Mitt. Münch. Ent. Ges.	87	3-21	München, 1.12.1997	ISSN 0340-4943

A generic study of the bees of the tribe Tapinotaspidini, with notes on the evolution of their oil-collecting structures

(Hymenoptera, Apidae)

Arturo Roig-Alsina

Abstract

The study addresses the scope and relationships of the genera *Tapinotaspis* Holmberg, 1903, *Chalepogenus* Holmberg, 1903, and *Lanthanomelissa* Holmberg, 1903, clarifies the identity of *Lanthanomelissa*, and studies the relationships of *Caenonomada* Ashmead, 1899, and *Monoeca* Lepeletier & Serville, 1828, two taxa which have been difficult to interpret in the past. The tribe Tapinotaspidini also comprises the genera *Paratetrapedia* Moure, 1941, *Arhysoceble* Moure, 1948, *Tapinotaspoides* Moure, 1944, and *Trigonopedia* Moure, 1941, the last three previously treated as subgenera. *Schrottkya* Friese, 1908, *Lanthanella* Michener & Moure, 1957, and *Tapinorhina* Michener & Moure, 1957, are new synonyms of *Chalepogenus* Holmberg, 1903; *Lanthanomelissa completa* Michener & Moure, 1957 = *Tetrapedia goeldiana* Friese, 1898, and *Tapinotaspis sabularum* Holmberg, 1903 = *Tetrapedia muelleri* Friese, 1899. The new species *Chalepogenus parvus* is described. Lectotype designations are made for the following species: *Exomalopsis chalybaea* Friese, 1899, *Tapinotaspis chacabucensis* Holmberg, 1903, *Lanthanomelissa discrepans* Holmberg,1903, *Tetrapedia muelleri* Friese, 1899, *Chalepogenus incertus* Holmberg, 1903, and *Tetrapedia goeldiana* Friese, 1899. *Chalepogenus caeruleus* (Friese, 1906), *C. goeldianus* (Friese, 1899), *C. nigripes* (Friese, 1899), and *C. herbsti* (Friese, 1906), are all new combinations in *Chalepogenus* Holmberg; *Tapinotaspis latitarsis* (Friese, 1899) is also a new combination.

A phylogenetic analysis of the genera of Tapinotaspidini is presented. The evolution of the diverse oil-collecting structures of these bees is discussed in the light of the new phylogenetic hypotheses. A key to the genera and illustrations are provided.

Introduction

The purpose of the present contribution is to study the relationships and classification of the bees previously placed in the genera *Tapinotaspis*, *Chalepogenus* and *Lanthanomelissa*, and to study the relationships of *Caenonomada* and *Monoeca*, two taxa which have been difficult to interpret in the past. Although the phylogenetic study includes species representing all the genera, some of them are better represented in the analyses. No attempt has been made to study the variability and subgeneric composition of the large genus *Paratetrapedia*, apart from removing from it *Arhysoceble* and *Trigonopedia*, which are given generic status.

Tapinotaspidines are small to medium sized bees, 4.2 mm to 14 mm long, usually with bare, polished apical areas on the metasomal terga. Many genera have pale bodied species and dark bodied species as well as dark species variously maculated with yellow, or less commonly with red. Bees of this tribe have the attributes usually shown by oil-collecting bees: the inner hind tibial spur is pectinate, and the scopa of the hind leg is composed of a mixture of branched hairs and stiff, simple hairs (Roberts & Vallespir 1978). Tapinotaspidines also have peculiar structures, groups of specialized hairs on the forelegs, middle legs, and metasoma, which are used in oil collecting (Vogel 1974, 1988; Neff & Simpson 1981). These structures are present in both sexes, though not as well developed in the males. Apomorphies of the tribe are the ventral membrane between meso and metasoma arising from the apical margin of the metasternum, and the lack of the lateral carina of the propleuron (Roig-Alsina & Michener 1993), although the latter character does not hold for a few species, which are thought to have reacquired the carina.

Bees of the tribe Tapinotaspidini have been variously treated. Early authors thought that *Caenonomada* and *Monoeca* were relatives of *Tetrapedia* Klug, or of the centridines. The latter point of view was revived recently by Snelling & Brooks (1985), who treated *Caenonomada* as the sister group of the tribes Centridini, Rhathymini, and Ericrocidini, and by Neff & Simpson (1981), who suggested a close relationship of *Monoeca* to the centridines based on the similarity of their oil-collecting organs. Other tapinotaspidines were confused with *Tetrapedia* until Moure (1941, 1948) separated the genera *Paratetrapedia*, *Trigonopedia*, and *Arhysoceble*. Still others, included later in *Tapinotaspis*, were treated as relatives of *Exomalopsis*.

Michener (1944) included all these taxa as part of the tribe Exomalopsini. Later Michener & Moure (1957) reviewed this tribe to the genus level and recognized five sections. They envisioned the Exomalopsini as probably a grade, and suggested possible relationships of the five groups to other tribes of bees. Their sections 1 (*Caenonomada*), 2 (*Monoeca*), and 5 (*Chalepogenus*, *Lanthanomelissa*, *Tapinotaspis*, and *Paratetrapedia*) were included by Roig-Alsina & Michener (1993) in the new tribe Tapinotaspini. Moure (1994a) independently proposed the tribe Tapinotaspidini, establishing the correct spelling for the tribal name, but with a more restricted scope: only *Tapinotaspis*, *Tapinotaspoides*, and *Tapinorhina*, the latter two considered as genera, were included. Simultaneously Moure (1994b) proposed the tribe Paratetrapediini for all the other taxa of section 5 of his paper with Michener (1957). The two tribes as they were proposed by Moure do not represent natural groups, as will be shown below.

Michener & Moure (1957) mentioned in their generic treatment that "A classificatory problem of great difficulty exists in section 5 ... These genera and their subgenera can be arranged in such a way as to form steps in a graded series from *Lophopedia* and *Paratetrapedia* at one extreme to *Tapinotaspis* at the other." This problem is addressed in the present contribution, studying the relationships between the genera, proposing new interpretations of them, and clarifying the use of certain generic names the type species of which were not properly recognized. The evolution of the oil-collecting structures of the tapinotaspidines is discussed in the light of the phylogenetic hypotheses obtained.

Material and Methods

Phylogenetic analyses were performed with the computer program HENNIG86, version 1.5 (Farris 1988). Phylogenetic inferences are based on the detailed morphological study of the following species of Tapinotaspidini: *Tapinotaspoides tucumana* (Vachal, 1904), *T. nigerrima* (Schrottky, 1909), *Tapinotaspis chalybaea* (Friese, 1899), *T. latitarsis* (Friese, 1899), *Lanthanomelissa discrepans* Holmberg, 1903, *Chalepogenus muelleri* (Friese, 1899), *C. herbsti* (Friese, 1906), *C. caeruleus* (Friese, 1906), *C. goeldianus* (Friese, 1899), *C. nigripes* (Friese, 1899), *Arhysoceble melampoda* Moure, 1948, *Trigonopedia oligotricha* Moure, 1941, *Paratetrapedia pygmaea* (Schrottky, 1902), *P. maculata* (Friese, 1899), *Monoeca lanei* (Moure, 1944), and *Caenonomada bruneri* Ashmead, 1899. Many other species in all genera were also examined. Species studied of the five outgroup tribes are the same as those used in Roig-Alsina & Michener (1993).

Three characters (Table 1) have more than two states; these were run as unordered. Part of the characters employed in the present study are those found to be variable within the Tapinotaspidini in the study of long-tongued bees of Roig-Alsina & Michener (1993: 128-138). Since the scope of the present study is narrower the relevance of the variability of several characters had to be reassessed. Some other characters used by Roig-Alsina & Michener (1993, characters 36, 71, 74, and 103) had to be excluded from the present study; the inclusion of more taxa of Tapinotaspidini made it difficult to define states due to a more or less continuous gradation of the characters.

For the description of the different structures of the legs of bees the system used by Neff & Simpson (1981) is followed. According to the system the strigillar concavity of the foretarsus is ventral, and the anterior and posterior surfaces are established considering the leg extended to the sides of the body of the bee. The tarsomeres 2-5 are considered here as depressed dorsoventrally. Their ventral surface not always corresponds with the ventral surface of the basitarsus due to rotation of the segments in some species.

Phylogenetic Analysis

The relationships of the Tapinotaspidini to other tribes of Apidae were studied by Roig-Alsina & Michener (1993). In their analyses based on adult characters the Tapinotaspidini are related to a group of tribes comprising the Emphorini, Ctenoplectrini, Eucerini, Ancylini, and the paraphyletic Exomalopsini. Their analyses A, B, and C show the Tapinotaspidini forming a monophyletic group together with these five tribes, while analysis D shows the Tapinotaspidini forming a clade with the first two tribes. Their analysis based on adult and larval characters combined also supports a close relationship to these five tribes (ROIG-ALSINA & MICHENER 1993, cladograms 1a, 1b, 2a, 2b, 3b, and 5). The relationships among the tribes are different in different analyses so, although the evidence suggests that the five tribes form a monophyletic group, their relationships are unresolved. SILVEIRA (1993) reanalyzed the data presented by ROIG-ALSINA & MICHENER (1993) adding the genus *Ancyla* LEPELETIER. He concluded that the data support a clade formed by the tribes Ancylini, Exomalopsini, Eucerini, Emphorini and Tapinotaspidini.

It should be noted that bees of the tribe Emphorini, excluding *Ancyloscelis* LATREILLE (i.e. the subtribe Emphorina sensu ROIG-ALSINA & MICHENER 1993), share with the tapinotaspidines some unique features not present in other bees. A remarkable one is the structure of the spatha, which has a median ventral projection that locks the produced basal margin of the penis valves. Another shared feature is the anterior expansion of the maxillary stipes. The similarity of the male hidden metasomal sterna, in particular the seventh sternum, of many emphorines and tapinotaspidines is striking; this feature was already mentioned by MICHENER & MOURE (1957: 403).

For the purpose of the present study the tribes Emphorini, Ctenoplectrini, Eucerini, Ancylini, and Exomalopsini are considered as outgroups for the Tapinotaspidini. Five outgroup hypotheses have been considered, taking the five tribes one at a time with the remaining four tribes forming outgroup vectors (Table 1). The results of the analyses using the five alternative outgroup hypotheses are compared and used to infer relationships within the Tapinotaspidini. Relationships that are stable under every outgroup combination are deemed to be valid regardless of how the outgroups are actually related. This is the outgroup substitution method proposed by DONOGHUE & CANTINO (1984), although the method is not used here for the assessment of ancestral states prior to the analysis; the outgroups themselves are used to root the trees.

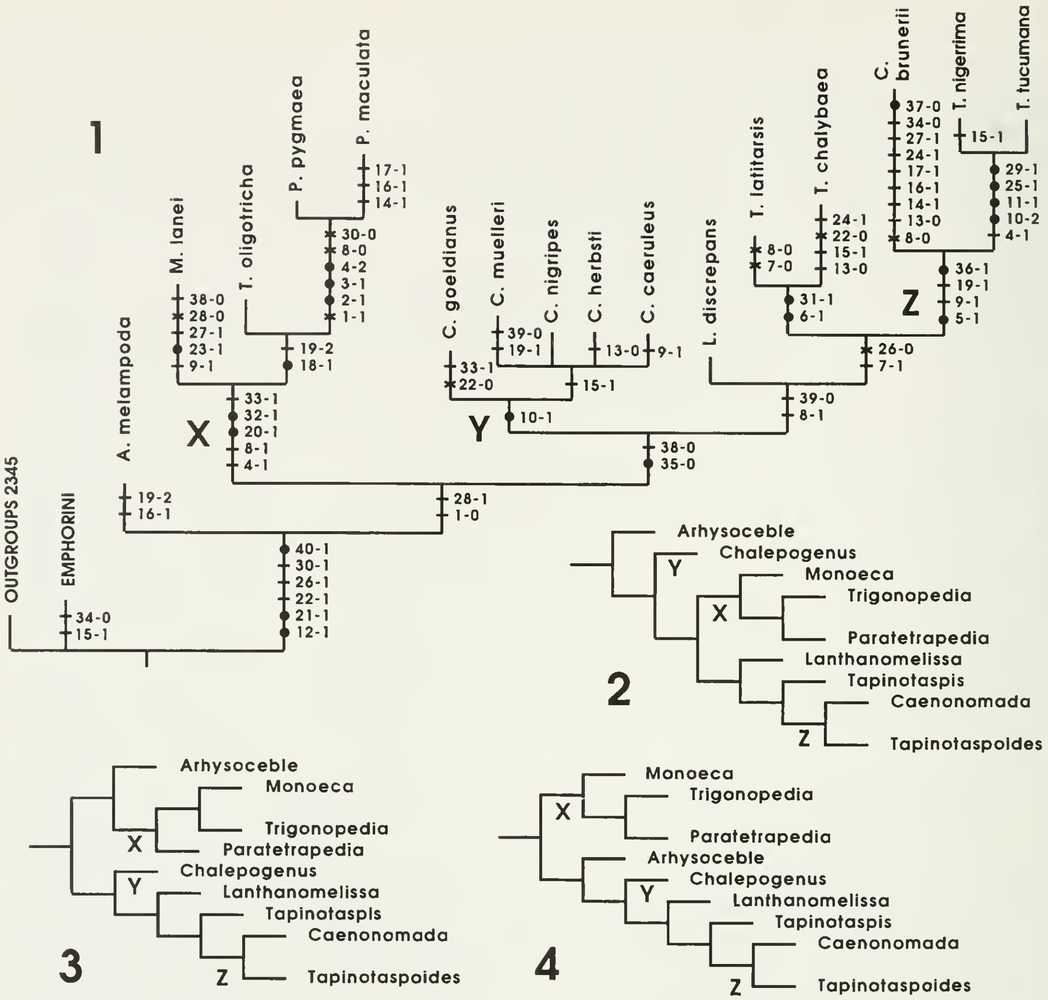
Table 1. Matrix of character states for outgroups and species of Tapinotaspidini. Character states explained in the text. Dashes in the outgroups indicate variability of the character within the group.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1Emphorini	1	–	0	0	0	0	–	0	–	0	0	–	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	0	1	0	–	1	–	–
2Ctenoplec	1	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	–	1	1	1	0	–	1	–	0
3Ancylini	0	0	0	0	0	0	0	–	1	0	0	0	0	1	0	0	0	0	0	0	0	1	–	–	0	0	0	0	0	0	0	0	0	1	1	0	0	1	–	0
4Eucerini	0	–	0	0	0	–	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
5Exomalops	1	–	0	0	0	–	–	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	1	0	0	0	0	–	0	0	0	0	0	–	0	0	1	0	1	0
outg2345	–	0	0	0	0	0	–	–	–	0	–	0	–	–	0	0	0	0	0	–	0	–	–	0	0	0	0	–	0	–	0	0	–	1	–	0	–	–	–	0
outg1345	–	0	0	0	0	0	–	0	–	0	0	0	–	–	–	0	0	0	0	0	0	–	–	0	0	0	0	–	0	0	0	0	0	–	–	0	–	–	–	0
outg1245	–	0	0	0	0	0	–	–	–	0	–	0	–	0	–	0	0	0	0	–	0	0	–	0	0	0	0	–	0	–	0	0	–	–	–	0	–	–	–	0
outg1235	–	0	0	0	0	0	0	–	–	0	–	0	–	–	–	0	0	0	0	–	0	–	–	0	0	0	0	0	0	–	0	0	–	–	–	0	–	–	1	0
outg1234	–	0	0	0	0	0	–	–	1	0	–	0	–	–	–	0	0	0	0	–	0	–	0	0	0	0	0	–	0	–	0	0	–	–	–	0	0	–	0	0
tucumana	0	0	0	1	1	0	1	1	1	2	1	1	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	1	0	0	0	1	0	1	1	0	0	1
nigerrima	0	0	0	1	1	0	1	1	1	2	1	1	1	0	1	0	0	0	1	0	1	1	0	0	1	0	0	1	1	1	0	0	0	1	0	1	1	0	0	1
chalybaea	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	1
latitarsis	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	1
discrepans	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0	1	0	0	1
muelleri	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	1	0	1	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0	1	0	0	1
herbsti	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0	1	0	1	1
nigripes	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0	1	0	1	1
caeruleus	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0	1	0	1	1
goeldianus	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	1	0	0	1	0	1	1
melampoda	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	2	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1	1	0	1	1	–	1
oligotricha	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	1	2	1	1	1	0	0	0	1	0	1	0	1	0	1	1	1	1	0	1	1	–	–
pygmaea	1	1	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	2	1	1	1	0	0	0	1	0	1	0	0	0	1	1	1	1	0	1	1	–	1
maculata	1	1	1	2	0	0	0	0	0	0	0	1	1	1	0	1	1	1	2	1	1	1	0	0	0	1	0	1	0	0	0	1	1	1	1	0	1	1	–	1
lanei	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	0	1	1	0	0	1	0	1	1	1	1	0	1	0	1	1
bruneri	0	0	0	0	1	0	1	0	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	1	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	1

List of characters

1. Lateral part of lower portion of clypeus. (0) Lateral part one third or less as long as median part, gently bent backward at an angle of 110° or more to median part. (1) Lateral part nearly half as long as median part, abruptly bent backward at an angle of 100°-105° to median part. This character is modified from Roig-Alsina & Michener (1993, character 6). Tapinotaspidines coded zero are variable in the degree of protuberance of the clypeus which, for example, is flattened in *Tapinotaspis* and much less so in species of *Monoeca* and *Caenonomada*. It was not possible to further divide the character due to intermediate conditions present in several species.
2. Paraocular area next to eye. (0) Flat. (1) Forming convex, sometimes cariniform, elevation along the eye margin. This elevation was considered homologous to the paraocular carina present in bees of other tribes, although it never is a sharply delimited carina.
3. Punctation of face. (0) Punctures on disc of clypeus and supraclypeal area fine, in a few cases punctures fairly strong, but in these cases due to long, stout hairs arising from them. (1) Punctures on disc of clypeus and supraclypeal area strong, giving rise to short or no hairs.
4. Preoccipital carina. (0) Vertex behind ocelli rounded, sometimes head more or less abruptly sloping behind, but not forming a ridge, nor a carina. (1) Vertex behind ocelli forming elevated ridge. (2) Vertex behind ocelli forming a lamellate carina. State 1 is present in both sexes of *Monoeca* and *Trigonopedia*, but only in the female sex in *Tapinotaspoides*, suggesting an independent origin of the ridge; nevertheless it was coded as homologous.
5. Face and gena of male. (0) Area between lateral ocellus and eye convex, flat, or slightly concave, vertex not depressed; when face depressed, only along paraocular areas; gena convex. (1) Area between lateral ocellus and eye, and also vertex, conspicuously depressed (Fig. 18); face above antennal sockets also depressed; gena flattened to slightly concave. State 1 is approached in some Eucerini, but the degree of depression seen in males of *Caenonomada* and *Tapinotaspoides* is not seen in the outgroups.
6. Antenna of male. (0) Not elongate; second flagellomere less than 1.5 times longer than wide. (1) Antenna elongate; second flagellomere at least 1.5 times longer than wide, and much longer than first flagellomere.
7. Antenna of female. (0) First flagellomere short, at most 1.5 times as long as its apical width, less than half of length of scape. (1) First flagellomere long, 1.8 times as long as its apical width or more, half or over half of length of scape.
8. Thickening of secondary tentorial bridge below antennal socket. Tapinotaspidines have a Y-shaped subantennal suture (Fig. 18), the mesial branch of which corresponds internally to the union of the thickening of the secondary tentorial bridge to the head wall. (0) Attachment of bridge to head wall close to antennal socket. (1) Attachment of bridge to head wall separated from antennal socket by 1 or more times thickness of bridge.
9. Postoccipital pouch below foramen magnum (Roig-Alsina & Michener 1993: Fig. 12, character 21). (0). Absent. (1) present.
10. Fan-shaped posterior sheets of tentorium. (0) Well developed. (1) Reduced, directed laterally so outer margin of sheet joins head wall at level of center of foramen magnum. (2) Reduced, but directed ventrally so outer margin of sheet joins head wall at level of ventral margin of foramen magnum. The reduction of the sheets follows a different pattern in the species of *Tapinotaspoides* and *Chalepogenus*. The character is treated as non-additive.
11. Attachment of secondary tentorial bridge to posterior wall of head (Roig-Alsina & Michener 1993: Figs. 11, 12, character 23; state coded 0 here corresponds to their state 2). (0) Bridge broadly fused to hypostoma. (1) Bridge attached above hypostoma, but connected to it by vertical broad septum.
12. Maxillary stipes with expansion on distal anterior margin. (0) Absent. (1) Present. In Roig-Alsina & Michener (1993: Fig. 14, character 32) *Monoeca* was coded 0, but a closer scrutiny revealed that the expansion is present, although bent mesially.
13. Paraglossa beyond apex of suspensorium. (0) Shorter than 1.3 times length of suspensorium. (1) Longer than 1.5 times length of suspensorium. State 1 unites states 1 and 2 of Roig-Alsina & Michener (1993, character 58).
14. Annular hairs of glossa (Roig-Alsina & Michener 1993: character 55). (0) Extending to base of flabellum. (1) Glossa with a bare section basal to flabellum.
15. Small sclerite lateral to subligular process (Roig-Alsina & Michener 1993: Fig. 16). (0) Absent. (1) Present. Among tapinotaspidines this sclerite, when present, is not very conspicuous.

16. Pre-episternal internal ridge (Roig-Alsina & Michener 1993: character 68; states 0 and 1 here correspond to their states 1 and 2). (0) Curved posteriorly toward scrobe. (1) Short, not reaching level of scrobe.
17. Ventrolateral extensions of pronotum (Roig-Alsina & Michener 1993, character 62). (0) Separated midventrally. (1) Fused midventrally.
18. Anterolateral angles of pronotum. (0) Rounded, in some species more or less flattened. (1) Angular.
19. Pubescence of scutum. (0) Long, consisting of hairs at least as long as width of flagellum. (1) Consisting of two strata, one of extremely short hairs as in 2 below, and another of scattered hairs usually as long as width of flagellum or longer. (2) Extremely short, under low magnification appearing as a plush; hairs at most 0.3 times as long as flagellar diameter.
20. Pubescence of venter of female thorax, coxae and trochanters. (0) Consisting of branched hairs or intermixed branched and simple hairs. (1) Hairs simple, not branched.
21. Membrane closing space behind metasternum and hind coxae and extending to base of first metasomal sternum (Roig-Alsina & Michener 1993: Fig. 24, character 72). (0) Arising basally to the free apex of metasternum. (1) Arising from apical margin of metasternum. This is a synapomorphy of tapinotaspidines.
22. Lateral carina of propleuron (Roig-Alsina & Michener 1993: Fig. 19, character 63). (0) Present. (1) Absent.
23. Internal longitudinal ridge (third phragma) on lower extremity of metapostnotum (Roig-Alsina & Michener 1993: Fig. 26, character 75). (0) Ridge extending as acute point visible through propodeal articulating orifice when metasoma is removed. (0) Ridge not extending beyond upper margin of propodeal articulating orifice.
24. Lower point of internal longitudinal ridge of metapostnotum. (0) Point small to absent. (1) Point exceedingly large, lamellate.
25. Hind coxal articulation (Roig-Alsina & Michener 1993: Figs. 25, 26, character 76). (0) At level of submarginal groove of propodeum. (1) Above submarginal groove.
26. Submarginal groove of propodeum. (0) Groove ending anteriorly near posterior margin of middle coxa. (1) Groove ending anteriorly at level of hind coxal articulation.
27. Sulcus above propodeal spiracle. (0) Absent. (1) Sulcus extending from dorsal margin of spiracle to margin of metanotum.
28. Sclerotized bridge isolating bases of hind tibial spurs. (0) Bridge almost complete, briefly interrupted in middle. (1) Bridge complete (Cane 1979: Fig. 16).
29. Sclerotized bridge isolating bases of hind tibial spurs. (0) Bridge moderately broad (Cane 1979: Fig. 16). (1) Bridge remarkably broad.
30. Inner hind tibial spur. (0) Margins of spur serrate. (1) Inner margin of spur pectinate.
31. Inner hind tibial spur. (0) Spur straight, sometimes sinuous apically or bent at apex. (1) Spur strongly curved and broadened basally, with sinuous shaft (Figs. 19, 20).
32. Hind basitarsus of female. (0) Distinctly projecting above articulation of second tarsomere (Figs. 25, 26). (1) Scarcely projecting, truncate (Figs. 23, 24).
33. Hind basitarsus of female, inner brush of hairs. (0) Hairs not specialized. (1) Hairs of brush apically forming comb of rigid, stout setae directed distally.
34. Trunk of anterior tibial spur. (0) Simple. (1) With expansion ("anterior velum" of Schönitzer, 1986) at right angles to velum.
35. Marginal cell of forewing. (0) Length of cell subequal to or shorter than distance from its apex to apex of wing. (1) Longer than distance from its apex to apex of wing (1.25 times or more).
36. Jugal lobe of hind wing. (0) Long, at least 0.35 times length of vannal lobe measured from wing base. (1) Short, 0.25 times length of vannal lobe or less.
37. Pubescence of female metasomal terga. (0) Apex of terga covered with hairs, usually forming apical bands. (1) Terga with bare apical areas, wider medially.
38. Pygidial plate of male. (0) Present, distinct at least apically. (1) Absent.
39. Pygidial plate of male. (0) Well defined, with lateral margins delimiting plate from rest of disc of tergum. (1) Distinct apically only, as sclerotized apical rim.
40. Spatha of penis, median ventral projection (Roig-Alsina & Michener 1993: Figs. 35, 36, character 128). (0) Absent. (1) Present.

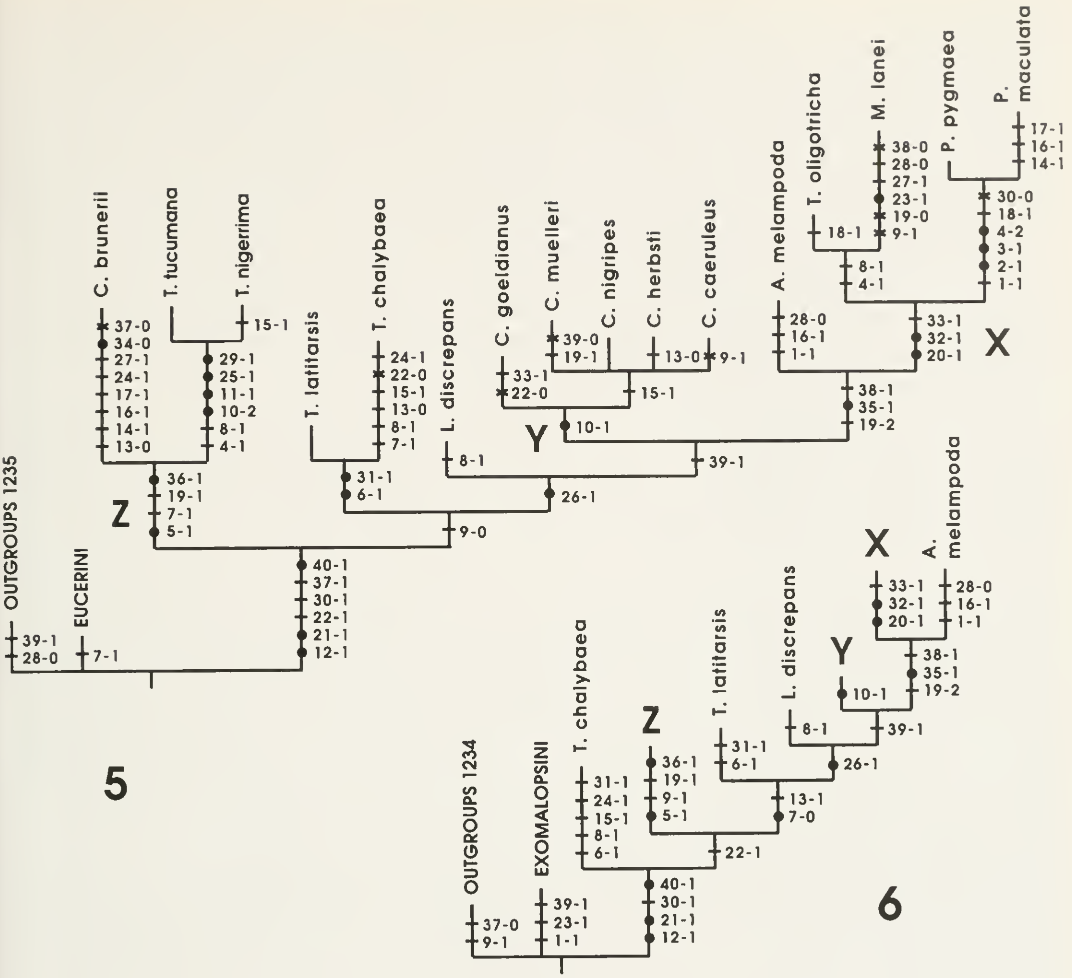


Figs. 1-4. Cladograms showing relationships within Tapinotaspidini according to analyses 1-3. Characters are numbered as in the List of characters and in Table 1. Bars indicate changes that occur in parallel or are reversed elsewhere in the tree, crosses indicate reversals, and dots indicate changes that occur only once in the tree.

Analyses

Analysis 1 (Emphorini as outgroup). Three minimum-length trees were obtained (length 74, ci 58, ri 66). Tree number one is shown in figure 1. Branches X and Y switch positions in the second tree (Fig. 2), according to a different interpretation of character state 8-1 (attachment of secondary tentorial bridge separated form antennal socket), which appears once in the tree, and character state 35-0 (marginal cell short), which reverses in branch X. *A. melampoda* and branch X form a monophyletic group in the third tree (Fig. 3), supported by character state 18-2 (extremely short pubescence of scutum). In this tree *M. lanei* and *T. oligotricha* have a sister group relationship supported by character states 1-0, 4-1, and 8-1.

Analysis 2 (Ctenoplectrini as outgroup). The analysis yielded two minimum-length trees (length 77, ci 55, ri 65). The topology of the trees is identical to trees 1 (Fig. 1) and 2 (Fig. 2) of analysis 1. The distribution of the character states in both trees is similar to that of analysis 1, except for character state 30-1 (pectinate hind tibial spur), which is shared by Ctenoplectrini and Tapinotaspidini, and five character states which are apomorphous for the Ctenoplectrini (8-1, 9-1, 11-1, 20-1, and 33-1).



Figs. 5-6. Cladograms showing relationships within Tapinotaspidini according to analyses 4 and 5. Symbols as in figures 1-4.

Analysis 3 (Ancylini as outgroup). The analysis yielded four minimum-length trees (length 76, ci 56, ri 65). Two trees are identical in topology to trees 1 and 2 of analyses 1 and 2 (Figs. 1, 2). The third tree is similar to tree number 3 of analysis 1 (Fig. 3), but *M. lanei* appears as the sister group of the clade (*T. oligotricha* (*P. pygmaea*, *P. maculata*)). The distribution of the character states is similar to that of previous analyses, except for those of the outgroups. Branch X is the sister group to all other tapinotaspidines in the fourth tree (Fig. 4).

Analysis 4 (Eucerini as outgroup). Two minimum-length trees were obtained (length 75, ci 57, ri 66). One of the trees is shown in figure 5. The other tree only differs in the position of *M. lanei*, which appears as the sister group of (*T. oligotricha* (*P. pygmaea*, *P. maculata*)).

Analysis 5 (Exomalopsini as outgroup). The analysis yielded two minimum-length trees (length 76, ci 56, ri 65). The two trees differ, as in analysis 4, in the position of *M. lanei*. Analysis 5 differs from all others in that *T. chalybaea* and *T. latitarsis* do not form a monophyletic group (Fig. 6).

Discussion of analyses

There are three groups of taxa which are stable throughout the five analyses, indicated as branches X, Y, and Z (Figs. 1-6). Branch X comprises *Paratetrapedia*, *Trigonopedia*, and *Monoeca*. The position of *Trigonopedia* in the branch varies, being alternatively the sister group of each one of the other two taxa. It should be noted that *Arhysoceble*, previously included as a subgenus of *Paratetrapedia*, in no case forms part of the clade. Branch Y is a monophyletic group including species previously placed in *Chalepogenus*, in the subgenus *Tapinorhina* of *Tapinotaspis*, and in the subgenus *Lanthanella* of *Lanthanomelissa*. Branch Z indicates the sister group relationship of *Caenonomada* and *Tapinotaspoides*.

The five analyses can be grouped in two major alternatives. When the tribes Emphorini, Ctenoplectrini, or Ancylini are taken as outgroups (Figs. 1-4) the clade (*Lanthanomelissa* (*Tapinotaspis* (*Caenonomada Tapinotaspoides*))) is constant and shown as a derived group, while *Arhysoceble*, *Chalepogenus*, and branch X represent basal branches of the trees. In the second alternative, when the tribes Exomalopsini or Eucerini are taken as outgroups, branch Z and *Tapinotaspis* species are the basal branches, while the other taxa form a constant derived clade as shown in the cladograms (Figs. 5, 6).

The results of the analyses lead to a new understanding of the scope of the genera of Tapinotaspidini. The genus *Tapinotaspis* as conceived by Michener & Moure (1957) was clearly polyphyletic, and should be restricted to include its type species and probably also *T. latitarsis*. Although analysis 5 (Fig. 6) does not support inclusion of the latter, the shared specialization of the oil-collecting structures of *chalybaea* and *latitarsis* would seem to favor the inclusion of the two taxa in the same genus.

Tapinotaspoides is recognized at the generic level. Its close relationship to *Caenonomada* was unsuspected before.

Lanthanomelissa is a distinct genus of Tapinotaspidini. Species attributed to this genus, apart from Holmberg's type species and four species described by Urban (1996) recently, belong elsewhere.

The scope of *Chalepogenus* is broadened to include all the species in branch Y (Figs. 1, 5). The length of the pubescence of the scutum and the color of the integument have been two misleading characters in the interpretation of the generic assignment of these species. The male of the type species has exceedingly short pubescence on the scutum and yellow integumentary bands on the metasoma, while the female has some long hairs on the scutum accompanying the short pile and dark metasoma. The female of *C. muelleri* was included in *Tapinotaspis* by Michener & Moure (1957, as *T. sabularum* Holmberg). There are pairs of species in the genus (many undescribed) in which one has pale and the other dark body color, and similarly pairs in which one species has short and the other long pubescence on the scutum.

Arhysoceble and *Trigonopedia* are given generic status. The sister group relationship between *Trigonopedia* and *Monoeca* suggested in several trees merits further study. The broad pygidial plate seen in females of *Trigonopedia* and the extremely broad pygidial plate of females of *Monoeca* may represent a shared derived character.

Evolution of the oil-collecting structures

Vogel (1974) demonstrated the existence of specialized tissues in flowers, which he called elaiophores, that produce oils as a reward for pollinators. He also demonstrated that certain groups of bees have specialized to exploit these resources. Since that time the literature on oil-producing plants, on oil-collecting bees, and on their relationships has steadily grown, as shown by the reviews of Neff & Simpson (1981), Simpson & Neff (1981), Buchmann (1987), and Vogel (1988). Nevertheless, the understanding of these relationships has been hampered by the lack of explicit phylogenetic hypotheses on the history of the groups of bees involved.

Oil collecting has arisen independently several times in the families Melittidae and Apidae. Among apids, oil-collecting groups are the Centridini, the Tetrapediini, the Ctenoplectrini, and the Tapinotaspidini. The number of times that oil collecting may have arisen in the family Apidae is 3 or 4, depending on the unresolved relationship between the last two tribes (Roig-Alsina & Michener 1993).

The Tapinotaspidini are the most diverse group in terms of number of genera and variety of oil-collecting adaptations. Some structures related to oil collecting, such as the mixed type of scopal hairs on the hind legs and the pectinate inner hind tibial spur, were undoubtedly present in the ancestral tapinotaspidine. Although these two features present variation (for example the inner hind tibial spur may be coarsely pectinate and twisted as in *Tapinotaspis* or may even change to a serrate condition as in some

Paratetrapedia), the following discussion pertains to other structures that are present only in certain genera of Tapinotaspidini.

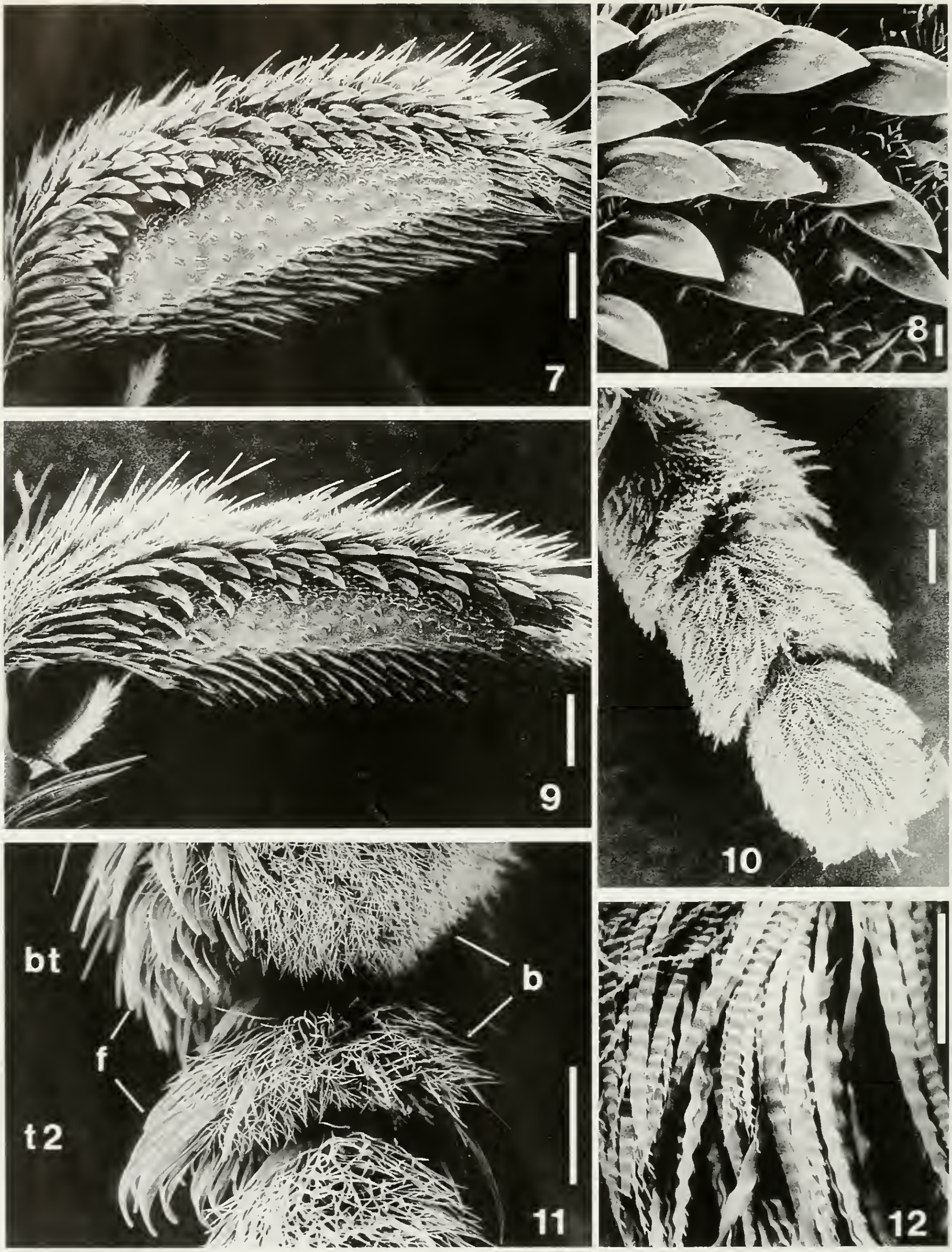
The structures that will be discussed are unknown in the outgroups, so inferences on their evolution can only be made a posteriori once we have established certain phylogenetic hypotheses. These structures are formed by modification of shape and size of some leg segments and particularly by the specialization of various groups of hairs on the legs and possibly also on the metasomal sterna. Some of these modified fields of hairs have been positively shown to participate in oil collecting, as for example the foretarsal pads of fine branched setae present in species of *Arhysoceble* and *Chalepogenus* (Vogel 1974). Evidence of use in oil collecting for other groups of hairs is indirect, as for the metasomal fringes of *Tapinotaspoides* (Neff & Simpson 1981). Still other groups of modified hairs, as the flattened hairs present on the anterior tarsomeres 2-4 of species of many genera, have not been paid attention to and should be investigated.

Six genera have modified foretarsi. Four of them, *Arhysoceble*, *Chalepogenus*, *Trigonopedia*, and *Paratetrapedia* present the same basic pattern. The anterior basitarsus is anteroposteriorly compressed, its anterior surface is convex, bearing simple setae, its posterior surface is flattened to moderately concave bearing an area of dense, fine branched hairs (Figs. 11, 13, b) which may cover the entire surface, and its dorsal margin has a compound comb of simple, stiff setae, variously developed (Fig. 13, c). The apex of the tibia and the tarsomeres 2-4 may also have areas of dense, fine branched hairs. This type of oil-collecting structure has been described and illustrated by Vogel (1974) and by Neff & Simpson (1981). It should be added that the tarsomeres 2-4 laterally, and sometimes the basitarsus apically, bear flattened setae (Figs. 11, 13, f). This type of structure is referred to hereafter as the *Arhysoceble* type. Other types evolved from it by magnification or loss of some of the groups of setae. Among species of *Paratetrapedia* the reduction of the area with fine branched hairs on the posterior surface of the basitarsus is common; these species have a well developed dorsal compound comb. The structure and function of the compound comb of a species of *Paratetrapedia* has been studied by Buchmann & Buchmann (1981). Another type of modification is seen in many species of *Chalepogenus*, in which the pad of fine branched hairs is outstandingly developed and the dorsal compound comb poorly differentiated. This is the case of *C. caeruleus*, a species that uses the pad for collecting oil from the trichome elaiophores of *Calceolaria* flowers (Vogel, 1974). Current studies of the phylogeny of the species of *Chalepogenus* (Roig-Alsina, in preparation) indicate that this is a derived condition within the genus.

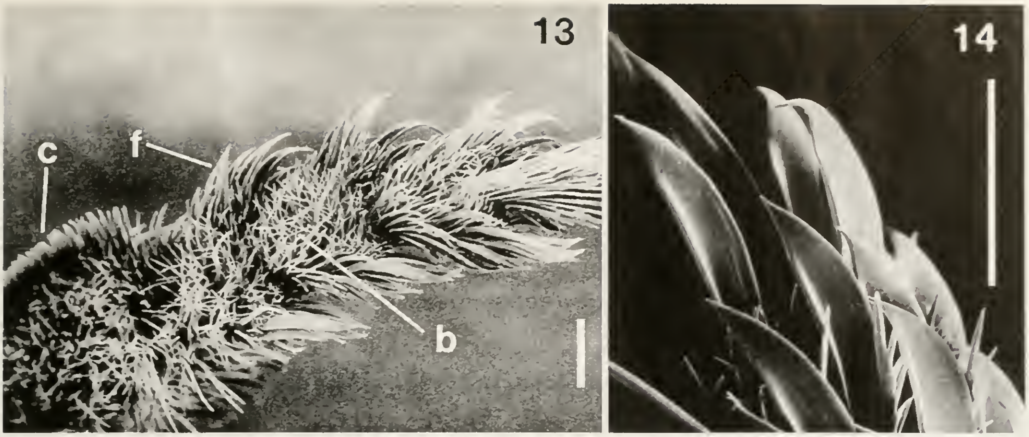
Lanthanomelissa has a unique type of modified foretarsus (Figs. 7-9). It is anteroposteriorly compressed and the posterior surface is covered with dense, fine branched hairs, much as in the *Arhysoceble* type, but the anterior surface is flat instead of convex and is almost bare medially. The anterior surface has a polished longitudinal area margined basally and dorsally by rows of flattened, short, lanceolate setae (Fig. 8); the polished area bears scattered minute setae. The basitarsus of the male (Fig. 9), although slenderer than that of the female (Fig. 7), has the same structure.

Caenonomada has flattened setae on the forebasitarsus as well as on the anterior tarsomeres 2-4; those of the forebasitarsus are well developed on the apical third of the anterior surface and along the dorsal margin. The flattened setae (Fig. 14) have the apex pointed and the outer surface somewhat concave with a shallow longitudinal furrow, much as in similar setae of the species of *Lanthanomelissa* and species with the *Arhysoceble* type of foretarsus. The posterior surface of the basitarsus has an area of fine branched hairs, although restricted to a triangular longitudinal band broadest apically. The tarsomeres 2-4 also have fine branched hairs on their dorsal and posterior surfaces. The tarsomeres 2-4 of *Caenonomada bruneri* closely resemble the tarsomeres of some *Chalepogenus* species (e.g. *C. goeldianus*). It is interesting to note that this combination of areas of flattened setae and areas of fine branched hairs on the anterior tarsus, and particularly on tarsomeres 2-4, is strikingly paralleled by the species *Centris hyptidis* (Vogel & Machado 1991), which collects oils on trichome elaiophores. The possibility that *Caenonomada* species are oil collectors needs to be investigated in the field. Many pinned specimens of *Caenonomada bruneri* in collections have the front, and also sometimes the middle legs, dirtied with a dark paste, much as is usually seen in some other tapinotaspidines. I have not seen collection specimens of *Caenonomada* bearing oily loads on the hind legs, and in those with pollen loads the pollen is dry and easily separable.

Monoeca species have combs on the ventral margin of the front and middle tarsi, which closely resemble in position the combs of *Epicharis* and *Centris*. Neff & Simpson (1981) described the combs of *Monoeca* in detail and pointed out the differences from the centridines, mainly the nature of the combs, which are formed by several rows of simple setae in *Monoeca*. Species of this genus lack the areas of fine branched hairs and the flattened setae present in other tapinotaspidines. Present understanding of the relationships of *Monoeca* (Figs. 1-6) indicates that their oil-collecting structures are derived from the *Arhysoceble* type. The



Figs. 7-12. *Lanthanomelissa discrepans* Holmberg: 7, left forebasitarsus of female, anterior surface; 8, same, close-up of flattened hairs; 9, left forebasitarsus of male, anterior surface. *Tapinotaspis latitarsis* (Friese): 10, left middle leg of female, dorsal view of tarsomeres 3-5. *Chalepogenus* sp.: 11, left foreleg of female, dorsal view of apex of basitarsus and second tarsomere: bt, basitarsus; t2, second tarsomere; f, flattened hairs; b, fine branched hairs. *Tapinotaspoides tucumana* (Vachal): 12, hairs of the apical fringe of the female second metasomal sternum. Scale lines: Figs. 7, 9-12 = 0.1 mm; Fig. 8 = 0.01 mm.



Figs. 13-14. *Chalepogenus muelleri* (Friese): 13, right foretarsus of female: apex of basitarsus, tarsomeres 2-4, and base of distotarsus; c, compound comb of setae; f, flattened hairs; b, fine branched hairs. *Caenonomada bruneri* Ashmead: 14, left foretarsus of female, flattened setae on apex of basitarsus. Scale lines = 0.1 mm.

ventral compound combs of *Monoeca* are unique among tapinotaspidines, although it should be noted that some *Paratetrapedia* (e.g. *P. maculata*) have developed a comb-like row of stout spiniform setae on the ventral margin of the posterior surface of the forebasitarsus.

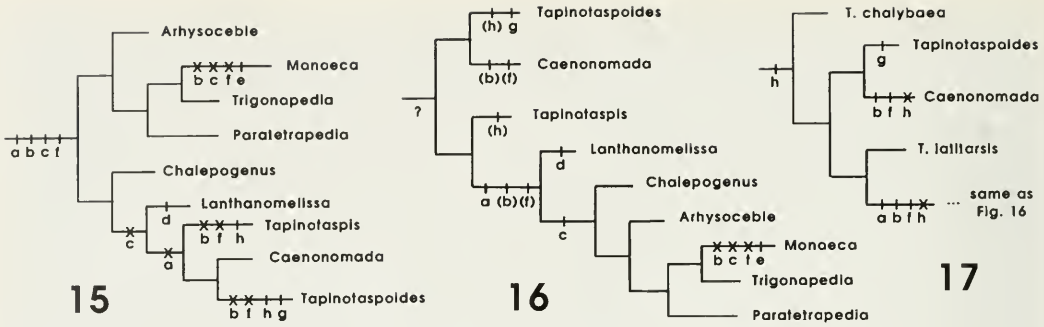
Tapinotaspis species have oil-collecting brushes on the tarsi of the middle legs (Fig. 10; Neff & Simpson 1981, Simpson & Neff 1981, Cocucci 1991), present in both sexes. The brushes are particularly well developed on the tarsomeres 2-4, but dense brushes may also be present on the basitarsus and the distotarsus depending on the species. The use of these brushes in oil collecting has been studied by Cocucci (1991).

The species of *Tapinotaspoides* also have brushes on the middle legs, but they are asymmetrical, and not as well developed as those of *Tapinotaspis*. The postero-dorsal margin of the basitarsus and the posterior sides of the tarsomeres 2-4 bear long branched hairs, while the anterior surface of the basitarsus is covered by a mixture of simple and branched short hairs. *Tapinotaspoides* species have the apical fringes of metasomal sterna 2-4 formed by ribbon-like, wavy hairs (Fig. 12); the fifth sternum bears a fringe of branched hairs, as is usual in other bees. Neff & Simpson (1981) have called attention to the fringes of specialized hairs of *Tapinotaspoides*, and offer indirect evidence of their use in oil collecting. Actual observations on the oil-collecting behavior of *Tapinotaspoides* species and their possible use of the middle legs and/or the metasomal fringes are still lacking.

Figures 15-17 show the possible evolution of the various structures mentioned above, according to the results obtained in the phylogenetic study. Characters a to h (Figs. 15-17) are plotted onto the trees and their points of origin are determined by minimizing the number of times that every character appears in the trees. Each character has two possible states: present or absent. Characters b and f (fine branched and flattened hairs of the anterior basitarsus respectively) are defined as if one type of hair could arise independently of the other, but this may not be the case since they can be functionally related. The brushes of hairs of the middle tarsus of *Tapinotaspis* and *Tapinotaspoides* are morphologically diverse, but have been treated as homologous (character h).

All the tree topologies obtained from analyses 1-3 (Figs. 1-4) render the same hypothesis of evolution for characters a-h, which is exemplified (Fig. 15) using the topology of figure 3. This hypothesis suggests that the *Arhysoceble* type of foretarsus is the ancestral condition for the whole tribe. In this hypothesis the distribution of characters h, b, and f in the clade (*Tapinotaspis* (*Caenonomada Tapinotaspoides*)) allows for several equally parsimonious interpretations. Character h may arise in parallel (as shown in Fig. 15) or only once, being then lost in *Caenonomada*; similarly, characters b and f may be lost twice independently, or may be lost in the ancestor of this clade and then regained in *Caenonomada*.

Plotting characters a-h onto figure 5 (Fig. 16) is inconclusive as to whether the foretarsal or the middle tarsal type of structure is ancestral for the tribe. The state of characters h, b and f cannot be unambiguously assigned to the root. Following this hypothesis the *Arhysoceble* type of foretarsus arose only once by the



Figs. 15-17. Trees showing different hypotheses of evolution of structures of Tapinotaspidini involved or possibly involved in oil collecting. Dashes indicate origin of the traits, crosses their loss. Characters in parentheses have ambiguous assignment, see text for explanation. **a**, forebasitarsus compressed anteroposteriorly. **b**, forebasitarsus with fine branched hairs on posterior surface. **c**, forebasitarsus with compound comb of setae on dorsal margin. **d**, forebasitarsus with anterior surface flattened with polished longitudinal area. **e**, forebasitarsus and middle tarsus with ventral combs of setae. **f**, forebasitarsus and/or tarsomeres 2-4 with flattened hairs. **g**, metasomal fringes with specialized hairs. **h**, tarsus of middle leg with dense brushes of hairs.

acquisition of the compound comb by an ancestor with compressed basitarsus and bearing areas of fine branched and flattened hairs.

Another alternative hypothesis results from plotting characters a-h onto the tree in figure 6 (Fig. 17). Here the foretarsal specializations of *Caenonomada* species (characters b, f) are shown as independently derived. The figure shows the presence of brushes on the middle tarsus (character h) as the ancestral condition for the whole tribe, but it is equally parsimonious to interpret that the presence of these brushes arose independently in *Tapinotaspis chalybaea*, in *T. latitarsis*, and in *Tapinotaspoides*.

Key to the genera of Tapinotaspidini

1 Middle tibial spur with angle close to apex, which appears as nearly notched (Fig. 21). Forebasitarsus with comb of strong setae along margin following strigilar concavity; middle basitarsus with similar comb on apical half. Venter of female thorax with hooked setae .... *Monoeca*

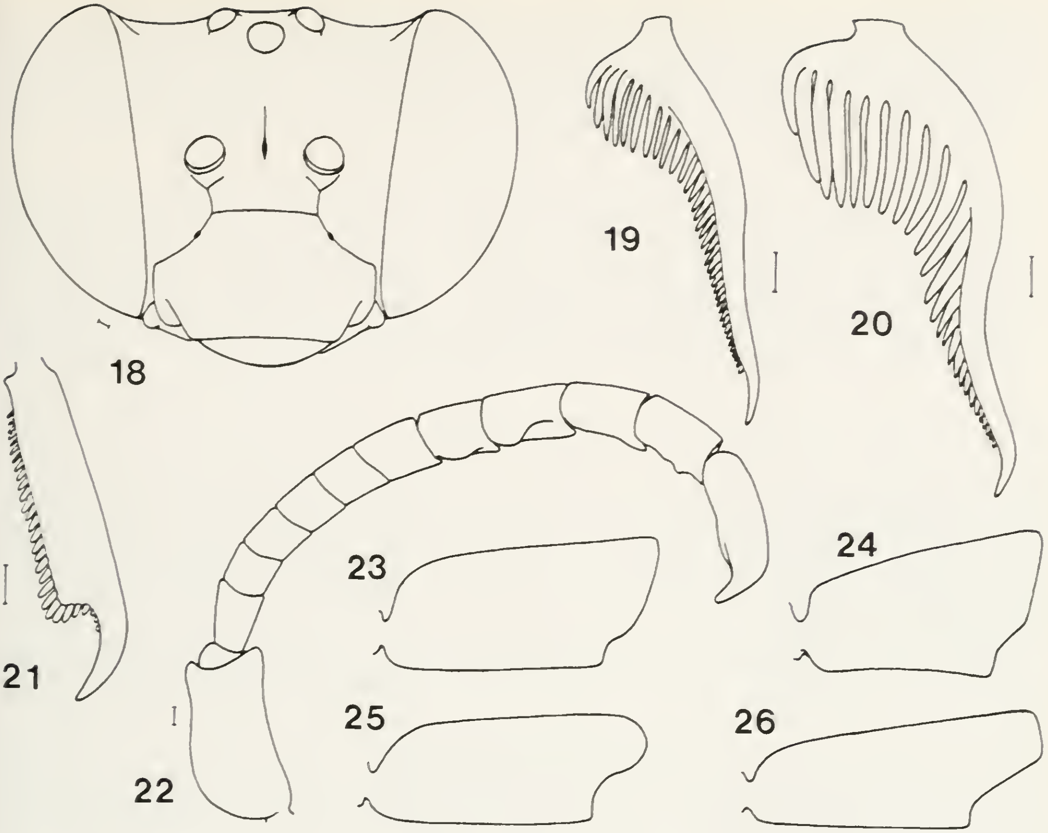
– Middle tibial spur tapering apically. Forebasitarsus without comb, or with comb along margin opposite to strigilar concavity. Middle basitarsus without comb. Venter of female thorax with hairs branched or simple, not hooked 2

2 Shaft of inner hind tibial spur strongly curved basally, sinuous; spur coarsely pectinate (Figs. 19, 20). Tarsomeres 2-4 of middle legs hairier than those of anterior or posterior legs, with dense brushes of hairs (Fig. 10); hairs of brushes of uniform length. Antenna of male elongate, with first flagellomere shorter than second, and second flagellomere 1.5 or more times longer than wide .... *Tapinotaspis*

– Shaft of inner hind tibial spur not curved basally, when sinuous only apically; spur either pectinate or serrate. Tarsomeres 2-4 of middle legs not hairier than those of anterior or posterior legs; in a few cases with brushes (*Tapinotaspoides*), but then brushes asymmetrical, with hairs longer posteriorly. Antenna of male with first flagellomere longer than second, and second flagellomere as long as or shorter than its apical width 3

3 First flagellomere 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 (Fig. 18). Jugal lobe of hind wing short, 0.3 times as long as vannal lobe measured from wing base, or less 4

– First flagellomere 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



Figs. 18-26. *Tapinotaspoides nigerrima* (SCHROTTKY): 18, face of male. *Tapinotaspis chalybaea* (FRIESE): 19, inner hind tibial spur of male; 20, inner hind tibial spur of female. *Monoeca lanei* (MOURE): 21, middle tibial spur of female. *Caenonomada bruneri* ASHMEAD: 22, antenna of male. *Trigonopedia oligotricha* MOURE: 23, hind basitarsus of female. *Monoeca lanei* (MOURE): 24, hind basitarsus of female. *Lanthanomelissa discrepans* HOLMBERG: 25, hind basitarsus of female. *Chalepogenus parvus* sp.n.: 26, hind basitarsus of female.

4 Integument of legs and metasoma extensively marked with yellow. Female metasomal sterna 2-4 with hairs of apical fringes branched, those of second sternum shorter than hairs of sterna 3 or 4. Scape of male swollen (Fig. 22). Hind leg of male with one tibial spur .... *Caenonomada*

– Integument of legs and metasoma black. Female metasomal sterna 2-4 with hairs of fringes ribbon-like, wavy (Fig. 12); apical fringes 2-4 of similar length. Scape of male slender. Hind leg of male with two tibial spurs .... *Tapinotaspoides*

5 Vertex of head behind ocelli carinate. Hind basitarsus of female scarcely projecting, truncate (Figs. 23, 24) 6

– Vertex of head behind ocelli rounded or sloping, not carinate. Hind basitarsus of female distinctly projecting above articulation of second tarsomere (Fig. 25, 26) 7

6 Face with fine punctures; punctures scarcely wider than arising hairs. Paraocular areas flat next to orbits .... *Trigonopedia*

– Face with at least some strong punctures on supraclypeal area and clypeus; punctures several times wider than arising hairs, frequently giving rise to no hairs at all. Paraocular areas convex next to orbits .... *Paratetrapedia*

7 Anterior surface of forebasitarsus flattened, with polished longitudinal area bearing minute setae; polished area margined basally and dorsally with rows of short flattened setae (Figs. 7-9). Forewing with two submarginal cells. Pygidial plate of male distinct, glabrous .... *Lanthanomelissa*

– Anterior surface of forebasitarsus convex, evenly covered with long setae. Forewing usually with three submarginal cells (exception are a few *Chalepogenus*). Pygidial plate of male either absent or upper surface covered by dense hairs 8

8 Scutum evenly covered by dense, extremely short 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 .... *Arhysoceble*

– Scutum usually with long hairs (as long as diameter of flagellum or longer); in a few species hairs extremely short, but some scattered, long hairs present and marginal cell length subequal to distance from its apex to apex of wing. Scutellum evenly rounded, not forming distinct posterior surface. Pygidial plate of male at least indicated apically by sclerotized, rounded margin .... *Chalepogenus*

Treatment of genera

As a result of the present study the scope of the genera *Tapinotaspis*, *Chalepogenus*, and *Lanthanomelissa* is modified. Brief diagnoses of the three genera are presented below, as well as notes on critical species. *Trigonopedia*, *Tapinotaspoides*, and *Arhysoceble* are accorded full generic status. Their scope is as defined originally by Moure (1941, 1944, and 1948 respectively). Redescriptions of these groups, as subgenera, are in Michener & Moure (1957).

The genus *Paratetrapedia* is understood to comprise the groups that Michener & Moure (1957) defined as *Xanthopedia* Michener & Moure, *Tropidopedia* Michener & Moure, *Amphipedia* Michener & Moure, *Lophopedia* Michener & Moure, and *Paratetrapedia* sensu stricto. *Lissopedia* Moure (1994b) is also included. All these bees share elevated paraocular areas, strong punctation on the face, a sharp preoccipital carina, and frequently the presence of a pronotal carina. The metasomal sterna of the males are variously modified; usually the fourth sternum is emarginate or with membranous areas and with groups of long hairs at least laterally, while sterna 2-3 have weak fringes of hairs, although groups of specialized hairs may also occur. This is a large genus in much need of revisionary study. *Monoeca* and *Caenonomada* have been redescribed by Michener & Moure (1957), and are not treated further here.

Tapinotaspis Holmberg

Tapinotaspis Holmberg, 1903: 413. Type species: *T. chacabucensis* Holmberg, by designation of Sandhouse, 1943: 603.

Bees 6.3-11.5 mm long. Integument dark, but males sometimes with yellow clypeus. Pubescence of head and thorax rather long; scutum with hairs longer than flagellar diameter. Female metasoma with bare, polished apical areas, at least on terga 1-3; males with conspicuous apical hair bands on terga 2-6. Vertex behind ocelli without carina, not depressed between lateral ocellus and eye. Clypeus flat, apically with short lateral parts. Paraglossa beyond apex of suspensorium 1.15-1.65 times as long as suspensorium. Antenna of female with first flagellomere long in the type species (1.8 times as long as its apical width), but not much so in *latitarsis* (1.3 times). Male with long antenna; first flagellomere shorter than second, and second longer than its apical width. Scutellum weakly convex; metanotum weakly to moderately convex, slanting to rear; metapostnotum and propodeum with a more or less distinct basal slanting area, then abruptly inclined. Basitarsus of foreleg with round section, bearing simple hairs. Middle tarsi of both sexes with dense brushes of hairs, specially on tarsomeres 2-4. Inner hind tibial spur broadened and curved basally, with sinuous shaft. Hind basitarsus projected above articulation of second tarsomere. Marginal cell of forewing 1.0-1.2 times as long as distance from its apex to apex of wing. Jugal lobe of hind wing 0.4 times as long as vannal lobe measured from wing base. Submarginal groove of propodeum ending anteriorly near posterior margin of middle coxa. Pygidial plate of male with distinct lateral margins, hairy.

Bees of the genus *Tapinotaspis* are characterized by the dense lateral brushes (Fig. 10) on the elongate tarsi of the middle legs, and the peculiar inner hind tibial spurs (Figs. 19, 20), both features present in the two sexes. Besides the type species, *Tapinotaspis latitarsis* (Friese) is also included in the genus (new combination). This small species (6.3-7.5 mm long), recently redescribed by Moure (1994a), also shares with *chalybaea* the elongate antennae of the males, but differs from this species in several features, as the longer paraglossa, the absence of propleural carina, and the shorter first flagellomere of the female. One of the 5 analyses does not support the inclusion of *latitarsis* in *Tapinotaspis*. The matter deserves further study.

Tapinotaspis chalybaea (Friese)

Exomalopsis chalybaea Friese, 1899: 267. Lectotype female, Brasil, Pará, 1890, Schulze (Zoologisches Museum Berlin, examined, present designation).

Tapinotaspis chacabucensis Holmberg, 1903: 415. Lectotype male, Argentina, Buenos Aires, Chacabuco (Museo Argentino de Ciencias Naturales, Buenos Aires, examined, present designation). Synonymized by Moure, 1948: 335.

Exomalopsis longicornis Friese, 1906: 170. Holotype male, Argentina, Córdoba, Stempelmann (Zoologisches Museum Berlin, examined). Synonymized with *T. chacabucensis* by Brethes, 1910: 290.

All the type specimens are conspecific and correspond to the usual interpretation of the species. The male genitalia and hidden sterna have been illustrated by Michener & Moure (1957). The female selected as lectotype of *E. chalybaea* is the one that better coincides with the original description in color and pubescence. Moure (1944), and Michener & Moure (1957) indicated that the specimen may be mislabeled. Three other specimens in the Zoologisches Museum of Berlin, designated paralectotypes of *E. chalybaea*, bear the following labels: "Brasil Sello" and "487". The lectotype of *T. chacabucensis* bears the following labels: a small whitish square without inscriptions, "chacabucensis Holmberg" and "Tapinotaspis Holmberg." The specimen has the antennae broken beyond the scapes. A second specimen, designated paralectotype, is in poor condition (only part of the head, part of the thorax, wings, and first metasomal tergum left); it only bears a small square paper similar to that of the lectotype.

Lanthanomelissa Holmberg

Lanthanomelissa Holmberg, 1903: 418. Type species *Lanthanomelissa discrepans* Holmberg, by monotypy.

Bees 4.5-7 mm long, with head, thorax, legs, and metasoma variously maculated with yellow. Head and thorax with long hairs, scutum of female with branched hairs at least as long as diameter of flagellum, those of male longer. Metasomal terga 1-3 in the female and 1-2 in the male with bare, polished apical areas. Female sterna 2-5 with well developed apical fringes of hairs, that of second sternum forming a dense median triangular area of long, simple hairs. Vertex of head rounded behind ocelli. Face finely punctured, without paraocular elevated ridges. Clypeus flat, apically with short lateral parts. Paraglossa long, beyond apex of suspensorium 2.6 times as long as suspensorium. Antenna of female with first flagellomere short, 1.2 times as long as its apical width, 0.35 times as long as scape; second flagellomere very short, 0.5 times as long as wide. Pronotum with rounded lateral angles, without pronotal carina. Scutellum moderately convex; metanotum convex; metapostnotum and propodeum uniformly convex. Forebasitarsus anteroposteriorly compressed; anterior surface largely bare and polished, margined basally and dorsally with short, flattened, lanceolate setae; posterior surface with dense pad of fine branched setae. Inner hind tibial spur of female finely pectinate, teeth rather short. Hind basitarsus with rounded projection above articulation of second tarsomere. Forewing with two submarginal cells; marginal cell as long as distance from its apex to apex of wing. Jugal lobe of hind wing half as long as vannal lobe measured from wing base. Submarginal groove of propodeum ending anteriorly at level of hind coxal articulation. Pygidial plate of male slender, glabrous, with distinct lateral margins.

This genus has not been properly recognized since its description by Holmberg. Besides the type species, *Lanthanomelissa* also includes four species recently described by Urban (1996). I have observed females of *L. discrepans* collecting oils from flowers of *Sysirinchium platense* Johnst. in the province of Buenos Aires.

Lanthanomelissa discrepans HOLMBERG

Lanthanomelissa discrepans HOLMBERG, 1903: 419. Lectotype female, Argentina, Buenos Aires, Chacabuco (Museo Argentino Ciencias Naturales, Buenos Aires, examined, present designation). URBAN, 1996: 775, 776, Fig. 4.

Tetrapedia (*Schrottkya*) *goeldiana*: FRIESE, 1908: 58 (females only, not FRIESE 1899, misidentification)

Anthophorula goeldiana: BRETHES, 1909: 222. SCHROTTKY, 1909b: 795.

The specimen designated lectotype is the only extant one of this species preserved in the HOLMBERG collection (Buenos Aires). It bears the following labels: a small whitish square without inscriptions, "discrepans HOLMBERG" and "Lanthanomelissa HOLMBERG." The specimen is in poor condition, lacking the head, the prothorax, the forelegs, and the right middle and hind legs beyond the trochanters. The specimen agrees with HOLMBERG's description, except for the presence of a yellowish spot on the metanotum not mentioned by HOLMBERG.

Regrettably the lectotype lacks the diagnostic forelegs. Due to its poor condition, it could be confused with some pale *Chalepogenus*. It differs from specimens of *C. goeldianus* because it has only two submarginal cells and smaller size. It can be separated from *goeldianus* and other pale *Chalepogenus* by the fringe of hairs of the second sternum, which forms medially a dense triangular area; in *Chalepogenus* such a fringe forms medially an irregular area of sparse hairs. It can be differentiated from *C. parvus*, a species of *Chalepogenus* with two submarginal cells, by the black scutellum (maculated with yellow in *parvus*), the hairs of the metapostnotum as long as those of the propodeum (shorter in *parvus*), and the shape of the hind basitarsus (compare Figs. 25 and 26).

FRIESE (1908) erroneously attributed 2 females of this species collected in Buenos Aires to his species *goeldiana*, which was based on males only. His mistake was followed by SCHROTTKY and BRETHES, as shown by specimens identified by the latter in Buenos Aires. The species identified by MICHENER & MOURE (1957) as *Lanthanomelissa goeldiana* does not correspond either with *goeldiana* FRIESE nor with *discrepans* HOLMBERG; it is a species of *Chalepogenus* described below as *C. parvus*.

Chalepogenus HOLMBERG

Chalepogenus HOLMBERG, 1903: 416. Type species: *Chalepogenus incertus* HOLMBERG, by monotypy.

Schrottkya FRIESE, 1908: 58 (as subgenus of *Tetrapedia*). Type species *Tetrapedia goeldiana* FRIESE, by monotypy.

Desmotetrapedia SCHROTTKY, 1909a: 223. Type species: *Tetrapedia muelleri* FRIESE, by original designation.

Lanthanella MICHENER & MOURE, 1957: 417 (as subgenus of *Lanthanomelissa*). Type species: *Lanthanomelissa completa* MICHENER & MOURE, by original designation.

Tapinorhina MICHENER & MOURE, 1957: 421 (as subgenus of *Tapinotaspis*). Type species: *Exomalopsis caerulea* FRIESE, by original designation.

Tapinorrhina MOURE, 1994a: 274. Emendation for *Tapinorhina* MICHENER & MOURE, 1957.

Bees 4.2-10.0 mm long. Integument black, or maculated with yellow on head, thorax, legs, and metasoma; some species with legs or metasoma partly red and others with bluish metallic reflections. Usually hairy species, with long hairs on scutum, but a few (like *C. muelleri)* with extremely short hairs on dorsum of thorax. Metasoma of both sexes with bare apical areas at least on terga 1-2. Posterior terga, and anterior terga laterally, frequently with apical hair bands, specially the males. Female second sternum with apical fringe forming medially an irregular area of sparse hairs. Vertex of head rounded behind ocelli. Clypeus flat to moderately protuberant. Paraglossa beyond apex of suspensorium 1.2-3.1 times as long as suspensorium. Antenna of female with first flagellomere 0.9-1.5 times as long as its apical width; second flagellomere usually half as long as wide. Scutellum and metanotum weakly convex to convex, former not forming distinct posterior vertical surface; profile of metapostnotum and propodeum variable, from gently slanting to rear (as in the type species) to convex. Forebasitarsus anteroposteriorly compressed; posterior surface flattened to moderately concave bearing pad of dense, fine branched hairs; anterior surface convex, bearing simple hairs; dorsal margin usually with compound comb of simple, stiff setae; in species in which the comb is weak, the pad of fine branched hairs is outstandingly developed. Apex of tibia and tarsomeres 2-4 also with areas of fine, branched hairs. Flattened hairs present on tarsomeres 2-4 and sometimes on basitarsus. Inner hind tibial spur of female moderately to finely pectinate. Hind basitarsus projected above articulation of second tarsomere. Marginal cell of forewing 1.05-1.15 times as long as distance from its apex to apex of wing. Jugal lobe of hind wing 0.35-0.5 times as long as vannal lobe measured from wing base.

Submarginal groove of propodeum ending anteriorly at level of hind coxal articulation. Pygidial plate of male distinct only on apical third of tergum or reduced to sclerotized apical margin; upper surface always hairy.

Chalepogenus caeruleus (FRIESE), *C. goeldianus* (FRIESE), *C. nigripes* (FRIESE), and *C. herbsti* (FRIESE), are all new combinations in *Chalepogenus*.

Chalepogenus muelleri (FRIESE)

Tetrapedia muelleri FRIESE, 1899: 291. Lectotype male, Brasil, SELLO (Zoologisches Museum Berlin, examined, present designation).

Chalepogenus incertus HOLMBERG, 1903: 417. Lectotype male, Argentina, Buenos Aires (Museo Argentino de Ciencias Naturales, Buenos Aires, examined, present designation). Synonymized by BRETHES, 1909: 222.

Tapinotaspis sabularum HOLMBERG, 1903: 415. Holotype female, Argentina, Buenos Aires (Museo Argentino Ciencias Naturales, Buenos Aires, examined). New synonym.

The specimen designated lectotype of *T. muelleri* bears the following labels: "Brasil Sello," "477," and "Tetrapedia muelleri, det. FRIESE 1898, n.sp." A second male specimen with the same labels in the Zoologisches Museum of Berlin is designated paralectotype. Both are in good condition and perfectly agree with the original description. The lectotype of *C. incertus* bears the following labels: a small orange square without inscriptions, "incertus HOLMBERG" and "Chalepogenus HOLMBERG." The specimen lacks part of the head, the antennae beyond the first flagellomere, and the right hind leg beyond the coxa. It agrees with the variety described by HOLMBERG as "alpha", which has the integument of the second metasomal tergum entirely dark. The holotype of *T. sabularum* only bears the label "sabularum HOLMBERG", and is in good condition.

Chalepogenus goeldianus (FRIESE)

Tetrapedia goeldiana FRIESE, 1899: 295. Lectotype male, Brasil, SELLO (Zoologisches Museum Berlin, examined, present designation).

Lanthanomelissa (*Lanthanella*) *completa* MICHENER & MOURE, 1957: 417, 448, figs. 25-27. Holotype male, Argentina, Buenos Aires, Olavarría, Sierras Bayas (Museo Argentino de Ciencias Naturales, Buenos Aires). New synonym.

The specimen designated lectotype of *T. goeldiana* bears the following labels: "Brasil Sello," "480" (handwritten), and "Tetrapedia goeldiana, det. FRIESE 1898, n.sp." A second male specimen has similar labels, but the number 480 is printed; it is designated paralectotype. Both are in good condition and agree with the original description.

Chalepogenus parvus sp.n.

Lanthanomelissa goeldiana: MICHENER & MOURE, 1957: 417, figs. 22-24; COCUCCI, 1991: 27 (not FRIESE, 1899, misidentification).

Lanthanomelissa discrepans: COCUCCI, 1984: 38, 39 (not HOLMBERG, 1903, misidentification).

Diagnosis. This species can be distinguished by its small size, extended yellow maculation, and by the forewing with only two submarginal cells. Proportions indicated below correspond to the holotype.

Description. Female. Length 5.5-6.0 mm (holotype 5.7 mm); length of forewing 4.5-5.0 mm (holotype 4.7 mm). Head, thorax, and propodeum black, with following parts yellow: clypeus, labrum, base of mandible, small supraclypeal spot in some paratypes, upper margin of pronotum, pronotal lobe, anterior spot on tegula, scutellum except axilla, and metanotum medially. Coxae, trochanters, and femora basally black; apex of femora, foretibia, and base of middle tibia yellow, rest of legs yellowish brown. Metasomal terga yellow with brown apical band broadened medially and laterally; first tergum with brownish spot basally. Sterna 1-5 yellowish brown with transverse brown band medially. Wings hyaline with veins and pterostigma dark brown. Vestiture mostly white, but yellowish on scutellum and light brown on metasomal terga and tarsi. Vestiture of scutum dense, short, hairs 0.6-1 times as long as flagellar diameter; scutellum with longer hairs, 1.5-2 times as long as flagellar diameter. Foreleg with areas of fine branched hairs on apex of tibia, posterior surface of basitarsus, and on tarsomeres 2-3; flattened hairs present on apex of basitarsus and tarsomeres 2-4. Proportion of upper interocular distance to lower interocular distance 1:0.79. Proportion of interantennal distance to antennocular distance 1:0.60. Clypeus laterally close to eye margin. Proportion of scape, pedicel, and first three flagellomeres, 2.85:1:1:0.3:0.5; first flagellomere as long as its apical width. Paraglossa long, beyond apex of suspensorium 2.6 times as long as suspensorium. Profile of scutellum and metanotum convex, that of metapostnotum and propodeum basally slanting, then abruptly so. Hind basitarsus with apical projection truncate. Forewing with two submarginal cells. Hind wing with second abscissa of M+Cu 1.85 times as long as vein cu-v; vein cu-v arched. Pygidial plate funnel-shaped, with subparallel apical margins and rounded apex.

Male. Length 4.2-5.5 mm; length of forewing 4.0-4.8 mm. Color and vestiture similar to those of the female, but legs with yellow more extended and metasomal sterna entirely yellow. Hairs of scutum dense, 1-1.5 times as long as flagellar diameter, those of scutellum 2-3 times as long as flagellar diameter. Metasomal sterna with apical fringes extended over entire width. Vertex of head not elevated behind ocelli. Preapical tooth of mandible subtruncate. Pygidial plate with lateral margins poorly defined, but with distinct sclerotized apex. Hidden sterna and genital capsule as illustrated by Michener & Moure (1957).

Material studied. Holotype female, from El Cadillal, Tucumán, Argentina, 7-11-1993, A. Roig Alsina. (on *Nierembergia* sp.) (Museo Argentino de Ciencias Naturales, Buenos Aires). Paratypes are deposited in the following institutions: American Museum of Natural History, New York (AMNH), Central Texas Melittological Institute, Austin (CTMI), Instituto de Biología Vegetal, Córdoba (Cocucci), Instituto Miguel Lillo, Tucumán (IML), Museo Argentino de Ciencias Naturales, Buenos Aires (MACN), Museo de La Plata, La Plata (MLP), Rutgers University, New Brunswick (Rutgers), and Snow Entomological Museum, Lawrence (SEM). All paratypes are from Argentina, from the provinces of Salta, Tucumán, Córdoba, and Entre Ríos. *Salta*: 2 males, Rosario de la Frontera, 10-11-1989, Rozen & Roig A. (AMNH). *Tucumán*: 2 males, Trancas, Tacanas, 1-30-11-1968, Stange (IML); 1 male, Trancas, Tacanas, 12-1946, Golbach (IML); 1 female, Trancas, 24-11-1940 (MLP); 6 females, 2 males, Tucumán, 24-11-1952, Ogloblin (MLP); 1 male, Tucumán, 12-2-1919, Chavanpe (MACN); 1 male, Guasapampa, 1-12-1940 (MLP); 4 females, 1 male, 6 km W Tapia, 20-11-1993, Roig A. (MACN); 5 females, 4 males, same data as holotype (MACN); 1 female, San Pedro de Colalao, 1-1949, Arnau (SEM); 1 male, San Pedro de Colalao, February (SEM); 7 females, 12 males, 11 km N Dique EL Cadillal, 11 & 18-11-1983, Roberts (Rutgers); 18 females, 4 males, 11 km NW El Cadillal, 7 & 8-11-1991, Rozen, Pena & Ugarte (AMNH); 3 females, 1 male, 11 km NW El Cadillal, 8 11-1991, Rozen (on *Nierembergia* sp.) (AMNH); 7 females, between Cadillal and Ticucho, 27-10-1989, Rozen & Roig A. (AMNH); 1 male, between Taruca Pampa and Río del Nío, 29-10-1989, Rozen & Roig A. (AMNH); 2 males, between Las Cejas and Gob. Garmendia, 29-10-1989, Rozen & Roig A. (AMNH). *Córdoba*: 3 males, San Roque, Dpto. Punilla, 28-11-1982, Cocucci (IML); 1 male, San Roque, Dpto. Punilla, 10-11-1983, Cocucci (Cocucci); 2 males, El Sauce, Dpto. Calamuchita, 12-1938, Viana (MACN); 2 females, Jesús María, 3-12-1973, Neff (1 on *Oxalis* sp., 1 on *Nierembergia hippomanica*) (CTMI); 1 male, Villa María, 17-11-1940 (MLP); 1 male, Alta Gracia, 7-11-1941 (MLP); 4 males, Córdoba, 10-11-1944 (MLP); 2 males, Dean Funes, 3-12-1942 (MLP); 1 male, Río Segundo, 20-12-1951 (MLP); 1 male, Río Tercero, 1-12-1941 (MLP); 19 males, Jesús María, 19-11-1940 (MLP). Entre Ríos: 1 male, Feliciano, 12-1972, Fritz (MACN).

Acknowledgements

Type specimens of critical species described by Friese were kindly lent for study by F. Koch. I am also indebted to A. A. Cocucci, M. Fritz, C. D. Michener, J. L. Neff, J. G. Rozen, Jr., A. Sersic, and A. Willink for the loan of specimens for study, and to C. D. Michener for reviewing the manuscript.

Literature

Brethes, J. 1909: Notas himenopterológicas. – An. Mus. Nac. Buenos Aires **19**, 219-223.
– – 1910: Himenópteros argentinos. – An. Mus. Nac. Buenos Aires **20**, 205-316.
Buchmann, S. L. 1987: The ecology of oil flowers and their bees. – Ann. Rev. Ecol. Syst. **18**, 343-369.

Buchmann, S. L., Buchmann, M. D. 1981: Anthecology of *Mouriri myrtilloides* (Melastomataceae: Memecyleae), an oil flower in Panama. – Biotropica **13** (Suppl.), 7-24.

Cane, J. H. 1979: The hind tibiotarsal and tibial spur articulations in bees. – J. Kansas Ent. Soc. **52**, 123-137.

Cocucci, A. A. 1984: Polinización en *Nierembergia hippomanica* (Solanaceae). – Kurtziana **17**, 31-47.

– – 1991: Pollination biology of *Nierembergia* (Solanaceae). – Pl. Syst. Evol. **174**, 17-35.

Donoghue, M. J., Cantino, P. D. 1984: The logic and limitations of the outgroup substitution approach to cladistic analysis. – Syst. Bot. **9**, 192-202.

Farris, J. S. 1988: Hennig86, version 1.5. Program and documentation, Port Jefferson.

Friese, H. 1899: Monographie der Bienengattungen *Exomalopsis, Ptilothrix, Melitoma* und *Tetrapedia*. – Ann. K. K. Naturhist. Hofmus. **14**, 247-304.

– – 1906: Neue Bienenarten aus Chile und Argentina. – Z. Hym. Dipt. **6**, 169-176.

– – 1908: Die Apidae (Blumenwespen) von Argentina nach der Reisenergebnissen der Herren A. C. Jensen-Haarup und P. Jörgensen in den Jahren 1904-1907. – Flora og Fauna 1908, 1-111.

Holmberg, E. L. 1903: Delectus hymenopterologicus argentinus. – An. Mus. Nac. Buenos Aires **9**, 377-517.

Michener, C. D. 1944: Comparative external morphology, phylogeny and a classification of the bees. – Bull. Amer. Mus. Nat. Hist. **82**, 151-326.

Michener, C. D., Moure, J.S. 1957: A study of the classification of the more primitive non-parasitic anthophorine bees (Hymenoptera, Apoidea). – Bull. Am. Mus. Nat. Hist. **112**, 399-451.

Moure, J. S. 1941: Notas sobre abelhas do grupo *Tetrapedia* Klug (Hym. Apoidea). – Revista Ent. Rio de Janeiro **12**, 515-521.

– – 1944: Apoidea da coleçao do Conde Amadeu Barbiellini (Hym. Apoidea). – Revista Ent. Rio de Janeiro **15**, 1-18.

– – 1948: Notas sobre algumas abelhas de Tacanas, Tucumán, Argentina (Hymenopt. Apoidea). – Revista Ent. Rio de Janeiro **19**, 313-346.

– – 1994a: Sobre a posiçao sistemática de *Exomalopsis latitarsis* Friese (Apoidea, Anthophoridae, Exomalopsinae). – Revista brasileira Zool. **9**, 273-276.

– – 1994b: *Lissopedia*, gen.n. de Paratetrapediini para a regiao Neotropical, com as descriçoes de três espécies novas (Hymenoptera, Apoidea, Anthophoridae). – Revista brasileira Zool. **9**, 305-317.

Neff, J. L., Simpson, B. B. 1981: Oil-collecting structures in the Anthophoridae (Hymenoptera): Morphology, function, and use in systematics. – J. Kansas Entomol. Soc. **54**, 95-123.

Roberts, R. B., Vallespir, S. R. 1978: Specialization of hairs bearing pollen and oil on the legs of bees (Apoidea: Hymenoptera). – Ann. Entomol. Soc. Amer. **71**, 619-627.

Roig-Alsina, A., Michener, C.D. 1993: Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). – Univ. Kansas Sci. Bull. **55**, 123-162.

Sandhouse, G. A. 1943: The type species of the genera and subgenera of bees. – Proc. U.S. Nat. Mus. **92**, 519-619.

Schönitzer, K. 1986: Comparative morphology of the antenna cleaner in bees. – Z. zool. Syst. Evolut.-forsch. **24**, 35-51.

Schrottky, C. 1909a: Hymenoptera nova. – An. Soc. Cientif. Argentina **67**, 209-228.

– – 1909b: Synonymical notes in: Sitzung der Deutschen Entomologischen Gesellschaft, vom 6.IX.1909. – Deutsch. Ent. Z. 1909: 795.

Silveira, F. A. 1993: Phylogenetic relationships of the Exomalopsini and Ancylini (Hymenoptera: Apidae). – Univ. Kansas Sci. Bull. **55**, 163-173.

Simpson, B. B., Neff, J.L. 1981: Floral rewards: alternatives to pollen and nectar. – Ann. Missouri Bot. Garden **68**, 301-322.

Snelling, R. R., Brooks, R.W. 1985: A review of the genera of cleptoparasitic bees of the tribe Ericrocini. – Contrib. Sci., Nat. Hist. Mus. Los Angeles County **369**, 1-34.

Urban, D. 1996: Espécies novas de *Lanthanomelissa* Holmberg e *Lanthanella* Michener & Moure (Hymenoptera, Anthophoridae, Exomalopsinae). – Rev. brasil. Zool. **12**(4): 767-777.

Vogel, S. 1974: Ölblummen und ölsammelnde Bienen. Trop.Subtrop. – Pflanzenwelt **7**, 285-547.

– – 1988: Die Ölblumensymbiosen – Parallelismus und andere Aspekte ihrer Entwicklung in Raum und Zeit. – Z. zool. Syst. Evolut.-forsch. **26**, 341-362.

Vogel, S., Machado, I. C. 1991: Pollination of four sympatric species of *Angelonia* (Scrophulariaceae) by oil-collecting bees in NE. Brazil. – Pl. Syst. Evol. **178**, 153-178.

Authors' address:

Dr. Arturo Roig-Alsina
Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia"
Av. A. Gallardo 470, 1405 Buenos Aires, Argentina

Zeitschrift/Journal: Mitteilungen der Münchner Entomologischen Gesellschaft

Jahr/Year: 1997

Band/Volume: 087

Autor(en)/Author(s): Roig-Alsina Arturo

Artikel/Article: A generic study of the bees of the tribe Tapinotaspidini, with notes on the evolution of their oil-collecting structures (Hymenoptera, Apidae). 3-21