** is the elevated part of the labrum, often called the "process of the labrum" in *Andrena* (see Sec. 10).

The **subgenal coronet** is a row of bristles or specialized hairs arising from a ridge on the paramandibular process of the hypostomal area, curving behind the mandibular base. The lateral part of this structure is concordant with the lateral extremity of the hypostomal carina (see Sec. 10).

The **flocus** or **flocculus** on the underside of the hind trochanter of females is a mass of long, branched hairs, curled distad, that closes the base of the femoral corbicula. When all the hairs on the underside of the trochanter are long and curled, the flocus is said to be **complete** (or perfect). When the hairs of the basal half of the trochanter are nearly straight and not particularly long, only the more distal hairs being long and curled, the flocus is considered **incomplete** (or imperfect).

Keys for the subgenera of three regions are provided below; the regions are North and Central America, the western palearctic region, and Japan.

Key to the Subgenera of *Andrena* of North and Central America (Females)

(Modified from LaBerge, 1986)

1. Inner hind tibial spur bent and broadened near base; tibial scopal hairs simple 2
- Inner hind tibial spur neither bent nor broadened near base, or *ifso*, then tibial scopal hairs plumose and spur only slightly broadened 4
- 2(1). Propodeal triangle coarsely sculptured *A. (Plastandrena)*
- Propodeal triangle finely sculptured 3
- 3(2). Thoracic dorsum with hairs short, forming a dense mat *A. (Aporandrena)*
- Thoracic dorsum with normal, long, plumose hairs not at all forming a mat obscuring surface *A. (Charitandrena)*
- 4(1). Middle and hind tibial spurs unusually thick, their apices abruptly hooked (terga without apical pale bands; facial fovea narrow) *A. (Euandrena)* (in part)
- Middle and hind tibial spurs long and slender, their apices usually evenly curved 5
- 5(4). Inner hind tibial spur rather abruptly bent and slightly twisted at about one-third of its length from apex (T2-T4 with conspicuous, usually medially interrupted, white fasciae) *A. (Leucandrena)* (in part)
- Inner hind tibial spur long, slender, not bent nor markedly twisted at apical third 6
- 6(5). Facial quadrangle broader than long; propodeal corbicula poorly formed, lacking long internal hairs, dorsal hairs extremely short, not flexed down over corbicular area (terga without pale apical fasciae) *A. (Oligandrena)*
- Facial quadrangle usually at least as long as broad and often slightly longer; propodeal corbicula with at least long, flexed dorsal hairs 7

- 7(6). Galeal blade as long as clypeus or slightly longer; maxillary and/or labial palpi greatly elongate (T2-T4 with pale apical fasciae, often weak) 8
 —. Galeal blade not as long as clypeus; maxillary and labial palpi not greatly elongate 10
- 8(7). Labial palpus greatly elongate, segments 1 plus 2 three to five times as long as segments 3 plus 4 and flattened; maxillary palpus of normal length, half as long as galeal blade; basal area of labrum not raised much above general level of surface *A. (Callandrena)* (in part)
 —. Labial palpus elongate, but first two segments not unusually long nor much flattened; maxillary palpus elongate, more than half as long as galeal blade; basal area of labrum distinctly raised above general level of surface 9
- 9(8). Maxillary palpus with second segment at least 1.5 times as long as first; stipes distinctly narrowed medially and tapering apically, the apical third thus less than half as broad as basal third, with weak, plumose hairs
 *A. (Iomelissa)*
 —. Maxillary palpus with second segment about as long as first; stipes linear, tapering from base to apex, with abundant, long, spinelike hairs *A. (Erandrena)*
- 10(7). Pronotum without dorsolateral angle, smoothly rounded posteriorly from one posterior pronotal lobe to the other, or *if* weak angle present, then without trace of lateral ridge or elevation 11
 —. Pronotum with dorsolateral angle on posterior margin just above and in front of pronotal lobe, usually with a ridge or elevation extending down side of pronotum from dorsolateral angle, often with depressed or flattened area posterior to this ridge; angle and ridge occasionally quite weak and rarely only that part of ridge immediately above front coxa present 13
- 11(10). Propodeal triangle coarsely sculptured, often bounded posteriorly by a strong transverse carina, or *if* finely sculptured, then with longitudinal rugae at least basally and with transverse carina at apex 12
 —. Propodeal triangle usually finely sculptured, usually tessellate, never with strong transverse posterior carina, or *if* coarsely sculptured, then without longitudinal basal rugae and/or without transverse apical carina 45
- 12(11). T2-T4 with depressed marginal zones less than half length of exposed part of each tergum medially
 *A. (Scapteropsis)*
 —. T2-T4 with depressed marginal zones half or more length of exposed part of each tergum medially
 *A. (Trachandrena)*
- 13(10). Pronotum laterally with deeply impressed groove cutting diagonally up and forward from pronotal spiracle to near midline anteriorly, this groove crossing and strongly depressing ridge extending down from dorsolateral angle; T2-T4 without apical pale fasciae or these weak and broadly interrupted; genal area broader than eye in side view; ocelloccipital distance about one and one-half to two and one-half ocellar diameters
 *A. (Tylandrena)*
 —. Pronotum without lateral diagonal groove, or groove not deeply impressed and not depressing dorsoventral ridge, or *if* diagonal groove present and depressing ridge, then terga with distinct pale apical fasciae; genal area often narrow; ocelloccipital distance often one ocellar diameter or less 14
- 14(13). Submarginal cells two 15
 —. Submarginal cells three 16
- 15(14). Propodeal triangle usually relatively coarsely sculptured; propodeal corbícula incomplete anteriorly, with internal hairs; integument usually metallic
 *A. (Diandrena)* (in part)
 —. Propodeal triangle finely tessellate; propodeal corbícula complete anteriorly, with few or no internal hairs; integument black or in part red, not metallic
 *A. (Parandrena)*
- 16(14). Propodeum with dorsal surface poorly defined, sloping evenly from base to apex, with complete lateral carina separating dorsoposterior and lateral surfaces; clypeus usually very short, produced beyond lower ends of eyes by less than one-fourth median clypeal length
 *A. (Hesperandrena)* (in part)
 —. Propodeum with well-defined dorsal surface and without complete lateral carina; clypeus normal, usually produced beyond lower ends of eyes by more than one-fourth median clypeal length 17
- 17(16). Tibial scopal hairs highly plumose throughout 18
 —. Tibial scopal hairs simple or largely so, occasionally weakly plumose throughout 22
- 18(17). Subgenal coronet absent; vestiture largely black or dark brown (Mexico) *A. (Celetandrena)*
 —. Subgenal coronet present; vestiture various but usually not all or mostly dark 19
- 19(18). Scopal hairs long and rather weak, with abundant short curved branches in outer half or more; maxillary palpal segments all exceptionally long
 *A. (Ptilandrena)* (in part)
 —. Scopal hairs relatively short, with short stiff branches; maxillary palpal segments not all elongate 20
- 20(19). Propodeal corbícula complete anteriorly, with few or no internal hairs; first flagellar segment scarcely, if any, longer than second segment
 *A. (Archandrena)* (in part)
 —. Propodeal corbícula incomplete anteriorly, with abundant long, simple internal hairs; first flagellar segment about 1.5 times as long as second segment or more 21
- 21(20). Scopal hairs entirely or mostly dark brown to black; pronotal dorsolateral ridge close to pronotal lobe; first recurrent vein usually meeting second submarginal cell near middle of cell *A. (Ptilandrena)* (in part)
 —. Scopal hairs pale ochraceous; pronotal ridge not distinct, or well separated from pronotal lobe; first recurrent vein meeting second submarginal cell at about two-thirds of its length from base of cell *A. (Belandrena)* (in part)
- 22(17). Galeal blade with abundant short, hooked hairs; body usually 11 mm long or more (integument usually metallic blue or black) *A. (Scolandrena)*
 —. Galeal blade without hooked hairs; often small bees, less than 10 mm in length 23
- 23(22). Frons below ocelli tessellate, without rugulae, or the rugulae sparse and extremely fine
 *A. (Derandrena)* (in part)
 —. Frons below ocelli with parallel longitudinal rugulae, in terrugal spaces narrow, weakly tessellate or shagreened 24
- 24(23). Facial fovea extremely elongate, almost reaching vertex above, occupying most of paracocular space below;

- ocelloccipital distance half an ocellar diameter or less; terga impunctate *A. (Oxyandrena)*
- Facial fovea shorter than above; ocelloccipital distance often more than half an ocellar diameter; terga often punctate 25
- 25(24). Hypostomal carina with longitudinal part longer than lateral part, lamellate, as high as two-thirds length of last labial palpal segment (clypeus with free apical margin elongate, moderately upturned; T2-T4 with pale apical fasciae interrupted medially) *A. (Geissandrena)*
- Hypostomal carina either with longitudinal part no longer than lateral part or carinate, not as high as half length of last labial palpal segment 26
- 26(25). Facial quadrangle considerably longer than broad 27
- Facial quadrangle at least almost as broad as long 28
- 27(26). Malar area more than half as long as broad; pleural hairs black to dark brown *A. (Dactylandrena)* (in part)
- Malar area about half as long as broad; pleural hairs pale ochraceous to white *A. (Conandrena)*
- 28(26). Middle basitarsus expanded medially (T2-T4 and usually T1 with complete apical pale fasciae of hairs with close-set, short barbs, giving them a dull appearance; basal area of labrum strongly bidentate and reflexed) *A. (Cnemidandrena)*
- Middle basitarsus not expanded medially, parallel-sided 29
- 29(28). Median third of clypeus impunctate, shiny; tibial scopal hairs weakly plumose throughout; scutellum shiny, unshagreened at least medially *A. (Larandrena)*
- Median third of clypeus punctate or dully by dense shagreening or tessellation or both, sometimes with impunctate and shiny area occupying much less than one-third of clypeus; tibial scopal hairs usually simple, at least medially; scutellum often opaque, dully by fine tessellation or shagreening 30
- 30(29). First flagellar segment only slightly longer than second, about as long as third segment; propodeal triangle with distinct longitudinal rugulae ending posteriorly in irregularly reticulate rugulae (propodeal corbícula incomplete anteriorly, with abundant internal hairs) *A. (Xiphandrena)*
- First flagellar segment considerably longer than either second or third; propodeal triangle with or without longitudinal rugulae, often with finely reticular rugulae forming small areolae 31
- 31(30). Propodeal triangle with coarse longitudinal rugulae; metasomal terga distinctly punctate *A. (Rhapandrena)*
- Propodeal triangle finely tessellate or with irregular anastomosing rugulae; metasomal terga often impunctate or only weakly punctate 32
- 32(31). Scutum with extremely fine longitudinal rugulae visible at an angle to light source *A. (Nemandrena)* (in part)
- Scutum variously shagreened, tessellate, or shiny, but without fine longitudinal rugulae 33
- 33(32). Genal area often with strong posterior carina; scutellum shiny, unshagreened; propodeal triangle with rather coarse irregular sculpturing; clypeus with apical margin usually broad, distinctly reflexed or turned upward *A. (Gonandrena)*
- Genal area without posterior carina; scutellum usually shagreened or tessellate, but *if* shiny, then propodeal triangle finely granular or tessellate; clypeal apical margin often narrow, not reflexed upward 34
- 34(33). Malar area extremely short, linear, its length one-sixth to one-tenth of its width; dorsolateral angle of pronotum weak; basal area of labrum simple, as long as broad or longer, strap-shaped or U-shaped with sides diverging slightly basad; propodeal triangle roughened at least mediobasally *A. (Leucandrena)* (in part)
- Malar area distinct, its length one-fourth to one-fifth of its width, but *if* linear, then dorsolateral angle of pronotum distinct and basal area of labrum distinctly bidentate or short and broad; propodeal triangle often finely tessellate, not roughened 35
- 35(34). Malar area extremely short, linear; terga without pale apical fasciae; vestiture entirely or largely black *A. (Onagrandrena)* (in part)
- Malar area often distinct, its length one-fifth to one-fourth of its width or more, but *if* linear, then terga sometimes with pale apical fasciae or at least vestiture not largely black 36
- 36(35). Malar area at least half as long as broad; propodeal corbícula incomplete, male-like; vestiture black *A. (Dactylandrena)* (in part)
- Malar area less than one-third as long as broad, usually one-fourth or one-fifth; propodeal corbícula usually complete anteriorly, but *if* incomplete, then not male-like; vestiture usually not entirely black 37
- 37(36). Scopal hairs long, simple, extremely sparse, scarcely obscuring surface of tibia; propodeal corbícula with long dorsal hairs but no anterior hairs, and with no or extremely few internal hairs *A. (Andrena s. str.)* (in part)
- Scopal hairs abundant, usually long, surface of tibia effectively hidden; propodeal corbícula complete anteriorly, or *if* lacking long anterior hairs, then with abundant long, simple or barbed internal hairs 38
- 38(37). Terga without pale apical fasciae, or fasciae diffuse, consisting of hairs of about same length and color as more basal hairs; basal area of labrum almost always bidentate and slightly reflexed; propodeal corbícula usually complete *A. (Andrena s. str.)* (in part)
- Terga with pale apical fasciae; basal area of labrum often simple; propodeal corbícula often incomplete anteriorly 39
- 39(38). Length 8-9 mm; stigma large, usually separated from vein r by two or three vein widths; pronotal dorsolateral angle distinct, dorsoventral ridge indistinct *A. (Notandrena)*
- Length usually 10 mm or more, or, *if* smaller, then stigma narrow, or pronotum with distinct dorsoventral ridge, or both 40
- 40(39). Malar area distinct, one-sixth to one-fourth as long as broad 41
- Malar area linear, less than one-sixth as long as broad 43
- 41(40). Basal area of labrum entire, short, three or more times as broad as long *A. (Anchandrena)*
- Basal area of labrum bidentate or emarginate apically, as long as broad at base or almost so 42
- 42(41). Pygidial plate large, as long as basal width; T1-T4 with pale apical fasciae *A. (Archandrena)* (in part)

- Pygidial plate narrower, longer than basal width, acute at apex unless worn; T2-T4 fasciate *A. (Leucandrena)* (in part) 43(40).
- Galeal blade sharply pointed, narrow, tapering directly from base to apex, spear-shaped *A. (Belandrena)* (in part) 44(43).
- Galeal blade broadened in basal half or more, and more or less obliquely tapered apically, not spear-shaped 44
- 44(43). Metasomal terga usually with weak, pale apical fasciae, weakly if at all punctate; pronotal dorsoventral ridge roughened below oblique groove; propodeal corbicula complete anteriorly *A. (Andrena s. str.)* (in part)
- Metasomal T2-T4 with distinct, pale apical fasciae often interrupted medially, the terga distinctly punctate; pronotal dorsoventral ridge usually sharp, subcarinate, or if rounded below, then propodeal corbicula incomplete anteriorly *A. (Holandrena)* 45(11).
- Submarginal cells two; tibial scopal hairs largely simple (propodeal corbicula incomplete anteriorly, with abundant internal hairs) 46
- Submarginal cells three, or if only two, then tibial scopal hairs largely plumose 47
- 46(45). Integument often metallic blue or blue-green; propodeum outside of triangle roughened by punctures *A. (Diandrena)* (in part)
- Integument not metallic; propodeum outside of triangle with punctures sparse, not roughening surface *A. (Pelicanandrena)* 47(45).
- Scutum between parapsidal lines with numerous, extremely fine, longitudinal rugulae *A. (Nemandrena)* (in part)
- Scutum shagreened, tessellate, punctate or shiny, but without fine longitudinal rugulae 48
- 48(47). Mandible tridentate; subgenal coronet composed of several rows (5-8) of short, thick hairs forming a dense brush *A. (Dasyandrena)*
- Mandible bidentate or simple; subgenal coronet composed of one or a few rows of short thick or plumose hairs 49
- 49(48). Propodeum with lateral surface completely set off from dorsal and posterior surfaces by a carina, profile declivous from base to apex; clypeus short *A. (Hesperandrena)* (in part)
- Propodeum with lateral surface not set off by a carina, profile showing a distinct dorsal surface; clypeus longer 50
- 50(49). Maxillary palpus short, usually not exceeding galea or occasionally exceeding galea by length of terminal segment; stigma narrow; tibial scopal hairs almost always plumose throughout 51
- Maxillary palpus exceeding galea by at least last two segments; stigma often broader than width of prestigma, as measured to wing margin; tibial scopal hairs usually simple, at least medially 53
- 51(50). Ocelloccipital distance about one-half ocellar diameter; integument usually slightly metallic blue-green; hind tibia cuneate with relatively short hairs; clypeal hairs plumose, all erect and only slightly curved near tips *A. (Augandrena)*
- Ocelloccipital distance usually one ocellar diameter, but if shorter, then integument black or red, not metallic and/or hind tibia not cuneate, with long scopal hairs; clypeal hairs plumose or largely so, not entirely erect, usually curving forward 52
- 52(51). Scopal hairs simple (ocelloccipital distance one ocellar diameter) *A. (Rhacandrena)* (in part)
- Scopal hairs largely plumose *A. (Callandrena)* (in part) 53(50).
- Tibial scopal hairs highly plumose 54
- Tibial scopal hairs simple or largely so 56
- 54(53). Propodeal corbicula complete; propodeum narrow at apex (at metasomal attachment); integument black, nonmetallic *A. (Simandrena)* (in part)
- Propodeal corbicula incomplete, without long anterior hairs but with internal hairs; propodeum not unusually narrow at apex; integument often metallic 55
- 55(54). Scopal hairs of distal part of tibia short; hind tibia cuneate; clypeus distinctly punctate; integument black, nonmetallic *A. (Genyandrena)* (in part)
- Scopal hairs longer; hind tibia not cuneate; clypeal punctures often obscured by dense tessellation or coarse shagreening; integument often metallic *A. (Euandrena)* (in part) 56(53).
- Length usually 9 mm or less; stigma large, first submarginal crossvein usually meeting marginal cell within two or three vein widths of stigma; propodeal corbicula usually incomplete anteriorly, often with internal hairs 57
- Length usually more than 9 mm; stigma narrow or only moderately broad, first submarginal crossvein usually meeting marginal cell several vein widths from stigma; but if length 9 mm or less and stigma broad, then propodeal corbicula complete anteriorly, without internal hairs 59
- 57(56). Vestiture of head, pleurae, and terga dark-brown; metasomal terga without pale apical fasciae; facial fovea narrow; facial quadrangle broader than long *A. (Cremnandrena)*
- Vestiture of head, pleurae, and terga not all dark brown; metasomal terga usually with pale apical fasciae; facial fovea usually broad; facial quadrangle usually as long as or longer than broad 58
- 58(57). Pronotum with weak dorsolateral angle, the dorsoventral ridge absent or extremely weak; face below ocelli tessellate, without distinct longitudinal rugulae or punctures *A. (Derandrena)* (in part)
- Pronotum without both dorsolateral angle and ridge; face below ocelli rugulate and/or punctate *A. (Micrandrena)* 59(56).
- Hind tibia cuneate; tibial scopal hairs along posterior margin usually short, less than half as long as greatest tibial width, shortest subapically 60
- Hind tibia not cuneate; tibial scopal hairs along posterior margin at least half as long as greatest tibial width 64
- 60(59). Subgenal coronet absent; ocelloccipital distance no more than half an ocellar width *A. (Genyandrena)* (in part)
- Subgenal coronet present; ocelloccipital distance often longer than half an ocellar diameter 61
- 61(60). Integument metallic blue or blue-black; terga with abundant, coarse, round punctures; tibial scopal hairs long anteriorly and longest anteroapically, where each hair equals length of tibial spur *A. (Scaphandrena)* (in part)

- Integument black; terga impunctate or with relatively small and/or sparse punctures; tibial scopal hairs short anteriorly as well as posteriorly, each anteroapical hair half length of tibial spur or less 62
- 62(61). Pleural hairs black; tergal vestiture black; facial fovea narrow, its upper end occupying about half ocellular distance *A. (Scaphandrena)* (in part)
- Pleural hairs white to fulvous and/or tergal vestiture not entirely black; facial fovea usually broad 63
- 63(62). Propodeal corbicula complete, bare internally *A. (Simandrena)* (in part)
- Propodeal corbicula incomplete, with long, simple internal hairs *A. (Scaphandrena)* (in part)
- 64(59). Vestiture entirely black or thoracic dorsum with reddish-brown hairs; propodeal triangle relatively coarsely and irregularly sculptured, forming small areolae; tibial scopal hairs long, simple, sparse *A. (Onagrandrena)* (in part)
- Vestiture not entirely black, or *if* so, then *either* propodeal triangle finely sculptured (tessellate or shagreened) *or* tibial scopal hairs simple but abundant 65
- 65(64). Labial palpal segments 2 and 3 each with next segment attached subapically, the third segment attached to second near middle of second segment; integument bright metallic blue-black; first recurrent vein meeting second submarginal cell about two-thirds of cell length from base *A. (Belandrena)* (in part)
- Labial palpal segments 2 and 3 attached terminally, or, *if* subapically, then third attached to second well beyond middle of second; integument often black or red, occasionally metallic; first recurrent vein meeting second submarginal cell usually not much, if any, beyond middle of cell 66
- 66(65). T2-T4 with pale apical fasciae of hair 67
- T2-T4 without pale apical fasciae of hair 73
- 67(66). T1 with pale apical fascia; basal parts of T2-T4 with abundant erect hairs arising from small punctures; wing membranes often infumate 68
- T1 without fascia; basal areas of T2-T4 without erect hairs, or these not arising from distinct punctures; wing membranes usually not infumate 69
- 68(67). Galeal blade pointed, its outer apical margin straight; clypeus, dorsum of thorax, and metasomal terga shiny; propodeum outside of triangle impunctate *A. (Rhacandrena)* (in part)
- Galeal blade with outer apical margin slightly convex, broader basally; at least clypeus and metasomal terga dulled or moderately dulled by coarse shagreening or tessellation; propodeum outside of triangle roughened by distinct punctures *A. (Euandrena)* (in part)
- 69(67). Terga distinctly punctate, their surfaces dulled by dense reticular shagreening; clypeus distinctly flattened posteromedially, with slightly elongate punctures, surface usually dulled by fine tessellation .. *A. (Taeniandrena)*
- Terga often not distinctly punctate, their surfaces dulled by fine reticular shagreening or shiny; clypeus not flattened posteromedially, or, *if* so, then shiny, not tessellate, and punctures round, not elongate 70
- 70(69). Terga punctate; clypeus sparsely punctate, punctures mostly separated by two to three or more puncture widths; pronotum with oblique groove impressed *A. (Rhacandrena)* (in part)
- Terga usually impunctate or weakly so; clypeal punctures more crowded; pronotum usually with oblique groove absent or scarcely impressed 71
- 71(70). Labrum below basal area with strong median crista, often lamellate, *and* with strong lateral crista and two shiny transverse sulci (metasomal terga tessellate, opaque) *A. (Psammandrena)*
- Labrum below basal area with one median crista, not lamellate, *or* without cristae, without transverse sulci 72
- 72(71). Propodeum outside of triangle with punctures moderately roughening surface; dorsal femoral hairs often with abundant short, S-shaped branches bent away from rachis, appearing highly plumose; galeal blade generally narrow, its outer margin in apical half usually straight *A. (Euandrena)* (in part)
- Propodeum outside of triangle without punctures, smoothly tessellate or shagreened; dorsal femoral hairs with relatively short, stiff barbs or simple; galeal blade with outer apical margin gently convex, broad at base *A. (Thysandrena)*
- 73(66). Vestiture entirely black; ocelloccipital distance one ocellar diameter or less *A. (Scaphandrena)* (in part)
- Vestiture in part or largely pale; or, *if* mostly black, then ocelloccipital distance one and one-half to two ocellar diameters *A. (Melandrena)*

Key to the Subgenera of *Andrena* of North and Central America (Males)

(Modified from LaBerge, 1986)

1. Submarginal cells two 2
- Submarginal cells three 6
- 2(1). First and often base of second flagellar segment excavated below *A. (Pelicanandrena)*
- First and second flagellar segments terete or flattened and expanded laterally but not excavated below 3
- 3(2). Clypeus metallic blue, often with violaceous reflections; basal area of labrum usually bidentate; propodeal triangle usually moderately coarsely sculptured *A. (Diandrena)*
- Clypeus yellow, white, or black; basal area of labrum bidentate or entire; propodeal triangle usually finely sculptured 4
- 4(3). Maxillary palpus short, when extended distad exceeding tip of galea by no more than length of last segment and usually less *A. (Callandrena)* (in part)
- Maxillary palpus exceeding tip of galea by at least length of two apical segments 5
- 5(4). Clypeus and paracocular areas black; propodeum outside of triangle roughened by coarse punctures *A. (Onagrandrena)* (in part)
- Clypeus and paracocular areas white to yellow; propodeum outside of triangle not roughened by coarse punctures *A. (Parandrena)*
- 6(1). Malar space one-third to one-half as long as broad, or longer, but *if* as short as one-third as long as broad, then anterior trochanter with spinelike process on anterior surface near apex; clypeus yellow; facial quadrangle usually as broad as long *A. (Dactylandrena)*
- Malar space less than one-third as long as broad, or, *if* as long as one-third width, then *either* clypeus black *or* facial quadrangle longer than broad; anterior trochanter never with apical spine 7

- 7(6). Scutum with fine longitudinal rugulae, often reduced to short rugulae on posteromedian area; basal area of labrum with short median horn, often as long as rest of area (metasomal terga without pale fasciae) *A. (Nemandrena)*
- Scutum without fine longitudinal rugulae; basal area of labrum without median horn 8
- 8(7). Mouthparts elongate, galeal blade as long as clypeus or slightly longer; maxillary palpus and/or labial palpus elongate; T2-T4 with pale, often weak, apical fasciae 9
- Mouthparts short, galeal blade usually not as long as clypeus; neither maxillary nor labial palpus greatly elongate, but *if* galeal blade as long as clypeus, then metasomal terga lacking pale apical fasciae 11
- 9(8). Labial palpus greatly elongate, segments 1 and 2 three to five times as long as segments 3 and 4 taken together, first two segments greatly flattened; maxillary palpus normal in length, half as long as galeal blade *A. (Callandrena)* (in part)
- Labial palpus elongate but normal, first two segments neither unusually long nor much flattened; maxillary palpus usually about as long as galeal blade or much longer 10
- 10(9). Maxillary palpus with second segment at least one and one-half times as long as first; stipes distinctly narrowed medially and tapering apically, the apical third less than half as broad as basal third, with relatively sparse, weak, plumose hairs *A. (Iomelissa)*
- Maxillary palpus with second segment about as long as first; stipes linear, tapering extremely slightly toward apex, apical third almost as broad as basal third, with abundant long, stout, spinelike hairs *A. (Erandrena)*
- 11(8). Malar area about one-third as long as wide; facial quadrangle distinctly longer than broad (clypeus yellow or partially so) *A. (Conandrena)*
- Malar area usually less than one-third as long as broad; facial quadrangle as long as broad or broader 12
- 12(11). Inner hind tibial spur slightly flattened basally with a membranous flange, spur often strongly curved, broader than outer spur near base 13
- Inner hind tibial spur not broadened basally, not unusually curved near base, usually about as broad as outer spur near base 15
- 13(12). Propodeal triangle coarsely sculptured *A. (Plastandrena)* (in part)
- Propodeal triangle finely sculptured, usually tessellate or shagreened 14
- 14(13). Flagellar segment 1 as long as segment 2 plus 3 or longer; maxillary palpus not reaching apex of galea *A. (Charitandrena)*
- Flagellar segment 1 about as long as segment 3, longer than segment 2; maxillary palpus exceeding galea by at least last palpal segment *A. (Aporandrena)*
- 15(12). Middle and hind tibial spurs unusually thick, their apices rather abruptly hooked; terga without pale apical fasciae; clypeus black *A. (Euandrena)* (in part)
- Middle and hind tibial spurs neither unusually thickened nor strongly hooked at apices; terga often with pale apical fasciae; clypeus usually black, occasionally yellow 16
- 16(15). Inner hind tibial spur rather abruptly bent and slightly twisted at about one-third length from apex; T3-T4 with pale apical fasciae and distinct punctures *A. (Leucandrena)* (in part)
- Inner hind tibial spur long, slender, neither bent abruptly nor twisted in apical third; T3-T4 with or without pale apical fasciae, often impunctate 17
- 17(16). Propodeum declivous, its dorsal surface slanting from basal margin to apex; clypeus often short, scarcely if at all protruding below lower margins of compound eyes 18
- Propodeum with distinct horizontal basal area; clypeus usually protruding below eyes, occasionally short 19
- 18(17). Propodeum with lateral surface separated from lower posterior surface by short lateral carina; clypeal punctures obscured by dense, fine tessellation *A. (Hesperandrena)*
- Propodeum with lateral surface not at all separated from lower posterior surface by a carina; clypeal punctures usually evident *A. (Celetandrena)*
- 19(17). Clypeus with lateral angle produced forward beyond base of mandible, to about same level as median apex of clypeus; head extremely broad, broader than thorax; dorsoventral pronotal ridges almost meeting mid-dorsally, far from dorsolateral angles *A. (Cremnandrena)*
- Clypeus with lateral parts not produced forward; head not much, if any, broader than thorax; dorsoventral pronotal ridge usually ending in dorsolateral angle, or pronotum lacking dorsolateral angle and ridge 20
- 20(19). Labial palpus with third segment arising near middle of second segment or slightly beyond, and fourth segment arising subapically from third; integument metallic blue (first recurrent vein meeting second submarginal cell two-thirds of length of cell from base; clypeus pale yellow) *A. (Belandrena)* (in part)
- Labial palpus with second and third segments attached to succeeding segments apically or almost so; integument usually black or red 21
- 21(20). Pronotum with distinct dorsolateral angle along posterior margin, and with more or less distinct dorsoventral ridge extending down from angle to anterior coxa, area between ridge and pronotal lobe often shiny and impunctate, occasionally deep and narrow or rugulose 22
- Pronotum without dorsolateral angle along posterior margin, without dorsoventral ridge 44
- 22(21). Maxillary palpus short, not exceeding galea (when extended distad) by more than length of apical segment of palpus; stigma usually narrower than prestigma, as measured to anterior margin of wing; clypeus yellow *A. (Callandrena)* (in part)
- Maxillary palpus usually exceeding galea by at least length of last two palpal segments; stigma variable, often broader than or equal to prestigma, as measured to wing margin; but *if* palpus short and stigma narrow, then clypeus black 23
- 23(22). Genal area immediately below posterior mandibular articulation with a short, shiny, often fingerlike process 24
- Genal area immediately below posterior mandibular articulation without a fingerlike process 25
- 24(23). Basal area of propodeum shorter than metanotum, triangle with fine but distinct, longitudinal rugulae;

- metasomal terga distinctly punctate *A. (Prilandrena)* (in part)
- Basal area of propodeum longer than metanotum, triangle tessellate or finely areolate, without longitudinal rugulae; metasomal terga impunctate or indistinctly punctate *A. (Derandrena)* (in part)
- 25(23). Genal area with a large, blunt process extending downward and somewhat forward from ventral surface, which is otherwise concave (poorly developed in a few specimens) 26
- Genal area without large process on ventral surface, which is flat, smoothly curved at sides 27
- 26(25). Clypeus yellow; propodeal triangle finely sculptured, shagreened or finely tessellate *A. (Genyandrena)*
- Clypeus black; propodeal triangle coarsely sculptured, irregularly rugulose *A. (Xiphandrena)*
- 27(25). Facial quadrangle distinctly broader than long; metasomal terga without pale apical fasciae; pronotum with dorsolateral angle indistinct, displaced toward midline (dorsoventral pronotal ridge distinct) *A. (Oligandrena)*
- Facial quadrangle about as broad as long, or, if broader, then either metasomal terga with distinct pale apical fasciae or dorsolateral angle of pronotum distinct or both 28
- 28(27). Clypeus partially or wholly yellow or cream-colored 29
- Clypeus entirely black 36
- 29(28). Pygidial plate well developed, narrow, V-shaped; first flagellar segment usually about two-thirds as long as second *A. (Archandrena)*
- Pygidial plate absent or vestigial (narrow and linear when present); first flagellar segment usually as long as or almost as long as second 30
- 30(29). Galeal blade sharply pointed and spear-shaped, evenly tapering from base to apex, narrow *A. (Belandrena)* (in part)
- Galeal blade not sharply pointed, not spear-shaped, more or less sharply tapered apically, broad in basal one-third to one-half 31
- 31(30). Clypeus with apical margin broad, turned forward; propodeal triangle finely areolate mediobasally (T2-T5 with distinct pale apical fasciae) *A. (Geisandrena)*
- Clypeus with apical margin short, not turned forward; propodeal triangle variously sculptured but usually tessellate 32
- 32(31). Genal area with posterior margin distinctly carinate; stigma large, first submarginal crossvein ending on marginal cell within two or three vein widths of stigma; first flagellar segment as long as or longer than second plus third *A. (Notandrena)*
- Genal area with posterior margin rounded, or, if carinate, then stigma narrow and first submarginal crossvein ending on marginal cell several vein widths from stigma; first flagellar segment shorter than second plus third 33
- 33(32). Stigma large, broader than prestigma as measured to anterior wing margin; first submarginal crossvein meeting marginal cell within three or four vein widths of stigma or less; pronotum with dorsoventral ridge crossed by distinctly impressed oblique groove 34
- Stigma narrower, or, if as broad as above, then first submarginal crossvein meeting marginal cell at more than four vein widths from stigma; pronotum with dorsoventral ridge relatively sharp, not depressed by oblique groove 35
- 34(33). Basal area of labrum trapezoidal, often with small but distinct median emargination; integument, except clypeus, black, nonmetallic *A. (Larandrena)*
- Basal area of labrum entire, rounded, short (several times broader than long), or, if trapezoidal and slightly emarginate, then integument largely metallic blue *A. (Derandrena)* (in part)
- 35(33). Malar area distinct, six times as broad as long or longer; metasomal terga usually impunctate or indistinctly punctate; propodeal triangle finely sculptured *A. (Anchandrena)*
- Malar area linear, six times as broad as long or shorter; metasomal terga more or less distinctly punctate; propodeal triangle moderately coarsely sculptured *A. (Holandrena)* (in part)
- 36(28). Pronotum with dorsoventral ridge extending down from dorsolateral angle interrupted by distinct, oblique, deeply impressed groove; T2-T4 usually without pale apical fasciae; clypeus short, not produced much beyond level of lower ends of compound eyes *A. (Tylandrena)*
- Pronotum with dorsoventral ridge extending down from dorsolateral angle not interrupted by distinctly impressed groove, or, if groove present, then a mere line; T2-T4 often with pale apical fasciae; clypeus often produced by one-fourth or more of median length beyond level of lower ends of compound eyes 37
- 37(36). Genal area with posterior margin distinctly carinate; clypeus with apical area long, distinctly turned forward; T2-T5 with more or less distinct pale apical fasciae *A. (Gonandrena)* (in part)
- Genal area with posterior margin not carinate; clypeus with apical area usually short, not turned forward; T2-T5 often without pale apical fasciae 38
- 38(37). T2-T4 with distinct pale apical fasciae; metasomal terga impunctate or with fine, indistinct punctures; propodeal triangle often areolate to coarsely rugulose (malar area linear) *A. (Leucandrena)* (in part)
- T2-T4 without pale apical fasciae; metasomal terga with small to coarse, distinct punctures; propodeal triangle smooth, tessellate to coarsely rugose 39
- 39(38). Malar area distinct, one-fourth to one-fifth as long as broad; terga without pale apical fasciae; mandible often with inferior basal tooth *A. (Andrena s. str.)* (in part)
- Malar area linear, much less than one-fifth as long as broad; terga with pale apical fasciae; mandible lacking inferior tooth 40
- 40(39). Metasomal terga coarsely punctate; dorsal propodeal triangle moderately coarsely to coarsely sculptured 41
- Metasomal terga impunctate or extremely finely punctate; dorsal propodeal triangle finely sculptured 42
- 41(40). Basal area of labrum short, four times as broad as long, entire to weakly emarginate *A. (Holandrena)* (in part)
- Basal area of labrum long, bidentate, usually reflexed *A. (Rhaphandrena)*
- 42(40). T1-T5 or T2-T5 with pale apical fasciae composed of long, blunt hairs with abundant, extremely short barbs, giving hairs an opaque appearance in strong light;

- basal area of labrum strongly bidentate and strongly reflexed, usually elevated well above margin of clypeus, its apical teeth turned under *A. (Cnemidandrena)*
- T2-T5 with pale apical fasciae weak, composed of moderately long, pointed, weakly barbed white hairs; basal area of labrum entire, weakly to strongly bidentate, often not strongly reflexed 43
- 43(42). T1 and usually T2 medially with abundant long, erect to suberect hairs; basal area of labrum usually bidentate; maxillary palpal segments not all elongate
..... *A. (Andrena s. str.)* (in part)
- T1 and T2 without long, erect to suberect hairs, T1 bare or with short, sparse, erect hairs; basal area of labrum entire or only weakly emarginate apically; maxillary palpal segments all moderately elongate
..... *A. (Ptilandrena)* (in part)
- 44(21). Maxillary palpus short, rarely exceeding galea when extended distad or exceeding galea by less than length of last two palpal segments 45
- Maxillary palpus long, exceeding galea when extended distad by at least length of last two palpal segments 47
- 45(44). Basal area of labrum large, entire, subtriangular, about as long as broad; first flagellar segment twice as long as second; integument dark metallic blue or blue-black
..... *A. (Scoliandrena)*
- Basal area of labrum smaller, usually bidentate or emarginate, broader than long; first flagellar segment often less than twice as long as second segment; integument occasionally metallic, usually black or in part red 46
- 46(45). Ocellocipital distance half an ocellar diameter or less, rarely slightly more; integument dull metallic blue; clypeus and paraocular areas pale yellow
..... *A. (Augandrena)*
- Ocellocipital distance usually one ocellar diameter or more, but *if* as short as half an ocellar diameter, then *either* integument not metallic *or* paraocular areas without pale maculae *or* both *A. (Callandrena)* (in part)
- 47(44). Stigma large, first submarginal crossvein ending one to three vein widths from stigma; body 9 mm or less in length 48
- Stigma narrower, first submarginal crossvein usually ending more than three vein widths from stigma; body usually more than 9 mm in length 49
- 48(47). Propodeal triangle margined by minutely carinate lateral bounding sutures; dorsal surface of propodeum not longer than scutellum *A. (Simandrena)* (in part)
- Propodeal triangle margined by acarinate lateral bounding sutures, mere lines or slight depressions; dorsal surface of propodeum often longer than scutellum
..... *A. (Micrandrena)*
- 49(47). Pleurae and propodeal triangle coarsely or moderately coarsely sculptured, or, *if* triangle finely sculptured, then genal area narrow, about as wide as eye in side view 50
- Pleurae and propodeal triangle usually finely sculptured, often merely granular or tessellate, or, *if* moderately coarsely sculptured, then genal area much broader than eye in side view 56
- 50(49). Inner hind tibial spur slightly broadened basally by a membranous flange, often strongly curved, broader than outer spur; S6 bent downward and forward apico-
laterally to form two reflexed blunt teeth; first recurrent vein meeting second submarginal cell near or only slightly beyond middle of cell
..... *A. (Plastandrena)* (in part)
- Inner hind tibial spur neither broadened basally nor unusually curved, about as narrow as outer spur; S6 relatively flat apically, or, *if* margin reflexed, then not forming apicolateral teeth; first recurrent vein often meeting second submarginal cell two-thirds of length of cell or more from base 51
- 51(50). Propodeal triangle coarsely areolate or irregularly rugose, with transverse posterior carina separating dorsal from posterior surface 52
- Propodeal triangle coarsely punctate or finely areolate, without transverse carina separating dorsal from posterior surface 53
- 52(51). Marginal zone of T2 one-third or more of median tergal length; third flagellar segment usually two-thirds as wide as long or longer, antennae in repose usually reaching beyond scutellum; first recurrent vein meeting second submarginal cell near middle of cell, rarely beyond *A. (Trachandrena)*
- Marginal zone of T2 less than one-third of median tergal length; third flagellar segment distinctly more than two-thirds as wide as long, antennae in repose usually not reaching beyond middle of scutellum; first recurrent vein meeting second submarginal cell two-thirds or more of length of cell from base *A. (Scapteropsis)*
- 53(51). Clypeus flattened mediobasally; metasomal terga distinctly punctate, surface and bottoms of punctures dulled by fine tessellation; T2-T5 with pale apical fasciae, but these often interrupted medially *A. (Taeniandrena)*
- Clypeus usually not flattened mediobasally; metasomal terga punctate but shiny or moderately so, at most dulled by fine reticulate shagreening; T2-T5 without pale apical fasciae 54
- 54(53). Clypeus yellow; terga bright metallic blue; S2-S5 with distinct, white, subapical fimbriae
..... *A. (Scaphandrena)* (in part)
- Clypeus black; terga dark metallic blue-black or black; sterna with or without subapical fimbriae, but these usually weak when present 55
- 55(54). First flagellar segment much shorter than second, second subequal in length to third; labial palpus short, second and third segments almost as broad as long; integument dark metallic blue-black with violaceous reflections
..... *A. (Melandrena)* (in part)
- First flagellar segment usually at least as long as second, rarely slightly shorter, second segment usually shorter than third; labial palpus normal, second and third segments slender, not nearly as broad as long; integument black or with extremely faint metallic reflections
..... *A. (Onagrandrena)* (in part)
- 56(49). Clypeus at least in part yellow or white 57
- Clypeus black or metallic blue or green 61
- 57(56). Metasomal terga without pale apical fasciae; integument usually dark metallic blue-black
..... *A. (Scaphandrena)* (in part)
- Metasomal terga with pale apical fasciae; integument usually dull black, nonmetallic 58
- 58(57). Clypeus dark except for small apicomедial spot or

- subapical band of yellow occupying less than half of clypeal area; S2-S5 with exceptionally long subapical fimbriae *A. (Dasyandrena)* (in part)
- . Clypeus at least two-thirds yellow; metasomal sterna with subapical fimbriae absent or consisting of hairs of moderate length 59
- 59(58). Metasomal terga dull, opaque, tessellation obscuring punctures if present; S6 flat apically *A. (Psammandrena)*
- . Metasomal terga strongly to moderately punctate, surface shiny or moderately shiny; S6 with apical margin often reflexed 60
- 60(59). Clypeus usually white or cream-colored; T2-T4, but rarely T1, with apical pale fasciae; S2-S5 with subapical fimbriae weak (short) or absent (*if* with weak sternal fimbriae, *then* without fascia on T1); hind tibia broad, cuneate *A. (Scaphandrena)* (in part)
- . Clypeus usually yellow; T1-T4 with apical pale fasciae; S2-S5 with well-formed pale subapical fimbriae; hind tibia not broadened apically, not cuneate *A. (Rhacandrena)*
- 61(56). Genal area narrow, at most slightly broader than eye in lateral view; metasomal sterna usually with pale subapical fimbriae 62
- . Genal area conspicuously broader than eye in lateral view; metasomal sterna without pale subapical fimbriae 67
- 62(61). Propodeum with lateral sutures delimiting triangle slightly raised; clypeus impunctate or punctures obscured by dense regular tessellation or coarse shagreening; integument black, never metallic *A. (Simandrena)* (in part)
- . Propodeum with lateral sutures demarcating triangle flat or slightly depressed, or, *if* raised and ridgelike, then integument at least slightly metallic; clypeus usually distinctly punctate, often shiny but occasionally impunctate and dull 63
- 63(62). T1-T5 with pale apical fasciae, bases of terga with abundant long, erect hairs; wing membranes moderately to deeply infumate *A. (Euandrena)* (in part)
- . T1-T5 or at least T1 without pale apical fasciae, bases of terga with or without erect hairs; wing membranes clear to moderately infumate 64
- 64(63). Metasomal sterna lacking pale subapical fimbriae; terga often without pale apical fasciae; propodeum outside of triangle distinctly punctate *A. (Euandrena)* (in part)
- . Metasomal sterna with distinct pale subapical fimbriae; T2-T4 with pale apical fasciae; propodeum outside of triangle impunctate or nearly so 65
- 65(64). Sternal subapical fimbriae exceptionally long; space between clypeus and antennal sockets less than one socket diameter (western USA) *A. (Dasyandrena)* (in part)
- . Sternal subapical fimbriae moderately long; space between clypeus and antennal sockets one socket diameter or more 66
- 66(65). Galeal blade narrow, spear-shaped, outer margin of apical half straight; basal area of labrum simple *A. (Oxyandrena)*
- . Galeal blade broad basally, outer margin of apical half or less gently concave; basal area of labrum usually emarginate apically *A. (Thysandrena)* (in part)
- 67(61). T2-T4 and often T5 with more or less distinct pale apical fasciae; ocelloccipital distance about one ocellar diameter, often less and rarely slightly more *A. (Leucandrena)* (in part)
- . T2-T5 without pale apical fasciae, or, *if* present on some terga, then weak, and ocelloccipital distance at least one and one-half ocellar diameters, often more *A. (Melandrena)* (in part)

Key to the Subgenera of *Andrena* of the Western Palearctic Region (Females)

(Modified from A. Molino-Pardo's translation (MS) of Warncke's 1968 key)

The subgenus *Oreomelissa*, containing the European *Andrena coitana* (Kirby), is omitted from the key to males, but see the key to Japanese subgenera. Warncke (1968) placed this species in *Stenomelissa* but neither described that subgenus nor placed it in his key. It presumably has nothing to do with the east Asian *Stenomelissa* Hirashima and LaBerge. Although *Carinandrena*, *Fuscandrena*, *Leimelissa*, *Longandrena*, *Osychnyukandrena*, and *Planandrena* are palearctic taxa, they not included in this key. Four of them are monotypic. *Malayapis* is included, although it is oriental. For couplet 17, see also couplet 49; the subgenus *Holandrena* would seemingly run to couplet 18. In Warncke's key these couplet numbers are 17 and 48, respectively.

1. Inner side of hind femur with a row of small peglike or thornlike projections 2
- . Inner side of hind femur without such projections 7
- 2(1). Tibial scopa of simple hairs; labrum not conspicuously divided 3
- . Tibial scopa of small to large plumose hairs; labrum divided conspicuously into median and lateral parts 4
- 3(2). Facial fovea broad in upper part, narrow and deeply channeled in lower part *A. (Orandrena)*
- . Facial fovea uniformly broad, occupying one-third of paraocular area *A. (Cryptandrena)* (in part)
- 4(2). Facial fovea short, rectangular, almost twice as long as broad; hind femur slender and almost cylindrical *A. (Avandrena)* (in part)
- . Facial fovea usually long and not rectangular; hind femur strong, its inner side flattened and limited above by a more or less conspicuously developed linear carina 5
- 5(4). Facial fovea short and drop-shaped; metasomal terga fairly strongly to strongly and densely punctate *A. (Rufandrena)*
- . Facial fovea long, or, *if* drop-shaped, then metasomal terga with scattered deep punctures 6
- 6(5). Inner side of hind femur with weak carina and sparse, long bristles; lateral area of labrum small; metasomal terga usually with scattered deep punctures *A. (Chlorandrena)*
- . Inner side of hind femur with strong carina and dense, short bristles; lateral area of labrum about as large as median area; metasomal terga strongly and densely punctate *A. (Lepidandrena)*
- 7(1). Inner hind tibial spur usually distinctly and strongly broadened at base 8
- . Inner hind tibial spur not broadened at base, at most distal half convexly broadened 13

- 8(7). Mesepisternum and propodeal triangle strongly honeycomb-areolate 9
 —. Mesepisternum and propodeal triangle finely roughened to smooth 11
- 9(8). Pronotum with dorsolateral angle elevated, abruptly cut off laterally *A. (Melanapis)*
 —. Pronotum with more rounded dorsolateral angle 10
- 10(9). Propodeal corbicula only weakly rugose in posterior part; body black to red *A. (Plastandrena)*
 —. Propodeal corbicula with strongly developed rugae, mostly lengthwise; body brilliant metallic blue *A. (Agandrena)*
- 11(8). Mesepisternum and propodeum glossy, coarsely and deeply punctate *A. (Scitandrena)*
 —. Mesepisternum and propodeum roughened, moderately finely lined, with asymmetrical (one-sided) punctures 12
- 12(11). Propodeal triangle weakly rugosely areolate to posterior margin; inner side of hind femur conspicuously carinate; basal area of labrum small and usually triangular *A. (Suandrena)*
 —. Propodeal triangle with middle area shagreened, covered with fine rugae; inner side of hind femur not carinate; basal area of labrum of medium size, deeply notched *A. (Pallandrena)*
- 13(7). Inner hind tibial spur distinctly convexly broadened a little beyond middle; inner side of hind femur almost always conspicuously carinate; pronotum not carinate 14
 —. Inner hind tibial spur not much broadened; inner side of hind femur more or less rounded; pronotum carinate or not 15
- 14(13). Glossa greatly elongated, at least six times as long as broad *A. (Charitandrena)*
 —. Glossa of normal length, about three times as long as broad *A. (Ulandrena)*
- 15(13). Propodeum declivous from the metanotum; facial fovea short and drop-shaped (head large) *A. (Cubiandrena)*
 —. Propodeum with basal area more or less horizontal, or, if declivous, then facial fovea not as above 16
- 16(15). Facial fovea short and rectangular, at most twice as long as broad *A. (Avandrena)* (in part)
 —. Facial fovea otherwise, usually conspicuously narrower below than above 17
- 17(16). Mesepisternum and propodeal triangle coarsely honeycomb-areolate 18
 —. Mesepisternum and propodeal triangle at most weakly wrinkled 20
- 18(17). Facial fovea small, upper part drop-shaped, lower part greatly reduced and fading out *A. (Brachyandrena)*
 —. Facial fovea normally long, deep, upper part broadly rounded, lower part almost reduced to a sulcus 19
- 19(18). Submarginal cells two *A. (Biareolina)*
 —. Submarginal cells three *A. (Trachandrena)*
- 20(17). Mesepisternum with remarkably minute to fine punctures; head usually elongate and narrower 21
 —. Mesepisternum strongly and deeply punctate; head short and broad 58
- 21(20). Dorsolateral angle of pronotum not strongly elevated as transverse ridge and without carina extending down from it, at most with hint of such carina 22
 —. Dorsolateral angle of pronotum weakly to strongly elevated as transverse ridge, abruptly cut off laterally, and with carina extending down from it 47
- 22(21). Mesepisternum behind attachment of foreleg conspicuously compressed and flat to deeply grooved; hairs of thorax squamose to minutely branched *A. (Aenandrena)*
 —. Mesepisternum behind attachment of foreleg normally rounded; thorax usually normally haired 23
- 23(22). Small to very small species; first submarginal crossvein reaching marginal cell near posterior margin of stigma 24
 —. Usually not small, generally medium-sized to large species; first submarginal crossvein reaching marginal cell at least three vein widths from stigma 27
- 24(23). Propodeal triangle strongly rugose to rugosely areolate; clypeus not grooved; facial fovea long, usually broad, and occupying about one-third of paraocular area *A. (Micrandrena)* (in part) and *A. (Fumandrena)*
 —. Propodeal triangle reticulated to shagreened, usually without rugae or weakly rugose at base, but if strongly rugose, then clypeus conspicuously grooved lengthwise; facial fovea usually not as above 25
- 25(24). Propodeal triangle near metanotum finely but conspicuously and evenly rugose; facial fovea moderately long, uniformly broad, and occupying about one-third of paraocular area *A. (Graecandrena)*
 —. Propodeal triangle without rugae; facial fovea conspicuously narrowed below 26
- 26(25). Facial fovea short, not extending below upper margin of antennal socket *A. (Aciandrena)*
 —. Facial fovea long, usually extending below upper margin of antennal socket *A. (Disandrena)*
- 27(23). Facial fovea long and narrow, deeply grooved at upper end, usually constricted somewhat at middle 28
 —. Facial fovea short or broad, not deeply grooved 29
- 28(27). Body under 10 mm long *A. (Parandrenella)*
 —. Body over 15 mm long *A. (Hyperandrena)*
- 29(27). Facial fovea short, comma- to drop-shaped, narrowed below 30
 —. Facial fovea longer, somewhat narrowed below to occupying almost whole paraocular area 32
- 30(29). Glossa much more than four times as long as broad; clypeus more or less distinctly snout-shaped, convex, or basal area of labrum broad *A. (Didonia)* (in part)
 —. Glossa not over about four times as long as broad; clypeus not to weakly protuberant; basal area of labrum usually normal, trapezoidal 31
- 31(30). Tibial scopa strongly plumose; glossa about four times as long as broad *A. (Chrysandrena)*
 —. Tibial scopa not to very briefly plumose; glossa less than three times as long as broad *A. (Euandrena)*
- 32(29). Surface of propodeal corbicula impunctate and bare, its margin entirely densely hairy; metanotum with dense, light tuft of hairs directed forward *A. (Simandrena)*
 —. Surface of propodeal corbicula either punctate and hairy or margin incomplete; metanotum usually not as above 33
- 33(32). Clypeus flattened and frequently more or less distinctly concave in middle; basal area of labrum short, as if strongly compressed in lengthwise direction; facial

- fovea occupying almost whole paraocular area
 *A. (Taeniandrena)* and *A. (Troandrena)*
- Clypeus more or less strongly convex, or, *if* flattened, then basal area of labrum always of normal size and trapezoidal *or* facial fovea not so broad..... 34
- 34(33). Mesepisternum and usually also propodeum finely punctate; propodeal triangle at most finely rugose like metanotum (metasoma not to indistinctly punctate) 35
- Mesepisternum and propodeum densely punctate; propodeum and especially triangle rugosely areolate 38
- 35(34). Facial fovea occupying almost whole paraocular area; clypeus strongly punctate; propodeal triangle finely reticulate, shagreened to glossy *A. (Hoplandrena)*
- Facial fovea occupying scarcely half of paraocular area; clypeus usually finely punctate; propodeal triangle minutely roughened to reticulately shagreened 36
- 36(35). Metasomal terga almost bare except for complete or interrupted hair bands; facial fovea fading away upward; clypeus elongate *A. (Nobandrena)*
- Metasomal terga usually distinctly hairy, without bands, or, *if* bands present, then propodeum densely punctate; facial fovea more distinctly defined above, but *if* vanishing, then clypeus not elongate 37
- 37(36). Very large species (body length 16-18 mm) with broad maxilla..... *A. (Melitoides)*
- Medium-sized to large species (less than 16 mm) with weakly developed maxilla *A. (Scaphandrena)*
- 38(34). Body under 10 mm long 39
- Body over 10 mm long 43
- 39(38). Mesepisternum moderately finely punctate and shagreened 40
- Mesepisternum rugosely areolate 41
- 40(39). Clypeus longer than broad, transversely convex; facial fovea long *A. (Poecilandrena)*
- Clypeus broader than long, flattened; facial fovea short, not extending below level of antennal bases
 *A. (Poliandrena)* (in part) and *A. (Tarsandrena)* (in part)
- 41(39). Clypeus distinctly broader than long; basal area of labrum very broad and short, rectangular
 *A. (Cryptandrena)* (in part)
- Clypeus as long as broad; basal area of labrum narrower.. 42
- 42(41). Terga uniformly densely punctate, apical marginal zones also punctate *A. (Cordandrena)*
- Terga impunctate or punctate and apical marginal zones distinctly less punctate to impunctate
 *A. (Micrandrena)* (in part)
- 43(38). T1 impunctate; metanotum with weak, forward-directed tuft of dense hairs *A. (Thysandrena)*
- T1 strongly and usually densely punctate; or, *if* impunctate, then metasoma without bands and metanotum usually differently hairy 44
- 44(43). Clypeus transversely wrinkled; basal area of labrum narrow and elongated; pygidial plate with elevated area
 *A. (Leucandrena)* (in part)
- Clypeus not transversely wrinkled; basal area of labrum usually trapezoidal; pygidial plate flat 45
- 45(44). Clypeus strongly convex; metasoma bare, without bands, at most with lateral, white hair patches (usually very large species) *A. (Melandrena)*
- Clypeus flattened; metasoma usually with distinct bands 46
- 46(45). Clypeus longitudinally grooved, appearing longer than broad *A. (Zonandrena)*
- Clypeus smooth to weakly transversely grooved, appearing broader than long *A. (Poliandrena)* (in part)
- 47(21). Glossa greatly elongated; clypeus usually distinctly elongated 48
- Glossa short; clypeus short, rarely elongated 49
- 48(47). Facial fovea occupying scarcely half of paraocular area; basal area of labrum trapezoidal; galea without hooked hairs *A. (Margandrena)*
- Facial fovea occupying almost whole paraocular area; basal area of labrum very large; galea covered with long, hooked hairs *A. (Didonia)* (in part)
- 49(47). Mesepisternum strongly honeycomb-areolated; propodeal triangle strongly rugosely wrinkled; dorsal surface of propodeum short and declivous
 *A. (Holandrena)*
- Mesepisternum and dorsal area of propodeum remarkably finely sculptured, at most weakly rugosely wrinkled; dorsal surface of propodeum normally developed, more or less at right angle to posterior surface 50
- 50(49). Facial fovea narrow, short to scarcely elongate drop-shaped, or, *if* broadened over half of paraocular area, then propodeal corbicular with surface free of hairs, margin densely hairy all around, and clypeus usually elongated *A. (Prilandrena)*
- Facial fovea broader, but *if* narrow, then not drop-shaped but constricted in middle and propodeal corbicular not as above, *or* clypeus not elongated 51
- 51(50). Mandible falcate, without preapical tooth, but with large, rounded tooth on inner margin at distal end of basal fourth (Malaysia) *A. (Malayapis)*
- Mandible with preapical tooth, but without tooth at end of basal fourth 52
- 52(51). Pygidial plate flat to weakly convex on disc and outer margin somewhat elevated; facial fovea narrow, constricted in middle, or, *if* broad, then metasoma strongly punctate 53
- Pygidial plate with distinctly limited, raised central area; facial fovea broad, or, *if* narrow, then metasoma finely punctate 55
- 53(52). Facial fovea broad; metasoma and scutum strongly punctate; clypeus flattened.....
 *A. (Poliandrena)* (in part) and *A. (Tarsandrena)* (in part)
- Facial fovea narrow; metasoma and usually also scutum weakly punctate to impunctate; clypeus convex 54
- 54(53). Propodeal triangle shagreened, on base almost weakly rugose; scutum and especially metasoma not to finely punctate, rarely strongly so *A. (Carandrena)*
- Propodeal triangle weakly rugosely wrinkled; scutum and especially metasoma strongly punctate
 *A. (Notandrena)*
- 55(52). Metasomal terga usually glossy and more or less bare; clypeus short, usually transversely grooved; basal area of labrum distinctly elongated or short-triangular, not notched on distal margin..... 56
- Metasomal terga usually shagreened and more or less densely, protrudingly haired; clypeus usually somewhat elongated, strongly punctate; basal area of labrum trapezoidal, distal margin usually notched 57
- 56(55). Basal area of labrum longer than broad.....
 *A. (Leucandrena)* (in part)

- Basal area of labrum short-triangular *A. (Lavandrena)* 57(55). Maxillary palpus surpassing galea by about last three segments; active in spring *A. (Andrena s. str.)*
- Maxillary palpus surpassing galea by about one segment; autumnal *A. (Cnemidandrena)*
- 58(20). Basal area of labrum large, notched; body length over 11 mm *A. (Campylogaster)*
- Basal area of labrum small, although strongly elevated, entire; body length 11 mm or less *A. (Oreomelissa)*

Key to the Subgenera of *Andrena* of the Western Palearctic Region (Males)

(Modified from A. Molino-Pardo's translation (MS) of Warncke's 1968 key)

1. Apex of S8 broadened, and on each side a long, bent spine distinctly visible among metasomal hairs *A. (Rufandrena)*
- Apex of S8 rarely strongly broadened, and never bearing visible spines 2
- 2(1). Mesepisternum and propodeal triangle strongly rugose-alveolar 3
- Mesepisternum and propodeal triangle at most strongly rugosely wrinkled, commonly not alveolar, usually distinctly weaker in sculpturing 9
- 3(2). Dorsolateral angle of pronotum distinctly elevated as transverse ridge, with dorsoventral carina extending down from it 4
- Pronotum without strong, elevated dorsolateral angle (ridge) and without well-developed dorsoventral carina below it 5
- 4(3). Clypeus yellow; propodeum largely declivous *A. (Holandrena)* (in part)
- Clypeus dark; propodeum with distinct more or less horizontal and vertical surfaces *A. (Melanapis)*
- 5(3). Length under 7 mm; metasoma strongly and very densely punctate *A. (Brachyandrena)*
- Length over 8 mm; metasoma strongly but usually only moderately densely punctate 6
- 6(5). Submarginal cells two; antenna of male short, like that of a female *A. (Biareolina)*
- Submarginal cells three; antenna of male longer than that of female 7
- 7(6). Marginal zones of T2 to T4 occupying half of tergal lengths *A. (Trachandrena)*
- Marginal zones of T2 to T4 normal, narrow 8
- 8(7). Metasoma shining like steel; body with whitish to yellowish-white hairs *A. (Agandrena)*
- Metasoma not so shiny; body dark-haired *A. (Plastandrena)*
- 9(2). Pronotum laterally smooth or weakly or interruptedly carinate below weak dorsolateral angle 10
- Pronotum laterally distinctly and sharply carinate below commonly strong dorsolateral angle 48
- 10(9). Mesepisternum and propodeum usually glossy, marked with deep and coarse, sievelike, dense punctures 11
- Mesepisternum and propodeum usually shagreened, marked with distinctly finer, often elongate punctures with raised edges, or surface rugosely finely areolate 12
- 11(10). Metasoma finely and densely punctate; genitalia complex *A. (Scitandrena)*
- Metasoma strongly to very strongly punctate; genitalia simple *A. (Campylogaster)* (in part)
- 12(10). Propodeum entirely declivous; ocellocipital distance almost as long as four midflagellar segments taken together *A. (Cubiandrena)*
- Propodeum with distinct more or less horizontal basal area; ocellocipital distance seldom longer than length of one midflagellar segment 13
- 13(12). First submarginal crossvein meeting marginal cell close to stigma or at most three vein widths distant (body length not over 8 mm) 14
- First submarginal crossvein meeting marginal cell more than three vein widths away from stigma 17
- 14(13). Propodeal triangle strongly to weakly rugose, usually areolate to posterior truncation of basal area (clypeus black) *A. (Micrandrena)* (in part) and *A. (Fumandrena)*
- Propodeal triangle minutely reticulate to shagreened, at most with rugae along anterior edge 15
- 15(14). First flagellar segment at least as long as second and third taken together; clypeus usually longitudinally grooved and weakly elongated, always black; genitalia simple with elongated gonostylus, which is uniformly broad to apex *A. (Distandrena)*
- First flagellar segment shorter than second and third taken together; clypeus never longitudinally grooved, black or yellow; genitalia usually shortened, gonostylus more or less shovel-shaped to strongly reduced 16
- 16(15). Clypeus yellow or rarely black; gonostylus slightly angled, shovel-shaped *A. (Aciandrena)*
- Clypeus black or exceptionally yellow; gonostylus not as above *A. (Graecandrena)*
- 17(13). Broad central area of clypeus flattened, anterior edge truncate, punctation not strong; basal area of labrum shortened and transversely wrinkled basally *A. (Taeniandrena)* and *A. (Troandrena)*
- Clypeus more or less distinctly convex, or, if flattened, then anterior edge convex and clypeus strongly shortened, or its punctation strong and deep; basal area of labrum not shortened 18
- 18(17). Glossa narrow, almost round in cross section and at least six times longer than broad 19
- Glossa broader, flattened, at most three times longer than broad 24
- 19(18). Malar area distinctly, even if narrowly, developed; glossa very long 20
- Malar area not developed; glossa not especially elongated 21
- 20(19). Clypeus yellow; mesepisternum with strongly inclined punctures having weak, downwardly elongated, raised margins *A. (Charitandrena)*
- Clypeus black; mesepisternum with round punctures lacking distinctly raised margins *A. (Didonia)* (in part)
- 21(19). Mesepisternum strongly rugosely areolate; metasoma strongly punctate and glossy; clypeus usually flat (clypeus broader than long) *A. (Cryptandrena)*
- Mesepisternum shagreened or weakly rugose because of raised edges of punctures; metasoma seldom strongly punctate; clypeus usually distinctly convex 22
- 22(21). T1 shagreened, with craterlike punctures (edges of punctures raised on all sides), or, if terga glossy and strongly punctate, then propodeal triangle toward metanotum at most weakly rugose *A. (Chlorandrena)*
- T1 glossy, coarsely and usually densely punctate; propodeal triangle variable 23

- 23(22). First flagellar segment as long as or shorter than second, *or*, if longer, then scutal disc strongly glossy and scarcely punctate *A. (Chrysandrena)*
- First flagellar segment longer than second; scutum strongly and densely punctate *A. (Lepidandrena)*
- 24(18). Clypeus black 25
- Clypeus yellow (sometimes dark in stylized individuals) 41
- 25(24). Propodeal triangle alveolarly areolate to posterior margin; mesepisternum not alveolar but punctures slightly sloped, with weakly raised margins (genitalia typically complex) *A. (Suandrena)*
- Propodeal triangle never alveolarly areolate; mesepisternum differently sculptured 26
- 26(25). Propodeal triangle more or less smooth and shining *A. (Hoplandrena)* (in part)
- Propodeal triangle rugosely areolated 27
- 27(26). First flagellar segment very short, at most half as long as second 28
- First flagellar segment more than half as long as second 30
- 28(27). Metasoma shining, strongly and densely punctate *A. (Cordandrena)*
- Metasoma shagreened to weakly shining, not very densely punctate 29
- 29(28). Clypeus and thorax shining, densely and strongly punctate *A. (Aenandrena)*
- Clypeus and thorax dull, sparsely and moderately finely punctate *A. (Thysandrena)*
- 30(27). First flagellar segment usually somewhat shorter than second, or at most as long as second 31
- First flagellar segment distinctly longer than second 32
- 31(30). Smaller species, less than 10 mm long; posterior metasomal terga usually with weakly developed, narrow bands *A. (Simandrena)*
- Larger species, over 10 mm long; posterior metasomal terga more or less bare *A. (Melandrena)* (in part)
- 32(30). Genitalia simple, gonostylus somewhat broadened toward apex and penis valve normally slender 33
- Genitalia distinctly complex, with gonostylus broadened, shovel-like, and/or penis valve laterally broadened 37
- 33(32). Length under 10 mm; mesepisternum and propodeum, including triangle, strongly rugosely wrinkled *A. (Micrandrena)* (in part)
- Length over 10 mm, *or*, if smaller, then mesepisternum and propodeum only shagreened to finely rugosely wrinkled 34
- 34(33). Mandibles long and sickle-shaped, crossed; terga finely and densely punctate with broad, shining marginal zones *A. (Hyperandrena)*
- Mandibles not long and crossed, *or*, if so, then terga with at most scattered punctures and marginal zones of normal width 35
- 35(34). Length less than 10 mm; mesepisternum shagreened and finely punctate *A. (Euandrena)*
- Length over 10 mm; mesepisternum abundantly rugosely wrinkled 36
- 36(35). Clypeus densely and deeply punctate; metasoma usually strongly punctate; first flagellar segment almost as long as second and third taken together *A. (Zonandrena)*
- Clypeus strongly convex, usually densely but shallowly punctate; metasoma usually finely and sparsely punctate; first flagellar segment usually only a little longer than second *A. (Melandrena)* (in part)
- 37(32). First recurrent vein meeting second submarginal cell usually distinctly before middle; marginal zones of terga usually strongly yellow to reddish yellow 38
- First recurrent vein at or usually beyond middle of second submarginal cell; marginal zones of terga at most weakly yellowish 39
- 38(37). First recurrent vein ending in vicinity of base of second submarginal cell; clypeus normally long and distinctly convex *A. (Pallandrena)*
- First recurrent vein ending little before middle of second submarginal cell; clypeus broader than long and flattened *A. (Ulandrena)* (in part)
- 39(37). Metasoma strongly and usually densely punctate; clypeus short and narrow, flattened *A. (Poliandrena)* (in part)
- Metasoma with scarcely perceptible to fine punctures; clypeus of normal length and convex or very broad 40
- 40(39). Small species; propodeal triangle shagreened, not rugose *A. (Avandrena)*
- Medium-sized species; propodeal triangle with conspicuous rugae near anterior margin *A. (Leucandrena)*
- 41(24). Mesepisternum and propodeum finely reticulately shagreened, shallowly and finely punctate; propodeal triangle reticulate to granularly shagreened 42
- Mesepisternum *or* propodeum *or* both rugosely areolate; propodeal triangle usually wrinkled to rugose 44
- 42(41). Malar area rather long *A. (Melitroides)*
- Malar area linear or very little elongated 43
- 43(42). Paraocular area in addition to clypeus yellow; scutum finely shagreened, finely, shallowly and sparsely punctate; metasoma almost bare *A. (Nobandrena)*
- Paraocular area and clypeus dark, rarely with small spot of yellow; scutum usually coarsely shagreened, punctures usually not evident or coarser and indistinct; metasoma usually relatively densely haired *A. (Scaphandrena)*
- 44(41). Small species; S8 strongly thickened on outer side, with several dense hair tufts *A. (Parandrenella)*
- Small to large species, if small, then S8 normal 45
- 45(44). Galeal blade short and narrow; labial palpus as long as or longer than glossa; paraocular area in addition to clypeus usually yellow 46
- Galeal blade normal to somewhat elongate; labial palpus shorter than glossa; paraocular area dark 47
- 46(45). Penis valve narrow, ventral lamella broadened laterally; apex of gonostylus narrowly shovel-shaped *A. (Poecilandrena)*
- Penis valve usually strongly bladder-shaped and enlarged; apex of gonostylus usually thickened and broadly shovel-shaped *A. (Ulandrena)* (in part)
- 47(45). Clypeus somewhat elongated; first submarginal crossvein meeting marginal cell only about three to four vein widths away from stigma *A. (Orandrena)*
- Clypeus short and relatively broad; first submarginal crossvein meeting marginal cell almost 10 vein widths away from stigma *A. (Poliandrena)* (in part) and *A. (Tarsandrena)* (in part)
- 48(9). Glossa conspicuously elongated and almost cylindrical 49
- Glossa short and more flattened 50

- 49(48). Body large; malar area well developed; genal area normally developed *A. (Didonia)* (in part)
 —. Body moderate-sized; malar area not unusual; posterior margin of genal area with tooth, or curved outward into carina *A. (Margandrena)*
 50(48). Mesepisternum strongly and deeply punctate; head thick, with short clypeus; genitalia simple
 *A. (Campylogaster)* (in part)
 —. Mesepisternum finely punctate or rugosely areolated; head not thickened; genitalia simple to complex 51
 51(50). Mandibles of normal length, apices at most somewhat crossed 52
 —. Mandibles long and sickle-shaped, apices more crossed over one another 54
 52(51). Mesepisternum alveolarly areolate; propodeum strongly and densely punctate, dorsal area sloping, scarcely developed *A. (Holandrena)* (in part)
 —. Mesepisternum shagreened and at most weakly rugosely wrinkled; propodeum shagreened to weakly rugose, shallowly and sparsely punctate, dorsal area, including triangle, more or less normally developed 53
 53(52). Propodeal triangle shagreened, with only a few flat and short rugae near anterior margin; metasoma shagreened and finely, inconspicuously punctate; clypeus dark; genitalia simple *A. (Cnemidandrena)*
 —. Propodeal triangle rugosely areolate; metasoma usually shiny and strongly punctate; clypeus usually yellow; genitalia complex
 *A. (Poliandrena)* (in part) and *A. (Tarsandrena)* (in part)
 54(51). Mesepisternum strongly rugose in longitudinal direction, almost undulate-areolate; clypeus and adjacent parts of face yellow; S8 with broad, isolated transverse carina on outer side before apex *A. (Holandrena)* (in part)
 —. Mesepisternum finely sculptured, never longitudinally undulate-areolate; paraocular area seldom yellow; S8 normal, with at most weak thickening before apex 55
 55(54). Posterior margin of genal area with outwardly curved carina, sometimes weak 56
 —. Posterior margin of genal area angular, forming a point 57
 56(55). Galeal blade of normal length; mesepisternum finely punctate; propodeal triangle shagreened with few short rugae near anterior margin; metasoma usually very finely punctate; gonostylar apex and penis valve scarcely broadened *A. (Carandrena)*
 —. Galeal blade short; mesepisternum strongly punctate; propodeal triangle shagreened and weakly rugosely areolate; metasoma usually conspicuously punctate; gonostylar apex and penis valve distinctly broadened
 *A. (Notandrena)*
 57(55). Clypeus yellow *A. (Larandrena)*
 —. Clypeus dark 58
 58(57). Clypeus flattened and broad, anterior margin usually distinctly indented; genitalia complex
 *A. (Andrena s. str.)*
 —. Clypeus usually distinctly convex, anterior margin not or weakly indented; genitalia simple 59
 59(58). Propodeal triangle rugosely wrinkled; first recurrent vein meeting second submarginal cell about in middle; first flagellar segment longer than second
 *A. (Ptilandrena)*
 —. Propodeal triangle smooth and shiny to shagreened,

without rugae; first recurrent vein meeting second submarginal cell far beyond middle; first flagellar segment usually very short, seldom longer than second
 *A. (Hoplandrena)* (in part)

Key to the Subgenera of *Andrena* of Japan (Females)
 (Modified from Hirashima, 1966a; I have not indicated here the doubts expressed by Hirashima concerning the placement of certain species of *Notandrena*, etc.)

1. Submarginal cells two *A. (Parandrena)*
 —. Submarginal cells three 2
- 2(1). Body length about or less than 7 mm; T1 impunctate or finely and sparsely punctate *A. (Micrandrena)*
 —. Body length about or more than 8 mm; if occasionally smaller, then T1 closely punctate 3
- 3(2). Propodeal triangle clearly indicated, coarsely roughened to strongly wrinkled, basal area bounded posteriorly by transverse carina or by strong wrinkles behind which surface is declivous 4
 —. Propodeal triangle finely sculptured, or, if coarsely sculptured, then apex of triangle not bounded by a transverse carina nor by irregular rugae 5
- 4(3). Facial fovea separated from eye by wide, shiny space; scutum and scutellum either foveolate-punctate or very strongly rugoso-punctate; inner hind tibial spur neither widened nor curved near base; trochanteral flocus incomplete, scanty; body length less than 10 mm
 *A. (Trachandrena)*
 —. Facial fovea and eye adjacent or separated by narrow space; scutum and scutellum rather strongly punctate but punctures not so close; inner hind tibial spur strongly widened and curved near base; trochanteral flocus complete or nearly so, dense; body length about or more than 12 mm *A. (Plastandrena)*
- 5(3). Tibial scopa well developed, composed of long, dense, branched hairs, and femoral scopal hairs also branched 6
 —. Tibial scopa and femoral scopa largely composed of simple hairs 7
- 6(5). Head elongate; clypeus protuberant *A. (Stenomelissa)*
 —. Head broader than long, more or less round in front view; clypeus not protuberant *A. (Chlorandrena)*
- 7(5). Third submarginal cell receiving second recurrent vein at end of cell or close to it *A. (Habromelissa)*
 —. Third submarginal cell receiving second recurrent vein well before end of cell 8
- 8(7). Middle basitarsus strongly expanded medially, subequal to or broader than hind basitarsus (the latter widened subbasally) *A. (Cnemidandrena)*
 —. Middle basitarsus slender, not widened medially (or at most only slightly so) 9
- 9(8). T1 densely, finely punctate; T2 and T3 progressively more sparsely, finely punctate; metasoma sparsely hairy, without distinct hair fringes; posterior margins of metasomal terga yellowish-transparent; clypeus densely tessellate, dull, sparsely and more or less weakly punctate, with broad, median, longitudinal, impunctate space; antenna short, swollen toward apical segments, first flagellar segment one and one-half times as long as broad, about as long as second plus third segments; scutum tessellate, more or less weakly punctate, covered with rather short, pale fulvous hairs; propodeal triangle well indicated, distinctly

- wrinkled all over; propodeum outside triangle densely rugulose or nearly shagreened; robust species, length about or less than 8 mm *A. (Poecilandrena)*
- T1 impunctate or nearly so, or, *if* densely punctate, then larger and without combination of characters listed above 10
- 10(9). Metasoma with integument densely tessellate, therefore dull, impunctate or with indications of weak, sparse punctures; posterior margins of T3 and T4 each with complete, narrow band of short, dense, appressed, white hairs, a similar hair band usually on posterior margin of T2; interior of propodeal corbícula with sparse, usually coarse, simple hairs throughout *A. (Hoplandrena)*
- Metasoma with integument either smooth or distinctly punctate, but *if* tessellate and impunctate (as in *Andrena* s. str. and some species of *Euandrena*), then appressed tergal hair bands lacking and/or propodeal corbícula without coarse hairs on interior surface 11
- 11(10). Metasoma tessellate, impunctate, dull or slightly shiny; trochanteral flocus complete, well developed *A. (Andrena* s. str.)
- Metasoma smooth and/or distinctly punctate, *if* tessellate and impunctate, then trochanteral flocus incomplete and scanty 12
- 12(11). Inner hind tibial spur widened and curved near base (usually rather large and robust species) 13
- Inner hind tibial spur at most gently curved, neither widened nor curved near base 14
- 13(12). Triangle of propodeum large, well indicated, sparsely wrinkled; propodeum outside triangle densely tessellate and densely rugose *A. (Plastandrena)*
- Triangle of propodeum rather large to small, more or less well defined, rugose to coarsely sculptured; propodeum outside triangle densely punctate *A. (Holandrena)* (in part)
- 14(12). Propodeal corbícula well developed, with dorsal fringe of long, dense, well-arranged, curled hairs, and with complete fringe of hairs anteriorly, interior of corbícula free of hairs medially; hind tibia rather short, dilated apically *A. (Simandrena)*
- Propodeal corbícula poorly developed or at most moderately so, without fringe of hairs anteriorly, usually hairy on interior; hind tibia normal 15
- 15(14). Propodeal corbícula moderately well developed, with dorsal fringe of long, dense, rather well- to well-arranged hairs, interior of corbícula with coarse, simple hairs throughout, no complete fringe of hairs anteriorly, but frequently sparse branched hairs present on dorsal portion of anterior margin; trochanteral flocus incomplete, scanty to dense; tibial scopa compact, well developed; facial fovea separated from eye by a narrow punctate space; medium-sized to large, robust species *A. (Melandrena)*
- Propodeal corbícula poorly developed, with dorsal fringe of short, scanty hairs; or, *if* propodeal corbícula more or less well developed, then without combination of characters listed above 16
- 16(15). Propodeal corbícula with sparse, coarse, simple hairs nearly throughout interior; dorsal fringe of corbícula rather well indicated but not well developed, rather short and not especially dense; no fringe of hairs on anterior margin of corbícula; trochanteral flocus complete, dense; metasoma smooth and shiny, weakly to very weakly punctate; interocellar distance equal to or a little longer than ocellocipital distance *A. (Holandrena)* (in part)
- Propodeal corbícula with soft, fine hairs in interior; or, *if* coarse hairs present in interior, then without combination of characters listed above 17
- 17(16). Metasoma short-oval, densely tessellate-punctate, nearly dull or weakly shiny, posterior margins of intermediate terga with narrow, appressed, pure-white hair bands, those of T3 and T4 complete; head broad and thin, nearly round in front view; clypeus hardly convex, tessellate, coarsely rugoso-punctate; basal area of labrum short, transverse, apex narrowly bilobed; scutum tessellate, rather densely punctate, covered with short, dull, pale, yellowish-brown hairs; propodeum roughened, triangle poorly defined, rugose basally, granulate apically; trochanteral flocus nearly complete, white; tibial scopa silver-white, narrowly brownish above basally, composed of rather coarse hairs *A. (Taeniandrena)*
- Metasoma elliptical or elongate, smooth and shiny, or, *if* terga tessellate as in some species of *Euandrena*, then without combination of characters listed above 18
- 18(17). Metasomal terga tessellate, sometimes weakly so, therefore nearly dull or weakly shiny, impunctate or rarely with weak punctures; metasoma more or less hairy, posterior margins of intermediate terga with loose to more or less compact hair fringes; propodeal corbícula poorly developed, with dorsal fringe of loose or more or less well-arranged, rather long hairs, interior with sparse, fine hairs; trochanteral flocus incomplete, scanty; tibial scopa well developed; dorsal surface of propodeum shagreened to roughened; propodeal triangle finely to rather finely sculptured, usually less coarsely sculptured than rest of dorsal surface of propodeum; facial fovea rather narrow, upper end occupying about or less than one-half distance between eye and posterior ocellus; head and thorax with rather abundant, not especially long hairs; rather small species *A. (Euandrena)*
- Metasomal terga, especially basal ones, smooth and shiny, or, *if* rarely very finely tessellate, then without combination of characters listed above; metasoma sparsely hairy, at least T1 bare dorsally 19
- 19(18). Mesopleura coarsely sculptured or at least rugose above, or with distinct punctures; dorsal surface of propodeum coarsely sculptured or at least shagreened; dorsal fringe of propodeal corbícula long, rather well to well arranged; trochanteral flocus usually complete *A. (Notandrena)*
- Mesopleura finely tessellate, with or without weak, well-separated small punctures; dorsal surface of propodeum nearly smooth or at most densely tessellate, usually with weak, well-separated, small punctures; dorsal fringe of propodeal corbícula poor, composed of rather short to short, rather sparse to sparse hairs; trochanteral flocus nearly incomplete 20
- 20(19). Facial fovea very broad, with upper end occupying full space between eye and posterior ocellus; propodeal triangle large, with lateral margins convex outward; mesopleura weakly tessellate with distinct, well-separated punctures; tibial scopa compact, with hairs well arranged, not loose *A. (Calomelissa)*
- Facial fovea much narrower; propodeal triangle large,

subtriangular, with sides not convex outward; mesopleura densely tessellate, impunctate or with an indication of weak punctures; tibial scopa large, composed of long, rather loose hairs *A. (Oreomelissa)*

Key to the Subgenera of *Andrena* of Japan (Males)
(Modified from Hirashima, 1966a)

1. Clypeus and frequently lower paraocular area ivory-white or yellow 2
- Clypeus black 9
- 2(1). Malar area approximately as long as broad; apical segment of antenna uncinata *A. (Stenomelissa)*
- Malar area linear; apical segment of antenna normal 3
- 3(2). Second recurrent vein at end of third submarginal cell, meeting third submarginal crossvein or nearly so *A. (Habromelissa)*
- Second recurrent vein much basad of third submarginal crossvein 4
- 4(3). Clypeus strongly convex mediosubapically, ivory white medially *A. (Notandrena)* (in part)
- Clypeus not strongly convex, largely yellow or ivory-white 5
- 5(4). Length about 6 mm, or occasionally slightly larger; metasomal terga, including T1, finely and densely punctate; propodeal triangle coarsely sculptured; dorsal surface of propodeum roughened; flagellum beneath yellowish brown; first flagellar segment approximately one and one-half times as long as broad, second much broader than long, about one-half as long as first, third as long as broad *A. (Poecilandrena)*
- Length more than 7 mm; or, *if* occasionally smaller, then without combination of characters listed above 6
- 6(5). Head and thorax with abundant brown to blackish hairs, or at least with admixture of brown hairs 7
- Head and thorax without admixture of brown hairs, primarily covered with yellowish hairs 8
- 7(6). Clypeus and lateral face marks ivory-white or only slightly yellowish; vertex strongly arched in front view *A. (Oreomelissa)*
- Clypeus yellow, lateral face marks usually lacking; vertex not arched or only slightly convex in front view *A. (Calomelissa)*
- 8(6). Basal area of labrum rather small, not reflexed at apex, slightly emarginate; propodeal triangle rugulose to rugose basally, tessellate apically, shiny; body length about or less than 9 mm *A. (Chlorandrena)* (in part)
- Basal area of labrum rather large, transverse, reflexed and deeply emarginate at apex; propodeal triangle rugulose or wrinkled all over; body length about 10 mm *A. (Holandrena)*
- 9(1). First flagellar segment at most as long as broad, about one-half as long as second; third and following segments about twice as long as broad, distinctly convex in front; malar area usually with sharp spine posteriorly in spring form (only) *A. (Hoplandrena)*
- First flagellar segment longer than broad, or, *if* occasionally shorter, then without combination of characters listed above 10
- 10(9). Mandible long, slender, falciform, with triangular tooth or projection near base of inner margin *A. (Andrena s. str.)* (in part)
- Mandible variable, without tooth basally 11
- 11(10). Mandible slender, curved, with sharp falciform apex; malar area evident, about one-third as long as broad; first flagellar segment slightly longer than broad, much shorter than elongate second segment (about 3:4.2); face covered with pale yellowish hairs; paraocular area, frons, and gena near eye with black hairs; length about 9 mm *A. (Andrena s. str.)* (in part)
- Mandible normal, or, *if* falciform, then without combination of characters listed above 12
- 12(11). Propodeal triangle strongly and rather sparsely wrinkled, bounded by a transverse carina posteriorly 13
- Propodeal triangle not bounded by a transverse carina posteriorly 15
- 13(12). Apical margins of metasomal terga reflexed *A. (Plastandrena)* (in part)
- Apical margins of metasomal terga normal 14
- 14(13). Length about 10 mm; lower paraocular area with punctures more obscure than those on clypeus; propodeal triangle with wrinkles irregular *A. (Plastandrena)* (in part)
- Length less than 9 mm; lower paraocular area with punctures distinct; propodeal triangle with wrinkles longitudinal *A. (Trachandrena)*
- 15(12). Length about or less than 7 mm; propodeal triangle large, weakly and rather coarsely sculptured; second submarginal crossvein ending close to stigma *A. (Micrandrena)*
- Length greater than 7 mm; propodeal triangle finely sculptured, or, *if* coarsely sculptured, then second submarginal crossvein ending well away from stigma 16
- 16(15). Basal area of labrum protuberant *A. (Cnemidandrena)*
- Basal area of labrum not protuberant 17
- 17(16). Gena well developed, carinate posteriorly *A. (Notandrena)*
- Gena normal 18
- 18(17). First flagellar segment slightly longer than second plus third, these broader than long *A. (Chlorandrena)* (in part)
- First flagellar segment shorter than next two segments taken together 19
- 19(18). Ocelloccipital distance about or more than twice as long as ocellar width *A. (Melandrena)*
- Ocelloccipital distance approximately equal to ocellar width 20
- 20(19). Propodeal triangle rather strongly wrinkled (metasoma very shiny, feebly tessellate, with an indication of sparse fine punctures; posterior margins of T2-T4 with lateral fringes of sparse white hairs; scutellum nearly smooth and shiny anteriorly; first flagellar segment much longer than second, second about as long as broad) *A. (Notandrena)* (in part)
- Propodeal triangle less strongly wrinkled 21
- 21(20). Propodeal triangle large, densely, rather weakly wrinkled all over *A. (Simandrena)*
- Propodeal triangle differently sculptured 22
- 22(21). Ocelloccipital distance longer than posterior ocellar diameter; metasomal terga tessellate, with distinct, close punctures *A. (Taeniandrena)*
- Ocelloccipital distance at most as long as posterior ocellar diameter; metasomal terga tessellate, impunctate *A. (Euandrena)*

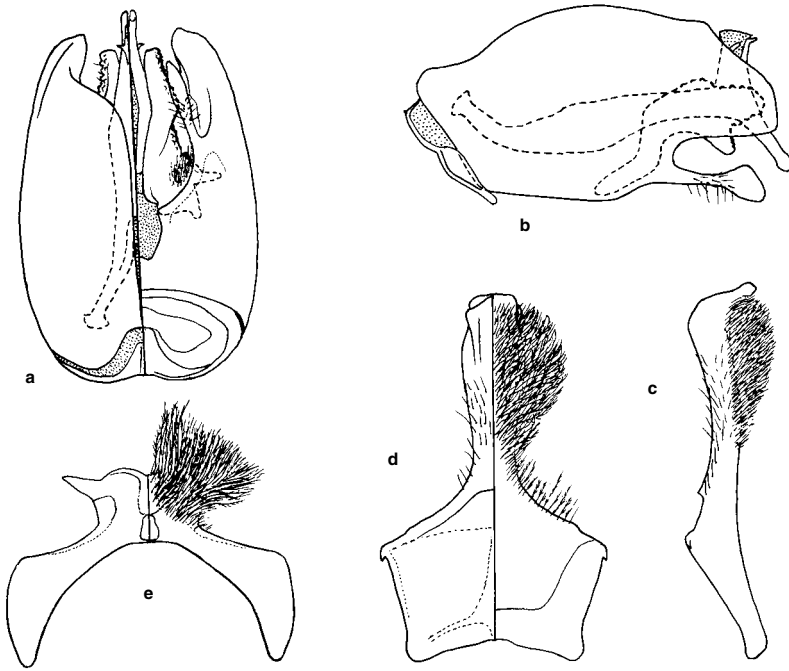


Figure 51-7. *Megandrena enceliae* (Cockerell). **a-e**, Male genitalia (dorsoventral and lateral views), S8 (dorsoventral and lateral views), and S7 (dorsoventral view). (Dorsal views are at the left.) Note the reduced gonobase and enormous volsella of the genitalia. From Michener, 1986c.

This genus contains two subgenera, both from the deserts of the southwestern United States. They were well differentiated by Zavortink (1972).

Key to the Subgenera of *Megandrena*

- 1. Long hairs of fore tarsus of female curved; gonobase of male absent or completely enclosed in bases of gonocoxites *M. (Erythrandrena)*
- Long hairs of fore tarsus of female straight; gonobase of male present, a narrow ring (Fig. 51-7a, b) *M. (Megandrena s. str.)*

Megandrena / Subgenus *Erythrandrena* Zavortink

Megandrena (Erythrandrena) Zavortink, 1972: 61. Type species: *Megandrena mentzeliae* Zavortink, 1972, by original designation.

In this subgenus the metasoma is largely red with apical white tergal hair bands. The head of the male is particularly large and broad. The body length is 12 mm. Structures including male genitalia were illustrated by Zavortink (1972). The characteristics of the subgenus are so distinctive (e.g., virtual absence of a gonobase) that subgeneric recognition seems justified even though the genus *Megandrena* contains only two species.

■ *Erythrandrena* is known only from southern Nevada, USA. The single species is *Megandrena mentzeliae* Zavortink, a visitor to flowers of *Mentzelia tricuspidis*.

Megandrena / Subgenus *Megandrena* Cockerell s. str.

Andrena (Megandrena) Cockerell, 1927a: 42. Type species: *Andrena enceliae* Cockerell, 1927, by original designation.

In this subgenus the metasoma is black with strong, white apical tergal hair bands. The body length is 13 to 16 mm. Noteworthy features of the male terminalia are the enormous volsellae, a distinct although membranous bridge between the volsellae, the apparently bifid gonocoxite (the slender, spatulate lower ramus probably represents the gonostylus, the upper one, a gonocoxal lobe), the reduced gonobase, and the divergent hairy lobes of S7. These structures were illustrated by Michener (1986c); see Figure 51-7.

■ This subgenus is found in the deserts of southern California, Nevada, and Arizona, USA. It, too, contains a single species, *Megandrena enceliae* (Cockerell), which visits, and may be oligolectic on, flowers of *Larrea*.

Genus *Orphana* Vachal

Orphana Vachal, 1909a: 35, 38. Type species: *Orphana inquirenda* Vachal, 1909, monobasic.

Leptoglossa Friese, 1925a: 9 (not Klug, 1839). Type species: *Leptoglossa paradoxa* Friese, 1925 = *Orphana inquirenda* Vachal, 1909, monobasic.

Proleglossa Friese, 1930: 127, replacement for *Leptoglossa* Friese, 1925. Type species: *Leptoglossa paradoxa* Friese, 1925 = *Orphana inquirenda* Vachal, 1909, autobasic.

This genus and *Euherbstia* differ from other Andreninae in their lack of depressed, hairy facial foveae in the

turgini and into the Panurgini, then the arrangements would be compatible. The distinctions indicated by Ruz (1986), and in the account below, between Melitturgini and Panurgini are not particularly impressive and Patiny's cladograms may be correct in associating *Mermiglossa* and *Plesiopanurgus* with the Panurgini rather than with the Melitturgini.

Since two major groups of Panurginae of the Eastern Hemisphere, Panurgini and Melitturgini, seem recognizable, I prefer to use them as tribes rather than recognizing six tribes, for the total number of genera (as recognized by Patiny, 1999b) is only nine; three of his tribes contain only one genus each. Recognition of subtribes might be appropriate.

A review of panurgine biology with many references to older literature was published by Rozen (1967a), and supplemented by Rozen (1989c) on the Protandrenini. The nests are burrows in the ground, with branches ending in isolated, usually subhorizontal cells or occasionally small series of cells. At least in the Perditini, Melitturgini, and Panurgini, many species are communal, and sometimes the nest burrows become many-branched systems. The cells are doubtfully flattened on their lower surfaces, or not flattened at all so that in cross section they appear to be circular. The walls of the cells are smooth, lined or partly lined with a secreted shiny "waxlike" membrane, except in the genus *Perdita*, in which the walls are unlined, or (in *P. graenicheri* Timberlake) are thinly lined, perhaps with nectar (Norden, Krombein, and Danforth, 1992). The larval food mass is spherical or somewhat flattened, the egg laid on top of it, and the food mass is covered with a waxy membrane in *Perdita*, *Calliopsis*, and at least some other Calliopsini (J. Rozen, personal communication, 1995). When the larva is large enough, it lies on its back, supported by large dorsal tubercles, with the partly eaten provisions on its venter, safeguarded from contact with the cell wall and possible moisture. When mature, the larva defecates onto the upper rear of the cell, except in the genus *Perdita*, in which the feces rest on the venter of the larva or prepupa. Prepupae pass any unfavorable season (e.g., winter) lying on their backs, supported by strong dorsal tubercles that reduce contact with the cell wall to several small points and thus perhaps reduce the probability of mold starting in extensive moist contacts with the cell wall.

Most Panurginae are oligolectic. Even within a single genus like *Perdita*, species are restricted to plants in diverse and unrelated families (see Sec. 6). Unlike Andreninae, most Panurginae transport pollen in a firm mass, apparently moistened with nectar, on each hind tibia, as do corbiculate Apidae. In *Panurgus* (Rozen, 1971b), however, and in certain subgenera of *Perdita*, pollen is carried dry on the scopa. Although for bees as a whole, dry transport is probably plesiomorphic, I suspect that it is derived in Panurginae. This behavior should be investigated more thoroughly in relation to phylogeny and scopal structure.

Key to the Tribes of Panurginae

1. S6 of female with curved (i.e., lateral parts oblique) marginal band of dense hairs (Fig. 59-3d), the band sometimes broken medially, elsewhere S6 with only widely scattered minute hairs; base of S6 of female with two

broad membranous lobes (visible only on dissection) occupying space between apodemes (Fig. 59-3d); S5 of female with distal margin convex medially; gonostylus of male absent or reduced to small projection usually not reaching middle of penis valve, the latter enormous and complex (Fig. 59-3a, e, h); anterior tentorial pit in outer subantennal suture (Fig. 59-1) (Western Hemisphere)

- Calliopsini (Sec. 59)
- S6 of female with marginal hair band undefined, poorly defined (Figs. 53-6g, 57-1d), or transverse (not curved), S6 commonly with moderate-sized hairs basal to band (in a few Melitturgini, especially *Plesiopanurgus*, very like Calliopsini but the band less curved); base of S6 of female without membranous lobes between apodemes (Figs. 53-6g, 57-1d); S5 of female with distal margin nearly straight to concave; gonostylus of male well developed, usually nearly reaching or exceeding apex of penis valve (or directed downward in *Neffapis*); penis valve variable in complexity; anterior tentorial pit at intersection of epistomal and outer subantennal sutures, or below, in epistomal suture, except in *Nolanomelissini* and some Melitturgini, in which it is in outer subantennal suture..... 2
- 2(1). Marginal cell usually much shorter than, usually about half as long as, distance from its apex to wing tip, broadly truncate, margin on costa little if any longer than stigma (Figs. 58-1, 58-2); submarginal cells two, or, rarely, a minute, petiolate intercalary cell between first and second; second submarginal cell (or third if there is a petiolate intercalary cell) less than two-thirds as long as first, rarely absent; integument often metallic and often with yellow markings; upper margin of hind tibia of male usually not toothed (North America) Perditini (Sec. 58)
- Marginal cell slightly shorter to longer than distance from its apex to wing tip, moderately to narrowly and often obliquely truncate, margin on costa usually longer than stigma; submarginal cells two or three, and if two, then second submarginal cell at least two-thirds as long as first on posterior margin; integument usually non-metallic, but if metallic, then with no yellow on metasoma; upper margin of hind tibia of male nearly always carinate or toothed (indistinctly carinate in *Nolanomelissini*) 3
- 3(2). Labial palpus with first two segments elongate (first over twice length of second), rather flattened; third segment arising preapically on second and directed laterally (as in L-T bees), third and fourth segments similar and small (Fig. 52-1c); basal vein strongly curved (uniformly curved, the curve not principally near base as in Halictinae); T7 of male strongly curled forward, with strong, blunt, apicolateral tooth (Brazil) 3
- Protomelitturgini (Sec. 57)
- Labial palpus with all segments similar to one another or only first strongly elongate (as in Fig. 52-1h), first three elongate in *Nolanomelissa* and *Plesiopanurgus*, or first shortest; third segment arising apically on second, last segments thus not directed laterally; basal vein straight or gently curved; T7 of male usually not strongly curled, lacking apicolateral tooth..... 4
- 4(3). Stigma slender, almost parallel-sided, margin within marginal cell straight or nearly so; facial fovea of male absent (weakly evident in some species of *Melitturgula*);

- valve of first valvula of sting reduced or absent (except in *Melitturgula*); inner orbits of male diverging below (except in *Plesiopanurgus*, which has the inner orbits sinuous, and the antenna thickened with the last segment pointed) 5
- Stigma wider, broadest at level of vein r (Figs. 53-1, 53-2), margin within marginal cell convex except in *Liphanthus*; facial fovea of both sexes present (weakly defined in some males of *Panurgus*); valve of first valvula of sting usually well developed; inner orbits of male parallel or converging below [except somewhat diverging below in *Psaenythia*, *Rhophitulus* (*Cephalurgus*), and *Panurgus* (*Flavipanurgus*)] 6
- 5(4). Hind tibia of male with dorsal carina distinct, toothed; inner orbits of female parallel or convergent below; labial palpus with segment 4 well developed, other segments variable but less sheathlike, second not the longest (palearctic region and Africa) *Melitturgini*
- Hind tibia of male with dorsal carina inconspicuous, not toothed; inner orbits of female divergent below; labial palpus with segment 4 minute, segments 1-3 elongate, 2 and 3 sheathlike, fitting around glossa, segment 2 longest (Chile) *Nolanomelissini*
- 6(4). Episternal groove absent, short, or curving into and joining scrobal groove; T2-T5 of male with marginal zones usually hairy; foramen of male genitalia in deep sinus between bases of gonocoxites, its two halves facing one another (Fig. 54-3a, e, k) (holarctic) *Panurgini* (Sec. 54)
- Episternal groove usually extending below scrobal groove, not curving to join scrobal groove; T2-T5 of male with marginal zones glabrous; genital foramen of male exposed at bases of gonocoxites (Fig. 53-6a, d) (Western Hemisphere) *Protandrenini* (Sec. 53)

53. Tribe Protandrenini

This is perhaps a paraphyletic tribe, one recognized principally by ancestral characters. Although Ruz (1986), in her taxonomic treatment, recognized it (as *Anthemurgini*) in its present sense for reasons of convenience, because the groups within it are morphologically similar and difficult to key out, in her phylogenetic treatment she divided it into four tribes. These were the *Lipanthini* (for *Lipanthus*), the *Protandrenini* (for *Protandrena*), the *Austropanurgini* (for *Austropanurgus*), and the *Anthemurgini* (for all other genera). The recognition of four tribes, three of them monotypic, that differ little from one another seems unnecessary and also unwise, considering the lack of robustness in this part of the cladogram (see the discussion under *Protandrena*).

The tribe *Protandrenini*, as here understood, consists of relatively slender, nearly all nonmetallic bees, almost always with yellow on the face of males, sometimes with yellow markings on all tagmata of both sexes, and occasionally with the metasoma red. Usually there are two submarginal cells, but in several genera there are three (Fig. 53-1). Apical hair bands on the metasomal terga are ordinarily absent. S7 of the male has two large apical lobes (small in *Lipanthus*, Fig. 53-4g-j) and the disc, to the extent that it is recognizable, is sometimes quite narrow (Figs. 53-3 to 53-6), suggesting the style common in Colletidae. The male gonostyli are rather large, at least half as long as the gonocoxites, and freely articulated to completely fused with the gonocoxites.

This tribe is abundant in North America and in temperate South America, and rare but present in the intervening moist tropics. It is not found in the Old World.

An Argentine bee of unknown relationship, but possibly a protandrenine, was named *Stenocolletes pictus* Schrottky; see the comments under that generic name below (it is not included in either key).

Key to the Genera of the Protandrenini (Males) (Modified from Ruz, 1986)

- 1. Forewing with three submarginal cells (Fig. 53-1) 2
- Forewing with two submarginal cells (Fig. 53-2) 6
- 2(1). Eye pilose; pronotum with strong transverse dorsal lamella; punctation on parts of thorax strong, contiguous (South America) *Parapsaenythia*
- Eye glabrous; pronotum with rounded ridge on dorsal margin; punctation well marked, usually not contiguous, to fine, weak 3
- 3(2). Stigma only slightly wider than prestigma, as measured to wing margin, sides subparallel or converging slightly basad from vein r, margin within marginal cell straight; T2 with narrow, deep postgradular depression, shallower on succeeding terga (South America)
..... *Lipanthus* (in part)
- Stigma clearly wider than prestigma, sides converging basad from vein r, margin within marginal cell at least slightly convex (Fig. 53-1); T2 with postgradular depression usually shallow, always similar on succeeding terga 4
- 4(3). Metasoma usually with yellow markings; T2 with lat-

- eral fovea well developed; mandible with preapical tooth (South America) *Psauenythia*
- Metasoma without yellow markings (except in *Protandrena maculata* Timberlake); T2 with lateral fovea shallow; mandible simple 5
- 5(4). Paraocular area medially depressed, flat below; tentorial pit at intersection between outer subantennal and epistomal sutures; propodeal triangle pilose (South America) *Anthrenoides*
- Paraocular area convex; tentorial pit in epistomal suture below intersection of outer subantennal suture; propodeal triangle usually glabrous (North and Central America) *Protandrena* s. str.
- 6(1). Glossa and labial palpus reaching middle of metasoma in repose, labial palpus three-segmented, third segment longer than first and second combined (Fig. 19-5c, d); maxillary palpus two-segmented; gonostylus directed downward at right angle to gonocoxite (Chile) *Neffapis*
- Glossa and labial palpus not reaching beyond base of metasoma in repose, labial palpus four-segmented; maxillary palpus six-segmented; gonostylus directed posteriorly at side of penis valve 7
- 7(6). Stigma only slightly wider than prestigma, as measured to wing margin, sides subparallel or converging slightly basad from vein r, margin within marginal cell straight; T2 with narrow, deep postgradular depression, shallower on succeeding terga (South America)
..... *Lipanthus* (in part)
- Stigma clearly wider than prestigma, sides converging basad from vein r, the margin within marginal cell at least slightly convex (Fig. 53-2); T2 with postgradular depression usually shallow, always similar on succeeding terga 8
- 8(7). Head wider than thorax; orbits somewhat divergent below [Some wide-headed species of *Rhopitulus* s. str. might run here; for additional characters, see account of the genus.] (South America) *Rhopitulus* (*Cephalurgus*)
- Head usually narrower than thorax; orbits at least slightly convergent below 9
- 9(8). Propodeal triangle hairless 10
- Propodeal triangle with hairs on at least lateral third .. 12
- 10(9). Punctation strong, punctures usually contiguous on some areas of thorax; omaulus sharp, at least dorsally; hind tibia with upper margin a strong, untoothed carina (Fig. 52-6j) (North and Central America)
..... *Pseudopanurgus*
- Punctation well marked but punctures not contiguous to fine, weak; omaulus smoothly curved from lateral to anterior mesepisternal surfaces; hind tibia with upper margin at least at base carinate with teeth or serrate (as in Fig. 53-6i) [but untoothed in *Protandrena* (*Pseudosarus*)] 11
- 11(10). Antennal flagellum about as long as head; propodeal triangle polished; tentorial pit far below intersection of outer subantennal and epistomal sutures (Brazil)
..... *Chaeturginus*
- Antennal flagellum clearly longer than head; propodeal triangle striate basally; tentorial pit at intersection of

- outer subantennal and epistomal sutures or just below it *Protandrena* (in part)
- 12(9). First flagellar segment about as long as second; genitalia with basal dorsal gonobase-like sclerotization; digitus (mesal lobe) of volsella prolonged, parallel-sided in ventral view, longer than rest of volsella (Fig. 53-3a) *Rhopitulus* s. str.
- First flagellar segment longer than second; gonobase entirely absent; digitus of volsella not parallel-sided, shorter than rest of volsella 13
- 13(12). Yellow on lower half of face, areas of thorax, and legs; antennal flagellum longer than head; glossa somewhat shorter than to longer than prementum; metasoma red or partly red (nearctic) *Protandrena* (*Metapsaenythia*)
- Yellow limited to small, faded spots on face; antennal flagellum shorter than head; glossa about half as long as prementum (Fig. 51-1a); metasoma black (nearctic) *Anthemurgus*

Key to the Genera of the Protandrenini (Females)
(Modified from Ruz, 1986)

1. Forewing with three submarginal cells (Fig. 53-1) 2
- Forewing with two submarginal cells (Fig. 53-2) 6
- 2(1). Eye pilose; pronotum with dorsal margin a strong lamella (at least laterally); T2 to T5 with complete or interrupted median (not apical) hair bands (South America) *Parapsaenythia*
- Eye glabrous; pronotum with dorsal margin a rounded ridge; metasomal terga without hair bands, except in some species of *Protandrena* s. str. 3
- 3(2). Metasomal terga usually with yellow markings; middle tibial spur with coarse teeth; hind femur on inner surface with longitudinal ridge (Fig. 53-6h); T1 to T5 densely punctate (South America) *Psaenythia*
- Metasomal terga with no yellow markings (except in *Protandrena maculata* Timberlake from Mexico); middle tibial spur with fine teeth; hind femur on inner surface without longitudinal ridge; T1 to T5 with punctures separated by spaces as wide as punctures or wider 4
- 4(3). Stigma little wider than prestigma, as measured to wing margin, sides of stigma subparallel or slightly convergent basad from vein r, margin within marginal cell straight (lower paraocular area slightly convex) (South America) *Lipanthus* (in part)
- Stigma about twice as wide as prestigma or wider, sides strongly convergent basad from vein r, margin within marginal cell at least slightly convex (Fig. 53-1) 5
- 5(4). Face black; paraocular area concave medially and below; tentorial pit at intersection of outer antennal and epistomal sutures; propodeal triangle pilose (inner orbits subparallel) (South America) *Anthrenoides*
- Face often with yellow on lower half; paraocular area convex; tentorial pit in epistomal suture below intersection with outer subantennal suture; propodeal triangle glabrous (North and Central America) *Protandrena* s. str.
- 6(1). Glossa and labial palpus reaching middle of metasoma in repose, labial palpus three-segmented, third segment longer than first and second combined (Fig. 19-5c, d); maxillary palpus two-segmented (Chile) *Neffapis*
- Glossa and labial palpus not reaching base of metasoma in repose, labial palpus four-segmented; maxillary palpus six-segmented 7

- 7(6). Stigma little wider than prestigma, as measured to wing margin, the margin within marginal cell straight (South America) *Lipanthus* (in part)
- Stigma about twice as broad as prestigma, as measured to wing margin, margin within marginal cell at least slightly convex (Fig. 53-2) 8
- 8(7). S2 to S5 or at least 54 each with irregular row of coarse setae on premarginal area (Fig. 53-3g) (face with conspicuous yellow marks; middle tibial spur finely toothed) (Brazil *Chaeturginus*
- S2 to S5 with normal hairs on premarginal areas 9
- 9(8). Fore coxa with well-developed, hairy, apical spine or process (Fig. 53-6k); middle tibial spur with small, fine, dense teeth (North and Central America) *Pseudopanurgus*
- Fore coxa unmodified; middle tibial spur usually with distal teeth larger and better spaced than basal ones 10
- 10(9). Glossa about half as long as prementum; first segment of labial palpus less than half length of second to fourth segments taken together (Fig. 52-1a) (nearctic) *Anthemurgus*
- Glossa somewhat shorter than to longer than prementum; first segment of labial palpus about as long as second to fourth segments taken together, or longer 11
- 11(10). Lateral third of propodeal triangle with hairs (South America) *Rhopitulus*
- Propodeal triangle bare *Protandrena* (in part)

Genus *Anthemurgus* Robertson

Anthemurgus Robertson, 1902b: 321. Type species: *Anthemurgus passiflorae* Robertson, 1902, monobasic.

At least superficially, the bees of this genus resembles *Protandrena* (*Heterosarus*), although slightly more robust. The female is entirely black and the male has very restricted yellowish facial marks. The body length is 6 to 8 mm. *Anthemurgus* differs from related Protandrenini in its short mouthparts, the glossa being about half as long as the prementum and less than twice as long as broad,

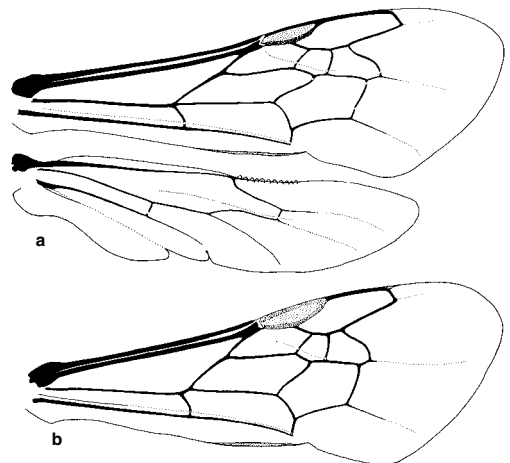


Fig. 53-1. Wings of Protandrenini with three submarginal cells. a, *Psaenythia bergi* Holmberg; b, *Anthrenoides meridionalis* (Schrottky).

Chaeturginus are the irregular, partly double row of very coarse setae on each sternum, S2 to S5, of the female (Fig. 53-3g) or on S4 only, in which case (*C. alexanderi* Ruz and Melo) similar setae are on the ventral part of the mesepisternum; and the few very long, coarse, setae arising from the lacinia (Fig. 52-1d, e). Moreover, the lower ends of the inner and outer subantennal sutures meet or are close together at the epistomal suture, so that the elongate subantennal area scarcely or only narrowly reaches the clypeus; no other panurgine exhibits this character. These and other features were illustrated by Lucas de Oliveira and Moure (1963) and Ruz (1986).

■ This genus is known from the states of Amazonas and Pará south to São Paulo, Brazil. *Chaeturginus testaceus* (Ducke) is from Amazonas and Pará. Another species, *C. alexanderi* Ruz and Melo from São Paulo and Minas Gerais, has the outer subantennal suture scarcely indicated, an unusual feature for a panurgine.

Genus *Liphanthus* Reed

Liphanthus consists of mostly minute (3-7 mm long) black bees frequently bearing yellow markings, sometimes including metasomal areas, and the metasoma sometimes red. Most species have three submarginal cells, a few species, only two. Although most small bees have a relatively large stigma, that of *Liphanthus* is narrow, scarcely widened toward vein r, and the margin within the marginal cell is straight. In most species the male anten-

nae are unusually long (Fig. 53-4a-c), the middle flagellar segments over twice as long as broad. S7 of the male is distinctive, with a small body but the usual large apodemal lobes, and without or with small apical lobes (Fig. 53-4g-j). The male gonostyli, much shorter than the gonocoxites, are articulated to the lower distal surfaces of the gonocoxites, and are thus quite different from those of other genera, in which the gonostyli are partly or fully fused to the gonocoxites or articulated to the extreme apices of the gonocoxites. Ruz and Toro (1983) illustrated male genitalia, sterna, and other structures; see also Figure 53-4.

Liphanthus is best known in Chile from Antofagasta to Chile Chico, but also occurs in Argentina from Jujuy to Santa Cruz Province. There are 26 described species. The genus was revised by Ruz and Toro (1983).

Key to the Subgenera of *Liphanthus* (Males)
(Based on Ruz and Toro, 1983)

- 1. Submarginal cells two; propodeal triangle laterally less than half length of metanotum (laterally) *L. (Neoliphanthus)*
- Submarginal cells three; propodeal triangle laterally more than half length of metanotum (laterally) or almost the same length 2
- 2(1). Hind tibial spurs with apices curved like claws, subequal in length; vertex concave or almost straight in frontal view *L. (Xenoliphanthus)*

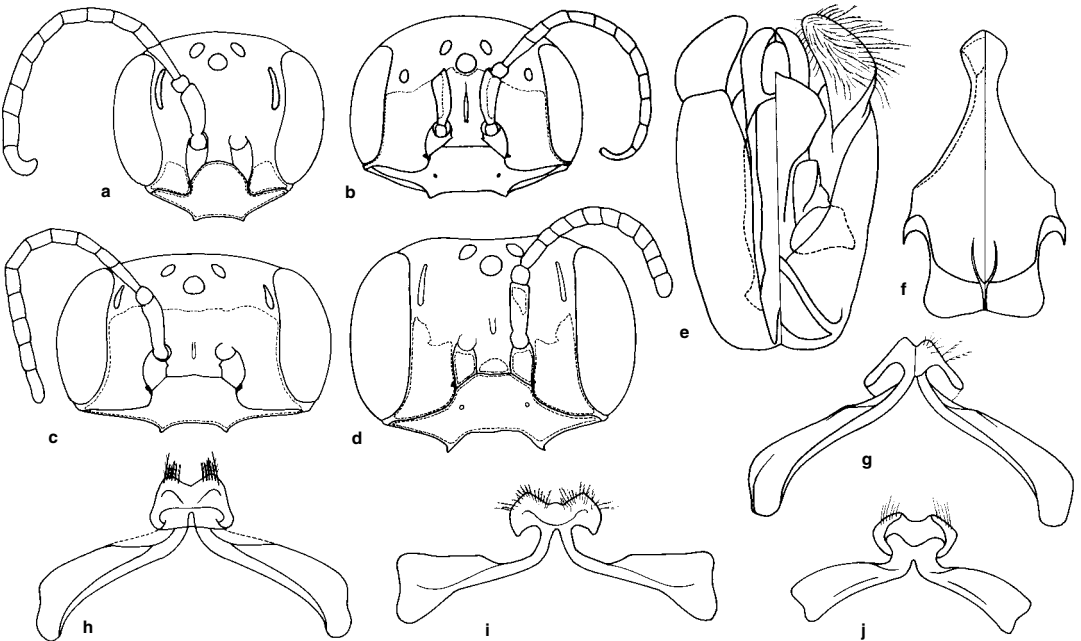


Fig. 53-4. Structures of males of *Liphanthus* (Protandreninae). a-d, Facial views; limits of yellow areas are indicated by dotted lines. **a**, *L. (Tricholiphanthus) leucostomus* Ruz and Toro; **b**, *L. (Liphanthus) sabulosus* Reed; **c**, *L. (Pseudoliphanthus) spiniventris* Ruz and Toro; **d**, *L. (Xenoliphanthus) parvulus* (Friese). **e-g**, Genitalia, S8, and S7 of *L. (Liphanthus) sabulosus* Reed.

h-j, S7 of the following species: **h**, *L. (Pseudoliphanthus) spiniventris* Ruz and Toro; **i**, *L. (Xenoliphanthus) parvulus* (Friese); **j**, *L. (Tricholiphanthus) leucostomus* Ruz and Toro. (In the divided figures, dorsal views are at the left.)
From Ruz and Toro, 1983.

- Hind tibial spurs with apices only slightly curved, inner somewhat longer than outer; vertex convex in frontal view 3
- 3(2). Distance between antennal socket and inner orbit shorter than or similar to interantennal distance 4
- Distance between antennal socket and inner orbit longer than interantennal distance 5
- 4(3). First flagellar segment about three times as long as broad; clypeus flattened basally *L. (Melalipanthus)*
- First flagellar segment less than twice as long as broad; clypeus convex *L. (Leptophanthus)*
- 5(3). S3 and S4 with posterior margins usually clearly concave (*if* only slightly concave, then with median, depressed, triangular, transparent area between apical thickenings) *L. (Tricholipanthus)*
- S3 and S4 with posterior margins convex or straight (without thickenings) 6
- 6(5). Pygidial plate present; head in ventral view with lateroventral area of clypeus widened mesally; frontal line in a very long and well-marked groove *L. (Lipanthus s. str.)*
- Pygidial plate absent; head in ventral view with lateroventral area of clypeus widened laterally; frontal line scarcely marked, not in groove *L. (Pseudolipanthus)*

Key to the Subgenera of *Lipanthus* (Females)

(Based on Ruz and Toro, 1983)

(Females of the subgenus *Tricholipanthus* are not known.)

- 1. Submarginal cells two; propodeal triangle laterally about half length of metanotum (laterally) *L. (Neolipanthus)*
- Submarginal cells three; propodeal triangle laterally slightly more than half length of metanotum (laterally) or almost same length 2
- 2(1). Hind tibial spurs with apices curved like claws, subequal in length; vertex concave or almost straight in frontal view *L. (Xenolipanthus)*
- Hind tibial spurs with apices only slightly curved, inner somewhat longer than outer; vertex convex in frontal view 3
- 3(2). Lateral ocellus, in frontal view, above upper orbital tangent; inner orbits divergent dorsally *L. (Leptophanthus)*
- Lateral ocellus, in frontal view, at same level as or slightly below upper orbital tangent; inner orbits convergent dorsally or almost subparallel 4
- 4(3). Outer subantennal suture almost straight; clypeus, inferior paraocular area, and base of mandible without yellow *L. (Melalipanthus)*
- Outer subantennal suture distinctly arcuate laterally; at least clypeus with yellow 5
- 5(4). Frontal line almost imperceptible; lower paraocular area and tegula without yellow *L. (Pseudolipanthus)*
- Frontal line distinct, in a groove; lower paraocular area and tegula with yellow *L. (Lipanthus s. str.)*

Lipanthus / Subgenus *Leptophanthus* Ruz and Toro

Lipanthus (Leptophanthus) Ruz and Toro, 1983: 277. Type species: *Psathyria nigra* Friese, 1916 (not Friese, 1908) = *Lipanthus nitidus* Ruz and Toro, 1983, by original designation.

In this subgenus the metasoma lacks yellow, although the face of the male has yellow or white markings.

■ *Leptophanthus* is known from Antofagasta to Malleco, Chile, and Santa Cruz province, Argentina. The seven known species were included in the revision by Ruz and Toro (1983).

Lipanthus / Subgenus *Lipanthus* Reed s. str.

Lipanthus Reed, 1894: 645. Type species: *Lipanthus sabulosus* Reed, 1894, monobasic.

In *Lipanthus* s. str. the face of the male is largely yellow and the metasoma is dark with broad yellow bands on T1 and T2 only. In the female, pale facial marks are limited and the metasoma is red or black.

■ The known range of *Lipanthus* s. str. is Coquimbo to Cautín, Chile. The four species were included in the revision by Ruz and Toro (1983).

Lipanthus / Subgenus *Melalipanthus* Ruz and Toro

Lipanthus (Melalipanthus) Ruz and Toro, 1983: 271. Type species: *Lipanthus atratus* Ruz and Toro, 1983, by original designation.

In this subgenus of largely black species, there are limited yellow areas on the clypeus of the male.

■ The known range is Malleco and Arauco, Chile. The two species were included in the revision by Ruz and Toro (1983).

Lipanthus / Subgenus *Neolipanthus* Ruz and Toro

Lipanthus (Neolipanthus) Ruz and Toro, 1983: 274. Type species: *Lipanthus bicellularis* Ruz and Toro, 1983, by original designation.

Neolipanthus is unique in the genus in having only two submarginal cells. It differs from other subgenera in other characters as well (see the key to subgenera); it is not merely a representative of another subgenus that has lost a submarginal crossvein.

■ This subgenus is known only from Linares, Chile. The only species is *Lipanthus bicellularis* Ruz and Toro.

Lipanthus / Subgenus *Pseudolipanthus* Ruz and Toro

Lipanthus (Pseudolipanthus) Ruz and Toro, 1983: 253.

Type species: *Lipanthus rozeni* Ruz and Toro, 1983, by original designation.

In appearance, males of this subgenus resemble *Lipanthus* s. str., because of the largely yellow face, a yellow band on T2, and usually another on T1.

■ *Pseudolipanthus* is known from Valparaíso to Malleco, Chile, and Neuquén, Argentina. The four species were included in the revision by Ruz and Toro (1983).

Lipanthus / Subgenus *Tricholipanthus* Ruz and Toro

Lipanthus (Tricholipanthus) Ruz and Toro, 1983: 267. Type species: *Lipanthus leucostomus* Ruz and Toro, 1983, by original designation.

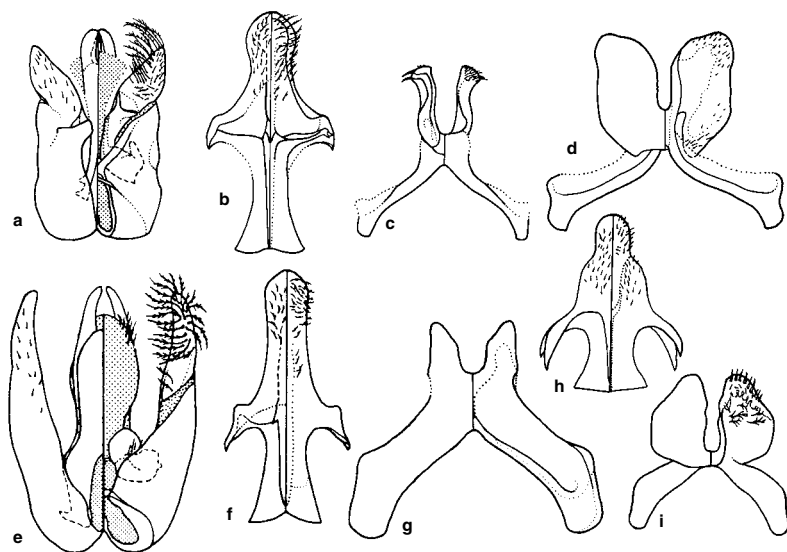


Figure 53-5. Structures of male Protandrenini. **a-c**, Genitalia, S8, and S7 of *Protandrena* (*Protandrena*) *mexicana* (Cockerell); **d**, S7 of *P. (Pterosarus) rudbeckiae* (Robertson); **e-g**, Genitalia, S8, and S7 of *Pseudopanurgus aethiops* (Cresson); **h, i**, S8 and S7 of *Anthemurgus passiflorae* Robertson. (In the divided figures dorsal views are at the left.) From Ruz, 1986.

(1986), but may not be justified because the relevant part of the cladogram appears to be far from robust. No apomorphies are shown for *Protandrena* s. str.; the apomorphies for the alternative line leading to nearly all other Panurginae are (1) a simple scopa, which reverses and appears elsewhere, probably in relation to the type of pollen being collected, and also is variable within *Protandrena* s. str. and (2) a relatively elongate glossa that also reverses and is probably related to floral type being utilized, and, moreover, is variable within *Protandrena* s. str.

The *Pseudopanurgus* to *Anthrenoides* clade of the Ruz cladogram involves the only polytomies in her cladogram (three and seven branches each). The synapomorphies are few and weak, unlike those in the rest of her cladogram, which is mostly strongly supported. As indicated above, I have chosen to incorporate several of these taxa into *Protandrena* on the basis that when the number of submarginal cells is ignored, the distinguishing features are not impressive. The taxa in this tribe that I retain at the genus level all differ in features with no known intermediate conditions closing the gaps between them and *Protandrena* s. l. Moreover, they have features that may be plesiomorphic relative to *Protandrena* s. l., such that a cladistic study of this group might show them to be branches basal to *Protandrena*.

Austropanurgus also has no obvious apomorphies, according to Ruz's cladogram, but does differ from the rest of *Protandrena* in the present sense in four characters, three of which also appear in one or more of the genera and subgenera of the *Pseudopanurgus* to *Anthrenoides* clade. Thus *Austropanurgus* also appears to be a member of the *Protandrena* group. For comments on *Pseudosarus* and *Xenopanurgus*, see the discussion of the subgenus *Heterosarus*. A species (*P. evansi* Ruz and Chiappa) that does not fall in any one of the subgenera as currently recognized was described by Ruz and Chiappa (2004).

I believe that *Protandrena* in the broad sense is comparable to *Calliopsis* in the degree of diversity among sub-

genera. It constitutes a much more useful taxon than the numerous genera sometimes recognized.

Key to the Subgenera of *Protandrena* (Males)

1. Submarginal cells three (occasional individuals have only two) (North and Central America) *P. (Protandrena) s. str.*
- Submarginal cells two (Fig. 53-2b) 2
- 2(1). Propodeal triangle basally pilose (metasoma often red or largely so) (nearctic) *P. (Metapsaenythia)*
- Propodeal triangle basally glabrous 3
- 3(2). Hind tibial spurs strongly curved at apices; first submarginal cell on posterior margin shorter than second (Chile) *P. (Austropanurgus)*
- Hind tibial spurs or at least one of them slightly curved or almost straight; first submarginal cell on posterior margin about as long as or longer than second 4
- 4(3). Gonostylus less than one-third as long as gonocoxite; S6 scarcely notched apically (face black) (South America) *P. (Parasarus)*
- Gonostylus over one-half as long as gonocoxite; S6 with deep midapical notch or slit 5
- 5(4). Scutum with punctures well marked, many of them separated by spaces larger than their diameters; S6 with midapical emargination narrow, deep (North and Central America) *P. (Pterosarus)*
- Scutum with punctures very small, homogeneous, commonly dense; S6 midapical emargination V-shaped *P. (Heterosarus)*

Key to the Subgenera of *Protandrena* (Females)

1. Forewing with three submarginal cells (only two in occasional individuals) (North and Central America) *P. (Protandrena) s. str.*
- Forewing with two submarginal cells (Fig. 53-2b) 2
- 2(1). Tibial scopa of rather long, abundant hairs with clearly visible branches (North and Central America) *P. (Pterosarus)*

- Tibial scopa of sparser hairs that lack branches, or some of them with few, minute branches 3
- 3(2). Propodeal triangle basally pilose (metasoma often largely red) (nearctic) *P. (Metapsaenythia)*
- Propodeal triangle basally glabrous 4
- 4(3). Hind tibial spurs not strongly curved at apices; anterior tentorial pit in epistomal suture slightly to distinctly below intersection between outer subantennal and epistomal sutures *P. (Heterosarus)*
- Hind tibial spurs strongly curved at apices; anterior tentorial pit at intersection between outer subantennal and epistomal sutures 5
- 5(4). First submarginal cell on posterior margin shorter than second; face with yellow areas (Chile) *P. (Austropanurgus)*
- First submarginal cell on posterior margin longer than second; face black (South America) *P. (Parasarus)*

Protandrena / Subgenus *Austropanurgus* Toro

Austropanurgus Toro, 1980: 209. Type species: *Austropanurgus punctatus* Toro, 1980, monobasic.

Austropanurgus consists of a small (6 mm long), slender, black species with yellow facial marks (these more extensive in the male); the metasoma is commonly reddish. Although *Austropanurgus* is widely separated from other taxa related to *Protandrena* by Ruz (1986), it falls in the weak part of her cladogram and seems to me to be best regarded as a subgenus of *Protandrena* s. l. Arguments in this connection are given in the discussion of the genus *Protandrena*. Distinctive features of *Austropanurgus* are the strongly curved apices of the subequal hind tibial spurs and the U-shaped emargination in the apex of S6 of the male. The latter appears in some of the related genera, such as *Rhophitulus* (*Cephalurgus*), and in some species of *Protandrena* s. str., but not in other groups of *Protandrena*. Also unlike most *Protandrena*, the two apical lobes of S7 of the male are only somewhat constricted in uniting to the sternal disc at their bases; in other subgenera the disc or body of the sternum from which the lobes arise is usually conspicuously small. Male genitalia, sterna, and other structures were illustrated by Toro (1980) and Ruz (1986).

■ This subgenus, found in Coquimbo, Chile, consists of a single species, *Protandrena punctata* (Toro).

Protandrena / Subgenus *Heterosarus* Robertson

Heterosarus Robertson, 1918: 91. Type species: *Calliopsis parvus* Robertson, 1892, by original designation. [New status.]

Xenopanurgus Michener, 1952: 24. Type species: *Xenopanurgus readioi* Michener, 1952, by original designation.

Pseudosarus Ruz, 1980: 25. Type species: *Pseudosarus virescens* Ruz, 1980, monobasic.

This subgenus consists of small (4–7 mm long) species having the appearance of the subgenus *Pterosarus* but differing in the simple (or very shortly and sparsely branched) scopal hairs and the rather broadly V-shaped midapical emargination of S6 of the male. Male genitalia and hidden sterna were illustrated by Mitchell (1960), Timberlake (1975), and Ruz (1980, 1986, 1990).

■ This subgenus is widespread in North America but scarce in the Pacific states, diverse in the Rocky Mountain states and Arizona, and reasonably common east to the Atlantic Ocean; it ranges from southern Canada to Argentina and Chile but is rare in the moist tropics (e.g., only one species is known from Panama). Timberlake recognized 52 species in North and Central America; only a few (perhaps about seven) are known from South America. Timberlake (1964b) gave a key to North and Central American species, and later revised them (Timberlake, 1975).

One central Chilean species, *Protandrena (Heterosarus) virescens* (Ruz), and two Mexican and Arizona species, *P. (Heterosarus) readioi* (Michener) and *platycephala* (Ruz), are weakly to strongly metallic greenish or blue. The Chilean species, which was placed in a genus *Pseudosarus* Ruz, differs from most *Heterosarus* not only in being weakly metallic but in having the middle tibial spur of the female finely serrate or ciliate, without coarser teeth distally as in other *Protandrena*. The two Mexican and Arizona species were placed in a genus *Xenopanurgus*. It was first named on the basis of the highly aberrant *P. (H.) readioi*, whose unusual features are described by Shinn (1964). *P. (H.) platycephala*, however, bridges the gap between *Heterosarus* and *P. readioi* (Ruz, 1990). D. Yanega has concluded that these two species are related to the group of *P. (Heterosarus) bakeri* (Cockerell) (personal communication, 1995).

Some South American species sometimes confused with *Protandrena (Heterosarus)* in collections are here removed to *Rhophitulus* (*Panurgillus*). They are so similar to *Heterosarus* that the male genitalic and sternal characters are the most convincing evidence that they belong in a different group. A relatively common South American species that remains in *Heterosarus* is *Protandrena (Heterosarus) nigra* (Spinola) (**new combination**); it is found in central Chile and in the lake district of Neuquén province, Argentina.

Protandrena / Subgenus *Metapsaenythia* Timberlake

Metapsaenythia Timberlake, 1969a: 89. Type species: *Calliopsis abdominalis* Cresson, 1878, by original designation.

This subgenus contains the only known species of *Protandrena* having two submarginal cells that also have hairs (inconspicuous) on the propodeal triangle. The thorax and metasoma are extraordinarily finely and closely punctate, the latter frequently red. Superficially, these bees are very like some of the species of *Protandrena* s. str. The V-shaped midapical notch of S6 of the male suggests *Heterosarus* and some *Protandrena* s. str. The long apical lobes of S7 with their retrorse apices also suggest *Protandrena* s. str. The scopa is of the simple type, but the hairs have a few short branches. Body length ranges from 4.5 to 9.0 mm. Male genitalia and hidden sterna were illustrated by Mitchell (1960) under the genus *Pseudopanurgus*, and by Ruz (1986).

■ This subgenus ranges from New Jersey to Georgia west to Kansas and Texas, USA, and south to Chihuahua and Sonora, Mexico. There are two species. The subgenus was revised by Timberlake (1969a).

At least the common species, *Protandrena abdominalis*

species of *Protandrena*. Length varies from 5 to 12 mm. They are usually more coarsely punctate, and males, in particular, usually have strong transverse postgradular depressions on T2 to T5. The body is black with yellow on the face of males and some females. All species have two submarginal cells. Distinctive generic characters are the large, hairy apical spine on the front coxa of females (Fig. 53-6k), not found in other Panurginae, and the strong but nondentate carina along the upper margin of the hind tibia of males (Fig. 53-6j). The scopa is strongly plumose, a feature seen among other Protandrenini only in *Protandrena* (*Pterosarus*) and some species of *P.* (*Protandrena*). The pronotum has a transverse carina or lamella, not found in other Protandrenini except *Parapsaenythia* and the female of *Chaeturginus*. The large anterior surface of the mesepisternum, a feature contributing to the robustness of the thorax, is flat, and the omaulus is represented by a narrowly rounded angle; these features are not duplicated in other Protandrenini. Likewise contributing to the short, robust appearance of the thorax is the short dorsal surface of the propodeum, only about one-half as long as the metanotum. In other Protandrenini it is nearly as long as the metanotum or longer. S7 of the male has two apical lobes; unlike *Protandrena* they arise from a relatively large disc and are not constricted at their bases (Fig. 53-5g). A probably plesiomorphic feature is the uniformly serrate or ciliate middle tibial spur of the females; in most related taxa the distal part of the spur has coarser and more widely separated teeth. Mitchell (1960) and Timberlake (1973) illustrated male genitalia and eighth sterna of *Pseudopanurgus* species; these and other structures were illustrated by Ruz (1986). See also Figure 53-5e-g.

■ This genus ranges from Wyoming, Kansas, and Texas west to southernmost California, USA, south through Mexico and Central America to Costa Rica. The 32 species were reviewed by Timberlake (1973).

The name *Pseudopanurgus* was formerly used (e.g., by Michener, 1944) in a broader sense to include the subgenera with two submarginal cells here placed in *Protandrena*. Although I have elected to maintain *Pseudopanurgus* as a genus distinct from *Protandrena* on the basis of the characters listed above, one could justify adding it to *Protandrena* as a subgenus.

Genus *Rhopitulus* Ducke

Rhopitulus is a genus of small (4-7 mm long) bees resembling *Protandrena* (*Heterosarus*). The clypeus of the male is partly or wholly yellow, whereas the female is wholly black or with yellow on the pronotum. The male resembles *Heterosarus* in the long apical lobes of S7, the lobes constricted at the bases and attached to a small discal area (Fig. 53-3c), and in the rather large V- or U-shaped midapical notch in S6. The male gonocoxite has an oblique lateral impression, and thus exhibits a lateral concavity (as in *Anthrenoides*; less developed in subgenus *Cephalurgus*) (Fig. 53-3a). The hind tibia of the female is commonly about twice as long as the basitarsus; in most other Protandrenini except *Liphanthus* it is less than twice the basitarsal length. Especially interesting is the distinct dorsal "remnant" of the gonobase, found among other Panurginae only in *Chaeturginus*.

As Ruz (1986) and Ruz and Melo (1999) correctly suggest, the dorsal "remnant" of the gonobase in *Rhopitulus* and *Chaeturginus* may be a new sclerotization of membrane rather than a remnant homologous to the gonobase found in most non-Panurgine bees.

Moure, in Schlindwein and Moure (1998), provided a new genus-group name for bees of this group, and a tentative key is provided below for subgenera of *Rhopitulus*. However, users should recognize that the classification is tentative, as was indicated by Ruz (1986) when she wrote "sometimes it is difficult to know exactly what *Rhopitulus* is." The close relationship of three subgenera is shown by the presence in the male of the dorsal sclerotization suggestive of a gonobase (shared only with *Chaeturginus*), the elongate digitus of the volsella, as well as the forms of S6, S7, and S8 of the male. Male genitalia and other structures were illustrated by Ruz (1986); see also Figure 53-3a-c.

Key to the Subgenera of *Rhopitulus*

1. Entire lower face strongly convex, clypeus protuberant for full eye width in lateral view and produced apicad so that lower ocular tangent crosses face near base of clypeus; S6 of male with apical emargination V-shaped although rounded at anterior extremity; male gonocoxite with small dorsal lobe (Fig. 53-3a) *R. Rhopitulus* s. str.)
- Lower face not unusually convex, clypeus protuberant for two thirds eye width or less in lateral view and not produced apicad, so that lower ocular tangent crosses lower half of clypeus; S6 of male with apical emargination U-shaped; male gonocoxite without middorsal lobe..... 2
2. Head commonly wider than thorax, inner orbits of male diverging below, of female closest medially; clypeus rather flat, protuberant about one seventh to one half width of eye in lateral view; S6 of male with lobe on each side of emargination rounded or obtuse *R. (Cephalurgus)*
- Head not wider than thorax, inner orbits converging below; clypeus protuberant one fourth to one half of width of eye in lateral view; S6 of male with lobe on each side of emargination acute (at least in some species) *R. (Panurgillus)*

Rhopitulus / Subgenus *Cephalurgus* Moure and Lucas de Oliveira

Cephalurgus Moure and Lucas de Oliveira, 1962: 2. Type species: *Cephalurgus anomalus* Moure and Lucas de Oliveira, 1962, by original designation.

This subgenus consists of more shiny species than the other subgenera, often with smooth integument between well-separated punctures. Unlike other species of *Rhopitulus*, some shiny species of *Cephalurgus* lack hairs on the propodeal triangle.

Ruz (1986) suggested that *Rhopitulus* and *Cephalurgus* might be synonymous; I suggest that subgeneric status would indicate their close relationship. Additional species may yet show that they grade one into the other.

■ This subgenus ranges from the state of Minas Gerais, Brazil, to Paraguay. Ruz (1986) listed the five described species.

54. Tribe Panurgini

Members of this holarctic tribe range from all black to those with extensive yellow maculation. The body form is similar to that of the Protandrenini. Most of the distinguishing tribal characters are indicated in the key to tribes, above. All Panurgini have two submarginal cells. The male gonocoxites are often more elongate than is usual in other tribes (Fig. 54-2a, e), and the inner margins of the penis valves usually have minute transverse ridges, otherwise known only in some Melitturgini. S7 of the male lacks the two large apical lobes arising from a small disc that are found in Protandrenini; the disc of the sternum is usually broad, but is narrow in *Camptopoeum* (Fig. 54-2g). The apodemal lobes in this same genus are long, as they are in Protandrenini, but they are much shorter in the other genera.

The Panurgini are found primarily in the palearctic region, but one genus, *Panurginus*, occurs also in North America, thus overlapping the distribution of the Protandrenini. *Panurginus* consists of largely black species, superficially resembling *Protandrena* (*Heterosarus*), but it can be distinguished quickly from such similar-looking Protandrenini by the first recurrent vein, which meets (or is slightly basal or distal to) the first submarginal crossvein (Fig. 54-1c). In North American *Protandrena* and other Protandrenini the first recurrent vein is considerably distal to the first submarginal crossvein. This is not, however, a tribal character outside of temperate North America.

The form of S7 of the male is particularly informative in indicating major groups within the tribe. In *Camptopoeum* the disc of the sternum is small and parallel-sided (Fig. 54-2g), the apex somewhat produced and ending in a large, broad notch, and the apodemal processes are long, as noted above and as in the Protandrenini. In *Panurgus* and *Panurginus*, S7 is a rather broad plate with two, three, or four apical spines, angles, or lobes and relatively short, broad apodemal processes (Fig. 54-3c, g, i). In some species of *Panurginus*, such as *P. clavatus* (Warncke), S7 is medially produced, the four angles possibly indicated. *Avpanurgus* falls in a group by itself on the basis of S7, which has a short, broad sternal disc or body and a small, slender, bifid apical process (Fig. 54-2c). These characters are extensively used in the generic classification proposed below.

Key to the Genera of the Panurgini

- 1. S7 of male with disc small, about as broad as long, almost parallel-sided, with broad apical notch (Fig. 54-2g) and sometimes [e.g., in *Camptopoeum ruber* (Warncke)] with lateral lobe at each side, and with long somewhat pedunculate apodemal lobes; body usually with yellow markings (episternal groove punctate, extending slightly below scrobal level) (palearctic) *Camptopoeum*
- S7 of male with disc rather large, usually apically with two, three, or four lobes, angles, or spines or a median process, disc much broader than long [except when drawn out as an apical process in *Panurginus* such as *P. clavatus* (Warncke)]; apodemal lobes of S7 not or little narrowed basally, relatively short (Figs. 54-2c, 54-3c, g,

- i); body often entirely black or only clypeus yellow, but body sometimes extensively yellow 2
- 2(1). S6 of male with posterior margin slightly to strongly produced medially, this projection with truncate to broadly concave apex margined by zone of short hairs (Fig. 54-3d); episternal groove entirely absent (body entirely black except for yellow clypeus of some males; first recurrent vein meeting or basal to first submarginal crossvein or nearly so, Fig. 54-1c) (holarctic) *Panurginus*
- S6 of male with posterior margin thin and more or less straight or usually broadly bilobed (Figs. 54-2d, 54-3h), [thickened, and medially bilobed, with dense, diverging apical brushes of plumose hair in *Panurgus* (*Flavipanurgus*)] but usually without an apical zone of very short hairs; episternal groove present but usually short, not reaching level of scrobe, or rarely absent..... 3
- 3(2). S7 of male with slender midapical bifid process (Fig. 54-2c); gonostylus short, simple, about one-fourth as long as gonocoxite (Fig. 54-2a), articulated well before apex of gonocoxite; dorsal surface of propodeum twice as long as metanotum (body with yellow areas) (northern Africa) *Avpanurgus*
- S7 of male without midapical process; gonostylus over one-fourth as long as gonocoxite, usually variously bidentate, bifid, or angulate, or with hair tufts or brushes (Fig. 54-3e, k); dorsal surface of propodeum little if any longer than metanotum (palearctic)..... *Panurgus*

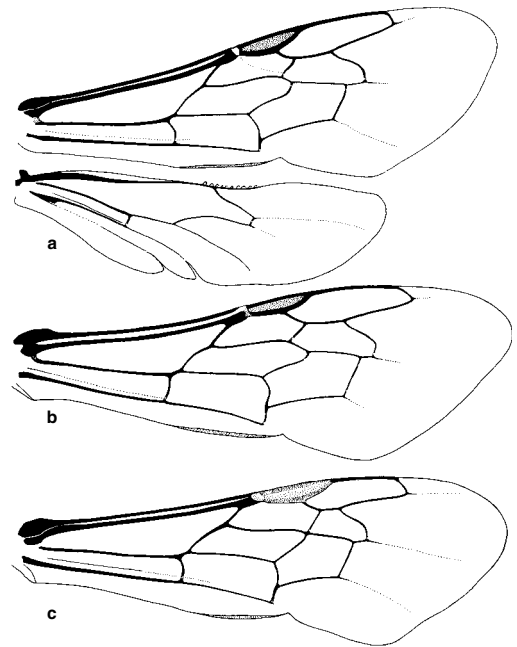
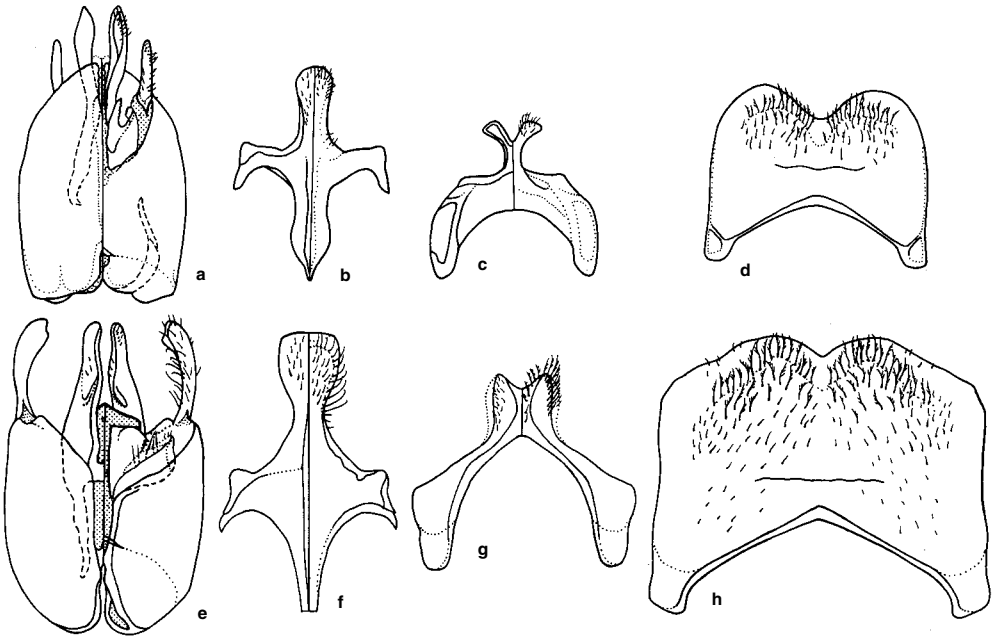


Figure 54-1. Wings of Panurgini. **a**, *Panurgus calcaratus* (Spinola); **b**, *Camptopoeum friesei* Mocsáry; **c**, *Panurginus occidentalis* (Crawford).



Genus *Avpanurgus* Warncke

Panurgus (*Avpanurgus*) Warncke, 1972: 70. Type species: *Panurgus flavofasciatus* Warncke, 1972, by original designation.

Avpanurgus consists of a species with extensive yellow markings on the head and thorax and with yellow tergal bands, narrowed medially. The body length is 7 to 8 mm. The male sterna and genitalia (Fig. 54-2a-d) are so different from those of other Panurgini that generic status seems warranted in spite of similarity in other features to *Panurgus*. The apex of S6 is broadly bilobed, with a rounded emargination between the lobes, not at all thickened or dentate. S7 has a short, transverse disc or body, extended basolaterally as the apodemal arms; at midapex is a slender, posteriorly directed process that is divergently bifid distally. The gonocoxites are elongate; the gonostylus is about one-fourth as long as the gonocoxite, simple, tapering, articulated well before the apex of the gonocoxite, and considerably exceeded by the slender penis valve. The episternal groove is distinct but short, not reaching down to the scrobal level. The first recurrent vein is distant from the first submarginal crossvein. The marginal cell is unusually narrowly truncate. The male genitalia and hidden sterna were sketched by Warncke (1972) and illustrated by Ruz (1986); see also Figure 54-2a-d.

■ This genus occurs in Algeria. It is known from a single species, *Avpanurgus flavofasciatus* (Warncke).

Genus *Camptopoeum* Spinola

In *Camptopoeum*, which consists of palearctic species, there are yellow maculations on the head and thorax and usually also the metasoma, the background color of which is occasionally red. The most distinctive feature is S7 of the male, which has a rather narrow, apically produced disc having a broad apical notch (Fig. 54-2g), with a lateral lobe in *C. ruber* (Warncke); the same sternum has

Figure 54-2. Structures of male Panurgini. **a-d**, Genitalia, S8, S7, and S6 of *Avpanurgus flavofasciatus* (Warncke); **e-h**, Same structures of *Camptopoeum* (*Epimethea*) *variegatum* (Morawitz). (In the divided figures, dorsal views are at the left.) From Ruz, 1986.

long apodemal arms that are frequently narrowed near the bases. These long arms may well be plesiomorphic, but the reduced disc lacking apical lobes is an apomorphy.

Panurgus nadigi Warncke (1972) was placed in *Camptopoeum* (then treated as a subgenus) by Warncke, but clearly belongs elsewhere, as shown by the broad S7 of the male, which is suggestive of *Panurginus*.

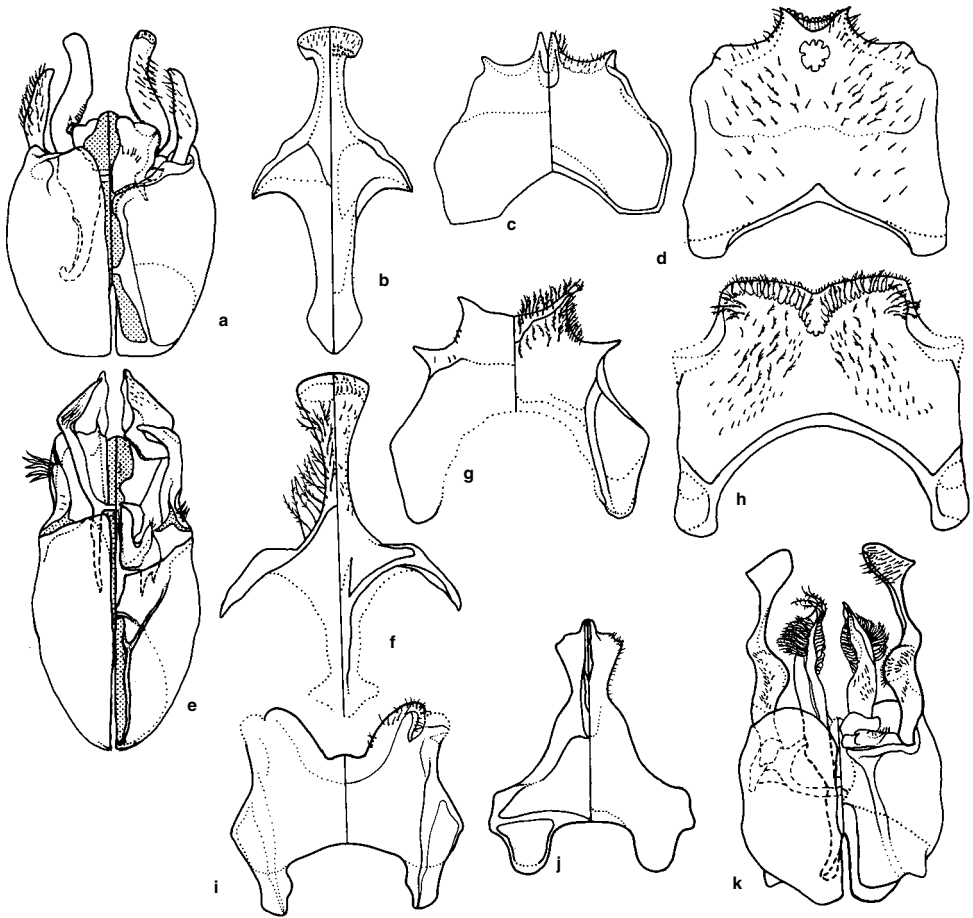
Warncke (1987) gave a key to Turkish and Middle Eastern species. Patiny (1999c) listed the species of both subgenera of *Camptopoeum*, 13 for *Camptopoeum* s.str. and 12 for *Epimethea*.

Key to the Subgenera of *Camptopoeum*

1. Labrum with basal area triangular, delimited by converging carinae, those in females meeting and forming longitudinal median carina that ends near apex of labrum, and in males ending together near apex of labrum; clypeus protuberant one-fourth to one-half or more of eye width in lateral view; glossa longer than prementum; first segment of labial palpus about as long as second to fourth segments taken together *C. (Camptopoeum* s. str.)
- Labrum with basal area delimited by transverse carina that curves basad laterally; clypeus not protuberant; glossa about one-half as long as prementum; first segment of labial palpus shorter than second to fourth segments taken together *C. (Epimethea)*

Camptopoeum / Subgenus *Camptopoeum* Spinola s. str.

Camptopoeum Spinola, 1843: 139. Type species: *Prosopis frontalis* Fabricius, 1804, by original designation.



Warncke. Finally, in the subgenus *Flavipanurgus* S7 has apical lobes instead of teeth (Fig. 54-3i). The gonostylus is commonly deeply bifid, but sometimes bidentate or with a mere tooth instead of a long branch, or simple except for a tuft of coarse hairs, as in *P. (Panurgus) calcaratus* (Scopoli). Genitalia and hidden sterna were illustrated by Rozen (1971b) and Ruz (1986); see also Figure 54-3e-h. Segment 1 of the labial palpus is shorter than 2 to 4 taken together.

The short, wide S7 of the male is an apomorphy, to judge by other Panurginae, but is shared with *Panurginus*. It is possible that *Panurgus* in my sense is paraphyletic, and *Panurginus* an ex-group derived from it.

Key to the Subgenera of *Panurgus*

- 1. Body without yellow markings; scopal hairs minutely spiraled or zigzag; galeal comb absent; glossa longer than prementum (episternal groove weak, not reaching down to scrobal level) *P. (Panurgus s. str.)*
- Body with yellow at least on face and metasoma; scopal hairs simple (female unknown in *Simpanurgus*); galeal comb present; glossa shorter than prementum 2
- 2(1). Episternal groove well marked, extending below scrobal level; inner orbits of male convex, closest to one another medially (Iberian peninsula) *P. (Simpanurgus)*

Figure 54-3. Structures of male Panurgini. **a-d**, Genitalia, S8, S7, and S6 of *Panurginus polytrichus* Cockerell; **e-h**, Same structures of *Panurgus (Panurgus) calcaratus* (Scopoli); **i**, S7 of *Panurgus (Flavipanurgus) venustus* Erichson; **j, k**, S7 and genitalia of *Panurginus clavatus* (Warncke). (In the divided figures, dorsal views are at the left.) From Ruz, 1986.

- Episternal groove weak, not reaching down to scrobal level; inner orbits of male diverging below (Iberian peninsula) *P. (Flavipanurgus)*

Panurgus / Subgenus *Flavipanurgus* Warncke

Panurgus (Flavipanurgus) Warncke, 1972: 69. Type species: *Panurgus flavus* Friese, 1897, by original designation.

Species of *Flavipanurgus* have yellow areas at least on the head and metasoma, and on the terga lateral spots sometimes uniting to form bands. The body length is 5 to 9 mm. The head is unusually large, and the inner orbits of the male diverge below, unlike those of other Panurgini. The most distinctive features are those of the male sterna and genitalia: S6 has four divergent projections, apicolateral teeth and midapical lobes, the latter well separated and covered with divergent, plumose hairs;

56. Tribe Melitturgini

The forms embraced by this tribe are more robust than most Protandrenini and Panurgini, the body being euciform or sometimes almost anthophoriform. Unusual features are the lack of facial foveae in most males and some females and the downwardly divergent inner orbits of most males. Coloration ranges from black to largely yellow, the metasoma sometimes red. The propodeal triangle is largely pilose. Tribal characters are presented in the key to tribes.

The Melitturgini are found in the palearctic and Ethiopian faunal regions.

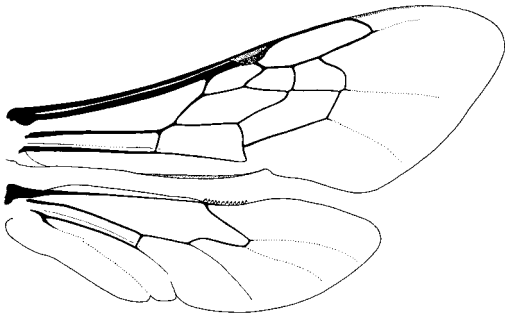


Figure 56-1. Wings of *Melitturga clavicornis* (Latreille).

Key to the Genera of the Tribe Melitturgini

- 1. Body with few to extensive yellow areas; submarginal cells three (Fig. 56-1); eyes of male large, inner orbits conspicuously convergent above; antennal flagellum of male at least somewhat clavate (Fig. 56-2g); labrum partially pilose, the hairs short; episternal groove usually extending below scrobal level 2
- Body without yellow markings; submarginal cells two; inner orbits of male not convergent above; antennal flagellum not clavate; labrum fully pilose, hairs long; episternal groove reaching but not extending below scrobal level 3
- 2(1). Posterior margins of submarginal cells subequal; tarsi of male with segments 2 to 4 expanded; stigma shorter than prestigma; T6 of male basally with conspicuous, broad, swollen hairy area (palearctic, Africa) *Melitturga*
- Posterior margin of first submarginal cell nearly as long as that of second and third taken together; tarsi of male with segments 2 to 4 unmodified; stigma almost as long as to longer than prestigma; T6 of male unmodified (Africa, southwest Asia) 4
- 3(1). Scape of male robust; last antennal segment of male strongly tapered at apex (Fig. 56-2k); pronotum with strong dorsolateral lamella or protuberance; metasoma black; T1 (lateral view) with dorsal and anterior surfaces rounding smoothly; T2 and T3 with gradulus not strongly carinate, lateral part rather short; head slightly wider than long (palearctic) *Plesiopanurgus*
- Scape and last antennal segment unmodified; pronotum with rounded and little-developed ridge on dorsal margin; metasoma red; T1 (lateral view) with dorsal and anterior surfaces meeting at almost 90 degrees; T2 and T3 with lateral part of gradulus strongly carinate, long; head conspicuously wider than long (Africa) *Mermiglossa*
- 4(2). First three segments of labial palpus elongate, fourth shorter; body usually partly or wholly yellow (glossa longer than face, at least in some species with apex broadly truncate (Fig. 52-1 f) *Flavomelitturgula*
- First segment of labial palpus elongate, as long as or longer than second to fourth segments together; body variable in coloration but often mostly dark, never wholly yellow; glossa pointed 5
- 5(4). Maxillary palpus “nearly absent” (Patin, 2001); glossa longer than face; first segment of labial palpus longer than second to fourth segments together *Gasparinabla*

- Maxillary palpus 6-segmented; glossa shorter than face; first segment of labial palpus about as long as second to fourth together 6
- 6(5). Scutum of female densely covered with short, thickened, appressed hairs among which are scattered erect hairs; male gonostylus very slender, as long as gonocoxite; volsella spiculate, extending beyond gonocoxites; T7 of male with bifid apex; S6 and S7 of male with deep median apical emarginations *Borgatomelissa*
- Scutum with scattered suberect hairs or in some species with appressed hairs, usually less dense than in *Borgatomelissa*; male gonostylus robust, half as long as gonocoxite or less (Fig. 56-2a); volsella not spiculate, extending little if at all beyond gonocoxites; T7 of male with apex simple; S6 and S7 with apical margins transverse or convex *Melitturgula*

Genus *Borgatomelissa* Patiny

Borgatomelissa Patiny, 2000: 101. Type species: *Andrena brevipennis* Walker, 1871, by original designation.
Sabulapis Patiny, 2002a: 43. This is a D. B. Baker manuscript name unnecessarily published by Patiny as a synonym of *Borgatomelissa*. Invalid because published with no type species designation and as a synonym. [New synonymy.]

This taxon could be considered as a subgenus of *Melitturgula* but Popov, Baker, etc., have thought it was generically distinct; see comments about the type species by Michener (2000) and as a *genus incertus* in Patiny (1999a,b). Distinctive characters, especially those of the male genitalia, are indicated in the key to the genera. The male genitalia were illustrated by Popov (1951a) as *Melitturgula arabica* Popov.

■ *Borgatomelissa* contains two species and is known from Saudi Arabia to Ethiopia and Mauritania.

Genus *Flavomelitturgula* Patiny

Flavomelitturgula Warncke, 1985: 229 *nomen nudum*.
Flavomelitturgula Patiny, 1999a: 251. Type species: *Poecilomelitta lacrymosa* Popov, 1967, by original designation.

Flavomelitturgula Warncke (1985) was tentatively listed under *Melitturgula* by Michener (2000). As origi-

in the relatively small size of the wings. In *M. (Macroteropsis) portalis* (Timberlake) and *M. (Macroterella) mellea* (Timberlake) the males are dimorphic, the larger ones being flightless and unable to leave the nests (Danforth, 1991b; Norden, Krombein, and Danforth, 1992), as in some *Lasioglossum* (*Chilalictus*) in Australia (Halictinae). Such males, at least in *M. portalis*, mate with the females, presumably their close relatives, that are provisioning cells in the communal nest. Of course, a new nest will not have any flightless males, and females there must mate with "normal" males, presumably on flowers.

Key to the Genera of the Perditiini

1. Outer groove of mandible broadened and fading away toward mandibular base (Fig. 58-5a); episternal groove usually curving posteriorly to scrobe (Fig. 58-6a) *Perdita*
- Outer groove of mandible narrow basally (as it is apically) and bent upward, cutting diagonally across mandible to acetabulum (Fig. 58-5b); episternal groove absent or short, not curving posteriorly to scrobe (Fig. 58-6b) *Macrotera*

Genus *Macrotera* Smith

Macrotera consists of four subgenera commonly placed in the genus *Perdita*. Danforth (1991a) retained them in the genus *Perdita* but showed that they constitute the sister group of *Perdita* as it is here understood. In addition to the characters indicated in the key to subgenera, *Macrotera* has the following features. The stigma is slender, little if any broader than the prestigma, as measured to the wing margin, its margin within the marginal cell not or scarcely convex (Fig. 58-2a); the paraglossae of females are expanded into broad, brushlike apices; the body is nonmetallic, the yellow maculation usually absent except on the face, although the body may be honey-colored and the metasoma, at least of males, is commonly reddish; and the head of the male tends to be broad and quadrate, often highly variable in size within a population (Figs. 58-3, 58-4). Interestingly, the male genitalia and hidden sterna do not differ markedly between *Macrotera* and *Perdita*; as shown in Figure 58-7, the hidden sterna of *Macrotera* resemble those of some groups of *Perdita*.

Some interesting behavioral plesiomorphies retained by *Macrotera* and unknown in *Perdita* include the following. In species of *Macrotera* that have been studied, the cells are lined with a water-repellant secretion, as in most ground-nesting bees; in *Perdita* the cells are very incompletely lined or not lined at all. In *Macrotera*, however, the pollen ball in each cell is not covered by a water-repellant secretion, whereas in *Perdita*, which lacks the cell lining, the food mass is so covered. In *Macrotera* the feces of larvae are applied to the inner part of the cell, as in many other ground-nesting bees, including other Panurginae. In *Perdita* the feces of larvae are deposited on the venter of the larva, and thus kept away from the cell wall, possibly keeping them dry and reducing their potential as a source of fungal development. References to literature on these topics are listed under the tribe Perditiini.

Key to the Subgenera of *Macrotera*

1. Facial fovea well developed and elongate; head of male usually enlarged, subquadrate, wider than long, inner orbits more or less divergent below; head of female as long as wide or slightly longer than wide; marginal cell about three times as long as wide, subequal in length to first submarginal cell 2
- Facial fovea small, oval or punctiform; head in both sexes sometimes wider than long but less quadrate, usually not much enlarged in male and inner orbits not divergent downward; marginal cell usually about twice as long as wide, yet shorter than or subequal to first submarginal cell 3
- 2(1). Glossa reaching hind coxae in repose, two to three times as long as prementum; head of male much broader than long, widened anteriorly; mandible of male inserted below eye, only posterior articulation behind posterior eye margin; metasoma of male lacking special modifications except for broad, depressed form; tibial spurs briefly hooked at apices and not serrate on inner margins *M. (Macrotera s. str.)*
- Glossa not over twice as long as prementum; head of male a little broader than long, only slightly widened anteriorly; mandible of male inserted partly behind posterior margin of eye; T7 and one or more metasomal sterna modified; tibial spurs strongly curved at apices and minutely serrate on inner margins *M. (Cockerellula)*
- 3(1). Head of male broader than long, rounded on sides and above, but truncate anteriorly, thus appearing almost semicircular in frontal view; mandible of male usually with half of base behind posterior margin of eye, either bidentate or simple at apex; stigma slender and tapering; maxillary palpus four- to six-segmented, apical segments short and more or less indistinct *M. (Macroteropsis)*
- Head of male not enlarged, ordinary in shape although more or less wider than long; mandible of male rather short, simple, tapering, and inserted largely below eye, only posterior articulation behind posterior eye margin; stigma small and usually rounded posteriorly, but varying to very small and lanceolate; maxillary palpus with six distinct segments *M. (Macroterella)*

Macrotera / Subgenus *Cockerellula* Strand

Perdita (Lutziella) Cockerell, 1922e: 1 (not Enderlein, 1922).

Type species: *Perdita opuntiae* Cockerell, 1922, by original designation.

Cockerellula Strand, 1932: 196, replacement for *Lutziella*

Cockerell, 1922. Type species: *Perdita opuntiae* Cockerell, 1922, autobasic.

This subgenus is related to *Macrotera s. str.* but differs in its smaller size (3.5-7.0 mm long) and shorter proboscis, the glossa in repose only reaching the front coxae or slightly beyond, whereas in *Macrotera s. str.* it reaches the hind coxae.

■ *Cockerellula* occurs from North Dakota south and southwest through western Texas to Arizona, USA, and on to Baja California Sur and Puebla in Mexico. There are 13 species. Keys and revisions were by Timberlake (1953b, 1954, 1960, 1968) and Danforth (1996).

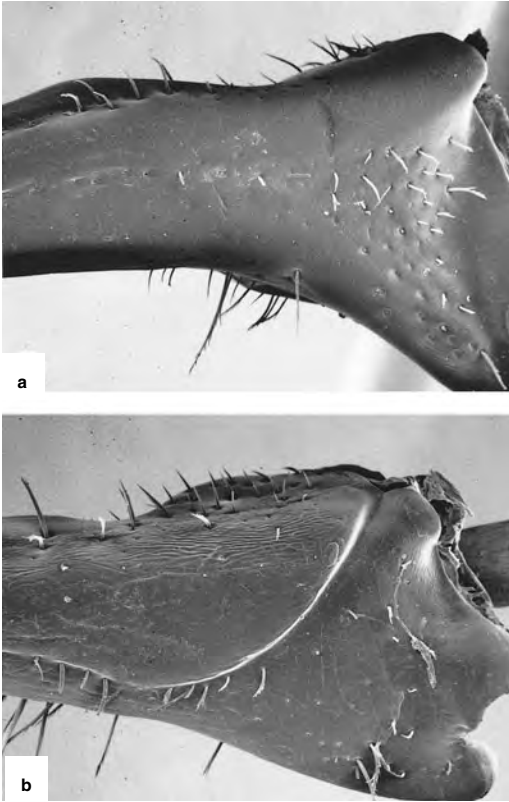


Figure 58-5. Outer surfaces of male mandibles (apices omitted) of Perditiini. **a**, *Perdita octomaculata* (Say); **b**, *Macrotera texana* Cresson. From Danforth, 1996.

Timberlake (1954) explained that the subgenera *Calomacrotera*, *Cockerellia*, *Hexaperdita*, *Pentaperdita*, *Procockerellia*, and *Xeromacrotera* are closely related, as shown by their unusually copious scopa, the simple claws in the female, the bilobed base of S8 of the males (as in *Heteroperdita*), and other characters. In these subgenera, pollen is carried partly dry in the scopa, not moistened and stuck together (with nectar?) as is the case with most *Perdita*. Danforth (1991a), in a cladistic analysis, found that these same subgenera (except *Xeromacrotera*, which he did not have) constituted a monophyletic group. Future workers might well consider uniting these six subgenera under a single name.

Key to the Subgenera of *Perdita*
(Modified from Timberlake, 1954)

- 1. Ocelli large, ocellular distance less than half ocellar diameter; body wholly pallid; intercalary cell present between first and second submarginal cells (Fig. 58-10) *P. (Xerophasma)*
 - Ocelli of ordinary size, ocellular distance much greater than ocellar diameter; if body pallid, then intercalary cell absent 2
- 2(1). Stigma small and slender, width about or not much over half maximum width of marginal cell and less than width of apical truncation of that cell; basitibial plate more or less distinct, at least in the male 3

- Stigma more or less large and broad, width ordinarily more than half width of marginal cell and as wide as apical truncation of that cell; basitibial plate usually absent or poorly developed, but sometimes well developed in both sexes, as in *Pygoperdita* 7
- 3(2). Metasoma broader than thorax and especially broad and depressed in male; hair of hind tibia and basitarsus of male unusually abundant, fine and appressed; basitibial plate developed in both sexes (head of male often greatly enlarged, facial fovea about three times as long as wide but weakly impressed; mandible of male with a broad biangulate or bidentate expansion on inner margin) *P. (Pseudomacrotera)*
 - Metasoma not broadened in female, and at most only moderately depressed and broadened in male; hair of hind tibia and basitarsus of male more or less long, curved, erect, and not much thickened by short, densely set branches; basitibial plate little developed in female 4
- 4(3). Marginal cell more or less shorter and smaller than first submarginal cell and squarely truncate at apex; stigma small and slender, but more or less rounded on posterior margin; facial fovea small and inconspicuous (very small bees with a satiny luster and appressed white pubescence; mandible simple and tapering in both sexes) *P. (Heteroperdita)*
 - Marginal cell subequal to first submarginal, apex a little obliquely truncate; stigma more or less narrowly lanceolate; facial fovea distinct 5
- 5(4). Glossa elongate, reaching middle coxae in repose (facial fovea of female considerably widened at lower end; metasoma of male at most moderately broadened; mandible of male simple) *P. (Glossoperdita)*
 - Glossa ordinary, not reaching much behind front coxae in repose 6
- 6(5). Stigma slender and tapering, hardly wide enough to show central pale streak; mandible of both sexes with a blunt inner tooth near apex; facial fovea of female slightly widened below; metasoma of male not broadened; front and middle femora of male subincrassate and apical segments of tarsi unusually large, with large claws *P. (Hesperoperdita)*
 - Stigma somewhat less slender; mandible of female with a small inner tooth, that of male usually simple and tapering; facial fovea of female very narrow; metasoma of male moderately depressed and broadened; legs of male ordinary *P. (Epimacrotera)*
- 7(2). Scopa of hind tibia copious, hairs long, often more or less crinkly or minutely branched, seemingly adapted for carrying pollen at least partly dry; claws of female simple; side of pronotum of male more or less deeply furrowed (except in *Allomacrotera*); S8 of male with bilobate base 8
 - Scopa of hind tibia composed of long, curved, simple, widely spaced hairs, seemingly adapted for carrying agglutinated pollen; claws of female more or less distinctly dentate within; side of pronotum of male usually not grooved; S8 of male with simple, median spiculum at base 14
- 8(7). Usually large species, 5 to 9 mm long; mandible of female dilated on inner margin and abruptly bent inward before apex, incurved part tapering and simple; metasoma of male no wider than thorax; claws of male hind

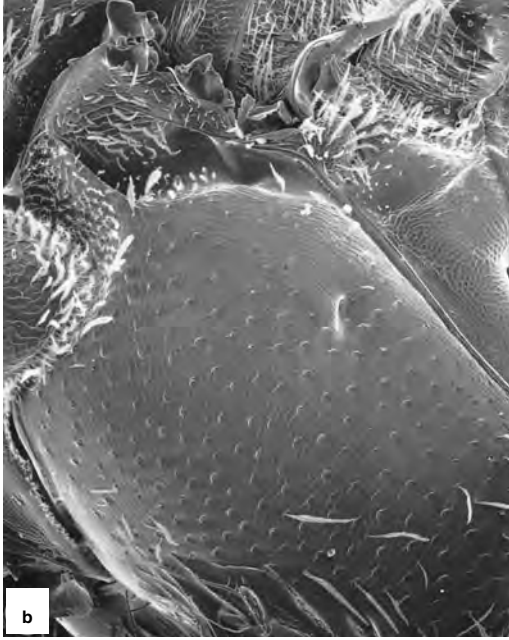


Figure 58-6. Lateral views of upper part of mesepisternum of Perditiini. **a**, *Perdita octomaculata* (Say); **b**, *Macrotera portalis* (Timberlake). *Perdita* has the episternal and scrobal groove (arrow), lacking in *Macrotera*. From Danforth, 1996; in his Figure 7 the legend for these two photographs is reversed.

- leg simple (except in *Allomacrotera* where cleft) 9
- Smaller species, rarely exceeding 6 mm in length; mandible of female ordinary or only moderately expanded within, and but little incurved at apex; metasoma of male usually moderately broad and depressed; claws of male hind leg cleft 11
- 9(8). Claws of male hind leg cleft; side of pronotum not furrowed (maxillary palpus three-segmented)
..... *P. (Allomacrotera)*
- Claws of male hind leg simple; side of pronotum more or less deeply furrowed 10
- 10(9). Maxillary palpus six-segmented; stigma moderately wide, sometimes less than half as wide as marginal cell; thorax green, mesonotum and scutellum never black but sometimes yellow; mandible of male long, slender, tapering, and curved *P. (Cockerellia)*
- Maxillary palpus three- to five-segmented; stigma considerably larger and broader, more than half as wide to fully as wide as marginal cell; thorax green, disc of mesoscutum and scutellum black; mandible of male long, simple, abruptly bent inward before middle, slightly dilated beyond bend *P. (Procockerellia)*
- 11(8). Maxillary palpus five-segmented (possibly indistinctly six-segmented in *Xeromacrotera*) 12
- Maxillary palpus six-segmented 13
- 12(11). Body metallic blue or green, usually with white facial marks (tibial scopa of female unusually copious; metasoma of male depressed, considerably broader than thorax and usually without light markings)
..... *P. (Pentaperdita)*
- Body yellow with black or nearly black markings on head and thorax [head of male very large, quadrate; malar area short but evident (almost obliterated in allies); disc of clypeus small, much narrower than lateral extensions of enormous paraocular areas] *P. (Xeromacrotera)*
- 13(11). Body large (length 6.5-9.0 mm), robust; metasoma with yellow bands and a definite pygidial plate in both

- sexes; mandible of female having triangular process on inner margin about one-fourth of length from base; tibial scopa copious for a *Perdita* and distinctly plumose
..... *P. (Callomacrotera)*
- Body small, of ordinary form; metasoma without distinct light markings, not subpygidiform at apex; mandible of female more or less dilated within; tibial scopa moderately copious, hairs simple and curved except on dorsal margin where they are mosslike with close-set, very short branches *P. (Hexaperdita)*
- 14(7). Marginal cell extremely short and oblique behind short, broad stigma; second submarginal cell triangular, first and second submarginal crossveins uniting at marginal cell (clypeus of male produced to sharp tooth or slender lobe on each side of base of labrum)
..... *P. (Perditella)*
- Marginal cell never excessively shortened and oblique; second submarginal cell not triangular 15
- 15(14). Small intercalary cell usually present between first and second submarginal cells (as in Fig. 56-10); mandible of male with small subapical tooth on inner margin *P. (Alloperdita)*
- Intercalary cell never present; mandible of male usually simple and acute at apex 16
- 16(15). T7 of male strongly emarginate on each side, setting off median pygidiform process or deeply bilobed process, or modifications thereof (female robust; head broader than long; margin of clypeus dentate on each side of labrum) *P. (Pygoperdita)*
- T7 of male usually simple, tapering, or, if somewhat

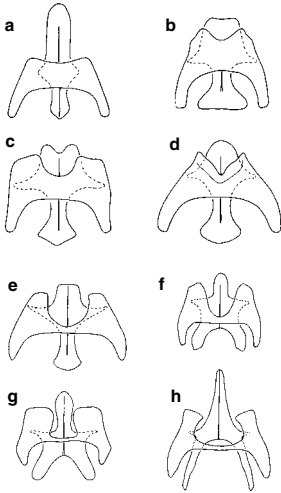


Figure 58-7. Diagrams of ventral views of S7 and S8 of male *Perditi*; S8 is indicated in part by broken lines behind S7. **a**, *Macrotera* (*Macrotera*) *texana* Cresson; **b**, *Perdita* (*Epimacrotera*) *euphorbiae* Timberlake; **c**, *P. (Perdita) sphaeralceae* Cockerell; **d**, *P. (P.) octomaculata* (Say); **e**, *P. (P.) zonalis* Cresson; **f**, *P. (Hexaperdita) bishoppi* Cockerell; **g**, *P. (Cockerellia) coreopsidis* Cockerell; **h**, *P. (Procockerellia) albonotata* Timberlake. Note that in f, g, and h, S8 is basally emarginate, in contrast to the basal spiculum of the others. From Danforth, 1996.

modified, then never deeply emarginate on each side nor strongly bilobed at apex *P. (Perdita s. str.)*

***Perdita* / Subgenus *Allomacrotera* Timberlake**

Perdita (*Allomacrotera*) Timberlake, 1960: 131. Type species: *Perdita stephanomeriae* Timberlake, 1954, by original designation.

This is a close relative of *Procockerellia*, from which it differs by the cleft hind claws of the male and the lack of lateral furrows on the pronotum. Body length is 5.5 to 6.0 mm.

■ *Allomacrotera* is found in southern California and Utah, USA. It includes two species. Timberlake (1971) gave a key to species of *Procockerellia* and *Allomacrotera*.

***Perdita* / Subgenus *Alloperdita* Viereck**

Perdita (*Alloperdita*) Viereck, 1917b: 241. Type species: *Perdita novaeangliae* Viereck, 1907, monobasic.

Like those of *Xerophasma*, bees of this subgenus have an intercalary submarginal cell in the forewing. This character distinguishes *Alloperdita* from *Perdita s. str.*, but the intercalary cell varies in size and is absent in an occasional individual. There may be no other character to separate *Alloperdita* from *Perdita s. str.* reliably, in which case *Alloperdita* should become a synonym. The size is like that of ordinary *Perdita*, 4 to 6 mm in body length.

■ This subgenus ranges from Massachusetts to Florida west to Texas, USA, and to Coahuila and Chihuahua, Mexico. All records in the USA are from coastal states. The six species were revised by Timberlake (1956).

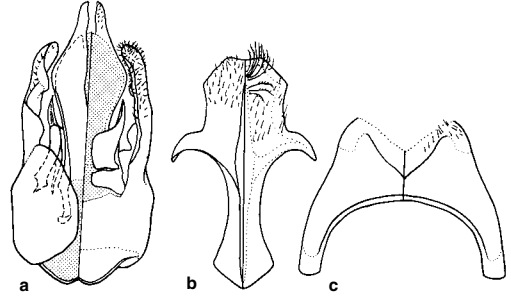


Figure 58-8. Male genitalia, S8, and S7 of *Perdita (Perdita) halictoides* Smith. (Dorsal views are at the left.) From Ruz, 1986.

***Perdita* / Subgenus *Callomacrotera* Timberlake**

Perdita (*Callomacrotera*) Timberlake, 1954: 413. Type species: *Perdita maritima* Timberlake, 1954, by original designation.

This subgenus consists of large species, 6.5 to 9.0 mm long, the head and thorax of which is dark green or blue green; the metasoma is blackish with yellow bands in females, largely yellow in some males. The transverse head, broad metasoma, and unusually short maxillary palpi are characteristic.

■ *Callomacrotera* is known only from the Pacific coast of Mexico, from Guerrero to Nayarit. There are two species; see Timberlake (1954).

***Perdita* / Subgenus *Cockerellia* Ashmead**

Cockerellia Ashmead, 1898: 284. Type species: *Perdita hyalina* Cresson, 1878 = *Perdita albipennis* Cresson, 1865, by original designation.

Philoxanthus Ashmead, 1898: 285. Type species: *Perdita beata* Cockerell, 1895, by original designation.

This subgenus consists of rather large species, 6 to 9 mm long, ranging from almost wholly yellow to the pattern of the commoner species, with broad yellow metasomal bands and metallic green head and thorax; rarely, the metasoma is entirely dark. As in *Procockerellia*, the claws of the female are simple, those of the male cleft on the front and middle legs, simple on the hind legs.

■ *Cockerellia* occurs in the southern prairie provinces of Canada, and from Idaho to New Jersey, USA, south to California and Georgia, USA, and to Veracruz and Zacatecas, Mexico. The 25 species were revised by Timberlake (1954), who also gave a separate key for the identification of females (Timberlake, 1953b).

All the species collect pollen from large-flowered Asteraceae, such as *Helianthus*.

***Perdita* / Subgenus *Epimacrotera* Timberlake**

Perdita (*Epimacrotera*) Timberlake, 1954: 377. Type species: *Perdita ainsliei* Crawford, 1932, by original designation.

Epimacrotera consists of small species (2.5-5.0 mm long) closely related to *Glossoperdita* except for the short proboscis, the glossa in repose extending little behind the head. It seems likely that the two subgenera should be

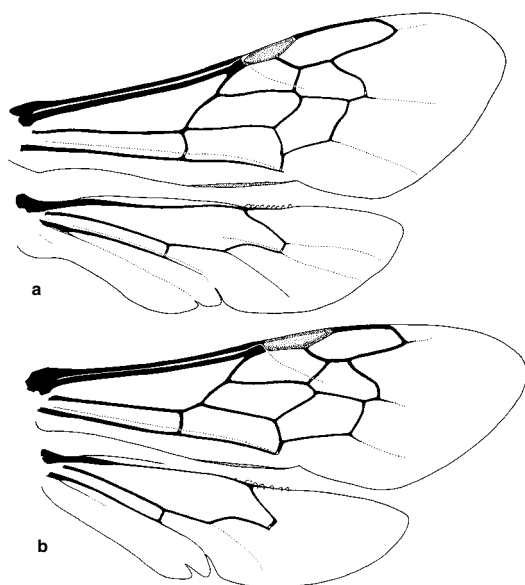


Figure 59-2. Wings of Calliopsini. **a**, *Calliopsis andreniformis* Smith; **b**, *Callonychium minutum* (Friese).

similar waterproofing, a feature duplicated, so far as is known, only in the Perditini. Details of nesting biology are provided by Rozen (1967a, 1970b), Shinn (1967), Danforth (1990), and Visscher and Danforth (1993).

The genera of this tribe were reviewed, and genitalia and other structures were illustrated, by Ruz (1986, 1991).

Key to the Genera of the Calliopsini (Males) (Modified from Ruz, 1991)

1. Inner orbits convergent below; tentorial pit clearly below middle of outer subantennal suture (Fig. 59-1) 2
- Inner orbits subparallel or divergent below; tentorial pit near middle of outer subantennal suture 4
- 2(1). T7 with median smooth area distally, area delimited by hairs and tapered at apex (S4 and S5 with distal margins straight or nearly so, without median projections) *Acampopoeum*
- T7 with pygidial plate rounded or truncate at apex, usually delimited by ridges or carinae laterally 3
- 3(2). S4 with distal margin usually produced in middle, its surface broadly concave mesally; S5 with median projection (sometimes inconspicuous) on distal margin *Calliopsis*
- S4 and S5 unmodified, transverse, without projections or concavity *Litocallipsis*
- 4(1). Orbits strongly divergent below; lower paraocular area flat; most of body yellow; hind tibial spurs strongly curved; metasoma much wider than head; body length about 10 mm or nearly so (South America) *Arhysosage*
- Orbits usually subparallel, but if not, then lower paraocular area very swollen mesally; body with yellow markings but usually predominantly black; inner hind tibial spur almost straight, outer spur straight or somewhat

- curved; metasoma as broad as head; body length 4 to 7 mm 5
- 5(4). Metasoma at apex slightly curved or straight; paraocular area yellow only on lower part; clypeus (in ventral view) with projection or convexity of lateral, downward-directed part beside lateral margin of labrum; antennal socket (lower margin) usually at lower third of face (South America) *Spinoliella*
- Metasoma at apex strongly curved downward and forward; paraocular area with yellow surpassing level of antennal socket, usually narrowly following orbit; clypeus (in ventral view) with inner margin of lateral area beside lateral margin of labrum usually almost straight; antennal socket (lower margin) usually at lower quarter of face (South America) *Callonychium*

Key to the Genera of the Calliopsini (Females) (Modified from Ruz, 1991)

1. Labrum with basal area excavated, distal part convex, protruberant in lateral view; inner orbits generally convergent below, or, if not, then lower paraocular area not swollen mesally 2
- Labrum flat or with smooth, rounded, nearly transverse ridge, distal area flat; inner orbits subparallel or divergent below and lower paraocular area swollen mesally 4
- 2(1). Labrum with basal area pilose at least laterally, its distal margin strongly salient; hind tibia with keirotichia widespread on most of inner surface (South America) 3
- Labrum with basal area usually glabrous, but if pilose, then flat (without ridge); hind tibia with keirotichia absent toward ventral margin to completely absent between basal and distal patches *Calliopsis*
- 3(2). Lower paraocular area mesally (immediately above sublateral concavity in upper clypeal margin) swollen and impunctate; apical hair bands of T1 to T4 with hairs short, scarcely surpassing tergal margins, and directed posterolaterally *Litocallipsis*
- Lower paraocular area mesally not or weakly swollen, sometimes with small, impunctate area; apical hair bands of T1 to T4 with hairs long, surpassing tergal margins, directed posteriorly *Acampopoeum*
- 4(1). Inner orbits divergent below; metasoma wider than thorax; middle and hind tibial spurs strongly curved at apices; lower paraocular area convex (South America) *Arhysosage*
- Inner orbits subparallel; metasoma about as wide as thorax or narrower; middle and hind tibial spurs slightly curved; lower paraocular area strongly convex only on inner corner 5
- 5(4). Gena black; lower paraocular area with yellow not extending upward as narrow band along orbit; antennal sockets (lower margins) at lower one-third of face; claws bifurcate; facial fovea not linear (South America) *Spinoliella*
- Gena with longitudinal yellow band to completely yellow; lower paraocular area with yellow spot, which is narrowed and extended upward along upper orbit; antennal sockets (lower margins) usually at lower one-fourth of face; claws simple; facial fovea linear (South America) *Callonychium*

species. Shinn (1965) gave a key to species. Compagnucci (2004) described three more species and gave a key to the species of Argentina. The nesting biology and immature stages of *Acamptopoeum* were described by Rozen and Yanega (1999).

Genus *Arhysosage* Brèthes

Arhysosage Brèthes, 1922: 121. Type species: *Arhysosage johnsoni* Brèthes, 1922 = *Camptopoeum ochraceum* Friese, 1908, monobasic.

Ruiziella Timberlake, 1952a: 105 (April) [not Cortés, 1952 (March)]. Type species: *Camptopoeum ochraceum* Friese, 1908, by original designation.

Ruziapis Timberlake, 1952b: 528, *lapsus* for *Ruizapis* and replacement for *Ruiziella* Timberlake, 1952.

Ruizapis Timberlake, 1953a: 598, emendation of *Ruizapis* Timberlake, 1952.

This genus is related to *Spinoliella* and *Callonychium*, sharing with them the yellow and black to largely yellow body (length about 10 mm) and the low position of the antennal sockets. Its members can be differentiated by their inner orbits, which are distinctly divergent below, and the hind tibial spurs, which are distinctly curved toward the apices. In the male the body is almost completely yellow, and the mandible is strongly curved and elongate, with a preapical tooth and a projection on the upper margin. Genitalic and other structures were illustrated by Ruz (1986, 1991).

■ This genus is found in Argentina, from the provinces of Formosa and Catamarca south to Córdoba. There were three known species (Ruz, 1991); they were reviewed by Moure (1958b). A revision of the six species of *Arhysosage* now recognized was by Engel (2000d).

Genus *Calliopsis* Smith

Calliopsis is used here in the sense of Ruz (1991) to include forms traditionally placed in the genera *Calliopsis*, *Hypomacrotera*, *Liopoeum*, and *Nomadopsis*. To judge from the study by Ruz, the genus *Calliopsis* in the old sense was a paraphyletic taxon from which the others arose. I have not hesitated to recognize various other probably paraphyletic taxa when strongly supported by large morphological gaps from derived taxa, but there is no such situation in this case.

This genus is similar to *Acamptopoeum*; the two are sister groups (Ruz, 1991). *Calliopsis* differs from *Acamptopoeum* by the usually shorter and less dense thoracic hair, the presence in most cases of a transverse but not strongly salient ridge on the labrum, the median marginal projection of S4 of the male (sometimes inconspicuous), and, usually, such a projection also on S5. The sting of the female does not reach the stylus and is pointed at the apex. Male genitalia and sterna of various subgenera were illustrated by Mitchell (1960) and Ruz (1986, 1991). These structures of the North American subgenera having integumental metasomal color bands (old *Nomadopsis*) were illustrated by Rozen (1958), and structures of the subgenera with metasomal hair bands (the old *Calliopsis*) were illustrated by Shinn (1967); see also Figure 59-3e-j.

The species of *Calliopsis* are oligolectic or narrowly polylectic. The subgenus *Calliopsis* s. str. visits mostly

small legumes, but at least some species, such as *C. (C.) andreniformis* Smith, are rather polylectic, utilizing pollen from other flowers as well (see Shinn, 1967). *Perissander* visits small Euphorbiaceae. *Calliopsisima* collects pollen from yellow Compositae. *Verbenapis* collects pollen from, and seems to be morphologically adapted to, certain species of *Verbena*. *Hypomacrotera* includes one species that is associated with *Sphaeralcea* (Malvaceae) and others that are associated with small Solanaceae such as *Physalis*. The subgenera *Nomadopsis* and *Micronomadopsis* are not oligolectic as subgenera, but many of the included species are oligolectic.

Nests of *Calliopsis* are short burrows in the soil with laterals leading to cells, which are sometimes isolated, sometimes in short series. The most extensive account is by Shinn (1967) on *C. andreniformis* Smith. The cell is lined with a thin secreted layer, and the ball of larval food, when completed, is covered with a similar film (Rozen, 1958, 1970b). In some species the loose tumulus material closes the nest entrance; on leaving or entering, the bee has to dig through the loose earth of the tumulus. *C. (Micronomadopsis) larreae* (Timberlake) nests in areas where loose sand 2 to 8 cm thick covers the sandy clay where the cells are constructed. Bees entering or leaving their nests have to dig through the loose sand; those entering evidently keep their pollen loads in place and quickly find their burrows under the loose sand layer (Rust, 1988). The life cycle and behavior of a tropical species, *Calliopsis (Calliopsis) hondurasicus* Cockerell, were discussed by Wcislo (1999a). Even in the lowlands of Panama, this species has a short season of flight, limited to the early part of the dry season.

Key to the Subgenera of *Calliopsis* (Males)

1. Hind basitarsus with pubescence of dorsal margin at least partly about as long as basitarsus or longer; apical area of labrum clearly convex, almost glabrous except at margin; labrum with no defined ridge separating basal and apical areas (South America) *C. (Liopoeum)*
- Hind basitarsus with pubescence of dorsal margin about half as long as basitarsus or shorter; apical area of labrum hairy, rather flattened; labrum with ridge or carina separating basal and apical areas [but entire labrum flat and pilose in *C. (Hypomacrotera) subalpina* (Cockerell)] 2
- 2(1). T2-T5 at least laterally with marginal hair bands 3
- T2-T5 without marginal hair bands 6
- 3(2). Subantennal area black; metanotum laterally without velvety area; propodeal triangle basally smooth, medially concave (nearctic) *C. (Verbenapis)*
- Subantennal area yellow; metanotum laterally with area (sometimes reduced to a small and narrow strip) of dense velvety hairs; propodeal triangle basally rugose or at least slightly roughened, medially flat 4
- 4(3). Clypeus (in lateral view) clearly protuberant; metanotum with conspicuous patch of velvet-brown hairs laterally (North and Central America) *C. (Calliopsis* s. str.)
- Clypeus (in lateral view) almost flat; metanotum with small patch of velvet-white hairs laterally 5
- 5(4). Labrum with basal area delimited by strong carinate ridge; middle basitarsus somewhat shorter than hind; propodeal triangle basally with strong striae, striated part delimited posteriorly by strong transverse ridge (nearctic) *C. (Calliopsisima)*

- Labrum with basal area delimited by weak ridge; middle basitarsus much longer than hind; propodeal triangle basally with weak striae, not delimited posteriorly by strong transverse ridge (nearctic) *C. (Perissander)*
- 6(2). Metasoma without yellow marks 7
- Metasomal terga almost always with interrupted or complete yellow bands 9
- 7(6). Antennal scape robust, less than three times as long as wide; stigma more than twice as broad as prestigma, as measured to wing margin, margin within marginal cell clearly convex (Argentina) *C. (Ceroliopoeum)*
- Antennal scape normal, over four times as long as wide; stigma less than twice as broad as prestigma, margin within marginal cell straight or nearly so (Fig. 59-5) 8
- 8(7). Inner orbits subparallel; marginal cell about twice as long as second submarginal cell or longer (Fig. 59-5); hind tarsomeres 2 to 5 unmodified (nearctic)
..... *C. (Hypomacrotera)*
- Inner orbits convergent below (Fig. 59-1f); marginal cell less than twice as long as second submarginal cell; hind basitarsus and tarsomeres 2 to 4 asymmetrical, and distitarsus widened medially (Argentina)
..... *C. (Liopoeodes)*
- 9(6). Front and middle tarsi slender, and tarsomeres 2 to 4 of hind tarsus often broadened laterally, asymmetrical (nearctic) *C. (Micronomadopsis)*
- Tarsi with tarsomeres broadened distally, symmetrical (nearctic) *C. (Nomadopsis)*

Key to the Subgenera of *Calliopsis* (Females)

- 1. Stigma more than twice as broad as prestigma as measured to wing margin; stigmal margin within marginal cell clearly convex; midfemoral comb less than half length of femur (Argentina) *C. (Ceroliopoeum)*
- Stigma less than twice as broad as prestigma as measured to wing margin; stigmal margin within marginal cell straight or nearly so; midfemoral comb about half length of femur 2
- 2(1). T2-T4 with marginal hair bands, at least laterally 3
- T2-T4 without marginal hair bands 8
- 3(2). Integument black (with some slight blue but no yellow); wing veins mostly dark; inner orbits subparallel; T1 and T2 polished, scarcely punctate (Argentina)
..... *C. (Liopoeodes)*
- Integument with at least some yellow marks; wing veins mostly yellowish; inner orbits convergent below; terga with rather abundant punctation 4
- 4(3). Middle tibial spur with about five coarse teeth, all on distal half; hind tibia with keirotrochia on inner surface at base and at apex only; S6 distally with fringe of hairs interrupted medially (South America)
..... *C. (Liopoeum)* (in part)
- Middle tibial spur with somewhat coarse teeth, not limited to distal half; hind tibia with keirotrochia on most of inner surface or absent toward ventral border; S6 distally with hairs forming a continuous curved fringe 5
- 5(4). Front tarsus with hairs on inner surface sparse, mostly stiff, curved and not tapered at apices (Fig. 59-3k); metanotum laterally without patch of velvety hairs (nearctic) *C. (Verbenapis)*
- Front tarsus with hairs on inner surface dense, unmod-

- ified; metanotum laterally with small (sometimes inconspicuous) patch of white, velvety hairs 6
- 6(5). Clypeus (in lateral view) protuberant, projecting forward one-third width of eye or more; paraocular area with lowest part noticeably wider than at level of antennal sockets, usually swollen on lower inner corner (North and Central America) *C. (Calliopsis s. str.)*
- Clypeus (in lateral view) less protuberant, projecting forward only about one-fourth width of eye or less; paraocular area with lowest part about as wide as at level of antennal sockets, only slightly convex 7
- 7(6). Propodeum mostly punctate, base with a conspicuously rugose triangle delimited by strong ridge or carina; metanotum laterally with clearly visible patch of white, velvety hairs (nearctic) *C. (Calliopsima)*
- Propodeum posteriorly with extensive impunctate area, base usually little or not very strongly rugose, triangle delimited by rather rounded ridge; metanotum laterally with inconspicuous (difficult to see) patch of white, velvety hairs (nearctic) *C. (Perissander)*
- 8(2). Middle tibial spur with most teeth much longer than those of hind tibial spurs; S6 with apical marginal fringe of hairs broken medially (South America)
..... *C. (Liopoeum)* (in part)
- Middle tibial spur with most teeth only slightly longer than those of hind tibial spurs; S6 with hairs forming a continuous curved fringe distally 9
- 9(8). Propodeal triangle polished; metasoma with no yellow markings (nearctic) *C. (Hypomacrotera)*
- Propodeal triangle at least slightly rugose basally; metasoma almost always with complete or interrupted yellow integumental bands 10
- 10(9). Body length less than 10 mm; middle tibial spur with four teeth on distal half (nearctic) *C. (Micronomadopsis)*
- Body length 10 mm or longer; middle tibial spur with more than four teeth on distal half (nearctic)
..... *C. (Nomadopsis)*

Calliopsis / Subgenus *Calliopsima* Shinn

Calliopsis (*Calliopsima*) Shinn, 1967: 834. Type species: *Calliopsis rozeni* Shinn, 1967, by original designation.

Most species of this subgenus are slightly more robust and larger (7-9 mm long) than most species of *Calliopsis* s. str. As in that subgenus, the body is black with yellow or cream-colored areas on the face and sometimes the pronotum. The glossa is longer than the prementum. The clypeus is flattened, and the distal margin of the basal area of the labrum is marked by a strong carina. The metanotum has a narrow patch of dense hairs basilaterally. The middle basitarsus is shorter than the hind basitarsus.

■ *Calliopsima* occurs from the southern prairie provinces of Canada to Chiapas in southern Mexico and across the continent from California to Florida, USA. It is unknown from the Northwest (Oregon, Washington, British Columbia) and from the Northeast (from Tennessee to the north and east). The 15 species were revised by Shinn (1967).

The biology of *Calliopsis pugionis* Cockerell was described in detail by Visscher and Danforth (1993).

ings limited to the head and pronotum. The genitalia and associated sterna are more similar to those of *Calliopsima* than to those of *Calliopsis* s. str. and *Perissander*. *Verbena* differs from all these subgenera in that the metanotum laterally lacks velvety hairs and the subantennal and supraclypeal areas are black. The glossa is as in *Calliopsima*. The middle basitarsus is shorter than the hind basitarsus (as in *Calliopsima*). The median projection of S6 of the male has a minute median distal emargination. Male genitalia and hidden sterna are illustrated in Figure 59-3h-j. The apical process of S8 lacks the angles basad to the median constriction found in other subgenera. The inner surface of the front tarsus of the female bears rather short, rigid hairs, curved at the blunt apices (Fig. 59-3k). ■ This subgenus ranges from North Dakota to New Jersey, south to Arizona and Texas, USA, and the state of México; it is not known in the southeastern USA. There are four species, as revised by Shinn (1967).

Species of this subgenus are probably all oligolectic on flowers of the genus *Verbena*. The hooked hairs of the front tarsi of the female (Fig. 59-3k) serve to pull pollen from the slender corolla tube.

Genus *Callonychium* Brèthes

Callonychium is a South American genus of black-and-yellow species 3 to 7 mm long. They differ from *Spinoliella* in the yellow on the genal area, the antennal sockets (lower margins), which are usually at the lower fourth of the face, and the lateral parts of the clypeus, which are strongly bent posteriorly. In the male the basitibial plate is flat and delimited by a carina, the metasomal apex is strongly curled forward, and the sterna are considerably modified with ridges and projections. Male genitalia, sterna, and other structures were illustrated by Toro and Herrera (1980), Cure and Wittmann (1990), and Ruz (1991); see also Figure 57-7a-c.

Key to the Subgenera of *Callonychium*

- 1. Axilla acute, yellow; S1 of male without premarginal process *C. (Callonychium* s. str.)
- Axilla rounded, depressed, black; S1 of male with premarginal process *C. (Paranychium)*

Callonychium / Subgenus *Callonychium* Brèthes s. str.

Callonychium Brèthes, 1922: 120. Type species: *Callonychium argentinum* Brèthes, 1922, monobasic.

■ This subgenus is found in Brazil, Paraguay, and Argentina. There are six described species and additional undescribed forms (Ruz, 1991).

Callonychium / Subgenus *Paranychium* Toro

Callonychium (Paranychium) Toro and Herrera, 1980: 213.

Not valid because no type species was designated.

Callonychium (Paranychium) Toro, 1989: 231. Type species: *Camptopoeum chilense* Friese, 1906, by original designation.

■ This subgenus is known in Chile and Argentina; J. Rozen (in litt., 1997) has found it in Peru. There are five

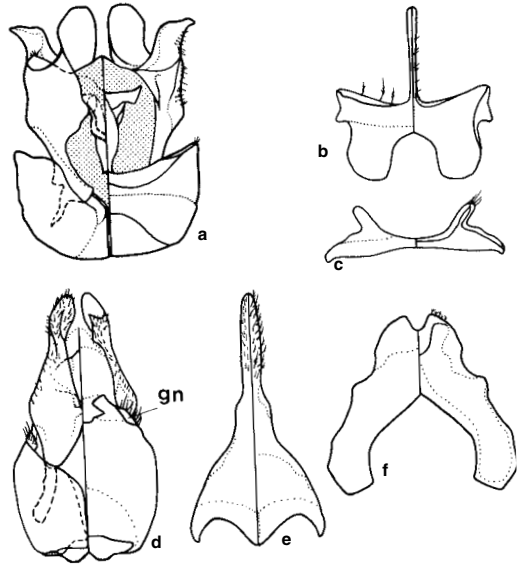


Figure 59-7. Genitalia, S8, and S7 of male Calliopsini. a-c, *Callonychium mandibulare* Brèthes; d-f, *Spinoliella nomadoides* (Spinola). (Dorsal views are at the left; gn is the gonostylus.) From Ruz, 1991.

named species (Ruz, 1991). The Chilean species were revised by Toro and Herrera (1980).

The male of *C. (P.) chilense* Friese has variously modified metasomal sterna. Toro (1985) has investigated the way in which these structures function during mating, when the male is curled around the apical part of the female's metasoma.

Genus *Litocalliopsis* Roig-Alsina and Compagnucci

Litocalliopsis Roig-Alsina and Compagnucci, 2003: 103.

Type species: *Litocalliopsis adesmia* Roig-Alsina and Compagnucci, 2003, by original designation.

Litocalliopsis combines some characters of *Acamptopoeum* and *Calliopsis*. Thus the simple male S4 and S5, the pilose labrum of the female, and the keirotrichia widespread on the inner surface of the hind tibia of the female are as in *Acamptopoeum* and the presence of a male pygidial plate is as in *Calliopsis*.

The single known species of this genus has been found in Buenos Aires Province, Argentina. It appears to be oligolectic on flowers of *Adesmia* (Fabaceae).

Genus *Spinoliella* Ashmead

Spinoliella Ashmead, 1899a: 84. Type species: *Camptopoeum nomioides* Spinola, lapsus for *Camptopoeum nomadoides* Spinola, 1851, by original designation.

Spinoliella (Peniella) Toro and Ruz, 1972: 146. Type species: *Camptopoeum maculatum* Spinola, 1851, by original designation.

Spinoliella consists of yellow-and-black species 4 to 9 mm long, and is closer to *Callonychium* than to

or even abuts against the inner surface of the clypeus without fusion (Michener, 1944: 206).

The larva is unusual, quite unlike other andrenid larvae, and in various characters is similar to that of the Nomadinae, an apparently unrelated taxon of L-T bees (Rozen, 1964a). The distinctive features of mature oxaeine larvae include the following: the apically cleft labrum, the much-reduced labiomaxillary region, the long and blade-like apex of the mandible, and the slitlike primary tracheal openings (Rozen, 1964a, 1993b).

The nests consist of deep (30-245 cm) vertical burrows in flat ground, and radiating, more or less horizontal laterals, each ending in a single, vertical cell lined with a "waxlike" film (Roberts, 1973). Provisions are somewhat liquid and fill the bottom of the cell. Thus the nests closely resemble those of Diphaglossinae (see Roberts, 1971) and are quite different from those of other Andrenidae. It may be significant that the cells of *Euherbstia*, here included in the Andreninae, are sloping to nearly vertical, although in other respects (e.g., firm spherical food mass) quite different from those of Oxaeinae.

The mutual similarity of all species of Oxaeinae is im-

pressive. Hurd and Linsley (1976) revised the subfamily and recognized four genera.

Key to the Genera of the Oxaeinae

1. Maxillary palpus present, six-segmented; male gonostylus partly differentiated from gonocoxite and hairy (Fig. 60-3a) 2
- Maxillary palpus absent; male gonostylus not recognizable, the apex of gonoforceps hairless (Fig. 60-3d) *Oxaea*
- 2(1). Mandible simple apically; clypeus and mandible of male without pale maculations 3
- Mandible with preapical tooth on inner margin; clypeus and mandible of male with pale maculations (South America) *Notoxaea*
- 3(2). S8 of male with apex convex, not emarginate (Fig. 60-3b); T6 of male and T5 of female without conspicuous lateral tufts of long white hairs (North America) *Protoxaea*
- S8 of male with median apical emargination (Fig. 60-3g); T6 of male and T5 of female each with lateral tuft of long white hairs (North America) *Mesoxaea*

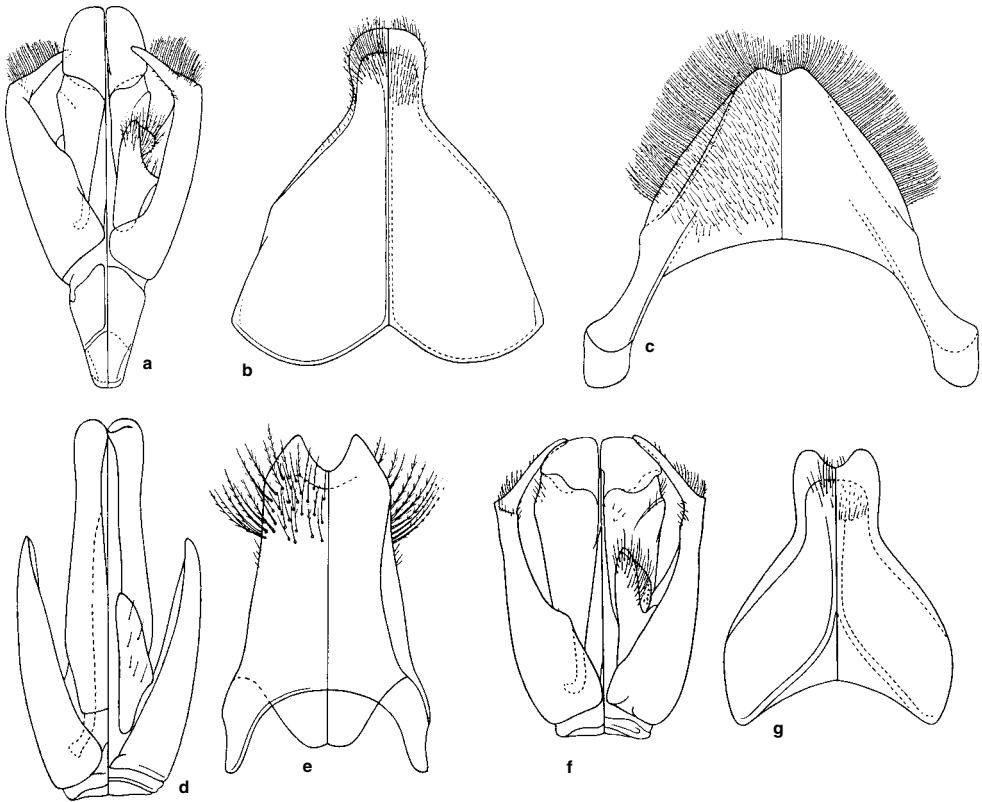


Figure 60-3. Structures of males of Oxaeinae. **a-c**, Genitalia, S8, and S7 of *Protoxaea* (*Protoxaea*) *gloriosa* (Fox); **d, e**, Genitalia and S8 of *Oxaea* *flavescens* Klug; **f, g**, Genitalia and S8 of *Protoxaea* (*Mesoxaea*) *nigerrima* (Friese). (Dorsal views are at the left.) From Hurd and Linsley, 1976.

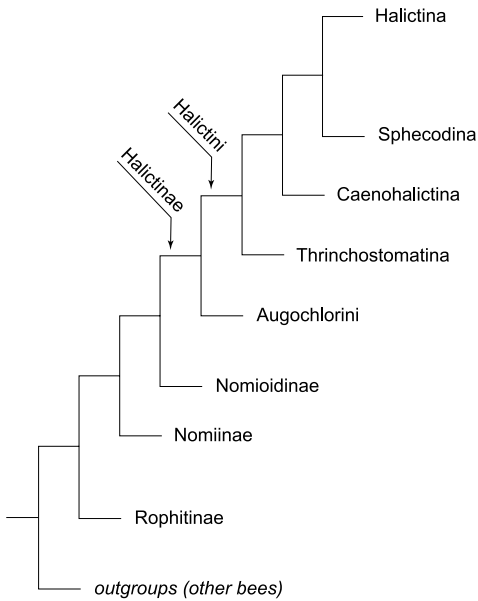


Figure 61-4. Phylogeny of Halictidae, modified from Danforth et al. (2004)

Key to the Subfamilies of the Halictidae

1. Antennae usually arising below midlength of eyes *and* antennal sockets separated from upper clypeal margin by little (if any) more than diameter of socket (Fig. 61-2); apex of labrum of female truncate or rounded (Fig. 61-2c), not produced to a process; hind basitarsus of female usually with apical angle or process but always without penicillus; trochanteral and femoral scopa reduced, longest hairs ordinarily shorter than those of tibial scopa Rophitinae (Sec. 62)
- . Antenna usually arising near midlength of eyes, or, *if*

below that level, then separated from upper clypeal margin by much more than diameter of antennal socket; apex of labrum of female, except in some cleptoparasitic forms, produced to a process commonly bearing a strong keel; hind basitarsus of female, except in some parasitic forms, with apical process bearing penicillus; trochanteral and femoral scopa well developed except in parasitic forms, longest hairs ordinarily longer than those of tibial scopa and forming femoral corbicula [but femoral scopa poorly developed in some *Lipotriches* (Nomiinae) such as *L. tulearensis* (Benoist)] 2

- 2(1). Episternal groove below scrobal groove absent or a weak depression, sometimes directed strongly forward; when there are three submarginal cells, third usually about as long as first, or, *if* shorter, *then* usually twice as long as second (apex of marginal cell rather broadly rounded, Fig. 63-1 (prepygidial fimbria of female not divided medially; S7 of male a transverse plate with short apodemal arms and no midapical projection) Nomiinae (Sec. 63)
- . Episternal groove distinct and directed strongly downward below scrobal groove; when there are three submarginal cells, third shorter than first and less than twice as long as second 3
- 3(2). Apex of marginal cell pointed or minutely truncate; prepygidial fimbria of female divided by longitudinal median zone or triangle of very fine, dense hairs and punctation or sometimes nearly bare integument, the fimbria and its median zone absent in some cleptoparasitic forms; S7 of male consisting of a small discal region, long basolateral apodemes, and usually a midapical angle or process; S8 of male broader than long, variable in shape (S7 and S8 aberrant in *Urohalictus*) Halictinae (Sec. 65)
- . Apex of marginal cell rounded or truncate; prepygidial fimbria of female not divided medially; S7 of male a broad and little modified sternum; S8 of male longer than broad, with broad spiculum and often long apical process (Eastern Hemisphere) Nomioidinae (Sec. 64)

Nests are burrows in the soil with lateral burrows leading to single cells or series of several cells. The cells are subhorizontal or slanting, short (only about 1.5 times as long as broad), and not or only slightly flattened on the lower surface; because the cells are short, observers are usually uncertain about any such flattening. The cell lining is a secreted membrane but it is dull and more pervious to water than that of the other subfamilies, and seems to be absent in *Protodufourea* (Rozen, Roig-Alsina, and Alexander, 1997); the larvae of Rophitinae may add a glistening lining during the feeding stage (Rozen, 1993a). The food mass in each cell is more or less spherical. Unlike those of all other Halictidae, most larvae spin cocoons, but those of one rophitine genus, *Conanthalictus*, do not do so (Rozen, 1993a). Overwintering is by prepupae, so far as is known.

Rozen (1993a) has described and compared various rophitine larvae. The larva of *Xeralictus* was described later by Snelling and Stage (1995a), although Rozen (1993a) had included it in a key to mature larvae. Rophitine larvae differ from those of other halictids in having paired, conical (not transverse) dorsolateral tubercles on most body segments, but those of the prothorax are either reduced, compared to those of other body segments, or absent. The larvae of *Conanthalictus* are very different from those of other known rophitine larvae, presumably because *Conanthalictus* does not spin a cocoon and has the recessed labiomaxillary region common to bee larvae that do not spin cocoons. Relevant details for *Conanthalictus* include fusion of the prementum and postmentum and loss of the lips of the salivary opening. *Xeralictus* may also not spin a cocoon; the one known postdefecating larva was not found in a cocoon, but it did not have the labiomaxillary reduction seen in *Conanthalictus*.

Warncke (1979b) revised the entire subfamily for the west palaearctic region, placing all species except those of *Systropha* under the generic name *Rophites*; he sketched male genitalia and other structures. Below, the genera of the Western Hemisphere are keyed separately from those of the Eastern Hemisphere.

Key to the Genera of the Rophitinae of the Western Hemisphere

1. Forewing with two submarginal cells (Fig. 62-1b, c) 2
- Forewing with three submarginal cells (Fig. 62-1a) 4
- 2(1). S8 of male without a spiculum but with a pair of basal lobes (Fig. 62-2b); penis valves large, elevated above bases of gonocoxites; volsella produced to a fingerlike hairy process (Fig. 62-2a); distance from apex of stigma to apex of marginal cell almost always at least as great as distance from apex of marginal cell to wing tip (Fig. 62-1b) (hol-arctic) *Dufourea*
- S8 of male pointed to truncate at base (Fig. 62-2f, i), without pair of basal lobes; penis valves but little elevated above bases of gonocoxites; volsella relatively short, not produced to a fingerlike process (Fig. 62-2e, h); distance from apex of stigma to apex of marginal cell sometimes less than distance from apex of marginal cell to wing tip (Fig. 62-1c) 3
- 3(2). Dorsal surface of propodeum more than twice as long as metanotum; male with major apical lobes of S7 slender basally and strongly incurved apically; gonostylus slender and straplike (nearctic) *Micralictoides*

- Dorsal surface of propodeum not or little longer than metanotum; male with apical lobes of S7 broad throughout and downcurved; gonostylus subtriangular and not well differentiated from gonocoxite (nearctic) *Sphécodosoma* (in part)
- 4(1). Subantennal area sharply defined, smooth, impunctate, and hairless, extending down broadly to epistomal suture; anterior tentorial pit adjacent to lower outer edge of antennal socket; labial palpus longer than prementum, at least first three segments flattened (South America) .. 5
- Subantennal area often evident as small triangle, impunctate area below antenna, if present, not sharply defined, with punctures and hairs at least marginally; anterior tentorial pit on or just above epistomal suture; labial palpus equal to or shorter than prementum, not flattened (North America) 7
- 5(4). Clypeus four or five times as broad as long; mandible of both sexes with medial or basal tooth or projection on upper margin, in addition to preapical tooth; pygidial plate of male nearly linear (Brazil) *Ceblurgus*
- Clypeus two or three times as broad as long; mandible with usual preapical tooth only; pygidial plate of male broad or absent 6
- 6(5). Maxillary palpus six-segmented; tibial scopal hairs simple; pygidial plate of male about as broad at base as long (Chile) *Penapis*
- Maxillary palpus four-segmented; tibial scopal hairs plumose; pygidial plate of male absent (Peru) *Goeletapis*
- 7(4). Outer hind tibial spur and middle tibial spur coarsely serrate, some teeth long enough to make the spurs briefly pectinate (Fig. 62-4); S7 of male a broad plate without or with small apical lobe on each side, much smaller than disc of sternum; body length 8 mm or more (nearctic deserts) *Xeralictus*
- Tibial spurs minutely ciliate, appearing simple; S7 of male with small disc to which are attached two or four large apical lobes, the lobes collectively much larger than disc; body length usually less than 7.5 mm 8
- 8(7). Dorsal surface of propodeum about two-thirds as long as scutellum and about one-half as long as posterior surface of propodeum, as seen from side (Fig. 62-3a); S7 of male with four apical lobes (nearctic) *Protodufourea*
- Dorsal surface of propodeum about as long as scutellum, more than one-half as long as posterior surface of propodeum, as seen from side (Fig. 62-3b); S7 of male with two apical lobes (Fig. 62-2g, k) 9
- 9(8). Clypeal truncation more than twice as long as length of clypeus; body surface minutely roughened and usually more or less dull; S7 of male relatively flat; spiculum of S8 of male pointed (Fig. 62-2f) (nearctic) *Conanthalictus*
- Clypeal truncation less than twice as long as length of clypeus; body surface smooth and shining between punctures; S7 of male with disc at right angles to basal arms and apical lobes (Fig. 62-2l); base of S8 of male broadly truncate (Fig. 62-2m) (nearctic) *Sphécodosoma* (in part)

Key to the Genera of the Rophitinae of the Eastern Hemisphere

1. Margin of marginal cell on costa shorter than stigma and less than half as long as distance from apex of marginal cell to wing tip; two submarginal cells, second less than

- half length of first; body with yellow integumental markings (paleartic) *Morawitzella*
- Margin of marginal cell on costa as long as or longer than stigma, and as long as or longer than distance from apex of marginal cell to wing tip; two or three submarginal cells, but if two, then second more than half as long as first; body without yellow markings 2
- 2(1). Flagellum of male with first six segments more or less normal, remaining segments abruptly more slender than preceding segments, tightly curled, and sometimes reduced in number; metasoma of both sexes, at least laterally, with abundant, long, more or less erect hair; S8 of male with apical process very broad, projecting, thus suggesting in undissected specimens an eighth tergum (forewing with three submarginal cells) *Systrophia*
- Flagellum of male not so modified; metasoma without abundant long hair; S8 of male with apical process slender, capitate, often projecting but not suggesting a tergal plate 3
- 3(2). Male without pygidial plate, or sometimes with shiny bare area but this area not defined by carinae and not elevated; base of S8 of male deeply bilobed (Fig. 60-2b); labial palpus with first two segments, or at least second, slender and similar in width to third and fourth segments (metasomal hair bands absent or sparse, integument thus visible through bands of hair) (holarctic) *Dufourea*
- Male with well defined, strongly elevated pygidial plate [not verified for *Rophites* (*Flavodufourea*)]; base of S8 of male rounded to weakly bilobed; labial palpus with first two segments broad and flattened in contrast to third and fourth segments (except that in *Rophites* s. str. third segment is on same axis as second and also rather broad basally, only fourth being freely articulated) 4
- 4(3). Metasomal terga with well-developed, dense, pale apical hair bands; forewing with two submarginal cells; pygidial plate of male margined by sharp carina (paleartic) *Rophites*
- Metasomal terga without pale apical hair bands; forewing with three submarginal cells; pygidial plate of male not margined by sharp carina (Turkey) *Morawitzia*

Genus *Ceblurgus* Urban and Moure

Ceblurgus Urban and Moure, 1993: 102. Type species: *Ceblurgus longipalpis* Urban and Moure, 1993, by original designation.

Ceblurgus consists of a robust nonmetallic species about 7.5 mm long. The base of the mandible of the male has a large tuft of long white hairs, directed mesad when the mandibles are closed. The lacinia, if correctly identified, is membranous, with few hairs, and high up on the labiomaxillary tube, as in *Penapis*. And as in *Penapis* and *Goeletapis*, an anterior tentorial root is located against the lower lateral margin of the antennal socket. The short, four-segmented maxillary palpi are as in *Goeletapis*, but the three-toothed mandibles are unique in Rophitinae; all other rophitines have six-segmented maxillary palpi and mandibles with a single preapical tooth, the tooth sometimes extremely reduced. S7 of the male is a broad plate with broad basolateral arms; the apex is truncate and lacks lobes. In this respect *Ceblurgus* is similar to *Penapis* (Fig. 62-2j) and *Goeletapis*. S8 of the male is subtruncate,

not bilobed, basally. The male gonostylus seems triangular, as is the case in many rophitines, but is indistinguishably fused to the gonocoxite; the volsella is elongate, without distinct digitus and cuspis, and is pointed apically (not a fingerlike, hairy projection as in *Dufourea*). The male genitalia and other structures were illustrated by Urban and Moure (1993).

■ *Ceblurgus* is known from the states of Bahia and Pernambuco, Brazil. It is the only rophitine from eastern South America. The single species is *C. longipalpis* Urban and Moure.

Genus *Conanthalictus* Cockerell

Conanthalictus consists of species with greenish or bluish coloration on at least some parts of the head and thorax, sometimes with a red metasoma; the body surface is minutely roughened. The basal area of the propodeum is as long as the scutellum (Fig. 62-3b). Plesiomorphic features include the small, chelate volsellae (Fig. 62-2e) (as usual in Halictidae) and the pointed spiculum of S8 of the male (Fig. 62-2f). S7 of the male is relatively flat, lacks the vertical disc of *Sphecodosoma*, and has two apical lobes (Fig. 62-2g). T6 of the male has a dense fringe that largely obscures T7. A flat-topped apical process on T7 of the male constitutes the pygidial plate, which is not elevated above the surface of the tergum as it is in *Rophites*. The male genitalia and hidden sterna of both subgenera were illustrated by Michener (1965c); see also Figure 62-2e-g.

All species of *Conanthalictus* appear to be oligolectic, mostly on certain genera of Hydrophyllaceae. The nesting biology has been described by Rozen and McGinley (1976) and Rozen (1993a). Except for their minute size, the nests are similar to those of *Dufourea*.

Key to the Subgenera of *Conanthalictus*

1. Head elongate oval, longer than broad; antennal bases twice as far from ocelli as from anterior clypeal margin *C. (Conanthalictus s. str.)*
- Head broader than long; antennal bases scarcely 1.5 times as far from ocelli as from anterior clypeal margin *C. (Phaceliapis)*

Conanthalictus / Subgenus *Conanthalictus* Cockerell s. str.

Halictus (Conanthalictus) Cockerell, 1901b: 209. Type species: *Halictus conanthi* Cockerell, 1901, monobasic.

Conanthalictus s. str. consists of minute, long-headed species, 3 to 4.5 mm long.

■ The range is western Texas to Arizona, USA. For the two species, see Timberlake (1961).

Conanthalictus / Subgenus *Phaceliapis* Michener

Conanthalictus (Phaceliapis) Michener, 1942a: 277. Type species: *Conanthalictus bakeri* Crawford, 1907, by original designation.

These are the broad-headed species of *Conanthalictus*, mostly larger than *Conanthalictus* s. str. (body length 3-7 mm).

■ The range is western Texas to southern California, USA, south at least to Chihuahua and Baja California,

in the number of submarginal cells and in the form of the four small apical lobes of the male S7, the disc of which is flat, not vertical as in *Sphēcodosoma*. The genitalia and hidden sterna were illustrated by Michener (1965c) and Bohart and Griswold (1997).

■ This genus is found in California and Arizona. The five species were revised by Bohart and Griswold (1997).

Protodufourea species appear to be oligolectic visitors to flowers of *Phacelia* and *Emmenanthe* (Hydrophyllaceae). The nesting behavior was described by Rozen, Roig-Alsina, and Alexander (1997).

Genus *Rophites* Spinola

Rophites is a close relative of *Dufourea*, and these two taxa could be regarded as congeneric. The principal differences are as follows: In *Rophites* the metasomal terga have dense apical hair bands. In other Rophitinae the bands are absent or thin, not hiding the surfaces of the tergal margins. As in *Ceblurgus* and *Penapis*, T7 of the male *Rophites* has a strongly elevated pygidial plate margined by a sharp, raised carina (not verified for the subgenus *Flavodufourea*). In male *Morawitzia* there is a raised pygidial area, but it is not margined by a sharp carina; other rophitine male pygidial areas, if recognizable, are not defined, except for being hairless. In *Rophites* the base of S8 of the male is convex to subtruncate or feebly emarginate; in *Dufourea* it is deeply bilobed. The *Dufourea*-like characters of *Rophites* include (1) the hairy apical projection of the volsellar digitus, although it is shorter than in *Dufourea* and the cuspis is nearly as long as the digitus, the two pressed together (in *Dufourea* the cuspis is unrecognizable or much shorter than the long digitus); (2) the moderately Z-shaped penis valve, with an angle produced apicad near the volsella; and (3) the capitate apical process of S8 of the male.

Three subgenera are distinguishable.

Key to the Subgenera of *Rophites*

1. First segment of labial palpus strongly broadened in apical half; apical lobes of S7 of male broad basally and tapering to points..... *R. (Flavodufourea)*
- First segment of labial palpus nearly parallel-sided; apical lobes of S7 of male slender basally, slightly enlarged and rounded apically..... 2
- 2(1). Labial palpal segments 1 to 3 flattened, fourth segment not flattened and sometimes divergent from axis of other segments; labial palpus longer than maxillary palpus; frons of female with several coarse bristles, these hooked or curved at tips (but bristles absent in *Rophites gusenleitneri* Schwammberger) *R. (Rophites s. str.)*
- Labial palpus with at least segment 3 (as well as 4) not flattened, commonly diverging from axis of 1 and 2; labial palpus shorter than maxillary palpus; frons of female without coarse bristles *R. (Rhophitoides)*

Rophites / Subgenus *Flavodufourea* Ebmer

Dufourea (Flavodufourea) Ebmer, 1984: 373. Type species: *Dufourea flavicornis* Friese, 1913, by original designation.

The type species of this subgenus was originally placed in *Dufourea*, and subsequently in *Rophites* (Popov, 1946) and *Rhophitoides* (Schwammberger, 1975a). Its strong

metasomal hair bands and the subtruncate or scarcely concave base of S8 of the male support its inclusion in *Rophites* in the sense of this work. The mouthparts are short; the maxillary palpus is shorter than the labial palpus, an unusual feature in Rophitinae but one that is found also in *Rophites s. str.* Mouthparts, genitalia, and hidden sterna were illustrated by Schwammberger (1975a) and Ebmer (1984).

■ *Flavodufourea* is known from Mongolia and Kazakhstan. Two species are recognized.

A. W. Ebmer (in litt., 1994) considers *Flavodufourea* to be closer to *Dufourea* than to *Rophites*. I have not seen specimens, and place it with *Rophites* because of the characters listed above, supported by Popov's (1946) judgment. *Flavodufourea* was returned to the genus *Dufourea* from its present placement, and a second species (from Kazakhstan) was described, by Patiny (2003a). The most distinctive feature of *Dufourea*, the deeply bilobed base of S8 of the male, was not reported by Patiny; therefore placement in *Dufourea* does not seem to be decisive.

Rophites / Subgenus *Rhophitoides* Schenck

Rhophitoides Schenck, 1861: 69 [for the date, see Michener, 1968a]. Type species: *Rhophitoides distinguendus* Schenck, 1861 = *Rhophites cana* Eversmann, 1852, monobasic.

This subgenus consists of forms 6 to 8 mm in length. For distinguishing characters, see the key to the subgenera.

■ The range is from Morocco and France to Turkey and the Caucasus. The four species were revised (along with *Flavodufourea*) by Schwammberger (1975a).

Nesting biology has been reported by various authors, such as Enslin (1921), Malyshev (1925a), and Wilkaniec, Wójtowski, and Szyma (1985). The nests are as described above for the subfamily; there are one to four subhorizontal cells per nest. *Rophites canus* Eversmann is a significant pollinator of alfalfa in Eurasia and an oligolectic on small legumes.

Rophites / Subgenus *Rophites* Spinola s. str.

Rophites Spinola, 1808: 8, 72. Type species: *Rophites quinquespinosus* Spinola, 1808, monobasic.
Rhophites Agassiz, 1846: 29, unnecessary emendation.

Members of this subgenus are usually larger than those of *Rhophitoides*, with a body length of 5 to 11 mm. The only species less than 8 mm long is *R. gusenleitneri* Schwammberger, which, in the absence of frontal bristles as well as in its size, resembles *Rhophitoides*. Male genitalia and other structures were illustrated by Schwammberger (1971b), Benedek (1973), Constantinescu (1974a), Ebmer and Schwammberger (1986), and Ebmer 1993a).

■ This subgenus ranges from Spain and Morocco to Asia Minor, southern Russia, and eastward to Mongolia, occurring north to 60°N in Europe. The 13 species were revised by Ebmer and Schwammberger (1986).

Müller (1996a) found that the bristles on the frons are used with buzzing to remove pollen from flowers of mints (Lamiaceae).

Genus *Sphecodosoma* Crawford

This genus consists of small to minute, nonmetallic, strongly punctate bees with the interspaces smooth, unlike those of *Conanthalictus*; the metasoma of the female is often red. Males differ from those of *Dufourea* in their short volsellae, without or with few hairs, the ordinary rather than elevated bases of the penis valves (so that the valves are not Z-shaped as seen in side view), the truncate base of S8 of the male (Fig. 62-2m), and the downcurved apical process of S8. Especially characteristic is the vertical disc of S7, lying more or less at right angles both to the basal arms and to the two apical lobes (Fig. 62-2l). The character of wing venation cited in the key to genera, couplet 2, is weak; it is therefore difficult to distinguish females from those of small *Dufourea*. The clypeus is not strongly protuberant as seen in side view, however, a helpful feature in distinguishing *Sphecodosoma* from *Dufourea*.

There are two subgenera of *Sphecodosoma*, each hitherto given generic status but actually closely related.

Key to the Subgenera of *Sphecodosoma*

1. Fore wing with two submarginal cells; dorsal surface of propodeum not or little longer than metanotum; body length about 6 mm *S. (Michenerula)*
- Fore wing usually with three submarginal cells; dorsal surface of propodeum much longer than metanotum; body length 4.5 mm or less *S. (Sphecodosoma s. str.)*

Sphecodosoma / Subgenus *Michenerula* Bohart

Michenerula Bohart, 1965: 320. Type species: *Michenerula beameri* Bohart, 1965, by original designation.

This subgenus contains small (6 mm long) species distinguishable from similar small rophitines by the robust body form with the apex of the metasoma strongly curled under in the male. The thorax is robust in part because the propodeum is short, its dorsal surface little longer than the metanotum. Genitalic, sternal, and other structures were illustrated by Bohart (1965).

■ *Michenerula* is found in western Texas, USA, and south to Durango, Mexico. It contains one described species and probably a second, undescribed species.

Sphecodosoma / Subgenus *Sphecodosoma* Crawford s. str.

Sphecodosoma Crawford, 1907: 182. Type species: *Sphecodosoma pratti* Crawford, 1907, by original designation.

This subgenus consists of minute species (length 3.0–4.5 mm) that appear more slender than *Michenerula*, at least in part because of the longer dorsal surface of the propodeum. Genitalia and hidden sterna were illustrated by Michener (1965c).

■ *Sphecodosoma* s. str. ranges from southeastern Kansas, Oklahoma, and western Texas to southern California, USA, and south to the state of Oaxaca, Mexico. The two species were differentiated by Timberlake (1961).

Sphecodosoma s. str. seems to be oligolectic on *Nama* (Hydrophyllaceae). The nesting biology was described by Rozen and McGinley (1976, as *Conanthalictus*) and by Rozen (1993a).

Specimens with only two submarginal cells, because of

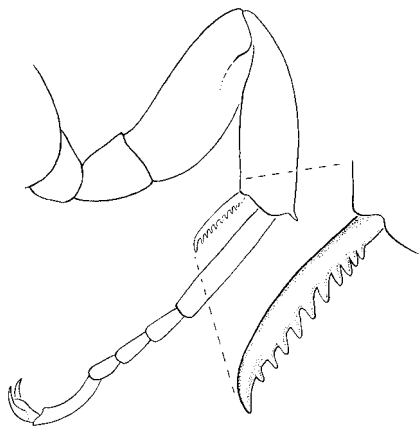


Figure 62-4. Middle leg of *Xeralictus timberlakei* Cockerell (Rophitinae), male, showing coarsely serrate tibial spur. That of the female has fewer but equally coarse teeth. From Michener, McGinley, and Danforth, 1994.

the loss of one of the transverse cubital veins, are sometimes found, as well as specimens in which both veins are present but unusually close together.

Genus *Systropha* Illiger

Systropha Illiger, 1806: 145. Type species: *Andrena spiralis* Olivier, 1789 = *Eucena curvicornis* Scopoli, 1770, monobasic.

Systropha (*Systrophidia*) Cockerell, 1936b: 477. Type species: *Systropha ogilviei* Cockerell, 1936, monobasic.

Systropha is a genus of rather robust rophitines, 6 to 14 mm long. Except in the smaller species, the head is noticeably small, distinctly narrower than the thorax. The mouthparts are elongate but variable. The first three segments of the labial palpus are flattened and sheathlike, only the fourth segment being not flattened and sometimes diverging from the main axis of the palpus. The maxillary palpus is usually longer than the labial palpus, but in *S. ogilviei* Cockerell from southern Africa the former is shorter, the glossa and labial palpi being greatly elongated; these characters are the basis for the subgeneric name *Systrophidia*. The apically curled antennae of males are among the most remarkable among bees; see the key to the genera. The number of male antennal segments varies from 11 to 13. S7 of the male has two large apical lobes and a small disc. The distal part of the apical process of S8 is greatly expanded, the apical margin convex. The male genitalia, sterna, and other structures were illustrated by Ponomareva (1967), Popov (1967), Constantinescu (1974a), Warncke (1976b), Ebmer (1994), and Baker (1996c).

■ This genus is widespread in the palearctic region from Spain and Morocco east to Tadzhikistan, north as far as southern Germany. Southward, the genus is known in both East and West Africa, south to Namibia, and in Asia south to Sri Lanka and Thailand. There are about 25 species. The palearctic species were revised by Ponomareva (1967); palearctic and Oriental species were re-

Key to the Genera of the Nomiinae of the Eastern Hemisphere

1. Malar space at least half as long as wide (apical tergal hair bands absent except sometimes at sides of T1 and T2; head only slightly, if any, wider than long) 2
 - Malar space nearly absent 3
- 2(1). Metanotum with median tubercle or projection (weak in *Mellitidia simplicinotum* Michener); mandible of female three-toothed; inner hind tibial spur of female pectinate with two large, broad teeth (Fig. 63-2k) (New Guinea region)..... *Mellitidia*
 - Metanotum strongly convex, slightly depressed medially, without median tubercle; mandible of female two-toothed; inner hind tibial spur of female minutely ciliate-serrate (as in Fig. 63-2f) (New Guinea) *Ptilonomia*
- 3(1). Ocelli enlarged, ocellular distance equal to or less than ocellar diameter; hind wing with dark area (due to dense minute hairs) along costal margin between hamuli and wing tip (body partly brown or testaceous; scutellum of male bituberculate) (New Guinea region)..... *Reepenia*
 - Ocelli not or only slightly enlarged, ocellular distance greater than ocellar diameter; hind wing without dark area 4
- 4(3). Marginal zones of T2 to T4 (or, in males, to T5), and often also T1, except near bases, hairless, impunctate, usually opaque white, yellow, green, or blue, although sometimes concolorous with rest of metasoma, the frequently opalescent bands sometimes broken medially (basal area of propodeum subhorizontal to vertical, sometimes incompletely distinguished from rest of propodeal triangle; anterior end of scutum not or only medially bent sharply down to meet pronotum; pronotum not lamellate)..... *Nomia* (in part)
 - Marginal zones of T1 to T4 variable, often hairy or punctate, and if impunctate, then often translucent, sometimes only that of T4 hairy or punctate, the zones never white, yellow, green, or blue 5
- 5(4). Tegula enormous, extending well behind level of scutoscuteellar suture (Fig. 63-4o) and preoccipital carina present; anterior end of scutum medially bent sharply downward, the angle sharp and commonly carinate (pronotum with strong, translucent lamella from posterior lobe mesad) *Pseudapis*
 - Tegula not reaching level of scutoscuteellar suture, or, if enlarged as above, then preoccipital carina absent; anterior end of scutum, if bent sharply downward, without sharp angle or carina along bend 6
- 6(5). Submarginal cells two; males and some females with translucent lamella on dorsolateral angle of pronotum, the lamella extending continuously mesad as carina all across pronotum; tegula large as in *Pseudapis* (Fig. 63-4o); mesepisternum of male, mesal to middle coxa, with tubercle or spine; antenna of male with last two segments enlarged and flattened, not pedunculate (African, oriental)..... *Steganomus*
 - Submarginal cells three; pronotum frequently without lamella, although often with carina that may or may not extend across pronotum, and in some *Lipotriches* s. str. [e.g., *notabilis* (Schletterer)] that do have a lamella there is a break or angular notch between lamella of posterior pronotal lobe and that of dorsolateral angle of pronotum; tegula only rarely enlarged as in *Pseudapis*; mesepisternum of male without ventral tubercle or spine; antenna of male usually not enlarged and flattened at apex [except in *Spatunomia* and *Lipotriches* (*Clavinomia*)] 7
- 7(6). Propodeal triangle sloping, curving down onto posterior surface of propodeum; basal area of propodeum neither sculptured distinctively nor defined by strong line or carina 8
 - Propodeal triangle vertical or its basal part subhorizontal and usually bending rather abruptly onto declivous surface; basal area of propodeum recognizable by having coarse sculpturing such as radiating striae, or the sharp angle or carina delimiting it, or being subhorizontal in contrast to declivous surface behind it 9
- 8(7). Basitibial plate of female delimited by carina only along posterior side; lateral carina of T1 strong, reaching posterior margin of tergum; pronotum with strong transverse carina at and usually extending mesad from dorsolateral angle, but the carina depressed and weak or absent medially; T6 of male with median, flat, apical projection resembling a pygidial plate (Madagascar) *Sphegocephala*
 - Basitibial plate of female delimited by carina on both sides; lateral carina of T1 absent; pronotum without or with weak carina; T6 of male without apical projection (Madagascar) *Halictonomia*
- 9(7). Mandible of female two- or three-toothed; last antennal segment of male not pedunculate, usually not modified (preoccipital carina absent) 10
 - Mandible of female simple; last antennal segment of male expanded, flattened, its base sometimes narrowly pedunculate 11
- 10(9). T2 to T4 with apical bands of hair or tomentum, at least on T4 and at least laterally, or if posterior marginal zones hairless as in some *Lipotriches* s. str., then pronotum with continuous transverse carina in front of posterior pronotal margin; male upper gonostylus directed mesoapically, not a broad plate (Fig. 63-3a) *Lipotriches* (in part)
 - T2 to T4 completely without apical bands of hair or tomentum, depressed marginal zones largely impunctate; pronotum without continuous transverse carina; male upper gonostylus directed apically and consisting of a broad, flat plate with ornate or incised margins (metanotum sometimes with broad lamelliiform projections).... *Nomia* (in part)
- 11(9). Last antennal segment of male narrowly pedunculate; male with preoccipital carina; inner hind tibial spur of female coarsely serrate (Africa) *Spatunomia*
 - Last antennal segment of male fully as wide at base as preceding flagellar segments; male lacking preoccipital carina; inner hind tibial spur of female with margin a simple, untoothed lamella (Iran) *Lipotriches* (*Clavinomia*)

Key to the Genera of Nomiinae of North America

1. Marginal zones of T2 to T4, except near base, hairless, impunctate, opaque green or blue; metasomal scopula absent; male gonostylus broad, flat, apex curved mesad and then basad (as in Fig. 63-3f) and usually ornamented with modified hairs *Nomia*
 - Marginal zones of T2 to T4 with hair bands (sometimes of dark hairs) and punctate except for margins, zones concolorous with adjacent areas; S2 to S5 and sides of T2

to T5 with well-developed scopa of long, straight hairs, those of medial region simple or nearly so, of lateral areas with branches; male gonostylus slender, directed apicad, with only a few simple hairs *Dieunomia*

Genus *Dieunomia* Cockerell

Dieunomia, the only strictly New World genus of Nomiinae, contains large (body length 7–23 mm), andreniform species not clearly related to any of the Old World genera. Except for a weak carina on the posterior lobe, the pronotum lacks a carina. The tibial spurs are unmodified. The basitibial plate of the female is completely margined by a carina that is often largely hidden by hairs; the plate is rounded apically. The hind legs of the males are usually moderately to greatly enlarged (Fig. 63-2a-d), and sometimes the middle legs are also modified. Features not found in other Nomiinae include (1) the dense scopa of S2 to S5 of the female, extending even onto the metasomal terga dorsolaterally, much as in *Systropha* (Rophitinae), (2) the form of T1 of both sexes, which has a longitudinal median depression extending to the summit of the anterior surface, the summit broadly V-shaped as seen from above and elevated above both the depressed zone behind it and the declivity in front of it, the profile of T1 thus angular, and (3) the thick head, such that the genal areas and vertex are broad and curve gradually onto its posterior surface. Male genitalia and hidden sterna were illustrated by Mitchell (1960).

Species of *Dieunomia* sometimes nest in great aggregations in sandy soil, even in land that is farmed, because the cells are below the level of plowing. The cells are vertical, “hanging” from rather long, horizontal laterals (Cross and Bohart, 1960). These bees are specialists on Asteraceae. Minckley et al. (1994) investigated the close seasonal relationship of *D. (Epinomia) triangulifera* (Vachal) to the flowering of *Helianthus annuus*.

Dieunomia has been divided into two subgenera.

Key to the Subgenera of *Dieunomia*

1. Labial palpus with first segment as long as or longer than segments 2 to 4 taken together; last antennal segment of male broader than preceding segments; tegula large, posterior end subtruncate and attaining level of scutocutellar suture, lateral margin sinuate *D. (Dieunomia s. str.)*
- Labial palpus with first segment shorter than remaining segments taken together; last antennal segment of male unmodified; tegula as above or shorter, its lateral and posterior margins then convex *D. (Epinomia)*

Dieunomia / Subgenus *Dieunomia* Cockerell s. str.

Eunomia Cresson, 1875: 723, not Hübner, 1818. Type species: *Eunomia marginipennis* Cresson, 1875 = *Nomia kirbii* Smith, 1865, by designation of Cockerell, 1910f: 290.

Dieunomia Cockerell, 1899a: 14, replacement for *Eunomia* Cresson, 1875. Type species: *Eunomia marginipennis* Cresson, 1875 = *Nomia kirbii* Smith, 1865, autobasic and by designation of Cockerell, 1910f: 290.

This subgenus consists of very large species, body length 11 to 23 mm.

■ *Dieunomia* is found from Manitoba, Canada, and Colorado, Wisconsin, Ohio, and Maryland south to Texas and Florida, USA, and Tamaulipas, Mexico. The five species were revised by Blair (1935).

Dieunomia / Subgenus *Epinomia* Ashmead

Epinomia Ashmead, 1899a: 88. Type species: *Nomia persimilis* Cockerell, 1898 = *Nomia triangulifera* Vachal, 1897, by original designation.

The species of this subgenus are smaller than most *Dieunomia* s. str., 7 to 13 mm long.

■ *Epinomia* ranges from Oregon, Minnesota, Illinois, and Florida, USA, south to the states of Baja California, Jalisco, and Morelos, Mexico. The four species were revised by Cross (1958).

Genus *Halictonomia* Pauly

Nomia (Halictonomia) Pauly, 1980a: 123. Type species: *Halictus decemmaculatus* Friese, 1900, by original designation.

Halictonomia is a genus of small (length 4–9 mm), andreniform species with the whole body or the metasoma largely yellow-brown in some species, although others are entirely black. The hairs are sparse and do not form metasomal bands, or form weak apical bands laterally. The punctation is weak and fine. The hind legs and exposed sterna of the male are unmodified, as are all the tibial spurs, except that in *H. minuta* (Benoist) (see below) the hind tibial spurs of the male are absent. Two characters that are unique in the Nomiinae are the absence of the episternal and scrobal grooves (or the former indicated only near the upper extremity) and the large stigma, two or more times as broad as the prestigma (as measured to the wing margin). In all other Nomiinae the episternal groove is indicated from its upper end down to a short distance below the scrobal groove, and the stigma is little if any wider than the prestigma, or wider in some small species. Another unusual feature of *Halictonomia* is the slender, more or less equally long, upper and lower male gonostyli, the upper with a mesal basal lobe bearing modified setae, at least in *H. decemmaculata* (Friese) and *minuta* (Benoist). Pauly (1990) diagramed the male genitalia and sterna.

■ This genus is found only in Madagascar. In his revision of Malagasy Nomiinae, Pauly (in Pauly et al., 2001) recognized 10 species of the genus *Halictonomia*.

Halictonomia minuta (Benoist) belongs here on the basis of its large stigma and lack of episternal and scrobal grooves. Unlike other species of *Halictonomia*, however, it lacks a strong longitudinal ridge on the supraclypeal area, and the scutellum is not biconvex. I consider its position tentative for the present.

Genus *Lipotriches* Gerstaecker

This is the largest genus of the Nomiinae, in its present sense including the species that Pauly (1990) segregated into several genera. Thus he segregated some African species related to the subgenus *Austronomia* into the genera *Afronomia*, *Macronomia*, and *Trinomia*. Asian material badly needs further study, but it either bridges the differences among these subgenera or could represent

additional taxa in this complex. I prefer to indicate the similarity among these forms by placing all of them as subgenera of the one genus. This may turn out to be a paraphyletic unit, and exclusion of *Sphegocephala* from it is rather arbitrary; nonetheless, recognition of a large genus *Lipotriches* is convenient and in accordance with current practices elsewhere among bees. A subgenus that differs from the rest in striking morphological characters (see the key), for example, in its mandibular dentition, is *Nubenomia*, but except for those characters, *Nubenomia* is almost like *Melanomia*, which is more difficult to separate from other subgenera of *Lipotriches*. I have therefore included both *Nubenomia* and *Melanomia* within *Lipotriches*, as subgenera. Because of its simple female mandibles, *Clavinomia* is also distinctive; the inner hind tibial spur of the female, with its margin consisting of a smooth, untoothed lamella, is suggestive of *Lipotriches* s. str. The body of *Lipotriches* is usually markedly more slender than that of most other nomiines, a tendency that culminates in the slender and petiolate males of some species of *Lipotriches* s. str. formerly segregated as *Rhopalomelissa*. Male genitalia, sterna, and other structures were diagrammed by Pauly (1990); see also Figure 63-3a-e.

As noted in the discussion of the Nomiinae above, *Lipotriches* is diverse in nest architecture, some species of *Lipotriches* s. str. having sessile horizontal cells dispersed along vertical burrows while a species of the subgenus *Austronomia* builds its cells in clusters. Great diversity in nest structure is also known in the genus *Nomia*.

Key to the Subgenera of *Lipotriches*

1. Mandible of female tridentate, of male usually bidentate; basal area of propodeum reduced to transverse line or fine groove *L. (Nubenomia)*
- Mandible of female bidentate, or simple in *Clavinomia*, of male simple (except bidentate in a few species of *Lipotriches* s. str.); basal area of propodeum larger, sometimes not defined medially or (rarely) entirely unrecognizable 2
- 2(1). Pronotum with continuous or medially or laterally notched transverse carina or lamella anterior to the scutum, at about level of scutum, the latter thus not bending down anteriorly (inner hind tibial spur of female commonly untoothed, margin a simple lamella, broadest near middle of spur, sometimes with a few teeth, Fig. 63-2i) *L. (Lipotriches* s. str.)
- Pronotum with transverse carina either absent or broadly interrupted medially, the anterior part of the scutum thus bending down medially to depressed pronotal margin 3
- 3(2). Mandible of female simple; inner hind tibial spur of female with simple, smooth-margined lamella; male with last two antennal segments curled to one side, the last segment much expanded, broader than long (Iran) *L. (Clavinomia)*
- Mandible of female with preapical tooth, thus bidentate; inner hind tibial spur of female pectinate, dentate, or minutely serrate (ciliate); male with apical antennal segments usually unmodified, but if modified, then not as above 4
- 4(3). Ocellular distance less than twice ocellar diameter; glossa very slender, as long as face; basitibial plate of female delimited on both sides but apex open; scape of fe-

- male short, not reaching median ocellus (Africa) *L. (Maynenomia)*
- Ocellular distance usually twice ocellar diameter or more; glossa shorter than face; basitibial plate of female, if carinate on both sides, with apex almost always closed; scape of female reaching to or beyond median ocellus 5
- 5(4). Head about as long as broad; clypeus with well-developed lip below row of large apical hairs (Madagascar) *L. (Melanomia)*
- Head distinctly broader than long; clypeus with row of large apical hairs very near lower margin except in a few *Austronomia* and *Macronomia* species in which lip extends below hair bases 6
- 6(5). Basitibial plate of female margined by carina only on posterior side (Africa, oriental region) *L. (Macronomia)*
- Basitibial plate of female with marginal carina complete except for base 7
- 7(6). Propodeal basal area more or less horizontal, only posterior part of propodeal triangle declivous (Australia, oriental region, Africa) *L. (Austronomia)*
- Propodeal basal area more or less vertical, at least medially, so that whole propodeal triangle, or most of it, is vertical 8
- 8(7). Terga, at least most of T1, minutely tessellate, dull, with only fine, sparse punctation; hind femur of male with three strong teeth on undersurface (Africa, Arabia) *L. (Trinomia)*
- Terga more shiny, often shagreened but not tessellate, usually more coarsely punctate; hind femur of male without or with one or two strong teeth (Africa, oriental region) *L. (Afromomia)*

Lipotriches / Subgenus *Afromomia* Pauly

Afromomia Pauly, 1990: 126. Type species: *Nomia picardi* Gribodo, 1894, by original designation.

Like *Trinomia*, this subgenus is similar to *Austronomia*, from which *Afromomia* differs in its more declivous propodeum (see the key to subgenera) and the presence of one or two teeth on the underside of the swollen hind femur of the male. *Afromomia* is larger (body length 10-12 mm) than African *Austronomia*, although some Australian *Austronomia* attain 12 mm. Males of *Afromomia* are not distinguishable by group characters from those of *Macronomia*.

■ This subgenus occurs from Ethiopia and Zaire south to Natal, Cape Province, and Namibia. The seven African species were revised by Pauly (1990).

At least three unidentified Asian species tentatively placed in this subgenus are smaller than African species (the smallest 7 mm long), and lack teeth on the hind femora of the males, although these femora are greatly swollen. Such species occur in India, Malaysia, and Java.

Lipotriches / Subgenus *Austronomia* Michener

Nomia (Austronomia) Michener, 1965b: 156. Type species: *Nomia australica* Smith, 1875, by original designation.

This is possibly a basal paraphyletic group from which arose various subgenera that have derived characters of various sorts. It is characterized by the complete basitibial plate of the female (either rounded or pointed), the lack of a continuous carina across the pronotum, the pres-

ored parts of the marginal zones are largely or entirely impunctate and hairless, although the bases of these zones often have some punctures and hairs. In some species that clearly belong to *Nomia*, however, colored bands are absent, although the depressed black tergal marginal zones are hairless and impunctate except at their bases. Thus *Nomia* (*Hoplonomia*) *amboinensis* Cockerell and *N. (H.) flavipennis* Friese have the characteristic thoracic structure of their subgenus, but have black rather than colored metasomal bands. Likewise in the subgenus *Acunomia*, within the group that has been called *Maculonomia* on the basis of distinctive genitalic structure, *Nomia terminata* Smith and *fuscipennis* Smith lack colored bands, whereas *N. megasoma* Cockerell and *viridicinctula* Cockerell are banded. Male genitalia and hidden sterna were illustrated by Mitchell (1960), Ribble (1965), Michener (1965b), and Wu (1982a, 1983e); see also Figure 63-3f-n.

Key to the Subgenera of *Nomia*

1. Metanotum with two broad, lamelliform projections, the two often united to one another 2
- Metanotum without projections 3
- 2(1). Lateral extremity of scutellum with lamelliform projection (Africa, oriental) *N. (Crocisaspidia)*
- Lateral extremity of scutellum not produced (oriental, Australia, Madagascar) *N. (Hoplonomia)*
- 3(1). Outer hind tibial spur of female and some males bent near apex, usually with projection at the bend continuing direction of main shaft (Fig. 63-2l); middle tibial spur usually with a few coarse preapical teeth (basitibial plate of female completely margined by carinae except at base; posterior femur of male without tooth) 4
- Outer hind tibial spur of female and most males tapering to unmodified apex (Fig. 63-2h); middle tibial spur with all teeth minute 5
- 4(3). S8 of male a small, compact sclerite with midapical peglike projection (as in Fig. 63-3g); S7 of male transverse, with two hirsute apical projections (as in Fig. 63-3h); male gonostylus flattened, commonly expanded, sometimes curved basad (as in Fig. 63-3f); S6 of male with apical margin emarginate, surface without oblique rows of setae; S5 of male with apex variously thickened, lobate, with hair tufts (as in Fig. 63-3j) (holarctic, Africa, oriental) *N. (Acunomia)*
- S8 of male relatively large, broadened basally and preapically, lateral margins thus concave, apical peglike projection absent (Fig. 63-3l); S7 of male relatively large, basolateral apodemal lobes long, length of sclerite thus much more than half its width (Fig. 63-3m); male gonostylus rather slender, not flattened, much exceeding penis valves, directed posteriorly, and arising from distal end of elongated gonocoxite (Fig. 63-3k); S6 of male with apex rounded, surface with oblique rows of flattened setae (Fig. 63-3n); S5 of male unmodified (Australia) *N. (Paulynomia)*
- 5(3). Male, in species with slender legs, with basitibial plate; T1 frequently without colored band and usually with pale hair band laterally; hind femur of male without tooth or with tooth near base on underside; body length 10 mm or less; colored bands white or nearly so (Africa, oriental) *N. (Leuconomia)*
- Male without basitibial plate; T1 with colored band, without hair band; hind leg enlarged, femur with one or

two preapical teeth on underside; body length 9 mm or more; bands more brightly colored (Africa, oriental)
..... *N. (Nomia s. str.)*

Nomia / Subgenus *Acunomia* Cockerell

Nomia (*Paranomia*) Friese, 1897b: 48, not Conrad, 1860.

Type species: *Nomia chalybeata* Smith, 1875, by designation of Cockerell, 1910f: 290.

Nomia (*Acunomia*) Cockerell, 1930, in Cockerell and Blair, 1930: 11. Type species: *Nomia nortoni* Cresson, 1868, by original designation.

Nomia (*Paranomia*) Michener, 1944: 251, not Hendel, 1907, replacement for *Paranomia* Friese, 1897. Type species: *Nomia chalybeata* Smith, 1875, by original designation and autobasis.

Nomia (*Curvinomia*) Michener, 1944: 251. Type species: *Nomia californiensis* Michener, 1937 = *Nomia tetrazonata* Cockerell, 1910, by original designation.

Nomia (*Maculonomia*) Wu, 1982a: 275. Type species: *Nomia terminata* Smith, 1876, by original designation.

The principal subgeneric characters of *Acunomia* are given in the key to subgenera. The body length is 8 to 16 mm. In the North American group that has been called *Curvinomia*, as well as in certain Old World species, the middle tibial spur is finely toothed to the apex or bears a few teeth near the apex that are scarcely larger than the more basal teeth. I agree with Pauly (1990) that the three North American species with tapering male antennal flagella, for which the name *Acunomia* was originally proposed, need not be separated at present from the other North American and Old World species that lack this feature. *Nomia* (*A.*) *yunnanensis* Wu from China also has tapering flagella, although its sternal characters do not agree with those of *N. (A.) nortoni* and its relatives in North America.

■ *Acunomia* is found from Eritrea and Senegal south throughout Africa to eastern Cape Province, South Africa, east to Madagascar, India, southeast Asia, China, Taiwan, the Philippines, and Indonesia. In North America it occurs from Washington State east to North Dakota and New Jersey, south to Florida, USA, the Bahamas, Cuba, and the states of Baja California, Guerrero, and Veracruz, Mexico. There are about 33 species. Nine African species were revised by Pauly (1990), three Malagasy species by Pauly (1991), and nine American species by Ribble (1965). The Australian species listed by Michener (1965b) belong to the subgenus *Paulynomia*, but many of the Asiatic species of *Acunomia* were listed in that same paper and by Pauly (1990).

The subgenus *Acunomia* is highly variable and may be a paraphyletic group that should be subdivided. The arolia of some African species are reduced or, as in *Nomia* (*A.*) *speciosa* Friese and *theryi* Gribodo, absent. As in the subgenera *Crocisaspidia*, *Hoplonomia*, and *Paulynomia*, the outer hind tibial spur in *Acunomia* usually is sharply bent preapically, perhaps because of a large apical or scarcely preapical tooth projecting to one side (Fig. 63-2l). This is not true, however, in a few species, e.g., those placed in *Maculonomia* by Wu (1982a) and *N. (A.) thoracica* Smith, a species with a protuberant male clypeus and large male mandibles each with a median tooth on the upper margin. The tegulae are unusually large and broad

rowly rounded, not attenuate, posteriorly and the tibial spurs simple, i.e., without large teeth. It is the only subgenus of *Nomia* having one or two preapical teeth on the underside of the hind femur of the male, and also with T6 of the male produced medially to a truncate projection resembling a pygidial plate and hiding T7.

■ *Nomia* s. str. occurs in China, Thailand, India, Pakistan, Madagascar, and Africa from Gambia to Sudan south to Angola, the Transvaal, and Mozambique. The six species were reviewed by Pauly (1990).

Nomia / *Paulynomia* Michener

Nomia (*Paulynomia*) Michener, 2000: 326. Type species: *Nomia aurantifer* Cockerell, 1910, by original designation.

This group has been included in the subgenus *Curvinomia*, here included in *Acunomia*. The male differs from *Acunomia* in the very striking characters of the genitalia and sterna (see the key to subgenera); in these particulars *Acunomia* agrees with the subgenus *Hoplonomia*. The simple S5, relatively elongate S7, and slender, unflattened gonostyli (Fig. 63-3k-n) are likely to be plesiomorphic relative to *Acunomia*, *Hoplonomia*, and perhaps various other Nomiinae. The middle tibial spurs of the female are dark in color and armed with coarse, thornlike teeth along both margins of their distal three-fifths; some Oriental species of *Acunomia* approach this condition. The body length is 10 to 13 mm. Some individuals have a broken yellow band on T1; in *Acunomia* the band on T1 is usually complete or absent, not broken.

■ *Paulynomia* occurs from northern New South Wales to northern Queensland, Australia. The two species listed by Cardale (1993) are *Nomia* (*Paulynomia*) *aurantifer* Cockerell and *swainsoniae* Cockerell. Three names for Australian species were listed by Michener (1965b), *N. luteofasciata* Friese being a synonym of *N. aurantifer*.

Genus *Pseudapis* Kirby

Pseudapis is the major genus having greatly enlarged tegulae (Fig. 63-4o), these extending far back behind the level of the scutoscuteellar suture. From other genera in which one or more species have precisely similar tegulae, presumably independently evolved, *Pseudapis* differs by the presence of a preoccipital carina behind the genal area and a carina across the anterior part of the scutum separating the small, vertical, anterior surface from the main part of the scutum. The lamella on the pronotal lobe (Fig. 63-4o) and extending mesad from it is translucent, larger than that of almost any other Nomiinae, and similar in the two sexes. The body form, especially of females, is short, markedly more robust than that of most other Nomiinae, eucuriform or even anthophoriform rather than andreniform as is usual for the Nomiinae. In most species the metasomal terga (except T1), or at least the more posterior ones, have both basal and apical bands of pale hairs or tomentum. The body length ranges from 6 to 11 mm. Male genitalia and numerous other structures were illustrated by Sakagami (1961), Wu (1983e), and Pauly (1990).

Relationships among the genera recognized by Pauly (1990) seem best shown by regarding some of them as subgenera or synonyms of *Pseudapis*.

Key to the Subgenera of *Pseudapis*

1. Basitibial plate of female delimited by a carina only on posterior margin; hind leg of male not enlarged, tibia without apical process but bearing two apical spurs; male upper gonostylus broadly fused to gonocoxite, directed apicad, with mosslike hair covering dorsal surface (Africa) *P. (Pachynomia)*
- Basitibial plate of female fully delimited, i.e., with a carina on both anterior and posterior margins; hind leg of male somewhat, often greatly, swollen, at least tibia with apical process, but without spurs or with only one spur; male upper gonostylus differentiated from gonocoxite, directed mesad across apex of genital capsule, and without mosslike hairs *P. (Pseudapis* s. str.)

Pseudapis / Subgenus *Pachynomia* Pauly

Nomia (*Pachynomia*) Pauly, 1980a: 124. Type species: *Nomia amoenula* Gerstaecker, 1870, by original designation.

Pachynomia looks superficially like *Pseudapis* s. str. but differs in the rather striking characters indicated in the key to subgenera. The male leg characters and part of the genitalic characters are probably plesiomorphic relative to *Pseudapis* s. str. As in *Pseudapis* s. str., the males of some species have a lateral, posteriorly directed tooth on the scutellum.

■ This subgenus is found from Senegal to Kenya south to Cape Province and Natal, South Africa. The four species were revised by Pauly (1990).

Pseudapis / Subgenus *Pseudapis* Kirby s. str.

Pseudapis W. F. Kirby, 1900: 15. Type species: *Pseudapis anomala* W. F. Kirby, 1900, monobasic.

Stictonomia Cameron, 1905: 192. Type species: *Stictonomia punctata* Cameron, 1905, monobasic.

Nomia (*Nomiapis*) Cockerell, 1919a: 208. Type species: *Nomia diversipes* Latreille, 1806, by original designation.

Nomia (*Lobonomia*) Warncke, 1976a: 99. Type species: *Nomia lobata* Olivier, 1811, by original designation.

Ruginomia Pauly, 1990: 103. Type species: *Nomia rugiventris* Friese, 1930, by original designation.

Pauly (1990) recognized all of the names listed above except *Lobonomia* as genera. The principal characters, however, appear in diverse combinations. In the females, the groups called *Pseudapis* and *Nomiapis* have the basitibial plate rounded, while in the groups called *Rugonomia* and *Stictonomia* it is pointed. No other characters appear to support this division into two groups. The lateral scutellar tooth of the male is present in *Stictonomia* but also in some species of both *Pseudapis* s. *strictissimo* and *Nomiapis* (and in some species of the subgenus *Pachynomia*). The lack of apical tergal hair bands is a character of *Nomiapis* and males of *Ruginomia*, but hair bands are sometimes absent on the basal half or more of the metasoma in *Pseudapis* s. *strictissimo*. There are no hind tibial spurs in males of *Ruginomia* and *Nomiapis*, but one spur is present in males of most but not all species of *Pseudapis* s. *strictissimo* and *Stictonomia*.

■ *Pseudapis* s. str. occurs in the Mediterranean basin (Morocco and Spain to Egypt), north in Europe to Aus-

64. Subfamily Nomioioidinae

In spite of the name, *Nomioioides* and its relatives do not resemble *Nomia*, either in appearance or in their combination of characters. They have usually been placed in the Halictinae, partly because of the curved basal vein of the forewing (Fig. 64-1a), but they differ from Halictinae in the unbroken prepygidial fimbria of the females and other characters listed below. In Alexander and Michener's (1995) study of the phylogeny of S-T bees, *Nomioioides* usually appeared among the rophitine genera, as part of a paraphyletic group from which the Nomiinae and Halictinae arose. *Nomioioides* differs from the Rophitinae in its most distinctive characters, however, and is here accorded subfamily rank, leaving the Rophitinae as monophyletic.

This Old World subfamily consists of minute (body length 2.5-6.5 mm), weakly sclerotized, andreniform bees, the head and thorax finely punctate and usually dull, usually metallic blue or green, and the metasoma flattened, especially in the female. All tagmata usually have yellow or cream markings (Fig. 64-3a-c), the metasoma sometimes being mostly yellow, although it may be wholly black. There are no pubescent fasciae on T1 to T4. Superficially, these bees closely resemble various groups of *Perdita* (Andrenidae, Panurginae) of North America, *Habralictus* (Halictinae) of the neotropics, *Eremaphanta* (Melittidae) of central Asia, and certain Euryglossinae (Colletidae) of Australia. The Nomioioidinae differ from the Halictinae in the presence of a sparse fimbria on T5 of the female that is not divided medially by an area of specialized, fine vestiture and texture. Also, the labrum of the female has a small but well-defined apical process that lacks a keel, thus differing from all other halictid groups; in nonparasitic Halictinae, this process is larger and strongly keeled. The inner orbits are distinctly and somewhat angularly emarginate (Figs. 64-1b, 64-3a, b), as is usual in the Augochlorini. The anterior tentorial pit is at the apex of an acutely pointed projection of the paraocular area (Figs. 64-1b, 64-3a, b) into the clypeus. This paraocular lobe is not elevated above the surrounding areas and thus differs from the elevated rounded paraocular lobe that projects into the clypeus in many Augochlorini. T7 of the male has a truncate apical projection that doubtless represents the pygidial plate, but the plate is not indicated on the tergal surface and the margin of the tergum is thin, not reflexed as in the Halictini. S7 of the male is a simple plate, like the preceding sterna but smaller. The group was further characterized by Michener (1978a) and in detail by Pesenko (1983, 2000b), who tabulated differences between Nomioioidinae and each tribe of Halictinae. Illustrations of the male genitalia, sterna, and other structures were provided by Ireland (1935) and Pesenko (1983, 2000b); see also Figure 64-2.

Pesenko (2000a) considered the nomioioidines as a tribe of the subfamily Halictinae, but his phylogenetic analysis placed them as the basal branch of the Halictinae (sister-group to all other Halictinae) and thus they could also logically be considered as a separate subfamily, the rank that I prefer for them.

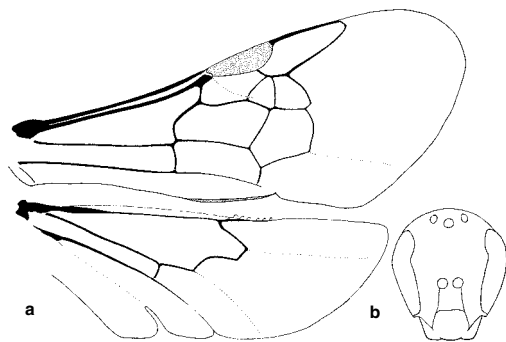


Figure 64-1. *Nomioioides minutissimus* (Rossi) (Nomioioidinae).

a, Wings; **b,** Face, showing acute paraocular lobes extending down into the clypeus.

It has been usual to place all members of this subfamily in the genus *Nomioioides*. Pesenko (1983, 1993), however, recognized three genera that seem to be as distinctive as genera elsewhere in the Halictidae.

The subfamily was revised by Blüthgen (1925) and, for the palearctic region, by Pesenko (1983), who also gave a good account of the morphology and a detailed statement of the differences among the genera. Pesenko (1996) revised the species of Madagascar. A large work by Pesenko and Pauly (2005) is on the nomioiid species of Africa. Pesenko (2000b) gave an account of the phylogeny and classification of the subfamily.

So far as is known, the Nomioioidinae are polylectic. Nests are slender vertical burrows in the soil with subhorizontal cells, one at the end of each lateral burrow, each lateral being filled with earth after the cell is completed. The cells and provisions are similar to those of the Halictinae. Some nests are occupied by presumably communal groups of females; there is no evidence of castes (Batra, 1966a; Radchenko, 1979). Unlike most Halictinae, both sexes overwinter as adults (Blüthgen, 1925).

Key to the Genera of the Nomioioidinae

1. S8 of male with long apical process (Fig. 64-2e), the process much longer than broad, thus sternum over 2.5 times as long as wide; posterior depressed marginal zone of T2 and frequently other terga translucent yellowish, so that yellow base of T3 shows through *Nomioioides*
- S8 of male without or with short apical process (Fig. 64-2b), the process not or scarcely longer than broad; sternum thus less than 2.5 times as long as broad; posterior depressed marginal zone of T2 and frequently other terga brown or dusky, at least basally (margin often narrowly pallid translucent) so that base of T3 does not show through conspicuously 2
- 2(1). Second submarginal cell petiolate from costal side (Fig. 64-3d); median flagellar segments of male little longer than broad; inner hind tibial spur of female with one large tooth (Fig. 64-3e); S8 of male with apical

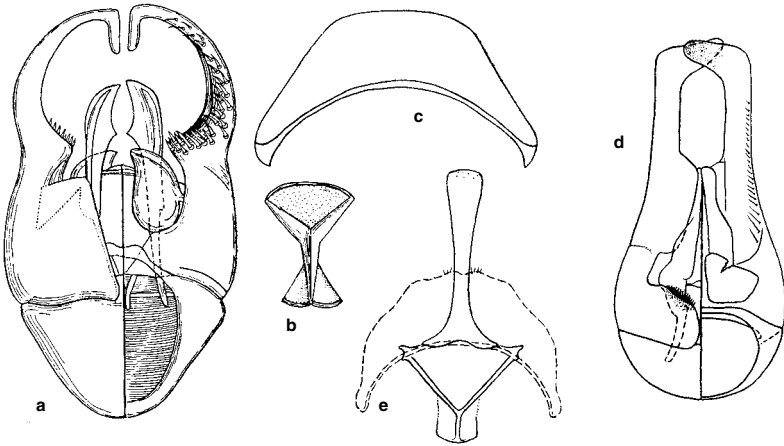


Figure 64-2. Structures of male Nomioioidinae. **a-c,** Genitalia, S8, and S7 of *Ceylalicthus variegatus* (Olivier); **d, e,** Genitalia, S8, and (in broken lines) S7 of *Nomioides minutissimus* (Rossi). (Divided drawings show dorsal views on the left.) a-c, based on Pesenko, 1983; d, e, from Michener, 1978a.

process short, broader than long or about as broad as long depending on how it is measured (Africa) *Cellariella*
— Second submarginal cell not petiolate (as in Fig. 64-1a), although sometimes pointed on marginal cell; median flagellar segments of male about 1.5 times as long as broad; inner hind tibial spur of female with two large teeth; S8 of male completely without apical process, apex Y-shaped with membrane between arms of Y (Fig. 64-2b) *Ceylalicthus*

Genus *Cellariella* Strand

Nomioides (Cellaria) Friese, 1913a: 575, not Ellis and Solander, 1786. Type species: *Nomioides arnoldi* Friese, 1913 = *Nomioides somalica* Magretti, 1899, monobasic.

Nomioides (Cellariella) Strand, 1926: 53, replacement for *Cellaria* Friese, 1913. Type species: *Nomioides arnoldi* Friese, 1913 = *Nomioides somalica* Magretti, 1899, autobasic.

■ *Cellariella* is widespread in Africa, from Somalia and Zaire south to Cape Province, South Africa. It also occurs in Madagascar. There are two species.

Genus *Ceylalicthus* Strand

This genus includes fewer species than *Nomioides*, but there is more diversity among them than among species of *Nomioides*, as indicated by the three subgenera recognized by Pesenko (1983). Pesenko considered *Ceylalicthus* a paraphyletic genus from which *Nomioides* arose. Another analysis by Pesenko (2000b) showed the same relationship, the subgenus *Atronomioides* being the sister group to all the rest of the Nomioioidinae. If this relationship is verified, *Atronomioides* should doubtless be given generic rank.

The subgeneric positions of most species are unknown to me, although the principal subgenus is evidently *Ceylalicthus* s. str.

Key to the Subgenera of *Ceylalicthus* (Males)

- 1. Gonostylus of male slender, eight or more times as long as wide (Fig. 64-2a) *C. (Ceylalicthus* s. str.)

- Gonostylus of male broad, not over about four times as long as wide 2
- 2(1). Gonostylus of male three or four times as long as wide, the apex narrowly rounded; penis valve rather straight *C. (Meganomioides)*
- Gonostylus of male about twice as long as broad, the apex broadly truncate; penis valve with strong bend near base *C. (Atronomioides)*

***Ceylalicthus* / Subgenus *Atronomioides* Pesenko**

Ceylalicthus (Atronomioides) Pesenko, 1983: 186. Type species: *Ceylalicthus warneckei* Pesenko, 1983, by original designation.

■ This subgenus is known from South Africa, equatorial Africa, and Madagascar to Iran, and southern China. There are eleven species.

***Ceylalicthus* / Subgenus *Ceylalicthus* Strand s. str.**

Halictus (Ceylalicthus) Strand, 1913a: 137. Type species: *Halictus horni* Strand, 1913, monobasic.

Nomioides (Eunomioides) Blüthgen, 1937: 3, nomen nudum. Type species: *Andrena variegata* Olivier, 1789, by original designation.

■ *Ceylalicthus* s. str. ranges from Senegal, the Canary Islands, and Portugal to western China, mostly south of 50°N. To the south it occurs to Cape Province, South Africa, Madagascar, the Arabian peninsula, and eastward to Sri Lanka, India, southeast Asia, Indonesia, and the northern half of Australia. No Nomioioidinae are known from New Guinea or islands to the eastward. One species, *C. (Ceylalicthus) variegatus* (Olivier), is found from the western outposts of the genus in Europe and Africa (south to Namibia) all the way to China. The total number of known species is 13.

***Ceylalicthus* / Subgenus *Meganomioides* Pesenko**

Ceylalicthus (Meganomioides) Pesenko, 1983: 183. Type species: *Nomioides karachensis* Cockerell, 1911, by original designation.

tions of the basal part of the labrum (Fig. 8-9d-f, 67-13d, g). For details and other features of the parasites, see Section 8 and Michener (1978b).

It may seem inconsistent to place the species formerly included in *Paralictus* into *Dialictus*, thus with no parasitic genus or subgenus, while retaining such taxa for the other parasitic species. This is done because the former *Paralictus* species are so similar to other *Dialictus*, from which the *Paralictus* must have evolved. For the other parasites, their derivation is less obvious or less certain.

Melittologists have long looked among nonparasitic Halictinae to seek the taxon most closely related to *Sphecodes*. I now believe that it is futile to seek a nonparasitic genus like *Halictus* or *Lasioglossum* as sister to *Sphecodes*. Rather, I suspect that *Sphecodes* and its relatives constitute an ancient parasitic halictine lineage that has spread worldwide and is here assigned subtribal status as the Sphecodina. A possible plesiomorphy retained by this group is the form of S7 and S8 of the males, which are less reduced than those of most other Halictini, often more or less quadrate with basolateral apodemal arms and with an obtuse spiculum on S8. Included genera would be *Eupetersia*, *Microsphecodes*, *Nesosphecodes*, *Prilocleptis*, and *Sphecodes*.

Most parasitic halictids parasitize their close relatives or at least bees of the same tribe, but some species of *Sphecodes* parasitize bees of other halictid tribes or subfamilies, the Augochlorini and Nomiodinae. Other species of *Sphecodes* parasitize quite unrelated bees, such as *Andrena*, *Calliopsis*, *Melitturga*, and *Perdita* in the Andrenidae and *Colletes* in the Colletidae. In most cases the parasitic female enters the nest of the host, destroys host eggs, and replaces them with her own; see Section 8 and Sick et al. (1994). This is quite unlike the method of parasitism used by most other groups of cleptoparasitic bees, in which it is the larva of the parasite that destroys the host egg or larva. In some species of *Sphecodes* and especially *Microsphecodes*, the parasitic female appears to remain in the nest with the host for a long period, suggesting social parasitism rather than cleptoparasitism; see Section 8.

Figure 61-4 is a phylogenetic tree for the Family Halictidae, and the basis for the classification. The Halictinae is divided into two tribes, the Augochlorini and the Halictini. The principal tribal characters are indicated in

the key to tribes, below. Presumably, these tribes are sister groups. An interesting plesiomorphic character is the galeal comb, retained among Halictinae only in certain South American Augochlorini such as *Corynura*, and lost in other Halictinae. Thus it is unlikely that the Augochlorini arose from within the Halictini, all of which lack the comb. On the other hand, it is the Halictini that have the plesiomorphic T5 of the female, lacking a cleft (Fig. 65-1j), and it is therefore unlikely that the Halictini arose from within the Augochlorini. My impression is that each tribe has both ancestral and derived characters relative to the other.

In addition to the tribal characters—often difficult to see—that are listed above and in the key to tribes below, there is a character of wing venation that frequently although not always distinguishes the two. In the Halictini the first recurrent vein usually meets the second submarginal cell, whereas in the Augochlorini it usually meets the second submarginal crossvein or the third submarginal cell. The difference is illustrated in Figure 65-5.

Fossil halictids have been described from late Eocene to Miocene deposits; see the review by Engel (1997a). The fossil augochlorine genus *Oligochlora* comprises three species from the Dominican amber (Engel, 1997b).

Key to the Tribes of the Halictinae

1. Longitudinal median specialized area of T5 of female of nonparasitic forms not divided by a notch or cleft (Fig. 65-1j); parasitic forms (recognized by loss or reduction of scopa and other pollen-carrying and -manipulating structures) nonmetallic or with dull greenish coloration; T7 of male with a transverse ridge, usually carinate, forming a false apex beneath which the tergum is strongly reflexed to the morphological apical margin, surface above the transverse ridge usually with a recognizable hairless pygidial plate Halictini (Sec. 66)
- . Longitudinal median specialized area of T5 of female of nonparasitic forms divided by a notch or cleft in tergal margin (Fig. 65-1k); parasitic forms mostly brilliant metallic green; T7 of male without pygidial plate and without transverse premarginal ridge or carina forming a false apex (Western Hemisphere) Augochlorini (Sec. 67)

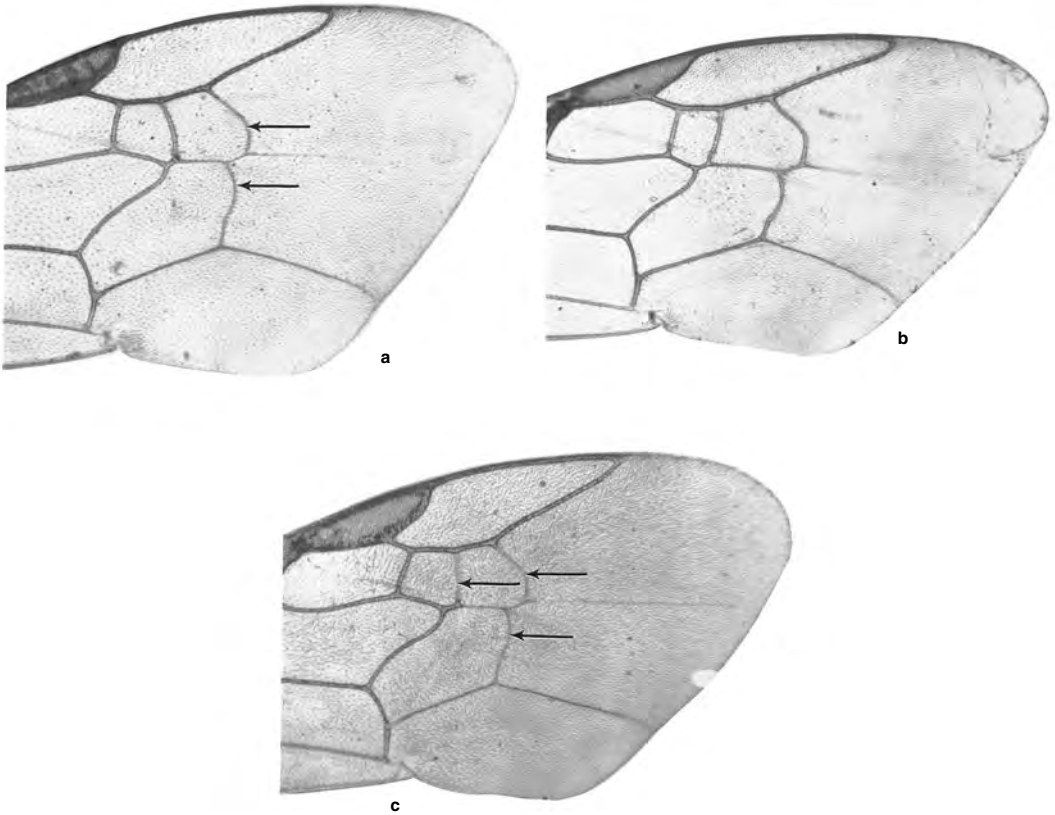


Figure 66-6. Distal venation in forewings of females of *Lasioglossum* and *Halictus*, showing weakening of veins in the former. **a**, Left, *L. (Lasioglossum) sisymbrii* (Cockerell); **b**, *H. rubicundus* (Christ); **c**, *L. (Evylaeus) quebecense* (Crawford). (Arrows indicate weakened veins.)

genera listed at the beginning of this paragraph) is a non-metallic flat or concave strip along the inner margin of the eye, from the emargination downward. This strip is suggestive of a facial fovea. *Caenohalictus* and *Habralictus* have a nonmetallic area in the lower paraocular area next to the lower inner orbit, as in *Homalictus*. This area might be equivalent to the lowest part of the nonmetallic area of *Agapostemon*. No consistent apomorphy is known for the *Caenohalictina*. Engel (2001b), as noted above, found one quite ordinary looking fossil halictine species, *Electrolictus antiquus* Engel, perhaps near *Patellapis*, in the Eocene Baltic amber. Considering the worldwide abundance of halictines now and their diversity in later deposits such as the Dominican amber, it is of interest that more fossil halictines of Eocene age have not been found.

Aside from faunal works on bees as a whole, there are several important regional catalogues or reviews of the Halictini, or of certain groups that cut across subtribal or even modern generic limits, especially *Halictus* and *Lasioglossum*. Such works are listed here, as follows: For the Western Hemisphere, Moure and Hurd (1987); for the Eastern Hemisphere, Blüthgen (1920, 1921, 1923a, b, 1924a, c, 1926, 1928a, 1930, 1931, 1933, 1936, 1955); Perkins (1922); Ebmer (1969, 1987a, 1988a, b); Warncke (1975b); Pauly (1984b, 1999b); Pauly (in Pauly et al., 2001); and Pesenko et al. (2000). Cockerell (1937) provided notes on many African species.

In order to simplify the keys, separate keys to genera

are given for the Western and Eastern hemispheres. In the first key, the temperate North American cleptoparasitic species sometimes placed in a subgenus or genus *Paralictus* run to *Lasioglossum (Dialictus)*; see the first option of the second couplet.

Key to the Genera of the Halictini of the Western Hemisphere (Females)

1. Scopa weak (Figs. 8-5a, 8-6) or absent; T5 with longitudinal median zone of fine punctation and short hairs weakly developed or absent; apical labral process without keel (as in Fig. 65-1i) or keel reduced to weak carina 2
- Scopa present from hind trochanter to tibia (Fig. 8-5b), forming corbícula on underside of femur; T5 with well-developed longitudinal median zone of fine punctation and commonly short, dense hairs, this zone dividing prepygidial fimbria (Fig. 65-1j); apical labral process with strong longitudinal keel on anterior surface (Fig. 65-1a, b, e) 5
- 2(1). Second and third submarginal crossveins and second recurrent vein weaker than first submarginal crossvein

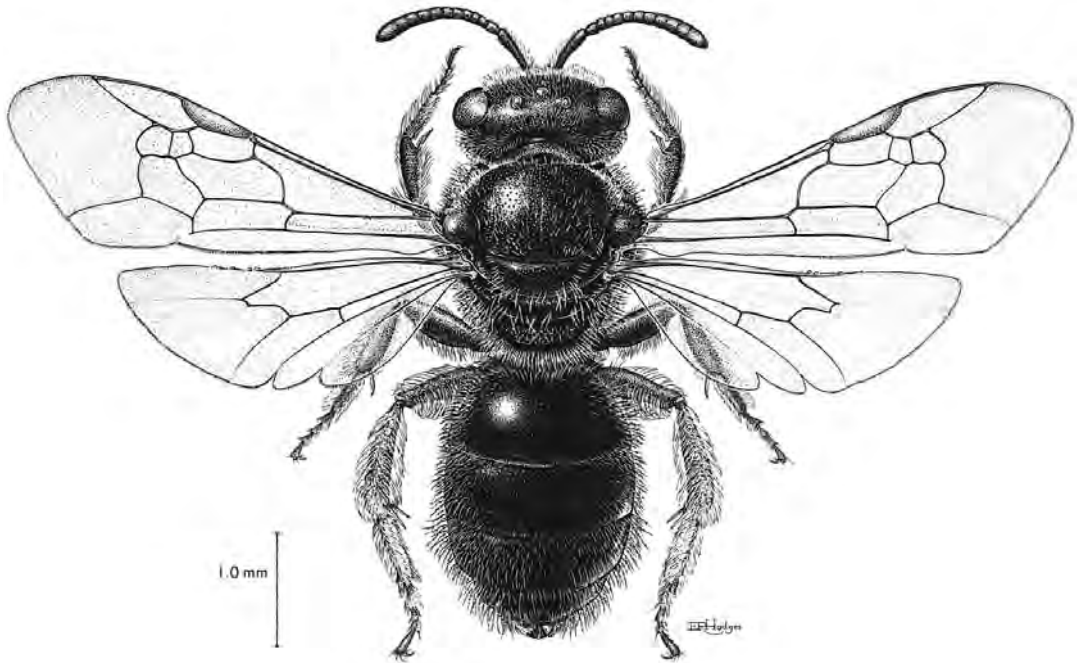


Figure 66-7. Female of *Lasioglossum (Dialictus) microlepidoides* (Ellis). At this magnification the weakness of the distal veins of the forewing is not evident. Drawing by E. R. S. Hodges, from Michener, McGinley, and Danforth, 1994.

and first recurrent vein (as in Fig. 66-6c); head and thorax largely dull greenish; inner hind tibial spur pectinate with two to four teeth (nearctic) *Lasioglossum (Dialictus)* (in part)

— . Distal veins of forewing as strong as first submarginal crossvein (as in Fig. 66-6b); body black, metasoma often red; inner hind tibial spur ciliate or minutely serrate 3

3(2). Inner orbits of eyes strongly converging below (Fig. 66-3c); head little wider than long; clypeus about twice as broad as long (Fig. 66-3c); carina across pronotum between dorsolateral angles continuous; surface of S2 conspicuously convex in profile, its base strongly depressed, suggesting strong constriction between S1 and S2 (neotropical) *Ptilocleptis*

— . Inner orbits of eyes usually not strongly converging; head distinctly wider than long, as seen from front (Fig. 66-3d); clypeus three or more times as wide as long, rarely only twice as broad as long (Fig. 66-3d); carina between dorsolateral pronotal angles incomplete; surface of S2 usually not strongly convex in profile, apparent constriction between S1 and S2 being weak 4

4(3). Free part of marginal cell about or more than three times as long as part subtended by submarginal cells (Fig. 66-5a); T1 slightly longer than broad; T5 with apical margin bare, like that of preceding terga (neotropical) *Microsphecodes*

— . Free part of marginal cell about or less than twice as long as part subtended by submarginal cells (Fig. 66-5b); T1 usually broader than long; T5 with margin more hairy than that of preceding terga 16

5(1). Third and often second submarginal crossvein and second recurrent vein weaker than first submarginal crossvein (Fig. 66-6a, b) in females and some males; body not brilliantly metallic except in a few, mostly Antillean,

species; metasomal terga without apical hair bands (Fig. 66-4a), basal hair bands present or absent *Lasioglossum* (in part)

— . Distal veins of forewing strong (Fig. 66-6b); coloration and hair bands variable 6

6(5). T1 to T4 with apical bands of posteriorly directed, plumose, tomental, pale hairs (Fig. 66-4b), sometimes limited to extreme sides of terga or to T5, terga sometimes also with basal bands; body not or weakly metallic 7

— . T1 to T4 without bands (Fig. 66-7) or with basal bands of hairs (Fig. 66-4a), and without apical bands (but bands sometimes suggested by the density of laterally directed hairs, as in *Mexalictus*); body coloration variable, sometimes bright metallic green or blue 8

7(6). Epistomal suture, at or lateral to tentorial pit, obtusely angulate *Halictus*

— . Epistomal suture, at or near tentorial pit, forming acute paraocular lobe protruding down into clypeus (as in Fig 67-6d) (South America) *Pseudagapostemon*

8(6). Posterior surface of propodeum enclosed by strong carina *Agapostemon*

— . Posterior surface of propodeum not or only partially surrounded by strong carina 9

9(8). T2 to T4 with basal bands or patches of white hair, bands or patches sometimes small and largely hidden under preceding terga (ignoring white hairs arising from gradulus) 10

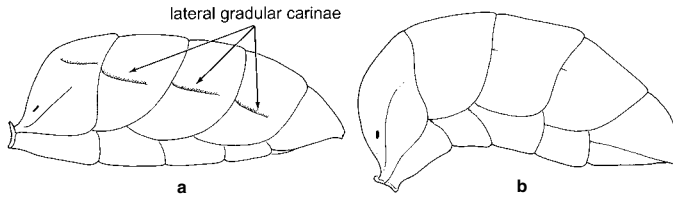


Figure 66-8. Side views of metasomas of female Halictini. **a**, *Rhinetaula denticrus* Friese; **b**, *Dinagapostemon sicheli* (Vachal). From Michener, McGinley, and Danforth, 1994.

- T2 to T4 without basal bands or patches of white hair except for series of pale hairs often arising from gradulus 11
- 10(9). Inner hind tibial spur with two or three teeth; hind tibia about as long as tarsal segments 1 to 4 taken together (South America) *Ruizantheda*
- Inner hind tibial spur with five or more teeth; hind tibia about as long as tarsal segments 1 to 5 taken together (neotropical) *Dinagapostemon* (in part)
- 11(9). Inner hind tibial spur coarsely to minutely serrate; epistomal suture near tentorial pit forming paraocular lobe protruding into clypeus (as in Fig. 67-6d) and body nonmetallic or weakly metallic greenish blue (Mesoamerica to Arizona) *Mexalictus*
- Inner hind tibial spur pectinate with two to eleven large teeth, the teeth longer than broad; epistomal suture near tentorial pit obtusely angulate or nearly straight (except forming paraocular lobe in *Paragapostemon*, which is brilliantly metallic blue or green) 12
- 12(11). Propodeal profile almost wholly steeply declivous, with only narrow sloping portion above, next to metanotum; T2 to T4 with lateral gradular carinae (Fig. 66-8a) and metasoma nonmetallic (neotropical) *Rhinetaula*
- Propodeal profile with subhorizontal or sloping upper portion about as long as or longer than metanotum; T2 to T4 without lateral gradular carina (Fig. 66-8b) or metasoma metallic blue or green or both 13
- 13(12). Eye bare or with scattered minute hairs; metasoma nonmetallic black or brown, rarely honey-colored, commonly with yellow markings (neotropical) *Habralictus*
- Eye with long hair, hair about as long as diameter of median ocellus or longer; metasoma metallic, without yellow markings 14
- 14(13). Inner hind tibial spur usually with three teeth; subhorizontal basal zone of propodeum over 1.5 times as long as metanotum (neotropical) *Caenohalictus*
- Inner hind tibial spur with 5 to 11 teeth; subhorizontal basal zone of propodeum about as long as metanotum 15
- 15(14). Body uniformly bright metallic green or blue; T2 to T4 with lateral gradular carinae (as in Fig. 66-8a); epistomal suture laterally forming prominent paraocular lobe protruding down into clypeus (Mexico) *Paragapostemon*
- Body not uniformly bright metallic; T2 and T3 and often T4 without lateral gradular carinae (Fig. 66-8b); epistomal suture obtusely angulate laterally (neotropical) *Dinagapostemon* (in part)
- 16(4). Anterior margin of mesoscutum abruptly declivous, well differentiated from dorsal surface; head and thorax coarsely pitted, dorsum of propodeum with coarse irregular rugae; second flagellar segment less than twice as long as

- first; free part or marginal cell less than twice as long as part subtended by submarginal cells (Fig. 66-5b) *Sphecodes*
- Anterior margin of mesoscutum in profile gently convex, not sharply differentiated from dorsal surface; head and thorax finely punctate, dorsum of propodeum with fine radiating ridges; second flagellar segment about twice as long as first; free part of marginal cell about twice as long as part subtended by submarginal cells. (Greater Antilles) *Nesosphecodes*

Key to the Genera of the Halictini of the Western Hemisphere (Males)

- 1. T1 to T4 with apical bands of posteriorly directed, plumose, tomental, pale hairs (Fig. 66-4b), these sometimes limited to extreme sides of terga; terga sometimes also with basal bands; body not or weakly metallic 2
- T1 to T4 without bands or with basal bands of hairs (Fig. 66-4a), but without apical bands (these sometimes suggested by the density of laterally directed hairs, as in *Mexalictus*); body coloration variable, sometimes bright metallic green or blue 3
- 2(1). Epistomal suture, at or lateral to tentorial pit, obtusely angulate (North America, rarely south to central Brazil) *Halictus*
- Epistomal suture, at or near tentorial pit, forming acute paraocular lobe protruding down into clypeus (as in Fig. 67-6d) (South America) *Pseudagapostemon*
- 3(1). T2 to T4 with lateral gradular carinae (Fig. 66-8a) (eye with abundant hair as long as ocellar diameter) 4
- T2 to T4 without lateral gradular carinae (Fig. 66-8b) 5
- 4(3). Paraocular lobe projecting down into clypeus prominent and narrowly rounded or acutely angulate (as in Fig. 67-6d); propodeal profile with basal subhorizontal portion about as long as metanotum; body bright green or blue (Mexico) *Paragapostemon*
- Paraocular lobe absent or obtuse, because epistomal suture not or obtusely angulate laterally; propodeal profile almost entirely declivous; head and thorax weakly metallic and metasoma not metallic (neotropical) *Rhinetaula*
- 5(3). Gonostylus (not including ventral gonostylus, which is often a large retrorse lobe) usually small and simple, less than half as long as and less than half as wide as gonocoxite (Fig. 66-16a), but if more than half as long as gonocoxite, then slender; distal veins of forewing sometimes weaker than first submarginal crossvein (see couplet 5 in the key for females above; this character is not reliable in males, although all males with the weakened distal veins belong here) *Lasioglossum*
- Gonostylus larger, more elaborate (Fig. 66-10c), often with long processes or folds or bifid, more than half as

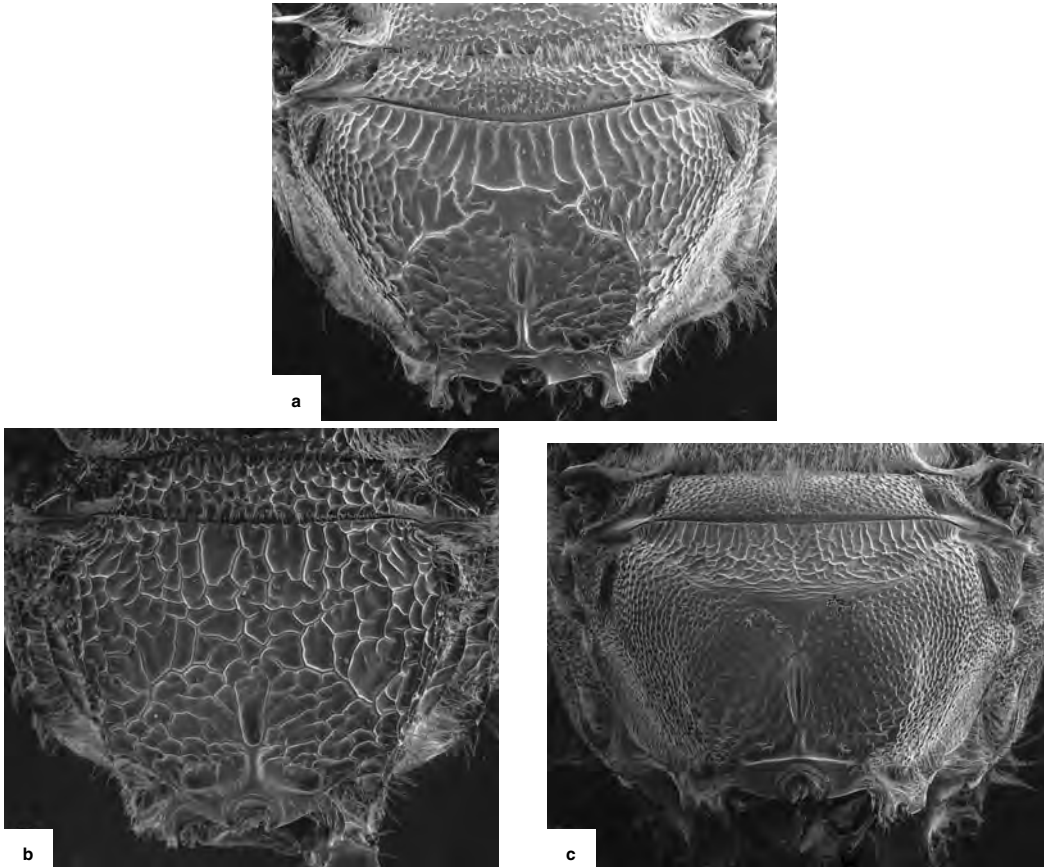


Figure 66-9. Posterodorsal views of propodeum of male Halictini. **a**, *Lasioglossum zonulum* (Smith); **b**, *Sphecodes monilicornis* (Kirby); **c**, *Halictus rubicundus* (Christ). From Michener, McGinley, and Danforth, 1994.

- long as or as wide as gonocoxite or both; distal veins of forewing as strong as first submarginal crossvein 6
- 6(5). Posterior surface of propodeum enclosed by strong carina *Agapostemon*
- . Posterior surface of propodeum not or only partially surrounded by strong carina, at least upper transverse part of carina absent 7
- 7(6). Epistomal suture near tentorial pit forming a paraocular lobe protruding down into clypeus (as in Fig. 67-6d); S7 with four basal apodemes (body weakly metallic or nonmetallic, eyes bare) (Mesoamerica) *Mexalictus*
- . Epistomal suture near tentorial pit nearly straight to obtusely angulate (or about right-angular in some *Caenohalictus*, which are bright green with long hairs on eyes); S7 with two basal apodemes, one at each lateral extremity 8
- 8(7). Metasoma very slender, almost petiolate, T1 over 1.5 times as long as wide; eyes bare or nearly so (neotropical) *Habralictus*
- . Metasoma more robust, T1 broader than long or, if nearly 1.5 times as long as broad, then eyes usually with abundant long hairs 9
- 9(8). Body generally coarsely sculptured (Figs. 8-2a, 66-9b) or sometimes with extensive shining impunctate areas; sides of propodeum coarsely reticulate; body nonmetallic, black or partly brown or red; eyes usually hairless or with few short hairs 10
- . Body much more finely sculptured, surface often dull

- (Fig. 66-9a, c); sides of propodeum punctate or granular, not coarsely reticulate; head and thorax usually with greenish or bluish reflections or strongly metallic; eyes usually with long hairs 11
- 10(9). Free part of marginal cell about or more than three times as long as part subtended by submarginal cells (Fig. 66-5a); T1 slightly longer than broad (neotropical) *Microsphecodes*
- . Free part of marginal cell about or less than twice as long as part subtended by submarginal cells (Fig. 66-5b); T1 usually broader than long 14
- 11(9). Hind femur swollen, with angle or tooth on underside; upper sloping part of propodeal profile about as long as metanotum (neotropical) *Dinagapostemon*
- . Hind femur slender, edentate; upper subhorizontal part of propodeal profile longer than metanotum 12
- 12(11). Legs with yellow areas or largely yellow (South America) *Ruizantheda*
- . Legs without yellow, or yellow restricted to front tibiae 13
- 13(12). Body usually metallic blue or green or with metallic areas, although sometimes nonmetallic; scutum and most of body entirely minutely granular and dull because

- of extremely fine, dense punctation (neotropical) *Caenohalictus*
- Body nonmetallic; scutum and most of body distinctly and in some areas rather coarsely punctate (neotropical) *Prilocleptis*
- 14(10). Anterior margin of mesoscutum abruptly declivous, well differentiated from dorsal surface; head and thorax coarsely pitted, dorsum of propodeum with coarse irregular rugae; free part of marginal cell less than twice as long as part subtended by submarginal cells (Fig. 66-5b) *Sphecodes*
- Anterior margin of mesoscutum in profile gently convex, not sharply differentiated from dorsal surface; head and thorax finely punctate, dorsum of propodeum with fine radiating ridges; free part of marginal cell about twice as long as part subtended by submarginal cells. (Greater Antilles) *Nesosphecodes*
-
- Key to the Genera of Halictini of the Eastern Hemisphere
1. Distal crossveins of forewing as strong as first submarginal crossvein (Fig. 66-6b); gonostylus of male broader or longer than indicated below, sometimes branched or otherwise complex (Fig. 66-11) 2
- Third and often second submarginal crossvein and second recurrent vein weaker than nearby veins (e.g., first submarginal crossvein) in females (Fig. 66-6a, c) and many males; gonostylus (not including ventral gonostylus or retrorse lobe) of male usually small and simple (as in Fig. 66-16a), less than half as long and less than half as wide as gonocoxite [although long and slender in some *Lasioglossum* (*Austrevylaeus*) and *Homalictus*, rather large in *Urohalictus*, and quite large and sometimes lobed in some *Lasioglossum* (*Ctenonomia*) and some Australian subgenera] 10
- 2(1). Scopa absent (Fig. 8-5a); median finely punctate and finely haired area on T5 of female absent, prepygidial fimbria, if present, thus not divided; S8 of male quadrate, somewhat longer than broad, with basolateral apodeme or arm [this unknown for *Halictus* (*Paraseladonia*)] [inner hind tibial spur of female ciliate or minutely serrate, or, in *Halictus* (*Paraseladelina*), coarsely serrate] 3
- Scopa present (Fig. 8-5b); T5 of female with longitudinal median finely punctate and haired or sometimes smooth area dividing prepygidial fimbria (Fig. 65-1j); S8 of male variable but not as above, disc usually much broader than long 6
- 3(2). Face fully as long as broad, clypeus produced and protuberant; paraocular lobe extending into clypeus strong, right-angular; labrum of both sexes with apical process (margined by bristles) with longitudinal carina, that of female high and keel-like apically (Madagascar) *Parathrincoctoma*
- Face much wider than long, clypeus neither produced nor protuberant; paraocular lobe absent, i.e., lateral segment of epistomal suture nearly straight; labrum of both sexes with apical part truncate or broadly rounded, without longitudinal carina or keel (Fig. 65-1i), or [in *Halictus* (*Paraseladonia*)] with keel scarcely evident 4
- 4(3). Inner hind tibial spur of female serrate with about eight teeth; metasomal terga with sparse, pale, apical hair bands, at least in male (body metallic blue-green; basal area of propodeum minutely reticulate) (Africa) *Halictus* (*Paraseladonia*)
- Inner hind tibial spur of female ciliate or minutely serrate, like other spurs of hind and middle legs; metasomal terga without apical hair bands 5
- 5(4). First two flagellar segments of male both distinctly broader than long; gonocoxite of male not striate, with dorsolateral depression margined by and usually traversed by flanges or ridges; body with moderate to fine punctation, rarely involving coarse pitting as is usual in *Sphecodes*; mandible of female simple (Africa, oriental) *Eupetersia*
- Second flagellar segment of male usually longer than broad, unlike first; gonocoxite of male usually striate, without depression; body and especially propodeum usually coarsely pitted; mandible of female nearly always with preapical tooth (except in neotropical *Austrosphecodes* group) *Sphecodes*
- 6(2). Female with margin of clypeal truncation, distal to preapical fimbria, extended downward at each side of labrum as a small, rather sharp, impunctate projection (except in some minute Asiatic species of the subgenus *Vestitohalictus* that lack such projections); S4 of male unmodified or at least without coarse apical setae; ventral gonostylus of male absent or directed apically, not retrorse (holarctic, Africa, oriental) *Halictus*
- Female with margin of clypeal truncation, distal to preapical fimbria, extending but little downward at each side of labrum, forming only a low, rounded projection (except in some species of *Thrincoctoma* in which there is a strong projection); S4 of male usually shortened, commonly hidden by S3, frequently with several coarse apical or subapical setae; ventral gonostylus of male usually present, directed ventrally or basally, forming a retrorse lobe 7
- 7(6). Apical marginal zones of terga with simple, laterally directed hairs usually forming apical bands that are conspicuous only in certain lights; profile of anterior part of scutum gently convex, rising but little above level of pronotum; pronotum with carina or lamella separating dorsal from declivous anterior surface (recurrent veins both entering third submarginal cell, or first recurrent entering extreme apex of second cell) (Africa, oriental) *Thrincoctoma*
- Apical marginal zones of terga variable, but without simple, laterally directed hairs; profile of anterior part of scutum strongly convex, subvertical surface thus rising well above level of pronotum and then curving strongly or angularly onto dorsum of scutum; pronotum medially without carina separating dorsal from anterior surface 8
- 8(7). Malar area about as long (female) to twice as long (male) as diameter of flagellum; pygidial plate of male not defined (dorsal gonostylus of male not bifurcate) (Asia Minor) *Thrincoctoma*
- Malar area usually linear, rarely about half as long as diameter of flagellum; pygidial plate of male defined at least posteriorly and posterolaterally by a carina 9
- 9(8). Glossa extremely long and slender, about twice as long as head; dorsal gonostylus of male broad, simple (Africa) *Glossodialictus*
- Glossa shorter than head or rarely about as long as head [somewhat longer in *Patellapis* (*Zonalictus*) *concinnum*]

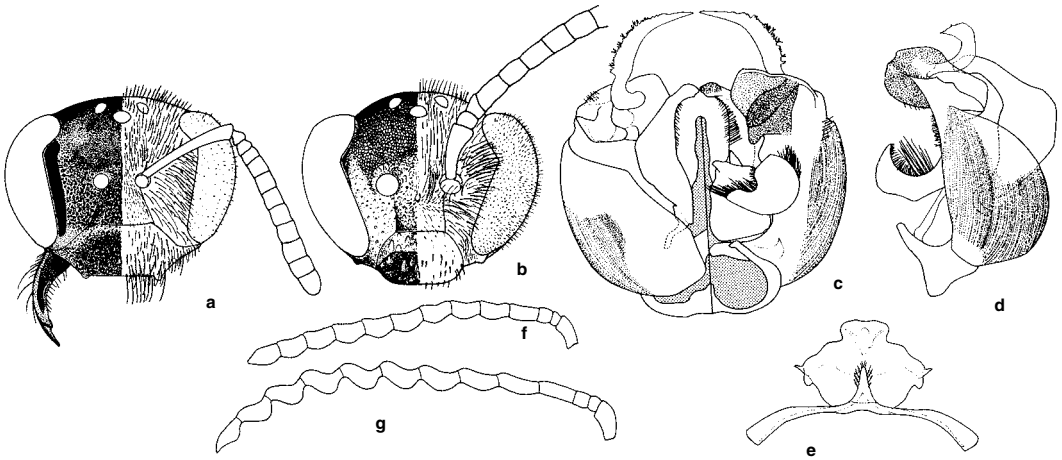


Figure 66-10. Halictini related to *Agapostemon*. **a, b**, Facial views of *A. (Agapostemonoides) hurdi* (Roberts and Brooks), female and male, showing hairy eyes.

c-f, *Dinagapostemon gigas* (Friese), male. **c**, Genitalia, dorsal view on left; **d**, Lateral view of same, showing the hairy lower

gonostylus (or retrorse lobe) midventrally; **e**, S7 and S8; **f**, Antenna.

g, Antenna of male of *D. orestes* Roberts and Brooks.

Original drawings of **a** and **b** by R. W. Brooks; others from Roberts and Brooks, 1987.

- (Cockerell)]; dorsal gonostylus of male deeply bifid, one branch sometimes slender and inconspicuous [or, in *P. (Madagalictus) suarezensis* (Benoist), small and simple] (Africa, oriental, Australia) *Patellapis*
- 10(1). S7 and S8 of male, taken together, longer than broad, as long as genital capsule, heavily sclerotized, with large lobes curved up into and around genitalia (Fig. 66-22b-d); pronotum and metanotum with middorsal yellow araeas (female unknown) (New Guinea) *Urohalictus*
- S7 and S8 of male transverse, much shorter than genital capsule, weakly sclerotic, without lobes curving upward (as in Figs. 65-1o, p; 66-10e); pronotum and metanotum not yellow middorsally 11
- 11(10). Femoral scopa reduced to few simple hairs less than two-thirds as long as diameter of femur; dorsolateral angle of pronotum produced to spine; mandible of female simple, acute; inner hind tibial spur of male coarsely pectinate (Samoa) *Echthralictus*
- Femoral scopa normal, of plumose or branched hairs enclosing ventral corbicula; dorsolateral angle or pronotum rounded, angulate (sometimes acute), or rarely lamellate, not produced to spine; mandible of female with preapical tooth; inner hind tibial spur of male finely serrate or ciliate 12
- 12(11). Metasomal terga of female, especially T1 to T3, usually sharply folded laterally, forming angle at margin between dorsal and ventrolateral parts of terga; scopal hairs plumelike with numerous lateral branches, those on sterna and ventrolateral parts of terga large, those of hind femur arising ventrally and especially at ends of femur forming femoral corbicula; gonobase of male genitalia, as seen from above, usually continuing contours of gonocoxites (Australia, oriental) *Homalictus*
- Metasomal terga rounded from dorsal to ventrolateral parts; scopal hairs with relatively few, longer branches,

less developed on metasomal venter, those of hind femur arising subdorsally and curling around femur to form femoral corbicula; gonobase of male genitalia, as seen from above, relatively broad, usually not at all continuing contours of gonocoxites *Lasioglossum*

Genus *Agapostemon* Guérin-Ménéville

In most species the head and thorax are bright metallic green or blue. In some females the metasoma is the same color, while in others it is black or amber, sometimes with basal tergal bands of white tomentum and very rarely with yellow integumental bands. In males the metasoma is black or weakly metallic, usually with broad yellow or white bands, thus contrasting sharply with the coloration of the head and thorax. Only in a few neotropical species is the body black with strong metallic reflections. The body is robust, 7.0 to 14.5 mm long. The inner hind tibial spur of the female is coarsely pectinate with three to seven large, spatulate teeth, and the hypostomal area is very coarsely striate. A strong carina usually completely surrounds the posterior surface of the propodeum.

Janjic and Packer (2003) made a phylogenetic study of species of *Agapostemon*. They regarded *Agapostemonoides* as a genus distinct from *Agapostemon*, but I think their close relationship is best indicated by the subgeneric level. These authors also recognized two clades in *Agapostemon* as subgenera. No one character distinguishes all species of these clades.

Nests of *Agapostemon* are deep, more or less vertical burrows in flat or sloping soil or sometimes in banks, with lateral burrows extending to the cells. Usually there is one cell per lateral, but sometimes there are two or three in series. In some species, burrows are frequently occupied by communal groups of two to two dozen females, and the main burrow may be branched. Accounts of life history,

nests, and behavior are by Eickwort and Eickwort (1969), Roberts (1969), Abrams and Eickwort (1980), and Eickwort (1981).

Key to the Subgenera of *Agapostemon*

1. Eyes with hairs about as long as ocellar radius (Fig. 66-10a, b); epistomal suture very obtusely angulate laterally (neotropical) *A. (Agapostemonoides)*
- Eyes bare or nearly so; epistomal suture, near tentorial pit, forming paraocular lobe protruding down into clypeus, basal margins of this lobe at right or acute angle to each other *A. (Agapostemon s. str.)*

Agapostemon / Subgenus *Agapostemon* Guérin-Ménéville s. str.

Andrena (Agapostemon) Guérin-Ménéville, 1844: 448. Type species: *Apis femoralis* Guérin-Ménéville, 1844 = *Apis viridula* Fabricius, 1793, monobasic.

Agapostemon (Notagapostemon) Janjic and Packer, 2003: 109. Type species: *Agapostemon mourei* Roberts, 1972, by original designation. [New synonymy.]

In this subgenus the eyes are bare or with minute scattered hairs, the paraocular lobe is strong and right-angular or acute, and the metasoma of the female lacks yellow markings, although there are sometimes basal tergal bands of pale tomentum. Male genitalia were illustrated by Michener (1954b), Mitchell (1960), and Roberts (1972).

■ *Agapostemon* s. str. is particularly common in North America, ranging from coast to coast and from southern Canada southward to the Bahamas and Antilles and through Mesoamerica. It is less common in South America, but occurs in the Andean countries south to northern Chile, especially the eastern slopes of the Andes, and in Brazil from Bahia, Minas Gerais, and Mato Grosso southward to Paraguay and northeastern Argentina. A total of 43 species are recognized, although some Antillean forms given specific rank may better be considered subspecies. The subgenus was revised by Roberts (1972).

Agapostemon / Subgenus *Agapostemonoides* Roberts and Brooks

Agapostemonoides Roberts and Brooks, 1987: 364. Type species: *Agapostemonoides hurdi* Roberts and Brooks, 1987, by original designation.

This subgenus differs from *Agapostemon* s. str. by the hairy eyes (the hairs being about as long as an ocellar radius), the absence of a paraocular lobe extending into the clypeus, and the presence of basal yellow bands on the metasomal terga of the female as well as the male. Curious features that may be involved in collecting pollen from the flowers of *Piper* (Piperaceae) are the fringes of long curved hairs on the posterior margins of the front and especially the middle trochanters of females. Male genitalia and other structures were illustrated by Roberts and Brooks (1987). Specimens of *Agapostemonoides* are small for *Agapostemon*, 7 to 8 mm long. This subgenus may well be the sister group of *Agapostemon* s. str. rather than a derivative from that subgenus; the paraocular lobes

of *Agapostemon* s. str. are likely to be derived relative to *Agapostemonoides*. In either case, *A. hurdi* could be considered as merely an unusual *Agapostemon*, not justifying recognition of the subgenera.

■ *Agapostemonoides* occurs from Costa Rica and Panama south probably along the eastern Andean zone to Bolivia. The only species is *Agapostemon hurdi* (Roberts and Brooks).

Genus *Caenohalictus* Cameron

Caenohalictus Cameron, 1903a: 231. Type species: *Caenohalictus trichioththalmus* Cameron, 1903, monobasic.

The name *Caenohalictus* was misapplied to *Rhinetula* by Michener (1954b). The resultant confusion was explained by Michener (1979b).

Caenohalictus consists of bright-green bees, rarely brassy, red, or nonmetallic black; in the last case the metasoma is usually blackish or partly amber. The body is more slender and usually much smaller than the bright-green members of the *Agapostemon* group of genera (see the account of the tribe Halictini); the length is 5 to 12 mm. The eyes have long hairs, about as long as an ocellar diameter to three times that length, sometimes lacking on the areas near the face; rarely, the eyes are nearly bare. Although there are occasionally areas of coarse punctation or reticulation on the thorax, the head and thorax are otherwise minutely and closely granular. There is much variation among the species; for example, most do not have paraocular lobes, but some of the larger species in which the clypeus is strongly protuberant and produced have strong paraocular lobes, about right-angular. Only the lower margin or lower two-fifths of the clypeus of the male is yellow. The first and second hind tarsal segments appear superficially to be articulated, but a cleared specimen showed the segments to be fused; the joint is rigid and wider than the more distal articulations. Male genitalia and hidden sterna were illustrated by Michener (1979b) and Packer (1993).

■ Although especially abundant and diverse in the Andean countries, *Caenohalictus* is found as far south as Chubut province in Argentina and over much of South America, but seems to be absent from the Amazon Valley and the Guianas; it also occurs uncommonly in Central America and north to the states of San Luis Potosí and Nayarit in Mexico. Rojas and Toro (2000) revised the 15 Chilean species of *Caenohalictus*, seven of which were new. About 55 species of *Caenohalictus* are known.

Because of similar color and hairy eyes, hasty examination is likely to result in confusion of *Caenohalictus* with *Caenagochloras* s. str. Of course the tribal characters readily differentiate these taxa, as does the dull, granular integument characteristic of *Caenohalictus*.

Nests of some species are similar to those of *Habralictus*, with lateral burrows each leading to a single horizontal cell (Michener and Lange, 1958a; Michener, Breed, and Bell, 1979). Other species, however, construct cells organized into a cluster of more or less horizontal cells in a cavity, suggestive of nests of some Augochlorini. Such nests were illustrated by Claude-Joseph (1926), and copied by Sakagami and Michener (1962, incorrectly

associated with the genus *Caenagochlora*). In view of the morphological and behavioral diversity among the species, it is likely that additional genera (or subgenera) will eventually be recognized.

Genus *Dinagapostemon* Moure and Hurd

Dinagapostemon Moure and Hurd, 1982: 46. Type species:

Halictus sicheli Vachal, 1901, by original designation.

This genus is a member of the *Agapostemon* group, having the large size (length 11.0–14.5 mm) and robust body form of that group. The color is metallic blue or green to nonmetallic brown or amber. The male antennal flagellum is long and strikingly crenulate (Fig. 66–10f, g), unlike that of all other genera. The hind legs of the male are dark in color and swollen, with femoral, tibial, and basitarsal teeth. I place *Dinagapostemon* near *Paragapostemon* because of their general similarity and especially the slender, tapering process of the male dorsal gonostylus (Fig. 66–10c). The male genitalia of *Dinagapostemon* are among the most complex of halictid genitalia (Fig. 66–10c, d); the lower gonostylus is large and usually projects downward; illustrations were presented by Roberts and Brooks (1987). Because the generic differences are substantial, including the lateral gradular carinae of T2 to T4 in *Paragapostemon* (as in Fig. 66–8a), I hesitantly retain the generic status for *Dinagapostemon*. According to Roberts and Brooks (1987), *Paragapostemon* is the sister group to *Dinagapostemon*.

■ *Dinagapostemon* is found in montane areas from the states of Tamaulipas and Guerrero, Mexico, through Central America to the Andean region of Colombia, Venezuela, and Ecuador. The eight described species were revised by Roberts and Brooks (1987).

Genus *Echthralictus* Perkins and Cheesman

Echthralictus Perkins and Cheesman, 1928: 14. Type species:

Halictus extraordinarius Kohl, 1908, by original designation.

This is probably a local, parasitic derivative of *Homalictus* s. str. It has, however, lost nearly all of the distinctive generic characters of *Homalictus*. The metasomal scopa is reduced to a few, scattered, very long hairs on the sterna. The femoral scopa is not recognizable except for the row of long, simple hairs on the posterior surface, the longest about two-thirds as long as the maximum femoral diameter. The tibia has a distinct, relatively bare undersurface, but the hairs margining it are not longer than those elsewhere on the tibia and have only short branches. The labral keel is reduced to a strong carina. Perhaps related to the loss of the tergal scopa and the great reduction of the sternal scopa, is the rounded lateral metasomal margin. By contrast, in *Homalictus* the metasoma is depressed so that its lateral margin is a strong bend or crease in the terga where their ventrolateral surfaces join the dorsal surfaces. T5 of the female *Echthralictus* has a bare, broad, shining, apical triangular area instead of the usual narrower area, usually with fine hairs, as is characteristic of nonparasitic Halictini. The body length is 5.5 to 6.0 mm.

■ *Echthralictus* is known only from Samoa, where there are two species; see Perkins and Cheesman (1928).

Since there are no intermediates between *Echthralictus* and *Homalictus*—i.e., there is in fact a major morphological gap—I have chosen to recognize *Echthralictus* as a genus. A cladistic study presumably would show that it is part of *Homalictus* s. str. if the features associated with parasitism in halictids (see Michener, 1978b) were ignored in the analysis. Probably, indeed, *Echthralictus* arose from a *Homalictus* group now found in its island range, as suggested by its metallic green or blue tints, among other characters.

Genus *Eupetersia* Blüthgen

Like *Prilocleptis*, this presumably parasitic genus may be derived from *Sphecodes*, but the moderate to fine punctation of the body, lacking the coarse pitting and reticulation found in *Sphecodes*, is probably plesiomorphic relative to *Sphecodes*. Exceptions exist, however; *Eupetersia seyrigi* Blüthgen has a coarsely pitted propodeum. *Eupetersia* is tentatively considered a basal branch of the *Sphecodes* clade. The lack of the striae on the gonocoxites of the male is probably also plesiomorphic relative to *Sphecodes*. Each gonocoxite has, however, a dorsolateral depressed area with a lamella or flange on each side and often one or more longitudinal ridges across the depression. As in *Prilocleptis* the antennae of the male are similar to those of the female, not long and robust as is usual in *Sphecodes*. The mandibles of the female are simple, unlike those of most *Sphecodes*. The coloration, also, is not usually like the black head and thorax and partly or wholly red metasoma of most *Sphecodes*; the body may be black (the thorax sometimes partly red), metallic blue, to wholly reddish yellow. The body length ranges from 5 to 12 mm.

Keys to species were provided by Blüthgen (1928b, 1936) and, to metallic species, by Pauly (1981b). Baker (1974a) gave a list of species with much useful detail. Pauly (1999b) listed the African species of *Eupetersia*, and Brooks and Pauly (in Pauly et al., 2001) revised the eight species from Madagascar.

Callosphcodes, here listed as a synonym of *Sphecodes*, could be a senior synonym of *Eupetersia*. It is known from a single specimen, now lost, believed to be from far outside the known range of *Eupetersia*. The problem of its position is not likely to be solved until more material is collected. See comments under *Sphecodes*.

Key to the Subgenera of *Eupetersia*

1. Scutum rather densely punctate; scutellum bigibbous, the two convexities not or scarcely punctate *E. (Eupetersia s. str.)*
- Scutum with widely separated punctures; scutellum gently convex, with punctation similar to that of scutum *E. (Nesoeupetersia)*

Eupetersia / Subgenus *Eupetersia* Blüthgen s. str.

Eupetersia Blüthgen, 1928b: 49. Type species: *Eupetersia neavei* Blüthgen, 1928, by original designation. [Also published as new by Blüthgen, 1928c: 165.]

Calleupetersia Cockerell, 1938: 329. Type species: *Halictus lasureus* Friese, 1910, by original designation.

The species placed in *Calleupetersia* seem to differ from the others only in the metallic blue coloration. The male

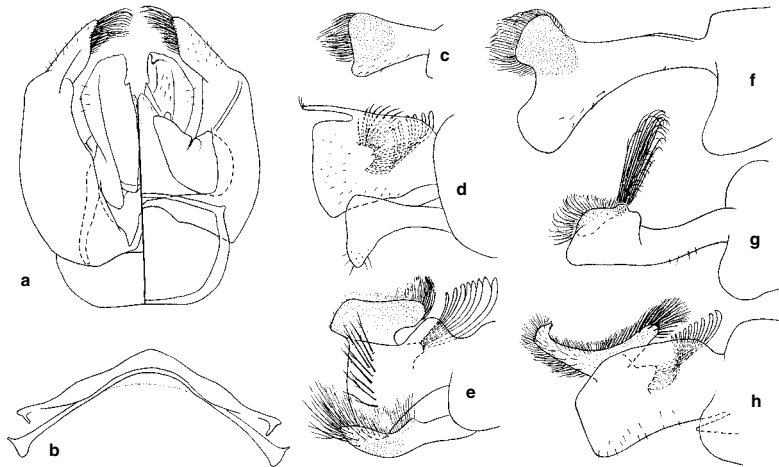


Figure 66-11. Genitalia and hidden sterna of males of *Halictus*.

a, Genitalia of *H. ligatus* Say (dorsal on left); **b**, S7 and S8 of same.
c-h, Posterolateral views of gonostyli: **c**, *H. (Odontalictus) ligatus*; **d**, *H. (Seladonia) confusus* Smith; **e**, *H. (Halictus) quadricinctus* (Fabricius); **f**, *H. (Argalictus) scabiosae* (Rossi); **g**, *H. (Monilapis)*

patellatus Morawitz; **h**, *H. (Protohalictus) rubicundus* (Christ). The gonostyli show the diversity within the genus *Halictus*. Only the subgenera *Halictus* s. str. and *Seladonia* have a well-developed lower gonostylus. From Michener, 1978a.

genitalia were illustrated by Michener (1978b) and Pauly (1981b).

■ The range is from Ethiopia and Uganda south to Natal Province in South Africa, and Madagascar. Pauly (1981b) listed 21 species. Blüthgen (1928b, 1936) gave a key to the species then known.

Eupetersia / Subgenus *Nesoeupetersia* Blüthgen

Eupetersia (*Nesoeupetersia*) Blüthgen, 1936: 182. Type species: *Sphecodes scotti* Cockerell, 1912, by original designation.

■ *Nesoeupetersia* occurs from Zaire and Uganda to Malawi, Madagascar, the Seychelles, and southern India. Pauly (1981b) listed eight species.

Genus *Glossodialictus* Pauly

Glossodialictus Pauly, 1984a: 704. Type species: *Glossodialictus wittei* Pauly, 1984, by original designation.

Because it has strong apical wing venation and occurs in Africa, this genus invites comparison with *Patellapis*. It differs from *Patellapis* in the blue-green metallic tints on the head and thorax; the strong, acute paraocular lobe extending down into the clypeus (but see the comments on *Patellapis braunsella* Michener); the protuberant clypeus; the very long, slender glossa; and the broad, simple, dorsal gonostylus of the male. The body length is 8.5 mm. Other characters include the retrorse ventral gonostylus of the male, the second submarginal crossvein approximately meeting the first recurrent vein, the basal tomentum on T2 and T3, and the lack of apical tergal hair bands although the tergal margins are yellowish brown. In spite of Pauly's (1984a) diagram that shows a substantial malar area, the malar area is said to be linear in the female, a little more developed in the male. Pauly (1984a) sketched the male genitalia and other structures.

■ *Glossodialictus* is known only from Shaba Province in Zaire. The only species is *G. wittei* Pauly.

Genus *Habralictus* Moure

Habralictus consists of small species (length 4.0-6.5 mm) with the head and thorax blackish (usually with metallic tints) to bright green, the surface dull and minutely granular to polished. The metasoma may be brown or black, rarely honey-colored, but in the female usually has yellow basal bands or basal lateral spots on the terga. Males usually lack such markings or have only lateral spots. The metasoma of the male is petiolate, widest at T4 and T5, T1 being much longer than broad. The male clypeus is more than half yellow. The usually bare eyes (although with short hairs in some species), as well as the form of the male metasoma, easily distinguish *Habralictus* from the only other small neotropical Halictini with strong wing venation, i.e., *Caenohalictus*. Male genitalia and hidden sterna were illustrated by Michener (1954b, 1979b).

The nests are burrows, usually in banks, with lateral branches each leading to a single horizontal cell (Michener and Lange, 1958a; Michener, Breed, and Bell, 1979).

Key to the Subgenera of *Habralictus* (Males)

(Two subgenera are tentatively recognized. One of them, *Zikaniella*, is known only in the male; subgeneric characters for females are unknown.)

1. Head not or scarcely wider than thorax; genal area much narrower than eye, as seen from side; clypeal surface not concave or with small median concavity; inner hind tibial spur simple, ciliate *H. (Habralictus) s. str.*
- Head much broader than thorax; genal area wider than eye, strongly angulate posteriorly; middle half of clypeal surface broadly concave; inner hind tibial spur pectinate with four teeth *H. (Zikaniella)*

Habralictus / Subgenus *Habralictus* Moure s. str.

Habralictus Moure, 1941a: 59. Type species: *Habralictus flavopictus* Moure, 1941, by original designation.

■ *Habralictus* s. str. is seemingly most abundant in Bolivia, but is found from that country and the state of Paraná in Brazil north to the state of Jalisco, Mexico. In the West Indies it is known from St. Vincent. The 21 described species were listed by Moure and Hurd (1987).

Habralictus / Subgenus *Zikaniella* Moure

Zikaniella Moure, 1941a: 57. Type species: *Zikaniella crassiceps* Moure, 1941, by original designation.

Zikaniella is known only from the male, which differs from *Habralictus* s. str. principally in its large head and the associated characters listed in the key to subgenera. Such features are usually not generic characters in bees, sometimes not even specific characters, and if the female of *Zikaniella* is a typical *Habralictus*, then *Zikaniella* should be regarded as a synonym of *Habralictus*, in spite of the page priority of *Zikaniella*; as first reviser, I consider *Habralictus* to have precedence over *Zikaniella*. *Zikaniella* resembles *Habralictus* s. str. not only in the characters indicated in the key to genera but also in the basal yellow spots of T3 and T4, the simple legs and sterna, and the nearly straight lateral segments of the episomal sutures. Its head and thoracic integument is shining green, largely smooth; this is also true of the basal area of the propodeum, which is minutely roughened in *Habralictus* s. str.

■ This subgenus is known only from the state of Rio de Janeiro, Brazil. The only species is *Habralictus crassiceps* (Moure).

Genus *Halictus* Latreille

Although in this genus the principal metasomal hair bands are on the apices of the terga (Pl. 4), in some species—especially in the subgenus *Seladonia*—there are also basal bands. In other species, especially most species of the subgenus *Vestitohalictus*, white tomentum covers the entire exposed tergal surfaces; the apical bands thus not very distinct or not recognizable. Distinctive attributes of the genus are indicated not only in the key to genera but in the discussion of the tribe Halictini and in Table 66-1. Illustrations of male genitalia and other characters were given by Sandhouse (1941), Mitchell (1960), Ebmer (1969), Pesenko (1985, 1986b), and Sakagami and Ebmer (1987); see also Figure 66-11.

It has been common in the past to recognize three subgenera, *Halictus* s. str., *Seladonia*, and *Vestitohalictus* (see Michener, 1978a), and Pesenko (1984a) recognized them as three genera. *Seladonia* (including *Pachycephale*) was distinguished from *Halictus* s. str. principally by the greenish, bluish, or brassy coloration, at least of the head and thorax; *Halictus* s. str. contained all the nonmetallic species (except for the few nonmetallic *Vestitohalictus*). The elaborate male genitalia of *Seladonia*, however, are similar to those of *Halictus* s. str. in the narrow sense of the present account (compare Fig. 66-11d with e), and there is no reason to make the integumental color deci-

sive in the taxonomic decision. There is such diversity among the black *Halictus* as to overshadow the difference between *Seladonia* and the black forms most similar to it. I have therefore followed Pesenko (1984a) in recognizing several subgenera of black *Halictus* and have retained *Seladonia* and *Pachycephale* as other subgenera among the black ones. The only other greenish *Halictus* are *Paraseladonia* and some species of the subgenus *Vestitohalictus*.

Danforth, Sauquet, and Packer (1999), in a phylogenetic study of 22 species of *Halictus* based on one nuclear gene, found groups mostly supportive of the subgenera recognized by Michener (2000). Recognition of *Vestitohalictus*, however, rendered *Seladonia* paraphyletic. In several analyses *Seladonia* plus *Vestitohalictus* appeared as the sister group of the rest of *Halictus*, but in other cases *Seladonia* plus *Vestitohalictus* arose within the rest of *Halictus*. Pesenko (2004b) made an extensive phylogenetic study of *Halictus* genus based on morphology. He found the genus to be monophyletic, and *Seladonia* s. l. to be the sister group to the rest of *Halictus*; he recognized *Seladonia* and *Halictus* as separate genera. I prefer to recognize *Halictus* as a genus including *Seladonia*; usually the former is black and the latter metallic greenish or bluish. However, a few species of *Seladonia* s. l. are nonmetallic black. The next most consistent difference between *Seladonia* s. l. and *Halictus* is a deep cleft in the upper gonostylus of the male. The lobe mesal to this cleft may be very long and slender, but in a few species it is lost so that there is no obvious cleft. I use the terms *Seladonia* group and *Halictus* group to distinguish the two groups given generic status by Pesenko.

A list of the species of *Halictus* (except *Seladonia* and *Vestitohalictus*), with synonymies, was given by Pesenko (1984b) and a list for the entire genus, 442 names, 182 recognized species, was provided by Pesenko (2004b), updated by Pesenko (2005). Lists of African species of the genus *Halictus* were given by Pauly (1999b). A revision of American species was by Sandhouse (1941).

The key below (modified from Pesenko, 2004b) has one obvious defect; females cannot be run past certain couplets for which only male characters are known. One must try running a female in both alternatives in such cases. Other keys should also be consulted. Michener (2000) gave keys for each sex, but that for females left five subgenera not distinguished. The key by Pesenko (2004b) is a useful alternative.

Key to the Subgenera of *Halictus*
(From Pesenko, 2004b)

1. Integument nonmetallic, usually black; S4 of male often broadly emarginate; dorsal gonostylus of male not cleft [*Halictus* group] 2
- Integument in at least some areas of head and thorax dull metallic green or bluish (very rarely black); S4 of male with posterior margin straight; dorsal gonostylus of male divided by deep cleft forming a slender inner (median) lobe that may be elongate or rarely lost (so that cleft is not evident) [*Seladonia* group] 12
- 2(1). Clypeus of female with rounded tubercle in middle of lower margin; S5 of male with deep, triangular but rounded incision in distal margin; metasoma, at least T1 to T3, red (Indian region) *H. (Ramalictus)*

- . Clypeus of female with lower margin straight; S5 of male with margin straight or broadly, weakly emarginate; metasoma usually black 3
- 3(2). Body length over 16 mm; scutum of female sparsely punctate; antennal flagellum of male flattened with long fringe on lower side, last segment flattened, curved; hind basitarsus of male curved (palearctic) *H. (Halictus s. str.)*
- . Body length less than 14 mm; scutum of female densely punctate; antennal flagellum of male not flattened, not fringed except rarely with short hairs, last segment unmodified; hind basitarsus of male nearly always straight. 4
- 4(3). Upper gonostylus of male broad with clump of very coarse bristles on inner surface; lower gonostylus a slender process, much reduced in *H. (Protohalictus) rubicundus* (Christ) and *hedini* Blüthgen 5
- . Upper gonostylus of male elongate, proximal half narrowed, without clump of coarse bristles on inner surface; lower gonostylus absent 7
- 5(4). Propodeal triangle densely and finely granulate; hind tibia of female black; male antenna reaching scutellum; S4 of male of normal length, posterior margin nearly straight (North America) *H. (Nealictus)*
- . Propodeal triangle rugose or rugulose; hind tibia of female usually red or reddish yellow, rarely black; male antenna reaching propodeum; S4 of male short, broadly emarginate 6
- 6(5). Sides and posterior surface of propodeum nearly smooth, polished; antennal flagellum of male with dense, short pubescence in proximal and distal bands on each segment; head of female as long as wide in frontal view, gena with large tooth (Central Asia) *H. (Lampralicutus)*
- . Sides and posterior surface of propodeum granulate or rugose, dull; antennal flagellum with pubescence inconspicuous; head of female shorter than wide in frontal view, genal area without tooth (holarctic) *H. (Protohalictus)*
- 7(4). Hypostomal and lower genal areas of male, at least in ventral view, slightly concave to deeply excavated; first flagellar segment of male broader than long, following segments often convex ventrally and thus moniliform and each with glabrous, shiny area or band mesally; S4 of male with posterior margin broadly and deeply emarginate with extreme lateral angle distinct 8
- . Hypostomal and genal areas of male convex or flat in lateral view; first flagellar segment of male as long as or longer than broad, following segments usually not convex, without glabrous areas; S4 of male with posterior margin straight or shallowly incised medially, without strong angle at side 9
- 8(7). Propodeal triangle with distinct wrinkles, shiny; malar areas of male more than one third as long as broad; hypostomal and genal areas deeply and sharply excavated (palearctic) *H. (Monilapis)*
- . Propodeal triangle obscurely rugulose, silk-shiny; malar area of male less than one fifth as long as broad; hypostomal and genal areas of male only slightly concave (palearctic) *H. (Platyhalictus)*
- 9(7). Male antenna at most reaching scutellum; S7 of male transverse without posterior median process; lower genal area of female with large tooth; inner hind tibial spur of female with one large basal tooth (North America to northern South America) *H. (Odontalictus)*
- . Male antenna usually reaching propodeum; S7 of male with median posterior projection; gena of female not toothed; inner hind tibial spur of female serrate with several teeth (palearctic) 10
- 10(9). Propodeum with carina bordering its posterior surface; last antennal segment of male usually hook-shaped; S4 of male trapezoidal, narrowed, and emarginate posteriorly (palearctic) *H. (Hexataenites)*
- . Propodeum without carina; last antennal segment of male of usual form; S4 of male not narrowed posteriorly, margin usually straight 11
- 11(10). Propodeum and metasomal terga distinctly punctate; metasomal hair bands broadly interrupted medially, consisting of fine hairs; S8 of male with median, apical prominence (palearctic) *H. (Tytthalictus)*
- . Propodeum and metasomal terga obscurely punctate; metasomal hair bands unbroken, consisting of coarser hairs; S8 of male without median, apical prominence *H. (Argalictus)*
- 12(1). Scopa almost absent; mandible of female simple; T5 without median specialized areas of minute hairs characteristic of most female Halictini [Cleptoparsitic, male unknown] (Africa) *H. (Paraseladonia)*
- . Scopa of female well developed; mandible of female with subapical tooth; T5 with specialized median area of minute hairs as normal for Halictini 13
- 13(12). Basitibial plate of female slender, pointed, its anterior margin incompletely defined; hairless propodeal triangle small, often not as long as metanotum, area lateral to triangle, and metasomal terga, largely covered with pale tomentum *H. (Vestitohalictus)*
- . Basitibial plate of female rounded or pointed, anterior margin defined; propodeal triangle about as long as metanotum, area lateral to triangle usually not densely hairy; terga usually with apical and basal bands of pale plumose hairs 14
- 14(13). Male antenna usually reaching only to scutellum, second flagellar segment 1.2 to 1.4 times as long as wide; S6 of male flat or with slight longitudinal median depression *H. (Seladonia)*
- . Male antenna usually reaching metasoma, second flagellar segment 1.7 to 2.0 times as long as wide; S6 of male with deep triangular depression behind gradulus *H. (Pachyceble)*

Halictus / Subgenus *Argalictus* Pesenko

Halictus / Subgenus *Argalictus* Pesenko

Halictus (Argalictus) Pesenko, 1984a: 348. Type species: *Hyalaenus senilis* Eversmann, 1852, by original designation.

■ The eight species of this subgenus are found in the southern palearctic region, especially the xeric parts of Asia.

Halictus / Subgenus *Halictus* Latreille s. str.

Halictus Latreille, 1804: 182. Type species: *Apis quadricincta* Fabricius, 1776, by designation of Richards, 1935: 170. For other type designations, see Michener, 1997b.

Mucoreohalictus Pesenko, 2004: 102. Type species: *Hylaeus mucoreus* Eversmann, 1852, by original designation. [New synonymy.]

I tentatively recognize *Vestitohalictus* in an older sense, including Pesenko's new subgenera, because the whole group seems distinctive (see the key to the subgenera) and because *Placidohalictus* seems to be paraphyletic in Pesenko's system.

The body in this subgenus is greenish or uncommonly nonmetallic, sometimes with the metasoma red, the metasoma often so densely covered with pale pubescence that the apical bands of the terga are not evident. The body length is 3.5 to 8.0 mm. The upper or principal gonostylus of the male is expanded distally and has a slender, hirsute preapical appendage arising from its upper mesal margin, as in *Halictus (Seladonia) virgatellus* Cockerell (see Sandhouse, 1941, fig. 7). There is also a very small cluster of anteromedially directed setae arising from near the upper margin of the basal part of the gonostylus. The lower gonostylus, when present, is rather slender, parallel-sided; it is sometimes absent.

■ *Vestitohalictus* is widespread in the palearctic region, mostly in xeric regions, from the Canary Islands to China. Pesenko (2004b) listed 35 species, under three subgeneric names.

Genus *Homalictus* Cockerell

In females of this genus the metasoma is flattened, at least T2 and T3 show distinct angles between their dorsal and lateroventral surfaces as in the Nomioidea, and there are enormous scopal hairs arising on the sterna and ventral parts of the terga (Fig. 66-12), those on the latter directed strongly mesad. The scopal hairs on the hind femora and metasoma are plumose, with numerous branches diverging from a distinct rachis. The hairs forming the hind femoral corbícula arise on the lower surface of the femur, not on the dorsal surface. The large hairs on the basal two-thirds of the lower surface of the hind tibia are pectinate, usually rather erect, and clearly differentiated from the usually short, erect hairs of the lower distal part of the outer surface of the tibia, which is often in a slightly different plane than the rest of the outer tibial surface. (Thus the tibia resembles that of some *Patellapis*, Fig. 66-19a.) All these characters differentiate females from *Lasioglossum*, with which *Homalictus* agrees in the weak third submarginal crossvein and second recurrent vein. Males, however, do not seem to differ from those of *Lasioglossum* in any thoroughly consistent character, although the gonobase character mentioned in the key to the genera usually works. Illustrations of male genitalia and other structures were published by Krombein (1951), Michener (1965b, 1980), and Walker (1986, 1997). For Indonesian and New Guinea species, Pauly (1980b, 1986) published sketches of male genitalia and other structures. In some species the gonostyli are much longer and more slender than those of *Lasioglossum*, as long, for example, as the gonocoxites in *Homalictus eurhodopus* (Cockerell) and *latitarsis* (Friese).

Because of the weakened distal wing venation, prior authors have regarded *Homalictus* as a derivative of *Lasioglossum*; this arrangement would make the latter paraphyletic. In the past I have recognized it nonetheless as a

genus because of the huge size of *Lasioglossum* and the distinctiveness of females of *Homalictus*. It now appears, however, that *Lasioglossum* may not be the closest relative of *Homalictus* and that the reduced distal venation of *Homalictus* possibly arose independently from that of *Lasioglossum*. Every one of the characters of *Homalictus* listed above except the weak distal venation is found also among the subgenera of *Patellapis*, which therefore may be the group from which *Homalictus* arose, and thus the group that *Homalictus* may make paraphyletic. In *Patellapis* (*Pachyhalictus* and *Archihalictus*) the metasoma is somewhat flattened, and T2 is somewhat angulate at the sides, especially in *Archihalictus* of the group of *joffrei* (Benoist), suggesting *Homalictus*. The metasomal scopa, in some species of these and other subgenera, is large, in the *joffrei* group fully as well developed as in *Homalictus*. The other characters of the female scopa and hind legs of *Homalictus* can all be duplicated in *Patellapis* subgenera such as *Pachyhalictus*. Although these are a complex set of features, *Homalictus* may none the less be closer to *Lasioglossum* than to *Patellapis*. In this case it could be incorporated into the former, making *Lasioglossum* an even larger and more cumbersome unit.

Unlike *Patellapis*, most *Homalictus* species are metallic blue or green, more rarely bronze or purple, often dull but sometimes as brilliant as in many Augochlorini. The metasoma is sometimes red. S4 of the male is not shortened and is not equipped with long bristles, features that are common in *Patellapis*.

The recognition of the presumably cleptoparasitic *Echthralictus* as a genus makes *Homalictus* paraphyletic. I have decided to recognize *Echthralictus* nevertheless, because there is a major structural gap between it and *Homalictus*. To synonymize it with *Homalictus* (*Homalictus*), which is undoubtedly where it goes cladistically, would make irrelevant virtually all of the indications of relations of *Homalictus* to *Patellapis*, *Lasioglossum*, etc., because most of these indications relate to structures that disappear or are modified in parasitic bees.

Key to the Subgenera of *Homalictus* (Females) (For males, see comments on the subgenera)

1. Hairs of lower distal part of outer surface of hind tibia short, uniform, erect, branched; undersurface of tibia concave *H. (Homalictus s. str.)*
- Hairs of lower distal part of outer surface of hind tibia not differentiated from those on rest of surface, and the hairs not erect; undersurface of tibia not or scarcely concave 2
- 2(1). T2 to T4 without bands of tomentum; hair on outer surface of hind tibia simple, sparse, almost bristle-like (New Guinea) *H. (Papualictus)*
- T2 to T4 with bands of tomentum, broken medially; hair on outer surface of hind tibia short, minutely plumose, appressed (Australia) *H. (Quasilictus)*

Homalictus / Subgenus *Homalictus* Cockerell s. str.

Halictus (Homalictus) Cockerell, 1919b: 13. Type species: *Halictus taclobanensis* Cockerell, 1915, by original designation.

Halictus (Indohalictus) Blüthgen, 1931: 291. Type species: *Halictus buccinus* Vachal, 1894, by original designation.

species as to subgenus. The subgenus *Dialictus* as here defined includes both greenish and nonmetallic species. So segregated, *Evyllaes* includes the species whose eusocial behavior is most complex, including species whose adults come in contact with the larvae and remove feces from larval cells, but it also includes solitary species such as *L. fulvicorne* (Kirby), as noted by L. Packer (in litt., 1997). *Dialictus*, on the other hand, includes many solitary species as well as species that are eusocial; so far as is known, the adults do not contact the larvae. I believe that my use of *Evyllaes* and *Dialictus* combines the recognition of useful groups with avoidance of a great many generic transfers that would probably not persist after future analyses.

The continued use of the generic name *Lasioglossum* makes it possible to conserve a current binomen for every species; thus such behaviorally well-known species as *Lasioglossum zephyrum* (Smith) do not get shifted to genera like *Dialictus*, *Evyllaes*, *Hemihalictus*, or *Sudila* (see below), to the certain confusion of nontaxonomists and probably of taxonomists as well. When or if *Lasioglossum* is to be split and species like *L. (Dialictus) zephyrum* are to be transferred to another genus, it should be done once, to some one other genus, something that is not yet possible because of uncertainties.

The keys to the subgenera of *Lasioglossum* below are divided geographically into three regions, thus: the Western Hemisphere; the Palearctic, Oriental, and African faunal regions; and the Australian region.

Several particulars concerning the keys bear comment here. For the first key, couplet 2, and second key, couplet 7: see the comments on the subgenera *Evyllaes* and *Dialictus* in the discussion of the genus *Lasioglossum*. The female of *Lasioglossum (Sellalictus) ankaratrense* (Benoist) from Madagascar does not agree with the characters given in the second key, first option of couplet 5, and would run to *Dialictus*, but the male is clearly a *Sellalictus*. Some small species of the subgenus *Parasphecodes* have coarsely serrate or pectinate hind tibial spurs and hence run to the second option of couplet 4 in the third key. They differ in having the metasoma red, and differ from most *Ctenonomia* in lacking basal bands of tomentum on the metasomal terga.

Key to the Subgenera of *Lasioglossum* of the Western Hemisphere

1. Second submarginal crossvein as strong as first (Figs. 66-1a, 66-6a) [usually rather large and robust, body length 6.8-12.0 mm, usually nonmetallic, although *Lasioglossum pavonotum* (Cockerell) of the Pacific Coast of USA is strongly green] (holarctic) *L. (Lasioglossum s. str.)*
- Second submarginal crossvein, at least in female, weaker than first, although not always as weak as third or as second recurrent vein (Fig. 66-6c) (*Hemihalictus* series) 2
- 2(1). Posterior surface of propodeum margined at side by vertical carina that extends upward to summit and then mesad at least partway across upper margin, so that there is a sometimes interrupted carina between dorsal and posterior surfaces; body nearly always nonmetallic (holarctic) *L. (Evyllaes)*
- Posterior surface of propodeum in nonmetallic species usually with lateral vertical carina extending only part-

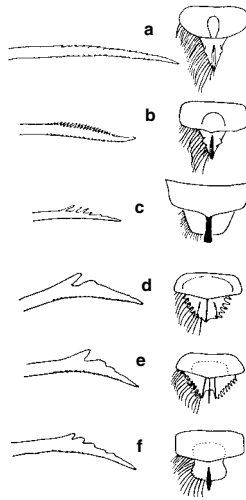


Figure 66-13. Inner hind tibial spurs and labra of females of Australian species of *Lasioglossum*. **a**, *L. (Parasphecodes) musicum* (Cockerell); **b**, *L. (Pseudochilalictus) imitator* Michener; **c**, *L. (Glossalictus) etheridgei* (Cockerell); **d**, *L. (Chilalictus) wahlenbergiae* Michener; **e**, *L. (C.) leai* (Cockerell); **f**, *L. (C.) helichrysi* (Cockerell). From Michener, 1965b.

- way to summit, or, if attaining summit, then usually not extending mesad across upper margin, so that there is usually no carina between dorsal and posterior surfaces, but in metallic species, with or without propodeal carinae, sometimes even more strongly carinate than in *L. (Evyllaes)*; body black or metallic greenish or bluish, rarely bright metallic green 3
- 3(2). Scopa sparse, consisting of a row of simple bristles on hind trochanter and lower edge of femur, shorter bristles on upper part of femur, and some long, nearly simple hairs on inner side of tibia (nonmetallic) (nearctic) *L. (Sphecodogastra)*
- Scopa normal, largely plumose (as in Fig. 8-5b) 4
- 4(3). Nonmetallic and with two submarginal cells; inner hind tibial spur of female serrate (nearctic) *L. (Hemihalictus)*
- Nonmetallic or metallic, with three submarginal cells or, in a few metallic species, with two; inner hind tibial spur of female pectinate with a few large teeth 5
- 5(4). Mandible of female strongly bidentate at apex; mid-dorsal length of male gonobase less than one-fourth as long as gonocoxite (Mesoamerica) *L. (Eickwortia)*
- Mandible of female with small, dorsal preapical tooth; middorsal length of male gonobase usually over one-third as long as gonocoxite *L. (Dialictus)*

Key to the Subgenera of *Lasioglossum* of the Palearctic, Oriental, and African Faunal Regions

1. Second submarginal crossvein as strong as first (to be verified using females) (as in Fig. 66-6a) (*Lasioglossum* series) 2
- Second submarginal crossvein, at least in female, weaker than first, although not always so weak as third or as second recurrent vein (as in Fig. 66-6c) (*Hemihalictus* series) 3
- 2(1). Inner hind tibial spur of female serrate or rarely pectinate with five or more teeth (holarctic) *L. (Lasioglossum s. str.)*
- Inner hind tibial spur of female pectinate with few large teeth, or with one large tooth followed by undulate margin (Africa, Oriental, Australia) *L. (Ctenonomia)*
- 3(1). Mandible of female with two preapical teeth on upper

- margin; body length 11 to 13 mm; S6 of male ending in thick, shining, uniformly curved and elevated margin (inner hind tibial spur of female serrate) (Siberia) *L. (Acanthalictus)*
- Mandible of female with one preapical tooth; body smaller; S6 of male not as described above 4
- 4(3). Basitibial plate of female absent (Fig. 66-17d); scopa of female represented by only a few hairs; propodeum with vertical lunate flange separating lateral from posterior surfaces (male unknown) (Africa) *L. (Paradialictus)*
- Basitibial plate of female distinct; scopa of female well developed, forming corbicula on underside of femur, evident but less well developed in parasitic species of *Dialictus* (Fig. 8-6a); propodeum with carina or rounded angle separating lateral from posterior surfaces 5
- 5(4). T2 of male with broad, basal band of erect white hairs; disc of labrum of female rather uniformly convex; inner hind tibial spur of female serrate or, if pectinate, then with five or more teeth, all longer than broad (Africa) *L. (Sellalictus)*
- T2 of male without basal band of white hairs, or, if present, then hairs more or less prostrate as on other terga; disc of labrum of female with elevated area or tubercles, not uniformly convex; inner hind tibial spur of female usually pectinate with less than five long teeth, but sometimes serrate or briefly pectinate with more teeth 6
- 6(5). Subpleural signum of female usually elevated as distinct tubercle in front of middle coxa; inner hind tibial spur of male briefly pectinate (Oriental) *L. (Sudila)*
- Subpleural signum of female inconspicuous or absent, not elevated as tubercle; inner hind tibial spur of male usually ciliate or minutely dentate 7
- 7(6). Posterior surface of propodeum margined at side by vertical carina that extends upward to summit and then mesad at least partway across upper margin, so that there is a sometimes interrupted, transverse carina between basal area and posterior surface, i.e., across posterior margin of basal area; rarely transverse carina present but vertical carina reduced or absent; usually rather large, non-metallic except for some Asian species (holarctic) *L. (Ervylaeus)*
- Posterior surface of propodeum usually with lateral vertical carina extending only partway to summit, or, if attaining summit, then usually not extending mesad across upper margin, so that there is usually no carina between basal area and posterior surface, i.e., so that basal area is usually not enclosed; body commonly smaller, sometimes metallic *L. (Dialictus)*
- 2(1). Females 3
- Males (unknown for *Pseudochilalictus*) 9
- 3(2). Apical labral process triangular (Fig. 66-13a, b), widest at base, tapering to pointed apex, apex usually simple except for being keeled (two keels in a few *Parasphcodes*, process broadened preapically in a few *Ctenonomia*) (basitibial plates usually rather elongate and pointed apically) 4
- Apical labral process broadened so that it does not taper uniformly to a pointed apex (Fig. 66-13c-f), lateral margins often pectinate, toothed, elevated, or otherwise modified 7
- 4(3). Inner hind tibial spur finely serrate, ciliate, or essentially simple (Fig. 66-13a, b) 5
- Inner hind tibial spur pectinate with a few coarse teeth (coarsely serrate in a few species) 6
- 5(4). Metasomal terga black with broad basal bands of tomentum; teeth of inner margin of inner hind tibial spur about half as long as diameter of spur *L. (Pseudochilalictus)*
- Metasomal terga red or black, metallic green in one species, without tomentum; teeth of inner hind tibial spur shorter *L. (Parasphcodes)*
- 6(4). Propodeum with triangle smooth, basal area not margined; thorax partially or wholly red or testaceous; metasomal terga without basal bands of tomentum *L. (Callalictus)*
- Propodeum with triangle variously roughened, basal area often margined by a carina; thorax black; metasomal terga usually with tomentum basally or basolaterally *L. (Ctenonomia)*
- 7(3). Inner hind tibial spur of female pectinate; glossa two-thirds as long as face; margin of labral process of female simple (Fig. 66-13c) *L. (Glossalictus)*
- Inner hind tibial spur of female not pectinate; glossa little more than one-half as long as face; margin of labral process of female variously modified 8
- 8(7). Inner hind tibial spur with a large tooth followed by a wavy margin (Figs. 66-13d, e), tooth in some cases reduced so that margin is almost simple, rarely a second tooth developed sufficiently that spur is almost pectinate; eyes usually bare, but in some cases with rather long hairs *L. (Chilalictus)*
- Inner hind tibial spur very finely serrate or ciliate, thus essentially simple; eyes with a few short hairs *L. (Australictus)*
- 9(2). Basitibial plate present in all but a very few species; mostly small to moderate-sized species (4.5-9.0 mm long, uncommonly to 12 mm); eyes bare 10
- Basitibial plate absent; large to moderate-sized species (8-11 mm long, uncommonly only 5.5 mm); eyes (except in some *Callalictus*) with scattered, very short hairs 13
- 10(9). Glossa two-thirds as long as face or longer 11
- Glossa about one-half as long as face 12
- 11(10). Glossa about two-thirds as long as face, which is broader than long *L. (Glossalictus)*
- Glossa longer than face, which is longer than broad *L. (Ctenonomia)* (in part)
- 12(10). Gonostylus less than half as long as gonocoxite (males of Australian species not available) *L. (Ctenonomia)* (in part)

Key to the Subgenera of *Lasioglossum* of the Australian Region

1. Second submarginal crossvein in both sexes narrower than first (as in Fig. 66-6c); small (less than 7 mm long); inner hind tibial spur of female ciliate, essentially simple, or in some cases bearing a few large oblique teeth (body dull, nonmetallic) (*Hemihalictus* series) *L. (Austrevylaeus)*
- Second submarginal crossvein as strong as first (as in Fig. 66-6a); if body less than 7 mm long, then inner hind tibial spur of female pectinate with one to several large teeth, teeth usually not so sloping or oblique as in the above (*Lasioglossum* series) 2

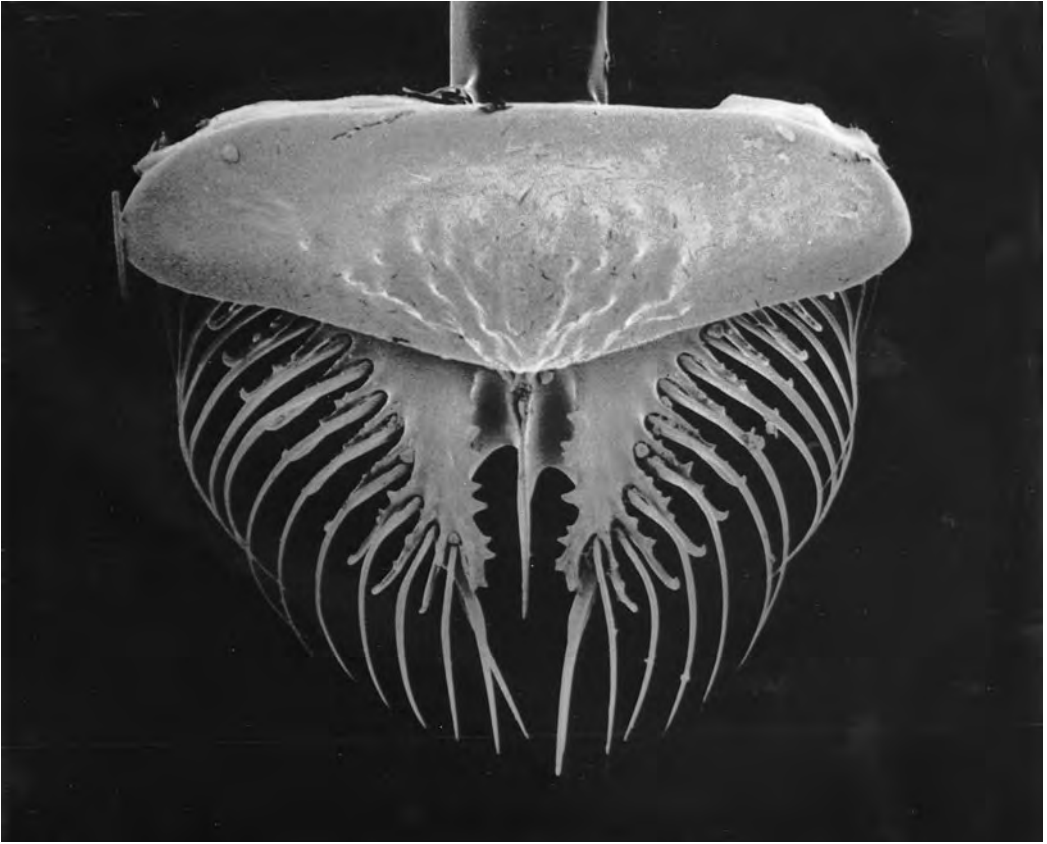


Figure 66-14. The most elaborate labral type among bees: the female of *Lasioglossum (Chilalictus) mirandum* (Cockerell). The function of the pectinations, or indeed of the whole labral process, is unknown. SEM photograph by Kenneth Walker.

- . Gonostylus more than half as long as gonocoxite (except in *L. idoneum* Cockerell), in some cases as long as gonocoxite *L. (Chilalictus)*
- 13(9). Gonostylus almost absent or at most short and triangular *L. (Australictus)*
- . Gonostylus distinct and longer than broad (metasomal terga without basal bands of tomentum) 14
- 14(13). Propodeal triangle smooth, basal area not margined; thorax partly or wholly red or testaceous *L. (Callalictus)*
- . Propodeal triangle roughened, basal area usually defined; thorax black *L. (Parasphcodes)*

***Lasioglossum* / Subgenus *Acanthalictus* Cockerell**

Acanthalictus Cockerell, 1924a: 184. Type species: *Halictus dybowskii* Radoszkowski, 1877, by original designation.

The tridentate female mandibles are unique in the genus. The body is nonmetallic, 9 to 12 mm long. The inner hind tibial spur of the female is finely serrate. The metasoma lacks hair bands, but the bases of T2 and T3 have very scattered bits of white tomentum.

■ This subgenus is known only from Siberia. The two species names are likely to represent queens and workers of a single social species, *Lasioglossum (Acanthalictus) dybowskii* (Radoszkowski).

Acanthalictus is likely to be a derivative of *Eurylaeus*; if so, it should be included in that subgenus.

***Lasioglossum* / Subgenus *Australictus* Michener**

Lasioglossum (Australictus) Michener, 1965b: 165. Type species: *Halictus peraustralis* Cockerell, 1904, by original designation.

In its size (length 7–10 mm), form, long male antennae, serrate inner hind tibial spur of the female, and genital structure, this subgenus resembles *Parasphcodes*. It differs from that subgenus in the blunt or truncated apex of the apical labral process of the female, the basal tomentum (sometimes weak) on the metasomal terga, and the short, broad, scarcely recognizable male upper gonostylus. The lower gonostylus is a strong retrorse lobe, as in many related bees. The male genitalia, labrum, and other structures were illustrated by Michener (1965b). ■ This subgenus occurs from Tasmania and South Australia to northern Queensland. Eleven specific names are listed by Michener (1965b).

As explained by Michener (1965b), *Australictus* and *Parasphcodes* almost merge and there may be no reason to maintain *Australictus* as a distinct subgenus.

to subgenera below separates groups that should have generic status, but characters distinguishing the males are unknown.

A feature especially noticeable in the subgenus *Pachyhalictus* is the area of short, nearly erect hairs on the distal half of the hind tibia of the female, this area separated from the rest of the external tibial surface by a slight change in the plane of the surface below a diagonal line across the tibial surface (Fig. 66-19a). Such an area is also evident in *Patellapis* (*Archihalictus*) *joffrei* (Benoist), *carinostriata* (Pauly), etc., and in the genus *Homalictus*. *Pachyhalictus* and these species of *Archihalictus* have rather broad hind tibiae, widest apically. The area is recognizable but less distinct, without a noticeable difference in the plane of the surface but with evident differences in hairs, in forms like *P. (Dictyohalictus) plicata* (Pauly). In species with more slender hind tibiae (the distal half parallel-sided, instead of broadest at apex), such as *P. (D.) retigera* (Cockerell), the outer surface of the tibia is uniformly convex, and the area of short hairs is recognizable only because the hairs are nearly erect. The hairs are more sloping in *P. (Archihalictus) laevata* (Benoist) and *P. (Lomatalictus) malachurina* (Cockerell), and the area is completely unrecognizable on the slender tibia of *P. (A.) perineti* (Benoist). The area of short hairs is associated with large hairs on the lower tibial margin that are more or less erect and pectinate or palmate; see couplet 1 in the key to subgenera. In such subgenera as *Zonalictus* these large pectinate hairs are evident even though the area of short, erect hairs is commonly not recognizable. The scopal hairs of the hind femur and, when developed, those of the sterna, tend to be plumose (i.e., with a central rachis and short branches in all directions along the rachis), although in the subgenus *Archihalictus* and in other genera, such as *Lasioglossum* or *Halictus*, they have a few long branches, and in *Lasioglossum* and *Halictus* the central rachis may not be readily recognizable. Plumose scopal hairs, like several other features listed above, are best developed in the subgenera having pectinate or palmate hairs on the lower margin of the hind tibia as well as the area of short hairs on the outer surface of the tibia. The inner hind tibial spur, which in many halictines is a group character, is variable within several of the subgenera of *Patellapis*, as indicated below.

Key to the Subgenera of *Patellapis*

1. Posterior tibia of female with fringe of long, pectinate to palmate hairs along basal two-thirds of lower margin, these hairs not curved strongly posteriorly toward apex of tibia or upward across outer surface of tibia, but *if* pectinate, then branches close together (thus approaching palmate) and tending to be at right angles to rachis; intermediates between large hairs of lower tibial margin and hairs of outer tibial surface very few; metasomal terga frequently with basal areas of pale tomentum, without strong apical hair bands (except in *Lomatalictus*) 2
- Posterior tibia of female with long hairs of lower margin strongly curved posteriorly toward apex of tibia, or distal parts usually curved upward across outer surface of tibia, with well-separated long branches directed in same general direction as rachis, or usually branched in such a way that the rachis is not identifiable except basally; distal

- parts of long marginal hairs overlapping hairs of outer tibial surface, and intermediate hair types seemingly present, thus there is no striking superficial contrast between long hairs of lower margin and hairs of outer surface (this is as in *Lasioglossum* and *Halictus*); metasomal terga without basal bands or lateral areas of tomentum, frequently with apical bands of pale hairs 6
- 2(1). Metasomal terga with apical hair bands, without basal bands or lateral areas of tomentum; claws of female simple or with inner tooth very small, those of male with teeth close together (S4 of male unmodified) (Africa)
..... *P. (Lomatalictus)*
 - Metasomal terga without strong apical hair bands, frequently with basal areas of pale tomentum; claws of both sexes toothed, as usual in halictines 3
 - 3(2). Posterior margins of terga, especially T1 to T3, bare, nearly always contrastingly white, yellow, greenish, or bluish (Africa, Arabia) *P. (Zonalictus)*
 - Posterior margins of terga brownish or translucent, commonly with weak or very weak apical hair bands 4
 - 4(3). Scutum and scutellum smooth or minutely roughened to coarsely striate, with punctures well separated at least in some areas; metasomal terga without areas of pale tomentum (ignoring pale hairs arising from graduli); S4 of male similar in size and shape to S3 and S5, without very large bristles (Madagascar) *P. (Archihalictus)*
 - Scutum and scutellum coarsely and closely punctate or punctures usually so large that surface is coarsely reticulate, rarely, as in *Pachyhalictus* (*Pachyhalictus*) *binghami* (Kirby), with partly smooth areas; metasomal terga (at least T2 and T3) with basal areas of pale tomentum, sometimes expanded to cover whole terga; S4 of male short, largely hidden, with a few large apical or preapical bristles 5
 - 5(4). Inner hind tibial spur of female pectinate with three to six long teeth; basitibial plate of male absent or indicated only at apex; S4 of male not produced posteriorly at side but with an enormous and complex lateral bristle, usually hidden by T4 (Fig. 66-20c); first two hind tarsal segments of male fused (Oriental to Australia)
..... *P. (Pachyhalictus)*
 - Inner hind tibial spur of female serrate or pectinate with ten or more teeth; basitibial plate of male present; S4 of male produced posteriorly at side with several large bristles usually hidden by T4; first two hind tarsal segments of male apparently articulated, but articulation broader than that between subsequent tarsomeres (Africa)
..... *P. (Dictyohalictus)*
 - 6(1). Terga with conspicuous apical hair bands; basitibial plate margined both in front and behind, its apex in female usually rounded (Africa) *P. (Patellapis s. str.)*
 - Terga without or with weak apical hair bands; basitibial plate not or incompletely defined on anterior margin, its apex in female angulate or pointed (Africa)
..... *P. (Chaetolictus)*

Patellapis / Subgenus *Archihalictus* Pauly

Archihalictus Pauly, 1984b: 132. Type species: *Halictus joffrei* Benoist, 1962, by original designation.

Madagalictus Pauly, 1984b: 125. Type species: *Halictus suarezensis* Benoist, 1962, by original designation.

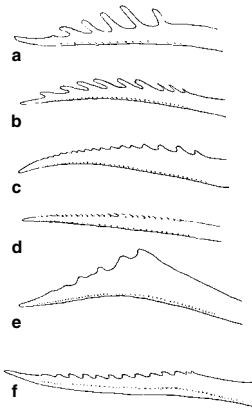


Figure 66-21. Inner hind tibial spurs of females of *Patellapis* and *Thrinchostoma*. **a**, *P. (Chaetalictus) pearstonensis* (Cameron); **b**, *P. (Zonalictus) partita* (Cockerell); **c**, *P. (Z.) albofasciata* (Smith); **d**, *P. (Z.) zacephala* (Cockerell); **e**, *T. (Thrinchostoma) afasciatum* Michener; **f**, *T. (Eothrinchostoma) productum* (Smith). From Michener, 1978a.

apical bands, at least laterally, on the metasomal terga. A paraocular lobe is well developed, extending down into the clypeus. The apical tergal bands, the lack of basal tergal tomentum, and the paraocular lobes are among the principal differences from the closely related genus *Ruizantheda*. Male genitalia, sterna, and other structures were illustrated by Moure and Sakagami (1984) and Cure (1989). For most *Pseudagapostemon* the bare or nearly bare eyes further differentiate the genus from *Ruizantheda*, which has long hair on the eyes. The subgenus *Brasilagapostemon*, however, has hairy eyes.

The species *Pseudagapostemon amabilis* and *cyanomelas*, attributed to Moure by Cure, were in fact first described by Cure (1989), who appears to have been responsible for the descriptions and figures.

Pseudagapostemon (Neagapostemon) cyanomelas Cure makes communal nests in earth banks; several females use the same nest entrance, and long laterals lead to cells far from the main burrow (Michener and Lange, 1958d, *P. perzonatus* Cockerell, misidentification). *P. (Pseudagapostemon) brasiliensis* Cure nests in flat ground, four females in the one nest studied; cells are close to the main burrows (Martins, 1993).

Key to the Subgenera of *Pseudagapostemon*

1. Eyes conspicuously hairy; malar area of male about one-third as long as second flagellar segment (Brazil) *P. (Brasilagapostemon)*
- Eyes nearly bare; malar area of male usually one-fifth as long as second flagellar segment or less 2
- 2(1). Clypeus usually with longitudinal median elevation or carina, and, in males, fine striae lacking or not converging on midline *P. (Neagapostemon)*
- Clypeus without longitudinal median ridge or carina except sometimes at uppermost end of clypeus, and, in males, with fine oblique striae converging downward to midline of clypeus *P. (Pseudagapostemon s. str.)*

Pseudagapostemon / Subgenus *Brasilagapostemon* Moure and Sakagami

Pseudagapostemon (Brasilagapostemon) Moure and Sakagami, 1984: 4. Type species: *Pseudagapostemon fluminensis* Schrottky, 1911, monobasic.

In addition to having hairy eyes, *Brasilagapostemon* differs from other subgenera in having a relatively broad head, the eyes strongly converging below. The male gonostyli are simple and rather broad.

■ This subgenus is known from Minas Gerais to Paraná, Brazil. The three species were revised by Cure (1989).

Pseudagapostemon / Subgenus *Neagapostemon* Cure

Pseudagapostemon (Neagapostemon) Cure, 1989: 295. Type species: *Pseudagapostemon cyanomelas* Cure, 1989, by original designation.

This subgenus includes nonmetallic species as well as species with the greenish or bluish tints usual to the genus. Aside from the median clypeal ridge, there are few common characters for this subgenus, and it may be an artificial assemblage of odd species of *Pseudagapostemon*. S4 of the males varies from unmodified in *P. cyanomelas* Cure to deeply emarginate, and in *P. jenseni* (Friese) it supports large lateral bristles and a series of marginal bristles reminiscent of some *Patellapis* species. The male gonostyli also are very diverse, as illustrated by Cure (1989).

■ *Neagapostemon* occurs from Mendoza and Buenos Aires provinces, Argentina, north to São Paulo, Brazil. The six species were revised by Cure (1989).

Pseudagapostemon / Subgenus *Pseudagapostemon* Schrottky s. str.

Pseudagapostemon Schrottky, 1909a: 145. Type species: *Agapostemon arenarius* Schrottky, 1902, by original designation.

The median clypeal ridge mentioned in the key to subgenera is weak or absent in *Pseudagapostemon* s. str. The convergent striae are part of the fine roughening of the clypeal surface; much coarser punctures, also present on the clypeus, interrupt the microstriae. A digitiform process arising at the base of the male gonostylus is characteristic of this subgenus, according to Cure (1989).

■ *Pseudagapostemon* s. str. ranges from the state of Pará, Brazil, south to the province of Río Negro, Argentina; one species is found in Chile from Aconcagua to Valdivia. The 16 species were revised by Cure (1989).

Genus *Ptilocleptis* Michener

Ptilocleptis Michener, 1978b: 315. Type species: *Ptilocleptis tomentosa* Michener, 1978, by original designation.

This presumably parasitic group may be derived from *Sphecodes*, but it has a number of characters that are probably plesiomorphic relative to *Sphecodes*, so that it may be a basal branch of the *Sphecodes* clade. Such characters include the moderate punctuation, without the coarse pitting found in *Sphecodes*; the face not broad as is usual in *Sphecodes*, the eyes being convergent below (Fig. 66-3c)

gonostylus is large and somewhat retrorse. The genitalia, sterna, and other structures were illustrated by Sakagami, Kato, and Itino (1991).

■ The genus has been found in Israel, islands of the Aegean Sea, Turkey, Iran, and Armenia. There is one species, *Thrincohalictus prognathus* (Pérez).

Genus *Thrinchostoma* Saussure

This is a genus of relatively large (length 8-16 mm), elongate bees. They are nonmetallic, black or with parts of the metasoma and even the whole body yellowish red. The clypeus is strongly produced downward and strongly protuberant forward. The malar area is distinct but variable, from less than one-third as long as wide to four times as long as wide, and as long as or longer than the eye. The paraocular lobe is strongly produced down into the clypeus. Both of the recurrent veins usually enter the third submarginal cell. The hind tibial spur of the female is finely to coarsely serrate or the margin is almost undulate. The hind tibia of the male has a broad yellowish enlargement that carries the tibial spurs. S4 of the male is usually shortened, largely hidden by S3, but the lateral parts extend far posteriorly on either side of a broad concavity. The dorsal gonostylus is large and rather elaborate, the ventral gonostylus erect or retrorse.

Strikingly distinct from most other Halictini, *Thrinchostoma* (with *Parathrinchostoma*) has been placed in a separate subtribe, Thrinchostomina; see Figure 61-4. The genus is found in southern Asia and in Africa, with an unusual concentration of species in Madagascar. The Asiatic species of *Thrinchostoma* were reviewed by Blüthgen (1926), the African and Malagasy species by the same author (1930, 1933). Various species have been described since those dates, however, as listed by Michener (1978a). Pauly (in Pauly et al., 2001) revised the twelve Madagascar species, all of which are in the typical subgenus.

Key to the Subgenera of *Thrinchostoma*
(Modified from Michener, 1978a)

- 1. Forewing without an area of dense hairs along second submarginal crossvein, this vein simple and straight; first submarginal crossvein arising far from base of vein r and margin of stigma; S4 of male with a series of enormous simple bristles arising from margin both medially under S3 and laterally, under the lateral extremity of T4, where the setae are largest (Africa)..... *T. (Eothrinchostoma)*
- Forewing with an area of dense hairs near median part of second submarginal crossvein, these hairs forming, in males, a conspicuous dark spot, this crossvein usually angulate or thickened medially, sometimes incomplete (not reaching marginal cell); first submarginal crossvein arising very near margin of stigma; S4 of male without coarse, specialized setae 2
- 2(1). Head extraordinarily produced below eyes, malar area nearly as long as or longer than eye, several times as long as wide (Fig 66-22b) *T. (Diagonozus)*
- Head only moderately produced below eyes, malar area much shorter than eye, three times as long as wide or less *T. (Thrinchostoma s. str.)*



Figure 66-22. Faces of unusual Halictini. **a**, *Urohalictus lieftincki* Michener, holotype male, from Michener, 1980; **b**, *Thrinchostoma (Diagonozus) lettoworbecki* Blüthgen, from Michener, 1978a.

***Thrinchostoma* / Subgenus *Diagonozus* Enderlein**

Diagonozus Enderlein, 1903: 35. Type species: *Diagonozus bicometes* Enderlein, 1903, monobasic.

The head in this subgenus is so elongate that the entire clypeus is below the lower ocular tangent (Fig. 66-22b). This construction provides space for folding an extremely long proboscis. The inner hind tibial spur of the female is as in *Thrinchostoma s. str.* The pronotum is longer than in the other subgenera, the collar medially being considerably longer than an ocellar diameter.



Figure 67-2. Cell cluster of *Pseudaugochlora sordicutis* (Vachal). **a**, Side view; **b**, Portion opened to show prepupae and pupae; **c**, Newer portion opened to show eggs and young larvae on food masses. Photos by C. D. Michener.

tween these two seemingly very distinct modes of construction is minimal. Cells built up in a space simply consist of cell linings. Exceptions to nests in soil occur in *Augochlora* s. str., which makes clumps of cells in rotting wood (Stockhammer, 1966), and *Megalopta*, which makes its cells, irregularly arranged, in rotting wood or vines (Sakagami, 1964). Many features of nest architecture were explained and illustrated by Sakagami and Michener (1962) and Eickwort and Sakagami (1979).

Cleptoparasitic Augochlorini are limited to the genus *Temnosoma* and one subgenus each of *Megalopta* and *Megommation*.

Key to the Genera of Augochlorini (Females)
(Modified from Eickwort, 1969b)

- 1. Proboscis extraordinarily slender, prementum 10 to over 20 times as long as broad (Fig. 67-4b); proboscoidal fossa about as wide as mandibular base 2
 - Proboscis not so slender (Fig. 67-4a, c-e), prementum four to eight times as long as broad; proboscoidal fossa much wider than mandibular base 6
- 2(1). Maxillary palpus much longer than stipes plus galea, reaching metasoma when mouthparts are in repose (basitibial plate moderately developed, much exceeding apex of femur, as in Fig. 67-5c) *Ariphanarthra*
 - Maxillary palpus not greatly lengthened 3
- 3(2). Eye greatly enlarged, projecting above vertex (Fig. 67-

- 7b), separated from lateral ocellus and from vertical part of epistomal suture above tentorial pit by one-fourth of ocellar diameter or less (basitibial plate not short, much surpassing apex of femur; ocelli much enlarged)
 - *Megaloptidia*
- Eyes not projecting above vertex, widely separated from lateral ocellus and from epistomal suture above tentorial pit (Fig. 67-6, 67-13g) 4
- 4(3). Pronotal dorsal surface swollen, dorsolateral angle and vertical ridge below angle absent; paraocular lobe long, lower end acute (Fig. 67-13a, b); head elongated, owing to greatly lengthened clypeus; inner hind tibial spur serrate *Chlerogelloides*
 - Pronotal dorsal surface normal, not swollen; paraocular lobe approximately right-angular (Fig. 67-7a); head not greatly elongated; inner hind tibial spur pectinate or serrate 5
- 5(4). Basitibial plate very short, scarcely surpassing apex of femur *Megommation*
 - Basitibial plate moderately developed (ocelli small; inner hind tibial spur serrate) (placed here on the basis of the description; I have seen no specimens)
 - *Micrommation*
- 6(1). Inner hind tibial spur serrate, teeth shorter than wide, pointed or rounded, or margin of spur undulate or ciliate (Fig. 67-5f, g, k-m) 7
 - Inner hind tibial spur pectinate, teeth longer than wide (Fig. 67-5h-j, n) 12
- 7(6). Scopa and median specialized area of T5 absent; integument coarsely punctate (Fig. 67-15); labral process truncate, without keel (Fig. 65-1i) *Temnosoma*
 - Scopa and median slit or notch and area of fine hairs on T5 present (Fig. 65-1k); integument rarely so coarsely punctate; labral process with strong median keel, usually pointed (Fig. 65-1a, e, g) 8
- 8(7). Inner hind tibial spur with rounded serrations (Fig. 67-5k-m); preoccipital ridge sharply angled or carinate .. 9
 - Inner hind tibial spur ciliate, with slender sharp teeth, as on outer spur, or with short, narrow teeth (Fig. 67-5f, g); preoccipital ridge sharply angled or rounded (epistomal suture forming obtuse paraocular lobe, Fig. 67-6a) 10
- 9(8). Epistomal suture forming acute paraocular lobe protruding into clypeus (Fig. 67-6d); clypeus relatively flat, green almost to apex; anterior angle of hypostomal carina usually a sharp right angle or produced into spine; apex of marginal cell narrowly truncate and usually appendiculate (Fig. 67-1a) *Augochlora*
 - Epistomal suture forming obtuse or right angle laterally (Fig. 67-6c); clypeus beveled, area below angle not green; anterior angle of hypostomal carina rounded; apex of marginal cell acute or very narrowly truncate
 - *Augochllorella*
- 10(8). Basal area of propodeum completely smooth or granular, without striae; eyes deeply emarginate (Fig. 67-6a) (preoccipital ridge gradually rounded)
 - *Corynura* (*Corynura*)
- Basal area of propodeum roughened or with weak plicae basally; eyes moderately emarginate 11
- 11(10). Preoccipital ridge sharply angled; mesoscutum strongly narrowed anteriorly, lip high and sharply angled; labral basal elevation suborbiculate *Paroxystoglossa*

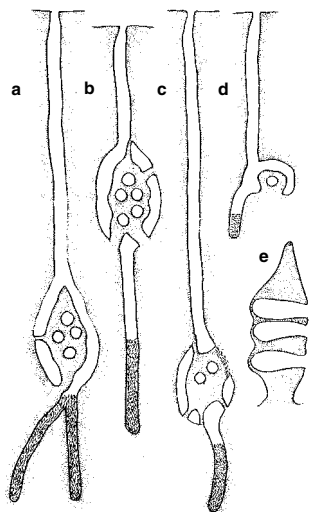


Figure 67-3. Nests of *Paroxystoglossa jocasta* (Schrottky) with cell clusters constructed of soft earth by the bees. **a, b**, Two normal nests; **c, d**, Other nests with abnormal or incomplete clusters. **e**, Sectional view of a cell cluster. From Sakagami and Michener, 1962.

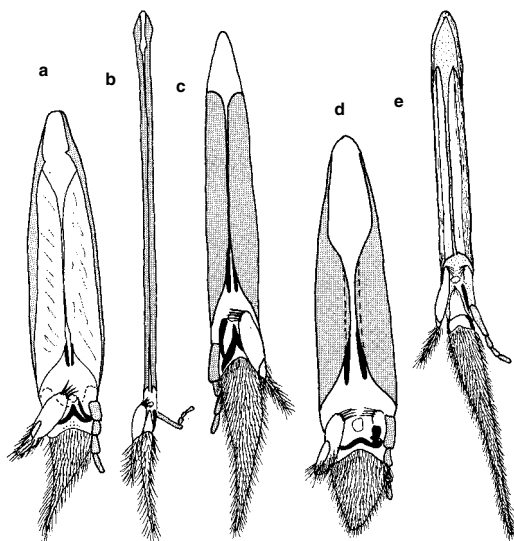


Figure 67-4. Labia (mentum and lorum omitted) of Augochlorini, each with one palpus and one paraglossa omitted. **a**, *Temnosoma smaragdinum* Smith; **b**, *Ariphanaethra palpalis* Moure; **c**, *Augochlora pura* (Say); **d**, *Corynura chilensis* (Spinola); **e**, *Pseudaugochlora graminea* (Fabricius). From Eickwort, 1969b.

- Preoccipital ridge rounded; mesoscutum very slightly narrowed anteriorly, lip low and rounded; labral basal elevation transverse *Megaloptilla*
- 12(6). Inner hind tibial spur closely pectinate with about ten teeth (Fig. 67-5n) (basitibial plate defined posteriorly but anterior margin evanescent) 13
- Inner hind tibial spur with not over six teeth, well-separated 14
- 13(12). Preoccipital carina strong, even almost lamella-like; apex of marginal cell minutely truncate; basal area of propodeum about as long as scutellum *Caenaugochlora* (*Ctenaugochlora*)
- Preoccipital ridge rounded; apex of marginal cell pointed; basal area of propodeum about as long as scutellum and metanotum taken together (head at least as long as broad) *Chlerogella* (*Ischnomelissa*)
- 14(12). Malar area as long as wide or longer; head greatly elongate (Fig. 67-7e-g) 15
- Malar area much shorter than wide; head not greatly elongate (Fig. 67-6) 16
- 15(14). Pronotum convex dorsally, dorsolateral angle and vertical ridge below angle absent; paraocular lobe acute (Fig. 67-7e); scutellum normal; flagellum ten-segmented *Chlerogella* (*Chlerogella*)
- Pronotum normal in form; paraocular lobe right-angular (Fig. 67-7f, g); scutellum produced into two convexities; flagellum nine-segmented *Chlerogas*
- 16(14). Epistomal suture acutely angled laterally, forming strong paraocular lobe into clypeus (Fig. 67-7d); apical labral process broad, without coarse marginal bristles and with weak keel (Fig. 67-5a); mandible with preapical teeth on inner surface (Fig. 67-5o) (in addition to preapical tooth on upper margin) except in forms with reduced scopa 17
- Epistomal suture variously angled, not forming strong lobe; apical labral process with coarse marginal bristles, usually narrow and pointed apically, and with strong keel (Figs. 65-1a, e, g; 67-5b, c); mandible without teeth on inner surface (eyes and ocelli not enlarged) 18
- 17(16). Eyes and ocelli enlarged, ocellular distance thus equal to or less than ocellar diameter (Fig. 67-7d, 67-13d); hamuli in a closely packed series (Fig. 67-1b); hind tibia covered with amber setae *Megalopta*
- Eyes and ocelli not enlarged, ocellular distance twice ocellar diameter or more; hamuli in series broken by gaps (as in most other Augochlorini), some hooks thus isolated; hind tibia and basitarsus largely covered with black setae *Xenochlora*
- 18(16). Tegula with inner posterior angle produced mesally, forming an emargination in the posterior part of the mesal tegular margin (Fig. 67-5t); basitibial plate very short, poorly defined, extending barely past apex of femur (Fig. 67-8a); labrum with distal process expanded and rounded, as broad as body of labrum (Fig. 65-1g), distal keel projecting beyond apex (pronotal dorsal ridge between lateral angle and pronotal lobe lamellate, forming flange from lateral angle to lobe) *Augochloropsis*
- Tegula with posterior end rounded; basitibial plate not short (Fig. 67-5q, r) [except in *Corynura* (*Callistochlora*) (Fig. 67-5p)]; labrum with distal process usually more slender and pointed (Figs. 65-1a, e; 67-5b, c), but may be expanded distally 19
- 19(18). Pronotal dorsal ridge lamellate, forming flange from dorsolateral angle to pronotal lobe (scutum strongly produced over pronotum, usually forming carinate or lamellate flange) 20
- Pronotal dorsal ridge not lamellate 21
- 20(19). Vertex swollen behind ocelli; clypeus usually armed

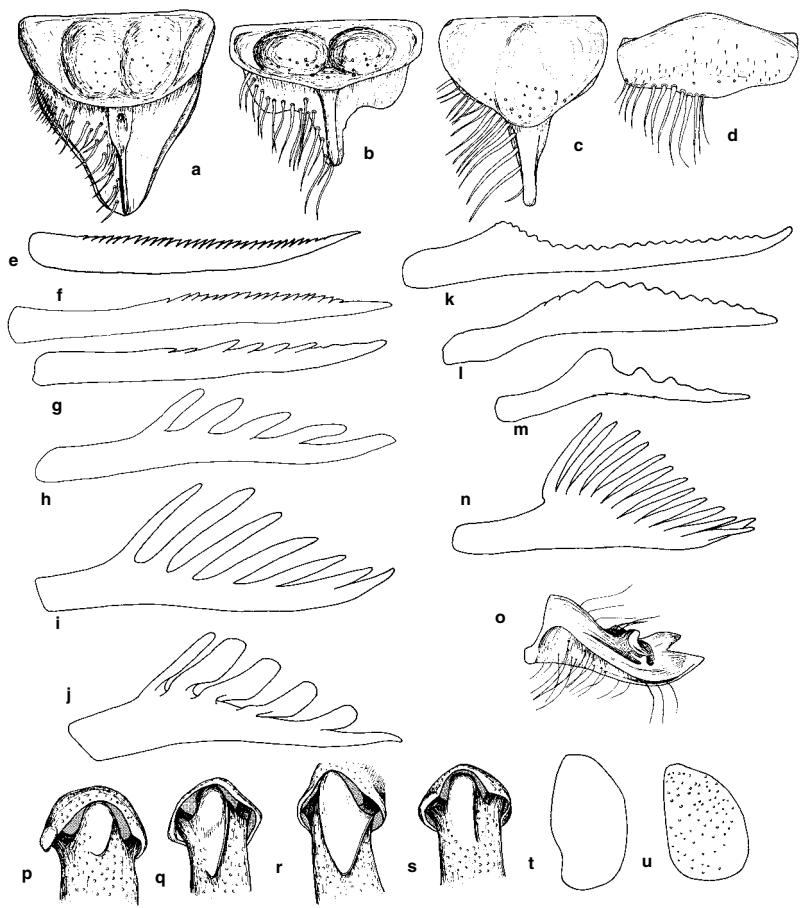


Figure 67-5. Structures of Augochlorini. **a**, Labrum of female, *Megalopta genalis* Meade-Waldo; **b**, Labrum of female, *Rhinocorynura briseis* (Smith); **c**, **d**, Labra of female and male, *Neocorynura pubescens* (Friese). (For labra of other Augochlorini, see Figure 63-1.)

e-n, Inner hind tibial spurs of females: **e**, *Temnosoma smaragdinum* Smith; **f**, *Corynura (Corynura) chilensis* (Spinola); **g**, *C. (C.) corynogaster* (Spinola); **h**, *C. (Callistochlora) chloris* (Spinola); **i**, *Augochloropsis ignita* (Smith); **j**, *Megalopta genalis* Meade-Waldo; **k**, *Augochlora nigrocyanea* (Cockerell); **l**, *Augochlorella (Ceratalictus) theia* (Schrottky); **m**, *Augochlorella (Pereirapis) sp.*; **n**, *Caenaugochlora (Ctenaugochlora) perpectinata* (Michener).

o, Inner view of female mandible of *Megalopta genalis* Meade-Waldo, showing tooth on inner surface; such modifications are characteristic of wood-nesting Augochlorini.

p-s, Basitibial plates of females: **p**, *Corynura (Callistochlora) chloris* (Spinola); **q**, *Andinaugochlora micheneri* Eickwort; **r**, *Pseudaugochlora graminea* (Fabricius); **s**, *Megalopta genalis* Meade-Waldo.

t, u, Tegular outlines, mesal margins to the left: **t**, *Augochloropsis metallica* (Fabricius); **u**, *Temnosoma smaragdinum* Smith.

From Eickwort, 1969b.

with spines or median tubercle (Fig. 67-7h); basal area of propodeum smooth, usually depressed transversely; base of T1 normal *Rhinocorynura*
— Vertex not swollen; clypeus not armed; basal area of propodeum short, striate, completely covered with short, dense pile; T1 with basal enclosure formed by dense plumose hairs near petiole, usually containing large mites *Thectochlora*
21 (19). Pronotal dorsolateral angle produced, strongly carinate anteriorly and laterally behind angle, dorsal ridge not carinate behind dorsolateral angle, but vertical ridge below angle carinate (mesoscutum slightly produced

over pronotum, low and sharply angled; preoccipital ridge rounded) *Rhectomia*
— Pronotal dorsolateral angle not strongly carinate anteriorly, if produced, then dorsal ridge carinate 22
22 (21). Epistomal suture forming right-angular or slightly acute paraocular lobe laterally (as in Fig. 67-6c), sometimes, as in *Andinaugochlora*, obtuse (about 100°) in laterofrontal view but not or scarcely obtuse in direct frontal view 23
— Epistomal suture forming distinctly obtuse angle laterally (Fig. 67-6a) 24
23 (22). Basitibial plate well-defined posteriorly, obsolescent

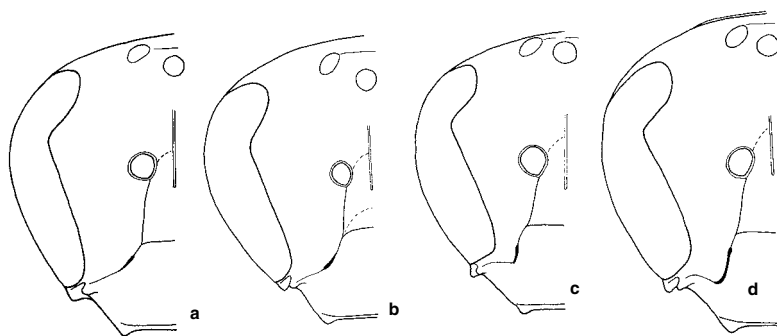


Figure 67-6. Faces of female Augochlorini. **a**, *Corynura chilensis* (Spinola); **b**, *Augochloropsis metallica* (Fabricius); **c**, *Augochlorella striata* (Provancher); **d**, *Augochlora pura* (Say). The paraocular lobe is progressively developed from b to d. From Eickwort, 1969b.

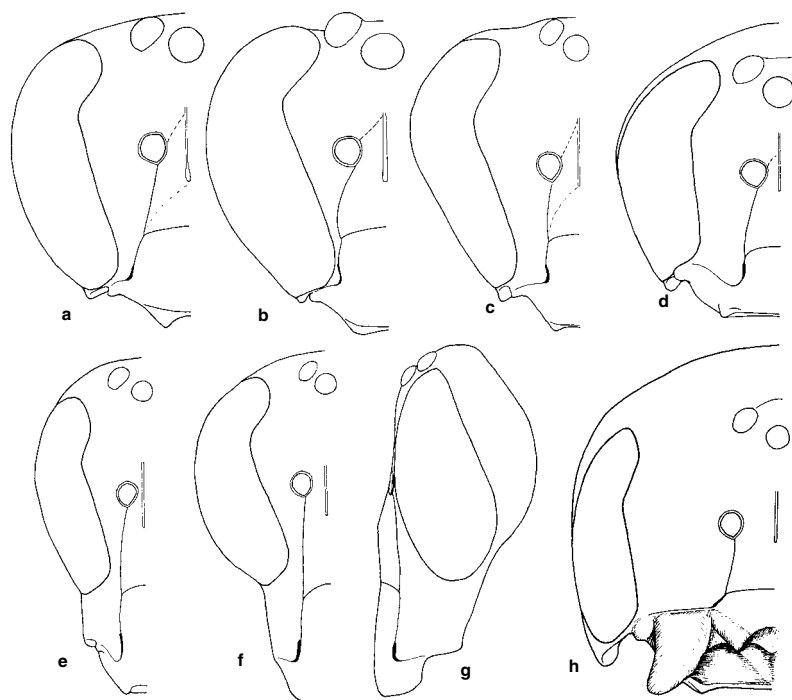


Figure 67-7. Faces of Augochlorini, females except for figures f and g. **a**, *Megommation insigne* (Smith); **b**, *Megaloptidia ? contradicta* (Cockerell); **c**, *Aripthartha palpalis* Moure; **d**, *Megalopta genalis* Meade-Waldo; **e**, *Chlerogella elongaticeps* Michener; **f, g**, *Chlerogas hirsutepennis* Cockerell, male; **h**, *Rhinocorynura inflaticeps* (Ducke). Note the well developed malar areas in e to g. From Eickwort, 1969b.

- anteriorly (Fig. 67-5q); pronotal dorsolateral angle not produced, obtuse; eye hairs short *Andinaugochlora* (*Andinaugochlora*)
- Basitibial plate well-defined on all edges (Fig. 67-5r); pronotal dorsolateral angle frequently produced, sometimes obtuse; eye hairs frequently long 29
- 24(22). Preoccipital ridge carinate or lamellate; mesoscutum *usually* narrowed anteriorly and anterior mesoscutal lip *usually* narrow, high, projecting forward and sharply angled; pronotal dorsolateral angle *usually* strongly produced, lateral ridge carinate or lamellate; propodeum *usually* narrowed posteriorly *Neocorynura*
- Preoccipital ridge rounded; mesoscutum not narrowed anteriorly, the mesoscutal lip *usually* not high or narrow; pronotal dorsolateral angle *usually* not produced, lateral ridge sharply angled or rounded; propodeum not narrowed posteriorly 25
- 25(24). Head, mesosoma, and metasoma brilliant green or orange or coppery; propodeal basal area weakly striate ..26
- Head and mesosoma dull metallic green or blue, black, or brownish; metasoma variously colored but not brilliant green; propodeal basal area smooth or roughened 28
- 26(25). Eyes with long hair; basitibial plate defined only posteriorly, very short (Fig. 67-5p) *Corynura* (*Callistochlora*)
- Eyes with short hair; basitibial plate well defined on all edges, of normal length 27
- 27(26). Pronotal dorsal ridge strongly carinate; marginal cell with apex acute; body length approximately 7 mm *Augochlorodes*
- Pronotal dorsal ridge rounded, not carinate; marginal cell with apex minutely rounded and appendiculate; body length 11.5-12.0 mm *Andinaugochlora* (*Neocorynurella*)

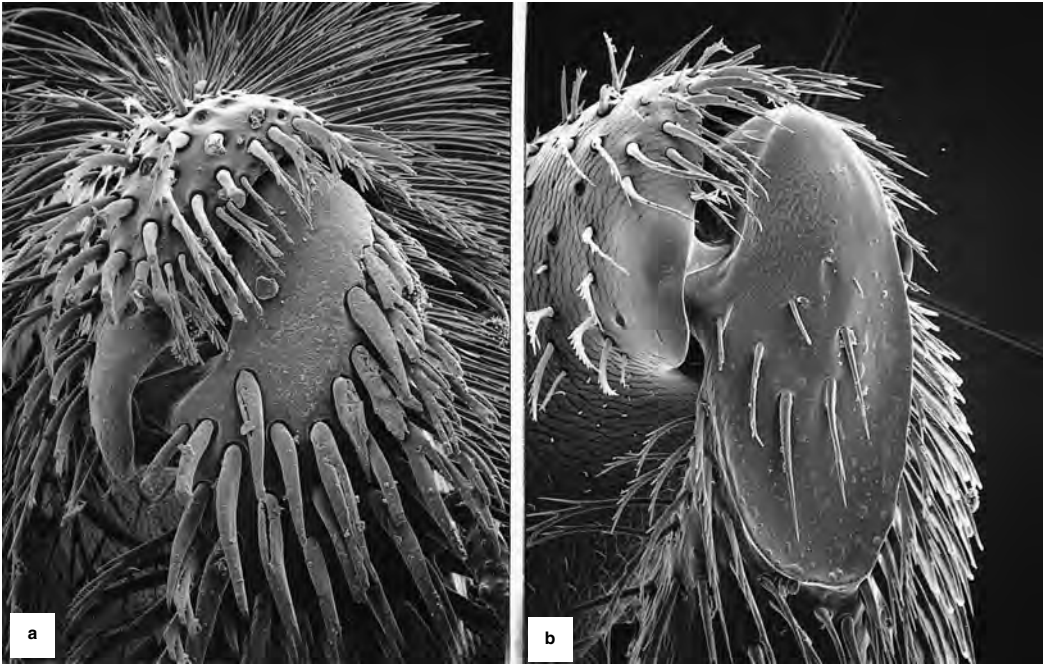


Figure 67-8. Apex of hind femur and basitibial plate of females. **a**, *Augochloropsis metallica* (Fabricius); **b**, *Augochlora pura* (Say). From Michener, McGinley, and Danforth, 1994.

- 28(25). Basal area of propodeum roughened; length 5-6 mm [body dull metallic, suggesting that of *Lasioglossum* (*Dialictus*)] *Halictillus*
— Basal area of propodeum smooth or granular; length usually over 6 mm *Corynura* (*Corynura*)
29(23). Vertex produced to rounded ridge behind ocelli (Fig. 67-14a); preoccipital ridge rounded; galea of maxilla with apex pointed, well sclerotized; basal elevation of labrum with apical surface flattened, rimmed (Fig. 65-1b) *Pseudaugochlora*
— Vertex not produced; preoccipital ridge usually sharply angled or carinate; galea normal, with apical lobe; basal elevation of labrum without flattened distal surface *Caenaugochlora* (*Caenaugochlora*)

Key to the Genera of Augochlorini (Males)
(Modified from Eickwort, 1969b; males unknown for *Xenochlora*.)

1. Proboscis extraordinarily slender, prementum 10 to over 20 times as long as broad (Fig. 67-4b); proboscoidal fossa about as wide as mandibular base 2
— Proboscis not so slender, prementum four to eight times as long as broad (Fig. 67-4a, c-e); proboscoidal fossa much wider than mandibular base 6
2(1). Maxillary palpus much longer than stipes plus galea, reaching metasoma when mouthparts are in repose
..... *Ariphanarthra*
— Maxillary palpus not greatly lengthened 3
3(2). Eyes greatly enlarged, projecting above vertex, separated from lateral ocellus and from vertical part of epistomal suture above tentorial pit by one-fourth of ocellar diameter or less (Fig. 67-7b); S4 bilobed with deep median notch, the lobes strongly pilose (ocelli much enlarged) *Megaloptidia*

- Eyes not projecting above vertex, widely separated from lateral ocellus and epistomal suture above tentorial pit (Fig. 67-6); S4 not bilobed 4
4(3). Pronotal dorsal surface swollen; paraocular lobe long, acute; head elongate owing to greatly lengthened clypeus; middle femur sometimes greatly swollen and flattened *Chlerogelloides*
— Pronotal dorsal surface normal, not swollen; paraocular lobe approximately right-angular (Fig. 67-7a); head not greatly elongate; middle femur unmodified 5
5 (4). Propodial spiracle surrounded by patch of dense, plumose setae, or ocelli greatly enlarged, or labrial distal process present. *Megommation*
— Propodeal spiracle not surrounded by dense, plumose setae and ocelli not enlarged, and labrial distal process absent *Micrommation*
6(1). Malar area as long as wide or longer; head greatly elongate (Fig. 67-7e-g) 7
— Malar area much shorter than wide; head not greatly elongate 8
7(6). Pronotum convex dorsally, lateral angle a mere convexity and vertical ridge below angle absent; epistomal suture forming acute paraocular lobe laterally; scutellum normal; flagellum 11-segmented *Chlerogella* (in part)
— Pronotum normal; epistomal suture forming right angle laterally (Fig. 67-7f, g); scutellum produced into two large tubercles; flagellum 10-segmented *Chlerogas*
8(6). Tegula with inner posterior angle produced mesally (Fig. 67-5t); posterior margins of T1 and T2 frequently

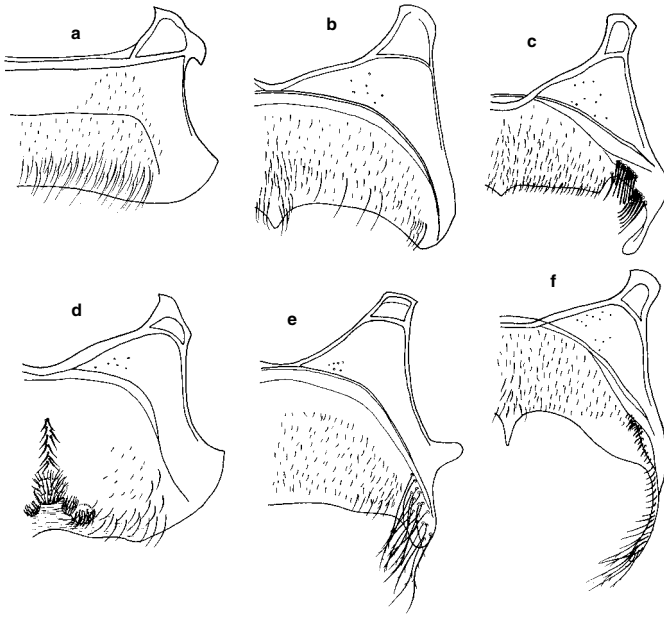


Figure 67-9. S4 of males of Augochlorini. **a**, *Augochlora pura* (Say); **b**, *Augochloropsis* (*Paraugochloropsis*) *chloera* (Moure), the species placed in *Glyptobasia* by Moure (1940, 1941a); **c**, *Augochloropsis* (*Augochloropsis*) *ignita* (Smith); **d**, *Caenauchochloa* (*Caenauchochloa*) *costaricensis* (Fries); **e**, *Augochlorodes turfaciens* Moure; **f**, *Augochloropsis* (*Paraugochloropsis*) *metallica* (Fabricius). From Eickwort, 1969b.

- each with a row of strong simple setae (pronotal dorsal ridge lamellate, forming flange from lateral angle to lobe; S4 usually with posterolateral appendage (Fig. 67-9c, f, but see also b), the appendage usually hidden or partly projecting from beneath T4; S4 posteriorly emarginate with median point; marginal cell truncate) *Augochloropsis*
- Tegula with posterior end rounded; posterior margins of T1 and T2 without rows of strong setae 9
- 9(8). S4 with conspicuous apical or median tufts of specialized setae (Fig. 67-14b) or strong cuticular ridges and depressions 10
- S4 usually not modified, apical margin at most emarginate or with usually hidden posterior lateral projections 13
- 10(9). Eyes and ocelli enlarged, ocellular distance usually less than ocellar diameter (Fig. 67-7d); S3 bilobed; S4 with posterior margin notched laterally, bilobed medially, and with median flap; pronotal dorsal ridge rounded and narrow, anterior edge of dorsolateral angle and vertical ridge below dorsolateral angle both carinate *Megalopta*
- Eyes and ocelli not enlarged (Fig. 67-6); S3 not strongly bilobed, sometimes medially emarginate; S4 not as above; pronotal dorsal ridge carinate or lamellate between dorsolateral angle and lobe, dorsolateral angle not strongly carinate on anterior margin, vertical ridge below dorsolateral angle variable 11
- 11(10). Pronotal dorsal ridge between dorsolateral angle and lobe, and anterior scutal lip, lamellate, forming flange; antenna long, scape less than 1.5 times length of flagellomere 2; S4 produced into caudally directed lateral processes bearing strong setae (usually hidden), posterior margin depressed and truncate, disc of S4 with median patch of short, erect, stout setae; S5 emarginate with long plumose pubescence *Thectochlora* (in part)
- Pronotum and scutum not lamellate; antenna of variable length, scape more than 1.5 times length of flagellomere 2; S4 and S5 not as above 12
- 12(11). Epistomal suture forming obtuse paraocular angle laterally (as in Fig. 67-6b); S4 without distinct median or posterior setal patches, posterior margin emarginate and centrally depressed and shiny, or with shiny median apical depression bordered by sharp ridges (S5 with median shiny depression usually bordered by strong ridges) *Paroxystoglossa*
- Epistomal suture forming right-angular paraocular lobe laterally; S4 with distinctive median or apical setal patches 28
- 13(9). Body very coarsely punctate; T1 to T3 strongly depressed basally (Fig. 67-15); T7 prolonged apically and bilobed *Temnosoma*
- Body not very coarsely punctate; T1 to T3 not strongly depressed basally (Fig. 67-11); T7 not prolonged or bilobed 14
- 14(13). Pronotal dorsal ridge lamellate from dorsolateral angle to lobe; scutum strongly produced over pronotum, the anterior lip usually carinate or lamellate 15
- Pronotal dorsal ridge not lamellate; scutum variable but anterior lip not carinate or lamellate 16
- 15(14). Vertex swollen above ocelli; basal area of propodeum smooth; S4 and S5 unmodified; scape more than twice length of second flagellar segment *Rhinocorynura*
- Vertex not swollen; basal area of propodeum striate; S4 produced into caudally directed lateral process bearing strong setae (usually hidden), posterior margin medially depressed and truncate, disc of S4 with a median patch of short, erect, stout setae; S5 emarginate, with long plumose pubescence; scape less than 1.5 times as long as second flagellar segment *Thectochlora* (in part)
- 16(14). Antenna very long, scape usually shorter than second flagellar segment, never more than 1.25 times length of that segment, which is usually subequal to or longer than preapical segment (preoccipital ridge rounded) 17

- Antenna of variable length, but scape over 1.25 times length of second flagellar segment, which is usually shorter than preapical segment 19
- 17(16). Basal area of propodeum about as long as scutellum and metanotum combined; propodeal pit narrow, not enclosed by V-shaped depression; paraocular lobe about right-angular; pronotal dorsal ridge not carinate; gonostylus not divided into dorsal and ventral gonostylar processes *Chlerogella* (*Ischnomelissa*) (in part)
- Basal area of propodeum about as long as scutellum alone; propodeal pit enclosed by V-shaped depression; paraocular lobe obtuse; pronotal dorsal ridge carinate; gonostylus divided to form dorsal and ventral gonostyli (dorsal gonostylus, however, present as a distinct setose ridge) 18
- 18(17). Metasoma elongate, not petiolate, dull metallic blue-green; body about 5 to 6 mm long; bridge of penis valves shifted apicad to level of apices of gonocoxites *Halictillus*
- Metasoma petiolate, first two segments long and narrow, or, if not, then body usually bright green or orange-green; body length usually over 6 mm; bridge of penis valves in usual position near level of middles of gonocoxites *Corynura*
- 19(16). Dorsolateral angle of pronotum produced and strongly carinate anteriorly and laterally (scutum slightly produced over pronotum; preoccipital ridge rounded) 20
- Dorsolateral angle of pronotum not strongly carinate anteriorly, if produced, then dorsal ridge between angle and lobe carinate 21
- 20(19). Mesoscutum weakly narrowed anteriorly; dorsal pronotal ridge between lateral angle and lobe carinate, vertical ridge below angle not carinate; apical margin of S5 unmodified *Megaloptilla*
- Mesoscutum broadly rounded anteriorly; dorsal pronotal ridge between lateral angle and lobe not carinate, vertical ridge below angle carinate; apical margin of S5 with weak median notch *Rhectomia*
- 21(19). Preoccipital ridge rounded 22
- Preoccipital ridge sharply angled or carinate 23
- 22(21). Basal area of propodeum smooth; S5 with dense clump of setae medially; S6 shallowly notched along apical margin; dorsal lobes of gonobase weakly defined; venter of penis valve without prong *Augochlorodes*
- Basal area of propodeum striate; S5 with scattered setae; S6 deeply notched along apical margin; dorsal lobes of gonobase strong; penis valve with ventral prong *Andinaugochlora* (*Neocorynurella*)
- 23(21). Epistomal suture forming distinctly obtuse lateral angle (as in Fig. 67-6b) 24
- Epistomal suture forming acute or right-angular paraocular lobe laterally (Fig. 67-6c, d), the lobe sometimes, as in *Andinaugochlora*, obtuse (about 100°) in laterofrontal view but nearly right-angular in direct frontal view 26
- 24(23). Antenna reaching about to scutellum, scape more than 2.5 times length of second flagellar segment, which is subequal to first; scutum not narrowed and not produced over pronotum (integument bright green; tibiae and tarsi orange) *Augochlorella* (*Ceratalictus*)
- Antenna long, frequently surpassing propodeum, scape less than 2.5 times length of second flagellar segment, which is longer than first, usually more than 1.5 times length of first; scutum usually narrowed and produced over pronotum 25
- 25(24). S4 and S5 depressed medially and shiny, posterior margin of S4 broadly emarginate (as in Fig. 67-9a); venter of head and mesosoma and lower surfaces of legs clothed with long plumose pubescence; metasoma not petiolate *Paroxystoglossa*
- S4 and S5 not modified; ventral surfaces without long plumose pubescence; metasoma frequently petiolate, S1 and S2 usually very long and narrow (compare with *Andinaugochlora*) *Neocorynura*
- 26(23). Antenna very long, surpassing propodeum; scape twice length of second flagellar segment or less; flagellum with plate areas containing only sensory plate-organs, these areas without setae; S6 strongly notched with deep concavities on either side of median notch *Andinaugochlora* (*Andinaugochlora*)
- Antenna of moderate length, usually not surpassing propodeum; scape over three times length of second flagellar segment; flagellum without specialized plate areas (rarely long and with plate areas in *Augochlora*); S6 without deep concavities on either side of median notch 27
- 27(26). Epistomal suture forming acute lateral angle or paraocular lobe protruding into clypeus (Fig. 67-6d); marginal cell truncate, usually appendiculate (Fig. 67-1a) *Augochlora*
- Epistomal suture forming right angle laterally (Fig. 67-6c); marginal cell acute, rarely very narrowly truncate *Augochlorella*
- 28(12). Apical flagellar segment tapering, hooked (Fig. 67-14c); preoccipital ridge rounded *Pseudaugochlora*
- Apical flagellar segment rounded; preoccipital ridge sharply angled or carinate *Caenaugochlora*

Genus *Andinaugochlora* Eickwort

This genus consists of bright metallic green or red, rather hairy bees, 8 to 10 mm long, often with brassy or blue reflections or a metallic red metasoma. They are probably related to *Neocorynura*, but differ in the lack of any pronotal or anterior scutal modifications and in the nonpetiolate metasoma of males. The paraocular lobe is 90° (or 100° in frontolateral view) to 135°, whereas in *Neocorynura* (also in *Paroxystoglossa*, a probable close relative) it is even more obtuse. As in some *Neocorynura* there is sometimes a weak galeal comb.

It is probable that relationships would be best indicated if *Andinaugochlora* and *Paroxystoglossa* were considered as subgenera of *Neocorynura*. A. Smith-Pardo, who has studied *Neocorynura* in detail, considers *Andinaugochlora* a basal branch (sister-group to the rest) of *Neocorynura* phylogeny.

Key to the Subgenera of *Andinaugochlora*

1. Preoccipital carina present although weak behind vertex; anterior margin of basitibial plate of female absent; paraocular lobe near right-angular (about 100°); penis valve without ventral prong *A. (Andinaugochlora s. str.)*
- Preoccipital carina absent; anterior margin of basitibial plate of female a distinct carina; paraocular lobe strongly obtuse (about 135°); penis valve with ventral prong *A. (Neocorynurella)*

***Andinaugochlora* / Subgenus *Andinaugochlora*
Eickwort s. str.**

Andinaugochlora Eickwort, 1969b: 407. Type species: *Andinaugochlora micheneri* Eickwort, 1969, by original designation.

The characters of the subgenus are indicated in the key to subgenera.

■ The subgenus is found in the mountains (2,500 m altitude or higher) of Venezuela, Colombia, Ecuador, and Peru. Two species have been described, but Eickwort (1969b) recognized three others. A Costa Rican species recently described (Engel and Smith-Pardo, 2004) is now considered to be a species of *Neocorynura* (A. Smith-Pardo, personal comm.).

***Andinaugochlora* / Subgenus *Neocorynurella* Engel**

Neocorynurella Engel, 1997, in Engel and Klein, 1997: 156.

Type species: *Neocorynurella seeleyi* Engel and Klein, 1997, by original designation.

Vachalius Moure, 1999b: 74. Type species: *Halictus cosmetor* Vachal, 1911, by original designation.

Although originally described as a genus, *Neocorynurella* seems to differ from *Andinaugochlora* only in the characters indicated in the key to subgenera.

■ *Neocorynurella* is known only from the Venezuelan Andes, at altitudes of 3,900 to 4,300 m for *Andinaugochlora seeleyi* Engel and Klein. Two species were distinguished by Engel and Klein (1997).

Genus *Ariphanarthra* Moure

Ariphanarthra Moure, 1951b: 137. Type species: *Ariphanarthra palpalis* Moure, 1951, by original designation.

This genus includes a bright blue-green species with extraordinarily long maxillary palpi and long and very narrow stipes and prementum (Fig. 67-4b). It is obviously a relative of *Megommation* but does not have the reduced female basitibial plate characteristic of that genus.

■ This genus occurs from Minas Gerais to Paraná in Brazil, and also in Paraguay and eastern Peru. The only species is *Ariphanarthra palpalis* Moure.

Genus *Augochlora* Smith

This genus consists of black to bright green, blue, or brassy bees of small to moderate size (length 5-11 mm). From similar forms, such as *Augochlorella*, it differs in its acute (but apically rounded) paraocular lobe protruding into the clypeus (Fig. 67-6d), the minutely truncate apex of the marginal cell (Fig. 67-1a), and the sharp angle or tooth at the bend of the hypostomal carina. Male genitalia were illustrated by Sandhouse (1937), as well as by Eickwort (1969b); see also Figure 67-10c, d.

Species found in the United States were revised by Sandhouse (1937).

The nests include clusters of more or less horizontal cells, or the cells are more scattered and excavated into the substrate. *Augochlora* s. str. builds in rotting wood (Stockhammer, 1966; Eickwort and Eickwort, 1973a), whereas the subgenus *Oxytroglossella* nests in the soil. At least some species of the latter subgenus have primitively social behavior with a worker caste (Michener and Lange, 1958a; Eickwort and Eickwort, 1972a; Sakagami and Moure, 1967). Their nests often have burrows that partly surround a cell cluster; this seems to be the first stage in forming isolated cell clusters. Another work on the nesting behavior of *Augochlora* s. str. is by Wcislo, Gonzalez, and Engel (2003).

Key to the Subgenera of *Augochlora*

1. Female: Mandible normal, preapical tooth not produced, far from apex of mandible; median area of T5 with long setae, not scale-like; S1 usually normal, rarely with slight median ridge or tooth; basitibial plate usually narrowly rounded, occasionally broadly rounded; basal elevation of labrum suborbicular. Male: Ventral gonostylus with long setae, greatly surpassing gonostylus *A. (Oxytroglossella)*
- Female: Mandible bidentate, preapical tooth and occa-

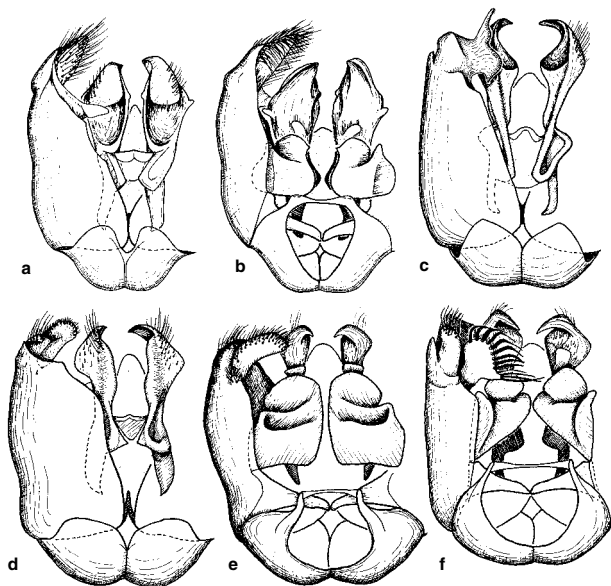


Figure 67-10. Male genitalia of Augochlorini, dorsal and ventral views. **a, b**, *Paroxystoglossa transversa* Moure; **c, f**, *Augochlorella striata* (Provancher); **d, e**, *Augochlora pura* (Say). See Figures 65-11, m, and 67-12 for genitalia of other augochlorines. From Eickwort, 1969b.

sionally outer ridge produced; median area of T5 with scale-like setae; S1 frequently with tooth or median ridge, sometimes unarmed; basitibial plate broadly rounded (Fig. 67-8b); basal elevation of labrum transverse. Male: Ventral gonostylus with short setae (Fig. 67-10d) *A. (Augochlora s. str.)*

Augochlora / Subgenus *Augochlora* Smith s. str.

Augochlora Smith, 1853: 73. Type species: *Halictus purus* Say, 1837, designated by Cockerell, 1923b: 448.

Oxytroglossa Smith, 1853: 83. Type species: *Oxytroglossa decorata* Smith, 1853, monobasic.

Augochlora Schrottky, 1901: 213, incorrect subsequent spelling (repeated) of *Augochlora* Smith, 1853.

Odontochlora Schrottky, 1909a: 141. Type species: *Augochlora mulleri* Cockerell, 1900, by original designation.

Augochlora (*Mycterochlora*) Eickwort, 1969b: 423. Type species: *Halictus repandirostris* Vachal, 1911, by original designation.

Mycterochlora is based on species of *Augochlora* having unusual derived characters; see Wcislo, Gonzalez and Engel (2003).

■ *Augochlora* s. str. is found from the province of Buenos Aires, Argentina, north through tropical South America (to Fernando Noronha off northeastern Brazil), Mesoamerica, and the Antilles; in North America, from Texas to Florida, north to Minnesota, USA, and Quebec, Canada. The species are particularly numerous in the moist tropics. Moure and Hurd (1987) recognized 86 species.

Augochlora / Subgenus *Oxytroglossella* Eickwort

Augochlora (*Oxytroglossella*) Eickwort, 1969b: 422. Type species: *Augochlora cordiaefloris* Cockerell, 1907, by original designation.

Augochlora (*Aethechlora*) Moure and Hurd, 1987: 275. Type species: *Augochlora matucanensis* Cockerell, 1914, by original designation.

This subgenus includes the more "ordinary" species of *Augochlora*. The female mandibles lack the characteristics presumably associated with nesting in rotting wood; nests are in the ground.

■ The range is from Buenos Aires Province, Argentina, north to southernmost Texas and Arizona, USA. Moure and Hurd (1987) listed 27 species.

Genus *Augochlorella* Sandhouse

This genus is understood here in a broader sense than in the past, to include the forms usually placed in *Ceratalictus* and *Pereirapis*. The three taxa are closely related; I believe the classification should serve to indicate relationships of such groups. The labrum of females has a broadly triangular elevated basal area in *Pereirapis* and a rounded, median elevation in the other subgenera, except that a small *Augochlorella* s. str., *A. edentata* Michener, is *Pereirapis*-like in labral structure. Most of the characters cited by Eickwort (1969b) to separate the three subgenera, however, do not intergrade; the three groups are quite distinctive, although sometimes, as a practical matter, difficult to separate without careful study and, for males, dissections.

Augochlorella consists of small (length 4.5–8.0 mm), bright green (Pl. 5), blue, or brassy species. They are common in the eastern and central United States and in Mesoamerica and can be distinguished from the superficially similar *Augochlora* most easily by the pointed rather than minutely truncate marginal cell. In South America they are less common.

Key to the Subgenera of *Augochlorella* (Females)

1. Epistomal suture forming obtuse paraocular lobe (as in Fig. 67-6b); inner hind tibial spur broadest near middle (Fig. 67-5l); basitibial plate poorly defined on anterior edge (preoccipital ridge carinate) *A. (Ceratalictus)*
- Epistomal suture forming right-angular or slightly obtuse paraocular lobe (Fig. 67-6c); inner hind tibial spur broadest at basal one-third to one-fifth; basitibial plate well defined on all edges 2
- 2(1). Inner hind tibial spur with few short, rounded teeth, basal tooth largest, forming broadest part of spur (Fig. 67-5m); basal area of propodeum strongly granular, striate basally; body length about 5 mm *A. (Pereirapis)*
- Inner hind tibial spur with rounded serrations, basal part broadened and serrate, i.e., not formed from a single tooth; basal area of propodeum not strongly granular; body length usually over 5 mm *A. (Augochlorella s. str.)*

Key to the Subgenera of *Augochlorella* (Males)

1. Epistomal suture forming obtuse paraocular lobe; dorsal gonostylus with long, narrow, hairless basal process extending mesad to midline *A. (Ceratalictus)*
- Epistomal suture forming right-angular paraocular lobe; dorsal gonostylus without such a mesal process 2
- 2(1). S4 broadly emarginate posteriorly, laterally bearing long, modified setae that are usually hidden; body length about 5 mm; inner lobe of ventral gonostylus without row of coarse setae *A. (Pereirapis)*
- S4 not broadly emarginate, without long lateral setae; body length usually over 5 mm; inner lobe of ventral gonostylus bearing marginal row of coarse, flattened setae (Fig. 67-10f) *A. (Augochlorella s. str.)*

Augochlorella / Subgenus *Augochlorella* Sandhouse s. str.

Augochlorella Sandhouse, 1937: 66. Type species: *Augochlora gratiosa* Smith, 1853, by original designation.

Oxytroglossidia Moure, 1943b: 473. Type species: *Oxytroglossidia uraniella* Moure, 1943 = *Oxytroglossa ephyra* Schrottky, 1911, by original designation.

Genitalia of this subgenus were illustrated by Sandhouse (1937) and by Eickwort (1969b); see Figure 67-10e, f.

■ This subgenus ranges from the province of Buenos Aires, Argentina, north through tropical and north-temperate America to Nova Scotia and Alberta, Canada, west to Utah and California, USA. It appears to be absent in the Antilles and in much of the Great Basin, the northwestern United States, and western Canada. Moure and Hurd (1987) listed 16 species. The species of America north of Mexico (with much information on the species in Mexico) were revised by Ordway (1966a). Coelho (2004) revised the subgenus *Augochlorella* s. str. She rec-

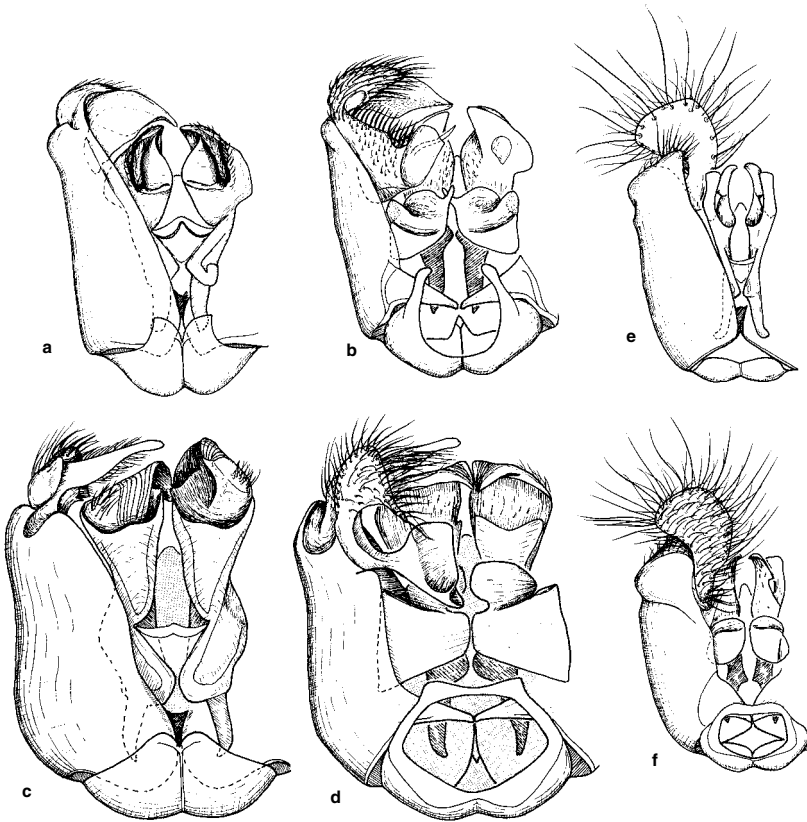


Figure 67-12. Male genitalia of Augochlorini, dorsal and ventral views. **a, b**, *Augochloropsis* (*Paraugochloropsis*) *metallica* (Fabricius); **c, d**, *Megalopta genalis* Meade-Waldo; **e, f**, *Temnosoma smaragdinum* Smith. From Eickwort, 1969b.

Nests are in the soil and include clusters of vertical cells opening into a common space usually joined by a horizontal burrow (lateroid) to the main burrow. The pollen masses, rectangular in outline (Fig. 7-4), are attached to the flatter side of the cell. Nests have been described by Michener and Lange (1959), Sakagami and Michener (1962), Sakagami and Moure (1967), and others.

Key to the Subgenera of *Augochloropsis*

1. Basal area of propodeum deeply and regularly pitted or strongly striate basally, smooth apically; S5 of male with apical margin notched, and with long, curved setae centrally; S6 of male with wide apical flange (broken medially) projecting beyond posterior border; distal process of male labrum truncate or notched apically; ventral gonostylus of male bearing row of strong, flattened, modified setae at apex *A. (Augochloropsis s. str.)*
- Basal area of propodeum smooth, irregularly roughened, or with light plicae; S5 of male with apical margin entire, setae not modified; S6 of male with apical flange little developed; distal process of male labrum rounded; ventral gonostylus of male bearing dense unmodified setae at apex (Fig. 67-12b) *A. (Paraugochloropsis)*

Augochloropsis / Subgenus *Augochloropsis* Cockerell s. str.

Augochlora (*Augochloropsis*) Cockerell, 1897b: 4. Type species: *Augochlora subignita* Cockerell, 1897 = *Augochlora ignita* Smith, 1861, by original designation.

Augochlora (*Augochloropsis*) Schrottky, 1901: 213, incorrect subsequent spelling for *Augochloropsis* Cockerell, 1897.

■ *Augochloropsis* s. str. is probably more strictly tropical than is *Paraugochloropsis*; it is found north as far as Veracruz, Mexico (see the account of the genus). I suggest that about one-third of the described species belong here, the rest in *Paraugochloropsis*.

Augochloropsis / Subgenus *Paraugochloropsis* Schrottky

Augochloropsis (*Paraugochloropsis*) Schrottky, 1906a: 312.

Type species: *Augochloropsis lycorias* Schrottky, 1906 = *Augochlora epipyrgitis* Holmberg, 1903, monobasic.

Augochloropsis (*Pseudaugochloropsis*) Schrottky, 1906a: 313.

Type species: *Augochloropsis sthena* Schrottky, 1906, by designation of Sandhouse, 1943: 593. [For an invalid type designation, see Michener, 1997b.]

Augochlora (*Tetrachlora*) Schrottky, 1909b: 481. Type species:

Halictus multiplex Vachal, 1903, monobasic.

Paraugochlora Schrottky, 1910: 540. Type species: *Augochlora*

spinolae Cockerell, 1900, by original designation.

Rivalisia Strand, 1921: 270. Type species: *Rivalisia metallica*

Strand, 1921 = *Augochlora aenigma* Engel, 1996, 2000b, monobasic.

Augochlora (*Glyptobasis*) Moure, 1940: 48 (not M'Lachlan,

1871). Type species: *Augochlora chloera* Moure, 1940, by original designation.

Augochlora (*Glyptobasia*) Moure, 1941a: 98, replacement for

Glyptobasis Moure, 1940. Type species: *Augochlora chloera* Moure, 1940, autobasic.

Augochloropsis (*Glyptochlora*) Moure, 1959: 188. Type species: *Megalopta ornata* Smith, 1879, by original designation.

■ This subgenus has the distribution of the genus; see the generic account above.

Two unusual, probably derived species have received the subgeneric names *Glyptobasis* and *Glyptochlora*. Both are unusually coarsely sculptured. Males of *Glyptobasis* lack the lateroapical processes of S4 that are generally characteristic of the genus (Fig. 67-9b), but the genitalic characters are as in *Paraugochloropsis*. Males of *Glyptochlora* are unknown. In the female the anterior part of the mesoscutum is narrowed, terminating in a forward-directed lamella, unlike that of other *Augochloropsis*. I follow Eickwort (1969b) in including these forms in *Paraugochloropsis*, although Engel (2000b) recognized *Glyptochlora* as a distinct subgenus.

Genus *Caenaugochlora* Michener

Caenaugochlora consists of moderate-sized to large (length 7-14 mm) bees, metallic green or coppery to black, in which the epistomal suture forms a right-angular paraoocular lobe laterally and S4 of the male has median or apical setal patches (Fig. 67-9d), sometimes raised on tubercles. The marginal cell is usually narrowly truncate at the apex. *Pseudaugochlora* differs from *Caenaugochlora* principally in certain derived characters; species of *Caenaugochlora* like *C. costaricensis* (Friese) that have large body size and short hairs on the eyes are particularly similar to *Pseudaugochlora*. The male gonostylus is quite different, but the volsellae are remarkably similar. My inclination is to regard *Caenaugochlora* and *Pseudaugochlora* as congeneric, but this view is not supported by M. Engel's phylogenetic study (MS).

Nest cells are mostly vertical, although the orientation may be variable. They are in rather large clumps with thick earthen walls. They have been studied by Michener and Kerfoot (1967), as *Pseudaugochloropsis costaricensis* (Friese). No great differences exist between nests of *Caenaugochlora* (*Caenaugochlora*) *costaricensis* (Friese) and those of species of the genus *Pseudaugochlora*.

Key to the Subgenera of *Caenaugochlora*

1. Basitibial plate of female well defined on all edges; inner hind tibial spur of female pectinate with well separated teeth (as in Fig. 67-5i); eye hair frequently long; S4 of male bearing distinctive setal clumps on raised tubercles on either side of apical median depression (Fig. 67-9d) *C. (Caenaugochlora s. str.)*
- Basitibial plate of female obsolescent anteriorly; inner hind tibial spur of female closely pectinate, with over ten teeth (Fig. 67-5n); eye hair short; S4 of male with V-shaped patch of setae bordering slight median depression *C. (Ctenaugochlora)*

Caenaugochlora / Subgenus *Caenaugochlora* Michener s. str.

Caenaugochlora (*Caenaugochlora*) Michener, 1954b: 76. Type species: *Caenaugochlora macswaini* Michener, 1954, by original designation.

Most species are brilliant metallic green or coppery red, but some rather dull greenish species are included.

■ This subgenus is primarily Mesoamerican, occurring as far north as Sinaloa and San Luis Potosí, Mexico, but is reported to occur also south to Ecuador. There are 13 species (Moure and Hurd, 1987). The species called *Caenaugochlora curticeps* (Vachal) by Michener and Lange (1958a) is in reality a *Caenohalictus* (tribe Halictini) and has nothing to do with *Caenaugochlora*.

Caenaugochlora / Subgenus *Ctenaugochlora* Eickwort

Caenaugochlora (*Ctenaugochlora*) Eickwort, 1969b: 435. Type species: *Neocorynura perpectinata* Michener, 1954, by original designation.

The species of this subgenus are greenish to blue or violet, sometimes nearly black, and superficially resemble some species of *Neocorynura*.

■ The known range is Panama to the state of Veracruz, Mexico. The four species were recognized and reviewed by Engel (1996c).

Genus *Chlerogas* Vachal

Chlerogas Vachal, 1904: 127. Type species: *Halictus chlerogas* Vachal, 1904, monobasic and absolute tautonymy.

In its long head and malar areas, this genus resembles *Chlerogella*, from which it differs in its large size (10.5-14.0 mm long) and bituberculate scutellum. The 12-segmented male and 11-segmented female antennae are unique in Augochlorini; indeed, in no other bees except some species of *Euryglossina* (Colletidae) are the number of antennal segments reduced in both sexes. Coloration varies from bright green to largely blackish.

■ *Chlerogas* is known in the Andes from Venezuela to Bolivia. There are nine described species; see the revision by Brooks and Engel (1999).

Genus *Chlerogella* Michener

This is a genus of rather slender Augochlorini, varying from largely testaceous with greenish tints to dark blue-green, the metasoma sometimes black. Most species are distinguishable from all other Augochlorini except *Chlerogas* and *Chlerogelloides* by their elongate head (Fig. 67-7e). *Chlerogelloides* is very different, the head elongation not involving the malar area (Fig. 67-13a), whereas in *Chlerogella*, if the head is elongate, the malar area is about as long as broad to much longer than broad. Major differences between *Chlerogas* and *Chlerogella* are indicated in the key to genera, in which *Chlerogella* emerges twice because of the variable elongation of the malar areas. In two species, *Chlerogella* (*Ischnomelissa*) *cyanea* Brooks and Engel and *zonata* Engel, the malar areas are linear, i.e., virtually absent.

I here place *Ischnomelissa* as a subgenus of *Chlerogella* because of their numerous common characters, such as the usually elongate malar area, the usually swollen dorsum of the pronotum (with mere convexities for dorso-lateral angles), the long propodeum (the length of the basal area being about equal to the combined lengths of the scutellum and the metanotum), and the dull, non-striate basal area of the propodeum.

Key to the Subgenera of *Chlerogella*

1. Inner hind tibial spur of female pectinate with over ten close teeth (as in Fig. 67-5n); paraocular lobe slightly acute; male gonostylus undivided *C. (Ischnomelissa)*
- Inner hind tibial spur of female with fewer, well-separated teeth (as in Fig. 67-5i); paraocular lobe strongly acute; male gonostylus divided into dorsal and ventral processes *C. (Chlerogella s. str.)*

Chlerogella / Subgenus *Chlerogella* Michener s. str.

Chlerogella Michener, 1954b: 75. Type species: *Chlerogella elongaticeps* Michener, 1954, by original designation.

Most species of this subgenus are largely testaceous. The dorsally convex pronotum, with convexities replacing the dorsolateral angles, is usually more prominent than in *Ischnomelissa*. Body length is 6 to 8 mm.

■ This subgenus ranges from Peru to Costa Rica, in the mountains. Three published names are associated with the subgenus (Moure and Hurd, 1987), and about 15 additional species are in a manuscript by M. Engel and R. Brooks.

Chlerogella / Subgenus *Ischnomelissa* Engel

Ischnomelissa Engel, 1997c: 42. Type species: *Ischnomelissa zonata* Engel, 1997, by original designation.

The name *Ischnomelissa* was given to a group of species that resemble *Chlerogella* in most features but differ in the characters given in the key to subgenera, and in their generally dark color, dark blue-green or with the metasoma black. Two species lack malar areas, whereas others have malar areas about as long as broad. The body length is 6.5 to 10.0 mm.

■ This subgenus occurs in the Andes from Colombia to Peru. Seven species have been described, and keys were provided by Brooks and Engel (1998) and Engel and Brooks (2000).

Genus *Chlerogelloides* Engel, Brooks, and Yanega

Chlerogelloides Engel, Brooks, and Yanega, 1997: 3. Type species: *Chlerogelloides femoralis* Engel, Brooks, and Yanega, 1997, by original designation.

In size (5.4-7.0 mm body length), form, coloration, and the elongate form of the head, *Chlerogelloides* resembles species of *Chlerogella* s. str. The cephalic elongation is produced by the greatly lengthened clypeus and supraclypeal region (Fig. 67-13a) in *Chlerogelloides*, whereas in both *Chlerogella* and *Chlerogella* the elongation involves the greatly lengthened malar spaces. Both *Chlerogella* s. str. and *Chlerogelloides* share a peculiar inflation of the pronotal dorsal surface, this surface being glabrous or finely imbricate. *Chlerogelloides* can be separated from *Chlerogella* by the short malar space, the serrate inner hind tibial spur of the female, the unique sharply pointed and slender paraocular lobes, and the slender proboscis, as in *Megommation*. Although the proboscis is long, the prementum being about as long as the head, the proboscoidal fossa is not so narrow as in *Megommation* and the slenderness of the proboscis is probably not homologous to that of *Megommation*. One of the strangest

features of *Chlerogelloides* is the long, toothless male mandible, its distal two-fifths strongly bent mesad and extremely attenuate, the apex compressed and blunt.

■ *Chlerogelloides* is found in the state of Amazonas, Brazil, and adjacent parts of Peru, Ecuador, Colombia, and French Guiana. Two species are known.

Genus *Corynura* Spinola

This genus contains diverse-looking elements, from brilliant green to dull metallic or black, the metasoma sometimes red. The body length is 6 to 11 mm. The lack of paraocular lobes is shown in Figure 67-6a, and male genitalia in Figure 65-11, m. The mouthparts are as described for *Halictillus*. The metasoma of males is petiolate or at least elongate.

The nests of both subgenera of *Corynura* were described and illustrated by Claude-Joseph (1926); see also Sakagami and Michener (1962). The cells, which range from horizontal to almost vertical, are in clusters.

The females of the two subgenera come out at different places in the key to genera because in *Corynura* s. str. the inner hind tibial spur is serrate, whereas in *Callistochlora* it is strongly pectinate.

Key to the Subgenera of *Corynura*

1. Integument bright green or orange-green; inner hind tibial spur of female pectinate (Fig. 67-5h); hairs on eyes long; metasoma of male elongate but not distinctly petiolate *C. (Callistochlora)*
- Integument not bright green, metasoma dull metallic black, brown, or red; inner hind tibial spur of female serrate (Fig. 67-5f, g); hairs on eyes short; metasoma of male usually distinctly petiolate *C. (Corynura s. str.)*

Corynura / Subgenus *Callistochlora* Michener

Callochlora Moure, 1964b: 269 (not Packard, 1864). Type species: *Halictus chloris* Spinola, 1851, by original designation.

Callistochlora Michener, 1997b: 12, replacement for *Callochlora* Moure, 1964. Type species: *Halictus chloris* Spinola, 1851, autobasic and original designation.

The male genitalia were illustrated by Moure (1964b).

■ *Callistochlora* contains three or four species (Moure and Hurd, 1987). It is well known in Chile but ranges north to Peru and Ecuador.

Corynura / Subgenus *Corynura* Spinola s. str.

Corynura Spinola, 1851: 296. Type species: *Corynura gayi* Spinola, 1851 = *Halictus rubellus* Haliday, 1836, by designation of Alfken, 1926a: 146.

Corynogaster Sichel, 1867: 146. Type species: *Corynura gayi* Spinola, 1851 = *Halictus rubellus* Haliday, 1836, by designation of Daly, Michener, Moure, and Sakagami, 1987: 104.

Rhopalictus Sichel, 1867: 146. Type species: *Corynura flavofasciata* Spinola, 1851 = *Halictus chilensis* Spinola, 1851, by designation of Sandhouse, 1943: 596.

Sandhouse (1943: 540) designated *gayi* as the type species of both *Corynura* and *Corynogaster*. For *Corynura*,

genus. They lack some derived features of *Megalopta* s. str., such as the supplementary mandibular teeth of females, and may therefore be a sister group to *Megalopta* s. str. rather than a derivative from it.

Key to the Subgenera of *Megalopta*

1. Female with scopa and poorly developed basitibial plate (Fig. 67-5s); mandible of female stout, bidentate, with supplementary teeth on inner surface (Fig. 67-5o); S5 of male narrowly emarginate; clypeus and scape of male partly white *M. (Megalopta* s. str.)
- Female without either scopa or basitibial plate (Fig. 67-13e); mandible of female simple, long and slender, without supplementary teeth (Fig. 67-13d); S5 of male broadly notched; clypeus and scape of male black *M. (Noctoraptor)*

Megalopta / Subgenus *Megalopta* Smith s. str.

Megalopta Smith, 1853: 83. Type species: *Megalopta idalia* Smith, 1853, designated by the Commission, Opinion 788 (1966). See Michener, 1997b.

Megaloptera Ashmead, 1899a: 92, incorrect spelling.

Megalopta (Megaloptella) Schrottky, 1906a: 312. Type species: *Halictus ochrius* Vachal, 1904, by original designation.

Tmetocelia Moure, 1943b: 481. Type species: *Megalopta sulciventris* Friese, 1926, by original designation.

■ *Megalopta* s. str. occurs from tropical parts of Mexico (state of Nayarit) to the state of Santa Catarina, Brazil. Of the 28 species listed by Moure and Hurd (1987), two have been transferred to *Xenochlora*. *Megalopta* was revised by Friese (1926), who included *Megaloptidia*. Engel (2006a) reviewed the Central American species and listed the species of the genus.

Megalopta / Subgenus *Noctoraptor* Engel, Brooks, and Yanega

Megalopta (Noctoraptor) Engel, Brooks, and Yanega, 1997: 12. Type species: *Megalopta byroni* Engel, Brooks, and Yanega, 1997, by original designation.

Females of *Noctoraptor* can be distinguished from other *Megalopta* by the common features of cleptoparasites—reduction of the scopa (Fig. 67-13e), large sickle-shaped mandibles (Fig. 67-13d), and the absence of a basitibial plate. Males are more difficult to recognize, but S5 is broadly notched. The ocelli are smaller than in most other *Megalopta*, the lateral one about an ocellar width from the ocular margin (Fig. 67-13d). The ocelli are large in *Megalopta* s. str., except for an undescribed, nonmetallic species from Panama and Costa Rica that has smaller ocelli like those of *Noctoraptor*. In ordinary diurnal augochlorines, including the related genus *Xenochlora*, the ocelli are much smaller, the lateral ocellus separated from the eye by two or three ocellar diameters (Fig. 67-6).

■ *Noctoraptor* is known from Panama and Guyana to Ecuador. A new record from Guyana was by Hinojosa-Díaz and Engel (2003) who gave a key to the three species of the subgenus.

One specimen was taken in a light trap at Barro Colorado Island in Panama. It is therefore likely that, in spite

of its smaller ocelli, *Noctoraptor* is nocturnal or crepuscular, like its possible hosts in the subgenus *Megalopta* s. str. It may be that *Noctoraptor* is a derivative of a *Megalopta* similar to the nonmetallic species from Central America.

Genus *Megaloptidia* Cockerell

Megalopta (Megaloptidia) Cockerell, 1900a: 373, 374. Type species: *Megalopta contradicta* Cockerell, 1900, by original designation.

This is a genus of large, *Megalopta*-like bees which, however, have a slender proboscis with a short glossa, like that of *Megommation*. *Megaloptidia* also differs from *Megalopta* in the approximately right-angular paraocular lobe (Fig. 67-7b), the broad clypeal teeth, the lack of teeth on the inner surface of the mandible of the female, etc. ■ The genus is found from Guyana and Colombia south to the Amazonian parts of Brazil and Peru. The three species were revised by Engel and Brooks (1998).

Genus *Megaloptilla* Hurd and Moure

Megommation (Megaloptilla) Moure and Hurd, 1987: 241.

Type species: *Halictus callopi* Vachal, 1911, by original designation.

The name *Megaloptilla* was originally proposed for a species thought to have a slender proboscis, as does *Megommation*. Examination by R. Brooks and M. Engel shows it to have an ordinary proboscis, and to be a genus similar to *Paroxystoglossa*. It contains species 8 to 11 mm in body length, with the inner hind tibial spur of the female ciliate, as in *Paroxystoglossa*. The type species looks superficially like a green *Augochlora*, whereas *M. byronella* Engel and Brooks is larger and nonmetallic, the metasoma and areas on the thorax honey-colored. The combination of produced and strongly carinate dorsolateral pronotal angle, the carina extending to the lobe, with lack of a carina on the ridge below the angle, is distinctive.

■ This genus occurs in Panama and eastern Peru. The known species are quite different in appearance (see above) but similar in structure. Three species were revised by Engel and Brooks (1999).

Genus *Megommation* Moure

Ariphanarthra, *Chlerogelloides*, *Megaloptidia*, *Megommation*, and *Micrommation* constitute a group having a remarkable, slender proboscis (Fig. 67-4b) that fits into an unusually narrow proboscisidial fossa. In addition to the large *Megommation* s. str., this genus contains some ordinary-looking species superficially like *Augochlora* or *Augochlora*. Except for the subgenus *Stilbochlora*, *Megommation* differs from the other genera having a slender proboscis in the greatly shortened basitibial plates of the female (absent in the subgenus *Cleptommmation*), obviously a derived feature.

The number of species is small, and a subgeneric classification is probably premature. The morphological diversity is great, however, and I have accepted the subgeneric classification below.

Species of this genus are rarely collected on flowers but appear in flight-intercept traps in forested areas.

Key to the Subgenera of *Megommation*

1. Ocelli much enlarged, ocellular distance equal to or less than ocellar diameter (Fig. 67-7a); body length 12 mm or more (inner hind tibial spur of female serrate) *M. (Megommation s. str.)*
- Ocelli not enlarged, ocellular distance more than ocellar diameter (Fig. 67-13g); body length 9 mm or less 2
- 2(1). Females 3
- Males 5
- 3(2) Scopa absent, femoral and tibial hairs simple; mandible long and simple (Fig. 67-13g); inner hind tibial spur serrate *M. (Cleptommaton)*
- Scopa present, hairs on outer surfaces of tibia and femur with long apical branches; mandible normal, with subapical tooth; inner hind tibial spur pectinate 4
- 4(3). Basitibial plate short and rounded, borders not defined; thorax metallic green blue, metasoma dark with green-blue metallic highlights *M. (Megaloptina)*
- Basitibial plate of normal length, narrowly rounded, posterior border well defined; both thorax and metasoma bright metallic green *M. (Stilbochlora)*
- 5(2). Area posterior to propodeal spiracle with evenly spaced sparse setae *M. (Stilbochlora)*
- Area posterior to propodeal spiracle with dense patch of plumose setae (Fig. 67-13h) 6
- 6(5). Apical margins of S2 and S3 simple; ocellular distance little more than one ocellar diameter *M. (Megaloptina)*
- Apical margins of S2 and S3 with medial projections; ocellular distance equal to about 1.5 ocellar diameters *M. (Cleptommaton)*

***Megommation* / Subgenus *Cleptommaton* Engel, Brooks, and Yanega**

Megommation (Cleptommaton) Engel, Brooks, and Yanega, 1997: 19. Type species: *Megalopta minuta* Friese, 1926, by original designation.

Females lack the scopa, basitibial plates, and labral keel, and have pointed mandibles; it therefore seems that this subgenus is cleptoparasitic. It is apparently a sister group to *Megaloptina*. The two subgenera share a dense patch of plumose setae behind the propodeal spiracle in the male (Fig. 67-13h) and have similar male genitalia. *Cleptommaton* can be separated easily from *Megaloptina* by its color (most of the head and all of the scutum are metallic green, and the rest of the body is yellow-brown to dark brown), the various features associated with parasitism, the serrate inner hind tibial spur of the female, and the projections on the apical margins of S2 to S5 of males.

■ *Cleptommaton* occurs from Costa Rica to the state of Amazonas, Brazil, and eastern Peru. The only known species is *Megommation minutum* (Friese).

***Megommation* / Subgenus *Megaloptina* Eickwort**

Megommation (Megaloptina) Eickwort, 1969b: 441. Type species: *Augochlora ogilviei* Cockerell, 1930, by original designation.

This subgenus contains largely black or brownish to strongly metallic green species, 7 to 9 mm long; most commonly, the head and thorax are metallic green and the metasoma dark brown with green highlights.

■ This subgenus ranges from Costa Rica to the Amazon Valley and eastern Bolivia. Moure and Hurd (1987) list two species. Eickwort (1969b) recognized five species, only one of them identified.

***Megommation* / Subgenus *Megommation* Moure s. str.**

Megommation Moure, 1943b: 479. Type species: *Halictus insignis* Smith, 1853, by original designation.

This is a subgenus containing a large (12-15 mm long), dark-brown species. The face is illustrated in Figure 67-7a.

■ The range is from the state of Espírito Santo, Brazil, to Misiones province, Argentina, and Paraguay. The only species is *Megommation insigne* (Smith).

The subterranean nests were described and illustrated by Michener and Lange (1958a) and Sakagami and Moure (1967). The vertical cells form a beautiful cluster in a chamber lateral to the main burrow.

***Megommation* / Subgenus *Stilbochlora* Engel, Brooks, and Yanega**

Megommation (Stilbochlora) Engel, Brooks, and Yanega, 1997: 15. Type species: *Megommation eickworti* Engel, Brooks, and Yanega, 1997, by original designation.

This subgenus can be distinguished by the combination of small ocelli, the bright metallic green thorax and metasoma in both sexes, the absence of a dense tuft of plumose hairs behind the propodeal spiracle in males, and the well-defined posterior margin of the basitibial plate in females.

■ *Stilbochlora* occurs from eastern Bolivia and Mato Grosso, Brazil, to Colombia. The only species is *Megommation eickworti* Engel, Brooks, and Yanega.

Genus *Micrommaton* Moure

Micrommaton Moure, 1969a: 247. Type species: *Micrommaton larocai* Moure, 1969, by original designation.

In its size (body length 10.4 mm) and small ocelli, this genus is similar to *Megommation (Megaloptina)*, but it differs in the female in the more ordinary basitibial plate, better-developed median specialized area of T5, and lack of metallic coloration (thus resembling *Megommation s. str.*). The male of *Micrommaton* was unknown until recently, but see Smith-Pardo and Engel (2005).

■ The genus is known only from the state of Paraná, Brazil. The only species is *Micrommaton larocai* Moure.

Genus *Neocorynura* Schrottky

Cacosoma Smith, 1879: 39 (not Felder, 1874). Type species: *Cacosoma discolor* Smith, 1879, by designation of Sandhouse, 1943: 532.

Neocorynura Schrottky, 1910: 540, replacement for *Cacosoma* Smith, 1879. Type species: *Cacosoma discolor* Smith, auto-basis.

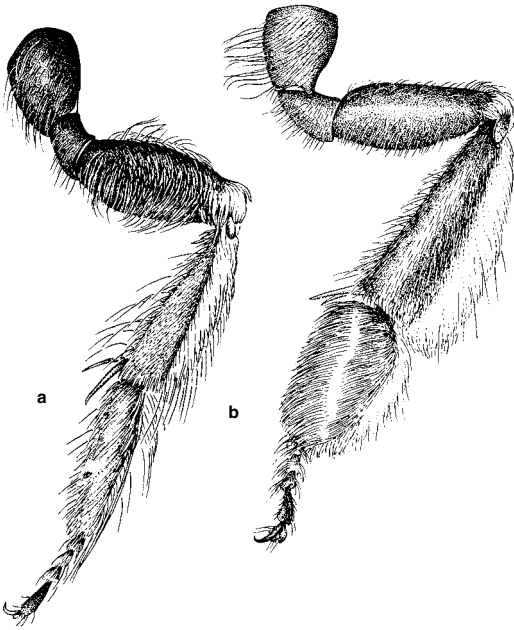


Figure 68-3. Hind legs of female Melittidae, showing the tibial and basitarsal scopae and reduced femoral to coxal scopae. **a**, *Hesperapis arida* Michener (Dasypodainae); **b**, *Macropis patellata* Patton (Melittinae). From Michener, McGinley, and Danforth, 1994.

Eremaphanta, *Macropis*, *Melitta*, *Promelitta*). In the nearctic region the family is rare except for *Hesperapis*, which occurs mostly in the Southwest of the USA; otherwise, the American genera are *Macropis* and *Melitta* (including *Dolichocheile*). Melittids are unknown in tropical America and in Australia, as well as in the Indo-Malayan area. Most species are oligolectic or at least have strong floral preferences, and some, *Macropis* and *Rediviva*, collect floral oils.

The family was reviewed to the generic and subgeneric levels by Michener (1981a); this work included a cladistic analysis. The west palearctic species were reviewed by Warncke (1973a), the Chinese species by Wu (1978). Keys to the Iberian species of Melittidae (11 species of *Melitta*, 10 of *Dasydoda*, 2 of *Macropis*) were provided by Ornos and Ortiz-Sanchez (2003).

The Melittidae are divided into three subfamilies (Michener, 1981a, and below). The relationships among the subfamilies are not clarified by the diverse relation-

ships found among the six melittid genera included in Alexander and Michener's (1995) phylogenetic study of S-T bees. More genera should be included in a new study directed toward learning about melittid relationships. As indicated above, the Melittidae will probably be confirmed as a paraphyletic group from which L-T bees arose. The Meganomiinae are deemed a holophyletic unit on the basis of numerous synapomorphies, and the Dasydodainae are probably holophyletic, for they possess several synapomorphies. The Melittinae, however, may not be holophyletic, and some of Alexander and Michener's (1995) cladograms show *Melitta* and *Macropis* as quite unrelated. One of Michener's (1981a) cladograms shows this subfamily as holophyletic on the basis of one weak synapomorphy. The other cladogram shows the Melittinae as two of the branches of a trifurcation. The numerous characters of the subfamily are mostly plesiomorphies.

Key to the Subfamilies of the Melittidae

1. Yellow or cream markings on head, thorax, and metasoma; body length over 10 mm; mandible of female simple; apex of marginal cell rounded, bent away from wing margin (Africa, Arabia) Meganomiinae (Sec. 73)
- Yellow or cream markings, if present, limited to male face and rarely areas on legs [except for *Eremaphanta* (Central Asia; length 6.5 mm or less) which often has abundant yellow markings, and *Macropis hedini* Popov, which has yellow on supraclypeal area of female]; mandible of female with preapical tooth on upper margin, sometimes two teeth; apex of marginal cell pointed, on or very near wing margin (Fig. 68-1) 2
- 2(1). Paraglossa largely bare, usually markedly shorter than suspensorium, its hairs largely limited to apex, or paraglossa absent (Fig. 72-1b); forewing with two submarginal cells, second usually shorter than first; first submarginal crossvein (= base of second submarginal cell) usually more or less at right angles to longitudinal veins (Fig. 68-1c, d) and usually close to first recurrent vein; known larvae do not spin cocoons Dasydodainae (Sec. 69)
- Paraglossa densely hairy; forewing with two or three submarginal cells, second (if only two) or second plus third as long as or longer than first; first submarginal crossvein (= base of second submarginal cell) slanting (Fig. 68-1a, b), usually well separated from first recurrent vein; larvae spin cocoons Melittinae (Sec. 74)

69. Subfamily Dasypodainae

The body of these bees is minute (4 mm long) to rather large (17 mm long), and lacks yellow markings, except for some *Eremaphanta*, the yellow clypeus of male *Promelitta*, and the partly yellow clypeus of male *Hesperapis rufipes* (Ashmead). The paraglossa is absent (Fig. 72-1b) or much shorter than the suspensorium, except in *Promelitta*. The forewing has two submarginal cells (Fig. 68-1c, d), the second shorter than the first or, in some Sambini, subequal to the first. The apex of the marginal cell is as in the Melittinae or, in *Eremaphanta*, not at all bent away from the costal margin of the wing. S7 of the male is a transverse plate with two apical lobes, not very different from the preceding sterna, or the disc is reduced but carries lateroapical lobes (Fig. 72-1f).

Larvae of *Dasypoda* and various subgenera of *Hesperapis* are known (Rozen and McGinley, 1974a). Although the larva of *Dasypoda* is quite different from that of *Hesperapis*, both exhibit several apomorphies that distinguish them from larvae of the Melittinae and Meganomiinae, and thus support recognition of the subfamily Dasypodainae. Unfortunately, larvae of the dasypodaine tribes Sambini and Promelittini are unknown.

The reduced paraglossae—they are absent in some Sambini—and the presence of only two submarginal cells, the base of the second one transverse, as well as the larval characters listed above, are synapomorphies of the subfamily. Such reduced paraglossae are not known in any other bees. The transverse base of the second submarginal cell (Fig. 63-1c, d), lying more or less at right angles to the longitudinal veins and close to the apex of the second recurrent vein, is an unusual feature. Unfortunately, it is less than satisfying as a key character because the difference between transverse (as in Dasypodainae) and slanting (as in *Macropis* and the genera having three submarginal cells) is small and sometimes bridged by variation within genera or even within species. Nonetheless, the character is a valuable one if used with caution, and does in general distinguish most Dasypodainae from other melittids.

Dasypodainae occur in the palearctic region, in North America (mostly western), and in Africa. They are most abundant in xeric areas but are present in mesic regions such as northern Europe and Japan.

Three tribes are recognized in the Dasypodainae. The

Promelittini is perhaps the sister group of the other two tribes. Its paraglossa is intermediate between that of Melittinae and the reduced type found in the other Dasypodainae. (See the discussion of the genus *Promelitta*.) The Dasypodaini and Sambini are sister groups, the most conspicuous synapomorphy of the former being the elevated vertex, whereas the latter has numerous synapomorphies, such as the strong, apically produced, mesal dorsal gonocoxal lobe of the male (Fig. 72-1d), the apically expanded and angulate gonostylus, and the elongate, nonopposable digitus of the volsella (quite different from, and evidently of independent origin from, the elongate, nonopposable digitus of *Melitta*).

The family-group name based on *Dasypoda*, Dasypodidae, is a junior homonym of the mammalian family Dasypodidae, which is based on *Dasypus*. Opinion 1926 (1999) of the Commission establishes the spelling Dasypodidae, hence Dasypodainae and Dasypodaini for the subfamily and tribal names (Alexander, Michener, and Gardner, 1998).

Key to the Tribes of the Dasypodainae

- 1. Vertex, as seen from front (except in *Eremaphanta* s. str.), elevated well above summits of eyes, usually convex; gonostylus of male (except in *Dasypoda*) robust, fused to gonocoxite; S7 of male without or (in some *Dasypoda*) with only one pair of straplike lateroapical lobes (Fig. 70-1f); paraglossa small, slender, more or less cylindrical Dasypodaini (Sec. 70)
- Vertex, as seen from front, little elevated above summits of eyes, gently convex to concave; gonostylus of male long, flexibly joined or articulated to gonocoxite; S7 of male with one or two pairs of broad lateroapical lobes (Fig. 72-1f, g); paraglossa tapering distally or absent 2
- 2(1). Clypeus of male largely yellow; metasomal terga with basal zones of pale hair; paraglossa nearly as long as its suspensorium; vertex weakly, uniformly convex, as seen from front (Egypt) Promelittini (Sec. 71)
- Clypeus of male concolorous with rest of head; metasomal terga usually without basal hair bands, but if bands present, then apical; paraglossa much shorter than its suspensorium or usually not recognizable (Fig. 72-1b); vertex straight or concave, as seen from front (Africa) Sambini (Sec. 72)

70. Tribe Dasypodaini

The clypeus of these bees is concolorous with the rest of the face, except in *Eremaphanta* from Central Asia; the lower part of the clypeus is yellowish in males of *Hesperapis rufipes* (Ashmead). The head is often narrower than the thorax; the vertex, as seen from in front, is almost always elevated above the summits of the eyes and is usually convex. The metasomal terga usually have apical hair bands. A longitudinal median elevated area of the female pygidial plate is absent except in *Hesperapis (Capicola)*. In the male, lateroapical lobes of S7 are absent or small and slender (Fig. 70-1c, g); the dorsal mesoapical lobe of the gonocoxite is absent and the gonostylus is short, broadly fused to the gonocoxite except in *Dasypoda*, and neither expanded nor angulate apically, and the volsellar digitus is normal (Fig. 70-1a, d).

The genus *Dasypoda*, which has numerous apomorphies, several of which are listed in the generic characterizations below, appears to be the sister group of the other Dasypodaini. Indeed Ascher and Engel (in Engel, 2005) provided the subtribal name Hesperapina to include *Hesperapis* and *Eremaphanta*, in contrast to the Dasypodaina for *Dasypoda*. Apomorphies for the genera of Hesperapina are the reduction of the gonostylus and its fusion to the gonocoxite, the loss of the lateroapical lobes of S7 of

the male, and the presence of a broad, transparent apical marginal zone with a deep median cleft on S1. *Eremaphanta*, with many synapomorphies, is probably the sister group to *Hesperapis*; a synapomorphy of the latter appears to be the plumose scopa with its long, emergent, bare hairs. Many illustrations of structures and phylogenetic trees were presented by Michener (1981a).

As shown by Rozen and McGinley (1974a) and Rozen (1978a), the known larvae also support the differentiation of *Dasypoda* from *Hesperapis*. The reduction in cephalic and mouthpart structures that characterizes the subfamily is carried to the extreme in *Hesperapis*, the maxilla and labium being fused and the prementum and postmentum not being separated.

Key to the Genera of the Dasypodaini

- 1. Yellow integumental markings present, at least on face and legs; stigma large, slightly shorter to slightly longer than costal margin of marginal cell; prepygidial and pygidial fimbriae of female absent (Central Asia) *Eremaphanta*
- Yellow integumental markings absent (except rarely on part of clypeus of male); stigma not enlarged, about half as long as costal margin of marginal cell (Fig. 68-1c, d);

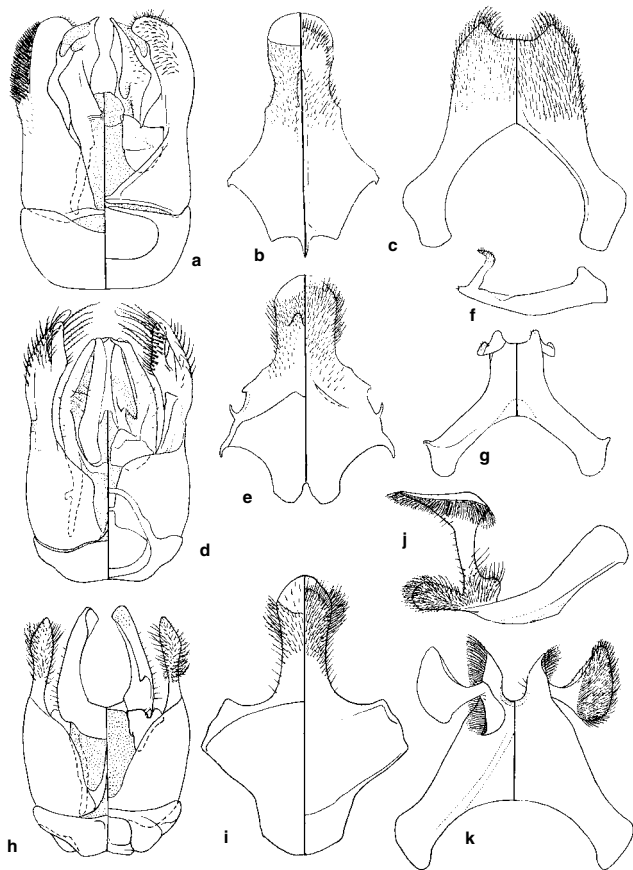


Figure 70-1. Male genitalia, S8, and S7 of Dasypodaini and Promelittini. Lateral views (f and j) are of S7. **a-c,** *Hesperapis (Capicola) braunsiana* (Friese); **d-g,** *Dasypoda hirtipes* (Fabricius); **h-k,** *Promelitta alboclypeata* (Friese). From Michener, 1981a.

- prepygidial and pygidial fimbriae of female well developed, or the former represented by a mere hair band similar to that of T4 2
- 2(1). Basitibial plate absent in both sexes; profile of propodeum all more or less in one plane; galeal comb absent or nearly so; male gonostylus well differentiated, nearly always deeply bifid (Fig. 70-1d) (palearctic) *Dasygoda*
- Basitibial plate of female and nearly all males present, rarely defined only along posterior margin; profile of propodeum more nearly horizontal at base than elsewhere [except in some *Hesperapis* (*Carinapis*)]; galeal comb present; male gonostylus broad, fully fused to gonocoxite, not bifid (Fig. 70-1a) but often with short inner process or lobe (nearctic, Africa) *Hesperapis*

Genus *Dasygoda* Latreille

Dasygoda Latreille, 1802a: 424. Type species: *Andrena hirtipes* Fabricius, 1793 = *Apis alterator* Harris, 1780, by designation of Blanchard, 1840: 414. [*Melitta swammerdamiella* Kirby, 1802, designated as the type species by Curtis (1831: 367), was not originally included in *Dasygoda* but is a synonym of *Andrena hirtipes* Fabricius = *Apis alterator* Harris.]

Podasys Rafinesque, 1815: 123, unnecessary replacement for *Dasygoda* Latreille, 1802. Type species: *Andrena hirtipes* Fabricius, 1793, autobasic.

Microdasygoda Michez, 2004, in Michez, Terzo, and Rasmont, 2004b: 427. Type species: *Dasygoda crassicornis* Friese, 1896, by original designation. [New synonymy.]

Megadasygoda Michez, 2004, in Michez, Terzo, and Rasmont, 2004b: 429. Type species: *Dasygoda argentata* Panzer, 1809, by original designation. [New synonymy.]

Heterodasygoda Michez, 2004, in Michez, Terzo, and Rasmont, 2004b: 428. Type species *Dasygoda pyrotricha* Förster, 1855, by original designation. [New synonymy.]

Dasygoda consists of large bees (length 11 to 17 mm) with abundant long hairs. The scopa consists of long, dense, minutely barbed hairs on both the inner and outer surfaces of the hind tibia and basitarsus; keitrichia are absent. Male genitalia and hidden sterna were illustrated by Radoszkowski (1887), Warncke (1973a), Wu (1978), and Radchenko and Pesenko (1989); see also Figure 70-1d-g.

■ This genus is widespread in the palearctic region from Portugal and the Canary Islands to Japan and is especially abundant in the Mediterranean basin. About 35 species are recognized. A review of the Spanish species was by Quilis (1928), of west palearctic species by Warncke (1973a), of Chinese species by Wu (1978), and of species of European Russia by Radchenko and Pesenko (1989). An annotated account of species of *Dasygoda* was provided by Baker (2002b), and a revision of the west palearctic species by Michez, Terzo, and Rasmont (2004a). In a phylogenetic study, Michez, Terzo, and Rasmont (2004b) recognized four subgenera.

The larva was described by Rozen and McGinley (1974a) and the nesting biology by several authors, including Müller (1884), Malyshev (1927a), Blagoveshchenskaya (1963), Lind (1968), and Radchenko (1987). An interesting feature of the pollen masses is the projec-

tions on their undersurfaces that reduce areas of contact with the cell wall and thereby reduce moist contacts and perhaps the likelihood of fungal infestation. Pollen masses of *D. hirtipes* (Fabricius) have three conical projections; those of *D. braccata* Eversmann have two parallel ridges and one conical projection. The cells are unlined, more or less horizontal, and isolated or in series at the ends of lateral burrows.

Genus *Eremaphanta* Popov

Eremaphanta consists of minute bees (4.0-6.5 mm long) whose male genitalia and hidden sterna are similar to those of *Hesperapis*. The body has extensive yellow markings, or at least yellow on the face and legs. The stigma is large and transparent, unlike that of other Melittidae, and more than three times as long as the prestigma. A large concavity in the posterior margin of the maxillary stipes, as in most L-T bees (Fig. 70-2), is a feature unique among S-T bees. Male genitalia, hidden sterna, and other structures were illustrated by Popov (1940, 1957b), Schwammburger (1971a), Michener (1981a), and Michez and Patiny (2006).

The minute size and yellow markings result in a superficial resemblance to *Perdita* (Panurginae), *Nomioides* and *Habralictus* (Halictidae), and certain Euryglossinae. Some common features of small bees, such as the large stigma, increase the resemblance. The genus was revised by Michez and Patiny (2006).

Key to the Subgenera of *Eremaphanta*

1. Terga without apical hair bands; head broader than long; vertex gently convex, scarcely above level of summits of eyes *E. (Eremaphanta) s. str.*
- Terga with apical hair bands; head longer than broad; vertex extending far above summits of eyes *E. (Popovapis)*

Eremaphanta / Subgenus *Eremaphanta* Popov s. str.

Eremaphanta Popov, 1940: 53. Type species: *Rhophites vitellinus* Morawitz, 1876, by original designation.

The low vertex is unlike that of other Dasygoda; presumably, it is a reversion to the condition found in most bees rather than a plesiomorphy.

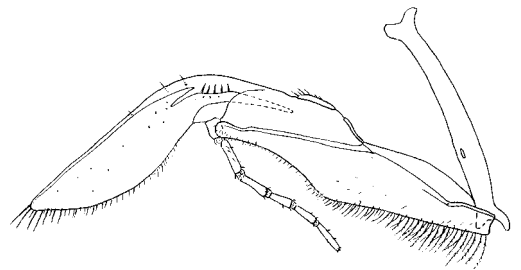


Figure 70-2. Inner view of maxilla of *Eremaphanta dispar* (Morawitz). Note the lower distal concavity of the stipes, otherwise unknown in S-T bees. From Michener, 1981a.

■ The subgenus is known from the Central Asian deserts and Iran south to Oman. It contains six species.

Eremaphanta / Subgenus *Popovapis* Michener

Eremaphanta (*Popovapis*) Michener, 1981a: 80. Type species: *Rhophites dispar* Morawitz, 1892, by original designation.

The characters indicated above in the key to subgenera are probably plesiomorphic, for they resemble other Dasypodaini rather than the apparently more derived subgenus *Eremaphanta* s. str. The reduced galeal comb (about five bristles) is an apomorphy, but has been observed in only one of the species.

■ *Popovapis*, from Central Asia to Pakistan (Baluchistan), contains two species.

Genus *Hesperapis* Cockerell

Species of this genus look superficially like *Halictus* or *Andrena* but the metasoma is very flat; when pinning specimens, one notes that the integument is soft so that a pin goes through the thorax more easily than with other bees. The male genitalia and hidden sterna were illustrated by Popov (1957b) and Michener (1981a); see also Figure 70-1a-c. As here understood, *Hesperapis* has an extraordinarily disjunct distribution, being found in North America, especially in xeric areas, and in xeric parts of southern Africa. Because of this disjunction, it has been common to recognize two genera, *Capicola* for Africa and *Hesperapis* for North America. There are in fact minor differences between the African and the North American species groups, but the differences are minute and have been hard to find (Cockerell, 1932b). By morphological standards for bee genera, the two groups without doubt belong in the same genus.

The principal differences between African and American *Hesperapis* are indicated in the first couplet of the key to the subgenera. (Michener, 1981a: 80, line 3 of diagnosis, inadvertently says for the African group "with" the inner basal process or lobe of the male gonocoxite; the word should have been "without.") The only other group differences known to me are that the galeal comb is weaker and the propodeal triangle larger in the American than in the African group. Among the few known mature larvae, the American species lack intrasegmental lines on S9 and S10 as well as paired dorsal segmental tubercles, characters found in African species whose larvae are known.

The nests are irregular burrows in the soil with long branches, each branch leading to a single cell or sometimes to a short series of cells (Rozen and McGinley, 1991). The cells are simply spaces, sometimes irregular and neither smoothed nor lined (Rozen, 1987b), but the walls are sometimes smooth and probably slightly firmer than the surrounding soil; they are dull and not waterproofed, and lack evident lining (Rozen and McGinley, 1991). This finding is much as in *Dasypoda*. Unlined cells are unusual because subterranean cells of other bee families are usually beautifully smoothed and lined with "waxlike" or cellophanelike films. The food mass in a cell is spherical, not coated; the egg is laid on top of it.

Xeralictoides has hitherto been considered a distinct genus, but it is similar to *Hesperapis* and its recognition as

a genus makes *Hesperapis* unnecessarily paraphyletic. I therefore include *Xeralictoides* as a subgenus within *Hesperapis*. The following treatment of American *Hesperapis* is modified from that of Stage (in Michener, 1981a).

Key to the Subgenera of *Hesperapis*

1. Pygidial plate of female with longitudinal median elevated area, or at least ridges representing edges of such an area; male gonostylus without inner lobe (Fig. 70-1a) (southern Africa) 2
- Pygidial plate of female without longitudinal median elevated or differentiated area (sometimes with triangular basal area); male gonostylus with inner lobe, usually bearing long, coarse, branched bristles or hairs (North America) 3
- 2(1). Outer surface of hind tibia of female with large, blunt, spinelike hairs among scopal hairs; S7 of male with disc narrowed, with diverging, densely hairy, lateroapical lobes *H. (Capicoides)*
- Outer surface of hind tibia of female without spinelike hairs interspersed among scopal hairs; S7 of male with disc broad, without diverging lateroapical lobes (Fig. 70-1c) *H. (Capicola)*
- 3(1). Mesoscutum as long as or longer than minimum intertegular distance; front tibia with series of five or more robust, amber apical and posteroapical spines on outer surface *H. (Xeralictoides)*
- Mesoscutum considerably shorter than minimum intertegular distance; front tibia without such spines 4
- 4(3). Propodeal triangle contiguously punctured throughout and dull, in contrast to sparsely punctured and shining posterior and lateral propodeal surfaces; pygidial plate of female more or less flat, with mesal area bearing patch of appressed plumose hairs *H. (Panurgomia)*
- Propodeal triangle smooth and shiny, at most anteriorly rugose or irregularly punctured, or, if dull and closely punctured, then posterior and lateral propodeal surfaces similar; pygidial plate of female often strongly convex with elevated basal triangle, always without mesal hair patch 5
- 5(4). Females 6
- Males 10
- 6(5). Hairs along upper (i.e., posterior) margin of hind basitarsus parted, margin being narrowly hairless and exposed 7
- Hairs along upper (i.e., posterior) margin of hind basitarsus not parted, arising on, as well as on both sides of, the margin 8
- 7(6). Pygidial plate with elevated, triangular basal area margined by carinae that meet posteromedially [except in *H. oliviae* (Cockerell), which lacks these carinae]; body length 7-16 mm *H. (Carinapis)*
- Pygidial plate flat with shallow longitudinal sulcus near apex, without elevated area; body length 4-7 mm *H. (Hesperapis* s. str.)
- 8(6). Head length only slightly less than width (9:10), head thus seemingly elongate; labial palpus with second segment much longer than first *H. (Zacesta)*
- Head length much less than width; labial palpus with second segment little if any longer than first 9
- 9(8). First flagellar segment at least 1.6 times length of second *H. (Disparapis)*

- First flagellar segment equal to or shorter than second *H. (Amblyapis)*
- 10(5). Labial palpus with second segment much longer than first; head about as long as broad *H. (Zacesta)*
- Labial palpus with second segment little if any longer than first; head distinctly broader than long (except in some *Hesperapis* s. str.)
..... *H. (Amblyapis, Carinapis, Disparapis, Hesperapis* s. str.) (see key below)

Key to the Subgenera of Certain Male *Hesperapis* from North America

Good subgeneric characters are difficult to find among many males. Because the following key, to certain males that run to the second alternative of couplet 10 in the above key, utilizes species-group characters, some subgenera come out in two or more places.

- 1. Body length 6 mm or less and metasomal terga with distinct, white, apical hair bands *H. (Hesperapis* s. str.)
- Body length greater than 6 mm or metasomal terga without white apical hair bands, sometimes with pale brown hair bands 2
- 2(1). Bare, subtriangular pygidial plate present, usually elevated and defined by carinae at least apically
..... *H. (Carinapis)* (in part)
- Pygidial plate absent, T7 covered with pubescence 3
- 3(2). Posterior lobe of pronotum produced into stout, weakly recurved spine; galea dark, sparsely punctured, glabrous *H. (Carinapis)* (in part)
- Posterior lobe of pronotum normal, not produced into spine; galea either pale, reticulate, heavily punctured, or bearing surface hair or apical fringe 4
- 4(3). S6 with apical lobes rounded, shiny and relatively free of hair except for apically directed marginal fringe; terga always with distinct pale apical hair bands
..... *H. (Disparapis)*
- S6 with apical lobes acute, dull, and bearing inner, subapical brush of suberect hair; terga with pale apical hair bands occasionally very weakly developed or absent 5
- 5(4). Terga dull with irregular-sized continuous punctures *H. (Amblyapis)* (in part)
- Terga shiny with uniform-sized, well-spaced punctures 6
- 6(5). Large species, more than 7.5 mm in length
..... *H. (Carinapis)* (in part)
- Small species, less than 7.5 mm in length 7
- 7(6). Apical lobes of S6 with subapical margins nearly straight and inner margin of each lobe bearing elongate, submarginal brush of suberect hairs
..... *H. (Carinapis)* (in part)
- Apical lobes of S6 with apices produced laterally and inner margin of each lobe bearing subovate, submarginal brush of hairs in a whorl *H. (Amblyapis)* (in part)

***Hesperapis* / Subgenus *Amblyapis* Cockerell**

Halictoides (Amblyapis) Cockerell, 1910b: 362. Type species: *Halictoides ilicifoliae* Cockerell, 1910b, by original designation.

This subgenus consists of small species (4-9 mm long). ■ *Amblyapis* occurs from west Texas to Nevada and central California, USA, and south to Baja California and Durango, Mexico. It contains six species.

***Hesperapis* / Subgenus *Capicola* Friese**

Capicola Friese, 1911a: 672. Type species: *Capicola braunsiana* Friese, 1911, = *Osmia? capensis* Cameron, 1905 [new synonymy], monobasic.

Rhinochaetula Friese, 1912a: 185. Type species: *Capicola cinctiventris* Friese, 1912, by designation of Cockerell, 1915: 343.

This subgenus has several apomorphies relative to *Capicoloides*, such as an area of dense setae on the outer side of the male gonostylus (Fig. 70-1a) and four apical lobes on S6 of males. S7 of the male has a rather broad disc and a bilobed apex (Fig. 70-1c). The body length is 3.5 to 13.0 mm.

■ This subgenus is found in xeric parts of South Africa and Namibia. It contains about six species; see list by Michener (1981a).

***Hesperapis* / Subgenus *Capicoloides* Michener**

Capicola (Capicoloides) Michener, 1981a: 83. Type species: *Capicola aliciae* Cockerell, 1932, by original designation.

This subgenus is largely characterized by plesiomorphies relative to *Capicola*, but the presence of spinelike hairs in the scopa is a unique apomorphy. The form of S7 of the male may also be an apomorphy, although, if so, it is a reversion toward the structure common in many melittids, colletids, and other bees, but otherwise not seen in the *Eremaphanta-Hesperapis* line. In appearance, the lone species of *Capicoloides* looks like a middle-sized species of the subgenus *Capicola* or of the American subgenus *Panurgomia*. The body length is 7.5 to 9.0 mm.

■ *Capicoloides* occurs in Namibia and Cape Province, South Africa. So far as is known, the subgenus contains a single species, *Hesperapis aliciae* (Cockerell).

***Hesperapis* / Subgenus *Carinapis* Stage**

Hesperapis (Carinapis) Stage, 1981, in Michener, 1981a: 98.

Type species: *Hesperapis carinata* Stevens, 1919, by original designation.

This subgenus contains moderate-sized to large (7-16 mm long) species.

■ *Carinapis* has the widest range of any subgenus of *Hesperapis*, from Oregon, North Dakota, and Illinois south to northern Florida, USA, and to Baja California and Morelos, Mexico. Of about 15 species, only seven are named.

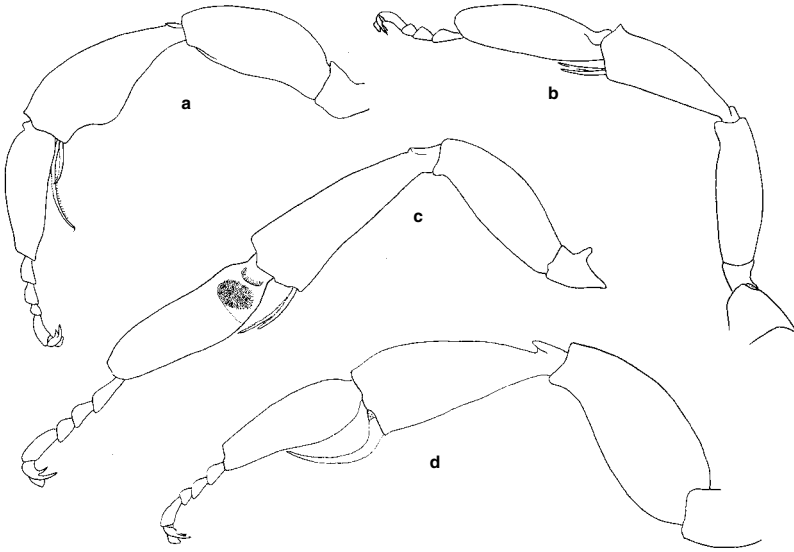
***Hesperapis* / Subgenus *Disparapis* Stage**

Hesperapis (Disparapis) Stage, 1981, in Michener, 1981a: 96.

Type species: *Hesperapis arenicola* Crawford, 1917, by original designation.

This subgenus contains species with body lengths of 8 to 14 mm.

■ *Disparapis* occurs in deserts from western Texas, California, and Utah, USA, to Zacatecas and Baja California, Mexico. Only one species has been named, but two others are known.



vergences, or separate the subgenera of *Haplomelitta* at the generic level. I would recommend the latter course, even though the genera would be monotypic, because of the great phenetic differences among them. I have delayed, however, until a phylogenetic analysis directed specifically toward the Sambini is made.

Key to the Genera of the Sambini

- 1. Female with only one hind tibial spur that is large and curved (Fig. 72-2d); vertex strongly concave, as seen from front; hind basitarsus of male with hairy pocket near base of outer surface (Fig. 72-2c) *Samba*
- Female with two hind tibial spurs; vertex not or scarcely concave; hind basitarsus of male without hairy pocket (Fig. 72-2a, b) *Haplomelitta*

Genus *Haplomelitta* Cockerell

This genus is sufficiently characterized in the discussion of the Sambini, above, and in the key to the genera of that tribe. All species of *Haplomelitta* occur in dry parts of western South Africa and Namibia.

Key to the Subgenera of *Haplomelitta*

- 1. With strong, pale apical tergal hair bands; legs of male with deformed hind and middle basitarsi and inner hind tibial spur (Fig. 72-2a) *H. (Metasamba)*
- Without metasomal hair bands; legs of male not deformed (hind basitarsus sometimes inflated) 2
- 2(1). Mandible of female tridentate (male unknown) *H. (Haplosamba)*
- Mandible of female bidentate (inner tooth sometimes reduced to a shoulder) 3
- 3(2). Propodeal triangle strongly differentiated, basal zone (and laterally entire length of triangle) with short longitudinal rugae; hind basitarsus of male strongly inflated (Fig. 72-2b), as broad as tibia *H. (Haplomelitta s. str.)*
- Propodeal triangle differentiated only by weak lines, without rugae on basal zone; hind basitarsus of male slender, much narrower than tibia 4

Figure 72-2. Hind legs of Sambini. **a**, *Haplomelitta (Metasamba) fasciata* Michener, male; **b**, *H. (Haplomelitta) ogilviei* (Cockerell), male; **c**, **d**, *Samba calcarata* Friese, male and female. Note the single tibial spur of the last. From Michener, 1981a.

- 4(3). Second submarginal cell about as long as first; first recurrent and first submarginal crossvein usually well separated; basal vein meeting cu-v or nearly so; S7 of male with two pairs of pedunculate membranous lobes *H. (Atrosamba)*
- Second submarginal cell distinctly shorter than first; first recurrent and first submarginal crossvein close together, meeting one another or the former on either side of the latter; basal vein much basad of cu-v; S7 of male with one pair of pedunculate membranous lobes and one pair of hairy areas *H. (Prosamba)*

Haplomelitta / Subgenus *Atrosamba* Michener

Haplomelitta (Atrosamba) Michener, 1981a: 65. Type species: *Haplomelitta atra* Michener, 1981, by original designation.

This subgenus includes a large (body length 11.0-11.5 mm), robust, dark species without metasomal hair bands. The subapical mandibular tooth (apex of pollex) is weak, often so worn as to be a mere shoulder. The hind basitarsus in both sexes has an apical spine projecting above the base of the second segment.

■ This subgenus is known only from western Cape Province, South Africa. It contains a single described species, *Haplomelitta atra* Michener.

Haplomelitta / Subgenus *Haplomelitta* Cockerell s. str.

Haplomelitta Cockerell, 1934a: 446. Type species: *Rhinochaetula ogilviei* Cockerell, 1932, by original designation.

The body is slender, coarsely punctate, and sparsely hairy, with the metasoma shining, not fasciate, and

73. Subfamily Meganomiinae

This subfamily contains medium-sized to large bees with yellow or cream-colored maculations on the body; the yellow pattern combined with large size differentiate them from all other Melittidae. The mandible of the female is simple. The paraglossa is longer than its suspensorium and densely hairy (Fig. 73-1). The forewing has three submarginal cells, the second and third together being shorter than or as long as the first. The stigma is extremely slender, the sides basal to vein r parallel or even converging apically, and the prestigma is two-thirds as long as the stigma to longer than the stigma. Vein r arises near the apex of the stigma. The apex of the marginal cell is rounded, bent away from the wing margin.

T4 and T5 of males of *Meganomia* and *Ceratonomia* each have two large, oval, finely striate, pregradular areas, probably strigilatory in function (Rozen, 1977a); no other bees have such structures. S7 of the male has a pair of sclerotized apical lobes arising medially and extending laterally or anterolaterally (Fig. 73-2c), often in contact with the disc of the sternum (so that one may not immediately see that the lobes join the sternum only near the midline). The volsella is much reduced, not at all chelate, as shown in the illustrations by Michener (1981a) and by Michener and Brooks (1987), and in Figure 73-2a.

The larva falls in the first of the two groups characterized in describing the larvae of the family, i.e., the larvae spin cocoons. Rozen (1977a: 14) suggested subfamilial status for *Meganomia* on the basis of the larval apomorphies of that genus. Larvae of other meganomine genera are unknown. The simple, acute mandibular apex, the lack of a dorsal transverse ridge on the perianal area, and the swollen cephalic margin behind the posterior mandibular articulation are among the apomorphies of *Meganomia*. The last may be unique among bees, but the others occur independently in various bees, including the Dasypodainae.

The Meganomiinae occur in xeric areas of eastern and southern Africa, but are not known south of the tropic of Capricorn. The subfamily also occurs in Yemen and Madagascar.

This subfamily contains only four small genera. Each genus is about equally different from the other three, owing largely to the derived features of each. Michener (1981a) showed two completely different and almost equally parsimonious cladograms for the genera. It seems best to recognize that we know nothing about their cladistic relationships.

Key to the Genera of the Meganomiinae

- 1. Arolia absent (although long, hairy, yellow plantae project between the claws); flagellum of male with apical segment or several segments curled and attenuate (Fig. 73-3c); hind basitarsus of male bent or contorted, or at least with curved carina on outer side *Meganomia*
- Arolia present, conspicuously black among associated pale interungual structures; flagellum of male with apex

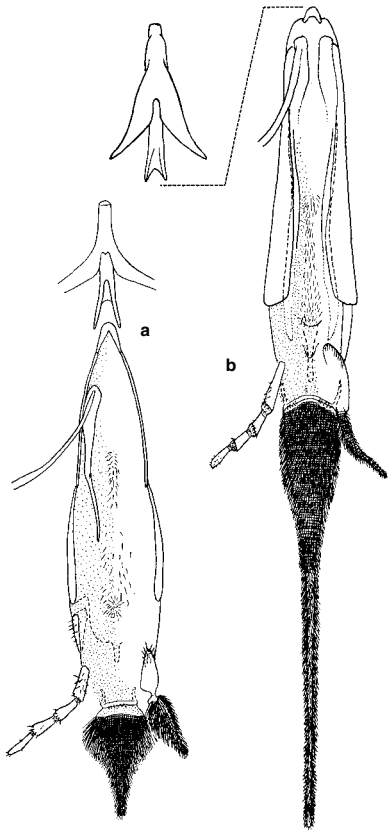


Figure 73-1. Anterior views of labia of Meganomiinae. a, *Ceratonomia rozenorum* Michener; b, *Pseudophilanthus tsavoensis* (Strand). One labial palpus and one paraglossa are omitted from each. From Michener, 1981a.

- simple or expanded as a plate; hind basitarsus of male simple 2
- 2(1). Ocelli much in front of posterior edge of vertex, posterior ocellus separated from that edge by more than two ocellar diameters; upper part of head gently convex, as seen from front; front edge of median ocellus little if any nearer to posterior edge of vertex than to antennal bases; glossa as long as prementum or nearly so (Fig. 73-1b) *Pseudophilanthus*
- Posterior ocellus separated from posterior edge of vertex by an ocellar diameter or a little more; upper part of head, as seen from front, feebly convex or flat or with ocellar region slightly elevated; front edge of median ocellus much nearer to posterior edge of vertex than to antennal bases; glossa three-fifths as long as prementum or shorter (Fig. 73-1a) 3
- 3(2). Flagellum of male not expanded at apex (Fig. 73-3a); T4 and T5 (both sexes) without sublateral stridulating areas; basitibial plate of female not defined (female un-

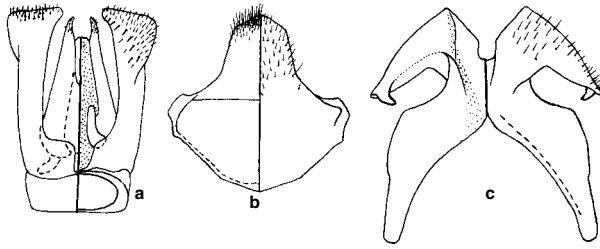


Figure 73-2. Male genitalia, S8, and S7 of *Meganomia binghami* (Cockerell). (Dorsal views are on the left.) From Michener, 1981a.

- known in subgenus *Nesonomia*); glossa one-half to three-fifths as long as prementum *Uromonia*
- Flagellum of male with apical segment expanded, plate-like, black (Fig. 73-3d); T4 and T5 (both sexes) with sublateral stridulating areas hidden under preceding tergal margins; glossa less than one-third as long as prementum (Fig. 73-1a) *Ceratonomia*

Genus *Ceratonomia* Michener

Ceratonomia Michener, 1981a: 20. Type species: *Ceratonomia rozenorum* Michener, 1981, by original designation.

The body is 13 to 15 mm long and more slender than in most meganomiines. The male flagellum is long, reaching beyond the scutellum, and flat and hairy beneath; the last segment is expanded, discoid (Fig. 73-3d). The labrum is a transverse strip, not produced medially. The basitibial plate of the female is well defined, conspicuous. Structures were illustrated by Michener (1981a).

■ *Ceratonomia* is known only from Namibia. There is one species, *Ceratonomia rozenorum* Michener.

Some aspects of behavior were described by Rozen (1977a) under the heading “*Meganomia* species B.”

Genus *Meganomia* Cockerell

Nomia (*Meganomia*) Cockerell, 1909a: 402. Type species: *Nomia binghami* Cockerell, 1909, monobasic.

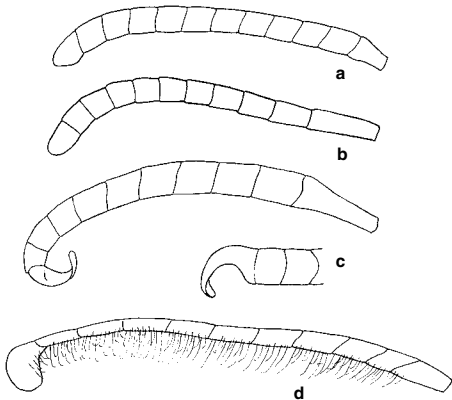


Figure 73-3. Lateral views of antennal flagella of male Meganomiinae. **a**, *Uromonia stagei* Michener (antennae 14-segmented); **b**, *Pseudophilanthus tsavoensis* (Strand); **c**, *Meganomia gigas* Michener, with separated, straightened apex in ventral view; **d**, *Ceratonomia rozenorum* Michener. From Michener, 1981a.

Maxschwarzia Pagliano and Scaramozzino, 1990: 5, unnecessary replacement for *Meganomia* Cockerell, 1909; see Michener, 1992a. Type species: *Nomia binghami* Cockerell, 1909, autobasic.

These are large bees (15–22 mm long). The male flagellum is thickened, without long hairs beneath, and curled apically (Fig. 73-3c), the last one to three segments slender. The labrum is two to three times as wide as long, its apex convex or medially emarginate. The basitibial plate of the female is hidden by hairs, not defined apically. Male genitalia, sterna, and other structures were illustrated by Michener (1981a); see also Figure 73-2.

■ This genus is found from Kenya to Namibia and northern Transvaal, South Africa, and in Yemen. There are four described species, and an additional one in Yemen. The genus was revised by Michener (1981a).

The nests and immature stages of *M. gigas* Michener were described by Rozen (1977a) under the name *M. binghami* (Cockerell). The nests are deep burrows leading to sloping cells that probably have an invisible, somewhat waterproof lining. The provisions are firm and elongate-subrectangular, with the egg on top.

Genus *Pseudophilanthus* Alfken

The body length is 13 to 15 mm. The vertex is convex, as seen from the front, and extends far behind the ocelli, its posterior margin separated from the posterior ocelli by at least two ocellar diameters. The male flagellum is simple. The labrum is less than four times as wide as long.

Key to the Subgenera of *Pseudophilanthus*

1. T7 of male bifid, without pygidial plate; galeal blade broad, shorter than stipes (Madagascar) *P. (Dicromonia)*
- T7 of male simple, with pygidial plate; galeal blade tapering, about as long as stipes (Africa)
- *P. (Pseudophilanthus s. str.)*

Pseudophilanthus / Subgenus *Dicromonia* Michener and Brooks

Agemmonia (*Dicromonia*) Michener and Brooks, 1987: 100.
Type species: *Agemmonia wenzeli* Michener and Brooks, 1987, by original designation.

The second to fourth segments of the male flagellum are broader than long. The labrum is less than three times as wide as long. Numerous other distinctive features are listed in the key to the subgenera, above, and by Michener and Brooks (1987), where illustrations of the male genitalia and hidden sterna were presented.

■ This subgenus is known from southwestern Madagas-

car. Only a single male specimen of *Pseudophilanthus wenzeli* (Michener and Brooks) has been collected.

Pseudophilanthus / Subgenus *Pseudophilanthus*
Alfken s. str.

Pseudophilanthus Alfken, 1939: 121. Type species:
Pseudophilanthus taeniatus Alfken, 1939, monobasic.
Agemmonia Michener, 1981a: 26. Type species: *Nomia*
tsavoensis Strand, 1920, by original designation.

Each of the first four segments of the male flagellum is much longer than broad (Fig. 73-3b). The labrum is over three times as wide as long. The basitibial plate of the female is not defined.

■ This subgenus is from Kenya and the Ethiopia-Kenya border region. The three nominal species, perhaps all variants of one species, were reviewed by Michener (1992a).

Genus *Uromonia* Michener

These are the smallest meganomiines, 10 to 13 mm long. The male flagellum is simple or crenulate. The labrum is over four times as wide as long, the apex convex or broadly truncate. The basitibial plate of the female is not defined (at least in *Uromonia* s. str.).

The two species, quite different from one another, are placed in separate subgenera. The female of *Nesomonía* is unknown.

Key to the Subgenera of *Uromonia*

1. Flagellum of male crenulate, 11-segmented; S8 of male with apical process narrower than disc of sternum (Madagascar)..... *U. (Nesomonía)*

- . Flagellum of male not crenulate, 12-segmented (Fig. 73-3a); S8 of male tapering toward subtruncate apex, without recognizable apical process (Africa) *U. (Uromonia* s. str.)

Uromonia / Subgenus *Nesomonía* Michener,
Brooks and Pauly

Uromonia (Nesomonía) Michener, Brooks, and Pauly, 1990: 135. Type species: *Nomia flaviventris* Benoist, 1963, by original designation.

In addition to the characters listed in the key to subgenera, *Nesomonía* differs from *Uromonia* s. str. in its simple penis valves and the shape and vestiture of its apical sterna. The male genitalia, hidden sterna, maxilla, and other structures were illustrated by Michener, Brooks, and Pauly (1990).

■ *Nesomonía* is known from southwestern Madagascar. The only known species is *Uromonia flaviventris* (Benoist).

Uromonia / Subgenus *Uromonia* Michener s. str.

Uromonia Michener, 1981a: 23. Type species: *Uromonia stagei* Michener, 1981, by original designation.

This subgenus is unique among all bees in its 14-segmented male antennae. The penis valves are large and complex, with processes projecting both dorsally and ventrally.

■ *Uromonia* s. str. is known only from the Kenya coast. The only species is *Uromonia stagei* Michener.

The relationships among the genera of Melittinae remain in doubt. Michener (1981a) gave two almost equally parsimonious cladograms, quite different from one another. There is no reliable evidence that one is “better” than the other. Engel (2001b), however, segregated *Rediviva* and *Redivivoides* as a separate tribe, Redivivini.

Key to the Genera of the Melittinae

- 1. Two submarginal cells (Fig. 68-1b); pygidial plate of male strongly developed; male with yellow face marks; gonostylus of male long, slender at least at base, articulated to gonocoxite; S8 of male not ending in beveled area suggestive of a pygidial plate (holarctic) *Macropis*
- Three submarginal cells (Fig. 68-1a); pygidial plate of male absent or weakly evident; male lacking yellow face marks; gonostylus of male broadly fused to gonocoxite (Fig. 74-2a, d); S8 of male ending in a beveled area suggestive of a pygidial plate 2
- 2(1). Propodeal triangle dull (finely granular), large (width at upper margin usually at least nearly equal to distance between transmetanotal sutures); second submarginal cell usually wider than long or about as long as wide (Fig. 68-1a); S7 of male a large plate, truncate or emarginate apically, the lobes or processes reduced to small sclerotic structures and sometimes hair patches at posterior lateral angles of sternum (Fig. 74-2f) (holarctic, Africa) *Melitta*
- Propodeal triangle shiny (usually smooth), often ill-defined, small (width at upper margin not over half distance between transmetanotal sutures and often much less); second submarginal cell usually longer than wide; S7 of male with a small disc, apex bifid or with membranous lobes or both (Fig. 74-2c) 3
- 3(2). Scopa of female consisting of simple bristles; hind tibia and basitarsus of female slender, the latter three or more times as long as wide; anterior tarsus ordinary, with ordinary vestiture; S7 of male with apex weakly emarginate, bearing, at each side, a large, flat, vertically expanded process with long erect hairs on outer surface (Africa) *Redivivoides*
- Scopa of female consisting of densely plumose understorey beneath long simple bristles; hind tibia and basitarsus of female broad, the latter about twice as long as broad; anterior tarsus thickened or elongate, with dense, short vestiture; S7 of male with apex deeply bifid or with two long, slender apical processes, lobes at each side (if present) hairless (although spiculate), not flattened, but coarsely striate or ribbed (Fig. 74-2c) (Africa) *Rediviva*

Genus *Macropis* Panzer

As indicated elsewhere, *Macropis* is the most distinctive genus of Melittinae. It differs from other Melittinae in having two submarginal cells, yellow on the face of the male, and a well-developed male pygidial plate elevated above the rest of the surface of T7. The form is rather robust, the body length 7 to 12 mm. Male genitalia and hidden sterna were illustrated by Saunders (1882), Popov (1958a), Mitchell (1960), Michener (1981a), and Snelling and Stage (1995b), and Michez and Patiny (2005). The oil-collecting and -transporting structures of

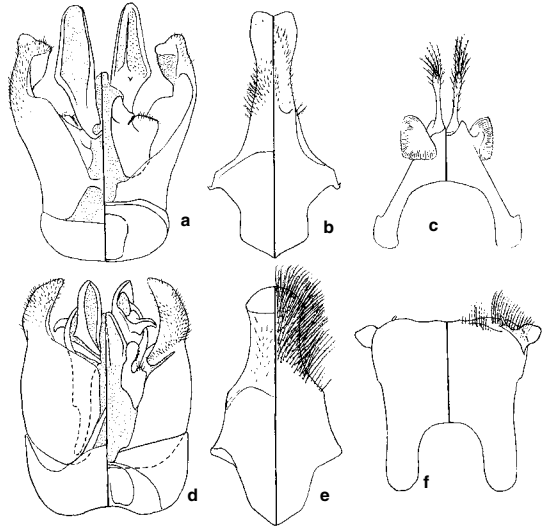


Figure 74-2. Male genitalia, S8, and S7 of Melittinae. **a-c**, *Rediviva peringueyi* (Friese); **d-f**, *Melitta dimidiata* Morawitz. From Michener, 1981a.

females are similar to those of *Rediviva*, although no *Macropis* has elongate front legs like some species of *Rediviva*. These structures of *Macropis* are the short, dense, velvety hairs on the small segments of all the tarsi, for collecting the oil, and the broad hind tibia and basitarsus with fine, dense, plumose scopal hairs (some with emergent simple apices), for oil transport; no function is known for the parted (i.e., diverging) hairs of the truncate apex of the hind basitarsus, leaving a narrow strip of integument visible along the basitarsal truncation.

So far as is known, all species of *Macropis* are dependent for larval food upon oil collected from flowers of *Lysimachia* (Primulaceae) and mixed with pollen from the same plant (Popov, 1958a; Wu, 1965a; Vogel, 1976, 1986; Rozen and Jacobson, 1980; Cane et al., 1983). Cane et al. showed that the oil is also used for lining the brood cells and accounts for the greenish color of the lining. Since *Lysimachia* produces no nectar, adults of *Macropis* visit other flowers for their own energy needs. The nests consist of short burrows in the soil with branches containing short series of subhorizontal cells (Rozen and Jacobson, 1980). The provision mass is firm, and a “foot” or projection holds the front part of the mass away from the floor of the cell, as in *Anthophorula* (Exomalopsini).

Three subgenera of *Macropis* are recognized. *Paramacropis* appears to be the sister group of the other two. *Macropis* s. str. and *Sinomacropis* are united by such synapomorphies as the expanded and bilobed or bifid gonostyli of the males and the hind basitarsal comb of the males. The hairy propodeal triangle of *Sinomacropis* is a striking apomorphy, unique in the Melittidae; the subgenus is clearly monophyletic. It may be, however, that *Macropis* s. str. is made paraphyletic by recognition of *Sinomacropis*, for apomorphies of *Macropis* s. str. are hard

to find. However, the bilobed ventroapical process of the male hind basitarsus of *Macropis* s. str. may be an apomorphy of that group; the process is not lobed in *Sinomacropis* and is absent in other bees. Moreover, the long comb on the same basitarsus may be an apomorphy of *Macropis* s. str.; the comb is short in *Sinomacropis* and absent in other bees. The genus was reviewed worldwide by Michez and Patiny (2005).

Key to the Subgenera of *Macropis*

1. Vertex broad behind ocelli, ending in a sharp preoccipital carina; gonostylus of male slender, simple; S6 of male with broadly truncate apical process, S7 with apical process broader than body of sternum, process densely hairy (eastern palearctic) *M. (Paramacropis)*
- Vertex declivous posteriorly, no carina separating it from concave occiput; gonostylus of male apically expanded and bilobed or bifid; S6 of male with attenuate apex, S7 with apical process narrow, pointed, bearing relatively sparse hairs 2
- 2(1). Propodeal triangle punctate, hairy except for small median area (China) *M. (Sinomacropis)*
- Propodeal triangle impunctate and hairless, smooth or rugose (holarctic) *M. (Macropis* s. str.)

Macropis / Subgenus *Macropis* Panzer s. str.

Macropis Panzer, 1809, no. 16. Type species: *Megilla labiata* Fabricius, 1805 = *Megilla fulvipes* Fabricius, 1805, monobasic. [*Macropis* has been attributed to Klug, but as pointed out in Commission Opinion 1383 (1986), Panzer provided the description.]

For a consideration of the name *Megilla* Fabricius (1804) and its relation to the name *Macropis*, see Michener (1983b, 1984) and Commission Opinion 1383 (1986).

■ This is a holarctic subgenus found in mesic (not xeric) regions from western Europe to Japan and in eastern and central North America, from Quebec, Canada, to Georgia and west to Montana and Colorado, with more western records in Idaho and Washington state, USA. This subgenus contains ten species. A key to palearctic species of the genus was given by Wu (1965a), to western palearctic species by Warncke (1973a), and to North American species by Snelling and Stage (1995a). See also Michez and Patiny (2005).

Nesting biology of species of this subgenus has been described by Malyshev (1929), Rozen and Jacobson (1980), and Cane et al. (1983).

Macropis / Subgenus *Paramacropis* Popov and Guiglia

Paramacropis Popov and Guiglia, 1936: 287. Type species: *Ctenoplectra ussuriiana* Popov, 1936, monobasic.

The status of this subgenus was reviewed by Wu and Michener (1986), who described the female for the first time and verified the position of *Paramacropis* in the genus *Macropis*. The lone species possesses striking presumably plesiomorphic characters as compared to other species of *Macropis*, such as the simple male gonostylus

and the simple hind basitarsus of the male. At the same time it has highly derived features, such as the male S7 and S8 (see the key to the subgenera). The male genitalia were illustrated by Popov (1936b) and Wu and Michener (1986).

■ This subgenus is from northeastern China and the Pacific maritime province of Russia. The only species is *Macropis ussuriiana* (Popov).

No observations have been made on the floral behavior of *Paramacropis*, but the female possesses oil-manipulating and -transporting structures like those of other *Macropis*. Presumably, *Paramacropis* uses oil from flowers of *Lysimachia*, as do the other subgenera.

Macropis / Subgenus *Sinomacropis* Michener

Macropis (Sinomacropis) Michener, 1981a: 51. Type species: *Macropis hedini* Alfken, 1936, by original designation.

Sinomacropis is widespread in China and occurs in Laos but is not known from other countries. See a key by Wu (1965a) and a review of the subgenus by Wu and Michener (1986); all four species were reviewed by Michez and Patiny (2005).

The floral biology was considered by Wu (1965a); the relation of *Sinomacropis* to *Lysimachia* appears to be the same as that for *Macropis* s. str.

Genus *Melitta* Kirby

These are melittine bees superficially resembling species of *Andrena*; the body length is 8 to 15 mm. The labrum has a lateral apical lobe, a character not found in other bees. The mouthparts are otherwise ordinary for the group except in the subgenus *Dolichochile*. The scopa on the outer sides of the hind tibia and basitarsus of the female is simple, these segments being slender. The propodeal triangle is large, dull. S7 of the male has a large disc and insignificant lateral apical lobes. The volsella has a long, blunt process extending much posterior to the cuspis and not opposable to it. The male genitalia were sketched by Warncke (1973a) and illustrated along with the hidden sterna by Wu (1978, 1982b), Michener (1981a), and Snelling and Stage (1995b); see also Figure 74-2d-f.

I reluctantly list two subgenera of *Melitta* below, for recognition of *Dolichochile* makes *Melitta* s. str. in its present sense paraphyletic. *Dolichochile* is phenetically remarkable, and I hope that its recognition will encourage investigators to learn the biological significance of its strange mandibular and proboscicidal characters. What is needed is a cladistic study of all species of *Melitta* to determine the real relationships of *M. (Dolichochile) melittoides* (Viereck). Then, since it is similar to *Melitta* except for a few remarkable features, the most informative classification might place *M. melittoides* within some species group of *Melitta*.

Key to the Subgenera of *Melitta*

1. Maxillary palpus reduced to two short, fused segments (Fig. 74-1e); mandible of female slightly longer than eye, distal half a long, flat, pointed blade, at base of which on inner side are two small teeth (Fig. 74-3); surface of

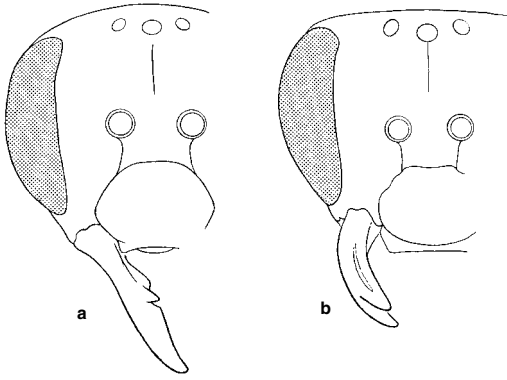


Figure 74-3. Facial views of female *Melitta*, showing mandible. **a**, *M. (Dolichochile) melittoides* (Viereck); **b**, *M. (Melitta) americana* (Smith).

labrum rather uniformly convex, impunctate except near apical margin (nearctic) *M. (Dolichochile)*
 —. Maxillary palpus six-segmented (Fig. 74-1a); mandible of female shorter than eye, of ordinary form with one subapical inner tooth; labrum with wedge-shaped, slightly depressed median punctate area partially dividing smooth area (holarctic region and Africa)
 *M. (Melitta) s. str.*

Melitta / Subgenus *Dolichochile* Viereck

Dolichochile Viereck, 1909: 49. Type species: *Dolichochile melittoides* Viereck, 1909, by original designation.

Unlike those of all other species of *Melitta*, both palpi of *Dolichochile* are short, the first segment of the maxillary palpus and segments 2 to 4 of the labial palpus being broader than long (Fig. 74-1d).

■ *Dolichochile* occurs in the eastern United States from New Hampshire to Tennessee and Georgia. The only species is *Melitta melittoides* (Viereck).

Melitta / Subgenus *Melitta* Kirby s. str.

Melitta Kirby, 1802: 117. Type species: *Melitta trilineata* Kirby, 1802, by designation of Richards, 1935: 172.

Cilissa Leach, 1812: 155. Type species: *Andrena haemorrhoidalis* Fabricius, 1775, by designation of Westwood, 1840a: 84. [A subsequent designation was listed by Michener, 1997b.]

Kirbya Lepeletier, 1841: 145 (not Robineau-Desvoidy, 1830). Type species: *Melitta trilineata* Kirby, 1802, by designation of Sandhouse, 1943: 561.

Pseudocilissa Radoszkowski, 1891: 241. Type species: *Cilissa robusta* Radoszkowski, 1876 = *Melitta dimidiata* Morawitz, 1876, monobasic.

Brachycephalapis Viereck, 1909: 47. Type species: *Melitta californica* Viereck, 1909, by original designation.

■ This is a holarctic and African subgenus. It is widespread in the Palearctic region (Canary Islands and England to Japan); it also occurs in Cape Province, South Africa, and in Kenya. In North America it occupies two disjunct areas: (1) the Sonoran desert of California and

Arizona, USA, and Baja California, Mexico, and (2) the eastern USA from New Hampshire to Florida and Mississippi. There are 20 palearctic species, three nearctic species, and three or four southern African species. Warncke (1973a) gave a key to west palearctic species, Wu (1978) gave a key to Chinese species, and Snelling and Stage (1995b) revised the North American species.

Most species are probably more or less oligolectic. *M. leporina* (Panzer) is a significant pollinator of alfalfa in Europe. Nesting behavior of *Melitta* has been described by Malyshev (1923a) and Tigrari (1968).

Genus *Rediviva* Friese

Andrena (Rediviva) Friese, 1911a: 671. Type species: *Andrena peringueyi* Friese, 1911, by designation of Cockerell, 1931a: 402.

Notomelitta Cockerell, 1933b: 128. Type species: *Rediviva neliana* Cockerell, 1931, by original designation and monobasic.

This genus is similar to *Redivivoides*, but the front tarsus of the female is covered with fine, dense hairs, and the segments are often thickened or elongate. Figure 6-1 illustrates variation in front tarsi related to the flowers from which oil is extracted. The scopa (on the outer sides of the broad hind tibia and basitarsus) is so densely plumose as to hide the surface; it also includes long, simple, emergent hairs (Fig. 68-3b). S7 of the male has a narrow disk that is bifid at the apex and usually has lateroapical lobes (Fig. 74-2c). The body length is 10 to 17 mm. Male genitalia and other structures were illustrated by Michener (1981a) and Whitehead and Steiner (1993).

■ *Rediviva* occurs in South Africa and Lesotho. There are about 23 species. Whitehead and Steiner (2001) revised the 15 species of *Rediviva* found in the winter-rainfall area of South Africa, providing a wealth of distributional, floral, and morphological information.

Although *Andrena*-like in superficial appearance, females of some species have front legs longer than the bee's body (Fig. 6-2). Probably all species collect oil with the front legs from oil-producing flowers, especially *Diascia* (Scrophulariaceae), which has slender floral spurs where oil is secreted, but less commonly from *Hemimeris* and *Bowkeria* (Scrophulariaceae), the latter having a floral pouch where oil is produced, and from flowers of terrestrial Orchidaceae (Vogel, 1984; Vogel and Michener, 1985; Steiner and Whitehead, 1990, 1991; Whitehead and Steiner, 1993). The female *Rediviva* inserts her front legs into the oil-producing spurs or pouches; the oil is collected by the dense tarsal vestiture. The length of the front legs varies among species and populations, parallel with the length of the oil-producing floral spurs of different forms of *Diascia*, suggesting a coevolutionary process. The structures for oil manipulation and transport are similar to those of *Macropis*.

Genus *Redivivoides* Michener

Redivivoides Michener, 1981a: 42. Type species: *Redivivoides simulans* Michener, 1981, by original designation.

These are *Melitta*-like bees the front tarsi of which are ordinary for the group, not densely hairy as in *Rediviva*.

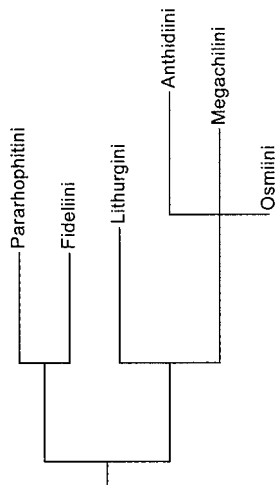


Figure 75-2. Consensus tree for tribes of Megachilidae, based on a phylogenetic study of L-T bees by Roig-Alsina and Michener (1993). The Dioxyini were not included by these authors; they would probably be a part of the multifurcation at the upper right. (Lengths of vertical lines are proportional to the numbers of derived characters.) The data were for particular genera thought to be representative of the tribes. Other analyses showed Pararhophitini as the sister group to all other Megachilidae.

dibular tooth and the rather narrow salivary lips of the larva (Rozen, 1973a) and the placement of the egg in the midst of the provisions (Rozen, 1970a, 1973b, 1977c); nearly all other mass-provisioning bees, including *Pararhophites* (McGinley and Rozen, 1987), place the egg on the surface of the provisions.

The Roig-Alsina and Michener (1993) phylogenetic study of L-T bees did not settle relationships among the tribes of Megachilinae, except for the basal position of Lithurgini. Except for *Lithurgus*, only six genera (two Anthidiini, two Megachilini, and two Osmiini) were included in the study, and although in some analyses each

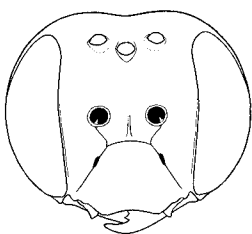


Figure 75-3. Face of male *Anthidium atripes* Cresson, showing subantennal sutures directed toward outer margins of antennal sockets. From Michener, 1944.

of the three tribes was holophyletic, in others the tribes were not supported. I believe that the Anthidiini (also the Dioxyini, which was not included in the study based on adults) and the Megachilini are easily shown to be monophyletic, but I suspect that the Osmiini are paraphyletic, and that at least the Megachilini arose from them. An attractive solution would be to divide the Osmiini; they are so diverse that such action seems desirable. Just how to do so will not be evident until a detailed analysis is made.

Key to the Subfamilies of the Megachilidae

- 1. Submarginal cells three (two in *Pararhophites*); mandible of female with preapical tooth (sometimes sufficiently enlarged that mandible is bilobed or bifid) or simple; dorsum of T6 of female hairless at least posteriorly, minutely roughened, often with a lateral ridge or carina suggesting that pygidial plate, if present, occupies most of exposed tergal surface; subantennal suture directed toward middle of lower margin of antennal socket, or usually so short that its direction cannot easily be determined.....Fideiinae (Sec. 76)
- Submarginal cells two; mandible of female with three or more teeth (except in Dioxyini and in a few *Megachile* that have a much elongated, bidentate mandible); dorsum of T6 of female usually with hairs, pygidial plate usually absent but, if present, then represented only by a narrow midapical process (Fig. 80-2); subantennal suture directed toward outer margin of antennal socket (Fig. 75-3)..... Megachilinae (Sec. 79)

76. Subfamily Fideliinae

This is an archaic subfamily with a disjunct distribution in xeric areas of Asia, Africa, and South America. It is formed by the union of the Fideliidae of authors and the supposedly anthophorine tribe Pararhophitini (Popov, 1949a). The minutely roughened surface of T6 of the female, commonly surrounded laterally and posteriorly by a ridge or carina in the Fideliini and therefore perhaps constituting the broad pygidial plate, may be a synapomorphy of the group. In the Fideliini, T6 is hairless; in the Pararhophitini, the basal part of T6 supports hairs but the hairless distal part, perhaps only a large marginal zone, projects and suggests the structure of Fideliini. Both inner and outer hind tibial spurs and also the middle tibial spur are coarsely serrate or bear widely separated small teeth, but are sometimes almost toothless, rather than having the usual fine close teeth, i.e., exhibiting the condition called ciliate. In the Megachilinae, the inner hind spur is sometimes coarsely toothed, but the others are ciliate. The premarginal lines of the terga are strongly arcuate forward medially, the hairless marginal zones thus extremely broad middorsally.

The peculiar cocoon of the mature larva, tapering at each end and incorporating sand that had been eaten by the mature larva and voided in strips tending to run on the inside of the cocoon, from one end of the cocoon to the other, is another subfamilial synapomorphy (Rozen, 1970a, 1973b; McGinley and Rozen, 1987). Such a cocoon is unknown in other bees; cocoon structure is therefore the most convincing synapomorphy of the subfamily. The unlined cells with walls no smoother than the burrow walls may also be synapomorphic, since except for Melittidae most other ground-nesting bees have smooth-walled and usually lined cells.

As indicated in Section 75, it may be best to give the Pararhophitini subfamily status; they are clearly quite different from the Fideliini.

Key to the Tribes of the Fideliinae

- 1. Submarginal cells three; stigma slender, parallel-sided, less than twice as long as prestigma, margin within mar-

- ginal cell straight or concave (Fig. 76-1b); T7 of male strongly sclerotized with distinct pygidial plate, or with the plate drawn out into a long and sometimes deeply bifid process; episternal groove present above level of scrobal groove and curving posteriorly to form scrobal groove; body densely hairy, without yellow markings except sometimes on T6 of the female and on clypeus of both sexes (Africa, Chile) Fideliini (Sec. 78)
- Submarginal cells two; stigma broad, about twice as long as prestigma, margin within marginal cell convex (Fig. 76-1a); T7 of male weakly sclerotized without distinct pygidial plate; episternal groove absent; body sparsely hairy, yellow or with yellow markings (palearctic) Pararhophitini (Sec. 77)

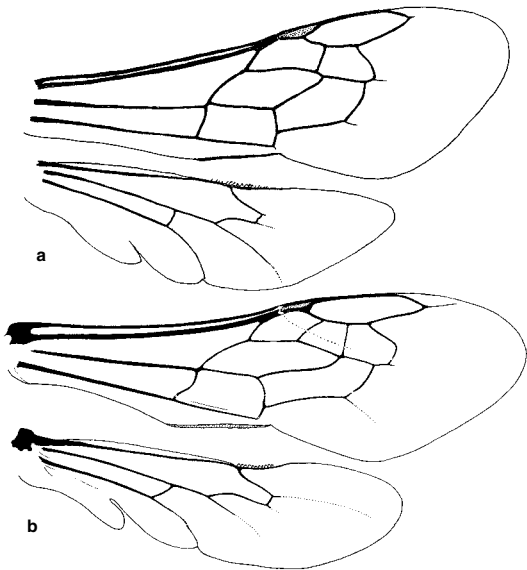


Figure 76-1. Wings of Fideliinae. **a**, *Pararhophites orobinus* (Morawitz); **b**, *Neofidelia profuga* Moure and Michener.

78. Tribe Fideliini

This tribe consists of apiform or euceriform bees with abundant long pale hair, giving them a pale appearance, but the integument is largely black except for the yellow clypeus of some; T6 of the female is sometimes yellow. The peculiar features of the group were described by Popov (1939b), Moure and Michener (1955a), and Rozen (1970a). They include the combination of a ventral metasomal scopa on which pollen is transported, three submarginal cells (Fig. 76-1b), and in some an enlarged and apically lobed S7 of the male, with the disc of the sternum reduced (Fig. 78-1c), suggesting that of many Colletidae. The posterior tibiae and basitarsi of females have long hairs that have sometimes been considered as a scopa. They are not used to carry pollen, however, but appear to function in throwing sand backward (for *Neofidelia*; Rozen, 1973b) or also laterally (for *Fidelia*; Rozen, 1970a) as the bee is digging. The male genitalia and hidden sterna were illustrated by Popov (1939b) and Warncke (1980b); see also Figure 78-1. Perhaps all species are oligolectic, different species on different and frequently unrelated flowers. The floral relations of the species of southern Africa were reported by Whitehead (1984).

Engel (2002b, 2004a) revised the tribe Fideliini and examined the phylogeny and floral relationships of its species. He placed each genus in its own tribe of his subfamily Fideliinae, presumably to emphasize the differences among the genera.

Key to the Genera of the Fideliini

- 1. Hind basitarsus of female slender, parallel-sided; hind legs of male enlarged, basitarsus forming two enormous curved talons; clypeus separated from antennal bases by much more than diameter of antennal socket (Chile) *Neofidelia*
- Hind basitarsus of female broadest near base, tapering to narrow apex; hind legs of male not enlarged or modified; clypeus separated from antennal bases by less than diameter of socket, subantennal suture thus difficult to observe (Africa) *Fidelia*

Genus *Fidelia* Friese

This genus contains robust, hairy, fast-flying bees. Some of the most distinctive generic characters are indicated in the key to the genera. The wings are hairless,

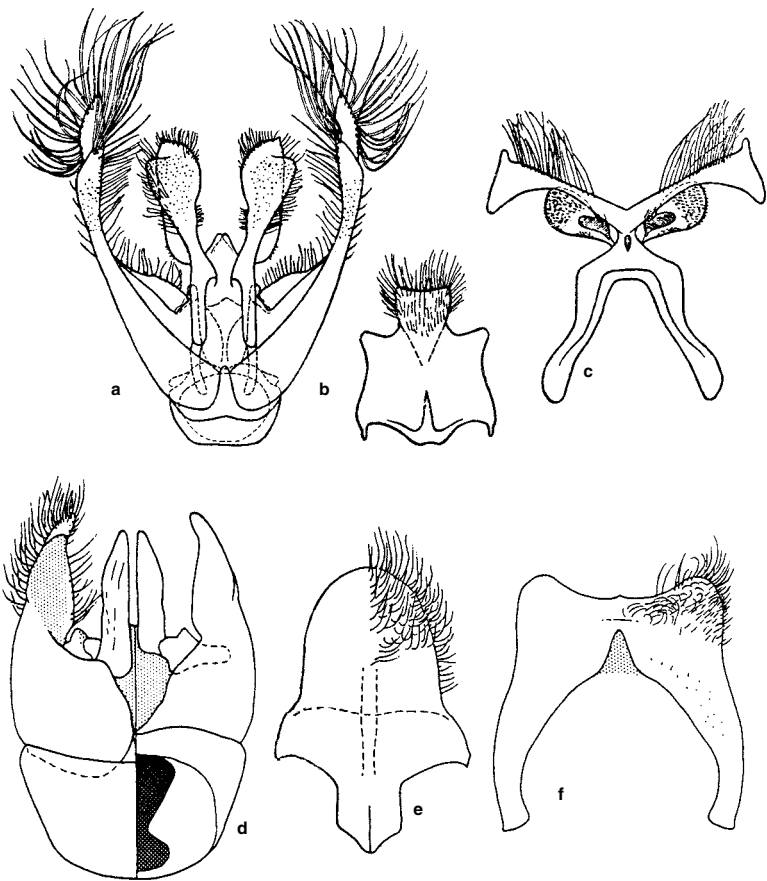


Figure 78-1. Male genitalia, S8, and S7 of Fideliini. **a-c,** *Fidelia villosa* Brauns, modified from Popov, 1939; **d-f,** *Neofidelia longirostris* Rozen, from Rozen, 1970a. (In d, the dorsal view is on the left.)

strongly papillate beyond the venation. The mandible in both sexes is often bifid or deeply bilobed, i.e., the preapical tooth is extended and similar in size and shape to the rutellum. Male genitalia and hidden sterna are illustrated in Figure 78-1a-c.

The nests are burrows in the soil consisting of several branches, each branch ending in an unlined cell. The provisions, which are packed into the distal part of the cell, completely enclose the egg (Rozen, 1970a) or eggs; Rozen (1977c) found that completed food masses contain up to three eggs or larvae, each in a chamber within the food. Thus, as in some *Megachile* (*Sayapis*), more than one larva can live and mature within one large cell. The cocoons are distinctive in having a nipple at each end, and as with other Fideliinae contain much sand that is presumably eaten by the mature larva and excreted with feces in cocoon formation.

Whitehead and Eardley (2003) revised the species of *Fidelia*, illustrating genitalia, hidden sterna, and other structures.

Key to the Subgenera of *Fidelia* (modified from Engel, 2002b)

1. Mandible strongly bidentate, teeth long, slender, and diverging from one another; pygidial plate of male present; midapical process of male T7 with apex emarginate *F. (Fideliopsis)*
- Mandible broadly bilobed (teeth broad and flat), or with short, subapical tooth, or simple; male pygidial plate absent; midapical process of male T7 deeply bilobed (essentially forming two processes) or simple 2
- 2(1). Marginal cell not extending beyond apex of submarginal cells, shorter than combined lengths of second and third submarginal cells; claws of female simple; front basitarsus of male flattened and extended laterally as lamella (only a weak lamella in *F. kobrowi* Brauns) *F. (Fidelia s. str.)*
- Marginal cell extending beyond apex of submarginal cells, as long as or longer than combined lengths of second and third submarginal cells; claws of female bifid or cleft; male front tarsus unmodified, segments cylindrical 3
- 3(2). Marginal cell about as long as combined lengths of second and third submarginal cells; apical flagellar segment of male antenna hooked, preceding segments ventrally crenulate; female T6 off-white; male T7 deeply emarginate (essentially forming two apical processes) *F. (Fideliana)*
- Marginal cell longer than combined lengths of second and third submarginal cells; male antenna simple, unmodified; female T6 black; male T7 with single midapical process, apex undivided *F. (Parafidelia)*

Fidelia / Subgenus *Fidelia* Friese s. str.

Fidelia Friese, 1899a: 244. Type species: *Fidelia paradoxa* Friese, 1899, monobasic.

This subgenus has unmodified male antennae, and yellow on the clypeus of both sexes and often on T6 of females. T7 of the male has a median, longitudinally elongate pit and a long, median, deeply bifid process that is somewhat elevated basally and might represent the pygidial plate; in addition, T7 has a large lateroapical

cal tooth, the whole tergum thus quadridentate. The claws of the female are simple. The body length is 12 to 16 mm.

■ This subgenus occurs in western South Africa and Namibia. There are three species. Probably all the species are oligolectic on Mesembryanthemaceae.

Fidelia / Subgenus *Fideliana* Michener

Fidelia (Fideliana) Michener, 2000: 422. Type species: *Fidelia braunsiana* Friese, 1905, by original designation.

This subgenus is characterized by modified male antennae [the apical segment is attenuate and hooked, the other flagellar segments slightly crenulate on the lower surface in *F. (F.) braunsiana* Friese or strongly crenulate and greatly thickened in *F. (F.) ulrikei* Warncke]. The clypeus is black, or, in the male of *F. braunsiana* Friese, yellow. The marginal cell is intermediate in length between the very short condition found in the subgenus *Fidelia* s. str. and the elongate condition characteristic of the subgenus *Parafidelia*. T7 of the male is bifid (profoundly so in *F. braunsiana*), lacks evidence of a pygidial plate, and has a lateral tooth that in *F. braunsiana* is largely hidden beneath and partly fused to the broad bifid part of the tergum. The claws of the female (at least in *F. braunsiana*) are bifid, the inner ramus much shorter than the outer, so that it could be described as a strong basal tooth. The mandible of the female is broadly bilobed (in *F. braunsiana*); that of the male, with a preapical tooth. The body length is 13 to 16 mm.

■ The distribution of this subgenus is disjunct, South Africa and Namibia in the south, Morocco in the north. The two species are *Fidelia braunsiana* Friese in southern Africa and *F. ulrikei* Warncke in Morocco.

Fidelia / Subgenus *Fideliopsis* Engel

Fideliopsis Engel, 2002b: 311. Type species: *Fidelia major* Friese, 1911, by original designation.

This subgenus can be recognized by the two long, pointed mandibular teeth of both sexes (in other *Fidelia*, mandible bilobed, or with small subapical tooth, or simple) and the greatly expanded front tarsal segments 1 and 3 (in other subgenera, front tarsi unmodified or only the basitarsus expanded). As in *Parafidelia* the marginal cell is about three fourths as long as the distance from its apex to the wing tip, and the female pygidial plate is black. (It is yellow and covers the entire exposed surface of T6 in the subgenera *Fidelia* s. str. and *Fideliana*.)

■ *Fideliopsis* is found in western South Africa and in Namibia and contains five species (see the key of Whitehead and Eardley, 2003).

There is nothing in the phylogenetic study to indicate whether *Fideliopsis* is best recognized as a genus or as a subgenus of *Fidelia*; according to Engel (2002b) it is the basal branch of *Fidelia* phylogeny, i.e. the sister group to the rest of *Fidelia*. Subjectively it is not more different than the other subgenera of *Fidelia* are from one another, and I have called it a subgenus of *Fidelia* here. Whitehead and Eardley (2003) in their revision of *Fidelia* also considered *Fideliopsis* as a subgenus.

79. Subfamily Megachilinae

This subfamily is the equivalent of the Megachilidae of most authors, i.e., those who have not placed the Fidelinae in the Megachilidae. Among the features that help us to recognize the Megachilinae are the hoplitiform to megachiliform (rarely anthophoriform) body, the two submarginal cells of roughly equal length, the strong sternal scopa (Fig. 8-7b) and lack of long hairs on the hind legs of females (except in *Aspidosmia*), the generally quadrate head with subantennal sutures directed toward the outer margins of the antennal sockets (Fig. 75-3), and usually the broad female mandibles with three or more teeth. T6 of the female is largely or entirely hairy, with no indication of a pygidial plate except in the tribe Lithurgini. An important feature of the subfamily is the reduced and often hairless S7 of the male. In Osmiini, Dioxyini, and Megachilini, S7 is a weakly sclerotized transverse band, sometimes divided medially. It is somewhat more developed in many Anthidiini, but in no case are there apical lobes or processes as in many other bees.

This is a large subfamily, common and diversified on every continent. Lithurgini is quite different from the other four tribes, and these four have common synapomorphies. A possible classification, therefore, would be to recognize two tribes, the Lithurgini and the Megachilini, the latter divided into four subtribes. It seems simpler, however, to recognize five tribes, of which the Lithurgini is the sister group to all the rest. The relationships among the remaining four tribes are not known; see the discussion of this topic in Section 75. As indicated there, I suspect that the Osmiini may be a paraphyletic unit from which one or all of the other three tribes (Anthidiini, Dioxyini, Megachilini) arose. Yet the Anthidiini have some features that seem plesiomorphic relative to the features of the other tribes, specifically a more or less recognizable male gonostylus and a better developed male S7. In Osmiini and Megachilini the gonoforceps show no indication of the separation of the gonostylus from the gonocoxites. See the account of *Aspidosmia*, an anthidiine bee, for a form exhibiting some mixture of the usual tribal characters.

The tribes Anthidiini, Dioxyini, Megachilini, and Osmiini contain the great majority of megachilid bees. The characters listed below differentiate these tribes jointly, as a group apart from the Lithurgini. The third and fourth segments of the labial palpus, both present, diverge from the axis of the second, and are not flattened (except that the third is flattened and not diverging in some species of *Chelostoma*). The dorsolateral angle of the pronotum is absent or weakly evident, but produced as a distinct tooth in some *Chelostoma* (Osmiini) and in most Dioxyini. The lower half of the metapleuron is not greatly narrowed (the lower quarter sometimes much narrowed; see the key to the tribes). The jugal lobe of the hind wing is half as long as the vannal lobe or less (Fig. 81-1a, b). The basitibial plate is not defined. The outer surfaces of the tibiae are usually not strongly tuberculate or spiculate, or the spicules terminate in bristles, but in some Anthidiini tubercles are present. The hind basitarsus is often flattened, shorter than the tibia. T1 is well developed, its posterior

margin transverse. T6 of the female lacks a posterior lateral spine except in many Anthidiini. The distal sterna of the male are commonly hidden, so that there are only one to five exposed sterna, but S6 is sometimes exposed, e.g., in most Anthidiini. The pygidial plate is absent in both sexes. Distinguishing characters of larvae are described by McGinley (1981), King (1984), and Romasenko (1995), who described and gave a key for mature larvae (prepupae) of 57 species. The characters differentiating these four tribes are summarized in Table 79-1.

The Megachilinae (except Lithurgini) almost always carry foreign materials from outside their nests to form cells, cell walls, partitions, etc. In this respect they differ from nearly all other bees except the corbiculate tribes of the Apinae and some species of *Centris*, also in the Apinae. The Apinae that carry building materials do so using the scopa or corbiculae of the hind tibiae, whereas the Megachilinae carry materials with the mandibles or held by the legs.

Megachiline building materials include leaf or petal pieces, chewed leaf pulp, plant hairs, nectar, resin, pebbles, mud, and various combinations of these; they commonly differ among different genera or species groups. Nectar as a construction material seems improbable, but the sticky substances used for partitions by various Osmiini may be nectar mixed with leaf fragments or other materials. Rozen and Eickwort (1997) report nectar in constructs of *Ashmeadiella* and suggest that it may also be used in construction by other Osmiini. Nests may be in the soil, in holes (made by other insects) in wood, in plant stems, and in diverse cavities, including the shells of dead snails, or may be free-standing constructs situated on rocks, walls, stems, twigs, or even leaves. Some species make their own burrows in soil or in pithy stems but the majority do not do so. In some cases, cells are made merely by partitions of resin, leaf pulp, or mud in a burrow, but in most cases cells are completely lined. Provisions are firm or somewhat sticky masses filling the bottom of each cell; an egg is laid on top of the provisions in each cell, after provisioning is complete. Partitions between cells are rarely omitted. Cocoons almost always have, at the anterior end, a projecting nipple in which the matrix that solidifies to fill the spaces between the silk fibers is incomplete, perhaps permitting gaseous exchange. Accounts of nests and nesting behavior are referenced below, under the tribes and genera.

There are several cleptoparasitic genera, nearly all species of which parasitize other Megachilinae.

Fries (1911b) summarized taxonomic knowledge of the whole subfamily, with keys to species, but species described after the period 1898 to 1901 were not included. The following key is supplemented by Table 79-1.

Key to the Tribes of the Megachilinae

1. Pygidial plate of male present (Fig. 80-4a, b), that of female represented by an apical process or spine (Fig. 80-2); metapleuron with lower half narrow (less than half as wide as upper end and five to six times as long as wide) to

Table 79-1. Characters of Four Tribes of Megachilinae (Tribe Lithurgini omitted).

Character	Megachilini	Osmiini	Anthidiini	Dioxyini
With yellow, white, or red maculations	no	no, except <i>Ochreriades</i> , face of male <i>Aspidosmia</i>	usually yes	no
Background of body	not metallic	frequently metallic	not metallic except for some <i>Stelis</i>	not metallic
Preaxilla ^a	sloping, with long hairs	vertical, nearly hairless	vertical, nearly hairless	vertical, nearly hairless
Stigma and prestigma	long (see key to tribes)	long except in <i>Aspidosmia</i> (see key to tribes)	short (see key to tribes)	as in Anthidiini
Arolia	absent (present on front and middle legs of <i>Megachile</i> (<i>Heriadopsis</i>))	present	present or absent	absent
Claws of female	simple or with basal tooth	simple, except cleft in <i>Osmia</i> (<i>Metallinella</i>)	cleft or with inner tooth, simple in <i>Trachusoides</i>	cleft or with inner tooth
Second recurrent vein	basal to second submarginal crossvein	basal to second submarginal crossvein	usually distal to second submarginal crossvein	basal to second submarginal crossvein
Dorsal lamella of metapleuron ^b	present	absent, except in <i>Pseudoheriades</i>	usually absent	absent
T6 of male with preapical transverse flange or carina	present, rarely two spines, absent in some <i>Megachile</i> (<i>Rhodomegachile</i>)	absent, except in <i>Hoplosmia</i>	absent	absent
Vestiture of outer surface of hind tibia	hairs	hairs	usually rather short, robust bristles	hairs
Juxtantennal carina	absent	sometimes present	sometimes present	absent

^a Often the tegula must be removed to see this character.
^b This is a narrow lamella or strong carina across the upper end of the metapleuron below the base of the hind wing.

linear; outer surfaces of tibiae, except hind tibiae of some males, with coarse tubercles that do not end in bristles (Fig. 80-3b) Lithurgini (Sec. 80)

— Pygidial plate absent; metapleuron with lower half little narrower than upper end (lower one-fourth sometimes considerably narrowed, about twice as long as wide); outer surfaces of tibiae commonly without tubercles, or with tubercles ending in bristles, but sometimes tuberculate as in Lithurgini 2

2(1). Metanotum with median spine or tubercle (except in *Allodioxyys* and *Ensliniana*); mandible of female slender apically, bidentate, similar to that of male; pronotum (except in *Prodioxyys*) with prominent obtuse or right-angular dorsolateral angle, below which a vertical ridge extends downward; sting and associated structures greatly reduced (scopa absent) Dioxyini (Sec. 83)

— Metanotum without median spine or tubercle; mandible of female usually wider apically, with three or more teeth, except rarely bidentate when mandible is greatly enlarged and porrect and clypeus is also modified; pronotum with dorsolateral angle weak or absent (or produced to a tooth in some *Chelostoma* but without vertical ridge below it); sting and associated structures well developed 3

- 3(2). Stigma less than twice as long as broad, inner margin basal to vein r usually little if any longer than width, rarely about 1.5 times width; prestigma commonly short, usually less than twice as long as broad; claws of female cleft or with an inner tooth (except in *Trachusoides*); outer surface of hind tibia usually with abundant simple bristles (but with long hairs in *Aspidosmia*); body commonly with yellow or white (sometimes red) integumental marks Anthidiini (Sec. 82)
- Stigma over twice as long as broad, inner margin basal to vein r longer than width (Fig. 81-1); prestigma much more than twice as long as broad; claws of female usually simple; outer surface of hind tibia with hairs, these sometimes plumose, but not bristles; body almost always without yellow or white integumental markings 4
- 4(3). Arolia absent, at least on hind legs, usually on all legs; preaxilla, below posterolateral angle of scutum, sloping and with small patch of hairs, these as long as those of adjacent sclerites; body nonmetallic or nearly so Megachilini (Sec. 84)
- Arolia present; preaxilla, below posterolateral angle of scutum, vertical, smooth and shining or with some hairs, these much shorter than those of adjacent sclerites; body sometimes metallic green, blue, or brassy Osmiini (Sec. 81)

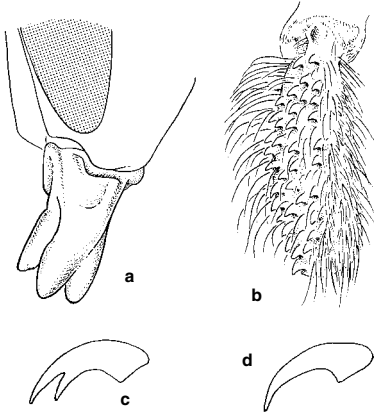


Figure 80-3. Structures of Lithurgini. **a**, Lower part of head and mandible of female *Lithurgus littoralis* Cockerell, showing the tridentate mandible with the middle tooth longest; **b**, Hind tibia of female *L. apicalis* Cresson; **c**, **d**, Claws of females of *Microthurge pharcidontus* (Moure) and *L. apicalis* Cresson. **a** and **b**, from Michener, McGinley, and Danforth, 1994; **c** and **d**, from Michener, 1983a.

synapomorphy, although this character arises independently in various other bees.

Lithurgus and *Microthurge* agree in several synapomorphies: the reduced lower mandibular tooth, such that the middle tooth is longest as well as more anterior than the others (Fig. 80-3a), the coarse tibial spicules or tubercles in areas of short and sparse hairs (Fig. 80-3b), and the low profile of the posterior part of the thorax and especially of the propodeum. Compared to *Trichothurgus*, with its many plesiomorphies, *Lithurgus* and *Microthurge* have few, the most noteworthy, perhaps, being the ordinary-sized labrum and the moderate to high density of hairs on the wing membrane.

Microthurge has few apomorphies. These include the short maxillary palpi and perhaps the larger stigma (plesiomorphic for Apoidea as a whole but perhaps derived in connection with small body size in this genus, as well as in some other small megachilids such as *Chelostoma* and *Heriades*). Bifid claws in females (plesiomorphic in bees in general) could be an apomorphy in *Microthurge*. Genes for this character must be retained in all species, because the claws of males are cleft. A regulatory change could therefore cause their reactivation in females, and would be apomorphic. The broad pygidial plate of males of *Microthurge* (Fig. 80-4b) seems to be plesiomorphic, as compared to all other megachilids, but one must question this idea in view of the slender produced plate in both *Trichothurgus* and *Lithurgus* (Fig. 80-4a). If this similarity is due to homology, then the broad plate of male *Microthurge* is a reversion toward the more primitive apoid condition, but for this genus it would be an apomorphy.

For *Lithurgus* the situation is equally confusing. If the stigmal, claw, and pygidial characters listed above are plesiomorphic for *Microthurge*, then the alternative characters are apomorphic for *Lithurgus*.

Key to the Genera of the Lithurgini (From Michener, 1983a)

1. Labrum longer than clypeus, often much longer; hind tibia of female rather uniformly hairy on outer, anterior, and posterior surfaces, spicules relatively inconspicuous among the hairs; lower mandibular tooth longer than middle tooth, *or*, in some females, lower and middle teeth equal (South America) *Trichothurgus*
- Labrum about as long as clypeus; hind tibia of female with hairs of broad, longitudinal outer zone shorter and sparser than those of anterior and posterior surfaces, spicules large and conspicuous in outer zone (Fig. 80-3b); lower mandibular tooth conspicuously shorter than middle tooth, which is the longest mandibular tooth (Fig. 80-3a) 2
- 2(1). Body small, slender, hoplitiform; claws of female bifid (Fig. 80-3c); stigma of moderate size, broadest at base of vein r, sides converging toward base; maxillary palpi two-segmented (South America) *Microthurge*
- Body broad, megachiliform; claws of female simple (Fig. 80-3d); stigma small, sides basal to vein r parallel or nearly so [in some small species of *Lithurgus* the stigma is larger, approaching the size of that of *Microthurge*.]; maxillary palpi three- or four-segmented ..
..... *Lithurgus*

Genus *Lithurgus* Berthold

Bees of this genus, 8 to 19 mm long, are robust, suggesting a slightly elongated *Megachile*, but the metasoma is somewhat flattened, and commonly has apical tergal and sternal hair bands. The midfacial prominence is almost always present in females, absent in most males. The labial palpus is four-segmented except in certain Old World species that lack the fourth segment. The fore and middle tibiae in the female each have two longitudinal rows of coarse spicules or tubercles extending basad, on the posterior part of the outer surface, from each of the two apical tibial spines, these rows outlining a channel on each tibia that extends basad to the middle of the tibia or beyond, sometimes nearly to the base. There are sometimes some spicules between the rows. In males the spicules are smaller, the rows shorter, sometimes absent. Scattered over the short-haired outer surface of the hind tibia of the female are coarse tubercles (Fig. 80-3b); the tubercles of the males are smaller, absent in many species. The wing membrane is hairy, often densely so. The pygidial plate of the female is a flat or concave dorsal surface of a long apical spine of T6 (Fig. 80-2c); of the male, it is a dorsally concave, broad, blunt projection or robust spine (Fig. 80-4a). The male genitalia and hidden sterna were illustrated by Mitchell (1960), Michener (1983a), and van der Zanden (1986); see also Figure 80-4c-e.

This genus is worldwide in distribution in tropical and warm to moderate temperate zones, except that in the Americas it may be largely absent from the wet tropics. Two subgenera are commonly recognized.

Key to the Subgenera of *Lithurgus*

1. Arolia absent or rudimentary in both sexes (except present in male of *L. rubricatus* Smith from Australia); facial

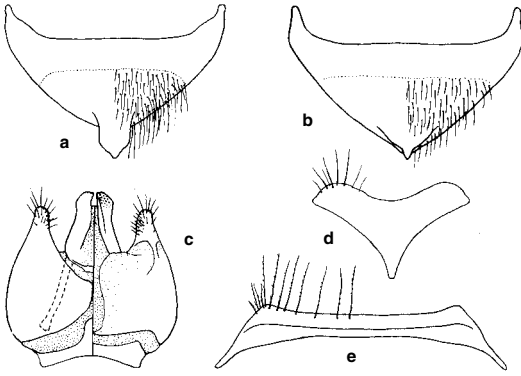


Figure 80-4. Structures of Lithurgini. **a, b**, T7 of males of *Lithurgus apicalis* Cresson and *Microthurge pharacidontus* (Moure), showing pygidial plates; **c-e**, Male genitalia, S8, and S7 of *L. apicalis* Cresson, the dorsal side of the genitalia on the right. The male genitalia of *Lithurgus* are the simplest of any bee, and the smallest relative to the size of the bee. From Michener, 1983a.

prominence of female involving upper part of clypeus and usually also part of supraclypeal area; first flagellar segment about twice as long as broad, more than twice as long as second, which is much broader than long

- *L. (Lithurgus s. str.)*
- Arolia present in males, absent in females; facial prominence of female entirely supraclypeal (absent in one species); first flagellar segment not or little longer than broad, slightly longer than to shorter than second, which is nearly as long as broad to longer than broad (Western Hemisphere) *L. (Lithurgopsis)*

Lithurgus / Subgenus *Lithurgopsis* Fox

Lithurgopsis Fox, 1902: 138. Type species: *Lithurgus apicalis* Cresson, by original designation. The presence of arolia in males is presumably a plesiomorphy showing that this subgenus did not arise from *Lithurgus s. str.*

The presence of arolia in *Trichothurgus* males suggests a relationship to that genus; arolia may have been independently lost in *Microthurge* and within *Lithurgus s. str.*

■ This subgenus is limited to the Western Hemisphere, where it ranges from South Dakota, USA, to Argentina. It is reported from Costa Rica, but is probably absent from broad areas in the tropics. In North America it occurs widely in the west and ranges east to Illinois, North Carolina, and Florida, but is absent from the northeastern part of the continent. These bees collect pollen from Cactaceae; possibly for this reason *Lithurgopsis* is largely restricted to xeric areas. *Lithurgopsis* appears to be absent in Chile as well as Brazil. There are seven North American species and another in the Greater Antilles; about three others that may belong here occur in Argentina. Snelling (1983b) reviewed the North American species; he later presented a new key to species (Snelling, 1986a).

Lithurgus / Subgenus *Lithurgus* Berthold s. str.

Lithurge Latreille, 1825: 463. Type species: *Andrena cornuta* Fabricius, 1787, monobasic. [The name *Lithurge* is French vernacular.]

Lithurgus Berthold, 1827: 467, emendation of *Lithurge* Latreille, 1825. Type species: *Andrena cornuta* Fabricius, 1787, monobasic. [Michener (1997b) listed a subsequent designation.]

Lithurgus Ashmead, 1899a: 77, *lapsus* for *Lithurgus* Berthold, 1827.

Since Sandhouse's (1943) list, certain authors have used the French vernacular form *Lithurge*. As noted by Michener (1979b) and others, the correct Latinized form is *Lithurgus*.

The loss of male arolia is an apomorphy for the subgenus, but arolia are found in the males of the Australian *Lithurgus rubricatus* Smith, which at least for the present is in the subgenus *Lithurgus s. str.* *L. rubricatus* does not agree with *Lithurgopsis* in subgeneric characters except in having long arolia in the male. It is difficult to polarize the other subgeneric characters. It is therefore not clear whether *Lithurgus s. str.* and *Lithurgopsis* are sister groups; the alternative is that the former is derived from a paraphyletic *Lithurgopsis*. No species of *Lithurgus s. str.*, however, is closely similar to any group or species of *Lithurgopsis*; I therefore hypothesize the sister-group relationship.

■ This subgenus is found in Eurasia, Africa, Australia, and intervening islands and includes all of the Old World species of the genus. In Africa it reaches the Cape, in Australia it reaches New South Wales but is apparently absent from southern parts of the continent, while in Eurasia it extends north to Japan, China, Russia, Germany, Spain, etc. To the east it occurs in the Philippines and as far as Tahiti, perhaps having been carried as nests in timbers of Polynesian boats. One species, *Lithurgus huberi* Ducke, occurs in Brazil; it is probably adventive there and the same as the Old World species *L. atratus* Smith. *Lithurgus (Lithurgus) scabrosus* (Smith) appears to have been introduced in Hawaii (Snelling, 2003). Another species, *L. chrysurus* Fonscolombe, has been recorded by Roberts (1978) as introduced, presumably from the Mediterranean region, into New Jersey. There are no subsequent records of this population, and the species is probably extinct in America. The subgenus is in need of revision; there are probably 15 species. The four species in sub-Saharan Africa were revised by Eardley (1988), and the roughly seven palearctic species by van der Zanden (1986).

Species of the subgenus *Lithurgus s. str.* are floral specialists, some on Malvaceae, others on Asteraceae. The length of the proboscis varies from extremely long (reaching the hind coxae or beyond) for species on Malvaceae and thistles (*Carduus*, *Cirsium*; see Banaszek and Romasenko, 1998; Pachinger, 2004) to much shorter for species on other Asteraceae (*Centuarea*; see Rust et al., 2004).

Genus *Microthurge* Michener

Microthurge Michener, 1983a: 181. Type species: *Lithurgus pharacidontus* Moure, 1948, by original designation.

This genus consists of small (5-8 mm long) lithurgines having the size and form of a *Heriades* or small *Hoplitis* (Osmiini). The metasomal terga have pale apical hair bands. The supraclypeal facial prominence is present in

Table 81-1. Grouping of Genera of Osmiini.

<i>Osmia</i> group (Subtribe Osmiina)	<i>Heriades</i> group (Subtribe Heriadina)
<i>Ashmeadiella</i>	<i>Afroheriades</i>
<i>Atoposmia</i>	? <i>Bekilia</i>
<i>Chelostoma</i>	<i>Heriades</i>
<i>Haetosmia</i>	<i>Hofferia</i>
<i>Hoplitis</i>	<i>Noteriades</i>
<i>Hoplosmia</i>	<i>Othinosmia</i>
<i>Ochreeriades</i>	<i>Protosmia</i>
<i>Osmia</i>	<i>Pseudoheriades</i>
<i>Stenosmia</i>	<i>Stenoheriades</i>
<i>Wainia</i>	<i>Xeroheriades</i>

without transverse humps; S3 but not S4 with discal hair short, velvety; S3 with lateral hyaline flaps (except in *Pseudoheriades*, *Noteriades*, *Afroheriades*); S5 with modified discal or marginal hair and/or its posterior margin emarginate; S6 without basal or lateral hyaline flaps. Female: clypeus not overhanging labrum [except in *Othinosmia* (*Megaloheriades*) and *Afroheriades primus* Peters]; labrum usually with apical or subapical tuft of hair, usually without marginal fringe of hair; T6 with preapical carina or with wide hyaline apical flange. Alternative features characterize most members of the *Osmia* group, or subtribe Osmiina.

Much of the difficulty in defining the *Heriades* group rests with the intermediate nature of *Protosmia* and *Othinosmia*. The rest of the *Heriades* group can be distinguished from all other Osmiini (except *Chelostoma*) by the ventrally elongate mesopleuron, the narrowly linear mesopleural signum, and the distally diverging stigmal margins. It must be remembered, however, that larger stigmata are commonly associated with relatively smaller body size (Danforth, 1989a); diverging margins characterize a larger stigma and may thus be a reflection of the generally small body size of species of the *Heriades* group, irrespective of relationships. The thoracic structure of *Protosmia* and *Othinosmia* is markedly like that of *Osmia*. All male *Protosmia* and *Othinosmia* have a brush of hair under the margin of S1. Such a brush is also present in some *Heriades*, but not elsewhere in the Megachilidae. A character of most of the *Heriades* group is the emarginate male S5 with its fringe of modified (often capitate) hairs, as found in *Protosmia*, *Othinosmia*, *Xeroheriades*, *Stenoheriades*, and *Heriades*. Such a fifth sternum is not found in other Osmiini. In *Afroheriades* and *Pseudoheriades* the modified hairs arise from the disc of the emarginate sternum, and *Hofferia* seems to lack both modified hairs and the emargination. The combination of a dense brush of hairs covering the disc of S3 with the absence of a similar covering on S4 will also serve to distinguish males of the *Heriades* group from those of the *Osmia* group. The presence of a preapical or apical tuft of hairs on the female labrum is also a character of importance; although not present in all species of the *Heriades* group, this tuft is present in most, and is not found in the *Osmia* group.

Because many authors have placed *Hoplitis* (including *Anthocopa*), *Osmia*, and related taxa together in the genus

Osmia, various keys and revisional works on *Osmia* of the palaearctic region include species in most genera of the *Osmia* group. Rather than mentioning such studies under each genus, I list some of them here: Schmiedeknecht (1885), Ducke (1900), Benoist (1931).

Likewise, various works on nesting biology include material on both *Osmia* and *Hoplitis* under the generic name *Osmia*. Examples are Malyshev (1937) and Westrich (1989).

Key to the Genera of the Osmiini of the Eastern Hemisphere (Males)
(Based on Griswold and Michener, 1998)

- 1. T7 weakly sclerotized, not exposed, hidden by large T6 2
 - T7 strongly sclerotized, exposed though sometimes small 5
- 2(1). Scutellum with transverse preapical carina, behind which it is vertical or overhanging metanotum; clypeus with longitudinal carina continued dorsally between antennal sockets (Africa, southern Asia) *Noteriades*
 - Scutellum not carinate, without such a posterior marginal zone; clypeus without longitudinal carina, or carina not continued dorsally between antennal sockets 3
- 3(2). Scutellum curved down posteriorly, posterior part of its surface thus steeply sloping, vertical, or overhanging; metanotum well below level of most of scutellum; posterior lateral angle of scutum frequently acutely produced posteriorly (Africa and Israel to the Philippines) *Wainia*
 - Scutellum flat or scarcely convex, not curved down posteriorly and not overhanging metanotum; metanotum medially about on the level of most of scutellum; posterior lateral angle of scutum obtuse 4
- 4(3). Posterior margins of S2 and S3 notched or stepped laterally; pronotal lobe without carinules in addition to carina (holarctic, Oriental, Africa, Central America) *Heriades*
 - Posterior margins of S2 and S3 not notched or stepped laterally; pronotal lobe with several minute carinules behind and parallel to carina, carina rarely absent but carinules present (except carinules absent in subgenus *Dolichosmia* from Burma) (holarctic, Burma) *Protosmia*
- 5(1). Parapsidal line punctiform or rarely short-linear, one-fifth as long as tegula or usually less (Fig. 81-2a); S3 of male commonly emarginate with fringe in emargination, the middle of S3 being largely or wholly covered by an enlarged S2, and S4 neither emarginate nor fringed like S3 (but some have S2 and S3 transverse and similar to one

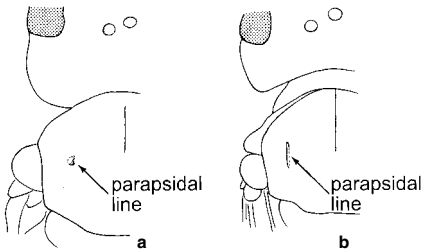


Figure 81-2. Dorsal views of thoraces of Osmiini. a, *Osmia* sp.; b, *Hoplitis* sp. From Michener, McGinley, and Danforth, 1994.

- another); body commonly with some greenish or bluish metallic color (holarctic) *Osmia* (in part)
- Parapsidal line linear (Fig. 81-2b), at least one-fourth as long as tegula; S3 of male neither emarginate nor fringed and not covered medially by S2 [except in *Hoplitis* (*Jaxartinula* and *Kumobia*) and except sometimes when S4 is similar to S3]; body nonmetallic 6
- 6(5). T6 with strong transverse preapical carina, the carina sometimes multidentate (Fig. 81-9b, c) 7
- T6 without preapical carina 10
- 7(6). Axilla angulate or spined posteriorly (Fig. 81-9a); S3 without dense, velvety discal hair; S5 with hairs unmodified and with reflexed lateral hyaline flaps (palearctic) *Hoplosmia*
- Axilla with posterolateral margin rounded (except pointed in the African *Othinosmia* subgenus *Afrosomia*); S3 with dense, velvety discal hair; S5 with modified hairs and without lateral hyaline flaps 8
- 8(7). Preapical carina of T6 smooth, neither crenulate nor spined; basal zone of propodeum not limited posteriorly by carina (Africa) *Othinosmia*
- Preapical carina of T6 crenulate or spined; basal zone of propodeum limited posteriorly by distinct carina, at least laterally 9
- 9(8). Metanotum vertical in lateral view; apical margin of S1 not produced; T7 emarginate (Mediterranean region to South Africa) *Stenoheriades*
- Metanotum nearly horizontal; apical margin of S1 produced; T7 not emarginate (Mediterranean region) *Hofferia*
- 10(6). T7 more or less quadrate, although sometimes with apical processes, and wrapped around laterally by T6, thus placed in large emargination of T6 11
- T7 variable in form but not quadrate, not wrapped around laterally by T6 12
- 11(10). Proboscis short, in repose not or scarcely exceeding fossa; upper end of metapleuron with shiny, shelflike projection; T1 with carina separating anterior and dorsal surfaces; S3 with median apical spike (Africa, India, Mediterranean region) *Pseudoheriades*
- Proboscis long, in repose much exceeding fossa; upper end of metapleuron without shiny projection; T1 without carina separating surfaces; S3 without median apical spike (South Africa) *Afroheriades*
- 12(10). Scutum elongate, its length at least equal to intertegular distance; mesopleural signum narrowly linear; stigma relatively large, its margin within marginal cell convex (Fig. 81-1c) 13
- Scutum not elongate, its length less than intertegular distance; mesopleural signum not linear; stigma relatively small, its margin within marginal cell usually not convex (Fig. 81-1b, d; but see *Stenosmia*) 14
- 13(12). Pronotum elevated so that scutum has no anterior surface; body (at least metasoma) with yellow or ivory markings; axilla lobate or angled laterally, extending beyond line from posterolateral angle of scutum to lateral margin of scutellum (Asia Minor, Namibia) *Ochreheriades*
- Pronotum medially not attaining level of dorsal scutal surface, so that anterior end of scutum is bent down, forming anterior scutal surface; body without yellow or

- ivory markings; axilla not produced (holarctic) *Chelostoma*
- 14(12). T6 with lateral tooth [a mere convexity in *Hoplitis* (*Formicapis*)], sometimes minute but sharp 15
- T6 without lateral tooth 16
- 15(14). Pronotal lobe with erect lamella (often hidden by hair); T7 broad, truncate, bulging dorsally; S6 without basal membranous flaps (Mediterranean region, East Africa to central Asia) *Haetosmia*
- Pronotal lobe without lamella but sometimes weakly carinate, usually without carina; T7, if truncate, not bulging dorsally; S6 usually with basal membranous flaps lying appressed against ventral surface of S6 (holarctic, Africa, India) *Hoplitis* (in part)
- 16(14). T7 tridentate; scutellum with profile distinctly convex, sloping so that posterior margin is below anterior margin; S6 with basal membranous flaps (palearctic) *Hoplitis* (*Megahoplitis*)
- T7 truncate, bilobed, or bidentate; scutellum flat or, if convex, then not sloping; S6 without basal membranous flaps 17
- 17(16). Stigma about half as long as marginal cell on wing margin; stigmal margin within marginal cell distinctly convex; lower half of omaulus carinate (Egypt to China) *Stenosmia*
- Stigma less than half as long as marginal cell on wing margin (Fig. 81-1d); stigmal margin within marginal cell weakly convex, straight or concave; omaulus sometimes a sharp angle and reinforced by abrupt changes in surface sculpture, but not carinate (holarctic) *Osmia* (in part)

Key to the Genera of the Osmiini of the Eastern Hemisphere (Females)

(Based on Griswold and Michener, 1998)

1. Posterolateral corner of scutum with marginal ridge not carinate, a dense patch of long pubescence on lateral surface (T6 with translucent apical lip extending beyond hairs and projecting at strong angle to surface of tergum) (South Africa) *Afroheriades*
- Posterolateral corner of scutum with strong marginal carina, pubescence absent lateral to carina 2
- 2(1). Apical part of labrum without long, erect hairs; body slender, elongate (Fig. 81-6), scutal length at least equal to intertegular distance 3
- Apical part of labrum with apical fringe of long, usually erect hairs or preapical tuft of such hairs or with at least some erect hairs on disc; body not elongate and slender (except *Osmia cephalotes* Morawitz, which is metallic), scutal length less than intertegular distance 5
- 3(2). Pronotum elevated, scutum thus lacking anterior surface; body (at least metasoma) with yellow or ivory markings (Near East, Namibia) *Ochreheriades*
- Pronotum medially not attaining level of dorsal scutal surface, anterior end of scutum thus bent down, forming anterior scutal surface; body without yellow or ivory markings 4
- 4(3). Preoccipital carina complete, reaching hypostomal carina, where it is produced into strong tooth; S6 with acute median apical spine (Mediterranean region) *Hofferia*
- Preoccipital carina incomplete, not reaching hypostomal carina, without strong tooth; S6 without or with small median apical tooth (holarctic) *Chelostoma*

- 5(2). Parapsidal line punctiform (Fig. 81-2a) or rarely short-linear, one-fifth as long as tegula or usually less; body commonly with some greenish or bluish metallic color (holarctic) *Osmia* (in part)
- Parapsidal line linear, at least one-fourth as long as tegula (Fig. 81-2b); body nonmetallic 6
- 6(5). Mesopleuron elongate ventrally, as long as scutum or nearly so; mesopleural signum narrowly linear; stigma relatively large, margin within marginal cell convex (as in Fig. 81-1c) 7
- Mesopleuron short ventrally, much shorter than scutum, mesopleural signum short, not slender; stigma smaller, margin within marginal cell usually not convex (as in Fig. 81-1b, d) 10
- 7(6). Posterior edge of scutellum with premarginal carina, surface behind carina a narrow vertical or overhanging zone; clypeus with strong longitudinal carina (Africa, southern Asia) *Noteriades*
- Posterior margin of scutellum not carinate, usually without vertical or overhanging marginal zone; clypeus without longitudinal carina 8
- 8(7). Hypostomal area margined laterally by carina and fringe of long curled hair; acetabular interspace of mandible with short, oblique secondary ridge (Africa, India, Mediterranean region) *Pseudoheriades*
- Hypostomal area not carinate or fringed laterally; acetabular interspace of mandible without secondary ridge 9
- 9(8). Mouthparts long, in repose well exceeding proboscis fossa [except in paleartic *Stenoberiades asiaticus* (Friese) and *coelostoma* (Benoist), which have medially emarginate clypeus and bidentate mandibles] (Africa, Mediterranean region) *Stenoberiades*
- Mouthparts short, in repose not or scarcely exceeding proboscis fossa [paleartic species with clypeus not emarginate medially and mandible with at least three teeth] (holarctic, oriental, Africa) *Heriades*
- 10(6). Labrum with apical or preapical tuft of erect hair 11
- Labrum without apical or preapical tuft of erect hair, though often with marginal fringe 12
- 11(10). Pronotal lobe carinate (holarctic, Burma) *Protosmia*
- Pronotal lobe usually not carinate (South Africa) *Othinosmia* (in part)
- 12(10). Axilla spined or angulate 13
- Axilla rounded or slightly lobate 14
- 13(12). Metapleuron with round dorsal projection; S1 with apical spine (East Africa) *Othinosmia* (*Afrosomia*)
- Metapleuron planar, without round dorsal projection; S1 without apical spine (paleartic) *Hoplosmia*
- 14(12). Labrum with fringe of hairs near or on margin [weak in *Hoplitis* (*Bytinskia*) and (*Anthocopa*) *matheranensis* (Michener)] 15
- Labrum without fringe of hairs, disc sometimes with erect hairs that may be longest near the margin but are relatively sparse, not forming a distinct fringe 17
- 15(14). Posterior lateral angle of scutum acute or right-angular, and produced posteriorly or in *Wainia algoensis* (Brauns) upward as strong lamella [except South African *W. elizabethae* (Friese), in which entire propodeum is densely shagreened] (Africa to Israel and east to the Philippines) *Wainia* (in part)
- Posterior lateral angle of scutum not sharp, not produced posteriorly; propodeum at most partly shagreened 16
- 16(15). Metanotum with medial, dorsal spine, or clypeus rugose (paleartic) *Osmia* (*Allosmia*, some *Erythrosomia*)
- Metanotum not spined medially; clypeus not rugose (holarctic, Africa, India) *Hoplitis* (most subgenera)
- 17(14). Clypeus strongly overhanging labrum 18
- Clypeus scarcely overhanging labrum 19
- 18(17). T6 with preapical carina visible through dense pubescence; mouthparts with hooked hairs; clypeus without longitudinal carina (Mediterranean region, East Africa to central Asia) *Haetosmia*
- T6 without preapical carina; mouthparts without hooked hairs; clypeus with longitudinal carina, carina sometimes obscured by dense pubescence (southern Africa) *Wainia* (*Wainiella*)
- 19(17). Omaulus strongly carinate below nearly to mid-ventral line; clypeus and mandibles obscured by dense plumose hair (Egypt to China) *Stenosmia*
- Omaulus not carinate below; clypeus and mandibles with hair sparse, not obscuring surfaces (Asia) *Hoplitis* (*Kumobia*)

Key to the Genera of the Osmiini of the Western Hemisphere

1. Propodeum with narrow horizontal basal zone, set off from declivous posterior surface by a carina, and divided by carinae into a series of large pits (Fig. 81-3); anterior surface of T1 broadly concave and delimited by strong carina; lines delimiting propodeal triangle absent or feeble (holarctic, Mesoamerica) *Heriades*
- Propodeum without such a horizontal basal zone (but if pits and a zone set off by a carina are evident, then zone is usually sloping, and anterior surface of T1 is neither broadly concave nor delimited by strong carina); lines delimiting propodeal triangle distinct, at least as sharp changes in sculpturing 2
- 2(1). Parapsidal lines punctiform (Fig. 81-2a) or at most three times as long as wide; body usually metallic (holarctic, Mesoamerica) *Osmia*
- Parapsidal lines linear (Fig. 81-2b); body rarely metallic although sometimes strongly so 3
- 3(2). Thorax elongate (Fig. 81-6), a line tangent to anterior

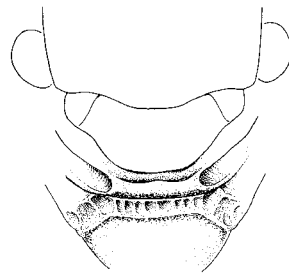


Figure 81-3. Middorsal part of metanotum and propodeum of *Heriades variolosa* (Cresson). Modified from Michener, McGinley, and Danforth, 1994.

- ends of tegulae is thus near middle of scutum, and ventral profile of mesepisternum, in front of middle coxa, is as long as dorsoventral thickness of thorax (seen in lateral view); apex of marginal cell curving away from wing margin only at extreme apex (Fig. 81-1c); S6 of male fully exposed; labrum of female with few and inconspicuous erect setae, thus often appearing hairless (holarctic) *Chelostoma*
- Thorax less elongate (Figs. 81-8, 81-10), a line tangent to anterior ends of tegulae is thus considerably anterior to middle of scutum, and ventral profile of mesepisternum, in front of middle coxa, is much shorter than dorsoventral thickness of thorax; apex of marginal cell usually curving away from wing margin in apical one-eighth or more of cell; S6 of male usually concealed or only its apical margin exposed; labrum of female with numerous erect setae 4
- 4(3). Posterior lobe of pronotum with several small vertical carinulae parallel to posterior margin; clypeus of female with apical, somewhat spatulate, slender horn (Fig. 81-13); T6 of male with median apical rounded flange and broad produced angle laterally (T7 of male not exposed) (paleartic; western North America) *Protosmia*
- Posterior lobe of pronotum usually without carinulae [but with carinulae in *Hoplitis* (*Aldidamea*) *pilosifrons* (Cresson) and others]; clypeus of female without apical horn; T6 of male not as described above 5
- 5(4). S1 of female with strong preapical bilobed process; S6 of female with median and apical spikes; posterior margins of T1 to T3 gently concave middorsally; S5 of male with deep midapical notch, its margin distally bearing a few capitate hairs (S6 of male without flaps such as are found in *Hoplitis*, broadly exposed; S1 convex in profile, its anterior surface not defined) (California) *Xeroheriades*
- S1 of female without strong preapical process; S6 of female without spikes or rarely with midapical spike; posterior margins of T1 to T3 straight middorsally; S5 of male not deeply notched, without capitate hairs on margin 6
- 6(5). S2 and S3 of male similar to one another; S5 and S6 of male hidden, largely membranous, only transverse apical marginal areas and lateral margins somewhat sclerotized, these sterna with large, basal, minutely hairy areas invaginated anteriorly into metasoma; distance from first submarginal crossvein to first recurrent usually twice distance from second recurrent vein to second submarginal crossvein (Fig. 81-1a); anterior surface of mesepisternum in front of omaulus smooth, shining, lower part usually sharply divided at omaulus from outer surface, lower part of omaulus carinate (except in subgenus *Iosmia*); male T6 with four strong teeth (Fig. 81-4) (except in subgenus *Iosmia*) (nearctic) *Ashmeadiella*
- S2 and S3 of male commonly quite different from one another; S5 or S6 of male, or both, usually exposed, broadly sclerotized, without large, anterior hairy areas; distance from first submarginal crossvein to first recurrent almost always less than twice distance from second recurrent vein to second submarginal crossvein; anterior surface of mesepisternum in front of omaulus usually with at least a few punctures near omaulus, which is not carinate; male T6 not four-toothed 7
- 7(6). S6 of male with basal, hairless translucent flaps (some-

times joined together) arising at gradulus and extending posteriorly, lying against ventral surface of sternum; body (except for most species of subgenera *Proteriades*, *Pentteriades*, and *Acrosmia*) rather elongate (Fig. 81-8), T1 with anterior surface not broadly concave or flat, not margined above by sharp line except sometimes medially, profile of T1 convex, not angulate; parapsidal line often over half as long as tegula (Fig. 81-2b); S2 of male usually not enlarged, not hiding middle of S3 margin, although the fully exposed S2 is sometimes emarginate and fringed, but rarely (subgenera *Pentteriades* and *Acrosmia*) S2 and S3 configured as in most species of *Osmia* and *Atoposmia* (holarctic) *Hoplitis*

— S6 of male without basal flaps; body robust, metasoma often almost globose; anterior surface of T1 a broad, concave or flat area margined above by a sharp line usually as long as one-half width of T1 although much less in some [e.g., *A. (Atoposmia) elongata* (Michener)], profile of T1 thus angulate at summit of anterior surface; parapsidal lines usually less than half as long as tegula; S2 of male nearly always much larger than S3, which is broadly emarginate and medially fringed, the fringe or at least sternal margin hidden medially by S2 (western North America, Mexico) *Atoposmia*

Genus *Afroheriades* Peters

Pseudoheriades (*Afroheriades*) Peters, 1970a: 157. Type species: *Pseudoheriades primus* Peters, 1970, by original designation.

Archeriades Peters, 1978a: 337. Type species: *Eriades larvatus* Friese, 1909, by original designation.

This genus contains heriadiform bees 4.0 to 8.5 mm long that differ from *Heriades* in having a relatively long proboscis (extending well beyond the fossa when in repose), in lacking a distinct carina surrounding the broadly concave anterior surface of T1, in lacking also an omaular carina, and in the large, exposed T7 of the male, which lies in a quadrate emargination of T6. As in *Chelostoma* the labrum of the female lacks the preapical tuft of large, erect hairs present in most *Heriades*, although a marginal row of erect hairs may be present. The inner margin of the mandible of the female sometimes bears a fringe of long hairs, as in *Chelostoma*. The preoccipital carina is present dorsally, absent laterally. The pronotal lobes are not carinate. The basal zone of the propodeum is not marked posteriorly by a carina. As in *Pseudoheriades*, the maxillary palpi are reduced to two segments, unlike those of nearly all other Osmiini. Illustrations of male genitalia and sterna are in Peters (1970a, 1978a).

■ *Afroheriades*, known only from South Africa, contains at least eight species, only five of them named (Griswold, 1985).

This genus contains a rather robust species, *Afroheriades primus* (Peters), and several slender species, such as *A. larvatus* (Friese), *dolicocephalus* (Friese), and *geminus* (Peters). The robust species could be called *Afroheriades* s. str., and the slender ones, subgenus *Archeriades*. In *A. primus*, which has a less elongate thorax, the metanotum is sloping and the basal area of the propodeum is well below the level of the scutellum and sloping, whereas, in the slender species, the scutellum, metanotum, and base of

the propodeum are almost in the same plane. Somewhat intermediate is *A. capensis* Griswold, MS. Females of *A. primus* are also unique among *Afroheriades* species in having a flat, polished hypostomal area bounded laterally by a carina and a row of curved hairs, thus suggesting females of *Pseudoheriades*, some *Stenoheriades*, *Osmia* (*Euthosmia*), *Hoplitis* (*Anthocopa*, *Chlidoplitis*), etc.

Genus *Ashmeadiella* Cockerell

Ashmeadiella consists of small (length 3.5–9.5 mm), robust, nonmetallic species with the metasoma sometimes red and the pubescence entirely pale and usually forming narrow apical fasciae on the terga. The distinctive and unique feature of the genus is the weak sclerotization of the hidden S5 and S6, and the invagination of each to form two minutely hairy flaps, as illustrated by Mitchell (1962), extending forward internally for a distance greater than the length of S4; because S2 and S3 are almost alike, the metasomal venter has four unmodified exposed sterna, S1 to S4. In almost all species the lower part of the omaulus is carinate, separating the smooth, impunctate, hairless preomaular part from the punctate and hairy postomaular part of the mesepisternum. In the subgenus *Isosmia*, although the carina is absent, the sharp change in sculpturing is evident. Some species of *Hoplitis* and *Osmia* have nearly as sharp a change in sculpturing at the omaulus. The venational character mentioned in the key to genera is likewise subject to variation. Except for *Isosmia*, the four-toothed T6 of the male, largely hiding the simple apex of T7 (Fig. 81-4), is also distinctive for the genus. Male genitalia and sterna were illustrated by Mitchell (1962).

The subgenus *Isosmia* has been included among the American group of “*Anthocopa*,” the other members of

which have been transferred to *Atoposmia* (Griswold and Michener, 1998). The sternal characters of the male, however, clearly show its relation to *Ashmeadiella*. A reasonable hypothesis is that *Isosmia* is the sister group to the rest of *Ashmeadiella*.

The genus is limited to North America. It was revised by Michener (1939a), and nearly all the species were revised by Hurd and Michener (1955).

Nests are made in holes in wood or stems, in burrows in the ground, or in spaces under rocks. Krombein (1967) reported on nests of several species of the subgenus *Ashmeadiella* s. str. and one of *Arogochila* in trap nests consisting of holes in wood. Cell partitions are made of gummy leaf pulp—probably leaf pulp mixed with nectar, gum, or resin—or less commonly of resin (or dried nectar?) alone, without leaf pulp. Rozen and Eickwort (1997) indicated the use of nectar mixed with leaf pulp as construction material by *Ashmeadiella*. Rozen (1987a) reported a nest of *A. (A.) leucozona* Cockerell in the ground with leaf pulp lining a cell. A nest of *A. (Isosmia) rubrella* (Michener) under a rock consisted of cells made of coarsely chewed flowers of *Dalea* (Yanega, 1994). But Rozen (1987a) reports cells of *A. (Chilosima) holtii* Cockerell in the ground, presumably in burrows made by the bees; the cells were made of soil somewhat harder than the surrounding soil, with no associated plant materials except probably nectar mixed with the soil of the cell walls.

The subgeneric name *Neoashmeadiella* Gupta (1990) is based on a species of *Megachile* (*Chelostomoda*).

Key to the Subgenera of *Ashmeadiella*

1. Omaulus not carinate; T6 of male not toothed
..... *A. (Isosmia)*
- . Omaulus carinate below; T6 of male with four teeth (Fig. 81-4) 2
- 2(1). Males 3
- . Females 5
- 3(2). Mandible tridentate *A. (Chilosima)*
- . Mandible bidentate 4
- 4(3). Lateral margin of T6 distinctly and rather evenly convex, ending at nearly right-angular apex of lateral tooth
..... *A. (Cubitognatha, Arogochila)*
- . Lateral margin of T6 straight, feebly convex, or sinuate, ending at acute apex of lateral tooth
..... *A. (Ashmeadiella s. str.)*
- 5(2). Outer side of mandible, as measured along lower carina, at most twice as long as scape [except in the group of *A. (A.) cubiceps* (Cresson)]; clypeus produced over base of labrum, clypeal apex usually truncate; well-developed pair of orange brushes beneath clypeal margin
..... *A. (Ashmeadiella s. str.)*
- . Outer side of mandible, as measured along lower carina, more than twice as long as scape; clypeus produced or not over base of labrum, but if produced, then not simply truncate; orange brushes beneath clypeal margin reduced or absent 6
- 6(5). Mandible bidentate, parallel-sided, elbowed; clypeal margin impunctate, upper margin protuberant
..... *A. (Cubitognatha)*
- . Mandible three- or four-toothed; clypeus punctured throughout, upper margin not protuberant 7

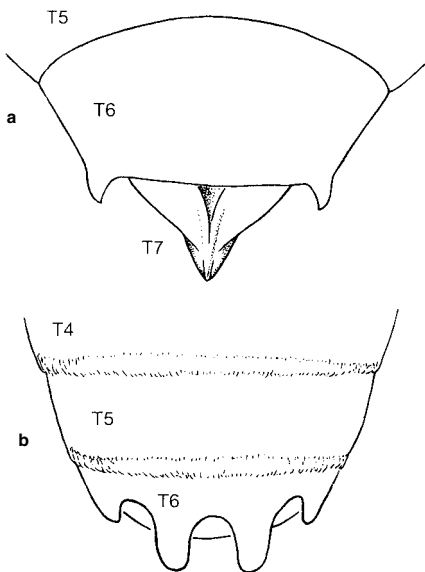


Figure 81-4. Apex of metasoma of male. **a**, *Hoplitis* (*Aldidamea*) *producta* (Cresson); **b**, *Ashmeadiella* (*Ashmeadiella*) *californica* (Ashmead). From Michener, McGinley, and Danforth, 1994.

- 7(6). Apex of clypeus irregularly rounded (not truncate or lobed) *A. (Chilosima)*
 —. Apex of clypeus with apical teeth or lobes, with at least a median broad truncation abruptly produced or with shoulder or small lobe at each side or a produced lateral angle *A. (Arogochila)*

Ashmeadiella / Subgenus *Arogochila* Michener

Ashmeadiella (Arogochila) Michener, 1939a: 58. Type species: *Ashmeadiella timberlakei* Michener, 1936, by original designation.

Ashmeadiella (Corythochila) Michener, 1939a: 74. Type species: *Ashmeadiella inyoensis* Michener, 1939, by original designation.

Ashmeadiella (Ramphorhina) Michener, 1939a: 8, *lapsus* for *Arogochila* Michener, 1939.

Ashmeadiella (Rhamphorhina) Michener and Sokal, 1957: 159, unjustified emendation of *Ramphorhina* Michener, 1939.

The relatively slender, three-toothed or occasionally four-toothed female mandible is similar to that of *Chilosima*. The female clypeal apex is often snoutlike or lobed, having at least a small lobe on each side of a truncation, or, in *Ashmeadiella (A.) foxiella* Michener, a truncation set off by an emargination at each side. In the group of *A. (A.) inyoensis* Michener, however, the middle of the clypeus is little produced, but there are strong apicolateral angles. This is the group formerly segregated as *Corythochila*.

■ *Arogochila* is found from western Texas and Idaho west to Baja California and Washington state, USA, and south to Puebla and Durango, Mexico. Most of the 18 species occur in xeric areas.

Ashmeadiella / Subgenus *Ashmeadiella* Cockerell s. str.

Ashmeadiella Cockerell, 1897c: 197. Type species: *Heriades opuntiae* Cockerell, 1897, by original designation.

Titusella Cockerell, 1906b: 445. Type species: *Titusella pronitens* Cockerell, 1906, monobasic.

This is by far the largest and most abundant subgenus of *Ashmeadiella*. Most females are characterized by the punctate, truncately produced clypeus resembling that found in most *Hoplitis* and *Osmia*, and the mandibles, which are somewhat shorter than those in other subgenera and tridentate. In the group of *A. (A.) cubiceps* (Cresson), formerly called subgenus *Titusella*, however, the clypeus is partly or largely impunctate, not produced and apically truncate, and the broad mandibles are longer, four- or five-toothed. This group intergrades completely with and seems to be a specialized derivative of ordinary *Ashmeadiella* s. str.; Figure 81-5 illustrates such an intermediate.

■ *Ashmeadiella* s. str. ranges from British Columbia, Canada, and Baja California, Mexico, east to North Dakota, Wisconsin, Indiana, and Texas, USA, with a disjunct area from North Carolina to Florida, USA; southward the subgenus reaches Yucatan and Morelos, Mexico. It is by far most abundant and speciose in the southwestern USA and northwestern Mexico. There are about 33 species.



Figure 81-5. *Ashmeadiella (Ashmeadiella) occipitalis* Michener. Above, male; Below, female. From Michener, McGinley, and Danforth, 1994.

Ashmeadiella / Subgenus *Chilosima* Michener

Ashmeadiella (Chilosima) Michener, 1939a: 78. Type species: *Ashmeadiella rhodognatha* Cockerell, 1924, by original designation.

Chilosima differs from all other subgenera in having three-toothed male mandibles. The lateral margins of T6 of the male are convex, about as in *Arogochila*, and the female resembles some species of that subgenus in having four-toothed, slender mandibles and lacking the orange brushes beneath the clypeal margin. Thus *Chilosima* shares derived characters with *Arogochila* and could be its sister group, possibly best treated as a group of *Arogochila*.

■ This subgenus ranges from western Texas to eastern California, USA, and south to Baja California, Sonora, and Coahuila, Mexico, in deserts. There are two species.

Ashmeadiella / Subgenus *Cubitognatha* Michener

Ashmeadiella (Cubitognatha) Michener, 1939a: 81. Type species: *Ashmeadiella xenomastax* Michener, 1939, by original designation.

Cubitognatha is easily recognized in the female by the unproduced clypeus and the slender, elbowed, bidentate mandibles. The male resembles that of *Arogochila*, suggesting that *Cubitognatha* may be nothing but a derivative of *Arogochila*. The lateral margins of T6 of the male *Cubitognatha*, however, are less convex than those of *Arogochila*, and *Cubitognatha* males might thus run to *Ashmeadiella* s. str. in the key to subgenera. The male of *Cubitognatha* differs from that of *Ashmeadiella* s. str. in the

strongly emarginate apex of its labrum, as in some *Arogochila*.

■ This subgenus occurs in the deserts of eastern California and Nevada, USA, and Baja California and Sonora, Mexico. The only species is *Ashmeadiella xenomastax* Michener.

Ashmeadiella / Subgenus *Isosmia* Michener and Sokal

Anthocopa (*Isosmia*) Michener and Sokal, 1957: 159. Type species: *Anthocopa rubrella* Michener, 1949, by original designation.

Isosmia lacks the derived features that have long been considered diagnostic for *Ashmeadiella*, i.e., the carina on the omaulus and the four teeth on T6 of the male. Its derived sternal characters clearly show that it is a member of the *Ashmeadiella* clade, however, and it is here included in that genus. It was formerly included in the group of American "*Anthocopa*," here relegated to the genus *Atoposmia*.

■ This subgenus occurs in deserts from western Texas to Nevada and eastern California, USA, and Coahuila to Sonora, Mexico. Two species are recognized.

Genus *Atoposmia* Cockerell

Atoposmia as here constituted contains most of the American species formerly placed in *Anthocopa*, which is here considered to be a palearctic subgenus of *Hoplitis*. *Atoposmia* differs from all American and most palearctic *Osmia* by the linear parapsidal lines, which are generally longer (one-third to one-half as long as the tegula) than those of the few palearctic species of *Osmia* that have linear parapsidal lines. Except for the subgenus *Hexosmia*, T6 of the male has a lateral tooth; occasional specimens of *Hexosmia* do have a very obtuse, rounded lateral angle. Lateral teeth on T6 are uncommon in *Osmia*. *Atoposmia* was at one time included in the *Anthocopa* group of *Hoplitis* because of the robust body form and linear parapsides, but it lacks the basal flaps on S6 of the male, which are characteristic of nearly all *Hoplitis*. The enlarged S2 and the medially emarginate, fringed, and largely hidden S3 are nearly always configured as in most *Osmia*; these are the principal characters that led me to transfer *Atoposmia* out of *Hoplitis*.

Key to the Subgenera of *Atoposmia*

1. Proboscis in repose extending behind fore coxa; first segment of labial palpus less than one-fourth as long as second *A. (Atoposmia s. str.)*
- Proboscis in repose hardly reaching fore coxa; first segment of labial palpus over one-half as long as second 2
- 2(1). Body with weak greenish tints; T6 of the male without lateral tooth or angle, or rarely with obtuse angle *A. (Hexosmia)*
- Body without greenish tints; T6 of male with lateral tooth or strong rounded angle *A. (Eremosmia)*

Atoposmia / Subgenus *Atoposmia* Cockerell s. str.

Osmia (*Atoposmia*) Cockerell, 1935a: 50. Type species: *Osmia triodontia* Cockerell, 1935, monobasic.

Atoposmia is black, the pubescence pale to partly black; the body length is 6 to 10 mm. T7 is exposed and basically with a pair of apical lobes between which is a tooth; either the lobes or the tooth, however, may be reduced. The proboscis is unusually long, and in some species the scope of the anterior and median sterna is unusually long. Mandibles of both sexes are three-toothed; those of the female vary from quite narrow medially to robust. The hind coxae are not or only weakly carinate.

■ This subgenus occurs from Baja California, Mexico, to Washington state, east to Montana, Colorado, and Arizona, USA, mostly in mountains. The 12 species were revised by Michener (1943) and Hurd and Michener (1955).

Atoposmia abjecta (Cresson) constructs clumps of cells of masticated plant material on the undersides of rocks (Parker, 1975b), whereas *A. elongata* Michener constructs clumps of cells of sand and masticated plant material in rock crevices (Parker, 1977a).

Atoposmia / Subgenus *Eremosmia* Michener

Anthocopa (*Eremosmia*) Michener, 1943: 66. Type species:

Osmia robustula Cockerell, 1935, by original designation.

Anthocopa (*Phaeosmia*) Michener, 1943: 77. Type species: *Osmia enceliae* Cockerell, 1935, by original designation.

Eremosmia consists of black, nonmetallic species with pale pubescence. The body length is 5.5 to 9.0 mm. The longitudinal carina on the inner ventral angle of the hind coxa is strong. T7 is rounded or has a median point; it is sometimes retracted and hidden.

■ *Eremosmia* ranges from Oklahoma and western Texas to coastal California, USA, and south to the states of Puebla and Morelos, Mexico. The 14 species were revised by Michener (1943) and Hurd and Michener (1955).

Parker (1975b, 1977a) described nests of *Atoposmia hypostomalis* (Michener) and *enceliae* (Cockerell) in pithy stems. Cell walls as well as partitions were made of a mixture of sand, chewed plant material, and probably secretions that resulted in a hard material. A nest of *A. beameri* (Michener) was in the soil, the cells composed entirely of soil particles possibly hardened with nectar (Yanega, 1994).

The mandibles of males vary from two- to three-toothed; this is one of the characters that led to the segregation of *Phaeosmia*. The reasons for not recognizing two subgenera are indicated by Hurd and Michener (1955).

Atoposmia / Subgenus *Hexosmia* Michener

Anthocopa (*Hexosmia*) Michener, 1943: 74. Type species: *Osmia copelandica* Cockerell, 1908, by original designation.

Hexosmia is the only group of *Atoposmia* with metallic coloration (weak, greenish). Body length is 5.5 to 7.0 mm. The carina of the hind coxa is weak or nearly absent. T6 of the male is edentate and broadly rounded, rarely with a vague obtuse angle laterally; T7 is hidden, but also broadly rounded.

■ This subgenus occurs from California to British Columbia, east to Wyoming, Colorado, and Arizona, USA. There are two species. A revision, in which probable geographic variants were regarded as species, was by Michener (1943); see also Hurd and Michener (1955).

Nests are in pithy stems, the cell walls and partitions being made of chewed plant material, sometimes mixed with sand (Parker, 1975b).

Genus *Bekilia* Benoist

Bekilia Benoist, 1962: 220. Type species: *Bekilia mimetica*

Benoist, 1962, by original designation.

This generic name was proposed for a *Heriades*-like bee presumed to be parasitic because of its lack of a distinct scopa. The type material cannot be found in the Paris Museum and it is not possible to determine its relationships; it is not included in the key to genera. It could be an anthidiine like *Afrostelis* rather than an osmiine.

■ *Bekilia* is from Madagascar. There is a single known species.

Genus *Chelostoma* Latreille

This genus consists of slender (Fig. 81-6), black heriadi-form bees, more attenuate and less coarsely sculptured than *Heriades*, mostly 3.4 to 9.0 mm long but some larger, *Chelostoma grande* (Nylander) attaining 14 mm. Although the preoccipital carina is present in the subgenus *Gyrodromella*, *Chelostoma* lacks the various other carinae found in *Heriades*. The parapsidal lines are usually half as long as the tegula to nearly as long as the tegula, but in *Chelostomas* str. they are shorter. T1, although somewhat concave on the anterior surface in the subgenus *Gyrodromella*, is usually convex except for the longitudinal depression, as in some *Hoplitis* (*Alcidamea*); T1 does not have a carina or even a line defining the anterior surface. The large depression or pit on the dorsal surface of T7 of the male is found also in many *Hoplitis* (*Alcidamea*); in some *Chelostoma* such as *C. (Prochelostoma) philadelphia* (Robertson) this depression reaches the tergal margin and is therefore not distinct. Also like some species of *Hoplitis* (*Alcidamea*), *Chelostoma* has a median elevation on S2 of the male. Females differ from most other osmiines in their nonfringed labrum, which is often elongate. Unlike *Alcidamea* and most other *Hoplitis*, the base of the labrum is exposed above the closed mandibles, and the mandible of the female is usually fringed with long hairs along the inner margin, and is usually widest at the base and taper-

ing to the rather narrow apex, which is bidentate or tridentate.

An unusual character of most species is that the axis of the third labial palpal segment continues the axis of the second, and only the fourth segment projects laterally. The known exceptions to this character (species with two laterally directed palpal segments) are the North American *Chelostoma philadelphia* (Robertson) (which has been placed in a separate genus or subgenus, *Prochelostoma*, primarily because of this character), the palearctic *C. petersi* (Tkalčú) (placed in *Ceraheriades*), and *C. aureocinctum* (Bingham) from Burma and neighboring countries (placed in *Eochelostoma*). These three species show no close relationship to one another, having in common principally the presumably ancestral palpal state.

Chelostoma is widespread in the holarctic region, ranging across North America and western and central Eurasia, but is unknown in China and Japan. It extends south to northern Mexico, northern Africa, and into the montane tropics in northeast India, Burma, and Thailand. In North America only nine native and two introduced species are known, but in Eurasia there are many species. Many and perhaps all species are oligolectic on particular floral taxa.

Nests are made in holes in wood, e.g., old beetle burrows, and in stems (see Westrich, 1989, and references therein; Krombein, 1967; and Parker, 1988). Partitions between cells are made of mud or sand grains, apparently stuck together with salivary secretion or nectar.

Key to the Subgenera of *Chelostoma*

(From Griswold and Michener, 1998)

1. Third segment of labial palpus flattened, its axis a continuation of that of second; T7 of male with dorsal pit 2
- Third segment of labial palpus not flattened, its axis directed laterally as in most megachilid bees; T7 of male without dorsal pit (male unknown in *Ceraheriades*) 4
- 2(1). Preoccipital carina present; propodeum with sloping basal zone little more than one-half as long as metanotum; T1 shallowly concave anteriorly (palearctic) *C. (Gyrodromella)*
- Preoccipital carina absent; propodeum with horizontal basal zone at least two-thirds as long as metanotum; T1 with anterior surface convex except for longitudinal groove 3
- 3(2). Parapsidal line half as long as tegula or more; S2 of male without sloping platform, or, if present, then not carinate; labrum of female less than twice as long as broad (longer in *C. isabellinum* Warncke) (holarctic) *C. (Foveosmia)*
- Parapsidal line less than half as long as tegula; S2 of male with median prominence, its posterior surface a flat sloping platform margined by carina; labrum of female elongate, nearly three times as long as broad or more (shorter in *C. nasutum* Pérez) (palearctic, introduced in nearctic) *C. (Chelostoma s. str.)*
- 4(1). Hind coxa not carinate (North America) *C. (Prochelostoma)*
- Hind coxa with longitudinal carina along inner ventral margin 5
- 5(4). T1 not concave on anterior surface; female mandible



Figure 81-6. Male of *Chelostoma (Foveosmia) californicum* Cresson. From Michener, McGinley, and Danforth, 1994.

- elongate, two-toothed; labrum apically thickened (central Asia) *C. (Ceraheriades)*
 —. T1 shallowly concave on anterior surface; female mandible not elongate, three-toothed; labrum not apically thickened (Himalayas to Thailand)
 *C. (Eochelostoma)*

Chelostoma / Subgenus *Ceraheriades* Tkalců

Archeriades (*Ceraheriades*) Tkalců, 1984a: 5. Type species:
Archeriades petersi Tkalců, 1984, by original designation.

This subgenus, known only in the female, resembles *Chelostoma* s. str. in its long mandibles, but differs from that genus in the labial palpi (see the key to subgenera) and in the elongate parapsides (half as long as the tegula or more). The head and other structures were illustrated by Tkalců (1984a).

■ The subgenus is from central Asia. The only species is *Chelostoma petersi* (Tkalců).

Chelostoma / Subgenus *Chelostoma* Latreille s. str.

Chelostoma Latreille, 1809: 161. Type species: *Apis maxillosa* Linnaeus, 1767 = *Apis florissomnis* Linnaeus, 1758, monobasic.

This subgenus differs from all other subgenera in the short parapsidal lines (see the key to subgenera). Most males differ from other subgenera in the carinate projection of S2, which often forms a margined platform on a large prominence, and in the dense covering of plumose or spatulate hairs on S4. The long labrum of the female (see the key to subgenera) (relatively short in *Chelostoma nasutum* Pérez) usually distinguishes this subgenus from others with similar labial palpi, and the elongate mandibles, the upper tooth of which is weak or absent, therefore bidentate, distinguish females from all others except *Ceraheriades*. In females of *C. (Foveosmia) foveolatum* (Morawitz), however, the mandibles are somewhat elongate and bidentate. Length ranges from 6 to 14 mm.

■ This is a palearctic subgenus, one species of which, *C. campanularum* (Kirby), is adventive in New York state, USA. Van der Zanden (in litt., 1993) indicated that there are 27 species.

Some variation among species is of interest. The projection of S2 in males is spatulate in *Chelostoma mocsaryi* Schletterer. In *C. diodon* Schletterer and *nasutum* Pérez, the platform is not margined by a carina, but, rather, weakly carinate, the carina not on the margin. In *C. transversum* (Friese) there is a low transverse carina on S2.

Chelostoma florissomne (Linnaeus) is oligolectic on *Ranunculus* (Ranunculaceae).

Chelostoma / Subgenus *Eochelostoma* Griswold

Chelostoma (*Eochelostoma*) Griswold, 1998, in Griswold and Michener, 1998: 216. Type species: *Heriades aureocincta* Bingham, 1897, by original designation.

This little-known subgenus differs from the others having plesiomorphic labial palpi (i.e., segments three and four directed laterally) in the concave anterior surface of T1 and the apically thickened labrum of the female. It is not possible to compare *Eochelostoma* fully with the subgenus *Ceraheriades*, the other Old World *Chelostoma*

with similar labial palpi, because the latter is known only in the female. *Ceraheriades*, however, has elongate, two-toothed mandibles in the female (as does *Chelostoma* s. str.), whereas they are short and three-toothed in *Eochelostoma*. Body length is 6 to 9 mm.

■ *Eochelostoma* is the only *Chelostoma* that occurs in the tropics; it is found in northeast India, Burma, and northern Thailand. The only species is *C. aureocinctum* (Bingham).

Chelostoma / Subgenus *Foveosmia* Warncke

Osmia (*Foveosmia*) Warncke, 1991c: 267. Type species: *Heriades foveolatus* Morawitz, 1868, by original designation.

Like those of the subgenus *Prochelostoma* but unlike those of *Chelostoma* s. str. and *Gyrodromella*, males of this subgenus have a low, rounded hump on S2. The labrum of the female is usually rather short, not much longer than broad although over 1.5 times as long as broad in *C. foveolatum* (Morawitz); that of the male has a transverse basal hump. The parapsidal lines are long (see the key to the subgenera). The gonostylus is slender apically (not clubbed), the penis valve being enlarged. Most species are small, but body length ranges from 4.5 to 10.0 mm. T7 of males varies from a single quadrate projection to trifid to four-toothed. *C. incisulum* Michener is four-toothed but the two median teeth are partly united, thus approaching the three-toothed condition. Male genitalia of American species were illustrated by Michener (1938b).

■ This subgenus is widespread in the palearctic region, although absent in China and Japan, and occurs also in the western part of North America, from Baja California, Mexico, to Washington and east to Utah, USA. There are 11 species in the palearctic region, according to van der Zanden (in litt., 1993), and eight in North America; all native American *Chelostoma* except *C. (Prochelostoma) philadelphia* (Robertson) fall in this subgenus. American species of the subgenus were revised by Michener (1938b) and Hurd and Michener (1955); Warncke (1991c) gave a key to Turkish species of the subgenus as he defined it.

Warncke (1991c) did not include such species as *Chelostoma campanularum* (Kirby), *distinctum* (Stoeckert), and *ventrale* Schletterer in *Foveosmia*. The pitted basal propodeal zone may distinguish *Foveosmia* from such forms, but since this character varies within *Chelostoma* s. str. and elsewhere, I do not think it alone is an appropriate subgeneric character.

The North American species are probably all oligolectic on *Phacelia* and *Eriodictyon* (Hydrophyllaceae) (personal observation), whereas European species are oligolectic on *Campanula* (Campanulaceae) (see Westrich, 1989).

Chelostoma / Subgenus *Gyrodromella* Michener

Gyrodroma Thomson, 1872: 259 (not Klug, 1807). Type species: *Heriades nigricornis* Nylander, 1848 = *Heriades rapunculi* Lepeletier, 1841, by designation of Cockerell, 1925b: 205.

Chelostoma (*Gyrodromella*) Michener, 1997: 27, replacement for *Gyrodroma* Thomson, 1872. Type species: *Heriades nigricornis* Nylander, 1848 = *Heriades rapunculi* Lepeletier, 1841, autobasic and by original designation.

Key to the Subgenera of *Heriades* (Males)
(Modified from Griswold, 1985)

1. S1 produced apically, with a brush of fine hair under margin (except in *Pachyheriades*); S2 depressed basomedially, with a hump or ridge apicolaterally; lateral line of T1 reaching spiracle 2
- S1 not produced apically, without a brush of hair under margin; S2 not depressed basomedially, without hump or ridge apicolaterally; lateral line of T1 not reaching spiracle 7
- 2(1). T6 with strong midapical projection below strong rounded carina; S1 produced posteriorly as keeled projection completely covering median part of S2; last antennal segment expanded, wider than preceding segments (central Asia to Israel) *H. (Rhopaloheriades)*
- T6 truncate or emarginate, transverse ridge, if present, apical; S1 produced as unkeeled projection not reaching apex of S2; last antennal segment not wider than other segments 3
- 3(2). Mandible with two teeth, though upper one may be broad and truncate; gradulus of S4 procurved medially 4
- Mandible with three teeth; gradulus of S4 straight, not procurved medially 5
- 4(3). Apex of S6 acutely angled; S2 at most angulate laterally, not notched (North and Central America) *H. (Neotrypetes)*
- Apex of S6 bilobate, truncate, or rounded; S2 distinctly notched laterally (Africa, oriental, palearctic) *H. (Michenerella)*
- 5(3). S2 without distinct fringe, at most with scattered hairs much shorter than hind basitarsal width; apical area of S2 transversely depressed below level of disc; basal zone of propodeum bounded posteriorly by a distinct carina that extends laterally behind spiracle; metanotum shallowly notched medially (Africa) *H. (Pachyheriades)*
- S2 with strong fringe of hair at least as long as width of hind basitarsus; apical area of S2 not depressed below level of disc; basal zone of propodeum not bounded posteriorly by a carina, or carina extremely weak, no carina posterior to spiracle; metanotum not notched medially 6
- 6(5). T6 with strong longitudinal crest abruptly terminated by a V-shaped, flattened apical area; mandible and hypostoma clothed in dense pubescence obscuring integument (southern Africa) *H. (Toxeriades)*
- T6 without longitudinal crest, contour not abruptly changed or flattened near margin; mandible with sparse hair not concealing surface, but hypostoma with narrow longitudinal strip of short plumose hair obscuring integument, surface otherwise visible (southern Africa) *H. (Tyttheriades)*
- 7(1). Frons and interantennal area with pair of juxtantennal carinae; T6 emarginate medially; T6 with U- or V-shaped raised area medially, without parallel-sided crest; S2 not notched laterally (Africa) *H. (Amboheriades)*
- Frons and interantennal area without juxtantennal carinae; T6 not emarginate medially and/or T6 medially with parallel-sided longitudinal crest (palearctic, Africa, India) *H. (Heriades s. str.)*

Key to the Subgenera of *Heriades* (Females)
(Modified from Griswold, 1985)

1. Frons and interantennal area with juxtantennal carinae (as in Fig. 10-3); S6 with short apical spike (Africa) *H. (Amboheriades)*
- Frons and interantennal area without juxtantennal carinae; S6 without apical spike 2
- 2(1). From North and Central America *H. (Neotrypetes)*
- From the Eastern Hemisphere 3
- 3(2). Lateral line of T1 short, not reaching spiracle (palearctic, Africa, India) *H. (Heriades s. str.)*
- Lateral line of T1 long, reaching spiracle 4
- 4(3). Scopa and ventral fringe of hind basitarsus strongly plumose (central Asia to Israel) *H. (Rhopaloheriades)*
- Scopa and ventral fringe of hind basitarsus consisting of simple hairs 5
- 5(4). Inner surface of fore tibia with a feltlike patch of hair (Africa, oriental, palearctic) *H. (Michenerella)* (in part)
- Inner surface of fore tibia without a feltlike patch of hair 6
- 6(5). Basal zone of propodeum horizontal or nearly so, bounded posteriorly by distinct carina, sometimes interrupted medially, that extends laterally behind spiracle 7
- Basal zone of propodeum sloping, without carina posteriorly, or with indistinct carina not extending laterally behind spiracle 8
- 7(6). Metanotum with shallow medial notch; scutum without transverse crest of dense, plumose hair anteriorly; acetabular carina prominent on basal half of mandible, abruptly truncated (Africa) *H. (Pachyheriades)*
- Metanotum with strong medial notch; scutum with transverse crest of dense, plumose hair anteriorly; acetabular carina absent or weak, not abruptly truncated (oriental, palearctic) *H. (Michenerella)* (in part)
- 8(6). Mandible with prominent acetabular carina above plane of outer surface of mandible; clypeal margin excavated, exposing base of labrum, thickened; majority of scopal hairs bent posteriorly near apices (southern Africa) *H. (Toxeriades)*
- Mandible without distinct acetabular carina; clypeal margin more or less straight, denticulate, slightly overhanging base of labrum, not thickened; scopal hairs straight, not bent near apices (southern Africa) *H. (Tyttheriades)*

Heriades / Subgenus *Amboheriades* Griswold

Heriades (Amboheriades) Griswold, 1998, in Griswold and Michener, 1998: 236. Type species: *Heriades canaliculata* Benoist, 1931, by original designation.

This is a subgenus having a particularly elongate, slender body form. The preoccipital carina is present at least laterally. The paired juxtantennal carinae are unique within the genus *Heriades*. The scutum is strongly curved down anteriorly, as in *Heriades s. str.* Illustrations of male genitalia and sterna were given for *H. pogonura* Benoist by Peters (1983).

■ This subgenus is widespread in Africa, from Gabon to Ethiopia, south to Namibia and South Africa. Eleven species were listed by Griswold (1985).

variations, the brushes are completely absent in some groups, such as *Hoplitis* (*Robertsonella*), that lack the translucent labroclypeal projections.

The American species of *Hoplitis* were revised by Michener (1947), by Timberlake and Michener (1950) for *Proteriades* in its traditional sense, and by Hurd and Michener (1955). Wu (1987b) gave a key to Chinese species. Van der Zanden (1988a) listed palearctic species.

Nests of *Hoplitis* are very diverse. Some species of the subgenus *Aldidamea* nest in pithy stems, and make partitions between cells from leaf pulp, sometimes supplemented with pith particles or pebbles (Parker, 1975b). Bees of the subgenus *Formicapis* make similar nests (Clement and Rust, 1975). Other *Hoplitis* nest in holes in wood, sometimes [as in *H. (Monumetha) fulgida* (Cresson)] making partitions from masticated leaf material and pebbles or bits of wood (Clement and Rust, 1976). *Hoplitis (Dasysmia) biscutellae* (Cockerell) constructs cells of resin and plant parts within abandoned cells of the wasp *Sceliphron* (Rust, 1980a) and in holes made by other insects in earthen banks. Even within the subgenus *Hoplitis* s. str. there is much diversity in nesting behavior, for *H. (H.) adunca* (Panzer) nests in holes in wood or stems, or in the soil, making partitions from sand, pebbles, and clay, while *H. (H.) anthocopoides* (Schenck) makes exposed nests of pebbles and mortar made of dry soil and saliva (Eickwort, 1973, 1975). Nests of at least some species of the subgenus *Anthocopa* are short burrows in the soil, each usually ending in a single cell lined with petals and closed with mud. Species making such nests were reported by Friese (1923), Cros (1937), Michener (1968c), and others; the most famous such species is *H. (Anthocopa) papaveris* (Latreille). Westrich (1989), Eickwort (1975), and Michener (1968a) describe nests and cells of various species, and give references to earlier works. Van der Zanden's (1988a) list will serve to show which of Westrich's "*Osmia*" species belong in *Hoplitis* (and in *Anthocopa*, here considered part of *Hoplitis*). In some cases, more details are given below in the accounts of subgenera.

In couplet 13 of the first key below, the options separate males and females. The female of *Exanthocopa* is not known to me but would run to couplet 30.

Key to the Subgenera of *Hoplitis* of the Eastern Hemisphere

(From Griswold and Michener, 1998)

1. Base of labrum exposed between closed mandibles and lower margin of clypeus; lateral basal extremity of labrum connected to lateral clypeal margin by yellowish membrane extending downward beside labral base (mandible of female rather slender, distinctly narrower at or before middle than at base) 2
- Base of labrum not or scarcely visible between closed mandibles and lower margin of clypeus [except in females of species like *H. (Anthocopa) cristatula* (Zanden) that have greatly modified clypeus and mandibles; in *H. (Microhoplitis)*; and in males of *Anthocopa* in which the basal labral zone is visible]; lateral basal extremity of labrum without yellowish membrane 13
- 2(1). Males 3
- Females 8
- 3(2). T7 bidentate, deeply emarginate between teeth 4

- T7 truncate, pointed, rounded, or tridentate, occasionally very shallowly emarginate medially but without deep medial notch 5
- 4(3). Mandible tridentate; S6 with truncate or bilobed apical extension densely haired throughout (palearctic to Sudan) *H. (Annosmia)*
- Mandible bidentate; S6 with longitudinal row of dense hairs on medial lobate extension (Iran, Baluchistan) *H. (Coloplitis)*
- 5(3). T7 tridentate, though lateral teeth may be reduced to right angles so that one sees principally a long median point; S6 with weak longitudinal ridge apically (eastern palearctic) *H. (Eurypariella)*
- T7 rounded or truncate; S6 without longitudinal ridge 6
- 6(5). T6 truncate produced between lateral teeth, margin of truncation with at least some irregularities, often crenulate; S6 with broad apical hyaline extension (palearctic) *H. (Hoplitis s. str.)*
- T6 roundly produced between lateral teeth, margin not irregular; S6 without differentiated apical extension 7
- 7(6). T7 very shallowly emarginate medially; clypeal margin weakly crenulate without narrow apical band (eastern Mediterranean) *H. (Bytinskia)*
- T7 truncate or rounded, not emarginate; clypeal margin smooth medially with narrow, impunctate apical band (central Asia) *H. (Kumobia)*
- 8(2). Mandible four-toothed; either clypeus thickened and modified or scopa reduced, longest hairs shorter than exposed parts of sterna 9
- Mandible three-toothed; clypeus not modified and scopa not reduced 10
- 9(8). Clypeus thickened, modified; scopa not reduced, sternal hairs erect (central Asia) *H. (Kumobia)*
- Clypeus neither thickened nor modified; scopa reduced, sternal hairs appressed, shorter than exposed parts of sterna (eastern Mediterranean; cleptoparasitic) *H. (Bytinskia)*
- 10(8). S6 with submarginal carina, sometimes extremely weak and visible only laterally, so that females may not differ appreciably from those of *H. (Annosmia)* (palearctic) *H. (Hoplitis s. str.)*
- S6 without submarginal carina 11
- 11(10). Labial palpus two-segmented, with abundant long, curled, capitate hair (Iran, Baluchistan) *H. (Coloplitis)*
- Labial palpus four-segmented, without hair or at most with scattered, short, straight hairs 12
- 12(11). Thorax steeply declivous behind posterior part of scutellum; apical spines of fore and middle tibiae each simple (palearctic to Sudan) *H. (Annosmia)*
- Thorax slanting posteriorly to posterior part of basal area of propodeum, behind which propodeum is steeply declivous; apical spines of fore and middle tibiae robust, each bifid or with preapical shoulder (eastern palearctic) *H. (Eurypariella)*
- 13(1). Males 14
- Females 27
- 14(13). T6 without lateral tooth; body length 13 mm or more (prestigma longer than stigma; T7 trifid) (Mediterranean region) *H. (Megahoplitis)*
- T6 with lateral tooth, sometimes weak, a mere angle in some small species (e.g., 6–8 mm long) 15

- 15(14). T7 deeply trifid, margins of middle tooth carinate to base; S6 without basal membranous flaps (T7 without middorsal pit) (palearctic south to Sudan) *H. (Pentadentostmia)*
- T7 pointed, truncate, rounded, bilobed, or four-lobed [except with three strong angles in *H. (Prionohoplitis) curvipes* (Morawitz) and trifid in *H. (Alcidamea) tridentata* (Dufour and Perris), in which middle tooth is not margined]; S6 with basal membranous flaps [except in *Exanthocopa*, *Nasutosmia*, and *H. (Anthocopa) matheranensis* (Michener)] 16
- 16(15). T7 medially bilobed, four-lobed, or produced and subtruncate, without middorsal pit 17
- T7 pointed, trifid, or rounded, commonly with middorsal pit 20
- 17(16). T1 without basal basin, with longitudinal depression not delimited above by transverse line or carina; T6 with low, obtuse lateral angle; T7 four-lobed, i.e., bilobed medially with large lateral tooth (northern holarctic) *H. (Formicapis)*
- T1 with basal flat or concave area delimited above at least medially by transverse line; T6 with strong, acute lateral tooth; T7 bilobed or produced and subtruncate [almost four-lobed in *H. (A.) matheranensis* (Michener) and *H. (A.) singularis* (Morawitz)] 18
- 18(17). S6 without differentiated triangular area (palearctic, Africa, India) *H. (Anthocopa)*
- S6 with differentiated median triangular area either margined by sharp carinae or projecting apically beyond rest of sternum 19
- 19(18). Flagellum slender, nearly cylindrical, flagellar segments 2-5 longer than broad, terminal flagellar segment simple; midtarsal segment 2 without elongate apical projection (northern Africa to Turkey) *H. (Platosmia)*
- Flagellum broad, concave ventrally, flagellar segments 2-5 twice as broad as long, terminal flagellar segment with apical buttonlike projection; midtarsal segment 2 with elongate anterior apical projection (Turkey) *H. (Chlidoplitis)*
- 20(16). Exposed part of S2 nearly half as long as metasoma, with strong basal transverse elevation and produced, truncate apex hiding median part of S3, which is strongly emarginate, fringed medially; S8 with two apical horns forming deep median emargination (Central and north-eastern Asia) *H. (Jaxartinula)*
- Exposed part of S2 much shorter, without elevation or tubercle at its base, S3 thus exposed medially, neither emarginate nor fringed medially; S8 not emarginate apically 21
- 21(20). S6 without membranous basal flaps (T7 with median apical point) 22
- S6 with membranous basal flaps appressed against undersurface of sternum (without transparent lateral inflexed flaps) 23
- 22(21). T7 with shallow middorsal depression or pit; S6 without lateral flaps; anterior surface of T1 with broad concave basin delimited above by transverse line and containing longitudinal median groove (northern Africa) *H. (Exanthocopa)*
- T7 without middorsal depression or pit; S6 with transparent inflexed flaps attached along lateral margins; T1 with anterior surface rather flat except for longitudinal medial groove not delimited above by transverse line (Mediterranean region) *H. (Nasutosmia)*
- 23(21). T7 scarcely exerted beyond T6, broadly rounded, without middorsal pit; S1 to S5 unmodified (Canary Islands) *H. (Microhoplitis)*
- T7 strongly produced beyond T6, variable in shape, often with middorsal pit or depression; sterna variously modified 24
- 24(23). T1 with distinct angle separating anterior and dorsal surfaces, angle extending across at least median half of width of tergum, anterior surface of T1 a broad basin; preoccipital ridge carinate or sharply angled (mandible bidentate) (palearctic) *H. (Prionohoplitis)*
- T1 without angle separating anterior and dorsal surfaces, or with angle extending less than half of tergal width, anterior surface of T1 without distinct broad basin; preoccipital ridge rounded [except *H. (Alcidamea) tridentata* (Dufour and Perris), in which mandible is tridentate] 25
- 25(24). S2 bearing strong transverse ridge with rather sharp crest; wings with dark papillae beyond closed cells; body with abundant yellow hair forming broad, distinct metasomal tergal bands (palearctic) *H. (Megalosmia)*
- S2 without strong transverse ridge, unmodified or with large tubercle; wings with weak papillae; body hairs not yellow, not forming broad, dense hair bands 26
- 26(25). S8 elongate, distal process ligulate, downcurved, undersurface of process with short modified hairs; S6 with midapical tuft of spreading hairs (holarctic) *H. (Monumetha)*
- S8 shorter, without long, downcurved distal process, hairs simple; S6 without apical tuft of spreading hairs (holarctic) *H. (Alcidamea)*
- 27(13). T1 with distinct angle separating anterior and dorsal surfaces, angle extending across at least median half of width of tergum; anterior surface of T1 a broad basin; fore basitarsus often with plumose hair 28
- T1 without angle separating anterior and dorsal surfaces, or angle extending less than half of tergal width [nearly half in *H. (Pentadentostmia) rufopicta* (Morawitz)]; anterior surface of T1 usually with longitudinal median depression; fore basitarsus without plumose hair 31
- 28(27). Preoccipital ridge carinate or sharply angled (palearctic) *H. (Prionohoplitis)*
- Preoccipital ridge rounded 29
- 29(28). Hypostoma shiny, with sparse punctures and hairs, but without differentiated area behind mandibular base and without fringe demarcating this area; fore basitarsus without plumose hairs (Canary Islands) *H. (Microhoplitis)*
- Hypostoma with somewhat differentiated, impunctate to sparsely punctate, shiny area near mandibular base, hair in this area sparse or absent [except in *H. (Anthocopa) bisulca* (Gerstaecker)], this area margined laterally by strong fringe of long curled hair [fringe weak in *H. (A.) bisulca* and *singularis* (Morawitz)]; fore basitarsus usually with plumose hair 30
- 30(29). Clypeal margin with narrow, parallel-sided median notch; hind tibial spurs stout, strongly hooked apically; fore basitarsus with simple hair; outer apex of middle tibia with acute spine (Turkey) *H. (Chlidoplitis)*
- Clypeal margin without notch, rarely with wide, angled

- emargination; hind tibial spurs slender, straight; fore basitarsus with plumose hair [but hair absent in *H. (A.) furcula* (Morawitz) and *H. (A.) picicornis* (Morawitz) and sparse and not evident in worn specimens of *H. (A.) matheranensis* (Michener)]; outer apex of middle tibia with narrow to broadly rounded lobe (paleartic, Africa, India) *H. (Anthocopa)*
- 31(27). Clypeus not overhanging labrum, with anteriorly projecting snout 32
- . Clypeus overhanging labrum, without anteriorly projecting snout 33
- 32(31). Mandible four-toothed; propodeum and anterior surface of T1 shiny (Mediterranean region) *H. (Nasutosmia)*
- . Mandible three-toothed (long, straight or undulate edge between middle and upper tooth); propodeum and anterior surface of T1 shagreened (northern holarctic) *H. (Formicapis)*
- 33(31). Mandible with long, slightly convex margin between second and uppermost teeth, thus possibly four-toothed; median part of metanotum elevated and strongly convex, attaining level of scutellar convexity, so that line tangent to scutal and scutellar convexities is also tangent to metanotum, as seen in profile (Central and northeastern Asia) *H. (Jaxartinula)*
- . Mandible without long margin between second and uppermost teeth; median part of metanotum not elevated and thus below line tangent to scutal and scutellar convexities, as seen in profile 34
- 34(33). Mandible four-toothed 35
- . Mandible three-toothed 36
- 35(34). Wings with dark papillae beyond closed cells; metasoma with distinct broad yellow hair bands (paleartic) *H. (Megalosmia)* (in part)
- . Wings with weak papillae beyond closed cells, papillae not dark; metasoma with weak white hair bands interrupted medially (holartic) *H. (Monumetha)*
- 36(34). Mandible greatly broadened apically, twice as wide as at narrowest point or nearly so; abductor swelling of mandible large, light-colored 37
- . Mandible scarcely broadened apically, little wider than at narrowest point; abductor swelling of mandible small, dark 38
- 37(36). Wings clear or only lightly stained; pubescence white or off-white; frons below anterior ocellus without impunctate polished area (paleartic south to Sudan) *H. (Pentadentosmia)*
- . Wings strongly stained, especially darkened in marginal cell; pubescence yellow; frons below anterior ocellus impunctate and polished (paleartic) *H. (Megalosmia)* (in part)
- 38(36). Apex of front basitarsus and second tarsal segment with strong, upcurved, capitate setae on outer surface; upper mandibular tooth truncate (Mediterranean region) *H. (Megahoplitis)*
- . Front tarsus without such modified setae; upper mandibular tooth acute 39
- 39(38). Proboscis in repose not or scarcely extending beyond fossa; clypeus quite flat, not convex above, somewhat flared outward to broad truncation; suture between clypeus and supraclypeal area weak; body form robust, suggesting subgenus *Anthocopa* (northern Africa to Turkey) *H. (Platosmia)*

- . Proboscis in repose extending at least a little beyond fossa; clypeus usually somewhat convex above, usually not flared toward truncation [except in *H. tridentata* (Dufour and Perris), *mitis* (Nylander), etc.]; suture between clypeus and supraclypeal area usually distinct; body form slender (holartic) *H. (Aldicamea)*

Key to the Subgenera of *Hoplitis* of the Western Hemisphere (Males)

1. S6 with longitudinal median hairy ridge, sometimes extending as median process beyond rest of sternum or consisting primarily of a midapical hairy process; T7 bilobed, sometimes only weakly so [except tridentate with lateral spine longer than median spine in *H. (Proteriades) xerophila* (Cockerell)]; metasoma commonly partly or wholly red, never metallic 2
- . S6 without longitudinal median hairy ridge or midapical process (but with a tuft of hairs in *Monumetha*); T7 ending in a truncation, convexity, or point [tridentate with median spine longer than lateral spine in *Cyrtosmia* and *H. (Dasysomia) biscutellae* (Cockerell)]; metasoma black or brownish black, sometimes metallic 5
- 2(1). Galeal blade and first two segments of labial palpus with numerous strong hairs that are hooked or wavy apically (western nearctic) *H. (Proteriades)*
- . Galeal blade and labial palpus without hooked or wavy hairs (or, in *Penteriades*, with very few) 3
- 3(2). Basal half of flagellum with some hairs as long as flagellar diameter; apex of last antennal segment produced laterally (western nearctic) *H. (Acrosomia)*
- . Flagellum with all hairs short; apex of last antennal segment unmodified or rarely tapering to a curved point 4
- 4(3). Proboscis scarcely extending beyond proboscoidal fossa in repose; hind coxa with longitudinal carina on inner ventral angle (western nearctic) *H. (Penteriades)*
- . Proboscis extending well beyond proboscoidal fossa in repose; hind coxa without longitudinal carina (western nearctic) *H. (Hoplitina)*
- 5(1). Mandible tridentate; T6 with median apical as well as lateral tooth; T7 tapering with three small adjacent teeth (western nearctic) *H. (Cyrtosmia)*
- . Mandible bidentate; T6 without median apical tooth except in *Dasysomia*; T7 pointed, rounded, or truncate or, if tridentate (one species of *Dasysomia*), then not tapering, teeth widely separated 6
- 6(5). Metanotum approximately on same level as scutellum, a line tangent to scutum and scutellum in profile thus nearly touching metanotum; stigma distinctly broader than prestigma, as measured to wing margin 7
- . Metanotum depressed below level of scutellum, which curves down posteriorly to meet metanotum, a line tangent to scutum and scutellum in profile thus well above metanotum; stigma smaller, about as broad as prestigma, as measured to wing margin 8
- 7(6). First recurrent vein nearly meeting first submarginal crossvein; T7 four-lobed (northern holarctic) *H. (Formicapis)*
- . First recurrent vein considerably distal to first submarginal crossvein; T7 rounded (eastern nearctic) *H. (Robertsonella)*

- 8(6). Hind coxa with large, flattened ventral tooth; T6 with median apical angle or tooth (western nearctic) *H. (Dasyosmia)*
- Hind coxa without tooth; T6 without median apical angle or tooth 9
- 9(8). Lateral basal extremity of labrum connected to clypeal margin by yellowish membrane extending downward beside labral base; S1 to S5 not modified (introduced, New York State) *H. (Hoplitis s. str.)*
- Lateral basal angles of labrum without yellowish membrane; one or more of S1 to S5 with projection, spine, or other modification 10
- 10(9). S8 elongate, distal process downcurved, ligulate, undersurface with short, modified hairs; S6 with midapical tuft of spreading hairs; antennal pedicel exposed [partly hidden in *H. (M.) spoliata* (Provancher)] (holarctic) *H. (Monumetha)*
- S8 without long, downcurved distal process, its hairs simple; S6 without tuft of spreading hairs; antennal pedicel largely hidden by invagination into apex of scape (holarctic) *H. (Alcidamea)*

Key to the Subgenera of *Hoplitis* of the Western Hemisphere (Females)

- Galeal blade and first two segments of labial palpus with numerous strong hairs, these hooked or wavy apically; proboscis short, in repose scarcely extending out of proboscival fossa (T6 not strongly concave in profile; posterior coxa with longitudinal carina on inner ventral angle; metasoma usually partly or wholly red) 2
- Galeal blade and labial palpus without hooked hairs; proboscis longer, in repose extending well beyond limit of proboscival fossa (except in *Acrosmia*) 3
- 2(1). Maxillary palpus five-segmented; clypeus with upper two-thirds strongly swollen and shining, nearly impunctate medially (western nearctic) *H. (Penteriades)*
- Maxillary palpus two- to four-segmented; clypeus uniformly convex, punctures moderately dense to crowded (western nearctic) *H. (Proteriades)*
- 3(1). Metanotum approximately on same level as scutellum, a line tangent to scutum and scutellum in profile thus nearly touching metanotum; stigma distinctly broader than prestigma, as measured to wing margin 4
- Metanotum depressed below level of scutellum, which curves down posteriorly to meet metanotum, a line tangent to scutum and scutellum in profile thus well above metanotum; stigma smaller, about as broad as prestigma, as measured to wing margin 5
- 4(3). Mandibular apical width nearly half of mandibular length; mandible tridentate; lower margin of clypeus entire; first recurrent vein considerably distal to first submarginal crossvein (eastern nearctic) *H. (Robertsonella)*
- Mandibular apical margin more than half of mandibular length; mandible with two lower apical teeth followed by long undulate margin; lower margin of clypeus with median snoutlike projection; first recurrent vein nearly meeting first submarginal crossvein (northern holarctic) *H. (Formicapis)*
- 5(3). Mandible clearly four-toothed (holarctic) *H. (Monumetha)*
- Mandible three-toothed, sometimes with a weak convexity between second and third teeth 6
- 6(5). Median mandibular tooth almost twice as far from upper tooth as from lower tooth, with a weak convexity between median and upper teeth, the convexity sometimes worn so as to yield a long undulating margin above median tooth; S6 with longitudinal median ridge ending in apical tooth (western nearctic) *H. (Cyrtosmia)*
- Median mandibular tooth more nearly midway between upper and lower teeth; S6 without median longitudinal ridge 7
- 7(6). Proboscis short, in repose not extending beyond proboscival fossa (western nearctic) *H. (Acrosmia)*
- Proboscis longer, in repose extending well beyond proboscival fossa 8
- 8(7). T6 nearly straight in profile; metasoma partly red (western nearctic) *H. (Hoplitina)*
- T6 distinctly concave in profile; metasoma without red 9
- 9(8). Apex of mandible nearly as broad as eye; distal part of fore wing with minute papillae, median part with very few hairs (western nearctic) *H. (Dasyosmia)*
- Apex of mandible much narrower than eye; fore wing uniformly finely hairy, without papillate areas 10
- 10(9). Base of labrum exposed when mandibles are closed; lateral basal extremity of labrum connected to clypeal margin by yellowish membrane extending downward beside labral base (introduced, New York State) *H. (Hoplitis s. str.)*
- Base of labrum hidden when mandibles are closed; lateral basal angles of labrum without yellowish membrane (holarctic) *H. (Alcidamea)*

Hoplitis / Subgenus *Acrosmia* Michener

Hoplitis (*Acrosmia*) Michener, 1947: 298. Type species: *Hoplitis plagiostoma* Michener, 1947, by original designation.

Acrosmia, a member of the *Proteriades* group of subgenera, is rather robust (like *Proteriades*), 7.5 to 8.5 mm in body length, usually black but the metasoma sometimes red, and the pubescence pale. The antenna of the male is distinctive, with a few long hairs on at least the basal half of the flagellum and with the last flagellar segment produced to one side. The clypeus of the male is unusually short and broad; that of the female has a large basal convexity suggestive of that of *Penteriades*. Although the proboscis lacks the specialized hairs characteristic of *Proteriades*, it is short as in that subgenus, not extending beyond the proboscival fossa in repose.

■ This subgenus is known from the mountains of California to Washington state, east to Idaho and Wyoming, USA. The five species were revised by Griswold (1983).

Parker (1978a) described nests of *Hoplitis plagiostoma* Michener in pithy stems; partitions and end plugs were made of masticated plant material containing sand, soil particles, or seeds.

Hoplitis / Subgenus *Alcidamea* Cresson

Alcidamea Cresson, 1864: 385. Type species: *Alcidamea producta* Cresson, 1864, by designation of Michener, 1941: 158.

Osmia (*Acanthosmia*) Thomson, 1872: 233. [Species first included by Schmiedeknecht, 1885: 21.] Type species: *Osmia*

are hooked or wavy at the tips; the maxillary palpi are two- to four-segmented. Male genitalia, sterna, and other structures were illustrated by Parker (1976, 1977c).

■ *Proteriades* occurs in California, Nevada, and New Mexico, USA, south to Coahuila and Baja California, Mexico. The 22 species were revised by Timberlake and Michener (1950) and by Hurd and Michener (1955).

The names *Cephalapis* and *Xerosmia* were proposed for single species that have numerous special derived features. There seems to be little point in giving such forms subgeneric recognition, although a second *Xerosmia*, *Hoplitis* (*Proteriades*) *zuni* (Parker), has been found.

Like species of the subgenus *Penteriades*, those of *Proteriades* visit the minute flowers of *Cryptantha* (Boraginaceae), drawing the pollen out with the hooked hairs on the proboscis. Nests of *Proteriades* have been found in holes in the ground, in old bee cells in a bank, and in holes in galls and stems. Parker (1976, 1977c, 1978a) described numerous nests in pithy stems. Partitions and nest closures are made of sand grains or pebbles and masticated plant parts, or, for a few species, resin and masticated plant material or sand.

Hoplitis Subgenus *Robertsonella* Titus

Robertsonella Titus, 1904a: 22. Type species: *Robertsonella gleasoni* Titus, 1904, by original designation.

Robertsonella contains small (5-8 mm long) black species with pale hair, having about the same slender hoplitiform aspect as small species of the subgenus *Alcidamea*. The thorax, however, has a more elongate form than that of *Alcidamea*, as shown by the elevated metanotum, reaching almost to the level of the scutellum and scutum, as indicated in the keys to subgenera. Among American *Hoplitis*, only *Formicapis* has a similar thorax. In the male, seven terga and six sterna are exposed; T7 is rounded posteriorly. On S6 of the male the basal flaps are very short, although recognizable. An unusual male character is the extremely dense, short white hair of the clypeus, completely concealing the clypeal surface and superficially suggesting the pale clypeus common in males of many other bees.

■ This subgenus is found in eastern North America from Connecticut to Georgia west to central Texas and Kansas. The three species were differentiated by Mitchell (1962).

Genus *Hoplosmia* Thomson

This genus consists of somewhat robust hoplitiform, nonmetallic bees, much like *Hoplitis* but with acutely pointed axillae (Fig. 81-9a). The pale pubescence usually forms tergal fasciae; body length is 6.5 to 10.0 mm. Unlike those of most *Hoplitis*, the maxillary palpi are four-segmented. T6 of the male is sometimes toothed laterally, as in most *Hoplitis*. A distinctive feature is the preapical, commonly nodulose or multidentate carina or thickening on T6 of the male. T7 of the male is variable: pointed, rounded, subtruncate, or bilobed (Fig. 81-9b, c). In females, except *H. fallax* (Pérez), the scopal hairs are crinkled, a feature not found in related taxa. Supporting the exclusion of *Hoplosmia* from *Hoplitis* is the lack of basal flaps on S6 of the male. Tkalců (1974c) illustrated male genitalia and other structures.

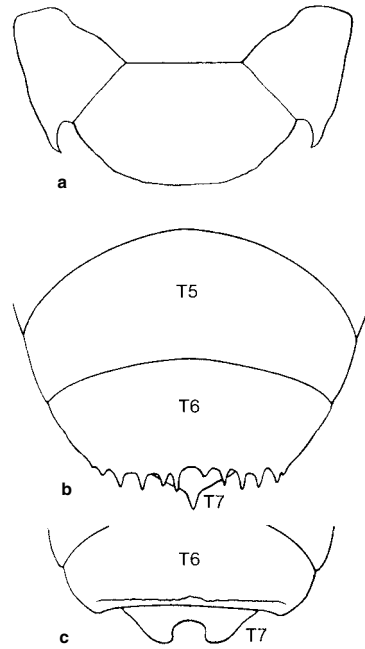


Figure 81-9. Structures of *Hoplosmia*. **a**, Scutellum and axillae of *H. (Hoplosmia) spinulosa* (Kirby); **b**, Apex of male metasoma of *H. (Hoplosmia) spinulosa* (Kirby), the terga numbered; **c**, Same, of *H. (Odontanthocopa) bidentata* (Morawitz). Modified from drawings by B. Tkalců, 1974c.

Recognition of *Hoplosmia* as a genus rather than as a subgenus of *Hoplitis* is arbitrary, given the few apomorphies recognized. *H. scutellaris* Morawitz (and possibly other species) is unusual in that there are carinae on the pronotal lobe, as in *Protosmia* and *Othinosmia*.

Key to the Subgenera of *Hoplosmia* (Males)

1. Carina of T6 with numerous spines (Fig. 81-9b); T6 with distinct lateral tooth; T7 produced to median spine (Fig. 81-9b) *H. (Hoplosmia) s. str.*
- Carina of T6 simple, irregularly crenulate or nodulose (Fig. 81-9c); lateral tooth of T6 absent or very blunt; T7 not produced to spine 2
- 2(1). T7 broad, subtruncate, much exserted, exposed part thus as long as T6 *H. (Paranthocopa)*
- T7 bidentate or bilobed with median apical emargination (Fig. 81-9c), or rounded, exposed part much shorter than T6 *H. (Odontanthocopa)*

Key to the Subgenera of *Hoplosmia* (Females)

1. Scutellum not overhanging metanotum *H. (Odontanthocopa)* (in part)
- Scutellum overhanging metanotum 2
- 2(1). Body clothed with reddish hair that obscures frons and scutum *H. (Paranthocopa)*
- Body clothed with off-white hair that does not obscure frons and scutum 3
- 3(2). Preoccipital margin carinate dorsally; scopal hairs slender, crinkly, not blunted apically; hind basitarsus at least four times as long as broad *H. (Hoplosmia) s. str.*
- Preoccipital margin not carinate dorsally though rather

abruptly angled; scopal hairs stout, smooth, blunted apically; hind basitarsus three times as long as broad
 *H. (Odontanthocopa)* (in part)

Hoplosmia / Subgenus *Hoplosmia* Thomson s. str.

Osmia (*Hoplosmia*) Thomson, 1872: 233, no included species; Schmiedeknecht, 1884: 23, included species. Type species: *Apis spinulosa* Kirby, 1802, by designation of Michener, 1941a: 161.

Distinctive characters are indicated in the key to subgenera, and in more detail by Tkalců (1974c).

■ This subgenus is found from Northern Europe to the Mediterranean and Egypt. The three species were included in the revision by Tkalců (1974c).

Hoplosmia / Subgenus *Odontanthocopa* Tkalců

Anthocopa (*Odontanthocopa*) Tkalců, 1974c: 125. Type species: *Osmia bidentata* Morawitz, 1876, by original designation.

Anthocopa (*Odonterythrosmia*) Tkalců, 1974c: 131. Type species: *Osmia fallax* Pérez, 1895, by original designation.

The subgeneric characters are indicated in the key to subgenera and in greater detail by Tkalců (1974c).

■ This subgenus is found in the Mediterranean basin and southeastern Europe. There are nine species (Zanden, 1988a).

Tkalců (1974c) separated one species, *Hoplosmia fallax* (Pérez), placing it by itself in a subgenus *Odonterythrosmia*, primarily on the basis of the broader hind basitarsus of the female and the largely red color of T1 to T3. Its relationship seems better indicated by including it in *Odontanthocopa*.

Hoplosmia / Subgenus *Paranthocopa* Tkalců

Anthocopa (*Paranthocopa*) Tkalců, 1974c: 132. Type species: *Osmia pinquis* Pérez, 1895, by original designation.

The subgeneric characters are indicated in the key to subgenera, and in more detail by Tkalců (1974c).

■ The subgenus is found in northern Africa and Israel. The only species is *Hoplosmia pinquis* (Pérez).

Genus *Noteriades* Cockerell

Heriades (*Noteriades*) Cockerell, 1931b: 332. Type species: *Megachile tricarinata* Bingham, 1903, by original designation.

This is a genus of short, compact hoplitiform bees, 4.5 to 10.0 mm long, that are characterized by the strong longitudinal carina on the clypeus, the complete preoccipital carina, the vertical propodeal profile (lacking a basal zone), and the posteriorly carinate scutellum. The wide apical hyaline rim of the female T6 is suggestive of *Pseudoheriades* and *Afroheriades*. *Noteriades* is the only osmiine, other than *Osmia* subgenus *Monosmia*, with two tibial spines on the front and middle legs, the anterior spine small and blunt. An unexpected plesiomorphy is the distinct volsella with recognizable digitus and cuspis.

■ *Noteriades* is found in both temperate and tropical parts of sub-Saharan Africa and in southern Asia (Thailand, Burma, India). There are nine recognized species

(Griswold, 1985, 1994a) and a few undescribed ones, for a total of possibly 15.

Nests are unknown, but a female was seen at the entrance to a burrow in wood (Griswold, 1985).

Genus *Ochreriades* Mavromoustakis

Ochreriades Mavromoustakis, 1956: 226. Type species: *Eriades fasciatus* Friese, 1899, by original designation.

This genus consists of heriadiform species 7 to 10 mm in body length, even more elongate and slender than *Chelostoma*, to which it is allied. It differs in having yellow or ivory integumental markings and an enlarged pronotum that extends the cylindrical shape of the thorax forward, well in front of the scutum, virtually eliminating the pre-aular surface of the mesepisternum as well as the anterior surface of the scutum. These are unique features in the Osmiini. The long mouthparts suggest that these bees may be floral specialists.

■ This rare genus appears to have a disjunct distribution; it is known from the Middle East (Israel, Jordan, Syria) and from Namibia, one species from each area. The two species were reviewed by Griswold (1994b).

Genus *Osmia* Panzer

This large genus includes the common, robust, megachiliform, more or less metallic Osmiinae. In addition, it includes many nonmetallic forms. Some subgenera, such as *Allosmia*, are rather elongate, more or less hoplitiform, but the elongate form in this case is due to the long metasoma, the thorax being rather short, and the posterior edge of the scutellum as well as the metanotum and propodeum being steeply declivous. Thus the thorax of *Osmia* and usually the whole body form is similar to that of *Hoplitis* subgenus *Anthocopa* (Fig. 81-10). An exception is *O. (Pyrosmia) cephalotes* Morawitz, in which the body, including the thorax, is elongate (scutellum nearly flat, metanotum and base of propodeum sloping but nearer horizontal than vertical), although other members of its subgenus are robust, like ordinary species of *Osmia*.

All Osmiini with punctiform or very short parapsidal lines belong to this genus, but the subgenus *Allosmia*, some species of the subgenera *Erythrosmia* and *Tergosmia*,



Figure 81-10. Female of *Osmia* (*Osmia*) *lignaria* Say. From Michener, McGinley, and Danforth, 1994.

palearctic and nearctic species of *Osmia*. In Europe, many are nonmetallic, and most of those that are metallic are only weakly so. On the other hand, many of the species in various subgenera are conspicuous because of abundant red or orange hair. American species, except *O. (Diceratosmia) azteca* Cresson, lack abundant red or orange hair; a few species of *Melanosmia* have reddish thoracic hairs. In America there are relatively few nonmetallic species, many are strongly metallic (Pl. 6), and a considerable group (including unrelated sections of the subgenus *Melanosmia* and one species of *Osmia* s. str.) consists of brilliantly metallic green, blue, or even purple species. (The generally nonmetallic genus *Hoplitis* includes three brilliant-green North American species in the subgenus *Monumetha*. Perhaps bees influence the evolution of color in their relatives living in the same area, possibly through mimetic complexes.)

In the two species mentioned in couplet 4 of the first key below, and in some others, the marginal groove of S4 is extremely narrow, the sternal margin is translucent, and a carina is extremely close to the margin. One would never recognize it by the description "two apical carinae," but it is not a simple, thin margin.

Key to the Subgenera of *Osmia* of the Eastern Hemisphere (Males)

1. Malar space with minimum length over half basal width of first flagellar segment; middle femur somewhat broadened basal to middle by rounded angle on undersurface; penis valves attaining apices of gonoforceps, which are slender and parallel-sided medially 2
- Malar space absent or linear, its minimum length half basal width of first flagellar segment or less; middle femur without rounded premedian angle on undersurface; penis valves not attaining apices of gonoforceps, or, if so, then gonoforceps usually robust and tapering throughout 4
- 2(1). Proboscis of ordinary length, usually not reaching beyond middle of thorax in repose; anterior surface of T1 shagreened; antenna usually reaching propodeum and middle flagellar segments usually over twice as long as broad *O. (Osmia* s. str.)
- Proboscis extremely long, reaching metasoma in repose; anterior surface of T1 shiny; antenna not reaching propodeum, middle flagellar segments less than twice as long as broad 3
- 3(2). Front tibia with two apical spines, a shorter one posterior to usual single spine; metasomal terga with diffuse pale hairs but no fasciae; S2 large, nearly completely hiding S3, which is emarginate and fringed; T6 entire, T7 with feeble apical emargination *O. (Monosmia)*
- Front tibia with usual single apical spine; metasomal terga with broad apical bands of dense white plumose hairs; S2 not enlarged, S3 fully exposed, not emarginate, with small, dense midapical fringe; T6 with small apical emargination, T7 entire *O. (Orientosmia)*
- 4(1). S4 with posterior margin not thin, with two apical carinae, at least laterally (the distal one being the sternal margin) and intervening narrow hairless groove along margin [often visible only in posterior view, and absent although margin rather thick in a few species such as *O. (Pyrosmia) versicolor* Latreille and *ferruginea* Latreille] 5

- S4 with posterior margin thin, without double carinae and groove 7
- 5(4). T7 ending in long, slender, heavily sclerotized, blunt-tipped process; S2 and S3 similar to one another, both exposed, transverse, each with transverse shining gibbosity, that on S3 broken medially *O. (Ozbekosmia)*
- T7 relatively short, margin medially emarginate, two-, three-, or rarely four-toothed, rarely entire and rounded; S2 large, covering much of S3, which has fringed emargination, these sterna without gibbosities 6
- 6(5). Margin of T6 medially projecting posteriorly or with median notch or crenulate; S5 simple, without velvety hair on disc or basal or lateral ridges; S6 without longitudinal groove, margin without projecting lobe *O. (Helicosmia)*
- Margin of T6 medially gently convex, not crenulate or notched; S5 with velvety hair on disc or ridges; S6 with longitudinal groove, margin with projecting lobe *O. (Pyrosmia)*
- 7(4). Mandible three-toothed, middle tooth well separated from upper tooth by deep notch, upper tooth sometimes broad, truncate or even concave, so that mandible could be considered four-toothed 8
- Mandible two-toothed, upper tooth sometimes broad, truncate or even concave, so that mandible could be considered three-toothed, but in the latter case middle angle not separated from upper angle by deep notch 10
- 8(7). T6 with strong posterolateral tooth; T7 not visible in dorsal view *O. (Hemiosmia)*
- T6 without posterolateral tooth; T7 visible in dorsal view 9
- 9(8). First flagellar segment at least three times as long as broad; apical margin of S3 with hair-filled notch *O. (Neosmia)*
- First flagellar segment at most two times as long as broad; apical margin of S3, like S2 and S4, transverse, without hair-filled notch *O. (Tergosmia)*
- 10(7). Hind coxa with strong longitudinal carina along inner ventral margin; parapsidal lines usually short-linear (nonmetallic) 11
- Hind coxa without longitudinal carina along inner ventral margin, or, if with ridge in location of carina, then ridge usually punctate, not raised and shining; parapsidal lines punctiform 12
- 11(10). T7 apically a simple process, much thickened and heavily sclerotized, flattened on dorsal surface and margined almost like a pygidial plate; S2 with flat-topped, bare longitudinal ridge apically almost to margin; maxillary palpus five-segmented *O. (Allosmia)*
- T7 bifid or bilobed, thin, not particularly heavily sclerotized, not flattened on dorsal surface; S2 apically thin, rounded or feebly emarginate medially, hairy; maxillary palpus four-segmented or with minute apical fifth segment *O. (Erythrosmia)*
- 12(10). Anterior margin of metanotum sharp, elevated approximately to level of scutellar surface and with space between metanotal crest and posterior margin of scutellum; S2 with posterior margin transverse *O. (Metallinella)*
- Anterior margin of metanotum below level of most of scutellum, which is curved down to metanotal margin; S2 with posterior margin broadly convex, sometimes with small median emargination *O. (Melanosmia)*

Key to the Subgenera of *Osmia* of the Eastern Hemisphere (Females)

1. Claws cleft, inner ramus shorter than outer; anterior edge of metanotum sharp, elevated approximately to level of scutellar surface; space present between crest of metanotum and scutellum *O. (Metallinella)*
- Claws simple; anterior edge of metanotum below level of most of scutellum, i.e., scutellar surface curved down to margin of metanotum [except in long-bodied species of *Pyrosmia* (e.g., *O. cephalotes* Morawitz) in which metanotum is horizontal, on level with scutellum]; ordinarily no space between edge of metanotum and scutellum 2
- 2(1). Head with small, usually bare and shiny depression immediately behind lower end of eye, i.e., below posterior margin of eye (body commonly covered with long, loose hairs rarely forming metasomal fasciae) *O. (Osmia s. str.)*
- Head without small depression immediately behind lower end of eye, although depression directly below or in front of lower end of eye, or occupying much of malar area, sometimes present 3
- 3(2). Depression across mandibular base deep and abruptly set off almost vertically from adjacent flat mandibular surface (Fig. 81-12d); orange hairs beneath clypeal margin arranged in four tufts, except when clypeus is highly modified, in which case there may be two broad tufts, or no orange hairs *O. (Helicosmia)*
- Depression across mandibular base absent or shallower, rarely completely separated from adjacent mandibular surface by vertical wall [some *Melanosmia*, e.g., *O. nigriventris* (Zetterstedt), approach the condition of *Helicosmia*]; orange hairs under clypeal margin in two tufts or brushes, or absent 4
- 4(3). Malar space, where shortest, as long as width of pedicel; proboscis extremely long, reaching metasoma in repose.....5
- Malar space, where shortest, much shorter than width of pedicel; proboscis not reaching beyond middle of thorax in repose 6
- 5(4). Front tibia with two apical spines, a short one posterior to usual single spine; metasomal terga with diffuse pale hairs not forming fasciae *O. (Monosmia)*
- Front tibia with single apical spine; metasomal terga with broad apical fasciae of dense, white plumose hairs.. *O. (Orientosmia)*
- 6(4). Hind coxa with strong longitudinal carina along inner margin and body nonmetallic, metasoma sometimes red; parapsidal lines usually short-linear, sometimes punctiform; erect tergal hair (middorsally on T2-T3, as seen in profile, ignoring apical tergal margins) sometimes no longer than minimum width of first flagellar segment 7
- Hind coxa not or weakly carinate, or, if carinate, then body metallic, if with ridge in location of coxal carina (as in some *Hemiosmia*, *Pyrosmia*, *Tergosmia*, etc.), then ridge usually punctate, not raised and shining as in above; parapsidal lines punctiform or sometimes short-linear in *Tergosmia*; erect tergal hair much longer than minimum width of first flagellar segment 8
- 7(6). Maxillary palpus distinctly five-segmented *O. (Allosmia)*

- Maxillary palpus four-segmented or with minute apical fifth segment *O. (Erythrosomia)*
- 8(6). First flagellar segment nearly three to more than three times as long as wide *O. (Neosmia)*
- First flagellar segment not over 2.5 times as long as wide 9
- 9(8). Anterior trochanter with longitudinal ventral carina or sharp ridge that is most prominent medially so that lower edge of trochanter, in side view, is convex; mandible in ventrolateral view with strong submedian tooth on inner margin of lower edge (mandible four-toothed or approaching that condition because of distinct cutting edge forming tooth in upper interspace) *O. (Hemiosmia)*
- Anterior trochanter without longitudinal ventral carina or sharp ridge, lower edge of trochanter, in side view, nearly straight; mandible usually without submedian tooth on inner margin of lower edge [but present in *O. (Melanosmia) inermis* (Zetterstedt)] 10
- 10(9). Hind coxa with longitudinal carina on inner ventral margin; clypeal margin usually with median impression (mandible usually three-toothed without cutting edge in upper interspace) *O. (Pyrosmia)*
- Hind coxa without longitudinal carina on inner ventral margin; clypeal margin without median impression 11
- 11(10). Body frequently slightly to strongly metallic; pubescence often including black or fuscous hairs; mandible commonly four-toothed, usually because of cutting edge in upper interspace *O. (Melanosmia)*
- Body black, nonmetallic; pubescence mostly yellowish white; mandible three-toothed without cutting edge in upper interspace 12
- 12(11). Anterior margin of clypeus produced and rounded; impunctate hairless area behind mandibular base overhung by long, curved hairs *O. (Ozbekosmia)*
- Anterior margin of clypeus produced and truncate; impunctate area behind mandibular base limited and not extensively overhung by long hairs *O. (Tergosmia)*

Key to the Subgenera of *Osmia* of the Western Hemisphere

1. Hind coxa with strong longitudinal carina along inner ventral angle; parapsidal line somewhat elongate *O. (Diceratosmia)*
- Hind coxa not carinate; parapsidal line punctiform 2
- 2(1). Malar space as long as width of scape; small shining depression in genal area below and behind lowermost point of eye margin *O. (Osmia s. str.)*
- Malar area shorter than width of scape, except in forms with anterior clypeal margin greatly swollen; no small shiny depression below eye 3
- 3(2). Males 4
- Females 10
- 4(3). S2 transverse, posterior margin feebly concave, straight, to slightly convex; S3 not or weakly emarginate medially, exposed from side to side, posterior margin not or gently concave 5
- S2 large, posterior margin strongly convex; S3 medially hidden by S2, posterior margin broadly emarginate with fringe of long hairs in emargination 7
- 5(4). Genal area wider than greatest width of eye, as seen from side; pubescence partly black *O. (Cephalosmia)*

- Genal area narrower than eye, as seen from side; pubescence white 6
- 6(5). Median flagellar segments 1.5 times as long as broad; T6 prolonged medially over T7 *O. (Mystacosmia)*
- Median flagellar segments 1.9 times as long as broad; T6 with posterior margin evenly convex, not conspicuously prolonged over T7 *O. (Euthosmia)*
- 7(4). S4 with apical margin laterally consisting of two carinae between which is a narrow, hairless, shiny groove *O. (Helicosmia)*
- S4 with apical margin thin, without groove 8
- 8(7). S2 with protuberance, tooth, or spine on median apical or subapical area (or median band of long hair in *O. integra* Cresson); male gonoforceps with small, slender appendage, usually arising preapically; mandible slender medially, apex (measured from apex of apical tooth to upper apical angle) at least 1.5 times width at constriction and usually wider than base (Fig. 81-12a) *O. (Acanthosmioides)*
- S2 without protuberance, tooth, or spine; male gonoforceps usually tapering from preapical angle to apex, rarely [as in *O. (Melanosmia) tanneri* Sandhouse] with distal preapical process; mandible usually widest at base or subequal at base and apex 9
- 9(8). Forewing with hairs about half as long as width of stigma; middle flagellar segments twice as long as wide *O. (Trichinosmia)*
- Forewing with hairs much less than half as long as width of stigma; middle flagellar segments less than twice as long as wide (except in *O. bucephala* Cresson) *O. (Melanosmia)*
- 10(3). Clypeal margin with strong lateral tooth and small median tooth; forewing with hairs half as long as width of stigma *O. (Trichinosmia)*
- Clypeal margin not so modified; forewing with hairs much less than half as long as width of stigma 11
- 11(10). Orange hairs beneath clypeal margin arranged in four tufts; depression across mandibular base deep and set off almost vertically from adjacent mandibular surface and commonly emphasized by mandibular swelling just distal to depression (Fig. 81-12d) *O. (Helicosmia)*
- Orange hairs beneath clypeal margin arranged in two tufts or brushes, or sometimes absent; depression across mandibular base usually less abrupt or absent and not emphasized by swelling distal to it [an exception is *O. (Melanosmia) bucephala* Cresson] 12
- 12(11). Clypeal punctures large, well separated by smooth ground or largely absent; genal area twice as wide as eye, as seen from side; eyes diverging downward *O. (Cephalosmia)*
- Clypeal punctures smaller, confluent at least on lower half of clypeus; genal area usually less than twice as wide as eye, as seen from side; eyes almost always converging downward or parallel 13
- 13(12). Mandible constricted near base, expanded distally to apex that is nearly twice as wide as constriction (Fig. 81-12a, c) (mandible tridentate or with small intercalary tooth between second and third teeth) *O. (Acanthosmioides, Melanosmia)* (in part)
- Mandible less constricted near base and less expanded apically, apex thus usually less than 1.5 times as wide as constriction 14

- 14(13). Clypeus without tufts or brushes of orange hairs beneath margin; scopal hairs restricted on each sternum to a band half as wide as distance from gradulus to sternal margin *O. (Euthosmia)*
- Clypeus with two tufts or brushes of orange hairs beneath margin; scopal hairs occupying larger area on each sternum *O. (Melanosmia)* (in part), *O. (Mystacosmia)*

Osmia / Subgenus *Acanthosmioides* Ashmead

Acanthosmioides Ashmead, 1899a: 76. Type species: *Osmia odontogaster* Cockerell, 1897, by original designation.
Acanthosmiades Titus, 1904b: 101, incorrect subsequent spelling of *Acanthosmioides* Ashmead, 1899.

This is a subgenus of metallic green or blue species, almost always with some black hairs; the body length ranges from 6 to 14 mm. *Acanthosmioides* is related to *Melanosmia* and is sometimes difficult to distinguish from that subgenus. The principal distinguishing characters are indicated in the key to subgenera.

■ *Acanthosmioides* is found throughout western North America, from Yukon, Canada, to Baja California, Mexico, east throughout the Rocky Mountain area and to North Dakota. There are 22 species. The subgenus was revised by White (1952), who also included Sinha's (1958) Group II of *Nothosmia*. White had no males of that group; males would have excluded this group from *Acanthosmioides*.

In a group of small desert species [Sinha's (1958) Group II of *Nothosmia*], the males fall in *Melanosmia* but the female mandible is constricted before the middle and broadened into a tridentate apex about twice as wide as the constriction. Thus the female mandible is like that of *Acanthosmioides* (Fig. 81-12d); tentatively I place this group in *Melanosmia*.

Another group that presents a similar problem is the species of "*Centrosmia*" as understood by Sinha and Michener (1958), except for *Osmia bucephala* Cresson, the type species of *Centrosmia*. The females are not distinguishable from those of *Acanthosmioides*, but the males lack the features of S2 and of the gonoforceps that characterize *Acanthosmioides*, although the gonoforceps of some species are rather intermediate.

This subgenus is almost certainly derived from *Melanosmia*, making the latter a paraphyletic group. Since there is no great morphological gap between *Melanosmia* and *Acanthosmioides*, the two could be united. I delay doing so until *Melanosmia* can be more fully studied and the relation of *Acanthosmioides* verified.

Some species of *Acanthosmioides* make shallow nest burrows in the soil (Rozen and Favreau, 1967). Other species excavate burrows in pithy stems or construct cells on sheltered surfaces, e.g., the underside of a rock. The cells are made of mud (Rust, Thorp, and Torchio, 1974) or of chewed plant material (Rozen and Favreau, 1967) or of both (Parker, 1975a). See also Gordon (2003).

Species of this subgenus have also been placed in the American subgenus *Diceratosmia*. Characters common to both *Diceratosmia* and *Pyrosomia* include the doubly carinate posterior margin of the male S4, at least laterally; the carinate hind coxae, at least in females; the slightly elongate rather than strictly punctiform parapsidal lines; and the short, mostly pale pubescence, often forming narrow white apical fasciae on the terga. Although both Warncke and van der Zanden have separated the palearctic species subgenerically from the American species, the differences are not very impressive, and recognition of a single holarctic subgenus is reasonable. The hind coxa in *Pyrosomia* is less strongly carinate or, in males, may lack a carina, whereas in *Diceratosmia* the carina is strong in both sexes and usually continues to the ventral apical angle of the coxa. In *Pyrosomia*, T6 of the male is simple or obtusely angulate laterally and not produced medially, whereas in *Diceratosmia* it is strongly angled laterally and has a broad median apical projection. S6, as noted above, has a longitudinal median groove in *Pyrosomia* that is lacking in *Diceratosmia*.

Osmia (*Pyrosomia*) *cephalotes* Morawitz belongs to this subgenus, as shown by the trifid male T7 and other characters, but as noted in the discussions of the tribe and the genus *Osmia*, it has an elongate body, like a *Chelostoma* or slender species of *Hoplitis*.

Nests are made in holes in wood, stems, galls, etc., and *Osmia versicolor* Latreille and *ferruginea* Latreille nest in snail shells. Cell partitions are of leaf pulp.

Osmia / Subgenus *Tergosmia* Warncke

Osmia (*Tergosmia*) Warncke, 1988a: 390. Type species: *Osmia tergestensis* Ducke, 1897, by original designation.

This subgenus contains rather ordinary-looking, robust, nonmetallic species 6.5 to 13.0 mm long. The clypeus of the female is truncate and overhangs the base of the labrum, as in most *Osmia* species, but lacks the brushes of orange hairs. The mandibles of the female are narrower medially than at the base, and three-toothed. The parapsidal lines are variable, more or less punctiform in *O. (T.) agilis* Morawitz and *lunata* Benoist, but short-linear in *O. (T.) rhodoensis* (Zanden). The most noteworthy character is the simple, transverse S2 to S4 of the male, as in the subgenus *Ozbekosmia* and the very different *Orientosmia*. An unusual character is the strong emargination of S5, which is usually filled with hair. T6 is simple, T7 bilobed to bispinose. Structures were illustrated by Tkalců (1994).

■ This subgenus occurs in the Mediterranean basin and in Uzbekistan and Turkmenistan. The six species were reviewed by Warncke (1988a). One of his species, *Osmia avosetta* Warncke, is out of place here and has been transferred to the subgenus *Ozbekosmia*, but another species was added by Tkalců (1994).

Osmia / Subgenus *Trichinosmia* Sinha

Osmia (*Trichinosmia*) Sinha, 1958: 244. Type species: *Osmia latisulcata* Michener, 1936, by original designation.

Among the relatives of *Melanosmia*, this subgenus can be recognized by the unusually long and branched hair of

the head and thorax as well as the long wing hairs and the female clypeal and male antennal characters indicated in the key to subgenera. The hairs are mixed black and white; the body is metallic green, its length 9 to 10 mm.

■ This subgenus occurs in the southwestern USA, from California and Arizona to Utah. The only species is *Osmia latisulcata* Michener.

Nests have been found in holes in wood blocks; cells are made of sand mixed with leaf pulp and apparently a secretion (Parker, 1984).

Genus *Othinosmia* Michener

This genus is related to *Protosmia* and has been included within that genus (e.g., Griswold, 1985), with which it agrees (except for *Othinosmia* subgenus *Afrosomia*) in the carinulae of the pronotal lobe. It also agrees with *Protosmia* (*Protosmia* s. str. and *Nanosmia*) in the general shape of the thorax, with its sloping metanotum and the indistinct, sloping basal zone of the propodeum. Distinctive features are the preapical transverse carina on the male T6, the lack of a lateral flap on the same tergum, and the exposed T7 of the male, which may be short and rounded to subtruncate or produced to a rather long point. Except in the subgenus *Afrosomia*, there is a mid-apical notch in S1 of the male; such a notch is absent in *Protosmia*. In both sexes the lateral line on T1 is long, attaining the level of the spiracle, and the summit of the metapleuron lacks a carina. In *Protosmia* the lateral line on T1 is shorter, and an upper metapleural carina is visible from beneath.

Unlike the holarctic genus *Protosmia*, *Othinosmia* is restricted to sub-Saharan Africa.

Key to the Subgenera of *Othinosmia* (Males)

(By Terry L. Griswold)

1. Front tibia with apical spine long, curved posteriorly; S2 not depressed medially, without dense covering of hair; hypostomal area with polished, impunctate area (southern Africa) *O. (Othinosmia) s. str.*
- Front tibia with apical spine short, straight; S2 depressed medially, densely covered with velvety hair; hypostomal area without polished, impunctate area 2
- 2(1). Metapleuron with large dorsal projection; axilla produced to acute angle (Kenya) *O. (Afrosomia)*
- Metapleuron without dorsal projection; axilla rounded (southern Africa) *O. (Megaloheriades)*

Key to the Subgenera of *Othinosmia* (Females)

(By Terry L. Griswold)

1. Metapleuron with dorsal projection; axilla produced to acute angle; body length 9 to 11 mm (pronotal lobe with carina) (Kenya) *O. (Afrosomia)*
- Metapleuron without dorsal projection; axilla rounded; body length 5 to 8 mm 2
- 2(1). Front tibia with long, curved apical spine; clypeus not overhanging labrum, base of labrum visible when mandibles are closed (pronotal lobe without carina) (southern Africa) *O. (Othinosmia) s. str.*
- Front tibial spine short, nearly straight; clypeus at least slightly overhanging labrum, base of labrum not visible when mandibles are closed (southern Africa) *O. (Megaloheriades)*

***Othinosmia* / Subgenus *Afrosmia* Griswold**

Protosmia (*Afrosmia*) Griswold, 1998, in Griswold and Michener, 1998: 239. Type species: *Othinosmia stupenda* Griswold, 1994, by original designation.

The lone species of this subgenus is larger than other *Othinosmia*, and differs further in lacking carinulae behind the carina on the pronotal lobe, and in the angularly produced axilla, and the upper metapleural projection. These features suggest a relationship to *Stenoheriades*, although none is unique to *Stenoheriades* and *Afrosmia*. The preapical carina of T6 of the male, the small (rounded) T7, etc., support placement in *Othinosmia*. Male genitalia and sterna were illustrated by Griswold (1994a).

■ *Afrosmia* is known only from Kenya. The only known species is *Othinosmia stupenda* Griswold.

***Othinosmia* / Subgenus *Megaloheriades* Peters**

Megaloheriades Peters, 1984: 366. Type species: *Osmia schultzei* Friese, 1909, by original designation.

In this subgenus the pronotal lobe is carinate or not (Griswold, 1985). The principal subgeneric characters are indicated in the key to subgenera.

■ This subgenus is known only from Cape Province, South Africa, and Namibia. Griswold (1985) listed seven species.

Nests are made of pebbles and resin, exposed on twigs or rocks, at least in the case of *Othinosmia* (*M.*) *globicola* (Stadelmann) (Michener, 1968a).

***Othinosmia* / Subgenus *Othinosmia* Michener**

s. str.

Anthocopa (*Othinosmia*) Michener, 1943: 86. Type species: *Thaumatostoma moniliferum* Cockerell, 1932, by original designation.

The principal subgeneric characters are indicated in the key to subgenera. Others are the convex margin of S4 of the male and the apically widened gonostylus. The receding clypeus of the female, exposing the base of the labrum, is characteristic of the subgenus. Peters (1984) illustrated the genitalia and hidden sterna.

■ This subgenus is known only from Cape Province, South Africa, and Namibia. The five known species were listed by Griswold (1985).

The elongate flagellum of males of some species led to placement of the type species in *Thaumatostoma*, a subgenus of *Megachile*. The only other osmiines with such antennae are the Burmese *Protosmia* (*Dolichosmia*) *burmanica* (Bingham) and some of the *Heriades* from southern Asia, such as *H. (Michenerella) testaceicornis* (Cameron).

Nests, so far as is known, are in holes in the ground, the cells lined with resin (Michener, 1968a).

Genus *Protosmia* Ducke

This genus contains more or less heriadiform or nearly megachiliform bees, generally of small size (body length 3.5–9.5 mm). In many ways, *Protosmia* and *Othinosmia* bridge the gap between the *Heriades*-like and *Osmia*-like sections of Osmiini, as indicated in the account of the

tribe Osmiini. In some *Protosmia* and some *Othinosmia* the pronotal lobe lacks a carina (as in many other Osmiini) but, except in *Othinosmia stupenda* (Griswold) and *P. burmanica* (Bingham), it has, behind the carina or the location where it would be, several small carinulae. Such carinulae are absent in most other Osmiini. The axillae are rounded. The basal zone of the propodeum is sloping, not delimited by a carina (except it is more horizontal and pitted in the subgenera *Chelostomopsis* and *Dolichosmia*). T1 lacks a carina, the anterior surface being flat or somewhat concave. T6 of the male lacks a preapical carina and has a lateral flap (this not verified for *Dolichosmia*) that is hidden when the metasoma is in repose. As in *Wainia*, T7 of the male is not exposed. Male genitalia and sterna were illustrated by Popov (1961) and Tkalců (1978b).

Four subgenera are recognized, as in the key below. The genus has a disjunct distribution—the Mediterranean region to northern India and Burma, and one species in western North America.

Key to the Subgenera of *Protosmia* (Males)

(By Terry L. Griswold)

1. S1 with large ventral projection; margin of T6 acutely angled laterally; flagellum modified 2
- S1 without ventral projection; margin of T6 not acutely angled laterally; flagellum not modified 3
- 2(1). Gena with elongate lateroventral fovea or crease; distal flagellar segments stout (palearctic) *P. (Protosmia s. str.)*
- Gena without lateroventral fovea; distal flagellar segments, except the last, threadlike (Burma) *P. (Dolichosmia)*
- 3(1). T6 in dorsal view with strongly projecting median lobe; pronotal lobe not carinate; S2 with median longitudinal line of short, appressed hairs, these quite different from long, erect hairs of adjacent areas (Mediterranean region, western nearctic) *P. (Chelostomopsis)*
- T6 in dorsal view with weakly projecting median lobe; pronotal lobe carinate; S2 without median longitudinal line of short hairs (Mediterranean region) *P. (Nanosmia)*

Key to the Subgenera of *Protosmia* (Females)

(By Terry L. Griswold)

1. Mandible elongate, its maximum length approximately equal to maximum clypeal width; gena much wider than eye in lateral view (Mediterranean region, western nearctic) *P. (Chelostomopsis)*
- Mandible not elongate, its maximum length at most two-thirds maximum clypeal width; gena little if any wider than eye in lateral view 2
- 2(1). Body slender, metasoma elongate; pronotal lobe without carinules in addition to carina; posterior surface of front tibia with patch of dense, velvety hair near apex (Burma) *P. (Dolichosmia)*
- Body stout, metasoma not elongate; pronotal lobe with carinules in addition to carina; posterior surface of front tibia sparsely haired 3
- 3(2). T1 (and usually T2) with narrow, distinct impunctate margins; flagellum clavate (palearctic) *P. (Protosmia s. str.)*
- T1 and T2 without impunctate margins; flagellum nearly cylindrical (Mediterranean region) *P. (Nanosmia)*

Key to the Subgenera of *Wainia*

1. Metasomal pale hair bands of T2 to T4, except laterally on basal terga, immediately behind graduli, not on posterior marginal zones of terga; mandible of male three-toothed (Africa to southern India and the Philippines) *W.* (*Wainia* s. str.)
- Metasomal pale hair bands on posterior marginal zones of terga; mandible of male two-toothed 2
- 2(1). Body heriadiform, 6-8 mm long; omaular carina distinct; female clypeus with longitudinal median carina; tibial spurs strongly hooked; labrum of female without well-formed fringe (Africa) *W.* (*Wainiella*)
- Body robust hoplitiform, 8.0-10.5 mm long; omaular carina absent; female without clypeal carina; tibial spurs weakly curved at apices; labrum of female with distinct fringe (southern Africa and Israel) *Caposmia*

***Wainia* / Subgenus *Caposmia* Peters**

Osmia (*Caposmia*) Peters, 1984: 378. Type species: *Osmia braunsi* Peters, 1984, by original designation.
Anthocopa (*Eremoplosmia*) Zanden, 1991b: 164. Type species: *Osmia eremoplana* Mavromoustakis, 1949, by original designation.

This subgenus contains species that look like *Hoplitis* (*Anthocopa*), with which group the type species of *Eremoplosmia* was affiliated by van der Zanden (1991b). *Caposmia* differs from *Hoplitis* in the lack of basal flaps on S6 of the male, the lack of lateral teeth on T6 of the male, and the generic characters of *Wainia*. The sterna and genitalia were illustrated by van der Zanden (1991b). Contrary to the original description of *Eremoplosmia*, the claws of the female are simple. The more or less obtuse posterior lateral angle of the scutum differentiates this subgenus from the others, except that in *W. algoensis* (Brauns) the angle is acute because the usual carina is elevated to form a rounded lamella. As in *Wainia* s. str., T6 of the male has a preapical carina, and the margin of the tergum is thus thickened. The body length is 8.0 to 10.5 mm.

■ *Caposmia* is known in Israel, where *Wainia eremoplana* (Mavromoustakis) occurs, and in South Africa, where *W. algoensis* (Brauns), *braunsi* (Peters), and *elizabethae* (Friese) are found. Peters (1984) differentiated these African species.

***Wainia* / Subgenus *Wainia* Tkalců s. str.**

Wainia Tkalců, 1980: 1. Type species: *Wainia lonavlae* Tkalců, 1980, by original designation.
Wainia (*Trichotomia*) Tkalců, 1980: 16. Type species: *Wainia consimilis* Tkalců, 1980, by original designation.

This subgenus contains species 4.5 to 6.5 mm long, more robust than those of *Wainiella* and smaller than those of *Caposmia* and lacking clypeal or hind coxal carinae. Either the omaulus is not carinate or the lower portion is weakly carinate. T6 of the male is convex, the apical margin thickened, sometimes carinate, as in *Caposmia*. The male gonoforceps are linear and bear long hairs. Tkalců (1980) illustrated the male genitalia and many other structures.

■ This subgenus occurs from Namibia and South Africa north to Kenya and east to Yemen, Pakistan, India, and, according to T. Griswold (in litt., 1997), the Philippines. Three species have been named.

***Wainia* / Subgenus *Wainiella* Griswold**

Wainia (*Wainiella*) Griswold, 1998, in Griswold and Michener, 1998: 234. Type species: *Heriades sakanienensis* Cockerell, 1936, by original designation.

This subgenus consists of small (6-8 mm long), cylindrical, heriadiform bees that resemble *Noteriades* in the narrow, longitudinal, median clypeal carina of females. The omaulus and hind coxa are carinate. T6 of males is flat, the apical margin simple. The male gonoforceps are enlarged apically, and lack fringes of long hairs.

■ This subgenus is found from South Africa to Kenya. The two known species are *Wainia albobarbata* (Cockerell) and *sakanienensis* (Cockerell).

Genus *Xeroheriades* Griswold

Xeroheriades Griswold, 1986b: 165. Type species: *Xeroheriades micheneri* Griswold, 1986, by original designation.

This is a genus of small, slender bees (length 4.5-7.0 mm) with the metasoma partly red. They lack the carinae (preoccipital, pronotal, omaular, and on T1) common in heriadine bees, but the hind coxa has a longitudinal ventral carina. Carinulae of the pronotal lobe are absent. As in *Chelostoma*, the male metasoma is relatively straight, T7 being exposed. S1 to S6 are all exposed, although S5 and S6 are less sclerotized than the others and only partly exposed. T1 is convex, with no angle between its anterior and dorsal surfaces, and there is a longitudinal median impressed line on the anterior surface. The basal zone of the propodeum is sloping, neither pitted nor defined by a carina.

■ This distinctive genus occurs in the isolated mountain ranges of the Mojave Desert, California. The only species is *Xeroheriades micheneri* Griswold.

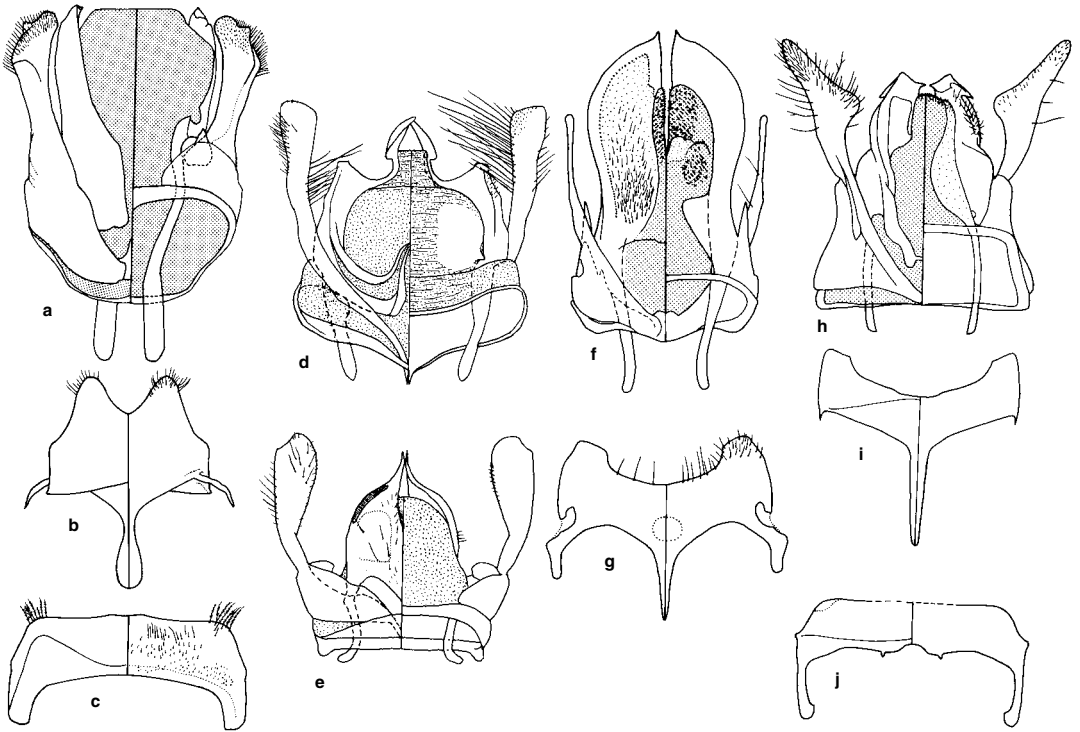


Figure 82-2. Male genitalia and hidden sterna of Anthidiini. **a-c,** Genitalia, S8, and S7 of *Trachusa* (*Ulanthidium*) *pueblana* Thorp and Brooks; **d, e,** Genitalia of *Acedanthidium* *flavoclypeatum* (Gupta) and *Pseudoanthidium* (*Tuberanthidium*) *brachiatum* Michener and Griswold; **f, g,** Genitalia and S8 of *Dianthidium*

(*Adanthidium*) *discophorum* Griswold and Michener; **h-j,** Genitalia, S8, and S7 of *D. (Deranchanthidium)* *chamela* Griswold and Michener. (In divided illustrations, the dorsal views are on the left.) a-c, from Thorp and Brooks, 1994; d, e, from Michener and Griswold, 1994a; f-j, from Griswold and Michener, 1988.

other insects. Pasteels (1977a) reviewed the nesting habits of Old World species, and the nests of various taxa are described below under the genera or subgenera concerned. Cleptoparasitic Anthidiini mostly parasitize other Megachilidae, although a few deviate and attack other bees; e.g., *Hoplostelis* s. str. parasitizes Euglossini. Larvae of Anthidiini are not known to present conspicuous generic or tribal characters. They have been described and illustrated by Michener (1953a), Grandi (1961), Clement (1976), and others.

Anthidiini can be divided, for convenience, into two series. Series A includes those taxa in which the mandibles of the females have three or four or rarely more teeth joined by shallow or at least rounded concavities, so that, except frequently for the lowermost and uppermost teeth, the teeth are obtuse or rounded and often mere angles on the mandibular margin (Fig. 82-3b). Sometimes the second and third teeth are indistinguishable (Fig. 82-3c) or represented by feeble convexities on a nearly straight margin. Except for the parasitic genera, species in this series make nests with resin, often supplemented by pebbles, earth, leaf fragments, or, in the case of at least one *Pachyanthidium*, plant hairs. Series B includes those in which the mandibles of the female have five or more, commonly sharp teeth, separated by acute, V-shaped notches (Fig. 82-3a). Series B is the group in which nests are made at least largely of fibers such as plant hairs. Se-

ries A is the more diverse of the two and is no doubt a paraphyletic group from which Series B arose one or more times. *Pachyanthidium* is placed in Series B but it includes some species that fall in Series A. The first couplet in each of the two keys that follow separates Series A and B, and Table 82-1 lists the genera in each.

Couplet 2 of the first key deals with T5. More anterior terga of both sexes and T6 of males reflect the same features, often less clearly. Taxa that are not clearly separable by this character can be run to either alternative.

Key to the Genera of the Anthidiini of the Eastern Hemisphere

(Modified from Michener and Griswold, 1994a)
(See also the Supplementary Key to Males, below.)

1. Mandible of female with 5 to 18, usually sharp teeth separated by acute notches (Fig. 82-3a) or (in one species of *Pachyanthidium*) minutely denticulate; maxillary palpus minute [relatively long in *Africanthidium* (*Zosteranthidium*)], two-segmented (arolia absent; base of propodeal triangle punctate or finely roughened, nearly always hairy; propodeum without basal series of pits and without fovea behind spiracle; juxtantennal carina absent) (Series B) 2
- Mandible of female with three or four teeth (Fig. 82-3b), or, if with five to ten, then the teeth are rounded and at least some of them separated by rounded emargina-

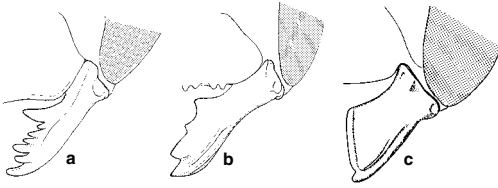


Figure 82-3. Mandible and adjacent structures of female Anthidiini. **a**, *Anthidium maculosum* Cresson; **b**, *Hypanthidium toboganum* (Cockerell); **c**, *Dianthidium* (*Deranchanthidium*) *chamela* Griswold and Michener. From Michener, McGinley, and Danforth, 1994.

- tions; maxillary palpus commonly three- or four-segmented but sometimes two-segmented (Series A) 11
- 2(1). T5 with posterior marginal zone depressed (except sometimes medially), more finely punctate than rest of tergum and usually densely so, not over half as wide laterally as medially, this zone ending in very narrow, smooth posterior margin, the anterior margin of depressed zone often obtusely angulate medially, whole zone thus very broadly triangular 3
- T5 with posterior marginal zone either not depressed or weakly to strongly depressed, but if recognizable, then punctate like rest of tergum to impunctate, often over half as wide laterally as medially, this zone often ending in broad, smooth posterior margin, the anterior margin of depressed zone straight or curved, not angulate, or with small basal median angular projection 4
- 3(2). T6 of female with margin usually not denticulate, sometimes with lateral tooth, with median apical notch or emargination accommodating sting [margin rarely denticulate, e.g., *A. (Proanthidium) oblongatum* Latreille]; T5 of female with basal edge of depressed marginal zone commonly obtusely angulate medially, zone thus broadly triangular; penis valves of male widely separated basally, united by long, narrow bridge; volsella projecting as lobe at apex of gonocoxite *Anthidium*
- T6 of female with margin denticulate, almost always without lateral tooth, usually without median apical notch; T5 of female with basal edge of depressed marginal zone not angulate medially; penis valves close together or fused basally, bridge therefore short or absent; volsella small or absent (Africa, palearctic) *Afranthidium* (in part)
- 4(2). First recurrent vein joining first submarginal cell; axilla acutely pointed; face with shiny longitudinal median ridge from frons to clypeus (Africa) *Serapista*
- First recurrent vein entering second submarginal cell; axillar margin rounded or straight; face without longitudinal median ridge 5
- 5(4). Basal area of propodeum hairless except laterally; pale markings absent; scutellum not angulate laterally; terga without impunctate margins (male unknown) (Africa) *Anthidioma*
- Basal area of propodeum with hairs, sometimes very short; pale markings usually present, but *if* not [as in *Gnathanthidium* and *Afranthidium* (*Immanthidium*), etc.], then scutellum usually angulate laterally and terga with impunctate marginal zones 6
- 6(5). Preoccipital ridge dorsally and omaulus produced as

- translucent lamellae (Africa, Oriental) *Pachyanthidium* (in part)
- Preoccipital ridge and omaulus rounded or at most carinate (except preoccipital ridge lamellate in *Gnathanthidium*) 7
- 7(6). Subantennal suture straight or weakly arcuate; S4 and S5 of male not strongly concave, rather simple, S3 to S5 without combs or areas of specialized bristles, posterior margins straight or weakly concave (with lateral projections in *Neanthidium* and on S5 in *Gnathanthidium*) 8
- Subantennal suture distinctly arcuate outward; S3 to S5 of male usually concave, S4 and S5 or at least the latter short and largely hidden (except in *Indanthidium*), at least S5 with posterior lateral projection [except in *Pseudoanthidium* (*Exanthidium*) and *Indanthidium*], S3 often with comb or area of wavy bristles 10
- 8(7). T6 and T7 of male each with four large equidistant teeth; S4 and S5 of male with lateral projections; T6 of female with lateral spine and median emargination (length 9–13 mm) (Mediterranean) *Neanthidium*
- T6 of male simple, T7 short, bidentate, bilobed, or tridentate; S4 and S5 without lateral projections or (in *Gnathanthidium*) S5 with such projections; T6 of female without or with very weak lateral spine and median emargination 9
- 9(8). Mandible of female with 13 or 14 teeth, apex broad, lower two teeth and upper one large, others small and subequal; scutellum transverse, truncate, carinate; tibiae coarsely tuberculate (Africa) *Gnathanthidium*
- Mandible of female with eight teeth or less; scutellum rounded as seen from above, sometimes weakly emarginate medially, not or incompletely carinate; tibiae tuberculate or not (Africa, palearctic) *Afranthidium* (in part)
- 10(7). T7 of male nearly as wide as T6, multidentate; subantennal suture arising at upper end of tentorial pit (S3 of male without wavy bristles; S5 with margin strongly concave but no lateral projections) (India) *Indanthidium*
- T7 of male markedly narrower than T6, two- or three-toothed or lobed; subantennal suture arising from epistomal suture well above tentorial pit [except in *P. (Royanthidium) reticulatum* Mocsáry] *Pseudoanthidium*
- 11(1). Hind tibia of female with scopula-like hairs, some of them at least as long as tibial width; basal vein of forewing curved (as in *Halictus* but less strongly) and meeting vein Cu at a right angle; jugal lobe of hind wing about half as long as vannal lobe (yellow markings absent except on clypeus of male) (Africa) *Aspidosmia*
- Hind tibia of female with relatively short hairs or bristles; basal vein of forewing nearly straight and meeting vein Cu at acute angle; jugal lobe of hind wing less than half as long as vannal lobe 12
- 12(11). Omaulus lamellate, continued onto venter of thorax and there separated from middle coxa by less than width of middle trochanter 13
- Omaulus lamellate or not, if lamellate then often not continued onto venter of thorax, but *if* so, then mesepisternum between middle coxa and omaulus (however recognized) as wide as or wider than width of middle trochanter 14

- 13(12). Propodeum with fovea defined by carina behind spiracle (as in Fig. 82-8); preoccipital ridge dorsally rounded or with low carina *Anthidiellum* (in part)
- Propodeum without fovea behind spiracle; preoccipital ridge behind vertex lamellate (Africa, oriental) *Pachyanthidium* (in part)
- 14(12). Lower part of preoccipital carina sloping forward and continuing directly to lower mandibular articulation; axilla frequently pointed posteriorly (anterior coxa with lamella in most species; hind trochanter of male with preapical ridge, carina, lamella or tooth on inner surface; arolia absent) (paleartic, Sahel) *Icteranthidium*
- Lower part of preoccipital carina absent, or, *if* present and extending to lower part of head, then ending below and mesal to lower mandibular articulation, or, *if* reaching mandibular articulation [in *Anthidiellum* (*Chloranthidiellum*)], directed below it and then curving up to articulation; axilla not pointed posteriorly (except in some parasitic genera that lack a scopa) 15
- 15(14). Face with three longitudinal ridges or carinae, two of them juxtantennal carinae and the third—a median longitudinal one on frons and supraclypeal area—often only a shiny ridge (body without yellow markings) *Euaspi*
- Face without a longitudinal median ridge or carina and usually without juxtantennal carinae 16
- 16(15). Vein cu-v of hind wing usually half as long as second abscissa of M+Cu or longer, oblique; middle tibia as broad as hind tibia or nearly so (T7 of male simple or bilobed) 17
- Vein cu-v of hind wing less than half as long as second abscissa of M+Cu (Fig. 82-1b, c), oblique or transverse; middle tibia usually narrower than hind tibia 19
- 17(16). Claws of female simple (male unknown) (India) *Trachusoides*
- Claws of female cleft or with inner median or preapical tooth 18
- 18(17). T7 of male curled under, dorsal surface thus facing downward; mandible of female dull, minutely roughened and bearing very short hairs, carinae absent on basal half of mandible; middle tibia with anterior margin strongly convex, at lowermost extremity usually at right angle to line across distal end of tibia (Fig. 82-4c) *Trachusa*
- T7 of male directed posteriorly although small, short, and transverse; mandible of female slightly shining, carinae strongly shining; middle tibia with anterior margin less strongly convex, at acute angle to line across distal end of tibia (Borneo) *Apianthidium*
- 19(16). Anterior part of axilla produced to a point or lobe directed laterally, behind which margin is concave; margin of T7 of male with median point and two lobes on each side, thus with five apical projections (India) *Acedanthidium*
- Axilla rounded, or sometimes pointed posteriorly, or, *if* with basal lateral projection, then curved posteriorly; margin of T7 of male with less than five apical projections 20
- 20(19). Axilla positioned and produced laterally, thus almost abutting posterior end of tegula; arolia absent; scopa absent (Africa) *Larinostelis*
- Axilla not abutting tegula; arolia present [except in *Eoanthidium* (*Salemanthidium*)]; scopa present (except in *Stelis* and *Aprostelis*) 21
- 21(20). Scopa present; front and middle tibiae each with one apical spine or angle (except *Cyphanthidium* and some *Eoanthidium*, which have two spines on middle tibia) 22
- Scopa absent; front and middle tibiae each with two spines, one midapical and one posterior apical 28
- 22(21). Juxtantennal carinae present although sometimes weak; interantennal distance usually less than, rarely equal to, antennocular distance; S6 of female (except in subgenus *Clistanthidium*) with spine or premarginal ridge, sometimes weak and lateral only, sternal margin thus appearing thick, sometimes elevated to lateral tooth (T7 of male over half as wide as T6) (paleartic, oriental) *Eoanthidium*
- Juxtantennal carinae completely absent; interantennal distance usually greater than antennocular distance; S6 of female unmodified, margin thin 23
- 23(22). Scutoscuteellar suture superficially similar to scutoaxillar suture, usually closed, but *if* smooth shining floor of groove visible, then usually not divided; subantennal suture approximately straight or only slightly arcuate; fovea behind propodeal spiracle absent; body usually over 10 mm long (although in *Cyphanthidium* as little as 6.5 mm long) 24
- Scutoscuteellar suture open to shiny bottom or fovea (as in Fig. 82-7a, b), thus very different from scutoaxillar suture, shiny area divided into two parts medially, or, *if* suture closed (as in *Anthidiellum* s. str.), then subantennal suture strongly arcuate outward (Fig. 82-5c); fovea behind propodeal spiracle present, defined posteriorly by carina, but fovea sometimes not larger than spiracle; body usually 8 mm long or less 27
- 24(23). T6 of male with median apical tooth or small projection; body length 8.5 mm or less and metasoma with continuous yellow bands [form and coloration as in *Afranthidium* (*Oranthidium*)] (Africa) *Cyphanthidium*
- T6 of male without median apical tooth; body length usually 8.5 mm or more, but *if* less [as in *Benanthis* and some *Plesianthidium* (*Spinanthidium*)], then metasoma without yellow, or yellow bands broken 25
- 25(24). Yellow or cream markings absent or limited to face of male; T3 and other terga with depressed premarginal zone sublaterally nearly one-half length of exposed part of tergum; T6 of male with median lobe (often subtruncate and elevated) and lateral tooth, thus trifid or (in subgenus *Spinanthidiellum*) truncate with a longitudinal median ridge at apex (Africa) *Plesianthidium*
- Body with yellow or reddish-yellow markings; T3 and other terga with depressed premarginal zone sublaterally one-third length of exposed part of tergum or less; T6 of male simple, bilobed, or with short, broad, rounded median lobe, sometimes (in *Rhodanthidium* s. str.) also with lateral tooth, thus trifid 26
- 26(25). Apex of T7 of male strongly bilobed; S4 and S5 of male simple, without combs or lateral teeth, margin of S6 with lateral lobe resembling a tooth in side view; ocellocapital distance about equal to ocellar diameter (Madagascar) *Benanthis*
- Apex of T7 of male with a median projection, thus with three projections (or five in subgenus *Meganthidium*); S4 or S5 of male frequently with marginal comb, S5 often

- with lateral tooth, S6 without lateral projection; ocellocapital distance two or more ocellar diameters (palearctic) *Rhodanthidium*
- 27(23). Omaular carina absent or extending down only to middle of mesepisternum; T7 of male, if trilobed, then with median lobe much longer than lateral lobe or spine; subantennal suture straight (eastern Asia) *Bathanthidium*
- . Omaular carina strong, sometimes lamellate, and extending onto ventral surface of thorax, sometimes across venter (except in subgenus *Clypanthidium*, in which omaular carina does not reach lower part of mesepisternum); T7 of male, if trilobed, then with median lobe small, either not separated from lateral lobe by emargination or not longer than lateral lobe; subantennal suture usually arcuate outward (Fig. 82-5c) *Anthidiellum* (in part)
- 28(21). Tegula of ordinary size and shape, widest medially and longer than wide (scutum wider than long, only moderately so in subgenus *Stelidomorpha*) *Stelis* (in part)
- . Tegula enlarged, especially posteriorly, width posteriorly almost as great as length 29
- 29(28). Scutum longer than wide; body without yellow markings (Africa) *Afrostelis*
- . Scutum slightly broader than long; metasoma with yellow markings (Yemen) *Xenostelis*

Supplementary Key to Males of the Anthidiine Genera of the Eastern Hemisphere (From Griswold and Michener, 1994a)

The preceding key will be frustrating for various reasons, chief among which will likely be that couplet 1 is based largely on a character of females; supplementary characters will help, but as indicated within the couplet, they are not always decisive. The following supplementary key for males leads either to certain genera or to numbered couplets in the main key, thus bypassing couplet 1. In reality, its main function is to help identify males of taxa that should run to 11 in the main key and that lack arolia, as do all taxa that run to 2.

- A. Arolia absent B
- . Arolia present go to 11
- B(A). Palearctic species C
- . Palearctic species go to 2
- C(B). Vein cu-v of hind wing more than half as long as second abscissa of M+Cu, oblique (as in Fig. 82-1a); middle tibia as broad as hind tibia or nearly so D
- . Vein cu-v of hind wing less than half as long as second abscissa of M+Cu (as in Fig. 82-1b, c), oblique or transverse; middle tibia narrower than hind tibia E
- D(C). T7 curled under, dorsal surface thus facing downward; middle tibia with anterior margin strongly curved, at lowermost extremity thus usually at right angle to line across distal end of tibia (Fig. 82-4c) *Trachusa* (in part)
- . T7 directed posteriorly although small, short, and transverse; middle tibia with anterior margin less strongly convex, thus at acute angle to line across distal end of tibia (as in Fig. 82-4d, e) *Apianthidium*
- E(C). Axilla almost entirely lateral to lateral margin of scutum; outer, apical margins of fore and middle tibiae each with two minute spines (placed on basis of female characters; male unknown) *Larinostelis*

- . Axilla at most extending slightly lateral to lateral margin of scutum; outer, apical margins of fore and middle tibiae each with at most one spine F
- F(E). Omaulus carinate for at least three-fourths of distance from upper end to midventral line G
- . Omaulus not carinate, or carinate for no more than one-half of distance from upper end to midventral line go to 2
- G(F). Preoccipital carina present dorsally, behind vertex H
- . Preoccipital carina absent dorsally, behind vertex I
- H(G). Hind tibia tuberculate on outer surface; scutellum very short, width greater than four times length, only slightly overhanging metanotum (for one-third its length) *Gnathanthidium*
- . Hind tibia not tuberculate; scutellum moderately long, width equal to or less than three times length, greatly overhanging metanotum (for one-half its length) *Pachyanthidium* (in part)
- I(G). Juxtantennal carinae present (as in Fig. 82-5a); T7 broadly truncate with small median projection *Eoanthidium* (in part)
- . Juxtantennal carinae absent (as in Fig. 82-5c); T7 with three apical spines *Serapista*

Key to the Genera of the Anthidiini of the Western Hemisphere

1. Mandible of female with five or more teeth separated by acute notches (Fig. 82-3a); with the following *combination* of other characters: arolia absent; basal vein of forewing several vein widths basal to cu-v; base of propodeal triangle minutely roughened, punctate, hairy, without series of pits; postspiracular fovea of propodeum absent; juxtantennal carina absent *Anthidium*
- . Mandible of female with three or four (rarely five) teeth, at least some of them separated by obtuse or rounded emarginations (Fig. 82-3b), rarely distal margin edentate except for small tooth near lower margin (Fig. 82-3c); without the combination of other characters listed above 2

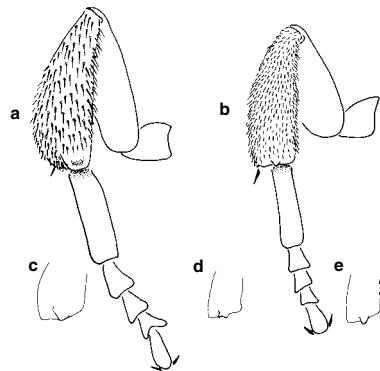


Figure 82-4. Middle legs, showing apices of tibiae, of anthidiine bees. **a**, *Paranthidium jugatorium perpictum* (Cockerell); **b**, *Dianthidium (Dianthidium) curvatum* (Smith); **c**, *Trachusa (Trachusomimus) gummiifera* Thorp; **d**, *D. (Adanthidium) arizonicum* (Rohwer); **e**, *Hypanthidiodes (Anthidulum) currani* (Schwarz). **a**, **b**, from Michener, McGinley, and Danforth, 1994; **c**-**e**, from Griswold and Michener, 1988.

and *Afranthidium*. The wide separation of the penis valves of *Anthidium* and the long bridge between their bases is the only known character consistently distinguishing *Anthidium* from *Afranthidium*, and as more species are dissected and examined, it too may fail.

Afranthidium differs from *Pseudoanthidium* as indicated in the key to genera, and in the simple male metasomal sterna. In *Afranthidium* the sterna are not strongly concave, do not bear lateral processes, and lack combs or specialized bristles. Usually, S1 to S6 are exposed, although S5 and rarely S4 may be largely hidden.

It is quite possible that *Anthidium* is derived from a paraphyletic taxon, *Afranthidium*, but there is no particular group of *Afranthidium* to which *Anthidium* appears most closely related. The characters of *Afranthidium* that distinguish it from *Anthidium* are possibly all plesiomorphies. It is a phenetically distinct group and recognition of it at this time seems reasonable. Recognition of the *Afranthidium* subgenera as genera seems undesirable because of their similarity and consequent difficulty of identification; moreover, there are a few, often unidentified and probably undescribed species that combine characters of different subgenera. Perhaps worse, placement of the *Afranthidium* subgenera as subgenera of *Anthidium* would make the latter an enormously diverse genus.

All *Afranthidium* are sub-Saharan except for the subgenus *Mesanthidium* and at least two species of *Capanthidium*, all of which are palearctic.

Key to the Subgenera of *Afranthidium*

(From Michener and Griswold, 1994a)

1. Marginal zones of T2 to T5 broadly impunctate, median lengths of impunctate zones usually one-sixth length of exposed parts of terga or more, these zones transparent, pale brown or cream-colored; male gonostylus enormous, broad, flat, and almost membranous; pronotal lobe not carinate, sometimes with small punctate and hairy ridge in position of carina (Africa) *A. (Immanthidium)*
- Marginal zones of T2 to T5 punctate or narrowly impunctate, median lengths of impunctate zones about one-seventh lengths of exposed parts of terga or less, these zones dark or translucent brownish; male gonostylus neither broad nor flat nor almost membranous although sometimes broadly paddle-shaped; pronotal lobe usually with transverse carina or low lamella that is hairless even when it extends only partway across lobe 2
- 2(1). Scutellum and axilla laterally not much overhanging as seen obliquely so as to show profiles; scutellum rounded in profile, not or scarcely overhanging metanotum; outer surfaces of tibiae not more coarsely punctate than mesepisternum, not tuberculate 3
- Scutellum laterally and usually axilla overhanging large fossa and usually acute or narrowly rounded, as seen obliquely so as to show profile of lateral part of scutellum and of axilla; scutellum acute, right-angular, or sometimes rounded in profile, medially often strongly overhanging metanotum; outer surfaces of tibiae, especially of female, coarsely, irregularly punctate, sometimes with extensive smooth areas between punctures, the punctures commonly coarser than those of mesepisternum, surfaces usually tuberculate (but not or weakly so in *Capanthidium* and *Mesanthidium*) 7
- 3(2). T2 to T5 with apical bands, broken medially, of white plumose hair; propodeal triangle with punctures (and hairs) widely separated from one another, surface between punctures strongly shagreened, dull; body and legs black, without pale markings (Africa) *A. (Zosteranthidium)*
- T2 to T5 without apical hair bands; propodeal triangle rather densely punctate and hairy, surface between punctures shining; body and legs usually with yellow or white markings, but *if* not, then at least anterior surfaces of front and middle tibiae brownish yellow 4
- 4(3). Hind basitarsus of female with apical projection over base of second tarsal segment; hind trochanter of male with apicoventral denticle; sterna of male with distinct basal hair fasciae arising at graduli; body black, with yellow or cream color usually limited to minute streak along inner margin of eye of both sexes (Africa) *A. (Nigranthidium)*
- Hind basitarsus of female with apex truncate, without apical projection; hind trochanter of male without apicoventral denticle; sterna of male without basal hair fasciae; body brown or black with yellow or cream-colored areas at least on face of male and metasomal terga of both sexes 5
- 5(4). T5 of female without lateral spine; T1 of female with carina separating anterior from dorsal surfaces abruptly strengthened laterally and thence extended lateroposteriorly; apex of T7 of male with two lobes, each lobe two or three times as broad as long, emargination between them with small median spine; S6 of male with small, pointed midapical process at base of which are two spines directed forward (Africa) *A. (Domanthidium)*
- T5 of female with lateral spine; T1 carina of female unmodified; apex of T7 of male two-lobed, usually with median angle or tooth, or three-lobed, each lateral lobe about as long as broad or longer; S6 of male without small apical process and spines 6
- 6(5). Gonostylus of male tapering, not or scarcely longer than gonocoxite, not attaining middle of penis valve; ventral surface of mesepisternum of female covered with strong, backward-directed, golden to black bristles that appear flattened, minutely barbed, and blunt or abruptly tapered at apices (S6 of male elongate, produced to narrowly rounded or bidentate apex) (Africa) *A. (Oranthidium)*
- Gonostylus of male expanded apically, about twice as long as gonocoxite, attaining apex of penis valve or nearly so; ventral surface of mesepisternum of female with pale, gradually tapering hairs similar to hairs of adjacent areas (Africa) *A. (Afranthidium s. str.)*
- 7(2). Posterior margins of metasomal terga not curved upward, lying near surfaces of following terga; axilla extending laterally beyond scutal margin; male gonostylus greatly reduced, attaining about middle of penis valves, which are completely fused to one another (palearctic) *A. (Mesanthidium)*
- Posterior margins of at least some metasomal terga, as seen in profile, curved upward away from following terga; axilla not extending laterally beyond scutum (except in some *Branthidium*); male gonostylus reaching to or beyond level of apical one-fourth of penis valves 8
- 8(7). T6 of female with preapical denticulate ridge parallel to denticulate apical margin (scutellum distinctly cari-

- nate except for small midapical emargination) (male unknown) (Africa) *A. (Xenanthidium)*
- T6 of female without preapical denticulate ridge 9
- 9(8). T6 of male with preapical, usually denticulate transverse ridge at least laterally; tibiae coarsely punctate but not or weakly tuberculate on outer surfaces (Africa, palearctic) *A. (Capanthidium)*
- T6 of male without preapical ridge; tibiae strongly tuberculate on outer surfaces 10
- 10(9). Preoccipital carina present laterally; male S3 with trapezoidal apical projection; T5 and T6 of male with lobate lateral carinae, T5 and T6 of female with lateral longitudinal carinae (Africa) *A. (Mesanthidiellum)*
- Preoccipital carina absent; male S3 margin not produced; T5 (usually) and T6 without lateral carinae in either sex (Africa) *A. (Branthidium)*

Afrantheidium / Subgenus *Afrantheidium* Michener s. str.

Anthidium (*Afrantheidium*) Michener, 1948a: 24. Type species: *Hypanthidium halophilum* Cockerell, 1936, by original designation.

Afrantheidium s. str. consists of small to medium-sized (6–10 mm long) robust species, black with the metasoma often brown, with limited cream or yellow markings, those of the metasoma forming narrow, unbroken tergal bands as in *Oranthidium* and *Domanthidium*. Unlike the male gonostyli of those subgenera, the gonostyli of *Afrantheidium* s. str. are slender, slightly expanded apically, and about twice as long as the gonocoxites, and they attain the apices of the penis valves or nearly so. The penis valves are broad, adjacent, and heavily sclerotized distally with retrorse preapical points, much as in *Oranthidium*. The lateral metasomal spines are strong, as in *Oranthidium*. ■ This subgenus is known from Cape Province, South Africa, and from Namibia. Pasteels (1984) included nine species, but some of them may belong elsewhere.

Afrantheidium murinum (Pasteels) does not completely fit the characterization of any recognized subgenus. Because the species is known only in the female, a firm decision on its placement is premature. The pronotal lobe lacks a carina, but in other respects *A. murinum* runs to couplet 3 in the key to subgenera, or to *Afrantheidium* s. str. if its tergal hair bands are ignored. It differs from *Afrantheidium* s. str. in its absence of lateral metasomal spines, although T3 to T5 have small lateral lobes, and from *Zosteranthidium* in the presence of yellow maculations and other characters.

Afrantheidium / Subgenus *Branthidium* Pasteels

Branthidium Pasteels, 1969a: 88. Type species: *Anthidium braunsi* Friese, 1904, by original designation.

Honanthidium Pasteels, 1969a: 88. Type species: *Anthidium honestum* Cockerell, 1936, by original designation.

Branthidium contains small (5–7 mm long), stout species, black with narrow pale metasomal bands, the bands often not interrupted, or with the metasoma largely yellow. *Branthidium* could reasonably be included in the subgenus *Capanthidium* but is retained for reasons given in the account of the latter. In most males the fore femur is flattened basoventrally and the mesosternum is

covered with long, silky, posteriorly directed, decumbent hair. Of all the subgenera of *Afrantheidium*, *Branthidium* and the closely related *Mesanthidiellum* are the ones that most resemble the genus *Pseudoanthidium*.

■ This subgenus is found from Lesotho to western Cape Province, South Africa, north to Shaba Province in Zaïre and to Kenya. Pasteels (1984) recognized ten species and revised the group.

Reasons for including *Honanthidium* in *Branthidium* are given by Michener and Griswold (1994a). As noted by those authors, *Afrantheidium* (*Branthidium*) *guillarmodi* (Mavromoustakis) resembles *Mesanthidium* in its laterally projecting axillae and *Mesanthidiellum* in its laterally carinate female T5.

Afrantheidium / Subgenus *Capanthidium* Pasteels

Capanthidium Pasteels, 1969a: 85. Type species: *Anthidium "capicole"* Friese, *lapsus* for *capicola* Brauns, 1905, by original designation.

Capanthidium consists of small (5–8 mm long) species, black with limited light markings on the head and thorax; the metasoma exhibits narrow unbroken light tergal bands or is almost entirely yellow. This subgenus is closely related to *Branthidium* and *Mesanthidiellum*, and the three could be regarded as a single subgenus. Characters previously used to distinguish among them do not hold true. For example, in his key to genera and subgenera, Pasteels (1984) indicates that the second recurrent vein almost meets the second submarginal crossvein in *Capanthidium* but is three to four vein widths beyond it in *Branthidium*, but the full range of this variation occurs even within the type species of *Capanthidium*. Further the lateral part of the scutellar margin and the margin of the axilla are sharper and irregularly crenulate in species placed in *Branthidium* and *Mesanthidiellum*, unlike those of species placed in *Capanthidium*, but this character, too, varies, and the difference is not consistent. In *Mesanthidiellum* and some *Branthidium* the marginal expansion of the axilla is sufficient that the axilla extends laterad behind the tegula. The male gonostyli are long and parallel-sided, although flat, in *Afrantheidium* (*Capanthidium*) *capicola* (Brauns) and *naefi* (Benoist), and long, apically expanded, and paddle-shaped, although sometimes bearing a marginal tooth, in species placed in *Branthidium*. In some species that have been included in *Capanthidium*, however, e.g., *A. (C.) rubellulum* (Cockerell), the gonostyli are as broadly expanded as those of *Branthidium*.

A number of characters, however, differentiate *Capanthidium* from *Branthidium* and *Mesanthidiellum*. The more flattened body (*Anthidium*-like rather than *Pseudoanthidium*-like) is distinctive. Other characters of *Capanthidium* not mentioned in the key to subgenera include the depressed marginal zones of terga that are finely and densely punctate and lack distinct impunctate margins except in *Afrantheidium capicola* (Brauns) and *naefi* (Benoist); the long, apical fringes of S7 and S8 of the male; the penis valves, which are flat dorsoventrally; and the semicircular disc of S6, usually with a lateral tooth near the margin. In addition, most females of *Capanthidium* have a median impunctate line on the clypeus (as in *Afrantheidium* s. str. and *Oranthidium*) and a blunt lateral tooth on T5, conditions never found in *Branthidium*

nearly so only in the median third. The inner surface of the hind tibia is rather flat; the upper edge, at least on the apical half of the tibia, is sharply marked by the limit of the keirottrichiate area, this limit sometimes carinate. This character is least evident in American species of *Anthidiellum* s. str., but even in these there is not a gradation from one hair type to the other as there is in the genus *Bathanthidium*. The subantennal sutures are usually strongly arcuate (Fig. 82-5c). The male gonostyli are expanded apically, commonly truncate or bilobed, or sometimes [*A. (Anthidiellum) strigatum* (Panzer)] extended to one side as though one lobe of a bilobed structure had been lost. The genitalia and hidden sterna were illustrated by Popov (1935) and Mitchell (1962).

Nests of *Anthidiellum* s. str. are constructed in the open, on stems, leaves, or rocks, and consist of isolated single cells made of resin (Pl. 8; Schwarz, 1928; Grigarick and Stange, 1968) or groups of cells (Friese, 1923). Bees of the subgenus *Ranthidiellum*, however, make nests in the soil, using resin for cells and entrance tubes (Pasteels, 1972).

Key to the Subgenera of *Anthidiellum*

1. Postgradular parts of T2 to T5 of females and to T6 of males swollen laterally, so that, from above, sides of metasoma seem lobed; S5 of male without comb; mandible of female with preapical shoulder on lower margin, below lower tooth 6
- Terga not swollen laterally; S5 of male with margin broadly concave and armed with comb of black teeth, at least laterally (male unknown in *Ananthidiellum*); mandible of female without preapical shoulder on lower margin (Eastern Hemisphere) 2
- 2(1). Mandible of female minutely sculptured, dull, almost without carinae, its apex expanded, 1.5 times as wide as basal width; subantennal suture straight; T1 to T4 without pale markings (oriental) *A. (Ananthidiellum)*
- Mandible of female somewhat shining, often coarsely punctate (somewhat dull distally in *Ranthidiellum* and *Chypanthidium*), with carinae, its apex but little wider than base (except in *Ranthidiellum*); subantennal suture arcuate [not clearly recognizable and perhaps not arcuate in *A. (Chypanthidium) bimaculatum* (Friese)]; T1 to T4 with yellow, cream, or reddish bands (except in subgenus *Chypanthidium* and some *Ranthidiellum*) 3
- 3(2). Preoccipital carina present at sides, behind eyes, but absent behind vertex; lamella on pronotal lobe tapering but extending nearly as far mesad from lateral margin of scutum as laterad; axilla extending laterally beyond margin of scutum (basal zone of propodeum laterally horizontal with well-developed pits) (Africa) *A. (Chloranthidiellum)*
- Preoccipital carina complete, or present only behind vertex, or absent; lamella or carina on pronotal lobe usually extending little mesad from lateral margin of scutum; axilla not extending laterally beyond lateral margin of scutum 4
- 4(3). Tegula narrowly rounded posteriorly; omalar carina reaching about halfway down oaulus (oriental) *A. (Chypanthidium)*
- Tegula broadly rounded or almost transverse posteriorly; omalar carina extending to venter (in some *Pyc-*

- nanthidium* very weak or perhaps absent on lower half of mesepisternum) 5
- 5(4). T1 with carina separating anterior and dorsal surfaces; apex of mandible but little wider than base; body black with yellow or cream markings on all tagmata (Africa, oriental) *A. (Pycnanthidium)*
- T1 without carina between anterior and dorsal surfaces; apex of mandible of female about 1.5 times as wide as base; body brown with red markings, or yellowish and black but without yellow on T1 to T4 (oriental) *A. (Ranthidiellum)*
- 6(1). Preoccipital ridge strongly carinate behind vertex; keirottrichiate area along upper margin of hind tibia not sharply defined (Western Hemisphere) *A. (Loyolanthidium)*
- Preoccipital ridge not or scarcely carinate; keirottrichiate area along upper margin of hind tibia sharply defined (palearctic region, India) *A. (Anthidiellum* s. str.)

Anthidiellum / Subgenus *Ananthidiellum* Pasteels

Anthidiellum (*Ananthidiellum*) Pasteels, 1969a: 49. Type species: *Anthidium anale* Friese, 1914, by original designation.

Like *Ranthidiellum*, this subgenus consists of species that do not resemble most anthidiines but are superficially suggestive of some species of *Trigona*. Yellow markings are greatly reduced, the apical terga are white, and the wings are infuscated apically and clear basally [in *Anthidiellum anale* (Friese)] or the reverse (in an undescribed species). In addition to the characters given in the key to subgenera, a distinctive feature is the impunctate vertical anterior margin of the scutum, sharply separated by a right angle from the punctate dorsal surface; no other subgenus has such a sharply differentiated and vertical anterior scutal margin. The length is 6.5 to 7.0 mm.

■ This subgenus is known from Sikkim and Malaysia. The only described species is *Anthidiellum anale* (Friese), known from only one specimen. An undescribed species is also known from one specimen.

Anthidiellum / Subgenus *Anthidiellum* Cockerell s. str.

Anthidium (*Anthidiellum*) Cockerell, 1904c: 3. Type species: *Trachusa strigata* Panzer, 1805, by original designation.

Anthidium (*Cerianthidium*) Friese, 1923: 304. Type species: *Trachusa strigata* Panzer, 1805, by designation of Cockerell, 1925a: 361.

The lobate aspect (as seen from above) of the sides of the metasoma is not found in other Old World subgenera. This is the only Old World subgenus that lacks the combs of small black teeth on the metasomal sterna of males. The species are mostly larger (5-7 mm long) than those of the other speciose subgenus, *Pycnanthidium*.

■ This subgenus occurs throughout Europe, north to Finland (63°N), but is better represented in the Mediterranean basin (Morocco and Portugal to the Balkan peninsula, Turkey, and Israel), south to Eritrea, and east to Tajikistan and India. There are about seven species.

fornia species; Pasteels (1984) for sub-Saharan Africa; Moure and Urban (1964) for Brazil; etc. Toro and Rodriguez (1998) revised the Chilean species of *Anthidiini*, including 15 species of *Anthidium* (*Anthidium*). North American species were reviewed by Schwarz (1927).

Anthidium makes nests of plant hairs in preexisting cavities in the soil, walls, wood, stems, etc., or in cavities excavated in loose soil. Masuda (1933) gave an extensive account of the nesting biology of *A. (Anthidium) japonicum* Smith and summarized many of the earlier accounts. The fragmentary information on nests of North American species is summarized by Grigarick and Stange (1968). Parker (1987) described nests of the subgenus *Callanthidium*, which are not strikingly different from those of *Anthidium* s. str. Westrich (1989) gave an excellent account of the nesting behavior of German species, with appropriate references to earlier work. [He includes other genera in *Anthidium*; his "Harzbienen" and *Anthidium lituratum* (Panzer) belong in other genera, according to the present classification.] Westrich (1989) also summarized accounts of territoriality and mating behavior in *Anthidium*. Unlike those of most bees, males are often larger than females, and large individuals hold territories that include food resources (Alcock, Eickwort, and Eickwort, 1977; Severinghaus, Kurtak, and Eickwort, 1981; and, for the subgenus *Callanthidium*, Alcock, 1977).

Key to the Subgenera of *Anthidium*
(From Michener and Griswold, 1994a)

1. T6 of female with deep median emargination about one-fifth as wide as tergum, and strong lateral tooth about midway between base and apex of exposed part of tergum, T6 thus appearing strongly four-toothed; S6 of male with two large, erect, heavily sclerotized, bare apical lobes between which lie the greatly elongated, retrorsely bent apices of the penis valves (nearctic) *A. (Callanthidium)*
- T6 of female with much smaller midapical emargination, lateral to which margin is entire or uncommonly denticulate, often with a relatively small lateral tooth; S6 of male variable but not as described above; penis valves not greatly elongate, not bent retrorsely 2
- 2(1). Scutellum rounded in profile, not carinate or lamellate, not greatly overhanging metanotum and propodeum; pronotal lobe with or without carina *A. (Anthidium s. str.)*
- Scutellum angulate in profile (at least as seen obliquely to show profile of lateral part of scutellum), strongly carinate or lamellate at least laterally, greatly overhanging metanotum and propodeum; pronotal lobe carinate or lamellate 3
- 3(2). Pronotal lobe carinate; axillar suture weak; scutoscuteellar suture not in deep depression, scutellum thus nearly continuing profile of scutum (scutellum strongly produced posteriorly as rather flat structure ending in lamella) (Africa) *A. (Nivanthidium)*
- Pronotal lobe with more or less anteriorly directed or erect, translucent lamella; axillar suture strong; scutoscuteellar suture in depression, scutellum thus independently convex in profile 4
- 4(3). Scutellum ending in lamella or large carina almost all

- the way across; hind basitarsus with longitudinal carina on outer surface; omaulus sharply angulate or weakly carinate 5
- Scutellar margin with broad median part neither carinate nor lamellate; hind basitarsus not carinate; omaulus rounded or forming rounded angle 6
- 5(4). Posterior scutellar margin subtruncate as seen from above, its lateral part curved forward and becoming more or less longitudinal; antennae arising below level of middles of eyes, which converge strongly below, rendering clypeus unusually small (Africa) *A. (Severanthidium)*
- Posterior scutellar margin broadly rounded as seen from above, with small median emargination, laterally oblique, only at extreme end next to axilla sometimes becoming longitudinal; antennae arising near level of middles of eyes, which converge slightly to moderately (palearctic) *A. (Gulanthidium)*
- 6(4). Scutellum as seen from above with margin gradually curved forward at each side to axillar margin; hind basitarsus of female less than four times as long as broad (palearctic) *A. (Turkanthidium)*
- Scutellum as seen from above with margin more or less transverse, curved forward rather abruptly or angled forward at each side to axillar margin, angle often protruding posteriorly; hind basitarsus of female four or more times as long as broad (palearctic) *A. (Proanthidium)*

Anthidium / Subgenus *Anthidium* Fabricius s. str.

- Anthidium* Fabricius, 1804: 364. Type species: *Apis manicata* Linnaeus, 1758, by designation of Latreille, 1810: 439.
- Stenanthidium* Moure, 1947a: 16. Type species: *Anthidium espinosai* Ruiz, 1938, by original designation.
- Tetranthidium* Moure, 1947a: 15. Type species: *Anthidium latum* Schrottky, 1902, by original designation.
- Melanthidium* Cockerell, 1947: 106, not *Melanthidium* Pasteels, 1969. Type species: *Melanthidium carri* Cockerell, 1947, by original designation.
- Anthidium (Melanoanthidium)* Tkalcü, 1967: 91. Type species: *Anthidium montanum* Morawitz, 1864, by original designation.
- Anthidium (Echinanthidium)* Pasteels, 1969a: 101. Type species: *Anthidium echinatum* Klug, 1832, by original designation.
- Anthidium (Pontanthidium)* Pasteels, 1969a: 105. Type species: *Anthidium pontis* Cockerell, 1933, by original designation.
- Anthidium (Ardenthidium)* Pasteels, 1969a: 103. Type species: *Anthidium ardens* Smith, 1879, by original designation.
- Anthidium (Morphanthidium)* Pasteels, 1969b: 423. Invalid because no type species designated; three included species. (Synonym of *Ardenthidium*, to judge by two of the included species, and was clearly intended by Pasteels to be the same as *Ardenthidium*.)

The metasoma in this subgenus is usually rather parallel-sided, T4 being about as wide as T1, and the whole perhaps a little flatter than in some related taxa, giving a characteristic form whereby the subgenus can often be tentatively recognized. The body length is variable, 8 to 19 mm. Females of most species differ from those of other subgenera in the strong outer ridge of the mandible,

head behind the eye, the partitions that form punctures in front of the carina extending up onto the anterior surface of the carina, which is thereby subdivided into numerous small segments. All species have arolia in both sexes, unlike most of the superficially similar species of *Hypanthidium* and *Hypanthidioides*, but like the equally similar *Hoplostelis* (*Austrostelis*). T7 of the male is small, rounded to bilobed; the terga lack spines.

Key to the Subgenera of *Anthodioctes*

1. Pronotal lobe shorter anteroposteriorly than tegula; stigma about twice as long as prestigma *A. (Anthodioctes s. str.)*
- Pronotal lobe as long anteroposteriorly as tegula; stigma about as long as prestigma *A. (Bothranthidium)*

Anthodioctes / Subgenus *Anthodioctes* Holmberg s. str.

Anthodioctes Holmberg, 1887b: 36, nomen nudum.

Anthodioctes Holmberg, 1903: 435. Type species: *Anthodioctes megachiloides* Holmberg, 1903, by designation of Cockerell, 1927b: 2. [*A. dasygastrinus* Holmberg, 1903, designated by Isensee (1927: 375), was not an originally included species name and was not a published name, so far as is known.]

Nananthidium Moure, 1947a: 26. Type species: *Nananthidium bettyae* Moure, 1947, by original designation.

Like the related genus *Hypanthidioides*, this subgenus has an unusually large stigma for an anthidiine. T7 of the male is entire or weakly bilobed. The slender, hoplitiform or heriadiform body of the species placed in *Nananthidium* seems to intergrade with the more robust form of most species of *Anthodioctes* s. str. Since no other characters distinguish *Nananthidium*, it is best regarded as a synonym of *Anthodioctes*.

■ *Anthodioctes* s. str. ranges through the tropics from as far north as Tamaulipas, Chihuahua, and Sinaloa, Mexico, south to Bolivia and Buenos Aires Province, Argentina. Urban (1998c) revised the nine species of the slender (*Nananthidium*) group of *Anthodioctes* and gave a key to the species. Urban (1999b) also gave a key to species of *Anthodioctes* s. str., exclusive of the slender species formerly placed in *Nananthidium*. She recognized 27 species, including 19 new ones.

The ecology and nesting biology of *Anthodioctes* in the Amazonian forest were described by Morato (2001). The nests, in trap nests (holes in wood blocks) mostly placed 15 m above the ground, consisted of series of cells made of resin mixed with particles of wood. Nests of another species in similar trap nests, much nearer to ground level, were described by Alves-dos-Santos (2004) along with observations on the nest-making behavior of females.

Anthodioctes / Subgenus *Bothranthidium* Moure

Bothranthidium Moure, 1947a: 23. Type species: *Bothranthidium lauroi* Moure, 1947, by original designation.

The hoplitiform body of species of this subgenus suggests the slender species of *Anthodioctes* s. str. formerly placed in *Nananthidium*. *Bothranthidium* differs from

such species in having an enormous combined prothoracic lobe and dorsolateral angle of the pronotum and a much smaller stigma (like that of most Anthidiini), as indicated in the key to subgenera. Additional distinctive features of *Bothranthidium* are the very broad scuto-scutellar foveae and other differentiating features cited by Moure (1947a: 27, 28). T7 of the male is strongly bilobed, the emargination between the lobes being deeper than a semicircle.

■ This subgenus occurs in Brazil (Esperito Santo to Santa Catarina), Paraguay, Bolivia, and Peru. The only species in *Anthodioctes lauroi* (Moure).

Genus *Apianthidium* Pasteels

Apianthidium Pasteels, 1969a: 41. Type species: *Anthidium apiforme* Meade-Waldo, 1914, by original designation.

Apianthidium appears to be a relative of *Trachusa*, as suggested by its megachiliform body and size (length 12–13 mm), the oblique, long cu-v (fully half the length of the second abscissa of M+Cu) of the hind wing, and the small T7 of the male. In the absence of arolia and the absence of all the usual anthidiine carinae, it agrees with some subgenera of *Trachusa*. In addition to the characters given in the key to distinguish it from *Trachusa*, it differs in the strongly hooked apices of the hind tibial spurs, the relatively slender hind basitarsus of the female (over three times as long as broad), and the yellow or reddish-yellow body with the posterior half of each tergum black.

■ *Apianthidium* occurs in Borneo. The only species is *A. apiforme* (Meade-Waldo).

Genus *Aspidosmia* Brauns

Osmia (Aspidosmia) Brauns, 1926: 208. Type species: *Osmia arnoldi* Brauns, 1926, monobasic.

This genus consists of dark, nonmetallic, robust bees, 8 to 10 mm long, having about the form of species of *Osmias* s. str. They are long-haired, without tergal fasciae. *Aspidosmia* was long included among the little-known genera related to *Osmia*, partly because the second recurrent vein enters the second submarginal cell, but Peters (1972a) demonstrated its relationship to the Anthidiini. The clypeus of the male is partly yellow, but there are no other yellow markings. The maximum width of the stigma is almost as great as the inner margin of the stigma basal to vein r. Peters (1972a) cited another character that *Aspidosmia* shares with Anthidiini, namely, a shortened thorax with a large propodeal triangle, but variations in both Anthidiini and Osmiini render this character weak. The prestigma is longer than the stigma. This is usually an osmiine feature but occurs also in a few anthidiines; thus the stigmal and prestigmal areas of *Aspidosmia* are similar to those of *Trachusa (Heteranthidium) larreae* (Cockerell). The cleft claws of the female, a presumed plesiomorphy, also resemble those of nearly all Anthidiini, but cleft claws also appear in females of *Osmia*, subgenus *Metallinella*, and simple claws appear in *Trachusoides*, an anthidiine. Because males all have cleft claws, the genes for such claws are present in every female, and a regulatory change could cause such claws to appear in females. On the preaxilla, below the posterior lateral angle of the

Aztecanthidium contains large (11–21 mm long), chalcidomiform species (Fig. 82–9), either black with yellow markings or red-brown with or without reddish-yellow markings. The clypeus of the female is more than twice as broad as long, sometimes protuberant. The preoccipital carina is complete, laterally joining the posterior end of the hypostomal carina. T5 of the male (and sometimes T4) has a lateral spine; T6 has two strong lateral spines, and T7 is deeply bilobed (Fig. 82–10b). The female is unusual in having a sublateral spine on T6 (Fig. 82–10a). The male genitalia, hidden sterna, and heads were illustrated by Snelling (1987).

■ This genus is known only from Mexico—Oaxaca to Puebla and Nayarit. The three species were revised by Snelling (1987).

Genus *Bathanthidium* Mavromoustakis

Bathanthidium is a small, little-known, Asiatic genus, its species all black to black with yellow on all tagmata, the yellow bands being broken on the anterior terga. These forms are united generically by the medially divided, smooth-floored scutoscuteellar sulcus (although the sulcus is narrow in the subgenus *Manthidium*), the absence of an omalar carina, the presence of at least a weak carina on the pronotal lobe, and the lack of other carinae. There is a fovea (small in *Manthidium*) behind the propodeal spiracle. The preoccipital ridge is not carinate. The scutellum is rounded or medially emarginate, in profile rounded or at least not sharp and not overhanging the metanotum. The inner surface of the hind tibia is rather convex, curving onto the upper margin, there being no sharp edge or carina marking the upper edge of the keirotrichiate area. Arolia are present. T6 of the male is simple; T7 ranges from simple (in *Bathanthidium* s. str.) to trilobed, with the median lobe longest.

This genus contains three taxa that have genus-group names, but because only four species are involved, it may seem unreasonable to recognize subgenera. I have done so partly because there is no assurance that the genus is monophyletic. The subgenera *Bathanthidium* s. str. and *Stenanthidiellum*, slender and hoplitiform, are quite clearly close relatives; e.g., both have a small median comb on S4 of the male. The subgenus *Manthidium* is more robust, megachiliform, resembling *Anthidiellum* subgenus *Ranthidiellum*, and may be misplaced in *Bathanthidium*. All, however, have a comb on S5 of the male occupying almost the entire width of the segment; this is an unusual feature suggesting a mutual relationship.

Key to the Subgenera of *Bathanthidium*

1. Fovea behind propodeal spiracle rounded, delimited by strong carina; T7 of male trilobed, median lobe longest (upper margin of propodeum without row of pits except laterally) (oriental) *B. (Bathanthidium* s. str.)
- Fovea behind propodeal spiracle elongate, weakly delimited; T7 of male simple or with slightly produced median lobe 2
- 2(1). Basal zone of propodeum not distinct, with irregular, sculptured, sloping pits laterally; T6 of male with elevated median section and concave lateral sections (oriental) *B. (Manthidium)*
- Basal zone of propodeum distinct laterally, with regular,

shiny, nearly horizontal pits; T6 of male with surface convex (eastern palearctic) *B. (Stenanthidiellum)*

Bathanthidium / Subgenus *Bathanthidium* Mavromoustakis s. str.

Dianthidium (*Bathanthidium*) Mavromoustakis, 1953a: 837.

Type species: *Dianthidium bifoveolatum* Alfken, 1937, by original designation.

This subgenus consists of a single small (8–9 mm long), slender hoplitiform species with yellow marks on all tagmata. It differs from the others in the dull mandibular surface of the female.

■ This subgenus occurs in southeastern China and Taiwan. The only known species is *Bathanthidium bifoveolatum* (Alfken).

Bathanthidium / Subgenus *Manthidium* Pasteels

Manthidium Pasteels, 1969a: 43. Type species: *Anthidium binghami* Friese, 1901 (first described under the homonymous name *Anthidium fraternum* Bingham, 1897), by original designation.

Manthidium consists of a megachiliform species, 8 mm long, without yellow marks on the head and thorax except on the face of the male, but with dark yellow bands on the terga, broken on T1 and T2. Contrary to Pasteels' (1969a) observations, the scutoscuteellar suture has a deeply invaginated part with a shiny bottom, divided medially to form two foveae. T6 of the male differs from both other subgenera as indicated in the key to subgenera; T7 has a weak midapical convexity, on each side of which is a shoulder.

■ This subgenus is known from northeastern India and Malaysia. The only species is *Bathanthidium binghami* (Friese).

Bathanthidium / Subgenus *Stenanthidiellum* Pasteels

Bathanthidium (*Stenanthidiellum*) Pasteels, 1968a: 1059.

Type species: *Anthidium sibiricum* Eversmann, 1852, by original designation. [Also described as new by Pasteels, 1969a: 53.]

?*Lasanthidium* Romankova, 1988: 26. Type species: *Stelis malaisei* Popov, 1941, by original designation.

Like *Bathanthidium* s. str., this is a subgenus containing small (5.5–8.0 mm long), slender, hoplitiform species with broken yellow tergal bands. It differs from the other subgenera in the evenly convex, simple T6 and T7 of the male and in the complete series of pits across the upper margin of the propodeum.

■ This subgenus occurs in eastern Siberia and Korea. There are apparently two species. Romankova (1988) considered the type species of *Stenanthidiellum* and *Lasanthidium* to be in different genera. The identity of *Anthidium sibiricum* Eversmann may be uncertain (see synonymy above). The genitalia of *Stelis malaisei*, the type species of *Lasanthidium*, are similar to those of *Bathanthidium* (*B.*) *bifoveolatum* Alfken (see Popov, 1941a), and it may be that *Bathanthidium* and *Stenanthidiellum* should be united.

and on the level of the scutal surface; (d) the tegula is as wide as long, the widest point behind the middle; and (e) impunctate tergal margins (rather broad) end abruptly at the side of the metasoma. In some other genera, such as *Hypanthidioides* and *Hypanthidium*, the anterior margin of the scutum bends down at an angle of about 45° to the adjacent scutal surface. This bend is not so abrupt, nor is the margin so nearly vertical, as in *Dianthidium*. Other characters of *Dianthidium* include the carinate omaulus, at least dorsally, the tridentate female mandible (in some species the preapical tooth is reduced to an angle at the end of a long cutting edge), the preapical crest or ridge of T6 of the female, and the apical fringe or tuft of hair (sometimes paired) on S3 of the male. The subgenus *Mecanthidium* was described in the genus *Paranthidium* because of the long, oblique apex of the female mandible, but it possesses the characters listed above, although the lateral feltlike patches of the metanotum and the transverse anterior crest of the scutum are less well developed than in other subgenera. Its relationship to *Dianthidium* was first noted by Moure (1965). The extreme male genitalic diversity among the subgenera (as in *Afranthidium*) is illustrated by Figures 82-2f and h.

Nests of *Dianthidium* usually consist of several cells and are made of pebbles stuck together by a matrix of resin and attached to rock surfaces or twigs of bushes or trees. Some species, however, make resin cells using pebbles and chaff in holes in banks or in holes in wood or stems. Exposed nests have been described for the subgenera *Mecanthidium* (Parker, 1977b), *Adanthidium* (Melander, 1902; Middleton, 1916), and *Dianthidium* s. str. (Fig. 7-1; also Grigarick and Stange, 1968; Clement, 1976). Subterranean nests have been described for *Dianthidium* s. str. by Custer and Hicks (1927), Fischer (1951), and Michener (1975a). [Through an error, the last were reported as nests of *Paranthidium jugatorium* (Say), but the bees were in fact *Dianthidium curvatum* (Smith).] Nests in holes in wood were described for *Dianthidium* s. str. (Krombein, 1967); one species, *D. (D.) ulkei* (Cresson) nests in holes in the ground, among rocks, and in pithy stems (Frohlich and Parker, 1985). In all cases cells are made of resin, usually intermixed with pebbles, chaff, seeds, and the like.

Key to the Subgenera of *Dianthidium* (Modified from Griswold and Michener, 1988)

1. Hind coxa with elongate ventral, apical spine in male, short tooth (best seen in lateral view) in female; hypostomal area dulled by fine, dense punctation (nearctic) *D. (Dianthidium s. str.)*
- Hind coxa without tooth or spine; hypostomal area shiny between punctures 2
- 2(1). Arolia absent; mouthparts in repose scarcely exceeding proboscis fossa (male S5 without sclerotized apical comb) (Mexico) *D. (Deranchanthidium)*
- Arolia present; mouthparts in repose considerably exceeding proboscis fossa 3
- 3(2). Male S5 with sclerotized apical comb; female mandible short, its length considerably less than maximum clypeal width (North America) *D. (Adanthidium)*
- Male S5 without sclerotized apical comb; female

mandible long, its length equal to maximum clypeal width (Mexico) *D. (Mecanthidium)*

Dianthidium / Subgenus *Adanthidium* Moure

Adanthidium Moure, 1965: 29. Type species: *Anthidium texanum* Cresson, 1878, by original designation.

This subgenus contains species 8 to 10 mm long that superficially resemble those of *Dianthidium* s. str. The comb on S5 of the male of *Adanthidium* is not found in other subgenera. The male genitalia, hidden sterna, and other structures were illustrated by Griswold and Michener (1988); see also Figure 82-2f, g.

■ The subgenus is found from Arizona to Texas (with a record for Kansas), USA, south to Oaxaca, in Mexico. There are four species.

Dianthidium / Subgenus *Deranchanthidium* Griswold and Michener

Dianthidium (Deranchanthidium) Griswold and Michener, 1988: 34. Type species: *Dianthidium chamela* Griswold and Michener, 1988, by original designation.

Species of *Deranchanthidium*, by their somewhat elongate form and restricted thoracic markings, superficially resemble *Anthodiocetes*, *Hypanthidium*, or *Hypanthidioides* more than *Dianthidium* s. str. Body length is 7.5 to 9.0 mm. The male genitalia, hidden sterna, and other structures were illustrated by Griswold and Michener (1988); see also Figure 82-2h-j.

■ This subgenus is found in western Mexico from Jalisco to Oaxaca. There are two species.

Dianthidium / Subgenus *Dianthidium* Cockerell s. str.

Anthidium (Dianthidium) Cockerell, 1900b: 412. Type species: *Anthidium curvatum* Smith, 1854, by original designation.

This is the principal group of *Dianthidium*, consisting of small to moderate-sized (5.5-13.0 mm long) species, mostly with abundant yellow markings. Male genitalia and hidden sterna were illustrated by Mitchell (1962) and Grigarick and Stange (1968).

■ *Dianthidium* s. str. is found from southern British Columbia and Ontario, Canada, and Maine south to Florida, USA, and the states of Nuevo Leon, Durango, and Baja California, Mexico. The 20 species were reviewed in papers by Timberlake (1943a) and Grigarick and Stange (1968).

Dianthidium / Subgenus *Mecanthidium* Michener

Paranthidium (Mecanthidium) Michener, 1942a: 278. Type species: *Paranthidium sonorum* Michener, 1942, by original designation.

Mecanthidium contains large species (body length 11-23 mm). The elongate body is largely red-brown, sometimes with yellowish-red markings. Because of size and color *Mecanthidium* superficially resembles *Aztecantidium* more than it does other subgenera of *Dianthidium*.

■ This subgenus ranges through western Mexico from

Oaxaca and Morelos north to Sonora and to southern Arizona, USA. There are two species.

Genus *Duckeanthidium* Moure and Hurd

Duckeanthidium Moure and Hurd, 1960: 2. Type species:

Anthidium megachiliforme Ducke, 1907, by original designation.

Grafanthidium Urban, 1995b: 435. Type species: *Grafanthidium amazonense* Urban, 1995, by original designation.

Atropium Pasteels, 1984: 132. Type species: *Megachile atropos* Smith, 1853, by original designation.

Ketianthidium Urban, 1999a: 160. Type species: *Ketianthidium zanolae* Urban, 1999, by original designation. (doubtful synonymy).

Urban (1999a) described *Ketianthidium* on the basis of one male from Argentina. She suggested that it is close to *Duckeanthidium*, differing by the very short omaular carina, the weakly emarginate apex of T7, etc., features that can be duplicated among species of *Duckeanthidium* of the the group called *Grafanthidium*. Unfortunately the stigma was not described, so that its agreement with the small stigma of *Duckeanthidium* cannot be determined. It probably runs to 8 in the key to genera of the Western Hemisphere. Michener (2002c) showed that *Atropium* Pasteels is a junior synonym, having been previously incorrectly included in the African fauna.

Duckeanthidium consists of robust, chalicodomiform bees 8.5 to 16.0 mm in length. They vary from wholly black, as in the female of *D. megachiliforme* (Ducke), with limited yellow markings in males, to forms with extensive yellow markings and the ground color of the metasoma brown. The juxtantennal carinae are distinct, unlike those of other large and robust American anthidiines except *Hoplostelis*. Arolia are well developed in males, absent or nearly so in females. There is a fovea margined by a carina behind the propodeal spiracle. T7 of males is produced to lateral lobes, often strongly developed, and sometimes a median spine, all projecting posteriorly. S1 to S6 of males are exposed and lack combs.

■ This genus is known from Costa Rica to Amazonas and Rondônia, Brazil, to Peru and probably Argentina. Five species were recognized by Urban (1995b) in *Duckeanthidium* and *Grafanthidium*.

Duckeanthidium megachiliforme (Ducke), the type species of the genus, was rather fully described by Moure and Hurd (1960), see also Michener (2002c). *D. cibeles* Urban is clearly congeneric with the species placed in *Grafanthidium* by Urban (1995b). *D. megachiliforme* and *thielei* Michener could be generically or subgenerically different from the other four species because they are large (13–16 mm long) and the male has a strong median carinate spine between the lobes of T7. The only equivalent of this spine in other species is a small median angle in *D. rondonicola* (Urban). The species placed in *Grafanthidium* by Urban have a weak lateral angle on the margin of the scutellum, but only a suggestion of such an angle can be seen in *D. cibeles*. Thus *Grafanthidium* and *Duckeanthidium* show a tendency to grade one into the other.

Thiele (2002) found the nests of *Duckeanthidium thielei* Michener, a close relative of *D. megachiliforme* (Ducke), in holes in wood blocks placed high in the for-

est canopy in Costa Rica; the pollen collected was almost exclusively that of *Bauhinia* (Fabaceae, Caesalpinioideae).

Genus *Eoanthidium* Popov

This is a genus of yellow-and-black bees (the metasoma yellow and brown in the subgenus *Clistanthidium*), mostly more elongate and slender than those of *Anthidiellum*. The most distinctive feature is the juxtantennal carinae, which in some species, however, are small, short ridges mesal to and slightly above the antennal bases. As indicated in the key to genera, there are certain other features that seem associated with the juxtantennal carinae. Nonetheless, the subgenera are quite different from one another (see the key to subgenera) and could have evolved the juxtantennal carinae independently. Generic characters other than those indicated above include the following: the preoccipital ridge is not carinate; the pronotal lobe has a strong carina or low lamella; the omaular carina is present at least on the upper half of the mesepisternum; the scutellum is rounded posteriorly with a small midapical emargination as seen from above, and is produced well over the metanotum, being narrowly rounded or acute as seen in profile; the fovea behind the propodeal spiracle is small (larger in the subgenus *Clistanthidium*), only partly enclosed, or absent; the row of pits across the upper margin of the propodeum is absent except as indicated at the extreme sides; S6 of the female is modified, with either a spine or a premarginal carina; the male sterna lack combs; T6 of the male is simple except for a tooth at each side; the male gonostylus is rather simple, slightly flattened distally, and often has a median bend or angle. The gonostylus is more broadened apically in the subgenera *Clistanthidium* and *Hemidiellum* than in others, and both have an apical brush of dense gonostylar hairs that is absent in the others. The penis valves are large (especially in some *Clistanthidium*) and pointed apically.

Key to the Subgenera of *Eoanthidium*

(Modified from Michener and Griswold, 1994a)

1. Subantennal suture straight; inner surface of hind tibia curving onto upper margin without sharp line between keirotrichiate area and region of longer hairs (arolia present; scutoscuteellar suture closed, similar to scutoaxillar suture; T4 to T6 of female and T5 and T6 of male with small lateral spines) (India) *E. (Hemidiellum)*
- Subantennal suture strongly arcuate outward; inner surface of hind tibia flat, keirotrichiate area ending abruptly at sharp, often carinate line along upper margin of tibia 2
- 2(1). Arolia absent; profile of T6 of female convex; T4 to T6 with lateral spines (scutoscuteellar suture closed, similar to scutoaxillar suture) (India) *E. (Salemanthidium)*
- Arolia present; profile of T6 of female concave (convex distally in subgenus *Clistanthidium*); T4 and T5 without lateral spines 3
- 3(2). Front coxa with strong carina or lamella transverse to axis of body or bending posteriorly and becoming longitudinal mesally; S6 of female not thickened apically, without lateral carina or spine; T6 of male with lateral tooth; scutoscuteellar suture sometimes not very different from scutoaxillar suture (palaearctic, Africa) *E. (Clistanthidium)*
- Front coxa without transverse carina or lamella; S6 of

female thickened apically, with lateral carina or spine; T6 of male without lateral tooth; scutoscutellar suture open, with shiny impunctate floor divided medially to form two foveae (paleartic, Africa) *E. (Eoanthidium s. str.)*

Eoanthidium / Subgenus *Clistanthidium* Michener and Griswold

Eoanthidium (Clistanthidium) Michener and Griswold, 1994a: 315. Type species: *Dianthidium turnericum* Mavromoustakis, 1934, by original designation.

This subgenus differs from its closest relative, *Eoanthidium s. str.*, in the often closed scutoscutellar suture (see the key to subgenera); the strong juxtantennal carina; the strong transverse carina or lamella, produced to a median angle in most males, on the front coxa, or, in *Eoanthidium nasicum* (Friese), the mesal part of the lamella extending distad toward the coxal spine and thus longitudinal; and the form of S6 of the female, which lacks marginal thickening but has a small preapical median spine. The body length is 8 to 9 mm.

■ *Clistanthidium* occurs in Turkey, Israel, Iran, and Pakistan, thence south in eastern Africa to Natal in South Africa, west to Shaba Province in Zaire, and to Namibia. There are probably six species; five named species were listed by Michener and Griswold (1994a).

Eoanthidium / Subgenus *Eoanthidium* Popov s. str.

Dianthidium (Eoanthidium) Popov, 1950a: 316. Type species: *Anthidium insulare* Morawitz, 1873, by original designation.

Eoanthidium (Eoanthidiellum) Pasteels, 1969a: 51. Type species: *Anthidium elongatum* Friese, 1897 = *Anthidium clypeare* Morawitz, 1873, by original designation.

Eoanthidium s. str. consists of strongly marked, yellow-and-black species 8 to 10 mm long. Pasteels (1969a) divided this group into two, as shown in the synonymy above. The differences, however, are weak or incorrect. Contrary to Pasteels' account, *Eoanthidium clypeare* (Morawitz), the type species of *Eoanthidiellum*, has juxtantennal carinae, although they are weak. In *E. insulare* (Morawitz), the type species of *Eoanthidium*, the omar carina continues onto the thoracic venter, a feature that might serve to distinguish it from *Eoanthidiellum*.

■ This subgenus occurs in the eastern Mediterranean basin, including Greece and the Balkans, southwestern Asia, thence east to Iran and southern Russia and south to Kenya. There are about five species.

Eoanthidium / Subgenus *Hemidiellum* Pasteels

Eoanthidium (Hemidiellum) Pasteels, 1972: 112. Type species: *Eoanthidium semicarinatum* Pasteels, 1972, monobasic.

Hemidiellum consists of a small species (6.0-6.5 mm long) sufficiently different from other *Eoanthidium* that it may deserve generic rank. As in some *Eoanthidium s. str.*, the omar carina is present only on the upper half of the mesepisternum.

■ This subgenus is known only from southern India. The lone species is *Eoanthidium semicarinatum* Pasteels.

Eoanthidium / Subgenus *Salemanthidium* Pasteels

Eoanthidium (Salemanthidium) Pasteels, 1969a: 51. Type species: *Hypanthidium salemense* Cockerell, 1919, by original designation.

Salemanthidium consists of species with more limited and paler yellow marks than is usual in *Eoanthidium s. str.*; body length is 8 to 9 mm. The substantial morphological differences from *Eoanthidium s. str.* are indicated in the key to subgenera. Lack of arolia, the most unusual feature, is duplicated among those Old World forms that do not have multidentate female mandibles only in *Icteranthidium*, *Apianthidium*, and some subgenera of *Trachusa*. The upper and lower parts of the base of the mandible are elevated, resulting in a broad concavity between them that is more conspicuous than in other subgenera. T7 of the male, rather large and long, has a longitudinal median carina; the apex is subtruncate except for a small median projection.

■ *Salemanthidium* is known only from southern India. There are two species (Pasteels, 1972).

Genus *Epanthidium* Moure

This genus consists of bees with a body form similar to that of *Dianthidium s. str.* or more elongate, such that the only Mexican species resembles an *Aztecantidium*. Some species are black with yellow or cream maculations but in most some of the pale areas or the background of parts of the metasoma are red. The pronotal lobe has an anteriorly sloping lamella as in *Dianthidium*; otherwise, the lettered (a to e) characters in the discussion of *Dianthidium* do not apply to *Epanthidium*. As noted in the key to genera, most *Epanthidium* have at least a minute indication of a juxtantennal carina, arising abruptly at the middle of the mesal margin of the antennal socket and extending upward. This carina thus differs from the generally larger juxtantennal carina of genera such as *Anthodioctes* and *Hypanthiodes*, which extends both up and down from the middle of the inner margin of the antennal socket and does not necessarily involve the margin of the socket proper. Although arolia are distinct in most species, they are extremely small in females (not males) of *E. (Epanthidium) tigrinum* (Schrottky) and could sometimes be considered absent. An interesting feature of all species except those in the subgenus *Ananthidium* is the strong submarginal carina of S6 of the female, which has one to four teeth. Male genitalia and other structures were illustrated by Stange (1983, 1995).

Epanthidium, except for *Ananthidium*, was revised by Stange (1983); *Ananthidium* was revised by Urban (1991). A nest, according to Stange (1983), consisted of cells made of clay, not resin as in *Dianthidium* and many other Anthidiini. Stange (personal communication, 1993) questioned this and reported exposed nests of *Epanthidium* each consisting of a single cell made of resin with embedded plant fibers. G. Melo (in litt., 1996) reported multicellular nests of *E. tigrinum* (Schrottky) made of resin and constructed in cavities.

Key to the Subgenera of *Epanthidium* (Males)

1. T7 three-lobed or with large median spine between two lobes (lamella of pronotal lobe translucent) (South America) *E. (Epanthidium s. str.)*

- T7 two-lobed 2
- 2(1). Tegula widest in front of middle; body length 9 to 12 mm; lamella of pronotal lobe opaque, black or dusky (South America, Mexico) *E. (Carloticola)*
- Tegula widest near middle; body length 6.5–8.0 mm; lamella of pronotal lobe translucent (South America)
..... *E. (Ananthidium)*

Key to the Subgenera of *Epanthidium* (Females)

- 1. T6 without longitudinal carina; lamella of pronotal lobe opaque, blackish (S6 with premarginal carina enlarged to form tooth on each side of apex of sternum)
..... *E. (Carloticola)*
- T6 with longitudinal median carina; lamella of pronotal lobe translucent 2
- 2(1). Clypeal apex truncate, nodulose, only slightly overhanging base of labrum, labrum therefore exposed when mandibles are closed; juxtantennal carina of *Epanthidium* type present although sometimes minute; S6 with premarginal carina enlarged to form one to four premarginal teeth *E. (Epanthidium s. str.)*
- Clypeal apex broadly rounded, rather thin, scarcely nodulose, overhanging base of labrum, labrum therefore hidden when mandibles are closed; juxtantennal carina absent or virtually so; S6 without premarginal carina or teeth, margin thin *E. (Ananthidium)*

***Epanthidium* / Subgenus *Ananthidium* Urban**

Ananthidium Urban, 1991: 73. Type species: *Anthidium inermis* Friese, 1908, by original designation.

This is the most distinctive of the subgenera of *Epanthidium*; both Urban (1991) and Stange (1995) gave it generic status. The principal characters are indicated in the key to subgenera and in Stange's (1995) key to genera. It consists of small species, 6.5 to 7.5 mm long. Male genitalia and hidden sterna were illustrated by Urban (1991) and Stange (1995).

■ *Ananthidium* is known from Argentina (provinces of Misiones and Salta to Chubut), Paraguay, and the state of Minas Gerais, Brazil. There are two species, distinguished by Urban (1991) and Stange (1995).

***Epanthidium* / Subgenus *Carloticola* Moure and Urban**

Carloticola Moure and Urban, 1990: 90. Type species: *Dianthidium paraguayense* Schrottky, 1908, by original designation.

This subgenus contains relatively large bees, 9 to 12 mm long, having a somewhat more elongate form than most species of *Epanthidium s. str.* Genitalia and other structures were illustrated by Moure and Urban (1990).

■ *Carloticola* occurs in two disjunct areas: (1) the states of São Paulo and Mato Grosso, Brazil, to Paraguay and the provinces of Catamarca and Misiones, Argentina; and (2) Mexico from Chiapas to Tamaulipas and Jalisco. There are three species, two in South America, one in Mexico.

***Epanthidium* / Subgenus *Epanthidium* Moure s. str.**

Epanthidium Moure, 1947a: 33. Type species: *Hypanthidium tigrinum* Schrottky, 1905, by original designation.

This subgenus includes species 6 to 10 mm long.

■ *Epanthidium s. str.* is found from the states of Pará and Paraíba, Brazil, south to Bolivia, Paraguay, and the provinces of Buenos Aires and Mendoza, Argentina. There are about 18 species. In the southern parts of its range, species of *Epanthidium s. str.* are the most common Anthidiini, particularly in xeric areas. Stange (1983) and Urban (1995c) gave keys to the species.

Genus *Euaspis* Gerstaecker

Euaspis Gerstaecker, 1857: 460. Type species: *Thynnus abdominalis* Fabricius, 1793, by original designation.

Dilobopeltis Fairmaire, 1858: 266. Type species: *Dilobopeltis fuscipennis* Fairmaire, 1858 = *Thynnus abdominalis* Fabricius, 1793, monobasic.

Parevaspis Ritsema, 1874: lxxi. Type species: *Parevaspis basalis* Ritsema, 1874, by designation of Sandhouse, 1943: 585.

This is a genus of moderate-sized to large (6–17 mm long) cleptoparasites. They are black, sometimes faintly bluish, and lack yellow markings, but the metasoma is commonly red. The interantennal area is elevated, with a strong, curved juxtantennal carina mesal to each antennal base and also with a smooth, longitudinal, median ridge or carina. The preoccipital carina is present laterally, behind the genal area, but not behind the vertex. The pronotal lobe has a carina, as does the omaulus. The hind coxa has a strong longitudinal carina on the inner margin; the outer surface is strongly expanded laterad to form a projecting lobe. The scutellum is strongly produced posteriorly, overhanging the propodeum, and forms a thin lamella in African species, but is thicker, punctate and hairy, in Asiatic species. The scopa is absent. T7 of the male is trilobed, small, extending little beyond T6. The male gonostylus is slender at the base, enlarged and flattened beyond the base, as illustrated by Viereck (1924b) and Baker (1995c). The volsellar lobe of the gonocoxite is large. A fuller generic description was given by Pasteels (1968a).

■ *Euaspis* is widespread in Africa, from Nigeria to Kenya and south to South Africa, and in southern and eastern Asia, from Nepal, India, and Sri Lanka east through Indonesia to the Moluccas and Kai (Key) and north through the Philippines, Taiwan, Japan, Korea, and China at least as far as Beijing. Of 12 species, two are African and ten Asian. Pasteels (1980) revised the genus and Baker (1995c) reviewed the Asiatic species.

Because of the scutellar character cited above, *Parevaspis* could be recognized as a subgenus for the Asiatic species, but no other distinguishing characters are known for the Asiatic group and recognition of subgenera seems unnecessary.

Euaspis species with red metasomas superficially resemble the similarly colored species of *Pachyanthidium*, with which they also agree in the produced, flat scutellum and the distally enlarged but rounded male gonostyli, the trilobed male S7, the presence of two apical spines on the

fore and middle tibiae (as in *Stelis*), and so forth. In fact, *Pachyanthidium* is the only nonparasitic anthidiine that usually has the last feature. *Euaspis*, however, differs from *Pachyanthidium* in lacking a scopa, a carina or lamella on the preoccipital ridge behind the vertex, and a broad toothed apex of the mandible of the female, and in having the juxtaantennal carinae and a vertical carina on the mesepisternum in front of the middle coxa. It is not clear whether *Euaspis* was derived from a *Pachyanthidium*-like ancestor. *Euaspis* also resembles *Stelis*, but in view of the differences listed in the key to genera as well as in the male genitalia, it may be that the similarities are convergent, resulting from the common parasitic habit.

Euaspis parasitizes other Megachilidae (*Lithurgus* and chalicodomiform *Megachile*), but unlike most cleptoparasitic bees, the female parasite enters the host nest by making a hole in the closure and burrowing through the nest (making holes in cell partitions), then throws out the host larvae and probably eats host eggs. Then, working toward the entrance, she reworks the pollen masses and lays an egg on each, often skipping cells near the entrance, and finally she closes the entrance with resin or pollen (Iwata, 1976: 420). *Stelis* (*Dolichostelis*) appears to have similar behavior (Parker et al., 1987).

Genus *Gnathanthidium* Pasteels

Gnathanthidium Pasteels, 1969a: 92. Type species: *Pachyanthidium prionognathum* Mavromoustakis, 1935, by original designation. [This is not *Gnathanthidium* Urban, 1994 = *Hypanthidioides* (*Michanthidium*).]

Gnathanthidium consists of a largely black species with only parts of the face of the male and lateral tergal spots of the female yellow. The metasoma tapers posteriorly so that T5 is much narrower than T1 or T2. The body is 9.5 to 10.0 mm long, coarsely punctate, and the tibiae are strongly tuberculate on the outer surfaces; there is a carina on the upper margin of the hind tibia. *Gnathanthidium* is a member of Series B related to *Pseudoanthidium* and should perhaps be regarded as a subgenus of that genus, related most closely to the subgenus *Micranthidium*, as indicated by the strongly carinate, almost lamellate preoccipital ridge, pronotal lobe, omaulus, and scutellar truncation; the lack of lateral teeth on T6 and T7 of the male; and the bilobed T7 of the male. It differs, however, in the nearly straight subantennal suture and the not particularly concave S3 to S5 of the male; the only unusual setae are on S3 and S4, which have median (not marginal) patches of dense white hairs, and the posterior margins of which are convex, translucent, and hairless. S5 of the male is reduced to a narrow band medially but laterally is produced to a short, hairless apical projection. An unusual feature is the broad, flat hind basitarsus of the female, conspicuously broader than the tibia and less than twice as long as broad.

■ This genus is found in eastern Africa from northern Natal Province, South Africa, to Kenya. The only species is *Gnathanthidium prionognathum* (Mavromoustakis).

Genus *Hoplostelis* Dominique

Austrostelis and *Hoplostelis* comprise the neotropical parasitic Anthidiini, i.e., the neotropical Anthidiini that

lack scopae. *Hoplostelis* has been recognized as a distinctive form, often at the genus level, for many years, formerly under the name *Odontostelis*. Various other neotropical bees have been described in the genus *Stelis* because they are anthidiines less distinctive than *Hoplostelis* and lack a scopa in the female and are therefore presumably cleptoparasites. However, they have only one apical spine on each front and middle tibia, and in other respects also do not agree with *Stelis*. For example, the male gonostyli do not have the characteristic angulate form found in *Stelis*. In fact, these neotropical *Stelis*-like bees are related to *Hoplostelis* and are now placed in the genus *Austrostelis*. They are also related to *Hypanthidioides*. *Austrostelis*, *Hoplostelis* and *Hypanthidioides* have lateral teeth on S5 and S6 of the male. The presence of arolia in both sexes of the parasitic genera suggests the subgenera *Dichanthidium* and *Ctenanthidium* of *Hypanthidioides*. The small and simple or weakly bilobed T7 of males of the parasitic genera is more similar to the bilobed T7 of *Ctenanthidium*, *Dichanthidium*, and *Saranthidium* than to other subgenera of *Hypanthidioides*. The male parasites do not have a comb on S5 as in *Saranthidium* or on S3 as in *Ctenanthidium*. Thus the parasites cannot be placed close to any one of the subgenera of *Hypanthidioides*.

Rozen (1966c), in describing the larva of *Hoplostelis* (as *Odontostelis*), regarded it as perhaps generically distinct from *Stelis*, a view that I strongly support. Young larvae of at least some species of *Stelis* have simple, pointed mandibles with which they kill eggs or larvae of the host. Larvae of *Hoplostelis*, however, have bidentate mandibles, as in most Anthidiini, and the adult, not the larva, destroys the host egg or larva.

Key to the Subgenera of *Hoplostelis*

1. Scutellum bigibbous; scutum bigibbous posteriorly; propodeum without foveae or pits; omaulus lamellate almost to lower end; T1 without transverse carina at summit of anterior surface; T4 to T6 (at least in female) each with longitudinal median carina (Brazil) *H. (Rhynostelis)*
- Neither scutellum nor scutum bigibbous; propodeum with well-defined fovea, divided by transverse carinae, behind spiracle, continued as basal propodeal zone divided into many pits or small foveae; omaulus carinate in upper one-half or one-third, rounded below; T1 with transverse carina at summit of anterior surface; terga without longitudinal median carinae *H. (Hoplostelis s. str.)*

Hoplostelis / Subgenus *Hoplostelis* Dominique s. str.

Hoplostelis Dominique, 1898: 60. No valid included species.

Type species: *Stelis abnormis* Friese, 1925 = *Anthidium bivittatum* Cresson, 1878, by inclusion and designation of Griswold and Michener, 1988: 36.

Odontostelis Cockerell, 1931d: 542. Type species: *Stelis abnormis* Friese, 1925 = *Anthidium bivittatum* Cresson, 1878, by original designation.

This subgenus includes relatively large (8–11 mm long), robust, chalicodomiform species having the special features indicated in the key as well as metasomal punctuation that is fine compared to that of the genus *Aus-*

trostelis. The clypeus of the female has an apical tubercle or two apical processes. Unlike those of *Austrostelis*, T1 and T2 are commonly black; the yellow of the remaining, smaller terga therefore contrasts sharply with the black metasomal base.

■ *Hoplostelis* s. str. occurs from Bolivia and Santa Catarina, Brazil, north through the tropics as far as Jalisco, Mexico. Moure and Urban (1994) gave a key to the three species of this subgenus. One of them, *H. cornuta* (Bingham), was described from Burma, no doubt in error, for it is known from Trinidad.

So far as is known, *Hoplostelis* s. str. parasitizes euglossine bees of the genus *Euglossa* (Bennett, 1966). The female parasite opens a host cell, kills the host egg or larva, lays her egg on the food mass, and reseals the cell. She then drives the adult host from its nest. Moreover, over a few days the parasite comes and goes from the nest, closing the nest entrance at each departure, all the while parasitizing the younger cells and killing larger larvae, pupae, and even unemerged adults in the older cells.

Hoplostelis s. str. has the body form of *Duckeanthidium cible* Urban and its congeners. It is tempting to believe that *Hoplostelis* s. str. is derived from *Duckeanthidium* and that the genus *Austrostelis* is derived from *Hypanthioides*, but other characters do not support a derivation from *Duckeanthidium*.

Hoplostelis / Subgenus *Rhynostelis* Moure and Urban

Rhynostelis Moure and Urban, 1994: 297. Type species: *Anthidium multiplicatum* Smith, 1879, by original designation.

This subgenus consists of a large (14 mm long), robust species similar to *Hoplostelis* s. str. Distinctive features are indicated in the key to subgenera; further, the clypeus of the female has a basomedian tubercle and the apex of the clypeus is simple. D. Urban (personal communication, 1994) writes, of a character not mentioned in the published description, that the juxtantennal carina is present but shorter than that in *Hoplostelis* s. str., arising at the level of the middle of the antennal alveolus and extending upward.

■ *Rhynostelis* occurs in Amazonas, Brazil. The only known species is *Hoplostelis multiplicata* (Smith), new combination.

This subgenus is known from only two female specimens; the male is unknown. One of the specimens was taken at the entrance to a nest site that had been occupied by *Eufriesea pulchra* (Smith); it is therefore likely that *Rhynostelis*, like *Hoplostelis* s. str., parasitizes Euglossini.

Genus *Hypanthioides* Moure

This is a neotropical genus of chalicodomiform or hoplitiform bees superficially similar to *Hypanthidium*, *Anthodiocetes*, and *Austrostelis*. Most species are dark, i.e., with limited yellow markings and dusky wings, but a few have extensive yellow areas. Many are smaller than most *Hypanthidium*; body length is from 5 to 9 mm. The presence of juxtantennal carinae distinguishes *Hypanthioides* from *Hypanthidium*; the lack of lateral preoccipital carinae distinguishes it from *Anthodiocetes*. The genus that

seems closest to *Hypanthioides* is *Austrostelis*, which lacks the scopa and is presumably cleptoparasitic. *Austrostelis* is essentially a *Hypanthioides* in the sense in which that generic name is used here. There is a strong tendency for loss of arolia in *Hypanthioides*; only the subgenera *Ctenanthidium* and *Dichanthidium* have arolia in both sexes.

Key to the Subgenera of *Hypanthioides*

1. Mandible of female with long, smooth apical margin between two small, lower apical teeth and upper apical angle or tooth; surface of distal half of mandible of female dull and minutely granular, without longitudinal carinae or with slender carinae that do not extend onto basal half of mandible; mandible of male with upper tooth separated from middle tooth by broad concave margin, upper interspace nearly twice as long as lower interspace; first segment of labial palpus of female with coarse, erect, curved or hooked hairs on undersurface..... 2
- Mandible of female with three or four more or less evenly spaced teeth; surface of female mandible not or less dull, with strong longitudinal carinae extending onto basal half; mandible of male with teeth more evenly spaced; first segment of labial palpus of female without erect, curved or hooked hairs..... 3
- 2(1). Mandible of female without distinct upper apical tooth, surface without carinae; hind coxa of male with small apical spine directed mesad; distal margin of T6 of male with lateral tooth but otherwise unmodified *H. (Michanthidium)*
- Mandible of female with strong upper apical tooth separated from long smooth margin by deep emargination, surface with usual carinae but carinae weak; hind coxa of male unarmed; distal margin of T6 of male with obtuse lateral tooth, margin medially expanded, elevated, sometimes bilobed *H. (Larocanthidium)*
- 3(1). Tegula large, with depressed translucent marginal area expanded anterolaterally, much wider there than midlaterally; body hoplitiform (arolia present in both sexes; T7 of male bilobed) *H. (Dichanthidium)*
- Tegula normal, its depressed translucent margin not much broader anterolaterally than midlaterally; body more robust, hoplitiform to chalicodomiform 4
- 4(3). Mandible of female three-toothed; S4 of male with small but strong basal median comb..... *H. (Mielkeanthidium)*
- Mandible of female four-toothed; S4 of male without comb 5
- 5(4). Arolia well developed in both sexes; S3 of male with median marginal comb of coarse black setae that are shorter than hairs of fringe on same margin laterally..... *H. (Ctenanthidium)*
- Arolia absent or extremely minute in females and some males; S3 of male without apical comb 6
- 6(5). Arolia of male absent; T7 of male bilobed, emargination between lobes about as wide as a lobe; S5 of male with apical comb; tegula widest in front of middle *H. (Saranthidium)*
- Arolia of male present; T7 of male with narrow apicolateral lobes, space between them much wider than a lobe or, rarely [as in *H. (Moureanthidium) capixaba* (Urban)], lobes triangular and separated by broad emargination; S5

- of male without apical comb (but with rows of coarse setae in *Dicranthidium*); tegula widest near middle 7
- 7(6). T6 and T7 of male curled anteriorly, their surfaces thus directed ventrad and processes of T7 overlapping S2; S3 or S4 to S6 of male hidden; hind coxa of male with one or more coarse peglike setae on mesal surface; omaral carina extending onto venter of thorax (scutellum produced to translucent apical carina except medially).....
..... *H. (Dicranthidium)*
- T6 and T7 of male not so strongly curled (except in *Moureanthidium*), T6 not clearly directed ventrad; S3 to S5 or S6 ordinarily visible; hind coxa of male without peglike setae; omaral carina on upper half of mesepisternum, disappearing or becoming irregular because of punctation below 8
- 8(7). Scutellum swollen, biconvex; omaral carina extending onto lower half of mesepisternum as irregular line (hind tarsus of male elongate, first two segments taken together as long as hind tibia) .. *H. (Hypanthidioides s. str.)*
- Scutellum not biconvex; omaral carina not extending onto lower one-half or one-third of mesepisternum 9
- 9(8). Hind tarsus of male elongate, first two segments taken together as long as hind tibia; S3 of male with small median bilobed projection; T7 of male strongly curled, surface thus directed ventrad; juxtantennal carina longer than diameter of antennal socket *H. (Moureanthidium)*
- Hind tarsus of male shorter, first two segments taken together shorter than hind tibia; S3 of male without median, bilobed projection; T7 of male not so strongly curled; juxtantennal carina about as long as diameter of antennal socket *H. (Anthidulum)*

Hypanthidioides / Subgenus *Anthidulum* Michener

Dianthidium (Anthidulum) Michener, 1948a: 19. Type species: *Dianthidium currani* Schwarz, 1933, by original designation.

Anthidulum contains small (4.5–6.5 mm long), moderately robust species, richly marked with yellow. S2 of the male is somewhat enlarged, suggesting *Dicranthidium*, but the metasoma is not tightly curled as in that subgenus, S3 to S6 being exposed. The male antennae are not elongate as in *Dicranthidium*, the middle flagellar segments being little longer than broad.

■ This subgenus is found from Costa Rica to the state of Paraná, Brazil, and the provinces of Misiones to Tucumán, Argentina. The four species were revised by Urban (1993b).

Hypanthidioides / Subgenus *Ctenanthidium* Urban

Ctenanthidium Urban, 1993a: 85. Type species: *Ctenanthidium gracile* Urban, 1991, by original designation.

Ctenanthidium includes species related to *Dicranthidium* and especially to *Anthidulum*, and similar in appearance to those subgenera, although the body is rather slender; the length is 5.5 to 7.0 mm. It differs from both of those subgenera in the form of the male T7, which is bilobed and lacks apicolateral projections, in addition to other characters indicated in the key to subgenera and in Urban (1993a).

■ The range is from Uruguay, the province of Córdoba,

Argentina, and Bolivia north to the state of Paraná, Brazil. The four species were revised by Urban (1993a).

Hypanthidioides / Subgenus *Dichanthidium* Moure

Dichanthidium Moure, 1947a: 30 (January); also described as new by Moure, 1947b: 235 (June). Type species: *Dichanthidium exile* Moure, 1947, by original designation.

Dichanthidium includes species having the size (body length 7 mm) and slender form of some *Anthidiocetes (Bothranthidium)* and the species formerly placed in *Nananthidium* but with all the principal features of *Hypanthidioides*, except that it has arolia in both sexes. In this respect *Dichanthidium* resembles *Hypanthidioides (Ctenanthidium)* and *Austrostelis*.

■ This subgenus is known from the provinces of Salta, Argentina, and Santa Cruz, Bolivia. The only described species is *Hypanthidioides exile* (Moure); the Bolivian species appears to be different.

Hypanthidioides / Subgenus *Dicranthidium* Moure and Urban

Dicranthidium Moure and Urban, 1975: 837. Type species: *Anthidium arenarium* Ducke, 1907, by original designation.

Dicranthidium, which was synonymized with the subgenus *Anthidulum* by Griswold and Michener (1988), appears to be a clearly distinct subgenus, though perhaps the sister group to *Anthidulum*, sharing with it small body size and the enlarged S2. The body is robust, the most robust of the subgenera of *Hypanthidioides*; length is 5 to 7 mm. The yellow markings are pale and limited in extent. As in *Moureanthidium*, the scutellum (except medially) and the axilla are produced to a translucent apical carina or lamella. Numerous structures, including male genitalia and sterna, were illustrated by Moure and Urban (1975).

■ This subgenus ranges from the states of Paraná and Paraíba, Brazil, to Trinidad (West Indies) and the province of Valle, Colombia. The six species were reviewed by Urban (1993b).

Some species differ from one another in certain striking features. For example, the male of *Hypanthidioides arenaria* (Ducke) lacks the hind tibial spurs that are present in other species.

Laroca and Rosado Neto (1975) described nests of *Hypanthidioides arenaria* (Ducke) consisting of one to several resin cells constructed in small cavities of various sorts.

Hypanthidioides / Subgenus *Hypanthidioides* Moure s. str.

Hypanthidioides Moure, 1947a: 35. Type species: *Anthidium flavofasciatum* Schrottky, 1902, by original designation.

Hypanthidioides Michener, 1948a: 22; Moure and Urban, 1975: 837; Urban, 1993b: 28; error for *Hypanthidioides* Moure, 1947.

Hypanthidioides Moure, 1947a: 18. Type species: *Anthidium flavofasciatum* Schrottky, 1902, by original designation.

Hypanthidioides / Subgenus *Saranthidium* Moure and Hurd

Hypanthidium (*Saranthidium*) Moure and Hurd, 1960: 6.

Type species: *Anthidium flavopictum* Smith, 1854, by original designation; incorrectly stated to be *Anthidium furcatum* Ducke, 1908, by Griswold and Michener, 1988: 31.

This subgenus consists of forms with limited yellow markings, an exception being *Hypanthidioides* (*S.*) *panamense* (Cockerell), which has much yellow, suggesting *H. (Anthidulum) currani* (Schwarz) from the same region. The body form is as in *Hypanthidioides* s. str.; the length is 6 to 7 mm. This is the only subgenus in which males as well as females lack arolia. It resembles *Dichanthidium* in the two moderately broad lobes of T7 of the male.

■ *Saranthidium* ranges from Paraguay and Santa Catarina, Brazil, north through the tropics to Oaxaca and Veracruz, Mexico. There are seven named species.

Genus *Hypanthidium* Cockerell

Although this neotropical genus comes out in the key next to *Epanthidium*, it does not resemble that genus superficially because of its chalicodomiform body and usually dark coloration; its species are thus similar to most *Anthodioctes*. Rarely, the metasoma is entirely red. The body length is 7.0 to 10.5 mm. The lack of juxtantennal carinae, of a strong carina around the basin of T1, and of arolia readily distinguishes *Hypanthidium* from *Anthodioctes*. T7 of the male is rather large, broadly rounded, subtruncate or weakly emarginate midapically, the exposed part about as long as that of T6, the distal margin often translucent.

Key to the Subgenera of *Hypanthidium*

1. Preoccipital carina present as a sharp although punctate ridge laterally, behind eye; mandible of male bidentate, with strong, broad emargination between teeth; S2 of male with strong projection on each side *H. (Tylanthidium)*
- Preoccipital carina absent; mandible of male with indications of three teeth; S2 of male with at most weak convexity on each side *H. (Hypanthidium* s. str.)

Hypanthidium / Subgenus *Hypanthidium* Cockerell s. str.

Hypanthidium Cockerell, 1904b: 292. Type species: *Anthidium flavomarginatum* Smith, 1879, = *Anthidium divaricatum* Smith, 1954, by original designation.

■ *Hypanthidium* s. str. occurs through the tropics from the states of Sonora, San Luis Potosí, and Yucatan, in Mexico, to Misiones, in Argentina, and to Paraguay and Bolivia. Urban (1998b) gave a key to the 16 species.

Hypanthidium / Subgenus *Tylanthidium* Urban

Tylanthidium Urban, 1994a: 277. Type species: *Tylanthidium tuberigaster* Urban, 1994, by original designation. [New status.]

In the male of *Tylanthidium* the lateral margins of T7 diverge apically to a broad apex that has a deeper midapical emargination than that in most other *Hypanthidium*, and the undersurface of T7 is densely hairy. In general,

however, the distinctive form of this tergum of *Tylanthidium* is as in *Hypanthidium* s. str. The hind tarsus of the male is more thickened than is usual in *Hypanthidium*, the second segment being about as long as broad and about as broad as the basitarsus, the fourth segment much broader than long because of its dorsal lobe. Other characters, including the carinate pronotal lobe, are as in *Hypanthidium* s. str., and *Tylanthidium* should probably be regarded as a synonym of *Hypanthidium*.

■ This subgenus occurs in the state of Amazonas, Brazil. It is based on a single species, *Hypanthidium tuberigaster* (Urban).

Genus *Icteranthidium* Michener

Icteranthidium Michener, 1948a: 25. Type species: *Anthidium limbiferum* Morawitz, 1875, by original designation.

Icteranthidium contains species with rich yellow markings or with the body largely yellow; the body form is similar to that of *Dianthidium*, and the size is variable (7.5–15.0 mm long). Arolia are absent. The preoccipital carina is absent behind the vertex but is strong laterally, and unlike that of other bees, its lower end extends nearly straight to the posterior mandibular articulation instead of extending more posteriad and approaching or joining the hypostomal carina or, rarely, curving forward to the mandibular articulation. The mandible of the female has four teeth separated by shallow concavities. The pronotal lobe has a strong lamella and the omaulus is carinate. The scutellum is produced to a lamella except medially, and the axilla is frequently produced to a posterior angle or point projecting beyond the contour of the scutellum. A strong carina or lamella between the ventral and anterior surfaces of the front coxa characterizes most species. T6 of the female is concave in profile, the margin convex with a median notch. The truncate T7 of the male has a midapical projection, sometimes also a lateral projection or tooth, and is thus trifid. Male genitalia and other structures were illustrated by Popov (1967).

■ This genus ranges from Morocco and Portugal to Mongolia. It is particularly well represented in the xeric areas of Asia, but occurs in southern Europe (north to Hungary), northern Africa south in the Sahel to Senegal, Mali, Chad, and northern Kenya, and southeast to Baluchistan in Pakistan. Warncke (1980a) reported 15 west palearctic species but did not include Central Asia, Mongolia, the Sahel, Pakistan, etc., in his study. There are probably about 25 species.

Genus *Indanthidium* Michener and Griswold

Indanthidium Michener and Griswold, 1994a: 315. Type species: *Indanthidium crenulicauda* Michener and Griswold, 1994, by original designation.

A member of Series B (see the discussion of the tribe), *Indanthidium* resembles a small (length 6.0–7.5 mm) *Anthidium*, largely because the yellow metasomal bands are divided into four spots each, as they are in some species of *Anthidium*. But in contrast to *Anthidium*, the depressed marginal zone of T5 is punctured like the rest of the tergum, or a little more densely so in the male, the zone not differentiated and its margin not angulate me-

dially; and the posterior margin of T5 and other terga is rather broadly impunctate. *Indanthidium* is similar to *Pseudoanthidium*, with which it agrees in its distinctly arcuate subantennal sutures. It differs from that genus in the unmodified S1 to S6 of the male, which lack combs or processes, and in S4 and S5, which are not especially concave. An unusual feature is T7 of the male, which is nearly as broad as T6 and has strong median and lateral spines (the latter the longest) and irregular smaller teeth between the median and lateral ones. Another distinctive feature is the maxillary palpus, which appears to consist of only one segment. The male genitalia were illustrated by Michener and Griswold (1994a).

■ This genus occurs in southern India. The only known species is *Indanthidium crenulaticauda* Michener and Griswold.

Genus *Larinostelis* Michener and Griswold

Larinostelis Michener and Griswold, 1994a: 317. Type species: *Larinostelis scapulata* Michener and Griswold, 1994, by original designation.

This genus, known only from the female, consists of a small (6.5 mm long), robust, black bee with extensive yellow markings. Like that of *Stelis*, the female lacks a scopa. *Larinostelis* is the most carinate of all *Stelis*-like bees, with juxtantennal carinae between the antennal sockets, and with carinae also on the pronotal lobe, the omaulus, the axilla, the scutellum (except for the median notch), the basal zone of the propodeum (except medially) and continuing behind the spiracle, the dorsal margin of the metapleuron, longitudinally on the hind basitarsus, transversely on S1, and across the base of S6. Arolia are absent. The axilla is greatly produced laterally, thus behind the regula. The two apical spines of the fore and middle tibiae are minute.

■ *Larinostelis* is known only from Kenya. The single species is *L. scapulata* Michener and Griswold, known from a single female specimen.

It is not clear whether *Larinostelis* is a derivative of *Stelis* or an independently cleptoparasitic form. In the former case, it would be best regarded as a subgenus of *Stelis*. When discovered, the male should help in resolving this question.

Genus *Neanthidium* Pasteels

Neanthidium Pasteels, 1969a: 93. Type species: *Anthidium octodentatum* Pérez, 1895, by original designation.

This genus consists of a rather elongate species (9–13 mm long) with abundant yellow markings; the broad metasomal bands are broken medially, the aspect being that of some *Rhodanthidium*. *Neanthidium* differs from that genus, however, in the characters of Series B (see the discussion of the tribe), e.g., the five-toothed female mandible and lack of arolia. Unique features of the male are the strongly four-toothed T6 and T7 and the strong, sharp lateral teeth of both S4 and S5; S1 to S6 are otherwise unmodified and exposed. The male gonostylus is slender, slightly broadened with numerous long hairs medially, and much longer than the short, wide gonocoxite; the penis valves are in contact through most of their lengths.

■ *Neanthidium* occurs in North Africa (Algeria, Morocco) and is represented by a single species, *N. octodentatum* (Pérez).

Some *Pseudoanthidium* species have lateral apical processes on S4 and S5 of the male, but the processes are blunt and often have modified setae, rather than being smooth and spinelike as in *Neanthidium*. T6, T7, and other features of *Neanthidium* are very different from those of *Pseudoanthidium*.

Genus *Notanthidium* Isensee

Notanthidium is used here in a broader than usual sense, to include *Allanthidium*. *Notanthidium* s. str. differs from *Allanthidium* principally in its slender, hoplitiform body. Equal variation in body form also occurs in other genera, e.g., *Anthodioctes* s. str., where heriadiform to chalicodomiform bodies are found among species of the same subgenus. The modified clypeus and mandibles of the female of *Notanthidium* s. str. do not seem to justify generic distinction for the single species of that subgenus. In both *Notanthidium* s. str. and *Allanthidium* there are individuals in which the postspiracular foveae of the propodeum are recognizable. In other individuals, they are completely absent or the area concerned is coarsely sculptured with ridges or carinae suggesting the carinae that delimit or subdivide the fovea when it is well defined. Likewise, the row of pits across the base of the propodeum is variable, recognizable if at all only laterally. Thus two characters other than body form used to differentiate *Notanthidium* and *Allanthidium* by Michener (1948a) do not work.

Notanthidium has yellow or cream markings at least on the metasoma, often also on the head and thorax. The pubescence is often but not always partly or wholly black. The body length is 7.5 to 11.5 mm. The pronotal lobe is strongly carinate, but the omaulus is not carinate or rarely feebly so. The scutellum is rounded posteriorly, not at all carinate, and not or weakly overhanging the metanotum. T7 of the male is moderately to strongly curled forward, and bilobed. S1 to S6 are all exposed, S4 to S6 or at least one of them with a lateral tooth. Male genitalia, sterna, and other characters were illustrated by Toro and Rojas (1970b).

Key to the Subgenera of *Notanthidium*

1. Body hoplitiform; clypeus of female largely impunctate, upper part tumescent, lower margin with sublateral projection; clypeus in both sexes not at all overhanging base of labrum; mandible of female porrect, with deep emargination in upper margin just beyond middle, width of its apex less than basal width, three-toothed *N. (Notanthidium s. str.)*
- Body chalicodomiform; clypeus of female punctate, not tumescent, without apical projections; apical margin of clypeus in both sexes overhanging base of labrum; mandible of female of the usual shape, width of its apex at least as great as basal width, vaguely four-toothed or with long straight margin above two lowermost teeth, sometimes undulate, thus producing a vaguely five-toothed margin 2
- 2(1). Omaulus carinate; mandible of female obscurely five-toothed *N. (Chrisanthidium)*

- . Omaulus rounded; mandible of female obscurely four-toothed *N. (Allanthidium)*

Notanthidium / Subgenus *Allanthidium* Moure

Allanthidium Moure, 1947a: 21. Type species: *Anthidium rodolfi* Ruiz, 1938, by original designation.

Trichanthidium Moure, 1947a: 20 (not Cockerell, 1930).

Type species: *Anthidium subpetiolatum* Schrottky, 1910, by original designation.

Allanthidium (Anthidium) Michener, 1948a: 13, replacement for *Trichanthidium* Moure, 1947. Type species: *Anthidium subpetiolatum* Schrottky, 1910, autobasic.

Moure (1947a) and Michener (1948a) recognized two taxa, here united under the name *Allanthidium*. The principal difference is that those then placed in *Allanthidium* are generally smaller, have pale pubescence, and have yellow areas on the head and thorax as well as the metasoma. Species formerly placed in *Anthidium* are generally larger, have abundant black hair, and lack yellow marks on the head and thorax except on the face of males. T7 of the male is two-lobed in the first group, two-lobed or four-lobed in the second; contrary to Michener (1948), then, this character does not distinguish the groups.

■ *Allanthidium* occurs from the provinces of Puno in Peru and Jujuy in Argentina south to south-central Chile and the province of Neuquén in Argentina. There are six described species and at least one undescribed.

The type species, *Notanthidium rodolfi* (Ruiz), differs from others in the short jugal lobe of the hind wing, little more than one-fourth as long as the vannal lobe. If it is considered subgenerically distinct, the name *Anthidium* is available for the remaining species.

Notanthidium / Subgenus *Chrsanthidium* Urban

Chrsanthidium Urban, 1997b: 181. Type species: *Anthidium bidentatum* Friese, 1908, by original designation. [New status.]

This subgenus resembles in appearance the well-marked, pale-haired species of *Allanthidium* such as *Notanthidium rodolfi* (Ruiz). It differs in the characters indicated in the key to subgenera.

■ *Chrsanthidium* occurs from Valparaíso to Atacama, Chile, and from Mendoza to Jujuy, Argentina. Urban (1997b) distinguished three species.

Notanthidium / Subgenus *Notanthidium* Isensee s. str.

Dianthidium (Notanthidium) Isensee, 1927: 373. Type species: *Anthidium steloides* Spinola, 1851, by original designation.

This slender-bodied subgenus, although characterized by partly black pubescence and a lack of pale marks on the thorax, does not present a black aspect, as do the dark species of *Allanthidium*.

■ This subgenus occurs in central and southern Chile and in the provinces of Neuquén and Chubut, Argentina. The one species is *Notanthidium steloides* (Spinola).

Genus *Pachyanthidium* Friese

These are robust, compact, megachiliform bees, 5 to 12 mm long. The metasoma tapers such that T5 is little more than half as wide as T1 and T2. The mandibles of the female are short and variable in dentition, from four-toothed (with at least some of the spaces between the teeth gently concave) to five- to ten-toothed (the teeth short and blunt, and the notches between them sometimes acute), to minutely denticulate with multiple, minute teeth. Thus some species fall in Series A, most in Series B (see the discussion of the tribe). For this reason the genus comes out twice in the key to genera. The color pattern is also variable, from black-and-yellow, as in most anthidiines, to black with a red metasoma, to wholly black. The arolia are absent except in males of the subgenus *Trichanthidium* and in both sexes of *Ausanthidium*. Pasteels' (1969a, 1984) statements that arolia are present but minute in *Pachyanthidium* seem to be based on the projecting, minutely setose plantae. *Pachyanthidium* is among the most carinate of the Anthidiini; the following are not merely carinate but are strongly lamellate: the preoccipital ridge behind the vertex, the pronotal lobe, the omaulus, the lateral margin of the axilla, and the posterior margin of the scutellum. The posterior margin of the scutellum is nearly straight (broadly rounded laterally in the subgenus *Ausanthidium*) and greatly overhangs the propodeum, which lacks basal pits and foveae (but see *Ausanthidium*). T7 of the male is trifid. The apices of the front and middle tibiae have two spines, as in *Stelis*, the two often reduced to one in the subgenus *Trichanthidium*.

Key to the Subgenera of *Pachyanthidium*

1. Eyes hairless; preoccipital carina absent laterally, behind eyes 2
- . Eyes with abundant, short hairs; preoccipital carina present laterally, behind eyes (mandible of female four-toothed) 3
- 2(1). Arolia present; mandible of female four-toothed (Namibia) *P. (Ausanthidium)*
- . Arolia absent; mandible of female usually five- to ten-toothed or denticulate (four-toothed only in *Pachyanthidium micheneri* Pasteels) (Africa) *P. (Pachyanthidium s. str.)*
- 3(1). T3 to T5 each with slender lateral spine; ocelli small, diameter about equal to width of base of first flagellar segment; hind coxa not carinate; arolia present in male, absent in female (Africa, oriental) *P. (Trichanthidium)*
- . T3 to T5 without lateral spines; ocelli of ordinary size, diameter greater than width of base of first flagellar segment; hind coxa carinate; arolia absent (possibly with very minute arolia in both sexes) (Africa, Arabia) *P. (Trichanthidioides)*

Pachyanthidium / Subgenus *Ausanthidium* Pasteels

Ausanthidium Pasteels, 1969a: 60. Type species: *Anthidiellum ausense* Mavromoustakis, 1934, by original designation.

In having arolia in both sexes, this subgenus differs from other *Pachyanthidium*. The body has abundant yellow markings, and the background of the metasoma is partly red-brown. The length is 7.0 to 7.5 mm. The terga

lack the strong lateral spines found in *Trichanthidium*, although T6 of the male has a moderate-sized sublateral spine. T6 of the female has a large apical emargination; females of the other subgenera do not.

■ This subgenus is known only from Namibia. The single species is *Pachyanthidium ausense* (Mavromoustakis).

This subgenus was placed in *Anthidiellum* by Pasteels (1969a), but nearly all its characters support affiliation with *Pachyanthidium*; see Michener and Griswold (1994a).

***Pachyanthidium* / Subgenus *Pachyanthidium* Friese s. str.**

Anthidium (*Pachyanthidium*) Friese, 1905a: 66. Also described as new by Friese, 1910b: 158. Type species: *Anthidium bicolor* Lepeletier, 1841, by designation of Cockerell, 1920b: 298.

Pachyanthidium consists of species 7.5 to 12.0 mm long, with yellow markings or a red metasoma, and without lateral spines on T2 to T5. The hypostomal carina is lamellate. The apices of the front and middle tibiae have two spines (as in *Stelis*). S5 of the male has a broad apical comb. A remarkable feature of the subgenus is the variability in dentition of the female mandibles, from four-toothed to multi-toothed and to minutely serrate. Males also are variable in mandibular dentition, from four-toothed to eight-toothed. In spite of this variation, the species are similar in most of their characters and constitute a morphologically rather homogeneous taxon.

■ The species of this subgenus are widespread in Africa, from Senegal to Ethiopia and south to Cape Province and Natal in South Africa. The 11 species were revised by Pasteels (1984).

The nest of *P. bicolor* (Lepeletier) consists of cells constructed adjacent to one another on leaves. The cells consist of resin or gum with intermixed plant hairs (Michener, 1968a). Females of another species were seen gathering solidifying latex from injured tips of a cactus-like *Euphorbia*.

***Pachyanthidium* / Subgenus *Trichanthidioides* Michener and Griswold**

Pachyanthidium (*Trichanthidioides*) Michener and Griswold, 1994a: 319. Type species: *Pachyanthidium semiluteum* Pasteels, 1981, by original designation.

Trichanthidioides resembles the subgenus *Trichanthidium* in its small size (body length 5 mm), hairy eyes, continuation of the ocellar carina across the thoracic venter, and lack or near lack of arolia in females (also in males). It differs from *Trichanthidium* in its extensive yellow areas, full-sized ocelli, lack of lateral tergal spines, and lack of a comb on S4 of the male, but presence of a comb on S5.

■ This subgenus is known from Kenya and Saudi Arabia. The only species is *Pachyanthidium semiluteum* Pasteels.

***Pachyanthidium* / Subgenus *Trichanthidium* Cockerell**

Pachyanthidium (*Trichanthidium*) Cockerell, 1930b: 52.

Type species: *Pachyanthidium occipitale* Cockerell, 1930 = *Anthidium benguelense* Vachal, 1903, monobasic.

Trichanthidium consists of small bees, 5 to 8 mm long, that are entirely black or have very restricted yellow areas, occurring only as sublateral spots on metasomal terga. The transverse carina of T1 is doubled laterally. The sides of T3 to T5 and sometimes T2 have long spines. The apices of the front and middle tibiae sometimes have two spines but usually only one is recognizable. The wings are strongly darkened as in *Pachyanthidium* s. str.

■ This subgenus ranges in Africa from the Ivory Coast to southern Egypt, south to Angola and Natal Province in South Africa, and in Asia from India to Yunnan Province, China. There are at least three species.

Genus *Paranthidium* Cockerell and Cockerell

Paranthidium (not to be confused with *Paraanthidium*, a subgenus of *Trachusa*) agrees with *Dianthidium* s. str. in general form and coloration; the body length is 7.5 to 11.0 mm. Most species have distinct postspiracular foveae; at the same time, in all species, the propodeal triangle is punctate and completely lacks a series of pits across its base. *Paranthidium* differs from *Dianthidium* not only in the characters indicated in the key but also in the lack of ocellar or preoccipital carinae and the short lamella of the pronotal lobe, which scarcely extends mesad from the lateral scutal margin. T7 of the male is three-lobed, the median lobe always larger and longer than the small lateral lobes. Arolia are present. Male genitalia and hidden sterna were illustrated by Mitchell (1960).

In no other anthidiines are the spines of the front and middle tibiae modified as they are in *Paranthidium*. Each of these tibiae terminates on the outer surface in a convex carina, subtended by short hairs, that forms the apex of a shallow apical concavity on the tibia's outer surface (Fig. 82-4a). In the subgenus *Rapanthidium* the carina is strongly convex, and in females is produced as a projection with a rounded apex. In males of *Rapanthidium* the projection (carina) is limited to the posterior half of each tibia, and the concavity basad to the carina is weak and broken up by hairs.

Evans (1993) described nests of *Paranthidium* (*P.*) *jagatorium* *perpictum* (Cockerell). They are burrows made by the bees in sandy soil, with cells, each made of a thin layer of resin or gum, in series in the burrows.

Key to the Subgenera of *Paranthidium*

1. Propodeum with postspiracular fovea; T6 of male without lateral lobe; S4 of male with median comb, S5 with comb laterally (nearctic, Mesoamerica)
..... *P.* (*Paranthidium* s. str.)
- Propodeum without postspiracular fovea or with fovea only about the size of the spiracle; T6 of male with lateral lobe; sterna of male without combs (Mesoamerica)
..... *P.* (*Rapanthidium*)

***Paranthidium* / Subgenus *Paranthidium* Cockerell and Cockerell s. str.**

Paranthidium Cockerell and Cockerell, 1901: 50. Type species: *Anthidium perpictum* Cockerell, 1898, by original designation.

■ This subgenus occurs from New York to Utah, south to Georgia, USA, and through Mexico to Panama. There are about four species. Forms found in the USA were treated by Schwarz (1926), along with *Dianthidium* (*Adanthidium*).

***Paranthidium* / Subgenus *Rapanthidium* Michener**

Paranthidium (*Rapanthidium*) Michener, 1948a: 11. Type species: *Anthidium vespoides* Friese, 1925, by original designation.

The lone described species, *Paranthidium vespoides* (Friese), and one undescribed species have limited white or yellow markings but another undescribed species has abundant yellow markings like those of the species of *Paranthidium* s. str.

■ *Rapanthidium* occurs from the state of Sinaloa, Mexico, south to Costa Rica. There are at least three species, two of them undescribed.

Genus *Plesianthidium* Cameron

Plesianthidium consists of four subgenera that agree in their robust megachiliform or (in the subgenus *Carinanthidium*) chalicodomiform bodies, lack of pale markings except on the face of the male, and in other characters indicated below and in the key to genera. The subgenera differ enough from one another that they have been given generic status. Common features, however, other than those indicated in the key to genera, are (1) a lack of carinae except sometimes on the pronotal lobe and sometimes on the preoccipital ridge behind the vertex, (2) the straight subantennal sutures arising at or near the tentorial pits, (3) the rounded scutellum, not or little overhanging the metanotum, in profile rounded or (in the subgenus *Spinanthidiellum*) angled, (4) the presence of arolia, (5) the tendency of T6 of the male to be trifold or trilobed (not in the subgenus *Spinanthidiellum*), (6) the small and little-exserted male T7, which is three-toothed or (in the subgenera *Plesianthidium* s. str. and *Carinanthidium*) has the middle tooth reduced to a minor convexity between two long, widely separated teeth, (7) the minimal modifications of the male sterna (S5 has an apical comb, absent in the subgenus *Spinanthidium*, and S6 is characteristically lobed or shows various convexities), and (8) the simple male gonostyli, which are slightly expanded and hairy apically, and in *Plesianthidium* s. str. have two small teeth at the apex. As in many other genera, the mandible of the female is four-toothed, that of the male three-toothed. The apical spines of the front and middle tibiae, particularly in females, are broad, the apices convex in *Carinanthidium* but truncate or emarginate (so that there are two spines) in *Spinanthidium* and *Plesianthidium* s. str.

Key to the Subgenera of *Plesianthidium*

1. Preoccipital ridge with carina behind vertex; T6 of male truncate, without lateral tooth, with longitudinal ridge distally, highest at posterior margin of tergum; mandible less than twice as long as broad *P. (Spinanthidiellum)*
- Preoccipital ridge not carinate; T6 of male with median truncate or rounded to pointed projection, rarely weakly produced, and a strong lateral tooth; mandible over twice as long as broad 2
- 2(1). S6 of female with strong longitudinal median carina; hind trochanter of male with mesal subapical spine; pubescence all black except for white on face of male *P. (Carinanthidium)*
- S6 of female not carinate; hind trochanter of male not spined; pubescence brown to gray, or with whitish on face and venter 3
- 3(2). T7 of male strongly trifold, median tooth or lobe exceeding lateral ones; S5 of male without apical comb; maxillary palpus two-segmented *P. (Spinanthidium)*
- T7 of male with median tooth reduced to low prominence, tergum thus essentially bifid; S5 of male with apical comb; maxillary palpus three-segmented *P. (Plesianthidium* s. str.)

***Plesianthidium* / Subgenus *Carinanthidium* Pasteels**

Carinanthidium Pasteels, 1969a: 42. Type species: *Megachile cariniventris* Friese, 1904, by original designation.

This subgenus consists of a wholly black, chalicodomiform species 12 to 14 mm long. Except for the white hairs on the lower face of the male, the hairs are all black. The *Megachile*-like appearance of this bee makes it the most distinctive *Plesianthidium*, although morphologically it shares various features with *Spinanthidium* and *Plesianthidium* s. str.

■ This subgenus is found in western Cape Province, South Africa, but the type specimen was reported to be from northern Transvaal, South Africa. The only species is *Plesianthidium cariniventris* (Friese).

***Plesianthidium* / Subgenus *Plesianthidium* Cameron s. str.**

Plesianthidium Cameron, 1905: 256. Type species: *Plesianthidium fulvopilosum* Cameron, 1905, by original designation.

This subgenus contains the largest species of the genus; it has brown or gray hair, and the face of the male is partly cream-colored. The body is robust (length 15–16 mm) but more elongate than that of *Spinanthidium*. Structurally, this subgenus is similar to *Spinanthidium*.

■ *Plesianthidium* s. str. occurs in northwestern Cape Province, South Africa. The only species is *Plesianthidium fulvopilosum* Cameron.

***Plesianthidium* / Subgenus *Spinanthidiellum*
Pasteels**

Spinanthidium (*Spinanthidiellum*) Pasteels, 1969a: 59. Type species: *Anthidium volkmanni* Friese, 1909, by original designation.

This is in some ways the morphologically most distinctive subgenus of *Plesianthidium*, although in general aspect the specimens look like small (7.0–8.5 mm long) *Spinanthidium*. The body, short and robust, has an almost globular metasoma, and the pubescence, brown or gray, is abundant. The face of the male has cream-colored areas. Because the three teeth of T7 of the male are short, the tergum is only weakly trifid.

■ This subgenus is found in western Cape Province, South Africa. The two species are *Plesianthidium volkmanni* (Friese) and *rufocaudatum* (Friese), the latter incorrectly synonymized by Pasteels (1984) (T. Griswold, in litt., 1995).

***Plesianthidium* / Subgenus *Spinanthidium*
Mavromoustakis**

Dianthidium (*Spinanthidium*) Mavromoustakis, 1951: 977.

Type species: *Anthidium trachusiforme* Friese, 1913, by original designation.

This subgenus contains gray- or brown-haired species, larger than *Spinanthidiellum* but smaller than *Plesianthidium* s. str. (8–12 mm long) and almost as robust as the former, with cream-colored areas on the face of the male. T7 of the male is deeply trifid, the median projection either truncate or pointed. Unlike that of the other subgenera, S5 of the male lacks a comb, but S4 has a comb in one species, *Plesianthidium calescens* (Cockerell) (T. Griswold, in litt., 1995).

■ This subgenus is found in Cape Province, South Africa. The five species were revised by Pasteels (1984).

This subgenus could reasonably be synonymized with *Plesianthidium* s. str.

Genus *Pseudoanthidium* Friese

Pseudoanthidium is here used in a broad sense to include numerous species having compact megachiliform bodies, commonly having the form of *Anthidium* s. str. Except in the subgenus *Micranthidium* the head is thick and the tibiae are tuberculate on the outer surfaces; but even in *Micranthidium* the tibiae are coarsely punctate. The integument is black with yellow markings, the metasomal bands broken or reduced to lateral spots. Commonly, the subantennal suture is arcuate outward (although not always visible); the pronotal lobe is lamellate; T6 of the male lacks lateral teeth except in the subgenus *Exanthidium*; and T7, not much exerted except in *Exanthidium*, is usually bilobed, the emargination between the lobes sometimes feeble or absent, the margin then being convex and sometimes undulate. The tergal margins, except in the subgenus *Royanthidium*, are rather broadly impunctate, slightly to strongly flared as seen in lateral view, and often translucent. S3 to S5 of the male are concave, the posterior margin of S3 with an area of wavy bristles except in *Royanthidium*, these bristles weak in *Pseudoanthidium*

(*Tuberanthidium*) *brachiatum* Michener and Griswold; the margin of at least S5 is concave and has an apical lateral process (merely a lobe in *Exanthidium*), the process frequently armed at the tip with a small comb.

**Key to the Subgenera of *Pseudoanthidium*
(From Michener and Griswold, 1994a)**

1. Gena margined posteriorly by distinct preoccipital carina (gena narrower than eye as seen from side) 2
- Gena without preoccipital carina (scutellum rounded or medially emarginate as seen from above; tibiae tuberculate on outer surfaces at least in female; male without lamellate lateral lobe on S3; clypeus of female with discal hairs straight) 3
- 2(1). Preoccipital carina behind vertex strongly produced back over front of thorax as a lamella; posterior basitarsus of male more than twice as long as broad (scutellum broadly truncate in dorsal view, posterior margin angulate laterally near axilla; tibiae not tuberculate but coarsely punctate; lateral lobe of S3 of male lamellate; clypeus of female with discal hairs bent down apically) (Africa, Arabia) *P. (Micranthidium)*
- Preoccipital carina behind vertex rather weakly carinate; posterior basitarsus of male less than twice as long as broad (Africa) *P. (Semicarinella)*
- 3(1). Propodeum shagreened; T6 of male with strong apical, medially emarginate flange; fore and middle basitarsi of female with long plumose hair (Africa) *P. (Tuberanthidium)*
- Propodeum shiny where not punctate; T6 of male without emarginate flange; fore and middle basitarsi of female with long but not plumose hair 4
- 4(3). T6 of female with surface broadly and conspicuously excavated; T5 of female with small, midapical, marginal projecting lobe; exposed part of T7 of male longer than exposed part of T6, very deeply bilobed; S5 of male without strong lateral tooth or lobe (palearctic, Sudan) *P. (Exanthidium)*
- T6 of female with surface largely convex; T5 of female without midapical lobe; exposed part of T7 of male shorter than exposed part of T6, weakly to strongly bilobed; S5 of male with strong lateral process 5
- 5(4). Clypeal apex of female fully exposed, coarsely denticulate, protruding; S3 and S4 of male broadly emarginate, or S3 with median V-shaped emargination, and S5 with apicolateral projection, all without combs or specialized hairs (palearctic) *P. (Royanthidium)*
- Clypeal apex of female largely hidden by hair, without shining premarginal ridge; S3 of male with comb of long, wavy bristles and S5 with comb at apex of apicolateral projection (palearctic, oriental) *P. (Pseudoanthidium* s. str.)

***Pseudoanthidium* / Subgenus *Exanthidium* Pasteels**

Exanthidium Pasteels, 1969a: 82. Type species: *Anthidium eximium* Giraud, 1863, by original designation.

This is a subgenus of small anthidiines, 7–9 mm long, having yellow areas on all tagmata. T6 of the female, in addition to exhibiting the excavated surface indicated in the key to subgenera, has a broadly rounded or truncate,

Mediterranean basin east to Central Asia. Pasteels (1969a) lists six species.

The species formerly placed in *Reanthidium* differ from other *Royanthidium* in having the preoccipital ridge carinate behind the vertex.

***Pseudoanthidium* / Subgenus *Semicarinella*
Pasteels**

Pseudoanthidium (*Semicarinella*) Pasteels, 1984: 32. Type species: *Pseudoanthidium latitarse* Pasteels, 1984, by original designation.

This subgenus may be based on a small species (length 6.5 mm) of *Micranthidium*, from which it appears to differ in the "subcarinate" preoccipital carina behind the vertex (it is lamellate in *Micranthidium*), the carina (rather than a lamella) on the pronotal lobe, the laterally rounded (rather than angulate) posterior margin of the scutellum, and the broad (less than twice as long as broad) hind basitarsus of the male. It should be noted that in *Pseudoanthidium* (*Micranthidium*) *truncatum* (Smith) the hind basitarsus is somewhat broadened and that the scutellar character listed above is doubtful because Pasteels' description, unlike his diagram, indicates that the scutellum is as in *Micranthidium*.

■ *Semicarinella* occurs in Senegal. The name is based on a single male specimen that I have not seen.

***Pseudoanthidium* / Subgenus *Tuberanthidium*
Pasteels**

Tuberanthidium Pasteels, 1969a: 87. Type species: *Anthidium tuberculiferum* Brauns, 1905, by original designation.

This subgenus consists of rather robust bees (showing the form of *Royanthidium*) 7 to 11 mm long. They are black with yellow markings on all tagmata, including lateral spots or broken bands on the metasoma. The dorsal bulge on the female mandible is unique in the genus, but absent in *Pseudoanthidium* (*Tuberanthidium*) *brachiatum* Michener and Griswold. The pronotal lobes are carinate; otherwise, the usual carinae are absent. The scutellum is rounded or feebly emarginate in the middle, as seen from above; in profile it is rounded or somewhat acute, but laterally it forms a sharp overhanging margin. S5 of the male is largely hidden medially beneath S4; its lateroapical projection is bare or in *P. brachiatum* with a comb. As in *Royanthidium* there is a medially emarginate flange on the margin of the male T6 and a semicircular emargination on T7. Whereas in *Tuberanthidium* as it was understood by Pasteels, S3 of the male is medially produced and carries long, wavy bristles, in *P. (T.) brachiatum* it is not produced and has much shorter, relatively inconspicuous wavy bristles. Male genitalia of that species were illustrated by Michener and Griswold (1994a).

■ *Tuberanthidium* is found in Namibia, South Africa (Cape Province to Natal), Lesotho, Botswana, and Tanzania. Pasteels (1984) treats three species of *Tuberanthidium*; a fourth is the more *Pseudoanthidium*-like species *P. (T.) brachiatum* Michener and Griswold.

Genus *Rhodanthidium* Isensee

This is a palearctic genus of moderate-sized to very large, chalicodomiform or euceriform bees with abundant yellow or reddish-yellow markings (Pl. 8), although some specimens of *Rhodanthidium* (*Asianthidium*) *glasunovii* (Morawitz) lack such markings on the thorax and metasoma. The metasomal color bands, when present, are broken medially at least on the anterior terga. Common features are (1) a lack of carinae, except commonly a carina or even a lamella on the pronotal lobe and sometimes a weak upper omaular carina, (2) the straight subantennal sutures, (3) the rounded or laterally sharp scutellum not or little overhanging the metanotum, (4) the presence of arolia, (5) the strongly trifold male T7 [lateral teeth rather small in *R. (Asianthidium) aculeatum* (Klug)], (6) the male gonostyli, which are about as described for *Plesianthidium*, their apices simple or having two small teeth, and (7) the male sterna, which are not greatly modified, although S4 and S5 sometimes carry median apical combs and S5 has a lateral tooth in *Rhodanthidium* s. str.

The number of segments in the maxillary palpus varies from two to three and perhaps four. It is difficult to determine the number; segments sometimes seem to be only partly separated, so that one must make arbitrary decisions.

Key to the Subgenera of *Rhodanthidium*

1. T6 of male with median, produced truncation or rounded process and lateral tooth or strong shoulder; S5 of male with strong lateral tooth and median marginal comb; omaulus weakly carinate above; margin of scutellum with sharp edge laterally; female with apical projection or spine of fore and mid tibiae narrowly bidentate *R. (Rhodanthidium) s. str.*
- T6 of male simple or with scarcely produced broad truncation, with or without strong shoulder or weak lateral tooth; S5 of male without lateral tooth, without comb; omaulus not carinate [or weakly so above in *R. (Asianthidium) caturigense* (Giraud) and its relatives]; margin of scutellum rounded, not forming sharp edge [except in *R. (Asianthidium) caturigense*]; female with apical projection of fore and mid tibiae either not notched or widely and shallowly emarginate 2
- 2(1). Trifold apex (median tooth sometimes broad and rounded or truncate) of T7 of male occupying full width of tergum; pronotal lobe with lamella or carina [weak in *R. (Asianthidium) glasunovi* (Morawitz)]; head with background color black *R. (Asianthidium)*
- Trifold apex of T7 of male much narrower than tergum, which has lateral angles rendering tergum five-toothed; pronotal lobe without or with very weak carina; head largely yellow *R. (Meganthidium)*

***Rhodanthidium* / Subgenus *Asianthidium* Popov**

Meganthidium (*Asianthidium*) Popov, 1950a: 315. Type species: *Anthidium glasunovii* Morawitz, 1894, by original designation.

Rhodanthidium (*Trianthidium*) Mavromoustakis, 1958: 435. Type species: *Anthidium caturigense* Giraud, 1863, by original designation.

Meganthidium (*Oxyanthidium*) Mavromoustakis, 1963a:

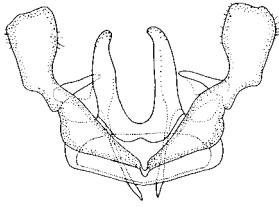


Figure 82-12. Male genitalia of *Stelis (Dolichostelis) louisae* Cockerell. Modified from Parker and Bohart, 1979.

and on the pronotal lobe, or in some species of the subgenus *Protostelis* the pronotal and omaular carinae are strong. The scutellum, little produced, is rounded, except in some oriental species. Behind the propodeal spiracle is sometimes a fovea, which forms the lateral extremity of a series of pits (often broken medially) commonly forming a narrow subhorizontal or slanting zone across the base of the propodeum (Fig. 82-14); this basal zone is often merely roughened, not pitted, or is pitted only laterally. The scopa is absent. T7 of the male is small and only a little exposed; its apex is rounded, weakly bilobed, or weakly trilobed, or it has a median angle exceeding a bilobed base. The male gonostylus has a slender base and an expanded, angulate distal part often directed mesad at an angle to the basal part (Fig. 82-12); there is a strong projecting angle, marked by an arrow in the figure, on the outer margin at the base of the expanded portion. The volsellar lobe is present. Popov (1938) and Mitchell (1962) illustrated the genitalia of diverse American species; see also Figure 82-12. Warncke (1992a) revised the west palearctic species. The genus *Afrostelis* agrees with the above comments except for the male genitalia characters.

The genus *Stelis* is primarily holarctic in distribution but extends south to Costa Rica (subgenus *Dolichostelis*), Malaysia (*Malanthidium*), and Kenya (*Stelidomorpha*). Griswold and Parker (2003) described a species of unknown subgeneric relationships on the basis of one female from western Cape Province, South Africa.

Pasteels (1968a, 1969a) believed that the closest non-parasitic relative of *Stelis* is *Bathanthidium*, partly because of its divided scutoscutellar fovea. The suggestion has been made that the subgenus *Protostelis* might be derived from *Trachusa*, and that *Stelis* therefore might be polyphyletic. *Protostelis*, however, does not have the reflexed male T7 characteristic of *Trachusa* and does have *Stelis*-like features such as the two spines on the apices of the front and middle tibiae (Fig. 82-6a). I therefore regard *Protostelis* as a subgenus of *Stelis*, not related to *Trachusa*.

The hosts of *Stelis* are other Megachilinae. In most cases the parasite, after locating a host nest, returns to it repeatedly to place an egg in each of several host cells before they are closed, as noted by Michener (1955) and others. In the subgenus *Dolichostelis*, however, the female opens the resin seal of the finished nest of the host and reseals it with the same resin on departure (Parker et al., 1987). Probably the behavior is similar to that of another parasitic genus, *Euaspid*. Larvae of *Stelis* are active and have sharp mandibles with which they destroy eggs or lar-

vae of the host. A possible exception is in the subgenus *Dolichostelis*, whose adults may destroy the host egg or larva.

Key to the Subgenera of *Stelis* of the Eastern Hemisphere

- 1. Clypeus produced well over mandibles, its apex bilobed, strongly so in females; anterior spine of front and middle tibiae conspicuous, enlarged, curved posteriorly *S. (Stelidomorpha)*
- Clypeus not greatly produced over mandibles, truncate or subtruncate; anterior spine of front and middle tibiae less than twice the size of posterior spine 2
- 2(1). Axilla projecting laterally beyond lateral margin of scutum; scutellum strongly projecting over metanotum and propodeum (oriental) *S. (Malanthidium)*
- Axilla not projecting laterally beyond margin of scutum; scutellum at most weakly projecting over metanotum and propodeum 3
- 3(2). Scutellum not carinate laterally; head and thorax without light markings; hind tibial apex with two spines or angles (Fig. 82-13b), one near outer middle of apical tibial margin (if with only one spine, as in *S. simillima* Morawitz, then not on posterior apical angle) or the spines united to form truncate margin, the area sparsely hairy and the structure thus easily seen; omaulus not carinate *S. (Stelis s. str.)*
- Scutellum carinate laterally; head and thorax with light markings; hind tibial apex with a single spine (sometimes a mere angle) largely hidden in hairs (Fig. 82-13a) near the posterior apical angle of the tibia, in front of which the apex of the tibia presents a convex margin; omaulus usually carinate 4
- 4(3). Hind basitarsus with carina along inner dorsal angle (Fig. 82-13a); middle tibia flattened, apically enlarged, twice as wide apically as basally; S1 with transverse carina overhanging apical margin *S. (Heterostelis)*
- Hind basitarsus without carina; middle tibia not flat-

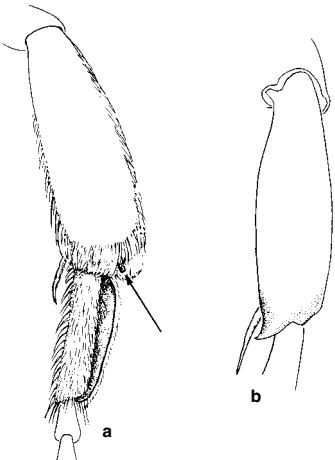


Figure 82-13. Hind tibiae of *Stelis*. **a**, *S. (Heterostelis) australis* Cresson. (The arrow indicates the spine largely and sometimes completely hidden by dense hairs); **b**, *S. (Stelis) rubi* Cockerell. Modified from Michener, McGinley, and Danforth, 1994.

- tened, little enlarged apically, at most 1.5 times as wide apically as basally; S1 without transverse carina 5
- 5(4). Pronotum without notch between lobe and rest of pronotum; omaulus not carinate; carinate pitted basal zone of propodeum extending behind spiracle
..... *S. (Protostelis)*
- Pronotum with notch between lobe and rest of pronotum; omaulus usually carinate; carinate pitted basal zone of propodeum not extending behind spiracle
..... *S. (Pseudostelis)*

Key to the Subgenera of *Stelis* of the Western Hemisphere

1. Hind tibia with a single prominent tooth or tibial spine (usually hidden among hairs) on margin near apex of posterior margin of tibia; hind basitarsus with strong lamella-like carina along posterior margin, separated by longitudinal depression from longitudinal thickening of outer surface of basitarsus (Fig. 82-13a) *S. (Heterostelis)*
- Hind tibia with an apical median tooth or tibial spine and a less prominent, rounded projection near apex of posterior margin of tibia; hind basitarsus unmodified 2
- 2(1). Base of propodeum with zone set off by carina and divided into a series of pits (Fig. 82-14), this zone projecting subhorizontally behind vertical metanotum; anterior surface of mesepisternum impunctate at least below and set off from lateral surface by sharp angle or weak omaular carina *S. (Dolichostelis)*
- Base of propodeum vertical or sloping, rarely subhorizontal, without series of pits or such pits usually present only laterally, this zone with about same slope as metanotum; anterior surface of mesepisternum punctate, omaular carina absent *S. (Stelis s. str.)*

Stelis / Subgenus *Dolichostelis* Parker and Bohart

Dolichostelis Parker and Bohart, 1979: 138. Type species:

Stelis laticincta Cresson, 1878, by original designation.

Dolichostelis, the species of which were formerly incorrectly placed in *Protostelis* (e.g., Hurd, 1979), contains rather elongate, chalicodomiform, black species, 6 to 10 mm long, richly marked with yellow, orange, or cream. As shown by Figure 82-11b, the aspect is similar to that of *Dianthidium*, but the costal part of the forewing is dark. Parker and Bohart (1979) regarded *Dolichostelis* as a genus allied to neotropical forms unrelated to *Stelis* (presumably *Hoplostelis* species), but this appears to be an error; the clubbed and angulate gonostylus (Fig. 82-12) is as in *Stelis*, as are the two apical spines on the front and middle tibiae (Fig. 82-6a). The characters of the subgenus all appear to be derivable from those of *Stelis* s. str. Distinctive features of *Dolichostelis* are (1) the angulate or weakly carinate omaulus, the surface in front of it more shiny and less closely punctate, at least below, than the surface behind it, (2) the subhorizontal, pitted to foveate base of the propodeum, extending back from the vertical metanotum (Fig. 82-14), (3) the rather sharp posterior marginal carina of the scutellum, and (4) the pair of broad translucent lobes forming much of the posterior margin of S3 of the male. The genitalic and sternal characters were illustrated by Parker and Bohart (1979); see also Figure 82-12.

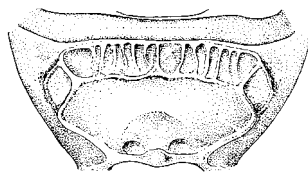


Figure 82-14. Posterodorsal view of propodeum of *Stelis* (*Dolichostelis*) *rudbeckiarum* Cockerell. From Michener, McGinley, and Danforth, 1994.

■ This subgenus occurs across North America from Maine to California, USA, and south to Costa Rica. The six species were revised by Parker and Bohart (1979).

So far as is known, this subgenus is cleptoparasitic in nests of *Megachile* (*Chelostomoides*) (Parker et al., 1987). For further details, see the account of the genus.

Stelis / Subgenus *Heterostelis* Timberlake

Stelis (*Heterostelis*) Timberlake, 1941: 125. Type species: *Stelis anthidioides* Timberlake, 1941, by original designation.

Doxanthidium Pasteels, 1969a: 28. Type species: *Anthidium paradoxum* Mocsáry, 1884, by original designation.

The subgeneric name *Heterostelis* replaces *Protostelis* of Michener (2000: 514) because the type species of *Protostelis* was incorrect in that work (see Sandhouse 1943).

This subgenus contains robust species 10 to 12 mm long with strong yellow markings on all tagmata. Unlike most *Stelis*, which have two-segmented maxillary palpi, those of *Heterostelis* appear to be three-segmented. The pronotal lobe is strongly carinate. The two surfaces of the mesepisternum are at right angles to one another and the omaulus is carinate, except in *S. hurdi* Thorp. The axillae are usually not angulate as in many palearctic *Stelis* s. str., but the margin often projects roundly as seen from above, not being a continuation of the curve of the scutellar margin; in *S. annulata* (Lepeletier) the axillae are somewhat angulate. The combined shape of the scutellum and axillae varies from semicircular to quadrate. The series of pits along the basal margin of the propodeum is broadly interrupted, and the median part of the propodeal surface is wholly vertical. The propodeum sometimes lacks a distinct pit or fovea behind the spiracle. Male genitalia, sterna, and other structures were illustrated by Thorp (1966).

■ *Heterostelis* is found throughout the southern USA from California to Florida, north to New Jersey, and south to Morelos, Mexico. In the palearctic region it is found in southern Europe north to Germany, in the Mediterranean basin, and east to Iran. There are about three palearctic species and six in North America. The latter were revised by Thorp (1966).

Heterostelis species may all be parasites of *Trachusa*. One species has been definitely associated with *Trachusa* (*Trachusomimus*) (see Thorp, 1966). A new species was observed entering nests of *Trachusa* (*Heteranthidium*) *catinula* Brooks and Griswold (T. Griswold, personal communication, 1995).

Stelidium Robertson, 1902b: 323. Type species: *Stelidium trypetinum* Robertson, 1902, monobasic. [See Michener, 1997b.]

Microstelis Robertson, 1903a: 170, 175. Type species: *Stelis lateralis* Cresson, 1864, by original designation.

Stelis (*Pavostelis*) Sladen, 1916b: 313. Type species: *Stelis montana* Cresson, 1864, monobasic.

Stelis (*Stelidina*) Timberlake, 1941a: 131. Type species: *Stelis hemirhoda* Linsley, 1939, by original designation.

Stelis (*Stelidiella*) Timberlake, 1941a: 133. *Lapsus* for *Stelidina* Timberlake, 1941.

Stelis (*Leucostelis*) Noskiewicz, 1961: 126, 132. Type species: *Gyroderma ornatula* Klug, 1807, by original designation (p. 132).

This is the principal subgenus of *Stelis*. There is usually a carina on the pronotal lobe, but elsewhere no carinae on the body. The axillae are sometimes angulate posteriorly. The body length is 4 to 11 mm. The coloration in the palearctic region is black, sometimes with cream-colored or yellow spots or tergal margins or bands on the metasoma. In the nearctic area the diversity among species is greater than elsewhere; some are wholly black or with cream or yellow markings, the metasoma sometimes red, while other species are strongly metallic blue or green, with or without cream or yellow markings. In North America, in certain species usually placed in the subgenus *Chelynia*, the second recurrent vein meets the second submarginal cell instead of flying beyond the apex of that cell as in most Anthidiini. In *S. (S.) labiata* (Provancher), the type species of *Chelynia*, however, the venation is intermediate, the second recurrent vein being at about the apex of the second submarginal cell. Likewise, the presence and development of postspiracular foveae varies. The various quite different groups of North American *Stelis* appear to merge, it is therefore not practical to recognize subgenera (T. Griswold, personal communication, 1992). Sterna of various species were illustrated by Mitchell (1962); together with the genitalia they show considerable homogeneity among the species of *Stelis* s. str.

■ Species of this subgenus are found almost throughout Europe and northern Africa, including the Canary Islands, and east at least to Mongolia. In North America *Stelis* s. str. ranges across the continent and from Canada south to the northern border states of Mexico. There are some 20 Eurasian species and 55 North American species. Warncke (1992a) gave a key to the west palearctic species, including species of other subgenera.

Hosts are other megachilids, species of *Anthidiellum*, *Anthidium*, *Ashmeadiella*, *Chelostoma*, *Heriades*, *Hoplitis*, *Megachile*, and *Osmia*. So far as is known, a *Stelis* egg is introduced while a cell is being provisioned by the host, or after it is provisioned but not yet closed. After hatching, the resultant *Stelis* larva kills the host egg or larva (Michener, 1955; Rust and Thorp, 1973). As with some other cleptoparasitic bees such as *Nomada*, two or more eggs are often found in a single host cell. Although in many other cleptoparasitic bees such as the *Nomadinae*, young larvae kill the host egg or larva, it may be that in *Stelis* it is older larvae that are most likely to do so (Rozen, 1987a).

Genus *Trachusa* Panzer

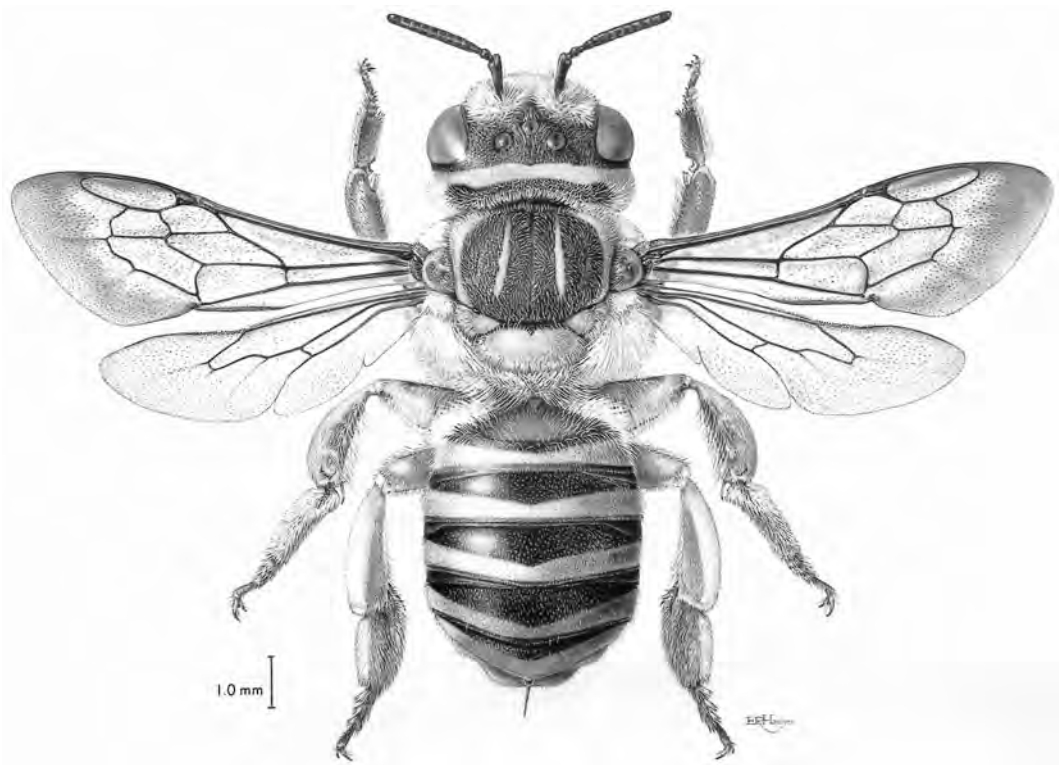
This genus consists of moderate-sized to large megachiliform anthidiines (Pl. 8; Fig. 82-15) without the usual carinae or with carinae or even lamellae on the pronotal lobe and the omaulus. The posterior part of the head is well-developed, the lateral ocellus thus nearer to the eye than to the preoccipital margin, except in the subgenus *Meta-trachusa*, in which these distances are about equal. The middle tibia is broad, usually nearly as broad as the hind tibia, and both anterior and posterior margins are convex; sometimes, however, in spite of these convexities, the middle tibia is distinctly narrower than the hind tibia. Vein cu-v of the hind wing is oblique and usually nearly half as long as the second abscissa of M+Cu or longer. In some *Meta-trachusa*, however, it is distinctly less than half as long as the abscissa of M+Cu, although oblique. T7 of the male is small, not strongly exerted, and flexed forward such that its morphologically dorsal surface is directed ventrad; sometimes (e.g., in subgenera *Archianthidium* and *Meta-trachusa*) T7 has a basal or median projection a small area of which is directed apicad or dorsad. Several characters that are often stable within a genus vary in *Trachusa*. Arolia are commonly present but sometimes greatly reduced or absent. Combs on S4 and S5 of the male are sometimes present but also often absent, and may vary even within a species (of the subgenus *Heteranthidium*; see Brooks and Griswold, 1988). The number of mandibular teeth of the female is commonly four but may be three, as in *Trachusa* s. str., or five, six, or seven, as in the subgenera *Massanthidium* and *Congotrachusa*. The number of segments in the maxillary palpus may be four or reduced to three.

So far as is known, species of *Trachusa* nest in the ground; unlike most anthidiines they make their own burrows. Cells are made from resin and pieces of green leaves by bees of the subgenera *Trachusa* s. str. and *Trachusomimus* (Hachfeld, 1926; Michener, 1941b; Westrich, 1989). In the subgenus *Heteranthidium*, cells are made of resin (Cane, 1996).

Trachusa is found in the holarctic, oriental, and African regions. Keys to the subgenera are separated for the Old World and New World forms; no subgenus occurs in both hemispheres.

Key to the Subgenera of *Trachusa* of the Eastern Hemisphere

1. Mandible of female with three more or less equidistant teeth; maxillary palpus as long as maximum width of galea, four-segmented (yellow markings absent except for face of male) (palearctic) *T. (Trachusa* s. str.)
- Mandible of female four- to seven-toothed; maxillary palpus shorter than width of galea, three- or four-segmented..... 2
- 2(1). Second recurrent vein entering second submarginal cell basal to second submarginal crossvein; T7 of male with median basal projection (palearctic) *T. (Archianthidium)*
- Second recurrent vein meeting or distal to second submarginal crossvein; T7 of male without basal projection 3
- 3(2). Subantennal suture distinctly arcuate outward; gonoforceps of male deeply bifid, Y-shaped (male unknown in *Orthanthidium*)..... 4



- . Subantennal suture nearly straight; gonoforceps of male not Y-shaped 5
- 4(3). Scutellum truncate posteriorly as seen from above, margin curved sharply forward laterally to meet longitudinal margin of axilla; eyes of female conspicuously diverging below; interocellar distance of female much less than half the ocelloccipital distance (male unknown) (oriental)..... *T. (Orthanthidium)*
- . Scutellum broadly rounded but medially emarginate; lateral margin of axilla convex but in general slanting; eyes of female subparallel; interocellar distance about half of ocelloccipital distance or somewhat greater (palearctic, oriental) *T. (Paraanthidium)*
- 5(3). Omaulus distinctly carinate, carina extending onto ventral surface of thorax close to middle coxa (Africa) *T. (Massanthidium)*
- . Omaulus not carinate 6
- 6(5). Arolia present in female, absent in male; S4 and S5 of male without combs (oriental) *T. (Metatrachusa)*
- . Arolia minute if present; S4 and S5 of male with combs as in *Paraanthidium* (Africa) *T. (Congotrachusa)*

Key to the Subgenera of *Trachusa* of North America

- 1. All tagmata with abundant yellow or cream-colored markings, including median tergal bands on metasoma *T. (Heteranthidium)*
- . Integument without yellow or cream-colored markings except usually on face of male and, in *Legnanthidium*, on apical metasomal tergal margins 2
- 2(1). Arolia absent..... *T. (Ulanthidium)*
- . Arolia present 3
- 3(2). Second recurrent vein joining second submarginal cell

Figure 82-15. *Trachusa (Heteranthidium) bequaerti* (Schwarz), female. Drawing by E. R. S. Hodges, from Michener, McGinley, and Danforth, 1994.

- basal to second submarginal crossvein; mandible of female four-toothed *T. (Legnanthidium)*
- . Second recurrent vein distal to second submarginal crossvein; mandible of female three-toothed *T. (Trachusomimus)*

Trachusa / Subgenus *Archianthidium*
Mavromoustakis

Archianthidium Mavromoustakis, 1939: 91. Type species: *Anthidium laticeps* Morawitz, 1873, by original designation.

Although this subgenus was not included in *Trachusa* by Pasteels (1969a), it falls easily within that genus. Superficially, because of its size (12.5-18.0 mm long), form, and abundant yellow markings, it resembles *Heteranthidium* and well-marked species of *Paraanthidium*, although, unlike those on the former, the yellow metasomal bands at least on T1 are broken medially. *Archianthidium* is indeed similar to and probably closely related to *Heteranthidium*, as indicated especially by the large, volsella-like process from the apex of the male gonocoxite. All of its characters fall within the range of variation for *Heteranthidium* except the broken metasomal bands, the position of the second recurrent vein (see the key to subgenera), and the midbasal, retrorse, blunt or truncate process of T7 of the male. Arolia are present

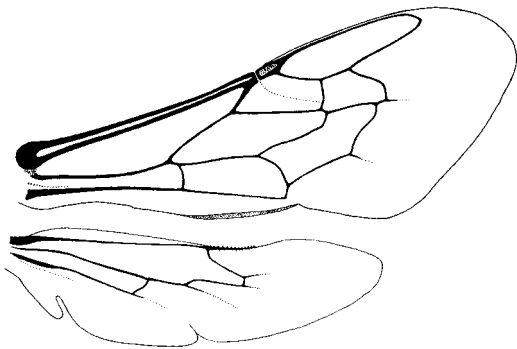


Figure 83-2. Wings of *Dioxys productus subruber* (Cockerell).

scribed by Rozen and Ozbek (2004), who noted various differences from the nearctic *D. pomonae* as well as pharate first instar larvae, frequently unrecognized in earlier accounts. Eggs of *Dioxys pomonae* are inserted through the cell wall of the host after the host female has closed the cell (Rozen and Favreau, 1967), but eggs of *D. cincta* (Jurine) appear to be deposited in open host cells (Rozen and Ozbek, 2005a).

Keys to the species of Dioxyini of the western palearctic region were provided by Warncke (1977b); for the nearctic region by Hurd (1958a).

Key to the Genera of the Dioxyini
(From Michener, 1996b)

- 1. Scutellum with posterior margin rounded 2
 - Scutellum produced laterally to form posteriorly directed tooth or spine (Fig. 83-3a) 3
- 2(1). Metanotum with median tooth; posterior lateral angle of scutum produced to a strong spine (as in Fig. 83-1); S5 of female without teeth (palearctic) *Allodioxys*
 - Metanotum without or with scarcely developed median tubercle or tooth; posterior lateral angle of scutum not produced; S5 of female with tooth on each side of base of S6 (palearctic) *Ensliniana*
- 3(1). Axilla produced to a strong, curved spine; metanotum without median tubercle or tooth (palearctic) *Eudioxys*
 - Axilla not spined or produced to a small, straight spine that lies close to and usually slightly below lateral margin

- of scutellum; metanotum with median tubercle or tooth, rarely weakly developed 4
- 4(3). Dorsolateral angle of pronotum unrecognizable; first recurrent vein entering first submarginal cell or nearly meeting first transverse cubital vein; jugal lobe of hind wing about one-seventh as long as vannal lobe, as measured from wing base; body covered with long red hair, branches short and inconspicuous (palearctic) *Prodioxys*
 - Dorsolateral angle of pronotum distinct; first recurrent vein entering second submarginal cell; jugal lobe of hind wing about one-third as long as vannal lobe, as measured from wing base; body with shorter, usually pale hairs, some of them densely plumose and superficially almost scale-like 5
- 5(4). Scutellum with strong carina, arcuate posteriorly, between lateral teeth; exposed part of T5 of female 2.5 to 4.0 times as long as exposed part of T6, tapering posteriorly to subtruncate apex only about one-seventh as wide as base of tergum; T6 of female with exposed part two or more times as long as broad, smooth and shining, hairless; S6 of female needle-like, extending well beyond apex of T6 (palearctic) *Paradioxys*
 - Scutellum without carina between lateral teeth; exposed part of T5 of female shorter than exposed part of T6, similar in form to preceding terga, its apex over two-thirds as wide as base of exposed part; T6 of female with exposed part about as broad as long or broader than long, punctured and setose like other terga; S6 of female broad, not or slightly exceeding T6, thus no needle-like metasomal apex (Fig. 83-4) 6
- 6(5). Labrum without transverse basal carina; male genitalia as a whole more than twice as long as width of gonobase; front coxa with anterior surface rounded (holarctic)
 - *Dioxys*
 - Labrum with transverse carina close to base (visible above closed mandibles); male genitalia as a whole much less than twice as long as width of gonobase (Fig. 83-3b); front coxa with tubercle or strong carina at summit of anterior surface 7
- 7(6). Front coxa with strong carina at summit of smooth anterior surface; metanotum with small median tubercle; third valvula (gonostylus) of female with row of coarse bristles (palearctic) *Metadioxys*
 - Front coxa with tubercle at summit of punctate anterior surface; metanotum with strong median spine (as in Fig.

Table 83-1. Positions of Spines and Carinae on Thoracic Sclerites of Dioxyini.
sp, spine; sm sp, small spine; c, carina; and l, lamella; — indicates no spine or carina present.

Taxon	Position				
	pronotum	scutum	axilla	scutellum	metanotum
<i>Ensliniana</i>	c	—	—	—	—
<i>Eudioxys</i>	c	—	sp	sp	—
<i>Prodioxys</i>	—	—	—	sp	sp
<i>Paradioxys</i>	c	—	—	sp	sp
<i>Dioxys</i>	c	—	— or sm sp	sp	sp
<i>Allodioxys</i>	c	sp	—	—	sp
<i>Metadioxys</i>	c	?	—	sp	sm sp
<i>Aglaopis</i>	c	—	sm sp	sp	sp

83-1); third valvula (gonostylus) of female with only minute hairs (palearctic, India, Africa)..... *Aglaoapis*

Genus *Aglaoapis* Cameron

Aglaoapis Cameron, 1901b: 262. Type species: *Aglaoapis brevipennis* Cameron, 1901, monobasic.

Dioxoides Popov, 1947: 89. Type species: *Coelioxys tridentata* Nylander, 1848, by original designation.

In external features *Aglaoapis* is similar to *Dioxys*, although the labral and other characters indicated in the key to genera (couplet 6) are distinctive. The male genitalia and female sting apparatus, however, are very different from those of *Dioxys*. The male genitalia are broader than long (Fig. 83-3b). In dorsal view the rather robust, curved gonostylus is easily distinguished from the gonocoxite and is hairy throughout its length. The male genital and hidden sterna were illustrated by Popov (1936a) and Michener (1996b); see also Figure 83-3b-d. In the female the large, discoid T7 hemitergite is quite different from that of all other Dioxyini [the female of *A. alata* (Michener) is unknown, and that of *A. brevipennis* Cameron has never been dissected]. Unlike those of *Dioxys*, the female gonostyli are covered with minute hairs (see Popov, 1953). The body length is 10 to 12 mm.

■ The distribution of *Aglaoapis* is disjunct, Europe and western Asia, western India, and South Africa. In the palearctic region it occurs north to 62°N in Finland, south to Spain, Italy, Greece, and Cyprus, and east to the Caucasus, the Urals, and Kazakhstan. In India it is known from Bombay. In Africa it is known only from the western Cape Province, South Africa; it is the only dioxyine from sub-Saharan Africa. Three species are recognized.

Genus *Allodioxys* Popov

Allodioxys Popov, 1947: 87. Type species: *Dioxys schultzei* Popov, 1936, by original designation.

The most noteworthy character of *Allodioxys* is the posterior lateral angle of the scutum, which is produced as a strong curved spine, whereas the axilla is small, its lateral margin convex, not angulate. The scutal spines and the median metanotal spine are the only thoracic spines. The propodeum has a sloping basal zone with irregular, anastomosing rugae. The last three metasomal segments of the female taper strongly, the exposed part of T6 at its base being about or more than half as wide as the base of T5, S6 having only the slender, pointed apex exposed and exceeding T6. The male genitalia and S7 and S8 were illustrated by Popov (1936a: fig. 16); the short and robust probable gonostylus is much shorter than the gonocoxite, unlike that of all other Dioxyini. The body length is 6 to 11 mm.

■ This genus is found in Israel and North Africa (Algeria and Libya). Warncke (1977b) listed four species.

Genus *Dioxys* Lepeletier and Serville

Dioxys Lepeletier and Serville, 1825: 109. Type species: *Trachusa cincta* Jurine, 1807, monobasic.

Hoplopassites Ashmead, 1898: 284. Type species: *Phileremus productus* Cresson, 1879, by original designation.

Chrysopheon Titus, 1901: 256. Type species: *Chrysopheon aurifuscus* Titus, 1901, monobasic.

In this genus the arcuate ridge from the pronotal angle to the pronotal lobe and the omaulus are both strongly carinate. The axilla is rounded or slightly angulate, its posterior lateral angle acute and sometimes produced as a small spine close to or in contact with the lateral margin of the scutellum. The scutellum has a strong lateral tooth or spine. The metanotum has a median spine, laterally compressed. The basal zone of the propodeum, which slopes steeply, is demarcated posteriorly by a carina and divided by numerous rugae into a series of shiny pits (Fig. 83-1). T6 of the female is broad, sculptured like T5, and its apex is broadly rounded or slightly angulate to weakly emarginate, the exposed part usually longer than the exposed part of T5. The exposed part of S6, not or slightly exceeding T6, is similar in shape to that of T6. Thus although the metasoma of the female tapers, it lacks the needle-like apex of some other genera (Fig. 83-4). Popov (1936a) illustrated the male genitalia and hidden sterna of several species, and Popov (1953) illustrated the structures associated with the sting; the female gonostyli or third valvulae are much reduced and hairless, and the T7 hemitergites are triangular or quadrate. The body length is 6 to 12 mm.

■ *Dioxys* ranges from the Canary Islands, Morocco, and Spain eastward through northern Africa and Europe (as far north as 49°N), and eastward into Central Asia. It is not known in China and Japan, but occurs in western North America from Oregon eastward to Wyoming, Colorado, and western Texas, USA, south to Baja California and Durango, Mexico. There are about ten palearctic species and five nearctic species. Warncke (1977b) gave a key to west palearctic species and Hurd (1958a) revised the nearctic species.

Genus *Ensliniana* Alfken

Ensliniana Alfken, 1938: 431. Type species: *Ensliniana cuspidata* Alfken, 1938 = *Stelis bidentata* Friese, 1899, by original designation.

This genus is similar to *Allodioxys* but the posterior lateral angle of the scutum is not produced and the meta-

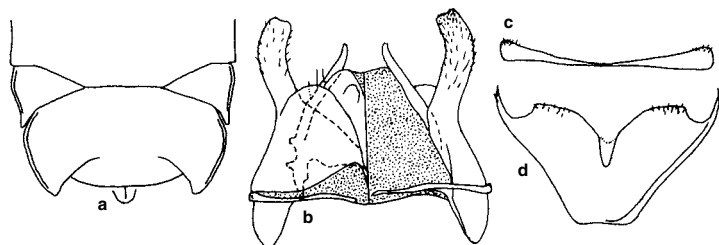


Figure 83-3. *Aglaoapis alata* (Michener). **a**, Dorsal view of axillae and scutellum; **b-d**, Male genitalia, S7, and S8, dorsal view of genitalia at left. From Michener, 1996b.

84. Tribe Megachilini

This vast tribe is distinguished by the characters indicated in the key to tribes and in Table 79-1. The more elongate stigma that differentiates the Megachilini from the Anthidiini is shown in Figure 84-1. In numerous illustrations of structures of Megachilini, Mitchell (1934-1980) and Pasteels (1965-1982) gave an idea of the diversity within the tribe. The aspect of some Megachilini is indicated by Figures 8-3, 8-7, 84-2, 84-3, 84-8, and 84-9, and by Plate 7.

The Megachilini are found in large numbers on all continents. And although the number of genera recognized is small, compared to those recognized in the Osmiini and Anthidiini, the morphological diversity within the major genus *Megachile* is great, perhaps as great as that found in all the Anthidiini. Nonetheless, the tribe Megachilini (thus *Megachile*) is not as readily divisible into distinctive types as are the other two tribes. In Anthidiini in particular, the presence or absence of various carinae and lamellae provide convenient characters that led to the tradition of recognizing numerous genera. In Megachilini, the tradition has been to recognize only one nonparasitic genus (*Megachile*) or three (*Chalicodoma*, *Creightonella*, and *Megachile*; Michener, 1962a), though Mitchell (1980) added several other genera to the list. Although my original manuscript for this group used several nonparasitic genera, I reluctantly retreated to the single genus *Megachile* for reasons that will be explained below.

Brood cells of the Megachilini made of leaf pieces (usually not masticated leaves as is common in Osmiini) are common in burrows in the ground or in cavities in wood, stems, or manmade objects. Other species make cells of mud, probably combining salivary material, or of resin, either in cavities or exposed on the surfaces of stones or walls or on branches of bushes or trees.

Cleptoparasitic species, mostly *Coelioxys*, are numerous; most of them attack bees of the related genus *Megachile*, but a few parasitize distantly related bees in the family Apidae.

Key to the Genera of the Megachilini (Females)

- 1. Scopa present on S2 to S5 or S6 (Fig. 8-7); metasoma not tapering throughout its length (Fig. 8-3) *Megachile*
— . Scopa absent; metasoma tapering from near base to narrow, often acutely pointed, apex (Figs. 8-2, 84-2, 84-3) 2
- 2(1). Omaular carina present; scutellum with dorsal and posterior surfaces usually separated by distinct, sometimes carinate, angle; axilla almost always produced posteriorly to angle or spine (Fig. 84-6a) *Coelioxys* (in part)
— . Omaular carina absent; scutellum with no distinct angle between dorsal and posterior surfaces; axilla rounded (Fig. 8-2) 3
- 3(2). Preoccipital carina absent; axilla and scutellum forming a single rounded posterior margin, not separated by incision; base of propodeum with row of strong pits (Africa) *Coelioxys*: *C. gracillima* Pasteels
— . Preoccipital carina present at sides of head; axilla sepa-

rated by incision from scutellar margin; base of propodeum finely wrinkled (palearctic) *Radoszkowskiana*

Key to the Genera of the Megachilini (Males)

- 1. T6 appearing multispinose because of two pairs of long, preapical spines, each spine of upper pair sometimes divided into two, or crenulate, rounded, or fused to other spine of pair (Figs. 84-6f, g; 84-7) *Coelioxys*
— . T6 with large preapical carina (apparent apex of metasoma), often crenulate, often emarginate medially, sometimes reduced to two spines or rarely absent (Figs. 84-14, 84-18) 2
- 2(1). Posterior lobe of pronotum with strong transverse lamella extending posterolaterally as flat spine (palearctic) *Radoszkowskiana*
— . Posterior lobe of pronotum usually with weak transverse ridge, sometimes with carina or low lamella, but without spine *Megachile*

Genus *Coelioxys* Latreille

This genus is easily recognizable by the characters indicated in the key to genera. Most species also differ noticeably from all other Megachilini by having abundant hairs on the eyes. Figures 84-2 and 84-3 illustrate the distinctive aspect of species of this genus. Species of *Coelioxys* are black, though the legs and metasoma are sometimes partly or wholly red, and, rarely, the metasoma is faintly bluish. Length varies from 5 to 22 mm, some of the largest species being in the subgenera *Torridapis* and *Liothyrapis*. Illustrations of male genitalia and, in some cases, metasomal apices of females were published by Erlandsson (1955), Mitchell (1962), and Tkalcû (1974b); see also Figure 84-4. Mitchell (1973) and Baker (1975) illustrated many structures of species from the Western Hemisphere.

Coelioxys consists of cleptoparasites related to *Megachile*. A series of apomorphies indicates that *Coelioxys* is a monophyletic unit; the transverse postgradular grooves of T2 and T3 are suggestive of hoplitiform taxa of *Megachile*, such as *Chelostomoides*. These hoplitiform taxa are probably ancestral forms of *Megachile*, and suggest either that *Coelioxys* is a sister group of *Megachile* or—if the grooves are homologous, i.e., constituting a single

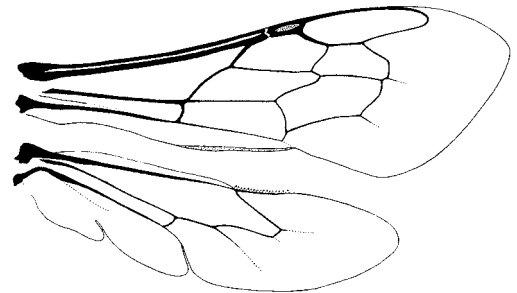


Figure 84-1. Wings of *Megachile chrysopyga* Smith.

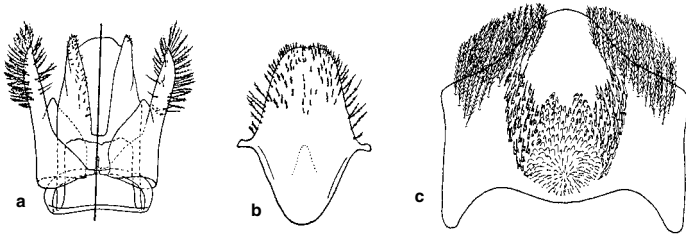


Figure 84-4. *Coelioxys* (*Xero-coelioxys*) *mesae* Cockerell. **a-c**, Male genitalia, S8, and S6. S7 is scarcely sclerotized, often only two minute remnants, in *Coelioxys*. From Baker, 1975.

Megachile, but there are also records of *Trachusa* s. str. (Anthidiini) and *Hoplitis* (*Anthocopa*) (Osmiini) serving as hosts of species that also attack *Megachile*. Baker (1975) summarized host records for North American species, and Westrich (1989) summarized European host records. Two European species known to attack *Megachile* are also reported as parasites of the apid, *Anthophora*, usually *A. (Clisodon) furcata* (Panzer), which nests in wood. Some such reports appear to be correct, but one has to wonder about the possibility that *Megachile* species nested in old *Anthophora* burrows, and were the true hosts. Some *Coelioxys*, however, do attack other apids, such as *Eucera*, *Tetraloniella*, *Centris*, and *Xylocopa*. Iwata (1976) reviewed host records worldwide up to that time. The most recent addition to the list of *Coelioxys* host genera is *Euglossa*; Ramírez-Arriaga, Cuadriello-Aguilar, and Martínez (1996) recorded *Coelioxys costaricensis* Cockerell laying eggs in provisioned but still open cells, as well as emerging as adults from cells of *Euglossa atrovirens* Dressler.

The long, tapering metasomal apex of females is usually used to insert the eggs through the food mass in an open cell into the cell wall, between or through leaf pieces in the case of leafcutter bees. In most cases, oviposition occurs while the host is foraging, and is into cells that have not yet been closed; see illustrations by Iwata (1939) and Baker (1971). In some species, however, eggs are laid after host cell closure, between the leaf pieces that form the closure. Little is known about oviposition sites for parasites of non-leafcutting hosts. Perhaps by analogy with

the Nomadinae, in which first-stage larvae have a sclerotized head and large mandibles, authors have assumed a similar arrangement for *Coelioxys*. Iwata (1939) and Baker (1971), however, both show that the brief first stage of *Coelioxys* is unsclerotized and equipped with rather short mandibles (Fig. 84-5c). It is the second and third stages that have the enormous jaws on a sclerotized head (Fig. 84-5a, d) with which they churn the food mass and destroy eggs or larvae of the host and of any conspecific competitors that may be in the cell. Older *Coelioxys* larvae, by contrast, have an ordinary head and are very *Megachile*-like (Fig. 84-5b).

Key to the Subgenera of *Coelioxys* of the Western Hemisphere

(Modified from Mitchell, 1973)

1. Postgradular grooves of T2 and T3 complete, clearly evident at midline (Fig. 84-2) 2
- Postgradular grooves of T2 and T3 interrupted medially, clearly evident only laterally 4
- 2(1). S6 of female with lateral subapical notch; T2 of male with sublateral pit or fovea just posterior to postgradular groove (Fig. 84-7) (holarctic) *C. (Boreocoelioxys)* (in part)
- S6 of female without lateral notches; T2 of male without foveae 3
- 3(2). Carina of pronotal tubercle conspicuously elevated, forming lamella anterior to regula; pubescence of thorax shorter, scutum nearly bare but with marginal lines or

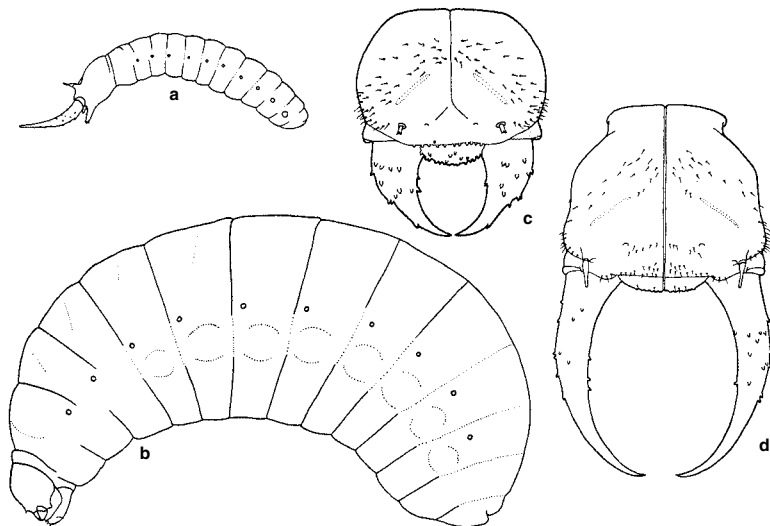


Figure 84-5. Larvae of *Coelioxys octodentata* Say. **a, b**, Side views of probable third-stage and mature larvae, showing the sclerotized head and falcate mandibles of the young larvae (compare with Fig. 4-1b, d); **c, d**, Dorsal views of heads of first- or second- and third-stage larvae. **a** and **b**, from Michener, 1953b; **c** and **d**, from Baker, 1971.

- spots of pale tomentum; gradulus of T2 approaching apical margin of tergum medially (nearctic) *C. (Xerocoelioxys)*
- Carina of pronotal tubercle not elevated, often obscured by long, dense, thoracic pubescence; scutum and scutellum more conspicuously pubescent, but without pale tomentose lines or spots; gradulus of T2 more nearly straight, not closely approaching apical tergal margin (holarctic) *C. (Coelioxys s. str.)*
- 4(1). Median ocellus partially surrounded by somewhat swollen and usually smooth portion of subocellar frontal area 5
- Subocellar area of frons usually closely punctate and quite flat, but *if* with smooth swollen area, then usually with a few punctures or divided medially by punctate zone 6
- 5(4). S6 of female rounded or broadly angulate apically, with marginal fringe of short hairs, without subapical notch; metasoma of male with four exposed sterna, dorsal processes of T6 forming a transverse, irregularly crenulate plate (North and Central America) *C. (Synocoelioxys)*
- S6 of female narrowed apically, without marginal fringe, with lateral subapical notch; metasoma of male with five exposed sterna, dorsal processes of T6 normal *C. (Neocoelioxys)*
- 6(4). Scutellum smooth, punctures well separated or sparse, hind margin carinate and usually angulate, projecting over metanotum and propodeum *C. (Acrocoelioxys)*
- Scutellum usually well punctured, hind margin not carinate and not overlying metanotum except sometimes for a median angle or tubercle 7
- 7(6). Concavity of T1 lacking marginal carina; T1 without dorsal basal fascia of pale hairs (S6 of female usually notched laterally) 8
- Concavity of T1 with dorsal marginal carina; T1 usually with more or less conspicuous pale basal fascia of hairs (i.e., on dorsum immediately behind basal concavity) 9
- 8(7). Axilla short, not reaching posterior transverse tangent of scutellum; scutellum broadly rounded or subtriangular;

- lar; T2 of male with sublateral, transverse, elongate fovea on surface behind gradulus (Fig. 84-7) (holarctic) *C. (Boreocoelioxys)* (in part)
- Axilla usually prominent; scutellum usually angulate or with median ridge or apical tubercle; T2 of male not foveate *C. (Glyptocoelioxys)*
- 9(7). S6 of female with small, lateral subapical notch; gena of male much narrowed below, hypostomal area lacking usual concavity (clypeus of female flattened, its apical margin straight and simple) *C. (Haplocoelioxys)*
- S6 of female without lateral subapical notch; hypostomal concavity present in male, though sometimes obscured by pubescence 10
- 10(9). Scutellum subtriangular, or, if broadly rounded posteriorly, then dorsal and posterior surfaces usually only indefinitely separated (S6 of female usually fringed with setae) *C. (Cyrtocoelioxys)*
- Hind margin of scutellum nearly or quite straight as seen from above, or, if broadly rounded, then dorsal and posterior surfaces separated by distinct or subcarinate edge (punctures of dorsal scutellar surface usually distinct, coarse and to some degree separated; S6 acute, without lateral notches or fringes) 11
- 11(10). S5 of female greatly expanded, hiding all but tip of S6; postgradular grooves of T3 to T5 in male not or only slightly fasciate; body length 6.5-7.2 mm (neotropical) *C. (Platycoelioxys)*
- S5 of female normal, S6 very narrow and elongate; postgradular grooves of T3 to T5 in male usually conspicuously fasciate; body usually much larger (clypeus in female variously modified) (neotropical) *C. (Rhinocoelioxys)*

Key to the Subgenera of *Coelioxys* of the Eastern Hemisphere

1. Eyes bare 2
- Eyes hairy 3
- 2(1). S5 of female greatly elongated, forming part of apical metasomal elongation, exposed part far longer than exposed parts of S4 and S6 (Fig. 84-6c); S6 of female narrow, without long hairs, not fringed; T6 of female with-

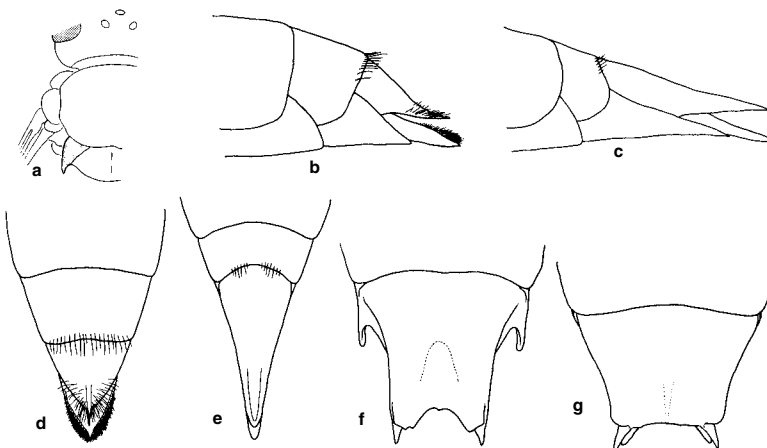


Figure 84-6. *Coelioxys*.
a, Thoracic dorsum of *C. sp.*, showing pointed axilla; **b**, **c**, Lateral views of apices of metasomas of females of *C. (Liothyrapis) scioensis* Gribodo and *C. (Torridapis) analis* Friese; **d**, **e**, Dorsal views of same; **f**, **g**, Dorsal views of T6 of males of *C. (Liothyrapis) decipiens* Spinola and *C. (Torridapis) analis* Friese. Drawings by D. Yanega.

- out keel, without long erect hairs; T6 of male without lateral tooth (Fig. 84-6g) (Africa, oriental, Australia) *C. (Torridapis)*
- S5 of female not attenuate, exposed part not much if any longer than exposed parts of S4 and S6; S6 of female broad, its apex bluntly pointed or rounded, fringed; T6 of female with keel ending in bare apical spine, with long erect hairs lateral to keel (Fig. 84-6b); T6 of male with lateral basal tooth (Fig. 84-6f) *C. (Liothyrapis)*
- 3(1). Transverse subocular carina (extending posteriorly from posterior mandibular articulation) joining preoccipital carina; subgenal fossa absent; T6 of male with eight teeth, two lateral, six apical *C. (Allocoelioxys)*
- Transverse subocular carina (extending posteriorly from posterior mandibular articulation) absent or ending free, without approaching preoccipital carina, except in some males in which subocular carina is extended as margin of subgenal fossa, the margin continuing upward as preoccipital carina; T6 of male with six teeth or projections, two lateral, four apical 4
- 4(3). Front and middle femora each with two strong but irregular longitudinal carinae on undersurfaces, one of the carinae of front femur elevated and keel-like, spaces between carinae densely covered with white, scale-like hairs; white areas or fasciae of body formed by white scales; T6 and S6 of female produced and slender but apices truncate *C. (Mesocoelioxys)*
- Front and middle femora unmodified; white areas of body formed by patches or fasciae of dense hairs or scale-like hairs; T6 and S6 of female usually pointed 5
- 5(4). T2 of male with sublateral pit or fovea on each side behind postgradular groove (Fig. 84-7); S6 of female with lateral subapical notch *C. (Boreocoelioxys)*
- T2 of male without foveae behind postgradular groove; S6 of female without lateral notch *C. (Coelioxys s. str.)*

Coelioxys / Subgenus *Acrocoelioxys* Mitchell

- Coelioxys (Acrocoelioxys)* Mitchell, 1973: 71. Type species: *Coelioxys otomita* Cresson, 1878, by original designation.
- Coelioxys (Melanocoelioxys)* Mitchell, 1973: 78. Type species: *Coelioxys tolteca* Cresson, 1878, by original designation. [New synonymy.]

The medially interrupted postgradular grooves of T2 and T3, the flattened and punctate subocellar area of the face, and the smooth, shining, and largely impunctate scutellum, with its conspicuously carinate and produced posterior margin, characterize this subgenus.

■ This primarily neotropical subgenus ranges from Argentina north to Sonora, Mexico, and North Carolina, USA. There are 25 or more species, of which Mitchell (1973) lists 18; only *Coelioxys dolichos* Fox occurs in the USA.

Coelioxys / Subgenus *Allocoelioxys* Tkalcü

- Allocoelioxys* Tkalcü, 1974b: 340. Type species: *Coelioxys afra* Lepelletier, 1841, by original designation.
- Coelioxita* Pasteels, 1977b: 180. Type species: *Coelioxys afra* Lepelletier, 1841, by original designation.
- Coelioxula* Pasteels, 1982: 110. Type species: *Coelioxys ruficaudata* Smith, 1854 = *Coelioxys ruficauda* Lepelletier, 1841, by original designation.

Coelioxys (Intercoelioxys) Ruzskowski, in Ruzskowski, Biliński, and Gosek, 1986: 117. Type species: *Coelioxys ruficaudata* (sic) Smith, 1854 = *C. echinata* Förster, 1853, monobasic.

Coelioxys (Lepidocoelioxys) Ruzskowski, in Ruzskowski, Biliński, and Gosek, 1986: 117. Invalid because no type species was designated; according to Pridal and Tkalcü (2001) the included species all would fall in *Allocoelioxys*.

Coelioxys (Tropicocoelioxys) Gupta, 1991: 425. Type species: *Coelioxys genoconcavitus* Gupta, 1991, by original designation. [New synonymy.]

Coelioxys (Orientocoelioxys) Gupta, 1992: 73. Type species: *Coelioxys quadrifasciatus* Gupta, 1992, by original designation. [New synonymy.]

Coelioxys (Nigrocoelioxys) Gupta, 1993: 235. Type species: *Coelioxys fuscipennis* Smith, 1854, by original designation. [New synonymy.]

Přidal and Tkalcü (2001) gave a useful translation from Polish to English of part of Ruzskowski's work. I see no justification for their belief that *Coelioxula* Pasteels is a *nomen nudum*, since a character and type species were specified by Pasteels (1982: 110).

The late Dr. Donald B. Baker (in litt., Nov. 2002) indicated that the three subgeneric names proposed by Gupta and synonymized under *Coelioxys* s. str. by Michener (2000) should all be placed instead as synonyms of the subgenus *Allocoelioxys*.

■ This subgenus is widespread in the Old World, including the palearctic region from Europe to China and Taiwan; to the south it occurs in all of Africa and southern Asia, at least to Java. Pasteels (1977b) reports 21 species in sub-Saharan Africa, and Warncke (1992e) reports 15 species in the western palearctic region. There are at least nine European species and a few additional species in southern Asia. The total may be about 40 species.

Coelioxys / Subgenus *Boreocoelioxys* Mitchell

- Coelioxys (Boreocoelioxys)* Mitchell, 1973: 37. Type species: *Coelioxys rufitarsus* Smith, 1854, by original designation.
- Coelioxys (Schizocoelioxys)* Mitchell, 1973: 50. Type species: *Coelioxys funeraria* Smith, 1854, by original designation. [The spelling *Schizococoelioxys* in the heading of Mitchell's description (p. 50) is corrected on the same page and elsewhere in the work.]

In *Boreocoelioxys* the postgradular grooves of T2 and T3 in both sexes vary from complete and often deep to widely interrupted. The subgenus therefore appears twice in the key to subgenera. The carina of the pronotal tubercle is elevated and conspicuous. S6 of the female has a distinct, though sometimes small, pair of lateral, subapical notches, and in the males T2 has a pair of usually small pits or foveae just posterior to the gradular groove and about midway between the median line and lateral margins (Fig. 84-7). In general, the included species are coarsely sculptured bees with abundant and often rather long pubescence on the head and thorax.

■ This subgenus is mainly holarctic. In America it occurs from northern Canada to Costa Rica, and from the Atlantic to the Pacific coast; in Eurasia it is known from Europe to Japan. The 11 North American species were re-

1991), and *M. campanulae* (Robertson), which collects pollen from *Campanula*.

The keys are divided geographically as follows: Western Hemisphere, palearctic and oriental, sub-Saharan Africa, and Australian and Papuan. For *Neochalicodoma* and *Stellenigris*, see the end of the section on the genus *Megachile*.

Zonomegachile is omitted from the following key to females of the Western Hemisphere because of lack of material. Females thought to be associated with males of *Zonomegachile* would run to couplet 23 (*Dasymegachile*, *Litomegachile*, *Megachiloides*) in the key, and differ from the last two in being South American rather than nearctic. There is a large but incomplete cutting edge in the second interspace (Mitchell, 1980, fig. 51); this character excludes *Zonomegachile* from both alternatives of couplet 23.

In keys to males, the number of exposed metasomal sterna is often important. In some cases, however, owing to artificial straightening of the metasoma, sterna that are ordinarily not or but little exposed become broadly exposed. Exposed sterna are usually punctate and hairy in a manner rather similar to one another, whereas hidden sterna, including those that become artificially exposed by straightening the metasoma, are more delicate, less punctate, with shorter and often flattened or otherwise modified hairs.

Key to the Subgenera of *Megachile* of the Western Hemisphere (Females)
(Partly from Mitchell, 1943, 1980)

1. S6 with at least posterior half bare or nearly so, except for subapical row of short hairs, behind which is bare, smooth rim directed posteriorly (body megachiliform) .. 2
- S6 with well-dispersed scopal hairs, or, if partly bare, then without bare apical rim behind transverse fringe of short hairs, or (in *Argyropile*) rim directed upward, or rim narrow and barely recognizable 6
- 2(1). Mandible five-toothed, a long cutting edge in second interspace, none elsewhere *M. (Melanosarus)*
- Mandible four-toothed, a well-formed cutting edge in third interspace 3
- 3(2). Second interspace distinct, with cutting edge usually present 4
- Second interspace lacking or small, without cutting edge 5
- 4(3). Inner angle of mandible truncate, or apical margin of clypeus impressed medially (S6 rather narrowly truncate) (neotropical) *M. (Moureapis)*
- Inner angle of mandible acute or rounded; clypeal margin straight and entire *M. (Pseudocentron)*
- 5(3). Mandible more robust, apical tooth more protuberant, much broader than other teeth; gena usually broader than eye in lateral view *M. (Acentron)*
- Mandible less robust, apical tooth not much broader than second or third; gena usually narrow *M. (Leptorachis)*
- 6(1). Mandible without cutting edges between teeth (Fig. 84-12e, f), or with incomplete cutting edge in second interspace only (Fig. 84-12c); mandible with less than five teeth, or, if five-toothed, then upper two teeth (4 and 5) usually closer together than teeth 3 and 4 7
- Mandible with cutting edges between teeth, if in second interspace only, then edge complete (in three-toothed mandible; Fig. 84-12b), or mandible clearly five-toothed, with teeth 4 and 5 about as far apart as 3 and 4 (body megachiliform) 16
- 7(6). Mandible with incomplete cutting edge in second interspace, and no cutting edges elsewhere (Fig. 84-12c) 8
- Mandible without cutting edges (Fig. 84-12e, f) 9
- 8(7). Body very large and robust (20 X 10 mm); vestiture entirely rufous; profile of T6 straight (Mexico) *M. (Grosapis)*
- Body not so large and robust; vestiture not entirely rufous, that of metasomal terga dark with pale apical bands; profile of T6 strongly concave distally because of projecting apical margin *M. (Sayapis)*
- 9(7). Megachiliform, the metasoma less than twice as long as wide unless unusually extended 10
- Heriadiform, hoplitiform, or chalicodomiform, the metasoma twice as long as wide or more 11
- 10(9). T6 distinctly concave in profile, without conspicuous erect pubescence except near base (holarctic) *M. (Megachile s. str.)* (in part)
- T6 nearly straight in profile, with abundant erect pubescence (neotropical) *M. (Chrysosarus)*
- 11(9). Pronotal lobe with transverse hairless lamella hidden among hairs; mandible with third interspace narrowly U-shaped and much deeper than others (South America) *M. (Schrottkyapis)*
- Pronotal lobe with transverse, unusually hairy ridge, sometimes with shiny but low carina; mandible with third interspace not narrower and deeper than others 12
- 12(11). Pubescence largely white, not fulvous, forming narrow white apical bands on metasomal terga and sometimes narrow bands on postgradular grooves *M. (Chelostomoides)*
- Pubescence with large areas of black or fulvous, forming striking color pattern (gray in American *Gronoceras*) 13
- 13(12). Mandible five-toothed; pubescence of thorax and metasoma black except for broad white band on T3 (Chile) *M. (Stelodides)*
- Mandible four-toothed; pubescence otherwise (introduced, Caribbean area) 14
- 14(13). Apex of front tibia with three distinct sharp spines or teeth on outer surface; clypeus with longitudinal elevation, highest at lower clypeal margin (?Jamaica) *M. (Gronoceras)*
- Apex of front tibia with two teeth or spines on outer surface; clypeus unmodified or not modified as above 15
- 15(14). Mandibular carinae minutely roughened, sometimes dull *M. (Callomegachile)*
- Mandibular carinae shining and smooth (at 40 X) *M. (Pseudomegachile)*
- 16(6). S6 with apical rim directed upward beyond fringe of hairs, this rim conspicuous if tergum and sternum are spread apart (nearctic) *M. (Argyropile)*
- S6 without apical rim, or, if rim present, then directed posteriorly and usually inconspicuous 17
- 17(16). Mandible three-toothed (Fig. 84-12b) or median tooth weakly divided and mandible thus obscurely four-toothed, with cutting edge limited to upper interspace (second if mandible tridentate, third if mandible quadridentate) (nearctic) *M. (Megachiloides)* (in part)

- . Mandible four- or five-toothed, with cutting edges in third and usually second interspaces, or rarely in second only (Figs. 84-11a-c, 84-12a) 18
- 18(17). Thoracic venter, including leg bases and S2, with dense covering of fine, plumose hairs, sharply differentiated from other scopal hairs (neotropical) *M. (Ptilosarus)*
- . Thoracic venter and leg bases with ordinary hairs, and scopal hairs all unbranched 19
- 19(18). Metasomal sterna with entire and conspicuous white apical hair fasciae beneath scopa 20
- . Metasomal sterna with white hair fasciae absent or broadly interrupted medially 21
- 20(19). Mandible four-toothed, no cutting edge in second interspace (introduced, North America, Antilles, Chile, Argentina) *M. (Eutricharaea)*
- . Mandible with fourth tooth emarginate, thus five-toothed, second interspace with conspicuous but incomplete cutting edge (South America) *M. (Trichurochile)*
- 21(19). Mandible four-toothed, upper tooth acute or right-angular (Fig. 84-12a) 22
- . Mandible four- or five-toothed, but *if* four-toothed, then upper tooth rounded, truncate, or incised (sometimes only minutely) and thus approaching the five-toothed condition (Fig. 84-11a-c) 25
- 22(21). Metasoma broadly conical, T3 narrower than T1 or T2 (neotropical) *M. (Tylomegachile)* (in part)
- . Metasoma more ovoid, T3 as broad as T1 23
- 23(22). T6 straight in profile; mandible with second tooth often rounded or obtuse (Fig. 84-12a), usually no cutting edge in second interspace (nearctic) *M. (Megachiloides)* (in part)
- . T6 usually concave in profile; mandible with second tooth acute, a small beveled cutting edge in second interspace 24
- 24(23). Scopa black; body usually covered with long, dense hairs (South America) *M. (Dasymegachile)*
- . Scopa white except on S6; body not densely covered with long hairs (nearctic) [The female of *Megachile (Xanthosarus) addenda* Cresson (couplet 24 of the first key) runs to *Litomegachile*, from which, usually, it is immediately distinguishable by its large size, 12-17 mm in body length] *M. (Litomegachile)*
- 25(21). Mandible clearly five-toothed, distance between upper two teeth not or only slightly less than distance between other pairs of teeth (holarctic) *M. (Megachile s. str.)* (in part)
- . Mandible four-toothed but upper tooth rounded, truncate, or itself bidentate (sometimes minutely), mandible thus five-toothed but distance between upper two teeth short compared to distances between other pairs of teeth (Fig. 84-11a-c) 26
- 26(25). Metasoma distinctly conical, T1 and T2 broader than T3 27
- . Metasoma more ovoid, T3 as broad as or broader than T1 28
- 27(26). Metasomal sterna with widely interrupted apical white hair fasciae; posterior apical angle of hind basitarsus slightly produced, that of segment 2 more conspicuously so (neotropical) *M. (Austromegachile)* (in part)
- . Metasomal sterna not at all fasciate; segments 1 and 2 of hind tarsus not or little produced apically (neotropical) *M. (Tylomegachile)* (in part)
- 28(26). Median area of clypeus somewhat elevated and strongly flattened, sloping away on each side (apical margin of clypeus medially emarginate) (neotropical) *M. (Austromegachile)* (in part)
- . Clypeus broadly convex or nearly flat, neither elevated nor flat medially 29
- 29(28). T6 with much conspicuous, erect pubescence visible in profile 30
- . Pubescence of T6 largely decumbent, with few or no erect hairs visible in profile 31
- 30(29). Lateral ocellus considerably nearer to posterior margin of vertex than to eye *M. (Cressoniella)*
- . Lateral ocellus usually as near as or nearer to eye than to posterior margin of vertex (holarctic) *M. (Xanthosarus)*
- 31(29). Preoccipital carina distinct behind gena; cutting edges of mandible obsolescent (lateral ocellus widely removed from occipital margin) (South America) *M. (Rhysomegachile)*
- . Preoccipital margin of gena usually not carinate, but *if* so, then cutting edges of mandible well formed 32
- 32(31). Thorax and metasoma above densely and minutely punctate throughout, largely covered with appressed or suberect tomentum (neotropical) *M. (Ptilosaroides)*
- . Punctures of thorax and metasoma distinctly separated, surface not tomentose to any considerable degree *M. (Neochelynia)*

Key to the Subgenera of *Megachile* of the Western Hemisphere (Males)

1. Middle tibial spur absent or much shorter than apical width of tibia, sometimes immovably fused to tibia, and middle basitarsus not or little modified (body megachili-form) 2
- . Middle tibial spur present, articulated to tibia, about as long as apical tibial width, or, *if* absent (as in some species of *Xanthosarus*), then middle basitarsus modified and swollen 6
- 2(1). Middle tibial spur present, articulated, but small *M. (Leptorachis)*
- . Middle tibial spur absent or represented by prong immovably fused to tibia 3
- 3(2). Middle tibia with a spurlike apical prong (spur presumably fused to tibia), prong sometimes reduced to large, acute tooth *M. (Pseudocentron)*
- . Middle tibia without such a process 4
- 4(3). Front and middle tibia and tarsus simple and unmodified; front tarsus slender, usually black (neotropical) *M. (Moureapis)*
- . Front and middle tibia and tarsus modified, middle tibia broadened apically or angulate on lower margin; basitarsus usually excavated along anterior margin; front tarsus dilated and brightly colored 5
- 5(4). Scutum finely and densely rugoso-punctate, punctures not individually distinguishable *M. (Acentron)*
- . Punctures of scutum usually well separated, but, if close, then individually distinguishable *M. (Melanosarus)*
- 6(1). S4 not exposed or only its posterior margin exposed (Fig. 84-13a); punctation and vestiture of S4 (except sometimes for posterior margin) reduced and different from those of S3 7

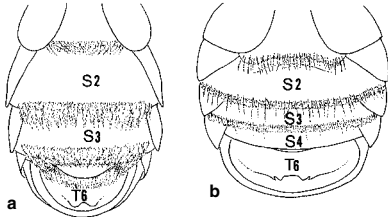


Figure 84-13. Undersurfaces of male metasomas of *Megachile*.
a, *M. (Chelostomoides) campanulae* (Robertson); **b**, *M. (Litomegachile) mendica* Cresson.

- S4 exposed, thus four exposed sterna (Fig. 84-13b), punctuation and vestiture of S4 similar to those of S3 8
- 7(6). Mandible three-toothed, toothed margin much shorter than distance from upper tooth to base of mandible; body not covered with rufous hairs *M. (Chelostomoides)*
- Mandible four-toothed, elongate, toothed margin as long as distance from upper tooth to base of mandible; body covered with long, rufous hairs (Mexico) *M. (Grosapis)*
- 8(6). Pronotal lobe with erect, hairless transverse lamella (clypeus protuberant medially; mandible as described for *Grosapis* in couplet 7) (South America) *M. (Schrottkeyapis)*
- Pronotal lobe rounded or with transverse, usually hairy ridge, sometimes with shiny, bare, but low carina 9
- 9(8). S8 with hairs on lateral margin (as in Fig. 84-10j, n); body chalicodomiform, with large areas of black or fulvous hairs forming a striking color pattern (except in our species of *Gronoceras*) (introduced into Caribbean region) 10
- S8 without marginal hairs (as in Fig. 84-10b, f) but discal hairs sometimes extending laterally beyond margin; body usually megachiliform, usually without a striking color pattern (but see *Stelodides*, couplet 25) 12
- 10(9). T6 with preapical brush of long hairs and two long, slender spines representing preapical carina (Fig. 84-18) *M. (Gronoceras)*
- T6 without brush of long hairs and without long spines.. 11
- 11(10). T6 with carina short, low, not or shallowly emarginate, not denticulate (Fig. 84-14c) *M. (Callomegachile)*
- T6 with carina strong, strongly dentate or denticulate (Fig. 84-14a), or sometimes scarcely undulate (Fig. 84-14b) *M. (Pseudomegachile)*
- 12(9). Mandible lacking inferior projection or tooth 13
- Mandible with definite projection, tooth, or angle on lower margin 24
- 13(12). Front coxal spine present 14
- Front coxal spine absent 19
- 14(13). Front coxal spine short, inconspicuous; basal segment of flagellum shorter than pedicel; T6 projecting posteriorly, thus nearly horizontal above carina (small, slender species) *M. (Neochelynia)* (in part)
- Front coxal spine longer, conspicuous; basal segment of flagellum usually longer than pedicel (but much shorter in *Rhyssomegachile*); T6 more nearly vertical, usually not visible from above 15

- 15(14). Carina of T6 without emargination but with small median apical point (neotropical) *M. (Tylomegachile)*
- Carina of T6 with a deep, rounded emargination (as in Fig. 84-14a) 16
- 16(15). Preoccipital carina strong behind genal area (front tarsus slender, dark) (South America) *M. (Rhyssomegachile)*
- Preoccipital carina absent 17
- 17(16). Anterior end of hypostomal area, immediately behind mandible, with strong, angular projection (South America) *M. (Zonomegachile)*
- Anterior end of hypostomal area unmodified 18
- 18(17). Front tarsus slender, black; carina of T6 represented principally by two spines, one on each side of emargination; mandible four-toothed (neotropical) *M. (Ptilosaroides)*
- Front tarsus enlarged, pale; carina of T6 better developed, not represented merely by two spines; mandible three-toothed (neotropical) *M. (Chrysosarus)* (in part)
- 19(13). First and second segments of flagellum subequal (mandible three-toothed, middle tooth sometimes notched, suggesting a four-toothed condition) (South America) *M. (Dasymegachile)*
- First segment of flagellum shorter than second 20
- 20(19). Carina of T6 with pair of acute spines or teeth 21
- Carina of T6 not bispinose, lateral portions on each side of emargination obtuse, if present 23
- 21(20). Large emargination between teeth of carina of T6 filled by dense fringes of long, plumose hairs largely arising from the teeth (mandible three-toothed) (South America) *M. (Trichurochile)*
- Emargination between teeth of carina of T6 not filled by fringe 22
- 22(21). Mandible four-toothed; body length often 12 mm or more; pubescence erect and rather long..... *M. (Cressoniella)*
- Mandible three-toothed; body smaller, length about 7 mm; pubescence short, appressed (neotropical) *M. (Ptilosarus)*
- 23(20). T6 more nearly horizontal, carina either deeply emarginate, with dorsal surface markedly concave, or surface convex, carina low, with only a small median notch *M. (Neochelynia)* (in part)
- T6 vertical, completely hidden in dorsal view of metasoma, carina low and entire or with small median emargination (neotropical) *M. (Austromegachile)*
- 24(12). Metasoma about twice as long as wide (carina of T6 usually emarginate medially; front tarsus usually enlarged and pale; front coxa with spine and usually with red bristles) 25
- Metasoma less than twice as long as wide 26
- 25(24). Pubescence of thorax and metasoma black except for broad white band on T3; mandible with small preapical inferior angle (Chile) *M. (Stelodides)*
- Pubescence not forming above color pattern; mandible with large basal inferior projection *M. (Sayapis)*
- 26(24). Carina of T6 entire or crenulate, median part the most produced, with no trace of a median emargination 27
- Carina of T6 commonly crenulate, median part emarginate (as in Fig. 84-14a) or sometimes irregular but not produced 29
- 27(26). Front tarsus slender and simple, black or fuscous;

- front coxa pubescent anteriorly, without red bristles, spine short and slender; lower tooth of mandible slender and acute; apical segment of antenna not at all dilated, fully three times as long as broad (nearctic) *M. (Argyropile)* (in part)
- Front tarsus usually dilated, ferruginous or yellowish; front coxa usually bare anteriorly, with broad, flat conspicuous spine and patch of red bristles; lower tooth of mandible usually robust; apical segment of antenna usually dilated, about twice as long as broad 28
- 28(27). S4 with small but distinct median tubercle on apical margin (large, robust species) (holarctic) *M. (Xanthosarus)* (in part)
- S4 without median apical tubercle, apical margin usually broadly membranous (nearctic) *M. (Megachiloides)*
- 29(26). Mandible four-toothed 30
- Mandible three-toothed 31
- 30(29). Front coxa usually largely bare anteriorly, often with patch of short red bristles in front of spine; front tarsus frequently modified, pallid (holarctic) *M. (Xanthosarus)* (in part)
- Front coxa hairy, without red bristles; front tarsus simple, dark-colored (nearctic) *M. (Argyropile)* (in part)
- 31(29). Mandible with low median or preapical inferior angle in place of usual tooth (neotropical) *M. (Chrysosarus)* (in part)
- Mandible with strong inferior basal tooth 32
- 32(31). Front tarsus broadly dilated, pale (holarctic) *M. (Xanthosarus)* (in part)
- Front tarsus simple, black or nearly so 33
- 33(32). Front coxal spine reduced to inconspicuous tubercle or absent (holarctic) *M. (Megachile s. str.)*
- Front coxal spine well developed 34
- 34(33). Morphological apical margin (not carina) of T6 without evident teeth (introduced) *M. (Eutricharaea)*
- Morphological apical margin of T6 with four small but distinct teeth (nearctic) *M. (Litomegachile)*
-
- Key to the Palearctic and Oriental Subgenera of *Megachile* (Females)
1. Mandible five- or six-toothed, teeth (except the first) similar and with similarly shaped incomplete cutting edges in second and third (and sometimes fourth) interspaces (Fig. 84-17d); apices of mandibular teeth roughly equidistant from nearest neighbors; preapical transverse mandibular groove distinct and filled with short, fine, pale hairs (these not found in other subgenera with cutting edges) *M. (Creightonella)*
- Mandible three- to five-toothed, without cutting edges, or, *if* with cutting edges, then teeth above first of different shapes and cutting edges often of different shapes, or only one cutting edge present; apices of mandibular teeth commonly separated from nearest neighbors by different distances; preapical transverse mandibular groove, in forms with cutting edges, absent, or, *if* present, then not filled with short, pale hairs 2
- 2(1). Mandible without cutting edges (Fig. 84-12d-f) (body chalicodomiform) 3
- Mandible with cutting edge in at least one interspace, sometimes hidden behind margin of interspace (Fig. 84-11) 8
- 3(2). Mandible with five fully distinct teeth, about equidistant (northern Africa) *M. (Parachalicodoma)*
- Mandible with three or four teeth 4
- 4(3). Anterior margin of clypeus rounded (rarely weakly emarginate medially), strongly crenulate, produced well over base of labrum, not thickened; head little developed posteriorly, ocelloccipital distance thus not greater than interocellar distance (palearctic) *M. (Chalicodoma)*
- Anterior margin of clypeus truncate or highly modified, usually not crenulate, often not much produced over base of labrum, but *if* rounded and somewhat crenulate (as in some *Pseudomegachile*), then margin thickened and impunctate; head usually much developed posteriorly, ocelloccipital distance thus greater than interocellar distance 5
- 5(4). Apex of front tibia with three spines, posterior one less acute and hidden by dense, short hairs; mandible strongly expanded apically, outer margin thus concave in basal half, narrowest part little more than half as wide as apical margin (oriental) *M. (Largella)*
- Apex of front tibia with one or usually two spines, posterior one absent; mandible not so expanded apically, outer margin not or weakly concave, narrowest part more than half as wide as apical margin 6
- 6(5). Mandible elongate, more or less parallel-sided or narrowest preapically, with teeth across apex *and* mandibular ridges smooth and shining (at 40X) (southwestern Asia) *M. (Maximegachile)*
- Mandible of ordinary shape or *if* elongated as above (as in some *Callomegachile*), then ridges minutely roughened and dull 7
- 7(6). Mandible with ridges largely shiny, not dulled by microsculpturing (at 40X) *M. (Pseudomegachile)*
- Mandible with ridges dulled by microsculpturing *M. (Callomegachile)*
- 8(2). Mandible with cutting edge only in second interspace (as in Fig. 84-12c); body heriadiform, hoplitiform (as in Fig. 84-9), or chalicodomiform 9
- Mandible with cutting edge in third interspace and frequently also in second; body megachiliform (Fig. 84-8) except metasoma over twice as long as broad in *Megella* 10
- 9(8). Metasomal sterna at least laterally with apical fasciae of white hair under scopa; mandible of ordinary shape, five-toothed *M. (Chelostomoda)*
- Metasomal sterna without apical fasciae; mandible over twice as long as basal width, four-toothed (palearctic) *M. (Eumegachile)*
- 10(8). Mandible with five teeth, distance between fourth and fifth little less than distance between other teeth (palearctic) *M. (Megachile s. str.)*
- Mandible with four teeth, or *if* with five, then distance between fourth and fifth less than half distance between third and fourth (Fig. 84-11a) 11
- 11(10). Metasoma over twice as long as broad; body over 20 mm long (cutting edge in third interspace, behind interspace margin and not or only slightly exposed in frontal view; Fig. 84-11h) (oriental) *M. (Megella)*
- Metasoma less than twice as long as broad; body 16 mm long or less 12

- 12(11). Cutting edges large, completely filling second and third interspaces, teeth thus not extending beyond cutting edges and, together with adjacent teeth, forming a thin, generally straight although irregular mandibular margin (Fig. 84-11e); cutting edge in second interspace at least in part indistinguishably fused to third tooth (oriental) *M. (Amegachile)*
- Cutting edges variable but not completely filling interspaces, teeth extending beyond cutting edges at least in some parts of mandibular margin (Fig. 84-11a-d, f, g); cutting edges usually nowhere indistinguishably fused to teeth 13
- 13(12). Upper mandibular tooth broad (convex or truncate) or emarginate so that the mandible is five-toothed (Fig. 84-11a); sterna without apical hair bands beneath scopa; third interspace of mandible frequently deeper than others (palearctic) *M. (Xanthosarus)*
- Upper mandibular tooth acute, sharply right-angular, or narrowly rounded; sterna frequently with apical white hair bands beneath scopa; third interspace of mandible not or little deeper than others 14
- 14(13). Mandible without or with only hidden or very small cutting edge in second interspace but with cutting edge in third interspace (rarely hidden behind interspace margin) (Fig. 84-11g) *M. (Eutricharaea)*
- Mandible with well-developed cutting edges in second and third interspaces (Fig. 84-11d) 15
- 15(14). Mandible with upper interspace as long as or longer than rest of apical margin, cutting edge in upper interspace complete, occupying full length of interspace and over twice as long as incomplete cutting edge in second interspace (oriental) *M. (Neocressoniella)*
- Mandible with upper interspace shorter than rest of apical margin, cutting edge in upper interspace complete or incomplete, sometimes hidden, less than twice as long as incomplete cutting edge in second interspace (oriental) *M. (Paracella)*

Key to the Palearctic and Oriental Subgenera of *Megachile* (Males)

(*Megella* is omitted because the male of the oriental species is unknown to me.)

1. S5 (sometimes also S6) exposed and generally similar to preceding sterna (sometimes S5 largely hidden but S6 exposed); lateral extremity of carina of T6 directed basad, away from apical margin of tergum *M. (Creightonella)*
- S5 and S6 retracted, variously modified, less sclerotized, less punctate, and less hairy than S1 to S4; lateral extremity of carina of T6 absent or directed toward lateral extremity of apical margin of tergum 2
- 2(1). S8 with lateral marginal hairs (Fig. 84-10j, n) (only one in *Eumegachile*); metasoma commonly strongly convex and twice as long as wide or more 3
- S8 without marginal hairs (Fig. 84-10b, f) but discal hairs sometimes extending beyond margin laterally; metasoma usually less strongly convex and usually less than twice as long as wide 12
- 3(2). S4 largely or wholly retracted (as in Fig. 84-13a), less sclerotized, less punctate, and less hairy than S2 and S3 (body heriadiform or hoplitiform) *M. (Chelostomoda)*
- S4 exposed, similar in punctuation and pubescence to preceding sterna (as in Fig. 84-13b) 4
- 4(3). T6 with carina dentate or denticulate, sometimes with

- median emargination but denticulate lateral to it (Fig. 84-14a), sometimes bilobed but margin with at least a few faint irregularities (Fig. 84-14b); surface of T6 above carina usually without median depression 5
- T6 with carina bilobed or sometimes simple, not at all toothed (Fig. 84-14c); surface of T6 above carina usually with median depression 8
- 5(4). T7 with narrow, median, apically truncate projection extending well beyond teeth of T6 carina (northern Africa) *M. (Parachalicodoma)*
- T7 a low sclerite largely hidden behind T6, sometimes produced to small median spine 6
- 6(5). Front coxa with erect spine *M. (Pseudomegachile)* (in part)
- Front coxa without spine or with tubercle or short spine 7
- 7(6). Toothed margin of mandible (three- to four-toothed) strongly oblique, nearly as long as distance from upper tooth to mandibular base *M. (Chalicodoma)*
- Toothed margin of mandible (three-toothed) less oblique, much shorter than distance from upper tooth to mandibular base *M. (Pseudomegachile)* (in part)
- 8(4). Hairs of middle of T6 above carina extremely long, extending well beyond carina; carina of T6 high, strongly bilobed (T6 conspicuously acute in lateral view) 9
- Hairs of middle of T6 immediately above carina not very long, not extending far beyond carina, although dorsum of T6 may have very long hairs laterally; carina of T6 usually lower, not or rather weakly bilobed 11
- 9(8). Posterior margin of T6 with strong lateral tooth (partly obscured by hair); apex of clypeus with small median nodule continued up clypeus for a distance as a carina (Asia Minor) *M. (Maximegachile)*
- Posterior margin of T6 without lateral tooth; clypeus without median nodule and carina 10
- 10(9). Front tibia with apical posterior angle, which is obtuse but distinct and covered with short hair (oriental) *M. (Largella)*
- Front tibia without apical posterior angle, or, if weakly evident, then angle not covered with short hair *M. (Pseudomegachile)* (in part)
- 11(8). Mandible with strong premedian projection from lower margin at right angles to axis of mandible; T7 with large, exposed, biconvex, punctate surface; mandibular carinae shining and smooth (at 40×) (palearctic) *M. (Eumegachile)* (in part)
- Mandible without inferior projection or with hairy convexity or basal lobe; T7 hidden or exposed as narrow rim; mandibular carinae usually dulled by minute sculpturing *M. (Callomegachile)*
- 12(2). T7 with large, exposed, biconvex, punctate surface; body chalcidomiform (palearctic) *M. (Eumegachile)* (in part)
- T7 hidden or exposed as narrow rim or crescentic sclerite, sometimes prolonged to median spine; body megachiliform *M. (Amegachile, Eutricharaea, Megachile s. str., Neocressoniella, Paracella, Xanthosarus)*

Key to the Sub-Saharan Subgenera of *Megachile* (Females)

(See the long note following the key to males, below.)

1. Mandible four- to six-toothed, all except lowermost teeth similar in shape with incomplete, similarly shaped cut-

- ting edges in second and third (sometimes also fourth) interspaces (Fig. 84-17d), rarely [*M. (C.) cornigera* (Friese)] in second interspace only; and if mandible four-toothed, then cutting edges sometimes dissimilar; metasoma strongly convex, often twice as long as broad, parallel sided, body chalicodomiform; preapical transverse mandibular groove distinct and filled with short, fine, pale hairs (this is diagnostic in combination with presence of cutting edges) *M. (Creightonella)*
- Mandible three- to five-toothed, rarely seven-toothed, without cutting edges, or, if with cutting edges, then second and higher teeth of different shapes and cutting edges of different shapes, or only one cutting edge present (Fig. 84-11); metasomal shape variable; preapical transverse mandibular groove, in forms with cutting edges, absent, or, if present, then not filled with short, pale hairs..... 2
- 2(1). Mandible without cutting edges between teeth (Fig. 84-12e, f); S6 usually with apical hairs like scopal hairs of nearby surface of sternum, sometimes with bare rim; body chalicodomiform, metasoma strongly convex, more or less parallel-sided, and commonly two or more times as wide as long (as in Fig. 84-9) 3
- Mandible usually with cutting edge in interspace between at least one pair of teeth, cutting edge rarely hidden behind interspace margin (Fig. 84-11); S6 with apical (or preapical if there is bare rim) fringe of dense, short, often plumose hairs different from scopal hairs; body megachiliform (except in *Megella*), thus metasoma more or less flattened, cordate, tapering to apical point, usually less than twice as long as wide 12
- 3(2). Apex of front tibia on outer surface with three distinct, sharp, fully exposed teeth or spines, spaces between them shining *M. (Gronoceras)*
- Apex of front tibia with one or two spines, or, if (rarely) with three spines, then posterior spine a mere tubercle or covered by a patch of short hairs, or if distinct and pointed, then spaces between spines with punctures and hairs, not noticeably shining 4
- 4(3). Arolia present on front and middle legs *M. (Heriadopsis)*
- Arolia absent 5
- 5(4). Anterior margin of clypeus rounded (rarely weakly emarginate medially), strongly crenulate, produced well over base of labrum, not thickened; head little developed posteriorly, ocelloccipital distance thus not greater than interocellar distance *M. (Chalicodoma)*
- Anterior margin of clypeus truncate or highly modified, usually not crenulate, often not much produced over base of labrum, but if rounded and somewhat crenulate (as in some *Pseudomegachile*), then margin usually thickened and impunctate; head much developed posteriorly, ocelloccipital distance thus usually greater than interocellar distance 6
- 6(5). Apex of front tibia with three spines, posterior spine less acute than others and hidden by dense, short hairs; mandible strongly expanded apically, outer margin thus concave in basal half and narrowest part little over half as wide as apical margin (Zanzibar) *M. (Largella)*
- Apex of front tibia with one or usually two spines, posterior spine as found in *Largella* being absent; mandible not so expanded apically, outer margin not or weakly concave, narrowest part more than half as wide as apical margin 7
- 7(6). Mandible elongate, approximately parallel-sided or narrowest preapically, and mandibular ridges smooth and shining (at 40×); posterior hypostomal area with strong tooth 8
- Mandible of ordinary shape, or, if elongate as above (as in some *Callomegachile*), then ridges minutely roughened and dull; posterior hypostomal area without a tooth, sometimes with obtuse angle 9
- 8(7). Mandible three-toothed *M. (Maximegachile)*
- Mandible four-toothed *M. (Stenomegachile)*
- 9(7). Mandible with ridges largely shiny, not dulled by microsculpturing (at 40×) 10
- Mandible with ridges dulled by microsculpturing 11
- 10(9). Apical margin of clypeus broadly and deeply emarginate, lower part of clypeus strongly depressed, separated from upper part by curved ridge *M. (Cuspidella)*
- Clypeus not or little modified, truncate, margin sometimes crenulate *M. (Pseudomegachile)*
- 11(9). Mandible five-toothed, with deep, rounded emargination between third and fourth teeth, fourth and fifth teeth (interpretable jointly as angularly truncate fourth tooth) connected by straight margin basal to level of first three teeth; clypeus with large, deep, triangular, shining, hairless area in middle of which, arising from impunctate surface, is a large tubercle (Madagascar) *M. (Cestella)*
- Mandible three- to seven-toothed, without especially deep emargination and with no teeth displaced basad; clypeus truncate to highly modified, but not as above *M. (Callomegachile)*
- 12(2). (See note at end of key to African male *Megachile*, below.) Mandible without or with only hidden cutting edge in second interspace but with cutting edge in third interspace, this edge sometimes hidden behind interspace margin (in a few species in the *Eurymella* group of *Eutricharaea*, such as *Megachile michaelis* Cockerell and *dolichognatha* Cockerell, second and third teeth fused, the long margin below upper tooth then with cutting edge on upper part only) 13
- Mandible with distinct cutting edges in second and usually third interspaces 15
- 13(12). Mandible five-toothed, upper two teeth close together (interpretable jointly as emarginate fourth tooth) but with small cutting edge between them, i.e., in fourth interspace, in addition to large but rather incomplete cutting edge in third interspace *M. (Platysta)*
- Mandible four-toothed or rarely three-toothed, with cutting edge only in uppermost interspace or sometimes also with faint indication of cutting edge (or cutting edge hidden behind interspace margin) in second interspace, attached to lower edge of third tooth 14
- 14(13). Mandible much broadened apically, outer margin thus strongly concave; body length 18 mm or more; metasoma more than twice as long as wide *M. (Megella)*
- Mandible of ordinary shape, outer margin not strongly concave; body length much less than 18 mm; metasoma less than twice as long as wide *M. (Eutricharaea)*
- 15(12). Mandible with third tooth truncate because fused to cutting edge of second interspace, fourth tooth acute; cutting edges usually crenulate (Fig. 84-11e) *M. (Amegachile)*

- Mandible with third tooth pointed or rounded, fourth tooth usually rather broad, rounded or truncate, rarely acute, rarely emarginate so that mandible five-toothed; cutting edges not crenulate *M. (Paracella)*

Key to the Sub-Saharan Subgenera of *Megachile* (Males)

(See the long note following this key.)

1. S5 (sometimes also S6) exposed and generally similar to preceding sterna (sometimes S5 largely hidden but S6 exposed); lateral extremity of carina of T6 directed basad, away from apical margin of tergum *M. (Creightonella)*
- S5 and S6 retracted, variously modified (less sclerotized, less punctate, and less hairy than S2 to S4); lateral extremity of carina of T6 absent or directed toward lateral extremity of posterior margin of tergum 2
- 2(1). S8 with lateral marginal hairs (Fig. 84-10j, n); metasoma commonly strongly convex and twice as long as wide or more, chalicodomiform 3
- S8 without marginal hairs (Fig. 84-10b, f) but discal hairs sometimes extending beyond margin laterally; metasoma usually less strongly convex and usually less than twice as long as wide, megachiliform 15
- 3(2). Front tibia on outer surface ending distally in three bare spines or teeth, the posteriormost extended as carina along much of outer posterior margin of tibia; T6 with carina represented by long spines or long lobes, partly hidden by extremely long hairs arising before carina (Fig. 84-18) *M. (Gronoceras)*
- Front tibia on outer surface ending in two spines or teeth (posterior tooth of *Gronoceras* sometimes represented by angle, which if strong is covered by short hair, see *Largella*); tibia usually without carina along outer posterior margin; T6 with carina variable, not represented by long spines, but if bilobed, then lobes much broader than long, surface of T6 usually without extremely long hairs, but if present, then such hairs sparse enough that carina almost always easily seen 4
- 4(3). Carina of T6 strongly produced medially to truncate, untoothed process with longitudinal median carina (T6 with strong lateral tooth) *M. (Cuspidella)*
- Carina of T6 dentate or medially emarginate, not produced medially, without longitudinal median carina but sometimes with broad ridge 5
- 5(4). T6 with carina dentate or denticulate, sometimes with median emargination but denticulate lateral to it, sometimes bilobed but margin with at least a few irregularities (Fig. 84-14a, b), rarely with median emargination forming two large teeth and an additional large lateral tooth (T6 thus four-toothed); surface of T6 above carina commonly without median depression 6
- T6 with carina bilobed (Fig. 84-14c) or sometimes simple, not at all toothed, or sometimes with small lateral tooth; surface of T6 above carina usually with median depression 9
- 6(5). Front coxa with erect spine *M. (Pseudomegachile)* (in part)
- Front coxa without spine or with tubercle or short spine 7
- 7(6). Toothed margin of mandible (three- to four-toothed) strongly oblique, nearly as long as distance from upper tooth to mandibular base *M. (Chalicodoma)*

- Toothed margin of mandible (three-toothed) less oblique, much shorter than distance from upper tooth to mandibular base 8
- 8(7). Eyes unusually large, ocellular distance thus much less than interocellar distance; T6 without lateral spine (Madagascar) *M. (Cestella)*
- Eyes of ordinary size, ocellular distance about equal to interocellar distance; T6 with strong lateral spine *M. (Pseudomegachile)* (in part)
- 9(5). Arolia present on front and middle legs *M. (Heriadopsis)*
- Arolia absent 10
- 10(9). Hairs of T6 above middle of carina extremely long, extending well beyond carina; carina of T6 high, strongly bilobed, T6 conspicuously acute in lateral view 11
- Hairs of T6 above middle of carina not very long, not extending far beyond carina, although laterally dorsum of T6 may have very long hairs; carina of T6 commonly lower, not or weakly bilobed [in *M. (Megella?) exsecta* Pasteels with deep median emargination leaving two teeth, not lobes] 14
- 11(10). Front tibia with longitudinal carina along outer posterior angle; hypostoma with large tooth close behind mandibular base; hairs of T6 so long and dense as to almost hide carina *M. (Stenomegachile)*
- Front tibia without longitudinal carina; no large tooth behind mandibular base; hairs of T6 not at all obscuring carina 12
- 12(11). Posterior margin of T6 with strong lateral tooth (partly obscured by hair); apex of clypeus with small median nodule continued up clypeus as carina *M. (Maximegachile)*
- Posterior margin of T6 without lateral tooth; clypeus without median nodule and carina 13
- 13(12). Apex of front tibia with posterior angle (indicating third apical spine) obtuse but distinct and covered with short hair *M. (Largella)*
- Apex of front tibia without posterior angle, or, if weakly evident, then not covered with short hair *M. (Pseudomegachile)* (in part)
- 14(10). Posterior margin of T6 simple *M. (Callomegachile)*
- Posterior margin of T6 with slender, mesally directed spine at each extreme side and a mediolateral convexity representing a tooth *M. (Megella)*

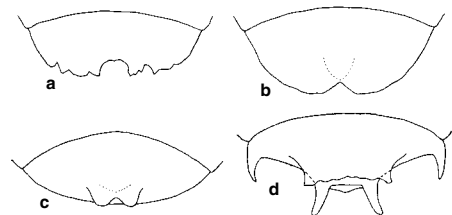


Figure 84-14. T6 of males of *Megachile*. **a**, *M. (Pseudomegachile) ericetorum* Lepeletier; **b**, *M. (P.) lanata* (Fabricius); **c**, *M. (Callomegachile) torrida* Smith; **d**, *M. (Austrochile) resinifera* Meade-Waldo. In a-c the actual posterior margin of T6, commonly with two or four small teeth, is out of sight behind the transverse carina or convexity. In d, however, the carina is the median truncate-undulate structure and the four marginal teeth are large. a-c, drawings by D. Yanega; d, from Michener, 1965b.

- 15(2). Carina of T6 short, occupying little over one-fifth width of tergum, high, rounded-truncate, slightly crenulate, not emarginate medially..... *M. (Platysta)*
 —. Carina of T6 much longer, usually occupying most of width of tergum, commonly crenulate, commonly emarginate medially.... *M. (Amegachile, Eutricharanea, Paracella)*

NOTE: The African subgenera of megachiliform, leafcutting species are much confused. Pasteels (1965) provided a subgeneric classification, but the diversity within some of his subgenera is so great that distinctions between subgenera almost vanish. I have eliminated some of his subgenera by synonymy, but I believe that a detailed study would result in recognition of additional groups that would be called subgenera by the standards used elsewhere. Moreover, various species are not assigned to subgenus at all, and one of the great, overriding problems is proper association of the sexes. The keys given above will certainly be found quite unsatisfactory. I hope that they suggest some useful major groupings. Further details are provided in accounts of the subgenera.

Key to the Australian and Papuan Subgenera of *Megachile* (Females)

1. Mandible with six teeth, incomplete cutting edges of similar shape (Fig. 84-17d) in second, third, and fourth interspaces, the last small and often inconspicuous (metasoma parallel-sided)..... *M. (Creightonella)*
 —. Mandible with two to five teeth, cutting edges absent or in second and third interspaces only, usually of quite different shapes in the two interspaces or absent in one or the other 2
 2(1). Mandible without cutting edges between teeth (Fig. 84-12d-f); metasoma parallel-sided, body thus heriadiiform or chalicodomiform (as in Fig. 84-9) 3
 —. Mandible with at least one cutting edge between teeth; metasoma usually broad, less than twice as long as broad, body thus megachiliform (but see *Mitchellapis* and *Chelostomoda*) 9
 3(2). S1 with large midapical spine *M. (Austrochile)*
 —. S1 without apical spine 4
 4(3). Claws each with two teeth on underside; proboscis fossa closed posteriorly by process from lower side of each genal area *M. (Schizomegachile)*
 —. Claws without or with but one ventral tooth each; proboscis fossa open posteriorly 5
 5(4). Metasomal integument red, and T2 and T3 without deep transverse postgradular grooves; glossa broad, ligulate *M. (Rhodomegachile)*
 —. Metasomal integument black, or, if red, then with deep postgradular grooves; glossa linear or only slightly broadened 6
 6(5). Mandible bidentate; T6, as seen from above, with strong, rounded, basolateral shoulders, lateral margins thus strongly concave immediately posterior to shoulders *M. (Thaumatoma)*
 —. Mandible with three or more teeth; T6 without shoulders, lateral margins gently convex to gently and rather uniformly concave 7
 7(6). T2 and T3 usually with deep, transverse postgradular grooves, these absent from some middle-sized and large species in which claws have strong basal tooth (except in *M. semiluctuosa* Smith); pubescence usually giving a gray

- aspect, often forming apical white tergal fasciae; fulvous pubescence often present but confined to apical part of metasoma, rarely (*M. ustulata* Smith) metasoma with extensive fulvous pubescence..... *M. (Hackeriapis)*
 —. Metasomal terga without deep, transverse postgradular grooves [except in *C. (Callomegachile) mcnamerae* Cockrell and others from New Guinea northward]; claws without basal teeth; pubescence black, fulvous, or with white patches, not grayish in aspect and not forming tergal fasciae; fulvous pubescence, if present, not confined to apical part of metasoma..... 8
 8(7). Mandible shining (although reticulate), apical margin very oblique, as long as distance from basal tooth to base of mandible; sharp hypostomal tooth behind base of mandible *M. (Chalicodomoides)*
 —. Mandible dull with minute roughening, apical margin shorter; no tooth behind base of mandible *M. (Callomegachile)*
 9(2). Mandible with incomplete cutting edge in second interspace, and without other cutting edges (as in Fig. 84-12c); body heriadiiform or chalicodomiform (Fig. 84-9) 10
 —. Mandible with cutting edge in third interspace and often also in second (Fig. 84-11); body megachiliform 11
 10(9). S6 with large smooth hairless area before apical fringe; T6 with many long hairs visible in profile, its apex produced and shallowly emarginate; pronotal lobe with rounded transverse ridge *M. (Mitchellapis)*
 —. S6 uniformly punctate and hairy; T6 with only very short hairs visible in profile, its apex rounded; pronotal lobe with strong transverse carina *M. (Chelostomoda)*
 11(9). Species with fulvous and black coloration suggestive of *Callomegachile*; third mandibular tooth broad and irregularly truncate because of fusion with cutting edge of second interspace (Fig. 84-11e), second (in Australian area) truncate (sometimes obliquely) or sinuate at apex *M. (Amegachile)*
 —. Species usually dull-colored, gray, often with pale metasomal bands of hair; third mandibular tooth as well as second angulate, cutting edge in second interspace usually present although incomplete and not indistinguishably fused to third tooth *M. (Eutricharanea)*

Key to the Australian and Papuan Subgenera of *Megachile* (Males)

1. S5 and usually S6 exposed (metasoma parallel-sided) *M. (Creightonella)*
 —. S5 and S6, and sometimes S4, hidden under preceding sterna 2
 2(1). S8 with lateral hairs (Fig. 84-10j, n); body heriadiiform or chalicodomiform, metasoma ordinarily twice as long as wide (Fig. 84-9) 3
 —. S8 without lateral hairs but sometimes discal hairs may extend slightly beyond lateral margins (Fig. 84-10b, f); body megachiliform, metasoma ordinarily less than twice as long as wide 12
 3(2). S1 with large midapical spine; carina of T6 very high and weakly crenulate to serrate medially, usually not emarginate, abruptly disappearing laterally so that general aspect is a large, truncate projection (Fig. 84-14d) *M. (Austrochile)*
 —. S1 at most apically tuberculate; carina of T6 low (rarely

- even absent), not crenulate or serrate, medially slightly emarginate (except in *Mitchellapis*, *Rhodomegachile*, and a few others) 4
- 4(3). Hind tibial spurs absent; S6 divided into two lateral sclerites by broad, median, membranous region *M. (Schizomegachile)*
- Two hind tibial spurs present (only one in *Thaumatoma*); S6 continuous, not divided into lateral hemisternites 5
- 5(4). Carina of T6, near the untoothed tergal margin, broadly rounded except for median tooth at apex of low, longitudinal median ridge *M. (Mitchellapis)*
- Carina of T6 variable, without median tooth 6
- 6(5). S4 retracted, or rear margin in some cases exposed (Fig. 84-13a) 7
- S4 more or less fully exposed (Fig. 84-13b) 10
- 7(6). Carina of T6 reduced to short, non-emarginate ridge or absent; metasomal integument red, without strong postgradular grooves on T2 and T3; glossa broad, ligulate *M. (Rhodomegachile)*
- Carina of T6 evident, in almost every case medially emarginate [merely an emarginate swelling, not carinate, in *M. (Hackeriapis) cliffordi* Rayment; a scarcely emarginate ridge in *M. (H.) apposita* Rayment]; metasomal integument usually black, but *if* red, then with strong transverse postgradular grooves on T2 and T3; glossa linear, rarely somewhat broadened 8
- 8(7). Distance between apices of first and third mandibular teeth nearly equal to distance from third tooth to base of mandible; apex of S1 produced as a broad, nearly hairless, median, suberect flap; large, robust species; metasoma without indications of pale tergal bands *M. (Chalicodomoides)*
- Distance between first and third (or second if mandible only bidentate) mandibular teeth much less than distance from uppermost tooth to base of mandible; apex of S1 not as above; usually smaller and more slender species; metasoma usually with indications of pale tergal bands 9
- 9(8). Region of carina of T6 swollen except at median emargination (northern Australia and northward) *M. (Chelostomoda)*
- Region of carina of T6 not swollen (common throughout Australia and Tasmania, rare in New Guinea, not known elsewhere) *M. (Hackeriapis)* (in part)
- 10(6). Only one hind tibial spur; clypeus with group of coarse, quill-like bristles arising near middle; flagellum exceedingly attenuate, first segment longer than others, last two segments expanded (Fig. 84-10q) *M. (Thaumatoma)*
- Two hind tibial spurs; clypeus without such bristles; flagellum rarely attenuate, first segment shorter than second, last segment rarely expanded 11
- 11(10). T2 and T3 usually without deep transverse postgradular grooves; pubescence all black or with pale or other areas not forming metasomal bands; posterior margin of T6 without teeth *M. (Callomegachile)*
- Terga usually with deep postgradular grooves; pubescence usually giving a gray appearance, in some cases fulvous on metasoma, usually forming metasomal bands; posterior margin of T6 usually with four teeth, median teeth absent in some cases *M. (Hackeriapis)* (in part)

- 12(2). Body with fulvous-and-black pubescence suggestive of *Callomegachile*; apical margin of T6 with four widely separated small teeth *M. (Amegachile)*
- Body usually appearing dull-colored, gray, often with pale metasomal tergal hair bands; apical margin of T6 with small lateral tooth only, or sometimes with weak indication of two submedian teeth *M. (Eutricharaea)*

Megachile / Subgenus *Acentron* Mitchell

Megachile (*Acentron*) Mitchell, 1934: 307. Type species: *Megachile albitarsis* Cresson, 1872, by original designation.

This is one of the group of megachiliform subgenera of Group 1 related to *Pseudocentron*. The female differs from the others in the broad base of the apical mandibular tooth, which is twice as broad as the second tooth. The male lacks the middle tibial spur, and the middle tibia has an apical angle on the undersurface. The subgenus was fully characterized and male genitalia and sterna illustrated by Mitchell (1937b).

■ This subgenus ranges from the southern USA (North Carolina to Arizona) south to Argentina. Only one species, *Megachile albitarsis* Cresson, occurs in the USA but there are at least ten additional species in the neotropical region.

Megachile / Subgenus *Amegachile* Friese

Megachile (*Amegachile*) Friese, 1909a: 326. Type species: *Megachile sjostedti* Friese, 1901 = *Megachile bituberculata* Ritsema, 1880, by designation of Cockerell, 1931c: 167. [Mitchell's (1934: 298) designation of *Megachile nasicornis* Friese, 1903, as the type species is subsequent and therefore invalid.]

Megachile (*Callochile*) Michener, 1962a: 27. Type species: *Megachile ustulatifomis* Cockerell, 1910 = *Apis mystacea* Fabricius, 1775, by original designation.

Megachile (*Platycheile*) Michener, 1965b: 205, nomen nudum. Type species: *Megachile foliata* Smith, 1861, monobasic. [*Platycheile* was introduced by error; *Callochile* was intended.]

This subgenus in Group 1 consists of large (12-20 mm long), broad-bodied megachiliform bees without pale metasomal bands, sometimes with areas of orange hair. The mandible of the female (Fig. 84-11e) is unusually broad, four-toothed, the second and third teeth broad, thin, and more or less truncate, often irregular or oblique. The third interspace has a large, complete cutting edge, the second interspace often appearing to be without a cutting edge, but in reality a large cutting edge seems to be fused with the third tooth to make a broad, thin, more or less truncate margin; an indication of the line between the third tooth and this edge can be seen in unworn mandibles of some species, but Pasteel's (1965) drawings are unrealistic in showing a clear separation of the tooth and cutting edge. Michener's (1965b) contention that the broad, thin margin arose from a cutting edge in *Amegachile* but from the tooth itself in *Callochile* seems to be an error; the two subgenera are synonymous. The cutting edges are often crenulate. The clypeal margin of the female is shallowly emarginate between two raised mar-

subfamily. Of these three excluded tribes, larvae are known for the Isepeolini and Protepeolini. These larvae are quite different from those of Nomadinae, at least partly because the mature larvae spin cocoons, unlike those of Nomadinae. Although recent authors such as Roig-Alsina and Michener (1993) and Roig-Alsina and Rozen (1994) have excluded these tribes from the Nomadinae, I believe there is still the possibility that they are basal groups of that subfamily, as was argued by Rozen, Eickwort, and Eickwort (1978).

The great diversity of the subfamily Apinae is an invitation to those who would like to subdivide it into several subfamilies, but it is not clear how such subdivision should be done. Although the tribes are mostly stable groups whose members remain together in various analyses, the arrangement of the tribes is different in different analyses (Roig-Alsina and Michener, 1993; Silveira, 1993b). Three tribes that might be transferred to the Nomadinae are discussed above; possible recognition of the corbiculate tribes as a separate subfamily is discussed under the subfamily Apinae. See also Section 21.

Because of frequent exceptions to group characters, it is difficult to construct a key to the subfamilies of Apidae. I have therefore prepared instead a key to the tribes of the family, with the subfamily subsuming each tribe indicated; a separate key to the tribes of Xylocopinae will be found under that subfamily, although the same tribes appear in the key below.

Considering that most of the tribes in the key are recognizable to an experienced mellittologist without microscopic examination, the difficulties of the key are surprising. A particular problem concerns the venation of the hind wing, which presents a continuum, as shown by Figures 106-2, 108-2, 108-3, 111-3, 112-4, 114-1, 116-4, and 117-3. Couplets in the key subdivide this continuum, but some species are intermediate and such couplets must be used with care.

Key to the Subfamilies and Tribes of the Apidae

1. Submarginal crossveins and second recurrent vein weak compared with other veins, commonly absent (Fig. 120-1); marginal cell open at apex or closed by weakened vein (hind tibial spurs absent).... Apinae, Meliponini (Sec. 120)
- All veins well developed, conspicuous; marginal cell closed by strong vein 2
- 2(1). Scopa of female, when present, forming a corbicula on posterior tibia (Figs. 10-11, 102-2a, 118-3, 121-1a); inner apical margin of posterior tibia of nonparasitic females (except in queens of Apini) with row of stiff bristles (the rastellum, Fig. 102-2); pygidial and basitibial plates absent; eyes hairy *or* jugal lobe of hind wing absent 3
- Scopa of female not forming a tibial corbicula [except in *Canephora* and *Hamatothrix* (Eucerini) from Argentina], and scopa sometimes absent; inner apical margins of posterior tibiae bare or hairy, without comb; pygidial and basitibial plates frequently present; eyes very rarely hairy *and* jugal lobe of hind wing almost always present 5
- 3(2). Eye hairy; jugal lobe of hind wing present although notch delimiting it shallow; hind tibial spurs absent; arolia present Apinae, Apini (Sec. 121)

- Eye bare; jugal lobe of hind wing absent; hind tibial spurs present; arolia absent 4
- 4(3). Proboscis in repose reaching beyond base of metasoma; body usually at least partly metallic; hind tibia of male with deep, hairy groove on upper surface (Fig. 118-4a-c); comb or group of bristles in position of jugal lobe of hind wing (Fig. 118-5) (neotropical) Apinae, Euglossini (Sec. 118)
- Proboscis in repose not reaching base of metasoma; body not metallic; hind tibia of male not grooved; no comb of bristles on base of hind wing Apinae, Bombini (Sec. 119)
- 5(2). Stigma absent (Fig. 88-2a); middle and hind basitarsi usually longer than tibiae; clypeus nearly flat, lower lateral areas not curved backward (Figs. 21-3c, g, 88-5b) Xylocopinae, Xylocopini (Sec. 88)
- Stigma present, although sometimes (e.g., in *Anthophora*, *Centris*; Figs. 113-1, 114-1) very small; middle and hind basitarsi usually shorter than tibiae; clypeus variable but usually more convex with lower lateral parts bent backward (Fig. 21-3d, h) 6
- 6(5). Pygidial plate absent, sometimes represented by spine in pygidial fimbria of female; scopa present (but reduced in parasitic Allodapini); epistomal suture between lateral extremity and subantennal suture usually bent mesad such that upper part of clypeus is almost parallel-sided; clypeus not or weakly protuberant 7
- Pygidial plate present in females and most males, or if absent in female, then scopa also absent; epistomal suture not or rarely bent mesad such that upper part of clypeus is nearly parallel-sided; clypeus commonly strongly protuberant, lower lateral parts bent strongly posteriorly (Fig. 21-3d, h) 9
- 7(6). Submarginal cells two (Fig. 90-11); clypeus typically slightly constricted at level of tentorial pits (Fig. 90-2), this level near middle of clypeus (Eastern Hemisphere) Xylocopinae, Allodapini (Sec. 90)
- Submarginal cells three (Fig. 89-4); clypeus not constricted at level of tentorial pits, this level above middle of clypeus 8
- 8(7). Jugal lobe of hind wing less than one-fifth as long as vannal lobe; female with spinelike pygidial plate arising from pygidial fimbria (Chile, Argentina) Xylocopinae, Manueliini (Sec. 87)
- Jugal lobe over one-third as long as vannal lobe; pygidial plate and pygidial fimbria absent Xylocopinae, Ceratinini (Sec. 89)
- 9(6). Labrum longer than broad (Fig. 96-3a) or rarely about as long as broad; scopa absent; body rather short-haired, or, *if* with long hairs, then metasoma usually with pattern of white, appressed hair-spots or bands 10
- Labrum broader than median length (Fig. 96-3b) [except rarely (e.g., *Epicharis*) longer than broad, in which case scopa present, body with long hairs, and metasoma without spots or bands of appressed white hair] 15
- 10(9). Distal parts of wings, beyond venation, hairless and coarsely papillate (Fig. 85-2a) Apinae, Melectini (in part) (Sec. 117)
- Distal parts of wings, beyond venation, with hairs (as in Fig. 85-2b), not or weakly papillate (most strongly so in *Ammobatoides*) 11
- 11(10). Arolia absent; preoccipital carina strong behind eye,

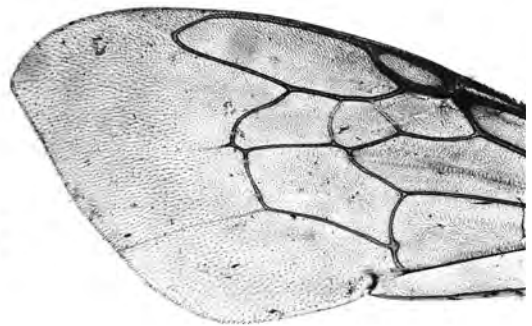


Figure 85-2. Papillate, hairless wing vs. nearly uniform hairy wing. Left, *Xeromelecta californica* (Cresson); Right, *Paratetrapedia lugubris* (Cresson). From Michener, McGinley, and Danforth, 1994.

- upper end curved forward to summit of eye; mandible with large tooth near middle of inner margin, projecting almost at right angle to mandibular axis (neotropical) Apinae, Tetrapediini, *Coelioxoides* (Sec. 109)
- Arolia present; preoccipital carina absent, or, if present, then not curved to summit of eye; mandible simple or with subapical tooth 12
- 12(11). Middle coxa much shorter than distance from its summit to posterior wing base; body coarsely punctured with patches of squamiform pubescence; each submarginal cell usually receiving a recurrent vein 13
- Middle coxa at least nearly as long as distance from its summit to posterior wing base; body finely punctate without patches of squamiform hairs; second submarginal cell receiving both recurrent veins 14
- 13(12). Episternal groove extending well below scrobal groove; scutellum and axilla lamellate or produced laterally; T5 of female without longitudinal ridge; preoccipital carina present (South America) Nomadinae, Caenoprosopidini (Sec. 101)
- Episternal groove not extending below scrobal groove; scutellum and axilla neither lamellate nor produced; T5 of female with median, rounded longitudinal ridge; preoccipital carina absent (holarctic) Nomadinae, Ammobatoidini (in part) (Sec. 96)
- 14(12). Pygidial plate of female absent or feebly defined; S6 of female produced to simple or bifid apex, without spinelike bristles (Fig. 91-2i); eyes of male not convergent above Nomadinae, Ammobatini (Sec. 100)
- Pygidial plate of female well defined; S6 of female broadly emarginate apically, lateral lobes with many blunt, spinelike bristles (as in Fig. 91-2a); eyes of male converging above Nomadinae, Ammobatoidini, *Ammobatoides* (Sec. 96)
- 15(9). Marginal cell at most but little larger than stigma (Fig. 99-1), truncate apically; one or two submarginal cells, the second, when present, much wider than long (nearctic) Nomadinae, Neolarrini (Sec. 99)
- Marginal cell far larger than stigma; two or three submarginal cells, if two, then second usually at least as long as broad 16
- 16(15). Second abscissa of vein M+Cu of hind wing shorter than cu-v (Figs. 116-4, 117-3), sometimes virtually absent, or as long as cu-v in some Rhathymini; scopa absent (posterior angle of mandible beneath middle of lower end of eye; claws of at least hind leg usually with inner ramus a broad lobe, Fig. 117-6b) 17
- Second abscissa of vein M+Cu of hind wing as long as

- to much longer than cu-v, but if about equal, then hairy bees with scopae 19
- 17(16). Wings hairy throughout, not papillate (as in Fig. 85-2b) neotropical [Some specimens of *Tetralonioidella* in Melectini have hairy, nonpapillate wings. They are Oriental whereas Rhathymini are Neotropical.] Apinae, Rhathymini (part) (Sec. 115)
- Wings bare beyond veins, coarsely papillate (Fig. 85-2a) 18
- 18(17). Middle tibial spur large, bifid or multidentate apically (Fig. 116-3); male gonostyli short, broad, often with slender projections (Fig. 116-5a, d, g); T6 of female with pygidial plate defined only at apex; marginal cell considerably exceeding last submarginal cell (Western Hemisphere) Apinae, Ericrocridini (Sec. 116)
- Middle tibial spur unmodified; male gonostyli elongate; T6 of female with well-defined pygidial plate; marginal cell in common genera not or scarcely exceeding last submarginal cell, but in certain rare Eastern Hemisphere genera much exceeding last submarginal cell Apinae, Melectini (in part) (Sec. 117)
- 19(16). Jugal lobe of hind wing small, less than one-fourth as long as vannal lobe (Figs. 108-2a, 109-1); scopa absent [except in *Caenonomada* (Tapinotaspidini) and *Tetrapedia* (Tetrapediini)] 20
- Jugal lobe of hind wing at least one-fourth as long as vannal lobe; scopa usually present 29
- 20(19). Hind tibial spur curved, coarsely pectinate (Fig. 109-2d), only one spur on hind tibia (scopa present; arolia absent) (neotropical) Apinae, Tetrapediini, *Tetrapedia* (Sec. 109)
- Tibial spurs unmodified, relatively straight, ciliate or serrate, two on hind tibia 21
- 21(20). Maxillary palpus absent and axilla small, not at all produced; epistomal suture absent below anterior tentorial pit so that clypeus and lower paraocular areas are fused Apinae, Rhathymini (part) (Sec. 115)
- Maxillary palpus present, if reduced to minute subspherical body as in some *Odyneropsis* (Epeolini), then axilla produced to point; epistomal suture usually complete 22
- 22(21). Arolia extremely small; scopa present; third submarginal cell larger than others (Fig. 108-2a) (neotropical) Apinae, Tapinotaspidini, *Caenonomada* (Sec. 108)

- . Arolia of ordinary size; scopa absent; when three submarginal cells present, first largest 23
- 23(22). Scape, excluding basal bulb, less than twice as long as broad; T6 of female with apical margin broadly concave, without pygidial plate (except plate present in *Rhopalolemma*); sting sheath (third valvula) thickened (usually two submarginal cells) (holarctic)
..... Nomadinae, Biastini (Sec. 97)
- . Scape, excluding basal bulb, more than twice as long as broad; T6 of female not broadly concave apically, usually with pygidial plate; sting sheath slender, more or less parallel-sided 24
- 24(23). Submarginal cells two, second much shorter than first and receiving only second recurrent vein (Fig. 97-3a), or sometimes also first recurrent very near its base; S6 of female broadly emarginate, lobes at either side of emargination armed with a series of large, spinelike bristles (Fig. 91-2c) (nearctic)
..... Nomadinae, Townsendiellini (Sec. 98)
- . Submarginal cells three, or, if two, then second at least nearly as long as first and receiving both recurrent veins (except very rarely in genus *Nomada*, in which marginal cell is pointed on wing margin, unlike that of Townsendiellini); S6 of female not broadly emarginate, although sometimes with spinelike bristles 25
- 25(24). Front coxae quadrate, trochanters arising from outer distal angles of coxae, trochanters thus far apart; axilla nearly always produced to acute angle or spine (Fig. 93-1c); S6 of female largely invaginated, disc reduced and lateral distal portions produced to form a pair of long, dentate or spinose processes (Fig. 95-3c, d)
..... Nomadinae, Epeolini (Sec. 95)
- . Front coxae somewhat triangular, trochanters (except in *Paranomada*, Brachynomadini) arising close to one another from apices of coxae (except lateral to apical coxal spine if spine present); axilla usually rounded; S6 of female not much invaginated, disc not greatly reduced, spinose processes, if present, short or mere lobes (Fig. 91-2e, f) .. 26
- 26(25). Mesal margin of front coxa with carina that usually bends laterad at base and extends across base of coxa; S6 of female curved to form tubular guide for sting, without blunt, spinelike bristles
..... Apinae, Osirini (in part) (Sec. 104)
- . Mesal and basal margins of front coxa not carinate; S6 of female bifid to subtruncate with blunt, spinelike bristles 27
- 27(26). S6 of female with apex elongate, bifurcate (Fig. 91-2f); maxillary palpus usually less than half as long as maxillary blade (body without yellow markings) (Western Hemisphere) Nomadinae, Brachynomadini (Sec. 93)
- . S6 of female truncate to bilobed (Fig. 91-2d, e); maxillary palpus over half as long as maxillary blade 28
- 28(27). Apex of marginal cell sharply pointed (Fig. 94-2); metasomal terga without distinct apical hair bands (Fig. 94-1); S6 of female subtruncate or feebly emarginate (Fig. 91-2e); body frequently with white or yellow markings Nomadinae, Nomadini (Sec. 94)
- . Apex of marginal cell rounded; metasomal terga with strong apical hair bands (Fig. 92-1); S6 of female emarginate (Fig. 91-2d); body without pale markings
..... Nomadinae, Hexepeolini (Sec. 92)
- 29(19). First two segments of labial palpus somewhat flattened but neither long nor sheathlike (Fig. 110-1c, d), thus as in S-T bees; S2 to S5 of female with oblique areas of long, sigmoid, oil-collecting hairs (Fig. 110-3) (rudiments on S3 to S5 even in parasitic species); inner hind tibial spur of female a fine comb of long teeth, in non-parasitic species with base greatly broadened across tibia (Fig. 110-2a, c, d) (Africa, oriental, eastern palearctic)
..... Apinae, Ctenoplectrini (Sec. 110)
- . First two segments of labial palpus long, flattened, sheathlike as in L-T bees [except in *Ancyla* (Ancylini)]; sterna of female without oil-collecting hairs; inner hind tibial spur variable but not greatly broadened at base 30
- 30(29). Scopa present; basitibial plate present except in some males; S6 of female not curled upward laterally; body euceriform to anthophoriform, with abundant plumose hairs 31
- . Scopa absent; basitibial plate absent; S6 of female curled to form guide for sting; body epeoliform, not noticeably hairy 38
- 31(30). Paraglossa as long as first two segments of labial palpus taken together (except in *Eucerinoda* from Chile); jugal lobe of hind wing about half as long as vannal lobe or sometimes more; antenna of males commonly elongate
..... Apinae, Eucerini (Sec. 112)
- . Paraglossa much shorter than first segment of labial palpus; jugal lobe of hind wing usually less than half as long as vannal lobe (more than half as long in *Ancyloscelis*); antenna of males not unusually elongate 32
- 32(31). Stigma small, usually shorter than prestigma, parallel-sided, vein *r* arising near its apex (Figs. 113-1, 114-1); distal parts of wings usually strongly papillate, basal parts usually with large bare areas (as in Fig. 85-2a) 33
- . Stigma larger, longer than prestigma, tapering beyond vein *r*, which arises near middle of stigma (Fig. 111-3); wings usually pubescent throughout and only weakly papillate apically (as in Fig. 85-2b, but see *Isepeolini*) 34
- 33(32). First submarginal cell larger than second, posterior margin longer than that of second (Fig. 113-1); scopal hairs of female largely simple, sometimes plumose along upper margin of tibia Apinae, Anthophorini (Sec. 113)
- . First submarginal cell usually smaller than second, posterior margin shorter than that of second (Fig. 114-1); scopal hairs of female mostly plumose, often intermixed with simple hairs or with projecting simple apices (Western Hemisphere) Apinae, Centridini (Sec. 114)
- 34(32). Vertex seen in facial view uniformly convex (Fig. 111-2a); second abscissa of vein M + Cu of hind wing not much longer than vein cu-v and half as long as vein M (Fig. 111-3b, c); first submarginal cell on posterior margin commonly longer than either of the others (Fig. 111-3), second shortest, third intermediate or sometimes equal to first (mandible simple) (Western Hemisphere)
..... Apinae, Emphorini (in part) (Sec. 111)
- . Vertex seen in facial view depressed between eye and ocelli, the ocellar area a little elevated (as in Fig. 111-2b); second abscissa of vein M + Cu of hind wing much longer than vein cu-v and usually more than half as long as vein M (Figs. 106-2a, 107-1, 108-2b, 108-3); first submarginal cell on posterior margin often not conspicuously longest when there are three submarginal cells, usually shorter than or subequal to third (Figs. 108-2, 108-3) 35

- 35(34). Clypeus strongly protuberant, in side view protruding in front of eye by about width of eye; vertex gently convex as seen from front; hind leg of male (femur to basitarsus) enlarged (Fig. 111-2c) (Western Hemisphere) Apinae, Emphorini (*Ancylscelis*) (Sec. 111)
- . Clypeus rather flat, in side view protruding in front of eye by much less than width of eye; vertex not or scarcely convex as seen from front; hind leg of male almost never enlarged 36
- 36(35). Second abscissa of vein M+Cu of hind wing half as long as vein M or less (Fig. 107-1) (palearctic) Apinae, Ancylini (Sec. 107)
- . Second abscissa of vein M+Cu of hind wing over half as long as vein M (Figs. 106-2a, 108-2, 108-3) (Western Hemisphere) 37
- 37(36). Second abscissa of vein M of posterior wing less than twice as long as vein cu-v (Figs. 108-2b, 108-3); mandible with preapical tooth, rarely with two such teeth; scopa with simple hairs extending beyond plumosity Apinae, Tapinotaspidini (in part) (Sec. 108)
- . Second abscissa of vein M of posterior wing more than twice as long as vein cu-v (Fig. 106-2a); mandible nearly always simple; scopal hairs plumose to apices Apinae, Exomalopsini (Sec. 106)
- 38(30). Arolia much shorter than claws, scarcely capitate; pygidial plate present in both sexes Apinae, Osirini, *Epeoloides* (Sec. 104)
- . Arolia unusually large, capitate, nearly as long as claws or longer; pygidial plate absent in both sexes (but in female of Protepeolini represented by narrow, flat, process) 39
- 39(38). Wings with hairs sparse or largely absent, papillate beyond veins (as in Fig. 85-2a) (South America) Apinae, Isepeolini (Sec. 103)
- . Wings rather uniformly hairy, not or weakly papillate distally (as in Fig. 85-2b) (Western Hemisphere) Apinae, Protepeolini (Sec. 105)

86. Subfamily Xylocopinae

An assemblage of bees, very diverse in size and appearance but united by a series of common characters, constitutes the Xylocopinae. As noted in Section 85 on the family Apidae, in some of Roig-Alsina and Michener's (1993) cladograms based on L-T bees, the tribes here placed in the subfamily Xylocopinae appeared together but among tribes of Apinae. In other analyses (when cleptoparasites were omitted), however, the Xylocopinae appeared as the sister group to the Apinae or to Apinae + Nomadinae; we therefore decided to recognize the Xylocopinae as a subfamily, and I have followed that decision here.

Xylocopinae includes two superficially very different sorts of bees; species of the tribe Xylocopini are large to very large, robust euceriform to anthophoriform bees, whereas the other three tribes consist of small, slender, andreniform to almost hylaeiform bees. Except in parasitic species that lack it, the scopa is reduced and slender compared to that of most pollen-collecting noncorbiculate Apinae. Presumably, some of the pollen carried to the nest is in the crop rather than on the scopa. The front coxae are considerably wider than long, with a tendency to be quadrate. This character, although variable, is to some degree evident in all Xylocopinae, but not in other bees except in some Nomadinae. The basitibial plates are often much modified, scarcely recognizable (Fig. 88-3b, c). The prepygidial fimbria is absent or evident only at the sides of T5 of the female. The pygidial plate of the female is usually absent (Fig. 89-2) or reduced to a spine (Fig. 88-3e, f), although in *Xylocopa* subgenus *Xylocopoides* the possible homologue of a broad plate is indicated by series of small teeth on the surface of T6 (Fig. 88-3d), and in the subgenus *Proxylocopa* there is a possible homologue of a broad plate. S7 of the male is reduced to a transverse bar, without or with a minute to small median disc area (largest in *Manueliini*) but no apical lobes. S8 is similarly reduced, without an apical process but with a spiculum, except in the *Manueliini*, in which the disc is large and an apical process is present; see Fig. 88-6c, d. The long, slender, scarcely flattened hind basitarsus, lacking both an apical process and a penicillus, is characteristic of the subfamily. So also is the relatively flat face, with the clypeus not or little protuberant (Fig. 88-5b), its lower lateral parts not curved back or only small areas curved back on either side of the labrum. As in most L-T bees the flabellum at the apex of the glossa is well developed (Fig. 86-1). The Xylocopini are unusual in that the flabellum is at the apex of a bare shank (Fig. 86-1a-c). In McGinley's (1981) study of larvae, the Xylocopinae (he did not have *Manueliini*) came out together in a nearest-neighbor analysis. The circular or oval salivary opening, without lips, is unique among larvae of nonparasitic bees. Mature larvae do not spin cocoons.

Unifying features of the nesting biology include the following: Except for *Xylocopa* (*Proxylocopa*), all species nest in dead plant material—hollow stems or galls or burrows made in pithy stems or galls or in rotten or solid wood. The cells (the *Allocladapini* make no cells) are un-

lined or the secreted lining is weak and scarcely detectable, except in the ground-nesting *X.* (*Proxylocopa*). Provisions (except for the progressive feeders, the *Allocladapini*) are loaf-shaped, firm, rather dry pollen masses, often partly separated from the cell walls, being supported in part by the egg (Figs. 89-3; 90-5a). There is a tendency toward social behavior, two or more adults being frequently found in nests (Michener, 1990b). Although one to several young adults commonly are present in a nest with the old mother, only a minority of nests in most species contain two or more older bees, with division of labor and eusocial or semisocial relationships. Some storage of food for adult consumption, a practice found in no other bees except the corbiculate Apinae, is common in the Xylocopinae. The view that Xylocopinae is the sister group to the corbiculate Apinae, as indicated by Sakagami and Michener (1987), was strengthened by this attribute (food storage for adult consumption), but is no longer a tenable idea, as shown by Roig-Alsina and Michener (1993).

The relationships among the four tribes of Xylocopinae were dealt with by Sakagami and Michener (1987), Roig-Alsina and Michener (1993), and Engel (2001b). Roig-Alsina and Michener, in a separate analysis of Xylocopinae, derived two minimum-length cladograms differing in the positions of *Manuelia* and *Xylocopa*. In agreement with Sakagami and Michener, one of the cladograms showed *Manuelia* as the first branch, *Xylocopa* next. The other reversed these positions. It seems likely that *Manuelia* is the sister group to all the others because of its less reduced and presumably plesiomorphic S7 and S8 of the male (Fig. 87-1b, c). If the ground-nesting behavior and associated structures of *Xylocopa* (*Proxylocopa*) were plesiomorphic, as advocated by Malyshev (1913) and Hurd (1958b), the basal position of *Xylocopa* rather than *Manuelia* would be probable, but it seems likely that in *Proxylocopa* these are not ancestral features. This matter is discussed in more detail in Section 88, on the Xylocopini.

Engel (2001b) proposed the tribe Boreallodapini for the three Eocene Baltic amber species of *Boreallodape*. This appears to be the sister group of the Recent *Allocladapini*, from which it differs most conspicuously by having an ordinary shaped clypeus with the lateral margins concave so that it is much narrower above the tentorial pits than below.

A key to the Recent tribes of Xylocopinae is incorporated into the key to tribes of the Apidae in Section 85; a separate key to the xylocopine tribes nevertheless may be useful.

Key to the Tribes of the Xylocopinae (Modified from Sakagami and Michener, 1987)

1. Stigma virtually absent (Fig. 88-2a); wings distally strongly papillate; flagellar segment 1 as long as or longer than 2 and 3 taken together; arolia absent; robust forms usually more than 13 mm long Xylocopini (Sec. 88)

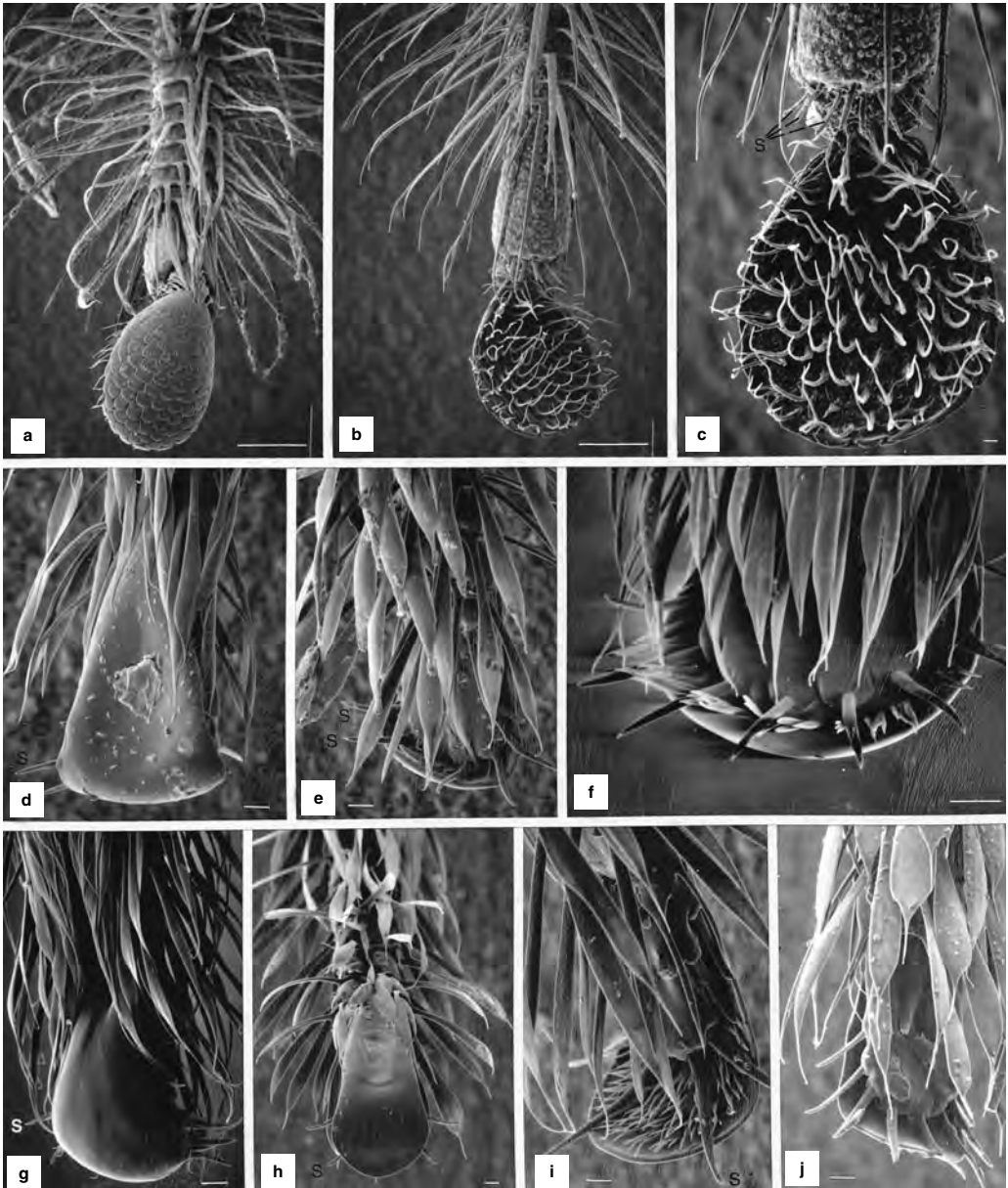


Figure 86-1. SEM photos of apices of glossae of Xylocopinae. **a-c**, *Xylocopa augusti* Lepeletier, posterolateral view and two anterior views; **d, e**, *Ceratina neomexicana* Cockerell, posterior and anterior views; **f, g**, *Manuelia gayi* (Spinola), anterior and posterior views; **h, i**, *Allodape ceratinoides* Gribodo, posterior and anterior

views; **j**, *Macrogalea candida* (Smith), anterior view.

(For a and b, Scale lines = 0.1 mm; for c-j, 0.01 mm; S indicates seta.) SEM photos by R. W. Brooks, from Michener and Brooks, 1984.

— Stigma large (Figs. 28-4, 89-4, 90-11a-c, 90-13) or at least recognizable (smallest in *Megaceratina* and *Macrogalea*, Fig. 90-12); wings distally pubescent but not papillate; flagellar segment 1 shorter than 2 and 3 taken together; arolia present; usually slender forms, usually less than 12 mm long 2
2(1). Submarginal cells two (Figs. 28-4, 89-4, 90-11a-c, 90-13) (or only one in *Eucondylops reducta* Michener);

clypeus above tentorial pits not greatly narrower than below (Fig. 90-2); apical metasomal terga of female depressed (Eastern Hemisphere) Allodapini (Sec. 90)
— Submarginal cells three (Fig. 89-4); clypeus above tentorial pits much narrower than below; apical metasomal terga strongly convex, not depressed 3
3(2). S8 of male simple, without apical process (Fig. 89-5c); male gonostylus [except in *Ceratina* (*Euceratina*)] short,

- more or less fused with gonocoxite (Fig. 89-5a, b); female labrum without basal elevated area; pygidial plate absent (Fig. 89-2)

Ceratinini (Sec. 89)
- . S8 of male robust, with distinct apical process (Fig. 87-1b); male gonostylus several times as long as broad, not fused with gonocoxite (Fig. 87-1a); female labrum with basal smooth elevated area; T6 of female with apical spine, flat or concave on dorsal surface, that may represent pygidial plate (South America)

Manueliini (Sec. 87)

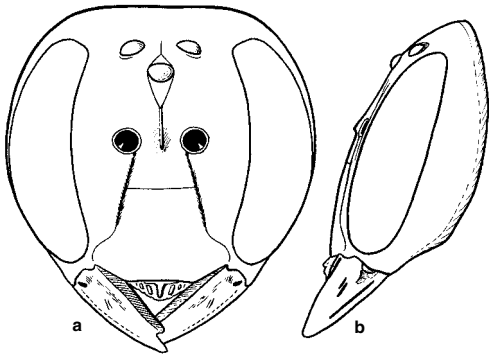


Figure 88-5. Head of *Xylocopa tabaniformis orpifex* Smith, female. **a**, Frontal view; **b**, Lateral view, showing the flat clypeus. See also Figure 21- 3. From Michener, 1944.

Western Hemisphere to certain Pacific islands that lie in the Eastern Hemisphere.

Much of this account of *Xylocopa* is based on Minckley (1998) and Hurd and Moure (1963). Minckley's phylogenetic analysis has been useful in indicating that various small or monotypic subgenera of Hurd and Moure are based on unusual species that, on the basis of other characters, fit into larger subgenera. One result is a key (modified from Hurd and Moure, 1963) in which several subgenera come out in two or more places. Revisional studies of *Xylocopa* include the following: Hurd and Moure, 1963, for the world; Eardley, 1983, for southern Africa; Leys, 2000, for Australia; Ma, 1938, for India; Maa, 1954, for Afghanistan; Lieftinck, 1955, for the Lesser Sunda Islands and Tanimbar; Lieftinck, 1956b, for the Moluccas; Vecht, 1953, for Sulawesi (Celebes); Brèthes, 1916, for Argentina; Ackerman, 1916, for the USA; and Hurd, 1955, for California. Wu (1982c) gave a key to Chinese species. Pérez (1901) and Maidl (1912) made contributions toward a monograph of *Xylocopa*. Hurd (1978a) provided a detailed catalogue of subgenera and species of the Western Hemisphere, Ospina (2000) presented a list of the neotropical species, and Eardley (1987) published a catalogue for sub-Saharan Africa.

Key to the Subgenera of *Xylocopa* of the Western Hemisphere (Males)

(Modified from Hurd and Moure, 1963)

(Males are unknown for the subgenera *Monoxylocopa* and *Diaxylocopa*.)

1. Clypeus black, or, if with pale area, then (1) vertex in frontal view at most only scarcely raised above level of eye summits, usually at or below this level; (2) apex of scape not or scarcely surpassing level of eye summits unless T1 to T4 integument maculated with yellowish white; (3) occipitocular distance nonexistent or much shorter than first flagellar segment; and (4) eyes frequently enlarged and often markedly convergent above 2
- Clypeus invariably maculated with pale coloration and with (1) vertex in frontal view strongly elevated above level of eye summits; (2) apex of scape much surpassing level of eye summits; (3) occipitocular distance longer than first flagellar segment; and (4) eyes always small, never strongly convergent above 10

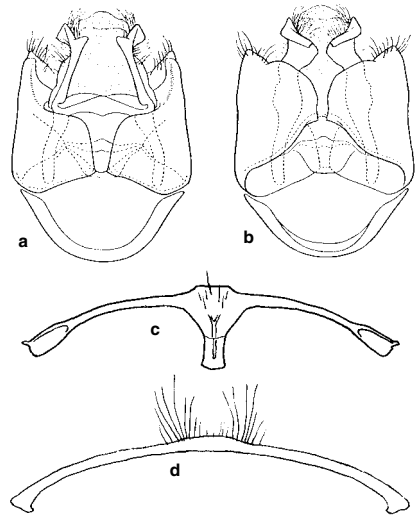


Figure 88-6. Structures of male *Xylocopa virginica* (Linnaeus). **a**, **b**, Dorsal and ventral views of genitalia; **c**, **d**, S8 and S7. **a** and **b**, from Hurd and Moure, 1963.

- 2(1). Tegula punctate throughout or thickly pubescent circummarginally 3
- Tegula impunctate, glabrous and shining on at least posterolateral third 4
- 3(2). T1 to T4 integument broadly banded with yellowish white; interantennal distance shorter than interocellar distance; subantennal suture longer than interantennal distance; scape surpassing upper eye margins; posterolateral margin of tegula thickly pubescent; apical margin of S1 entire *X. (Schonnherria)* (in part)
- Metasomal tergal integument entirely black; interantennal distance longer than interocellar distance; subantennal suture much shorter than interantennal distance; scape not surpassing upper eye margins; posterolateral margin of tegula not pubescent; apical margin of S1 deeply emarginate medially (South America) *X. (Nanoxycopa)*
- 4(2). Scutellum flat, not convex in profile, exposed on same subhorizontal plane as median portion of metanotum and anterodorsal margin of propodeum; propodeum more or less horizontal anterodorsally before declivous posterior surface 5
- Scutellum convex in profile, well above metanotal and propodeal levels, and median portion of metanotum steeply inclined; propodeum declivous, not horizontal along anterodorsal margin 6
- 5(4). Hind tibia with high, thin lamella beneath, beginning near base of inner hind tibial spur and extending obliquely forward across ventral surface of tibia; inner distal end of hind tibia not modified (South America) *X. (Xylocopoda)*
- Hind tibia without lamella beneath and without inner hind tibial spur; inner distal end of hind tibia bearing an enlarged, flattened, highly polished tubercle (South America) *X. (Cirroxylocopa)*
- 6(4). Outer distal end of hind tibia with two denticles or spines 7

- Outer distal end of hind tibia with one denticle or spine 8
- 7(6). T7 armed with two well-separated, posterolateral, dentiform projections; antennal sockets closer to upper clypeal margin than to anterior margin of median ocellus *X. (Notoxylocopa)*
- T7 without posterolateral, dentiform projections; antennal sockets nearly midway between upper clypeal margin and anterior margin of median ocellus (North and Central America) *X. (Xylocopoides)* (in part)
- 8(6). Triangular area of propodeum well developed, broadly transverse, its surface nonmetallic; anterior half of T3 broadly depressed on each side of basally carinate median line, anterior margin of each depression bearing a transverse row of very long, posteriorly directed plumose hairs that overlie the depression (North and Central America) (*Calloxylocopa* group) *X. (Xylocopoides)* (in part)
- Triangular area of propodeum not recognizable; T3 normal, not modified as above 9
- 9(8). T3 to T5 with graduli deeply incised, medially interrupted, and near anterior tergal borders; integument weakly metallic (South America) *X. (Xylocopsis)*
- Metasomal terga without graduli; integument frequently brilliantly metallic *X. (Schonherria)* (in part)
- 10(1). Mandible, as seen from side, expanded at apex, its lower apical tooth markedly projected or expanded below lower mandibular margin 11
- Mandible, as seen from side, not expanded at apex, its lower apical tooth not projected or expanded below lower mandibular margin 12
- 11(10). Body integument extensively ferruginous or yellowish, richly clothed with ferruginous or fulvous pubescence; tegula ferruginous; scape entirely ferruginous or with longitudinal yellow frontal stripe *X. (Neoxylocopa)*
- Body integument chiefly black at least on dorsal surface, with predominantly blackish, whitish, or griseous pubescence; tegula black; scape largely or entirely black, without longitudinal frontal stripe *X. (Stenoxycopa)* (in part)
- 12(10). Upper lateral margin of clypeus abruptly and steeply elevated above adjacent paraocular area; tegula transversely expanded, posterolateral margin greatly thickened in contrast with anterolateral margin (*Xylocopina* group) *X. (Stenoxycopa)* (in part)
- Upper lateral margin of clypeus scarcely raised, rounded, not abruptly and steeply elevated above adjacent paraocular area; tegula normal, not transversely expanded or modified as above 13
- 13(12). Propodeum steeply inclined, almost without a basal horizontal surface; hind basitarsus longer than tibia (South America) *X. (Dasxylocopa)*
- Propodeum broadly arched and greatly exposed anterodorsally, thus subhorizontal basally; hind basitarsus shorter than tibia *X. (Schonherria)* (in part)

Key to the Subgenera of *Xylocopa* of the Western Hemisphere (Females)

(Modified from Hurd and Moure, 1963)

- 1. Pygidial spine armed on each side with subapical spine preceded anteriorly by strongly divergent row of spine-like teeth (Fig. 88-3d), the two rows outlining broad py-

- gidial area on disc of T6; basitibial plates usually markedly excavated subapically (Fig. 88-3b) (North and Central America) *X. (Xylocopoides)*
- Pygidial spine simple or armed on each side with a single subapical spine (Fig. 88-3e, f), without rows of teeth or other indication on disc of T6; basitibial plates at most only weakly excavated subapically 2
- 2(1). Head with greatly elevated ridges or prominences adjacent to ocelli; posterior margin of posterior ocellus above level of eye summits; clypeus separated from eye by more than minimum diameter of first flagellar segment; anterolateral corners of clypeus strongly protuberant (*Megaxylocopa* group) *X. (Neoxylocopa)* (in part)
- Head without greatly elevated ridges or prominences adjacent to ocelli; posterior margin of posterior ocellus below level of eye summits; clypeus separated from eye by much less than minimum diameter of first flagellar segment; anterolateral corners of clypeus flat, not protuberant 3
- 3(2). Lower tooth of mandible much narrower than upper tooth or teeth, as measured across mandible at level of apex of notch(es) between teeth *X. (Stenoxycopa)*
- Lower tooth of mandible at least equal to, usually much wider than, upper tooth or teeth, as measured across mandible at level of apex of notch(es) between teeth 4
- 4(3). Longitudinal midventral carina of metasoma strongly developed, raised above integumental surface as high, sharply carinate ridge; dorsolateral margin of clypeus strongly raised above adjacent paraocular area, separated from clypeal punctation by prominent, subcarinate polished ridge that extends upward on each side of clypeus, and curves mesad to join its fellow beneath transverse section of epistomal suture; apical margin of S1 entire (*Neoxylocopa* group) *X. (Neoxylocopa)* (in part)
- Longitudinal midventral carina of metasoma absent, or, if present, then not raised above integumental surface as high, sharply carinate ridge and not evident on all sterna; dorsolateral margin of clypeus on same level as adjacent paraocular area, or, if elevated, then rounded and not modified as above, ridge following upper clypeal margin discontinuous or absent; apical margin of S1 usually indented or incurved medially 5
- 5(4). Eyes more convergent above than below; body integument often brilliantly metallic 6
- Eyes equally convergent above and below or, usually, more convergent below than above; body integument at most feebly metallic as seen in bright light 9
- 6(5). Propodeal triangle absent; antennocular distance less than interantennal distance *X. (Notoxylocopa)*
- Propodeal triangle present, well differentiated, and margined; antennocular distance equal to or more than interantennal distance 7
- 7(6). Flagellum at most approximately as long as maximum length of eye; T2 to T6 without graduli; body integument brightly metallic *X. (Schonherria)* (in part)
- Flagellum much exceeding maximum length of eye; T3 and T4 each with gradulus; body integument feebly metallic as seen in bright light 8
- 8(7). Labrum with five tubercles or multituberculate; clypeus much less than half as long as broad; dorsum of metasoma clothed with very short hairs, not shaggy in appearance (South America) *X. (Xylocopsis)*

- Labrum with three tubercles; clypeus about half as long as broad; dorsum of metasoma clothed with very long hairs, decidedly shaggy in appearance (South America) *X. (Dasxylocopa)*
- 9(5). Clypeus less than half as long as broad; median clypeal length shorter than clypeocellar distance; gradulus of T1 not continued posteriorly near lateral margin of tergum 10
- Clypeus at least half as long as broad; median clypeal length longer than clypeocellar distance; gradulus of T1 continued posteriorly near lateral margin of tergum 13
- 10(9). Parapsidal line less than half as long as first flagellar segment; subantennal sutures parallel or diverging above, meeting antennal sockets at their lower margins 11
- Parapsidal line more than half as long as first flagellar segment; subantennal sutures converging above, meeting antennal sockets near their inner margins 12
- 11(10). Apex of basitibial plate strongly asymmetrical, dentiform anteriorly, lobate posteriorly; subantennal sutures parallel, nearly as long as interantennal distance; upper portion of gena broadly glabrous and pruinose, very sparsely punctate; scutum broadly impunctate medially, punctuation adjacent to parapsidal line sparse *X. (Schonnherria)* (in part)
- Apex of basitibial plate nearly symmetrical, produced into two dentiform processes; subantennal sutures divergent above, much shorter than interantennal distance; upper portion of gena narrowly impunctate, hirsute, without a pruinose bloom; scutum narrowly impunctate medially, punctuation adjacent to parapsidal line dense, nearly confluent (South America) *X. (Xylocopoda)*
- 12(10). Mandible tridentate apically, with prominent preapical internal tooth on upper margin; clypeus conspicuously depressed transversely near apical margin, depression emphasized by bulging upper portion of clypeus (Brazil) *X. (Diasxylocopa)*
- Mandible bidentate apically, without preapical internal tooth on upper margin; clypeus flat, neither transversely depressed subapically nor bulging above (Brazil) *X. (Monoxylocopa)*
- 13(9). Frontal carina short, transverse, tuberculiform, not extending between antennal sockets, lower end considerably closer to anterior ocellus than to upper margin of clypeus; metasomal tergal discs sparsely pubescent; outer apex of hind tibia with two dentiform processes, i.e., tibial spines (South America) *X. (Nanoxylcopa)*
- Frontal carina elongate, longitudinal, cariniform, extending between antennal sockets, lower end considerably closer to upper margin of clypeus than to anterior ocellus; metasomal tergal discs densely hirsute; outer apex of hind tibia with single dentiform process, i.e., tibial spine (South America) *X. (Cirraxylcopa)*
- T1 with subhorizontal dorsal surface abruptly and angularly separated from declivous anterior surface or at least subangularly rounded (*Alloxylocopa*) into that surface; gradulus of T1 transverse, lateral extremities not or scarcely directed posteriorly 18
- 2(1). Parapsidal line short, at most three times as long as broad, situated anterior to posterior end of median scutal line (palearctic) *X. (Proxylocopa)*
- Parapsidal line usually elongate-linear, but if short, then situated well behind posterior end of median scutal line .. 3
- 3(2). First and second submarginal crossveins nearly parallel; undersurface of flagellum crenulate; maxillary palpus four-segmented (Australia) *X. (Lestis)*
- First submarginal crossvein strongly slanting, second submarginal cell thus more than twice as long on posterior margin as on anterior margin; undersurface of flagellum not crenulate; maxillary palpus six-segmented or apparently five-segmented 4
- 4(3). Antennocular distance approximately equal to, or usually much less than, length of subantennal suture; ocellular distance less than length of subantennal suture 5
- Antennocular distance nearly two or more times length of subantennal suture; ocellular distance much greater than length of subantennal suture 13
- 5(4). Apex of basitibial plate strongly bifid; first flagellar segment at most scarcely longer than combined lengths of succeeding two segments 6
- Apex of basitibial plate entire; first flagellar segment considerably longer than combined lengths of succeeding two segments 7
- 6(5). Posterior lobe of pronotum prolonged posteriorly well onto mesepisternum; spiracle of T3 with an elevated scale-like process near its mesal border; ocelli normal, not globose; ocelloccipital distance greater than occipitocular distance (Africa, Asia) *X. (Ctenoxylocopa)*
- Posterior lobe of pronotum not prolonged posteriorly onto mesepisternum; spiracle of T3 without elevated, scale-like process; ocelli greatly enlarged, globose; ocelloccipital distance equal to or shorter than occipitocular distance (oriental) *X. (Nyctomelitta)*
- 7(5). Eyes enlarged, maximum width of eye in frontal view equal to or usually greater than minimum upper interocular distance; face narrow, minimum upper interocular distance shorter than length of antennal scape 8
- Eyes small, maximum width of eye in frontal view considerably less than minimum upper interocular distance; face broad, minimum upper interocular distance equal to or greater than length of antennal scape 12
- 8(7). Outer apex of hind tibia with two teeth (tibial spines); subantennal suture longer than interantennal distance; apical margin of labrum entire 9
- Outer apex of hind tibia with one tooth; subantennal suture shorter than interantennal distance; apical margin of labrum emarginate 10
- 9(8). Face narrowest at middle; inner orbit convex, bowed toward antennal socket; frontal line sulciform, not elevated at lower end; apex of scape much surpassing upper eye margin; scutellum modified, dorsal surface rounding into vertical posterior surface (Madagascar) *X. (Prosopoxylcopa)*
- Face narrowest near eye summits; inner orbit concave, curved toward central eye axis; frontal line cariniform, el-

Key to the Subgenera of *Xylocopa* of the Eastern Hemisphere (Males)

(Modified from Hurd and Moure, 1963)

(The subgenus *Neoxylocopa* has been introduced into some Pacific islands, such as the Marianas, that lie in the Eastern Hemisphere; it is not included in this key.)

1. T1 with subhorizontal dorsal surface sloping or rounding into declivous anterior surface; gradulus of T1 curved posteriorly at side, becoming more or less longitudinal at lateral extremity 2

- evated at lower end above supraclypeal integument; apex of scape not surpassing upper eye margin; scutellum unmodified, convex in profile (eastern Asia) *X. (Bomboixylocopa)* (in part)
- 10(8). Disc of scutum punctate throughout; antennal sockets about midway between upper margin of clypeus and anterior margin of median ocellus; tegula punctate nearly throughout, marginally thickly pubescent; ocelli without adjacent swellings or ridges (oriental) *X. (Zonohirsuta)*
- Disc of scutum narrowly impunctate medially; antennal sockets very close to upper margin of clypeus; tegula with posterolateral third impunctate, glabrous and shining; lateral ocellus usually bounded below by conspicuous transverse ridge (oriental, palearctic) 11
- 11(10). Thoracic declivity beginning as abrupt although narrowly rounded angle in scutellar profile *X. (Maaiana)*
- Beginning of thoracic declivity not defined, scutellum evenly rounded in profile *X. (Nodula)*
- 12(7). Clypeus black; propodeal spiracle asymmetrical, complex, lower extremity broadened, anterior margin limited by deeply impressed line forming elongate triangular flap with lower anterior margin projecting strongly forward; outer apex of hind tibia with acute tooth (palearctic) *X. (Rhysoxylocopa)*
- Clypeus blackish, stained with ferruginous; propodeal spiracle simple, not modified as above; outer apex of hind tibia unarmed (Africa) *X. (Xylomelissa)* (in part)
- 13(4). Outer apex of hind tibia with at least one tooth; punctuation of supraclypeal area and upper margin of clypeus so strong as to obscure or virtually obliterate transverse section of epistomal suture 14
- Outer apex of hind tibia unarmed; punctuation of supraclypeal area and upper margin of clypeus at most only moderate, not obscuring transverse section of epistomal suture 17
- 14(13). Outer apex of hind tibia with two teeth; posterior margin of metanotum straight, not angulately lengthened medially; median length of metanotum less than combined lengths of second and third flagellar segments; apex of gonocoxite simple 15
- Outer apex of hind tibia with one tooth; posterior margin of metanotum angulately lengthened medially; median length of metanotum greater than combined lengths of second and third flagellar segments; apex of gonocoxite complex 16
- 15(14). Clypeus black; scutum narrowly impunctate medially; subantennal suture much shorter than interantennal distance; malar area short, linear; propodeum entirely declivous; interantennal distance less than interocellar distance (palearctic) *X. (Xylocopa s. str.)*
- Clypeus blackish, maculated with yellow; scutum punctate throughout; subantennal suture longer than interantennal distance; malar area long, minimum length equal to length of second flagellar segment; propodeum subhorizontal along upper margin; interantennal distance greater than interocellar distance (eastern Asia) *X. (Bomboixylocopa)* (in part)
- 16(14). Apex of basitibial plate bifid; tegula punctate nearly throughout and marginally thickly pubescent; clypeus long, median length greater than clypeoocellar distance; apex of scape much surpassing summit of eye; disc of scutum punctate throughout (Africa) *X. (Gnathoxylocopa)*
- Apex of basitibial plate simple; tegula with posterolateral third impunctate, glabrous and shining; clypeus short, median length less than clypeoocellar distance; apex of scape not or very slightly surpassing eye summit; disc of scutum narrowly impunctate medially (palearctic) *X. (Copoxyla)*
- 17(13). Basitibial plate present; anterior ocellus not bordered laterally by impunctate, crescent-shaped swellings; outer apex of middle tibia with acute tooth (Africa) *X. (Xylomelissa)* (in part)
- Basitibial plate absent; anterior ocellus bounded on each side by impunctate, crescent-shaped swelling; outer apex of middle tibia rounded, without tooth (oriental) *X. (Biluna)*
- 18(1). Eyes enlarged, maximum width of eye in frontal view equal to or usually greater than minimum upper interocular distance; face narrow, minimum upper interocular distance less than length of scape; apex of scape not surpassing eye summit; occipitocular distance short or nonexistent, at most scarcely longer than second flagellar segment 19
- Eyes small, maximum width of eye in frontal view much less than minimum upper interocular distance; face broad, minimum upper interocular distance greater than length of scape; apex of scape much surpassing eye summit; occipitocular distance about as great as or greater than length of first flagellar segment 23
- 19(18). Ocelli high on face, ocelloccipital distance equal to or less than ocellar diameter *X. (Koptortosoma)* (in part)
- Ocelli low on face, ocelloccipital distance considerably greater than ocellar diameter 20
- 20(19). Posterior trochanter with inner apex produced into long spine; scutellum on approximately same subhorizontal plane as metanotum; scutellar profile not angled, thus not divided into horizontal and vertical surfaces 21
- Posterior trochanter not produced into a long spine; scutellum conspicuously above metanotum, its profile angled posteriorly and thus divided into a long horizontal surface and a short vertical surface; surface of metanotum vertical 22
- 21(20). Metasomal terga brilliantly metallic, without gradulus on T3; clypeus black, densely punctate; punctuation on supraclypeal area and upper part of clypeus so strong as to obscure or virtually obliterate transverse section of epistomal suture; middle trochanter with inner apex produced as acute spine *X. (Koptortosoma)* (in part)
- Metasomal terga dull, scarcely metallic, with widely interrupted gradulus on T3; clypeus blackish, maculated with yellow, sparsely to moderately punctate; punctuation of supraclypeal area and upper part of clypeus sparse, not obscuring transverse section of epistomal suture; middle trochanter unarmed (Africa, oriental) *X. (Mesotrichia)* (in part)
- 22(20). Tegula elongate, posterolateral third impunctate, glabrous, and shining; tarsi of middle and hind legs greatly flattened, expanded, and maculated (Africa, oriental) *X. (Mesotrichia)* (in part)
- Tegula normal, rounded behind, punctate throughout,

- thickly pubescent marginally; tarsi of all legs normal, not modified as above (oriental) *X. (Alloxylocopa)*
- 23(18). Face less broad, maximum interocular distance less than eye length; paraocular area not modified as below *X. (Koptortosoma)* (in part)
- Face very broad, maximum interocular distance greater than eye length; paraocular area strongly elevated along inner eye margin, forming groove adjacent to inner orbit that continues for a short distance around summit of eye 24
- 24(23). Face black; mandible edentate at apex; labrum trapezoidal in outline, much longer than clypeus; metanotum obliquely inclined, shortened medially; tegula with posterolateral third impunctate, glabrous, and shining; interantennal distance greater than interocellar distance (Africa, oriental) *X. (Mesotrichia)* (in part)
- Face blackish, maculated with yellow; mandible bidentate at apex; labrum transverse, much shorter than clypeus; metanotum subhorizontal, lengthened medially; tegula punctate nearly throughout, thickly pubescent marginally; interantennal distance less than interocellar distance (Africa) *X. (Xenoxyclopa)*

Key to the Subgenera of *Xylocopa* of the Eastern Hemisphere (Females)

(Modified from Hurd and Moure, 1963)

1. Pygidial plate or spine armed on each side with subapical spine 2
- Pygidial plate or spine unarmed 17
- 2(1). Outer apex of hind tibia rounded or armed with single tooth or spiniform process 3
- Outer apex of hind tibia armed with two teeth or two spiniform processes 12
- 3(2). Ocelli with adjacent cariniform ridges or anterior ocellus bounded on either side by an impunctate, crescent-shaped swelling, but if occasionally cariniform ridges vestigial or absent (some species of subgenus *Nodula*), then ventral surface of hind femur impunctate, glabrous, and highly polished 4
- Ocelli without adjacent cariniform ridges; anterior ocellus without lateral impunctate crescent-shaped swellings; ventral surface of hind femur not as above 11
- 4(3). Mandible tridentate at apex; rear basal angle of mandible behind posterior margin of eye 5
- Mandible bidentate at apex; rear basal angle of mandible before posterior margin of eye 6
- 5(4). Malar area short, minimum length much less than length of pedicel; clypeus less than half as long as broad, median length less than clypeocellar distance (upper clypeal margin to median ocellus); clypeocular distance less than minimum diameter of first flagellar segment; first flagellar segment at most about as long as next two segments taken together; triangular area of propodeum present (Africa, Asia) *X. (Ctenoxyclopa)*
- Malar area long, minimum length greater than length of pedicel; clypeus longer, more than half as long as broad, median length longer than clypeocellar distance; clypeocular distance greater than minimum diameter of first flagellar segment; first flagellar segment about as long as or longer than next three segments taken together; triangular area of propodeum absent (Africa) *X. (Xylomelissa)* (in part)
- 6(4). Apex of basitibial plate entire, much before middle of tibia; outer apex of middle tibia unarmed, with cushion of short, densely compacted, bristle-like hairs; anterior ocellus bounded on each side by impunctate, crescent-shaped swelling (oriental) *X. (Biluna)*
- Apex of basitibial plate bifid, well beyond middle of tibia; outer apex of middle tibia with tooth or spiniform process; anterior ocellus not bounded laterally by impunctate, crescent-shaped swellings 7
- 7(6). Scutellum convex in profile, not divided into dorsal and posterior surfaces 8
- Scutellum angulate or subangulate in profile, divided into a subhorizontal dorsal surface and a vertical posterior surface (oriental, palearctic) 10
- 8(7). Punctuation adjacent to mesal border of spiracle of T4 very fine and dense, markedly differentiated from punctuation elsewhere on that tergum (Africa) *X. (Xylomelissa)* (in part)
- Punctuation adjacent to mesal border of spiracle of T4 not markedly differentiated from punctuation elsewhere on that tergum 9
- 9(8). Discal hairs of T1 simple or sparsely plumose; first flagellar segment shorter than combined lengths of next three segments; median longitudinal groove of propodeum complete, clearly impressed (Africa) *X. (Xylomelissa)* (in part)
- Discal hairs of T1 thickly plumose; first flagellar segment equal to or longer than combined lengths of next three segments; median longitudinal groove of propodeum indistinct, virtually obliterated (palearctic) *X. (Rhysoxyclopa)*
- 10(7). Scutellum, in profile forming rounded projection, overhanging entire metanotum *X. (Nodula)*
- Scutellum not bulging over metanotum *X. (Maaiana)*
- 11(3). Mandible bidentate at apex, lower inferior surface not modified as below; ocelli greatly enlarged, globose; eyes more convergent above than below; maximum interocular distance less than eye length; antennal sockets approximately midway between upper margin of clypeus and anterior tangent of median ocellus; disc of scutum narrowly impunctate medially; body integument chiefly reddish brown (oriental) *X. (Nyctomelitta)*
- Mandible tridentate at apex, lower surface bearing a long, stout, curved hook; ocelli normal, not globose; eyes more convergent below than above; maximum interocular distance greater than eye length; antennal sockets below midpoint between upper margin of clypeus and anterior tangent of median ocellus; disc of scutum punctate throughout; body integument chiefly black (Africa) *X. (Gnathoxyclopa)*
- 12(2). Scutellum convex in profile, not divided into subhorizontal dorsal surface and subvertical posterior surface; apical margin of S1 emarginate medially; dorsolateral margin of clypeus and side of supraclypeal area not or at most scarcely raised above adjacent paraocular area 13
- Scutellum subangulate or angulate in profile, divided into subhorizontal dorsal surface and subvertical posterior surface; apical margin of S1 entire, not emarginate medially; dorsolateral margin of clypeus and lateral side of supraclypeal area conspicuously raised above adjacent paraocular area 15

- 13(12). Malar area long, minimum length half as long as first flagellar segment; clypeocular distance greater than minimum diameter of first flagellar segment; median length of clypeus shorter than clypeocellar distance; triangular area of propodeum absent; vertical fold of T1 narrowly and deeply sulcate (eastern Asia) *X. (Bomboixylocopa)* (in part)
- Malar area short, minimum length much less than half as long as first flagellar segment; clypeocular distance less than minimum diameter of first flagellar segment; median length of clypeus longer than clypeocellar distance; triangular area of propodeum present; vertical fold of T1 linear, shallowly impressed 14
- 14(13). Mandible bidentate at apex; apex of basitibial plate before middle of tibia; maximum interocular distance less than length of eye (Africa) *X. (Xylomelissa)* (in part)
- Mandible tridentate at apex; apex of basitibial plate well beyond middle of tibia; maximum interocular distance greater than length of eye (palearctic) *X. (Xylocopa s. str.)*
- 15(12). Rear basal angle of mandible slightly behind posterior margin of eye; apex of basitibial plate considerably before middle of tibia; vertical fold of T1 broadly and deeply sulcate; gradulus of T1 virtually coincident with anteroventral margin of metasoma, not continued posteriorly adjacent to lateral margin of T1 (Africa) *X. (Xenoxyllocopa)*
- Rear basal angle of mandible before posterior margin of eye; apex of basitibial plate beyond middle of tibia; vertical fold of T1 linear, shallowly impressed; gradulus of T1 obliquely curved away from anteroventral margin of metasoma and continued posteriorly adjacent to lateral margin of T1 16
- 16(15). Subantennal suture longer than interantennal distance; disc of scutum narrowly impunctate medially; apex of basitibial plate simple; supraclypeal area strongly swollen, bigibbose; antennal sockets slightly above midpoint between upper margin of clypeus and anterior tangent of median ocellus (Madagascar) *X. (Prosopoxyllocopa)*
- Subantennal suture conspicuously shorter than interantennal distance; disc of scutum punctate virtually throughout; apex of basitibial plate feebly bifid; supraclypeal area only moderately elevated, not swollen or bigibbose; antennal sockets below midpoint between upper margin of clypeus and anterior tangent of median ocellus (oriental) *X. (Zonohirsuta)*
- 17(1). Scutellum convex in profile, not divided into a subhorizontal dorsal surface and a subvertical posterior surface; vertical fold of T1 sometimes inconspicuous, without a foveate depression or an invaginated orifice 18
- Scutellum with subhorizontal dorsal surface rounding into or abruptly and angulately separated from subvertical posterior surface; vertical fold of T1 with a foveate depression or an invaginated orifice at or near its summit 21
- 18(17). Pygidial plate raised above surface of T6 and extending basad across that surface, its margins entire; basitibial plate with apex at or before basal fourth of tibia, its apex not a raised scale; parapsidal line at most three times as long as broad, anterior to end of median scutal line (palearctic) *X. (Proxyllocopa)*
- Pygidial plate dorsally flat or concave apical spine, sometimes hidden among hairs; basitibial plate with apex

- beyond basal one-fourth of tibia, commonly elevated as a scale; parapsidal line usually elongate-linear, but *if* short, then behind posterior end of medial scutal line.... 19
- 19(18). Paraocular area below antenna with strong protuberance; first and second submarginal crossveins almost parallel; maxillary palpus four-segmented (Australia) *X. (Lestis)*
- Paraocular area without protuberance; first submarginal crossvein strongly slanting, second submarginal cell thus more than twice as long on posterior margin as on anterior margin; maxillary palpus six-segmented or apparently five-segmented 20
- 20(19). Mandible bidentate at apex; metasomal terga at most only faintly metallic in bright light; malar area with minimum length half as long as first flagellar segment or more; outer apex of hind tibia with two teeth; apex of scape much surpassing summit of eye (eastern Asia) *X. (Bomboixylocopa)* (in part)
- Mandible tridentate at apex; metasomal terga brilliantly metallic; malar area with minimum length considerably less than half length of first flagellar segment; outer apex of hind tibia with one tooth; apex of scape not surpassing summit of eye (palearctic) *X. (Copoxyla)*
- 21(17). Posterodorsal margin of scutellum projecting beyond posterior margin of metanotum *X. (Koptortosoma)*
- Posterodorsal margin of scutellum not surpassing posterior margin of metanotum 22
- 22(21). Posterodorsal margin of scutellum not acutely angled in profile and not projecting posteriorly beyond posterior surface of scutellum as a thin-edged flange; T1 without an invaginated chamber and hence without an opening on anterior surface (oriental) *X. (Alloxylocopa)*
- Posterodorsal margin of scutellum in profile sharply and acutely angled, projecting posteriorly beyond posterior surface of scutellum as a thin-edged flange; T1 with an invaginated chamber opening at or near summit of vertical fold on anterior surface (Africa, oriental) *X. (Mesotrichia)*

Xylocopa / Subgenus *Alloxylocopa* Hurd and Moure

Xylocopa (*Alloxylocopa*) Maa, 1939: 155. Nomen nudum because no characters given, although a type species was designated; see ICZN, 3rd ed., art. 13(a)(i).

Xylocopa (*Alloxylocopa*) Hurd and Moure, 1963: 239. Type species: *Xylocopa appendiculata* Smith, 1852, by original designation.

Alloxylocopa resembles *Xenoxyllocopa*, but the female lacks the lateral spine at the base of the pygidial spine and the male is dark-colored with a fovea on the anterior surface of T1.

■ This subgenus is found from Japan and China south to Sumatra. Hurd and Moure (1963) listed six species.

Xylocopa / Subgenus *Biluna* Ma

Xylocopa (*Biluna*) Ma, 1938: 276. Type species: *Xylocopa nasalis* Westwood, 1842, by original designation.

This is a group of rather large species with elongate bodies that nest, so far as is known, only in stems of bamboo. According to Minckley (1998) it is related to *Xy-*

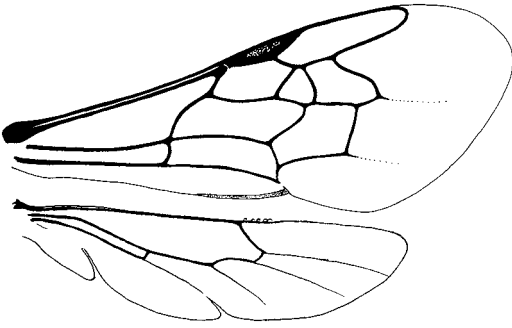


Figure 89-4. Wings of *Ceratina dupla* Say.

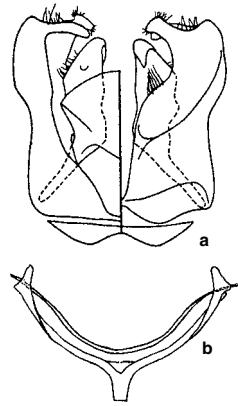


Figure 89-5. Structures of male *Ceratina* (*Zadontomerus*) *calcarata* Robertson.

a, Genitalia, dorsal view at the left; b, S8 (with truncate median spiculum) and S7. These two sterna are in contact, not separated as here shown. a, from Daly, 1973.

that do not fall in any recognized subgenus. An example is *Ceratina laticeps* Friese, which was incorrectly included in *Zadontomerus* by Michener (1954b). In addition, many of the 120 or more names proposed for neotropical species have never been placed to subgenus.

Regional studies of *Ceratina* are as follows: Vecht (1952), oriental species; Yasumatsu and Hirashima (1969), Japan; Hirashima (1971a), southern and eastern Asia and the Pacific; Daly (1983a), North Africa and the Iberian peninsula; Daly (1973), North America north of Mexico; Friese (1896a), the palearctic region; Terzo and Rasmont (2004), Turkestan.

Key to the Subgenera of *Ceratina* of the Eastern Hemisphere

(In part modified from Hirashima, 1971a)

1. Prestigma about as long as distance from base of stigma to vein r; stigma not wider than prestigma, as measured to wing margin; margins of stigma basal to vein r parallel, margin in marginal cell not convex; distal halves of middle and hind femora with sharp, bladelike edges ventrally (Africa) *C. (Megaceratina)*
- Prestigma much shorter than distance from base of stigma to vein r (Fig. 89-4); stigma wider than prestigma, as measured to wing margin (except in large species like *Ceratina chalcites* Germar); margins of stigma basal to vein r convergent basally, margin in marginal cell convex except in largest species; middle and hind femora without sharp ventral edges 2
- 2(1). T2 to T6 without graduli (punctuation very strong; punctures of lower part of paraocular area usually large, as close as they can be, flat-bottomed so that the pattern is a network of ridges; supraclypeal area with transverse carina below antennae; basal area of propodeum not longer than metanotum; notaulus extending nearly to posterior margin of scutum; hind tibia of female with no evidence of basitibial plate) 3
- At least T2 and T3, and sometimes subsequent terga, with graduli 4
- 3(2). Axilla produced to posterior angle separated from scutellum; basal area of propodeum separated from posterior surface by carina; T7 of male rounded or pointed (Africa, oriental) *C. (Pithitis)*
- Axilla not angulate, abutting scutellum; basal area and posterior surface of propodeum not separated by carina; T7 of male bidentate (Africa) *C. (Protopithitis)*
- 4(2). Paraocular area above antennal socket impunctate; body usually with yellow, or yellow and ferruginous, or rarely red, at least paraocular area with yellow marking in both sexes; pregradular areas of metasomal terga often yellow or ferruginous (usually medium-sized to large species) 5
- Paraocular area above antennal socket punctate, at least with a few distinct punctures on space between eye and ocellus or with row of fine punctures along inner margin of eye, or, if this area impunctate, then body small, without pale markings except sometimes on head, pronotal lobe, and legs; paraocular areas without yellow marking in female (except for *Ceratinidia*); pregradular areas of metasomal terga neither yellow nor ferruginous 8
- 5(4). Basal area of propodeum horizontal, sharply separated from posterior surface, which is steeply declivous; antenna of male long, third segment of flagellum longer than broad (apex of T7 of male bluntly tridentate, the median tooth large, triangular; S6 of male with large concavity in middle of subapical portion; head and thorax largely impunctate; dark parts of body slightly to distinctly metallic blue or green (Philippines) *C. (Chloroceratina)*
- Basal area of propodeum usually strongly slanting, not abruptly separated from posterior surface; antenna of male short, third segment of flagellum broader than long 6
- 6(5). Preoccipital carina present, especially strong in male, forming angle between vertex and occiput (vertex impunctate or nearly so; large, robust, black species with more or less rich yellow markings on head, thorax, and metasoma) (oriental) *C. (Catoceratina)*
- Preoccipital carina absent, vertex rounded onto occiput 7
- 7(6). Basitibial plate of female rudimentary; at least median part of clypeus finely coriaceous in female; basal area of propodeum also finely coriaceous, not coarsely sculptured; genitalia of male without bundles of hairs (oriental) *C. (Lioceratina)*
- Basitibial plate of female distinct, although small; clypeus polished, not coriaceous, or rarely finely coriaceous in female as in *Lioceratina*; basal area of propodeum often slightly more coarsely sculptured than in *Lioceratina*; genitalia of male with four bundles of hairs (oriental) *C. (Xanthoceratina)*
- 8(4). Posterior margins of T2 to T5 and S2 to S5 each with

- row of coarse, posteriorly directed setae that are usually thickened, sometimes scalelike, the rows on terga sometimes interrupted middorsally; graduli limited to T2, T3, S2, and S3 and sometimes S6 of male 9
- Terga and sterna without apical rows of specialized setae; graduli present on T2, T3, and usually T4 of female and on T2 to T4 of male, also usually present behind S3 but sometimes weak on S4, etc. 10
- 9(8). Scutellum strongly convex in profile, its posterior part nearly vertical; profile of metanotum and propodeum strongly declivous (Africa) *C. (Simioceratina)*
- Scutellum gently convex, its posterior part and metanotum and propodeum forming a single slope as seen in profile (Africa) *C. (Ctenoceratina)*
- 10(8). T5 with distinct gradulus in both sexes 11
- T5 without gradulus (or with gradulus in male of *Copoceratina* which can be recognized by leg characters listed in couplet 16) 14
- 11(10). Black with yellow markings on head, thorax, metasoma, and legs (frons and vertex densely and rather coarsely punctate; mesopleura densely punctate; medium-sized to large, robust species) (oriental, east palearctic) ..
..... *C. (Ceratinidia)*
- Black or metallic, with only a few pale markings, if any, on head, pronotal lobe, and legs; metasoma without yellow markings 12
- 12(11). Genal and frontal areas smooth, largely impunctate except on upper part of genal area, which is punctate, sometimes scattered punctures along frontal margin of eye [But see note on *C. parvula* Smith under the subgenus *Ceratina* s. str.] *C. (Ceratinula)*
- Genal and frontal areas punctate, at least a row of dense punctures along frontal margin of eye and scattered punctures on most of genal area 13
- 13(12). Maxillary palpus five- or six-segmented; S5 of female with gradulus; T6 of male without gradulus; T7 of male truncate or rounded or pointed posteriorly; S2 of male without tubercle; gonostylus of male without down-curved projection (palearctic, Africa, oriental)
..... *C. (Ceratina s. str.)*
- Maxillary palpus five-segmented; S5 of female without gradulus; T6 of male usually with gradulus; T7 of male usually extending posteriorly as long projection that is simple or bidentate at apex; S2 of male usually with tubercle in middle; gonostylus of male with down-curved projection (palearctic, oriental, Australia)
..... *C. (Neoceratina)*
- 14(10). Palearctic. Male gonostylus several times as long as broad, simple, hairy, well separated from gonocoxite; T6 with median longitudinal keel; T7 of male strongly extending posteriorly, simple or bidentate at apex
..... *C. (Euceratina)*
- Africa or Madagascar. Male gonostylus short, less than twice as long as broad, with one or two pointed processes or hooks and without hairs or with hairs on restricted areas; T6 not keeled; T7 variable, not so extended 15
- 15(14). Body dark metallic blue; posterior femur of male without tooth or comb of hairs (Madagascar)
..... *C. (Malgatina)*
- Body nonmetallic black or with weak bronze reflections; posterior femur of male with ventrobasal tooth or with ventral comb of hairs 16
- 16(15). Posterior femur of male with ventrobasal tooth, without median ventral comb of hairs; T6 of male without median convexity; terga without apical plumose hairs (Africa, Madagascar) *C. (Copoceratina)*
- Posterior femur of male without tooth, with median ventral (sometimes interrupted) comb of hairs; T6 of male with large median convexity with punctuation much finer than on nearby areas; T1 to T4 (or at least T1 and T2) with apical bands of white plumose hairs laterally (Africa, Madagascar) *C. (Hirashima)*

Key to the Subgenera of *Ceratina* of the Western Hemisphere

1. Pronotum with distinct transverse carina sometimes interrupted medially, in front of posterior margin of pronotum, curving strongly downward at each side to front coxa 2
- Pronotum without transverse carina (or such carina almost coincident with posterior margin of pronotum), and carina usually not extending downward to front coxa 3
- 2(1). Female without yellow or white on paraocular area; posterior tibia of female and some males on outer side basally usually with oblique carina representing posterior margin of basitibial plate; body usually brilliantly metallic, at least in some areas; maxillary palpus five- or six-segmented (neotropical) *C. (Calloцерatina)*
- Female with yellow or white on paraocular area; posterior tibia of both sexes without oblique carina, usually with protuberant angle or tooth representing apex of basitibial plate; body dark metallic; maxillary palpus six-segmented (South and Central America) *C. (Crewella)*
- 3(1). Extensive impunctate regions on genal and frontal areas; maxillary palpus five- or six-segmented (preoccipital carina present or absent; paraocular area with pale marks in males and some females) *C. (Ceratinula)*
- Genal and frontal areas with punctures; maxillary palpus six-segmented 4
- 4(3). Preoccipital carina absent or weak; male gonostylus several times as long as broad, hairy (California; introduced) *C. (Euceratina)*
- Preoccipital carina strong; male gonostylus little longer than broad 5
- 5(4). Paraocular area with pale marking in both sexes; T5 without gradulus; frons punctate throughout; T6 of female with strong carina extending from apex anterolaterally, separating dorsal from lateroventral surface of tergum (South America) *C. (Rhyssoceratina)*
- Paraocular area dark in females and nearly all males; T5 with gradulus; frons with smooth convexity on each side of midline; T6 of female without carina (North and Central America) *C. (Zadontomerus)*

Ceratina / Subgenus *Calloцерatina* Cockerell

Ceratina (*Calloцерatina*) Cockerell, 1924d: 77. Type species: *Ceratina amabilis* Cockerell, 1897 = *C. exima* Smith, 1862, by original designation.

The species of *Calloцерatina* are usually brilliantly metallic green or blue, or the metasoma sometimes red, pale areas limited to the face, pronotal lobe, and legs. Even when the body appears only weakly metallic, like *Zadontomerus*, as it does in *Ceratina* (*Calloцерatina*) *capitosa*

E. bicolor there is division of labor into four classes of individuals, the males participating in two of these classes.

Although there are no known parasitic forms of Xylocopini or Ceratinini, several socially parasitic species are known or surmised in the Allodapini (Michener, 1961b, 1970, 1977b, 1983c; Reyes and Michener, 1990; Batra, Sakagami, and Maeta, 1993). The parasites have reduced scopa, shortened mouthparts, and frequently projections on the head as though for pushing hosts. They do not feed from flowers, so far as is known; they live more or less as colony members in nests of hosts. Batra et al. found that they not only eat from food stores placed in the nest by hosts, but solicit food from hosts and participate in many host activities such as grooming larvae, feeding larvae, and guarding at the nest entrance. In all known cases, the parasites and hosts are related, i.e., in the same genus or the same clade.

The parasites differ from their hosts to various degrees. Three parasitic species, *Macrogalea mombasae* Cockerell, *Braunsapis breviceps* (Cockerell), and *B. kaliago* Reyes and Sakagami, and four probable but little-known parasites, *Allodapula guillarmodi* Michener, *B. natalica* Michener and *pallida* Michener, and *Allodape greatheadi* Michener, are sufficiently similar to their host or probable host genera that they have not received generic names of their own. It has been the custom among melittologists to give parasites such generic names, however, in spite of similarity to host genera, as for example *Psithyrus* (here placed as a subgenus within *Bombus*) and *Paralictus* (here placed within *Dialictus*, a subgenus of *Lasiglossum*). In most cases, such parasitic taxa probably make the host genera paraphyletic. I continue to recognize parasitic and host genera as distinct when they are markedly different and lack intermediates, but when similar and differing principally in loss or reduction of the scopa and similar features, I relegate the parasitic taxon to synonymy or subgeneric status. Thus, as noted above, *Paralictus* is a synonym of *Dialictus* and *Psithyrus* is a subgenus of *Bombus*. For allodapines, rather arbitrarily I consider *Inquilina* a subgenus of *Exoneura*, but I recognize *Effractapis*, *Nasutapis*, and *Eucondyllops* as genera. *Braunsapis breviceps* (Cockerell) and *kaliago* Reyes and Sakagami could also be placed in a separate genus or subgenus, for in numerous characters they differ from their nonparasitic relatives in the genus *Braunsapis*. The same can be said for *Braunapis bislensis* Michener and Borges. Contrarywise, persons so inclined could reasonably synonymize *Effractapis* and *Nasutapis* under *Braunsapis*, and *Allodapula* under *Eucondyllops*, to eliminate probable paraphyly of the nonparasitic genera.

An old and informal phylogenetic study of the genera of Allodapini was by Michener (1977c). A recent phylogenetic study by Reyes (1998) was based on nine larval characters, ten characters of adult morphology, and three characters of adult behavior or life history. Both of these authors considered *Compsomelissa* in the present broad sense (i.e., as those species that use partial or complete mass provisioning of larvae) as the sister group to all other Allodapini. The Allodapini other than *Compsomelissa* were then shown by Reyes to consist of two clades. One was the Australian genera plus the Near Eastern *Exoneuridia* and the African *Macrogalea*; the other consisted

of the African *Allodapula* and its relatives that lay small eggs, plus the large-egged *Allodape* (Africa) and *Braunsapis* (widespread). Similarity to the cell series of mass provisioned larvae found in many bees (such as the Ceratinini) seemed to support the idea (Michener, 1977c; Reyes, 1998) that *Compsomelissa* is the sister group to all other Allodapini, conserving as a plesiomorphy the behavior that results in series of young with the oldest at the bottom of the nest and youngest near the nest entrance. See *C. (Halterapis) nigrinervis* (Cameron) (Michener, 1971a). More recent phylogenetic studies (Schwarz, Bull, and Cooper, 2005) show, however, that *Macrogalea* is the sister to all the rest, and Engel (2005) has even provided a subtribal name, *Macrogaleina*, for *Macrogalea*. It seems that the sequence of stages in nests of *C. nigrinervis*, with mass provisioned larvae, is an apomorphy derived from the behavior of progressive feeders. Viewed in this light, laying of eggs before provisioning and firmly attaching the eggs to the nest wall, as does *C. nigrinervis*, are features not found in ordinary bees like *Ceratina* and are supportive of a relationship between *Allodapula* and *Compsomelissa*.

Reyes (1998) was not always certain whether a social parasite is derived from within a nonparasitic genus, or is a sister group to such a genus. Regardless of phylogenetic details, it is clear that larvae provide important information about diversity and phylogeny among genera with similar adults, because they have changed but little even when adults diverge strikingly as parasites.

Some of the nonparasitic genera of Allodapini are so similar in adult characters that they might not have been recognized as genera in the absence of larval characters. Particularly *Compsomelissa (Halterapis) nigrinervis* (Cameron) and its relatives would have been included in *Braunapis* if nests and male genitalia were unknown. I have therefore given a key to genera based on larvae, in addition to that based on adults.

Key to the Genera of the Allodapini Based on Adults

1. Body rather robust, head and thorax hairy, female with transverse fasciae of short, appressed plumose hairs on T2 to T5; stigma slender (Fig. 90-12b), basal part parallel-sided; prestigma about as long as distance from base of stigma to base of vein r; jugal lobe of hind wing enormous (Fig. 90-12b), almost as long as vannal lobe (Africa) *Macrogalea*
- Body slender, inconspicuously hairy and lacking metasomal fasciae of plumose hairs; stigma broad, not parallel-sided (Figs. 28-4, 90-11a-c, 90-13); prestigma usually half as long as distance from base of stigma to base of vein r; jugal lobe of hind wing of ordinary size, extending little if any beyond vein cu-v [except in *Braunsapis trochanterata* (Gerstaecker)] 2
- 2(1). Labial palpus with apical segments not diverging from axis of first two segments; maxillary palpus three- to five-segmented (proboscis short; no functional scopa, no midfemoral brush in female) 3
- Labial palpus with apical segments small and in ordinary position sharply divergent from axis of first two segments; maxillary palpus five- to six-segmented 5
- 3(2). Labial palpus three-segmented; frons and apex of clypeus without projections (Madagascar) *Effractapis*

- . Labial palpus four-segmented; frons or apex of clypeus with projection 4
- 4(3). Second recurrent vein absent (Figs. 90-10b, 90-13d); facial projection on frons, bilobed or paired (Africa) *Eucondylops*
- . Second recurrent vein present (Fig. 90-13c); facial projection on apex of clypeus, snoutlike, not bilobed or paired (Africa) *Nasutapis*
- 5(2). Second recurrent vein absent 6
- . Second recurrent vein present 9
- 6(5). Malar space nearly as long as broad; T5 and T6 of female each with sharp, lateral lamella or strong carina (southwestern Asia) *Exoneuridia*
- . Malar space much wider than long; T5 and T6 without lateral lamellate carinae, at most T5 with lateral part of gradulus as on preceding terga 7
- 7(6). Maxillary palpus six-segmented; thorax and metasoma with yellow or white markings (Africa, Arabia) *Compsomelissa* (in part)
- . Maxillary palpus five-segmented; thorax and metasoma without yellow or white markings except sometimes on pronotum, tegula, and axillary sclerites, and rarely bands on metasomal terga 8
- 8(7). Costal margin of second submarginal cell short, often less than half as long as first submarginal crossvein [except almost as long as that crossvein in *E. tridentata* (Houston)]; basitibial plate not indicated; T6 of female with apex strongly produced, upturned, bidentate or tridentate, not at all hidden by pubescence (Australia) *Exoneurella*
- . Costal margin of second submarginal cell usually almost as long as first submarginal crossvein; basitibial plate of female usually indicated by carina strongly raised across apex of plate; T6 of female with apex little produced, not or weakly upturned, not or minutely bidentate, not tridentate, and usually hidden by pubescence denser at apex of tergum than elsewhere (Australia) *Exoneura*
- 9(5). T6 of female with lateral parts bent under rather abruptly, usually a rather abrupt change in vestiture along this bend, dorsal part of tergum rather flat or even concave [*Compsomelissa* (*Halterapis*) *nigrinervis* (Cameron) shows these features only weakly]; apex of T6 of female without minute, median, apical pygidial plate, or plate completely covered by hairs; gonostylus of male much reduced or slender, if thin and flattened, then more than three times as long as broad 10
- . T6 of female with lateral parts bent under in a broadly rounded way (i.e., bend broad in transverse section), change in vestiture at bend gradual, dorsal part of tergum convex [exceptions are in those species in which T6 is laterally projecting or angulate scoop-shaped: *Allodape mucronata* Smith, *Braunsapis angolensis* (Cockerell), *associata* (Michener), and *paradoxa* (Strand, etc.)]; apex of T6 of female usually with minute, median, apical, elevated spine or pygidial plate (absent in the species with modified T6 listed above); gonostylus of male broad, flattened, concave on inner surfaces, flaplike, less than twice as long as broad 11
- 10(9). Ventroapical plate across apex of male gonocoxite with long, apically directed projection arising mesally; upper margin of clypeus often strongly concave between subantennal sutures (Africa, Arabia) *Compsomelissa* (in part)
- . Ventroapical plate across apex of male gonocoxite without projection from mesal portion; upper margin of clypeus not or less strongly concave (Africa) *Allodapula*
- 11(9). Outer surface of tibia of female, on distal half, with brush of dense, usually coarse hairs, commonly coarser or of different form and color than hairs of adjacent areas, and indications of brush present in most males; distance from first submarginal crossvein to first recurrent vein much greater than from second recurrent to second submarginal crossvein in most species; yellow along inner and outer orbits of most females (Africa) *Allodape*
- . Outer surface of tibia of both sexes without dense brush [except in *Braunsapis trochanterata* (Gerstaecker)]; distance from first submarginal crossvein to first recurrent vein subequal to that from second recurrent to second submarginal crossvein in most species; yellow along inner and outer orbits absent (except in female *B. aureoscapa* Michener) *Braunsapis*

Key to Genera of Allodapini Based on Mature Larvae (Illustrated in Figure 90-6; larvae of *Effractapis* and *Exoneuridia* are unknown)

- 1. Antenna tapering to attenuate, acute point; ventrolateral area of head swollen, tending to hang down on either side of mouthparts, bearing large curved hairs; body sharply bent in middle rather than uniformly curved (Australia) *Exoneurella*
- . Antenna blunt or almost absent; lateral area of head, if enlarged and with large hairs, then dorsolateral, not lobed down on either side of mouthparts; body uniformly curved or rather straight 2
- 2(1). Head or lateral protuberances of first body segment with enormous curved hairs; antenna represented by feeble convexity 3
- . Anterior end of body without large hairs; head hairs, if present, usually not much if any longer than those found elsewhere on body; antenna strongly projecting 4
- 3(2). Large, curved hairs on upper and lateral parts of head 10 to 18 or more; first ventrolateral projection of body without such hairs [except that *Braunsapis trochanterata* (Gerstaecker) has three to five]; ventral or ventrolateral parts of body with hairs (limited to first and last two segments in *B. simplicipes* Michener) *Braunsapis*, *Nasutapis*
- . Large, curved hairs on head eight or less, on vertex; first ventrolateral projection of body with seven to about 20 much larger hairs; ventral and ventrolateral parts of body hairless except for first ventrolateral projections (Africa) *Allodape*
- 4(2). Body curled, covered all over with short hairs, some of those of dorsum hooked (Africa) *Macrogalea*
- . Body naked or nearly so, or, if hairy, then nearly straight and without hooked hairs 5
- 5(4). Body curled, hairless or nearly so, with lateral projections corresponding to second and third body segments but otherwise without tubercles; maxilla and labium without projecting sensory areas (Africa, Arabia) *Compsomelissa*
- . Body rather straight, hairy or multituberculate; maxilla and labium with projecting sensory areas representing palpi 6
- 6(5). Australian *Exoneura*
- . African *Allodapula*, *Eucondylops*

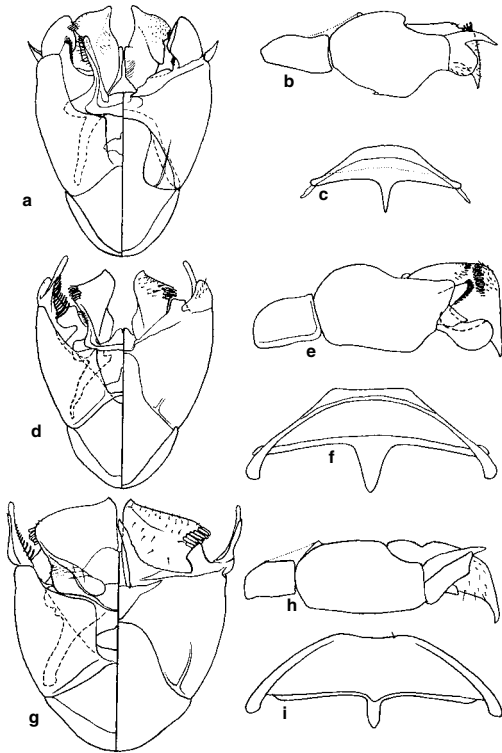


Figure 90-8. Apical metasomal structures of male Allodapini. **a-c**, Genitalia, in dorsal (at left), ventral, and lateral views, and S7 and S8 taken together, of *Allodapula (Dalloapula) dichroa* (Strand); **d-f**, Same structures, *A. (Allodapulodes) xerica* Michener; **g-i**, Same structures, *Compsomelissa (Halterapis) nigrinervis* (Cameron). From Michener, 1975b.

fed individually. Larvae of *Allodapula* were illustrated by Michener (1975c).

Allodapula was revised by Michener (1975b). Since that revision did not take into account the subgenera, the following listing may be useful: *Allodapulodes*: *hessei* Michener, *maculithorax* Michener, *palliceps* (Fries), *xerica* Michener. *Dalloapula*: *acutigera* Cockerell, *dichroa* (Strand). *Allodapula* s. str.: all other species.

Key to the Subgenera of *Allodapula* Based on Adult Males

- 1. Gonostylus of male minute, stylus-shaped (Fig. 90-8a), with short, slender hairs; penis valve and ventroapical plate much exceeding gonostylus; roof of genital chamber weakly convex, not or scarcely folded, each half over twice as long as broad *A. (Dalloapula)*
- Gonostylus variously shaped, not styluslike, with hairs as long as width of gonostylus and often robust (Fig. 90-8d); penis valve and projections from gonocoxite not exceeding gonostylus; convexities of roof of genital chamber strong, about as in *Braunsapis*, each half broad, folded or not 2
- 2(1). Gonobase reduced, consisting of narrow sclerotized bands; penis valves slender, only weakly downcurved, without coarse setae *A. (Allodapula) s. str.*

- Gonobase of ordinary form; penis valves robust, strongly downcurved, with cluster of coarse setae on outer angle (Fig. 90-8d) *A. (Allodapulodes)*

Key to the Subgenera of *Allodapula* Based on Mature Larvae

- 1. Body without conspicuous tubercles, with scattered hairs (Fig. 90-6o) *A. (Allodapulodes)*
- Body with several longitudinal rows of conspicuous tubercles or projections (Fig. 90-6l-n); hairs few and minute or absent 2
- 2(1). Labium with median apical projection; maxilla not bulbous; projections of body without basal shoulders or branches (Fig. 90-6n) *A. (Dalloapula)*
- Labium with median apical emargination; maxilla bulbous; several anterior projections of lateral and ventrolateral series with basal shoulders or branches (Fig. 90-6l, m) *A. (Allodapula) s. str.* and genus *Eucondylops*

***Allodapula* / Subgenus *Allodapula* Cockerell s. str.**

Allodape (Allodapula) Cockerell, 1934c: 220. Type species: *Allodape variegata* Smith, 1854, by original designation.

This subgenus consists of relatively slender species, 4.5 to 7.5 mm long, with a red or rarely reddish-black metasoma and nearly always a yellow band or spot on the scutellum.

■ *Allodapula* s. str. is widespread in South Africa, and occurs as far north as Zimbabwe, with a doubtful record for Tanzania. The nine species were included in the revision by Michener (1975b).

Allodapula guillarmodi Michener was based on a female with reduced scopa, presumably a social parasite in nests of another species.

***Allodapula* / Subgenus *Allodapulodes* Michener**

Allodapula (Allodapulodes) Michener, 1969b: 291. Type species: *Allodape palliceps* Fries, 1924, by original designation.

Like *Dalloapula*, this subgenus includes rather robust species, 5 to 7 mm long. The metasoma is black to red, and the scutellum sometimes has a cream-colored or yellow spot. In males of some species the legs are wholly yellow.

■ This subgenus is known only from Cape Province, South Africa. The four or five species were included in the revision by Michener (1975b).

***Allodapula* / Subgenus *Dalloapula* Michener**

Allodapula (Dalloapula) Michener, 1975c: 246. Type species: *Allodape dichroa* Strand, 1915, by original designation.

This subgenus consists of somewhat robust species 4.5 to 9.0 mm long, with the metasoma black or partly red, and without yellow on the scutellum.

■ This subgenus occurs in Cape Province and Natal, South Africa. The two species were included in the revision by Michener (1975b).

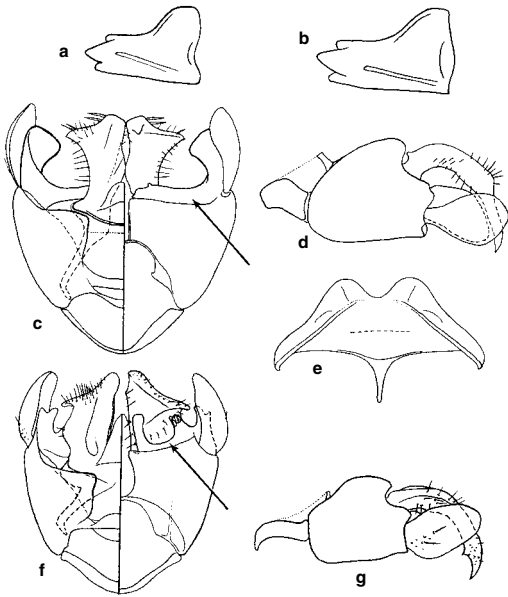


Figure 90-9. Structures of Allodapini. **a, b,** Mandibles of male and female of *Allodape obscuripennis* Strand. **c, d,** Male genitalia of *Allodape obscuripennis* Strand, in dorsal (at left), ventral, and lateral views; **e,** S7 and S8 of male of *A. mucronata* Smith; **f, g,** Male genitalia of *Braunsapis leptozonia* (Vachal), in dorsal (at left), ventral, and lateral views. The arrows indicate the ventroapical plate, which frequently supports peglike setae, as in **f**. The ventroapical plate appears to be a mesad extension of the lower gonostylus. From Michener, 1975b.

Genus *Braunsapis* Michener

Allodape (*Braunsapis*) Michener, 1969b: 290. Type species: *Allodape facialis* Gerstaecker, 1857, by original designation.

Most species of *Braunsapis* are black with ivory or yellow marks on the face and often on the pronotal lobes and tarsi. Females lack such marks on the paraocular and genal areas except for strong marks in *B. aureoscapa* Michener, and occasionally very small paraocular marks, e.g., in *B. maculata* Reyes. Rarely the metasoma is red, and in *B. pallida* Michener the body is largely testaceous. The size is commonly smaller than that of *Allodape*, body length being 3 to 9 mm. The gonostylus of the male is flat, usually broad (Fig. 90-9f, g), and there is no projecting lower gonostylus or process mesal to it, as in *Compsomelissa* and *Allodape*. Except in *B. aureoscapa* there are one to several peglike setae on the ventroapical plate (?lower gonostylus) (Fig. 90-9f). The hind femur of the male is rather slender, not angulate at its extreme base, but sometimes with a more distal angle. The male genitalia and other structures were illustrated by Michener (1975b, 1977b) and Reyes (1991a, c, 1993, 1998); see also Figure 90-9f, g.

■ *Braunsapis* ranges from southernmost Africa north to Senegal, Ethiopia, and Madagascar and eastward from Pakistan, India, and Sri Lanka to southernmost China, Taiwan, the Philippines, the Solomon Islands, and Aus-

tralia south as far as New South Wales and South Australia. This is by far the largest genus of the Allodapini. There are well over 45 species in Africa and Madagascar, 19 in the oriental region, and 23 in the Australian region. The African figure is clearly low, for unplaceable specimens are numerous, and many names thought to be synonymous probably represent recognizable species. Revisions were by Michener (1975b) for Africa, and by Reyes (1991a, b, 1993, 1998) for Madagascar, the oriental region, and the Australian region. Australian species were listed by Cardale (1993).

Studies of nesting behavior (Figs. 90-4) and social behavior were presented by Michener (1962b, 1971a) on Australian and African species and in a series of papers on a Taiwan species, of which one is *Maeta*, Sakagami, and Michener (1992). Social behavior with two or occasionally more females working in a single nest is common. As indicated in the discussion of the tribe, several species of *Braunsapis* are known or probable social parasites of other species of *Braunsapis*; behavioral information on *B. breviceps* (Cockerell) and *kaliago* Reyes and Sakagami was provided by Reyes and Michener (1990) and Batra, Sakagami, and Maeta (1993). In addition social parasites probably derived from *Braunsapis* constitute the genera *Effractapis* and *Nasutapis*. Limited biological information on the latter was presented by Michener (1971a).

Genus *Compsomelissa* Alfken

This genus is here used in a broad sense to include species formerly placed in *Halterapis*. The mature larvae, robust and nearly hairless, have weak lateral tubercles on two thoracic segments, but otherwise lack tubercles (Fig. 90-6h, i). The male gonostylus consists of two elements, the upper and lower gonostyli, appressed together (Fig. 90-8g, h). They are rather slender, or, if broad, are broadly attached to the gonocoxite. The structure that I call the ventral gonostylus with some confidence is continuous with the ventroapical plate, which is probably part of the ventral gonostylus. It is produced as a long mesal process parallel to and beneath the penis valve. The male genitalia and other structures were illustrated by Michener (1975b) and Reyes and Michener (1992); see also Figure 90-8g-i).

The two subgenera are weakly separated on adult and larval characters, although the manner of feeding larvae differs, being by mass provisioning in the subgenus *Halterapis* and by progressive feeding of young larvae and mass provisioning of older larvae in the subgenus *Compsomelissa* s. str., so far as is known.

Key to the Subgenera of *Compsomelissa*

1. All tagmata with some yellow or white integument, or integument largely pale, but metasoma sometimes red
..... *C. (Compsomelissa)* s. str.
- Pale areas limited to head, pronotal lobe and legs, but metasoma sometimes red *C. (Halterapis)*

Compsomelissa / Subgenus *Compsomelissa* Alfken s. str.

Compsomelissa Alfken, 1924a: 251. Type species: *Compsomelissa borneri* Alfken, 1924, monobasic.

Exoneurula Michener, 1966b: 573. Type species: *Exoneurula*

At least in *Compsomelissa* (*Halterapis*) *nigrinervis* (Cameron) and probably in *C. (H.) angustula* (Cockerell), larvae are fully and individually mass provisioned, as described by Michener (1971a). This practice differs from that of all other allodapine bees. One collection of nests of *C. (H.) minuta* (Brooks and Pauly) in Madagascar revealed an extraordinary, and so far as known, unique mode of feeding larvae. Three to eleven eggs are glued to the wall of the nest burrow, near the bottom of the nest. Then a firm pollen-honey mixture is provided, covering the eggs and extending up the burrow wall toward the nest entrance. The larvae move slowly upward, consuming the common food mass as they go (Schwarz et al., 2005). It is not certain whether food is added to this mass by the one to several adult females in the nest, as the larvae feed.

Genus *Effractapis* Michener

Effractapis Michener, 1977b: 6. Type species: *Effractapis furax* Michener, 1977, by original designation.

Effractapis is the generic name used for a small species (length 4 mm) no doubt derived from *Braunsapis* and presumably parasitic on species of that genus. Interesting characters in addition to those indicated in the key to genera are the entirely black face of both sexes, the gently convex whole face, and the presence of two setae, longer than the scape, extending forward from near the upper clypeal margin, and of a few long hairs on the front tibiae and basitarsi. Male genitalia and other structures were illustrated by Michener (1977b).

■ This genus occurs in Madagascar. The only known species is *Effractapis furax* Michener.

Genus *Eucondylops* Brauns

Eucondylops Brauns, 1902: 377. Type species: *Eucondylops konowi* Brauns, 1902, monobasic.

Eucondylops consists of elongate (5.5–7.0 mm), dark brown or blackish parasitic species that differ from nearly all other Allodapini in lacking pale markings on the face in both sexes, a character also found in another social parasite, *Effractapis furax* Michener. The head is unusually small, the eyes too are small, and the malar area is therefore large (Fig. 90-10); a bilobed projection or two projections arise from the upper part of the frons. The reduction of the proboscis is extreme, the mentum being a small, weakly sclerotized structure, wider than long, and the lorum being a transverse bar, not V- or Y-shaped as in all other L-T bees. One species, *Eucondylops reducta* Michener, has only one submarginal cell (Fig. 90-10b), an unusual feature among bees, but the type species has two submarginal cells (Fig. 90-13c). Male gonostyli are absent; penis valves are slender and nearly straight, not curved strongly downward. Male genitalia were illustrated by Michener (1975b).

■ This genus occurs in South Africa in nests of *Allodapula*. The two species were revised by Michener (1970).

Although larvae (Fig. 90-6l) look like those of *Allodapula* s. str., suggesting that *Eucondylops* is derived from that subgenus, the adult structure is so extraordinary that I do not hesitate to regard *Eucondylops* as a genus, even though the result may be a paraphyletic *Allodapula*.

Genus *Exoneura* Smith

Exoneura differs from most other Allodapini in lacking the second recurrent vein (Fig. 90-11a-b). In most species the metasoma is red, but some are black; because most have limited yellowish marks on the face, sometimes also the pronotal lobe, those with a black metasoma superficially resemble the common species of *Braunsapis*. The gonostyli of males are absent or at least unrecognizable (as in Fig. 90-11d). The larvae (Fig. 90-6q-t) tend to have a pair of large and often branched thoracic appendages.

Exoneura is the common allodapine genus in the temperate parts of Australia and does not occur on other continents. Its nesting biology has been discussed by various authors, e.g., Michener (1965a) and a series of papers by M. P. Schwarz and coauthors, of which Schwarz and O'Keefe (1991) and Silberbauer and Schwarz (1995) are examples. The subgenus *Inquilina* consists of social parasites in nests of *Exoneura* s. str.

Key to the Subgenera of *Exoneura*

1. Female with scopa reduced to mass of short, dense hairs; mandible of female with ventral tooth reduced to mere

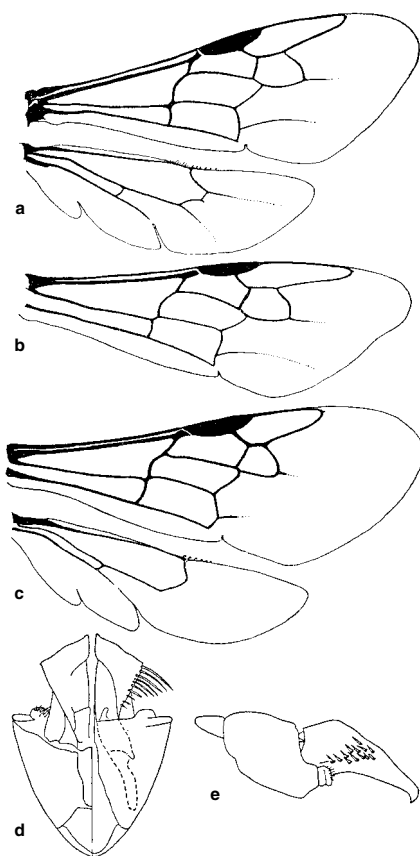


Figure 90-11. Australian Allodapini. **a**, Wings of female *Exoneura* (*Exoneura*) *bicolor* Smith; **b**, Forewing of male of same species; **c**, Wings of *Exoneurella lawsoni* (Rayment); **d**, **e**, Male genitalia of *Exoneurella lawsoni* (Rayment), in dorsal (at left), ventral, and lateral views, showing the greatly reduced gonostyli. From Michener, 1965b.

- convexity so that mandible is bidentate; face concave; middle and hind tibial spurs robust, in female strongly curved apically, less than one-half as long as basitarsi; anterior margin of pronotum in both sexes with a sharp angle or small spine at level of base of fore coxa *E. (Inquilina)*
- Female with ordinary tibial scopa; mandible of female three-toothed (as in Fig. 90-9b); face not noticeably concave; middle and hind tibial spurs slender, in female gently curved, one-half as long as basitarsi or longer; anterior margin of pronotum with an inconspicuous rounded angle at level of base of fore coxa 2
- 2(1). Vein Cu_1 of forewing usually long and gradually tapering (Fig. 90-11a, b); clypeus usually widely separated from antennal sockets, subantennal suture thus about as long as diameter of socket; fore tarsus of male attenuate, first two segments taken together longer than tibia; hind basitarsus of male dilated (scarcely so in species such as *E. asimillima* Rayment), nearly as wide as tibia (except in *E. asimillima*), not parallel-sided *E. (Exoneura s. str.)*
- Vein Cu_1 of forewing a short stub, ending abruptly (as

in Fig. 90-11c), although in some cases continued as a pigmented line; clypeus usually closely approaching antennal sockets, subantennal suture thus much shorter than diameter of socket; fore tarsus of male of ordinary form, first two segments taken together shorter than or as long as tibia; hind basitarsus of male much more slender than tibia, parallel-sided *E. (Brevineura)*

Exoneura / Subgenus *Brevineura* Michener

Exoneura (*Brevineura*) Michener, 1965b: 224. Type species: *Exoneura concinnula* Cockerell, 1913, by original designation.

Brevineura includes mostly smaller species (body length 3.5-7.0 mm), none of which have the enlarged eyes and associated features found in most males of *Exoneura s. str.*

■ The distribution is Australia, north to the latitude of southern Queensland. The 26 species names were listed by Michener (1965b) and Cardale (1993).

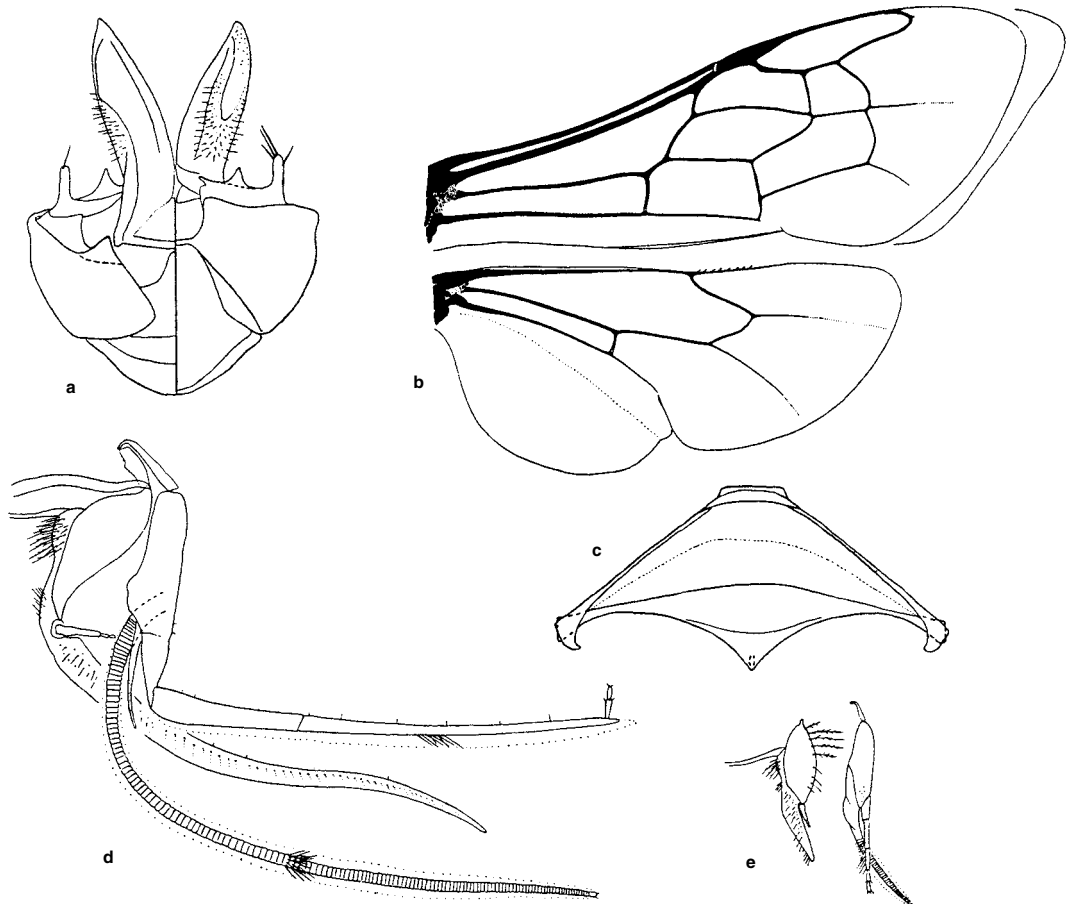


Figure 90-12. Structures of *Macrogalea candida* Smith. **a**, Dorsal (at left) and ventral views of male genitalia; **b**, Wings of female and (at right) the outline of forewing of male; **c**, S7 and S8 of male; **d**, Lateral view of proboscis of female; **e**, Proboscis of male (cardo and lorum omitted) to same scale. From Michener, 1971b.

lives in small colonies and has large and small female morphs (Houston, 1977). Reyes and Schwarz (1997) gave an account of the phylogeny and behavior of the four species of *Exoneurella*, which differ greatly in their social levels. Reyes, Cooper, and Schwarz (2000) revisited the phylogeny and the relations of *Exoneurella* to similar genera.

Genus *Exoneuridia* Cockerell

Exoneura (*Exoneuridia*) Cockerell, 1911d: 232. Type species: *Exoneura libanensis* Friese, 1899, by original designation.

Like *Exoneura*, *Exoneurella*, and most species of *Comp-somelissa* s. str., *Exoneuridia* lacks the second recurrent vein (as in Fig. 90-11a-c). The long malar space and the strong lateral carina on T5 and T6 of the female distinguish *Exoneuridia* from its relatives. The body length is 6 to 9 mm. Unfortunately, its larval characters remain unknown. It is the only palearctic genus of Allodapini.

Terzo (1999) has placed the three species of *Exoneuridia* in two subgenera. Although this seems like excessive splitting, the subgenera are quite different and I tentatively recognize them:

Key to the Subgenera of *Exoneuridia*

1. All tagmata richly marked with yellow; mandible of female with median tooth longer than others; maxillary palpus 5-segmented; gonobase of male nearly as long as midventral length of gonocoxite.....*E. (Alboneuridia)*
- Body dark except for clypeus and limited pale marks elsewhere (thus coloration as in most *Braunsapis*); mandible of female with lower tooth longer than others; maxillary palpus 6-segmented; gonobase much shorter than midventral length of gonocoxite.....*E. (Exoneuridia* s str.)

Exoneuridia / Subgenus *Alboneuridia* Terzo

Exoneuridia (*Alboneuridia*) Terzo, 1999: 147. Type species: *Allodape oriola* Warncke, 1979, by original designation.

The principal subgeneric characters are indicated in the key to the subgenera above.

■ This subgenus is known only from southwestern Iran. The only species is *Exoneuridia oriola* (Warncke); see Terzo (1999).

Exoneuridia / Subgenus *Exoneuridia* Cockerell s. str.

Exoneura (*Exoneuridia*) Cockerell, 1911: 232. Type species: *Exoneura libanensis* Friese, 1899, by original designation.

The principal subgeneric characters are indicated in the key above to subgenera.

■ *Exoneuridia* s. str is found in Turkey, Lebanon, Israel, and Syria. The two species were included in the revision by Terzo (1999).

Genus *Macrogalea* Cockerell

Macrogalea Cockerell, 1930f: 291. Type species: *Allodape candida* Smith, 1879, by original designation.

This is the only hairy, robust allodapine. Body length is 7.5 to 10.5 mm. The integument is blackish with a pale

clypeal mark in most females. The female metasoma is flattened. The males, which are extremely rare in collections, have enlarged eyes, very short antennae, and extremely long, dense, erect hair on the clypeus and hypostomal areas; the male mandible tapers to the apex and has a small tooth on the upper margin; the male proboscis is one-half to one-third (depending on what structures are measured) the size of the female's (Fig. 90-12d, e) and does not project out of the proboscidial fossa. The maxillary palpus is three-segmented, the first segment being elongate. The male genitalia and numerous other structures were illustrated by Michener (1971b); see also Figure 90-12. As in *Exoneura*, the male upper gonostyli appear to be absent; the gonostylus-like projection is fused with the ventroapical plate and is presumably part of the lower gonostylus. ■ This genus occurs in Madagascar and in Africa from Ethiopia to Tanzania and Namibia. Like *Liotrigona* and certain other taxa, the genus *Macrogalea* is widespread in Africa but represented there by only one nonparasitic species (plus one known only from Zanzibar and one parasitic species), but it has speciated in Madagascar, where nine species are known (Brooks and Pauly, in Pauly et al., 2001). The genus was reviewed by Michener (1971b), with supplementary information by Michener (1977b).

Tierney et al. (2002) provided an account of nests of *Macrogalea zanzibarica* Michener and its frequently social organization. When other genera are also considered, implications exist for the monophyletic origin of social behavior in the ancestral Allodapini.

As shown by Michener (1971b), one species of *Macrogalea*, *M. mombasae* Cockerell, is a social parasite in nests of *M. candida* (Smith). The parasite shares features of various parasitic bees, such as a reduced scopa; see Michener (1970). Larvae of *Macrogalea*, unlike those of other Allodapini, have abundant short hairs, many of them hooked, all over the body (Fig. 90-6j) and lack the tubercles and large hairs found in other allodapines. Presumably, the short hairs serve to hold the larvae, which are typically curled, in their positions in vertical burrows in pithy stems.

Genus *Nasutapis* Michener

Nasutapis Michener, 1970: 208. Type species: *Nasutapis straussorum* Michener, 1970, by original designation.

Like *Effractapis*, *Nasutapis* is a probable parasitic derivative of *Braunsapis* and could well be included in that genus as was done by Reyes (1998); its larvae do not differ from those of *Braunsapis* by any known group characters, and its wing venation (Fig. 90-13d) is not different from that of small species of *Braunsapis*. Unusual characters of adults include a broad head, a snoutlike lower median clypeal projection, and the yellow clypeus and paracocular areas of the female, which are similar to those of the male. Body length is 4.5 to 5.5 mm.

■ *Nasutapis* is known from Natal Province, South Africa, in nests of *Braunsapis facialis* (Gerstaecker). The only species is *N. straussorum* Michener.

93. Tribe Brachynomadini

This American group was recognized as the melanomachine complex by Rozen (1977b), Ehrenfeld and Rozen (1977), Snelling and Rozen (1987), and Alexander (1990), and given the present tribal status after phylogenetic analysis by Roig-Alsina and Michener (1993).

The bees of this tribe have the general aspect of small Nomadini or of Ammobatini and have usually been placed in the Nomadini. Brachynomadini are nomadiform or small epeoliform bees, black or with the metasoma or much of the body red. The yellow or white integumental markings found in most *Nomada* species are absent. The two basal mandibular articulations are about equidistant from the eye (Fig. 93-1b), except that in some *Brachynomada* and especially in *Trichonomada* the anterior articulation is more distant; the anterior angle is farther from the eye in Nomadini (Fig. 93-1a). The maxillary palpus is three- to six-segmented and usually less than half as long as the blade of the galea; it is six-segmented and longer in Nomadini. Except in *Kelita* the pseudopygidial area of females is clothed with minute posterolaterally directed hairs, parted on the midline, such that in most positions half of the area appears silvery, the other half dark. Except in *Trichonomada*, S5 of the female is produced to a median hairy process or lobe, not found in Nomadini. S6 of the female has a deep midapical cleft between the two pointed or narrowly rounded lobes, and the lobes are close together and armed mesally with a few coarse setae (Fig. 91-2f) or, in *Kelita*, armed apically with a few short, blunt setae; this configuration is altogether unlike the subtruncate apex with coarse blunt setae of Nomadini.

Bees of this tribe are found only in the Western Hemi-

sphere. Larvae were described by Rozen (1977b, 1994b, 1997a), and Ehrenfeld and Rozen (1977). Hosts include Colletinae, Exomalopsini, and Panurginae. Eggs are thought to be inserted into the cell wall as in Nomadini.

Kelita appears to be the most distinctive brachynomachine taxon. The genera *Brachynomada*, *Paranomada*, and *Triopasites* are similar to one another; unique specimens in various collections indicate that there are undescribed species of this group in Mexico and South America. As such additional species become known in both sexes, it is likely that these three genera will merge and be synonymized or recognized as subgenera.

Key to the Genera of the Brachynomadini (From Rozen, 1997a)

- 1. Hind coxa normal, not expanded, with carina along mesal dorsal edge but without carina along outer dorsal edge; antennal scape, exclusive of basal bulb, shorter than twice maximum diameter; graduli of terga and sterna simple (South America) *Kelita*
- Hind coxa broadly expanded laterally, with pronounced longitudinal carina along mesal dorsal edge and strong carina along outer dorsal edge, the two separated by strongly concave, mostly glabrous surface; antennal scape, exclusive of basal bulb, distinctly longer than twice maximum diameter; graduli of T2 to T4 and S2 to S4 and others produced as distinct, clear, thin, posteriorly directed lamellae (not just carinae) appressed against postgradular areas 2
- 2(1). Anterior mandibular articulation separated from eye by distance almost as great as ocellar diameter 3
- Anterior mandibular articulation almost as close to eye as posterior articulation, separated from eye by distance no greater than half ocellar diameter (Fig. 93-1b)..... 4
- 3(2). Thorax not strongly flattened, width about equal to depth; eyes with sparse setae about half as long as ocellar diameter; frons in front of ocelli punctate, not particularly shiny; scutal disc punctate; maxillary palpus five-segmented (counting minute segment I); S5 of female broadly rounded apically; clypeus of male with low lateral carina in addition to deep suture immediately above it, extending from anterior tentorial pit to anterior mandibular articulation (South America) *Trichonomada*
- Thorax strongly flattened, width distinctly greater than depth; eyes with sparse minute setae, scarcely noticeable; frons in front of ocelli nearly glabrous, polished; scutal disc virtually glabrous, highly polished; maxillary palpus usually four-segmented (counting minute segment I); S5 of female with apical margin produced as round, median, hairy projection; clypeus of male without lateral carina but with very deep suture from anterior tentorial pit to anterior mandibular articulation (North America) *Paranomada*
- 4(2). Median apical triangle of S1 projecting downward; male with dorsal gonostylus short, laterally flattened, bladelike near base, tapering evenly toward apex as seen in lateral view (North America) *Triopasites*

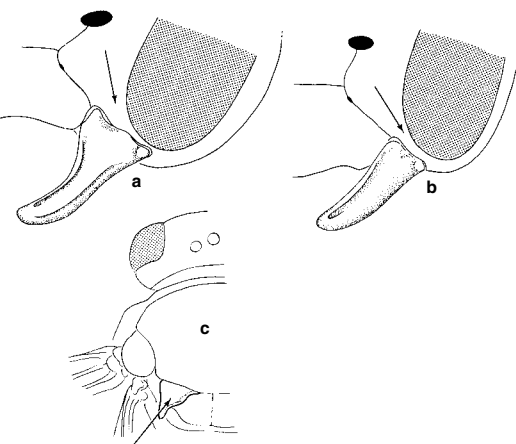


Figure 93-1. Cephalic and thoracic structures of Nomadinae. **a, b,** Mandibular articulations of *Nomada imbricata* Smith and *Brachynomada* (*Melanomada*) *grindeliae* (Cockerell), with arrows indicating distinguishing feature; **c,** Dorsum of thorax showing produced axilla (arrow) of *Doeringiella* (*Triepeolus*) sp. From Michener, McGinley, and Danforth, 1994.

- . Median apical triangle of S1 scarcely produced; male with dorsal gonostylus short or attenuate, but slender, sometimes widening near apex, neither laterally flattened nor bladelike..... *Brachynomada*

Genus *Brachynomada* Holmberg

The number of submarginal cells is two or three, differing among species of this genus, and the number of segments in the maxillary palpus is five or six. Nonetheless, the genus is morphologically rather homogeneous, with punctures on all parts of the body although widely separated by shiny ground in some parts of some species. The body length is 3.5 to 9.0 mm. The scutellum is biconvex. T5 of the female has a large median pseudopygidial area about twice as wide as long, covered with extremely fine, dense, simple hairs. The male genitalia and apical sterna of both sexes were illustrated by Linsley and Michener (1939) and Rozen (1994b, 1997a).

Key to the Subgenera of *Brachynomada*

1. Hind femur of male without basal thornlike projection or other modification; S8 of male elongate, strongly produced distally, its apex broadening before ending abruptly (South America) *B. (Brachynomada s. str.)*
- . Hind femur of male with thornlike projection ventrally and, in some species, with other modifications on ventral surface; S8 of male less elongate, not strongly produced, tapering to apex (North America) *B. (Melanomada)*

***Brachynomada* / Subgenus *Brachynomada* Holmberg s. str.**

Brachynomada Holmberg, 1886b: 233, 239, 272. Type species: *Brachynomada argentina* Holmberg, 1886, designated by Sandhouse, 1943: 531.

■ This subgenus occurs from Peru and the state of São Paulo, Brazil, to the province of Buenos Aires, Argentina. Probable members of this subgenus are reported from areas as distant as Ceará, Brazil, and Mendoza, Argentina, but I have not seen specimens from such distant areas; they might belong to similar-looking bees such as *Trichonomada*. Eight species have been described. Several species of this subgenus were misplaced in *Doeringiella* (Epeolini) by Friese (1908b), who gave a key to certain species.

Species of *Brachynomada* s. str. are cleptoparasites of *Exomalopsis* (Exomalopsini), as shown by Rozen (1997a), and *Psaenythia* (Panurginae), as shown by Rozen (1994b). The use of such dissimilar hosts, belonging to different families of bees, is of interest. The larva of *B. scotti* Rozen was described by Rozen (1997a).

***Brachynomada* / Subgenus *Melanomada* Cockerell**

Nomada (Melanomada) Cockerell, 1903d: 587. Type species: *Nomada grindeliae* Cockerell, 1903, by original designation.

Hesperonomada Linsley, 1939b: 5. Type species: *Hesperonomada melanantha* Linsley, 1939, by original designation.

■ *Brachynomada (Melanomada)* occurs from California and Nebraska south to Texas, USA, and Durango and Jalisco, Mexico. The seven species were revised by

Snelling and Rozen (1987), supplemented by Rozen (1994b).

Species of *Melanomada* are cleptoparasites in nests of *Anthophorula* (*Anthophorisca*) (Exomalopsini) (Rozen, 1977b, 1997a; Rozen and Snelling, 1986). Host records are summarized by Snelling and Rozen (1987), supplemented by Rozen (1994b, 1997a).

Genus *Kelita* Sandhouse

This is a distinctive genus of Brachynomadini, as indicated by the first couplet of the key to genera. Moreover, the antennal scape is not flattened as it is in the other genera, and the species are often smaller, the body length being from 2.8 to 5.8 mm. The pseudopygidial area is partly covered by broad, scalelike, posteriorly directed, appressed hairs; in all other Brachynomadini the hairs are slender and directed posterolaterally.

Key to the Subgenera of *Kelita* (From Rozen, 1997a)

1. Submarginal cells two; maxillary palpus six-segmented; hind tibia of male normal in shape; hind tibial spurs of male normal in size, subequal in length; dorsal and median processes of gonostylus shorter than gonocoxite (Chile) *K. (Kelita s. str.)*
- . Submarginal cells three; maxillary palpus five-segmented; hind tibia of male broadly expanded apically with anterior edge forming apical curved spine; hind tibial spurs of male very different, inner one normal-sized, outer one extremely short or absent; dorsal and median processes of gonostylus elongate, distinctly longer than gonocoxite (Argentina) *K. (Spinokelita)*

***Kelita* / Subgenus *Kelita* Sandhouse, s. str.**

Herbstiella Friese, 1916: 168 (not Stimpson, 1871). Type species: *Herbstiella chilensis* Friese, 1916, monobasic.

Kelita Sandhouse, 1943: 561, replacement for *Herbstiella* Friese, 1916. Type species: *Herbstiella chilensis* Friese, 1916, autobasic.

Numerous structures were excellently illustrated by Ehrenfeld and Rozen (1977); see also Rozen (1997a).

■ *Kelita* s. str. occurs from Atacama province to Nuble, Chile. The four species were revised by Ehrenfeld and Rozen (1977).

Two species of *Kelita* s. str. are known to be cleptoparasites in nests of *Liphanthus* and *Protandrena* (*Panasarus*) (Panurginae), as reported by Ehrenfeld and Rozen (1977); one of the *Liphanthus* host species was placed incorrectly in *Psaenythia* by these authors. A third species parasitizes *Leioproctus* (*Perditomorpha*) (Colletinae) (Rozen, 1994b).

***Kelita* / Subgenus *Spinokelita* Rozen**

Kelita (Spinokelita) Rozen, 1997a: 5. Type species: *Kelita argentina* Rozen, 1997, by original designation.

The male genitalia and other structures were illustrated by Rozen (1997a).

■ *Spinokelita* is known from Santa Cruz to San Juan provinces, Argentina. The only described species is *Kelita argentina* Rozen.

Subtribe Epeolina, *Epeolus*

Subtribe Thalestriina, *Doeringiella**, *Pseudepeolus**,
Rhinepeolus, *Thalestria*, *Triepeolus*

*Considered subgenera of *Doeringiella* by Michener (2000).

The monogeneric subtribes are characterized by the generic characters indicated below. The subtribe Thalestriina is characterized especially by the form of S6 of the female (Figs. 8-10f and 95-3c; Rightmyer, Figs. 7 and 10).

As in other Nomadinae, first-stage larvae have large, heavily sclerotized heads and jaws (Fig. 91-6a, b); Rozen (1989b) illustrated the larvae and distinguished those of *Epeolus* from *Triepeolus*.

The Epeolini are found on all continents except Australia and are cleptoparasites in the nests of various groups of bees.

Key to the Genera of the Epeolini

(part of this key is based on that of Rightmyer, 2004)

1. Body largely covered by minute, appressed, plumose, scalelike, metallic blue or green hairs, and similar white hairs on metasoma limited to small lateral patches; eyes closest at upper ends, strongly converging above in male; T5 of female with apical transverse area densely covered with long, stiff, black hairs but without distinct pseudopygidial area; preoccipital carina behind vertex strong but on posterior surface of head much below level of ocelli (neotropical)..... *Thalestria*
- Body nonmetallic, usually with extensive areas of minute, appressed, plumose, white to pale-tan hairs on metasoma; eyes usually converging below (but in *Odyneropsis* slightly closer above than below in both sexes); T5 of female with apical area covered with short brown to white hairs (but long black hairs in *Rhogepeolus*), often well enough defined to be called a pseudopygidial area; preoccipital carina behind vertex (upper sector, see Fig. 95-4) absent or at summit of posterior surface of head, little below level of ocelli 2
- 2(1). Inner margins of eyes subparallel, usually slightly closer above than below; metasoma without conspicuous areas of pale pubescence except sometimes on T1; stigma rather large, vein r arising near middle (Fig. 95-2a); marginal cell as long as three submarginal cells combined; T5 of female with small middorsal depressed area often surrounded by ridges (often hidden by T4) (neotropical)..... *Odyneropsis*
- Inner margins of eyes distinctly converging below; metasoma usually with conspicuous areas of pale pubescence; stigma smaller, with vein r arising well beyond middle (Fig. 95-2b, c) [except in *Epeolus* (*Trophocleptria* group)]; marginal cell shorter than submarginal cells combined [except in *E. (Trophocleptria* group)]; T5 of female without middorsal depressed area 3
- 3(2). Scutellum with median longitudinal strip of appressed, pale setae between convexities; pseudopygidial area of female with apical margin strongly concave, with medioapical slit, apical margin fringed with relatively long, curved, simple setae; first flagellar segment longer than second..... *Rhogepeolus*
- Scutellum rarely with distinct median longitudinal strip of appressed setae; pseudopygidial area of female variable but apex rarely strongly concave, without median apical slit (except in *T. roni* Genaro); first flagellar segment not longer than second 4
- 4(3). Males 5
- Females..... 9
- 5(4). Scape dramatically swollen (Fig. 95-4b) or, if not, forming subbasal angle on lateral surface (seen with antenna directed upward) so that only basal third or fourth tapers toward basal bulb; metafemur with setae on undersurface (rarely lacking); basitibial plate completely bordered by carina; S3 with elongate, curled setae on apical margin *Doeringiella*
- Scape not swollen, not forming subbasal angle on lateral surface, basal half or more of scape tapering toward basal bulb; metafemur very rarely with conspicuous setae on undersurface; basitibial plate absent to completely bordered by carina; S3 with apical setae variable, rarely curled 6
- 6(5). Supraclypeal area produced into bulbous protrusion with weak median carina; preoccipital carina continuous; scutum anteriorly with median longitudinal band of appressed setae (sometimes faint); scutellum relatively flat but bearing two mammiform tubercles; second abscissa of hindwing vein M+Cu over twice as long as cu-v..... *Rhinepeolus*

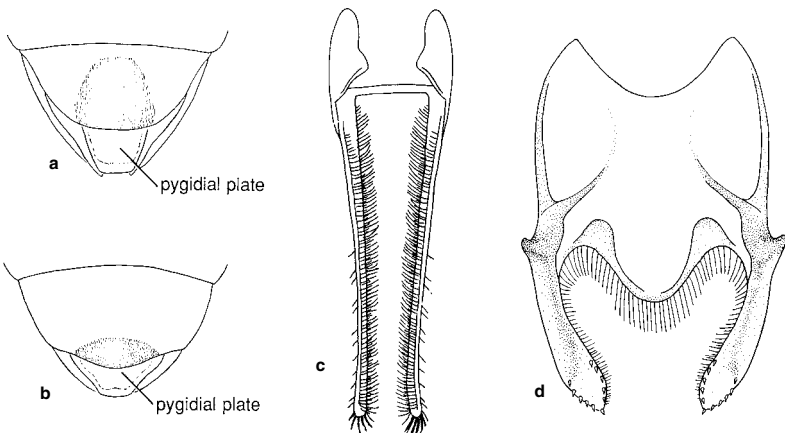


Figure 95-3. Apical metasomal structures of female Epeolini. **a**, Dorsal view of T5 and T6, indicating (by shading) the pseudopygidial area on T5, of *Triepeolus texanus* (Cresson) (see also Fig. 93-5); **b**, Same, of *Epeolus compactus* Cresson; **c**, S6 of *Triepeolus concavus* (Cresson); **d**, S6 of *Epeolus* (*Trophocleptria* group) sp.? From Michener, McGinley, and Danforth, 1994.

- Supraclypeal area and median carina variable, rarely produced into bulbous protrusion; preoccipital carina absent at least on upper corners of head; scutum usually lacking median longitudinal band of appressed setae (sublateral bands can be present); scutellum variable but not bearing mammiform tubercles; second abscissa of hindwing vein M+Cu usually less than twice as long as cu-v 7
- 7(6). Scape relatively short (length approximately 1.5 times width), flattened on condylar surface; basitibial plate incompletely or completely bordered by carinae; S3 with mostly straight, elongate setae on apical margin (curved in *Pseudepeolus willinki* Roig-Alsina) *Pseudepeolus*
- Scape length variable, not flattened on condylar surface; basitibial plate absent or rarely incompletely bordered by carinae; S3 with setae usually undifferentiated on apical margin, rarely elongate or curled 8
- 8(7). Mandible lacking distinct preapical tooth; pygidial plate usually with median constriction, often apically differentiated to form distinct, down-turned, posterior surface; S7 usually with median emargination on distal margin, apicolateral lobes not attaining apical margin between lobes, and apical setae mostly ventral, forming distinct pocket near apicolateral lobe; gonostylus lacking basal lobe; penis usually lacking lateral projections or sometimes with subapical, lamellate projection; dorsobasal lobe of penis valve covering basolateral margin of penis; antennal pedicel usually set into scape *Triepeolus*
- Mandible usually with preapical tooth; pygidial plate almost always all in one plane, broadly rounded posteriorly; S7 usually lacking median emargination on distal margin, apicolateral lobes exceeding apical margin between lobes, and with apical setae mostly dorsal, on surface leading to lateral lobe; gonostylus with basal angle or lobe; penis with widely divergent, fleshy lateral lobe, lacking in *Trophocleptria* group; dorsobasal lobe of penis valve not covering basolateral margin of penis; antennal pedicel usually largely exposed *Epeolus*
- 9(4). Processes of S6 spatulate, with apical principal setae indicated by small denticles (Fig. 95-3d); pseudopygidial area forming wide apical lunule of silvery setae (Fig. 95-3b); apical ventral surface of pygidial plate with two medial, flattened, rounded processes, sometimes very reduced *Epeolus*
- Processes of S6 rodlike, with apical principal setae elongate and hooked (Fig. 95-3c); pseudopygidial area variable, very rarely forming wide lunule of silvery setae on apical margin; apical ventral surface of pygidial plate with lateral, curled, scroll-like processes 10
- 10(9). Supraclypeal area produced into bulbous protrusion with weak median carina; scutellum relatively flat but bearing two mammiform tubercles; pseudopygidial area with median longitudinal row of dark, stout setae, and with apical margin convex; preoccipital carina continuously curved, not angulate at upper corners of head *Rhinepeolus*
- Supraclypeal area not bulbous, with strong or weak protrusion and carina; scutellum variable but not bearing mammiform tubercles; pseudopygidial area variable but lacking median, longitudinal row of dark, stout setae;

- preoccipital carina forming angles or broken at upper corners of head (Fig. 95-4a) 11
- 11(10). Scape length about twice width, forming subbasal angle on lateral surface (seen with antenna directed upward) so that only basal third or less tapers toward basal bulb; preoccipital carina complete or absent at upper corners of head; basitibial plate completely bordered by carina; first and second flagellar segments of about same length *Doeringiella*
- Scape length usually only 1.5 times its width, rarely twice, not forming subbasal angle on lateral surface, basal half or more tapering toward basal bulb; preoccipital carina absent at upper corners of head or along entire upper border of head; basitibial plate absent to completely bordered by carina; first flagellar segment usually shorter than second, rarely the same length 12
- 12(11). Scutum almost always with elongate longitudinal bands of appressed setae reaching middle; preoccipital carina absent on upper corners of head or entire sector absent *Triepeolus*
- Scutum with longitudinal bands of appressed setae often reduced, usually restricted to anterior fourth; preoccipital carina absent at upper corners of head only *Pseudepeolus*

Genus *Doeringiella* Holmberg

Doeringiella Holmberg, 1886a: 151; 1886b: 233. Type species: *Doeringiella bizonata* Holmberg, 1886, monobasic.

Doeringiella (*Orfilana*) Moure, 1954b: 266. Type species: *Doeringiella variegata* Holmberg, 1886 = *Epeolus holmbergi* Schrottky, 1913, by original designation.

This is the *Doeringiella* s. str. of Michener (2000). Superficially, the species of *Doeringiella* are similar in appearance to those of *Triepeolus*. The distinguishing characters are indicated in the key to genera.

In some males of this genus the scape is greatly enlarged, with a cavity opening on the lower surface (Fig. 95-4b). Moure (1945b) proposed the name *Orfilana* for the species of *Doeringiella* that do not have the antennal scape of the male thus enlarged. Illustrations of various structures were provided by Roig-Alsina (1989b) and Rightmyer (2004).

■ *Doeringiella* occurs from Cautín, Chile, north to Lima, Peru, and from Chubut province north to Formosa province, Argentina, to Bolivia and the state of Pará, Brazil. The 31 species then known were revised by Roig-Alsina (1989b). Compagnucci and Roig-Alsina (2003) reviewed *Doeringiella*, recognizing 35 species, and prepared a new phylogenetic analysis of the species. This analysis indicated that, contrary to earlier conclusions, swollen male antennal scapes arose only once.

So far as known, species of this genus are cleptoparasites in nests of Apinae, mostly Eucerini (Roig-Alsina, 1989b). The only firm host record is *Svastrides* (Eucerini); probable hosts, also Eucerini, are in the genera *Svastra* and *Melissoptila*. Other possible hosts are in the genera *Diadasia* (Emphorini) and *Caupolicana* (Colletidae).

of the egg and other aspects of cleptoparasitic behavior of *Epeolus* have been published by Rozen and Favreau (1968) and Torchio and Burdick (1988).

Key to the Groups of *Epeolus*

1. Scape, excluding basal bulb, 1.5 times as long as broad or little more; venter of mesothorax with anterior vertical part set off from horizontal part by a transverse carina, the lower part of omaular carinae continued across the venter, often irregular or broken medially and rarely weak; lateral angle of pronotum rounded but well developed, its anteroposterior length about equal to diameter of pronotal lobe (but *if* only moderately developed, then transverse ventral mesothoracic carina strong); scutellum coarsely punctate or reticulate, often produced to two posteriorly directed teeth *Trophocleptria* group
- Scape, excluding basal bulb, twice as long as broad or nearly so; venter of mesothorax with anterior vertical part rounding onto horizontal part with no intervening transverse carina; lateral angle of pronotum weakly developed, its anteroposterior length much less than diameter of pronotal lobe; scutellum punctured, biconvex *Epeolus* group

The *Trophocleptria* group differs from the *Epeolus* group not only in the characters listed in the key above, but also in the larger stigma and the longer marginal cell, typically longer than the distance from its apex to the wing tip. These wing characters suggest the very different genus *Odyneropsis*. *Epeolus bifasciatus* Cresson, the only *Trophocleptria* in temperate North America, is intermediate in wing characters. It also has areas of white pubescence on the metasoma that are poorly developed in other species. It was regarded as intermediate between *Epeolus* s. str. and *Trophocleptria* by Michener (1954b). Male genitalia and hidden sterna of the *Trophocleptria* group were illustrated by Michener (1954b) and Rightmyer (2004).

■ The *Epeolus* group occurs across the entire holarctic region, north to the latitudes of subarctic Alaska and Finland, from coast to coast in North America, and in the Eastern Hemisphere from the Canary Islands, Portugal, and Britain to Japan. Southward, the *Epeolus* group is not known from tropical India or southeast Asia but occurs through Africa to the Cape and through the Americas to Cuba, Central America, and Colombia. About 55 species are known from North and Central America, about 35 from the palearctic region, and 11 from sub-Saharan Africa. The species of western North America were revised by Brumley (1965), those of sub-Saharan Africa were revised by Eardley (1991b). Yasumatsu (1933) and Hirashima (1955) gave keys to Japanese species; Bischoff (1930) and Lith (1956) gave accounts of palearctic species. Richards (1937) revised British species and gave an extensive account of the relations of those species and their morphs to their *Colletes* hosts.

■ The *Trophocleptria* group occurs from Connecticut, Minnesota, and Colorado, USA, south through the tropics to the province of Buenos Aires, Argentina. There are about eight species.

Genus *Odyneropsis* Schrottky

Odyneropsis consists of moderate-sized to rather large (body length, 9 to 17 mm), slender species without areas of white, appressed pubescence, except sometimes on the pronotum, propodeum, and anterior surface of T1. The entire body is sericeous because of short, appressed, brown hairs. The body shape and long wings cause large species to closely resemble *Polistes* wasps, and some species have yellowish areas reinforcing the resemblance. An unusual feature is the near absence of the maxillary palpus in most species of *Odyneropsis* s. str.; it is probably represented by a minute subspherical body in approximately the position of the palpus. By contrast, Moure (1955) observed one specimen with three segments on one side, only the basal one on the other, and some species of the subgenus *Parammobates* have three segments. The pseudopygidial area of T5 of the female is rather large, covered with dark hairs, and the posterior margin has a broad notch, from the apex of which a narrow, smooth, shining, longitudinal line extends forward, bisecting the area. This line is posterior to the median depression of T5, which is surrounded by a ridge (absent anteriorly in the subgenus *Parammobates*). The structure of T5 suggests that of *Rhogepeolus*, which, however, is a much more ordinary epeoline. Unlike that of *Rhogepeolus*, the frontal carina is strong along the summit of the interantennal prominence. S6 of the female has a relatively broad disc, as in *Epeolus* and *Rhogepeolus*; the apicolateral process is hairy and bears at its apex a row of curved, thickened setae, enlarged and broadened at their blunt apices. Illustrations of numerous structures were provided by Rightmyer (2004).

Key to the Subgenera of *Odyneropsis*

1. T5 of female with small oval middorsal depression surrounded by an apparent carina formed by short, blunt, multiridged setae; body length 14 mm or more *O. (Odyneropsis)* s. str.
- T5 of female with such middorsal depression not well defined, entirely open anteriorly; body length 11 mm or less *O. (Parammobates)*

Odyneropsis / Subgenus *Odyneropsis* Schrottky, s. str.

Odyneropsis Schrottky, 1902a: 432. Type species: *Odyneropsis holosericea* Schrottky, 1902 = *Rhathymus armatus* Friese, 1900, by original designation.

This subgenus contains the large species of the genus that often resemble vespid wasps of the genus *Polistes*.

■ This subgenus occurs from southern Arizona, USA, and the states of Puebla and Jalisco, Mexico, south through the tropics to Bolivia, Tucumán province, Argentina, and the state of Santa Catarina, Brazil. The ten species were listed and annotated by Moure (1955).

Known hosts are species of the colletid genus *Priloglossa* (Rozen, 1966a, 1994b).

Odyneropsis / Subgenus *Parammobates* Friese

Parammobates Friese, 1906e: 118. Type species: *Parammobates brasiliensis* Friese, 1906, monobasic.

96. Tribe Ammobatoidini

This tribe was called the Neopositini by Linsley and Michener (1939) and Michener (1944), and the Holcopositini by Rozen (1966a). Recognition of Neopositini (*sensu* Michener, 1944) or Holcopositini suggests the placement of *Ammobatoides* in a different tribe from *Holcopasites* and its relatives, but the differences lie mostly in size and size-related characters such as the stigmal size; *Ammobatoides* is large with a relatively small stigma. The name Ammobatoidini has priority over Holcopositini (Michener, 1986a), and the name Neopositini is not applicable to members of this tribe, since *Neopasites* is a genus of the Biastini. See the account of the subgenus *Neopasites* (Sec. 97) for details.

These are pasitiform bees, often coarsely punctate, commonly with a red metasoma, and with short, sparse pubescence that commonly includes patches of pale, often white, scalelike appressed hairs, the metasoma thus often having a spotted rather than banded appearance (Fig. 96-1a). In banded species, however, the metasomal bands are usually at the bases of terga rather than at the apices as they are in most bees, and are usually broken medially or, in *Aethammobates*, there are both basal and apical bands; in *Ammobatoides*, however, the bands are apical, although in females largely missing dorsally except on T4. The labrum appears longer than broad (Fig. 96-3), although sometimes only as long as broad, particularly in small species. In both sexes, there is a pygidial plate, that of the male well defined on a strongly projecting process, that of the female almost always hidden by T5, which has a longitudinal median rounded ridge and no recognizable pseudopygidial area. The ridge and sometimes adjacent parts of T5 are minutely punctate and may represent the pseudopygidial area. The marginal cell is rounded at the apex, which is away from the wing margin (Fig. 96-2); the second submarginal cell is much smaller than the first, and the first recurrent vein joins either cell. S5 of the female is apically emarginate. S6 of the female (Fig. 91-2a) is similar to that of Biastini. (The female of *Aethammobates* is unknown.)

Except for a South African *Ammobatoides* species, this is a holarctic tribe of four genera, one or two of which are so similar to *Schmiedeknechtia* that they could reasonably be considered as subgenera.

Key to the Genera of the Ammobatoidini

- 1. Body length 10 mm or more; eyes of male strongly converging above; inner orbits of female gently concave (palearctic) *Ammobatoides*
- Body length 7.5 mm or less; eyes of male diverging above; inner orbits of female straight or slightly convex 2
- 2(1). Pronotum with well-developed, horizontal dorsal collar surface extending across between dorsolateral angles; scutum without vertical anterior surface; T1 with anterior surface deeply concave, separated from dorsal surface by strongly arcuate carina that forms strong anterolateral tergal angles (Egypt) *Aethammobates*
- Pronotum with dorsal surface of collar broadly inter-

- rupted medially, where scutum curves down to form vertical anterior surface; T1 with anterior surface shallowly to deeply concave, without or with only suggestion of carina between anterior and dorsal surfaces, anterolateral part of T1 rounded 3
- 3(2). Male antenna 12-segmented; middle flagellar segments broader than long; metasomal terga with graduli strong, shelflike, a deep transverse furrow immediately behind each gradulus on at least T2 to T4; clypeus and nearby structures dark (nearctic) *Holcopasites*
- Male antenna 13-segmented; middle flagellar segments as long as or longer than broad; metasomal terga with weaker graduli, not emphasized by furrow behind each gradulus; clypeus (at least lower margin), bases of mandibles, labrum, and antennal scape yellow (palearctic) *Schmiedeknechtia*

Genus *Aethammobates* Baker

Aethammobates Baker, 1994: 155. Type species: *Aethammobates prionogaster* Baker, 1994, by original designation.

This genus, known from a single male specimen, differs from the other genera in the striking characters indicated in the key. Some of the other characters suggest that it may be more like a large species (body length 7.5 mm) of the otherwise small *Schmiedeknechtia* than was recognized when *Aethammobates* was described. The middle femora are much expanded below; an approach to this feature occurs in large species of *Holcopasites*. The posterior margins of the discs of the terga are elevated and strongly denticulate; this feature is also approached in large *Holcopasites*. Thus some of the apparent generic characters may be merely features of large species of the *Holcopasites-Schmiedeknechtia* group. In the 13-segmented, rather long antennae and probably in the lack of a groove behind each tergal gradulus, *Aethammobates* resembles *Schmiedeknechtia*.

■ *Aethammobates* is known only from Egypt. The one species is *A. prionogaster* Baker.

Genus *Ammobatoides* Radoszkowski

Ammobatoides Radoszkowski, 1867: 82 (not Schenck, 1869).

Type species: *Phileremus abdominalis* Eversmann, 1852, by designation of Sandhouse, 1943: 525.

Phiarus Gerstaecker, 1869: 147. Type species: *Phileremus abdominalis* Eversmann, 1852, monobasic.

Euglages Gerstaecker, 1869: 149. Type species: *Euglages scripta* Gerstaecker, 1869, monobasic.

Paidia Radoszkowski, 1872b: 10 (not Herrich-Schaffer, 1847), unnecessary replacement for *Ammobatoides* Radoszkowski, 1868. Type species: *Phileremus abdominalis* Eversmann, 1852, autobasic.

Paedia Dalla Torre, 1891: 147, unjustified emendation of *Paidia* Radoszkowski, 1872.

This genus contains the largest pasitiform bees except for those in the Malagasy genus *Melanempis* and some large species of *Pasites* in the Ammobatini; the body

97. Tribe Biastini

This is a holarctic tribe of small, black epeoliform bees, often with the metasoma red; thus the appearance is as in various groups of pasitine bees (Fig. 97-1). The pubescence is not largely scalelike, as it is in the Townsendiellini and Neolarrini, although the hairs may be short and plumose. The labrum is much broader than long (Fig. 96-3b). The antennae are short, the scape less than twice as long as broad. T5 of the female has a pseudopygidial area or a median marginal lunule with slightly distinctive short pubescence. T6 usually lacks a pygidial plate in the female, but in *Rhopalolemma* the plate is recognizable. The marginal cell is pointed or narrowly rounded, the apex bent away from the wing margin (Figs. 97-2, 97-3b), and there are two submarginal cells, the second at least two-thirds as long as the first and receiving both recurrent veins, but in some specimens of *Rhopalolemma* there are three submarginal cells. The apex of S6 of the female has two lobes, each bearing a few coarse, blunt bristles, these lobes separated by a broad concavity, as illustrated by Linsley and Michener (1939) and Roig-Alsina (1991b); see also Figure 91-2b. The sting is reduced, sometimes bifurcate at the tip, and the gonostylus of the female is enlarged medially (in *Rhopalolemma* apically), unlike that of other bees.

The recent discovery of the genus *Rhopalolemma* demolished some of the long-recognized tribal characters. For example, the Biastini were unique among small pasitiform bees because of their preapical mandibular tooth, but *Rhopalolemma* has simple mandibles.

So far as is known, all Biastini are cleptoparasites in nests of Rophitinae; known hosts for *Biastes* are *Dufourea*, *Rophites*, and *Systropha*; for *Neopasites*, *Dufourea*; and for *Rhopalolemma*, *Protodufourea*.

Key to the Genera of the Biastini

- 1. Mandible simple; T6 of female produced medially, with pygidial plate; gonostylus of female clubbed; scape 1.75 times as long as its maximum diameter (basal bulb excluded) (nearctic) *Rhopalolemma*
- Mandible with preapical tooth; T6 of female without indication of pygidial plate, produced to sharp point at each side, the margin between lateral projections strongly, broadly concave, hairy; gonostylus of female thickened medially; scape about 1.5 times as long as its maximum diameter (basal bulb excluded) 2
- 2(1). T5 of female with small, raised, semicircular, sloping pseudopygidial area covered with appressed pale hairs; metanotum with median elevation well above level of adjacent part of scutellum; second submarginal cell longer than first (palearctic) *Biastes*
- T5 with ill-defined lunule of pale or black hairs, not raised, not sloping, and usually broader than semicircular; metanotum without median elevation, not or little above level of adjacent part of scutellum; second submarginal cell as long as or shorter than first (nearctic) *Neopasites*

Genus *Biastes* Panzer

Biastes Panzer, 1806: 239. Type species: *Tiphia brevicornis* Panzer, 1798, monobasic.

Rhineta Illiger, 1807: 198. Type species: *Nomada schottii* Fabricius, 1804 = *Tiphia brevicornis* Panzer, 1798, monobasic.

Melittoxena Morawitz, 1873: 154. Type species: *Nomada truncata* Nylander, 1848, monobasic.

Biastoides Schenck, 1874: 252. Type species: *Pasites punctatus* Schenck, 1870 = *Phileremus emarginatus* Schenck, 1853, monobasic.

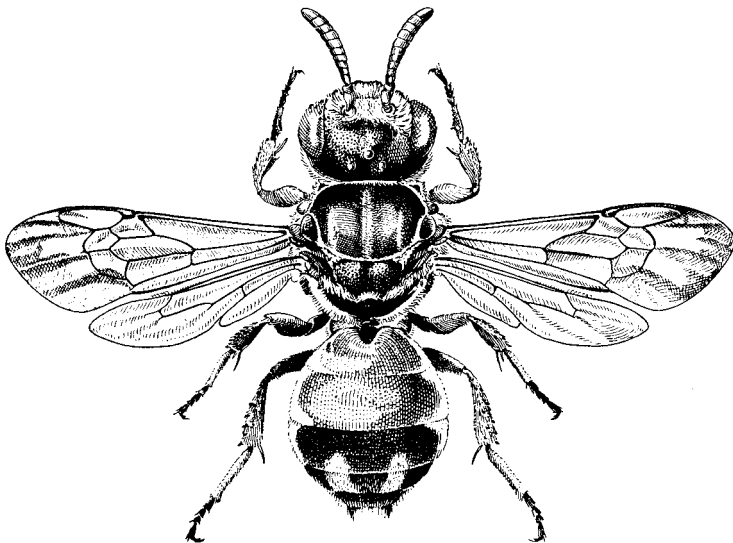


Figure 97-1. *Neopasites fulviventris* (Cresson), female. Length 8 mm. Drawing by F. Abernathy, from Linsley, 1943c.

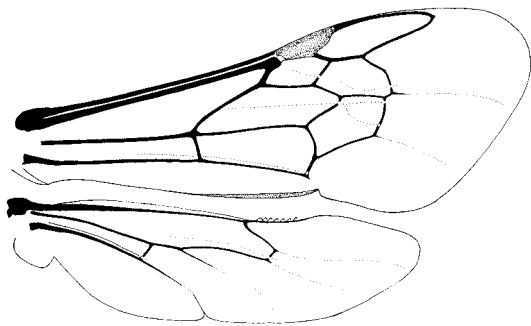


Figure 97-2. Wings of *Biastes brevicornis* (Panzer).

Biastes is similar to *Neopasites*; the two could be considered as only subgenerically distinct. The principal differences are indicated in the key to genera. In some species the male antennae have only 12 segments. The body length is 5 to 9 mm. In species that I have studied, the maxillary palpus is less reduced than that in *Neopasites*, four- or five-segmented. Male genitalia and hidden sterna were illustrated by Popov (1933a), who recognized *Biastoides* and *Melittoxena* as subgenera. These structures were also illustrated by Radoszkowski (1885) and Iuga (1958). For comments on S6 of the female, see the account of *Neopasites*.

■ This genus occurs in Europe, north to 55°N in Finland, and east to the Urals and Caucasus. The four species were revised by Warncke (1982).

Species of this genus are believed to parasitize *Dufourea*, *Rophites*, and *Systropha* (Rophitinae). The larva was briefly described by Rozen (1993a). The egg is laid lying in a groove in the host cell wall, parallel to the surface. Thus one whole side of the egg, rather than just one end, is exposed.

Genus *Neopasites* Ashmead

This is the North American counterpart of *Biastes*, from which it differs in the characters indicated in the key to genera. In *Neopasites* the punctuation of the body is finer than that in some *Biastes*, but the general appearance is similar. Michener (1944) indicated that S6 of the female in *Biastes* might differ from that of *Neopasites*, because Grütte (1935) illustrated the sternal disc in *Biastes* as reduced to a transverse bar while Linsley and Michener (1939) illustrated a moderate-sized disc for *Neopasites*. Actually, in both genera there is a well sclerotized, curved bar along the emargination between the two apical lobes, and the rest of the disc, which is rather membranous, was omitted by Grütte. The structure is alike in the two gen-

era; see Figure 91-2b. The male genitalia and apical sterna of both sexes were illustrated by Linsley and Michener (1939); see Figure 91-3e-g.

Neopasites was revised by Linsley (1943c) under the name *Gnathopasites*.

Key to the Subgenera of *Neopasites*

1. Maxillary palpus shorter than or as long as greatest galeal width, one- or two-segmented; second submarginal cell about as long as first; body length 3.5 to 6.0 mm *N. (Micropasites)*
- Maxillary palpus much longer than greatest galeal width, four-segmented; second submarginal cell much shorter than first; body length 6 to 8 mm. *N. (Neopasites s. str.)*

Neopasites / Subgenus *Micropasites* Linsley

Gnathopasites (Micropasites) Linsley, 1942: 130. Type species: *Neopasites cressoni* Crawford, 1916, by original designation.

■ *Micropasites* is found from California to New Mexico, USA. The three species were revised by Linsley (1943c); at least one undescribed species is known.

The hosts of *Micropasites* are in the genus *Dufourea* (Rophitinae); Torchio et al. (1967) gave an account of the biology of two species, and Rozen (1966a) described the larva.

Neopasites / Subgenus *Neopasites* Ashmead s. str.

Neopasites Ashmead, 1898: 284. Type species: *Phileremus fulviventris* Cresson, 1878, by original designation.

Gnathopasites Linsley and Michener, 1939: 272. Type species: *Phileremus fulviventris* Cresson, 1878, by original designation.

■ *Neopasites* s. str. is known only from California. The two species were revised by Linsley (1943c).

Neopasites s. str. is a parasite of *Dufourea* (Rophitinae), according to Torchio et al. (1967).

Ashmead's (1898) description of *Neopasites*, as well as the specimen on which he based it, show that he actually had before him a specimen of what is now called *Holcopasites*, which he misidentified as *Phileremus fulviventris* Cresson. Linsley and Michener (1939) therefore transferred the name *Neopasites* to *Holcopasites* and proposed a new name, *Gnathopasites*, for what is now called *Neopasites*, as shown in Table 97-1. The Code, 3rd ed., art. 70, however, specifies that the name used in designating a type species is to be followed, unless the Commission rules otherwise. There is no need to request a Commission opinion for uncommon and little-known insects like these, especially since for many years the Linsley and Michener proposal has been rejected by melittologists and the names have been applied as they are here.

Genus *Rhopalolemma* Roig-Alsina

Rhopalolemma Roig-Alsina, 1991b: 33. Type species: *Rhopalolemma robertsi* Roig-Alsina, 1991, by original designation.

Table 97-1. Equivalents of Certain Generic Names in the Nomadinae.

Tribe	Linsley & Michener (1939)	Other authors and current usage
Biastini	<i>Gnathopasites</i>	<i>Neopasites</i>
Ammobatoidini	<i>Neopasites</i>	<i>Holcopasites</i>

99. Tribe Neolarrini

This nearctic tribe, consisting of the single genus *Neolarra*, contains minute to small, slender, pasitiform bees, black or with the metasoma red, the body pruinose because of being more or less covered with short, appressed, scalelike, pale pubescence. The wing venation is distinctive, often not extending beyond the middle of the forewing (Fig. 99-1); the broadly truncate marginal cell is little if any longer than the stigma, and the second submarginal cell is either absent or very short, receiving only the second recurrent vein, which may be absent. Veins C and R of the forewing are very close together. In small species, e.g., of the subgenus *Phileremulus*, these veins are in contact, leaving no costal cell between them; therefore they do not run properly in most keys to superfamilies of Hymenoptera. T5 of the female is sometimes notched or cleft midapically, but it has nothing resembling a pseudopygidial area. S6 of the female has a narrow apical emargination, and the lobe on each side lacks coarse setae (Fig. 91-2g, h). The male lacks a pygidial plate but T7 is produced to a short, bare process. The male genitalia and apical sterna of both sexes were illustrated by Linsley and Michener (1939).

The tribe Neolarrini is found only in North America; its species are cleptoparasites in the nests of *Perdita* and perhaps *Calliopsis* (*Micronomadopsis*) (Panurginae)

(Shanks, 1978). The larva was described by Rozen (1966a).

Neolarrini is not particularly similar to any other tribe; its closest relative is best considered undecided. Michener (1944) thought it was closest to Townsendiellini but gave no analysis of characters. Rozen (1966a), on the basis of larval characters, placed it as the sister group of *Neopasites* (Blastini). Alexander (1990), using adult characters, reached the same conclusion, but other phylogenetic studies (Roig-Alsina, 1991b; Rozen, Roig-Alsina, and Alexander, 1997; see Fig. 87-5) placed it far from the Blastini, e.g., as the sister group of Ammobatini + Caenoprosopidini.

Genus *Neolarra* Ashmead

The principal characters of the genus are those of the tribe. The two subgenera are separable by the following key. Revisions were by Michener (1939b) and Shanks (1978).

Key to the Subgenera of *Neolarra*

- 1. Scutellum widest at or in front of middle; outer margin of axilla rounded *N. (Neolarra s. str.)*
- Scutellum widest behind middle; axilla produced to acute tooth *N. (Phileremulus)*

Neolarra / Subgenus *Neolarra* Ashmead s. str.

Neolarra Ashmead, 1890: 8. Type species: *Neolarra pruinosa* Ashmead, 1890, monobasic.

Neolarra s. str. contains the larger species of *Neolarra*, 3 to 7 mm in body length; most species have two submarginal cells (Fig. 99-1a), although some have only one.

■ The range of *Neolarra* s. str. is from California north and east to Idaho, Montana, North Dakota, and Texas, USA, and south to Jalisco and Durango, Mexico. The 11 species were revised by Shanks (1978).

Neolarra / Subgenus *Phileremulus* Cockerell

Phileremulus Cockerell, 1895: 9. Type species: *Phileremulus vigilans* Cockerell, 1895, by original designation.

This subgenus contains minute species, 2.0 to 3.7 mm in body length, having only one submarginal cell, and lacking also the second recurrent vein (Fig. 99-1b).

■ *Phileremulus* occurs from southern Alberta and Saskatchewan, Canada, to Tennessee, Georgia, Texas, and California, USA, and Hidalgo to Baja California, Mexico. The three species were revised by Shanks (1978).

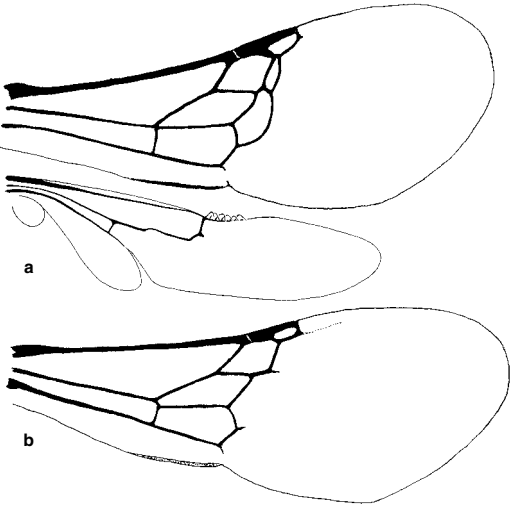


Figure 99-1. Wings of *Neolarra*. a, *N. (Neolarra) verbesinae* Cockerell; b, Forewing of *N. (Phileremulus) vigilans* (Cockerell).

100. Tribe Ammobatini

In this tribe of cleptoparasitic pasitine bees the body is typically black, the metasoma usually wholly or partly red; rarely, the head and thorax also are reddish. The pubescence is not scalelike, usually sparse, although apical patches or broken bands of white, appressed hair are common on the metasomal terga (Fig. 100-1). The long labrum (longer than broad, as in Figure 96-3, or about as long as broad) is unusual in Apidae but is shared with Ammobatoidini and Caenoprosopidini. The antennae are not so short as in the Biastini, the scape (excluding the basal bulb) being 2.5 or more times as long as broad. T5 of the female completely lacks a pseudopygidial area, and T6 usually lacks a recognizable pygidial plate, although there is a distinct area usually having erect hairs or bristles; sometimes, as in *Melanempis*, there is an area, defined by a carina, that is probably not homologous to a pygidial plate. In males there may be a well-defined projecting pygidial plate or a flat, rounded or truncate but otherwise undefined projection of T7. S5 of the female is usually strongly curved up laterally, around the apical process of S6 and the sting, and covering the lateral parts of T6. S6 of the female has a slender apical process, sometimes completely retracted; sometimes it is a simple spine but usually it is notched (Fig. 91-2i) or bifurcate; it lacks the coarse setae found in most Nomadinae.

Interesting features found in the tribe include 12-segmented male antennae in *Pasites*, *Melanempis*, and *Parammobatodes*, and extreme variability in the maxillary palpi. For example, in the genus *Pasites*, these palpi vary from absent to five-segmented; in *Ammobates* from one- to six-segmented (one- to five-segmented in the subgenera *Euphileremus* and *Parammobatodes*); and in *Oreopasites*, from four- to six-segmented. Both Popov (1951c) and Warncke (1983) tabulated the number of segments in palpi of various species. In *O. barbarae* Rozen the labial palpi are three-segmented instead of four-segmented. A distinctive feature of males of the tribe, not found in other bees and also absent in *Melanempis*, is a tuft or fringe of

long, pale hairs arising from the lower lateral part of the clypeus and curved back adjacent to the side of the labrum.

Popov (1951c) recognized two tribes, Ammobatini and Pasitini, for the bees here included in the Ammobatini. Rozen (1992b) discussed the tribal characters in detail without deciding whether to recognize the two tribes; Rozen and McGinley (1974b) had shown that larval characters do not seem to support recognition of two tribes. In a phylogenetic study of genera and a revision of afrotropical species, Eardley and Brothers (1997) recognized only one tribe. I believe that recognition of two tribes would obscure the close relationships among all genera here included in the Ammobatini. Warncke (1983) placed the entire tribe in one genus, *Pasites*.

Key to the Genera of the Ammobatini

- 1. Mandibles in repose directed posteromesally, so that, except when badly worn, they cross one another well before their apices, their anterior margins forming angle of 90° to 145° 2
- Mandibles in repose directed mesally, so that they overlap one another and cross, if at all, at extremely obtuse angle 4
- 2(1). Vein Rs of hind wing transverse or directed basad from costal margin, discal cell (R) thus not extending distad from base of vein Rs; first recurrent vein joining distal half of second submarginal cell, second medial cell thus greatly narrowed toward costa (palearctic, oriental) *Parammobatodes*
- Vein Rs of hind wing directed strongly distad, discal cell (R) thus extending beyond base of vein Rs; first recurrent vein joining basal half of second submarginal cell, second medial cell thus not greatly narrowed toward costa 3
- 3(2). Labrum pointed apically, entirely exposed in front of crossed mandibles in repose; male without defined pygidial plate; S5 of female without preapical collar of long hairs (Africa) *Sphecodopsis*
- Labrum truncate or broadly rounded apically, extend-

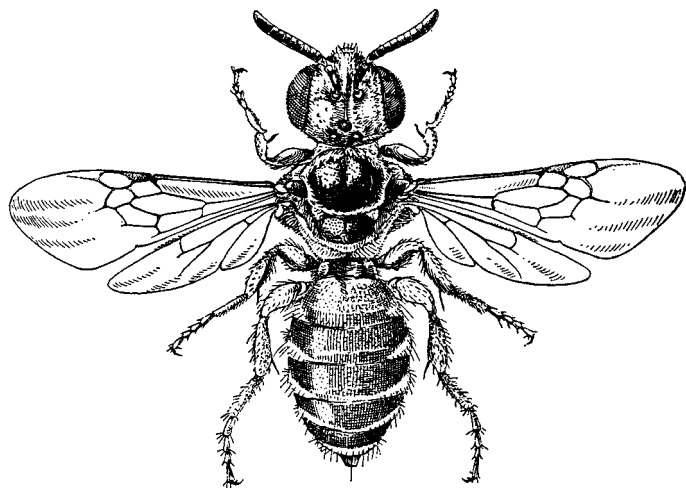


Figure 100-1. *Oreopasites euphorbiae* Cockerell, female. Drawing by F. Abernathy, from Linsley, 1941.

- ing under and beyond crossed mandibles; male with pygidial plate; S5 of female with preapical V- or U-shaped collar of long hairs (nearctic) *Oreopasites*
- 4(1). S5 of female with posterior margin (curved up and sometimes around process of S6 and sting) unmodified, covered with fine hairs; labrum not extending under or posterior to mandibles in repose (male antenna 12-segmented) (palearctic, oriental, Africa) *Pasites*
- S5 of female with posterior margin bare at least medially, usually with median protuberance or troughlike projection that may look superficially like another sternum; labrum commonly extending under and sometimes beyond mandibles in repose 5
- 5(4). Female with nearly circular, hairless pygidial plate margined by circular carina, on posterior subvertical surface of T6; jugal lobe of hind wing essentially absent; maxillary palpus absent; body length 15 to 18 mm; male antennae 12-segmented (Madagascar) *Melanempis*
- Female without circular pygidial plate; jugal lobe of hind wing present, but small as in most Nomadinae; maxillary palpus one- to six-segmented; body length 4 to 13 mm; male antenna 13-segmented (male unknown in *Spinopasites*) 6
- 6(5). S6 of female ending in a single spine; S5 of female with posterior part bent upward and not visible from below, preapical concavity V-shaped and not defined by hairy ridge (northwest Africa) *Spinopasites*
- S6 of female bifurcate; S5 of female with posterior part not so strongly bent upward, visible from below, preapical concavity more U-shaped and defined by hairy ridge (palearctic, oriental, southern Africa) *Ammobates*

Genus *Ammobates* Latreille

This is the largest genus of the Ammobatini. Its species have the usual pasitiform aspect; usually the metasoma is partly or wholly red, the whole body rarely red-brown. Unlike those of *Pasites*, the male antennae are 13-segmented; S5 of the female exhibits generic characters as indicated in the key to genera.

Revisional studies were by Popov (1951c) and Warncke (1983); the former includes excellent illustrations of male genitalia and hidden sterna as well as habitus drawings; the latter includes sketches of diverse structures. Good illustrations were also published by Radoszkowski (1885), Iuga (1958), and Mavromoustakis (1968b).

There are three groups here considered as subgenera; certain of them have been considered as genera by other authors in the past.

Key to the Subgenera of *Ammobates*

1. Second submarginal crossvein meeting second recurrent vein (S5 of female with deep longitudinal channel, the apex deeply emarginate; maxillary palpus six-segmented; S8 of male with disc and spiculum forming triangle; apical process of S8 broad, membranous, sometimes spiculate, not cleft) *A. (Xerammobates)*
- Second submarginal crossvein distal to second recurrent vein 2
- 2(1). T6 of female more or less rooflike with longitudinal median ridge, sides sloping, densely hairy; labrum relatively short, 1.5 times as long as its basal width *A. (Euphileremus)*

- T6 of female flat or convex, not longitudinally ridged, sparsely or at most only partially hairy, often with specialized median area, or posterior part bent down and vertical, or both; labrum more than twice as long as its basal width *A. (Ammobates s. str.)*

Ammobates / Subgenus *Ammobates* Latreille s. str.

Ammobates Latreille, 1809: 169. Type species: *Ammobates rufiventris* Latreille, 1809, by designation of Latreille, 1810: 439. [A subsequent and invalid designation was listed by Michener, 1997b.]

Phileremus Latreille, 1809: 169. Type species: *Epeolus punctatus* Fabricius, 1804, by designation of Latreille, 1810: 439. [A subsequent and invalid designation was listed by Michener, 1997b.]

Ammobatoides Schenck, 1869: 349 (not Radoszkowski, 1867). Type species: *Ammobates bicolor* Lepeletier, 1825 = *Epeolus punctatus* Fabricius, 1804, monobasic.

Ammobates (Caesarea) Friese, 1911d: 142. Type species: *Ammobates depressa* Friese, 1911, by designation of Sandhouse, 1943: 532.

In species of this subgenus the labrum is over twice as long as its basal width, and the face, especially the clypeus, is strongly protuberant. The body length is 4 to 11 mm.

■ *Ammobates* s. str. occurs from Portugal and Morocco north in Europe to 53° latitude, east to Uzbekistan, and south to southern India, with one disjunct species in Namibia and South Africa (Eardley and Brothers, 1997). Of a total of about 30 species, those of the palearctic region were revised by Warncke (1983).

Probable hosts include *Ancyla* (Ancylini), *Tetraloniella* (Eucerini), and *Anthophora* (Anthophorini) (Warncke, 1983).

Ammobates / Subgenus *Euphileremus* Popov

Ammobates (Euphileremus) Popov, 1951c: 906. Type species: *Phileremus oraniensis* Lepeletier, 1841, by original designation.

In *Euphileremus*, as in *Xerammobates* and the genus *Parammobatodes*, the labrum is about 1.5 times as long as the basal width and the face is almost flat. T6 of the female is more or less horizontal, commonly with a median ridge and thus roof-shaped. The body length is 5.0 to 8.5 mm.

■ *Euphileremus* occurs from the Canary Islands, Morocco, and Spain east through southwestern Asia and southern Russia to Uzbekistan. About seven species were revised by Warncke (1983).

So far as is known, species of this subgenus parasitize *Tetraloniella* (Eucerini) (Warncke, 1983).

Ammobates / Subgenus *Xerammobates* Popov

Ammobates (Xerammobates) Popov, 1951c: 904. Type species: *Ammobates oxianus* Popov, 1951, by designation of the Commission, Opinion 1853 (1996). [See Michener, 1997b. Popov (1951c) misidentified the original type species of *Xerammobates* as *Ammobates biastoides* Friese, 1895, which is actually a species of *Ammobates* s. str. (Baker, 1995b).]

Omachthes Friese, 1909a: 436, unjustified emendation of *Omachthes* Gerstaecker, 1869.

Pasitomachthes Bischoff, 1923: 596. Type species: *Pasitomachthes nigerrimus* Bischoff, 1923, by original designation. [See note by Michener, 1997b.]

Pasitomachthes Sandhouse, 1943: 586, unjustified emendation of *Pasitomachthes* Bischoff, 1923.

The species of *Pasites* resemble superficially those of *Ammobates*, usually having a red metasoma and varying in body length from 2.3 to 12.5 mm. The labrum is variable, from about as long as broad to much longer than broad; its apex is pointed or truncate and visible in front of the closed mandibles which usually cross, forming a very obtuse angle. The pygidial plate is recognizable or not in each sex. The male genitalia and sterna and female sting were illustrated by Radoszkowski (1885), Popov (1931b), and Iuga (1958).

■ *Pasites* ranges from Portugal and Morocco to Mongolia and Japan, south to India and through the whole of Africa. Of about 21 species, two are palearctic, 15 are from sub-Saharan Africa, three from Madagascar, and one is from India. African species were revised by Bischoff (1923) and Eardley and Brothers (1997); Malagasy species, by Eardley and Pauly (in Pauly et al., 2001).

Pasites maculatus Jurine parasitizes *Pseudapis* (Nomiinae) (Rozen, 1986); and Nomiinae are probable hosts of other species. The egg of *Pasites* is folded into a U and inserted in the cell wall of the host, the truncate anterior end flush with the cell wall, all this much as in *Oreopasites* (Rozen, 1986).

The palearctic species, *Pasites maculatus* Jurine, differs enough from some of the sub-Saharan and Indian species that the latter have usually been regarded as generically distinct, being placed in *Morgania* or *Omachthes*. Eardley and Brothers (1997) united them, and their phylogenetic analysis showed *P. maculatus* Jurine falling among African species. The swollen upper paraocular area and the depression above the antennal sockets to accommodate the scapes are features of *P. maculatus* not well developed in other species; further, in some African species the antennal pedicel is firmly set in the apex of the scape, whereas it seems to be more freely articulated in others, including *P. maculatus*. Moreover, *P. maculatus* lacks maxillary palpi, whereas in other species (except *P. gnoma* Eardley) they are present, although highly variable. Baker (1974b) emphasized a distinction between *Pasites* and *Morgania* (including *Omachthes*) based on T6 and S5 of the female. In *Morgania* the pygidial plate, or at least its posterior margin, is clearly defined by a carina behind which the tergum is vertical, covered with short, dense, dark-colored, specialized hairs, and the apical lobes of S5 are bent upward, forming with the posterior surface of T6 a truncate apex of the metasoma. *Pasites maculatus* has almost these same features but they are less developed. T6 has the pygidial plate weakly defined, not margined by a carina, and the surface behind it is relatively short, less vertical, and the specialized dark hairs are limited to a small space, while the apical lobes of S5 are less strongly bent upward. Thus the apex of the metasoma is less truncate than that of *Morgania*. Comparable structures are found in each group, and intergradation in various features exists; I

agree with Eardley and Brothers (1997) in not recognizing *Morgania* as a genus.

Genus *Sphecodopsis* Bischoff

This southern African genus consists of rather small, black forms 4 to 9 mm long, the metasoma usually partly or wholly red. The male antennae are 13-segmented. The scutellum is gently and evenly curved as seen in profile. S5 is either strongly or shallowly concave apically when viewed from behind and has a midapical prominence, sometimes weak or even included in an apical emargination.

Eardley (1994a) was entirely correct in emphasizing the close relationship of *Pseudodichroa* to *Sphecodopsis*. He did not recognize subgenera, but I retain *Pseudodichroa* for the present as a subgenus, since it is quite different and he did not show how it is related to *Sphecodopsis* s. str.; it could be the sister group to that subgenus.

Key to the Subgenera of *Sphecodopsis*

1. S6 of female produced to a long, slender, median spine; S5 of female with midapical process that is truncate and longer than broad *S. (Pseudodichroa)*
- S6 of female produced to a process with bifurcate apex; S5 with midapical projection rounded or truncate, much broader than long, sometimes scarcely recognizable, sometimes in emargination that is broader than projection *S. (Sphecodopsis* s. str.)

Sphecodopsis / Subgenus *Pseudodichroa* Bischoff

Pseudodichroa Bischoff, 1923: 595. Type species: *Omachthes capensis* Friese, 1915, by designation of Sandhouse, 1943: 593.

Males of species probably belonging to this subgenus do not exhibit distinctive subgeneric characters. The body length is 6 to 11 mm. Diverse structures were well illustrated by Rozen (1968a).

■ *Pseudodichroa* is known only in western Cape Province, South Africa. The two species were revised by Rozen (1968a).

The hosts are species of *Scapter* (Colletinae); the behavior and mode of parasitism were described by Rozen and Michener (1968). The egg is inserted into the cell wall of the host; a flange around the outer end fits against the cell wall so that the egg would probably be difficult to detect.

Sphecodopsis / Subgenus *Sphecodopsis* Bischoff s. str.

Sphecodopsis Bischoff, 1923: 593. Type species: *Omachthes capicola* Strand, 1911, by original designation.

Sphecodopsis (Pseudopasites) Bischoff, 1923: 593. Type species: *Pasites pygmaeus* Friese, 1922, by designation of Sandhouse, 1943: 594.

The body length is 4 to 9 mm.

■ *Sphecodopsis* s. str. is found in southern Africa from Namibia and Zimbabwe south through South Africa; most species are in western Cape Province and Namibia. The eight species were revised by Bischoff (1923) and Eardley and Brothers (1997).

101. Tribe Caenoprosopidini

The Caenoprosopidini consist of strongly punctate bees with a red metasoma and short, appressed, plumose hairs forming narrow, white, apical tergal bands. T5 of the female lacks a pseudopygidial area. The antennae arise far below the middle of the face. The preoccipital carina is strong. Unlike that of other L-T bees, the episternal groove is very long, extending to the thoracic venter; it is perhaps not homologous to the comparable groove frequently found in S-T bees. The omaulus is angular, the upper part almost carinate but often hidden by hair. An unusual feature among the small groups of Nomadinae is the presence of small basitibial plates in both sexes. The sting is reduced. S6 of the female is elongate, consisting of two longitudinal rods pointed distally and connected by a narrow membrane (Fig. 91-2j). The male genitalia are small and simple, the gonostyli, gonocoxites, and gonobase being fused into a single unit (Roig-Alsina, 1987; Fig. 101-2).

All studies of relationships of the tribes of Nomadinae have shown this tribe to be affiliated with the Ammobatini. Rozen and Roig-Alsina (1991) found larvae to be almost identical. Phylogenetic studies (Roig-Alsina, 1987, 1991b; Alexander, 1990; Eardley and Brothers, 1997) show *Caenoprosopis* or the Caenoprosopidini as the sister group to the Ammobatini. The major differences, such as fusion of male genitalic parts and division of S6 of the female into two parts, lead me to recognize the two tribes.

Bees of this tribe occur in Argentina, Paraguay, and southern Brazil. They have no relatives in South America; the Ammobatini are found in the palearctic region, Africa, and western North America.

Key to the Genera of Caenoprosopidini

- 1. Total length of marginal cell much greater than that of stigma, about as long as distance from its apex to wing tip (Fig. 101-1); second submarginal cell about two-thirds as long as first; axillae and scutellum not spined, but with projecting convex lateral edges; middle flagellar segments about as long as broad *Caenoprosopis*
- Total length of marginal cell as long as stigma, much less

than distance from its apex to wing tip; second submarginal cell less than half as long as first; axillae and posterior lateral angles of scutellum produced to posteriorly directed spines; middle flagellar segments much broader than long *Caenoprosopina*

Genus *Caenoprosopina* Roig-Alsina

Caenoprosopina Roig-Alsina, 1987: 312. Type species: *Caenoprosopina holmbergi* Roig-Alsina, 1987, by original designation.

This genus consists of a species that superficially resembles a small *Holcaspites*. The body length is 4 to nearly 5 mm. Many structures were illustrated by Roig-Alsina (1987).

■ *Caenoprosopina* is known from Catamarca to Salta, Argentina. The only species is *C. holmbergi* Roig-Alsina.

Rozen and Roig-Alsina (1991) found *Caenoprosopina* to be a parasite of *Callonychium* (Panurginae).

Genus *Caenoprosopis* Holmberg

Caenoprosopis Holmberg, 1886b: 235, no included species; 1887a: 22, one included species. Type species: *Caenoprosopis crabronina* Holmberg, 1887, first included species. *Austrodioxys* Cockerell, 1916a: 432. Type species: *Austrodioxys thomasi* Cockerell, 1916 = *Caenoprosopis crabronina* Holmberg, 1887, monobasic.

This genus consists of a species that looks superficially like a *Holcaspites*. The body length is 6.0 to 8.5 mm. Many structures were illustrated by Roig-Alsina (1987). The fusion of the genitalic parts (Fig. 101-2), shared also with *Caenoprosopina*, is one of the unusual features that emphasize the distinctness of the tribe from the Ammobatini.

■ *Caenoprosopis* occurs from the province of Neuquén, Argentina, to the state of São Paulo, Brazil. There is a single species, *C. crabronina* Holmberg.

Rozen and Roig-Alsina (1991) found *Caenoprosopis* to be a cleptoparasite in nests of *Arhysosage* (Panurginae).

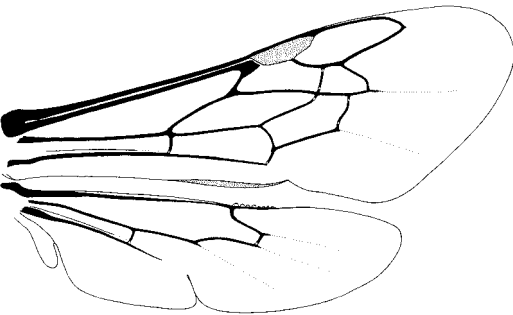


Figure 101-1. Wings of *Caenoprosopis crabronina* Holmberg.

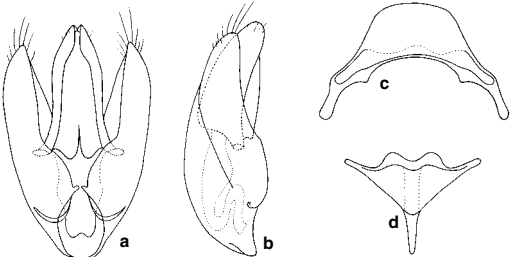


Figure 101-2. Structures of male of *Caenoprosopis crabronina* Holmberg. a, b, Genitalia, in dorsal and lateral views; c, d, S7 and S8. From Roig-Alsina, 1987.

103. Tribe Isepeolini

The Isepeolini have frequently been placed among the Nomadinae. The tribe consists of South American cleptoparasitic epeoliform bees, usually with conspicuous patches of white or rarely blue pubescence on the metasoma (Fig. 103-2g). Like the Protepeolini, it could be a basal branch of the Nomadinae, but in the absence of synapomorphies showing this relationship, it is here regarded as a tribe of the subfamily Apinae. This position is supported by Rozen's (1991a) suggestion, which is based on larval characters, of a relationship between Isepeolini and Ericrocidini, another tribe of Apinae.

Some characters of Isepeolini include the apically fimbriate and emarginate T6 of the female, without spine-like setae, and the apically pointed S6 of the female, sometimes with a series of spinelike or peglike preapical setae laterally (Fig. 103-2a-c). The axillae are rounded, not pointed as in Epeolini. As in Protepeolini the three submarginal cells are subequal in the lengths of their posterior margins (Fig. 103-1). The wings have bare areas basally; distally they are strongly papillate. The pygidial plate is entirely absent in both sexes. S7 of the male has a hairless median apical projection but no lobes (Fig. 103-2e); S8 sometimes has a median apical projection, sometimes does not. The male genitalia usually have both dorsal and ventral gonostyli (Fig. 103-2d); sometimes both are much reduced and fused to the gonocoxite.

This tribe was revised by Roig-Alsina (1991a), who provided numerous illustrations of structures, including the male genitalia and hidden sterna. Male genitalia were also illustrated by Toro and Rojas (1968), who provided a key to Chilean species.

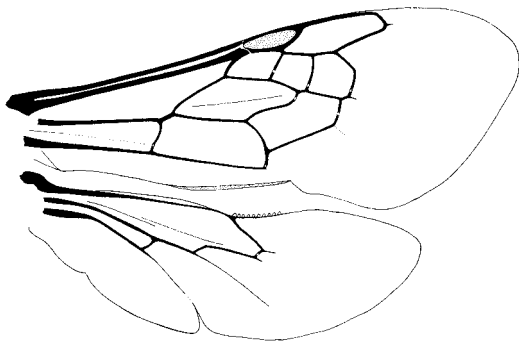


Figure 103-1. Wings of *Isepeolus viperinus* (Holmberg).

Key to the Genera of the Isepeolini (Modified from Roig-Alsina, 1991a)

- 1. Vertex of head between lateral ocellus and eye slightly rounded to flat as seen in frontal view, at most with shallow depression; first flagellar segment of male conspicuously widened apically, as in female; sclerotized apex of female S6 bordered by long spinelike setae (Fig. 103-2c), and lateral apical margin folded down, partially covering such setae; apex of female T5 prolonged by membranous rim bordered by upcurved hairs; male S6 without preapical tubercle *Melectoides*
- Vertex of head with conspicuous depression between eye and ocelli as seen in frontal view; first flagellar segment of male slightly widened apically, contrasting with conspicuous widening in female; sclerotized apex of female S6

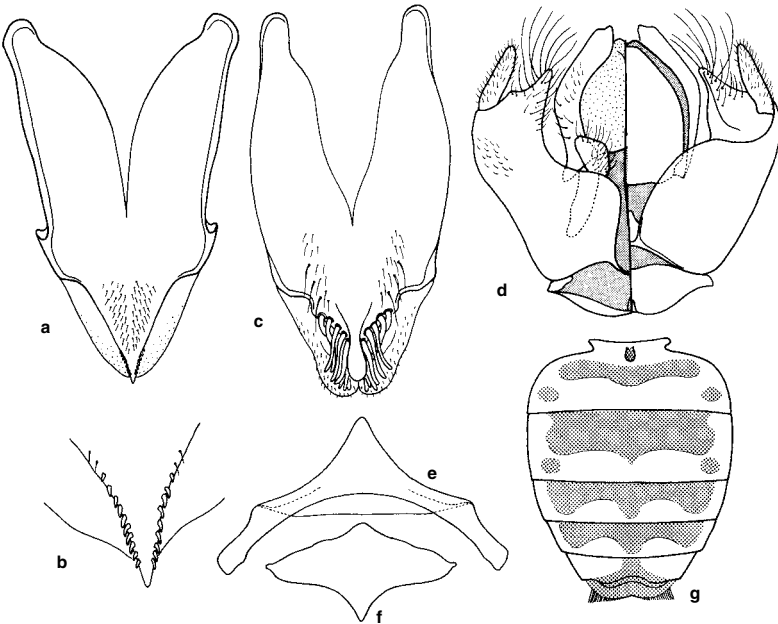


Figure 103-2. Structures of Isepeolini. a, S6 of female of *Isepeolus viperinus* (Holmberg); b, Apex of same, enlarged; c, S6 of female of *Melectoides kiefferi* (Jørgensen); d, Male genitalia of *Melectoides triseriatus* (Friese), dorsal view on the right; e, f, S7 and S8 of the same; g, Dorsal metasomal pattern of *Melectoides politus* Roig-Alsina. From Roig-Alsina, 1991a).

with spinelike setae absent or short (Fig. 103-2a), barely visible at low magnification, lateral apical margin not expanded, not folded down; apex of female T5 without membranous rim; male S6 with large preapical tubercle

..... *Isepeolus*

Genus *Isepeolus* Cockerell

Isepeolus Cockerell, 1907b: 64. Type species: *Isepeolus albopictus* Cockerell, 1907 = *Epeolus viperinus* Holmberg, 1886, monobasic.

Palinepeolus Holmberg, 1909b: 77. Type species: *Epeolus viperinus* Holmberg, 1886, by original designation.

Calospiloma Brèthes, 1909b: 68 footnote. Type species: *Epeolus viperinus* Holmberg, 1886, by original designation.

Isepeolus consists of species with the metasoma white spotted, 6 to 11 mm in body length.

■ This genus occurs from Santa Cruz province, Argentina, and Magallanes, Chile, north to the state of Ceará, Brazil; there is a possibly erroneous record from Cali, Colombia. Eleven species were recognized in the revision by Roig-Alsina (1991a).

Isepeolus has been reared from nests of *Colletes* (Michener, 1957; Lucas de Oliveira, 1966); the first-stage larva, with its sclerotized head and large, curved mandibles, was described in those papers and by Rozen (1991a); mature

larvae were described by Lucas de Oliveira and by Rozen (1966a).

Genus *Melectoides* Taschenberg

Melectoides Taschenberg, 1883: 75. Type species: *Melectoides senex* Taschenberg, 1883, by original designation.

Most species in this genus are nonmetallic, white-spotted or banded, and rather small in size (length 7.5-11.0), thus resembling species of *Isepeolus*. Two species, however, *Melectoides senex* Taschenberg and *tucumanus* (Fries), have metallic blue or green metasomal pubescence, in the latter species lacking white patches; these two species, both large (length 12.5-16.0 mm), resemble *Mesoplia* or *Mesonychium* (Ericrocidini) in superficial appearance.

■ *Melectoides* occurs in Chile from Atacama to Cautín and in Argentina from Salta province to Chubut province. The ten species were revised by Roig-Alsina (1991a).

The large species of *Melectoides* are too large to parasitize *Colletes*; perhaps they attack diphaglossine Colletidae. However, *Melectoides bellus* (Jørgensen) is a cleptoparasite of *Canephorula apiformis* (Fries) in the Eucerini, as shown by Michelette, Camargo, and Rozen (2000).

104. Tribe Osirini

The tribe Osirini is composed of cleptoparasitic genera that were long included in the Nomadinae. Roig-Alsina (1989a), however, found that these genera do not possess some of the principal apomorphies of the Nomadinae, such as (1) the largely retracted, truncate, emarginate to bifid or pointed S6 of the female, usually with spinelike apical or preapical setae, (2) the specialized median area usually present on T5 of the female, sometimes clearly defined and called the pseudopygidial area, and (3) the simple stipital margin presumably resulting from loss of the stipital comb. The Osirini possess various features also found in nonparasitic Apinae but absent in the Nomadinae, such as a little-modified (although attenuate and tubular in *Osiris*) S6 of the female; a ridge on the outer surface of the stipes; and a translucent, impunctate lamella at the posterior end of the metasternum. It therefore seems likely that the Osirini evolved parasitic habits independently from the Nomadinae, a conclusion supported by the phylogenetic analysis of Roig-Alsina and Michener (1993); see Figure 102-1. Other distinctive characters of Osirini include a small, round, central sclerite in the cervical membrane (unique among bees); a ventral carina along the inner and basal margins of the fore coxa; a large stigma, nearly three to about eight times as long as the prestigma; and a marginal cell that is narrowly separated from the wing margin throughout its length (Fig. 104-1), so that there is a membranous rim in front of the marginal cell. There are three submarginal cells. The body is nomadiform (Fig. 104-2a) or epeoliform. The male genitalia, diverse in structure, usually have both dorsal and ventral gonostyli, but only one is present in *Epeoloides* and *Osiris*.

It is likely that Osirini (except *Epeoloides*) are all cleptoparasites of Tapinotaspidini. Rozen (1984a) found a

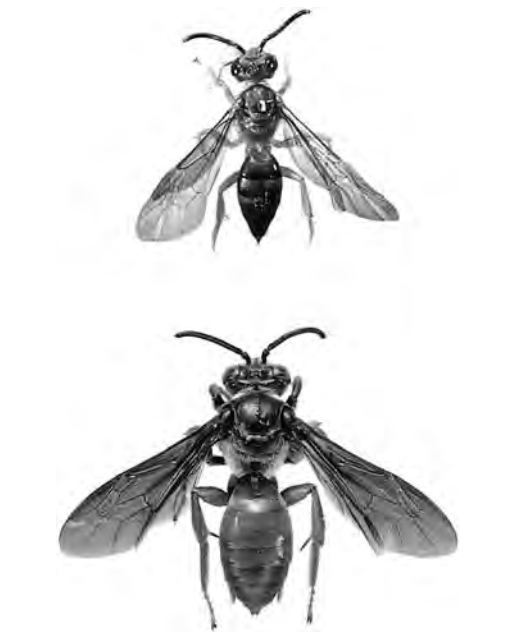


Figure 104-2. Cleptoparasitic Apidae. Above, *Osiris* sp., female; Below, *Rhathymus* sp., male. From Michener, McGinley, and Danforth, 1994.

Parepeolus (*Parepeolus*) *niger* Roig-Alsina in a nest of *Tapinotaspoides tucumana* (Vachal), and Roig-Alsina (1989a) published records of occurrence of *Parepeolus* (*Ecclitodes*) *stuardi* (Ruiz) around nest sites of *Chalepogenus caeruleus* (Friese). Rozen et al. (2006) studied the biology of *Parepeolus minutus* Roig-Alsina in nests of *Chalepogenus* (*Lanthanomelissa*) *betinae* (Urban) and *Protosiris gigos* Melo in nests of *Monoeca haemorrhoidalis* (Smith). *Osiris* has been reared from nests of *Paratetrapedia* by Camillo, Garófalo, and Serrano (1993). In contrast, the holarctic genus *Epeoloides* is a parasite of *Macropis* in the Melittidae.

Key to the Genera of the Osirini (Modified from Roig-Alsina, 1989a)

1. Jugal lobe of hind wing rounded; basal vein of fore wing basal to cu-v or sometimes meeting it; lateral margin of clypeus not continued by paraocular carina above level of anterior mandibular articulation; labrum with pair of preapical tubercles or two to four teeth near middle of disc; ventral gonostylus of male bifid, dorsal gonostylus large, flattened (South America) *Parepeolus*
- Jugal lobe of hind wing elongate (Fig. 104-1); basal vein of fore wing apical to cu-v or sometimes meeting it; lateral margin of clypeus continued by paraocular carina above level of anterior mandibular articulation; labrum with single preapical tubercle or several small preapical denticles; ventral gonostylus of male simple, dorsal gonostylus small, cylindrical or absent 2

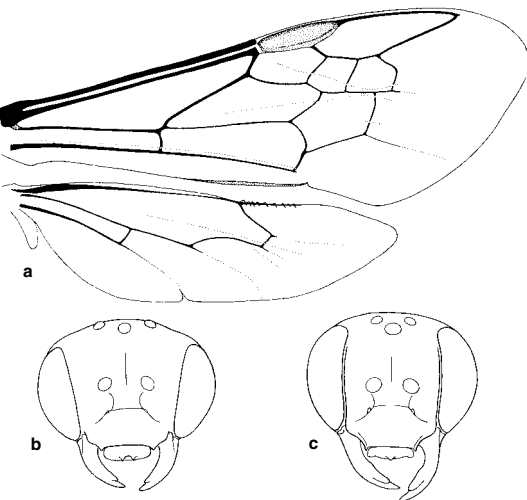


Figure 104-1. Osirini. a, Wings of *Osiris* sp.?; b, c, Faces of females of *Parepeolus minutus* Roig-Alsina and *Epeoloides pilosula* (Cresson). b, c, from Roig-Alsina, 1989a.

2(1). Apex of marginal cell curved away from wing margin (Fig. 104-3a); paraocular carina almost reaching summit of eye (Fig. 104-1c); eyes of male strongly converging above, those of female slightly so; labrum with strong preapical tubercle; stigma 2.8-3.2 times as long as prestigma; rami of male claws similar and adjacent (holartic)..... *Epeoloides*

— Apex of marginal cell terminating close to wing margin (Fig. 104-1a); paraocular carina fading near lower margin of eye; eyes of both sexes parallel or diverging above; labrum with several small denticles; stigma more than 5.5 times as long as prestigma; inner ramus of male claws shorter than outer, flattened 3

3(2). Collar of pronotum dorsally bulging, with a distinct subhorizontal portion connecting swollen, rounded dorsolateral angles; inner margin of eye with shallow emargination near upper third; mandible with two subapical teeth; S6 of female usually exceeding T6 (Fig. 104-4c); apex of pygidial plate of female not reaching margin of tergum, a wide rim present apical to plate; pygidial plate of male reduced to sclerotization on tergal margin; male gonostylus simple (neotropical) *Osiris*

— Transverse middorsal part of pronotal collar short or absent, dorsolateral lobes or angles thus not connected by elevated collar; inner margin of eye almost straight; mandible with one subapical tooth or simple (an inner angle sometimes present); S6 of female not exceeding T6; apex of pygidial plate of female constituting apex of tergum; pygidial plate of male present; male gonostylus double, i.e., upper and lower gonostyli well separated 4

4(3). Inner margins of eyes almost parallel; mandible long, strongly curved, outer basal width 0.33 to 0.35 times length of mandible; mesepisternum with hairs simple or at most with one or two basal barbs; legs slender; strigular concavity 0.26 to 0.27 times length of basitarsus; scutum as long as intertegular distance (neotropical) *Protosiris*

— Inner margins of eyes convergent below; mandible short, outer basal width 0.40 to 0.45 times length of mandible; at least anterior part of mesepisternum with plumose hairs; legs short, stout; strigular concavity shallow, 0.38 to 0.41 times length of basitarsus; scutum shorter than intertegular distance (South America)..... *Osirinus*

Genus *Epeoloides* Giraud

Epeoloides Giraud, 1863: 44. Type species: *Epeoloides ambiguus* Giraud, 1863 = *Apis coecutiens* Fabricius, 1775, monobasic.

Viereckella Swenk, 1907: 298. Type species: *Viereckella obscura* Swenk, 1907 = *Nomada pilosula* Cresson, 1878, by original designation.

In this genus the vestiture of the head and thorax is relatively long and plumose (although not hiding the surface), unlike that of other Osirini. The body is epeoliform, black or with the metasoma red; length is 7 to 10 mm. A striking character of the male is the small, elongate, strongly elevated pygidial plate margined by strong carinae that nearly enclose the plate anteriorly as well as posteriorly.

Because it is parasitic on the melittid genus *Macropis*

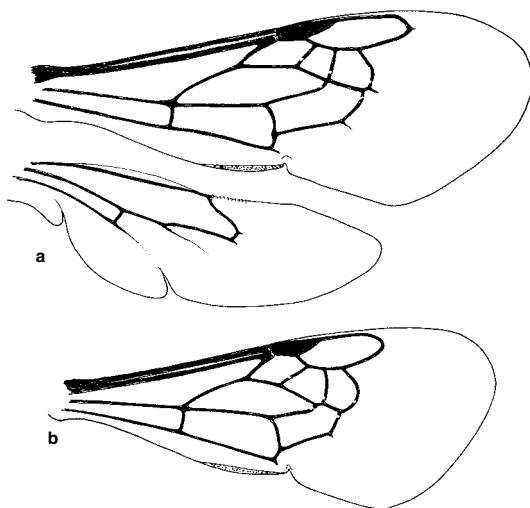


Figure 104-3. Wings of Osirini. **a**, *Epeoloides coecutiens* (Fabricius); **b**, Forewing of *Parepeolus niger* Roig-Alsina. From Roig-Alsina, 1989a.

rather than on Tapinotaspidini, and because it is holarctic (the other Osirini are strictly neotropical), *Epeoloides* might be convergent with the other Osirini rather than phylogenetically closely related. Roig-Alsina (1989a) was the first to note the similarity; *Epeoloides* was previously placed by itself in a tribe Epeoloidini. At present there is no good reason to disagree with Roig-Alsina's decision to include *Epeoloides* in the Osirini; convergence in characters like the separation of the marginal cell from the wing margin (Fig. 104-3) seems unlikely.

■ The range of *Epeoloides* includes Northern and Central Europe from the Netherlands and France to western Russia, and North America from Quebec, Canada, to Georgia west to North Dakota and Nebraska, USA. There are probably only two species, one in Europe, the other in America. Linsley and Michener (1939) gave a description of the genus; that work, Iuga (1958), Popov (1958a), Mitchell (1962), and Roig-Alsina (1989a) all illustrated the male genitalia and other structures.

The American species, *Epeoloides pilosula* (Cresson), seemed not to have been collected in the USA since 1942 and in Canada since 1960. However, it was rediscovered in 2002 in Nova Scotia, Canada (Sheffield et al., 2004). The biology of the European *E. coecutiens* (Fabricius) was dealt with by Bogush (2005). Its presumed host, *Macropis*, remains widespread but localized to patches of its required flower, *Lysimachia* (Primulaceae).

Genus *Osirinus* Roig-Alsina

Osirinus Roig-Alsina, 1989a: 17. Type species: *Osirinus lemniscatus* Roig-Alsina, 1989, by original designation.

Compsocepta Moure, 1995b: 143. Type species: *Compsocepta fasciata* Moure, 1995 = *Osirinus lemniscatus* Roig-Alsina, 1989, by original designation.

Osirinus and *Protosiris* resemble *Osiris*, with which they have usually been confused, in their nomadiform

body, shiny reddish, yellow, or testaceous integument (dark in some *Osirin*), and pointed marginal cell. They differ from *Osiris* in the shorter head, absence of a malar space, more abundant plumose hairs, and other characters described in the key to genera. S6 of the female is relatively short and blunt (Fig. 104-4a), not attenuate and pointed as in *Osiris*. The body length is 5.5 to 10.0 mm.

■ This genus occurs from the provinces of Córdoba and Entre Ríos, Argentina, north to northeastern Brazil. The seven species were revised by Melo and Zanella (2003).

Genus *Osiris* Smith

Osiris Smith, 1854: 288. Type species: *Osiris pallidus* Smith, 1854, by designation of Sandhouse, 1943: 580.

Euthyglossa Radoszkowski, 1884a: 21. Type species: *Euthyglossa fasciata* Radoszkowski, 1884 = *Eucera euthyglossa* Dalla Torre, 1896, monobasic.

Osiris consists of slender, nomadiform, smooth, shiny, almost completely impunctate species (Fig. 104-2a) 6.2 to 18.0 mm long, the whole body often yellow or testaceous but sometimes blackish. The head is somewhat elongate compared to other *Osirini*, the length of the malar area being one-fifth to one-half as long as the basal width of the mandible. Behind the ocelli is a preoccipital carina. S6 of the female is elongate, usually exceeding T6, the lateral margins upturned to form a guide for the enormous sting (Fig. 104-4b, c), which at least in death is often exerted and reflexed above the metasoma. Male genitalia and hidden sterna were illustrated by Popov (1939c), Michener (1954b), and Shanks (1986).

■ *Osiris* occurs from the states of Nayarit and San Luis Potosí, Mexico, south through the tropics to Bolivia, Misiones Province, Argentina, and the state of Santa Catarina, Brazil. Shanks (1986, 1987) revised the 21 species of the genus.

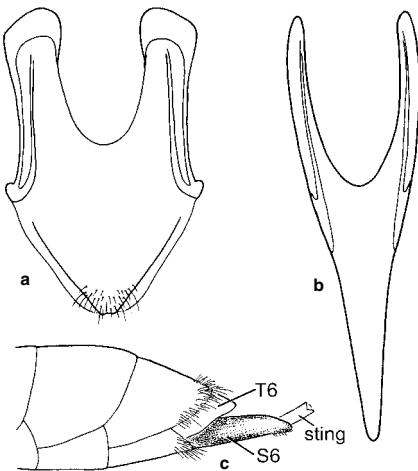


Figure 104-4. Apical structures of female *Osirini*. **a**, S6 of *Osirin rutilans* (Fries); **b**, S6 of *Osiris variegatus* Smith; **c**, Side view of apex of metasoma of *Osiris* sp., the distal part of the sting omitted. **a**, **b**, from Roig-Alsina, 1989a; **c**, from Michener, McGinley, and Danforth, 1994.

Genus *Parepeolus* Ducke

This South American genus includes epeoliform species 6 to 13 mm in length. The two subgenera have hitherto been regarded as genera, but are so similar and contain so few species that subgeneric rank, which emphasizes their close relationship, seems preferable.

Key to the Subgenera of *Parepeolus*

1. Propodeal triangle microstriate; posterior margin of first submarginal cell about twice as long as apical margin; maxillary palpus six-segmented; metasomal terga with apical bands of pale hairs; supratergular carina curved cephalad of tegula, following tegular margin, reaching mesoscutum-pronotal lobe boundary close to tegula *P. (Ecclitodes)*
- Propodeal triangle polished, smooth or with few scattered punctures; posterior margin of first submarginal cell less than 1.5 times as long as apical margin (Fig. 104-3b); maxillary palpus four- to five-segmented; metasomal terga black or variously patterned with pale hairs, an apical band, when present, appearing only on T1; supratergular carina slightly curved, directed anteriorly, diverging from tegular margin and reaching mesoscutum-pronotal lobe boundary near middle of that margin *P. (Parepeolus s. str.)*

Parepeolus / Subgenus *Ecclitodes* Roig-Alsina

Ecclitodes Roig-Alsina, 1989a: 9. Type species: *Epeolus stuardi* Ruiz, 1935, by original designation.

Ecclitodes includes bees with apical zones of white, appressed hairs on T1 to T5. They therefore superficially resemble *Epeolus* in the Nomadinae.

■ This subgenus occurs from Nuble to Valdivia, Chile, and in the province of Río Negro, Argentina. The only described species is *Parepeolus (Ecclitodes) stuardi* (Ruiz); Roig-Alsina (1989a) gave a full account of the subgenus (as a genus) and indicated that there may be two species.

Parepeolus / Subgenus *Parepeolus* Ducke s. str.

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

Parepeolus s. str. consists of largely black species, sometimes having spots of pale pubescence on the metasomal terga, the pubescence sometimes forming an apical pale band on T1 only. To the distinguishing characters listed in the key to subgenera can be added the usually rounded rather than somewhat truncate apex of the marginal cell (Fig. 104-3b) and the occurrence of the subgenus in warmer environments.

■ *Parepeolus* s. str. occurs from the provinces of Buenos Aires and La Pampa, Argentina, north to the state of Pará, Brazil. The four species were revised by Roig-Alsina (1989a).

Genus *Protosiris* Roig-Alsina

Protosiris Roig-Alsina, 1989a: 20. Type species: *Osiris obtusus* Michener, 1954, by original designation.

(1947, 1980b). Silveira (1995b) has catalogued the species of Exomalopsini.

This tribe is found only in the New World and is primarily neotropical, although one species of *Anthophorula* extends north to the central USA.

Key to the Genera of the Exomalopsini

1. Hind tibial and basitarsal scopa consisting of sparse, simple or sparsely branched hairs; mandible with preapical tooth that is sometimes minute; S7 of male with disc pentagonal (Fig. 106-3l), median apex separating two apical margins, apicolateral angle with short, robust process; male gonocoxite with apicolateral process from apex of which arises rather long gonostylus, the process and gonostylus sometimes appearing together as basally elbowed gonostylus (Fig. 106-3j) (subtribe Teratognathina) 2
- Scopa consisting of strongly plumose hairs; mandible simple (but with preapical tooth in *Eremapis*); S7 of male variable, not as above; male gonocoxite without apicolateral process from which gonostylus arises (Figs. 106-3, 106-4) (subtribe Exomalopsina) 3
- 2(1). Stigma broad, three times as long as prestigma; pronotal lobe produced to horizontal lamella in female, strong ridge in male, rounded as seen from above (Argentina) *Teratognatha*
- Stigma small, less than twice as long as prestigma; pronotal lobe rounded (South America) .. *Chilimalopsis*
- 3(1). Second medial cell of forewing about as long as second cubital; labrum and clypeus of female yellow; margin of T7 of male produced into a broad, sharp lamella, rounded as seen from above; S7 of male broadly trilobed; hind basitarsus of female without apical process and penicillus (Argentina) *Eremapis*
- Second medial cell of forewing much shorter than second cubital (Fig. 106-2); labrum and clypeus of female entirely dark; margin of T7 of male not produced into a carina or lamella, or, if carina present, then its posterior margin elevated as margin of pygidial plate; S7 of male not trilobed; hind basitarsus of female with apical process and penicillus 4
- 4(3). Basitibial plate of female small, with surface planar, or, if margins of plate raised and central area with velvety pilosity, then transverse carina of T1 of female absent; labrum and clypeus of male yellow or white [except dark in *A. (Anthophoriscia) levigata* Timberlake and *linsleyi* Timberlake and in *A. (Isomalopsis) niveata* (Friese)]; outer side of penis valve without or with small lateral process (Fig. 106-3a, d, g); dorsal flange of male gonocoxite absent *Anthophorula*
- Basitibial plate of female large, central area with velvety pilosity separated from raised margin by groove, and transverse carina of T1 of female present; labrum and clypeus of male entirely dark; outer side of penis valve with strong lateral process; dorsal flange of male gonocoxite present *Exomalopsis*

Genus *Anthophorula* Cockerell

This genus has usually been included in *Exomalopsis* but was differentiated by Silveira (1995a, b). In addition to the characters indicated in the key to genera, it differs from *Exomalopsis* in having the areas between the ocelli

and the eyes convex. The stigma is commonly smaller than in *Exomalopsis*, less than half as long as the length of the marginal cell on the wing margin, but this character is consistent only for the subgenus *Anthophorula* s. str. In *Anthophoriscia* the stigma is often as large as in those *Exomalopsis* having smaller stigmas, although never as large as those in some *Exomalopsis* s. str. The body length ranges from 2.5 to 8.0 mm; the smallest species are in the subgenus *Anthophorula* s. str., but one species of *Anthophoriscia* is only 3.5 mm long. Male genitalia and hidden sterna were illustrated by Michener and Moure (1957), Mitchell (1962), Timberlake (1980b), and Silveira (1995a, b).

As in *Exomalopsis* but not *Eremapis*, nests of *Anthophorula* are usually communally occupied burrows, each being inhabited by several females (Rozen, 1984c). Cells are oval, with a thin waterproof lining. As in the genus *Exomalopsis*, the provision mass is partly lifted off the cell surface by a projection, called a "foot" by Rozen (1977b, 1984a); it presumably reduces the area of moist contact between the provision mass and the cell surface, and thus may reduce the danger of mold. In *A. (Anthophoriscia) sidae* (Cockerell) and *nitens* (Cockerell), larvae of the autumn generation spin cocoons, but those of the summer generation do not (Rozen, 1984a; Rozen and Snelling, 1986), although they retain the cephalic structures characteristic of cocoon-spinning larvae.

Key to the Subgenera of *Anthophorula*

1. Transverse carina of T1 at summit of anterior surface weak or absent in female, that of male absent; peglike setae present on mesal side of male gonostylus (Fig. 106-3d) [not visible in *A. linsleyi* (Timberlake)] (North America) *A. (Anthophoriscia)*
- Transverse carina of T1 of female strong, that of male present; peglike setae absent from male gonostylus 2
- 2(1). Stigma large, four times as long as prestigma, its inner breadth (i.e., not counting marginal veins) much greater than breadth of its marginal veins; yellow marks on clypeus of male absent or restricted to apical transverse line; S6 of male with two apicolateral flanges that bear a series of spicules on their inner margins (Argentina) *A. (Isomalopsis)*
- Stigma small, no more than three times as long as prestigma, its inner breadth (i.e., not counting marginal veins) as great as or less than breadth of its marginal veins; clypeus of male entirely yellow; S6 of male simple (North America) *A. (Anthophorula* s. str.)

Anthophorula / Subgenus *Anthophoriscia* Michener and Moure

Exomalopsis (Anthophoriscia) Michener and Moure, 1957:

433. Type species: *Melissodes pygmaea* Cresson, 1872, by original designation.

Exomalopsis (Panomalopsis) Timberlake, 1980b: 82. Type species: *Exomalopsis linsleyi* Timberlake, 1980, by original designation.

I follow Silveira (1995a, b) in regarding *Panomalopsis* as a derived *Anthophoriscia*; it has unusual male genitalia but does not seem to require subgeneric status.

■ This subgenus occurs across the southern USA from

(1957), Mitchell (1962), Timberlake (1980b), and Silveira (1995a, b).

As in *Anthophorula*, nests, so far as is known, are communal. Zucchi (1973) showed that nests of *Exomalopsis* (*Exomalopsis*) *aureopilosa* Spinola may contain hundreds of females (up to 884) and attain a depth of over 5 meters. Probably females of generation after generation return to the nest and extend it. The cells, which as in most ground-nesting bees are lined with "waxlike" material, are usually vertical, isolated at the ends of lateral, down-curved burrows, but in other species the cells are horizontal or variable in orientation, sometimes seemingly in series (Norden, Krombein, and Batra, 1994). The food mass often lacks the "foot," well known in the genus *Anthophorula*. Larvae may or may not spin cocoons, and those species that do not, such as *E. bruesi* Cockerell, have recessed labiomaxillary regions and reduced salivary lips so that they cannot do so (Rozen, 1997a). There is evidence, summarized by Rozen (1984a), of cooperative provisioning of cells by females; if that is verified, such colonies are probably semisocial or quasisocial. The evidence for such behavior is that females with undeveloped ovaries sometimes collect pollen, and that there are sometimes more pollen gatherers inhabiting a nest than cells being provisioned. The nesting biology of two additional species of *Exomalopsis* with 2 to 12 and 2 to 19 bees per nest was described by Raw (1976, 1977).

median elevated area that broadens toward apex of sternum, forming carina or spine at each side (S7 and S8 of male without peglike setae; vertex of female, between ocellus and eye, excavated) *E. (Exomalopsis s. str.)*

Almeida and Silveira (1999) presented an alternative key to the subgenera of *Exomalopsis*.

Exomalopsis / Subgenus *Diomalopsis* Michener and Moure

Exomalopsis (*Diomalopsis*) Michener and Moure, 1957: 431.

Type species: *Exomalopsis bicellularis* Michener and Moure, 1957, by original designation.

In the genus *Anthophorula*, species with two submarginal cells are close relatives of those with three submarginal cells. In *Exomalopsis*, however, the only two-celled species is distinctive in other respects and appears to warrant its own subgenus. Distinctive characters are the large stigma, longer than the length of the marginal cell on the wing margin, and the pedunculate, apically broad and truncate process of S8 of the male (Fig. 106-4b). The genitalia and hidden sterna were illustrated by Michener and Moure (1957) and Silveira (1995a, b); see also Figure 106-4a-c.

■ This subgenus is known from Paraná and São Paulo, Brazil, and Paraguay. The two species were distinguished by Almeida and Silveira (1999).

Key to the Subgenera of *Exomalopsis*

1. Vertex in frontal view convex; area between lateral ocellus and eye not excavated (except in *E. arcuata* Timberlake) and lateral ocelli below level of summit of head; marginal zones of T1 and T2 of female smooth and glabrous; T2 to T4 of female with white apical fringes sometimes interrupted medially; S7 of male with apical sclerotization forming short transverse sclerite across apex of sternum and fused to arms of disc; S8 of male with apical process a single bare lobe (North and Central America) *E. (Stilbomalopsis)*
- Vertex in frontal view straight; area between lateral ocellus and eye excavated and/or lateral ocelli above level of summit of head; marginal zones of T1 and/or T2 of female punctate and pilose; T2 to T4 of female with apical fringes absent; S7 of male with apical process absent or complex and with two free basolateral lobes under ventral surface; S8 of male with apical process bearing two apical arms (short or long), or, if consisting of a single broad lobe, then lobe hairy (Fig. 106-4) 2
- 2(1). Submarginal cells two (vertex of female, between ocellus and eye, not excavated; T1 of female with premarginal line not depressed; S6 of male entirely flat; S7 and S8 of male with peglike setae) *E. (Diomalopsis)*
- Submarginal cells three 3
- 3(2). T1 of female with premarginal line depressed, forming transverse sulcus, and marginal zone between dorsolateral convexities smooth and shining, comprising no more than two-thirds of dorsal surface of tergum; S6 of male entirely planar *E. (Phanomalopsis)*
- T1 of female with premarginal line not depressed, or, if depressed, then marginal zone between dorsolateral convexities punctate and/or comprising much more than two-thirds of dorsal surface of tergum; S6 of male with

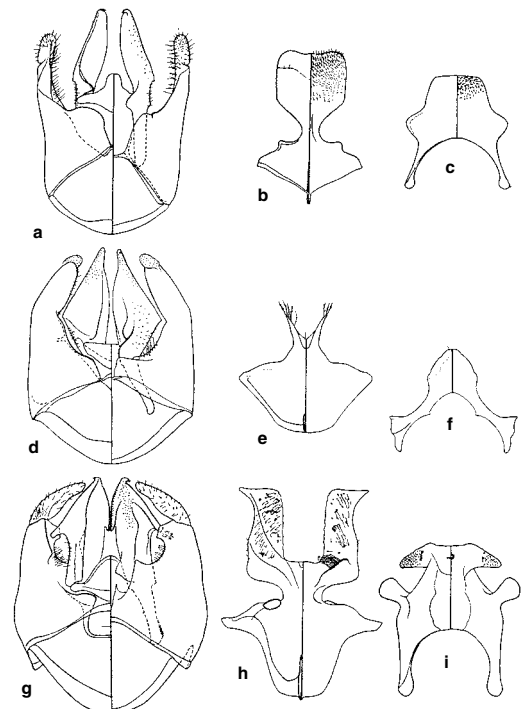


Figure 106-4. Male genitalia, S8, and S7 of *Exomalopsis*. **a-c**, *E. (Diomalopsis) bicellularis* Michener and Moure; **d-f**, *E. (Exomalopsis) aureopilosa* Spinola; **g-i**, *E. (Phanomalopsis) aureosericea* Friese. From Michener and Moure, 1957.

107. Tribe Ancylini

The Ancylini are rather small to moderate-sized (5-13 mm long, mostly under 10 mm), euceriform to almost anthophoriform palearctic Apinae, similar in appearance to and perhaps closely related to the Eucerini or the American tribe Exomalopsini. These relationships, as well as those between the two included genera (*Ancyla* and *Tarsalia*, regarded as congeneric by Warncke, 1979c), were investigated by Silveira (1993a, b), who reached no decisive conclusions. Silveira (1995a, b), however, in another analysis, considered the Ancylini to be probably holophyletic. Baker (1998) restudied the two genera with much more abundant material and considered them not closely related; he removed *Tarsalia* from the Ancylini and placed it as a basal member of the Eucerini, leaving *Ancyla* as the only genus of Ancylini. But since he used only two eucerine genera in his study, and since parsimony analyses are often sensitive to the taxa included, and especially since the characters that he used are not known to me, I have not accepted his conclusions, although they may be correct. Some of the distinctive features of *Ancyla* involve its reduced glossa; some other characters of *Ancyla* may also be loss characters.

In males and some females the clypeus and lower paraoxular areas are partly yellow. The Ancylini differ from the Exomalopsini (other than *Anthophorula* s. str.) by the small stigma, little broader than the prestigma as measured to the wing margin, the stigmal margin in the marginal cell being not or scarcely convex. The base of the propodeum has a subhorizontal zone, best developed in *Tarsalia*, and better developed than in most Exomalopsini. The wings have three submarginal cells, and the marginal cell bends gradually away from the wing mar-

gin distally (Fig. 107-1), not being obliquely truncate as in most Exomalopsini. The scopa on the hind tibia is rather large and consists of plumose hairs. T7 of the male is medially produced and weakly bidentate.

The male genitalia and hidden sterna are similar in *Ancyla* and *Tarsalia* and fundamentally similar to those of the Exomalopsini and Eucerini that have long gonostyli, a somewhat elaborate distal part of S7, and a bilobed apex of S8; these structures are asymmetrical in *Tarsalia*. Silveira (1993b) called attention to a character that appeared to distinguish *Ancyla* and *Tarsalia* from Exomalopsini, namely, a sulcus dividing the male gonocoxite (see Roig-Alsina and Michener, 1993). This sulcus, however, also occurs in some *Exomalopsis*; for example, in *E. mellipes* (Cresson) it is very strong, whereas it is very weak in *Ancyla* and absent in many Exomalopsini.

Key to the Genera of the Ancylini

- 1. Glossa and labial palpus much shorter than prementum (Fig. 107-2); labial palpus with first and second segments not sheathlike, second segment not much longer than broad; clypeus nearly flat, scarcely bent back at side of labrum; T7 of male densely hairy, pygidial plate narrow, triangular, pointed posteriorly, strongly elevated, nearly bare; clypeus of female black; flagellum of male crenulate on undersurface *Ancyla*
- Glossa and labial palpus longer than prementum; labial palpus with first two segments long, sheathlike; clypeus more protuberant, strongly bent back at side of labrum; T7 of male sparsely hairy throughout, pygidial plate, if correctly interpreted, occupying most of dorsum of tergum, defined laterally by strong carinae, and ending in truncate or bidentate apex; clypeus of female often yellow; flagellum of male not crenulate *Tarsalia*

Genus *Ancyla* Lepeletier

Ancyla Lepeletier, 1841: 294. Type species: *Ancyla oraniensis* Lepeletier, 1841, monobasic.

Plistotrichia Morawitz, 1874: 134. Type species: *Nomia flavilabris* Lucas, 1846 = *Ancyla oraniensis* Lepeletier, 1841, monobasic.

Ancyla is extraordinary among L-T bees in that the glossa and labial palpi are short (Fig. 107-2), the mouthparts thus suggesting those of the Melittidae. The labial palpi are robust, little longer than the glossa, and the second segment is but little longer than the third (Silveira, 1993a), an unusual character for an L-T bee. Nonetheless, *Ancyla* has basic features of L-T bees, such as the presence of a stipital comb and the lack of a galeal comb; presumably, the short glossa and labial palpi result from reduction, possibly in response to regular use of shallow flowers such as those of Apiaceae. Silveira (1993a) described these and other characters of the mouthparts. The body length is 5 to 10 mm. The male genitalia were illustrated by Silveira (1995a, b).

■ *Ancyla* is found in the Mediterranean area from Spain (one specimen) and Morocco east through northern

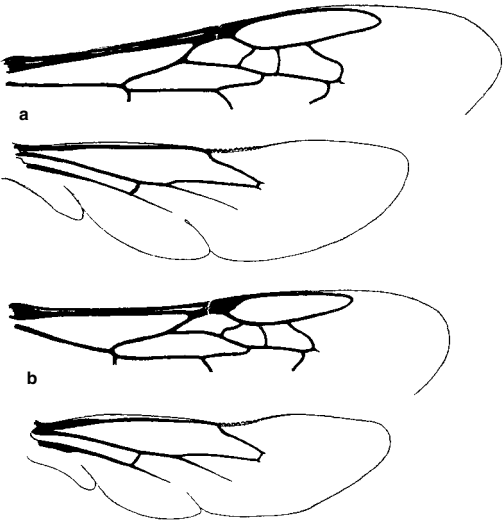


Figure 107-1. Wings (posterior parts of forewings omitted) of Ancylini. **a**, *Tarsalia ancyliformis mediterranea* Pittioni; **b**, *Ancyla holtzi* Friese. Based on drawings by D. B. Baker.

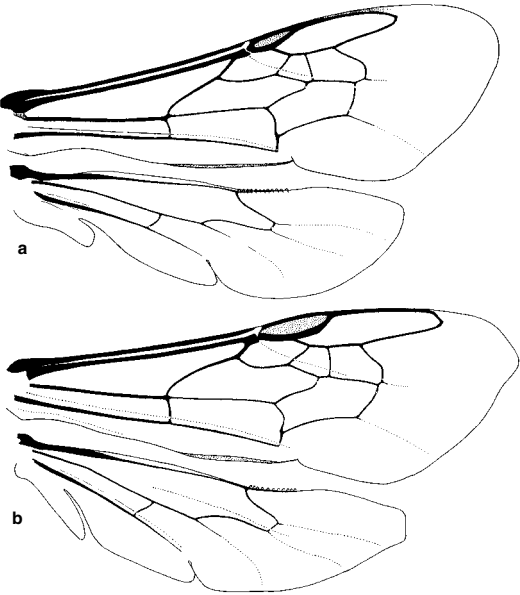


Figure 108-3. Wings of Tapinotaspidini. **a**, *Chalepogenus caeruleus* (Friese); **b**, *Trigonapedia* sp.

108-4d). Males also have combs, in *Paratetrapedia* as well developed as those of females, but presumably functionless.

The Tapinotaspidini were revised to the subgeneric level as part of the Exomalopsini by Michener and Moure (1957); Roig-Alsina (1997) reevaluated the classification as part of a phylogenetic study.

All the genera are South American, but *Paratetrapedia* and *Monoeca* also occur widely in Mesoamerica.

Key to the Genera of the Tapinotaspidini
(by Arturo Roig-Alsina)

1. Middle tibial spur with angle close to apex, apex thus notched; fore basitarsus with comb of strong setae along

margin following strigilar concavity (Fig. 108-4c); middle basitarsus with similar comb on apical half; venter of female thorax, coxae, and trochanters with hooked bristles *Monoeca*

- Middle tibial spur tapering apically; fore basitarsus without comb, or with comb along margin opposite to strigilar concavity (Fig. 108-4d); middle basitarsus without comb; venter of female thorax and leg bases with hairs branched or simple, not hooked 2

- 2(1). Shaft of inner hind tibial spur strongly curved basally, sinuous; spur coarsely pectinate; second to fourth tarsal segments of middle leg hairier than those of other legs, with dense brushes of hairs of uniform length; antenna of male elongate, with first flagellar segment shorter than second, and second 1.5 or more times longer than wide *Tapinotaspis*

- Shaft of inner hind tibial spur not curved basally, sometimes sinuous apically; spur either pectinate or serrate; second to fourth tarsal segments of middle leg not hairier than those of other legs [in a few cases with brushes (*Tapinotaspoides*), but then brushes asymmetrical, with hairs longer posteriorly]; antenna of male with first flagellar segment as long as or longer than second, and second as long as or shorter than its apical width 3

- 3(2). First flagellar segment of female twice as long as its apical width and over half of length of scape; face of male in frontal view with area between lateral ocellus and eye, and also vertex, conspicuously depressed; jugal lobe of hind wing short, 0.3 times as long as vannal lobe or less 4

- First flagellar segment of female at most 1.5 times as long as its apical width, less than half of length of scape; face of male in frontal view with area between lateral ocellus and eye slightly convex to flat, vertex not depressed; jugal lobe of hind wing over 0.4 times as long as vannal lobe 5

- 4(3). Integument of legs and metasoma extensively marked with yellow; S2 to S4 of female with hairs of apical fringes branched, those of S2 shorter than hairs of S3 or S4; scape of male swollen; hind leg of male with one tibial spur *Caenonomada*

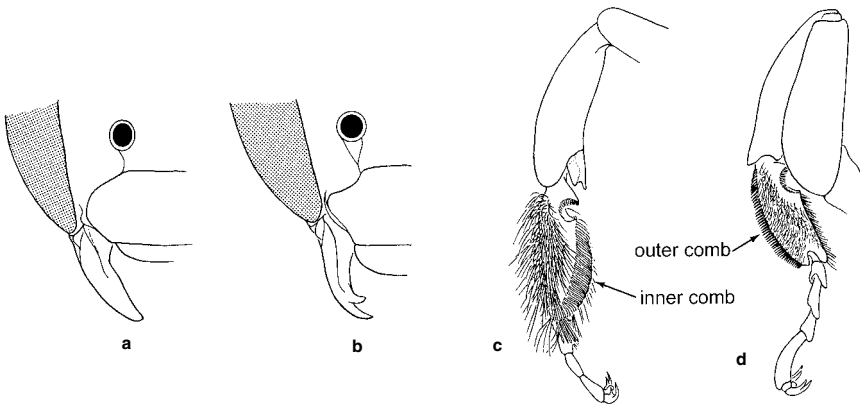


Figure 108-4. Structures of Exomalopsini and Tapinotaspidini. **a, b**, Faces of females of *Exomalopsis solani* Cockerell and *Paratetrapedia* sp.; **c, d**, Fore basitarsi of females of *Monoeca lanei* (Moure) and *P. lugubris* (Cresson). From Michener, McGinley, and Danforth, 1994.

- Integument of legs and metasoma black; S2 to S4 of female with hairs of fringes ribbonlike, wavy, and apical fringes of S2 to S4 of similar length; scape of male slender; hind leg of male with two tibial spurs *Tapinotaspoides*
- 5(3). Vertex of head behind ocelli carinate; hind basitarsus of female scarcely projecting above articulation of second segment, truncate at apex 6
- Vertex of head behind ocelli rounded or sloping, not carinate; hind basitarsus of female distinctly projecting at apex above articulation of second tarsal segment, projection rounded or ending obliquely 7
- 6(5). Face with fine punctures, scarcely wider than hairs arising from punctures; paraocular areas flat next to orbits *Trigonopedia*
- Face with at least some strong punctures on supraclypeal area and clypeus, such punctures several times wider than hairs arising from punctures or frequently giving rise to no hairs at all; paraocular areas convex next to orbits *Paratetrapedia*
- 7(5). Inner surface of fore basitarsus flattened, with polished longitudinal area bearing minute setae, the polished area margined basally and dorsally with rows of short flattened setae; forewing with two submarginal cells; pygidial plate of male distinct, glabrous *Chalepogenus* (*Lanthanomelissa*)
- Inner surface of fore basitarsus convex, evenly covered with long setae; forewing usually with three submarginal cells (but with two in a few *Chalepogenus*); pygidial plate of male either absent or upper surface covered by dense hairs 8
- 8(7). Scutum evenly covered by extremely short, dense setae (0.1–0.2 times flagellar diameter); marginal cell 1.25 times as long as distance from apex of cell to wing apex, or longer; scutellum strongly convex, with distinct dorsal and posterior surfaces; pygidial plate of male absent *Arhysocele*
- Scutum usually with long hairs (as long as diameter of flagellum or longer); in a few species most hairs extremely short, but some scattered hairs long and marginal cell length subequal to distance from its apex to apex of wing (Fig. 108-3a); scutellum evenly rounded, not forming distinct posterior surface; pygidial plate of male at least indicated apically by sclerotized, rounded margin *Chalepogenus* s. str.

Genus *Arhysocele* Moure

Arhysocele Moure, 1948: 335. Type species: *Arhysocele xanthopoda* Moure, 1948, by original designation.

Roig-Alsina (1997) has called attention to the very distinctive features of *Arhysocele*; in his phylogenetic analyses it appeared in diverse positions but not near *Paratetrapedia*, where it was placed by Michener and Moure (1957). *Arhysocele* has yellow markings on the slender, almost nomadiform, black body, the markings sometimes lacking on the metasoma. The body length is 6 to 8 mm. The pronotum lacks a transverse carina. The front basitarsus has a strong comb on the outer margin; the outer surface, moreover, is covered by a dense pad of fine hairs as in *Chalepogenus* s. str., the pad more extensive than that in *Paratetrapedia*. The inner hind tibial spur of the female is more broadly pectinate than the

outer spur. The pygidial plate of the female is concave laterally, and the apical part is thus parallel-sided or slightly expanded. Male genitalia and hidden sterna were illustrated by Michener and Moure (1957); see Figure 108-5a-c.

■ This genus occurs from Tucumán province, Argentina, and Rio Grande do Sul, Brazil, north to the state of Ceará, Brazil. The five known species were listed by Michener and Moure (1957).

Genus *Caenonomada* Ashmead

Caenonomada Ashmead, 1899a: 68. Type species: *Caenonomada bruneri* Ashmead, 1899, by original designation.

Chacoana Holmberg, 1887b: 225, nomen nudum.

Chacoana Holmberg, 1903: 432. Type species: *Chacoana melanoantha* Holmberg, 1903 = *Caenonomada bruneri* Ashmead, 1899, monobasic.

Caenonomada consists of yellow-and-black to largely yellow euceriform or apiform bees with a rather broad and flat metasoma; the posterior margin of T1 is convex, and the exposed part of T2 is thus shorter medially than laterally. The body length is 9 to 14 mm. Although mor-

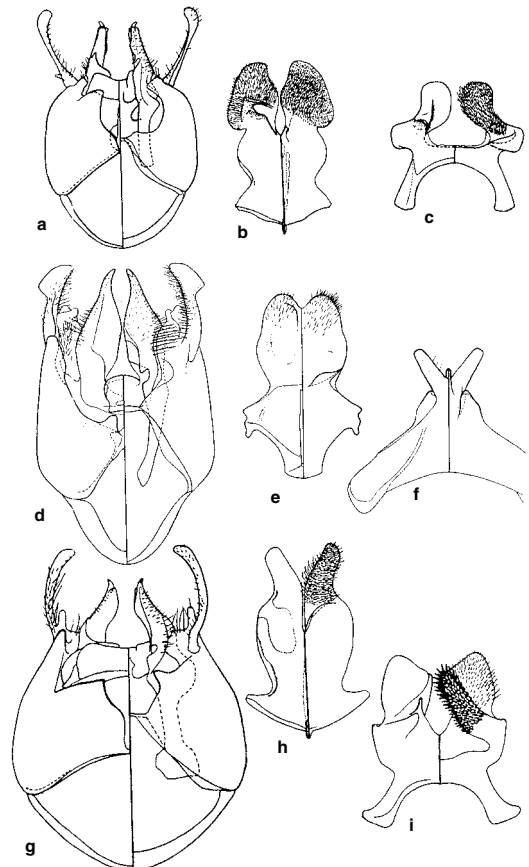


Figure 108-5. Male genitalia, S8, and S7 of Tapinotaspidini. a-c, *Arhysocele melampoda* Moure; d-f, *Caenonomada bruneri* Ashmead; g-i, *Chalepogenus goeldiana* (Friese). (Dorsal views are on the left.) From Michener and Moure, 1957.

phologically very distinctive, this genus is the sister group to *Tapinotaspoides*, according to a cladistic analysis by Roig-Alsina (1997). Additional features include the sharply pointed and somewhat hooked last flagellar segment of the male, the the third submarginal cell which is larger than either of the others, the lack of basitarsal combs (although some modifications suggest that this, like other Tapinotaspidini, is an oil-collecting bee), and the broadly pectinate inner hind tibial spur of the female. The stigma is usually not wider than the prestigma (measured to the wing margin) but extends well beyond vein r, the margin of the stigma in the marginal cell being convex (Fig. 108-2a). Male genitalia and hidden sterna were illustrated by Michener and Moure (1957); see Figure 108-5d-f.

■ This genus ranges from Buenos Aires and Tucumán provinces, Argentina, to the state of Ceará, Brazil. In his revision of the genus, Zanella (2002a) recognized three species.

Genus *Chalepogenus* Holmberg

This genus is used here in a broader sense than in the past, to include *Lanthanomelissa* and the species formerly placed in the subgenus *Tapinorrhina* of *Tapinotaspis*. *Chalepogenus* consists of small, euceriform species some of which have yellow tergal bands on the metasoma. As in *Tapinotaspis* the comb on the outer margin of the front basitarsus is weakly developed or absent, unlike that of related genera, in which it is conspicuous. The outer surface of the front basitarsus is covered by a broad, dense pad of fine branched setae, as in *Arhysoceble*. The species of the subgenus *Lanthanomelissa* differ from those placed in *Chalepogenus* s. str. in the shape and vestiture of the front basitarsus of both sexes, as indicated in the key below. There are almost no other differences between *C. discrepans* (Holmberg), the type species of *Lanthanomelissa*, and some species of *Chalepogenus* s. str., such that if the front tarsi are broken off, it is difficult to determine the subgenus. A. Roig-Alsina (in litt., 1996) found that Michener and Moure (1957) based their account of *Lanthanomelissa* on species of *Chalepogenus* s. str. In Roig-Alsina's (1997) phylogenetic analysis, *Lanthanomelissa* and *Chalepogenus* come out in such a way that if united, the resultant genus is paraphyletic. I nonetheless unite them, (1) because of their great similarity and (2) because unlike most of the rest of Roig-Alsina's cladograms, this part is not strongly supported, each clade having only one or two, not necessarily unique, synapomorphies. Additional characters or taxa might easily modify this portion of the cladogram.

A key to the subgenera is provided for convenience and to emphasize certain characters, even though the subgenera come out separately in the key to genera.

Key to the Subgenera of *Chalepogenus*

1. Inner surface of anterior basitarsus in both sexes flat or gently concave, shiny, with a few short hairs; hairy upper margin of front basitarsus with rows of small, flat hairs above the nearly bare, smooth area; fore wing with two submarginal cells *C. (Lanthanomelissa)*
- Inner surface of anterior basitarsus convex and hairy, much as on adjacent parts of basitarsus; small, flat hairs of front basitarsus absent; fore wing in most species with three submarginal cells *C. (Chalepogenus* s. str.)

Chalepogenus / Subgenus *Chalepogenus* Holmberg s. str.

- Chalepogenus* Holmberg, 1903: 416. Type species: *Chalepogenus incertus* Holmberg, 1903 = *Tetrapedia muelleri* Friese, 1899, by designation of Sandhouse, 1943: 537. [See note by Michener, 1997b.]
- Schrottkeya* Friese, 1908c: 170, no included species. Friese, 1908b: 58, included a species. Type species: *Tetrapedia goeldiana* Friese, 1899, first included species.
- Desmotetrapedia* Schrottkey, 1909d: 223. Type species: *Tetrapedia muelleri* Friese, 1899, by original designation.
- Lanthanomelissa* (*Lanthanella*) Michener and Moure, 1957: 417. Type species: *Lanthanomelissa completa* Michener and Moure, 1957 = *Tetrapedia goeldiana* Friese, 1899, by original designation.
- Tapinotaspis* (*Tapinorrhina*) Michener and Moure, 1957: 421. Type species: *Exomalopsis caerulea* Friese, 1906, by original designation.
- Tapinorrhina* Moure, 1994a: 274, unjustified emendation of *Tapinorrhina* Michener and Moure, 1957.

Like *Lanthanomelissa*, some *Chalepogenus* s. str. have basal yellow fasciae on the metasomal terga. Others lack such yellow markings; *C. herbsti* (Friese) has strong white tergal hair bands, and in *C. caeruleus* (Friese) the metasomal terga are dark metallic blue. Male genitalia and hidden sterna were illustrated by Michener and Moure (1957) under the generic names listed in the synonymy above as well as *Lanthanomelissa*; see also Figure 108-5g, h. The body length is 4 to 9 mm.

■ This subgenus is known from Valdivia, Chile, and Chubut, Argentina, north to Paraíba, Brazil and in the Andes to Ecuador. Roig-Alsina (1999) revised the 21 species included in the subgenus.

Chalepogenus / Subgenus *Lanthanomelissa* Holmberg

- Lanthanomelissa* Holmberg, 1903: 418. Type species: *Lanthanomelissa discrepans* Holmberg, 1903, monobasic.

Lanthanomelissa consists of small species, 4 to 6 mm in body length, exactly resembling small species of *Chalepogenus* s. str. that have yellow tergal bands.

■ The known range is Buenos Aires province to Tucumán, Argentina, north to Paraná, Brazil. The five species were reviewed by Urban (1995e). Rozen et al. (2006) gave an account of nesting behavior of *Lanthanomelissa*, together with descriptions of larvae.

Genus *Monoeca* Lepeletier and Serville

- Monoeca* Lepeletier and Serville, 1828: 528. Type species: *Monoeca brasiliensis* Lepeletier and Serville, 1828, monobasic.
- Epeicharis* Radoszkowski, 1884a: 18. Type species: *Epeicharis mexicanus* Radoszkowski, 1884, monobasic.
- Fiorentinia* Dalla Torre, 1896: 334, replacement for *Epeicharis* Radoszkowski, 1884 (not *Epicharis* Klug). Type species: *Epeicharis mexicanus* Radoszkowski, 1884, autobasic.
- Florentina* Ashmead, 1899a: 67, error for *Fiorentinia* Dalla Torre, 1896.
- Pachycentris* Friese, 1902: 186. Type species: *Pachycentris schrottkeyi* Friese, 1902, monobasic.

Chaetostetha Michener, 1942a: 281. Type species: *Exomalopsis pyropyga* Friese, 1925, by original designation.

Monoeca consists of robust black bees, sometimes with the metasoma red or with yellow integumental bands on terga. The body length varies from 8 to 12 mm. This genus is not close to any other. As in *Epicharis* and most *Centris*, the front basitarsus has a strong comb on the inner margin (next to the strigilis) (Fig. 108-4c), and the middle basitarsus has a comb in the equivalent position. The thoracic venter, leg bases, and S2 to S4 of the female are covered with strong, hooked bristles, a feature unique to this genus. The inner hind tibial spur is broadly and coarsely pectinate, as in *Caenomada*. Male genitalia and hidden sterna were illustrated by Michener and Moure (1957); see Figure 108-6a-c.

■ This genus occurs from San Luis Potosí and Jalisco, Mexico, south to southernmost Brazil. Six named species were listed by Michener and Moure (1957). There are at least two or three additional species.

Cunha (2002) described and illustrated the nests, which are branching burrows in the soil. More extensive information is in Rozen et al. (2006), along with descriptions of larvae.

Genus *Paratetrapedia* Moure

Paratetrapedia is by far the largest genus of the Tapinotaspidini, and the only one except the relatively rare *Monoeca* that is found throughout the moist tropics of the Americas. All the species, whether all black, all red, black with a red metasoma, or with extensive yellow or reddish-yellow markings, resemble species of *Trigona* to such an extent that one must often catch specimens to determine whether they are *Paratetrapedia* or *Trigona*; females of the

former sting, those of *Trigona* do not! The lack of long hairs and the smooth and largely hairless margins of the metasomal terga enhance the resemblance to *Trigona*. The body length is 6 to 12 mm. The comb on the outer margin of the front basitarsus is strongly developed, and the outer surface of the basitarsus has a rather narrow zone of fine, dense hairs, unlike the broad pad of such hairs found in *Arhysocele* and *Chalepogenus*. Male genitalia and hidden sterna were illustrated by Michener (1954b) and Michener and Moure (1957); see also Figure 108-6d-f.

Many of the species described in *Tetrapedia* by earlier authors belong in *Paratetrapedia*, but some of the types have not been reexamined to determine their proper placements. Thus more named species fall in this genus than are indicated in the following accounts of subgenera.

Key to the Subgenera of *Paratetrapedia*

1. Inner hind tibial spur much more broadly (but finely) pectinate or ciliate basally than outer; basitibial plate of female large (or small in *Amphipedia*), dull, without shining excavated zone; basitibial plate of male distinct, with lateral margins clearly defined; pygidial plate of female variable, only rarely with depressed spatulate apical portion and, if so, then with marginal carinae of anterior portion meeting in obtuse angle at base of spatulate portion..... 2
- Inner hind tibial spur finely ciliate and not or little broader than outer; basitibial plate of female very small, with shining excavated submarginal zone; basitibial plate of male obsolete, with lateral margins not clearly defined; pygidial plate of female with depressed spatulate apical portion, marginal carinae of anterior portion meeting in acute angle at base of spatulate portion 4
- 2(1). Pronotum with narrowly rounded transverse subapical ridge but without transverse carina; S4 and S5 of male with strong, continuous, apical fringes; lower margin of supraclypeal area unmodified *P. (Xanthopedia)*
- Pronotum with transverse carina; S4 and S5 of male almost unfringed or with remnants of fringe sublaterally; lower margin of supraclypeal area with transverse carina, at least in male 3
- 3(2). Pygidial plate of female broadly triangular; basitibial plate of female large; preoccipital carina not extending behind eyes; comb of anterior basitarsus of male a mere fringe, inconspicuous because of nearby hairs *P. (Tropidopedia)*
- Pygidial plate of female with apical spatulate portion (much as in *Paratetrapedia* s. str.); basitibial plate of female small; preoccipital carina extending behind eyes; comb of anterior basitarsus of male distinct *P. (Amphipedia)*
- 4(1). Preoccipital carina separated from eye by antennal diameter or less; pronotum with high, translucent, transverse lamella, surface immediately anterior to lamella thus concave in profile; second anterior tarsal segment of female without hooked bristle *P. (Lophopedia)*
- Preoccipital carina separated from eye by more than antennal diameter; pronotum with strong transverse carina, surface immediately anterior to carina convex; second anterior tarsal segment of female with greatly thickened hooked bristle on outer margin *P. (Paratetrapedia* s. str.)

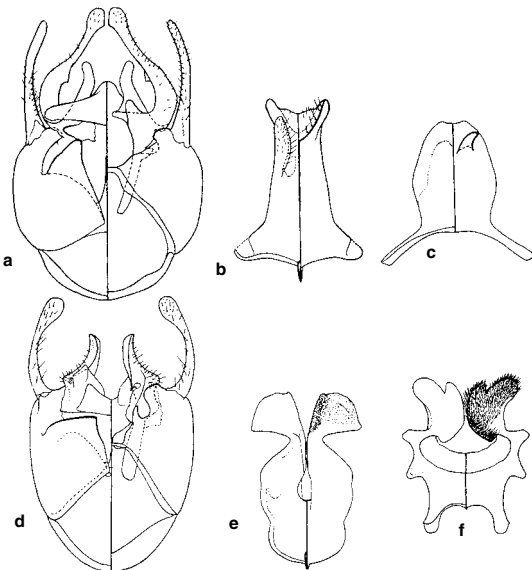


Figure 108-6. Male genitalia, S8, and S7 of Tapinotaspidini.

a-c, *Monoeca lanei* (Moure); d-f, *Paratetrapedia (Lophopedia) pygmaea* (Schrodtky). (Dorsal views are on the left.) From Michener and Moure, 1957.

109. Tribe Tetrapediini

Tetrapediini includes two very different genera, one (*Coelioxoides*) being cleptoparasitic, the other (*Tetrapedia*) consisting of nest-making species. Roig-Alsina (1990), who first recognized that *Coelioxoides* is related to *Tetrapedia*, lists features that indicate this relationship and constitute tribal characters. They include bending of the marginal cell away from the costa for much of its length, the small jugal lobe of the hind wing (Fig. 109-1), the long antennal pedicel, 1.3 to 1.7 times as long as wide, combined with a short scape, little more than 2.5 times as long as the pedicel (in most other Apinae the pedicel is at most as long as wide, but if elongate, the scape is also long); the slanting propodeal profile, with no separation into horizontal and vertical surfaces; the hairy propodeal triangle (bare medially in *Coelioxoides*); the short, broad middle tibial spur with elongate points forming pectination on both margins, the teeth largest near the apex of the spur (Fig. 109-2b, c); the lack of arolia (although in *Coelioxoides* the compressed inner rami of the claws are often approximate, superficially resembling an arolium); and the simple S7 of the male, lacking apical lobes.

The nesting biology and immature stages of both genera of Tetrapediini were treated by Alves-dos-Santos, Melo, and Rozen. (2002). *Coelioxoides* was established as a cleptoparasite of *Tetrapedia*; *Coelioxoides* places its eggs into cells shortly after they are closed by the host.

Key to the Genera of the Tetrapediini

- 1. Scopa absent; metasoma tapering posteriorly, in the female to a point (Fig. 109-3), suggesting *Coelioxys*; metepisternum almost linear except at upper end (Fig. 109-2a), pits united to form one large pit; hind tibia with two spurs in female, none in male *Coelioxoides*
- Scopa present on hind tibia and basitarsus of female; metasoma not tapering; metepisternum narrow but not linear, pits separate although close together; hind tibia in both sexes with one short, strongly pectinate spur (Fig. 109-2d) *Tetrapedia*

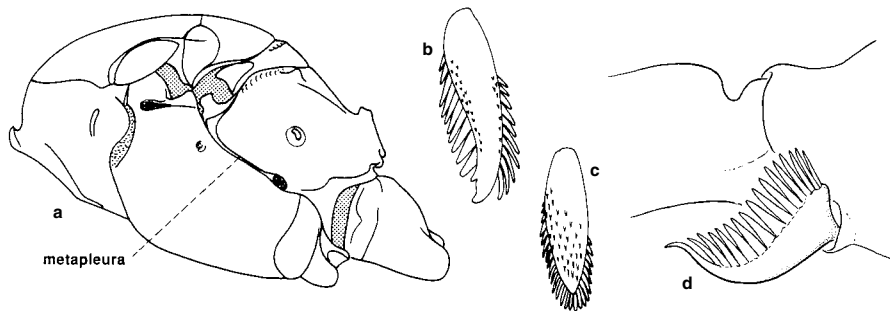


Figure 109-2. Structures of Tetrapediini. **a**, Lateral view of thorax of *Coelioxoides punctipennis* (Cresson), showing the reduced metapleuron; **b**, **c**, Middle tibial spurs of females of *Tetrapedia clypeata*

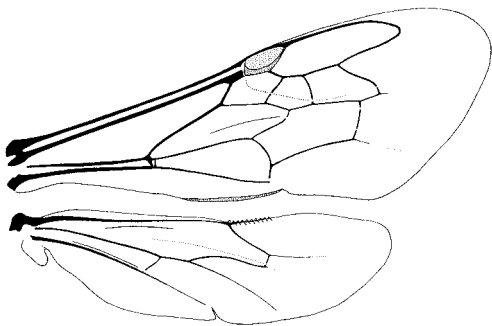


Figure 109-1. Wings of *Tetrapedia* sp.

Genus *Coelioxoides* Cresson

Coelioxoides Cresson, 1878: 94. Type species: *Coelioxoides punctipennis* Cresson, 1878, monobasic.

Among apine bees, *Coelioxoides* can be recognized immediately by the *Coelioxys*-like aspect, particularly of females. The wings are dark with a hyaline spot or transverse band distal to the closed cells (Fig. 109-4). The body length varies from 7.5 to 13.0 mm. Some derived characters include the one-segmented maxillary palpus, the enormous sting, and the produced, sharply pointed apex of the metasoma of the female, accentuated by S6, which extends beyond T6 (Fig. 109-3) and forms a nearly closed tube for the sting. Characters that are probably ancestral relative to *Tetrapedia* include the double (upper and lower) male gonostyli (Fig. 109-5), the complete gonobase, and the presence of a volsella. These features suggest that *Coelioxoides* and *Tetrapedia* are sister groups, not that *Coelioxoides* is derived from *Tetrapedia*.

■ *Coelioxoides* occurs from the states of Jalisco and San Luis Potosí in Mexico to Bolivia and the province of Córdoba, Argentina. The three species were revised by Roig-Alsina (1990).

Friese and *C. waltherae* Ducke; **d**, Hind tibial spur of *T. peckoltii* Friese, female. **b**, **c**, from Roig-Alsina, 1990; **d**, from Michener, McGinley, and Danforth, 1994.

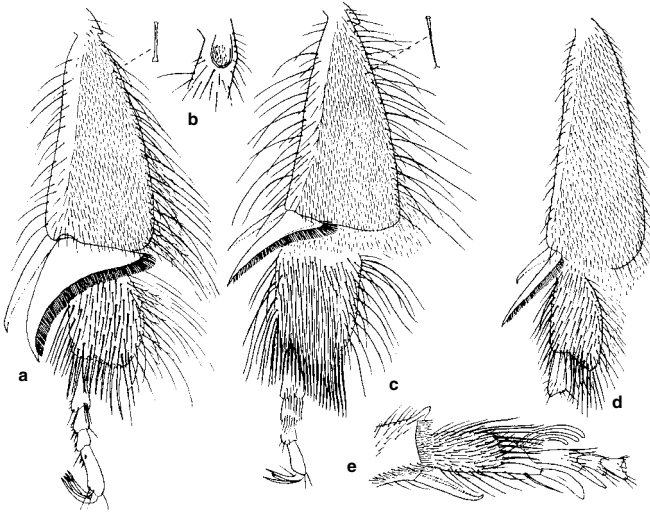


Figure 110-2. Leg structures of female Ctenoplectrini. **a**, Inner surface of posterior tibia and tarsus of *Ctenoplectra albolimbata* Magretti; **b, c**, Basitibial plate and inner surface of posterior tibia and tarsus of *C. bequaerti* Cockerell (note the enlargements of the keirotrichia); **d**, Inner surface of posterior tibia and tarsus of *Ctenoplectrina politula* (Cockerell); **e**, Inner view of middle tarsus of *Ctenoplectra bequaerti* Cockerell, showing modified setae. From Michener and Greenberg, 1980.

thus crescentic (Fig. 110-2a, c); the margin is finely comblike. Even in parasitic species (Fig. 110-2d) the spur is broadly and finely comblike. The term “pectinate” often used for these spurs is confusing for one familiar with that term as it is used elsewhere among bees, especially in the Colletinae and Halictidae, where it means having a very few long, coarse teeth. In the Ctenoplectrini the spur has many long fine teeth, presumably prolongations of the processes of the ciliate spurs found in many bees. To avoid changing established, even if none too appropriate, terminology, I am simply calling ctenoplectrine inner hind tibial spurs comblike. Arolia are absent. The distal part of the pygidial plate of the female is slender, parallel-sided, or, in parasitic species, scarcely evident. S2 to S5 of females have oblique bands, broken medially, of long, coarse, distally curved and serrate or squamose hairs (Fig. 110-3) used in wiping floral oils from the cucurbitaceous genera *Thladiantha* and *Momordica* (Vogel, 1981, 1990). These hairs are present but reduced in the parasitic *Ctenoplectrina* (Fig. 110-3b). Many structures were illustrated by Michener and Greenberg (1980); genitalia and hidden sterna were illustrated by Popov and Guiglia (1936) and

Wu (1978). As shown in Figure 110-4b, the spatha is well developed and there are two gonostyli; the dorsal gonostylus is greatly reduced in some species, however.

Ctenoplectra is known to nest in beetle holes in old wood (Williams, 1928) and in abandoned mud-and-resin megachilid nests (Rozen, 1978); probably they utilize small holes of various kinds. Floral oil may be added to earth that is carried to the nest on the scopa, as observed by Williams. Rozen described the larva and the cocoon spun by the mature larva.

Key to the Genera of the Ctenoplectrini
(Females Only)

- 1. Hind tibial and basitibial scopa consisting largely of long simple hairs, many of them nearly as long as tibial width; inner hind tibial spur expanded at base across apex of tibia, sometimes to full width of tibia, so that spur is crescentic, its margin finely comblike (Fig. 110-2a, c) *Ctenoplectra*
- Hind tibia and basitarsus without scopa, hairs much shorter than width of tibia; inner hind tibial spur not expanded at base, relatively slender, not crescentic, but finely comblike (Fig. 110-2d) *Ctenoplectrina*

Genus *Ctenoplectra* Kirby

Ctenoplectra Kirby in Kirby and Spence, 1826: 681, no species. Type species: *Ctenoplectra chalybea* Smith, 1857, by inclusion and designation of Sandhouse, 1943: 542. *Ctenoplectra* Smith, 1857: 44. Type species: *Ctenoplectra chalybea* Smith, 1857, monobasic.

This genus includes the nonparasitic species of the tribe. In addition to the characters indicated in the key to genera, females of *Ctenoplectra* have long dense sternal fringes (Fig. 110-3a), as described in the account of the tribe, the apical margins of S4 and S5 are deeply emarginate, and the setae on the midtarsal segments 1 and 2 (Fig. 110-2e) are curiously modified. The basitibial and pygidial plates of females are sharply defined, and the prepygidial fimbria on T5 is strong. The hind tibia of the female is triangular, broadest apically, and tapering to-

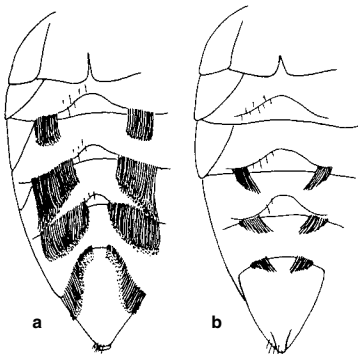


Figure 110-3. Undersurfaces of metasomas of female Ctenoplectrini. **a**, *Ctenoplectra bequaerti* Cockerell, showing oil-collecting hairs; **b**, *Ctenoplectrina politula* Cockerell, showing the reduction in oil-collecting hairs. From Michener and Greenberg, 1980.

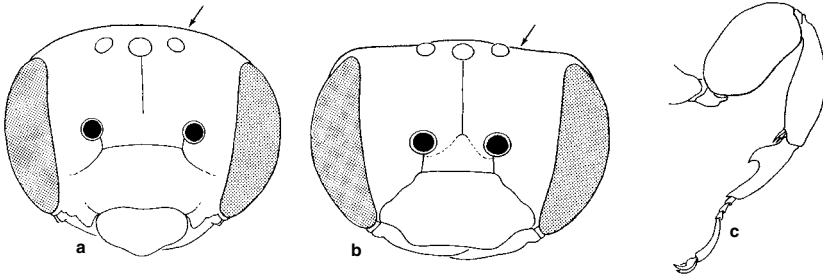


Figure 111-2. Structures of Apinae. **a**, Face of female of *Diadasia sphaeralcearum* Cockerell (Emphorini); **b**, Face of female of *Melisoides lupina* Cresson (Eucerini); **c**, Hind leg of male of *Ancyloscelis toluca* (Cresson) (Emphorini). Arrows indicate the vertex, the shape of which is characteristic of Emphorini and Eucerini. From Michener, McGinley, and Danforth, 1994.

from ponds and puddles to soften the soil for excavation and cell construction. The cells are urn-shaped, with smooth earthen walls such that in some forms, such as *Melitoma*, they can easily be separated intact from the earthen matrix in which they are constructed. They are lined with a very thin secreted membrane, or such a lining may appear to be absent. The cells are either isolated, one in each branch of a nest, or alone in an unbranched nest, or more commonly they are in short series; in most species their orientation is variable, horizontal to vertical. The provisions are firm masses occupying the distal ends of the cells. After the provisions for a cell are collected and shaped, an egg is laid, underneath the provisions in the subtribe Emphorina; this is a unique feature of the subtribe. It is likely that the observation by D. Dias (in Michener and Lange, 1958c) of eggs on top of food masses of *Ptilothrix plumatus* Smith (see also Michener, 1974c) is an error. Studies of several *Ptilothrix* species by Hazeldine (1997a) show eggs beneath food masses as in other Emphorina. The females show no evident apical structures for inserting eggs under the pollen masses. In the subtribe Ancyloscelina, the egg is laid on top of the food mass (Rozen, 1984a). The emphorine larva is unusually elongate, almost wormlike, and curls around the food mass, eating its way around it. After feeding is completed, the larva deposits a layer of fecal material covering the whole interior of the cell except sometimes for the closure, and then covers it with a thin cocoon. Such a layer of feces, which appears as a layer of pollen exines without recognizable fecal pellets, is also a unique emphorine characteristic. Various distinctive features of the nest, as described above, support the placement of *Ancyloscelis* in the Emphorini.

Perhaps all species of Emphorini are oligolectic, but as indicated in the accounts of the genera, the tribe as a whole and even different species of the genus *Diadasia* visit a wide variety of flowers for pollen.

Key to the Genera of the Emphorini (Modified from a key by A. Roig-Alsina, 1998a)

1. Paraocular carina present along most of inner eye margin; vein cu-v of hind wing less than half as long as second abscissa of vein M+Cu (Fig. 111-3a); second abscissa of vein M+Cu of hind wing at least three-fourths as long as vein M; maxillary palpus with sparse, short hairs; T7 of male rounded apically; hind leg of male modified, femur dilated, at least twice as thick as middle femur (Fig. 111-5); S7 of male with broad disc and two or four small apical lobes, shorter than disc (Fig. 111-4c) (subtribe Ancyloscelina) *Ancyloscelis*
- Paraocular carina absent except sometimes along lower

- or upper extremity of eye; vein cu-v of hind wing about half as long as (in *Melipholipsis*), or nearly as long as, second abscissa of vein M+Cu (Fig. 111-3b, c); second abscissa of vein M+Cu of hind wing half as long as vein M or less; maxillary palpus, at least in female, with brush of hairs on one side of segment 3 and usually also 2 and 4; T7 of male with two apical points or angles; hind leg of male not or moderately modified, femur less than twice as thick as middle femur (except about twice as broad but flattened in some *Melitoma*); S7 of male with short and often narrow disc and large apical lobes, much longer than disc (Fig. 111-4f) (subtribe Emphorina) 2
- 2(1). Second segment of labial palpus 1.1-3.0 times as long as first, and usually longer than eye (except in *Melitoma*, in which it is 0.95 times eye length); proboscis in repose reaching well beyond front coxae and usually surpassing middle coxae 3
- Second segment of labial palpus shorter, 0.5-0.8 times as long as first, and usually shorter (0.3-0.6 times) than eye; proboscis in repose reaching at most front coxae 6
- 3(2). T2 to T4 with broad, bare, median apical areas occupying much of terga in female; anterior surface of T1 largely bare; T7 of male apically truncate, with apical points far apart, separated by long straight margin; center of T7 bare, polished (South America) *Melipholipsis*
- T3 and T4, usually also T2, with pubescence reaching apices, frequently forming conspicuous apical hair bands; anterior surface of T1 hairy; T7 of male apically with two close points or lobes; center of T7 hairy 4
- 4(3). Clypeus with yellow area; middle tibia with strong outer apical spine easily seen because of sparse vestiture of tibia; first flagellar segment as long as apical width (South America) *Toromelissa*
- Integument of clypeus dark; middle tibia with small apical point hidden by dense, appressed vestiture of tibia; first flagellar segment over 1.5 times as long as apical width 5
- 5(4). Second labial palpal segment two to three times as long as first; labrum of female parallel-sided, more or less quadrate, apical margin with a median tubercle and one to three smaller tubercles on each side; hind femur of male with lower margin strongly carinate *Melitoma*

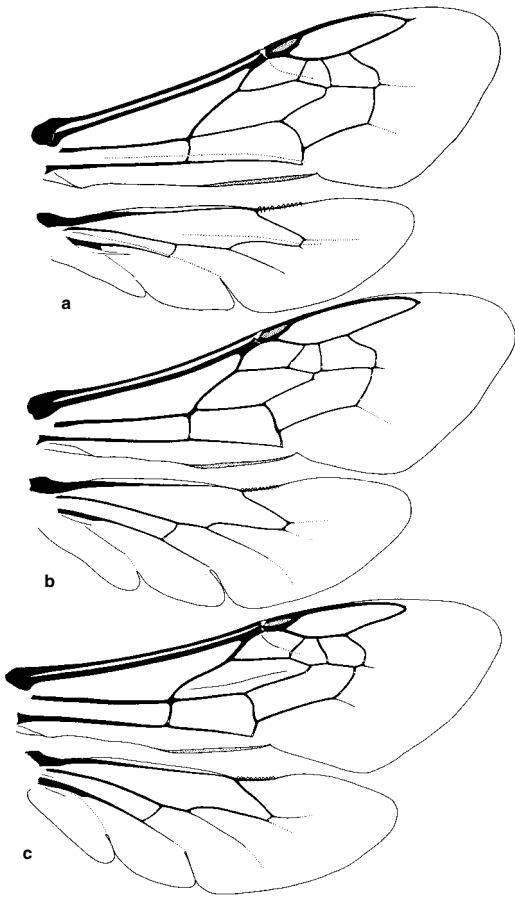


Figure 111-3. Wings of Emphorini. **a**, *Ancyloscelis panamensis* Michener; **b**, *Diadasia afflictata* (Cresson); **c**, *Ptilothrix fructifer* (Holmberg).

- Second labial palpal segment 1.5 times as long as first; labrum of female with sides diverging apically, pentagonal, apical margin without tubercles; hind femur of male with lower margin narrowly rounded *Melitomela*
- 6(2). Arolia absent; first flagellar segment usually two or more times as long as apical width; branches of tibial scopal hairs mostly directed distad, most of them not curved basad *Ptilothrix*
- Arolia present; first flagellar segment less than twice as long as apical width; branches of tibial scopal hairs mostly curved basad at their apices [except in *Alepidosceles* and *Diadasina* (*Leptometriella*)] 7
- 7(6). Gradulus of S2 medially angulate posteriorly, graduli of S3 and S4 often weakly so; basal half of front femur of female commonly with dense brush of long hairs; propodeal triangle of male bare or, rarely, with some hairs close to posterior margin of triangle, but then posterior claws with rounded apices *Diadasia*
- Graduli of metasomal sterna with median parts gently recurved; front femur of female with long hairs not forming dense basal brush; propodeal triangle of male hairy [or in *Diadasina* (*Leptometriella*) sometimes largely bare]; claws pointed 8

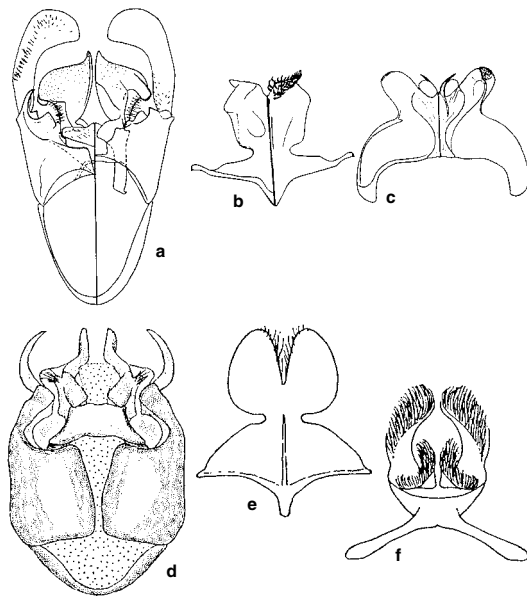


Figure 111-4. Male genitalia, S8 and S7 of Emphorini. **a-c**, *Ancyloscelis ursinus* Haliday, dorsal view on the left; **d-f**, *Melitoma taurea* (Say), dorsal view in d, ventral views in e and f. **a-c**, from Michener and Moure, 1957; **d-f**, from Mitchell, 1962.

- 8(7). Basitibial plate of female absent; mandible of male broadened preapically; apex of labrum of male medially with bilobate tubercle *Alepidosceles*
- Basitibial plate of female distinct; mandible of male tapering apically (or, in subgenus *Leptometriella*, slightly broadened preapically); apex of labrum of male with or without simple median tubercle *Diadasina*

Genus *Alepidosceles* Moure

Alepidosceles Moure, 1947b: 244. Type species: *Ancyloscelis imitatrix* Schrottky, 1909, by original designation.

Alepidosceles is the only emphorine genus that lacks a basitibial plate in the female. The metasoma is covered with yellowish hairs, sometimes denser on the apical parts of terga than elsewhere, forming weak bands. The body length is 7 to 11 mm. The branches of the hairs of the tibial scopa are directed distad. In both sexes the propodeal triangle is hairy. The male upper and lower gonostyli are both rather long and slender, the lower exceeding the upper. Male genitalia and hidden sterna were illustrated by Moure (1947b).

■ This genus occurs from Mendoza province, Argentina, north to Minas Gerais, Brazil. Six species have been described; those of Argentina were revised by Roig-Alsina (1998b).

Genus *Ancyloscelis* Latreille

Ancyloscelis Berthold, 1827: 466, nomen nudum. Latinization of *Ancyloscele* Latreille, 1825: 463.
Ancyloscelus Berthold, 1827: 565, nomen nudum.
Ancyloscelis Latreille, 1829: 355, no included species; Hali-

branches of the hairs of the tibial scopa commonly curve basad. Males mostly have only one long gonostylus; a few species, e.g., *D. enavata* (Cresson), have a second (dorsal) gonostylus about half as long as the first. Male genitalia and hidden sterna were illustrated by Adlakha (1969), Toro and Ruz (1969), and Snelling (1994).

■ *Diadasia* has an amphitropical distribution, from Washington, Utah, Nebraska, and California to Texas, USA, south through Mesoamerica to Costa Rica and from Colombia and Rio Branco, Brazil south to Bio-Bío, Chile, and Río Negro, Argentina. Only the *Dasiapis* group (see below) is known from moist tropical locations. About 30 species occur in North America; about 15 additional species are known from South America. It is difficult to know from descriptions which named South American species actually belong in *Diadasina* instead of *Diadasia*; revisional studies involving examination of types will be needed to clarify such problems. Timberlake (1941b) gave a key to species found in the United States and Adlakha (1969) revised the same species. Toro and Ruz (1969) revised the species (including the genus *Toromelissa*) of Chile. Snelling (1994) revised the North American species of the *Dasiapis* group.

The species are rather diverse in appearance. Those that are oligolectic on *Helianthus* (Asteraceae) and on Cactaceae are large and distinctly banded. Those oligolectic on Malvaceae and Onagraceae are mostly small and tend to have a uniform covering of pale hairs on the metasoma. The one species on Convolvulaceae, *Diadasia bituberculata* (Cresson), is intermediate in size and has more dark hair. The diversity among species led to the recognition of four subgenera, characters of which were tabulated, along with those of the genus *Diadasina*, by Michener (1954b). Unfortunately, certain Holmberg genus-group names were misinterpreted at that time by both Moure and Michener, but the group characters remain of interest. Subgenera may not be desirable for *Diadasia*, and need not be recognized until the genus is more fully studied; the names are shown as synonyms above. The only subgenus usually recognized is that having yellow on the clypeus or at least on the bases of the mandibles, i.e., *Dasiapis* = *Leptometria*; I term this the *Dasiapis* group.

Nests of *Diadasia* are rather shallow burrows, sometimes in large aggregations, commonly with earthen turrets at the entrances, leading to one to several cells at the ends of branch burrows. Unlike *Melitoma* and *Ptilothrix*, the bees do not alight on water and do not carry water to nest sites; they may soften hard earth with nectar. Cells are made of hardened earth but do not come free from the substrate, like those of *Melitoma*. Accounts of nesting biology are by Linsley, MacSwain, and Smith (1952), Linsley and MacSwain (1957), Adlakha (1969), Snyder, Barrows, and Chabot (1976), Eickwort, Eickwort, and Linsley (1977), Neff, Simpson, and Dorr (1982), Ordway (1984), and Hazeldine (1997b).

Genus *Diadasina* Moure

Diadasina is here used in a broad sense to include *Diadasia*-like species in which the gradulus of S2 is straight or gently convex medially, not angulate as in *Diadasia*; and the claws of the male are pointed, not broadened and

rounded on at least the posterior legs as in many *Diadasia*. S6 of the male has a broad, rounded, longitudinal ridge densely covered with long hair in the subgenus *Diadasina* s. str.; such a ridge is also found in *Melitomella grisescens* (Ducke). *Diadasina* is probably paraphyletic, to judge from the preliminary results of a phylogenetic study by A. Roig-Alsina (manuscript). His cladograms show the two subgenera (see the key below) as separate, usually basal branches of the clade that includes *Alepidosceles* and *Ptilothrix*. Since the phylogeny remains speculative, I prefer to indicate the similarity and relationship of the two subgenera by including them in a single genus.

All species of *Diadasina* are South American.

Key to the Subgenera of *Diadasina*

1. Propodeal triangle with hairs covering entire surface, except sometimes a narrow longitudinal median bare band; apex of labrum of female with margin rounded, lacking denticle; S6 of male with hairs longer along median longitudinal convexity, frequently forming dense tuft *D. (Diadasina* s. str.)
- Propodeal triangle with upper bare area bordering metanotum, or triangle largely bare; labrum of female with distal margin elevated, smooth, frequently with median denticle; S6 of male evenly covered with short hairs *D. (Leptometriella)*

Diadasina / Subgenus *Diadasina* Moure s. str.

Diadasina Moure, 1950d: 392. Type species: *Melitoma paraensis* Ducke, 1912, by original designation.

Diadasina Michener, 1954b: 130. Incorrect subsequent spelling.

Diadasina consists of small species 6 to 8 mm in length.

■ This subgenus is found from Pará, Brazil, to Buenos Aires province, Argentina. At least four species are included; probably other little-known species currently included in *Diadasia* will be found to be species of *Diadasina* s. str. or *Leptometriella*.

The nesting biology of one species, *Diadasina distincta* (Holmberg), has been described by Martins and Antonini (1994). The nests were in aggregations in more or less flat ground. Each burrow ended in a single cell; each female must make several nests.

Diadasina / Subgenus *Leptometriella* Roig-Alsina

Leptometriella Roig-Alsina, 1998a: 23. Type species: *Leptometria tucumana* Brèthes, 1910, by original designation.

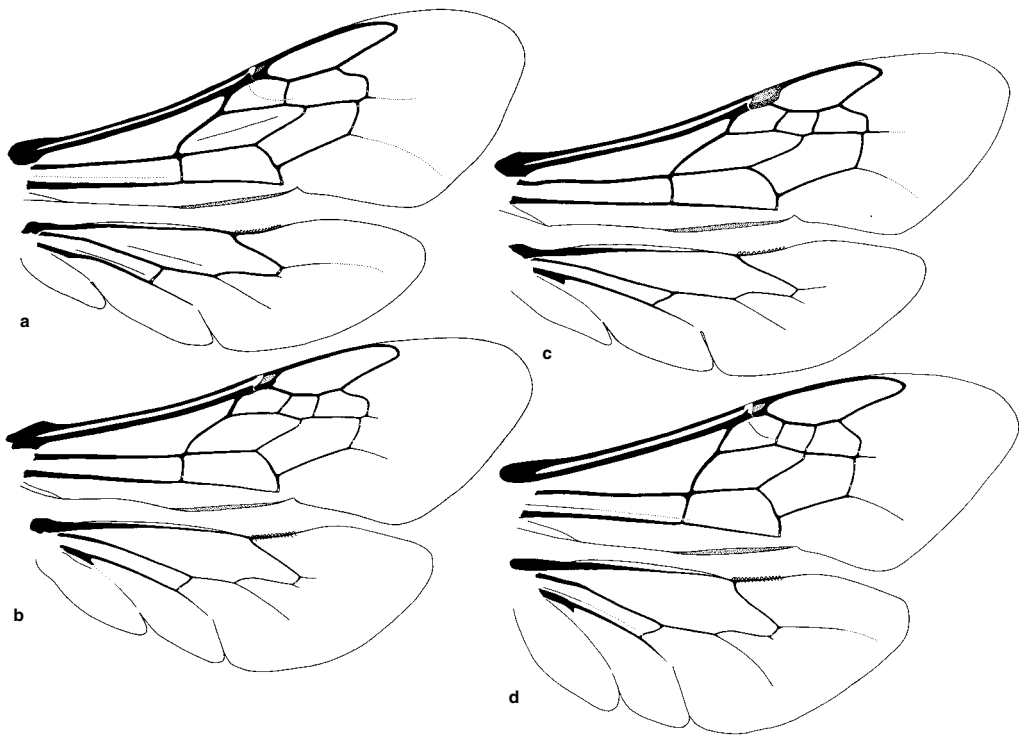
Like *Diadasina* s. str., subgenus *Leptometriella* consists of small species 6 to 8 mm in length. The branches of the scopal hairs are mostly directed distad rather than retrorsely curved as they are in many other Emphorina.

■ This subgenus is known from Salta to Mendoza, Argentina. Three named species are included.

Genus *Meliphilopsis* Roig-Alsina

Meliphilopsis Roig-Alsina, 1994: 183. Type species:

Meliphilopsis melanandra Roig-Alsina, 1994, by original designation.



ably be easily distinguished from other Eucerini, except *Pachysvastra*, by the lack of arolia. *Platysvastra* is known only in the female; the scutellar characters described in the key to females probably distinguish males also.

Users will find difficulties with portions of these keys, particularly in distinguishing *Tetraloniella* from *Eucera* (*Synbalonia*). These genera should be restudied, on a world-wide basis, before further reclassification; perhaps the subgenera of *Tetraloniella* should be included in *Eucera*.

Key to the South American Genera of Eucerini

- 1. Paraglossa much shorter than first segment of labial palpus; paraocular area of male with yellow (gradulus of S2 simple, recurved) (subtribe Eucerinodina) *Eucerinoda*
 - Paraglossa attaining apex of second segment of labial palpus; paraocular area of male not yellow 2
- 2(1). Outer surface of hind tibia of female with corbicula on distal half; corbicula margined posteriorly by comb of long, stiff, closely spaced bristles; wings nearly bare, strongly papillate beyond veins; vein cu-v of hind wing well over half as long as second abscissa of M+Cu (Fig. 112-16); gradulus of S2 simple, recurved (subtribe Canephorulina) *Canephorula*
 - Scopa formed of more or less uniformly spaced hairs, not forming a corbicula except for bare area on distal fourth of tibia, and without row or comb of long, stiff bristles; wings hairy more or less throughout, not strongly papillate; vein cu-v of hind wing commonly more or less oblique, but little if any more than half as long as second abscissa of M+Cu; gradulus of S2 birecurved, i.e., with two convexities to the rear, one on ei-

Figure 112-4. Wings of Eucerini. **a**, *Eucera chrysopyga* Pérez; **b**, *Melissodes agilis* Cresson; **c**, *Melissoptila* (*Ptilomelissa*) sp.; **d**, *Thygater analis* (Lepeletier).

- ther side of midline (Fig. 112-5a, b) (subtribe Eucerina) 3
- 3(2). Males 4
 - Females 23
- 4(3). Clypeocular distance at least as great as minimum diameter of first flagellar segment (Fig. 112-6e); lower part of paraocular carina completely absent (indicated by ridge in a few *Thygater*); lateral parts of clypeus, parts of paraocular area above latter, and part of paraocular area adjacent to eye all nearly in one plane; labrum at least three-fourths as long as broad; clypeus very strongly protuberant, i.e., lower end, as seen in side view, in front of lower anterior eye margin by about 1.5 times maximum eye width in same view (Fig. 112-6e) [except in *Thygater* (*Nectarodiaeta*)] 5
 - Clypeocular distance usually less than minimum diameter of first flagellar segment (Fig. 112-6a-d); lower part of paraocular carina present, or, if absent, then indicated by a ridge such that a narrow zone adjacent to eye is in a very different plane from adjacent regions (this may not be evident in forms in which clypeus, and hence paraocular carina, is very close to eye); labrum less than three-fourths as long as broad (In *Mirnapis*, labrum nearly three fourths as long as broad, apex deeply emarginate.); clypeus weakly to strongly protuberant, usually not very strongly so, i.e., lower end, as seen in side view, in front

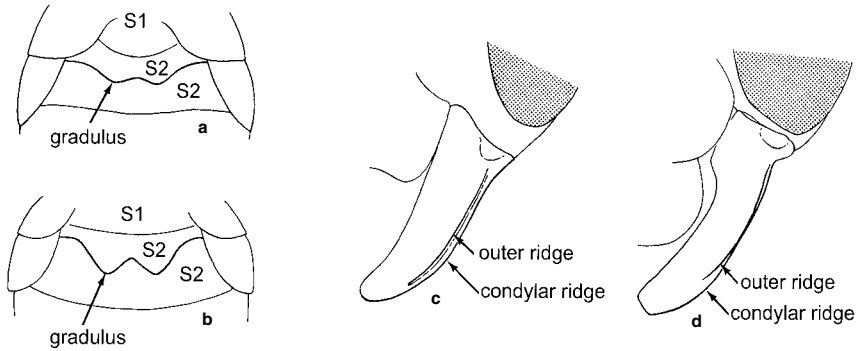


Figure 112-5. Eucerini. **a, b**, Ventral surface of base of metasoma of female of *Thygater* sp. and *Peponapis* sp., showing gradulus of S2; **c, d**, Mandible of female of *Thygater* sp. and *Peponapis* sp. From Michener, McGinley, and Danforth, 1994.

- of lower anterior eye margin by about maximum width of eye or less (except for *Santiago* and some *Peponapis* that have very protuberant clypeus) 6
- 5(4). T7 ending in two lobes or blunt teeth, merely weakly emarginate in one species; pygidial plate unrecognizable or indicated only by weak, incomplete, lateral carinae; segments of antennal flagellum of approximately uniform diameter, without long hairs *Thygater*
- T7 not bilobed; pygidial plate clearly defined; eighth and following flagellar segments more slender than preceding ones, with row of hairs on one side *Trichocenerpis*
- 6(4). Flagellum tapering, its apical segment thus less than half as broad as its second segment; vertex with strong preoccipital carina *Lophothygater*
- Flagellum not or less strongly tapering; vertex without preoccipital carina 7
- 7(6). Pygidial plate absent, reduced and ending in an acute apex, or with lateral carinae ending preapically, the apical portion of the plate truncate or rounded and without raised margins; S7 usually with median apical projection between elaborate, hairy apical lobes (Fig. 112-7c) *Alloscirtetia*
- Pygidial plate with distinct raised margin or carina laterally and posteriorly (broken posteriorly only in a few forms with the apex of the plate bilobed or bidentate); S7 without median apical projection 8

- 8(7). T7 with gradular tooth or strong angle on each side of pygidial plate, sometimes hidden in dense hair or by T6 9
- T7 without lateral teeth 13
- 9(8). Arolia absent; pygidial plate deeply notched medially; antenna scarcely reaching beyond scutellum, median flagellar segments less than twice as long as broad and about 1.5 times broader than ocellar diameter *Pachysvastra*
- Arolia present; pygidial plate entire; antenna usually much longer, median flagellar segments more than twice as long as broad and little broader than ocellar diameter 10
- 10(9). First segment of flagellum at least one-fourth as long as second; maxillary palpus two- to three-segmented; stigma large for the tribe, longer than prestigma; second submarginal cell large for the tribe, posterior margin often almost as long as that of first; inner and outer apical lobes of S7 almost indistinguishably fused and usually hairless (Fig. 112-9i); spatha over four times as wide as long *Melissoptila*

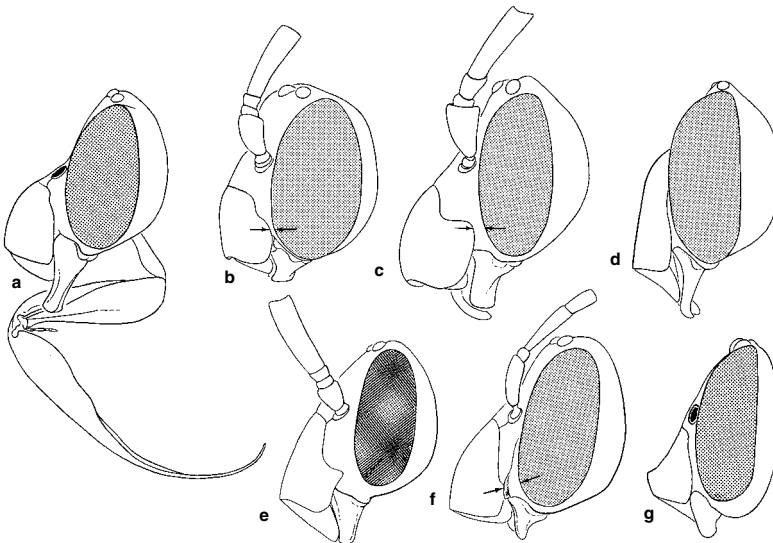


Figure 112-6. Heads of Eucerini. **a**, *Tetraloniella* (*Loxoptilus*) *longifellator* (LaBerge), male; **b**, *T. (Tetraloniella)* *albata* (Cresson), male; **c**, *Eucera* (*Synhalonia*) *atriventris* (Smith), male; **d**, *Tetraloniella* (*Pectinapis*) sp., male; **e**, *Thygater analis* (Lepelletier), male; **f**, *Tetraloniella* (*Loxoptilus*) *longifellator* (LaBerge), female; **g**, *Simanthesdon* *linsleyi* Zavortink, male. (Arrows indicate clypeoocular distance.) From Michener, McGinley, and Danforth, 1994.

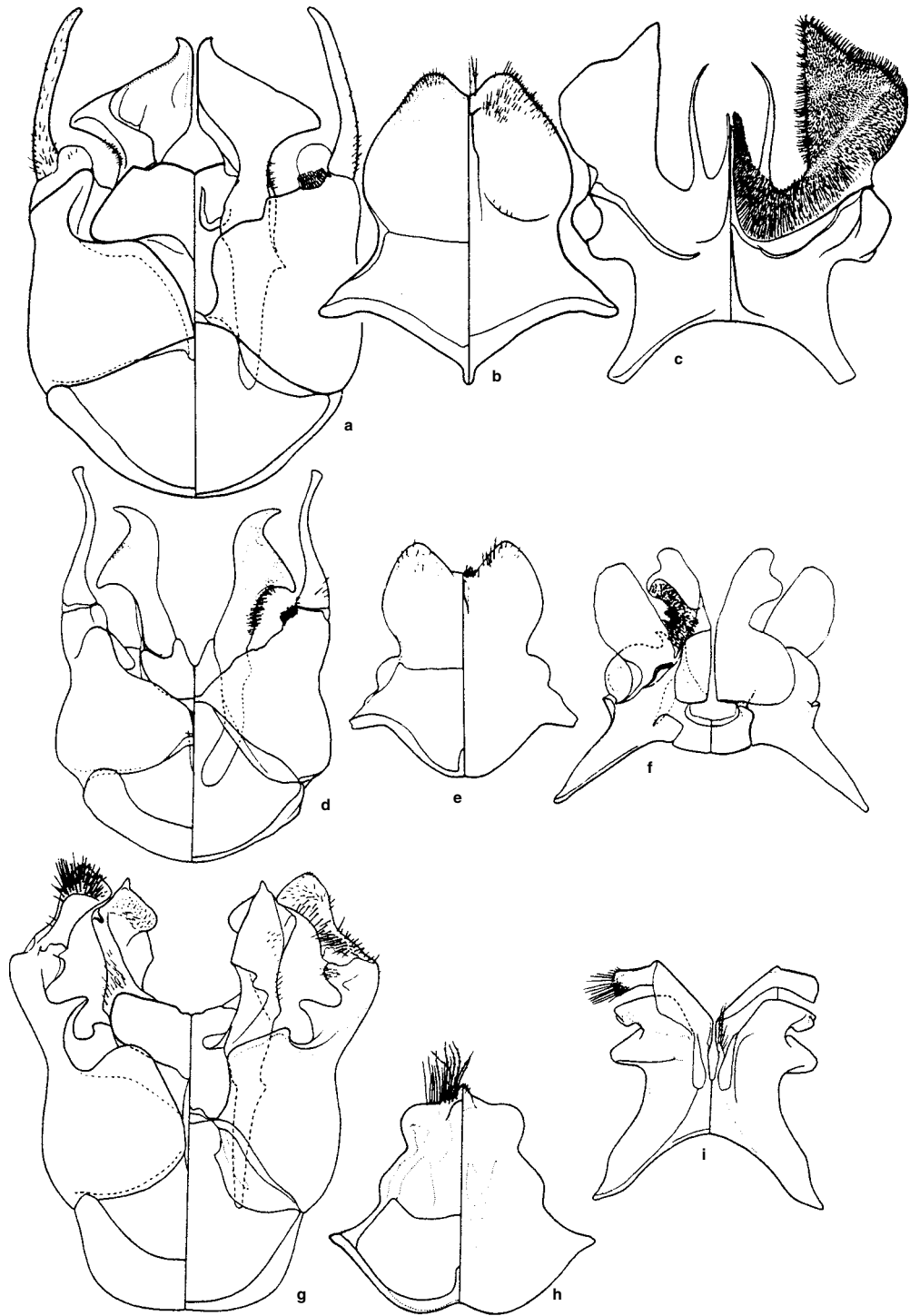


Figure 112-7. Male genitalia, S8, and S7 of Eucerini. **a-c,** *Alloscirtetica* (*Megascirtetica*) *mephistophelica* (Schrottky); **d-f,** *Trichocerapis* (*Trichocerapis*) *mirabilis* Smith; **g-i,** *Florilegus* (*Eufleurilegus*) *barbiellinii* Moure and Michener. From Moure and Michener, 1955b.

- First segment of flagellum not over one-fifth as long as second (Fig. 112-8e); maxillary palpus four- to five-segmented, very rarely three-segmented; stigma and second submarginal cell usually smaller; inner and outer apical lobes of S7 separated by transparent zone, the inner lobe either curled or reflexed or large with scattered hairs (Figs. 112-7i, 112-9c, f); spatha less than four times as wide as long 11
- 11(10). Pygidial plate with strong, transverse, preapical carina separating depressed apical part of plate from main part of plate; scutellum flat in profile *Gaesochira*
- Pygidial plate without transverse preapical carina; scutellum convex in profile [except in *Florilegus* (*Floriraptor*)] 12
- 12(11). Anterior femur slender, distinctly more than three times as long as broad, and broadest near base; maxillary palpus four-segmented, rarely three-segmented; anterolateral margin of tegula (commonly hidden by hair) gently concave (Fig. 112-8a) *Melissodes*
- Anterior femur somewhat robust, nearly three times as long as broad, and broadest near or beyond middle; maxillary palpus five-segmented; lateral margin of tegula continuously convex (as in Fig. 112-8b) *Florilegus*
- 13(8). Anterior mandibular articulation nearly twice as far from eye margin as posterior one; clypeocular distance about half of minimum width of first flagellar segment 14
- Anterior mandibular articulation little farther from eye margin than posterior one; clypeocular distance less than half (more than half in *Mirnapis*) of minimum width of first flagellar segment (inner apical lobes of S7 except in *Svastra*, large, much exceeding outer lobes) 15
- 14(13). Gonostylus bent downward near middle; clypeus protuberant by eye width in front of eye margin as seen in lateral view; S6 with pair of strong converging carinae on lateral margins (Fig. 112-10d); S7 with inner apical lobes small, not much exceeding outer lobes *Peponapis*
- Gonostylus not bent near middle; clypeus protuberant by about 1.4 times eye width; S6 with converging carinae weak and confused with margin; S7 with inner apical lobes much exceeding outer lobes *Santiago* 15(13). Arolia absent; posterior trochanters with strong ventral prominence *Svastrina*
- Arolia present; posterior trochanters usually without such a prominence 16
- 16(15). Pygidial plate ending in two upturned points; middle and hind legs thickened and somewhat contorted, tibial spurs robust, inner hind spur only about four times as long as its greatest breadth *Micronychapis*
- Pygidial plate rounded or truncate; legs not so modified, tibial spurs of the usual slender form 17
- 17(16). Distal process of gonocoxite as long as rest of gonocoxite and extending much beyond distal margin of spatha (S6 without converging carinae, with median basal elevated area; labral emargination scarcely evident; middle femur hairy, without tuft of short dense hair; flagellum scarcely wider than diameter of middle ocellus) *Hamatothrix*
- Distal process of gonocoxite shorter than rest of gonocoxite and extending little if any beyond margin of spatha 18
- 18(17). Labrum nearly three fourths as long as broad, apex deeply emarginate, sides of emargination at about right angle to one another and lobe on each side of emargination narrowly rounded (S6 with pair of strong, converging carinae near tergal margins; first flagellar segment on shortest side slightly longer than broad) *Mirnapis*
- Labrum much less than three fourths as long as broad, broadly emarginate, lobes gently convex 19
- 19(18). S6 without a pair of converging carinae but with median, basal, somewhat elevated area or longitudinal median lamella; labral emargination deep and broad, oc-

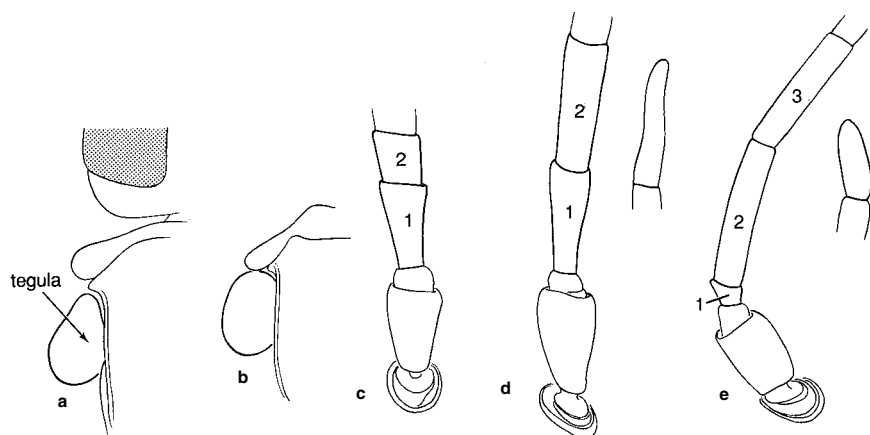


Figure 112-8. Tegula and antennal structures of Eucerini. **a, b,** Tegulae of *Melissodes* sp. and *Eucera* (*Synhalonia*) *atriventris* (Smith); **c,** Antennal base of male of *Xenoglossa kansensis* Cockerell; **d, e,** Antennal bases and apices of males of *Martinapis luteicornis* (Cockerell) and *Gaesischia exul* Michener, LaBerge, and Moure. (The flagellar segments are numbered.) From Michener, McGinley, and Danforth, 1994.

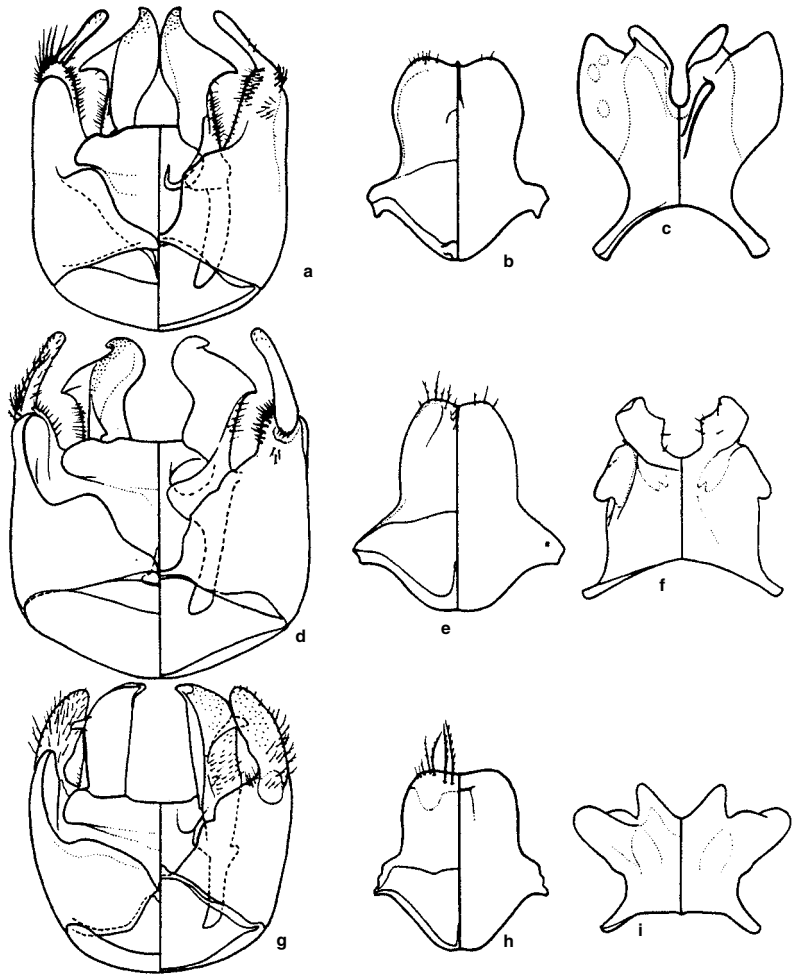


Figure 112-9. Male genitalia, S8, and S7 of Eucerini. **a-c,** *Melissodes (Melissodes) tepaneca* Cresson; **d-f,** *Melissodes (Ectoplectica) nigroaenea* (Smith); **g-i,** *Melissoptila (Ptilomelissa) bonaerensis* Holmberg. (Dorsal views are on the left.) From Moure and Michener, 1955b.

- cupying well over one-third of apical margin; middle femur usually nearly bare beneath except for a mass or tuft of short, dense hairs; flagellum much thicker than diameter of ocellus *Gaesischia* (in part)
- S6 with pair of strong converging carinae but without basal elevated area; labral emargination shallow and occupying less than one-third of margin; middle femur without hair mass or tuft; flagellum little thicker than ocellar diameter 20
- 20(19). First flagellar segment longer than broad, more than one-fifth as long as second; inner apical lobes of S7 not reflexed basally, not diverging apically; vertex usually not elevated behind ocelli, which are on dorsal surface of head; clypeus almost reaching eye and almost without lateroclypeal carina 21
- First flagellar segment much broader than minimum length, less than one-sixth as long as second; inner apical lobes of S7 strap-shaped or expanded apically, reflexed near bases and diverging apically; vertex elevated to form a weak ridge behind ocelli, which are thus to some extent on anterior slope of head; clypeus distinctly separated from eye and with distinct lateroclypeal carina 22
- 21(20). First flagellar segment more than half as long as sec-

- ond (Fig. 112- 8d); inner apical lobes of S7 large, strap-like, expanded and converging apically, much exceeding lateral lobes; metasoma without spatuloplumose hairs; lateral carina of pygidial plate with tooth subapically *Martinapis (Svastropsis)*
- First flagellar segment less than half as long as second; inner apical lobes of S7 very small, much exceeded by lateral lobes; basal hair bands of T2 and sometimes T3 with spatuloplumose hairs (Fig. 112-10b); lateral carina of pygidial plate not toothed subapically..... *Svastra*
- 22(20). T2 and T3 without appressed pale pubescence, sometimes with basal pale bands of semierect pubescence, without median or apical pale bands; length over 10 mm; median apical lobe of S7 usually straplike and not expanded apically; gonostylus with coarse plumose hairs *Suastrides*
- T2 and T3 with appressed pale pubescence, usually

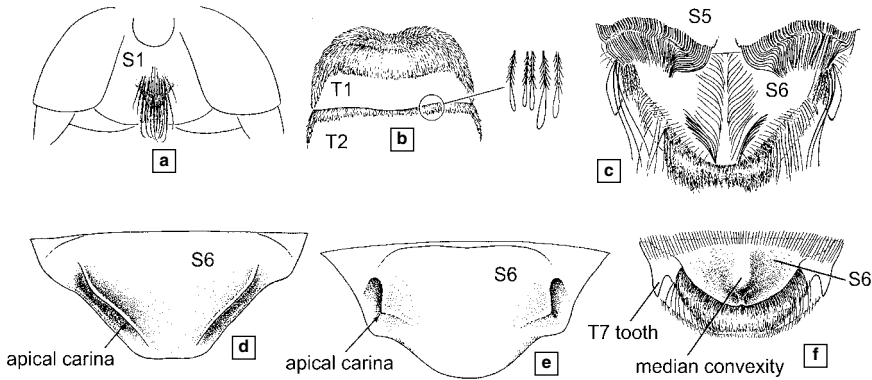


Figure 112-10. Structures of Eucerini. **a**, Ventral surface of base of metasoma of *Syntrichalonia exquisita* (Cresson), male, showing the hairy tubercle of S1; **b**, Dorsal surface of base of metasoma of *Svastra* (*Epimelissodes*) *obliqua* (Say), with enlargement of spatuloplumose hairs; **c**, S5 and S6 of male of *Svastra* (*Idiomelissodes*)

duplocincta (Cockerell); **d**, **e**, S6 of males of *Peponapis pruinosa* (Say) and *Eucera* (*Synhalonia*) *atriventris* (Smith); **f**, S6 and adjacent sclerites of male of *Florilegus condignus* (Cresson). From Michener, McGinley, and Danforth, 1994.

- forming apical as well as basal bands; length under 10 mm; median lobe of S7 expanded apically; gonostylus without coarse plumose hairs *Gaeschia* (in part) 23(3). Gradulus of S2 weakly biconvex (Fig. 112-5a); blade of galea at least 1.4 times as long as eye; mandible with condylar ridge expanded forward and thus at least as salient as and usually more salient than outer ridge; gradulus of T6 without lateral parts; labrum usually two-thirds as long as broad 24
- Gradulus of S2 strongly biconvex, forming angle of 140° or less between two convexities (Fig. 112-5b); blade of galea as long as eye or slightly longer (nearly 1.5 times as long as eye in *Santiago*); mandible normal, with condylar ridge less salient than outer ridge; gradulus of T6 often with lateral parts; labrum usually less than two-thirds as long as broad 26
- 24(23). Vertex with strong preoccipital carina; scape almost as long as interantennal distance; first flagellar segment slightly shorter than scape *Lophothygater*
- Vertex without preoccipital carina; scape much shorter than interantennal distance; first flagellar segment as long as or longer than scape 25
- 25(24). Scape little if any more than twice as long as broad; clypeus black, without pair of ridges diverging below; pygidial plate narrower, margins at angle of about 65°; metasomal terga without bands of appressed pubescence [or, in group of *Thygyter analis* (Lepeletier), with basal bands completely hidden by preceding terga] *Thygyter*
- Scape more than twice as long as broad; clypeus usually with a pair of yellowish spots and with a pair of weak ridges or carinae diverging below; pygidial plate very broad, margins at angle of 80° or more; T2 to T4 with basal bands of sparse, appressed, pale, plumose pubescence *Trichocerapis*
- 26(23). Apical bare area on outer surface of hind tibia nearly one-fourth as long as tibia, delimited posteriorly near base by clump of strong, amber-colored bristles; hairs of metasomal sterna strongly hooked (clypeus almost entirely yellow) *Hamatothrix*
- Apical bare area on outer surface of hind tibia absent or

- not over one-fifth as long as tibia, delimited posteriorly by ordinary hairs; hairs of metasomal sterna not hooked 27
- 27(26). Posterior basitarsus with hairs of inner surface sparse except for a narrow band of dense hairs near lower margin (Fig. 112-11a); clypeus strongly protuberant; labrum about two-thirds as long as broad *Peponapis*
- Posterior basitarsus densely hairy on inner surface (Fig. 112-11b), a band of especially dense hairs near lower margin; clypeus variable but usually moderately protuberant (strongly so in *Santiago*); labrum usually nearly one-half as long as broad or broader 28
- 28(27). Basitibial plate with margin entirely exposed (Fig. 112-12a), surface often bare; T6 with lateral arm of gradulus lamelliform and ending in strong tooth *Florilegus*
- Basitibial plate with margin exposed, if at all, only posteriorly, surface covered with hair (Fig. 112-12b); T6 with gradulus variable, usually not ending in tooth 29
- 29(28). Scutellum half as long as scutum, flattened, projecting well beyond metanotum over whole propodeum, profile of which is vertical *Platysvastra*

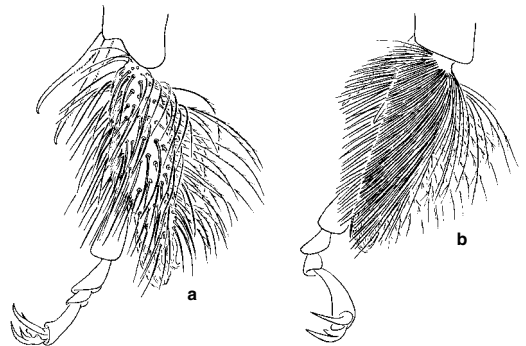


Figure 112-11. Inner views of hind tarsi of females. **a**, *Peponapis pruinosa* (Say); **b**, *Melissodes desponsa* Smith. From Michener, McGinley, and Danforth, 1994.

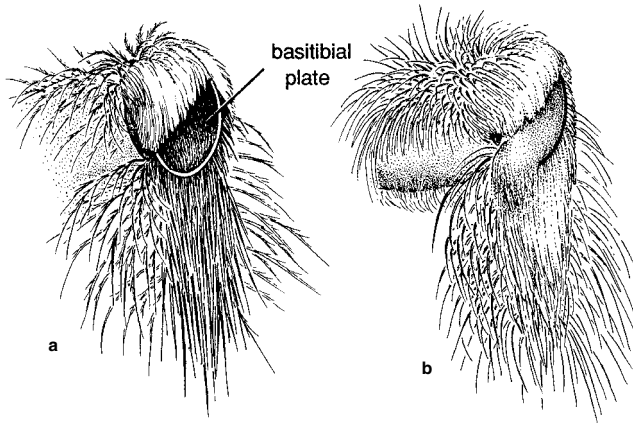


Figure 112-12. Basitibial plates of female Eucerini. **a**, *Florilegus condignus* (Cresson); **b**, *Tetraloniella albata* (Cresson). From Michener, McGinley, and Danforth, 1994.

- . Scutellum nearly always less than half as long as scutum, rarely flattened, not projecting beyond metanotum and over propodeum, profile of which has subhorizontal to steeply sloping basal zone 30
- 30(29). Arolia absent; flagellum thicker than ocellar diameter, first segment about one and one-half times as long as thick (gradulus of T6 with lateral part lamelliform, ending in strong tooth; maxillary palpus five-segmented) 31
- . Arolia present; flagellum little if any thicker than ocellar diameter, first segment over twice as long as thick (this antennal character not verified for *Platysvastra*) 32
- 31(30). Hairs of prementum sparse, simple; first flagellar segment slender at base, twice as long as greatest width *Svastrina*
- . Hairs of prementum dense, undulate, or bent at apices; first flagellar segment robust from base, about 1.5 times as long as greatest width *Pachysvastra*
- 32(30). Maxillary palpus two- or three-segmented; gradulus of T6 with lateral part elevated and terminating in strong tooth; stigma usually longer than prestigma (Fig. 112-4c); second submarginal cell distinctly longer than broad *Melissoptila*
- . Maxillary palpus four- to six-segmented, rarely three-segmented; gradulus of T6 with lateral part weak, cariniform, or, if lamelliform, then not ending in tooth or with tooth low and usually rounded; stigma usually shorter than prestigma (Fig. 112-4b); second submarginal cell variable, usually shorter than or as long as broad 33
- 33(32). Clypeus strongly protuberant, extending forward for distance greater than width of eye as seen in lateral view; blade of galea about 1.5 times as long as eye *Santiago*
- . Clypeus protuberant for less than width of eye as seen in lateral view; blade of galea not much if any longer than eye 34
- 34(33). Maxillary palpus four-segmented, rarely three-segmented; anterior coxa without spine; paraocular carina, when lower part is visible, independent of lateroclypeal carina; anterolateral margin of tegula straight or gently concave (Fig. 112-8a) *Melissodes*
- . Maxillary palpus usually five- or six-segmented, rarely four-segmented; anterior coxa with large apical spine

- (Fig. 112-13c); paraocular carina, when lower part is visible, connected to lateroclypeal carina (except in *Svastra*); lateral margin of tegula continuously convex (Fig. 112-8b) 35
- 35(34). Basal parts of T2 and T3 with dense pilose bands, in strong contrast to remainder of these terga; T6 with lateral parts of gradulus lamellate or strongly carinate; maxillary palpus five-segmented 36
- . Basal parts of T2 and T3 without dense basal bands of pubescence or with median or apical bands as well (very broad basal bands only, in some *Gaesischia*); T6 with lateral parts of gradulus absent, cariniform, or occasionally lamellate; maxillary palpus four-, five-, or six-segmented 37
- 36(35). Pubescent bands of T2 and T3 with spatuloplumose hairs (Fig. 112-10b); eyes converging below; clypeus closely approaching eye; lateroclypeal carina not connected to paraocular carina *Svastra*
- . Pubescent bands of T2 or T3 or both with plumose hairs; eyes subparallel; clypeocular distance about half flagellar width or more; lateroclypeal carina connected to paraocular carina when latter is traceable *Svastrides*
- 37(35). Claws very small, outer rami little exceeding inner teeth; S6 deeply and narrowly notched at apex; middle basitarsus less than two-thirds as long as tibia *Micronychapis*
- . Claws normal, outer rami much exceeding inner teeth (latter rarely absent); S6 only slightly notched or emarginate; middle basitarsus about as long as tibia 38
- 38(37). Scutellum more than one-third as long as scutum, flattened and nearly on same plane as posterior part of scutum; clypeus extraordinarily flat; middle and posterior tibial spurs robust and almost as long as basitarsi *Gaeschira*
- . Scutellum less than one-third as long as scutum, convex; clypeus moderately to strongly protuberant; tibial spurs normal, two-thirds as long as basitarsi or less 39
- 39(38). Vertex elevated behind ocelli, which are therefore on anterior surface; paraocular carina strong; anterior coxa usually with strong apical spine (Fig. 112-13c); maxillary palpus four- or five-segmented, rarely six-segmented *Gaesischia* (in part)
- . Vertex not elevated behind ocelli, which are dorsal; paraocular carina variable, weak if vertex slightly elevated

- behind ocelli; anterior coxa without strong apical spine; maxillary palpus six-segmented, occasionally five-segmented 40
- 40(39). Gradulus of T6 with lateral parts long and strongly carinate or lamellate *Gaesischia* (in part)
- Gradulus of T6 with lateral parts usually absent or very short (indicated as a long but weak carina only in some *Alloscirtetica*) 41
- 41(40). Mandible with apex strongly bidentate (perhaps sometimes simple due to wear); first flagellar segment nearly as long as scape (Fig. 112-8d); maxillary palpus five-segmented *Martinapis*
- Mandible with apex simple; first flagellar segment clearly shorter than scape; maxillary palpus six- or rarely five-segmented *Alloscirtetica*

Key to the North and Central American Genera of the Eucerini (Females)

(Often, hairs must be removed to see the first character in couplet 5(4). In *Melissodes stearnsi* Cockerell, although the tegula is shaped much as in other *Melissodes*, the relevant tegular margin is feebly convex; this species runs to couplet 19 and fails to agree with either alternative.)

1. Gradulus of S2 weakly biconvex (Fig. 112-5a); mandible with condylar ridge expanded forward, at least as salient as and usually more salient than outer ridge (Fig. 112-5c); gradulus of T6 without lateral parts; labrum two-thirds as long as broad or longer (tropical) *Thygater*
- Gradulus of S2 strongly biconvex (Fig. 112-5b), forming angle of 140° or less between two convexities;

- mandible normal, with condylar ridge less salient than outer ridge (Fig. 112-5d); gradulus of T6 usually with lateral parts; labrum usually less than two-thirds as long as broad 2
- 2(1). Apical clypeal margin trilobed, with median lobe short, broad, and often slightly emarginate (Fig. 112-13d) (eastern and central USA) *Cemolobus*
- Apical clypeal margin truncate 3
- 3(2). Inner margin of mandible with tooth near base (Fig. 112-13e) *Xenoglossa*
- Inner margin of mandible without basal tooth (Fig. 112-13f) 4
- 4(3). Posterior basitarsus with inner surface sparsely hairy except for narrow band of dense hairs near lower margin ((Fig. 112-11a) *Peponapis*
- Posterior basitarsus with inner surface uniformly densely hairy or more densely hairy near lower margin (Fig. 112-11a) 5
- 5(4). Tegula narrowed anteriorly (Fig. 112-8a), lateral margin slightly concave or straight in anterior half or less; maxillary palpus usually four-segmented, rarely three- or five-segmented 6
- Tegula not narrowed anteriorly, lateral margin convex (Fig. 112-8b); maxillary palpus three- to six-segmented 7
- 6(5). Mandible simple or scarcely notched at apex, widest preapical part less than three-fourths as wide as base (Fig. 112-14a); last antennal segment much less than twice as long as wide *Melissodes*
- Mandible strongly notched and therefore bilobed at apex (but often worn, so that this structure is lost), ex-

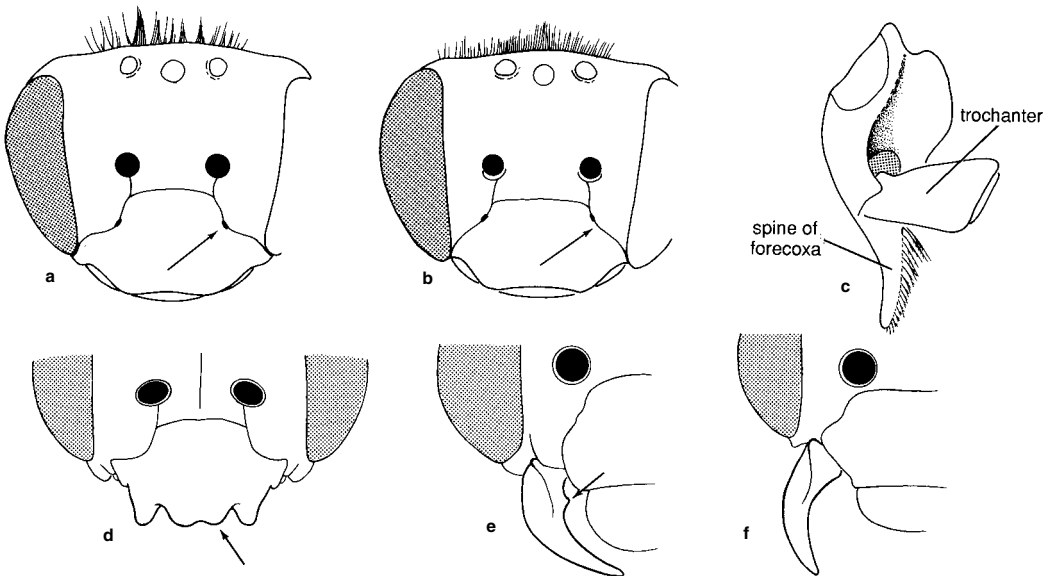


Figure 112-13. Eucerini. **a, b,** Faces of females of *Gaesischia (Gaesischiana) exul* Michener, LaBerge, and Moure and *Tetraloniella (Tetraloniella) albata* (Cresson), showing the angle in the epistomal suture at the tentorial pit (arrows) in the former; **c,** Fore coxa and trochanter of female of *Gaesischia (Gaesischiopsis) flavoclypeata* Michener, LaBerge, and Moure, showing the coxal

spine; **d,** Lower face of male of *Cemolobus ipomoeae* (Robertson), showing the lobate clypeus; **e, f,** Mandible of female of *Xenoglossa strenua* (Cresson) and *Peponapis pruinosa* (Say), showing basal tooth (arrow) of the former. From Michener, McGinley, and Danforth, 1994.

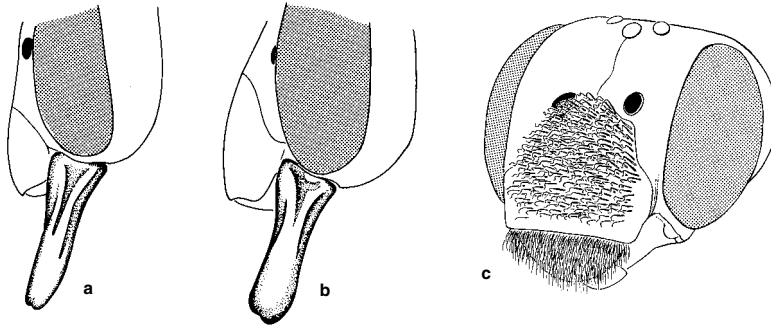


Figure 112-14. Structures of female Eucerini. **a, b,** Mandibles of *Melissodes agilis* Cresson and *Martinapis luteicornis* (Cockerell); **c,** Face of *Tetraloniella (Pectinapis)* sp., showing hooked clypeal hairs. From Michener, McGinley, and Danforth, 1994.

- panded apically and preapical part thus nearly as wide as base (Fig. 112-14b); last antennal segment about twice as long as broad (deserts of southwestern USA and Mexico) *Martinapis*
- 7(5). Scopal hairs simple or with minute barbs 8
- Scopal hairs with branches 14
- 8(7). Clypeal hairs short, erect, robust especially basally, bristle-like, and apically hooked or wavy (Fig. 112-14c) *Tetraloniella (Pectinapis)*
- Clypeal hairs slender, not hooked, not bristle-like 9
- 9(8). Pale pubescent bands of metasomal terga with abundant, basally plumose, apically spatulate hairs; maxillary palpus four-segmented *Svastra (Anthedonia)*
- Pale pubescent bands of metasomal terga without spatuloplumose hairs; maxillary palpus five- or six-segmented, rarely four-segmented 10
- 10(9). Minimum oculoclypeal distance much greater than minimum width of first flagellar segment (Fig. 112-6f); clypeus strongly protuberant; stipes with long, dense, coarse, apically hooked or wavy hairs (Mexico) *Tetraloniella (Loxoptilus)*
- Minimum oculoclypeal distance not greater than minimum width of first flagellar segment; clypeus variable; stipes without area of hooked hairs 11
- 11(10). Blade of galea longer than eye; clypeus protuberant 12
- Blade of galea not longer than eye; clypeus flat to slightly protuberant (slightly less so than in male) 13
- 12(11). Middle ocellus not as broad as flagellum [or, in *Eucera venusta* (Cresson), as wide as flagellum]; maxillary palpus six-segmented; pygidial plate rather broad, rounded apically, apicolateral margin convex (except in *E. venusta* and others) *Eucera (Synhalonia)*
- Middle ocellus broader than flagellum; maxillary palpus

- five-segmented; pygidial plate tapering and bluntly pointed apically, apicolateral margin concave (deserts of southwestern USA and Mexico) *Smantnedon*
- 13(11). Scopal hairs with minute barbs; clypeus with margin indented at anterior tentorial pit to form almost right-angular notch (Fig. 112-13a) (tropical to Arizona) *Gaesischia* (in part)
- Scopal hairs simple; clypeus with margin at level of anterior tentorial pits straight or slightly concave (Fig. 112-13b) *Tetraloniella* (in part)
- 14(7). Fore coxa with inner apical hairy spine (Fig. 112-13c) (tropical to Arizona) *Gaesischia* (in part)
- Fore coxa without spine 15
- 15(14). Vertex elevated, median ocellus thus below summit in facial view; hairs of upper and outer parts of scopa with abundant, uniform, short branches, mostly with ten or more branches on each side of rachis and often with as many as 15; apical part of rachis extending beyond last branch usually shorter than average length of branches (Mexico, southwestern USA) *Syntrichalonia*
- Vertex weakly elevated if at all, median ocellus thus near or on summit in facial view; scopal hairs mostly with six to eight branches on each side of rachis, rarely with as many as ten; apical part of rachis long, extending beyond last branch by at least average length of branches 16
- 16(15). Tibial spurs weak, on middle leg less than half as long as tibia, as measured from base of spur to anterior tibiofemoral articulation; lateral arm of hypostomal carina prominent, sublamelliform; T2 and T3 with short, dense, white pubescence in broad basal bands, with short, relatively simple, dark, appressed hairs from basal bands almost to apices of terga (Baja California, California) *Agapanthinus*

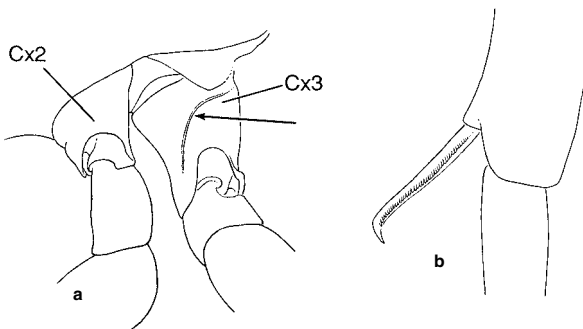


Figure 112-15. Structures of females of Eucerini. **a,** Middle and hind coxae of *Ptilomelissa* (*Ptilomelissa*) sp., the lateral hind coxal carina marked by an arrow; **b,** Middle tibial spur of *Svastra (Idiomelissodes) duplocincta* (Cockerell). From Michener, McGinley, and Danforth, 1994.

- Tibial spurs strong, on middle leg more than half as long as tibia; lateral arm of hypostomal carina weak, cariniform; T3 and usually T2 without basal pale pubescent bands, or with distal pale band in addition, or entirely covered by pale pubescence 17
- 17(16). Prestigma shorter than stigma (as in Fig. 112-4c); lateral hind coxal carina sharp, bent strongly posteriad basally to form a rounded angle of almost 90° (Fig. 112-15a); maxillary palpus two- or three-segmented (tropical to Texas) *Melissoptila*
- Prestigma as long as or longer than stigma (as in Fig. 112-4b); lateral hind coxal carina absent or reduced to short apical portion, straight or only slightly curved toward rear; maxillary palpus four- to six-segmented 18
- 18(17). Maxillary palpus usually four-segmented, but *if* five-segmented, then basal pubescent band of T2 with at least a few spatuloplumose hairs (Fig. 112-10b); lateral arms of gradulus of T6 lamelliform, often with a small tooth *Svastra*
- Maxillary palpus five- or six-segmented; basal pubescent band of T2 without spatuloplumose hairs; lateral arms of gradulus of T6 cariniform to lamelliform 19
- 19(18). Basitibial plate with margin entirely exposed, surface often bare; T6 with lateral parts of gradulus lamelliform and ending in strong tooth *Florilegus*
- Basitibial plate with anterior and apical part of margin hidden, surface usually hairy; T6 with lateral parts of gradulus cariniform, never toothed *if* sublamelliform *Tetraloniella* (in part)
-
- Key to the North and Central American Genera of the Eucerini (Males)
- (*Peponapis timberlakei* Hurd and Linsley runs *either* to *Svastra* in couplet 14, except that the last antennal segment is not tapering and acuminate, *or* to couplet 15, except that the last flagellar segment is more than twice as long as broad.)
1. Minimum length of malar area greater than minimum width of first flagellar segment (Fig. 112-6e); pygidial plate unrecognizable or indicated by weak lateral carinae, mostly covered by long, appressed hairs, T7 bidentate apically; labrum at least three-fourths as long as broad (tropical) *Thygater*
- Minimum length of malar area equal to or less than minimum width of first flagellar segment; pygidial plate prominent, exposed, with short hairs or bare, T7 truncate or rounded apically; labrum variable but usually less than three-fourths as long as broad 2
- 2(1). Clypeal margin trilobed, median lobe broad and often shallowly emarginate medially (Fig. 112-13d); first flagellar segment as long as second segment; S6 with large, laterally directed, lateral tooth (eastern and central USA) *Cemolobus*
- Clypeal margin truncate; first flagellar segment usually shorter than second segment; S6 usually without lateral teeth 3
- 3(2). T7 with lateral gradular tooth or strong angle on each side of pygidial plate, sometimes hidden in dense hair or *by* T6 4
- T7 without lateral teeth (occasionally S6 with lateral teeth that can be seen from above and may be confused with tergal teeth) 7
- 4(3). Stigma slightly longer than prestigma (Fig. 112-4c); maxillary palpus two- or three-segmented; lateral hind coxal carina prominent, curved (Fig. 112-15a) (tropical to Texas) *Melissoptila*
- Stigma small, usually as short as or shorter than prestigma (Fig. 112-4b); maxillary palpus usually four- or five-segmented, rarely three-segmented; lateral hind coxal carina reduced or absent 5
- 5(4). S6 with prominent median convexity; fore femur broadest about one-fourth or one-third of its length from apex; maxillary palpus five-segmented *Florilegus*
- S6 flat or with exceedingly shallow, longitudinal median depression; fore femur broadest basal to middle; maxillary palpus usually three- or four-segmented, rarely five-segmented 6
- 6(5). Tegula narrowed anteriorly, lateral margin slightly concave or straight in anterior one-half or one-third (Fig. 112-8a) (often hidden by hairs); clypeus little or moderately protruding, extending in front of eye by eye width or less as seen in lateral view *Melissodes*
- Tegula not narrowed anteriorly, lateral margin continuously convex (Fig. 112-8b); clypeus strongly protuberant, extending in front of eye by more than eye width as seen in lateral view *Peponapis* (in part)
- 7(3). First flagellar segment longer than second; inner margin of mandible with tooth near base (Fig. 112-13e) *Xenoglossa*
- First flagellar segment no longer than second segment and often much shorter (longer in *Peponapis timberlakei*, Hurd and Lindsey); inner margin of mandible without tooth near base 8
- 8(7). Clypeus strongly protuberant, abruptly beveled and snoutlike apically (Fig. 112-6g), its profile forming distinct preapical angle and concave above angle (rare, southwestern deserts) *Simanthes*
- Clypeus uniformly convex or straight in profile 9
- 9(8). Tibial spurs weak, middle tibial spur about half or less than half as long as tibia, as measured from base of spur to anterior tibiofemoral articulation 10
- Tibial spurs strong, middle tibial spur more than half as long as tibia 13
- 10(9). First flagellar segment only slightly shorter than second (Fig. 112-8d); last flagellar segment tapering to apex; flagellum bright yellow (deserts of southwestern USA and Mexico) *Martinapis*
- First flagellar segment half as long as second or less (Fig. 112-8e); last flagellar segment not tapering; flagellum tan to black 11
- 11(10). Last flagellar segment with short, pointed, hooked apex twisted slightly laterad (Baja California, California) *Agapanthinus*
- Last flagellar segment with rounded apex 12
- 12(11). Hind basitarsus flattened, shining, largely hairless on outer surface; distal two flagellar segments often slightly compressed (tropical to Arizona) *Gaesischia*
- Hind basitarsus normal, hairy; distal two flagellar segments not compressed (central and western USA and Mexico) *Tetraloniella* (in part)
- 13(9). Maximum length of first flagellar segment as great as or slightly greater than minimum length of second segment; last flagellar segment at least twice as long as broad 14
- Maximum length of first flagellar segment usually much

- less than length of second segment or, *if* about the same, then last flagellar segment less than twice as long as broad and rounded apically 15
- 14(13). S1 with hairy median convexity (Fig. 112-10a), profile thus convex; last flagellar segment rounded apically (Mexico, southwestern USA) *Syntrichalonia*
- S1 relatively flat, profile straight and lacking prominent median eminence; last flagellar segment tapering and acuminate apically *Svastra* (*Anthedonia*)
- 15(13). Maxillary palpus usually four-segmented, but *if* five-segmented, then T2 with basal pubescent band at least a few hairs of which are basally plumose and apically spatulate (Fig. 112-10b) *Svastra*
- Maxillary palpus five- or six-segmented, and T2 without spatuloplumose hairs 16
- 16(15). Blade of galea twice as long as eye or longer (Fig. 112-6a); clypeus strongly protuberant; lower part of paraocular carina prominent; antenna long, reaching stigma or beyond in repose (Mexico) *Tetraloniella* (*Loxoptilus*)
- Blade of galea 1.5 times as long as eye or shorter; clypeus variable, often flat; paraocular carina variable, lower part often obsolete; antenna variable in length 17
- 17(16). Oculoclypeal distance extremely short (Fig. 112-6b), not more than about one-fourth of minimum width of first flagellar segment *Tetraloniella* (in part)
- Oculoclypeal distance short to long, equal to one-third of minimum width of first flagellar segment or more 18
- 18(17). S6 with oblique lateral apical carina straight, sternum not toothed or angled laterally (Fig. 112-10d); antenna of moderate length, not reaching stigma in repose *Peponapis* (in part)
- S6 almost always with oblique lateral apical carina curved outward and thickened basally, ending in a lateral blunt tooth or obtuse angle of sternum (Fig. 112-10e); antenna usually long, reaching stigma or beyond in repose 19
- 19(18). Profile of clypeus distinctly convex *Eucera* (*Synhalonia*)
- Profile of clypeus nearly straight, in spite of rather strong protuberance (Mexico) *Tetraloniella* (*Pectinapis*)

Key to the Genera of the Eucerini of the Eastern Hemisphere

1. Forewing with two submarginal cells (Fig. 112-4a) 2
- Forewing with three submarginal cells 3
- 2(1). Maxillary palpus six-segmented, very rarely five-segmented; first submarginal cell of front wing smaller than second (Fig. 112-4a), and distance from first submarginal crossvein to first recurrent vein greater than distance from second recurrent to second submarginal crossvein; first segment of flagellum of male short, 0.9 to 2.5 times as long as broad, second segment 1.7 to 5.0 times as long as first; gradulus of S6 of male arcuate; medial area of S7 of male more or less flat (palearctic) *Eucera* (in part)
- Maxillary palpus three- or four-segmented; first submarginal cell of front wing equal to second, and distance from first submarginal crossvein to first recurrent vein about equal to that from second recurrent to second submarginal crossvein; first segment of flagellum of male long, 3.3 to 4.0 times as long as broad, second segment 0.7 to 1.2 times as long as first; gradulus of S6 of male sharply angulate to rear near lateral extremity (sometimes weakly so in subgenus *Cubitalia* s. str.); medial area of S7 of male produced downward posteriorly (palearctic) *Cubitalia*
- 3(1). Maxillary palpus three- to four-segmented or with minute fifth segment, often not longer than maximum width of galeal blade; keirotrichiate area of female apically at least half as wide as hind tibia and extending basad beyond middle of tibia; scopa consisting of sparse, strongly plumose hairs on outer surface of tibia, each arising from tubercle separated from its neighbors by full width of tubercle *Tetralonia*
- Maxillary palpus five- or six-segmented, often longer than maximum width of galeal blade; keirotrichiate area and associated finely and closely punctate surface of female usually less than half as wide as hind tibia and extending basad only to middle of tibia, rarely absent; scopa consisting of denser hairs, often simple, *if* plumose, then arising from tubercles less widely separated from one another 4
- 4(3). Blade of galea more than twice as long as eye; first flagellar segment of male much longer than scape and as long as second flagellar segment, that of female about as long as scape and distinctly longer than second and third flagellar segments taken together (Turkmenistan) *Notolonia*
- Blade of galea shorter; first flagellar segment of male shorter than scape and much shorter than second flagellar segment, that of female shorter than scape and not or scarcely longer than second and third flagellar segments taken together 5
- 5(4). S6 of male with the two converging carinae each usually angulate near anterior end, forming lateral angle usually reflecting marginal sternal angle or lobe (Fig. 112-10e), which is often strengthened by lateral branch carina arising at angle of converging carina, sometimes carinae absent except for branch and mesally directed anterior end of converging carina, together forming transverse carina directed anteromesally from marginal sternal angle or lobe; clypeus usually protuberant for width of eye or more as seen in lateral view; blade of galea 1.2 or more times length of eye; middle femur of male on undersurface commonly with area of dense, appressed, red-brown hair hiding surface *Eucera* (*Synhalonia*)
- S6 of male with the two converging carinae each usually simple and more or less straight; clypeus usually protuberant for less than width of eye as seen in lateral view; blade of galea usually not much longer than length of eye; middle femur of male sometimes with area of sparse, appressed whitish hair not hiding surface, more commonly with unspecialized sloping or erect hair *Tetraloniella*

The genus *Ulugombakia* Baker (known only in the female) runs to 3 in the Key to the Genera of Eucerini of the Eastern Hemisphere. If one ignores characters of males and the number of maxillary palpal segments (justified by the palpal length even though there are only four segments), it runs to *Tetraloniella*, from which it can be distinguished by characters cited in the account of the genus.

Genus *Agapanthinus* LaBerge

Agapanthinus LaBerge, 1957: 35. Type species: *Melissodes callophila* Cockerell, 1923, by original designation.

Although *Melissodes*-like in general appearance, 9 to 11 mm in length, *Agapanthinus* is not closely related to *Melissodes*. The small midtibial spur and modified apex of the male antenna (see the key to genera) suggest a relation to *Gaesischia*. Other characters include the large and complex apical lobes of S7 of the male, somewhat as in *Gaesischia*. The male gonostylus is unique among Eucerini, being shorter than the apical process of the gonocoxite, almost as broad as long, tapering, and bearing long hairs. Male genitalia and hidden sterna were illustrated by LaBerge (1957).

■ *Agapanthinus* occurs in the desert of Baja California and California. The single species is *A. callophilus* (Cockerell).

Genus *Alloscirtetica* Holmberg

In this South American genus the pygidial plate of the male is reduced, at least the lateral carinae ending before the apex of the pygidial area and the plate often unrecognizable or ending in a point. Elsewhere in the Eucerini such reduction of the male pygidial plate occurs in *Thygater*, a very different genus. S7 of the male nearly always has an unpaired median projection between the apical lobes, which are rather large, delicate, hairy, and elaborate (Fig. 112-7c). S6 of the male lacks the carinae common thereon in many Eucerini. Except for the subgenus *Megascirtetica*, which looks like a large black *Thygater*, the species of *Alloscirtetica* look rather like *Melissodes*. The six-segmented maxillary palpi of most species resulted in many of them being described in the genus *Tetralonia*.

Alloscirtetica is largely restricted to temperate and Andean South America, with a few species occurring in tropical Brazil. Urban (1971, 1982) revised the genus and provided keys to its species, except for *Megascirtetica*. Michener, LaBerge, and Moure (1955a), Moure and Michener (1955b), and Urban (1971, 1977) recognized up to four subgenera in *Alloscirtetica* (not including *Megascirtetica*). In those works *Alloscirtetica* s. str. consisted simply of those species that did not fall into any other subgenus. As more species became known, it became increasingly difficult to recognize the subgenera, and Urban (1982), after studying all known species, decided that the subgenera could not be maintained. I agree with her decision.

Megascirtetica has hitherto been regarded as a genus related to *Alloscirtetica*. Its distinctive features, however, are all probably derived; it is thus a specialized derivative of *Alloscirtetica*, and its relationships are best indicated by its inclusion in that genus.

Key to the Subgenera of *Alloscirtetica*

1. Claws of female simple; arolia unusually small; mandible with large, right-angular preapical tooth separated from apex by deep notch; head strongly elevated behind ocelli; body length over 15 mm *A. (Megascirtetica)*
- Claws of female with inner tooth; arolia of ordinary size; mandible simple, preapical tooth vestigial or absent; head

not or weakly elevated behind ocelli; body length 12 mm or less *A. (Alloscirtetica* s. str.)

Alloscirtetica / Subgenus *Alloscirtetica* Holmberg s. str.

- Scirtetica* Holmberg, 1903: 389 (not Saussure, 1884). Type species: *Scirtetica antarctica* Holmberg, 1903, monobasic.
- Alloscirtetica* Holmberg, 1909a: 77, replacement for *Scirtetica* Holmberg, 1903. Type species: *Scirtetica antarctica* Holmberg, 1903, autobasic.
- Neoscirtetica* Schrottky, 1913a: 256, replacement for *Scirtetica* Holmberg, 1903. Type species: *Scirtetica antarctica* Holmberg, 1903, autobasic.
- Holmbergiapis* Cockerell, 1918b: 36, replacement for *Scirtetica* Holmberg, 1903. Type species: *Scirtetica antarctica* Holmberg, 1903, autobasic.
- Alloscirtetica (Dasyscirtetica)* Michener, LaBerge, and Moure, 1955a: 218. Type species: *Tetralonia gilva* Holmberg, 1884, by original designation.
- Alloscirtetica (Ascirtetica)* Moure and Michener, 1955b: 260. Type species: *Eucera herbsti* Friese, 1906, by original designation.
- Alloscirtetica (Scirteticops)* Moure and Michener, 1955b: 261. Type species: *Tetralonia gayi* Spinola, 1851, by original designation.

This is a highly variable taxon having a generally *Melissodes*-like form, although its members are highly variable in hair color. The body length is 8 to 12 mm. Some of the characters of males that vary, and that led to recognition of four subgenera in what is here called *Alloscirtetica* s. str., are enumerated below. Females are less variable and the subgenera recognized on the basis of males were not easily (or at all) separable among females. T7 of males may be rounded, the dorsal surface almost without evidence of a pygidial plate, but usually there is at least a well-defined bare area, often margined by carinae, these margins converging posteriorly to a point on or in front of the tergal margin. In other species the carinae do not meet, and sometimes the apical part of a subtruncate pygidial plate is recognizable, but the carinae do not extend to its apex. Urban (1982) diagrammed the variation in T7 of males. The length of the first flagellar segment of males varies from very short to almost two-thirds as long as the second segment. Urban (1982) illustrated this variation also. The posterior claws are sometimes asymmetrical. In the form formerly placed in *Scirteticops*, the profile of the propodeum is wholly declivous, whereas in others there is a sloping zone behind the metanotum. The jugal lobe of the hind wing is only about half as long as cell Cu in the former *Scirteticops*, whereas it is variably longer in others. In spite of such variation, *Alloscirtetica* s. str. is a distinctive, unified taxon. Male genitalia and hidden sterna as well as other characters were illustrated by Michener, LaBerge, and Moure (1955a), Moure and Michener (1955b), and Urban (1971, 1977, 1982). The hairs of the male S7 are particularly elaborate, and Urban illustrated many of them.

■ This subgenus ranges from Magallanes, Chile, and the province of Chubut, Argentina, north to Pará, Brazil, and in the Andean uplift to Ecuador. Most species occur in Chile and the xeric parts of Argentina. The 36 species

onymized by Michener (2000) under *Eucera* (*Heteroecura*). (Note that “*Donatica*,” which appears in Risch’s abstract as though it were a genus, is in fact a specific name, the type species of *Opacula*.)

Key to the Subgenera of *Cubitalia* (Males Only)

1. Postgradular area of S5 with two tufts of bristly hairs directed laterally; front basitarsus slightly curved, of normal length, about 1.8 times as long as three following segments taken together; gonostylus sharply curved medially, with pointed ventral lamellar projection; clypeus gently convex in profile, lower part extended down and facing forward; middle tibia slightly curved *C. (Opacula)*
- Postgradular area of S5 more or less uniformly pubescent; front basitarsus straight, shortened, 1.2 to 1.5 times length of three following segments taken together; gonostylus broadened at apex, not bent medially, without ventral projection; clypeus obtusely angulate in profile, lower part curved back and facing somewhat downward; middle tibia not curved 2
- 2(1). Mandible longer than eye, bidentate, acetabular carina not forming preapical tooth; inner orbits diverging downward; antenna reaching propodeum; front margins of middle and hind basitarsi with broad excisions or emarginations; S7, as seen from beneath, with large convexity on each side of median carina *C. (Cubitalia s. str.)*
- Mandible shorter than eye, acetabular carina ending in preapical tooth, mandibular apex thus three-toothed; inner orbits parallel; antennae long, reaching metasoma; front margins of middle and hind basitarsi unmodified; S7 without large ventral convexities *C. (Pseudeucera)*

Cubitalia / Subgenus *Cubitalia* Friese s. str.

Friese, 1911d: 136. Type species: *Eucera breviceps* Friese, 1911, monobasic.

Cubitalia s. str. consists of large (16–18 mm long), robust bees. The head of the male, and especially the mandibles, is large. Hidden sterna and other structures were illustrated by Tkalců (1984b) and Pesenko and Sitdikov (1988).

■ This subgenus occurs in the Balkans and Greece east to the Caucasus. The four species were revised by Tkalců (1984b).

Cubitalia / Subgenus *Opacula* Pesenko and Sitdikov

Opacula Pesenko and Sitdikov, 1988: 849. Type species: *Opacula donatica* Sitdikov, 1988, by original designation. [New status.]

This subgenus, like *Pseudeucera*, consists of species smaller than those of *Cubitalias* s. str., body length 13 mm. As in *Pseudeucera*, the male mandible is three-toothed, because the acetabular carina ends in a preapical tooth; and the middle and hind basitarsi do not have emarginations in their anterior margins. Illustrations of male genitalia, sterna, legs, etc., were provided by Pesenko and Sitdikov (1988).

■ *Opacula* is known only from Kirghizia, in Central Asia. The only species is *Cubitalia donatica* (Sitdikov).

Cubitalia / Subgenus *Pseudeucera* Tkalců

Pseudeucera Tkalců, 1978a: 157, 158. Type species: *Eucera parvicornis* Mocsáry, 1878, by original designation. [New status.]

In addition to the characters indicated in the key, *Pseudeucera* differs from *Opacula* in having relatively short, straight male gonostylus; the distal one-third is broadened, quite unlike the fanlike enlargement of the extreme apex in *Cubitalias* s. str. and the incurved, slender apex in *Opacula*. The gonostylus and various other structures were illustrated by Pesenko and Sitdikov (1988). The body length is 12 to 14 mm.

■ *Pseudeucera* occurs from Hungary, Italy, and Greece east to the Ukraine. The only species is *Cubitalia parvicornis* (Mocsáry), an oligolege on Boraginaceae (Müller, 1995).

Genus *Eucera* Scopoli

Eucera includes most of the palearctic Eucerini that have two submarginal cells, *Cubitalia* being the only other such group, as shown in the key to genera. *Eucera* also includes, however, many species with three submarginal cells, commonly placed in *Tetralonia* or *Synhalonia*, but here considered to constitute the subgenus *Synhalonia* of *Eucera*. The loss of the second submarginal crossvein, resulting in two instead of three submarginal cells, is widespread among bees and frequently is not a generic character. Given the variability in both two-celled *Eucera* and in three-celled *Synhalonia*, there is no character other than the number of submarginal cells that separates the two-celled from the three-celled groups. *Eucera* as usually recognized may be polyphyletic, its species derived from different three-celled ancestors. This possibility is supported by the similar variability of other characters within two-celled and three-celled groups. For example, in both groups the male gonostylus is sometimes elbowed and sometimes arcuate or nearly straight, suggesting that two-celled *Eucera* with the elbowed gonostylus may have arisen from *Synhalonia* with the elbowed gonostylus, and two-celled *Eucera* with the straight gonostylus, from comparable *Synhalonia*. The structure of the male gonostylus, however, is particularly useless for recognition of groups in this section of Eucerini, and appears to have led various authors astray. In the related genus *Tetraloniella*, within its *ruficornis* species group, there are species with gently curved gonostyli and others with weakly and strongly elbowed gonostyli (Tkalců, 1979b). On the basis of other characters, at least certain groups of *Eucera* do not appear to have immediate ancestors among *Synhalonia* species. For example, in the large subgenus *Eucera* s. str., the keirotrichiate area of the hind tibia of females is large, occupying most of the inner surface of the hind tibia, whereas in related Eucerini it is small, limited to the distal half of the tibia and occupying less than one-third of the tibial width; the large area is presumably plesiomorphic.

Evidence for the close relationship of two-celled *Eucera* to *Synhalonia* is found in the strongly protuberant clypeus, the long proboscis, such that the blade of the galea is conspicuously longer than the eye, and the lack of paraocular carinae or, if present, the carinae not reaching

the carinate lateral margins of the clypeus. Further, S6 of the male usually has a lateral marginal projection commonly strengthened by the anterior end of one of the converging carinae of S6, or by a lateral branch from that carina, the main axis of which often bends mesad near its anterior end, producing an angle that is often produced laterally. Sometimes, in both two-celled and three-celled species, the convergent carina is largely absent, but its anterior end remains, combined with its lateral branch, as a transverse carina on each side of the sternum strengthening the lateral marginal projection of the sternum. With minor adjustments, these are all characters of *Eucera* that help to distinguish it from *Tetraloniella*; as noted elsewhere, I recognize *Tetraloniella* as a genus largely for historical reasons, awaiting proper studies of the species worldwide, for all of the characters that separate it from *Eucera* (*Synhalonia*) break down. *Synhalonia* and most two-celled *Eucera* resemble one another superficially; they are all large, and the males often lack pale metasomal hair bands.

The two large two-celled subgenera, *Eucera* s. str. and *Heteroeucera*, which contain the great majority of two-celled species of Eucerini, are clearly congeneric with *Synhalonia*. The subgenera *Oligoeucera*, which I have not seen, and *Preneucera*, however, the two together comprising only five species, are quite different from the large subgenera and may deserve generic rank. The latter has paraocular carinae near the eye margins, reaching the lateral clypeal carinae or nearly so. I include them in *Eucera* only because it is not clear where else they might be placed. Neither seems to be a *Tetraloniella*.

Key to the Subgenera of *Eucera*

1. Forewing with three submarginal cells (holarctic)
..... *E. (Synhalonia)*
— Forewing with two submarginal cells (paleartic) 2
- 2(1). Males 3
— Females 6
- 3(2). Gonostylus, as seen in lateral view, straight or gently arcuate *E. (Heteroeucera)*
— Gonostylus as seen in lateral view angled, i.e., base directed dorsoapically, then bent ventroapically 4
- 4(3). Hind femur with angular protuberance in middle of lower margin; body length 7.5 to 8.0 mm; first flagellar segment broader than long *E. (Oligoeucera)*
— Hind femur with middle of lower margin more or less straight; body length 10.0 to 16.5 mm; first flagellar segment longer than broad 5
- 5(4). Gonostylus with retrorse ventral spine; S4 and S5 with lateral areas of strong yellowish bristles; body length 10.0 to 12.5 mm *E. (Preneucera)*
— Gonostylus without ventral spine; S4 and S5 without lateral tufts of bristles (except in *Eucera interrupta* Bör); body length 12.0 to 16.5 mm *E. (Eucera s. str.)*
- 6(2). Hind tibia with keirotrichiate area occupying most of inner surface; scopal hairs limited to outer surface and margins of inner surface of tibia (scopal hairs simple; body length 12–17 mm) *E. (Eucera s. str.)*
— Keirotrichiate area a longitudinal band or triangle less than half as wide as tibia and limited to distal half of tibia;

- scopal hairs occupying not only outer surface of tibia but also inner surface, except for keirotrichiate area 7
- 7(6). Lower half of clypeus largely yellow; S2 to S5 with twisted hairs; body length 7 mm (scopal hairs simple) *E. (Oligoeucera)*
— Clypeus entirely dark; S2 to S5 with straight hairs; body length 8 to 17 mm 8
- 8(7). Scopal hairs on outer surface of hind tibia coarsely branched *E. (Preneucera)*
— Scopal hairs simple (or, in *E. furfurea* Vachal, with very short branches) *E. (Heteroeucera)*

Eucera / Subgenus *Eucera* Scopoli s. str.

Eucera Scopoli, 1770: 8. Type species: *Apis longicornis* Linnaeus, 1758, by designation of Latreille, 1810: 439.

Eucera s. str. is a distinctive subgenus of large bees (see the key to subgenera) with long and usually dark-colored male antennae, like those of *Synhalonia*. The large keirotrichiate area of the hind tibia of the female, in particular, distinguishes *Eucera* s. str. from related Eucerini. In view of the distribution of keirotrichiae in other bees, the large area here may be a plesiomorphy, not an apomorphy as interpreted by Sitdikov and Pesenko (1988). Male genitalia, hidden sterna, and other structures were illustrated by Iuga (1958), Tkalců (1978a, 1984c), and Sitdikov and Pesenko (1988).

■ *Eucera* s. str. occurs from the Canary Islands, Spain, and Britain to Japan. Of over 130 named species of two-celled *Eucera*, only about 20, representing about 10 species, have been shown to belong to *Eucera* s. str., but about 50 of the proposed species names of *Eucera* probably relate to this subgenus.

Eucera / Subgenus *Heteroeucera* Tkalců

- Eucera (Heteroeucera)* Tkalců, 1978a: 167. Type species: *Eucera hispana* Lepeletier, 1841, by original designation.
- Eucera (Pareucera)* Tkalců, 1978a: 164. Type species: *Eucera caspica* Morawitz, 1873, by original designation.
- Eucera (Stilbeucera)* Tkalců, 1978a: 162. Type species: *Eucera clypeata* Erichson, 1835, by original designation.
- Eucera (Atopeucera)* Tkalců, 1984c: 71. Type species: *Eucera seminuda* Brullé, 1832, by original designation.
- Eucera (Agatheucera)* Sitdikov and Pesenko, 1988: 87. Type species: *Eucera bidentata* Pérez, 1887, by original designation.
- Eucera (Hemieucera)* Sitdikov and Pesenko, 1988: 88. Type species: *Eucera paraclypeata* Sitdikov, 1988, by original designation.
- Eucera (Pileteucera)* Sitdikov and Pesenko, 1988: 87. Type species: *Eucera cineraria* Eversmann, 1852 = ?*E. cinerea* Lepeletier, 1841, by original designation.
- Eucera (Rhyteucera)* Sitdikov and Pesenko, 1988: 87. Type species: *Eucera parvula* Friese, 1895, by original designation.

As here understood, *Heteroeucera* is a second major subgenus of two-celled *Eucera*, *Eucera* s. str. being the first. Sitdikov and Pesenko broke it up into eight subgenera,

and Spain eastward throughout the Mediterranean countries, north to Slovakia, south to India (Punjab), and through Asia to Japan. There are 54 North American species and perhaps as many palearctic species. Many species from the latter region have not been reliably placed to genus, because *Tetralonia*, *Tetraloniella*, and *Eucera* (*Synhalonia*) have been commonly regarded as a single unit usually called *Tetralonia*. The nearctic species of *Synhalonia* were revised by Timberlake (1969b).

The nesting biology of *Eucera hamata* (Bradley) was described by Miliczky (1985).

Genus *Eucerinoda* Michener and Moure

Eucerinoda Michener and Moure, 1957: 445. Type species: *Anthophora gayi* Spinola, 1851, by original designation.

This genus constitutes the subtribe Eucerinodina. Its distinctive features are indicated not only in the key to South American genera, but also in the account of the tribe Eucerini. It consists of a rather robust species with a body length of 10.5 to 11.0 mm. The pubescence is pale, and forms broad bands on the metasomal terga, especially apically. It differs from most but not all other Eucerini in having a rather flat clypeus, the lateral parts of which are not much bent posteriorly, and in its stigma, which, although small, is longer than the prestigma with vein *r* arising near its middle, about as in *Melissoptila*. In the male the clypeus and paraocular areas below the antennae are yellow; the antennae reach the base of the scutellum, the first flagellar segment being almost as long as the second and third segments taken together; and the hind leg is enlarged, the basitibial plate and tibial spurs absent, and the basitarsus highly modified. A full description and figures of genitalia and sterna were provided by Michener and Moure (1957); see also Figure 112-17, presented here to demonstrate the similarity of *Eucerinodato* other Eucerini (compare Figs. 112-7, 112-9). ■ *Eucerinoda* occurs in central Chile. There is only one species, *E. gayi* (Spinola).

Genus *Florilegus* Robertson

Florilegus consists of *Melissodes*-like bees of North and South America having weak iridescent reflections on the metasomal terga and five-segmented maxillary palpi. Females differ from those of all similar genera in the exposed and often bare margin of the basitibial plate (Fig. 112-12a), and from those of most others in the lamellate lateral arm of the gradulus of T6, ending in a strong tooth. The male differs from that of *Melissodes* and other similar bees by the relatively large and complex apical lobes of S7 (Fig. 112-7i), suggesting those of some *Gaesischia*. Unlike the male gonostyli of that genus, those of *Florilegus* are relatively short, robust, and expanded apically. The male genitalia and hidden sterna were illustrated by Michener (1954b), Moure and Michener (1955b), LaBerge (1957), Mitchell (1962), and Urban (1970); see also Figure 112-7g-i.

This genus was revised by Urban (1970).

Key to the Subgenera of *Florilegus* (Males) (Modified from Moure and Michener, 1955b)

1. Hind tibia at least slightly contorted with band of dense hairs on otherwise largely bare inner surface; hind femur concave beneath; inner apical lobe of S7 much longer

- than broad, terminating in relatively short, sparse hairs (South America) *F. (Eu)florilegus*)
 —. Hind tibia unmodified; hind femur convex beneath; inner apical lobe of S7 broader than long, terminating in fringe of long hairs 2
 2(1). Large black forms without pale fasciae on first three metasomal terga; scutellum relatively flat, its profile nearly a continuation of that of scutum (neotropical)
 *F. (Floriraptor)*
 —. Smaller forms with pale fasciae (sometimes broken) on T2 and T3; scutellum more convex *F. (Florilegus s. str.)*

Key to the Subgenera of *Florilegus* (Females) (Modified from Moure and Michener, 1955b)

1. Hairs of maxilla and mentum erect, hooked; marginal cell slightly shorter than distance from apex to wing tip (South America) *F. (Eu)florilegus*)
 —. Hairs of maxilla and mentum simple, inconspicuous; marginal cell longer than distance from apex to wing tip 2
 2(1). Scutellum more than one-third as long as scutum, flattened and nearly on same plane as posterior part of scutum; first flagellar segment as long as distance between posterior ocelli; first three terga largely glabrous (neotropical) *F. (Floriraptor)*
 —. Scutellum less than one-third as long as scutum, convex; first flagellar segment distinctly shorter than distance between posterior ocelli; at least T3 with band (sometimes broken) of pale pubescence *F. (Florilegus s. str.)*

Florilegus / Subgenus *Euflorilegus* Ogloblin

Florilegus (*Euflorilegus*) Ogloblin, 1955: 231. Type species: *Florilegus riparius* Ogloblin, 1955, by original designation.

Members of this subgenus look much like those of *Florilegus s. str.* in size and coloration.

■ *Euflorilegus* occurs from Buenos Aires Province, Argentina, north to Pará and Amazonas, Brazil. The five species were revised by Urban (1970).

Florilegus / Subgenus *Florilegus* Robertson s. str.

Florilegus Robertson, 1900: 53. Type species: *Melissodes condigna* Cresson, 1879, monobasic.

Like *Euflorilegus*, species of this subgenus are relatively small, 9 to 11 mm long, with much yellowish hair.

■ This subgenus occurs from New Jersey to Colorado, USA, southward through the Antilles (at least Cuba), Mexico, and the American tropics to Buenos Aires and La Rioja provinces, Argentina. The five species were revised by Urban (1970).

LaBerge and Ribble (1966) gave an account of nesting biology, larval structure, and the like, for *Florilegus condignus* (Cresson).

Florilegus / Subgenus *Floriraptor* Moure and Michener

Florilegus (*Floriraptor*) Moure and Michener, 1955b: 268. Type species: *Melissodes atropos* Smith, 1879 = *Tetralonia melectoides* Smith, 1879, by original designation.

This subgenus consists of large species, 12 to 14 mm long, with much black pubescence, therefore rather dif-

ferent in appearance from members of the other subgenera.

■ *Floriraptor* occurs from Panama south to Santiago del Estero, Argentina, and Paraná, Brazil. The single species, *Florilegus melectoides* (Smith), was treated by Urban (1970).

Genus *Gaesischia* Michener, LaBerge, and Moure

A substantial group of neotropical Eucerini is here placed in the genus *Gaesischia*. They are superficially *Melissodes*-like bees (Fig. 112-1), 9 to 16 mm long. They were separated into two genera, *Gaesischia* and *Dasyhalonia*, by Moure and Michener (1955b) and Urban (1967c, 1968a) and come out in separate couplets of the key to South American genera of Eucerini, above. However, as shown by LaBerge (1958), they are much alike and merge, the Mexican subgenus *Prodasyhalonia* being intermediate in various features. Common characters that differentiate them from genera such as *Melissodes*, *Melissoptila*, and *Svastra* are (1) the broad, complex apical lobes of S7 of the male, the basolateral part of the lateral lobe usually elaborated, and without the midapical projection found in most *Alloscirtetica*, and (2) the long and usually weakly sigmoid male gonostyli. *Svastrides*, *Santiago*, and *Hamatothrix* have the same features and might also be included in *Gaesischia*.

Species formerly placed in *Gaesischia* (i.e., in the three subgenera *Gaesischia* s. str., *Gaesischipsis*, and *Gaesischiana*) have the head elevated behind the ocelli, which face somewhat forward. Among Eucerini, similar construction is found in some *Alloscirtetica*, especially in the subgenus *Megascirtetica*, and to a lesser degree in the genus *Svastrides*. The three subgenera of *Gaesischia* listed above also have a pair of converging carinae on S6 of the male, as in many Eucerini. Species formerly placed in *Dasyhalonia* (i.e., in the subgenera *Dasyhalonia* and *Pachyhalonia*), on the contrary, have the head horizontal behind the ocelli, which face upward. The males lack converging carinae on S6. The subgenus *Prodasyhalonia* is intermediate in head formation and has its own distinctive type of male S6, with a longitudinal lamella ending in a posteriorly directed spine. In the subgenera *Dasyhalonia* and *Pachyhalonia*, as well as *Prodasyhalonia*, S4 and S5 of the male, sometimes also S3, have long, coarse, curled subapical hairs, not found in other subgenera. Long, straight hairs are present in the same position on S5 of *Gaesischipsis*. The male flagellum of *Gaesischiana* and *Prodasyhalonia* is tapering, the last segment strongly compressed and sometimes broadened. In the extreme case, *G. (Gaesischiana) patellicornis* (Ducke), the antenna is suggestive of that of *Trichocerapis* but less threadlike preapically and is certainly an independent development. LaBerge (1958) gave a useful tabulation of subgeneric characters. Male genitalia were illustrated by Moure and Michener (1955b) and Urban (1967c, 1968a, 1989b).

Key to the Subgenera of *Gaesischia* (Males)

1. S6 with pair of carinae converging posteriorly [except in *Gaesischia patellicornis* (Ducke)]; labral emargination shallow or occupying less than one-third of distal labral margin; middle femur without mass or tuft of dense hair; flagellum little thicker than diameter of ocellus 2

- S6 without such carinae, but with elevated basal area or median lamella; labral emargination deep and occupying over one-third of distal labral margin; middle femur nearly bare beneath except sometimes for mass or tuft of short, dense hairs; flagellum much thicker than diameter of ocellus 4
- 2(1). Maxillary palpus four-segmented; S5 with subapical row of long, bristle-like hairs (South America) *G. (Gaesischipsis)*
- Maxillary palpus five- or six-segmented; S5 without long bristle-like hairs 3
- 3(2). Posterior leg modified, femur enlarged with area of short, dense hairs near posterior margin of bare under-surface, basitarsus with row of long hairs on anterodistal margin; flagellum tapering, last segment compressed and sometimes expanded (neotropical, Arizona) *G. (Gaesischiana)*
- Posterior leg unmodified; flagellum unmodified (South America) *G. (Gaesischia* s. str.)
- 4(1). S6 with longitudinal median lamella, ending posteriorly in a tooth; penultimate flagellar segment more than twice as long as broad (Mexico) *G. (Prodasyhalonia)*
- S6 with elevated basal area sometimes ending in a tooth, but without lamella; penultimate flagellar segment less than twice as long as broad 5
- 5(4). Antennal flagellum greatly thickened, thickest from sixth to eighth segments, whence it tapers both basally and apically; lateral carinae of pygidial plate dentate subapically; underside of middle femur with small dense hair tuft (South America) *G. (Dasyhalonia)*
- Antennal flagellum of approximately uniform thickness or second and third segments thickest; lateral carinae of pygidial plate not dentate; underside of middle femur with large oblique band of dense hairs (South America) *G. (Pachyhalonia)*

Key to the Subgenera of *Gaesischia* (Females)

1. Anterior coxa with apical spine reaching to middle of trochanter or beyond (Fig. 112-13c) 2
- Anterior coxa without apical spine or with short, triangular projection 3
- 2(1). Anterior coxal spine reaching apex of trochanter (Fig. 112-13c); maxillary palpus four-segmented; lateral part of gradulus of T6 absent or nearly so (South America) *G. (Gaesischipsis)*
- Anterior coxal spine reaching about or somewhat beyond middle of trochanter; maxillary palpus five- or six-segmented; lateral part of gradulus of T6 evident as carina (South America, Mexico) *G. (Gaesischia* s. str., *Prodasyhalonia*)
- 3(1). Head elevated behind ocelli such that ocelli face strongly forward (clypeus closely approaching eye margin) (neotropical, Arizona) *G. (Gaesischiana)*
- Head not elevated behind ocelli, which face upward 4
- 4(3). Clypeus separated from eye margin by about one-third of minimum flagellar diameter; margins of basitibial plate entirely hidden except posteriorly (South America) *G. (Pachyhalonia)*
- Clypeus very closely approaching eye margin; margins of basitibial plate evident although covered with hairs except posteriorly (South America) *G. (Dasyhalonia)*

Genus *Gaesochira* Moure and Michener

Gaesochira Moure and Michener, 1955b: 283. Type species: *Gaesochira complanata* Moure and Michener, 1955 = *Eucera obscurior* Dalla Torre, 1896, by original designation.

This genus has a broad, flat scutellum suggestive of that of *Florilegus* (*Florinaptor*). The female differs from that of *Florilegus* in the hidden basitibial plates and the lack of gradular teeth on T6. The tibial spurs, curved apically, are very large, almost reaching the apices of the basitarsi, and the clypeus is very flat, longitudinally strigose; these two features are unique among the Eucerini. The body length is 10 to 12 mm. Male genitalia and hidden sterna were illustrated by Michener and Moure (1956) and Urban (1974b).

■ *Gaesochira* is known from Colombia and from Amazonas, Pará, and Rondônia, Brazil. The single species is *G. obscurior* (Dalla Torre). In view of the Code, 3rd ed., art. 59(b), Dalla Torre's replacement name is to be used rather than *obscura* Smith; this disposition is contrary to the decision of Urban (1974b).

Genus *Hamatothrix* Urban

Hamatothrix Urban, 1989c: 121. Type species: *Hamatothrix silvai* Urban, 1989, by original designation.

This genus is based on a rather small species (8-9 mm long) from Argentina. As in some species of both *Alloscirtetica* and *Gaesischia*, S6 of the male lacks the usual convergent carinae. The well-developed pygidial plate of the male, as well as the lack of a median apical process on S7 of the male, show that *Hamatothrix* is not *Alloscirtetica* but is close to *Gaesischia*; on the basis of the male alone I would have included it in that genus, although its combination of characters differs from that of any *Gaesischia* subgenus. Thus the lack of carinae and presence of a basal median elevated area on S6 and the more or less uniform width of the flagellum suggest the subgenus *Pachyhalonia*, but the labral emargination is so small and weak as to be nearly absent, and the middle femur lacks an area of dense hairs. It is the remarkable features of the female that may justify recognition of *Hamatothrix* as a genus (see the key to genera). The clump of strong bristles behind the small tibial corbicula (or apical bare space, as in other Eucerini) suggests the single row of stronger bristles behind the larger corbicula in *Canephorula*. Other characters of *Canephorula*, however, such as the simple curvature of the gradulus of S2 of the female, the long, oblique vein cu-v of the hind wing, and the papillate wings, suggest that *Canephorula* and *Hamatothrix* are not closely related and evolved strong bristles behind the bare areas of the hind tibiae independently. The completely exposed marginal carina of the basitibial plate of the female suggests *Florilegus*, but in most respects, *Hamatothrix* females, like males, resemble *Gaesischia*. In the key to the subgenera of *Gaesischia*, the female would run to *Dasyhalonia* except for the exposed margin of the basitibial plate. Male genitalia and other structures were illustrated by Urban (1989c).

■ *Hamatothrix* occurs in the provinces of Santiago del Estero and La Rioja, Argentina. The only species is *H. silvai* Urban.

Genus *Lophothygater* Moure and Michener

Lophothygater Moure and Michener, 1955b: 313. Type species: *Tetralonia decorata* Smith, 1879, by original designation.

Lophothygater is a member of the *Thygater-Trichocrepis* group, as shown by the gradulus of S2 of the female and other characters. It differs in having a strong preoccipital carina across the posterior margin of the vertex, and in the long scape of the female, which is almost as long as the interantennal distance. The male differs from other members of the *Thygater* group in the reduced clypeocular distance, etc., so that it runs to 6 at couplet 4 of the key to genera. The male genitalia, hidden sterna, and other structures were illustrated by Urban (1967b). Body length is from 11.0 to 13.5 mm.

■ This genus is known only from the Amazon valley. There is a single species, *Lophothygater decorata* (Smith). Its characters and distribution were reported by Urban (1967b).

Genus *Martinapis* Cockerell

This is a genus of bees that are similar in form to species of *Svastra* or large *Melissodes*; the body length is 12 to 16 mm. *Martinapis* differs in the long first flagellar segment of the male, more than half as long as the second (Fig. 112-8d), and in the elongate median apical lobes of S7 of the male (these lobes are small and short in *Svastra* and in most *Melissodes*). The outer margin of the tegula, anteriorly, is rather broadly expanded, translucent, and impunctate, even more so than in *Simanthredon*. As in *Melissodes* but unlike *Simanthredon* and other Eucerini, this margin is slightly concave, at least in North American species.

■ The distribution of *Martinapis* is disjunct, with one species in Argentina and two in the southwestern United States and northern Mexico. The Argentine species is so different from the others that a different subgeneric name has been proposed for it.

Key to the Subgenera of *Martinapis*

1. Antenna of male rather short, reaching propodeum, entirely yellow, first flagellar segment over 0.7 times as long as second; last flagellar segment of male tapering to blunt point (Fig. 112-8d) (nearctic) *M. (Martinapis s. str.)*
- Antenna of male reaching beyond propodeum, black, flagellum red-yellow beneath, first flagellar segment nearly 0.6 times as long as second; last flagellar segment of male with ordinary rounded apex (South America) *M. (Svastropsis)*

Martinapis / Subgenus *Martinapis* Cockerell s. str.

Melissodes (*Martinella*) Cockerell, 1903c: 450 (not Jousseume, 1887). Type species: *Melissodes luteicornis* Cockerell, 1896, monobasic.

Martinapis Cockerell, 1929f: 19, replacement for *Martinella* Cockerell, 1903. Type species: *Melissodes luteicornis* Cockerell, 1896, autobasic.

The male genitalia and hidden sterna were illustrated by LaBerge (1957) and Zavortink and LaBerge (1976).

■ *Martinapis* s. str. occurs in deserts from western Texas to California, USA, and south to Puebla and Morelos,

Mexico. The two species were revised by Zavortink and LaBerge (1976).

***Martinapis* / Subgenus *Svastropsis* Moure and Michener**

Martinapis (*Svastropsis*) Moure and Michener, 1955b: 291.

Type species: *Tetralonia bipunctata* Friese, 1908, by original designation.

The male genitalia and hidden sterna were illustrated by Moure and Michener (1955b).

■ This subgenus occurs in Mendoza, Argentina. The only known species is *Martinapis bipunctata* (Friese).

Genus *Melissodes* Latreille

This is the major North American genus of Eucerini, although there are also a few South American species. Males differ from those of *Svastra* in the strong lateral arm of the gradulus of T7, ending in a tooth at the side of the pygidial plate. Both sexes differ from those of nearly all *Svastra* in lacking the spatuloplumose hairs. Both sexes differ from other Eucerini except *Martinapis* in tegular shape, although the character is subtle, and removal of hairs is often necessary in order to see it. Although the anterior part of the lateral tegular margin is usually gently concave, in some species it is straight or even feebly convex. It is not, however, simply a convex continuation of the rest of the tegular margin, as in nearly all other Eucerini. The males are also similar to those of *Florilegus*. The maxillary palpi have four or rarely three segments whereas those of *Florilegus* have five. The characters of the male genitalia and hidden sterna also differ from those of *Florilegus*; in *Melissodes* S7 has small apical lobes and the gonostyli are small and simple (Fig. 112-9a-f). In the female *Melissodes*, the basitibial plate is largely hidden by short hair and T6 lacks gradular teeth. Male genitalia and hidden sterna were illustrated by Michener (1954b), LaBerge (1956a, b, 1961), and Mitchell (1962); see also Figure 112-9a-f.

Key to the Subgenera of *Melissodes* (Males)
(Modified from LaBerge, 1961)

1. Clypeus protuberant in front of eye for one-half to three-fourths of eye width, as seen in lateral view and antenna long, minimum length of first flagellar segment less than one-third maximum length of second segment; T2 to T5 fringed with narrow apical bands of appressed white pubescence, bands much narrower than basal areas (nearctic) *M. (Apomelissodes)*
- Clypeus usually not protruding in front of eye by as much as half of eye width, as seen in side view, or, if protruding by half of eye width or more, then minimum length of first flagellar segment one-third or more of maximum length of second segment; terga often not fringed by apical pubescent bands, bands when present interrupted medially and/or preapical 2
- 2(1). Posterior margin of S4 (and usually S3) broadly convex, or produced into a broad, thin, hyaline, colorless flap (nearctic) *M. (Callimelissodes)*
- Posterior margins of S3 and S4 straight to slightly concave, never produced into flaps 3
- 3(2). Clypeus protuberant in front of eye by at least three-

- fourths of width of eye, as seen in side view; maximum length of first flagellar segment 0.4 or more of maximum length of second segment (nearctic) .. *M. (Heliomelissodes)*
- Clypeus usually protruding one-half or less of width of eye, as seen in side view, or, if protruding more, then maximum length of first flagellar segment less than 0.4 of maximum length of second segment 4
- 4(3). Maximum length of first flagellar segment as great as or almost as great as maximum length of second segment and longer than third segment (antenna female-like); clypeus wholly black (nearctic)..... *M. (Psilomelissodes)*
- Maximum length of first flagellar segment less than maximum length of second segment and distinctly less than that of third; clypeus usually pale, occasionally partly or wholly black 5
- 5(4). Minimum length of first flagellar segment distinctly more than half maximum length of second segment; T2 to T5 with pubescent bands apical, of nearly uniform width across each tergum, and subequal in width to each other (nearctic) *M. (Tachymelissodes)*
- Minimum length of first flagellar segment half of maximum length of second segment or less; T2 to T5 with pale pubescent bands usually not all apical or not subequal in width, often interrupted medially and usually subapical 6
- 6(5). Median apical lobes of S7 without hairs on ventral surfaces, usually small, curled ventrally along an oblique axis to form half or more of an oblique cylinder or scroll (Fig. 112-9c), but often secondarily flattened and expanded, or secondarily reduced in size *M. (Melissodes s. str.)*
- Median apical lobes of S7 thin, hyaline, with short to moderately long hairs on ventral surfaces, not curled ventrally, relatively large 7
- 7(6). Gonostylus often less than half as long as gonocoxite, in lateral view at least twice as broad near base as near apex, narrowing abruptly near middle, not capitate; median lobes of S7 relatively small, with several short hairs ventrally (Fig. 112-9f) (neotropical) *M. (Ecliptica)*
- Gonostylus at least half as long as gonocoxite, in lateral view not twice as broad near base as near apex, often somewhat capitate; median lobes of S7 large, with abundant short to moderately long hairs ventrally (North and Central America) *M. (Eumelissodes)*

Key to the Subgenera of *Melissodes* (Females)
(Modified from LaBerge, 1961)

1. Scopal hairs simple or, if weakly branched, then clypeus in profile protruding in front of eye by at least two-thirds width of eye, as seen in lateral view (pygidial plate not narrow) (nearctic) *M. (Apomelissodes)*
- Scopal hairs branched, usually abundantly so, but if weakly branched, then clypeus in profile not protruding in front of eye by as much as two-thirds width of eye, as seen in lateral view 2
- 2(1). Clypeus protruding anteriorly in front of eye by one-half to two-thirds width of eye, as seen in lateral view; inner orbits of eyes often parallel; inner surface of hind basitarsus with hairs dark brown to black (scopal hairs highly plumose, often yellowish) (nearctic).....*M. (Heliomelissodes)*
- Clypeus protruding in front of eye by less than half width of eye, as seen in lateral view, or, if protruding by as much as half width of eye, then inner orbits distinctly

- converging below *and/or* inner surface of hind basitarsus with hairs bright red to yellow (scopal hairs occasionally only weakly branched) 3
- 3(2). Scopai hairs weak, with few branches, not hiding outer surfaces of hind basitarsus and tibia; metasomal terga very sparsely and weakly punctate, dulled by dense, fine shagreening and weakly banded with sparse pubescence; pygidial plate V-shaped with broadly rounded apex (nearctic) *M. (Psilomelissodes)*
- Scopai hairs strongly branched and hiding outer surfaces of hind basitarsus and tibia; or, *if* weak and with few branches, then terga coarsely punctate at least basally, or moderately shiny to shiny and strongly banded with abundant pubescence, *or* pygidial plate narrowly U-shaped 4
- 4(3). T2 to T4 with distal pale pubescent bands reaching apical margins of terga, of about same width across each tergum and subequal in width to one another, as narrow as or narrower than basal areas of dark pubescence (nearctic) *M. (Tachymelissodes)*
- T2 to T4 with distal pale pubescent bands (at least on T2) not reaching apices of terga, or, *if* reaching apices of terga, then diffuse over entire tergum or much wider than basal area of dark pubescence or of varying width across each tergum or between terga *M. (Callimelissodes, Eclectica, Eumelissodes, Melissodes s. str.)*

Melissodes / Subgenus *Apomelissodes* LaBerge

Melissodes (Apomelissodes) LaBerge, 1956a: 1175. Type species: *Melissodes fimbriata* Cresson, 1878, by original designation.

In *Apomelissodes* the clypeus is protuberant, extending in front of the eye by much more than half the eye width in lateral view, and often by the full eye width. The blade of the galea is over twice to nearly three times as long as the clypeus. The scopal hairs are simple to weakly plumose, with two to four branches on each side. The body length is 9 to 14 mm. Male genitalia and hidden sterna were illustrated by LaBerge (1956a, b).

■ This subgenus occurs primarily in eastern North America from Maine to Florida, USA, but ranges westward as far as Kansas. The four species were revised by LaBerge (1956b).

Melissodes / Subgenus *Callimelissodes* LaBerge

Melissodes (Callimelissodes) LaBerge, 1961: 294. Type species: *Melissodes lupina* Cresson, 1878, by original designation.

This subgenus is similar to *Eumelissodes*, from which it differs in the broad, hyaline apical flap on S4 and usually S3 of the male. On T6 of the female, the lateral arm of the gradulus is lamelliform and often ends in a small tooth, whereas in *Eumelissodes* it is short and carinate. Body length is 7.5 to 16.0 mm. Male genitalia and hidden sterna were illustrated by LaBerge (1961).

■ *Callimelissodes* is found from Alberta, Canada, Washington state, Wisconsin, and Indiana south to Texas and North Carolina, USA, and Baja California, Mexico. The 14 species were revised by LaBerge (1961).

Melissodes / Subgenus *Eclectica* Holmberg

Eclectica Holmberg, 1884: 123. Type species: *Eclectica tintinnans* Holmberg, 1884, monobasic.

Eclectica is the only entirely neotropical subgenus of *Melissodes*. It is similar to *Melissodes* s. str. but differs in the faint violaceous reflections nearly always evident on the metasomal terga, the short male gonostylus, often not over one-third as long as the gonocoxite and twice as broad basally as in the narrowed apical section, and the characters indicated in the key. The body length is 7.5 to 11.0 mm. Male genitalia and hidden sterna were illustrated by LaBerge (1956a) and Urban (1973); see also Figure 112-9d-f.

■ This subgenus occurs from Veracruz, Mexico, and Puerto Rico in the Antilles south to Tarapacá, Chile, Buenos Aires Province, Argentina, and Uruguay. There are about eight species; three found in Mesoamerica and the Antilles were revised by LaBerge (1956a) and five found in South America were revised by Urban (1973).

Melissodes / Subgenus *Eumelissodes* LaBerge

Melissodes (Eumelissodes) LaBerge, 1956a: 1177. Type species: *Melissodes agilis* Cresson, 1878, by original designation.

This is the largest and most abundant subgenus of *Melissodes*. The clypeus is not or little protuberant, usually yellow or white in the male. The labrum of the male is variable in color. The first flagellar segment of the male is less than half, usually less than one-third, as long as the second segment. The scopa of the female is plumose, usually strongly so. The body length is 8 to 16 mm. The male genitalia and hidden sterna were illustrated by LaBerge (1956a, 1961).

■ *Eumelissodes* is found from British Columbia, Canada, to Maine, USA, and south throughout North and Central America to Panama and to Cuba. The 72 species were revised by LaBerge (1961).

Melissodes / Subgenus *Heliomelissodes* LaBerge

Melissodes (Heliomelissodes) LaBerge, 1956a: 1172. Type species: *Melissodes desponsa* Smith, 1854, by original designation.

In this small subgenus the clypeus is protuberant in front of the eye by at least half the width of the eye as seen in lateral view, and the blade of the galea is more than twice as long as the clypeus. The labrum of the male is black. The first flagellar segment of the male is one-third the length of the second segment or slightly longer. Body length is 9 to 17 mm. Male genitalia and hidden sterna were illustrated by LaBerge (1956a, b).

■ *Heliomelissodes* occurs from Nova Scotia to British Columbia, Canada, south to North Carolina, Alabama, Texas, and Arizona, USA. The two species were revised by LaBerge (1956b).

The species of *Heliomelissodes* are oligolectic on flowers of thistles of the genus *Cirsium* (Asteraceae).

Genus *Platysvastra* Moure

Platysvastra Moure, 1967b: 148. Type species: *Platysvastra macraspis* Moure, 1967, by original designation.

Platysvastra can be recognized in the female and probably also in the unknown male by the robust body, 13.5 mm long, with the flat scutellum that projects over the metanotum and propodeum. In this character it suggests, but is more extreme than, *Gaesochira*. The female differs further from *Gaesochira* in its shorter middle tibial spur, only half as long as the basitarsus, and in the strong gradular tooth on T6 (it is lamellate but not toothed in *Gaesochira*). The male will be needed to learn whether *Platysvastra* is actually closely related to *Gaesochira* or convergent in scutellar form. Moure (1967b) illustrated various characters, including the thoracic profile.

■ This genus is known from Guyana. There is one species, *Platysvastra macraspis* Moure.

Genus *Santiago* Urban

Santiago Urban, 1989c: 117. Type species: *Santiago mourei* Urban, 1989, by original designation.

Santiago is probably close to *Gaesischia*. It differs from that genus in having a strongly protuberant clypeus and long proboscis, as indicated in the key to genera. The somewhat tapering male flagellum resembles that of many *Gaesischia*, as does the large mesal apical lobe of S7 of the male; it bears an apical straplike process, expanded apically. *Santiago* resembles *Svastrides* in its large size (body length 10.0–14.5 mm) and most of the generic characters indicated, but it lacks the fuscous or black hairs found in all known *Svastrides*. In the female the basitibial plate is completely hidden by short, dense, appressed hair; the plate is largely but incompletely hidden in *Svastrides*. The male gonostylus lacks the strongly plumose hairs found in *Svastrides*. The male genitalia and other structures of *Santiago* were illustrated by Urban (1989c). ■ *Santiago* was described from Minas Gerais, Brazil, on the basis of *S. mourei* Urban. A second species, from Peru, was described by Urban (2003).

Genus *Simanthedon* Zavortink

Simanthedon Zavortink, 1975: 232. Type species: *Simanthedon linsleyi* Zavortink, 1975, by original designation.

This genus contains a species 12 to 15 mm long that is similar in appearance and many other features to *Martinapis* s. str. For example, the male antenna tapers to a rounded point, the scape of the male is yellow, and the outer margin of the tegula is broadly impunctate and translucent. It differs from *Martinapis* s. str., however, in the longer male antennae, convex outer tegular margin, the narrow V-shaped pygidial plate of the female, lack of a gradular tooth on T6 of the male, the strongly sclerotized lateral apical lobe of S7 of the male, and the tapering male gonostylus. Male genitalia and other structures were illustrated by Zavortink (1975).

■ *Simanthedon* occurs in New Mexico and Arizona, USA, south to Durango, Mexico. The only species is *S. linsleyi* Zavortink.

Genus *Svastra* Holmberg

This genus contains species that are usually larger (length 8.5–20.0 mm) than most *Melissodes*. Spatuloplumose hairs (Fig. 112-10b) are usually present among other hairs of the basal band (sometimes also in the apical band) of T2 and sometimes T3 and T4. The tegula is of the usual shape, the outer margin convex throughout, not as configured in *Melissodes*. The lateral arm of the gradulus of T6 of the female is lamellate, ending in a weak tooth. T7 of the male lacks gradular teeth. The male gonostylus is long compared to that of most *Melissodes*.

Most species of this genus are North and Central American, but a small group (*Svastra* s. str.) is found on the other side of the tropics, in temperate South America.

Key to the Subgenera of *Svastra*

1. Scopal hairs simple; first flagellar segment of male as long as second, last segment tapering, attenuate (nearctic) *S. (Anthedonia)*
- Scopal hairs plumose; first flagellar segment of male much shorter than second, last segment cylindrical with rounded apex 2
- 2(1). Middle tibial spur hooked near apex (Fig. 112-15b); front tibial spur of male as long as basitarsus or slightly longer; posterior margin of male S5 with shallow lateral emargination bordered by long, posteriorly directed, hooked hairs overlying shallow, bare depression of S6 (Fig. 112-10c) (nearctic) *S. (Idiomelissodes)*
- Middle tibial spur not hooked; front tibial spur of male shorter than basitarsus; S5 of male without lateral emarginations, without hooked hairs 3
- 3(2). Hairs of basal band of T2 and elsewhere plumose, spatuloplumose hairs absent; antenna of male scarcely reaching scutellum, undersurface of scape bright yellow *Brachymelissodes*
- Spatuloplumose hairs present in basal band of T2 and elsewhere; antenna of male reaching beyond scutellum, scape without yellow 4
- 4(3). Maxillary palpus five-segmented; scutoscuteellar suture without, and basal band of T3 with, spatuloplumose hairs like those of T2; S6 of male with pair of converging carinae (South America) *S. (Svastra s. str.)*
- Maxillary palpus usually four-segmented; scutoscuteellar suture with, and T3 without, spatuloplumose hairs like those of T2; S6 of male without pair of converging carinae, sometimes with ridges instead (North and Middle America) *S. (Epimelissodes)*

Svastra / Subgenus *Anthedonia* Michener

Anthedon Robertson, 1900: 53 (not Agassiz, 1847). Type species: *Melissodes compta* Cresson, 1878, monobasic.

Anthedonia Michener, 1942a: 282, replacement for *Anthedon* Robertson, 1900. Type species: *Melissodes compta* Cresson, 1878, autobasic.

Abda Sandhouse, 1943: 521, replacement for *Anthedon* Robertson, 1900. Type species: *Melissodes compta* Cresson, 1878, autobasic.

Anthedonia consists of large (13–18 mm long), robust species similar to other *Svastra*, although usually given separate generic status. The female differs from other *Svastra* in having the scopal hairs simple. Males differ

arolia. Other characters are the deeply notched apex of the labrum and the rather long vein cu-v of the hind wing, two-thirds as long as the second abscissa of M + Cu. The male differs from that of *Pachysvastra* in the lack of lateral (gradular) teeth on T7, the long antennae, and the un-notched pygidial plate. The male genitalia and hidden sterna were illustrated by Moure and Michener (1955b) and by Urban (1974a). The female differs from that of *Pachysvastra* in the lack of hooked and undulate hairs on the prementum and the slender base of the first flagellar segment (see key). The female was first described by Urban (2003); I have not seen specimens.

■ The genus is known from the provinces of Sante Fe and Formosa, Argentina, and the state of Mato Grosso, Brazil. The only species is *Svastrina subapicalis* (Brèthes).

Genus *Syntrichalonia* LaBerge

Syntrichalonia LaBerge, 1957: 10. Type species: *Melissodes exquisita* Cresson, 1878, by original designation.

This genus includes large (body length 14–17 mm), robust species well covered with erect ochraceous to fulvous pubescence, the weak metasomal bands being formed by longer and less erect apical hairs of the same color. The male antennae are relatively short, not reaching the posterior end of the thorax, and the first flagellar segment is subequal to the second, characters that distinguish *Syntrichalonia* from most of its relatives. The clypeus is little protuberant, the blade of the galea is no longer than the eye, and on S6 of the male the convergent carinae are simple; these are characters of *Tetraloniella*, to which *Syntrichalonia* may be related. Male genitalia and hidden sterna were illustrated by LaBerge (1957).

■ *Syntrichalonia* occurs from southern Arizona to Texas, USA, south to Oaxaca, Mexico. The two species were differentiated by LaBerge (1994).

Genus *Tetralonia* Spinola

For many years, especially early in this century, the name *Tetralonia* was used for almost all Eucerini with three submarginal cells. More recently it has been restricted, for example, to the forms here placed in *Tetralonia*, *Tetraloniella*, and *Eucera* (*Synhalonia*), or only to the last, and it is now further restricted to a small group of species including *T. malvae* (Rossi) plus the species of the related subgenera *Eucara* and *Thygatina*, both of which have usually been given generic status.

The sparse tibial scopa, consisting of branched hairs, often with most of the branches on one side, is distinctive, as are the other characters indicated in the key to genera. The male antennae are relatively short but may reach the base of the metasoma. The males usually have unusually large claws, particularly on the middle and hind legs. In side view the clypeus protrudes forward usually less than the width of the eye, less in *Tetralonia* s. str. than in the other subgenera. The body length is 10 to 16 mm, the larger species being in the subgenus *Eucara*.

The American genera *Peponapis* and *Xenoglossa* share various features—especially the sparse scopa, which consists of coarsely branched hairs, and the relatively short antennae of males—with *Tetralonia*. If these features are

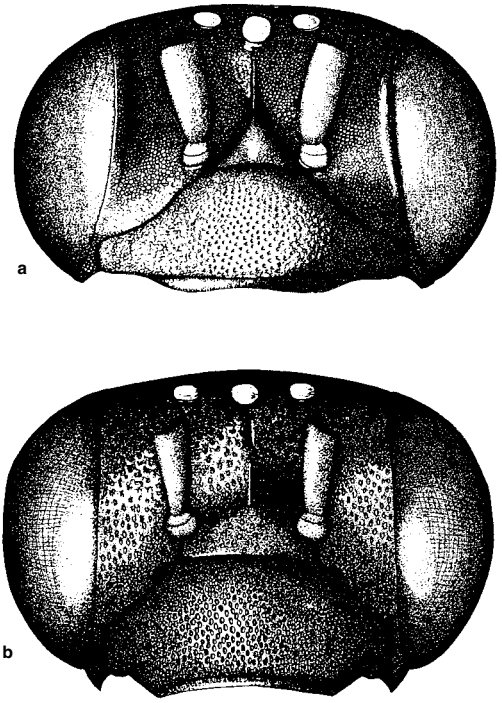


Figure 112-18. Faces of female Eucerini. **a**, *Tetralonia* (*Eucara*) *macrognatha* (Gerstaecker); **b**, *Tetraloniella* (*Tetraloniella*) *junodi* (Friese). From Eardley, 1989.

determined to be homologous rather than convergent, the relations could be indicated by placing those genera as subgenera of *Tetralonia*.

At least some species of this genus are specialist collectors of pollen of Malvaceae, perhaps also of *Ipomoea* (Convolvulaceae), and the distinctive scopa may be an adaptation to the coarse pollen of these plants.

Key to the Subgenera of *Tetralonia*

1. T7 of male with lateral tooth; male gonostylus gently arcuate in side view; maxillary palpus five-segmented, fifth segment minute and indistinct; antenna of male reaching base of metasoma (palearctic)..... *T. (Tetralonia* s. str.)
- T7 of male without lateral tooth; male gonostylus elbowed as seen in lateral view; maxillary palpus three- to four-segmented; antenna of male reaching scutellum..... 2
- 2(1). Lower clypeal margin mesal from mandibular articulation nearly transverse and rounding onto transverse or weakly concave median part of clypeal margin; lower lateral part of clypeus, as seen from beneath, curved back on either side of labrum in such a way that margins are at angle of about 45° to long axis of body (Africa).... *T. (Eucara)*
- Lower clypeal margin mesal from mandibular articulation diagonal, separated by distinct angle from transverse median part of clypeal margin; lower lateral part of clypeus, as seen from beneath, curved back on either side of labrum in such a way that margin at each side is nearly parallel to long axis of body (Africa, oriental) *T. (Thygatina)*

Key to the Subgenera of *Tetraloniella*

1. Gonostylus of male about three times as long as basal width, as seen in side view; basitibial plate of female almost bare, margin fully exposed and not at all raised but curving down to level of rest of tibia; claws of female with inner tooth minute, its axis parallel to that of distal part of claw (palearctic Asia) *T. (Glazunovia)*
- Gonostylus of male five or more times as long as basal width; basitibial plate of female with small, more or less appressed hairs that usually hide part of margin, which is often minutely raised; claws of female with inner tooth larger, diverging from axis of distal part of claw 2
- 2(1). Clypeus of female broadly flattened, covered with short, erect, robust hairs with hooked or wavy apices (Fig. 112-14c) (oculoclypeal distance of male 0.5 to 1.0 times minimum width of first flagellar segment) (Mexico, Texas) *T. (Pectinapis)*
- Clypeus of female convex, with ordinary vestiture 3
- 3(2). Maxillary stipes of female with longitudinal band of coarse bristles having hooked or wavy apices; oculoclypeal distance greater than minimum width of first flagellar segment (Fig. 112-6a, f) (Mexico) *T. (Loxoptilus)*
- Maxillary stipes without such bristles; oculoclypeal distance variable but often minute, less than one-fourth of minimum width of first flagellar segment (holarctic and Africa) *T. (Tetraloniella s. str.)*

Tetraloniella / Subgenus *Glazunovia* Baker

Glazunovia Baker, 1998: 846. Type species: *Tetralonia nigriceps* Morawitz, 1895, by original designation.

Glazunovia consists of a black species with abundant white hair forming basal white bands on T2 to T4 and apical white bands on T3 and T4 of the female, T2 to T6 of the male. In both sexes, the face lacks yellow or white areas. The body length is 9 to 12 mm. The following are some characters other than those indicated above and in the key to subgenera: the paraocular carina is broken by punctuation before reaching the lateroclypeal carina; the maxillary palpus is six-segmented, about as long as the basal width of the galeal blade, the last segment minute; the marginal cell is unusually short and broad; the scopa is plumose, the keirotrichiate area absent (in this respect, *Glazunovia* is unlike other *Tetraloniella*, which have such an area on the distal half of the tibia); T6 and T7 of the male each have a rather small, right-triangular, lateral tooth; and S6 of the male lacks a lateral tooth but has two rather short carinae converging posteriorly, as is usual in *Tetraloniella*.

■ This subgenus occurs in Central Asia. The only known species is *Tetraloniella nigriceps* (Morawitz).

Popov (1962a) recognized the distinctiveness of the species now placed in *Glazunovia* and illustrated the male genitalia, hidden sterna, wing, and faces of both sexes. He placed it in the genus *Melissina*, which he had not seen, and which is a synonym of *Tetraloniella* s. str., as shown by its slender, elbowed male gonostyli, the presence of a keirotrichiate area on the female hind tibia, and other characters indicated in the key to subgenera.

Tetraloniella / Subgenus *Loxoptilus* LaBerge

Loxoptilus LaBerge, 1957: 28. Type species: *Loxoptilus longifellator* LaBerge, 1957, by original designation. [New status.]

This is a probable derivative of *Tetraloniella* s. str. The strongly protuberant clypeus, in males produced by a distance nearly equal to the eye width as seen in lateral view, the long blade of the galea, much exceeding the eye length, and the great oculoclypeal distance, greater than the minimum width of the first flagellar segment (Fig. 112-6a, f), are not typical of *Tetraloniella*, although each of these characters can be found in one or another species of *Tetraloniella* s. str. The strong paraocular carinae, joining the lateroclypeal carinae, and the simple converging carinae on S6 of the male, are features of *Tetraloniella*. The only unique feature of *Loxoptilus* is the strong, hooked or wavy bristles on the stipes of the female. These bristles and the long proboscis suggest a specialist on some deep-flowered plant, as yet unknown. The body length is 9 to 15 mm. The male genitalia and hidden sterna were illustrated by LaBerge (1957).

■ *Loxoptilus* is found from Sonora to Morelos, Puebla, and Yucatan, Mexico. There are two species, differentiated by LaBerge (1957).

Tetraloniella / Subgenus *Pectinapis* LaBerge

Pectinapis LaBerge, 1970: 322. Type species: *Pectinapis fasciata* LaBerge, 1970, by original designation. [New status.]

Pectinapis has hitherto been given generic rank. It is readily recognized by the clypeal characters of the female given in the key to subgenera. Females of *Tetraloniella fasciata* (LaBerge) but not other species are further remarkable for the comb of erect bristles across the supraclypeal area below the antennae, and females of that species and of *T. auricauda* (LaBerge) are noteworthy for the expansion of the clypeus upward almost to the antennal bases. In various other groups of bees, specialist collectors of *Salvia* pollen have a flattened clypeus with erect hooked or wavy bristles, as in *Pectinapis*. These features by themselves are not elsewhere regarded as generic characters, and I see no reason why they should be generic characters in the Eucerini. The greater oculoclypeal distance as compared to most *Tetraloniella*, is duplicated in some palearctic species. The body length of *Pectinapis* varies from 10 to 15 mm. Male genitalia and hidden sterna were illustrated by LaBerge (1970).

■ *Pectinapis* occurs from Texas, USA, and Jalisco, Mexico, south to Oaxaca, Mexico. The four species were revised by LaBerge (1989b).

Tetraloniella / Subgenus *Tetraloniella* Ashmead s. str.

Tetraloniella Ashmead, 1899a: 61. Type species: *Macrocera graja* Eversmann, 1852, by original designation.

Xenoglossodes Ashmead, 1899a: 63. Type species: *Melissodes albata* Cresson, 1872, by original designation.

Melissina Cockerell, 1911e: 670. Type species: *Melissina viator* Cockerell, 1911, monobasic.

Tetraloniella s. str. contains all of the species of the genus that have not been placed in other subgenera. The

body length ranges from 7 to 14 mm. Among its species, there exist many combinations of the characters that vary. As in *Eucera* (*Synhalonia*), the male gonostylus varies from elbowed near the base to gently curved. No other character seems to be correlated with this gonostylar character. Variations in other characters discussed under the generic heading all occur within the subgenus *Tetraloniella* s. str. *Tetraloniella dentata* (Klug) is unusually large for the subgenus (body length 11–14 mm), and T7 of the male, unlike that of other species, has a blunt tooth on each side of the pygidial plate. It is further remarkable for the broadly truncate distal part of the female mandible, which is about three-fourths as broad as the mandibular base. Male genitalia and hidden sterna of the subgenus were illustrated by Mitchell (1962, as *Xenoglossodes*) and Tkalců (1979b).

■ This subgenus occurs in North America from South Dakota and Illinois to Texas, west to California, USA, and south to Panama. In the palearctic region it occurs from Spain to India and Central Asia, ranging north as far as northern Germany. In sub-Saharan Africa it occurs from northern Nigeria and Ethiopia south through east Africa to South Africa and Namibia, and also occurs in Madagascar. There are about 35 North American species (mostly Mexican), revised by LaBerge (2001); about 30 sub-Saharan species, revised by Eardley (1989); four species from Madagascar were revised by Pauly (in Pauly, et al., 2001); and an unknown number [because of confusion with *Eucera* (*Synhalonia*)], perhaps 50, of palearctic species.

Melissina, from Pakistan, was characterized by Cockerell (1911e), who noted the robust five-segmented maxillary palpi with the long fourth segment. His count, based on more than one specimen, was probably accurate, but on examining the type (London) I could not be certain of the segmentation beyond the two basal segments. The clypeus of the female, largely white, is protuberant for a distance little over one-third of the eye width as seen in lateral view. The tibial and basitarsal scopa is dense, hiding the surface or nearly so, the hairs simple except plumose along the upper margins of both segments. The margin of the basitibial plate of the female is entirely exposed, unlike that of other *Tetraloniella* s. str.; this is the only character known to me that might justify recognition of *Melissina* as a taxon distinct from the variable *Tetraloniella*. When *Tetraloniella* is well studied, however, *Melissina* may well be the appropriate name for one of its segregates.

Genus *Thygater* Holmberg

This is one of the more distinctive genera of Eucerini, as indicated in the key to genera. Useful characters not mentioned there are the very long male antennae, the black male clypeus often contrasted with a white or yellowish labrum, the strongly protuberant clypeus, and the long first flagellar segment of the female, longer than the scape. Genitalia and hidden sterna of males were illustrated by Michener (1954b) and, for both subgenera, by Moure and Michener (1955b) and Urban (1961, 1962, 1967a). The body length is 10 to 16 mm.

The genus was revised by Urban (1967a).

Key to the Subgenera of *Thygater* (Males) (Modified from Moure and Michener, 1955b)

1. First flagellar segment one-sixth as long as second or less; flagellum reaching far beyond stigma, greatest breadth nearly equal to basal width of mandible; malar space one-third as long as wide or longer (neotropical) *T. (Thygater s. str.)*
- First flagellar segment one-fourth to one-third as long as second; flagellum reaching stigma, greatest breadth about two-thirds basal width of mandible; malar space less than one-fourth as long as wide (South America) *T. (Nectarodiaeta)*

Key to the Subgenera of *Thygater* (Females) (Modified from Moure and Michener, 1955b)

1. Eyes strongly diverging below; antenna less than twice as long as eye; middle flagellar segments usually less than twice as long as broad (neotropical) *T. (Thygater s. str.)*
- Eyes not or scarcely diverging below; antenna nearly twice as long as eye or longer; middle flagellar segments almost twice as long as broad or longer (South America) *T. (Nectarodiaeta)*

Thygater / Subgenus *Nectarodiaeta* Holmberg

Nectarodiaeta Holmberg, 1887b: 225, nomen nudum.

Nectarodiaeta Holmberg, 1903: 420. Type species: *Nectarodiaeta oliveirae* Holmberg, 1903, monobasic.

In this subgenus the clypeus is less protuberant than in *Thygater* s. str., the inner orbits of the female are subparallel, and the male flagellum is somewhat shorter and less flattened than in *Thygater* s. str. Thus it is less extreme in its differences from typical Eucerini than is *Thygater* s. str. ■ *Nectarodiaeta* occurs in Buenos Aires Province, Argentina, and the state of Paraná, Brazil. There are two species, revised by Urban (1961).

Urban (1962, 1967a) placed under the subgeneric name *Nectarodiaeta* all those species of *Thygater* having four rather than three segments in the maxillary palpi. No other characters are perfectly correlated with the palpal segmentation. This characterization seems arbitrary, since the fourth palpal segment is sometimes minute, as was noted by Urban, and since other characters, for example the lobes of S7 of the male, suggest that some species with four-segmented maxillary palpi are close relatives of species with three-segmented maxillary palpi. On the whole, I think that the characterization of this subgenus by Moure and Michener (1955b) results in natural groups probably worth recognizing. If characterized as by Urban, *Nectarodiaeta* should be regarded as a synonym of *Thygater*.

Thygater / Subgenus *Thygater* Holmberg s. str.

Thygater Holmberg, 1884: 133. Type species: *Tetralonia terminata* Smith, 1854 = *Macrocera analis* Lepeletier, 1841, monobasic.

Macroglossa Radoszkowski, 1884a: 17 (not Ochsenheimer, 1816). Type species: *Macroglossa oribazi* Radoszkowski, 1884 = *Macrocera analis* Lepeletier, 1841, monobasic.
Macroglossapis Cockerell, 1899c: 14, replacement for

Macroglossa Radoszkowski, 1884. Type species:
Macroglossa oribazi Radoszkowski, 1884 = *Macrocera*
 analis Lepeletier, 1841, autobasic.

■ This subgenus occurs from Córdoba Province, Argentina, and the state of Rio Grande do Sul, Brazil, north through the tropics to the states of San Luis Potosí, Chihuahua, and Sonora, Mexico. It contains 23 species, which were revised, partly under the subgeneric name *Nectarodiaeta*, by Urban (1967a).

Genus *Trichocerapis* Cockerell

This genus is used here in a broader sense than in prior studies, in order to demonstrate the close relationship of *Dithygater* and *Trichocerapis* as these taxa were understood by Moure and Michener (1955b). The genus differs in many characters from *Thygater*. Such characters are the yellow clypeus of the male; the short apical spine on the front coxa of the female; and the slender segments 8 to 11 of the male flagellum, each with a fringe of hairs on one side, in contrast to the more robust segments 1 to 7. The genitalia and hidden sterna of both subgenera were illustrated by Moure and Michener (1955b); see also Figure 112-7d-f.

Key to the Subgenera of *Trichocerapis* (Males) (Modified from Moure and Michener, 1955b)

1. Pygidial plate rounded posteriorly, marginal carina uniform; last flagellar segment longer than any of the others, not broadened; submarginal cells two *T. (Dithygater)*
- Pygidial plate narrowed subapically and ending in small upturned process, marginal carina elevated subapically; last flagellar segment shorter than others except first, broad and flat; submarginal cells three *T. (Trichocerapis s. str.)*

Key to the Subgenera of *Trichocerapis* (Females) (Modified from Moure and Michener, 1955b)

1. Clypeus without carinae but strongly declivous in upper lateral areas forming a pair of rounded ridges diverging below; malar area one-fifth as long as wide; submarginal cells two *T. (Dithygater)*
- Clypeus with two distinct carinae diverging below; malar area about one-third as long as wide; submarginal cells three *T. (Trichocerapis s. str.)*

Trichocerapis / Subgenus *Dithygater* Moure and Michener

Dithygater Moure and Michener, 1955b: 309. Type species:
Dithygater seabrai Moure and Michener, 1955, by original designation. [New status.]

This is the only New World eucerine taxon with two submarginal cells. Although it is related to *Thygater* and *Trichocerapis* s. str., it is by no means merely a *Thygater* or *Trichocerapis* having two submarginal cells. It differs from both in the five-segmented (rather than three- or four-segmented) maxillary palpus and the broad, weak ridges diverging from the upper median part of the clypeus toward the lower lateral angles (such ridges are present but carinate in *Trichocerapis* s. str.). *Dithygater* looks like a small (11.5–15.0 mm long) *Trichocerapis* s. str.

■ This subgenus is known from the states São Paulo to

Minas Gerais, Brazil. There is only one species, *Trichocerapis seabrai* (Moure and Michener) [new combination].

Trichocerapis / Subgenus *Trichocerapis* Cockerell s. str.

Trichocerapis Cockerell, 1904b: 292. Type species: *Tetralonia mirabilis* Smith, 1865, monobasic and by original designation.

The threadlike eighth to tenth flagellar segments of the male and the broad, flat, black eleventh segment are unique and unmistakable. S6 of the male has a strong sub-lateral tubercle and a pair of carinae converging posteriorly (S6 is simple in *Dithygater*). The labrum is as long as wide or, in the male, nearly so; in *Dithygater* it is much wider than long. The body length is 11 to 15 mm.

■ *Trichocerapis* occurs from Pernambuco, Brazil, to Paraguay and northwest to Peru. A key to the five species was published by Urban (1989a).

Genus *Ulugombakia* Baker

Ulugombakia Baker, 2003: 124. Type species: *Ulugombakia platytarsus* Baker, 2003, by original designation.

Because the male is unknown, this genus is not included in the Key to the Genera of Eucerini of the Eastern Hemisphere. See the note following the key.

Ulugombakia, based on a single female specimen, is most similar to *Tetraloniella* s. str. It differs in the 4-segmented maxillary palpus which, however, as in *Tetraloniella*, is longer than the maximum width of the galeal blade, and in the relatively large stigma, longer than the prestigma and (from Baker's photograph) extending well beyond the base of vein r. Such a stigma is unusual in Eucerini although approached in the unrelated American genus *Melissoptila*. The paraocular carinae become lamelliform and convergent anteriorly, unlike the simple and anteriorly reduced carinae of *Tetraloniella*. Baker (2003) enumerated other distinctive features.

■ *Ulugombakia* is known from West Malaysia. The single species is listed above.

Genus *Xenoglossa* Smith

Like *Peponapis*, *Xenoglossa* consists of robust, nearly anthophoriform rather than euceriform species (Pl. 11). The male antennae are shorter than those of *Peponapis*, not surpassing the tegulae. The first flagellar segment of the male is longer than the second (Fig. 112-8c); this condition is rare in *Peponapis*. The mandible of both sexes has a tooth on its inner margin near the base (Fig. 112-13e). The clypeus of the female is frequently maculated with yellow; it is black in *Peponapis*. In the female the inner surface of the hind basitarsus is tan with black spots representing the bases of the widely dispersed large hairs, except for a densely hairy band along the lower margin. This presumably derived condition is as in *Peponapis* and supports the view that *Peponapis* should be regarded as a subgenus of *Xenoglossa*. The possibility exists, however, that these characters are adaptive, related to the extremely coarse pollen of *Cucurbita*, and that the two genera originated from different ancestors. The arrangement used by

LaBerge (1957) suggests that this was his view. Male genitalia and hidden sterna were illustrated by LaBerge (1957) and Mitchell (1962).

Like species of *Peponapis*, those of *Xenoglossa* are oligolectic collectors of pollen of *Cucurbita*. *Xenoglossa* has been divided into two subgenera; they seem more distinct than the subgenera that have been proposed for *Peponapis*.

Key to the Subgenera of *Xenoglossa*

1. Eyes weakly diverging below, antennal socket closer to eye margin than to lateral ocellus; ocelli scarcely larger than antennal sockets *X. (Eoxenoglossa)*
- . Eyes markedly diverging below, antennal socket farther from eye margin than from lateral ocellus; ocelli enlarged, much larger than antennal sockets *X. (Xenoglossa s. str.)*

Xenoglossa / Subgenus *Eoxenoglossa* Hurd and Linsley

Xenoglossa (Eoxenoglossa) Hurd and Linsley, 1970: 34. Type species: *Melissodes strenua* Cresson, 1878, by original designation.

Species of this subgenus look much like *Peponapis*; their body length is 11 to 18 mm.

■ *Eoxenoglossa* occurs from Maryland to Florida west to Wisconsin and California, USA, and south to San Luis Potosí, Durango, and Baja California, Mexico. The two species were revised by Hurd and Linsley (1964, 1967a).

Xenoglossa / Subgenus *Xenoglossa* Smith s. str.

Xenoglossa Smith, 1854: 315. Type species: *Xenoglossa fulva* Smith, 1854, monobasic.

This subgenus includes large Eucerini, 16 to 24 mm long. The enlarged ocelli, large body size, and, for some species, the largely fulvous body (Pl. 11) suggest earlier matinal activity than for either *Eoxenoglossa* or the genus *Peponapis*.

■ *Xenoglossa* s. str. occurs from California to Texas, USA, and south through Mesoamerica to Nicaragua and possibly Panama and Venezuela. The five species were revised by Hurd and Linsley (1964, 1967a).

113. Tribe Anthophorini

This is a tribe of robust, fast-flying, anthophoriform (Pls. 12, 13) or rarely euceriform or apiform, pollen-collecting bees, apparently most closely related to the Centridini. The wings are largely bare, the distal parts beyond the veins being strongly papillate (as in Fig. 85-2a). The stigma is small, usually ending at the base of vein r. The marginal cell is slightly shorter than or about as long as the distance from its apex to the wing tip, and rounded and often appendiculate at the apex (Fig. 113-1). The first submarginal cell is short, much shorter than the combined lengths of the second and third submarginal cells, all measured along the posterior margins. The jugal lobe of the hind wing is less than one-half as long as the vannal lobe, usually about one-third as long.

Some authors divide this tribe to form the separate tribes Habropodini and the Anthophorini s. str., distinguishing them in part by the characters indicated in the first couplet of the key to genera. To me these groups of genera appear very similar and I do not recognize a tribe Habropodini. It seems important that the classification show the relationship of *Habropoda* and its allies to *Anthophora*.

Nests of Anthophorini are burrows in the soil, either in banks or in flat ground, with the exception of *Anthophora* subgenus *Clisodon*, which nests in rotten wood or pithy stems. The best-known species nest in aggregations in vertical clay banks, but probably the majority of species make nonaggregated nests in flat ground. The bees may facilitate excavation by moistening clay with regurgitated water or nectar. The barrel-shaped cells are either isolated or in series in the burrows, and are made of earth or clay in such a way that they can be separated from

the surrounding matrix. Separation is possible because the cell wall is constructed in a larger cavity from clay particles moistened by Dufour's gland secretion and tamped into place with the pygidial plate. In the case of *Clisodon*, similar cells are made from chewed pith or wood particles. The cells are lined with more or less liquid triglyceride-rich material from Dufour's gland, which solidifies into a solid diglyceride-rich membranous "waxlike" lining on contact with salivary secretion in the food mass. This lining waterproofs the cell but is later eaten by the large larva. The provisions are a viscous or quite liquid mixture of pollen and nectar and Dufour's gland and salivary gland products that has a distinctive yeasty smell. This odor has been attributed to the action of yeast, but Batra and Norden (1996) noted it (they say the odor is that of butyric acid) from the moment that the triglyceride lining begins to be converted to solid diglycerides; the odor must therefore be a product of that reaction. After a cell is provisioned and an egg laid on the provisions, the cell is closed with a spirally constructed mud or earthen closure, in the center of which a small hole remains. The bee may insert the glossa through this hole to apply the lining material to the inner surface of the plug, then finally close the central hole with earth. Thus the entire inner surface of the cell—except for a small plug, less than 1 mm in diameter, in the center of the cell closure—is lined with the "waxlike" diglyceride material. Gess and Gess (1996) do not accept this explanation, at least for certain *Amegilla* species. Since there appears to be wax on the inner surface of the central closure, they believe that wax is added with the mud of the closure. Some of the works on anthophorine nesting behavior in earth are Malyshev (1928), Stephen (1961), Torchio and Youssef (1968), Rozen (1969c), Thorp (1969c), Torchio (1971), Brooks (1983), Norden (1984), Torchio and Trostle (1986), Houston (1991b), Batra and Norden (1996), and Alcock (1996b, 1997a,b, 1999). For nesting in rotten wood or pith (*Anthophora* subgenus *Clisodon*), see Medler (1964b).

Amegilla dawsoni (Rayment) in Australia has males of two different sizes, as do some species of *Centris* in the Western Hemisphere. Tomkins, Simmons, and Alcock (2001) relate this phenomenon to the provisioning strategy of females.

Unlike those of most Apinae, the mature larvae of Anthophorini do not spin cocoons and have lost much of the labial structure of cocoon-spinning larvae. Presumably, overwintering is usually as prepupae, but some species of *Anthophora* (*Lophanthophora*) (Brooks, 1988) and *Habropoda* (Stephen, 1961) pass the winter as adults in natal cells.

Key to the Genera of the Anthophorini

1. First recurrent vein joining second submarginal cell near middle; third submarginal cell subquadrate, with front and rear margins of about equal length, and basal and distal margins of about equal length (Fig. 113-1a); male gonostylus usually less than one-third as long as gono-

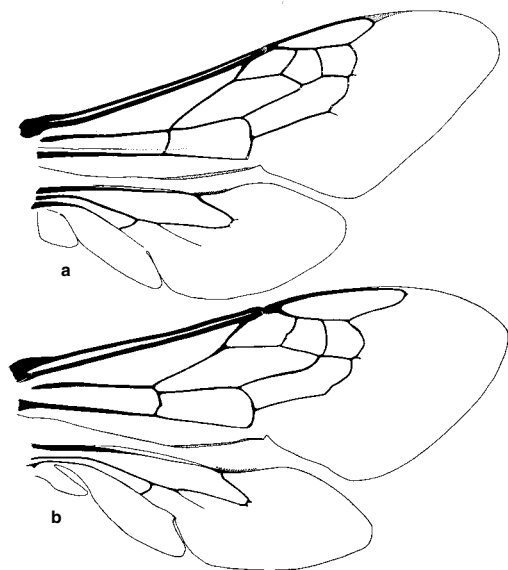


Figure 113-1. Wings of Anthophorini. **a**, *Anthophora occidentalis* Cresson; **b**, *Deltoptila montezumia* (Smith).

- coxite (Fig. 113-2a, d), often not double, sometimes reduced to almost nothing 2
- First recurrent vein terminating at or near apex of second submarginal cell (Fig. 113-1b); third submarginal cell (except in *Habrophorula*) with front margin much shorter than rear margin because of curvature of third submarginal crossvein, such that distal margin of the cell is longer than basal margin; male gonostylus double, dorsal and ventral gonostyli usually both one-third as long as gonocoxite or more 3
- 2(1). Arolia present (worldwide except Australian region) *Anthophora*
- Arolia absent (Eastern Hemisphere) *Amegilla*
- 3(1). Stigma almost absent, represented by minute area broader than long; T2 to T5 or at least T3 with lateral, longitudinal parts of graduli strong, sometimes reaching posterior marginal zones of terga; pygidial plate of male present as a well-defined apical process of T7, margined by carinae across apex and at sides, at least apically (Africa, Madagascar) *Pachymelus*
- Stigma at least as long as broad, usually much longer than broad (Fig. 113-1b); T2 to T5 commonly without lateral longitudinal parts of graduli; pygidial plate of male absent or indicated by smooth bare area margined by carina only across apex 4
- 4(3). Malar space at least twice as long as antennal pedicel; vein cu-v of hind wing nearly transverse, at angle of 50° or more to first abscissa of M+Cu (Mesoamerica) *Deltoptila*
- Malar space linear to about as long as antennal pedicel; vein cu-v of hind wing usually conspicuously oblique, at angle of 45° or less to first abscissa of M+Cu (except nearly transverse in *Habrophorula*) (holarctic and oriental) 5
- 5(4). Mandible with two preapical teeth, thus tridentate; T7 and S6 of male somewhat attenuate apically, apices rounded or pointed (S7 of male weakly sclerotized, without transverse ridge at base of apical process; hind leg of male enlarged, trochanter with broad rounded projection) (oriental) *Elaphropoda*
- Mandible with one preapical tooth, thus bidentate; T7 and S6 of male not attenuate, apex of T6 nearly always bidentate or with emarginate apical truncation 6
- 6(5). Third submarginal cell about as wide on anterior margin as on posterior margin; male with first flagellar segment about as broad as long and shorter than second; S7 of male weakly sclerotized, transverse, disc broader than long, without apical process (oriental) *Habrophorula*
- Third submarginal cell with anterior margin much shorter than posterior margin; male with first flagellar segment much longer than broad and longer than second; S7 of male strongly sclerotized, disc giving rise to large apical process, base of which often bears transverse ridge (holarctic, oriental) *Habropoda*

Genus *Amegilla* Friese

- Podalirius* (*Amegilla*) Friese, 1897a: 18, 24. Type species: *Apis quadrifasciata* Villers, 1789, by designation of Cockerell, 1931e: 277.
- Alfkenella* Börner, 1919: 168. Type species: *Apis quadrifasciata* Villers, 1789, by original designation.

- Asaropoda* Cockerell, 1926b: 216. Type species: *Saropoda bombiformis* Smith, 1854, by original designation.
- Amegilla* (*Aframegilla*) Popov, 1950b: 260. Type species: *Anthophora nubica* Lepeletier, 1841, by original designation.
- Amegilla* (*Zonamegilla*) Popov, 1950b: 260. Type species: *Apis zonata* Linnaeus, 1758, by original designation.
- Amegilla* (*Zebramegilla*) Brooks, 1988: 502. Type species: *Anthophora albigena* Lepeletier, 1841, by original designation.
- Amegilla* (*Dizonamegilla*) Brooks, 1988: 505. Type species: *Megilla sesquicincta* Erichson and Klug, 1842, by original designation.
- Amegilla* (*Megamegilla*) Brooks, 1988: 505. Type species: *Apis acraensis* Fabricius, 1793, by original designation.
- Amegilla* (*Ackmonopsis*) Brooks, 1988: 508. Type species: *Anthophora mimadvena* Cockerell, 1916, by original designation.
- Amegilla* (*Micramegilla*) Brooks, 1988: 508. Type species: *Anthophora niveata* Friese, 1905, by original designation.
- Amegilla* (*Notomegilla*) Brooks, 1988: 511. Type species: *Anthophora aeruginosa* Smith, 1854, by original designation.
- Amegilla* (*Glossamegilla*) Brooks, 1988: 512. Type species: *Anthophora mesopyrrha* Cockerell, 1930, by original designation.

These bees have the form of *Anthophora*. Some common groups have metallic blue or green pubescence, especially on the metasoma (Pl. 13). Such coloration does not occur in *Anthophora*, and species of *Amegilla* lacking such coloration are most easily separated from *Anthophora* by the lack of arolia. The face of both sexes usually shows yellow or white markings. The tibial scopa includes a band of plumose hairs near the upper margin of the tibia, as in most *Anthophora*. The hind leg of the male is ordinarily unmodified, without a basitarsal tooth, and the middle tarsus lacks brushes. The pygidial plate of the male is absent. The mentum has a submedian tooth on its anterior surface except in *Amegilla nonconforma* Brooks. Illustrations of male genitalia and other structures for all species groups were presented by Brooks (1988); Eardley (1994b) illustrated the species of southern Africa; additional such illustrations were published by Liefertinck (1944, under the genus *Anthophora*; 1956a, 1975), Popov (1950b), Iuga (1958), Michener (1965b), and Wu (1983d); see Figure 113-2d-f. The body length is 8 to 24 mm.

I have arbitrarily decided not to recognize the numerous subgenera of *Amegilla* defined by Brooks (1988). They are largely indistinguishable in females, and in males differ from one another considerably less than do most subgenera of *Anthophora*. They probably do constitute natural groups and are available for use by anyone wishing to use them; the names and type species are listed in the synonymy above. The great number of species of *Amegilla* supports recognition of groups or subgenera.

■ This genus is found throughout Africa (including Madagascar) and the Mediterranean basin and from the Canary Islands east across southern Europe to Japan, Korea and northeast China, south to Yemen, Sri Lanka, Indonesia, New Guinea, and the whole of Australia (including Tasmania), and east to the Solomon Islands.

and Cockerell (1906e) for North America. Brooks (1988) listed the species for the world, placing them into subgenera and in many cases species groups. Marikovskaya (1976, 1979, 1980) proposed a very different classification, using the name *Clisodon* for a major segment of what is here called the genus *Anthophora*.

Key to the Subgenera of *Anthophora* (Males)
(Modified from Brooks, 1988)

1. Middle distitarsus with brush of dense hairs, middle basitarsus often with brush; apex of S7 with lateral margin forming two low lobes, one sometimes partly above the other 2
- Middle tarsus simple, without any brushes; apex of S7 laterally simple or with two lobes 5
- 2(1). Basitibial plate absent; pygidial plate absent 3
- Basitibial plate present; pygidial plate present 4
- 3(2). Flabellum apically entire; S7 apically narrowed, elongate, apodemes at least 1.3 times as long as length of disc;
 - apex of gonocoxite deeply bilobed (palearctic) *A. (Anthophora s. str.)*
 - Flabellum apically with fingerlike projections (as in Fig. 113-4a-c); S7 apically broad, short, apodemes no more than 0.4 times as long as length of disc; apex of gonocoxite weakly trilobed (palearctic) *A. (Caranthophora)*
 - 4(2). Distal half of S6 with a pair of apically diverging oblique ridges; apex of gonocoxite simple, flattened, hooked ventrad (holarctic) *A. (Lophanthophora)*
 - Distal half of S6 simple, without ridges; apex of gonocoxite bilobed or triangular, not flattened and hooked ventrad (holarctic, Africa) *A. (Pyganthophora)* (in part)
 - 5(1). Mandible tridentate because of preapical convexity or tooth on lower margin in addition to usual preapical tooth on upper margin; gonostylus concolorous with apex of gonocoxite, perhaps absent; flabellum apically simple (holarctic) *A. (Clisodon)*
 - Mandible bidentate or sometimes simple; gonostylus lightly sclerotized, thus clearly demarcated from gono-

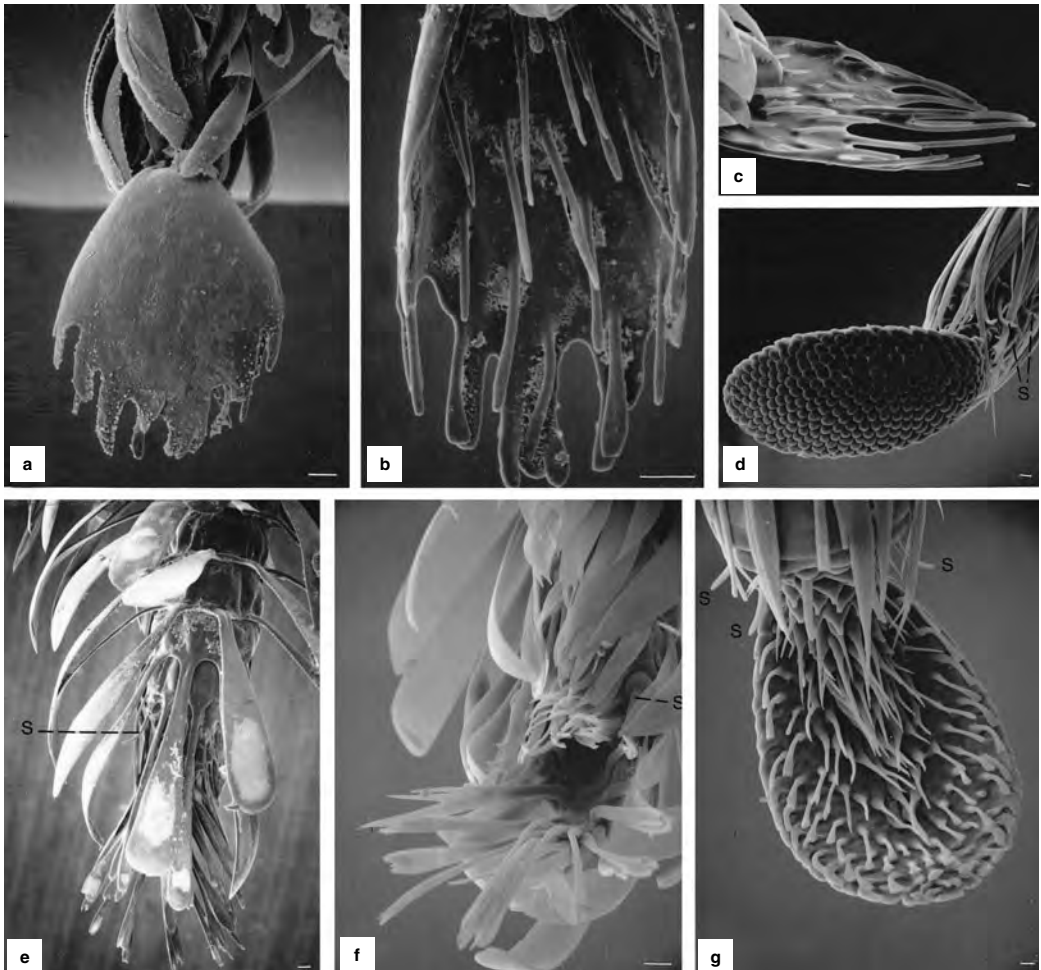


Figure 113-4. Apices of glossae of Anthophorini. **a, b,** *Anthophora (Heliophila) cockerelli* Timberlake, posterior and anterior views; **c,** *A. (Mystacanthophora) walchii* Cresson, anterior view; **d,** *Deltoptila* n. sp., posterolateral view; **e,** *Habropoda miserabilis* (Cresson), an-

terior view; **f,** *H. pallida* (Timberlake), posteroapical view; **g,** *Deltoptila* n. sp., anterior view.

Habropoda is extraordinary for an L-T bee in that it lacks a flabellum. From Michener and Brooks, 1984.

- coxite; flabellum apically with fingerlike lobes (Fig. 113-4a-c) 6
- 6(5). Mentum with submedian tooth on anterior surface; apex of S7 with one lateral lobe (Fig. 113-2c) (hind basitarsus with anterior tooth or strong ridge) 7
- . Mentum without tooth near middle of anterior surface, or, *if* tooth present, then hind basitarsus simple, almost parallel-sided, and without anterior tooth or ridge; apex of S7 with two lateral lobes on each side, sometimes only weakly developed, or, *if* apex simple laterally or with one lobe, then body small (7.5-13.5 mm long) and/or S6 with thick pad of hair 8
- 7(6). Body length at most 13 mm; hind tibial spur arising near apex of an apical tibial spine; apex of gonocoxite heavily sclerotized with a distinct melanized demarcation (seen only in cleared preparations of genital capsule) between apex and base; face with white integumental markings (yellow in *Anthophora vallorum* Cockerell and *californica* Cresson) (North and Central America) *A. (Anthophoroides)*
- . Body length greater than 13 mm; hind tibia simple, without apical spine; apex of gonocoxite not more heavily sclerotized than base, no demarcation between the two; face with yellow integumental markings (holarctic) *A. (Melea)*
- 8(6). Malar space more than one-third as long as wide; flabellum elongate, apically entire or with numerous small apical lobes 9
- . Malar space almost always short and linear, at most one-third as long as wide; flabellum short and wide, apically with three to ten fingerlike projections (Fig. 113-4a) or if entire, then apical two-thirds not narrowed and flabellum lacking numerous short apical lobes (S6 almost always medioapically emarginate) 10
- 9(8). Flabellum apically entire, elongate, with apical two-thirds narrowed; T7 of male with longitudinal median ridge not reaching apex, with two small, weakly developed, submedian projections; penis valve bridge short, basally emarginate (paleartic) *A. (Anthomegilla)*
- . Flabellum apically with numerous small lobed divisions, broom-shaped, lateral margins almost parallel; T7 of male apicomediaally, dorsoventrally flattened with longitudinal median ridge reaching apex; penis valve bridge long, basally pointed (Asia) *A. (Rhinomegilla)*
- 10(8). Body length usually 7.5-13.5 mm and/or S6 with thick pad of hair (often hidden until sternum is relaxed and pulled apically); gradular process of T7 often prolonged into tooth when body size is small; apex of disc of T7 laterally simple, not with two lobes, lateral margins of disc usually parallel or apically converging, rarely narrowed medially (holarctic, Africa) *A. (Heliophila)*
- . Body length usually 9-24 mm; S6 simple, without pad of hair; gradular process of T7 at most obtusely projecting, usually not developed; apex and base of disc of S7 wider than middle, apex laterally angulate or with two small lobes on each side 11
- 11(10). Pygidial plate present, lateral tooth below pygidial plate sometimes also present; gradular process of T7 sometimes present 12
- . Pygidial plate and lateral tooth both absent, apex of T7 with two submedian teeth; gradular process of T7 absent 13
- 12(11). Basitibial plate present, and hind basitarsus simple,

- nearly parallel-sided; pygidial plate with margin carinate and not concave; gradular process of T7 sometimes present (holarctic, Africa) *A. (Pyganthophora)* (in part)
- . Basitibial plate absent, or, *if* present, then hind basitarsus not parallel-sided, with anterior process dilated; pygidial plate with margin rounded, almost never carinate, but *if* carinate, then lateral margin concave; gradular process of T7 absent (holarctic, Africa) *A. (Paramegilla)* (in part)
- 13(11). S7 with disc broad, its minimum width over half of distance between tips of apodemes; S8 with broad, deep, apical emargination (weak in *A. calcarata* Lepeletier), lateral margin on apical half concave 14
- . S7 with disc narrow, its minimum width less than half of distance between tips of apodemes; S8 with narrow shallow apical emargination, lateral margin on apical half angulate or concave 15
- 14(13). S8 with apicolateral margin angulate, spiculum projecting somewhat basally; S7 with apex shallowly emarginate, with two weakly developed apicolateral lobes, basal apodeme with lateral angle or process; apex of gonocoxite somewhat bilobed in profile, lower lobe weakly developed, not carinate, sometimes with a tooth on lower inner margin of gonocoxite; face almost always with yellow markings (paleartic) *A. (Petalosternon)*
- . S8 with apicolateral margin prolonged and rounded, spiculum not easily visible from ventral aspect but projecting dorsally at a 90° angle; S7 with apex distinctly emarginate, with two strong apicolateral lobes, basal apodeme without lateral process or angle; apex of gonocoxite complex in profile with dorsoventral and lateral carinae; face with white markings (Western Hemisphere, paleartic) *A. (Mystacanthophora)*
- 15(13). T7 with two short submedian teeth, their bases separated by convex lamellate or angular apical margin, and median longitudinal carina often present; apical zone of T7, as seen from ventral view, narrow where bent ventroanteriorly; hind basitarsus anteriorly with tooth, blunt process, or longitudinal ridge; apodemes of S7 almost always short, 0.34-0.78 as long as length of disc, lateral process absent; apex of gonocoxite in profile simple to weakly bilobed (holarctic, Africa) *A. (Paramegilla)* (in part)
- . T7 with two long submedian teeth, their bases separated by rounded apical margin; apical zone of T7, as seen from ventral view, wide where bent ventroanteriorly; hind basitarsus almost parallel-sided, anterior margin simple; apodemes of S7 long, 1.00-1.75 times as long as length of disc, lateral process present; apex of gonocoxite in profile deeply bilobed (paleartic) *A. (Dasymegilla)*

Key to the Subgenera of *Anthophora* (Females) (Modified from Brooks, 1988)

1. Apex of mandible with lower subapical tooth and thus tridentate; basitibial plate about twice as long as broad, tapering to pointed apex (flabellum entire) (holarctic) *A. (Clisodon)*
- . Apex of mandible without lower subapical tooth, bidentate; basitibial plate less slender, apex rounded 2
- 2(1). Flabellum narrowly elongate, apically entire or with numerous short, small lobes; first flagellar segment equal in length to next 3.2-4.0 segments taken together 3
- . Flabellum wide, with few long fingerlike apical lobes

- (Fig. 113-4a-c); first flagellar segment equal in length to next 2.2-5.5 segments taken together 5
- 3(2). Malar area almost always short, rarely well developed, at most one-third as long as wide; flabellum more or less parallel-sided or lanceolate, not attenuate in apical two-thirds, apex entire; upper margin of hind tibia with scopal hairs plumose (palearctic) *A. (Anthophora s. str.)*
- Malar area more than one-third as long as wide; flabellum elongate with apical two-thirds narrowed or flabellum with numerous small apical lobes; upper margin of hind tibia with scopal hairs simple 4
- 4(3). Flabellum apically entire, elongate, with apical two-thirds narrowed (palearctic) *A. (Anthomegilla)*
- Flabellum apically with numerous small lobes (Asia) *A. (Rhinomegilla)*
- 5(2). Mentum with a well-developed submedian tooth on anterior surface; first flagellar segment equal in length to next 2.4-3.3 segments taken together 6
- Mentum without tooth on anterior surface [rarely with tooth in old world species having upper zone of scopa plumose, e.g., *Anthophora (Dasymegilla) excisa* Morawitz]; first flagellar segment equal in length to next 2.2-5.5 segments taken together 7
- 6(5). Hind basitarsus with upper distal process acute; S6 with subapical tooth; upper margin of hind tibia with simple hair; body 13 mm long or longer (holarctic) *A. (Melea)*
- Hind basitarsus with upper distal process blunt; S6 without subapical tooth; upper margin of hind tibia with plumose hair; body no longer than 13 mm (North and Central America) *A. (Anthophoroides)*
- 7(5). Upper margin of hind tibia with simple hair; length 6-15 mm 8
- Upper margin of hind tibia with plumose hair; length 10-24 mm 9
- 8(7). Face black; body length 12-14 mm (palearctic) *A. (Paramegilla)* (in part)
- Face almost always with yellow to white integumental markings and body length 6-15 mm, but *if* face black, then length 11-13 mm and southern African in distribution (holarctic, Africa) *A. (Heliophila)*
- 9(7). Clypeus with pale integumental marking in shape of inverted T, and first flagellar segment equal in length to next 2.2-3.0 segments taken together (palearctic) *A. (Caranthophora)* (in part)
- Clypeus almost always black, rarely with pale integumental marking, or, *if* marking present, then not in shape of inverted T, or, *if* in shape of inverted T, then first flagellar segment longer than combined lengths of next three segments 10
- 10(9). Metasoma with apical bands of hair interrupted medially or surface covered evenly with appressed hair (holarctic, Africa) *A. (Paramegilla)* (in part)
- Metasoma with apical bands of hair complete and/or surface covered with semierect to erect hair 11
- 11(10). Clypeus normal, without apically hooked or wavy hairs or basal pecten; first flagellar segment equal in length to next 2.2-5.5 segments taken together *A. (Caranthophora* [in part], *Dasymegilla*, *Lophanthophora*, *Mystacanthophora* [in part], *Paramegilla* [in part], *Petalosternon*, *Pyganthophora*)
- Clypeus flattened, with hairs apically hooked or wavy,

sometimes with a basal pecten; first flagellar segment equal in length to next 2.2-3.4 segments taken together (Western Hemisphere, palearctic) *A. (Mystacanthophora)* (in part)

Anthophora / Subgenus *Anthomegilla* Marikovskaya

Anthomegilla Marikovskaya, 1976: 688. Type species: *Anthophora arctica* Morawitz, 1883, by original designation.

Anthomegilla has a well-developed malar space, two or three times as wide as long. The flabellum is widest near the base, distally attenuate, four or more times as long as wide, rounded or subtruncate at the apex, and not divided into distal processes; it is thus quite different from that of the other subgenera that lack an apically divided flabellum, *Anthophora s. str.* and *Clisodon*. As in *Melea*, *Rhinomegilla*, and *Heliophila*, the scopa of the female hind tibia consists entirely of simple hairs. The male lacks basitibial and pygidial plates. The body length is 9 to 14 mm. Wu (1986) and Brooks (1988) illustrated male genitalia and other structures.

■ This subgenus occurs in the Siberian subarctic south to the mountains of Central Asia and China to Tibet. There are eight species (Brooks, 1988). Wu (1986) gave a key to species.

Anthophora / Subgenus *Anthophora* Latreille s. str.

Podalirius Latreille, 1802a: 430. Type species: *Apis pilipes* Fabricius, 1775 = *Apis plumipes* Pallas, 1772. *Podalirius* was suppressed by Commission Opinion 151 (1944) (Direction 4).

Anthophora Latreille, 1803: 167, replacement for *Podalirius* Latreille, 1802. Type species: *Apis pilipes* Fabricius, 1775 = *Apis plumipes* Pallas, 1772, designated by Commission Opinion 151 (1944). [See Michener, 1997b.]

Lasius Panzer, 1804b: tab. 16. Type species: *Lasius salviae* Panzer, 1804 = *Anthophora crinipes* Smith, 1854, monobasic. Suppressed by Commission Opinion 151 (1944) (Direction 4). [According to Opinion 151 (1944), the correct date for *Lasius* Panzer is [1801-1802]; see Literature Cited.]

Megilla Fabricius, 1804: 328. Type species: *Apis pilipes* Fabricius, 1775 = *Apis plumipes* Pallas, 1772, designated by Commission Opinion 1383 (1986). [For previous type designations, see Sandhouse (1943) and Michener (1997b).]

Anthophora s. str. differs from other subgenera in having an elongate, simple flabellum, without the deep sinuses forming apical lobes found in most other subgenera. The basitibial plate of the male is weakly delimited or absent, and the pygidial plate is absent in the male. The apex of the male gonocoxite is strongly bifid. The body length is 10 to 19 mm.

■ This subgenus occurs from Spain and Britain to Korea and eastern China. Brooks (1988) listed 11 species.

Most of the studies on nesting biology of this subgenus concerned *Anthophora acervorum* of authors, which is now called *A. plumipes* Pallas because *Apis acervorum* Linnaeus is a species of *Bombus* (see Brooks, 1988).

Habropoda Smith, 1854: 320, replacement for *Habrophora* Smith, 1854. Type species: *Habrophora ezonata* Smith, 1854 = *Tetralonia tarsata* Spinola, 1838, by designation of Patton, 1879a: 477.

Emphoropsis Ashmead, 1899a: 60, no included species; Cockerell and Cockerell, 1901: 48, included species. Type species: *Anthophora floridana* Smith, 1854 = *Bombus laboriosus* Fabricius, 1804, by designation of Cockerell and Cockerell, 1901: 48.

Meliturgopsis Ashmead, 1899a: 62, no included species; Cockerell, 1909c: 414, included a species while synonymizing *Meliturgopsis* under *Emphoropsis*. Type species: *Emphoropsis muribirta murina* Cockerell, 1909, first included species, monobasic. [For a subsequent designation, see Michener 1997b.]

Psithyrus (*Laboriopsithyrus*) Frison, 1927: 69. Type species: *Bombus laboriosus* Fabricius, 1804, by original designation. [The specific name was misapplied by Frison and others, who considered it to be a species of *Psithyrus*, a subgenus of *Bombus*.]

Habropoda consists of anthophoriform bees; indeed, various species are so *Anthophora*-like in form and coloration, matching color patterns of diverse species of *Anthophora*, that the generic characters of wing venation mentioned in couplet 1 of the key to genera of Anthophorini must be examined in order to place specimens to genus correctly. The body length is 10 to 18 mm. *Habropoda* appears to differ from all other genera of Anthophorini, and indeed from most other L-T bees, in the absence of the flabellum (Michener and Brooks, 1984; Fig. 113-4e, f); although many species of *Habropoda* have been examined for this character, others, particularly additional palearctic species, should be examined for verification. The hind leg of the male varies from simple to enlarged and variously modified. Likewise, the front coxa of the male sometimes has a long apical spur. Such modifications are found especially in palearctic species and are not or rarely developed in oriental and nearctic species. Male genitalia, hidden sterna, and other structures were illustrated by Iuga (1958), Mitchell (1962), Liefertinck (1974), and Wu (1979, 1983a).

■ This genus is found in the Eastern Hemisphere from southern France and Algeria eastward through Europe as far north as Hungary, and through Asia Minor, Central Asia, to northeastern China, and southward to northern India, Thailand, Viet Nam, and Taiwan. In the Western Hemisphere it occurs from British Columbia, Canada, to Baja California, Mexico, east across the continent to Connecticut to Florida, USA. Most of the American species are Californian; only one occurs east of Texas and the Great Plains. There are approximately 50 species, equally divided between the Eastern and Western hemispheres. Most of the Asiatic species were revised by Liefertinck (1974); Wu (1979, 1991) gave a key to Chinese species.

According to Stephen (1961), *Habropoda miserabilis* (Cresson) nests in sand and makes only one cell at the end of each burrow. The young metamorphose in autumn, pass the winter as quiescent adults in their natal cells, and emerge in the spring.

Genus *Pachymelus* Smith

This genus of large to very large anthophoriform bees from Africa and Madagascar differs from all other Anthophorini in having a greatly reduced stigma. The marginal cell is longer and more slender than that of most Anthophorini, longer than the distance from its apex to the wing tip. Numerous structures, including male genitalia, were illustrated by Eardley (1993).

The two subgenera of *Pachymelus* have not been distinguished in the past. Morphological diversity among the species is sufficiently great that multiple genera or subgenera may eventually be proposed.

Key to the Subgenera of *Pachymelus*

1. Arolia absent; first flagellar segment shorter than scape; labrum with transverse preapical ridge, often broken; T2 with lateral gradulus reaching about middle of exposed part of tergum *P. (Pachymelopsis)*
- Arolia present; first flagellar segment as long as or usually longer than scape; labrum without transverse preapical ridge; T2 with lateral gradulus usually strong and reaching posterior marginal zone of tergum *P. (Pachymelus s. str.)*

Pachymelus / Subgenus *Pachymelopsis* Cockerell

Pachymelus (Pachymelopsis) Cockerell, 1905a: 331. Type species: *Pachymelus conspicuus* Smith, 1879, by original designation.

Pachymelopsis consists of species 14 to 19 mm long with the metasoma pale-fasciate or covered with tan or orange appressed hair. In both sexes the clypeus and usually the labrum and mandibles are marked with yellow. The clypeus is moderately convex, as seen in profile.

■ This subgenus occurs from Namibia and South Africa north through East Africa to Ethiopia. The five species were revised [with *Pachymelus (Pachymelus) peringueyi* (Friese) included] by Eardley (1993).

The African "*Habropoda*" mentioned by Liefertinck (1966) was a *Pachymelopsis*.

Pachymelus / Subgenus *Pachymelus* Smith s. str.

Pachymelus Smith, 1879: 116. Type species: *Pachymelus microcephalus* Smith, 1879, by designation of Sandhouse, 1943: 581. [For comments, see Michener, 1997b.]

Pachymelus s. str. includes species 15 to 30 mm in length, the latter the largest of the Anthophorini. The appressed metasomal pubescence varies from pale apical tergal fasciae to all-black, largely red, or various shades of brown.

■ This subgenus is found only in Madagascar, with the exception of *Pachymelus peringueyi* (Friese), which occurs in western Cape Province, South Africa, and in Namibia. There are about 15 species. Saussure (1890) gave a key to the species then known. Brooks and Pauly (in Pauly et al., 2001) revised the Malagasy species.

The type species is one of the enormous species with the clypeus of the female angularly produced, as seen in profile, and without yellow facial marks. Among the very large species with an angulate clypeal profile, females of some, *Pachymelus microcephalus* Smith and *ocularis* Saus-

larvae spin cocoons but *Epicharis* larvae do not, and have the reduced labiomaxillary region and antennae characteristic of larvae of all taxa that have lost cocoon-spinning behavior.

Key to the Genera of the Centridini

1. Marginal cell longer than distance from its apex to wing tip (Fig. 114-1b); a few long, whiplike setae arising from preoccipital ridge behind summit of eye and usually reaching anterior margin of tegula (but scarcely reaching anterior margin of scutum in subgenus *Trieipicharis*) *Epicharis*
- Marginal cell shorter than distance from its apex to wing tip (Fig. 114-1a); whiplike setae arising behind summit of eye absent, or, if present (subgenus *Ptilotopus*), then reaching only to anterior margin of scutum *Centris*

Genus *Centris* Fabricius

In *Centris* not only is the marginal cell short, as indicated in the key to genera, but its apical part is usually abruptly bent away from the costal margin of the wing, and is thus obliquely truncate (Fig. 114-1a), a shape not found in *Epicharis*. Species of most subgenera are very compact, strikingly robust, anthophoriform, and capable of hovering as well as extremely rapid flight. The largest species, however, those of the subgenera *Melacentris* and *Ptilotopus*, are more elongate and less adept at both hovering and rapid flight. The genus contains some of the largest neotropical bees, often with colorful pubescence: black, yellow and black, fulvous, white, etc. The integument is black or black and yellow, sometimes with the metasoma

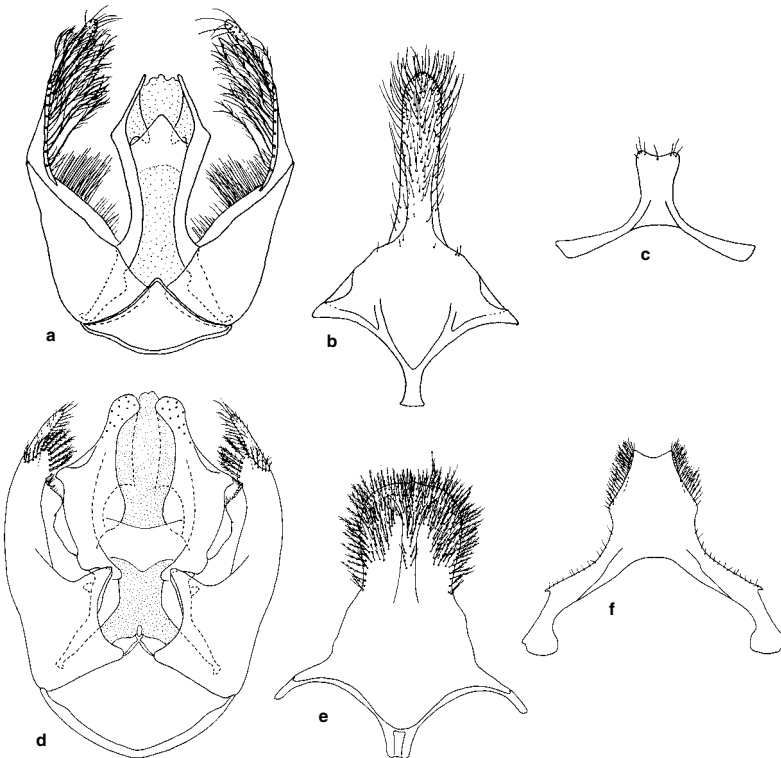
red or metallic bluish or greenish, often with yellow markings. Male genitalia and hidden sterna were illustrated by Michener (1954b), Moure (1969c), and Snelling (1984); see also Figures 114-2 and 114-3a-f.

At one stage (e.g., Michener, 1944) this genus was called *Hemisia*, and the tribe, Hemisiini, because the type species of *Centris* was considered to be a species now placed in *Eulaema* in the Euglossini. *Centris*, however, was conserved in its traditional sense by Commission Opinion 567 (1957). *Ptilotopus*, given generic rank by Snelling (1984), is here regarded as a subgenus of *Centris*, since it is no more distinctive than some of the other subgenera.

A cladistic study by Ayala (1998) indicates that *Centris* is divisible into three groups, as follows: (1) *Acritocentris*, *Centris* s. str., *Exallocentris*, *Paracentris*, *Xanthemisia*, *Xerocentris* (*Exallocentris*, lacking giant setae on the male genitalia in a group otherwise characterized by such setae, may be out of place in group 1); (2) *Heterocentris*, *Trachina*; (3) *Melacentris*, *Ptilocentris*, *Ptilotopus*, *Wagenknechtia*. These three groups could be regarded as genera, although such a division poses some problems, as indicated above for *Exallocentris*. Ayala's work resulted in two new subgenera (Ayala, 2002); to incorporate them I present a new key to the subgenera kindly made available by Dr. Ayala. An additional reason for the new key is that the old key (in Michener, 2000) contains errors.

Papers reviewing the subgenera of *Centris* are by Michener (1951b), Snelling (1974, 1984), and Ayala (1998). Revisions at the species level are found in the above papers by Snelling for North and Central America, and in

Figure 114-2. Dorsal views of genitalia and ventral views of S8 and S7, of male *Centris*. **a-c**, *C. (Centris) aethiocesta* Snelling; **d-f**, *C. (Ptilotopus) zonata* Mocsáry. From Snelling, 1984.



Friese (1900). Roig-Alsina (2000) revised the 31 Argentine species of *Centris*.

In various species of *Centris*, in diverse subgenera, some males are much larger than the usual form and commonly have more extensive yellow markings, more enlarged hind legs, and other distinctive features. Such "metanders" or "Beta males" have often been described as distinct species. Moure (1969c) illustrated the nearly identical male genitalia of "normal" males and metanders of *C. (Centris) aenea* Lepeletier and *flavifrons* (Fabricius). The behavioral correlates involved in the production of such individuals, as well as their mating and other activities, are in need of study.

Mating systems have been investigated in several species of *Centris* and vary greatly among the species. In some species, like *C. pallida* Fox and *caesalpiniae* Cockerell, males dig into the ground where females are emerging (Alcock, 1989; Rozen and Buchmann, 1990). The largest males have an advantage in mating with the virgin females, for they can push aside smaller, weaker males, which must, however, be at an advantage somewhere, perhaps where nests are widely scattered, or they would probably not be produced generation after generation. Males of other species establish territories, probably for mating, marked by pheromones secreted either by the mandibular glands (*Centriss.* str.) or by glands in the enlarged hind legs of some species (subgenera *Heterocentris*, *Trachina*, and *Xanthemisia*) (Coville et al., 1986; Frankie, Vinson, and Williams, 1989). Coville et al. show such a gland as occupying part of the interior of both the femur and the tibia and opening through a pore at the apex of the tibia.

Key to the Subgenera of *Centris*

(By Ricardo Ayala)

1. Scutellum with two lobes, tubercles, or convexities (except in males of *Ptilocentis* in which scutellum is convex with lobes not well defined) 2
 - Scutellum rounded, without lobes, tubercles or separate convexities 6
- 2(1). Hypoepimeral area with strong tubercle on anterior lower part (except in *C. americana* Klug); scutellum, and sometimes scutum with glabrous areas; female with basitibial plate simple, clearly without secondary plate (body length 30–32 mm) *C. (Ptilotopus)*
 - Hypoepimeral area without tubercle; scutellum, and scutum hairy, without glabrous areas except sometimes apices of scutellar tubercles; female with secondary basitibial plate on disc of primary plate 3
- 3(2). Mandible of female 5-toothed, of male 4-toothed, the two basal teeth flat and blunt; pygidial plate of female with apex notched *C. (Schisthemisia)*
 - Mandible of female 4-toothed, of male 3-toothed, the basal teeth acute (sometimes robust) in female (in some *Melacentris* basal tooth obtuse, somewhat divided in two); pygidial plate of female with apex acute or obtuse, not notched 4
- 4(3). Secondary basitibial plate of female with apex broadly rounded, behind central axis of primary plate; wings dark, almost black, with blue, violet, or green iridescence (metasomal terga with abundant pubescence and usually without metallic tints) *C. (Melacentris)*
 - Secondary basitibial plate of female with apex acute, near central axis of primary plate; wings dark but not black, somewhat translucent, with magenta and green iridescence 5
- 5(4). Clypeus in both sexes yellow with median black area narrowed toward lower margin; ocellocular distance equal to median ocellar diameter or less; metasomal terga without long plumose hairs (terga sometimes strongly metallic) *C. (Aphemisia)*
 - Clypeus black in female, in male with median yellow area; ocellocular distance greater than median ocellar diameter; T2 and T3 with abundant plumose hairs *C. (Ptilocentris)*
- 6(1). Maxillary palpus 3- or 4-segmented (counting robust basal segment, i.e., with two or three free segments); hind femur and tibia of male usually swollen; hind basitarsus of male usually with spine or elevated carina on posterior margin 7
 - Maxillary palpus 5- or 6-segmented (4 or 5 free segments); hind leg of male usually not swollen; hind basitarsus of male without spine or elevated carina 8
- 7(6). Male labrum broader than long with sparse or abundant hairs on whole surface; female basitibial plate simple, without secondary plate or with tendency to form secondary plate covered with short, dense hairs *C. (Heterocentris)*
 - Male labrum longer than broad with abundant hairs on distal margin only, sparse hairs elsewhere; female basitibial plate with elevated secondary plate not hidden by hairs, apex of secondary plate near posterior margin of primary plate *C. (Trachina)*
- 8(6). Females 9
 - Males 15
- 9(8). Mandible 5-toothed, one of these teeth on inner surface at base of distal tooth; pygidial plate with longitudinal groove from apex of secondary plate toward spatulate apex of pygidial plate *C. (Xanthemisia)*
 - Mandible 3- or 4-toothed, without tooth on inner surface at base of distal tooth; pygidial plate without longitudinal groove and spatulate apex 10
- 10(9). Front and mid tibiae without combs for collecting floral oil, or in South America sometimes with vestigial combs 11
 - Front and mid tibiae with well developed combs for collecting oil 12
- 11(10). Pubescence completely black; mandible 4-toothed; mid basitarsus with area of dense, spatulate hairs; T2 and T3 with sparse, usually short pubescence; basitibial plate traversed by two more or less transverse lines *C. (Exallocalcentris)*
 - Pubescence largely pale; mandible 3-toothed; mid basitarsus with hairs simple, not spatulate (South American species with vestigial comb); T2 and T3 with abundant short pale pubescence; basitibial plate variable but without transverse lines *C. (Xerocentris)*
- 12(10). Front basitarsus with comb for collecting floral oil only on distal half; tergal integument black with intense metallic blue reflections *C. (Wagenknechtia)*
 - Front basitarsus with comb on full length of anterior margin; terga with or without metallic reflections, sometimes with transverse yellow bands 13
- 13(12). Basitibial plate with defined secondary plate that lacks sharp projecting margin, margin of secondary plate extending basad near anterior margin of basitibial plate

- and distad near posterior margin of plate *C. (Paracentris)*
- Basitibial plate with defined secondary plate with sharp projecting margins; margins of secondary plate extending basad both anteriorly and posteriorly 14
- 14(13). Clypeus without yellow or white markings *C. (Acritocentris)*
- Clypeus with yellow or white inverted T or Y *C. (Centris s. str.)*
- 15(8). Middle basitarsus with comb presumably for collecting oil (as also in some *Paracentris*); pygidial plate well defined with exposed, elevated margins *C. (Acritocentris)*
- Middle basitarsus without comb for collecting oil (except in some *Paracentris*, which lack pygidial plate); pygidial plate absent or not well defined, if present lateral margins covered by pubescence and not elevated 16
- 16(15). Mandible with acetabular groove ending between apical and subapical teeth (acetabular carina ending between the two most proximal teeth); posterior femur swollen *C. (Xanthemisia)*
- Mandible with acetabular groove ending between proximal and subapical (median) teeth; posterior femur not swollen 17
- 17(16). Basitibial plate well defined, distal margin elevated; pygidial plate well defined, lateral margins not elevated, covered by pubescence medially (integument black, pubescence black and whitish) *C. (Exallocentris)*
- Basitibial plate absent; pygidial plate absent, apical margin of T7 bilobed 18
- 18(17). Clypeus yellow with upper lateral margins black . . . *C. (Centris s. str.)*
- Clypeus black or reddish brown or if yellow, then its upper lateral margins yellow, not black 19
- 19(18). Metasomal terga black with strong, usually dark blue, reflections (clypeus black) *C. (Wagenknechtia)*
- Metasomal terga black or brown without metallic reflections 20
- 20(19). Lateral ocellus separated from eye by less than ocellar diameter; T2 to T4 with abundant whitish pubescence *C. (Xerocentris)*
- Lateral ocellus separated from eyes by at least ocellar diameter; T2 to T4 usually with dark pubescence, rarely whitish *C. (Paracentris)*

Centris / Subgenus *Acritocentris* Snelling

Centris (Acritocentris) Snelling, 1974: 36. Type species: *Centris ruthannae* Snelling, 1966, by original designation.

This subgenus consists of species 15 to 19 mm in body length that resemble large *Paracentris*, to which males run in the key. Females, however, differ from *Paracentris* in their three-toothed mandibles and the overhanging margin of the secondary basitibial plate, although the overhang may be worn off in old specimens. It should be noted that in the related subgenus *Xerocentris* some species have three-toothed female mandibles whereas others have four-toothed mandibles. Further, *Centris (Paracentris) autrani* Vachal from Chile has a partially overhanging margin of the secondary basitibial plate, thus resembling *Acritocentris*.

■ *Acritocentris* occurs from southern Arizona, USA, to Tamaulipas and southward to Chiapas, Mexico. The four species were revised by Snelling (1984).

Centris / Subgenus *Aphemisia* Ayala

Centris (Aphemisia) Ayala, 2002: 1. Type species: *Centris plumipes* Smith, 1854, by original designation.

The species of this subgenus resemble *Melacentris* but differ in the more translucent wings. In the female the acute apex of the secondary basitibial plate, more or less on the longitudinal axis of the primary plate, distinguishes it from *Melacentris*. The apical process of S8 of the male is widest medially, not basally as in related groups; the articulation of the male gonostylus, slightly preapically on the gonocoxite, also differs from related groups.

■ *Aphemisia* occurs from Panama and French Guiana south to Bolivia. The three species were reviewed by Moure (2002). (The replacement name given by Moure to the type species is unnecessary since *Centris plumipes* Smith is, in fact, not a junior homonym of *Apis plumipes* Fabricius, which, although listed in *Centris* by Fabricius in 1804, was transferred to *Anthophora* in 1854.)

Centris / Subgenus *Centris* Fabricius s. str.

Centris Fabricius, 1804: 354. Type species: *Apis haemorrhoidalis* Fabricius, 1775, designation by Commission Opinion 567 (1959). [See Michener, 1997b.]

Hemisia Klug, 1807, in Illiger, 1807: 198, nomen nudum.

Hemisia Klug, 1807b: 213, 227. Type species: *Apis haemorrhoidalis* Fabricius, 1775, by designation of Cockerell, 1906: 105.

Centris (Cyanocentris) Friese, 1900: 244, 251. Type species: *Apis versicolor* Fabricius, 1775, by designation of Sandhouse, 1943: 543.

Centris (Poecilocentris) Friese, 1900: 244, 252. Type species: *Centris fasciatella* Friese, 1900, by designation of Sandhouse, 1943: 589.

Centris s. str. consists of species usually having metallic metasomal background color. Yellow metasomal markings occur in many species and in some, e.g., *C. eisenii* Fox, the yellow bands are so extensive that the metallic background is essentially eliminated. Rarely, the metasoma is red and nonmetallic. The body length is 12 to 24 mm. A unique character of the subgenus is the long, slender, apical projection of the male gonocoxite, extending parallel to the gonostylus; this gonocoxal projection bears giant branched setae (Fig. 114-2a).

■ This subgenus occurs from Baja California, Mexico, and southern Arizona to southern Florida, USA, and the Bahamas, south through the Antilles and the continental tropics to Santa Catarina, Brazil. Of perhaps 35 species in all, about 20 occur in North and Central America and the Antilles. The species of Mexico and Central America were reviewed by Snelling (1984). Moure (1945c) listed 11 mostly South American species.

Centris / Subgenus *Exallocentris* Snelling

Centris (Exallocentris) Snelling, 1974: 35. Type species: *Centris anomala* Snelling, 1966, by original designation.

male gonostyli (Fig. 114-3g) in *Epicharis* are plesiomorphic relative to *Centris*. At the same time, the short, two- or three-segmented maxillary palpi and the reduced larval mouthparts and loss of cocoon-spinning activity are derived relative to *Centris*. Although most *Centris* have four- or five-segmented palpi, two of its subgenera have three-segmented maxillary palpi, but these subgenera are in other ways derived and their palpal reduction is presumably independent from that of *Epicharis*.

The subgenera of *Epicharis* were reviewed by Moure (1945b), Snelling (1984), and Ayala (1998). The three subgenera *Epicharis* s. str., *Epicharana*, and *Hoplepicharis* taken together were the sister group to all others in Ayala's cladistic analyses.

Key to the Subgenera of *Epicharis*

(Modified from Snelling, 1984)

1. Female with secondary basitibial plate; male with obsolete pygidial plate, its margins more or less coextensive with margins of T7, its apex thin and bilobate or bidentate 2
- Female without secondary basitibial plate; male with distinct, sharply margined pygidial plate, no more than one-half as wide as T7, its apex narrowly truncate or rounded 4
- 2(1). Lateral margins of female pygidial plate nearly straight, apex narrowly truncate; female hind tibia longer than basitarsus; hind leg of male with long, scopa-like hairs and basitarsus with prominent tooth at basal one-third *E. (Hoplepicharis)*
- Lateral margins of female pygidial plate distinctly concave as seen in dorsal view, apex broadly truncate; female hind tibia no longer than basitarsus; male without scopa-like hairs on hind leg and hind basitarsus without tooth at basal one-third 3
- 3(2). Female: Frontal carina ending more than diameter of anterior ocellus below that ocellus; apical pygidial truncation narrower than diameter of anterior ocellus; disc of T5 with short hairs mostly simple or barbed. Male: Mesosternal tubercles absent; hind basitarsus without carinate ridge on outer margin; hind trochanter and femur without ventral patch of short, dark, plumose setae (South America) *E. (Epicharis* s. str.)
- Female: Frontal carina to anterior ocellus ending less than diameter of anterior ocellus below that ocellus; apical pygidial truncation broader than diameter of anterior ocellus; disc of T5 with short hairs distinctly plumose. Male: Two mesosternal tubercles or teeth projecting posteriorly between middle coxae; hind basitarsus with carinate ridge on outer margin, terminating in toothlike process; hind trochanter and femur with ventral patch of short, dark, plumose setae *E. (Epicharana)*
- 4(1). First flagellar segment of female equal to length of second to fourth segments combined, of male longer than scape and longer than following two segments combined; posterior margin of dorsal surface of scutellum deeply impressed in middle; maxillary palpus two-segmented *E. (Parepicharis)*
- First flagellar segment short, in female usually no longer than second and third segments combined and always shorter than second to fourth combined, and in male shorter than scape; posterior margin of dorsal surface of

- scutellum not or weakly impressed in middle, or, if deeply impressed, then maxillary palpus three-segmented 5
- 5(4). Lateral ridges of clypeal disc absent or, on basal one-half or less of clypeus, weakly evident; male hind basitarsus with carinate ridge on inner margin, terminating in large tooth at about midlength 6
- Lateral ridges of clypeal disc strong and sharply defined to near apical margin of clypeus; male hind basitarsus without carinate ridge or tooth on inner margin 7
- 6(5). Maxillary palpus two-segmented; flagelliform preoccipital setae distinct and extending beyond anterior margin of mesoscutum; ocellular distance in male less than diameter of lateral ocellus (South America) *E. (Anepicharis)*
- Maxillary palpus three-segmented; flagelliform preoccipital setae short, not projecting beyond occipital hairs and scarcely reaching anterior margin of mesoscutum; ocellular distance in male equal to diameter of lateral ocellus (South America) *E. (Triepicharis)*
- 7(5). Dorsal surface of scutellum bigibbous; prepygidial fimbria of female not preceded by shiny, glabrous area (Brazil) *E. (Cyphepicharis)*
- Dorsal surface of scutellum flat; prepygidial fimbria of female preceded by a shiny, nearly glabrous area 8
- 8(7). Jugal lobe of hind wing about one-half as long as vannal lobe, nearly attaining apex of cubital cell; female hind basitarsus about twice as long as broad, its posterior margin nearly straight; male pygidial plate broad, covering most of T7 *E. (Epicharoides)*
- Jugal lobe of hind wing about one-third as long as vannal lobe, its apex well short of that of cubital cell; female hind basitarsus about one-third longer than broad, its posterior margin strongly curved; male pygidial plate narrow, covering less than half of T7 *E. (Epicharitides)*

Epicharis / Subgenus *Anepicharis* Moure

Anepicharis Moure, 1945b: 302. Type species: *Epicharis dejeanii* Lepeletier, 1841, by original designation.

■ *Anepicharis* is found in Brazil from the state of Rio Grande do Sul to Goiás. Three species were recognized by Moure (1945b).

Epicharis dejeanii Lepeletier nests in aggregations in flat ground. Floral oils from Malpighiaceae are used to waterproof the cells and not as a larval food. Overwintering in the temperate climate of southern Brazil is as prepupae (Hiller and Wittmann, 1994).

Epicharis / Subgenus *Cyphepicharis* Moure

Cyphepicharis Moure, 1945b: 306. Type species: *Cyphepicharis borgmeieri* Moure, 1945, by original designation.

■ *Cyphepicharis* is known from the states of São Paulo and Minas Gerais, Brazil. The only species is *Epicharis borgmeieri* (Moure).

Epicharis / Subgenus *Epicharana* Michener

Epicharis (Epicharana) Michener, 1954b: 144. Type species: *Apis rustica* Olivier, 1789, by original designation.

This is the group that Moure (1945b) considered to be *Epicharis* s. str.; for an explanation, see Michener

115. Tribe Rhathymini

This tribe of tropical American cleptoparasitic bees consists of large (13–28 mm long), elongate, nomadiform species (Fig. 104-2b). Various studies, e.g., Michener (1944) and Roig-Alsina and Michener (1993), place the Rhathymini among the apine bees, not in the Nomadinae, in spite of superficial resemblance to the large species of the epeoline genus *Odyneropsis*. The tribe is easily distinguished from *Odyneropsis* by tribal characters, such as the oblique vein cu-v of the hind wing, longer than to slightly shorter than vein M+Cu; the short first submarginal cell, little if any longer than the second on its posterior margin; the tapering rather than quadrate anterior coxa with a slender, hairy, apical spine mesal to the articulation of the trochanter; and the tapering, somewhat tubular (because of upturned lateral margins) S6 of the female, which is not produced into processes armed with specialized setae as in Epeolini. From the Ericrocidini, the Rhathymini differs in its slender body; the hairy, not papillate wings; the presence of arolia; and the unmodified middle tibial spur. Other characters are the simple mandibles, the absence of maxillary palpi, the often bi-convex scutellum, its posterior part declivous, and the slender, parallel-sided middle and hind tarsi, the former and sometimes the latter as long as the corresponding tibia. S4 and S5 of the male are strongly fringed; in most species the margin of S5 is broadly concave and produced posterolaterally under T5 as a hairy projection, resulting in preapical metasomal tufts of long hair that are visible from above, as shown in Figure 104-2b. A fuller characterization of the tribe was by Engel, Michener, and Rightmyer (2004a).

Larvae of Rhathymini were described by Rozen (1969a) and Camargo, Zucchi, and Sakagami (1975). The absence of galeae and the elongate labiomaxillary region are derived characters of mature larvae in common with those of Ericrocidini and Melectini. The first-stage larva has a less sclerotized and more globose and hypognathous head than that in other cleptoparasitic Apinae, and the antennae are scarcely noticeable convexities, unlike those of Melectini and Ericrocidini (Rozen, 1991a). The egg is evidently laid through an aperture opened in the closure of the host cell, and the young larva presumably kills the egg or young larva of the host.

Key to the Genera of Rhathymini

- 1. Mesepisternum with large submedian tubercle; vein cu-v of hind wing strongly oblique and distinctly longer than second abscissa of M+Cu; supraclypeal area strongly elevated, crested medially, not continuing convexity of clypeus *Rhathymus*
- Mesepisternum without tubercle; vein cu-v of hind wing less strongly oblique and shorter than or subequal to second abscissa of M+Cu; supraclypeal area with surface, in general, a continuation of convexity of clypeus although with small frontal tubercle at lower end of frontal line *Nanorhathymus*

Genus *Nanorhathymus* Engel, Michener, and Rightmyer

Rhathymodes Engel, Michener, and Rightmyer, 2004a: 6 (not Turner, 1911). Type species: *Rhathymus acutiventris* Friese, 1906, by original designation.

Nanorhathymus Engel, Michener, and Rightmyer, 2004b: 316, replacement for *Rathymodes* Engel, Michener, and Rightmyer. Type species: *Rathymus acutiventris* Friese, 1906, autobasic.

This genus includes species smaller than most *Rhathymus* (13–18 mm in body length; 16–28 mm for *Rhathymus*). The most prominent morphological differentiating characters are indicated in the key above. Others include the nearly flat (rather than strongly depressed) area between the lateral ocellus and the eye and the position of the second recurrent vein near the middle or apical third (rather than near the apex) of the second submarginal cell.

■ *Nanorhathymus* is known from central Mexico to Paraguay. The two species were differentiated by Engel, Michener, and Rightmyer (2004a).

Nanorhathymus superficially resembles large *Osirinus* (tribe Osirini) but differs in the much smaller stigma, absence of maxillary palpi, lack of separation of the anterior wing margin from vein R1, absence of a mesal carina on the anterior coxa, etc.

Genus *Rhathymus* Lepeletier and Serville

Colax Lepeletier and Serville, 1825: 4, 213, nomen nudum.
Colax Lepeletier and Serville, 1828: 448 (not Hübner, 1819).

Type species: *Rhathymus bicolor* Lepeletier and Serville, 1828, monobasic. [See Michener, 1997b.]

Rhathymus Lepeletier and Serville, 1828: 448. Type species: *Rhathymus bicolor* Lepeletier and Serville, 1828, monobasic.

Liogastra Perty, 1833: 146. Type species: *Liogastra bicolor* Perty, 1833 = *Rhathymus bicolor* Lepeletier and Serville, 1825, monobasic.

Rathymus Smith, 1854: 278 (not Dejean, 1831), unjustified emendation of *Rhathymus* Lepeletier and Serville, 1828.

Bureauella Dominique, 1898: 61. Type species: *Bureauella insignis* Dominique, 1898, monobasic.

The characters of *Rhathymus* are indicated in the discussion of the tribe and in the key to genera. Species vary from black, the metasoma frequently red, to largely yellow.

■ The range is from the state of San Luis Potosí, Mexico, south through the tropics to eastern Bolivia and the province of Misiones, Argentina. There are about eight species. Friese (1912b) gave a key to the species, along with *Odyneropsis* in the Epeolini.

Rhathymus species are cleptoparasites of *Epicharis* in the Centridini (Rozen, 1969a; Camargo, Zucchi, and Sakagami, 1975; Hiller and Wittmann, 1994).

116. Tribe Ericrocidini

This is a Western Hemisphere tribe formerly sometimes called Ctenioschelini. It consists of anthophoriform to euceriform cleptoparasitic bees having the size and form of species of the largely Eastern Hemisphere tribe Melectini (Fig. 116-1). In the phylogenetic study of Roig-Alsina and Michener (1993) these tribes appear as sister groups, but this apparent relationship could be a result of convergence as parasites rather than genuine phylogenetic relationship; that work emphasized the major influence of adaptations to cleptoparasitism on adult morphology and apparent phylogeny. It is a reasonable assumption that the Ericrocidini is actually related to its principal host group, the Centridini, and Melectini to *its* host group, the Anthophorini. A unique feature of the Ericrocidini is the bipartite flabellum, consisting of an elongate preflabellum with a rounded apex curved anteriorly and a smaller postflabellum arising preapically from the anterior surface of the preflabellum and curved posteriorly (Fig. 116-2e-g). The convex side of each has a cobblestone pattern. Another unique feature of the tribe is the large, bifurcate or multidentate apex of the middle tibial spur (Fig. 116-3). This character is approached in some Centridini (species of *Epicharis*) by the preapical shoulder of the same spur, a fact supporting the suggested relationship of Ericrocidini to the Centridini. In

the ericrocidines *Epiclopus gayi* Spinola and *wagenknechti* (Ruiz), there is merely a preapical group of larger teeth on the midtibial spur rather than the usual ericrocidine structure. Ericrocidini differs further from the Melectini in its long marginal cell, extending well beyond the third submarginal cell (Fig. 116-4); the short, broad male gonostylus, sometimes having a slender dorsal process that in some *Hopliophora* arises at the base of the gonostylus like a separate dorsal gonostylus (Fig. 116-5); and the flattened middle basitarsus, usually with a carina (Fig. 116-3c). The middle and hind tibiae have scattered spinelike setae on the outer surfaces. Arolia are absent. Parts of the body commonly appear metallic blue or green; this is usually because of appressed metallic hairs or scales, but in *Epiclopus lendliana* (Friese) the integument itself is metallic. Conversely, the genus *Ericrocis* and some species of *Hopliophora* and *Epiclopus* lack metallic coloration entirely.

Snelling and Brooks (1985) presented a generic revision of the tribe, including illustrations of male genitalia, hidden sterna, and other structures (see also Fig. 116-5). Larvae have been described by Rozen (1969a) and Rozen and Buchmann (1990). First-stage larvae described by Rozen (1991a) suggested a possible close relationship between Ericrocidini and Isepeolini, but are not similar to those of Melectini or Rhathymini.

So far as is known, Ericrocidini, like Melectini and Rhathymini, introduce their eggs into closed cells of the host by breaking a hole in the cell closure. The egg is then left attached to the closure or nearby cell wall, or in *Ericrocis* it may drop onto the food mass, where such eggs, already killed by a young larva from another egg, were found by Rozen (1991a).

Key to the Genera of the Ericrocidini (Modified from Snelling and Brooks, 1985)

- 1. Third submarginal cell of forewing large, receiving both recurrent veins; hind tarsus very long, in male with dense brush of long, dark, plumose hairs; maxillary palpus absent (South America) *Acanthopus*
- Second and third submarginal cells each receiving a recurrent vein, or first recurrent vein and second submarginal crossvein meeting; hind tarsus without dense brush of long, dark, plumose hairs; maxillary palpus present, although sometimes very short 2
- 2(1). Juncture of anterior and dorsal surfaces of T1 slightly humped and subangulate in middle (Fig. 116-6b); middle basitarsus without distal, flattened process; mandible simple 3
- Juncture of anterior and dorsal surfaces of T1 evenly rounded, not subangulate (Fig. 116-6a); middle basitarsus almost always with distal, flattened process on posterior margin, often continued basad as a raised, cariniform ridge (Fig. 116-3c); mandible usually with preapical tooth 5
- 3(2). Scutellum with two flat and platelike processes directed caudad (Fig. 116-7b); forewing with an apical cloud in marginal cell in addition to that at wing apex *Mesocheira*



Figure 116-1. Female Ericrocidini. Above, *Ericrocis lata* (Cresson); Below, *Mesoplia azurea* (Lepeletier and Serville). From Michener, McGinley, and Danforth, 1994.

- . Scutellum bituberculate, the projections stout, subconical, and suberect; forewing with apex dark but without dark area in marginal cell 4
- 4(3). Pronotum carinate between collar and lobe; omaulus lamellate; male antenna normal, not extending much beyond tegula *Aglaomelissa*
- . Pronotum not carinate between collar and lobe, lateral end of collar clearly defined; omaulus abruptly rounded; male flagellar segments greatly elongate, flagellum extending well beyond apex of metasoma (Fig. 116-7a) *Ctenioschelus*
- 5(2). Middle and hind distitarsi with a group of appressed, black setae on each side (inner eye margins divergent above; male gonostylus without dorsal lobe or process) 6
- . Middle and hind distitarsi with normal setae 7
- 6(5). Metasomal scales contrasting black and white (may be somewhat tawny); labrum with erect preapical median tubercle; scutellum without tubercles (nearctic, Mexico) *Ericrocis*
- . Metasomal scales or hairs iridescent blue or green, with or without small, contrasting, whitish hair patches; labrum with transverse preapical ridge; scutellum with pair of mammiform tubercles (South America) *Mesonychiium*
- 7(5). Eyes diverging above; scutellum not bituberculate (in *E. gayi* Spinola with median depression, thus weakly bi-convex) (South America) *Epiclopus*
- . Eyes not diverging above, inner orbits usually more or less parallel; scutellum with two large tubercles 8
- 8(7). Metasoma covered with minute blue-green scales, often with small patches of white or yellow pubescence *Mesoplia*
- . Metasoma black or faintly metallic, without patches of pale pubescence (South America) *Hopliphora*

Genus *Acanthopus* Klug

Acanthopus Klug, 1807, in Illiger, 1807: 199; Klug, 1807b: 226. Type species: *Apis splendida* Fabricius, 1793 = *Apis palmata* Olivier, 1789, monobasic. [See the annotation by Michener, 1997b.]

Acanthopus consists of large (body length 20-25 mm), dark blue species, the color resulting from appressed blue pubescence. These bees have extremely long hind legs, the hind tarsus of the male being densely hairy and thus appearing broader than the tibia. Unlike that of other Eriocridini, the inner ramus of the claw of *Acanthopus* is a strong tooth, not a compressed lobe as in many other parasitic bees. Unlike the mentum of almost all long-tongued bees, as indicated by Snelling and Brooks (1985), that of *Acanthopus* is a slender transverse bar, and the lorum is a stronger bar extending between the apices of the cardines, but not fused to them.

■ This genus occurs from the state of Goiás, Brazil, north to the Guianas and Trinidad, with a doubtful report from Panama. There are at least two species, although five names have been proposed (Snelling and Brooks, 1985).

Acanthopus parasitizes *Centris* (*Ptilotopus*) (Rozen, 1969a), which nests in arboreal termite nests.

Genus *Aglaomelissa* Snelling and Brooks

Aglaomelissa Snelling and Brooks, 1985: 25. Type species: *Melissa duckei* Friese, 1906, by original designation.

Aglaomelissa resembles a rather small *Mesoplia* (length 9-10 mm), from which it differs in having a carinate omaulus and a subangulate profile of T1, the angle separating the anterior from the dorsal surface of this tergum (as in Fig. 116-6b). The metasoma is green because of its metallic scales.

■ This genus occurs from Costa Rica to Colombia, Venezuela, Trinidad, and the state of Pará, Brazil. The only species is *Aglaomelissa duckei* (Friese).

Genus *Ctenioschelus* Romand

Ctenioschelus Romand, 1840: 336. Type species: *Acanthopus goryi* Romand, 1840, monobasic. Taschenberg, 1883: 78, designated *Melissodes latreillei* Lepeletier, 1841 = *Acanthopus goryi* Romand, 1840.

Ischnocera Shuckard, 1840: 166, no included species; Smith, 1854: 284, included *Ischnocera* as a synonym of *Ctenioschelus*, with the single species *latreillii* Lepeletier. Type species: *Melissoda latreillii* Lepeletier, 1841 = *Acanthopus goryi* Romand, 1840.

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

Various authors, from Smith (1854) to Snelling and Brooks (1985), have recognized the existence of the name *Ischnocera*, while calling this genus *Ctenioschelus*. Shuckard's (1840) brief comments could apply to no other bee. Smith recognized the priority of *Ctenioschelus*, on the basis of Romand's (1841) publication. Romand (1840), however, proposed *Ctenioschelus* earlier, probably before the date of Shuckard's work. Romand's paper appeared in November, 1840. Shuckard's work is in a volume whose preface includes a note dated "Nov. 1840." It is therefore unlikely to have been published before December, 1840, and a copy in the Natural History Museum, London, bears the handwritten notation, "Dec. 1840" (this information thanks to J. Harvey, Librarian). Romand's name is here considered to have priority, as well as universal usage; *Ischnocera* has not appeared in print except as a synonym since 1840, so far as I know. Article 69(a)(i)(1) and (vii) of the Code, ed. 3, appears to require the type designation indicated above for *Ischnocera*.

The male of *Ctenioschelus* is unmistakable because of its antennae, which look like those of a cerambycid beetle and extend well beyond the apex of the metasoma (Fig. 116-7a). The female looks superficially like a *Mesoplia* about 15 mm long with the metasoma more green or gold than in the usually blue *Mesoplia*. It differs from *Mesoplia* in its carinate omaulus, backward-directed scutellar tubercles extending over the propodeum (but not flat as in *Mesochœira*), the angle between the anterior and dorsal surfaces of T1, and the lack of slender apical points on the male gonostyli.

■ *Ctenioschelus* ranges from the state of Jalisco, Mexico, south through tropical America to Uruguay and Paraguay. There are two species.

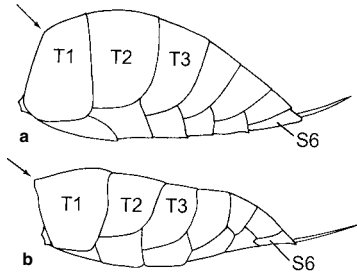


Figure 116-6. Lateral views of metasomas of Ericrocidini. **a**, *Mesoplia imperatrix* (Friese); **b**, *Mesoscheira bicolor* (Fabricius). (The angle of T1 is marked by an arrow.) From Michener, McGinley, and Danforth, 1994.

M[eso]chira Agassiz, 1846: 20; Schulz, 1906: 257, unjustified emendation of *Mesoscheira* Lepeletier and Serville, 1825.

A unique character of this genus is the broad, flat, shelflike scutellar lobes that extend horizontally back over the base of T1 (Fig. 116-7b). The wings are more strongly maculate than in other genera, there being separate, well-defined separate dark areas in the apex of the marginal cell and at the wing tip. The metasoma is covered with metallic blue scales. This genus includes some of the smallest Ericrocidini (body length 9-14 mm). Male genitalia and hidden sterna were illustrated by Michener (1954b) and Snelling and Brooks (1985); see Figure 116-5g-i.

■ *Mesoscheira* occurs from the Mexican states of Sonora and Veracruz and the Greater Antilles south through the tropics to Paraguay. There is probably only one species, *M. bicolor* (Fabricius), although six names have been proposed, as listed by Snelling and Brooks (1985).

Genus *Mesonychium* Lepeletier and Serville

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

In size (10-16 mm long) and coloration, including the metallic scale-like hairs on the metasoma, this genus is similar to *Mesoplia*, and the two genera have usually been confused. A distinctive character of the genus is the greatly reduced maxillary palpus consisting of an obscure (doubtful) first segment and an ovoid second segment not over twice as long as broad; related genera have a much longer palpus and the second segment is parallel-sided and several times as long as broad.

■ *Mesonychium* occurs from central Chile and Argentina north to Peru, and through Brazil to French Guiana. The 12 species names in this genus, as here understood, were listed by Snelling and Brooks (1985).

Two species included in *Mesonychium* by Snelling and Brooks (1985) are here removed to *Epiclopus*. These species are responsible for the morphological diversity indicated for *Mesonychium* in their key and description.

Circumstantial evidence indicates that *Mesonychium* species parasitize *Centris* (Wagenknecht Huss, 1969).

Genus *Mesoplia* Lepeletier

In *Mesoplia* the metasoma is bright metallic blue or green-

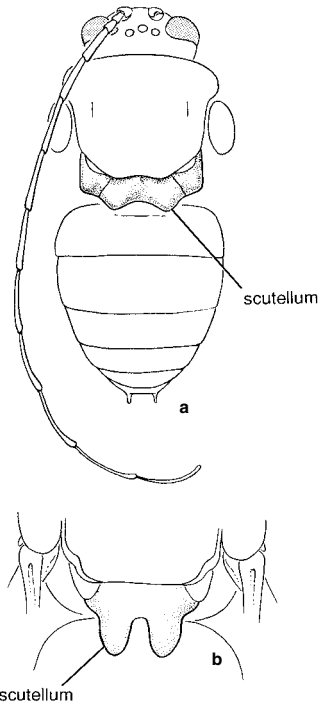


Figure 116-7. Ericrocidini. **a**, *Ctenioschelus goryi* (Romand), male; **b**, Dorsal view of scutellum of *Mesoscheira bicolor* (Fabricius). From Michener, McGinley, and Danforth, 1994.

ish blue because of colored scales, each about the size of a puncture; sometimes there are also small patches of pale hairs on the terga. The maxillary palpus is elongate, three- or four-segmented. S5 of the male is broadly emarginate and largely hidden under S4. The body length is 11.5 to 20.0 mm. Male genitalia and hidden sterna were illustrated by Michener (1954b) as well as Snelling and Brooks (1985); see also Figure 116-5a-c.

This genus is known to parasitize both *Centris* and *Epicharis* (Rozen, 1969a). As with Melectini and Rhythmini, the parasite commonly attains access to closed cells by opening a hole in the cell closure and inserting an egg, which is attached to the upper cell walls (Vinson, Frankie, and Coville, 1987). In some cases an egg was found in a cell that showed no signs of having been opened; presumably in these cases the egg was laid before the cell was closed.

Key to the Subgenera of *Mesoplia*

- 1. Hind tibial spurs of male not reaching beyond basal third of basitarsus, sometimes only one spur present; hind tibia of male with inner distal patch of dense black hairs; pygidial plate of female broad, occupying exposed dorsal surface of T6, covered with hairs or scales *M. (Mesoplia s. str.)*
- Hind tibial spurs of male both present, reaching to or beyond middle of basitarsus; hind tibia of male without inner distal hair patch; pygidial plate of female narrow, bare *M. (Eumelissa)*

laid before the host cell was closed, but Torchio and Trosle showed that this was an erroneous interpretation.

Popov (1955c) and Lieftinck (1968) suggest that the Melectini are polyphyletic, *Thyreus* being derived from *Amegilla*-like ancestors and *Melecta* and its allies from *Anthophora*-like ancestors. This may be correct, but the evidence is weak because loss of arolia and palpal reduction, cited as common characteristics of *Thyreus* and *Amegilla*, are both also found in some *Melecta*-like taxa.

Separate keys are provided for genera of the Western and of the Eastern hemispheres.

Key to the Genera of the Melectini of the Western Hemisphere

1. Wings with two submarginal cells; metasoma densely and uniformly covered with appressed, cinereous pubescence *Brachymelecta*
 - Wings with three submarginal cells; metasoma all black with erect hair or with patches of appressed hair producing a pattern of pale spots or bands 2
- 2(1). Marginal cell scarcely longer than stigma (Fig. 117-3b); maxillary palpus one- to three-segmented; flagellum of male greatly thickened, median segments thus more than twice as wide as long (Fig. 117-4); pygidial plate of male present; arolia absent *Zacosmia*
 - Marginal cell much longer than stigma (Fig. 117-3a); maxillary palpus four- to six-segmented; flagellum of male not thickened, median segments at most twice as broad as long; pygidial plate of male usually absent; arolia present 3
- 3(2). Inner ramus of claws of middle and posterior legs broad, vertically expanded, lobelike although subtruncate or pointed (Fig. 117-6d); T1 without or almost without long hair similar to that of thorax *Xeromelecta*
 - Inner ramus of claws of middle and posterior legs pointed, shaped somewhat like outer ramus (Fig. 117-6b) (does not hold for species of the Eastern Hemisphere); T1 with long hair like that of thorax (except in subgenus *Melectomimus*) *Melecta*

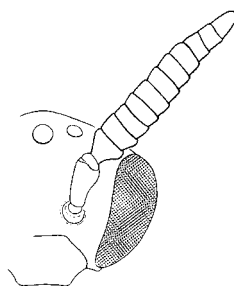


Figure 117-4. Antenna of *Zacosmia maculata* (Cresson), male. From Michener, McGinley, and Danforth, 1994.

Key to the Genera of the Melectini of the Eastern Hemisphere

1. Scutellum flat or nearly so, produced posteriorly over metanotum, propodeum, and, in some positions, base of T1, as sharply margined plate, bidentate with broad V- or U-shaped emargination between teeth, and posterior part of scutellar surface on underside of plate, facing downward; body with areas of appressed plumose hairs forming white, blue, or green spots or broken bands (arolia absent; maxillary palpus absent or minute, zero- to four-segmented) *Thyreus*
 - Scutellum convex, biconvex, bituberculate, or bispinose, surface curving downward posteriorly, and posterior part of scutellar surface thus declivous, facing posteriorly; body with or without areas of appressed plumose hairs, but if present, then these hairs white, not at all bluish or greenish 2
- 2(1). Marginal cell longer than distance from its apex to wing tip; body without spots of white pubescence, metasomal pubescence brown, orange, or yellowish (oriental) *Tetralonioidella*
 - Marginal cell equal to or shorter than distance from its apex to wing tip; body commonly with spots of white, appressed pubescence, metasomal pubescence entirely black or with such white spots, or pale and forming apical fasciae on terga 3
- 3(2). Submarginal cells two; body without patches of appressed white hair; metasomal terga with apical white fasciae; first flagellar segment over 1.5 times as long as broad and about twice as long as second segment (China) *Sinomelecta*
 - Submarginal cells three; body usually with patches of appressed white hair and without pale apical tergal fasciae (but *Melecta oreina* Baker agrees with *Sinomelecta* in these features of vestiture); first flagellar segment less than 1.5 times as long as broad and less than twice as long as second segment 4
- 4(3). T1 with dorsal surface longer than to scarcely shorter than T2 in normal position; arolia absent or nearly so 5
 - T1 with dorsal surface distinctly shorter than T2 in normal position; arolia present (palearctic) *Melecta*
- 5(4). Marginal cell exceeding third submarginal cell and only slightly shorter than distance from its apex to wing tip; apex of labrum with median emargination (Africa) *Afromelecta*
 - Marginal cell not or scarcely extending beyond third submarginal cell and distinctly shorter than distance

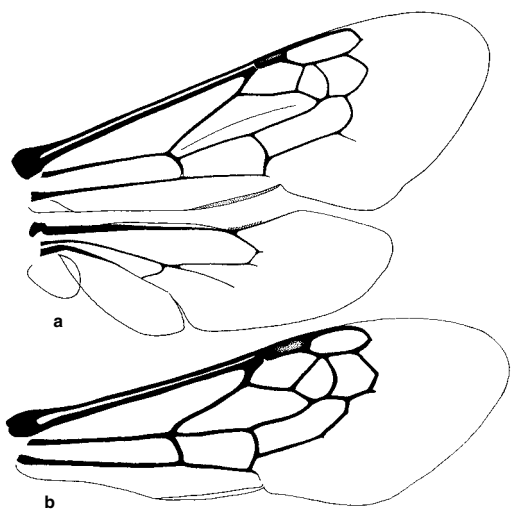
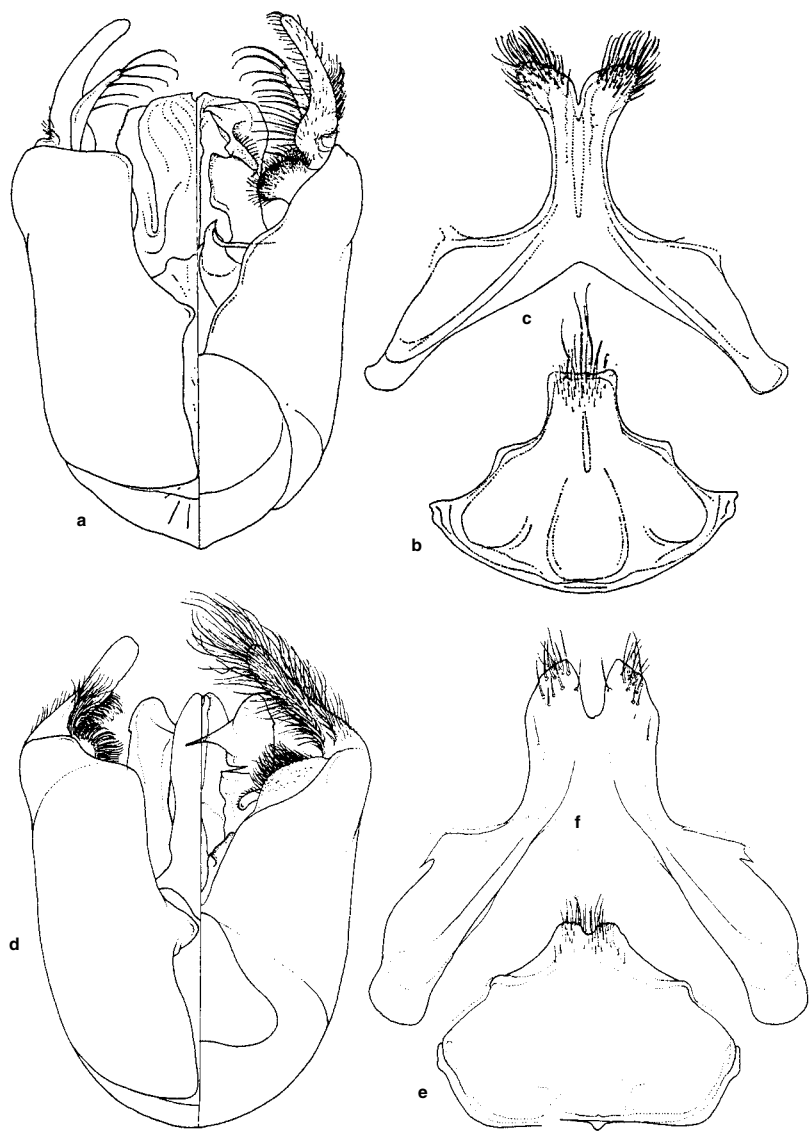


Figure 117-3. Wings of Melectini. **a**, *Xeromelecta* (*Melectomorpha*) *californica* (Cresson), see also Figure 83-1a; **b**, Forewing of *Zacosmia maculata* (Cresson).



from its apex to wing tip; apical margin of labrum gently convex (Palearctic Asia and North Africa)
..... *Thyreomelecta*

Genus *Afromelecta* Liefstinck

This is a *Melecta*-like genus from sub-Saharan Africa. The scutellar spines are strongly lateral in position. The marginal cell exceeds the third submarginal cell and is only slightly shorter than the distance from its apex to the wing tip. The general appearance and areas of white appressed pubescence on the metasoma are as in *M. (Paracrocisa)* or even *Xeromelecta (Melectomorpha)*. Body length is 13 to 16 mm. Male genitalia and other structures were illustrated by Liefstinck (1972); see also Figure 117-5a.

Key to the Subgenera of *Afromelecta*

1. Maxillary palpus six-segmented; scutellar spines as long as middorsal length of scutellum *A. (Acanthomelecta)*

Figure 117-5. Male genitalia (dorsal views on the left side), S8, and S7 of Melectini. **a-c**, *Afromelecta (Acanthomelecta) bicuspis* (Stadelmann); **d-f**, *Melecta (Melecta) fumipennis* Liefstinck. From Liefstinck, 1972, 1980.

— . Maxillary palpus minute, one- to two-segmented; scutellar spines at most half as long as middorsal length of scutellum *A. (Afromelecta s. str.)*

***Afromelecta* / Subgenus *Acanthomelecta* Liefstinck**

Acanthomelecta Liefstinck, 1972: 316. Type species: *Crocisa bicuspis* Stadelmann, 1898, by original designation. [New status.]

The six-segmented maxillary palpi are strikingly different from the short palpi of *Afromelecta s. str.*, but variation within taxa of Melectini is often considerable. The dorsal branch of the male gonostylus in *Acanthomelecta* is

slender, pointed, and sparsely haired (Fig. 117-5a), in contrast to the robust, densely hairy structure in *Afrolelecta* s. str.; see Liefstinck (1972).

■ *Acanthomelecta* occurs in Tanzania. The only species is *Afrolelecta bicuspis* (Stadelmann), which was fully described and its genitalia and hidden sterna illustrated by Liefstinck (1972); see also Figure 117-5a-c.

Afrolelecta / Subgenus *Afrolelecta* Liefstinck s. str.

Afrolelecta Liefstinck, 1972: 309. Type species: *Crocisa fulvo-hirta* Cameron, 1905, by original designation.

The contrast with *Acanthomelecta* is indicated in the text for that subgenus. The maxillary palpus of *Afrolelecta* s. str. is no longer than the two apical segments of the labial palpus taken together. Unlike better known taxa, the marginal cell extends well beyond the third submarginal cell.

■ *Afrolelecta* s. str. occurs from Cape Province and Natal, South Africa, north to Kenya and Ethiopia. Liefstinck (1972) revised the subgenus, and Eardley (1991c) gave a key to the two named species.

Genus *Brachymelecta* Linsley

Brachymelecta Linsley, 1939a: 458. Type species: *Melecta mucida* Cresson, 1879, by original designation.

This genus contains a small anthophoriform species (9 mm in body length) lacking all indication of the spots or broken bands of appressed pale metasomal pubescence found in most Melectini. Instead the metasoma is uniformly covered with short, appressed, pale hair. Unlike that of the similarly small *Zacasmia*, the male flagellum is slender, the first segment cylindrical and scarcely longer than the second, and the pygidial plate of the male is absent. The marginal cell, rounded at the apex, is short, about attaining the apex of the last (second) submarginal cell. The male genitalia and hidden sterna have never been dissected and are therefore unknown.

■ *Brachymelecta* is known from a single male specimen collected before 1878 in "Nevada."

Genus *Melecta* Latreille

This large holarctic genus includes some rather diverse forms, some of which have been given generic status by Popov (1955c) and Liefstinck (1972). These are small, divergent groups that seem likely to be derived from among the large mass of *Melecta*, making the latter paraphyletic. In the absence of a phylogenetic analysis, however, this interpretation is not well founded, for they are clearly so similar to *Melecta* that differentiating them at the generic level is not easily justified, given the nature of most apoid genera. The problem is illustrated by Liefstinck's (1972) "descriptive key," which separates *Eupavlovskia*, *Paracrocisa*, and *Pseudomelecta* from *Melecta* at the generic level. For very few characters is the state of one taxon matched by an alternative in others; rather, the combination of characters of one taxon differs from combinations or from variability found in others. I have elected to recognize the taxa listed below as subgenera.

Melecta consists of robust, anthophoriform species. These bees are black, frequently with patches of appressed

white hairs on the metasomal terga, and usually with long hair like that of the thorax on T1, at least laterally.

Key to the Subgenera of *Melecta*

1. S3 to S5 (sometimes also S2 and S6) of male with subapical fringes of strong, backward-directed, black bristles often forming dense brushes; T1 without long, erect pale hair either basally or laterally (middle and hind tarsal claws with inner rami shorter and broader than outer, often subtruncate)..... 2
- S2 to S6 of male without subapical brushes of black, posteriorly directed bristles, although often with abundant subapical hairs; T1 usually with long, erect pale hair, at least basolaterally 3
- 2(1). Marginal cell short, 2.2 to 3.0 times as long as broad; hind tibia of male unmodified; inner hind tibial spur of male straight or gently curved, not undulate, little if any longer than outer spur (palearctic) *M. (Pseudomelecta)*
- Marginal cell 3.3 to 4.0 times as long as broad; hind tibia of male expanded toward apex with spiculate ventroapical process extending laterally beyond bases of spurs; inner hind tibial spur of male much longer than outer, gently curved in different directions, thus weakly undulate (palearctic) *M. (Paracrocisa)*
- 3(1). Hind tibia of male expanded toward apex with strong ventroapical process extending laterally beyond bases of spurs; inner hind tibial spur of male much longer than outer, gently curved in different directions so as to be weakly undulate; hind basitarsus of male broadened distally, widest about two-thirds of distance from base to apex; S7 of male with disc slender, over twice as long as broad (palearctic)..... *M. (Eupavlovskia)*
- Hind tibia of male not or weakly expanded apically; inner hind tibial spur of male usually not modified [but in *M. albifrons* (Forster) and its relatives modified somewhat as in *Eupavlovskia*]; hind basitarsus less broadened [although somewhat so in group of *M. albifrons* (Forster)]; S7 of male with disc ordinarily less than twice as long as broad, often little longer than broad 4
- 4(3). Male flagellar segments about 1.5 times as long as broad; pygidial plate of female broadly triangular, occupying much of distal part of T6; metasoma without patches of white appressed hairs; T1 without long hairs like those of thorax (nearctic)..... *M. (Melectomimus)*
- Male flagellar segments mostly little longer than broad, often broader than long; pygidial plate of female narrowed apically, nearly parallel-sided to spatulate (but in *M. megaera* Liefstinck and *aegyptiaca* Radoszkowski about as in *Melectomimus*); metasoma usually with patches of appressed white pubescence; T1 usually with long pale hairs like those of thorax, often especially well developed laterally (holartic)..... *M. (Melecta* s. str.)

Melecta / Subgenus *Eupavlovskia* Popov

Eupavlovskia Popov, 1955c: 330. Type species: *Melecta funeraia* Smith, 1854, by original designation.

This subgenus consists of robust species 12.5 to 16.0 mm long with a densely hairy thorax. The metasomal terga usually have lateral patches of white appressed hair. The scutellum overhangs the metanotum and bears two straight, divergent spines about two-thirds as long as the

Asia, including the islands of Taiwan, the Philippines, and Indonesia, eastward to the Solomon Islands and southward in Australia as far as the state of Victoria and central Western Australia. In the palearctic and Indo-Australian areas a total of 83 species are recognized, after revision and elimination of many synonyms and subspecies. For sub-Saharan Africa nearly 40 species have been recognized, after revision. Revisions are by Lieftinck (1958, 1959, 1962 for Indo-Australian species, 1968 for palearctic species), Vergés (1967, for Spanish species), and Eardley (1991c, for sub-Saharan species). Meyer (1921) listed described species and reproduced descriptions.

Genus *Xeromelecta* Linsley

Xeromelecta is an American genus closely related to *Melecta*, although the body is more slender than that of most species of *Melecta*. The body length is 8 to 16 mm. As in *M. (Pseudomelecta)* and *Paracrocisa*, the integument of much of the scutum and scutellum is clearly exposed, with only short hairs or rather sparse hairs. This sparsity of pubescence is in contrast to that of most *Melecta* species, as well as *Tetralonioidella*, in which the thoracic hair is long and rather dense, more or less completely hiding the scutellar spines even when they are long. *Xeromelecta* also differs from most *Melecta*, although not from the subgenera *Pseudomelecta*, *Paracrocisa*, and *Melectomimus*, in its lack of long hair like that of the thorax on T1 (Fig. 117-2). Such hair is especially well developed at the sides of T1 in most Old World *Melecta* (*Melecta*); in most American species it extends across T1 from side to side. As the genera are here understood, *Xeromelecta* differs from *Melecta* in the absence of a dorsobasal lobe or process of the male gonostylus [not verified for *Xeromelecta* (*Nesomelecta*)]. Except for *X. (Xeromelecta) larreae* (Cockerell), *Xeromelecta* differs from *Melecta* in its shorter maxillary palpi, four- or five-segmented in *X. (Melectomorpha)* and much shortened, three-segmented or possibly sometimes two-segmented in *X. (Nesomelecta)*. The male genitalia and hidden sterna were illustrated by Mitchell (1962). The broad inner ramus of the claws of the middle and hind legs (see the key to North American genera above and Figs. 28-5, 117-6c, d) is a common feature in this genus, found for some reason in many other groups of cleptoparasitic bees.

Although *Xeromelecta* resembles *Melecta* (*Pseudomelecta*) in some characters, it differs in having a longer marginal cell, and unmodified hind legs in the male, and in lacking brushes of black bristles on the male metasomal sterna; see the key to the subgenera of *Melecta*. Except for the marginal cell, the same characters differentiate it from the subgenus *Paracrocisa*.

Xeromelecta was revised by Linsley (1939a) and Hurd and Linsley (1951).

The subgeneric names *Xeromelecta* and *Melectomorpha* were published simultaneously. The precedence of *Xeromelecta* was established by Hurd and Linsley (1951), and the genus name is *Xeromelecta*.

Key to the Subgenera of *Xeromelecta*

1. Scutellum biconvex, with only the faintest suggestion of

a posterior tooth on each convexity; maxillary palpus more than half as long as first segment of labial palpus, six-segmented; body without patches of appressed pale pubescence; wings blackish..... *X. (Xeromelecta s. str.)*

— Scutellum convex, with two distinct, posteriorly directed teeth or spines; maxillary palpus less than half as long as first segment of labial palpus, three- to five-segmented (possibly two-segmented); body with patches of appressed, pale pubescence; wings rather clear with apical dusky areas 2

2(1). Scutellar lobes each ending in acute spine or tooth; maxillary palpus three-segmented (possibly sometimes two-segmented), less than one-fourth as long as first segment of labial palpus (Antilles) *X. (Nesomelecta)*

— Scutellar lobes each ending in approximately right-angular tooth; maxillary palpus four- to five-segmented, little less than one-half as long as first segment of labial palpus *X. (Melectomorpha)*

Xeromelecta / Subgenus *Melectomorpha* Linsley

Melecta (*Melectomorpha*) Linsley, 1939a: 451. Type species:

Melecta californica Cresson, 1878, by original designation.

This subgenus includes the commonest American melectines. They have patches of appressed white or rarely pale brownish pubescence, forming medially broken bands on the metasomal terga.

■ *Melectomorpha* occurs from British Columbia, Canada, to California, east to Minnesota, Wisconsin, Illinois, and Texas, USA, and south to Baja California, Sonora, Zacatecas, and Puebla, Mexico. There are two species.

Xeromelecta / Subgenus *Nesomelecta* Michener

Melecta (*Nesomelecta*) Michener, 1948b: 15. Type species:

Melecta haitensis Michener, 1948, by original designation.

Nesomelecta resembles *Melectomorpha* in its areas of white appressed pubescence, although the pattern is more elaborate on the head and thorax (Michener, 1988; Fig. 117-2) and in one species the pale tergal bands are not broken medially.

■ This subgenus is found on Puerto Rico, Hispaniola, and Cuba. The three species were differentiated by Michener (1988).

This is the only tropical American group of Melectini. The Puerto Rican species has been known as *Xeromelecta pantalon* (Dewitz), but according to D. B. Baker (in litt., 1992) a senior synonym is *Nomada tibialis* Fabricius, 1793, hence *X. tibialis* (Fabricius).

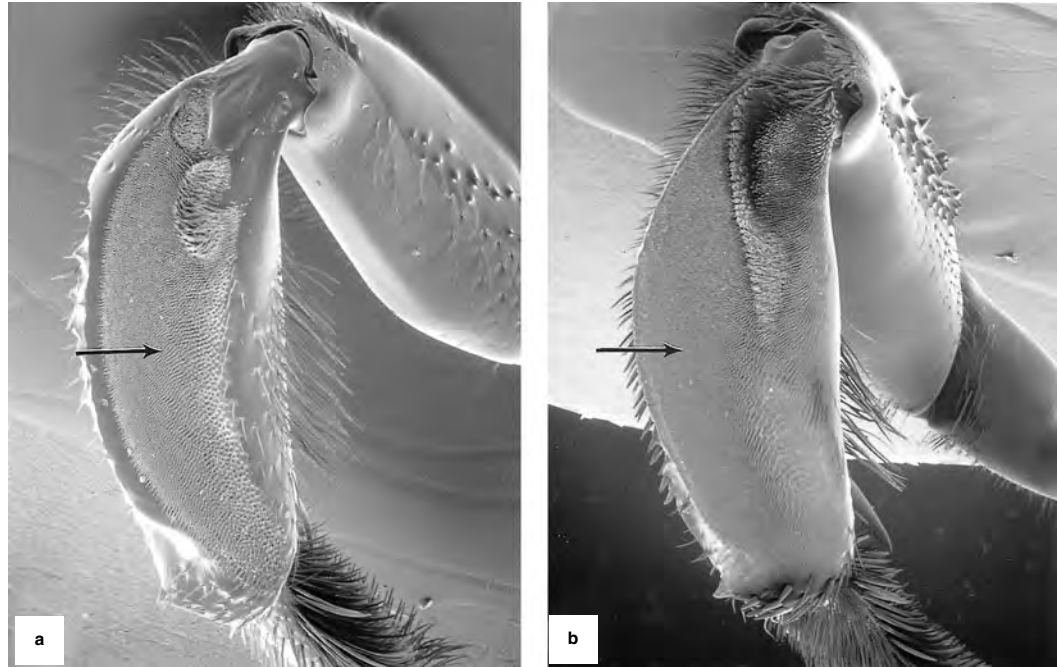
Xeromelecta / Subgenus *Xeromelecta* Linsley s. str.

Melecta (*Xeromelecta*) Linsley, 1939a: 450. Type species:

Bombomelecta larreae Cockerell, 1900, by original designation.

This subgenus contains a slender species, black-haired except for fulvous hairs on the thoracic dorsum.

■ *Xeromelecta* occurs in xeric areas from California to New Mexico, USA. The single species is *Xeromelecta larreae* (Cockerell).



arable in general appearance also: *Exaerete* species are large, all green (rarely all purple), not conspicuously hairy; *Aglae* is slender, blue; and *Euglossa* is small to moderate-sized and usually brilliantly metallic (but there are a few dull-colored species). *Eufriesea* and *Eulaema*, similar to one another superficially, are large, robust, and conspicuously hairy, except that some species of *Eufriesea* are less hairy and are brilliantly metallic, resembling *Euglossa*. There are cases of probable Müllerian mimicry involving *Eufriesea* and *Eulaema* (Dressler, 1979), and close examination may be needed to recognize the usually rarer *Eufriesea*.

Key to the Genera of the Euglossini
(Modified from Kimsey, 1987)

- 1. Hind tibia three or more times as long as broad in both sexes (Fig. 118-4c); female hind tibia somewhat inflated, without corbícula; cleptoparasitic species 2
- Hind tibia twice as long as broad or less in females (Fig. 118-3) and most males (Fig. 118-4a, b); female hind tibia flat and shieldlike with enormous corbícula (Fig. 118-3); nonparasitic species 3
- 2(1). Hind femur swollen and usually denticulate ventrally (Fig. 118-4c); hind tibia curved and expanded apically; scutellum dorsally convex, with sublateral tubercle or welt (Fig. 118-4d) *Exaerete*
- Hind femur slender and unmodified; hind tibia straight and apically narrowed; scutellum flat *Aglae*
- 3(1). Labrum whitish with two large, dark oval spots; male hind tibial slit short, not reaching apical margin of tibia, and basally curved (Fig. 118-4b); male middle tibia with two, or less commonly one or three, small felty patches in basal end of large patch (Fig. 118-9a); female usually with median, black scutellar tuft *Euglossa*
- Labrum dark in color; male hind tibial slit long, reach-

Figure 118-9. Middle tibiae of males of Euglossini, with small felt patches at bases of large felt areas marked by arrows. **a**, *Euglossa cordata* (Linnaeus); **b**, *Eufriesea concava* (Friese). From Michener, McGinley, and Danforth, 1994.

- ing apical margin, broad and not curved basally (Fig. 118-4a); male middle tibia with one relatively large basal felty patch adjacent to large patch (Fig. 118-9b); female with (*Eulaema*) or without (*Eufriesea*) scutellar tuft 4
- 4(3). Labial palpus four-segmented; face metallic without white markings; clypeal ridging various, usually without single medial ridge *Eufriesea*
- Labial palpus two-segmented; face black or brown, often with white markings; clypeus with single strong medial ridge *Eulaema*

Genus *Aglae* Lepeletier and Serville

Aglae Lepeletier and Serville, 1825: 105. Type species: *Aglae coerulea* Lepeletier and Serville, 1825, monobasic.
Aglaa Schulz, 1906: 258, unjustified emendation of *Aglae* Lepeletier and Serville, 1825.

This is a monotypic genus of relatively slender, steel-blue bees 20 to 28 mm in length, reported to be cleptoparasites of *Eulaema*. It is the most distinctive euglossine genus, as indicated by Kimsey (1982), who considered it the sister group of all the other genera, and by Kimsey (1987), who documents its many autapomorphies. In the latter work she regards it as the sister group of *Eulaema*, but see my comments, in the account of the Tribe Euglossini, on relationships among the genera.

■ *Aglae* occurs in the moist forests from Bolivia to Colombia with a doubtful report for eastern Panama. There is only one species, *A. coerulea* Lepeletier and Serville.

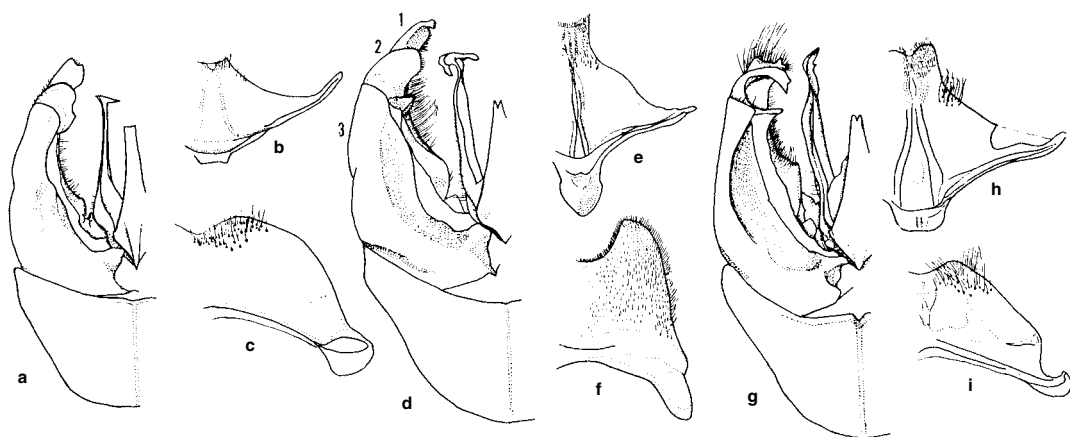


Figure 119-8. A sample of genitalic and sternal variation in male *Bombus*; dorsal views of genitalia and ventral views of S8 and S7. **a-c**, *B. (Melanobombus) lapidarius* (Linnaeus); **d-f**, *B. (Frater-nobombus) frater-nobombus* (Smith); **g-i**, *B. (Rubicundobombus) rubicundus* Smith. See also Figures 117-4b and 117-9c, d. (1, volsella; 2, gonostylus; 3, gonocoxite.) From Ito, 1985.

North America); LaBerge and Webb, 1962 (Nebraska, USA); Mitchell, 1962 (eastern North America); Moure and Sakagami, 1962 (Brazil); Medlar and Carney, 1963 (Wisconsin, USA); Milliron, 1970-1973; Thorp, Horning, and Dunning, 1983 (California, USA); Laboulge, 1990 (Mesoamerica); Lavery and Harder, 1998 (eastern Canada); Rasmussen, 2003 (Peru); Abrahamovich and Diaz, 2002 (neotropics); Abrahamovich, Diaz, and Lucia, 2005 (Argentina).

EUROPE: Friese and Wagner, 1910 (Germany); Krüger, 1917, 1920 (Central Europe); Richards, 1927 (Britain); Pittioni, 1937 (east Tirol), 1938, 1939a (Balkans); Kru-seman, 1947 (Netherlands); Knechtel, 1955 (Romania); May, 1959 (Czechoslovakia); Yarrow *in* Free and Butler, 1959 (Britain); Elfving, 1960 (Finland); Hammer and Holm, 1970 (Denmark); Løken, 1973, 1984, 1985 (Scandanavia); Alford, 1975 (Britain); Delmas, 1976 (France); Rasmont, 1983 (west palearctic region); D'Albore, 1986 (Italy); Prýs-Jones and Corbet, 1987 (Britain); Hagen, 1990 (Central Europe); Rasmont and Adamski, 1995 (Corsica).

ASIA: Frison, 1928 (Philippines), 1930 (Indonesia); Maa, 1948 (*Psithyrus* of eastern Asia); Özbek, 1983 (eastern Turkey); Williams, 1991 (Kashmir); Starr, 1992 (Taiwan); Pawlikowski, 1996, 1999 (Poland); Özbek, a series on the bumble bee fauna of Turkey, 1997, 1998, 2000, 2002.

Of course, keys to species of Bombini are also found in the various regional works on bees or on Hymenoptera, such as are listed in Section 30.

A few "couplets" in the keys that follow offer three alternatives instead of two. These are "couplet" 25 in the key to males and "couplets" 21 and 22 in the key to females; each of these is marked "triplet" to assure proper use. Given the intricacy of Richards' (1968) key on which the key below is based, I have not risked introducing errors by converting these items to a dichotomous format. *Exilobombus* is omitted from the key to males.

Key to the Subgenera of *Bombus* (Males) (Modified from Richards, 1968, with additions based on Williams, 1991)

1. Volsella weakly or strongly sclerotized, inner corner near midpoint of its length, without any inwardly directed

- hooks, distal half of volsella thus usually nearly triangular (Fig. 119-9d); gonostylus without an inner basal process, or, *if* process present, then associated with many long, branched hairs; apex of penis valve nearly straight in dorsal view 2
- Volsella always strongly sclerotized, inner corner usually much closer to apex than to base, forming an inner apical corner often bearing two inwardly directed hooks or a single inwardly directed process; gonostylus usually with distinct inner basal process or shelf, not associated with long hairs; apex of penis valve much modified, often curved strongly toward midline as sickle-shaped hook, otherwise curved outward in some individuals, but *if* nearly straight in dorsal aspect, then volsella with pronounced inner hooks 3
- 2(1). Volsella weakly sclerotized, yellowish in color; gonostylus with pronounced inner basal process associated with many long, branched hairs (Fig. 119-9d); apex of penis valve, as defined by an outer lateral ridge, accounting for less than one-fourth of total length of penis valve, not strongly curved but shaped like slender arrowhead in lateral aspect (holarctic) *B. (Psithyrus)*
- Volsella strongly sclerotized, dark brown in color; gonostylus without inner basal process or hairs; apex of penis valve, as defined by an outer lateral toothed ridge, accounting for nearly one-half of total length, ventrally curved and sabre-shaped in lateral aspect (Eurasian mountains) *B. (Mendacibombus)*
- 3(1). Apex of mandible with two preapical teeth (palearctic) *B. (Alpigenobombus)*
- Apex of mandible with one preapical tooth 4
- 4(3). Penis valve narrow and pointed; ocellular distance equal to 3.0 to 3.5 ocellar diameters; hind tibia bare on disc; second flagellar segment 1.1 to 1.4 times as long as first (Himalayas to Southeast Asia) *B. (Orientalibombus)*
- If penis valve narrow and pointed, then lateral ocellus

- much closer to eye, *or* hind tibia hairy, *or*, if with a small, bare disc, then second flagellar segment about half as long as first 5
- 5(4). Penis valve curved outward into a rounded, recurved hook; second and third flagellar segments 1.2 and 1.5 times as long as first segment, and middle and hind basitarsi without long fringes (paleartic) *B. (Kallobombus)*
- Penis valve not curved outward into a recurved hook; second and third flagellar segments relatively short (second shorter than first) except in a few species with short basitarsal fringes 6
- 6(5). Second and third flagellar segments 0.36 to 0.56 and 0.48 to 0.78 times as long as first segment; penis valve narrow and pointed, or finger-shaped, only in one group curved inward with flange on outside of curve; ocellular distance one ocellar diameter or less 7
- Second and third flagellar segments relatively longer and penis valve usually of a different shape, particularly if antenna approaches above description; ocellular distance usually more than one ocellar diameter (although sometimes less, e.g., in *Brachycephalibombus*) 9
- 7(6). Penis valve curved inward with small flange on outside of curve; hind basitarsus with short dorsal fringe (North America) *B. (Fraternobombus)*
- Penis valve pointed or finger-shaped; hind basitarsus with long dorsal fringe 8
- 8(7). Gonostylus V-shaped in section, formed of two plates set at an angle and joined at outer edges; S7 crescentic but with rounded-triangular median process; S8 crescentic, little produced, apex subtruncate; hind tibia with fringe of long hairs (Europe) *B. (Confusibombus)*
- Gonostylus not V-shaped in section, all angles rounded; S7 broadly triangular, apex feebly emarginate; S8 broadly triangular, apex deeply emarginate; hind tibia with fringe of very short hairs (North America) *B. (Bombias)*
- 9(6). Penis valve in form of wide sinuate vertical plate (holarctic) *B. (Bombus s. str.)*
- Penis valve of quite different form 10
- 10(9). Penis valve ending in strong, inwardly directed, recurved hook; middle basitarsus usually with short fringe 11
- Penis valve rarely ending in strong, inwardly directed, recurved hook, but *if* so, then middle basitarsus with long fringe 17
- 11(10). Ocellular distance less than one ocellar diameter; malar area shorter than second flagellar segment; sides of spatha strongly convergent posteriorly 12
- Ocellular distance greater than one ocellar diameter; malar area longer than second flagellar segment, as long as or longer than first flagellar segment; sides of spatha subparallel, little convergent posteriorly 14
- 12(11). S7 trapezoidal, apex broadly emarginate; S8 with apical process broadly emarginate; penis valve ending in broadened apex with acute point directed mesad (Mesoamerica) *B. (Brachycephalibombus)*
- S7 trapezoidal or crescentic, apex not or scarcely emarginate; S8 with apical process narrower, apex convex; penis valve ending in broadened apex with blunt or slender point 13
- 13(12). Penis valve ending in rounded hook, tip not acute; impression of gonocoxite wide but ill-defined; third flagellar segment shorter than first; S7 trapeziform, apex feebly emarginate; S8 subtriangular (North America) *B. (Separatobombus)*
- Penis valve ending in somewhat smaller hook, tip acute; impression of gonocoxite wide and well-defined; third flagellar segment longer than first; S7 subcrescentic; S8 with parallel-sided, tongue-like projection (California, Mexico) *B. (Crotchibombus)*
- 14(11). Gonostylus considerably longer than broad, inner side emarginate; impression of gonocoxite strong, sharp-edged; third flagellar segment clearly shorter than first (paleartic) *B. (Sibiricobombus)*
- Gonostylus not clearly longer than broad, inner side not emarginate; impression of gonocoxite feebly defined; third flagellar segment longer than first 15
- 15(14). Volsella scarcely projecting beyond gonostylus (more so in *Festivobombus*) (gonostylus small and rounded-triangular); ocellular distance at least three ocellar diameters; S8 with parallel-sided, tongue-like projection *B. (Pyrobombus, Festivobombus)*
- Volsella very long, projecting well beyond gonostylus; ocellular distance less than three ocellar diameters; S8 broadly subtriangular 16
- 16(15). Gonostylus transverse with inner side emarginate; hind basitarsus with short or long fringe; malar area not longer than first flagellar segment; ocellular distance one and three-fourths to two and one-fourth ocellar diameters (holarctic) *B. (Cullumanobombus)*
- Gonostylus S-shaped, inner end pointed, almost the whole of it lying inside inner margin of gonocoxite; hind basitarsus with short fringe; malar area longer than first flagellar segment; ocellular distance two and one-half ocellar diameters (Southeast Asia to Java and Taiwan) *B. (Rufipedibombus)*
- 17(10). Gonostylus almost as long as gonocoxite, attaining midline of genitalia, directed mesad at right angle to gonocoxite, without lobe or process; volsella produced as slender, hairy fingerlike apical projection almost as long as gonostylus (Mesoamerica) *B. (Dasybombus)*
- Gonostylus less than half as long as gonocoxite, not approaching midline of genitalia, and *if* directed mesad, then commonly with lobe or process; volsella without long, slender apical projection, but with tooth or lobe or apically pointed, not fingerlike 18
- 18(17). Middle and hind basitarsi with long fringes 19
- Middle and hind basitarsi with short fringes 25
- 19(18). Penis valve not curved inward or outward at apex, but with two external teeth, one of which is sometimes small; second flagellar segment not much shorter than first, third segment 1.25 times longer than first; malar area in most species distinctly longer than first flagellar segment (arctic and alpine, holarctic) *B. (Alpinobombus)*
- Penis valve sometimes curved inward at apex, never with more than one outer tooth; second flagellar segment not more than three-fourths as long as first, third segment not more than 1.1 times longer than first; malar area rarely longer than first flagellar segment 20
- 20(19). Volsella projecting far beyond gonostylus; malar area as long as first flagellar segment or a little longer 21
- Volsella projecting at most a moderate distance beyond gonostylus (gonostylus with rounded angles and an inner emargination); malar area usually shorter than first flagellar segment 22

- 21(20). Gonostylus completely fused with gonocoxite, produced into long acute process directed downward and backward; penis valve at apex with small pointed flange on inside and large pointed one on outside; S7 broadly trapezoidal; S8 with parallel-sided projection; gonocoxite with broad, sharp-edged impression; volsella twisted, its plane thus oblique distally, with dense short hairs at apex and on inner side; ocellular distance equal to three ocellar diameters (Himalayas) *B. (Pressibombus)*
- Gonostylus separate from gonocoxite, rounded-transverse with small, proximal inner process; penis valve with acute apex and acute inner flange (half-arrowhead-shaped); S7 crescentic; S8 broadly triangular; gonocoxite narrow, without inner impression; volsella not twisted, with few hairs; ocellular distance variable, equal to one to three ocellar diameters (palearctic) *B. (Melanobombus)*
- 22(20). Third flagellar segment a little longer than first; impression of gonocoxite wide and deep 23
- Third flagellar segment distinctly shorter than first; impression of gonocoxite not more than half as wide as long 24
- 23(22). Penis valve curved inward at apex with serrate flange on outside; gonostylus markedly transverse, widening inward, inner edge emarginate; volsella with rounded-angular projection on inner edge, inner corner of apex with long curved hook; S7 crescentic; S8 with tongue-like projection the sides of which converge posteriorly; malar area hardly more than half as long as first flagellar segment; ocellular distance equal to less than one ocellar diameter (Central and South America) *B. (Robustobombus)*
- Penis valve slightly curved inward at apex and with small inner tooth; gonostylus rounded-quadrangular with large subcircular inner emargination; volsella wide, posterior end with a short hook, apex with dense tuft of relatively long bristles; S7 transverse with central one-fourth produced; S8 subtriangular; malar area a little shorter than first flagellar segment; ocellular distance equal to 1.5 ocellar diameters (western South America) *B. (Rubicundobombus)*
- 24(22). Gonocoxite with strong impressions; volsella short, apex with small posteriorly directed hook (outer and ventral sides with dense short hairs); S7 transverse, apex biemarginate; S8 with long, parallel-sided midapical process; malar area slightly longer than first flagellar segment; ocellular distance equal to two ocellar diameters (South America) *B. (Coccineobombus)*
- Gonocoxite with small, ill-defined depressions; volsella moderately long, apex with small hooklike projection at inner end; S7 crescentic, weakly emarginate; S8 subtriangular; malar area three-fourths as long as first flagellar segment; ocellular distance less than two ocellar diameters (South America) *B. (Funebriobombus)*
- 25(18) [triplet]. Volsella long and narrow, produced inward at apex as process shaped like toe and heel; penis valve narrow, outer side distally strongly serrate [a character otherwise seen only in *B. (Thoracobombus) pascuorum* (Scopoli)], no tooth beneath; gonostylus forming a large, elongate, vertical, curved plate on inner side two-thirds enclosing an oval space, anterior lower corner produced upward as sharp spike; malar area as long as combined lengths of pedicel and first and second flagellar segments (palearctic) *B. (Megabombus)*
- Volsella long and narrow, produced inward at apex as spurlike process with several points; penis valve narrow, sinuate, with apical outer flange forming a small tooth at its proximal end, emarginate beneath but not forming a real tooth; gonostylus narrow and transverse, posterior inner corner produced into thumb-shaped process, anterior inner corner with long curved hook extending as far back as posterior margin; malar area as long as pedicel and first flagellar segment combined (Asia) *B. (Diversobombus)*
- Differing in character combinations from both *Megabombus* and *Diversobombus*; volsella at apex produced at most into a small hook or serrate, rounded lobe (in *Senexibombus* somewhat similar to *Megabombus* but penis valve serrate only on recurved distal quarter) 26
- 26(25). Length of third flagellar segment 1.5 to 1.9 times length of first segment 27
- Length of third flagellar segment 1.0 to 1.3 times length of first segment 29
- 27(26). Second flagellar segment less than 0.7 times as long as first; spatha very narrow (Malaysia to Philippines) *B. (Senexibombus)*
- Second flagellar segment as long as or longer than first segment; spatha very broad with convergent sides 28
- 28(27). Volsella very wide, not extending far beyond outer part of gonostylus, on inner side proximally with very long acute hook, inner edge behind hook straight-truncate, somewhat serrate, with long bristles; gonostylus sclerotized, with elongate outer lobe set in oblique plane, on inner side at a lower level produced into two very long acute processes directed obliquely forward and backward respectively; penis valve with feebly serrate outer flange apically, with a tooth beneath; malar area about as long as first and second flagellar segments combined (metasoma very closely punctured) (Asia) *B. (Tricornibombus)*
- Volsella very long, broadly digitiform, inner side near center produced into strong, parallel-sided process with expanded end with sharp angles; gonostylus with large, outer part pale and submembranous, generally transverse but posteriorly produced on inside into rounded lobe, before this deeply emarginate and then produced into a large subcircular lobe (mainly in a vertical plane) with its dorsal edge serrate and the whole attached to gonostylus by narrow stalk; penis valve narrow, simply pointed at apex, not toothed beneath; malar area as long as second flagellar segment (palearctic) *B. (Laesobombus)*
- 29(26). Penis valve at end somewhat hooked inward, with two large teeth on outer side, midpoint beneath with bifid or trifid tooth (holarctic) *B. (Subterraneobombus)*
- Penis valve at end curved or hooked outward, or pointed, not toothed, or in one species serrate 30
- 30(29). Malar area normally a little longer than combined lengths of first and second flagellar segments; penis valve curved outward at end [except in *B. (Fervidobombus) brevivillus* Franklin], this end-piece serrate or truncate, with central tooth beneath; gonocoxite with rather well-defined inner impressions 31
- Malar area a little shorter than combined lengths of first

- and second flagellar segments; penis valve with small, pointed external lobe, or pointed, or serrate; gonocoxite without distinct inner impressions 32
- 31(30). Mandible without beard; gonostylus on inside produced obliquely downward and backward as twisted anterior plate; volsella with apex produced on inside to small lobe with small tooth; volsellar region with no conspicuous bristles (palearctic) *B. (Rhodobombus)*
- . Mandible with beard; gonostylus on inside usually produced into a vertical platelike anterior lamella and a wider, more dorsal, rounded process (details vary considerably among species); volsella with apex produced on inside to small hook or angular process; volsellar region with dense bristles (Western Hemisphere) *B. (Fervidobombus)*
- 32(30). Volsella wide but not very long, apex more or less pointed, center of inner edge produced into spike or at least narrow, truncate process, pubescence widespread but not dense; penis valve variable but with central tooth beneath (palearctic) *B. (Thoracobombus)*
- . Volsella long and broad, finger-shaped, center of inner edge produced as wide lobe defined at each end by small tooth or else simple, inner and often ventral surface with dense, quite long pubescence; penis valve simple or emarginate beneath, with no distinct tooth 33
- 33(32). Volsella with center of inner edge produced into wide lobe defined at each end by small tooth; penis valve simply pointed; fringe of hind tibia long (palearctic) *B. (Mucidobombus)*
- . Volsella with inner edge straight or feebly concave, with no lobe or process; penis valve at end hardly acute, with slight outer, feebly serrate flange; fringe of hind tibia short (palearctic) *B. (Eversmannibombus)*

Key to the Subgenera of *Bombus* (Females)
(Modified from Richards, 1968, with additions based on Williams, 1991. This key is based primarily on gynes and may not work for some workers.)

1. Hind tibia convex and hairy on outer surface, corbicula thus absent (Fig. 119-9b), and rastellum absent; hind basitarsus without auricle; apex of metasoma curved downward; S6 with lateral carina; worker caste absent (holartic) *B. (Psithyrus)*
- . Hind tibia with corbicula (Fig. 119-9a) and rastellum; hind basitarsus with strong auricle; apex of metasoma not curved downward; S6 without carinae; worker caste usually present 2
- 2(1). Apex of mandible with six teeth; hind basitarsus proximally near ventral margin often with a number of bristles almost as long as corbicular bristles (palearctic) *B. (Alpigenobombus)*
- . Apex of mandible with one or two small dorsal teeth and sometimes a small preapical notch setting off an apical tooth; hind basitarsus with no bristles as long as corbicular bristles (except in *Mendacibombus* and *Pressibombus*) 3
- 3(2). Middle basitarsus with posterior apical angle obtuse, more or less rounded [except for some *Sibiricobombus*, most of which have ocellular distance equal to about two ocellar diameters and differ further from *Subterraneobombus*, which they often most resemble, in having whole surface of auricle of hind basitarsus densely hairy; *B. (Melanobombus) tanguticus* Morawitz has apical angle of middle basitarsus produced but has a strong, bare subcircular boss on T6 such as is not found in alternative] 4
- . Middle basitarsus with posterior apical angle right-angular or acute and usually coarsely bristled [see exceptions in first alternative of this couplet] 22
- 4(3). Outer surface of hind tibia densely reticulate, dull, some long bristles arising from upper half of corbicular disc; malar area very elongate; first flagellar segment fully three times as long as median width (Eurasian mountains) *B. (Mendacibombus)*
- . Outer surface of hind tibia less coarsely reticulate, rarely if ever so dull, long bristles confined to corbicular margins except very near base, or, if bristles more widespread in corbicula, then malar area transverse; first flagellar segment nearly always shorter 5
- 5(4). Malar area longer than combined lengths of pedicel and first flagellar segment; first flagellar segment about four times as long as broad; middle basitarsus with posterior apical angle somewhat produced (some species difficult to separate from some *Subterraneobombus*; see couplet 3) (palearctic) *B. (Sibiricobombus)* (in part)
- . Malar area clearly shorter, or, if not, then first flagellar segment about 2.5 times as long as broad; middle basitarsus with posterior apical angle quite obtuse 6
- 6(5). Corbicular hairs unusually dense, tibial surface between them covered throughout with rather sparse but quite distinct, very short feathered hairs (southeast Asia to Java and Taiwan) *B. (Rufipedibombus)*
- . Corbicular hairs less dense, tibial surface between them without short feathered hairs [except in a few *Melanobombus* (couplet 8)] 7
- 7(6). Frons with very large unpunctured areas, most of area for some distance in front of ocelli being unpunctured and only narrow band of punctures between ocelli and eyes; area immediately behind ocelli also unpunctured; ocellular distance equal to three ocellar diameters (Himalayas to Southeast Asia) *B. (Orientalibombus)*
- . Frons without large unpunctured area, especially in front of ocelli, or else densely punctured right up to ocelli posteriorly; ocelli closer to eyes 8
- 8(7). T6 with a bare, convex, more or less rounded boss not divided by furrow; hind tibia with dorsal apical inner corner not or rarely somewhat produced; hind basitarsus as a rule with unusually dense, short, feathery hairs (palearctic) *B. (Melanobombus)*
- . T6 without a bare, convex, rounded boss or with boss divided by furrow; hind tibia with dorsal apical inner corner more or less strongly, angularly produced [except in *Kallobombus* and a few *Pyrobombus*—e.g., *Bombus pratorum* (Linnaeus) and *atrocinctus* Smith]; hind basitarsus rarely so densely haired 9
- 9(8). Whole corbicular surface of hind tibia with scattered but quite numerous, short, unbranched hairs; frons crossed by wide transverse band of microscopic punctures across unpunctured area; T6 with raised boss (almost as in *Melanobombus*) divided by deep, well-defined furrow (South America) *B. (Coccineobombus)*
- . Hind tibia with at least a considerable distal corbicular

- area bare; frons without band of microscopic punctures across unpunctured area; T6 without deep, well-defined furrow 10
- 10(9). Malar area distinctly transverse; either a definite band of close punctures along inner margin of eye, *or* ocellular distance equal to about two ocellar diameters, *or* both 11
- Malar area variable, i.e., elongate, quadrate, or transverse (if distinctly transverse as in *Pyrobombus*, then without fine punctures along inner eye margin *and* ocellular distance equal to three ocellar diameters) 16
- 11(10). Ocellular distance equal to three ocellar diameters, *and* corbicular surface of hind tibia entirely bare and shining; mandible with strong notch above apical tooth; clypeus strongly punctured on almost whole surface (holarctic) *B. (Bombus s. str.)*
- Ocellular distance not more than two ocellar diameters, *or* proximal one-half or one-third of corbicular surface bristly and whole surface more or less strongly reticulate, *or* both; mandible with notch above apical tooth weak or absent; clypeus sometimes with some sparse, large punctures, but *if* punctures are close, then they are small 12
- 12(11). Hind tibia with corbicular surface bare (North and Central America) 13
- Hind tibia with proximal one-half or one-third of corbicular surface bristly (Central and South America) 15
- 13(12). Frons with rather strong, close punctures along inner margin of eye; clypeus elongate, impressions feeble, finely and closely punctured; labral furrow deep and wide, nearly as wide as length of first flagellar segment (North America) *B. (Separatobombus)*
- Frons rather sparsely punctured all around ocelli except for a densely punctured area immediately behind them, unpunctured areas large and ill-defined, without band of fine punctures near eye (although in *Crotchibombus* fine punctures may be seen, but not close to eye margin); clypeus short, impressions with coarse punctures; labral furrow deep and narrower 14
- 14(13). Malar area clearly shorter than first flagellar segment, which is less than twice length of second; clypeus more coarsely though shallowly punctured, impressions weaker; labral tubercle more convex but less angular, furrow deep and wider than length of first flagellar segment; corbicular hairs shorter than half tibial width and dense (North America) *B. (Fraternobombus)*
- Malar area clearly longer than first flagellar segment, which is nearly twice length of second; clypeus more finely punctured, impressions stronger; labral tubercle less raised but more angular at inner end, furrow deeper but much narrower than length of first flagellar segment; corbicular hairs mostly longer than half tibial width and less dense (California, Mexico) *B. (Crotchibombus)*
- 15(12). Frons rather closely punctured, with large but well-defined unpunctured areas and a band of fine punctures along inner margin of eye; ocellular distance equal to three ocellar diameters; ocelli a little in front of postocular tangent; clypeus swollen, with lower third flattened, with numerous, mostly rather large punctures and apical impressions; labral furrow narrow; hind basitarsus not unusually bristly (western South America) *B. (Rubicundobombus)*
- Frons with large unpunctured or very sparsely punctured area in front of and around ocellus, without especially defined unpunctured areas and without band of punctures along inner margin of eye; ocellular distance equal to two ocellar diameters; ocelli well in front of postocular tangent; clypeus strongly swollen, sometimes somewhat flattened ventrally, little or moderately punctured, apical impressions feeble; labral furrow wide or very wide; hind basitarsus with bristles on outer surface longer and more numerous than usual (Central and South America) *B. (Robustobombus)*
- 16(10). Malar area distinctly longer than broad, at least as long as combined lengths of pedicel and first flagellar segment, often as long as first and second flagellar segments taken together (arctic and alpine, holarctic) *B. (Alpinobombus)*
- Malar area transverse, quadrate or scarcely longer than broad, at most a little longer than first flagellar segment 17
- 17(16). Mandible with no notch above apical tooth but with ventral apical angle produced as small process (South America) *B. (Funebribombus)*
- Mandible sometimes with notch above apical tooth, ventral apical angle not produced as short process 18
- 18(17). Labral tubercles little raised and much rounded, furrow shallow and ill-defined; ocellular distance about 2.5 times ocellar diameter or less (ocelli well in front of postocular tangent); first flagellar segment as long as or slightly longer than combined lengths of second and third segments 19
- Labral tubercles more or less raised and flattened, inner ends more or less angled, furrow deeper and well-defined; lateral ocellus more widely separated from eye (except in some *Cullumanobombus*); first flagellar segment clearly shorter than combined lengths of second and third segments 20
- 19(18). Malar area a little longer than broad and a little longer than first flagellar segment; clypeus with wide flattened disc; frons mostly closely and rather finely punctured, unpunctured areas well-defined, a wide band of close fine punctures along inner margin of eye (Europe) *B. (Confusibombus)*
- Malar area roughly quadrate, about as long as first flagellar segment; clypeus long, strongly swollen; frons moderately strongly and closely punctured, unpunctured areas large and ill-defined, a narrow band of rather fine sculpture along inner margin of eye (North America) *B. (Bombias)*
- 20(18). Ocellular distance somewhat or distinctly less than three ocellar diameters; ocelli well in front of postocular tangent (holarctic) *B. (Cullumanobombus)*
- Ocellular distance equal to fully three ocellar diameters; ocelli scarcely in front of postocular tangent 21
- 21(20) [triplet]. Clypeus rather strongly and evenly punctured, impressions strong but not more closely punctured; frons rather closely punctured, unpunctured areas small and well-defined, a wide band of fine sculpture along inner margin of eye; mandible without preapical notch; hind basitarsus with sparse pubescence and no long bristles (paleartic) *B. (Kallobombus)*
- Clypeus, except impressions, largely unpunctured [more strongly and closely punctured in *B. lapponicus* (Fabri-

- cus)]; frons mostly rather sparsely punctured, unpunctured areas ill-defined, fine punctures along inner margin of eye absent, margin largely shining; mandible with well-marked notch above apical tooth; hind basitarsus not usually very densely haired, without long bristles
 *B. (Pyrobombus, Festivobombus)*
- Clypeus with fairly numerous scattered punctures, mostly small but some large; frons neither closely nor coarsely punctured, unpunctured areas ill-defined, not large; fine punctures along inner margin of eye absent, margin largely shining; mandible with feeble notch above apical tooth; hind basitarsus densely pubescent along lower edge for its whole length and its disc in part with long bristles (Himalayas) *B. (Pressibombus)*
- 22(3) [triplet]. Malar area twice as long as first flagellar segment 23
- Malar area less than 1.3 times as long as first flagellar segment 25
- Malar area 1.4 to 1.8 times as long as first flagellar segment 29
- 23(22). First flagellar segment a little shorter than combined lengths of second and third segments (10.5:11.0); furrow between labral tubercles narrower; middle basitarsus acutely spinosely produced at apex (paleartic)
 *B. (Megabombus)*
- First flagellar segment clearly shorter than combined lengths of second and third segments (at most 11.5:13.0); furrow between labral tubercles wider; middle basitarsus with apical projection wider, scarcely spinose 24
- 24(23). Inner dorsal angle of hind tibia not or scarcely produced apically; much of clypeus rather strongly and closely punctured, midline on upper third with several rows of fine punctures (Western Hemisphere)
 *B. (Fervidobombus)* (in part)
- Inner dorsal angle of hind tibia pointed apically though point short and broad; clypeus finely or little punctured, midline dorsally without rows of punctures (holarctic)
 *B. (Subterraneobombus)* (in part)
- 25(22). Ocellular distance about 1.6 to 1.8 ocellar diameters; ocelli well in front of postocular tangent 26
- Ocellular distance about three ocellar diameters; ocelli just in front of postocular tangent 27
- 26(25). Impunctate area of frons small, ill-defined, punctured area reaching anterior margins of ocelli, a few coarse punctures between lateral ocellus and eye (Mesoamerica)
 *B. (Dasybombus)*
- Impunctate area of frons larger, well-defined, large area in front of ocelli impunctate, only few minute punctures between lateral ocellus and eye (Mesoamerica)
 *B. (Brachycephalibombus)*
- 27(25). Frons with large unpunctured area separated from eye by narrow band of close, fine punctures (paleartic)
 *B. (Laesobombus)*
- Frons with small unpunctured area separated from eye by wide band of fine punctures 28
- 28(27). Middle basitarsus broadly produced at apex; band of fine punctures along inner edge of eye not spreading over unpunctured area of frons; labral lamella not prominent; malar area with many fine punctures (paleartic)
 *B. (Eversmannibombus)*
- Middle basitarsus spinosely produced at apex; band of fine punctures along inner edge of eye spreading halfway across unpunctured area of frons; labral lamella considerably thickened; malar area unpunctured (northeastern Asia) *B. (Exilobombus)*
- 29(22). Metasomal terga with very close, coarse punctures, except T6, which has coarse granules (Asia)
 *B. (Tricornibombus)*
- Metasomal terga without close, coarse punctures 30
- 30(29). Frons with no band of close, fine punctures along inner margin of eye (Malaysia to Philippines)
 *B. (Senexibombus)*
- Frons with band of close, fine punctures along inner margin of eye 31
- 31(30). Malar area very long; first flagellar segment about four times as long as broad; auricle of hind basitarsus with dense brown pile even on surface not apposed to hind tibia (paleartic) *B. (Sibiricobombus)* (in part)
- Malar area shorter; first flagellar segment shorter; auricle with dense pile, if present, limited to surface apposed to end of hind tibia (and present only in a few species of *Subterraneobombus* that are similar to *Sibiricobombus*) 32
- 32(31). Middle basitarsus acutely spinosely produced 33
- Middle basitarsus acutely but not spinosely produced 37
- 33(32). Malar area about as long as combined lengths of pedicel and first two flagellar segments 34
- Malar area not longer than combined lengths of first and second flagellar segments 35
- 34(33). Third flagellar segment clearly longer than second, which is transverse rather than quadrate; hind basitarsus little produced apically (Asia) *B. (Diversobombus)*
- Third flagellar segment very little longer than second, which is at least quadrate; hind basitarsus distinctly produced apically (paleartic) *B. (Thoracobombus)*
- 35(33). Large area in front of median ocellus unpunctured; lateral unpunctured areas large but well-defined, band of fine sculpture along inner margin of eye narrow; first flagellar segment slightly longer than combined length of second and third segments; inner dorsal angle at apex of hind tibia not or scarcely produced (paleartic)
 *B. (Rhodobombus)* (in part)
- Area in front of median ocellus coarsely but not closely punctured, lateral unpunctured areas of moderate size and fairly well-defined, band of fine sculpture along inner margin of eye wide or rather wide; first flagellar segment shorter than or as long as combined lengths of second and third segments; inner dorsal angle at apex of hind tibia more acutely produced 36
- 36(35). Malar area as long as combined lengths of first and second flagellar segments; apical impressions of clypeus rather strong, with close, moderately coarse punctures; labral tubercles flattened, furrow shallow (paleartic)
 *B. (Thoracobombus)* (in part)
- Malar area not quite as long as combined lengths of pedicel and first flagellar segment; apical impressions of clypeus weak, with narrow deeper strip of close, moderately coarse punctures; labral tubercles somewhat raised and angular at inner ends, furrow moderately deep (paleartic) *B. (Mucidobombus)*
- 37(32). Clypeus swollen with no furrow or lines of punc-

- tures on upper third of midline; hind tibia with inner dorsal apical angle sharp, although projection rather broad (holarctic) *B. (Subterraneobombus)* (in part)
- Clypeus with slight furrow or distinct lines of punctures on upper third of midline; hind tibia with inner dorsal apical angle not or scarcely produced 38
- 38(37). Clypeus with dispersed, sparse, fine punctures; middle basitarsus more spinosely produced; frons less punctured, with a larger unpunctured area in front of and at sides of ocelli (paleartic) *B. (Rhodobombus)* (in part)
- Clypeus generally with closer and coarser punctures; middle basitarsus often not very distinctly produced; frons more punctured, with unpunctured areas smaller (Western Hemisphere) *B. (Fervidobombus)* (in part)

Bombus / Subgenus *Alpigenobombus* Skorikov

- Alpigenobombus* Skorikov, 1914a: 128. Type species: *Alpigenobombus pulcherrimus* Skorikov, 1914 = *Bombus kashmirensis* Friese, 1909, by designation of Williams, 1991. [See Williams (1991) for explanation of other supposed type species.]
- Alpigenobombus* Skorikov, 1938a: 145, unjustified emendation of *Alpigenobombus* Skorikov, 1914.
- Bombus (Mastrucatobombus)* Krüger, 1917: 66. Type species: *Bombus mastrucatus* Gerstaecker, 1869 = *Bombus wurflenii* Radoszkowski, 1859, monobasic.
- Nobilibombus* Skorikov, 1933a: 62. Invalid because no type species was designated. [For subsequent designations in synonymy, see Michener (1997b) and Williams (1991).]
- Nobilibombus* Richards, 1968: 216, 222. Type species: *Bombus nobilis* Friese, 1904, by original designation.
- *Alpigenobombus* occurs from northern Spain and Norway east to the Himalayas and China. Six species were listed by Williams (1998).

Bombus / Subgenus *Alpinobombus* Skorikov

- Bombus (Alpinobombus)* Skorikov, 1914a: 122. Type species: *Apis alpinus* Linnaeus, 1758, by designation of Frison, 1927: 66.
- Alpinobombus* Skorikov, 1937: 53, unjustified emendation of *Alpinobombus* Skorikov, 1914.
- This subgenus occurs in the high arctic almost as far north as there is land, and southward in arctic-alpine habitats as far as California, New Mexico, and the European Alps. Five species were listed by Williams (1994, 1998).
- Bombus (Alpinobombus) arcticus* (Quenzel) (= *B. hyperboreus* Schönherr) is a workerless social parasite in nests of *B. (A.) polaris* Curtis, at least in some areas (K. Richards, 1973).

Bombus / Subgenus *Bombias* Robertson

- Bombias* Robertson, 1903a: 176. Type species: *Bombias auricomus* Robertson, 1903, by original designation.
- Nevadensibombus* Skorikov, 1922b: 149. Type species: *Bombus nevadensis* Cresson, 1874, by designation of Frison, 1927: 64.
- Bombus (Boopobombus)* Frison, 1927: 62. Type species: *Bombias auricomus* Robertson, 1903, by designation of

Williams, 1994: 339. [A sectional name that, according to Article 10(e) of the Code (3rd ed.) must be treated as a subgenus.]

- This subgenus is widespread across North America from southern Canada south to Texas and California, USA, and the state of Hidalgo, Mexico. The two closely related forms of *Bombias* are *Bombus nevadensis* Cresson and its subspecies or close relative, *B. auricomus* (Robertson).

Bombias is unusual among bumble bees in that each egg is laid in a separate small cell; thus eggs are not laid in clumps (Michener, 1974a) as is usual for *Bombus* species.

Bombus / Subgenus *Bombus* Latreille s. str.

- Bremus* Jurine, 1801: 164. Type species: *Apis terrestris* Linnaeus, 1758, by designation of Morice and Durrant, 1915: 428. Invalidated by Commission Opinion 135 (1939).
- Bombus* Latreille, 1802a: 437. Type species: *Apis terrestris* Linnaeus, 1758, monobasic. [Westwood, 1840a: 86, designated *Apis muscorum* Linnaeus, 1758, as type species; it was not an originally included species.]
- Bremus* Panzer, 1804a: 19. Type species: *Apis terrestris* Linnaeus, 1758, by designation of Benson, Ferrière, and Richards, 1937: 93. [For other designations and a comment on the date, see Michener, 1997b.]
- Bombus (Leucobombus)* Dalla Torre, 1880: 40. Type species: *Apis terrestris* Linnaeus, 1758, by designation of Sandhouse, 1943: 564.
- Bombus (Terrestribombus)* Vogt, 1911: 55. Type species: *Apis terrestris* Linnaeus, 1758, by designation of Frison, 1927: 67.
- *Bombus* s. str. ranges from the Canary Islands, Madeira, Spain, and Britain to Japan, south to the Himalayas, Southeast Asia, and Taiwan, north to Norway, Finland, and northeastern Siberia; in North America, Alaska to Nova Scotia, south to California to Florida. Ten species were listed by Williams (1998).

Bombus / Subgenus *Brachycephalibombus* Williams

- Bombus (Brachycephalibombus)* Williams, 1985: 247. Type species: *Bombus brachycephalus* Handlirsch, 1888, by original designation.
- This subgenus occurs from Nayarit to San Luis Potosí, Mexico, south to Honduras. Two species were included by Williams (1998).
- Of the two species of this subgenus, the rare *Bombus haueri* Handlirsch has been placed in *Crotchiibombus* by Labougle (1990), who did not know the male, and by G. Chavarría (in litt., 1995). Williams' (1994) analysis, however, shows its close relationship to *B. brachycephalus* Handlirsch.

Bombus / Subgenus *Coccineobombus* Skorikov

- Alpigenobombus (Coccineobombus)* Skorikov, 1922b: 157.
- Type species: *Bombus coccineus* Friese, 1903, by designation of Sandhouse, 1943: 539.
- This subgenus occurs from western Argentina and Bolivia north to Ecuador. Two species were listed by Williams (1994, 1998).

males, and the identification of a male, not accompanied by workers, will often be difficult. Fortunately, males are almost always found with workers. Queens have been available for only a few taxa, and their characters have not been incorporated into the keys. Keys are presented separately for the neotropics, Africa, Asia (including the Sunda Islands), and Australia (including New Guinea).

Key to the Neotropical Genera of the Meliponini

1. Base of marginal cell broad, basal angle (between stigmal margin and vein *r*, within marginal cell) slightly acute (not under 68°) to right-angular (Fig. 120-1f); marginal cell, at apex of stigma, broader than submarginal cell area; forewing less, usually much less, than 4 mm long *Trigonisca*
- Base of marginal cell of usual shape, basal angle strongly acute (not over 50°) (Fig. 120-1a-e) (except about 80% in *Nogueirapis*); marginal cell, at apex of stigma, little if any broader than submarginal cell area; forewing usually over 4 mm long 2
- 2(1). Inner surface of hind tibia with strongly depressed, shining, upper marginal zone, which at least apically is usually about as broad as longitudinal median keirottrichiate ridge, and midway of tibial length is at least half as wide as keirottrichiate ridge (Fig. 120-10a) 3
- Inner surface of hind tibia with depressed upper marginal zone more narrow (much less than half as wide as area with keirottrichia) or absent, keirottrichia extending to or close to margin (Fig. 120-10b) 6
- 3(2). Eyes hairy; rastellum reduced to tapering hairs (Brazil) *Trichotrigona*
- Eyes bare; rastellum strongly developed 4
- 4(3). Face short and broad, minimum distance between eyes

- much greater than length of eye; clypeus less than twice as broad as long; malar space almost twice as long as flagellar diameter; keirottrichiate zone on inner surface of worker hind tibia nearly twice as wide as depressed upper marginal zone at midlength of tibia *Oxytrigona*
- Face of ordinary shape, minimum distance between eyes little more than to less than length of eye; clypeus usually more than twice as broad as long; malar space little over 1.5 times as long as flagellar diameter or usually much less; keirottrichiate zone on inner surface of worker hind tibia usually narrower (Fig. 120-10a), rarely over 1.5 times as wide as depressed upper marginal zone at mid length of tibia 5
- 5(4). Preoccipital carina strong and shining across full width behind vertex; lower face and genal area shining and coarsely punctate in contrast to dull, densely, minutely punctate upper face, genal area and scutum *Cephalotrigona*
- Preoccipital carina absent; lower face and genal area finely sculptured like upper part of head and scutum *Trigona*
- 6(2). First flagellar segment of worker nearly as long as second plus third taken together, of male nearly as long as second; outer surface of hind tibia convex, without corbicula, lower margin convex like upper margin; penicillum absent; rastellum consisting of tapering hairs *Lestrimelitta*
- First flagellar segment of worker shorter than second plus third taken together, of male much shorter than second; outer surface of hind tibia of worker (and some males) flat or concave at least distally, forming corbicula, lower margin gently convex to concave, unlike largely or

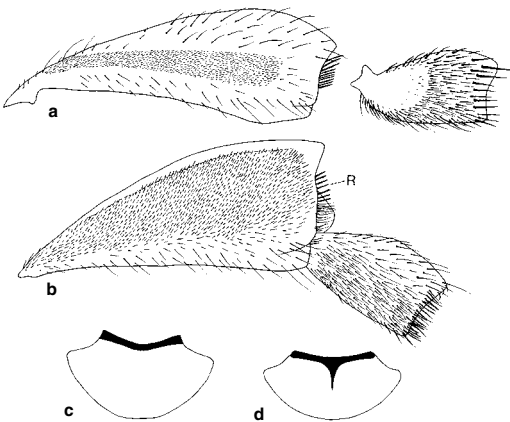


Figure 120-10. Structures of workers of Meliponini. **a**, Inner surfaces of hind tibia and basitarsus of *Trigona* (*Trigona*) *amalthea* (Olivier), showing the keirottrichia on the tibial ridge and the sericeous area on the base of the basitarsus (for the outer surfaces, see Fig. 120-11); **b**, Inner surfaces of hind tibia and basitarsus of *Plebeia* (*Plebeia*) *frontalis* (Friese), showing the keirottrichiate area extending nearly to the upper tibial margin (for the outer surfaces, see Fig. 10-11); **c, d**, Scutellum of *Partamona bilineata* (Say) and *Scaptotrigona mexicana* (Guérin-Méneville) (R, rastellum). From Michener, 1990a.

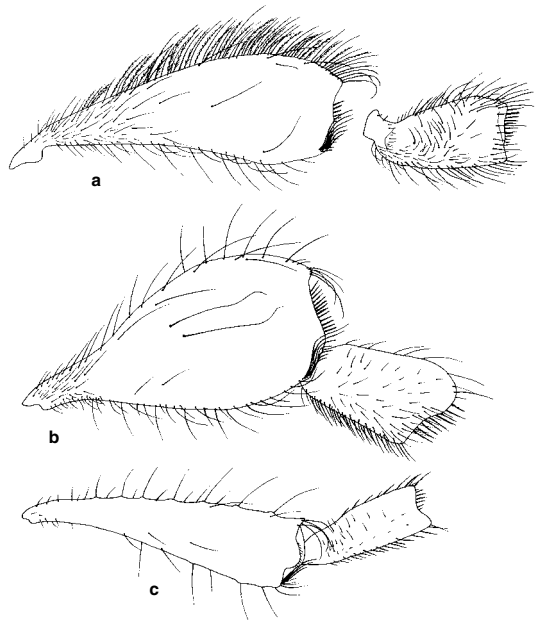


Figure 120-11. Outer surfaces of hind tibiae and basitarsi of workers of Meliponini. **a**, *Trigona* (*Trigona*) *amalthea* (Olivier) (for the inner surfaces, see Fig. 120-10); **b**, *Partamona bilineata* (Say); **c**, *Trigonisca longitarsis* (Ducke). From Michener, 1990a.

- wholly convex upper margin (Fig. 120-11); penicillum present (Fig. 120-11); rastellum variable 7
- 7(6). Hamuli 9-14 (rarely 8); wings extending little if any beyond apex of metasoma; stigma with margin within marginal cell straight or weakly concave (Fig. 120-1a) (body apiform; basal propodeal area dull, hairy) *Melipona*
- Hamuli 5-7, rarely up to 9 or even 10; wings long, extending well beyond apex of metasoma; stigma with margin within marginal cell slightly convex (Fig. 120-1b-f) 8
- 8(7). Anterior part of scutellum with shining, longitudinal V- or U-shaped median depression opening anteriorly into scutoscuteellar fossa (Fig. 120-10d); preoccipital carina present, extending far down on each side of head 9
- Anterior part of scutellum without such a shining, median depression (Fig. 120-10c); preoccipital carina absent or with transverse part only, behind vertex and weakly indicated, except in *Paratrigonoides* 10
- 9(8). Head and thorax, or at least scutellum, with extremely coarse, cribriform punctation; posterior margin of scutellum notched or emarginate medially as seen from above; anterior margin of pronotal lobe with strong, transverse carina *Nannotrigona*
- Head and thorax with fine punctation; posterior margin of scutellum entire; anterior margin of pronotal lobe rounded *Scaptotrigona*
- 10(8). Mandible of worker with four apical teeth (lower two sometimes united by translucent septum but teeth still recognizable); scutellum, as seen in lateral view projecting posteriorly as thin shelf over median part of metanotum *Paratrigona*
- Mandible of worker with (rarely without) one or two denticles at upper end of apical margin, otherwise without teeth; scutellum, as seen in lateral view, rather thick and rounded, not projecting as thin shelf over metanotum 11
- 11(10). Hind tibia of worker greatly broadened, spoon-shaped (Fig. 120-11b), about three times as wide as femur, outer surface largely occupied by corbicula, lower margin of tibia with distal one-half convex; basal area of propodeum densely hairy *Partamona*
- Hind tibia of worker not greatly broadened, less than three times as wide as femur (Fig. 10-11), corbicula extending but little if at all basad of middle of tibia, lower margin of tibia convex only in distal one-fourth or less; basal area of propodeum usually hairless 12
- 12(11). Malar space about one-fifth as long as eye; upper margin of hind basitarsus strongly convex medially; yellow markings absent *Meliwillea*
- Malar space much less than one-fifth as long as eye; upper margin of hind basitarsus gently convex (Fig. 120-10b); yellow markings almost always present, at least on face 13
- 13(12). Upper margin of inner surface of hind tibia strongly depressed, shiny, in sharp contrast to keirottrichiate area [except not depressed in apical third of tibia of *Plebeia (Scaura) timida* (Silvestri)]; concave surface of corbicula usually not occupying whole distal half of hind tibia *Plebeia*
- Upper margin of inner surface of hind tibia not depressed, although shiny and in contrast to keirottrichiate area; concave surface of corbicula occupying full width of distal half of hind tibia 14
- 14(13). Integument of head and thorax dull, microreticulate; preoccipital carina lamellate across upper part of head, with row of coarse setae, branched apically; supraclypeal area expanded laterally, forming flange partly covering antennal socket *Paratrigonoides*
- Integument largely shiny; preoccipital carina absent, without row of coarse setae; supraclypeal area not expanded laterally *Nogueirapis*

Key to the African Genera of the Meliponini

1. Forewing length less than 3.5 mm; hind wing without closed cells (as in Fig. 120-1f), veins closing cells R and Cu, if visible at all, clear and unpigmented; forewing with submarginal crossveins almost always completely absent, thus indications of submarginal cells absent; at least distal part of cell second Cu of forewing undefined or defined by completely unpigmented vein traces; vein M of forewing terminating without bend at about position of anterior end of first recurrent vein (as in Fig. 120-1f), which, however, is absent 2
- Forewing length about 4 mm or more; hind wing commonly with cells R and Cu closed by at least weakly brownish veins; forewing with one or two submarginal crossveins usually weakly indicated, first submarginal cell thus usually recognizable; cell second Cu of forewing completely indicated, at least by faint veins; vein M of forewing extending at least slightly beyond position of anterior end of first recurrent vein and angulate at end of that vein (Fig. 120-1d, e; as in 120-1c), which is usually at least faintly visible 4
- 2(1). Outer surface of hind tibia of worker convex, without corbicula; penicillum absent; clypeus much more than twice as wide as long *Cleptotrigona*
- Distal part of outer surface of hind tibia of worker flat or concave, margined by long hair, forming corbicula; penicillum present; clypeus twice as wide as long or less 3
- 3(2). Upper apical part of hind tibia of worker forming distinct angle; gonostyli of worker much longer than broad, flat, adjacent or separated by less than one gonostylar diameter, without setae but with minute hairs (as in Fig. 120-6e-g) *Liortrigona*
- Upper apical part of hind tibia of worker rounded; gonostyli of worker minute, tuberculiform, separated by several gonostylar diameters, with setae but without minute hairs (as in Fig. 120-6c) *Hypotrigona*
- 4(1). Inner surface of hind tibia with strongly depressed, shining, upper marginal area nearly as broad apically as longitudinal median keirottrichiate ridge, and about half as wide as keirottrichiate ridge midway of tibial length; first metasomal segment longer than broad *Dactylurina*
- Inner surface of hind tibia with depressed upper marginal area narrow (much less than half as wide as broad area with keirottrichia) or absent, keirottrichia extending to or close to margin; first metasomal segment broader than long 5
- 5(4). Hind tibia of worker rather spoon-shaped, upper apical angle rounded but with coarse, amber-colored to blackish bristles (posterior parapenicillum); sting stylet of worker distinct, acute (Fig. 120-6e, g) *Meliponula*
- Hind tibia of worker slender, triangular with distinct up-

per apical angle supporting long, pale hairs (not especially coarse); sting stylet of worker a mere rounded con-vexity *Plebeina*

Key to the Genera of the Meliponini of Asia and the Sunda Islands

1. Forewing length commonly (but not always) over 4 mm, wing venation usually not greatly reduced (for a meliponine), but if minute and with some of the wing reduction characters listed below, then upper margin of hind tibia with plumose hairs intermixed with simple ones (as in Fig. 120-11a); hind wing commonly with cells R and Cu closed by at least weakly brownish veins; forewing with one or two submarginal crossveins usually weakly indicated, first submarginal cell usually recognizable; cell second Cu of forewing completely indicated at least by faint veins; vein M of forewing usually extending at least slightly beyond position of anterior end of first recurrent vein and angulate at end of that vein (as in Fig. 120-1c), which is usually at least faintly visible *Trigona*
- Forewing length less than 3 mm, wing venation greatly reduced; upper margin of hind tibia without plumose hairs; hind wing without closed cells, veins closing cells R and Cu, if visible at all, clear and unpigmented; forewing with submarginal crossveins almost always completely absent, thus without indications of submarginal cells; at least distal part of cell second Cu of forewing undefined or defined by completely unpigmented vein traces; vein M of forewing terminating without bend at about position of anterior end of first recurrent vein which, however, is absent (as in Fig. 120-1f) 2
- 2(1). Malar space almost one-fifth as long as eye, much longer than flagellar diameter; gonostylus of worker with setae but without minute hairs *Pariotrigona*
- Malar space shorter than flagellar diameter; gonostylus of worker with many minute hairs, in addition to setae along outer and distal margins *Lisotrigona*

Key to the Genera of the Meliponini of Australia and New Guinea

1. Scutellum and usually face and scutum with well-developed yellow markings; inner surface of hind tibia with keirottrichiate area broad, nearly reaching upper margin of tibia (as in Fig. 120-10b) *Austroplebeia*
- Head and thorax without distinct yellow markings; inner surface of hind tibia with strong longitudinal keirottrichiate ridge above which is a broad depressed, shining marginal area (Fig. 120-10a) *Trigona*

Genus *Austroplebeia* Moure

Austroplebeia Moure, 1961: 195. Type species: *Trigona cassiae* Cockerell, 1910, by original designation.

This genus includes bees that closely resemble species of the neotropical group *Plebeia* (*Plebeia*) as well as the African *Plebeina*. *Austroplebeia* consists of rather robust species, 3 to 4 mm long, with distinct yellow areas on the scutellum and axillae, usually also on the lateral margins of the scutum and on the face. It differs from *Plebeia* and resembles African genera in the abundant, minute hairs and few small setae on the worker gonostyli and the slender and pointed bristles of the rastellum. The sting stylet,

however, is a rounded projection, not pointed as in most African genera. On the inner side of the hind tibia, the keirottrichiate area closely approaches the upper margin of the tibia, leaving a narrow shiny margin as in *Plebeia* s. str. but less depressed or not depressed.

■ *Austroplebeia* is found in the northern half of Australia and in New Guinea. There are several species; nine names were listed by Michener (1965b) and Cardale (1993).

Nests are found in cavities in rather small tree trunks. An outstanding feature is the cluster of spherical brood cells (Michener, 1961a).

No bees similar to *Austroplebeia* are found in Asia or Indonesia north and west of New Guinea; the relationship of this genus to African or possibly American genera gives rise to a biogeographical puzzle—how and when did such bees reach Australia? Almost certainly they have been in Australia longer than the Australian *Trigona* species, which are close relatives of Indo-Malaysian forms.

Genus *Cephalotrigona* Schwarz

Trigona (*Cephalotrigona*) Schwarz, 1940: 10. Type species: *Trigona capitata* Smith, 1854, by original designation.

This genus is closely related to *Trigona* and could be considered a subgenus of that genus. The body seems more strongly sclerotized than in *Trigona* and is larger than most species of that genus (body length 6–10 mm). Unique features include (1) the strongly, coarsely punctate and shining clypeus, lower supraclypeal area, lower paraocular area, and lower genal area contrasting with the dull, reticulate frons, the dull, closely punctate vertex and scutum, and the extremely dull and minutely punctate upper genal area; and (2) the distal margin of the mandible of the worker, which has a single large tooth at the upper extremity, separated by a broad, shallow concavity from the rest of the margin, which is edentate (Fig. 119-5b). The propodeal triangle has conspicuous hair bases and, like the rest of the propodeum, abundant plumose hairs. The characters of the genus are well illustrated by Schwarz (1940, 1948) and described comparatively by Moure (1951a).

■ *Cephalotrigona* is found from Jalisco and Tamaulipas, Mexico, to Santa Catarina, Brazil, and Misiones, Argentina. It contains at least three species (listed as varieties by Schwarz, 1948).

Nests are typically in cavities in large tree trunks, although also recorded from the ground. The large honey pots contain excellent honey.

Genus *Cleptotrigona* Moure

Lestrimelitta (*Cleptotrigona*) Moure, 1961: 219. Type species: *Lestrimelitta cubiceps* Friese, 1912, by original designation.

This African robber genus is strongly convergent with the American robber, *Lestrimelitta*, and Moure (1961) regarded them as congeneric; common characters are listed above in the subsection on convergence in the Meliponini. Wille (1979b), however, emphasized their distinctness and recognized their resemblances as convergent. This genus contains small (3.5–4.0 mm long) black bees. In workers the gonostyli are flat and divergent, the bases separated by about half a gonostylar width; they bear many minute hairs in addition to several setae along the edges of

ground. In nesting biology, *Melipona* is unique among the Meliponini in rearing numerous small queens in comb cells that are among and identical to worker cells. In all other genera only a few large queens are produced, usually in special large cells. Caste determination of *Melipona* is presumably partly genetic, in the sense that a combination of trophic and genetic factors determines caste. The long-established idea was that some females lack the potential to become queens, while others have such a potential but do so only under favorable trophic conditions. Velthuis and Sommeijer (1991) reviewed the matter and presented a more complex and probably more realistic theory of the interactions of genetic and trophic factors.

In *Melipona*, the production of numerous gynes, nearly all of which were believed to be killed by workers, has long been puzzling. It seemed to indicate wastage of space, provisions, and energy for producing nearly 25% of the female progeny in some cases (see review in Michener, 1974, p. 105-107). Recent studies of *Melipona favosa* (Fabricius) indicate that many virgin gynes leave the nest alive, that they stay alive for some time and visit flowers outside the nest, that they search for and find nests of their own species, and that they can sometimes pass the guards and enter such nests. Possible acceptance and reproductive behavior remain unknown but the existence of searching and entering behavior suggests that the young gynes sometimes survive and reproduce (Sommeijer and de Bruijn, 2003; Sommeijer, de Bruijn, Meeuwssen, and Slaa, 2003).

The method of recruitment to resources by *Melipona* workers is also different from that of other Meliponini; see review by Michener (1974a).

Although four subgenera have been recognized and constitute recognizable groups, the species of *Melipona* are morphologically similar and I have not recognized the subgenera. Male genitalia of 25 species studied by Rego (1990) are monotonously similar, as shown by her illustrations; her preferred cladogram (Rego, 1992), based on male genitalia, suggests that *Melikerria* and *Eomelipona* might constitute clades different from that of *Melipona* s. str. Fernandez-Salomão et al. (2005) prepared a phylogeny for eight species, two of each subgeneric group of *Melipona*, based on nuclear DNA in an internal transcribed spacer. For whatever it means with only two species per group, all four groups were supported, and *Melikerria* was basal, i.e., sister group to all the others.

Genus *Meliponula* Cockerell

This genus includes not only the type species, *Meliponula bocandei* (Spinola), but also a series of smaller African forms placed in other genera (see the subgenera, below) by Wille (1979b) and Moure (1961); see Michener (1990a). *Meliponula* shares with most other African Meliponinae the flattened worker gonostyli with their many minute hairs (Fig. 120-6e-g) (sometimes also with a few setae), the presence of a conspicuous remnant of the gonobase attached to the male gonocoxite lateroventrally (Fig. 120-9), the schizogonol (presumably permanently) male genital capsule with the gonocoxites longer than broad, at least in ventral view, and the strongly reflexed median apical process of S6 of the male. *Meliponula* dif-

fers from *Plebeina* in the reduction of the rastellum to slender hairs, no coarser than those of similar length on adjacent parts of the tibial apex; the rounded or very obtuse upper apical angle of the worker hind tibia, the tibia thus being rather spoon-shaped; the presence of coarse, amber or blackish bristles arising from or near this angle, forming what Wille (1979b) called the posterior parapencilum in *M. bocandei* (Spinola); the presence of hairs, at least laterally, on the basal area of the propodeum; and the acute worker sting stylet (Fig. 120-6e, g). Like *Plebeina* and unlike other African genera, *Meliponula* has a broad area of keirotichia on the inner surface of the worker hind tibia; the upper margin may be depressed and shining, almost as in *Plebeia* s. str., only slightly depressed (e.g., in *Meliponula* s. str.), or poorly defined and not at all depressed (subgenus *Axestotrigona*). The smaller species of *Meliponula* resemble the larger species of *Plebeia* s. str. superficially, but differ from most *Plebeia* not only in the character states indicated above but in the very fine, dense punctation at least of the mesoscutum.

Key to the Subgenera of *Meliponula*

1. Propodeal profile largely vertical; corbicula occupying less than distal half of hind tibia; apical reflexed process of S6 of male short and rounded; metasomal terga dull, minutely sculptured *M. (Meliponula) s. str.*
- Propodeal profile with slanting dorsal portion rounding onto vertical portion; corbicula occupying more than distal half of hind tibia; apical reflexed process of S6 of male longer than body of sternum; metasomal terga at least partly shining 2
- 2(1). Head and thorax without yellow markings; inner surface of worker hind tibia without well-defined, shining, depressed upper margin, although keirotichiate area does not reach margin at least distally *M. (Axestotrigona)*
- Head and thorax with yellow markings; inner surface of worker hind tibia with shining upper margin, at least slightly depressed *M. (Meliplebeia)*

Meliponula / Subgenus *Axestotrigona* Moure

Axestotrigona Moure, 1961: 237. Type species: *Melipona ferruginea* Lepeletier, 1836, by original designation.

This subgenus consists of moderate-sized (length 5.5-7.0 mm) robust species. There are delicate plumed hairs among the marginal bristles at the upper apical angle of the worker hind tibia and across the apex of the tibia.

■ The subgenus ranges from Gambia to Kenya, south to Angola and the Transvaal, South Africa. The 12 species names, some probably representing only color forms of others, were listed by Moure (1961).

Nest sites include both tree cavities and terrestrial termite nests; brood cells form combs.

Meliponula / Subgenus *Meliplebeia* Moure

Meliplebeia Moure, 1961: 229. Type species: *Trigona beccarii* Gribodo, 1879, by original designation.

Plebeilla Moure, 1961: 226. Type species: *Trigona lendliana* Friese, 1900, by original designation.

Apotrigona Moure, 1961: 233. Type species: *Trigona nebulata* Smith, 1854, by original designation.

Genus *Paratrigonoides* Camargo and Roubik

Paratrigonoides Camargo and Roubik, 1905; 34. Type species: *Paratrigonoides mayri* Camargo and Roubik, 2005, by original designation.

As the generic name suggests, *Paratrigonoides* resembles species of *Paratrigona*, for example in the dull integument and yellow markings on the face and thorax. Indeed Camargo and Roubik (2005) in a phylogenetic analysis found it to be the probable sister group to *Paratrigona* (both *Aparatrigona* and *Paratrigona* proper, which might well be recognized as a subgenera). However, it differs from *Paratrigona* in the two denticles (instead of four teeth) on the mandible, the relatively short scutellum, the lamellate upper part of the preoccipital carina, the laterally expanded supraclypeal area, etc. It differs from *Nogueirapis* in the features indicated in the key to genera. ■ *Paratrigonoides* is known only from the Cauca Valley region of Colombia. The only species is *P. mayri* Camargo and Roubik.

Genus *Pariotrigona* Moure

Pariotrigona Moure, 1961: 192. Type species: *Trigona pendleburyi* Schwarz, 1939, by original designation.

This is another genus of minute Meliponini (body length 2.5–3.0 mm), sharing the character states listed in couplet 1 of the above keys to the genera of Asia and Africa. Because it is known only from workers, its generic status and its position relative to other genera remain in doubt. The gonostyli of workers bear setae and lack minute hairs. The only other minute genus with such gonostyli is *Hypotrigona*. Those of *Pariotrigona*, however, are quite different, being broadened at the bases and separated by little more than a stylar width. The hind tibia has a distinct although rounded upper apical angle in *Pariotrigona* that is lacking in *Hypotrigona*. The long malar space of *Pariotrigona* suggests some species of the neotropical genus *Trigonisca*, a similarity strengthened by the nearly right-angular basal angle of the marginal cell and the transverse rows of hairs on the inner surface of the hind basitarsus. *Trigonisca*, however, has quite different worker gonostyli.

■ *Pariotrigona* is found from the Malay Peninsula to Vietnam, Borneo, and Sumatra. The male of *Pariotrigona* was described, and the two specific names synonymized, by Michener (2002a); thus the genus now contains only one species.

Genus *Partamona* Schwarz

This genus is composed of relatively robust forms, 4.5 to 7.0 mm long, that are superficially suggestive of *Scaptotrigona*, *Trigona* (*Geotrigona*), and some species of *Trigona* s. str. *Partamona* differs from such forms in having yellowish face marks (often restricted), in the rather dense covering of erect hair on the basal propodeal area, and in the hind tibial structure of workers. This tibia is spoon-shaped and greatly broadened, about three times as wide as the femur, the outer surface mostly occupied by the enormous corbicula (Fig. 120-11b). On the inner surface of the tibia the broad keirotrichiate area extends nearly to the upper margin, which is shining but not depressed.

Key to the Subgenera of *Partamona*

1. Cuticle of thorax shining with minute, widely separated punctures; yellow of face pale and inconspicuous; metasomal terga without yellow maculations; worker gonostylus a rounded tubercle with few setae (Fig. 120-6c) *P. (Partamona) s. str.*
- Cuticle of thorax dull and minutely roughened; paraocular areas largely bright yellow; metasomal terga usually with yellow bands or lateral spots; worker gonostylus about 1.5 times as long as broad, and setose *P. (Parapartamona)*

Partamona / Subgenus *Parapartamona* Schwarz

Trigona (*Parapartamona*) Schwarz, 1948: 428. Type species: *Trigona zonata* Smith, 1854, by original designation.
[New status.]

Parapartamona differs from *Partamona* not only in the characters indicated in the key to subgenera, but also in having conspicuously long wings and an elongate propodeum, its dorsal surface being about twice as long as the scutellum.

■ This subgenus occurs in the mountains from Colombia to Peru. The group was dealt with by Schwarz (1948), and the seven species were revised by Moure (1995a); Bravo (1992), however, recognized only two species.

Partamona / Subgenus *Partamona* Schwarz s. str.

Trigona (*Patera*) Schwarz, 1938: 475 (not Lesson, 1837).
Type species: *Melipona testacea* Klug, 1807, by original designation.

Trigona (*Partamona*) Schwarz, 1939b: 23, replacement for *Patera* Schwarz, 1938. Type species: *Melipona testacea* Klug, 1807, autobasic and original designation.

This subgenus lacks the special features listed for *Parapartamona*. In the species examined, the worker gonostylus is more reduced than that in other Meliponini.

■ *Partamona* ranges from Sonora, Chihuahua, and San Luis Potosí, Mexico, to Santa Catarina, Brazil, and eastern Peru, but appears to be absent from southernmost Brazil and adjacent countries. The species with testaceous bodies were revised by Camargo (1980), and the entire subgenus was revised (as a genus) by Pedro and Camargo (2003). They recognized 34 species. An account by Camargo and Pedro (2003a) provided a further review, phylogenetic and biogeographic patterns for the species, accounts of nests, and magnificent illustrations of the nests and nest entrances.

Although some *Partamona* species frequently occupy tree cavities, the commonly found nests are in partly or fully exposed sites, such as cavities in bank or cliff surfaces, or on walls of buildings, frequently below protecting eaves. The bees are usually highly aggressive when disturbed. The brood cells are arranged in combs.

Partamona grandipennis (Schwarz) and *xanthogastra* Pedro and Camargo from Costa Rica and Panama have unusually long wings, suggesting those of *Parapartamona*, but are otherwise like *Partamona* s. str. Moure (1995a) excluded *P. grandipennis* from *Parapartamona*, but by error placed it in *Parapartamona* in the same paper.

Genus *Plebeia* Schwarz

Bees of this genus have shiny cephalic and thoracic integument with minute [somewhat larger in *Plebeia* (*Plebeia*) *caerulea* (Friese)], well-separated punctures, varying to dull, densely and minutely punctate in the subgenus *Schwarziana* and in *P. (P.) schrottkyi* (Friese). The scutellum is rounded in lateral view, not shelflike, and often but not always overhangs and hides the median part of the metanotum, as seen from above. The scutellum lacks a median depression in the anterior margin like that of *Nannotrigona* and *Scaptotrigona*, but in some species there is a weak indication of such a depression. The broad area with keirotichia on the inner side of the hind tibia extends nearly to the upper margin of the tibia (Fig. 120-10b) but the margin is shiny, largely bare, and abruptly depressed, except on the distal third of the tibia of *P. (Scaura) timida* (Silvestri), where it is not depressed.

The forms listed above with dull cephalic and thoracic integument are not closely related to one another as judged by tibial and other characters. In *Trigona*, also, there is a subgenus with fine, dull thoracic integument (*Lepidotrigona*) and a subgenus with a somewhat more shining and less closely punctate thoracic integument (*Papuatrigona*), in addition to the majority, which are shiny with well-separated, minute punctures. In *Partamona*, also, there are dull as well as shiny species. The idea that integumental dullness is necessarily a generic or subgeneric character should be abandoned.

Key to the Subgenera of *Plebeia*

1. Hind basitarsus thickened, nearly as broad as or broader than tibia (Fig. 120-13) (face without yellow markings) *P. (Scaura)*
- Hind basitarsus flat, much narrower than tibia (Fig. 120-10b) 2
- 2(1). Body (including metasomal terga) dull, minutely and closely punctured; forewing length about 6 mm; S3 of male with enormous procurved band of erect hooked hairs, behind which is a concave membranous area with erect hairs (South America) *P. (Schwarziana)*
- Body (or at least metasoma) shining; forewing length less than 5 mm, usually 4 mm or less; S3 of male unmodified *P. (Plebeia s. str.)*

Plebeia / Subgenus *Plebeia* Schwarz s. str.

Trigona (*Plebeia*) Schwarz, 1938: 480. Type species: *Trigona mosquito* Smith, 1863, by original designation.

Mourella Schwarz, 1946, in Moure, 1946a: 442. Type species: *Melipona caerulea* Friese, 1900, by original designation.

Friesella Moure, 1946a: 441; 1946b: 611. Type species: *Melipona schrottkyi* Friese, 1900, by original designation.

This is a subgenus of small bees (body length 3–6 mm), mostly with whitish or yellow markings on the face and thorax. Unlike *Scaura*, which commonly has a more slender metasoma, that of *Plebeia* s. str. is as broad as the thorax. Special features of two species resulted in each receiving a genus-group name, as shown in the above synonymy. I doubt if subgeneric names are needed for them. *Mourella* was described and illustrated by Schwarz (1948).

■ *Plebeia* s. str. ranges from Sinaloa and Tamaulipas,

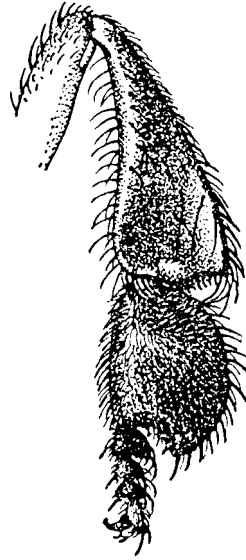


Figure 120-13. Hind tibia and tarsus of *Plebeia* (*Scaura*) *latitarsis* (Friese), worker. From Schwarz, 1948.

Mexico, to San Luis province, Argentina. There are about 30 species; several occur in most areas. Two unusual species, *P. (Plebeia) schrottkyi* (Friese) and *caerulea* (Friese) [*Friesella* and *Mourella*], occur in southern Brazil and adjacent countries; *P. (P.) intermedia* (Wille), an unusually large species, is from Bolivia. Thus most of the diversity in the subgenus is found in southern South America. The possibility exists that *P. schrottkyi* and *caerulea* are distinct taxa convergent with *Plebeia* s. str.

Species of this subgenus nest in tree cavities, artificial containers, or in the ground. Brood cells of most species form combs, but in a small species, *Plebeia schrottkyi* (Friese), the combs are irregular, and in *P. tica* (Wille) and related minute species the cells are in clusters. The former is an unusual species constituting *Friesella* but the latter is morphologically a rather ordinary although small *Plebeia* s. str.

Plebeia / Subgenus *Scaura* Schwarz

Trigona (*Scaura*) Schwarz, 1938: 479. Type species: *Trigona latitarsis* Friese, 1900, by original designation.

Schwarzula Moure, 1946a: 439. Type species: *Trigona timida* Silvestri, 1902, by original designation.

This subgenus differs from other Meliponini in the form of the hind basitarsi, which are nearly as broad as or broader than the tibia (Fig. 120-13) and convex on the outer surfaces, at least apically, as illustrated along with other character states (including those of male genitalia and sterna) of the *latitarsis* group by Schwarz (1948). These are small bees (body length 4.0–5.5 mm). *Plebeia timida* (Silvestri) has the form of a *Plebeia* s. str.; the others have variably more slender metasomas. An interesting feature, best developed in *P. latitarsis* (Friese), is the series of flat, curved bristles on the posterior margins of S4 and S5 of the worker. The head and thorax of *Scaura* are black, without the yellow markings characteristic of nearly all species of *Plebeia* s. str. The body surface is shining with small, scattered punctures like those of most *Plebeia* s. str.

Cockerell) are intermediate (see Michener, 1961a). *Trigona* (*H.*) *canifrons* Smith and the whole subgenus *Friesiocomelitta* also arrange their cells in clusters. Probably the cluster arrangement within the genus *Trigona* is derived, presumably independently in the Indo-Australian and American taxa, the ancestral pattern for the genus being horizontal combs.

Separate keys to the subgenera are provided for the Western Hemisphere and for the Indo-Australian region. Oliveira (2002) gave a new key to the subgenera of *Trigona*, using the presence or absence of the middle tibial spur as an important character.

Key to the Neotropical Subgenera of *Trigona*

1. Mandible of worker with four or five teeth along distal margin (Fig. 119-5c); inner surface of hind basitarsus of males and workers with basal sericeous area (Fig. 120-10a) *T. (Trigona s. str.)*
- Mandible of worker with lower half or two-thirds of distal margin edentate, upper part of margin with one or usually two teeth; inner surface of hind basitarsus of males without basal sericeous area, that of workers, variable 2
- 2(1). Metasoma short, about as wide as thorax, dorsoventrally flattened; upper margin of hind tibia of worker usually with few plumose hairs, most of them with only two to six scattered branches not concentrated toward apices; yellow markings absent; vein M of forewing dark almost to wing margin *T. (Geotrigona)*
- Metasoma usually narrower than thorax, often noticeably elongate; upper margin of hind tibia of worker with numerous strongly plumose hairs (Fig. 120-11a), usually with abundant branches toward apices; yellowish or reddish markings present on face of some species; vein M of forewing usually fading away near widest part of wing 3
- 3(2). Inner surface of hind basitarsus of worker with basal sericeous area covered with minute setae or sometimes lacking setae (Fig. 120-10a) *T. (Tetragonisca)*
- Inner surface of hind basitarsus of worker without basal sericeous area, rather uniformly setose 4
- 4(3). Posterior margin of vertex elevated as strong, hairy ridge between summits of eyes; upper distal angle of hind tibia of worker acute (Brazil) *T. (Duckeola)*
- Posterior margin of vertex not elevated; upper distal angle of hind tibia of worker broadly rounded 5
- 5(4). Labial palpi with large, sinuous setae on first two segments (Fig. 120-12e) *T. (Friesiocomelitta)*
- Labial palpi with setae no longer than palpal width and straight or nearly so (Fig. 120-12c) *T. (Tetragona)*

Key to the Indo-Australian Subgenera of *Trigona*

1. Hairs along upper margin of hind tibia of workers and males all simple, or some plumose only on apical fifth or sixth of margin; elevated, keirotrichiate median zone of inner surface of hind tibia separated from shining upper marginal zone by gentle slope 2
- Hairs along upper margin of hind tibia of workers (Fig. 120-11a) and some males partly plumose; elevated, keirotrichiate median zone of inner surface of hind tibia separated from shining upper marginal zone by abrupt slope 3
- 2(1). Head and thorax dull, with minute close punctures;

- propodeal dorsum finely reticulate; upper margin of hind tibia of worker without plumose hairs; scutum margined with whitish, densely plumose ("scale-like") hairs (South-east Asia) *T. (Lepidotrigona)*
- Head and thorax shining, although with minute, rather close punctures; propodeal dorsum smooth, shining; upper margin of hind tibia of worker with plumose hairs among bristles on apical one-fifth or one-sixth of margin; scutum without conspicuous plumose hairs (New Guinea) *T. (Papuatrigona)*
- 3(1). Inner surface of hind basitarsus of worker with basal sericeous area covered with minute setae or sometimes lacking setae (Fig. 120-10a) *T. (Heterotrigona)*
- Inner surface of hind basitarsus of worker without basal sericeous area, rather uniformly setose (Southeast Asia) *T. (Homotrigona)*

Trigona / Subgenus *Duckeola* Moure

Duckeola Moure, 1944a: 71. Type species: *Trigona huberi* Friese, 1901 = *Trigona ghilianii* Spinola, 1853, by original designation.

This subgenus consists of large (8-9 mm long), rather robust species so different from other *Tetragona*-like bees that they must be placed in their own subgenus. It resembles *Tetragona* in lacking a sericeous area on the inner surface of the hind basitarsus of the worker. It differs from *Tetragona* and all other subgenera in the strong, hairy ridge on the posterior margin of the vertex between the summits of the eyes (this differs from the shiny, hairless carina in a similar position in the genus *Cephalotrigona*); in the rather slender hind tibia of the worker, its upper apical angle strongly produced apicad and acute; and in the roughly 20 large setae of the labial palpi, which are at most only about 1.5 times as long as the palpal width, yet are mostly curved or slightly sinuous (Fig. 120-12d). Males are unknown.

■ *Duckeola* is found in Brazil and Colombia. There are two species.

Trigona / Subgenus *Friesiocomelitta* Ihering

Friesiocomelitta Ihering, 1912: 5. Type species: *Trigona silvestrii* Friese, 1902, monobasic.

This subgenus consists of slender, delicate-looking species 4.0 to 6.5 mm long that agree with *Tetragona* in subgeneric attributes except that the labial palpus of the worker possesses many (19-23 in species examined) large, sinuous setae (Fig. 120-12e). Such setae are absent in *Tetragona*, although present in *Tetragonisca*. *Friesiocomelitta* is further distinguished from all other American groups of the genus *Trigona* in the arrangement of the brood cells—in clusters rather than in combs. This architectural character does not separate subgenera among the Indo-Australian *Trigona* and in the genus *Plebeia*, but appears to do so in American *Trigona*. Another architectural character state of *Friesiocomelitta* is the elongate storage pots, which are also found in the genus *Trigonisca* and in some species of *Trigona* (*Heterotrigona*).

■ *Friesiocomelitta* ranges from Sinaloa and Veracruz, Mexico, to Minas Gerais, Brazil. There are about ten species.