

SOME IMPORTANT MORPHOLOGICAL FEATURES OF THE CHALCIDINI (HYMENOPTERA: CHALCIDIDAE) AND THEIR IMPLICATIONS IN THE CLASSIFICATION OF THE TRIBE

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ABSTRACT. A detailed morphological study of an extensive material revealed some important features of the Chalcidini and, within the tribe, of *Spilochalcis*. The main characters are: Malar sulcus, foraminal cavity, preapical carina of scutellum, dorsellum, propodeum, mesopleuron, prepectus, procoxal bristles, abdominal petiole, and the male genitalia. Among the described genera of Chalcidini, three are regarded as valid: *Chalcis* Fabricius (type species *Sphex sispes* Linné, 1761), *Spilochalcis* Thomson, 1876 (type species *Chalcis xanthostigma* Dalman, 1820), and *Melanosmicra* Ashmead, 1904 (type species *Melanosmicra immaculata* Ashmead, 1904). A phylogenetic tree is suggested. Synapomorphies for twenty-three groups of *Spilochalcis* are given. The following genera are synonymized under *Spilochalcis*: *Thaumapus* Kirby, 1883 (type species *Smicra decora* Walker, 1871), *Epinaeus* Kirby, 1883 (type species *Smiera dux* Walker, 1861), *Metadontia* Ashmead, 1888 (type species *Smicra montana* Ashmead, 1887), *Ceratosmicra* Ashmead, 1904 (type species *Ceratosmicra petiolata* Ashmead, 1904), *Xanthomelanus* Ashmead, 1904 (type species *Chalcis dimidiata* Fabricius), *Psychidosmicra* Blanchard, 1935 (type species *Psychidosmicra australis* Blanchard, 1935), *Mixochalcis* Blanchard, 1935 (type species *Mixochalcis sibinecola* Blanchard, 1935), and *Eterochalcis* Burks, 1939 (type species *Smiera maculipennis* Cameron, 1884). *Platychalcis* Cameron, 1904 (type species *Platychalcis flavicollis* Cameron, 1904) is synonymized under *Melanosmicra*.

Introduction

The Chalcidini comprise several hundred described species, but the taxonomy of the tribe is rather poorly understood. Attempts were made by Walker (1864 and 1871), Sichel (1865), Cresson (1872) and Ashmead (1904) to provide keys to the species, but these keys included only a small number of them, mainly those described by the authors themselves.

Ashmead's key to genera (1904) has most often been used to distinguish the various taxa. Burks (1940) revised the Nearctic species, which constitutes only a small part of the whole fauna of the group.

The objective of the present study, started four years ago, was to (1) assess the limits of the genera and propose a revised classification of the Chalcidini through a character analysis based on the examination of an extensive material, (2) look for synapomorphies defining natural groups within *Spilochalcis* Thomson, (3) update the nomenclature of the species after examining the type material.

The original confusion made by the earlier authors concerning the genus *Chalcis* Fabricius, 1787 and the fact that the genus *Spilochalcis* Thomson (1876) was established rather late, doubtless explain that, in the nineteenth century, most species of the tribe were described under *Smiera* or *Smicra*. The distinction between *Chalcis* and *Spilochalcis* appeared clearly for the first time in Thomson (1876) and in

Ashmead's key for the Chalcididae (1888). Later, Ashmead (1904) established several new genera, mainly on the basis of the metafemoral teeth. Most of them were, however, synonymized under *Spilochalcis* by Burks (1940).

The present study is based on a survey of about 400 species of *Spilochalcis*, among which 215 described species, 10 *Chalcis*, 7 *Melanosmicra*, 335 types and more than 4000 specimens. The male genitalia of 90 species of *Spilochalcis* belonging to 25 natural groups were also studied. The same was also studied in 4 species of *Chalcis* and 3 of *Melanosmicra*.

The Chalcidini may be recognized from other Chalcididae by the following combination of characters: Antenna inserted in the middle of the head, never immediately above the mouth; metatibia obliquely truncate at the end and bearing one apical spur; and gaster with a distinct petiole having a basal lamina and never bearing strong longitudinal grooves or keels.

In the present study all available species are treated disregarding their previous generic separation. Among the described genera of the tribe only three of them, *Chalcis* Fabricius, 1787, *Spilochalcis* Thomson, 1876 and *Melanosmicra* Ashmead, 1904 (better known by its junior synonym *Platychalcis* Cameron), are recognized.

A new genus will be probably necessary to include *S. corumbicola* Ashmead, 1904. I do not know *Schizosmicra* Blanchard, 1943 including its type species, *S. tucumana* Blanchard, 1943. It is not discussed further.

The three valid genera are characterized as follows:

Chalcis: Male hypopygium enlarged and posteriorly emarginate (Fig. 114); female hypopygium posteriorly protruding in its median part (Fig. 111); no apical spur on the mesotibia or apical spur fine and short (Fig. 105); male claws strongly pectinate and bifid at apex (Fig. 73); female claws unarmed (Fig. 72); claws only little curved in both sexes.

Melanosmicra: Female hypopygium densely pubescent at apex (Fig. 112); female metafemur with a strong and curved inner basal tooth (Fig. 62); apical spine of metatibia long and curved (Fig. 60); mandibles either 2-3 with the upper teeth longer than the other (Fig. 77) or 2-2 and fine, with the lower teeth longer than the upper (Fig. 78); in the latter case thorax strongly flattened and very sparsely punctured, with interspaces smooth and shiny; claws normally curved, similar in both sexes; apical spur always present on mesotibia; mouth never very broad.

Spilochalcis: Apical spur nearly always present on mesotibia (Fig. 106); claws normally curved, similar in both sexes (Fig. 107); hypopygium normal in both sexes (Fig. 113 and 115); metafemur sometimes with an inner tooth, but the latter never strong; if mandibular formula 2-3, then upper teeth not longer than the lower; if mandibular formula 2-2, then thorax never strongly flattened and sparsely punctured with interspaces smooth.

The tribe Chalcidini is mainly Neotropical. The distribution of the genera is summarized in Table I below:

Region	Number of valid species		
	<i>Chalcis</i>	<i>Melanosmicra</i>	<i>Spilochalcis</i>
Paleartic + Oriental	3	0	2
Australian	1	0	0
Afrotropical	1	0	4
Nearctic	9	0	38
Neotropical ¹	10	5	280 ²

Character analysis

The character analysis is based not only on the examination of an extensive material belonging to the Chalcidini, but also to other groups of Chalcididae: Brachymeriini, Cratocentrini, Phasgonophorini, Haltichellinae, Dirhininae and Eplitraninae. I tried to determine the polarity of the character states mainly by the outgroup method, i.e., by comparing their distribution within the family, then within the whole Chalcidini + Brachymeriini, within the Chalcidini, and finally, within the genus *Spilochalcis*. If no contradiction appeared, I considered the character states exhibited by the largest number of groups within Chalcididae or species groups of *Spilochalcis* as primitive or plesiomorphic. In this reasoning, attention has been paid mainly to the species belonging to *Brachymeria*. On the other hand, character states evidently correlated with other ones, otherwise viewed apomorphic or derived, or resulting of a specialization were also considered as apomorphies.

However, it must be remembered that the polarity of a character must be considered within a grade. For example, a synapomorphy of the Chalcidini within the Chalcididae is a plesiomorphy for the species groups of *Spilochalcis* within the genus.

General features of *Spilochalcis*

Reversibility of characters states is one of the typical features exhibited by *Spilochalcis*; it makes the character analysis and the evolution of the genus difficult to understand. For example, most species of the *mariae* and *femorata* groups have the mandibles 2-3; most of those of the *pygmaea* group are of the 2-2 formula and different subgroups within the *nigricornis* and *xanthostigma* groups are of the 2-3 formula. The analysis of other characters showed that all these groups are rather far apart from each other. However, I know one species of the *mariae* group with the

1. Some species are found in the Nearctic and Neotropical regions.
2. 362 described species but about 280 still valid after examination of the type material.

3-3 mandibular formula and so are some species of the *femorata* and the *pygmaea* groups, and a subgroup of species within the *nigricornis* and *xanthostigma* groups. Many other cases may be quoted. This fact proves that, a character state though not visible in the phenotype of a species, is present in its genotype and might be expressed in other close species. It appears to establish the genetic unity of the genus.

The development of carinae or keels, which emphasizes structures and sculpture, is another typical feature of *Spilochalcis*. It includes carinae bordering the gena and the mandible, on the top of the interantennal projection, bordering the malar furrow, pronotal carina, preapical carina of the scutellum, transverse carina of the mesopleuron, ventral metapleural keels; apical carinae of pro- and metacoxae which cover the articulations with the trochanters and femora. These carinae are often expanded into foliaceous laminae.

Mandibular formula

This is the number of teeth in left and right mandibles; thus mandibles 2-3 means that the left mandible bears two teeth and the right one three teeth. Five character states were observed:

- a - Mandibles 2-3: Considered plesiomorphic because of general occurrence within the Chalcididae and Chalcidini (Fig. 85).
- b - Mandibles 3-3: Apomorphic but mostly without significance because noted in isolated species within various species groups of *Spilochalcis* (Fig. 81, 84 and 86).
- c - Mandibles 2-2: Apomorphic and significant although appears four different times within the Chalcidini (Fig. 78, 82, 87 and 88).
- d - Mandibles 2-2(+1): Apomorphic; intermediate between states a and c: a small tooth is hardly visible on the right mandible between the two other ones (Fig. 89).
- e - Mandibles 3(+1)-3(+1): Apomorphic; a distinctive character state supported by species of the *maculipennis* group (Fig. 90).

In fact the mandibular formula must be used with other characters - mandible length, mandible shape, presence or absence of lower carina - to define synapomorphies.

Malar sulcus

We must here take into account the depth and breadth of the malar furrow, and the expansion of the carinae bordering it. The following states were observed:

- a - Malar furrow deep but narrow, bordered by a distinct external carina and a weaker internal one (Fig. 17): in most *Spilochalcis* of the *oiketicusi* group; some species of the *mariae*, *fulvomaculata* and the *nigricornis* groups.

- b - Malar furrow present but superficial, the external carina quite distinct, the internal one absent or visible towards the mouth (Fig. 18): in *Spilochalcis* of the *mariae*, *fulvomaculata*, *blanda*, *biannulata* and *nigricornis* groups; some species of the *xanthostigma* and *oiketicusi* group; some *Melanosmicra*.
- c - Malar furrow very shallow and internal carina absent or virtually absent, only or mostly the external carina present (Fig. 19): *Spilochalcis* of the *apaiis* and *rufodorsalis* groups; some species of the *xanthostigma* and *blanda* groups.
- d - Malar furrow very narrow and superficial, arched, not bordered by carinae (Fig. 20): *Spilochalcis* of the *rufoscutellaris* and *debilis* groups; some species of the *fulvomaculata* group; some *Melanosmicra*.
- e - Neither malar furrow nor carina (Fig. 21): all *Spilochalcis* of the *side* group; some species of the *debilis* and the *rufoscutellaris* groups.
- f - Malar furrow narrow, rather deep and arched, with the internal carina distinct the external one present only towards the mouth (Fig. 22): *Spilochalcis* of the *maculipennis* group.
- g - Malar furrow broad and deep, bordered by two strong carinae (Fig. 23): *Spilochalcis* of the *dimidiata*, *transitiva*, *N*, *discolor*, *alienata*, *pygmaea*, *hollandi*, *referator*, *flava* and *femorata* groups; some species of the *blanda* group.

The presence of a distinct malar furrow is the groundplan of the *Melanosmicra* + *Spilochalcis* complex, because it can be seen only here within the family. I consider states **d**, **e**, and **f** as apomorphic because they occur in a minority of species groups of *Spilochalcis*. I consider also state **g** as apomorphic because before the malar furrow could be expanded, it must have been present; so state **g** evidently follows one of the states **a** or **b**. States **a**, **b** and **c** represent a transformation series, the polarity of which is not evident. Moreover two different states are sometimes observed within a natural group, i. e., states **a** and **b** within the *mariae* group, states **b** and **c** within the *xanthostigma* group.

However, from the distribution of state **c** within the tribe, there is little chance that it would be the plesiomorphic one.

As I could not decide with certainty between the two other states (**a** or **b**), I consider them equivalent and not significant for the character analysis.

Antennal scrobe and interantennal projection

The form of the antennal scrobe and the interantennal projection in the Chalcidini are characteristic and may represent the groundplan of the tribe. Generally in the other members of the family the scrobe is either shallow and little distinct, or very deeply impressed but carinately margined (Fig. 1). In the Chalcidini the scrobe is impressed in the form of an inverted V; its shows no or a very superficial sculpture relative to the front, but there is neither a margin nor a abrupt change in the sculpture (Fig. 2, 5 and 10). The following states were observed:

- a1 - Scrobe distinctly impressed; interantennal projection convex but not strongly protruding, only finely carinated at its top, the carina not expanded into a foliaceous lamina (Fig. 2 and 3): *Spilochalcis* of the *oiketicusi*, *mariae*, *pygmaea*, *referator*, *flava*, *hollandi*, *alienata* and *apaiis* groups; some species of the *xanthostigma* and *debilis* groups;
- a2 - Similar to state **a1**, but the carina expanded into a foliaceous lamina (Fig. 24): *Spilochalcis* of the *femorata* group.
- b1 - Scrobe deeply impressed; interantennal projection strongly protruding, forming sometimes dorsally a lamina (Fig. 4, 5, 6, 7, 8 and 9): *Spilochalcis* of the *nigricornis*, *blanda*, *dimidiata*, *transitiva*, *N*, *biannulata*, *discolor* groups; most of the species of the *xanthostigma* group; some species of the *debilis* group; *Chalcis* spp.
- b2 - Similar to state **b1** but scrobe less impressed (Fig. 10): some species of *Melanosmicra*.
- c - Scrobe virtually absent (Fig. 11, 12, 13 and 14); interantennal projection hardly visible: *Spilochalcis* of the *maculipennis*, *rufoscutellaris*, *rufodorsalis*, *fulvomaculata* and *side* groups; some species of the *pygmaea* group; some *Melanosmicra*.

It is difficult to assess the polarity of the character within the tribe and then within *Spilochalcis*. States **a1** or **b1** could be considered as the primitive ones. State **c** is clearly a derived one but this does not necessarily demonstrate a close relationship because it is the result of a simplification of the structures due to the reduction in size of the individuals, which occurred several times. On the other side, the detailed examination of the species shows that each group bearing state **b1** of the character shows a unique derived state. In this matter the dorsal part of the interantennal lamina seen in lateral view is very useful for recognition of the natural groups.

Foraminal cavity

Some natural groups of *Spilochalcis* have a very deep foraminal cavity, at least dorsally delimited by a carina (Fig. 25); in its center the foramen magnum can be seen. This state is always correlated with the expansion in curved laminae of the anterior margins of the pronotum and prosternum (Fig. 30). A transverse furrow, called here the basal furrow, is sometimes formed between the lamina and the edge of the collum. In the *N* group a postbasal furrow has also been observed (Fig. 103); it is impressed on the collum. A foraminal cavity can also be seen in *Brachymeria* species, but it is different. First it is not so deep and never carinately margined ; secondly it is not correlated with the expansion of the anterior margin of pronotum, but by the development of the ventral part of the foraminal margin. So the two structures are not homologous.

The different states observed within the tribe are the following:

- a - Foraminal cavity deep and dorsally delimited by a sharp carina (Fig. 25): *Spilochalcis* of the *nigricornis*, *oiketicusi*, *blanda*, *transitiva*, *N*, *alienata* and *hollandi* groups.
- b - Foraminal cavity more or less distinct but not carinately margined at all (Fig. 26): *Spilochalcis* of the *dimidiata* and *biannulata* groups; some species of the *apais*, *blanda*, *flava* and *femorata* groups;
- c - Back of the head with a deep and large depression, this one not margined, and surmounted by a transverse carina expanded into a foliaceous lamina (Fig. 99 and 100): *Spilochalcis* of the *hollandi* group.
- d - A similar depression, by not surmounted by a foliaceous lamina; basal furrow of the pronotum well expanded (Fig. 102): *Spilochalcis* of the *referator* group; some species of the *discolor* and *flava* groups.
- e - Foraminal cavity indistinct or absent (Fig. 27): many natural groups of *Spilochalcis*; *Chalcis* and *Melanosmicra* spp.

State **a** seems to constitute a derived one within the Chalcidini. However the character analysis revealed that it is present in a number of different species groups of *Spilochalcis*. It also demonstrated that the absence of foraminal cavity may be a primitive state, or the result of a secondary loss. These regressions are attested by states **b**, **c** and **d** which correspond to different vestiges of the foraminal cavity. We can postulate that it appeared rather early and may represent the plesiomorphic condition of the character for the genus *Spilochalcis*.

The construction of the cladogram will indeed depend on the stage when the foraminal cavity appeared.

Hypostomal process

In some *Spilochalcis* the hypostomal carina is expanded into a lamina. In several cases a process, called here the hypostomal process has been seen at the upper corner of the proboscidial fossa (Fig. 26 and 102).

Antennal scape

This character was used by Burks (1940) for recognition of natural groups of *Spilochalcis*. In order to define the apomorphic states, the following conditions should be considered:

- Length of the female scape.
- Relative breadth of female scape.
- Sexual dimorphism in length of scape.
- Sexual dimorphism in shape of scape.

The first two conditions can define the following apomorphy: "scape short and compact, as well as the flagellum; apex of scape at most reaching ventral level of median ocellus" (Fig. 91); in *Spilochalcis* of the *xanthostigma* and *biannulata* groups;

in some species of the *discolor* group. However such a state does not mean a close relationship between these groups, because it evidently results from parallel evolutions.

Generally the scape is a little broader and shorter in the male than in the female (Fig. 92 and 93). In the *flava*, *femorata* and *pygmaea* groups, this feature is outstanding; this state is correlated with an also outstanding sexual dimorphism of the head: in the males of these groups the frontovertex is distinctly narrower than in the females (Fig. 95).

In *Spilochalcis* of the *mariae* group and most of the species of the *fulvomaculata* group, the scape is longer in the male and enlarged at its apex (Fig. 28 and 29). In many species of the *side* group the whole male scape is expanded, and bears a distinct sensilla on its ventral margin (Fig. 94).

Pronotal carina

In many different species groups of *Spilochalcis* a pronotal carina, setting off the collar, is expanded laterally into a foliaceous translucid lamina (Fig. 30). It is most often broken mesally where a small arched carina takes place.

As this character state has been found in many different species groups (*xanthostigma*, *nigricornis*, *oiketicusi*, *mariae*, *blanda*, *transitiva*, *dimidiata*, *N*, *biannulata* and *apaiis* groups) of *Spilochalcis*, it is considered to be the primitive state of the character for the genus. However several regressions or secondary evolutions of this carina occurred which cannot be quoted here.

In *Chalcis* and *Melanosmicra* this carina is absent and no vestige of it could be found. Thus this carina is supposed to be a derived character state which would distinguish *Spilochalcis* within the tribe.

Mesoscutal sculpture

The following states were observed in the Chalcidini:

- a - Mesoscutum deeply and closely punctured (Fig. 33): in most of the natural groups of *Spilochalcis*; *Chalcis* spp.
- b1 - Mesoscutum transversely punctate-strigose (Fig. 34): some species of the *mariae* and *fulvomaculata* groups.
- b2 - Mesoscutum transversely strigose, the carinae strong (Fig. 35 and 36): *Spilochalcis* of the *mariae*, *biannulata* and *dimidiata* groups; most of the species of the *pygmaea* group.
- c - Mesoscutum superficially and sparsely punctured, the punctures alternating with squamae (Fig. 37): *Spilochalcis* of the *rufoscutellaris* and *maculipennis* groups.
- d - Mesoscutum alutaceous (Fig. 38): the smallest species of the *fulvomaculata*, *rufodorsalis* and *rufoscutellaris* groups.
- e - Mesoscutum sparsely punctate, the interspaces alutaceous or smooth (Fig. 39): *Melanosmicra* spp. and *S. xantha* Burks, which belongs to the *xanthostigma* group.

State **a** is considered as the primitive one since it is generalized in Chalcididae. A transformation series evidently occurred leading, from state **a** to state **b2**. States **b2**, **c** are apomorphic but do not mean close relationships between the groups which exhibit them, as they result from parallel evolution. State **e** is correlated with other significant characters and considered to be a synapomorphy for *Melanosmicra*.

Preapical carina of the scutellum

In many species of Chalcididae a preapical carina is conspicuous at the posterior margin of the scutellum; this is also the case in Chalcidini. The following states were observed:

- a - Preapical carina developed as well in its median part as its sublateral parts, broadly rounded, with distinct crenulae on the rim formed dorsally (Fig. 42) : *Spilochalcis* of the *xanthostigma*, *nigricornis*, *oiketicusi* and *biannulata* groups; *Chalcis* spp.
- b - Preapical carina developed as well in its median part as its sublateral parts but distinctly angular at its apex (Fig. 43): *Spilochalcis* of the *apaiis*, *rufodorsalis*, *rufoscutellaris*, *debilis*, *mariae*, *fulvomaculata* and *side* groups; the primitive species of *Melanosmicra*.
- c - Preapical carina expanded sublaterally into transverse or rounded lobes, united by a distinct and sometimes foliaceous lamina (Fig. 44): *Spilochalcis* of the *blanda*, *N*, *discolor*, *alienata*, *pygmaea*, *hollandi*, *referator*, *flava* and *femorata* groups; some *Chalcis*.
- d - Preapical carina expanded into two lateral rounded or triangular lobes, these always broadly separated (Fig. 45): *Spilochalcis* of the *dimidiata* and *transitiva* groups.
- e - Preapical carina very close to the posterior margin of the scutellum, mainly in its median part, the frenal area transverse or absent (Fig. 46); some species of the *nigricornis*, *apaiis*, *rufodorsalis* and *rufoscutellaris* groups; all the species of the *maculipennis* group; some *Melanosmicra*.

State **a** is considered as the plesiomorphic one for the tribe. The other ones are supposed to be derived. However, they are significant only when correlated with other synapomorphies. The distribution of state **b** within the tribe shows that it cannot be used for the character analysis, as well as state **e**. States **c** and **d** are really synapomorphies for the species groups of *Spilochalcis* which exhibit them.

Prepectus

In the Chalcididae the prepectus has generally the shape of a semi-annular and transverse sclerite. It bears in its median part various processes, typical for each group of the family. In the Chalcidini it bears two submedian keels delimiting a median areola (Fig. 49). I consider this state as an apomorphic one for the tribe within the Chalcididae. Within *Spilochalcis* two derived states were observed. In *S*.

biannulata Ashmead, for example, the submedian keels are fused in a median carina; this apomorphic feature has been observed several times within the genus. In the *maculipennis* group the submedian carinae are regressed.

Mesopleuron

In some species groups of *Spilochalcis* there is a transverse ventral carina on the mesopleuron, delimiting anteriorly a horizontal ventral area, sometimes called "mesosternal shelf" (Fig. 48). Such a carina can also be seen in other Chalcididae, but it is not homologous with the preceding one. For instance, in *Brachymeria*, the epicnema is rather distinct because it is margined by continuous lateral and ventral epicnemial carinae. Moreover, in that genus, the mesopleural area situated between the femoral groove and the epicnema is laterally oriented (Fig. 47).

In *Spilochalcis* the transverse carina of the mesopleuron, when present, in fact prolongs a carina bordering anteriorly to the femoral groove, and consequently it is not homologous with the ventral part of the epicnemial carina of *Brachymeria*. Moreover, the space preceding the femoral groove is anteriorly rather than laterally oriented and can be distinguished from the epicnema by a large areola.

Whether or not a transverse carina is present, the mesopleuron in Chalcidini shows a unique structure within the family and represents an apomorphy of the tribe. Within the tribe the following states were noted:

- a - A ventral transverse carina present and distinct on the mesopleuron, delimiting anteriorly a horizontal ventral area (Fig. 48): *Spilochalcis* of the *nigricornis*, *oiketicusi*, *xanthostigma*, *biannulata*, *transitiva*, *dimidiata*, *blanda*, *debilis*, *apais* and *rufodorsalis* groups.
- b - Transverse carina absent or hardly visible but mesopleuron with an angular outline (seen in lateral view), because a horizontal ventral area is more or less distinct: *Spilochalcis* of the *discolor*, *alienata* and *referator* groups.
- c - Transverse carina absent, mesopleuron with a rounded outline (Fig. 49): *Chalcis* and *Melanosmicra* spp.; *Spilochalcis* of the *maculipennis*, *rufoscutellaris*, *mariae*, *fulvomaculata*, *side*, *pygmaea*, *hollandi*, *flava* and *femorata* groups.
- d - Transverse carina present, continuous with the true epicnemial carina: *Spilochalcis mesomelas* (Walker).

We can see an evident transformation series from state a to state c.

The character analysis shows that the complex of groups exhibiting state a is strongly heterogeneous. If the transverse carina of the mesopleuron did appear only once during the evolution of the tribe, it may probably represent the primitive condition of the character for *Spilochalcis*. In this case four complete and parallel regressions of this carina must be considered.

Such regressions can be seen within some aggregates comprising closely related groups, or within some species groups, i. e., State a to state b within the *nigricornis* group; State b in the *alienata* group to state c in the *flava* group.

Conversely, if state **c** is supposedly the primitive one for the genus we must consider five or six independent acquisitions of the same feature. Because it seems much more reasonable to consider parallel evolutions resulting in regressions, than resulting in the same acquisition, I think that state **a** is really the plesiomorphic one for the genus *Spilochalcis*.

Dorsellum

Three main different states could be observed in the Chalcidini:

- a - Dorsellum little distinct, impressed or crenulate, pubescent (Fig. 51, 53, 54 and 57): *Chalcis* and *Melanosmicra* spp.; *Spilochalcis* of the *apaiis*, *rufodorsalis*, *maculipennis*, *rufoscutellaris*, *nigricornis*, *oiketicusi*, *blanda*, *mariae*, *fulvomaculata* and *side* groups; some species of the *dimidiata* and *xanthostigma* groups.
- b - Dorsellum well distinct, smooth and shining, not impressed, glabrous, delimited on each side by a deep fovea (Fig. 56): *Spilochalcis* of the *biannulata*, *transitiva*, *alienata*, *femorata*, *flava*, *referator* and *pygmaea* groups; the other species of the *dimidiata* group.
- c - Dorsellum well distinct, but dull, often with a transverse areolate furrow laterally (Fig. 42); the other species of the *xanthostigma* group.

As state **a** is generalized within the Chalcididae and also within the tribe, it is considered to be the plesiomorphic one. State **b** seems to be significant when correlated with other important characters (malar sulcus, preapical carina of the scutellum). It is supposed to have appeared only two times during the evolution of the tribe.

Propodeum

The structure of the propodeum in *Spilochalcis* is typical within the family and must be described in detail. I describe here what seems to be the groundplan character for the genus (Fig. 54 and 56).

First the spiracular aperture is longitudinally oriented instead of being transversely or obliquely oriented. In front of it, a little laterally, a transverse, pubescent area may be seen: this is the unusually small callus. A median keel is always developed in the anterior half of the propodeum; it is split in two posterior costulae. These costulae delimit anteriorly an articular area preceding the petiolar cavity. The medio-anterior part of the propodeum often shows anterior costulae; behind them there are longitudinal keels. A combination of these keels and the costulae gives to this part an areolate appearance. However all these keels are sometimes absent and this area is then rugose or reticulate. Laterally, between the anterior and posterior costulae, is the spiracular areola (a1). Still more laterally, above the metacoxa, is the supracoxal areola (a2). The petiolar cavity is at least laterally bordered by the para-articular areolae (a3) and ventrally by a triangular areola, the subarticular areola (a4). The spiracular areola is often little distinct because it may be anteriorly open or fused with a secondary areola.

From this groundplan several apomorphies have been noted (for instance development of apophyses, expansion of the foraminal margin, regression of the anterior costula...) which cannot be quoted in detail here.

Procoxal carina

A carina, sometimes expanded into a foliaceous lamina, is present in many species groups of *Spilochalcis* (Fig. 31). It is always correlated with the presence of the transverse carina of the mesopleuron; refer to the analysis concerning this character.

Procoxal bristles

In all the Chalcidini, a very distinctive line of bristles is present on the posterior side of the procoxa (Fig. 32). It constitutes a unique apomorphy of the tribe within the family.

Mesocoxal bristles

In the *Melanosmicra* + *Spilochalcis* aggregate, distinct isolated hairs can be seen on the laterodorsal side of the mesocoxa, in the center of a bare area (Fig. 40): they are called the mesocoxal bristles. The mesocoxa of *Chalcis* is uniformly pubescent in this area and does not show such bristles (Fig. 41). Similar mesocoxal bristles are also present in *Brachymeria* and seem to be the groundplan for the Chalcidinae. In such a case their absence should be interpreted as a regression.

Metafemur: marginal bristles

In all the Chalcidini, a line of distinct bristles (distinct by their length and their breadth) is visible along the ventral margin of the metafemur, on its internal side (Fig. 58 and 59): they are called here the marginal metafemoral bristles. They are followed by submarginal bristles which are intermediate between the usual bristles and the marginal ones.

Metafemur: teeth (Fig. 60, 63, 64, 65, 66 and 67)

The teeth of the metafemur were used by Ashmead (1904) to erect several new genera among the Chalcidini. The survey of an extensive material showed that Burks (1940) was right in including these genera in *Spilochalcis*. There is not only an intrageneric variation of the character states, but also a variation within some of the natural groups of *Spilochalcis*, the best representatives in this matter being the *nigricornis* group (Fig. 108) and the *blanda* group (Fig. 109). It seems that the plesiomorphic state for the character is: metafemur with a distinct but short basal tooth, followed by many short and closely set teeth; a short internal basal tubercle or tooth is also often present. This state is generalized within the subfamily.

Claws

In Chalcididae the claws are usually curved and show a basal lobe (Fig. 107). Two significant apomorphies have been observed within the Chalcidini, both concerning the genus *Chalcis*. In this genus the claws are little curved in both sexes. Moreover the claws - which are normally pectinate in both sexes in the other Chalcidini - are unarmed in females, while there are strongly pectinate and bifid at apex in males (Fig. 72 and 73).

Abdominal petiole: structure and length

The structure of the abdominal petiole of the Chalcidini is unique within the Chalcididae and represents an apomorphy of the tribe (Fig. 76).

The petiole first shows a basal part articulated with the propodeum, followed by the basal lamina. This lamina is generally not continuous and comprises a dorsal and a ventral part; at the lateral break a small longitudinal carina is visible; the ventral lamina is situated a little behind the dorsal one. The basal lamina is followed by the body of the petiole, the length of which is extremely variable (Fig. 110) : the petiole may be annelliform like in *Spilochalcis fusiformis* Ashmead or *S. leucotelus* (Walker) or very long and fine in some species of the *debilis* group. But as many intermediates of these extreme states have been encountered, the length of the abdominal petiole is not considered significant at the generic level.

Female hypopygium

The position of the female hypopygium, mainly the position of its apex relative to the apex of the gaster was used by Burks (1939) to distinguish several genera of Chalcidini, such as *Chalcis*, *Melanosmicra* (mentioned as *Platychalcis*) and *Metadontia*. It must be noticed that Burks (1940) defined *Metadontia* in a more restricted sense than Ashmead (1888) did originally. Ashmead used the metafemoral teeth to erect the genus.

The position of the apex of the hypopygium, relative to the apex of the gaster is variable within *Spilochalcis*. Many intergrades have been found between a hypopygium removed from the apex of the gaster to other ones situated at or near it.

Thus both preceding character states, used to separate *Metadontia*, do not appear to have any taxonomic value.

In the Chalcididae, the female hypopygium is mesally emarginate on its posterior margin, and a small median lobe can be seen within the emargination (Fig. 113). This character state, considered as the primitive one for the Chalcidini, has been observed in all *Spilochalcis* species.

In *Chalcis* the female hypopygium projects backwards in its median part (Fig. 111). This state is considered as a significant derived one.

In *Melanosmicra*, the female hypopygium does not protrude posteriorly. However it is sclerotized at apex in the median part, and densely pubescent (Fig. 112). This character state is also considered to be a significant apomorphy.

Male hypopygium

In *Chalcis* the male hypopygium is enlarged and posteriorly emarginate (Fig. 114). This is also considered to be a significant apomorphy. It is probably related with the shape of the female hypopygium; this point must however be confirmed by the observation of the mating behaviour.

Male genitalia

A short description of the male genitalia in the Chalcidini is necessary before mentioning the different variations observed.

As in the other Chalcididae, the male genitalia are composed of two independently mobile parts: a sheath and the aedeagus (Fig. 116 and 117).

The sheath has a basal phallobase which is laterally prolonged into parameres, each bearing generally one apical parameral bristle. Between the parameres the median ventral lamina is distinguished, separated from them by an emargination or an incision of the phallobase. Mesad of the parameres are inserted the volsellar digiti. The phallobase itself appears as two lateral parts broadly separated dorsally and more or less united ventrally. They were called lamina parameralis by Boucek (1952). When separated, their ventral margin is strengthened by a sclerotized line, the ventral frame. The edge of the median ventral lamina shows also a marginal frame.

Several apomorphies concerning the following characters of the male genitalia are significant: the ventral frame, the median ventral lamina, the shape of digiti and of the aedeagus.

Phallobase

In *Spilochalcis* of the *apaisi*, *nigricornis*, *oiketicusi*, *mariae*, *fulvomaculata*, *side*, *alienata*, *pygmaea*, *hollandi*, *flava* and *femorata* groups, in some species of the *xanthostigma* group and in *Chalcis*, the phallobase is completely open ventrally and the ventral frame is present (state a) (Fig. 121, 122, 124, 125, 132, 133 and 134).

In some *Spilochalcis* of the *xanthostigma*, *N*, *rufodorsalis* and *debilis* groups, in *S. biannulata* and in some species of *Melanosmicra*, the phallobase is partly open ventrally and traces of the ventral frame can be observed. While these traces are situated near the base of the sheath in the *xanthostigma* group (state b1), in the *N* group (Fig. 118 and 127) and in other cases they are near the median ventral lamina (state b2) (Fig. 116, 119 and 128).

In *Spilochalcis* of the *rufodorsalis*, *rufoscutellaris*, *dimidiata*, *transitiva* groups, in some species of the *discolor* group, in one species of the *N* group and in some *Melanosmicra*, the phallobase is completely closed ventrally and no ventral frame is seen (state c) (Fig. 117, 120, 129, 131 and 135).

As state a is the most frequently encountered condition in the Chalcidini, it is considered as the primitive one for the tribe. It also agrees with the groundplan of the Hymenoptera where the sheath is composed of two series of lateral pieces: the

gonocoxites and gonostyli. If we consider state **c** as the primitive one, we must suppose that states **b1** and **b2**, complementary in relation to state **a**, appeared independently, which would not seem reasonable.

Concerning the median ventral lamina, three extreme states are observed:

- State **a1**: Median ventral lamina broadly rounded and separated from the parameres by an emargination of the phallobase or a small incision (Fig. 116, 117, 118, 121 and 122): *Spilochalcis* of *xanthostigma*, *rufodorsalis*, *oiketicusi*, *dimidiata*, *N*, *biannulata* groups and some species of the *discolor* group; *Chalcis* and *Melanosmicra* spp.
- State **a2**: In the *Spilochalcis* of the *debilis*, *mariae*, *fulvomaculata* and *side* groups and some species of the *nigricornis* group, the ventral lamina is somewhat narrower, often truncate or subtriangular at its apex (Fig. 123, 125 and 126).
- State **b**: Median ventral lamina long and narrow, separated from the parameres by a deep incision (Fig. 132 and 133): In *Spilochalcis* of the *alienata*, *pygmaea*, *hollandi*, *referator*, *flava*, and *femorata* groups.

As state **a1** is the generalized one within the Chalcididae and Chalcidini, it is considered to be the plesiomorphic one. State **a2** represents only a variation of this state. State **b** is very significant because it is correlated with many phenotypic characters and also (and mostly) with some important apomorphies (malar sulcus, preapical carina of the scutellum, dorsellum, propodeum).

Parameres

In *Chalcis* the parameres are rather long and slender, their apex sometimes exceeding the apex of the digiti (Fig. 116).

Volsellar digiti

The digiti as figured for *Spilochalcis* aff. *oiketicusi* (Cameron) seem to be the groundplan for the Chalcidini (state **a**) (Fig. 122). Several apomorphies were encountered concerning the shape, the length or the ornamentation of the digiti:

- State **b**: Digiti with the apical part (between the condyle and the apex) short; hooks in small number (Fig. 116): *Chalcis* spp.
- State **c**: Digiti long and slender (Fig. 121, 123 and 125): *Spilochalcis* of the *nigricornis*, *debilis*, *mariae* and *fulvomaculata* groups.
- State **d**: Digiti slender but emarginate, the condyle distinctly protruding (Fig. 126): *Spilochalcis* of the *side* group.
- State **e**: Digiti strongly emarginate, angular at the condyle level (Fig. 128): *Spilochalcis biannulata*.
- State **f**: Digiti broad and short, basal hooks distinctly longer than the apical ones (Fig. 117 and 118): *Melanosmicra* spp; some species of the *xanthostigma* group.

Aedeagus

Several apomorphies were observed concerning the following characters: phallotreme; relative length of apodemes; aedeagus ornamentation and aedeagus shape.

In the *mariae* group (and some species groups close to it but not quoted here) the phallotreme is broadly open (Fig. 124). In the same groups, the aedeagus is very long but the apodemes are unusually short.

In *Melanosmicra* and some species of the *xanthostigma* and *nigricornis* groups the aedeagus is broadly rounded apically (Fig. 117 and 118).

In *Chalcis*, the aedeagus bears in the apical part two pairs of dorsal laminae (Fig. 116); the first ones are inserted in the middle of this part, the second ones on each side of the phallotreme.

Cladogram construction

In the present analysis, I have excluded several undescribed species, belonging to undescribed natural groups. I have also excluded some described species, the names of which could not be used for natural groups. This exclusion is done because of unsolved nomenclatural problems (i.e. *variegata* Sichel, homonym of *variegata* Fabricius) or because the necessary analysis could not be completed. In both cases these species are rare and their exclusion does not change the general scheme suggested here. The construction of a cladogram or a phylogenetic tree depends mainly on the relative weight of the characters used during the analysis. Therefore a cladogram represents a phylogenetic hypothesis.

Within the Chalcididae, the Chalcidini are distinguished by the following apomorphies: prepectus with two submedian keels, structure of the mesopleuron, structure of the propodeum, procoxal bristles, marginal metafemoral bristles, structure of the abdominal petiole.

The species belonging to *Chalcis* share very distinct apomorphies: apical mesotibial spur absent; claws little curved in both sexes (Fig. 72 and 73); male claws pectinate and bifid at apex; female hypopygium strongly protruding in median part (Fig. 111); male hypopygium enlarged and posteriorly emarginate (Fig. 114); phallobase with a dorsal expansion; parameres long and slender; aedeagus with dorsal expansions (Fig. 116); species parasitizing Stratiomyidae; eggs deposited in eggs or larvae.

Melanosmicra Ashmead, 1904 was forgotten by subsequent authors. *Melanosmicra immaculata* Ashmead, 1904, its type species, is evidently congeneric with *Platychalcis flavicollis* Cameron, 1904, the type species of the genus *Platychalcis*, which is a junior synonym of *Melanosmicra*.

The species of *Melanosmicra* share also distinct apomorphies: metafemur in females with a long and curved inner tooth, this tooth inserted close to its base (Fig. 61 and 62); female hypopygium densely pubescent medially at apex (Fig. 112) and distinctly protruding when valvulae are extended. Other characteristics are: thorax somewhat or strongly flattened, the punctuation sparse; metapleuron densely pubescent dorsally; apical spine of the metatibia always long and curved (Fig. 60); phal-

lobase closed on its ventral side, the ventral frame absent or hardly visible, digits short and broad, with a reduce number of hooks, the basal ones being longer than the apical ones; aedeagus broad and apically rounded (Fig. 117).

The propodeum is also typical (Fig. 52): a basal median projection is always visible, followed by a median keel. This keel is split posteriorly into costulae which delimit a very distinct articular area; the propodeum, in the primitive species, is rather long and protrudes a little backwards in its median part.

Two species groups can be distinguished within the genus. In the primitive *immaculata* group the mandibular formula is 2-3 (Fig. 77), upper teeth being longer than the other; interantennal projection is well protruding (Fig. 10); thorax is somewhat flattened with a rather dense punctuation (Fig. 3f); preapical carina of scutellum is complete, not fused with its posterior margin; propodeum is long and protruding backwards; metacoxa and metafemur are long and slender. In *flavicollis* group, which includes the evolved species of the genus, the head is transverse; mandibles are very fine and of the 2-2 formula with lower tooth longest (Fig. 78); antennal scrobe is shallow and interantennal projection hardly visible; thorax is strongly flattened with a very sparse punctuation; preapical carina of the scutellum is fused mesally with its posterior margin; propodeum is shorter; metacoxa and metafemur are short and compact.

Melanosmicra seems to make a link between *Chalcis* and the *xanthostigma* group of *Spilochalcis*. With the former genus, the primitive species of *Melanosmicra* share the same states of the following characters: mandibles, metacoxa and metafemur. Moreover, some *Chalcis*, like *C. myrifex* (Sulzer), exhibit the inner metafemoral tooth found in females of *Melanosmicra*; in both cases they are regressed in males. The propodeum in *Chalcis*, although more rugose than in *Melanosmicra*, shows the same features (Fig. 51): general shape, basal projection, posterior costulae and articular area. At last in both genera the female hypopygium is protruding.

Conversely the male genitalia of both preceding genera are strongly different. In fact the male genitalia of *Melanosmicra* are very similar to some species of the *xanthostigma* group, like *Spilochalcis pulchripes* (Cameron) (Fig. 117 and 118).

Owing to the diversity of the genus, I could not find any evident apomorphy to distinguish the set of species groups which I have included in *Spilochalcis*. However, it seems that the presence of several carinae (pronotal carina, procoxal carina and transverse carina of the mesopleuron) are synapomorphies for *Spilochalcis*.

Although it is possible that these structures regressed in *Chalcis* and *Melanosmicra* as a result of secondary evolutions, I have not seen any transformation series which would give evidence of these regressions.

The *xanthostigma* group is distinguished by the following apomorphies (Fig. 3, 5 and 6): head transverse in frontal view, subquadrate; mouth very broad; mandibles either very long or robust with the teeth blunt. It is considered a sister group of all other *Spilochalcis* because I could not find any evident apomorphy common to the *xanthostigma* group and other strains or species groups of *Spilochalcis*.

Classification of the Chalcidini

Thaumapus Kirby, 1883 is based on *Smicra decora* Walker, 1861 (a junior synonym of *S. masus* Walker, 1841) which belongs to the *dimidiata* group in the present paper. The type species of *Xanthomelanus* Ashmead, 1904 is *Chalcis dimidiata* Fabricius, 1804, and is therefore a junior synonym of *Thaumapus*.

The distribution of the character states within the Chalcidini indicates that *Thaumapus* must be included in *Spilochalcis*. The following genera are also synonyms of *Spilochalcis*:

Metadontia Ashmead, 1888 based on *Smicra montana* Ashmead, 1887 which is a junior synonym of *Chalcis amoena* Say, 1836 and corresponds to the *flava* group.

Mischosmicra Ashmead, 1904 (type species *Mischosmicra kahlui* Ashmead, 1904 which is a junior synonym of *Chalcis debilis* Say, 1836): it is equivalent to the *debilis* group of *Spilochalcis*.

Ceratosmicra Ashmead, 1904 (type species *Ceratosmicra petiolata* Ashmead, 1904), regarded as the *fulvomaculata* group because *C. petiolata* belongs to this group.

It may be mentioned that Burks (1940 and 1968) placed in *Ceratosmicra* at least three different species groups:

C. debilis (Say) and *C. paya* Burks in the *debilis* group of *Spilochalcis*.

Smiera immaculata Cresson, *C. meteori* Burks and *C. campoplegicis* Burks [a junior synonym of *S. petioliventris* (Cameron)] in the *fulvomaculata* group of *Spilochalcis*.

I am not sure of the position of *C. provancheri* Burks, which may belong to the *xanthostigma* group of *Spilochalcis*.

Psychidosmicra Blanchard, 1935 (type species *Psychidosmicra australis* Blanchard, 1935) is the same as the *oiketicusi* group of *Spilochalcis*.

Mixochalcis Blanchard, 1935 (type species *Mixochalcis sibinecola* Blanchard, 1935) corresponds to the *nigricornis* group.

Eterochalcis Burks, 1939 (type species *Smicra maculipennis* Cameron, 1884) is equivalent to the *maculipennis* group of *Spilochalcis*.

Epinaeus Kirby, 1883 is based on *Smicra dux* Walker, 1861, which can be included in the *femorata* group of *Spilochalcis*.

The distribution of the derived character states within the tribe shows that if we regard them as valid genera, we must divide *Spilochalcis* following the natural groups previously mentioned.

Must also be taken into account the fact that for most of the characters, transformation series occur and intergrades linking the extreme states of the same character can be found. The character analysis shows that parallel evolutions occur frequently, as a result of the reversibility of character states. As natural groups of *Spilochalcis* can hardly be distinguished by using synapomorphies, each group is mainly defined by a combination of multiple apomorphies. Consequently I propose to synonymize *Thaumapus*, *Xanthomelanus*, *Metadontia*, *Ceratosmicra*, *Psychidosmicra*, *Mixochalcis* and *Eterochalcis* with *Spilochalcis* Thomson, 1876.

Conclusions

No significant synapomorphy could be found to distinguish *Spilochalcis*. There is thus a little doubt concerning the origin of *Chalcis* and *Melanosmicra*. They might have arisen within a strain of *Spilochalcis*. However I consider this to be very unlikely. The position of the *xanthostigma* group, the validity of the *blanda*, *discolor*, *alienata*, *flava* and *apaiis* groups must be confirmed by the study of further material and by biological data.

References

- ASHMEAD, W. H., 1888. A revised generic table of the Chalcidinae. Amer. Entomol., 4: 87-88.
- ASHMEAD, W. H., 1904. Classification of the Chalcid flies or the superfamily Chalcidoidea, with descriptions of new species in the Carnegie Museum, collected in South America by Herbert H. Smith. Mem. Carnegie Mus., 1 (4): I-XI, 225-551.
- BOUČEK, Z., 1952. The first revision of the European species of the family Chalcididae. Acta Entomol. Mus. Nat. Pragae, 27 (Suppl.1): 1-108, 150 figs.
- BURKS, B. D., 1939. Two new species of *Platychalcis* from Costa Rica. (Hymenoptera: Chalcidoidea). Arb. Morph. Taxon. Entomol. Berlin-Dahlem, 6 (3): 275-278. -
- BURKS, B. D., 1940. Revision of the Chalcid-flies of the tribe Chalcidini in America North of Mexico. Proc. U. S. Natl. Mus., 88: 237-354.
- BURKS, B. D., 1968. New North American species of *Ceratosmicra* Ashmead (Hymenoptera: Chalcididae). Proc. Entomol. Soc. Washington, 70 (2): 170-174.
- CRESSON, E. T., 1972. Synopsis of the North American species belonging to the genera *Leucospis*, *Smicra* and *Chalcis*. Trans. Amer. Entomol. Soc., 4: 29-60.
- SICHEL, J., 1865. Essai d'une monographie des genres *Phasganophora* Westwood, et *Conura* Spinola, Hyménoptères de la famille des Chalcidides. Ann. Soc. Entomol. France, 5: 345-396.
- THOMSON, C. G., 1876. Skandinaviens Hymenoptera. 4: 1-192. Lund.
- WALKER, F., 1864. Characters of undescribed species of *Smiera* (Chalcidites). Trans. Entomol. Soc. London, 2: 181-207.
- WALKER, F., 1871. Notes on Chalcididae. Part III. Torymidae and Chalcididae. Pp. 39-54. London.

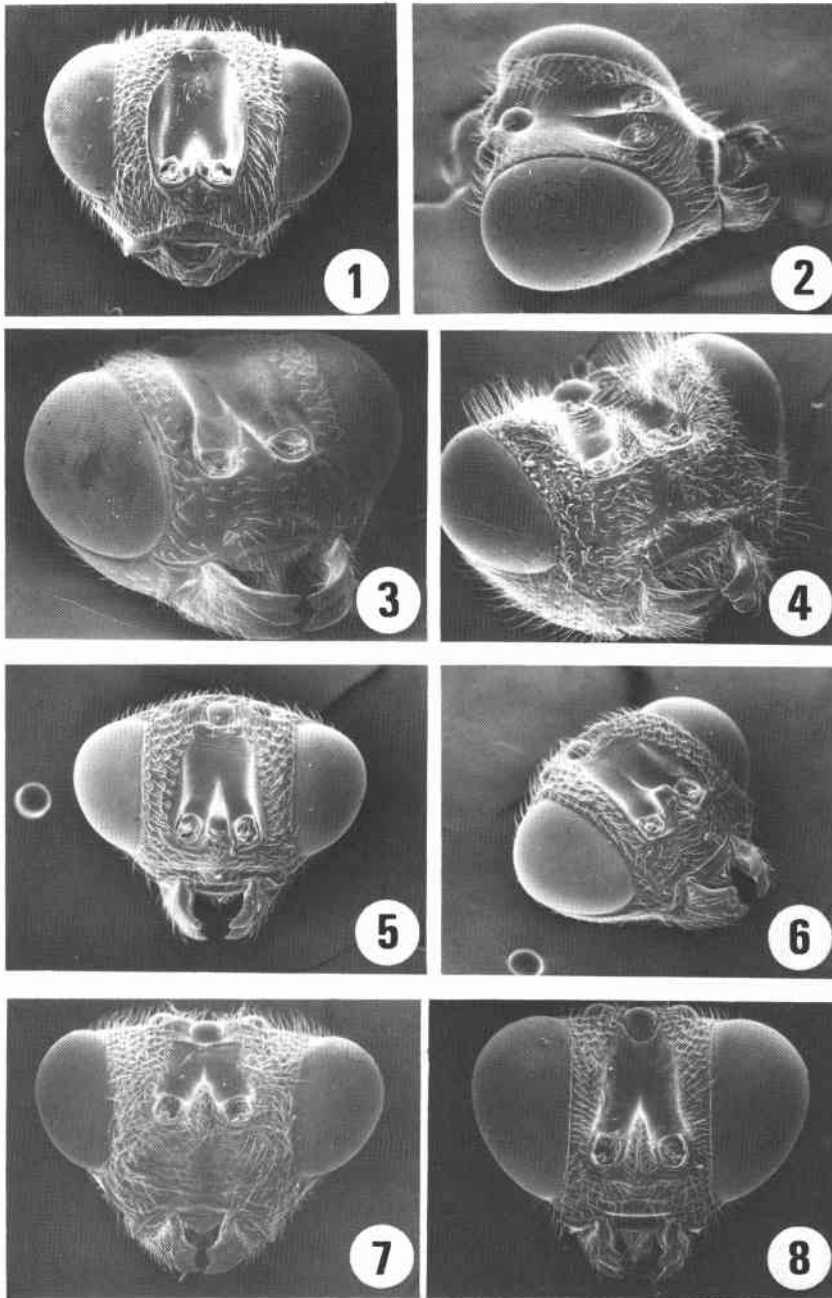
Table II. Derived character states in the Chalcidini, based on outgroup comparisons.

No.	Attribute	Derived character state
1	Female hypopygium	protruding backwards (Fig. 111).
2	Male hypopygium	enlarged and posteriorly emarginate (Fig. 114).
3	Apical spur of the mesotibia	absent.
4	Claws, ornamentation	sexual dimorphism: female claws unarmed; male claws strongly pectinate (Fig. 72, 73).
5	Claws, shape	little curved claws (Fig. 72).
6	Hosts	Stratiomyidae.
7	Oviposition behaviour	eggs laid in eggs or larvae.
8	Malar furrow	present and bordered by an external carina
9	Female hypopygium	pubescent at apex in the median part (Fig. 112).
10	Nesoscutum, sculpture	sparsely punctured, smooth between the punctures (Fig. 39).
11	Inner basal tooth of the metafemur	present, long and curved in females (Fig. 61, 62).
12	Apical spine of the metatibia	long and curved (Fig. 60).
13	Pronotal carina	present and laterally expanded into foliaceous laminae of rounded outline (seen in frontal view); replaced mesally by a weaker arched carina (Fig. 30).
14	Procoxal carina	present, delimiting a flat anterior area (Fig. 31).
15	Transverse carina of the mesopleuron	present, delimiting a ventral area. (Fig. 48).
16	Head, shape	transverse in frontal view, mouth very broad (Fig. 3).
17	Mandibles, shape	either long or robust with blunt teeth (Fig. 79, 80).
18	Foraminal cavity	present, deep and delimited, at least dorsally, by a sharp carina (Fig. 25).
19	Notauli	deep and crenulate, strongly convergent (Fig. 33).
20	Metafemur, teeth.	basal ones regressed, apical ones progressively larger (Fig. 64).
21	Hosts	Psychidae of the genus <i>Oiketicus</i> .
22	Volsellar digiti	long and slender (Fig. 121, 123, 125).
23	Mandibles	robust, with truncate teeth (Fig. 83, 84).
24	Propodeum	with conspicuous pubescence.

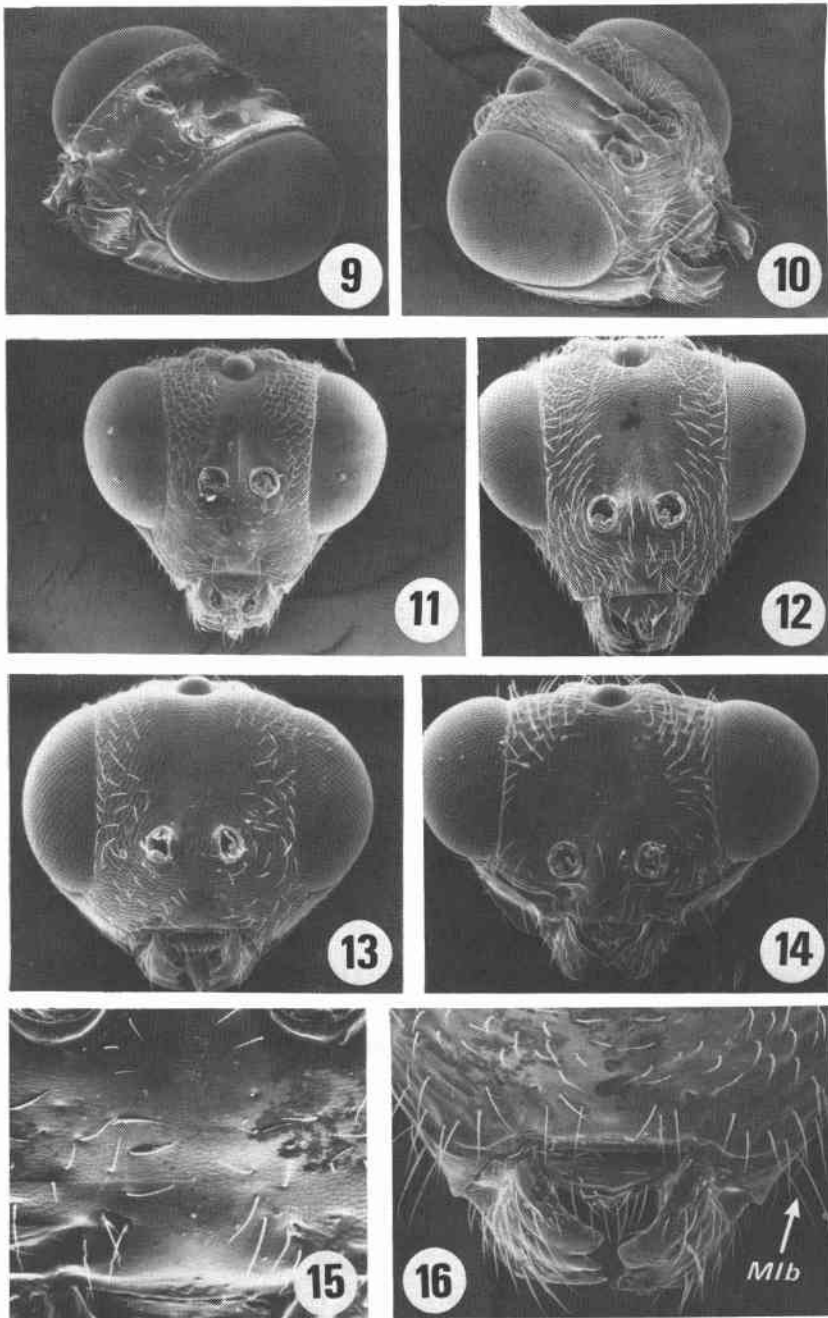
No.	Attribute	Derived character state
25	Metacoxa	long and slender.
26	Claws	strongly pectinate in both sexes (Fig. 74).
27	Hosts	Limacodidae and Megalopygidae.
28	Median ventral lamina	narrow (Fig. 123, 125, 126).
29	Propodeum	articular areola distinct; anterior costula absent (Fig. 54).
30	Propodeum	para-articular apophyses strongly protruding backwards; articular areola distinctly enlarged; subarticular areola sometimes enlarged and delimited by foliaceous laminae (Fig. 55).
31	Phallobase	arms of the ventral frame fused apically on a long distance (Fig. 123).
32	Mesoscutum, sculpture	mesoscutum strigose (Fig. 34, 35).
33	Scape	sexual dimorphism: scape longer (sometimes strongly so) in male than in female, at least apically enlarged (Fig. 28).
34	Foraminal cavity	regressed (Fig. 27).
35	Transverse carina of the mesopleuron and procoxal carina	regressed (Fig. 49).
36	Pronotal carina	regressed.
37	Malar bristles	present and outstanding in males (Fig. 16).
38	Phallotreme	broadly open (Fig. 124d).
39	Scrobe and interantennal projection	scrobe shallow; interantennal projection hardly expanded (Fig. 11).
40	Malar space, sculpture	malar space with elongate squamae (Fig. 21).
41	Malar sulcus	absent because regressed (Fig. 21).
42	Malar space	unusually long (Fig. 12).
43	Volsellar digiti	distinctly emarginate, with a protruding condyle (Fig. 126).
44	Hypostomal process	present and conspicuous (Fig. 26).
45	Preapical carina of the scutellum	present and sublaterally expanded into lobes or laminae (Fig. 44).
46	Malar furrow	broad and deep, bordered by two distinct carinae (Fig. 23).
47	Face, sculpture.	finely alutaceous, with sparse and fine punctures (Fig. 15).
48	Occipital vertical furrow	present.
49	Dorsellum	well delimited; convex, bare and shining (Fig. 56).

No.	Attribute	Derived character state
50	Ventral frame and phallobase	ventral frame regressed; phallobase at least partly closed on its ventral side. (Fig. 128, 131).
51	VolSELLar digiti	emarginate on their external margin (Fig. 127).
52	Prepectus	submedian carinae fused.
53	VolSELLar digiti	strongly emarginate; angular at the level of the condyle (Fig. 128).
54	Antennal scrobe	dorsally delimited by a carina (Fig. 96).
55	Pronotum	a transverse post-basal furrow impressed on collum (Fig. 103).
56	Parameres	two apical bristles on the right paramere (Fig. 127).
57	Mandibles	2-2 formula; the teeth bordered ventrally by a foliaceous lamina (Fig. 87).
58	Preapical carina of the scutellum	bilobed, the lobes widely separated (Fig. 45).
59	Basal lamina of the abdominal petiole	only ventrally expanded; sloping forwards (Fig. 75).
60	Interantennal projection	compressed into a well expanded translucent lamina (Fig 9).
61	Metafemur, teeth	metafemur four-toothed, the last tooth large and triangular (Fig. 65).
62	Phallobase	deeply incised apically; median ventral lamina long and narrow (Fig. 132).
63	Metafemur, teeth	metafemur with 5-8 long teeth (Fig. 67).
64	Head	a broad foraminal depression, surmounted by a transverse and high foliaceous lamina, this latter forming a deep furrow with the occiput (Fig. 99, 100).
65	Head	a broad foraminal depression (Fig. 101, 102).
66	Head	face with an arched subantennal carina (Fig. 97, 98).
67	Mandibles	2-2 formula, but fine; the teeth of equal length, acute (Fig. 88).
68	Scutellum	distinctly convex, mostly at base.
69	Metafemur, teeth	metafemur with closely set teeth, the basal one indistinct or short.
70	Metatibia	with a short to very short apical spine.
71	Phallobase	short (Fig. 133).

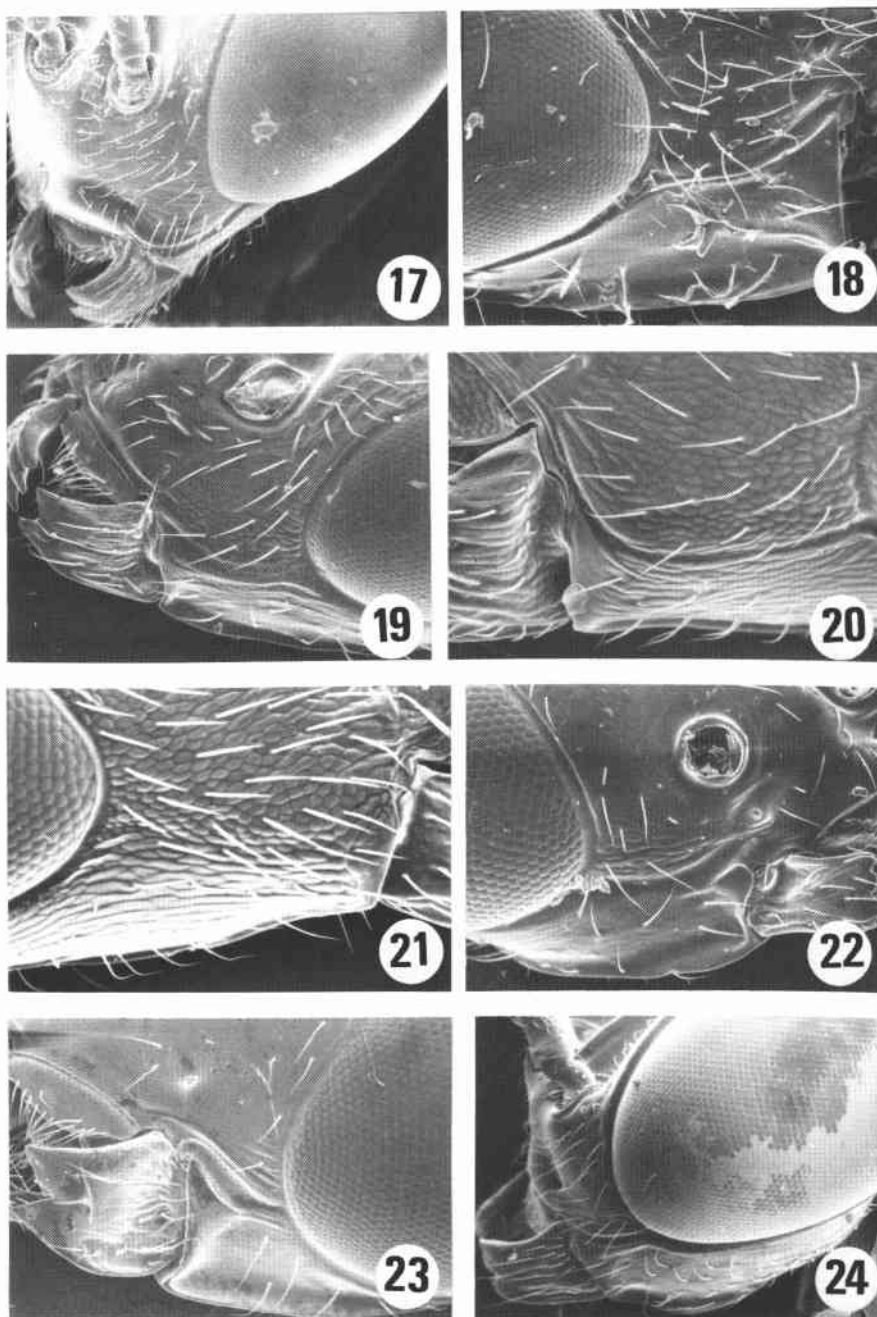
No.	Attribute	Derived character state
72	Metafemur, teeth	basal tooth distinctly longer than the following ones; inner acute tooth (Fig. 68, 69)
73	Interantennal projection	never strongly protruding, but dorsally compressed into a translucent lamina. (Fig. 24).
74	Propodeum	rather long, but irregularly areolate, the articular area hardly or not distinct (Fig. 57).
75	Scape	short but not compact.
76	Malar furrow	shallow or absent; internal carina absent or present only towards the mouth; external carina complete (Fig. 19).
77	Mesoscutum, sculpture	punctuation sparse, superficial ; punctures alternating with squamae (Fig. 37).
78	Preapical carina of the scutellum	mesally fused with the posterior margin of the scutellum or very close to it ; frenal area reduce (Fig. 46).
79	Head	rounded in frontal view (Fig. 13).
80	Malar furrow	narrow, superficial and not bordered by carinae (Fig. 13).
81	Head	very transverse in frontal view, with antennal scrobe hardly set up (Fig. 14).
82	Mandibles	aberrant, 3+1 - 3+1 toothed (Fig. 90).
83	Prepectus	submedian carinae regressed.



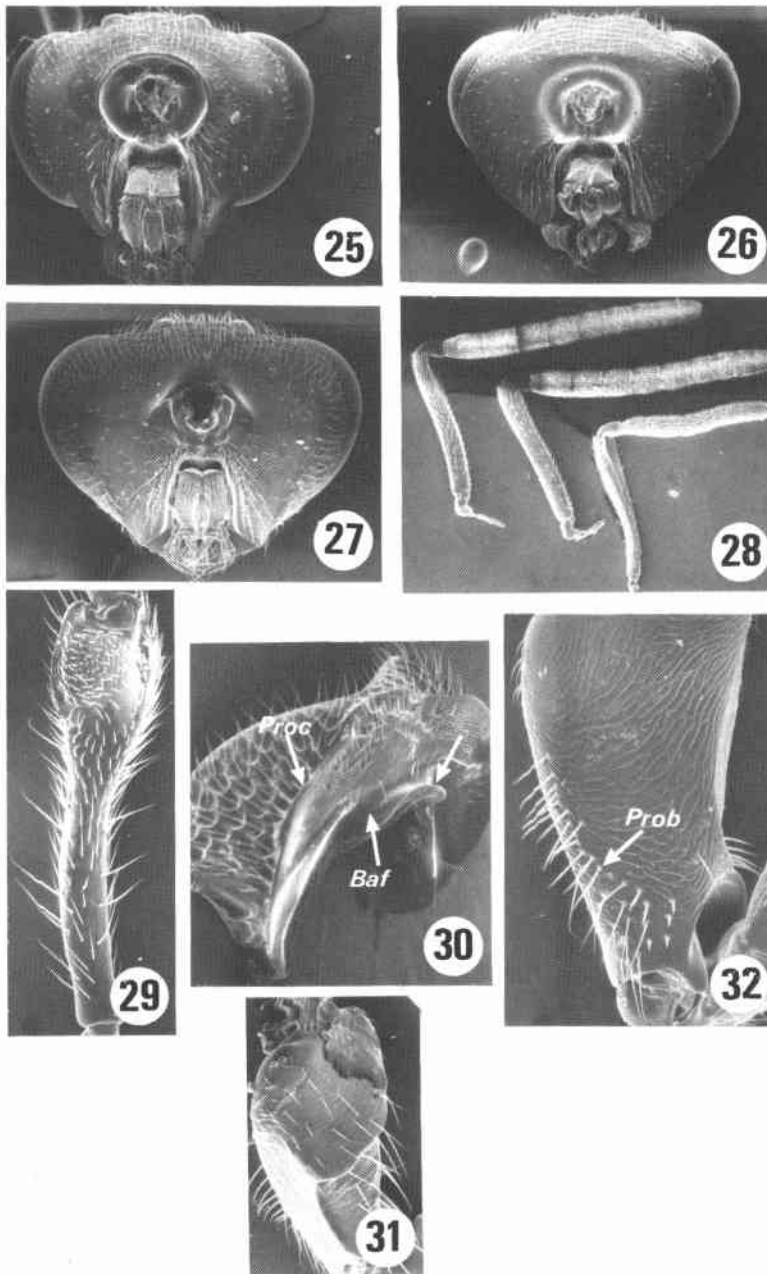
Figs. 1-8. 1, Head of Brachymeriini (female): *Brachymeria* sp. (x50). 2-8. Heads of selected species of Chalcidini (females): 2, *Spilochalcis miniata* (Cameron) (*mariae* group) (x50); 3, *S. lecta* (Cresson) (*xanthostigma* group) (x75); 4, *Chalcis myrifex* (Sulzer) (x50); 5-6, Undetermined *Spilochalcis* of the *xanthostigma* group (x50); 7, Undetermined *Spilochalcis* of the *nigricornis* group (x35); 8, *S. santaremensis* Ashmead (x50).



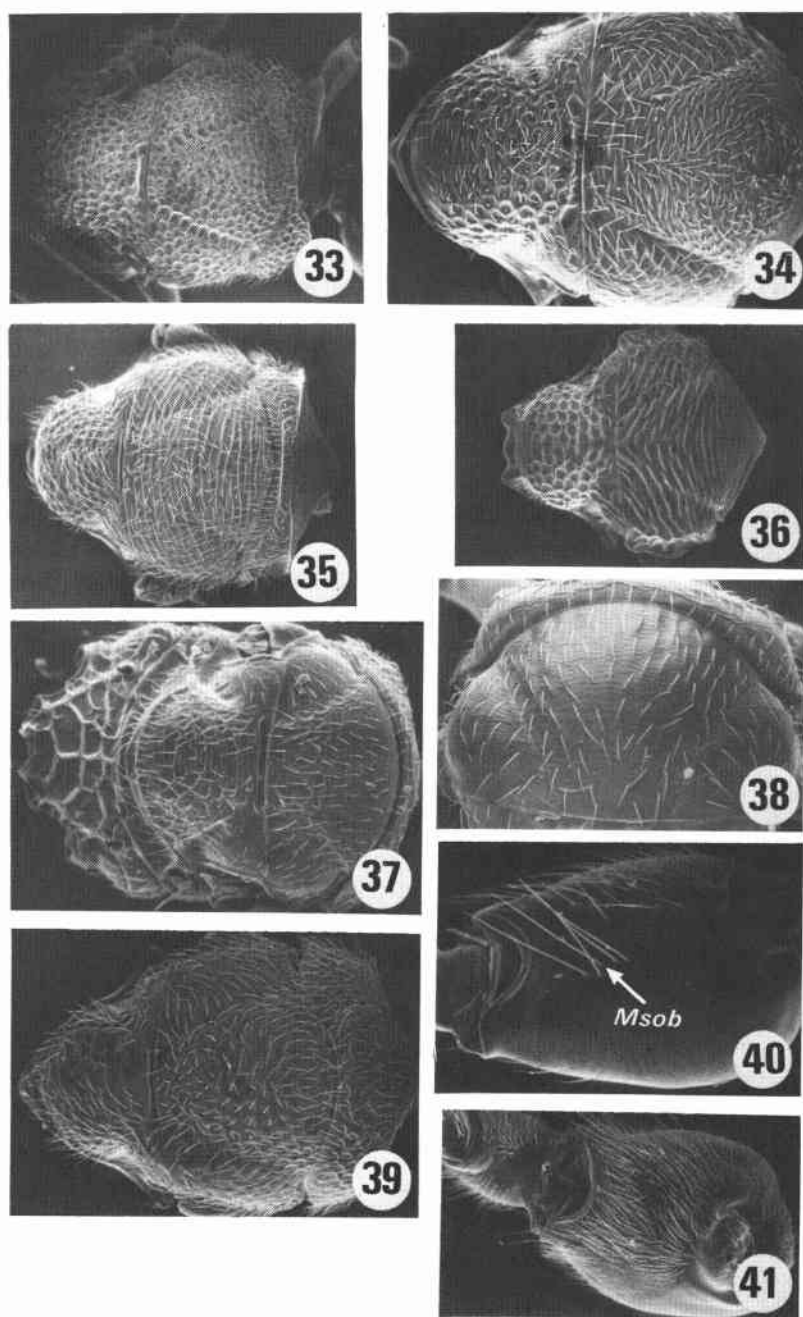
Figs. 9-16. Heads of selected species of Chalcidini (females except otherwise mentioned): 9, *Spilochalcis decisa* (Walker) (*transitiva* group) (x50); 10, *Melanosmicra variventris* (Cameron) (x75); 11, *S. fulvovariegata* (Cameron) (*fulvomaculata* group) (x75); 12, Undetermined *Spilochalcis* of the *side* group (x100); 13, Undetermined *Spilochalcis* of the *rufoscutellaris* group (x150); 14, *S. maculipennis* (Cameron) (*maculipennis* group) (x100); 15, Undetermined *Spilochalcis* of the *blanda* group: sculpture of the face (x200); 16, *S. miniata* (Cameron), male: face showing the malar bristles (Mlb) (x150).



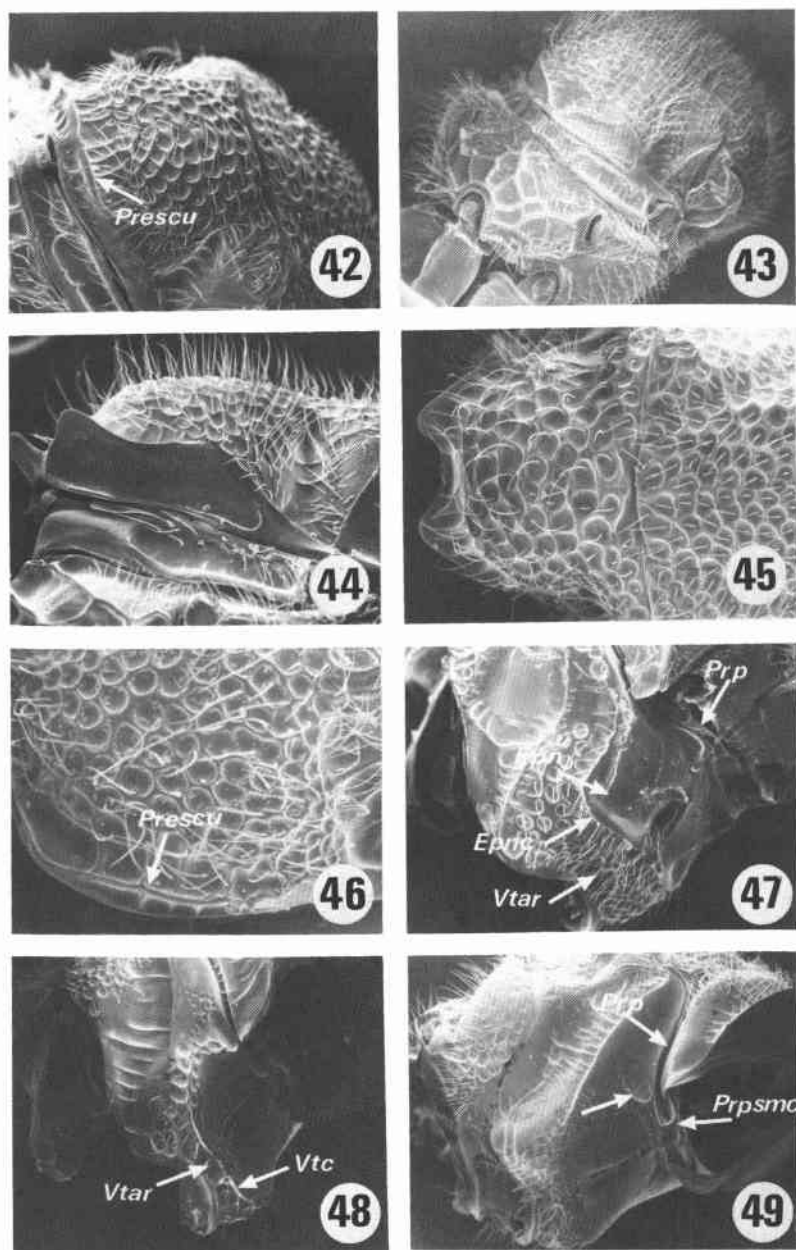
Figs. 17-24. Malar furrow of selected species of *Spilochalcis*: 17, *S. miniata* (Cameron) (*mariae* group) (x100); 18, Undetermined species of the *oiketicusi* group (x150); 19, Undetermined species of the *apaiis* group (x150); 20, *S. fulvovariiegata* (Cameron) (*fulvomaculata* group) (x350); 21, Undetermined species of the *side* group (x350); 22, *S. maculipennis* (Cameron) (*maculipennis* group) (x200); 23, *S. decisa* (Walker) (*transitiva* group) (x150); 24, *S. femorata* (F.) (*femorata* group) (x100).



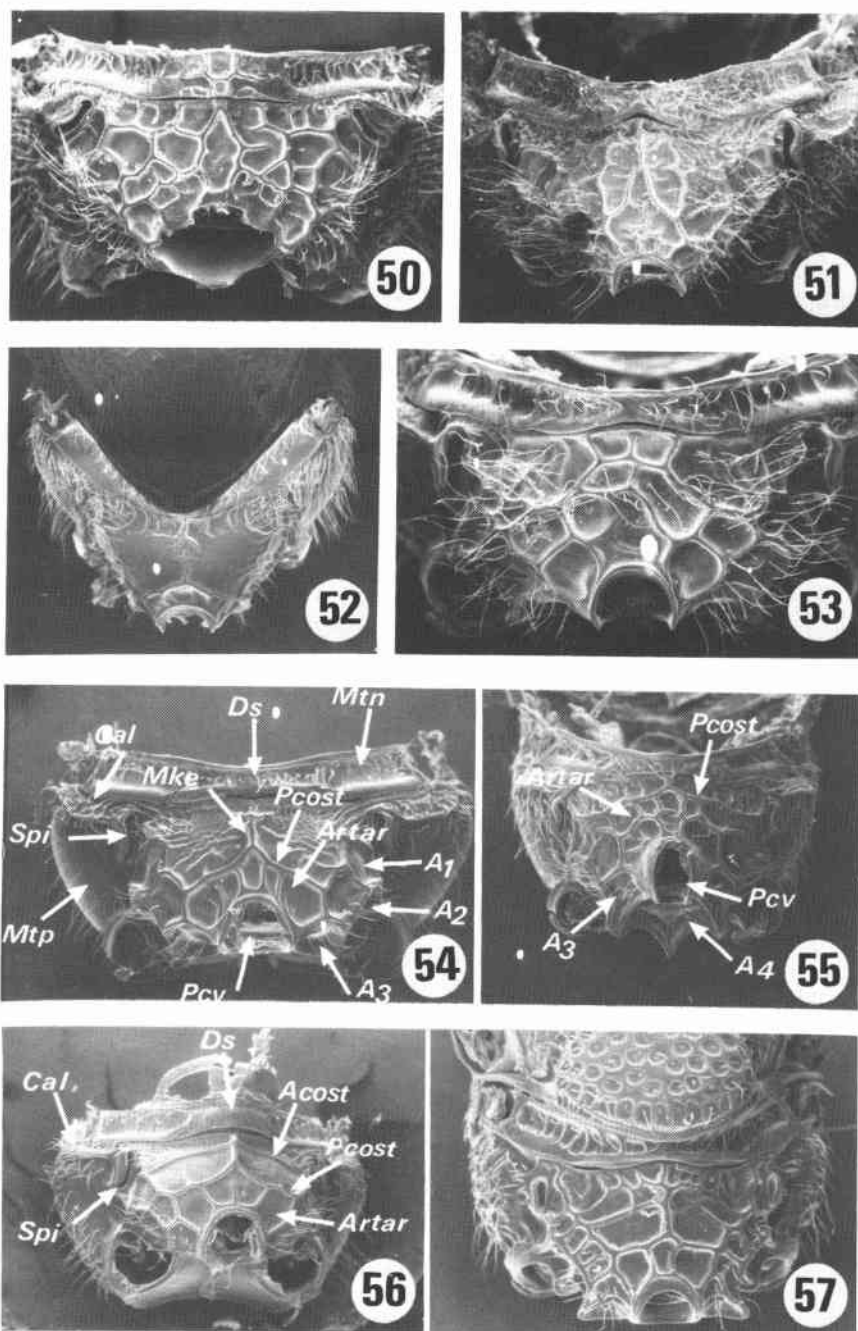
Figs. 25-32. 25-27. Heads of selected species of *Spilochalcis* in posterior view: 25, *S. decisa* (Walker) (x50); 26, Undetermined species of the *blanda* group (x50); 27, *S. santaremensis* (Ashmead) (x50). 28-29. Antenna of some *Spilochalcis*: 28, *S. fulvomaculata* (Cameron): from left to right: female antenna in outer view; the same in inner view; male antenna (x50); 29, *S. miniata* (Cameron): male scape in ventral view (x150). 30-32. Pronotal structures of Chalcidini: 30, *Spilochalcis decisa* (Walker): pronotum showing the pronotal carina (Proc) and the basal furrow (Baf) (x75); 31, Undetermined *Spilochalcis* of the *xanthostigma* group: procoxa (x150); 32, *S. santaremensis* Ashmead: procoxa in posterior view showing the procoxal bristles (Prob) (x200).



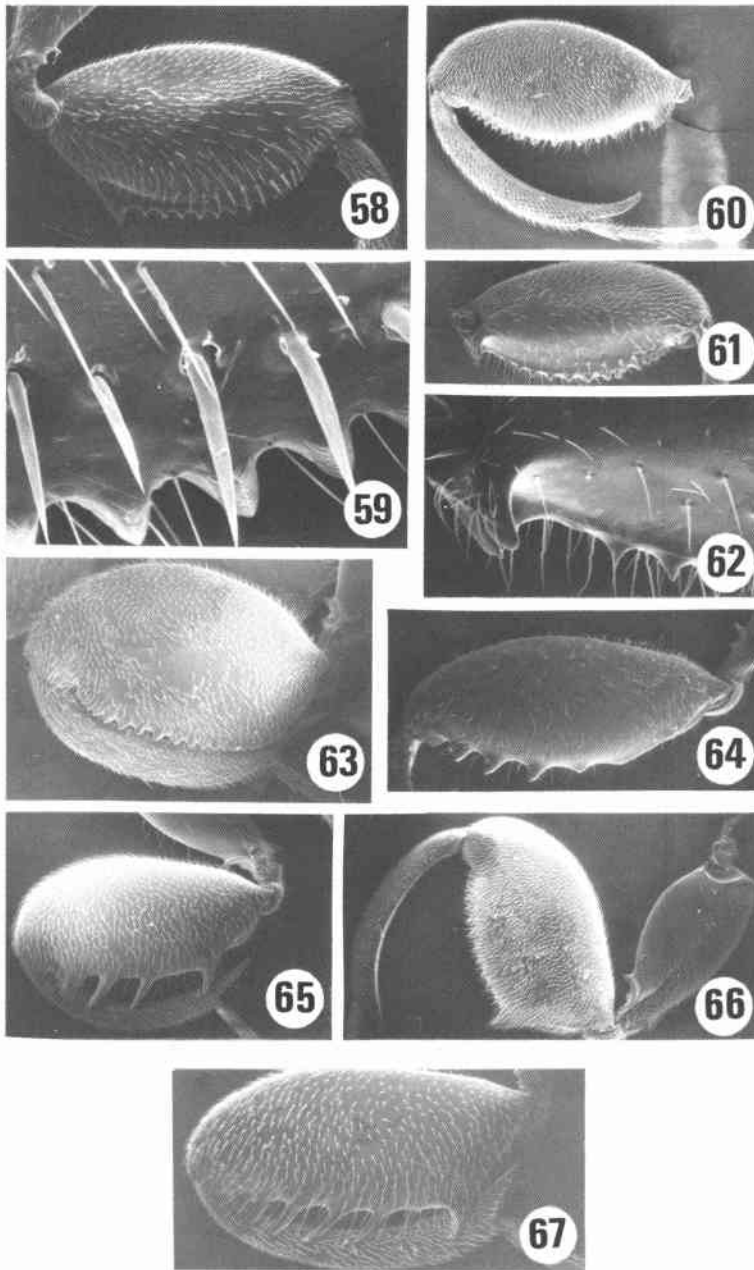
Figs. 33-41. 33-39. Mesoscutal sculpture of Chalcidini: 33, Undetermined *Spilochalcis* of the *oiketicusi* group (x35); 34, *S. fulvomaculata* (Cameron) (*fulvomaculata* group) (x75); 35, *S. miniata* (Cameron) (*mariae* group) (x50); 36, *S. dimidiata* (F.) (*dimidiata* group) (x35); 37, Undetermined *Spilochalcis* of the *rufoscutellaris* group (x150); 38, Undetermined *Spilochalcis* of the *fulvomaculata* group (x150); 39, *Melanosmicra variventris* (Cameron) (x75). 40-41. Mesocoxa of Chalcidini: 40, *Spilochalcis santaremensis* Ashmead: mesocoxa in inner view showing the mesocoxal bristles (Msob) (x200); 41, *Chalcis myrifex* (Sulzer): mesocoxa in dorsal view (x100).



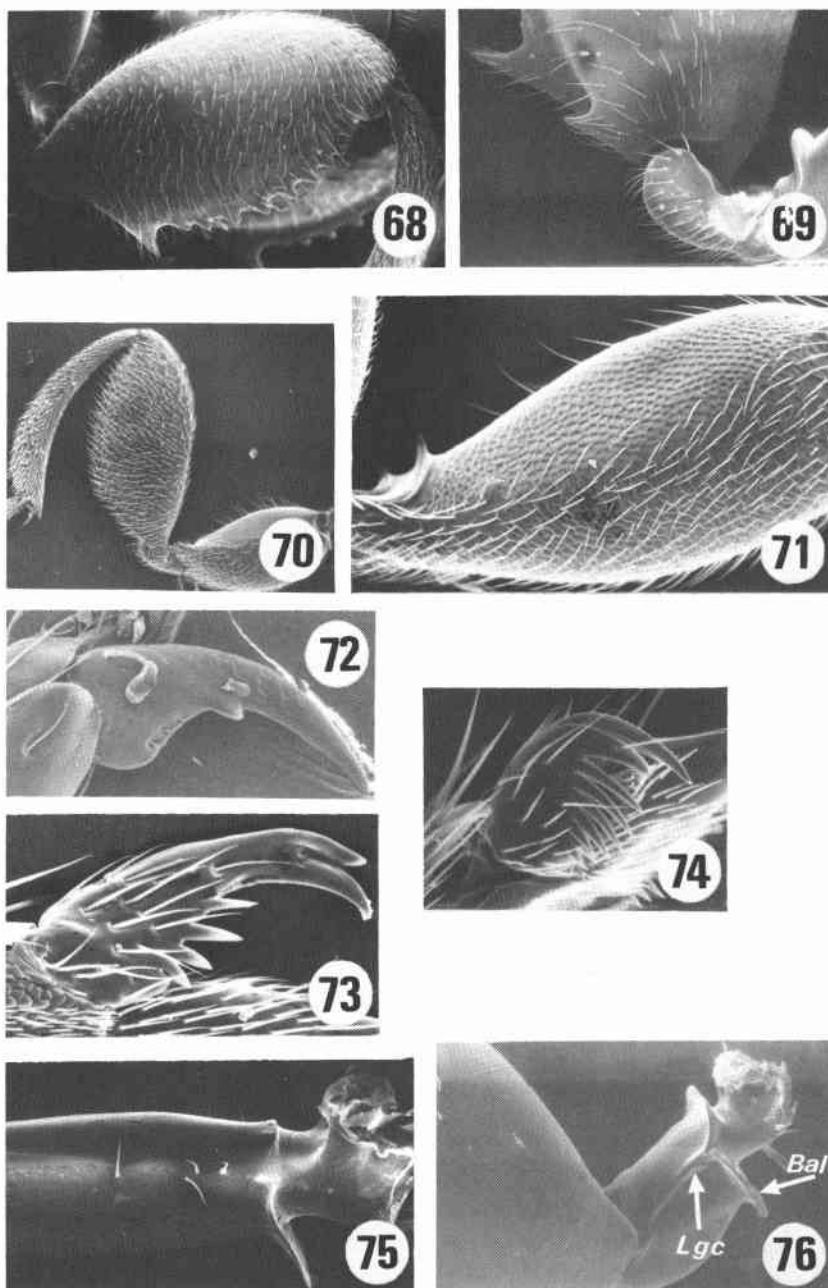
Figs. 42-49. 42-46. Preapical carina of the scutellum in selected species of Chalcidini: 42, Undetermined *Spilochalcis* of the *xanthostigma* group: scutellum in posterior view showing the preapical carina (Prescu) (x75); 43, *S. maculata* (F.): idem (x50); 44, *S. flava* (F.): scutellum in lateral view (x75); 45, *S. destinata* (Walker): scutellum in dorsal view (x75); 46, Undetermined *Spilochalcis* of the *nigricornis* group: scutellum in laterodorsal view (x100). 47, Mesopleuron of Brachymeriini: *Brachymeria* sp. in lateroventral view (x75). 48-49. Mesopleuron of Chalcidini: 48, *Spilochalcis decisa* (Walker) (x50); 49, *S. miniata* (Cameron) (x50). Epn, epicnemium; Epic, epicnemial carina; Prp, prepectus; Prpsmc, submedian carinae of the prepectus; Vtar, ventral area of the mesopleuron; Vtc, ventral transverse carina of the mesopleuron.



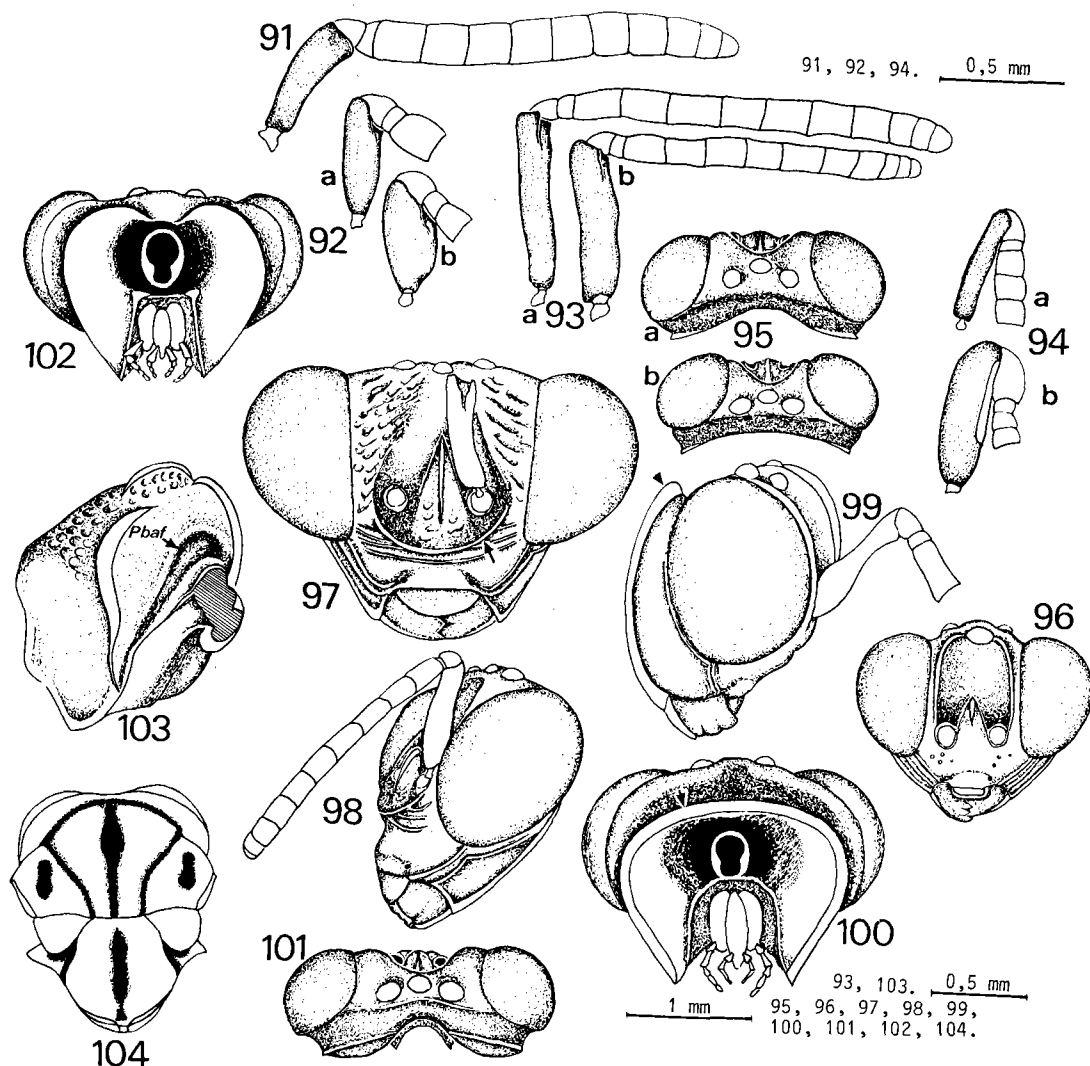
Figs. 50-57. 50, Propodeum of Brachymeriini: *Brachymeria* sp., propodeum and metanotum in dorsal view (x75). 51-57. Propodeum of Chalcidini: 51, *Chalcis myrifex* (Sulzer) (x50); 52, *Melanosmicra variventris* (Cameron) (x75); 53, Undetermined *Spilochalcis* of the *oiketicusi* group (x75); 54, *Spilochalcis fulvomaculata* (Cameron) (x75); 55, *S. longipetiolata* (Ashmead) (*debilis* group) (x100); 56, *S. longicaudata* (Ashmead) (*flava* group) (x50); 57, *S. maculipennis* (Cameron) (x100). Acost, anterior costula; A1, spiracular areola; A2, supracoxal areola; A3, para-articular areola; A4, subarticular areola; Artar, articular area; Cal, callus; Ds, dorsellum; Mke, median keel; Mtn, metanotum; Mtp, metapleuron; Pcost, posterior costula; Pcv, petiolar cavity; Spi, spiracular aperture.



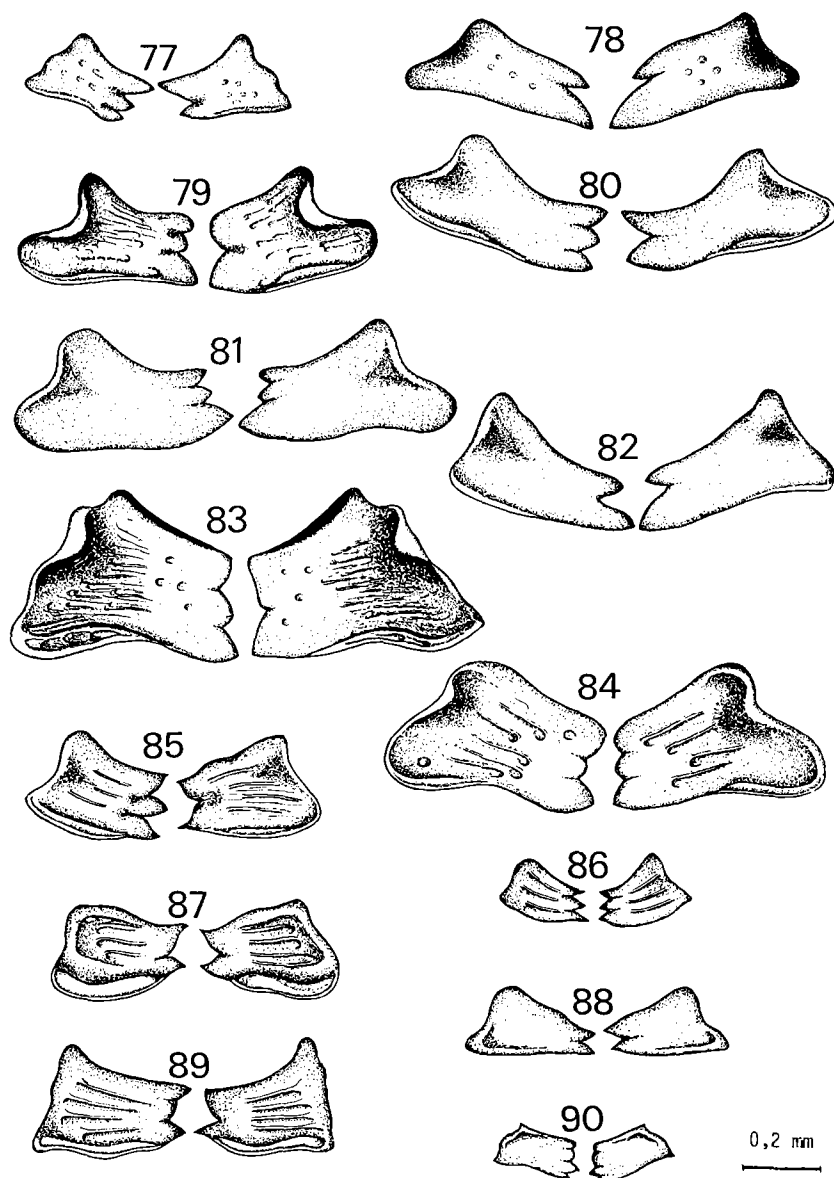
Figs. 58-67. Metafemoral structures in Chalcidini: 58, *Spilochalcis fulvomaculata* (Cameron): metafemur in inner view showing marginal metafemoral bristles (x50); 59, Part of the same enlarged (x350); 60, *Melanosmicra variventris* (Cameron), female: hind leg in outer view showing external basal tooth of metafemur and apical spine of metatibia (x50); 61, Same species, female: metafemur in inner view (x50); 62, Same species: base of metafemur enlarged showing inner basal tooth (x200); 63, *Spilochalcis lecta* (Cresson), metafemur (x50); 64, Undetermined species of the *oiketicusi* group, metafemur (x35); 65, *Spilochalcis decisa* (Walker), metafemur (x50); 66, *S. santaremensis* Ashmead, metafemur (x50); 67, *S. longicaudata* (Ashmead), metafemur (x50).



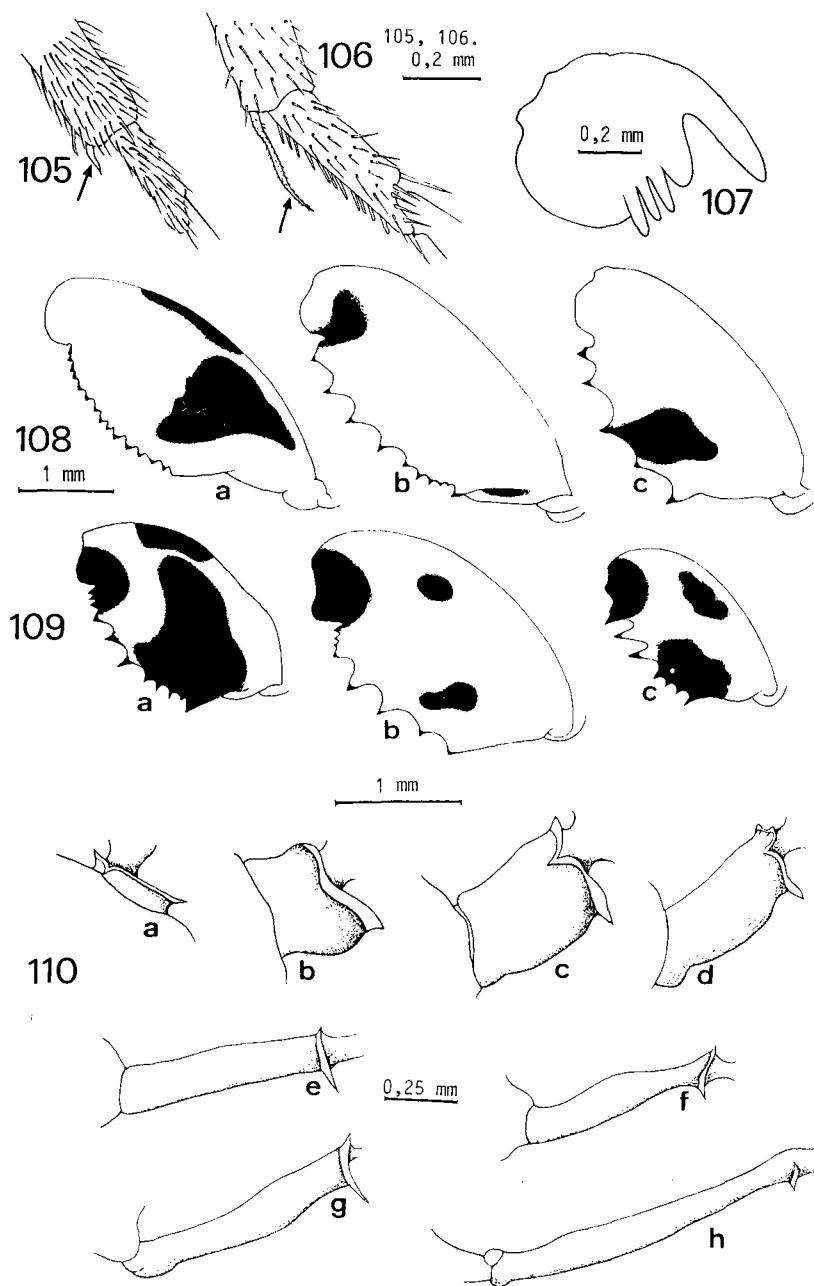
Figs. 68-76. 68-71. Hind legs of Chalcidini: 68, *Spilochalcis femorata* (F.), metafemur showing the outer basal tooth (x50); 69, Same species, enlarged base of metafemur in inner view showing inner basal tooth (x75); 70, *S. pygmaea* (F.), hind leg (x35); 71, Undetermined *Spilochalcis* of *side* group, metacoxa showing reticulation of outerdorsal area (x200). 72-74. Claws of Chalcidini: 72, *Chalcis myrifex* (Sulzer), female (x350); 73, *C. myrifex*, male (x500); 74, Undetermined *Spilochalcis* of the *nigricornis* group, female (x350). 75-76. Abdominal petiole of Chalcidini: 75, *Spilochalcis decisa* (Walker) (x150); 76, *S. femorata* (F.) (x100).



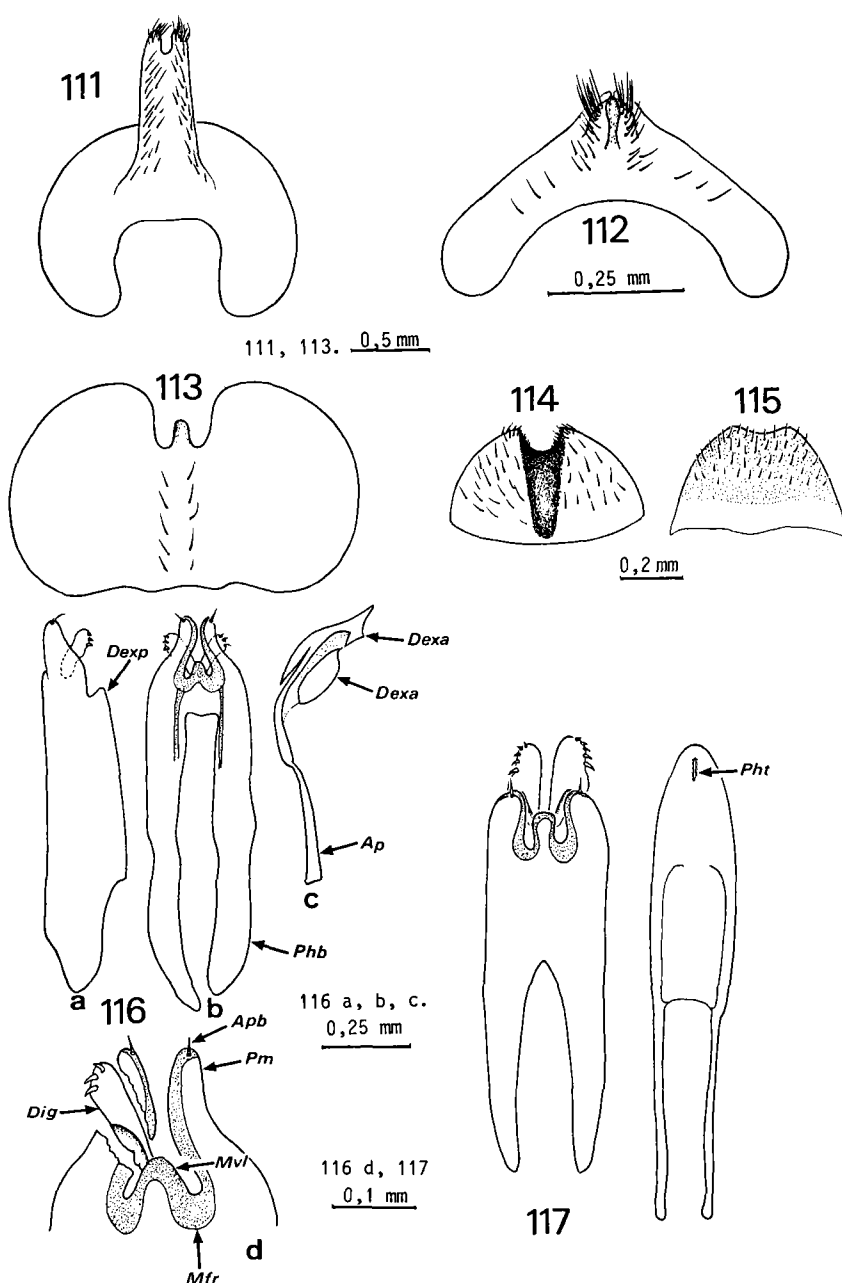
Figs. 91-104. 91, Antenna of an undetermined *Spilochalcis* of the *xanthostigma* group, female. 92-94, Sexual dimorphism in the antenna of *Spilochalcis*, female (a), male (b): 92, Undetermined species of the *pygmaea* group, scape and base of flagellum; 93, *S. longicaudata* (Ashmead); 94, *S. side* (Walker). 95, Sexual dimorphism in head of *Spilochalcis longicaudata* (Ashmead), dorsal view, female (a), male (b). 96-102, Heads of some species of *Spilochalcis*: 96, *Spilochalcis* of the *N* group, head in frontal view showing antennal scrobe; 97, *S. referator* (Walker), head in frontal view showing subantennal carina; 98, the same in lateral view; 99, *S. hollandi* Ashmead, head in lateral view; 100, Undetermined species of the *hollandi* group, head in posterior view showing foraminal depression; 101, *S. exaniens* (Walker), head in dorsal view; 102, the same, head in posterior view showing foraminal depression. 103, Pronotal structures of an undetermined species of the *N* group of *Spilochalcis*, pronotum in anterolateral view showing the postbasal furrow (Pbaf). 104, Mesonotal maculation of *Spilochalcis maculata* (F.) (*mariae* group).



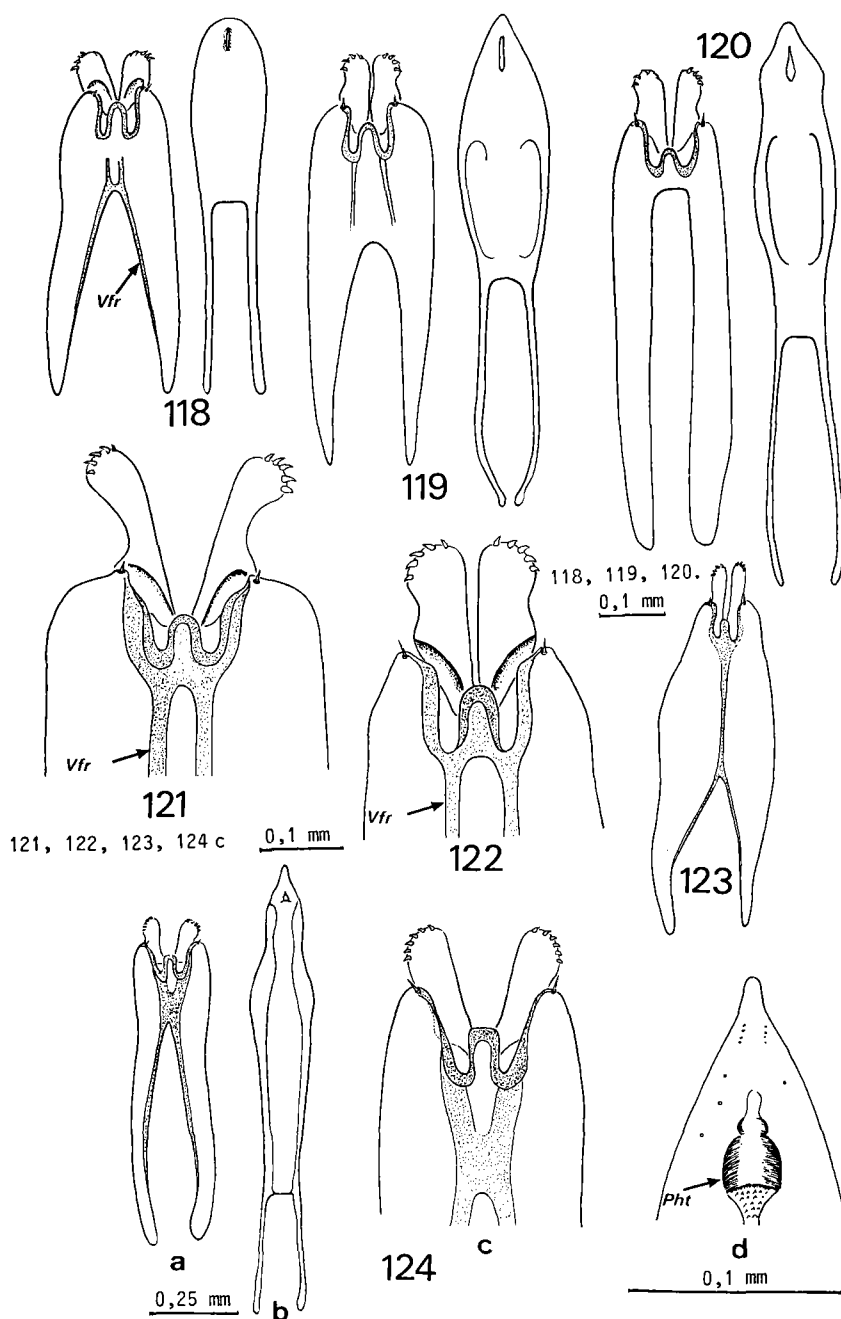
Figs. 77-90. Mandibles of selected species of Chalcidini (females): 77, *Melanosmicra variventris* (Cameron); 78, *M. flavicollis* (Cameron); 79, Undetermined *Spilochalcis* of the *xanthostigma* group; 80, *S. lecta* (Cresson); 81-82, Undetermined species of *Spilochalcis* of the *xanthostigma* group; 83-84, Undetermined species of *Spilochalcis* of the *nigricornis* group; 85, *S. miniata* (Cameron); 86, Undetermined *Spilochalcis* of the *side* group; 87, *S. decisa* (Walker); 88, *S. pygmaea* (F.); 89, Undetermined *Spilochalcis* of the *alienata* group; 90, *S. maculipennis* (Cameron).



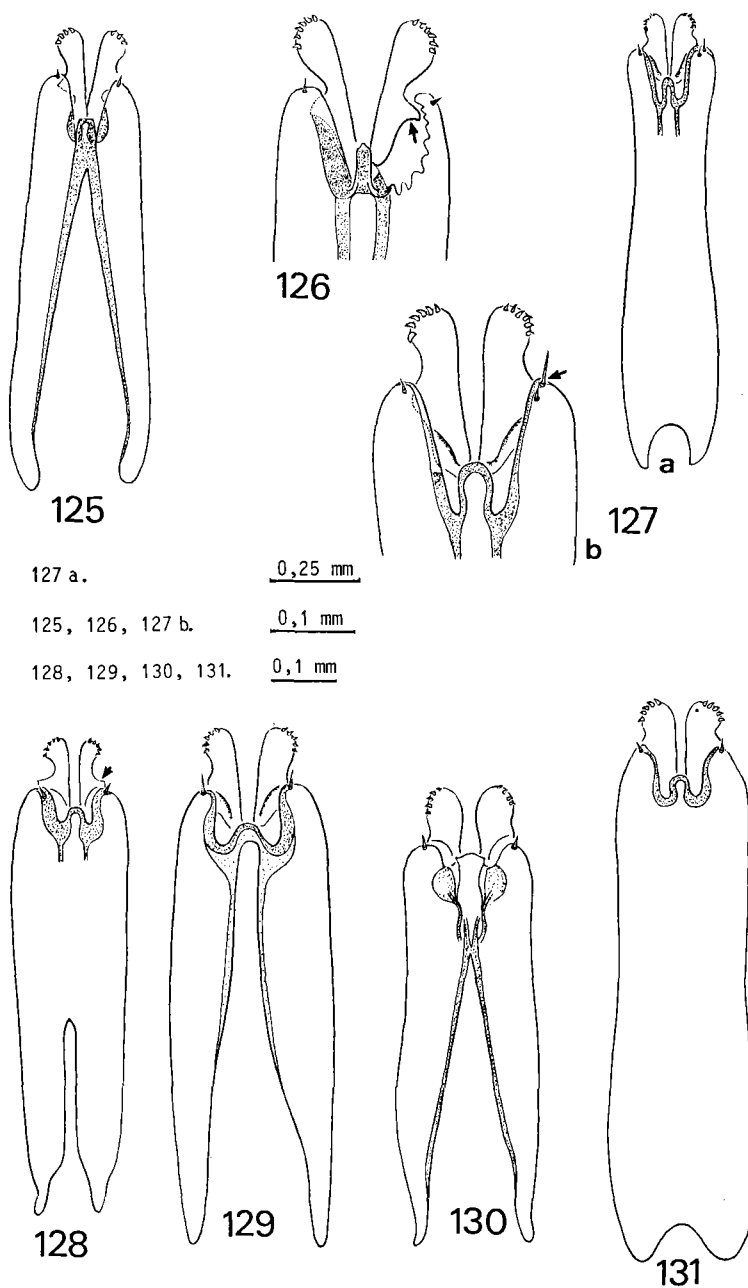
Figs. 105-110. 105-106. Apical spur of mesotibia in Chalcidini: 105, Undetermined species of *Chalcis*; 106, *Spilochalcis flava* (F.). 107, Claws of *Spilochalcis decisa* (Walker). 108, Teeth of metafemur in *nigricornis* group of *Spilochalcis*: a, b, undetermined species; c, *S. lasnierii* (Guérin). 109, Teeth of metafemur in the *blanda* group of *Spilochalcis*: a, *S. marginata* Ashmead; b and c, undetermined species. 110. Abdominal petiole of *Spilochalcis*: a, *S. fusiformis* Ashmead; b, *S. rodriguezi* (Cockerell); c, *S. miniata* (Cameron); d, undetermined species of the *xanthostigma* group; e, *S. megalospilus* Cameron; f, *S. petioliventris* Howard; g, *S. paya* (Burks); h, *S. debilis* (Say).



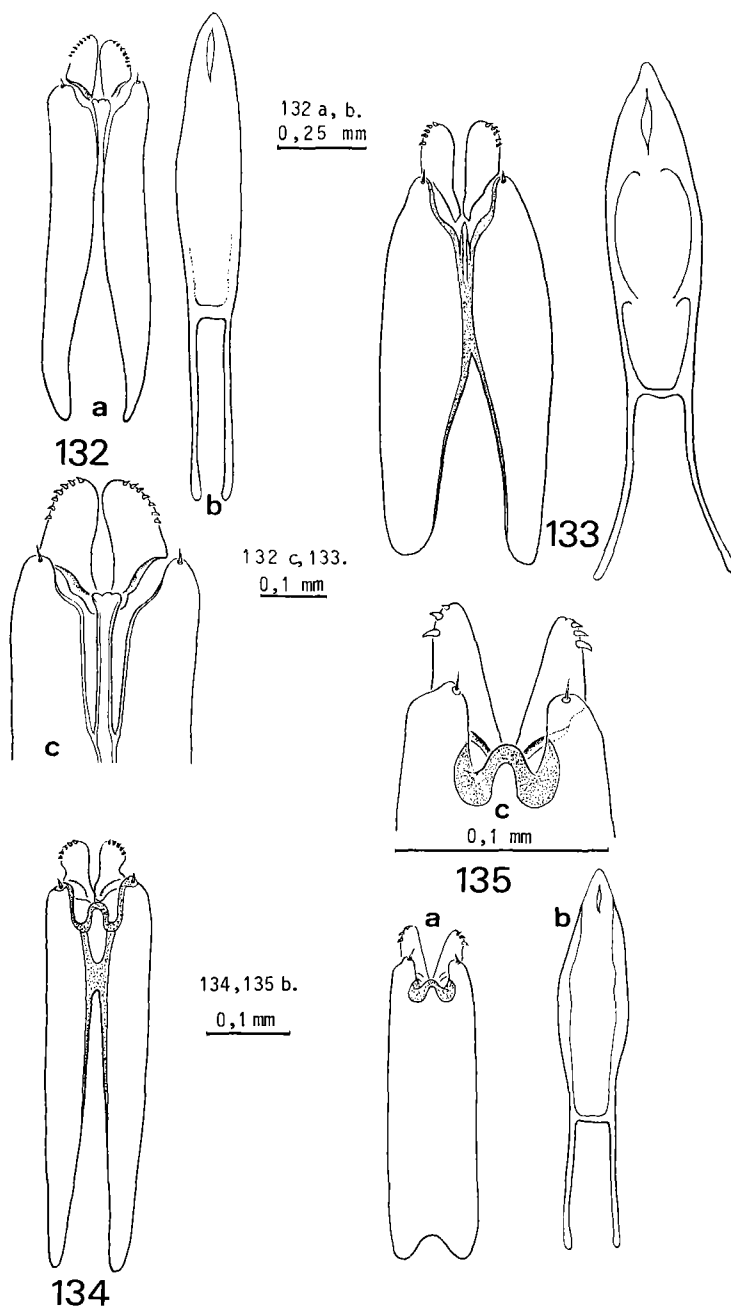
Figs. 111-117. 111-112. Female hypopygium of Chalcidini: 111, *Chalcis myrifex* (Sulzer); 112, *Melanosmicra variventris* (Cameron); 113, *Spilochalcis quadripunctata* (F.). 114-115. Male hypopygium of Chalcidini: 114, Undetermined species of *Chalcis*; 115, *Spilochalcis flava* (F.). 116-117. Male genitalia of Chalcidini: 116, Undetermined species of *Chalcis*: *a*, sheath in lateral view; *b*, the same in ventral view; *c*, aedeagus in lateral view; *d*, apex of phallobase enlarged; 117, Undetermined species of *Melanosmicra*, ventral view. *Ap*, apodeme; *Apb*, apical parameral bristle; *Dexa*, dorsal expansions of aedeagus; *Dexp*, dorsal expansion of phallobase; *Dig*, volsella digiti; *Mfr*, marginal frame; *Mvl*, median ventral lamina; *Phb*, phallobase; *Pht*, phallotreme; *Pm*, paramere.



Figs. 118-124. Male genitalia of *Spilochalcis* (ventral view): 118, Undetermined species of the *xanthostigma* group; 119, *S. lecta* (Cresson) (*xanthostigma* group); 120, Undetermined species of the *xanthostigma* group; 121, Undetermined species of the *nigricornis* group: apex of phallobase enlarged; 122, Undetermined species of the *oiketicusi* group: apex of phallobase enlarged; 123, *S. debilis* (Say) (*debilis* group); 124, *S. mariae* (Riley) (*mariae* group): a, sheath; b, aedeagus; c, apex of phallobase enlarged; d, apex of aedeagus showing phallotreme (Pht). Vfr, ventral frame.



Figs. 125-131. Male genitalia of *Spilochalcis* (ventral view): 125, *S. fulvovariegata* (Cameron) (*fulvomaculata* group); 126, *S. delumbis* (Cresson) (*side* group): apex of phallobase; 127, Undetermined species of the *N* group: *a*, sheath; *b*, apex of phallobase enlarged; 128, *S. biannulata* (Ashmead); 129, *S. exinaniens* (Walker); 130, Undetermined species of the *discolor* group; 131, *S. santaremensis* Ashmead.



Figs. 132-135. Male genitalia of *Spilochalcis* (ventral view): 132, *S. flava* (F.): a, sheath; b, aedeagus; c, apex of phallobase enlarged; 133, *S. pygmaea* (F.); 134, Undetermined species of the *apaiis* group; 135, Undetermined species of the *rufodorsalis* group: a, sheath; b, aedeagus; c, apex of phallobase enlarged.

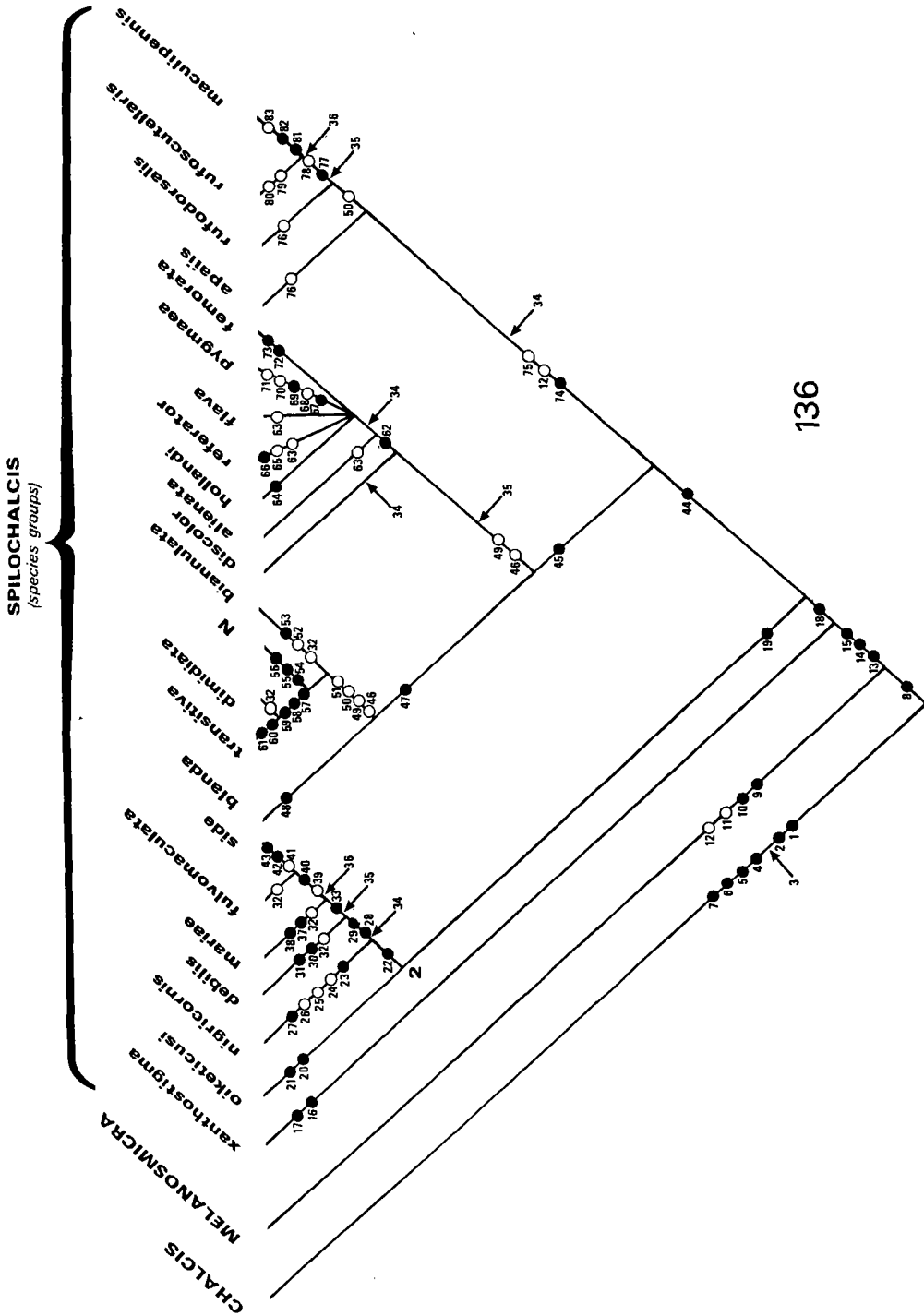


Fig. 136. Cladogram showing the distribution of shared derived characters in genera of Chalcidini and species groups of *Spirochalcis*. Characters defined in Table II. O = synapomorphies; O = multiple apomorphies; --- = reversals.