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THE COMPARATIVE EXTERNAL MORPHOLOGY AND SYSTEMATICS OF THE NEOTROPICAL PARASITIC FIG WASP GENUS *IDARNES* (HYMENOPTERA: TORYMIDAE)

By

GORDON GORDH

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The Comparative External Morphology and Systematics of the Neotropical Parasitic Fig Wasp Genus *Idarnes* (Hymenoptera: Torymidae)

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The Comparative External Morphology and Systematics of The Neotropical Parasitic Fig Wasp Genus *Idarnes* (Hymenoptera:Torymidae)[1]

GORDON GORDH[2]

ABSTRACT

The external morphology of the parasitic fig wasp genus *Idarnes* is examined and compared to more primitive and advanced hymenopterous forms. Several secondary features, noticed by earlier workers, have been named in the present paper. These features include setal tracts in the forewing and mesosomal apodemes of the female.

In spite of its distinctive appearance, *Idarnes* has never been properly characterized. Therefore, the genus has been redefined and a neotype designated. Eleven species are described as new and numerous species erroneously included earlier in *Idarnes* are discussed.

Although *Idarnes* has been considered pantropical, the present work develops the hypothesis that it is exclusively neotropical. Moreover, evidence is presented which suggests *Idarnes* is found exclusively associated with the subgenus *Urostigma*. Ramírez has demonstrated that a high degree of specificity exists between species of agaonid pollenator and *Ficus* host. Data collected throughout México and Central America indicate a similar pattern exists for *Idarnes*. However, it is uncertain whether the specificity exhibited by *Idarnes* is connected to the pollenator, host fig, or both.

INTRODUCTION

Since its description in 1843 by Francis Walker, the genus *Idarnes* has never been properly characterized, although numerous identifications of *"Idarnes carme"* have been made (Wolcott, 1951; Butcher, 1964; cf. remarks of Burks, 1969). This study is intended to provide a firm systematic foundation for *Idarnes* and to elucidate its external morphology.

Of the earlier workers, Mayr (1885, 1906) probably came closest to guessing the true identity of *Idarnes*. Unfortunately, the original generic description of *Idarnes* is so vague that Mayr supposed his material to be new and erected the genus *Tetragonaspis* for it in spite of his suspicions about *Idarnes*. Subsequent taxonomic studies (Ashmead, 1904; Girault, 1913) only obscured the issue. Aside from an occasional remark (Risbec, 1951; Joseph, 1964, 1967; Wiebes, 1966b, 1968, 1970; Hill, 1967a; Burks, 1969), *Idarnes* has remained essentially untouched systematically.

Nonetheless, *Idarnes* represents the largest, most conspicious element of the neotropical fauna of fig wasp parasites. Although other parasitic genera are found, they are never collected in the diversity or abundance of *Idarnes*.

ACKNOWLEDGMENTS

Numerous individuals were in part responsible for bringing this work to fruition. Mr. William Ramírez provided much of the material studied from his personal collection of Central American figs and fig wasps; Dr. P. D. Ashlock (University of Kansas) gave many helpful suggestions regarding a cladistic analysis of the group; Dr. R. E. Beer (University of Kansas) aided in collecting material in México during the summer of 1970; and Dr. B. D. Burks of the United States

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National Museum lent material from which a neotype was designated. Dr. J. T. Wiebes (Rijksuniversiteit, Leiden) had the onerous task of comparing much of the material with that of the Mayr collection and gave several taxonomic suggestions. Professor C. D. Michener (University of Kansas) has offered encouragement, suggestions, and a critical evaluation of the entire project. To Professor J. H. Camin (University of Kansas) I am deeply indebted for the generous loan of equipment, facilities, and space during the entire gestation of this revision.

Linda Gordh typed rough drafts of the manuscript and rendered much clerical assistance.

MATERIALS AND METHODS

The material studied came from three sources: collections by the author from México during the summers of 1969 and 1970; material provided by William Ramírez from Central America; and representatives of previously described species provided by J. T. Wiebes.

Collecting in México was by the methods described by Ramírez (1970b). For a tabulation of Central and North American host trees, *Blastophaga* pollinators, and associated *Idarnes* parasites, see Table 1. For each collection, ripened syconia of the *Ficus* were preserved in 70% alcohol; branches, including young figs and leaves, were pressed. In addition, samples of all fig species collected during 1970 were halved, photographed, and close-up photographs of branches taken. Identification of host figs was based on the classification of Standley (1917). When applicable, the work of DeWolf (1960) was consulted; Condit's (1969) work also proved useful. Plant material collected during the summer of 1969 was retained by Ramírez; plant material collected during the summer of 1970 is retained by the author.

All wasp material was collected into 70% alcohol. Associated pollinators (agaonids) were given to Ramírez and Wiebes, while voucher specimens of torymids collected during the 1970 trip were given to Professor Wiebes. The bulk of the material remained with the author. For the deposition of types, see Table 2.

Specimens were dissected in depression slides filled with 70% alcohol. Dissections were made with *minuten nadeln* hooks embedded in heat-treated glass rods. The following parts were separated from intact female wasps: antennae, head, pro-, meso-, and metathoracic legs, pronotum, mesosternum, labiomaxillary complex, gaster and wings. Parts separated from intact male wasps included antennae, legs and occasionally the gaster. When each dissection was completed, wings and the labiomaxillary complex were mounted on a slide in Hoyer's medium. Other structures were cleared in 10% KOH at 50° C for 12-16 hours, depending upon size and sclerotization. The parts were then transferred to 70% alcohol for several hours and subsequently mounted in Hoyer's. Material sent to the U.S. National Museum of Natural History and many paratypes were mounted in Canada balsam.

After Hoyer's medium slides were dried for several days at 50° C (with the aid of a slide warmer), each coverslip was sealed with Zut's Ringing Medium. This procedure proved excellent for preventing deterioration of the mount due to evaporation of water from the Hoyer's.

Illustrations were prepared with a microprojector and a binocular phase contrast Zeiss microscope with drawing tube attachment.

THE EXTERNAL MORPHOLOGY OF *IDARNES*

1. *Female Head* (Figs. 1-3)

Based upon the axis of the gnathal appendages and the position of the occipital foramen, the cranium of female *Idarnes* may exhibit two distinct conditions: it may be prognathous (as in *I. bucatoma*) or more generally hypognathous (as in *I. barbigera, I. galbina*). The shape of the cranium is highly variable, ranging from elongate *(I. bucatoma)* to round *(I. galbina)*.

The sculpture of the head capsule is also variable, depending upon the degree of sclerotization. Species such as *I. galbina* have lightly sclerotized heads and hence are nearly smooth; *I. obtusifoliae* females have honeycomb-like sculpturing which results in heavy sclerotization.

When viewed from above, 3 triangularly arranged ocelli are visible; when viewed from the front, the position of the anterior ocellus is variable, ranging from the level of the upper third of the compound eyes to the crest of the vertex. Position of the ocelli seems correlated with the axis of the cranium: species with prognathous heads have ocelli located higher on the vertex than do species with hypognathous heads.

The epicranial suture represents a cardinal landmark of the generalized insect head. Within the Hymenoptera an epicranial suture has been identified in the Symphyta (Pergidae), some braconids, and evanoids. Michener (1944b) indicated the suture was not present in bees.

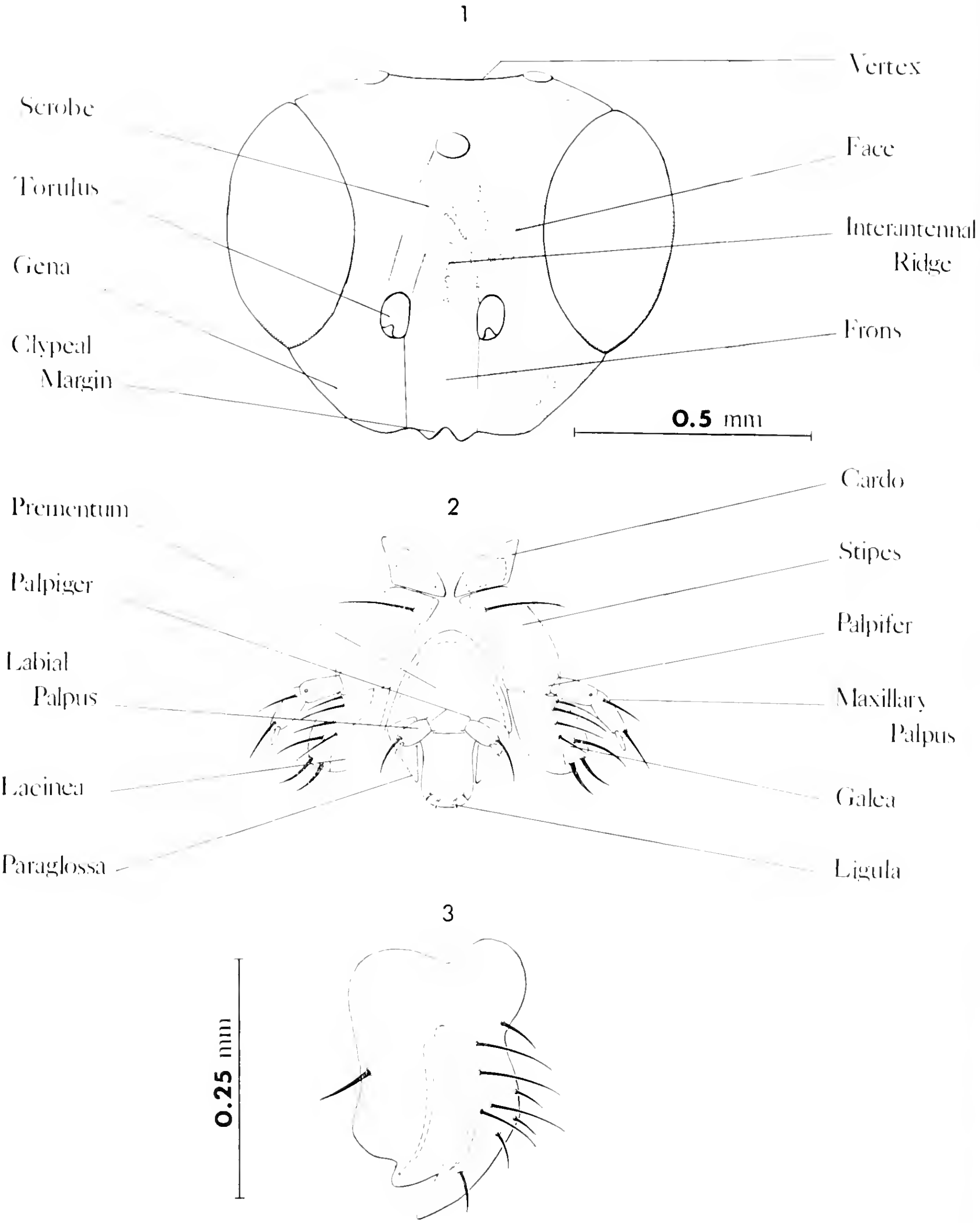
The epicranial suture is not evident in *Idarnes* or any other chalcid examined morphologically. As a consequence standard regions of the cranium are poorly defined and homology with more primitive insect heads is difficult. Michener (1944b) recognized this problem in bees and created artificial boundaries for the area between the anterior ocellus and toruli. He applied the term "supra-antennal" which is noncommital with regard to homology; however, this term has not been retained in the present work because the scrobal cavity and interantennal ridge are well defined and are more familiar terms.

Immediately lateral to the scrobal cavity and adjacent to the compound eye inner margin is another ill-defined region termed the "face" in the present work. It is bounded by imaginary transverse lines extending from the anterior ocellus dorsally, and the toruli ventrally. The region is called paraocular by Michener (1944b), parafrontal by Pratt (1940) and parietal by Bucher (1948). The face and scrobal cavity together are regarded as the frontovertex by some chalcid taxonomists. However, because the scrobe is so well defined in *Idarnes* it is again useful to separate these regions terminologically.

The compound eyes of *Idarnes* are lateral to the face. They vary in shape, ranging from round *(I. galbina)* to oval *(I. carme)*, but are never emarginate. The eyes are never setose in *Idarnes*, though this characteristic is common in other chalcidoids such as *Aphytis* (Aphelinidae). Many Hymenoptera (some braconids, evanoids, vespids, and bees) have a circumocular sulcus that circles the compound eye. If the sulcus is present in *Idarnes*, it must coincide with the margin of the eye itself since no conspicuous ring has been observed. Some chalcids (e.g., *Brachymeria*, Chalcididae) bear a distinct line of favose punctations which surround the eye margin. However, this condition is also absent from *Idarnes*.

Heads cleared in KOH or bleach reveal the presence of a large, well defined ocular sclerite. This feature has been found in all chalcids examined (including representatives of 12 families). Presumably the ocular sclerite supports the compound eye and provides a shelf upon which the eye rests. The ocular sclerite of *Idarnes* is peninsulate along the inner margin, but the function of this feature is unknown.

The gena (= malar space) is immediately beneath the compound eye. When the head is viewed in lateral aspect it is



Figs. 1-3. **1,** Head of *Idarnes* female, anterior aspect; **2,** labiomaxillary complex of *Idarnes* female, external aspect; 3, left mandible of *Idarnes* female, inner aspect.

bounded dorsally by the eye, ventrally by the pleurostome, and anteriorly and posteriorly by imaginary lines extending from the lateral margins of the compound eye to the mandibular articulations. In most chalcids a subocular suture (= malar sulcus) bisects the gena, extending from the ventral margin of the eye to the pleurostome. In many encyrtids, eupelmids, and pteromalids the suture is bold and presumably serves as a secondarily developed reinforcement for the cranium. In *Monodontomerus* spp. also it is well developed, but all species of *Idarnes* lack the suture. In the related genus *Critogaster* the subocular suture is incipient, represented only by a weak, dark, incomplete line.

The insertion of the antennae in *Idarnes* ranges from the midline of the compound eyes to their ventral margins. Moreover, the toruli may be nearly contiguous *(I. bucatoma)* or separated by one to several times the diameter of a single torulus *(I. camini)*. The antennal suture circling the torulus is well defined. The antennifer is variable, being conspicuous in some species *(I. simus)* and reduced in others *(I. galbina)*. Between the toruli and anterior ocellus, a shallow depression (scrobe) which receives the scapes when the antennae are in repose is always present. The scrobe is divided by a mesal interantennal ridge of variable length and height. When well developed, it creates two distinct channels which merge at the anterior ocellus.

Since the epicranial and frontal sutures are absent from *Idarnes,* the boundaries of the frons are not certain. The frons is taken to be a region below an imaginary transverse line below the toruli and between perpendicular lines extending from the outer margin of each torulus to the pleurostome.

The anterior tentorial pits are minute and can be located only with a compound microscope by tracing the course of the anterior tentorial arms to the surface of the head. The epistomal and subgenal sutures are absent from *Idarnes*. Thus, the boundary separating the ventral margin of the frons from the dorsal margin of the clypeus is arbitrary. For the purpose of the present paper, it is taken to be an imaginary transverse line between the anterior tentorial pits. Bucher (1948) noted *M. dentipes* and James (1926) indicated *Harmolita graminicola* have epistomal and subgenal sutures.

The labrum of *Idarnes* consists of a membranous flap concealed beneath the clypeus. This condition seems common to most chalcids though some species of *Leucospis* exhibit a lightly sclerotized retractile sclerite and in *Perilampus* this sclerite resembles a comb.

The mandibles (Fig. 3) of *Idarnes* are highly sclerotized, bi- or tri-dentate. The toothed margin may be sharply *(I. flavicollis)* or weakly *(I. galbina)* incised. Mandibles bear 2 hollow, internal, cone-like cavities extending into the primary and secondary teeth. The third tooth of tri-dentate species lacks such a feature. These cavities seem universal in the Chalcidoidea. In some Pteromalidae (*Pachycrepoideus vindemiae, Pteromalus* spp.) and Perilampidae (Perilampus spp.) the left mandible may have 3 cavities. However, in all cases the function of this adaptation is unknown.

The maxillae and labium (Fig. 2) are bound together by membrane, forming the labiomaxillary complex. Maxillary components include cardo, stipes, galea, lacinea, and segmented palpus. The cardo shape is variable, but it always flexes mesally along the posterior margin of the elongate stipes, except in isolated instances (some individuals of *I. micheneri*) where it is fused to the stipes. Each stipes characteristically bears a basal acuminate seta. The maxillary palpus arises from the antero-lateral margin of the stipes and consists of a proximal palpifer and 2 distal segments. Lengths of the palpifer and palpal segments are variable and the palpifer and basal palpal segment may be fused. The basal segment bears a scolopophorous sensillum at the distal end and the terminal segment is characterized by sensory spines and acuminate setae. The galea and lacineae are membranous, enveloping the ligula and paraglossae. These modifications contrast sharply with the condition found in aculeate Hymenoptera (Matsuda, 1965) but conform to other chalcidoids.

The labium consists of a medio-distal ligula (fused glossae), prementum, paraglossae, and lateral labial palpi. The ligula is surrounded by a crown of pilus dentilae (flattened pronged setae) and is arched sharply forward, bearing 2 or 4 sensory pegs along its anterior margin. (Sensory pegs along the margin of the ligula seem characteristic of all chalcidoids, though the number varies considerably among species. Encyrtids such as *Comperia merceti* have as many as 10 pegs; 2 pegs seems to be the minimum number.) The ligula is broadly attached to the prementum (which is always larger than the ligula in *Idarnes*), which also bears the labial palpi on the distal margin. The 1-segmented labial palpi are always shorter than the maxillary palpi, with the palpiger irregular. The apex of each palpus bears a long, acuminate seta, and there is often a long basal one.

The paraglossae arise from the prementum lateral to the labial palpi. Each is blade-like, lightly sclerotized, and projects anteriorly along the lateral margin of the ligula. They are exceedingly difficult to see except with high magnification (> 250X). The mentum and submentum are not differentiated, a feature noted by Matsuda (1965) for other chalcidoids.

The posterior surface of the chalcid head has undergone considerable modification, making homology difficult or impossible. In *Idarnes* it may be flat or concave, depending upon the species. The occipital suture (preoccipital ridge of Michener, crassa of Ross) is inconsistently developed in the Hymenoptera and altogether lacking in *Idarnes*. Bucher (1948) indicated *Monodontomerus* bears a well developed carina he chose to call an occipital suture, but it is doubtful that this carina is homologus with the occipital suture of more primitive insects.

The dorsal margin of the occipital foramen of *Idarnes* exhibits a thickening which diminishes laterally. The post occipital suture is poorly developed and does not circle the foramen. The dorsal thickening may contain remnants of the post occipital suture, but they have not been observed in any species of *Idarnes* yet examined.

In *M. dentipes, H. graminicola,* and most other chalcids the occipital foramen is bisected by an apodeme which originates at the posterior tentorial pits. This structure has been termed the corporotentorium, body of the tentorium, or primary tentorial bridge by various writers on Hymenoptera morphology. It is lacking from all species of *Idarnes*. Posterior tentorial arms do project from the posterior tentorial pits to the ventral margin of the foramen in *Idarnes,* but these are not fused.

The posterior tentorial pits are small and may be recognized by tracing the tentorial arms to the surface of the head. The pits are ventro-lateral to the foramen.

The sclerite which separates the foramen from the proboscidial fossa exhibits two conditions. In some species *(I. ashlocki),* faint post occipital sutures run parallel from the posterior tentorial pits to the proboscidial fossa. The sclerite thus formed is a gula according to the definition of Snodgrass (1935). Bucher (1948) has made a similar observation for *Monodontomerus*. However, in each instance the gula has developed on a hypognathous head. Alternatively, a faint median suture may be present *(I. simus)* and extend from the ventral margin of the foramen to the proboscidial fossa. The postgenae are separated by a postgenal groove. This mesad migration of weakly developed postoccipital sutures has drawn the lateral walls of the proboscidial fossa together thereby forming a hypostomal bridge.

II. *Female Antenna* (Fig. 4)

Antennae are either 12- or 13-segmented because there may be 1 or 2 annuli at the base of the flagellum. The first annulus is always constricted basally; the second, when present, appears to be a fragment of the first flagellomere. The annuli have been counted in numbering the flagellomeres.

Surface features of individual flagellomeres are highly variable among species, but constant intraspecifically. The most conspicuous modifications include longitudinal carinae and three forms of setae, inflexible (obdurate) setae (Figs. 25, 27, 28), flexible setae (Figs. 29, 34), and acicular setae (Fig. 26). Setal types may be distinguished on the basis of appearance when mounted under a coverslip and viewed with a low power compound microscope objective. Flexible setae are recurved, appear hollow and are often apically blunt; inflexible setae are not recurved or hollow, and are shorter than flexible setae. Acicular setae are long and transmit light in such a way as to make the base resemble the eye of a needle. Each type of seta, when present, forms a whorl around each flagellomere. These setae usually originate at the base of a flagellomere, but minute inflexible setae may, in addition, be randomly dispersed in some species. For a given species, one setal form predominates.

A club may or may not be present. When present, it is composed of the last 3 flagellomeres, and may be compact *(I. bucatoma, I. micheneri)* or loosely formed *(I. ashlocki)*. Regardless of club formation, the distal 3 flagellomeres (=clavus) always show the carinal and setal patterns found on previous segments. A nipple-like terminal protuberance is always present, although sometimes weakly developed. It bears clusters of short, thick setae and minute discoid sensilla. This feature seems to be a characteristic of the family Torymidae.

III. *Female Thorax* (Figs. 6-9)

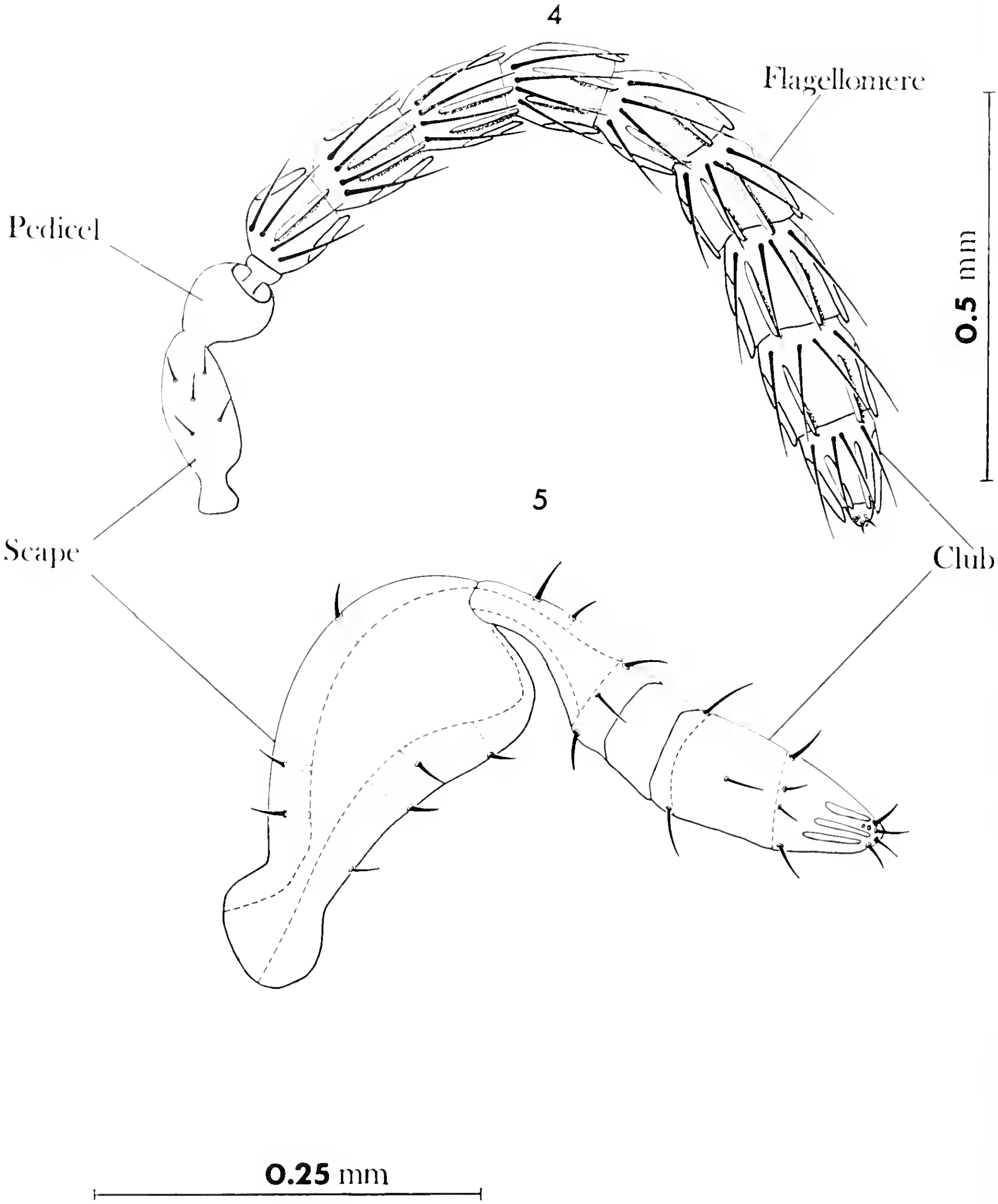
Aside from a few incomplete statements regarding specific features (cf. Compere, 1962; Compere and Rosen, 1970; Richards, 1956; Matsuda, 1960, 1970) of the pleurosternum, no attempt has been made to homologize the chalcidoid thorax with that of more primitive and advanced hymenopterous forms. Although *Idarnes* is seemingly specialized biologically, it is a member of a chalcidoid family considered to be primitive (Malyshev, 1966; Breland, 1938). Morphological features of *Idarnes* tend to bear out this hypothesis.

The central portion of the chalcidoid body (mesosoma, *sensu* Michener, 1944b) consists of four regions: pro-, meso-, metathorax and propodeum. Morphologically, the last represents the first abdominal segment which has fused with the thoracic components, a condition characteristic of all clistogastrous Hymenoptera. The term thorax will be used to refer only to the three anterior segments of the mesosoma; when the term mesosoma is used the propodeum is also included in the discussion.

The Notum (Figs. 6, 7)

The pronotum (Figs. 6, 7) of female *Idarnes* is rigid, collar-like, and envelops the anterior edge of the mesoscutum. The pronotum is not sharply angular at the anterior end, but is latero-ventrally expanded, forcing the proepisterna into ventral positions; it usually possesses the notal sculpture pattern only along the postero-dorsal edge, with the remainder of the sclerite smooth or bearing distorted striations.

The mesonotum (Fig. 6) comprises the bulk of the thoracic notum. It has been



FIGS. 4-5. **4**, Left antenna of *Idarnes* female, inner aspect; **5**, left antenna of *Idarnes* male, dorsal aspect.

subdivided into 7 distinct regions, separated by sutures, sulci, and apodemes.[1] Anterior-most of the mesonotal regions is the prescutum, which is not visible from a dorsal view and may be seen only when the pro- and mesosternum have been separated. The prescutum is bounded dorsally by the mesoscutum to which it is united at the transverse notal suture. In *Idarnes,*

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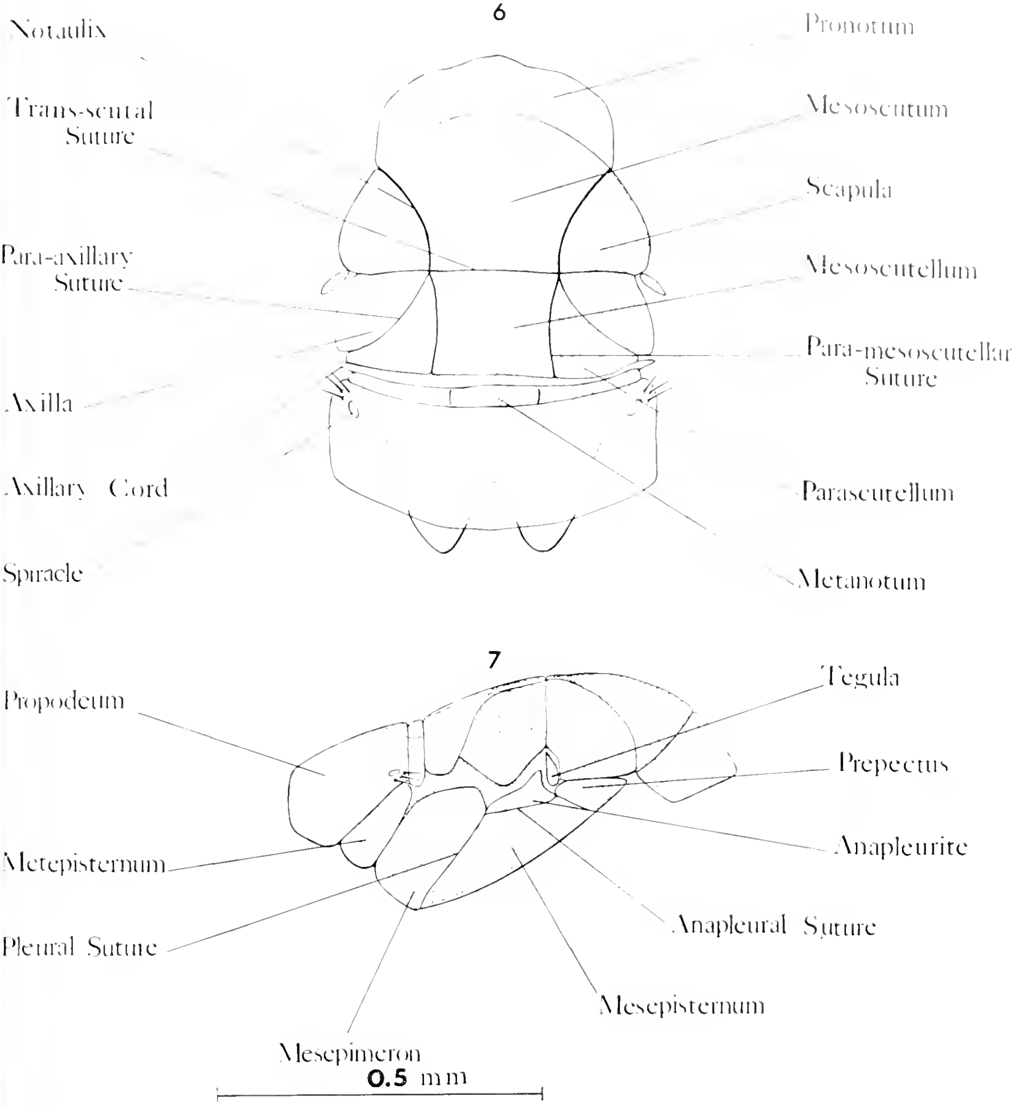
[1] Snodgrass (1962) has indicated that the first two terms have been used interchangeably and that it is often impossible to distinguish between them. As a consequence, the term suture is used throughout the text.



Figs. 6-7. Mesosoma of *Idarnes* female in dorsal (6) and lateral (7) aspects.

however, this suture is poorly defined. Moreover, the prescutum represents a lightly sclerotized, pendulous lip which projects posteriorly beneath the mesoscutum and effectively forms an anterior rim that contains the dorsal longitudinal flight muscles.

The mesoscutum (in a restricted sense, including scapulae) lies immediately behind the pronotum and is bounded laterally by notaulices[2] and posteriorly by the

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[2] Various authors have referred to these longitudinal inflections of the mesonotum as "parapsidal sutures." Tulloch (1929) indicated that parapsidal sutures are distinct from notaulices, with the former extending anteriorly from the scutoscutellar suture while the latter extend posteriorly from the anterior margin of the mesoscutum. Functionally, parapsidal sutures represent the site of attachment for rudimentary indirect flight muscles, while notaulices are associated with the distribution of connective tissue during metamorphosis (Daly, 1964). Some chalcids bear both structures, but *Idarnes* has only notaulices.

trans-scutal suture. The shape of the mesoscutum in *Idarnes* is constant. In lateral aspect the posterior margin is flat, but where the notaulices begin to diverge anteriorly, the mesoscutum is arched (Fig. 7). The regions lateral to the mesoscutum, bounded by the notaulices, are the scapulae.[3] In *Idarnes* these sclerites are large and constant in shape. They are bordered posteriorly by the lateral parts of the trans-scutal suture.

The trans-scutal suture of *Idarnes* is transverse and straight. The principal landmark posterior to this suture is the mesoscutellum which is characteristically quadrate. As with the scutum, the term here is used in a restricted sense, the lateral fragments being named separately for convenience. Laterally, the mesoscutellum is bounded by a secondary suture which I have chosen to call the *para-mesoscutellar suture*. Posteriorly, the mesoscutellum is bounded by a bold suture-like impression which Graham (1969) terms the frenal groove. Immediately posterior to the frenal groove and anterior to the metanotum is a narrow, transverse region termed the postscutellar zone in contradistinction to the postscutellum of Burks (1943). The postscutellar zone extends laterally to the base of the forewing and forms the axillary cord, a fact which indicates that it is a fragmentum of the scutellum.

Lateral to the mesoscutellum and posterior to the trans-scutal suture another secondary suture has been formed. Originating adjacent to the intersection of the notaulices, trans-scutal and para-mesoscutellar sutures, a *para-axillary suture*[4] extends obliquely rearward to the base of the forewing. The suture separates the axilla from a region termed the *para-scutellum* by Grandi (1921). Grandi recognized the presence of the para-axillary suture, but chose to refer to it as a "rinforzo endoscheletrico della linea che separa l'ascella dal parascutello." Subsequent taxonomic studies on chalcid parasites associated with figs have illustrated this suture, but not indicated a name or its morphological significance (cf. work of Joseph, Hill, etc.). The suture separates the para-scutellum and axilla into two equal regions. Incipient para-axillary sutures exist in other families of chalcidoids, notably Eulophidae (Brothers and Moran, 1969) and Agaonidae (Grandi, 1929).

The second phragma (Fig. 6) is a large, lightly sclerotized, bilobed plate which provides attachment for the dorsal longitudinal flight muscles. In *Idarnes* the sclerite may be viewed only when the mesonotum is separated from the propodeum and metathorax, since it develops beneath the metanotum and dorsum of the propodeum. Weber (1924) and Snodgrass (1910) both believed the postphragma to be double-walled; however, it appears single-walled and arises from the metanotal antecosta.

The metathorax represents the final thoracic subdivision of the mesosoma; it is a narrow transverse band when viewed from above (the general condition in Hymenoptera), and upon closer inspection appears superficially divided into three regions.[5] The distinctness of the areas is emphasized by different sculpture patterns found on the meson and lateral regions. The meson (dorsellum of Graham, 1969)

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[3] Graham (1969), in agreement with general-morphological usage, regards the entire region cephad to the scutoscutellar suture in chalcids as the mesoscutum, with development of notaulices subdividing the region into a mid- and two lateral sclerites. But since the scapulae are so distinct in many chalcidoids, it is convenient to separate them terminologically.

[4] Graham (1969) calls this the "scutello-axillar suture," a term less descriptive. The sclerotized area just behind this suture was regarded by Graham as the "Axillula." Bucher (1948) noted the presence of an incomplete suture in this region of the mesonotum of *M. dentipes*, but chose to call it "suture of the postscutum."

[5] Owing to the reduction of the metanotum, homologies with the mesonotum are difficult. The terms meson and lateron will be applied.

is characteristically elevated from the lateral areas (metanotum of Graham, 1969). The three regions are more or less equal in size. While plicae may be evident in some species of *Idarnes*, no longitudinal sutures are present to separate the three areas into distinct sclerites. The metanotal postphragma is obsolete.

The Pleurosternal Region (Figs. 7-9)

Several theories regarding the origin and development of the pleurosternal region of the insect thorax have been put forward. The primitive pleural region must have been membranous. To account for the origin and development of sclerotization, Heymons (1899) developed the subcoxal theory of the sternal and pleural sclerites. While most subsequent morphologists have subscribed to this concept in principle, their opinions regarding homologies of various sclerites have diverged sharply (Weber, 1924, 1928; Snodgrass, 1935; Ferris, 1940; Richards, 1956; DuPorte, 1965).

The pleurosternal region of *Idarnes* is primitive compared to that of most chalcidoids. As in other pterygotes, the prothorax is simple when compared with a wing-bearing segment. Hanna (1935) interpreted the pleuron of *Euchalcidia caryobori* (Chalcididae) to be exclusively episternal and the proepimeron to be absent. *Idarnes* conforms to this pattern, for reasons indicated below. Earlier workers sometimes regarded the episternal plates as the prosternum; however, this interpretation is untenable for *Idarnes*.

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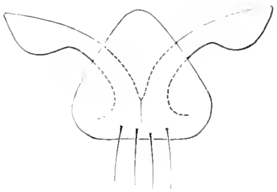

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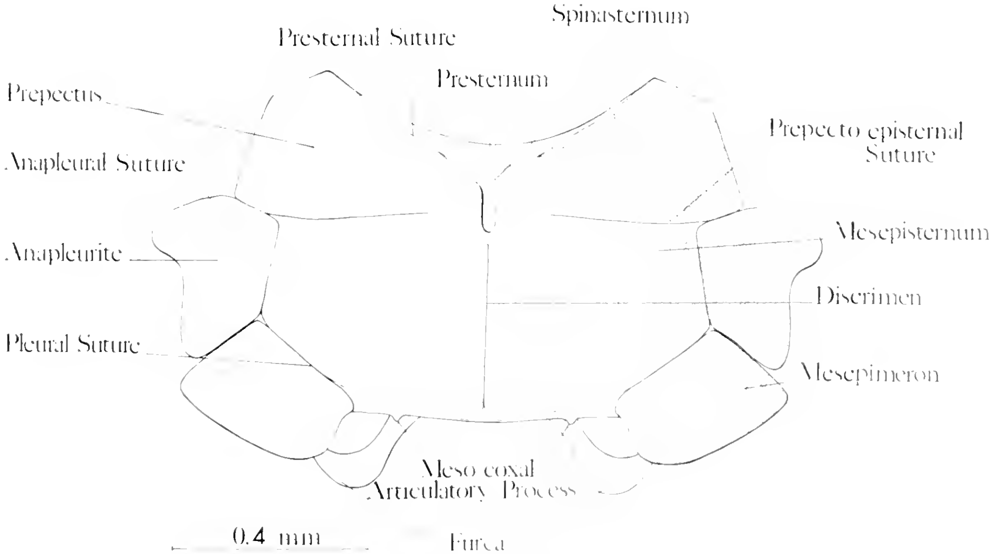


Figs. 8-9. **8**, Prosternum of *Idarnes* female, ventral aspect with furca flexed cephalad; **9**, mesothoracic pleurosternum of *Idarnes* female, ventral aspect with furca flexed caudad.

Idarnes lacks lateral cervical sclerites. Instead, the anterior cranial processes (Snodgrass, 1910) of the proepisterna articulate directly with the posterior surface of the head. As in other Hymenoptera, it is not possible to state conclusively if the cranial processes represent a fusion of cervical sclerites with the proepisterna or whether the processes are modifications of the anterior-most portion of the proepisterna.

The mesal surfaces of the proepisterna are flat and contiguous along their anterior ends. The proepisterna are ventral in position, seemingly having been pushed ventromesally by the expanding pronotum.

The prosternum (Fig. 8) is a small sclerite which lies immediately behind the posterior proepisternal margins and between the forecoxae. It is highly variable in shape, ranging from nearly round to trapezoidal. Superficially, the prosternum may be rugose to smooth with scattered setae projecting posteriorly.

The discrimen of the prosternum is evident and variably developed. In one species *(I. bucatoma)* it extends nearly the entire length of the sclerite; in some species it is barely evident. Internally, the prosternum bears 2 conspicuous apodemes, the prosternal furca.

Idarnes appears to retain only proepisterna, proepimera being absent. Internally a ridge extends from each cranial process rearward, running the entire length of the propleuron along its lateral margin. This ridge has been called by Snodgrass the *internal pleural ridge,* in spite of the fact that the upper ends leads to the cranial process. At the level of the apex of each strenal apophysis, the internal pleural ridge is extended further inward, forming a pleural apophysis. By definition (Snodgrass, 1935), the episternum and epimeron are separated by the pleural suture. Although the *pleural suture* is evanescent (since it is the lateral proepisternal margin), the pleural apophysis and ridge are evident.

The mesothoracic pleurosternum (Fig. 9) (=mesopectus of Compere, 1962) of *Idarnes* is large and conspicuous. The mesothoracic legs arise ventrally along the posterior edge of the mesepisterna and are mesally contiguous. The points of articulation with the mesothorax are unmistakable, and the pleural suture is quite distinct; consequently, homologizing the various mesothoracic sternal components is comparatively simple. Interestingly enough, the coxal condyles are apparently sternal in origin since they are continuous apodemes which originate along the discrimen and fuse with the posterior margin of the mesepisternum. This condition has been observed in all trichogrammatids, aphelinids and encyrtids examined morphologically.

The anterior-most region of the mesothoracic pleuron is a lightly sclerotized, nearly membranous presternum. Immediately posterior to this is the area commonly called the prepectus. An internal submarginal ridge (= presternal suture) separates the two structures.

The triangular prepectus (Figs. 7, 9) is large and not completely separated from the rest of the mesepisternum. Numerous other species of chalcidoids have the prepectus more nearly separated from the sternal plate *(Microterys, Encyrtidae).* I call the suture which separates the prepectus from the mesepisternum the *prepecto-episternal suture,* and this should not be confused with the pleural suture which lies posteriorly.

Immediately behind the prepectus is the main mesepisternal plate, which comprises the bulk of the pleural region of the mesothorax. The discrimen separates the mesepisterna midventrally. Internally, a large, conspicuous furca is evident on the posteromesal surface of the episternum. The spinasternum has fused to the episterna mesally at the anterior end of the discrimen.

The mesothoracic pleural suture is identifiable by the position of the articulatory process of the mesothoracic coxa. The coxal articulation is on the posterior edge of the mesepisternum, halfway between the mesepimeron and the discrimen. The pleural suture runs obliquely forward separating the epimeron from the episternum. Prepectus, epimeron, and episternum are moderately sclerotized and bear sculpture patterns that range from favose to lightly shagreened.

Lateral to the main mesepisternal plate is a conspicuous anapleural suture (=pleural ridge of Bucher, 1948; = sternopleural suture of Snodgrass, 1910, 1935). The sclerite lateral to this suture has been termed "epansione marginale anteriore del mesopleurum terminante nel denza della regione epimerale" by Grandi (1929) for *Blastophaga psenes.* The anapleural suture must be a secondary development and consequently the sclerite formed must be part of the mesepisternum. It is here called the anapleurite, and it arches dorsally beneath the forewing, providing a fulcrum for wing movement. The upper part of the pleural suture which leads to this fulcrum in primitive insects is absent. Here the anapleurite may have an epimeral as well as an episternal component.

The metasternum of *Idarnes* is unusual. The hind legs are latero-ventrally situated, and from a lateral view only a metepisternum is visible. The metepisternum meets the mesepimeron along the lateral thoracic wall. However, the two sclerites have not formed a suture between one another since they are readily separable upon dissection. Together, the metepisterna form a moderate sized oblique plate which confines the mesothoracic coxae posteriorly. The metepisterna extend ventrally and meet along the longitudinal central axis of the body, forming an internal keel between the hind coxae. The keel splays out laterally, forming a lightly sclerotized plate which separates the hind coxae from the longitudinal flight muscles.

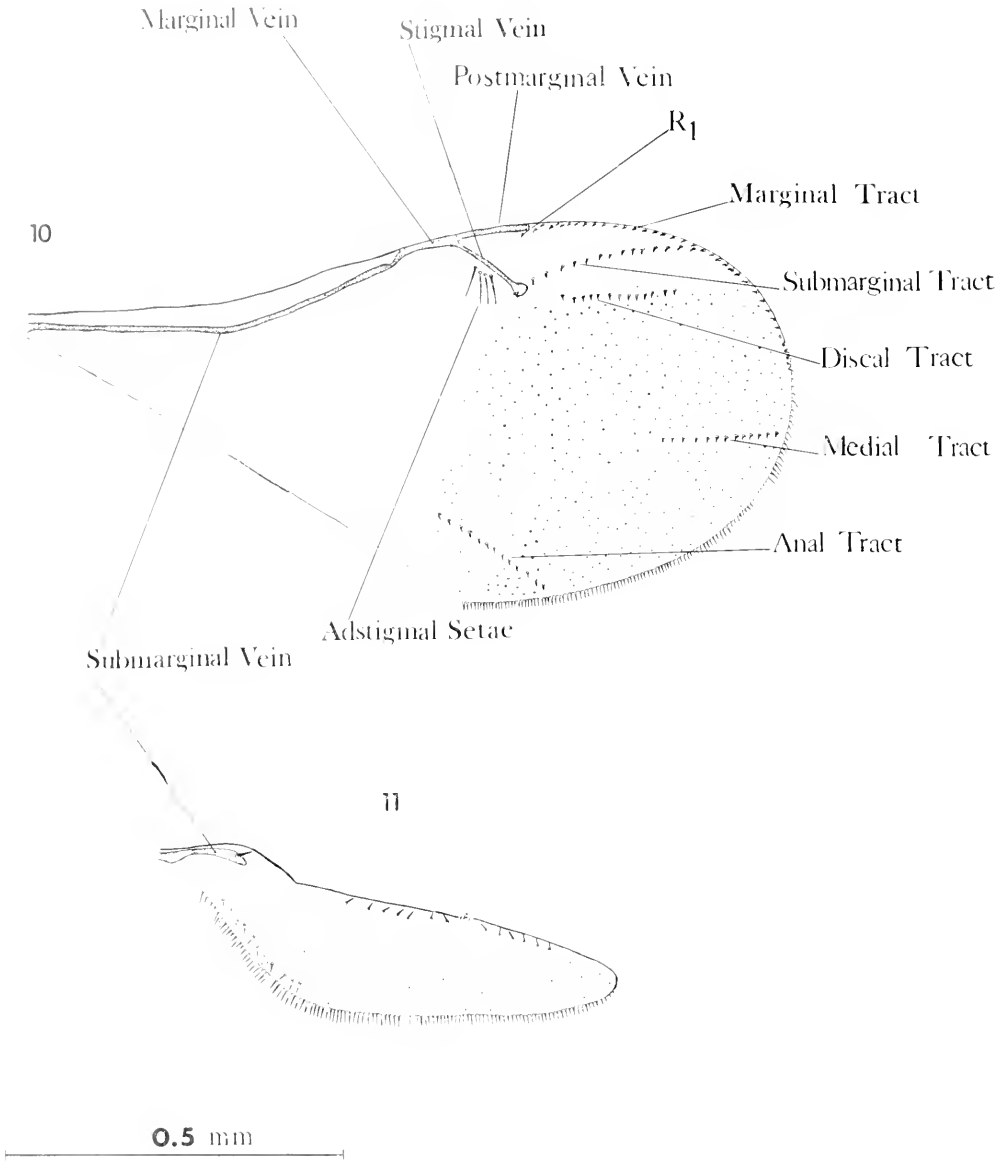
The metathoracic pleural suture (Fig. 7) originates at the metathoracic leg articulatory point (seen as a notch along the dorsal surface of the coxa) and continues obliquely forward, terminating beneath the hind wing. Immediately behind the pleural suture is the propodeum; the metathoracic epimera have been nearly obliterated. All that remains of the metepimera are two thin, transverse bands, one on each side, which converge mesally behind the metathoracic coxae and connect to the mesepisternal keel.

IV. *Wings* (Figs. 10, 11)

The Forewing

The forewing (Fig. 10) of *Idarnes* conforms to the typical chalcidoid pattern: veination is reduced to a single vein which has been subdivided into submarginal, marginal, postmarginal, and stigmal regions (Howard, 1887). The submarginal vein angles forward along its distal third and at the extreme end is notched; at the notch two campaniform sensilla are always present. The portion of the submarginal vein between the bend and the notch is often called the parastigma. The notch represents the beginning of the marginal vein, which continues to the fork where the stigmal and postmarginal veins originate. The stigmal vein may have a distal bulb which is called the stigma. The stigma invariably bears campaniform sensilla. The degree of stigmal development appears to be a species characteristic. The postmarginal vein is variable in length and usually bears a few small setae.

Close examination of the wing reveals distinct setal tracts which converge along the distal edge of the wing. Burks (1938), using representatives of 8 chalcid families



FIGS. 10-11. Right forewing (**10**) and hindwing (**11**) of *Idarnes* female.

(no torymids), attempted to correlate extensive setal tracts and obsolete venation with the hypothetical forewing venation of Ross. Unfortunately, the setal tracts of the *Idarnes* forewing do not reach the basal portion of the wing or connect with existing wing venation. Thus it is not possible to identify the setal tracts of *Idarnes* with the system of Burks.

Recently, Doutt and Viggiani (1968)[6]

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[6] The systems of nomenclature employed by Burks and by Doutt and Viggiani are useful from a taxonomic standpoint, but imply a vestige of wing venation and hence homology. Since the tracts found in *Idarnes* are not from the same region of the wing and cannot be homologized with extant venation in other Hymenoptera, new terms seem necessary. Names used in the present work refer to areas with which the reader may be familiar and no presumptions of homology are intended.

have indicated that setal tracts provide taxonomic characters among species of trichogrammatids. Oldroyd and Ribbands (1936) found that these tracts of macrotrichae in *Trichogramma evanescens* were influenced by the size of the host from which the wasps emerged. Taxonomists of Torymidae have not used the tracts in classification, although they have been illustrated. Tracts have not been observed in other Sycophagini but in *Idarnes* have proven quite reliable in separating species and appear constant in their formation. Some variation of the type found by Oldroyd and Ribbands has been noted, but this has not proven a problem taxonomically.

The setal tracts of *Idarnes* all seem to merge with the conspicuous marginal fringe. The anterior-most tract may be called the *marginal tract;* it is always present in *Idarnes.* In some species it extends to the postmarginal vein *(I. micheneri),* while in others it terminates abruptly well in front of the postmarginal vein *(I. oscrocata).* Immediately behind the marginal tract is sometimes found a very short "R_1" which terminates behind the postmarginal vein *(I. simus).* A *submarginal tract* in some species originates along the apical wing margin and arches to the area of the stigma *(I. obtusifoliae).* Posterior to the submarginal tract and perpendicular to the distal edge of the wing is sometimes a variable *discal tract (I. barbigera).* This tract is absent from most species, and difficult to interpret when present owing to the random dispersal of microtrichae over the general wing surface. The microtrichae are widespread on the wing surface behind and beyond the stigma. *Idarnes jimenezi, I. obtusifoliae,* and *I. ashlocki* bear a tract composed of microtrichiae that are densely arranged along an imaginary longitudinal line which would conform to a median vein, hence the name *medial tract. I. jimenezi* also bears an *anal tract.*

Adstigmal setae, long, acuminate and located just mesad to the stigma, provide an additional forewing feature. Species tend to exhibit some variation in number, but distinct trends (clusters vs. 1 or 2 setae) are useful in determining species.

The Hindwing

The hindwing (Fig. 11) of *Idarnes* has proven to be of some taxonomic value. It is slender and elongate. The entire posterior margin bears a conspicuous fringe which is longer than the corresponding forewing fringe. Venation is much reduced from that of other Sycophagini, consisting of a short, stubby, submarginal vein. The region between the tip of the submarginal vein and hamuli may be setose and gives the appearance of a vestigial marginal vein. Other genera of Sycophagini have marginal veins. The entire wing surface bears microtrichiae.

V. *Female Legs* (Figs. 12-15)

The coxae conform in part to the typical torymid pattern: the hind coxa (Fig. 15) is larger than the fore coxa (Fig. 12), but the middle coxa (Fig. 14) is reduced, globular, and easily detached from the mesosoma. Sculpturing of coxae may be evident. The trochanters usually have sensilla near the apical margins. The mesothoracic femur is slender and atrophied. Additionally, it is basally constricted, giving the impression of a second trochanter being present. Femora of all legs may be mesally setose. The fore leg tibia posseses an apical bifurcate calcar (Fig. 13). Sensory spurs beneath the calcar form a comb which presumably facilitates antennal cleaning. Various authors (Grandi, Joseph) have used the number of apical tibial setae and spurs as a specific character. The present study has revealed the number to be variable, and not a good diagnostic character for *Idarnes* (cf. Wiebes, 1968). The middle tibia (Fig. 14) generally has a single large spur, while the rear tibia generally has 2 subequal spurs. The smaller spur may often be confused with part of the setal tract which runs along the length (mesad) of the hind tibia.

The ratio of basitarsal length to that of other tarsomeres proves to be reliable in separating species of *Idarnes.* The basitarsus of the fore leg possesses a mesal setal comb (the number of setae is again not constant) and invariably is shorter than the other basitarsi. The middle basitarsus is usually as long as the remaining tarsomeres, while the hind basitarsus is variable. All tarsomeres are clothed with variable numbers of setae which are not constant within species in number or arrangement.

VI. *Female Abdomen* (Figs. 6, 7, 23, 24)

The propodeum (Figs. 6, 7) is large with spiracles along the antero-lateral margin. Subparallel carinae and costulae are never present, but sculpturing may be developed. The gaster attaches to the propodeum via abdominal segment 2 (petiole), but the attachment is somewhat broad for clistogastrous Hymenoptera. The relatively broad attachment restricts the amount of flexibility possible for the gaster.

The gaster (Fig. 23) is comparatively simple. Its general shape ranges from ovoid with flat sterna to nearly spherical with the sterna convex. Tergal and sternal plates are conspicuous, though the extent of development of the sterna may be somewhat variable. The surface of each tergal sclerite may be lightly shagreened or smooth. These plates may be glabrous or setose along the posterior margin. The posterior margins of terga 2-6 may be either straight *(I. flavicollis)* or strongly sinuate *(I. obtusifoliae).* The latter condition appears to be an adaptation for movement within the fig, since tergal margins which are sinuate permit more flexibility than straight margins. All sterna have posterior margins which are straight; sternal texture varies from coriaceous to smooth. Abdominal pleurites are absent.

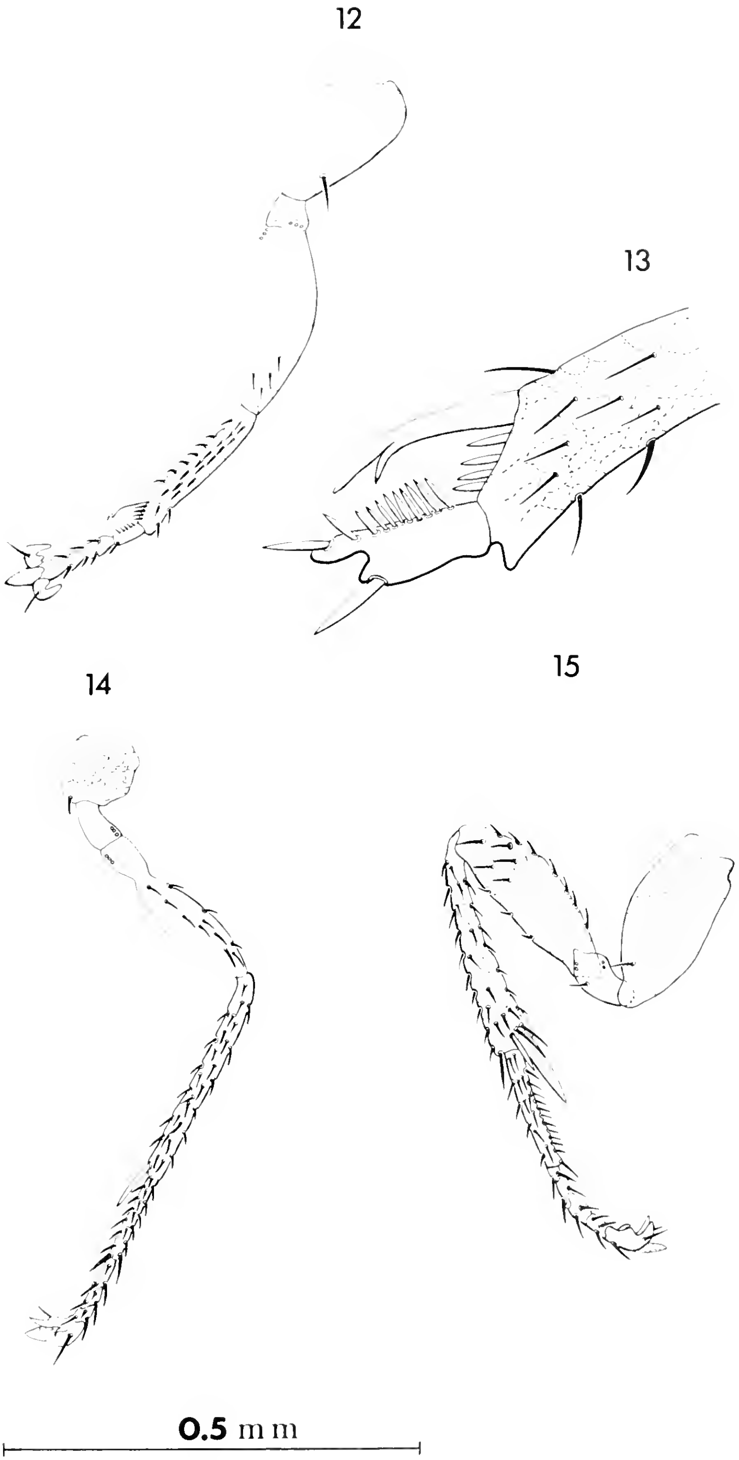
VII. *Female Genitalia* (Figs. 23, 24)

The most conspicuous feature of the female torymid gaster is the ovipositor. Morphologically, the external female genitalia represent lateral projections (gonostyli = sheath) and mesal extensions (gonapophysis = ovipositor) from gonocoxites of the eighth and ninth abdominal segments (seventh and eighth metasomal segments). *Idarnes* conforms to the rest of the Pterygota in that the gonostyli of gonocoxite 8 have been lost. The gonostyli of gonocoxite 9 are equal in length to the ovipositor, serving as a sheath.

In the ovipositor gonapophysis 8 is ventral, while 9 is dorsal. Smith (1969) has observed that gonapophysis 9 is inverted and interconnected with 8 along the long axis. The euventral surface of 9 provides a tongue (rachis) which fits within a trough (aulax) of gonapophysis 8. Smith calls the track locking gonopophysis 8 and 9 together an olistheter. His hypothesis is applicable to *Idarnes* since gonapophyses 8 and 9 are connected along their entire lengths.

In all species of *Idarnes,* the external female genitalia (Fig. 23) are several times longer than the gaster. The long ovipositor is an adaptation for penetrating the fig receptacle and depositing eggs inside the gall flowers. *Idarnes* is not adapted for entering the fig through the ostiole. During oviposition, only the gonapophyses penetrate the receptacle of the fig while the gonostyli diverge perpendicularly to the axis of penetration of the ovipositor. The mesal surface of each gonostylus appears transversely striated and is sparsely setose. The extreme tip of each gonapophysis is serrated to facilitate penetration of the receptacle.

As indicated by Smith (1969), insects retaining both gonapophysis 8 and 9 are



Figs. 12-15. **12,** Right fore leg of *Idarnes* female; **13,** enlarged calcar and strigil of *Idarnes* female fore leg; **14,** right middle leg of *Idarnes* female; **15,** left hind leg of *Idarnes* female.

limited in the distance 8 can be thrust in relation to 9 (for movement of the egg), and little vertical leverage can be applied against the ovipositional surface. In *Idarnes*, the problem is further complicated by the length of the gonapophysis. The former problem has been alleviated to an extent in most Hymenoptera by the development of an articulation of gonocoxite 8 with tergum 9.

The pygostyli (Fig. 24) are well developed and situated at the apex of the gaster. Three apical setae are present and are presumably sensory, indicating to the female precisely how deep the ovipositor has been thrust into the fig.

VIII. *Male Head* (Fig. 16)

All male *Idarnes* exhibit moderately sclerotized, depressed, subtrapezoidal, cranial capsules. The occipital foramen is located on the posterior surface of the head which is prognathous. The mandibles are located on the extreme anterior end of the head and are articulated in a horizontal plane. Dentition is variable among species, but hollow cones (of the type mentioned in females) are always present in the first and second teeth (cf. Figs. 74-82). Immediately posterior to the mandibles and along the lateral margins of the head are the compound eyes, identifiable only by red pigment spots. The ocular suture and ocelli are absent. Mesal to the compound eye, along the base of the mandible, two conspicuous, thick-walled toruli are present.

IX. *Male Antenna* (Fig. 5)

Antennae are 4- or 5-segmented. The basal segment is spoon-shaped and thick-walled, with setae over the dorsal surface and along the lateral margins. The distal surface is mesally concave, allowing the second segment (pedicel) to fit within. The second segment is elongate with thick walls, and often bears thickened setae along the apical end. The third segment is translucent (except *I. bucatoma*), lacks setae or thickened walls, and resembles a collar. Internally, a canal is visible which communicates between segments 2 and 4. In species with 5 segments, a small segment is present immediately distal to the third; species that have 4 antennal segments have this region completely fused with the club. The apical segment represents the fusion of 3 segments into a club. Setae are randomly dispersed over the club, with longitudinal carinae, thick setae, and sensilla on the terminus.

The labiomaxillary complex is completely absent, leading to the conclusion that males do not feed (a supposition supported by the comparatively short life of the male).

X. *Male Mesosoma* (Fig. 17)

The mesosoma is dorso-ventrally compressed, lightly sclerotized, and bears few external surface features. Internally, however, numerous heavily sclerotized ridges are conspicuous. Presumably these are for structural support. The pronotum represents the largest single sclerite of the mesosoma.[7] It is sometimes invested with setae, but more often is glabrous. The posterior margin of the pronotum is indicated by a distinct lateral constriction. Setae are often found in this region of the pronotum (cf. *I. micheneri*). A prescutum is not present in the male, hence the pronotum attaches directly to the mesoscutum.

Since males are apterous, the mesothorax is not fully developed as in the female. The lateral margins of the mesonotum project outward and these margins may or may not be setose. The remainder of the mesonotum is devoid of surface

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[7] Reid (1941) has indicated that with the reduction of wings, the mesonotal region may become reduced; concomitant with this change, other regions of the thorax become enlarged. *Idarnes* conforms to Reid's observations in that the pronotum is much larger in the male than in the female.

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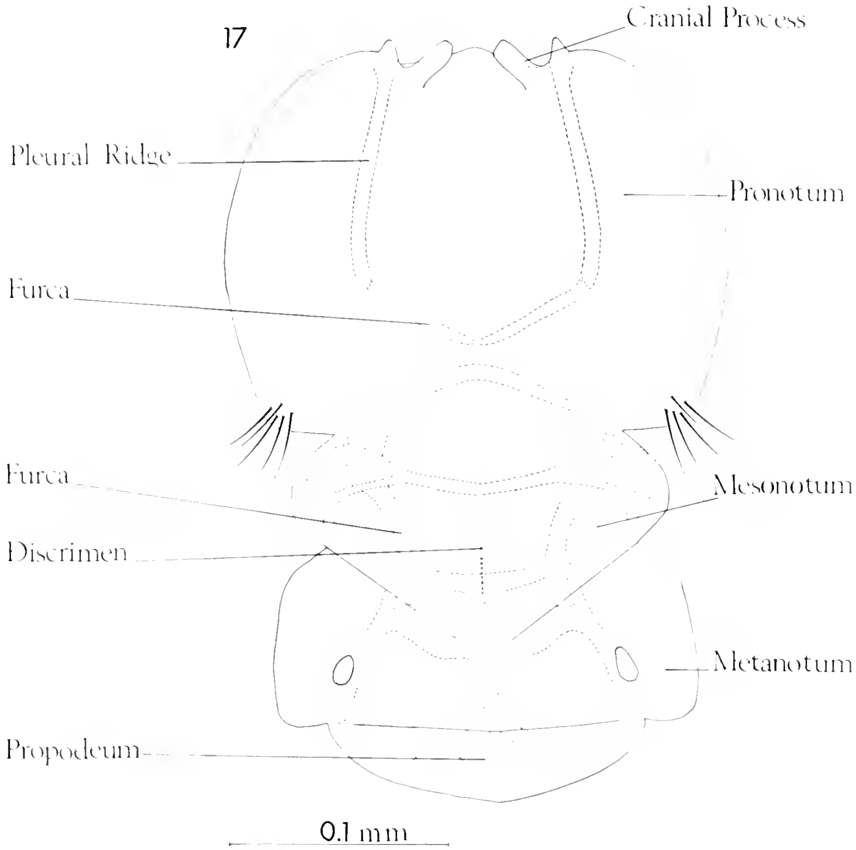


Figs. 16-17. Head (**16**) and mesosoma (**17**) of *Idarnes* male, dorsal aspects.

features: notauli, scapulae, axillae, parascutella, and other features found on the female are absent from the male. Internally, however, an exceedingly complex network of apodemes may be noted. These provide points for muscle attachment which are presumably highly modified. In many species *(I. micheneri)* the mesothoracic discrimen is reduced. However, the internal apodemes (= furca) which it produces seem well developed. The furca of the male projects forward, joining other apodemes (see Fig. 17).

The posterior margin of the metanotum is marked by two very faint lines which project obliquely rearward but do not connect. The metanotum is slightly smaller than the mesonotum and there are numerous internal apodemes evident, but no external surface features are present. The metathoracic discrimen appears to be more fully developed than the corresponding mesothoracic structure. The furca is attached to parallel apodemes that connect to other apodemes of the mesothorax. The propodeal spiracles are located near the antero-dorsal edge of the propodeum.

Immediately beneath the pronotum lies the propleuron which is subdivided into a mesal proepisternum and a lateral proepimeron. Each region is about the same size, being separated by a large, conspicuous, internal pleural ridge. The ridge provides points of attachment for the sternal apophysis (furca) as well as for coxal pro- and remotors. This enlarged apodeme presumably provides strength for the legs, which are used to rip open the gall flowers in which the females develop. Anteriorly, the pleural ridge forms a very large bilobed cranial process. Unlike females, all males exhibit a ball-and-socket type cranial process into which the cranial lobe fits. The position of the paired cranial processes limits movement of the head to dorso-ventral flexion.

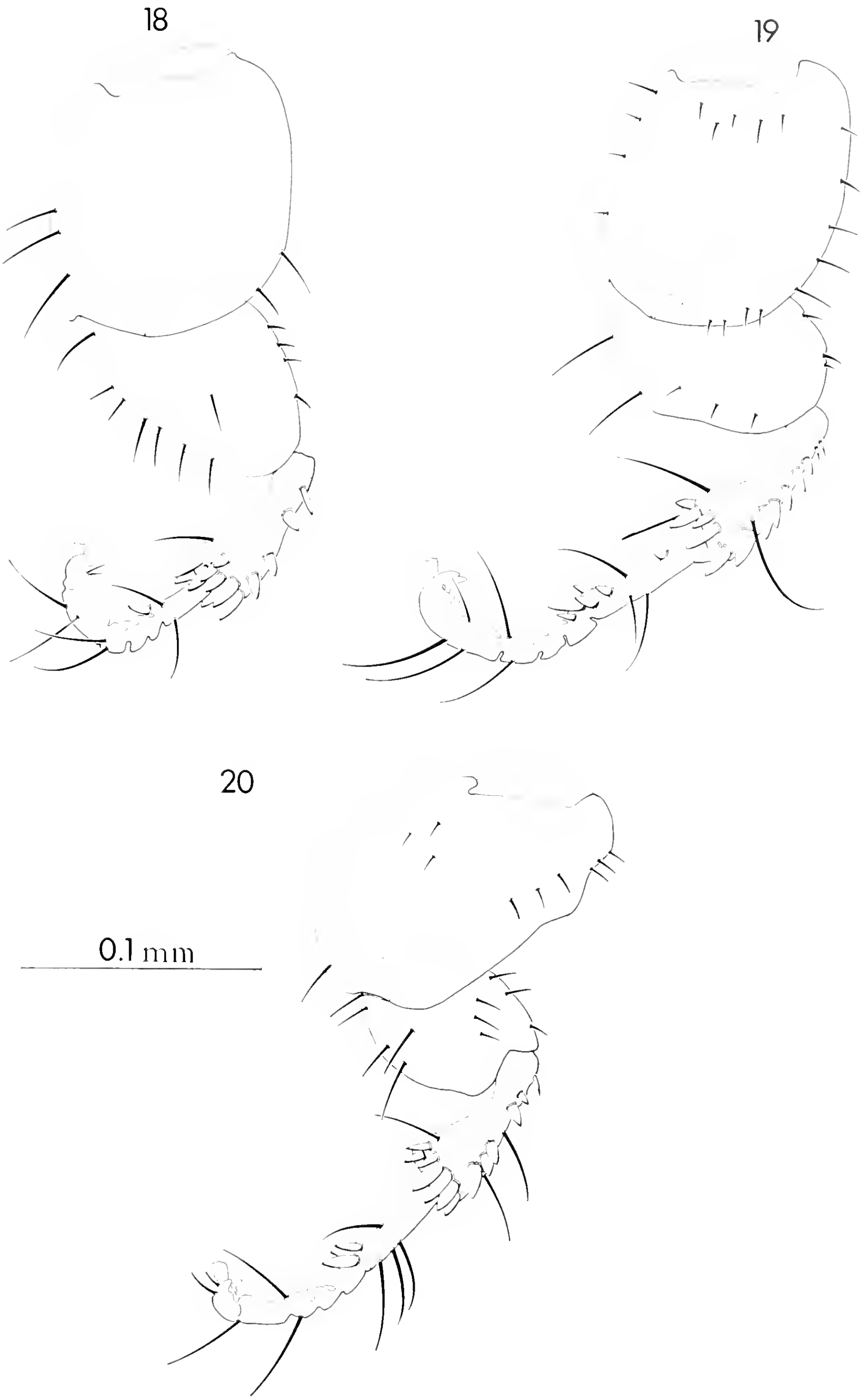
Immediately posterior to the mesally contiguous proepisterna is a small prosternum. It is variable in shape and bears apophyses which serve as endoskeletal support for the prothorax.

XI. *Male Legs* (Figs. 18-20)

The legs of the males are uniform in appearance. In fact, the legs of virtually all male fig-inhabiting wasps are strikingly similar, differing only in number of tarsal segments (cf. work of Joseph, Wiebes, Hill, and Grandi). All coxae are large, disc-like, and flattened dorso-ventrally, with setules and campaniform sensillae scattered over the surfaces. The trochanters are fused to the femora, and each appears as a sclerotized articulatory process on the basal portion of the femur. In some males a faint impression of the surface indicates the separation of the trochanter from the femur. All femora are smaller than the coxae and appear uniformly flat, disc-like, and lightly invested with setules and sensillae. Each femur is articulated in such a way that the dorsal surface may be rotated beneath and pressed against the ventral surface of the coxa. This feature permits the wasp to move among compact flowers within the fig receptacle.

Each tibia is heavily sclerotized, elongate, and invested with heavy spine-like setae along the outer and apical margins. These spines permit the wasp to wedge its body into narrow spaces. The fore tibia (Fig. 18) of the male lacks the strigil found in the female.

Five tarsomeres are found in male *Idarnes* (except in *I. bucatoma* which has 4). The basitarsus is more heavily sclerotized than the remaining segments and often bears apical spines similar to those found on the tibia. The remaining tarsomeres are lightly sclerotized and easily shed; many males collected from receptacles lack tarsomeres 2 to 5 on the fore legs. This probably results from tearing open gall flowers which contain females.



Figs. 18-20. Right fore leg (**18**), middle leg (**19**), and hind leg (**20**) of *Idarnes* male.

XII. *Male Gaster* (Fig. 21)

The gaster is globular and white. There are seven distinct terga and sterna with spiracles only on the seventh (eighth abdominal) tergum. Abdominal segments 8 and 9 are reduced and serve only as the origin of genital components. The posterior tergal margins of most species are sinuous, corresponding to the condition found in some females. Terga may be either glabrous or with distinct transverse rows of setae. The length and number of setae vary from species to species. Sterna are always glabrous.

XIII. *Male Genitalia* (Fig. 22)

The external genitalia of chalcidoids are relatively featureless when compared with other insects. The basic pattern of *Idarnes* is indicated below and except for size, little or no variation exists among species.

The basal ring which supports the external genitalic components is not evident in *Idarnes*. Instead, support seems drawn from aedaegal rods. The parameres are elongate, undivided lobes, united to the aedaegus basally. Volsellae lie between the parameres and the aedaegus.

The free portion of the aedaegus projects between the parameres and bears a pair of lateral rods. Beck (1933) considers these rods gonapophyses of the ninth abdominal sternum in bees; Michener (1944a) calls these "mesal basal processes of the gonocoxopodites"; Snodgrass (1951) calls them "lateral sclerotizations of the aedaegus supporting the aedaegal apodemes."

The volsellae appear unique to the Hymenoptera. Each one consists of an elongate, ventral plate which lies adjacent to the paramere. At the distal end are the digitus and cuspis. These are strongly musculated and form pincers. Snodgrass (1941, 1951) and Michener (1944a) have indicated these are used by most Hymenoptera to grasp and spread female genital membranes during copulation. They presumably function in a similar manner for *Idarnes*.

SYSTEMATICS, MORPHOLOGY, AND DISTRIBUTION OF *FICUS*

The genus *Ficus* (Moraecae) includes over 900 described species placed in four subgenera: *Urostigma* (Banyans), *Pharmacosycea*, *Sycomorus*, and *Ficus* (Croizat, 1952; Corner, 1958, 1965). Of these, only the first two are native in the New World. All members of the genus bear conspicuous hollow syconia (when mature, these are the fig "fruits") which enclose the flowers which line the syconial cavities. Three types of flowers exist: male flowers that contain anthers, female flowers, and gall flowers. Condit and Flanders (1945) indicated that the term gall flower is a misnomer since this floral type represents short-styled female flowers. The term will be retained, however, because it is convenient and well established. The arrangement and location of staminate or pistillate flowers within the syconium provide the foundation of fig classification. In monoecious species, male, female, and gall flowers are randomly interspersed within the same syconium; dioecious species bear male and female flowers on separate trees with male flowers usually arranged in rows around the ostiole, which is the opening into the syconial cavity.

Most species of figs yield 3 or 4 crops per year. A tree will usually have all fruits in the same stage of development, but within a region, trees of the same species may be in different floral stages. This adaptive feature insures pollination by agaonids.

Ficus is absolutely dependent upon insects for pollination; all pollinators belong to the family Agaonidae. Recent studies (Ramírez, 1970a, 1970b; Hill, 1967a, 1967b, 1969; Joseph, 1966; Wiebes, 1964, 1966a) have indicated a high degree of host spe-

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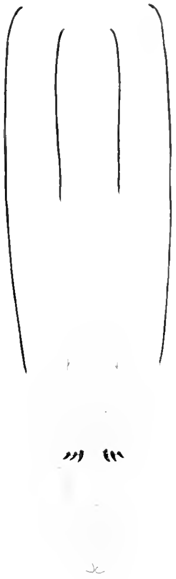

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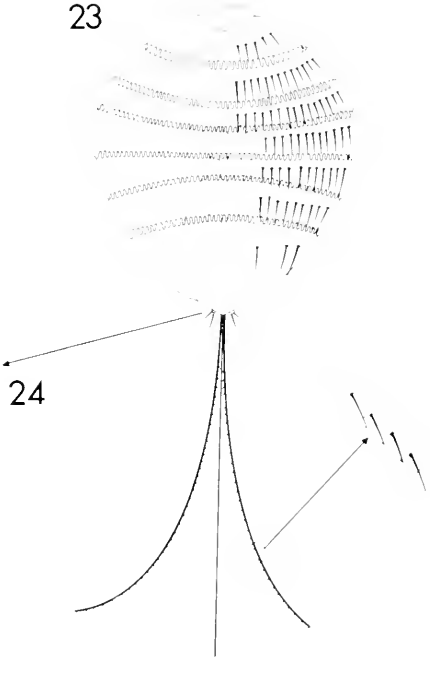

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Figs. 21-24. **21**, Metasoma of *Idarnes* male, dorsal aspect; **22**, genitalia of *Idarnes* male, ventral aspect; **23**, metasoma of *Idarnes* female, dorsal aspect; **24**, pygostyle of *Idarnes* female, ventral aspect.

cificity between pollinating wasp and tree.

The life history and pollination ecology of numerous agaonids have been established (Baker, 1913; Galil and Eisikowitch, 1968; Ramírez, 1969; Williams, 1928; Eisen, 1896; Carmin and Scheinkin, 1931; Cunningham, 1889). Within a mature syconium the insects develop inside the gall flowers. The wingless males emerge first and move around within the syconium in search of females of the same species. The male locates a gall flower containing a female, gnaws a hole in the gall, and mates with the immobile female. Emergence from the syconium is achieved by the males tunneling through the fig wall or ostiolar scales. Several males may work in the tunnel simultaneously, and if the tunnel is not completed, all the inhabitants of a syconium will die.

The winged females, before leaving their natal fig, gather pollen from the male flowers which are ripe at this time. Some female pollinators collect pollen in sternal or coxal corbiculae. Upon emergence from the fig, the females fly to a tree of the same species in the proper floral phase and enter the figs via the ostiole.

Once inside the fig, the agaonid wanders about, pollinating long-styled female flowers; subsequently, she oviposits in the short-styled gall flowers. Female pollinators always die inside the receptacle. The young of the next generation mature during the male phase of the same fig.

THE PARASITES IN FLORAL ECOLOGY

Many non-pollinating hymenopterous inhabitants of figs, members of the families Torymidae and Eurytomidae, have been described. The relationship between *Idarnes* and the pollinating agaonids has not been completely established. Kattamathiathu (= Joseph) (1955) has indicated that *Philotrypesis caricae,* another torymid fig inhabitant, develops "cleptoparasitically" at the expense of *Blastophaga psenes,* pollinator of the edible fig, *Ficus (Ficus) caricae. P. caricae* lacks the so-called "poison glands" which Grandi (1930, 1961) indicated are necessary for the preparation of gall flower endosperm. *B. psenes* presumably induces gall formation (hence "gall flowers") when its eggs are deposited inside a short-styled flower. Later, the parasite lays its eggs in the same flower and both larvae begin to develop. Both *Blastophaga* and *Philotrypesis* develop through the second instar at which time the parasite kills the pollinator but does not feed upon it.

Concerning the development of *Idarnes,* the following observations can be made:

Examination of preserved syconia of *Urostigma* figs reveals that the parasites also develop within short-styled flowers. Each flower appears to contain only one pollinator or parasite. Wiebes (1968) has shown that in rare instances two wasps may develop within the same flower. A similar observation has not been made for *Idarnes.* It has not been established if the male *Idarnes* mates with the female before or after her emergence from the gall flower or if the male parasites aid the male agaonids in digging an exit tunnel through the wall of the receptacle. One interesting feature of the material examined appears to be the constancy of the tunnel site. Each species of fig appears to have a unique site for the emergence hole.

Joseph (1956) has indicated that female torymid parasites will live up to 35 days in the laboratory. *Idarnes* females have been kept alive at high humidity (+70%) for 9 days without feeding.

Observations of *I. oscrocata* have revealed that newly emerged females do not immediately oviposit within receptacles of proper age. Instead, they congregate on the undersides of leaves and on branches of the host tree. Branches and leaves having quiescent *Idarnes* also bear fruits into which pollinating agaonids are burrowing. If the hypothesis of Grandi regarding atrophied poison glands is correct, the torymids would delay oviposition until after pollination and egg laying by the agaonids.

Females of *Idarnes* do not enter the fig through the ostiole. Instead, they use their long ovipositors to penetrate the receptacle of the fig. Initially the female moves rapidly over the receptacle, but eventually she slows down. Movement over the syconium continues for a few minutes to half an hour. Several females may be noted on one receptacle. Upon selection of a suitable place for oviposition, the wasp moves forward slightly, raises the gaster and elevates the body by extending the legs. After the tip of the ovipositor has been inserted into the receptacle surface, the wasp moves the body on an anterior-posterior axis, forcing the ovipositor deeper into the receptacle. The wasp moves rearward as the ovipositor penetrates more deeply. Occasionally, females have been observed to discontinue drilling and search for another oviposition site on the same fig. As the ovipositor penetrates the receptacle, the gonostyli project rearward or postero-laterally. After laying is completed, the female pulls herself forward, extracting the ovipositor.

Developmental time of the parasite varies with the species but is approximately the same as that of the agaonid pollinators. Ramírez (1970b) has observed that for most New World species of *Ficus*, almost every syconium on a tree is pollinated during a single day. Oviposition by *Idarnes* is not as restricted since many parasites may be collected from trees several days after oviposition by the pollinators.

HOST SPECIFICITY AND *IDARNES*

The following data indicate that *Idarnes* develops exclusively within *Urostigma* figs: (1) In 17 collections of figs of the subgenus *Pharmacosycea* made throughout México during two successive years, only parasites of the genus *Critogaster* emerged from receptacles or were found ovipositing into these figs. (2) In 56 collections of *Urostigma* figs made in México and Central America, 3 genera of parasites were collected: *Heterandrium*, *Physothorax*, and *Idarnes*. *Idarnes* was always the most abundant. (3) At two localities (Izucar de Matamoros, Puebla, México and 12 miles west of Veracruz, México) species of *Urostigma* and *Pharmacosycea* were growing sympatrically and wasps were emerging from each fig species. *Idarnes* aggregated on *Urostigma* and *Critogaster* aggregated on *Pharmacosycea*, even though the trees were separated by only 15 to 20 meters. In personal communications, Ramírez has indicated his finding of *Idarnes* only in figs of the subgenus *Urostigma*, not only in México and Central America but also in Venezuela.

Host specificity is also indicated by a study of ovipositor lengths. Ovipositors must be long enough to penetrate the syconial walls. Informal study, not supported by data on wall thicknesses, shows that species of *Idarnes* with long ovipositors inhabit figs with thick walls and those with short ovipositors inhabit small figs with thin walls. Obviously, the *Idarnes* with short ovipositor could not successfully infest figs with thick walls.

Recent authors (cf. Wiebes, Ramírez, Hill, and Joseph, loc. cit.) have indicated a high level of host specificity between pollinator and species of *Ficus*. Although the proof is not conclusive, a similar tendency exists between *Idarnes* and *Ficus*. Ten different species of *Idarnes* have been collected from 10 different species of fig. Moreover, where collections were made in different areas from the same species of fig, the wasps in all instances were presumably conspecific. At least they were morphologically more similar to one another than to different species of *Idarnes* collected on different fig species in the same or adjacent areas.

It is entirely unknown whether host specificity is based on host fig alone or also on the pollinator species. Table 1 lists the known *Urostigma* pollinators and their parasites.

REDEFINITION OF *IDARNES*

Idarnes Walker, 1843

Idarnes Walker, 1843, Ann. Mag. Nat. Hist. 12:47, ♀.
Type species: *Idarnes carme* Walker (monotypic).
Tetragonaspis Mayr, 1885, Verh. Zool. Bot. Gesell. Wien 35.205, ♀.
Type species: *Tetragonaspis flavicollis* Mayr.
Ganosoma Mayr, 1885, Verh. Zool. Bot. Gesell. Wien 35.204, ♂.
Type species: *Ganosoma robustum* Mayr.
Idarnes Ashmead, 1904, Mem. Carnegie Mus. 1:238-239; 395.

Female—Head, mesosoma metallic green; gaster tan with metallic luster; compound eye asetose, red; scape, pedicel amber, remaining segments darker. Head sculptured; antenna inserted below transverse middle line of compound eyes; scrobe cavity extending to anterior median ocellus or vertex; inter-antennal ridge present, but variable. Antenna 12-segmented with 1 annulus or 13-segmented with 2 annuli; flagellomeres carinate and setose; club variable, terminal protuberance present. Mandible bi- or tridentate; stipes with basal acuminate seta; maxillary palpus 2-segmented, segment 1 with disc-shaped sensillum along distal margin, terminal segment with proximal acuminate seta and distal margin excindate; labial palp 1-segmented, ligula with 2 to 5 sensory pegs; galea with numerous acuminate setae.

Pronotum sculptured, collar-like; mesoscutum sculptured, separated from scapula by well developed notaulix; mesoscutellum quadrate; forewing with parastigmal notch sensillate; stigma sensillate; adstigmal setae present; setal tracts conspicuous; hindwing with submarginal vein only. Fore leg with bifurcate calcar; basitarsus with conspicuous strigil; middle leg with coxa small, globular; middle femur slender, with 1 or 2 subapical spurs; hind coxa 3 times as large as fore coxa; hind femur setose, sculptured; hind tibia with 1 or 2 subapical spurs. Proepisterna sculptured,

Table 1. Neotropical *Urostigma* figs, pollinators *(Blastophaga)*, and their known *Idarnes* parasites.

Tree	Pollinator	Parasite	Collections	Known distribution
Ficus aurea Nuttall	*B. mexicana* Grandi	*I. carme* Walker	2	West Indies, Florida
F. cervantesiana Standley		*I. bucatoma* sp. nov.	1	Costa Rica
F. colubrinae Standley	*B. orozcoi* Ramírez	*I. galbina* sp. nov.	1	Costa Rica
F. goldmanii Standley		*I. oscrocata* sp. nov.	2	Mexico, Costa Rica
F. hemsleyana Standley	*B. tonduzi* Grandi	*I. barbigera* sp. nov.	2	Mexico, Costa Rica
F. isophlebia Standley	*B. urbanae* Ramírez	*I. micheneri* sp. nov.	1	Costa Rica
F. jimenezii Standley	*B. jimenezii* Grandi	*I. jimenezi* sp. nov.	1	Costa Rica
F. lapithifolia Liebmann	*B. aguilari* Grandi	*I. simus* sp. nov.	1	Costa Rica
F. obtusifolia H. B. K.	*B. hoffmeyeri* Grandi	*I. obtusifoliae* sp. nov.	3	Mexico, Costa Rica
F. oerstediana Miguel	*B. standleyi* Ramírez	*I. camini* sp. nov.	2	Mexico, Costa Rica
F. tuerckheimii Standley	*B. mariae* Ramírez *B. carlosi* Ramírez	*I. ashlocki* sp. nov.	4	Mexico, Costa Rica
F. velutina Willd.	*B. torresi* Grandi	*I. flavicollis* Mayr	1	Brazil, Costa Rica

prepectus not completely separated from mesepisternum; discrimen well developed; anapleurite present.

Male—Head, mesosoma tan, depressed; gaster white, globular; compound eye reduced to pigmented spot or absent; ocelli absent; antenna 4- or 5-segmented, basal segment with thick walls, segment 3 translucent; mandible bi- or tridentate, often scythe-like; labiomaxillary complex absent.

Pronotum depressed, larger than remaining thoracic components; wings absent; coxae, femora disc-shaped, dorsoventrally flattened; tibiae with large conspicuous spines; basitarsi with apical spurs.

Propodeum reduced, demarcated from metanotum by faint, transverse line, spiracles along antero-lateral margin; gaster with tergites setose; posterior tergal margin often sinuate.

KEY TO SOME SPECIES OF *IDARNES*

1. Head and mesosoma bronze; gaster tan with metallic luster; antenna 12- or 13-segmented; 3 ocelli and compound eyes present; wings present; ovipositor longer than remainder of body .... Females 2
– Head and mesosoma tan; gaster white; antenna with 4 or 5 segments; ocelli, compound eyes, and wings absent .... Males 13
2. Mandible tridentate; clypeal margin bilobed; antenna 13-segmented with 2 ring segments; mesoscutellum lightly shagreened or smooth; posterior tergal margin straight 3
– Mandible bidentate (except *I. obtusifoliae*); clypeal margin variable; antenna 12-segmented with single ring segment (except *I. simus*); mesoscutellar sculpture variable; posterior tergal margin strongly sinuate 6
3. Head prognathous; antennal scape and pedicel strongly setose (Fig. 26); pedicel twice as long as wide; flagellar setae not verticillate; club compact; pronotum as large as mesoscutum and scapulae combined; adstigmal setae of forewing forming a dense cluster (Fig. 54) .... *I. bucatoma*
– Head hypognathous; antennal scape and pedicel bearing few setae; pedicel not elongate; flagellomeres with distinct whorls of setae basally; club not compact; pronotum smaller than mesoscutum and scapulae combined; forewing with fewer adstigmal setae 4
4. Vertex of head flat; frons weakly rugose .... *I. camini*
– Vertex of head convex; frons smooth 5
5. Toruli just below middle line of compound eyes; scrobe shallow, smooth; clypeus bilobed; ovipositor 4.5 times gaster length; gonostyli bearing only a few small setae .... *I. flavicollis*
– Toruli at lower margin of compound eyes; scrobe cavity deep, rugose; clypeus trilobed; ovipositor 3.5 times gaster length; gonostyli bearing large conspicuous setae along mesal surface .... *I. micheneri*
6. Antennal flagellomeres, 2 times as long as wide (Fig. 34); ovipositor 5 times gaster length .... *I. simus*
– Flagellomeres less than 2 times as long as wide; ovipositor less than 5 times gaster length 7
7. Antenna inserted at or just below middle line of compound eyes; mesoscutellum lacunose or smooth; stigma not tumid 8
– Antenna inserted at level of ventral margin of compound eyes; mesoscutellum smooth; stigma tumid 9
8. Interantennal ridge acute; marginal tract not extending to postmarginal vein (Fig. 56); prepectus laterally favose, mesally rugose; ovipositor 4 times gaster length; gonostylar setae minute .... *I. barbigera*
– Interantennal ridge flat; marginal tract reaching postmarginal vein (Fig. 50); prepectus uniformly rugose; ovipositor 2.5 times gaster length; gonostylar setae conspicuous .... *I. galbina*
9. Anal tract absent; ovipositor at least 3.0 times gaster length 10
– Anal tract present (Fig. 59); ovipositor 2.5 times gaster length .... *I. jimenezi*
10. Scape extending to vertex; frons smooth; prepectus favose, pattern fading mesally, mesepisternum laterally rugose, shagreened at discrimen; ovipositor 6 times gaster length;

gonostylar setae minute .... *I. oscrocata*

– Scape not reaching vertex; frons not smooth (except *I. carme*); ovipositor several times more or less than 6 times gaster length 11

11\. Vertex sinuous as seen from front; frons, prepectus favose; mesepisternum laterally favose, smooth at discrimen; ovipositor 8 times gaster length .... *I. obtusifoliae*

– Vertex flat; frons not lacunose; prepectus rugose; mesepisternum laterally rugose; ovipositor considerably less than 8 times gaster length 12

12\. Frons favose; terga smooth; ovipositor 4 times gaster length ...... *I. ashlocki*

– Frons smooth; gastral terga shagreened; ovipositor 3 times gaster length .... *I. carme*

13\. Antenna 4-segmented (Fig. 43), segment 3 not translucent; legs with 4 tarsomeres (Figs. 116-118). .. *I. bucatoma*

– Antenna 4- or 5-segmented, segment 3 translucent; legs with 5 tarsomeres 14

14\. Antenna 4-segmented with no constriction at base of club 15

– Antenna 5-segmented or 4-segmented with a constriction at base of club 18

15\. Mandible tridentate, not scythe-like; posterior tergal margin sinuate 16

– Mandible bidentate, occasionally scythe-like; posterior tergal margin straight or sinuate 17

16\. Antenna 4-segmented (Fig. 46), flagellomeres moderately setose; middle and hind tibiae with long apical spurs (Figs. 105, 106) .... *I. micheneri*

– Antenna 4-segmented, flagellomeres sparsely setose (Fig. 37); tibiae without long apical spurs (Figs. 86-88) .... *I. galbina*

17\. Hind tibia with large apical spur; middle and hind basitarsi spinose, elongate (Figs. 99, 100); gastral sterna with minute setae .... *I. camini*

– Tibiae with apical spurs of intermediate length; basitarsi with few apical spines (Figs. 110-112) .... *I. jimenezi*

18\. Tibiae without large spurs 19

– Middle and/or hind tibiae with long apical spurs 20

19\. Hind basitarsus lacking apical spines, nearly as long as tibia (Fig. 115); clypeal margin with 2 small mesal spines .... *I. oscrocata*

– Hind basitarsus with apical spines, less than half as long as tibia (Fig. 91); clypeal margin lacking mesal spines .... *I. simus*

20\. Mandible tridentate (Fig. 75) .... *I. flavicollis*

– Mandible bidentate 21

21\. Mandible scythe-like; posterior tergal margin straight 22

– Mandible not scythe-like; posterior tergal margin sinuate 23

22\. Head with small setae uniformly distributed on dorsal surface; clypeal margin straight; middle and hind tibiae with apical spurs (Figs. 108, 109) .... *I. barbigera*

– Dorsal surface of head sparsely setose; clypeal margin concave; tibiae lacking long apical spurs (Figs. 95-97) .... *I. carme*

23\. Middle tibia with long apical spur (Fig. 102) .... *I. obtusifoliae*

– Middle tibia without long apical spur (Fig. 84) .... *I. ashlocki*

SYSTEMATIC TREATMENT

All of the named species that fall in *Idarnes* as here restricted are listed in this section. Locations of type material and voucher specimens for newly described species or species treated in detail appear in Table 2. Etymological origins of new names are given in Table 3.

Characters are sequentially numbered in each description for convenient comparison among descriptions. For example, mandibular dentition may be ascertained for females of all species by looking for number 21 in each description.

Idarnes ashlocki, new species

Female—Body length 1.5 mm, ovipositor 4.0 mm long. (1, 2) Head, mesosoma metallic mossy green; (3) gaster bronze with metallic luster; (4) scape, pedicel smoky brown, remaining segments ebony; (5) legs uniformly tawny; (6) prosternum, mesosternum metallic green.

(7) Head hypognathous, in frontal aspect wider than long; compound eye weakly protuberant; (8) entire head with

TABLE 2. Disposition of types and voucher specimens of *Idarnes*.[a]

	K.U.	U.S.N.M.N.H.	Pret.	Lenin.	B.M.	Leiden	Canberra	Ramírez
I. ashlocki	♀ H ♂ A	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P
I. barbigera	♀ H ♂ A	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P
I. bucatoma	♀ H ♂ A	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P
I. camini	♀ H ♂ A	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P
I. carme	1 ♀ 1 ♂	♀ Neo 1 ♂	1 ♀	1 ♀	1 ♀	1 ♀	1 ♀	1 ♀
I. flavicollis	1 ♀ 1 ♂	1 ♀	1 ♀	1 ♀	1 ♀	1 ♀	1 ♀	1 ♀
I. galbina	♀ H ♂ A	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P
I. jimenezi	♀ H ♂ A	1 ♀ P 1 ♂	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P
I. micheneri	♀ H ♂ A	1 ♀ P 1 ♂	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P
I. obtusifoliae	♀ H ♂ A	1 ♀ P 1 ♂	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P
I. oscrocata	♀ H ♂ A	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P
I. simus	♀ H ♂ A	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P	1 ♀ P

[a] Abbreviations used. Names in parentheses refer to individual to whom material was sent.
K.U. = Snow Entomological Museum, University of Kansas, Lawrence, Kansas (G. W. Byers).
U.S.N.M.N.H. = U.S. National Museum of Natural History, Washington, D.C. (B. D. Burks).
Pret. = Plant Protection Research Institute, Pretoria, Republic of South Africa (D. P. Annecke).
Lenin. = Zoological Institute, Academy of Science, Leningrad, U.S.S.R. (V. Trjapitzin).
B. M. = British Museum (Natural History), England (R. D. Eady).
Leiden = Rijksuniversiteit, Leiden, Netherlands (J. T. Wiebes).
Canberra = C.S.I.R.O., Canberra, Australia (E. Riek).
Ramírez = W. Ramírez.
H = Holotype; P = Paratype; A = Allotype; Neo = Neotype.

TABLE 3. Etymological origin of new *Idarnes* species names.

Epithet	Origin
I. ashlocki	Patronym of P. D. Ashlock, Hemipterist
I. barbigera	barbigera = bearded
I. bucatoma	bu = large; catoma = shoulders
I. camini	Patronym of J. H. Camin, Acarologist
I. galbina	galbina = jaundiced
I. jimenezi	*Ficus jimenezii*
I. micheneri	Patronym of C. D. Michener, Hymenopterist
I. obtusifoliae	*Ficus obtusifolia*
I. oscrocata	os = mouth; crocatus = saffron yellow
I. simus	simus = flat nosed

bold, uniform favose sculpture; setae sparse; (9) margin of vertex flat; (10) antenna inserted at ventral margin of compound eye; (11) toruli separated by twice diameter of torulus; (12) scrobe with 2 favose, shallow channels converging at anterior ocellus; (13) interantennal ridge not strongly convex. (14) Antenna 12-segmented (Fig. 28); (15) scape shagreened, setose, extending to median ocellus; (16) pedicel shagreened, setose; (17) flagellomeres as wide as long, verticillate; setae inflexible; setae and carinae equal in number; (18) club weak; terminal protuberance inconspicuous. (19) Frons favose, asetose; (20) clypeal margin weakly bilobed; (21) mandible (Fig. 63) tridentate, tooth margin sharply incised. (22) Maxillary palpus 2-segmented, palpifer not evident; (23) palpiger not evident; (24) ligula with 2 sensory pegs; (25) paraglossa enveloping 3/4 of ligular margin; (26) galea strongly setose.

(27) Pronotum favose along posterodorsal margin, remainder shagreened; (28, 29, 30, 31) mesoscutum, scapula, parascutellum and axilla favose; (32) mesoscutellum lacunose; (33) meson of metanotum favose, lateron smooth. (34) Forewing (Fig. 51) with submarginal vein 3.5 times as long as marginal vein; postmarginal vein 2 times stigmal vein; (35) stigma weakly tumid; (36) 2 adstigmal setae; (37) marginal tract ending well before postmarginal vein; R_1 tract ending before terminus of marginal tract; submarginal tract reaching stigma; medial tract present; discal, anal tracts absent. (38) Fore and hind coxae lightly sculptured, middle coxa smooth; (39) femora sculptured; (40) middle and hind tibiae each with single large apical spur; (41) fore basitarsus as long as tarsomere 2; middle basitarsus as long as tarsomeres 2-5; hind basitarsus as long as tarsomeres 2-4. (42) Proepisternum bronze, lightly sculptured, smaller than fore coxa, bearing single cranial process; (43) prosternum triangular, lightly shagreened; discrimen short; (44) prepectus rugose; (45) mesepisternum laterally rugose, pattern becoming shagreened at discrimen; (46) mesepimeron uniformly rugose; (47) anapleurite lightly shagreened.

(48) Propodeum 3.5 times as wide as long; meson favose, with pattern laterally evanescent; (49) gaster larger than head and mesosoma; (51) sterna glabrous; (52) ovipositor and gonostylus 4 times gastral length; (53) gonostylar setae short.

Male—Body length 2.0 mm. (54, 55) Head, mesosoma tan; mandible dark red; (56) gaster milky white; (57) third antennal segment translucent, remaining segments tan; (58) leg segments concolorous with mesosoma.

(59) Head with lateral margin bearing short setae; (60) mandible (Fig. 71) bidentate, scythe-like; tooth margin not sharply incised; (61) antenna (Fig. 39) 4-segmented, basal portion of segment 4 constricted, nearly forming a distinct segment; (62) all legs with 5 tarsomeres (Figs. 83-85); hind tibia with long apical spur, basitarsi elongate. (63) Gastral terga smooth, with long setae; posterior tergal margins sinuate; (64) sterna smooth, asetose.

Material—Described from 16 females and 3 males collected at San Rafael, Heredia, Costa Rica on 23 May 1964 by William Ramírez; 14 females and 2 males collected 7 miles northeast of Coscomatepec, Veracruz, México on 8 August 1969 by the author and Ramírez; 12 females and 1 male collected 10 August 1969 at Córdoba, Veracruz, México by Ramírez; and 16 females and 4 males collected by the author at Campeche, Campeche, México on 7 July 1970. In each instance the host fig was *Ficus tuerckheimii* Standley.

Ficus tuerckheimii is distributed throughout Central America and México. Standley (1917) indicates it is closely related to *F. jimenezii,* but differs in leaf shape and venation.

Holotype—A dissected female mounted in Hoyer's medium on 2 slides, each with 3 coverslips. Both labels are inscribed: "*Idarnes ashlocki.* San Rafael, Heredia, Costa Rica. 23 May 1964, leg. W. Ramírez, ex. *F. tuerckheimii.* HOLOTYPE." *Allotype*—One dissected male mounted in Hoyer's medium on 1 slide under 3 coverslips. The label bears the same data as indicated above. *Paratypes*—Nine females mounted in the manner indicated for the holotype above with a simliar label inscription.

Variation—Idarnes ashlocki females are quite constant in appearance. Some variation in the vertex shape (9), length of setal tracts in the wings (37), number of adstigmal setae (36), and shape of the prosternum (27) have been noted. Males from the northern limit of the species may have scythe-like mandibles (60).

Comparative Comments—I. ashlocki seems most nearly related to *I. obtusifoliae,* but may be distinguished from this and other species of *Idarnes* on the basis of the following characters: females with favose sculpture on head (8) and mesosoma (28, 29, 30, 31), antenna inserted at ventral margin of compound eye (10), wings with short marginal and R_1 vein tracts (37), and mesepimeron rugose (46).

Idarnes barbigera, new species

Female—Body length 1.8 mm, ovipositor 4.0 mm long. (1, 2) Head and mesosoma brown with tawny luster; margin of oral fossa light; (3) gaster chestnut brown; (4) scape tan, remaining segments rust red; (5) fore coxa basally tan, remaining segments dull translucent white; (6) prosternum translucent; mesosternum concolorous with gastral sterna.

(7) Head hypognathous, in frontal aspect wider than long; compound eye protuberant; (8) gena setose, smooth; face rugose with pattern progressively bolder dorsally, vertex favose; (9) vertex sinuate; (10) antenna inserted just below middle line of compound eye; antennifer large; (11) toruli separated by single torulus diameter; (12) scrobe deep, lacunose, extending to anterior ocellus; (13) interantennal ridge acute. (14) Antenna (Fig. 25) 12-segmented; (15) scape with minute setae along dorsal and mesal surface extending to vertex; (16) pedicel elongate, smooth, with few setae; (17) flagellomeres slightly longer than wide, verticillate, setae inflexible; setae more numerous than carinae; (18) club terminal protuberance weakly formed. (19) Frons glabrous with marginal setae; (20) clypeal margin with single lobe; (21) mandible bidentate (Fig. 61), tooth margin sharply incised. (22) Maxillary palpus 2-segmented; palpifer not evident; (23) palpiger not evident; (24) ligula bearing 4 sensory pegs; (25) paraglossa enveloping 5/6 of ligular margin; (26) galea with moderate number of acuminate setae.

(27) Pronotum postero-dorsally favose, remainder smooth; (28, 29, 30, 31) mesoscutum, scapula, axilla, parascutellum favose; (32) mesoscutellum smooth; (33) meson of metanotum lacunose, lateron smooth. (34) Forewing (Fig. 56) with submarginal vein 3 times as long as marginal vein; postmarginal vein 2 times stigmal vein; (35) stigma weakly tumid, sensillae small; (36) 2 short adstigmal setae; (37) marginal tract ending well before postmarginal vein; R_1 tract absent; submarginal tract reaching stigma; discal tract present; median and anal tracts absent. (38) Hind coxa sculptured, remaining coxae smooth; (39) middle femur with setal tract; (40) middle tibia with single tibial spur; hind tibia with 2 setal tracts, 2 subequal apical spurs; (41) fore basitarsus as long as tarsomeres 2-4; middle basitarsus as long as remaining tarsomeres; hind basitarsus as long as tarsomeres 2-4. (42) Proepisternum smaller

than fore coxa, shagreened, with single large cranial process; (43) prosternum semicircular, glabrous; discrimen extending half length of structure; (44) prepectus laterally favose, pattern rugose mesally; (45) mesepisternum rugose laterally, pattern fading mesally, glabrous at discrimen; (46) mesepimeron lacunose; (47) anapleurite lacunose.

(48) Propodeum 4 times as wide as long, smooth, median longitudinal carina absent; (49) gaster ovoid, slightly larger than mesosoma; (50) tergum shagreened, pattern lightly incised; posterior tergal margins sinuate; (51) strena coriaceous, weakly setose; (52) ovipositor and gonostylus 4 times gaster length; (53) gonostylar setae along mesal surfaces minute.

Male—Body length 1.2 mm. (54, 55) Head, mesosoma tan; (56) gaster milky white; (57) antennal scape, base of segment 2 amber, club pale; (58) coxae, femora concolorous with mesosoma, tibiae marginally red.

(59) Head with small setae uniformly distributed over dorsal surface; clypeal margin straight, bearing 2 moderately sized acuminate setae; (60) mandible (Fig. 80) scythe-like, bidentate; (61) antenna (Fig. 44) 4-segmented; club spindle-shaped; (62) legs with 5-segmented tarsi; tibio-tarsal complex (Figs. 107-109) with middle and hind basitarsi elongate; (63) terga asetose, posterior tergal margins straight; (64) sterna smooth.

Material—Described from 16 females and 4 males collected at Sarchi Garcia, Alajuela, Costa Rica on 17 June 1964 from *Ficus hemsleyana* by William Ramírez, and 241 females collected by the author at 4 miles south of Rio Hondo, Oaxaca, México on 6 July 1970 from *F. hemsleyana*.

Condit (1969) indicates *F. hemsleyana* is synonymous with *F. citrifolia*. Although Standley (1917) did not have material available from México, the voucher specimen collected in 1970 agrees with Standley's description. DeWolf (1960) lists 29 synonomous names for *F. citrifolia*, among which is *F. hemsleyana*. He cites the distribution as Florida to Paraguay. Among the major synonyms are *F. laevigata* Vahl, *F. judunculata* Dryand, *F. pyrifolia* Desfontaines and *F. brevifolia* Nuttall. Collections of *Idarnes* and *Blastophaga* from these figs should be compared with the type description to examine host specificity and the validity of DeWolf's synonymy.

Holotype—A dissected female mounted in Hoyer's medium on 2 slides each bearing 3 coverslips. Both labels are inscribed: "*Idarnes barbigera*. Sarchi Garcia, Costa Rica. 17 June 1964, leg. W. Ramírez, ex. *Ficus hemsleyana*. HOLOTYPE." *Allotype*—A single dissected male mounted in Hoyer's medium on 1 slide with the parts under 3 coverslips. The inscription on the label is the same as above. *Paratypes*—Eight females are balsam-mounted in the manner indicated above, with the same label inscription, and the parts of each insect are on 1 slide.

Variation—All females from México have strongly sculptured fore coxae (38), unlike those from Costa Rica. Individuals collected in México are virtually identical in other features to those collected in Costa Rica.

Comparative Comments—Females may be recognized by the following key characters: gena smooth and setose (9), frons glabrous with marginal setae (19), smooth mesoscutellum (32), cranial process of proepisternum very large (42), and mesepimeron lacunose (46). Males are recognized by the short setae on the dorsal surface of the head (59), scythe-like, bidentate mandible (60), 4-segmented antenna (61), and asetose terga (63).

Idarnes brevicolis (Mayr)

Tetragonaspis brevicolis Mayr, 1885, Verh. Zool. Bot. Gesell. Wien 35:209, ♀.

Mayr described *I. brevicolis* from the female only. I have not examined the type material but it was collected in Brazil. It is considered a species of *Idarnes* as here restricted.

Idarnes bucatoma, new species

Female—Body length 3.4 mm, ovipositor 3.7 mm long. (1, 2) Head and mesosoma brassy green; (3) gaster reddish dark brown with iridescent sheen; (4) scape, pedicel tan with remaining segments darker; (5) coxae concolorous with head and mesosoma; fore femur entirely dark brown, hind femur apically dark brown; remaining segments tan; (6) prosternum, mesosternum concolorous with notum.

(7) Head subprognathous, in frontal aspect longer than wide; compound eye not protuberant, or weakly so; (8) face and gena rugose, asetose; (9) vertex weakly sinuate seen from front; (10) antenna inserted at level of lower third of compound eye; (11) toruli nearly contiguous; (12) scrobe evanescent, lightly shagreened, extending to anterior ocellus; (13) interantennal ridge acute, short. (14) Antenna 13-segmented (Fig. 26); (15) scape elongate, setose, reaching anterior ocellus; (16) pedicel elongate, setose; (17) flagellar segments as long as wide, bearing more carinae than setae; setae irregularly dispersed, not verticillate; each seta with a distinct socket; (18) club distinct; terminal protuberance conspicuous. (19) Frons smooth; (20) clypeal margin trilobed, mesal lobe small; (21) mandible tridentate (Fig. 64), tooth margin sharply incised. (22) Maxillary palpus 2-segmented; palpifer evident; (23) palpiger not evident; (24) ligula with 4 sensory pegs; (25) paraglossa enveloping basal 3/4 of ligular margin; (26) galea with numerous acuminate setae.

(27) Pronotum as large as mesoscutum and scapulae combined, shagreened, sparsely setose; (28, 29) mesoscutum, scapula rugose; (30, 31) axilla, parascutellum weakly rugose; (32) mesoscutellum elutely shagreened; (33) meson of metanotum rugose, lateron with longitudinal plicae. (34) Forewing (Fig. 54) with submarginal vein 4 times as long as marginal vein; stigmal vein 2 times postmarginal vein; (35) stigma weakly tumid, sensilla evident; (36) dense cluster of adstigmal setae conspicuous; (37) marginal tract ending well before postmarginal vein; R_1 tract ending before marginal tract; submarginal tract not reaching stigma; distal, medial, and anal tracts absent. (38, 39) Coxae, femora all lightly sculptured; (40) middle and hind tibiae with 2 subequal apical spurs each; (41) fore basitarsus as long as tarsomeres 2-4; middle and hind basitarsal longer than tarsomeres 2-5. (42) Proepisternum as large as fore coxa, rugose, bearing 2 apparent cranial processes; (43) prosternum heart-shaped, shagreened; discrimen extending entire length; (44) prepectus laterally favose, mesally rugose; (45) mesepisternum laterally favose, mesally shagreened, smooth at discrimen; (46) mesepimeron rugose; (47) anapleurite smooth.

(48) Propodeum 3 times as wide as long, rugose, with pattern distorted laterally; median longitudinal carina weakly formed; (49) gaster ovoid, slightly larger than mesosoma; (50) tergum lightly shagreened, rear half of each tergum weakly setose, posterior margins straight; (51) sterna coriaceous; (52) ovipositor and gonostylus 2.5 times gastral length; (53) mesal surface of gonostylus setose basally, becoming sparsely setose distally.

Male—Body length 2.3 mm. (54, 55) Head and mesosoma chestnut; (56) gaster dirty white; (57) basal antennal segment dark reddish-brown, segment 2 tan, remaining segments dirty white; (58) coxae, femora concolorous with mesosoma; remaining segments castaneous.

(59) Head with dorsal surface lightly setose; clypeal margin with single conspicuous lobe; labiomaxillary complex represented by 2 large sensory pegs; (60)

mandible tridentate (Fig. 74), tooth margin sharply incised; third tooth weakly developed; (61) antenna 4-segmented (Fig. 43); segment 3 not translucent or collar-like; (62) all legs with 4 tarsomeres; tibio-tarsal complexes (Figs. 116-118) with basitarsi elongate; (63) each tergum bearing transverse row of long setae at center axis of plate; posterior tergal margins straight; (64) sterna smooth, asetose.

Material—Described from 27 females and 9 males collected at Turrialba, Cartago Province, Costa Rica by William Ramírez on 29 July 1964 from *Ficus cervantesiana*.

Holotype—A dissected female mounted in Hoyer's medium on 3 slides under 9 coverslips. Each label is inscribed: "*Idarnes bucatoma*. Turrialba, Cartago, Costa Rica. 29 July 1964, leg. W. Ramírez, ex. *Ficus cervantesiana*. HOLOTYPE." *Allotype*—One dissected male mounted in Hoyer's medium on 1 slide under 3 coverslips. The label is inscribed with the same data indicated above. *Paratypes*—Ten dissected females mounted in Hoyer's as the above holotype, with a similar label inscription.

Comparative Comments—This species is readily identifiable since the female antennal scape, pedicel, and second annulus are strongly setose (15, 16), the head is subprognathous (16), the pronotum (26) is exceedingly large; the adstigmal setae (37) of the forewing form a dense cluster, and the propodeum (46) is sculptured and bears a longitudinal carina. Males are recognized by the combination of tridentate mandible (60), 4 tarsomeres on each leg (62), and long tergal setae at the middle line of each plate, and straight posterior tergal margin (63).

Idarnes bucatoma does not appear closely related to any other *Idarnes* species, yet it clearly falls within the generic limits. The subprognathous head in the female presumably represents a derived character. The male is the only *Idarnes* which has a pigmented third antennal segment and 4-segmented tarsi.

Idarnes camini, new species

Female—Body length 1.4 mm, ovipositor 3.7 mm long. (1, 2) Head and mesosoma chestnut brown with sheen, margin of oral fossa light; (3) gaster brown with tawny luster, posterior margins of terga each bearing dark transverse band; (4) antenna tawny; (5) leg segments uniformly gold; (6) prosternum translucent, mesosternum concolorous with head and mesosoma.

(7) Head hypognathous; in frontal aspect nearly round; compound eye not protuberant; (8) face weakly rugose; gena strongly asetose; (9) vertex flat; (10) antenna inserted at middle line of compound eye; (11) toruli separated by diameter of single torulus; (12) scrobe cavity shallow, smooth, lateral walls carinate, extending to anterior ocellus; (13) interantennal ridge not acute. (14) Antenna 13-segmented (Fig. 33); (15) scape extending to vertex; (16) pedicel with few setae; (17) flagellomeres longer than wide, verticillate; setae inflexible, more numerous than carinae; (18) club present; terminal protuberance conspicuous. (19) Frons weakly shagreened, setose; (20) clypeal margin bilobed; (21) mandible tridentate (Fig. 67), tooth margin sharply incised. (22) Maxillary palpus 2-segmented; palpifer well formed; (23) palpiger not evident; (24) ligula with 2 sensory pegs; (25) paraglossa enveloping basal 1/2 of ligula; (26) galea moderately setose.

(27) Pronotum smaller than scapulae and mesoscutum, campanulate, uniformly shagreened; (28, 29) mesoscutum, scapula rugose; (30, 31) axilla, parascutellum strongly shagreened; (32) mesoscutellum lightly shagreened; (33) meson of metanotum smooth, lateron lightly sculptured. (34) Forewing (Fig. 55) with submarginal vein 3 times as long as marginal vein;

stigmal vein 3 times postmarginal vein; (35) stigma tumid, sensilla conspicuous; (36) 5 adstigmal setae; (37) marginal tract ending before postmarginal vein; R_1 tract extending to postmarginal vein; submarginal tract reaching stigma; discal, medial, anal tracts absent. (38) Fore and hind coxae lightly sculptured; (39) femora lightly setose; (40) middle tibia bearing 1 subapical spur; hind tibia setose, bearing 1 apical spur; (41) fore basitarsus as long as tarsomeres 2-5. (42) Proepisternum slightly larger than fore coxa, shagreened, bearing single cranial process; (43) prosternum triangular, smooth, setose along posterior margin; furca broadly attached to posterior margin of prosternum; (44) prepectus rugose; (45) mesepisternum laterally shagreened, smooth at discrimen; (46) mesepimeron weakly shagreened; (47) anapleurite smooth.

(48) Propodeum 3.5 times as wide as long, meson smooth, lateral region shagreened; (49) gaster ovoid; (50) terga shagreened, setose; posterior tergal margins straight; (51) sterna coriaceous; (52) ovipositor and gonostylus 3.5 times gaster length; (53) gonostylar setae along mesal surface large.

Male—Body length 1.1 mm. (54, 55) Head, mesosoma tan; mandible red; (56) gaster milky white; (57) antennal scape red; (58) legs straw colored.

(59) Head with long setae along posterior and lateral margins; (60) mandible (Fig. 79) bidentate with tooth margin sharply incised; (61) antenna (Fig. 38) 5-segmented; (62) legs with 5 tarsomeres (Figs. 98-100); middle and hind tibiae with single long apical spur; fore basitarsus short, middle and hind basitarsi spinose, elongate. (63) Gastral terga asetose, posterior margins sinuate; (64) sterna with minute setae.

Material—Described from 24 females and 3 males collected by William Ramírez at La Virgen, Heredia, Costa Rica on 31 May 1964 and 9 females and 2 males collected 15 June 1969 by the author and Ramírez 7.1 miles northeast of Coscomatepec, Veracruz, México. *Ficus oerstediana* Miquel was the host tree in both instances.

Ficus oerstediana is distributed throughout Mexico, Central America, and into Colombia.

Holotype—One dissected female mounted in Hoyer's medium on 2 slides under 6 coverslips. Each label is inscribed: "*Idarnes camini*. La Virgen, Heredia, Costa Rica. 31 May 1964, leg W. Ramírez, ex. *Ficus oerstediana*. HOLOTYPE." *Allotype*—One dissected male mounted in Hoyer's medium on a single slide under 3 coverslips. The label is inscribed as is the holotype label. *Paratypes*—Eight dissected females mounted in the manner indicated above for the holotype. Each label is inscribed as above.

Variation—Some females have setae on the vertex (9); the frons may be smooth and glabrous (19); 4 ligular spines (24) and 4 adstigmal setae (36) may be present. The series of males was too small to show variation.

Comparative Comments—*Idarnes camini* females may be recognized by the combination of setose gena (8), distinctive antennal appearance (14-18), mesoscutum lightly shagreened (32), long postmarginal vein (34), and large setae on the gonostylus (53). Males are identifiable by the long setae on the head (59), bidentate mandible (60), 5-segmented antenna (61), and sinuous posterior tergal margins (63).

Idarnes carme Walker

Idarnes carme Walker, 1843, Ann. Mag. Nat. Hist. 12:47, ♀.

Female—Body length 1.5 mm, ovipositor 2.2 mm long. (1, 2, 3) Head, mesosoma, and gaster reddish brown with faint sheen; (4) antenna concolorous with head; (5) legs tan; (6) prosternum nearly yellow, mesosternum reddish brown.

(7) Head hypognathous, in frontal aspect distinctly wider than long; compound eye not protuberant; (8) face lightly setose, favose, pattern bolder toward vertex; gena setose, lacunose; (9) vertex flat; (10) antenna (Fig. 32) inserted at ventral margin of compound eye; (11) toruli separated by twice diameter of torulus; antennifer small; (12) scrobe evanescent, lacunose, not extending to anterior ocellus; (13) interantennal ridge setose, broad, nearly smooth; (14) antenna 12-segmented; (15) scape short, weakly setose; (16) pedicel not elongate, smooth, lightly setose; (17) flagellomeres longer than wide, longitudinal carinae more numerous than inflexible setae; (18) club weakly formed; terminal protuberance inconspicuous. (19) Frons smooth, setose; (20) clypeal margin straight; (21) mandible (Fig. 72) bidentate, tooth margin moderately incised. (22) Maxillary palpus 2-segmented; palpifer weak; (23) palpiger absent; (24) ligula with 4 sensory pegs; (25) paraglossa enveloping 3/4 of ligular margin; (26) galea with numerous acuminate setae.

(27) Pronotum with postero-dorsal surface favose, remainder shagreened; (28) mesoscutum favose; (29) scapula lacunose, weakly setose; (30, 31) axilla, parascutellum rugose; axilla weakly setose; (32) mesoscutellum lacunose, nearly smooth, lateral margin setose; (33) meson of metanotum lacunose, nearly smooth; lateron shagreened. (34) Forewing (Fig. 53) with submarginal vein 3 times as long as marginal vein; postmarginal vein over 2 times stigmal vein; (35) stigma tumid, sensillae large; (36) single adstigmal seta present; (37) marginal tract ending before postmarginal vein; R_1 tract short; submarginal tract reaching to stigma; discal, medial, and anal tracts absent. (38) Coxae all lightly shagreened, weakly setose; (39) femora lightly shagreened, weakly setose; (40) middle and hind tibiae each with single apical spur; (41) fore basitarsus as long as tarsomeres 2-3; middle and hind basitarsi as long as tarsomeres 2-4. (42) Proepisternum larger than forecoxa, shagreened, with single cranial process; (43) prosternum hemispherical, smooth; discrimen short; (44, 45) prepectus, mesepisternum laterally rugose, mesally smooth; (46) mesepimeron shagreened; (47) anapleurite smooth.

(48) Propodeum 3 times as wide as long, smooth; median longitudinal carina absent; (49) gaster as large as mesosoma; (50) terga lightly shagreened, setose; posterior tergal margins sinuate; (51) sterna smooth; (52) ovipositor and gonostylus 3 times gaster length; (53) gonostylus with setae along mesal surface, progressively more numerous distally.

Male—Body length 0.8 mm. (54, 55) Head, mesosoma tan; (56) gaster milky white; (57) antenna pale, nearly white; (58) legs concolorous with mesosoma, tibial margins red.

(59) Head with few short setae along dorsal surface; clypeal margin concave; (60) mandible (Fig. 73) bidentate, tooth margin not sharply incised; (61) antenna (Fig. 40) 4-segmented, with few setae; (62) all legs with 5 tarsomeres (Figs. 95-97); tibiae lacking long apical spurs; basitarsi elongate, with few apical spines. (63) Gastral terga asetose, posterior tergal margins straight; (64) sterna smooth, asetose.

Material—Redescribed from 6 females collected in part by H. H. Smith on St. Vincent and Barbados, West Indies (date of collection not indicated), and 27 females and 3 males collected by R. E. Beer on 10 April 1968 from the Florida Keys. In each instance the host tree was *Ficus aurea*.

Walker's type material should be in the British Museum (Natural History) but cannot now be located. Material borrowed from the U.S. National Museum of Natural History through the courtesy of B. D. Burks had been collected in the

West Indies and identified as *Idarnes carme* by Ashmead and Girault. Walker did not describe the male of this species, nor are any males present in the U.S. National Museum of Natural History from the West Indies. The females collected by Beer in Florida are considered conspecific with the material from the West Indies.

The epithet "aurea" has been used to describe varieties of *Ficus elastica* Roxburgh and *F. macrophylla* Desfontaines. However, these are not to be confused with *F. aurea* Nuttall, the Florida Strangling Fig. The species is found in southern Florida and the Bahamas, in addition to the West Indies.

Neotype—A dissected female mounted in Canada balsam on 2 slides with 3 coverslips each. Both labels are inscribed: "*Idarnes carme* Walker. St. Vincent, W. I., female, leg. H. H. Smith 209. NEOTYPE."

Variation—Some variation may be noted in the sculpturing of the female head (8) and mesosoma (28-33). Males were not collected in large enough numbers to detect variation.

Comparative Comments—*Idarnes carme* may be distinguished from other species by females with brunneous color (1, 2, 3), antenna inserted at level of ventral margin of compound eyes (10), shallow scrobe (12), setose interantennal ridge (13), mesosoma with setae on dorsal surface (29-32), and setae of the gonostylus becoming progressively more numerous distally (53). Males have a bidentate mandible (60), 4-segmented antenna (61), and straight posterior tergal margins (63).

Idarnes coriaria (Mayr)

Tetragonaspis coriaria Mayr, 1885, Verh. Zool. Bot. Gesell. Wien 35:209.

This species was adequately described by Mayr from Brazilian material collected by Fritz Müller. The male remains undescribed and the *Ficus* host is unknown. The species belongs in *Idarnes* as here limited but differs from the more northern species described herein.

Idarnes flavicollis (Mayr)

Tetragonaspis flavicollis Mayr, 1885, Verh. Zool. Bot. Gesell. Wien 35:207-208, ♀.

Ganosoma robustum Mayr, 1885, Verh. Zool. Bot. Gesell. Wien 35:204, ♂.

Female—Body length 2.5 mm, ovipositor 5.0 mm long. (1, 2) Head, mesosoma metallic dark green; (3) gaster smoky brown; (4) scape basally tan, becoming progressively darker distally; pedicel and remaining segments reddish brown; (5) fore and hind coxae tawny brown; remaining leg segments dirty white; (6) prosternum, mesosternum concolorous with head and mesosoma.

(7) Head hypognathous, in frontal aspect oval, nearly round; (8) face progressively more rugose above toruli; vertex favose; gena rugose along margin of compound eye, remainder smooth; genal surface setose; (9) vertex convex; (10) antenna (Fig. 29) inserted just below midline of compound eye; (11) toruli separated by 1.5 times diameter of torulus; (12) scrobe shallow, glabrous, terminated at anterior ocellus; (13) interantennal ridge short. (14) Antenna 13-segmented; (15) scape setose, shagreened, extending beyond vertex; (16) pedicel not elongate, setose; (17) flagellomeres longer than wide, verticillate, with flexible setae; (18) club not distinct; terminal protuberance conspicuous. (19) Frons smooth, asetose; (20) clypeal margin bilobed; (21) mandible tridentate (Fig. 69), tooth margin not sharply incised. (22) Maxillary palpus 2-segmented; palpifer evident; (23) palpiger evident; (24) ligula with 4 sensory pegs; (25) paraglossa enveloping 2/3 of ligular margin; (26) galea with numerous acuminate setae.

(27) Pronotum with postero-dorsal surface rugose, remainder shagreened; (28, 29, 30, 31) mesoscutum, scapula, axilla, parascutellum uniformly rugose; (32) mesoscutellum shagreened with pattern lightly incised; lateral margin asetose;

(33) meson of metanotum rugose, lateron smooth, setose. (34) Forewing (Fig. 48) with submarginal vein 3 times as long as marginal vein; stigmal vein 2 times postmarginal vein; (35) stigma tumid with large sensillae; (36) adstigmal setae variable; (37) marginal tract ending at postmarginal vein; R$_1$ tract absent; submarginal tract reaching stigma; discal, medial, anal tracts absent; (38) all coxae sculptured, setose; (39) femora setose; hind femur and coxa subequal in size; (40) middle tibia with single apical spur; hind tibia with 2 subequal apical spurs; (41) fore basitarsus as long as tarsomeres 2-3; middle basitarsus longer than remaining tarsomeres; hind basitarsus as long as tarsomeres 2-5. (42) Proepisternum as large as fore coxa, asetose, rugose, bearing single elongate cranial process; (43) prosternum subtrapezoidal, rugose; discrimen extending to center; (44) prepectus laterally rugose, pattern fading mesally; (45) mesepisternum uniformly shagreened; spinasternum smooth, well developed; (46) mesepimeron laterally rugose, shagreened at pleural suture; (47) anapleurite smooth.

(48) Propodeum 3 times as wide as long, smooth; area antero-lateral to spiracles setose; median longitudinal carina absent; (49) gaster larger than head and mesosoma combined; (50) terga lightly shagreened; posterior half of each tergum uniformly setose; posterior tergal margins straight; (51) sterna smooth, glabrous; (52) ovipositor 4.5 times gaster length; (53) gonostylus with few small setae along mesal surface.

Male—Body length 1.9 mm. (54, 55) Head, mesosoma tan; (56) gaster pale, nearly dirty white; (57) antenna tan; (58) legs concolorous with mesosoma, tibial margins reddish.

(59) Dorsal surface of head smooth; clypeal margin weakly concave; (60) mandible tridentate (Fig. 75), front tooth margin sharply incised; (61) antenna (Fig. 47) 5-segmented; (62) each leg with 5 tarsomeres; tibio-tarsal complex (Figs. 92-94) with fore basitarsus short, middle and hind tibiae with long spurs. (63) Gastral terga asetose, posterior margins straight; (64) sterna smooth.

Material—Twenty-one female and 8 male wasps collected at La Cañada, Cartago, Costa Rica by William Ramírez on 31 January 1963 from *Ficus velutina* Willd.

Comparative Comments—Superficially this species resembles *Idarnes simus*, but it may be distinguished on the basis of the following female characters: *I. flavicollis* has a rugose face (8), the antenna 13-segmented (14), frons asetose (19), lateral margin of mesoscutellum asetose (32), lateron of metanotum setose (33), the stigmal vein twice as long as the postmarginal vein (34), the prosternum subtrapezoidal in shape (43), the anapleurite smooth (47), and the posterior tergal margins straight (50).

Mayr (1885) described *Ganosoma robustum* from Brazil as developing in receptacles of the same tree as *Idarnes flavicollis*. The material from Costa Rica reveals two distinct male morphs, neither of which conforms to *G. robustum* very well. The marked male dimorphism may be due to nutrition, which could also account for the discrepancy between the material examined from Costa Rica and Mayr's *G. robustum*. Since the larger form is more common, and since the smaller form could conceivably be the male of another symbiont, I have described above only the larger of the two morphs. The problem of association of sexes is still not satisfactorily solved, and the Costa Rican material may represent a new species. The female from Costa Rica, however, agrees with *I. flavicollis* from Brazil.

Mayr failed to give the species of fig from which *Idarnes flavicollis* emerged. *Ficus velutina* Willd. if found throughout

Central America, but it is uncertain whether or not it grows in South America.

Type Locality—Santa Catarina, Brazil.

Idarnes forticornis (Mayr)

Tetragonaspis forticornis Mayr, 1885, Verh. Zool. Bot. Gesell. Wien 35:208, ♀.

This species was described from material collected in Brazil. The male remains undescribed and the *Ficus* host unrecorded. This is a species of *Idarnes* as here restricted.

Idarnes galbina, new species

Female—Body length 1.0 mm, ovipositor 1.9 mm long. (1, 2, 3) Head, mesosoma, gaster shining brown; (4) antenna concolorous with body; (5) legs uniformly straw colored; (6) prosternum chestnut brown; mesosternum shining brown.

(7) Head hypognathous, in frontal aspect nearly round; compound eye weakly protuberant; (8) face shagreened at toruli, pattern becoming progressively bolder toward vertex; (9) vertex convex; gena hispidous, smooth; (10) antenna inserted just below midline of compound eye; (11) toruli separated by 2 times torulus diameter; (12) scrobe cavity short, not reaching anterior ocellus; lateral walls carinate; (13) interantennal ridge broad, flat. (14) Antenna 12-segmented (Fig. 31); (15) scape weakly setose, smooth, reaching lower margin of anterior ocellus; (16) pedicel with very few setae; (17) flagellomeres as long as wide, carinae long; carinae more numerous than setae; (18) club nearly absent; terminal protuberance not conspicuous. (19) Frons lightly shagreened, marginally setose; (20) clypeal margin convex; (21) mandible bidentate (Fig. 68), tooth margin not sharply incised. (22) Maxillary palpus 2-segmented; palpifer not evident; (23) palpiger not evident; (24) ligula with 2 sensory pegs; (25) paraglossa enveloping entire ligular margin; (26) galea with few acuminate setae.

(27) Pronotum lightly shagreened; (28) mesoscutum favose along scuto-scutellar suture, pattern distorted cephalad; (29, 30, 31) axilla, scapula, parascutellum rugose; (32) mesoscutellum glabrous; (33) meson of metanotum lacunose, lateron weakly sculptured. (34) Forewing (Fig. 50) with submarginal vein 3 times as long as marginal vein; postmarginal vein 2 times stigmal vein; (35) stigma not tumid, sensillae small; (36) 2 adstigmal setae; (37) marginal tract ending at postmarginal vein; R_1 tract present, ending behind postmarginal vein; submarginal tract not reaching stigma; discal, anal tracts absent; medial tract present. (38) Fore coxa lightly shagreened, hind coxa rugose; (39) femora shagreened, setose; (40) middle tibia with medial setal tract, single apical spur; hind tibia bearing setal tract, several subequal apical spurs; (41) fore basitarsus as long as tarsomeres 2-3; middle and hind basitarsi as long as tarsomeres 2-4. (42) Proepisternum as large as fore coxa, glabrous, bearing single elongate cranial process; (43) prosternum nearly round, glabrous; discrimen only at base of structure; (44) prepectus rugose; (45) mesepisternum shagreened, pattern evanescent at discrimen; (46) mesepimeron uniformly shagreened; (47) anapleurite smooth.

(48) Propodeum 5 times as wide as long, lacunose; median longitudinal carina absent; (49) gaster ovoid; (50) posterior tergal margins sinuate; each tergum with transverse row of small, inconspicuous setae; (51) sterna smooth; (52) ovipositor and gonostylus 2.5 times gaster length; (53) gonostylus with setae becoming progressively longer, more numerous distally.

Male—Body length 0.9 mm. (54, 55) Head and mesosoma chestnut; (56) gaster dirty white; (57) scape light tan, club white; (58) all leg segments concolorous with head and mesosoma.

(59) Head with postero-dorsal surface setose; clypeal margin sinuate; (60) man-

dible tridentate (Fig. 77). tooth margin moderately incised; (61) antenna 4-segmented (Fig. 37), inserted at base of mandible; segment 3 translucent, collar-like; lateral walls of scape not thick; (62) all legs with 5 tarsomeres; tibio-tarsal complexes (Figs. 86-88) as figured; (63) each tergum bearing transverse row of very long setae; posterior tergal margins sinuate; (64) sterna smooth.

Material—Described from 42 females and 16 males collected at Puerto Viejo, Heredia, Costa Rica, by William Ramírez on 16 May 1964 from *Ficus colubrinae.*

Holotype—A dissected female mounted in Hoyer's medium on 2 slides, each bearing 3 coverslips. Both labels are inscribed: "*Idarnes galbina.* Puerto Viejo, Heredia, Costa Rica. 16 May 1964, leg. W. Ramírez, ex. *Ficus colubrinae.* HOLOTYPE." *Allotype*—A single male, dissected, on 1 slide with the parts under 3 coverslips. The inscription on the label is the same as above. *Paratypes*—Eight females, Canada balsam or Hoyer's medium, mounted in the manner indicated above for the holotype, with a similar label inscription.

Variation—While this species is exceedingly small, occasionally a large (1.4 mm) female may be found; the antennal scape may bear some setae (15), the ligula has a variable number of sensory pegs (24), and the mesoscutellum may bear a shagreened sculpture pattern (32). Males also exhibit some variation in size, and in setal number on the antennal club (61).

Comparative Comments—This species of *Idarnes* may be distinguished from others on the basis of the following key female characters: smooth, hispidous gena (8), 12-segmented antenna (13), flagellomeres with more carinae than setae (17), clypeal margin convex (20), mesoscutum with distorted favose sculpture (28), medial vein tract present (37), and a thin, transverse, lacunose propodeum. Males may bear long setae on the dorsum of the head (59), and antenna (61) may appear 5-segmented, with the base of the club constricted.

Idarnes galbina seems most closely related to *I. carme.* The female antennae of both species are similar, the sculpturing patterns of the mesosoma overlap, and the labiomaxillary complexes resemble one another.

Idarnes gracilicornis (Mayr)

Ganosoma attenuatum Mayr, 1885, Verh. Zool. Bot. Gesell. Wien 35:204, ♂.

Tetragonaspis gracilicornis Mayr, 1885, Verh. Zool. Bot. Gesell. Wien 35:208, ♀.

Ashmead (1904) originally associated the female *T. gracilicornis* with the male *G. attenuatum,* but offered no reason for doing so. Thus some question remains as to the correct association between the species synonomized under *I. gracilicornis.* I have not had an opportunity to examine the material Ashmead used and from the original descriptions it is not possible to correctly associate the sexes.

Idarnes jimenezi, new species

Female—Body length 2.1 mm, ovipositor 2.3 mm long. (1, 2) Head, mesosoma dark metallic green; (3) gaster rusty red; (4) antenna reddish brown; (5) coxae concolorous with mesosoma; remaining leg segments tan; (6) prosternum gold.

(7) Head hypognathous, in frontal aspect nearly round; eye weakly protuberant; (8) vertex favose, pattern evanescent over remainder of head; setae irregularly dispersed over face; (9) margin of vertex strongly sinuate; (10) antenna inserted at ventral margin of compound eye; (11) toruli separated by diameter of torulus; (12) scrobe cavity deep, lacunose, lateral margins carinate; (13) interantennal ridge acute. (14) Antenna 12-segmented (Fig. 36); (15) scape extending to anterior ocellus; (16) pedicel not elongate, setose; (17) flagellomeres slightly longer than wide, verticillate, setae inflexible; setae, carinae equal in number; (18) club absent; ter-

minal protuberance inconspicuous. (19) Frons favose, glabrous; (20) clypeal margin straight; (21) mandible bidentate (Fig. 65), tooth margin deeply incised. (22) Maxillary palpus 2-segmented; palpifer small; (23) palpiger not evident; (24) ligula very reduced, bearing 2 sensory pegs; (25) paraglossa enveloping basal 3/4 of ligular margin; (26) galea with moderate number of acuminate setae.

(27) Pronotum favose along posterodorsal margin; (28) mesoscutum rugose, pattern evanescent along posterior margin near scapula; (29, 30) scapula, axilla shagreened; (31) parascutellum rugose; (32) mesoscutellum smooth; (33) meson of metanotum rugose, lateron smooth. (34) Forewing (Fig. 59) with submarginal vein 3 times as long as marginal vein; postmarginal vein 1.5 times stigmal vein; (35) stigma tumid, with small sensilla; (36) 2 adstigmal setae; (37) marginal tract ending at postmarginal vein; R_1 tract absent; submarginal tract not reaching stigma; discal tract absent; medial, anal tracts present. (38, 39) Coxae, femora shagreened, setose; (40) middle tibia with single apical spur; hind tibia with 2 subequal large apical spurs; (41) fore basitarsus as long as tarsomeres 2-3; middle basitarsus as long as tarsomeres 2-4; hind basitarsus as long as tarsomeres 2-3. (42) Proepisternum as large as fore coxa, shagreened, bearing single cranial process; (43) prosternum semicircular, glabrous; discrimen long; (44) prepectus rugose, pattern evanescent mesally; (45) mesepisternum shagreened, pattern absent at discrimen; (46) mesepimeron rugose; (47) anapleurite smooth.

(48) Propodeum 3 times as wide as long, meson favose, lateral regions smooth; median longitudinal carina absent; (49) gaster larger than head and thorax; (50) tergum glabrous, posterior tergal margins sinuate; (51) sterna glabrous; (52) ovipositor and gonostylus 2.5 times gaster length; (53) gonostylus glabrous or bearing minute setae mesally.

Male—Body length 1.8 mm. (54, 55) Head and mesosoma amber; (56) gaster white; (57) scape, pedicel reddish brown; segment 3 translucent; remaining segments tan. (58) Coxae concolorous with mesosoma; tibiae lacteous.

(59) Head with short setae; clypeal margin arched inward, with single large mesal spine; (60) mandible (Fig. 78) scythe-like, bidentate, tooth margin sharply incised; (61) antenna (Fig. 41) 4-segmented, basal part of segment 4 nearly a distinct segment; (62) all legs with 5 tarsomeres; tibio-tarsal complexes as figured (Figs. 110-112), basitarsi with apical spines. (63) Each tergum bearing a few long setae; posterior margins sinuate; (64) sterna smooth, asetose.

Material—Described from 31 females and 6 males collected by William Ramírez on 24 August 1964 at Santa Domingo, Heredia, Costa Rica from *Ficus jimenezii*.

Holotype—One dissected female mounted in Hoyer's medium on 2 slides under 6 coverslips. Each label is inscribed: "*Idarnes jimenezi*. Santa Domingo, Heredia, Costa Rica. 24 August 1964, leg. W. Ramírez, ex. *Ficus jimenezii*. HOLOTYPE." *Allotype*—A dissected male mounted in Hoyer's medium under 3 coverslips on 1 slide. The label is inscribed as indicated above. *Paratypes*—Eight dissected females each mounted on 1 slide under 3 coverslips in Canada balsam. Each label is inscribed as indicated above.

Variation—Variations in the facial sculpturing pattern (8, 19), setae on the coxae and femora (38, 39), and propodeal sculpture pattern (48) are exhibited by females. Males were not collected in large enough numbers to determine the extent of variation.

Comparative Comments—Females may be distinguished from other species of *Idarnes* on the basis of the following characters: antennal configuration (14-18), mesoscutellum smooth (32), and the presence of an anal vein tract (37). All males examined have the scythe-like mandible (60) and a 4-segmented antenna (61) in which the club base is constricted.

Idarnes micheneri, new species

Female—Body length 1.8 mm, ovipositor 3.9 mm long. (1, 2, 3) Head, mesosome, gaster brassy green; margin of oral fossa tan; (4) antenna uniformly dark brown; (5) all coxae, hind femur shining brown; remaining segments tan; (6) prosternum, mesosternum fusco-rufeous.

(7) Head verging on prognathous, in frontal aspect nearly round; (8) face progressively more rugose above toruli; gena smooth, setose; (9) vertex weakly convex; (10) antenna inserted just above ventral margin of compound eye; (11) toruli separated by twice diameter of torulus; (12) scrobe cavity moderately deep, extending to anterior ocellus at level of upper 1/3 of compound eye; (13) interantennal ridge not acute. (14) Antenna (Fig. 27) 13-segmented; (15) scape lightly setose, extending to anterior ocellus; (16) pedicel lightly setose, elongate; (17) flagellomeres as long as wide, verticillate, setae inflexible; (18) club present; terminal protuberance not conspicuous. (19) Frons smooth, often lateral margin setose; (20) clypeus trilobed; (21) mandible tridentate (Fig. 60), tooth margin not sharply incised. (22) Maxillary palpus 2-segmented; palpifer conspicuous; (23) palpiger large; (24) ligula with 4 sensory pegs; (25) paraglossa enveloping basal 1/3 of ligular margin; (26) galea with numerous acuminate setae.

(27) Pronotum postero-dorsally rugose, remainder shagreened; (28, 29) mesoscutum, scapula rugose; (30, 31) axilla, parascutellum shagreened; (32) mesoscutellum eleutely shagreened; (33) meson of metanotum shagreened, lateron smooth. (34) Forewing (Fig. 58) with submarginal vein 3 times as long as marginal vein; stigmal vein 2 times postmarginal vein; (35) stigma tumid, sensillae conspicuous; (36) 3 adstigmal setae present; (37) marginal tract reaching postmarginal vein; R_1 tract ending behind postmarginal vein; submarginal tract reaching stigma; discal tract conspicuous; medial, anal tracts absent. (38) Fore and hind coxae shagreened; hind coxa larger than hind femur; (39) femora setose, lightly shagreened; (40) middle and hind tibiae each with 2 subequal apical spurs; hind tibia with setal tract, large apical spurs; (41) fore basitarsus as long as tarsomeres 2-3; middle and hind basitarsi as long as tarsomeres 2-5 of respective legs. (42) Proepisternum larger than fore coxa, weakly shagreened, setose along posterior margin, bearing single elongate cranial process; (43) prosternum campanulate, shagreened, setose; discrimen extending cephalad 1/4 length of structure; (44) prepectus rugose; (45) mesepisternum shagreened; (46) mesepimeron rugose; (47) anapleurite smooth.

(48) Propodeum 3 times as wide as long, eleutely shagreened, median longitudinal carina absent; (49) gaster 2.5 times longer than wide; (50) terga lightly setose, strongly shagreened; posterior tergal margins straight; (51) sterna coriaceous; (52) ovipositor and gonostylus 3.5 times gaster length; (53) gonostylus bearing long conspicuous setae.

Male—Body length 1.4 mm. (54, 55) Head and mesosoma tan; (56) gaster white; (57) scape, pedicel tan with margin reddish; (58) coxae, femora concolorous with mesosoma; remaining segments reddish.

(59) Head with long conspicuous setae; clypeal margin concave; (60) mandible tridentate (Fig. 76), tooth margin sharply incised; (61) antenna 4-segmented (Fig. 46); base of club nearly separated from distal portion; (62) all legs with 5 tarsomeres (Figs. 104-106); middle and hind tibiae each with 1 long apical spur;

basitarso spinose; (63) all terga smooth, setose, posterior margins sinuate; (64) sterna smooth, lightly setose.

Material—Described from 83 females and 12 males collected by William Ramírez at Ciruelas, Alajuela, Costa Rica on 20 August 1964 from *Ficus isophlebia.*

Ficus isophlebia is related to *F. jimenezii* according to Standley (1917). Both species of *Ficus* grow throughout Central America and northward into México.

Holotype—One dissected female mounted in Hoyer's medium on 2 slides under 6 coverslips. Each label is inscribed: "*Idarnes micheneri.* Ciruelas, Alajuela, Costa Rica. 20 August 1964, leg. W. Ramírez, ex. *Ficus isophlebia.* HOLOTYPE." *Allotype*—One dissected male mounted in Hoyer's medium on 1 slide under 3 coverslips. The label is inscribed as indicated above. *Paratypes*—Eight dissected females mounted in Canada balsam or Hoyer's medium, each on 2 slides under 6 coverslips. Each label is inscribed as above.

Variation—Some female wasps from México have the hind coxae and femora bronze (4), the genae shagreened (7), a minute mesal clypeal lobe (20), and fewer than 4 adstigmal setae (36). Males sometimes have a setose pronotum and some variation in the development of setae on the sternum of the gaster (64).

Comparative Comments—*Idarnes micheneri* females may be recognized by the rugose face (8), 13-segmented antenna (14), smooth, setose frons (19), tridentate mandible (21), large labial palpiger (23), well developed submarginal and discal vein tracts (37), straight posterior tergal margin (50), and long, conspicuous gonostylar setae (53). Males can be recognized by the tridentate mandible (60), 4-segmented antenna (61), and lightly setose gastral sterna (64).

Idarnes obtusifoliae, new species

Female—Body length 2.4 mm, ovipositor 7.0 mm long. (1, 2) Head and mesosoma brassy green; (3) gaster chestnut brown; (4) antenna uniformly shining brown; (5) coxal bases brassy green, legs otherwise dirty white; (6) prosternum castaneous; mesosternum concolorous with head and mesonotum.

(7) Head hypognathous, in frontal aspect slightly wider than long; compound eye not protuberant; (8) face asetose, uniformly favose; gena favose; (9) vertex sinuous; (10) antenna inserted just above ventral margin of compound eye; (11) toruli separated by 3 times diameter of torulus; antennifer conspicuous; (12) scrobe with 2 shallow channels, favose; lateral walls not carinate; (13) interantennal ridge not acute. (14) Antenna 12-segmented (Fig. 30); (15) scape shagreened, setose, elongate, but not reaching vertex; (16) pedicel shagreened, setose; (17) flagellomeres 1.5 times as long as wide, verticillate; setae inflexible, more numerous than carinae; (18) club absent; terminal protuberance evident. (19) Frons favose; (20) clypeus bilobed, meson incised; (21) mandible tridentate (Fig. 62), tooth margin sharply incised. (22) Maxillary palpus 2-segmented; palpifer evident; (23) palpiger not evident; (24) ligula with 2 sensory pegs; (25) paraglossa enveloping entire margin of ligula; (26) galea with numerous acuminate setae.

(27) Pronotum with postero-dorsal surface favose, remainder shagreened; (28, 29, 30, 31) mesoscutum, scapula, axilla, parascutellum lacunose; (32) mesoscutellum lacunose; (33) meson of metanotum favose, lateral regions with numerous parallel plicae. (34) Forewing (Fig. 52) with submarginal vein 4 times as long as marginal vein; postmarginal vein 2 times stigmal vein; (35) stigma tumid, sensilla small; (36) 1 adstigmal seta present; (37) marginal tract not extending to postmarginal vein; R_1 tract absent; submarginal tract reaching stigma; medial tract present; discal, anal tracts absent. (38) Fore

and middle coxae mesally setose; hind coxa asetose; (39) middle femur shorter than middle tibia; hind femur setose; (40) middle tibia with single apical spur; hind tibia with 2 mesal, longitudinal setal tracts, 2 subequal apical spurs; (41) fore basitarsus as long as tarsomere 2; middle basitarsus as long as tarsomeres 2-5; hind basitarsus as long as tarsomeres 2-4. (42) Proepisternum smaller than fore coxa, rugose, bearing single elongate cranial process; (43) prosternum oval, glabrous, lightly setose; discrimen extending along basal third of structure; (44) prepectus favose; (45) mesepisternum laterally favose, smooth at discrimen; (46) mesepimeron rugose; (47) anapleurite favose.

(48) Propodeum 4 times as wide as long, lacunose; medial longitudinal carina present; (49) gaster ovoid; (50) tergum shagreened, small setae irregularly distributed; posterior margin of each tergum sinuate; (51) sterna smooth; (52) ovipositor and gonostylus 8 times gaster length; (53) gonostylus with small setae along mesal surface.

Male—Body length 2.1 mm. (54, 55) Head and mesosoma tan; (56) gaster milky white; (57) scape tan with margin reddish; segments 2, 4, and 5 tan; (58) coxae, femora concolorous with mesosoma; tibiae, tarsomeres reddish.

(59) Head prognathous; lateral margin with short, inconspicuous setae; (60) mandible bidentate (Fig. 70), not scythe-like, tooth margin not sharply incised; (61) antenna 4-segmented (Fig. 45); clypeal margin flexed inward; (62) all legs with 5 tarsomeres; tibio-tarsal complexes (Figs. 101-103) with elongate basitarsi, apical basitarsal spines; (63) all gastral terga smooth, setose; posterior margins sinuate; (64) sterna smooth.

Material—Described from over 100 females and 38 males collected by William Ramírez at Playon Aguirre, Puntarenas Province, Costa Rica on 15 August 1964 from *Ficus obtusifolia* H. K. B.; by the author and Ramírez from Coiclagus, Veracruz, México, 11 August 1969 on *Ficus obtusifolia;* and by the author at El Salto, San Luis Potosí, México, 12 June 1970, also from *Ficus obtusifolia.*

Ficus obtusifolia ranges throughout México and Central America. DeWolf (1960) indicates *Ficus bonplandiana* (Liebm.) Miquel is a synonym of *Ficus obtusifolia* H. B. K. The association between *Ficus obtusifolia* and *Idarnes obtusifoliae* appears to be one of the better documented examples of host specificity between torymid and fig, since the wasp has been collected from this host at 3 widely separated localities on 3 separate occasions.

Holotype—One dissected female mounted in Hoyer's medium on 2 slides under 6 coverslips. Each label is inscribed: "*Idarnes obtusifoliae.* Playon Aguirre, Costa Rica. 15 August 1964, leg. W. Ramírez, ex. *Ficus obtusifolia.* HOLOTYPE." This locality is inland from Parrita, Puntarenas Province. *Allotype*—A dissected male mounted on 1 slide under 3 coverslips in the manner indicated above and similarly labeled. *Paratypes*—Eight dissected females slide-mounted in the manner indicated for the holotype above, with labels inscribed in a similar manner.

Variation—Females from México sometimes have a unilobed clypeus (20), antennae inserted a little higher on the head (10), head with flat vertex (9), and the propodeal carina absent (48).

Comparative Comments—*Idarnes obtusifoliae* may be easily recognized by the following combination of female characters: Head uniformly favose (8), toruli widely separated (11), 12-segmented antenna (14), flagellomeres as illustrated (17), and forewing with medial setal tract (37). Males are difficult to separate from other species since some have a scythe-like mandible (60), and some have an antenna that appears 5-segmented (61). Several large setae are arranged in transverse rows along each tergum (63) and appear to be a distinctive, constant male character.

Idarnes oscrocata, new species

Female—Body length 1.9 mm, ovipositor 5.0 mm long. (1, 2) Head and mesosoma brassy green; margin of oral fossa tan, extending to occipital foramen; (3) gaster brown; (4) scape tan with luster; pedicel brunneous; remaining antennal segments bronze; (5) all leg segments tan; (6) prosternum tan.

(7) Head hypognathous, in frontal aspect wider than long; compound eye moderately protuberant; (8) head above toruli favose; gena lacunose, weakly setose; (9) vertex flat; (10) antenna inserted at midline of compound eye; (11) toruli separated by twice diameter of torulus; antennifer conspicuous; (12) scrobe cavity deep, favose, lateral walls carinate; (13) interantennal ridge acute, short. (14) Antenna 12-segmented (Fig. 35); (15) scape asetose, elongate, extending to vertex; (16) pedicel asetose, 2 times longer than maximum width; (17) flagellomeres 1.5 times longer than wide; (18) club present but weak; terminal protuberance conspicuous. (19) Frons smooth, setose; (20) clypeal margin straight; (21) mandible bidentate (Fig. 66), tooth margin moderately incised. (22) Maxillary palpus 2-segmented; palpifer evident; (23) palpiger not evident; (24) ligula elongate with 4 sensory pegs; (25) paraglossa enveloping 2/3 of ligular margin; (26) galea with numerous acuminate setae.

(27) Pronotum postero-dorsally favose, remainder shagreened; (28, 29, 30, 31) mesoscutum, scapula, axilla, parascutellum favose; (32) mesoscutellum lacunose; (33) meson of metanotum favose, lateron with numerous longitudinal plicae. (34) Forewing (Fig. 57) with submarginal vein 3.5 times as long as marginal vein; postmarginal vein 2 times stigmal vein; (35) stigma tumid, sensilla small; (36) 3 adstigmal setae present; (37) marginal tract with few microtrichae, ending well before terminus of postmarginal vein; R_1 tract absent; submarginal tract reaching stigma; discal, medial, anal tracts absent. (38) Fore and hind coxae sculptured; middle coxa smooth; (39) femora setose, hind femur smaller than hind coxa; (40) middle tibia with single apical spur; hind tibia with 2 subequal apical spurs; (41) fore basitarsus slightly longer than tarsomere 2; middle basitarsus as long as tarsomeres 2-5; hind basitarsus as long as tarsomeres 2-4. (42) Proepisternum bronze, rugose, slightly smaller than fore coxa, bearing single elongate cranial process; (43) prosternum heart-shaped, smooth, setose on posterior quarter; (44) prepectus favose laterally, smooth mesally; (45) mesepisternum rugose laterally, shagreened mesally; (46) mesepimeron smooth along pleural suture, laterally rugose; (47) anapleurite rugose.

(48) Propodeum 3 times as wide as long, glabrous, asetose; median longitudinal carina absent; (49) gaster slightly larger than head and mesosoma combined; (50) terga lightly shagreened, posterior margins sinuate; (51) sterna coriaceous; (52) ovipositor and gonostylus 6 times gaster length; (53) gonostylus bearing small inconspicuous setae along mesal surface.

Male—Body length 1.5 mm. (54, 55) Head, mesosoma tan; (56) gaster light tan, nearly white; (57) antenna pale; (58) all leg segments concolorous with mesosoma; tibial spines amber.

(59) Head with dorsal surface lightly setose; clypeal margin concave, bearing 2 small mesal spines; (60) mandible bidentate (Fig. 82), tooth margin not sharply incised; large spines on mesal surface of mandible; (61) antenna (Fig. 42) 5-segmented; (62) all legs with 5 tarsomeres; tibio-tarsal complexes (Figs. 113-115) with

tibiae lacking apical spurs; basitarsi lacking thickened walls; (63) terga smooth, asetose; posterior tergal margins sinuate; (64) sterna smooth, asetose.

Material—Described from 6 females collected on 6 August 1969 and 87 females and 4 males collected on 20 August 1969, 2 miles north of Izucar de Matamoros, Puebla, México, along the Rio Balsas, by the author and William Ramírez. In both instances the host tree was *Ficus goldmanii.*

Ficus goldmanii Standley ranges throughout México and into Central America. In Puebla this species grows in a riparian situation; in Sinaloa it was observed growing in a xeric habitat. *Idarnes* was not recovered from figs taken in Sinaloa.

Holotype—One dissected female mounted in Hoyer's medium on 2 slides under 6 coverslips. Each label is inscribed: "*Idarnes oscrocata.* 2 mi. N. Izucar de Matamoros, Puebla, México. 20 August 1969, leg. Gordh and Ramírez, ex. *Ficus goldmanii.* HOLOTYPE." *Allotype*—One dissected male mounted in Hoyer's medium under 3 coverslips on a single slide, with the label inscribed as indicated above. *Paratypes*—Eight dissected females, each on one slide under 3 coverslips in Canada balsam.

Variation—Some females have 2 sensory pegs on the ligula (24), the frons may be lacunose (19), the medial vein tract is sometimes obscure (37), the metanotal meson may be lacunose (33), and the propodeum may be mesally and postero-laterally rugose (48). Aside from the fourth antennal segment being nearly fused to the club (61), little variation was detected in males.

Comparative Comments—Females of this species may easily be recognized by the conspicuous tan margin of the oral fossa (1), straight clypeal margin (20), elongate ligula with 4 sensory pegs (24), medial vein tract (37), rugose anapleurite (47) and coriaceous sterna (51). Males are identifiable by their bidentate mandible (60), 5-segmented antenna (61), and asetose terga with sinuate posterior margins (63).

Idarnes oscrocata appears most closely related to *I. obtusifoliae* and may be distinguished from that species on the basis of facial sculpture pattern (8), and clypeal margin conformation (20).

Idarnes parallela (Mayr)

Ganosoma parallelum Mayr, 1885, Verh. Zool. Bot. Gesell. Wien 35:204, ♂.

The female of *I. parallela* remains undescribed. From the original description by Mayr, it is not possible to state with certainty that a synonymy has not been made in the present work or that a previously described species is not synonymous with *I. parallela.* Until further collections have been made in Brazil and *I. parallela* females are collected and associated with the males, positive statements regarding the taxonomic status of *I. parallela* cannot be made.

Idarnes punctata (Mayr)

Tetragonaspis punctata Mayr, 1885, Verh. Zool. Bot. Gesell. Wien 35:209, ♀.

The female of this species was adequately described by Mayr, but the male remains undescribed. It is a species of *Idarnes* as here restricted, from Brazil.

Idarnes simus, new species

Female—Body length 2.0 mm, ovipositor 6.2 mm long. (1, 2) Head, mesosoma bright metallic green; margin of oral fossa pale; (3) gaster dorsally tawny; sterna tan with pale transverse stripes; (4) scape brownish yellow, remaining segments chestnut brown; (6) prosternum tan; mesosternum pale at discrimen, remainder concolorous with head and mesonotum.

(7) Head hypognathous, in frontal aspect slightly wider than long; compound eye not protuberant; (8) face favose above

level of toruli; gena smooth, strongly setose; (9) vertex weakly sinuate; (10) antenna inserted at lower third of compound eye; antennifer conspicuous; (11) toruli separated by 3 times diameter of torulus; (12) scrobe nearly absent, 2 widely separated channels, short, smooth; (13) interantennal ridge broad, not acute. (14) Antenna (Fig. 34) 13-segmented; (15) scape elongate, setose, extending to vertex; (16) pedicel not elongate, bearing few setae; (17) flagellomeres 2 times as long as wide, verticillate; setae flexible, more numerous than carinae; (18) club absent; terminal protuberance conspicuous. (19) Frons smooth, setose; (20) clypeal margin straight; (21) mandible bidentate, tooth margin sharply incised. (22) Maxillary palpus 2-segmented; palpifer small; (23) palpiger not evident; (24) ligula with 2 sensory pegs; (25) paraglossa enveloping basal 2/3 of ligular margin; (26) galea with numerous acuminate setae.

(27) Pronotum postero-dorsally favose, remainder shagreened, pattern lightly incised; (28, 29, 30, 31) mesoscutum, scapula, axilla, parascutellum favose; (32) scutellum lacunose, nearly smooth; (33) meson of metanotum favose, lateron bearing several longitudinal plicae. (34) Forewing (Fig. 49) with submarginal vein 3 times as long as marginal vein; postmarginal vein 2 times stigmal vein; (35) stigma tumid, sensilla small; (36) 2 adstigmal setae; (37) marginal tract ending at postmarginal vein; R_1 tract absent; submarginal tract ending at stigma; discal, medial, anal tracts absent. (38) Fore and hind coxae lightly shagreened; (39) femora shagreened, setose; (40) middle tibia heavily setose, bearing single apical spur; hind tibia with setal tract, 2 subequal apical spurs; (41) fore basitarsus as long as tarsomeres 2-3; middle basitarsus longer than remaining tarsomeres; hind basitarsus as long as tarsomeres 2-4. (42) Proepisterna smaller than fore coxa, shagreened, bearing setae basally, single wide cranial process; (43) prosternum nearly round, smooth, bearing few setae; discrimen extending 1/3 the length of structure; (44) prepectus favose mesally, smooth laterally; (45) mesepisterna setose, laterally favose with pattern centrally rugose, absent at discrimen; (46) mesepimera favose; (47) anapleurite rugose.

(48) Propodeum 4 times as wide as long, mesally rugose, laterally smooth; median longitudinal carina absent; (49) gaster ovoid, slightly larger than head and mesosoma combined; (50) terga lightly shagreened; posterior tergal margins strongly sinuate; (51) sterna coriaceous; (52) ovipositor and gonostylus 5 times gaster length; (53) gonostylus bearing small setae along mesal surface.

Male—Body length 1.2 mm. (54, 55) Head and mesosoma tan; (56) gaster white; (57) antenna, except segment 3, amber; (58) legs honey colored with tibial margins red.

(59) Head with small setae sparsely arranged over dorsal surface; clypeal margin strongly concave, without setae or spines; (60) mandible bidentate (Fig. 81), not scythe-like; (61) antenna (not figured) 5-segmented; (62) tarsi 5-segmented; tibiae (Figs. 89-91) without large apical spurs; basitarsi with few apical spurs; (63) terga asetose; posterior tergal margins sinuate; (64) sterna smooth, asetose.

Material—Described from 31 female and 14 male specimens collected by William Ramírez at Rio Aguilar, Hatillo, San José, Costa Rica on 14 June 1964 from *Ficus lapithifolia*. This species of fig is widespread in México and Central America.

Holotype—One dissected female mounted in Hoyer's medium on 2 slides under 5 coverslips. Each label is inscribed: "*Idarnes simus*. Rio Aguilar, Hatillo, Costa Rica. 14 June 1964, leg. W. Ramírez, ex. *Ficus lapithifolia*. HOLOTYPE."

Allotype—One dissected male mounted on 1 slide under 3 coverslips in the manner indicated above. *Paratypes*—Eight dissected females, slide mounted in the manner indicated for the holotype, with a similar label inscription.

Variation—In some females the face may be rugose at the level of the toruli and become progressively more favose towards the vertex (8), the entire pronotum may be shagreened (27), the mesosternum may be asetose (45, 46) or the anapleurite may be shagreened (47). Males exhibit some size variation, but appear remarkably constant morphologically. Occasionally, a male may have a mandible verging on scythe-like (60).

Comparative Comments—This wasp is easily recognized by the following combination of female characters: widely separated toruli (11), broad, flat interantennal ridge (13), flexible, blunt setae on each flagellomere (17), smooth frons bearing setae (19), straight clypeal margin (20), and mesopectus favose (44, 45, 46). Males have small setae on the head (59), bidentate mandible (60), and asetose terga (63).

SPECIES INCORRECTLY ATTRIBUTED TO *IDARNES*

The species listed below have at one time or another been placed in *Idarnes*, but this assignment is probably or certainly incorrect as explained in each case.

Idarnes australis Froggatt, 1900, Agr. Gazette N.S.W. 11:452, ♀.

The illustration of this species indicates the forewing lacks setal tracts and adstigmal setae, and the hindwing bears a fully developed marginal vein. Froggatt's description makes the species difficult to place, but it has been recognized by Mayr (1906) as *Sycoryctes australis*. It is an Australian species and for that reason alone unlikely to fall in *Idarnes* as that genus is here defined.

Otitesella gnaphalocarpae Risbec, 1951, Mém. Inst. Français d'Afr. Noire 13:332, ♀.

I have not had the opportunity to examine this species. Wiebes (1970) regards it as an *Idarnes* species. It was described from Senegal emerging from *Ficus gnaphalocarpa* and for these reasons probably does not belong to *Idarnes* as here restricted.

Idarnes gracilie Wiebes, 1968, Zool. Meded. 42:318, ♀.

Described from Africa, this species bears a strong resemblance to *Idarnes*. However, I consider the species extralimital not only because of its continent of origin but because: (1) the forewing lacks setal tracts; (2) the hindwing has a completely developed marginal vein; (3) the terminal segment of the maxillary palpus is not excindate; (4) an acuminate seta is found on the first maxillary palpal segment rather than at the base of the terminal one; and (5) as pictured, the female lacks the discoid sensillum on the base of the first palpal segment of the maxilla.

Idarnes nigra Risbec, 1951, Mém. Inst. Français d'Afr. Noire 13:123, ♀, ♂.

Wiebes (1970) examined Risbec's material and indicated that the females are probably *Sycoscapter* and the males *Apocrypta*. The continent of origin is sufficient to exclude the material from *Idarnes* as here defined.

Idarnes orientalis Walker, 1875, Entomologist 8:17, ♀.

I have not had the opportunity to examine the material. Walker indicated *I. orientalis* was recovered from Hindustan and Ceylon. On the basis of distribution it is excluded from *Idarnes* as here defined. Grandi (1928) considered *I. orientalis* a synonym of *Sycoscapter stabilis*.

Idarnes pteromaloides Walker, 1871, Notes on Chalcidiae 4:63, ♀.

Wiebes (1967) has considered the material as *Micransia pteromaloides* (Walker). The material described by Walker came from Hindustan, and hence is excluded from *Idarnes* in the present work.

Idarnes stabilis Walker, 1871, Notes on Chalcidiae 4:62, ♀.

Wiebes (1967) has demonstrated that *I. stabilis* is *Sycoscapter stabilis* (Walker). The original material came from India and is also excluded from *Idarnes* on the basis of distribution.

Idarnomorpha subaenea Girault, 1915, Mem. Queensland Mus. 4:282, ♀, ♂.
Idarnes subaenea Girault, 1917, Insec. Inscit. Menstr. 5:37, ♀.

Girault (1917) considered *Idarnomorpha* to be synonymous with *Idarnes;* thus the Australian species *subaenea* was transferred to *Idarnes.* Girault considered the antenna 13-segmented, counting the terminal protuberance as a distinct segment. Girault indicates the female is 1.75 mm and the male is 2.8 mm long. In all described species of *Idarnes*, the female is larger than the male. If the sexes are correctly associated, a typographical error has probably been made. Assuming the sexes to be correctly associated, *Idarnes subaenea* must be considered extra-limital both geographically and morphologically. *Idarnomorpha* is probably a good genus on the basis of the male antenna being 3- and tarsi 5-segmented. The wasps were reared from figs with *Ceratosolensis ficophaga* Girault. *Idarnes* has been shown in all other instances to parasitize tropical American *Blastophaga*; hence, biological information also suggests that *Idarnomorpha* is a valid genus.

Idarnes transiens Walker, 1871, Notes on Chalcidiae 4:62, ♀.

Idarnes transiens was described from the female from Ceylon and India. Morphologically, the species is clearly not *Idarnes,* and Wiebes (1967) has called it *Philotrypesis transiens.*

Tetragonaspis testacea Mayr, 1885, Verh. Zool. Bot. Gesell. Wien 35:157, ♀.
Eukoebelea testacea Mayr, 1906, Wien. Ent. Ztg. 25:165, ♀.
Sycophagella agraensis Joseph, 1953, Agra Univ. J. Sci. 2:54, ♀, ♂.
Idarnes testacea (Mayr), Joseph, 1956, Ann. Soc. Ent. Fr. 125:103, ♀, ♂.

Illustrations do not accompany the original description of *Tetragonaspis testacea.* Joseph (1953) described *Sycophagella agraensis* from the receptacles of *Ficus glomerata* collected in India and illustrated the female. In 1956, he considered *S. agraensis* synonymous with *Idarnes testacea* (Mayr). If Joseph's description is correct, and if he has correctly associated *S. agraensis* with *T. testacea,* then this material cannot be considered *Idarnes* for the following reasons: (1) the maxillary palpus is unisegmented; (2) the forewing lacks a parastigmal notch and sensilla; (3) the forewing lacks setal tracts; and (4) the hindwing bears a fully developed marginal vein. Geographically, also, this species is outside the known range of *Idarnes* as here delimited.

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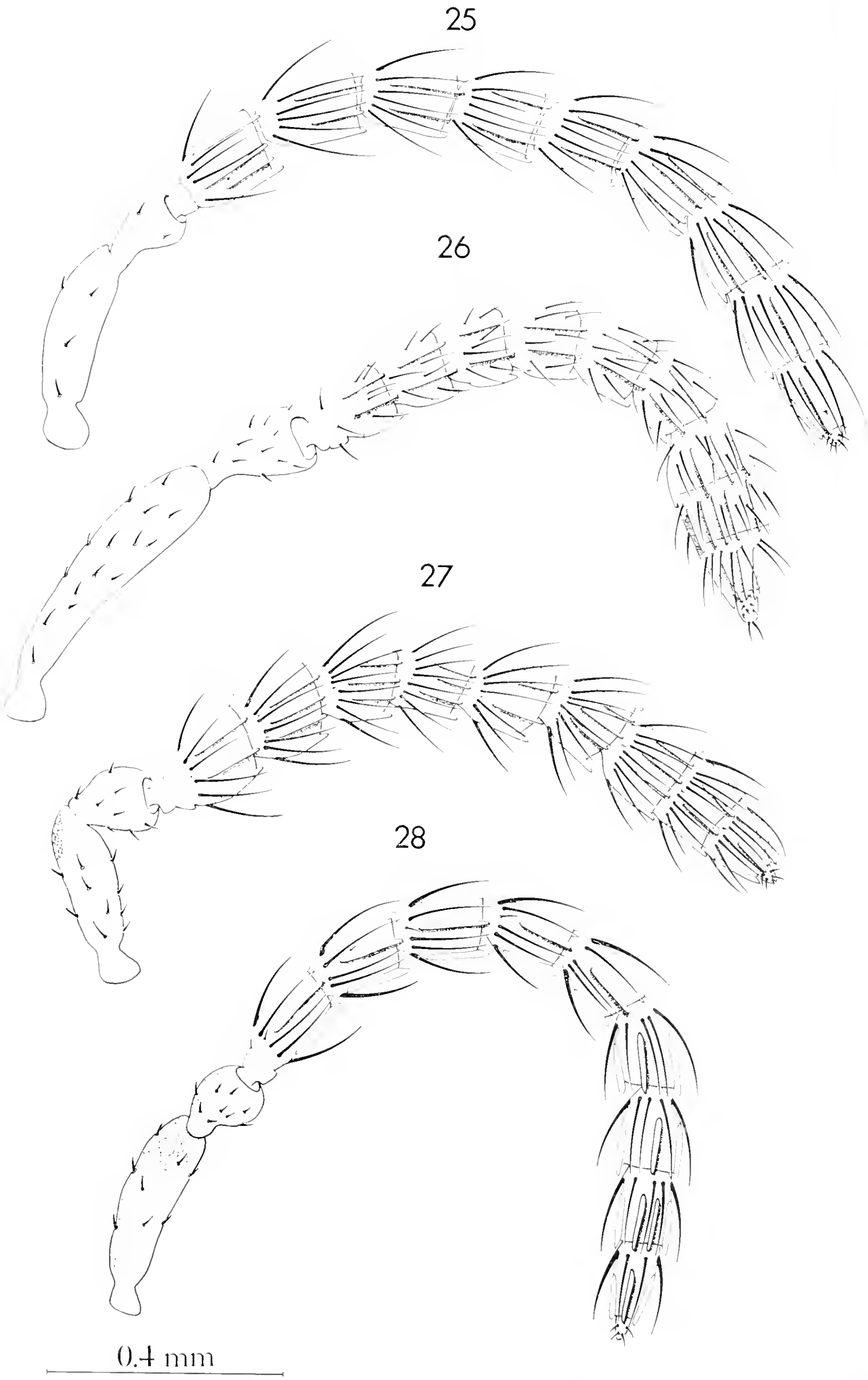
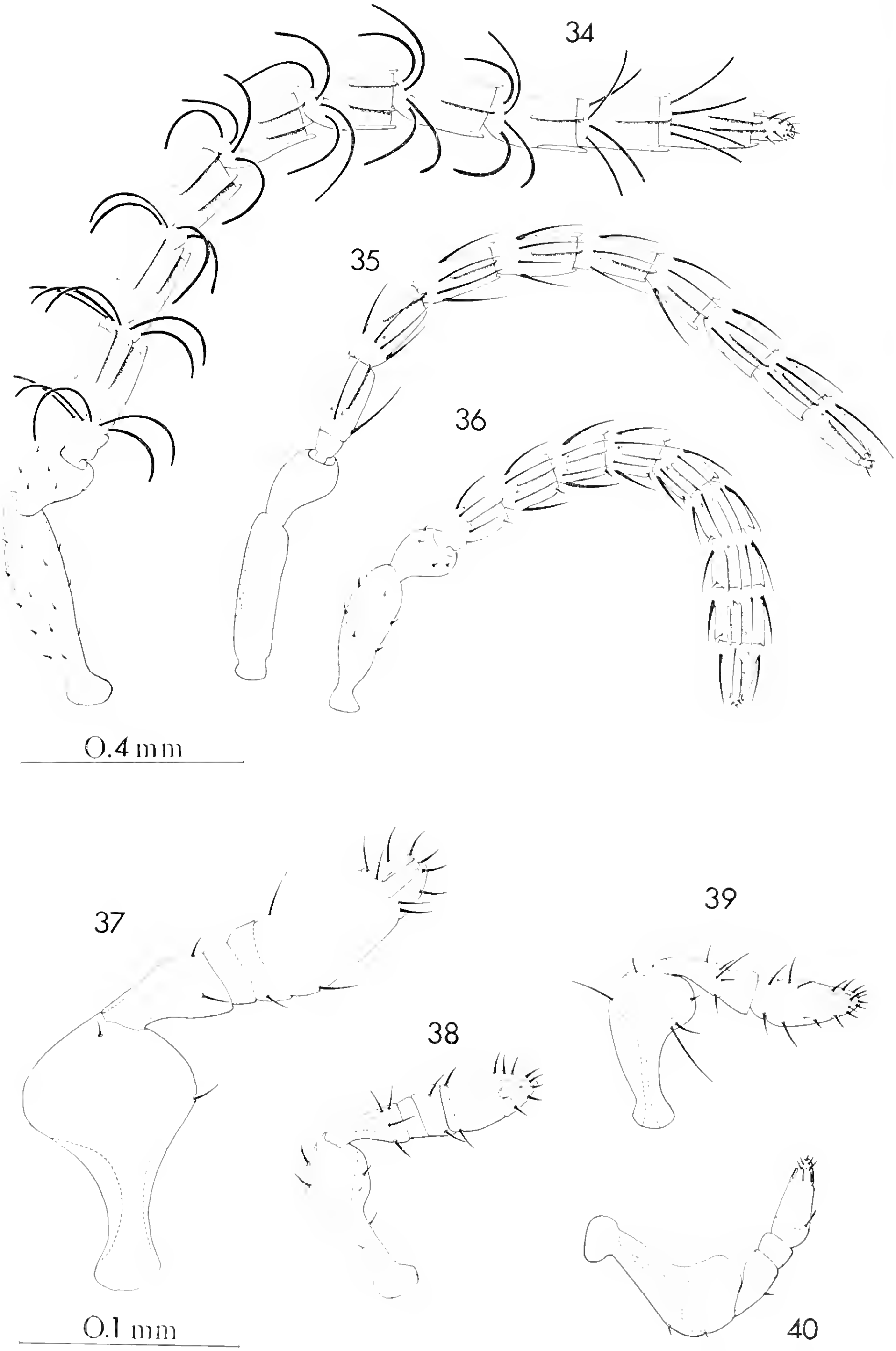
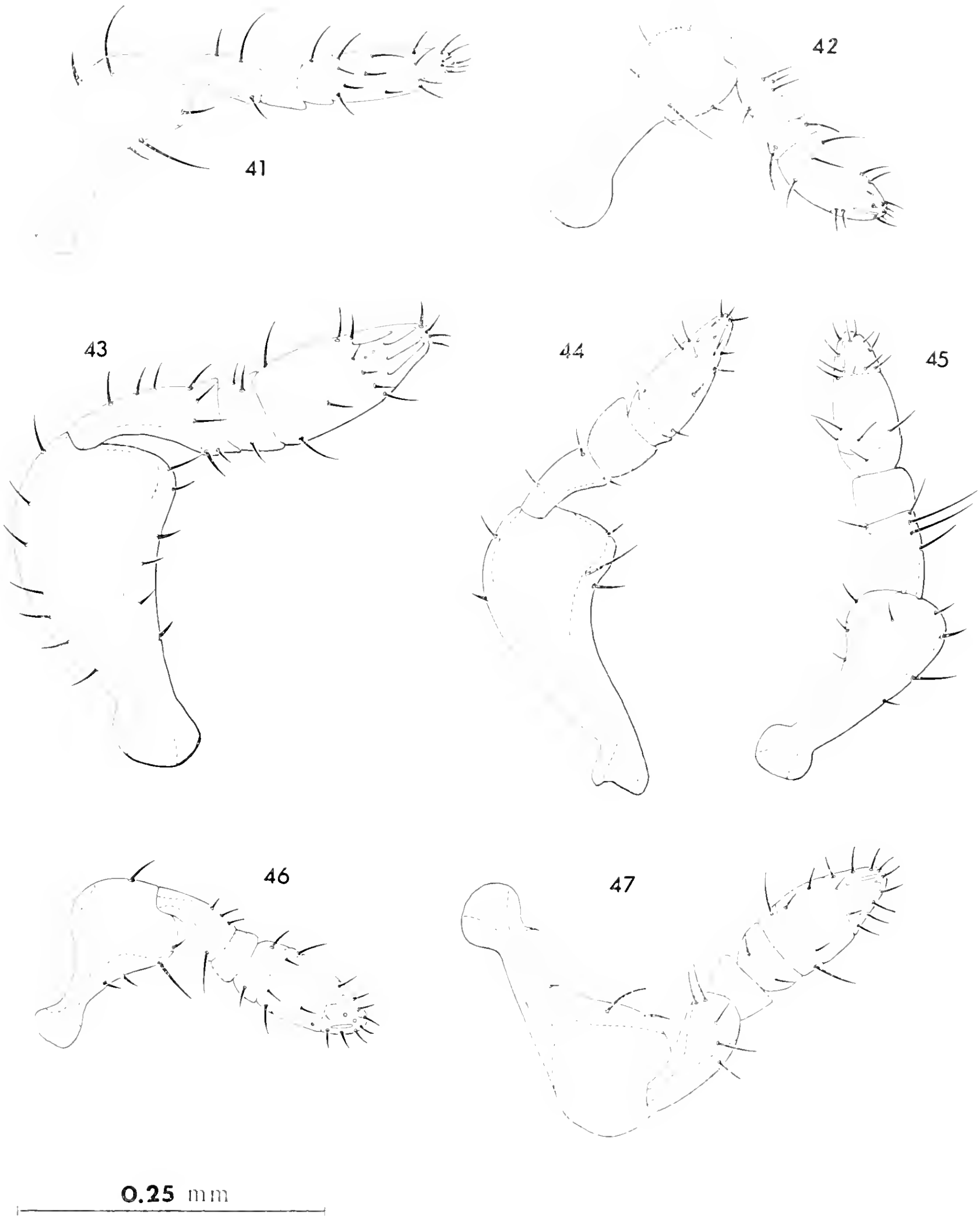


Figs. 25-28. Left antenna of *Idarnes* females, inner aspect. **25,** *I. barbigera;* **26,** *I. bucatoma;* **27,** *I. micheneri;* **28,** *I. ashlocki.*

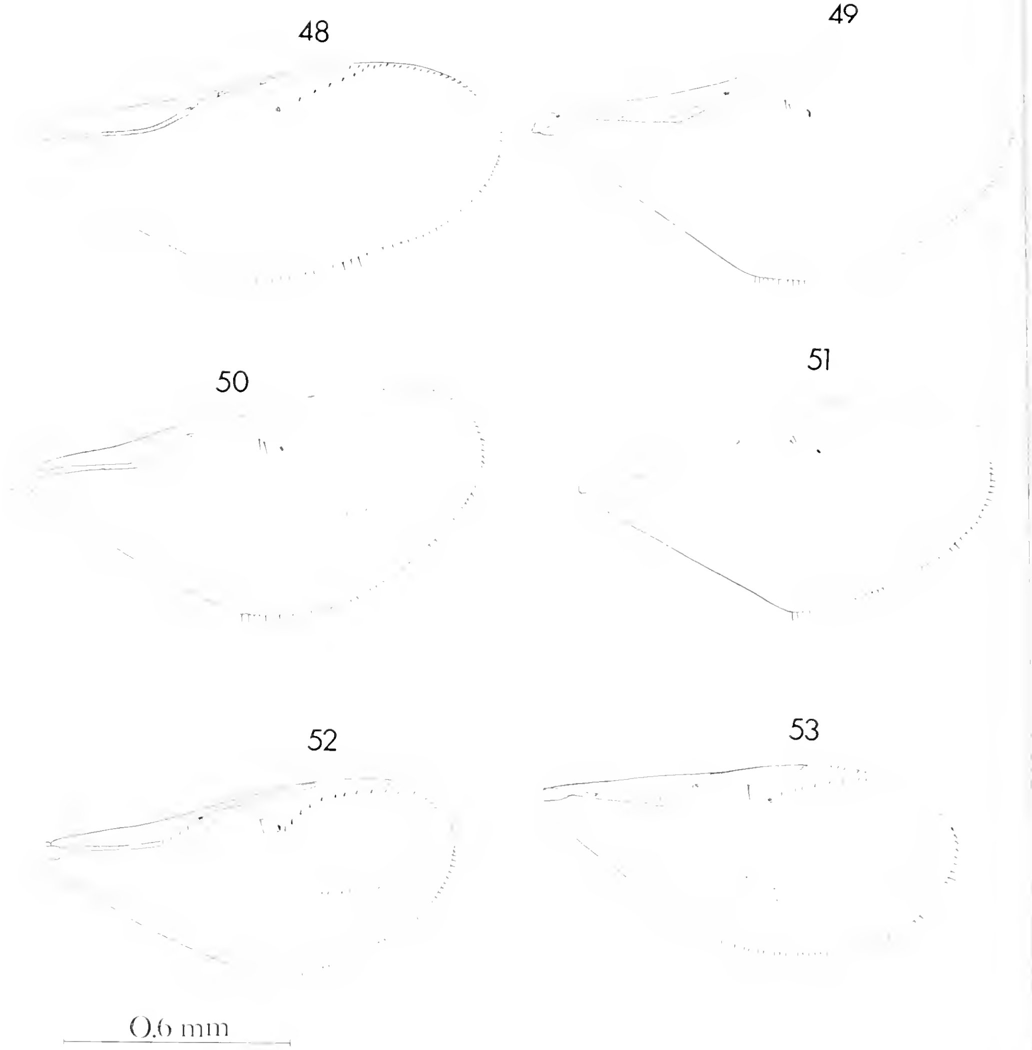
Figs. 29-33. Left antenna of *Idarnes* females, inner aspect. 29, *I. flavicollis;* 30, *I. obtusifoliae;* 31, *I. galbina;* 32, *I. carme;* 33, *I. camim.*



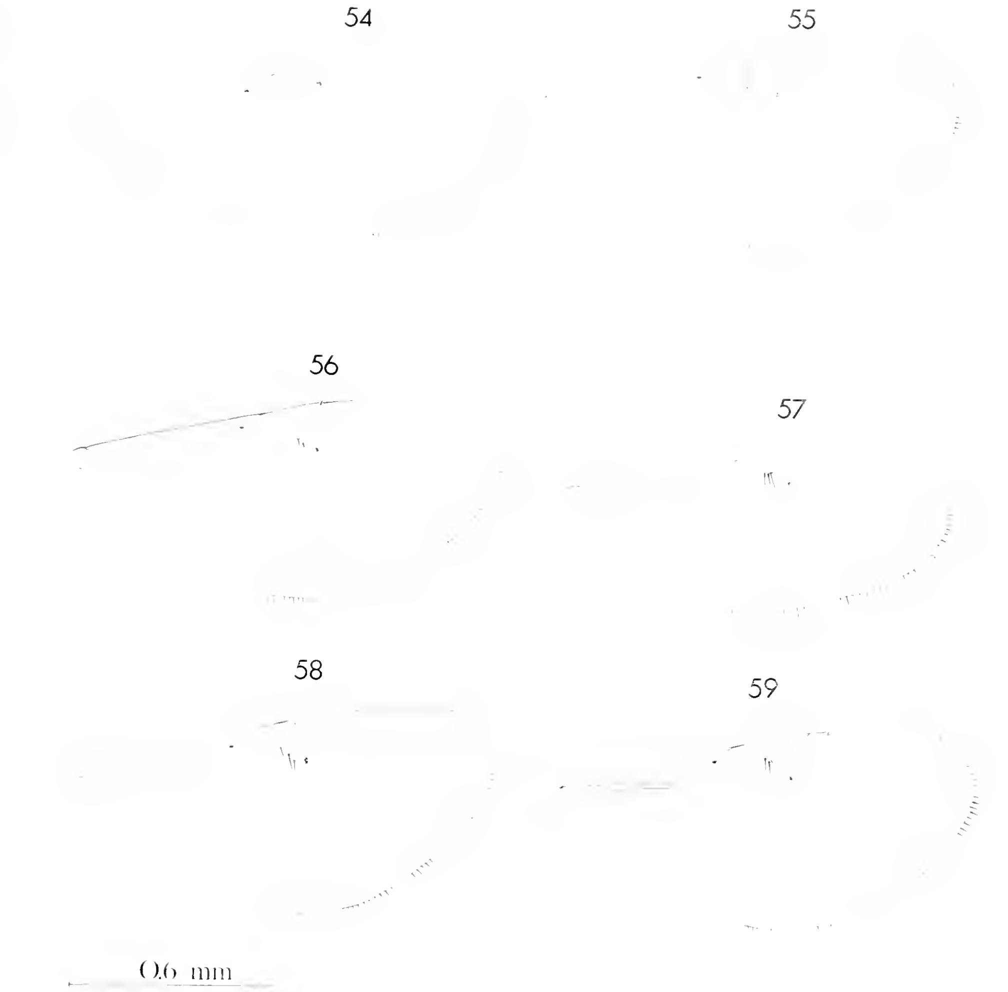
FIGS. 34-40. Left antenna of *Idarnes* females (34-36) and males (37-39), inner aspect; right antenna, male, dorsal aspect (40). **34,** *I. simus;* **35,** *I. oscrocata;* **36,** *I. jimenezi;* **37,** *I. galbina;* **38,** *I. camini;* **39,** *I. ashlocki;* **40,** *I. carme.*



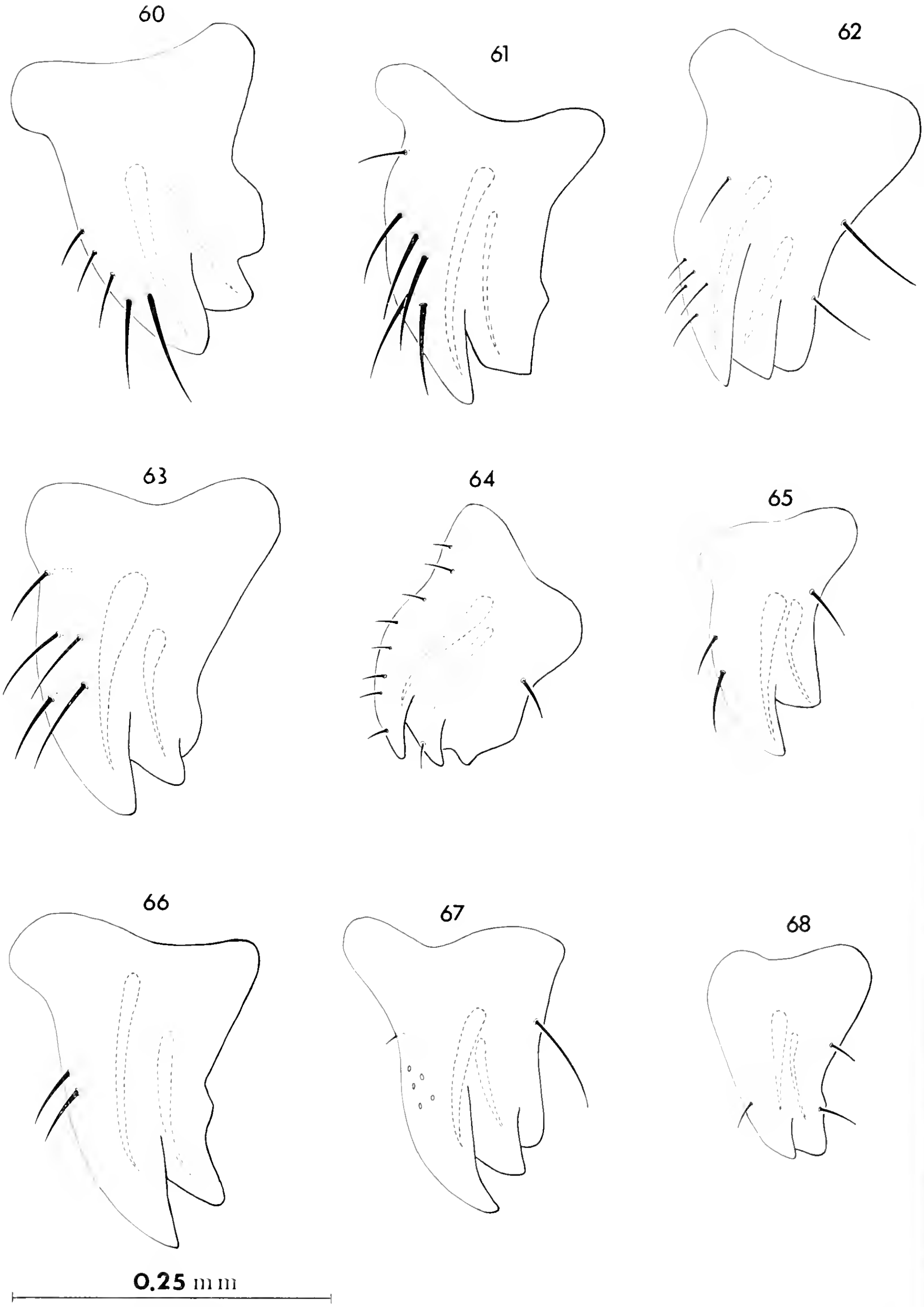
Figs. 41-47. Antennae of *Idarnes* males, dorsal aspect; 45, 47 right antenna, remainder left. **41**, *I. jimenezi*, **42**, *I. oscrocata:* **43**, *I. bucatoma;* **44**, *I. barbigera;* **45**, *I. obtusifoliae;* **46**, *I. micheneri;* **47**, *I. flavicollis.*



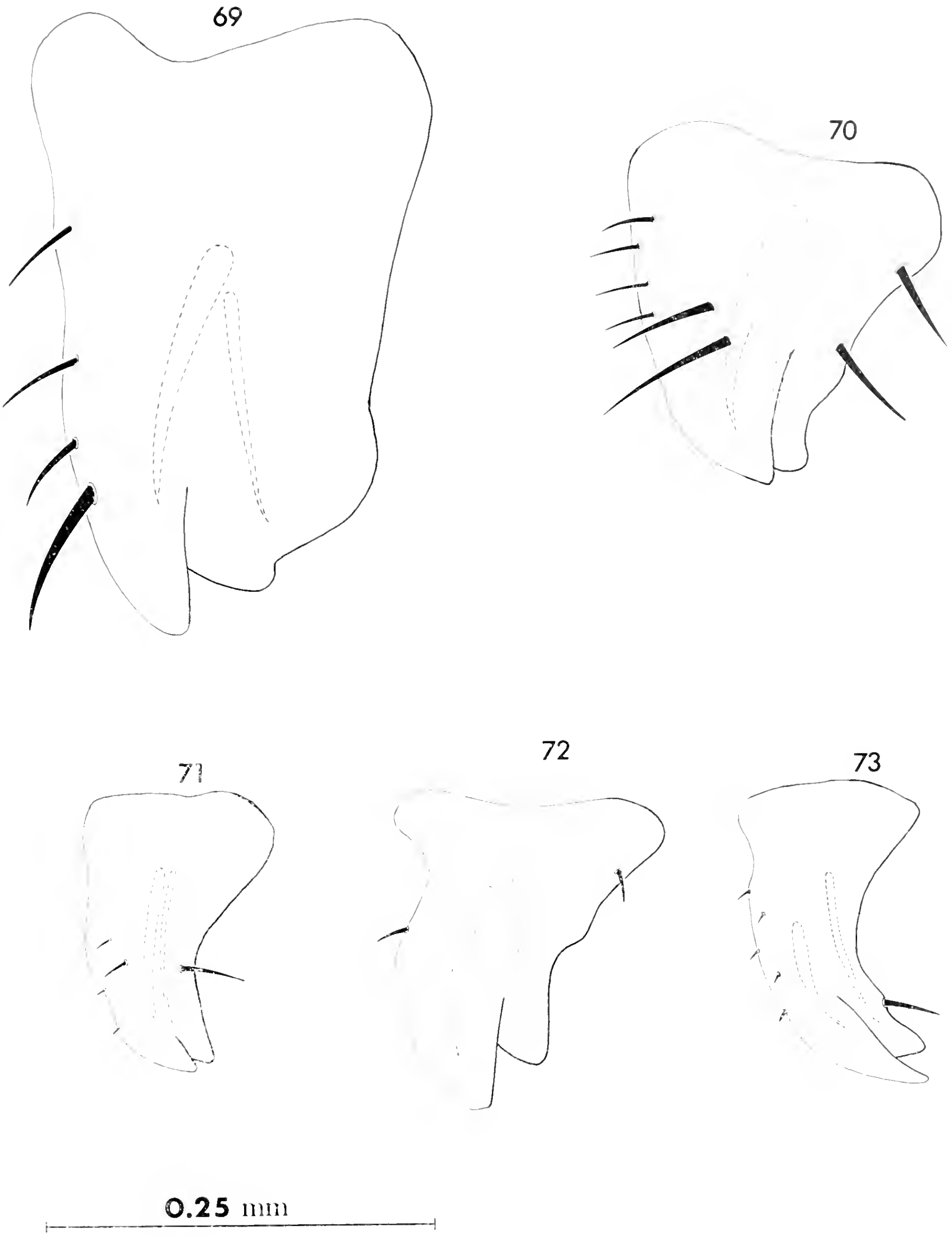
FIGS. 48-53. Right forewing of *Idarnes* females. **48**, *I. flavicollis;* **49**, *I. simus;* **50**, *I. galbina;* **51**, *I. ashlocki;* **52**, *I. obtusifoliae;* **53**, *I. carme.*



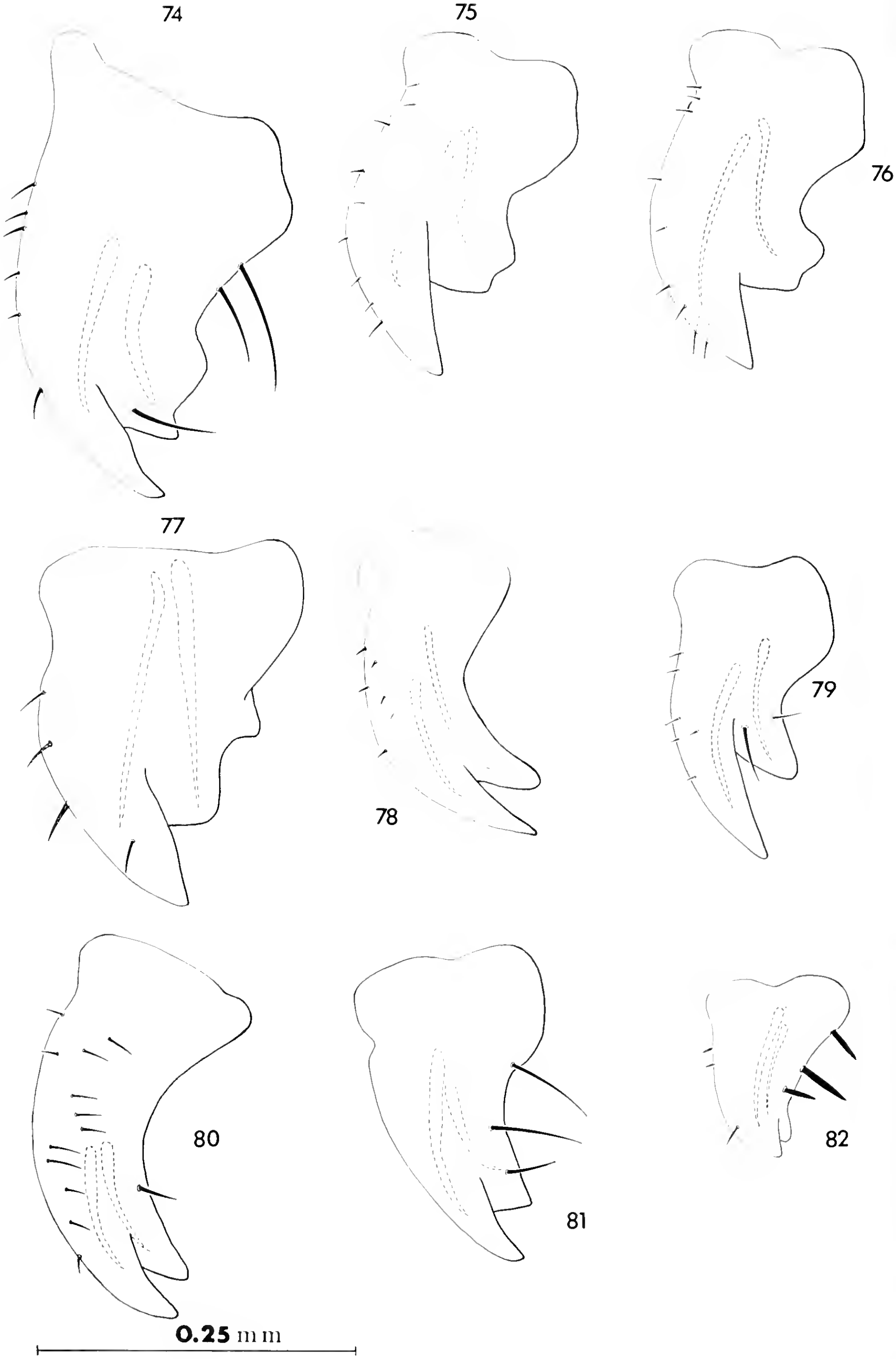
Figs. 54-59. Right forewing of *Idarnes* females. **54,** *I. bucatoma;* **55,** *I. camini;* **56,** *I. barbigera;* **57,** *I. oscrocata;* **58,** *I. micheneri;* **59,** *I. jimenezi.*



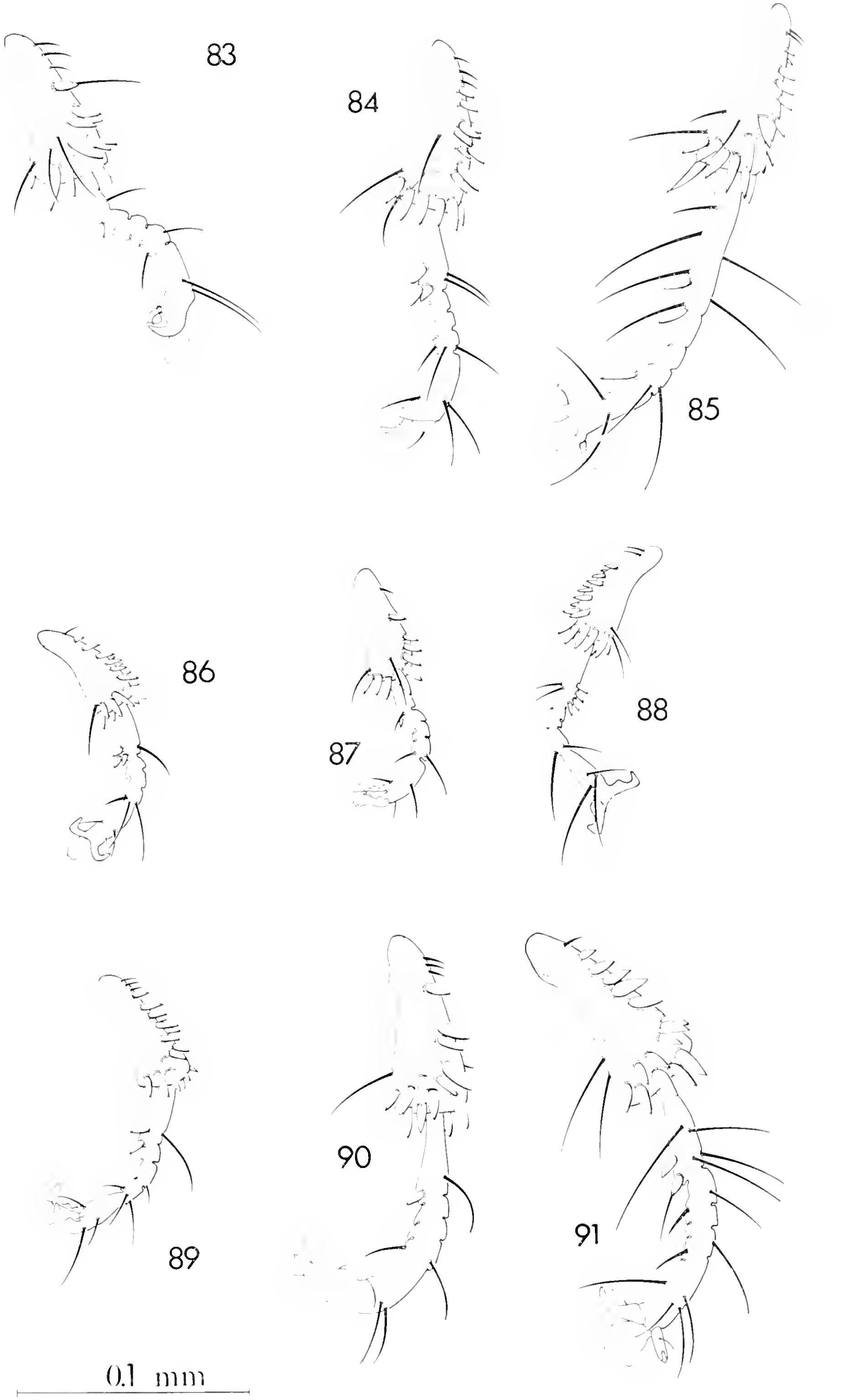
FIGS. 60-68. Right mandible of *Idarnes* females, inner aspect. **60**, *I. micheneri;* **61**, *I. barbigera;* **62**, *I. obtusifoliae;* **63**, *I. ashlocki;* **64**, *I. bucatoma;* **65**, *I. jimenezi;* **66**, *I. oscrocata;* **67**, *I. camini;* **68**, *I. galbina.*



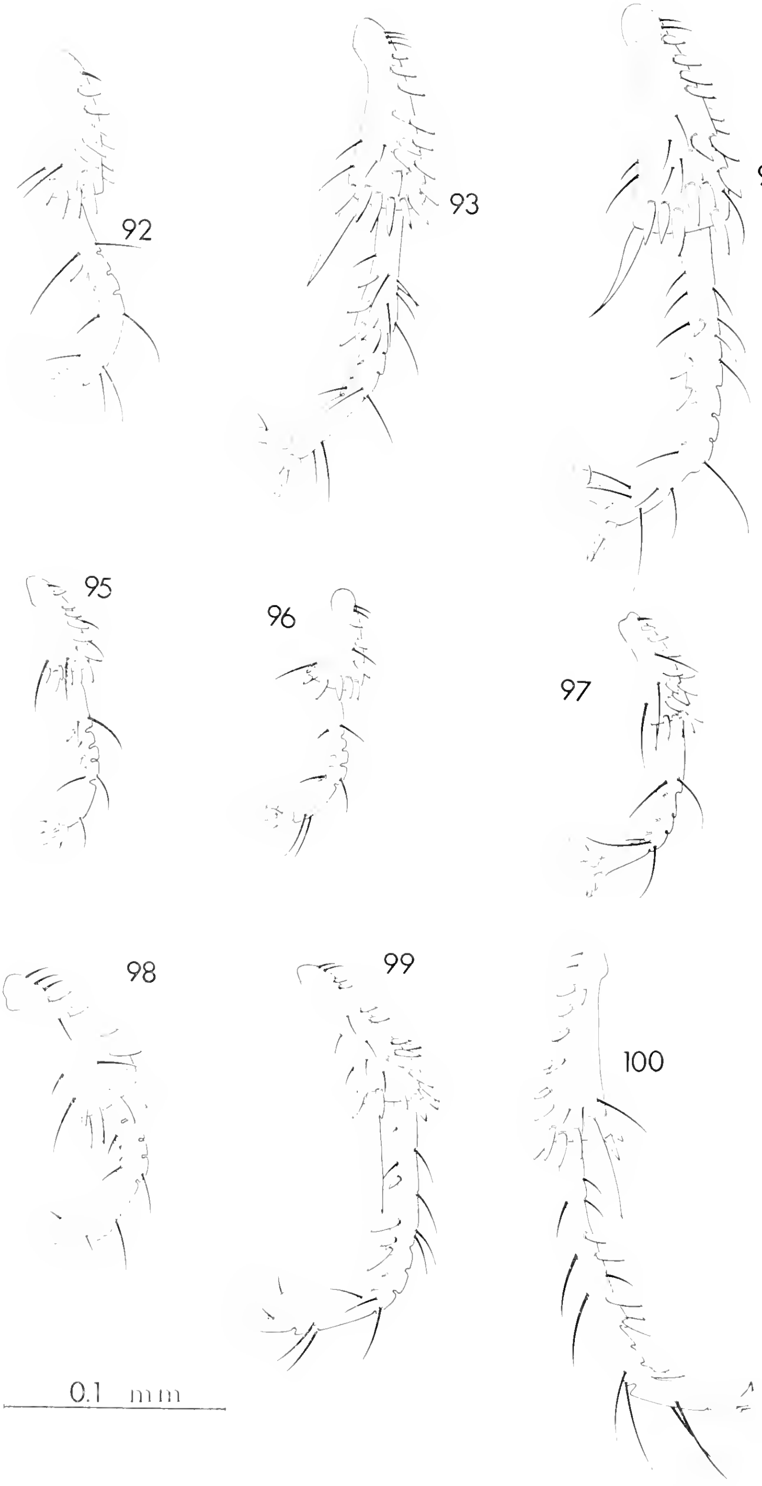
Figs. 69-73. Right mandible of *Idarnes* females (69, 72) and males (70, 71, 73), inner aspect. **69**, *I. flavicollis*; **70**, *I. obtusifoliae*; **71**, *I. ashlocki*; **72**, *I. carme*; **73**, *I. carme*.



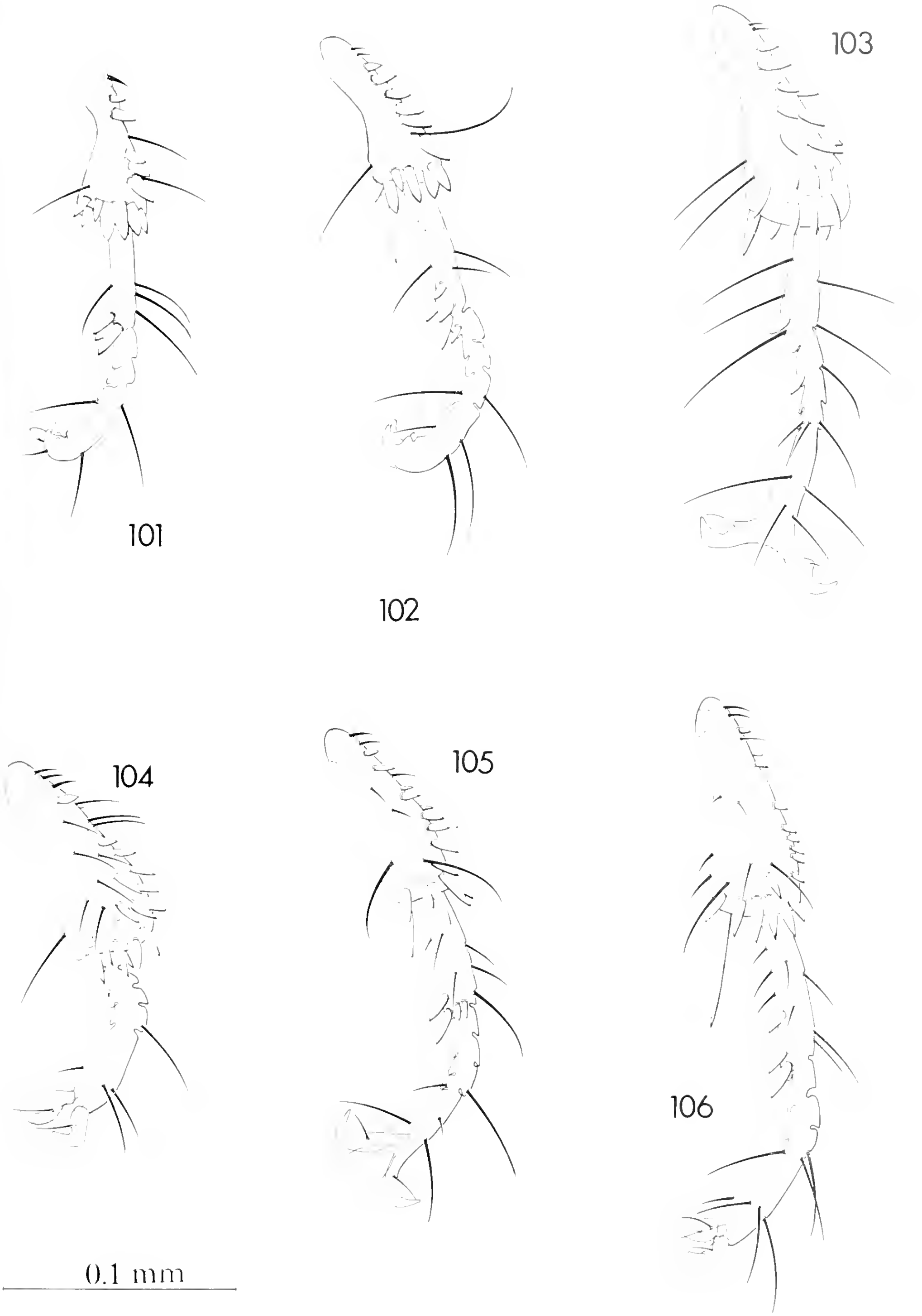
FIGS. 74-82. Right mandible of *Idarnes* males, inner aspect. **74,** *I. bucatoma;* **75,** *I. flavicollis;* **76,** *I. micheneri;* **77,** *I. galbina;* **78,** *I. jimenezi;* **79,** *I. camini;* **80,** *I. barbigera;* **81,** *I. simus;* **82,** *I. oscrocata.*



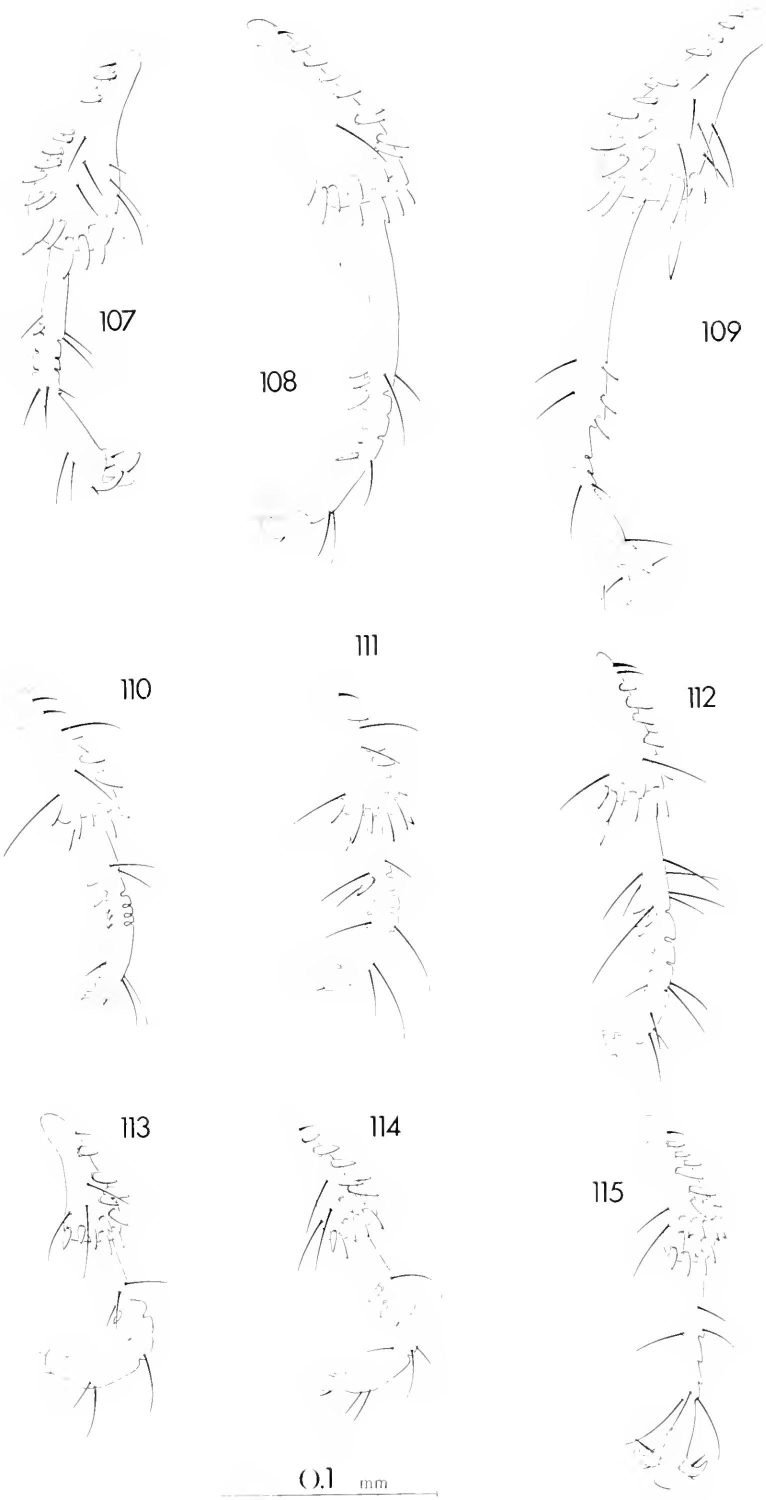
FIGS. 83-91. Fore, middle and hind tibiotarsi of *Idarnes* males, inner aspect. **83-85**, *I. ashlocki;* **86-88**, *I. galbina;* **89-91**, *I. simus.*



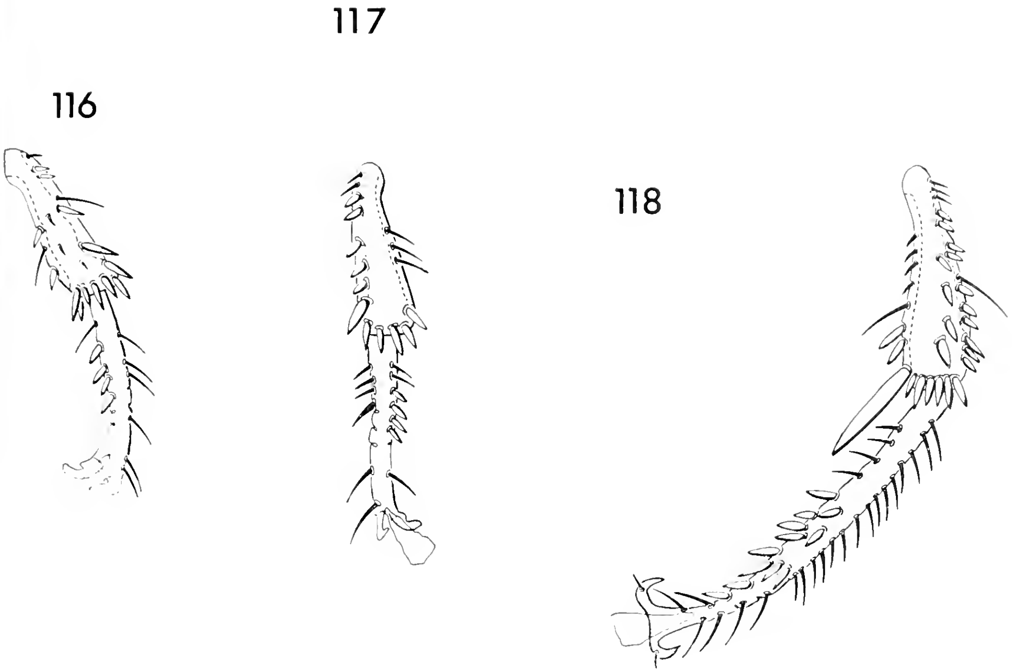
Figs. 92-100. Fore, middle and hind tibiotarsi of *Idarnes* males, inner aspect. **92-94**, *I. flavicollis;* **95-97**, *I. carme;* **98-100**, *I. camini.*



Figs. 101-106. Fore, middle and hind tibiotarsi of *Idarnes* males, inner aspect. **101-103**, *I. obtusifoliae*; **104-106**, *I. micheneri*.



FIGS. 107-115. Fore, middle and hind tibiotarsi of *Idarnes* males, inner aspect. **107-109,** *I. barbigera;* **110-112,** *I. jimenezi;* **113-115,** *I. oscrocata.*



FIGS. 116-118. Fore, middle and hind tibiotarsi of *Idarnes bucatoma* male, inner aspect. (Hind tibiotarsus = 0.2 mm.)

THE UNIVERSITY OF KANSAS

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THORACIC POLYMORPHISM IN *MESOVELIA MULSANTI* (HEMIPTERA: MESOVELIIDAE)

By

JANET E. GALBREATH

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Thoracic Polymorphism in *Mesovelia mulsanti* (Hemiptera: Mesoveliidae)

Janet E. Galbreath

Thoracic Polymorphism in *Mesovelia mulsanti* (Hemiptera: Mesoveliidae)[1]

Janet E. Galbreath[2]

ABSTRACT

Three thoracic morphs are recognized: winged, wingless and intermediate (new term to identify flightless adults that develop from nymphs with wing pads). The wingless morph may be recognized in the fourth nymphal instar by the absence of wing pads. An individual of the fourth instar with wing pads must be observed in the fifth instar to identify the morph. In an intermediate morph of the fifth instar, the wing pads may reach to the second abdominal segment, remain short, become vestigial, or be absent. A winged morph of the fifth instar has long wing pads which extend to the third abdominal segment or beyond.

Results of crossing studies gave little evidence to suggest that any one of the nine kinds of crosses (three morphs, sexes taken reciprocally) would yield significantly more of any one kind of morph. The occurrence of morphs (as nymphs) was related to field temperatures, called "the estimated mean air temperature" and derived from the climatologist's "march of monthly mean temperatures." Fourth and fifth instars of the wingless morph were collected when the estimated mean air temperature ranged from a spring low of 16.7° C to a summer high of 28.3° C and to a fall low of 8.3° C. Fourth and fifth instars of the winged and intermediate morphs were found primarily, but irregularly, when estimates of the mean air temperature were 21.5° C or higher.

Nymphs have one or two morph-determining points in development. The first, whether or not wing pads develop, occurs in all nymphs. The sentitive stage for the first critical point is unknown, but it is thought to occur prior to the late third instar. In the field, high temperatures and unknown factors during the first critical period are apparently necessary for a high frequency (11-45%) of nymphs with wing pads. In the laboratory, a high frequency of nymphs with wing pads was reared from a parental stock with a frequency of 11 to 45% and when the fluctuating temperatures averaged 25.6° C or higher. The second critical period occurs early to midway in the fourth stadium of nymphs with wing pads. A fourth instar with wing pads is more likely to become a winged morph in the field than in a laboratory rearing, but it is not known why.

INTRODUCTION

Historical background. Thoracic polymorphism is typical of members of the superfamily Gerroidea; Usinger (1956) gave examples of it in six families. In *Mesovelia*, thoracic polymorphism occurs in both sexes. Heretofore, two morphs have been recognized: the common wingless, or apterous, morph lacking wing pads as a nymph and wings as an adult, and the winged, or macropterous, morph known to have long wing pads in the fifth instar and wings in the adult. A third term, short-winged or brachypterous, has been used in two ways: to name the wingless adults mentioned above (Jaczewski, 1928; Gupta, 1963) and to denote winged adults with broken wings, an error first recognized by Horváth (1915).

The literature concerning *Mesovelia* shows that the winged morph is rare in areas where the average monthly mean for July is 21° C or lower. The relative abundance of the winged and wingless morphs of *M. furcata* Mulsant and Rey was observed between 59° and 45° north latitude in Europe where the average monthly means of July are 17° C to about 21° C, respectively. In Sweden, where this species is univoltine, wingless adults are common; only one winged adult is recorded (Ekblom, 1930; Wesenberg-

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Lund, 1943). Leth (1943) reported 20 (=7%) winged adults from the southern half of Denmark. In Germany and France, where there are one or two annual generations, the winged morph is infrequent. Jordan (1931, 1936), who studied in Oberlausitz, found only wingless adults in 1925 to 1927, five winged among many hundred wingless adults in 1928, and three specimens of the winged morph (one adult, two nymphs) in 1934. Apparently no more winged adults were collected until 1950, when he was astonished to find 16 (Jordan, 1951). Schumacher (1919) found one winged adult near Brodown, Germany; Müller (1919) reported winged adults and the more common wingless adults on July 5, 1911, on a pond near Walkenried, Thüringia. Poisson (1922, 1933) stated that he had never collected the winged morph in the Department of Calvados.

Likewise near Pellston, Michigan (45° 34′ north latitude; average monthly mean of July, 18.8° C), Hungerford (1953) reported few winged (none, 1923-1950; a total of five, 1951-1952) and a preponderance of wingless adults of *M. douglasensis* Hungerford (taxonomy not clear; possibly a synonym of *M. amoena* Uhler). In contrast, he gave data from pinned specimens from southern states (37° to 25° north latitude; average monthly means of July, 25.5° C or higher) showing a frequency of 20% (N = 174) for the winged morph.

The literature pertaining to *M. mulsanti* White near Pellston gives some information on the morphs of adults. Hussey (1919) listed only the wingless morph taken in general collecting in the years 1913, 1914, and 1918. Hoffmann (1932) for the year 1930 and Neering (1954) for the year 1950 reported that winged adults occurred with the more common wingless morph. Pinned adults from this area in the Snow Entomological Museum, University of Kansas, include no winged (N = 63) in seven years (1923-1925, 1927, 1930-1931, 1937) and 54 winged (= 11%) in three years (1939, 1941, 1950).

In laboratory crossing experiments, only the wingless morph of the European *M. furcata* has been reared (Poisson, 1922; Jordan, 1931). Poisson used wingless parents and Jordan used winged and wingless parents. Hoffmann (1932) worked with wingless parents and obtained wingless progeny in rearings of the North American *M. cryptophila* Hungerford and *M. douglasensis*. One record of three winged adults reared from eggs of *M. japonica* Miyamoto was reported by Miyamoto (1964); the morphs of the parents were not known.

Questions to be answered. This paper describes the developmental pathways of morphs and discusses the extent of environmental and genetic causation of morphs in *M. mulsanti*. To understand the developmental divergence of the thorax, observations were made on the form of the first three instars, of the fourth instar with wing pads and of the fifth instar and adult of the heretofore unrecognized intermediate morph. Data were accumulated on the percentages of morphs among pinned adults, nymphs and adults in field samples in three geographical areas (Fig. 1), and nymphs in laboratory rearings. Study of these data suggested three tests. Field data on the occurrence of the winged morph as nymphs and as adults showed the need to observe whether or not migration could be influencing the frequencies of winged adults. Field data on the occurrence of morphs as nymphs indicated that a test could be made on whether or not the occurrence of nymphs with wing pads could be related to high temperatures. Data from laboratory crosses were tested to determine if any one kind of cross would yield significantly more of any one kind of morph.

In the field, other problems included the sequence of the life history stages, where these stages lived, variations of temperatures and how temperature influenced the rate of nymphal development. In the laboratory, records were made on the duration of the nymphal stage.

ACKNOWLEDGMENTS

This work, which initially was directed by the late H. B. Hungerford, was completed under the supervision of C. D. Michener. I am grateful to my husband, E. C. Galbreath, for his dedicated interest in this study and assistance with the preparation of this manuscript. The opportunity to carry on research at the University of Michigan Biological Station was made possible by a Summer Fellowship from the National Science Foundation and by an Ida H. Hyde Scholarship from the University of Kansas. I am grateful for use of facilities at the University of Kansas and at Southern Illinois University at Carbondale.

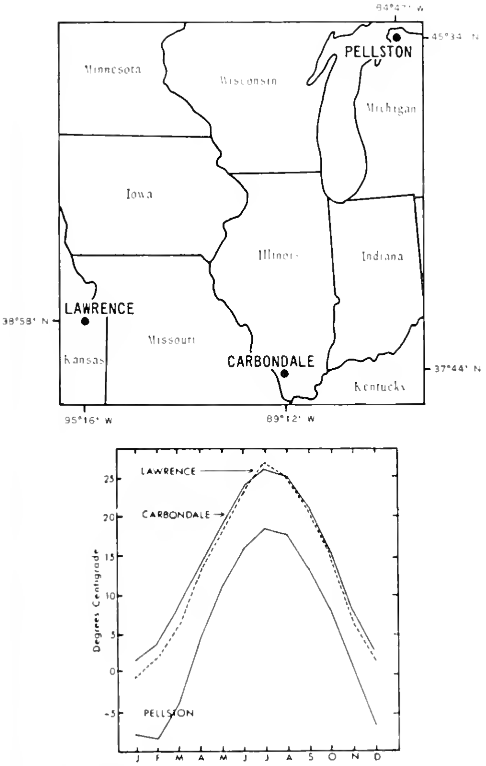

FIG. 1. Map of the central United States showing where populations of *M. mulsanti* were studied, and graph of the average monthly mean air temperatures for these three areas.

MATERIALS AND METHODS

Field work. Data were accumulated on the percentages of morphs among adults (15,000) and nymphs (9,765 fourth and fifth instars) in field samples. A dip net and an aspirator were used for collecting. The insects survived collecting best in an aspirator with a piece of moistened paper toweling; otherwise they often died by desiccation if left too long in dry containers and by drowning if caught in a condensation of moisture in wet containers.

In making a field count, a stereoscopic microscope with a magnification of 45× was used to identify the morphs of nymphs. Fourth instars were recognized as having wing pads (Fig. 2A) or as the wingless morph (Fig. 2B). Fifth instars were recognized as the winged morph (Fig. 2C), as intermediates (Fig. 2D, E, F) or as without wing pads (Fig. 2G, H), the latter being grouped as the wingless morph. Adults were recognized as winged (Fig. 2I) or flightless, because some individuals of the intermediate morph (Fig. 2L) are not distinguishable from the wingless morph (Fig. 2M). When the count was finished, nymphs and adults not used in other studies were returned to the locality where they had been found.

During a field count, fourth instars with wing pads and fifth instars of the intermediate morph (Fig. 2D, E, F) were placed in separate containers for rearing in the laboratory. A fourth instar with wing pads was reared until the fifth instar to recognize the winged or the intermediate morph. When an individual did not survive, a dissection was made to learn if the exoskeleton of the fifth instar was sufficiently developed for identification. Often such an individual was early in the instar and was listed as "morph unknown" in the tables containing field data. Fifth instars of the intermediate morph were reared to observe the thoracic form of the adult. Unless used for rearing studies, each specimen with its exuviae was preserved in a separate vial of alcohol.

Routine field counts were made once a week and frequently more often. In the vicinity of the University of Michigan Biological Station near Pellston, Michigan, between June 18 and August 10, 1955, 29 counts were made at 15 places (Cheboygan County: two open beach pools at Black Lake; Black River; Bryant's Bog; vicinity of Douglas Lake—marsh near mouth of Bessey Creek, mouth of Bessey Creek, open beach pool at Hook Point, Maple River Bay, two closed beach pools at Sedge Point; two drainage ditches near Duncan Bay; mouth of Indian River; Emmet County: Maple River Swamp; Pellston Pool). Most collections and observations were made in the habitats around Douglas Lake because they were most accessible. Near Lawrence, Kansas, field samples were made regularly at The Pond, University of Kansas Natural History Reservation, from September 30 to October 19, 1955; July 12 to November 18, 1956; and May 1 to September 6, 1957; with a few collections at Eudora Pond in 1956 and 1957 and one sample at Bagsby Pond in 1956. All of these places are in Douglas County. Near Carbondale, Illinois, routine field collections were made at Fisher Pond during periods of seasonal activity from April 28, 1959 through September 6, 1962. More frequent collections were made in 1961: 22 samples of nymphs from May 18 to June 18 and 23 samples of adults from May 26 to June 18. Each day all unmarked adults were marked on the thorax with model paint applied with a crow quill pen. In addition, some samples were made at LaRue Swamp in 1959 through 1961, at Lewis Swamp in 1959, and at Lake-on-the-Campus and at Tar Hill Pond in 1961. LaRue Swamp is in Union County; the other collecting places are in Jackson County.

Records were kept on the duration of seasonal activity, i.e., when first instars hatched in the spring and when nymphs and adults were last observed in the fall.

The temperature data came from the following sources: for Europe, from the United States Department of Agriculture (1941); and for the areas of study, from "Climatological Data: Michigan" (1955), "Climatological Data: Kansas" (1955-1957), "Climatological Data: Illinois" (1910-1962), "Local climatological data. Carbondale, 1910-1962," the operating records of the Murphysboro Water Plant, Murphysboro, Illinois, and from a thermograph placed at Fisher Pond, Carbondale, during the seasonal activity of *M. mulsanti* in 1961-1962. Freeze probabilities were determined from the dates of threshold freezes of 0° C or lower for Carbondale for the years 1910-1962. Freeze probabilities are statistics used by climatologists (Thom and Shaw, 1958) and are derived from threshold freezes, the last vernal and the first autumnal freeze.

To relate seasonal temperatures to the dates of collection, a graph of the monthly mean air temperatures was made for each year of research from the records of the U.S. Weather Bureau Station closest to the area of study. An estimated mean air temperature for any specific date was obtained by reading the temperature indicated by the intersection of a line drawn through the date and the line connecting the monthly mean temperatures. For example, in Figure 4, line C (for September 1) intersects the line of the mean air temperature at 23.3° C. Estimates of the mean temperature of pond water were determined for 1961-1962 from graphs of the monthly means from data obtained at Fisher Pond.

Laboratory work. Data were accumulated on the percentages of morphs among pinned adults (3,000 specimens, Snow Entomological Museum, University of Kansas) and among nymphs (2,355) reared primarily from virgin crosses in the laboratory.

The laboratory rearings required handling over 8,000 individuals within one month's time. To rear *M. mulsanti*, freshly killed insects for food, a rearing container with a cover, a moist environment, and a matrix for the insertion of eggs must be provided. Care was needed in handling of insects used for food (primarily *Drosophila*) to be sure that the ether fumes had evaporated and the bodies remained moist for piercing and sucking. First, second, and third instars required one fruit fly per day; fourth and fifth instars and adults needed two per day. Circular, plastic, covered containers, 35 mm in diameter and 28 mm tall, were used. A humid environment was maintained in two ways. The eggs and the first through third instars were kept in containers partially filled with distilled water. For fourth and fifth instars and for adults, two layers of paper toweling moistened with distilled water were placed on the bottom of the rearing containers. The toweling also served as a matrix into which the ovipositor was inserted and to which the eggs were usually attached.

The toweling was not likely to influence development. Abnormal development in some pyrrhocorids was recognized to be caused by a "paper factor," now known to be juvabione (Gilbert and King, 1973). Carlisle and Ellis (1967) observed that toweling did not modify growth when the manufacturer had used a chemical process or if the wood pulp did not include the balsam fir. The toweling used in my work was made by a chemical process from wood pulp with no balsam fir (personal communication from the manufacturer).

Some progeny were reared from eggs laid by females collected as adults in the field (Table 5: Pellston, expt. 1-4; Lawrence, expt. 1-2; Carbondale, expt. 4); in these studies the morph of just the one parent was known. In 1955, virgin crosses were set up from parental stocks in which the percentages of nymphs with wing pads were unknown. Beginning in 1957, crossing experiments were set up with parental stocks taken when field counts indicated 0 to 10% or alternatively 11 to 45% nymphs with wing pads. Differing conditions of temperature and light were used (Table 5). Each experiment started with collecting fourth and fifth instars from the field and rearing each nymph in isolation in the laboratory. When the adults emerged, single-pair crosses were established. The matrix of toweling with eggs from one female for one day of oviposition was placed in a separate rearing container. In about five days (average temperatures 25° C or higher) the eggs were examined for embryos; if there were few embryos, the eggs and parents of the particular cross were discarded. When the fertility rate was high, the toweling was separated to place five or six eggs in a container—a precaution to reduce future cannibalism. For each group of eggs records were kept of the number and kinds of morphs produced.

During the rearings, observations were made on the thoracic form of the first three instars. Dead third instars were dissected to observe in late instars the presence or absence of wing pads. Fourth instars of the wingless morph were preserved. Fourth instars with wing pads were isolated and reared as long as possible; those which died were dissected to

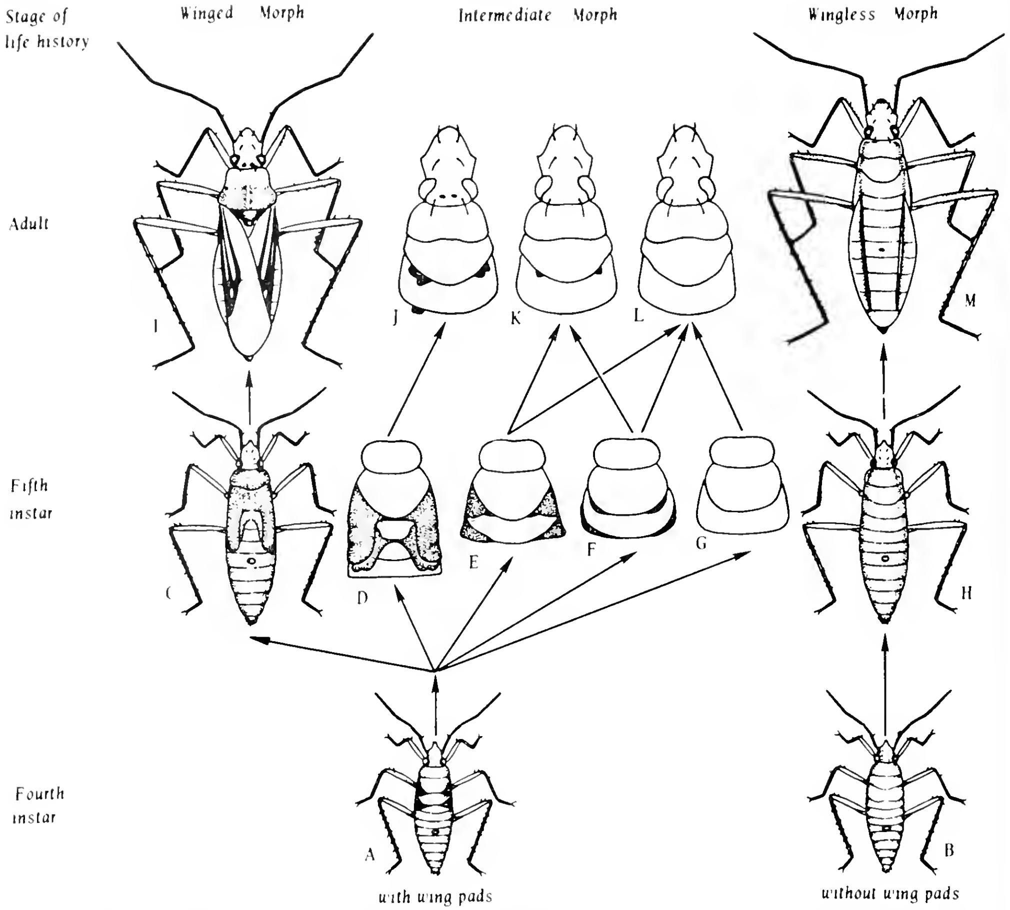

FIG. 2. Diagrams to show developmental divergence in *M. mulsanti*. **A**, Fourth nymphal instar with wing pads, morph unknown. *Winged morph.* **C**, Fifth instar; **I**, young adult female. *Intermediate morph.* **D-G**, Thoraxes of fifth instars: **D**, with short wing pads; **E**, with shorter wing pads; **F**, with vestiges of wing pads; **G**, without wing pads. **J-L**, Thoraxes and heads of adults: **J**, with three vestiges of wing pads and reduced ocelli; **K**, with two vestiges of wing pads and no ocelli; **L**, without vestiges of wing pads and ocelli. The individual illustrated as a fifth instar, D, and as an adult, J, represents the maximum development toward wingedness observed in the intermediate morph. *Wingless morph.* **B**, Fourth instar; **H**, Fifth instar (thorax as in G); **M**, adult female (details as in L). (Parts B, C, I and M are from Hungerford, 1917.)

observe in late instars the winged or the intermediate morph. Some nymphs with wing pads, the dissected late third and early fourth instars, were grouped as "morph unknown" in the tables of progeny counts. Each individual of the winged and intermediae morphs was preserved as a fifth instar or as an adult with its exuviae in a separate vial.

Measurements were made of the wing pads of exuviae of the fourth instar of each preserved specimen known to be a winged or an intermediate morph. The thorax of the exuviae of the fifth instar and of the adult of the same intermediate morph individual was studied from preserved specimens.

The duration of the nymphal stage was observed at 23.9° and 30.0° C.

Near the end of the summer, the duration of the incubation period was used to determine whether the eggs were nondiapause or diapause (Galbreath, 1973).

MORPHS

Developmental divergence. Three thoracic morphs are recognized: winged, intermediate and wingless (Fig. 2). Individuals do not seem to deviate from the norm of five nymphal instars. The mesotergum and the metatergum remain undifferentiated through the third instar of all nymphs and through the adult of the wingless morph (Fig. 2B, H, M). Wing pads are present in some fourth instars (Fig. 2A) and may be observed in dissections of some late third instars, but the morph of such individuals cannot be recognized. Measurements of the length and width of the wing pads on exuviae of fourth instars of preserved specimens known to be either a winged or an intermediate morph did not show a morph-related difference. However, differences in the development of the wing pads during the fourth stadium are evident after the molt into the fifth instar: the growth is normal (winged morph, Fig. 2C), some growth occurs (intermediate, Fig. 2D), growth is suppressed (intermediate, Fig. 2E), or reduction occurs (intermediates, Fig. 2F, G). These thoracic differences may also be observed in dissections of late fourth instars with wing pads. Adults have wings (winged morph, Fig. 2I), vestiges of wing pads (intermediates, Fig. 2J, K), or no sign of wings (intermediate, Fig. 2L; wingless morph, Fig. 2M). Vestiges of wing pads (Fig. 2F, J, K) retain the mesal position characteristic of wing pads and in adults lack the differentiation of wings.

Each morph has a stage or stages when it may be recognized.

The winged morph may be identified as a fifth instar (Fig. 2C) by the long wing pads which reach to the third abdominal segment or farther, and as a young adult (Fig. 2I) by the well-developed wings themselves, as well as by two prominent ocelli, the pronotal lobe, and the exposed mesonotal and metanotal scutella. In older individuals, the apices of the hemelytra and wings are broken and the indirect flight muscles undergo autolysis.

The one feature common to all intermediates is the presence of wing pads in the fourth instar. The rarest intermediate lacks vestiges of wing pads in the fifth instar and may not be distinguished from the fifth instar of the wingless morph (Fig. 2G, H, respectively). Fifth instars with short wing pads (Fig. 2D, E) and, more frequently, with vestiges of wing pads (Fig. 2F) are recognizable as intermediates. A few of the adults may be identified as intermediate by having ocelli or vestiges of wing pads; some have both of these features (Fig. 2J). However, the majority of intermediate adults (Fig. 2L) are inseparable from wingless adults (Fig. 2M).

To recognize an individual of the wingless morph, one must know that wing pads are absent in the fourth instar (Fig. 2B). This knowledge is important in designing rearing experiments with virgin crosses.

In flightless adults, the intermediate and wingless morphs, the pronotal lobe is absent; the mesonotum and the metanotum remain simple, subequal segments; flight muscles are absent; and the phragmata are reduced. The wings of some intermediates are reduced to stubs called vestiges of wing pads or to minute, distorted areas visible only with a stereoscopic microscope at a magnification of 60×.

Discussion. "Polymorphism can usually be interpreted as the outcome of developmental divergence after a critical point which may be anywhere from the egg to the adult stage. The fate of the individual is thought to become fixed or determined at this critical point. However, as in studies of growth and development of tissues and organs, words like 'determined' often turn out to have relative rather than absolute meanings . . . Determination does not always occur at the same stage in all individuals of a species" (Michener, 1961:47).

My research with *M. mulsanti* and study of papers by Ekblom (1949), Miyamoto (1953), Sprague (1956) and Brinkhurst (1963) on developmental divergence in members of three other families of semiaquatic Hemiptera show that there are several ways that the development of the nymphs may differ: the nymphs may or may not have wing pads, the wing pads may not appear in the same instar, the wing pads may show differences in rates of growth or amounts of regression, the number of kinds of flightless morphs may vary, and the morphs may not be recognizable at the same stage of development. The wingless morph of *M. mulsanti* does not have wing pads; all nymphs of the species reported on in the literature cited above have wing pads. In *Hydrometra martini* Kirkaldy, wing pads are found in the third instar; in *Microvelia diluta* Distant, wing pads appear in the fourth instar. Most of the differences in the development of wing pads appear to be a result of different rates of growth, although regression or loss of wing pads occurs in some intermediate nymphs of *M. mulsanti*. The kinds of morphs may vary from two (*H. martini* with one winged and one flightless) to several (one winged and several flightless). In some species (*M. mulsanti, M. diluta, Gerris lateralis* Schummel = *Gerris asper* Fieber of Ekblom) the thoraxes of flightless morphs show much variation as nymphs and adults. The stage when the morphs first become recognizable ranges from the third instar (*H. martini*) to the adult (*Gerris odontogaster* [Zetterstedt]).

A critical point has been suggested for only one species, *G. odontogaster*. The hypothesized critical point of the egg during vitellogenesis (Brinkhurst, 1959) was not substantiated. Instead, the critical point is thought to occur during the first four stadia (Vepsäläinen, 1971b).

Study of the developmental divergence of *M. mulsanti* suggests that all individuals could undergo a critical point sometime before the late third instar, when the pathway for the wingless morph may be recognized in dissections. Then it is possible that fourth instars with wing pads undergo a second critical point which determines whether the individual becomes a winged or an intermediate morph. See later sections for answers to these questions.

RESULTS OF FIELD STUDIES

Seasonal temperatures. To study the effect of seasonal temperatures on *M. mulsanti*, one must know where the individuals live during their various stages. It is now known that the egg overwinters (Galbreath, 1969). Diapause eggs embedded in plant tissue overwinter below the surface film and post-diapause nymphs hatch below the film and swim upward to attain their position on the surface. Non-diapause eggs, inserted in aquatic plant tissue just above the water line, must remain in a moist environment. Then, depending upon the position of the plant, a nymph hatches from a non-diapause egg and either climbs onto the surface of the floating plant or emerges below the surface and swims upward as described above. Nymphs and adults live on the surface film but in the air.

This study is concerned with the subsurface water temperatures, surface film temperatures, and air temperatures influencing nymphal development. However, daily fluctuations in temperatures mask the overall point of view that is needed to relate the occurrence of morphs to different temperatures. The climatologist's

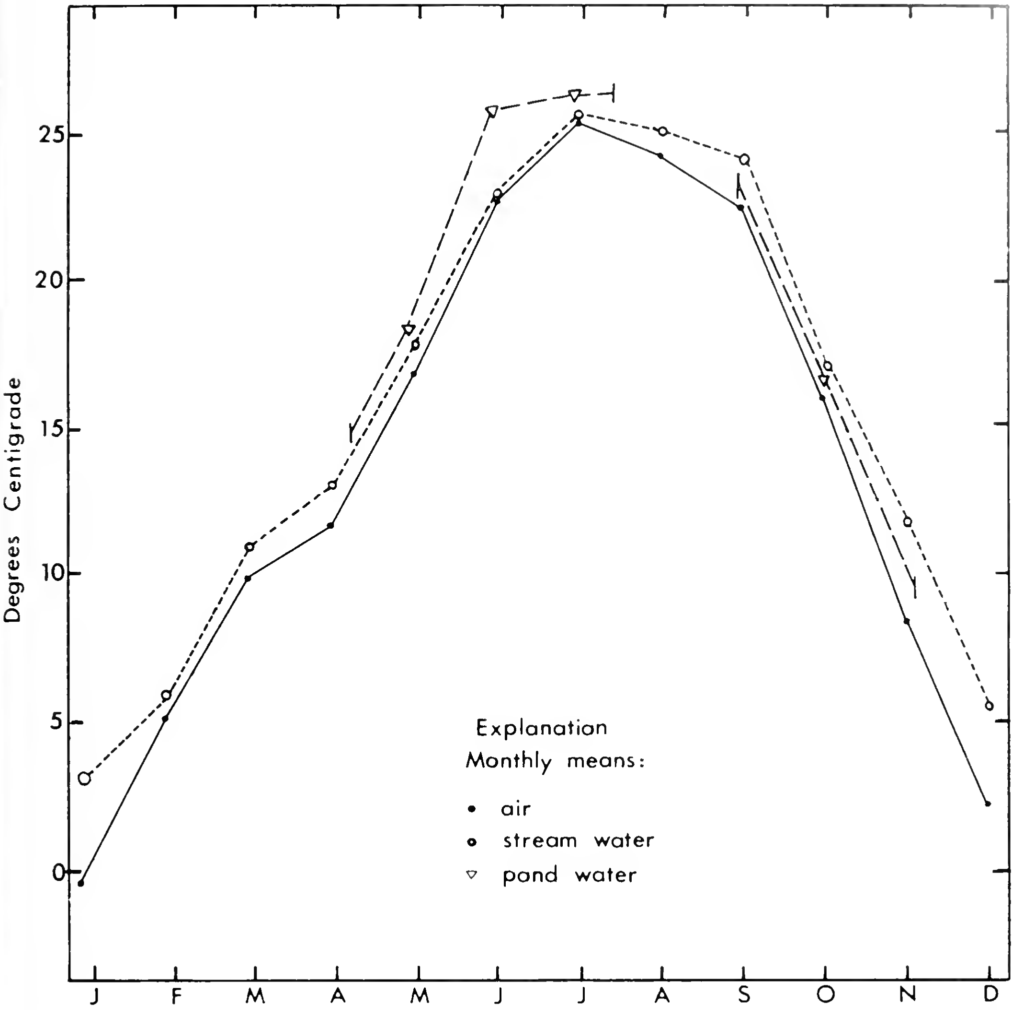

Fig. 3. Comparison of the monthly mean temperatures of air, stream water, and water of Fisher Pond for 1961 at Carbondale, Illinois. Data on air temperatures were obtained from the U.S. Weather Bureau Station at Carbondale. Temperatures for stream water were compiled from daily records of the Big Muddy River made at the Murphysboro Water Plant. The mean for the month was the sum of the daily temperatures divided by the number of days in the month. Water temperatures for Fisher Pond were obtained from a thermograph for April 23 to July 28 and September 15 to November 21. The monthly mean temperatures were calculated from the average of the maximal water temperature plus the average of the minimal water temperature divided by two.

"march of monthly mean air temperatures" smooths these variations.

The graphs and data of Harmeson and Schnepper (1965) record a marked similarity in the average monthly mean temperatures of air and surface waters in Illinois for 38 stations, 27 flowing streams and 11 impoundments of flowing streams. Analysis of their data shows that the average monthly means of surface waters are generally (90% of the 456 sets of water and air data compared) equal to or higher than those of air. Figure 3 is a graph plotted after Harmeson and Schnepper but comparing the monthly mean temperatures of air and stream water to those of the water in Fisher Pond where field studies were made. From April 23

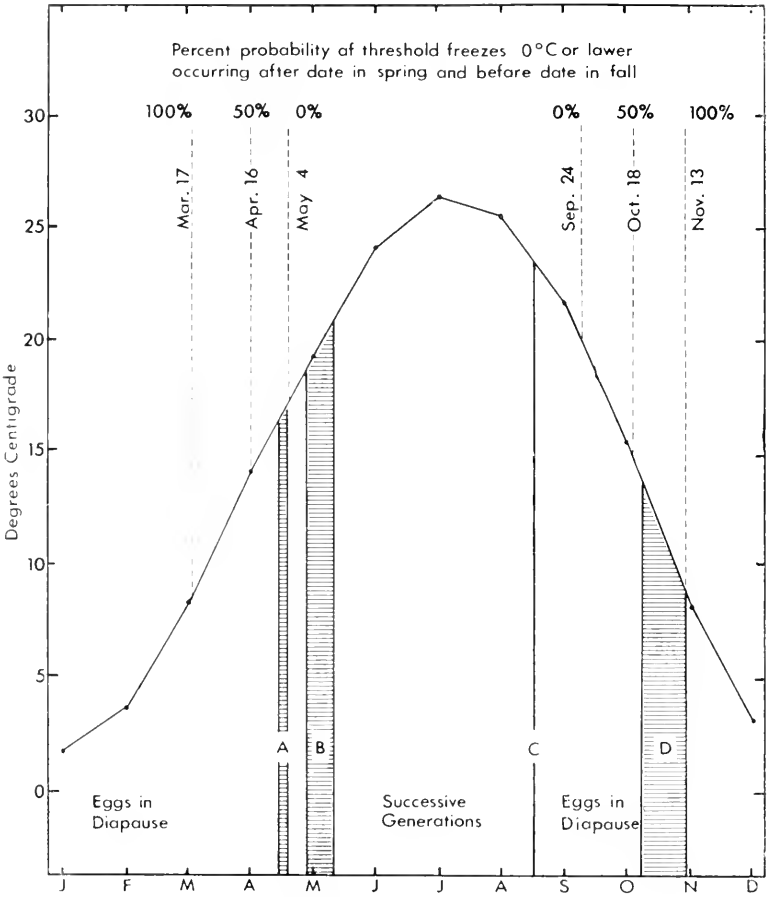

FIG. 4. Graph relating seasonal activity of *M. mulsanti*, probabilities of threshold freezes, and the average monthly mean air temperatures at Carbondale, Illinois. First records of first instars (A) were as early as April 28 and as late as May 2. First records of adults (B) were as early as May 12 and as late as May 26. The last record of nymphs or adults (D) occurred as early as October 22 and as late as November 14. The earliest record of eggs in diapause (C) was obtained from eggs laid in the laboratory on September 1, 1971, by females collected as adults on August 31 (unpublished data).

through July 28, the average temperatures of pond water were warmer than those of stream water and air. The biggest difference occurred in June (25.7° C for pond water, 22.8° C for stream water, 22.0° C for air). From September 15 until November 21, the average temperatures of the pond water were cooler than those of the stream water but warmer than those of air.

Because water temperatures were available for but two out of seven years involved in this study, seasonal temperatures were determined from air data because of the close similarity in the monthly mean temperatures of air and water.

Seasonal activity at Carbondale. Seasonal activity refers to the time when nymphs and adults are found on the surface film. Figure 4 shows the variations in seasonal activity observed at Fisher Pond from 1959 to 1962. Hatching of the first instars occurred after the last vernal freeze of each year, when the freeze probability was 10% or lower (Fig. 4A) and

TABLE 1. Field records of the first generation at Fisher Pond, Carbondale, Illinois. All temperatures are °C. (Average monthly mean of May: 19.3°.)

Year	Monthly mean temp. of May	First records of first instars	Estimates of mean temp.		First records of adults	Estimates of mean temp.		Duration of nymphal stage in days
			Air	Surface water		Air	Surface water	
1959	21.5	Apr. 28	17.2	..	May 16	21.4	..	18
1960	17.6	May 2	16.7	..	May 22	20.8	..	20
1961	16.7	May 2	14.4	16.0	May 26	20.9	21.1	24
1962	23.7	Apr. 28	17.2	19.4	May 12	22.8	23.8	14

the estimated mean air temperature was 14.4° C or higher (Table 1). The first records of adults were obtained during the freeze-free period (Fig. 4B) and when the estimated mean air temperature was 20.8° C or higher. There are five or more successive generations per year. In this study, records of diapause eggs were obtained in October. Figure 4C shows the earliest record of diapause observed in subsequent work. Also, see section on diapause under results of laboratory studies. The lowest estimated mean air temperature on the last date of observed activity was 8.3° C. Much variation occurred in the last dates of seasonal activity (Fig. 4D). Surely this variation must be related to the kind of freeze and the freeze resistance of *M. mulsanti*. In 1960, only two nymphs in poor physiological condition were found after the first freeze of -2.7° C; in 1961, a few nymphs and adults were alive after eight freezes, the lowest being -6.7° C.

Influence of climate and weather. An understanding of the differences in climate in the three areas of study and of features of the weather of the specific years of research is an integral part of the interpretation of the field data. As shown in Figure 1, Pellston, Michigan, normally has cool summers; whereas Lawrence, Kansas, and Carbondale, Illinois, have warm to hot summers. Rainfall is important to the ecology of *M. mulsanti* because it determines the area and the number of places that can be inhabited. At Pellston and Carbondale the rainfall is relatively dependable; Lawrence is characterized by intermittent periods of drought.

Seasonal activity at Lawrence has the same duration as at Carbondale (average duration of freeze-free periods: 196 and 186 days, respectively; average monthly means of July: 27.0° C and 26.3° C, respectively). Study of the records of temperatures for Pellston suggest that seasonal activity would begin there in late May or early June and continue into September with one or more generations per year (average duration of freeze-free period: 92 days; average monthly mean of July: 18.8° C). The approximate changes in day length during the periods of seasonal activity are: at Lawrence and Carbondale, 13.9 hr on May 1 to 15.0 hr on June 15 to 10.0 hr on November 15; at Pellston, 15.4 hr on June 1 to 15.6 hr on June 15 to 11.7 hr on October 1 (Beck, 1968).

At Pellston, in 1955, the summer was warmer and drier than average. It is probable that the warm temperatures of June caused an early molt into adults. I found adults on June 18, the first date of collection, whereas the earliest dates on the labels of pinned adults from this area in the Snow Entomological Museum show June 28 in 1950 and June 30 in 1923 and 1939. In 1955, the continued warm temperatures in July and August may have resulted in three generations; in the laboratory adults of the second generation emerged on July 21 and those of the third generation on August 26. The dryness brought about low water levels in aquatic habitats in late July (an accumulated deficiency of 14.1 cm of precipitation); shallow habitats were dry in early August.

Near Lawrence, in 1955 and 1956, a widespread drought, the longest and most severe on record (Climatological Data: Kansas, 1957), reduced The Pond at the Natural History Reservation to three small pools. In contrast, heavy rains in May and June of 1957 raised the water level of The Pond causing it to overflow the dam.

At Carbondale during the period of study from 1959 through 1962, precipitation was normal. Whether the temperatures were warmer or cooler than average during May was observed to influence the duration of the nymphal stage and the time when the first generation became adults (Table 1).

Use of data to determine frequencies of morphs. One problem was to decide which data were the most meaningful to determine if a relationship could exist between any one kind of morph and the environment.

Percentages of the winged morph often showed great disparities. For example, between May 18 and June 18, 1961, at Fisher Pond, Carbondale, among 577 nymphs and 920 adults, none of the nymphs were the winged morph but 54% of the adults were winged. In this series of data, the unmarked adults were counted each day, marked and released. Because this sampling started at the beginning of seasonal activity, it was possible to observe when the different stages were most numerous: fourth instars on May 22, fifth instars on May 28, flightless adults on June 1 and winged adults on June 11. Two facts, the absence of nymphs of the winged morph and the numerical dominance of the winged adults when there were few fourth and fifth instars, suggest the possibility of long distance migration. These results showed that the frequencies of the morphs as nymphs would be more reliable to show ratios among kinds of morphs.

Data from all field samples of fourth and fifth instars showed a range of 0 to 21% for the winged morph, 0 to 24% for the intermediate morph and 55 to 100% for the wingless morph.

However, the primary problem was whether or not the environment could influence the development of wing pads. A percentage based on the number of nymphs with wing pads, i.e., fourth instars with wing pads and fifth instars of the winged and intermediate morphs, in the total sample was used to compare the results obtained in different field samples.

A secondary problem was whether or not the environment could influence the development of wings; the percentage was based on the number of nymphs of the winged morph among all of the nymphs with wing pads.

The first critical period. "It must, indeed, be common ground that the diverse potentialities latent in the gene system become manifest only when the cell or organism are in the appropriate environment or at the appropriate stage of development" (Wigglesworth, 1961:112). I think that the frequency of nymphs with wing pads in *M. mulsanti* must be related to temperature during the first critical period.

The stage of the insect when the development of the thorax is sensitive to the environment is unknown. The first critical point does not appear to occur at fertilization because results of laboratory crossing experiments did not suggest a genetic relationship between the morphs of the progeny and those of their parents. The embryo does not appear to be the sensitive stage because there are records from the field of high frequencies of nymphs with wing pads when embryonic development took place at low as well as at high temperatures. For example, at Fisher Pond in 1962, the embryonic development which took place in April with a monthly mean of 12.8° C resulted in May in 18% (N = 571) of the nymphs with wing pads; the embryonic development which took place in May with a monthly mean of 23.7° C resulted in June in 15% (N = 572) of the nymphs with wing pads. Therefore, the sensitive stage appears to take place in the nymph sometime in the interval beginning with the first stadium and prior to the late third stadium.

At Pellston, normally all nymphs regardless of generation pass through the first critical period when the monthly means are low. In July, 1955, some nymphs of a second generation underwent their first critical period when the monthly mean was 21.7° C. However, in field samples the frequency of nymphs with wing pads remained 3%.

At Lawrence and Carbondale, most nymphs of the first generation undergo the first critical period in May when normally the monthly mean is low. This was the case in four years (Lawrence, 1957—18.3° C; Carbondale, 1959—20.5° C, 1960—17.6° C and 1961—16.7° C); 1.6% (N = 1,447) of the nymphs had wing pads. On the other hand, in 1962 at Carbondale when the monthly mean of May was 23.7° C, 18% (N = 571) of the nymphs had wing pads in three field samples: 0% on May 8 (N = 1), 5.3% on May 12 (N = 189), 24.1% on May 14 (N = 381). For this example, Figure 5 shows the sequence of life history stages and the ambient air temperatures and Table 1 records the estimated mean air and water temperatures.

Comparison of the duration of the nymphal stage and temperature data from the field and laboratory (Tables 1 and 8) suggests that nymphs in the field may respond to the warmer temperatures of water rather than to the lower temperatures of air. Indeed, a method of measuring temperatures at the surface film is needed.

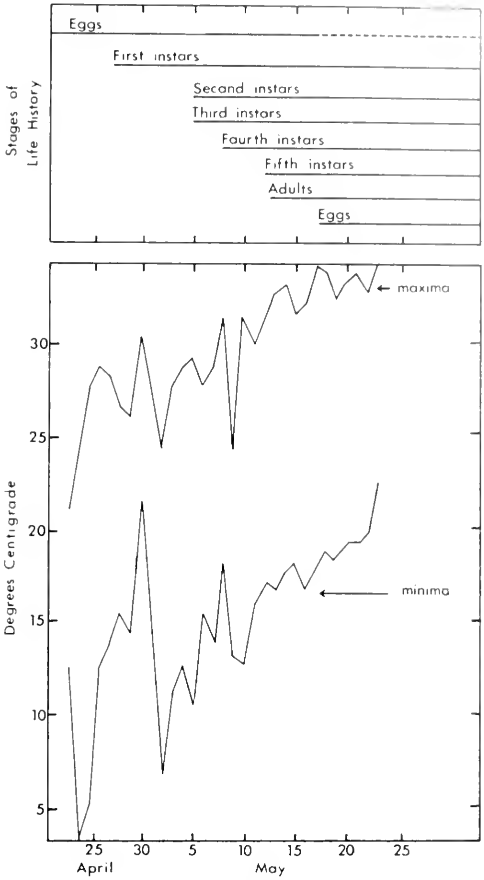

FIG. 5. The sequence of the life history stages of the first generation of *M. mulsanti* at Fisher Pond, and the daily fluctuations of air temperatures from April 23 through May 23, 1962, at Carbondale, Illinois. The data for the maxima and minima came from Climatological Data: Illinois (1962). Monthly means were: 12.8° C, April, and 23.7° C, May.

Nymphs with wing pads and temperature. To relate the percentages of nymphs with wing pads in field samples to seasonal temperatures, an estimate of the mean air temperature was made for the date of each field sample. Study of the

TABLE 2. Numbers of the morphs found as nymphs in field samples during the three temperature intervals. Collections were made at Pellston, Michigan, 1955; Lawrence, Kansas, 1955-1957; and Carbondale, Illinois, 1959-1962; and pooled.

Estimates of mean air temp. in °C	With wing pads				Without wing pads
	Winged morph	Intermediate morph	Morph unknown[1]	% with wing pads	Wingless morph
16.7–21.4	23	5	2	1.9	1,589
21.5–28.3–21.5	702	302[2]	47	14.9	5,994[2]
21.4–8.3	16	9	9	3.1	1,067

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[1] Fourth instar with wing pads for which the morph could not be recognized.

[2] Field count of intermediate and wingless morphs incomplete due to collecting technique.

data suggested three temperature intervals: low temperatures of seasonal warming, 16.7° to 21.4° C; high temperatures of summer, 21.5° to 28.3° to 21.5° C; low temperatures of seasonal cooling, 21.4° to 8.3° C (Table 2). Fourth and fifth instars of the wingless morph were collected when the estimated mean air temperature ranged from 16.7° C in the spring to 28.3° in the summer to 8.3° C in the fall. When estimates of the mean air temperature were 21.4° C or lower, whether there was seasonal warming or cooling, the frequency of nymphs with wing pads was consistently low, averaging 2.4% (N = 2,720). When estimates of the mean air temperature were 21.5° C or higher, the frequency of nymphs with wing pads averaged 15% (N = 7,045) but in individual samples ranged from 0 to 45%.

Differences in the percentages of nymphs with wing pads because of latitudinal differences in temperature were also observed: 2.9% (N = 445) at Pellston in contrast to 13.7% (N = 2,654) at Lawrence and 11.1% (N = 6,666) at Carbondale.

Nymphs with wing pads and unknown factors. Much variation (0 to 45%) occurred in the frequency of nymphs with wing pads when the estimate of mean air temperature was 21.5° C or higher. During this temperature interval at Fisher Pond in 1961, first 0% (N = 92, 10 samples, June 10 to 18) of the nymphs had wing pads. Later 5.7% (N = 743, Table 3, June 19 to July 3) of the nymphs had wing pads; percentages ranged from 0.0 to 11.5%. At the same time, at Tar Hill Pond, another shallow, man-made pond only one quarter of a mile away, 17% (N = 795, June 24 to 30) of the nymphs had wing pads. Subsequently, at Fisher Pond 44.7% (N = 85, July 29) of the nymphs had wing pads. At Tar Hill Pond between July 24 and 30 the population was drastically reduced so that no accurate frequency of nymphs with wing pads could be determined on July 30.

Table 4 records differences in the percentages of nymphs with wing pads observed during the temperature interval of 21.5° C or higher. Few nymphs with wing pads were observed in the populations studied in 1956, 1959 and 1960. At Lawrence in 1957 at The Pond, the occurrence of a high frequency (11-45%) of nymphs with wing pads was the longest on record; it began when the estimated mean air temperature was 24.4° C on June 22 and lasted at least through August 18. At Carbondale, in 1961 and 1962, high frequencies of nymphs with wing pads were observed for shorter durations of time: examples already given in Table 3; Fisher Pond: 17.7% (N = 656), estimates 23.3° to 22.8° C, August 30 to September 7, 1961, 17.9% (N = 571), estimates 21.5° to 23.6°

TABLE 3. Records of nymphs with wing pads at Fisher and Tar Hill Ponds, Carbondale, Illinois from June 19 to July 30, 1961. Estimated mean air temperatures changed from 22.8° to 25.5° to 24.4° C.

Date	Fisher Pond				Tar Hill Pond			
	With wing pads			Without wing pads	With wing pads			Without wing pads
June-July	Winged morph	Intermediate morph	% with wing pads	Wingless morph	Winged morph	Intermediate morph	% with wing pads	Wingless morph
19	1	0	3.7	26	..	..	....	....
20	0	3	4.5	63	..	..	....	....
21	1	1	2.4	80	..	..	....	....
22	2	2	3.4	113	..	..	....	....
23	7	13	11.5	154	..	..	....	....
24	2	6	5.1	148	26	33	32.1	125
25	..	..	....	....	25	30	13.8	344
28	1	3	5.0	76	..	..	....	....
30	..	..	....	....	16	7	10.8	189
1	..	..	....	....	17	2	....	N.C.[1]
3	0	0	0.0	41	..	..	....	....
4–15	..	..	....	....	10	N.C.	....	N.C.
24	..	..	....	....	1	N.C.	....	N.C.
29	18	20	44.7	47	..	..	....	....
30	..	..	....	....	0	0	....	2

[1] Not collected.

C, May 8 to 14, 1962 and 15.0% ($N = 572$), estimates 23.7° to 24.2° C, June 7 to 24, 1962.

When estimates of the mean air temperatures were 21.5° C or higher, there were years when few nymphs with wing pads were found as opposed to years when samples contained high percentages of nymphs with wing pads. Consequently, one must conclude that unknown factors plus high temperatures during the first critical period are necessary for a frequency of 11 to 45% of nymphs with wing pads.

TABLE 4. Percentages of nymphs with wing pads collected when the estimated mean air temperature was 21.5° C or higher.

% with wing pads	N	Collecting data: dates, area
0.5	1,118	July 12[1]-Sep. 11, 1956, Lawrence
36.5[2]	890	June 5-Aug. 18, 1957[3], Lawrence
6.3	586	May 16-Aug. 18, 1959[4], Carbondale
1.7	479	June 10-Sep. 11, 1960, Carbondale
14.5[2]	2,551	June 9-Sep. 16, 1961, Carbondale
21.4[2]	1,421	May 8-Sep. 6, 1962, Carbondale

[1] First date of field work.
[2] Field count of intermediate and wingless morphs incomplete due to collecting technique.
[3] No collections between Aug. 19 and Sep. 5.
[4] No collections between Aug. 19 and Sep. 12.

The second critical period. The percentage of nymphs with wing pads that are of the winged morph gives a basis for comparing the influence of the environment on the developing wings. In different samples at Fisher Pond, this percentage ranged from 33 to 85%: 33.3% ($N = 42$, June 19 to 28, 1961, Table 3), 47.3% ($N = 38$, July 29, 1961, Table 3), 75.0% ($N = 116$, August 30 to September 7, 1961), 84.8% ($N = 92$, May 14, 1962). The reason for the differences in percentage is unknown. Because these data show statistical significance, I think that a second critical period takes place early to midway in the fourth stadium of nymphs with wing pads.

Table 5. Percentages (numbers) of the morphs present as nymphs in field samples when adult females and fourth and fifth instars were selected for parental stocks, compared with the morphs reared from them in the laboratory (filial generation).

	Field samples Parental generation					Laboratory reared progeny Filial generation				
Area, year, number of experiment, locality, date[1]	Winged morph	Inter-mediate morph	Morph un-known[2]	Total with wing pads	Wing-less morph	Winged morph	Inter-mediate morph	Morph un-known	Total with wing pads	Wing-less morph
Pellston 1955										
1. Pellston Pool, June 18	.. (0)	.. (0)	.. (0)	.. (0)	.. (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (1)
2. Black Lake Pool, June 19	.. (5)	.. (0)	.. (0)	.. (5)	.. (5)	8.3 (1)	0.0 (0)	0.0 (0)	8.3 (1)	91.7 (11)
3. Duncan Bay, July 2	.. (0)	.. (0)	.. (0)	.. (0)	.. (0)	30.0 (12)	0.0 (0)	5.0 (2)	35.0 (14)	65.0 (26)
4. Duncan Bay, July 6	.. (0)	.. (0)	.. (0)	.. (0)	.. (0)	4.3 (1)	0.0 (0)	4.3 (1)	8.7 (2)	91.3 (21)
5. Sedge Point Pool, July 12	.. (0)	.. (0)	.. (0)	.. (0)	.. (6)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (7)
6. Virgin crosses set up from reared progeny of expts. 2, 3, 4	.. ..	.. ..	.. ..	.. ..	.. ..	1.5 (1)	0.0 (0)	0.0 (0)	1.5 (1)	98.5 (66)
Lawrence 1955										
1. The Pond, Sep. 28-Oct. 6	.. (4)	.. ..	.. ..	.. ..	.. ..	0.0 (0)	0.0 (0)	1.6 (2)	1.6 (2)	98.4 (122)
1956										
2. The Pond, July 12-Sep. 11	0.5 (6)	0.0 (0)	0.0 (0)	0.5 (6)	99.5 (1,112)	0.9 (3)	4.3 (15)	1.1 (4)	6.3 (22)	93.7 (329)
1957										
3. The Pond, May 11-June 18	4.0 (8)	0.0 (0)	0.0 (0)	4.0 (8)	96.0 (190)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (21)
4. The Pond, June 19-Sep. 6[3]	24.3 (240)	7.1 (70)	3.7 (36)	35.1 (346)	64.9 (640)	0.0 (0)	7.9 (7)	5.6 (5)	13.5 (12)	86.5 (77)
Carbondale 1959										
1. Lewis Swamp, May 31	4.9 (3)	3.3 (2)	0.0 (0)	8.2 (3)	91.8 (56)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (5)
2. Fisher Pond, June 27	1.1 (1)	5.5 (5)	0.0 (0)	6.6 (6)	93.4 (85)	0.0 (0)	9.1 (1)	0.0 (0)	9.1 (1)	90.9 (10)

1960										
3. Fisher Pond, July 8	7.7 (3)	0.0 (0)	0.0 (0)	7.7 (3)	92.3 (36)	0.0 (0)	16.7 (5)	6.7 (2)	23.3 (7)	76.7 (23)
4. Fisher Pond, Sep. 30-Oct. 13	0.0 (0)	0.5 (1)	0.0 (0)	0.5 (1)	99.5 (182)	0.0 (0)	28.6 (18)	6.3 (4)	34.9 (22)	65.1 (41)
1961										
5. Tar Hill Pond, June 24-July 12[3]	11.4 (94)	8.7 (72)	0.0 (0)	20.1 (168)	79.9 (658)	8.3 (58)	30.6 (215)	15.6 (110)	54.5 (383)	45.5 (320)
6. Fisher Pond, Aug. 30-Sep. 7	13.3 (87)	4.3 (28)	0.2 (1)	17.7 (116)	82.3 (540)	4.9 (33)	19.8 (134)	4.7 (32)	29.4 (199)	70.6 (477)
7. Fisher Pond, Sep. 27-28	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	100.0 (142)	0.0 (0)	3.0 (4)	4.5 (6)	7.6 (10)	92.4 (122)
					Total	109	399	168	676	1,679

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[1] Laboratory conditions. *Pellston.* Expts. 1-6, natural light plus artificial during work at night. Expts. 1-6, fluctuating temperatures, no data, but based on rate of development estimate an average of about 24° C. Expts. 1-4 were done at Pellston between June 18 and Aug. 11; expts. 5-6 were started at Pellston and moved on Aug. 12 to Winnebago, Ill. and on Aug. 30 to Lawrence, Kans. *Lawrence.* Expts. 1-2, natural light plus artificial light during work at night; expts. 3-4, artificial light during research. Expts. 1-4, air conditioned temperatures: expts. 1-2, no data; expts. 3-4, mean 23.9° C, range 18.8°-27.2°. *Carbondale.* Expts. 1-2, no data on light for first part of rearing for fifth instars from field, preoviposition period of adults, or incubation of eggs in controlled chamber set at 20.0° C, range 18.3°-20.0°; then transferred to laboratory with natural light plus artificial during work at night for rearing of nymphal progeny, no data on fluctuating temperatures. Expts. 3-6, natural light plus artificial during work at night; fluctuating temperatures: expt. 3, mean 30.0° C, range 27.7°-33.3°, expt. 4, mean 23.9° C, range 21.1°-27.2°, expt. 5, mean 26.7° C, range 21.1°-32.2°, expt. 6, mean 25.6° C, range 19.4°-31.1°. Expt. 7, natural light through glass door of incubator plus artificial during work at night; controlled temperatures: incubator set at 27.7° C, range 26.1°-30.0°.

[2] Nymphs with wing pads for which the morph could not be recognized.

[3] Field count of intermediate and wingless morphs incomplete due to collecting technique.

TABLE 6. Summary of Table 5 showing percentages of morphs in laboratory rearings relative to the percentages of nymphs with wing pads in parental stocks.

Nymphs with wing pads in parental stocks	Laboratory reared progeny						Temp. in °C	Area, number of expt.[2]
	Winged morph	Intermediate morph	Morph unknown[1]	Total with wing pads	Wingless morph	N		
0–10	0.5	7.0	2.6	10.1	89.9	613		Lawrence
							----	expt. 2
							23.9	expt. 3
								Carbondale
							----	expt. 1
							----	expt. 2
							30.0	expt. 3
							23.9	expt. 4
							27.7	expt. 7
11–45	8.3	30.6	15.6	54.5	45.5	703	26.7	Carbondale expt. 5
	4.9	19.8	4.7	29.4	70.6	676	25.6	Carbondale expt. 6
	0.0	7.9	5.6	13.5	86.5	89	23.9	Lawrence expt. 4

[1] Nymphs with wing pads for which the morph could not be recognized.
[2] Laboratory conditions given in Table 5.

RESULTS OF LABORATORY STUDIES

Purpose of crossing experiments. The intent was to learn what kind of morphs would be produced from different parental stocks, where field samples indicated 0-10% or 11-45% of the nymphs with wing pads. These studies also gave information on the kinds of crosses which can give rise to the three morphs. Totals for each laboratory sample are given; data on the progeny reared from individual crosses and from females fertilized in nature are available from the author.

Parental stock and filial generation. As previously mentioned, 2.9% (N = 445) of the nymphs had wing pads in field samples at Pellston in 1955. However, when rearing stocks (primarily adults) were collected, the localities contained few or no fourth and fifth instars. Few progeny with wing pads were obtained in all but one reared sample, for which the adult females were collected on July 2 at Duncan Bay (Table 5: Pellston expt. 3). This high percentage (35%) of nymphs with wing pads is an unusual occurrence among mesoveliid nymphs of 45° north latitude. It was not obtained in the field; a trip to Duncan Bay at the appropriate time showed that 9.5% (N = 21) of the nymphs had wing pads.

The percentage of nymphs with wing pads in the parental stock was unknown for the Lawrence expt. 1. Among the progeny, 1.6% of the nymphs had wing pads.

In seven studies, the parental stocks contained 0-10% nymphs with wing pads (Table 5: Lawrence expts. 2-3; Carbondale expts. 1-4, 7). In the filial generation, the percentages of nymphs with wing pads varied; there were but three winged, a few intermediate and a preponderance of wingless young (Tables 5, 6). The winged progeny were produced by two females which had been fertilized in nature.

When the parental stocks contained 11-45% nymphs with wing pads, the filial generation reared in the laboratory gave

TABLE 7. Thoracic morphs of the parents of the 109 winged progeny reared in the laboratory.

Area, year, number of expt., locality, date[1]	Morphs of parents		Winged progeny		N
	Female	Male	%	(N)	
Pellston, 1955					
2. Black Lake Pool, June 19	flightless[2]	unknown	10.0	(1)	10[3]
3. Duncan Bay, July 2	winged	unknown	33.0	(9)	27
	flightless	unknown	23.1	(3)	13
4. Duncan Bay, July 6	winged	unknown	6.2	(1)	16[3]
6. Virgin cross no. 43	wingless	winged	5.0	(1)	20[3]
Lawrence, 1956					
2. The Pond, July 12-Sep. 11	winged	unknown	0.8	(1)	127
	flightless	unknown	0.9	(2)	224
Carbondale, 1961					
5. Tar Hill Pond, June 24-July 12	winged	winged	7.2	(22)	305
	winged	intermediate	6.8	(5)	73
	intermediate	winged	8.6	(20)	233
	intermediate	intermediate	12.0	(11)	92
Carbondale, 1961					
6. Fisher Pond, Aug. 30-Sep. 7	winged	winged	2.6	(5)	190
	winged	wingless	4.1	(9)	219
	intermediate	winged	29.4	(5)	17
	intermediate	intermediate	9.3	(6)	64
	intermediate	wingless	0.0	(0)	8
	wingless	winged	0.0	(0)	38
	wingless	intermediate	0.0	(0)	14
	wingless	wingless	6.3	(8)	126

[1] Laboratory conditions given in Table 5.

[2] A flightless adult could be an intermediate or a wingless morph.

[3] The reason for the difference in this total and the one in Table 5 is because only part of the sample is being considered here.

high frequencies of nymphs with wing pads, but no nymphs of the winged morph were obtained when the fluctuating temperatures averaged 23.9° C (Table 5: Lawrence expt. 4; Carbondale expts. 5, 6; Table 6).

Laboratory conditions (Table 5) will be discussed under "influence of laboratory conditions."

Morphs of progeny in relation to those of their parents. Individuals of the wingless morph were reared from each of the nine possible kinds of crosses (three morphs, sexes taken reciprocally). Among the samples of laboratory reared progeny (Table 5), the frequency of the wingless morph ranged from 46 to 100%. The 46% was obtained in the Carbondale expt. 5. In this sample of 76 crosses, 74 yielded 14 to 100% wingless offspring. The two remaining crosses lacked wingless progeny—the only time that this occurred in all of the research. There was no evidence that any kind of cross would consistently produce more wingless progeny than other kinds of crosses.

The intermediate morph was also reared from all nine possible kinds of crosses. Among the samples of laboratory reared progeny (Table 5), the frequency of the intermediate morph ranged from 0 to 31%, the latter obtained in the Carbondale expt. 5. Among the 76 crosses, 27 had no intermediate offspring; in the others the numbers of intermediates ranged from one to 16 and the percentages from 6 to 71%. In the Carbondale expt. 6, 20% of the reared progeny were intermediates; 20 crosses had no intermediate progeny and 36 yielded from one to 11, equalling 5 to 50%. There was no evidence that any one kind of cross would produce more intermediate progeny than other kinds of crosses.

Winged progeny were obtained from seven kinds of crosses (Table 7), but not as yet from crosses of intermediate female × wingless male and wingless female × intermediate male. The frequency of the winged morph ranged from 0 to 30% among laboratory reared samples (Table 5). Among the 76 crosses in the Carbondale expt. 5, 26 yielded from one to five winged progeny, the percentages being 5 to 57%. Among the 56 crosses in the Carbondale expt. 6, 16 gave one to five winged progeny, the percentages being 4 to 67%.

In the Carbondale expt. 5 where the morphs of both parents were known, the frequencies of the winged morph showed no statistically significant relation to the four kinds of crosses (Table 7). In the Carbondale expt. 6 where the morphs of both parents were known, the frequencies of the winged morph likewise showed no statistically significant relation to four kinds of crosses (Table 7), those yielding 3 to 9% of the winged morph. The frequency of the winged morph (29%) for the two crosses of intermediate female × winged male, although statistically significant, is thought not to be meaningful. In these two crosses, the percentages of winged progeny were 21% (N = 14) and 67% (N = 3). As mentioned already for this experiment, 16 out of 56 crosses gave winged progeny. Study of the 16 percentages on winged progeny indicated that 14 crosses for which the percentages ranged between 4 and 23% did not show statistical significance. It is thought to be a matter of chance that two crosses gave higher percentages (43%, N = 7, intermediate female x intermediate male, cross no. 3; 67%, N = 3, intermediate female × winged male, cross no. 2). In expt. 6 three kinds of crosses lacked winged progeny. I do not understand these results.

I think that winged progeny may be equally derived from the nine kinds of crosses; however, further work is needed to prove the point. The winged morph has yet to be reared from two crosses, intermediate female × wingless male and its reciprocal. The results of Carbondale expt. 6 show that additional work with the cross of intermediate female × winged male is required.

Influence of laboratory conditions. Apparently laboratory conditions did not influence the percentages of the different morphs as these data show good agreement among different samples in the laboratory and in the field. The observed limits in laboratory rearings were 0 to 30% for the winged morph, 0 to 31% for the intermediate morph, and 46 to 100% for the wingless morph. The observed limits recorded for field samples were 0 to 21% for the winged morph, 0 to 24% for the intermediate morph, and 55 to 100% for the wingless morph.

Proportionately more nymphs had wing pads in laboratory rearings (observed upper limit—54% in the Carbondale expt. 5, Table 5) than in field samples (observed upper limit—45% in the sample of July 29, 1961, Table 3). A suggested reason is the difference in temperature. For example, from June 24 to July 31, 1961, in the laboratory the temperature averaged 26.7° C, range 21.1°-32.2°. In July in the field the monthly mean air temperature was 25.5° C, extremes 9.4°-35.0°, and the monthly mean pond water temperature was 26.4° C, extremes 12.8°-38.3°.

The percentage of nymphs with wing pads that were the winged morph ranged from 0 to 86% in the laboratory (Table 5: Carbondale: 0%, N = 22, expt. 4; 15.1%, N = 383, expt. 5; 16.6%, N = 199, expt. 6; Pellston: 85.7%, N = 14, expt. 3).

Comparison of these data on the second critical period with those obtained in field samples show that nymphs with wing pads are more likely to become the winged morph in the field than in laboratory rearings. The reason for this difference is unknown.

In this study there was no evidence that day length could influence thoracic development; see "Discussion."

Because of later work with diapause (see next side heading), I now think that long day lengths could have stimulated the laying of non-diapause eggs in the following experiments: Table 5, Lawrence expt. 1 and Carbondale expts. 4, 6, 7.

Diapause. Records of diapause eggs were obtained in 1960 (Table 5: Carbondale expt. 4). Non-diapause eggs with an average incubation period of 11.7 days, range 11 to 12, were recognized from diapause eggs with an incubation period lasting from 20 to 227 days. One female, collected in the field as a fourth instar on September 30, matured in the laboratory, was mated and 7% (N = 130) of the eggs were diapause. Six females were collected as adults, four on October 9 and two on October 13, and in the laboratory 84% (N = 172) of the eggs were diapause.

In a subsequent study on diapause at Carbondale, the work started with the collection of adult females (Galbreath, 1973). In 1971, among females collected on August 28, 3% (N = 496) of the eggs laid in the laboratory between August 28 and September 12 were diapause; among females collected on September 17, 85% (N = 748) of the eggs laid between September 17 and 21 were diapause.

Mortality. The mortality from egg to fourth instar was 91% among progeny in the Carbondale expt. 5 and 85% in the Carbondale expt. 6. This agrees with Hungerford's estimate (1917) of 90% mortality. I do not think that any significance should be attached to the high mortality of nymphs. Everyone who has reared semiaquatic Hemiptera knows about the high mortality in the laboratory. I see no reason to think that a lethal factor exists for any one kind of individual of *M. mulsanti* as has been postulated for individuals with the AA genetic constitution in *Gerris* (in *G. lacustris*, Poisson, 1924; in *G. lacustris* and *G. lateralis*, Guthrie, 1959; in *Gerris*, Brinkhurst, 1959). Vespsäläinen (personal communication in 1973) reported that in rearing studies of *G. lacustris* he found such an individual to be viable.

Survival. More of the progeny were reared from eggs laid early in the period of oviposition because these eggs yielded a higher proportion of progeny that survived to a recognizable morph. Records from the Carbondale expt. 6 showed that the percentages of survival were 19.5% (592 progeny from 3,132 eggs) from days one through four of oviposition and 6.2% (84 progeny from 1,352 eggs) from days five through nine. Consequently, in crossing studies it is advantageous to start with large numbers of crosses and rear only the eggs laid early in the period of oviposition.

Duration of the nymphal stage. The nymphal stage averaged 12 days at 30.0° C and 20.5 days at 23.9° C (Table 8). These records agree with my calculations for Hungerford's data (1917) and the data for *M. mulsanti* reported by Hoffmann (1932), respectively.

DISCUSSION

Differing environments are known to produce different thoracic morphs in some aquatic Hemiptera (*Aphelocheirus*, Larsén, 1931; Corixidae, Young, 1965). In the case of *M. mulsanti*, field samples of nymphs and results from laboratory experiments indicate environmental control of the morphs. In some species of gerrids, the main influence seems to be environ-

Table 8. Duration in days of nymphal stage in the laboratory.

Source of data	Mean air temp. in °C			Stadia			Duration of nymphal stage
		I	II	III	IV	V	
Carbondale expt. 3[1]	30.0	2.1[2] (2–3)[3] 30[4]	1.9 (2–3) 30	2.1 (1–4) 30	2.7 (2–4) 17	3.5 (3–4) 2	12.0 .. 2
Hungerford (1917)	..	2.4 (2–5) 9	2.1 (1–3) 9	2.4 (2–3) 9	2.4 (2–3) 9	2.8 (2–3) 9	12.2 (11–14) 9
Carbondale expt. 4[1]	23.9	3.6 (3–4) 23	3.1 (3–4) 23	3.4 (3–6) 22	4.8 (4–7) 18	6.5 (6–7) 4	20.5 (20–22) 4
Hoffmann (1932)	..	3.4 (2–6) 71	3.2 (2–5) 71	3.5 (2–5) 61	4.4 (3–6) 59	5.4 (3–9) 47	20.0 (17–24) 47

[1] Details of laboratory conditions given in Table 5.
[2] Average in days.
[3] Range in days.
[4] Number of individuals.

mental; in others, both genetic factors and environmental influences appear to be involved (Vepsäläinen, 1971a).

In *G. odontogaster,* rearing data gave no evidence of genetic control (Ekblom, 1950; Brinkhurst, 1959, 1961; Guthrie, 1959; Vepsäläinen, 1971b). Laboratory experiments suggested that photoperiod directed development toward short-winged, non-diapause individuals or winged, diapause individuals (Vepsäläinen, 1971b). The critical period appeared to be the first four stadia. Nymphs from populations in southern Finland responded to increasing day lengths of 18 hours or longer to become short-winged adults; nymphs undergoing the critical point after the summer solstice became winged adults. Field samples of morphs supported this hypothesis. Populations were univoltine and winged in northern Finland and Sweden (Vepsäläinen, 1971b; Ekblom, 1950; respectively). Populations showing a dimorphic first generation with short-winged adults emerging first and winged adults emerging later and a partial second generation of winged adults were observed in southern Finland and Denmark (Vepsäläinen, 1971b; Andersen, 1973; respectively). Two studies, a rearing experiment by Guthrie (1959) and observations on seasonal differences in ovarian development between morphs by Andersen (1973), substantiated Vepsäläinen's observations that short-winged adults were non-diapause individuals. Overwintering populations in southern Finland consisted of winged adults from both generations and only a few short-winged adults, 0.6% in 1970.

The interaction of genetic factors and environmental influences is not understood for any gerrid. In *G. lateralis,* for which polygenetic control was hypothesized by Ekblom (1928, 1941, 1949), and in *G. lacustris,* for which monogenic control was hypothesized by Poisson (1924), the effects of temperature and photoperiod on nymphs (reported by Guthrie, 1959; discounted by Brinkhurst, 1963) have been considered. In a preliminary report on *G. lacustris,* Vepsäläinen (1971a) thought that monogenes could be the major control in univoltine populations but that photoperiod also could be involved in determining the short-winged morph in the first generation of bivoltine populations. Andersen (1973) pointed out that this hypothesis did not account for the increase of short-winged adults that he observed in autumn.

It should be noted that causation of morphs in gerroids is not likely to be explicable on the basis of any one environmental variable. Undoubtedly there are a number of interacting influences that contribute to the environmental control of development of morphs. Temperature and unknown factors acting on the nymphs were involved in *M. mulsanti* because of the irregular occurrence of nymphs with wing pads. If photoperiod were involved in *M. mulsanti* there would have been a simultaneous occurrence of nymphs with wing pads among localities within the same geographical area and a predictable occurrence of these nymphs from one year to another.

The possibility of hormonal imbalances causing flightless morphs in gerroids has been mentioned (Southwood, 1961; Brinkhurst, 1963; Wigglesworth, 1964; Novák, 1966; Chapman, 1971; Puchkova, 1971; Vepsäläinen, 1971b), but there are no published results to substantiate the hypothesis. In gerroids, the physiological causation of the developmental differences between morphs is unknown.

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ADDENDUM

Critical point, page 466, column 2, line 5; page 480, column 1, line 13. Vepsäläinen (1974c) stated that among individuals of this species there could be variation in the duration of the critical period.

Mortality, page 479, column 2, line 14. Subsequent studies of *G. lacustris* (Darnhofer-Demar, 1973; Vepsäläinen, 1974c) gave no basis for the hypothesis of a lethal factor. On the other hand, review of the available data on *G. lateralis* by Vepsäläinen (1974c) suggested that the hypothesis could be plausible in this species.

G. odontogaster, page 480, column 1, line 7. Add Vepsäläinen, 1974a.

G. lacustris, page 481, column 1, line 3. Subsequent studies of *G. lacustris* have been published (Darnhofer-Demar, 1973; Vepsäläinen, 1974b, 1974c).

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PHYLOGENY AND CLASSIFICATION OF THE ACULEATE HYMENOPTERA, WITH SPECIAL REFERENCE TO MUTILLIDAE

By

DENIS J. BROTHERS

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Denis J. Brothers

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Phylogeny and Classification of the Aculeate Hymenoptera, With Special Reference to Mutillidae[1]

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ABSTRACT

The phylogeny (and classification) of the aculeate Hymenoptera has not been examined as a whole since Börner's limited study of the entire Hymenoptera 55 years ago. The relationships of the members of the "Scolioidea," especially the tiphioid-mutilloid complex, have been especially confused. This investigation attempts to rectify this situation.

Representatives of 25 taxa of aculeate Hymenoptera (the taxa varying in categorical level from tribe to superfamily in a traditional classification, the emphasis being on the "Scolioidea") were examined with respect to 92 characters. Primitive-derived sequences of states were determined for these characters and cladograms were constructed by electronic computer ("Wagner trees") and by hand using the principles of Hennig. The most variable characters were eliminated and cladogram construction was repeated until similar cladograms were derived by both methods. All derived states of all characters were inserted on the cladogram and numerical measures of distinctness, considering the number of derived states per internode, the number of species subtended by (i.e., resulting from) each internode and the efficiency (in terms of unique, parallel or convergent occurrences) of each derived state on each internode, were calculated. Taxonomic distinctness of each taxon from every other was calculated, and this measure was used as a guide in establishing the categorical levels to which the taxa were assigned in a classification.

Representatives of 89% of the valid described genera and subgenera of myrmosids and mutillids were examined and cladograms were derived as for the Aculeata. The final cladogram of the mutillid-myrmosid group was based on 43 characters (involving 61 derived states), 20 of females and 23 of males. Distinctness measures were calculated, based on these characters only.

These investigations suggest that the aculeate Hymenoptera comprise three superfamilies, each with numerous families: 1. Bethyloidea, containing Plumariidae, Bethylidae, Scolebythidae, Cleptidae, Chrysididae, Loboscelidiidae, Dryinidae, Sclerogibbidae and Embolemidae; 2, Sphecoidea, containing two informal groups, one (Spheciformes) consisting of Ampulicidae, Sphecidae, Larridae, Mellinidae, Pemphredonidae, Astatidae, Philanthidae and Nyssonidae, and the other (Apiformes) consisting of Colletidae, Halictidae, Oxaeidae, Andrenidae, Melittidae, Fideliidae, Megachilidae, Anthophoridae and Apidae; and 3, Vespoidea, containing two informal groups, one (Vespiformes) consisting of Tiphiidae, Sapygidae, Mutillidae, Sierolomorphidae, Rhopalosomatidae, Pompilidae, Bradynobaenidae, Scoliidae, Masaridae, Eumenidae and Vespidae, and the other (Formiciformes) consisting of Formicidae only.

The composition of most families of Vespoidea is unchanged, but the Tiphiidae consists of only the subfamilies Anthoboscinae, Thynninae, Myzininae, Methochinae, Tiphiinae and Brachycistidinae. The Bradynobaeninae, with Typhoctinae (including Eotillini), Chyphotinae and Apterogyninae, is placed in the family Bradynobaenidae. The Mutillidae consists of seven subfamilies: Myrmosinae, Pseudophotopsidinae, Ticoplinae, Rhopalomutillinae, Sphaeropthalminae (comprising two tribes, Dasylabrini and Sphaeropthalmini, the latter with the subtribes

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Pseudomethocina and Sphaeropthalmina), Myrmillinae and Mutillinae (comprising two tribes, Mutillini and Ephutini, the former with the subtribes Mutillina and Smicromyrmina).

The cladogram of the Mutillidae and the geographic distributions of its component taxa suggest that the family arose on Laurasia and differentiated in northeastern Africa. The New World members were possibly derived almost entirely from two independent stocks introduced to South America from Africa, and the Australasian fauna probably resulted in the main from a few introductions from South America across Antarctica.

INTRODUCTION

The Hymenoptera is a well-defined order of endopterygote insects, often considered to comprise a distinct superorder (e.g., Mackerras, 1970), and is undoubtedly holophyletic (Ashlock, 1971, 1972; = monophyletic *sensu* Hennig, 1966a). Within the Hymenoptera, the suborder Apocrita (= Clistogastra) is also holophyletic, being characterized by development of a constriction between the first and second abdominal segments and fusion of the first abdominal segment with the thorax to form the propodeum. This situation is unique in the Insecta. (Because of these morphological modifications, the tagmata of apocritans are referred to below as "head," "mesosoma," and "metasoma," for the head, apparent thorax and apparent abdomen, following the suggestion of Michener, 1944.) By contrast, the Symphyta (= Chalastogastra) is almost certainly a paraphyletic group (*sensu* Ashlock, 1971, 1972; not Nelson, 1971) as Rasnitsyn (1969: p. 168, Fig. 273) has demonstrated, the Apocrita possibly having been derived from within the Siricoidea.

Although the Apocrita is often formally considered to comprise a number of equivalent superfamilies (e.g., Riek, 1970), an informal division into two groups is useful. One of these groups, the Aculeata, is holophyletic, being characterized mainly by modification of the ovipositor as a stinging apparatus (see Oeser, 1961, for various characters involved). The other group, the Terebrantia (= Parasitica) is undoubtedly paraphyletic, comprising the remaining apocritans. Richards (1956b) considers these groups more formally as sections.

The Aculeata is commonly considered to comprise seven superfamilies ("Bethyloidea," "Scolioidea," "Pompiloidea," "Formicoidea," "Vespoidea," "Sphecoidea" and "Apoidea") of which the first two are judged to be the most primitive in general (e.g., Evans & West Eberhard, 1970). (Since this study has led to conclusions which involve changes in the limits of taxa previously recognized at the family and superfamily levels, names used in the old sense are enclosed in quotation marks throughout.) Most of these superfamilies are readily characterized by one or more unique specializations and thus are clearly holophyletic. The "Scolioidea" is an exception, however, since this group appears to contain those aculeates which do not clearly fall into any of the other superfamilies. It is thus probably paraphyletic or even polyphyletic (*sensu* Hennig, 1966a; Ashlock, 1971, 1972; not Nelson, 1971), although shown as holophyletic in the dendrogram of Evans & West Eberhard (1970). The "Scolioidea" further contains various taxa the placement of which has been confused. The main purpose of this investigation is thus the clarification of the interrelationships of the various taxa comprising the "Scolioidea," with special emphasis on the "Mutillidae," and the derivation of a classification which reflects these interrelationships adequately. Coincidentally, the study has been extended to cover the entire Aculeata.

There have been widely differing classifications at the higher levels for the members of the scolioid complex, notably the "Tiphiidae" (*sensu lato*). Thus, de Saussure (1892) considered the entire complex to be a single family *(Hétérogynes)* and Ashmead (1900, 1903-1904) differentiated eight families in this group. Pate (1947a) provided some clarification of the genera related to *Tiphia, Myzinum,* etc., and Krombein (1951) included six families in the "Scolioidea" of North America. Tobias (1965) elevated one of these families ("Sapygidae") to the superfamily level so that he could designate its two subordinate taxa as families. The "Mutillidae" has consistently been considered an important member of the "Scolioidea."

The "Mutillidae" is a large, cosmopolitan group of wasps, the classification of which has also long been in a state of confusion. The group included by Linnaeus (1758) and other early workers in the genus *Mutilla* was much broader than the present family "Mutillidae." (The following outline excludes those sections more recently considered to fall in other families.) Although there were preliminary attempts by workers such as Latreille (1809, 1825, 1829), Wesmael (1851), Sichel & Radoszkovsky (1869), Thomson (1870), Blake (1871, 1886), Burmeister (1874) and de Saussure (1892) to develop a higher level classification within the group (often by merely describing a few new genera or subgenera for species which were superficially aberrant), subsequent workers such as Fox (1899, 1900) again reduced most genera to synonymy of *Mutilla,* although suggesting species groups within the genus. However, André (1899-1903, 1902) and Ashmead (1900, 1903-4) described many new genera and each proposed a different classification for the group. The differences between the two schemes resulted mainly from tendencies by André to lump many taxa into a single family (Mutillidae), while Ashmead placed the equivalent taxa in four families (Cosilidae, Thynnidae, Myrmosidae and Mutillidae). Bischoff (1920-21) based his classification of African species mainly on that of André (1902), with the addition of various tribal divisions and taking into account Börner's (1919) phylogeny of the Hymenoptera. Bradley & Bequaert (1923, 1928) formulated a scheme that combined features of those of André (1902) and Ashmead (1900, 1903-4). Concurrently they placed most members of two of Bischoff's tribes (Trogaspidiini and Smicromyrmini) in a single genus *(Smicromyrme).* Skorikov (1935) proposed a classification which essentially raised the previously recognized taxa by one categorical step, placing the two tribes of Bischoff in question as subfamilies. Schuster (1947, 1949) recognized that previous attempts at a classification of the group had often been rendered inapplicable because they had been based on too limited material. He proposed a scheme which attempted to take this into account even though he apparently saw few specimens from the Old World. This scheme was adopted by Krombein (1951) for Nearctic species. By contrast, Invrea (1964) used a classification essentially based only on Old World species for the Italian fauna, thus perpetuating the type of arrangement that Schuster had attempted to eliminate.

The present study was initiated as an attempt to derive a broadly applicable classification of the "Mutillidae" from consideration of the entire world fauna (specimens were available for approximately 90 percent of the described taxa at the genus level). After initial investigations it became apparent that the "Mutillidae" as previously delineated was almost certainly polyphyletic, as had been suggested by Schuster (1949). As a result, the investigation was extended to other members of the "Scolioidea" in an attempt to find the smallest holophyletic group upon which a classification could be based. The superfamily "Scolioidea" proved to be at most paraphyletic (as suggested above), so that the remaining divisions were added to the investigation.

Although the study was thus broadened to include the entire Aculeata, the levels of accuracy and completeness vary considerably, depending on the problem being investigated at each stage. Thus the study of the "Mutillidae" and closely related groups is the most complete and hopefully the most accurate. As higher and higher level taxa were added into the study, time and logistics militated against each being considered as completely as were the taxa originally investigated. Further inaccuracies may have been caused by the unavailability of specimens of rare groups, resulting in the absence of data for some characters of these. The unavoidable inaccuracies introduced at the higher levels as a result of these factors are, however, of minor importance for the main focus of the study, viz., the relationships of the "Mutillidae."

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METHODS

The methods by which the final cladistic diagrams were derived were essentially the same no matter which taxonomic grouping was involved. First, the operational taxonomic units (OTU's) under consideration were surveyed in an attempt to discover as many differentiating character states as possible. Each character was re-examined to ensure that the different states could be unambiguously recognized and placed in a coded sequence of "primitive" (or ancestral) to "derived." If there was much uncertainty, the character was rejected. Then, using the selection of least equivocal characters remaining, a cladistic dendrogram was constructed, using two methods. First, a diagram was constructed by hand using the principles of Hennig (1966a) as elaborated by Brundin (1966) and others, i.e., basing all groups on common possession of the derived state of one or more characters (synapomorphies). Second, a diagram was derived by use of a computer program for construction of "Wagner trees" (Farris, 1970; Kluge & Farris, 1969). The hand- and machine-derived trees, representing different approaches to the problem (Moss & Hendrickson, 1973), were then compared. All characters were re-examined in the light of their distribution on the trees and those characters which showed many separate derivations or reversals of the same state were eliminated because of their instability. Certain characters were found to be in need of re-coding, either because of inappropriate delimitation of states or misinterpretation of the primitive-derived sequence. Judgments were based on the principle that most parsimonious placement of states on the trees was the most likely to be correct, unless logically contraindicated (e.g., a most parsimonious placement requiring the re-appearance of a complex structure in an identical form after being lost). During the process of consideration and rejection or retention of characters, due importance was given to the complexity of the character concerned. Thus, for example, a character involving a complex of morphological features was considered to be less likely to have undergone multiple independent changes to a similar derived state than was a simple character involving a single structure. During the examination process various additional characters were discovered and incorporated into the data matrix.

Once all the characters had been re-evaluated, cladistic diagrams were again constructed by hand and using the computer. These were again compared, the characters re-evaluated and new characters added, etc. This process was repeated until highly similar or identical cladograms were derived using the two methods of construction, indicating that the characters used presented a distribution of derived states that were meaningfully correlated. This final scheme (or highly similar schemes) also most likely embodied the maximal number of "uniquely derived character [states]" and the lowest "coefficient of character-state randomness" (Le Quesne, 1969, 1972) possible.

The initial studies were done using selected genera traditionally included in the "Mutillidae" (*sensu* Schuster, 1947, 1949) as well as representatives of the various subordinate taxa considered to comprise the "Tiphiidae" (*sensu* Pate, 1947a), the family thought to be most closely related to the "Mutillidae." These investigations led to two independent lines of study, viz., relationships between the Mutillidae *(sensu stricto)* (the characteristics of which had been established by the initial study) and other taxa within the traditional "Scolioidea" and eventually the Aculeata (taxa being added at higher and higher levels as the study progressed), and the relationships within the Mutillidae.

For the studies involving the Aculeata the characteristics for the various taxa were derived from relatively few species chosen to cover the variation within the taxon as completely as possible, but with emphasis on the presumably least specialized forms. The categorical levels of the taxa involved varied from tribe (in the "Mutillidae") to family (for most other "Scolioidea") or superfamily (for the non-scolioid aculeates). The material examined in each instance is listed in the account of the primitive characters of each taxon, below.

The general usefulness of any classification depends on the purposes for which it was drawn up. In the present study the attempt has been made to formulate a classification of as general applicability as possible. A classification appears to be of broadest use when it is based neither exclusively on raw phenetic data divorced from any consideration of evolutionary pathways ("pure phenetics," as advocated by Sneath & Sokal, 1973, and others) nor derived from a rigid insistence upon strictly holophyletic taxa, paraphyletic groups being inadmissible ("pure cladistics," as proposed by Hennig, 1966a, 1969, necessitating a complex numbering system; and others), but considers both these aspects, as well as chronistic information (which is present in a relative sense in any cladogram), and may be termed "natural."

Such a classification may be based on a cladogram, with the limits and ranks of the included taxa being delineated by phenetic considerations. Sneath & Sokal (1973) consider that "basing taxonomy on all three approaches [i.e., phenetics, cladistics and chronistics] requires art or compromise, both of which are inadmissible as bases for a precise science." The present study is an attempt to achieve the ideal by minimizing this "requirement," as has been called for by Hull (1970).

As Tuomikoski (1967) and Ashlock (1971, 1972) have pointed out, paraphyletic groups fulfill the basic requirements of monophyly which have always been regarded as essential properties of good taxa. There is thus no reason to discard taxa which are found to be paraphyletic if they are phenetically about as homogeneous as are holophyletic taxa at the same categorical level. On the other hand, a classification including paraphyletic taxa should not be used as the basis for studies (e.g., zoogeography) which require accurate knowledge of branching patterns displayed in the cladogram from which the classification was derived. (The numerical methods used to obtain indices of phenetic distinctness for the various groups in a cladogram are discussed below, in the section on "derivation of a classification" for the Aculeata.)

Previous classifications and evolutionary schemes of the higher Hymenoptera have generally not been based on strict consideration of synapomorphies. This defect was encouraged by the presence of trends which appear in various lines apparently independently but are characteristic of many of the more derived groups. For example, there is a general tendency toward reduction of the degree of articulation between the various mesosomal sclerites, especially in the pleural region, expressed in various ways in the higher Aculeata. The consideration of such trends as being characteristic of a single line has been responsible for the conventional (inadequate) view involving sequential divergence of various taxa from a single evolutionary line (e.g., the scheme provided by Evans & West Eberhard, 1970).

A detailed study of the hymenopteran ovipositor by Oeser (1961) has, however, used Hennigian principles in the derivation of a very limited cladogram which demonstrates that the Aculeata in the broad sense are holophyletic [females have lost the cerci, section 1 of the gonocoxite IX is dorsoventrally constricted, and the basal portion of the "notum" of gonapophysis IX is detached (terminology of Smith, 1970a & b); all three are derived states occurring in the Aculeata only], as are its two component sister groups, the "Bethyloidea" and the remaining Aculeata *(sensu stricto)*. This study, admittedly based on a limited suite of characters albeit ones involved in a structural system of great complexity, has provided the rationale for restricting the present study to the Aculeata. Comparisons were also made to the Trigonalidae (Terebrantia) since these have been considered representative of the possible ancestors of the Aculeata (Lanham, 1951; Riek, 1970). Decisions as to the direction and course of evolution of some characters were also aided by reference to a few members of the Symphyta (Argidae, Cimbicidae, Diprionidae, Siricidae, Tenthredinidae, Xyelidae) and Terebrantia (Braconidae, Chalcididae, Gasteruptiidae, Ibaliidae, Ichneumonidae).

INVESTIGATION OF THE ACULEATA

States of the Characters Considered

The characters used in the analysis of the Aculeata vary greatly in scope and plasticity. Some characters are uniform in all taxa examined except for a single taxon, these representing unique evolutionary innovations serving to differentiate only the taxon bearing the derived state. Such autapomorphies do not associate taxa and are of minor phylogenetic significance. They do, however, contribute to the phenetic component of the degree of differentiation of the taxon in question from its sister group. In such cases it is usually relatively easy to decide which state is primitive and which is derived; the more common state is primitive. Other characters present synapomorphies which serve to associate two or more taxa on a common branch of the cladogram by virtue of their sharing the uniquely derived state of the character. The direction of evolution in such characters may sometimes not be obvious and must then be determined with reference to the states in forms presumed to be generally more primitive than the Aculeata. The degree of congruence with the patterns of derivations presented by other characters is also significant.

Some states that are seemingly synapomorphous may not represent unique derivations; a superficially similar derived state may occur in more than one location on the cladogram but in remote sections of it (resulting in convergences). Such a situation reduces the usefulness of the character to some extent. Other characters show tendencies toward the evolution of similar derived states numerous times, often in the same general section of the cladogram, expressed as parallelisms. Although such plastic characters are mostly of minor use in associating taxa on particular branches, they are often useful in indicating which of two taxa associated on the basis of other characters may be considered the more highly derived. In such cases the character involves the "tendency toward" a particular derived state. If formulated in this way the derived state may be envisioned as having evolved (in some preliminary but unexpressed fashion) some time before its appearance on any of the branches of the cladogram, perhaps as the result of accumulated mutations in a non-functional set of gene loci producing a "frozen accident" (see Ohno, 1973).

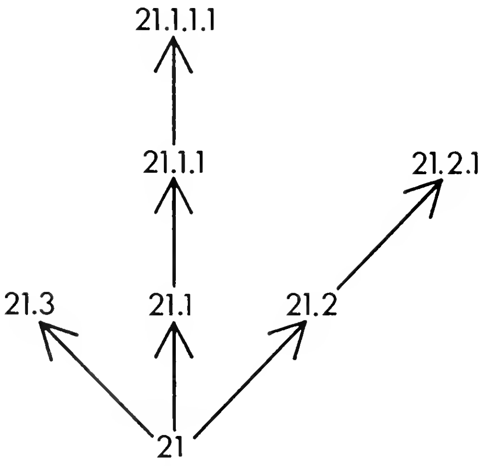


FIG. 1. Diagram of evolution of character 21, showing scheme for numbering the states.

The numbering system for character states reflects the pattern of evolution for the character involved. Each subsequent digit, reading from the left, refers to a state derived from that expressed by the digits preceding it. This is illustrated in Fig. 1, which shows the pattern of evolution of character 21. Where a particular derived state is characteristic of an entire taxon it is referred to below as being present "in" the group concerned. If a derived state is found in only some members of a taxon and is not characteristic of the entire taxon, it is referred to as occurring "within" the group involved. Placement of the various derived states on "internodes" refers to the final cladogram (Fig. 2). Where examples are given below, the use of a genus name does not necessarily imply that all members of the genus show that character state, but that one or more species do; nor are examples of groups containing a few members with a particular state meant to encompass all such groups. The ending "-id" also does not imply family status.

Although it is inappropriate to refer to taxa as being "primitive" or "advanced," since each taxon exhibits characters in both the "primitive" and "advanced" (or "derived") states, it is convenient to refer to taxa in this way on occasion. When a taxon is referred to as being "primitive" this generally means that it originates low on the cladogram and bears relatively few characters in derived states.

Those characters considered to be most useful in the final construction of the cladogram are marked with an asterisk (*). Even in these, all derived states are usually not equally useful and in some instances one state is practically of no significance whereas another is of great importance.

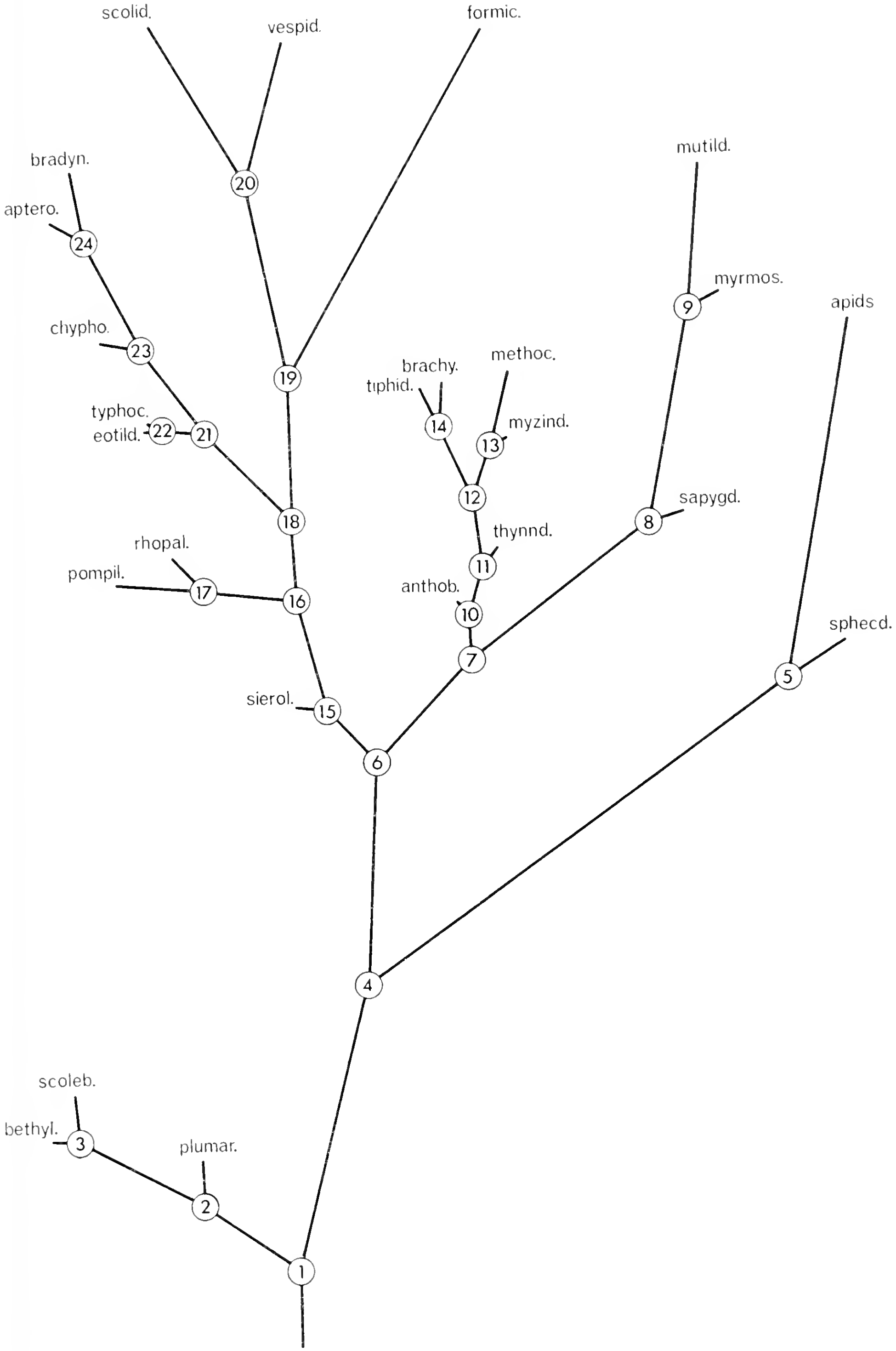


Fig. 2. Cladogram of 25 taxa of Aculeata, based on 92 characters. Lengths of branches (measured from the circumference of each circle) are proportional to the distinctness measures (DC) derived below.

Certain characters were confirmed or derived from studies by Reid (1941) on the mesosoma, Snodgrass (1941) on the male genitalia and Oeser (1961) on the female genitalia. Genitalic terminology is that of Smith (1969, 1970a & b). Wing venation is based on the terminology of Hamilton (1971, 1972a & b), derived from that of Ross (1936). The number of closed cells includes the costal cell if that cell is present and closed. The symbols used for the behavioral formulae are based on those of Iwata (1942, 1950) as used by Evans (1966b) but with some modifications, mainly those necessary to include the bees in the same scheme. The symbols are as follows: Preparation of next = I *(instruere);* Searching for larval provisions = V *(venari);* Transport of provisions = T *(transferre);* Preparation of provisions—paralysis of animal prey = P *(pungere),* preparation (often "mixing") of pollen-nectar mass = M *(miscere);* Oviposition = O *(ovum parere);* Final closure = C *(claudere);* Provisions—of animal origin = subscript *a,* of vegetable origin = subscript *v.* Other terminology is explained where necessary in the section on the character involved, below.

*1. *Sexual dimorphism, general form.* Primitively, sexual dimorphism in general body form is minimal except that the male may be slightly smaller than the female and sometimes members of one sex may be apterous. 1.1—The male is considerably more slender than the female and is very elongate, thus being of quite different form.

No or only slight sexual dimorphism is considered primitive because this is the condition in most non-aculeate Hymenoptera and also in most members of the Aculeata.

State 1.1 is uniquely derived, occurring on internode 12-13 and forming a synapomorphy which links the myzinid and methochid groups. However, *Pterombrus* (myzinid) has the general sexual dimorphism only slight, indicating that state 1.1 may have been reversed within the myzinid group, or it may have arisen within the myzinid group. There is actually a tendency toward increased slenderness in the males within the entire branch subtended by internode 7-10 except for the tiphiid and brachycistidid groups, but its development to a very similar extreme in the myzinid and methochid groups leads to male slenderness being placed as above. Further, some members of the scoliid (e.g., *Campsomeris*) and apid (e.g., *Corynura;* Eickwort, 1969) groups have moderately slender males, but these are not of the same form as those included in the groups possessing state 1.1.

2. *Sexual dimorphism, aptery.* Primitively, both sexes are fully winged, or, rarely, both sexes have the wings equally reduced. 2.1—Sexual dimorphism is considerable, with the male winged and the female apterous.

No sexual dimorphism in wing development is considered primitive because this is the condition in most non-aculeate Hymenoptera and also in most aculeates.

Aptery in the female only has occurred on numerous occasions independently throughout the Aculeata. State 2.1 has developed on internodes 8-9 (associating the myrmosid and mutillid groups) and 18-21 (where it links five taxa), and in the plumariid, thynnid, methochid and brachycistidid groups. In view of its sporadic occurrence, little weight should be attached to it even where it does indicate synapomorphy. Furthermore, female aptery (or brachyptery) has arisen within the bethylid (e.g., *Deinodryinus, Pristocera;* Evans, 1964a), myzinid (e.g., *Braunsomeria*), tiphiid (e.g., *Pseudotiphia;* Nagy, 1969b) and formicid (all workers, some queens, e.g., *Dorylus, Eciton;* Wilson, 1971) groups. [Aptery or brachyptery in both sexes has arisen within the rhopalosomatid (e.g., *Olixon*) group; brachyptery in males only occurs within the apids (e.g., *Lasioglossum;* Houston, 1970: *Perdita;* Rozen, pers. comm.).]

3. *Sterile caste.* Primitively, all female individuals are capable of reproduction. 3.1—There is a specialized caste of females with reduced or no reproductive capability.

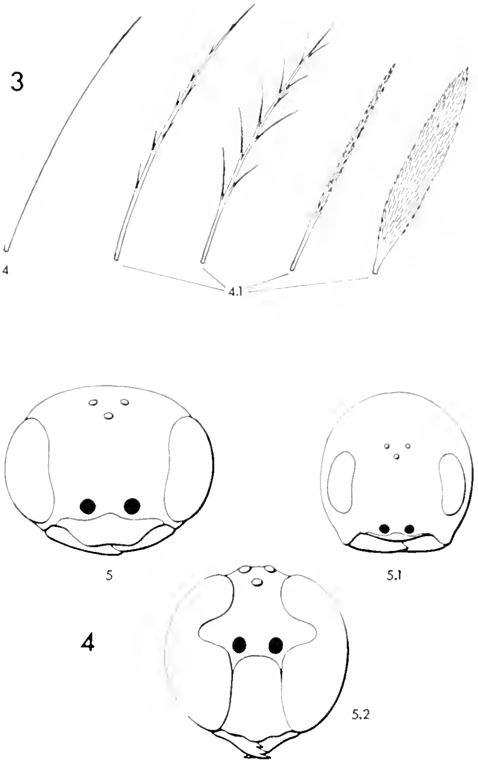
The lack of a sterile female caste is considered primitive because this is the condition in all non-aculeates and the vast majority of aculeate Hymenoptera.

The development of a sterile worker caste (3.1) is characteristic of the entire formicid group only, and thus provides no information on relationships at the higher levels. However, a similar derived state has evolved independently on various occasions within the apid (e.g., *Lasioglossum, Bombus, Apis, Trigona;* Michener, 1974) and vespid (e.g., *Vespa, Vespula;* Wilson, 1971) groups.

4. *Pubescence* (Fig. 3). Primitively, all pubescence is simple and unbranched. 4.1—Some of the body setae, especially those dorsally at the base of the metasoma, are branched to some extent, being subplumose or plumose.

Simple pubescence is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

The presence of plumose pubescence is characteristic of the apid group and is one of the classical characters for distinguishing this group from the sphecids. State 4.1 also occurs on internode 21-22, however, associating the eotillid and typhoctid groups. A similar state has developed within the anthoboscid (e.g., *Lalapa*) and mutillid (e.g., *Sphaeropthalma, Pseudomethoca*) groups at least, so that the importance of this character and its usefulness for establishing higher groupings is somewhat diminished.



Figs. 3-4. Characters of **Aculeata.** 3, body seta, showing primitive and derived states of pubescence; 4, head, anterior view, showing primitive and derived states of clypeus (5 based on *Anthobosca,* ♂; 5.1 on *Clystopsenella,* ♀; 5.2 on *Apoica,* ♂).

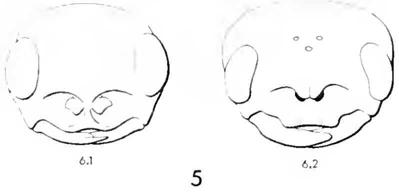
5. *Clypeus* (Fig. 4). Primitively, the clypeus is rather short and transverse so that the antennae are inserted below the middle of the face but not immediately above the oral cavity, i.e., the clypeus is termed "moderate." 5.1—The clypeus is extremely short and reduced to a transverse strip so that the antennae appear to be inserted just above the oral cavity. 5.2—The clypeus is somewhat dorsally produced and increased in height so that the antennae are inserted at or slightly above the middle of the face.

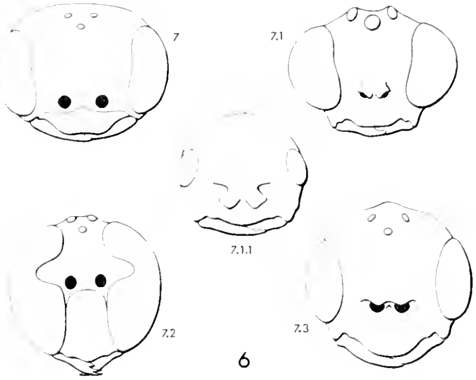
A moderate clypeus is considered primitive because this is the condition in most Aculeata and in particular in those considered primitive on the basis of other, stronger characters. Most non-Aculeata appear to have a slightly larger clypeus, although the Trigonalidae seem to fall more or less midway between clear expression of either the primitive state or state 5.2.

The clypeal form is difficult to interpret and is somewhat variable so that the states are fairly equivocal. However, state 5.1 represents an extreme and is characteristic of the scolebythid group as well as the females of the brachycistidid group. It also occurs within at least the myzinid group (e.g., female of *Braunsomeria*) and there is a tendency toward this state in the females of the bradynobaenid group. State 5.2 (representing the opposite trend) is present in the scoliid group (although somewhat equivocally so) and more clearly in the vespids (thus arising on internode 19-20), and in the males of the apterogynid group. It has also arisen within various other taxa such as the apid (practically all members except e.g., *Brachyhesma*), sphecid (e.g., *Sphex*, *Zyzzyx*) and formicid (especially males, e.g., *Paltothyreus*, *Camponotus*) groups. In view of the sporadic occurrence of both derived states and their equivocal nature, the clypeal form is accorded little weight in the analysis of relationships.

*6. *Antennal socket* (Fig. 5). Primitively, the antennal socket is an approximately circular foramen bordered evenly by a slightly raised rim. 6.1—The dorsomesal region of the rim is much produced, forming a projecting "tubercle" which is semicircular in cross-section and well-differentiated from the interantennal frontal region. 6.2—The interantennal front dorsomesal to the antennal socket is produced into a "frontal ledge" which is not highly differentiated from the front dorsally and is thus distinguishable from state 6.1.

A simple antennal socket is considered primitive because this is the condition in most non-aculeate Hymenoptera as well as most Aculeata.





Figs. 5-6. Characters of Aculeata. 5, head, anterior view, showing derived states of antennal socket (6.1 based on *Aureotilla*, ♀; 6.2 on *Meria*, ♀); 6, head, anterior view, showing primitive and derived states of eye form (7 based on *Anthobosca*, ♂; 7.1 on *Apterogyna*, ♂; 7.1.1 on *Apterogyna*, ♀; 7.2 on *Apoica*, ♂; 7.3 on *Methocha*, ♂).

State 6.1 occurs twice on the cladogram, on internodes 7-8 (where it associates the sapygid, myrmosid and mutillid groups) and 21-23 (linking the chyphotid and apterogynid groups), being subsequently modified into state 6.2 in the bradynobaenid group. State 6.2 occurs elsewhere on internode 12-13 thus linking the myzinid and methochid groups although it is not as well-developed in many of the methochids as in most myzinids. Although there is a tendency toward a state like 6.2 in female *Plumarius*, this state is not considered to be fully developed in the plumariid group. States 6.1 and 6.2 are not as distinct as the notation would indicate, as witness the apparent derivation of 6.2 directly from 6.1 in the bradynobaenid group. A state similar to 6.1 also occurs within the bethylid group (e.g., *Apenesia*, *Pristocera*), so that this character is actually not an extremely efficient indicator of groupings.

7. *Eye form* (Fig. 6). Primitively, each compound eye is large, oval and with the inner margin (seen from directly anteriorly) shallowly sinuate. 7.1—The eye is somewhat rounded but retains the sinuate inner margin. 7.1.1—The eye is rounded and the inner margin is convex. 7.2—The eye is essentially oval but the inner margin is deeply incised so that the shape is reniform. 7.3—The eye is oval but the inner margin is convex.

An oval eye with sinuate inner margin is considered primitive because this is the condition in most non-Aculeata and also in those aculeates considered to be the most primitive on the basis of other characters.

The differences between the various states of eye form are very subtle and often equivocal. Nevertheless, they do seem to provide useful information on higher groupings. Although state 7.1 has apparently evolved in parallel in both the chyphotid and apterogynid groups and its derivative occurs in the females of both these groups, there is a trend toward this state in the bradynobaenid group also, so that state 7.1 may logically be placed on internode 21-23 as another synapomorphy shared by these three taxa. A limitation is, however, inherent in the usefulness of this state since similar states have occurred within the plumariid (e.g., *Plumarius* male —7.1), brachycistidid (e.g., *Brachycistis*—7.1), mutillid (e.g., *Chrestomutilla*—7.1; *Sphaeropthalma*—7.1.1), formicid (most females—7.1.1) and other groups. State 7.2 is uniquely derived on the tree and links the scoliid and vespid groups, falling on internode 19-20. The strength of this is somewhat lessened by the occurrence of a similar condition within the sphecid (e.g., *Trypargilum*), anthoboscid (e.g., *Lalapa*), sapygid (e.g., *Sapyga*), mutillid (*Rhopalomutilla*, *Mutilla* males), myzinid (e.g., *Myzinum* male) and rhopalosomatid (e.g., *Rhopalosoma*) groups also. State 7.3 has occurred on at least four separate occasions, in the plumariid (female), scolebythid, methochid and brachycistidid (female) groups. It also has arisen within various taxa such as the bethylid (e.g., *Parnopes*), sphecid (e.g., *Cerceris*) and rhopalosomatid (e.g., *Olixon*) groups so that it is of little significance in delineating relationships.

8. *Eye contour.* Primitively, the compound eye more or less follows the general contours of the head. 8.1—The eye is protuberant and very prominent, being highly differentiated from the surrounding cuticle.

A non-protuberant eye is considered primitive because this is the condition in most non-aculeates and also in most aculeate Hymenoptera.

Although state 8.1 has apparently occurred as a parallelism in both the chyphotid and apterogynid groups, it may actually be that there has been a reversal in the bradynobaenid group to a situation similar to the primitive state, a hypothesis possibly supported by the fact that the eyes do not merge smoothly into the surrounding cuticle but present a discontinuity at their margins in the males of the bradynobaenids. In this case state 8.1 would have arisen on internode 21-23. In the absence of any further indications, parallel derivations are considered more likely than is the reversal. Elsewhere, state 8.1 occurs in the brachycistidid group and also within the plumariid (e.g., *Plumarius* male), mutillid (e.g., *Sphaeropthalma*) and formicid (e.g., *Paraponera* male) groups, especially in those species of nocturnal or crepuscular habit. This character is probably thus of minimal significance in establishing relationships between the taxa investigated.

9. *Eye pores and setae.* Primitively, the compound eye has scattered pores which penetrate the cuticle between the ommatidia and which bear minute setae which are not readily distinguishable except under extreme magnification (referred to as "not evident"). 9.1—The setae are readily visible at magnifications of approximately 100×, and are referred to as "short." 9.2—The sensory setae are obvious at magnifications of 20× or less and are referred to as "moderately long." 9.3—The pores and setae are apparently completely absent and are not visible under magnifications of 100×.

An eye with pores and minute setae is considered primitive because this is the condition in most non-aculeates (in particular the Terebrantia, including Trigonalidae) and also in most Aculeata.

It is often extremely difficult to distinguish the various states involved in this character and each has apparently arisen independently on several occasions, so that they are of minimal significance in the delineation of the cladogram. State 9.1 is characteristic of the scolebythid, brachycistidid (male), sierolomorphid, rhopalosomatid and formicid groups and also links the eotillid, typhoctid and males of the chyphotid groups (on internode 18-21). It has apparently been modified in the females of the chyphotids and both sexes of the apterogynid and bradynobaenid groups, the last three groups being associated by possession of state 9.3 (on internodes 21-23 for the female and 23-24 for the male). State 9.1 has also evolved independently within the bethylids (e.g., *Pristocera*). State 9.2 appears in the myrmosids and methochids and also within the apids (e.g., *Apis, Coelioxys*) and mutillids (e.g., *Areotilla*). Apart from its occurrences in the branch subtended by internode 21-23, state 9.3 appears in the plumariid (female), brachycistidid (female) and scoliid groups and also within the plumariid (e.g., *Plumarius* male) and mutillid (e.g., *Pseudophotopsis*) groups at least.

10. *Ocelli.* Primitively, three ocelli are present on the vertex. 10.1—The ocelli are completely absent, not even traces being retained.

The presence of ocelli is considered primitive because this is the condition in most Hymenoptera (both Aculeata and non-aculeates) and also in most insects.

The complete loss of ocelli is almost invariably associated with aptery although the inverse relationship does not always hold. Thus state 10.1 has appeared in the females of the plumariid and brachycistidid groups and also in the females of the entire branch subtended by internode 18-21. It is also present within the bethylid (e.g., *Pristocera* female; Evans, 1964a), mutillid (all females except some *Pseudophotopsis*), myrmosid (e.g., *Myrmosula* female), rhopalosomatid (e.g., *Olixon*) and formicid (most workers) groups. In addition, some or all of the ocelli are greatly modified or reduced (although traces generally remain) in various members of the sphecid group (e.g., some *Bembix;* Evans, 1966a). State 10.1 is thus of little or no cladistic significance.

*11. *Genal organ* (Fig. 7). Primitively, the gena is simple, without any specialized organ. 11.1—The gena bears an apparently secretory organ opening externally via an invaginated line or scattered pores.

A simple gena is considered primitive because this is the condition in most non-Aculeata (if not all of them) and also in most aculeates.

The development of a genal secretory organ in the apterogynid and bradynobaenid groups is apparently unique in the Aculeata and thus provides a very good synapomorphic character associating these two groups (on internode 23-24). The organ has a slightly different appearance in the two groups, forming a slight pro-

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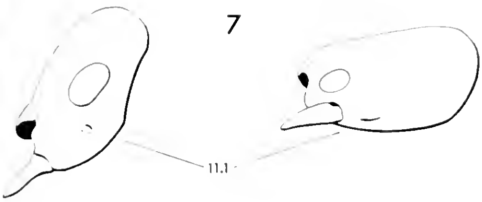

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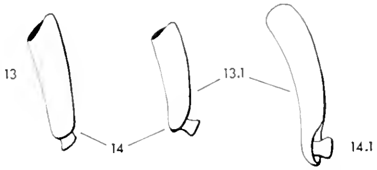

FIGS. 7-8. Characters of Aculeata. 7, head, lateral view, showing derived state of genal organ (11.1 based on *Apterogyna*, ♀, and *Bradynobaenus*, ♀, left to right); 8, antennal scape, anteromesal view, showing primitive and derived states of radicle axis and radicle-scape insertion (13, 14 based on *Zyzzyx*, ♀; 13.1, 14 on *Chyphotes*, ♂; 13.1, 14.1 on *Aureotilla*, ♂).

tuberance in the female of apterogynids and not being raised in the female bradynobaenids. Nevertheless it seems clear that the two forms are homologous. In male apterogynids it forms a patch of scattered pores and is not clearly distinguishable in bradynobaenid males. The organ may be analogous to the "felt line" on the second metasomal tergum (character 70).

*12. *Antennal dimorphism*. Primitively, the antenna comprises the same number of segments (usually 13) in both sexes. 12.1—The number of antennal segments is 12 in the female and 13 in the male.

A condition with the antenna 13-segmented in the male and 12-segmented in the female is unique in the Hymenoptera to most groups of Aculeata, those aculeates in which it does not occur being considered primitive on the basis of other characters also. This particular sexual dimorphism is thus considered derived.

Almost all groups of Aculeata show state 12.1 with great consistency, this apparently being a condition which evolved early and which serves to link almost all the aculeates into a holophyletic group (on internode 1-4). Only the plumariid, bethylid and scolebythid groups typically show no sexual dimorphism in the number of antennal segments. Within the bethylid group there is much variation in the number of segments (from 10 to 40; Riek, 1970) but the number is usually the same in both sexes or fewer in the males. The importance of state 12.1 is not much diminished by the fact that it has apparently been reversed on rare occasions within some taxa, such as in the pompilid group (e.g., *Ctenizipbontes;* Evans, 1972) and the mutillid group (*Atillum, Hoplocrates*) where both sexes have the antenna 13-segmented. In addition, the number of segments has been reduced to 12 in both sexes in a few instances, for example within the vespids (e.g., *Belonogaster*) and apids (e.g., *Neopasites;* Linsley & Michener, 1939), and some dacetine ants have as few as four antennal segments in the female (Brown & Taylor, 1970).

13. *Radicle axis* (Fig. 8). Primitively, the axis of the radicle does not deviate much from that of the remainder of the scape, so that the scape merely has a somewhat differentiated annulus basally. 13.1—The axis of the radicle forms a marked angle with that of the remainder of the scape.

A scape with a simple radicle is considered primitive because this is the condition in most non-aculeates as well as most Aculeata.

An angulate radicle (13.1) appears three times on the cladogram, in the plumariids (female) and on internodes 8-9 (linking the myrmosids and mutillids) and 21-23 (associating the chyphotid, apterogynid and bradynobaenid groups). Nevertheless, similar states are present within various other taxa such as the bethylids (e.g., *Bethylus, Anisepyris*), myzinids (e.g., *Meria*) and thynnids (e.g., *Elaphroptera*) so that this state is actually not very useful in delineating relationships.

*14. *Radicle-scape insertion* (Fig. 8). Primitively, the radicle is demarcated by a simple annular constriction. 14.1—The scape is produced externally into a flange that forms a cup-shaped depression or invagination into which the radicle is set.

A simple radicle-scape insertion is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

The invagination of the radicle appears once on the tree, on internode 8-9, thus associating the myrmosid and mutillid groups strongly. Although a similar development has occurred within the bethylid group (e.g., *Anisepyris*), such species are almost certainly only remotely related to the myrmosid-mutillid group, so that this affects the usefulness of this character minimally.

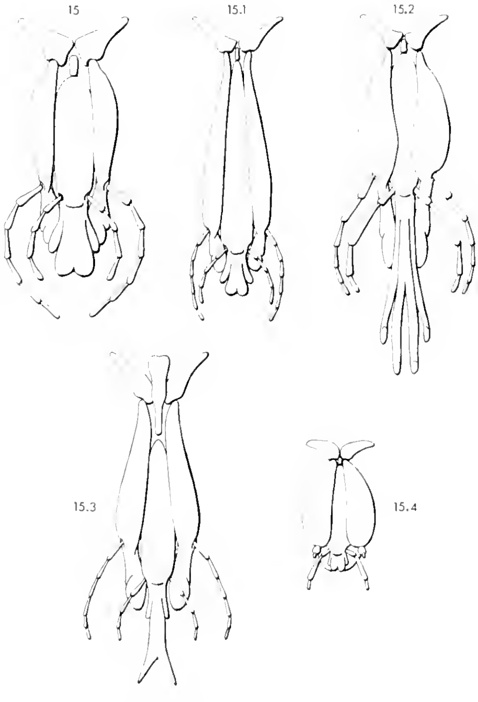

FIG. 9. Labio-maxillary complex, ventral view, somewhat diagrammatic, showing primitive and derived states (15 based on *Anthobosca*, ♂; 15.1 on *Callomelitta*, ♀; 15.2 on *Monobia*, ♀, modified; 15.3 on *Fedtschenkia*, ♀; 15.4 on *Bradynobaenus*, ♀, cardines may differ from form shown).

15. *Labio-maxillary complex* (Fig. 9). Primitively, the labio-maxillary complex is well-developed but relatively short and adapted for lapping. 15.1—The labio-maxillary complex is elongated by production of the prementum and stipes only. 15.2—The labio-maxillary complex is elongated by production of the glossa and paraglossa only. 15.3—The labio-maxillary complex is elongated by production of the glossa only. 15.4—The labio-maxillary complex is much reduced in size.

A well-developed but relatively short labio-maxillary complex is considered primitive because this is the condition in most non-Aculeata and also in most aculeates.

Derived states 15.1, 15.3 and 15.4 are each present in only one taxon, the apid, sapygid and bradynobaenid groups respectively, thus not contributing any information on higher groupings. State 15.2 is apparently possessed in common by the scoliid and vespid groups, seemingly having arisen on internode 19-20. There is some uncertainty about this, however, since the labio-maxillary complex is somewhat different in form in the two taxa, although its slight elongation in both has involved the same structures. In addition, many bees have a modification similar to state 15.2 superimposed on state 15.1.

16. *Maxillary palpus.* Primitively, the maxillary palpus is six-segmented. 16.1—The maxillary palpus is five-segmented. 16.2—The maxillary palpus is two-segmented.

A six-segmented maxillary palpus is considered primitive because this is the condition in most aculeates and many non-aculeates, this being the maximal number of segments in the Hymenoptera. This is also probably the primitive condition for the Insecta (Matsuda, 1965).

A five-segmented palpus (16.1) is characteristic of the female of the plumariid group. Nevertheless, similar reductions in the number of segments have occurred within many of the other taxa, such as the bethylid group (e.g., *Dissomphalus* male; Evans, 1964a), the male of *Plumaroides* in the plumariid group, and the apid group (where the number of segments ranges from 6 to 0). This state is thus not of great significance, especially since it involves the loss of only one segment. State 16.2 involves the loss of four segments and has occurred in the bradynobaenid group and elsewhere such as within the bethylid (e.g., *Dissomphalus* female; Evans, 1964a), mutillid (*Rhopalomutilla* female) and apid (e.g., *Apis*) groups. It is thus of no use in establishing higher groupings.

17. *Labial palpus.* Primitively, the labial palpus is four-segmented. 17.1—The labial palpus is three-segmented.

A four-segmented labial palpus is considered primitive because this is the condition in many non-Aculeata and in most aculeates; it also represents the maximal number of segments in the Hymenoptera. The primitive condition for the Insecta is, however, probably three segments (Matsuda, 1965).

The loss of one segment in the labial palpus has apparently occurred on the tree at least three times independently, in the plumariid (female), bethylid and bradynobaenid groups. It is also found within the plumariid group (e.g., males of *Myrmecopterina*, *Plumarius*). It is thus of no use in delimiting higher groupings.

*18. *Hind margin of pronotum* (Fig. 10). Primitively, the pronotum is large and somewhat saddle-shaped with its hind margin nearly straight and only very slightly anteriorly arcuate. 18.1—The pronotum is shortened with its hind margin strongly concave in a fairly regular and somewhat acute parabolic curve (roughly V-shaped). 18.2—The pronotum is shortened with its hind margin shifted anteriorly over almost its entire width (broadly U-shaped).

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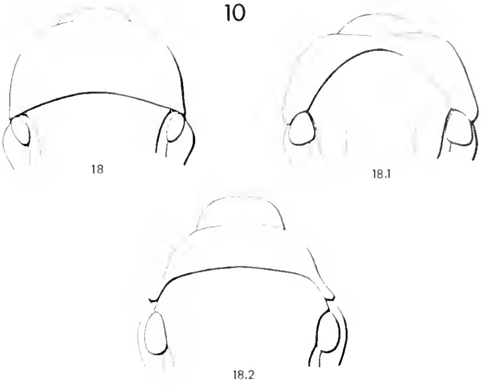

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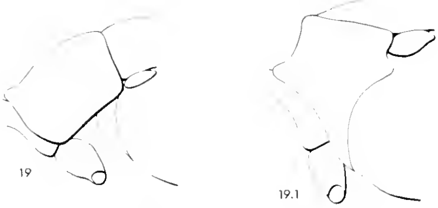


Figs. 10-11. Characters of Aculeata. 10, anterior region of mesosoma, dorsal view, showing primitive and derived states of hind margin of pronotum (18 based on *Anthobosca*, ♀; 18.1 on *Trielis*, ♀; 18.2 on *Cerceris*, ♀); 11, anterior region of mesosoma, lateral view, showing primitive and derived states of pronotal articulation (19 based on *Anthobosca*, ♀; 19.1 on *Scolia*, ♀).

A large pronotum with approximately straight hind margin is considered primitive because this is the condition in those groups of Aculeata considered primitive on the basis of other characters, and also in various of the most primitive non-aculeates (e.g., xyelids). Furthermore, elsewhere in the insects reduction in relative size of the pronotum is generally derived.

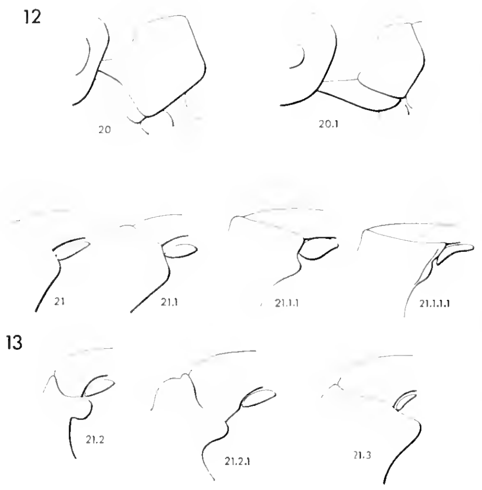
State 18.1 has arisen independently on at least six occasions, on internodes 18-19 and 21-23 (males), and in the plumariids (male), mutillids, brachycistidids (male) and rhopalosomatids. It is thus of little use in establishing relationships. By contrast, state 18.2 has apparently arisen only once, on internode 4-5, thus associating the sphecid and apid groups. A vaguely similar condition is present in some members of the bethylid group (e.g., *Deinodryinus, Euchroeus*) causing some authors to consider *Ampulex* (definitely a sphecid although it has the pronotum larger than most other sphecids; see Evans, 1959a; Leclercq, 1954) closer to (or even a member of) the bethylid group (e.g., Nagy, 1969a). The condition in the Trigonalidae is also vaguely similar to state 18.2. However, in all three of these instances there are marked differences in detail (especially in the form of the posterolateral angle and the spiracular lobe) so that these superficially similar states appear definitely to have had independent origins.

*19. *Pronotal articulation* (Fig. 11). Primitively, the attachment of the pronotum to the mesothorax is loose and freely articulating. 19.1—The pronotum is very closely attached and coadapted to the mesothorax so that no or extremely little movement is possible between them, although the sclerites are not actually fused.

A freely movable connection between the pronotum and mesothorax is considered primitive because this is the condition in most non-aculeates as well as in most Aculeata.

Apparently immovable association of the pronotum and mesothorax has occurred in only two taxa, the scoliid and vespid groups, and is so similar in both that it is considered as very good evidence for their association, this state thus having arisen on internode 19-20.

20. *Pronotal collar* (Fig. 12). Primitively, the pronotum is expanded anteriorly as a well-developed flange or "collar" which aids in the support of the head and provides protection to the neck region dorsally. 20.1—The pronotum is somewhat flattened anteriorly and not at all expanded, so that the neck region is dorsally exposed.



FIGS. 12-13. Characters of Aculeata. 12, prothorax and base of head, lateral view, showing primitive and derived states of pronotal collar (20 composite; 20.1 based on *Clystopsenella*); 13, anterodorsal region of mesosoma, lateral view, showing primitive and derived states of posterolateral angle of pronotum (21 based on *Anthobosca*, ♂; 21.1 on *Pseudophotopsis*, ♂; 21.1.1 on *Scolia*, ♀; 21.1.1.1 on *Rygchium*, ♀; 21.2 on *Callomelitta*, ♀; 21.2.1 on *Trypargilum*, ♀; 21.3 on *Bradynobaenus*, ♂).

A well-developed pronotal "collar" is considered primitive because this is the condition in most non-Aculeata (although generally not well-developed in Symphyta) as well as in practically all aculeates.

Although the derived state is approached in various taxa (e.g., the vespids), it is fully expressed only in the plumariid (female) and scolebythid groups, and in a different fashion in each. State 20.1 is thus of no use in establishing relationships between taxa.

*21. *Posterolateral angle of pronotum* (Fig. 13). Primitively, the posterolateral angle of the pronotum is evenly rounded, reaching the tegula but not exceeding its anterior margin. 21.1—The posterolateral angle is very slightly dorsally produced so as to appear truncate anterior to the tegula; it attains the tegula but does not exceed its anterior margin. 21.1.1—The posterolateral angle is dorsally produced and exceeds the anterior margin of the tegula very slightly so that the lobe is notched. 21.1.1.1—The posterolateral angle is markedly produced dorsally and posteriorly so that it exceeds the level of the tegula and forms an acute lobe above it. 21.2—The posterolateral angle is reduced dorsally above and slightly anterior to the spiracular operculum; the operculum forms a highly differentiated lobe reaching the tegula. 21.2.1—The posterolateral angle is reduced anterodorsal to the spiracular operculum and is somewhat retracted anteriorly so that the highly differentiated operculum does not reach the level of the tegula. 21.3—The posterolateral angle is slightly posteriorly produced below the tegula and thus exceeds its anterior margin slightly, forming a fairly acute lobe.

A simple posterolateral angle which reaches the tegula is considered primitive because this is the condition in many non-aculeates (especially Symphyta; many Terebrantia show differing modifications) and also in many Aculeata, in those taxa which are generally considered most primitive on the basis of other characters.

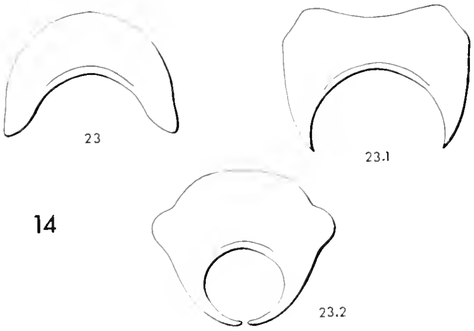
A slight dorsal production of the pronotal angle (22.1) has apparently occurred on at least four occasions, on internodes 12-14 and 18-19 and in the mutillid and rhopalosomatid groups, and is thus not of much use in establishing relationships. However, further development of this structure has occurred in both taxa derived from internode 19-20; state 21.1.1 arose on internode 19-20, being present in the scoliid group, and its further elaboration (21.1.1.1) is present in the vespid group. This derivation of state 21.1.1 is unique and thus provides good evidence of the close relationship of the scoliid and vespid groups. State 21.2 arose uniquely on internode 4-5 and thus is a very good indicator of the holophyly of the sphecid and apid groups. Its elaboration (21.2.1) has occurred in the entire sphecid group, although it is not very well-developed in some (such as *Astata*) and a similar state is present in most of the apids (but 21.2 in *Callomelitta* and *Megachile*, e.g.). A superficially similar condition is also present within the bethylid group (e.g., *Chrysis, Euchroeus*) but this anterior retraction of the spiracular operculum differs in detail from the state in the sphecids, so that it does not diminish the significance of state 21.2.1 or its antecedent. State 21.3 is apparently unique to the bradynobaenid group although a slight tendency toward this state is distinguishable in the apterogynids, so that its importance in delimiting higher groupings is minimal.

22. *Posteroventral margin of pronotum.* Primitively, the posteroventral margin of the pronotum is approximately straight. 22.1—The posteroventral margin is distinctly concave.

An approximately straight posteroventral margin is considered primitive because this is the condition in many non-aculeates (in particular Symphyta) and also in many of the Aculeata which are considered to be the most primitive on the basis of other characters.

The derived state represents a widespread tendency that has arisen on at least four occasions and has been reversed at least once. Thus, state 22.1 appears on internodes 4-5, 12-14 and 6-15, and in the methochid group. The apparently primitive state has been regained on internode 21-22. Because of its plasticity and the somewhat equivocal nature of this character, it is not of much utility in demonstrating relationships, although it does seem to have some value in indicating which taxa are relatively more advanced than others.

*23. *Ventral angle of pronotum* (Fig. 14).



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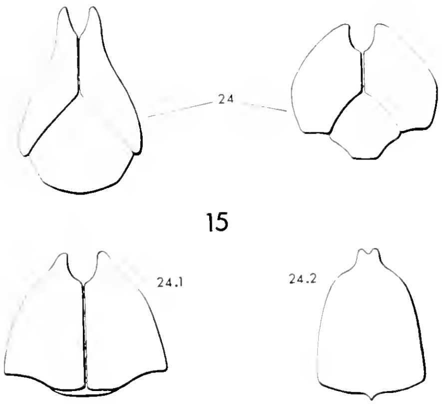

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Figs. 14-15. Characters of Aculeata. 14, pronotum, anterior view, showing primitive and derived states of its ventral angle (23 based on *Anthobosca*, ♀; 23.1 on *Synoeca*, ♀; 23.2 on *Cerceris*, ♀); 15, prothorax, ventral view, showing primitive and derived states of propleural separation (24 based on *Clystopsenella*, ♀, and *Euchroeus*, ♂, left to right; 24.1 on *Euclavelia*, ♀; 24.2 on *Plumarius*, ♀).

Primitively, the ventral angle of the pronotum is rounded and does not much (or at all) exceed the level of the base of the forecoxa ventrally. 23.1—The ventral angle is acute and produced ventrally beyond the forecoxal base. 23.2—The ventral angle is greatly produced so that it almost contacts its counterpart midventrally.

A rounded ventral angle is considered primitive because this is the condition in most non-aculeates as well as in most Aculeata.

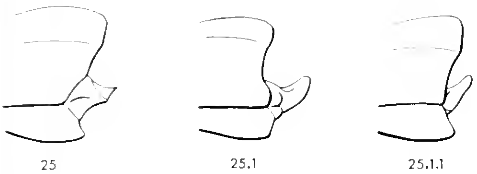
State 23.1 has apparently arisen twice on the cladogram, on internodes 18-19 (associating the formicid, vespid and scoliid groups) and 21-23 (associating the chyphotid, apterogynid and bradynobaenid groups). Although it is also weakly present within the plumariid group (e.g., male of *Plumarius*), it seems to be fairly useful and may actually represent a trend originating on internode 16-18. The extreme development of the ventral angle (23.2) is uniquely present in the sphecid and apid groups and apparently arose on internode 4-5, thus forming a strong indicator of the holophyly of this grouping.

*24. *Propleural separation* (Fig. 15). Primitively, the propleura are separated posteriorly, diverging at an angle and thus exposing the prosternum anterior to the forecoxae. 24.1—The propleura are mesally contiguous posteriorly and do not diverge at an angle; their posterior margins form a more or less straight line, so that the prosternum is not visible between the propleura. 24.2—The propleura are modified similarly as in 24.1 but they are fused along the midline both dorsally and ventrally.

Posteriorly diverging propleura are considered primitive because this is the condition in many non-Aculeata (except that various taxa highly specialized in other respects, as well as the Trigonalidae, show a tendency toward a state approaching 24.1) and in those aculeates which possess many other characters in their primitive states.

The primitive extreme is apparently present in the scolebythid group where the prosternum is remarkably well-developed anteriorly and is extensively exposed between the widely diverging propleura. Since this condition is more extreme than in any other taxon, it may be a secondary development, however. State 24.1 is uniquely developed in all the taxa subtended by internode 4-6, although the superficially similar 24.2 is present in the female plumariids where the propleura form a rigid tube. This character is probably not as reliable as might be supposed, however, since some members of the sphecid (e.g., *Crabro*) and apid (e.g., *Sericogaster*) groups show conditions approaching state 24.1.

*25. *Prosternum* (Fig. 16). Primitively, the prosternum forms an approximately uniform plane and is not sunken except perhaps for a very short posterior section. 25.1—The prosternum is sunken over most of its surface so that only a short anterior section (shorter than the sunken section) is visible ventrally, this section being in a different plane from the remainder of the sternum. 25.1.1—The prosternum is entirely sunken and not visible ventrally.



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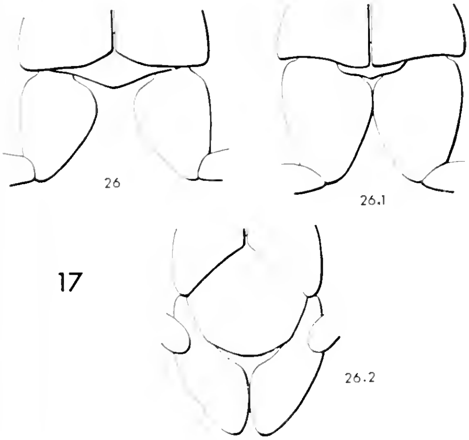

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Figs. 16-17. Characters of Aculeata. 16, posterior region of propleura and prosternum, oblique ventrolateral view, showing primitive and derived states of prosternum (25 based on cleptid sp.; 25.1 on *Anthobosca*, ♀; 25.1.1 on *Polybia*, ♀); 17, posterior region of prothorax, ventral view, showing primitive and derived states of forecoxal contiguity (26 based on cleptid sp.; 26.1 on *Anthobosca*, ♂; 26.2 on *Clystopsenella*, ♀).

A prosternum with most of its surface in a single plane is considered primitive because this is the condition in most non-aculeates. (Even though the prosternum may be somewhat hidden in many, e.g., the Trigonalidae, even in these it generally forms a single plane.)

State 25.1 has apparently arisen on at least two occasions in the aculeates, in the plumariid group and on internode 1-4. It is additionally present within the bethylid group (e.g., *Pristocera*). The second derived state (25.1.1) apparently has a unique origin (on internode 19-20) and associates the vespid and scoliid groups. Since the difference between 25.1 and 25.1.1 is not very great, however, this state may not be as valuable as its apparent unique derivation would indicate.

*26. *Forecoxal contiguity* (Fig. 17). Primitively, the forecoxae are somewhat separated basally by the width of the relatively well-developed prosternum. 26.1—The forecoxae are contiguous basally due to reduction in the posterior width of the sternal region. 26.2—The forecoxae are basally separated but are posteriorly produced beyond the trochanteral insertions so as to become contiguous apically only.

Separated forecoxae are considered primitive because this is the condition in most non-Aculeata, although there is much variation and the forecoxae approach contiguity in various groups (including the Trigonalidae).

Although there is variation in the intercoxal distance in the bethylid and plumariid groups so that some members have the forecoxae almost contiguous, actual contiguity (26.1) apparently arose uniquely on internode 1-4. State 26.2 is uniquely derived and occurs only in the scolebythid group, thus not contributing information on relationships.

27. *Mesonotum*. Primitively, the mesonotum does not extend anteriorly much beyond the level of the tegulae. 27.1—The mesonotum is mesally anteriorly produced so that its anterior margin extends much anterior to the level of the tegulae.

A short mesonotum is considered primitive because this is the condition in those Aculeata considered to be generally the most primitive on the basis of other characters, and is also the condition in the most primitive non-aculeates (e.g., Xyelidae).

State 27.1 has arisen on at least six separate occasions, on internodes 18-19 and 21-23 (males), in the plumariid (male), brachycistidid (male) and rhopalosomatid groups, and somewhat less obviously on internode 4-5. It is thus essentially useless for associating groups. This state is logically linked with the derived states of character 18, but does not present an identical distribution on the cladogram and is thus not considered a duplication.

*28. *Scutellum* (Fig. 18). Primitively, the mesoscutellum is simple, more or less flattened and not highly differentiated from the remaining notal area. 28.1—The scutellum is enlarged, being posterodorsally swollen and evenly protuberant. 28.1.1—The scutellum is extremely enlarged and produced so that it overhangs the metanotum.

A simple scutellum is considered primitive because this is the condition in most non-aculeates as well as in most members of the Aculeata.

Although there are scattered instances of enlargement of the scutellum (e.g., apids, *Euglossa;* mutillids, *Trispilotilla;* formicids, *Atta*) these are of varying types, and a swollen scutellum is characteristic of only two of the taxa considered, the apterogynid and bradynobaenid groups. State 28.1 has thus apparently arisen on internode 23-24 and is considered to be quite good evidence of the grouping of these two taxa although it has been taken a step further in the bradynobaenids where state 28.1.1 is present.

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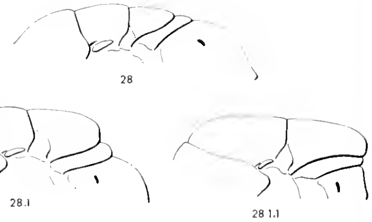

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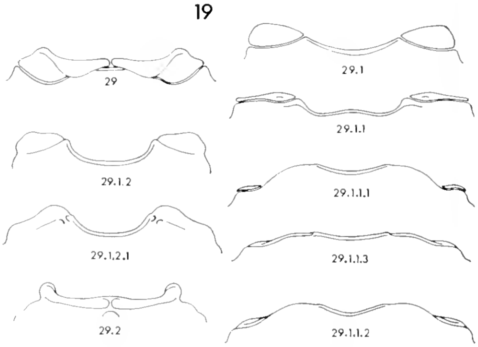


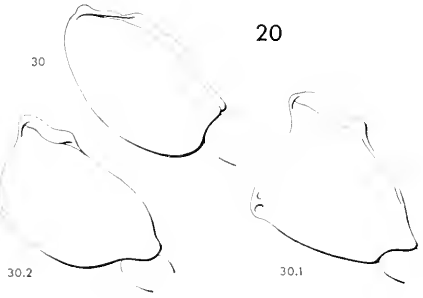
FIGS. 18-19. Characters of Aculeata. 18, dorsal region of mesosoma, lateral view, showing primitive and derived states of scutellum (28 based on *Anthobosca*, ♀; 28.1 on *Apterogyna*, ♂; 28.1.1 on *Bradynobaenus*, ♂); 19, anterior region of mesopleurosternum, ventral and lateral view (as if flattened), showing primitive and derived states of prepectus (29 based on *Cleptes*, ♀; 29.1 on *Sierolomorpha*, ♀; 29.1.1 on *Chyphotes*, ♂; 29.1.1.1 on *Polistes*, ♀; 29.1.1.2 on *Trielis*, ♂; 29.1.1.3 on *Paraponera*, ♂; 29.1.2 on *Fedtschenkia*, ♀; 29.1.2.1 on *Pseudophotopsis*, ♂; 29.2 on *Chlorion*, ♀).

*29. *Prepectus* (Fig. 19). Primitively, the prepectus (= epicnemium) is a transverse sclerite divided midventrally but with the halves contiguous (or almost so), extending across the anterior margin of the mesopleurosternum and articulating freely with this margin. 29.1—Each half of the prepectus is narrowed so that the two sections become widely separated and do not extend to the ventral surface of the mesosoma but do extend the entire height of the pleural region laterally. 29.1.1—Each section of the prepectus is widely separated from its counterpart and is shortened so that each half forms a very short but elongate strip at the anterior margin of the mesepisternum; the articulation is retained and the prepectal sclerite is hidden under the posteroventral margin of the pronotum. 29.1.1.1—Each prepectal sclerite is very narrow and short, extending over only the dorsal half or less of the mesepisternum and articulating with it; the sclerite is hidden under the posterolateral angle of the pronotum. 29.1.1.2—Each prepectal sclerite is extremely short and narrow, extending over less than the dorsal half of the mesepisternum and fused to it with almost no trace of differentiation; the sclerite is hidden under the posterolateral angle of the pronotum. 29.1.1.3—Each prepectal sclerite is shortened but extends over most of the height of the mesepisternum and is fused to it; the sclerite is hidden under the posteroventral margin of the pronotum. 29.1.2—Each prepectal sclerite is not shortened and extends the height of the mesepisternum, being fused to it with the line of fusion forming a sulcus. 29.1.2.1—Each prepectal sclerite is not shortened and extends the height of the mesepisternum, being fused to it but with the line of fusion obliterated except for a pair of pits ventrally. 29.2—The prepectus extends completely across the anterior margin of the mesopleurosternum, is fused in the midline and is also fused to the pleurosternum, forming a depressed anterior margin to it.

The allocation of states of the prepectus is that which shows greatest correlation with the groupings made on the basis of other characters. A state similar to 29.2 is present in Trigonalidae and some chalcidoids, however. Although the sequence and pattern of modification forms a logical scheme, the homologies of the sclerites involved are somewhat uncertain despite the studies by Snodgrass (1910, 1935), Matsuda (1970) and others. In particular, the possibility of confusion of the "postspiracular sclerite" (probably the anepisternum) and the "epicnemium" (prepectus) has been noted by Richards (1956a; see also 1956b, 1971). Additional investigations, especially of groups not critically studied hitherto, should clarify the situation.

The primitive state is present in the bethylid, scolebythid and plumariid groups, although some members of the last (e.g., *Plumaroides*) have the prepectus tending towards state 29.1. Apart from this, state 29.1 has apparently been derived only on internode 4-6, thus associating the remainder of the aculeates except for the sphecids and apids. State 29.1.1 has apparently arisen on three occasions, on internode 16-18 (where it groups eight taxa) and in the brachycistidid and rhopalosomatid groups. The next modification (29.1.1.1) has occurred only in the vespid group. Even greater fusion and reduction (29.1.1.2) has occurred in the scoliid group and state 29.1.1.3 is characteristic only of the formicid group. Modification in a different direction (29.1.2) has apparently occurred twice, on internode 7-8 (associating the sapygid, myrmosid and mutillid groups) and in the pompilid group. The next step in this sequence (29.1.2.1) has occurred once, on internode 8-9, linking the myrmosid and mutillid groups even more strongly. State 29.2 is characteristic of the sphecid and apid groups and serves to emphasize their relatively basal position, this state occurring on internode 4-5. A few members of the bethylid group (e.g., *Pseudisobrachium coxalis*) show a similar condition, however, this fact somewhat reducing the strength of this state in associating the sphecids and apids. Although a more detailed investigation of these structures is necessary, the pattern of evolution derived here seems to provide useful phyletic information. Although Reid (1941) misinterpreted the situation in some taxa (e.g., Mutillidae, *sensu stricto*), he also suggested that the prepectus provided useful information for establishing relationships.

*30. *Mesepimeron* (Fig. 20). Primitively, the mesepimeron is differentiated from the mesepisternum by a distinct pleural sulcus which is continuously distinguishable from the pleurointersegmental suture, and extends from the pleural wing process to a point just dorsal to the mesocoxa. 30.1—The pleural sulcus is indistinct or invisible over its ventral half so that the mesepimeron is not differentiated ventrally although it is apparently not reduced in size. 30.2—The pleural sulcus is coincident with the pleurointersegmental suture over its ventral half or more, so that the mesepimeron is reduced to a small sclerite at the posterodorsal angle of the mesopleuron.



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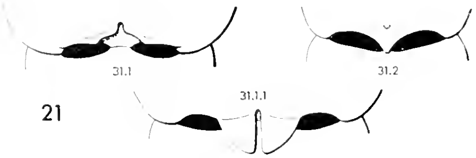

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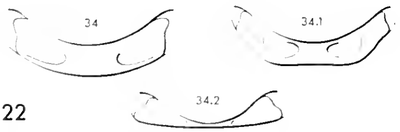

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FIGS. 20-22. Characters of Aculeata. 20, mesopleuron, lateral view, showing primitive and derived states of mesepimeron (30 based on *Plumarius*, ♂; 30.1 on *Areotilla*, ♂; 30.2 on *Chyphotes*, ♂); 21, posterior region of mesosternum, ventral view, showing derived states (31.1 based on *Fedtschenkia*, ♀; 31.1.1 on *Anthobosca*, ♂; 31.2 on *Apoica*, ♂); 22, metanotum, dorsal view, showing primitive and derived states (34 based on *Anthobosca*, ♂; 34.1 on *Pseudophotopsis*, ♂; 34.2 on *Clystopsenella*).

A complete and distinct mesopleural sulcus is considered primitive because this is the condition in most non-aculeates as well as in those Aculeata considered the most primitive on the basis of other characters.

Reduction of the mesepimeron is apparently a general tendency in the more advanced Hymenoptera and is thus useful only in indicating relative position on the tree. Such a general trend cannot, however, be adequately divided into discrete states. State 30.1 has apparently been attained twice, in the mutillid and scoliid groups, and is thus of no importance in associating taxa. State 30.2 is characteristic of the apid and formicid groups and also occurs within the sphecid (e.g., *Gorytes*) and vespid (e.g., *Belonogaster*) groups. It has also arisen on internode 18-21 where it serves to associate five taxa. Its apparent weakness because of multiple origins is somewhat offset in this last instance in that some fine details of the modification are constant in these five taxa but differ from those in other groups. State 30.2 is thus considered quite good evidence for the association of the eotillid, typhoctid, chyphotid, apterogynid and bradynobaenid groups.

*31. *Mesosternum* (Fig. 21). Primitively, the mesosternum is moderately convex and smoothly truncate posteriorly without any protuberances or carinae. 31.1—The mesosternum has a short transverse carina or dentate projection anteromesal to each coxal cavity. 31.1.1—The mesosternum has a platelike projection originating anteromesal to each coxal cavity and projecting posteriorly over it. 31.2—The mesosternum is posteriorly produced mesally, carrying the mesal points of articulation (condyles) of the mid-coxae posteriorly and with the anteromesal margins of the coxal cavities thus somewhat produced.

A simple mesosternum is considered primitive because this is the condition in most non-aculeate and in most aculeate Hymenoptera.

The development of a transverse carina or small tooth anterior to each mid-coxa (state 31.1) has apparently occurred on at least three occasions, on internodes 6-7 and 16-17 and in the sierolomorphid group. This is thus a rather weak state for demonstrating relationships. The further development of lamellae overlying the coxae (31.1.1) has occurred twice, on internode 7-10 (where it links six taxa) and in the rhopalosomatid group. Within the branch subtended by internode 7-10 the lamellae have been reduced to small teeth (an apparent reversal to state 31.1) in the methochid group. Nevertheless, 31.1.1 appears to provide rather good evidence for the grouping of the anthoboscid, thynnid, myzinid, tiphiid, brachycistidid (and methochid) groups. The posteromesal production of the mesosternum (31.2) has apparently occurred twice, on internodes 4-5 (linking the sphecids and apids) and 19-20 (associating the scoliid and vespid groups), although the presence of state 32.2 in the scoliids obscures this relationship.

32. *Mesocoxal contiguity.* Primitively, the mid-coxae are slightly separated basally. 32.1—The mid-coxae are contiguous as a result of a reduction in the intercoxal region of the mesosternum. 32.2—The mid-coxae are very widely separated as a result of considerable lateral expansion of the intercoxal region of the mesosternum.

Slightly separated mid-coxae are considered primitive because this is the condition in most groups of Aculeata and in particular those taxa considered most primitive on the basis of other characters.

Contiguity of the mid-coxae (32.1) has apparently arisen on at least three occasions, on internodes 8-9 (in the myrmosids and mutillids) and 16-17 (linking the pompilid and rhopalosomatid groups), and in the vespid group. It thus does not provide very strong evidence of relationships. Broad separation of the mid-coxae (32.2) has occurred twice, on internode 23-24 (female), thus associating the apterogynid and bradynobaenid groups, and in both sexes of the scoliid group. Details differ in these two occurrences of the derived state, so that the presence of 32.2 on internode 23-24 is considered strong evidence of relationship.

33. *Meso-metapleural suture.* Primitively, the meso- and metapleura articulate freely with each other. 33.1—The meso- and metapleura are closely associated and not mutually movable although not fused. 33.1.1—The meso- and metapleura are fused, at least over the dorsal half, although the suture is distinct.

Mutually movable meso- and metapleura are considered primitive because this is the condition in most non-Aculeata and most insects in general.

Immobility of the meso-metapleural suture has occurred on at least four occasions, and is an expression of the general trend toward consolidation of the mesosoma in the aculeates. State 33.1 has arisen on internodes 4-5, 12-14 and 16-18 and in the pompilid group, and is thus of little utility except in indicating approximate relative advance on the tree. The further fusion of the meso- and metapleura (33.1.1) has occurred independently in the formicid and chyphotid groups and is thus of no use in indicating relationships.

34. *Metanotum* (Fig. 22). Primitively, the metanotum is a transverse sclerite of approximately the same length mesally as laterally. 34.1—The metanotum is slightly shortened mesally so that it is only a little more than half as long mesally as laterally. 34.2—The metanotum is extremely con-

stricted mesally and reduced to a minute strip connecting the lateral areas.

A well-developed metanotum of even length is considered primitive because this is the condition in most non-aculeates (including Trigonalidae) as well as in most Aculeata.

Mesal shortening of the metanotum (34.1) has occurred at least twice, on internode 23-24 (linking the apterogynid and bradynobaenid groups, in which this state is at least partly correlated with the mesoscutellar enlargement) and in the mutillid group. It is thus not of great utility in establishing relationships. It has also occurred elsewhere, such as within the myrmosid group (e.g., *Myrmosa*). Extreme reduction of the metanotum so that the scutellum and propodeum are almost in contact (34.2) has occurred on the tree only in the scolebythid group. A similar state is present within the bethylid group (e.g., Epyrinae; Evans, 1964), however, and this may be of significance in associating these groups.

*35. *Metapostnotum* (Fig. 23). Primitively, the metapostnotum forms a transverse groove at the anterior margin of the propodeum, being fused to the propodeum and slightly depressed. 35.1—The metapostnotum is very considerably shortened and invaginated so that it is barely visible mesally between the propodeum and the metanotum. 35.1.1—The metapostnotum is completely invaginated and not visible mesally, the propodeum being in contact with the metanotum, but the metapostnotum is still visibly continuous with the metepimeron laterally. 35.2—The metapostnotum is obscurely distinguishable laterally but merges completely with the propodeum mesally although it is apparently not invaginated. 35.3—The metapostnotum is greatly enlarged and posteriorly produced mesally, forming a "triangular area" which occupies most of the apparent disc of the propodeum. It carries the muscles between the second and third phragmata to their insertion apparently far posteriorly on the propodeum.

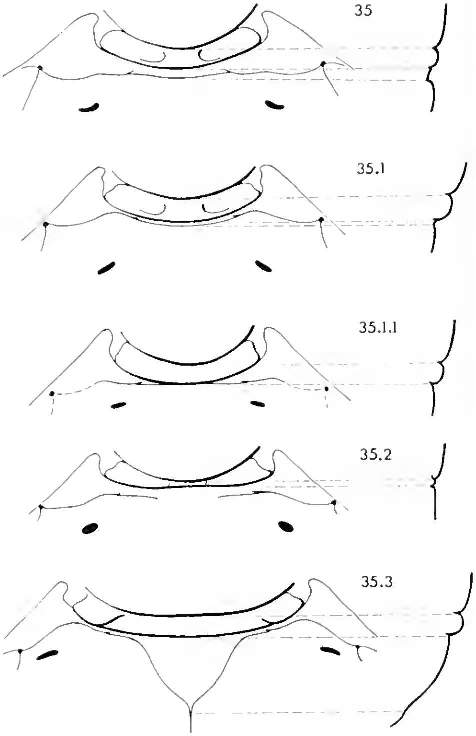
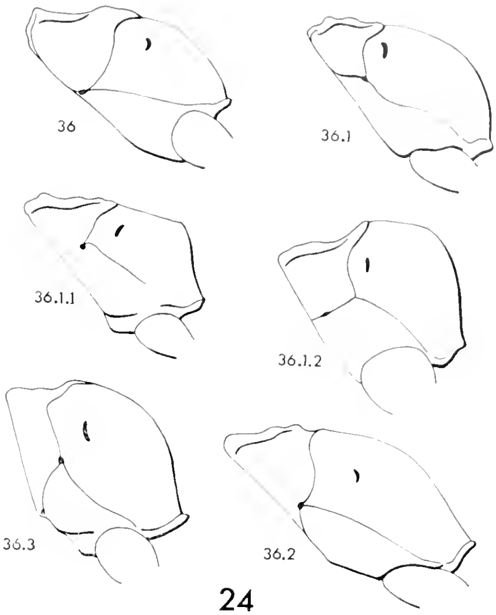


FIG. 23. Anterodorsal region of metathorax and propodeum, dorsal and lateral view (as if flattened) on left and profile on right (dorsal to right), showing primitive and derived states of metapostnotum (35 based on *Euclavelia*, ♀; 35.1 on *Anthobosca*, ♂; 35.1.1 on *Methocha*, ♂; 35.2 on *Clystopsenella*, ♀; 35.3 on *Cerceris*, ♀).

A distinct and depressed metapostnotum of approximately uniform length is considered primitive because this is the condition in many non-aculeates, especially Terebrantia (including Trigonalidae).

There is a general tendency above internode 4-6 toward shortening and invagination of the metapostnotum as part of the trend toward mesosomal consolidation. Although state 35.1 appears only once on the tree (on internode 6-7), its derivative (35.1.1) appears at least three times, in the tiphiid and myzinid groups, and apparently *de novo* on internode 16-18. This last derivation thus weakens the unique placement of state 35.1 somewhat, although 35.1 is logically not absolutely necessary as an antecedent to 35.1.1. State 35.2 is present in the bethylids and scolebythids, thus having arisen once (on internode 2-3) and providing useful information associating these taxa. State 35.3 is unique in the Aculeata and apparently in the Hymenoptera as a whole. This remarkable modification of the metapostnotum which is present in the sphecid and apid groups provides extremely strong evidence of the holophyletic association of these groups, having arisen on internode 4-5.

Although the various modifications of the metapostnotum need further investigation and clarification, the scheme outlined here provides useful information. In particular, the above interpretation of the origin of the "triangular area" in bees and sphecids (35.3) seems to be upheld by the arrangement of sutures (or sulci) in various sphecids (e.g., *Cerceris*) and by the placement of the muscles between the second and third phragmata (*2ph-3ph*). Daly (1964) concluded that in *Apis* the transpropodeal lines (defining the propodeal triangle) do not result from the migration of muscles *2ph-3ph* from the sides of the propodeum to the median pit, but he apparently did not consider that the propodeal triangle might represent the metapostnotum, a condition which is actually obscure in this highly evolved bee.



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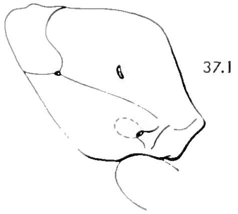


Figs. 24-25. Characters of Aculeata. 24, metapleuron and propodeum, lateral view, showing primitive and derived states of metapleuron (36 based on *Anthobosca*, ♂; 36.1 on *Pseudophotopsis*, ♂; 36.1.1 on *Colocistis*, ♂; 36.1.2 on *Trielis*, ♀; 36.2 on *Euclavelia*, ♀; 36.3 on *Cerceris*, ♀); 25, metapleuron and propodeum, lateral view, showing derived state of metapleural gland (37.1 composite).

36. *Metapleuron* (Fig. 24). Primitively, the metepimeron is dorsally quite long, with the pleural sulcus almost or quite coincident with the meso-metapleural suture dorsal to the endophragmal pit. Below the pit the pleural sulcus is coincident with the metapleural-propodeal suture. The pit is very close to the anterior margin of the metapleuron which is constricted at this point. 36.1—The metepisternum and to a slightly lesser extent the metepimeron are expanded anteroventral to the endophragmal pit which is thus some distance posterior to the meso-metapleural suture. The pleural sulcus distinctly curves anterodorsally from the pit and the transepisternal groove may be visible ventrally. 36.1.1—The metepisternum and metepimeron are expanded anterior to the endophragmal pit so that the pit is some distance posterior to the meso-metapleural suture. The pleural sulcus and transepisternal suture are very indis-

tinct and barely distinguishable if distinguishable at all. 36.1.2—The metepisternum is posteriorly produced behind the endophragmal pit, in addition to slight anterior expansion of the metepisternum and metepimeron. The pleural sulcus is angulate behind the pit which is a short distance from the anterior margin of the metapleuron. 36.2—The metepimeron is expanded and somewhat produced anteroventrally so that the endophragmal pit is shifted posteriorly and the pleural sulcus is angulate. 36.3—The metepimeron is greatly expanded anteroventrally so that the pleural sulcus issues from a pit just above the mesocoxa and passes posterodorsally to the endophragmal pit.

The allocation of states for the metapleuron is that which is best correlated with the branching pattern derived from consideration of other characters, the primitive state in particular being that present in the taxa which are considered to be the most primitive on other grounds. Further investigations are needed to clarify the situation, however.

The various modifications of the metapleuron, based mainly on the position of the endophragmal pit as a marker, are somewhat equivocal and most have occurred more than once, so that they are not as strong in indicating relationships as might be expected. State 36.1 has had at least three origins, on internodes 8-9, 18-19 and 21-23. Since state 36.1.1 occurs on internode 12-14, a modification similar to 36.1 perhaps also occurred here. State 36.1.1 is also present in the bradynobaenid group. State 36.1.2 is uniquely present in the scoliid group. State 36.2 is present in the sierolomorphid, pompilid, rhopalosomatid, eotillid and typhoctid groups and thus probably arose three times (on internodes 16-17 and 21-22 and in the sierolomorphids); however, if 36.2 could have been a precursor to 36.1, then 36.2 probably arose only once, on internode 6-15. A decision is, however, not possible at this stage so that 36.2 has been placed three times on the tree. State 36.3 has arisen once, on internode 4-5, and serves to associate the sphecid and apid groups strongly.

37. *Metapleural gland* (Fig. 25). Primitively, there is no gland opening to the exterior on the metapleuron. 37.1—There is a gland developed on the metapleuron and opening via a bulla and meatus just above the hind coxa.

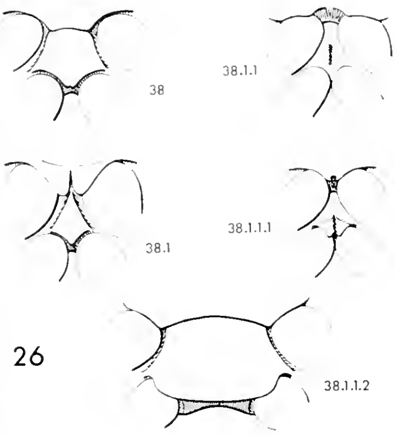
Absence of a metapleural gland is considered primitive because this is the condition in the non-aculeate Hymenoptera and in most Aculeata.

The metapleural gland is a unique feature of the formicid group and thus does not serve to indicate any groupings of the taxa considered here (see Wilson, Carpenter & Brown, 1967).

38. *Metasternum* (Fig. 26). Primitively, the mesal section of the metasternum is in approximately the same plane as the mesosternum. The metasternal area is depressed laterally to accommodate the mid-coxae, the metasternum being differentiated into approximate thirds. 38.1—The metasternum is depressed anteriorly and laterally but not completely so posteromesally, the mid-coxae being contiguous. 38.1.1—The metasternum is entirely depressed, the mid-coxae being contiguous. 38.1.1.1—The metasternum is entirely depressed but small teeth are developed just anterior to the metacoxal cavities, the mid-coxae being contiguous. 38.1.1.2—The metasternum is entirely flat and broad but not depressed, being at the same level as the mesosternum, with the mid-coxae widely separated.

A metasternum with only the lateral thirds depressed is considered primitive because this is the condition in various aculeates that are considered to be the most primitive on the basis of other characters.

Although state 38.1 has apparently



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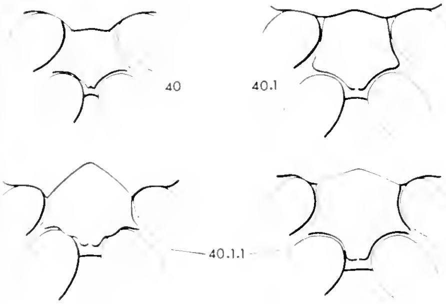

FIGS. 26-27. Characters of Aculeata. 26, posterior region of mesosoma, ventral view, showing primitive and derived states of metasternum (38 based on *Pristocera*, ♂: 38.1 on *Anthobosca*, ♀; 38.1.1 on *Fedtschenkia*, ♀; 38.1.1.1 on *Pseudophotopsis*, ♂; 38.1.1.2 on *Trielis*, ♀); 27, posterior region of mesosoma, ventral view, showing primitive and derived states of metasternal anterior production (40 based on *Pristocera*, ♂; 40.1 on *Typhoctoides*, ♀; 40.1.1 on *Apterogyna*, ♀, and *Bradynobaenus*, ♂, left to right).

arisen only twice (on internode 4-6 and in the plumariid group), its presumed utility is diminished by the frequent additional modifications of the metasternum. Thus, 38.1.1 has arisen three times, on internodes 7-8 and 6-15, and in the plumariid group (male), and has apparently been reversed on internode 18-21. State 38.1.1.1 is uniquely characteristic of the mutillid group and 38.1.1.2 is present in the scoliids only, so that these two states are of no use in grouping the taxa.

39. *Metasternal differentiation.* Primitively, the meso- and metasterna are clearly differentiated by a definite discontinuity in the form of a deep sulcus or difference in level. 39.1—The meso- and metasterna are barely differentiated because of fusion and loss of any definite sulcus, especially mesally.

Well-differentiated meso- and metasterna are considered primitive because this is the condition in most non-aculeates as well as in most Aculeata.

Loss of differentiation of the metasternum is most probably another expression of the general tendency toward consolidation of the mesosoma. It has occurred at least three times, on internodes 4-5 and 18-21 and in the scoliid group, so that it is of little use in establishing relationships.

*40. *Metasternal anterior production* (Fig. 27). Primitively, the metasternum has the anterior margin approximately straight. 40.1—The metasternum is slightly anteriorly produced mesally between the mid-coxae so that its anterior margin attains the level of the anterior extremities of the mid-coxae. 40.1.1—The anterior margin of the metasternum is anteriorly produced mesally and reaches a point anterior to the level of the anterior extremities of the mid-coxae.

A metasternum with approximately straight anterior margin is considered primitive because this is the condition in most non-Aculeata as well as in most aculeates.

Anterior production of the metasternum has taken place in only one line, providing good evidence of the holophyletic relationship of the eotillid, typhoctid, chyphotid, apterogynid, and bradynobaenid groups. State 40.1 has arisen on internode 18-21, and its derivative (40.1.1) reinforces the association of the apterogynids and bradynobaenids, appearing on internode 23-24.

41. *Metacoxal contiguity.* Primitively, the metacoxae are nearly or actually contiguous. 41.1—The metacoxae are broadly separated as a result of lateral expansion of the intercoxal region of the metasternum.

Contiguous metacoxae are considered primitive because this is the condition in most non-aculeate and in most aculeate Hymenoptera.

The derived state is characteristic of the scoliid group only, and is thus of no importance in the derivation of higher groupings.

42. *Metathoracic-propodeal pleural suture.* Primitively, the metathoracic-propodeal intersegmental pleural suture is clearly discernible over its entire length, both dorsal and ventral to the endophragmal pit. 42.1—The metathoracic-propodeal pleural suture is completely obliterated ventral to the endophragmal pit but is distinct dorsally. 42.1.1—The metathoracic-propodeal pleural suture is completely obliterated, both dorsal and ventral to the endophragmal pit.

A completely discernible metathoracic-propodeal pleural suture is considered primitive because this is the condition in most non-aculeates.

The obliteration of the metathoracic-propodeal pleural suture has occurred on numerous occasions and this character is thus almost valueless for determining higher groupings. State 42.1 has apparently arisen on six occasions, on internodes 1-2, 12-14 and 18-21, and in the apid, methochid and sierolomorphid groups. State 42.1.1 has occurred twice, in the tiphiid group and (apparently *de novo*) on internode 8-9. The placement of this state on internode 8-9 is especially interesting in the light of Krombein's (1940) statement that a major difference between the "Myrmosinae" and "Mutillidae" lay in the complete absence of this intersegmental suture in the myrmosids and its presence in the mutillids. It actually appears that the suture is completely obliterated in both, but in some of the more highly developed mutillids there is a secondary development of a weak carina along the apparent line of this suture. State 42.1.1 is thus a condition linking the myrmosid and mutillid groups, rather than one differentiating them.

43. *Propodeal length* (Fig. 28). Primitively, the propodeum is of moderate length, being at least as long as high. 43.1—The propodeum is much shortened in its entirety but especially dorsally, so that the metanotum extends posteriorly to a point almost perpendicularly above the base of the metasoma.

A propodeum of moderate dorsal length is considered primitive because this is the condition in most non-aculeates as well as in most aculeates.

The shortening of the propodeum may

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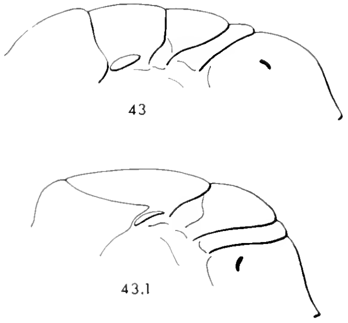

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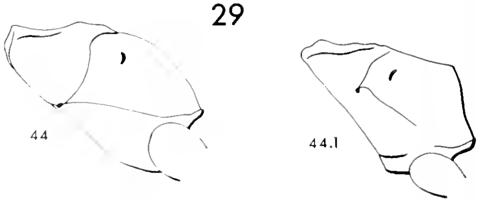

Figs. 28-29. Characters of Aculeata. 28, dorsal region of mesosoma, lateral view, showing primitive and derived states of propodeal length (43 based on *Anthobosca*, ♀; 43.1 on *Ceramius*, ♀, modified); 29, metapleuron and propodeum, lateral view, showing primitive and derived states of discal distinction (44 based on *Anthobosca*, ♂; 44.1 on *Colocistis*, ♂).

be another expression of the general tendency toward consolidation of the mesosoma. State 43.1 has occurred twice, the mechanism differing slightly in detail, in the vespid and bradynobaenid groups. It is thus of no use in the derivation of higher groupings.

44. *Discal distinction* (Fig. 29). Primitively, the disc and declivity of the propodeum are not distinct but merge gradually into each other. 44.1—The disc and declivity form distinct dorsal and posterior surfaces, often separated by a carina.

A propodeum with merging disc and declivity is considered primitive because this is the condition in most non-aculeates as well as in most members of the Aculeata.

The degree of distinctness between the disc and declivity is difficult to quantify. State 44.1 is considered to be fully developed when the two surfaces involved are almost perpendicular to one another. Such a condition has arisen on at least three occasions, on internode 12-14 (linking the tiphiid and brachycistidid groups) and in the bradynobaenid and scoliid groups. Since this state is approached in many other instances, its presence is not a good indicator of higher groupings.

*45. *Extent of forewing venation.* Primitively, the longitudinal veins of the forewing attain the apical margin of the wing membrane. 45.1—The venation of the forewing is reduced or retracted so that the veins extend into the apical half of the wing membrane but do not reach the margin. 45.1.1—The venation of the forewing is extremely reduced so that it does not extend beyond the basal half of the wing membrane.

Venation which attains the apical margin of the wing membrane is considered primitive because this is the condition in most Symphyta and many Terebrantia (including Trigonalidae).

Retraction of the venation from the apex of the wing membrane is extremely common, and state 45.1 has apparently occurred on at least nine occasions, on internodes 1-2, 12-14 and 18-21, and in the apid, mutillid, anthoboscid (female), sierolomorphid, rhopalosomatid and scoliid groups. This state is thus of little utility in determining relationships. The extreme reduction of venation in relatively large individuals without an associated tendency toward brachyptery is apparently present in only the apterogynid and bradynobaenid groups (on internode 23-24, state 45.1.1) and is thus considered quite good evidence of their relationship. There are, however, some members of the myzinid group which show a somewhat similar reduction in venation but with an accompanying decrease in wing or body size (e.g., "*Meria*" *infradentata; Myzinella patrizii*, Guiglia, 1968).

*46. *Cells of forewing* (Fig. 30). Primitively, there are ten closed cells in the forewing, viz., C, SC+R+S, SC+R, R, 1S, 2S, S+M, 1M, M+Cu, 1Cu. 46.1—There are eight closed cells in the forewing, viz., C, SC+R+S, SC+R, R, 1S, S+M, M+Cu, 1Cu. 46.1.1—There are seven closed cells in the forewing, viz., C, SC+R+S, SC+R, R, S+M, M+Cu, 1Cu. 46.1.1.1—There are six closed cells in the forewing, viz., C, SC+R+S, SC+R, R, S+M, M+Cu. 46.2—There are seven closed cells in the forewing, viz., C, SC+R+S, (SC+R)+1S, R, S+M, M+Cu, 1Cu. 46.3—There are nine closed cells in the forewing, viz., C, SC+R+S, R, (SC+R)+1S, 2S, S+M, 1M, M+Cu, 1Cu; vein S is obliterated proximal to its fusion with r-s. 46.4—There are nine closed cells in the forewing, viz., C, SC+R+S, R, (SC+R)+1S, 2S, S+M, 1M, M+Cu, 1Cu; vein S is obliterated just distal to its separation from vein M. 46.5—There are five closed cells in the forewing, viz., C, SC+R+S, SC+R, M+Cu, 1Cu. 46.5.1—

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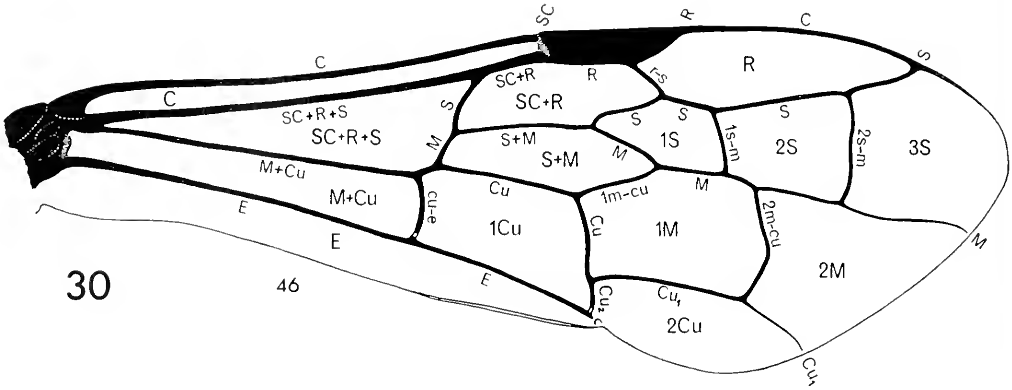

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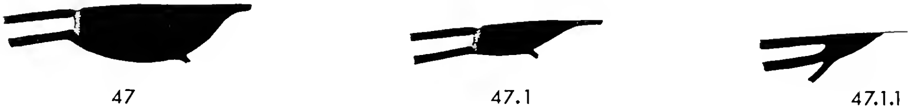

47 47.1 47.1.1

FIGS. 30-31. Characters of Aculeata. 30, forewing, showing primitive state of cells; veins (smaller letters) are: C = costa, Cu = cubitus, E = empusal, M = media, R = radius, S = sector, SC = subcosta (46 based on *Anthobosca*, ♂); 31, pterostigma, showing primitive and derived states of its size (47 based on *Anthobosca*, ♀; 47.1 on *Chirodamnus*, ♀; 47.1.1 on *Apterogyna*, ♂).

There are three closed cells in the forewing, viz., C, SC+R+S, M+Cu.

Ten closed cells is considered the primitive condition because this is the state in the Trigonalidae and also in many aculeate taxa which are considered relatively primitive on the basis of other characters. The trend has apparently been toward reduction in cell number in the Terebrantia, and ten is the maximal number of cells found in the aculeates.

Losses of various veins and thus reductions in the number of cells have been quite common although most appear to be characteristic of single taxa only and are thus of no use in establishing groupings. State 46.1 has arisen at least three times, on internode 1-2 and in the rhopalosomatid and formicid groups, as well as within many of the other groups. State 46.1.1 is present on internode 2-3, and 46.1.1.1 is characteristic of the scolebythid group and also some species within the bethylid group (e.g., *Lytopsenella;* Evans, 1964). State 46.2 appears in the sierolomorphids; 46.3 is developed in the methochid group; 46.4 is present in the tiphiids. State 46.5 has apparently arisen on internode 23-24, linking the apterogynid and bradynobaenid groups, with its derivative (46.5.1) being present in the bradynobaenids; these last states are very characteristic and considered good evidence of this relationship.

47. *Pterostigmal size* (Fig. 31). Primitively, the pterostigma is large and prominent. 47.1—The pterostigma is reduced although nevertheless distinct and is moderate to small in size. 47.1.1—The pterostigma appears as a mere swelling in the venation, and is thus very small.

A large pterostigma is considered primitive because this is the condition in most non-aculeates and in many aculeates which are considered relatively primitive on the basis of other characters.

There appears to be a tendency towards reduction in the size of the pterostigma in various of the more highly developed groups. Thus, state 47.1 has apparently occurred on at least two occasions, on internodes 4-5 and 15-16. This trend has been reversed, however, in the eotillid and chyphotid groups, where the apparent primitive state is present. Extreme reduction (47.1.1) is characteristic of the apterogynid and bradynobaenid groups, and has thus developed on internode 23-24; it also occurs within the sphecid (e.g., *Zyzzyx*) and apid (e.g., *Apis*) groups. These states are thus not considered to provide good evidence of relationships.

48. *Pterostigmal sclerotization.* Primitively, the pterostigma is heavily sclerotized and uniformly thickened. 48.1—The sclerotization of the pterostigma is reduced so that the pterostigma appears to be bounded by a distinct vein, although some sclerotization of the cell so formed is generally retained.

A heavily sclerotized pterostigma is considered primitive because this is the condition in many non-aculeates as well as in most Aculeata.

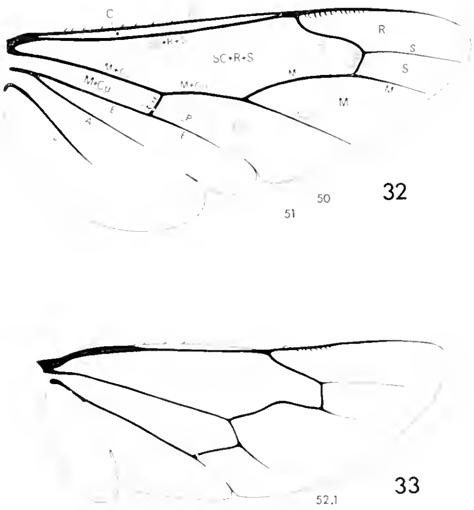
Reduction of pterostigmal sclerotization has occurred at least twice, on internodes 16-17 (associating the pompilid and rhopalosomatid groups) and 19-20 (linking the vespids and scoliids) as well as within various other groups such as the mutillids (e.g., *Mutilla*) and sphecids (e.g., *Pseudoplisus*). This character is thus only of use in confirming the indications of relationships provided by other characters.

49. *Extent of hind wing venation.* Primitively, the longitudinal veins of the hind wing attain the apical margin of the wing membrane. 49.1—The venation of the hind wing is retracted or reduced so that the veins extend into the apical half of the wing membrane but do not attain the margin. 49.1.1—The venation of the hind wing is greatly reduced and restricted to the basal half of the wing membrane.

Venation which attains the apical margin of the wing membrane is considered primitive because this is the condition in most Symphyta and many Terebrantia (including Trigonalidae).

Retraction of the veins away from the apical margin of the hind wing has occurred on numerous occasions, as with the forewing, although the pattern of derivations is not identical for both wings. State 49.1 is present on internodes 2-3, 12-14 and 18-21, and in the mutillid, sierolomorphid, rhopalosomatid and scoliid groups, as well as within various other groups. State 49.1.1 has occurred on internode 23-24 and in the scolebythid group, as well as within the bethylid group (e.g., *Pristocera*). This character is thus of minimal utility in determining relationships.

50. *Cells of hind wing* (Fig. 32). Primitively, there are three closed cells in the hind wing, viz., C, SC+R+S, M+Cu. 50.1—There are two closed cells in the hind wing, viz., SC+R+S, M+Cu; vein C is reduced distally. 50.2—There are two closed cells in the hind wing, viz., C,



Figs. 32-33. Characters of Aculeata. 32, hind wing, showing primitive state of cells and veins; veins as in forewing, plus A = anal, J = jugal bar, P = plical fold (50, 51 based on *Prionyx*, modified); 33, hind wing, showing derived state of crossvein cu-e (52.1 based on *Anthobosca*, ♂).

(SC+R+S)+(M+Cu); vein M+Cu is obliterated. 50.3—There is one closed cell in the hind wing, viz., C; vein M+Cu and all cross-veins are obliterated. 50.3.1—There are no closed cells in the hind wing.

Three closed cells is considered the primitive condition because this is the maximum number of cells found in the Aculeata. In the Terebrantia the trend has apparently been toward reduction in cell number.

The distal reduction of the costal vein (state 50.1) has occurred on numerous occasions, on internodes 7-8 and 16-17, as well as in the apid, methochid, sierolomorphid, formicid, eotillid and chyphotid groups. This state is thus of no use as an indicator of higher groupings. State 50.2 is uniquely present in the bradynobaenid group. State 50.3 is present in the bethylid group, and its derivative (50.3.1) is present in the scolebythids as well as within the bethylid group (e.g., *Pristocera*), so that this modification is probably significant in associating these groups.

*51. *Hind wing anal and jugal veins* (Fig. 32). Primitively, one anal vein and a veinlike jugal bar are present in the hind wing, i.e., veins A and J are present. 51.1—An anal vein is present in the hind wing but vein J is obliterated. 51.2—Both veins A and J are obliterated in the hind wing.

The presence of both an anal vein and a jugal bar is considered primitive because this is the maximal number of such veins found in the Aculeata. In the non-aculeates the trend has been toward loss of these veins; they are generally both absent in Terebrantia, including Trigonalidae, but are present in the most primitive Symphyta (e.g., Xyelidae). Although the jugal "vein" is not a true vein, but rather a development from the jugal bar (Hamilton, 1972a), as shown by its position in the jugal lobe, it is most convenient to treat it in the same way as the true veins for reference purposes.

Both the anal and jugal veins are retained in only the sphecid group and the anal vein only is retained in the apid group, which is thus characterized by state 51.1. Both veins have apparently been lost in all other groups, so that state 51.2 has arisen on internodes 1-2 and 4-6, as well as within the sphecid (most species, but both veins present in *Sphex, Prionyx,* e.g.) and apid (e.g., *Megachile, Mesocheira*) groups. Vein A has apparently reappeared as a minute spur within the anthoboscid (e.g., *Anthobosca* sp. male) and thynnid (e.g., *Hemithynnus*) groups, although its origin on vein E is shown as a basal thickening of that vein in many other groups. This character is thus only useful in so far as it emphasizes the presence of a very primitive state in a taxon (the sphecids) otherwise considered highly derived, thus indicating a remote separation of the sphecid (and apid) line from the other aculeates.

52. *Hind wing cross-vein cu-e* (Fig. 33). Primitively, in the hind wing cross-vein cu-e originates basal to the point of separation of veins M and Cu. 52.1—Cross-vein cu-e originates distal to the point of separation of veins M and Cu.

A basal position for cross-vein cu-e is considered primitive because this is the condition in most taxa of Aculeata. In taxa showing both states, state 52.1 generally occurs in those members considered most derived on the basis of other characters.

Although state 52.1 appears on the tree only once (on internode 6-7) and thus seems to provide good evidence of the relationship of nine mutilloid and tiphioid taxa, its strength is considerably diminished by its presence within various other taxa such as the sphecids (e.g., *Gorytes*) and vespids (e.g., *Synoeca*). There have also rarely been apparent reversals to the

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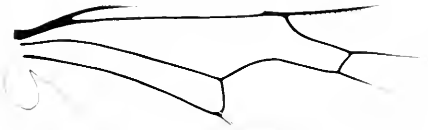

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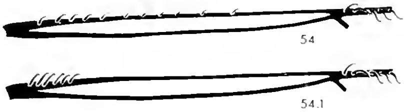

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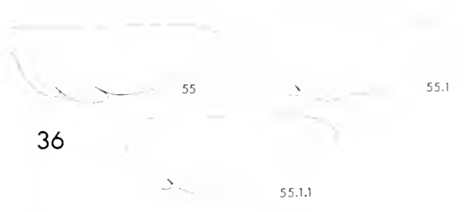

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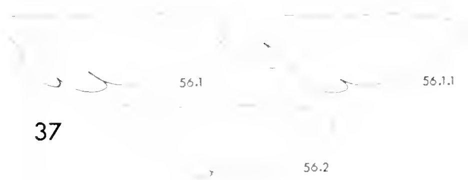

FIGS. 34-37. Characters of Aculeata. 34, hind wing, showing derived state of vein Cu (53.1 based on *Myrmosa*, ♂); 35, anterior basal region of hind wing, showing primitive and derived states of basal hamuli (54 based on sphecid; 54.1 on pompilid); 36, hind wing, showing primitive and derived states of plical lobe (all composite); 37, hind wing, showing derived states of jugal lobe (all composite).

primitive state, within the myzinid and tiphiid groups (some females, e.g., *Myzinum*, *Tiphia*).

*53. *Hind wing vein Cu* (Fig. 34). Primitively, vein Cu is distinctly present in the hind wing distal to its point of separation from vein M. 53.1—Vein Cu is obliterated distal to its separation from vein M.

Presence of vein Cu distally is considered primitive because this is the condition in most non-aculeate and in most aculeate Hymenoptera.

The loss of the free section of vein Cu has apparently occurred on a single occasion, on internode 7-8, thus strongly associating the sapygid, myrmosid and mutillid groups. There is some confusion regarding the mutillids, however. The mutillid genus with the greatest proportion of primitive character states (*Pseudophotopsis*) has a condition like state 53.1, but the more derived members often seem to show the primitive state (e.g., *Tricholabiodes*). Such a direct reversal is logically unlikely, since it involves the regaining of a lost structure. The mutillids commonly have the venation of the hind wing considerably modified, however, various veins or sections of them being lost or suppressed so that there are no closed cells. Such modification could conceivably have caused the apparent redevelopment of a free spur in the position of vein Cu, perhaps actually as a result of a break in and displacement of vein E.

54. *Basal hamuli* (Fig. 35). Primitively, the basal hamuli are dispersed along the costal margin (on vein C) of the hind wing distal to the point of separation of veins C and SC+R+S. 54.1—The basal hamuli are concentrated into a basal cluster approximately at the point of separation of veins C and SC+R+S. 54.2—The basal hamuli are completely absent.

A dispersed series of basal hamuli is considered primitive because this is the condition in the Trigonalidae as well as in those Aculeata judged to be most primitive on the basis of other characters. Lanham (1951) considered the Braconidae (Terebrantia) to have a very primitive condition, merely bearing a dispersed series of strong, straight bristles. By contrast, Rasnitsyn (1969) showed both a basal cluster and a dispersed series in his putative generalized symphytan.

State 54.1 has occurred on two occasions, apparently, on internodes 8-9 and 15-16. State 54.2 is present on internodes 18-19 and 23-24 and in the brachycistidid group, as well as within others such as the mutillid group (most species, except *Pseu-*

dophotopsis) so that these states are useful only as confirmatory indicators rather than prime establishers of relationships.

55. *Plical lobe* (Fig. 36). Primitively, the plical lobe is indicated by a moderate incision of the hind margin of the hind wing. 55.1—The plical lobe is indicated by a shallow notch in the hind margin of the wing. 55.1.1—The plical lobe is not indicated by any modification of the margin of the wing although the plical furrow indicates its extent within the wing membrane.

A plical lobe indicated by a moderate incision is considered primitive because this is the condition in those Aculeata judged to be most primitive on the basis of other characters. As Hamilton (1971) has pointed out, the jugal and vannal folds are alternative mechanisms of wing folding and thus are mutually exclusive; the presence of both jugal and vannal lobes in the same wing is thus impossible. In Hymenoptera there is no true vannal fold, the anterior margin of the supposed "vannal" lobe being formed by the plical furrow. This lobe may thus conveniently be called the "plical lobe" to maintain morphological consistency.

Modification of the depth of the notch indicating the plical lobe has apparently occurred a number of times. Thus state 55.1 has arisen on at least three occasions, on internodes 7-8 and 6-15 and in the thynnid group; 55.1.1 has developed twice, on internode 18-21 and in the scoliid group. An apparently primitive state has, however, been redeveloped in both the rhopalosomatid and eotillid groups independently, and the condition varies within many of the taxa, so that this character is not of fundamental value in indicating groupings.

*56. *Jugal lobe* (Fig. 37). Primitively, the jugal lobe is long, being indicated by a slight notch in the margin of the hind wing. 56.1—The jugal lobe is moderately long and indicated by an axillary incision which extends about half the anterior length of the lobe. 56.1.1—The jugal lobe is small and indicated by a well-developed axillary incision which extends almost to the base of the hind wing. 56.2—The jugal lobe is absent.

A long jugal lobe indicated by a notch is considered primitive because this is the condition in most Symphyta and also in the more generalized members of a few taxa of Aculeata judged to be relatively primitive on the basis of other characters (especially of the wings). The Terebrantia have generally lost this lobe and so do not provide any useful information relative to this character.

The development of a marked incision (56.1) has apparently occurred only once on the tree, on internode 4-6, although it is also present within the sphecid (e.g., *Philanthus*) and apid (e.g., *Megachile*) groups. State 56.1.1 has also arisen on the tree only once, on internode 7-8, associating the sapygids, myrmosids and mutillids, although a similar tendency is rarely present within the sphecids (e.g., *Trypargilum*). By contrast, complete absence of the jugal lobe (56.2) has occurred at least three times, on internode 1-2 (associating the plumariids, bethylids and scolebythids) and in the sierolomorphid and typhoctid groups. This state is also present within the mutillid group (all members except *Pseudophotopsis*). Despite the fact that these states are somewhat equivocal, this character seems to provide useful information on groupings.

57. *Leg form* (Fig. 38). Primitively, the legs are relatively slender and of generalized form, all three pairs being similar. 57.1—The legs have the femora and tibiae expanded to some degree so that they are rather stout, especially the middle and hind pairs. 57.2—The legs have only the femora much inflated. 57.3—The legs have

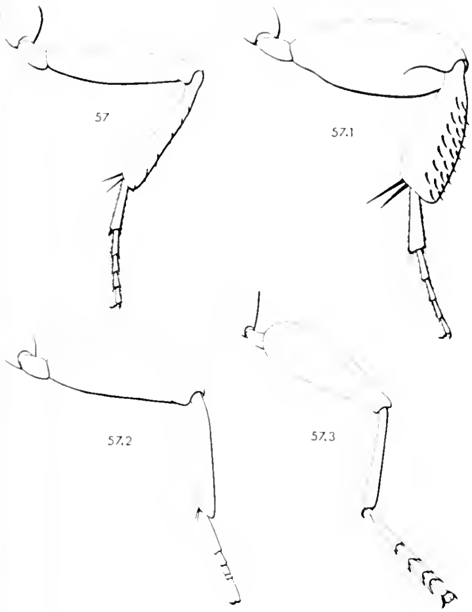

Fig. 38. Leg, showing primitive and derived states of leg form (57 based on *Anthobosca*, ♂, hind leg; 57.1 on *Anthobosca*, ♀, hind leg; 57.2 on *Clystopsenella*, ♀, hind leg; 57.3 on *Olixon*, ♀, front leg).

the tarsi expanded and flattened and the fore-tibiae swollen.

Slender, unspecialized legs are considered primitive because this is the condition in most non-aculeates as well as in most Aculeata.

Modifications of the legs have occurred numerous times, often being correlated with burrowing or prey manipulation. State 57.1 has arisen on at least four occasions, always only in females, on internodes 7-10 and 21-23, and in the plumariid and scoliid groups. The legs have reverted to a slender condition in the methochid group and within the myzinid (e.g., *Pterombrus*) and thynnid (e.g., *Diamma*) groups, so that this state is additionally weakened as an indicator of relationships. State 57.2 is uniquely characteristic of both sexes of the scolebythid group, and 57.3 is present in only the females of the rhopalosomatid group (and is of some importance here since it associates *Rhopalosoma* and *Olixon*, the latter genus having been placed elsewhere on occasion—e.g., in the Pompilidae, by Reid, 1939).

58. *Arolium*. Primitively, each arolium forms a well-developed pad between the tarsal claws. 58.1—The arolium is completely reduced and absent, or at least not distinguishable under a magnification of 100×.

A well-developed arolium is considered primitive because this is the condition in most non-aculeate and aculeate Hymenoptera as well as the Insecta in general.

The arolium has been lost on a number of occasions, in the females of the myrmosid group, both sexes of the eotillids and in the female on internode 21-23 and the male on internode 23-24, so that the chyphotids possess arolia in males only (although much reduced in some males in the subgenus *Pitanta*, e.g., *Chyphotes mojave*; Mickel, 1967), and the apterogynids and bradynobaenids lack them in both sexes. Loss or extreme reduction of the arolium has also occurred within the apids (e.g., *Megachile*) at least. Because of its multiple occurrences this state is not a good indicator of groupings.

59. *Claws* (Fig. 39). Primitively, each claw bears one or more processes on the ventral margin, these forming teeth or producing a cleft appearance; in either case the claw is referred to as "toothed." 59.1—Each claw is simple, with a smooth ventral margin and no trace of any tooth.

Toothed claws are considered primitive because this is the condition in many non-aculeates (including Trigonalidae) and in many Aculeata considered relatively primitive on the basis of other characters.

The loss of teeth on the tarsal claws has occurred on numerous occasions. State 59.1 is characteristic of the entire brachycistidid, scoliid and bradynobaenid groups and the females of the plumariid and myrmosid groups. It has also occurred within the bethylids (e.g., *Chrysis*), mutil-

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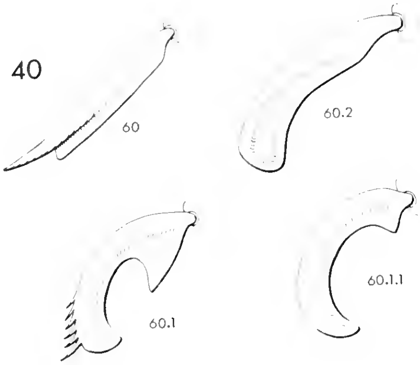


FIGS. 39-40. Characters of Aculeata. 39, claw, showing primitive and derived states (59 based on *Anthobosca*, ♀, *Apterogyna*, ♂, and *Sphex*, ♀, left to right then below; 59.1 on *Bradynobaenus*, ♀); 40, foretibial calcar, posterior view, showing primitive and derived states (60 based on *Anthobosca*, ♂; 60.1 on *Apterogyna*, ♂; 60.1.1 on *Bradynobaenus*, ♀; 60.2 on *Tielis*, ♂).

lids (all except *Pseudophotopsis*), eotillids (e.g., *Eotilla*), typhoctids (e.g., *Typhoctoides*), sphecids (e.g., *Bembix*) and apids (e.g., *Megachile*) at least. The primitive state also covers a variety of forms of teeth which cannot readily be separated into distinct states, some of which may even be secondary derivations (see the section on the mutillids below for a discussion of *Rhopalomutilla*). This character is thus very weak and of essentially no significance in determining relationships.

*60. *Foretibial calcar* (Fig. 40). Primitively, the single calcar of the foretibia is approximately straight with an elongate inner lamina which may be somewhat shortened. 60.1—The foretibial calcar is strongly curved inward and is more or less even in width but with a small outer spine present at the apex. 60.1.1—The foretibial calcar is strongly curved inward and is more or less even in width with the apex obtuse. 60.2—The foretibial calcar is inwardly curved, spatulate at the apex and hollowed along the posterior surface.

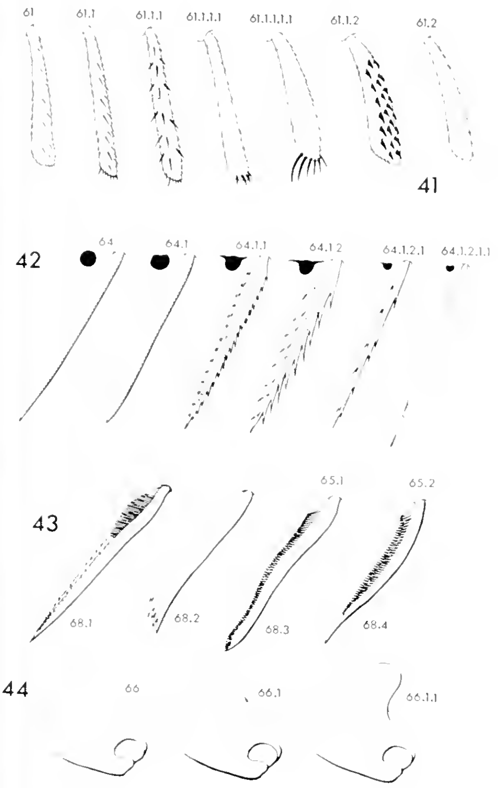
An approximately straight calcar is considered primitive because this is the condition in most non-Aculeata as well as in most aculeates.

There is actually greater variation in the foretibial calcar than would appear from the above. The primitive state covers many rather subtle variations which could not unequivocally be divided into separate states. Further, 60.1, 60.1.1 and 60.2 are actually quite similar and it is thus possible that they should really be considered as expressions of the same series. Nevertheless, 60.1 (apterogynids) and its derivative, 60.1.1 (bradynobaenids) do serve to associate the groups subtended by internode 23-24, as has previously been noted by Reid (1941). State 60.2 characterizes the scoliid group.

61. *Middle tibial spines* (Fig. 41). Primitively, each middle tibia bears many scattered setae, a few of which are slightly stronger than the remainder and are termed "spiniform." 61.1—Each middle tibia bears scattered spiniform setae which are readily identifiable as weak spines. 61.1.1—Each middle tibia bears scattered spines which are fairly strong and are termed "moderate." 61.1.1.1—Each middle tibia bears moderate spines which are absent basally and present only apically. 61.1.1.1.1—Each middle tibia bears very strong spines apically only. 61.1.2—Each middle tibia bears scattered spines which are extremely strong and prominent. 61.2—Each middle tibia is completely spineless and bears only a few weak setae.

An essentially spineless but setose middle tibia is considered primitive because this is the condition in most non-aculeates.

The tibial spines are very variable



Figs. 41-44. Characters of Aculeata. 41, middle tibia, showing primitive and derived states of spines (61 based on *Pristocera*, ♂; 61.1 on *Plumarius*, ♂; 61.1.1 on *Anoplius*, ♀; 61.1.1.1 on *Paraponera*, ♀; 61.1.1.1.1 on *Bradynobaenus*, ♂; 61.1.2 on *Trielis*, ♀; 61.2 on *Clystopsenella*, ♀); 42, middle tibial spur, cross section and dorsal view, showing primitive and derived states (64, 64.1, 64.1.1 composite; 64.1.2 based on *Apterogyna*, ♂; 64.1.2.1 on *Bradynobaenus*, ♂, hind spur; 64.1.2.1.1 on *Bradynobaenus*, ♀, hind spur); 43, middle or hind tibial spur, showing derived states of calcaria (65.1, 68.3 based on *Paraponera*, ♀; 65.2, 68.4 on *Methocha*, ♀; 68.1 on *Pepsis*, ♀; 68.2 on *Euparagia*, ♀); 44, hind coxa, showing primitive and derived states (66 based on *Anthobosca*, ♂; 66.1 on *Sierolomorpha*, ♂; 66.1.1 on *Myrmosa*, ♂).

within and among taxa and the states described are somewhat equivocal so that assignment of the various states to the different taxa is sometimes almost arbitrary. This character is thus of minimal use in determining relationships. State 61.1 has apparently arisen on internode 1-4 and in the plumariid group, some development of tibial spines being characteristic of almost all aculeates. State 61.1.1 has developed on internodes 6-7 and 21-23, and in the sphecid, pompilid and typhoctid groups as well as female plumariids. The spines have been somewhat reduced in the methochid group, however, so that it is assigned state 61.1. State 61.1.1.1 has developed in the formicid group and also on internode 23-24, while its derivative, 61.1.1.1.1, is present in the bradynobaenids. State 61.1.2 is present only in the scoliids. Complete loss of spines (61.2) has taken place only in the scolebythid group.

62. *Hind tibial spines* (Fig. 41). The allocation of states for the hind tibial spines is as for the middle tibia (character 61).

The same comments apply to the hind tibial spines as to those of the middle legs. The allocation of states is similar except that 62.1.1 is not present in female plumariids and 62.1.1.1 is developed on internode 21-23, being present in the chyphotid group. Because of these differences, this character is not considered to duplicate the previous one.

63. *Middle tibial spur number.* Primitively, each mid-tibia bears two spurs apically. 63.1—Each mid-tibia bears one spur apically. 63.2—Each mid-tibia bears no spurs apically.

A middle tibia with two spurs is considered primitive because this is the condition in most non-Aculeata and also in most aculeates.

The loss of middle tibial spurs has occurred on a number of occasions, each time in a single taxon, so that this character is of no use in establishing relationships. State 63.1 is present in the apid, methochid (female only), brachycistidid and scoliid groups, and 63.2 has arisen in the bradynobaenids. One spur has also been lost within various other taxa such as the bethylid (e.g., *Deinodryinus*), mutillid (e.g., *Acanthophotopsis*) and sphecid (e.g., *Larra, Zyzzyx*) groups, and both spurs have been lost within the formicid group (e.g., *Crematogaster*).

64. *Basic form of middle and hind tibial spurs* (Fig. 42). Primitively, each spur is simple and approximately circular in cross-section, forming a very narrow cone. 64.1—Each tibial spur is slightly flattened dorsally but retains simple margins. 64.1.1—Each tibial spur is dorsally flattened and has serrate margins. 64.1.2—Each tibial spur is dorsally flattened and with deeply dentate margins. 64.1.2.1—Each tibial spur is dorsally flattened and somewhat elongated, with a few teeth on the margins. 64.1.2.1.1—Each tibial spur is dorsally flattened and threadlike (nematiform) with simple margins.

Conical tibial spurs are considered primitive because this is the condition in many non-Aculeata, particularly Terebrantia, and in those aculeates considered relatively primitive on the basis of other characters.

Although the modifications of spur form have occurred on various occasions, there does seem to be a logical progression in the pattern shown in at least the chyphotid, apterogynid and bradynobaenid groups which serves to associate them. State 64.1 is present in females only on internodes 6-7 and 21-23, and in both sexes of the pompilid and scoliid groups. 64.1.1 has arisen in females on internode 7-8 and in both sexes on internode 4-5. State 64.1.2 is present in both sexes on internode 23-24, and its modification (64.1.2.1) occurs in the males of bradynobaenids while the females of that taxon are even more modified and exhibit state 64.1.2.1.1.

65. *Middle tibial calcar* (Fig. 43). Primitively, the mid-tibial spurs are similar, showing no signs of modification as calcaria. 65.1—The inner spur of the mid-tibia is modified as a calcar by formation of a dorsal pectinate carina. 65.2—The (inner?) spur of the mid-tibia is modified as a calcar by the development of dorsal pectination but without carina formation.

Unmodified spurs are considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

The formation of a calcar on the middle tibia is uncommon and has occurred twice, each time in a slightly different fashion. State 65.2 is present only in the females of the methochid group and 65.1 occurs in both sexes of the formicids, although the modification is minimal in some (e.g., *Camponotus*). This character is therefore of no use in establishing higher groups.

66. *Form of hind coxa* (Fig. 44). Primitively, each hind coxa is smoothly rounded dorsally. 66.1—Each hind coxa bears a definite longitudinal carina along the dorsal surface, especially basally. 66.1.1—Each hind coxa bears a dorsal carina which is expanded and lamellate.

A simple hind coxa is considered primitive because this is the condition in most non-Aculeata (although the coxa is carinate in Trigonalidae) and in those aculeates judged to be the most primitive on the basis of other characters.

The development of a dorsal carina or tooth on the hind coxa has occurred on various occasions, sometimes rather equivocally. Such projections have also been lost again within some groups such as the mutillids (see section below for discussion) and brachycistidids (present in males of most species but absent in *Brachycistis*). This character is thus of little importance in establishing groupings. State 66.1 has developed on internodes 7-8, 12-14 and 21-22, in the thynnid, sierolomorphid and apterogynid groups, and in the males of the methochid and chyphotid groups. The expansion of the tooth into a lamella (66.1.1) is characteristic of the myrmosid group only, although it may be approached within the brachycistidid group (*Colocistis* male).

67. *Hind tibial spur number.* Primitively, each hind tibia bears two spurs apically. 67.1—Each hind tibia bears a single spur apically.

A hind tibia with two spurs is considered primitive because this is the condition in most Hymenoptera, both nonaculeates and aculeates.

The loss of one of the hind tibial spurs has occurred on the tree only in the methochid group, thus not providing any information on higher relationships. A similar state is, however, found within the bethylid group (e.g., cleptid sp.) and a more extreme state, involving the loss of both spurs, has occurred within the apid (e.g., *Apis*) and formicid (e.g., *Crematogaster*) groups.

*68. *Hind tibial calcar* (Fig. 43). Primitively, the hind tibial spurs are similar, showing no evidence of modification as calcaria. 68.1—The inner spur of the hind tibia is modified as a calcar by the formation of a basal dorsal tuft of bristles with little modification of the cuticular portion of the spur. 68.2—The inner spur of the hind tibia is modified as a calcar by a dorsal carinate expansion of the cuticle over a considerable length. 68.3—The inner spur of the hind tibia is modified as a calcar by pectinate elaboration of a dorsal carina. 68.4—The inner spur of the hind tibia is modified as a calcar by development of dorsal pectination but without carina formation.

Unmodified spurs are considered primitive because this is the condition in nonaculeates as well as in most Aculeata.

The formation of a calcar on the hind tibia has occurred at least four times but in different ways on each occasion. State 68.1 has developed on internode 16-17, thus associating the pompilid and rhopalosomatid groups quite strongly, as has been noted by Rick (1970). States 68.2, 68.3 and 68.4 are characteristic of the vespid, formicid and methochid groups respectively (the last two are similar to the condition of the middle tibial spurs in these taxa). Different forms of hind tibial calcaria have also been developed within the sphecid (present in most but absent in a few such as *Astata*) and myzinid (e.g., *Myzinum* female) groups. Although some members of the apid group (e.g., *Halictus*) have the inner hind tibial spur with large teeth, this state does not appear to be comparable to calcar formation in the other groups.

*69. *Modified mesosoma of apterous female* (Fig. 45). Primitively, the mesosoma of the female is essentially unmodified and similar to that of the male. 69.1—The female is apterous with the mesosoma modified so that there are movable sutures between the pro- and meso- and the meso- and metathorax, the mesonotal subdivisions are distinguishable, the prepectal sclerite is free and the mesepimeron is distinct. 69.1.1—The female has the mesosoma modified as in 69.1 except that the mesepimeron is not distinguishable externally. 69.1.1.1—The female has the mesosoma modified as in 69.1.1 except that the mesonotal subdivisions are not distinguishable and the prepectal sclerite is reduced although free. 69.2—The female is apterous with the mesosoma modified so that the pleura are flattened, there is a functional suture between the pro- and mesothorax, the metathoracic-propodeal suture is distinct but not functional dorsally, and the prepectal sclerite is fused to the mesepisternum. 69.2.1—The female has the mesosoma modified as in 69.2 except that the metathoracic-propodeal suture is obliterated dorsally. 69.2.2—The female has the mesosoma modified as in 69.2 except that the suture between the pronotum and mesothorax is non-functional but distinct, and the metathoracic-propodeal suture is

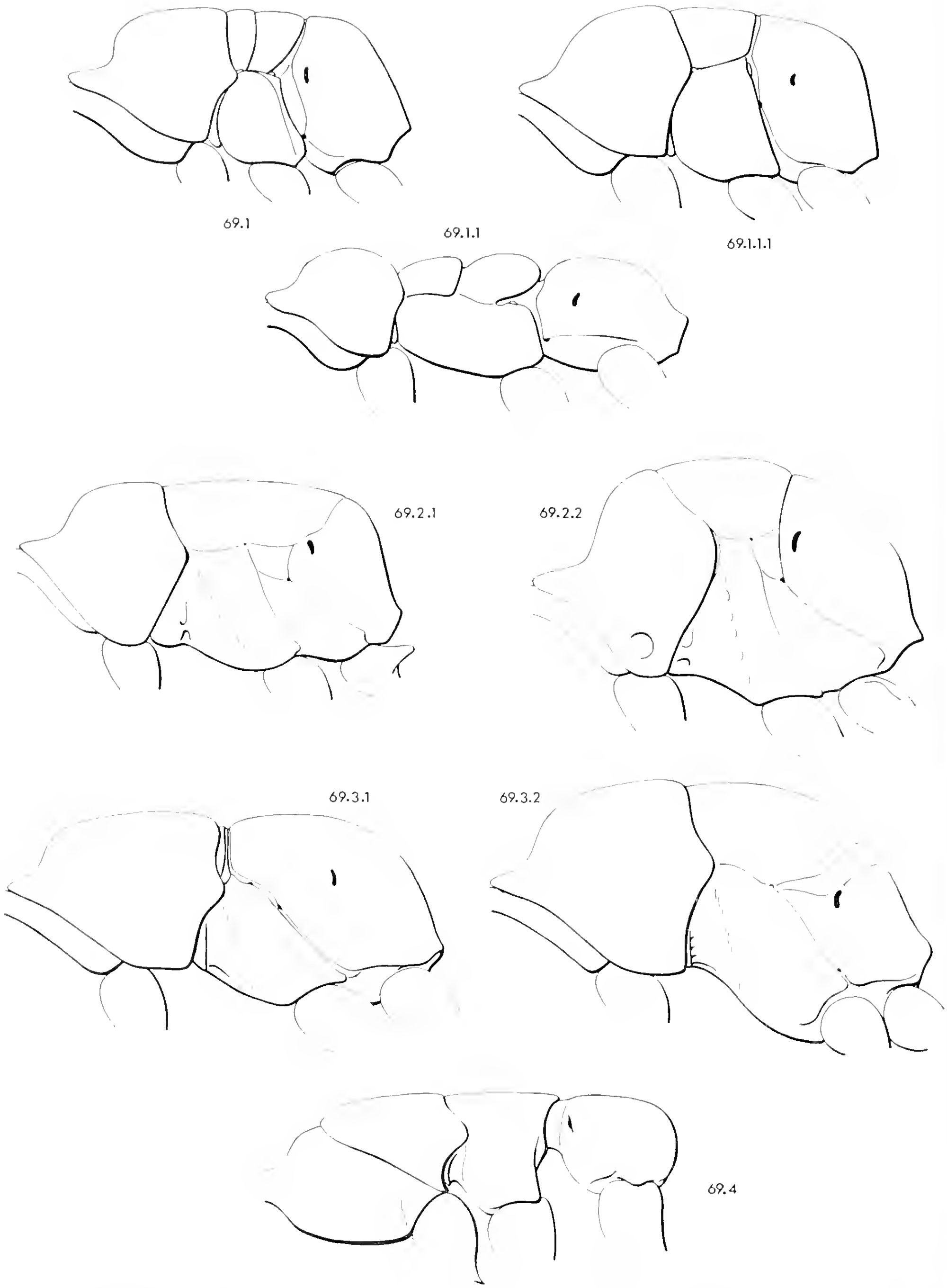


Fig. 45. Mesosoma, lateral view, showing derived states in apterous females (69.1 based on *Zaspilothynnus;* 69.1.1 on *Methocha;* 69.1.1.1 on *Bruesiella;* 69.2.1 on *Myrmosa;* 69.2.2 on *Pseudophotopsis;* 69.3.1 on *Typhoctoides;* 69.3.2 on *Apterogyna;* 69.4 on *Plumarius*).
]

indistinct dorsally. 69.3—The female is apterous with the mesosoma modified so that the pleura (especially the mesopleuron) are somewhat protuberant, the suture between the pronotum and the mesothorax is functional, the meso-metathoracic suture is visible but non-functional, the mesonotum is neither reduced nor enlarged, and the prepectal sclerite is fused to the mesepisternum. 69.3.1—The female has the mesosoma modified as in 69.3 except that the mesonotum is very short and transverse. 69.3.2—The female has the mesosoma modified as in 69.3 except that the meso-metathoracic suture is only indistinctly visible and the mesonotum is somewhat posteriorly produced. 69.4—The female is apterous with the mesosoma modified so that the pro-meso- and meso-metathoracic articulations are retained, the propleura are fused to form a rigid tube, and the meso- and metathoraces are separated by a deep lateral and ventral constriction, causing the metacoxal cavities to be considerably separated from the mesocoxal cavities.

An unmodified mesosoma in the female is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

Associated with aptery in the females (state 2.1), the mesosoma has been variously modified, as was shown by Reid (1941). (Although worker ants are primitively apterous and thus show mesosomal modifications, they are not included here because the queens are winged with no such mesosomal changes, except in a few highly specialized forms. The primitive condition in the formicids is thus not considered to involve this character.) There are at least four different basic patterns along which such modification has occurred, three of them linking various taxa into higher groupings. Because of the complexity and extent of the various modifications involved, each line of development is considered to provide very good evidence of the relationships demonstrated.

The line based on 69.1 associates various members of the tiphioid complex. In this line it is apparent that each of the derived states is expressed only when accompanied by state 2.1, but that the potential for such expression exists even in the absence of winglessness in the female. Although state 69.1 is displayed in the thynnid group only, it has logically arisen on internode 10-11 since its derivatives are expressed in other taxa derived from that internode. State 69.1.1 is expressed in the entire methochid group and also in some members of the myzinid group (e.g., *Braunsomeria*), so that it must have arisen below node 13. In addition, its derivative state (69.1.1.1) is present in the brachycistidid group, so that state 69.1.1 is logically placed on internode 11-12. The line based on state 69.2 associates the myrmosid and mutillid groups. State 69.2 is logically derived on internode 8-9 and has apparently subsequently been modified in different directions in its two derivative groups, so that 69.2.1 appears in the myrmosids and 69.2.2 in the mutillids. The line based on 69.3 associates five taxa in the typhoctoid and bradynobaenoid lines, state 69.3 having been derived on internode 18-21. Its two derivative states are expressed in different lines; 69.3.1 appears on internode 21-22, strongly associating the typhoctid and eotillid groups, and 69.3.2 is placed on internode 21-23, strongly linking the chyphotid, apterogynid and bradynobaenid groups. State 69.4 has occurred in only the plumariid group. Apart from these states, aptery and various mesosomal modifications have occurred within certain other taxa, as is indicated in the discussion of character 2.

*70. *"Felt lines"* (Fig. 46). Primitively, there are no modifications of the second metasomal segment in the form of differ-

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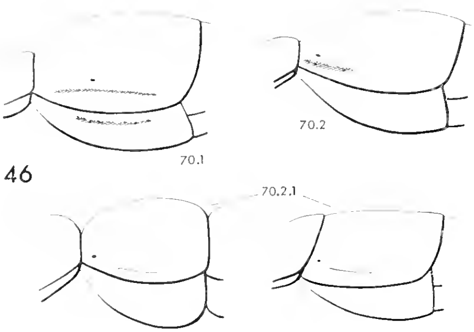

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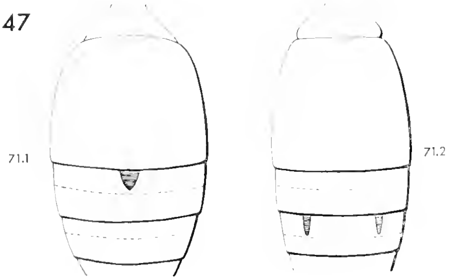


FIGS. 46-47. Characters of Aculeata. 46, second metasomal segment, lateral view, showing derived states of "felt lines" (70.1 based on *Pseudophotopsis*, ♂; 70.2 on *Typhoctes*, ♂; 70.2.1 on *Apterogyna*, ♀, and *Bradynobaenus*, ♀, left to right); 47, second to fourth metasomal segments, dorsal view, somewhat expanded, showing derived states of stridulitra (both composite).

entiated areas for the openings of subcuticular glandular organs. 70.1—There are longitudinally elongate and narrow depressed areas ("felt lines") on each side of the second metasomal segment on both tergum and sternum, each bearing dense short pubescence and the openings of secretory organs. 70.2—There is a longitudinally oval area ("felt line") developed on each side of the second metasomal segment on the tergum only, this bearing dense moderately long pubescence and the openings of secretory organs. 70.2.1—There is a longitudinal area on each side of the second metasomal tergum consisting of a line of cuticular depression or invagination but without dense pubescence.

A second metasomal segment without "felt lines" is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

Although it would at first seem likely that a structure as complex as a "felt line" would most probably have a single derivation, this is apparently not so. Despite the similarities between states 70.1 and 70.2, these do exhibit slight morphological differences, as was found by Debolt (1973). In addition, similar structures, in gross appearance at least, are present on the first metasomal tergum within the tiphiid group (*Paratiphia*) and ventrally on the pronotum within the mutillids (*Pseudophotopsis*). Some primitive members of the apid group (e.g., *Brachyhesma, Sericogaster*) bear a lateral "fovea" on the second metasomal tergum, which is apparently secretory although not as densely pubescent as in state 70.2; this is probably analogous (or even homologous) to a "felt line." Structures which are probably analogous are also found on the sixth metasomal sternum in some vespids (e.g., *Paravespula;* Spradbery, 1973).

State 70.1 is characteristic of the mutillid group only, within which it has undergone various modifications involving loss of the sternal or tergal elements or both. State 70.2 has occurred on internode 18-21 and links five taxa. Loss of the pubescence in the "felt line" resulting in a mere cuticular depression or invagination (70.2.1) has apparently taken place in the female on internode 23-24 so that male apterogynids have pubescent lines whereas the female has cuticular grooves. In the bradynobaenids the loss of pubescence has occurred in the male also and both sexes have lines along which the cuticle is apparently slightly invaginated. These structures have not previously been recorded in this group, and their presence is strong evidence of the relationship between the bradynobaenid, apterogynid and chyphotid groups and of these to the typhoctids and eotillids.

*71. *Stridulitra* (Fig. 47). Primitively, there are no specialized stridulatory organs on the metasoma. 71.1—There is a single stridulitrum developed as a small shield-shaped, finely transversely striated area mesally at the base of the third metasomal tergum. This rubs against a plectrum (ridge) on the underside of the posterior margin of the second tergum. 71.2—There is a pair of stridulitra developed as a fairly narrow, finely transversely striated, shield-shaped area on each side at the base of the fourth metasomal tergum. This rubs against a plectrum on the underside of the posterior margin of the third metasomal tergum on each side.

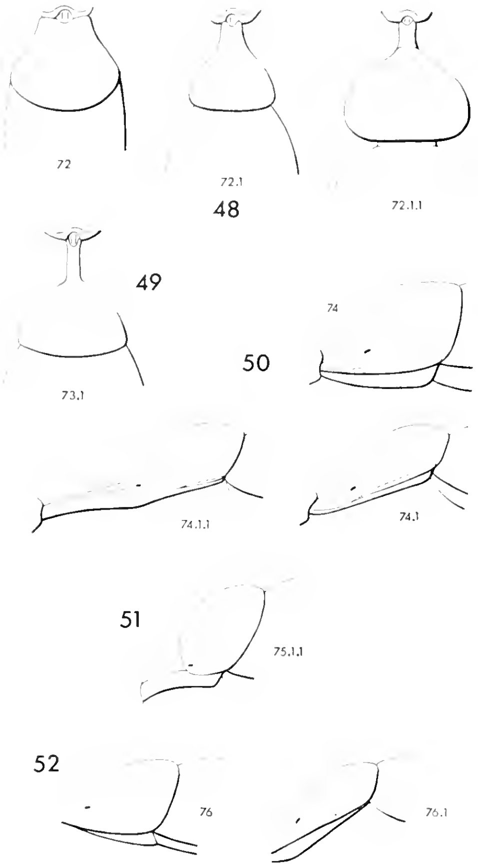
The absence of metasomal stridulitra is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and Aculeata. The terminology is derived from that of Ashlock & Lattin (1963), although the "instrument" is moved against the plectrum in the Hymenoptera rather than the plectrum being the movable part. The fine structure of the mesal stridulitrum has been investigated by Hinton, Gibbs & Silberglied (1969).

The development of a mesal stridulitrum (71.1) has occurred on internode 8-9 and thus strongly associates the myrmosid and mutillid groups. The strength of this state is, however, slightly reduced by the fact that a similar development has taken place within the formicid group (present in the poneroid and pseudomyrmecoid complexes but absent in the myrmecioid line; see Haskins & Ensman, 1938; Markl, 1973) and within the rhopalosomatids (e.g., *Olixon*), where the form is somewhat different, however. Lateral stridulitra (71.2) are present in the typhoctid, eotillid and chyphotid groups and apparently arose on internode 18-21; they were subsequently lost on internode 23-24, being absent in the apterogynids and bradynobaenids. It seems more likely that such a structure, apparently unique in the aculeates (although a very few members of the sphecid group, e.g., *Pseudoplisus*, possess lateral stridulitra on the fourth and fifth terga) should have arisen once only, than that it had two independent origins resulting in identical expressions. Similar loss of stridulitra has apparently occurred in the *Ligyrocoris* group of Lygaeidae (Hemiptera) (Ashlock & Lattin, 1963), so that this possibility should not be rejected out of hand.

72. *Constriction of first metasomal tergum* (Fig. 48). Primitively, especially as viewed from above, the first metasomal tergum overlies the second and its surface contour merges smoothly with it in a continuous arc. 72.1—The posterior margin of the first metasomal tergum is slightly constricted so that there is a definite discontinuity between the contours of the first and second terga, but the first segment is not nodose. 72.1.1—The posterior margin of the first metasomal tergum is markedly constricted and differentiated from the second so that the first segment is definitely nodose.

An unconstricted first tergum is considered primitive because this is the condition in most Symphyta and many Terebrantia as well as in those Aculeata considered primitive on the basis of other characters.

Slight posterior constriction of the first metasomal tergum has apparently occurred on numerous occasions so that this state is of minimal use in establishing groups. State 72.1 has arisen on at least seven occasions, on internodes 8-9 and 11-12 in males only, 12-14 in females also, and 18-21 in both sexes, and in addition in the rhopalosomatid, formicid and scoliid groups. It is also present within various other taxa such as the sphecids (e.g., *Trypargilum*), apids (e.g., *Osiris* female), sierolomorphids (e.g., *Sierolomorpha canadensis*) and vespids (e.g., *Monobia*).



FIGS. 48-52. Characters of Aculeata. 48, base of metasoma, dorsal view, showing primitive and derived states of constriction of first tergum (72 based on *Anthobosca*, ♂; 72.1 on *Typhoctes*, ♀, modified; 72.1.1 on *Apterogyna*, ♀); 49, base of metasoma, dorsal view, showing derived state of petiole (73.1 based on *Bradynobaenus*, ♀); 50, first metasomal segment, lateral view, showing primitive and derived states of lateral margin of tergum (74 based on *Sierolomorpha*, ♀; 74.1 on *Typhoctes*, ♀; 74.1.1 on *Chyphotes*, ♂); 51, first metasomal segment, lateral view, showing derived state of width of tergum (75.1.1 based on *Chyphotes*, ♀; Fig. 50, 74.1.1 represents 75.1 also); 52, base of metasoma, lateral view, showing primitive and derived states of differentiation of first sternum (76 based on *Anthobosca*, ♂; 76.1 on *Tiphia*, ♂, modified).

State 72.1.1 occurs only in the apterogynid group and also within the formicid group (all members except Amblyoponini; Wilson, Carpenter & Brown, 1967).

73. *Metasomal petiole* (Fig. 49). Primitively, the first metasomal segment is evenly constricted anteriorly toward its articulation with the mesosoma. 73.1—The anterior extremity of the first metasomal segment is highly differentiated from the main body of the segment as a short petiole which is more or less cylindrical.

A non-petiolate first metasomal segment is considered primitive because this is the condition in the Symphyta and most other non-aculeates as well as in most Aculeata.

The formation of a definite petiole has occurred on internode 18-21 where a short, cylindrical petiole is characteristic of five taxa, and also in the formicid group. The strength of this character is, however, weakened by the fact that various petiolar modifications of the first metasomal segment have occurred within many other taxa such as the sphecids (e.g., *Ammophila*), myzinids (e.g., *Meria, Mesa*) and vespids (e.g., *Belonogaster, Eumenes*).

*74. *Lateral margin of first metasomal tergum* (Fig. 50). Primitively, the first metasomal tergum broadly overlies the sternum laterally and is freely movable against it. 74.1—The first metasomal tergum overlies the sternum only posteriorly and narrowly, being closely associated with it but not fused except perhaps at the extreme base. 74.1.1—The first metasomal tergum overlies the sternum only posteriorly and narrowly and is fused to it along the petiole.

A first tergum that broadly overlies the sternum is considered to be primitive because this is the condition in most non-aculeates and in most members of the Aculeata.

The tendency toward fusion of the first tergum and sternum has apparently been established on internode 18-21 since state 74.1 associates the typhoctid and eotillid groups, and its derivative (74.1.1) has arisen on internode 21-23, linking the chyphotid, apterogynid and bradynobaenid groups. This trend is almost unique and good evidence of these relationships although a rather similar condition is shown within the myzinid group (e.g., *Meria*). Different forms of fusion have occurred within other taxa such as the sphecid (e.g., *Chlorion*) and vespid (e.g., *Zethus*) groups.

*75. *Width of first tergum* (Fig. 51). Primitively, the first metasomal tergum is broader than the sternum over its entire length due to its overlap of the sternum. 75.1—The first tergum is very narrow anteriorly, its lateral margin running along the dorsal surface of the petiole on each side. 75.1.1—The first tergum is completely absent anteriorly, the sternum apparently forming the petiole in its entirety.

A broad first tergum is considered primitive because this is the condition in most non-aculeates and in most members of the Aculeata.

Extreme reduction in width of the first tergum anteriorly (75.1) is characteristic only of the chyphotid, apterogynid and bradynobaenid groups and has occurred on internode 21-23. Complete absence of the tergum along the petiole (75.1.1) has apparently occurred only in the females of the chyphotid group, traces of the tergum being distinguishable to the base of the petiole in the males of that taxon. A state similar to 75.1 has, however, occurred within the myzinid group (e.g., *Meria*) and the absence of the tergum along the petiole has taken place within the sphecid group (e.g., *Prionyx*), although in a slightly different fashion from state 75.1.1. Despite these separate origins, this character provides quite good evidence of the relationship of the taxa subtended by internode 21-23.

76. *Differentiation of first sternum* (Fig. 52). Primitively, the first metasomal sternum overlies the second posteriorly and is not differentiated from it by any marked discontinuities. 76.1—The first sternum is depressed and differentiated from the second by a deep constriction.

An undifferentiated first sternum is considered primitive because this is the condition in most non-aculeates and also in those members of the Aculeata considered to be primitive on the basis of other characters.

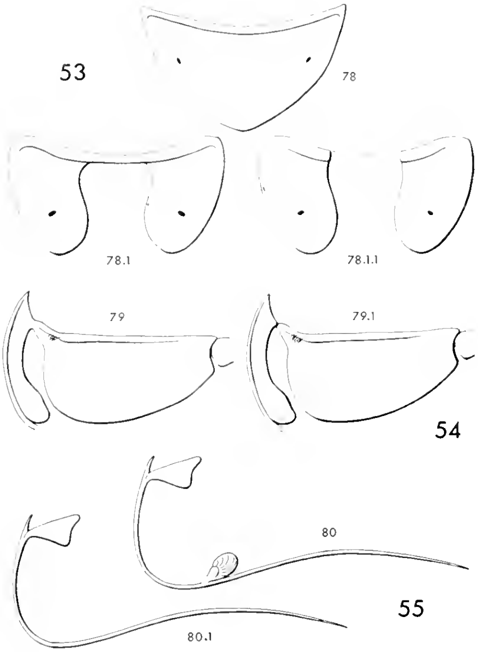
Posterior differentiation of the first sternum has apparently occurred at least three times, on internodes 8-9, 11-12 and 16-18 and also within the thynnid (e.g., *Diamma* female) and sphecid (e.g., *Cerceris*) groups at least, so that it is of little importance in establishing relationships, although there are differences in detail in the various occurrences.

77. *Constriction of second metasomal segment.* Primitively, the second metasomal segment is not at all constricted apically but its contours merge evenly with those of the third. 77.1—The second metasomal segment is strongly constricted apically, dorsally and ventrally as well as laterally, and is strongly differentiated from the third.

An unconstricted second metasomal segment is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

A nodose second metasomal segment is characteristic only of the apterogynid group and is thus not of any importance in determining higher groupings. A similar state is also present within the formicid group (e.g., *Atta*).

*78. *Seventh tergum of female* (Fig. 53). Primitively, the seventh metasomal tergum (eighth abdominal tergum) is somewhat exposed. It is evenly sclerotized over its entire length, forming a fairly long transverse sclerite. 78.1—The seventh metasomal tergum is retracted and entirely hidden. Its sclerotization is reduced to a short strip across the anterior margin con-



FIGS. 53-55. Characters of Aculeata. 53, seventh tergum of female, dorsal view, showing primitive and derived states (all composite); 54, gonocoxite IX of female, lateral view, showing primitive and derived states (both composite); 55, gonapophysis VIII of female, lateral view, showing primitive and derived states (both composite).

necting the lateral plates which bear the spiracles. 78.1.1—The seventh metasomal tergum is retracted and entirely hidden. Its sclerotization is entirely reduced mesally so that the lateral spiracular plates are linked by membrane only.

An exposed and fully sclerotized seventh tergum is considered primitive because this is the condition in the non-aculeate Hymenoptera.

Concealment and partial desclerotization of the seventh tergum in the female is characteristic of the entire group comprising the Aculeata *(sensu stricto)* as defined by Oeser (1961). Since this state (78.1; internode 1-4) has been attained only once in the entire Hymenoptera, it provides extremely good evidence of the holophyletic nature of this grouping. Although the seventh tergum is concealed in the plumariids, this has occurred by enlargement of the sixth sternum which enfolds the seventh tergum, and not by anterior retraction of the seventh tergum under the sixth. State 78.1.1 is uniquely characteristic of the apid group and so does not serve to indicate any further higher groups.

*79. *Gonocoxite IX of female* (Fig. 54). Primitively, section 1 of gonocoxite IX (Smith, 1970a) is dorsoventrally constricted but is not completely divided. 79.1—Section 1 of gonocoxite IX is dorsoventrally constricted and completely divided by an internal articulation.

The absence of an articulation within section 1 of the gonocoxite is considered primitive because this is the condition in all non-aculeate Hymenoptera as well as in most Aculeata.

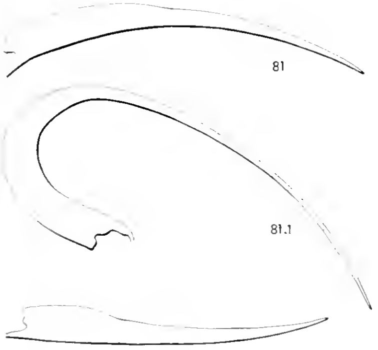
The development of an articulation within section 1 of the gonocoxite is uniquely characteristic of the bethylid, scolebythid and plumariid groups (it even occurs in the highly modified genitalia of the Chrysididae; Oeser, 1961). This is thus a very strong character uniting these taxa into a holophyletic group, and has arisen on internode 1-2.

80. *Gonapophysis VIII of female* (Fig. 55). Primitively, each gonapophysis VIII bears a lamellate valve dorsally near the base. 80.1—Each gonapophysis VIII is simple and smooth dorsally with no trace of a valve.

A valve on the gonapophysis VIII is considered primitive because this is the condition in most Aculeata including those which are judged to be most primitive on the basis of other characters. A valve is also present in at least some non-aculeates (e.g., Ichneumonidae; Oeser, 1961).

The loss of the gonapophyseal valve has occurred on at least seven occasions, on internode 21-22 (in the typhoctids and most likely the cotillid group although the actual condition in the cotillids is unknown) and in the plumariid, sapygid, pompilid, vespid, chyphotid and bradynobaenid groups. Alternatively the valve could have been lost on internode 18-21 and then been redeveloped in the apterogynids. Although this would be more parsimonious placement on the cladogram, it seems intuitively less likely than multiple losses. In view of its large number of independent derivations, this state is not of any use in establishing higher groupings.

81. *Gonapophysis IX of female* (Fig. 56). Primitively, the gonapophysis IX (fused to its counterpart) is gently arcuate dorsally so that the apex is directed obliquely ventrally. 81.1—The gonapophysis IX is strongly curved dorsally, especially basally, being somewhat elongated and with the apex directed downward. 81.2—The gonapophysis IX is almost straight or even slightly ventrally arcuate so that the apex is directed slightly upward or directly posteriorly.



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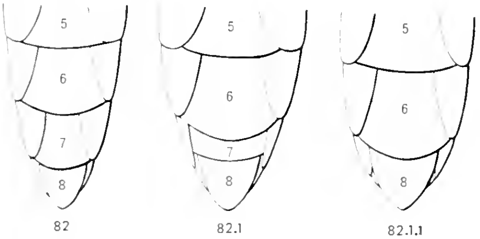

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Figs. 56-57. Characters of Aculeata. 56, gonapophysis IX of female, showing primitive and derived states (all composite); 57, posterior region of metasoma of male, ventral view, showing primitive and derived states of seventh sternum, sterna numbered (all composite).

A gently arcuate gonapophysis IX with the apex obliquely ventrally-directed is considered primitive because this is the condition in many Aculeata which are judged to be relatively primitive on the basis of other characters.

The degree and type of curvature of the gonapophysis IX is difficult to assign unequivocally to one of the designated states, and even when such decisions have been made, both derived states have apparently originated on numerous occasions. Nevertheless, the states do give some general indications of relationship and are somewhat useful. State 81.1 has apparently been derived on internodes 8-9 and 12-14 and in the methochid group. These taxa are all on the branch subtended by internode 6-7, the other members of which also show tendencies toward possession of this state, especially in elongation of the gonapophysis. State 81.1 is also present in the bradynobaenid group. State 81.2 has apparently been derived on internodes 4-5 and 18-21 (modified to 81.1 in the bradynobaenids) and in the rhopalosomatids and formicids. These are mostly groups on the branch subtended by internode 6-15, the other members of which also show a tendency toward a less elongate and less flexible gonapophysis.

82. *Seventh sternum of male* (Fig. 57). Primitively, the seventh metasomal sternum (eighth abdominal sternum) is well-developed, not much smaller than the sixth and clearly visible and exposed. 82.1—The seventh metasomal sternum is reduced and much smaller than the sixth although it is partly exposed. 82.1.1—The seventh metasomal sternum is greatly re-

duced, much smaller than the sixth and completely hidden by it.

A well-developed seventh sternum is considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates.

Reduction of the seventh sternum has apparently occurred on numerous occasions. State 82.1 has arisen on internodes 6-7, 16-17 and 18-21, as well as in the plumariid and vespid groups. Furthermore, re-enlargement of the seventh sternum has apparently occurred on internode 12-13 and in the myrmosid group. State 82.1.1 has been derived on internode 12-14 and in the apid group. As in all characters involving relative sizes, it is difficult to assign the various states unequivocally, and it appears that because of multiple derivations this character cannot be used to provide reliable information on higher groupings.

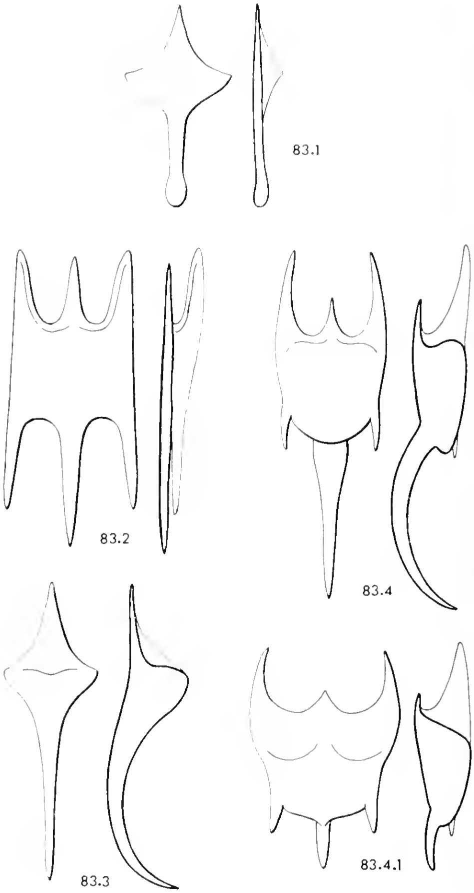


Fig. 58. Hypopygium of male, dorsal view and medial longitudinal section (approximate), showing derived states (83.1 based on *Sierolomorpha;* 83.2 on *Triclis;* 83.3 on *Paratiphia;* 83.4 on *Apterogyna;* 83.4.1 on *Bradynobaenus*).

*83. *Form of male hypopygium* (Fig. 58). Primitively, the hypopygium (eighth metasomal or ninth abdominal sternum) is simple, unmodified and apically rounded although it may be reduced in size and concealed. 83.1—The hypopygium is much narrowed, forming a peglike structure, but is not acute apically. 83.2—The hypopygium bears three subequal spines apically, the spines about equal to the base in length (excluding the anterior process). 83.3—The hypopygium is modified to form a single upcurved spine or aculeus. 83.4—The hypopygium is apically produced as three spines, the middle one upcurved and much longer than the laterals which are considerably shorter than the base (excluding the anterior process). 83.4.1—The hypopygium is modified as in 83.4 except that the middle spine is only very slightly longer than the laterals and not upcurved.

A simple hypopygium is considered primitive because this is the condition in most Hymenoptera, both non-Aculeata and Aculeata.

Each modification of the hypopygium has apparently only occurred once and where any one modification is present in more than one taxon it thus provides very good evidence of relationships. State 83.1 is characteristic of the sierolomorphids only and 83.2 of the scoliids. State 83.3 has been derived on internode 11-12 and associates four taxa in the tiphioid group, although this condition is approached within the thynnids (Salter, 1957). State 83.4 has originated on internode 21-23 and links three taxa in the bradynobaenoid group; the derived form of this state (83.4.1) is present in the bradynobaenid group only. States 83.2 and 83.4.1 are superficially similar but apparently have different origins and do appear somewhat different, especially when considered in conjunction with the following character (84). Within some of the other groups the hypopygium has often been modified in various ways but apparently never like any of the above states (except perhaps for 83.1).

84. *Concealment of male hypopygium.* Primitively, the hypopygium (eighth metasomal or ninth abdominal sternum) is not concealed by the preceding sterna. 84.1—The hypopygium is partially (up to the basal half) concealed by the preceding sterna. 84.2—The hypopygium is completely or almost completely concealed by the preceding sterna.

An unconcealed hypopygium is considered primitive because this is the condition in most Hymenoptera, both nonaculeates and aculeates.

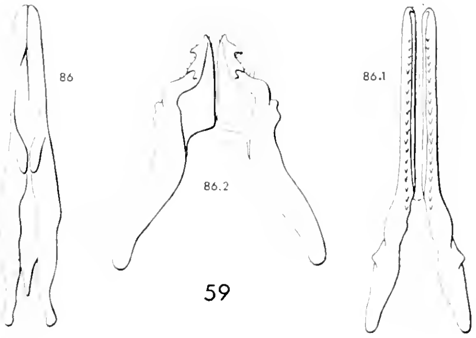
Partial or complete concealment of the hypopygium has apparently occurred on various occasions, mostly in single taxa, and is thus of minimal use in establishing relationships. State 84.1 has arisen in the anthoboscid and chyphotid groups and state 84.2 is present on internode 12-14 and in the apid, myrmosid, sierolomorphid and scoliid groups.

85. *Cercus of male.* Primitively, a cercus is present on each side of the composite tenth and eleventh abdominal tergum of the male. 85.1—The cercus is absent.

Presence of a cercus in the male is considered primitive because this is the condition in most Hymenoptera, both nonaculeate and aculeate, and also in insects in general. The cercus is absent in the female of all members of the Aculeata, however.

Loss of the cercus in the male has apparently occurred on at least four occasions and is thus not a strong character for indicating higher groups. State 85.1 has apparently arisen on internodes 12-14, 19-20 and 23-24 (in each case associating two taxa) and in the apid group.

*86. *Gonapophysis IX of male* (Fig. 59). Primitively, the gonapophyses IX are fused dorsally to form a chitinous "notum" (Smith, 1970a) over much of their length. 86.1—The notal fusion between the gonapophyses is desclerotized so that the gonapophyses are linked by a membrane along their entire length dorsally. 86.2—The notal fusion between the gonapophyses is



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Figs. 59-61. Characters of Aculeata. 59, gonapophyses IX of male, ventral view, showing primitive and derived states (86 based on *Sierolomorpha;* 86.1 on *Trielis;* 86.2 on *Fedtschenkia*); 60, mandible of larva, showing primitive and derived states of teeth (all composite); 61, first and second spiracles of final instar larva, showing derived state (88.1 based on *Pseudomethoca*).

retracted basally and desclerotized so that the gonapophyses are linked only basally by a membrane, and are completely free apically, over much more than half their length.

Dorsally fused gonapophyses are considered to be primitive because this is the condition in most Hymenoptera, both non-Aculeata and Aculeata, as well as in insects in general (Smith, 1969, 1970a).

The particular modifications of the aedeagal notum have each apparently arisen only once in the taxa considered. State 86.1 is characteristic of the scoliid group only. State 86.2 has apparently arisen on internode 7-8 and associates the sapygid, myrmosid and mutillid groups strongly. The form in *Fedtschenkia* (sapygid) for example, is remarkably similar to that in *Pseudophotopsis* (mutillid), and the myrmosid type is easily derived by increased production of the dorsal area of the apex of each gonapophysis, a tendency which is present in the sapygids also. There are various other modifications involving desclerotization of the notum within other taxa such as the apids (Snodgrass, 1941), but generally not in detail like the described states.

87. *Larval mandibular teeth* (Fig. 60). Primitively, the final instar larva has strongly sclerotized mandibles which are quadridentate. 87.1--The final instar larva has tridentate mandibles. 87.2—The final instar larva has bidentate mandibles. 87.3—The final instar larva has simple unidentate mandibles.

Quadridentate mandibles are considered to be primitive because this is the condition in various aculeate taxa considered to be relatively primitive on the basis of other characters.

Although evaluation of the states of the larval mandibular teeth is considerably hampered by the complete absence of information on the larvae of the plumariid, scolebythid, brachycistidid, sierolomorphid, typhoctid, eotillid, chyphotid, apterogynid and bradynobaenid groups, there nevertheless appear to be trends which may reflect the evolution of the mandible. Thus state 87.1 may have arisen on internode 15-16 (or possibly on internode 6-15 if it is present in the sierolomorphids). State 87.2 is present in the apids and sapygids but this may not be the primitive state for the latter group since the larvae of *Fedtschenkia* (the most generally primitive member) are unknown. State 87.3 is present in the rhopalosomatids, although it does occur within the apid group (e.g., *Apis*) and so is weakened, as well as not indicating higher groups.

*88. *Larval spiracles* (Fig. 61). Primitively, the final instar larva has ten pairs of fully developed spiracles, all of similar size and complexity. 88.1—The final instar larva has only nine pairs of fully developed spiracles, the second thoracic spiracle being much reduced in size and complexity although still distinguishable.

Ten pairs of fully developed spiracles are considered primitive because this is the condition in most Hymenoptera, both non-aculeates and aculeates (Riek, 1970).

Reduction of the second thoracic spiracle in the final instar larva (88.1) has apparently occurred at least twice, on internode 6-7 and in the pompilid group. Unfortunately, as for character 87, information is lacking for nine taxa. The condition observed in the larva of *Sapyga* (Torchio, 1972) in which the spiracle is apparently not reduced (included on the tree as an apparent reversal to the primitive condition) may have resulted from the specialized cleptoparasitic habits of this genus; a more generalized member such as *Fedtschenkia* may have the spiracle reduced. Apart from this uncertainty, the usefulness of this character is also somewhat lessened by the fact that the second spiracle is reduced in early instar larvae of various other taxa like the bethylids (e.g., *Chrysis;* Grandi, 1961). It is also apparently somewhat reduced in even the final instar larva of some vespids (e.g., *Dolichovespula;* Grandi, 1961). Nevertheless, because of various differences in detail, this character does seem to provide useful information on the relationship of the taxa above internode 6-7, as was suggested by Evans (1965), although his projection of the condition in the anthoboscid group has proved incorrect.

89. *Number of prey.* Primitively, each larva is supplied with a single host or prey individual and completes its development on this individual (V, P or M, and T appear once in the behavioral formula). 89.1—Each larva is supplied with numerous individuals of the host or prey and develops at the expense of many such individuals (V, P or M, and T appear repeatedly in the behavioral formula).

Use of a single prey individual for each larva is considered primitive because this is the situation in many Terebrantia and in various Aculeata considered relatively primitive on the basis of other characters.

The use of many prey individuals is apparently a trend shown in various taxa. Thus state 89.1 has arisen in the formicid and vespid groups and also in the apid group but in a somewhat different sense since the "prey" in the last instance is of vegetable and not animal origin. State 89.1 has also arisen within the sphecid group (in many members but not in *Ampulex,* e.g.). Although an evaluation is greatly hampered by the lack of biological information on the plumariid, scolebythid, brachycistidid, sierolomorphid, typhoctid, eotillid, chyphotid, apterogynid and bradynobaenid groups, it appears that state 89.1 is of no use in delineating groups because of its multiple origins. It does, however, give some indication of relative advance on the tree.

90. *Nest construction.* Primitively, the prey is left exposed or in a natural cavity and no nest construction or excavation is undertaken by the female (T, I and C do not appear in the behavioral formula). 90.1—The prey is relocated by the female but no nest construction or excavation is undertaken (T appears in the behavioral formula but I and C do not). 90.1.1—The prey is relocated by the female which also constructs a specialized nest or excavation in which the prey is placed and which is closed after provisioning and oviposition (T, I and C appear in the behavioral formula). 90.1.2—The prey is relocated by the female which also constructs a specialized nest or excavation in which the prey is placed but which is not closed after oviposition since provisioning is continuous during the development of the young (T and I but not C appear in the behavioral formula). 90.1.3—The prey is relocated by the female which does not construct any specialized nest or excavation but which does close off the cavity in which the prey is placed (T and C but not I appear in the behavioral formula). 90.2—The prey is not relocated and no specialized nest construction or excavation is undertaken by the female which merely closes off the cavity in which the prey was discovered, after oviposition (C but not T and I appears in the behavioral formula).

Lack of any type of prey transportation or nest construction is considered primitive because this is the situation in many Terebrantia and in various Aculeata considered primitive on the basis of other characters.

As with character 89, it is difficult to determine the evolution of nest construction since data are lacking for nine of the taxa considered. Nevertheless, state 90.1 has apparently arisen at least twice, on internodes 4-5 (associating the sphecid and apid groups) and 18-19 (linking the formicid, vespid and possibly the scoliid groups). State 90.1.1 has arisen independently in the apid and vespid groups; 90.1.2 is characteristic of the formicids; and 90.1.3 has arisen (apparently *de novo,* without prior origin of state 90.1) in the pompilid group. State 90.2 is characteristic of the myrmosid and mutillid groups and probably of the sapygids also, thus most likely having arisen on internode 7-8. This state is also present in the methochid group. Since behavior is by its very nature more plastic and thus probably more susceptible to evolutionary change than is morphology, thus aggravating problems of parallelism and convergence, this character appears to be of minimal significance in delineating groups, although it does provide some general indications of possible groupings.

91. *Oviposition sequence.* Primitively, oviposition occurs on the prey or host after it has been located [V (and usually P or M, and T) appears before O in the behavioral formula]. 91.1—Oviposition occurs in the empty nest chamber before the prey or host has been located (O appears before V, P or M, and T in the behavioral formula).

Oviposition after location of the host is considered primitive because this is the situation in the Terebrantia and in most Aculeata.

Early oviposition (91.1) has apparently arisen independently in the formicid and vespid groups and is thus not of any significance in establishing relationships, although some connection may be implied by the fact that both occurrences have appeared on the branch subtended by internode 18-19.

92. *Type of provisions.* Primitively, the larvae are reared on food of animal origin, viz., other arthropods (subscripts "a" appear in the behavioral formula). 92.1—The larvae are reared on food of vegetable origin, usually pollen and nectar (subscripts "v" appear in the behavioral formula).

Provisions of animal origin are considered primitive because these are the type used by most Terebrantia and by most Aculeata, including those considered relatively primitive on the basis of other characters.

The use of provisions of vegetable origin is characteristic of only the apid group, although a similar state has arisen within the vespid group (most Masaridae but not *Euparagia;* Williams, 1927) and within the formicid group (the more advanced members; Wilson, 1971). This character is thus of no use in the derivation of higher groupings.

Character States Primitive for the Taxa Considered

The following accounts are composite and intended to apply to primitive members of the taxa concerned, i.e., the character states are those possessed by the ancestral members of the taxon. Such an ancestral form may be hypothetical since no particular extant member may show all the characters in the states given for a taxon. However, all the states listed are present in at least some modern species for each taxon. The accounts are thus usually not diagnostic in the usual sense for the taxa involved. Unless otherwise specified, each character state applies to both sexes of the adults, except for some characters of the mesosoma in taxa where the female is apterous, in which case the character states are those of the male. The numbers refer to the preceding discussion of the characters themselves.

The taxa are referred to below by informal names (the ending "-id" does not necessarily connote a group at the family level) so that the final classification derived from the cladogram may be more readily constructed from the taxa actually considered, without the accounts of these taxa appearing under names which may differ from those adopted in the classification, or which may bear connotations at variance with those suggested by the final result. Nevertheless, the order in which the taxa are presented is as close to one reflecting evolutionary advance as possible, given the limitations of a linear arrangement. The taxa vary greatly in scope and categorical level, as may be judged from the listing of species examined for each, as well as the citation of which commonly recognized groups are included. Since it has proved impossible to check all previously identified specimens for accuracy of identification, the names used are those appearing on the determination labels associated with the specimens used, except for a few instances where changes in generic assignation have been made following recent revisions. Any misidentifications that may exist are actually of little or no significance for the derivation of the character states for the taxon concerned.

1. *Plumariid group.*

Material examined: *Myrmecopterina filicornis* (♂); *Plumarius* spp. (♂, Argentina; ♀, Peru); *Plumaroides andalgalensis* (♂). ("Plumariidae")
(Data also from Evans, 1967; Nagy, 1969a; Bradley, 1972. Nagy's "Heterogyninae"—*Heterogyna*—is also considered a member of this group.)

General—Sexual dimorphism considerable although male not more slender than female; male winged, female apterous (*Heterogyna* also; Nagy, *in litt.*) (1-2). No sterile caste (3). All pubescence simple (4).

Head—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (upper rim slightly produced in female) (6). Eye oval with inner margin shallowly sinuate (margin convex in female), not protuberant; scattered short setae present (glabrous in female) (7-9). Three ocelli present (absent in female) (10). Genal secretory organ absent (11). Antenna with 13 segments in both sexes; axis of radicle not deviating much from that of scape (at an oblique angle in female); radicle not inserted into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented (5-segmented in female); labial palpus 4-segmented (3-segmented in female) (15-17).

Mesosoma—Pronotum large, not reduced mesally (reduced and short mesally in male), freely articulating with mesothorax; hind margin arcuate, almost straight (strongly concave in male); anterior "collar" very short (absent in female); posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura mesally somewhat separated and shallowly diverging posteriorly (24). Prosternum somewhat sunken except anteriorly (25). Forecoxae somewhat separated (almost contiguous in female) (26). Mesonotum not anteriorly produced (enlarged, anteriorly produced in male); scutellum not much enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves contiguous (29). Mesepimeron running the height of mesopleuron (30). Mesosternum essentially simple, without posterior projections (31). Mid-coxae slightly separated (almost contiguous in female) (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum forming a distinct transverse area, fused to propodeum, slightly sunken but not invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae (entirely depressed in male), well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae slightly separated (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, obliterated ventral to pit (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation reduced apically; eight closed cells; veins 2s-m and 2m-cu absent (45-46). Pterostigma large and sclerotized (47-48). Hind wing with venation well-developed; three closed cells; veins A and J absent; cu-e originating proximal to point of separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along costa, not clustered (54). Plical lobe indicated by a moderate incision; jugal lobe absent (55-56). Legs slender, generally unmodified (femora and tibiae somewhat enlarged in female); arolia well-developed; claws toothed (simple in female) (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered weak spines (moderate spines in female); two simple spurs (61, 63-65). Hind coxa simple (66). Hind tibia with scattered weak spines; two simple spurs (62, 64, 67-68). Modified mesosoma of female with pronotum articulating with mesonotum; propleura fused ventrally and dorsally forming a rigid tube, slightly posteriorly produced in the midline ventrally; mesothorax with all sclerites fused, not distinguishable; metathorax much reduced, fused to propodeum; meso-metathoracic articulation very narrow and constricted; metacoxal cavities considerably separated from mesocoxal cavities so that mid-coxae are closer to forecoxae than hind coxae (69).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate (anteriorly narrowed and almost petiolate in female); first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, more or less continuous in contour with the second and overlying it (first sternum barely depressed and separated from second in female) (72-76). Second segment not apically constricted (77). Female with seventh tergum not mesally reduced (although enclosed by enlarged sixth sternum); articulation present within section 1 of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with seventh sternum reduced but not entirely hidden; hypopygium simple, little modified although slightly narrowed; cercus present; gonapophyses IX with notal fusion well-developed, especially basally (82-86).

LARVA—Unknown (that ascribed to *Plumarius* by Janvier, 1933:324, appears to be that of a mutillid from the figure and description).

BEHAVIORAL FORMULA—Unknown.

2. *Bethylid group.*

MATERIAL EXAMINED: *Anisepyris subviolaceus* (♂, ♀); *Apenesia columbana* (♂); *Bethylus amoenus* (♀); *Chrysis grandis* (♂, ♀); cleptid spp. (♂, California; ♀, India); *Deinodryinus henshawi* (♀); dryinid sp. (♀, Brazil); *Euchroeus purpuratus* (♂); *Goniozus foveolatus* (♀); *Goniozus* spp. (♂, New York; ♀, Florida); *Hedychridium carinulatum* (♂); *Omalus auratus* (♂); *Parasierola* spp. (♂, ♀, California); *Parnopes grandior* (♂); *Pristocera armifera* (♂); *Prosierola bicarinata* (♀); *Pseudisobrachium coxalis* (♂); *P. flavinervis* (♂); *Rhabdepyris megacephalus* (♂, ♀). ("Bethylidae," "Chrysididae," "Cleptidae," "Dryinidae") (Data also from Haupt, 1938; Grandi, 1961; Maa & Yoshimoto, 1961; Evans, 1964a. The following taxa are also considered to be members of this group: "Embolemidae," "Loboscelidiidae," "Sclerogibbidae.")

GENERAL—Sexual dimorphism minimal, both sexes of similar form and fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in both sexes; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 3-segmented (15-17).

MESOSOMA—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin arcuate, almost straight; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura mesally separated and diverging posteriorly (24). Prosternum not sunken (25). Forecoxae somewhat separated (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, divided midventrally, the two halves contiguous (29). Mesepimeron running the height of mesopleuron (30). Mesosternum without posterior projections (31). Midcoxae somewhat separated (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum indistinct, indistinguishable from propodeum medially, apparently not invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed laterally to accommodate mid-coxae, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae almost contiguous (41). Metathoracic-propodeal pleural suture barely visible dorsal to endophragmal pit, obliterated ventral to pit (42). Propodeum not shortened; disc and declivity slightly distinct but merging (43-44). Forewing with venation reduced apically; seven closed cells; vein M absent distal to separation from S; vein Cu_1 absent distal to separation from Cu_2; crossveins 1s-m, 2s-m and 2m-cu absent (45-46). Pterostigma large and sclerotized (47-48). Hind wing with venation reduced apically; one closed cell (C); vein M+Cu and all crossveins absent; veins A and J absent; traces of cu-e originating proximal to separation of M and Cu (49-52). Basal hamuli dispersed along costa, not clustered (54). Plical lobe indicated by a moderate incision; jugal lobe absent (55-56). Legs slender, unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with some scattered setae spiniform; two simple spurs (61, 63-65). Hind coxa simple (66). Hind tibia with some scattered setae spiniform; two simple spurs (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, more or less continuous in contour with the second (72-76). Second segment not apically constricted (77). Female with seventh tergum partially exposed, not much reduced; articulation present within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with seventh sternum not reduced nor hidden; hypopygium simple, unmodified; cercus present; gonapophyses IX with notal fusion well-developed (82-86).

FINAL INSTAR LARVA—Mandible quadridentate (87). Ten pairs of fully developed spiracles (88).

BEHAVIORAL FORMULA—V_aP_aO (89-92).

3. *Scolebythid group.*

MATERIAL EXAMINED: *Clystopsenella longiventris* (♀). ("Scolebythidae")
(Data also from Evans, 1963, 1967.)

GENERAL—Sexual dimorphism minimal, both sexes of similar form and fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus very short, reduced; antennae inserted very low on face (5). Antennal socket simple, with mesal margin only slightly raised, no tubercle (6). Eye oval with inner margin convex, not protuberant; scattered pores with short setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in both sexes; axis of radicle not deviating much from that of scape; radicle not inserted in basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin arcuate, almost straight; anterior "collar" absent; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura mesally considerably separated and diverging posteriorly (24). Prosternum large, not sunken (25). Forecoxae broadly separated basally but posteriorly produced, thus becoming contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum without posterior projections (31). Mid-coxae somewhat separated (32). Meso- and metapleura articulating (33). Metanotum reduced and very short medially; metapostnotum forming an indistinct transverse area, not clearly distinguishable from propodeum medially, not invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed laterally to accommodate mid-coxae, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, obliterated ventral to pit (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation reduced apically; six closed cells; vein M absent distal to separation from S; vein Cu_1+Cu_2 reduced distal to junction with 1m-cu; vein E absent distal to junction with cu-e; crossveins 1s-m, 2s-m and 2m-cu absent (45-46). Pterostigma large and sclerotized (47-48). Hind wing with venation much reduced; no closed cells; veins A and J absent; origin of cu-e not determinable (49-52). Basal hamuli dispersed along costa, not clustered (54). Plical lobe indicated by a moderate incision; jugal lobe absent (55-56). Legs stout with femora inflated; arolia small but distinct; claws with blunt basal tooth (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia spineless; two simple spurs (61, 63-65). Hind coxa simple (66). Hind tibia spineless; two simple spurs (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, more or less continuous in contour with the second and overlying it (72-76). Second segment not apically constricted (77). Female with seventh tergum barely exposed, not mesally reduced; articulation present within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with hypopygium simple, unmodified (83) (additional character states of terminalia unknown).

LARVA—Unknown.

BEHAVIORAL FORMULA—Unknown.

4. *Sphecid group.*

MATERIAL EXAMINED: ampulicid spp. (♂, Costa Rica; ♀, Sri Lanka); *Aphilanthops taurula* (♂, ♀); *Astata occidentalis* (♂, ♀); *Bembix hinei* (♂, ♀); *Cerceris bicornuta* (♂, ♀); *Chlorion aerarium* (♂, ♀); *Crabro largior* (♂, ♀); *Dasyproctus simillimus* (♂, ♀); *Epinysson bellus* (♂, ♀); *Gorytes provancheri* (♂, ♀); *Hapalomellinus albitomentosus* (♂, ♀); *Hoplisoides gulielmi* (♂, ♀); *Larropsis conferta* (♂, ♀); *Lyroda subita* (♂, ♀); *Mellinus* sp. (♂, ♀; Michigan); *Motes argentata* (♂, ♀); *Nysson aequalis* (♂, ♀); *Oxybelus cornutus* (♂, ♀); *Philanthus gibbosus* (♂, ♀); *Podalonia communis* (♂, ♀); *Prionyx foxi* (♂, ♀); *Pseneo montezuma* (♂, ♀); *Pseudoplisus phaleratus* (♂, ♀); *Sphex ichneumoneus* (♂, ♀); *Tachysphex tarsatus* (♂, ♀); *Trypargilum politum* (♂, ♀); *Zyzzyx chilensis* (♂, ♀). ("Sphecidae" *sensu lato*) (Data also from Williams, 1919; Leclercq, 1954; Evans & Lin, 1956; Evans, 1959a, 1966.)

GENERAL—Sexual dimorphism minimal, male slightly smaller than female; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum reduced mesally, eliminating laterodorsal surface, fairly freely articulating with mesothorax, especially dorsally; hind margin broadly U-shaped; anterior "collar" well-developed; posterolateral angle much reduced above spiracular lobe, not reaching tegula; posteroventral margin slightly concave; ventral angle considerably produced mesally, almost meeting its counterpart midventrally (18-23). Propleura mesally slightly separated and shallowly diverging posteriorly (24). Prosternum sunken except for moderately large anterior rim (25). Forecoxae contiguous (26). Mesonotum somewhat anteriorly produced; scutellum not much enlarged (27-28). Prepectus depressed, fused to mesepisternum, continuous midventrally (29). Mesepimeron reduced, very short but distinguishable the entire height of mesopleuron (30). Mesosternum slightly posteriorly produced between coxal bases but not overlying them (31). Mid-coxae slightly separated (32). Meso- and metapleura not mutually movable but not completely fused (33). Metanotum not reduced medially; metapostnotum mesally greatly expanded posteriorly, forming most of apparent disc of propodeum, neither sunken nor invaginated (34-35). Metepimeron expanded ventrally anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron, additional ventral pit developed; no metapleural gland (36-37). Metasternum depressed laterally to accommodate mid-coxae, well-differentiated from mesosternum except mesally, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture entirely visible, more distinct dorsal to endophragmal pit than ventrally (42). Propodeum effectively not shortened dorsally except as a result of development of metapostnotum; disc essentially absent but merging with declivity (43-44). Forewing with venation not much reduced apically; ten closed cells (45-46). Pterostigma fairly small and sclerotized (47-48). Hind wing with venation not much reduced apically; three closed cells; veins A and J present; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along costa, not clustered (54). Plical lobe indicated by a moderate incision; large jugal lobe indicated by a shallow notch (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not much modified (60). Mid-tibia with scattered moderate spines; two spurs, both slightly dorsally flattened with serrate margins (61, 63-65). Hind coxa simple (66). Hind tibia with scattered moderate spines; two spurs, both slightly dorsally flattened with serrate margins (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, not differentiated from second but overlying it (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden and reduced but with continuous anterior sclerotization; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX almost straight with apex directed slightly upward (78-81). Male with seventh sternum neither reduced nor hidden; hypopygium simple, unmodified; cercus present; gonapophyses IX with notal fusion well-developed (82-86).

FINAL INSTAR LARVA—Mandible quadridentate (87). Ten pairs of fully developed spiracles (88).

BEHAVIORAL FORMULA—$V_aP_aT_aO$ (89-92).

5. *Apid group.*

MATERIAL EXAMINED: *Andrena striatifrons* (♂, ♀); *Apis mellifera* (♂, ♀, ☿); *Aztecanthidium xochipillium* (♂, ♀); *Brachyhesma incompleta* (♂, ♀); *Callomelitta* sp. (♂, ♀; Australia); *Colletes nudus* (♂, ♀); *Euglossa cordata* (♂, ♀); *Fidelia kobrowi* (♂); *Fidelia* sp. (♀, South Africa); *Halictus ligatus* (♂, ♀); *Hylaeus basalis* (♂, ♀); *Leioproctus herbsti* (♂, ♀); *Lithurgus apicalis* (♂, ♀); *Megachile parallela* (♂, ♀); *Megalopta centralis* (♂, ♀); *Melissodes microsticta* (♂, ♀); *Melitta tricincta* (♂, ♀); *Mesocheira bicolor* (♂, ♀); *Nomada superba* (♂, ♀); *Nomadopsis zebrata* (♂, ♀); *Nomia melanderi* (♂, ♀); *Osiris* spp. (♂, Brazil; ♀, Panama); *Protoxaea ferruginea* (♂, ♀); *Ptilothrix fructifer* (♂, ♀); *Sericogaster fasciata* (♂, ♀); *Systropha curvicornis* (♂, ♀); *Xylocopa micans* (♂, ♀). ("Colletidae," "Halictidae," "Oxaeidae," "Andrenidae," "Melittidae," "Fideliidae," "Megachilidae," "Anthophoridae," "Apidae")

(Data also from Snodgrass, 1941; Michener, 1944, 1953, 1965, 1974; Daly, 1964; Exley, 1968; Eickwort, 1969; Stephen, Bohart & Torchio, 1969.)

GENERAL—Sexual dimorphism minimal, male slightly smaller than female; both sexes fully winged (1-2). No sterile caste (3). Much erect pubescence plumose (4).

HEAD—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex slightly elongated, especially in stipes and prementum; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum reduced mesally, eliminating laterodorsal surface, fairly freely articulating with mesothorax, especially dorsally; hind margin broadly U-shaped; anterior "collar" well-developed; posterolateral angle much reduced above spiracular lobe, reaching tegula; posteroventral margin slightly concave; ventral angle considerably produced mesally, almost meeting its counterpart midventrally (18-23). Propleura mesally slightly separated and shallowly diverging posteriorly (24). Prosternum sunken except for fairly long anterior region (25). Forecoxae contiguous (26). Mesonotum somewhat anteriorly produced; scutellum not greatly enlarged (27-28). Prepectus depressed, fused to mesepisternum, continuous midventrally (29). Mesepimeron much reduced, vaguely distinguishable only at dorsal extreme (30). Mesosternum very slightly posteriorly produced between coxal bases but not overlying them (31). Mid-coxae slightly separated (32). Meso- and metapleura not mutually movable but apparently not fused (33). Metanotum not reduced medially; metapostnotum mesally greatly expanded posteriorly, forming most of apparent disc of propodeum, neither sunken nor invaginated (34-35). Metepimeron ventrally expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron, additional ventral pit developed; no metapleural gland (36-37). Metasternum depressed laterally to accommodate midcoxae, mesally not well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, not distinguishable ventrally (42). Propodeum effectively not shortened dorsally except as a result of development of metapostnotum; disc essentially absent but merging with declivity (43-44). Forewing with venation somewhat reduced apically; ten closed cells (45-46). Pterostigma fairly small and sclerotized (47-48). Hind wing with venation only very slightly reduced apically; two closed cells; vein C reduced distally; vein A present, vein J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along margin, not clustered (54). Plical lobe indicated by a moderate incision; large jugal lobe indicated by a moderate incision (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, little modified (60). Mid-tibia with scattered weak spines; a single spur, slightly dorsally flattened with serrate margins (61, 63-65). Hind coxa simple (66). Hind tibia with scattered weak spines; two spurs, both slightly dorsally flattened with serrate margins (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, not differentiated from second but overlying it (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced, forming two separate sclerites; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX almost straight with apex directed slightly upward (78-81). Male with seventh sternum reduced and concealed; hypopygium simple but concealed; cercus absent; gonapophyses IX with notal fusion well-developed (82-86).

Final instar larva—Mandible bidentate (87). Ten pairs of fully developed spiracles (88).

Behavioral formula—I$(V_vT_v)^n$MOC (89-92).

6. *Anthoboscid group.*

Material examined: *Anthobosca erythronota* (♂, ♀); *A. ?flavicornis* (♂, ♀); *Anthobosca* spp. (♂, South Africa; ♀, Argentina); *Lalapa lusa* (♂, ♀). ("Anthoboscinae" of the "Tiphiidae")
(Data also derived from Turner, 1912; Janvier, 1933; Pate, 1947a; Evans, 1965.)

General—Sexual dimorphism moderate, male somewhat more slender than female; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

Head—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

Mesosoma—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for relatively large anterior rim (25). Forecoxae very nearly contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum with platelike projections posteromesally over coxal cavities (31). Mid-coxae slightly separated (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum visible medially, somewhat invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae, slightly raised posteromesally, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae only slightly separated (41). Metathoracic-propodeal pleural suture entirely distinct (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically (slightly reduced in female); ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation not reduced apically; three closed cells; veins A and J absent; cu-e originating distal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along margin, not clustered (54). Plical lobe indicated by a moderate incision; moderate jugal lobe present (55-56). Legs slender, generally unmodified (stouter in female with femora and tibiae enlarged); arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (61, 63-65). Hind coxa simple (66). Hind tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (62, 64, 67-68).

Metasoma—No specialized "felt lines" or

stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, not highly differentiated from second (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with seventh sternum somewhat reduced although not hidden; hypopygium slightly narrowed, lingulate, little modified, concealed basally; cercus present; gonapophyses IX with notal fusion well-developed, especially basally (82-86).

FINAL INSTAR LARVA—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88) (pers. obs.).

BEHAVIORAL FORMULA—V_aP_aO (89-92).

7. *Thynnid group.*

MATERIAL EXAMINED: *Diamma bicolor* (♀); *Eirone* sp. (♂, Australia); *Elaphroptera scoliaeformis* (♂, ♀); *Elidothynnus basalis* (♂, ♀); *Hemithynnus apterus* (♂, ♀); thynnine spp. (♂, ♀; Argentina, Australia); *Thynnoides fumipennis* (♂, ♀); *Zaspilothynnus dilatatus* (♂, ♀). ("Thynninae" of the "Tiphiidae")
(Data also from Turner, 1910; Janvier, 1933; Clausen, 1940; Reid, 1941; Pate, 1947a; Given, 1954, 1958, 1959; Salter, 1957; Ridsdill Smith, 1970a & b.)

GENERAL—Sexual dimorphism considerable although male only slightly more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size, slightly dorsally produced; antennae inserted fairly low on face (5). Antennal socket simple although slightly raised dorsomedially, without true tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum with platelike projections posteromesally over coxal cavities (31). Mid-coxae slightly separated (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum visible medially, somewhat invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae, slightly raised posteromesally, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic propodeal pleural suture entirely distinct (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically; ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation not much reduced apically; three closed cells; veins A and J absent; cu-e originating distal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along costa, not clustered (54). Plical lobe barely indicated; moderate jugal lobe present (55-56). Legs slender, generally unmodified (somewhat stouter in female with femora and tibiae somewhat enlarged); arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (61, 63-65). Hind coxa with weak dorsal carina (66). Hind tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; mesonotum short; scuto-scutellar suture present; separate prepectal sclerite present; mesepimeron differentiated from mesepisternum; meso- and metapleura articulating; mesonotum very short and transverse; endophragmal pit very close to anterior margin of metapleuron; metathoracic-propodeal notal and pleural sutures visible (69).

Metasoma—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum very slightly posteriorly depressed, not highly differentiated from second (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with seventh sternum somewhat reduced although not hidden; hypopygium simple, unmodified; cercus present; gonapophyses IX with notal fusion well-developed, especially basally (82-86).

Final instar larva—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88) (pers. obs.).

Behavioral formula—V_aP_aO (89-92).

8. *Myzinid group.*

Material examined: *Braunsomeria mutilloides* (♀); *B. quadraticeps* (♂, ♀); *Meria infradentata* (♀); *M. perornata* (♂, ♀); *M. semirufa* (♂, ♀); *Mesa capitata* (♂, ♀); *Myzinum dubiosum* (♂, ♀); *M. quinquecinctum* (♂, ♀); *Pterombrus* spp. (♂, Mexico; ♀, Argentina). ("Myzininae" of the "Tiphiidae")
(Data also from Williams, 1928; Krombein, 1937, 1968; Clausen, 1940; Pate, 1947a; Evans, 1965.)

General—Sexual dimorphism marked, male much more slender than female; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

Head—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim somewhat raised by protuberance of frons, forming a frontal ledge (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpi 6-segmented; labial palpi 4-segmented (15-17).

Mesosoma—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae very nearly contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum with platelike projections posteromesally over coxal cavities (31). Mid-coxae slightly separated (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae, slightly raised posteromesally, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae slightly separated (41). Metathoracic-propodeal pleural suture entirely distinct (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically; ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation not much reduced apically; three closed cells; veins A and J absent; cu-e originating distal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along margin, not clustered (54). Plical lobe indicated by a moderate incision; long jugal lobe marked by a deep incision (55-56). Legs slender, generally unmodified (stouter in female with femora and tibiae enlarged); arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Midtibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (61, 63-65). Hind coxa simple (66). Hind tibia with scattered moderate spines; two simple spurs (spurs slightly flattened in female) (62, 64, 67-68).

Metasoma—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate (slightly constricted in male); first tergum with lateral margin overlying sternum, not fused to it; first sternum extensively depressed, most strongly so posteriorly, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with seventh sternum neither reduced nor hidden; hypopygium a single upcurved spine, hardly concealed basally; cercus present; gonapophyses IX with notal fusion extensive (82-86).

Final instar larva—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88).

Behavioral formula—V_aP_aO (89-92).

9. *Methochid group.*

Material examined: *Methocha haemarrhoidalis* (♀); *M. minima* (♀); *M. mosotuana* (♂, ♀); *M. stygia* (♂, ♀). ("Methochinae" of the "Tiphiidae")
(Data also from Williams, 1919; Pate, 1947a; Burdick & Wasbauer, 1959; Hamann, 1960; Evans, 1965; Wilson & Farish, 1973.)

General—Sexual dimorphism considerable, male much more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

Head—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim only very slightly raised, forming a very slight frontal ledge (6). Eye oval with inner margin obliquely convex, not protuberant; many scattered pores with moderately long setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

Mesosoma—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin slightly concave; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum essentially simple but with dentate projections anteromesal to coxal cavities (31). Mid-coxae slightly separated (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum barely visible medially, invaginated (34-35). Endophragmal pit very close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae, slightly raised posteromesally, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, not distinguishable ventrally (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically; nine closed cells; vein S incomplete just proximal to junction with r-s (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation only slightly reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e originating distal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along margin, not clustered (54). Plical lobe indicated by a moderate incision; moderate jugal lobe present (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Midtibia with scattered weak spines; two simple spurs (only one, modified as calcar by dorsal pectination in female) (61, 63-65). Hind coxa simple (with well-developed dorsal carina in male) (66). Hind tibia with scattered weak spines; two spurs, the inner modified as calcar by dorsal pectination (only one spur, similarly modified, in female) (62, 64, 67-68). Modified mesosoma of female much narrowed; pronotum large, articulating with mesothorax; separate prepectal sclerite present; mesothorax long dorsally; scuto-scutellar suture present; mesepimeron not differentiated from mesepisternum; meso- and metapleura freely articulating; metathorax with notum very short and transverse; metapleuron reduced anterior to endophragmal pit; metathoracic-propodeal notal and pleural sutures visible dorsal to pit, not discernible ventrally; metacoxal cavities somewhat separated from mesocoxal cavities although mid-coxae still closer to hind coxae than to forecoxae (69).

Metasoma—No specialized "felt lines" or

stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate (slightly constricted in male); first tergum with lateral margin overlying sternum, not fused to it; first sternum depressed, especially posteriorly, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX considerably curved, especially basally, with apex directed downward (78-81). Male with seventh sternum not reduced nor hidden; hypopygium a single upcurved spine not concealed basally; cercus present; gonapophyses IX with notal fusion extensive (82-86).

Final instar larva—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88).

Behavioral formula—V_aP_aOC (89-92).

10. *Tiphiid group.*

Material examined: *Krombeinia nayarita* (♂, ♀); *Neotiphia rostrata* (♂, ♀); *Paratiphia aequalis* (♂, ♀); *P. neomexicana* (♂, ♀); *Tiphia letalis* (♂, ♀); *T. popilliavora* (♂, ♀). ("Tiphiinae" of the "Tiphiidae")
(Data also from Allen & Jaynes, 1930; Clausen & Gardner, 1932; Pate, 1947a; Allen & Krombein, 1964; Evans, 1965; Nagy, 1967; Allen, 1972.)

General—Sexual dimorphism slight, male only a little more slender than female; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

Head—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

Mesosoma—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle very slightly dorsally produced anterior to tegula, thus appearing truncate but reaching tegula; posteroventral margin somewhat concave; ventral angle more or less acute but not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum with platelike projections posteromesally over coxal cavities (31). Mid-coxae somewhat separated (32). Meso- and metapleura not mutually movable although not fused (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepisternum somewhat expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron but pleural sulcus is very indistinct; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae, raised posteromesally, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae slightly separated (41). Metathoracic-propodeal pleural suture not distinguishable (42). Propodeum not shortened; disc and declivity distinctly separated by a transverse carina (43-44). Forewing with venation reduced apically; nine closed cells; vein S incomplete just distal to separation from M (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation reduced apically; three closed cells; veins A and J absent; cu-e originating distal to separation of M and Cu; free section of Cu present although reduced to a spur (49-53). Basal hamuli dispersed along margin, not clustered (54). Plical lobe marked by a moderate incision; long jugal lobe marked by an incision (55-56). Legs fairly slender, little modified (stouter in female with femora and tibiae enlarged); arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Midtibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (61, 63-65). Hind coxa with weak dorsal carina basally (66). Hind tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment slightly constricted apically, not petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum posteriorly depressed, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX considerably curved, especially basally, with apex directed downward (78-81). Male with seventh sternum reduced and hidden; hypopygium a single upcurved spine, almost entirely concealed; cercus absent; gonapophyses IX with notal fusion extensive (82-86).

FINAL INSTAR LARVA—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88).

BEHAVIORAL FORMULA—V_aP_aO (89-92).

11. *Brachycistidid group.*

MATERIAL EXAMINED: *Acanthetropis* spp. (♂; Arizona, New Mexico); *Aglyptacros sulcatus* (♀); *Brachycistis alcanor* (♂); *B. alutacea* (♀); *B. emarginata* (♀); *B. inaequalis* (♂); *Bruesiella* sp. (♀, Arizona); *Colocistis* spp. (♂; Arizona, New Mexico); *Quemaya perpunctata* (♂). ("Brachycistidinae" of the "Tiphiidae")
(Data also from Mickel & Krombein, 1942; Pate, 1947a; Wasbauer, 1966, 1968; Krombein, 1967.)

GENERAL—Sexual dimorphism considerable although male not more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size (very short in female); antennae inserted fairly low on face (5). Antennal socket simple, without tubercle (6). Eye broadly oval, almost round, with inner margin shallowly sinuate, somewhat protuberant, scattered pores with short setae (eye reduced, oval with inner margin convex, flattened, glabrous, without pores in female) (7-9). Three ocelli present (absent in female) (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate (deeply arcuate in male); anterior "collar" well-developed; posterolateral angle very slightly dorsally produced anterior to tegula thus appearing truncate but reaching tegula; posteroventral margin somewhat concave; ventral angle rounded, almost acute but not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae very nearly contiguous (26). Mesonotum somewhat anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated and much reduced in length (29). Mesepimeron running the height of mesopleuron (30). Mesosternum with platelike projections posteromesally over coxal cavities (31). Mid-coxae somewhat separated (32). Meso- and metapleura not mutually movable although not fused (33). Metanotum not reduced medially; metapostnotum barely visible medially, invaginated (34-35). Metepisternum somewhat expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron but pleural sulcus is very indistinct; no metapleural gland (36-37). Metasternum depressed anterolaterally to accommodate mid-coxae, slightly raised posteromesally, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, barely discernible ventrally (42). Propodeum not shortened; disc and declivity fairly distinct (43-44). Forewing with venation reduced apically; ten closed cells (45-46). Pterostigma large and sclerotized (47-48). Hind wing with venation reduced apically; three closed cells; veins A and J absent; cu-e originating distal to separation of M and Cu; free section of Cu present although reduced to a spur (49-53). Basal hamuli absent (54). Plical lobe indicated by a shallow incision; moderate jugal lobe present (55-56). Legs slender, generally unmodified (stouter in female with femora and tibiae enlarged); arolia well-developed; claws simple (57-59). Foretibia with single calcar almost straight, not highly modified (58). Midtibia with scattered moderate spines; a single simple spur (spur slightly dorsally flattened in female) (61, 63-65). Hind coxa with weak dorsal carina basally (66). Hind tibia with scattered moderate spines; two simple spurs (spurs slightly dorsally flattened in female) (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax, its hind margin almost straight; mesonotum short; scuto-scutellar suture obliterated; separate prepectal sclerite present although much reduced; mesepimeron not differentiated from mesepisternum externally; meso- and metapleura articulating; metanotum extremely short and transverse, fused to propodeum, essentially not discernible; metapleuron greatly shortened anterior and dorsal to endophragmal pit; metathoracic-propodeal notal and pleural sutures discernible dorsal to pit, completely obliterated ventrally (69).

Metasoma—No specialized "felt lines" or stridulatory apparatus (70-71). First segment slightly constricted apically (more so in male), not petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum entirely depressed, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but completely sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX considerably curved, especially basally, with apex directed downward (78-81). Male with seventh sternum reduced and hidden; hypopygium a single upcurved spine, mostly concealed; cercus absent; gonapophyses IX with notal fusion extensive (82-86).

Larva—Unknown.

Behavioral formula—Unknown.

12. *Sapygid group.*

MATERIAL EXAMINED: *Fedtschenkia anthracina* (♂, ♀); *Polochrum repandum* (♂); *Sapyga clavicornis* (♀); *S. martinii* (♀); *Sapyga* sp. (♀, Colorado). ("Sapygidae") (Data also from Pate, 1947c; Bradley, 1955; Oeser, 1961; Guiglia, 1963, 1969; Tobias, 1965; Bohart & Schuster, 1972; Torchio, 1972.)

GENERAL—Sexual dimorphism minimal, both sexes of similar form and fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim somewhat raised, forming small tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex slightly elongated, with glossa slightly produced and broadened; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not much reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for fairly large anterior rim (25). Forecoxae very nearly contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not much reduced although discontinuous midventrally, the halves considerably separated, fused to mesepisternum, the line of fusion sulcate (29). Mesepimeron running the height of mesopleuron (30). Mesosternum essentially simple but with weak transverse carinae anteromesal to coxal cavities (31). Mid-coxae slightly separated (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum barely discernible medially, invaginated (34-35). Endophragmal pit close to anterior margin of metapleuron; no metapleural gland (36-37). Metasternum entirely depressed, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture entirely visible although less distinct dorsal to endophragmal pit (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically; ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation not much reduced apically; two closed cells; vein C reduced distally; veins A and J absent; origin of cu-e probably distal to separation of M and Cu, not absolutely determinable; free section of Cu absent (49-53). Basal hamuli dispersed along margin, not clustered (54). Plical lobe barely indicated; short jugal lobe present (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs (spurs flattened and marginally serrate in female) (61, 63-65). Hind coxa with well-developed dorsal carina (66). Hind tibia with scattered moderate spines; two simple spurs (spurs flattened and marginally serrate in female) (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, not highly differentiated from second (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX moderately curved with apex directed obliquely downward (78-81). Male with seventh sternum somewhat reduced but not hidden; hypopygium simple, unmodified, not hidden; cercus present; gonapophyses IX with notum desclerotized, gonapophyses linked by membrane basally only (82-86).

Final instar larva—Mandible bidentate (87). Ten pairs of fully developed spiracles (88) (data for *Sapyga* only).

Behavioral formula—V_aP_aO (89-92)

13. *Myrmosid group.*

Material examined: *Myrmosa bradleyi* (♀); *M. frater* (♂); *M. melanocephala* (♂, ♀); *M. nigriceps* (♂); *M. nocturna* (♂); *M. unicolor* (♂, ♀); *Myrmosula parvula* (♂, ♀); *M. rutilans* (♀); *Protomutilla microsoma* (♀). ("Myrmosinae" of the "Tiphiidae")
(Data also from Bischoff, 1915; Bridwell, 1920; Krombein, 1940; Pate, 1947a & b; Suárez, 1960; Wasbauer, 1973; Brothers, 1974b.)

General—Sexual dimorphism considerable although male not more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

Head—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim much produced, forming well-developed tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; many scattered pores with moderately long setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle perpendicular to that of scape; radicle set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

Mesosoma—Pronotum large, not much reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum barely anteriorly produced; scutellum not much enlarged (27-28). Prepectus not much reduced although discontinuous midventrally, the halves considerably separated, fused to mesepisternum, the line of fusion only marked by two pits ventrally (29). Mesepimeron running the height of mesopleuron (30). Mesosternum essentially simple but with weak transverse carinae anteromesal to coxal cavities (31). Midcoxae very nearly contiguous (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum barely discernible medially, invaginated (34-35). Metepisternum and metepimeron slightly expanded anterior to endophragmal pit so that pit is shifted slightly posteriorly; no metapleural gland (36-37). Metasternum entirely depressed, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture almost entirely obliterated, position barely discernible (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically; ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation not much reduced apically; two closed cells; vein C reduced distally; veins A and J absent; origin of cu-e probably distal to separation of M and Cu, not absolutely determinable; free section of Cu absent (49-53). Basal hamuli clustered near point of separation of veins C and SC+R+S (54). Plical lobe barely indicated; short jugal lobe present (55-56). Legs slender, unmodified; arolia well-developed (reduced in female); claws toothed (simple in female) (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs (spurs flattened and marginally serrate in female) (61, 63-65). Hind coxa with lamellate dorsal carina (66). Hind tibia with scattered moderate spines; two simple spurs (spurs flattened and marginally serrate in female) (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; prepectal sclerite fused to mesepisternum; meso- and metathorax and propodeum fused completely dorsally; pleura with only meso-metapleural suture faintly visible, flattened (69).

Metasoma—No specialized "felt lines" (70). Stridulitrum present as a single small shield-shaped area medially at base of third tergum (71). First segment neither apically constricted nor petiolate (slightly constricted in male); first tergum with lateral margin overlying sternum, not fused to it; first sternum posteriorly depressed, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX considerably curved, especially basally, with apex directed downward (78-81). Male with seventh sternum not reduced nor hidden; hypopygium simple but concealed; cercus present; gonapophyses IX with notum desclerotized, gonapophyses linked by membrane basally only (82-86).

Final instar larva—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88) (pers. obs.).

Behavioral formula—V_aP_aOC (89-92).

14. *Mutillid group.*

Material examined: Specimens of approximately 150 genera and subgenera. (See section on Mutillidae below, Table III, for complete list.) ("Pseudophotopsidinae - Sphaeropthalminae - Mutillinae - Rhopalomutillinae" of the "Mutillidae") (Data also from Bischoff, 1920-21; Mickel, 1928; Schuster, 1947, 1949; Brothers, 1972; Debolt, 1973.)

General—Sexual dimorphism considerable, although male not more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

Head—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim much produced, forming well-developed tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; scattered sensory pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle perpendicular to that of scape; radicle set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

Mesosoma—Pronotum fairly large, somewhat reduced mesally; articulation with mesothorax slightly restricted but with no fusion; hind margin concave; anterior "collar" well-developed; posterolateral angle very slightly dorsally produced anterior to tegula, thus appearing truncate but reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum only slightly anteriorly produced; scutellum not enlarged (27-28). Prepectus not much reduced although discontinuous midventrally, the halves considerably separated, fused to mesepisternum, the line of fusion marked by two pits ventrally (29). Mesepimeron running the height of mesopleuron although poorly differentiated ventrally (30). Mesosternum essentially simple but with weak transverse carinae anteromesal to coxal cavities (31). Mid-coxae very nearly contiguous (32). Meso- and metapleura articulating (33). Metanotum slightly reduced medially; metapostnotum barely discernible medially, invaginated (34-35). Metepisternum and metepimeron slightly expanded anterior to endophragmal pit so that pit is shifted slightly posteriorly; no metapleural gland (36-37). Sternum entirely depressed but slightly ventrally produced anteromesal to coxal cavities, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture almost entirely obliterated, position barely discernible (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation reduced apically; ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e apparently originating distal to separation of M and Cu; free section of Cu apparently absent (49-53). Basal hamuli clustered near point of separation of veins C and SC+R+S (54). Plical lobe barely indicated; extremely short jugal lobe present (55-56). Legs slender, unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs (spurs flattened and serrate in female) (61, 63-65). Hind coxa with weak dorsal carina basally (66). Hind tibia with scattered moderate spines; two simple spurs (spurs flattened and serrate in female) (62, 64, 67-68). Modified mesosoma of female with pronotum fused to mesothorax but with suture visible; prepectus fused to mesepisternum; meso- and metathorax fused completely dorsally, with pleurointersegmental suture faintly visible laterally; metathoracic-propodeal notal and pleural sutures visible only above endophragmal pit; pleura flattened (69).

Metasoma—Tendency toward development of felted secretory areas ("felt lines") on second segment, on both tergum and sternum laterally (70). Stridulitrum present as a small shield-shaped area medially at base of third tergum (71). First segment neither apically constricted nor petiolate (slightly constricted in male); first tergum with lateral margin overlying sternum, not fused to it; first sternum posteriorly depressed, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section I of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX considerably curved, especially basally, with apex directed downward (78-81). Male with seventh sternum somewhat reduced but not hidden; hypopygium simple, unmodified, not hidden; cercus present; gonapophyses IX with notum desclerotized, gonapophyses linked by membrane basally only (82-86).

Final instar larva—Mandible quadridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88).

Behavioral formula—V_aP_aOC (89-92).

15. *Sierolomorphid group.*

Material examined: *Sierolomorpha ?apache* (♂); *S. canadensis* (♂,♀); *S. nigrescens* (♂,♀); *S. similis* (♂). ("Sierolomorphidae")
(Data also from Evans, 1961; Nagy, 1971.)

General—Sexual dimorphism minimal, both sexes of similar form and fully winged (1-2). No sterile caste (3). All pubescence simple (4).

Head—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple but with dorsomesal rim very slightly raised, no true tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; scattered pores with short setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

Mesosoma—Pronotum large, not reduced mesally, freely articulating with mesothorax; hind margin shallowly arcuate (somewhat more deeply so in male); anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin slightly concave; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum not anteriorly produced (very slightly produced in male); scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum essentially simple but with weak ridges anteromesal to coxal cavities (31). Mid-coxae slightly separated (32). Metanotum not reduced medially; metapostnotum visible medially, slightly depressed but not invaginated (33-34). Metepimeron slightly expanded anteroventral to endophragmal pit so that pit is a short distance from anterior margin of metapleuron; no metapleural gland (35-36). Metasternum entirely depressed except for slight ridges anterior to coxae, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture barely discernible dorsal to endophragmal pit, not visible ventrally (42). Propodeum not shortened; disc and declivity somewhat distinct although merging (43-44). Forewing with venation reduced apically; seven closed cells; vein S absent between its separation from M and junction with r-s; crossveins 2s-m and 2m-cu absent (45-46). Pterostigma large and sclerotized (47-48). Hind wing with venation reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli dispersed along margin although tending toward concentration at separation of vein SC+R+S from margin (54). Plical lobe barely indicated; jugal lobe absent (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered weak spines; two simple spurs (61, 63-65). Hind coxa with weak dorsal carina (66). Hind tibia with scattered weak spines; two simple spurs (62, 64, 67-68).

Metasoma—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, not highly differentiated from second (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX gently curved, almost straight, with apex only weakly directed obliquely downward (78-81). Male with seventh sternum not reduced nor hidden; hypopygium reduced, very narrow, hidden except for extreme apex; cercus present; gonapophyses IX with notal fusion well-developed, especially basally (82-86).

Larva—Unknown.

Behavioral formula—Unknown.

16. *Pompilid group.*

Material examined: *Anoplius amethystinus* (♂, ♀); *Ceropales maculata* (♂, ♀); *Chirodamnus pyrrhomelas* (♀); *Cryptocheilus severini* (♂, ♀); *Episyron quinquenotatus* (♂, ♀); *Euclavelia fasciata* (♀); *Evagetes parvus* (♂, ♀); *Paracyphononyx funereus* (♂, ♀); *Pepsis thisbe* (♂, ♀); *Poecilopompilus interruptus* (♂, ♀); *Pompilus scelestus* (♂, ♀); *Psorthaspis connexa* (♂, ♀); *Tachypompilus ferrugineus* (♂, ♀). ("Pompilidae")
(Data also from Evans, 1953, 1959b, 1972; Daly, 1955.)

General—Sexual dimorphism minimal, male slightly smaller than female but of similar form; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

Head—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

Mesosoma—Pronotum large, not mesally reduced, freely articulating with mesothorax; hind margin arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin slightly concave; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum not anteriorly produced; scutellum not enlarged (27-28). Prepectus not much reduced although discontinuous midventrally, the halves considerably separated, fused to mesepisternum, the line of fusion retained as a sulcus (29). Mesepimeron running the height of mesopleuron (30). Mesosternum essentially simple but with weak ridges anteromesal to coxal cavities (31). Mid-coxae contiguous (32). Meso- and metapleura not mutually movable although not fused (33). Metanotum not reduced medially; metapostnotum well-developed, visible medially, slightly depressed but not invaginated (34-35). Metepimeron slightly expanded anteroventral to endophragmal pit so that pit is a short distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum entirely depressed except for slight ridges anterior to coxae, well differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture entirely visible (42). Propodeum not shortened; disc and declivity somewhat distinct although merging (43-44). Forewing with venation not reduced apically; ten closed cells (45-46). Pterostigma fairly small with sclerotization reduced (47-48). Hind wing with venation not reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli strongly concentrated into a basal cluster at separation of vein SC+R+S from margin (54). Plical lobe barely indicated; moderate jugal lobe present (55-56). Legs slender, generally unmodified although somewhat elongated; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Midtibia with scattered moderate spines; two spurs slightly dorsally flattened (61, 63-65). Hind coxa simple (66). Hind tibia with scattered moderate spines; two spurs slightly dorsally flattened, the inner one modified as a calcar by development of basal brush of setae dorsally (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed, not highly differentiated from second (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX gently curved, almost straight, with apex only weakly directed obliquely downward (78-81). Male with seventh sternum reduced but not hidden; hypopygium essentially simple, not reduced nor hidden; cercus present; gonapophyses IX with notal fusion well-developed (82-86).

FINAL INSTAR LARVA—Mandible tridentate (87). Nine pairs of fully developed spiracles, i.e., second pair reduced (88).

BEHAVIORAL FORMULA—$V_aP_aT_aOC$ (89-92).

17. *Rhopalosomatid group.*

MATERIAL EXAMINED: *Olixon banksii* (♂, ♀); *O. testaceum* (♀); ?*Olixon* sp. (♂, Cameroon); *Rhopalosoma* spp. (♀; Madagascar, Panama). ("Rhopalosomatidae") (Data also from Perkins, 1908; Reid, 1939; Brues, 1943; Gurney, 1953.)

GENERAL—Sexual dimorphism minimal, male slightly smaller than female but of similar form; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores with short setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum somewhat reduced mesally, fairly freely articulating with mesothorax; hind margin concave; anterior "collar" fairly well-developed; posterolateral angle rounded, very slightly produced dorsally and thus truncate although reaching tegula; posteroventral margin slightly concave; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum somewhat anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, much reduced, short and tall, hidden under pronotum, discontinuous midventrally, the halves considerably separated (29). Mesepimeron running the height of mesopleuron (30). Mesosternum with platelike projections posteromesally over coxal cavities (31). Mid-coxae contiguous (32). Meso- and metapleura articulating (33). Metanotum not reduced medially; metapostnotum visible medially, depressed but not invaginated (34-35). Metepimeron somewhat expanded anteroventral to endophragmal pit so that pit is some distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum entirely depressed, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture entirely visible (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation slightly reduced apically; eight closed cells, including cell C which is much reduced by fusion of veins C and SC+R+S except distally; crossveins 2s-m and 2m-cu absent (45-46). Pterostigma small with sclerotization reduced (47-48). Hind wing with venation slightly reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli strongly concentrated into a basal cluster at separation of vein SC+R+S from margin (54). Plical lobe well-marked by a deep incision; moderate jugal lobe present (55-56). Legs slender, little modified (tarsi flattened and broadened, forefemur swollen and arolia enlarged in female); arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered weak spines; two simple spurs (61, 63-65). Hind coxa simple (66). Hind tibia with scattered weak spines; two simple spurs, the inner one modified as a calcar by development of basal brush of setae dorsally (62, 64, 67-68).

Metasoma—No specialized "felt lines" or stridulatory apparatus (70-71). First segment apically somewhat constricted, not petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum not depressed although fairly well-differentiated from second (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX gently curved, with apex directed obliquely upward (78-81). Male with seventh sternum reduced but not hidden; hypopygium essentially simple, not reduced nor hidden; cercus present; gonapophyses IX with notal fusion well-developed (82-86).

Final instar larva—Mandible essentially unidentate (inner margin serrate) (87). Ten pairs of fully developed spiracles (88).

Behavioral formula—$V_a(P_a?)O$ (89-92).

18. *Formicid group.*

Material examined: *Aphaenogaster fulva* (♂, ♀, ☿); *Atta cephalotes* (♂, ♀, ☿); *Camponotus herculeanus* (♂, ♀, ☿); *Crematogaster coarctata* (♂, ♀, ☿); *Dinoponera* sp. (☿, Argentina); *Eciton vagans* (♂, ☿); *Ectatomma tuberculatum* (♂, ♀, ☿); *Labidus coecus* (♂, ☿); *Liometopium apiculatum* (♂, ♀, ☿); *Myrmecia* spp. (☿, Queensland); *Neoponera villosa* (♀, ☿); *Nomamyrmex crassicornis* (♂, ☿); *Odontomachus haematoda* (♂, ♀); *Paltothyreus* sp. (♂, ♀, ☿; Mozambique); *Paraponera clavata* (♂, ♀, ☿); *Pogonomyrmex barbatus* (♂, ♀, ☿). ("Formicidae")

(Data also from Haskins & Ensman, 1938; Brown & Nutting, 1950; Creighton, 1950; Haskins & Haskins, 1950; Wheeler & Wheeler, 1952, 1971; Brown, 1954, 1969; Brown & Wilson, 1959; Hermann & Blum, 1966; Wilson, Carpenter & Brown, 1967; Gotwald, 1969; Wilson, 1971; Markl, 1973.)

General—Sexual dimorphism moderate,

male somewhat smaller but not much more slender than female; both sexes fully winged (1-2). Wingless sterile female worker caste present (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin shallowly sinuate, not protuberant; scattered pores with short setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, somewhat reduced mesally, fairly freely articulating with mesothorax; hind margin deeply arcuate; anterior "collar" well-developed; posterolateral angle very slightly dorsally produced posteriorly, thus appearing truncate although reaching tegulae; posteroventral margin slightly concave; ventral angle acute, somewhat mesally produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum slightly anteriorly produced; scutellum not enlarged (27-28). Prepectus fused to mesepisternum, not distinguishable, apparently very short and narrow, hidden under pronotum (29). Mesepimeron reduced, distinguishable only at dorsal extreme (30). Mesosternum simple, without posterior projections (31). Mid-coxae slightly separated (32). Meso- and metapleura fused, not mutually movable (possibly not fused in *Sphecomyrma*) (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepisternum and metepimeron expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron; metapleural gland present, opening above hind coxa (36-37). Metasternum entirely depressed, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture entirely distinguishable (42). Propodeum not shortened; disc and declivity not distinct but merging (43-44). Forewing with venation not much reduced apically; eight closed cells; veins 2s-m and 2m-cu absent (45-46). Pterostigma moderate and sclerotized (47-48). Hind wing with venation not much reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli absent (54). Plical lobe indicated by a shallow notch; moderate jugal lobe present (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not much modified (60). Mid-tibia with few moderate spines apically only; two spurs, the inner dorsally carinate-pectinate forming a calcar, the outer simple (61, 63-65). Hind coxa simple (66). Hind tibia with few moderate spines apically only; two spurs, the inner dorsally carinate-pectinate forming a calcar, the outer simple (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment somewhat apically constricted, not petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum slightly depressed, differentiated from second by a slight constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX almost straight, with apex weakly directed obliquely upward (78-81). Male with seventh sternum not reduced nor hidden; hypopygium simple, unmodified, not hidden; cercus present; gonapophyses IX with notal fusion well-developed (82-86).

Final instar larva—Mandible tridentate (87). Ten pairs of fully developed spiracles (88).

Behavioral formula—$I[1O^{n}(V_{a}P_{a}T_{a})^{x}]^{i}$ (89-92).

19. *Scoliid group.*

Material examined: *Austroscolia nitida* (♂); *Campsomeris marginella* (♂, ♀); *Scolia nobilitata* (♂, ♀); *Trielis octomaculata* (♂, ♀); *Trisciloa zonata* (♂). ("Scoliidae")
(Data also from Betrem, 1928; Bradley, 1950; Grandi, 1961; Iuga, 1968.)

General—Sexual dimorphism slight, male only slightly more slender than female; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

Head—Clypeus somewhat enlarged; antennae inserted moderately high on face (somewhat higher in male) (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin deeply incised, not protuberant; pores and setae absent (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex somewhat elongated, with both glossa and paraglossa produced; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

Mesosoma—Pronotum considerably reduced and short mesally, not freely movable against mesothorax but tightly appressed to it; hind margin strongly concave; anterior "collar" well-developed; posterolateral angle slightly produced above tegula, thus appearing notched but reaching tegula; posteroventral margin strongly concave; ventral angle acute, somewhat produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum entirely sunken, without differentiated anterior rim (25). Forecoxae contiguous (26). Mesonotum enlarged and anteriorly produced; scutellum not enlarged (27-28). Prepectus fused to mesepisternum, much reduced but tall, discontinuous midventrally, the halves considerably separated, hidden under pronotum (29). Mesepimeron running the height of mesopleuron although pleural sulcus much reduced and not differentiated externally (30). Mesosternum flat, laterally broadened, with small plate-like projections over coxal cavities (31). Midcoxae very broadly separated (32). Meso- and metapleura not mutually movable although not fused (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Endophragmal pit a short distance from anterior margin of metapleuron and metepisternum posteriorly expanded; no metapleural gland (36-37). Metasternum large, laterally broadened, with small plate-like projections over coxal cavities, little differentiated from mesosternum but not anteriorly produced (38-40). Hind coxae broadly separated (41). Metathoracic-propodeal pleural suture entirely distinct (42). Propodeum not much shortened; disc and declivity fairly distinct (43-44). Forewing with venation reduced apically; ten closed cells (45-46). Pterostigma reduced and partially desclerotized (47-48). Hind wing with venation reduced apically; three closed cells; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli absent (54). Plical lobe not indicated; long jugal lobe indicated by a deep incision (55-56). Legs fairly slender, unmodified (stouter in female with femora and tibiae somewhat enlarged); arolia well-developed; claws simple (57-59). Foretibia with single calcar slightly curved, posteriorly hollowed and spatulate (60). Mid-tibia with scattered stout spines; one spur, slightly dorsally flattened (61, 63-65). Hind coxa simple (66). Hind tibia with scattered stout spines; two slightly flattened spurs (62, 64, 67-68).

METASOMA—No specialized "felt lines" or stridulatory apparatus (70-71). First segment slightly apically constricted, not petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum entirely depressed, highly differentiated from the second by a marked constriction (72-76). Second segment not constricted apically (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX moderately curved, with apex directed obliquely downward (78-81). Male with seventh sternum neither reduced nor hidden; hypopygium apically produced as three subequal spines, almost entirely concealed (except only for tips of spines); cercus absent; gonapophyses IX with notum desclerotized, gonapophyses linked by membrane along most of their length (82-86).

FINAL INSTAR LARVA—Mandible tridentate (87). Ten pairs of fully developed spiracles (88).

BEHAVIORAL FORMULA—$V_aP_a(?T_a)O$ (89-92).

20. *Vespid group.*

MATERIAL EXAMINED: *Ancistrocerus antilope* (♂, ♀); *Belonogaster* spp. (♂, Uganda; ♀, South Africa); *Brachygastra lecheguana* (♂, ♀); *Ceramius bicolor* (♂, ♀); *C. lichtensteinii* (♂, ♀); *Eumenes fraternus* (♂, ♀); *Euodynerus annulatus* (♂, ♀); *Euparagia scutellaris* (♂, ♀); *E. timberlaki* (♂, ♀); *Monobia quadridens* (♂, ♀); *Polistes metricus* (♂, ♀); *Polybia sericea* (♀); *Provespa barthelemyi* (♂, ♀); *Pseudomasaris vespoides* (♂, ♀); *Pterocheilus quinquefasciatum* (♂, ♀); *Stenodynerus papagorum* (♂, ♀); *Symmorphus canadensis* (♂, ♀); *Synagris cornuta* (♂); *Synoeca surinama* (♀); *Vespa crabro* (♂, ♀); *Vespula norvegicoides* (♂, ♀); *Zethus matzicatzin* (♂, ♀). ("Masaridae," "Eumenidae," "Vespidae") (Data also from Duncan, 1939; Reid, 1942; Grandi, 1961; Richards, 1962; Evans, 1966; Torchio, 1970; Charnley, 1973.)

GENERAL—Sexual dimorphism minimal, male not much more slender than female; both sexes fully winged (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus somewhat enlarged; antennae inserted moderately high on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin fairly deeply incised, not protuberant; scattered pores without evident setae (7-9). Three ocelli present (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex slightly elongated, with both glossa and paraglossa somewhat produced; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum extremely reduced and short mesally, not freely movable against mesothorax but tightly appressed to it; hind margin strongly concave; anterior "collar" slightly reduced; posterolateral angle slightly produced above tegula and exceeding its anterior margin, the angle thus appearing acute; posteroventral margin strongly concave; ventral angle acute, slightly ventrally produced (18-23). Propleura posteriorly contiguous mesally

(24). Prosternum entirely sunken, without differentiated anterior rim (25). Forecoxae contiguous (26). Mesonotum enlarged and anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, much reduced, very short, discontinuous midventrally, the halves very considerably separated, hidden under pronotum (29). Mesepimeron running the height of mesopleuron although much reduced (30). Mesosternum essentially simple but with anteromesal rims of coxal cavities acutely produced posteriorly (31). Mid-coxae contiguous (32). Meso- and metapleura not mutually movable although apparently not fused (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepisternum and metepimeron expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum entirely depressed except for anteromesal ridge, to accommodate mid-coxae, well-differentiated from mesosternum, not anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture entirely distinct (42). Propodeum shortened dorsomedially so that disc virtually absent, merging with declivity (43-44). Forewing with venation not much reduced apically; ten closed cells (45-46). Pterostigma fairly small and slightly desclerotized (47-48). Hind wing with venation not much reduced apically; three closed cells; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli absent (54). Plical lobe barely indicated; moderate jugal lobe present (55-56). Legs slender, unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not much modified (60). Mid-tibia with scattered weak spines; two simple spurs (61, 63-65). Hind coxa simple (66). Hind tibia with scattered weak spines; two spurs, the inner carinate and fringed dorsally, forming a calcar, the outer simple (62, 64, 67-68).

Metasoma—No specialized "felt lines" or stridulatory apparatus (70-71). First segment neither apically constricted nor petiolate; first tergum with lateral margin overlying sternum, not fused to it; first sternum depressed, especially posteriorly, highly differentiated from second by a marked constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX almost straight, with apex only weakly directed obliquely downward (78-81). Male with seventh sternum reduced although not entirely hidden; hypopygium simple, unmodified, not hidden; cercus absent; gonapophyses IX with notal fusion well-developed (82-86).

Final instar larva—Mandible tridentate (87). Ten pairs of fully developed spiracles (88).

Behavioral formula—$IO(V_aP_aT_a)^nC$ (89-92).

21. *Eotillid group.*

Material examined: *Eotilla mickeli* (♂, ♀); *E. superba* (♂). ("Eotillinae" of the "Mutillidae")

(Data also from Schuster, 1949; Mickel, 1968.)

General—Sexual dimorphism considerable, male not much more slender than female; male winged, female apterous (1-2). No sterile caste (3). Much pubescence of sub-plumose setae and plumose scales (4).

Head—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin very shallowly sinuate, not protuberant; scattered pores with short setae (7-9). Three ocelli present (absent in female) (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

Mesosoma—Pronotum large, very little reduced medially, freely articulating with mesothorax; hind margin arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae nearly contiguous (26). Mesonotum not much anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum (probably—not determinable without dissection), discontinuous midventrally, the halves considerably separated, very short and tall (29). Mesepimeron reduced, distinguishable only at dorsal extreme (30). Mesosternum simple, without posterior projections (31). Midcoxae somewhat separated (32). Meso- and metapleura not mutually movable although not fused (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepimeron very slightly expanded anteroventral to endophragmal pit so that pit is a short distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed only laterally to accommodate mid-coxae, mesally little differentiated from mesosternum and slightly anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, not distinguishable ventrally (42). Propodeum not shortened; disc and declivity somewhat distinct although merging (43-44). Forewing with venation reduced apically; ten closed cells (45-46). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli strongly clustered at separation of vein SC+R+S from margin (54). Plical lobe well-marked by a deep incision; moderate jugal lobe present (55-56). Legs slender, generally unmodified; arolia reduced; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered weak spines; two simple spurs (61, 63-65). Hind coxa with weak dorsal carina basally (66). Hind tibia with scattered weak spines; two simple spurs (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; mesonotum extremely short and transverse; scutoscutellar suture absent; prepectus probably fused to mesepisternum but hidden under pronotum; mesepimeron not differentiated from mesepisternum; meso- and metapleura fused but suture distinct; metathorax not distinguishable but apparently transverse (69).

Metasoma—"Felt line" developed on second segment, on tergum only, as line of dense pubescence (70). Stridulitrum present as a shield-shaped area on each side at base of fourth tergum (71). First segment somewhat apically constricted, with short petiole; first tergum with lateral margin only very slightly overlying sternum, apparently not movable against sternum although not fused to it except perhaps at basal extreme; first sternum entirely depressed, slightly more so posteriorly, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden; apex of gonapophysis IX not directed downward (additional details of female terminalia unknown) (78, 81). Male with seventh sternum somewhat reduced although not hidden; hypopygium simple, unmodified; cercus present; gonapophyses IX with notal fusion well-developed (82-87).

Larva—Unknown.

Behavioral formula—Unknown.

22. *Typhoctid group.*

Material examined: *Typhoctes peculiaris* (♂, ♀); *T. striolatus* (♀); *T. williamsi* (♂); *Typhoctoides aphelonyx* (♀). ("Typhoctinae" of the "Mutillidae") (Data also from Reid, 1941; Schuster, 1949; Krombein & Schuster, 1957; Brothers, 1970.)

General—Sexual dimorphism considerable, male smaller but not much more slender than female; male winged, female apterous (1-2). No sterile caste (3). Much pubescence of sub-plumose setae (4).

Head—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket simple, without tubercle (6). Eye oval with inner margin very shallowly sinuate (slightly incised in male), not protuberant; scattered pores with short setae (7-9). Three ocelli present (absent in female) (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle not deviating much from that of scape; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

Mesosoma—Pronotum large, very little reduced medially, freely articulating with mesothorax; hind margin arcuate; anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin approximately straight; ventral angle rounded, not produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae nearly contiguous (26). Mesonotum not much anteriorly produced; scutellum not enlarged (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated, each half very short and tall (29). Mesepimeron reduced, distinguishable only at dorsal extreme (30). Mesosternum simple, without posterior projections (31). Mid-coxae somewhat separated (32). Meso- and metapleura not mutually movable although not fused (33). Metanotum not reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepimeron very slightly expanded anteroventral to endophragmal pit so that pit is a short distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed only laterally to accommodate mid-coxae, mesally little differentiated from mesosternum and very slightly anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, not distinguishable ventrally (42). Propodeum not shortened; disc and declivity somewhat distinct although merging (43-44). Forewing with venation reduced apically; ten closed cells (45-46). Pterostigma small and sclerotized (47-48). Hind wing with venation reduced apically; three closed cells; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli strongly clustered at separation of veins C and SC+R+S (54). Plical lobe not indicated; jugal lobe absent (55-56). Legs slender, generally unmodified; arolia well-developed; claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with scattered moderate spines; two simple spurs

(61, 63-65). Hind coxa with weak dorsal carina basally (66). Hind tibia with scattered moderate spines; two simple spurs (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; mesonotum extremely short and transverse; scuto-scutellar suture absent; prepectus fused to mesepisternum; mesepimeron not differentiated from mesepisternum; meso- and metapleura fused but suture distinct; metanotum very short and transverse, not distinguishable, fused to propodeum; endophragmal pit barely distinguishable, apparently within meso-metapleural suture; metathoracic-propodeal pleural suture barely visible dorsal to endophragmal pit, not distinguishable ventrally (69).

METASOMA—"Felt line" developed on second segment, on tergum only, as line of dense pubescence (70). Stridulitrum present as a shield-shaped area on each side at base of fourth tergum (71). First segment somewhat apically constricted, with short petiole; first tergum with lateral margin only very slightly overlying sternum posteriorly, not movable against sternum although not fused to it except perhaps at extreme base; first sternum entirely depressed, slightly more so posteriorly, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX almost straight with apex weakly directed obliquely upward (78-81). Male with seventh sternum somewhat reduced although not hidden; hypopygium simple, unmodified; cercus present; gonapophyses IX with notal fusion well-developed although slightly desclerotized (82-86).

LARVA—Unknown.

BEHAVIORAL FORMULA—Unknown.

23. *Chyphotid group.*

MATERIAL EXAMINED: *Chyphotes attenuatus* (♂); *C. auripilus* (♀); *C. belfragei* (♂, ♀); *C. elevatus* (♂); *C. evansi* (♀); *C. melaniceps* (♂); *C. nubeculus* (♂); *C. petiolatus* (♀); *C. similis* (♂); *Chyphotes* spp. (♂, ♀; Mexico). ("Chyphotini" of the "Mutillidae")
(Data also from Buzicky, 1941; Reid, 1941; Mickel, 1967; Debolt, 1973.)

GENERAL—Sexual dimorphism considerable, although male not much more slender than female; male winged, female wingless (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim produced, forming a moderate tubercle (6). Eye almost round with inner margin sinuate (convex in female), protuberant; scattered pores with short setae (apparently without pores and glabrous in female) (7-9). Three ocelli present (absent in female) (10). Genal secretory organ absent (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle deviating from that of scape at an oblique angle; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not reduced medially (somewhat reduced in male), freely articulating with mesothorax; hind margin almost straight (strongly arcuate in male); anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin very slightly concave; ventral angle more or less acute, slightly produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae nearly contiguous (26). Mesonotum not anteriorly produced (slightly produced in male); scutellum not enlarged (27-28). Prepectus fused to mesepisternum, discontinuous midventrally, the halves considerably separated, each half very short and tall (29). Mesepimeron reduced, distinguishable only at dorsal extreme (30). Mesosternum simple, without posterior projections (31). Mid-coxae somewhat separated (32). Meso- and metapleura not mutually movable, apparently fused (33). Metanotum not reduced medially; metapostnotum barely visible medially, invaginated (34-35). Metepisternum very slightly expanded anteroventral to endophragmal pit so that pit is a short distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed only laterally to accommodate mid-coxae, mesally little differentiated from mesosternum and very slightly anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, not distinguishable ventrally (42). Propodeum not shortened; disc and declivity somewhat distinct although merging (43-44). Forewing with venation reduced apically; ten closed cells (45-56). Pterostigma fairly large and sclerotized (47-48). Hind wing with venation reduced apically; two closed cells; vein C reduced distally; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli strongly concentrated into a very small basal cluster at separation of vein SC+R+S from margin (54). Plical lobe not indicated; moderate jugal lobe present (55-56). Legs slender, generally unmodified (slightly stouter in female); arolia well-developed (much reduced in female); claws toothed (57-59). Foretibia with single calcar almost straight, not highly modified (60). Mid-tibia with few moderate spines; two simple spurs (spurs dorsally flattened in female) (61, 63-65). Hind coxa apparently simple (with moderate dorsal carina in male) (66). Hind tibia with very few moderate spines apically only; two simple spurs (spurs dorsally flattened in female) (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; meso- and metathorax and propodeum entirely fused dorsally and laterally; no sutures visible except that meso-metanotal suture barely evident; mesonotum large, posteriorly expanded; prepectus fused to mesepisternum; propodeum reduced dorsally; disc lost (69).

Metasoma—"Felt line" developed on second segment, on tergum only, as line of dense pubescence (70). Stridulitrum present as a shield-shaped area on each side at base of fourth tergum (71). First segment somewhat apically constricted, with marked petiole; first tergum with lateral margin only very slightly overlying sternum posteriorly, not movable against sternum and fused to it basally, much narrowed along petiole (tergum apparently absent from petiole in female); first sternum depressed, slightly more so posteriorly, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX almost straight, with apex weakly directed obliquely upward (78-81). Male with seventh sternum somewhat reduced, not entirely hidden; hypopygium basally concealed by sixth and seventh sterna, apically produced as three spines, the middle one produced and upcurved; cercus present; gonapophyses IX with notal fusion extensive (82-86).

Larva—Unknown.

Behavioral formula—Unknown.

24. *Apterogynid group.*

Material examined: *Apterogyna algirica*

(♂); *A. aliwalica* (♀); *A. bembesia* (♀); *A. bimaculata* (♀); *A. bulawayona* (♂); *A. geyri* (♂); *A. globularis* (♂); *A. guillarmodi* (♀); *A. karroa* (♂); *A. kochi* (♂); *A. olivieri* (♂, ♀); *A. patrizii* (♂); *A. savignyi* (♂, ♀); *A. schultzei* (♂, ♀); *A. villiersi* (♂). ("Apterogynini" of the "Mutillidae")

(Data also from Reid, 1941; Giner Marí, 1944; Invrea, 1957.)

GENERAL—Sexual dimorphism considerable, although male not more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

HEAD—Clypeus of moderate size; antennae inserted fairly low on face (somewhat higher in male) (5). Antennal socket with dorsomesal rim produced, forming well-developed tubercle (6). Eye oval, somewhat shortened and almost round, with inner margin extremely shallowly sinuate (convex in female), protuberant; pores and setae apparently absent (7-9). Three ocelli present (absent in female) (10). Genal secretory organ well-developed (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle deviating from that of scape at an oblique angle; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex not elongated; maxillary palpus 6-segmented; labial palpus 4-segmented (15-17).

MESOSOMA—Pronotum large, not reduced medially (much reduced in male), freely articulating with mesothorax; hind margin shallowly arcuate (deeply concave in male); anterior "collar" well-developed; posterolateral angle rounded, reaching tegula; posteroventral margin very slightly concave; ventral angle acute, slightly mesally produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for anterior rim (25). Forecoxae contiguous (26). Mesonotum not anteriorly produced (considerably produced in male); scutellum somewhat enlarged and swollen posterodorsally (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated, each half extremely short and tall (29). Mesepimeron reduced, distinguishable only at dorsal extreme (30). Mesosternum simple, without posterior projections (31). Mid-coxae somewhat separated (considerably separated in female) (32). Meso- and metapleura not mutually movable although apparently not fused (33). Metanotum somewhat reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepisternum expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron; no metapleural gland (36-37). Metasternum depressed only laterally to accommodate mid-coxae, mesally little-differentiated from mesosternum and considerably anteriorly produced (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, not distinguishable ventrally (42). Propodeum slightly shortened dorsally; disc and declivity somewhat distinct although merging (43-44). Forewing with venation much reduced apically; five closed cells; cells R, 1S, 2S, S+M, 1M absent (45-46). Pterostigma very small and sclerotized (47-48). Hind wing with venation considerably reduced apically; three closed cells; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli absent (54). Plical lobe not indicated; moderate jugal lobe present (55-56). Legs slender, generally unmodified (slightly stouter in female); arolia much reduced; claws toothed (57-59). Foretibia with single calcar considerably curved and flattened with an outer spine apically (60). Mid-tibia with very few moderate spines apically only; two spurs flattened and with strongly toothed margins (61, 63-65). Hind coxa with moderate dorsal carina (66). Hind tibia with very few moderate spines apically only; two spurs flattened and with strongly toothed margins (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; meso- and metathorax and propodeum entirely fused dorsally and laterally; meso-metanotal suture barely evident; mesonotum large, somewhat posteriorly expanded; prepectus fused to mesepisternum; meso- and metapleura fused but suture visible; line of fusion between nota and pleura of meso- and metathorax weakly marked; metathoracic-propodeal suture entirely obliterated; propodeum reduced dorsally; disc lost (69).

Metasoma—"Felt line" developed on second segment, on tergum only, as line of dense pubescence (as invaginated cuticular line in female) (70). Stridulitrum absent (71). First segment considerably constricted apically, nodose, with marked petiole; first tergum with lateral margin only very slightly overlying sternum posteriorly, not movable against sternum and fused to it basally, much narrowed along petiole; first sternum depressed, slightly more so posteriorly, separated from the second by a deep constriction (72-76). Second segment considerably constricted apically (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; valve present on gonapophysis VIII; gonapophysis IX almost straight with apex weakly directed obliquely downward (78-81). Male with seventh sternum reduced but not entirely hidden; hypopygium not concealed basally, apically produced as three spines, the middle one produced and upcurved; cercus absent; gonapophyses IX with notal fusion extensive (82-86).

Larva—Unknown.

Behavioral formula—Unknown.

25. *Bradynobaenid group.*

Material examined: *Bradynobaenus australis* (♂); *B. gayi* (♂, ♀); *B. wagenknechti* (♂); *Bradynobaenus* spp. (♀ ♀; Chile, Argentina). ("Bradynobaeninae" of the "Tiphiidae")
(Data also from Spinola, 1851; Zavattari, 1910; Reid, 1941; Pate, 1947a; Pérez D'Angello, 1968.)

General—Sexual dimorphism considerable although male not more slender than female; male winged, female apterous (1-2). No sterile caste (3). All pubescence simple (4).

Head—Clypeus of moderate size; antennae inserted fairly low on face (5). Antennal socket with dorsomesal rim very slightly produced but no true tubercle; interantennal frons slightly produced and forming a weak frontal ledge (6). Eye broadly oval with inner margin extremely shallowly sinuate, not protuberant; pores and setae apparently absent (7-9). Three ocelli present (10). Genal secretory organ present (not clearly distinguishable in male) (11). Antenna with 13 segments in male, 12 segments in female; axis of radicle deviating from that of scape at an oblique angle; radicle not set into basal invagination of scape (12-14). Labio-maxillary complex reduced; maxillary palpus 2-segmented; labial palpus 3-segmented (15-17).

Mesosoma—Pronotum large, not reduced medially (extremely reduced in male), freely articulating with mesothorax; hind margin shallowly arcuate (very deeply concave in male); anterior "collar" moderate; posterolateral angle rounded, reaching tegula, slightly posteriorly produced below tegula; posteroventral margin slightly concave; ventral angle acute, slightly mesally produced (18-23). Propleura posteriorly contiguous mesally (24). Prosternum sunken except for small anterior rim (25). Forecoxae nearly contiguous (26). Mesonotum not anteriorly produced (greatly produced in male); scutellum much enlarged and swollen posterodorsally, overhanging metanotum (27-28). Prepectus not fused to mesepisternum, discontinuous midventrally, the halves considerably separated, each half extremely short and tall (29). Mesepimeron reduced, distinguishable only at dorsal extreme (30). Mesosternum simple, without posterior projections (31). Mid-coxae somewhat separated (considerably so in female) (32). Meso- and metapleura not mutually movable although apparently not fused (33). Metanotum somewhat reduced medially; metapostnotum not visible medially, invaginated (34-35). Metepisternum expanded anterior to endophragmal pit so that pit is some distance from anterior margin of metapleuron but sutures anterior to pit are indistinct; no metapleural gland (36-37). Metasternum depressed only laterally to accommodate mid-coxae, mesally little differentiated from mesosternum and considerably anteriorly produced (moderately produced in female) (38-40). Hind coxae contiguous (41). Metathoracic-propodeal pleural suture visible dorsal to endophragmal pit, very indistinctly distinguishable ventrally (42). Propodeum considerably shortened dorsally; disc virtually non-existent, distinct from declivity (43-44). Forewing with venation extremely reduced apically; three closed cells; cells R, SC+R, 1S, 2S, S+M, 1M, 1Cu absent (45-46). Pterostigma very small and sclerotized (47-48). Hind wing with venation extremely reduced apically; two closed cells; vein M+Cu absent; veins A and J absent; cu-e originating proximal to separation of M and Cu; free section of Cu present (49-53). Basal hamuli absent (54). Plical lobe not indicated; moderate jugal lobe present (55-56). Legs fairly slender, little modified (considerably stouter in female); arolia much reduced; claws simple (57-59). Foretibia with single calcar considerably curved and flattened with an outer spine apically (spine absent in female) (60). Mid-tibia with few strong spines apically only; no spurs (61, 63-65). Hind coxa simple (66). Hind tibia with few strong spines apically only; two spurs flattened with a few teeth on margins (nematiform and smooth in female) (62, 64, 67-68). Modified mesosoma of female with pronotum large, articulating with mesothorax; meso- and metathorax and propodeum entirely fused dorsally and laterally; meso-metanotal suture barely evident; mesonotum large, somewhat posteriorly expanded; prepectus fused to mesepisternum; meso-metapleural suture faintly visible; line of fusion between nota and pleura of meso- and metathorax distinct; metathoracic-propodeal suture entirely obliterated; propodeum reduced dorsally; disc lost (69).

Metasoma—"Felt line" developed on second segment, on tergum only, as invaginated cuticular line in both sexes (70). Stridulitrum absent (71). First segment slightly constricted apically, with short petiole; first tergum with lateral margin only very slightly overlying sternum posteriorly, not movable against sternum and fused to it basally, much narrowed along petiole; first sternum depressed, more so posteriorly, separated from second by a deep constriction (72-76). Second segment not apically constricted (77). Female with seventh tergum hidden, reduced but continuously sclerotized anteriorly; no articulation within section 1 of gonocoxite IX; no valve on gonapophysis VIII; gonapophysis IX strongly curved, especially basally, with apex downwardly directed (78-81). Male with seventh sternum reduced but not entirely hidden; hypopygium not concealed basally, apically produced as three subequal spines; cercus absent;

gonapophyses IX with notal fusion extensive (82-86).

LARVA—Unknown.

BEHAVIORAL FORMULA—Unknown.

Discussion

CLADISTIC RELATIONSHIPS

Surprisingly, there have apparently been few intensive attempts to derive a phylogeny of the aculeate Hymenoptera. Although various schemes have been proposed (e.g., Ashmead, 1896b; Börner, 1919; Evans, 1958, 1966b; Ross, 1965; Evans & West Eberhard, 1970), these generally do not explicitly state the data on which they are based, or else they are based on a very limited data set so that detailed comparisons with the present scheme are of little value. A recent scheme of the evolution of the Hymenoptera is that of Evans & West Eberhard (1970), the upper section of which is shown in Fig. 62. This diagram expresses the commonly accepted ideas on aculeate evolution and should be used as the frame of reference for discussion of the present scheme (Fig. 2).

Basically, a sequence of more or less straight-line evolutionary advancement seems to have been emphasized, so that the more "primitive" groups (e.g., bethyloids and scolioids) are shown as arising early and the more "advanced" groups (e.g., apoids) are derived at the apex of the tree (Fig. 62). It now seems that some of the most "advanced" groups originated near the base of the tree and subsequently diverged greatly from the original stock. (This in essence reemphasizes the inappropriateness of the terms "primitive" and "advanced" as applied to entire taxa.) It is of some interest that Spradbery (1973) has recently presented a diagram which is somewhat more similar to that derived here in that he shows the line leading to the bees arising above the bethyloids but below the scolioids. On the other hand, he places the chrysidids in the Terebrantia, which is at variance with most other schemes.

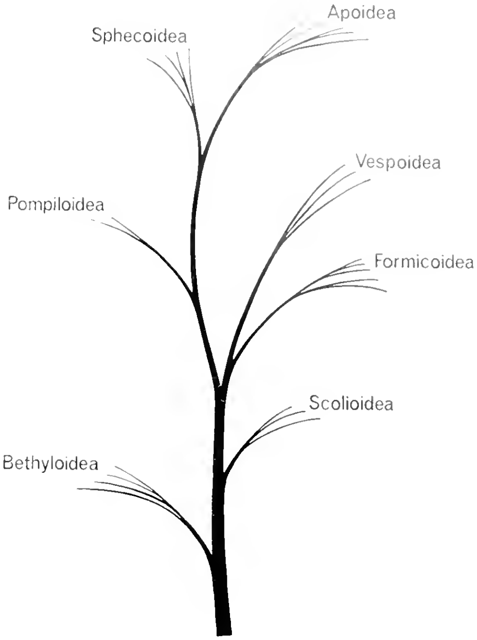


FIG. 62. Phylogeny of the traditional superfamilies of Aculeata, according to Evans & West Eberhard (1970).

In the present cladogram the scolebythids are extremely close to the bethylid group and may even have been derived from a stock very similar to modern "Bethylidae," indicating that this group is clearly more strongly associated with the bethylid group than any other. (Evans, 1963, by contrast, included the scolebythids in the "Scolioidea.") Although the plumariids possess many characters in states which have otherwise occurred only in lines on or above internode 1-4, they are linked to the bethylids and scolebythids by the common development of an articulation within section 1 of gonocoxite IX in the female and by the loss of the jugal lobe in the hind wing.

The remaining aculeates are strongly associated, most strikingly by common possession of sexual dimorphism in the number of antennal segments (13 segments in male and 12 segments in female), and reduction and desclerotization of the seventh metasomal tergum in the female. Thus the basal division of the Aculeata into two holophyletic lines as proposed by Oeser (1961) is not contradicted here.

The common ancestor of the sphecid and apid lines apparently diverged very early from the other aculeates, thus establishing a separate and highly divergent line. This is most strikingly characterized by the forms of the pronotum, metapostnotum and metapleuron, which serve to associate the apid and sphecid groups very strongly.

The remaining line of aculeates is not associated by any very strong character states, although the posterior approximation of the propleura, shortening of the prepectus, anterior depression of the metasternum, loss of veins A and J (hind wing) and deepening of the axillary incision may all have occurred on a line (internode 4-6) associating this group. These character states have also evolved elsewhere, however, although the first and second are probably the strongest and appear on the cladogram only once each.

Within this grouping there appear to be two lines, one of which is much more firmly established than the other. The group containing the tiphiids, mutillids and their relatives (subtended by internode 6-7) is associated by a number of reasonably good character states, such as the distal position of crossvein cu-e (hind wing), the partial invagination of the metapostnotum and the reduction of the second larval spiracle (which has apparently been reversed in, or within, the sapygids). Although these are individually not particularly impressive, the entire complex of character states involved is evidently significant. Within this group the association of the sapygids, myrmosids and mutillids is based on some quite strong character states, especially the loss of the free section of vein Cu (hind wing) (although with apparent reversal within the mutillid group), reduction of the jugal lobe of the hind wing, and desclerotization and basal retraction of the gonapophyseal notum in the male. Although the myrmosids have recently commonly been included in the "Tiphiidae" (e.g., Krombein, 1940; Pate, 1947a), their association with the mutillids appears much stronger, being based particularly on the form of the scape, fusion of the prepectus to the mesepisternum, the form of the modified female mesosoma, and the mesal stridulitrum. The general similarity between the myrmosids (males) and *Fedtschenkia* (sapygid group) is also quite marked, especially in wing venation, reinforcing the grouping of these taxa. It is of some interest that *Fedtschenkia* was first described as a member of the Mutillidae (Saussure, 1880) and a short time later was placed in a separate tribe of the mutillids since "ils forment le trait d'union entre les Mutillines et les Sapygides" (Saussure, 1892). If indeed *Fedtschenkia* is correctly considered to be a relatively "primitive" member of the "Sapygidae" (a placement that was not found to be contradicted during the present study), then the present investigation supports this relationship which was first suggested more than 80 years ago. (Guiglia, 1955, 1969, has outlined the taxonomic history of *Fedtschenkia*.)

The group containing the tiphiids consists of six taxa associated (on internode 7-10) by rather few characters of which the major one is probably the development of lamellate projections over the mid-coxae (although these have been reduced in the methochids). The group is also associated by a somewhat similar body form, especially of the females. The five taxa beyond the anthoboscids share a tendency towards reduction or loss of the wings in the female, resulting in similar mesosomal modifications, although the tiphiid group does not exhibit complete aptery in any member. The four taxa beyond the thynnids are strongly associated by the modification of the male hypopygium as a simple upcurved aculeus. The myzinid and methochid groups share males of a peculiar elongate form, in particular, and the tiphiids and brachycistids both have the seventh sternum and hypopygium of the male almost completely concealed, amongst other shared character states.

The remaining taxa (subtended by internode 6-15) are very weakly associated basally and may not represent a holophyletic group. Internodes 6-15, 15-16 and 16-18 are all rather weak (each bearing relatively few character states, most of which occur numerous times elsewhere on the cladogram) and may not be supported when additional data are considered. Despite these limitations, the sierolomorphids do appear to be similar to the pompilid group and also the typhoctids, especially in the structure of the female genitalia. The pompilids and rhopalosomatids are quite strongly associated, particularly by the similar development of a calcar on the hind tibia, and to some extent by the venation of the hind wing (especially the loss of the apical section of vein E).

The ten taxa above the sierolomorphids are associated (on internode 15-16) by the clustering of the basal hamuli, the reduction in the size of the pterostigma and perhaps the reduction in the number of teeth on the larval mandible (tridentate or less), all rather weak characters, especially the last since the larva is unknown for the entire branch subtended by internode 18-21. Association of the eight apical groups (above internode 16-18) is mainly on the basis of the complete invagination of the metapostnotum, which has also occurred elsewhere.

The formicid-vespid-scoliid line is associated by the common production of the ventral angle of the pronotum and anterior expansion of the metepisternum and metepimeron (which is least obvious in the scoliids). These are probably not very strong character states. However, the formicid and vespid groups share other states, such as the extreme reduction of the prepectus, the use of numerous prey individuals and early oviposition, which may additionally indicate some association based on parallel development of these character states. By contrast, the somewhat unexpected association of the scoliids and vespids seems to be based on a number of good character states. These include especially the form of the pronotum and its close association with the mesothorax, as well as the reniform eyes, dorsally produced clypeus, sunken prosternum and membranous pterostigma. (They of course also share all derived states appearing on internodes below internode 19-20.) Both of these taxa also possess highly muscular and similarly modified venom reservoirs with the muscle strands running transversely (Robertson, 1968), which supports this relationship, although Robertson came to somewhat different conclusions in her study which was based on a rather limited data set.

The remaining five taxa are very strongly associated (on internode 18-21) by a number of characters, such as the form of the metasternum, the basic form of the modified mesosoma in females (all of which are apterous), the presence of dorsal "felt lines" and the paired stridulitra (which are, however, lost in the apterogynids and bradynobaenids). Within this group the eotillids and typhoctids are strongly linked by the form of the mesosoma in the female. The other three taxa share an angulate scape, a similarly modified mesosoma in the female, a similarly modified first metasomal segment, and a trispinose hypopygium in the male. The association of the apterogynids and bradynobaenids has been mentioned previously by Reid (1941) and in passing by Bischoff (1927); it is strongly supported, particularly by the specialized genal organ, the enlarged scutellum, the identical modification of wing venation and the form of the foretibial calcar.

When life history data are considered, the cladogram does not contradict the idea that the ancestral aculeates were associated with hemimetabolous insects, such as Orthoptera or Hemiptera, which may have been more plentiful than the more recently evolved holometabolous groups. Thus, for example, various members of the bethylid group attack Hemimetabola [dryinids and embolemids on Homoptera (Ponomarenko, 1972; Evans, 1964a), mesitiines on Orthoptera (Gryllidae) (Nielsen, 1932)—although Nagy, 1969c, found *Mesitius horvathi* parasitic on a clythrine beetle—and sclerogibbids on Embioptera (Callan, 1939; Richards, 1939)], as do the most generalized sphecoids [ampulicids on Blattodea and sphecines mainly on Orthoptera (Clausen, 1940)], these taxa representing the most basal groups on the cladogram. Within each of these taxa there have been departures to the use of Holometabola [e.g., Coleoptera larvae by many "Bethylidae" (Evans, 1964a), Diptera and Lepidoptera by higher "Nyssoninae" (Evans, 1966a)]. The rhopalosomatids attack Orthoptera (Gryllidae) (Gurney, 1953) and the pompilids utilize spiders (Evans, 1953), another ancient group. Above internode 4-5, the apids have undergone a drastic change to the use of pollen and nectar (Malyshev, 1968). On internode 7-8 a change to parasitization of other Hymenoptera nesting in the soil apparently occurred. This is the basic habit of the sapygid (Bohart & Schuster, 1972), myrmosid and mutillid (Mickel, 1928) groups, although many sapygids have become cleptoparasitic on bees (Malyshev, 1968; Torchio, 1972) and a few mutillids parasitize hosts other than Hymenoptera (Brothers, 1972). All the taxa above internode 7-10 utilize cryptic coleopterous larvae (Pate, 1947a), as do the scoliids (Clausen, 1940) (this probably resulting in the convergence of body form between various tiphioids and the scoliids). (The hosts are actually unknown for the brachycistidid group, but see Wasbauer, 1966.) Primitive formicids have adopted a predatory habit connected with their sociality (Wilson, 1971). The vespids use many prey individuals of various types with which they provision their complex nests, and a large group of these (the masarids) has adopted pollen and nectar (although some of the most primitive masarids—*Euparagia*—use the larvae of weevils; Williams, 1927). Unfortunately, nothing is known of the life histories of plumariids, scolebythids (although parasitism of woodboring beetle larvae is probable; Evans, 1963), sierolomorphids, typhoctids, eotillids, chyphotids, apterogynids or bradynobaenids, so that they cannot be related to this scheme.

Although such attempts can be made to correlate prey or host group with a cladogram derived almost entirely from morphological characters, much more work is needed on the life histories of most groups of Aculeata before any more definite indications of the patterns of evolution of host relationships can be given. Data on entirely new aspects of behavior will also undoubtedly prove useful. For example, Farish (1972) examined grooming behavior in 51 species of aculeates (as well as other Hymenoptera) and applied the results to a somewhat unusual phylogeny which he had constructed from previously published information. Although very incomplete (due to poor representation in some groups), the patterns derived seem to confirm the distinctness of the Aculeata. Again, additional investigations are needed, but these initial results seem promising. Despite the prematurity of the attempts by workers such as Iwata (1942) and Malyshev (1968) to derive a unified scheme of the evolution of behavioral patterns in the Hymenoptera, such studies are of great heuristic value in emphasizing those areas most needing additional study.

Geographic distribution patterns often supply additional data which may support or refute a particular cladogram, especially when considered in the light of recent advances in the understanding of plate tectonics (see e.g., Axelrod & Raven, 1972), and using the principles derived by Hennig (1966b). Unfortunately, such data are of minimal use in the present study since most groups are essentially cosmopolitan. Furthermore, members of at least the bethylid (*Procleptes*), sphecid (*Archisphex* and *Lisponema*), formicid (*Sphecomyrma*) and possibly plumariid (*Cretavus*) groups are known from the Cretaceous (Sharov, 1957; Evans, 1967, 1969b; Wilson, Carpenter & Brown, 1967), suggesting that most of the gross evolution within the aculeates took place before the breakup of Pangaea had proceeded very far. The existence of fossil ants older than any pompilids (Evans, 1969b) places further doubt on the accuracy of the internodes associating these groups; although the cladogram does not preclude an earlier origin for the ants than for the pompilids, such a condition would seem unlikely. The incompleteness of the fossil record may be the most important factor in this regard, however.

When the present cladogram (Fig. 2) is compared with a commonly accepted scheme such as that given by Evans & West Eberhard (1970) (Fig. 62), a few striking differences may be noted. The most important of these involves the position and arrangement of the "Scolioidea." This group, which contains many of the taxa generally considered primitive in the Aculeata, is shown as a holophyletic unit in Evans & West Eberhard's scheme. The taxa included in this group appear on four distinct branches in the present cladogram, however, as emphasized in Fig. 63, and the scolebythids and plumariids (considered by some authors to belong to the "Scolioidea" and by Evans & West Eberhard to be intermediate between the "Bethyloidea" and "Scolioidea") form two additional branches. Thus the "Scolioidea" is a highly paraphyletic (if not polyphyletic) group. If the ancestral aculeate (below node 1) is considered to be a scolioid, then most of the other commonly accepted superfamilies have independently evolved from various points within the "Scolioidea," a situation which can be expressed as in Fig. 64. This closely resembles the scheme provided by Evans (1958) (Fig. 65), except as regards the "Pompiloidea." Actually, in view of the fundamental de-

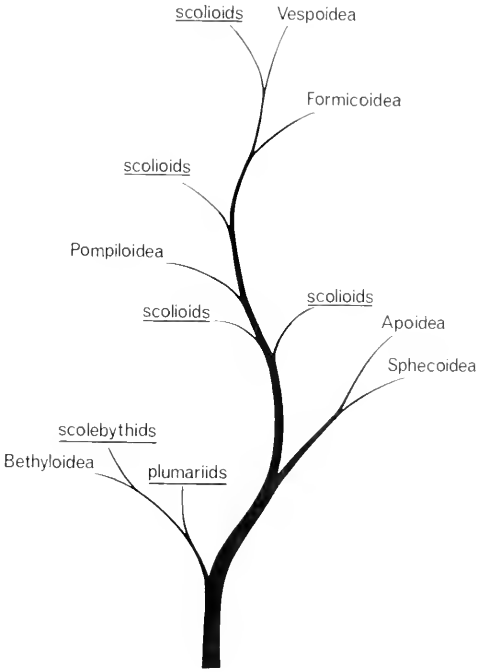
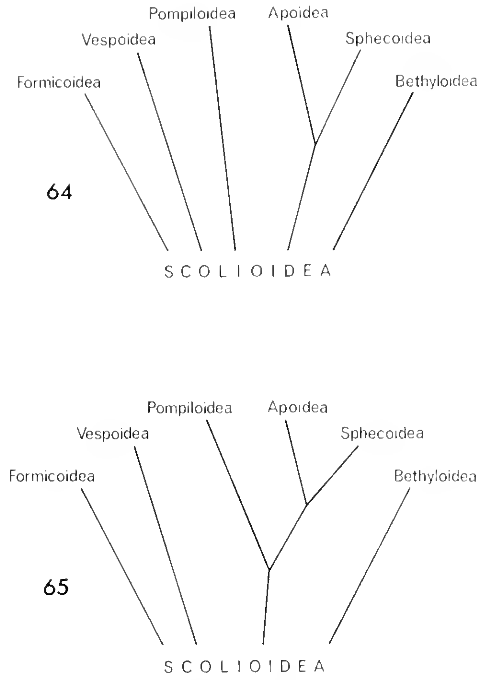


FIG. 63. Phylogeny of the traditional superfamilies of Aculeata, from the present study (see Fig. 2), emphasizing the paraphyletic (or polyphyletic) nature of the Scolioidea (scolioids).



FIGS. 64-65. Relationships of the traditional superfamilies of Aculeata. 64, from the present study, considering the ancestral aculeate to be a member of the Scolioidea; 65, according to Evans (1958).

rived characters present on internode 1-4, it is not appropriate to consider the ancestor below node 1 to be a member of the "Scolioidea," so that this scheme is also inadequate. It is also singularly lacking in information content.

The "Pompiloidea" has commonly been considered as derived from the line leading to the sphecoids and apoids, apparently because the posterolateral angle of the pronotum is rather rounded in the pompilids, a condition which has been regarded as a precursor to that in the sphecoids and apoids. Actually the primitive condition in the pompilids is not unlike that in many of the more generalized scolioids, such as *Anthoboscа* or *Sierolomorpha,* although the lobe over the spiracle is somewhat emphasized by the presence of a dorsoventral groove in the pompilids. Furthermore, the pompilids do not possess any of the other unique modifications, such as the form of the metapostnotum and metapleuron, which are characteristic of the apoids and sphecoids. It is thus clear that there is no good character to link the pompilids to the sphecoid-apoid line. Instead, the pompilids show more affinities with the formicoid-vespoid line.

DERIVATION OF A CLASSIFICATION

Given the present cladogram (Fig. 2), the question arises as how best to translate it into a classificatory scheme and whether the traditional superfamilies ("Bethyloidea," "Scolioidea," "Pompiloidea," "Vespoidea," "Formicoidea," "Sphecoidea" and "Apoidea") should logically continue to be recognized as such. The basic branching pattern (the result of cladogenesis) is only one aspect to be considered; degree of relative morphological or phenetic distinctness of taxa (the result of anagenesis) is another. The latter is difficult to measure objectively in such a way that it can be incorporated directly into a cladogram.

A simple method of estimating phenetic divergence might merely involve summing the number of derived character states on each particular internode, thus deriving an index of phenetic divergence for that internode. (For any taxon in which the state of a character is unknown, the primitive state is assumed unless otherwise indicated by the distribution of derived states in related taxa.) This is not sufficient, however, since degree of classificatory (or taxonomic) distinctness is somewhat dependent on the sizes of the groups involved, as is expressed in Mayr's (1969:92) recommendation that, for taxa above the species level, "the size of the [phenetic] gap [separating a taxon from another of the same categorical level] be in inverse ratio to the size of the taxon." This is purely a formalistic requirement designed to facilitate the data retrieval or reference functions of a classification by minimizing the proliferation of named taxa each containing only one or a few rather distinctive species. It has further been suggested by Ashlock (pers. comm.) that it may be logical to judge the relative importance of the various internodes in terms of the "success" of the groups derived from those internodes, possibly by considering the number of species in each group. Although "success" undoubtedly involves many other factors, most of these, such as biomass, number of individuals or energy flow, are incapable of adequate quantification in practice. (See Van Valen, 1973, for a discussion of criteria for comparison of taxa at the same categorical level in different phyla.)

The importance ("distinctness") of a particular internode may thus be estimated by devising some index that combines the number of evolutionary innovations (most conveniently represented as hatch marks) on that internode and the number of species that has been produced by the various lines derived from it. A simple product of these numbers appears to serve this purpose, as has been suggested by Ashlock (pers. comm.). Such a distinctness measure based on numbers or frequencies *(df)* may be expressed as

$$df_m = k_m S_m \qquad (1)$$

where k_m equals the number of derived character states (hatch marks) on internode (or final branch) m (assuming each such state to appear once on the branch) and S_m equals the total number of species subtended by internode m.

There is, however, an additional factor to consider: the fact that the distinctness of a group depends on the uniqueness of the derived character states delimiting the group. Thus a group characterized by the possession of many states uniquely derived (i.e., possessed by that group only) may logically be regarded as more distinct than one which possesses an equal number of states which have been derived more than once on the tree. The weight to be attached to any derived character state in assessing its significance as a delimiter of taxa for any internode, may logically be considered to be proportional to the ratio of its frequency of occurrence on that internode (assumed as unity) to its total frequency on the entire tree. This value is the reciprocal of the total number of times that it appears on the tree. Based on these considerations, another measure of distinctness for each internode (and final branch) utilizes the reciprocal of the harmonic mean (i.e., the mean of the reciprocals) of the number of times that each derived character state falling on that internode appears on the entire tree. (Although some character states appear only once on the tree, they may have been derived within other groups elsewhere on the tree. Such states are obviously not as efficient in delimiting groups as are those which appear only once on the tree and have not been derived elsewhere. It is impossible to differentiate between these two types in practice when dealing with very large groups, however, so that only occurrences shown on the tree can be included.) Maximal distinctness of a branch (all character states uniquely derived) is given by a value of 1, with decreased distinctness being less than 1 but greater than 0 (unless the internode bears no derived states). This distinctness measure based on character state efficiencies *(de)* may be expressed as

$$de_m = \frac{\left(\sum_{j=1}^{k} N_j^{-1} \right)_m}{k_m} \qquad (2)$$

where N_j equals the total number of times that derived character state j appears on the entire cladogram and k_m (as before) equals the number of derived character states (hatch marks) on internode (or final branch) m (assuming each such state to appear once on the branch). This index is identical to the mean of the "unit character consistencies" (Farris, 1969) for the "characters" on the internode if each character state is considered as a separate "character" (i.e., each has a range of one unit).

Neither of these measures alone is sufficient to provide an adequate idea of distinctness; since all the factors mentioned must be taken into account, a combination should be more useful. This is easily derived as the product of *df* and *de*. Thus, a more complete measure of distinctness *(dc)* for any internode or final branch m may be given as

$$dc_m = df_m de_m = S_m \left(\sum_{j=1}^{k} N_j^{-1} \right)_m \quad (3)$$

Once such a measure of distinctness has been obtained for each branch, it is a simple matter to construct a matrix presenting the taxonomic distinctness *(dt)* of each taxon from every other taxon. This is done by summing the distinctness values for each branch linking the two taxa (X and Y) under consideration. This may be expressed as

$$dt_{X,Y} = \sum_{m=1}^{p} dc_m$$
$$= \sum_{m=1}^{p} \left[S_m \left(\sum_{j=1}^{k} N_j^{-1} \right)_m \right] \quad (4)$$

where p is the number of internodes and final branches between taxon X and taxon Y including the most recent common ancestor of X and Y, and the other symbols have the same meaning as before. These final figures are essentially weighted measures of total "patristic difference" (Farris, 1967) or "number of steps" in the sense of Camin & Sokal (1965). They may be used in judging appropriate levels of distinctness for allocating the various taxa to different categorical levels (such as genus, family, etc.) in the final classification.

There is a complication introduced into the present study as a result of differential evolution of the two sexes. In some instances a particular derived state is present in one sex only although it could potentially occur in both. Such a derived state is obviously not as effective in distinguishing between taxa as is one which does not exhibit such dimorphic development, and thus should not be given equal weight in the calculation of a distinctness measure. (This of course does not deny that such a character state may be equally valid in a cladistic sense as a reflection of significant genetic modification as is one which occurs in both sexes.) For states appearing on the tree at least once in both sexes, it thus seems logical to score each occurrence of the state in one sex only as 0.5, and when affecting both sexes as 1.0. Character states occurring on the tree in only one sex or logically applicable to one sex only (such as those of the female genitalia) should also be coded as 1.0 since there is no *a priori* reason to consider these less significant than those appearing in both sexes.

These adjustments (or any other type of weighting to take similar factors into account) invalidate the assumptions made earlier that each state appearing on an internode appears there once. The previously derived equations (1-4) must thus be made more general. When this is done it becomes obvious that k_m in equation 2 is not the same factor as that symbolized by k_m in equation 1. The generalization follows:

Assume no limitation on the number of occurrences of each derived character state j on any internode m. Now,

$$DF_m = \left(\sum_{j=1}^{k} i_j \right)_m S_m \quad (5)$$

where i_j is the number of occurrences i of each derived state j, and k is the number of derived states, both on internode (or final branch) m; and S_m equals the total number of species subtended by internode m, as before.

Since unitary occurrence of each derived state on any one internode is now not assumed, the measure of distinctness based on efficiencies can no longer be based directly on the harmonic mean of the number of times each state appears on the entire tree. Instead, the "efficiency" of each state j is directly calculated as the ratio of the frequency of its occurrence on the internode to its frequency on the entire cladogram, and the mean of these ratios for all k states is then utilized. The limits of 0 and 1 still hold, as long as no state is considered to occur less than once in the entire tree. Thus,

$$DE_m = \frac{\left[\sum_{j=1}^{k}\left(\frac{i_{j_m}}{\sum_{m=1}^{n} i_{j_m}}\right)_j\right]_m}{k_m} \qquad (6)$$

where i_{j_m} is the number of occurrences of derived character state j on internode (or final branch) m, k_m is the number of derived character states (hatch marks) on internode m (as before), and n is the number of internodes (and final branches) in the cladogram.

There is no longer any cancellation of terms in the formula when the product of *DF* and *DE* is found, so that *DC* cannot be calculated directly. Now,

$$DC_m = DF_m DE_m \qquad (7)$$

The taxonomic distinctness of any two taxa, X and Y, is thus measured as

$$DT_{XY} = \sum_{m=1}^{p} DC_m \qquad (8)$$

where p is the number of internodes and final branches between taxon X and taxon Y, including the most recent common ancestor of X and Y.

These generalized equations (5-8) are those used in the present study. For investigations where the assumption of one occurrence on any internode for each derived state is valid, the earlier equations (1-4) are easier to apply, especially since *DC* can then be calculated directly.

A word is necessary to clarify the method of determining the number of occurrences of a character state. There are two aspects which may cause confusion. First, a particular derived state is sometimes apparently reversed to the primitive or a less derived condition. Since the original primitive state cannot be placed on any internode, the only appearances of the "primitive" state will be the result of such reversals. As such, it seems most appropriate to consider these as "pseudoprimitive" states and treat them like any other derived state, merely totalling the number of times that each appears on the tree. On the other hand, a reversal to an already derived state (e.g., from state C.2.1 to C.2) represents another appearance of a state which is already placed elsewhere on the tree. Although this actually represents a further derivation (in the above example it might be numbered C.2.1.1) in a cladistic sense, it nevertheless is equivalent to the less-derived state (C.2) in a phenetic sense, and so should be counted among the occurrences of that less-derived state. The second problem concerns instances in which a highly derived state apparently arises *de novo*, there being no evidence of an intermediate state which is found elsewhere on the tree (e.g., state C.3.1.1 is derived directly from C.3 although elsewhere on the tree it is derived from C.3.1). The usual practice in constructing the cladogram is to enter the missing intermediate state on the internode with its logical derivative. If there is absolute certainty that such an intermediate is required for that subsequent derivation to be possible, then this placement of states is justified. Such certainty is usually not possible, however, since a similar highly derived state may often logically have arisen in different ways from different intermediates. Some of these intermediates may not be present in the material examined, so that they do not appear in the coding of character states. Thus, inferring the occurrence of a particular derived state on an internode merely because of the presence of a state which may logically be derived from it, is probably unwarranted in most instances. Such inferred derivations should thus not usually be included when counting the occurrences of a particular state.

It should be emphasized at this point that the measures of taxonomic distinctness *(DT)* should not be considered to provide absolute criteria or definite numerical values at which groups are automatically considered distinct at some predetermined taxonomic level. (As Sneath & Sokal, 1973, emphasize, groups delimited in an analogous fashion on phenograms by means of phenon lines "approach natural taxa more or less closely" but are more appropriately termed "phenons" and are not allocated levels in the formal taxonomic hierarchy.) Instead, these measures may be used as indices from which some indication of the size of the phenetic gap between two groups, as well as the relative variation within a cluster of groups, may be gauged. As is indicated by Sneath & Sokal (1973), the most important criteria on which to base decisions on taxonomic rank are probably the internal diversity of a taxon and the sizes of the gaps between a taxon and those adjacent to it. Despite the significance generally attached to the "gap criterion" by practicing taxonomists of the "evolutionary" school (Michener, 1970), it is rejected by Sneath & Sokal (mainly because a gap is almost incapable of being measured using the usual numerical phenetic techniques). The distinctness measures derived above seem to be interpretable in terms of both criteria, however.

Because of the branching structure of a cladogram, involving hierarchical levels of dichotomy, use of the absolute number of species for calculation of *DF* is not appropriate. Instead, a multiplicative (logarithmic or exponential) conversion

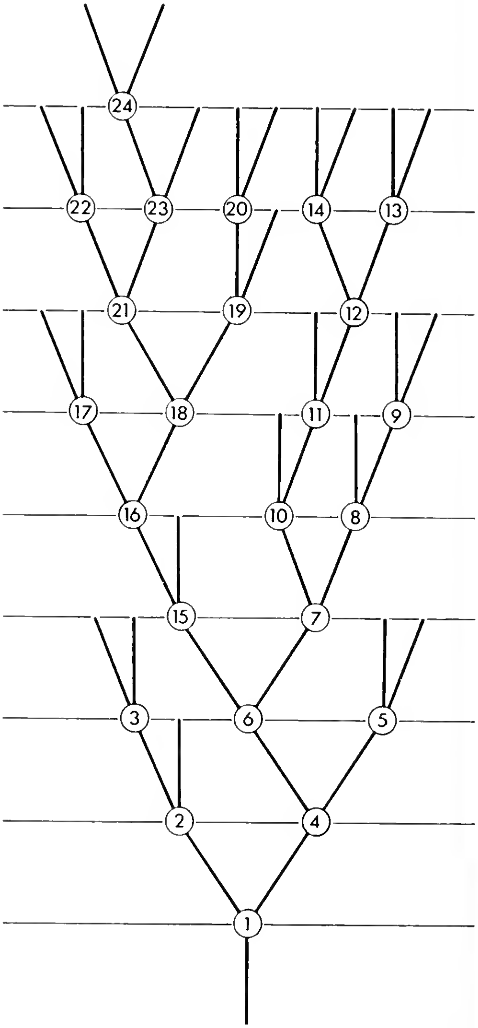


FIG. 66. Cladogram of 25 taxa of Aculeata, as in Fig. 2, emphasizing the number of levels of dichotomy.

scale should be used. It may be proposed that the logarithm to the base 2 is appropriate since this represents the number of levels of dichotomy in a perfectly regular tree which gives rise to the number of end points (species) involved. Cladograms are practically never perfectly regular, however. If one were able to count the number of levels involved in an actual cladogram, the number would almost invariably be greater than for a perfectly regular branching pattern involving the same number of species. For example, the present cladogram of the Aculeata (with 25 final branches) may be considered to involve 9 levels of dichotomy (see Fig. 66 for derivation) although a perfectly regular dendrogram with the same number of final taxa would have about half that number of levels ($4 < \log_2 25 < 5$). A scale based on consideration of the number of levels of dichotomy is thus not logically required. Furthermore, a logarithmic scale has the effect of drastically reducing the weight of a very large group in comparison with the small ones. This effect is not as extreme if an exponential scale is used. In the present study some groups were extremely large, and the cube root of the estimated number of species in each group was thus used for the values of S_m. (The number of species in each group is a best estimate based on the information contained in a wide variety of papers cited elsewhere in this account.)

Values of Σi, k, S, DF, DE and DC for the Aculeata appear in Table I, and those of DT are shown in Table II. The taxa are arranged from the base of the tree to the apex, taking each branch in turn.

The taxonomic distinctness measures *(DT)* for the Aculeata range from 5 to 1048 (mean 454). In general, the long diagonal in Table II contains the values between the closest pairs on the tree except where different branches are involved. These values are all below the mean for the study, except for two. These are the values between the plumariids and sphecids (566) and between the apids and anthoboscids (713). Furthermore, the values between all the basal taxa on the branches represented by these taxa (considering in addition sphecids to sierolomorphids, 489) are greater than the mean. This suggests a fundamental division into three groups, these subtended by internodes 1-2, 4-5, and 4-6 respectively.

Within the first of these groups (containing plumariids, bethylids and scolebythids) the values of *DT* are all quite low (mean is 77) although that between the scolebythids and bethylids is much lower than the others. This indicates relatively slight internal variation within this group. Furthermore, none of these values is much more than one quarter of the lowest value between an included taxon and a taxon in one of the other large groups (389, plumariids to sierolomorphids), again indicating a large gap between the three groups already identified.

The second group (sphecids and apids) has somewhat greater internal variation (246), but the value is only about half the mean value for the entire study. Furthermore, this figure is also only about half of the lowest value between a member of this group and one of the others (489, sphecids to sierolomorphids), reemphasizing the presence of a large gap.

The third group contains 20 taxa and is more complex to analyze. The variation within this group is quite considerable, and the mean value of *DT* within the group (339) is insignificantly less than the minimal value between a member of this group and one of the other two (389, sierolomorphids to plumariids). The most distinct taxon included here is the formicids, which is more distinct from every other taxon (minimal *DT* is 373, to typhoctids, and mean is 507) than the mean value for the group. It is also about as distinct within the group as the group is from one of the other groups. This suggests that the formicids may form a fourth group of the same rank as the three already recognized. The scoliids and vespids are almost as distinct from other members of this group as are the formicids (minimal value is 323, vespids to typhoctids) but less so from each other (183).

TABLE I. Occurrences (Σi) and numbers (k) of derived states, number of species subtended (S) and various distinctness measures (DF, DE, DC) for the internodes and final branches of the cladogram of Aculeata (Fig. 2).

Internode	Σi	k	S[a]	DF	DE	DC
1-2	6.0	6	10030	129.42	0.41	53.06
2-Plumar.	17.0	22	20	46.07	0.42	19.35
2-3	4.0	4	10010	86.20	0.78	67.24
3-Bethyl.	1.0	1	10000	21.54	0.40	8.62
3-Scoleb.	12.0	12	10	25.80	0.78	20.12
1-4	6.0	6	58500	232.92	0.69	160.71
4-5	15.0	15	32000	476.25	0.63	300.04
5-Sphecd.	3.0	3	12000	68.67	0.48	32.96
5-Apids	16.0	16	20000	434.24	0.49	212.78
4-6	5.0	5	26500	149.05	0.80	119.24
6-7	7.5	8	7700	148.12	0.46	68.14
7-8	10.5	11	5200	181.86	0.56	101.84
8-Sapygd.	4.0	4	150	21.24	0.66	14.02
8-9	12.5	13	5050	214.50	0.54	115.83
9-Myrmos.	6.0	7	50	22.08	0.55	12.14
9-Mutild.	9.0	9	5000	153.90	0.52	80.03
7-10	2.0	2	2500	27.14	0.38	10.31
10-Anthob.	1.5	2	100	6.96	0.31	2.16
10-11	1.0	1	2400	13.39	1.00	13.39
11-Thynnd.	3.0	3	1000	30.00	0.21	6.30
11-12	3.5	4	1400	39.16	0.63	24.67
12-13	3.0	3	600	25.29	0.67	16.94
13-Myzind.	1.0	1	500	7.94	0.33	2.62
13-Methoc.	17.0	18	100	78.88	0.48	37.86
12-14	13.5	14	800	125.28	0.25	31.32
14-Tiphid.	3.0	3	700	26.64	0.68	18.12
14-Brachy.	11.0	14	100	51.04	0.36	18.37
6-15	3.0	3	18800	79.77	0.33	26.32
15-Sierol.	12.0	12	20	32.52	0.33	10.73
15-16	3.0	3	18780	79.68	0.67	53.38
16-17	7.0	7	3050	101.50	0.39	39.58
17-Pompil.	8.0	8	3000	115.36	0.39	44.99
17-Rhopal.	14.0	14	50	51.52	0.37	19.06
16-18	4.0	4	15730	100.32	0.31	31.10
18-19	7.0	7	15500	174.51	0.40	69.80
19-Formic.	18.0	18	12000	412.02	0.57	234.85
19-20	9.0	9	3500	136.62	0.77	105.20
20-Vespid.	10.0	10	3000	144.20	0.55	79.31
20-Scolid.	23.0	23	500	182.62	0.57	104.09
18-21	19.0	19	230	116.47	0.50	58.24
21-22	6.0	6	20	16.26	0.52	8.46
22-Typhoc.	3.0	3	10	6.45	0.26	1.68
22-Eotild.	4.0	4	10	8.60	0.38	3.27
21-23	14.5	17	210	86.13	0.54	46.51
23-Chypho.	8.5	9	100	39.44	0.42	16.56
23-24	16.0	18	110	76.64	0.75	57.48
24-Aptero.	5.5	6	100	25.52	0.61	15.57
24-Bradyn.	21.5	22	10	46.22	0.77	35.59

[a] Estimated number of species (including those yet to be described). Calculations utilize $\sqrt[3]{S}$.

Table 11. Taxonomic distinctness (DT) for the taxa of Aculeata.

	SCOLEB.	BETHYL.	PLUMAR.	SPHECD.	APIDS	ANTHOR.	THYNND.	MYZIND.	METHOC.	TIPHID.	BRACHY.	SAPYGD.	MYRMOS.	MUTILD.	SIEROL.	POMPIL.	RHOPAL.	FORMIC.	VESPID.	SCOLID.	TYPHOC.	EOTILD.	CHYPHO.	APTERO.
BETHYL.	29																							
PLUMAR.	107	95																						
SPHECD.	631	623	566																					
APIDS	814	802	746	246																				
ANTHOR.	501	489	433	533	713																			
THYNND.	518	507	450	550	730	22																		
MYZIND.	556	545	488	588	768	60	50																	
METHOC.	592	580	524	624	803	95	86	40																
TIPHID.	586	575	518	618	798	90	80	69	104															
BRACHY.	586	575	518	618	798	90	81	69	104	36														
SAPYGD.	604	593	536	636	816	128	146	184	219	214	214													
MYRMOS.	718	707	650	750	930	242	260	298	333	328	328	142												
MUTILD.	786	775	718	818	998	310	328	366	401	396	396	210	92											
SIEROL.	457	446	389	489	669	118	135	173	208	203	203	221	335	403										
POMPIL.	585	573	517	616	796	245	262	300	336	330	330	348	462	530	149									
RHOPAL.	559	547	491	590	770	219	236	274	310	304	304	322	436	504	123	64								
FORMIC.	836	824	768	868	1048	496	514	552	587	581	582	599	713	781	400	420	394							
VESPID.	785	774	717	817	997	446	463	501	536	531	531	549	663	731	350	370	344	419						
SCOLID.	811	799	742	842	1022	470	488	526	561	556	556	574	688	756	374	395	369	444	183					
TYPHOC.	600	588	532	631	811	260	277	315	350	345	345	363	476	545	164	184	158	373	323	347				
EOTILD.	601	590	533	633	813	261	279	317	352	347	347	365	478	547	165	186	160	375	324	349	5			
CHYPHO.	652	641	584	684	864	313	330	368	403	398	398	416	529	598	217	237	211	426	376	400	73	75		
APTERO.	709	697	641	741	921	369	387	425	460	454	455	473	586	654	273	293	268	482	432	457	130	131	90	
BRADYN.	729	717	661	761	941	389	407	445	480	474	475	493	606	674	293	313	288	502	452	477	150	151	110	51

These two may thus also form a separate group.

The remaining taxa form a paraphyletic group and show a wide range of variation, although no one taxon is minimally as distinct from any other as are the formicids, vespids and scoliids. Thus, the basal taxa on each of the three major branches involved have the following values: anthoboscids to sapygids—128; anthoboscids to sierolomorphids—118; sapygids to sierolomorphids—221. This indicates that these branches are not highly distinct, these values all being less than the mean value for all included taxa (280). When members at the extremes of the included branches are considered, however, it is seen that some of the taxa are highly distinct from each other (e.g., mutillids to bradynobaenids, 674). Furthermore, each pair of taxa along these branches does not show great differentiation of its members, so that at no point is it possible to identify a further distinct group. Since a paraphyletic taxon should logically only be recognized if it is approximately as homogeneous as other recognized holophyletic taxa at the same categorical level, the extreme variability of this group suggests that it should not be recognized as such. Further subdivision is, however, impossible because of the absence of internal gaps. If the formicids, vespids and scoliids are again added in, it is found that the total variation within the group is only increased by about one-sixth (maximum is now 781, mutillids to formicids). This produces a holophyletic group only slightly more variable than the paraphyletic one, so that the recognition of this large holophyletic group is probably the best course of action. The Aculeata is thus considered to comprise three subgroups of equal categorical rank, which may be designated as superfamilies, viz., Bethyloidea, Sphecoidea and Vespoidea. This is somewhat reminiscent of the suggestion by Bradley (1958) who proposed two superfamilies, Vespoidea (including those taxa here placed in the Bethyloidea) and Sphecoidea.

Within the Bethyloidea, in the absence of any detailed studies of the included taxa other than those of previous workers, it seems best to maintain the commonly accepted family groups (cf., Maa & Yoshimoto, 1961), Bethylidae, Scolebythidae, Cleptidae, Chrysididae, Loboscelidiidae, Dryinidae, Embolemidae, Sclerogibbidae and Plumariidae. (Krombein, 1957 & *in litt.*, has suggested that the Cleptidae and Loboscelidiidae may more appropriately be considered to fall within the Chrysididae.) Various of these taxa contain few species with apparently relict distributions, probably indicative of a remote origin. For example, recent Scolebythidae occur in Brazil and Madagascar (Evans, 1963), and Plumariidae (including Heterogyninae) occur in arid areas in South America, South Africa and the Mediterranean area (Rhodes) (Bradley, 1972; Nagy, 1969a).

Within the Sphecoidea the two main taxa have been treated differently in the past. The wasp component has recently been considered to comprise a single family, the Sphecidae (Leclercq, 1954; Evans, 1964b) while the bees comprise nine families (Michener, 1965; Rozen, 1965; Roberts, 1973). Since both groups contain comparable numbers of species and appear to include an approximately equivalent range of phenetic variation, it seems reasonable to subdivide both groups to a similar degree. If this is done, the Sphecoidea may be considered to contain either two families (one of wasps and one of bees) or two groups each consisting of a number of families. Since an important function of a classification involves information retrieval, the size of the group involved is of some concern, for efficiency is lost if a group is very large. Based on this consideration, it is suggested that the eight subfamilies of sphecids recognized by Evans (1964b) be considered valid taxa at the family level, and that the presently accepted bee families be retained at that level. The Sphecoidea then consists of the Ampulicidae, Sphecidae, Larridae, Mellinidae, Pemphredonidae, Astatidae, Philanthidae, Nyssonidae, Colletidae, Halictidae, Oxaeidae, Andrenidae, Melittidae, Fideliidae, Megachilidae, Anthophoridae and Apidae. The first eight may be included in an informal grouping, the Spheciformes, and the last nine in the Apiformes. (It is of some interest that, despite his suggestion in 1944 that the bees should be placed "as a division of the Sphecoidea," Michener has retained the superfamily "Apoidea" in his subsequent papers, illustrating that some collective term for "bees" is necessary.)

Despite the general absence of marked gaps within the Vespoidea, recognition of subtaxa, mainly on the basis of areas of low distinctness, is possible. Thus the six taxa above internode 7-10 show generally low mutual distinctness and a slightly higher minimal value to surrounding taxa. They may thus logically be recognized as a single taxon at the family level with the component taxa designated as subfamilies. The Tiphiidae thus comprises the Anthoboscinae, Thynninae, Myzininae, Methochinae, Tiphiinae and Brachycistidinae. Although many of the values are somewhat higher for the five taxa subtended by internode 18-21, the gaps between any of these and any member of the larger group are considerably greater. Here again it is probably appropriate to recognize these taxa as a group at the family level. The lowest value in the matrix is that between two members of this group, a figure so small (5) that the question arises as to whether recognition of these taxa as separate is justified. In the absence of convincing evidence to the contrary, recognition of these members at a very low level is probably appropriate. The Bradynobaenidae thus comprises the Typhoctinae (with tribes Eotillini and Typhoctini), Chyphotinae, Apterogyninae and Bradynobaeninae.

The only other relatively low values (less than 100) are those between the pompilids and rhopalosomatids (64) and the myrmosids and mutillids (92). In both instances consideration should be given to inclusion of both taxa in the same family. In the case of the rhopalosomatids and pompilids this does not seem appropriate since the habits of the two groups are completely different (rhopalosomatids develop as ectoparasites of active crickets and pompilids store paralyzed spiders as larval provisions). The myrmosids and mutillids, however, have extremely similar habits, both being parasitoids of the prepupae or pupae of other Hymenoptera (see Knerer, 1973, e.g.). This suggests that they may be considered to fall in a single family, the Mutillidae (see section on Mutillidae below for details).

Each remaining taxon is best considered as valid at the family level at the least. The vespid group may additionally be considered to comprise three families (Masaridae, Eumenidae, Vespidae) as recommended by Richards (1962). Since the formicid group is highly distinctive within the Vespoidea, it also seems appropriate to recognize the Formiciformes informally to contain the family Formicidae, the remainder of the Vespoidea being the Vespiformes. (Incidentally, it is of some interest that a form more similar to *Sierolomorpha* than to *Anthobosca* seems to be indicated as the ancestral type that gave rise to ants; Anthoboscinae have in the past been considered to be the closest to the ancestral form, Wilson, Carpenter & Brown; 1967.)

The superfamily Vespoidea is therefore considered to contain the following 12

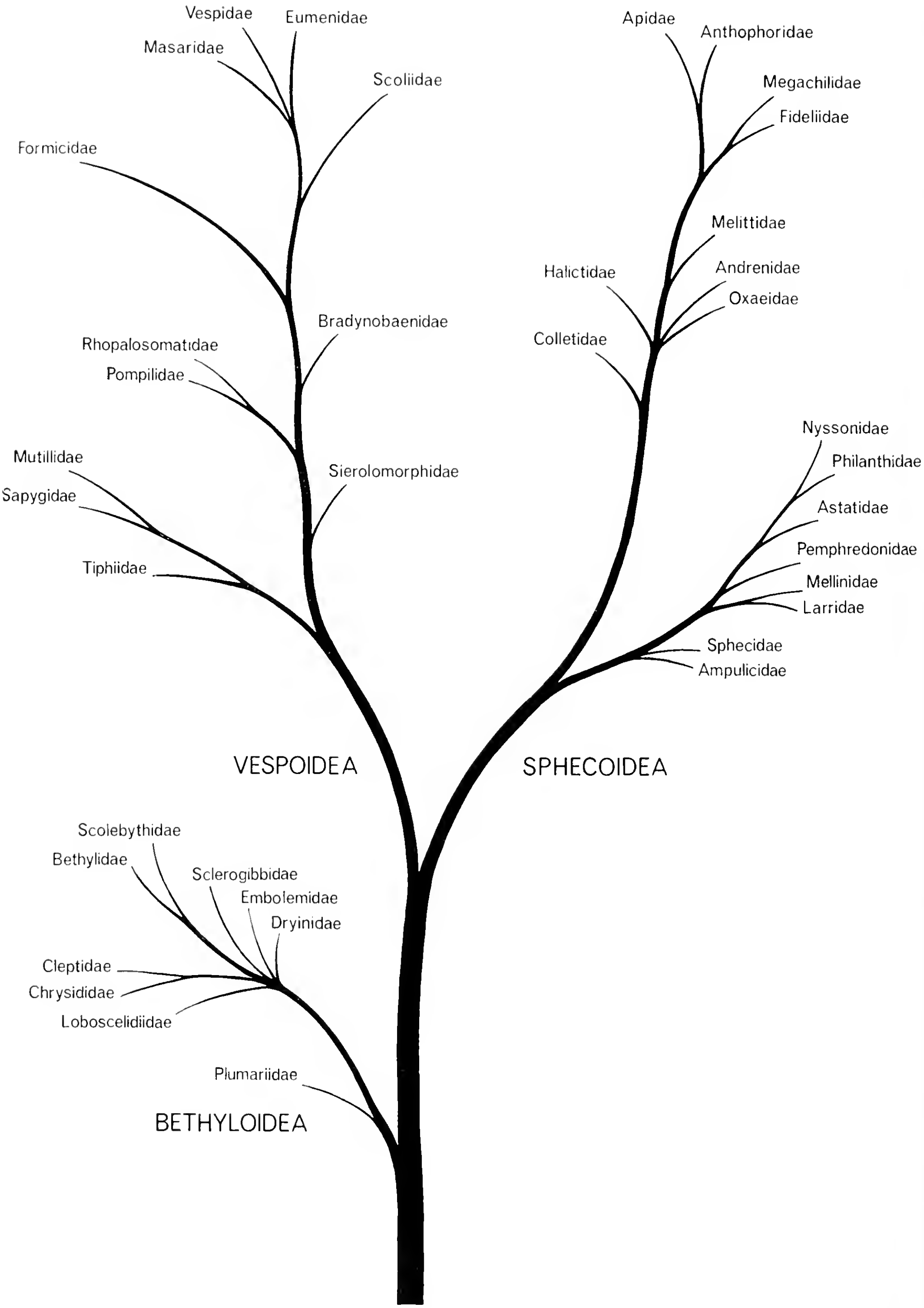


FIG. 67. Phylogeny of the families of Hymenoptera Aculeata (relationships within the Vespoidea from the present study; within the Sphecoidea from Michener, 1974, for the Apiformes, and Evans, 1964b, for the Spheciformes; within the Bethyloidea from the present study and personal impressions).

families: Tiphiidae, Sapygidae, Mutillidae, Sierolomorphidae, Pompilidae, Rhopalosomatidae, Scoliidae, Masaridae, Eumenidae, Vespidae and Bradynobaenidae in the Vespiformes, and Formicidae in the Formiciformes.

The phylogeny of the Aculeata to the level of family thus appears as in Fig. 67.

INVESTIGATION OF THE MYRMOSID-MUTILLID COMPLEX (MUTILLIDAE)

The methods used in the study of the myrmosid-mutillid group were similar to those utilized in the study of the entire Aculeata. Initially, all available specimens (approximately 10,000, in about 1250 species and including representatives of 89 per cent of the valid described genera and subgenera as well as many undescribed genera) were surveyed for about 50 characters, mainly ones which had been used previously to differentiate members at the generic and suprageneric levels. (The material examined is summarized in Table III. This is actually a highly conservative estimate since the extensive collections of many museums on four continents were also surveyed, but only the most significant specimens were borrowed and thus included in the figures given here.) This survey demonstrated that many characters were highly variable, and these were discarded. New characters were discovered and incorporated. On the basis of the initial survey, and considering published views such as those of Bischoff (1920-21) and Schuster (1947, 1949), members of 135 genera and subgenera of mutillids were tentatively grouped into 16 suprageneric complexes and these were surveyed with respect to 46 characters. At this point various genera (or subgenera) showed identical distributions of the character states and many such superfluous members were discarded, one genus generally being retained for each such set of concordant states. Wagner trees (by electronic computer) and cladograms (by hand) were constructed, and characters having states with many independent origins or reversals were discarded. Additional characters were discovered and added, and further groups showing concordance of character states were reduced to representative genera. Representatives of three genera of myrmosids were added and a few additional characters were introduced as a result.

The machine- and hand-derived cladograms were then compared and refined as a few more characters were added, eliminated or coding was modified. Finally, identical cladograms based on 43 characters (involving 61 derived states) were derived both by the machine and by hand. When the characters were allocated to two data sets, one containing the 20 characters of females and the other those of males, and cladograms were derived using these data sets independently, the resulting schemes were fully compatible although not identical because of the lack of characters for females on two of the internodes. A final check was made that the character states differentiating each taxon on the tree were present in all the genera and subgenera represented by that taxon.

States of the Characters Considered

The 43 "best" characters used in the analysis of the myrmosid-mutillid complex are listed below, with comments on their evolutionary patterns. This is followed by a listing of the characters which were eliminated during the analysis, with the reasons for their elimination. In both cases characters of females are listed before those of males, the applicable sex being indicated by the prefixes F (female) and M (male). Even in cases where characters are apparently identical in the two sexes, they have been considered separately be-

TABLE III. Genera and subgenera of Mutillidae, including the approximate number of species examined. (* indicates that the type species was seen. Information on synonymies and new sex associations will be presented elsewhere.)

MYRMOSINAE	Myrmosa (3 *spp.*,*; ♂, ♀; *incl.* Ischioceras) Myrmosina (1 *sp.*,*; ♂) Myrmosula (2 *spp.*,*; ♂, ♀) Protomutilla (1 *sp.*; ♀)
Not examined: Krombeinella (*incl.* Paramyrmosa *Suárez*), Leiomyrmosa, Morysmula, Paramyrmosa *Saussure.*	
PSEUDOPHOTOPSIDINAE	Pseudophotopsis (10 *spp.*; ♂, ♀; *incl.* Alloneurion, Ephutomma, Sphinctomutilla *André, 1899*)
TICOPLINAE	Areotilla (5 *spp.*,*; ♂, ♀) Nanomutilla (3 *spp.*,*; ♂, ♀) Smicromyrmilla (17 *spp.*; ♂, ♀)
Not examined: Ticopla.	
RHOPALOMUTILLINAE	Rhopalomutilla (13 *spp.*,*; ♂, ♀)
SPHAEROPTHALMINAE	
DASYLABRINI	Apteromutilla (4 *spp.*,*; ♂, ♀; *incl.* Apterotilla) Brachymutilla (7 *spp.*,*; ♂, ♀) Chrestomutilla (5 *spp.*,*; ♂, ♀) Dasylabris (28 *spp.*,*; ♂, ♀; *incl.* Allomutilla) Dasylabroides (21 *spp.*,*; ♂, ♀) Seyrigilla (1 *sp.*,*; ♀) Stenomutilla (16 *spp.*,*; ♂, ♀; *incl.* Xenomutilla) Tricholabiodes (14 *spp.*,*; ♂, ♀)
Not examined: Craspedopyga.	
SPHAEROPTHALMINI	
PSEUDOMETHOCINA	Ancipitotilla (1 *sp.*,*; ♂) Anomophotopsis (1 *sp.*,*; ♂) Atillum (9 *spp.*,*; ♂, ♀) Calomutilla (3 *spp.*,*; ♀) Darditilla (10 *spp.*; ♂, ♀) Dimorphomutilla (6 *spp.*; ♂, ♀) Euspinolia (11 *spp.*,*; ♂, ♀; *incl.* Reedia *Ashmead*) Gurisita (2 *spp.*,*; ♀) Hoplocrates (15 *spp.*,*; ♂, ♀; *incl.* Hoplomutilla *André*) Hoplognathoca (3 *spp.*,*; ♀) Hoplomutilla *Ashmead* (18 *spp.*,*; ♂, ♀; *incl.* Tilluma) Horcomutilla (6 *spp.*,*; ♀) Invreiella (3 *spp.*,*; ♀) Jamaitilla (1 *sp.*,*; ♂, ♀) Lynchiatilla (4 *spp.*; ♂, ♀) Mammomutilla (1 *sp.*,*; ♂) Mickelia (1 *sp.*; ♀) Myrmilloides (1 *sp.*,*; ♂, ♀) Pappognatha (5 *spp.*; ♂, ♀) Patquiatilla (1*sp.*,*; ♀) Pertyella (6 *spp.*,*; ♀) Pseudomethoca (23 *spp.*,*; ♂, ♀; *incl.* Nomiaephagus) Seabratilla (1 *sp.*,*; ♀) Sphinctopsis (33 *spp.*,*; ♂, ♀; *incl.* Sphinctomutilla *André, 1909*) Tallium (13 *spp.*,*; ♂, ♀) Vianatilla (1 *sp.*,*; ♀)
Not examined: Allotilla.	

TABLE III. Genera and subgenera of Mutillidae, including the approximate number of species examined. (* indicates that the type species was seen. Information on synonymies and new sex associations will be presented elsewhere.) (Continued.)

SPHAEROPTHALMINA	Acanthophotopsis (2 _spp._,*; ♂) Acrophotopsis (1 _sp._,*; ♂) Ascetotilla (8 _spp._,*; ♂, ♀) Bothriomutilla (1 _sp._,*; ♂, ♀) Cephalomutilla (7 _spp._: ♀) Ceratophotopsis (2 _spp._,*; ♂) Cystomutilla (2 _spp._,*; ♂, ♀) Dasymutilla (110 _spp._,*; ♂, ♀ ; _incl._ Bruesia, Pycnomutilla) Dilophotopsis (6 _spp._,*; ♂, ♀) Ephutomorpha _sensu stricto_ (6 _spp._,*; ♀) Eurymutilla (11 _spp._,*; ♂, ♀) Huacotilla (1 _sp._; ♀) Leucospilomutilla (1 _sp._,*; ♂, ♀) Limaytilla (4 _spp._,*; ♂, ♀) Lomachaeta (6 _spp._,*; ♂, ♀) Lophomutilla (3 _spp._,*; ♀) Lophostigma (6 _spp._: ♀) Micromutilla (7 _spp._,*; ♂, ♀) Morsyma (3 _spp._,*; ♂, ♀) Nanotopsis (1 _sp._,*; ♂) Neomutilla (3 _spp._,*; ♂, ♀) Odontophotopsis (16 _spp._,*; ♂ ; _incl._ Tetraphotopsis) Paramutilla (2 _spp._?,*?; ♂, ♀ ?) Periphotopsis (1 _sp._,*; ♂) Photomorphina _Schuster, 1952_ (8 _spp._: ♂, ♀ ; _incl._ Photomorphina _Schuster, 1958_) Photomorphus (3 _spp._,*; ♂, ♀) Photopsioides (5 _spp._,*; ♂, ♀) Physetapsis (1 _sp._,*; ♂) Photopsis (13 _spp._,*; ♂, ♀; _incl._ Agama _Blake_, Neophotopsis, Pyrrhomutilla) Protophotopsis (2 _spp._,*; ♂, ♀) Ptilomutilla (4 _spp._,*; ♀) Reedomutilla (4 _spp._,*; ♂, ♀ ; _incl._ Reedia _André_) Scaptodactyla (6 _spp._,*; ♂, ♀) Smicromutilla (1 _sp._,*; ♂, ♀) Sphaeropthalma (2 _spp._,*; ♂, ♀ ; _incl._ Sphaerophthalma) Suareztilla (6 _spp._; ♂, ♀) Tobantilla (4 _spp._: ♂, ♀) Traumatomutilla (31 _spp._,*; ♂, ♀) Xenophotopsis (1 _sp._,*; ♂) Xystromutilla (6 _spp._: ♂, ♀)

Not examined: Chasquitilla, Protophotopsiella, Xenomorphus.

In addition to other scattered undescribed genera, representatives of at least 20 undescribed genera from the Australasian region, mainly Sphaeropthalmina but a few Pseudomethocina, were examined.

MYRMILLINAE	Blakeius (2 _spp._,*; ♂, ♀ ; _incl._ Bisigilla) Ceratotilla (9 _spp._,*; ♂, ♀) Clinotilla (1 _sp._,*; ♂, ♀) Labidomilla (12 _spp._,*; ♂, ♀) Liomutilla (1 _sp._,*; ♀) Liotilla (1 _sp._,*; ♀) Myrmilla (10 _spp._,*; ♂, ♀ ; _incl._ Edrionotus, Eurygnathilla, Pseudomutilla, Rudia) Myrmotilla (1 _sp._,*; ♀) Odontotilla (9 _spp._,*; ♂, ♀) Platymyrmilla (1 _sp._,*; ♂, ♀) Pygomilla (6 _spp._,*; ♀)

TABLE III. Genera and subgenera of Mutillidae, including the approximate number of species examined. (* indicates that the type species was seen. Information on synonymies and new sex associations will be presented elsewhere.) (Concluded.)

	Sigilla (1 *sp.*,*: ♂, ♀) Spilomutilla (3 *spp.*: ♂, ♀) Squamulotilla (26 *spp.*: ♂, ♀) Viereckia (9 *spp.*,*: ♂, ♀)
Not examined: Omotilla, Saganotilla.	
MUTILLINAE MUTILLINI MUTILLINA	Hadrotilla (1 *sp.*,*: ♀) Mutilla (23 *spp.*,*: ♂, ♀; *incl.* Barymutilla, Pycnotilla, Ronisia) Odontomutilla (40 *spp.*: ♂, ♀; *incl.* Peringueya, Radoszkowskius) Tropidotilla (4 *spp.*,*: ♂, ♀)
Not examined: Physetopoda.	
SMICROMYRMINA	Antennotilla (4 *spp.*,*: ♂) Artiotilla (1 *sp.*,*: ♀) Aureotilla (2 *spp.*,*: ♂, ♀) Bisulcotilla (1 *sp.*,*: ♂) Carinotilla (3 *spp.*: ♂, ♀) Chrysotilla (4 *spp.*: ♀) Corytilla (3 *spp.*: ♂, ♀) Ctenotilla (15 *spp.*,*: ♂, ♀; *incl.* Cephalotilla, Pseudocephalotilla) Dolichomutilla (7 *spp.*,*: ♂, ♀) Eremomyrme (6 *spp.*: ♂) Glossotilla (16 *spp.*,*: ♂, ♀) Gynandrotilla (2 *spp.*: ♂) Lophotilla (4 *spp.*: ♂, ♀) Mimecomutilla (3 *spp.*,*: ♂, ♀) Pristomutilla (10 *spp.*: ♂ ?, ♀) Promecilla (18 *spp.*,*: ♂, ♀) Psammotherma (2 *spp.*,*: ♂) Smicromyrme (100 *spp.*,*: ♂, ♀) Spinulotilla (6 *spp.*,*: ♂, ♀) Sulcotilla (3 *spp.*,*: ♂, ♀) Timulla (175 *spp.*,*: ♂, ♀; *incl.* Lobotilla, Trogaspidia) Trispilotilla (5 *spp.*: ♂, ♀)
Not examined: Hildebrandtia, Rhombotilla, Sylvotilla, Zeugomutilla. Chaetotilla *probably also falls here.*	
EPHUTINI	Ephuamelia (1 *sp.*: ♂) Ephuchaya (1 *sp.*,*: ♂) Ephuscabra (1 *sp.*,*: ♂) Ephusuarezia (2 *spp.*: ♂, ♀ ?) Ephuta (50 *spp.*,*: ♂, ♀; *incl.* Ephutopsis) Xenochile (1 *sp.*: ♂)
Not examined: Arcasina.	

cause the distribution of the various states often differs in the females from that in the males. (See below for treatment in calculations, however.) Some of the less useful characters that had been used in the study of the Aculeata and which differentiate the myrmosids and mutillids (e.g., subtle differences in the form of the posterolateral angle of the pronotum, extent of the mesopleural sulcus, length of the metanotum, size of the seventh metasomal sternum and hypopygium, all in the male) were not included here at any stage. The system of coding for the various states is as for the investigation of the Aculeata. The names of taxa are those used in the final classification resulting from consideration of these data. (The final cladogram appears after the figures of characters, as Fig. 92.)

Characters Utilized for Derivation of the Final Cladogram

F1. *Ocelli.* Primitively, the ocelli are well-developed or at least readily distinguishable. F1.1—The ocelli are completely obliterated and indistinguishable.

Presence of ocelli is considered primitive because this is the condition found generally throughout the Aculeata including the taxa most closely related to the Mutillidae.

Loss of the ocelli in apterous forms is common throughout the Insecta. Such loss is characteristic of all Mutillidae except some Myrmosinae (ocelli present in species of *Myrmosa*) and a few species of *Pseudophotopsis* (Pseudophotopsidinae). Thus state F1.1 has been derived within the Myrmosinae and at least twice within the remaining Mutillidae, once within *Pseudophotopsis* and once on the line leading to all other Mutillidae. Nevertheless, the derived state appears only once on the tree, on internode 2-3. In view of its multiple derivations, state F1.1 cannot be considered strong evidence for the holophyletic nature of the Mutillidae above *Pseudophotopsis,* but indeed the presence of the primitive condition in many species of Myrmosinae and Pseudophotopsidinae serves to emphasize the basal position of those taxa.

F2. *Eye form.* Primitively, the compound eye is somewhat flattened in profile, merging smoothly with the surrounding cuticle, and is also broadly oval in outline. F2.1—The compound eye is highly convex in profile, strongly differentiated from the surrounding cuticle and approximately hemispherical, being more or less circular in outline.

A flattened, ovate eye is considered primitive because this is the condition in most Aculeata and in particular those taxa most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae).

Although there is a tendency for the eye to be circular in a few groups where it is also reduced in size (e.g., *Rhopalomutilla, Nanomutilla*), the specialized hemispherical form of the eye has apparently evolved only once, in the Sphaeropthalmini, and is characteristic of almost all members of this tribe. In a few related genera (e.g., *Euspinolia, Tallium, Atillum, Hoplocrates*) the eye has become somewhat flattened once more although retaining some of the other characteristics of the tribe such as the basically circular shape. Despite this apparent partial reversal within the Sphaeropthalmini, state F2.1 provides strong evidence for the holophyletic origin of this taxon.

F3. *Eye pubescence.* Primitively, the compound eye is pubescent, bearing setae set into minute pores between the ommatidia. The setae may be prominent at relatively low magnification or they may be essentially indistinguishable although the pores may be discerned. F3.1—The compound eye is completely glabrous and all pores are lost.

A pubescent eye is considered primitive because most groups of Aculeata have eyes which are either obviously pubescent or which have well-developed pores bearing minute setae. In particular this is true of the Fedtschenkiinae and most Tiphiidae, the taxa most closely related to the Mutillidae.

Loss of pubescence and pores in the compound eye has apparently occurred at least twice, in the Pseudophotopsidinae and on internode 3-4, so that the only groups with the eye prominently pubescent or with pores are the Myrmosinae and Ticoplinae. Within the latter group *Areotilla, Nanomutilla* and *Ticopla* all have the eyes with dense and quite long setae (as do the Myrmosinae), whereas *Smicromyrmilla* has the setae reduced but still possesses a few pores in most species. The presence of the primitive state in the Ticoplinae is thus significant in emphasizing the relatively basal position of this taxon, rather than the derived state being useful in defining holophyletic groups.

F4. *Maxillary palpus.* Primitively, the maxillary palpus consists of six segments. F4.1—The maxillary palpus comprises only two segments.

A six-segmented maxillary palpus is considered primitive because this is the condition in most Aculeata, including the taxa most closely related to the myrmosid-mutillid group, and also in practically all members of this group.

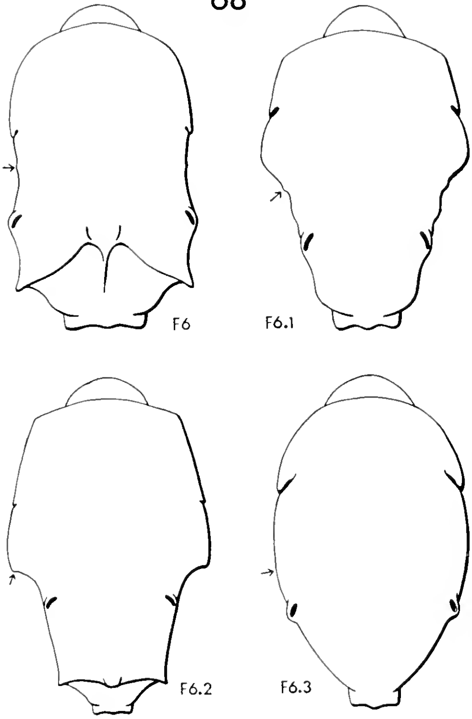
Reduction of the maxillary palpus in the female to two segments has occurred in only one genus, *Rhopalomutilla,* and so serves to emphasize the distinctness of the Rhopalomutillinae rather than to establish any higher groupings.

F5. *Labial palpus.* Primitively, the labial palpus consists of four segments. F5.1—The labial palpus is reduced to two segments.

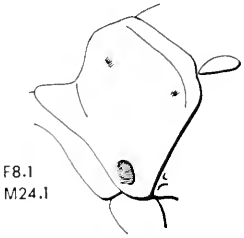
A four-segmented labial palpus is considered primitive because this is the condition in almost all Aculeata, including those taxa most closely related to the Mutillidae, and also in most members of this family.

Reduction of the labial palpus to two segments in the female has occurred once only, in the Rhopalomutillinae, thus not providing any essential information on higher level groups.

68



69



Figs. 68-69. Characters of Mutillidae. 68, mesosoma of female, dorsal view, showing primitive and derived states of form, with position of second spiracle arrowed (F6 based on *Areotilla;* F6.1 on *Sphaeropthalma;* F6.2 on *Rhopalomutilla;* F6.3 on *Ephuta*); 69, prothorax, lateral view, showing derived state of pronotal pit (F8.1, M24.1 based on *Pseudophotopsis*).

F6. *Form of mesosoma* (Fig. 68). Primitively, the mesosoma has an approximately constant width although subtle variations may involve depression of the mesopleuron and/or lateral expansion of the propodeum. Thus the mesosoma is more or less parallel-sided, narrower at the mesopleural level than elsewhere or broader posteriorly than anteriorly. F6.1—The mesopleuron is protuberant at about half its length, predominantly as a result of broad development of the mesopleural ridge which is dorsally separated from the prothoracic spiracle. The mesosoma thus broadens behind the prothoracic spiracle and then narrows from a point some distance anterior to the second mesosomal spiracle, the metapleural-propodeal region being narrower than the pronotum. F6.2—The metapleuron and lateral face of the propodeum are somewhat depressed and the mesopleuron is very slightly protuberant. The mesosoma thus broadens gently and evenly from the anterolateral angle of the pronotum to a point at the approximate level of the second mesosomal spiracle, behind which it is abruptly constricted. F6.3—The mesosoma is oval with the mesopleuron very slightly protuberant although the mesopleural ridge is undeveloped. The mesosoma is thus evenly broadened from the anterolateral region of the pronotum to the mesosomal midpoint and then evenly narrowed to the posterior region of the propodeum which is about as wide as the pronotum.

An approximately parallel-sided mesosoma is considered primitive because this is the condition in the Myrmosinae which are considered to occupy a basal branch on the cladogram on the basis of other characters. It is also the condition in some of the less-derived members of the Ticoplinae such as *Areotilla* and *Nanomutilla,* this being a group with many other characters in the primitive states. The primitive state also includes some variations in mesosomal form that occur in various genera but do not characterize particular groups. The particular derived states considered seem to involve the most distinct modifications, each having originated independently.

Some of the variations included in the primitive type have occurred sporadically. For example, the mesopleuron is somewhat depressed in *Pseudophotopsis* (Pseudophotopsidinae), *Squamulotilla* (Myrmillinae) and *Aureotilla* (Mutillini), amongst others; the propodeum is broadened in *Smicromyrmilla* (Ticoplinae), *Labidomilla* (Myrmillinae) and some *Timulla* (Mutillini). State F6.1, by contrast, is characteristic of a single group, the Sphaeropthalminae, having arisen on internode 5-6. It is thus a useful state establishing this group as holophyletic. Unfortunately, the strength of this state is slightly lessened by the fact that the mesopleuron is somewhat similarly expanded in *Odontomutilla* (Mutillini) in which, however, the propodeum is not markedly narrower than the pronotum. State F6.1 is also slightly modified in the Pseudomethocina, a subgroup of the Sphaeropthalmini, mainly by a slight dorsal flattening and anterior displacement of the mesopleural ridge.

State F6.2 is present only in *Rhopalomutilla* and state F6.3 is characteristic of the various members of the Ephutini only. These states are thus of minimal use in establishing higher groups. Actually the various forms of the mesosoma in the female are difficult to describe and are more distinct than might be indicated by the particular designation of derived states. Thus the Pseudophotopsidinae, Myrmillinae and Mutillini also have somewhat characteristic forms of the mesosoma although these are impossible to describe and code adequately.

F7. *Pro-mesonotal suture.* Primitively, the suture between the pronotum and mesonotum is freely articulating and is approximately straight. F7.1—The pro-mesonotal suture, although distinct, is fused and immovable and is also strongly curved so that the posterior margin of the pronotum is concave. F7.1.1—The pro-mesonotal suture is obliterated and indistinguishable (at least dorsally) or is barely indicated by a slight variation in sculpturing, when it is seen to be strongly curved.

An articulating pro-mesonotal suture is considered primitive because this is the condition in other Aculeata and almost all male mutillids. An approximately straight posterior margin to the pronotum is also considered primitive because this is the situation in those taxa most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae).

Fusion of the pro-mesonotal suture has occurred in the Aculeata only in the Mutillidae and is characteristic of the entire family except for the Myrmosinae. Strong concavity of the posterior margin of the pronotum is found in a number of the generally more derived taxa in the Aculeata and this condition is also characteristic of almost all the Mutillidae. Thus, state F7.1 arose once only, on internode 1-2, and is a very strong indicator of the holophyletic nature of the six higher subfamilies of the Mutillidae. Further obliteration of the pro-mesonotal suture (F7.1.1) has occurred on internode 2-3, thus providing further strong evidence of the holophyletic origin of the remainder of the family and emphasizing the low position of the Pseudophotopsidinae within the family. Although the position of the suture is sometimes discernible because of slight variations in sculpturing (e.g., some species of *Dasylabris, Neomutilla*), this condition is obviously more advanced than that in all species of *Pseudophotopsis* and cannot be confused with it, despite the fact that a few pseudophotopsidines have the fusion more developed than others.

F8. *Pronotal pit* (Fig. 69). Primitively, the pronotum is more or less evenly sculptured without any specialized pitlike structures. F8.1—The pronotum has a shallow pit at the ventral angle, which is filled with setae forming a structure similar to that on the first metasomal tergum in *Paratiphia* or the second metasomal tergum in some species of *Odontomutilla*, so that it may be analogous to the felt lines of the second metasomal segment.

A simple pronotum is considered primitive because this is the condition in practically all Aculeata, including the taxa most closely related to the mutillids, and also in most of the Mutillidae.

The development of specialized ventral pits on the pronotum has occurred in only one genus, *Pseudophotopsis*, so that this is a strong character separating the Pseudophotopsidinae from the remaining Mutillidae but it is not of any use in

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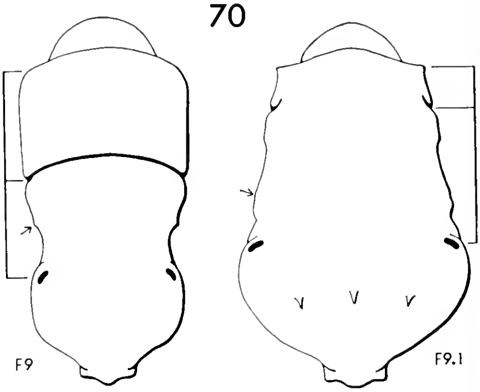

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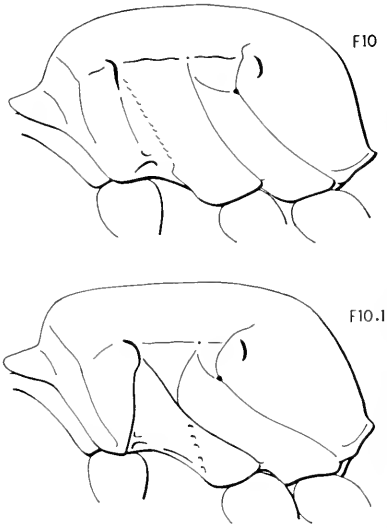


Figs. 70-71. Characters of Mutillidae. 70, mesosoma of female, dorsal view, showing primitive and derived states of length of pronotum, with position of second spiracle arrowed (F9 based on *Myrmosa;* F9.1 on *Labidomilla*); 71, mesosoma of female, lateral view, showing primitive and derived states of meso-metapleural suture (F10 based on *Myrmilla;* F10.1 on *Smicromyrme*).

establishing holophyletic groups at the higher levels.

F9. *Length of pronotum* (Fig. 70). Primitively, the dorsolateral margin of the pronotum is about as long as the distance between the prothoracic and propodeal spiracles. F9.1—The dorsolateral margin of the pronotum is much shorter than (about two-thirds the length of) the distance between the prothoracic and propodeal spiracles.

A long pronotum (laterally) is considered primitive because the pronotum in *Fedtschenkia* and most of the generalized Aculeata such as the Anthoboscinae is quite long and well-developed. Shortening of the pronotum has occurred in various of the more derived groups of the Aculeata.

Shortening of the pronotum in the female has apparently occurred only once in the Mutillidae, on internode 4-5, and is thus characteristic of most members of the family, excepting only the four most basal subfamilies. This is thus quite a good indication of the holophyletic origin of the three higher subfamilies. Its strength is, however, perhaps diminished by the fact that a superficially similar derived state has occurred within the Myrmosinae (e.g., in *Myrmosula*), although here the apparent reduction in size of the pronotum appears to have resulted from a posterior displacement of the propodeal spiracle. The similarity to state F9.1 may thus be more apparent than real in this case.

This measure for describing the lateral shortening of the pronotum was chosen for convenience, but it cannot express the complex changes in proportion which occur in the mesosoma as a whole (such as have apparently occurred in *Myrmosula*). The change which has taken place on internode 4-5 is actually more distinct than might be thought from the description alone, and consideration of the mesosoma as a whole strengthens the use of this character.

F10. *Meso-metapleural suture* (Fig. 71). Primitively, the meso-metapleural suture passes from a point just posterior to the midcoxa dorsally directly to the second mesosomal spiracle, and is approximately straight. This suture is thus also separated from the dorsoventral mesopleural ridge. In some cases the meso-metapleural suture is slightly anteriorly curved and approaches the mesopleural ridge, usually if this ridge is dorsally separated from the prothoracic spiracle and thus somewhat posteriorly shifted. F10.1—The meso-metapleural suture passes anterodorsally from the midcoxa and becomes continuous with the mesopleural ridge which is dorsally contiguous with the pronotal spiracle. The dorsal section of the meso-metapleural suture (between the mesopleural ridge and the second mesosomal spiracle) is at an acute angle to the ventral section. In many instances the dorsal section of the meso-metapleural suture and the ventral portion of the mesopleural ridge are obliterated so that there is an apparently continuous suture extending from a point just posterior to the mid-coxa anterodorsally to the prothoracic spiracle. [These modifications were first noted by Reid (1941) who considered the mesopleural ridge to be the prepectal suture. His interpretation of the evolutionary sequence was also slightly different since he considered the mesopleural ridge to be primitively separated from the prothoracic spiracle.]

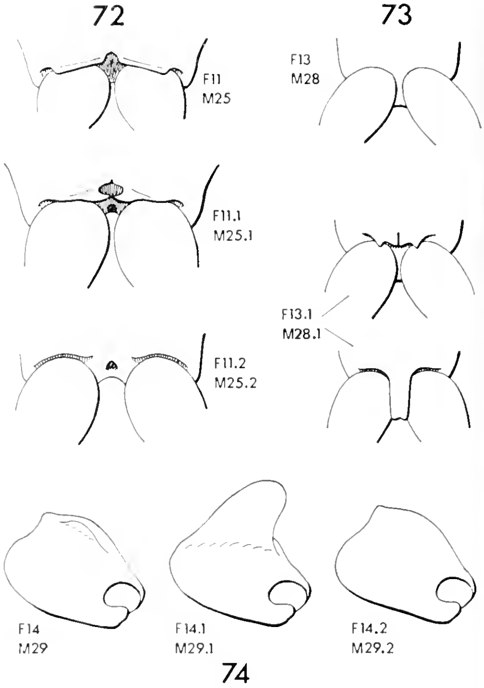
An approximately straight meso-metapleural suture is considered primitive because this is the condition in most other members of the Aculeata, including those taxa most closely related to the Mutillidae, and also in mutillid males, especially those of the more generalized subfamilies (but see character M26).

Strong angulation of the meso-metapleural suture is characteristic of all genera of Mutillini except for *Odontomutilla* in which this state is approached but where the mesopleural ridge is separated from the prothoracic spiracle dorsally, this apparently secondary condition obscuring the situation. State F10.1 is thus shown on the cladogram on the branch leading to the Mutillini despite the fact that it is not definitely present in *Odontomutilla* (which falls into the Mutillini by virtue of a combination of different characters). This state is also considered to be good evidence for the holophyletic derivation of the Mutillini, the significance of which is increased by the fact that this is one of the largest tribes of the family.

F11. *Mesosternal teeth* (Fig. 72). Primitively, the mesosternum bears a simple transverse carina anterior to each mid-coxa. F11.1—The mesosternum has a pair of toothlike projections, one anterior to each mid-coxa, being elaborations of the primitive carinae. F11.2—The mesosternum is simple, without any protuberances or carinae.

A mesosternum with simple carinae is considered primitive because this is the condition in the Fedtschenkiinae and is the precursor to the state in the Tiphiidae, these being the taxa most closely related to the Mutillidae.

The presence of small dentate projections on the mesosternum anterior to the coxae in females (F11.1) is characteristic only of *Pseudophotopsis*. Since this is an autapomorphic state, it does not provide any data on higher groupings. By contrast, loss of the carinae (F11.2) is characteristic of the females of Myrmosinae and also of the remaining Mutillidae, the latter derivation having occurred on internode 2-3. Since this state has occurred twice, it is not a strong indicator on which to base higher groups. Furthermore, a state somewhat similar to the primitive one has been redeveloped in some of the more highly derived members of the Sphaeropthalmina (e.g., *Ascetotilla* and some other genera in the "*Ephutomorpha* complex"), further weakening this state.



Figs. 72-74. Characters of Mutillidae. 72, posterior region of mesosternum, ventral view, showing primitive and derived states of mesosternal teeth (F11, M25 based on *Myrmosa*, ♂; F11.1, M25.1 on *Pseudophotopsis*, ♂; F11.2, M25.2 on *Areotilla*, ♂); 73, posterior region of metasternum, ventral view, showing primitive and derived states of metasternal process (F13, M28 based on *Myrmosa*, ♂; F13.1, M28.1 on *Dasylabris*, ♂, and *Hoplocrates*, ♂, top to bottom; 74, hind coxa, showing primitive and derived states (F14, M29 based on *Pseudophotopsis*, ♂; F14.1, M29.1 on *Myrmosa*, ♂; F14.2, M29.2 composite).

F12. *Contiguity of mid-coxae.* Primitively, the mid-coxae are contiguous mesally. F12.1—The mid-coxae are slightly separated and do not contact each other along the midventral line.

Contiguous mid-coxae are considered primitive because this is the condition in the Myrmosinae and Pseudophotopsidinae, which are the taxa considered to be the most basal on the cladogram on the basis of other characters.

Separated mid-coxae are characteristic of the entire Mutillidae except for Myrmosinae and Pseudophotopsidinae, so that state F12.1 provides good evidence for the holophyletic nature of the Mutillidae above internode 2-3. The strength of this character is, however, somewhat diminished by the fact that the middle coxae show various degrees of contiguity or separation throughout the Aculeata.

F13. *Metasternal process* (Fig. 73). Primitively, the metasternum is simple and flattened anteromesal to the hind coxa. F13.1—The metasternum bears a process anteromesal to each hind coxa. This may be a transverse carina, or the mesal extremity of this carina may be produced as a tooth which may be fused with the process of the opposite side to form a single mesal projection on the metasternum.

A simple metasternum is considered primitive because this is the condition in the Sapygidae, the sister group of the Mutillidae. Although there is slight development of a mesal longitudinal ridge in *Fedtschenkia,* this is developed anterior to the position of the protuberances involved in state F13.1 and is furthermore obviously not a paired structure. A simple metasternum is also present in the Myrmosinae, which forms a basal branch of the cladogram on the basis of other characters.

A dentate metasternum is characteristic of the entire family Mutillidae except for the Myrmosinae. Since this state is apparently unique in the Aculeata, it provides very good evidence of the holophyletic nature of the group above internode 1-2. This may, however, not be quite as strong as at first considered since the metasternum is apparently somewhat plastic elsewhere in the Aculeata and has been modified in various ways.

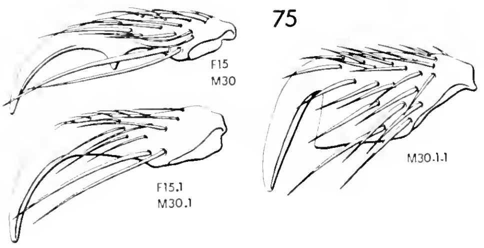
F14. *Hind coxal tubercle* (Fig. 74). Primitively, each hind coxa bears a carinate tubercle dorsally. F14.1—Each hind coxa bears a lamellate process dorsally. F14.2—Each hind coxa is simple, without any dorsal tubercle or lamella.

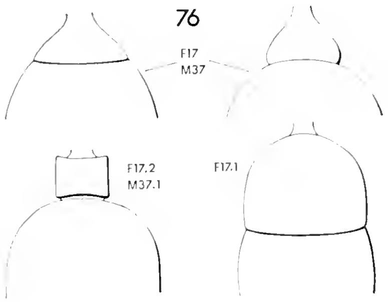
The presence of a carinate tubercle on the hind coxa is regarded as primitive because this is the condition in the Fedtschenkiinae, which is the group most closely related to the Mutillidae, and also in most of the basal members of the Mutillidae (so considered in the light of other characters).

Elaboration of the hind coxal carina into a lamellate process (F14.1) is uniquely characteristic of the Myrmosinae and is thus an important character state differentiating this group. Loss of the coxal tubercle is often difficult to establish with certainty since the tubercle is never very highly developed even when obviously present. Nevertheless, a hind coxal tubercle is definitely present in *Pseudophotopsis, Areotilla* and *Smicromyrmilla.* The small size of *Nanomutilla* makes determination very difficult, but a tubercle does appear to be present in this genus and in *Rhopalomutilla* also. Thus state F14.2 appears to have evolved once only, on internode 4-5. In view of the difficulties involved in determining the condition of the hind coxa and since it seems likely that such insignificant structures may have been lost on various occasions, the presence of state F14.2 should probably not be regarded as of great significance in establishing the holophyly of the Mutillidae above internode 4-5. Instead, the presence of the primitive state in three subfamilies serves to emphasize the basal position of these.

F15. *Tarsal claws* (Fig. 75). Primitively, each tarsal claw bears a sharp tooth about halfway along the ventral margin. F15.1—Each tarsal claw is simple, the ventral tooth having been lost.

A toothed tarsal claw is considered primitive because this is the condition in most Aculeata and in particular those taxa most closely related to the Mutillidae, a





Figs. 75-76. Characters of Mutillidae. 75, claw, showing primitive and derived states (F15, M30 based on *Pseudophotopsis*, ♀; F15.1, M30.1 on *Mutilla*, ♀; M30.1.1 on *Rhopalomutilla*, ♂); 76, base of metasoma, dorsal view, showing primitive and derived states of form of first segment (F17, M37 composite; F17.2, M37.1 based on *Ephuta*, ♀; F17.1 on *Rhopalomutilla*, ♀).

single tooth being present in Fedtschenkiinae and many Tiphiidae.

Simple tarsal claws in the female are characteristic of the entire subfamily Myrmosinae and all other Mutillidae except for the Pseudophotopsidinae, having been derived in the latter instance on internode 2-3. State F15.1 has thus arisen on two occasions within the myrmosid-mutillid group, and also elsewhere in the Aculeata; its presence is thus not particularly good evidence for the association of most of the Mutillidae into a single holophyletic group. Instead, the presence of the primitive condition in *Pseudophotopsis* again serves to emphasize the basal position of this taxon.

F16. *Arolium*. Primitively, the arolium is well-developed, forming a definite padlike structure between the tarsal claws and being distinct under magnifications of 50× or less. F16.1—The arolium is obliterated (or at least extremely reduced) so that no such structure is distinguishable, even at magnifications of 100×.

A well-developed arolium is considered primitive because this is the condition in most Aculeata, including the Fedtschenkiinae and Anthoboscinae, those groups most closely related to the Mutillidae.

Complete loss of arolia has occurred on a single occasion, this condition being characteristic of the Myrmosinae. Within the other Mutillidae there is some variation in the degree of development of the arolia. These are most reduced (but nevertheless still distinct) in, for example, *Pseudophotopsis* (Pseudophotopsidinae) and *Reedomutilla* (Sphaeropthalmina).

F17. *Form of first metasomal segment* (Fig. 76). Primitively, the first metasomal segment (especially the tergum) is gradually and evenly broadened posteriorly and merges more or less smoothly in contour with the second. Although it may be somewhat constricted apically and narrower than the second, the first segment is never predominantly cylindrical (parallel-sided). F17.1—The first metasomal segment (notably the tergum) is much enlarged and almost parallel-sided, approximately as broad as the second segment and more than half its length. F17.2—The first metasomal segment, and especially the tergum, forms a constricted cylinder which is much narrower than and less than one quarter the length of the second segment.

A flaring first metasomal segment is considered primitive because this is the most widespread form amongst the Aculeata and in particular those taxa most closely related to the Mutillidae.

Both derived states are uniquely characteristic of single taxa on the cladogram. F17.1 is present only in the Rhopalomutillinae and F17.2 characterizes the tribe Ephutini. Since these are autapomorphic states, they do not provide useful information on the grouping of the higher taxa but merely emphasize the specializations of the particular taxa involved.

F18. *Base of first metasomal tergum* (Fig. 77). Primitively, the first metasomal tergum is simple basally without any lateral protuberances. F18.1—The first metasomal tergum bears a pair of protuberances, one on each side, at the base, forming "auricles" which tend to cup the apex of the propodeum.

A simple first metasomal tergum is considered primitive because this is the condition in most Aculeata, and in particular in those taxa which are most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae).

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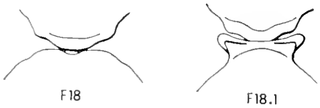

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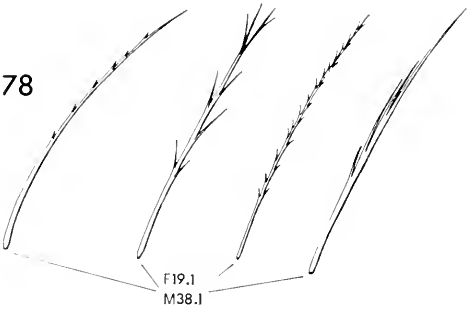

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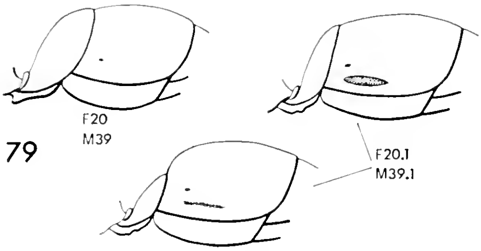


Figs. 77-79. Characters of Mutillidae. 77, articulation of meso- and metasoma of female, dorsal view, showing primitive and derived states of base of first metasomal tergum (F18 based on *Myrmosa;* F18.1 on *Pseudophotopsis*); 78, seta from first metasomal tergum, showing derived state of pubescence (F19.1, M38.1 based on *Cystomutilla, Dasymutilla, Reedomutilla, Bothriomutilla,* left to right); 79, anterior region of metasoma, lateral view, showing primitive and derived states of tergal felt line (F20, M39 based on *Areotilla,* ♀; F20.1, M39.1 on *Odontomutilla,* ♀, and *Smicromyrme,* ♀, top to bottom).

The development of auricles has apparently occurred only once. These structures are present in all members of the Mutillidae except for the Myrmosinae, so that state F18.1 was apparently derived on internode 1-2. The degree of development of the auricles varies, but they are smallest in the groups below internode 4-5, except for *Pseudophotopsis* where they are quite large. (This may in part be a result of the generally large body size of these species; the ancestral form may have been relatively small, if "Cope's Rule" is applicable—Stanley, 1973.)

F19. *Pubescence of first metasomal tergum* (Fig. 78). Primitively, all the pubescence is composed of simple, smooth setae. F19.1—Some erect setae at the base of the first metasomal tergum are plumose or subplumose, bearing fine branches. Much of the pubescence elsewhere on the body may also be plumose.

Simple pubescence is considered primitive because this is the condition in most Aculeata, including those groups most closely related to the Mutillidae.

Development of plumose pubescence has apparently occurred on a single occasion, being characteristic of the entire tribe Sphaeropthalmini. A few scattered genera within this group appear to have lost the plumosity, however (e.g., *Euspinolia, Atillum, Hoplocrates, Neomutilla, Cephalomutilla, Traumatomutilla*). Despite these few apparent reversals, the presence of state F19.1 is considered strong evidence for the holophyletic origin of the tribe Sphaeropthalmini. Although some species of *Stenomutilla* (Dasylabrini) have setae with trifurcate apices, their condition is unlike that in the Sphaeropthalmini and thus does not diminish the significance of this state.

F20. *Tergal felt line* (Fig. 79). Primitively, the second metasomal tergum is simple, without any development of specialized lateral felt lines or other secretory structures. F20.1—The second metasomal tergum bears a specialized felt line with recumbent setae and secretory pores, laterally on each side.

The absence of felt lines is considered primitive because this is the condition in most Aculeata, and in particular in the Sapygidae and Tiphiidae, those groups most closely related to the Mutillidae. Felt lines of similar form occur elsewhere only in the Bradynobaenidae, although some primitive bees (various Colletidae) possess foveae on the second metasomal tergum in a similar position, and these may be analogous to felt lines. The detailed anatomy of the felt lines in Mutillidae and Chyphotinae (Bradynobaenidae) has recently been elucidated by Debolt (1973).

A tendency toward development of felt lines on the second metasomal tergum appears to be characteristic of the family Mutillidae except for the Myrmosinae, although the actual development of such lines has apparently occurred on two occasions, once in *Pseudophotopsis* and again on internode 4-5. The presence of the felt line in a relatively basal taxon (Pseudophotopsidinae) as well as most higher members, indicates that its development is probably a general tendency in the family (at least above Myrmosinae). Since a tergal felt line has secondarily been lost in some higher genera (e.g., *Stenomutilla*, many *Ephuta*), it may be that the absence of the line is secondary in Ticoplinae and Rhopalomutillinae also. In both these groups there are, however, no traces of even rudimentary development of a felt line. It is thus more parsimonious to consider state F20.1 to have been fully expressed on two occasions rather than for it to have been developed on internode 1-2 and then to have been lost on two subsequent occasions (in the Ticoplinae and Rhopalomutillinae). Nevertheless, the "tendency toward" development of a tergal felt line may be visualized as having been uniquely derived on internode 1-2 (as in the above investigation of Aculeata), this being a fairly strong state uniting most Mutillidae. (The development of felt lines seems to be correlated with the derived states of characters F53r, F54r, M79r and M80r, which apparently do not occur in the Myrmosinae, so that the tendency toward development of felt lines is considered to have been established after the divergence of the Myrmosinae.)

M21. *Eye form.* Primitively, the compound eye in the male is somewhat flattened in profile, merging smoothly with the surrounding cuticle. M21.1—The compound eye is highly convex in profile, strongly differentiated from the surrounding cuticle and approximately hemispherical.

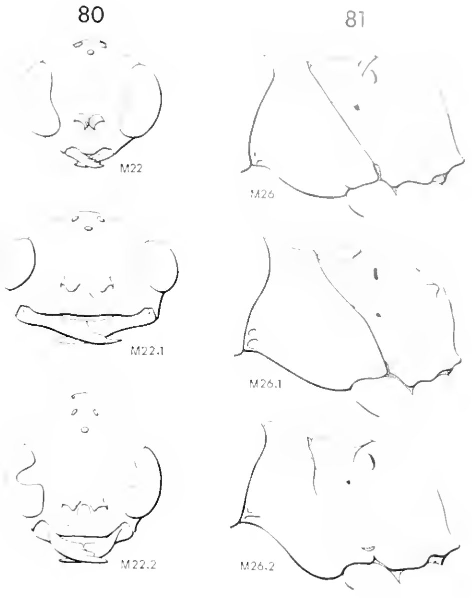
A flattened eye is considered primitive because this is the condition in most Aculeata and in particular those taxa most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae).

The specialized hemispherical form of the eye in the male parallels the development of a similar eye form in the female (F2.1) quite closely. Thus, all members of the Sphaeropthalmini have hemispherical eyes in the male also, except that *Cystomutilla* has this state somewhat less well-developed than in most of the other genera. In addition, the group including *Euspinolia*, *Tallium*, *Atillum* and *Hoplocrates* also has the eyes less protuberant than other Sphaeropthalmini, as in the females. In contrast to the females, the males of *Tricholabiodes* (Dasylabrini) also have well-developed and protuberant eyes, although they are less nearly circular than in the Sphaeropthalmini. This means that if state M21.1 evolved once only, then the Sphaeropthalmini and *Tricholabiodes* share a common ancestor not also shared with the remaining Dasylabrini. Alternatively, state M21.1 may have arisen twice, once in the ancestral Sphaeropthalmini and again in *Tricholabiodes.* Although there are no good characters indicating holophyly of the Dasylabrini, it seems that forms similar to *Tricholabiodes* (all the species of which are nocturnal and highly specialized) would probably have been too specialized to have given rise to the Sphaeropthalmini. Two separate derivations of state M21.1 thus seem the more probable. Independent development of this condition in *Tricholabiodes* was probably associated with their nocturnal habit since other nocturnal Aculeata often have the eyes larger and more protuberant than do their relatives (e.g., Brachycistidinae in the Tiphiidae, *Megalopta* in the halictid bees, and even *Pseudophotopsis* and *Eremomyrme* elsewhere in the Mutillidae to a lesser extent). Despite the uncertainty regarding the exact pattern of evolution of this character, state M21.1 provides quite good evidence for the holophyletic origin of the Sphaeropthalmini.

M22. *Eye shape* (Fig. 80). Primitively, the compound eye is broadly oval with the inner margin sinuately concave. M22.1—The compound eye is subcircular with the inner margin approximately evenly convex. M22.2—The compound eye is broadly oval with the inner margin strongly incised and emarginate, the angle of the emargination at its apex being less than 90°.

A broadly oval eye with sinuate inner margin is considered primitive because this is the condition in most Aculeata and in particular in those groups (such as Fedtschenkiinae and most Tiphiidae) which are most closely related to the Mutillidae.

An approximately circular compound eye with a convex inner margin in the male is characteristic only of the Sphaeropthalmini, so that state M22.1 apparently arose only once on the cladogram. However, a few genera (such as *Euspinolia* and *Tallium*) have eyes which are almost circular but with the inner margins very slightly sinuate. A few members of the Dasylabrini (such as *Apteromutilla, Brachymutilla* and *Dasylabroides*) also have the inner margins of the eyes convex although the eyes are not as nearly circular as in the Sphaeropthalmini. Actually, there seems to be a tendency toward reduction in the size of the eyes in many of the higher Mutillidae and especially in the Sphaeropthalminae, which sometimes makes accurate determination of the occurrence of state M22.1 difficult. Nevertheless, this does seem to be a fairly good indicator of the holophyletic nature of the Sphaeropthalmini.



Figs. 80-81. Characters of Mutillidae. 80, head of male, anterior view, showing primitive and derived states of eye shape (M22 based on *Smicromyrmilla;* M22.1 on *Ascetotilla;* M22.2 on *Rhopalomutilla*); 81, meso- and metapleura and propodeum of male, lateral view, showing primitive and derived states of meso-metapleural suture (M26 based on *Pseudophotopsis;* M26.1 on *Areotilla;* M26.2 on *Squamulotilla*).

Emargination of the eye (M22.2) is characteristic of the entire subfamily Mutillinae and thus arose on internode 7-8. A similar condition is, however, present in Rhopalomutillinae. *Areotilla* shows a marked tendency toward development of this state also, with *Smicromyrmilla* and *Nanomutilla* (all three Ticoplinae) having the inner margin slightly more deeply sinuate than in *Pseudophotopsis*. Thus the presence of state M22.2 in the Mutillinae is not as useful an indication of the association of the members of this subfamily as could be wished, although it is obvious that its occurrences in the Rhopalomutillinae and *Areotilla* were independent of its origin in the Mutillinae.

M23. *Eye pubescence.* This character shows the same pattern of evolution and occurrence as in the female (F3), with the derived state (M23.1) having occurred in all members of the Mutillidae except the Myrmosinae and Ticoplinae. It thus provides no additional information on higher groupings.

M24. *Pronotal pit* (Fig. 69). This character shows the same pattern of occurrence as in the female (F8), with the derived state (M24.1) being characteristic of the Pseudophotopsidinae. This condition was one of the main characters used by Schuster (1950) to associate the sexes of this group.

M25. *Mesosternal teeth* (Fig. 72). The states of this character are as for the female (F11), although their distribution is slightly different. The elaboration of the mesosternal carinae into dentate projections in the male (M25.1) coincides with a similar development in the female (F11.1), being found only in *Pseudophotopsis*. By contrast, the obliteration of the carinae (M25.2) has occurred in all other Mutillidae except for most Myrmosinae, unlike the situation in females. Thus, simple carinae are developed in the males of *Myrmosa* but they have been lost in *Myrmosula* (the condition in *Protomutilla* is unknown). State M25.2 thus appears only once on the cladogram, on internode 2-3. Nevertheless, its parallel occurrence within the Myrmosinae tends to weaken it, so that it should not be considered a particularly good indicator of the holophyletic nature of the Mutillidae above internode 2-3. It appears that there is never any redevelopment of mesosternal carinae or teeth in the males of the more highly derived Mutillidae similar to that in the females of *Ascetotilla* and other genera related to *Ephutomorpha*. A few genera in the *Sphaeropthalma* complex (such as *Odontophotopsis*) bear mesosternal teeth of varying types, but these are placed anterior to the position of the primitive carinae and are obviously not an expression of this character.

M26. *Meso-metapleural suture* (Fig. 81). Primitively, the meso-metapleural suture is approximately straight. M26.1—The meso-metapleural suture is curved posteriorly so that the hind margin of the mesopleuron is convex. M26.2—The meso-metapleural suture is sinuate so that the hind margin of the mesopleuron is concave over at least the ventral half and is convex dorsally; the metapleuron thus appears to be expanded anteriorly below the endophragmal pit.

An approximately straight meso-metapleural suture is considered primitive because this is the condition in those Aculeata most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae) and also in those groups considered on the basis of other characters to be the most basal on the cladogram (i.e., Myrmosinae, Pseudophotopsidinae).

A posteriorly curved meso-metapleural suture (M26.1) is found only in *Areotilla*, *Nanomutilla* and *Smicromyrmilla* so that this forms a very good characteristic establishing the Ticoplinae as a holophyletic group (the condition in *Ticopla* is, however, unknown to me). A sinuate meso-metapleural suture (M26.2) is characteristic of the entire Mutillidae except for the Myrmosinae, Pseudophotopsidinae and Ticoplinae. This state apparently arose uniquely on internode 3-4 and is thus a very useful indicator of the holophyletic origin of the four higher subfamilies.

M27. *Meso-metapleural "bridge"* (Fig. 82). Primitively, the meso- and metapleura are closely associated but not fused at any point. The anterior margin of the metapleuron is simple ventrally with only a slight protuberance approaching the hind margin of the mesopleuron but not contacting it. M27.1—The metapleuron ventrally bears a marked tubercle which is fused with a similar protuberance on the mesopleuron, so that a "bridge" is formed between these pleura which are additionally fused for some distance over their ventral halves.

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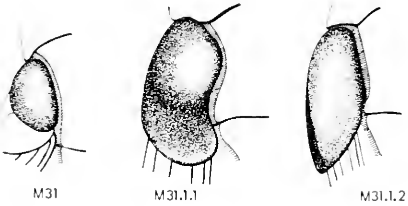

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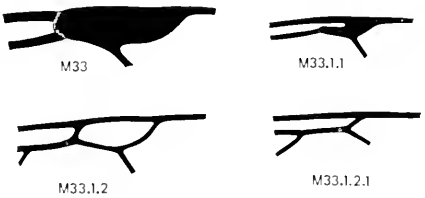

FIGS. 82-84. Characters of Mutillidae. 82, ventral region of meso-metapleural suture of male, lateral view, anterior to left, showing primitive and derived states of meso-metapleural "bridge" (M27 based on *Myrmosa*; M27.1 on *Squamulotilla*); 83, left tegula of male, dorsal view, showing primitive and derived states (M31 based on *Myrmosa;* M31.1.1 on *Odontomutilla;* M31.1.2 on *Ephuta*); 84, pterostigma of forewing, showing primitive and derived states (M33 based on *Pseudophotopsis;* M33.1.1 on *Viereckia;* M33.1.2 on *Dolichomutilla;* M33.1.2.1 on *Ephuta*).

A simple metapleuron not fused to the mesopleuron is considered primitive because this is the condition in most Aculeata and in particular in the Fedtschenkiinae and Tiphiidae, those taxa most closely related to the Mutillidae. The development of a slight protuberance at the anteroventral angle of the metapleuron has not occurred in these related taxa but is actually another derived state associating the myrmosid-mutillid complex, and is thus considered primitive for the complex.

The development of a meso-metapleural "bridge" is characteristic of all Mutillidae except for the Myrmosinae, Pseudophotopsidinae and Ticoplinae, in which there is merely a small tubercle ventrally on the metapleuron. Thus state M27.1 apparently arose on internode 3-4, strongly associating most of the Mutillidae into a holophyletic group.

M28. *Metasternal process* (Fig. 73). The evolution and occurrences of the various states of this character are the same as in the female (F13). Thus state M28.1 is characteristic of the entire Mutillidae except for the Myrmosinae, apparently having arisen on internode 1-2.

M29. *Hind coxal tubercle* (Fig. 74). The pattern of modifications of this character is the same as for the female (F14), so that state M29.1 is characteristic of the Myrmosinae, and M29.2 has apparently arisen on internode 4-5. As in the female, a tubercle is never very well-developed in the male, except in Myrmosinae, so that determination of the state involved is often difficult, reducing the significance of this character.

M30. *Tarsal claws* (Fig. 75). Primitively, each tarsal claw bears a sharp tooth about halfway along the ventral margin. M30.1—Each tarsal claw is simple, the ventral tooth having been lost. M30.1.1—Each tarsal claw is broadened into a dentate lamella basally but is simple apically, so that it appears cleft.

A tarsal claw with a single distal ventral tooth is considered primitive because most aculeates have toothed claws and this is the condition in the Fedtschenkiinae and many Tiphiidae, the groups most closely related to the Mutillidae. The subsequent development of a basal lamella is considered to be derived from the simple condition because this state is unlike that in most other Aculeata and also because it appears in only one sex of a single genus within the Mutillidae, a genus which seems on the basis of other characters to have arisen on the cladogram above the point of derivation of state M30.1.

Loss of the tooth on the tarsal claws of the male does not quite coincide with this condition in the female (F15.1). Thus, the males of Myrmosinae have armed claws whereas the females do not. State M30.1 has thus apparently arisen only once, on internode 2-3, being characteristic of all Mutillidae except for Myrmosinae, Pseudophotopsidinae and Rhopalomutillinae. The last group is uniquely characterized by possession of state M30.1.1. Thus state M30.1 is useful as an indicator of the holophyletic nature of the Mutillidae above Pseudophotopsidinae while M30.1.1 merely serves to emphasize the distinctness of the Rhopalomutillinae and does not aid in establishing higher groupings. This interpretation of the origin of the condition in the male of *Rhopalomutilla* differs from that of Schuster (1947) who considered it to be primitive and comparable to that in *Pseudophotopsis.*

M31. *Tegula* (Fig. 83). Primitively, each tegula is an evenly convex, subcircular sclerite with its hind margin not attaining the level of the transscutal suture. M31.1—Each tegula is posteriorly produced so that its hind margin exceeds the level of the transscutal suture, the tegula being subovate. M31.1.1—The hind margin of the elongate tegula is reflexed, forming a posterior upcurved rim. M31.1.2—The elongate tegula is longitudinally angulate basally so that it has two distinct surfaces approximately perpendicular to one another, at least anteriorly.

A short, evenly convex tegula is considered primitive because this is the condition in most Aculeata, including those groups most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae).

Elongation of the tegula (M31.1) is characteristic of the entire subfamily Mutillinae and has apparently arisen on the cladogram only once, on internode 7-8. Elongate tegulae are found in scattered genera elsewhere, however, but in these their form is generally not identical to that in the Mutillinae. Thus *Smicromyrmilla* has tegulae which reach the transscutal suture but do not exceed it, and *Nanomutilla* and *Areotilla* have tegulae which do exceed this line but which are mesally curved posteriorly, those in *Areotilla* in particular being very elongate and more or less reniform, a condition unlike that in the Mutillinae. (These modifications do, however, indicate that there is a tendency toward some type of tegular elongation in the Ticoplinae as a whole, but this does not appear on the cladogram. It does not fall into any of the designated states since it is rather indefinite.) A few of the more highly derived members of the Sphaeropthalmina, like *Bothriomutilla*, also have the tegulae posteriorly produced to or slightly beyond the level of the transscutal suture, but in these this appears to be partly the result of anterior displacement of this suture laterally, and the tegulae are not as elongate as in the

Mutillinae. The presence of state M31.1 is thus considered quite good evidence for the holophyletic origin of the Mutillinae.

State M31.1.1 is present only in the tribe Mutillini, although a few of the more derived members of the Sphaeropthalmina such as *Bothriomutilla* exhibit a similar tendency toward reflexion of the posterior margin of the tegula. Also, a few genera of Mutillini such as *Ctenotilla* and *Mimecomutilla* show a secondary reversal of this state with the hind margin of the tegula not upturned but forming a more or less extensive flat area. Despite these few anomalies, state M31.1.1 appears to be a strong indicator of the holophyletic nature of the tribe Mutillini.

State M31.1.2 is uniquely characteristic of the tribe Ephutini and is not approached elsewhere in the Mutillidae, thus providing good evidence of the holophyletic nature of this tribe but not proving useful in the establishment of any higher groupings.

M32. *Extent of venation of forewing.* Primitively, the venation of the forewing attains the distal margin of the wing membrane or ends only a very short distance from it. M32.1—The venation of the forewing is obliterated apically so that the longitudinal veins do not reach the distal margin of the membrane but end a considerable distance from it; although there may be dark lines which do almost attain the margin, these are merely pigmentary and not differentiated cuticular structures.

Venation attaining the apical margin of the forewing is considered primitive because this is the condition in those groups most closely related to the Mutillidae [viz., Sapygidae (although venation slightly retracted in *Fedtschenkia*) and Anthoboscinae].

Retraction of the venation of the forewing to end a considerable distance from the apical margin of the wing is characteristic of the entire family Mutillidae except for the Myrmosinae, and thus apparently arose on internode 1-2. Although this is a unique derivation here, a similar condition has occurred in various other groups of Aculeata, including some Tiphiidae, thus weakening this state somewhat as an indicator of the holophyletic nature of most of the Mutillidae. Instead its absence serves to emphasize the basal position of the Myrmosinae.

M33. *Pterostigma* (Fig. 84). Primitively, the pterostigma is entirely heavily sclerotized and thus not cell-like. M33.1—The pterostigma has the sclerotization reduced, somewhat more so anteriorly than posteriorly, so that it appears as a small cell bounded basally by vein SC and with vein R much heavier than vein C. M33.1.1—The pterostigma is apparently formed entirely by the relatively heavy vein R, the free section of vein SC being lost. M33.1.2—The pterostigma is entirely desclerotized, with all the bounding veins of approximately equal width. M33.1.2.1—The pterostigma is absent as a result of the loss of the free section of vein R (or its fusion with vein SC) eliminating any cell.

A completely sclerotized pterostigma is considered primitive because this is the condition in most Aculeata, including those taxa most closely related to the Mutillidae (e.g., Fedtschenkiinae, Anthoboscinae).

A pterostigma with the sclerotization reduced anteriorly (M33.1) is not found in any extant members. Since all the taxa subtended by internode 5-7 show some degree of pterostigmal desclerotization, all with conditions which are logically derivable from a state such as M33.1, this state may have arisen uniquely on this internode. State M33.1 is thus apparently a good indicator of the holophyletic nature of the group comprised of the Myrmillinae and Mutillinae, despite the fact that this state is hypothetical. There is actually a tendency toward a similar development in *Protophotopsis* (Sphaeropthalmina) although in this genus the reduction of sclerotization is more even, veins R and C being approximately equally heavy, both heavier than any of the other veins.

Loss of vein SC is characteristic of the entire subfamily Myrmillinae, although this state (M33.1.1) is not very obvious in some members where the reduction of sclerotization is not very marked (e.g., *Viereckia*) and the loss of vein SC merely results in a basal emargination of the pterostigma. Since this state is uniquely characteristic of all members of the subfamily, it is useful in establishing the holophyletic nature of the Myrmillinae but does not aid further in higher groupings.

Complete desclerotization of the pterostigma (M33.1.2) is found only in the Mutillinae and is thus a strong indicator establishing the holophyly of the group, having arisen on internode 7-8. Some slight uncertainty is introduced by the fact that the Ephutini is characterized by complete loss of the pterostigma, although this condition seems logically more readily derivable from a state such as M33.1.2 rather than from the primitive condition. Loss of the pterostigma in the Ephutini (M33.1.2.1) has apparently occurred as a result of the elimination of its apical region, whether by loss of vein R or by its fusion with vein SC cannot be established. In any case it is apparent that vein SC is retained since the "crossvein" joins vein SC+R just distal to the weak point in vein SC+R. This point is at the base of the pterostigma, just proximal to vein SC, in other mutillids. This loss of the pterostigma provides a strong indication of the holophyletic nature of the Ephutini. A superficially similar loss of the pterostigma has occurred in *Odontomutilla* (Mutillina) but in this case it is apparently the result of the obliteration of the free section of vein SC since the "crossvein" joins vein "SC+R" at a point some distance distal to the weak point in vein "SC+R."

M34. *Forewing cell 1S* (Fig. 85). Primitively, cell 1S (second submarginal) is sessile anteriorly, sharing a section of vein S with cell R (marginal). M34.1—Cell 1S is petiolate anteriorly, not reaching cell R (crossvein r-s reaches vein S distal to the junction of vein S and crossvein 1s-m).

A sessile cell 1S is regarded as primitive because this is the condition in most Aculeata, including those taxa most closely related to the Mutillidae (e.g., Fedtschenkiinae, Anthoboscinae).

A petiolate cell 1S is found only in the Ticoplinae where it is characteristic of all the genera (except perhaps for *Ticopla* where cell 1S is apparently lost). This state thus provides very good evidence of the holophyletic nature of this subfamily but does not aid further in higher level groupings. Elsewhere, state M34.1 is approached within the Myrmosinae (*Myrmosa* has cell 1S anteriorly acute and

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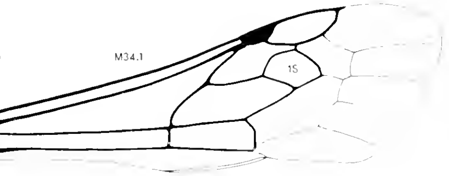

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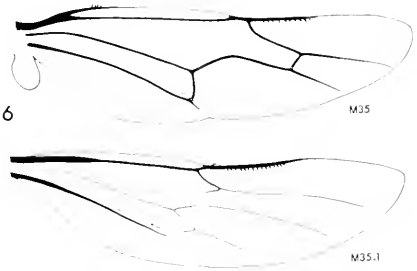

Figs. 85-86. Characters of Mutillidae. 85, forewing of male, showing derived state of cell 1S (M34.1 based on *Areotilla*); 86, hind wing of male, showing primitive and derived states of jugal lobe (M35 based on *Myrmosa;* M35.1 on *Areotilla*).

barely reaching cell R although not actually petiolate).

M35. *Jugal lobe* (Fig. 86). Primitively, the hind wing bears a small but well-differentiated jugal lobe basally. M35.1—The jugal lobe is completely lost so that the hind wing has a smooth posterior margin.

Presence of a jugal lobe is considered primitive because this is the condition in most Aculeata, including the Fedtschenkiinae and Anthoboscinae, i.e., those taxa most closely related to the Mutillidae.

The complete absence of a jugal lobe in the hind wing is characteristic of the entire Mutillidae except for the Myrmosinae and Pseudophotopsidinae. This state has thus apparently arisen on internode 2-3 and provides strong evidence for the holophyletic nature of the higher Mutillidae, despite the fact that a similar condition has occurred elsewhere in the Aculeata (e.g., in Bethyloidea).

M36. *Propodeal disc* (Fig. 87). Primitively, the propodeal disc is fairly heavily and evenly sculptured, often reticulately so. M36.1—The disc of the propodeum bears four subparallel longitudinal carinae linked posteriorly by a zig-zag transverse carina.

An evenly sculptured propodeal disc is considered primitive because this is the condition in those Aculeata most closely related to the Mutillidae (viz., Fedtschenkiinae, Anthoboscinae) and in most members of the Mutillidae.

A characteristic pattern of carinae on the disc of the propodeum is most highly developed in *Nanomutilla* (and *Ticopla*) and slightly less so in *Areotilla*. In *Smicromyrmilla* the fully winged species have similar carinae on the anterior region of the disc but the apterous species have the sculpturing modified so that the carinae are lost. Although a few species of *Rhopalomutilla* show a superficially similar condition (differing in detail, however), this pattern of sculpturing is considered to be present in these genera only, and thus is useful in associating them into the holophyletic subfamily Ticoplinae. (Nagy, 1970, however, cited this as a character in which *Ticopla* was similar to some Bethylidae, although the pattern differs in detail in the groups involved.)

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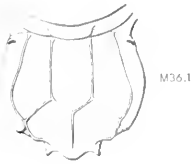

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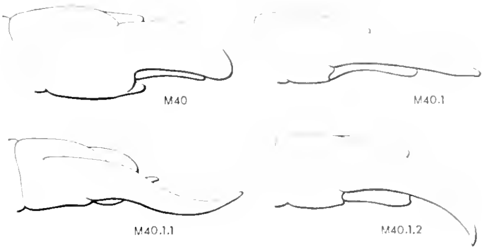


FIGS. 87-88. Characters of Mutillidae. 87, posterior region of mesosoma of male, dorsal view, showing derived state of propodeal disc (M36.1 based on *Nanomutilla*); 88, posterior region of male genitalia, lateral view, showing primitive and derived states of gonostylus (M40 based on *Pseudophotopsis;* M40.1 on *Nanomutilla;* M40.1.1 on *Protophotopsis;* M40.1.2 on *Antennotilla*).

M37. *Form of first metasomal segment* (Fig. 76). Primitively, the first metasomal segment (especially the tergum) is evenly expanded from base to apex and is only slightly constricted apically so that it is not highly differentiated from the rest of the metasoma. Although it may be somewhat constricted apically and narrower than the second, the first segment is never predominantly cylindrical (parallel-sided). M37.1—The first metasomal segment (notably the tergum) is approximately cylindrical and short, being highly differentiated from the remainder of the metasoma.

An evenly dilated first metasomal segment is considered primitive because this is the condition in most Aculeata, including those taxa most closely related to the

Mutillidae (e.g., Fedtschenkiinae, Anthoboscinae), and also in most mutillids.

The development of a cylindrical, parallel-sided first metasomal segment in the male follows the same pattern as a similar development in the female (F17.2), being characteristic only of the Ephutini and providing a strong indication of the holophyly of that tribe but not providing additional information above that supplied by the female.

M38. *Pubescence on first metasomal tergum* (Fig. 78). The development of plumose pubescence in the males (M38.1) exactly parallels that in the females (F19.1), being characteristic of the entire Sphaeropthalmini except for a few genera in which plumosity has apparently been lost secondarily. This strengthens the importance of this state in establishing the Sphaeropthalmini as a holophyletic group, but does not provide more information on groupings than that given by females.

M39. *Tergal felt line* (Fig. 79). The pattern of development of a tergal felt line in the male is exactly the same as that in the female (F20), the derived state being present in the Pseudophotopsidinae and above internode 4-5 except for a few species. The tendency toward expression of state M39.1 may thus be considered to have been established on internode 1-2, although actual expression has occurred on at least two occasions. This state does not provide any additional information on higher groupings beyond that provided by females, but does serve to strengthen the conclusions based on that in the female.

M40. *Gonostylus* (Fig. 88). Primitively, each gonostylus is about twice as long as high, being lamellate with a rounded apex. M40.1—Each gonostylus is at least three times as long as its basal height, being approximately straight and tapered so that the apex is acute. M40.1.1—Each acute gonostylus is upcurved at the apex. M40.1.2—Each acute gonostylus is downcurved apically.

A broad, rounded gonostylus is considered primitive because this is the condition in various of the more generalized groups of the Aculeata (e.g., Plumariidae, Sierolomorphidae) and especially in those taxa most closely related to the Mutillidae, such as Fedtschenkiinae and Anthoboscinae.

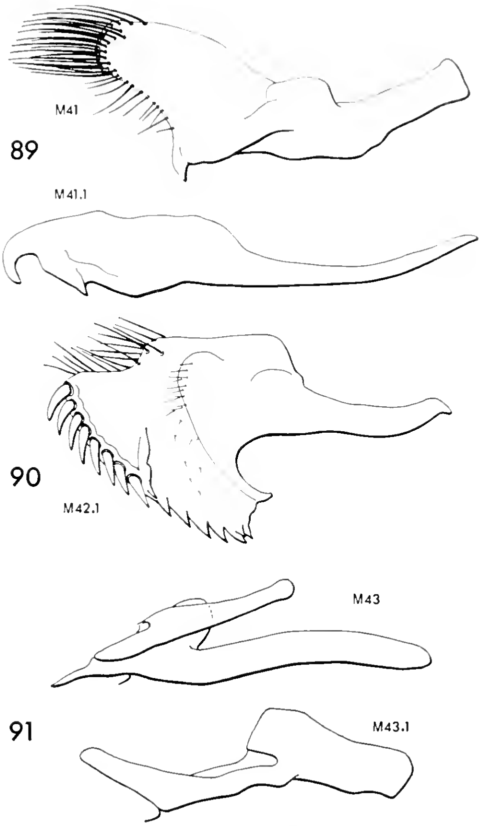
The development of an acute gonostylus (M40.1) has apparently occurred on a single occasion on the cladogram, on internode 2-3, since this condition is characteristic of all Mutillidae except for Myrmosinae and Pseudophotopsidinae. There are, however, a few instances in which somewhat of a reversal has occurred, so that in *Brachymutilla* (Dasylabrini), *Atillum* and *Hoplocrates* (both Pseudomethocina) the gonostyli are fairly broad and their apices are somewhat rounded, a similar but less marked tendency being shown in *Hoplomutilla, Myrmilloides* (both Pseudomethocina) and *Ctenotilla* (Smicromyrmina). Although state M40.1 is best placed on internode 2-3, *Nanomutilla* (Ticoplinae) has gonostyli which are narrowed but with apices which are somewhat blunt. In sum, the gonostyli in *Nanomutilla* appear to be more similar to those of the higher Mutillidae than to *Pseudophotopsis,* however. Thus the possession of narrow, acute gonostyli is quite a good characteristic associating the Mutillidae above internode 2-3 into a holophyletic group. In the Myrmosinae, however, a somewhat similar development has taken place in some members of the genus *Myrmosa,* although *Myrmosula* has gonostyli of the primitive type.

Dorsal curvature of the gonostylar apex (M40.1.1) is characteristic of the entire subfamily Sphaeropthalminae and is present in all members of that taxon except for a few specialized genera in which the gonostylus has been further modified and the apex is more or less straight (e.g., *Hoplomutilla, Myrmilloides, Atillum, Hoplocrates, Lomachaeta*). Although the apical curvature of the gonostylus may often be rather subtle, this seems to be a useful state for associating the Sphaeropthalminae in a holophyletic group, having arisen on internode 5-6.

Ventral curvature of the apex of the gonostylus (M40.1.2) is characteristic of the entire branch bearing both the Myrmillinae and Mutillinae although the degree of curvature is somewhat reduced in *Ctenotilla* (Smicromyrmina). This is thus a useful state establishing that these two subfamilies form a holophyletic group. Although *Nanomutilla* in the Ticoplinae has the gonostylus approximately straight, both *Areotilla* and *Smicromyrmilla* have the gonostyli strongly ventrally curved but with the conformation of the gonostyli in other respects unlike that of the myrmilline-mutilline group. This occurrence thus almost certainly represents an independent but somewhat similar modification of the gonostylus and does not materially weaken the significance of state M40.1.2 on internode 5-7.

M41. *Gonapophysis IX* (Fig. 89). Primitively, each gonapophysis IX has the apex much produced dorsally and posteriorly into a marked lobe and bears a tooth about halfway along the ventral margin. M41.1—Each gonapophysis IX has the dorsal apical lobe much reduced or lost and bears a tooth on the apical half of the ventral margin.

A gonapophysis IX with a large dorsal lobe apically is considered primitive because this is the condition in the Fedtschenkiinae, the group most closely related to the Mutillidae, and also in the Myrmosinae which forms a basal branch of the cladogram on the basis of other characters.



Figs. 89-91. Characters of Mutillidae. 89, right gonapophysis IX of male, lateral view, anterior to right, showing primitive and derived states (M41 based on *Myrmosa nigriceps;* M41.1 on *Areotilla* sp.); 90, right gonapophysis IX of male, lateral view, anterior to right, showing derived state of gonapophyseal spines (M42.1 based on *Pseudophotopsis ?continua*); 91, right volsella, mesal view, anterior to left, showing primitive and derived states of digitus (M43 based on *Dasymutilla nigripes;* M43.1 on *Areotilla* sp.).

The form of the gonapophysis IX is somewhat more complex than can be concisely described, but, basically, each has lost the dorsal lobe or has it greatly reduced in all taxa except the Myrmosinae, so that state M41.1 has apparently evolved once, on internode 1-2. Actually the form of the dorsal lobe in the Fedtschenkiinae is slightly different from that in the Myrmosinae where it often seems to be more strongly developed distally. Within the Myrmosinae its form differs also, being a large lamella often bearing long marginal setae in *Myrmosa;* it is non-setose in

Myrmosula but with a large apical ventral tooth, so that its condition appears to be more similar to that in both the Fedtschenkiinae and other Mutillidae.

M42. *Gonapophyseal spines* (Fig. 90). Primitively, each gonapophysis IX does not bear any articulating spines but is merely armed with one or more simple cuticular teeth ventrally. M42.1—Each gonapophysis IX bears stout spines articulating at the base along the distal ventral margin in addition to simple cuticular teeth.

Simply toothed gonapophyses IX are considered primitive because this is the condition in the group most closely related to the Mutillidae (i.e., Fedtschenkiinae) and also in almost all mutillids.

A gonapophysis IX with stout, articulating spines is found only in *Pseudophotopsis*. This is thus a good state establishing the Pseudophotopsidinae as a highly differentiated taxon, but it does not provide any information on higher groupings. Although such stout spines are unique to *Pseudophotopsis,* they may actually be modified setae such as are present in similar positions on the gonapophysis IX in most Mutillidae.

M43. *Digitus* (Fig. 91). Primitively, the volsella of the male genitalia comprises both a cuspis and a digitus. M43.1—The volsella consists of only the cuspis, the digitus having been obliterated.

A volsella with both digitus and cuspis is considered primitive because this is the condition in most Hymenoptera, including those taxa most closely related to the Mutillidae.

A digitus is present in practically all Mutillidae although it is often somewhat reduced and apparently not movable relative to the cuspis. In both the Ticoplinae and Rhopalomutillinae, however, the digitus has been completely lost, apparently independently in these two subfamilies, the volsella otherwise appearing quite different in these taxa. Nevertheless, the presence of state M43.1 is quite a useful characteristic associating at least three genera in the Ticoplinae (the condition in *Ticopla* is unknown to me).

Characters Rejected for Derivation of the Final Cladogram

The following characters were considered but were rejected for the construction of the final cladogram, for various reasons. Some showed a high incidence of parallel or convergent derivations which lessened their usefulness. Others could not be described unequivocally in terms of one or a few states which could be readily distinguished. Instead they varied gradually, making it impossible to include them in the formal scheme. Other characters were considered and used early in the study before it had been established that the Mutillidae as then constituted was actually a polyphyletic group. When the Typhoctinae, Apterogyninae and Chyphotinae (Bradynobaenidae) had been removed from the Mutillidae, these characters became invariant, even after the Myrmosinae had been added to the study. Further characters were found to vary only within the final tribal or other divisions which were used as the basic taxa in the cladogram, and thus did not provide any information on higher groupings at the tribal level or above.

Of course most of these characters do provide useful information which was utilized mainly early in the investigation to obtain indications of probable groupings. Many will also be found useful in establishing groups within the final taxa used in the cladogram. However, the limitations of each have to be borne in mind at each stage.

Each character is briefly described below and the reasons for its rejection are given. The numbering is continuous with that for the characters utilized, but the suffix "r" indicates rejection.

F44r. Absence (primitive) or presence (derived) of laterally flattened, lanceolate setae in the female.

This character varies only within the tribe Sphaeropthalmini in which those genera in the Pseudomethocina possess the derived state, as do other genera scattered in the Sphaeropthalmina. This character is thus variable within the group, provides no information on higher groupings at the levels involved in the cladogram and is also somewhat equivocal in that the degree of modification of the setae varies, making the determination of setae as lanceolate or not difficult in many cases.

F45r. Compound eye large (primitive) or small (derived).

Although relatively large eyes are retained in most members of the Mutillinae as well as the Pseudophotopsidinae and Myrmosinae, most members of the Sphaeropthalminae have the eyes reduced in size, as do many Myrmillinae, the Rhopalomutillinae and some Ticoplinae. There have been many parallel and convergent derivations of small eyes, and it is impossible to define the two states unequivocally.

F46r. Compound eye with ommatidia individually convex and differentiated (primitive) or with entire surface smooth and ommatidia undifferentiated (derived).

The derived state is found only within the Sphaeropthalmini (where it is developed in many of the genera of the Sphaeropthalmina and a few of those in the Pseudomethocina) and in *Tricholabiodes* in the Dasylabrini. Although the two states can be defined reasonably unequivocally, the derived state has occurred (or has been reversed) on many parallel occasions, thus not delimiting any groupings.

F47r. Antennal socket simple (primitive) or with dorsomesal antennal tubercle (derived).

After removal of the Typhoctinae, Apterogyninae and Chyphotinae from the Mutillidae, all members of the myrmosid-mutillid complex possess the derived state.

F48r. Scape approximately straight and relatively short (less than 1.5 times as long as thick) (primitive) or sigmoid and more than twice as long as thick (derived).

All members of the myrmosid-mutillid complex have the derived state, the primitive scape being found in some of the genera that were excluded from the Mutillidae.

F49r. First flagellar segment subequal in length to the second (primitive) or more than twice the length of the second (derived).

Apart from a few members of the Myrmillinae, the derived state is found only in various members of the Sphaeropthalmini, where it is most commonly developed in the Pseudomethocina. This character shows numerous parallel and convergent derivations and also is incapable of unequivocal formulation.

F50r. Antenna with 12 (primitive) or 13 (derived) segments.

Only two genera possess the derived state (*Atillum* and *Hoplocrates* in the Pseudomethocina) so that this is of no use in establishing groups at the tribal (or even the subtribal) level.

F51r. Absence (primitive) or presence (derived) of a ventral excision forming a basal tooth on the mandible.

Although most members show the primitive state, the derived state appears in scattered genera throughout the Mutillidae so that many parallelisms and convergences are involved.

F52r. Mesosomal pleura approximately flat or convex (primitive) or markedly concave (derived).

Although the derived state is particularly characteristic of the Myrmillinae, it also occurs in one or more members of the Myrmosinae, Ticoplinae and Mutillinae and thus shows some parallel and convergent developments. The states are also difficult to define and identify unequivocally.

F53r. Lateral face of pronotum dorsally without (primitive) or with (derived) a small tubercle bearing fine setae and perhaps secretory pores.

Although the derived state appears to be characteristic of the entire Mutillidae except for the Myrmosinae, an unequivocal decision on the state involved, especially in small species, is often impossible because of the small size and minimal differentiation of this structure. The tubercle may be analogous to the felt line of the second metasomal segment.

F54r. Anterior face of pronotum dorsally without (primitive) or with (derived) a short transverse ridge bearing fine setae and perhaps secretory pores.

As for the previous character, the derived state is apparently characteristic of the entire Mutillidae expect for the Myrmosinae, but certainty is impossible. This structure may also be analogous to the felt line of the second metasomal segment.

F55r. Pronotum with posteroventral margin distinct so that pronotum is well-differentiated from mesopleuron (primitive) or with posteroventral margin obliterated so that pronotum and mesopleuron are not differentiated (derived).

The primitive state is generally present in the Pseudophotopsidinae, Mutillini and many Sphaeropthalmini; the derived state is found in the other groups, generally differing in details in the different taxa. This means that many of the higher taxa can be characterized by detailed formulations of the type of derived state involved in each. Nevertheless, it is difficult to do this unequivocally. These states also would provide no information on supratribal groupings. Furthermore, there is much variation in the degree of expression of these derived states, especially in the Sphaeropthalmini.

F56r. Mesopleuron dorsally protuberant (primitive) or depressed (derived).

Although the derived state is generally characteristic of the Mutillini (except for *Odontomutilla*) and Pseudophotopsidinae, it is also present in a few other genera so that it has occurred in parallel or convergently on various occasions. Furthermore, the range of variation present precludes accurate delimitation of these states.

F57r. Mesopleural ridge with ventral (often carinate) section anterior to (primitive) or dorsal to midpoint of (derived) mid-coxae.

Although the derived state tends to be characteristic of the Ticoplinae, unequivocal determination of the state is often difficult because of intermediates and also because of lack of development of the ridge.

F58r. Ventral section of mesopleural ridge not (primitive) or sharply (derived) carinate.

The derived state is found in most members of the Ticoplinae, Myrmillinae and Mutillini, and sporadically elsewhere, so that it shows many instances of parallel or convergent development. Intermediates also preclude unequivocal assignation of various members to one or the other state.

F59r. Meso-metapleural suture distinct (primitive) or obliterated and indistinguishable (derived).

Since the meso- and metapleura are fused in all members, there is a general tendency for the meso-metapleural suture to become obliterated, so that the derived state is expressed in many members independently in the various subfamilies and tribes involved. Furthermore, unequivocal categorization of the degree of distinctness of the suture is impossible because of continuous variation from a quite distinct state to one in which the suture is completely indistinguishable.

F60r. Metapleural-propodeal suture distinct (primitive) or obliterated (derived).

As for character F59r, there is a general tendency for this suture to become obliterated so that the derived state shows many parallel and convergent occurrences, and also cannot be characterized unequivocally.

F61r. Calcar on front tibia with an elongate, narrow blade (primitive) or with a short, broad blade (derived).

Although all Mutillidae except Myrmosinae, Ticoplinae and Rhopalomutillinae tend to have the derived state, there is actually continuous variation so that definite decisions on which state is present are impossible in many instances.

F62r. Pectinal spines on fore tarsi barely developed (primitive) or highly elaborated (derived).

Although highly developed pectinal spines are mainly characteristic of many members of the Sphaeropthalminae and Mutillini, and also Pseudophotopsidinae, there is much variation within these groups so that it is impossible to decide unequivocally which state is involved in many cases. The derived condition has also arisen independently in various groups.

F63r. Mesotibia with two or more longitudinal rows of spines (primitive) or with only one or no rows of spines (derived).

Although degree of spininess is vaguely correlated with tribal groupings, the derived state has arisen on many independent occasions. There is also essentially continuous variation in the character so that meaningful states are impossible to define.

F64r. Metatibia with two or more longitudinal rows of spines (primitive) or with one or no rows of spines (derived).

As with character F63r, the less spiny tibiae are mainly characteristic of some Sphaeropthalmini, Ephutini, Myrmillinae, Rhopalomutillinae and Ticoplinae, but extreme variability and impossibility of precise definition preclude the use of this character.

F65r. First metasomal segment sessile and not apically constricted (primitive) or petiolate, narrowed and apically constricted (derived).

Although the derived state tends to be restricted to various members of the Sphaeropthalminae, it has arisen on numerous occasions independently within the subfamily and is, furthermore, difficult to describe unequivocally since there is considerable variation in form. The derived state is also present in a less extreme form in many members of the Smicromyrmina.

F66r. First metasomal tergum extending over entire length of segment (primitive) or absent on anterior half of segment which is thus comprised of the sternum only (derived).

The derived state occurs in the Chyphotinae (Bradynobaenidae), so that with removal of this taxon from the Mutillidae, this character becomes invariant in the myrmosid-mutillid complex.

F67r. Second metasomal sternum without (primitive) or with (derived) a secretory felt line on each side.

The derived state occurs in scattered genera throughout the Mutillidae except for the Myrmosinae, Rhopalomutillinae, Sphaeropthalmini and Mutillinae, and thus may reflect a general tendency for the development of felt lines (whether tergal or sternal) in the Mutillidae (above the Myrmosinae), or may simply show numerous independent derivations.

F68r. Mesal stridulitrum on third metasomal tergum absent (primitive) or present (derived).

After removal of the Typhoctinae, Apterogyninae and Chyphotinae, this character is invariant in the myrmosid-mutillid complex, being present only in the derived state.

M69r. This character is the same as F44r, but for the male, and the same comments apply.

M70r. Head in anterior view tending to be vaguely triangular with the clypeal margin fairly short (primitive) or more rounded with the clypeal margin longer (derived) (see Fig. 80).

Although there is a striking difference in the shape of the head, the derived state being characteristic of all taxa except the Ticoplinae and less obviously the Myrmosinae and Pseudophotopsidinae, and thus providing useful information establishing the holophyly of all Mutillidae above the three basal subfamilies, it is impossible to formulate the character states unequivocally so that they can be objectively applied.

M71r. Compound eye large (primitive) or small (derived).

Although this character is similar to F45r, and it was rejected for the same reasons, the distribution of the derived state is somewhat different. In the male small eyes occur in some Dasylabrini, most Sphaeropthalmini and most Myrmillinae.

M72r. This character is the same as F46r and the same comments apply.

M73r. Antennal scrobe dorsally unarmed (primitive) or with a tooth or transverse carina (derived).

Although the derived state tends to be present in most members of the Sphaeropthalminae, it also occurs sporadically in almost all the other subfamilies of Mutillidae. Unequivocal decisions on which state is present are also often impossible, mainly because of the heavy sculpturing of many species.

M74r. This character is the same as F47r and the same comments apply.

M75r. This character is the same as F48r and the same comments apply.

M76r. First flagellar segment subequal to the second (primitive) or less than half the length of the second (derived).

The derived state is characteristic of most members of the Ticoplinae and also some Dasylabrini and a few Sphaeropthalmini and Mutillini, but cannot be unequivocally determined because of continuous variation between the two states.

M77r. This character is the same as F51r, but the derived state is more commonly present in the male, appearing in many members scattered throughout the Mutillidae.

M78r. Hind margin of pronotum shallowly arcuate (primitive) or deeply concave or angulate (derived).

Although the derived state tends to be characteristic of the Rhopalomutillinae, Myrmillinae and Mutillinae, scattered members of the other three higher subfamilies of Mutillidae also show it. The Myrmosinae have a more primitive condition than most other Mutillidae for this character. In addition, continuous variation precludes unequivocal decisions on which state is involved in many instances.

M79r. This character is the same as F53r and the same comments apply.

M80r. This character is the same as F54r and the same comments apply.

M81r. Mesoscutum with the parapsidal sutures and the parapsidal furrows both present (primitive) or with one (or both) of these paired “sutures” obliterated (various derived states).

Although most members show the

primitive state, some scattered members of the Sphaeropthalmini have lost the parapsidal sutures, as has *Smicromyrmilla*. The parapsidal furrows have been lost only rarely, e.g., in *Stenomutilla*. Both "sutures" are never lost simultaneously, it appears. Apart from the limitations caused by scattered occurrence, it is often difficult to ascertain the state, both because the degree of reduction of the "suture" varies and because it may be obscured by the sculpturing.

M82r. Axilla smoothly rounded posterolaterally (primitive) or produced into an obtuse or acute tooth (derived).

Although most members have the primitive state, various scattered genera, especially in the Sphaeropthalminae, show the derived state, which is furthermore difficult to designate unequivocally because of continuous variation.

M83r. Meso-metapleural suture fused for only a short distance ventrally (primitive) or fused for half its length or more (derived).

This character is associated with M27 in that only those members possessing state M27.1 have the meso-metapleural suture at all fused. This excludes the Myrmosinae, Pseudophotopsidinae and Ticoplinae from consideration. Most other mutillids possess the derived state of M83r, but various scattered members of the Sphaeropthalminae in particular have the primitive condition. Since there is also continuous variation it is impossible to designate the states unequivocally.

M84r. Metasternal process bidentate (primitive) or acute (derived).

This character is related to M28 in that it only applies to members possessing state M28.1. The Myrmosinae are thus excluded. The derived state of M84r has occurred on various occasions, being present in *Nanomutilla* (Ticoplinae), Rhopalomutillinae, some scattered Sphaeropthalmini and Ephutini. Although the details of modification differ among the different groups involved, the differences are often subtle and difficult to designate unequivocally.

M85r. Metapleural-propodeal suture below the endophragmal pit not evident (primitive) or marked by a secondarily developed ridge (derived).

The primitive state is present in the Myrmosinae, Pseudophotopsidinae and Ticoplinae, and also in various scattered members of the Sphaeropthalminae, so that the derived condition must have arisen on numerous independent occasions. Because of essentially continuous variation and obscuration by sculpturing, unequivocal determination of the state represented is often impossible.

M86r. Tegula with inner margin approximately straight (primitive) or markedly concave as a result of posteromesal expansion of the tegula (derived).

Although most members possess the primitive state, a very few scattered genera (e.g., *Areotilla, Odontomutilla, Ctenotilla, Dolichomutilla*) show the derived state, the definition of which is also somewhat equivocal.

M87r. The forewing has three (primitive) or two (derived) or even one (further derived) submarginal cells (i.e., cell 2S or both 2S and 1S obliterated in the two derived states, respectively).

Many members scattered throughout the Mutillidae possess the first derived state (within some genera, e.g., *Dasylabris*, both the primitive and first derived states are found). Relatively few members possess the second derived state, but these are also scattered (e.g., *Ticopla, Atillum*). Thus both derived states have arisen on numerous independent occasions.

M88r. This character is the same as F61r and the same comments apply.

M89r. An arolium is distinctly present (primitive) or is absent (derived).

This character is comparable to F16 but shows a different distribution of states. After the removal of Typhoctinae, Chyphotinae and Apterogyninae, all members of the myrmosid-mutillid complex show the primitive state for character M89r. This character is thus invariant despite the fact that the females of Myrmosinae possess the comparable derived state (F16.1).

M90r. This character is the same as F65r except that in the primitive state the first metasomal segment is not as broad as in the female. Similar comments apply as to F65r, except that the derived state of M90r is present in the Rhopalomutillinae also. Furthermore, a different derived condition in which the first metasomal segment is apparently broadened seems characteristic of the Mutillina and to a lesser extent of the Ticoplinae and some Myrmillinae.

M91r. This character is the same as F66r and similar comments apply. It appears, however, that the derived state of this character is actually not present in the males of at least some Chyphotinae, but has been misinterpreted in the past.

M92r. Second metasomal sternum without (primitive) or with (derived) a secretory felt line on each side.

This character is the same as F67r but shows a different distribution in that the derived state is much more commonly present in the male, being found in scattered members of all taxa of the Mutillidae except for Myrmosinae, Rhopalomutillinae and Ephutini. (In addition some species of *Dasymutilla* and *Traumatomutilla* bear midventral felt lines on the second sternum.)

M93r. This character is the same as F68r and the same comments apply.

M94r. Hypopygium simple (primitive) or with an upcurved aculeate spine (derived).

After removal of the Apterogyninae and Chyphotinae, all members of the myrmosid-mutillid complex possess the primitive state, although *Myrmosa* and *Rhopalomutilla* have the hypopygium modified in various ways.

M95r. Base of gonostylus approximately vertical (i.e., at right angles to longitudinal axis of genitalia) (primitive) or oblique (i.e., originating dorsally at a point more proximal than the ventral point of origin) (derived).

Although the derived condition is the more common, the primitive state occurs in the Pseudophotopsidinae and many scattered members of the Sphaeropthalminae so that there must have been numerous independent derivations. Also, because of continuous variation, unequivocal designation of the states is impossible.

M96r. Gonapophyses IX symmetrical (primitive) or with the right gonapophysis larger and more elaborate than the left (derived).

The derived state occurs in only a few members of the Smicromyrmina (viz., *"Lobotilla," "Timulla," "Trogaspidia"*) and is thus only of use at the generic level.

Discussion

TAXONOMIC CONCLUSIONS

The final cladogram (Fig. 92) includes nine taxa, each of which is internally homogeneous for the various states of the particular characters considered (except for the few instances detailed in the above section describing these characters). As for the study of the Aculeata, values of *DF, DE, DC* and *DT* (various weighted measures of distinctness) were calculated (Tables IV and V). Although various characters occurring in both sexes were considered separately in cladogram con-

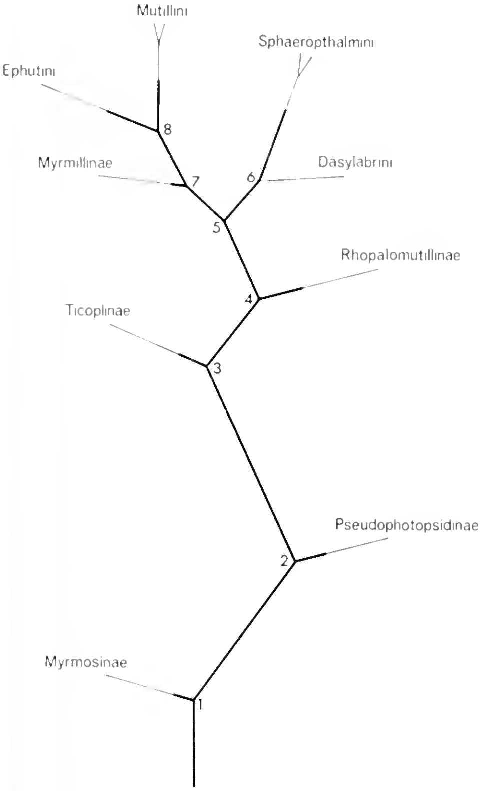


Fig. 92. Cladogram of nine taxa of Mutillidae; lengths of heavy lines are proportional to the distinctness measures (DC). Mutillini (comprising Mutillina and Smicromyrmina) + Ephutini = Mutillinae; Dasylabrini + Sphaeropthalmini (comprising Pseudomethocina and Sphaeropthalmina) = Sphaeropthalminae.

struction, they were combined and coded as to occurrence in the same fashion as for the aculeates for calculation of these values (i.e., a derived state occurring in only one sex on a particular internode was scored as 0.5 if it occurred in both sexes elsewhere on the tree). It should be noted that only the characters considered the most significant in deriving the cladogram have been included here, unlike for the Aculeata where all the characters considered were used. What influence this may have on the conclusions is unclear, although "poor" characters might be expected to occur at random on the tree and thus not affect the relative proportions of "distinctness" for the various internodes. Certainly, the intuitive impressions gained during both investigations were supported by the values derived in each case.

The highest value for taxonomic distinctness (*DT*; Table V) between adjacent taxa is that for pseudophotopsidines and ticoplines, despite the fact that the myrmosines have commonly been excluded from the Mutillidae and so might be expected to show the greatest distinctness. The fact that the pseudophotopsidines are more distinct from the higher mutillids (minimum, 136) than from the myrmosines (108) strengthens the inclusion of the myrmosines in the Mutillidae. The ticoplines are also quite distinct from the rhopalomutillines (79) which in turn are slightly more distinct from the closest higher taxa (97 to myrmillines, 91 to dasylabrines). This suggests that the four basal taxa at least should each be recognized as distinct at the subfamily level. The myrmillines are somewhat less distinct from neighbouring taxa but approximately equally so (60 to both mutillines and dasylabrines). The two lowest values are those between the mutillines and ephutines (50) and the dasylabrines and sphaeropthalmines (37) indicating that these pairs should perhaps not be recognized at the subfamily level. The intermediate position of the myrmillines between two complexes which are highly distinct (minimum value 106, mutillines to dasylabrines) suggests that the three groups containing myrmillines, mutillines and dasylabrines each be recognized at the subfamily level.

The cladogram is thus interpreted to encompass one family, the Mutillidae, consisting of seven subfamilies, two of which comprise two tribes each. Two of these tribes (in different subfamilies) are in turn divided into two subtribes each, in both instances mainly on the basis of characters excluded in cladogram construc-

Table IV. Occurrences (Σi) and numbers (k) of derived states, number of species subtended (S) and various distinctness measures (DF, DE, DC) for the internodes and final branches of the cladogram of Mutillidae (Fig. 92).

Internode	Σi	k	S[a]	DF	DE	DC
1-Myrmos.	3.0	4	50	11.04	0.83	9.16
1-2	5.0	5	4850	84.65	1.00	84.65
2-Psdpht.	5.0	5	50	18.40	0.80	14.72
2-3	7.0	7	4800	118.09	0.90	106.28
3-Ticopl.	4.0	4	75	16.88	0.88	14.85
3-4	3.0	3	4725	50.34	0.83	41.78
4-Rhopal.	7.0	7	50	25.76	0.86	22.15
4-5	3.0	3	4675	50.16	0.83	41.63
5-6	2.0	2	2475	27.06	1.00	27.06
6-Dasyla.	0.0	0	550	0.00	0.00	0.00
6-Sphaer.	3.0	3	1925	37.32	1.00	37.32
5-7	2.0	2	2200	26.00	1.00	26.00
7-Myrmil.	1.0	1	400	7.37	1.00	7.37
7-8	3.0	3	1800	36.48	0.83	30.28
8-Mutiln.	2.0	2	1500	22.90	1.00	22.90
8-Ephutn.	4.0	4	300	26.76	1.00	26.76

[a] Based on the sum of the estimated number of species in each genus (including those yet to be described). Calculations utilize $\sqrt[3]{S}$.

tion. The genera and subgenera included in these various taxa are listed in Table III.

Mutillidae Latreille, 1802

The Mutillidae as a whole is characterized by some quite strong synapomorphies, as outlined in the section on the Aculeata, above. The most significant of these are probably the development of a complex basal angulation of the scape, fusion of the moderately large prepectus to the mesepisternum, form of the modified mesosoma of the female (which is invariably apterous) and the development of a mesal stridulitrum on the third metasomal tergum.

Despite past attribution of the name Mutillidae to a wide variety of authors, it appears that Latrielle's treatment was the first in which a group based on a genus included in this taxon was allocated a rank at the family group level.

Table V. Taxonomic distinctness for the taxa of Mutillidae.

	MYRMOSINAE	PSEUDOPHOTOPSIDINAE	TICOPLINAE	RHOPALOMUTILLINAE	DASYLABRINI	SPHAEROPTHALMINI	MYRMILLINAE	MUTILLINI
PSEUDOPHOTOPSIDINAE	108							
TICOPLINAE	215	136						
RHOPALOMUTILLINAE	264	185	79					
DASYLABRINI	310	231	125	91				
SPHAEROPTHALMINI	348	269	163	128	37			
MYRMILLINAE	317	238	132	97	60	98		
MUTILLINI	363	284	177	150	106	144	60	
EPHUTINI	366	287	181	154	110	147	64	50

Myrmosinae Fox, 1894

With the suite of characters in use here, the Myrmosinae has only five characters in the derived state, three of these being unique to this subfamily. In two there is parallel development of a derived condition in the Myrmosinae and also within the remaining Mutillidae, viz., unarmed claws and an unarmed mesosternum, both in the female only. Of the other three characters, the development of a dorsal lamella on the hind coxa in both sexes is probably the most significant. The remaining Mutillidae are distinguished from the Myrmosinae by the presence of six characters in the uniquely derived state. Of these, two involve the development of an armed metasternum in both males and females, considered a single character for calculation of distinctness. The most useful character states uniting these higher taxa are the fusion of the pronotum with the mesothorax in the female and the form of the gonapophysis IX in the male. Although the absence of felt lines in the Myrmosinae has been considered to exclude them from the Mutillidae (e.g., Krombein, 1940), the development of felt lines in the higher subfamilies is somewhat irregular, so that this is not as fundamental a character as has been considered in the past.

The Myrmosinae is a relatively homogeneous group without any obvious subdivisions so that there does not seem to be any reason to subdivide it, at least not at this time. *Protomutilla* is perhaps the most anomalous member, and it may later be found that this genus is distinct enough to warrant the erection of a separate suprageneric taxon to contain it. Until the male is discovered, however, any such decision would be premature. Although Ghesquière (1951) placed the genera *Obenbergerella* Strand (= *Alienus* Bridwell) and *Alieniscus* Benoit as the tribe Obenbergerellini in the subfamily Myrmosinae of the Tiphiidae, Krombein (1957) included these genera in the Amiseginae, placed by him in the Chrysididae (Bethyloidea). Nagy (1969c) considered this group to fall in the Cleptidae. The females have 13-segmented antennae, only four exposed metasomal segments and only one spur on the hind tibia, among other characters. These characteristics exclude the group from the Myrmosinae but not from the Cleptidae or Chrysididae (*sensu lato*).

Handlirsch (1925) cites Ashmead (1896a) as the first to base a taxon of the family group on the genus *Myrmosa*. It appears, however, that Fox should be cited as the author since the paper in which he established the tribe Myrmosini was published before that of Ashmead.

Pseudophotopsidinae Bischoff, 1920

The Pseudophotopsidinae is distinguished from the higher Mutillidae (those above internode 2-3) by a relatively large number of characters. The most important of these are probably the retention of ocelli (or their rudiments) in the female in many species, retention of a distinct suture between the pronotum and mesonotum in the female, retention of a straight meso-metapleural suture in the male, retention of teeth on the claws in both sexes, retention of a jugal lobe in the hind wing of the male, retention of a rounded gonostylus in the male (all primitive states), development of a felted pronotal pit and mesosternal teeth in both sexes and development of articulating spines on the gonapophysis IX in the male in the Pseudophotopsidinae.

Although Schuster (1950) suggested that Krombein (1940) should be considered the author for this group, he apparently overlooked the fact that Bischoff, in his 1920-21 monograph, had based a tribe on the genus *Pseudophotopsis*, in the section of that work published in 1920.

Ticoplinae Nagy, 1970

The Ticoplinae differ from the higher groups of Mutillidae (i.e., those subtended by internode 3-4) by a number of characters, of which the following are probably the most significant: retention of setae and minute pores in the compound eye of both sexes, retention of an articulating meso-metapleural suture in the male (i.e., no development of a ventral bridgelike fusion) (both primitive characters although only the latter is shared with both the Myrmosinae and Pseudophotopsidinae), development of a posteriorly convex mesopleural margin in the male and development of a petiolate cell 1S in the forewing of the male. In addition the form of the head (especially in the male) tends to be quite different from the other Mutillidae where the oral fossa appears to have been laterally expanded (less markedly so in the Pseudophotopsidinae, and barely so in the Myrmosinae, however). In general facies the females of the Ticoplinae appear to be more similar to the Myrmosinae than do any of the other higher Mutillidae. This is especially true of *Nanomutilla* which is uncannily similar to *Protomutilla*, whereas *Areotilla* is more similar to some species of *Myrmosa*. *Smicromyrmilla* is more highly modified in many respects and so shows less obvious similarity to the Myrmosinae.

In 1970 Nagy described the genus *Ticopla* (comprising two species) from two male specimens, both from the Jordan region. He made this genus the type of a new subfamily of his family Heterogynidae. (It appears that *Heterogyna* Nagy is actually a member of the Plumariidae—especially on the basis of wing venation—and it has been treated as such in the above investigation of the Aculeata.) Although it has been impossible for me to examine Nagy's specimens, it seems certain from his figure and description that *Ticopla* is very similar to *Nanomutilla*. *Ticopla* has the wing venation more reduced, however, and the genitalia may be somewhat different although Nagy's description of these is not detailed enough for certainty. In particular, these genera are similar in various characteristics cited by Nagy as indicating relationships of *Ticopla* to the Bethylidae rather than the Mutillidae, such as the position of the compound eye (very short malar space), setae on the eye, acute posterolateral angle and pattern of sculpturing of the propodeum, and the prominent setae on the major wing veins. It thus seems that *Ticopla* is in actual fact a member of the Mutillidae, closely related to *Nanomutilla*. On this basis, the subfamily including *Nanomutilla* (and thus *Ticopla*) must be designated the Ticoplinae since Nagy has already based the name of a taxon of the family group on that genus. It may even be that a species of *Ticopla* is actually the male of *Nanomutilla vaucheri* (Tournier), females of which have been collected in the same region (André, 1902). If this should prove to be true, then *Ticopla* would have to be synonymized with *Nanomutilla*, although the subfamily name would be unchanged.

Within the Ticoplinae there are no particularly marked groupings (other than that of *Nanomutilla* and *Ticopla* already mentioned), so that tribal divisions are unwarranted. The most distinct genus is probably *Smicromyrmilla* which possesses sternal felt lines as well as a variously armed mesosoma. The female in particular has a superficial similarity to some members of the Myrmillinae, especially in mesosomal form, as has been noted by Suárez (1965). The males of *Smicromyrmilla* also show a complete gradation from fully winged forms to species without any trace of sutures on the mesosomal dorsum, a condition found elsewhere only in *Brachymutilla* (Dasylabrini). Nevertheless, the least-modified members (especially the males) are reasonably similar to *Nanomutilla* and were placed in this genus by Bischoff (1920-21). This placement may, however, have been due in considerable part to the fact that Bischoff had seen neither the type species *(N. vaucheri)* nor the only other species placed in *Nanomutilla* by André (the author of the genus) up to that time, but apparently based his generic allocation mainly on the presence of a petiolate cell 1S, which is now seen to be a subfamily characteristic. Although Nonveiller (1973) recognized the confusion then existing between *Nanomutilla* and *Smicromyrmilla*, he had apparently not seen any male specimens of *Nanomutilla*.

Rhopalomutillinae Schuster, 1949

The Rhopalomutillinae differ from the higher Mutillidae (i.e., those subtended by internode 4-5) in the retention of a relatively long pronotum in the female, the absence of any felt lines and the retention of a small metacoxal tubercle in both sexes (all primitive states) and from all other members of the family in the reduced maxillary and labial palpi of the female, the form of the mesosoma and first metasomal segment in the female (although a somewhat similar but less extreme development of the metasoma has occurred in the Sphaeropthalmini in the complex of species related to "*Ephutomorpha*" *addenda*), and the development of a basal lamella on the tarsal claws in the male. In addition, the hypopygium of the male is much modified, being reduced and often with complex protuberances, a condition unlike that in other Mutillidae (the hypopygium is also reduced but differently modified in many Myrmosinae).

Although Schuster in 1947 considered *Rhopalomutilla* to be of doubtful position, in or near the Sphaeropthalminae, he did not designate any family level group to contain it at that time. However, in his 1949 treatment, Schuster used the term "Pseudophotopsidinae-Sphaeropthalminae-Mutillinae-Rhopalomutillinae complex" when referring to the taxon here considered to comprise the Mutillidae (except for the Myrmosinae). He also gave a few characters (pp. 123, 125) differentiating the Rhopalomutillinae from other groups. This is apparently the first instance in which a family level group name was based on *Rhopalomutilla*.

Sphaeropthalminae Schuster, 1949 (1903)

The Sphaeropthalminae differ from the two higher subfamilies (subtended by internode 5-7) in their retention of a completely sclerotized pterostigma and also in the form of the mesosoma in the female and the direction of curvature of the gonostylus in the male.

In his classification of the Mutillidae, Ashmead (1903-4) based two tribes on genera which are included in the present concept of the Sphaeropthalminae. These were the Photopsidini (in his subfamily Mutillinae) and the Sphaerophthalmini (sic) (in his Ephutinae). Although the name "Photopsidinae" was used by Bradley & Bequaert (1928) and by Schuster in the first paragraph of his 1947 paper, Schuster in the same paper later specifically designated this group as the Sphaerophthalminae (sic), because "*Photopsis* is not generically distinct from *Sphaerophthalma*" (sic). [The confusion in the spelling of the generic name has arisen because Blake's (1871) original spelling, *Sphaeropthalma*, was an incorrect transliteration from the Greek—*σφαιρα* a ball, and *οφθαλμος* an eye—which Blake corrected in 1886 to *Sphaerophthalma*. This corrected spelling was used uniformly from then on until Schuster (1949) reverted to the original spelling as the basis for the name "Sphaeropthalminae." The "corrected" (1886) form is an unjustified emendation under the provisions of Articles 32(a) & 33(a) of the International Code of Zoological Nomenclature (1964), since Blake's change was obviously intentional, appearing consistently in many places in his 1886 paper. As such, *Sphaerophthalma* Blake, 1886 must be considered a junior objective synonym of *Sphaeropthalma* Blake, 1871, rather than merely a misspelling.] This change in the name has won general acceptance and was used by Krombein (1951) in his catalog of the Mutillidae of America North of Mexico, with the additional change of spelling resulting from Schuster's (1949) correction of the spelling of the type genus. The appropriate name to be conserved under Article 40 of the International Code of Zoological Nomenclature

(1964) is thus "Sphaeropthalminae," which is considered to date from 1903 when it was in effect first used by Ashmead. (The citation of author and date, as in the heading to this section, follows Recommendation 40A of the Code.)

Dasylabrini Invrea, 1964

The Sphaeropthalminae contains two distinct groups, one of which (Sphaeropthalmini) is recognized by a few quite distinct derived states. The Dasylabrini, however, does not possess any particular derived characteristics which would indicate it as a holophyletic group. It may thus be that it is actually paraphyletic, representing those members of the Sphaeropthalminae which do not fall in the holophyletic tribe Sphaeropthalmini. Since homogeneous paraphyletic groups fulfill the criteria of monophyly generally required of named taxa (Tuomikoski, 1967; Ashlock, 1971), recognition of the Dasylabrini as a named taxon is not illegitimate. Within the Dasylabrini there are no particular subgroups recognizable, so that the entire taxon is best regarded as a single tribe. Although Skorikov (1935) seems to have been the first to propose a family level group name based on one of the genera *(Dasylabris)* included here, he did not characterize the group. Apparently Invrea (1964) was the first to fulfill all the requirements of the International Code of Zoological Nomenclature (1964).

Sphaeropthalmini Schuster, 1949 (1903)

The tribe Sphaeropthalmini is distinguished from other members of the subfamily by some unique derived states in both sexes. These are the form of the eye which is approximately hemispherical and often smooth and polished (particularly in the male) and the development of plumose pubescence. These characteristics unite a large and varied group of genera which Schuster (1947) considered to comprise at least five taxa, each apparently at the tribal level, although this was not explicitly stated. In 1958 Schuster revised one of these groups and Krombein (1967) designated it a tribe, so that his "Sphaeropthalmini" is more restricted than the group included here under that name.

When the members of the Sphaeropthalmini were examined more closely, using many of the characters which were rejected for the study as a whole, no very distinct groupings were recognizable. The most distinct subgroup is that including *Pseudomethoca* and related taxa, mainly based on the form of the female mesosoma and the tendency for both sexes to have the metasoma sessile. The remaining members are associated by a tendency toward development of a petiolate metasoma in the male and sometimes in the female, but do not fall into any further clear subgroups. There is instead a continuum from those genera with fewest derived states to those with many. Although no final decisions can now be made on the evolutionary relationships among these genera, since additional investigations and clarification of generic limits are needed, it is nevertheless clear that the genera nearest the base of the line are those like *Cystomutilla, Photomorphus* and *Protophotopsis,* with the moderately advanced ones being similar to *Sphaeropthalma, Lomachaeta* and *Dasymutilla,* and the most highly derived ones being some members of the "*Ephutomorpha* complex," such as *Ascetotilla* and the group of *"Ephutomorpha" paradisiaca.*

At this point it seems best to consider the tribe Sphaeropthalmini to consist of two more or less equal subdivisions which may be given the status of subtribes. The group with a generally sessile metasoma is the **Pseudomethocina.** [Although Schuster (1947) characterized this group, he referred to it as the "Pseudomethocine complex." Suárez (1962) was apparently the first to Latinize the name (as Pseudomethocini), but he did not accompany it with any differentiating characters, nor has this been done since. It thus seems that the name should formally be considered to date from the present paper.] The group with the metasoma tending to be petiolate (in the male at least) is the **Sphaeropthalmina** Schuster, 1949 (1903). Additional and more detailed investigations of this tribe may quite likely indicate that fewer or more such subtribal divisions are warranted.

Myrmillinae Bischoff, 1920

The Myrmillinae differ from the Mutillinae in the retention of a simple, short tegula and broadly oval eye with shallowly sinuate inner margin in the male (both primitive states) and also in the form of the pterostigma in the male. The form of the mesosoma in the female is also different, with the pleura in the Myrmillinae tending to be evenly concave and rather smooth (except that the mesopleural ridge tends to form a strong carina or lamella ventrally just anterodorsal to the mid-coxa), and the pronotal-mesopleural suture is essentially obliterated. Female Myrmillinae also tend to have the head rather heavy, often roughly quadrate with the gena somewhat swollen and with the mandible very strong and broad apically. Although the females of Myrmillinae are sometimes difficult to allocate unequivocally to this subfamily without prior experience, having few good features to distinguish them from Mutillini, the males are quite distinct.

Since this family is confined to the Old World, its members were apparently not included by Schuster (1947) in his general scheme. Interestingly, Skorikov (1927, 1935) placed this subfamily in the Myrmosidae. Bischoff (1920-21), apparently the first to base the name of a group at the family level on that of one of the genera included here in the Myrmillinae, derived the myrmillines as a separate branch from a myrmosid ancestor but included them in his Mutillinae and not the Myrmosinae!

Within the Myrmillinae there are no definite subgroups of genera which could be designated as tribes. It is of some interest that this subfamily includes the highest proportion of species with brachypterous or apterous males of all the subfamilies. Various genera contain both fully winged and wingless species (e.g., *Myrmilla*, *Labidomilla*) although the range of variation in these is not as great as in *Smicromyrmilla* (Ticoplinae) where the most advanced forms have in addition lost all traces of sutures dorsally on the mesosoma.

Mutillinae Latreille, 1802

The Mutillinae is characterized by development in the male of a posteriorly produced tegula, deeply and sharply emarginate eye and a completely membranous pterostigma. (The pterostigma is further entirely lost in some members.)

Mutillini Latreille, 1802

This tribe is distinguished by the development of a recurved posterior margin of the tegula in almost all genera and, in the female, by the dorsal depression of the mesopleural ridge and modifications of the meso-metapleural suture (except for *Odontomutilla*).

The tribe Mutillini itself consists of a large number of genera which fall into two reasonably distinct groups. The smaller group consists of a few genera with males which tend to have the mesosoma somewhat compact and the metasoma completely sessile, with the first tergum somewhat broadened. The females also have the first metasomal tergum broadened and often almost disclike. This group may be designated the subtribe **Mutillina** Latreille, 1802. The other, larger, group has males which are generally slightly more slender, with the first metasomal tergum almost campaniform, narrower and weakly demarcated from the second. The females also have the first metasomal segment narrower and sometimes almost petiolate. This second group is the subtribe **Smicromyrmina** Bischoff, 1920. Actually this subtribe includes two of Bischoff's (1920-21) tribes, his Smicromyrmini and Trogaspidiini. In contrast to Bischoff's treatment, Bradley & Bequaert (1923) placed many of the genera included in both "tribes" under the genus *Smicromyrme.* Mickel (1933) once more considered *Smicromyrme* and *Trogaspidia* to be generically distinct (although he placed the latter as a subgenus of *Timulla*). Since that time various authors of major works have treated *Trogaspidia* either as a subgenus of *Timulla* (e.g., Mickel, 1935; Krombein, 1971) or as a distinct genus (e.g., Olsoufieff, 1938; Chen, 1957). Furthermore, Krombein (1972) returned to Bischoff's (1920-21) concepts of tribal classification, but changed the name of the Trogaspidiini to the Timullini (a procedure disallowed under Article 40 of the International Code of Zoological Nomenclature, 1964). In view of the confusion surrounding the name *Trogaspidia* it thus seems best to use *Smicromyrme* (which is also the older name) as the type genus for this subtribe.

Ephutini Ashmead, 1903

The Ephutini is a very distinct group, characterized by the peculiar cylindrical form of the first metasomal segment in both sexes, the form of the mesosoma in the female and the tegula in the male, as well as the loss of the pterostigma.

There are no distinct subgroups within this tribe so that no subdivisions can be recognized, although much work needs to be done to clarify generic limits. It appears that Ashmead (1903-4) was the first to base a family-level name on the genus *Ephuta,* first doing so adequately in the section of his paper published in 1903.

The morphological investigation thus indicates that the family Mutillidae may be considered to be composed of seven subfamilies, five of these being monotypic; the other two subfamilies each contain two tribes and, in each, one of the tribes comprises two subtribes. This arrangement should be found to be useful and stable provided that it is based on an accurate interpretation of the patterns of evolution within the family. Some indication of the probable accuracy of a cladogram may often be obtained when external data are superimposed on it and their fit to the scheme is judged. Such data may be biological (information on life histories, hosts, etc.) or distributional, and these two types of data will be evaluated below.

Life Histories and Host Relationships

Unfortunately, rather little work has been done on the life histories of the Mutillidae. Detailed, although nevertheless incomplete, information is available for *Chrestomutilla glossinae* (Lamborn, 1915, 1916; Heaversedge, 1968, 1969a & b, 1970) (Dasylabrini), *Dasymutilla bioculata* (Mickel, 1924; Cottrell, in Brothers, 1972) and *Sphaeropthalma (Photopsis)* spp. (Ferguson, 1962) (Sphaeropthalmina), and *Pseudomethoca frigida* (Brothers, 1972) (Pseudomethocina) in the Sphaeropthalminae, and also for *Smicromyrme rufipes* (Crèvecoeur, 1930; Maréchal, 1930) (Smicromyrmina) and *Mutilla europaea* (Hoffer, 1886; Jordan, 1935; Pouvreau, 1973) (Mutillina) in the Mutillini. Reasonably detailed information also exists for *Myrmosula parvula* in the Myrmosinae, although this is as yet unpublished (Brothers, in prep.). There are only brief observations on mating, feeding and other details for the subfamilies Pseudophotopsidinae, Rhopalomutillinae and Myrmillinae, as well as the Ephutini. There is essentially no information on the Ticoplinae.

In view of the paucity of data, it is impossible to ascertain whether life history information supports the cladogram or not. The time and method involved in mating seem to differ according to taxonomic unit. Sphaeropthalmini such as *Dasymutilla* (Cottrell, in Brothers, 1972; Linsley, MacSwain & Smith, 1955), *Photopsis* (Ferguson, 1962; Salman, in Mickel, 1938) and *Pseudomethoca* (Brothers, 1972) mate on the substrate, intromission lasting a few seconds. The males of Smicromyrmina (Mutillini) such as *Timulla* (Linsley, 1960; Sheldon, 1970), *Smicromyrme* (Bertkau, 1884; Crèvecoeur, 1930; Pagden, 1934) and *Sulcotilla* [specimens in British Museum (Natural History) collected by Risbec] often transport the female in flight before settling and mating. They may even mate in flight, the male clasping the female with his mandibles and legs. In the Rhopalomutillinae also, the male transports the female (Bridwell, 1917; Pagden, 1938), but in this case the female is supported entirely by the attachment of the male genitalia and by modifications of the apical sterna of the male. In *Rhopalomutilla tongaana* at least, the relative positions of the male and female are similar to those figured by Evans (1969a) for *Apenesia* (Bethylidae) (and thus unlike most Thynninae), although the size difference between the sexes is greater in *Rhopalomutilla* (pers. obs.). In the instance observed, the male was visiting the flowers of *Zizyphus* with the female attached passively to his metasomal apex. In some Myrmosinae, also, the male transports the female during copulation, with the female below the male and venter to venter, the only support of the female being provided by the genitalia of the male (*Myrmosa*; Townes, in Pate, 1947a; Krombein, 1956). It is obvious that phoretic copulation is most likely to occur in species where the male is appreciably larger and stronger than the female. This condition occurs most markedly in the Rhopalomutillinae, many but not all Smicromyrmina and some Myrmosinae, as well as some species in other groups. Thus, information on mating may elucidate phyletic relationships within the higher groups but will probably not be particularly useful in confirming (or refuting) the present cladogram based on adult morphology.

Other biological data which have been found to be useful in other parasitic groups, are host relationships. If the parasites tend to be at all host specific, they should show a pattern of evolution which is compatible with that of the host organisms, unless there have been transfers to unrelated hosts. Such data have, for example, proved to be useful in studies of mammalian ectoparasites (see Traub, 1972, for a discussion of the interrelationships of evolutionary patterns and geographic distributions of fleas and mammals). From the available host records, it appears that no parallels can be drawn between the evolution of the Mutillidae and that of their hosts. Members of this family were almost certainly originally parasitoids of ground-nesting Hymenoptera, as are the Fedtschenkiinae (Bohart & Schuster, 1972). However, host specificity is apparently often not strict [e.g., *Stenomutilla argentata* parasitizes Eumenidae (Vespoidea), Megachilidae (Sphecoidea) and Clythrinae (Coleoptera; Chrysomelidae) (Giner Marí, 1944); *Pseudomethoca frigida* attacks at least eight species of halictine bee and perhaps a eumenid wasp (Brothers, 1972)], and transfers to entirely unrelated hosts (even in different orders) have apparently occurred sporadically. Thus, Coleoptera and Diptera are utilized by a few members of the Dasylabrini and Smicromyrmina, Lepidoptera only by *Stenomutilla* (Dasylabrini) and at least some *Odontophotopsis* may parasitize cockroach oothecae (Mickel, 1928, 1974; Seyrig, 1936). As a result, it appears that host information is of no use in confirming or refuting the cladogram. Instead, members of the Mutillidae seem to be capable of parasitizing a wide variety of hosts, the one requirement perhaps being that the stage of the host attacked be in the form of a more or less immobile "package" sealed off from the environment, whether in a closed cell or a hard cocoon, puparium or ootheca.

GEOGRAPHIC DISTRIBUTION

Since the Mutillidae comprises exclusively species with low vagility as a result of the winglessness of the females, it might be expected that the geographic distributions of the various subtaxa would reflect their places (and times) of origin when considered in the light of the theory of plate tectonics and continental drift, if the group is of appropriate age. This should be more clearcut than for a group with high vagility which could more easily cross water gaps. In fact it appears that the cladogram of the Mutillidae is consistent with the data on geographic distribution, and is thus supported (or at least not refuted) by it. The distribution of the more primitive subfamily (Fedtschenkiinae) of the sister group to the Mutillidae (the Sapygidae) is also of importance in this regard, since it provides a clue as to the area in which the ancestor of the Mutillidae arose. [The more derived Sapyginae are essentially cosmopolitan—absent only from the Australian region (Pate, 1947c)—and thus do not provide any useful data.] Although the cladogram is not being used here as evidence for former land connections, as was the purpose of Hennig (1966b) in his survey of the Diptera fauna of New Zealand, the rigorous principles which he outlined in that paper still apply.

Reconstructions of Pangaea and the sequence of events leading to fragmentation and rearrangement of the components, together with estimates of the times involved, have been attempted by various authors and are being steadily refined. The following sequence has been derived from information presented by Dietz & Holden (1970), Axelrod & Raven (1972), Fooden (1972), Raven & Axelrod (1972) and Heirtzler *et al.* (1973). Most of these authors have based their concepts on data derived from a wide variety of sources, in large part geophysical. This sequence should, nevertheless, be regarded merely as the best estimate derivable from their data.

About 200 million years (m.y.) ago (during the Triassic) there was apparently a single land mass, Pangaea, surrounded by the universal ocean, Panthalassa, an arm of which formed the Tethys Sea separating Eurasia and Africa. The first rift occurred in the west and separated North America from South America and Africa, resulting in two continental areas, Laurasia and Gondwana, with tenuous contact maintained across the Gibraltan area (180 m.y., late Triassic—early Jurassic). About 150 m.y. ago (middle Jurassic), the Indian Ocean first opened from the east, separating East Gondwana (consisting of Australia-New Guinea, New Zealand and Antarctica) from West Gondwana (India, Madagascar, Africa and South America) although contact was maintained between Antarctica and South America. The next rift occurred within West Gondwana when South America split off from Africa (110 m.y., mid-Cretaceous), although these two continents remained reasonably close to each other for perhaps another 20 m.y. because their relative movement in the north resulted from a shear fault (similar to the San Andreas Fault in California). The next separation was that of New Zealand from

West Antarctica (80 m.y., late Cretaceous), thus splitting East Gondwana. Shortly thereafter (70 m.y.) India separated from Africa and Madagascar and began its migration north-eastward. About 60 m.y. ago (late Cretaceous—Paleocene) Madagascar split off from Africa and, as a result of rotational movements, the Arabian section of the African plate came into contact with Eurasia, cutting off the Mediterranean Sea from the western extremity of the Tethys. Not long after this (50 m.y., Eocene) North America and Greenland finally separated from Europe, although this rift had gradually been extending northwards since its initiation more than 80 million years before. At about the same time, Australia-New Guinea split off from East Antarctica and moved northward, contacting the eastern region of the Asian plate about 20 m.y. ago (Miocene). India collided with Asia about 15 m.y. ago and North and South America were linked only about 10 m.y. ago (early Pliocene). In addition, Antarctica only moved to its polar position within the last 40 m.y., after Australia had separated from it, its climate up to that time having been much milder than presently. Also, New Caledonia remained linked to (or at least close to) Australia for a short time after New Zealand had separated from the rest of East Gondwana.

The present disjunct Holarctic distribution of *Fedtschenkia* (Fig. 93; Guiglia, 1972) probably represents the relicts of a more widespread group which was undoubtedly of Laurasian origin. (The Sapyginae have apparently radiated from this area, perhaps relatively recently since they are not found in the Australian region.) The Myrmosinae (Fig. 94) are also confined to the Holarctic region although the single modern representative of the derived genus *Protomutilla* occurs in the Oriental region. Fossil specimens of *Protomutilla* are, however, from Baltic amber (Bischoff, 1915), so that members of this group were probably present throughout Eurasia. Apparently both the Fedtschenkiinae and the Myrmosinae originated on Laurasia and dispersed throughout this area after the splitting of Pangaea into Laurasia and Gondwana. Even after this break, however, there was still contact (at least intermittently) across the region of Gibraltar, which may explain the presence of *Myrmosa* in North Africa (although this is perhaps more likely a later development).

By contrast, the Pseudophotopsidinae (Fig. 95) is presently distributed across the northern section of Africa, Arabia and into southwestern Asia. The Ticoplinae (Fig. 96) is predominantly African although apparently absent from the Saharan area (perhaps a secondary development because of ecological changes), and also occurs in India and Spain. The Rhopalomutillinae (Fig. 97) is again mainly tropical African but with representatives in the Oriental region.

Since these three are the most basal groups of Mutillidae (apart from the Myrmosinae), it seems that the center of origin for this section of the family was the African plate, and probably its northern section. This likely resulted from the introduction of an ancestral form across the Gibraltan region at about the time that the final break occurred between Laurasia and Gondwana. The ancestral form gave rise to the Pseudophotopsidinae which apparently spread to the east and eventually across the Arabian area and on to the Eurasian plate after contact was reestablished there. The most generalized species of *Pseudophotopsis* is probably *P. continua* (ocelli and dorsal mesosomal sutures in the female the least reduced) which is widespread in North Africa. The more eastern species are generally more highly derived (e.g., *P. syriaca*), which supports this pattern of dispersal.

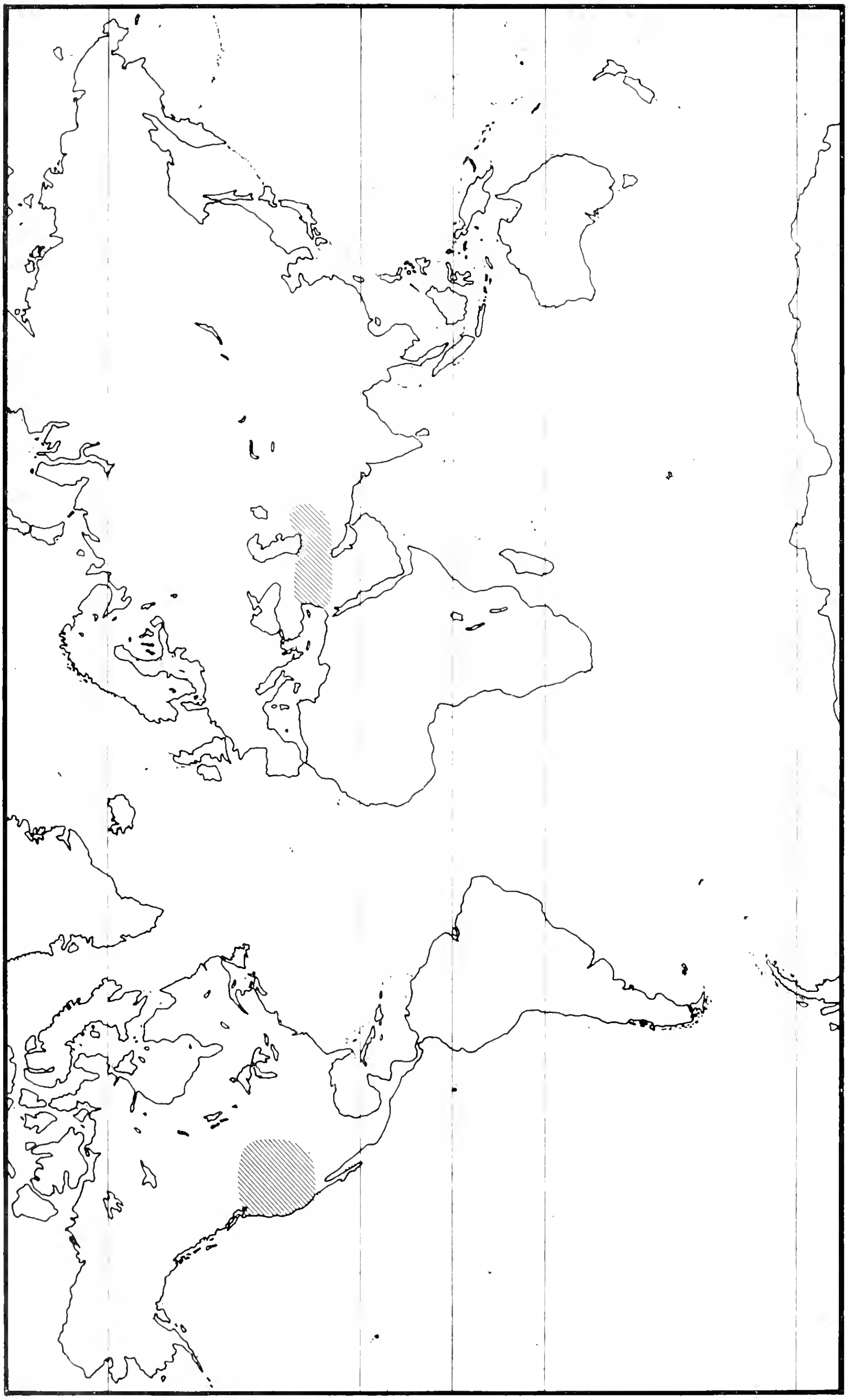


FIG. 93. Geographic distribution of Fedtschenkiinae (Sapygidae).

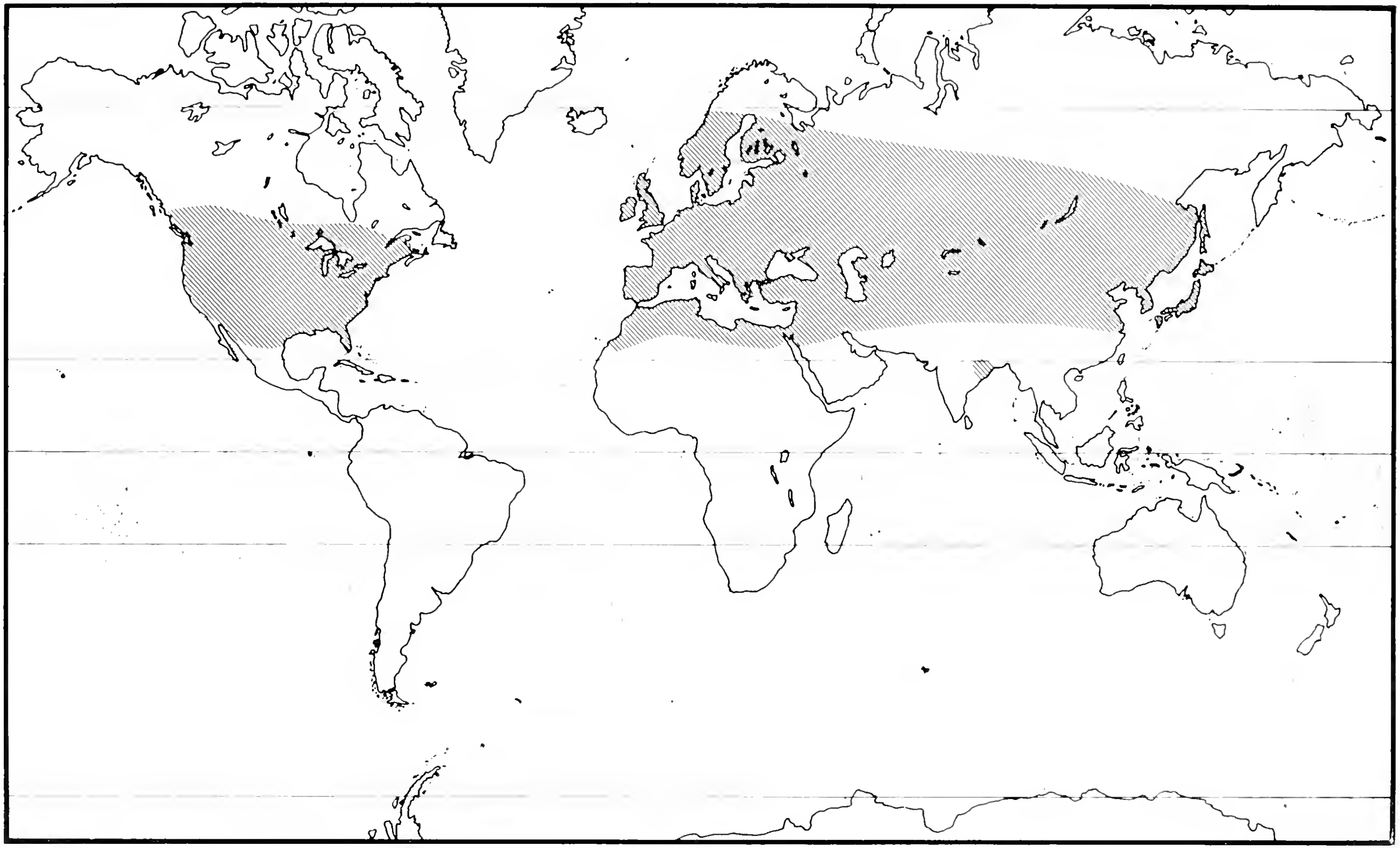
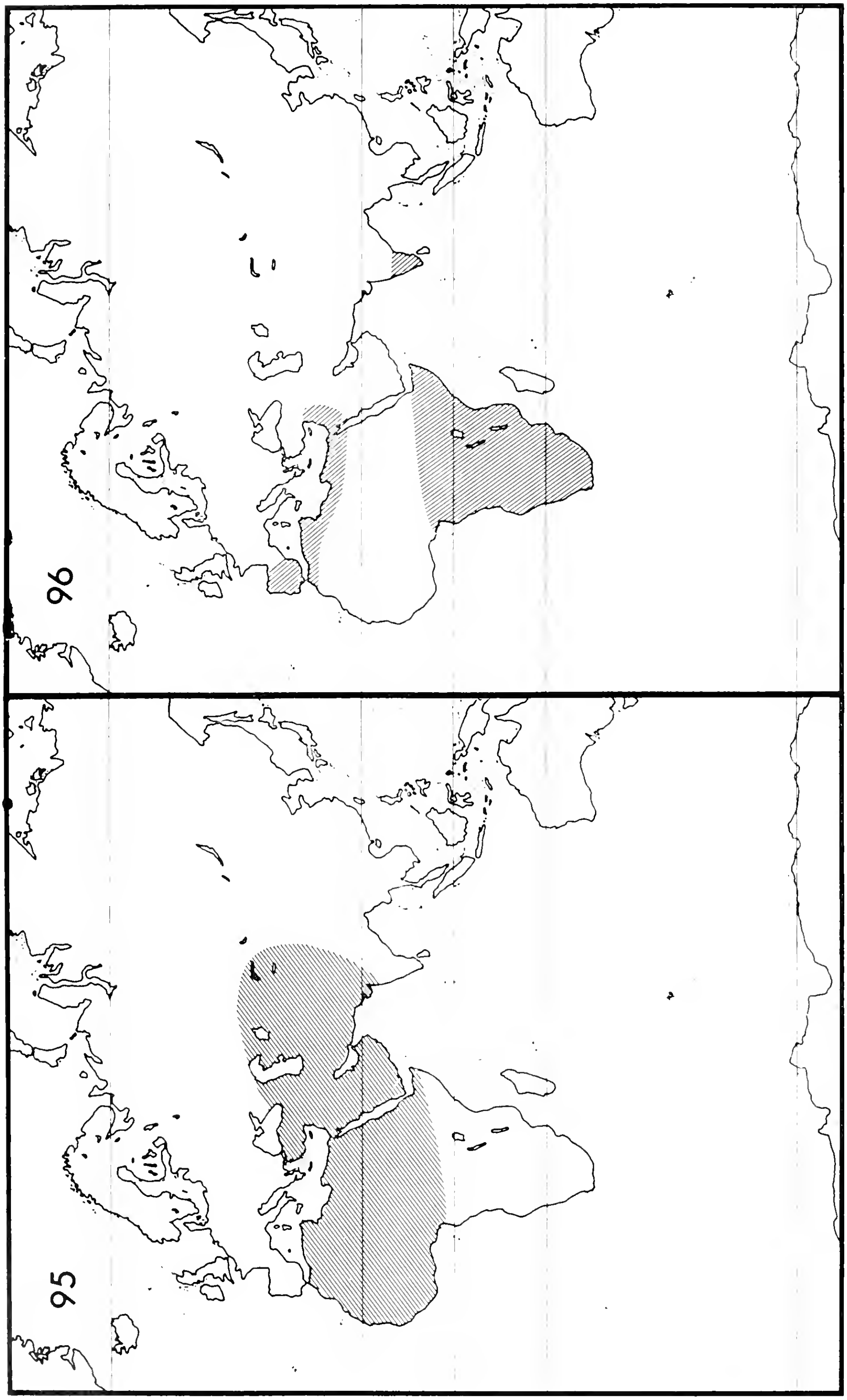
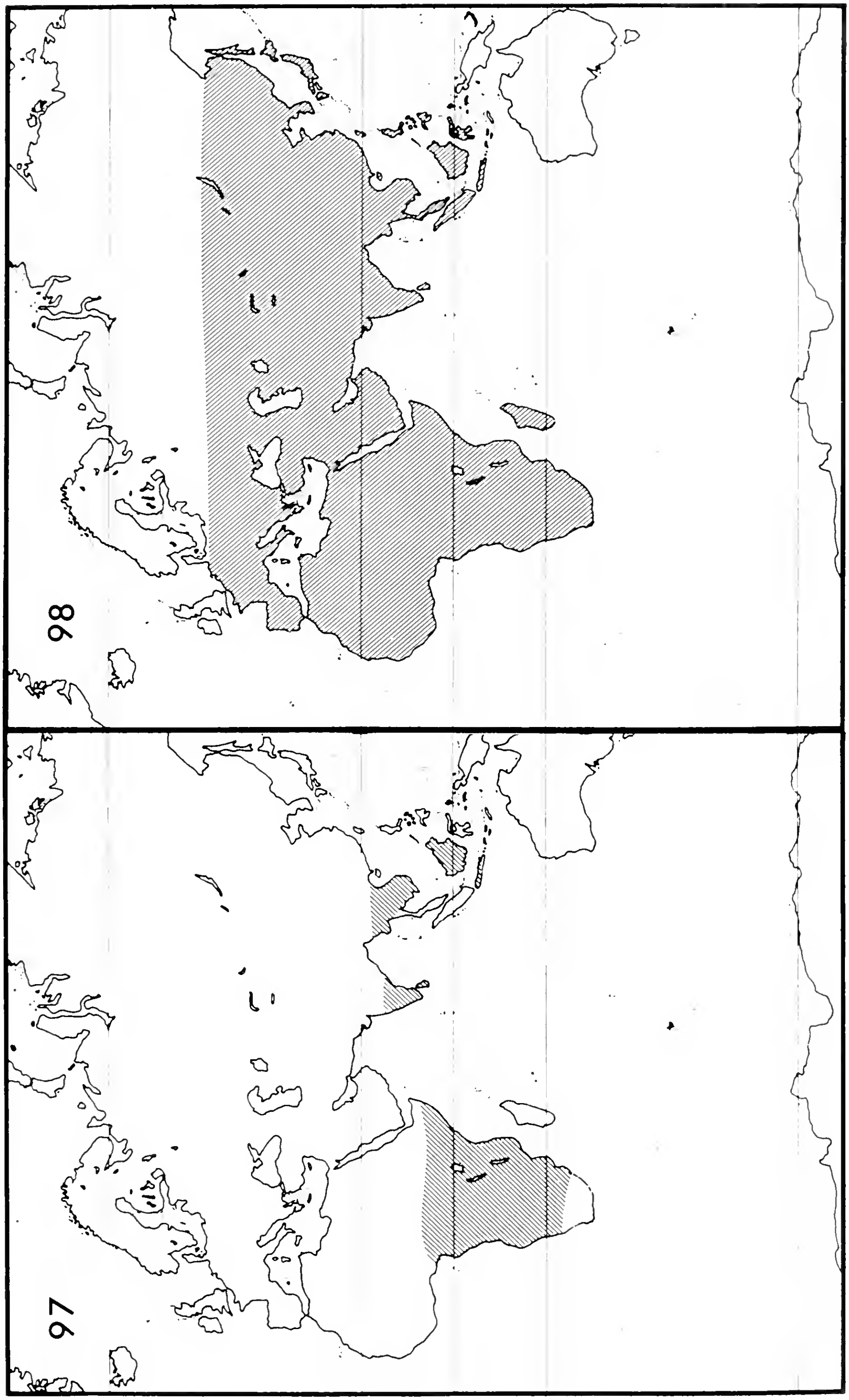


FIG. 94. Geographic distribution of Myrmosinae (Mutillidae).



FIGS. 95-96. Geographic distribution of subfamilies of Mutillidae. 95, Pseudophotopsidinae; 96, Ticoplinae.



FIGS. 97-98. Geographic distribution of subfamilies of Mutillidae. 97, Rhopalomutillinae; 98, Myrmillinae.

The ancestral Ticoplinae probably arose somewhat farther south and east on the African plate. This group then may have diversified and spread on to the Indian plate while it was still in contact with Africa or at least close to it. At least one member apparently crossed the Gibraltan area to Europe, probably much more recently. Although it is difficult to state which genus of Ticoplinae is the most generalized, it seems clear that the most specialized morphologically is *Smicromyrmilla,* which is also the most widespread at present, and the one which occurs in both Spain and India, as well as Africa. (Some Indian species have the most highly derived males of the subfamily since they are completely apterous and lack any traces of sutures on the mesosomal dorsum.) This is not inconsistent with the concept of diversification of the group from an African center.

A similar sequence may have led to the origin of the Rhopalomutillinae, which seem to be adapted to more tropical conditions than the Ticoplinae. Rhopalomutillinae also probably spread from the African to the Indian plates, and when India came into contact with the Eurasian plate there was apparently additional diversification and dispersal of this subfamily to the east into Indo-China and further to Borneo and Java. From morphological considerations it appears that the most generalized species of *Rhopalomutilla* occur in Africa (e.g., *R. tongaana*; least modified hypopygium in the male) and some of the more highly derived are the Asian species (e.g., *R. oceanica*), a distribution not inconsistent with the above ideas.

These three basal subfamilies were probably confined to the east African region, at least initially, since none of them occurs in the New World. This may have resulted from the presence of epicontinental seas over much of northern and western Africa during the Cretaceous (Cracraft, 1973). The absence of the Ticoplinae and Rhopalomutillinae in Madagascar is somewhat puzzling and requires further elucidation. These groups may, however, have become extinct there, perhaps as a result of competition from the more advanced subfamilies. Until more data have been gathered on these groups, further speculation is pointless.

The subfamily Sphaeropthalminae is cosmopolitan in distribution (Fig. 99). However, the more generalized tribe (Dasylabrini) is confined to the Ethiopian, southern Palearctic and Oriental regions (with one species of *Stenomutilla* on the Solomons in the Australasian region). The most widespread genera are *Dasylabris* and *Stenomutilla,* both of which extend over approximately the entire range of the subfamily. The most derived genera are probably *Apteromutilla* and *Brachymutilla* (both with apterous males), both of which are confined to the southern tip of Africa. This distribution is not inconsistent with an origin for the group in north-eastern Africa with the spread of two vigorous genera into Eurasia, either across Arabia when contact was established there or by transport on the Indian plate, or both. Diversification and dispersal also apparently occurred toward the south and west across Africa.

The tribe Sphaeropthalmini (Fig. 99) occurs entirely in the New World and the Australasian region, apart from the genus *Cystomutilla* (two species) which now occurs in the Mediterranean region and Japan, a somewhat enigmatic situation. Except for *Cystomutilla* (which may actually be misclassified as a result of parallel development of certain characters), this distribution may have resulted from a single introduction of an ancestral sphaeropthalmine from Africa into South America at about the time that these two continents separated. After becoming es-

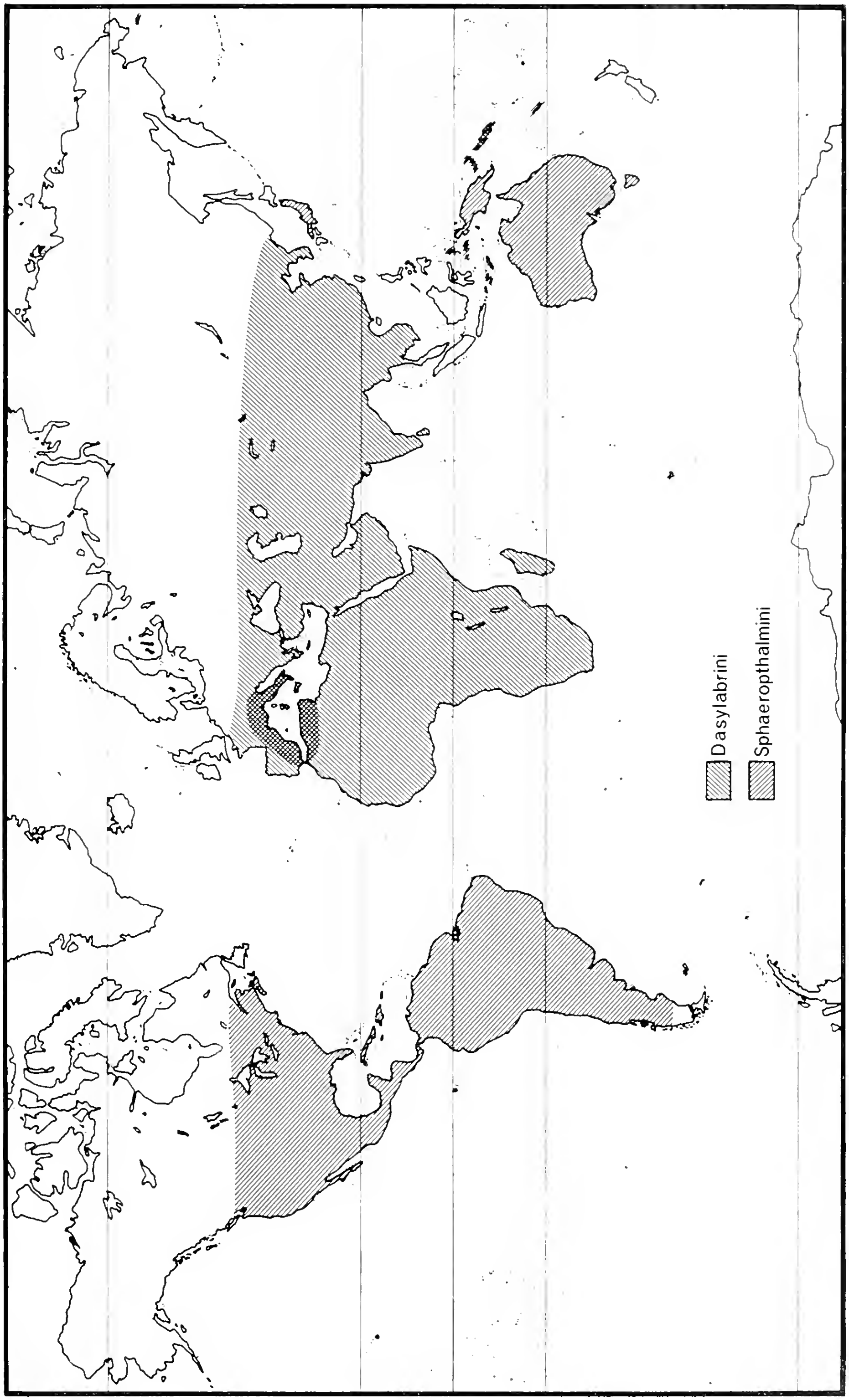


FIG. 99. Geographic distribution of both tribes of Sphaeropthalminae (Mutillidae).

tablished in South America, the Sphaeropthalmini apparently radiated extensively and rapidly, establishing two basic lines at this time (viz., Pseudomethocina and Sphaeropthalmina). Since Australia and South America were linked via Antarctica until much more recently (50 m.y. ago), most of the Australian fauna (predominantly Sphaeropthalmina, very few Pseudomethocina and Mutillini) could easily have been derived from the South American. In fact the most highly derived members of the Sphaeropthalmina seem to be various members of the "*Ephutomorpha* complex," especially those on New Guinea. (This type of progression is an important factor in establishing probable routes of dispersal; Hennig, 1966b.) Furthermore, there are various Australian species which share some highly characteristic derived features with a few South American genera (e.g., the flangelike expansions of the antennal tubercles in the females of *Scaptodactyla*), and the females of the South American (southern Chile and Argentina) genus *Neomutilla* are remarkably like some "*Ephutomorpha*" species in general facies. It may also be significant that there are many highly metallic species (often blue or green) in the Australasian region (especially New Guinea), whereas the only other metallic Sphaeropthalminae occur in the southern section of South America (e.g., females of *Neomutilla* and *Dimorphomutilla suavissima*). (Marked similarities have been found between the Australian and southern South American representatives of various insect groups—see Brundin, 1966; O'Brien, 1971.) That the introduction of mutillids into Australia by this route was probably relatively recent, is indicated by their absence in New Zealand, so that this dispersal probably occurred less than 80 m.y. ago. Furthermore, there are very few species (although at least two) on New Caledonia, which probably split from Australia soon after the New Zealand—Antarctica separation. The North American sphaeropthalmine fauna is not as rich as that of South America and was apparently derived from it by a few introductions, probably when contact between the two continents was established relatively recently (10 m.y. ago).

The subfamily Myrmillinae (Fig. 98) is distributed across the Ethiopian, most of the Palearctic and the Oriental regions. The richest representation is in Africa with fewer genera in the peripheral areas and only two species in Madagascar. (These last are species of *Pygomilla*, and not *Ctenotilla* as was indicated by Krombein, 1972.) In some respects the Indian fauna is more similar to that of Africa than that of Europe. The genus *Squamulotilla*, for example, is present in Africa, India and farther east in the Oriental region. This may merely reflect ecological similarities, but perhaps indicates spread of this genus, at least, on to the Indian plate from Africa and subsequent dispersal from India on to Asia. The most highly derived species of *Squamulotilla* also tend to be those which occur the farthest east (e.g., *S. byblis*, with extreme development of the ventral lamella on the mesopleural ridge in the female, in the Philippines). Again, it appears that this subfamily originated in north-eastern Africa with subsequent dispersal, probably on to the Indian plate as well as more direct movement into Eurasia across the Arabian region.

The subfamily Mutillinae is worldwide in distribution, like the Sphaeropthalminae. Unlike the Sphaeropthalminae, however, this subfamily is richest in the Old World, except for the Australian region. The two tribes of Mutillinae also have essentially complementary distributions (Fig. 100). The Mutillini is entirely an Old World group except for one genus (*Timulla*), which is cosmopolitan. This genus shows signs of recent rapid specia-

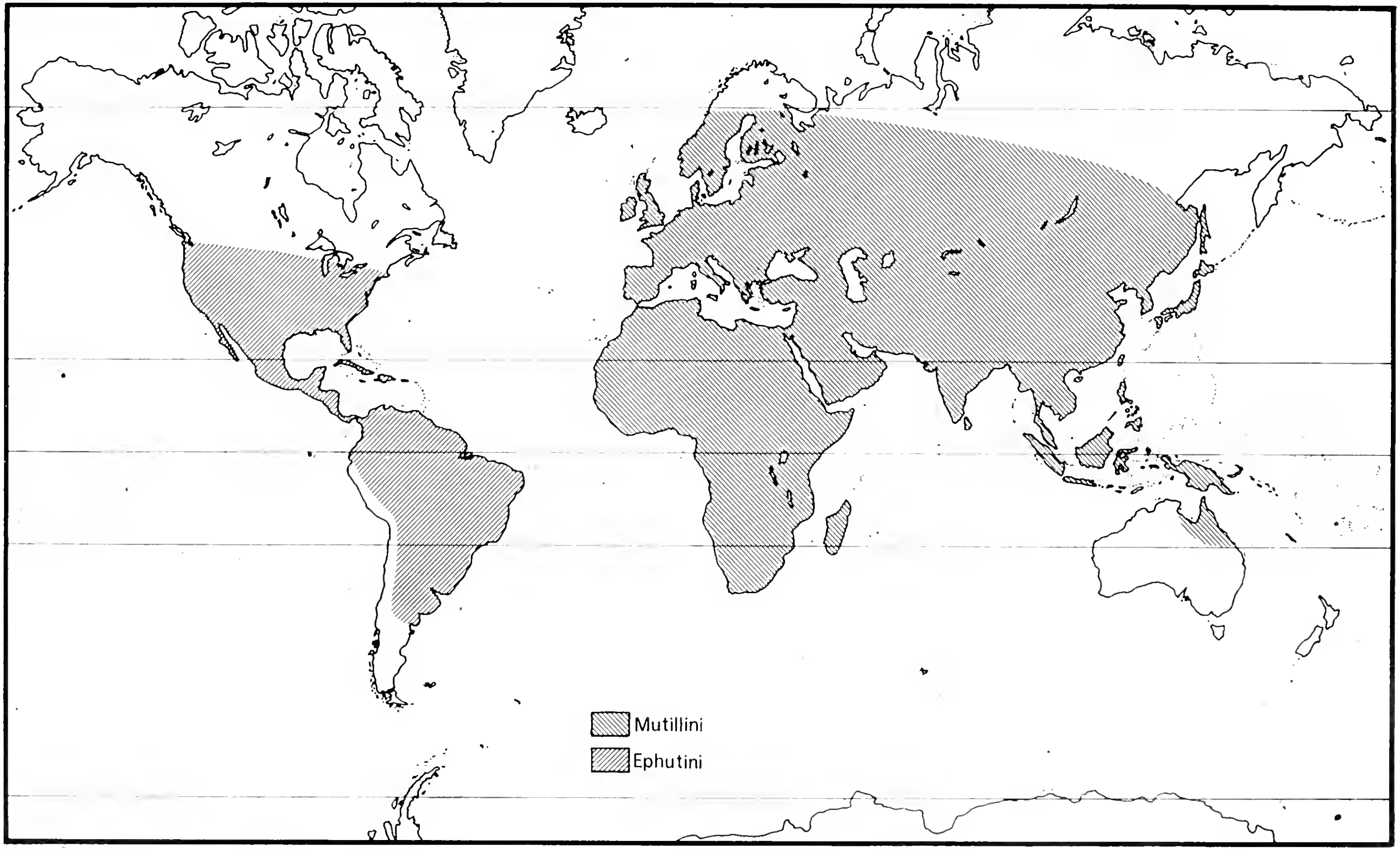


Fig. 100. Geographic distribution of both tribes of Mutillinae (Mutillidae); however, that of Mutillini excludes *Timulla* (cosmopolitan), and *Chaetotilla* and *Physetopoda* (each known from one specimen from the New World and not seen by me).

tion and so may represent a more recent introduction into the New World, perhaps via the Beringian connection. [A problem is that the species of *Timulla* with the most highly complex male genitalia (in terms of asymmetry and development of the endophallus) are African and Indian, but various species from eastern Asia and most New World species have the genitalia more nearly symmetrical (Peterson, *in litt.*). The latter would thus intuitively seem to be the less highly derived forms, which would suggest dispersal from the New World through Asia to Africa. Additional work is definitely necessary to clarify the complexities of this genus and its relatives before these problems can be solved.] The Mutillini is most richly represented in Africa, and only two species (*Odontomutilla australica* and *Timulla cooki*) extend into northern Australia. The spread into the Australasian region is thus obviously very recent and has probably occurred since the Australian and Asian plates came into contact. There are in addition two genera of Mutillini in the New World, *Chaetotilla* from Argentina and *Physetopoda* from Haiti, each known from only one specimen and not seen by me (I could not find the types in the Paris Museum), so that comment on their distribution and origin is impossible at this time.

The tribe Ephutini (Fig. 100) is entirely New World in distribution and has its greatest diversity in northern South America. It seems likely that this group also arose from a single introduction of the ancestral form from Africa to South America at about the time that these two continents separated. There was later dispersal from South America to North America, probably when these continents came into contact, but apparently no dispersal to Australia. This may have been because the ephutines seem generally to be adapted to more tropical conditions than are many sphaeropthalmines.

It thus appears (Fig. 101) that the Mutillidae probably arose in Laurasia and diversified on the northern and eastern part of the African plate less than 180 million years ago, from where dispersal occurred on numerous occasions to India and Eurasia. Two introductions from Africa into South America probably gave rise to almost the entire New World fauna and also to most of the Australasian fauna by a few introductions across Antarctica from South America less than 80 million years ago.

Since the cladogram can be applied in this way to explain the distribution of Mutillidae in accordance with the sequences of events involved in the breakup of the continents (derived from other evidence), it appears to be supported (or at least not contradicted) by the distributional data. The likelihood that the cladogram reflects the true phylogeny of the Mutillidae is thus enhanced.

GENERAL CONCLUSIONS

The entire investigation of the Aculeata, including the section on the Mutillidae, has led to the proposed classification presented in Tables VI and VII. Since it has not been possible to examine each taxon with equal thoroughness, the lower levels remain to be clarified by subsequent workers in the majority of instances. Furthermore, it is quite possible that the conclusions drawn at the higher levels may in some cases prove to be unwarranted when more complete representation is obtained for various groups. Certainly, some of the relationships shown on the cladogram (such as the proximity of Scoliidae to Vespidae and their remoteness from Tiphiidae) are unexpected. These definitely warrant more intensive examination. In fact, even if the only result of this investigation is the stimulation

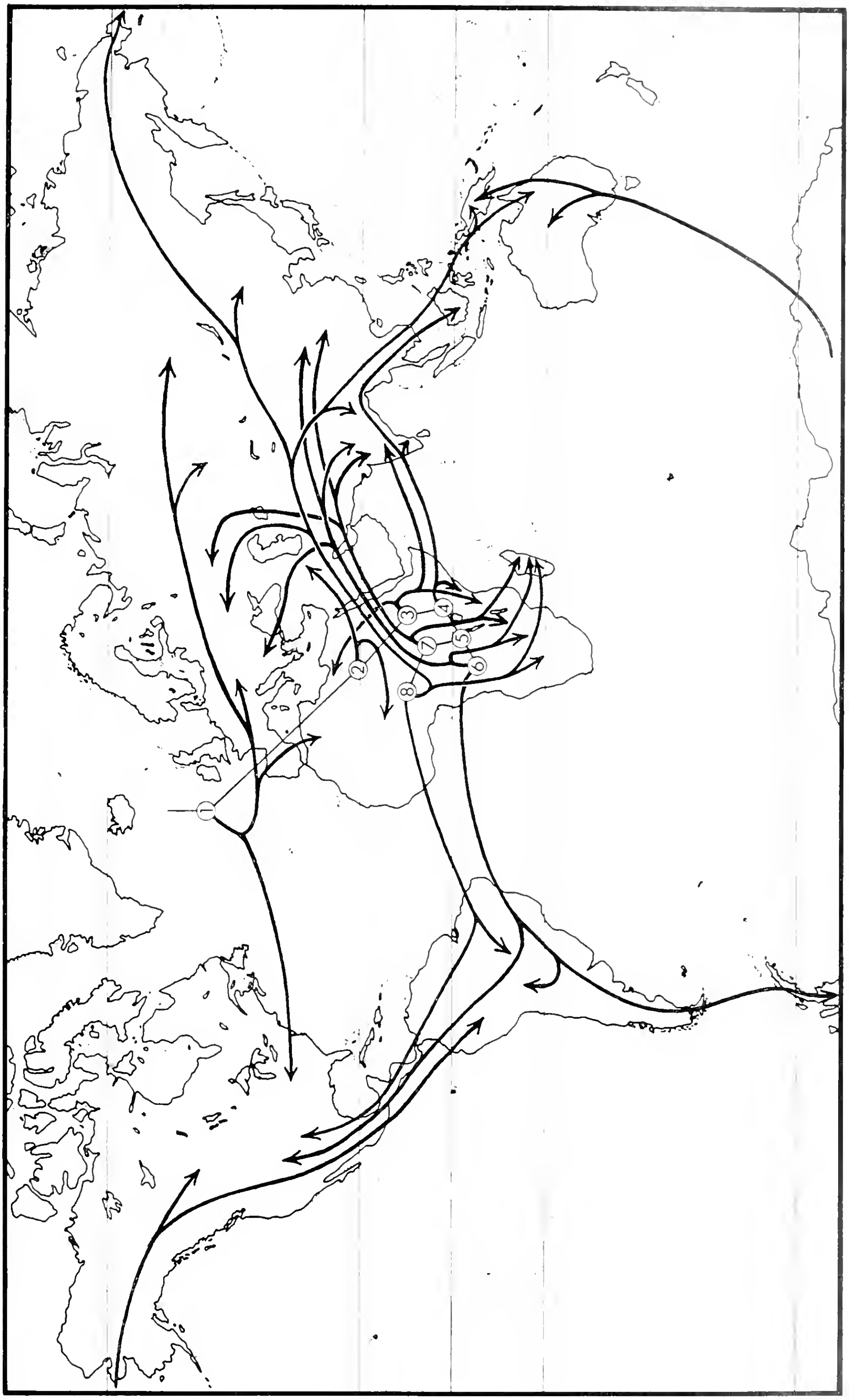


FIG. 101. Cladogram of nine taxa of Mutillidae (light straight lines and numbered nodes) and probable routes of dispersal (heavy lines) (see text for discussion).

TABLE VI. Proposed classification of the Hymenoptera Aculeata.

Superfamily	Family	Subfamily[a]
BETHYLOIDEA	Plumariidae	
	Bethylidae	
	Scolebythidae	
	Cleptidae	
	Chrysididae	
	Loboscelidiidae	
	Dryinidae	
	Sclerogibbidae	
	Embolemidae	
SPHECOIDEA		
(Spheciformes)	Ampulicidae	
	Sphecidae	
	Larridae	
	Mellinidae	
	Pemphredonidae	
	Astatidae	
	Philanthidae	
	Nyssonidae	
(Apiformes)	Colletidae	
	Halictidae	
	Oxaeidae	
	Andrenidae	
	Melittidae	
	Fideliidae	
	Megachilidae	
	Anthophoridae	
	Apidae	
VESPOIDEA		
(Vespiformes)	Tiphiidae	Anthoboscinae
		Thynninae
		Myzininae
		Methochinae
		Tiphiinae
		Brachycistidinae
	Sapygidae	Fedtschenkiinae
		Sapyginae
	Mutillidae[b]	
	Sierolomorphidae	
	Rhopalosomatidae	
	Pompilidae	
	Bradynobaenidae	Typhoctinae[c]
		Chyphotinae
		Apterogyninae
		Bradynobaeninae
	Scoliidae	
	Masaridae	
	Eumenidae	
	Vespidae	
(Formiciformes)	Formicidae	

[a] Subfamilies indicated only for taxa previously considered to comprise the tiphioid-mutilloid group, and the Sapygidae.

[b] For details of subfamily divisions see Table VII.

[c] Comprises two tribes, Eotillini and Typhoctini.

Table VII. Proposed classification of the Mutillidae.

Subfamily	Tribe	Subtribe
Myrmosinae		
Pseudophotopsidinae		
Ticoplinae		
Rhopalomutillinae		
Sphaeropthalminae	Dasylabrini	
	Sphaeropthalmini	Pseudomethocina
		Sphaeropthalmina
Myrmillinae		
Mutillinae	Mutillini	Mutillina
		Smicromyrmina
	Ephutini	

of critical studies which may refute the conclusions presented here, then it will have accomplished its purpose.

Those conclusions which are most at variance with the current ideas on the classification of the Hymenoptera Aculeata, may be summarized as follows:

a) The Aculeata should be considered as comprising only three superfamilies (Bethyloidea, Vespoidea, Sphecoidea) as opposed to the previously commonly accepted seven.

b) The Scolebythidae and Plumariidae should be included with seven other familes in the Bethyloidea.

c) The Vespoidea should be divided into two informal groups, the Vespiformes (with 11 families) and the Formiciformes (1 family).

d) The Sphecoidea should be divided into two informal groups, the Spheciformes (with 8 families) and the Apiformes (9 families).

e) The Myrmosinae and Bradynobaeninae should be removed from the Tiphiidae.

f) The "Eotillinae," "Typhoctinae" and "Apterogyninae" ("Chyphotini" and "Apterogynini") should be removed from the Mutillidae.

g) The family Bradynobaenidae should be recognized as comprising the subfamilies Typhoctinae, Chyphotinae, Apterogyninae and Bradynobaeninae.

h) The subfamily Typhoctinae should be recognized as comprising two tribes, the Typhoctini and Eotillini.

i) The family Mutillidae should be divided into seven subfamilies, the Myrmosinae, Pseudophotopsidinae, Ticoplinae, Rhopalomutillinae, Myrmillinae, Mutillinae and Sphaeropthalminae.

j) The subfamily Mutillinae should be recognized as comprising two tribes, the Mutillini and Ephutini.

k) The tribe Mutillini should be recognized to comprise two subtribes, the Mutillina and Smicromyrmina.

l) The subfamily Sphaeropthalminae should be divided into two tribes, the Dasylabrini and Sphaeropthalmini.

m) The tribe Sphaeropthalmini should be recognized as comprising two subtribes, the Pseudomethocina and Sphaeropthalmina.

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THE UNIVERSITY OF KANSAS
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TAXONOMY OF FIVE NEARCTIC SUBGENERA OF *COELIOXYS* (HYMENOPTERA: MEGACHILIDAE)

By

J. R. BAKER

Vol. 50, No. 12, pp. 649-730 August 18, 1975

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Taxonomy of Five Nearctic Subgenera of *Coelioxys* (Hymenoptera: Megachilidae)[1]

By J. R. Baker[2]

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ABSTRACT

The taxonomy of five subgenera of *Coelioxys* which are restricted primarily to the North American continent are reviewed. The recognition of a surprising amount of infraspecific variation in many species allowed the synonymization of 64 names into 25 presumably valid species. The following species are described as new: *C. mitchelli*, *C. nodis*, *C. oaxacana*, and *C. serricaudata*. Keys are presented to the subgenera of North American *Coelioxys* and to species in the five subgenera treated herein. Distribution maps, host records where known, season of flight, a discussion of habitat where remarkable, of geographic variation where noticed and of comparative comments complete the description or redescription of each species in the five subgenera.

INTRODUCTION

Five of fourteen New World subgenera of bees in the genus *Coelioxys* are almost entirely confined to the North American continent. This paper concerns these five nearctic subgenera and is intended to complement a review of the New World subgenera of *Coelioxys* by Mitchell (1973) which set up 13 new subgenera. Therefore this paper may appear to be shallow in the diagnostic treatment at the subgeneric level. Mitchell provides a thorough diagnosis of each subgenus, however, and it seems unnecessary to repeat such information here. Almost none of Mitchell's work is concerned with taxonomy at the species level.

Bees of the genus *Coelioxys* are so distinctive that since Latreille (1809) erected the genus, not a single bee now considered to be in *Coelioxys* has been described in another genus. So distinctive are these bees, in fact, that Dalla Torre and Friese (1894) set up the subfamily Coelioxinae based upon the genus *Coelioxys*. Cockerell and Robbins (1910) changed the spelling

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to Coelioxynae. The group was last given this rank by Hicks (1926). Robertson (1903), slightly more conservative, erected the tribe Coelioxyini but was the only and last (1929) person to use this rank for *Coelioxys.*

The genus *Coelioxys* shares certain characters with the genus *Megachile:* The notaulices are linear, arolia between the claws are lacking, and the basal metasomal tergum is shallowly concave anteriorly. *Megachile* and *Chalicodoma* are the most closely related genera. However, *Coelioxys* differs from them in that the metasoma has no scopa, the axilla is elongate, the pronotal tubercle is carinate, and the mesepisternum has an anterior and a lateral surface separated by a vertical carina. The metanotum and posterior surface of the scutellum are perpendicular, and the fore coxae of both sexes possess spines which are usually distinct. In general, *Coelioxys* species are black or very dark brown bees with white fasciae on the metasoma. The metasomas of females taper posteriorly, and the metasomas of males are denticulate or spinose apically. A character separating New World *Coelioxys* from all other New World megachilids is the presence of ocular hairs (however, the name *Coelioxys* does not mean "hairy eyes" as interpreted by Stephen, Bohart and Torchio (1969:54) but rather, according to Shuckard (1866), is derived from two Greek words, *koilia* and *oxus,* which mean "acute abdomen").

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Of the many people who have contributed to this study, special thanks must be extended to Dr. Charles D. Michener whose time, constructive criticism, advice and encouragement were frequently made available. Special thanks are also extended to Dr. T. B. Mitchell who originally encouraged the idea of working with this group and who made his personal collection available for my use.

The following people and institutions loaned specimens and made types available and are gratefully thanked: W. W. Moss, Academy of Natural Sciences of Philadelphia; J. G. Rozen, American Museum of Natural History; F. G. Werner, University of Arizona; E. P. Rouse, University of Arkansas; V. M. Tanner, Brigham Young University; G. R. Else, British Museum (Natural History); J. J. Pasteels, University Libre de Bruxelles; P. H. Arnaud, Jr., California Academy of Sciences; P. D. Hurd, then of the University of California, Berkeley; R. O. Schuster, University of California, Davis; E. I. Schlinger, P. H. Timberlake (personal collection) University of California, Riverside; A. R. Moldenke, (personal collection) University of California, Santa Cruz; H. E. Milliron, Canada Department of Agriculture; G. Wallace, Carnegie Museum of Natural History; U. N. Lanham, University of Colorado Museum; G. I. Stage (personal collection), University of Connecticut; L. L. Pechuman, Cornell University; M. E. Prokop, Field Museum of Natural History; H. V. Weems, Florida Department of Agriculture and Consumer Services, Division of Plant Industry; W. T. Atyeo, University of Georgia; H. W. Smith, University of Idaho; W. E. LaBerge, Illinois Natural History Survey; D. W. Ribble, University of Indiana, Kokomo; C. D. Michener, University of Kansas; H. D. Blocker, Kansas State University; R. R. Snelling, Los Angeles County Museum of Natural History; T. E. Moore, University of Michigan; K. MacArthur, Milwaukee Public Museum; P. J. Clausen, University of Minnesota; B. C. Ratcliffe, University of Nebraska; T. B. Mitchell (personal collection), North Carolina State University; E. Cross, Northwestern State College, Natchitoches, Louisiana; C. A. Triplehorn, Ohio State University; C. E. Hopla, University of Oklahoma; W. A. Drew, Oklahoma State University; R. B. Roberts, Oregon State University; K. C. Kim, Pennsylvania State University; W. Ferguson, San Jose College; H. R. Burke, Texas A and M University; G. I. Stage, then of the National Natural History Museum; W. J. Hanson, Utah State University; J. D. Eves and M. T. James, Washington State University; L. J. Bayer, University of Wisconsin; R. J. Lavigne, University of Wyoming.

Finally I wish to thank my wife, Faye H. Baker, for her exceeding patience and help during the preparation and typing of this manuscript.

METHODS

Approximately 8,000 specimens were examined. Examination of type specimens was expedited by carrying a synoptic collection to various museums. Thus "homotypes" could be selected and later scrutinized at a more leisurely pace. When none of the specimens in the synoptic collection agreed (within a reasonable degree) with a type, notes describing the variation and photographs were made. Type specimens were run through the appropriate keys and compared with the appropriate descriptions so that all descriptions agree with all type specimens in each synonymy. After consideration of the general lack of reliability of the characters of hidden sterna and genital armature at the species level, a decision was made not to dissect out these parts of type specimens. At least these structures will be intact should a future systematist discover more stable characters than I have been able to find in these hidden segments.

Drawings of adults were made with the aid of an ocular grid except for the hidden sterna of males which were cleared in hot KOH, mounted on slides, and projected through a microscope for drawing. Use of an incandescent bulb in the illuminator of the binocular microscope seemed to be more effective than fluorescent lighting in the differentiation of dark brown areas of the integument.

Literature citations in the synonymies are restricted to articles in which synonymies were made and to biological studies. Extensive citations are given in a thesis by Baker (1972).

Characters are numbered throughout each description in order to facilitate comparisons among species. To save space, references to characters of a species are deleted when they agree with the description of those characters for the first species treated in the group. Thus if a number does not appear in a description, that character agrees with the description of the first species in the group. Although this method may at first seem confusing, the value in space saved will undoubtedly outweigh the value of redundancy.

Flower records are given in a thesis by Baker (1972).

Host records and season of flight were taken from specimen labels (or from the literature, as noted).

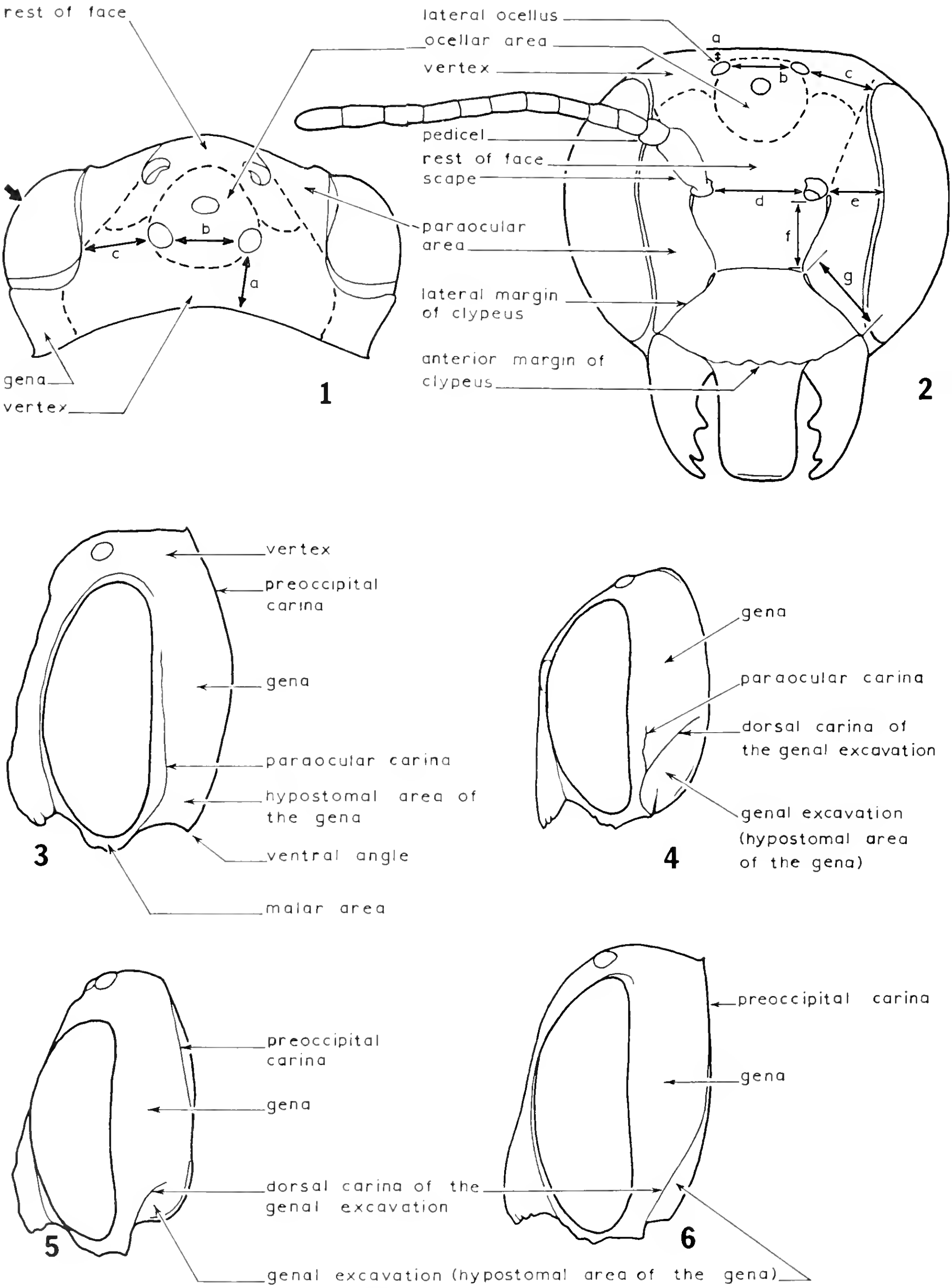
Küchler's (1964) map of potential vegetation types of the contiguous United States was used to try to find some correlation between species distributions and vegetation types. Many species extend through so many types that they appear to be distributed regardless of vegetation type. Some of the more restricted bees, however, seem to be associated with a group of vegetation types such as western coniferous forests or western shrub and grassland.

The distribution of any intraspecific variants noted was examined to see if there was a relation to geography. Size, color (of the legs especially), and crenulations of the sixth tergum in males, were all found to vary geographically in some species.

CHARACTERS

The following list enumerates characters found to vary among the species of the five subgenera of *Coelioxys* in this study. Explanatory comments are added wherever they seem to facilitate understanding. The Characters are numbered to correspond to the numbers used in descriptions (the first number for females, the second number for males).

(1, 24) LENGTH: measured in a dor-



FIGURES 1-6. 1, 2, Dorsal and frontal views of head of *Coelioxys texana* female (arrow, angle from which measurement of ocular hair made). a, ocelloccipital distance; b, interocellar distance; c, ocellocular distance; d, interantennal distance; e, antennocular distance; f, clypeoantennal distance; g, lateral margin of clypeus. 3-6. Lateral views of male *Coelioxys* heads. 3, *C. texana;* 4, *C. funeraria;* 5, *C. sodalis;* 6, *C. edita.*

sal view by an ocular scale in a binocular microscope. Length is the distance (in mm) from the bases of the antennae to the tip of the metasoma. By measuring from the bases of the antennae, compensation was made for specimens in which the normally hypognathous head is turned up to the prognathous position.

(2, 25) Integument: punctation and color.

(3, 26) Pubescence: color, density, form. Pubescence of the tarsi is almost invariably golden.

(4, 27) Ocular hairs: length. Ocular hairs are longest along the posterior margin of the compound eye. The measurement for all descriptions was made on the disc of the eye (Fig. 1) at the middle.

(5, 28) Clypeus: amount and type of pubescence, texture of integument, and conformation of the anterior margin.

(6, 29) Clypeoantennal Distance and the Lateral Margin of the Clypeus (*f* and *g* in Fig. 2): relative lengths.

(7, 30) Paraocular Area (Fig. 2): amount and type of pubescence (subject to wear), and integumental characters (when the integument is normally exposed in most specimens).

(8, 31) The Rest of the Face (Fig. 2): pubescence, conformation, and punctation.

(9, 32) The Clypeoantennal, Interantennal, and Antennocular Distances (*f*, *d*, and *e* in Fig. 2): relative lengths.

(10, 33) The Ocellar Area (Figs. 1, 2, roughly equivalent to Mitchell's (1973) subocellar area): conformation.

(11, 34) Ocelloccipital, Ocellocular, and Interocellar Distances (*a*, *c*, and *b* in Figs. 1, 2): relative lengths.

(12, 35) Vertex: punctation and pubescence.

(13, 36) Gena: width in relation to the width of the eye (measured at the broadest part of both structures in lateral view).

(14, 37) Hypostomal Area of the Gena: conformation, pubescence, angle of the posteroventral carina (the ventral angle). The hypostomal area of the gena varies greatly in pubescence and conformation between sexes among species and groups. This problem is most acute in males in which many times the ventral portion of the gena is deeply excavated. In *Coelioxys texana* the paraocular carina almost surrounds the eye and more or less defines the posterior margin of the malar area (Fig. 3). The gena sweeps from the vertex to the hypostomal carina without interruption. In *C. funeraria* a remnant of the paraocular carina remains posterior to the eye and another carina, the dorsal carina of the genal excavation, separates the gena from the genal excavation (Fig. 4). In *C. sodalis*, no remnant of the paraocular carina remains in the area of the gena (Fig. 5). In *C. edita* the dorsal carina of the genal excavation recurves dorsally where it merges with preoccipital carina (Fig. 6). In *C. rufitarsis* the condition of the genal excavation approximates that of *C. funeraria*.

(15, 38) Mandible: conformation. Wear may give the mandibles a more robust appearance.

(16, 39) Scutum: punctation and pubescence.

(17, 40) Mesepisternum: pubescence and punctation. The mesepisternum is divided into anterior and posterior surfaces by a distinct carina (Fig. 7). The lateral surface sometimes has minute punctures as well as larger punctures (Fig. 8). The anterior surface of the mesepisternum shows little variation throughout the five groups considered herein.

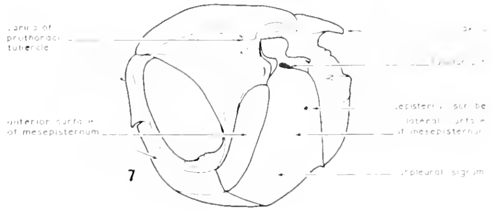
(18, 41) Scutellum: punctation, pubescence, and conformation of carina separating the dorsal and posterior surfaces in both dorsal and lateral views (Figs. 10 and 14 F).

(19, 42) Axilla: length.

(20, 43) Metanotum: pubescence.

(21, 44) Fore Coxal Spine: shape, size, and the direction of protrusion.

(22, 45) Metasomal Terga: color, pubescence, punctation, and the presence or absence of graduli and foveae (Fig. 9). The shapes of the apices of the sixth and seventh terga are sometimes specifically distinct (especially in males), and the general conformation of these segments is important at the subgeneric level.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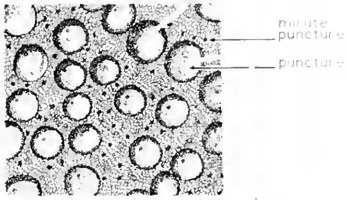
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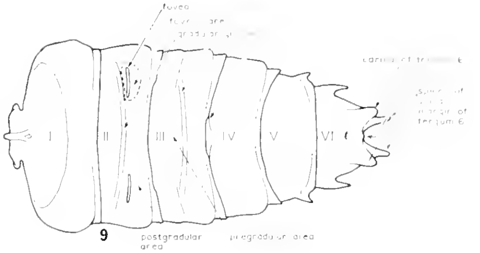
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Figures 7-9. Various *Coelioxys* parts. 7, Anterolateral view of mesosoma of female *C. texana;* 8, Portion of integument of mesepisternum showing minute and larger punctures of female *C. texana;* 9, Dorsal view of metasoma of male of *C. rufitarsis.* Roman numerals indicate tergum numbers.

(23, 46) Exposed Metasomal Sterna: punctation, pubescence, and conformation of the graduli. The apical margin of the sixth sternum of females displays a number of characters useful at the subgeneric and specific levels.

(47) Hidden Sterna and Genital Armature of Males: punctation, pubescence, and conformation. These characters are useful at the subgeneric level but are of less use, if any, at the species level.

KEYS TO SUBGENERA OR SPECIES

The following keys separate species of North American *Coelioxys* into subgenera or species (for species not included in the five subgenera covered by this study). All *Coelioxys* species for which specimens were available from Mexico and northward are included.

Distribution is used as a character only in the two following keys, where species not otherwise treated in this paper can be separated by range. Careful taxonomic studies will have to be done before morphological characters are found to separate the members of several groups of similar species, and some species currently separated may be found to be synonymous. For example, the western forms *Coelioxys gilensis* and *C. deani* will probably be found synonymous when a systematic review is made of that group as will likely also be the case with *C. modesta* and *C. scitula,* two eastern forms. However, the morphological differences separating *C. gilensis* and *C. deani* from *C. modesta* and *C. scitula* are subtle, and the decision to recognize these four names as two or one species will be a difficult one. Distribution separates the two groups readily, although the separation may be an artificial one.

Key to Females of North American *COELIOXYS.*

1. Ocellar area (Figs. 1-2) swollen, impunctate 2
   Ocellar area not swollen or if raised then closely punctate. 8
2. Sixth metasomal sternum broadly rounded to acute apically, not notched subapically (Fig. 14A-D) .... *Synocoelioxys*

Sixth metasomal sternum apically or subapically notched 3

3. Vertex between lateral ocellus and compound eye completely or almost impunctate, shining; scutellum almost impunctate medially, with a large, rounded projection posteriorly; sixth metasomal tergum blunt or truncate. 4

Vertex moderately to closely punctured; scutellum variously punctured, but with no projection; sixth metasomal tergum usually rounded 5

4. Wings blackish-brown; large bee (13-16 mm); southeastern United States .... *dolichos* Fox

Wings pale brown; medium sized bee (10-12 mm); Mexico and southward .... *laevigata* Smith, *laevis* Friese, *tolteca* Cresson

5. Scutellum impunctate medially or with scattered punctures, posterior margin of dorsal surface elevated 6

Scutellum closely, evenly and deeply punctured, posterior margin of dorsal surface not raised 7

6. Only basal metasomal tergum ferruginous across entire width; scutellum impunctate medially; Mexico and southward .... *assumptionis* Schrottky

Basal two or three metasomal terga ferruginous across entire widths; scutellum punctured medially; northern Mexico and northward .... *menthae* Cockerell

7. Thoracic and metasomal fasciae dense, conspicuous .... *slossoni arenicola* Crawford

Thoracic and metasomal fasciae narrow, inconspicuous .... *slossoni slossoni* Viereck

8. Sixth metasomal sternum notched subapically (as in Fig. 21) 9

Sixth metasomal sternum with margin entire 12

9. Scutellum without medioposterior projection 10

10. Scutellum with longitudinal, raised, impunctate line medially .... *mexicana* Cresson

Scutellum without raised, impunctate line medially 11

11. Metasomal terga two and three with graduli complete .... *Boreocoelioxys*

Metasomal terga two and three with graduli incomplete ...... *Schizocoelioxys*

12. Sixth metasomal tergum and sternum attenuate apically, sixth sternum without conspicuous, erect subapical setae; Mexico and southward .... *zapoteca* Cresson

Sixth metasomal tergum and sternum variable but not conspicuously elongate, sixth sternum usually with erect subapical setae 13

13. Scutellum with posterior margin in dorsal view medially subangulate or with medioposterior projection; Mexico and southward 14

Scutellum with posterior margin in dorsal view gently rounded to straight .. 15

14. Scutum and axilla black .... *chichimeca* Crawford

Scutum and axilla with distinct ferruginous areas .... *gonaspis* Cockerell

15. Axilla with projecting portion as long as basal portion .... *obtusiventris* Crawford

Axilla with projecting portion about half as long as basal portion 16

16. Scutum and axilla with ferruginous areas; Mexico and southward .... *sanguinicollis* Friese

Scutum and axilla black; usually northern Mexico and northward 17

17. Sixth metasomal tergum in lateral view upturned apically 18

Sixth metasomal tergum in lateral view tapering horizontally 19

18. Metasoma with postgradular areas evenly punctured (one to two puncture widths between punctures) with small punctures; west of Rocky Mountains .... *deani* Cockerell, *gilensis* Cockerell

Metasoma with postgradular areas less closely punctured medially (four or five puncture widths between punctures) with medium sized punctures; east of Rocky Mountains .... *scitula* Cresson, *modesta* Smith

19. Prothoracic tubercle expanded into thin, plate-like structure .... *Xerocoelioxys*

Prothoracic tubercle with strong carina but not expanded into thin, plate-like structure .... *Coelioxys*

20. Eastern United States .... *germana* Cresson

Mexico and southward .... *totonaca* Cresson

KEY TO MALES OF NORTH AMERICAN *COELIOXYS*.

1. Ocellar area impunctate and swollen .. 2

Ocellar area closely punctured or not swollen 9

2\. Sixth metasomal tergum with dorsal spines modified into a crenulate plate (Fig. 12B-G) .... *Synocoelioxys*

Sixth metasomal tergum with two distinct dorsal spines (sometimes with a third median spine in specimens from Mexico and southward 3

3\. Metasomal terga three to five with longitudinal, median ridge; vertex with scattered punctures; scutum practically impunctate on disc; scutellum impunctate medially with a large, rounded projection posteriorly 4

Metasomal terga three to five without longitudinal, median ridge; vertex variably punctured; scutum variably punctured; scutellum moderately to closely punctured, with or without large projection 5

4\. Wings blackish-brown; large bee (10-14 mm); southeastern United States .... *dolichos* Fox

Wings pale brown; medium sized bee (8-10 mm); Mexico and southward .... *laevigata* Smith, *tolteca* Cresson

5\. Vertex between lateral ocellus and eye impunctate; scutum, axilla, and scutellum with large ferruginous areas; scutellum with large, rounded posterior projection medially .... *azteca* Cresson

Vertex variously punctured; scutum, axillae usually black; scutellum without large, rounded posterior projection 6

6\. Scutellum evenly, closely, deeply punctured on dorsal surface; carina separating dorsal and posterior surfaces incomplete laterally, only a small median portion raised above level of dorsal surface 7

Scutellum sparingly punctured or impunctate medially; carina separating dorsal and posterior surfaces entire, median half raised above level of dorsal surface 8

7\. Thoracic and metasomal fasciae dense, conspicuous .... *slossoni arenicola* Crawford

Thoracic and metasomal fasciae narrow, inconspicuous .... *slossoni slossoni* Viereck

8\. Only the basal metasomal tergum ferruginous across entire width .... *assumptionis* Schrottky

Basal two or three metasomal terga ferruginous across entire width .... *menthae* Cockerell

9\. Foveae (Figs. 9, 25B-H) on metasomal tergum two (in *C. mexicana* foveae may be very small on tergum two, but they are in an otherwise impunctate area) 10

Foveae not present or present on metasomal tergum three only 12

10\. Foveae present on metasomal tergum three .... *mexicana* Cresson

Foveae absent on metasomal tergum three 11

11\. Graduli complete on metasomal terga two and three .... *Boreocoelioxys*

Graduli incomplete medially on metasomal terga two and three .... *Schizocoelioxys*

12\. Foveae absent, foveal area may be closely punctured on metasomal terga two and three 13

Foveae present only on tergum three 17

13\. Scutellum impunctate medially, posterior margin with flat, rounded projection .... *azteca* Cresson

Scutellum punctured medially except sometimes for an impunctate longitudinal line, posterior margin variable 14

14\. Scutellum in dorsal view with a conical projection posteriorly .... *gonaspis* Cockerell

Scutellum in dorsal view without a projection 15

15\. Metasomal tergum six with inner margins of dorsal spines forming a broad V .... *zapoteca* Cresson

Metasomal tergum six with inner margins of dorsal spines forming a broad U 16

16\. Thoracic and metasomal fasciae distinct; prothoracic tubercle produced into thin, plate-like structure; gradulus of tergum two curved toward apical margin medially .... *Xerocoelioxys*

Thoracic and sometimes metasomal fasciae inconspicuous; carina of prothoracic tubercle conspicuous but not expanded into thin, plate-like structure; gradulus of tergum two almost straight .... *Coelioxys*

17\. Posterior margin of scutellum in dorsal view with a median projection half as long as axilla 18

Posterior margin of scutellum without median projection 19

18\. Eastern United States .. *germana* Cresson

Mexico and southward .... *totonaca* Cresson

19\. Scutellum with narrow, impunctate, longitudinal median carina .... *mexicana* Cresson

Scutellum without longitudinal median carina 20

20\. Posterior margin of scutellum medially subangulate in dorsal view; basal metasomal terga with ferruginous areas; Mexico and southward .... *chichimeca* Cresson

Posterior margin of scutellum broadly rounded in dorsal view; metasoma black or very dark brown throughout; northern Mexico and northward 21

21\. Metasoma with postgradular areas closely and evenly punctured (maximum of one to two puncture widths between punctures) with small punctures; west of Rocky Mountains .... *deani* Cockerell, *gilensis* Cockerell

Metasoma with postgradular areas less closely punctured medially (maximum of four to five puncture widths between punctures) with medium sized punctures; east of Rocky Mountains .... *scitula* Cresson, *modesta* Smith

Subgenus *Synocoelioxys* Mitchell

Synocoelioxys Mitchell, 1973. A subgeneric revision of the genus *Coelioxys* of the Western Hemisphere. Cont. Dept. Entomol. North Carolina State Univ. p. 57. Type species: *Coelioxys texana* Cresson.

Table 1. Known host-parasite relationships for North American *Megachile* and *Coelioxys*. References to sources for species not covered by this review are given in footnotes. B = *Boreocoelioxys*, Co = *Coelioxys*, Cy = *Cyrtocoelioxys*, M = *Melanocoelioxys*, Sc = *Schizocoelioxys*, Sy = *Synocoelioxys*, X = *Xerocoelioxys*.

MEGACHILE and CHALICODOMA		COELIOXYS
Subgenus	species	species
Chelostomoides	campanulae	modesta (Cy)[3]
Chelostomoides	subexilis	gilensis (Cy)[3]
Delomegachile	frigida	funeraria (Sc), moesta (B), porterae (Co)
Delomegachile	melanophoea	rufitarsis (B), sodalis (Co)
Delomegachile	melanophoea wootoni	rufitarsis (B), sodalis (Co)
Eutricharaea	concinna	moesta (B)
Eutricharaea	rotundata	funeraria (Sc), gilensis (Cy)[4], moesta (B), novomexicana (B), octodentata (B), sodalis (Co)
Litomegachile	brevis	novomexicana (B), octodentata (B), sayi (B)
Litomegachile	gentilis	novomexicana (B)
Litomegachile	mendica	octodentata (B), sayi (B)
Litomegachile	onobrychidis	octodentata (B)
Litomegachile	texana	octodentata (B), moesta (B), rufitarsis (B), sodalis (Co)
Megachile	centuncularis	modesta (Cy)[5], moesta (B), octodentata (B)
Megachile	inermis	funeraria (Sc)
Megachile	montivaga	rufitarsis (B)
Megachile	relativa	funeraria (Sc), modesta (Cy)[6], moesta (B), porterae (Co)
Megachiloides	umatillensis	mesae (X)
Melanosarus	xylocopoides	dolichos (M)[1]
Phenosarus	fortis	rufitarsis (B)
Pseudocentron	sidalceae	novomexicana (B)
Sayapis	policaris	texana (Sy)
Sayapis	pugnata pugnata	alternata (Sy)
Xanthosarus	latimanus	funeraria (Sc), rufitarsis (B)
Xanthosarus	perihirta	grindeliae (X), octodentata (B), rufitarsis (B)

[3] Krombein (1967).

[4] From specimen labels in Washington, Canada.

[5] Graenicher (1927).

[6] Fye (1965).

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FIGURE 10. Dorsal view of female *Coelioxys texana*, left half showing punctations, right half with melanization and pubescence added.

FIGURE 11. Frontal view of females of *Synocoelioxys*. A, Head of *C. texana*. B-C, Left half of clypeus and mandible. B, *C. alternata;* C, *C. hunteri.*

Other bees in the subgenus *Synocoelioxys* are *C. alternata, C. apacheorum, C. hunteri,* and *C. erysimi*. This group of bees, although possessing many derived characters, possesses several characters which appear to be ancestral: the seventh sternum of males is complete, the sixth sternum of females has a simple margin and is not unduly lengthened, and the sixth tergum of males appears to be most ancestral (i.e. resembles most closely the condition found in some species of *Megachile* and *Liothyrapis*) of any of the New World *Coelioxys.*

Certain host bees are known for two species in *Synocoelioxys: Coelioxys texana* and *C. alternata.* Both utilize *Megachile* hosts of the subgenus *Sayapis* (Table 1).

Most of the characters in the list below are found in other subgenera of New World *Coelioxys* and even in some of the Old World *Liothyrapis,* but never in this combination. The simple seventh sternum and the crenulate margin of the sixth tergum of males are found in no other New World *Coelioxys.* Italicized characters most clearly differentiate *Synocoelioxys* from other subgenera in North America.

A. *Ocellar area raised, impunctate.* Median ocellus margined anteriorly by small group of anteriorly directed setae (Figs. 10, 11A, 12A).

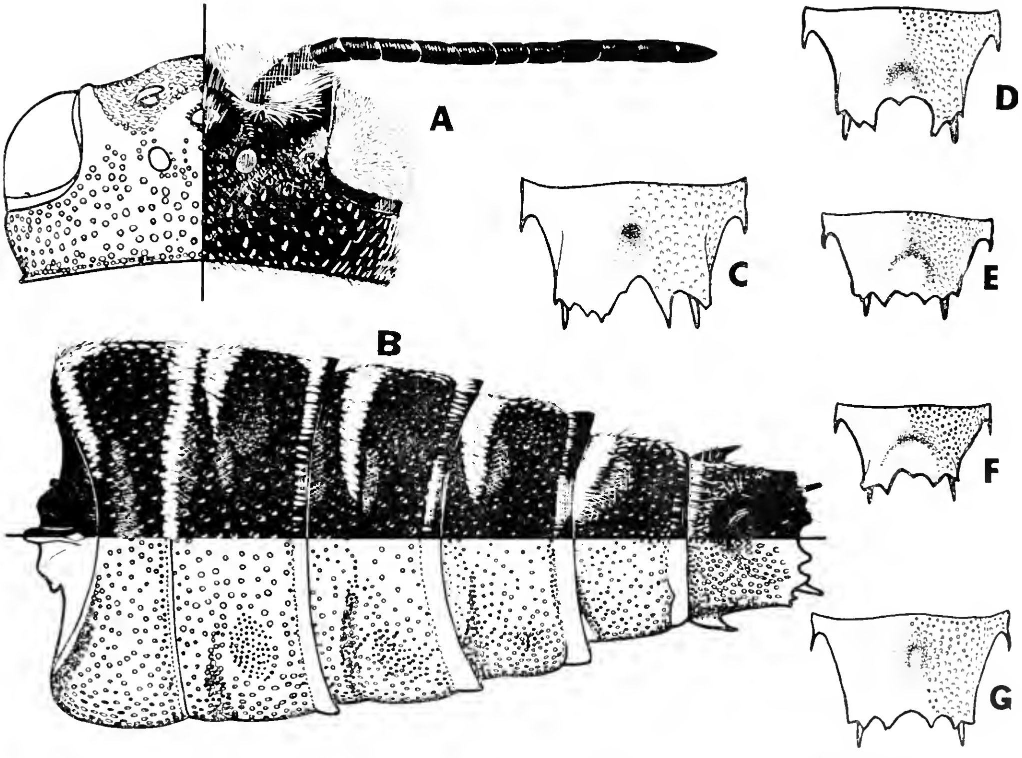

FIGURE 12. Dorsal views of males of *Synocoelioxys*. A-C, *C. texana*. A, Head; B, Metasoma; C, Sixth metasomal tergum. D-G, Sixth metasomal terga. D, *C. alternata;* E-F, *C. apacheorum;* G, *C. hunteri.*

B. Preoccipital carina complete medially (Fig. 3).

C. Mandible robust to slender (Fig. 11A-C).

D. Prothoracic tubercle with carina produced into thin plate-like structure.

E. Scutum moderately punctured (Fig. 10), fasciae indistinct to distinct.

F. Scutellum not flattened and usually without a projection although a small carina may be present (Fig. 14E).

G. Axilla well produced except in *Coelioxys alternata* (Figs. 10, 14E).

H. Mesepisternum moderately punctured, with minute punctures as well as larger punctures (Fig. 8).

I. *Gradular grooves incomplete medially, becoming filled with squamose setae laterally* (Figs. 10, 12B).

J. Female: front coxal spine variable but well produced in some species.

K. Female: *lateral margin of sternum six*

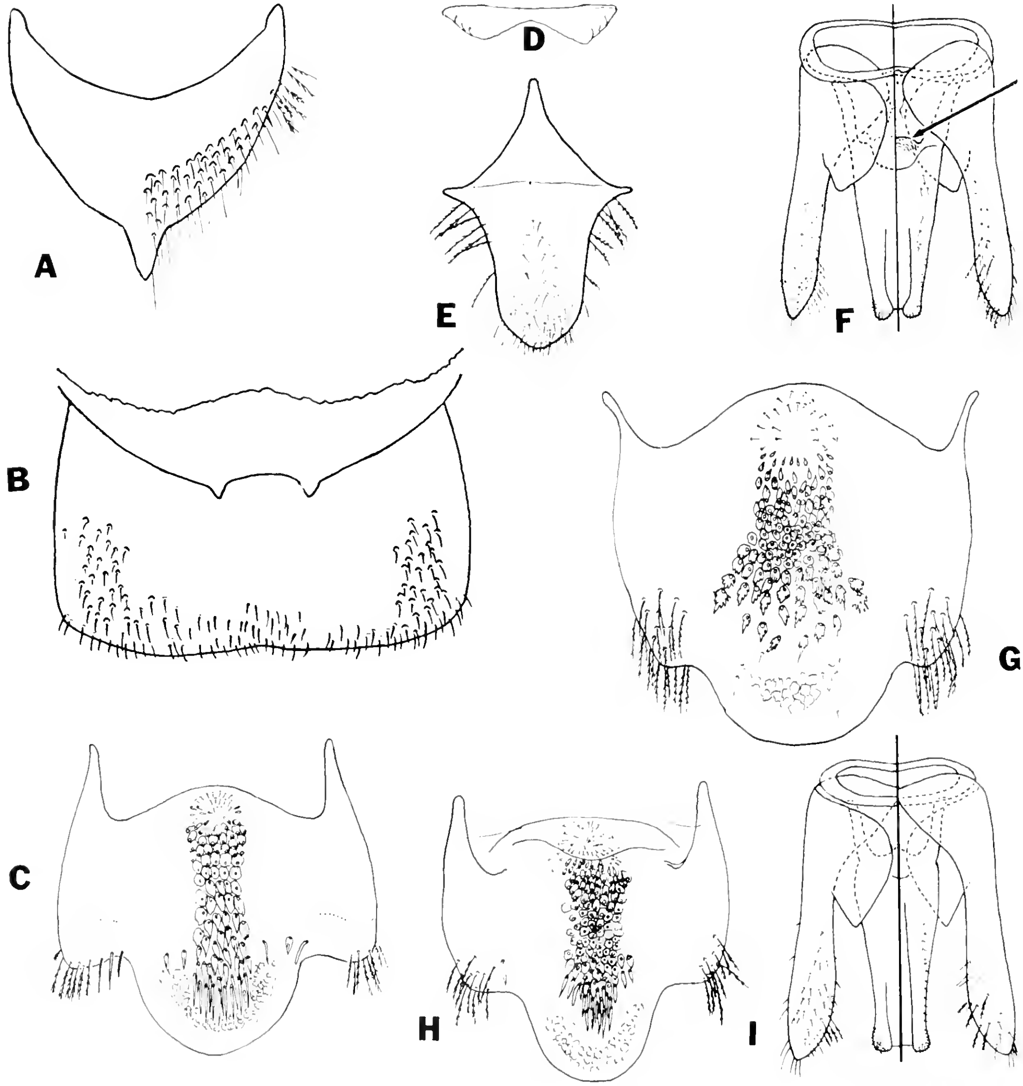

FIGURE 13. Hidden sclerites of males of *Synocoelioxys*. A-F, *C. texana*. A, Seventh tergum; B, Margin of fourth sternum, fifth sternum; C, Sixth strenum; D, Seventh sternum; E, Eighth sternum; F, Genital armature (arrow indicates rugulose area). G, Sixth sternum, *C. alternata:* H, Sixth sternum, *C. apacheorum;* I, Genital armature, *C. alternata*.

entire, acute or rounded apically (Figs. 10, 14A-C).

L. Male: hypostomal area of the gena *not* modified into excavation (Fig. 3).

M. Male: *foveal area of tergum two sometimes very closely punctate* (Fig. 12B).

N. Male: fifth tergum with lateral spine close to apical margin.

O. Male: *carina of tergum six forming a crenulate plate* (Fig. 12B-G).

P. Male: *apex of tergum seven with a conspicuous spine* (Fig. 13A).

Q. Male: apex of sternum four with a pair of teeth (Fig. 13B).

R. Male: *sternum seven undivided, bilobed* (Fig. 13D).

Key to Females of *Synocoelioxys*

1. Sixth sternum acute apically (or very narrowly rounded) (Fig. 14A, C) 2
   Sixth sternum rounded apically (Figs. 10, 14B, D) 3
2. Axilla short (Fig. 14 E); mandible slender (Fig. 11B) .... *alternata*
   Axilla longer (as in Fig. 10); mandible intermediate (Fig. 11C) .... *hunteri*
3. Lateral ocellus closer to occipital margin than to eye 4
   Lateral ocellus equidistant from occipital margin and eye .... *texana*
4. Sternum six broadly rounded (Fig. 14D) .... *erysimi*
   Sternum six more narrowly rounded (Fig. 14B) .... *apacheorum*

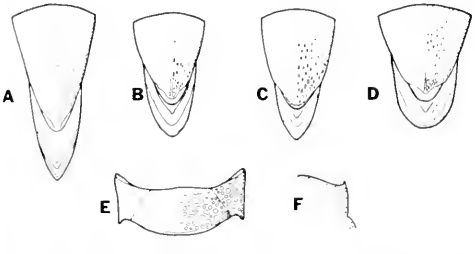

FIGURE 14. A-D, Sixth metasomal terga and sterna of females of *Synocoelioxys*. A, *C. alternata;* B, *C. apacheorum;* C, *C. hunteri;* D, *C. erysimi.* E-F, Dorsal (E) and optical section (F) of scutellum and axillae of *C. alternata.*

Key to Males of *Synocoelioxys*

1. Hypostomal area of the gena bare or with small slender setae which do not obscure integument 2
   Hypostomal area of the gena obscured by setae at least as wide if not as long as setae on gena 3
2. Anterior portions of raised, impunctate ocellar area (Figs. 1, 2) separated by about one puncture width, usually a longitudinal row of punctures in the space; scutellum usually without a carina separating dorsal and posterior surfaces .... *hunteri*
   Anterior portions of raised, impunctate ocellar area separated by about two or three puncture widths; scutellum usually with a carina separating dorsal and posterior surfaces (Fig. 14E) .... *alternata*
3. Ocellocular distance less than ocelloccipital distance; scape and pedical usually ferruginous .... *texana*
   Ocellocular distance subequal to or greater than ocelloccipital distance; scape and pedicel usually piceous or black 4
4. Posterior surface of scutellum with no appressed setae or a few slender appressed setae restricted to middle .... *erysimi*
   Posterior surface of scutellum with squamose appressed setae across the full width .... *apacheorum*

Coelioxys texana Cresson

Figures 10, 11A, 12A-C, 13A-F, 15

Coelioxys texana Cresson, 1872, Trans. Amer. Entomol. Soc. 4:272 (♀, ♂ Texas, type ♀, in Philadelphia Academy of Sciences); Schwarz, 1896, Proc. Entomol. Soc. Washington 4:24 (Sleeping); Robertson, 1926, Psyche 33: 177 (Phenology); Krombein, 1967, Trap-nesting Wasps and Bees: Life Histories, Nests and Associates, Washington, D.C. 570 p.

Coelioxys texanus; Banks, 1902, J. New York Entomol. Soc. 10:212 (Sleeping).

Coelioxys texana sonorensis Cockerell, 1914, Entomologist 47:116 (♂, Sonora, Mexico, type in the National Museum of History) NEW SYNONYMY.

Coelioxys texana texana: Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:193, 194, 228 (Redescription, key).

FEMALE. (1) Length 9-14 mm; (2) integument between punctures granular on vertex, weakly so on thorax, dull on metanotum and propodeum, shiny elsewhere; black; scape, pedicel, apical portion of labrum, pronotal lobe, tegula, front coxal spine, trochanters, femora, tibiae, ventral or medioventral portion of hind coxa, lateroposterior margins of terga 1-4, sometimes 5, and posterior portions of sterna 1-5 ferruginous to reddish brown; (3) pubescence white, slightly brown below antenna, golden on tarsi, brown on apices of tergum 6 and sternum 6; (4) ocular hairs short (about 0.05 mm); (5) clypeus visible medially, margin irregular (Fig. 14A); (6) clypeoantennal distance subequal to lateral margin of clypeus; (7) paraocular area hidden laterally by setae about 0.2 mm long; (8) rest of face punctured up to ocellar area; (9) clypeoantennal and interantennal distances equal, greater than antennocular distance (Fig. 11A); (10) ocellar area with impunctate areas broad (Figs. 10, 11A); (11) ocelloccipital distance subequal to ocellocular distance, greater than or subequal to interocellar distance (Fig. 10); (12) vertex moderately punctate (Figs. 10, 11A); (13) gena narrower than eye, setae not obscuring integument, ventral angle about 90°; (14) hypostomal area of the gena with setae shorter than on disc; (15) mandible short, broad (Fig. 11A); (16) scutum with conspicuous fasciae (Fig. 10); (17) lateral surface of mesepisternum with punctures well separated, many more minute punctures than punctures, pubescence short; (18) scutellum with posterior margin of dorsal surface subangulate in dorsal view (Fig. 10); (19) axilla well produced (Fig. 10); (20) metanotal setae appressed medially, erect laterally; (21) front coxal spine subtriangular, flattened, directed ventrally or slightly forward, inconspicuous; (22) terga 1-5 with conspicuous fasciae, tergum 6 rounded (Fig. 10); (23) sterna 1-5 fasciate apically, fasciae less conspicuous posteriorly, punctures on sterna 1-4 with short setae, punctures exceedingly small and close medially on sternum 5 and subapically on sternum 6, ventral apical margin of sternum 6 bare, shining, broadly rounded (Fig. 10).

MALE. (24) Length 10-12.3 mm; (25) integument as in female (2 above); (26) pubescence white, golden on tarsi; (27) ocular hairs of medium length (about 0.075 mm, Fig. 12A); (28) clypeus hidden by setae in some specimens, coarsely rugose; clypeal margin as in female (5 above); (29) clypeoantennal distance as in female (6 above); (30) paraocular area hidden by setae about 0.3 mm long; (31) rest of face hidden up to ocellar area; (32) antennocular distance less than clypeoantennal distance which is less than interantennal distance; (33) ocellar area as in female (10 above); (34) interocellar and ocellocular distances equal, less than ocelloccipital distance (Fig. 12A); (35) vertex as in female but longer (12 above, Fig. 12A); (36) gena as in female (13 above); (37) hypostomal area of the gena with setae as long as on discs; (38) mandible as in female (15 above); (39) scutum as in female (16 above) but with slender erect setae on disc; (40-43) mesepisternum, scutellum, axilla, metanotum as in female (17-20 above); (44) front coxal spine about twice as long as broad; (45) terga 1-6 fasciate, carina of tergum 6 crenulate, or with sharp denticles, deeply emarginate, often asymmetric (Fig. 12B-C), tergum 7 with apical spine (Fig. 13A); (46) sterna 1-4 evenly punctate with squamose setae filling most punctures, sterna 1-3 apically with irregular fasciae about 0.35 mm wide; (47) sternum 4 submarginally carinate, apex bidentate (Fig. 13B); margin of sternum 5 slightly emarginate (Fig. 13B); sternum 6 with unbranched setae medioapically (Fig. 13C); sternum 7 simple (Fig. 13D); sternum 8 with small, unbranched setae medially (Fig. 13E); genital armature with area at base of penis valves (arrow on Fig. 13F) sometimes rugulose.

HOST RECORDS. Krombein (1967) reported rearing *Coelioxys texana* from trap nests provisioned by *Megachile policaris.*

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys texana* is most abundant in the southwestern United States (Fig. 15). Exceptionally long series have been taken at the Southwestern Research Station five miles west of Portal, Arizona.

This bee has been collected from March 27 to November 2 in Texas. One specimen of *Coelioxys texana* was taken November 17 at Ciudad Victoria, Tamualipas, Mexico.

HABITAT. *Coelioxys texana* has been taken at altitudes ranging from close to sea level (Indian Wells, California) to 9,000 feet. Habitats range from humid areas such as mangrove and floodplain forests of Florida to xeric habitats in Arizona and southern California where major vegetational types include *Larrea, Opuntia, Cercidium, Bouteloua, Hilaria, Quercus, Juniperus, Flourensia,* and *Franseria. Coelioxys texana* is apparently not common at higher altitudes although specimens from two localities indicate it may range up into coniferous forests (Shannon Peak, Pinalena Mountains, Arizona, 9,000 feet and Madera Canyon, Santa Rita Mountains, Pima County, Arizona, 4,800 feet).

GEOGRAPHIC VARIATION. Specimens of *Coelioxys texana* from Florida have wings which are noticeably darker and a deeper yellow than wings of *C.*

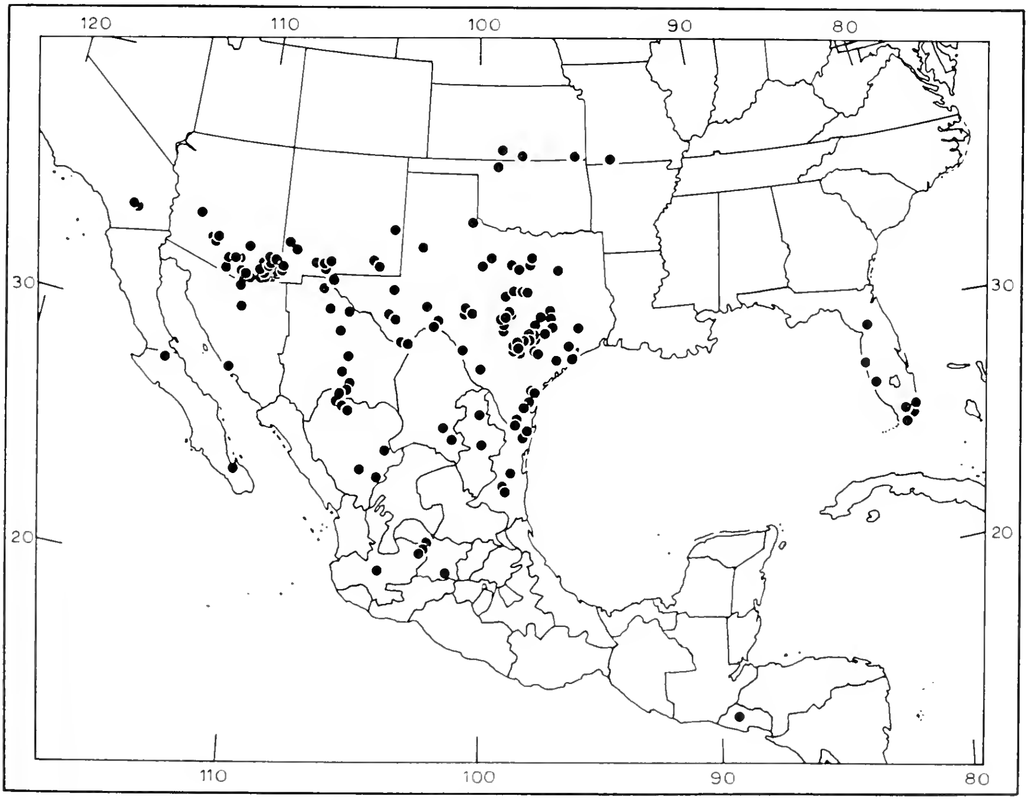

FIGURE 15. Distribution of *Coelioxys texana.*

texana from other areas. All (seven) males from Florida also have the margin of the carina of the sixth tergum produced into sharp denticles (Fig. 12 C); elsewhere the margin of the sixth tergum is crenulate (Fig. 12 B). A single female from the Lower Matecumbe Key with dark, yellowish wings (but typical in other characters) has been associated with these males.

COMPARATIVE COMMENTS. In both sexes of *Coelioxys texana* the antennal scape and pedicel are usually ferruginous, a condition found in no other North American *Coelioxys* spp. Of the females in this group, *C. texana* has the lateral ocelli furthest removed from the occipital margin (subequally distant from the occipital margin and eye).

Coelioxys alternata Say
Figures 11B; 12D; 13G, I; 14A, E-F; 16

Coelioxys alternata Say, 1837, Boston J. Natur. Hist. 1: 401 (♂, ♀, Indiana, type probably destroyed); Robertson, 1929, Flowers and Insects, Lancaster, Pennsylvania Sci. Press (Flower records); Graenicher, 1935, Ann. Entomol. Soc. Amer. 28:304; Medler, 1964, Can. Entomol. 96:918, 920, 921; Medler and Lussenhop, 1968, Univ. Wisconsin Research Bull. 274:51, 52 (Biology, key).

Coelioxys texana; Graenicher, 1911, Bull. Publ. Mus. Milwaukee 1:243 (Wisconsin, misidentification).

Coelioxys texana vegana Cockerell, 1912, Can. Entomol. 44:166, 169 (New Mexico, ♂, key, type in the American Museum of Natural History) NEW SYNONYMY.

Coelioxys cockerelli Crawford, 1915, Insecutor Inscitiae Menstruus 3:108 (♀, Colorado, type in the National Museum of Natural History) NEW SYNONYMY.

Coelioxys wisconsinensis Cockerell, 1925, Pan-Pacific Entomol. 1:145 (♀, ♂, Wisconsin, type in the University of Colorado Museum) NEW SYNONYMY.

Coelioxys alternata alternata; Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:193-195 (Redescription, key).

Coelioxys alternata wisconsinensis; Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:193, 194, 196; Medler, 1964, Can. Entomol. 96:920, 921 (Host record).

FEMALE. Agrees with description and figures of *Coelioxys texana* except as follows: (1) Length 10-16 mm; (2) integument black or becoming dark reddish-brown to ferruginous on femora, tibiae, and metasoma; (3) pubescence white except golden on tarsi; (4) ocular hairs 0.08 mm long; (5) clypeus with setal fringe scant; (6) clypeoantennal distance shorter than lateral margin of clypeus; (7) paraocular area rugose, almost hidden by 0.3-0.4 mm setae; (8) rest of face with median impunctate ridge; (9) antennocular distance subequal to clypeoantennal distance and to interantennal distance; (10) ocellar area with impunctate ridges not as conspicuous as those in Fig. 10; (11) interocellar distance greater than ocelloccipital distance and less than ocellocular distance; (12) vertex with longer, more copious setae than shown in Fig. 10; (13) gena with ventral angle acute, approaching 60°; (14) hypostomal area of the gena appearing bare; (15) mandible slender (Fig. 11B); (16) scutum with peripheral fasciae less conspicuous than shown in Fig. 10; thin setae on disc longer than shown in Fig. 10; (17) mesepisternum with lateral surface closely punctate, pubescence long and slender, lateral surface with as many or more punctures than minute punctures; (18) scutellum not angulate medially as seen from above, with carina separating surfaces (Fig. 14E, F); (19) axilla short (Fig. 14E); (21) front coxal spine reduced, sometimes slightly curved posteriorly; (22) terga 1-6 in general more slender than those of Fig. 10; (23) sterna 1-5 with apical fasciae of sparse hairs, punctures laterally with short, slender setae, punctures rather uniform throughout; sternum 6 acute apically (Fig. 14A), ventrad with punctures contiguous basally, in parallel rows.

MALE. Agrees with description and figures of *Coelioxys texana* except as follows: (25) integument as in female (2 above); (27) ocular hairs of medium length (about 0.1 mm); (28) clypeus hidden by setae in some specimens, coarsely punctured, shining when revealed; (29) clypeoantennal distance as in female (3 above); (30) paraocular area as in female (7 above); (31) rest of face with weak impunctate line to subocellar area; (32) clypeoantennal distance subequal to interantennal distance, greater than antennocular; (33) ocellar area as in female (10 above); (34) ocelloccipital distance subequal to ocellocular distance and greater than interocellar distance; (35) vertex with more slender upright setae than shown in Fig. 12A; (36-42) gena, hypostomal area of the gena, mandible, scutum, mesepisternum, scutellum, axilla as in female (13-19 above); (43) metanotum with almost no appressed setae; (44) front coxal spine pointing ventrally, about as long as broad; (45) tergum 1 with median fascia not as complete as shown in Fig. 12 B, tergum 6 with carina denticulate (Fig. 12D), tergum 7 with apical projection slightly recurved, shorter than shown in Fig. 13A; (46) sterna 1-4 with apical fasciae interrupted medially, sternum 6 with a few slender scattered setae medioapically (Fig. 13G), genital armature with ventral lobe of gonocoxite acute apically (Fig. 13I).

HOST RECORDS. Medler (1964) reported rearing *Coelioxys alternata* from trap nests provisioned by *Megachile (Sayapis) pugnata pugnata.*

DISTRIBUTION AND SEASON IN FLIGHT. Although rare throughout its range, *Coelioxys alternata* occurs as far north as Edmonton, Alberta (Fig. 16). In the southernmost extensions of its range, *C. alternata* occurs only at higher elevations. One specimen from the American Museum of Natural History labeled "Tex. Collection Belfrage" is probably mislabeled. Somewhat surprising in view of its coast to coast distribution is a lack of specimens from California. The host bee, *Megachile pugnata pugnata* occurs as far west in California as the eastern sides of the Sacramento and San Joaquin Valleys.

Coelioxys alternata has been collected from June 24 to October 13.

HABITAT. Mesic conditions prevail throughout most of the localities from which *Coelioxys alternata* has been collected. Dryer vegetational types include areas classified as bluestem prairie *(Andropogon),* oak savana *(Quercus, Andropogon),* and oak-juniper woodland *(Quercus, Juniperus).* Further north, *C. alternata* appears to be associated with various coniferous and hardwood forests.

GEOGRAPHIC VARIATION. Variation in *Coelioxys alternata* does not seem to be related to geography. The color of the legs and tegulae grades from black (previously considered to be *C. alternata wisconsinensis*) to ferruginous. Medler (1964) reared both black and ferruginous forms from the same domicile. Actually most specimens exhibit an intermediate condition, and all degrees of melanism are found throughout the range. The coexistence of forms with all degrees of melanism throughout the range, morphological agreement among forms, and identical host data were major factors contributing to the synonymyzing of *C. alternata wisconsinensis* and *C. alternata alternata.*

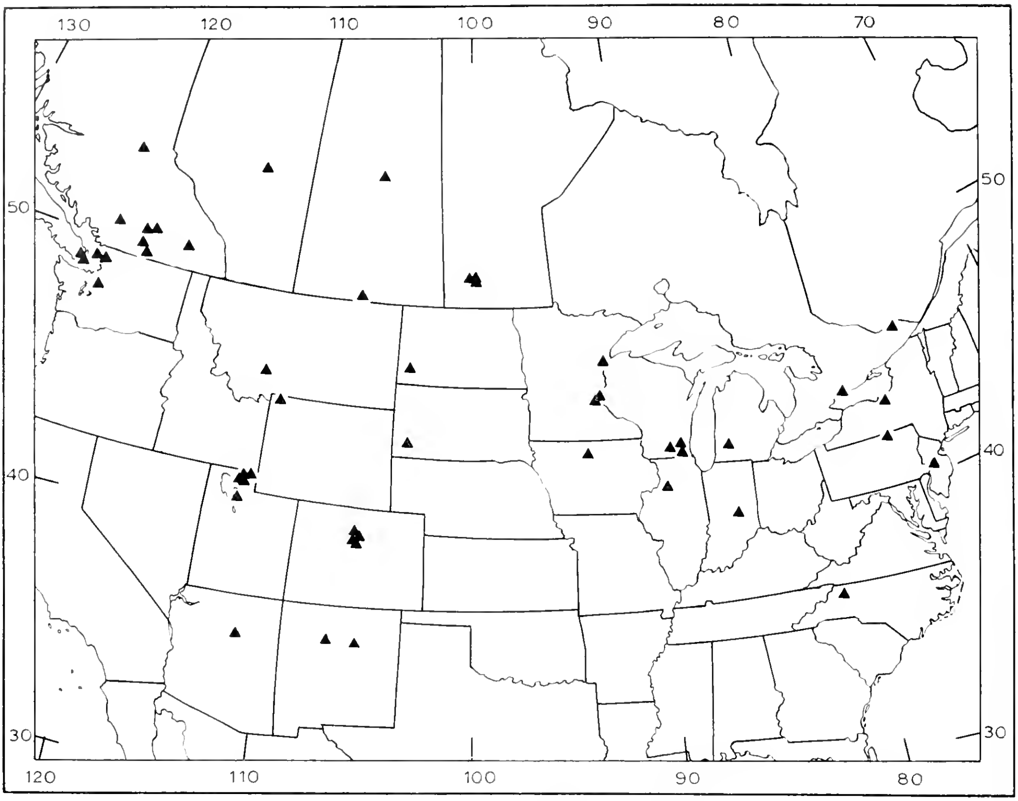

FIGURE 16. Distribution of *Coelioxys alternata*.

COMPARATIVE COMMENTS. Males of *Coelioxys alternata* are known from other males in *Synocoelioxys* (except *C. hunteri*) by the bare appearance of the hypostomal area of the gena. Unlike all other species of *Synocoelioxys*, the axillae in both sexes are usually very short (Fig. 14E). Females of *C. alternata* possess sixth strena more acute apically (compare Figs. 14A and 14C) and mandibles more slender than those of *C. hunteri* (compare Figs. 11B and 11C).

Coelioxys apacheorum Cockerell
Figures 12E-F, 13H, 14B, 17

Coelioxys apacheorum Cockerell, 1900, Can. Entomol. 32:297, 299-307 (♀, New Mexico, key, type in the National Museum of Natural History); Linsley *in* Muesebeck *et al.,* 1951. Hymenoptera of America North of Mexico; Synoptic Catalog USDA Agric. Mono. 2:1183 (=*fragariae*).

Coelioxys fragariae Cockerell, 1912, Can. Entomol. 44:167-169 (♂, California, key, type in the American Museum of Natural History); Cockerell, 1921, Amer. Mus. Novitates 21:3, 8-10 (Colorado, redescription).

Coelioxys quercina Cockerell, 1912, Can. Entomol. 44:167-169 (♂, Arizona, key, type in the American Museum of Natural History) NEW SYNONYMY.

FEMALE. Agrees with description and figures of *Coelioxys texana* except as follows: (1) Length 9-13 mm; (2) integument grainy on vertex, dull on thorax, shiny on abdomen; black; scape, front coxal spine, and coxae piceous; pronotal lobe and tegula dark brown to brown;

femora, tibiae and basitarsi dark brown to dark brown with ferruginous spots or segments to ferruginous throughout; lateroposterior margins of terga 1-4 and sometimes 5, and posterior margins of sterna 1-5 black to dark reddish-brown; (3) pubescence brown on apex of sternum 6; (4) ocular hairs 0.05-0.1 mm long; (5) margin of clypeus with 6 teeth about 0.05 mm long; clypeus sometimes with irregular impunctate line; (6) clypeoantennal distance shorter than lateral margin clypeus; (7) paraocular area hidden laterally by 0.2-0.3 mm setae; (8) rest of face with an indefinite impunctate line up to ocellar area; (9) clypeoantennal distance greater than antennocular distance and less than or subequal to interantennal distance; (10) ocellar area with arms of impunctate area medially separated by punctures in a band 2 or 3 punctures wide; impunctate area sometimes not as broad as in Figures 10, 11A; (11) ocelloccipital distance less than or subequal to interocellar distance which is less than ocellocular distance; (12) vertex with slender erect setae longer than shown in Figure 10, especially in interocellar area; (13) gena with ventral angle slightly acute; (14) hypostomal area of gena with setae as long as or longer than on disc; (15) mandible with outer tooth longer than shown in Figure 11 A, more like Figure 11C; (16) scutum with erect setae longer and more copious than shown in Figure 10; (17) mesepisternum with lateral face closely punctate, more punctures than minute punctures, pubescence slender and long (about 0.35 mm); (18) scutellum with posterior margin of dorsal surface almost straight to broadly curved in dorsal view; (21) front coxal spine flattened and rounded apically, slightly recurved posteriorly, inconspicuous; (22) tergum 6 rounded apically (Fig. 14B); (23) sternum 6 moderately to narrowly rounded apically (Fig. 14B).

MALE. Agrees with description and figures of *Coelioxys texana* except as follows: (24) Length 8.5-10.5 mm; (25) integument as in female (2 above); (27) ocular hairs 0.05-0.1 mm long; (28) clypeal margin and median line as in female (5 above); (29) clypeoantennal distance as in female (6 above); (32) clypeoantennal distance subequal to or greater than antennocular distance, less than interantennal distance; (33) ocellar area as in female (10 above); (34) ocellocular distance subequal to ocelloccipital distance, greater than interocellar distance; (35) vertex with more erect, slender setae than shown in Figure 12A; (36) gena as in female (13 above); (37) hypostomal area of gena as in female (14 above); (39) scutum as in female (16 above); (40) lateral surface of mesepisternum closely but distinctly punctured, pubescence as in female (17 above); (41) scutellum as in female (18 above); (44) front coxal spine 1.5 times longer than wide; (45) terga 3-5 sometimes lacking apical fasciae medially or entirely, carina of tergum 6 with irregular denticulations (Fig. 12E, F); (46) sterna 1-4 evenly punctate with squamose setae filling most or only a few punctures, apically with irregular fasciae 0.25-0.3 mm (maximum) wide; (47) sternum 6 with lateral setae resembling *C. alternata* (Fig. 13H).

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys apacheorum* ranges from southwestern Canada to California and east to South Dakota, Colorado, and to the edge of the Edwards Plateau in Texas (Fig. 17).

Extremes of the flight period are April 10 (Abilene, Texas) and September 23 (Sequoia National Park, California) with the majority of specimens taken from June to August.

HABITAT. In its northern range, *Coelioxys apacheorum* is associated with areas classified as a variety of western coniferous forests, and one specimen was taken at the edge of alpine meadow west

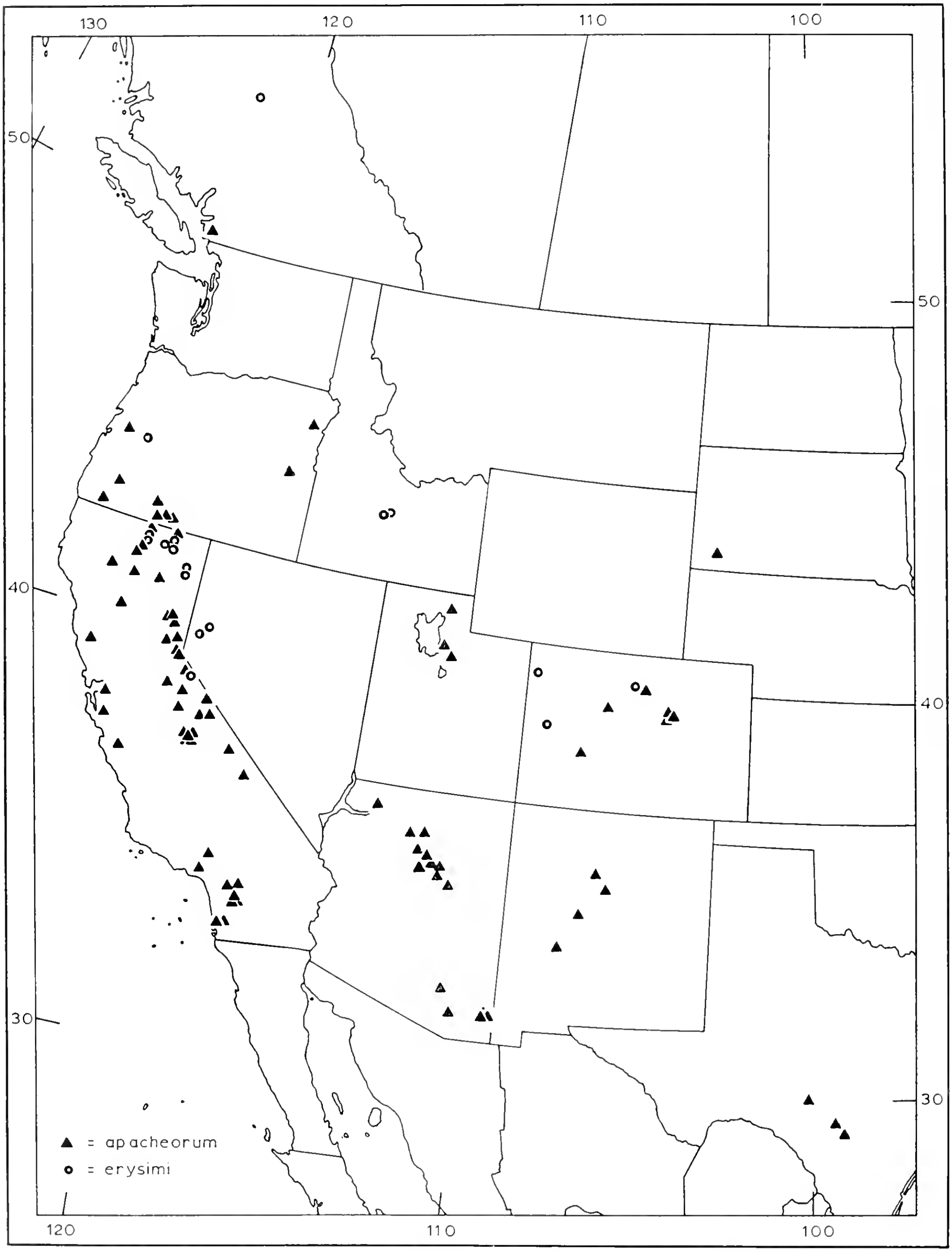

FIGURE 17. Distributions of *Coelioxys apacheorum* (△) and *C. erysimi.* (o).

of Boulder, Colorado. Further south the bee spreads into areas classified as western shrub and grassland and forest-grassland in Texas.

GEOGRAPHIC VARIATION. As with *Coelioxys alternata,* variation in *C. apacheorum* does not seem to be related to geography. Color of the legs varies from black to ferruginous with an intermediate condition in which the tibia is dark medially with ferruginous proximal and distal areas. Bees exhibiting all degrees of melanism occur throughout the range.

The decision to synonymize *Coelioxys quercina* and *C. apacheorum* is based upon morphological agreement of the darker males (earlier associated with the females of *C. apacheorum*) with the lighter colored males which resemble the type of *C. quercina*.

COMPARATIVE COMMENTS. Specimens of *Coelioxys apacheorum* are usually smaller than the other species of *Synocoelioxys*. Dark males of *C. apacheorum* most closely resemble those of *C. erysimi* but have a fascia of squamose setae on the posterior surface of the scutellum. Dark females of *C. apacheorum* resemble females of *C. erysimi* and dark females of *C. alternata* but differ by the narrowly to moderately rounded sixth sterna (compare Fig. 14B and D).

Coelioxys erysimi Cockerell
Figures 14D, 17

Coelioxys erysimi Cockerell, 1912, Can. Entomol. 44:166 (♂ Colorado, type in the American Museum of Natural History).

FEMALE. Agrees with the figures and description of *Coelioxys texana* except as follows: (1) Length 12-14 mm; (2) integument black, sometimes piceous on tibiae; (3) pubescence white, sometimes brownish below antennae, pale brown on apices of tergum 6 and sternum 6; (4) ocular hairs of medium length (about 0.08 mm); (5) clypeus with fringe of setae shorter than shown in Figure 11; (6) clypeoantennal distance shorter than lateral margin of clypeus; (7) lateral quarter of paraocular area hidden by setae, erect setae about 0.3 mm long; (8) rest of face with an indistinct impunctate median line; (9) interantennal distance slightly greater than clypeoantennal distance which is greater than antennocular distance; (11) interocellar distance slightly greater than ocelloccipital distance and less than ocellocular distance; (14) hypostomal area of gena with setae as long or longer than on disc; (15) mandible with apical tooth longer than shown in Figure 11A, more like Figure 11C; (16) fasciae of scutum not as distinct as shown in Figure 10; (17) mesepisternum with lateral surface closely punctate, many more punctures than minute punctures, pubescence long (about 0.35 mm) and slender; (18) scutellum with posterior margin of dorsal surface broadly rounded; (19) axilla shorter than shown in Figure 10, longer than shown in Figure 14E; (20) metanotum with small amount of setae appressed medially; (21) front coxal spine with anterior surface 1.5 times as long as wide, small but conspicuous; (22) terga 1-5 with gradular fasciae inconspicuous; (23) sterna 1-5 with irregular fasciae.

MALE. Agrees with the figures and description of *Coelioxys texana* except as follows: (24) Length 10-12.5 mm; (25) integument as in female (2 above); (27) ocular hairs as in female (4 above); (28) clypeal margin as in female (5 above); (29) clypeoantennal distance as in female (6 above); (30) paraocular area hidden by setae about 0.4 mm long; (34) interocellar distance equal to or less than ocellocular distance, less than ocelloccipital distance; (38) mandible as in female (15 above); (36) scutal fasciae indistinct or lacking; (40-42) mesepisternum, scutellum, axilla as in female (17-19 above); (43) metanotum with little or no appressed setae medially; (45) tergum 2 with median portion of gradular groove bare, carina of tergum 6 denticulate, apical spine of tergum 7 shorter than shown in Figure 13A; (46) setae filling punctures of sterna 1-4 not squamose.

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys erysimi* is probably restricted to the higher elevations of the western United States and Canada (Fig. 17). Judging from the small number of specimens examined, this bee appears to be rare throughout its distribution.

This bee has been taken between June 21 and September 9.

HABITAT. *Coelioxys erysimi* has been taken from areas classified as grand fir-Douglas fir *(Abies-Pseudotsuga)* and pine-Douglas fir *(Pinus-Pseudotsuga)* forests, from juniper-pinyon and juniper-steppe woodland *(Juniperus, Pinus, Artemisia, Agropyron)*, from Montane chaparral *(Arctostaphylos, Castanopsis, Ceanothus)*, and from Great Basin sagebrush and sagebrush steppe *(Artemisia, Agropyron)* vegetation types.

GEOGRAPHIC VARIATION. Varition within *Coelioxys erysimi* does not seem to be related to geography.

COMPARATIVE COMMENTS. *Coelioxys erysimi* is variable in size but seems to be invariably dark (black or piceous) throughout. Females most closely resemble dark females of *C. apacheorum* but the sixth sternum is as broad as that of *C. texana* (compare Figs. 10 and 14D). Males of *C. erysimi* are distinguished from dark males of *C. apacheorum* by the lack of a fascia across the posterior area of the scutellum.

Coelioxys hunteri Crawford

Figures 11C, 12G, 14C, 18

Coelioxys hunteri Crawford, 1914, Ann. Entomol. Soc. Amer. 7:151 (♀, Texas, type in the National Museum of Natral History); Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:193, 209 (Key, redescription).

FEMALE. Agrees with figures and description of *Coelioxys texana* except as follows: (1) Length 10.5-13.5 mm; (2) integument with scape, legs and metasoma darker than ferruginous, scape and metasome sometimes black; (5) clypeus medially with slightly raised impunctate line, apically with 0.1 mm fringe of slender setae barely obscuring margin, medioapically with 5-10 setae 0.2-0.3 mm long; (6) clypeoantennal distance shorter than lateral margin of clypeus; (7) lateral third of paraocular area hidden by setae, medial area visible between erect setae; (8) rest of face closely punctate except for slightly raised median line; (11) interocellar and ocelloccipital distances equal, greater than ocellocular distance; (15) mandible more slender than Figure 11A (Fig. 11C); (17) lateral surface of mesepisternum with about as many or more punctures than minute punctures; (21) front coxal spine rounded in frontal view; (22) tergum 6 narrowly rounded apically (Fig. 14C); (23) sternum 6 acute apically (Fig. 14C).

MALE. Agrees with figures and description of *Coelioxys texana* except as follows: (24) Length 10-12.5 mm; (25) integument as in female (2 above); (29) clypeoantennal distance as in female (5 above); (30) paraocular area hidden except for small inner area by setae 0.4 mm long; (34) interocellar distance less than ocellocular distance which is less than ocelloccipital distance; (37) hypostomal area of gena with setae much shorter than genal setae; (38) mandible as in female (15 above); (40) mesepisternum as in female (17 above); (45) carina of tergum 6 crenulate or more commonly denticulate, asymmetrical (Fig. 12G) tergum 7 with apical projection slightly more attenuate than shown in Figure 13A.

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys hunteri* has a range similar to that of *C. texana* except *C. hunteri* has been taken further north (Fig. 18). As with *C. texana*, the longest series has been taken in the vicinity of the Southwestern Research Station five miles west of Portal, Arizona.

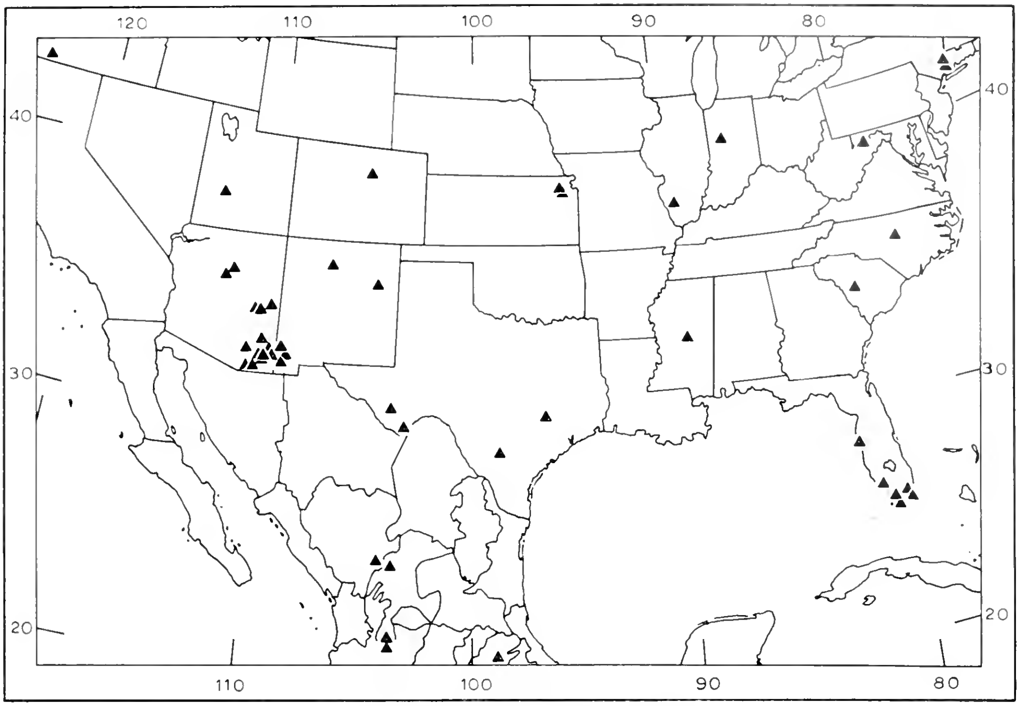

FIGURE 18. Distribution of *Coelioxys hunteri.*

Coelioxys hunteri has been taken from March 14 (Florida) to September 18 (Oregon).

HABITAT. *Coelioxys hunteri* extends through a wide variety of vegetation types in the United States. In the West, it is associated with areas classified as fir-hemlock *(Abies-Tsuga)*, pine-spruce *(Pinus-Picea)*, juniper-pinyon *(Juniperus-Pinus)* forests as well as western shrub *(Atriplex-Sarcobatus)* and shrub-grassland *(Bouteloua, Hilaria, Larrea)* vegetation types. In the central United States, *C. hunteri* has been collected in shinnery *(Quercus-Andropogon)*, bluestem prairie *(Andropogon, Panicum, Sorghastrum)*, and oak-hickory *(Quercus-Carya)* vegetation types. Further east, it extends from the northern hardwood forests down to marl-everglades (*Mariscus* and *Persea, Taxodium*), subtropical-pine *(Pinus-Tetrazygia)*, and mangrove *(Avicennia-Rhizophora)* vegetation types.

GEOGRAPHIC VARIATION. Size, using head width of males as an index, was found to vary geographically in *Coelioxys hunteri* (Females were not used in this study because sample sizes from the eastern United States were too small to yield meaningful results). Head widths of nine males from Florida (3.64 ± 0.133 mm) were significantly larger than those of 15 males from the rest of the eastern United States (3.48 ± 0.130 mm) or 109 males from Southern California, Arizona, New Mexico, western Texas and Mexico (3.38 ± 0.144).

COMPARATIVE COMMENTS. *Coelioxys hunteri,* a medium to large bee, most closely resembles *C. texana* but differs in the males by the bare appearance of the hypostomal area and in the females by the apically very narrowly rounded sixth sternum. Also in the males of *C. hunteri*, the lateral ocellus is subequally distant from the eye and occipital margin, whereas in *C. texana* the lateral ocellus is closer to the eye than to the occipital margin.

Subgenus *Schizocoelioxys* Mitchell

Schizocoelioxys Mitchell, 1973. A subgeneric revision of the genus *Coelioxys* of the Western Hemisphere. Cont. Dept. Entomol. North Carolina State Univ. p. 50. Type species: *Coelioxys funeraria* Smith.

Coelioxys funeraria is the lone New World representative of an Old World group of bees (Mitchell, 1973). The lateral widening of the apical fascia on the first metasomal tergum as well as the medial obliteration of the metasomal graduli is characteristic of many Old World *Coelioxys* spp. Host records of *C. funeraria* fall into four subgenera of *Megachile* (Table 1). Two host subgenera, *Eutricharaea* and *Megachile*, are Holarctic in distribution (the first by recent introduction); and the other two host subgenera, *Delomegachile* and *Xanthosarus*, are closely resembled by two Palearctic groups (Mitchell, personal communication). One of the five known hosts of *C. funeraria* has had only *C. funeraria* reported as a parasite: *M. inermis*. The other four bees are exploited by one to three other species of *Coelioxys*. This bee seems to be a more generalized parasite than the endemic groups of North American *Coelioxys* such as *Boreocoelioxys* and *Synocoelioxys*. The host range and resemblance of *C. funeraria* to Palearctic species suggest that this bee may be a fairly late arrival on the North American scene.

Schizocoelioxys is distinguished from other subgenera of *Coelioxys* by the following list of characters. The absence of fasciae on the scutum and the hump on the inner surface of the mandible (Fig. 22A) are found in no other species of North American *Coelioxys*. Italicized characters most clearly differentiate *Schizocoelioxys* from other subgenera in North America.

A. Ocellar area closely punctured.

B. Preoccipital carina incomplete.

C. *Mandible with hump on inner surface* (Fig. 22A).

D. Prothoracic tubercle with carina moderately produced.

E. *Scutum moderately punctured, lacking fasciae.*

F. Scutellum moderately punctured (Fig. 23A).

G. *Axilla short* (Fig. 23A).

H. Mesepisternum moderately punctured with a few minute punctures in female, contiguously punctured in male.

I. *Metasomal terga with graduli incomplete medially.*

J. Female: *fore coxal spine carinate, blending with medioanterior surface of coxa.*

K. Female: sixth metasomal sternum elongate and notched (Fig. 24A).

L. Male: hypostomal area of gena with excavation bare, shining (Fig. 4).

M. Male: *conspicuous fovea on metasomal tergum two.*

N. Male: spine reduced but present on metasomal tergum five.

O. Male: sixth metasomal tergum with conspicuous spines (Fig. 25A).

P. Male: apex of tergum six rounded apically (Fig. 19A).

Q. Male: sternum four emarginate apically (Fig. 19B).

R. Male: sternum seven represented by two small sclerites (Fig. 19D).

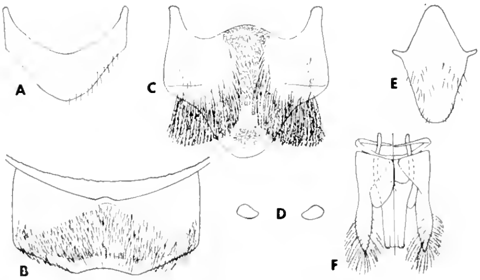

FIGURE 19. Hidden sclerites of male of *Coelioxys funeraria*. A, Seventh tergum; B, Margin of fourth sternum, fifth sternum; C, Sixth sternum; D, Seventh sternum (represented by two sclerites); E, Eighth sternum; F, Genital armature.

Coelioxys funeraria Smith
Figures 19A-F, 20, 22A, 25A-B

Coelioxys funeraria Smith, 1854, Catalogue of British Hymenoptera in the collection of the British Museum I: 272 (♂, Canada, type in the British Museum); Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152: 195, 203 (Key, redescription, = *C. lateralis* Cresson, = *C. lucrosa* Cresson);

Hobbs, 1968, Can. Entomol. 100: 783 (Host).

Coelioxys lateralis Cresson, 1864, Proc. Entomol. Soc. Philadelphia 2:405 (♂, Pennsylvania, type # 2498 in Academy of Natural Sciences of Philadelphia).

Coelioxys lucrosa Cresson, 1878, Trans. Amer. Entomol. Soc. 7:97 (♀, New York, Colorado, type # 2496 in Academy of Natural Sciences of Philadelphia); Graenicher, 1905, Bull. Natur. Hist. Soc. Wisconsin 3:160 (Biology); Graenicher, 1927, Entomol. News 38: 233 (Biology); Graenicher, 1935, Ann. Entomol. Soc. Amer. 28:300, 304 (Biology); Medler, 1958, Can. Entomol. 90: 326-327 (Biology); Medler and Koerber, 1958, Ann. Entomol. Soc. Amer. 51:343 (Biology).

Coelioxys hicksi Cockerell, 1934, Amer. Mus. Novitates 732:3 (♀, Colorado, type in the American Museum of Natural History) NEW SYNONYMY.

FEMALE. (1) Length 12-16 mm; (2) integument finely rugulose between punctures, dull on propodeum; black to very dark brown; (3) pubescence white to light golden brown, golden on tarsi; (4) ocular hairs of medium length (about 0.05 mm); (5) clypeus visible medially, slightly convex, closely punctured with small (about 0.018 mm) punctures; margin gently outcurved, with 5 small denticulations (Fig. 22A); (6) clypeoantennal distance less than lateral margin of clypeus; (7) paraocular area visible between 0.35 mm long setae, closely punctured; (8) rest of face closely punctured up to ocellar area except for longitudinal median area indented by a longitudinal median line; (9) interantennal distance greater than clypeoantennal distance which is greater than antennocular distance; (10) ocellar area sloping, coarsely punctured; (11) interocellar distance greater than ocelloccipital distance, less than ocellocular distance; (12) vertex with punctures slightly larger and slightly more crowded than shown in Figure 10; (13) gena subequal in width to eye, tapering dorsally and ventrally; (14) hypostomal area of gena with setae slightly longer than on gena; (15) mandible with a distinct hump on inner surface (Fig. 22A); (16) scutum with inconspicuous, slender setae; median line extending slightly more than half the distance from anterior margin; disc less closely punctured than periphery; (17) lateral surface of mesepisternum punctured like scutum in Figure 10, but with a few minute punctures among punctures; (18) scutellum with posterior margin of dorsal surface broadly rounded in dorsal view (Fig. 23A); (19) axilla reduced in length (Fig. 23A); (20) metanotum with inconspicuous, long, slender setae; (21) front coxal spine a thickened carina blending with medioanterior surface of coxa; (22) terga 1-5 with graduli incomplete medially, with apical fasciae wider laterally; graduli bare; tergum 6 elongate with raised, impunctate median line (Fig. 24A); (23) sterna 1-5 fasciate apically; 1-4 more closely punctured laterally; sternum 5 very closely and minutely punctured apically; sternum 6 minutely and closely punctured with elongate punctures, elongate, notched subapically (Fig. 24A).

MALE. (24) Length 9-12 mm; (25) integument as in female (2 above); (26) pubescence as in female (3 above); (27) ocular hairs of medium length (about 0.08 mm); (28) clypeus and clypeal margin hidden by setae 0.5 mm long, conformation as in female (5 above); (29) clypeoantennal distance shorter than lateral margin of clypeus; (30) paraocular area almost hidden by setae about 0.45 mm long, closely punctured; (31) rest of face visible through setae 0.5 mm long, punctures contiguous to ocellar area; (32) clypeoantennal distance less than interantennal distance and greater than antennocular distance; (33) ocellar area contiguously punctured; (34) ocelloccipital distance less than ocellocular distance and subequal to or greater than interocellar distance; (35) vertex coarsely but contiguously punctured; (36) gena slightly narrower than eye (Fig. 4); (37) hypostomal area bare, separated from gena by carina (Fig. 4); (38) mandible as in female (15 above); (39) scutum as in female (16 above); (40) mesepisternum contiguously punctured; (41) scutellum as in female (18 above); (43) axilla slightly more produced than shown in Figure 23A; (43) metanotum as in female (20 above); (44) front coxal spine robust, about twice as long as broad; (45) terga 1-6 fasciate lateroapically; graduli incomplete medially, mostly bare; tergum 2 with conspicuous foveae (Fig. 25B); tergum 6 with conspicuous dorsal, ventral, and lateral spines (Fig. 25A); tergum 7 rounded apically (Fig. 19A); (46) sterna 1-4 fasciate apically, evenly punctured; (47) sternum 4 submarginally carinate, weakly bidentate apically (Fig. 19B); sternum 5 incurved apically (Fig. 19B); sternum 6 with abundant, long setae (Fig. 19C), sternum 7 represented by 2 small sclerites (Fig. 19D); sternum 8 broadly rounded apically (Fig. 19E); (47) genital armature with long, copious setae on gonocoxites (Fig. 19F).

HOST RECORDS. *Coelioxys funeraria* has been reported from more hosts than any other North American *Coelioxys*. Graenicher (1927) reported *C. funeraria* to be a parasite of *Megachile latimanus*. Medler (1958) reported *C. funeraria* from the nest of *M. inermis*, and Medler and Koerber (1958) reported *C. funeraria* from the nest of *M. relativa*. Mitchell (1962) listed *M. frigida* as a host of *C. funeraria*, and Hobbs (1968) found a fifth host species, *M. rotundata*.

DISTRIBUTION AND SEASON OF FLIGHT. The distribution of *Coelioxys funeraria* extends from above the arctic circle to southern New Mexico (Fig. 20). Such a broad distribution, however, is no more remarkable than the distribution of one of the host bees, *Megachile frigida*, which ranges from Alaska to Arizona.

Season of flight lasts at least from May 26 (Ottawa, Ontario) to September 18 (Banff, Alberta) with most specimens taken from mid-June through August.

HABITAT. In the northern portion of its range, *Coelioxys funeraria* is associated with areas designated as various coniferous forests, tundra-coniferous forest, northeastern oak-pine forests, northern floodplain forests, Appalachian oak forest, northern grassland, oak savana, and fescue-wheatgrass vegetation types. Further south *C. funeraria* is associated only with vegetation types which occur at higher elevations such as alpine meadow barrens in Colorado and southwestern spruce-fir forest in New Mexico. In California (Gilroy), *C. funeraria* was taken near an area classified as the ecotone between California oakwoods and fescue-oatgrass vegetation types.

GEOGRAPHIC VARIATION. Although there is considerable variation in size in *Coelioxys funeraria*, larger and smaller specimens occur throughout the range. One explanation for such variation may be that its size is an expression of host size. The large bees may utilize the nests of *Megachile inermis* (15-22 mm). Medium sized *C. funeraria* may utilize the nests of *M. frigida* (12-15 mm) and *M. latimanus* (13-14 mm), and the small *C. funeraria* may utilize the nests of *M. relativa* (9-12 mm) and *M. rotundata* (8-9 mm). The distributions of the host bees overlap over thousands of square miles, and perhaps this overlap accounts for the considerable variation within and between populations of *C. funeraria* from any one area.

COMPARATIVE COMMENTS. *Coelioxys funeraria* is most easily confused with the usually smaller *C. moesta*, but it

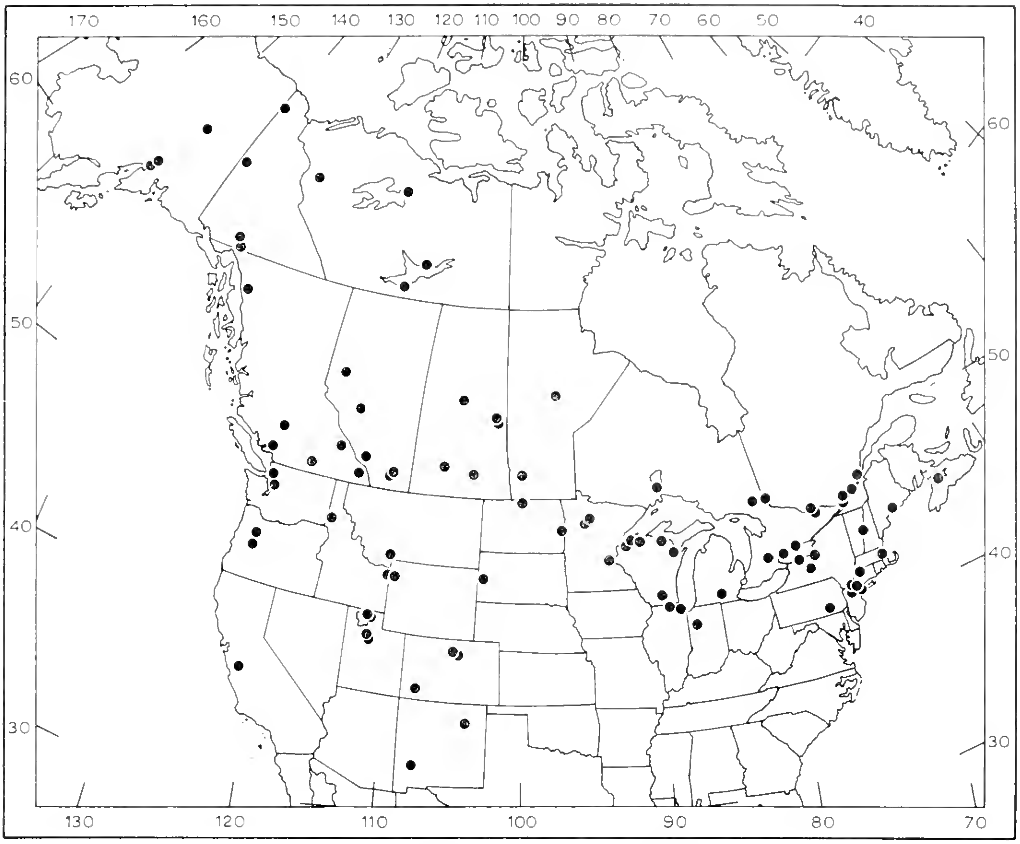

FIGURE 20. Distribution of *Coelioxys funeraria*.

is distinguished from *C. moesta* males by the foveae of the second metasomal tergum which are large and almost open along the anterior margin in *C. funeraria* (Fig. 25B) and small and enclosed in *C. moesta* (Fig. 25E). The female of *C. funeraria* possesses a convex clypeus with a slightly outcurved margin (Fig. 22A) whereas the female of *C. moesta* possesses a flat clypeus with a triangularly produced margin (as in Fig. 22D).

Subgenus ***Boreocoelioxys*** Mitchell

Boreocoelioxys Mitchell, 1973. A subgeneric revision of the genus *Coelioxys* of the Western Hemisphere. Cont. Dept. Entomol. North Carolina State Univ. p. 37. Type species: *Coelioxys rufitarsis* Smith.

Other bees in the subgenus *Boreocoelioxys* are *C. banksi*, *C. insita*, *C. moesta*, *C. novomexicana*, *C. oaxacana*, *C. octodentata*, *C. porterae*, *C. pratti*, and *C. sayi*. These bees are usually black or dark brown except for the legs which may vary from black to bright ferruginous.

Host-parasite relationships are not clear-cut for *Boreocoelioxys*. The large number of hosts utilized probably reflects a generalized response of female *Coelioxys* to nests of *Megachile* occurring within the habitat. Species from the group have been reared from the following subgenera of *Megachile*: *Delomegachile*, *Eutricharaea*, *Litomegachile*, *Megachile*, *Pseudocentron*, and *Xanthosarus* (Table 1).

Most of the characters in the list below are found in other subgenera of New World *Coelioxys* and even in some of the Old World *Liothyrapis*, but never in this combination. This group is the only North American group with complete graduli on meta-

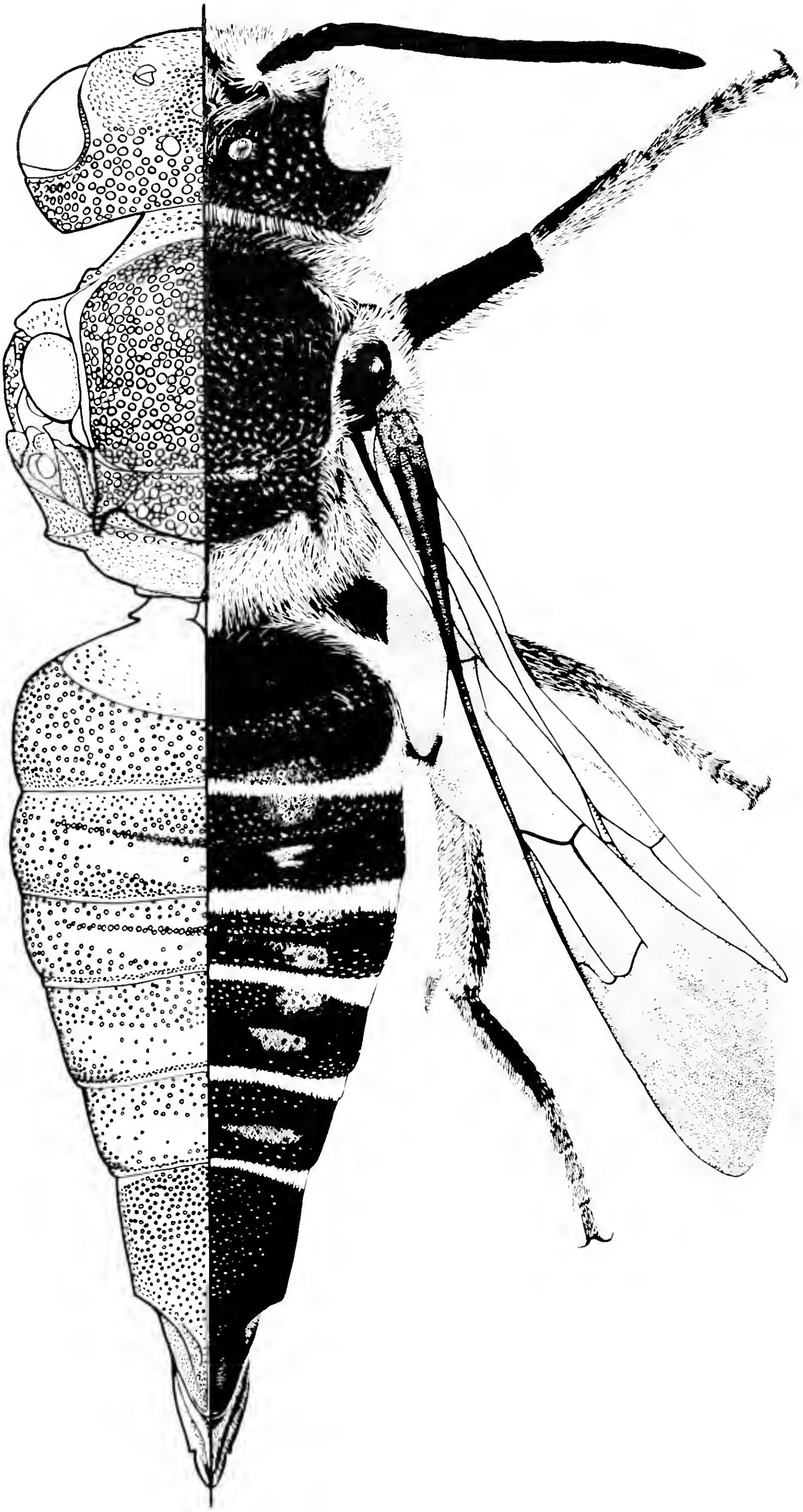

Figure 21. Dorsal view of female *Coelioxys rufitarsis*, left half showing punctation, right half with melanization and pubescence added.

somal terga two and three and notched sixth metasomal sterna in females or foveae on metasomal tergum two in males. Italicized characters most clearly differentiate *Boreocoelioxys* from other subgenera in North America.

A. Ocellar area closely punctured (Fig. 21).

B. Preoccipital carina incomplete medially.

C. Mandible with outer surface broadly rounded to humped (Fig. 22B-G).

D. Prothoracic tubercle with carina usually produced into thin, plate-like structure.

E. Scutum closely punctured, sometimes with conspicuous fasciae (Fig. 21).

F. Scutellum contiguously to moderately punctured (Fig. 23B-D).

G. Axillae well produced (Fig. 21, 23B-D).

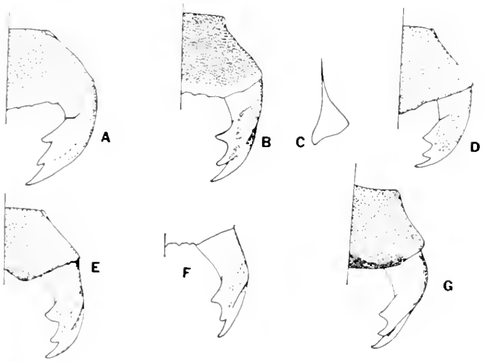

FIGURE 22. Left half of clypeus and mandible of females of *Coelioxys*. A, *C. funeraria;* B, *rufitarsis;* C, Lateral view of clypeus of *C. banksi;* D, *C. banksi;* E, *C. novomexicana;* F, *C. porterae;* G, *C. sayi.*

H. Mesepisternum with lateral surface closely punctured.

I. *Graduli complete on metasomal terga two and three* (Figs. 21, 25B).

J. Female: fore coxal spine small, inconspicuous.

K. Female: *sixth metasomal sternum elongate and notched* (Figs. 21, 24B-L).

L. Male: hypostomal area of gena with excavation bare, shining.

M. Male: *conspicuous foveae on metasomal tergum two* (Fig. 25B).

N. Male: fifth metasomal tergum with lateral spine (Fig. 25B).

O. Male: sixth metasomal tergum with conspicuous spines (Fig. 25B).

P. Male: apex of metasomal tergum seven rounded (Fig. 26A).

Q. Male: apex of metasomal sternum four conspicuously emarginate (Fig. 26B).

R. Male: sternum seven represented by two small sclerites (Fig. 26D).

FIGURE 23. Scutellum and axillae of females of *Coelioxys*. A, *C. funeraria;* B, *C. moesta;* C, *C. oaxacana.*

KEY TO FEMALES OF *Boreocoelioxys*

1. Clypeal margin with distinct emargination evident in frontal view with full compliment of setae 4
Clypeal margin otherwise 2
2. Clypeal margin outcurved 3
Clypeal margin straight 5
3. Clypeus concave in profile .... *banksi*
Clypeus straight in profile .... *moesta*
4. Clypeal margin with dense fringe of white setae almost perpendicular to surface .... *sayi*
Clypeal margin with dense fringe of yellowish setae almost parallel to surface .... *novomexicana*

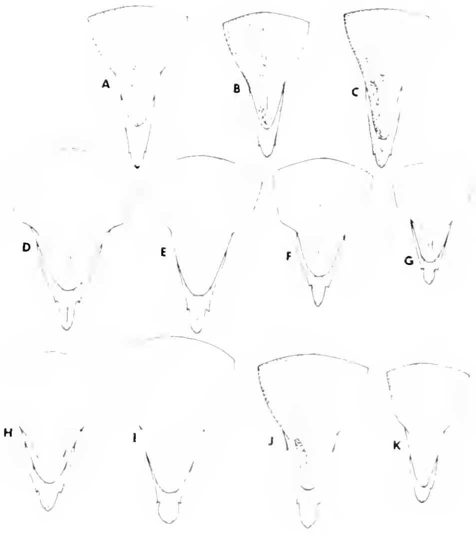

FIGURE 24. Sixth metasomal tergum and sternum of females of *Coelioxys*. A, *C. funeraria;* B, *C. banksi;* C, *C. moesta;* D-I, *C. octodentata* showing variation in lateral angles of tergum, apex of sternum; J, *C. porterae*, K, *C. oaxacana.*

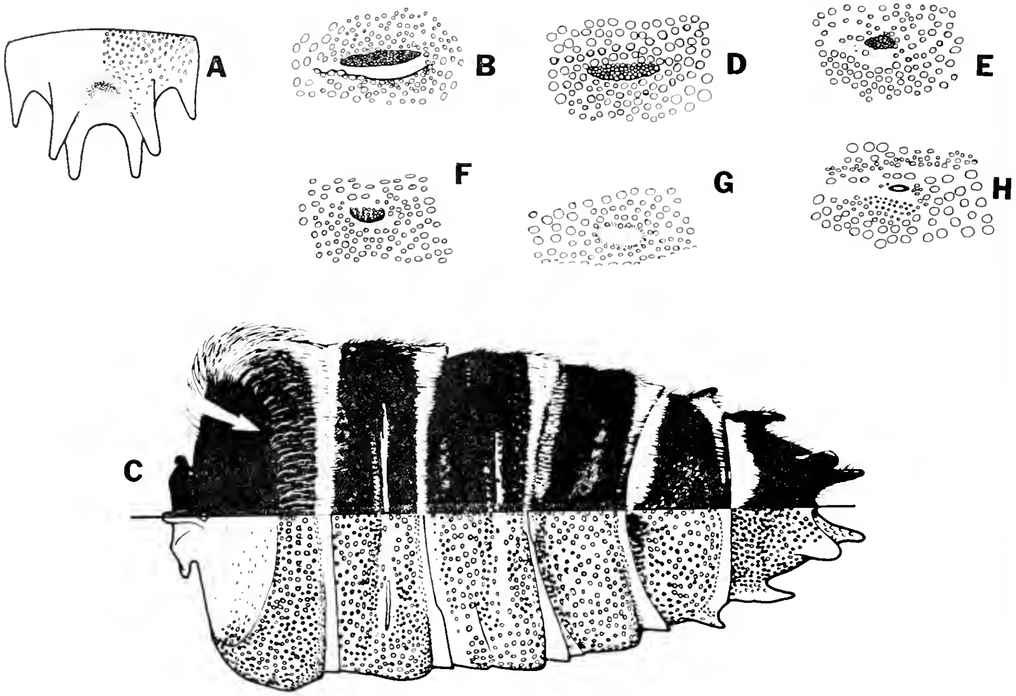

Figure 25. Various parts of males of *Coelioxys*. A-B, *C. funeraria*. A, Sixth metasomal tergum; B, Fovea. C, Metasoma, *C. rufitarsis* (arrow indicates median fascia). D-H, Foveal areas. D, *C. banksi;* E, *C. moesta;* F, *C. porterae;* G, *C. octodentata;* H, *C. grindeliae*.

5. Scutellum with median longitudinal ridge .... *oaxacana*
   Scutellum without median longitudinal ridge 6
6. Tergum six in dorsal view angulate as in Figure 21 7
   Tergum six in dorsal view less angulate than shown in Figure 24 J 8
7. Ocular hairs long (about 0.15 mm); tergum six with tiny setae ventral to angles which have a velvety appearance; tergum one with median fascia (see arrow on Fig. 25C) of long, slender, erect setae .... *rufitarsis*
   Ocular hairs short (about 0.05 mm); tergum six with squamose white setae ventral to angles; tergum one with median fascia of prostrate setae, if slender than short .... *octodentata**
8. Conspicuous fasciae laterally and anteriorly around scutum; ocular hairs long (about 0.15 mm) .... *pratti*
   Scutum with no conspicuous fasciae; ocular hairs variable 9
9. Sterna one to five ferruginous apically. .... *octodentata**
   Sterna one to five very dark to black apically 10
10. Legs black or very dark brown .. *porterae*
    Legs brownish to ferruginous 11
11. Tergum six broadly rounded apically (Fig. 24E-J) .... *octodentata**
    Tergum six narrow apically (as in Fig. 24B) .... *insita*

* Occurs more than once in key.

Key to Males of *Boreocoelioxys*

1. Fovea on metasomal tergum two wide, deep, short, conspicuous; margins of fovea impunctate (Fig. 25C); bee robust .... *rufitarsis*
   Fovea on metasomal tergum two variable, if wide, then anterior margin punctate; bee variable in form 2
2. Fovea on metasomal tergum two shallow (as in Fig. 25D) or with anterior margin lower than posterior margin (as in Fig. 25F) and sometimes closely punctate 3
   Fovea on metasomal tergum two deep (as in Fig. 25G) with margins the

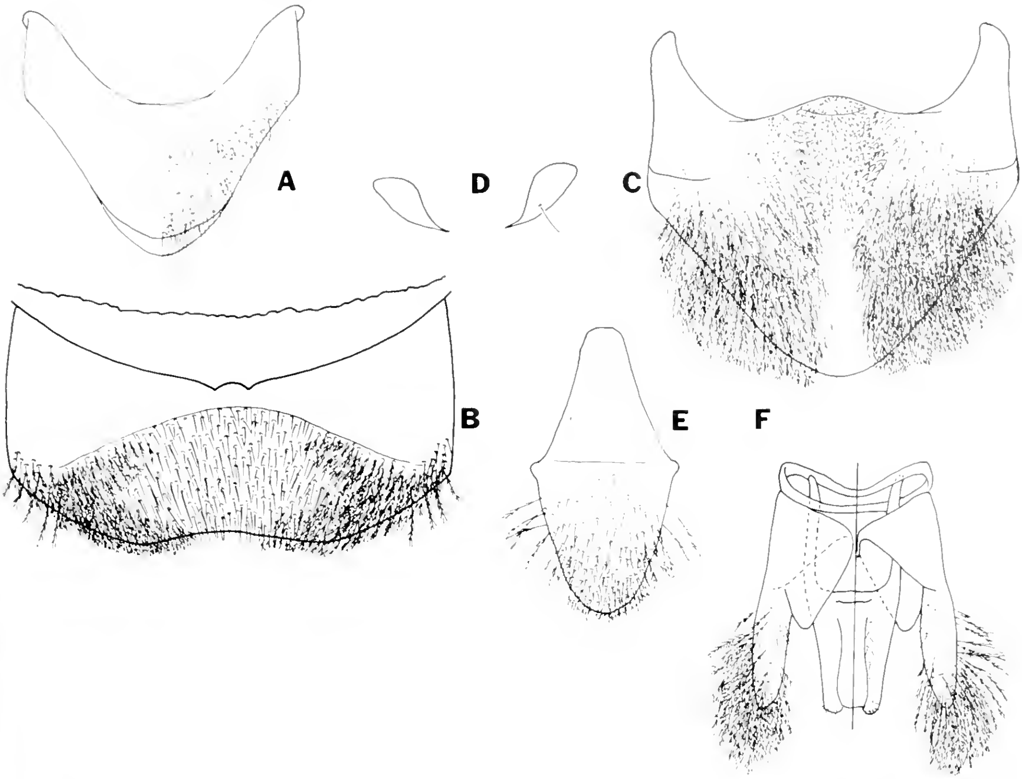

FIGURE 26. Hidden sclerites of male of *Coelioxys rufitarsis*. A, Seventh tergum; B, Margin of fourth sternum, fifth sternum; C, Sixth sternum; D, Seventh sternum (represented by two sclerites); E, Eighth sternum F, Genital armature.

same height, anterior margin may be moderately punctate 4

3. Scutellum with dorsal and posterior surfaces separated medially by a carina, punctures deep and contiguous; legs usually with ferruginous areas; fovea on metasomal tergum two complete or with anterior margin weak (as in Fig. 25D .... *banksi, insita*

   Scutellum convex, punctures contiguous but so broad that edges become minute carinae above the flat surfaces of the puncture floors; legs usually black or blackish-brown; fovea on metasomal tergum two with anterior margin weaker than posterior margin (Fig. 25F) .... *porterae*

4. Fovea on metasomal tergum two inconspicuous, sometimes shallow (Fig. 25E); integument usually black; medium to small, slender bee .... *moesta*

   Fovea on metasomal two deep and conspicuous (as in Fig. 25G) with small, contiguous punctures immediately posterior to it; integument variable in color; medium to large bee 5

5. Posterior margins of gradular grooves on metasomal terga two and three almost obliterated medially .... *sayi*

   Posterior margins of gradular grooves on metasomal terga two and three distinct medially 6

6. Ocular hairs long (about 0.15 mm); punctation of vertex with conspicuous interspaces; scutum with conspicuous anterolateral fasciae; posterior surface of scutellum with conspicuous fascia .... *pratti*

   Ocular hairs short (about 0.06 mm); punctation of vertex variable; scutum laterally and scutellum posteriorly without conspicuous fasciae. .... *novomexicana, octodentata*

Coelioxys rufitarsis Smith

Figures 21, 22B, 25C, 26A-F, 27, 28

Coelioxys rufitarsis Smith, 1854, Catalogue of Hymenoptera in the British Museum 2:271 (♂, United States, type in the British Museum); Graenicher, 1905, Bull. Wisconsin Natur. Hist. Soc. 3: 162-163 (Host); Graenicher, 1906, Bull. Wisconsin Natur. Hist. Soc. 4:138 (Biology); Robertson, 1926, Psyche 33: 116 (Host); Hicks, 1926, Univ. Colorado Stud. 15:230 (Host); Graenicher, 1927, Entomol. News 38:233 (Biology); Robertson, 1929, Flowers and Insects, Lancaster Pennsylvania Sci. Press: 9-142 (Flower Records); Medler and Lussenhop. 1968, Univ. Wisconsin Research Bull. 274:57 (Key, diagnosis, biology).

Coelioxys dubitata Smith, 1854, Cat. Hymenoptera Brit. Mus. 2:272 (♀, Florida, type in the British Museum); Robertson, 1897, Trans. Acad. Sci. St. Louis 7:345 (= *rufitarsis*); Graenicher, 1935, Ann. Entomol. Soc. Amer. 28: 300, 304 (Distribution, host).

Coelioxys comstockii Cresson, 1878, Trans. Amer. Entomol. Soc. 7:96 (♀, New York, type # 2497 in the Academy of Natural Sciences of Philadelphia) NEW SYNONYMY.

Coelioxys coloradensis Cresson, 1878, Trans. Amer. Entomol. Soc. 7:98 (♂, Colorado, type # 2500 in the Academy of Natural Sciences of Philadelphia) NEW SYNONYMY; Hicks, 1926, Univ. Colorado Stud. 15:233 (Host); Graenicher, 1935, Ann. Entomol. Soc. Amer. 28:300 (Host).

Coelioxys rufitarsis rhois Cockerell, 1903, Ann. Mag. Natur. Hist. 12:452 (♀, New Mexico, type in the American Museum of Natural History).

Coelioxys rufitarsis claripes Cockerell, 1925, Pan-Pacific Entomol. 1:146, 150 (♂, California, type # 1633 in the California Academy of Sciences).

Coelioxys rufitarsis rufitarsis; Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:193-194, 220 (Key, redescription).

FEMALE. (1) Length 11-13 mm; (2) integument granular on vertex between punctures and on thorax; black, dark brown on ventral surface of tergum 1, legs distal to coxae black to ferruginous; (3) pubescence white, golden on tarsi; (4) ocular hairs long (about 0.15 mm); (5) clypeus uniformly covered with short, appressed setae, surface visible, margin irregular (Fig. 22B); (6) clypeoantennal distance shorter than lateral margin of clypeus; (7) paraocular area hidden by setae about 0.25 mm long; (8) rest of face rugose, closely punctured up to ocellar area except for small median impunctate ridge between antennae; (9) clypeoantennal distance less than interantennal and greater than antennocular distances; (10) ocellar area closely punctate; (11) interocellar distance greater than ocelloccipital and less than ocellocular distances; (12) vertex moderately punctate (Fig. 21); (13) gena narrower than eye, integument visible, ventral angle about 90°; (14) hypostomal area of gena with setae longer than on disc; (15) mandibles short, broad (Fig. 22B); (16) scutum with slender, erect hair on disc (Fig. 21); (17) lateral surface of mesepisternum closely punctate with long (about 0.35 mm), slender setae which usually form anterior and posterior fasciae; (18) scutellum with posterior margin of dorsal surface rounded (Fig. 21); (19) axilla well produced (Fig. 21); (20) metanotal setae erect except for 1-3 or 4 prostrate in center; (21) front coxal spine subtriangular, inconspicuous; (22) terga 2, 3 with conspicuous gradular grooves, terga 1-5 with conspicuous apical fasciae, tergum 6 angled with very small setae at angles which resemble velvet in dorsal view (Fig. 21); (23) sterna 1-5 fasciate apically, fasciae of sterna 2-4 usually interrupted medially, sterna 1-4 and basal area of sternum 5 deeply and evenly punctured, sternum 5 apically very closely and shallowly punctured, sternum 6 with indistinct elongate punctures medially, broadly lanceolate apically (Fig. 21).

MALE. (24) Length 9.5-12 mm; (25) integument as in female (2 above), venter of abdomen black to dark brown; (26) pubescence white, white to yellow on face, white to pale brown on thorax, golden on tarsi; (27) ocular hairs long (about 0.15 mm); (28) clypeus hidden by copious long (about 0.45 mm) setae, surface rugose and shiny; clypeal margin slightly emarginated with 5 small denticles; (29) clypeoantennal distance as in female (6 above); (30) paraocular area hidden by long setae (about 0.6 mm); (31) rest of face rugose with median, short (0.25 mm), impunctate line usually obscured by copious setae up to 0.45 mm long; (32) interantennal, clypeoantennal, antennocular distances as in female (9 above); (33) ocellar area as in female (10 above); (34) interocellar and ocelloccipital distances equal, less than ocellocular distance; (35) vertex as in female (12 above); (36) gena as in female (13 above) but ventral angle greater than 90°; (37) hypostomal area of gena modified into distinct excavation (as in Fig. 4), anterior portion with setae as in female (14 above), posterior portion with integument clearly visible; (38) mandible, scutum, mesepisternum, scutellum, axilla, metanotal setae as in female (15-20 above); (44) front coxal spine long (about 0.25 mm) and broad (about 0.2 mm) with setae on dorsal and ventral surfaces, rounded apically, directed anteriorly; (45) terga with apical fasciae diminishing posteriorly, gradular grooves of terga 4-6 with fasciae, fovea on tergum 2 less than 0.05 mm long and 0.3-0.5 mm wide (Fig. 25C), tergum 6 with dorsal spines stouter than ventral spines (Fig. 25C); tergum 7 unmodified (Fig. 26A); (46) sterna 1-4 evenly punctate with small slender seta in each puncture, fasciate apically, sternum 1 fasciate medially; (47) sternum 4 submargically carinate, apex emarginate to bidentate, margin of sternum 5 slightly emarginate (Fig. 26B), sternum 6 with copious setae lateroapically (Fig. 26C), sternum 7 with two sclerotized areas (Fig. 26D), sternum 8 with base broad (Fig. 26E), genital armature with abundant setae on gonocoxite apically (Fig. 26F).

HOST RECORDS. Graenicher (1905) reared *Coelioxys rufitarsis* from nests of *Megachile latimanus* and *M. melanophaea.* He later (1935) reported *C. rufitarsis* to be a parasite of *M. melanophaea wootoni.* Hicks (1926) reared *C. rufitarsis* (= *C. coloradensis*) from a nest of *M. montivaga.* Medler and Lussenhop (1968) reported that D. H. Pengelly found *C. rufitarsis* to be a parasite of *M. texana.* Mitchell (1973) indicated *M. fortis* is another host of *C. rufitarsis.* A new host record from a label of *C. rufitarsis* from Alberta, Canada, is *M. perihirta.*

DISTRIBUTION AND SEASON OF FLIGHT. This bee extends from middle Canada well into Mexico (Fig. 27). Although Smith (1854) described the female of *Coelioxys rufitarsis* from Florida, specimens from south of the 35° parallel are rare.

Coelioxys rufitarsis is in flight at least from April 22 (Texas) and May 21 (Idaho) to October 3 (central California).

HABITAT. *Coelioxys rufitarsis* ranges through areas which have been classified as a variety of forest, savana, and open grassland vegetation types. In the West this bee has been taken from areas classified as forests containing such dominant trees as spruce *(Picea),* cedars *(Thuja Librocedrus),* hemlock *(Tsuga),* fir *(Abies),* and pine *(Pinus);* from areas classified as scrub and savana such as chaparral, mountain mahogany-oak scrub and oak savana *(Cercocarpus, Quercus, Andropogon),* juniper-oak savana *(Juniperus, Quercus, Andropogon),* sagebrush *(Salvia, Eriogo-*

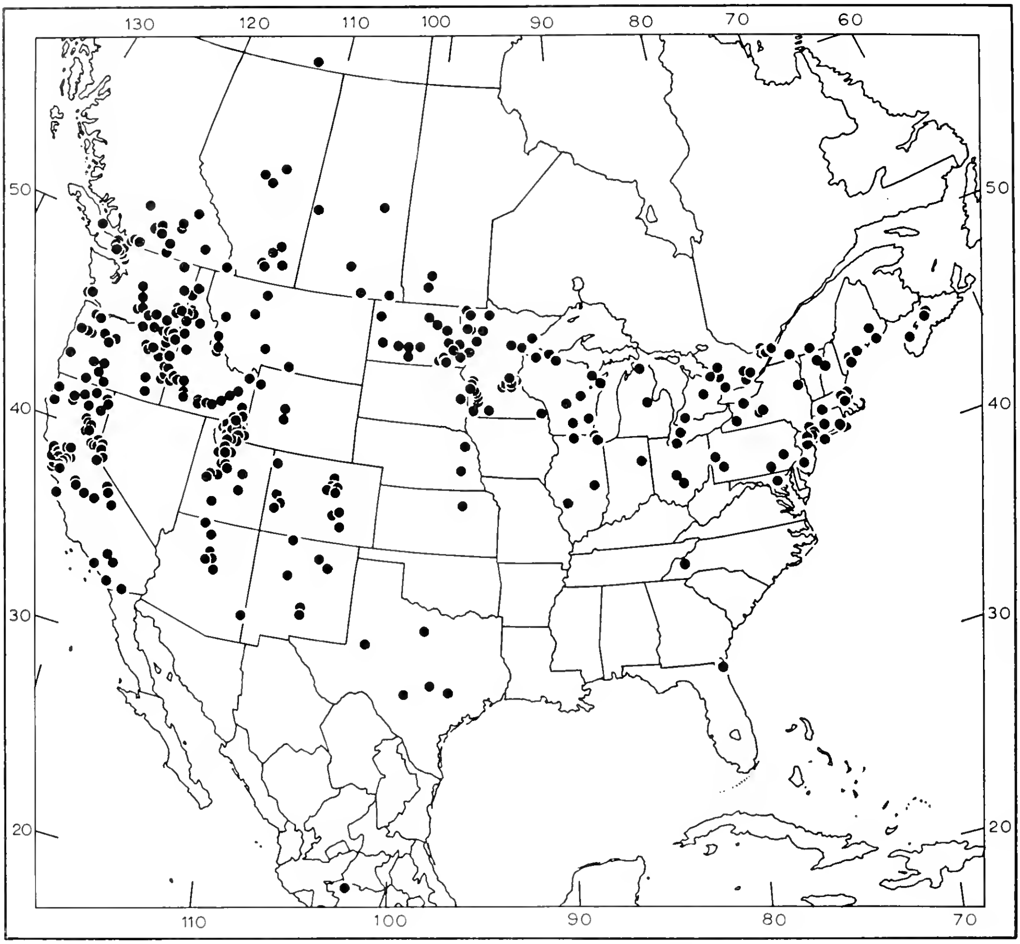

Figure 27. Distribution of *Coelioxys rufitarsis*.

num, Artemisia), and creosote bush (*Larrea*); from areas classified as various grasslands containing grasses such as fescue (*Festuca*), oatgrass (*Danthonia*), tule (*Scirpus*), cattail (*Typha*), grama grass (*Bouteloua*), and bluestem (*Andropogon*); and from an area classified as alpine meadows and barren.

In the East *Coelioxys rufitarsis* has been taken from areas classified as a variety of northern coniferous, hardwood and mixed forests. In Florida it has been collected in southern mixed forest.

GEOGRAPHIC VARIATION. As with *Coelioxys alternata*, leg color of *C. rufitarsis* varies throughout its distribution and seemingly without respect to geography. However, an exceptionally large series of *C. rufitarsis* from California showed possible geographic variation (Fig. 28). The proportion of bees with dark legs was greater for bees from higher elevations than for bees from the San Joaquin and Sacramento Valleys. However, bees with both dark and ferruginous legs occurred at high and low elevations.

Color of the pubescence of males seemed to vary geographically. Some males from the western portion of the distribution of *Coelioxys rufitarsis* possess yellowish facial pubescence and slightly brownish thoracic pubescence. This con-

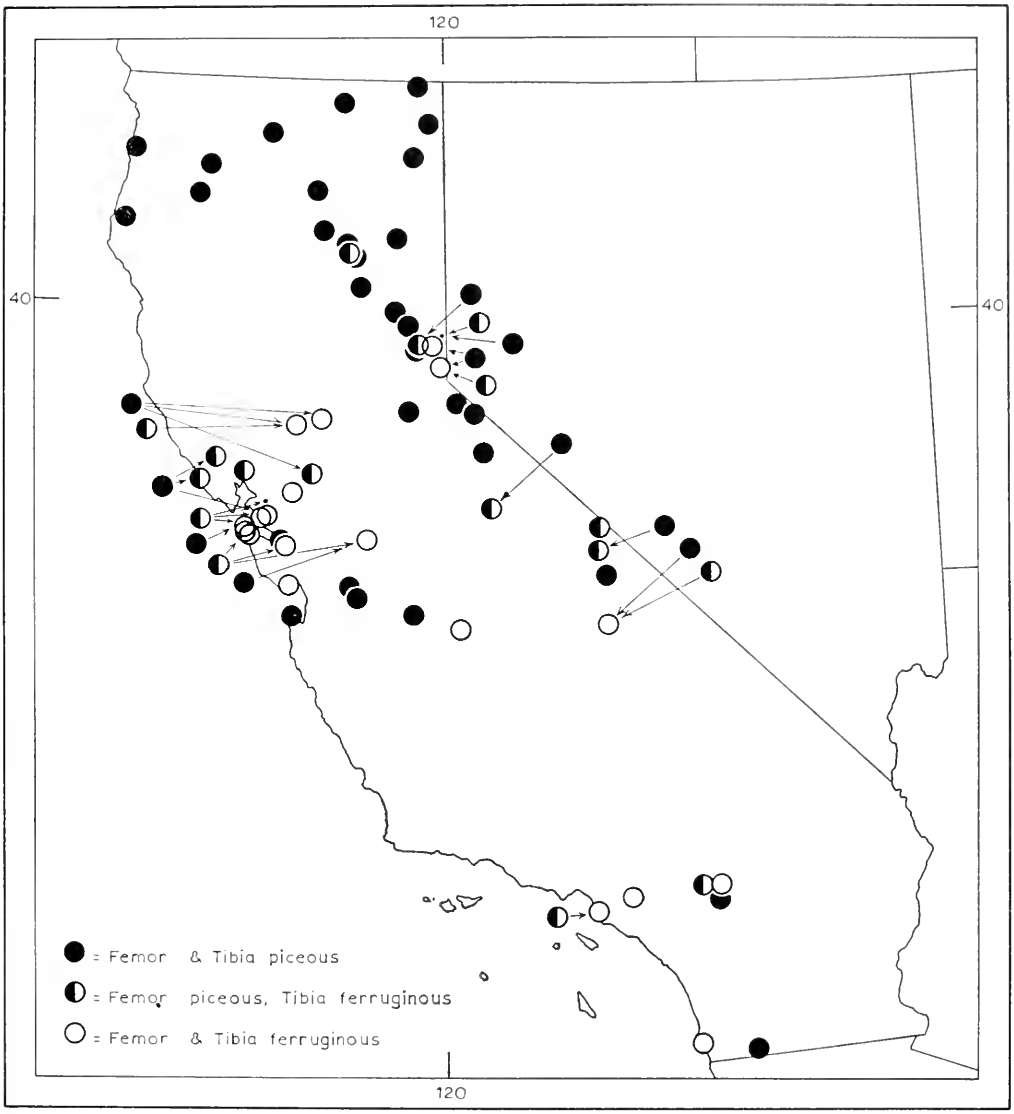

FIGURE 28. Distribution of *Coelioxys rufitarsis* in California showing variation in leg color.

dition was especially evident in bees from Zacapu, Michoacan, Mexico. However, bees in this condition were also taken in southwestern Canada and Ithaca, New York. Perhaps the yellow or brown condition of the pubescence is due to the teneral conditions of these specimens. Teneral adults of *Megachile brevis* and *M. mendica* possess bright yellow (almost orange-yellow in *M. mendica*) pubescence whereas that of specimens from the field is white.

The name *Coelioxys comstockii* is represented only by the type specimen in the Academy of Natural Sciences of Philadelphia and seems to be a teratological specimen. The metasoma appears to be discolored; the metasoma is asymmetrically punctured (some punctures appear to be missing on one side); and the apex of tergum six appears to be broken. Pollen on the sixth metasomal sternum indicates the bee may have been worn before collection. In other respects, however, the specimen agrees with the description above.

COMPARATIVE COMMENTS. *Coelioxys rufitarsis* is most easily confused with the larger western specimens of *C. octodentata* but differs in the females by the basal fascia on metasomal tergum one which is composed of long, slender, erect setae in *C. rufitarsis* (Fig. 21) and at least partially composed of squamose setae in *C. octodentata*. Males of *C. rufitarsis* possess foveae (Fig. 25C) which are wider, deeper, and shorter than those of *C. banksi* and *C. insita* (Fig. 25D) and are unlike the more oval foveae of all other North American *Coelioxys* which possess foveae on the second tergum of the metasoma.

Coelioxys banksi Crawford
Figures 22C-D, 24B, 25D, 29

Coelioxys banksi Crawford, 1914, Ann. Entomol. Soc. Amer. 7:155 (♀, Virginia, type # 18221 in the National Museum of Natural History); Medler and Koerber, 1958, Ann. Entomol. Soc. Amer. 51:343 (Biology); Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:213 (= *C. moesta,* misidentification).

Coelioxys angulifera Cockerell, 1916, Pomona J. Entomol. Zool. 8:61 (♀, ♂, California, type in the American Museum of Natural History) NEW SYNONYMY.

FEMALE: Agrees with description and figures of *Coelioxys rufitarsis* except as follows: (1) Length 10-13 mm; (2) integument black, becoming brown to ferruginous on tegula, legs distal to base of femora, and metasomal venter; (4) ocular hairs short (about 0.05 mm); (5) clypeal margin outcurved and produced anteriorly, clypeal profile concave (Fig. 22C-D); (7) paraocular area almost hidden by appressed setae about 0.15 mm long; (10) ocellar area in some specimens with irregular, impunctate areas, usually narrower than puncture width anterior to median ocellus; (11) interocellar distance equal to ocelloccipital distance, less than ocellocular distance; (13) gena equal in width to light portion of eye; (14) hypostomal area of gena with setae as long as or slightly longer than setae on lower disc; (16) scutum with slender, erect setae and with anterolateral fascia sometimes less conspicuous than shown in Figure 21; (17) mesepisternum in some specimens with an occasional minute puncture among large punctures, usually closely punctured; (22) terga 2-5 slightly more closely punctured on postgradular area than shown in Fig. 21, gradular groove of tergum 3 less conspicuous than shown in Fig. 21, tergum 6 not angled laterally but produced posteriorly (Fig. 24B); (23) sternum 6 elongate, apex lanceolate (Fig. 24B).

MALE: Agrees with figures and description of *C. rufitarsis* except as follows: (24) Length 9.5-11.5 mm; (25) integument faintly rugulose on metasoma between punctures; tegula black to brown; (26) pubescence as in female (3 above); (27) ocular hairs of medium length (about 0.09 mm); (31) rest of face coarsely, contiguously punctured, with long (0.3 mm), slender setae; (33) ocellar area contiguously punctured; (34) ocelloccipital distance greater than interocellar distance, less than ocellocular distance; (37) hypostomal area of gena with pubescence on anterior portion shorter than on gena; (39) scutum as in female (16 above); (43) metanotum with erect, slender setae; (45) fovea on tergum 2 about 0.06 mm long and 0.3 mm wide (Fig. 25D); tergum 6 with depression between dorsal spines slightly deeper and wider than shown in Figure 25C.

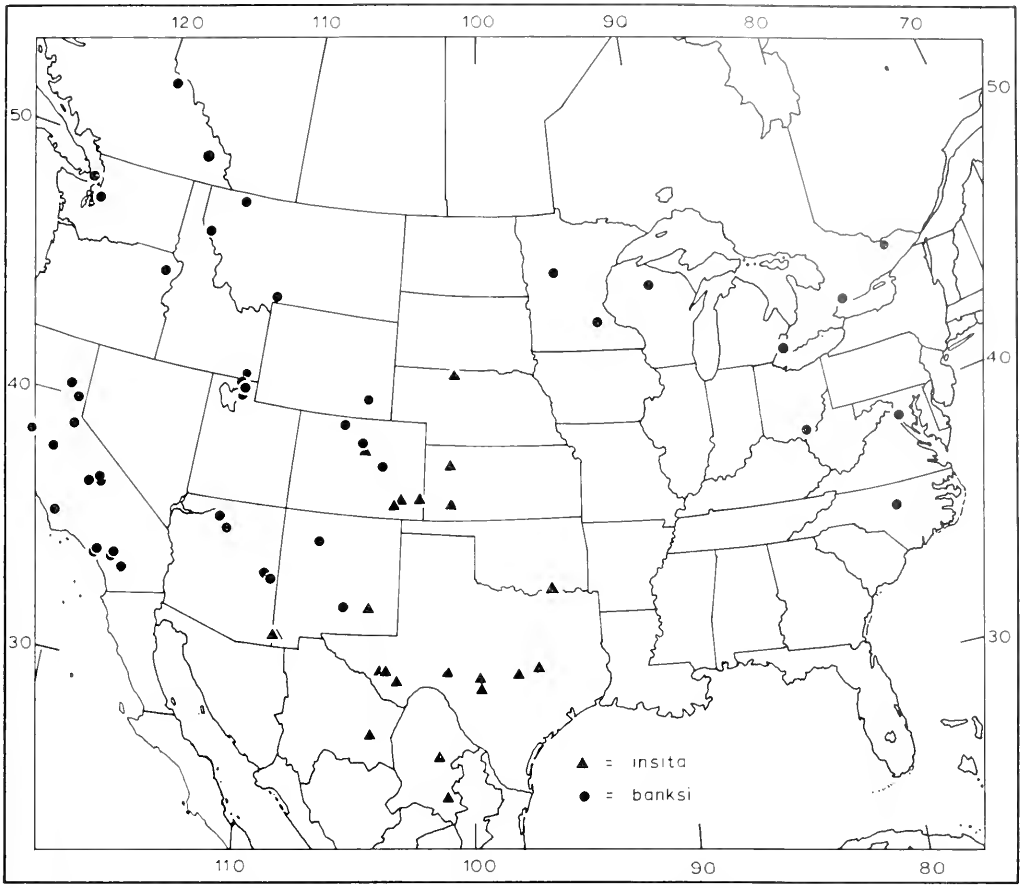

FIGURE 29. Distributions of *Coelioxys banksi* and *C. insita*.

HOST RECORDS. Medler and Koerber (1958) reported rearing *Coelioxys banksi* from nests of *Megachile relativa*.

DISTRIBUTION AND SEASON OF FLIGHT. This species has been collected throughout the western half and northeastern quarter of the United States (Figure 29). It appears to be rare throughout its range.

Coelioxys banksi is in flight from at least April 16 (central California) to September 20 (Toronto, Ontario).

HABITAT. *Coelioxys banksi* has been taken mainly from areas classified as western coniferous and northern hardwood forests. The western forests are dominated by such trees as cedar *(Thuja)*, hemlock *(Tsuga)*, and Douglas fir *(Pseudotsuga)*, grand fir *(Abies)*, pine *(Pinus)*, and spruce *(Picea)*. Two areas, one in California, classified as coastal sagebrush *(Salvia, Eriogonum)* and the other in Utah classified as mountain mahogany-oak shrub *(Cercocarpus, Quercus)*, were the only western areas not dominated by conifers. In the East this bee was taken from an area classified as mixed mesophytic forest *(Acer, Aesculus, Fagus, Liriodendron, Quercus, Tilia)* and an area classified as northern hardwoods forest *(Acer, Betula, Fagus, Tsuga)*. Perhaps *C. banksi* is excluded from the western, central, and eastern grasslands by *C. insita*.

GEOGRAPHIC VARIATION. The variation described above does not seem to be related to geography. *Coelioxys banksi* shows a problem that is recurrent in New World *Coelioxys;* this species and *C. insita* (treated next) differ largely in the configuration of the anterior margin of the clypeus of the female (males are indistinguishable). In *C. banksi* the clypeal margin is produced medially (Fig. 22C-D) whereas the clypeal margin is almost straight to slightly outcurved in *C. insita.* There seem to be no intermediates (15 specimens of *C. banksi* and 20 specimens of *C. insita*). Whether these alternate conditions are the result of polymorphism within one species or indicate the presence of two species cannot be determined from dead specimens. Unless it is demonstrated that there is only one species, it seems best to recognize two.

Similar pairs of species separated by the anterior margin of the clypeus of the female (males indistinguishable) are found again in this group (*Coelioxys octodentata* and *C. novomexicana,* further discussion below) and in a Neotropical group (*C. zapoteca* and *C. clypeata*).

COMPARATIVE COMMENTS. Females of *Coelioxys banksi* differ from all other females in this group by the anterior margin of the clypeus which is produced and raised medially, making the profile distinctly concave (Fig. 22C-D). Males of *C. banksi* differ from other males in this group (except those of *C. insita* which are distinguishable by distribution only) by the almost linear shape of the fovea on the second metasomal tergum (Fig. 25D). The anterior margin of the fovea is usually very closely punctured.

Coelioxys insita Cresson
Figure 29

Coelioxys insita Cresson, 1872, Trans. Amer. Entomol. Soc. 4:273 (♀, Texas, type # 2499 in the Academy of Natural Sciences of Philadelphia).

Coelioxys rudis Cockerell, 1934, Amer. Mus. Novitates 732:3-4 (♀, Colorado, type in the American Museum of Natural History) NEW SYNONYMY.

FEMALE. Agrees with description and figures of *Coelioxys banksi* except as follows: (5) clypeal margin almost straight to slightly undulating or slightly outcurved; clypeal profile straight.

MALE. Agrees with description and figures of *Coelioxys banksi.*

DISTRIBUTION AND SEASON OF FLIGHT. This bee ranges from Nebraska to northern Mexico and to Arizona (Fig. 29).

Coelioxys insita is in flight at least from April 11 (Texas) to September 15 (Arizona) and October 15 (Mexico).

HABITAT. The distribution of *Coelioxys insita* extends westward to an area classified as pine-Douglas fir forest *(Pinus, Pseudotsuga)* in Colorado and eastward to an area classified as oak-hickory forest *(Quercus, Carya)* in Texas. This bee has also been taken from areas classified as eastern ponderosa pine forest, oak-juniper woodland *(Juniperus),* mesquite-oak savana *(Prosopis, Quercus, Andropogon),* mesquite-buffalo grass *(Buchloe),* creosote bush-tarbush *(Larrea, Flourensia),* and grama-tobosa-shrubsteppe *(Bouteloua, Hilaria)* vegetation types. The remaining areas are classified as western grassland and central and eastern grassland containing such dominant grasses as grama, tobosa, buffalo grass *(Buchloe),* bluestem *(Andropogon),* switchgrass *(Panicum),* and Indian grass *(Sorghastrum).*

Coelioxys moesta Cresson
Figures 23B, 24C, 25E, 30

Coelioxys moesta Cresson, 1864, Proc. Entomol. Soc. Philadelphia 2:403 (♀, Connecticut, type # 2491 in the Academy of Natural Sciences of Philadelphia); Graenicher, 1927, Entomol. News 38:233, 274 (Biology); Medler and Koerber, 1958, Ann. Entomol. Soc. Amer. 51:337, 343 (Biology); Medler, 1959, Can. Entomol. 91:114-115 (Biology); Bohart, 1970, Utah State Univ. 41st Faculty Honor Lecture, p. 9 (Immature).

Coelioxys tristis Provancher, 1882, Natur. Can. 13:241 (Lapsus for *C. moesta*).

Coelioxys lutzi Cockerell, 1921, Amer. Mus. Novitates 21:5-6 (♀, ♂, Utah, Colorado, type in the American Museum of Natural History) NEW SYNONYMY.

FEMALE. Agrees with description and figures of *Coelioxys rufitarsis* except as follows: (1) Length 10-12 mm; (2) integument black, tegula, legs and apex of metasoma black to dark brown; (3) pubescence white, scattered golden erect setae on clypeus, golden setae on tarsi; (4) ocular hairs short (about 0.7 mm); (5) clypeus covered by short appressed setae and erect golden setae which are more numerous near apical margin, margin broadly outcurved, clypeal profile straight; (7) paraocular area almost obscured by setae about 0.2 mm long; (11) interocellar distance slightly greater than ocelloccipital distance and less than ocellocular distance; (14) hypostomal area with setae subequal in length to those on disc; (16) scutum with almost no squamose setae; (17) setae of mesepisternum usually not forming discrete fasciae; (19) axilla short (Fig. 23B); (20) metanotal setae erect, (22) terga 2, 3 with less conspicuous gradular grooves than shown in Figure 21, gradular groove of tergum 3 almost obliterated medially, postgradular areas more closely punctured than shown in Figure 21, fasciae of terga 4, 5 almost obliterated medially, tergum 6 not angled, elongate (Fig. 24C); (23) sternum 6 elongate, lanceolate apically (Fig. 24C).

MALE. Agrees with description and figures of *Coelioxys rufitarsis* except as follows: (24) Length 7-11 mm; (25) integument as in female (2 above); (26) pubescence white, golden on tarsi; (27) clypeal margin irregular with 5 or 6 small denticles; (30) paraocular area with integument rugose, visible among long (0.35 mm), slender, erect setae; (31) rest of face contiguously, deeply punctured to ocellar area, visible among slender setae (about 0.5 mm long); (34) ocelloccipital distance subequal to or greater than interocellar distance, less than ocellocular distance; (35) vertex more closely punctured than shown in Figure 21; gena in lateral view subequal in width to eye, ventral angle greater than 90°; (37) hypostomal area of gena with dorsal carina of excavation extending to the preoccipital carina, excavation with setae of anterior fascia denser ventrally and longer than setae on disc; (39) scutum as in female (16 above); (41) fasciae of mesepisternum indistinct; (42) axilla as in female (19 above); (43) metanotum as in female (20 above); (45) terga 1-4 with apical fasciae incomplete medially, apical fascia missing on tergum 5; gradular grooves on terga 4-6 with fasciae weak; gradular groove on tergum 2 almost obliterated medially; fovea on tergum 2 inconspicuous, shallow, about 0.05 mm long, 0.1 mm wide (Fig. 25E); (47) setae on gonocoxites not as copious as shown in Figure 26F.

HOST RECORDS. Medler and Koerber (1958) reported *Coelioxys moesta* to be a parasite of *Megachile relativa;* Medler (1959) recorded *M. centuncularis* as a host; and Medler and Lussenhop (1968) related that D. H. Pengelly reared *C. moesta* from the nests of *M. texana* and *M. frigida.* Hobbs (1968) noted *C. moesta* as a probable parasite of *M. rotundata.* A new host record is from an anonymous label on a pin with a female of *C. moesta* from Tucson, Arizona: *M. concinna.*

DISTRIBUTION AND SEASON OF FLIGHT. The distribution of *Coelioxys moesta* is practically the same as that of *C. funeraria* (compare Figs. 20 and 30).

Coelioxys moesta is in flight at least

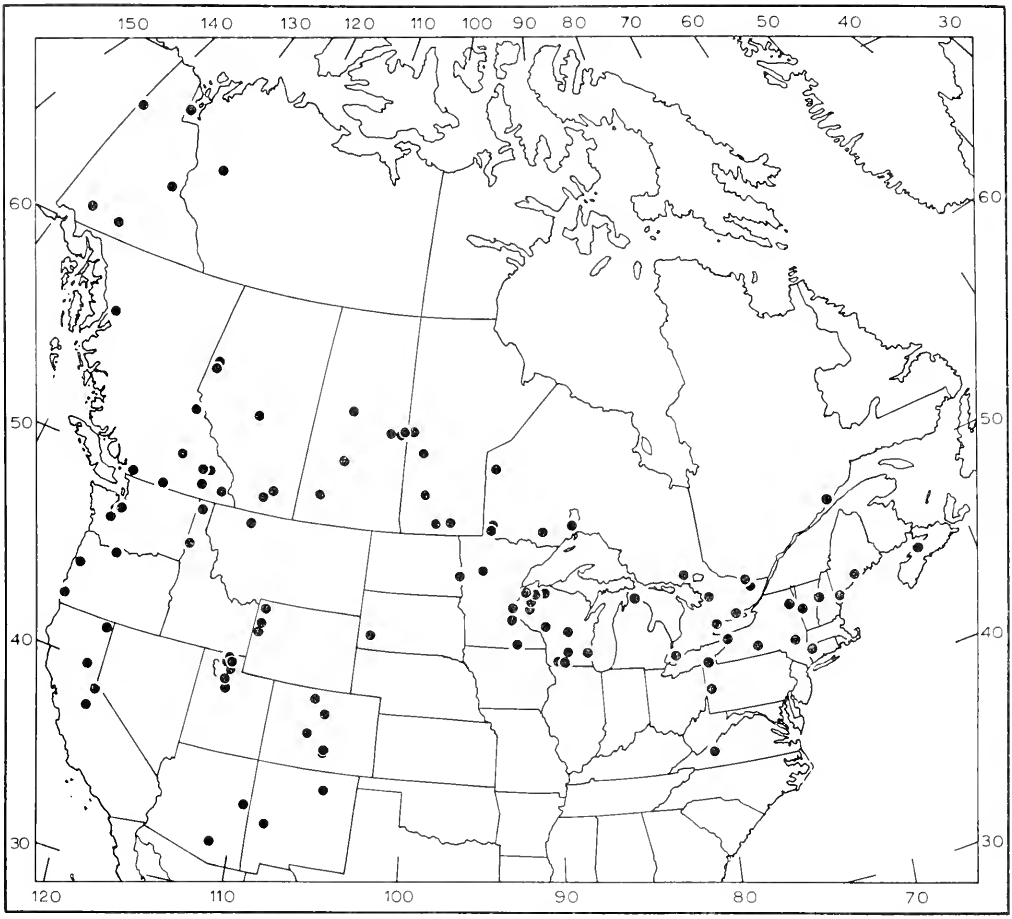

FIGURE 30. Distribution of *Coelioxys moesta*.

from May 27 (Virginia) to September 29 (Ontario, Canada).

HABITAT. The habitat of *Coelioxys moesta* agrees closely with that of *C. funeraria* with both bees taken at many of the same localities.

GEOGRAPHIC VARIATION. The variation in *Coelioxys moesta* described above does not seem to be related to geography.

COMPARATIVE COMMENTS. Females of *Coelioxys moesta* are probably most easily confused with dark females of *C. banksi* but differ in that the profile of the clypeus is straight in *C. moesta.* Males of *C. moesta* are probably most easily confused with dark males of *C. banksi* but differ by the dorsal carina of the genal excavation which extends to the preoccipital carina in *C. moesta.* Both sexes of *C. moesta* differ from all others in this group by the prothoracic tubercles which are *not* produced into a thin, almost translucent carina. Axillae of both sexes are shorter than those of other species in this group. The prothoracic tubercles and axilla of *C. moesta* more closely resemble those of *C. funeraria* than those of other bees in the rufitarsis group. However, *C. moesta* possesses complete graduli on metasomal terga two and three (incomplete in *C. funeraria*).

Coelioxys novomexicana Cockerell
Figures 22E, 31

Coelioxys sayi novomexicana Cockerell, 1909, Entomol. News 20:9 (♀, New Mexico, type in University of Colorado Museum).

Coelioxys novomexicana; Crawford, 1914, Ann. Entomol. Soc. Amer. 7:149 (Key); Bechtel, 1958, Pan-Pacific Entomol. 34:12-13 (Host).

Coelioxys texana; Bohart, 1970, Utah State Univ. 41st Faculty Honor Lecture, p. 8 (Misidentification).

FEMALE. Agrees with description and figures of *Coelioxys rufitarsis* except as follows: (1) Length 8-13 mm; (2) integument black; scape, pedicle, and apical portions of metasomal sterna black to dark reddish-brown; apical portion of clypeus, tegula, and legs distal to trochanters ferruginous; (3) pubescence white; golden on tarsi; clypeus and face with scattered erect light brown setae; (4) ocular hairs short (about 0.05 mm long); (5) clypeus uniformly covered by short, appressed setae and scattered erect setae, margin produced into 2 lobes (Fig. 22E); (7) paraocular area obscured by setae about 0.2 mm long plus scattered erect setae; (8) rest of face rugose, closely punctured up to ocellar area, with or without a small median impunctate ridge; (10) ocellar area raised, impunctate to closely punctured; (11) interocellar distance subequal to ocelloccipital, less than ocellocular distance; (12) vertex moderately punctate, usually with small impunctate area lateroposterior to ocelli; (13) gena practically obscured by prostrate setae; (14) hypostomal area of gena with setae equal in length to those on disc; (16) scutum with long erect setae on disc less conspicuous and anterior fascia more distinct than shown in Figure 21; (17) lateral surface of mesepisternum with setae shorter (about 0.15 mm) and sometimes squamose on disc; (18) scutellum with posterior margin straight as in Figure 23C; (20) metanotal setae erect or prostrate medially; (21) front coxal spine acute, directed ventrally, inconspicuous; (22) tergum 6 angled as in Figure 24E-G; (23) sternum 6 ovate to broadly lanceolate as in Figure 24E-G.

MALE. Agrees with description and figures of *Coelioxys rufitarsis* except as follows: (25) Integument black; tegula, venter of metasoma brown; leg distal to coxae ferruginous; (26) pubescence white, golden on tarsi; (27) ocular hairs short (about 0.06 mm); (28) clypeus obscured by short (about 0.33 mm) setae; (30) paraocular area obscured by short setae (about 0.4 mm); (31) rest of face rugose, obscured by copious setae up to 0.2 mm long; (32) interantennal distance subequal to clypeoantennal distance, greater than antennocular distance; (33) ocellar area as in female (10 above); (34) ocelloccipital and ocellocular distances subequal, greater than interocellar distance; (35) vertex as in female (12 above); (36) anterior portion of gena practically obscured by prostrate setae; (37) hypostomal area of gena with distinct excavation (as in Fig. 4), anterior and ventral portion of excavation with fascia shorter than setae on gena; dorsal carina of the excavation reaches preoccipital carina; (39) scutum as in female (16 above); (40) mesepisternum as in female (17 above); (41) scutellum as in female (18 above); (43) metanotum as in female (20 above); (45) fovea on tergum 2 about 0.03 mm long, about 0.13 mm wide (as in Fig. 25G); tergum 6 with dorsal spines variable: sometimes reduced, sometimes as in Fig. 25C, sometimes more slender than shown in Fig. 25C; (47) sternum 4 with apical emargination less conspicuous than shown in Fig. 26B; apical margin of sternum 5 straight, lateral setae more plumose than shown in Fig. 26B.

HOST RECORDS. Bechtel (1958) re-

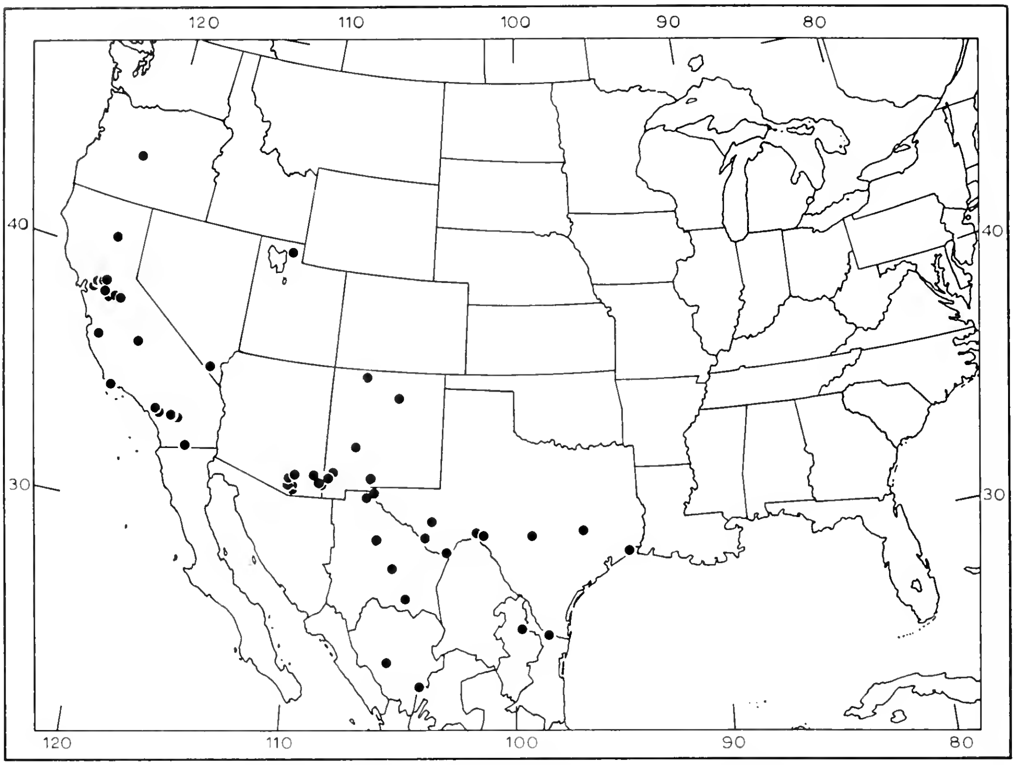

Figure 31. Distribution of females of *Coelioxys novomexicana.*

ported males of *Coelioxys novomexicana* (See comparative comments for *C. novomexicana.*) emerged from a nest of *Megachile gentilis.* Another possible host is indicated by a bee collected by Dr. F. Werner at Tucson, Arizona, close to a nest of *M. sidalceae.* A third host bee is *M. brevis* from the labels of female *C. novomexicana* from three localities in California: Summerville, Sacramento, and Turlock. A fourth host record is from the labels of four small (8-10 mm) females from Davis and College City, California, where Dr. R. W. Thorp reared *C. novomexicana* from nests of *M. rotundata.*

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys novomexicana* is most common in the southwestern United States and northern Mexico (Fig. 31).

Season of flight is at least from April 12 (Texas) to October 1 (southern California).

HABITAT. *Coelioxys novomexicana* ranges from various areas classified as western pine forests *(Pinus)* into areas classified as juniper-pine *(Juniperus),* oak-juniper *(Quercus),* mountain mahogany-oak *(Cercocarpus)* scrub and woodlands. In California *C. novomexicana* also has been taken from areas classified as chaparral *(Adenostoma, Archtostaphylos, Ceanothus),* coastal sagebrush *(Salvia, Eriogonum),* California steppe *(Stipa),* and tule marshes *(Scirpus, Typha).* Areas classified as creosote bush-bur sage *(Larrea, Fanseria)* and creosote bush-tarbush *(Flourensia),* Trans-Pecos shrub savana, juniper-oak savana (with *Andropogon*) are more southerly vegetation types. This bee also occurs in areas classified as open habitats such as alpine meadows and barren *(Agrostis, Carex, Festuca, Poa),* and grama tobosa prairie and shrubsteppe *(Bouteloua, Hilaria, Larrea).* In the easternmost portion of its range, *C. novomexicana* has been taken from an area classified as oak-hickory forest *(Carya)*.

GEOGRAPHIC VARIATION. Size (using head width as an index) of females of *Coelioxys novomexicana* from central California was found to vary significantly from size of females outside this region. Head widths of 59 females from central California (3.06 ± 0.153 mm) were highly significantly less than the head widths of 125 females from the rest of the range (3.39 ± 0.186 mm). Perhaps, as was postulated for *C. funeraria* (p. 102), this difference in size is an expression of host size. The only evidence for this explanation is that three small females from Summerville, Sacramento, and Turlock, California were reared from nests of *Megachile brevis* whereas a large female was taken close to a nest of *M. sidalceae* in Tucson, Arizona. Since *M. sidalceae* (11-14 mm) is a larger bee than *M. brevis* (7-12 mm), the cells of *M. sidalceae* are doubtless larger and could support a larger parasite.

Females of *Coelioxys novomexicana* are smaller in size in central California, but in the same general area males have been taken which had earlier been considered to be *C. novomexicana* but which are larger than true *C. novomexicana*. It seems improbable that these males belong to the same species (assuming that *C. octodentata* and *C. novomexicana* are not the same species, see discussion under *C. octodentata*) as the smaller females. A more likely explanation is that these males belong to *C. octodentata*.

COMPARATIVE COMMENTS. Females of this species are most likely to be confused with *Coelioxys octodentata* although the females of *C. novomexicana* have the clypeal margin modified into two conspicuous lobes (Fig. 22E). The only other bee in this group possessing a bilobed clypeal margin is *C. sayi* from which *C. novomexicana* differs by the fringe of setae on the clypeal margin which is directed ventrally (directed posteriorly in *C. sayi*). Males of *C. novomexicana* are most likely to be confused with males of *C. octodentata* from which they are separable only by distribution (where the distributions of the females do not overlap). Males of *C. sayi* are similar but in *C. sayi* the posterior margin of the gradular groove on the third metasomal tergum is almost obliterated medially (distinct in *C. novomexicana*). In the southern extreme of their range, males of *C. novomexicana* may be confused with males of *C. pratti* from which they differ by their short ocular hairs (long in *C. pratti*).

Coelioxys oaxacana, new species

Figures 23C, 24K

FEMALE. Agrees with description and figures of *Coelioxys rufitarsis* except as follows: (1) Length 12.5 mm; (2) integument black; mandible rufous medially; legs, tegula ferruginous; (3) pubescence white, ochreous on face, golden on tarsi; (4) ocular hairs short (about 0.06 mm); (5) clypeus hidden by appressed setae about 0.15 mm long, margin obscured by dense fringe 0.45 mm wide medially; margin widely emarginate; (6) paraocular area hidden by setae about 0.2 mm long; rest of face visible between short, appressed setae, strongly punctured, broadly conical; (9) clypeoantennal distance subequal to interantennal distance, greater than antennocular distance; (10) ocellar area with impunctate median longitudinal line anteriorly; (12) vertex sparsely punctured anteriorly, moderately punctured posteriorly; (14) hypostomal area of gena with setae shorter than those on gena; (16) scutum with fasciae more distinct than shown in Figure 21; (17) lateral surface of mesepisternum moderately punctured with many more very small punctures than larger punctures;

disc with very short, scattered, slendered setae; distinct fasciae anteriorly and posteriorly; (18) scutellum with median longitudinal impunctate line (Fig. 23C); (19) axilla slender, acute (Fig. 23C); (22) terga 2, 3 with gradular grooves complete but almost obliterated medially; tergum 6 elongate (Fig. 24K).

COMPARATIVE COMMENTS. *Coelioxys oaxacana* is distinguished from all other females in this group by the broadly conical condition of the ventral portion of the rest of the face; the divergent, acute axillae (Fig. 23C); and the elongate, conspicuously angled sixth metasomal tergum (Fig. 24K).

TYPE. Holotype female, ten miles southeast Tapanatepec, Oaxaca, Mexico, August 8, 1963 (F. D. Parker, L. A. Stange) in the collection of the University of California, Davis.

Coelioxys octodentata Say

Figures 24D-I, 25G, 32

Coelioxys octodentata Say, 1824, *In* Keating, Narrative of Long's 2nd Expedition etc. 2:353 (♂, type probably destroyed); Say, 1837, Boston J. Nat. Hist. 1:400 (♀); Robertson, 1897, Trans. St. Louis Acad. Sci. 7:345 (= *C. altilis*, = *C. brevis*); Fox, 1900, Entomol. News 11:553 (Host); Hicks, 1926, Univ. Colorado Stud. 15:22 (Biology); Robertson, 1926, Psyche 33:116 (Host); Robertson, 1929, Flowers and Insects, Lancaster Pennsylvania Sci. Press 9-217 (Flower records); Graenicher, 1935, Ann. Entomol. Soc. Amer. 28:300, 304 (Host, Wisconsin); Michener, 1953, Univ. Kansas Sci. Bull. 35: 1059-1060, 1737-1742 (Biology); Linsley, 1958, Hilgardia 27:582 (Ecology); Medler, 1965, Proc. Entomol. Soc. Washington 67:113-115 (Biology); Stephen, Bohart and Torchio, 1969, Biology and External Morphology of Bees: 29 (Immatures); Baker, 1971, J. Kansas Entomol. Soc. 44:225-235 (Immatures).

Coelioxys brevis Cresson (nec Eversmann), 1864, Proc. Entomol. Soc. Philadelphia 2:402-403, (♀, Connecticut, New Jersey, Pennsylvania, Maryland, type # 2490 in the Academy of Natural Sciences of Philadelphia).

Coelioxys altilis Cresson, 1878, Trans. Amer. Entomol. Soc. 7:219 (new name for *C. brevis* Cresson, not Eversmann).

Coelioxys cressoni Dalla Torre, 1896, Catalogus Hymenopterorum 10:485 (new name for *C. brevis* Cresson, not Eversmann).

Coelioxys coquilletti Crawford, 1914, Ann. Entomol. Soc. Amer. 7:157 (♀, California, type # 18224 in the National Museum of Natural History) NEW SYNONYMY.

Coelioxys megatricha Cockerell, 1916, J. Entomol. Zool. 8:60 (♂, California, type in the American Museum of Natural History) NEW SYNONYMY.

Coelioxys crassula Cockerell, 1919, Can. Entomol. 51:27 (♀, Colorado, type in the American Museum of Natural History) NEW SYNONYMY.

Coelioxys mediata Cockerell, 1925, Pan-Pacific Entomol. 1:146-147 (♀, California, type # 1634 in the California Academy of Sciences) NEW SYNONYMY.

Coelioxys atlantica Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:193, 195, 198 (♀, ♂ Canada to Florida in the eastern United States, type in the collection of T. B. Mitchell) NEW SYNONYMY.

FEMALE. Agrees with descriptions and figures of *Coelioxys rufitarsis* and *C. novomexicana* except as follows: (1) Length 7-12 mm; (2) integument black; scape, pedicle, apical portions of metasomal sterna black to dark ferruginous; tegula, tibiae, tarsi fulvous; femora black to fulvous; (5) clypeus slightly convex, clypeal margin straight or slightly emarginate as in Figure 22B; (22) tergum 6 with lateral angles variable (Fig. 24D-I); (23) sternum 6 with apex variable, broadly ovate to lanceolate (Fig. 24D-I).

MALE. Agrees with descriptions and figures of *Coelioxys rufitarsis* and *C. novomexicana* except as follows: (45) tergum 6 with dorsal spines usually slightly more slender than shown in Figure 25G.

HOST RECORDS. Fox (1900) reared *Coelioxys octodentata* from a nest of *Megachile mendica,* a record repeated later by Medler (1965). Hicks (1926) reared *C. octodentata* from a nest of *M. brevis,* repeated later by Michener (1953) and Baker (1971). Medler (1958) reared this bee from a nest of *M. centuncularis,* and Hobbs (1956) reared it from a nest of *M. perihirta.* Medler and Lussenhop (1968) reported that D. H. Pengelly reared *C. octodentata* from a nest of *M. texana.* A new host record is a female of *C. octodentata* labeled: Cornish, Utah, IX-10-59, reared from cell of *Meg. onobrychidis.* Another new host record is from three females from College City, California reared from three nests of *M. rotundata* by Dr. R. W. Thorp (as would be expected, these bees are small, 7-8.5 mm).

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys octodentata* ranges from southern Canada to the southern United States (Fig. 32). In the southwestern portion of its range the distribution of *C. octodentata* overlaps with that of *C. novomexicana* (compare Figs. 31 and 32).

This bee is in flight at least from May 8 (Kansas) to October 22 (central California).

HABITAT. In the western United States, *Coelioxys octodentata* has been collected from a variety of areas classified as needleleaf forests and broadleaf and needleleaf forest combinations. This bee has also been taken from a number of western shrub lands, western grasslands and western shrub and grassland combinations. Elsewhere this bee has been taken from central and eastern grasslands, grassland and forest combinations, and eastern broadleaf and broadleaf and needleleaf forests.

However, more specific habitat observations have been reported for *Coelioxys octodentata* (Hicks, 1926; Michener, 1953). The host bee, *M. brevis,* nests in open meadows and unshaded sites usually in, on or near the ground. These are also types of areas in which *C. octodentata* is found flying near the ground and from which nests containing *C. octodentata* larvae have been recovered (Hicks, 1926; Michener, 1953). Occasionally *M. mendica* nests in the ground at the edges of open areas, a situation which *C. octodentata* might exploit.

GEOGRAPHIC VARIATION. Six characters of *Coelioxys octodentata* were analyzed for geographic variation: size, degree of angulation of the sixth tergum, density of the medial fascia of the first metasomal tergum, leg color, punctation of the vertex, and degree of elongation of the sixth metasomal sternum. Females were used for this analysis as the males in southern Oregon, California, northern Arizona and New Mexico, Utah, and Colorado cannot be distinguished from those of *C. novomexicana.* In Figure 32 each of the six sides of a symbol summarizes data on one character in the form of a histogram for the group of bees from the area indicated (a key to characters and scale appears in the upper right portion of the map).

Size varies markedly even in bees from the same general area (in Fig. 32 size was scored as small, 0-9.0 mm; medium, 9.1-10.9 mm; large, 11-12 mm). Perhaps, as was postulated for *Coelioxys funeraria* and *C. novomexicana,* size is an expression of host size in *C. octodentata.*

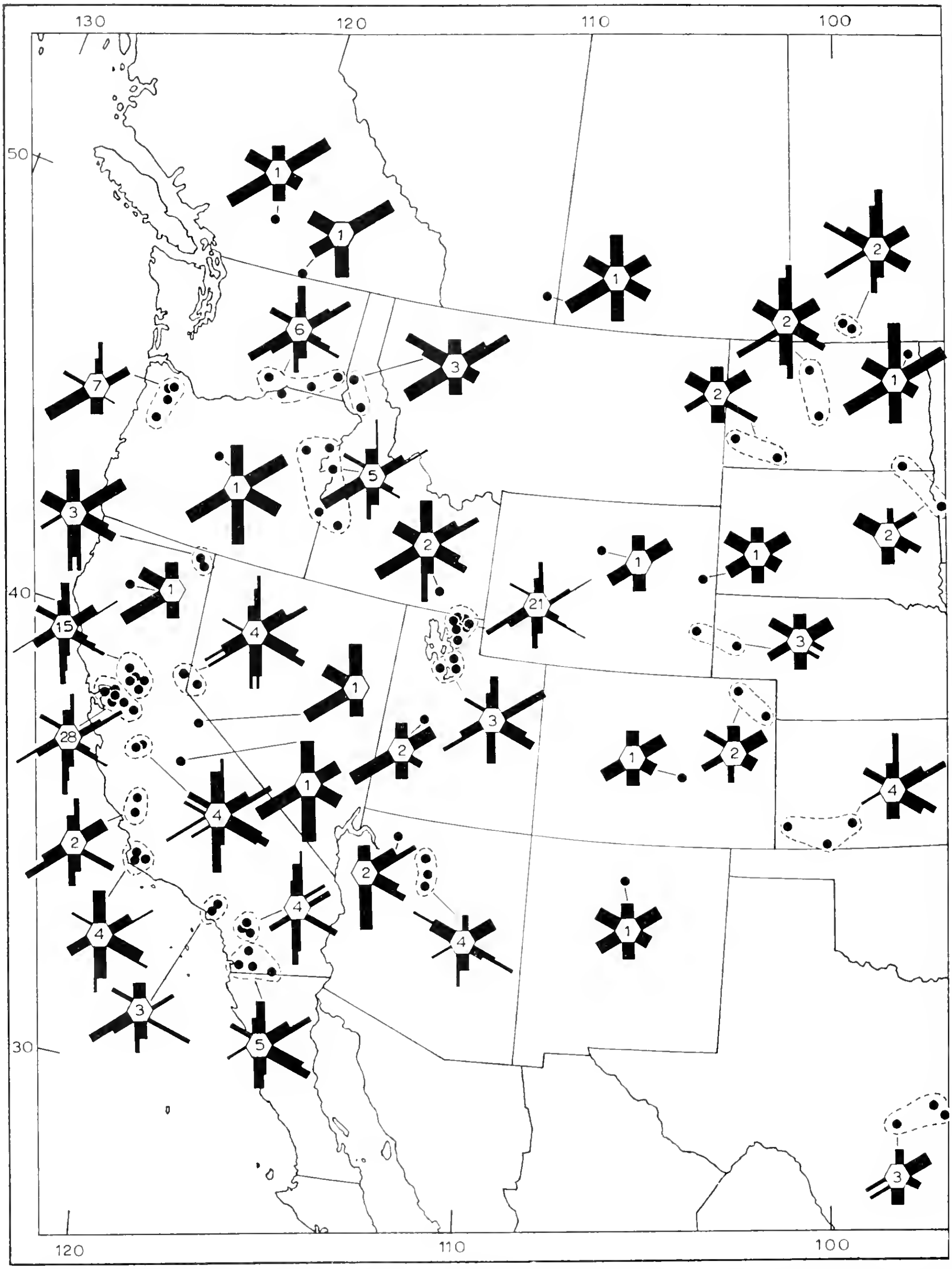

FIGURE 32. Distributions of females of *Coelioxys octodentata* showing variation of six characters given in (upper right) key.

Degree of development of the lateral angle of the apical tergum does not seem to vary geographically except perhaps for bees from the Southeast. Bees from the East with well developed angles and apical sterna were formerly considered to be

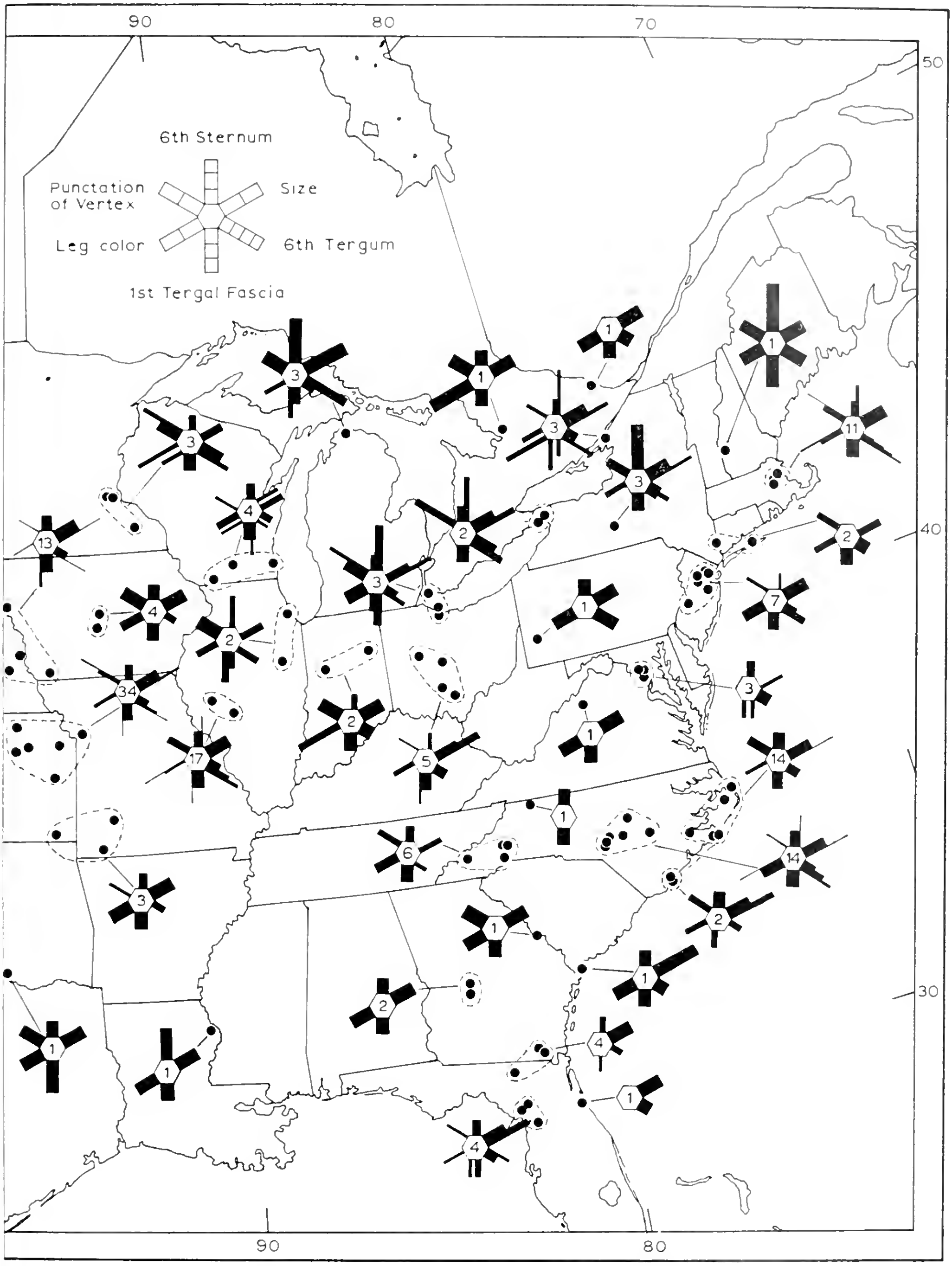

Figure 32. (continued) Each side of the hexagon is the base line of a histogram. The number inside each hexagon is the number of specimens examined from the area indicated.

Coelioxys atlantica. Bees from the West with well developed angles and apical sterna and medial fasciae of the first metasomal tergum were considered to be *C. coquilletti.* Bees intermediate in all conditions were considered to be *C. octo-*

dentata throughout the distribution. Bees, especially small specimens, with poorly developed sixth tergal angles, apical sterna, and medial fasciae were formerly considered to be *C. salinaria* or *C. pratti* (a misidentification; original description of *C. pratti* emphasizes the long, brown ocular hairs). Specimens with poorly developed angles and long sterna and specimens with extreme angles and short sixth sterna (Fig. 24D-I) represent mixed conditions among the extreme examples. Most bees from the Southeast have the lateral angles moderately developed (Fig. 32).

The medial fascia of the first metasomal tergum in general is poorly developed in the Southeast (minimum in Fig. 32) but well developed in large specimens from the northwestern and western United States (maximum in Fig. 32). In the West there seems to be a correlation between size and density of this medial fascia in that larger bees (formerly considered to be *Coelioxys coquilletti*) usually have medial fasciae which are more dense and contain more squamose setae than those of smaller bees (formerly considered to be *C. crassula* and *C. octodentata*). However, if only the larger bees are considered, the medial fascia of the first metasomal tergum gradually becomes less dense and the proportion of squamose setae drops as a cline across the northern United States from west to east.

Leg color, especially color of the femora, varies from black to fulvous with the color of most specimens intermediate (ferruginous). Bees of the eastern United States have fulvous to ferruginous legs whereas western specimens vary from fulvous to black with both large and small bees displaying both extremes of leg color.

Punctation of the vertex varies from closely punctate to a condition in which impunctate areas occur lateroposteriorly to the ocelli (in Fig. 32 this character was scored as impunctate areas, minimum; closely punctured, maximum). Most bees were intermediate or with impunctate areas, but a few (mainly from the Northeast) were closely punctured.

The apex of the female sixth sternum seemed to be highly variable in contrast to most species of North American *Coelioxys* in which the apex of the sixth sternum may be uniform throughout the whole series. In *C. octodentata*, however, the apex of the sixth sternum ranged from broadly ovate (Fig. 24I, minimum in Fig. 32) to lanceolate (Fig. 24D, maximum in Fig. 32).

Females with maximum lanceolate apices of the sixth metasomal sternum were generally medium to large, although some small bees had moderately lanceolate apices (as in Fig. 24G-H).

COMPARATIVE COMMENTS. The large specimens of this species are most likely to be confused with *Coelioxys rufitarsis* although the ocular hairs are short and the medial fascia of the first metasomal tergum is composed of short, appressed setae in *C. octodentata* (long ocular hairs and long, erect setae on tergum one in *C. rufitarsis*). In the West, females of *C. octodentata* differ from those of *C. novomexicana* by their almost straight clypeal margin (bilobed in *C. novomexicana*) although males of *C. octodentata* are not separable from those of *C. novomexicana*. Females of *C. octodentata* differ from females of *C. sayi* in the same way as from females of *C. novomexicana* and males differ from *C. sayi* by the well produced posterior margins of the gradular grooves of metasomal terga two and three (posterior gradular margin almost obliterated medially in males of *C. sayi*).

Coelioxys porterae Cockerell
Figures 22F, 24J, 25F, 33

Coelioxys (*lucrosa* var?) *porterae* Cockerell, 1900, Can. Entomol. 32:297-301 (♀, ♂, New Mexico, key, type #

20230 in the National Museum of Natural History).

Coelioxys porterae; Cockerell, 1904, Ann. Mag. Natur. Hist. (7) 13:34 (at flowers of *Frasera* sp.).

Coelioxys dubitata melanopoda Viereck, 1916, Connecticut Geol. Hist. Surv. Bull. 22:747 (♂, Connecticut, type # 66187 in the National Museum of Natural History); Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:220 (=*C. rufitarsis,* misidentification).

Coelioxys hypodonta Cockerell, 1925, Pan-Pacific Entomol. 1:150-151 (♂, California, type # 1637 in the California Academy of Sciences) NEW SYNONYMY.

FEMALE. Agrees with description and figures of *Coelioxys rufitarsis* except as follows: (1) Length 9-14.5 mm; (2) integument granular on vertex between punctures, rugulose on thorax, faintly rugulose on metasoma; black; tegula, venter of metasoma black to piceous; (3) pubescence white to faintly brownish on clypeus; (4) ocular hairs of medium length (about 0.1 mm); (5) clypeus also with erect setae (about 0.16 mm long) scattered on surface; (7) paraocular area obscured laterally by setae up to 0.4 mm long; (11) ocelloccipital distance slightly greater than interocellar distance and much less than ocellocular distance; (13) gena with ventral angle less than 90°; (14) hypostomal area of gena with setae subequal to setae on disc; (15) mandible with hump on middle of outer surface (Fig. 22F); (18) scutellum with posterior margin of dorsal surface slightly less rounded than shown in Figure 21; (19) axilla as or slightly less produced than shown in Figure 21; (20) metanotal setae erect; (22) terga 2 and 3 posterolaterally less closely punctured than shown in Figure 21; tergum 6 less conspicuously angled than shown in Figure 21 (Fig. 24J); sternum 6 lanceolate apically (Fig. 24J).

MALE. Agress with description and figures of *Coelioxys rufitarsis* except as follows: (24) Length 9-12 mm; (25) integument black; tegula, legs distal to coxae, venter of metasoma black to piceous; (26) pubescence white, golden on tarsi; (27) ocular hairs of medium length (about 0.13 mm); (28) clypeus obscured by copious setae about 0.5 mm long; (31) rest of face closely punctured up to ocellar area, almost obscured by setae up to 0.7 mm long; (37) hypostomal area of gena with setae on anterior portion of excavation shorter than on disc; (41-43) scutellum, axilla, metanotum as in female (18-20 above); (45) terga 1-5 with apical fascia sparse but complete; gradular grooves of terga 5 and 6 fasciate; fovea on tergum 2 about 0.1 mm long, about 0.25 mm (Fig. 25E); dorsal spines of sternum 5 with denticles slightly more conspicuous than shown in Fig. 25C.

HOST RECORDS. Mitchell (1962) listed *M. relativa* as a host of *C. porterae.* A bee from Pibrach, Alberta was reared from the nest of *M. frigida* by Dr. G. A. Hobbs. Hobbs also collected two females at a log in which *M. frigida* was nesting in Scandia, Alberta.

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys porterae* ranges across southern Canada and down the major mountain ranges of the United States (Fig. 33).

This bee is in flight at least from June 1 (Massachusetts) to September 9 (Medicine Hat, Alberta).

HABITAT. In the Southwest *C. porterae* occurs only at higher elevations in areas classified as various western needleleaf forests. From central California northward it occurs in areas classified as western needleleaf forests and western shrub and grasslands. In the Northeast and mountains of the Southeast, *C. porterae*

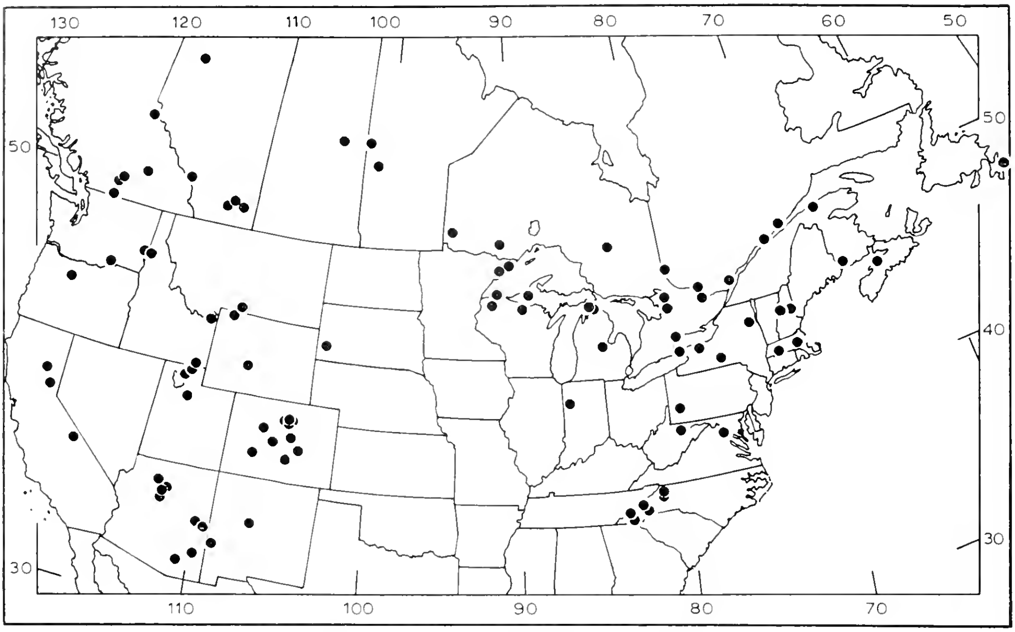

FIGURE 33. Distribution of *Coelioxys porterae*.

occurs in areas classified as eastern needleleaf and broadleaf forests and combinations of these two vegetation types.

GEOGRAPHIC VARIATION. The variation described above does not seem to be related to geography.

COMPARATIVE COMMENTS. *Coelioxys porterae* is most likely to be confused with dark specimens of *C. octodentata* from which it can be distinguished by the medium length of the ocular hairs (short in *C. octodentata*) in females and the larger fovea of the second metasomal tergum (Fig. 25F) in males (small in *C. octodentata*, Fig. 25G). Another similar bee is *C. sodalis* which has long ocular hairs and no subapical notches on the sixth sternum in the female and no foveae on the second tergum in the male.

Coelioxys pratti Crawford
Figure 34

Coelioxys pratti Crawford, 1914, Ann. Entomol. Soc. Amer. 7:159 (♀, Texas, type # 18225 in the National Museum of Natural History).

FEMALE. Agrees with description and figures of *Coelioxys rufitarsis* except as follows: (1) Length 9.5-13 mm; (2) integument black; tegula, legs ferruginous to fulvous; lateral margins of metasomal terga 1 and 2, posterior areas of sterna 2-5 ferruginous; (3) pubescence white, brownish tinge on face and thorax; ocular hairs light brown; golden on tarsi; (4) ocular hairs medium to long (about 1.3 mm); (5) clypeus uniformly covered with short appressed setae and erect brown setae (about 0.25 mm long); (7) paraocular area obscured laterally by setae about 0.3 mm long; (11) interocellar and ocellocipital distances subequal, less than ocellocular distance; (12) vertex slightly more closely punctured than shown in Figure 21; (13) gena with ventral angle slightly less than 90°; (15) mandible with hump on outer surface slightly less conspicuous than shown in Figure 22F; (16) scutum with anterolateral fascia more conspicuous and erect setae on disc less conspicuous than shown in Figure 21; (18) scutellum with posterior margin less rounded than shown in Figure 21; (20) metanotum with erect setae; (22) tergum 6 not as angled laterally as shown in Figure 21, more like Figure 24J.

MALE. Agrees with description and figures of *Coelioxys rufitarsis* except as follows: (24) Length 9-11 mm; (25) integument as in female (2 above), terga 2-4 with lateral margins ferruginous; (26) pubescence as in female (3 above); (27) ocular hairs long (about 0.15 mm); (28) clypeus obscured by copious long (about 0.5 mm) setae; (30) paraocular area obscured laterally by long (up to 0.6 mm) setae; (31) rest of face rugose with long (up to 0.6 mm) setae sometimes obscuring integument; (34) ocelloccipital distance greater than interocellar distance, less than ocellocular distance; (35) vertex as in female (12 above); (36) gena as in female (13 above); (37) hypostomal area of gena with anterior fascia of excavation shorter than genal setae; (39) scutum as in female (16 above); (41) scutellum as in female (18 above); (43) metanotum as in female (20 above); (45) fovea on tergum 2 about 0.05 mm long, about 0.1 mm wide as shown in Figure 25G; (47) margin of sternum 5 slightly emarginate; sternum 8 with setae longer, more abundant than shown in Figure 26E; genital armature with copious, long (half the length of gonocoxite) setae on gonocoxite.

DISTRIBUTION AND SEASON OF FLIGHT. Although the type was collected in Texas, most specimens of *Coelioxys pratti* were taken in Mexico and southward (Fig. 34).

Coelioxys pratti is in flight from at least March 21 (Cuernavaca, Morelos) to December 24 (Tamazunchale, San Luis Potosi).

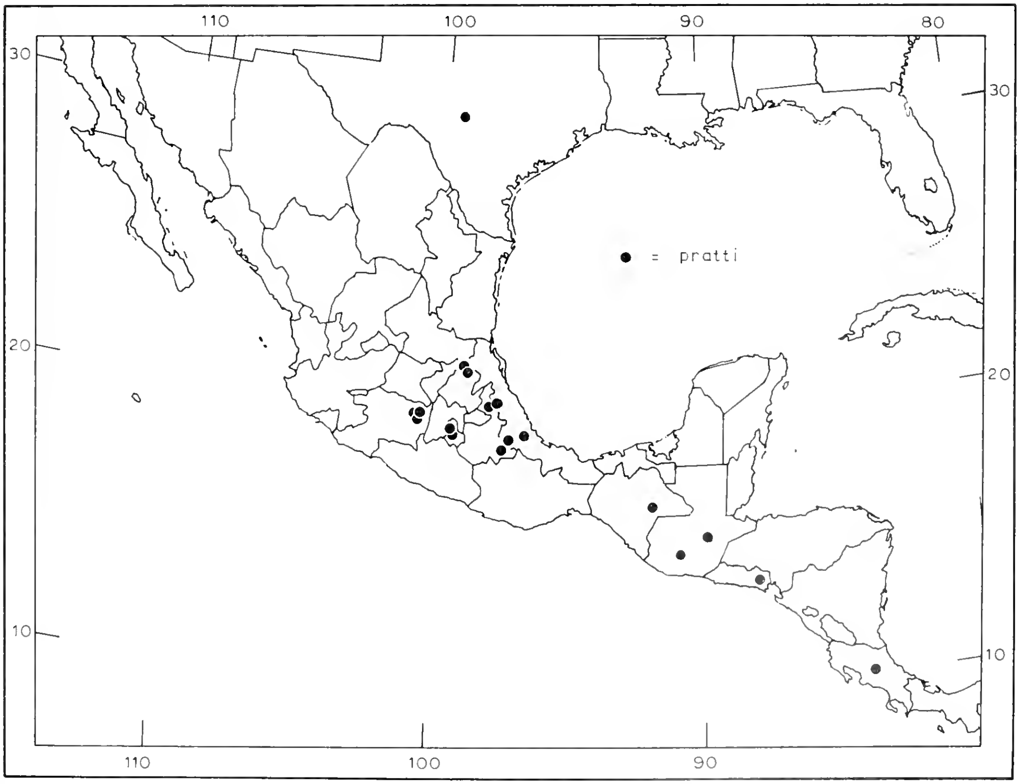

FIGURE 34. Distribution of *Coelioxys pratti*.

HABITAT. The type locality (Kerrville, Texas) is in an area classified as juniper-oak savana *(Juniperus, Quercus, Andropogon)*. The remaining localities are at least 600 miles farther south and at elevations above 1,000 feet.

COMPARATIVE COMMENTS. Both sexes of *Coelioxys pratti* are most similar to *C. octodentata* but can be distinguished by the long, brown ocular hairs (short and yellowish to white in *C. octodentata*).

Coelioxys sayi Robertson
Figures 22G, 35

Coelioxys sayi Robertson, 1897, Trans. Acad. Sci. St. Louis 7:346 (♀, ♂, Florida, Illinois, type in the Illinois Natural History Survey); Robertson, 1926, Psyche 33:116 (Host); Robertson, 1929, Flowers and Insects, Lancaster Pennsylvania Science Press, p. 9-216 (Flower records); Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152: 192, 195, 222 (Key, redescription, = *C. mendacina*); Medler, 1965, Proc. Entomol. Soc. Washington 67:113-115 (Host); Krombein, 1967, Trap-nesting Wasps and Bees, Smithsonian Press, P. 322 (Host); Baker, 1971, J. Kansas Entomol. Soc. 44:225-235 (Immatures).

Coelioxys mendacina Cockerell, 1921, Amer. Mus. Novitates 21:3, 7 (♀, Virginia, type in the American Museum of Natural History).

FEMALE. Agrees with description and figures of *Coelioxys rufitarsis* except as follows: (1) Length 9.5-12 mm; (2) integument granular on vertex between punctures, less so on thorax; (3) pubescence white, slight golden-brown tinge on clypeus, golden on tarsi; (4) ocular hairs of medium length (about 0.08 mm); (5) clypeus covered with short appressed setae plus scattered erect setae; surface visible, margin thickened and slightly bilobed (Fig. 22G); (7) paraocular area almost obscured by appressed and erect setae about 0.2 mm long; (8) rest of face rugose with long (0.45 mm) mediosagittal impunctate ridge extending from ocellar area; (9) clypeoantennal distance subequal to antennocular distance and less than interocellar distance; (10) ocellar area coarsely punctured; (14) hypostomal area of gena with setae subequal to setae on disc; (15) mandible with outer margin straight (Fig. 22G); (16) scutum with erect setae shorter and less conspicuous than shown in Figure 21; (17) lateral surface of mesepisternum moderately punctured with short (0.2 mm) slender setae on disc and distinct anterior and posterior fasciae; (18) scutellum with posterior margin less rounded than shown in Figure 21; (20) metanotal setae sometimes erect, sometimes prostrate medially; (22) tergum 3 with gradular groove medially, fasciae on terga 1-5 not as conspicuous as shown in Figure 21; tergum 6 with lateral angles as shown in Figure 24H.

MALE. Agrees with description and figures of *Coelioxys rufitarsis* except as follows: (24) Length 9-10 mm; (26) pubescence as in female (3 above); (27) ocular hairs short (about 0.8 mm); (28) clypeus obscured by long, copious setae (about 0.3 mm); (30) paraocular area obscured by copious setae (about 0.3 mm long); (31) rest of face rugose, punctured closely up to ocellar area, with copious setae (about 0.3 mm long); (33) ocellar area as in female (10 above); (34) ocelloccipital distance greater than interocellar distance, less than ocellocular distance; (35) vertex usually with impunctate areas lateroposterior to ocelli; (36) gena with ventral angle about 90°; (37) excavation of hypostomal area of gena with setae of anterior fascia shorter than setae on disc; (39-43) scutum, mesepisternum, scutellum, axilla, metanotal setae as in female (16-20 above); (45) gradular grooves of

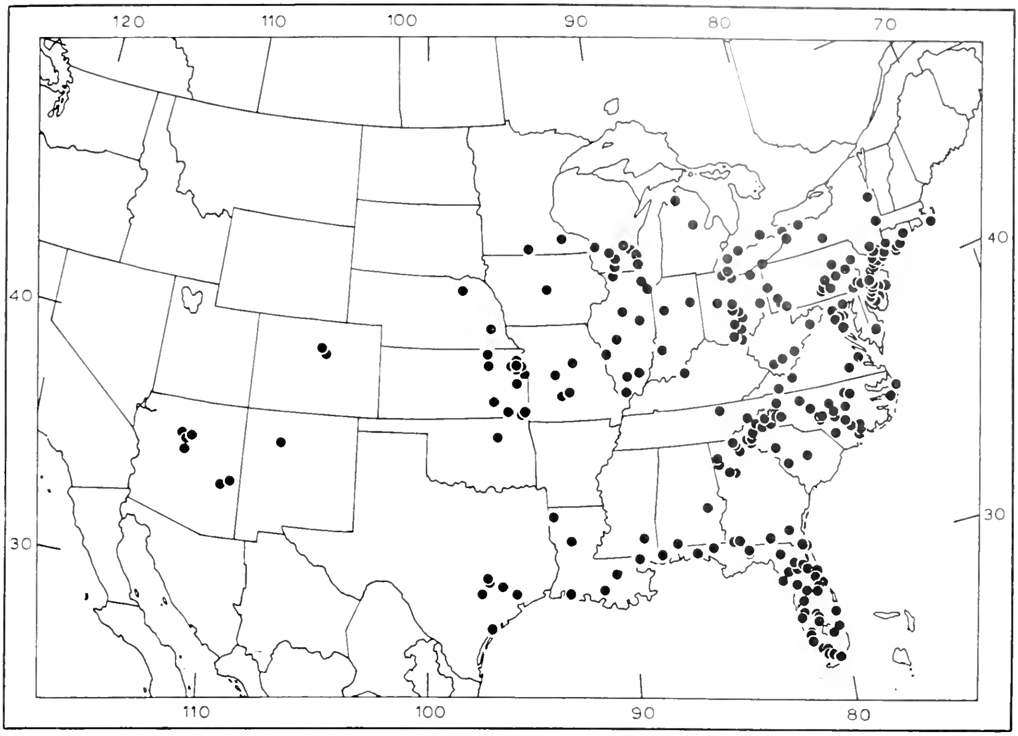

Figure 35. Distribution of *Coelioxys sayi*.

terga 2, 3 as in female (22 above); fovea on tergum 2 about 0.03 mm long; 0.06 mm wide (as in Fig. 25G); dorsal spines of tergum 6 variable, sometimes more, as, or less slender than shown in Figure 25C; (47) genital armature with setae not as abundant on gonocoxite apically as shown in Figure 26F.

HOST RECORDS. Medler (1965) reported *Megachile mendica* to be a host of *Coelioxys sayi*. This bee has also been recovered from nests of *M. brevis*.

DISTRIBUTION AND SEASON OF FLIGHT. Except for scattered records from the West, *Coelioxys sayi* is confined to the eastern United States (Fig. 35).

This bee is in flight from at least March 3 in Florida, April 30 in Texas, and May 8 in Kansas to October 3 in New York and October 23 in Texas.

HABITAT. In the eastern United States, *Coelioxys sayi* has been collected from areas classified as eastern broadleaf, eastern broadleaf and needleleaf forests, and eastern grassland and forest combinations. In the West, *C. sayi* has been taken from areas classified as western needleleaf forests. However, as with *C. octodentata*, more specific habitats have been reported for its host *Megachile mendica*, as well as for *C. sayi* (Medler, 1965). These bees have been reared from trap nests placed in open woodland, savana, and forest-edge habitats. The nests usually occur well above the ground (although *M. mendica* has been observed to nest in the ground). *C. sayi* has been taken from *M. brevis* nests at ground level, and has been observed at a woodland edge flying slowly along the ground as though searching for host nests.

GEOGRAPHIC VARIATION. As in the case of *Coelioxys alternata*, leg color in *C. sayi* does not seem to be meaningfully correlated to geography. Bees with all degrees of leg color occur at many localities throughout the range, and the chance of finding any particular condition at a given location appears to hinge on the sample size rather than latitude and longitude. As with *C. texana,* however, wing color does vary geographically. Bees from Florida to Texas have slightly darker, very slightly more yellowish wings than those from elsewhere in the distribution.

COMPARATIVE COMMENTS. Females of *Coelioxys sayi* are most similar to those of *C. rufitarsis* and *C. octodentata* although the clypeus is bilobed in *C. sayi* and straight in the other two species. In the West, *C. sayi* might be confused with dark females of *C. novomexicana* but differs conspicuously in the setal fringe of the clypeus which is posteriorly directed (ventrally directed in *C. novomexicana*). Males of *C. sayi* are most easily confused with those of *C. octodentata,* differing mainly in the reduced posterior margins of the gradular grooves of terga two and three (well formed in *C. octodentata*).

Subgenus *Xerocoelioxys* Mitchell

Xerocoelioxys Mitchell, 1973. A subgeneric revision of the genus *Coelioxys* of the Western Hemisphere. Cont. Dept. Entomol. North Carolina State Univ. p. 44. Type species: *Coelioxys edita* Cresson.

Xerocoelioxys is intermediate between *Boreocoelioxys* and the subgenus *Coelioxys.* The distinct foveae of males of *Boreocoelioxys* are represented in some members of *Xerocoelioxys* by densely punctate foveal areas. The notched sixth sternum of females of *Boreocoelioxys* is also found in one species of *Xerocoelioxys* although the configuration is not exactly reproduced (compare Figs. 21 and 38B). The subgenus *Coelioxys* is separable from *Xerocoelioxys* by the reduced fasciae of the mesosoma and metasoma and by the reduced carina of the prothoracic tubercles.

Bees in *Xerocoelioxys* fall clearly into two subgroups: (1) *Coelioxys edita, C. boharti, C. mesae, C. galactiae, C. grindeliae, C. nodis, C. piercei,* and *C. soror;* and (2) *C. aperta* and *C. bisoncornua.* Reasons for this subdivision are given under the comparative comments for *C. aperta.*

Host records are known for two species, *Coelioxys mesae* and *C. grindeliae* (Table 1), and the host bees fall into two subgenera of *Megachile.*

Most of the characters in the list below are found in other subgenera of New World *Coelioxys* and even in some of the Old World *Liothyrapis,* but never in this combination. Italicized characters most clearly differentiate *Xerocoelioxys* from other subgenera in North America.

A. Ocellar area variously punctured.

B. Preoccipital carina complete or incomplete medially.

C. Mandible robust, variously modified (Fig. 36A-C).

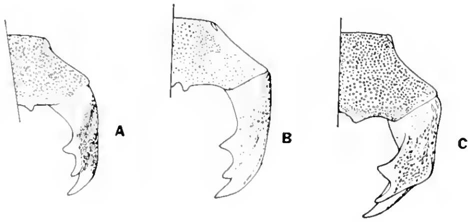

Figure 36. Left half of clypeus and mandible of females of *Xerocoelioxys.* A, *C. edita;* B, *C. aperta;* C, *C. bisoncornua.*

D. *Prothoracic tubercle with carina produced into thin, plate-like structure.*

E. *Scutum moderately to closely punctured, with conspicuous fasciae.*

F. Scutellum closely punctured (Fig. 37A-E).

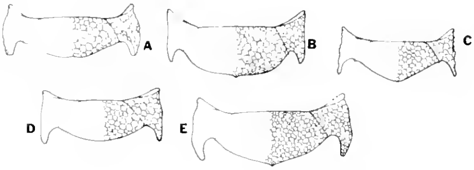

Figure 37. Scutellum and axillae of females of *Xerocoelioxys.* A, *C. edita;* B, *C. aperta;* C, *C. grindeliae;* D, *C. soledadensis;* E, *C. bisoncornua.*

G. Axillae well produced (Fig. 37A-E).

H. Mesepisternum with lateral surface moderately to closely punctured, with distinct fasciae.

I. *Graduli complete on metasomal terga two and three.*

J. Female: fore coxal spine variable.

K. Female: *sixth metasomal sternum with apical margin straight or constricted* (notched in *Coelioxys bisoncornua*, Fig. 38B) *as in Figures 42A and 38A.*

L. Male: hypostomal area of gena with excavation (Fig. 6).

M. Male: foveal area of metasomal tergum two densely punctured in some species.

N. Male: fifth metasomal tergum with lateral spine.

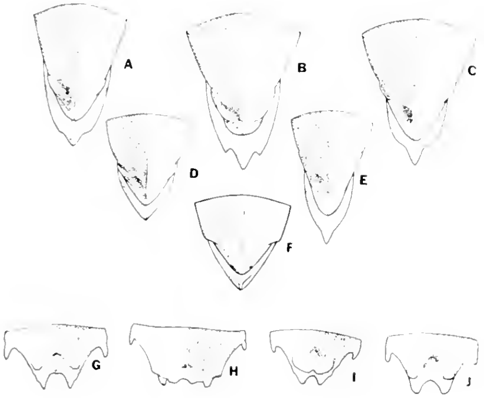

Figure 38. A-F, Sixth metasomal tergum and sternum of females of *Xerocoelioxys*. A, *C. edita;* B, *C. bisoncornua;* C, *C. galactiae;* D, *C. soledadensis;* E, *C. grindeliae;* F, *C. piercei.* G-J, Sixth metasomal tergum of males of *Xerocoelioxys*. G, *C. edita;* H, *C. aperta;* I, *C. soledadensis;* J, *C. nodis.*

O. Male: sixth metasomal tergum with dorsal spines variable, reduced in some species (Fig. 38G-J).

P. Male: seventh metasomal tergum variable apically.

Q. Male: apex of metasomal sternum four conspicuously emarginate (Fig. 39R).

R. Male: sternum seven represented by two small sclerites (Fig. 39B).

Key to Females of *Xerocoelioxys*

1. Fore coxal spine reduced to obtuse angle 2
   Fore coxal spine conspicuous, directed anteriorly or ventrally 3
2. Mandible with distinct flange on outer surface (Fig. 36C); ocular hairs very short (about 0.03 mm) ...... *bisoncornua*
   Mandible without distinct flange on outer surface (Fig. 36B); ocular hairs short (about 0.06 mm) .... *aperta*
3. Sixth metasomal tergum with distinct subapical protrusions (Fig. 38F) .... *piercei*
   Sixth metasomal tergum without protrusions 4
4. Sixth metasomal sternum elongate, constricted subapically (Fig. 38E); legs black to piceous; gena usually hidden by dense setae; scutellum sometimes with raised longitudinal median line .... *grindeliae*
   Sixth metasomal sternum variable, if elongate then legs ferruginous; gena visible through subappressed setae; scutellum without longitudinal medial line 5
5. Sixth metasomal sternum not or little constricted subapically (Figs. 38D, 38E) 6
   Sixth metasomal sternum more conspicuously constricted subapically (Figs. 38A, 38C 7
6. Lateral surface of mesepisternum with posterior margin with conspicuous fascia of appressed, squamose setae; scuto-scutellar suture with dense fascia ...... *soror*
   Lateral surface of mesepisternum with posterior margin with fascia sparse, indistinct or formed from erect, slender setae; scuto-scutellar suture with fascia indistinct .... *mesae*
7. Mesepisternum with lateral surface contiguously punctured; axilla usually with small carinae defining dorsal surface (Fig. 37A); scutum closely punctured .... *edita*
   Mesepisternum with lateral surface moderately punctured; axilla not carinate; scutum moderately to sparsely punctured .... *galactiae*

Key to Males of *Xerocoelioxys*

1. Sixth metasomal tergum with dorsal spines reduced, broad as in Figures 38H, 38I 2
   Sixth metasomal tergum with dorsal spines at least as conspicuous as shown in Figure 38G 4
2. Hypostomal area of the gena with distinct excavation (as in Figs. 5-6); fore coxal spine conspicuous, without brown setae .... *soror*
   Hypostomal area of the gena without distinct excavation; fore coxal spine reduced, with fascia of brown setae 3

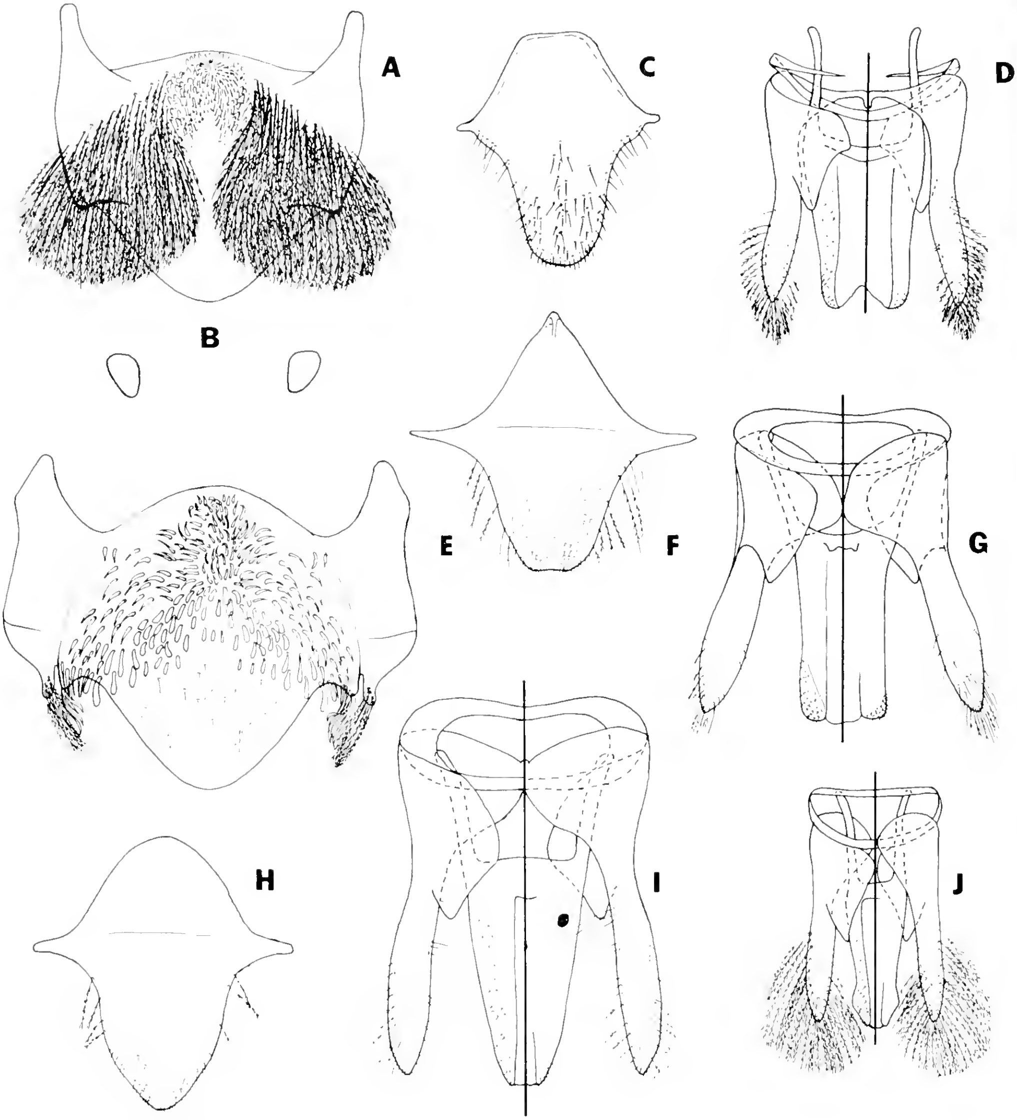

FIGURE 39. Hidden sclerites of males of *Xerocoelioxys*. A-D, *C. edita*. A, Sixth sternum; B, Seventh sternum (represented by two sclerites); C, Eighth sternum; D, Genital armature. E-G, *C. aperta*. E, Sixth sternum; F, Eighth sternum; G, Genital armature. H-I, *C. bisoncornua*. H, Eighth sternum; I, Genital armature. J, *C. boharti*, genital armature.

3. Clypeal margin tridentate medially (Fig. 36B); legs, venter of metasoma usually black or piceous .... *aperta*

Clypeal margin bidentate medially (Fig. 36C); legs, venter of metasoma usually with ferruginous areas .... *bisoncornua*

4. Lateral surface of mesepisternum almost covered by appressed, squamose (almost scale-like) setae; axilla without carina on dorsal surface; ocelloccipital distance at least subequal to ocellocular distance .... *boharti*

Lateral surface of mesepisternum without appressed squamose setae, or if with squamose setae then axilla with small carina (Fig. 37A) or ocelloccipital distance less than ocellocular distance 5

5. Gena with dense fascia hiding surface;

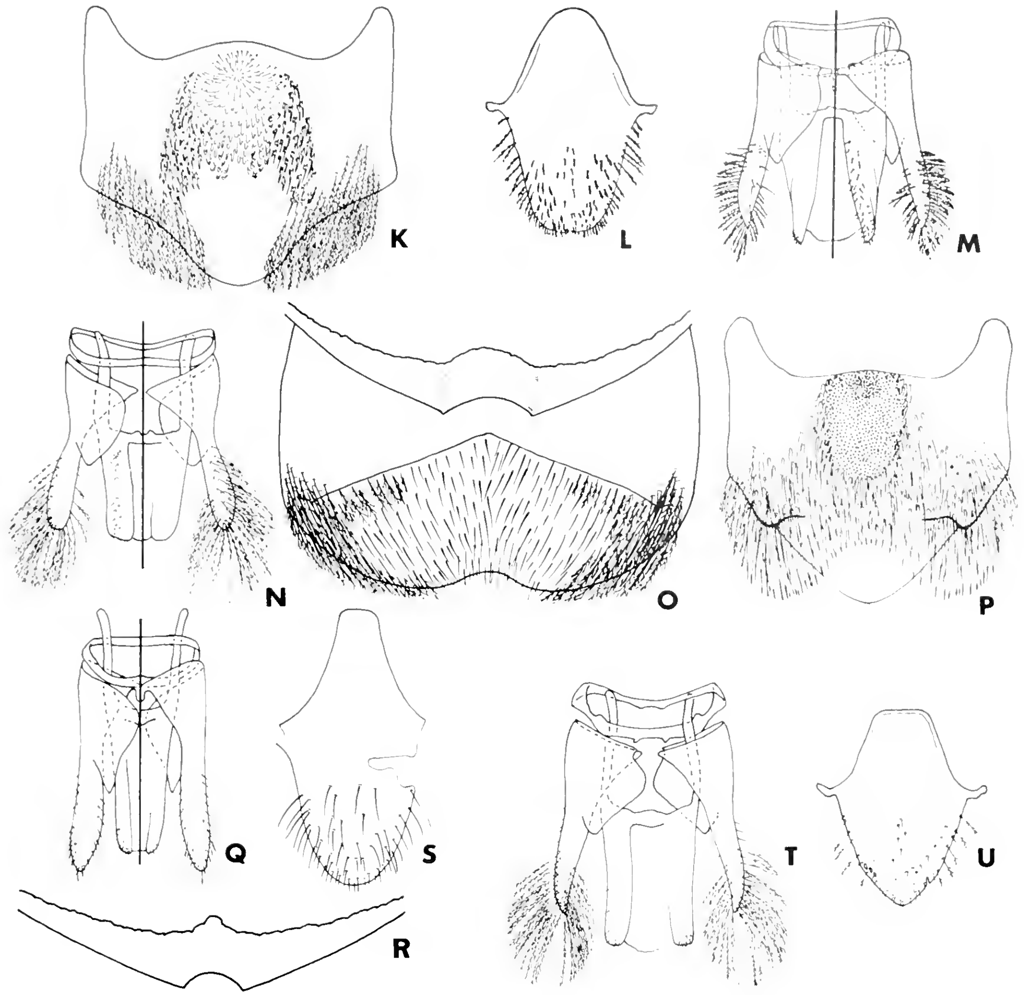

FIGURE 39. (continued) K-M, *C. mesae*. K, Sixth sternum; L, Eighth sternum; M, Genital armature. N, *C. galactiae*, genital armature. O-Q, *C. grindeliae*. O, apical margin of fourth sternum, fifth sternum; P, Sixth sternum; Q, Genital armature. R-T, *C. nodis*. R, margin of fourth sternum; S, Eighth sternum; T, Genital armature. U, *C. soledadensis*, eighth sternum.

foveal area of metasomal tergum two with raised, impunctate area (Fig. 25H) .... *grindeliae*

Gena usually with surface visible; foveal area of metasomal tergum two without raised impunctate area 6

6. Lateral surface of mesepisternum with squamose setae; scutum with anterior fascia distinct, of squamose setae .. *edita*

Lateral surface of mesepisternum with plumose but slender setae; scutum with anterior fascia variable, of plumose but slender setae 7

7. Scutum moderately to sparsely punctured; ocular hairs short (about 0.06 mm) 8

Scutum closely punctured; ocular hairs medium length (about 0.09 mm) .... *mesae*

8. Usually 10 mm or longer, midwestern distribution .... *nodis*

Usually 10 mm or less; eastern distribution .... *galactiae*

Coelioxys edita Cresson

Figures 36A, 37A, 38A, G, 39 A-D, 40

Coelioxys edita Cresson, 1872, Trans. Amer. Entomol. Soc. 4:272 (♂, Texas, type # 2502 in the Academy of Natural Sciences of Philadelphia); Crawford, 1914, Ann. Entomol. Soc. Amer. 7:153 (? = *deplanata*); Hill, 1936, Entomol. News 47:207 (= *deplanata*).

Coelioxys deplanata Cresson, 1878, Trans. Amer. Entomol. Soc. 7:96 (♀, Kansas, Colorado, type # 2487 in the Academy of Natural Sciences of Philadelphia).

FEMALE. (1) Length 9.5-14 mm; (2) integument granular on vertex, very finely rugulose on thorax and metasoma, black; antenna black to piceous; coxae, trochanters, venter of metasoma piceous to ferruginous; legs piceous to ferruginous; basal metasomal terga black to ferruginous; (3) pubescence white, yellowish on clypeus, golden on tarsi; (4) ocular hairs short (about 0.03 mm); (5) clypeus with surface rounded horizontally, rugose, contiguously punctured, covered with very short setae; margin with two strong denticles (Fig. 36A) obscured by dense setal fringe; (6) clypeoantennal distance less than lateral margin of clypeus; (7) paraocular area hidden by appressed setae about 0.1 mm long; (8) rest of face coarsely, closely punctured, upper median area bare; (9) clypeoantennal distance greater than antennocular distance and less than interantennal distance; (10) ocellar area with impunctate areas slightly less conspicuous than shown in Figures 10, 11A; (11) interocellar distance greater than ocelloccipital distance and less than ocellocular distance; (12) vertex less closely punctured anteriorly and more closely punctured posteriorly than shown in Figure 10; (13) gena narrower than eye, strongly constricted ventrally, surface visible; ventral angle greater than 90°; (14) hypostomal area of gena with setae shorter than those on disc; (15) mandible with outer surface closely punctured (Fig. 36A); (16) scutum moderately punctured medially, closely punctured laterally; distinct anterior fascia interrupted medially; slender, suberect setae in every puncture on disc; (17) lateral surface of mesepisternum contiguously punctured with large punctures, scattered squamose setae on disc; conspicuous fasciae anteriorly and posteriorly; (18) scutellum with posterior margin slightly emarginate in some specimens (Fig. 37A); (19) axilla with small carina defining dorsal surface (Fig. 37A); (20) metanotal setae prostrate medially; (21) fore coxal spine about 0.16 mm long, rounded apically, directed ventrally; (22) terga 2, 3 with conspicuous gradular grooves, terga 1-5 with conspicuous apical fasciae, tergum 1 with sparse basal fascia; punctures moderately (tergum 1) to closely punctured (tergum 6), tergum 2 with foveal area closely punctured; tergum 6 with subapical carina (Fig. 38A); (23) sterna 1-5 fasciate apically, fascia of sternum 1 interrupted submedially, fascia of sternum 5 incomplete medially; punctures on sterna 1-4, basally on 5, 6 moderately spaced; sterna 5, 6 apically very closely punctured; sternum 6 with margin constricted subapically (Fig. 38A).

MALE. (24) Length 8.5-10.5 mm; (25) integument as in female (2 above); (26) pubescence white, golden on tarsi; (27) ocular hairs short (about 0.05 mm); (28) clypeus hidden by copious setae about 0.3 mm long; surface rugulose and shiny; margin as in Figure 36A; (29) clypeoantennal distance as in female (6 above); (30) paraocular area hidden by setae about 0.3 mm long; (31) rest of face coarsely punctured, hidden by setae about 0.3 mm long; (32) interantennal distance subequal to clypeoantennal distance, greater than antennocular distance; (33) ocellar area as in female (10 above); (34) interocellar and ocelloccipital distances subequal, less than ocellocular distance; (35) vertex more closely punctured than shown in Figure 10; (36) gena narrowed ventrally; surface visible; ventral angle greater than 90°; (37) hypostomal area of gena modified into distinct excavation (Fig. 6); anterior, posterior portions with setae shorter than on disc of gena; (38-43) mandible, scutum, mesepisternum, scutellum, axilla, metanotal setae as in female (15-20 above); (44) front coxal spine conspicuous (0.3 mm long, 0.15 mm wide) with setae on dorsal and ventral surfaces, rounded apically, directed anteriorly; (45) terga 1-5 with distinct apical fasciae diminishing posteriorly, gradular grooves of terga 5, 6 with conspicuous fasciae; foveal area of tergum 2 closely punctured but not sunken; tergum 6 with dorsal spines stout (Fig. 38G); tergum 7 unmodified (as in Fig. 26A); (46) sterna 1-4 with punctures and fasciae as in female (23 above); (47) sternum 4 submarginally carinate (as in Fig. 26C), fascia incomplete, apex entire; sternum 5 as in Figure 19C except margin with small, median emargination; sternum 6 with conspicuous shoulders (Fig. 39A); sternum 7 represented by two sclerites (Fig. 39B); sternum 8 with base broad (Fig. 39C); genital armature with gonobase incomplete, setae on gonocoxite sparse (Fig. 39D).

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys edita* ranges from southern Canada into northern Mexico (Fig. 40). Few specimens have been collected east of the Mississippi River.

This bee is in flight at least from April 10 (Texas) to October 11 (Baja California).

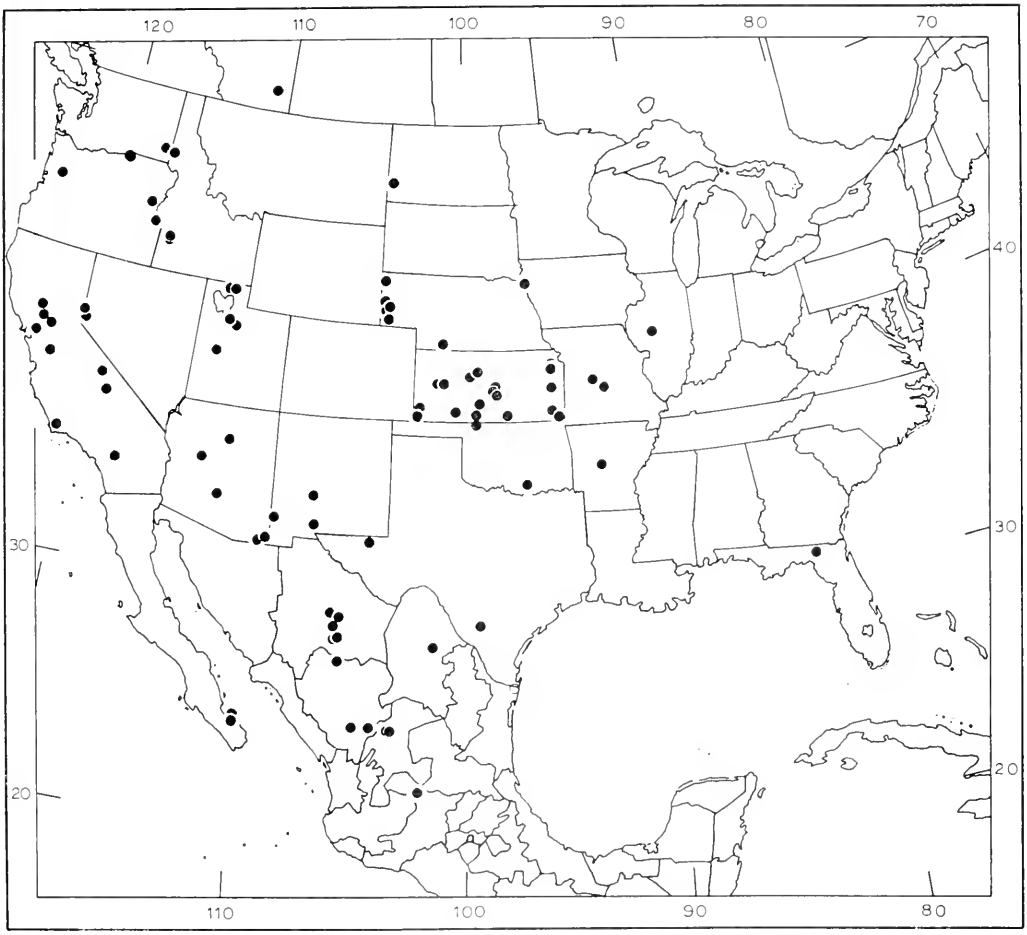

FIGURE 40. Distribution of *Coelioxys edita.*

HABITAT. *Coelioxys edita* has been collected from areas classified as a wide variety of vegetation types. Its distribution does not seem to be related to vegetation type.

COMPARATIVE COMMENTS. *Coelioxys edita* most closely resembles *C. bisoncornua* from which it can be distinguished by the slightly carinate axilla and slightly emarginate scutellum (non-carinate axilla and slightly produced scutellum in *C. bisoncornua*, compare Figs. 37A and 37E).

Coelioxys aperta Cresson

Figures 36B, 37B, 38H, 39E-G, 41

Coelioxys aperta Cresson, 1878, Trans. Amer. Entomol. Soc. 7:95 (♀, Colorado, type # 2488 in the Academy of Natural Sciences of Philadelphia); Cockerell, 1921, Amer. Mus. Novitates 21:4-10 (♂ described, key).

FEMALE. Agrees with description and figures of *Coelioxys edita* except as follows: (1) Length 11-15.5 mm; (2) integument black; antenna, tegula, piceous; legs piceous to dark ferruginous; (4) ocular hairs short (about 0.05 mm); (5) clypeus slightly convex to rounded horizontally, rugose, shining; surface visible except for longitudinal median line covered with short, appressed setae, lateral and dorsal margins bare; margin with three strong denticles (Fig. 36B); setal fringe scant; (7) paraocular area visible between setae about 0.3 mm long; (8) rest of face closely, coarsely punctured except for irregular mediosagittal line; (10) ocellar area closely punctured; (11) interocellar and ocelloccipital distances subequal, less than ocellocular distance; (12) vertex closely punctured; (14) hypostomal area of gena with setae longer than those on disc; (15) mandible with outer surface rounder than shown in Figure 36A (Fig. 36B); (16) scutum closely punctured, longitudinal median line complete; anterior fascia represented by median patch, weaker lateral line; (17) mesepisternum with anterior and posterior fasciae sparse; (18) scutellum with posterior margin produced slightly (Fig. 37B); (19) axilla without carina (Fig. 37B); (21) front coxal spine reduced; (22) tergum with foveal area unmodified; (23) fascia of sternum 1 represented by median patch, fascia of sternum 5 complete.

MALE. Agrees with description and figures of *Coelioxys edita* except as follows: (24) Length 9.5-12.5 mm; (25) integument as in female (2 above); (27) ocular hairs of medium length (about 0.1 mm); (28) clypeus obscured by long setae (about 0.45 mm); (30) paraocular area obscured by setae about 0.45 mm long; (32) clypeoantennal distance less than interantennal distance, greater than antennocular distance; (33) ocellar area as in female (10 above); (34) ocellocular distance greater than interocellar distance, less than ocelloccipital distance; (36) gena with ventral angle less than 90°; (37) hypostomal area of gena *not* excavated, but as in female (14 above); (38-43) mandible, scutum, mesepisternum, scutellum, axilla, metanotal setae as in female (15-20 above); (44) front coxal spine reduced, with dense, brown anteroventrally directed spot of setae; (45) terga 3-5 with apical fasciae incomplete medially, median fasciae becoming more distinct posteriorly; tergum 2 with foveal area unmodified; tergum 6 with dorsal spines reduced (Fig. 38H); tergum 7 with apical spine about half as long as shown in Figure 13A; (46) sterna 1-4 with punctures and fasciae as in female (23 above) except each puncture with seta becoming more conspicuous posteriorly; gradular grooves with fasciae; (47) sternum 4 subapically carinate, fascia complete; emargination of sternum 5 broad; shoulders of sternum 6 bifid, setae inflated medioposteriorly (Fig. 39E); sternum 8 with lateral angles extended,

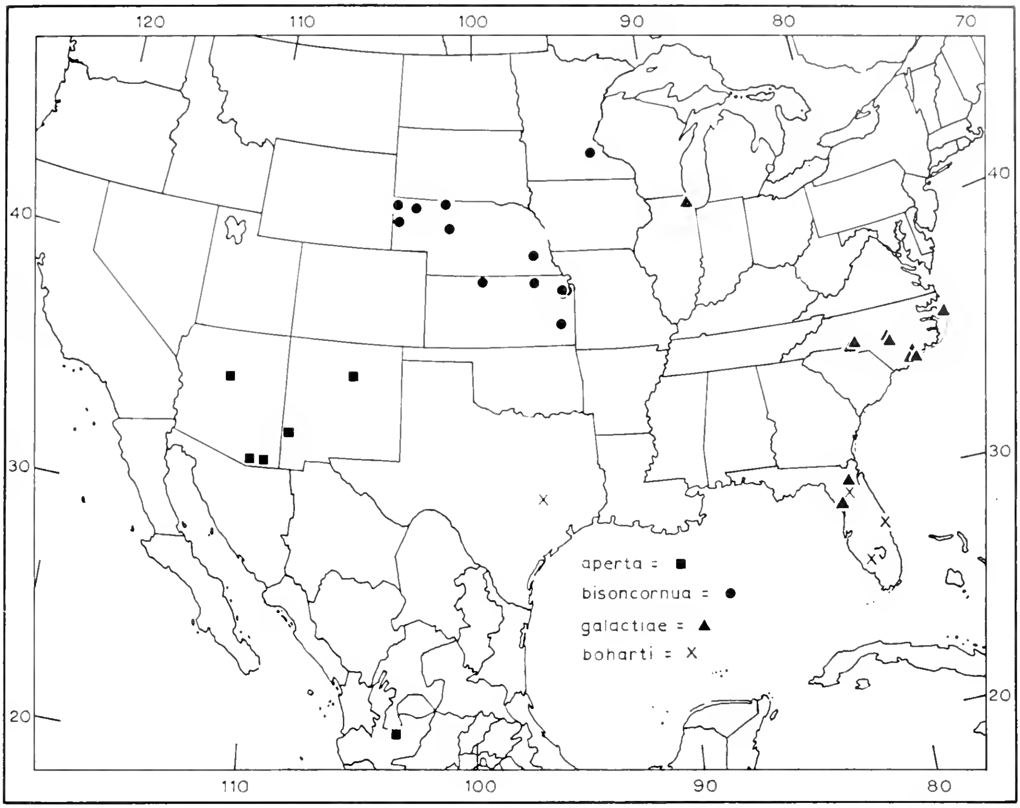

FIGURE 41. Distributions of *Coelioxys aperta*, *C. bisoncornua*, *C. boharti*, and *C. galactiae*. *Coelioxys aperta* is also known from Colorado (state record only).

base narrow (Fig. 39F); genital armature with slender branched setae on gonocoxites (Fig. 39G).

DISTRIBUTION AND SEASON OF FLIGHT. This bee ranges from Colorado to Guadalajara, Mexico (Fig. 41).

Coelioxys aperta is in flight at least from July 19 (New Mexico) to October 5 (Arizona) and to October 16 (Guadalajara, Mexico).

HABITAT. Areas classified as western coniferous forests (*Abies, Picea, Pinus, Pseudotsuga*) appear to be the principal habitat of *Coelioxys aperta* although it has been collected in oak-juniper woodland (*Quercus, Juniperus*) and perhaps has been collected in grama-tobosa shrubsteppe (*Bouteloua, Hilaria, Larrea*).

GEOGRAPHIC VARIATION. Although the series of this species is small, specimens from the southern part of the range are larger with the clypeal marginal denticles longer and the metasomal fascial more distinct.

COMPARATIVE COMMENTS. *Coelioxys aperta* resembles the larger, darker specimens of *C. edita* but differs in both sexes by the conspicuous median tooth of the clypeal margin (Fig. 36B), the small median projection of the scutellum (Fig. 37B), and the lack of carinae on the axillae (Fig. 37B). The reduced fore coxal spines of both sexes, the spine on tergum seven of males, the bifid shoulders of sternum six in males, the wide eighth sternum, and the complete gonobase of the genital armature are different from other bees in *Xerocoelioxys* except for *C. bisoncornua*. The lack of an excavation of the hypostomal area of the gena suggests males of *Synocoelioxys* (Fig. 3).

Coelioxys bisoncornua Hill
Figures 36C, 37E, 38B, 39H-I, 41

Coelioxys bisoncornua Hill, 1936, Entomol. News 47:205 (♀, ♂, Nebraska, Kansas, type in the collection of The University of Nebraska, Lincoln).

FEMALE. Agrees with description and figures of *Coelioxys edita* except as follows: (1) Length 12-15 mm; (2) integument black, antenna black to ferruginous; mandibles rufous; legs, venter of metasomal rufous to ferruginous; tegula brown; (4) ocular hairs very short (about 0.16 mm); (5) clypeus slightly convex; bare or visible through short (about 0.15 mm) appressed setae; margin with sparse fringe, two strong denticles (Fig. 36C); (7) paraocular area with ventral half bare or with scattered appressed setae; (8) rest of face bare except for area about 0.3 mm wide around base of antenna; (10) ocellar area closely punctate; (11) ocellocular distance subequal to ocelloccipital distance, greater than interocellar distance; (12) vertex very closely punctured laterally, contiguously punctured with slightly smaller punctures medially; (13) gena constricted ventrally; (15) mandible with flange on outer surface (Fig. 36C); (16) scutum with indistinct anterior fascia complete; slender, erect setae on disc sparse, short; (17) lateral surface of mesepisternum contiguously punctured with medium sized punctures, fascia indistinct; (18) scutellum with posterior margin rounded, produced medially (Fig. 37E); (19) axilla without carinae (Fig. 37E); (20) metanotum with dorsal setae subprostrate; (21) front coxal spine reduced; (22) tergum 3 with gradular groove shallow or incomplete medially; terga 1, 5 closely punctured, tergum 6 very closely punctured, terga 2-4 moderately punctured; foveal area of tergum 2 unmodified; tergum 6 broadly rounded (Fig. 38B); (23) sterna 1-5 sparsely fasciate apically, fascia of sternum 1 a median patch; sterna 1-5 moderately punctured, sternum 6 with contiguous, elongate, irregular punctures, subapically notched in some specimens (Fig. 38B).

MALE. Agrees with description and figures of *Coelioxys edita* except as follows: (24) Length 11-14.5 mm; (25) integument as in female (2 above); (28) clypeus obscured by long (about 0.45 mm) copious setae; (30) paraocular area obscured by setae about 0.45 mm long; (31) rest of face obscured by setae about 0.45 mm long; (32) clypeoantennal distance greater than antennocular distance, less than interantennal distance; (33) ocellar area as in female (10 above); (34) ocelloccipital distance less than ocelloccipital distance, greater than interocellar distance; (37) hypostomal area of gena *not* excavated, but as in female (14 above); (38) mandible with outer margin slightly rounder than shown in Figure 36B; (39-43) scutum, mesepisternum, scutellum, axilla, metanotal setae as in female (16-20 above); (44) front coxal spine as described for male of *C. aperta;* (45) foveal area of tergum 2 unmodified; tergum 6 as in Figure 38H; tergum 7 as described for *C. aperta;* (46) sterna 1-4 with conspicuous apical fasciae, 2-4 with conspicuous basal fasciae in gradular grooves; (47) margin of sternum 4 broadly emarginate; margin of sternum 5 entire, sternum 6 as in Figure 39E but with slightly more copious setae; sternum 8 broadly rounded basally (Fig. 39H); genital armature large (Fig. 39I).

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys bisoncornua* ranges from Minnesota through Nebraska and Kansas (Fig. 41).

This bee is in flight at least from July 28 to September 13.

HABITAT. *Coelioxys bisoncornua* has

been taken in areas classified mostly as central and eastern grasslands, grassland and forest combinations but also in eastern ponderosa pine forest, northern flood plain forest and oak-hickory forest.

Flower records indicate an open, disturbed habitat as all but one are sunflower, a flower of open areas rather than woodlands. Furthermore, Mr. K. W. Richards captured a female "searching" along a dirt bank near Lawrence, Kansas.

COMPARATIVE COMMENTS. This bee is most likely to be confused with large specimens of *Coelioxys edita* because *C. edita* is far more common than the more similar *C. aperta*. Females of *C. bisoncornua* have a conspicuous flange on the outer surface of the mandible (Fig. 36C) which is lacking in *C. edita* and *C. aperta*. Males of *C. bisoncornua* lack small carinae on the axillae evident in *C. edita* (compare Figs. 37A and 37E) and have more ferruginous areas on the legs and venter of the metasoma than the darker *C. aperta*.

Coelioxys boharti Mitchell

Figures 39J, 41

Coelioxys boharti Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:194, 206-207 (♂, Florida, type in the collection of the National Museum of Natural History).

MALE. Agrees with description and figures of *Coelioxys edita* except as follows: (24) Length 12-13.5 mm; (25) integument black; antenna, tegula, legs piceous; venter of metasoma dark ferruginous; (26) pubescence white, slightly yellow on face, golden on tarsi; (31) rest of face hidden ventrally by appressed setae about 0.15 mm long, dorsally by subappressed setae about 0.45 mm long; (32) clypeoantennal distance greater than antennocular distance, less than interantennal distance; (33) ocellar area moderately punctured; (34) ocellocular distance less than ocelloccipital distance, greater than interocellar distance; (37) excavation of hypostomal area of gena almost bare; (38) mandible with outer surface rounded as in Figure 67E; (39) scutum with anterior fascia sparse medially; (40) mesepisternum with lateral surface closely punctured with large punctures; punctures filled with appressed, squamose setae which may hide the surface; (42) axilla not carinate; (45) foveal area of tergum 2 closely punctured with small punctures, very slightly sunken; tergum 6 with dorsal spines as in Figure 38G; (47) apical margin of sternum 4, sternum 5 as in Figure 26B; sternum 8 as in Figure 26 E; genital armature with gonobase entire, setae on gonocoxite long (Fig. 39J).

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys boharti* has been collected in Texas (College Station) and Florida (Alachua County, Cocoa, and Labelle, Fig. 41).

This bee is in flight at least from June 21 to August 17.

HABITAT. This bee, known only from the male, has been taken from areas classified as oak-hickory *(Quercus-Carya)*, southern mixed forest *(Fagus, Liquidambar, Magnolia, Pinus, Quercus)*, and palmetto prairie *(Serenoa-Aristida)*.

COMPARATIVE COMMENTS. *Coelioxys boharti* resembles males of *C. galactiae* but is larger. The lateral surface of the mesepisternum is almost hidden by appressed squamose setae in *C. boharti* but is almost bare with scattered, erect, plumose (but slender) setae in *C. galactiae*.

Coelioxys galactiae Mitchell

Figures 38C, 39N, 41

Coelioxys galactiae Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:193-195, 204-206 (♀, ♂ North Carolina, Florida, Illinois, type is collection of T. B. Mitchell).

FEMALE. Agrees with description and figures of *Coelioxys edita* except as follows: (1) Length 9-11 mm; (2) integument granular on vertex, thorax; finely rugulose on metasoma; black; antenna, tegula piceous; mandible, venter and dorsum (basally) of metasoma black to rufous; legs rufous to ferruginous; (3) pubescence white, yellowish on face, golden on tarsi; (4) ocular hairs short (about 0.06 mm); (5) clypeus almost flat, margin with 4-6 denticles obscured by apical fringe; (10) ocellar area moderately punctate anteriorly; (11) interocellar distance slightly greater than ocelloccipital distance, less than ocellocular distance; (12) vertex punctured as in Figure 10; (13) gena constricted ventrally; surface almost obscured; (15) mandible as in Figure 22E; (16) scutum punctured as vertex in Figure 10; anterior fascia indistinct; (17) lateral margin of mesepisternum moderately punctured, fasciae distinct; (18) scutellum sparsely punctured; (19) axilla without conspicuous carinae; (22) tergum 1 with basal fascia inconspicuous; postgradular areas less closely punctate than pregradular areas; tergum 6 narrowly rounded apically (Fig. 38C); (23) fascia of sternum 5 sparse but complete medially; apical portion of sternum 6 longer than shown in Figure 38A (Fig. 38C).

MALE. Agrees with description and figures of *Coelioxys edita* except as follows: (24) Length 9-10 mm; (25) integument as in female (2 above); (26) pubescence white, yellow on face, golden on tarsi; (32) clypeoantennal distance greater than antennocular distance, less than interantennal distance; (33) ocellar area as in female (10 above); (34) ocelloccipital distance greater than interocellar distance, greater than ocellocular distance; (38) mandible as in female (15 above); (39) scutum moderately punctured; (40) mesepisternum moderately punctured, almost obscured by setae about 0.45 mm long; (41, 42) scutellum, axilla as in female (18-19 above); (45) gradular groove of tergum 4 with conspicuous fasciae laterally; tergum 6 with apical spines slightly more elongate than shown in Figure 39G; (47) sternum 4 with subapical carina indented medially, apical margin bidentate as in Figure 39O; sternum 6 as in Figure 39A; sternum 8 with base about half as broad as shown in Figure 39C; abundant setae apically on gonocoxite (Fig. 39N).

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys galactiae* is confined to the eastern United States (Fig. 41).

This bee is in flight at least from June 23 to August 6.

HABITAT. *Coelioxys galactiae* has been collected from areas classified as a mixture of bluestem prairie and oak-hickory forest *(Andropogon, Panicum, Sorghastrum, Quercus, Carya)*, oak-hickory forest, oak-hickory-pine forest *(Pinus)*, southern mixed forest *(Fagus, Liquidambar, Magnolia, Pinus, Quercus)*, and pocosin *(Pinus, Ilex)*.

COMPARATIVE COMMENTS. This bee is similar to *Coelioxys edita* but differs by the more attenuate sixth sternum of females (compare Figs. 38C and 38A) and more attenuate apical spines of males (longer than shown in Fig. 38G). Also the axillae of *C. galactiae* in both sexes are not carinate and are more sparsely punctured than those of *C. edita* (Fig. 37A).

Coelioxys grindeliae Cockerell
Figures 25H, 37C, 38E, 39O-Q; 44

Coelioxys grindeliae Cockerell, 1900, Can. Entomol. 32:297-301 (♂, ♀ New Mexico, key, type in the American Museum of Natural History;

Coelioxys grindeliae denverensis Cockerell, 1912, Can. Entomol. 44:166-170 (♂, Colorado, key, type in the National Museum of Natural History);

Coelioxys lamellicauda Cockerell, 1921, Amer. Mus. Novitates 21:6-8 (♂, Colorado, type in the American Museum of Natural History).

FEMALE. Agrees with description and figures of *Coelioxys edita* except as follows: (1) Length 9-11.5 mm; (2) integument black; antenna, legs, tegula, venter of metasoma black to piceous; (3) pubescence white, golden on tarsi; (5) clypeus almost flat, very closely punctate, almost hidden by dense, 1.5 mm long, plumose setae and scattered erect setae; margin with 5 small evenly spaced denticles; (7) paraocular area hidden by dense, plumose setae 2.0 mm long; (8) rest of face closely punctured except for longitudinal median line, almost hidden by appressed, plumose setae; (10) ocellar area moderately to closely punctured; (12) vertex punctured as in Figure 21; (13) gena constricted ventrally, surface visible anteriorly; (15) mandible as in Figure 22E; (16) scutum closely punctured; anterior fascia sparse medially; (17) lateral surface of mesepisternum nearly to completely contiguously punctured, disc bare or with scattered, suberect setae; (18) scutellum sometimes with longitudinal median impunctate ridge (Fig. 37C); (19) axilla long (Fig. 37C); (22) tergum 1 with basal fascia inconspicuous; tergum 2 with foveal area unmodified; tergum 6 more slender than shown in Figure 38A (Fig. 38E); (23) sterna 1-5 moderately to sparsely punctured, punctures very shallow medially, surface shining; sternum 5 apically contiguously punctured with small punctures; sternum 6 elongate apically (Fig. 38E).

MALE. Agrees with description and figures of *Coelioxys edita* except as follows: (24) Length 9.5-11 mm; (25) integument as in female (2 above); (28) clypeal margin with 3 distinct denticles; (33) ocellar area as in female (10 above); (36) ventral half of gena hidden by dense setal fascia; (38, 39) mandible, scutum as in female (15, 16 above); (40) mesepisternum with lateral surface almost hidden in some specimens; (41-43) scutellum, axilla, metanotal setae as in female (18-20 above); (45) foveal areas of tergum 2 with small, raised, impunctate area (Fig. 25H); (46) sterna 1-4 with conspicuous fasciae posteriorly; sternum 4 carinate subapically, margin with 2 projections (Fig. 39O); sternum 6 with mostly expanded, rather than plumose setae, heavily pigmented laterally (Fig. 39P); sternum 8 with base broadly rounded; genital armature with gonobase complete (Fig. 39Q).

HOST RECORDS. Hicks (1926) reported *Coelioxys grindeliae* to be a parasite of *Megachile perihirta*.

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys grindeliae* is confined to southern Canada and the western United States (Fig. 44).

This bee is in flight at least from June 4 (northern California) to September 26 (Middle California).

HABITAT. *Coelioxys grindeliae* has been taken from a diversity of western forest, shrub and grassland vegetation types, as well as central and eastern grassland vegetation types and northern floodplain forest.

COMPARATIVE COMMENTS. Most specimens of *Coelioxys grindeliae* have the gena obscured by a dense, white fascia, a condition found in no other species in this group. Males of *C. grindeliae* are distinguished from other males by the raised, impunctate area of the foveal area (Fig. 25H). Females are distinguished by the elongate sixth metasomal sternum (Fig. 38E), dark legs, and sometimes by the raised longitudinal median line of the scutellum (Fig. 37C).

Coelioxys mesae Cockerell
Figures 39K-M, 42A, 43

Coelioxys mesae Cockerell, 1921, Amer.

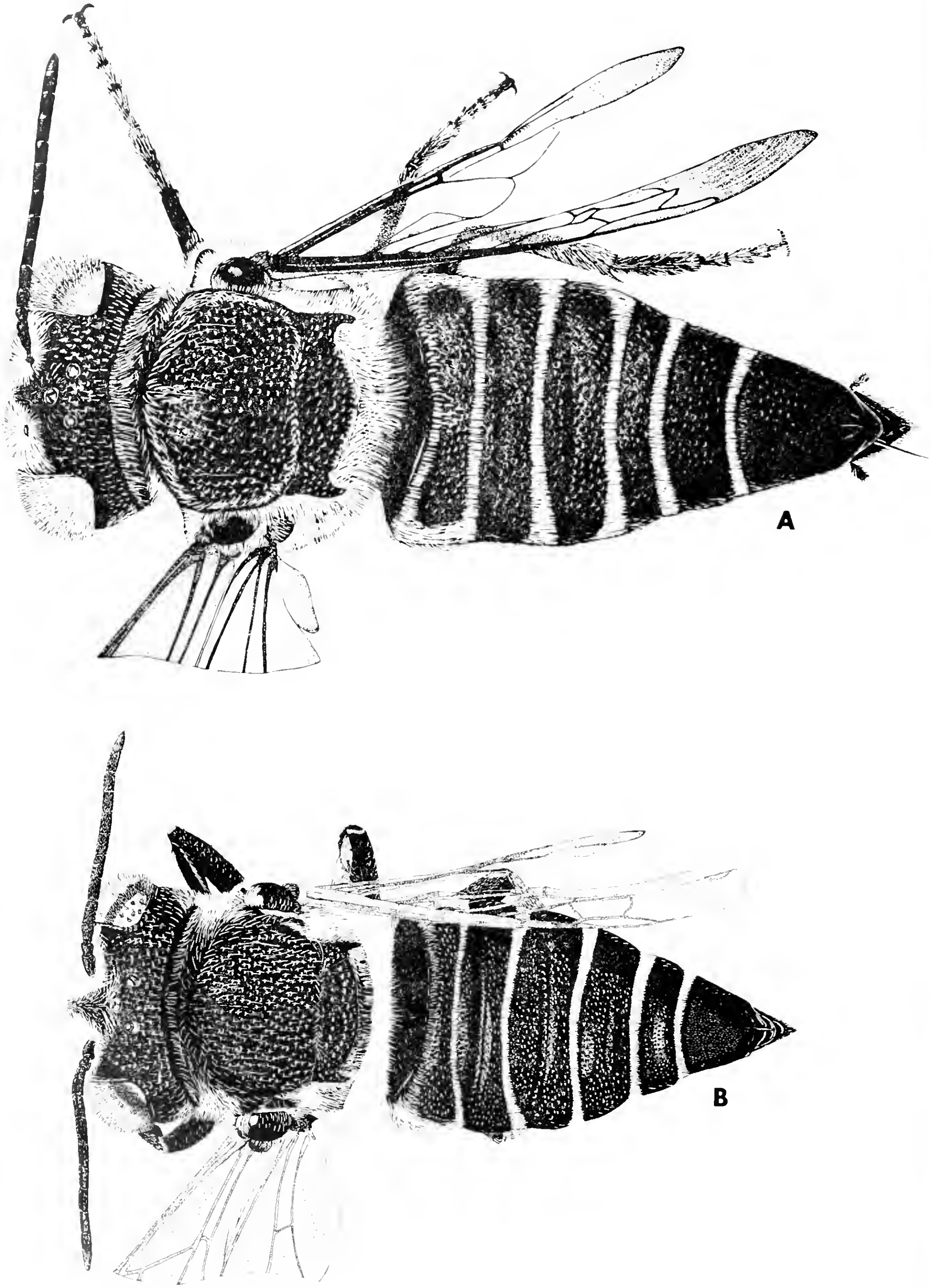

FIGURE 42. Dorsal views of female *Coelioxys*. A, *C. mesae;* B, *C. mitchelli.*

Mus. Novitates 21:6 (♂, Colorado, type in the American Museum of Natural History).

FEMALE. Agrees with description and figures of *Coelioxys edita* except as follows: (2) Integument finely granular, dull on vertex, metasoma; black; antenna, legs, venter of metasoma black to piceous; (3) pubescence white, sometimes brownish on mesosoma, golden on tarsi; (4) ocular hairs medium length (0.08 mm); (5) clypeus convex, rugose, closely punctured, shiny; disc bare, margin with 5 small denticles; apical fringe conspicuous but not dense; (7) paraocular area hidden by setae up to 0.3 mm long; (8) ventral portion of face with sparse, appressed setae about 0.1 mm long; dorsal portion with mediosagittal portion bare or obscured by longer setae; (10) ocellar area closely punctured; (12) vertex coarsely, evenly punctured (Fig. 42A); (13) gena with ventral angle about 90°; (15) mandible with outer margin rounded as in Figure 22E; (16) scutum closely, evenly punctured; disc with short, inconspicuous erect setae (Fig. 42A); (17) lateral surface of mesepisternum largely bare, fasciae sometimes indistinct; (18) scutellum with posterior margin almost straight medially (Fig. 42A); (19) axilla not carinate (Fig. 42A); (21) front coxal spine directed anteriorly; (22) metasomal terga closely punctured; tergum 2 with foveal area unmodified; tergum 6 subtriangular (Fig. 42A); (23) sternum 5 complete medially; sternum 6 subtriangular apically (Fig. 42A).

MALE. Agrees with description and figures of *Coelioxys edita* except as follows: (24) Length 9-11 mm; (25) integument as in female (2 above); (27) ocular hairs medium (about 0.1 mm); (28) clypeus hidden by copious setae about 0.36 mm long; margin as in female; (30) paraocular area hidden by setae about 0.45 mm long; (31) rest of face closely punctured; hidden by setae about 0.4 mm long; (32) clypeoantennal distance less than interantennal distance, greater than antennocular distance; (33) ocellar area as in female (10 above); (34) interocellar distance greater than ocelloccipital distance, less than ocellocular distance; (35) vertex slightly more irregularly punctured than shown in Figure 42A; (36) gena slightly narrowed ventrally; (38, 39) mandible, scutum as in female (15, 16 above); (40) mesepisternum with slender, plumose setae on disc; (41-43) scutellum, axilla, metanotal setae as in female (18-20 above); (45) tergum 6 with dorsal spines more conspicuous than shown in Figure 38G; (47) sterna 4, 5 as in Figure 39O except for longitudinal ridges on rim of sternum 4; sternum 6 as in Figure 39K; sternum 8 with base rounded (Fig. 39L); gonocoxite with abundant, plumose setae (Fig. 39M).

HOST RECORDS. Dr. G. E. Bohart has reared this bee from a nest of *Megachile umatillensis* at Cornish, Utah.

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys mesae* is confined to the western half of the United States (Fig. 43).

This bee is in flight at least from May 15 (Texas) and June 10 (Oregon) to August 29 (Utah).

HABITAT. Most localities from which *Coelioxys mesae* has been collected are classified as sagebrush steppe (*Artemisia-Agropyron*). Two specimens were collected from areas classified as grama-tobosa prairie (*Bouteloua, Hilaria*) and pine-Douglas fir forest (*Pinus, Pseudotsuga*).

COMPARATIVE COMMENTS. Females of *Coelioxys mesae* differ from those of *C. edita* by darker integument and entire lateral margin of the sixth sternum (compare Figs. 42A and 38A) and from those of *C. mitchelli* by the greater amount of appressed, squamose setae on

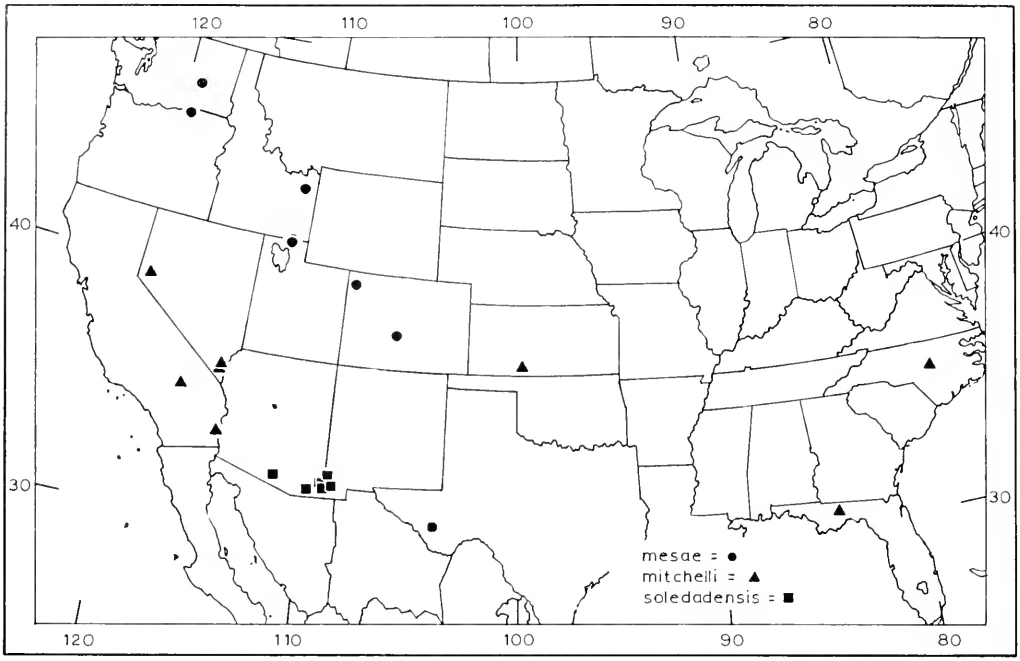

Figure 43. Distributions of *Coelioxys mesae*, *C. mitchelli*, and *C. soledadensis*.

the scutum, scutellum, and metanotum (compare Figs. 42A and B). Males of *C. mesae* differ from those of *C. edita* by longer ocular hairs, longer facial setae, and darker integument. Males of *C. mesae* differ from those of *C. mitchelli* by the entire, distinct basal fascia of tergum one (incomplete in *C. mitchelli*).

Coelioxys nodis, new species
Figures 38J, 39R-T, 48

MALE. Agrees with description and figures of *Coelioxys edita* except as follows: (24) Length 10-11 mm; (25) integument black, antenna, dorsum of metasoma black to piceous; legs, tegula, venter of metasoma piceous to ferruginous; (28) margin of clypeus with six small denticles; (30) paraocular area hidden by setae about 0.45 mm long; (31) rest of face hidden by appressed setae about 0.25 mm long; (33) ocellar area with small, irregular impunctate areas anteriorly; (34) ocelloccipital distance greater than interocellar distance, less than ocellocular distance; (38) mandible with outer surface simple as in Figure 22E; (39) scutum moderately punctured, anterior fascia indistinct; (40) lateral surface of mesepisternum closely punctured, setae squamose to slender, fascia indistinct; (41) scutellum slightly rounded posteriorly, sparsely punctured; (42) axilla without carinae; (45) tergum 6 with dorsal spines reduced, broad (Fig. 38J); (47) sternum 4 with submarginal carina indented medially (Fig. 39R); sternum 8 with base truncate (Fig. 39S); genital armature with gonobase lobed, gonocoxite with long, abundant setae (Fig. 39T).

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys nodis* has been collected in Illinois, Kansas, and Nebraska (Fig. 48) from July 3-12.

HABITAT. *Coelioxys nodis* has been collected in bluestem grama prairie (*Andropogon*, *Bouteloua*).

COMPARATIVE COMMENTS. *Coelioxys nodis* resembles larger males of *C. edita* but differs by lack of carinae on

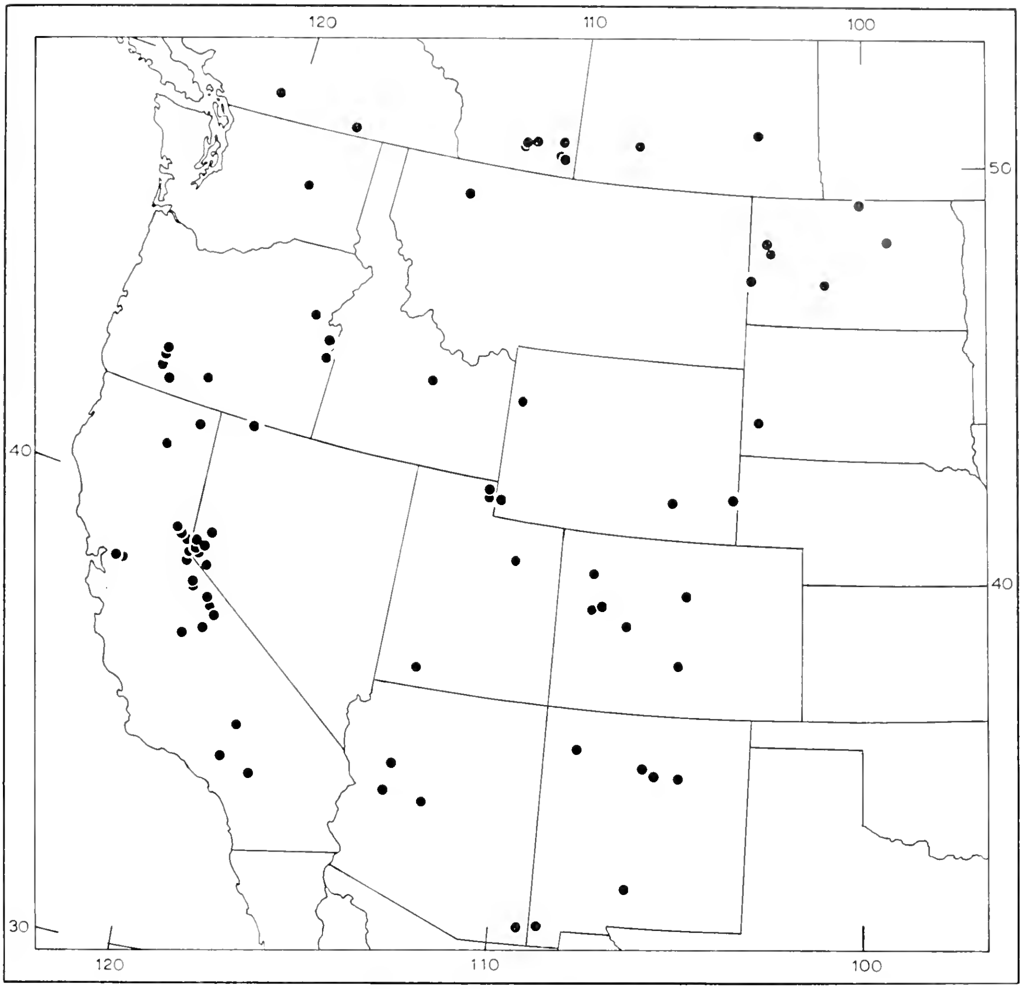

FIGURE 44. Distribution of *Coelioxys grindeliae*.

the axillae, by the subapical carina of sternum four which is indented medially (Fig. 39R), and by the dorsal spines of tergum six which are broad (compare Figs. 38J and 38G).

TYPES. Holotype male, Carns, Nebraska, July 3, 1902, *Verbena* (W. D. Pierce), in the collection of the University of Nebraska at Lincoln. Paratypes males; one, Sioux Co., Nebraska; one, Trego Co., Kansas, 2450 feet, July 12, 1912 (F. X. Williams); one, 35530, Sands, Illinois (Hart), 128. Paratypes in the collections of the University of Nebraska and the University of Kansas.

The specific names refer to the lobes on the gonobase which are more conspicuous in this species than any other in this study.

Coelioxys piercei Crawford
Figure 38F

Coelioxys piercei Crawford, 1914, Ann. Entomol. Soc. Amer. 7:152-153 (♀, Texas, type # 18219 in the National Natural History Museum).

FEMALE. Agrees with description and figures of *Coelioxys edita* except as follows: (1) Length 9.5 mm; (2) integument black; antenna, legs, tegula piceous; (4) ocular hairs short (about 0.05 mm long); (5) clypeus with surface almost convex, clypeal margin with 3 small denticles; (10) ocellar area closely punctate; (12) vertex moderately punctured; (15) mandible with outer margin rounded, resembling that shown in Figure 22E; (16) scutum moderately punctured, fascia slightly more conspicuous laterally than anteriorly; (17) lateral surface of mesepisternum dorsally with slender, scattered setae on disc; (18) scutellum with posterior margin as in Figure 42B; punctures as in Figure 37D; (19) axilla elongate as in Figure 37B; (22) tergum 2 with foveal area unmodified; tergum 6 with subapical flattened projections (Fig. 38F); sterna 1-5 fasciate apically; sternum 6 with lateral margin entire (Fig. 38F).

DISTRIBUTION AND SEASON OF FLIGHT. Type specimen from Cotulla, Texas, taken on April 17. No other specimens are known.

HABITAT. The area surrounding Cotulla has been classified as mesquite-acacia savana *(Prosopis, Acacia, Andropogon, Setaria)*.

COMPARATIVE COMMENTS. *Coelioxys piercei* resembles the females of *C. mesae* and *C. mitchelli* but differs by the flattened lateral projections of tergum six (Fig. 38F).

Coelioxys soledadensis Cockerell
Figures 37D; 38D, I; 39U; 43

Coelioxys soledadensis Cockerell, 1909, Entomol. News 20:9 (♂, New Mexico, type in the American Museum of Natural History).

FEMALE. Agrees with description and figures of *Coelioxys edita* except as follows: (1) Length 8-12 mm; (2) integument shiny on vertex; black, antenna, tegula black to piceous; legs, metasoma basally and ventrally piceous to rufous; (3) pubescence white, yellowish dorsally, golden on tarsi; (5) clypeus slightly convex, visible through minute setae, margin with two denticles not as conspicuous as shown in Figure 36A; (7) paraocular area hidden by appressed setae about 0.05 mm; (8) lower portion of rest of face plus longitudinal median line up to ocellar area visible, closely punctured; (9) clypeoantennal distance subequal to antennocular distance, less than interocellar distance; (10) ocellar area moderately punctured; (12) vertex moderately punctured; (14) hypostomal area of gena with setae subequal in length to those on disc; (15) mandible with outer surface rounded as in Figure 22E; (16) scutum evenly, contiguously punctured; anterior fascia distinct, narrowly interrupted medially; disc with minute suberect setae in each puncture; (17) lateral surface of mesepisternum moderately punctured, disc bare, fasciae distinct; (18) scutum with posterior margin rounded (Fig. 37D); (19) axilla not carinate (Fig. 37D); (22) terga 1, 2 very closely punctured; terga 3-5 moderately punctured; tergum 6 very closely, minutely punctured (Fig. 38D); (23) sternum 6 slightly constricted subapically (Fig. 38D).

MALE. Agrees with description and figures of *Coelioxys edita* except as follows: (24) Length 8-10 mm; (25) integument black; antenna, legs, tegula, venter of metasoma black to rufous; (27) ocular hairs medium length (about 0.8 mm); (28) clypeal margin as in female (5 above); (31) rest of face closely punctured, rugulose; (32) clypeoantennal distance greater than antennocular distance, less than interantennal distance; (33) ocellar area as in female (10 above); (34) interocellar distance greater than ocelloccipital distance, less than ocellocular distance; (35) vertex as in female (12 above); (37) hypostomal area of gena covered with small erect setae through which surface is visible, anteroventral portion of excavation with setae longer than those on disc; (38-43) mandible, scutum, mesepisternum, scutellum, axilla, metanotal setae as in female (15-20 above); (45) terga 3-6 with gradular grooves conspicuous, tergum 6 with dorsal spines reduced (Fig. 38I); (47) sterna 4, 5 as in Figure 39O; sternum 6 much like Figure 19C, shoulders slightly more distinct; sternum 8 with base broad, apex narrowly rounded (Fig. 39U); gonocoxite with dense setae, gonobase complete, much like Figure 39J.

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys soledadensis* has been collected in southern Arizona and New Mexico (Fig. 43).

This bee is in flight at least from July 5 to October 7.

HABITAT. *Coelioxys soledadensis* has been collected in areas classified as Arizona pine forest *(Pinus)*, oak-juniper woodland *(Quercus, Juniperus)*, creosote bush-bur sage *(Larrea, Franseria)*, and grama-tobosa shrubsteppe *(Bouteloua, Hilaria, Larrea)*.

COMPARATIVE COMMENTS. *Coelioxys soledadensis* most closely resembles *C. edita* from which it differs by the shiny vertex, moderately punctured lateral surface of the mesepisternum, slightly constricted sixth sternum of the female (compare Figs. 38A and 38D), and reduced dorsal spines of the sixth tergum of the male (compare Figs. 38I and 38G).

Subgenus *Coelioxys* Latreille

Coelioxys Latreille, 1809. Genera crustaceorum et insectorum secundum ordinen naturalem in familias disposita . . . 4: 166.
Type species: *Coelioxys quadridentata* Linnaeus.

The subgenus *Coelioxys* contains *C. hirsutissima, C. immaculata, C. mitchelli,* and *C. serricaudata*. This subgenus differs from *Xerocoelioxys* mainly in the reduced carina of the prothoracic tubercle.

Three hosts, all in different subgenera of *Megachile*, have been reported for *Coelioxys sodalis* (Table 1). Hosts have not been discovered for the remaining species in this group.

Most of the characters listed below are found in other groups of New World *Coelioxys* (particularly in *Xerocoelioxys* and *Boreocoelioxys*) and even in some Old World *Liothyrapis*, but never in this combination. This group is the only North American subgenus with reduced carinae of the prothoracic tubercles, complete graduli on metasomal terga two and three, sixth metasomal sterna in females entire (as in Fig. 42B) or constricted (as in Fig. 45E, not notched as in Fig. 21), and foveal areas of metasomal terga two in males closely punctured. Italicized characters below most clearly differentiate the subgenus *Coelioxys* from others in North America.

A. Ocellar area moderately to closely punctured.

B. Preoccipital carina incomplete medially.

C. Mandible with inner surface simple (as in Figs. 45A, B).

D. *Prothoracic tubercle with carina distinct but not expanded into thin plate-like structure.*

E. Scutum moderately to closely punctured, fasciae usually indistinct.

F. Scutellum usually rounded posteriorly (Figs. 45C, D).

G. Axilla usually well produced (Figs. 45C, D).

H. Mesepisternum closely to contiguously punctured, no minute punctures.

I. *Gradular grooves complete on metasomal terga two and three.*

J. Female: fore coxal spine small, inconspicuous.

K. Female: *sixth metasomal sternum with margin entire* (as in Fig. 42B) *or constricted subapically* (as in Fig. 45E, F), not notched as in Figure 21.

L. Male: hypostomal area of gena with distinct excavation (as in Fig. 5).

M. Male: *foveal area of metasomal tergum two closely punctured.*

N. Male: fifth metasomal tergum with lateral spines present but not conspicuous.

O. Male: sixth metasomal tergum with dorsal spines long (as in Fig. 45G) or short (as in Fig. 45I).

P. Male: seventh metasomal tergum broadly rounded apically (Fig. 46A).

Q. Male: fourth metasomal sternum sub-

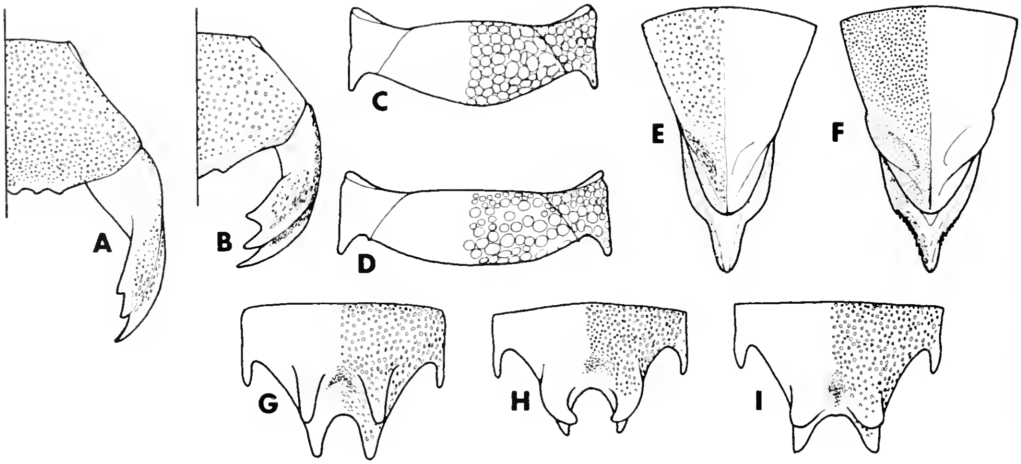

Figure 45. Parts of spp. of the subgenus *Coelioxys*. A-B, Left half of clypeus and mandible. A, *C. sodalis;* B, *C. serricaudata.* C-D, Scutellum and axillae. C, *C. sodalis;* D, *C. immaculata.* E-F, Sixth metasomal tergum and sternum of females. E, *C. sodalis;* F, *C. serricaudata.* G-I, Sixth metasomal tergum of males. G, *C. sodalis;* H, *C. serricaudata;* I, *C. immaculata.*

apically carinate, apex bidentate (as in Fig. 26B).

R. Male: seventh sternum represented by two small sclerites (as in Fig. 19D).

Key to Females of the Subgenus *Coelioxys*

1. Clypeus strongly convex, in lateral view almost half the width of eye; ventral portion of rest of face convex .... *serricaudata*
   Clypeus less convex, in lateral view much less than half the width of eye; ventral portion of rest of face flat or slightly rounded 2
2. Ocular hairs long (about 1.5 mm) .... *sodalis*
   Ocular hairs medium or short (about 1.0 to 0.5 mm) 3
3. Sixth metasomal sternum not or little constricted subapically (Fig. 42 B) .... *mitchelli*
   Sixth metasomal sternum conspicuously constricted subapically 4
4. Clypeus slightly raised, shining, medioapically depressed or flat ...... *immaculata*
   Clypeus not raised, slightly rounded vertically .... *hirsutissima*

Key to Males of the Subgenus *Coelioxys*

1. Metasomal tergum six with dorsal spines curved inward, upper surfaces sloping ventrally from outer margin (Fig. 45 H) .... *serricaudata*
   Metasomal tergum six with dorsal spines directed posteriorly or slightly outward, upper surfaces not sloping 2
2. Ocular hairs long (about 0.17 mm) .... *sodalis*
   Ocular hairs shorter (0.12-0.05 mm) 3
3. Excavation of hypostomal area appearing bare 4
   Excavation at least half covered by short setae .... *hirsutissima*
4. Interocellar distance greater than ocelloccipital distance; coast to coast distribution .... *mitchelli*
   Interocellar distance subequal to or slightly less than ocelloccipital distance; distribution limited to southeastern United States .... *immaculata*

Coelioxys sodalis Cresson

Figures 45A, C, E, G; 46A-D; 47

Coelioxys quadridentata; Cresson, 1864, Proc. Entomol. Soc. Philadelphia 2: 409 (United States, Trenton Falls, misidentification); Hicks, 1926, Univ. Colorado Stud. 15:226 (Searching behavior, misidentification).

Coelioxys sodalis Cresson, 1878, Trans. Amer. Entomol. Soc. 7:99 (♂, New York, Colorado, type in the Academy of Natural Sciences of Philadelphia); Mitchell, 1962, North Carolina Agr.

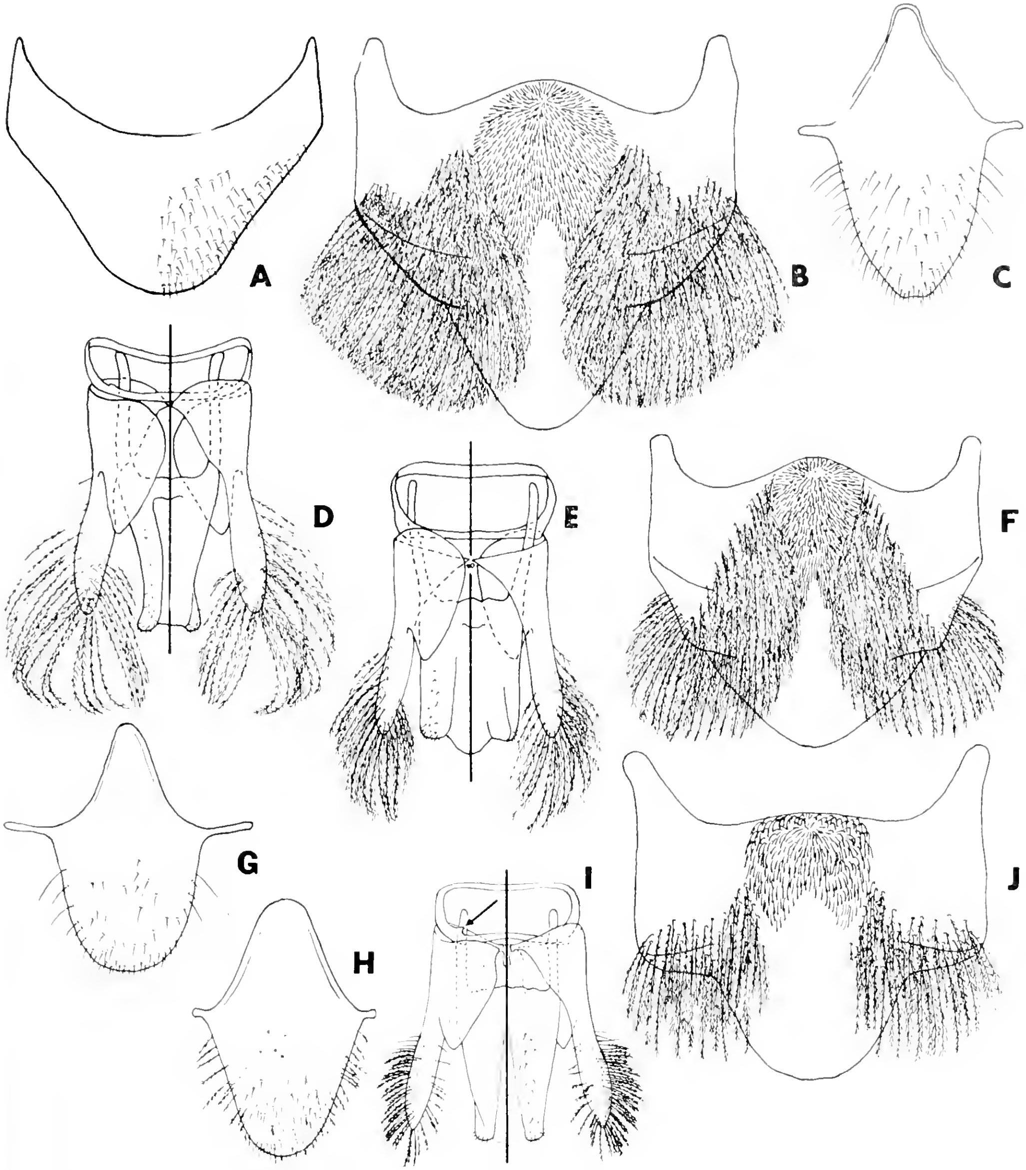

FIGURE 46. Hidden sclerites of males of the subgenus *Coelioxys*. A-D, *C. sodalis*. A, Seventh tergum; B, Sixth sternum; C, Eighth sternum; D, Genital armature. E, *C. hirsutissima*, genital armature. F-G, *C. immaculata*. F. Sixth sternum; G, Eighth sternum. H-I, *C. mitchelli*. H, Eighth sternum; I, Genital armature. J, *C. serricaudata*, sixth sternum.

Exp. Sta. Tech. Bull. 152:193, 195, 226 (Key, redescription, = *C. tristis*, = *C. ribis*).

Coelioxys ribis Cockerell, 1900, Can. Entomol. 32:297, 301, 308 (♂, New Mexico, key, type in the National Museum of Natural History); Graenicher, 1935, Ann. Entomol. Soc. Amer. 28: 300, 304 (Biology); Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:226 (= *C. sodalis*).

Coelioxys ribis var. *kincaidi* Cockerell, 1904, Ann. Mag. Nat. Hist. (7) 13:33 (♀, ♂, Washington, type in the American Museum of Natural History); Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:226 (= *C. sodalis*).

FEMALE. (1) Length 11-13 mm; (2) integument very finely rugulose, moderately shiny between punctures; black, antenna, legs, tegula, metasoma black to piceous; (3) pubescence white, pale ochraeous on face, mesosoma, golden on tarsi; (4) ocular hairs long (about 0.15 mm); (5) clypeus convex, almost hidden by appressed setae, longer, erect, scattered setae; margin with 6 small denticles (Fig. 45A); (6) clypeoantennal distance shorter than lateral margin of clypeus; (7) paraocular area almost hidden by setae up to 0.35 mm long; (8) rest of face rugose except for a small impunctate median area, closely punctured up to ocellar area; (9) clypeoantennal distance subequal to antennocular distance, less than interantennal distance; (10) ocellar area closely punctate; (11) interocellar distance greater than ocelloccipital distance, less than ocellocular distance; (12) vertex closely punctured; (13) gena narrower than eye, constricted below; ventral angle greater than 90°; (14) hypostomal area of gena with setae subequal to or longer than those on disc; (15) mandible with short teeth (Fig. 45A); (16) scutum closely punctured; erect, slender setae on disc about 0.33 mm long; (17) lateral surface of mesepisternum closely punctured, with erect, slender setae about 0.35 mm long; (18) scutellum with posterior margin strongly rounded (Fig. 45C) or slightly produced, carina separating dorsal and posterior surfaces indistinct; (19) axilla sometimes less produced than shown in Figure 45C; (20) metanotal setae erect; (21) fore coxal spine small (about 0.08 mm), triangular, directed anteriorly; (22) terga 1-5 with apical fasciae less conspicuous than shown in Figure 21, punctured as in Figure 21 but with slightly smaller punctures; tergum 6 elongate (Fig. 45E); (23) sterna 1 to basal portion of sternum 5 moderately punctured, apical portion of sternum 5, sternum 6 very closely punctured; sternum 6 constricted subapically (Fig. 45E).

MALE. (24) Length 8-12 mm; (25) integument as in female (2 above); (26) pubescence white, golden on tarsi; (27) ocular hairs long (about 0.15 mm); (28) clypeus hidden by setae about 0.6 mm long; surface rugose, shiny; margin as in female (5 above); (29) clypeoantennal distance as in female (6 above); (30) paraocular area almost hidden by setae up to 0.6 mm long; (31) rest of face closely punctured, almost hidden by setae up to 0.6 mm long; (32) clypeoantennal, antennocular, interantennal distances as in female (9 above); (33) ocellar area closely punctate; (34) interocellar distance subequal to ocelloccipital distance, less than ocellocular distance; (35) vertex closely punctured, sometimes with small, irregular, impunctate areas lateral to ocelli; (36) gena as in female (13 above); (37) hypostomal area of gena with distinct excavation (Fig. 5) covered with setae shorter than those on disc; (38-39) mandible, scutum as in female (15-16 above); (40) lateral surface of mesepisternum with setae about 0.45 mm long; (41-43) scutellum, axilla, metanotal setae as in female (18-20); (44) front coxal spine long (about 0.33 mm), narrow (about 0.12 mm) with setae on dorsal and ventral surfaces; rounded apically; directed anteriorly; (45) terga 1-5 with fasciae and punctures as in female (22 above); tergum 2 with postgradular area very closely punctured and rounded to densely punctured and slightly but broadly sunken laterally; tergum 6 with dorsal spines slender (Fig. 45G); tergum 7 slightly protuberant apically (Fig. 46A); (46) sterna 1-4 moderately punctured, inconspicuous seta in each puncture; (47) margin of sternum 4, sternum 5 as in Figure 26B except den-

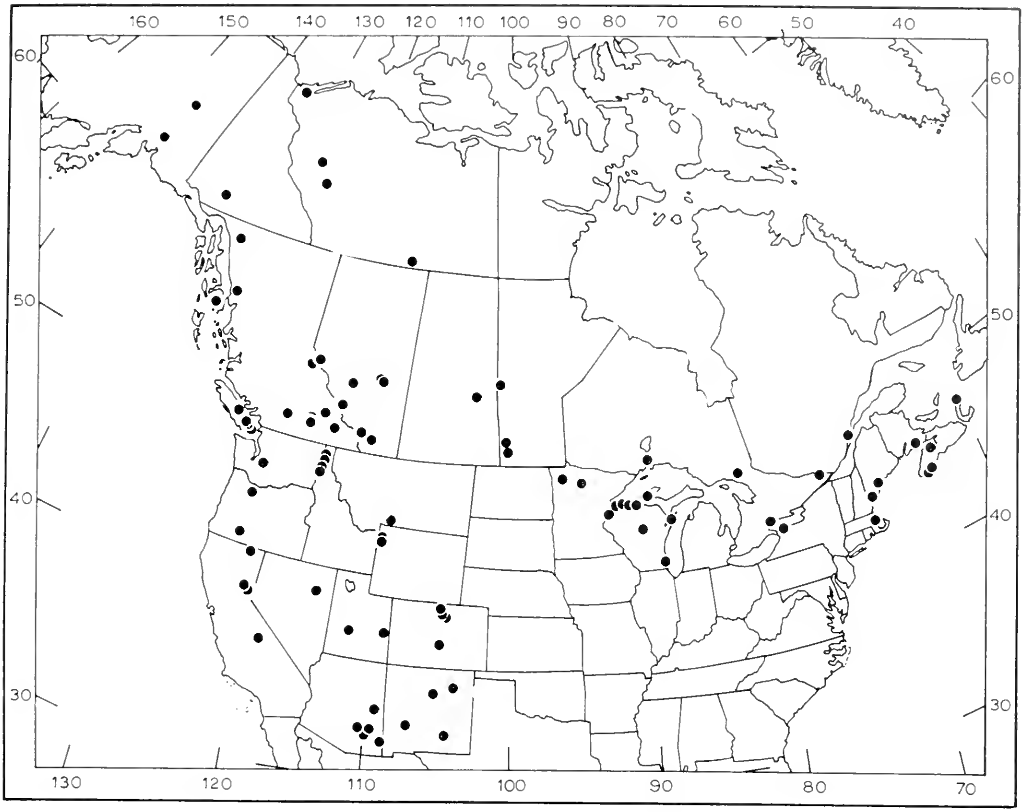

Figure 47. Distribution of *Coelioxys sodalis*.

ticles of sternum 4 more rounded; sternum 6 with shoulders inconspicuous (Fig. 46B); sternum 7 represented by 2 small sclerites; sternum 8 with narrow base (Fig. 46C); gonocoxite with long setae, gonobase complete (Fig. 46D).

HOST RECORDS. Graenicher (1927) reared *Coelioxys sodalis* from nests of *Megachile melanophoea wootoni*. Medler (1968) reared *C. sodalis* from the cells of *M. texana*. Hobbs (1968) reared *C. sodalis* from a third host bee, *M. rotundata*.

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys sodalis,* like *C. funeraria* and *C. moesta*, ranges from Alaska to high altitudes in Arizona and eastward in the north to Nova Scotia (Fig. 47).

This bee is in flight at least from April 17 (Arizona) and June 5 (Yukon Territory) to September 8 (Alberta).

HABITAT. *Coelioxys sodalis* has been collected mainly from areas classified as coniferous forests, although it does range down into sagebrush steppe *(Artemisia, Agropyron)* in the northwestern United States. In Canada it has been collected in the ecotone between tundra and coniferous forest, in the boreal forest, in the coastal or moist coniferous forest, and in coniferous and deciduous forest combinations in the east. In the Southwest, *C. sodalis* is associated with various coniferous forests dominated mainly by pine *(Pinus)*.

GEOGRAPHIC VARIATION. Specimens of *Coelioxys sodalis* from the southern part of its range tend to have more distinct setal fasciae. In addition, the foveal area on the second metasomal tergum of males tends to be more closely punctured and very slightly and broadly sunken in males from the Southwest. Western specimens closely resemble specimens of the Old World *Coelioxys quadridentata* in that western specimens of *C. sodalis* are more coarsely punctured.

COMPARATIVE COMMENTS. *Coelioxys sodalis* is a fairly large, dark bee which resembles *C. funeraria* and dark specimens of *C. rufitarsis*. Females of *C. sodalis* differ from the latter two species by the unnotched sixth metasomal sternum. Males of *C. sodalis* differ from *C. funeraria* and *C. rufitarsis* by the lack of a distinct fovea on the second metasomal tergum.

Coelioxys hirsutissima Cockerell

Figures 46E, 48

Coelioxys hirsutissima Cockerell, 1912, Can. Entomol. 44:168-169 (♂, California, key, type in the American Museum of Natural History).

FEMALE. Agrees with description and figures of *Coelioxys sodalis* except as follows: (1) Length 9-12 mm; (2) integument black; antenna, venter of metasoma black to piceous; mandible piceous to rufous; legs, tegula, subapical portion of 6th tergum piceous to ferruginous; (3) pubescence white, white to pale ochreous on mesosoma, golden on tarsi; (4) ocular hairs medium length (about 0.8 mm); (5) clypeus visible to almost hidden by short, appressed setae; slightly convex, margin with 3-5 small denticles; (14) hypostomal area of gena with setae shorter than those on rest of gena; (16) scutum closely punctured anteriorly and laterally, rest moderately to closely punctured; erect setae inconspicuous, about 0.2 mm long; (20) some metanotal setae appressed medially; (22) terga 1-5 with apical fasciae as or less conspicuous than shown in Figure 21; (23) sternum 6 with portion distal to constriction 2/3-1/2 as long as shown in Figure 45E.

MALE. Agrees with description and figures of *Coelioxys sodalis* except as follows: (24) Length 8-10 mm; (25) integument as in female (2 above); (28) clypeus hidden by setae about 0.45 mm long, margin as in female (5 above); (30) paraocular area hidden by setae up to 0.45 mm long; (31) rest of face almost hidden by setae up to 0.45 mm long; (35) vertex moderately punctured; (37) excavation of hypostomal area of gena covered anteriorly or completely by setae shorter than those on gena; (39) scutum as in female (16 above); (40) lateral surface of mesepisternum with setae about 0.35 mm long; (45) terga 1-5 with fasciae as in female (22 above); (47) margin of sternum 4, sternum 5 as in Fig. 26B; sternum 6 as in Fig. 46B, apical margin rounder (as in Fig. 46F); gonocoxites blunter than shown in Fig. 46D, gonobase simple (Fig. 46E).

DISTRIBUTION AND SEASON OF FLIGHT. This bee ranges from northern California southeastward into Texas (Fig. 48) and is in flight at least from March 15 (Texas) to July 16 (California).

HABITAT. *Coelioxys hirsutissima* ranges from areas classified as mixed coniferous forest *(Abies, Pinus, Pseudotsuga)*, red fir forest *(Abies)*, and oak-juniper woodland *(Quercus, Juniperus)* to areas classified as chaparral *(Adenostoma, Arctostaphyllos, Ceanothus)*, and coastal sagebrush *(Salvia, Eriogonum)* and into areas classified as California steppe *(Stipa)*, creosote bush-bur sage *(Larrea, Franseria)*, grama-tobosa prairie and shrubsteppe *(Bouteloua, Hilaria, Larrea)*, sagebush steppe *(Artemisia, Agropyron)*, and trans-Pecos shrub savana *(Flourensia, Larrea*, also with *Juniperus*).

COMPARATIVE COMMENTS. *Coelioxys hirsutissima* resembles *C. sodalis* and *C. immaculata* closely, but females differ from *C. sodalis* by shorter ocular hairs and brighter coloration of the legs and from *C. immaculata* by the flat or

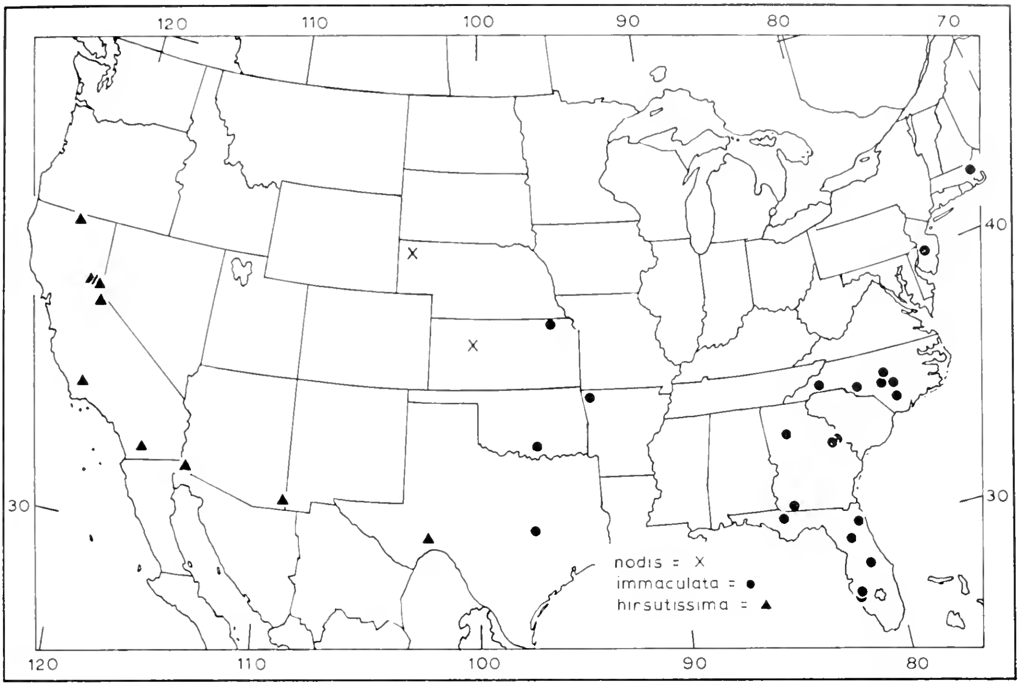

FIGURE 48. Distributions of *Coelioxys hirsutissima* (△), *C. immaculata* (o), and *C. nodis* (X).

slightly rounded clypeus (slightly raised in *C. immaculata*). Males of *C. hirsutissima* differ from males of *C. sodalis* by shorter ocular hairs and brighter coloration of the legs and from males of *immaculata* by pubescence on the excavation of the hypostomal area of the gena (almost bare in *C. immaculata*).

Coelioxys immaculata Cockerell
Figures 45D, I, 46F-G, 48

Coelioxys immaculata Cockerell, 1912, Can. Entomol. 44:165 (♂, Indiana, type in the American Museum of Natural History).

Coelioxys sculptifrons Crawford, 1914, Ann. Entomol. Soc. Amer. 7:153 (♀, New York, type # 18220 in the National Museum of Natural History); Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:210 (= *C. immaculata*).

FEMALE. Agrees with description and figures of *Coelioxys sodalis* except as follows: (1) Length 10-13 mm; (2) integument black; antenna black to rufous; legs piceous to ferruginous apically; tegula ferrruginous; (4) ocular hairs medium (about 0.08 mm long); (5) clypeus as in *C. sodalis* to bare, shining; raised, medioapically flat or slightly depressed; margin with 5 small denticles; (9) clypeoantennal distance slightly greater than antennocular distance, less than interantennal distance; (10) ocellar area moderately to closely punctured; (11) interocellar slightly greater than ocelloccipital distance, less than ocellocular distance; (12) vertex moderately punctured; (13) gena with ventral angle less than 90°; (16) scutum closely punctured anteriorly, posteriorly with 2 submedian slightly swollen, sparsely punctured areas; (17) lateral surface of mesepisternum contiguously punctured; erect slender setae about 0.4 mm long; (18) scutellum with posterior margin broadly rounded (Fig. 45D); (23) sternum 6 with portion beyond constriction 2/3 to 1/2 as long as shown in Figure 45E.

MALE. Agrees with description and figures of *Coelioxys sodalis* except as follows: (24) Length 9-11 mm; (25) integument as in female (2 above), venter of metasoma black to piceous; (26) pubescence as in female (3 above); (27) ocular hairs long (about 0.12 mm); (28) clypeus hidden by setae about 0.45 mm long; margin as in female (5 above); (30) paraocular area hidden by setae about 0.45 mm long; (31) rest of face with setae about 0.45 mm long; (32) clypeoantennal, antennocular, interantennal distances as in female (9 above); (33) ocellar area shallowly punctured by large punctures; (37) hypostomal area of gena with posterior portion bare; (39) scutum as in female (16 above), submedian swollen areas moderately punctured; (41) scutellum slightly more rounded posteriorly than shown in Figure 45D; (43) axilla as in Figure 45C; (45) tergum 6 with dorsal spines blunt (Fig. 45I); (47) margin of sternum 4, sternum 5 as in Figure 26B; sternum 6 with thin apical portion broad (Fig. 46F); sternum 8 broad apically (Fig. 46G).

DISTRIBUTION AND SEASON OF FLIGHT. This bee ranges throughout the eastern United States (Fig. 48) and is in flight at least from March 30 (Florida) to July 14 (Massachusetts).

HABITAT. *Coelioxys immaculata* has been collected from areas classified as bluestem prairie (*Andropogon, Panicum, Sorghastrum*) and cross timbers (*Quercus, Andropogon*) in the western portion of its range. Further east it has been taken from areas classified as various deciduous forests such as Appalachian oak forest (*Quercus*), oak-hickory forest (*Carya*), northeastern oak-pine forest (*Pinus*), oak-hickory-pine forest, southern mixed forest (*Fagus, Liquidambar, Magnolia, Pinus, Quercus*), and southern floodplain forest (*Quercus, Nyssa, Taxodium*).

COMPARATIVE COMMENTS. *Coelioxys immaculata* closely resembles *C. sodalis* and *C. hirsutissima* but differs from both by submedial areas of the scutum which are usually conspicuously less closely punctured than the surrounding areas. In females the clypeus is slightly raised and indented medioapically (flat or slightly convex in *C. sodalis* and *C. hirsutissima*).

Coelioxys mitchelli new species

Figures 42B, 43, 46H-I

Coelioxys piercei; Mitchell, 1962, North Carolina Agr. Exp. Sta. Tech. Bull. 152:217 (misidentification).

FEMALE. Agrees with description and figures of *Coelioxys edita* except as follows: (1) Length 9-10 mm; (2) integument black; antenna, legs proximal to tibia piceous; tegula, legs distal to femur, apical margins of sterna 5, 6 piceous to fulvous; (3) pubescence white; white to pale yellow on face, dorsal mesosoma; golden on tarsi; (4) ocular hairs short (about 0.06 mm long); (5) clypeus convex, surface with scattered slender setae 0.05-0.1 mm long; margin with three distinct teeth almost hidden by fringe of slender setae 0.3 mm wide; (7) paraocular area hidden by setae about 0.3 mm long; (8) rest of face visible to hidden; setal length about 0.25 mm around antenna to about 0.09 mm medially; (10) ocellar area closely punctured; (12) vertex moderately punctured (Fig. 42B); (15) mandible resembles Figure 36B; (16) scutum closely punctured medially, contiguously punctured laterally (Fig. 42B); (17) lateral surface of mesepisternum moderately to closely punctured with large punctures; fasciae variable; surface bare to almost hidden by slender setae about 0.3 mm long; (18) scutellum slightly curved posteriorly (Fig. 42B) to broadly rounded; (19) axilla not carinate (Fig. 42B); (21) fore coxal spine about 0.09 mm long, directed anteroventrally; (22) basal fascia of tergum 1 as or more conspicuous than shown in Figure 42B; tergum 2 with foveal area not modified; (23) sterna 1-5 fasciate apically (medially on sternum 1 and fascia complete on sternum 5); sternum 1 medially closely punctured; sternum 6 with lateral margin entire (Fig. 42B).

MALE. Agrees with description and figures of *Coelioxys edita* except as follows: (24) Length 9.5-10 mm; (25) integument as in female (2 above); (26) pubescence as in female (3 above); (27) ocular hairs medium length (0.12 mm); (28) clypeal margin as in female (5 above); (30) paraocular area hidden by setae about 0.45 mm long; (31) rest of face with setae about 0.45 mm long; (32) clypeoantennal distance less than interantennal distance, greater than antennocular distance; (33) ocellar area as in female (10 above); (34) interocellar distance greater than ocelloccipital distance, less than ocellocular distance; (35) vertex as in female (12 above); (37) posterior portion of excavation of hypostomal area of gena almost bare; (38) mandibles as in female (15 above); (39) scutum without fasciae; (40-42) mesepisternum as in female (17-19 above); (43) metanotum with few appressed setae medially; (45) gradular grooves of terga 4-6 with conspicuous fasciae; tergum 6 resembles Figure 39K; (46) fasciae complete on sterna 1-4; (47) margin of sternum 4, sternum 5 as in Figure 19B; sternum 6 as in Figure 26C; sternum 8 as in Figure 46H; genital armature with small projection on gonobase (arrow on Fig. 46I).

DISTRIBUTION AND SEASON OF FLIGHT. *Coelioxys mitchelli* ranges from coast to coast (Fig. 43).

This bee is in flight from at least April 1 (Florida) and April 24 (southern California) to June 22 (Nevada).

HABITAT. In the East, *Coelioxys mitchelli* has been collected in areas classified as oak-hickory-pine (*Quercus, Carya, Pinus*) and southern mixed (*Fagus, Liquidambar, Magnolia, Pinus, Quercus*) forests. In Kansas it was taken from bluestem-grama prairie (*Andropogon, Bouteloua*). Further west *C. mitchelli* was taken from areas classified as sagebrush steppe (*Artemisia, Agropyron*), creosote bush-bur sage (*Larrea, Franseria*), creosote bush, and saltbush-greasewood (*Atriplex, Sarcobatus*) vegetation types.

GEOGRAPHIC VARIATION. Western specimens of *Coelioxys mitchelli* in general have lighter colored tegulae and legs as well as denser, more conspicuous pubescence on the face, lateral surface of the mesepisternum, and metasoma.

COMPARATIVE COMMENTS. *Coelioxys mitchelli* closely resembles *C. mesae* (for this reason the description was compared with *C. edita* rather than *C. sodalis*) but differs by its smaller size, shinier integument, and lesser quantity of appressed setae on the scutum, posterior surface of scutellum, and on the metanotum. Western specimens of *C. mitchelli* possess ferruginous or fulvous tegulae and legs whereas those of *C. mesae* are black or piceous.

TYPES. Holotype female, Raleigh, North Carolina, May 23, 1959 (T. B. Mitchell). Allotype male, Wake Co., N.C., May 22, 1960, on *Oenothera* (T. B. Mitchell), both deposited in the North Carolina State University Museum. Paratypes females, Raleigh, N.C., May 1930, May 19, 1932, May 9, 1935 (T. B. Mitchell), May 23, 1959, May 18, 1922, May 17, 1951, May 25, 1933, last three of *Oenothera*, Wake Co., N.C., May 21, 1960, May 26, 1960; males, 3 from Tallahassee, Florida, April 1, 1944 (R. & G. Bohart), Raleigh, N.C., May 23, 1922, on *Oenothera*

(T. B. Mitchell). Paratypes are deposited in the collections of the North Carolina State University Museum, Utah State University, the National Museum of Natural History, Snow Entomological Museum, University of Kansas, and the Florida State Collection of Arthropods, Division of Plant Industry.

This species is named in honor of Professor emeritus T. B. Mitchell of the North Carolina State University.

Coelioxys sericaudata, new species

Figures 45B, F, H, 46J, 49

FEMALE. Agrees with description and figures of *Coelioxys sodalis* except as follows: (1) Length 10-12 mm; (2) integument black; antenna, legs, tegula, venter of metasoma black to piceous; (3) pubescence white; white to golden on head, mesosoma; golden on tarsi; (4) ocular hairs medium (0.08 mm long); (5) clypeus with slender, inconspicuous setae; strongly convex; closely punctured, shiny; margin with 3-5 denticles (Fig. 45B); (8) ventral portion of rest of face convex; (9) clypeoantennal distance greater than antennocular distance, shorter than interantennal distance; (14) hypostomal area of gena with setae subequal or shorter than those on disc; (15) mandible with hump on outer surface (Fig. 45B); (17) lateral surface of the mesepisternum with slender, prostrate setae up to 0.45 mm long; (18) scutellum similar to Figure 45D; (19) axilla as in Figure 37D; (20) metanotum with setae prostrate medially; (22) terga 1-5 with apical fasciae similar to or more conspicuous than those shown in Figure 21; uniformly, closely punctured with smaller punctures than shown in Figure 21; tergum 6 very closely punctured (Fig. 45F); (23) sterna 1 to basal portion of 5 closely, uniformly punctured; most of sternum 5, 6 very closely punctured; sternum 6 with subapical margin serrate (Fig. 45F, serrations visible in silhouette against light source).

MALE. Agrees with description and figures of *Coelioxys sodalis* except as follows: (24) Length 9-11 mm; (25-26) integument, pubescence as in female (2-3 above); (28) margin of clypeus as in female (5 above); (32) clypeoantennal, antennocular, interantennal distances as in female (9 above); (35) vertex closely punctured; (38) mandible as in female (15 above); (41-42) scutellum, axilla as in female (18-19 above); (45) terga 1-5 with fasciae and punctures as in female (22 above); tergum 6 with dorsal spines curved and sloped medially (Fig. 45H); (47) margin of sternum 4 as in Fig. 39O, lacking longitudinal carinae; sternum 6 with shoulders distinct (Fig. 46J); gonocoxites with setae 2/3 length shown in Fig. 46E.

DISTRIBUTION AND SEASON OF FLIGHT. This bee has been collected from May 5 to July 6 in the Pacific coast states (Fig. 49).

HABITAT. *Coelioxys sericaudata* has been taken from areas classified as mixed conifer forest *(Abies, Pinus, Pseudotsuga)*, lodgepole pine-subalpine forest *(Pinus, Tsuga)*, ponderosa pine shrub forest, and California mixed evergreen forest *(Quercus, Arbutus, Pseudotsuga)*; areas classified as open grassland such as fescue-oatgrass *(Festuca, Danthonia)*, fescue-wheatgrass *(Agropyron)*, California steppe *(Stipa)*, tule marshes *(Scirpus, Typha)*, and alpine meadows and barrens *(Agrostis, Carex, Festuca, Poa)*.

COMPARATIVE COMMENTS. Females of *Coelioxys sericaudata* are slender, dark bees which resemble *C. moesta*, but differ from all other North American *Coelioxys* by the strongly convex clypeus and serrated margin of the sixth metasomal sternum (Fig. 45F). Males of *C. sericaudata* are darker than most *Coelioxys* males and differ from all

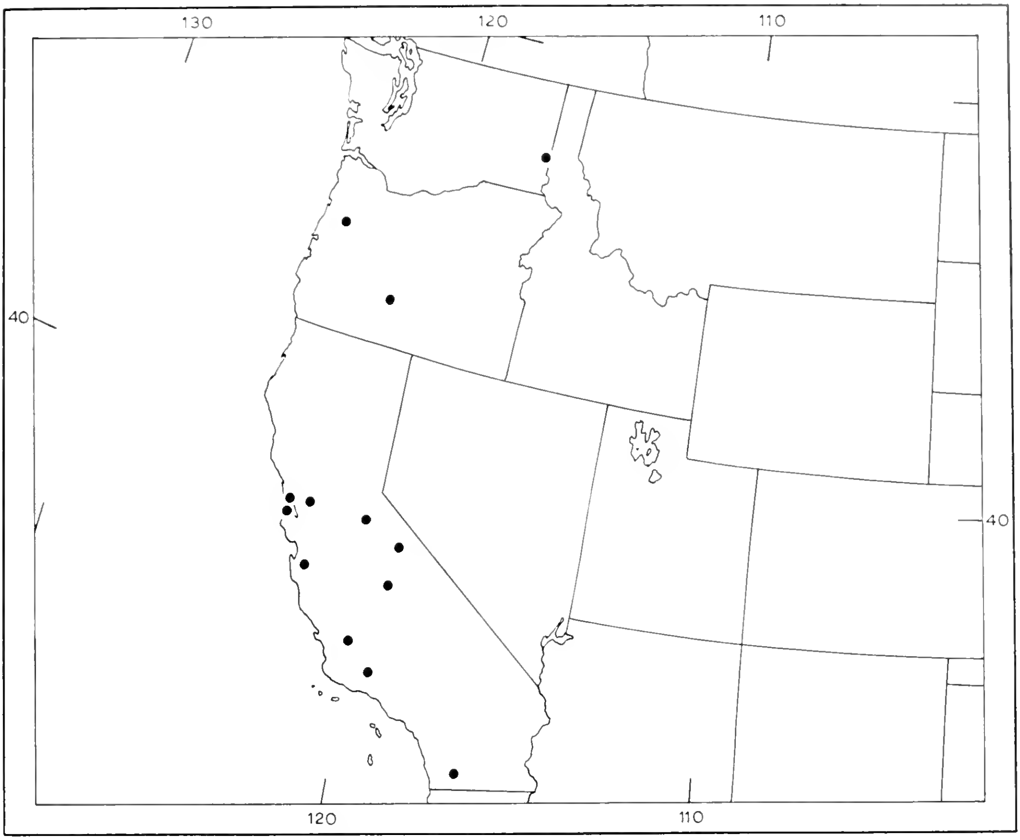

Figure 49. Distribution of *Coelioxys serricaudata.*

other North American *Coelioxys* by the dorsal spines of the sixth metasomal tergum which are strongly curved and sloped medially.

TYPES. Holotype female, Hastings Nat. Hist. Reservation, Santa Lucia Mts., Jamesburg, Monterrey Co., California, 1900-2700 ft., June 12, 1938 (C. D. Michener), deposited in Snow Entomological Museum, the University of Kansas. Paratypes females, one, Prospect, Oregon, June 20, 1924 (C. L. Fox); one, Antelope Mt. L. O., Grant Co., Oregon, El. 6500 ft., August 7, 1941 (M. & R. E. Rieder); one, Corvallis, Oregon, July 1, 1910 (J. C. Bridwell); one, Palouse, Washington, June 26, 1961 (R. W. Dawson); the remaining paratypes are from California; one, Tanbark Flat, Los Angeles Co., June 20, 1956 (R. C. Bechtel); one, Twaine-Harte, Tuolumne Co., 4000 ft., July 1937, *Grindelia* sp. (F. E. Blaisdell); one, Chile Bar, Eldorado Co., July 5, 1948 (C. Chan); Redwood City, San Mateo Co., June 10, 1961 (P. H. Arnaud, Jr.); one, 16 mi. E. Glenville, Kern Co., June 25, 1961 (R. L. Macdonald); one, Mormon Bar, 2 mi. S., Mariposa Co., June 16, 1959 (G. I. Stage); one, Miguel Meadows, Yosemite National Park, Elev. 5200, July 6, 1940 (E. G. Linsley); one, Pine Flat, Tulare Co., June 14, 1961 (G. I. Stage, R. R. Snelling); one, Ryan Creek, Mendocino Co., June 27, 1954, *Godetia amoena* (P. D. Hurd); one, Nipinnawasee, Madera Co., July 4, 1960 (G. I. Stage, R. R. Snelling); one, Santa Margarita, 6 mi. N. E., S. L. Obispo Co., June 22, 1958 (E. G. Linsley); two, Arroyo Seco, Monterey Co., May 2, 1959 (Don Burdock), May 5, 1956 (Dave Ribble); two, California Hot Springs, Tulare Co., June 4, 1934 (E. C. VanDyke), (E. R. Leach); five, Antioch, Contra Costa Co., two, May 6, 1939, one, May 16, 1936 (M. Cazier), one, April 25, 1936 (M. Cazier), one, June 23, 1957 (G. I. Stage). Paratypes are in collections of the California Academy of Sciences; the University of California at Berkeley and Davis; the Los Angeles County Museum; the National Natural History Museum; San Jose State College; Utah State University; G. I. Stage, the University of Connecticut; and P. H. Timberlake, the University of California, Riverside.

The specific name refers to the serrate margin of the apical sternum of the female.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

PARASITID MITES ASSOCIATED WITH BUMBLEBEES IN ALBERTA, CANADA (ACARINA: PARASITIDAE; HYMENOPTERA: APIDAE). I. TAXONOMY

By

LYNN A. RICHARDS

Vol. 50, No. 13, pp. 731-773 February 4, 1976

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

Vol. 50, No. 13, pp. 731-773 February 4, 1976

Parasitid Mites Associated with Bumblebees in Alberta, Canada (Acarina: Parasitidae; Hymenoptera: Apidae). I. Taxonomy[1]

Lynn A. Richards

TABLE OF CONTENTS

ABSTRACT

Four new species of mites in the Genus *Parasitus*, found associated with bumblebees of the Genus *Bombus* in Alberta, Canada, are described. They are: *Parasitus hobbsi; P. favus; P. inquilinobombus; P. perthecatus.* For each of these new species the deutonymph, female and male are described and for *P. perthecatus* the protonymph and larva, also. A fifth species *P. fimetorum* Berlese, 1903, found in nests of bumblebees of the Genus *Bombus* in Alberta, Canada, is also briefly discussed.

INTRODUCTION

The purpose of this study is to describe new species of mites of the Genus *Parasitus* found with the Canadian bumblebees of the Genus *Bombus,* species listed below. Field work was done in southwestern Alberta, Canada, from May 26 through August 25, 1970, and April 25 through August 25, 1971, on the east side of Prairie Bluff Mountain, 49° 20′ N, 114° 06′ W, at about 5200 feet elevation. The biology of these new species of *Parasitus* is to be reported in Richards and Richards (in press).

Previous work on *Parasitus* associated

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[1] Contribution number 1529, Department of Entomology, University of Kansas, Lawrence, Kansas, 66045.

with *Bombus* has mainly been taxonomic: Oudemans (1902, 1903, 1904, 1905, 1906), Berlese (1903, 1905), Trägardh (1904, 1910, 1912), Vitzthum (1930), Willmann (1939), Schweizer (1949), Karg (1965), Holzmann (1969), and Micherdzinski (1969).

Bumblebees of the following species of *Bombus* and *Psithyrus* were encountered in the study area: *B. appositus* Cresson; *B. bifarius nearcticus* Handlirsch; *B. californicus* F. Smith; *B. centralis* Cresson; *B. flavifrons* Cresson; *B. frigidus* F. Smith; *B. huntii* Greene; *B. melanopygus* Nylander; *B. mixtus* Cresson; *B. nevadensis* Cockerell; *B. occidentalis* Greene; *B. rufocinctus* Cresson; *B. ternarius* Say; *B. terricola* Kirby; *B. vagans* F. Smith; *P. insularis* (F. Smith); *P. suckleyi* (Greene); and *P. fernaldae* Franklin.

METHODS AND MATERIALS

Mites were mounted and cleared in Hoyer's solution. Measurements in millimeters were taken from the specimens used in figures, employing an ocular micrometer. The measurements given are maximal lengths and widths. No attempt was made to measure more specimens because the measurements have only general value. Differences in size are often caused by handling (i.e., pressure applied to the cover slip; amount of medium used; time between collecting and preserving) and by the condition of each mite at the time it was collected (e.g., starved, engorged). When males or females are referred to in the text it can be assumed that they are adults. Nomenclature for setae follows Hirschmann (1957).

DESCRIPTIONS OF SPECIES

Mites in the family Parasitidae are heavily sclerotized, with the dorsal shield entire or divided into two plates. The palpal tarsus has a three-pronged seta. The female has a triangular genital shield with its anterior apex flanked by large metasternal plates. The male has a large apophysis on leg II, and the spermatophoral process on the moveable digit of the chelicera is fused to the distal area of the digit.

Genus *Parasitus* Latreille, 1795

Both sexes have divided dorsal shields, generally with 21 to 24 pairs of setae on the propodosoma and 20 to 70 pairs on the hysterosoma. Dorsal chaetotaxy of the propodosomal shield in larvae resembles that of *Pergamasus* Berlese, 1903, with nine pairs of setae. Larval hysterosoma have eight pairs of setae (Micherdzinski 1969). Protonymphs resemble those of *Pergamasus*. Micherdzinski (1969) found 14 propodosomal setae and 15 hysterosomal setae on protonymphs of *Parasitus kraepelini* Berlese. Sellnick (1938) and Karg (1969) record more setae for *Parasitus immanus* Berlese and *P. remberti* Oudemans than are noted in previous protonymphal descriptions. Dorsal chaetotaxy of deutonymphs is similar to that of adults.

The epigynum of females in many species is not clearly separated from the ventro-anal shield. The vaginal sclerite is either heavily sclerotized or present as a weakly defined element. The male genital opening is set far back from the sternal shield. The gnathosoma of males is sometimes modified, with cleft corniculi and nontypical rows of deuterosternal teeth. The *digitus mobilus* of female chelicera have one to three teeth, seldom four; of the male, zero to four teeth, seldom three. The anal shield of the larva has three setae (i.e., an adanal pair and a long postanal hair). There are three pairs of sternal setae, four pairs of setae between coxa III. An anal shield is present; stigma and paratreme, absent. The protonymph has three pairs of sternal setae, two lyrifissures, one pair of genital setae, five pairs of opistogastral setae, and three anal setae. A stigma and short paratremes are present, but the anal shield and paratremal shields are not always clearly defined. Deutonymphs have pre-endopodal shields and a distinct sternal shield with four pairs of setae and three lyrifissures.

Legs II and III are shorter than I and IV; legs II are usually thicker than I, III, or IV. Tarsus I of most deutonymphs is divided (distinguishing this genus from other genera in the family, except *Poechlochirus*).

Parasitus hobbsi, new species

DEUTONYMPH (Fig. 1): Idiosomal length 0.78 mm, width 0.62 mm. Propodosoma with 21 pairs of pilose setae; m 5 and i 2 longer; m 1, 2, and 3 shorter than other setae on propodosomal shield. Hysterosomal shield rounded posteriorly. Sculpturing on dorsal shields netlike.

Pre-endopodal shield rectangular, 0.03 mm long, 0.01 mm wide. Front border of sternal shield distinct, sclerotization heavier behind first pair of pores. Sternal setae smooth. Sculpturing of shield, netlike polygons. Metapodal shields comma-shaped, with truncate ends; 0.05 mm long.

Tectum (Fig. 2C) three pointed, middle point broad, blunt, all about same length. Chelicera (Fig. 2B): *Digitus mobilus* with three large teeth; *digitus fixtus* with three large and two small teeth.

Length of leg I, 1.04 mm; II, 0.80 mm; III, 0.80 mm; IV, 1.17 mm. Leg II (Fig. 2D) setae pilose; leg IV (Fig. 2E) setae sparsely pilose or smooth, longer than setae of leg II; tarsus IV pd 2 longest setae on entire leg.

FEMALE (Fig. 3): Idiosomal length 1.16 mm, width 0.83 mm. Propodosomal shield wider than long, with 21 pairs of setae; all setae pilose except m 1, 2, and 3; m 5 longer than other setae; m 1, 2, and 3 shorter than 4. Hysterosomal shield and propodosomal shield separate. Hysterosomal shield shorter than propodosomal shield, semicircular. All hysterosomal setae about the same length, pilose. Sculpturing of dorsal shield, netlike. Peripheral lines of propodosomal shield form netlike pattern, becoming closer together, following edge of plate; lines indistinct nearer center.

First pair of sternal setae borne off heavily sclerotized part of sternal shield. All ventral setae pilose, except five pairs of short setae and adanal setae. Ventro-anal plate, V-shaped and fused with paratremal shield, has polygonal netlike sculpturing. Metasternal shield and anterior halves of ventro-anal shield have netlike sculpturing.

Gnathosoma (Fig. 4B) has 11 rows of deuterosternal teeth. Tectum (Fig. 4A) three-pointed, the middle point longest. G 1 smooth, G 2, 3, and 4 pilose. Chelicera (Fig. 4C): *Digitus mobilus* has three teeth in upper half, two more apical about the same size, third larger; *digitus fixtus* has four teeth, the middle two larger.

Length of leg I, 1.35 mm; II, 1.01 mm; III, 1.04 mm; IV, 1.54 mm (Fig. 5B, C). Setae pilose; leg II (Fig. 5A) setae needlelike, except tarsus av 1 and pv 1, which are short and thornlike; setae on tarsus longer than other leg setae, especially pd 2, except al 1 and pl 1 which are short and needlelike.

MALE (Fig. 6): Idiosomal length 1.11 mm, width 0.80 mm. Twenty-two pairs of setae on propodosomal shield, all pilose except m 1, 2, and 3; m 5 longer than other setae; m 1, 2, and 3 shorter than 4. Line dividing propodosomal shield from hysterosomal shield extends to body margins. All hysterosomal setae pilose. Dorsal sculpturing like that of female.

Ventral setae pilose. Tritosternum, base about ⅓ the total length, with lacinia pile long. Sculpturing over entire sclerotized ventral area has a polygonal netlike pattern.

Gnathosoma (Fig. 7E) has 11 rows of deuterosternal teeth. Tectum (Fig. 7D) varies, has one to three points; only G4 pilose. Chelicera (Fig. 2A): *Digitus mobilus* curved apically, with one tooth; *digitus fixtus* curved apically, with two teeth; cheliceral brush not stalked.

Length of leg I, 1.35 mm; II, 1.04 mm; III, 0.98 mm; IV, 1.43 mm. Apophysis on femur II well developed, axillary process rounded. Genu and tibia II have smaller, rounded apophyses. Leg setae mostly smooth, some sparsely pilose. Leg II (Fig. 7C) and IV (Fig. 7A, B), setae needlelike; tarsus IV, setae longer, especially pd 2.

P. hobbsi resembles *P. traegardhi* (Micherdzinski, 1969) (= *bombophilus* Vitzthum, 1930), but differs in the following ways: The female hysterosomal shield is shorter than the propodosomal shield. The dorsal hysterosomal setae are the same length throughout: they are not longer posteriorly as they are in *P. traegardhi*. The male of *P. hobbsi* is similar to the male of *P. traegardhi*, but *P. hobbsi* has pilose setae, whereas *P. traegardhi* has smooth setae. The setae on and off the hysterosomal shield of the deutonymph are about the same length, with lateral setae being somewhat shorter, whereas in *P. traegardhi* the setae off the shield are shorter.

Adult mites are found in *Bombus* nests; deutonymphs in nests and on adult bumblebees.

TYPES: Holotype of the deutonymph collected 9 August 1970, at Prairie Bluff Mountain, Alberta, Canada (49° 20′ N, 114° 06′ W), 5200 feet, from *Bombus bifarius* nest; collector L. A. Richards. Specimen located in Canadian National Collection (CNC) no. 13187. Morphotype of the male collected 9 August 1970, and of the female collected 7 August 1971, both from *B. occidentalis* nests; same locality and collector as the holotype; both specimens in CNC. Paratypes, all from same locality as holotype. Eighteen deutonymphs: Five collected 11 August 1971, from *B. occidentalis* nest; three 20 August 1971, from *B. occidentalis* nest; two 14 August 1970, from *B. californicus* nest; one 9 August 1971, from *B. bifarius* nest; one 14 August 1971, from *B. bifarius* nest; one 8 August 1970, from *B. bifarius* nest; one 17 July 1970, from *B. occidentalis* nest; one 18 July 1970, from *B. huntii* queen; one 8 July 1971, from *B. figidus* nest; one 9 June 1970, from *B. huntii* queen; and one 19 August 1970, from *B. californicus* nest. Twelve females: Three collected 11 August 1971, from *B. occidentalis* nest; three 20 August 1971, from *B. occidentalis* nest; two 11 August 1971, from *Bombus* nest; one 14 August 1971, from *B. bifarius* nest; one 22 August 1971, from *Bombus* nest; two 14 August 1970, from *B. californicus* nest and *Bombus* sp. nest. Fourteen males: Five collected 20 August 1971, from *B. occidentalis* nest; four 11 August 1971, from *B. occidentalis* nest; one 9 August 1971, from *B. bifarius* nest; one 9 August 1970, from *B. frigidus* nest; one 22 August 1970, from *B. mixtus* nest; one 2 August 1970, from *B. frigidus* nest; and one 22 August 1971, from *Bombus* nest. Five deutonymphs, three females and four males, are deposited in the CNC. Four deutonymphs, three females and three males, are deposited in the British Museum (Natural History) (BMNH). Four deutonymphs, three females and three males, are deposited in the United States National Museum (USNM). Five deutonymphs, three females and four males, are deposited at the University of Kansas.

The species was named in honor of Dr. Gordon A. Hobbs for his help and encouragement with this project.

Parasitus favus, new species

DEUTONYMPH (Fig. 8): Idiosomal length 0.77 mm, width 0.59 mm. Propodosomal and hysterosomal shields have scalelike surface; m 5 and i 2 longer than other setae; m 5 and d 1 pilose. All hysterosomal setae smooth and needlelike. Setae off the shield about the same length as the short setae on the shield.

Pre-endopodal shields triangular. Front borders of sternal shield indistinct, heavily sclerotized part beginning at first pair of pores. First pair of sternal setae pilose, second pair with scarce pile or none, all others smooth. Metapodal shields oval, 0.03 mm long.

Tectum (Fig. 9B) three-pointed, middle point longer and wider than others. Chelicera (Fig. 9A): *Digitus mobilus* has three teeth, two in upper half of digit about $\frac{1}{3}$ size of third tooth in middle of digit; *digitus fixtus* has four teeth, all similar in size.

Length of leg I, 0.83 mm; II, 0.68 mm; III, 0.68 mm; IV, 0.98 mm. Leg II (Fig. 9C), setae needlelike, except av 1 and pv 1 of tarsi, which are thornlike. All setae about same length, pilose. Leg IV (Fig. 9D), setae needlelike, pilose, al 3, pd 3, and av 2 very long. All coxal setae pilose.

FEMALE (Fig. 10): Idiosomal length 1.29 mm, width 0.88 mm. Propodosomal shield has 21 pairs of setae; m 5 and i 2 longer than other setae on shield; m 1, 2, and 3 shorter, than 4. Setae sparsely pilose. Propodosomal shield wider than long; separated from hysterosomal shield by a slightly concave line. Propodosomal shield wider than hysterosomal shield, about the same length. Dorsal sculpturing, netlike. Hysterosomal shield as wide as long, triangular. Setae on hysterosoma all about same length, most smooth; some on membranous portion of dorsum, pilose.

Ventro-anal shield fused with paratremal shield, rounded posteriorly, pointed posterior to anus, has nestlike sculpturing. Ventral setae, moderately to sparsely pilose.

Gnathosoma (Fig. 11A) has 10 rows of deutosternal teeth. Tectum (Fig. 11B) has three points, middle one larger and wider than lateral ones. G 1, 2 smooth, G 3, 4 pilose. Chelicera (Fig. 12C): Each digit with three teeth set wide apart.

Length of leg I, 0.98 mm; II, 0.83 mm; III, 0.80 mm; IV, 1.12 mm. Setae thick; pd 2 of genu II (Fig. 12B) longer than other setae; av 1 and pv 1 of tarsi II, III, IV thornlike, other tarsal setae longer than setae on rest of leg. Tibia and trochanter pv 1 thicker than other setae of these segments. Leg IV (Fig. 12A) setae needlelike, ad 3 and pd 2 of tarsus IV very long.

MALE (Fig. 13): Idiosomal length 0.98 mm, width 0.68 mm. Propodosomal shield has 22 pairs of setae, all smooth; m 5 and i 2 longer than other setae. Hysterosomal and propodosomal shield divided by a concave line. Dorsal sculpturing similar to that of female. Hysterosoma polytrichous; setae smooth.

Tritosternum slender, base about same length as lacinia. First pair of sternal setae borne off heavily sclerotized portion of sternal shield. First pair of sternal setae pilose. Ventro-anal and sternal shields have netlike sculpturing.

Gnathosoma (Fig. 11C) has nine rows of deuterosternal teeth. Tectum (Fig. 11D) has one large, rounded point. G 1, 2, and 3 smooth, G 4 pilose. Chelicera (Fig. 14C): *Digitus mobilus* $\frac{4}{5}$ the length of the *digitus fixtus*, curved apically, with one tooth; *digitus fixtus* slender, with three widely spaced teeth, cheliceral brush on a short stalk.

Length of leg I, 0.98 mm; II, 0.80 mm (Fig. 14B); III, 0.74 mm; IV, 1.04 mm (Fig. 14A). Femur II has well-developed apophysis on ventral side. Genu and tibia II also have small rounded apophyses, tarsal setae longer except av 1 and pv 1 which are thornlike, pd 2 of tarsus very long.

P. favus appears to be closely related to *P. numismaticus* Vitzthum 1930, according to the description by Micherdzinski (1969). The description of the dorsum of *P. numismaticus* by Vitzthum (1930) differs from that by Micherdzinski (1969) as having smooth, dorsal setae which are shorter towards the posterior. The ventral surface of the female of *favus* is similar to that of *P. numismaticus* except that areas of small circles on sternal plate are absent and the epigenial shield has a broad elliptical apex (in *P. numismaticus* it is narrow). The paragynial shield is like that of *P. numismaticus*, but the setae are smooth. In *P. numismaticus* only G 4 is pilose, but in *P. favus* both G 3 and 4 are pilose. *P. favus* females have 10 rows of deuterosternal teeth compared to 11 in females of *P. numismaticus*.

Adults of *P. favus* are found in the nests of *Bombus;* deutonymphs occur both in the nests and on adult bumblebees. These mites were the most common *Parasitus* in the studied area.

TYPES: Holotype of the deutonymph collected 9 May 1971, at Prairie Bluff Mountain, Alberta, Canada (49° 20′ N, 114° 06′ W), 5200 feet, from a *Bombus bifarius* queen: collector L. A. Richards. Located in CNC, no. 13188. Morphotypes of male and female collected 30 May 1970, and 15 June 1970, respectively, from a *B. frigidus* nest at the same locality as holotype, collector L. A. Richards; specimens located in CNC. Paratypes, all collected from same locality as the holotype. Twenty-three deutonymphs: Three collected on 18 August 1970, from *B. bifarius* nest; three 5 June 1970, from *P. insularis* queen; two 18 August 1970, from *B. bifarius* nest; two 19 May 1971, from *B. occidentalis* queen; one 3 August 1970, from *B. frigidus* nest; one 29 May 1971, from *B. rufocintus* queen; one 28 May 1970, from *B. frigidus* queen; one 28 May 1970, from *B. occidentalis* queen; one 4 June 1970, from *B. melanopygus* queen; one 3 August 1970, from *B. occidentalis* nest; one 6 August 1970, from *B. flavifrons* nest; one 28 July 1971, from *B. rufocinctus* queen; one 16 June 1971, from *B. nevadensis* queen; one 3 June 1971, from *B. rufocinctus* queen; one 16 May 1971, from *P. suckleyi* female; one 11 August 1970, from *B. flavifrons* nest; and one 16 May 1971, from *B. frigidus* queen. Twelve males: Four collected 20 August 1971, from *B. occidentalis* nest; two 14 August 1971, from *B. bifarius* nest; two 9 August 1970, from *B. occidentalis* nest; one 2 August 1970, from *B. frigidus* nest; one 6 August 1970, from *B. californicus* nest; one 14 August 1971, from *B. vagans* nest; and one 28 July 1970, from *B. mixtus* nest. Fourteen females: Three collected 11 August 1971, from *B. occidentalis* nest; two 14 August 1971, from *B. bifarius* nest; one 9 August 1970, from *B. occidentalis* nest; one 30 June 1971, from *B. huntii* nest; one 30 June 1970, from *B. bifarius* nest; one 8 August 1970, from *B. bifarius* nest; one 14 August 1971, from *B. vagans* nest; one 9 August 1971, from *B. frigidus* nest; one 28 July 1971, from *B. bifarius* nest; one 30 July 1971, from *B. huntii* nest; and one 20 August 1971, from *B. occidentalis* nest. Six deutonymphs, four females and three males; located in CNC. Six deutonymphs, three females and three males; in the BMNH. Five deutonymphs, three females and three males; in the USNM. Six deutonymphs, four females, and three males; at the University of Kansas.

The specific name, *favus* (i.e., honeycombed) refers to the honeycomb pattern on the sclerotized areas.

Parasitus inquilinobombus, new species

DEUTONYMPH (Fig. 15A, B): Idiosomal length 0.62 mm, width 0.40 mm. All propodosomal setae smooth; m 5 longer than other setae; l 4, l 5, d 3, and i 2 also long; m 1, 2, 3 and 4 short. Hysterosomal shield semicircular, polytrichous, setae smooth. Dorsal sculpturing, netlike.

Pre-endopodal shields 0.02 mm long, teardrop-shaped. Sternal shield lacks distinct front border; has heavily sclerotized area of netlike sculpturing which begins at first pair of pores. All sternal setae smooth. Metapodal shields sac-shaped, have two anterior projections: one short and round, the other long, tail-like, curving back, about ⅓ the length of the shield from its anterior extremity. Shield 0.03 mm long, 0.15 mm wide.

Tectum three-pointed, middle point twice as long as wide. Chelicera: *Digitus mobilus* has three teeth in apical half, all about same size; *digitus fixtus* has four teeth, three in apical half, fourth in distal half, all about same size.

Length of leg I, 0.63 mm; II, 0.58 mm; III, 0.52 mm; IV, 0.74 mm (Fig. 16A). Most leg-setae slightly pilose, some smooth. Genu II pd 2 longer than other setae. Leg II (Fig. 16B) with most tarsal setae thick, av 1 thornlike. No division of tarsus I.

FEMALE (Fig. 17): Idiosomal length 0.94 mm, width 0.68 mm. Propodosomal shield has 24 pairs of setae. Setae smooth and needlelike; m 5 longer than other setae on propodosoma; m 1, 2, and 3 shorter than 4. Other setae of equal length. Propodosomal shield wider than long, larger than hysterosomal shield. Dorsal sculpturing netlike; shield lines forming pattern near the edges follow the edges and become closer. Hysterosomal shield wider than long, rounded posteriorly.

Sternal shield has netlike, polygonal sculpturing, beginning at first pair of pores. First two pairs of sternal setae pilose, all other ventral setae smooth. Ventro-anal plate v-shaped, covered by a netlike pattern, fused with paratremal shield.

Gnathosoma (Fig. 18D) with 11 rows of deuterosternal teeth. Tectum (Fig. 18C) with three points, middle point largest. G 1, 2, and 3 smooth, G 4 pilose. Chelicera (Fig. 19C, D): *Digitus mobilus* with three teeth, two evenly spaced in the upper half and about half the size of the third tooth in the lower half; *digitus fixtus*, with four teeth, successively smaller from the most proximal to the most distal tooth.

Length of leg I, 0.77 mm; II, 0.62 mm; III, 0.57 mm; IV, 0.89 mm. Tarsus II (Fig. 19A) av 1, pv 1 heavy thornlike setae, other setae also thick, most smooth. Tarsus IV (Fig. 19B), setae longer than other leg IV setae, pd 2 very long; av 1 and pv 1 of tibia and genu IV longer and thicker than other setae of tibia and genu IV.

MALE (Fig. 20): Idiosomal length 0.83 mm, width 0.59 mm. Propodosomal shield has 24 pairs of setae, all smooth; m 5 and i 2 longest; m 1, 2, and 3 shorter than 4. Line dividing propodosomal shield and hysterosomal shield not extended to body margins. Hysterosoma polytrichous, setae all smooth and the same length. Dorsal sculpturing like that of female.

Tritosternum stout, base about ¼ the total length. First pair of sternal setae anterior to distinct part of sternum. Netlike sculpturing of sternum extending to coxa IV. All ventral setae smooth.

Gnathosoma (Fig. 18B) has 11 rows of deuterosternal teeth. G 1, 2, and 3 smooth, G 4 pilose. Tectum (Fig. 18A) has a single point, with row of teeth on middle third of the edge of point. Chelicera (Fig. 21A): *Digitus mobilus* curved and pointed apically, with one tooth; *digitus fixtus* slender, also curved apically and with one tooth; cheliceral brush on long stalk with few bristles.

Length of leg I, 0.98 mm; II, 0.62 mm; III, 0.55 mm; IV, 0.83 mm. Femur II has well developed apophysis, rounded apically, axillary process pointed apically. Genu and tibia II have smaller apophyses. Genual apophysis is round, tibial apophysis longer and rounded apically (Fig. 21D). Coxal setae smooth or scarcely pilose. Leg setae smooth and needlelike. Tarsus II, III, IV, av 1, and pv 1 thornlike, mv, pl 3, al 3, pv 2, and al 2 thicker than other tarsal setae. Most setae of tarsus IV (Fig. 21B) thicker and longer than other leg IV setae (Fig. 21C). Genu and tibia IV with av 1, pv 1, thicker than other genal and tibial setae.

This mite is distinguished by its small size when compared to other *Parasitus* collected from bumblebees at Prairie Bluff Mountain. The deutonymphs are about the same size as those of *P. crinitus* Oudemans, 1903, and *P. crinitosimilis* Vitzthum, 1930. *P. inquilinobombus* differs from *P. crinitus* by the lack of short setae between the long ones on the hysterosomal shield (Vitzthum 1930), and from *P. crinitosimilis* by having shorter setae posteriorly. The deutonymph of *P. inquilinobombus* differs from that of other *Parasitus* species by the lack of the division of tarsus I.

Adults of this mite are found in *Bombus* nests; deutonymphs occur both in nests and on adult bumblebees.

TYPES: Holotype of the deutonymph collected 18 August 1970, at Prairie Bluff Mountain, Alberta, Canada (49° 20′ N, 114° 06′ W), at 5200 feet, from *B. bifarius* nest; collector L. A. Richards. Specimen located in CNC, no. 13189. Morphotypes: Male collected 11 July 1970, from *B. frigidus* nest; female collected 12 August 1970, from *B. occidentalis* nest; both from same locality as holotype; collector L. A. Richards, both specimens in CNC. Paratypes, all from same locality as holotype. Sixteen deutonymphs: Thirteen collected 11 August 1971, from *B. occidentalis* nest; one 18 August 1971, from *B. bifarius* nest; one 9 August 1971, from *B. bifarius* nest; and one 14 August 1971, from *B. bifarius* nest. Fourteen males: Five 11 August 1971, from *B. occidentalis* nest; two 11 August 1971, from *Bombus* nest; one 11 July 1970, *B. frigidus* nest; one 9 August 1971, from *B. bifarius* nest; one 22 July 1970, from *B. occidentalis* nest; one 3 August 1970, from *B. frigidus* nest; one 14 August 1970, from *B. californicus* nest; one 31 July 1970, from *B. mixtus* nest; and one 9 August 1970, from *B. frigidus* nest. Fifteen females: Five 11 August 1971, from *Bombus* nest; four 8 August 1970, from *B. bifarius* nest; three 11 August 1971, from *B. occidentalis* nest; one 2 August 1970, from *B. appositus* nest; one 9 August 1971, from *B. bifarius* nest; and one 3 August 1970, from *B. frigidus* nest. Four deutonymphs, four females and four males, in the CNC. Four deutonymphs, three females and three males, in the USNM. Four deutonymphs, four females, three males, in BMNH. Four deutonymphs, four females, and four males at the University of Kansas.

The speces is named for its habitat, the *Bombus* nest.

Parasitus perthecatus, new species

DEUTONYMPH (Fig. 22): Idiosomal length 1.04 mm, width 0.74 mm. Propodosomal shield has 22 pairs of setae, all pilose and needlelike; m 5 longer, m 1, 2, 3, and 4 shorter than other propodosomal setae. Hysterosomal shield, triangular. Setae off hysterosomal shield shorter than those on shield, pilose. Dorsal sculpturing netlike, similar to that of female. Pre-endopodal shields, triangular, 0.03 mm long and 0.05 mm wide. Sternal shield has distinct front border. All ventral setae pilose. Sternal shield has netlike polygonal sculpturing. Metapodal shields, oval to pear-shaped, 0.33 mm long, 0.02 mm wide.

Tectum (Fig. 24A) has three points, middle one largest and rounded apically. Chelicera (Fig. 24F): Both digits slender; *Digitus mobilus* has three teeth in upper half; *digitus fixtus* has four teeth, apical one smaller.

Length of leg I, 1.11 mm; II, 0.80 mm (Fig. 23A); III, 0.86 mm; IV, 1.26 mm (Fig. 23B, C). Setae pilose. Tarsus IV with ad 3, pd 2, very long.

FEMALE (Fig. 25): Idiosomal length 1.48 mm, width 1.04 mm. Twenty-two to twenty-three pairs of setae on propodosomal shield; m 5 longer than other setae, all dorsal setae pilose, l 2, d 4, and i 2, spatulate. Propodosomal shield smaller than hysterosomal shield. Hysterosomal shield covers entire hysterosoma. Hysterosoma polytrichous.

First pair of sternal setae arise off heavily sclerotized portion of sternal shield. First two pairs of sternal setae and genital setae, pilose. Anterior half of ventro-anal shield has smooth setae, other ventral setae pilose. Ventro-anal shield v-shaped. Setae on posterior half of ventral surface broader towards tip, similar to l 2, d 4, and i 2 of propodosomal shield. Surface of sternal shield has netlike sculpturing which continues through epigynium, with smaller polygons anteriorly. Ventro-anal shield has netlike pattern.

Gnathosoma (Fig. 26A) has 11 rows of deuterosternal teeth. Tectum (Fig. 24B) has three points, the middle one larger and rounded apically. G1 and 2 smooth, G 3 and 4 pilose. Chelicera (Fig. 24D): Both digits slender, each has four evenly-spaced large teeth.

Length of leg I, 1.23 mm; II, 0.98 mm (Fig. 27A); III, 1.04 mm; IV, 1.54 mm (Fig. 27B, C). Setae thick, pilose. Tarsus II, III, IV with av 1 and pv 1 thornlike. Coxal setae pilose.

MALE (Fig. 28): Idiosomal length 1.29 mm, width 0.98 mm. Propodosomal shield has 22 setae; m 5 longer than other setae; m 1, 2, and 3 shorter than m 4; d 4 and i 2 knife-shaped. Propodosomal shield and hysterosomal shield are divided by a line extending to body margins. All dorsal setae pilose. Hysterosoma polytrichous. Dorsal sculpturing like that of female.

Tritosternum short, about same length as coxa I, lacinia three times the length of base. Sternal and genital setae conspicuously pilose, other setae slightly pilose. Surface of sternal area has netlike pattern which becomes less distinct towards anal area.

Gnathosoma (Fig. 26B) has six rows of deuterosternal teeth; tectum (Fig. 24C) triangular, rounded apically. G 1, 2, and 3 smooth, G 4 pilose. G 2 shorter than G 1, 3, and 4. Chelicera (Fig. 24E): *Digitus mobilus* strongly curved apically, with one tooth just above the middle; *digitus fixtus* triangular, with dorsal point; cheliceral brush a thick stalk 2/5 length of *digitus mobilus*, with few bristles.

Length of leg I, 1.18 mm; II, 0.92 mm (Fig. 29C); III, 1.01 mm; IV, 1.48 mm (Fig. 29A, B). Femur II has well-developed apophysis; both axillary process and apophysis rounded apically. Genu and tibia II have smaller, rounded apophyses. Leg-setae like those of female.

PROTONYMPH (Fig. 30): Idiosomal length 1.18 mm, width 0.62 mm. Dorsal shields not distinguishable. Propodosoma and hysterosoma each with 14 pairs of smooth setae. Tritosternum, base only slightly shorter than lacinia. Three pairs of sternal setae. No sternal shield visible.

Anal shield shaped like an upside-down teardrop, with three setae, the adanal pair and postanal or anal seta. Five pairs of setae between sternal region and anal shield, plus one seta on each side of anal shield. Paratreme not visible.

Length of leg I, 1.23 mm; II, 1.04 mm; III, 1.17 mm; IV, 1.63 mm. Setae of tarsus IV two to three times as long as setae on other tarsi.

LARVA (Fig. 31): Idiosomal length 0.83 mm, width 0.55 mm. Nine pairs of propodosomal setae, seven pairs of setae on hysterosoma; m 5 longer than other setae. Setae simple, smooth.

Ventral surface has three pairs of sternal setae and four pairs of setae between coxa III and anal shield. Adanal pair of setae long, at least 2½ times the length of other ventral setae. Anal setae barely distinguishable. Postanal setae very long, four times length of adanals. Base and lacinia of tritosternum about same length; two smooth lateral branches accompany lacinia. Gnathosoma has two pairs of setae, 11 rows of deuterosternal teeth.

Length of leg I, 1.04 mm; II, 0.77 mm; III, 0.86 mm.

This species is similar to *P. fucorum*. The shapes of l 2, d 4, and i 2 of the female are like those of the *P. fucorum* female. The chelicera is similar to that of the *P. fucorum* female. In *P. fucorum* the female has a large hysterosomal shield not completely covering the hysterosoma, as it does in *P. perthecatus*. On *P. perthecatus* the sternal shield differs, the anterior portion being less sclerotized than that of *P. fucorum*.

The ventral setae of the male *P. perthecatus* are pilose, whereas on *P. fucorum* males most ventral setae are smooth. The cheliceral brush of males of *P. fucorum* is not a stalk.

Ventral surfaces of deutonymphs of *P. fucorum* and *P. perthecatus* are similar, except for the absence of the vertical lines in the sculpturing on the sternal shield of *P. perthecatus*.

P. perthecatus are the largest *Parasitus* found with the bumblebees in the study area. Adults, protonymphs and larvae were collected from nests, and deutonymphs from nests and on adult bees. These mites have also been collected at Lake Hazen, Ellesmere Island, Northwest Territories in association with *Bombus polaris* Curtis and *B. hyperboreus* Schönherr by K. W. Richards in the summers of 1967 and 1968.

TYPES: Holotype of the deutonymph collected 12 June 1971, at Prairie Bluff Mountain, Alberta, Canada (49° 20′ N, 114° 06′ W), at 5200 feet, from *B. appositus* nest; collector L. A. Richards. Specimen located in CNC no. 13190. Morphotypes: Male collected 29 June 1970, from *B. bifarius* nest; female collected 30 May 1970, from *B. frigidus* nest; both from same locality and by the same collector as the holotype. Larva reared 15 July 1971, from mating of male and female from *Bombus* nest. Protonymph reared 25 July 1971, from same source as larva, both parents from same locality as holotype. All these specimens located in the CNC. Paratypes all from same locality as holotype. Nineteen deutonymphs: Two collected 18 August 1970, from *B. bifarius* nest; two 6 July 1970, from *B. occidentalis* queen; one 14 August 1971, from *B. bifarius* nest; one 24 May 1970, from *Bombus* sp. nest; one 29 May 1970, from *B. frigidus* nest; one 14 June 1970, from *B. bifarius* queen; one 19 June 1971, from *B. californicus* queen; one 22 May 1971, from *B. bifarius* queen; one 20 June 1971, from *B. frigidus* nest; one 6 June 1970, from *B. flavifrons* queen; one 3 June 1971, from *B. appositus* queen; one 3 June 1971, from *B. rufocinctus* queen; one 19 May 1971, from *B. occidentalis* queen; one 1 August 1970, from *B. occidentalis* nest; one 16 June 1971, from *B. nevadensis* queen; one 6 June 1970, from *Hydrophyllum capitatum* flower; and one 25 May 1971, from *B. flavifrons* queen. Seven males: Two collected 9 August 1970, from *B. occidentalis* nest; one 5 June 1970, from *B. bifarius* nest; one 8 August 1971, from *B. bifarius* nest; one 14 August 1970, from *B. californicus* nest; one 9 August 1971, from *B. bifarius* nest; and one 13 August 1970, from *B. appositus* nest. Seven females: Two 6 June 1970, from *B. occidentalis* nest; two 2 August 1970, from *B. appositus* nest; one 9 July 1971, from *Bombus* sp. nest; one 2 August 1970, from *B. appositus* nest; and one 14 August 1970, from *B. californicus* nest. Five deutonymphs; two females, and two males; located in the CNC. Five deutonymphs; two females, and two males; located in the BMNH. Four deutonymphs; one female, and one male; located in the USNM. Five deutonymphs; two females and two males; located at the University of Kansas.

The specific name is derived from Latin, meaning well sheathed, referring to the heavy dorsal and ventral shields covering most of the body of the adult mites.

Parasitus fimetorum Berlese, 1903

Gamasus fimetorum Berlese, 1903, Redia, 1 (1904):238.

Parasitus affinis Oudemans, 1904, Ent. Ber. nederl. Ver., Gravenhage, 1:120.

Parasitus fimetorum Schweitzer, 1949, Res. Rech. Scient. Parc Nation. Suisse (N. F.) 2:8-9.

Parasitus fimetorum Costa, 1961, Ann. Mag. Nat. Hist. (13)4:261.

Eugamasus fimetorum Holzmann, 1969, Acarologie 13:14.

Parasitus fimetorum Micherdzinski, 1969, Panstwowe Wydawnictwo Naukowe. p. 478.

The specimens from southern Alberta differ slightly from those previously described. Differences include the shape of the tectum of the deutonymph, which is triangular for the Alberta specimens; other descriptions call it three-pointed. On the gnathosoma of the male, according to Costa (1961), eight rows of deuterosternal teeth are present; Micherdzinski (1969) shows only a single basal row, which is the same condition as in the specimens from Alberta; Holzmann (1969) shows two to three rows. Male, female and deutonymphs of this species have been described.

These mites are common in Europe and have also been collected in Israel. They are found in manure, but also occur under wood, stones, bark, and in soil habitats. Generally the deutonymphal stage is the most commonly encountered. They have not previously been reported from *Bombus* nests. Two specimens received from Dr. R. Husband were collected from nests of *B. fervidus* (Fabricius) and *B. americanorum* (Fabricius) in Michigan. In Alberta this species was found in *Bombus* nests, but not on the bees. Thus it is likely to be a soil inhabitant with no specific relationship to *Bombus* such as seems to exist for the preceding species.

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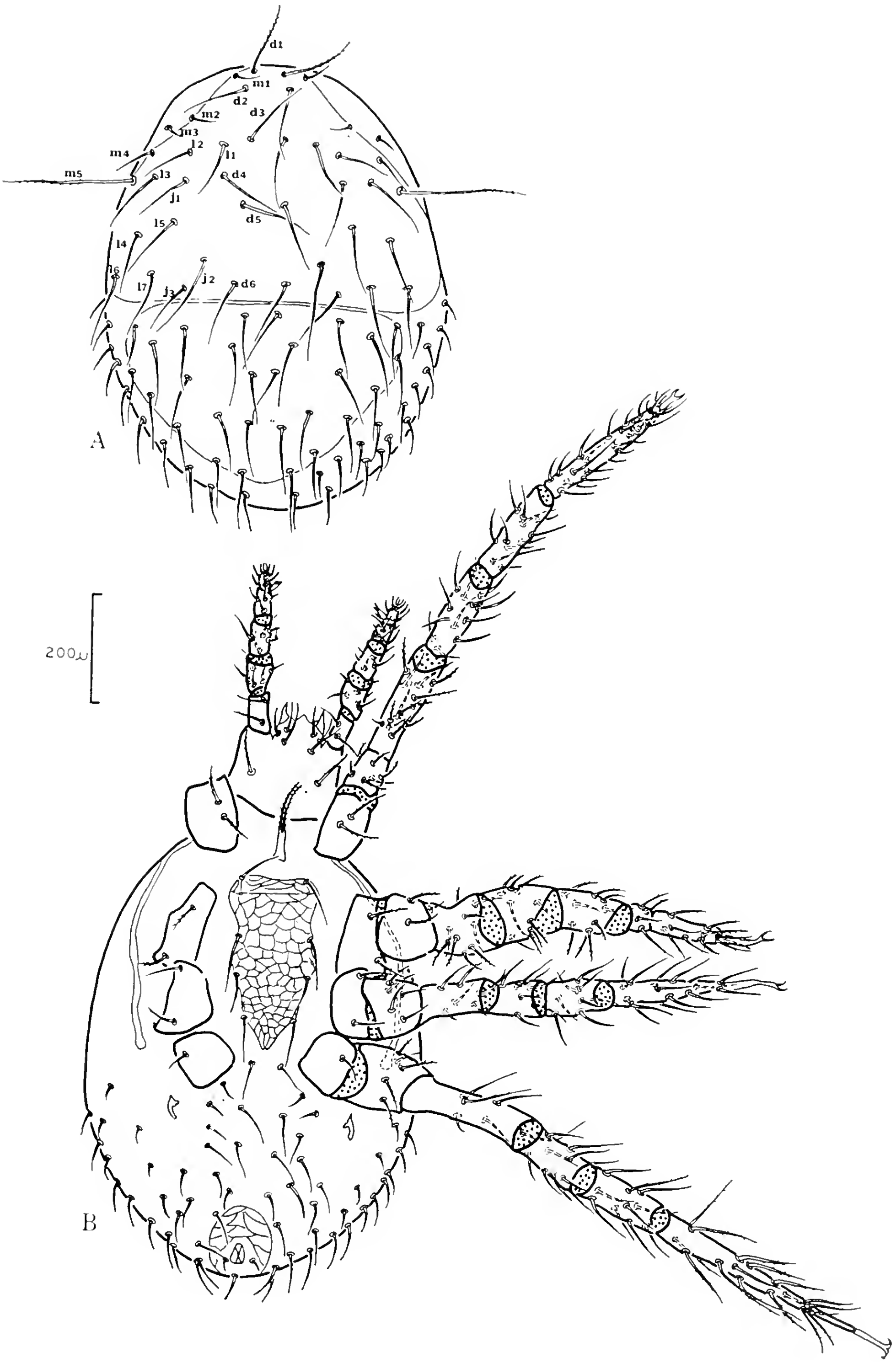

Fig. 1. *Parasitus hobbsi*, deutonymph. A. dorsal chaetotaxy, B. ventral side.

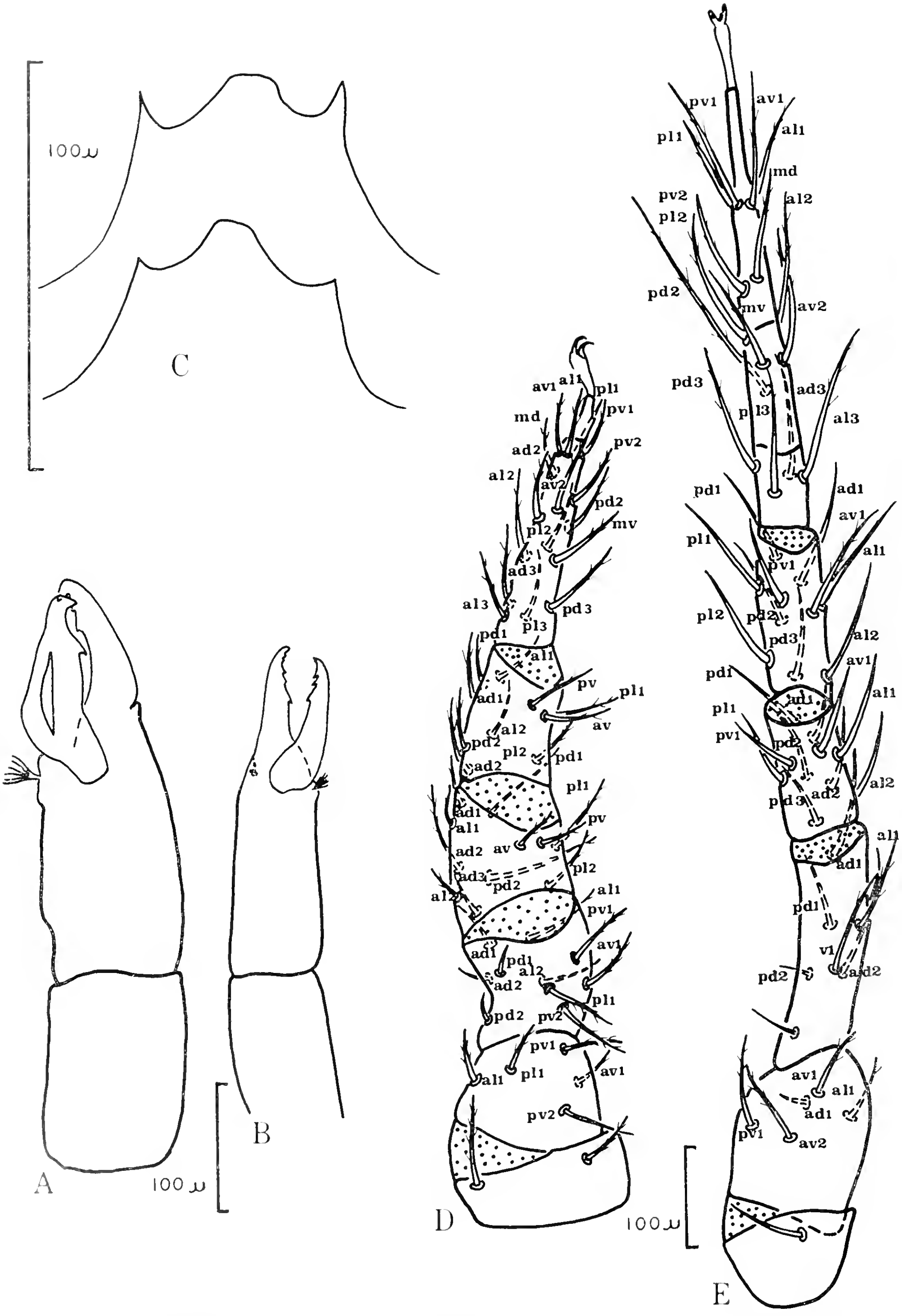

FIG. 2. *Parasitus hobbsi* A. male chelicera, B. deutonymph chelicera, C. deutonymph tectum, D. deutonymph leg II, E. leg IV.

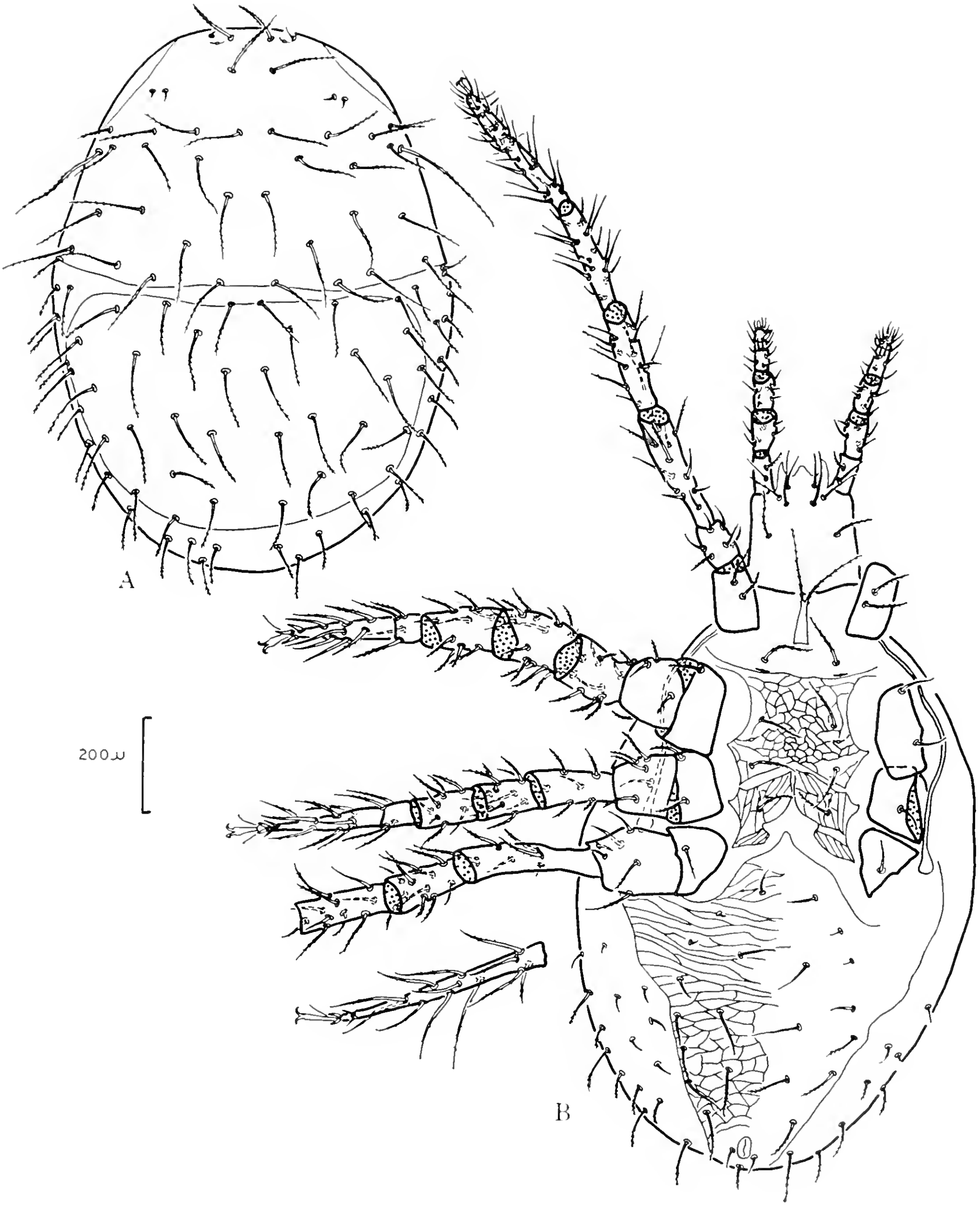

Fig. 3. *Parasitus hobbsi,* female. A. dorsal chaetotaxy, B. ventral side.

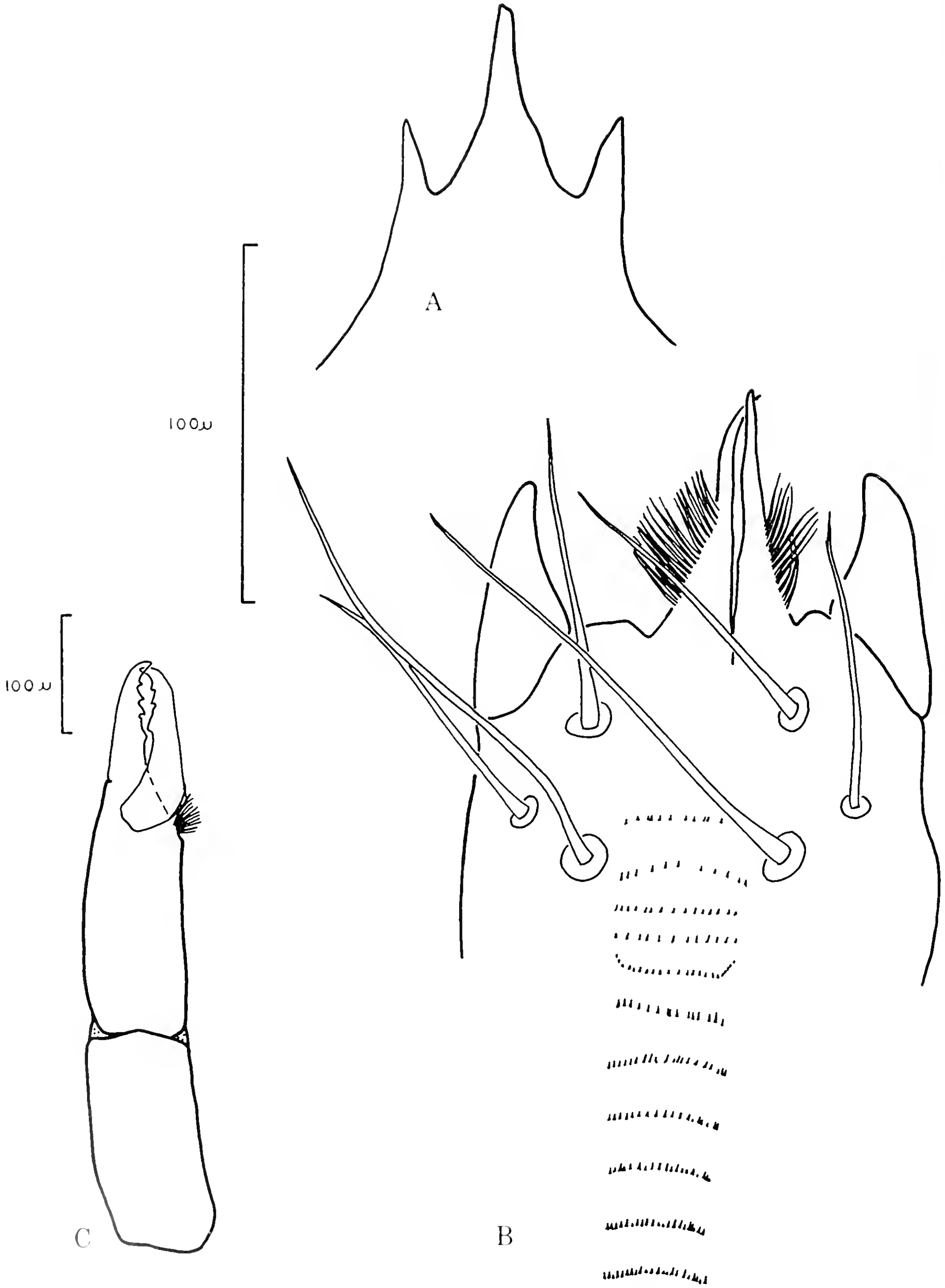

Fig. 4. *Parasitus hobbsi,* female. A. tectum, B. gnathosoma, C. chelicera.

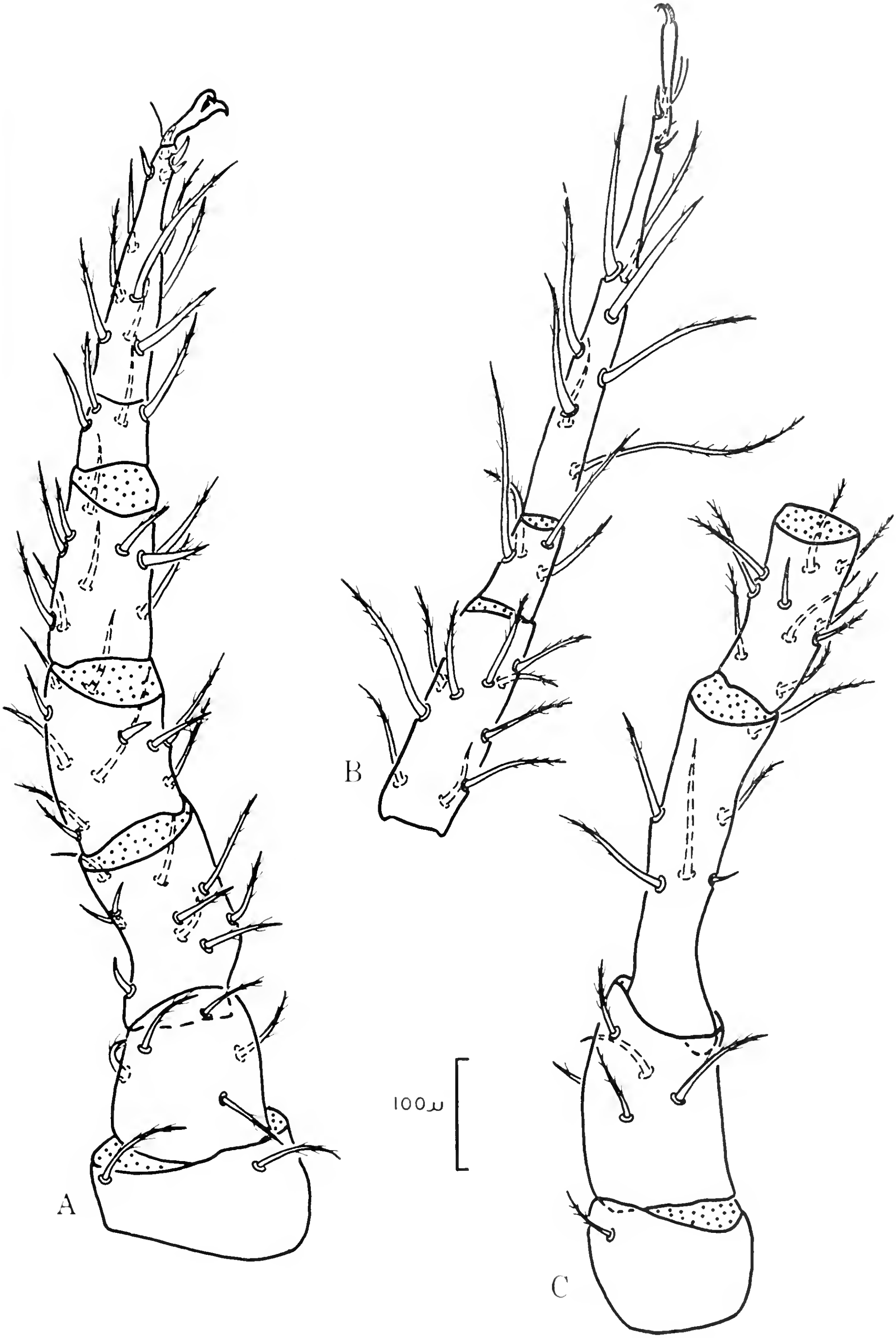

Fig. 5. *Parasitus hobbsi,* female. A. leg II, B. tibia IV and tarsus IV, C. coxa, genu, trochanter, femur.

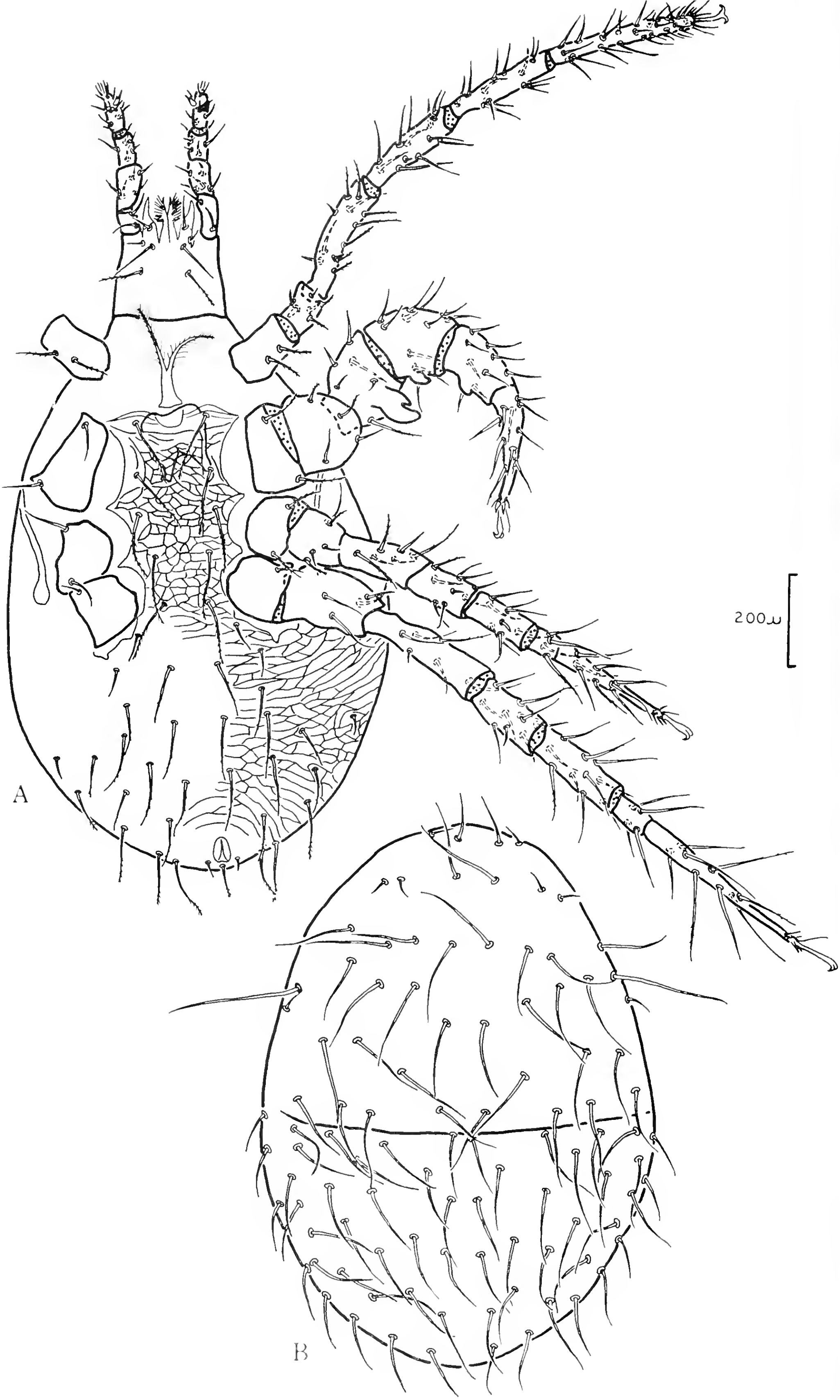

FIG. 6. *Parasitus hobbsi*, male. A. ventral side, B. dorsal chaetotaxy.

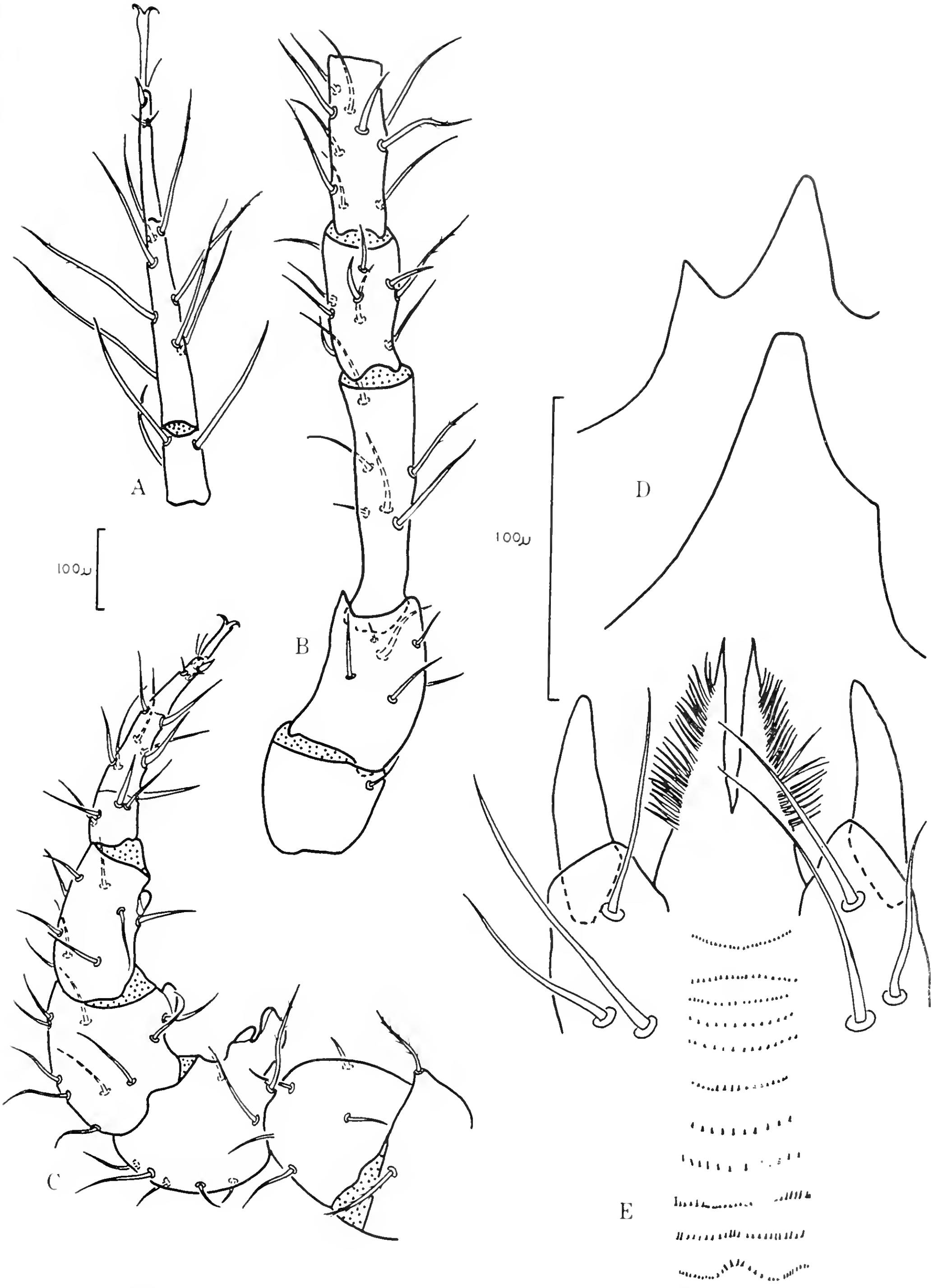

Fig. 7. *Parasitus hobbsi*, male. A. tarsus IV, B. coxa, trochanter, femur, genu, tibia IV, C. leg II, D. tectum, E. gnathosoma.

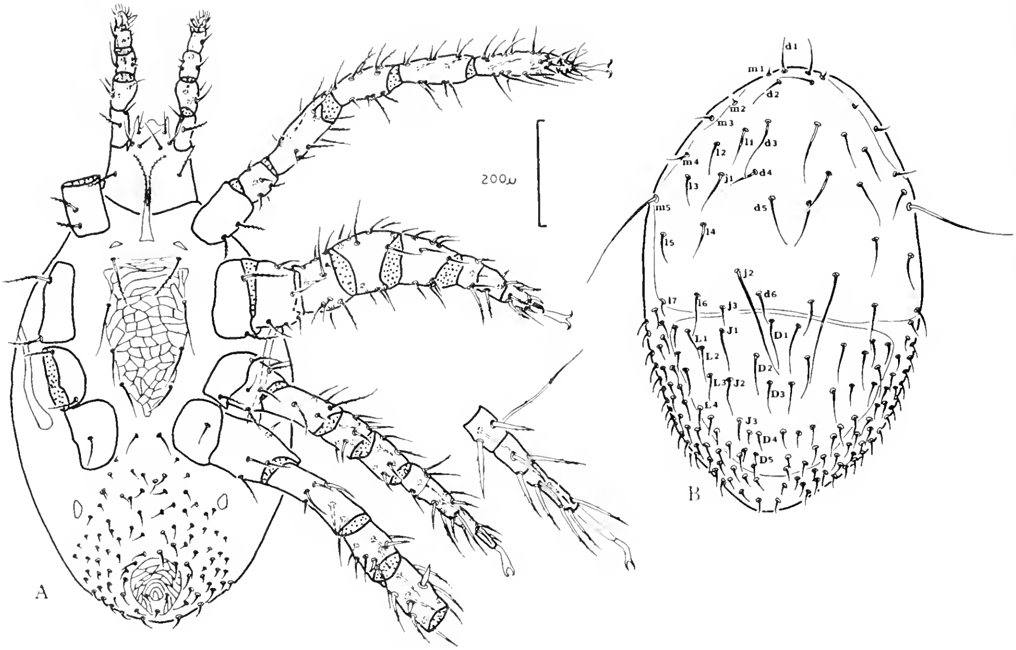

FIG. 8. *Parasitus favus*, deutonymph. A. ventral side, B. dorsal chaetotaxy.

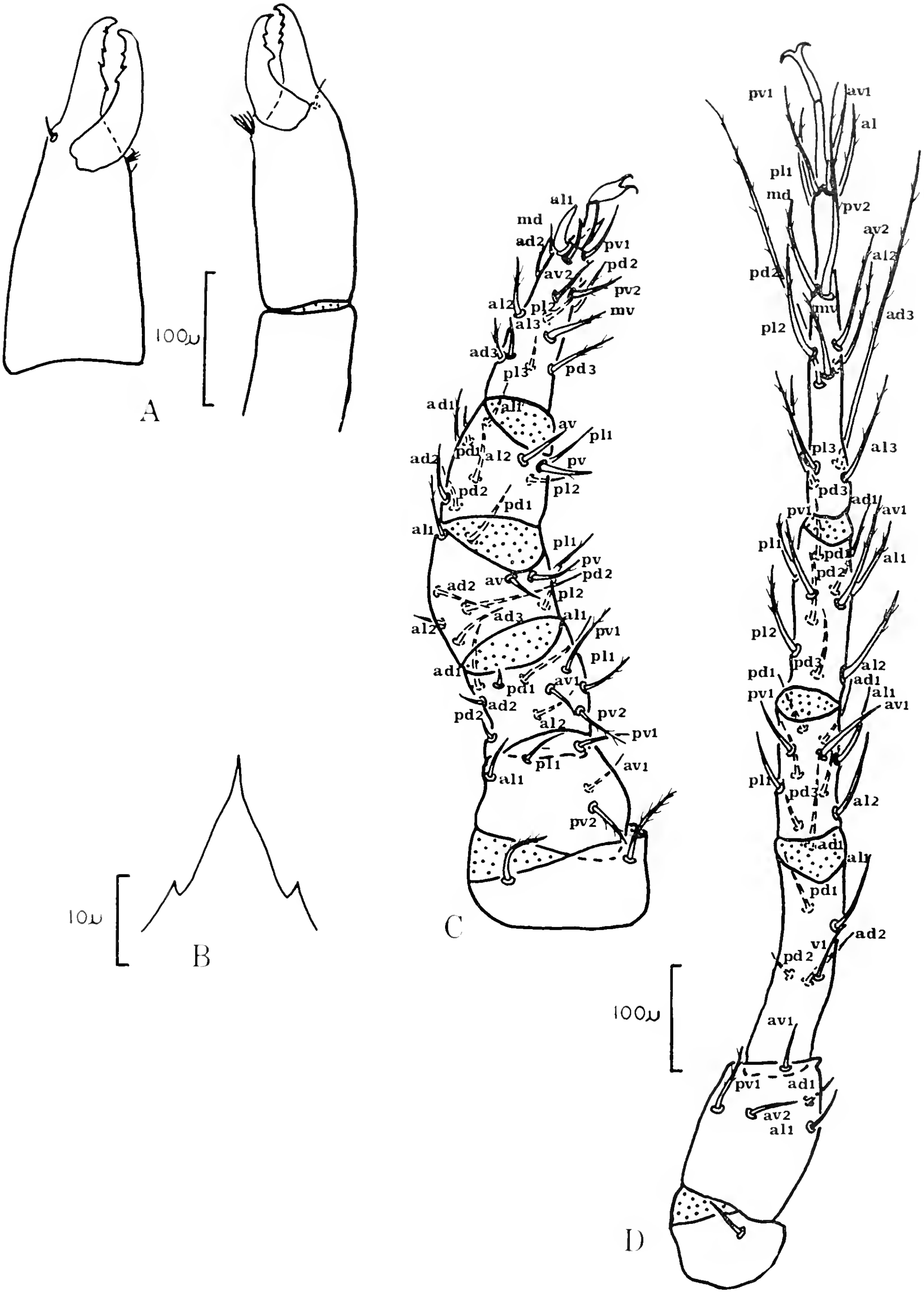

Fig. 9. *Parasitus favus,* deutonymph. A, chelicera, B, tectum, C, leg II, D, leg IV.

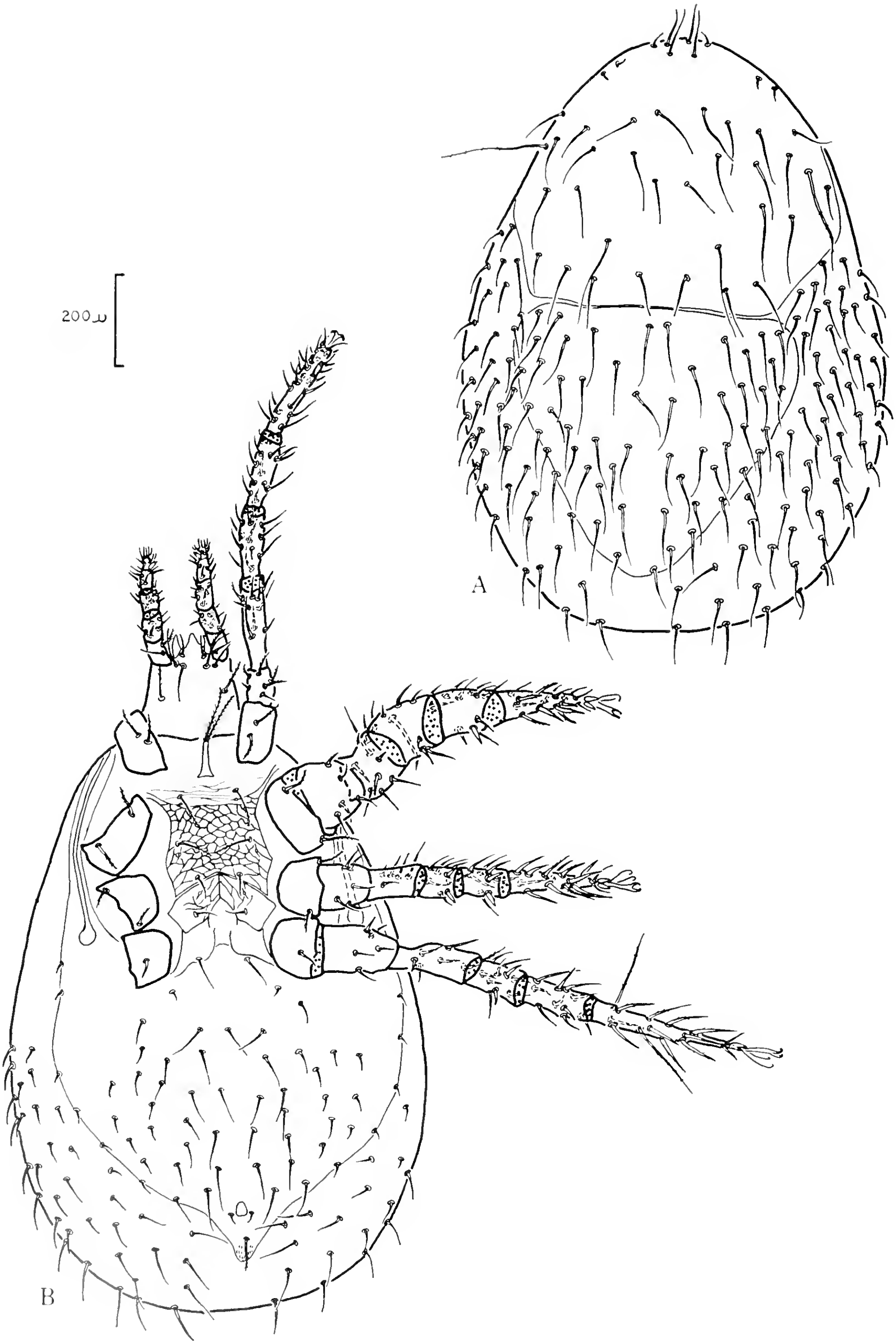

Fig. 10. *Parasitus farus,* female. A. dorsal chaetotaxy, B. ventral side.

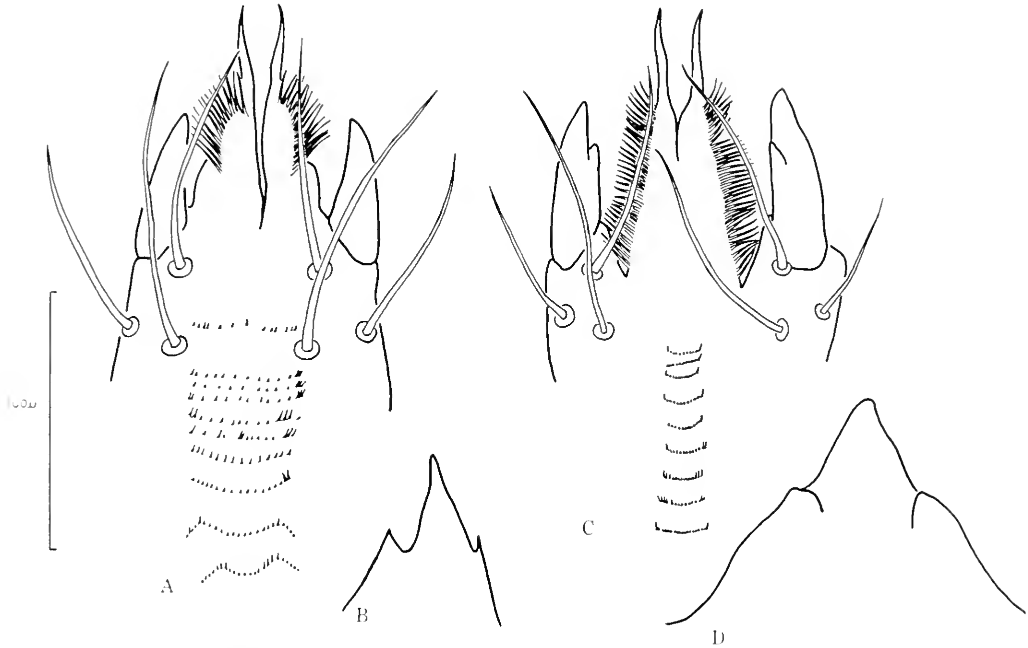

Fig. 11. *Parasitus favus* A. female gnathosoma, B. female tectum, C. male gnathosoma, D. male tectum.

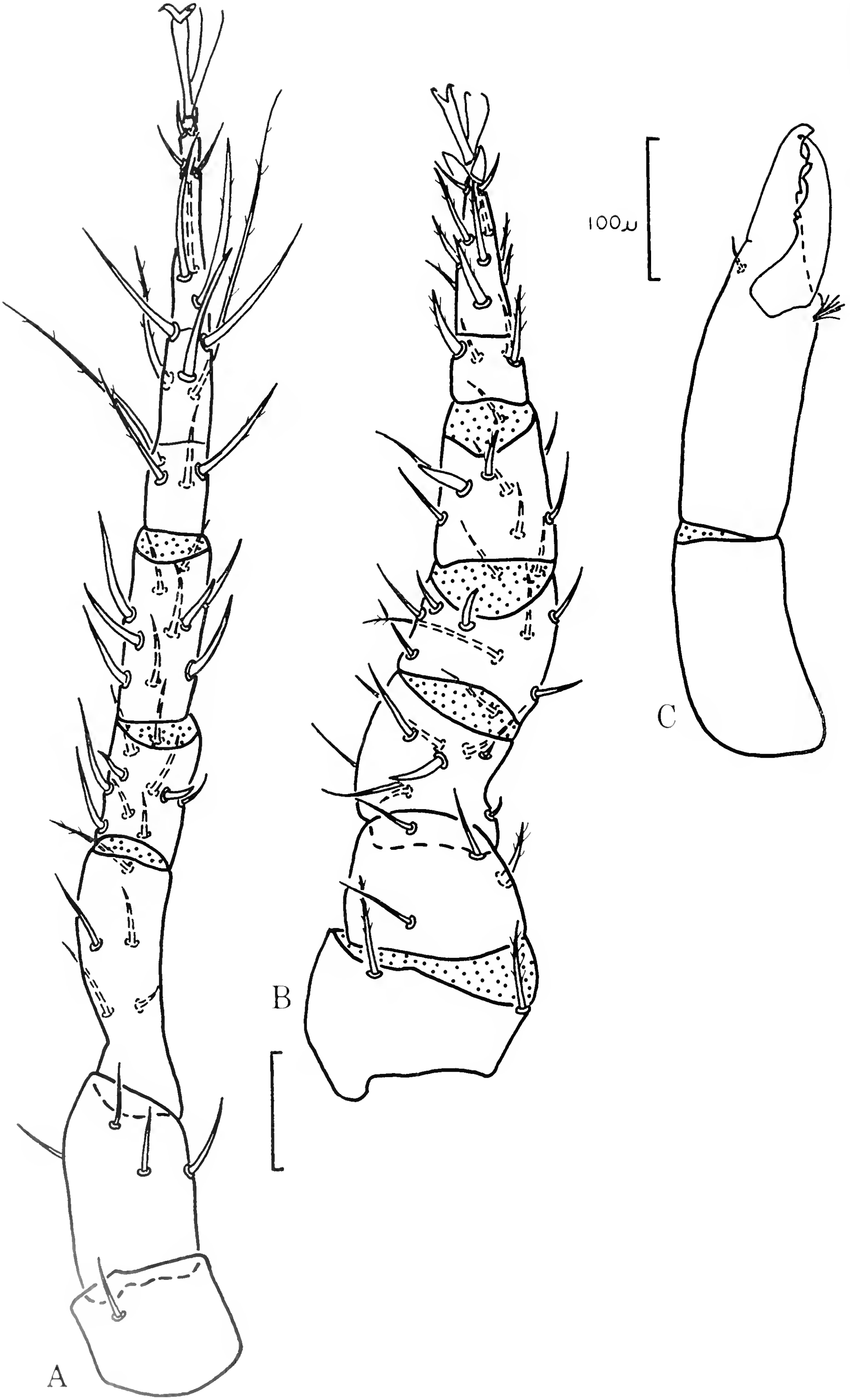

Fig. 12. *Parasitus favus*, female. A. leg IV, B. leg II, C. chelicera.

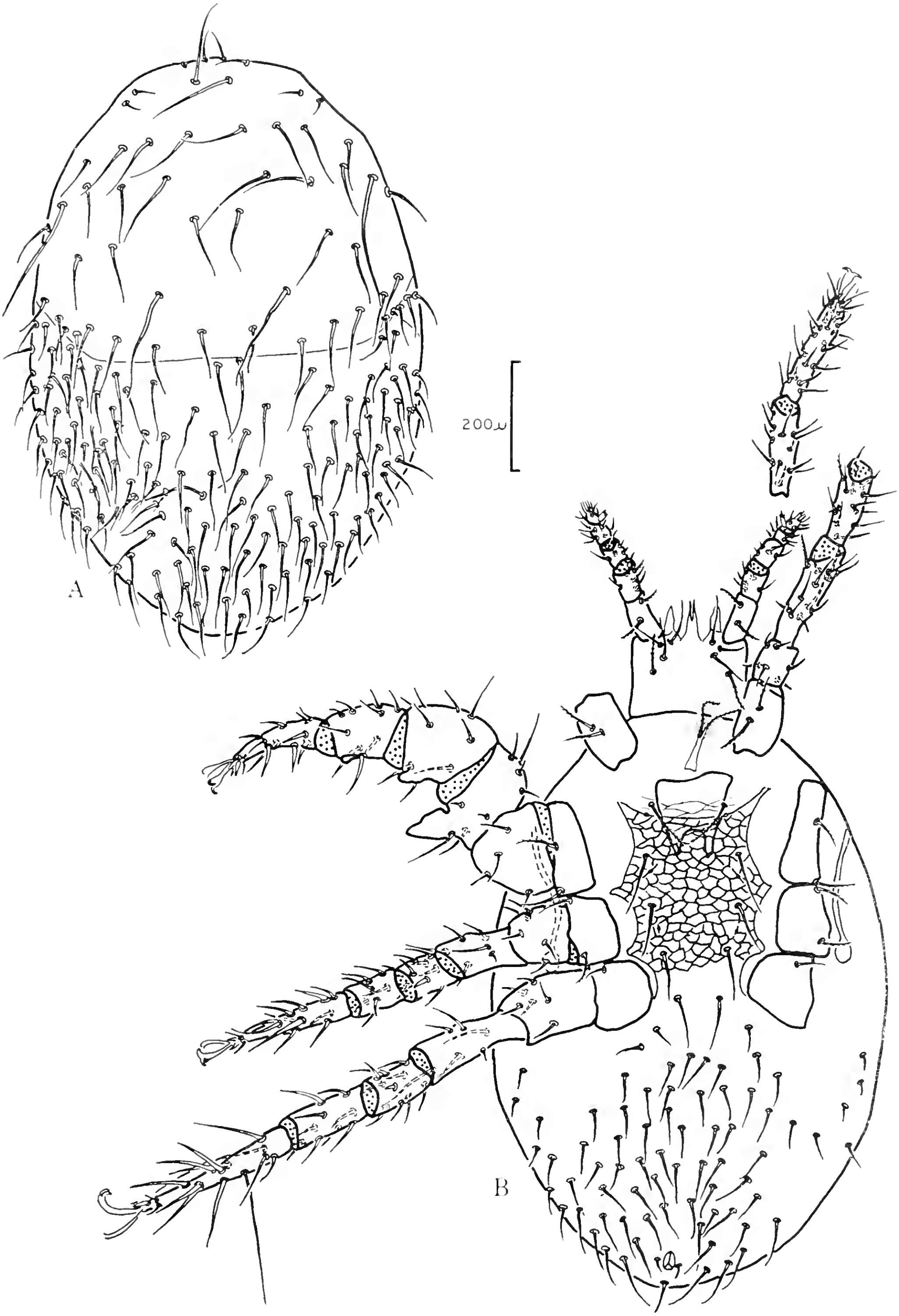

Fig. 13. *Parasitus favus*, male. A. dorsal chaetotaxy. B. ventral side.

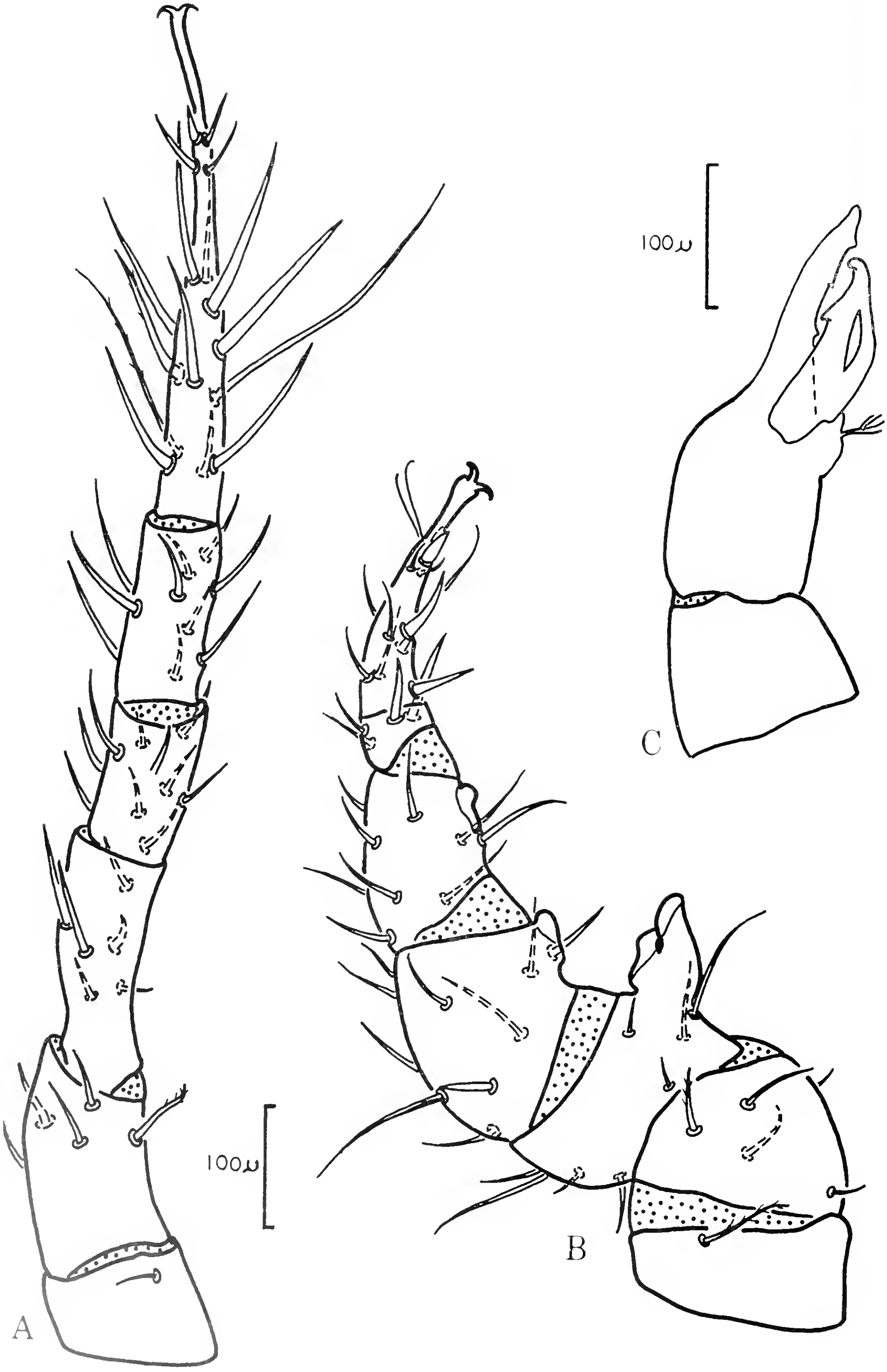

Fig. 14. *Parasitus favus,* male. A. leg IV, B. leg II, C. chelicera.

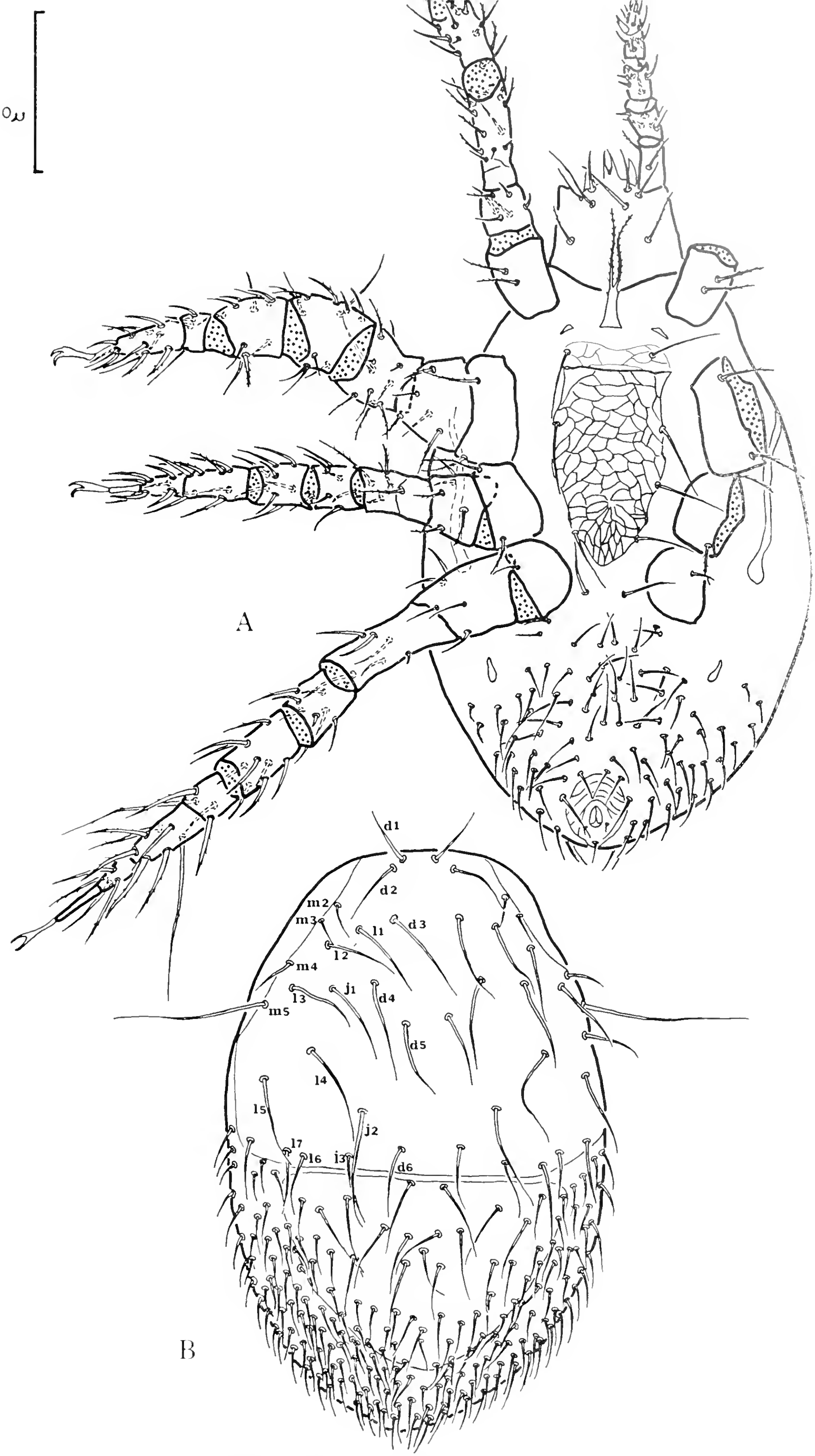

FIG. 15. *Parasitus inquilinobombus*, deutonymph. A. ventral side, B. dorsal chaetotaxy.

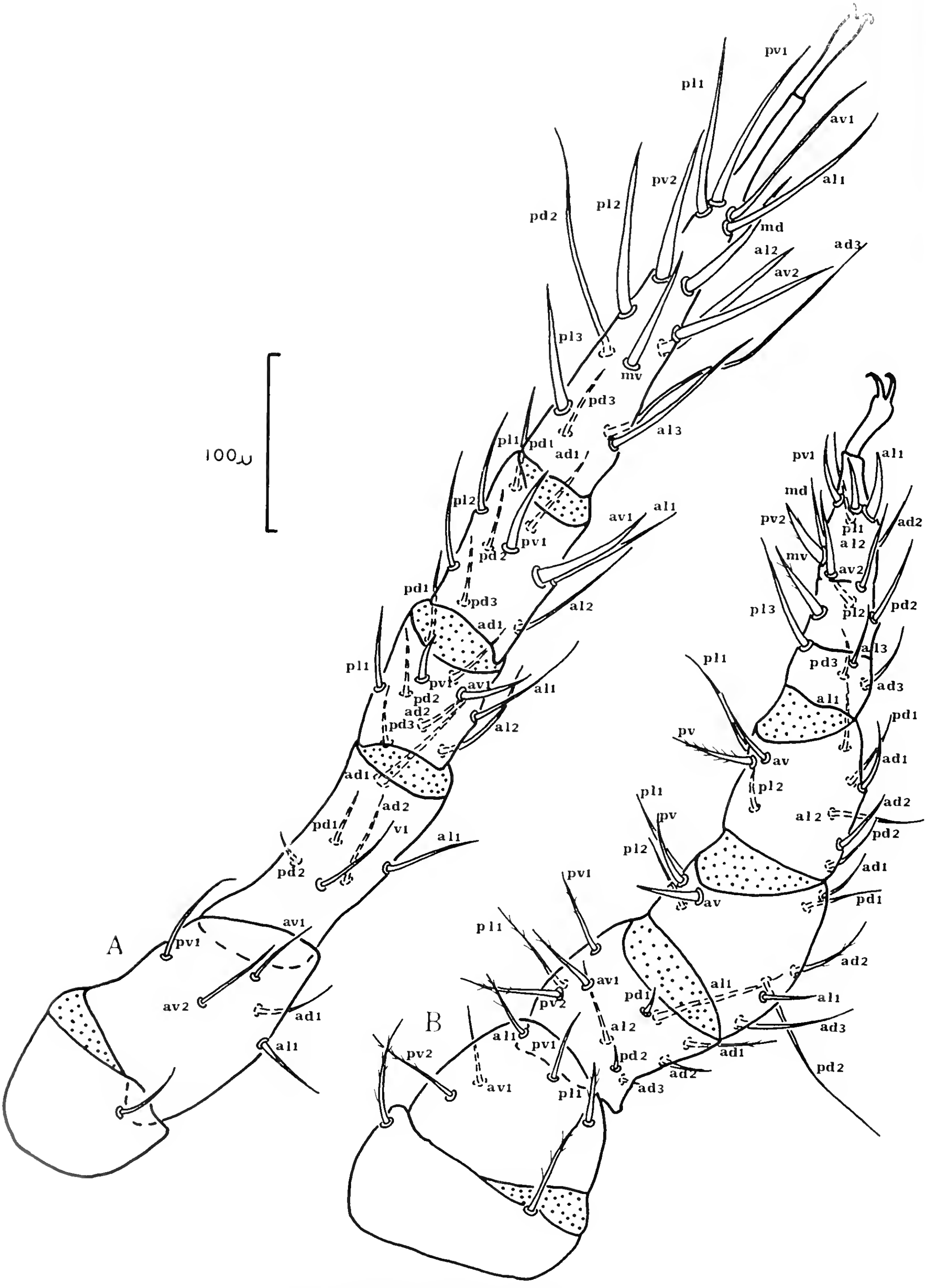

Fig. 16. *Parasitus inquilinobombus*, deutonymph. A. leg IV, B. leg II.

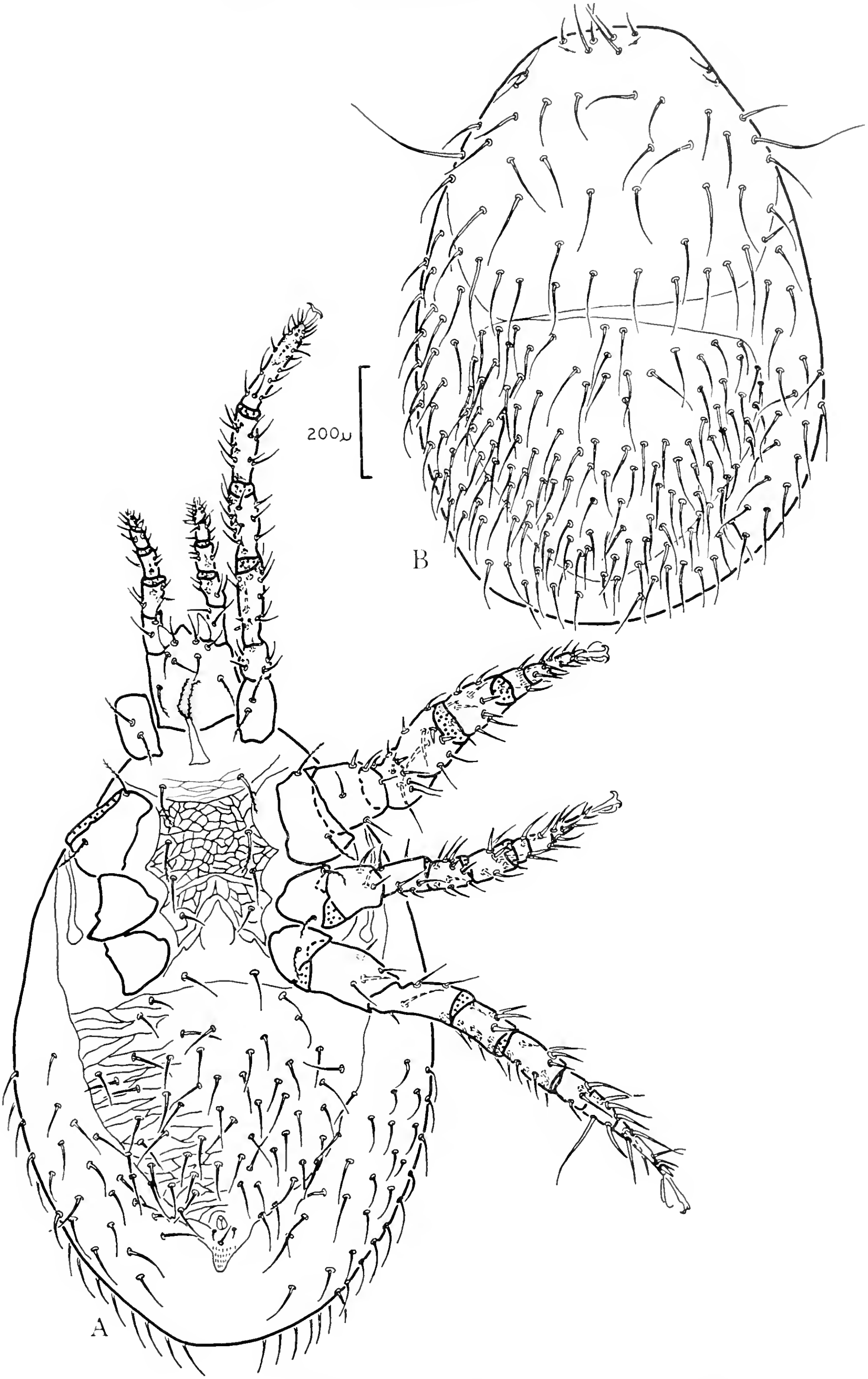

Fig. 17. *Parasitus inquilinobombus*, female. A. ventral side, B. dorsal chaetotaxy.

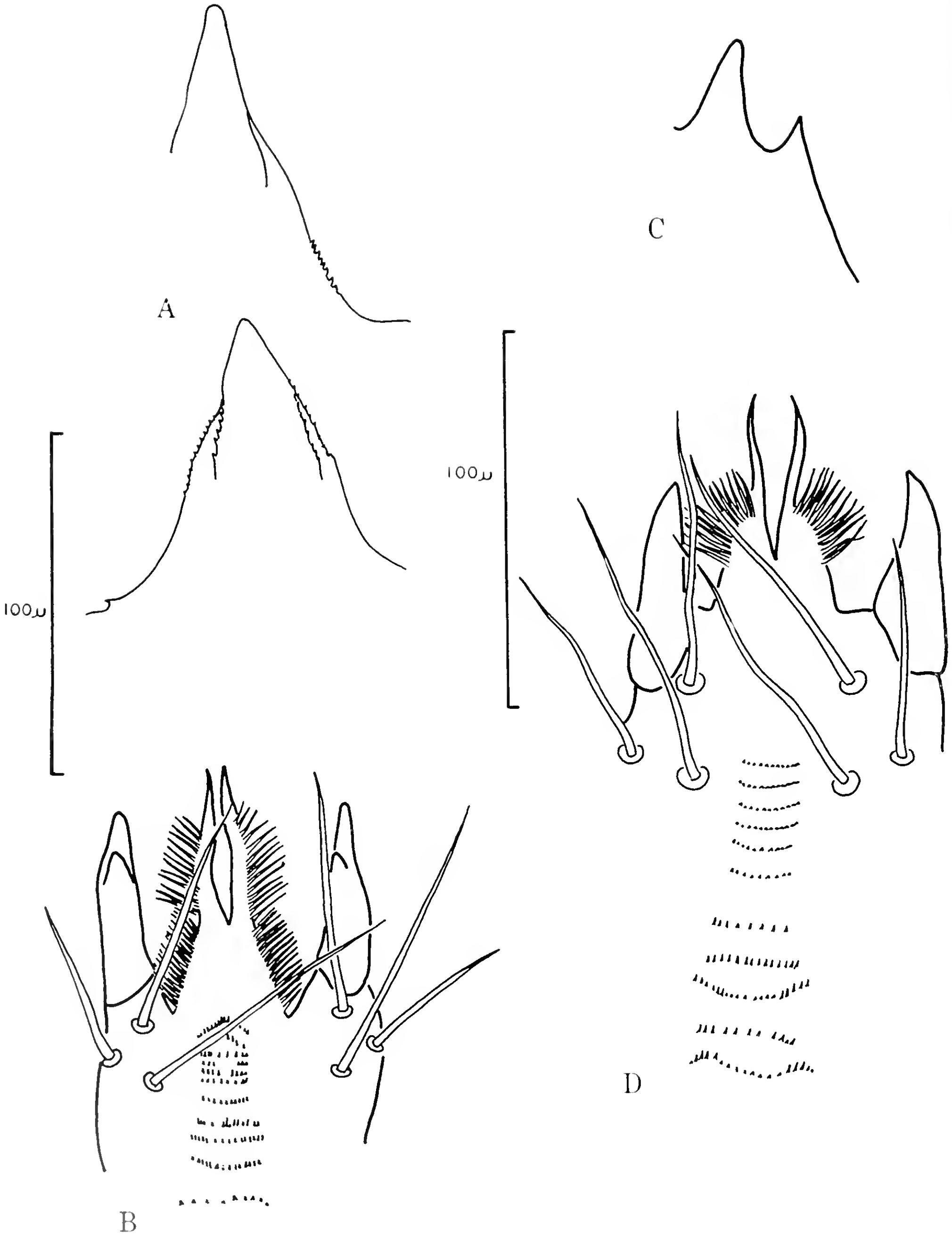

FIG. 18. *Parasitus inquilinobombus* A. male tectum, B. male gnathosoma. C. female tectum, D. female gnathosoma.

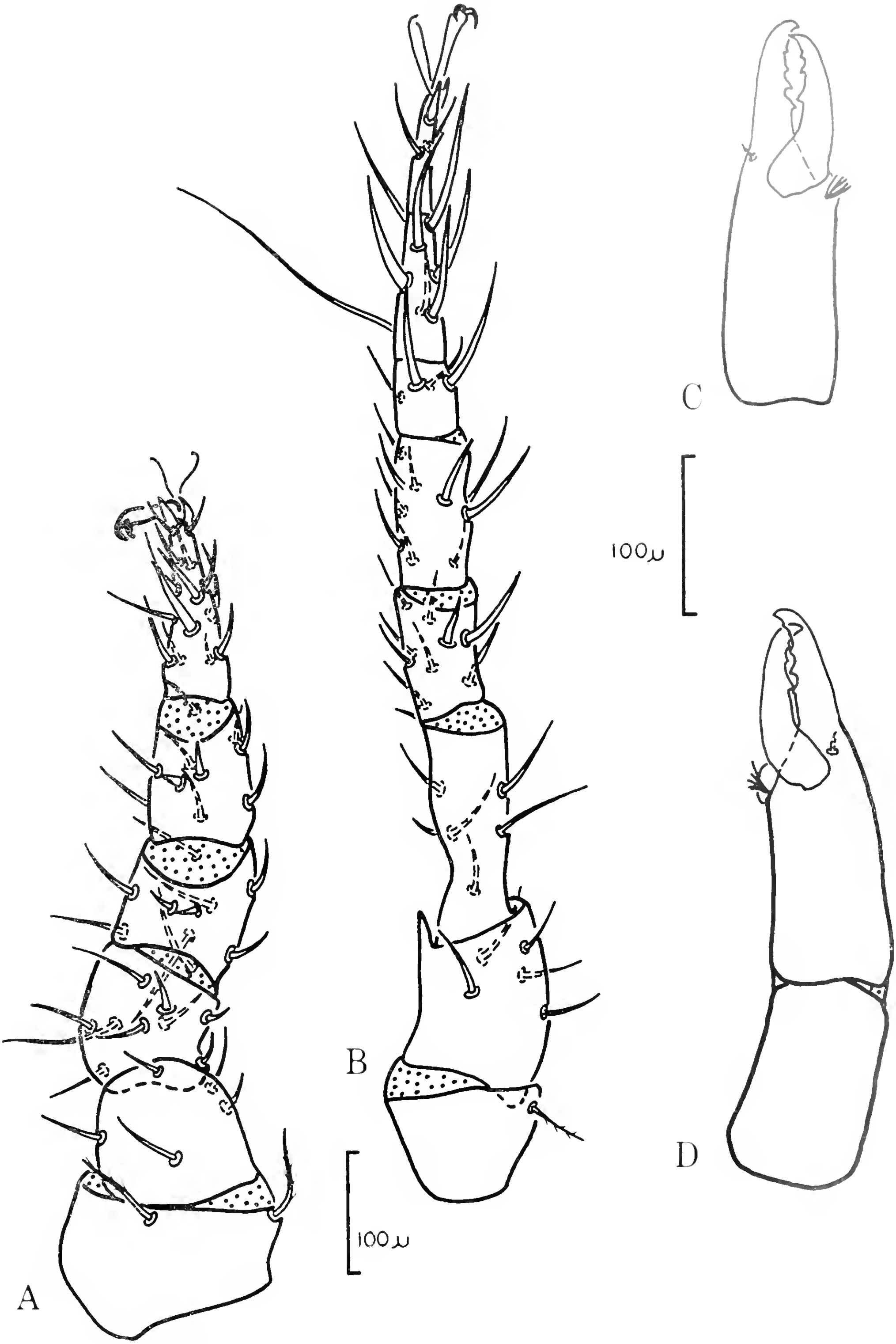

FIG. 19. *Parasitus inquilinobombus,* female. A. leg II, B. leg IV, C. chelicera left, D. chelicera right.

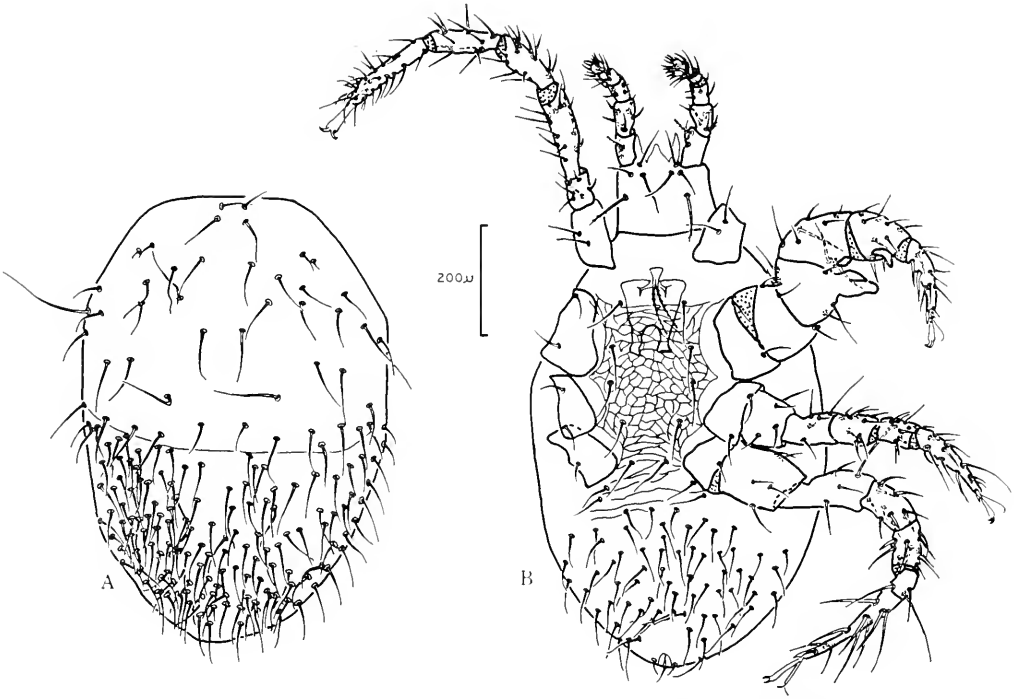

FIG. 20. *Parasitus inquilinobombus*, male. A. dorsal chaetotaxy, B. ventral side.

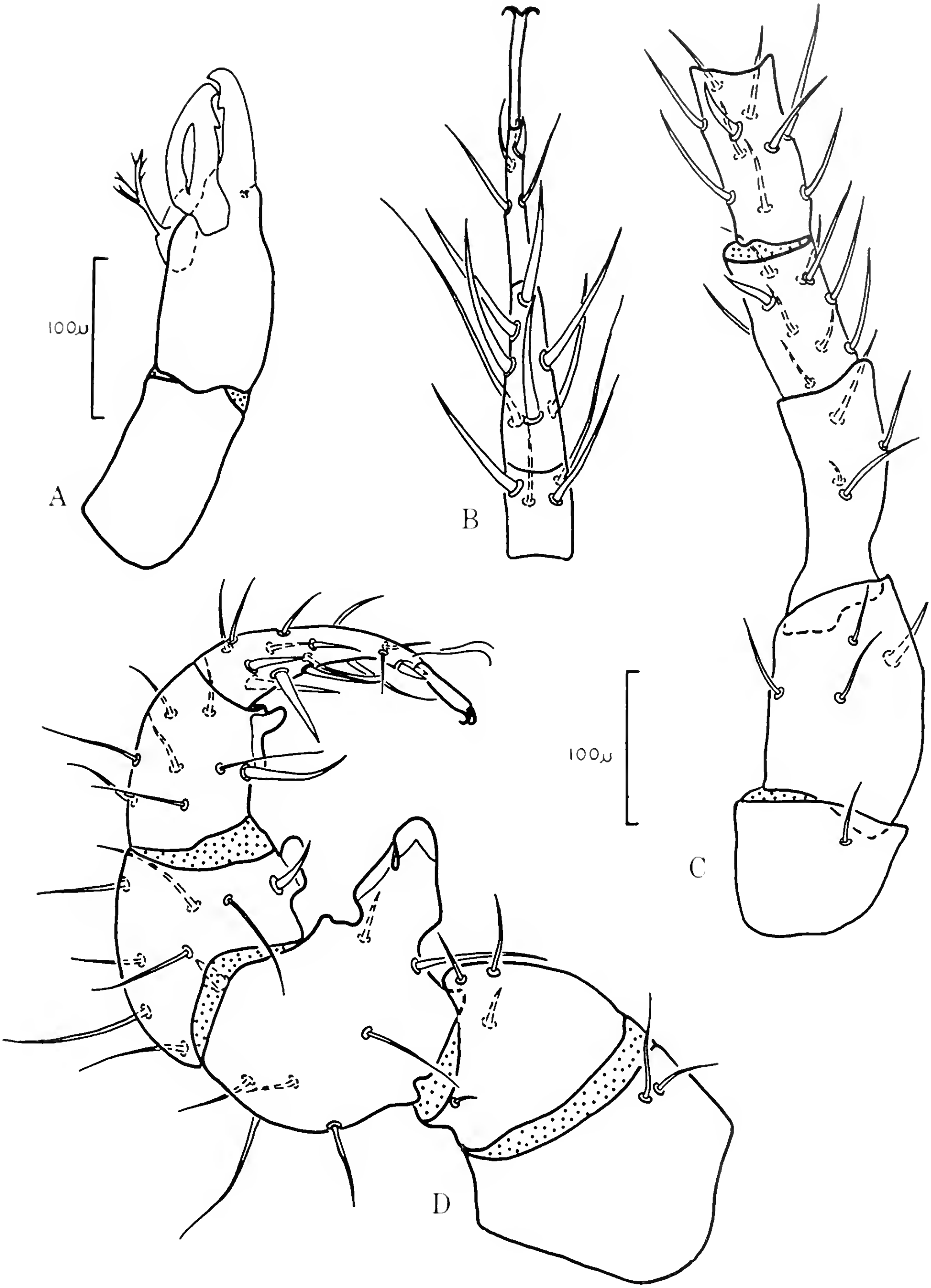

FIG. 21. *Parasitus inquilinobombus,* male. A. chelicera, B. tarsus IV, C. coxa, trochanter, femur, genu, tibia IV, D. leg II.

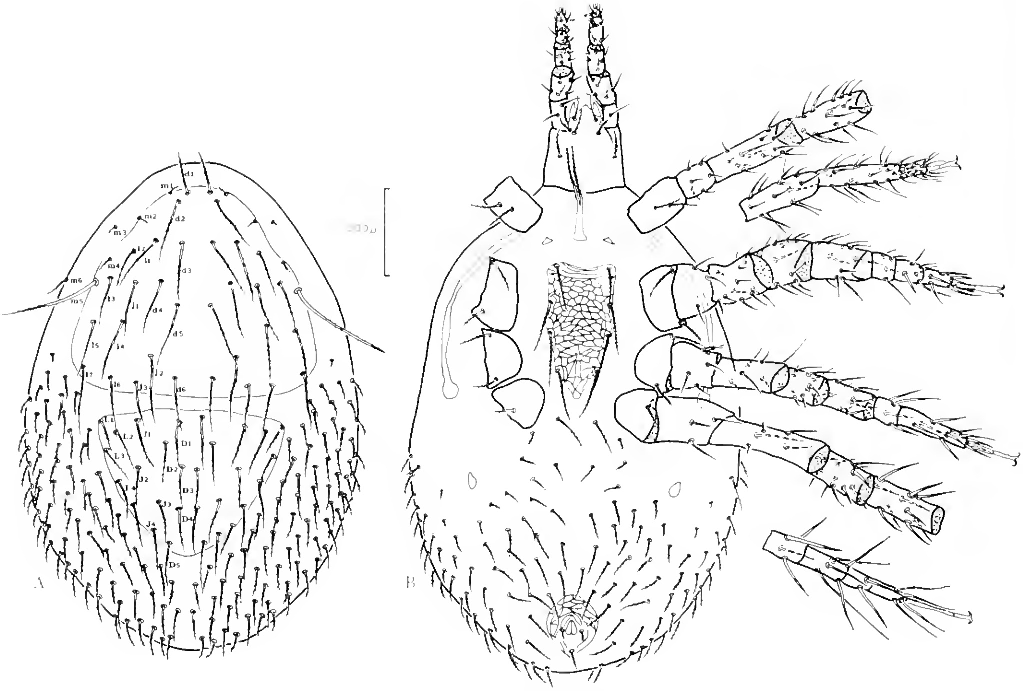

FIG. 22. *Parasitus perthecatus*, deutonymph. A. dorsal chaetotaxy, B. ventral side.

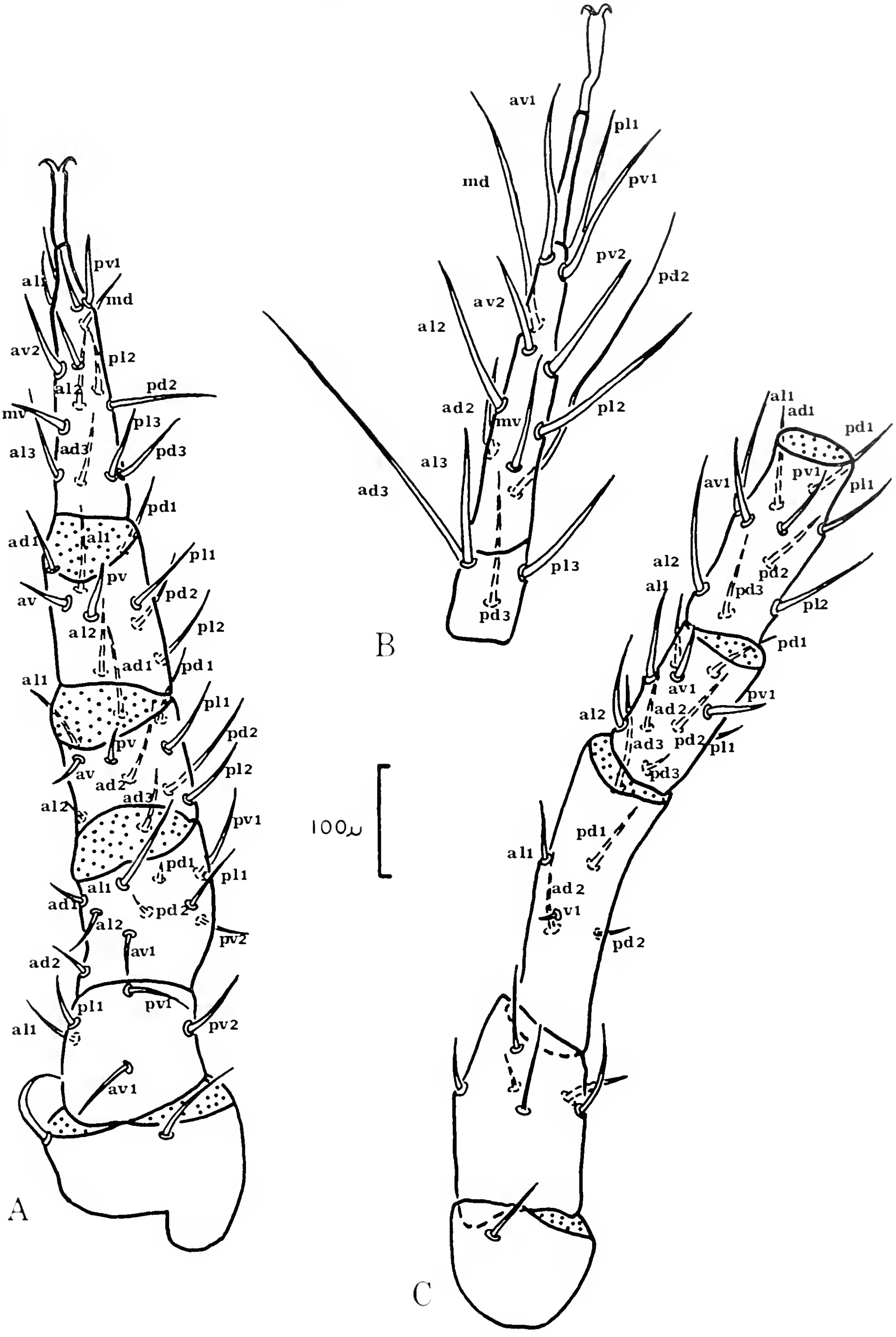

Fig. 23. *Parasitus perthecatus,* deutonymph. A. leg II, B. tarsus IV, C. coxa, trochanter, femur, genu, tibia IV.

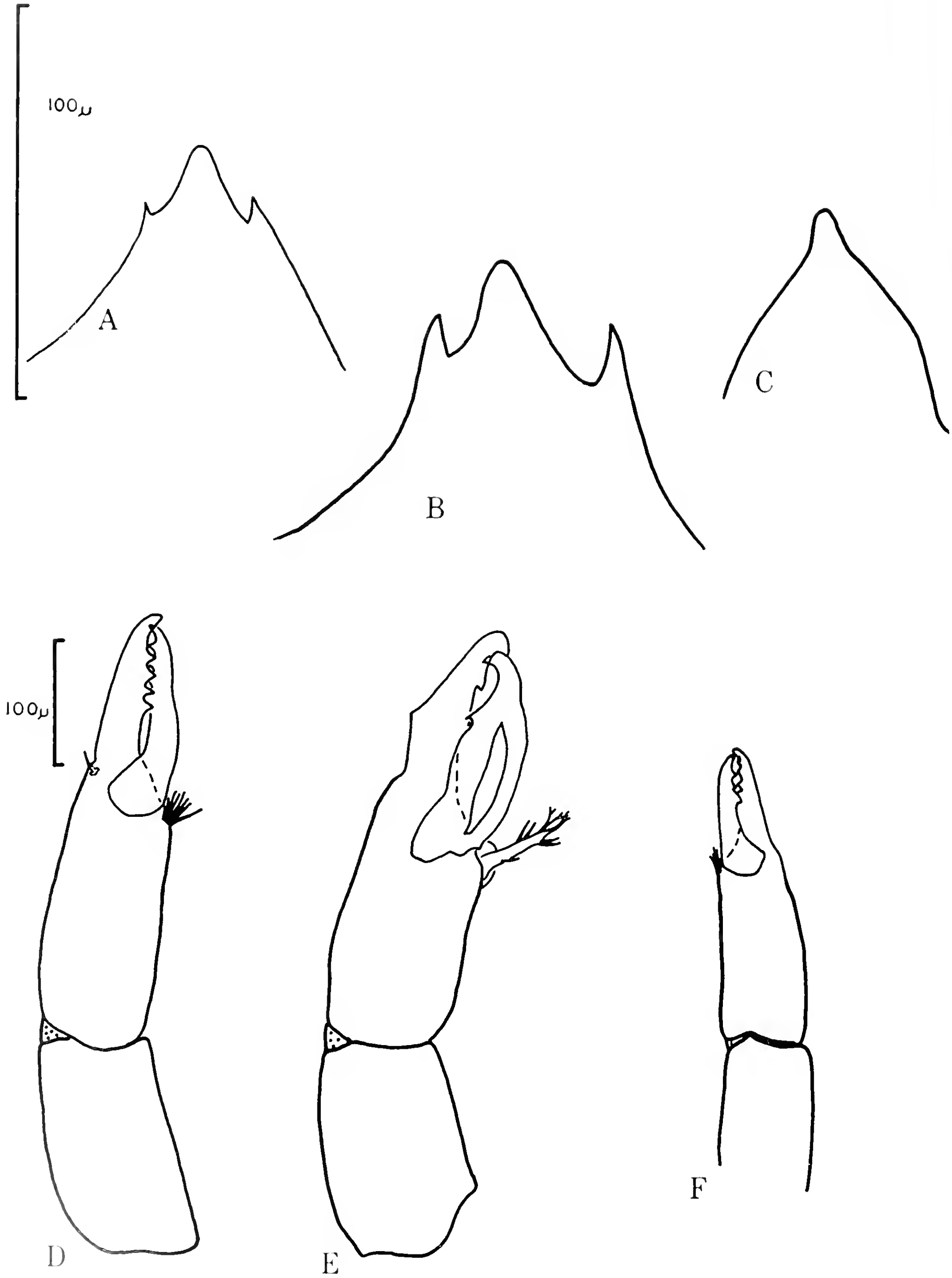

FIG. 24. *Parasitus perthecatus* A. deutonymph tectum, B. female tectum, C. male tectum, D. female chelicera, E. male chelicera, F. deutonymph chelicera.

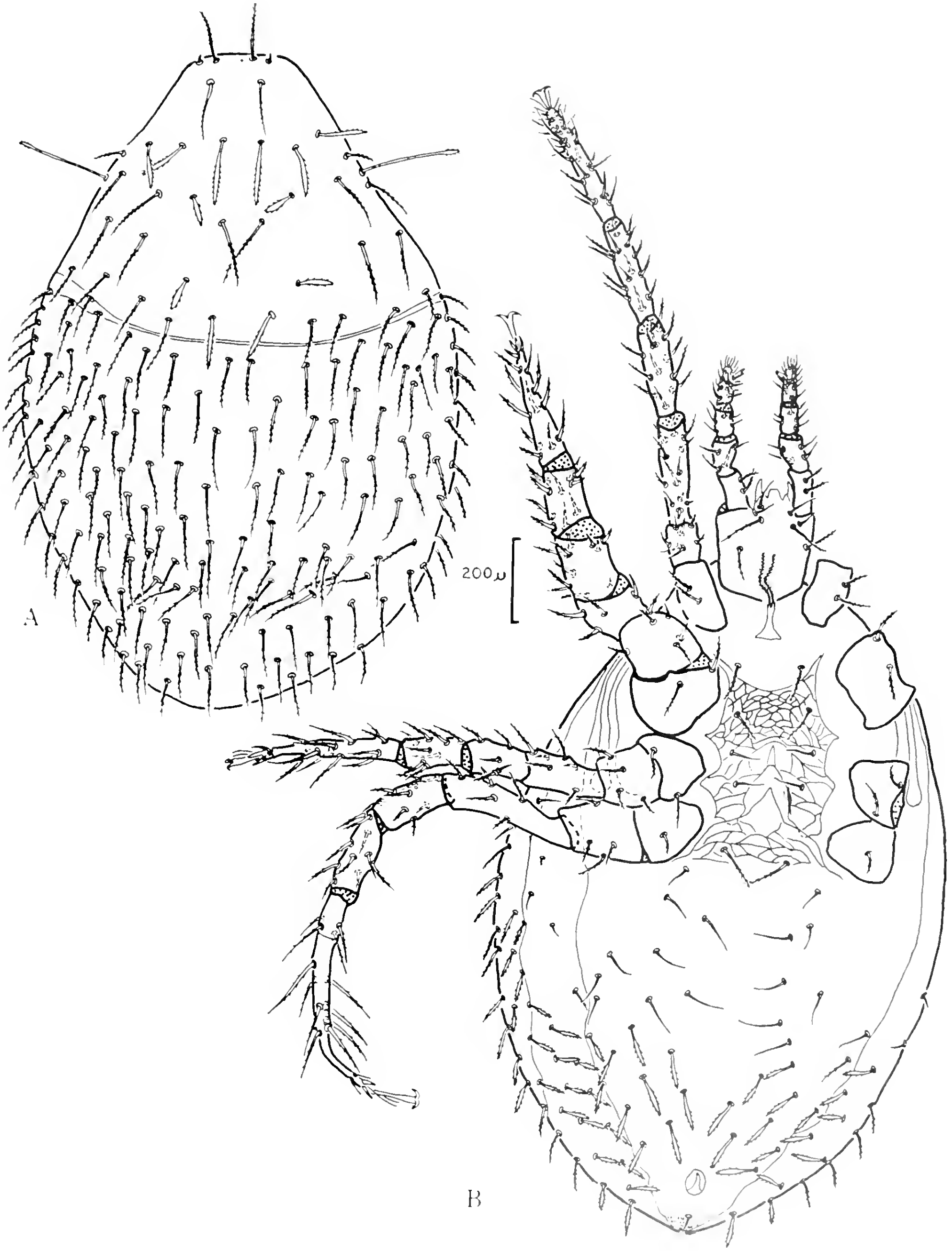

FIG. 25. *Parasitus perthecatus,* female. A. dorsal chaetotaxy. B. ventral side.

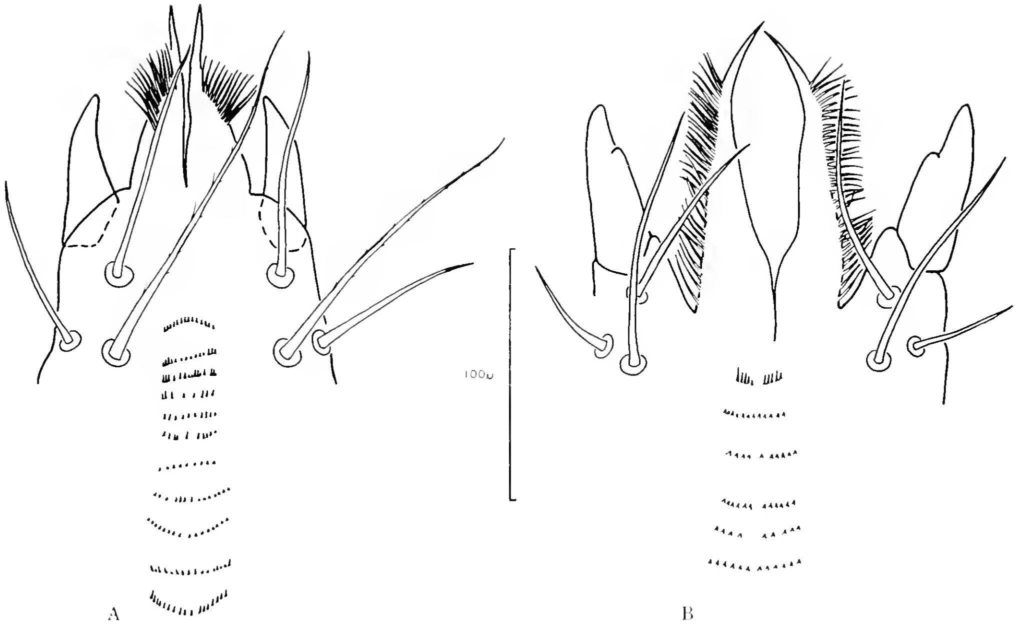

FIG. 26. *Parasitus perthecatus* A. female gnathosoma, B. male gnathosoma.

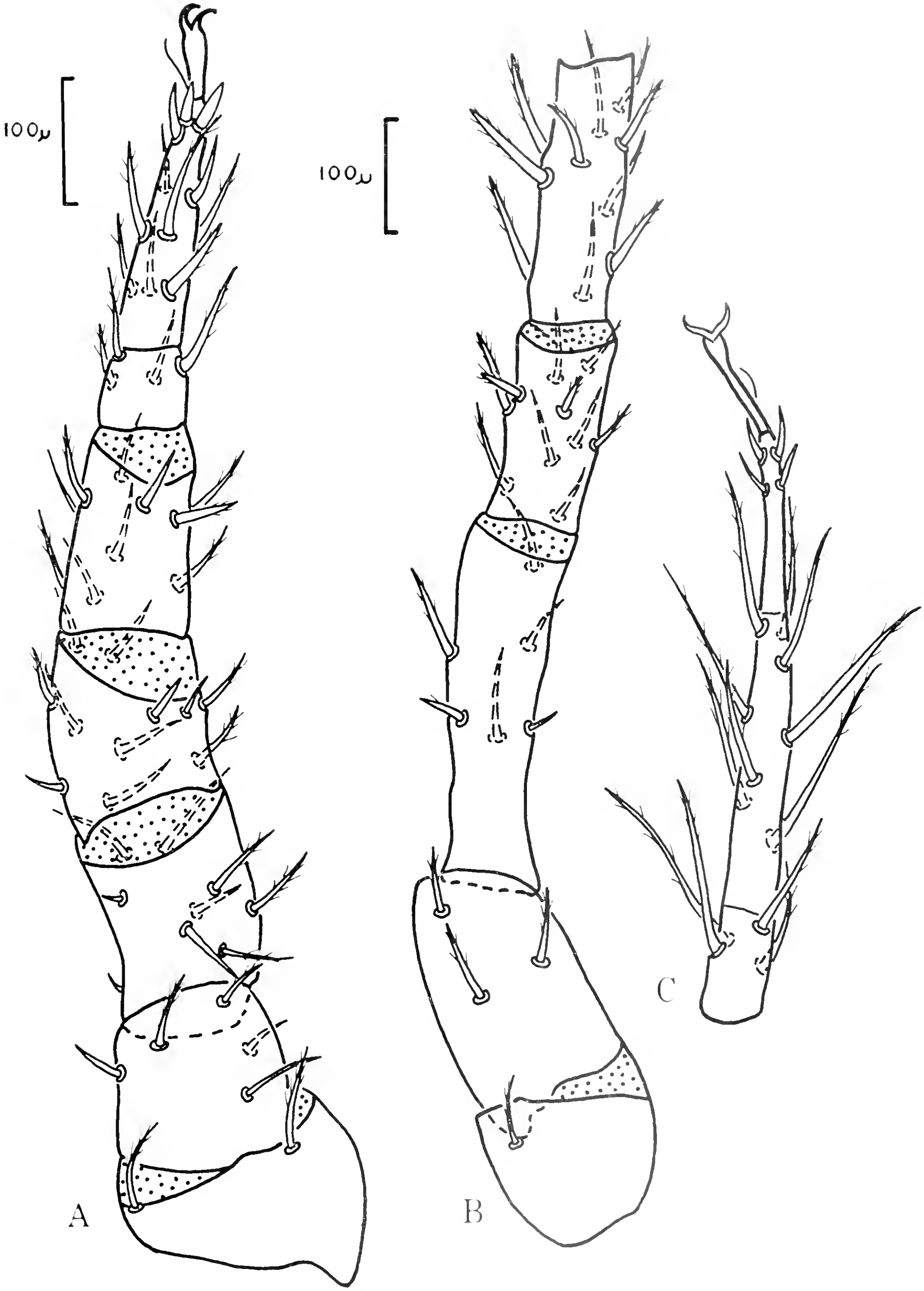

Fig. 27. *Parasitus perthecatus,* female. A. leg II. B. coxa, trochanter, femur, tibia IV. C. tarsus IV.

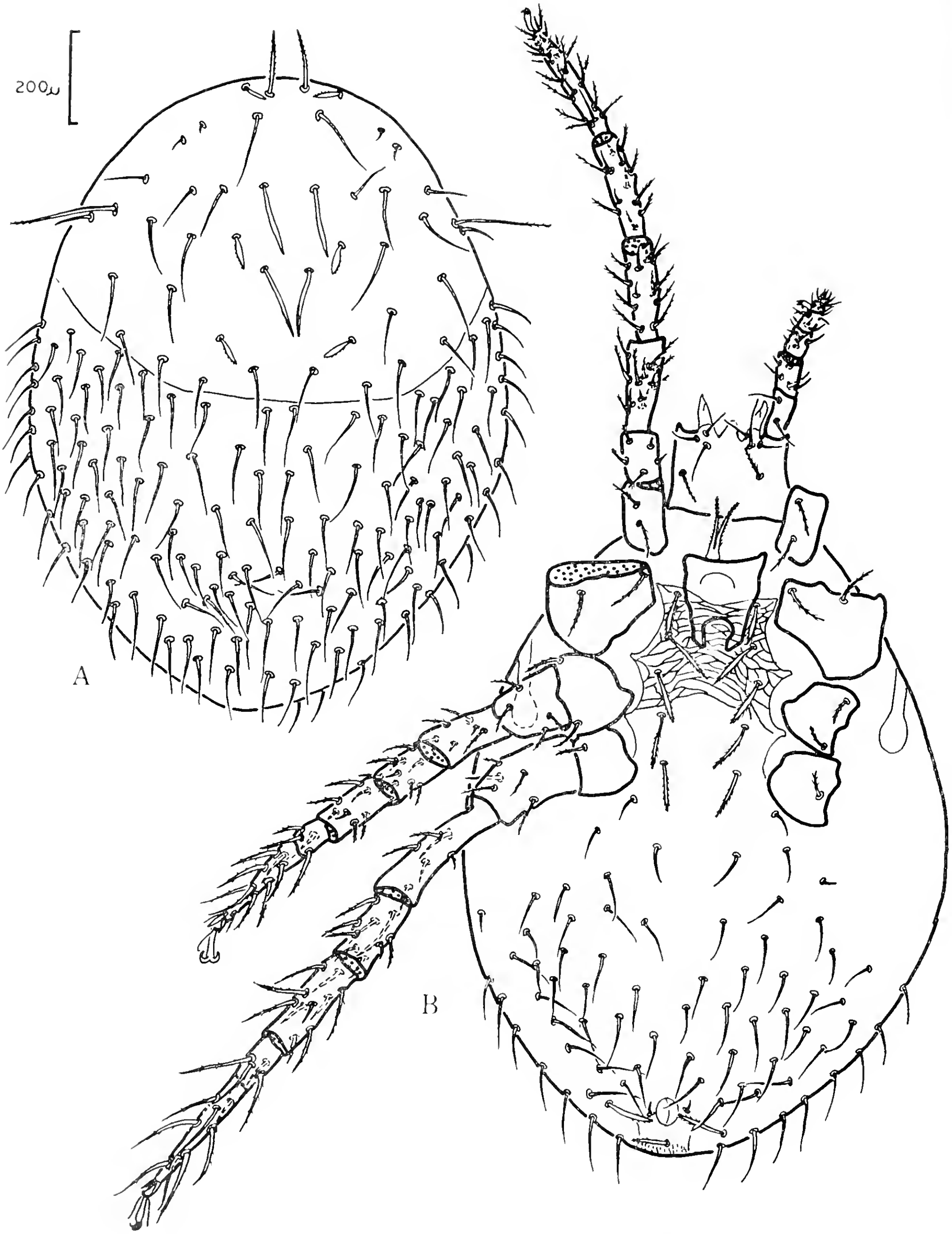

FIG. 28. *Parasitus perthecatus*, male. A. dorsal chaetotaxy, B. ventral side.

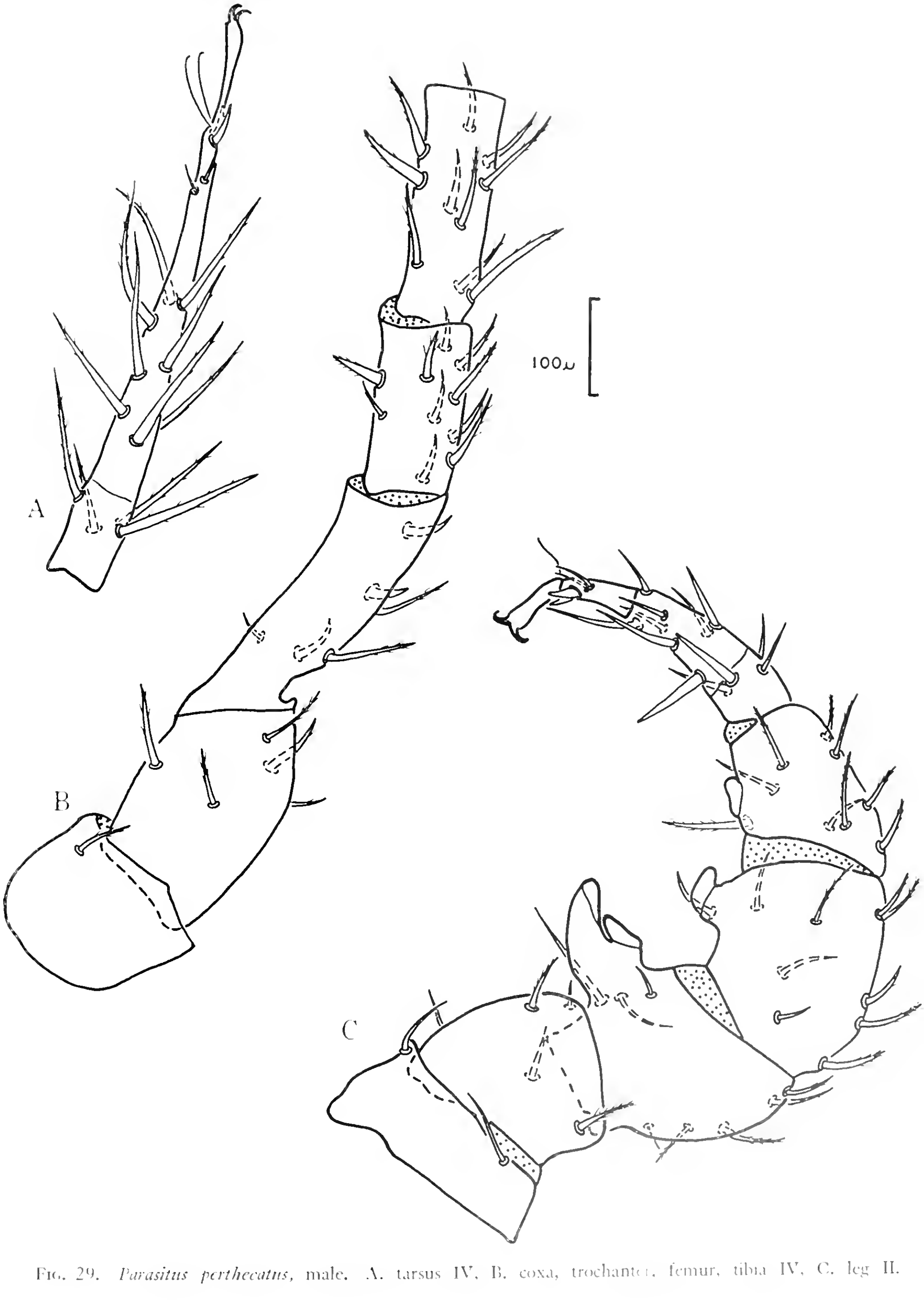

FIG. 29. *Parasitus perthecatus,* male. A. tarsus IV, B. coxa, trochanter, femur, tibia IV, C. leg II.

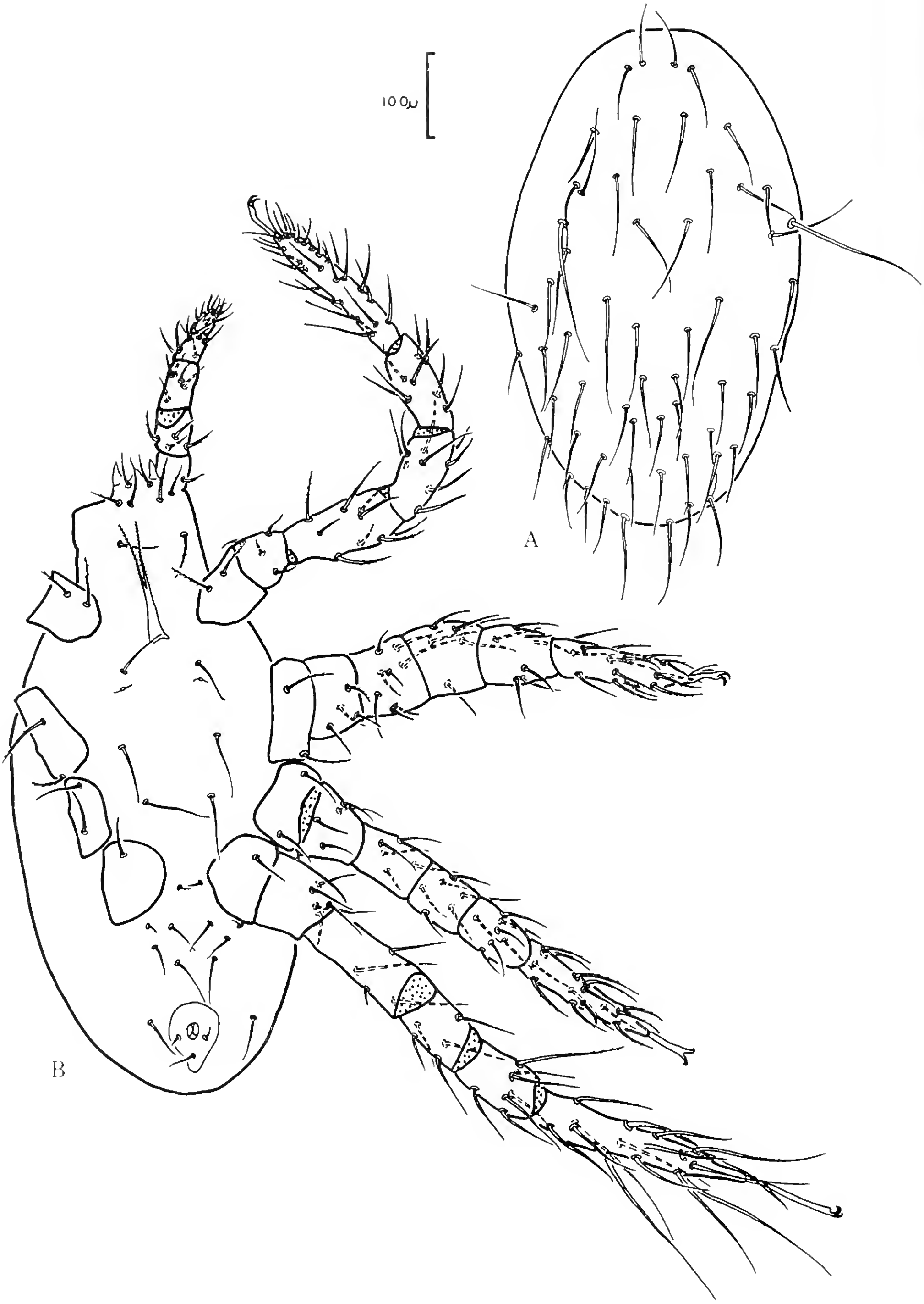

FIG. 30. *Parasitus perthecatus,* protonymph. A. dorsal chaetotaxy, B. ventral side.

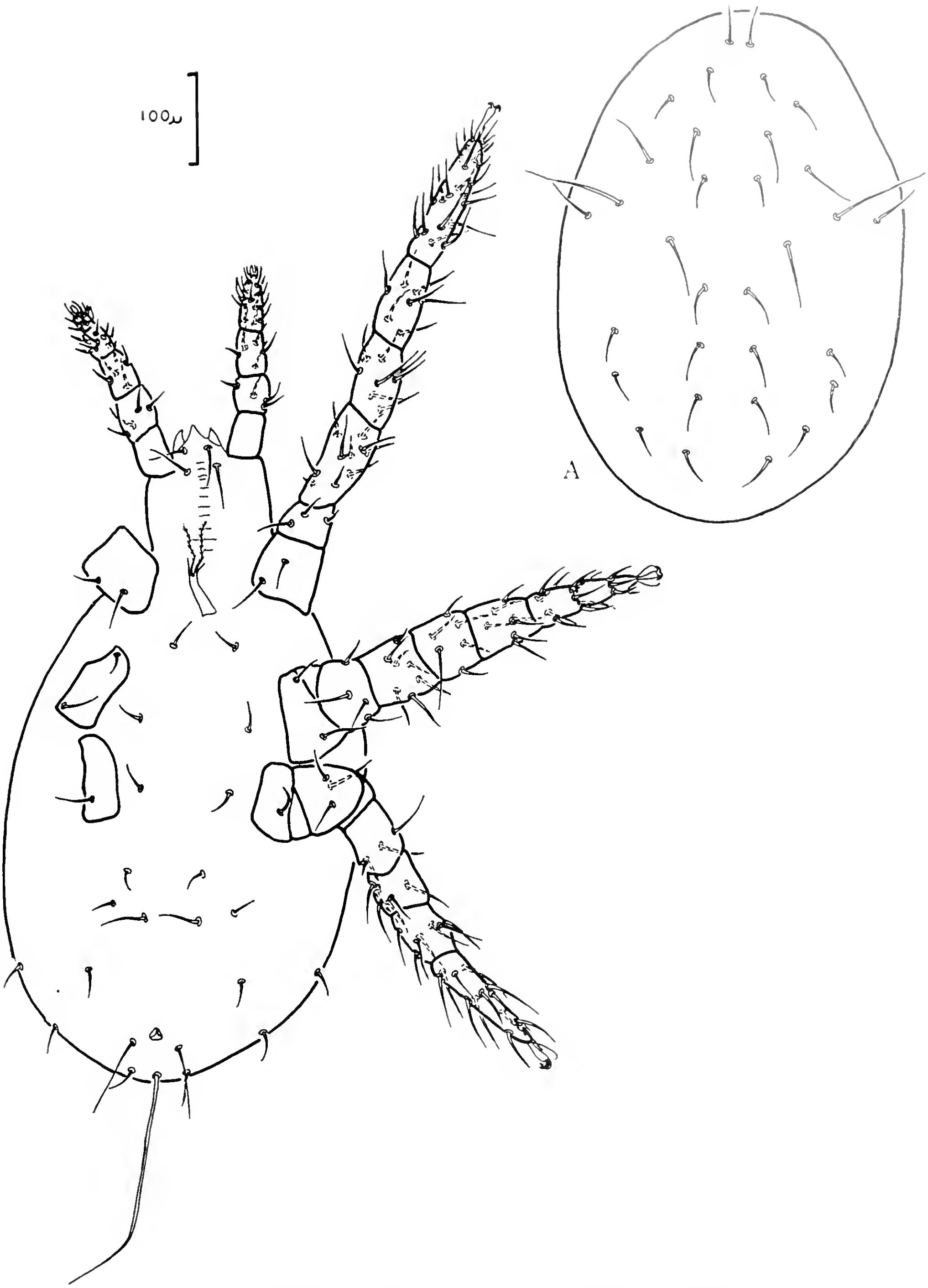

FIG. 31. *Parasitus perthecatus*, larva. A. dorsal chaetotaxy. B. ventral side.