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The Parasitic Groups of Halictidae (Hymenoptera, Apoidea)

Charles D. Michener
University of Kansas

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THE PARASITIC GROUPS OF HALICTIDAE (HYMENOPTERA, APOIDEA)

By

Charles D. Michener

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The Parasitic Groups of Halictidae
(Hymenoptera, Apoidea)

CHARLES D. MICHENER

Departments of Entomology and of Systematics and Ecology, and Snow Entomological Museum, University of Kansas

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ABSTRACT

Eight parasitic genera of halictid bees are recognized, derived from five different nonparasitic ancestral groups. The parasites vary from those, like Para/ictus, which are similar to their nonparasitic relatives and are presumably recent derivatives of them, to others, like Sphecodes, which appear to be ancient parasitic groups derived from nonparasitic ancestral genera that quite likely no longer exist. Convergent morphological features among parasites include reduction or loss of structures for pollen collecting and carrying and of structures used in nest construction.

A review of host relationships is provided, as is speculation on the relationships between type of parasitization and structure within the genus Sphecodes.

In the taxonomic treatment, a new genus (Ptilocleptis) and three new species (P. tomentosa, polybioides, and eickworti) are described, as are Sphecodes subgenus Austrosphecodes and the species S. (A.) convergens and Eupetersia guillarmodi and flavic.

INTRODUCTION

Among most families of bees there are genera or species that do not make or provision their own nests, but put their eggs in, or actually live in, the nests of other species of bees. Larvae of such social parasites or cleptoparasites do not feed on the hosts, but eat the provisions supplied by the host. In some cases, adult hosts are killed by the female parasite, but in most cases only the eggs or young larvae in cells are killed, either by the adult female parasite or by the young larvae of the parasite. In the large bee family Halictidae, parasitic forms have arisen at least five times from different nest-making ancestors. The subjects of this paper are the parallel evolution that has occurred among these forms, their host relationships, and their taxonomic groupings.

Although some of them have not yet been reared from nests of their hosts, parasitic halictids can be recognized by the absence of pollen-gathering and pollen-carrying structures in the females. There are parasitic species of other families of bees that have not lost pollen-handling equipment (Bombus, Braunsapis; see Michener, 1974), but no such forms are known in Halictidae, although individuals of nest-making species sometimes usurp nests of the same or other species (Knerer and Plateaux-Quénu, 1967).

The parasitic halictid genera and their antecedents are listed in Table 1. Characters supporting the judgments as to which are the ancestral groups are indicated in the taxonomic treatment. Convergent features characteristic of the parasitic groups are listed below and in Table 2.

CONVERGENT FEATURES

Parasitic halictids are characterized by numerous similarities. These are among the principal characteristics by which they differ from the nonparasitic or nest-making genera from which they arose. Many of these features involve reduction or loss of pollen-gathering, pollen-carrying, and nest-making structures, while others appear to be defensive and offensive equipment for encounters with nest owners. In either case, the structures are those of females, and the rest of this section pertains only to female characters. Some of these characters, such as the reduced hairiness, relatively coarse punctation, and sometimes even spine-like setae on the hind tibiae, occur in males of some species also. Their functional significance is probably limited to females, however; presumably the de-
Developmental mechanisms happen to operate in some males.

In this section each feature which seems to be an adaptation of parasites to their way of life and which appears to have arisen independently in different parasitic groups, is lettered a to s. Each of these features is scored on a scale 0 to 1, 0 representing the structure as found in nest-making ancestral halictids, 1 representing the extreme modification found among parasites. The intermediate conditions are subjectively assigned scores such as 0.2 or 0.6 to give an idea of the morphological degree of difference from the extremes, 0 and 1. Scores for the parasitic genera are shown in Table 2 and many of them are indicated in parentheses in the following account.

**Reduction and Loss of Structures of Nest-Making Halictids:**

(a) The body and legs of nest-making Halictidae are usually hairy, most of the longer hairs and many short ones being plumose (Fig. 1). This extensive vestiture presumably serves to capture loose pollen, which can later be brushed together and transferred to the scopa by modified grooming movements (Jander, 1976).

Comparison of the right sides of Figures 1 and 2 shows the difference in vestiture of a typical host and a highly modified parasite. *Paralictus* (0) has the hairiness of its presumed ancestor; all other parasites (1) are markedly less hairy than their presumed ancestors. In *Ptiloleptis* and some species of *Austrosphecodes* a dense covering of short plumose hairs occurs on certain parts of the body, but this is very different from the longer, more or less erect hairs of nest-making halictids.

(b) The front basitarsus of most pollen collecting halictids is somewhat flattened with a sharp ridge or carina along the posterior (i.e., outer) margin of the segment, the distal half or more of this ridge giving rise to a row of closely placed setae forming a comb, the anterior basitarsal comb (the anterior basitarsal brush of Eickwort, 1969b). The entire segment except for the strigilar area is covered with a brush of hairs which are usually longer than those of the comb, so that the latter may be inconspicuous. The hairs of the brush are usually rather dense but are sparse in small forms like *Homalictus* and *Lasigoglossum* (*Diaictus*). The brush and the comb contained within it appear to be important in removing pollen from anthers.

### Table 1. Parasitic Halictidae and the Groups from which they Presumably Arose.

<table>
<thead>
<tr>
<th>Parasites</th>
<th>Probable Ancestors</th>
<th>Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>Paralictus</em></td>
<td><em>Lasigoglossum</em> (<em>Diaictus</em>)</td>
<td>North America</td>
</tr>
<tr>
<td>2. <em>Echthralictus</em></td>
<td><em>Homalictus</em> s. str.</td>
<td>Samoa</td>
</tr>
<tr>
<td>3. <em>Paralirincostoma</em></td>
<td><em>Thrincotoma</em></td>
<td>Madagascar</td>
</tr>
<tr>
<td>4. <em>Temnozoma</em></td>
<td><em>Augochlorini</em></td>
<td>Neotropical</td>
</tr>
<tr>
<td>The Sphecodes Group:</td>
<td><em>Halictus-Lasigoglossum Group</em> of Genera</td>
<td>Neotropical</td>
</tr>
<tr>
<td>5. <em>Ptiloleptis</em></td>
<td><em>Sphecodes</em> (<em>Austrosphecodes</em>)</td>
<td>Neotropical</td>
</tr>
<tr>
<td>6. <em>Microsphecodes</em></td>
<td><em>Sphecodes</em> (<em>Austrosphecodes</em>)</td>
<td>Neotropical</td>
</tr>
<tr>
<td>7. <em>Eupetersia</em></td>
<td><em>Sphecodes</em> s. str.</td>
<td>Neotropical</td>
</tr>
<tr>
<td>8. <em>Sphecodes</em></td>
<td><em>Sphecodes</em> s. str.</td>
<td>Neotropical</td>
</tr>
<tr>
<td>8b. <em>Austrosphecodes</em></td>
<td></td>
<td>Neotropical</td>
</tr>
</tbody>
</table>

**Note:**

- Table 1 continues on the next page.
as well as various parts of the body. The posterior ridge and the comb arising from it vary from essentially unmodified (0) to lacking (1) among parasitic groups. When they are lacking, the basitarsus is more nearly round in cross-section, less flattened than in nest making forms. Although development of the comb varies in the Augochlorini and it seems to be absent in some unrelated, nonparasitic genera, its loss especially in the Halictini seems clearly related to parasitism.

(c) The base of the mid femur and the apex of the mid tibia of pollen collecting halictids each bears a comb or brushlike row of hairs on the under surface, that on the tibia arising from an oblique ridge. They were termed the mesofemoral brush and mesotibial comb by Eickwort (1969b). As pointed out by Jander (1976), these structures are opposable and serve to remove pollen from the fore legs. In parasites the tibial brush is retained but the femoral brush varies from little modified (0) to absent (1). Usually the tibial brush is more brushlike, less comblike, than in many nest making bees.

(d) In pollen-carrying forms, there are
long and usually branched hairs on the underside of the hind trochanter (Fig. 4). On the femur in the Halictini, there are some long branched hairs at the base on the underside, but otherwise the underside is nearly bare. Long branched hairs from the anterior (= outer) surface (Figs. 4, 5) and a longitudinal row of similar hairs from near the middle of the posterior (= inner) surface (Fig. 6) curl down and meet below the femur to form a femoral corbicula, the cavity of which is somewhat enlarged by the straight or usually concave, rather than convex, under surface of the femur. The pollen carrying corbicula is less specialized in the Augochlorini. Long branched hairs arise from a more extensive basal area on the underside of the femur; on the posterior surface, while the hairs are directed downward, there is no row of unusually long curled hairs. The corbicula is shorter than in Halictini because of the larger basal hairy area and is open, since very long curled hairs arise only from the anterior side of the femur. Earlier illustrations and accounts of halictid scopas are those of Eickwort (1969) and Eickwort and Fischer (1963). In all parasitic forms the scopa is reduced (Figs. 3, 7-14). In Para/hictus the trochanteral hairs are unmodified while the long branched femoral hairs are either somewhat reduced in number and density but curled to form a corbicula which often contains some pollen grains (0.2), or the scopa is further modified by loss of the long hairs on the anterior surface of the femur (0.5). In all other parasitic genera the trochanteral hairs are short and the femoral hairs are short, relatively sparse, and not or little branched. The underside of the femur is relatively bare, however, and the hairs are directed about as in the pollen carrying forms. In some (0.9) the underside of the femur is about as in the pollen collecting ancestral groups (concave in Echthralictus, straight in Temnosoma) while in others (1) the curvature of the under surface is slightly to markedly convex.

(c) The posterior tibia in nest making forms is covered with long plumose pollen carrying hairs except for the relatively bare under surface. Near the anterior (outer) margin of the bare area, i.e., along the lower margin of the outer surface of the tibia, the hairs are especially long (except in Homalictus) and coarsely branched and while the main axes are directed downward and distally, the apical parts are curled upward and distally. The tibial scopa is modified in all the parasitic groups (Figs. 7-14). In Paralictus (0.3) the long hairs near the lower margin of the outer surface are not much larger than other tibial hairs, are only gently curved, and lack the characteristic coarse plumosity of these hairs in pollen carrying forms. In Echthralictus (0.5) the same is true but the hairs are even shorter, those of the lower margin of the outer surface being quite short. In other parasitic genera, the ventral relatively bare area is not or weakly evident, the hairs have few barbs or are simple, and those along the lower margin of the outer surface are smaller than those elsewhere on the tibia. Forms having a relatively uniform coverage of simple hairs are scored (1) while those with more plumose hairs and a sparsely hairy under surface are scored as (0.8) or (0.9).

(f) The hind basitarsus is flattened, usually as long as the remaining tarsal segments, the hairs of its lower margin unusually long, coarse, straight, simple or with branches only basally. Probably these features function to comb pollen off of the metasoma. In parasitic genera they vary from almost unmodified (0.2), to less flattened and lacking most or all of the coarse, straight hairs (0.7), to those in which the basitarsus is also markedly shorter than the remaining tarsal segments (1). Because of variability this feature is rather weak, but seems worth more
Fig. 3. Outer (= anterior) surface of hind leg, *Sphecodes monilicornis* (Kirby), female. Fig. 4. Same, *Lasio-glossum malacharum* (Kirby). Figs. 5, 6. Anterior and posterior views of hind femur of *Lasio-glossum malacharum* (Kirby), female. Most hairs are indicated only by their sockets. Scale line represents 0.5 mm.
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FIGS. 7-14. Outer views of posterior femora and tibiae of females. Fig. 7. Paralictus asteris Mitchell. Fig. 8. Echthralictus extraordinarius (Kohl). Fig. 9. Parathrinocostoma seyrigi Blüthgen. Fig. 10. Temnosoma smaragdinum Smith. Fig. 11. Philocleptis tomentosa Michener. Fig. 12. Eupetersia coerules Blüthgen. Fig. 13. Sphecodes (Austrosphecodes) chilensis Spinola. Fig. 14. Sphecodes (Sphecodes) confertus Say. Scale lines represent 1.0 mm.
Table 2. Scores for Various Characters of Females of Parasitic Halictid Genera 1 to 8.*

<table>
<thead>
<tr>
<th>Character</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>a. Vestiture</td>
<td>0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>b. Tarsus I</td>
<td>0</td>
<td>0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>c. Mid-femoral brush</td>
<td>0.5</td>
<td>0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>d. Femoral scopa</td>
<td>0.2-0.5</td>
<td>0.9</td>
<td>1.0</td>
<td>0.9</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>e. Tibial scopa</td>
<td>0.3</td>
<td>0.5</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>0.9</td>
</tr>
<tr>
<td>f. Hind basitarsus</td>
<td>0.2</td>
<td>0.7</td>
<td>0.7</td>
<td>0.7</td>
<td>0.7</td>
<td>0.7</td>
<td>0.7</td>
<td>0.7-1.0</td>
</tr>
<tr>
<td>g. Ventral scopa</td>
<td>0.2</td>
<td>0.6</td>
<td>1.0</td>
<td>0.8</td>
<td>0.9</td>
<td>0.9</td>
<td>1.0</td>
<td>0.9-1.0</td>
</tr>
<tr>
<td>h. Basitibial plate</td>
<td>0.1-0.3</td>
<td>0</td>
<td>0.9</td>
<td>0.7</td>
<td>1.0</td>
<td>1.0</td>
<td>0.7</td>
<td>0.7-1.0</td>
</tr>
<tr>
<td>i. Prepygidial region</td>
<td>0.5</td>
<td>0.6</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>j. Sixth tergum</td>
<td>0.3</td>
<td>0.3</td>
<td>0.4</td>
<td>0.6-1.0</td>
<td>0.9</td>
<td>0.9</td>
<td>0.9</td>
<td>0.9</td>
</tr>
<tr>
<td>k. Labrum</td>
<td>0.5-0.7</td>
<td>0.2</td>
<td>0.2</td>
<td>0.8</td>
<td>1.0</td>
<td>0.9</td>
<td>0.9</td>
<td>0.9</td>
</tr>
<tr>
<td>l. Tibial spur</td>
<td>0.2</td>
<td>0.2</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>m. Penicillus</td>
<td>0.5-0.8</td>
<td>0.8</td>
<td>0.5</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>n. Sculpturing</td>
<td>0</td>
<td>0</td>
<td>0.8</td>
<td>1.0</td>
<td>0</td>
<td>0</td>
<td>0.6</td>
<td>0.4-0.8</td>
</tr>
<tr>
<td>p. Mandible</td>
<td>0.5-1.0</td>
<td>1.0</td>
<td>0</td>
<td>0.5</td>
<td>0.5</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>q. Head</td>
<td>0.5-1.0</td>
<td>1.0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>r. Legs</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td>s. Spines</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1</td>
<td>0.1-0.3</td>
</tr>
<tr>
<td>Mean</td>
<td>0.25-0.38</td>
<td>0.44</td>
<td>0.64</td>
<td>0.72-0.74</td>
<td>0.76</td>
<td>0.83</td>
<td>0.82-0.87</td>
<td>0.69-0.97</td>
</tr>
</tbody>
</table>

*1 = Paralictus, 2 = Echthralictus, 3 = Parathirincostoma, 4 = Tennosoma, 5 = Pillocleetis, 6 = Microsphecodes, 7 = Eupetersia, 8 = Sphecodes.

consideration than mere inclusion under general hairiness (feature a, above).

(g) Nest making Halictinae vary in the extent to which there is a ventral metasomal scopa for carrying pollen. Usually there is a preapical zone of rather long plumed hairs, often simple but curled at the tips, across each metasomal sternum, these hairs being longer and more erect and therefore more important in pollen carrying on basal than on apical sterna. In Homalictus, however, the ventral scopa becomes the main pollen carrying structure. The bands of hairs are reduced, usually to a single row on each sternum, but these hairs are enormous, coarsely plumed, directed posteriorly and at their tips often upward toward the sternum to form a corbicula behind each row. Moreover, similar giant hairs arise on the lateral, ventral parts of the terga and are directed postero-mesally. In all parasitic forms the sternal scopa is reduced. In Paralictus (0.2) the hairs are only somewhat shorter and less plumose than in the presumed ancestral type. In Echthralictus (0.6), a Homalictus derivative, the large sternal hairs are much reduced in numbers, curvature, and in plumosity, some being simple, but are still evident as a few, unusually large hairs; large lateral tergal hairs are absent. The other parasitic genera have only simple hairs of moderate length on the areas concerned, and are scored 0.8 to 1 depending on the density of the hairs, the latter indicating the lower density.

(h) The basitibial plate is defined, at least along its posterior margin, and commonly around the whole margin by an elevated carina in nest making species (Fig. 15). It functions to support the bee working in the nest as it pushes its legs out against the burrow walls (Batra, 1964). In parasitic genera (Figs. 16-22) it may be essentially normal (0), less well defined with the marginal carina lower (0.1-0.3), feebly defined and often only posteriorly (0.7), barely detectable (0.9) or entirely absent (1).

(i) The fifth metasomal tergum of nest-
making species has a dense prepygidial fimbria of hairs extending across the segment, apically. This hair band is broadened middorsally where the hairy region extends toward the base of the segment. In the middle of this broad area is a sharply defined specialized longitudinal zone lacking ordinary hairs but covered with minute dense hairs. The surface in this zone is very minutely punctate. There is a deep cleft in the tergal margin, dividing this zone longitudinally in the Augochlorini but not in the Halictini. In all parasitic forms this elaborate structure is modified. In no case is there a sharply defined specialized longitudinal zone. In *Paralictus* there is an ill-defined longitudinal area or a small, median, apical region of minute punctation and fine hairs. Although superficially the tergal surface and vestiture are uniform from side to side, there is a broad triangular, median wedge lacking long hairs but with scattered hairs of moderate length. This zone includes the small median apical region and is roughly an equilateral triangle; posterolaterally it is continuous with the apical impunctate tergal margin (0.5). In *Echthralictus*, the specialized zone is also broadened posteriorly to form a wide, hairless, triangular wedge, only minutely roughened and shiny, cutting into the hairy part of the
tergum (0.6). Posterolaterally this zone is continuous with the bare posterior marginal band of the tergum. The posterior margin of the zone is longer than the other two margins which are about at right angles to one another. The zone is similar to that of Paralictus but it is larger and much better defined. Both genera have hairs along the extreme tergal margin. In other parasitic genera the tergal surface and margin show no specialized region, dense to sparse hairs being distributed across it (1). When the hairs form a dense fimbria it is often less dense medially; such a sparsely hairy area may or may not be a rudiment of the specialized zone found in nest-making forms. In all cases it lacks the short fine hairs and dense minute punctuation of this zone in nest making forms.

(j) The sixth metasomal tergum of pollen-collecting halictids is provided with two heavily sclerotized plates (Fig. 23) which perhaps contribute to the effectiveness of the tamping movements characteristic of halictid nest building (Batra, 1964). The gradulus is strongly arched to the rear and forms a carina delimiting posteriorly and laterally the more anterior, elevated plate, the suprapygidial plate of Eickwort (1969b). An inclined zone, broad anteriorly and tapering posteriorly, slopes downward as it extends backward from the suprapygidial plate and merges

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Figs. 23-25. Median parts of sixth metasomal terga of females. Fig. 23. Lasio glossum malachurum (Kirby). Fig. 24. Paralictus asteris Mitchell. Fig. 25. Ptilocleptis polybioides Michener.

Figs. 26-28. Labra of females. Fig. 26. Lasio glossum malachurum (Kirby). Fig. 27. Sphecodes monilicornis (Kirby). Fig. 28. Ptilocleptes tomentosa (Michener).
with the median basal part of the pygidial plate, which is a flat process projecting beyond the rest of the tergal margin. On either side of the pygidial plate is a hairy region, the hairs constituting the pygidial fimbria, which is broken by the pygidial plate and the inclined zone anterior to it. All parasitic forms have these plates less well developed (Figs. 24, 25). In *Paralictus* (0.3), the arch of the gradulus is less prominent although distinct, the suprapygidial plate being a relatively small elevated area, delimited by a carina which is angulate rather than rounded posteriorly. The inclined zone is absent, and the pygidial fimbria is sparse, but continuous, across the tergum where the inclined zone would be if it were present. *Echthralictus* (also 0.3) is similar, but the gradulus is very weak, not carinate, and the suprapygidial plate therefore is inconspicuous; however, the pygidial fimbria is interrupt ed medially. *Parathrinocostoma* (0.4) agrees with the comment on *Echthralictus* except that the whole gradulus is almost invisible and some *Temnosoma* (0.6) likewise agree except that the gradulus is absent lateral to the suprapygidial plate. In the *Sphecodes* group (0.9) the gradulus is only weakly arcuate posteriorly in the middle, there being no hint of a suprapygidial plate, and the fimbria or hairy zone is continuous or narrowly interrupted medially. In some *Temnosoma* (1) the gradulus and of course the suprapygidial plate are absent and the fimbria is continuous.

(k) The labrum of nest making forms (Fig. 26) consists of a transverse, more or less rectangular, thick sclerite or body, sometimes called the basal area of the labrum, from the distal margin of which projects an apical process which is flattened, depressed below the surface of the body, relatively thin, pointed or rounded, and provided with a strong dorsal keel and a row of coarse bristles along the margins. The keel is reduced in parasitic forms, and the process is usually less pointed (Figs. 27, 28). In the genera scored 0.2 in Table 2, the labrum is modified principally by the reduction of the keel on the process to a carina. In *Paralictus* (0.5-0.7) the line between the body of the labrum and the process is not sharp, the surfaces sometimes being at or nearly at the same level, and the process is broad and lacks the keel completely, and is bluntly pointed, rounded, or subtruncate at the apex. In one species there are scattered bristles on the surface of the process. In *Temnosoma* (0.8) the labrum is similar, but the process is relatively short, truncated or emarginate, and its bristles scattered. In the *Sphecodes* group, the body of the labrum is reduced to a transverse basal ridge, the process lacks a keel and is broadly rounded, truncate, or bilobed, and there are often bristles other than the marginal ones or the row of bristles is mesal to the margin (Figs. 27, 28). Most members of this group are scored 0.9, but *Ptilocleptis*, because of the greatly shortened process, is scored 1.0.

(l) The hind tibial spurs each has two margins between which is a concave surface. Both margins of the outer spur and the outer margin of the inner spur are minutely serrate. The inner margin of the inner spur, in nest making species, varies from more coarsely serrate to wavey, even almost straight, to produced into one or a few long processes. In genera scored 0.2 the inner margin of the inner hind tibial spur is produced into a few large projections, as in the forms ancestral to these parasites, but the projections are smaller (as noted for *Paralictus* by Eickwort and Fischer, 1963). In all the rest (1), that margin is minutely serrate like the other margins.

(m) In nest-making forms, the apex of the hind basitarsus, on the outer surface, is prolonged as a flat process bearing a dense brush of hairs, the penicillus,
shaped like a paint brush and used for spreading liquid on the cell lining (Batra, 1964). A small but slender penicillus is present in *Parathrincostoma* (0.5); in genera scored 0.8, a small projection remains but the brush is absent, while in those scored 1 both projection and brush are absent.

**Enlargement and Specialization of Structures Among Parasites:**

(n) Nest-making Halictinae vary greatly in the coarseness of the punctuation and propodeal areolation. Moreover, there is no single measure of such coarseness for a specimen or species. Yet in general it seems clear that parasitic forms are more coarsely sculptured, and the cuticle firmer, than in their nest-making relatives. *Temnosoma* is noteworthy for the coarse pitting of the first two metasomal terga which end in thickened margins instead of thin margins as in other forms, for the coarse transverse ridges on the constricted bases of the second and third terga, and for the coarsely punctate tegulae. Presumably such features provide defense against the stings and jaws of host bees. The numbers in Table 2 for this feature are more subjective than for others, but nonetheless give a general idea of sculpturing.

(o) The proccipital carina and the anterolateral angles of the pronotum are highly variable in nest-making forms, as also in the parasites. In general, however, they appear to be more prominent in parasites, probably providing defense for the neck. Acute produced prothoracic angles occur in *Ecthralcitus* and *Parathrincostoma*. The latter also has an unusually prominent proccipital carina. In *Temnosoma* the head is unusually produced backward forming a sharp ridge behind the vertex, protecting the neck region. Perhaps this explains the lack of enlargement of the pronotal angles in this genus. These features are not scored for Table 2.

(p) Mandibles in nest-making Halictinae have a preapical inner tooth. They are unmodified in forms scored 0 in Table 2. In those scored 0.5, the mandibles are of more or less normal length but lack the inner tooth, or in some *Paradictus*, are elongate with a small inner tooth; 1 indicates mandibles that are very long, pointed, and simple.

(q) Most nest-making Halictinae have heads about as wide as the thorax, the clypeus less than three times as wide as high, and the eyes usually converging below. Various parasitic groups (0) retain these characteristics. Others (1) have heads usually wider than the thorax, the clypeus over three times as wide as high, and the eyes not converging below. This places the mandibles farther apart, presumably making them more effective in grasping hosts, and is generally associated with long mandibles.

(r) In nest-making species the legs are relatively slender, the hind femur being straight or concave on the under surface (see d) (Figs 5, 6). Similarly shaped femora are found in some parasitic forms (0). In *Parathrincostoma* the legs are extraordinarily slender but the under surface of the hind femur is slightly convex (0.1). In others, the under surface of a moderately slender femur is slightly convex (0.5) or the femur is more thickened (1), with the under surface slightly convex and the upper surface especially near the base strongly so. Thickened legs presumably house stronger muscles for pushing resistant host bees along the burrows (see Figs. 7-14).

(s) Nest-making Halictinae lack spine-like tibial setae and the outer surface of the apex of the hind tibia often has a mere tubercle representing the apical tibial spine. Some parasitic groups (0) are similar, others (0.1) differ only in having a some-
what more recognizable tibial spine, but broader than long. *Echthralictus* (0.2) has the numerous setae of the outer margin of the hind tibia thickened, tapering, mostly simple, and thus spinelike. Other forms (0.3) have spinelike setae intermixed among hairs on the outer margin of the hind tibia, although the tibial spine is broader than long. In many *Sphecodes* the spinelike setae become more prominent, shorter, stouter, often almost peglike and in some species similar setae occur on the middle tibia. Along with such strengthening of the spinelike setae, the hind tibial spine is much better developed, becoming two or three times as long as broad. Such forms are scored as 1 (Fig. 3). Probably the spinelike setae and the apical tibial spines provide for a firm grip on the burrow walls when a parasite pushes a host bee.

The means in Table 2 give an idea of the amount of morphological evolution that a parasitic group has undergone since diverging from its nest making ancestors. Obviously *Paralictus* is less different from *Lasioglossum* (*Dialictus*) than other parasitic genera are from their nest making ancestral groups. *Echthralictus*, also, is moderately close to *Homalictus* from which it was derived. Every genus has scores ranging from 0 to 1, showing that acquisition of the characteristics of parasites has not followed the same sequence in all. The genera from *Temnosoma* to *Sphecodes* are all highly modified as parasites, *Temnosoma* being more specialized than the least modified *Sphecodes*, according to the table. This is probably true, but it should be noted that the range of means for a genus is based on the scores in the column above. There may not be any species having such extreme means, however. For example, in *Paralictus*, there is no species that combines all the low scores, nor is there a species that combines all the high scores. Thus there is no *Para- lictus* species with a mean score as low as .25, nor is there one with a mean score as high as .38.

**SIMILARITY OF PARASITIC FEMALES TO MALES**

Males of halictids leave the nests early and play no roles in nest making, defense, or parasitization. It is therefore not surprising that in most features relating to pollen gathering and transport and nest construction, the parasites approach males. Specifically, this applies to characters b to m of the preceding sections and Table 2. In character p also, parasites often resemble halictid males and it may be that loss of the mandibular tooth should be looked at as loss of a structure important in nest-making, rather than as acquisition of simple, sicklelike mandibles for fighting. Indeed, the *Sphecodes* species famous for fighting and killing hosts with its mandibles [*S. monilicornis* (Kirby)] is one that retains the inner mandibular tooth.

In gross appearance, however, most halictid males, whether belonging to parasitic genera, or not, are quite different from females, having longer, more slender metasomas and longer antennae than females. Some nest-making forms have males that look like females [*e.g.*, *Lasioglossum lustrans* (Cockerell)], and some parasites have sexes that look alike, more or less intermediate in shape between typical halictid males and females (*e.g.*, *Eupetersia*).

**RELATIVE DIVERSITY OF PARASITIC AND NONPARASITIC HALICTINAE**

The nonparasitic Halictinae constitute an enormous group of species of impressive, morphological homogeneity. The similarity in morphology is suggested by the series of papers by Vachal and Blüthgen. Vachal, who was a specialist in halictines early in this century, placed all non-
parasitic species of the subfamily in a single genus, *Halictus*. Blüthgen, a later specialist who was a “splitter” at the generic level in other groups with which he worked, placed nonparasitic groups as isolated as *Homalictus, Lasioglossum, Pachyhalictus*, and *Halictus* in a single genus. Only intensive studies and long searches for group characters have made possible the present classification of nonparasitic halictines, dividing the subfamily into two tribes, Augochlorini and Halictini, and many genera (Eickwort, 1969a, b).

By contrast, parasitic halictines have almost consistently been accorded generic rank since their species were first studied, and it is perfectly obvious that they are morphologically markedly different from the nonparasitic forms and from one another. No numerical phenetic study has been made to demonstrate the differentiation of the parasitic genera quantitatively, but such a study hardly seems necessary for that purpose alone.

It seems clear that on all continents, in spite of a wide diversity of habitats, social organizations, nesting substrates, and floral relationships, the nonparasitic forms remained basically similar, presumably as a result of selection favoring their various characteristic structures. The peculiarities of the labrum, scopa, pygidial plates and pygidial and prepygidial fimbriae, for example, vary only within narrow limits.

Among parasites, however, these structures and others listed above, mostly involved in nest construction and pollen gathering and carrying, appear to have escaped from the forces that elsewhere limit their variation. The result is the structural diversity found among parasitic genera.

**HOST RELATIONSHIPS**

Most parasitic bees have their own close relatives as hosts. This rule appears to apply to the majority of parasitic Halictinae, although some species of *Sphecodes* are exceptions. Table 3 gives known or probable hosts for parasitic halictids. All hosts are halictids except as otherwise indicated.

Of course, the most indisputable host data are those in which the parasite has been reared from host cells, or its larvae, pupae, or teneral adults found there. Such records are annotated (R) in the table. Finding a female parasite in the burrow of another bee is not entirely convincing, unless repeated, since parasitic bees may enter various burrows at night, in bad weather, or in searching for host nests. Such records, as well as reports of the parasites flying about nesting sites of the hosts, are annotated (N) in Table 3. Reports of hosts based on finding the parasite in the vicinity of or on the same flowers as the supposed host, the latter being the only local bee of the appropriate size and seasonality, are mere surmises, but probably are commonly correct, and are annotated (S). Less definite associations have been ignored, except for genera like *Echthralictus* and *Parathrinocostoma* for which no host data exist, but whose hosts are probably correctly surmised.

In the table, each parasite name begins a separate paragraph. Specific names of hosts are omitted to save space when different host species of the same genus or subgenus are reported. The publications cited after host names provide such information.

Examination of the table suggests no high level of host specificity by most species of parasites. Some appear to attack any halictines of the right size that are available to them, while different-sized individuals of a parasitic species are reported by several authors to be associated with host species of different sizes. Other parasites are doubtless more host specific. Some are primarily or exclusively parasites
of halictids, others of andrenids. Certain species of *Sphecodes* are believed to parasitize both halictids and andrenids, however, and *S. albitalbris* has been reared from an andrenid and probably from a colletid, but appears to be primarily a parasite of large halictids.

Larvae of parasitic Halictinae are very similar to those of other Halictinae, having no specialized structures and behavior, such as characterize the parasitic anthophorid and megachilid larvae that attack host eggs or larvae. In halictid parasites whose behavior has been examined, the adult female parasite opens a host cell, destroys the egg, replaces it with her own egg, and recloses the cell. Evidence for this statement is largely that in repeated excavations of nests parasitized by *Paralictus* (Michener, unpublished), *Microsphecodes* (Eickwort and Eickwort, 1972), and *Sphecodes* (various authors), many cells containing immature stages and presumably eggs of parasites must have been seen, although often such cells were not distinguished from unparasitized cells. G. Eickwort (personal communication) was able to distinguish the shorter, straighter eggs of *Sphecodes autumnalis* and sp.? from those of hosts (*Perdita* and *Evylaeus*). The *Sphecodes* eggs were in the typical halictine egg position on the provisions and were not easily distinguishable from those of the hosts in the field, although measurements served to permit recognition in the laboratory. All cells, both those examined by Eickwort and by other authors, contained only one egg or young, indicating destruction of the host-egg by the adult parasite. All were closed, except, no doubt, in those of species of *Lasiglossum (Evylaeus)* whose cells are left open part of the time. In no case was a partly eaten pollen ball found with an egg, indicating that the parasites do not destroy host larvae and replace them with eggs, but only attack fully provisioned cells in which the host larva has not started to feed. Hosts quickly oviposit in and close any fully provisioned cell. Hence, in nearly all cases, destruction of a host egg or possibly freshly hatched larva must precede laying of the egg of a parasite.

Parasites enter the nests of both solitary and eusocial hosts. After ovipositing in appropriate cells, they close the cells and either leave, or remain inside the nest to deposit more eggs on subsequent days, depending at least in part on the number of cells available for parasitization (Knerer and Atwood, 1967; Ordway, 1964). *Paralictus, Microsphecodes*, and some species of *Sphecodes* accomplish parasitization without killing adult hosts (Ordway, 1964; Eickwort and Eickwort, 1972; Michener, unpublished) while other *Sphecodes* species regularly do so. Legewie (1925) recorded the results of 76 attacks of *Sphecodes monilicornis* on colonies of *Lasiglossum malachurum*. The *Sphecodes* succeeded in 75 cases and 283 *Lasiglossum* were killed. *S. pimpinellae*, however, appears to chase away the hosts, *Augochlorella* spp., without killing them (Ordway, 1964).

Species such as *Sphecodes monilicornis* and *pimpinellae* attack social hosts and the attack appears to result in destruction of the colony.

In the case of solitary hosts, the *Sphecodes* may lay in appropriate cells and depart before the host returns, thus being cuckoo-like, as is *Nomada*.

Eickwort and Eickwort (1972) give an account of *Microsphecodes kathleenae*, females of which enter nests of *Lasiglossum (Dialictus) umbripenne*, a eusocial host, either by passing the guard like a *Lasiglossum* or by locating unguarded nests. Female *Microsphecodes* were found in nests along with workers and queens of the host and are believed to locate the host cells, open them, eat the eggs, deposit their own, and close the cells. More than
Table 3. Hosts of Parasitic Halictid Bees. (R) = reared or immature parasite taken from host cell, (N) = found in or about nests, (S) host surmised on the basis of seasonal and local occurrence.

| **Paraliclus asteris** Mitchell—Lasioglossum (Dialictus) imitatum (Smith), (R) Michener and Wille, 1961, parasite misidentified as *P. cephalotes* (Dalla Torre); (N) Michener, unpublished. |
| **Paraliclus cephalotes** (Dalla Torre)—Lasioglossum (Dialictus) zephyrum (Smith), (N) Robertson, 1901, 1926. |
| **Paraliclus simplex** Robertson—Lasioglossum (Dialictus) versatum (Robertson), (N) as unidentified Paraliclus, Michener, 1966; (N) Michener, unpublished. |
| Echthralictus spp.—Homaliictus spp. Homaliictus is the only possible host in the islands where Echthralictus occurs. |

**Parathrincostoma** sp.—*Trinchkostoma* sp. Probable host as judged by size and relationship. **Temnosoma** spp.—Augochlorini such as *Augochloropsis* or *Augochlorora*. Probable hosts as judged by size, abundance, similar coloration, and relationship. **Microsphecodes kathleeneae** (Eickwort)—Lasioglossum (Dialictus) umbripenne (Ellis), (R) Eickwort and Eickwort, 1972. **Microsphecodes rusticetypicus** (Sakagami and Moure)—Lasioglossum (Dialictus) seabrai (Moure), (N) Sakagami and Moure, 1962. **Microsphecodes** sp.—Lasioglossum (Erylaeus) sp., (R) Michener, unpublished. **Microsphecodes** sp.—*Habralictus* sp., (N) Michener, unpublished. **Sphecodes albidophrus** (Kirby) (= fuscipennis Germar)—Halictus spp., (N) Blagoveschenskaya, 1955; (N) Blüthgen, 1919; (N) Fahringter, 1922; (N) Friese, 1926; (?) Stoeckhert, 1954. Colletes curricularius (Linnaeus), COLLETIDAE, (N) Alfken, 1912; (S) Blüthgen, 1930; (R?) Malyshev, 1927; (N) Möschler, 1938. **Mellitogna clavicornis** Latreille, ANDRENIIDAE, (N) Rozen, 1965. Andrena ovina Klug, ANDRENIIDAE, (N) Friese, 1926. Major hosts of this species are apparently Halictus quadririctus (Fabricius) and sexinctus (Fabricius) but the only actual rearings from cells are from Colletes and Mellitogna. **Sphecodes alternatus** Smith—Lasioglossum (Erylaeus) nigripes (Lepeletier) (N) Knerer, 1968; (N) Knerer and Plateaux-Quéru, 1970. **Sphecodes arvensis** Patton (det. Cockrell)—Halictus rubicundus (Christ), (N) Hicks, 1934. **Sphecodes atlantis** Mitchell—Lasioglossum (Dialictus) pilosus (Smith), (R) G. Eickwort, personal communication. **Sphecodes autumnalis** Mitchell—Perdita octomaculata (Say), ANDRENIIDAE, (R) G. Eickwort, personal communication. **Sphecodes barbatus** Blüthgen—Lasioglossum (Lasioglossum) caspicum (Morawitz), (S) A. W. Ebner, personal communication. **Sphecodes brachycephalus** Mitchell—Calliopsis andreniformis Smith, ANDRENIIDAE, (S) Mitchell, 1956. **Sphecodes chilensis** Spinola—Corynura lepida Alfken, (R?, N) Claude-Joseph, 1926; (R? N) Janvier, 1933. **Sphecodes crassus** Thomson (= variegatus Hagens)—Lasioglossum (Erylaeus) spp., (N) Alfken, 1912; (N) Blüthgen, 1919, 1923a; (R) Blüthgen, 1934; (N) Rapp, 1945; (R) Stoeckhert, 1933. Stoeckhert (1933) deprecates reports that Halictus maculatus Smith is a host and Valkeka (1962) reports but gives no evidence that Lasioglossum (Lasioglossum) sexnotatum Schenk is a host. **Sphecodes cristatus Hagens—Lasioglossum (Erylaeus) nigripes** (Lepeletier), (S) Blüthgen, 1934. **Sphecodes darisii** Robertson—Agaponeemon virescens (Fabricius), (R) G. Eickwort, personal communication. **Sphecodes divisus** Kirby—Lasioglossum (Erylaeus) spp., L. (L.) spp., and Halictus spp., (N) Alfken, 1913a; (N) Blüthgen, 1916, 1919, 1934; (N) Chambers, 1949; (S) Morice, 1901; (N) Rapp, 1945; (N) Scholz, 1912. There are also scattered records of this species entering *Andrena* nests, ANDRENIIDAE, (N) Alfken, 1913a; (N) Morice, 1901. **Sphecodes fasciatus** Hagens—Lasioglossum (Dialictus) spp., L. (Erylaeus) spp., and Halictus (Seladonia) tumulorum (Linnaeus), (N, S) Alfken, 1912, 1913b; (S) Blüthgen, 1934; (S) Morice, 1901; (N) Perkins, 1887. **Sphecodes ferruginatus** Hagens (= trifasciatus Hagens)—Lasioglossum (Erylaeus) spp., (S) Blüthgen, 1934; (N) Stoeckhert, 1933. **Sphecodes near fragariae** Cockerell—Perdita nuda Cockerell, ANDRENIIDAE, (R) Torchio, 1975. **Sphecodes friesei** Herbst—Leiopterus (Lonchoptria) zonalis (Reed), COLLETIDAE, (R?) Janvier, 1933. **Sphecodes gibbus** (Linnaeus)—Halictus spp., (N) Alfken, 1913a, 1939; (N) Blüthgen, 1923a, 1934; (R) Breitenback, 1878; (N) Fahringter, 1922; (S) Friese, 1926; (N) Möschler, 1938; (R) Nielsen, 1903; (S) Perkins, 1887; (S) Sanders, 1948; (N) Stoeckhert, 1933. Lasioglossum (Erylaeus) malachorum (Kirby), (N) Blüthgen, 1934; (N) Stoeckhert, 1933. Lasioglossum (Lasioglossum) leucozontion, (N) Perkins, 1887. Records of
this species in or near nests of unrelated bees involve Dasypoda hirtipes (Fabricius), MELITIIDAE (Friese, 1920, 1923, 1926), ANDrena spp., ANDRENIDAE (Morice, 1901; Minkiewicz, 1935, but see Stoeckhert, 1954), and Eucera longicornis (Linnæus), ANTHIOPHORIDAE (Friese, 1920). Of these only the Dasypoda record appears to be based on repeated observations.

Sphecodes granulosus Siebel and rugulosus Siebel—Caenohalictus rostriceps (Friese), (R, N) Claude-Joseph, 1926; (R, N) Janvier, 1933. Corynura (Callochloa) chloris (Spinola), (R) Janvier, 1933.

Sphecodes hyalinus Hagens—Lasioglossum (Eucera) spp., (N) Blüthgen, 1934; (R, N) Stallknecht, 1933.

Sphecodes levis Lovell and Cockerell (?)—Lasioglossum (Eucera) quebecense (Crawford), (R) G. Eickwort, personal communication.

Sphecodes longuloides Blüthgen—Lasioglossum (Eucera) aglyphum (Pérez), (N) Blüthgen, 1934.

Sphecodes longulus Hagens—Lasioglossum (Eucera) and Dialectus spp., (N) Alfken, 1912; see also Blüthgen, 1934 and Valkéla, 1962.

Sphecodes majalis Pérez—Lasioglossum (Lasioglossum) pallens (Brullé), (S) Blüthgen, 1934; (S) Stallknecht, 1954.

Sphecodes marginatus Hagens (= nigeritulus and atratus Hagens)—Lasioglossum (Eucera) spp., (N) Alfken, 1913a, 1939; (N) Blüthgen, 1934; (S) Möschler, 1938.

Sphecodes miniatius Hagens (= dimidiatus Hagens)—Lasioglossum (Eucera) spp., (N) Alfken, 1939; (N) Blüthgen, 1919; (S) Perkins, 1887; (N) Stoekhert, 1933. Blüthgen (1916) reported Halictus (Seladonia) tumidulus as a probable host.

Sphecodes minor Robertson—Lasioglossum (Eucera) cinctipes (Provancher), (R) Knérer and Atwood, 1967. (R, Atwood, 1933, probably also concerns S. minor.)

Sphecodes monilicornis Kirby (= subquadratus Smith, quadratus Meyer)—Lasioglossum (Eucera) malachurum (Kirby), (N) Blüthgen, 1934; (N) Ferton, 1898, 1923; (N) Grandi, 1961; (N) Knérer, 1968, 1973; (R) Legewie, 1925; (N) Marechal, 1894; (N) Rapp, 1895; (N) Stoekhert, 1933, 1954. L. (Eucera) spp., (N) Alfken, 1913a, b; (N) Blüthgen, 1934; (N) Färhringer, 1922; (N) Grandi, 1961. Halictus rubicundus (Christ), (N) Alfken, 1913a, b; (S) Perkins, 1887. L. (Lasioglossum) spp., (N) Alfken, 1913a, b; (N) Frisby, 1914. Many of the references marked (N) report the Sphecodes killing nest guards or burrowing into nest entrances.


Sphecodes puncticeps Thomson—Lasioglossum (Eucera) spp., (N) Alfken, 1912, 1913a, but see 1939; (N) Blüthgen, 1919, 1934.

Sphecodes reticulatus Thomson—Andrena spp., ANDRENIDAE, (N) Alfken, 1913a, b; 1939; (N) Blüthgen, 1919, 1934; (N) Legewie, 1925; (S) Perkins, 1919; (S) Richards, 1944. Dasypoda hirtipes (Fabricius), MELITIIDAE, (N) Friese, 1920, 1923.

Sphecodes rubicundus Hagens—Andrena spp., ANDRENIDAE, (N) Alfken, 1912, 1913a; (N) Blüthgen, 1934; (N) Chambers, 1949; (N) Möschler, 1938; (S) Perkins, 1919; (N) Saunders, 1898; (R) Saden, 1895; (N) Stoekhert, 1919, 1933; (N) Torka, 1913.

Sphecodes rufipes (Erickson) (= hispanicus Wesmael)—Lasioglossum malachurum (Kirby), (N) Ferton, 1898.

Sphecodes rufiventris (Panzer) (= suboralis Schenck)—Halictus maculatus Smith, (N) Blüthgen, 1934; (N) Stoekhert, 1933. Lasioglossum (Eucera) spp., L. (Lasioglossum) spp. and Halictus (Seladonia) sp., (S) Blüthgen, 1923.

Sphecodes schencki Hagens—Lasioglossum (Lasioglossum) ducum (Smith) (= morbillosum Kriechbaum), (R) Grozdanić, 1971.

Sphecodes spinulosus Hagens—Lasioglossum xanthopus (Kirby), (?) Alfken, 1912; (S) Blüthgen, 1916, 1934; (N) Perkins, 1889. Halictus rubicundus (Christ), (S) Yarrow, 1943. Records for Andrena are probably incorrect (Stoeckhert, 1933).


one *Microsphecodes* was often found in a single nest and the parasites appear to remain in the host-nest for up to a day or so. The Chilean *Sphecodes* reported upon by Claude-Joseph (1926) and Janvier (1933), all of them probably in the subgenus *Austrosphecodes*, probably behave similarly. The several North American species of *Paralictus* are parasites in *Lasioglossum* (*Dialictus*) nests and adults of host and parasite are regularly found together in the same nest. Probably they, too, have habits similar to those of *M. kathleenae*.

There are probably morphological correlates in females of *Sphecodes* related to the manner of parasitization. Thus, those that actively dig and push their way into nests, against the defense of hosts, have heavy legs, strong hind-tibial spines, spine-like or peglike tibial setae, and a partially recognizable basitibial plate, all features which presumably make the parasite more effective in pushing its hosts. *S. monilicornis* has these features very well developed (Figs. 3, 22) and also has a heavy, quadrate head, which provides space for the strong mandibular musculature; the females of this species puncture or crush the heads of the host with their long mandibles. On the contrary, the subgenus *Austrosphecodes* and the genus *Microsphecodes*, whose females apparently live more or less peacefully in nests of the host, have slender legs without the projections and basitibial plates to improve traction.

Unlike many *Sphecodes*, which commonly visit flowers, adults of *Microsphecodes* perhaps feed only in cells of their hosts. Most of the known specimens have been collected only recently, by persons studying nests of halictine bees. No specimens are known to have been taken on flowers although *M. russellypeatius* was obtained in a place where much floral collecting has been done by me and by those associated with Padre J. S. Moure. Published observations of *M. kathleenae* in Costa Rica indicate that it was not found on flowers (Eickwort and Eickwort, 1972). I found the unnamed species listed in Table 3 as parasites of *Hablacticus* and *Lasioglossum* (*Evelia*) to be common flying about nesting sites of their hosts in Colombia, as well as in the nests, yet not one was seen on a flower. Another Colombian species was taken about a bank inhabited by *Lasioglossum* (*Dialictus*) where extensive sweeping of the flowers visited by the *Dialictus* failed to reveal even one *Microsphecodes*. These observations suggest that the principal, if not the only, feeding place of *Microsphecodes* adults may be in the nest of the host, where they probably feed on food masses stored in cells. Such behavior is suggestive of that of the parasitic genera of allodapine bees which likewise do not visit flowers but feed in the nests of the host.

**SYSTEMATIC TREATMENT**

For genera 1 to 4 of Table 1, the commentary in this section indicates the placement relative to their nonparasitic ancestors. For genera 5 to 8, the *Sphecodes* group, however, more detailed, comparative descriptions are given, because these genera are closely related and require substantiation. Moreover, they probably had a common parasitic *Sphecodes* or *Sphecodes*-like ancestor and thus constitute a natural group, unlike genera 1 to 4, each of which arose from a different nest-making ancestor (Table 1).

**GENUS PARALICTUS ROBERTSON**

(Figs. 7, 24, 29)

*Paralictus* Robertson, 1901, Canadian Ent., 33:229. Type species: *Halictus cephalicus* Robertson, 1892 (not Morawitz, 1873) = *Halictus cephalotes* Dalla Torre, 1896, by original designation.

This is a North American group of several species, resembling and presumably
derived from the subgenus *Dialictus* of *Lasioglossum*. It resembles *Dialictus* in small size, presence of some greenish coloration on the head and thorax, weakened second and third transverse cubital veins (second sometimes absent) and second recurrent vein, presence of a few (two to four) coarse teeth on the inner margin of the inner, hind tibial spur (but these teeth smaller than is usual in *Dialictus*), male genital structure including the large, retrorse, ventral lobe on the base of the gonostylus, as well as various other features marked as zero or near zero in column 1, Table 2.

*Para/ictus* differs from *Dialictus* in those features having high numbers in column 1, Table 2. Included among these are reductions in various pollen-handling and nest-making structures, such as characters *e* to *j* and *m*. (For details, see the explanations for the characters listed in Table 2). Other outstanding features of *Para/ictus* are the following: (*k*) Apical process of labrum of female rounded at apex, without keel. (*p*) Mandible of female large, sometimes with subapical tooth, although mandible narrower and more pointed than in most *Dialictus*, sometimes acutely pointed, without distinct, subapical tooth. (*q*) Head of female often quadrate, inner margins of eyes sometimes parallel or diverging below so that face is wide below, genal areas commonly greatly broadened, much wider than eye.

The males are not distinguishable from those of *Dialictus* by characters that appear to be of generic importance (but see Mitchell, 1960).

As emphasized to me by Dr. George C. Eickwort, who has studied *Para/ictus* in some detail and who provided me with an identified set of specimens for study, there is considerable diversity among the species, some being more like *Dialictus* than others (see variation indicated in column 1, Table 2). *P. michiganensis* Mitchell and *simplex* Robertson are perhaps the most *Dialictus*-like, having a relatively unmodified head (especially in *simplex*), bidentate mandibles (inner tooth smaller and narrower than in *Dialictus*), the body of the labrum distinctly elevated above the apical process, and the carina margining the basitibial plate strong. On the other hand, in some features the same species are quite different from *Dialictus*. Thus the hind femur lacks long, scopal hairs on the anterior surface, the penicillus is much reduced, and the labral process in *simplex* is subtruncate and bears scattered bristles other than those near the margin. At the other extreme are species such as *P. cephalotes* (Dalla Torre) and *asteris* Mitchell which have large heads, the inner orbits nearly parallel or diverging below, the mandibles enormous and untoothed, the labral process weakly differentiated from the body of the labrum, and the carina margining the basitibial plate weak. The long, curled, scopal hairs on the anterior surface of the hind femur in *asteris* and the well formed penicillus in *cephalotes*, however, are *Dialictus*-like features of these species. (The largest penicillus, but still reduced compared to *Dialictus*, occurs in an undescribed species from Lawrence, Kansas.)

The question arises as to whether *Para/ictus* is a monophyletic group or consists of parasites derived independently from different species of *Dialictus*. Perhaps this question can be answered if *Dialictus* becomes well enough known that the group or groups from which *Para/ictus* arose can be determined. At present it is impossible to reach a decision. Obviously, if *Para/ictus* is polyphyletic it must either be divided into two or more genera (or subgenera of *Lasioglossum*) or synonymized with *Dialictus*. For the present, I maintain *Para/ictus* as a genus because it differs from *Dia-
lictus by many more, and more striking, characters than those that separate the non-parasitic groups such as Dialictus, Evyllaeus, Lasioglossum s. str., and even Halictus from one another.

**Genus ECHTHRALICTUS**

**PERKINS AND CHEESEMAN**

(Figs. 8, 16, 30)


This genus contains at least two species restricted to Samoa, where it presumably arose from Homalictus (Homalictus) species. As indicated by Michener (1965) it resembles Homalictus proper in the following features: small size; presence of some greenish or bluish coloration on the head and thorax; presence of a frontal carina; weakened third transverse cubital and second recurrent veins; presence of a few, coarse teeth on the inner margin of the inner, hind tibial spur; presence of a few, very long hairs representing the distinctive sternal scopa of Homalictus; rather elongate male genitalia with short gonostyli and without a basal, retrorse, gonostylar lobe, as well as various other features marked as zero or near zero in column 2 of Table 2.

Echthralictus differs from Homalictus in those features having high numbers in column 2, Table 2. Among these are reductions in pollen-carrying structures (characters d to g) and in some probable nest-making structures (characters i, j, m), as explained in the paragraphs about characters listed in Table 2. The femoral scopa is not recognizable, except for the row of long hairs on the posterior surface which is reduced to simple hairs, the longest about two-thirds as long as the maximum femoral diameter. The tibia has a distinct, relatively bare, under surface, but the hairs margining it are not longer than those elsewhere on the tibia and have only short...
branches. Except for some long hairs arising near the tibial spurs, the longest tibial hairs are the thick, mostly-simple bristles along the outer margin (character s). Other outstanding generic characters of *Echthralicetus* are: (k) Apical process of labrum of female rather narrowly rounded (rather than pointed) at apex; the keel reduced to a strong carina. (o) Dorsolateral angle of pronotum produced to acute spine, rounded at apex. (p) Mandible of female acute, without subapical tooth. (q) Head of female quadrate, inner margins of eyes subparallel, so that face is wide below, genal area much wider than eye.

Another distinctive feature, perhaps related to the loss of the tergal and great reduction of the sternal scopal, is the rounded lateral metasomal margin. In *Homalictus*, the metasoma is compressed so that its lateral margin is a strong bend, or crease, in the terga where their ventral surfaces join the dorsal surfaces. The inner margin of the inner, hind-tibial spur of the male is coarsely pectinate, suggesting a female.

In features such as the wide head and the coarse teeth on the inner hind-spur of the male, *Echthralicetus* suggests *Homalictus ctenander* Michener from Australia, but in the labral process, female mandible, scopal, etc., that species does not show evidence of parasitic behavior (Michener, 1965). While the male of *Echthralicetus* is easily distinguished from that of most *Homalictus*, species like *H. ctenander* eliminate useful, constant, generic characters for males.

**Genus PARATHRINCOSTOMA**
Blüthgen
(Figs. 9, 31-38)


This genus, known only from Madagascar, was first described from the male. Although Blüthgen could not determine whether the pollen-carrying scopal of the female was present or absent, he suggested that the genus was probably a parasite derived from *Thrinchostoma*. Benoist (1962) described the female and noted the absence of the "brosse collectrice aux tibias III," but made no point of this finding, nor did he note the lack of a femoral scopal. Presumably he was confused by the fact that one of his two, supposed species was a *Nomia* with pollen-collecting apparatus (see Appendix). Thus the parasitic nature of the genus is here established for the first time, based on the lack of the pollen-carrying apparatus.

*Parathrincostoma* agrees with *Thrinchostoma* subgenus *Eothrinicostoma* in the characters listed below:

**Both sexes:** Nonmetallic black, large and slender, 11-14 mm long; metasoma elongate, widest at third segment. Clypeus produced downward and strongly protuberant forward, a line tangent to the lower ends of eyes crossing clypeus near middle or at lower third; malar space conspicuous, but shorter than basal mandibular width. Paraocular area extending as a strong, right-angular lobe into clypeus. Mouthparts long and slender, glossa linear and much exceeding the short galea and palpi. Pronotum with horizontal, dorsal surface rather broad, margined anteriorly by high carina or lamella, not overhung by scutum. Dorsal surface of propodeum much longer than metanotum. Apical wing veins strong; first transverse cubital arising well away from margin of stigma, vein *r* being about three times as long as wide, first recurrent vein approximately interstitial (or in one specimen of *P. seyrigi*, second transverse cubital absent so that there are only two submarginal cells); no area of dense hair along second transverse cubital vein, this vein not angular or thick-
Ened; anterior margin of third submarginal cell about half as long as posterior margin; marginal cell minutely truncate and appendiculate at apex. Apical margins of terga 1-4 of females and 1-6 of males broadly impunctate and slightly depressed.

**Male:** Labrum with strong, median, apical process similar to that of female, this process margined with bristles, without keel, but with feeble, longitudinal, median ridge. Basitibial plate an elongate, hairless, shining area, not defined by a carina.

*Parathrincostoma* differs from *Thrinchostoma* in the features represented by high scores in column 3, Table 2, and discussed in the paragraphs associated with that table as well as below: (a) Body and legs largely without short hairs except behind pronotal lobe, sparsely across dorsum of pronotal collar, and in males on large areas with short, dense, brown hairs on terga 3-5. Depressed apical tergal margins without laterally directed hairs in female or in male with such hairs poorly represented. (b) Basitibial plate of female feebly elevated, shining, not clearly defined. (i) Fifth metasomal tergum of female hairy, with hairs nearly to margin, without any evidence of median specialized area, surface not hidden by hairs, apical margin weakly produced medially. (j) Sixth tergum with pygidial and supra-pygidial plates united, the gradulus weak or absent. (k) Labral keel of female reduced to a strong carina, high and almost a keel apically.

Other distinctive features of *Parathrincostoma* are as follows: Dorsolateral, pronotal angle obtuse or produced to acute spine, connected mesally with carina or lamella across anterior margin of collar. Propodeal triangle broader than in *Thrinchostoma*, posterior margin curving onto posterior pronotal surface. Male: Face and legs black; flagellum of moderate length, all segments longer than broad or second
as broad as long; hind tibia slender, black, unmodified, the spurs in normal positions; first two hind tarsal segments not fused, but articulation much broader than more distal articulations; seventh tergum without pygidial plate, but with broadly rounded, apical margin as seen from above, this margin being a sharp separation of dorsal and ventral surfaces of tergum. Sterna 4 and 5 unmodified.

It is interesting that the unmodified fourth and fifth sterna and hind tibia of the male and the nonfused first and second hind tarsal segments of the male appear to be ancestral to those of any Thrincostoma. Relative to most Thrincostoma, several other characters, especially those of the wings, are ancestral, being more like ordinary halictids. It is in these latter characters that Parathrincostoma resembles the subgenus Eothrincostoma. Eothrincostoma is restricted to Africa, so far as known not being found in Madagascar or Asia. Unless the ancestral wing, leg, and sternal characters are reversions somehow related to parasitic behavior, the implications are that Parathrincostoma is an ancient parasite that arose from a common ancestor with Eothrincostoma either in Africa or at a time when Eothrincostoma was in Madagascar. Eothrincostoma and Thrincostoma have the common derived male features of modified sterna, fused first and second hind tarsal segments, and enlarged and modified hind tibiae.

**Genus TEMNOSOMA Smith**
(Figs. 10, 18)


This genus, which ranges from southern Arizona to Argentina, consists of brilliant metallic-green species with coarse punctation (suggestive of chrysidids), the only known parasites in the tribe Augochlorini. (All other forms treated in this paper are in the tribe Halictini). *Temnosoma* has been described and illustrated by Eickwort (1969b) and its features related to the presumed parasitic behavior are summarized in Table 2 and the accompanying text and figures. More detailed treatment is not necessary here.

In some respects there is more variation in the genus than Eickwort recognized. Thus the labral process of the female is sometimes emarginate instead of truncate and the body of the labrum may have a single median elevation instead of a pair of them. The gradulus of the sixth tergum of the female may be absent, so that there is no suprapygidial plate and the hairy zone or pygidial fimbria extends across the tergum in front of the pygidial plate uninterruptedly. On the other hand, as illustrated by Eickwort, there may be a weakly defined, small, suprapygidial plate and behind it, a break in the hairy zone.

**THE SPHECODES GROUP**

The content of this large and widespread group is indicated in Table 1. It contains halictids that are highly modified as parasites. Probably because of its antiquity, its most closely related nonparasitic relatives are not readily identifiable. The distal veins of the forewing are strong, a character shared with *Halictus* and differentiating the parasites from *Lasioglossum, Homalictus*, and their rela-

Figs. 39-43. Ptilocleptis tomentosa Michener, male. Fig. 39. Seventh tergum. Figs. 40, 41. Dorsal-ventral and lateral views of genitalia. Figs. 42, 43. Seventh and eighth metasomal sterna, dorsal at left.

Figs. 44-46. Ptilocleptis eickworti Michener, male. Fig. 44. Seventh tergum. Figs. 45, 46. Dorsal-ventral and lateral views of genitalia. Scale lines represent 0.5 mm.
tives. Unlike *Halictus*, however, the distal margins of the metasomal terga are usually rather broadly hairless, never with hair bands. Also, unlike *Halictus*, the male gonostylus often has a small basal ventral lobe, probably homologous to the retrorse lobe that is widespread in the *Lasioglossum-Homalictus* group. The rather large gonostylus, however, are suggestive of those of some *Halictus*.

Partly because of the great variability among species of *Sphecodes*, the genera of the *Sphecodes* group are not easily defined. The more diagnostic characters are italicized in the following descriptions.

**PTILOCLEPTIS New Genus**

(Figs. 11, 17, 25, 28, 39-54)

Type species: *Ptilocleptis tomentosa* new species.

The three species of this genus, all of them described in the Appendix, resemble certain polybiine wasps because of the elongate body, dark costal margins of the forewings, and in some cases the yellowish integumental markings, in others the pattern of yellow brown pubescence.

**Both sexes**: *Punctuation moderate, dense on head and thorax, not involving coarse pitting as is usual in *Sphecodes*. Head little wider than long, eyes strongly converging below, clypeus only about twice as broad as long, not biconvex. Eyes with scattered hairs, extremely short to about one-fourth as long as diameter of scape. Hypostomal carina a very high, thin lamella, gradually reduced toward posterior end, abruptly reduced near angle so that transverse part is low. Hairs of flagellum mostly short, but dorsal side with some hairs one fifth as long as diameter of flagellum, basal segments with some as much as one third that length. *Preoccipital carina present, complete*. Pronotum with horizontal surface of collar very-short medially, a strong carina across anterior margin of collar between lateral angles; lateral angle right-angular, extended downward as strong vertical carinate ridge which merges with a laterally directed lamella that extends toward coxal base; a carina from lateral angle of pronotum onto posterior lobe, continuing at least two thirds of way across lobe. Anterior extremity of scutum narrowly vertical, then abruptly curving onto dorsal surface, vertical area that lacks punctures present, but small, or absent in *P. polybioides* Michener. Scutellum rather flat medially or biconvex. Propodeum with dorsal area bearing strong longitudinal carinae, the area about as long as or longer than metanotum, distinctly shorter than scutellum; posterior and lateral surfaces of propodeum with short plumose hairs. First metasomal tergum as long as or longer than wide.

Wings with rather long hairs over entire surface; stigma of moderate size; marginal cell with apex narrowly rounded almost on wing margin, free part beyond submarginal cells much longer than part subtended by marginal cells; *marginal cell unusually broad because vein beyond submarginal cells is gently curved almost its entire length*; submarginal cells extending well beyond apex of stigma; second and third submarginal cells each receiving a recurrent vein, or second transverse cubital vein absent, so that there are only two submarginal cells, the second receiving both recurrent veins.

Female: *Mandible without subapical tooth, relatively short*. Labrum with apical process a little over twice as wide as long to four times as wide as long.

**Legs slender**, hind femur well over four times as long as wide; basitibial plate totally absent; *tibia rather densely covered with relatively short, slender, essentially simple hairs*, some near upper margin with a few short barbs, some shorter plumed hairs interspersed, no spinelike setae; *hind tibial spine absent*. 

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**THE PARASITIC GROUPS OF HALICTIDAE (HYMENOPTERA,apoidea) 315**
Figs. 47-54. Prioleptis. Figs. 47-49. P. tomentosa Michener, holotype female. Fig. 50. Face of allotype male of P. tomentosa. Figs. 51, 52. P. polybioides Michener, holotype female. Fig. 53. Wing of P. tomentosa, allotype male. Fig. 54. Propodeum and base of metasoma of P. tomentosa; holotype female.
Fifth tergum with apical fringe of plumose hairs longer than those of preceding terga. Pygidial plate a thin slightly upturned apical process in front of which a bare zone extends anteriorly toward middle of tergum in *P. tomentosa*.

**Male:** Antenna of moderate length as in female, not thickened, first flagellar segment broader than long or as long as broad, others longer than broad or second about as long as broad. Labrum with apical process two to four times as broad as long.

Second hind tarsal segment shorter than to longer than third, base broader than base of third.

Gonocoxite not striate, without depression; gonostylus without basal lobe.

This genus is known from Mexico (unknown locality) to southern Brazil. It differs from *Sphecodes* in the features italicized above, especially those of the labrum, clypeus, and hind tibia. Moreover, it does not look like a *Sphecodes*, not only because of its form and relatively fine punctuation, but because of lack of red coloration and the extensive coverage of the body with short plumed hair, as indicated in the descriptions of the species.

In its elongate body, slender legs and relatively fine punctuation this genus suggests *Eupetersia*. It is much less similar to *Sphecodes* than is *Eupetersia*, however. Presumably it is an independent derivative of *Sphecodes*, as indicated by the characters emphasized above as well as by the relatively narrow head and short mandibles, features suggestive of *S. convergens* which may represent the group from which *Ptilocleptis* arose.

The generic name is based on *ptilon*, feather or plume, and *kelptis*, thief, and is feminine in gender.

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**GENUS MICROSPHECODES**

EICKWORT AND STAGE

(Figs. 55-57)


**Both sexes:** Punctuation rather weak, not involving such coarse pitting as is usual in *Sphecodes*. Clypeus three to four times as broad as long, not biconvex. Eyes with only very short, scattered hairs. Hairs on upper surface of antennal flagellum often one third as long as diameter of flagellum or more, such long hairs present on all flagellar segments. Preoccipital carina present or absent. Pronotum with horizontal surface or collar poorly defined, rounded onto declivous anterior surface, narrow medially, lateral angle rounded or obtusely angulate with no marked vertical ridge extending downward from it and no carina or lamella extending toward coxal base; a weak ridge extending to pronotal lobe, but not continued as a carina across lobe. *Anterior extremity of scutum gently convex* except adjacent to pronotum, no large strongly convex or vertical region, but with small transverse more or less vertical area without punctures. Scutellum biconvex or not, the midlateral areas (convexites when present) largely impunctate. Propodeum with dorsal area slightly shorter than or as long as scutellum, semilunar, with a few, often irregular carinae. Posterior and lateral surfaces of propodeum with numerous, short, plumose, white hairs in addition to scattered longer hairs.

Wings with rather long hairs over entire surface; stigma large; marginal cell pointed at or near wing margin; *free part of marginal cell more than twice as long as part subtended by submarginal cells, which do not extend beyond apex of stig-
Figs. 55-57. Microsphecodes kathleenae (Eickwort and Stage). Figs. 55, 56. Faces of female paratype and allotype male. Fig. 57. Wing of allotype male.
Figs. 58, 59. Eupetersia flavo Michener, face and dorsum of propodeum and base of metasoma.

ma; second and third submarginal cells each receiving a recurrent vein.

First tergum slightly longer than broad, more elongate in male; metasoma moderately elongate, more slender in male than in female. Almost no constriction between first and second terga as seen in lateral view.

Female: Mandible without subapical tooth. Labrum as usual in Sphecodes, with broad rounded apical process about twice as broad as long.

Legs slender, hind femur over three times as long as wide, upper surface near base scarcely convex; basitibial plate entirely absent; hairs on outer side of hind tibia simple or nearly so, upper margin of hind tibia without spinelike setae or pegs; hind tibial spine absent or nearly so.

Fifth tergum with apical margin bare, broadly impunctate, like preceding terga.

Pygidial plate narrow, rounded apically, parallel-sided, marginal carinae extending only a short distance onto tergal disc.

Male: Antenna not much longer than in female, flagellum not thickened, first two flagellar segments both a little broader than long. Labrum as in female.

Second hind tarsal segment slightly longer than third, narrowed toward base and articulated like third.

Gonocoxite not striate, without depressed area. Gonostylus broadly rounded, its basal ventral setose lobe rather small and directed apically.

This is a neotropical genus of minute species, 3.25 to 6 mm long, often with more or less extensive yellowish areas on the head and thorax. Species are known from Costa Rica to southern Brazil. The characters italicized in the above description separate Microsphecodes from most
Sphecodes. Some of these characters, such as the simple mandibles, occur also in various groups of Sphecodes, but others seem very distinctive and have led me to elevate Microsphecodes to the genus-level. Among such characters are the gently convex anterior part of the scutum, the enlarged stigma and short submarginal cells relative to the marginal cell, and the lack of an apical fringe on the fifth tergum of the female. Thus Microsphecodes is fully as distinctive as Eupetersia.

The described species of the genus are listed and discussed by Eickwort and Stage (1972).

Various small species of Sphecodes resemble Microsphecodes in appearance and some species of Austrosphecodes from South America may represent a group of Sphecodes related to Microsphecodes. In other areas, similar species obviously result from convergence. For example, Sphecodes (Sphecodes) antennariae Robertson has the size, coloration, shining thorax with small punctures, lack of areolation, and simple female mandibles of Microsphecodes. However, the distinct origin of S. antennariae is shown by most of the above italicized characteristics and by the presence of a few spinelike setae on the outer margin of the hind tibia of the female, the partially recognizable basitibial plate of the female, the thickened articulation between the first and second hind tarsal segments of the male, etc.

**Genus Eupetersia Blüthgen**

(Figs. 12, 19, 58-66)

Both sexes: Punctuation moderate to fine, varying from dense to sparse, not involving such coarse pitting as is usual in Sphecodes. Head much wider than long, clypeus three or more times as wide as long, not or feebly biconvex. Eyes hairless or with scattered very-short hairs. Hairs of antennal flagellum all short or some as much as one-fifth as long as diameter of flagellum. Preoccipital carina present, at least at sides where lower extremities approach or join posterior extremities of hypostomal carinae.

Pronotum with horizontal surface of collar reduced almost to the vanishing point medially (broader in guillarmodi), but forming lateral angle which is usually prominent (weak and rounded in coerulea Blüthgen and rusticus Blüthgen and relatives) and below which vertical ridge extends downward, a carina usually evident from lateral angle onto posterior lobe. Anterior extremity of scutum strongly convex, the vertical anterior surface sometimes lacking punctures and therefore with an area sharply different from rest of scutum.
Scutellum variable. Propodeum with dorsal area coarsely-rugose, acrolate, *markedly longer than scutellum*, usually slightly concave, broad laterally so that it is semilunar and broadly rounded posteriorly (not triangular); *posterior and lateral surfaces of propodeum with numerous short plumose pale hairs in addition to scattered longer hairs.*

Wings with rather long hairs over entire surfaces; stigma of moderate size; marginal cell narrowly truncate to pointed on or near wing margin; *free part of marginal cell beyond submarginal cells much longer than part subtended by submarginal cells*, which usually extend but little beyond apex of stigma.

First tergum usually about as long as broad; *metasoma in both sexes moderately elongate*, usually more slender than in most female *Sphecodes* and not as slender and parallel sided as in most male *Sphecodes*. (In *E. guillarmodi*, metasoma relatively robust, same shape in male and female.) In lateral view, a constriction between first and second terga (except in *E. guillarmodi*). Posterior margins of terga 2-4 broadly depressed, hairless, impunctate.

**Female:** Mandible without subapical tooth. Labrum as usual in *Sphecodes* with broad, rounded apical process about twice as broad as long.

**Legs slender:** hind femur over three times as long as wide; upper surface near base scarcely convex; basitibial plate entirely absent or slightly elevated; long hairs on outer side of hind tibia simple or nearly so; upper margin of hind tibia with or without spinelike setae; hind tibial spine broad, blunt, not longer than broad.

Fifth tergum with apical margin fringed, unlike preceding terga, and sometimes with a conspicuous hairless zone in front of fringe. *Pygidial plate usually narrow, the sides parallel*, but broad in *E. guillarmodi* and *flava*.

**Male:** Antenna short as in female, *flagellum not thickened, first two flagellar segments both distinctly broader than long*. Labrum with apical process short so that it is three to several times as broad as long.

Second hind tarsal segment about as long as third, base broader than base of third.

**Gonocoxite not striate, with dorsolateral depressed area with lamella or flange on either side** and often with one or more longitudinal ridges across depressed area. Gonostylus long, with basal setose lobe broad and directed mesobased.

This genus ranges widely through sub-Saharan Africa, south as far as Cape Province; it also occurs in Madagascar, the Seychelles, and has recently been found in southern India. Baker (1974) has catalogued the described species. [He missed records of *E. sakalava* Blüthgen by Benoist, 1962, as well as a species, *E. constricta* (Benoist), new combination, described in the same paper as a *Sphecodes* and here transferred to *Eupetersia* on the basis of the description.] Keys to the species were given by Blüthgen (1928, 1935).

Compared to *Sphecodes*, the body form is rather elongate, about the same in the two sexes, with the antennae of the male short as in females. In species such as *E. bequaerti* (Meyer), the pitting of the mesoscutum, mesepisterna, and to a lesser degree the rest of the thorax is quite coarse, suggestive of *Sphecodes*. Also, the first metasomal tergum is not as elongate as in most species (length to breadth about as 9:10) and the part of the marginal cell subtended by submarginals extends well beyond the stigma. In these respects as well as coloration *E. bequaerti* resembles *Sphecodes*. Unfortunately, I have not seen males of this species, but it is a reasonable assumption that such *Sphecodes*-like forms were ancestral to the species typical of *Eupetersia*.

The existence in Africa of *Sphecodes*
species (unidentified, Karen, Nairobi, Kenya, Univ. of Kansas) with simple mandibles in the female, a strong preoccipital carina, and a narrow pygidial plate, nearly bridges the gap between *Sphecodes* and *Eupetersia* and supports the suggestion of Benoist (1962, p. 124) that *Eupetersia* is not generically distinct from *Sphecodes*. I have concluded, however, that *Eupetersia*, although an offshoot of *Sphecodes*, is different enough to receive generic status. The distinctive combination of characters is italicized in the above description, but it must be noted that few of these characters, by themselves, are diagnostic.

Most *Eupetersia* are distinguished from *Sphecodes* by the fine thoracic punctuation, either rather dense or sparse, as well as the body form. The coloration is commonly unlike that typical of *Sphecodes*, ranging from entirely black or dark metallic blue (*E. coerulea* Blüthgen and allies, placed in *Callenpetersia* by Cockerell (1938) only because of the blue color) to specimens with the thorax red and the rest of the body black (some specimens of *E. para doxa* Blüthgen) to the entirely reddish yellow *E. flava* described below.

Slender legs are diagnostic for females. The slender, parallel-sided pygidial plate occurs in some otherwise ordinary *Sphecodes*, such as *S. crassus* Thompson, *gibbus* (Linnaeus), *heraclei* Robertson, etc. The antennae of known males do not resemble those of any *Sphecodes* known to me. The flagellum is relatively short, not thickened as in *Sphecodes*, the middle segments slightly broader than long to longer than broad. The first two segments are both much broader than long. In *Sphecodes*, even species with relatively short male antennae, such as *S. cressonii* Robertson, *atlantis* Mitchell, and *costaricensis* Friese, the flagellum is longer and thicker than in the female and although the first segment is much broader than long, the second is nearly as long as broad or longer than

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**Fig. 62-65. Eupetersia guillarmodi Michener.** Figs. 62, 63. Faces of holotype female and allotype male. Figs. 64, 65. Dorsal views of median parts of body, holotype female and allotype male.
broad. Unfortunately males of the most Sphecodes-like Eupetersia, such as E. bequaerti, are not known to me. For the same reason the genitalic characters listed above cannot with certainty be considered diagnostic of all species.

**Subgenus EUPETERSIA**

Blüthgen s. str.


Scutum more or less densely punctate. Scutellum with surface bigibbous, the two convexities not or sparsely punctate, punctures denser around them and on midline separating them. Recurrent veins both entering third submarginal cell or the first interstitial. Depressed area of male gonocoxite preapical.

This subgenus is limited to Africa and Madagascar. Calleupetersia is distinctive only in its metallic blue integumental coloration and does not warrant subgeneric status.

**Subgenus NESOEUPETERSIA**

Blüthgen


Scutal punctures scattered. Scutellum gently convex, not bigibbous, with scattered punctuation similar to that of scutum. Second and third submarginal cells each receiving a recurrent vein, or the first vein interstitial. Depressed area of male gonocoxite extending much of length of gonocoxite, without carinae across it (examined only in P. sakalava Blüthgen).

This subgenus is known from Madagascar, the Seychelles, and south India, with a possibly incorrectly placed species from Zaire (see Baker, 1974).

**Genus SPHECODES Latreille**

(Figs. 13, 14, 20-22, 27, 67-72)

Both sexes: Punctuation of head and thorax usually coarse, but punctures, especially of mesoscutum, sometimes widely separated by shining ground. Head much wider than long (or scarcely so in S. convergens Michener), clypeus about two to usually more than three times as wide as long, often biconvex due to longitudinal median depression which is often reduced to a closely punctate zone or absent. Eyes usually nearly hairless, but with variably long hair in S. biroi Friese and in an unidentified Argentine species, and with scattered short hairs in various other species. Hairs of antennal flagellum all or nearly all very short. Preoccipital carina usually absent in the holarctic region (occasionally present as in S. scabricollis Wesmael), but distinct in some groups from South America, south Asia to Australia, and Africa.

Pronotum with horizontal surface of collar almost absent medially, but forming lateral angles which are usually prominent (weak and rounded in brachycephalus Mitchell and some small Neotropical species) and below which a vertical ridge extends downward (ridge weak in forms with weak lateral angles and in S. convergens Michener, persimilis Lovell and Cockerell, etc.), vertical ridge approaching or merging with a more laterally directed ridge that extends toward coxal base, or laterally directed ridge weak or absent in many species; a carina from lateral angle across posterior lobe of pronotum. Anterior extremity of scutum strongly convex, vertical anterior surface nearly always with area that lacks punctures (or has them smaller and sparser than in adjacent areas.
in *S. convergens* Michener) and is therefore sharply different from rest of scutum. Scutellum gently convex or sometimes weakly biconvex due to feeble longitudinal median depression. Propodeum with dorsal area coarsely rugose, usually strongly areolate, usually about as long as scutellum, shorter than scutellum in a few species [e.g., *S. spinulosus* Hagens, *albilabris* (Kirby), and *ruschelis* Strand], area broadly rounded posteriorly; posterior and lateral surfaces of propodeum usually without or with few short plumose hairs in addition to longer hairs, but such hairs
sometimes rather conspicuous (e.g., in S. heraclei Robertson, prosphorus Lovell and Cockerell, pulsatillae Cockerell, pecozensis Cockerell, rubicundus Hagens, and in the subgenus Austrosphecodes).

Wings with hairs short and dense apically, somewhat longer and less dense toward bases [hairs rather long and dense throughout in S. manskii (Rayment)]; stigma of moderate size; marginal cell pointed to narrowly truncate at apex; free part of marginal cell beyond submarginal cells as long as to twice as long as part subtended by submarginal cells, which extend well beyond apex of stigma. Second and third submarginal cells each receiving a recurrent vein, or as occasional variants first recurrent and second transverse cubital interstitial, or in some species first transverse cubital absent so that there are only two submarginal cells.

First tergum usually broader than long, in various Neotropical Austrosphecodes species as wide as long or even longer than wide. In lateral view base of second tergum sometimes depressed so that there is a weak constriction between first and second terga. Posterior margins of terga 2-4 broadly depressed, hairless, commonly impunctate.

Female: Mandible with or without subapical tooth. Labrum with broad, flat apical process which is rounded, truncate, or bilobed and usually about twice as broad as long, but varies to nearly as long as broad [e.g., in S. monilicornis (Kirby)].

Legs commonly robust, hind femur little over twice as long as wide (S. monilicornis Kirby) to three or more times as long as wide, nearly always strongly convex on upper surface near base except in some Austrosphecodes; basitibial plate absent to demarked along posterior margin and at apex; long hairs on outer side of hind tibia plumose, barbed, or (rarely) mostly simple (e.g., in S. monilicornis (Kirby), profugus Cockerell); upper margin of hind tibia with or without spine-like setae; hind tibial spine variable.

Fifth tergum, unlike preceding terga, with apical margin fringed except in S. brachycephalus Mitchell, often with dense prepygidial fimbria in front of apical fringe, fringe sometimes interrupted medially. Pygidial plate typically broader than in Eupetersia, but slender in various species [e.g., S. gibbus (Linnaeus), pulsatillae Cockerell].

Male: Antennae long to as short as in female, flagellum often thickened, first flagellar segment broader than long, second variable, but usually longer than first, the first and second never both very short as in Eupetersia. Labrum with apical process shorter than in female, usually several times as wide as long, but rarely (e.g., S. chilensis Spinola) little over twice as broad as long.

Second hind tarsal segment shorter than to longer than third, base broader than or equal to base of third.

Gonocoxite usually striate, sometimes with dorsal basal depression, but without dorsolateral margined depression as in Eupetersia. Gonostylus variable, commonly with basal setose lobe.

This genus consists of hundreds of species and is found on all continents, although it is nearly absent in Australia, being represented there by only two species found in the northern part of the continent. Major papers on the taxonomy of Old World species of the genus are by Blüthgen (1923b, 1924, 1927, 1928); comprehensive taxonomic treatment of New World species is limited to those of eastern North America by Mitchell (1960). Meyer (1919) listed and gave copies of descriptions of the species of all geographical regions.

The genus is quite variable and doubtless, with adequate study, could be divided into various subgenera. For the present, however, only two major groups are ac-
corded subgeneric rank, the Neotropical *Austrosphecodes* and the rest of the genus, *Sphecodes* proper.

The mandible of the female usually has a subapical inner tooth. Sometimes it is reduced to a small tooth close to the main axis of the mandible (e.g., in *S. brachycephalus* Mitchell, *costaricensis* Friese sensu Michener, 1954, and *pyrenanthemi* Robertson). In various species the subapical tooth is absent so that the mandible is simple and sharply pointed. Such mandibles characterize *Austrosphecodes*, as well as species such as *S. antennariae* Robertson, *confertus* Say and *stygius* Robertson. The related genera *Eupetersia*, *Ptilocleptis*, and *Microsphecodes* also have simple mandibles. It seems likely that this feature has arisen independently in different species groups.

Male antennae are usually quite elongate, with most flagellar segments, including the second, much longer than broad, and with the first, by contrast, much shorter and broader than long. In various species, however [e.g., most *Austrosphecodes* and *antennariae* Robertson, *atlantis* Mitchell, *costaricensis* Friese, *cressonii* Robertson, *illinoensis* (Robertson)], the first and second segments are not very different in length, each a little broader than long. The second antennal type is most common in small species. All intergrades between the two types exist (e.g., in *heraclei* Robertson, *confertus* Say, and *chilensis* Spinola).

The legs of females are usually robust, the upper surface of the hind femur strongly convex basally, near the trochanter. To a variable extent this is not so in *Austrosphecodes* and in a few other species (S. *brachycephalus* Mitchell). The hind tibia of the female typically has some spinelike or even peglike setae, shorter than the nearby hairs, along the outer margin. At the apex, on the outer surface of the tibia, there is a strong tibial spine. These features are reduced in some, but not all, small species. In some small species like *S. brachycephalus* Mitchell, the spinelike setae are few in number and pale, hence difficult to see. The tibial spine is sometimes only a rounded prominence [e.g., in *S. illinoensis* (Robertson)]. In *Austrosphecodes* the spinelike setae are absent or are as long as nearby hairs and sometimes with barbs or branches. The same is true of the very large *S. rufichelis* Strand. The spinelike setae are usually absent in males, but are present in some species [e.g., *S. ruficus* (Erichson), *spinulosus* Hagens].

The preoccipital carina is usually absent, the posterior surface of the head being rounded peripheral to its central concavity, but such a carina is present and very strong in *S. manskii* (Rayment), distinct in *S. chilensis* Spinola and some other *Austrosphecodes* as well as in *profugus* Cockerell, *scabricollis* Wesmael, and an unidentified African species (see discussion under *Eupetersia*).

The male gonocoxites are typically longitudinally striate over most of the upper and outer surfaces. Such striae are absent or weak and limited to certain areas in *Austrosphecodes*.

**Subgenus SPHECODES Latreille s. str.**

*Sphecodes* Latreille, 1804, Nouvelle dictionnaire d'histoire naturelle [Deterville], Paris, Tableaux methodiques, 24:182. Type species: *Sphecodes falcifer* Ulmer.


*Drepanium* Robertson, 1903, Ent. News., 14:103. Type species: *Sphecodes falcifer*

**Proteraner** Robertson, 1903, Ent. News, 14: 103. Type species: *Sphecodes ranunculi* Robertson, 1897, monobasic.

**Sphecodium** Robertson, 1903, Ent. News, 14: 103. Type species: *Sphecodium cressonii* Robertson, 1903, by original designation.

**Machaeris** Robertson, 1903, Ent. News, 14: 104. Type species: *Sphecodes stygius* Robertson, 1893, by original designation.

**Dialonia** Robertson, 1903, Ent. News, 14: 104. Type species: *Sphecodes antennariae* Robertson, 1891, monobasic and original designation.


Mandible of female usually with subapical tooth. Labral process of male much shorter than in female, three or more times as wide as long. Preocicipital carina usually absent. *Legs almost always robust*, hind femur two to three times as long as broad, strongly convex on upper surface near base. *Hind tibia of female almost always with spinelike setae on outer margin; basitibial plate of female defined along posterior margin and sometimes also at apex*. Second hind tarsal segment of male shorter than or equal to, rarely longer than, third, *its base broader than base of third*, so that articulation to first is broader than articulation of third to second. Posterior surface of propodeum usually without short plumose hairs among long erect hairs. First metasomal tergum considerably broader than long. Male gonoxites striate on most of outer and dorsal surfaces. This subgenus is not known in South America, but is found on all other continents. As indicated by the discussion and descriptions above, it is quite diverse and may well be subdivided.

The status of the name *Callosphecodes* remains in doubt. It was described by Friese from a large, robust specimen with a metallic blue-black metasoma from New Britain in the Bismarck Archipelago. Unfortunately, Dr. Jeno Papp of the Hungarian Natural History Museum reports that the type (and only specimen) cannot be found. The blue color suggests some species of *Eupetersia* but it is not likely that *Callosphecodes* is a senior synonym of that name. The locality is far to the east of the known range of *Eupetersia*, and metallic species of that genus are known only in Africa. Moreover, the robust form (Friese says 3 mm wide, 9.95 mm long) does not suggest *Eupetersia*.

It seems likely that *Sphecodes* (*Callosphecodes*) *ralunensis* Friese is related to *S. manskii* (Rayment) from northern Australia, as suggested by Michener (1965). Rayment described this form as having a metallic purplish green abdomen, although the type entirely lacks such coloration at present, the metasoma being shining black. *S. manskii* is a very unusual *Sphecodes*, and if it is similar to *S. ralunensis*, the subgeneric name *Callosphecodes* may be used to unite the two species. Interesting features of *S. manskii* (Figs. 67, 68) include the unusually large subapical mandibular tooth of the female, the very strong preocicipital carina, the tooth at the posterior end of the hypostomal carina, and the unusually well defined, shining, slightly elevated basitibial plate of the female. The hind femur of the female is more slender (3 times as long as wide) and less convex on the dorsal surface near the base than usual for *Sphecodes s. str.*, especially for a large species with conspicuous spinedlike setae on the outer margin of the hind tibia and a large, long tibial spine. The fifth tergum has a less dense prepygidial fimbria than most large species, the apical fringe being absent in the middle part of the margin, and a smooth shining hairless area being in front of this fringeless area. A unique feature of *S. manskii* among *Sphecodes* that I have seen is the vestiture
of the wings, the hairs being long and dense as in *Eupetersia*. Unfortunately the species is known from only a single female specimen.

**AUSTROSPHECODES New Subgenus**

Type species: *Sphecodes chilensis* Spinola, 1851.

This subgenus includes the rather numerous South American species of the genus. I have studied unidentified specimens of many species, and identified specimens of *S. mutillaeformis* Schrottky, specimens of *S. chilensis* compared with Spinola's type by H. Toro, and of course *S. convergens* described below.

Mandible of female simple. Labral process of male two to three or more times as broad as long. Preoccipital carina often present. *Legs relatively slender*, hind femur not strongly convex on upper surface near base. Tegula usually larger than in *Sphecodes s. str*. *Hind tibia of female without spinelike setae on outer margin* or if present they are as long as the nearby hairs; *basitibial plate of female entirely absent*. Second hind tarsal segment of male as long as or longer than third, *narrowed at base like third* so that its articulation to first is similar to that of third to second. Posterior surface of propodeum with short plumose hairs among long erect hairs. First metasomal tergum variable but often as long as broad or longer than broad. Male gonocoxites without striae or striae fine, inconspicuous, and occurring only in limited areas.

In various features *Austrosphecodes* resembles *Eupetersia*. Both have simple mandibles and rather slender legs; some species of *Austrosphecodes* have the slender body and even a somewhat female-like body form in the male, suggestive of *Eupetersia*; some also have a preoccipital carina. *Austrosphecodes* also has short pale plumose hairs on the vertical surfaces of the propodeum, as does *Eupetersia*. *Austrosphecodes*, however, looks much more like *Sphecodes* than does *Eupetersia*, resembling *Sphecodes* in wing vestiture and venation, in basal flagellar segments of the male, and in lacking the margined depressed area of the male gonocoxite found in *Eupetersia*.

Presumably the similarities of *Austrosphecodes* and *Eupetersia* are convergences since the latter probably arose from African *Sphecodes* and not from South American forms.

The subgeneric name, meaning southern *Sphecodes*, refers to the South American range of the group.

**APPENDIX**

Descriptions of new species needed for inclusion in the preceding account, together with other taxonomic conclusions at the specific level, are presented here.

Moreover, a revision of the new genus *Ptiloplectis* is included.

**Parathrincostoma seyrigi** Blühgen


New localities are as follows: Madagascar: District de Fanovana, Region orientale de forêts humides, September - October, 1938 (C. Lamberton); east Madagascar, forest 600-1200 m, December-February, 1930-31 (C. Lamberton); Manombo s.l., Tulear Province, March 31, 1968 (K.M.G. and P.D.). The Lamberton material is in the American Museum of Natural History, New York; the other specimen is in the British Museum (Natural History).

The female (one specimen from "east Madagascar") has a strongly produced clypeus, almost as in the male; the anterolateral angles of the pronotum are produced to acute, almost spinelike angles; the punctuation is relatively sparse, punc-
tures of the frons below the ocelli being separated by much more than puncture widths; and metasomal segments 4-6 are brown, the rest of the body brownish black and the legs more noticeably reddish.

*Parathrincostoma elongatum* Benoist


This species, known only from the type female, has a less produced clypeus than *P. seyrigi*; the anterolateral angles of the pronotum are obtuse; the punctation is denser, punctures of the frons below the ocelli being separated by less than a puncture width, and metasomal segments 5 and 6 are brown, the rest of the body and legs being black.

*Nomia ambrensis* (Benoist) new combination


As indicated above, the remaining specific name proposed in *Parathrincostoma* is based on a specimen of *Nomia* in the broad sense. It is a slender black bee, with wings dark except for the clear bases, and thus is superficially extraordinarily similar to *Parathrincostoma*. However the lack of a preepisternal groove, the short pronotum without a transverse carina or lamella, the pale femoral scopa, the elongate third submarginal cell, and the short face clearly show the incorrect placement.

**Genus PTILOCLEPTIS**

This genus, described above, is known from only seven specimens taken in the American tropics from Mexico to southern Brazil. Three species are easily recognizable, separated by the following key.

**Key to the Species of PTILOCLEPTIS**

1. Terga 2-6 with extensive areas of dense, yellow brown, plumose hair; scutellum of male with an impunctate area on each side, but not strongly bigibbous...*

2. Scutum with many plumose hairs although surface not entirely obscured; scutellum and metanotum yellow (female) ... *polybioides*

    Scutal hairs mostly simple and surface not at all obscured; scutellum and metanotum black (male) ... *eickworti*

*Ptilocleptis tomentosa* new species (Figs. 11, 17, 28, 39-43, 47-50, 53, 54)

This middle American species is markedly larger than the other members of the genus, from which it also differs by having conspicuously hairy eyes and areas of dense, plumose, brown hair on the metasoma.

**Female**: Length 10 mm; forewing length 8 mm (7 mm in paratype). Black; the following parts red-brown: labrum, mandible, lower two-thirds of clypeus (entire clypeus in paratype), scape, pedicel, underside of flagellum (almost whole of two basal segments, red-brown coloration more restricted in area and darker in color toward apex), posterior pronotal lobe, tegula, axillary sclerites, tibiae (mid and hind with infuscated postmedian band in paratype), tarsi, apices of femora, apical half of sixth metasomal segment (the last blackish in paratype). Metasomal segments 2-5 with apical translucent brown bands, narrow on terga 2-3, progressively broader on 4-5. Wings light yellowish-brown, costal area of forewing from stigma to apex of wing (including entire marginal cell) dark brown; veins and stigma brown.

Pubescence yellow-brown to yellow-testaceous, on sixth metasomal segment dusky except laterally, that on venter of thorax and in paratype also on side of
thorax and posterior surface of propodeum whitish. Hairs of head rather short, yellow-testaceous, plumose ones hiding most of paraocular area, frons, vertex, and genal area. Thorax with hairs rather short and simple, some long hairs on scutellum and metanotum, surface easily visible except for the following areas which have dense coverings of short, plumose, yellow-testaceous hairs obscuring the surface: dorsum of pronotal collar, margin of pronotal lobe and corresponding mesepisternal depression, pre-episternal groove (not entirely covered), line along mesepisternal-metaplural suture, rest of metapleuron (not entirely covered), line along scuto-scutellar suture, posterior margin of scutellum, disc of metanotum, posterior and posterolateral surfaces of propodeum. Metasoma with scattered, moderately long, erect, simple hairs, very sparse on disc of first tergum, longer and slanting posteriorly on apical terga dorsally, on all terga laterally, and on all sterna; second to fifth tergum also with short hairs which are plumose, dense and form broad, yellow-testaceous basal band across tergum 2, basal half of tergum 3 similar, otherwise plumose hairs less dense and light brown; short, simple hairs on mid-dorsal convex part of tergum 2 and across posterior parts of terga 2-4; hairs on both terga and sterna extending almost to posterior margins, on terga 2-4 short hairs, more erect and laterally directed than the rest, forming weak, narrow, subapical, yellow-testaceous bands. Fifth tergum with hairs somewhat longer than on preceding terga, some arising almost to apex of tergum, but no recognizable subapical band and no dense prepygidial fimbria. Eye with rather abundant hairs about one-fourth as long as diameter of scape.

Head narrower than thorax, somewhat wider than long (100:88), upper and lower interorbital distances as 59:45, shorter than eye length (65). Clypeus convex, longer than clypeoantennal distance (27:20). Antennocular:interantennal:antennocellular:intercellular:ocellocular distances as 15:14.5:25:13.5:15. Labrum with broad, transverse, basal, elevated area covered with short hairs, apical process as long as basal area, about four times as wide as long, rounded at apex, margined with narrow band of slender hairs. Supraclypeal area gently elevated up to frontal tubercle, above which it is gently declivous to frons. Scape, pedicel, and upper surface of flagellum near base with rather conspicuous hairs, under surface of flagellum with only very short hairs; flagellum with first two segments broader than long, third longer than broad, middle segments slightly longer than broad. Dorsal area of propodeum slightly shorter than metanotum. Hamuli 8-10. First metasomal segment about as long as broad.

Head closely punctate, ground between punctures minutely roughened, anterior part of clypeus most coarsely punctate, rest of clypeus and lower supracylpeal area more coarsely so than frons and vertex, which are rather finely punctate except for area of coarser, sparser punctures above antennal base; genal area finely and rather sparsely punctuate, lower genal area near foramen magnum striate. Mesoscutum closely punctate, punctures similar in size to largest clypeal punctures, anterior part rugose, punctate. Scutellum much more finely punctate than scutum, with some shining ground between punctures; metanotum closely and rather finely punctate; mesepisternum above scrobe somewhat more finely punctate than scutum, elsewhere coarsely reticulopunctate, strigose below; pre-episternal groove a series of pits separated by carinae; mesepisternal-metapleural suture marked by similar series of smaller pits; upper convexity of metapleuron with about four horizontal striae, rest of metapleuron with fine punctures and less conspicuous transverse striae,
especially above. Basal area of propodeum with irregular, longitudinal carinae, seven or eight on each side, connected by a carina posteriorly and separating pits which middorsally are twice as long as wide, or more; posterior surface and posterior part of lateral surface of propodeum irregularly coarsely areolate. First metasomal tergum shining with only scattered minute punctures. Remaining terga with numerous small punctures, mostly separated by a puncture width or less, extending onto the slightly depressed brownish margins of terga 2-5, but punctures on these margins smaller and sparser than elsewhere; ground between punctures shining, but minutely lineolate, especially on more posterior terga; sterna shining, coarsely and sparsely punctate, apical margins of more anterior sternae broadly impunctate, surface between punctures minutely lineolate, progressively more strongly so on more posterior sternae.

Male: Similar to description of female, differing as follows: Forewing length 7 mm. Black, the following parts red-brown: scape, first flagellar segment, anterior tibia (darker brown along outer surface). Other parts described as red-brown in female are dark brown. Metasomal terga 1-2 without translucent margins, 3 with a rather narrow translucent brown margin. 4-6 with such margins broad.

Hairs of head as well as sides of thorax largely whitish, sparser than in female, partially obscuring surface only on paraocular area, scutoscutellar line and center of metanotum, fully hiding surface under dense plumose yellowish hair only on dorsum of pronotal collar. Basal band of plumose, yellowish hairs across tergum 2 supplemented by weaker preapical band, strongest dorsolaterally; similar, yellowish, plumose hairs occupying most of dorsum, anterior to translucent margins, of terga 3-6. Hair of eyes very short.

Structure, including facial proportions, about as in female. Second flagellar segment as long as broad, succeeding segments all longer than broad. Scutellum as in female.

Genal area somewhat more sparsely, but no more finely punctate than vertex. Upper part of metapleura with only two or three horizontal striae, rest of metapleuron areolate. First metasomal tergum shining with sparse large punctures and sparse smaller punctures intermixed.


Ptilocleptis polybioides new species (Figs. 25, 51, 52)

This Peruvian species differs from the other members of the genus in the yellow pronotum, scutellum, metanotum, and much of the first metasomal tergum, a pattern which enhances its wasplike aspect.

Female: Length 7 mm; forewing length 6 mm. Black, the following parts yellow (reddish-yellow in paratype): labrum, mandible (apex red-brown), clypeus, scape, pedicel, first two flagellar segments (reddish-yellow) (second dark brown in paratype), prothorax (lamella across front of collar dark), tegula (translucent), axillary sclerites, scutellum (reddish), metanotum, legs, basal two-thirds of first metasomal tergum, first sternum, and base of second sternum. Lower anterior part of meseptisternum with diffuse, yellow brown area (absent in paratype, which has sides of thorax dark brown). Metasomal terga and sternae with narrow, apical, dark,
brownish bands; fifth and sixth segments more extensively brownish. Wings light yellowish brown, costal area of forewing from about level of vein cu-v to apex of marginal cell (including marginal cell except for narrow strip along its posterior border, or entire marginal cell in paratype) dark brown; stigma and veins proximal to it including basal vein dark brown, other veins yellow brown.

Pubescence yellowish-white (that of head and thorax more golden in paratype), that of posterior half of metasoma more brownish-white and of sixth segment dusky. Hair pattern of head and thorax as described for *P. tomentosa*, but scutum with abundant, plumose hair partly obscuring surface, plumose hairs (white) otherwise perhaps less dense and obscuring surface less than in *P. tomentosa*, conspicuously less abundant on scutellum. Hair pattern of metasoma as described for *P. tomentosa*, but short hairs are longer, and none are plumose. Eye with scattered, very short hairs.

Head about as wide as thorax, somewhat wider than long (75:63), upper and lower interorbital distances as 45:34.5, shorter than eye length (48.5). Clypeus convex, longer than clypeoantennal distance (18:12). Antennocular:interantennal:antennocellar:interocellar:ocellocular distances as 11:12:22.5:10.5:12. Labrum with broad, transverse, basal, elevated area covered with short hairs; apical process about twice as wide as long. Supraclypeal area and antennal pubescence as described for *P. tomentosa*; flagellum with first segment broader than long, second as long as broad or appearing longer than broad in paratype, the remainder all distinctly longer than broad. Scutellum biconvex, summits of convexities impunctate. Dorsal area of propodeum longer than metanotum. Hamuli 8. First metasomal tergum about as long as broad.

Punctuation similar to that of *P. tomentosa*, differing from description of that species as follows: ground between punctures of clypeus and supracycpeal area smooth and shining, these areas similarly punctate; striae of lower genal area weak. Anterior part of mesoscumum punctate, but scarcely rugose; mesepisternum above scrobe as coarsely punctate as adjacent areas. Basal area of propodeum with more regular longitudinal carinae, pits between median ones about three times as long as wide. Impunctate tergal margins broader. Sterna less coarsely punctate, less lineolate.

Holotype female: Tingo Maria, Peru, 620 m altitude, October 5-12, 1964 (H. C. Porter), in the Museum of Comparative Zoology, Harvard University. Paratype female: Monzon Valley, Tingo Maria, Peru, November 2, 1954 (E. I. Schlinger, E. S. Ross), in the California Academy of Sciences.

The specific name is based on the wasp genus *Polybia*, because of the bee’s resemblance in general form and coloration to such polybiine wasps.

Unlike other known specimens of the genus, the paratype of *P. polybioides* has only two submarginal cells through loss of the second transverse cubital vein.

*Ptilocephis eickworti* new species
(Figs. 44-46)

This species from southern Brazil is the smallest of the genus and also the darkest, having neither the rather extensive yellow markings of *P. polybioides*, nor the large areas of yellowish plumose hairs of *P. tomentosa*.

**Male:** Length 6 mm; forewing length 5 mm. Black, the following parts red-brown: scape, pedicel, first flagellar segment, tibiae, tarsi, and parts of femora; the following dark brown, sometimes blackish: labrum, mandible, clypeus, pronotal lobes and diffuse area on side of pronotum, tegula, axillary sclerites,
coxae, trochanters, much of femora, and much of first tergum. Extreme base of first tergum yellow, this color continued middorsally to behind middle of tergum. Wings light brownish, marginal cell of forewing dark brown, dark color extending less intensely beyond apex of marginal cell as well as basal to stigma; veins and stigma brown.

Pubescence yellowish white, yellow on legs, brownish on metasoma, longer hairs of posterior segments dusky. Plumose hairs (white) less dense than in other species, not covering surface, most conspicuous on face and pronotal collar, present also on sides of thorax and sides and posterior surface of propodeum and surface clearly visible in these areas; plumose hairs largely absent on scutum so that surface is clearly visible. Hairs of metasoma and eyes as in *P. polybioides*.

Head about as wide as thorax, wider than long (64:57), upper and lower interorbital distances as 40:28, shorter than eye length (42). Clypeus convex, longer than clypeoantennal distance (15:11). Antennocular :interantennal :antennocellar :interocellar :ocellocular distances as 8:11:21:10:10.5. Labrum with broad, transverse, basal, elevated area with short hairs; apical process over twice as broad as long. Supraclypeal area and antennal pubescence as described for *P. tomentosa*; flagellar segments as described for *P. polybioides*. Scutellum bigibbous, with a strong elevation, impunctate at summit, on each side of midline. Dorsal area of propodeum longer than metanotum. Hamuli 7. First metasomal tergum distinctly longer than broad. Punctation as described for *P. polybioides*.

Holotype male: Nova Teutonia, Santa Catarina, Brazil, March 24, 1966 (Fritz Plaumann) in the Museum of Comparative Zoology, Harvard University. Paratype male, same locality and collector (27°11' S, 52°23' W), no date, in the same collection.

This species is named for Dr. George C. Eickwort, who assembled most of the known specimens of *Ptilocleptis* and kindly permitted me to study them.

_Eupetersia (Eupetersia) guillarmodi_ new species (Figs. 60-66)

This species differs from other species of the genus by the black body and red scape and legs; other species have the body partly red, yellow, or blue. The species is larger than other species except *E. neavei* Blüthgen, from which it differs in the black metasoma, the broad pygidial plate of the female, the largely black pubescence, and other characters.

_Female:_ Length 10 mm (9.5 mm in one paratype); forewing length 8 mm. Black, the following parts red brown: labrum, mandible (except blackish apex which grades into the red basally), scape, pedicel, first two flagellar segments, legs including apices of coxae (but greater part of coxae black). Posterior lobe of pronotum, tegula, and axillary sclerites of wings slightly darker red-brown; third and following flagellar segments dark-brown. Wings fuliginous, veins and stigma dark brown.

Longer hairs black, those of labrum, mandible and lower clypeal margin reddish black, apical fringe of fifth tergum reddish. Anterior surface of front tibia and posterior surfaces of mid and hind tibiae with hair pale-red. Hairs of undersides of tarsi red. Short, white hair present among longer black hairs on much of head and thorax; most of hair of frons and metapleuron pale; short, pale hairs conspicuous among longer black hairs on pronotal collar, around hind wing base and on lateral and posterior faces of propodeum. Dense fringe on posterior pronotal
lobe and dense hairs in corresponding depression of mesepisternum white.

Head as wide as thorax, much wider than long, upper and lower interorbital distances subequal (71:70.5), greater than eye length (60.5). Clypeus scarcely biconvex, higher than clypeoantennal distance (19.5:15). Antennocular:interantennal:antennocellar : interocellar : ocellocular distances as 22:12.5:27:16:20. Labrum with sharp, transverse, basal ridge with only a few short hairs on distal surface; process beyond ridge about twice as broad as long, rounded, margined with strong hairs, two or three irregularly placed preapical hairs. Supraclypeal area strongly elevated to frontal tubercle, then abruptly declivous upward between antennal bases. Flagellum with first two segments much broader than long, third longer than broad, middle segments slightly broader than long. Preoccipital carina continuous, but weak dorsally. Pronotal collar broader medially than in other species, anterolateral angles sharp although somewhat obtuse, a strong, high carina extending across pronotal lobe. Scutum with longitudinal median depression extending from anterior almost to posterior margin. Scutellum distinctly biconvex. Legs rather slender; basitibial plate with posterior margin indicated by distinct smooth line which curves anteriorly at apex and indicates end of plate; hairs along upper margin of hind tibia with branches along convex surfaces, spinelike setae absent, but there are some simple bristles especially near base and apex; hairs of outer surface of hind tibia appearing simple in lateral view, but with a few short branches on convex sides visible from above. Apex of marginal cell narrowly subtruncate with appendage. Hamuli seven. Pygidial plate rather broad, but lateral margins converging somewhat anteriorly so that plate is nearly round.

Head dull, coarsely and closely punctate, transversely rugose-punctate on vertex between ocelli and preoccipital carina, punctures finer and arranged to suggest weak striae on genal area; hypostomal area shining, with widely scattered, coarse punctures, surface between them minutely shallowly punctulate. Scutum and metanotum dull, closely punctate, more coarsely so than head, transversely rugose anteriorly on scutum. Scutellum more finely, closely punctate except for the two large, shining, convexities with scattered punctures. Mesepisternum coarsely rugose-punctate, becoming more coarsely reticulate below and ventrally; preepisternal groove consisting of a series of pits separated by carinae, a similar series of pits along anterior margin of metapleuron; upper convexity of metapleuron with about four horizontal striae, rest of metapleuron rugose-punctate, more finely so below. Dorsal surface of propodeum shining, longitudinal carinae irregular and connected by numerous transverse carinae, so that surface is areolate, at margins areolae of similar size extending down on lateral and posterior surfaces of propodeum, except that anterior, lateral surface is finely punctate. First metasomal tergum polished, at first glance impunctate, but with scattered small punctures laterally and even less conspicuously extending across tergum mid-dorsally. Terga 2-5 with punctures densest laterally, quite fine on 2, progressively coarser on 3-5; posterior marginal zones of terga 2-5 broadly shining, impunctate, hairless; marginal zones as well as surface between punctures nearly smooth on 2, progressively more distinctly lineolate on 3-5; marginal zones slightly depressed, most noticeably so sublaterally because of gently elevated, less closely punctate convexities of punctate areas in front of marginal zones; marginal zone of tergum 2 occupies one third exposed length of tergum, the zones being progressively broader on terga 3-5, occupying most of exposed length of 5. Anterior sterna with only scattered
coarse punctures and large median im-punctate areas; sternae progressively more closely and more finely punctate posteriorly.

Male: Length 10 mm (to 8 mm in one paratype); forewing length 8 mm (to 7 mm in one paratype). Coloration as in female, but posterior lobe of pronotum black; tegular and axillary sclerites brownish black.

Pubescence colored as in female, but hairs of sixth and seventh sternae black or dusky.

Upper interocular distance somewhat longer than lower (64:58), subequal to eye length (60). Clypeal length to clypeoantennal distance as 20:15. Antennocellular:interantennal:antennocellar:interocellar:ocellocellar distances as 19:13:26:16.5:18.5. Labral process shorter than in female, about three times as broad as long. Third as well as middle flagellar segments about as broad as long. Longitudinal scutal depression weaker than in female and not noticeable behind middle of scutum. Hairs of hind tibia with fewer and shorter branches, those of outer surface simple. Apex of pygidial plate broadly rounded with margin slightly raised. Gonocoxite with depressed area about as broad as long with several longitudinal carinae across it; gonostylius over half length of gonocoxite, broad, rounded, with broad basal ventral lobe.

Terga much as described for female, but 5 should read 6 throughout; second sternum with punctures sparse dorsally and surface between them not or scarcely lineolate.

Holotype female: Mamathes, Lesotho (= Basutoland), March 8, 1953 (C. Jacot-Guillarmod). Allotype male, same data but January 2, 1960. Two female and five male paratypes, all from same locality, females taken January 12, 1947 (L. Bevis) and February 18, 1945 (A. Jacot-Guillarmod), the males on November 19 and 22, 1945 (L. Bevis), January 12, 1947 (L. Bevis), February, 1940 (C. Jacot-Guillarmod), and February 11, 1945 (C. Jacot-Guillarmod).

The holotype and allotype are in the British Museum (Natural History), paratypes in the Albany Museum in Grahamstown and the Snow Entomological Museum, University of Kansas.

This species is named for one of its collectors, Charles Jacot-Guillarmod, Director of The Albany Museum, Grahamstown, South Africa.

Eupetersia (Nesoeupetersia) flavus new species (Figs. 58, 59)

This species differs from other members of the genus by the uniformly reddish-yellow color, so that the insect is suggestive of various nocturnal Hymenoptera. E. scotti (Cockerell) and madagascablitthgen are species of Nesoeupetersia with partly red head and thorax, but no others have the wholly reddish yellow body of E. flavus.

Female: Length 6 mm; forewing length 5.5 mm. Reddish yellow, apices of mandibles red, upper surface of flagellum brown; wings nearly clear, veins and stigma brown.

Hairs yellowish white, longer hairs of lower part of face dusky yellow, hairs of tarsi yellow, longer hairs of posterior sternae and sides of posterior sternae dusky in certain lights.

Head slightly wider than thorax, much wider than long, upper and lower interorbital distances as 35:34, about equal to eye length (36). Clypeus uniformly convex, upper margin concave medially, height of clypeus greater than clypeoantennal distance (8:6). Antennocellular:interantennal:antennocellar:interocellar:ocellocellar distances as 11:5:23:7.5:11. Labrum with sharp transverse basal ridge with a
few hairs on distal surface; labral process over twice as broad as long, margined with strong hairs and without premarginal hairs. Supracypeal area weakly elevated to frontal tubercle, then gently descending above, between antennal bases. Flagellum with first three segments all much broader than long, middle segments broader than long. Preoccipital carina continuous, but weak dorsally. Anterolateral angles of pronotum nearly right angular, a weak carina extending across pronotal lobe. Scutum without longitudinal depression. Legs slender, basitibial plate slightly elevated and short; hairs along upper margin of hind tibia with branches along convex surfaces, these intermixed with some coarse, simple, curved, pointed bristles about half as long as longest hairs or longer; hairs of outer surface of tibia as described for E. guillarmodi. Apex of marginal cell pointed almost on wing margin. Hamuli six. Pygidial plate rather broad, sides diverging anteriorly.

Body shining, with scattered minute punctures, lower half of face and entire genal area minutely roughened between punctures, upper part of frons smooth between punctures separated by several puncture widths, vertex almost impunctate; thorax with punctures coarser than those of head, punctures of scutum separated by one to two puncture widths, scutellum with similar sized punctures separated by three of four puncture widths, space between punctures minutely roughened, more conspicuously so on scutum than scutellum; sides and venter of thorax smooth, with scattered small punctures, about two horizontal striae on upper convex part of metapleuron. Dorsal surface of propodeum with longitudinal, slightly irregular carinæ, terminating at posterior margin; posterior and lateral surfaces of propodeum finely roughened and punctate, not areolate except for a few, large, incomplete areolæ just above attachment of metasoma, carinæ delimiting them extending only about half way up from metasomal attachment to summit of posterior face of propodeum. Metasomal terga entirely shining and nearly impunctate, minutely lineolate except on first tergum, weakly so on second; dorsal hairs almost absent except on fifth and sixth terga; basal parts of terga and apical marginal zones not differentiated except sublaterally on terga 1-4, which have distinct sublateral swellings in front of marginal zones. Sterna 1-2 nearly impunctate, 3-6 with coarse punctures posteriorly and laterally, interspaces conspicuously lineolate.


The specific name refers to the uniformly yellow color of the body.

**Spécodes (Austrospécodes) convergens**

new species

(Figs. 69, 71, 72)

This species differs from other Spécodes known to me by the relatively narrow face, with eyes strongly converging below. In this and other respects it resembles the genus *Ptilocelptis* and suggests the origin of that group from Austrospécodes. The abundant, snow white hair is unusual, and the areas of dense, white hair at the sides of the terga probably distinguish it from other species such as *S. cordillerensis* Jörgensen.

**Female:** Length 7 mm; forewing length 5.5 mm. Black, the following parts light red: labrum, mandible (apex red-brown), antenna (upper surface red-brown, basal half of scape brown in some paratypes), pronotal lobe, legs (coxae and in some paratypes trochanter infuscated, front coxa essentially black; hind tarsal segments 1-3 infuscated in some para-
types), metasomal terga 1-3 and basal half of 4, sterna (fifth and sixth brownish). Clypeus dark brown. Tegula and basal wing sclerites translucent testaceous. Wings transparent, veins and stigma dark brown.

Hairs snowy-white, those of apex of abdomen yellowish; shorter hairs largely densely plumose, obscuring paraocular area and extreme sides of clypeus, slightly less dense on frons and supraclypeal area, most of clypeus with only scattered sparse simple hairs; genal area hidden by dense hair. Thoracic surface largely hidden by plumose hairs in the following areas: posterior margin of pronotum and outer surface of pronotal lobe, anterolateral, lateral and posterior margins of mesoscutum, lateral part of scutellum, metanotum, lateral and ventral surface of thorax, posterior and lateral surfaces of propodeum. Hair of legs rather abundant, longer hairs of hind tibia longer than tibial diameter, mostly branched, none thickened or spikelike; hairs of under surfaces of tarsi pale-yellowish. Lateral parts of terga 1-5 with diffuse areas of white hairs, mostly not quite dense enough to hide surface, these areas extending medially toward midline on middle parts of terga 2 and 3 as areas of laterally directed hairs, conspicuous from some angles. Api cal fringe of fifth tergum broadly interrupted medially so that medially this tergum has broad, hairless margin like preceding terga; prepygidial fimbria rather weak, nowhere fully obscuring surface of fifth tergum. Eye with scattered short hairs.

Head as wide as thorax, broader than long (about 80:70); eyes strongly converging below, upper and lower interorbital distances as 48:38, both less than eye length (50). Clypeus slightly biconvex, only slightly more than twice as wide as long (37:16), longer than subanten nal distance (16:14). Antennocular:interantennal:antennocellar:intero cellular:ocellocular distances as 14:65:19.5:14.5:11. Mandible simple. Labrum with transverse basal elevated area about four times as wide as long, summit of this area feebly emarginate medially, distal surface of this area with short hairs; process beyond elevated area rounded, about twice as broad as long, hairs of marginal row slender, not bristles. Supraclypeal area gently convex, frontal carina not steeply declivous above frontal tubercle. Flagellum with first segment almost twice as broad as midventral length, segments 2-9 subequal in length, slightly longer than broad (3.5 most distinctly so) to about as broad as long. Preoccipital carina absent dorsally, distinct laterally and extending to posterior end of hypostomal carina where the two form a posteriorly directed acute angle. Anterolateral angle of pronotum with dorsal, transverse, horizontal carina, angle about right-angular seen from above, no strong ridge, but only a rounded surface extending downward from angle, but ventrolaterally directed ridge extending toward coxal base distinct. Scutum with vertical, anterior surface convex, with punctures and therefore less sharply differentiated from rest of scutum than usual. Scutellum feebly biconvex. Legs slender, hind femur width to length as 12.5:47. Hind tibia without basitibial plate, apical spine, or spikelike setae; hairs of outer surface of hind tibia with branches along convex sides. Apex of marginal cell narrowly truncate with short appendage. Hamuli five. First metasomal tergum nearly as broad as long. Pygidial plate rather broad, margins diverging anteriorly.

Head closely and rather finely punctate, dull because of punctuation except clypeus, which is shining with coarser round punctures separated by about a puncture width, and hypostomal area which has only very scattered punctures, but whose surface is minutely roughened, dull. Scutum with punctures nearly as large as those of cly-
peus, separated by about one-third puncture width or almost contiguous anteriorly; scutellum more finely punctate; metanotum finely reticulate; sides of thorax reticulate punctate, finely so above, weakly and finely so on metapleuron and anterior part of propodeum; upper part of metapleuron with about three horizontal striae. Dorsal surface of propodeum rather finely reticulate, nearly smooth around the arcuate posterior margin; posterior and posterior lateral surfaces of propodeum more coarsely reticulate-areolate. First metasomal tergum shining, with small punctures mostly separated by three or four puncture widths, except laterally in some areas where they are coarser and closer and posteromiddorsally, where they are finer and sparser. Second tergum similarly punctured, depressed apical margin not differently punctured, coarsest punctures widely separated and on elevation anterior to depressed margin. Remaining terga with punctures closer, surface between them somewhat less shining, marginal areas impunctate posteriorly but basal parts with punctures. Sterna with surface rather dull, finely-lineolate.

Holotype female and three female paratypes (one headless): Zapala, Prov. Neuquén, Argentina (Juan Foerster). One paratype is dated March, the others have no dates. One female paratype: Tornquist, 500 m altitude, Sierra de la Ventana, Prov. Buenos Aires, Argentina, December, 1954 (F. H. Walz). The holotype is in the Snow Entomological Museum, University of Kansas. Paratypes are in that collection, the American Museum of Natural History, and the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia.”

The specific name refers to the inner ocular margins which are strongly convergent below, unlike other *Sphecodes*.

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