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# PSYCHE

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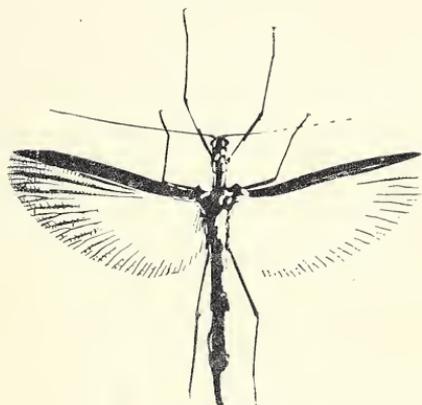
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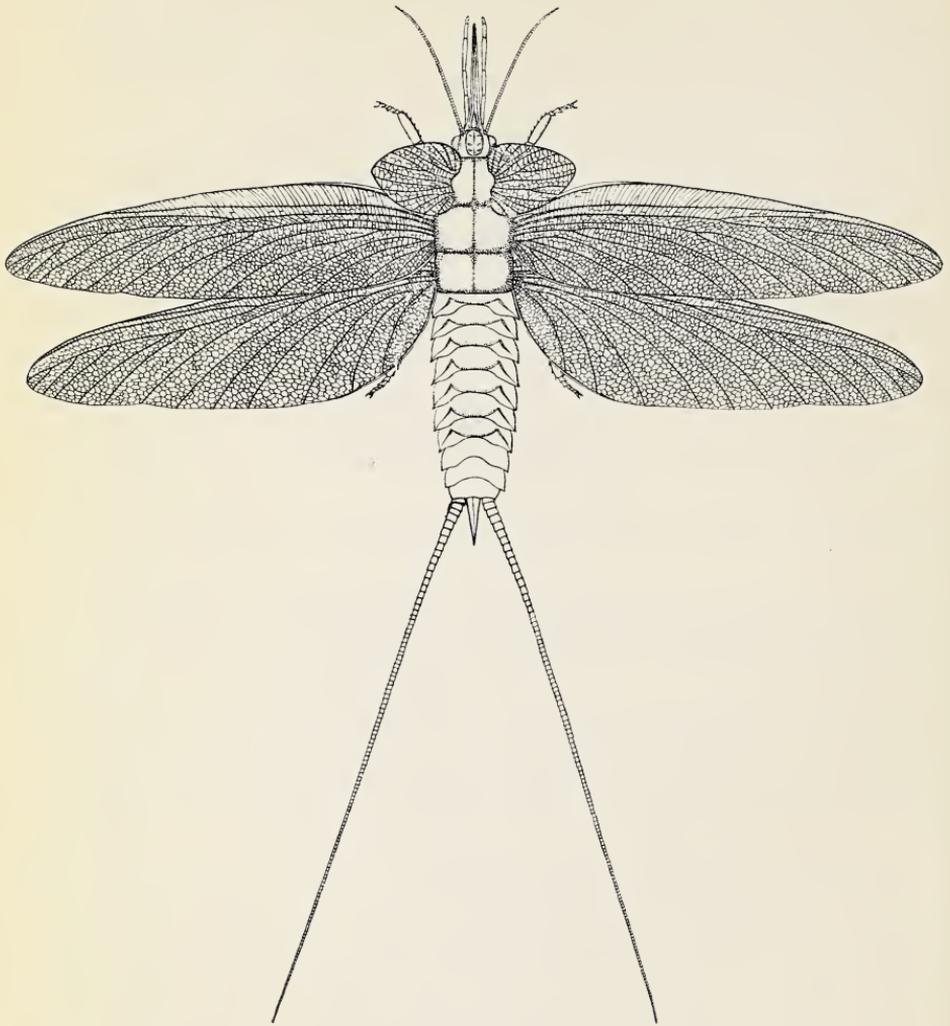


Figure 50. Reconstruction of *Stenodictya* based on specimens in the Institut de Paléontologie, Paris. For explanation, see text.

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## REVISIONAL STUDY OF THE ORDER PALAEODICTYOPTERA IN THE UPPER CARBONIFEROUS SHALES OF COMMENTRY, FRANCE. PART III<sup>1</sup>

BY JARMILA KUKALOVA<sup>2</sup>  
Charles University, Prague

The first two parts of these studies have dealt with eight families of the Palaeodictyoptera in the Commeny collection at the Institut de Paléontologie in Paris. The introductory discussion in Part I summarized the background of this investigation and the extent of the collection studied. The present part deals with the remaining family, the Dictyoneuridae, which is well represented in the Commeny shales. Some of the fossils of this group provide us with structural details that are otherwise unknown in the Palaeodictyoptera. In the concluding paragraphs of this paper I have summarized what is known of the wing and body structures of this extinct order of insects.

### Family Dictyoneuridae Handlirsch<sup>3</sup>

Stenodictyoptera Brongniart, 1885: 60; Brongniart, 1893: 380.

Stenodictyopteridae Pruvost, 1919: 98; Laurentiaux, 1953: 419.

Dictyoneuridae Handlirsch, 1906: 63; Handlirsch, 1911: 297; Lameere, 1917: 102; Handlirsch, 1919: 3.

Stenodictyidae Laurentiaux, 1952: 234.

<sup>1</sup>Published with the aid of a grant from the Colles Fund of the Museum of Comparative Zoology at Harvard College and a Grant-in-Aid of Research from the Society of the Sigma Xi. This study has also been supported in part by grants numbered GB2038 and GB7038 (F. M. Carpenter, Principal Investigator) from the National Science Foundation. Part I, dealing with the family Spilapteridae, was published in *Psyche*, Vol. 76, pp. 163-215; part II, dealing with seven additional families, was published in *Psyche*, Vol. 76, pp. 439-486.

<sup>2</sup>Alexander Agassiz Lecturer in Zoology, Harvard University, 1969.

<sup>3</sup>As noted by Handlirsch (1906) the name Stenodictyopteridae, which was not based on a generic name, is invalid. The name Stenodictyidae, used by Laurentiaux and based on *Stenodictya*, presumably in an attempt to retain a name similar to the one used by Brongniart, is, of course, a synonym of Dictyoneuridae, which was correctly formed by Handlirsch in 1906.

Type Genus: *Dictyoneura* Goldenberg, 1854.

Brongniart originally conceived of this family as characterized by the presence of a dense archedictyon and a specialized venation in which there were few branches. Marked attention was given to this family in later years and it played an important role in hypotheses on insect phylogeny. Brongniart's original and apparently correct conclusion on the specialized nature of the venation in this family was rejected or modified by subsequent investigators. Handlirsch, who considered the morphology of *Stenodictya* as supporting his theory of trilobite ancestry of insects [by having the prothoracic lobes and abdominal expansions derived from the trilobite cephalon and pleura (1908, p. 1304)], believed the Dictyoneuridae to be the most primitive of all Pterygota. He also thought the order Palaeodictyoptera was ancestral to all other insect orders. This latter view was rejected by Martynov (1925, 1938), who did, however, follow Handlirsch (1938, p. 19, 21) in his conviction that the Dictyoneuridae were the most primitive of the Palaeodictyoptera. Martynov based his conclusions on the presence of four features in the family: a uniform archedictyon, well developed prothoracic lobes, paranotal expansions along the abdomen, and a primitive venational pattern, the veins having few branches.

In the light of information acquired in recent years, the archedictyon seems to be only one of these traits that can be considered as primitive. In the geological record of insects, the archedictyon appears repeatedly in the more ancient forms of primitive groups, becoming irregular or reduced to cross veins in more advanced forms (e.g., Paleozoic Blattodea, Protorthoptera, etc.). On the other hand, the prothoracic lobes of *Stenodictya* and of other Dictyoneuridae, as far as known, do not differ from those of other Palaeodictyoptera and cannot be considered as being more primitive. Previous interpretations of the so-called expansions of the abdomen in *Stenodictya* seem to be very questionable, after careful study of the type specimens concerned. Incorrectly figured by Brongniart, who considered them to be homologous to the tracheal gills of mayfly nymphs, the expansions seemed to Handlirsch and Martynov as evidence for their respective hypotheses on insect evolution. Handlirsch assumed that the paranotal expansions of the abdomen of insects were derived from the pleura of trilobites because of the presence of an "oblique furrow." In his hypothesis on the origin of the Pterygota, Martynov assumed that wings of insects arose from the paranotal expansions which developed in hypothetical ancestral

forms on both the thorax and the abdomen, as they are still partially present in some Recent Thysanura (*Lepismatidae*). He considered the lateral abdominal expansions of *Stenodictya* to represent a very primitive stage of this development at a time when they were not yet completely reduced.

My examination of the Commeny dictyoneurids throws an entirely different light on the problem. The abdominal tergites of *Stenodictya* are heavily sclerotized with pointed and even prolonged posterolateral angles directed obliquely backwards. They are provided with oblique ridges, which, of course, have nothing to do with the "oblique furrow" of trilobite pleura, but are secondary structures, undoubtedly serving to strengthen the lateral parts of tergites. The longitudinal suture, separating the lateral parts of tergites in some other families of Palaeodictyoptera, is completely missing. Since the abdomen of *Stenodictya* was relatively broad, decomposition processes had a marked effect on the relationship of abdominal segments, as preserved. They were widely separated from each other so that much of the intersegmental membrane between the tergites is visible in most specimens. The prolonged posterolateral angles of tergites consequently overlap the following segments much less and they protrude much more towards the sides. Simply by cutting out single segments of an exact figure and arranging them back to normal position, the abdomen becomes shorter, with the tergites slightly protruding. The abdomen, so reconstructed, is very suggestive of that of many Neoptera (e.g., roaches) and undoubtedly represents a derived, specialized state of development. Other body parts of *Stenodictya* were heavily sclerotized as well, with deep, dense pits, exceptional for the Palaeodictyoptera. This strengthened cuticle probably provided protection against injury. Much more primitive, in my opinion, is the abdomen of some Palaeodictyoptera that have lateral lamellae present, i.e., with lateral parts of tergites separated by a longitudinal suture extending from the notum. These structures are probably homologous with lateral lamellae of some living mayfly nymphs but their function is not yet explained.

Martynov considered the venation of the Dictyoneuridae as the most primitive in the Palaeodictyoptera because of the presence of only a few branches (Comstock and Needham, 1898-99). The geological record, on the other hand, supports Redtenbacher's (1886) concept of the richer wing venation being present in the more ancient groups. This idea was followed and developed further by Lameere

(1922). For that reason I consider the venation of the Fouqueidae, and to a lesser extent that of the Spilapteridae, as more primitive and much closer to the supposedly ancestral type than that of Dictyoneuridae. Especially primitive, perhaps, are those genera with richly branched, convex and concave parts of M and Cu.

The venation of the Dictyoneuridae is an extremely simplified one for the Palaeodictyoptera and provides little basis for differentiation of taxa. It is therefore necessary to study the specimens in as much detail as possible in order to obtain full information. From my study of the Commeny material I am of the opinion that differences in cell shape of the archedictyon, the detailed outline of the posterior margin on the wings and distribution of cross veins and of the archedictyon may be useful for taxonomy. Nevertheless, the classification of isolated wings at both specific and generic levels is less satisfactory than in other families of the order.

In the Dictyoneuridae, the postcostal area is differently developed from that of all other families of Palaeodictyoptera. Arising from the very base of C, a single postcostal vein follows along the subcosta and terminates shortly on this vein. Commonly in the Palaeodictyoptera this subcostal vein is directed obliquely towards the costa, delimiting a triangular area and giving rise to several fine twigs. In the Dictyoneuridae also the precostal strip is very pronounced and broad, extending over the first third of the wing. Examining the other more specialized families, such as Eugereonidae, Calvertiellidae and Archaemegaptilidae, we note that the postcostal vein is completely reduced; on the other hand the precostal membranous strip is enlarged to form a true precostal area. The Dictyoneuridae apparently show the way in which the postcostal area became reduced in favor of the precostal area in the more advanced and specialized families. There is no doubt that the precostal area is a "younger" feature than the postcostal area, which developed by radial evolution in some groups only.

Thanks to Handlirsch's reconstruction, published in numerous textbooks of entomology and palaeontology, *Stenodictya lobata* is undoubtedly the most famous fossil insect known. Unfortunately, as this revisional study shows, no one feature given in Handlirsch's reconstruction is correct. In contrast to what he figures, the mouthparts of *Stenodictya* are actually modified for sucking, the head is provided with a large clypeal region, the prothoracic lobes have a venation and a cross venation, the wings are more slender distally than represented, Rs has more numerous branches, the arche-

dictyon is replaced by cross veins in the subcostal and sc-r areas, the tarsal segments are five in number, the abdomen shorter and narrower than represented, the lateral lamellae are not present (the posterolateral angles of tergites projecting only slightly), and the cerci are robust and long. Finally, Handlirsch's figure includes a combination of male and female features. His reconstruction of the prothoracic lobes, wings and part of the abdomen were based on Brongniart's specimen 22-1, which is a female, as shown by the presence of an ovipositor (see Figure 50). On the other hand, the end of the abdomen of Handlirsch's reconstruction was based upon Brongniart's specimen 22-2, which turns out to be a male and which probably represents a distinct species. The male claspers, incidentally, were misinterpreted by Handlirsch (Lameere, 1917, p. 158).

Following the significant discovery by Laurentiaux (1952) of the presence of the sucking beak in a previously unstudied specimen of *Stenodictya* (collection of the Institut, Paris), doubts about the presence of a beak in all Palaeodictyoptera have disappeared. On the basis of the photograph in Laurentiaux's paper, Sharov (1966, p. 118) gave a new reconstruction of *Stenodictya*. However, this reconstruction is also incorrect, mainly because the specimen itself was preserved so as to show a ventral view, although this was not apparent from the photograph. As a result, Sharov erroneously interpreted several features as dorsal in position. For example, the prothoracic lobes, appearing from underneath the body, were interpreted as a prothoracic shield; and vague outlines of a structure shown on the photograph only as the result of shading (but completely invisible in the specimen itself) is represented in the restoration as a separate small segment at the base of the beak in the place where, in the dorsal surface of the Palaeodictyoptera, there is the triangular, elongate labrum. Furthermore, the beak as represented in Sharov's reconstruction, should be longer than drawn, with long palpi present; the wings should have cross veins in the subcostal and the sc-r areas, the legs should have five tarsal segments; the cerci should be somewhat longer and the posterolateral angles of the tergites less projecting.

In the accompanying illustration (Figure 50) I am including a reconstruction of *Stenodictya* which, it should be noted, is a composite of structures present in several species of the genus, as follows: *S. lobata* Brongniart, specimen 22-1, for head, eyes, clypeus, prothoracic lobes, venation of fore and hind wings (in part), thorax,

abdomen, ovipositor, cerci; *S. pygmaea* Meunier for the shape of the prothoracic lobes; *S. oustaleti* Brongniart, specimen 22-3, and *S. agnita* (Meunier) for the five-segmented tarsi and legs; and *S. laurentiauxi*, n.sp., for the beak. It should also be pointed out that since the maxillary palpi are incompletely preserved in any specimen of *Stenodictya*, they have been represented in the restoration to the length of those in *Eugereon boeckingi* Dohrn; the labrum, which is indistinct in specimens of *Stenodictya*, is drawn as it is in various species of Palaeodictyoptera belonging to other genera; and the length of the ovipositor, also incomplete in specimens of *Stenodictya*, is drawn to its length in *Homaloneura ornata* Brongniart.

A dense archedictyon, more or less approaching that of the Dictyoneuridae and related families, occasionally occurs within the homoiopterid and spilapterid groups of families. In the Homoiopteridae it is very dense, for example in *Boltopruvostia nigra* (Kukalová, 1958), and it is well developed in *Homoioptera woodwardi*. In the Spilapteridae, the archedictyon is presumably completely reduced in all genera and the anastomoses between the cross veins are only rarely present, but the cross veins themselves are exceptionally dense. Nevertheless, in the closely related family Eubleptidae, there is a dense archedictyon between the cross veins. A special case of modified archedictyon occurs in the Fouqueidae, particularly in the genus *Fouquea*. The coarse, extremely dense cross venation in that genus recalls very much the process which has taken place in some roaches, in which the dense reticulation in the more primitive Carboniferous forms became restricted into markedly dense patterns in Permian forms. Nevertheless, among all Palaeodictyoptera, the archedictyon of the Dictyoneuridae is certainly the most even and tends least to form cross veins. Its presence, together with specialized morphological features, is not surprising, this phenomenon being known as mosaic evolution.

Of the genera included in the Dictyoneuridae by Laurentiaux (1953), *Athymodictya* Handlirsch is to be referred to the Eubleptidae, *Dictyoneurella* Laurentiaux to Archaemegaptilidae, *Mecynoptera* Handlirsch perhaps to Archaemegaptilidae and *Boltopruvostia* Pruvost to the Homoiopteridae.

The following are the basic characteristics of the Dictyoneuridae: Fore and hind wings very similar. Main veins without coalescence. Sc ending on costal margin beyond midwing; R<sub>1</sub> extending nearly to apex; R<sub>s</sub> with several branches; MA unbranched, usually strongly

curved; MP simple or branched; CuA unbranched; CuP simple or having several branches. Archedictyon well developed over most of the wings and usually dense.

Body structures: head with small projecting eyes and large clypeus. Antennae multisegmented, long. Prothoracic lobes large, with about eight radiating veins, often branched, and numerous, anastomosing cross veins; thoracic segments uniformly long, though the prothorax may be somewhat shorter than the others. Legs short, robust, tarsus 5-segmented, with claws and arolium. Abdomen relatively broad and short. Cerci in females long, multisegmented. Ovipositor in female curved, stout, reaching beyond the end of the body. Males with claspers arising laterally from the subgenital plate, composed of homonomous, carinated plates, directed obliquely and touching distally. Body and wings completely and densely covered by deep pits. All body parts heavily sclerotized.

The family Dictyoneuridae is related to the Eugereonidae, Archaemegaptilidae and Protagrionidae and is more distantly related to the Megaptilidae and Calvertiellidae.

The genera included in the Commeny shales: *Stenodictya* Brongniart, *Microdictya* Brongniart. The following genera, also in the family Dictyoneuridae, are from the Stephanian of Germany: *Dictyoneura* Goldenberg, *Stilbocrocis* Handlirsch, *Gleffia* Guthörl, *Rotundopteris* Guthörl, *Polioptenus* Scudder, *Dictyoneurula* Handlirsch, *Goldenbergia* Scudder, *Sagenoptera* Handlirsch, *Kallenbergia* Guthörl and possibly *Gegegenemene* Handlirsch.

#### Genus *Stenodictya* Brongniart

*Scudderia* Brongniart, 1885: 61; Brongniart, 1885: 277 (*nomen nudum*).

*Scudderia* Brongniart, 1890: 5 (nec *Scudderia* Grote, 1873).

*Stenodictya* Brongniart, 1893: 383; Handlirsch, 1906: 63; Handlirsch, 1919: 3; Pruvost, 1919: 308; Crampton, 1919: 54; Lameere, 1917: 157; Laurentiaux, 1953: 419; Sharov, 1966: 118.

Type species: *Scudderia lobata* Brongniart, 1890, SD Brongniart, 1893.

This genus was based originally on two species, *lobata* and *spinosa*, which Brongniart subsequently (1893) and incorrectly merged under one species, *lobata*.

In the Commeny collections in the Institut in Paris there are 22 specimens not figured or described by previous workers. These are mostly isolated wings and fragments of wings. Presumably, the flatness of the dictyoneurid wings and the indistinct venation prevented Brongniart and Meunier from making satisfactory observations on these specimens. By using glycerin, however, I was able

to work out the venation satisfactorily and to add descriptions of these specimens to the account included here.

Since the venation of the Dictyoneuridae is very simplified, as well as homogenous but individually variable, it does not offer much basis for taxonomy. The relative positions of the Rs origin and the M division into MA and MP, used as specific and even generic characters by many authors, may vary even within one individual specimen's fore and hind wings (see for example *Stenodictya laurentiauxi* sp. nov.). Also, the number of branches can only be used to a limited extent, as additional twigs are frequently formed by the archedictyon, elements of which may or may not reach the posterior margin. Having rich material for comparison at my disposal, I find that the general outline of the wings, especially the degree of undulation of the posterior margin and the detailed structure of the archedictyon (shape and size of cells, areas occupied by cross veins, presence of twigs) are the same in fore and hind wings and are therefore additional and useful taxonomic characters.

In view of the situation noted above, I believe it is not advisable to form new genera in this family unless they are completely obvious and necessary, since such taxa just cannot be satisfactorily substantiated. I have not been able to study Dictyoneuridae in deposits other than that of Commeny but it seems very probable that the total number of genera will diminish after revisional studies.<sup>4</sup>

The wings of the Dictyoneuridae are about equal in length or the hind pair may be a little shorter; they are similar in venation and in the undulation of the posterior margin. Fore wing with the anterior margin strongly curved near the base. Precostal strip pronounced; postcostal veins simple, arising from the very base of C, ending on Sc or forming a fork towards C and Sc. Sc terminating beyond midwing. Rs pectinate, originating at about mid-wing; MA, MP, CuA, CuP usually simple and parallel, sometimes with additional twigs formed by the archedictyon. Anal area relatively broad, with about five anal veins, sometimes forked. Archedictyon irregular, occasionally producing twigs. In the costal, sc-r and proximal part of r-m areas there are dense, regular cross veins,

<sup>4</sup>In the collections of the Institut, I was not able to find the type specimen of *S. vasseurii* Meunier, 1914. Since the specimen was not present in the collection in 1938 (pers. comm., F. M. Carpenter) and since no photograph of it exists, I have not included this species in my present account. *S. minima* Brongniart, 1893, is based on a very fragmentary specimen and since it shows no other characteristic than the small size, I am referring this species to Dictyoneuridae inc. gen.

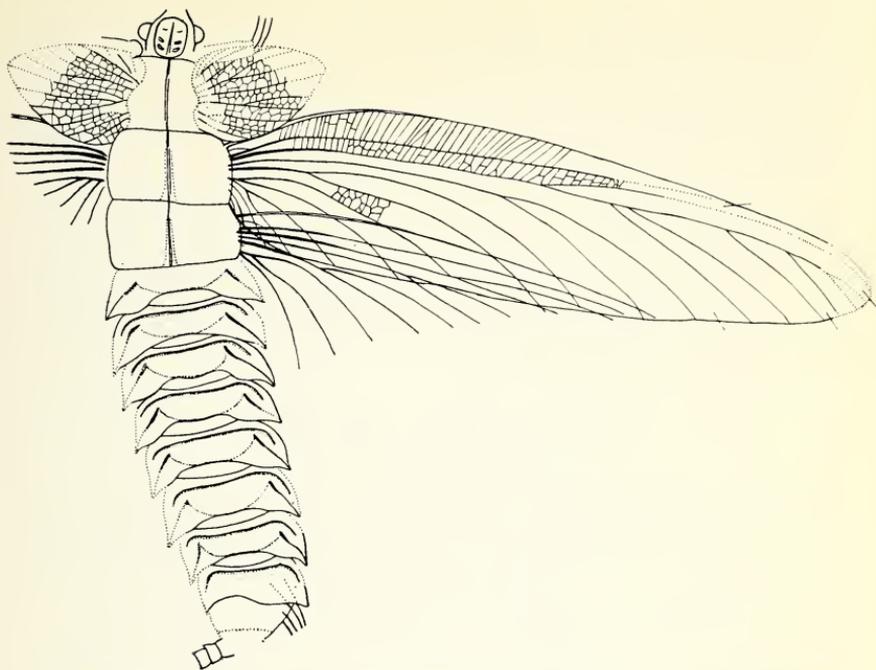


Figure 51. *Stenodictya lobata* (Brongniart); specimen 22-1. Holotype.

connected by anastomoses. Hind wing slightly broader, broadest shortly beyond the first quarter of wing length.

Body structures: Head small, narrower than prothorax. Eyes projecting, clypeus large. Antennae composed of narrow and long segments. Beak long, with long palpi. Prothoracic lobes large, cordate, with fan-like venation and irregular, anastomosing cross venation. Thoracic segments either equal in length or the prothorax shortest. Legs short, tibiae only slightly prolonged, sometimes provided with spines. Tarsi with long claws. Abdomen slightly longer than half the wings. Posterior margin of terga convexly curved in the central part. Posterolateral angles pointed, more or less produced. Lateral parts of terga with oblique ridges. Females with a stout, curved ovipositor and robust cerci. Males with claspers, arising posterolaterally from beneath the 9th tergite and composed of about 12 small segments of equal size, each with a short median carina.

*Stenodictya* differs from *Dictyoneurula* Handlirsch by the short Sc and simple MP. From another related genus, *Microdictya*

Brongniart, it differs in having its wings broadest just beyond the base, narrower in the apical third, and by having the costal area broader, C, Sc and R more curved towards the base, MP and CuP usually simple, the anal area larger, the hind wing broader and of triangular shape. From all other genera it differs in its simplified venation with unbranched MP and CuP.

Species included in Commeny shales: *Stenodictya lobata* (Brongniart, 1885); *S. spinosa* (Brongniart, 1885); *S. agnita* (Meunier, 1908); *S. pygmaea* (Meunier, 1911); *S. grandissima* (Meunier, 1911); *S. oustaleti* (Brongniart, 1893); *S. arnaudi* (Brongniart, 1893); *S. klebsi* (Meunier, 1908); *S. laurentiauxi* spec. nov.; *S. parisiana* spec. nov.

### *Stenodictya lobata* (Brongniart)

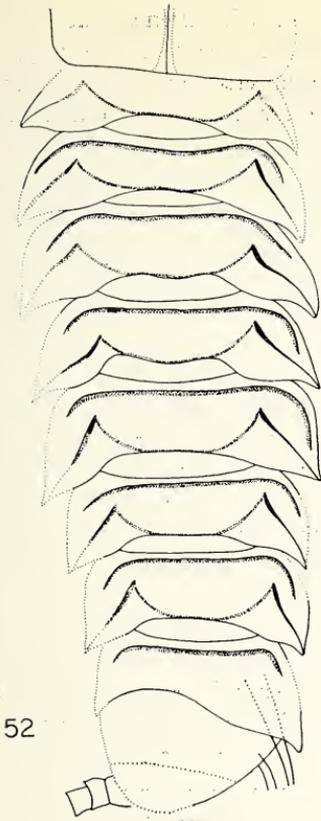
Figures 50, 51, 52

*Scudderia lobata* Brongniart, 1890: pl. II, fig. 2, 3.

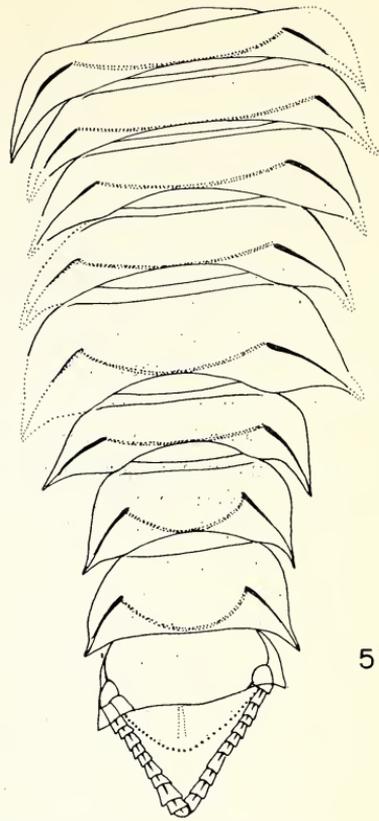
*Stenodictya lobata* Brongniart, 1893: 386, pl. 22, fig. 1; Handlirsch, 1906: 64, pl. 8, fig. 20; Handlirsch, 1911: 181, pl. 6, fig. 1 (reconstruction); Handlirsch, 1913: 513 (reconstruction); Handlirsch, 1921: 129, fig. 54 (reconstruction); Handlirsch, 1919: 3; Pruvost, 1919: 98, fig. 24; Laurentiaux, 1952: 237; Sharov, 1966: 118, fig. 52 (reconstruction).

The type specimen of this species was first figured by Brongniart in 1890 (pl. 2, fig. 2, 3) as *Scudderia lobata*; in 1893 it was illustrated with the name *Stenodictya lobata* (22-1). The specimen which Brongniart figured in his latter paper (pl. 22-2) as *lobata* was the one on which he previously (1890) based *spinosa*. As stated in the footnote on page 386 of the 1893 work, he considered *spinosa* to be a synonym of *lobata*. However, I believe that Brongniart was in error in this conclusion and I am convinced that *spinosa* is a distinct species. In all figures, Brongniart showed *lobata* (specimen 22-1) as having the incompletely preserved claspers similar to those of *spinosa* (specimen 22-2). This is not correct, however, the end of the abdomen on specimen 22-1 being distorted and showing on the left side bases of the cerci and on the right side the base of the ovipositor.

Some confusion has existed in the literature about the lateral portions of the tergites. Lameere (1917, p. 158) correctly noted that the lateral parts of the tergites have the same surface texture and sclerotization as the median part of the tergites and that they are not separated by any suture from the rest of the tergites. The transverse ridge, running near and parallel to the anterior margin of the abdominal segments, Lameere considered to be a suture



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Figure 52. *Stenodictya lobata* (Brongniart); specimen 22-1; detail of abdomen.

Figure 53. *Stenodictya spinosa* (Brongniart); specimen 22-2; detail of abdomen.

dividing the tergites. The oblique ridge which extends out from the posterolateral angles of the segment ends freely on the tergite surface and is not connected with the transverse ridge. All structures mentioned in all probability served to strengthen the abdominal wall.

Fore wing: length 66 mm, width 17.5 mm. Anterior margin convex, posterior margin with a convex curvature at the end of MA; apical third of wing very narrow; subcostal area broad, but narrowing a short distance beyond the base of the wing. Rs with 5 simple branches. Anal area with 6 veins, mostly unbranched. Cross veins in the subcostal area and the sc-r area dense, regular, with but few anastomoses.

Body structures: Head 1.5 mm long; 7 mm broad. Clypeus very large, quadrangular in form and having a median ridge and three pairs of transverse ridges, the anterior pair being weakly indicated. Prothoracic lobes reaching about  $\frac{2}{3}$  the width of the fore wing, with 7 branched veins. Thoracic segments about equal in length and each with a median furrow. Length of mesothorax, 7.8 mm, of metathorax 7.2 mm. Prothorax narrower than mesothorax. Abdomen slightly broader than thorax, about 39 mm long. Lateral parts of abdominal segments laterally dilated; posterolateral angles pointed, projecting somewhat laterally. First abdominal segment slightly narrower than the following ones, the other abdominal segments almost equal in size; transverse tergal suture well developed.

*Stenodictya lobata* differs from *spinosa* in having longer thoracic segments, a narrower abdomen, less pronounced posterolateral angles on the tergites; and a broader forewing, which lacks the pronounced convex curve along the hind margin.

*Stenodictya spinosa* (Brongniart)

Figures 53, 54

*Scudderia spinosa* Brongniart, 1890: 6, pl. II, fig. 1.

*Stenodictya lobata* Brongniart, 1893: pl. 22, fig. 2.

Brongniart's attempt to synonymize *spinosa* with *lobata* has already been noted. The original figure of specimen 22-2 showed some significant differences as compared with the type specimen of *lobata*, such as the size of the thoracic segments, the length of legs, the shape of the wings and the structure of the abdomen — all of which are certainly acceptable as the bases for specific differentiation in the Palaeodictyoptera. Sexual dimorphism, of course, can not be excluded as an explanation of these differences, *spinosa* obviously

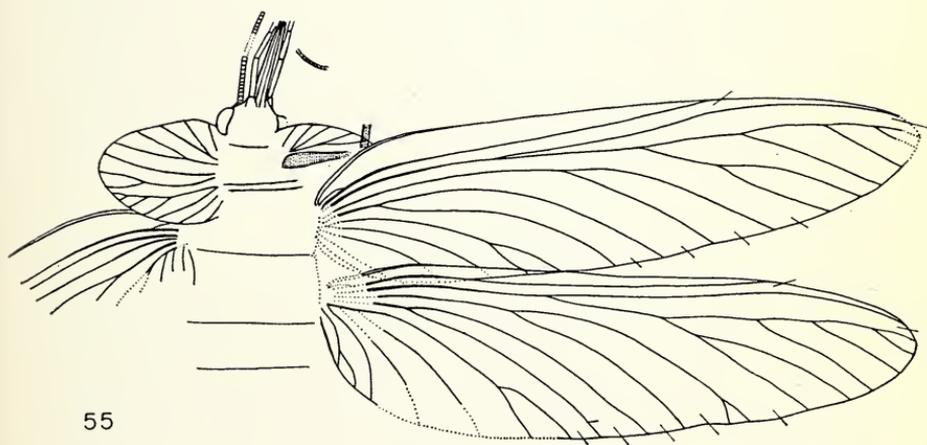
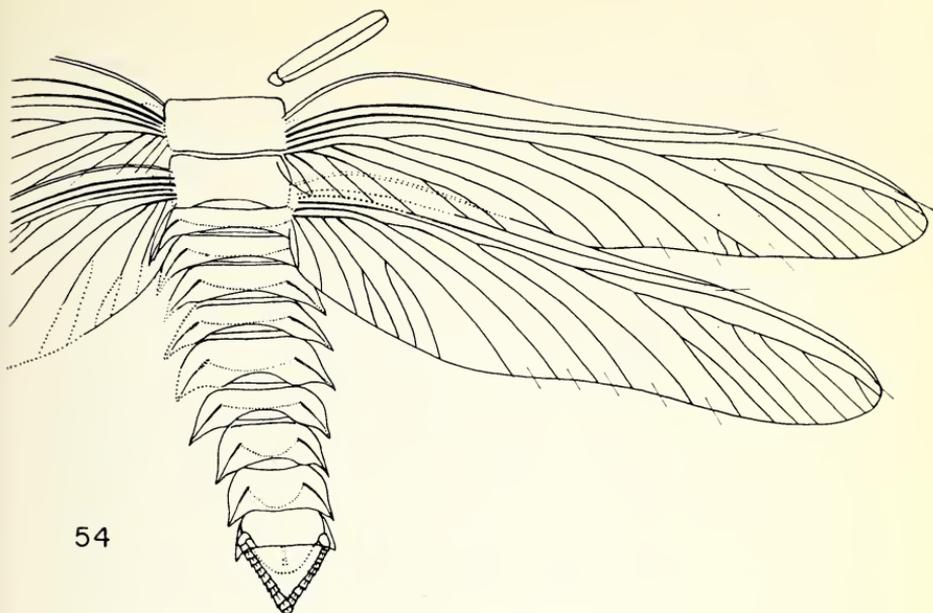


Figure 54. *Stenodictya spinosa* (Brongniart); specimen 22-2. Holotype.  
Figure 55. *Stenodictya laurentiauxi* sp. nov. Holotype.

being a male and *lobata* a female; but since there is no information at all about the sexual dimorphism in the Palaeodictyoptera, I consider it preferable to retain Brongniart's *spinosa* as a distinct species.

*Stenodictya spinosa* represents the only male known of the Commeny Palaeodictyoptera with claspers preserved. A study of them under glycerin has added some further details. They are much more primitive than those of the Permian Megasecoptera (Carpenter, 1939) and of the Permian and Recent Ephemeroptera. In both of these latter orders, the claspers are jointed at about the middle. The Palaeodictyoptera is the only known order in which the claspers are directed towards each other beyond the basal segment, which is slightly larger than the following ones.

The following account is based on specimen 22-2: Fore wing length 61 mm, width 13 mm. Anterior margin strongly convex proximally, very slightly concave at about mid-wing; posterior margin slightly concave from MP to CuP. Apical part narrowed. Subcostal area broadened, narrowing abruptly towards the base. Rs with 6 branches, the first branch forked; anal area large with 6 veins, two of them forked. Hind wing: length 61 mm, width 15 mm.

Body structures: mesothorax 5.4 mm long, metathorax 4.5 mm long. Abdomen about 40 mm long. Abdominal segments unequal, segments one and two shorter than the following ones. First tergite 2.2 mm long, 19.6 mm wide; 5th tergite 5 mm long; 7th tergite 11 mm wide. Claspers 9.2 mm long.

The differences between the *spinosa* and *lobata* have been discussed above. From *S. laurentiauxi* spec. nov., *spinosa* differs in the narrower wings, especially in their distal portions by the presence of the concavity along the posterior margin and by the more distal origin of Rs.

### *Stenodictya laurentiauxi* sp. nov.

Figures 55, 56

*Stenodictya lobata* Laurentiaux (*nec* Brongniart), 1952: 233-247, pl. 10, 10a.

The type specimen of this species has historical significance for the study of insect evolution. For many years the general belief of the students of fossil insects was that the paleopterous orders of the Paleozoic, being generally primitive in nature and geologically old, must have had chewing mouthparts. The erroneous nature of this concept was apparent when Laurentiaux (1952) described the presence of a long, haustellate beak in the "classical" representative

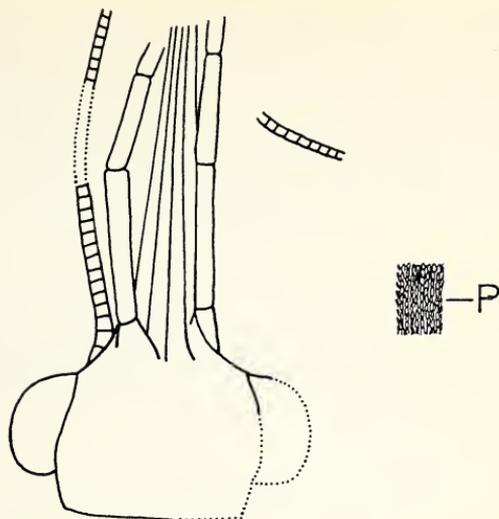


Figure 56. *Stenodictya laurentiauxi* sp. nov.; head, ventral view. P, surface of palpus, enlarged.

of the Palaeodictyoptera, *Stenodictya*, in a previously unstudied specimen which he found in the collections of the Sorbonne in Paris (subsequently deposited in the Institut).

Laurentiaux called attention to the similarities of the structure of the mouthparts of this specimen to that of *Eugereon boeckingi* Dohrn, from the Permian of Germany. He correctly concluded that the specimen as preserved shows the head and mouthparts from the ventral surface. Of all the specimens which I have seen, this is the only one showing the ventral view of the beak. The long palpi can be seen to arise beneath the stylets (more probably under the inner pair), which explains their close position to the base of the outer stylets when the beak is observed from the dorsal view in other specimens. The base of the beak itself is very indistinct so that other structures, such as the labium, cannot be distinguished. From my examination of the wings and body structures of the specimen which Laurentiaux described, I am convinced that this cannot be referred to *lobata* or *spinosa* and that it represents still another species. The formal description of this species, which I have the pleasure to name for Dr. Laurentiaux, Professor of Geology at Reims, is as follows: Fore wing length 64 mm, width 17 mm. Anterior margin convexly curved at the base, then straight; posterior margin with a slight indentation at MP. Apical part broad, apex

obtuse. Costal area only slightly broadened; Rs originating well before the middle of the wing, with four branches. Anal area small, with five branches. Hind wing length 64 mm, width 18 mm. There are minor venational peculiarities in the wings of this fossil but these are almost certainly individual traits and not specific ones. For example the level of the division of M is anterior to the origin of Rs in the fore wing but it is posterior to the origin of Rs in the hind wing.

Body structures: length of head 5 mm, width about 9 mm. Antennae composed of many short segments. The length of the beak, incompletely preserved, 8.6 mm. The palpi originate beneath the stylets, probably under the inner pair; segments of palpi with longitudinal, rugose ridges; first segment length .8 mm, 2nd 3.9 mm and 3rd 2.3 mm.

*Stenodictya agnita* (Meunier)

Figures 57, 58, 61

*Microdictya agnita* Meunier, 1908: 155; Meunier, 1908: 39, fig. 3; Meunier, 1909: 136, pl. 1, fig. 7.

*Stenodictya gaudryi* Meunier, 1908: 139; Meunier, 1909: 42, fig. 2.

*Stenodictya fayoli* Meunier, 1909: 134, pl. 1, fig. 5; Lameere, 1917: 153; Handlirsch, 1919: 4, fig. 2.

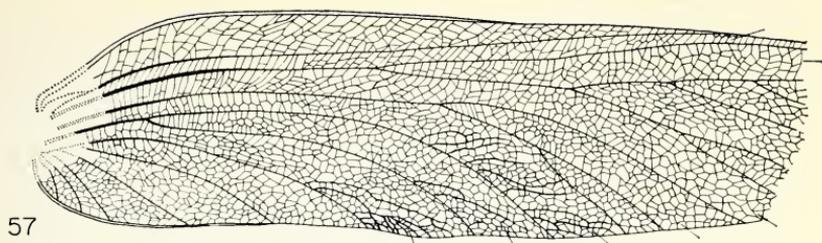
*Stenodictya agnita* Handlirsch, 1919: 3, fig. 6.

This species was based by Meunier on an isolated, incomplete fore wing with a well preserved archedictyon that forms numerous twigs. In the collections of the Institut in Paris I found another fore wing, completely preserved, which I am referring to the same species.

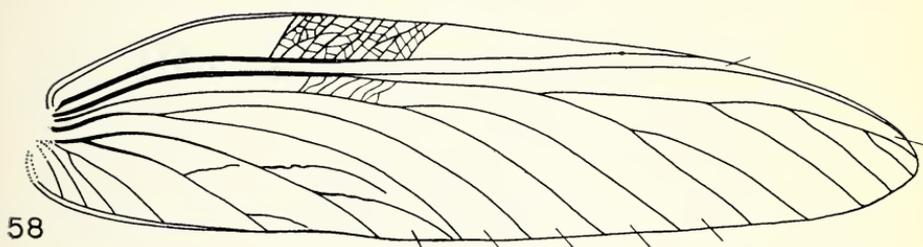
Comparing the type specimen of *agnita* with the type of *fayoli* (originally referred by Meunier to *S. gaudryi* Brongniart), I was unable to find any significant differences. Both the specimens are very similar in venation, in the details of the form of the posterior margin, in the nature of the archedictyon and the general shape of its cells. I am therefore synonymizing *fayoli* with *agnita*.

The following account is based on all three specimens of *agnita*.

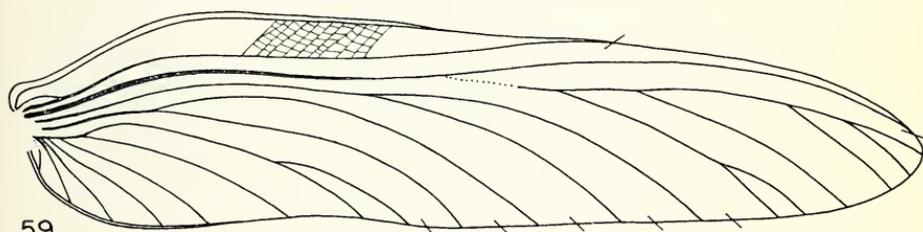
Fore wing: length 70-74 mm, width 15.5-18 mm. Anterior margin convexly curved proximally, then almost straight. Posterior margin with two concavities between 1A and CuP and at the end of CuA. Apical part of wing gradually narrowing. R-rs area broad; Rs originating before mid-wing, with 4-6 branches; MP simple or with an additional branch. Anal area with six veins. Archedictyon dense, strong, forming extra twigs. Many anastomoses between cross veins.



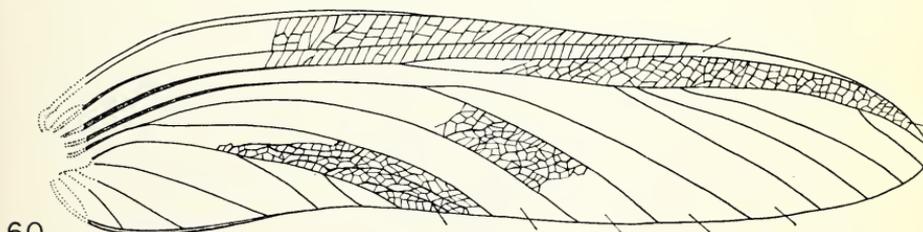
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Figure 57. *Stenodictya agnita* (Meunier); fore wing. Holotype.

Figure 58. *Stenodictya agnita* (Meunier); fore wing.

Figure 59. *Stenodictya perrieri* Brongniart; fore wing, specimen 22-4. Holotype.

Figure 60. *Stenodictya perrieri* Brongniart; fore wing.

Body structures: Prothoracic lobes large, cordate, their 8 veins often forked and having numerous, irregular cross veins connected by anastomoses. Length of mesothorax 7.9 mm. Legs relatively long, with slender tibiae, long tarsi and claws. Mesothoracic tibia 9.6 mm long; tarsus and claws combined 11.03 mm; metathoracic tibia 12.4 mm long.

*Stenodictya agnita* is related to *perrieri* Brongniart from which it differs only in details of form of the posterior margin and in the more proximal origin of Rs. These two species may eventually turn out to be synonymous.

*Stenodictya perrieri* Brongniart

Figures 59, 60

*Stenodictya perrieri* Brongniart, 1893: 384, pl. 22, fig. 4; Handlirsch, 1906: 64, pl. 8, fig. 22; Handlirsch, 1919: 3.

This species was based by Brongniart on specimen 22-4, a complete fore wing. The cross veins in the subcostal area are more regular than shown in Brongniart's figure. I am referring to this species another undescribed fore wing, which differs from the type specimen in the more pronounced convex curvature of the posterior margin.

Fore wing: length 65 mm, width 15 mm. Anterior margin convexly curved basally, then almost straight. Posterior margin with pronounced convex curvature at the end of the basal third of the wing length, then straight. Apical part of wing moderately narrowing. Subcostal area relatively broad and short; Rs originating at the mid-wing, with 4 branches. Anal area large, with 7 branches.

As noted above this species is closely related to *agnita* from which it differs in the minor respects already noted.

*Stenodictya thevenini* Meunier

Figure 62

*Stenodictya thevenini* Meunier, 1908: 154; Meunier, 1908: 37, fig. 1; Meunier, 1909: 133, pl. 1, fig. 2; Handlirsch, 1919: 5, fig. 5.

This species was based by Meunier on a perfectly preserved fore wing, distinct from any other known species of *Stenodictya*.

Fore wing: length 78 mm, width 18 mm. Anterior margin very convex proximally, with a pronounced concavity just beyond mid-wing. Posterior margin slightly concave. Apical part of wing gradually narrowing. Sc extending far beyond mid-wing; Rs originating beyond first third of wing length, with four branches. Anal area large, with 5 veins. Archedictyon with elongate cells.

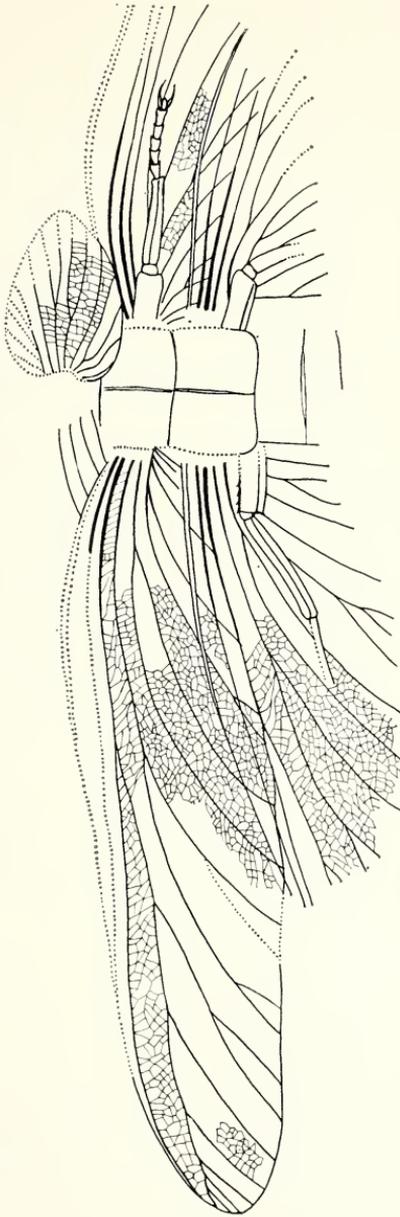


Figure 61. *Stenodictya agnita* (Meunier) (holotype of *Stenodictya fayoli* Meunier).

*Stenodictya thevenini* differs from all other known species by its very long and narrow wing, pronounced concavity of the anterior margin and the presence of elongate cells in the archedictyon.

*Stenodictya pygmaea* Meunier

Figure 64

*Stenodictya pygmaea* Meunier, 1911: 120, fig. 3; Meunier, 1912: 10, pl. 6, fig. 3; Handlirsch, 1919: 5, fig. 4.

This species was based by Meunier on a specimen consisting of fragments of fore and hind wings and on a perfectly preserved prothoracic lobe. The structure of the lobe, which is unusually broad and exceptional in the branching of its veins, would seem to justify the recognition of this specimen as a separate species.

The prothoracic lobe of the specimen of *pygmaea*, being unusually large and very well preserved, presents a rare opportunity to study this highly interesting structure of the Palaeodictyoptera in detail. Its narrow attachment, the shape of the lobe itself, the presence of veins and cross veins support Brongniart's conclusion about the homology of this structure with the functional wings. The lobes are attached to the prothorax along a cuticular thickening in the middle part of the base, from which the veins radiate. Actually, the nature of the attachment corresponds to that of the functional wings. Since the veins lack any trace of concentration along the costal margin ("costalization"), and since the base of the lobe shows no articular sclerites, the lobes probably never functioned as active organs of flight.

The venational pattern of prothoracic lobes does not completely follow Lameere's (1922) hypothetical scheme of the original venation of true wings, the veins (R, Rs, MA, MP) always arising from the ridge separately, not from two common stems. This is true of all prothoracic lobes which I have been able to study. Nevertheless, the "cubitus" in almost all of the prothoracic lobes is very much like that of the functional wings, being characteristically S-shaped and two-branched. The number of branches arising from the cuticular ridge is variable and differs to some extent in each specimen. This is because in most specimens the twigs of "Sc" arise from the base separately and also because the number of independent "anal" veins varies. There is no homologizing of the veins by convexities and concavities, since, in all of the lobes which I have had the opportunity to study, the fluting is absent.

The independent origin of the branches of veins in the prothoracic lobes (excepting Cu and sometimes Sc) seems to me to be a derived

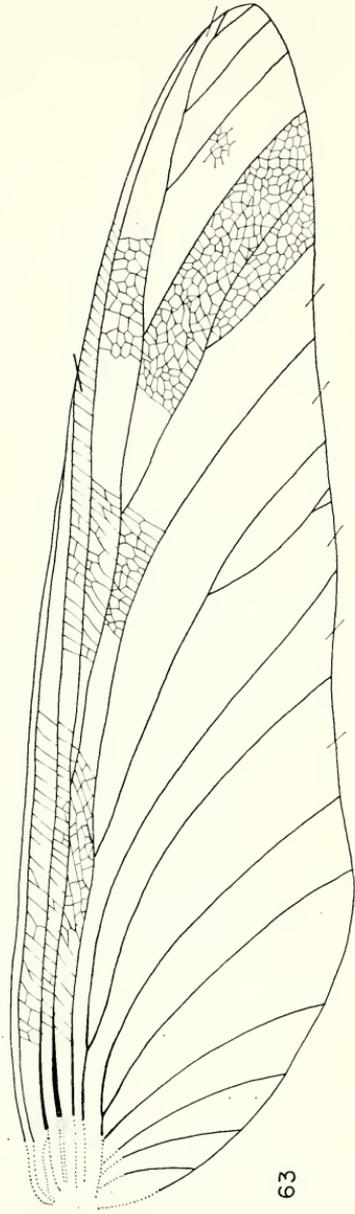
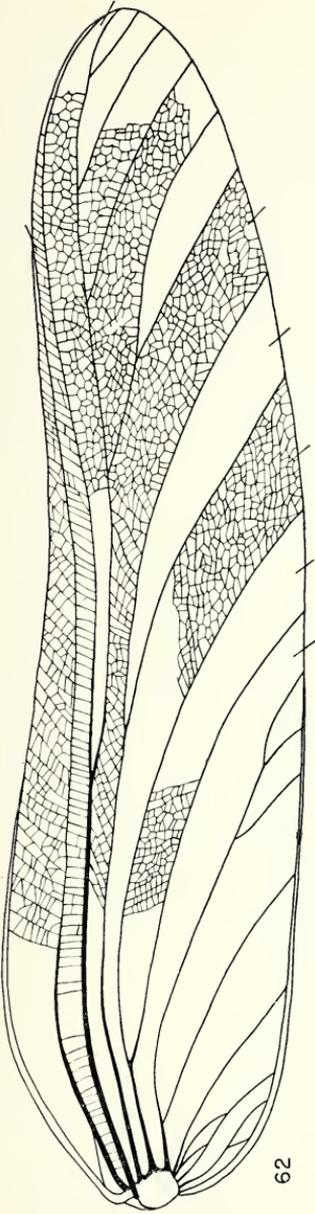


Figure 62. *Stenodictya thevenini* Meunier; fore wing, Holotype.

Figure 63. *Stenodictya grandissima* Meunier; hind wing, Holotype.

condition and not an original, primitive one. On the other hand, the almost symmetrical radiation of the veins in the lobes seems to indicate what was probably the original distribution of venation, before the veins were arranged more nearly longitudinally especially to support the anterior margin of the wing in connection with flight.

In figure 63 I have attempted to identify the pronotal veins of *pygmaea*. Although Sc seems to be obvious by its position and its pectinate series of branches and Cu by its position and sigmoidal course, the designation of the other veins is purely arbitrary.

One of the surprising features of the prothoracic lobes is the extent to which they overlap the forewings. But in all probability the lobes were high on the prothorax, which was presumably rounded above, so that there was probably enough space for the movement of the fore wings without there being any interference by the lobes. At the same time, the lobes, which were attached along a very narrow ridge, were probably capable of being moved by the action of the fore wings or perhaps by air currents.

In the collections of the Institut there are several fragments of Palaeodictyoptera labeled by Meunier as *Stenodictya pygmaea*. These are so incomplete that they can only be referred to Dictyoneuridae inc. gen. The following account is based on the type specimen of *pygmaea* only. Fore and hind wings of the typical *Stenodictya* character. Body structures: prothoracic lobe, 15 mm long, 14 mm wide. Anterior and posterior margins strengthened near the base; the apex pointed, directed somewhat anteriorly. Veins of lobe radiating independently from a basal, cuticular ridge. Sc apparently sending out a pectinate series of 4 branches; "R" and "Rs" simple; "MA" forked, directed above apex, "MP" simple, curved; Cu sigmoidal, dividing into "CuA" and "CuP", both of these being forked. One "anal" vein. Cross veins numerous, irregular, anastomosed. Prothoracic lobe sclerotized, covered by numerous deep pits.

### *Stenodictya grandissima* Meunier

#### Figure 63

*Stenodictya grandissima* Meunier, 1911: 121, fig. 4; Meunier, 1912: 11, pl. 7, fig. 5; Handlirsch, 1919: 3, fig. 1.

*Microdictya grandissima*, Lameere, 1917: 159.

This species was based by Meunier on the largest wing so far known within the Dictyoneuridae. Lameere (1917, p. 159) believed that, because of the branched MP, this species should be referred to the genus *Microdictya* Brongniart, close to "*Microdictya*"

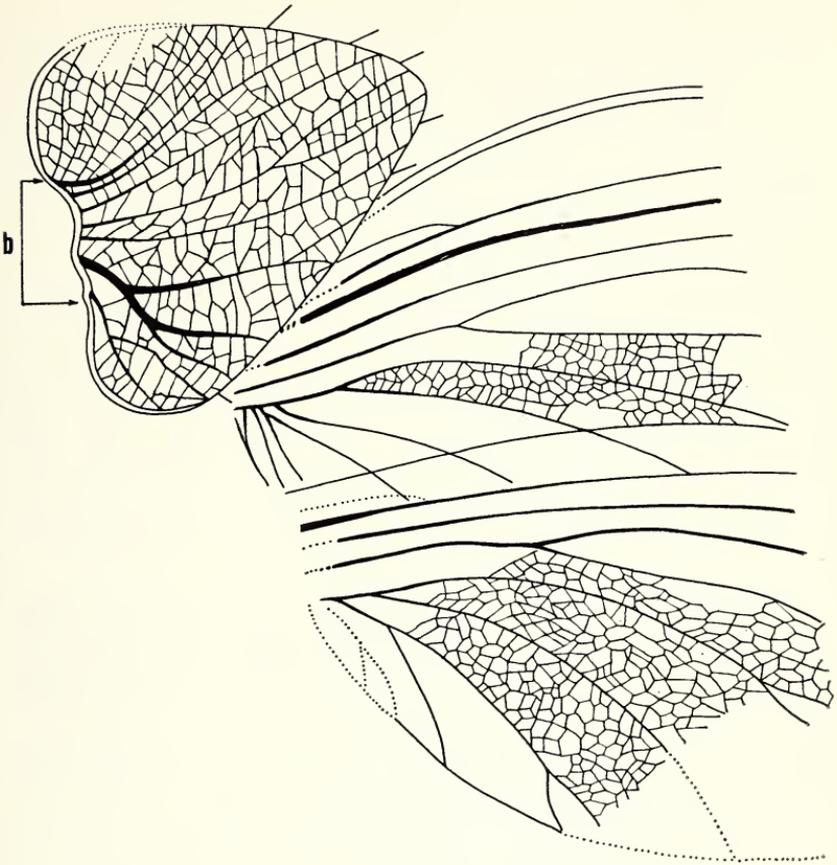


Figure 64. *Stenodictya pygmaea* Meunier. Holotype. Prothoracic lobe, basal parts of fore and hind wings; b, basal attachment of prothoracic lobe.

*agnita* Meunier. However, this is not correct, because though both branches of M and Cu are usually simple in *Stenodictya*, additional twigs may be formed by the archedictyon. The triangular shape of the stenodictyid hind wing, which is very different from the oval shape of the microdictyid hind wing, with its narrow cubital area and simple CuP, provides the more reliable basis for determining the generic position of *grandissima*.

*Stenodictya oustaleti* Brongniart

Figure 65

*Stenodictya oustaleti* Brongniart, 1893: 388, pl. 22, fig. 3; Handlirsch, 1906: 65, pl. 9, fig. 1; Handlirsch, 1919: 3.

This species was based by Brongniart on specimen 22-3, consisting of a complete hind wing, indistinct body and three legs. The legs are very well preserved, showing tiny tibiae, tarsal segments and short claws. Lameere (1917, p. 159) considered *oustaleti* synonymous with *fritschi* Brongniart. This may be so but it cannot be verified since the type and only known specimen of *fritschi* is fragmentary.

Hind wing: length 70 mm, width 19.5 mm. Anterior margin slightly convex proximally, then straight; posterior margin with slight concavity at MA and CuA; apical part of wing long and narrow. Rs originating before mid-wing with six branches. Anal area large, with 6 veins, 1A forked.

Body structures: legs short and stout, tibiae only a little longer and more slender than femora, with distinct spines; a deep suture extends across the femora proximally just before the end; tarsus stout, composed of 5 subequal segments; claws short. Mesothoracic femora 7 mm long, tibia 8.5 mm long and tarsus 8 mm long; metathoracic tibia 10 mm long (incompletely preserved).

*S. oustaleti* differs from all other known species of the genus by the elongate and narrow apical part of the wing, by the numerous densely arranged branches of Rs; it is somewhat similar to *S. arnaudi* Brongniart by the large anal area, with a forked 1A.

*Stenodictya arnaudi* Brongniart

Figure 66

*Stenodictya arnaudi* Brongniart, 1893: 385, pl. 22, fig. 6; Handlirsch, 1905: 64, pl. 8, fig. 23; Handlirsch, 1919: 3; Lameere, 1917: 158.

This species was based by Brongniart on specimen 22-6, a hind wing, lacking the apex. Lameere (1917, p. 158) noted that the hind wing of *arnaudi* could well belong to the same species as the

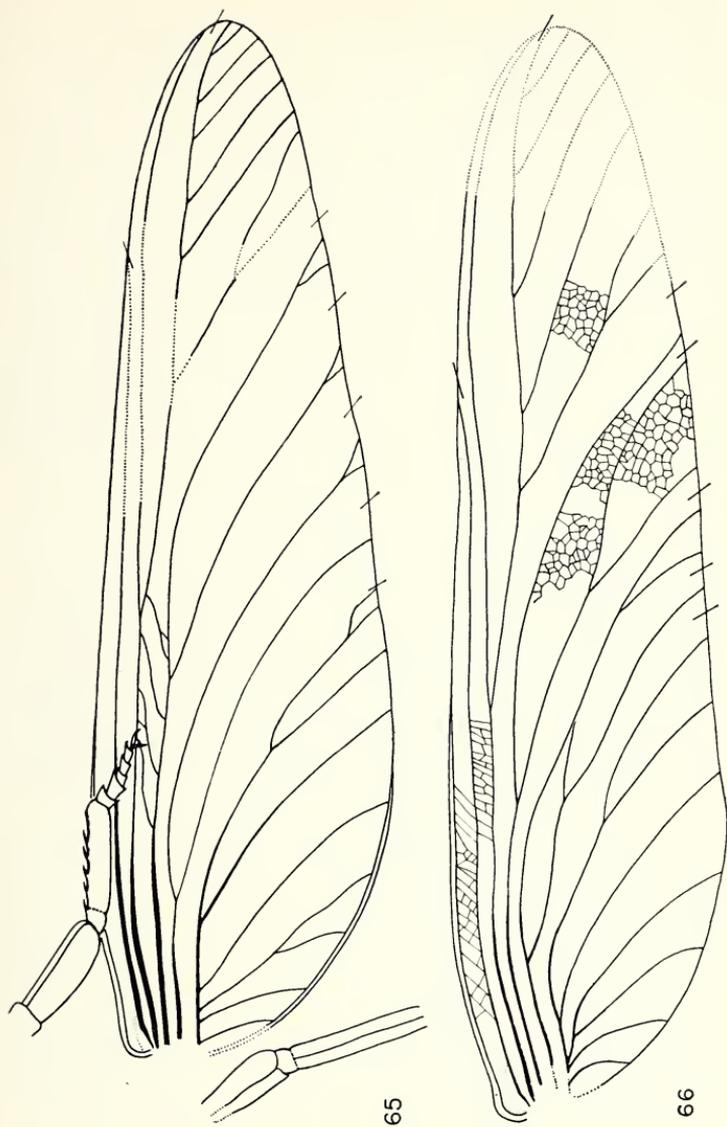


Figure 65. *Stenodictya oustalei* Brongniart; hind wing. Holotype.

Figure 66. *Stenodictya arnaudi* Brongniart; hind wing. Holotype.

fore wing described under the name *thevenini*. This statement is not correct as *thevenini* has an unusual type of archedictyon, with elongate cells, and it also has a deeply concave anterior margin.

Hind wing: probable length 80 mm, width 18 mm. Anterior margin slightly convex proximally and slightly concave just beyond the midwing; posterior margin convex at the end of 2A. Apical part of wing narrow and elongate. R-rs area broad; Rs originating well before mid-wing, with about five branches. MP and CuA giving rise to one irregular branch, probably secondarily formed by the archedictyon. Cubital area very narrow; course of CuP irregular. Anal area large with side branches, sometimes forked.

*S. arnaudi* differs from all other species by the irregular course of MP and CuP (which, of course, may be an individual trait only). It is similar to *S. oustaleti* in having a large anal area with 1A forked.

#### *Stenodictya klebsi* (Meunier)

Figure 67

*Microdictya klebsi* Meunier, 1908: 154; Meunier, 1908: 38, fig. 2; Meunier, 1908: 135, pl. 2, fig. 1.

*Stenodictya klebsi* Handlirsch, 1919: 6, fig. 7.

This species was based by Meunier on a complete hind wing. Unfortunately, I could not find the type specimen in the collection at the Institut. The accompanying figure was made from a very good photograph which Dr. Carpenter made in 1938 and in which all features are clearly visible.

Hind wing: length 72 mm, width 21 mm. Anterior margin slightly convex proximally, then straight. Posterior margin with only a small convex curvature at 1A. Apical part short and broadly rounded. Rs originating shortly before mid-wing, with 5 branches. Anal area large, with 4 veins, 1A forking. Archedictyon with a tendency to form additional twigs.

*S. klebsi* has the broadest hind wing of all related species, especially in the apical part. Its outline resembles that of *laurentiauxi* sp. nov. and *parisiana* sp. nov.

#### *Stenodictya parisiana* sp. nov.

Figure 68

This species is based on a complete hind wing in the Institut collection. Its position is remote from the other species by the more advanced modification of the archedictyon into cross veins, which

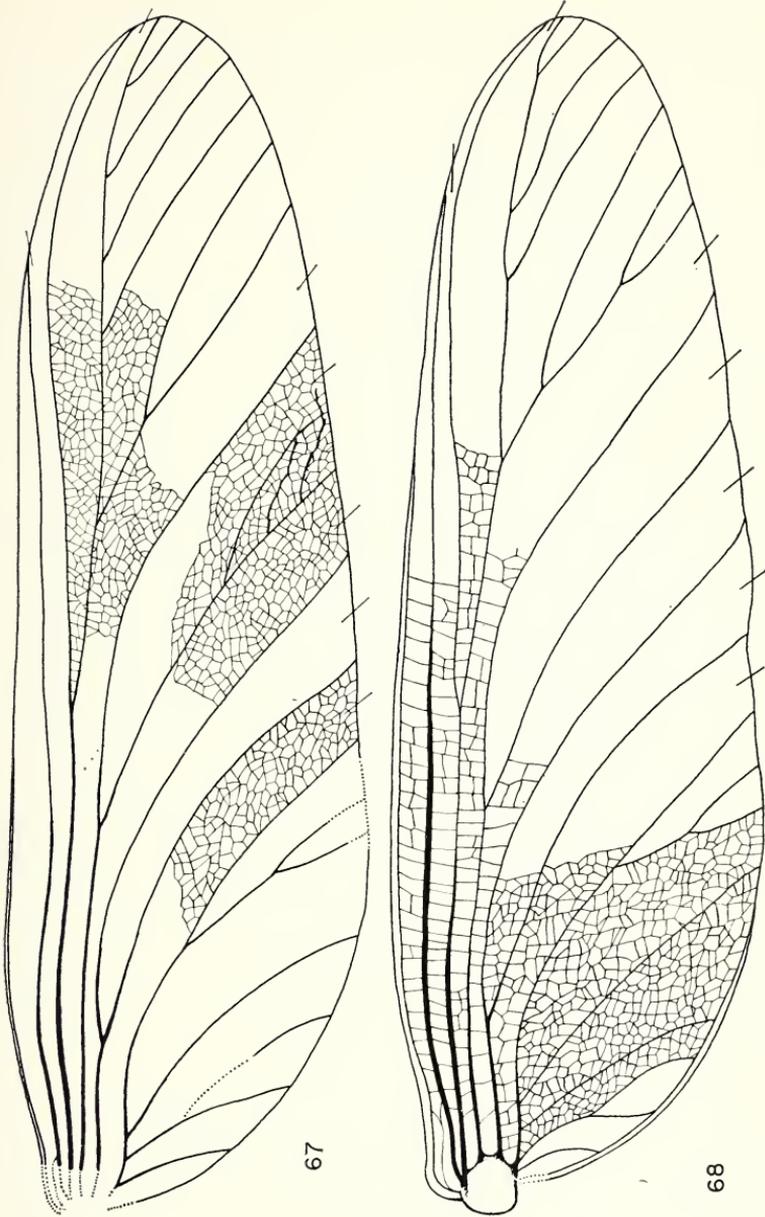


Figure 67. *Stenodictya klebsi* (Meunier); hind wing. Holotype.  
Figure 68. *Stenodictya parisiana* sp. nov.; hind wing. Holotype.

are relatively much less dense than in other species and which are oriented more perpendicularly to the axis of the wing.

Hind wing: length 56 mm, width 16.5 mm. Anterior margin very slightly convex, posterior margin with a small convex curvature at CuP. Apical part short and broad, broadly rounded. R-rs area broad. Rs originating shortly before the mid-wing, with 4 branches. Anal area large with 5 veins, 1A forking. Cross veins in subcostal area, r-m and m-cu areas relatively sparse and almost perpendicular to the wing axis.

This species differs from all others in the genus by the smaller number of cross veins and by their arrangement on the wing. It is related to *klebsi* by its broadly rounded apex and forked 1A.

*Stenodictya fritschi* Brongniart

Figure 69

*Stenodictya fritschi* Brongniart, 1893: 385, pl. 22, fig. 7; Handlirsch, 1906: 65 pl. 8, fig. 24; Lameere, 1917: 158; Handlirsch, 1919: 3.

This species was based by Brongniart on specimen 22-7, represented by a fragment which does not show enough features to enable comparison with the other species of the genus. It is probably part of a hind wing; the length of the fragment is 38 mm, the width 20 mm. The wing probably narrowed gradually towards the apex; the anal area had a forked 1A. The species may be related to *Stenodictya* with broad wings, such as *klebsi*.

Two additional fragments of hind wings are included in the collection at the Institut. These are too incomplete to justify formal description but figures of them are included here because they show a few features not noted in other species. One of these (figure 70) is a fragment (*Stenodictya* sp. A) which shows clearly the basal subcostal plate and the branching of 2A, which is probably an individual variation. The anal area has 5 veins, 1A is forked and 2A has three branches arising pectinately. Wing fragment 37 mm long and 21 mm wide.

The other specimen is a fragment of a hind wing (*Stenodictya* sp. B), which I could not find in the Institut but which was photographed there by Dr. Carpenter in 1938. The accompanying drawing (Figure 71) was made from the photograph. Rs originates shortly before mid-wing, MP has one additional branch. The anal area is large with 6 veins and 1A is forked twice. The archedictyon is irregular and dense.

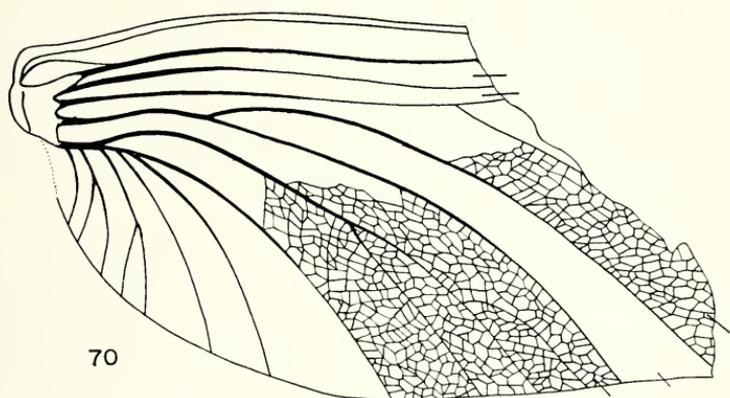
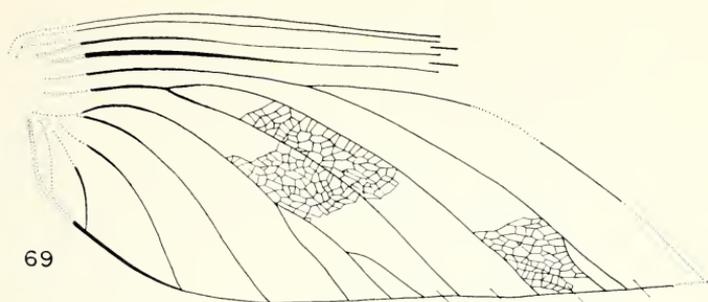


Figure 69. *Stenodictya fritschi* Brongniart; specimen 22-7; hind wing fragment. Holotype.

Figure 70. *Stenodictya* sp. Hind wing.

*Microdictya* Brongniart

*Heeria* Brongniart, 1893: 338.

*Microdictya* Brongniart, 1893 (pro *Heeria* Brongniart, nec Scudder, 1890) (Atlas): 28; Handlirsch, 1919: 6; Lameere, 1917: 159.

Type species: *Heeria vaillanti* Brongniart, SD Handlirsch, 1922.

Brongniart established the genus *Heeria* on two species, *vaillanti* and *hamyi* but in a foot-note of the same publication (1893, p. 28, Atlas) he changed the name to *Microdictya* because of the homonymy indicated above.

This genus includes less specialized species than *Stenodictya*, with richer venation and with the archedictyon much more developed. Both pairs of wings are more alike in shape than in *Stenodictya*. Bolton (1917, p. 9) was of the opinion that *Microdictya* and *Sagenoptera* Handlirsch were junior synonyms of *Goldenbergia* Scudder, 1885. Although this is possible, I am not recognizing this synonymy at this time; it is necessary that the specimens on which *Goldenbergia* were based be examined with special reference to this question.

The characteristics of *Microdictya* are as follows: wings very much alike in shape and venation. Fore wings usually broadest at about mid-wing; anterior margin convex near the base; precostal strip pronounced; postcostal vein short, simple, terminating on Sc. Sc not reaching the apical part of the wing; Rs originating before the end of the first third of the wing length; MA simple, MP branched twice, CuA simple, CuP branched once or twice. Anal area narrow with three to five pectinate branches. Hind wings a little broader, usually with the posterior margin slightly convex. The hind wing broadest at about mid-wing. Anal area a little broader than in the fore wing. Archedictyon very irregular, changing into irregular cross veins with many anastomoses in subcostal and sc-r areas. Wing membrane, veins and archedictyon with a dense covering of pits.

*Microdictya* differs from *Stenodictya* in having both wings broadest at about the middle, in having MP and CuP branched, the anal area narrower and by the generally oval shape of the wings.

Species included in Commeny shales: *Microdictya vaillanti* Brongniart, 1893; *Microdictya hamyi* Brongniart, 1893; *Microdictya lacroixi* Meunier, 1910; *Microdictya villeneuvei* Meunier, 1908.

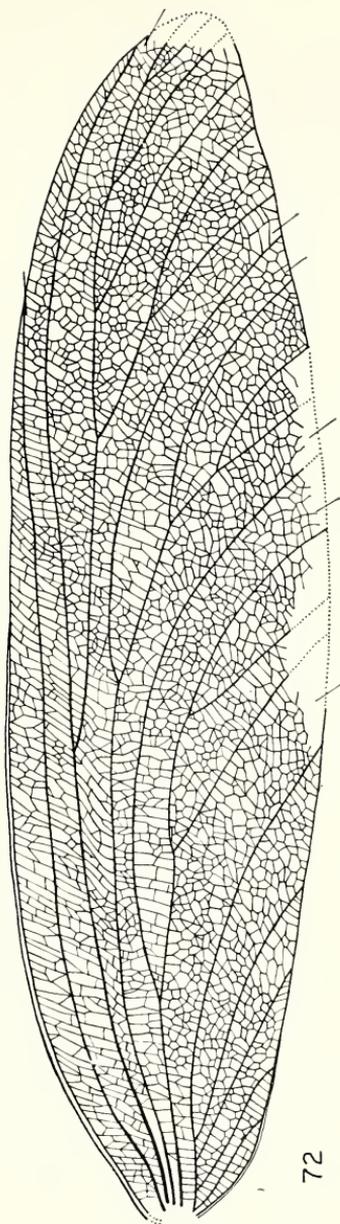
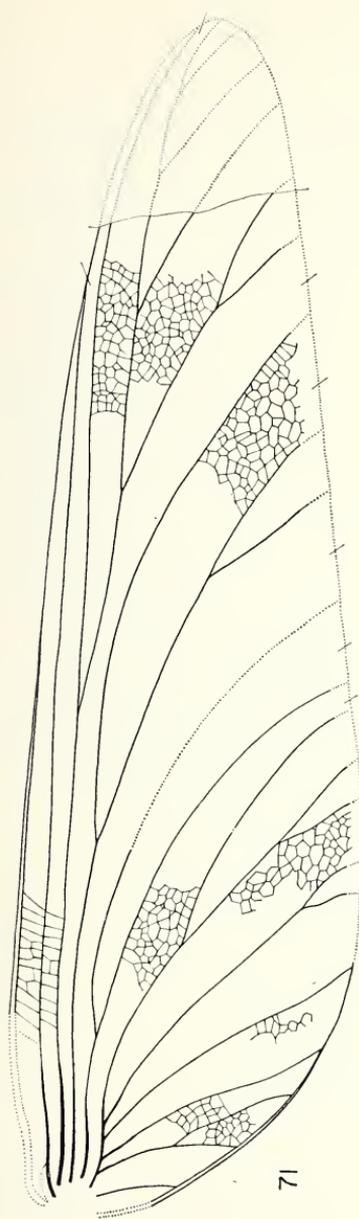


Figure 71. *Stenodictya* sp. Brongniart. Hind wing.

Figure 72. *Microdictya hamyi* Brongniart; specimen 23-3; fore wing. Holotype.

*Microdictya vaillanti* (Brongniart)

Figures 73, 74, 75

*Heeria vaillanti* Brongniart, 1893: 389.*Microdictya vaillanti* Brongniart, 1893, Atlas: 28, pl. 22, fig. 12, pl. 23, fig. 1, 2; Handlirsch, 1906: 65, pl. 9, fig. 6; Lameere, 1917: 159; Handlirsch, 1919: 6.*Stenodictya gaudryi* Brongniart, 1893: 384, pl. 22, fig. 5; Handlirsch, 1906: 64, pl. 8, fig. 21; Handlirsch, 1919: 3.

This species was based by Brongniart on two specimens: 23-1 (and its counterpart 23-2), an incomplete body and four remarkably preserved wings; and 22-12, a fore wing with a small fragment of a hind wing. I designate specimen 22-12 (figure 72) as the lectotype of *vaillanti*, since the other specimen is not present in the collection of the Institut in Paris and is presumed lost. The figure of that fossil (figure 73) included here is based on an excellent photograph of it made by Dr. Carpenter in 1938; in the photograph, all features of the wings, including the archedictyon, are perfectly clear. The body (best preserved in the reverse half of the fossil) shows the head, prothoracic lobes and part of the abdomen but unfortunately I was not able to work out these details reliably enough from the photograph for inclusion in the drawing.

Specimen 22-5, described by Brongniart in 1893 as *gaudryi* (figure 74) is clearly *vaillanti*. The fore wing is very faintly preserved and Brongniart, with the methods he used, was unable to see the characteristic branches on MP and CuP, which do become distinct under glycerin.

The characteristics of *vaillanti* are as follows: fore wing, length 60 to 70 mm, width 15 to 18 mm. Fore wing oval, broadest at about mid-wing; anterior margin slightly convex; posterior margin slightly concave. Rs originating well before mid-wing, with four branches. MP giving rise to two branches, CuP with one or two branches. Anal area narrow, with four veins, some of them forked. Archedictyon denser than in most other species, the components bordering the cells irregular, giving the cells the character of a "loose" network. Hind wing, width 16.5 - 19.5 mm. Posterior margin slightly more concave.

*Microdictya vaillanti* is related to *hamyi* in having a dense archedictyon but differs in having the veins directed more obliquely and by having narrower rs, m and cu areas. From *lacroixi* Meunier, which has a similar shape of hind wing and similar venation, it differs in the much denser archedictyon.

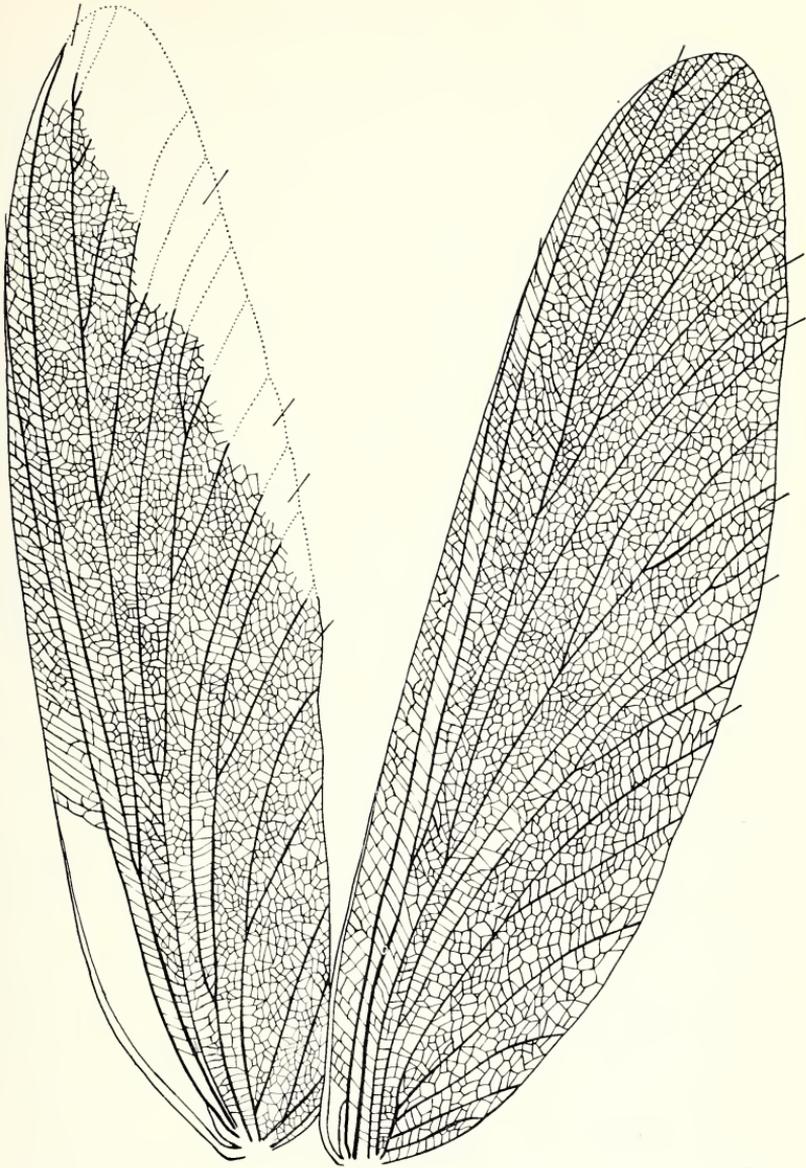


Figure 73. *Microdictya vaillantii* Brongniart; specimen 23-1; fore and hind wings.

*Microdictya hamyi* (Brongniart)

## Figure 72

*Heeria hamyi* Brongniart, 1893: 390.

*Microdictya hamyi* Brongniart, 1893: 390, pl. 22, fig. 3; Handlirsch, 1906: 66, pl. 9, fig. 7; Handlirsch, 1919: 6.

This species was based by Brongniart on two well preserved fore wings of specimen 23-3. Bolton (1917, p. 8) identified as the same species a fragment (apical part of a wing), from Commentry and now in the Mark Stirrup collection in Manchester. This probably does belong to *Microdictya* but its specific position is obscure.

Fore wing: length 80 mm, width 22 mm. Fore wing almost oval in shape, broadest at about mid-wing. Apex of wing directed posteriorly. Apical part of wing relatively broad and short. Subcostal area narrow, almost band-like; Sc-r area very broad, Rs originating not far before mid-wing, with four branches. MP and CuP with two branches. Cup-1a area very broad. Anal area long, narrow, with 5 anal veins. Branches of M and Cu strongly curved towards the posterior margin. Archedictyon dense.

This species differs from all others by the convex curvature of M and Cu branches towards the posterior margin and by the broad cup-1a area. The archedictyon is almost as dense as in *vallanti* but less irregular, tending to be arranged into cross veins.

*Microdictya lacroixi* Meunier

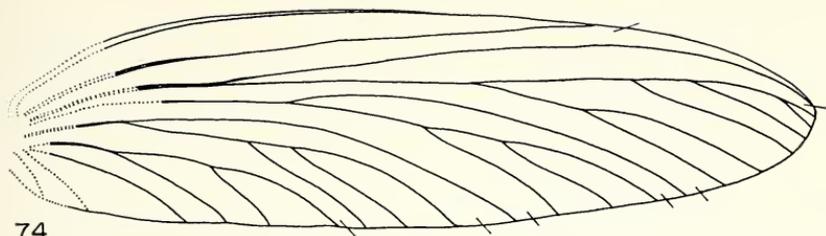
## Figure 76

*Microdictya lacroixi* Meunier, 1910: 235, fig. 2; Meunier, 1912: 6, pl. 6, fig. 2; Handlirsch, 1919: 6, fig. 8.

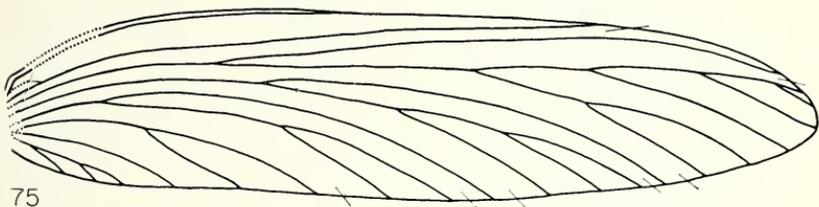
This species was based on a well preserved hind wing with a relatively sparse archedictyon. Unfortunately, I could not locate the type of this species in the Institut; the figure included here was made from Dr. Carpenter's 1938 photograph.

Hind wing: length: 51 mm, width 15 mm. Anterior margin almost straight; posterior margin regularly curved. Hind wing broadest shortly before midwing. Rs originating well before apex, with 3 branches, first of them forked three times. MP reaching the posterior margin with its 3 branches. CuP giving rise to one branch. Anal area long and narrow, with 5 pectinate branches. Archedictyon sparse, more in the form of irregular cross veins connected by anastomoses.

*Microdictya lacroixi* is related to *villeneuvei* by its sparse archedictyon but differs in wing shape. From the other species with similar wing shape, it differs in the archedictyon.



74



75

Figure 74. *Microdictya vaillanti* Brongniart; specimen 22-12; fore wing. Holotype.

Figure 75. *Microdictya vaillanti* Brongniart; specimen 22-5; fore wing. (Type of *Stenodictya gaudryi* Brongniart).

### *Microdictya villeneuvei* Meunier

#### Figure 77

*Microdictya villeneuvei* Meunier, 1908: 245, fig. 1; Meunier, 1908: Meunier, 1909: 136, pl. 1, fig. 4; Handlirsch, 1919: 6, fig. 9.

This species was based on a hind wing, which lacked the apex; the type could not be found in the collection of the Institut and the figure included here was made from Dr. Carpenter's photograph.

This species represents the most specialized one within the genus *Microdictya*. The development of veins along the costal area is very advanced and the outline of the hind wing, recalling some species of the related genus *Stenodictya*, has a pronounced convex curvature of the posterior margin in the apical half. At the same time, the proximal half of the wing retains the oval shape characteristic of other species of the genus.

Hind wing: length 50 mm, width 14 mm. Wing broadest shortly before mid-wing. Anterior margin convex near the base, slightly concave at about mid-wing. Posterior margin concave in proximal half, then forming a pronounced convex curvature at the end of the first branch of MP. Apex apparently directed backward. Rs long, originating before the first third of the wing length. MP and CuP giving off two branches. Anal area long and narrow, with four

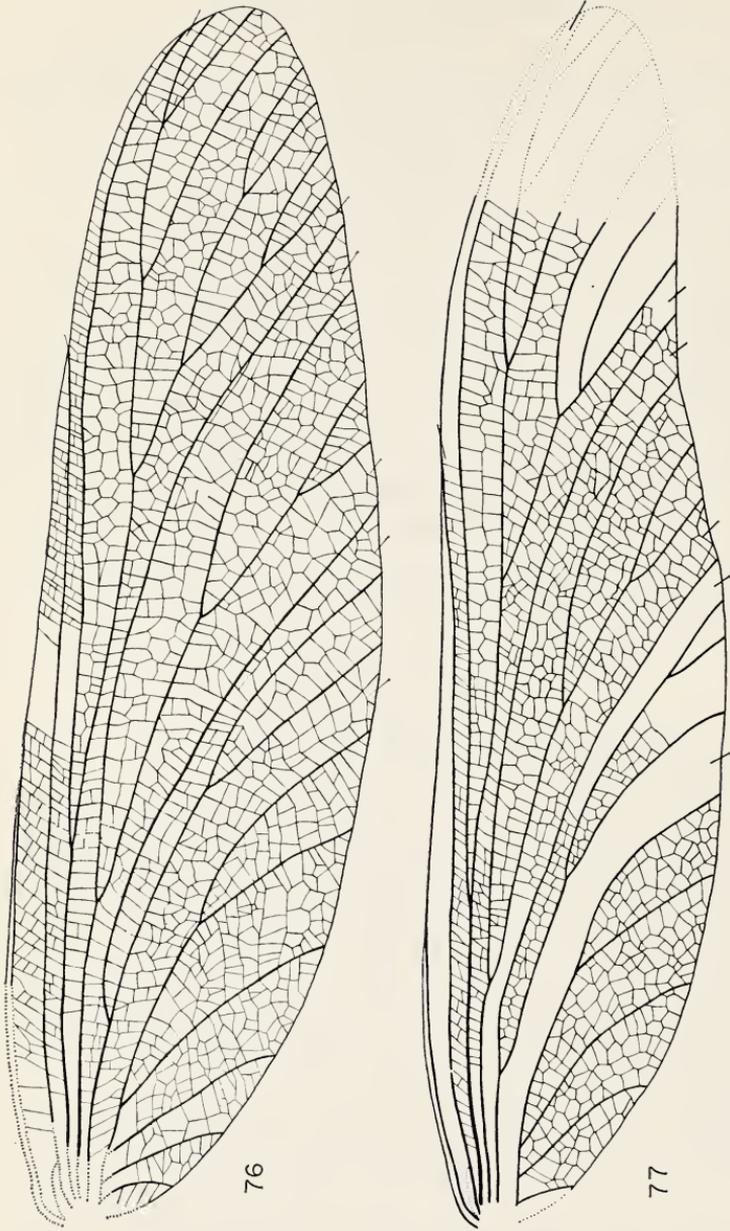


Figure 77. *Microdictya villeneuvei* Meunier; hind wing. Holotype.

Figure 76. *Microdictya lacroixi* Meunier; hind wing. Holotype.

veins. Archedictyon sparse, more like irregular cross veins connected with anastomoses.

*Microdictya villeneuvei* differs from all other species in the pronounced curvature of the distal part of the posterior margin.

#### SUMMARY

The Commeny shales in central France provide us with the most extensive and the best preserved collection of Palaeodictyoptera so far known. The information obtained from detailed study of these fossils shows that this extinct order was a very diverse one, with far more specialization and adaptations than have previously been suspected. The following is a general account of the structure of the Palaeodictyoptera, as it is now known.

The head was small, often very small, with slender antennae composed of numerous segments. The eyes were large and conspicuous. The mouthparts were haustellate, forming a prominent beak, resembling superficially that of the Hemiptera. However, the head was not opisthognathous but clearly hypognathous, perhaps with a tendency towards the prognathous condition: the beak is preserved in the fossils in front of the head, projecting somewhat obliquely in an anterior-ventral direction. Four long stylets were included in the beak, their basal portions being covered by a triangular or lanceolate labrum. The clypeal region was markedly swollen and enlarged, much as in the Hemiptera, and possessed a median longitudinal ridge as well as several transverse ridges. It seems almost certain that this enlarged clypeal region marked the presence of a sucking pump. The stylets were apparently held tightly together but were probably moveable, to some extent. The palpi, presumably the maxillary pair, were slightly longer than the beak and were attached to the head laterally at the base of the beak. The palpi were segmented, six segments being present in specimens in which the details can be ascertained; the first segment as well as the last one or two segments were much shorter than the others. The surface of the palpi was rugose. The beak itself was from 2 to 2.5 cm long in the moderate to large Palaeodictyoptera although in one such species (*Lycocercus goldenbergi*) the beak was only 1 cm long. In smaller specimens, such as some spilapterids, the beak was correspondingly shorter.

The thoracic segments were nearly equal in size, though the prothorax was frequently somewhat shorter and sometimes narrower than the others. A median, longitudinal ridge was often present.

The prothorax possessed a pair of lobes, which were usually cordate, and which were narrowly attached to the pronotum along a cuticular ridge. In most cases the lobes appear to have been membranous and to have possessed longitudinal as well as cross veins; the veins arose from the basal cuticular ridge and radiated into the lobe, some of them branching. In the fossils the convexities and concavities of the veins are not visible, and they were presumably not present in the original specimens. In exceptional instances, the lobes may be heavily sclerotized, all traces of the veins being lost. The lobes usually overlap the basal parts of the fore wings to a considerable extent; being situated high on the prothorax, they may have acted as immovable "fore sails", air passing under them and increasing the pressure on the functional wings. Prothoracic lobes of the Palaeodictyoptera were undoubtedly homologous with the functional wings; there is no evidence that they were used for active flight, the basal articulation and the distribution of the veins being unlike those of the functional wings.

The legs of the Palaeodictyoptera were relatively short or even very short and usually stout. The tibiae were slightly elongate, often spiny, and the tarsus was composed of five, subequal segments; two claws and an arolium were present in at least some species. The tibiae in some specimens show what appears to be a separate segment proximally, set off by a suture from the rest of the tibia; this seems to be comparable to the structure of the tibia in many existing Ephemeroptera. The three pairs of legs are similar except that the hind pair are slightly longer. The legs so far as known were adapted for walking and presumably were also used for holding onto vegetation or for climbing.

The wings of the Palaeodictyoptera had great diversity in size and shape. There are some species in which both pairs of wings were almost equal, others in which the hind wings were somewhat enlarged and then still others in which the hind wings were greatly enlarged. In several isolated lines of families, there was a tendency for the hind wings to be reduced, with respect to both width and length or a combination of both. The shape of the wing also extends over a very wide range, from relatively short to very long and slender. The articulation of the wings with the thorax is not preserved in detail in any specimens but it seems to be comparable to that in the existing Palaeoptera, the Ephemeroptera and Odonata. The convexity and concavity of the longitudinal veins is well known in the Palaeodictyoptera; a postcostal or a precostal area is present

at the base of both pairs of wings. There are also present in the basal part of the wings (especially if they are long or thin) transverse, supporting structures, generally in the form of cuticular thickenings, supporting cross veins or dark sclerotized bands. In some species there is a deep, oblique furrow crossing the basal part of the anal area and forming a line along which the wings appear to break readily; the function of this structure is not known.

The wings are often dark in color, with transverse light bands or with small, circular spots in varied patterns of distribution. There are also circular, cuticular thickenings on the wing membrane, which may have been the site of macrotrichia with a sensory function. The precostal strip, bordering the costa for varying lengths, is serrated in some species, as it is in the existing Odonata. The palaeodictyopterous wings were apparently consistently hairy, at least along the veins; the cross veins, the elements of the archdictyon and the wing membrane itself between veins also had hairs in some species. Sometimes long hairs formed clusters at the base of the wing and along the wing margin (recalling the submarginal condition of some mayflies) or on the wing membrane.

The abdomen was always shorter than the wing but, with few exceptions, it was not excessively broad. Often, the lateral parts of the tergites of the abdomen were separated from the main part of the tergum by a longitudinal suture, resembling in general the structure of the lateral lamellae of some mayfly nymphs. In a few cases, the tergites were strongly sclerotized, with lateral expansions, having oblique ridges along the expanded portions. The females had a robust ovipositor, usually curved but not really elongate. The general nature of the ovipositor resembled that of the Recent Zygoptera and some Anisoptera. The males of at least some Palaeodictyoptera had short but distinct claspers, apparently segmented, and arising from the ninth segment. The aedeagus was paired, at least in the few specimens in which this structure was preserved; a similar condition is known in the Protohymenidae of the Megaseoptera. Both males and females of the Palaeodictyoptera possessed long, robust, multisegmented cerci, approximately twice as long as the abdomen.

Very little is known about the nymphs of the Palaeodictyoptera. The evidence, such as it is (Carpenter and Richardson, 1969, p. 309), indicates that the nymphs were terrestrial and, like the adults, had haustellate mouthparts. The wing pads of the nymphs were held in oblique-lateral positions, independent of each other in all stages and

apparently articulated to the thorax in the same manner as were the wings. There is no evidence as to whether or not a subimaginal stage was present.

The Palaeodictyoptera, one of the most abundant and widely distributed orders of the oldest winged insects, apparently inhabited lowland of forests of the Upper Carboniferous and Lower Permian periods. It is clear from their haustellate mouthparts that they fed on liquid food only, this being almost certainly of plant origin. It is conceivable that the basic change in the plant life, which took place in the lower part of the Permian, may have been the principle reason for the extinction of this order of insects, along with the Megasecoptera and Diaphanopterodea, whereas the other contemporary paleopterous orders with chewing mouthparts, Ephemeroptera and Odonata, were able to survive the changes.

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## MIMICRY OF HYMENOPTERAN ANTENNAE BY SYRPHIDAE\*

BY G. P. WALDBAUER  
Department of Entomology  
University of Illinois

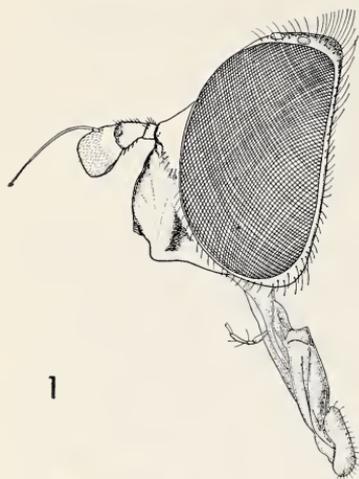
Many flies of the Family Syrphidae mimic aculeate Hymenoptera. The hymenopterans, particularly vespid wasps, which serve as models for these syrphids have relatively long, many segmented, filiform antennae which are often in motion and are usually a conspicuous feature. Most syrphids, like all of the other cyclorrhaphous Diptera, have three-segmented antennae which are usually short and decidedly inconspicuous as, for example, are those of the non-mimetic *Tropidia quadrata* (Say) (fig. 1). To human eyes the absence of conspicuous antennae decreases the resemblance of mimic to model, and the effect is presumably the same to at least some of the species of predators which are to varying degrees deceived by the mimetic resemblance. I have observed in nature several species of wasp-mimicking syrphids which either have or give the appearance of having long, filiform antennae. In each case the living mimic is remarkably deceptive and only close observation reveals that wasp-like antennae are not actually present.

The antennae of *Sphecomylia vittata* (Wiedemann) (fig. 2) and *Ceriana signifera* (Loew) (fig. 3) have been lengthened. The first and second segments of the antennae of *S. vittata* are very long while the third is short and bears an arista. The apparent length of the antennae is further increased by the forward-extending process of the head capsule which bears them. In *C. signifera* the first and third segments are quite long while the second is of only moderate length. The third segment bears a terminal style rather than an arista, further extending its length. In life both species hold the antennae in positions which suggest the geniculate antennae of vespids.

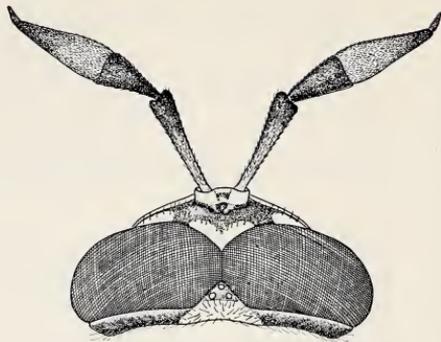
The antennae of *Tenthredomyia abbreviata* (Loew) (fig. 4) appear to be long because they are borne by a long, forward-extending process of the head capsule. The antennae themselves have been but slightly lengthened. The first segment is moderately long, but the second and third are short although the third bears a terminal style rather than an arista. As in the preceding two species living specimens of *T. abbreviata* hold the antennae in such a way that they appear

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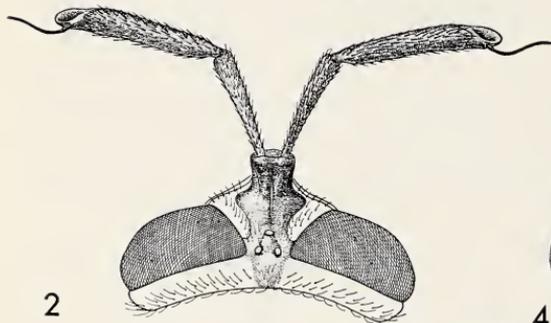
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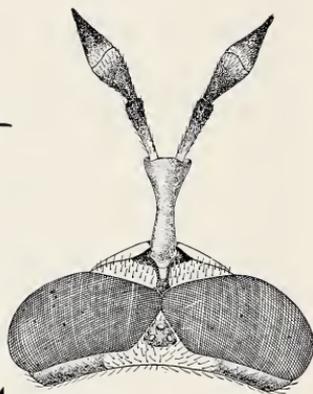
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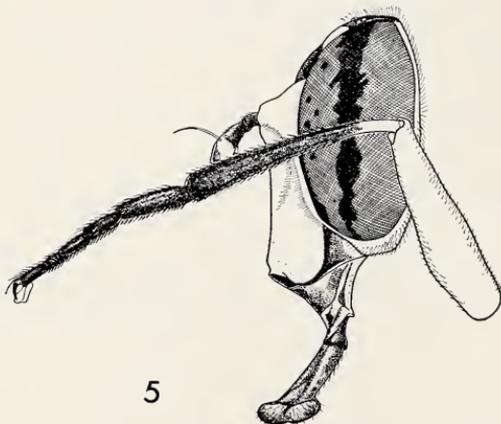
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to be geniculate as are the antennae of the models. This orientation is retained even in some dried specimens.

*Spilomyia hamifera* Loew (fig. 5) has antennae which are short and quite inconspicuous, similar in length and form to the antennae of non-mimetic Syrphidae (fig. 1). They are borne by a tubercle which is only slightly produced. In this case the long, dark, filiform antennae of the models are mimicked by the dark front legs which are held up and waved about in front of the head. The effect is very realistic and can easily deceive an inexperienced collector. The tarsi and the distal portion of the tibiae of the front legs are dark. The proximal portion of the front legs as well as the other two pairs of legs are yellow as are those of the models. I have observed this behavior in *S. hamifera* both while they were feeding on flowers or resting on foliage. Occasionally, all six legs are on the substrate, the usual position for most syrphids. I do not know in what position the legs are held in flight.

I have observed a similar use of the front legs in three other vespid-mimicking *Spilomyia*, *S. fusca* Loew, *S. longicornis* Loew and *S. quadrifasciata* (Say). In each of these species the front tarsi and a part of the front tibiae are dark. The remaining legs are yellow except for dark areas on the femora of *S. fusca* and *S. quadrifasciata*. The legs of *S. crandalli* Curran and *S. foxleei* Vockeroth are similar to those of the last two species mentioned although the meso- and metatarsi of *S. foxleei* are somewhat darkened distally. *S. kahli* Snow does not have the front legs darkened. I have seen only pinned specimens of the last three species. It may be that *S. kahli* does not use the front legs to mimic antennae, but it seems more likely that models with yellow antennae will be found to occur within its range in the southwestern United States. Curran (1951) stated that all species of *Spilomyia* rest on the four posterior legs and use the front legs to mimic antennae.

At least some of the North American species of *Temnostoma* use the front legs in the same manner. In nature I have seen this done by *T. balyras* Walker, *T. pictulum* Williston and *T. trifasciatum* Robertson. In each of these species the front legs are dark while the other two pairs are largely yellow. Although I have not seen them

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Figs. 1-5. Dorsal and lateral views of the heads of five species of Syrphidae.

Fig. 1. *Tropidia quadrata* (Say). Fig. 2. *Sphecomyia vittata* (Wiedemann). Fig. 3. *Ceriana signifera* (Loew). Fig. 4. *Tenthredomyia abbreviata* (Loew). Fig. 5. *Spilomyia hamifera* Loew.

in life I have examined dried specimens of *T. alternans* Loew and *T. vespiforme* (L.) and found the legs to be similarly marked.

These observations show that in the Family Syrphidae there are at least four ways of achieving the appearance of aculeate antennae. These four ways represent at least three and perhaps four independent evolutionary innovations. *Spilomyia* and *Sphecomyia* certainly present evolutionarily independent solutions to the problem of mimicking hymenopteran antennae. *Ceriana* and *Tenthredomyia* represent at least a third line and may have evolved solutions independently of each other. The antennae of both are stylate and otherwise similar. The antennae of *Tenthredomyia* are borne by a long process, but *Ceriana* exhibits a similar though very short process. Thus it is possible that these two genera present primitive and advanced versions of the same evolutionary line rather than two separate lines. The question cannot be decided on the basis of the present evidence.

Nicholson (1927) noted that among the Syrphidae long antennae are generally associated with those species in which the over-all mimetic resemblance to Hymenoptera is the most highly developed. My observations of living Syrphidae in the eastern United States confirm this view. I have seen very few non-mimetic syrphids which have or appear to have long antennae. In life the species mentioned above are remarkably vespid-like both in general appearance and behavior. However, they are not necessarily precise mimics of a particular species of vespid. I would, nevertheless, consider them to be specialized mimics which exhibit a number of different adaptations which imitate salient features of vespids. For example, of the four mimetic species illustrated, all have a more or less distinct dark area along the leading edge of the wing, suggesting the dark band produced by the longitudinal folding of the vespid wing at rest. The four species illustrated also have either a constriction at the base of the abdomen or markings which suggest such a constriction.

It is noteworthy that stylate antennae occur in only three of the 88 genera (*Ceriana*, *Tenthredomyia* and *Callicera*) and 17 of the 939 species of North American Syrphidae listed by Wirth *et al.* (1965). The genera *Ceriana* and *Tenthredomyia* include thirteen species which occur in America north of Mexico. All are wasp mimics. There are four species of *Callicera* in the same area. The one species which I have seen is not a wasp mimic and is probably not mimetic at all.

In my experience syrphids which mimic bees neither have nor give the appearance of having long antennae. From observations of living

insects in the field I have found this to be true of *Mallota bautius* (Walker), *M. posticata* (Fab.), *Eristalis bardus* (Say) and *E. bastardii* Macquart, all of which mimic bumblebees. It is also true of *Eristalis tenax* (L.) which is frequently cited as a mimic of the honeybee. Another bumblebee mimic, *Volucella bombylans* (L.), has a rather long and feathery arista which is somewhat conspicuous in the field, but does not suggest to me the antenna of a bumblebee. It would be interesting to know if it is a valid generalization that bee-mimicking syrphids do not appear to have long antennae and, if so, to attempt to discover why this is the case.

*Acknowledgment:* Thanks are due to Mrs. Alice Prickett who made the drawings.

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A DESCRIPTION OF  
THE LARVA OF *THYCE HARFORDI* CASEY  
(SCARABAEIDAE: MELOLONTHINI)

BY TERRY L. ERWIN  
Museum of Comparative Zoology

Mating flights of *Thyce harfordi* Casey adults were first noticed in San Jose, California in 1962. In subsequent years many adult beetles were collected, but attempts to excavate larvae proved unsuccessful until J. Gordon Edwards, Richard Penrose, and I found two specimens. These were destroyed in the mail when we sent them to P. O. Ritcher at Oregon State University. The following year, Charles Baker, Toby Schuh, Edwards, and I returned to the cherry orchard the larvae were taken from previously. This trip in May, 1965, proved successful in our search for one of the few large scarab genera with undescribed immature stages.

Five or six excavations were made, each one adjacent to a randomly chosen cherry tree. The holes were dug to a depth of six feet and were from five to eight feet square. Even with this amount of digging, only eleven larvae were found (two were so badly damaged by the shovel that they had to be discarded).

These larvae are here described and a key (for larvae) to the known genera of the Tribe Melolonthini is offered. For the most part, I have tried to follow the style and format used by Ritcher (1966) in order to make this single description fit into that author's excellent and recent work on white grubs and their allies.

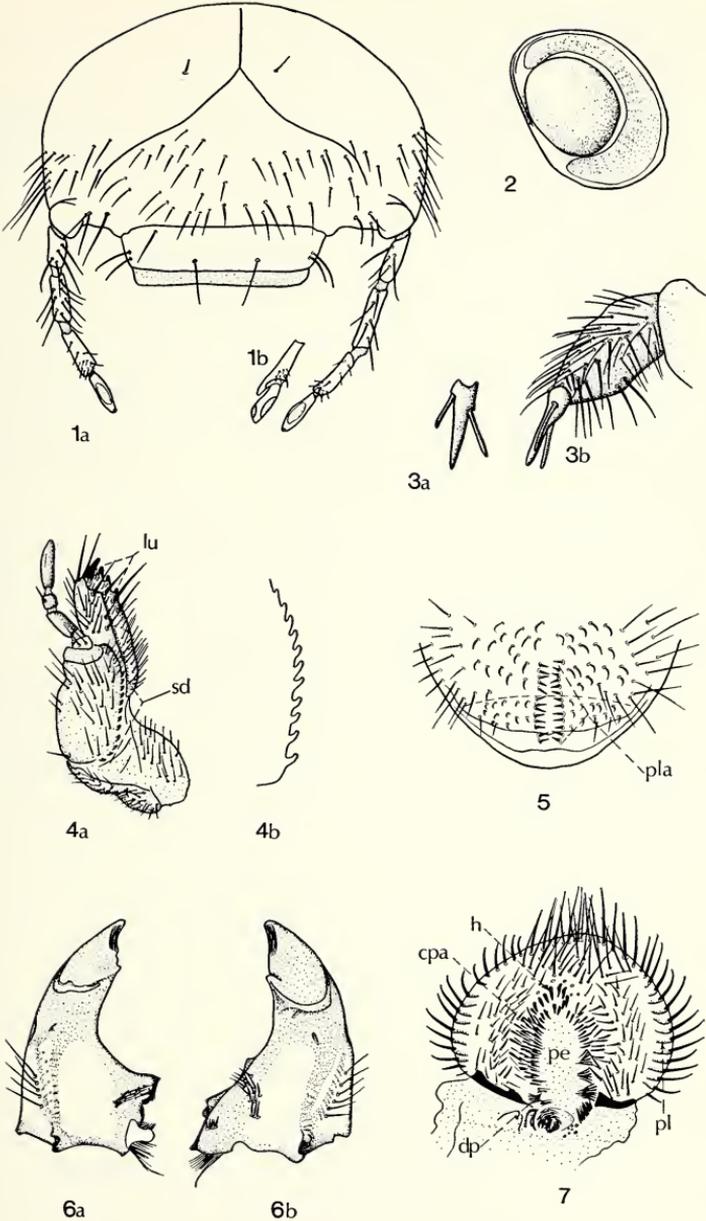
Tribe Melolonthini (*sensu* Ritcher)

Key to genera with known immature stages, third instar

1. Palidia present (fig. 5) ..... 2  
1'. Palidia absent ..... (in part) *Phyllophaga* Harris

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Figs. 1-7. *Thyce harfordi* Casey. 1a. Head capsule, frontal aspect. 1b. Ultimate and penultimate antennal articles, proximal aspect. 2. Abdominal spiracle, 4th segment left side. 3a. Prothoracic leg, left lateral aspect. 3b. Prothoracic claw, caudal aspect. 4a. Left maxilla, dorsal aspect. 4b. Maxillary stridulatory teeth of left maxilla, dorsal aspect. 5. Raster, ventral aspect. 6a. Left mandible, dorsal aspect. 6b. Right mandible, dorsal aspect. 7. Epipharynx, proximal aspect. Symbols used: cpa, chaetoparia; dp, dexiophoba; h, heli; lu, unci of lacinia; pe, pedium; pl, plegmata; pla, palidium; sd, maxillary stridulatory area.



- 2(1). Epipharynx with epizygmum (sclerotized strip or patch near apex). ..... 3
- 2'. Epipharynx without epizygmum ..... 4
- 3(2). Plegmata (fig. 7) short, not approaching outer chaetoparia; maxillary stridulatory teeth pointed .... *Amphimallon* Berthold
- 3'. Plegmata long, closely approaching outer chaetoparia; maxillary stridulatory teeth truncate .....  
 ..... (in part) *Phyllophaga* Harris
- 4(2'). Dexiophoba (fig. 7) ringing much of right side of pedium; maxilla (fig. 4a) with a row of 14 or more long, conical stridulatory teeth; haptomerum (fig. 7) with a group of 15 or more heli ..... *Polyphylla* Harris
- 4'. Dexiophoba short; maxilla with a row of 12-13 short, conical arcuate stridulatory teeth; haptomerum with a group of 14 heli (proximal ones small, setae-like) ..... *Thyce* LeConte

#### Genus *Thyce* LeConte, Third Instar Larva

The larvae of this genus are extremely similar to those of *Polyphylla* Harris. This similarity may indicate the monophyly of the two taxa which are retained as good genera on the basis of the adult antennal characteristics.

The following combination of characteristics is diagnostic of the larvae of the genus *Thyce*: Head without eye spots. Frons and gena with numerous scattered setae, lateral ones long. Labrum symmetrical. Epipharynx with epizygmum; zygmum indistinct. Haptomerum with a group of 14 heli. Plegmata present, plegmata short. Proplegmata absent. Dexiophoba short. Haptolachus with microsensilla. Maxilla with a row of 12-13 short, conical, arcuate stridulatory teeth. Lacinia with longitudinal row of 3 stout unci. Anal slit transverse, ventral anal lobe not cleft. Raster with 2 short, longitudinal, parallel palidia. Preseptular hamate setae numerous, lateral setae long. Claws of prothoracic and mesothoracic legs long and falcate, those of mesothoracic legs slightly smaller. Claws of hind legs minute.

#### *Thyce harfordi* Casey, Third Instar Larva (Figs. 1-7)

*Material.* Eleven specimens of third instar larvae found in pupal chambers and burrows beneath cherry trees, 2555 Meridian Avenue, San Jose, California, May, 1965; collected by Charles Baker, Toby Schuh, J. Gordon Edwards and me. Two specimens taken by Baker to Oregon, both subsequently reared by P. O. Ritcher to the adult stage. Both were females of *Thyce harfordi*.

*Description.* The following combination of characteristics is diagnostic of the larvae of this species: Maximum width of head capsule 7.0 to 7.3 mm. Head yellowish-brown in color, smooth, shiny. Hypotomerum of epipharynx with 14 heli. Epipharynx without proplegmata, the area covered instead with setae. Each plegmatium with 11-12 short plegmata. Haptolachus with seven microsensilla. Maxilla with row of 12-13 short, conical, arcuate stridulatory teeth. Thoracic spiracles slightly larger than spiracles on abdominal segments 1-5, which are all similar in size. Spiracles on abdominal segments 6 to 8 progressively smaller. Anal slit transverse, slightly curved. Raster with 2 short, parallel, longitudinal palidia, each with 13 short, sharp, pali. Septula narrow. Tegilla extending forward beyond the palidium for a distance equal to or slightly greater than half the length of the palidium. Preseptular setae more numerous than 50 (50-100), adjacent lateral setae long.

*Habitat.* The specimens were found in the "B horizon," 14 to 48 inches deep in sandy clay among the roots of cherry trees in what appeared to be an "old" orchard. The larvae found at 14 inches were upside down (supine) in pupal chambers, while the deeper ones were adjacent to the lower surface of roots of the cherry trees.

I would like to thank P. O. Ritcher and J. Gordon Edwards for critically reading this manuscript and offering suggestions.

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DESCRIPTIONS OF THE NESTS OF  
*PSEUDOCHARTERGUS FUSCATUS* AND  
*STELOPOLYBIA TESTACEA*,  
WITH A NOTE ON A PARASITE OF  
*S. TESTACEA* (HYMENOPTERA, VESPIDAE).\*

BY ROBERT L. JEANNE

The Biological Laboratories, Harvard University  
Cambridge, Mass.

The nest built by a colony of wasps is the tangible product of complex behavior patterns which have evolved in response to a variety of factors. Since the nest is a solid object which remains after the colony has gone, it provides a direct means of gaining insight into some of these factors. The remarkable architectural diversity of nests, especially among tropical species, suggests that the factors in question are many and varied.

Beyond their importance in studies of the adaptations of individual species, nests must be taken into consideration in studies of the phylogeny of the social vespids. Richards and Richards (1951) point out that the details of behavior as well as morphology must be carefully studied in deducing phylogenetic relations of each group so that those characters selected will combine to give the most consistent classification. Henri de Saussure (1853-8) was the first to classify nests of social wasps according to their structure. Adolph Ducke, to whom we are indebted for much of what we know about neotropical social wasps, attempted to construct a phylogeny of the Vespidae based on Saussure's classification (Ducke, 1914), but his success was limited by inadequate taxonomic knowledge of the wasps themselves, and a lack of knowledge of the details of nest-building behavior. Ducke also made no attempt to understand the adaptive functions of the various features of nest structure. Though a great deal has been accomplished since Ducke's time, especially through the work of Bequaert and of the Richardses, we still have much to learn before we can hope to understand the evolution of nest structure in this family. The nests of roughly 30% of the species of neotropical polistine wasps (exclusive of the genera *Polistes* and *Mischocyttarus*) remain completely unknown, and many of the descriptions that do exist are cursory and note only general architecture. Almost nothing is known of the behavior associated with the details of nest-building.

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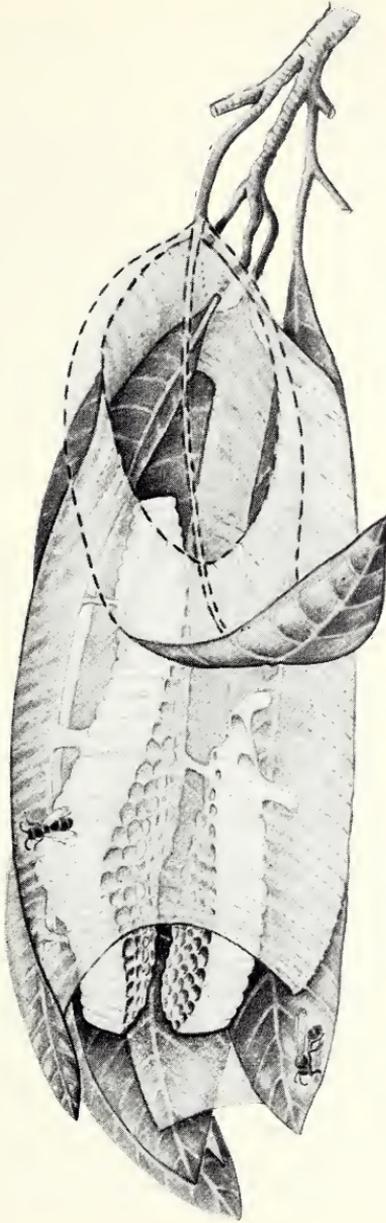


Fig. 1. Nest of *Pseudochartergus fuscatus*, showing structure. The leaf at the right is shown cut away. The proximal (right hand) end of the nest is completely sealed in by the transparent film, while the broad entrance to the nest is at the left.

*Pseudochartergus fuscatus* has been recorded only from the Amazon basin. Its nest is remarkable in that it is enclosed in a transparent envelope. This feature is shared with the congener *P. chartergoides*. *P. fuscatus* also has cells that open upward, an extremely rare trait in the Vespidae. The nest of *Stelopolybia testacea*, a species that ranges from northern South America to Bolivia, is very similar in structure to those of *S. pallipes* and *S. cajennensis*. The nest described here was unique, however, in having been constructed in a relatively exposed site, on the underside of a palm spathe. Moreover, it was one of the largest and most populous nests of any social vespid ever taken in the American equatorial tropics.

A sample of the adult population of each nest has been deposited in the collection of the Museum of Comparative Zoology at Harvard University. The field numbers are 71 and 265 for the colonies of *P. fuscatus* and *S. testacea*, respectively. One specimen of the parasite of *S. testacea* has also been placed in the MCZ collection.

#### *Pseudochartergus fuscatus*

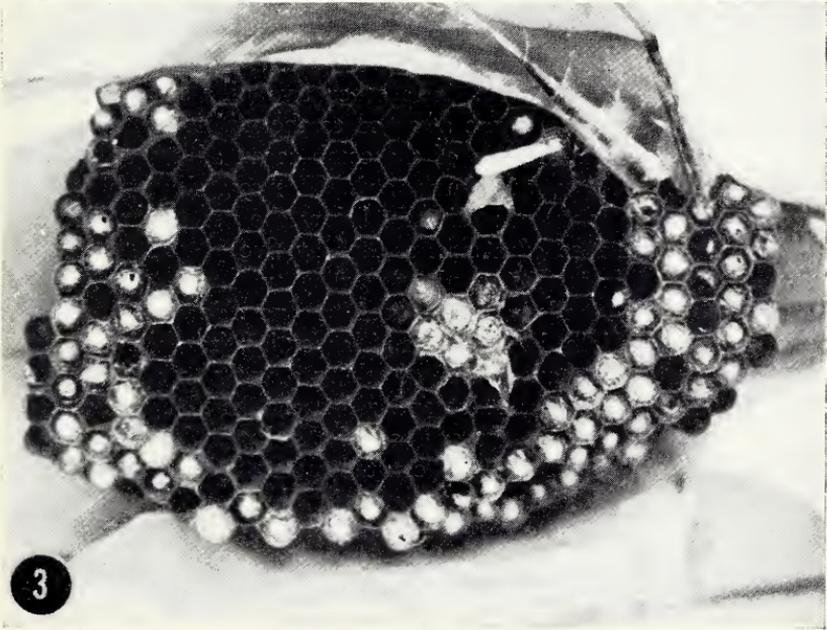
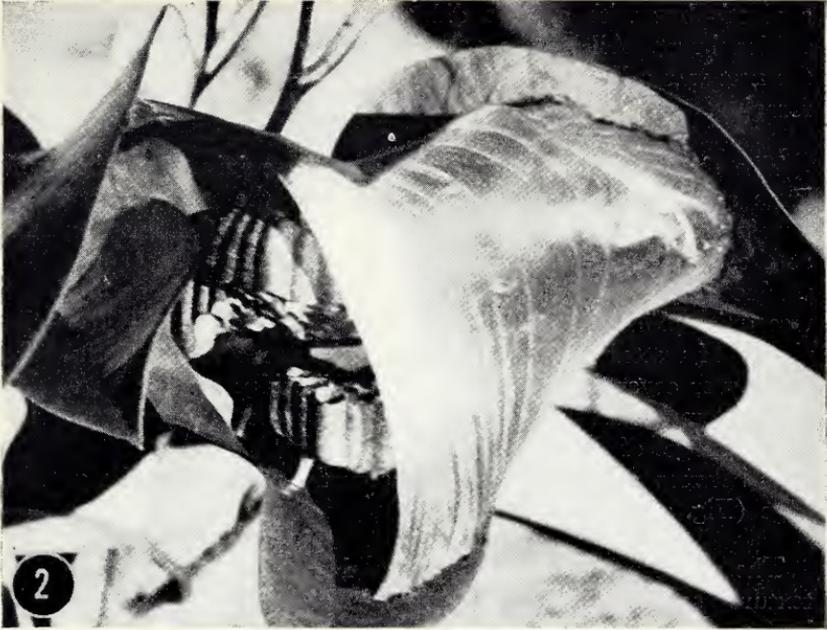
I found a single colony on November 30, 1967, in the Utinga district on the outskirts of Belém, Pará, Brazil ( $1^{\circ}27'S$ ,  $48^{\circ}29'W$ ). The nest was located in an isolated tree growing in marshy soil at the upper end of an arm of a reservoir. The trunk of the tree would stand in shallow water during the rainy season (January through June), when the reservoir is full. The tree was about eight meters tall and twenty meters distant from tall second-growth forest, which surrounded it on three sides. The nest was built in the thick foliage at the end of a small branch about four meters from the ground.

The adult wasps were very timid, and the slight shaking of the nest as I collected it caused them all to retreat inside. Even more violent shaking after the branch was clipped would not bring them out to defend their brood. Only when the colony was placed inside

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Fig. 2. Nest of *Pseudochartergus fuscatus*. The combs are visible through the entrance. The parallel ridges in the broad sheet of transparent film to the right of the combs probably mark boundaries between successive additions of the secretion. Slightly larger than natural size.

Fig. 3. Upper comb of *Pseudochartergus fuscatus* nest, showing brood distribution. The two dark cells just above the five pupae near the center contain eggs of the third generation of brood. Large larvae are visible in surrounding cells. Some of the cells among the outer pupae are empty but still have fragments of cocoon attached to them; these are cells from which adults emerged after the nest was collected.  $1\frac{1}{2}$  times natural size.



a plastic bag with cyanide did the adults fly from the nest in a sudden burst. All of the 230 adults present were females. Since the nest was collected during the day there were probably more out foraging.

The six leaves surrounding the nest were joined together with large amounts of a dry, transparent film, the resulting structure forming a watertight envelope around the nest, with a broad opening at the distal end (Figs. 1 & 2). The film, probably a secretion produced by the adult wasps, resembled thick cellophane in that it was quite pliable, crackled when flexed and tore much like cellophane. If wetted with water it softened but retained its form. The film never covered leaf surfaces, but did bridge gaps of up to four centimeters between leaves. Each sheet of the film had a series of curved ridges of thicker material; these probably marked the boundaries between successive applications of the material to the growing edge (Fig. 2).

The nest consisted of two horizontal combs constructed of a fine-textured carton. The upper comb was the larger, being 4.5 cm wide by 6.5 cm long. It was suspended below a single leaf by three carton pillars averaging 5 mm in length. The largest of these was 3 mm thick, located near the center of the comb and attached to the leaf surface next to the midrib. The other two pillars, one on either side of the central one, were attached to the midrib of the leaf. A fourth pillar joined one side of the comb to an adjacent leaf. The cells of this comb opened downward. The second comb (2.0 cm wide by 4.0 cm long) was directly below the upper one and fixed to the dorsal surface of a smaller leaf by five pillars 5 mm long. The cells of this comb opened upward, though there were several irregularly-placed cells which opened to one side (Fig. 1). The two combs were joined by a single pillar issuing from the face of the upper comb near its center and attaching directly to a pillar at one end of the lower comb. A second pillar connected the face of the upper comb directly to the surface of the lower leaf next to the lower comb. The pillars were constructed entirely of carton. The cells of each comb averaged 3.0 mm in diameter (measured from midpoints of opposite walls). Cells which had produced adults averaged 8.0 mm in depth. The silken cocoons spun by the larvae were slightly domed and were not covered with bits of carton, as they are in at least some species of the genera *Mischocyttarus*, *Clypearia* and *Epipona* (Jeanne, unpublished data).

The upper comb (Fig. 3) had 288 cells in 25 rows. There were three generations of brood<sup>1</sup> in this comb. Two cells in the center of the comb contained eggs of the third generation, and next to these were five second-generation pupae. Surrounding these were 58 cells containing meconia and second-generation larvae, decreasing in age away from the center of the comb, and they in turn were surrounded by a ring of 90 cells containing meconia and second-generation eggs. Thirteen empty cells were scattered throughout these egg and larval cells. Around the second-generation egg cells were the remaining brood of the first generation: 92 pupae surrounded by 25 larvae and three eggs.

The lower comb consisted of 52 cells. This comb was apparently younger than the upper one, and contained only two generations. The oldest part of this comb appeared to be at the proximal end (end nearest the leaf petiole), where the end cell contained a meconium and an egg, probably of the second generation. Moving distally along the comb, there were 37 pupae, three larvae and one egg of the first generation, with no empty cells.

The entire nest, therefore, contained 97 eggs, 86 larvae, 134 pupae and 13 empty cells for a total of 330 cells. Richards and Richards (1951) estimate the ages of nests in developmental units, one unit being the developmental period from egg to adult. By this measure the nest was just over two developmental units old.

There are three species of *Pseudochartergus*, and the nest of one, *P. chartergoides*, has previously been described by R. von Ihering (1904), A. Ducke (1905) and J. Bequaert (1938). It consists of a single, usually elongate comb, attached by pillars to the underside of a banana-like leaf or a palm leaflet. The comb is enclosed by a second leaf or leaflet fastened under the first with a secretion similar to that described above for *P. fuscatus*. The nest of *P. fuscatus* differs from nests of *P. chartergoides* in having a second comb, and from nests of most other vespids in that the cells of this comb open upward. To my knowledge the only recorded instance of a vespid nest with upward-opening cells is *Ropalidia flavopicta javanica* from Java (van der Vecht, 1962).

The transparent film enclosing the nest is likewise unusual but not unique to the genus. A nest of *Ropalidia opifex* described by

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<sup>1</sup>The term "generation of brood" as used here is defined such that the x<sup>th</sup> generation comprises all those brood in cells being used for the x<sup>th</sup> time. Since the adults of a colony may continue to add cells to the periphery of a comb that has developing brood in the center, several generations of brood may be present in a single comb at one time.

van der Vecht (1962) consisted of a single comb attached by a number of pillars to the underside of a fern frond and enclosed in a "silk-like canopy resembling polythene in colour and degree of transparency" (p. 70). The photographs of this nest reveal the striking resemblance of the canopy to the film described above for *P. fuscatus*, even down to the ridged thickenings. Van der Vecht mentions, however, that the covering was "very delicate" (p. 70), whereas that of *P. fuscatus* was quite tough.

To my knowledge *Pseudochartergus* and *Ropalidia* are the only genera to enclose their nests in a transparent film. However, wasps of the genera *Polistes*, *Mischocyttarus* and probably others produce a similar substance which they apply with their mouthparts to build up the very tough petioles from which their nests are suspended (Rau, 1933; Eberhard, 1969). It is possible that these two substances have a common glandular source.

Richards and Richards (1951) classify the nest of *Pseudochartergus chartergoides* as stelocytтарous and gymnodomous; that is, the comb is attached by petioles to the substrate and is not surrounded by an envelope. But they observed no nests in the field and apparently relied on the description written by Ducke (1910), which makes no mention of a clear film joining the leaves surrounding the nest. Bequaert (1938), however, mentions the film, and it was consistently present in the nests of *P. chartergoides* I found near Belém. Since the leaves and film form an envelope that surrounds the nest, much as do the more conventional carton envelopes of other genera, I am inclined to conclude that the nests of these two species can properly be called calyptodomous.

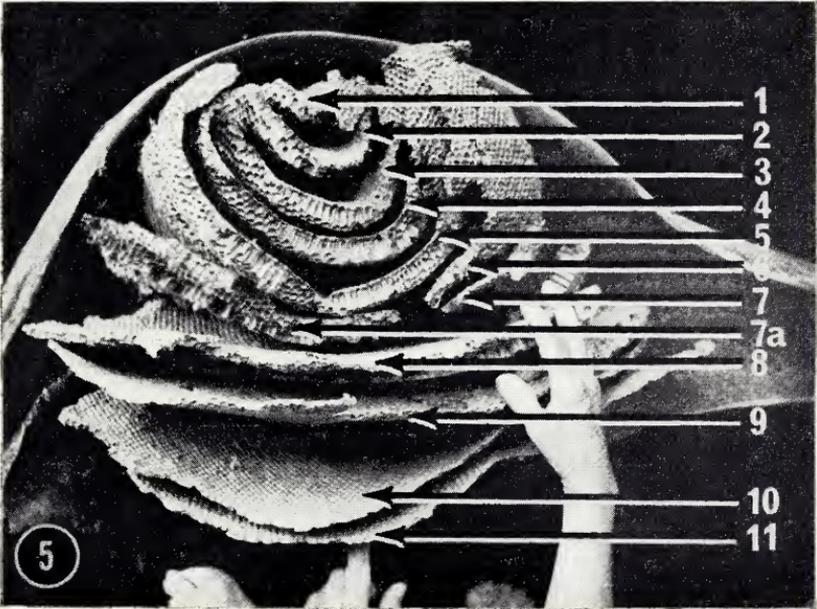
#### *Stelopolybia (Gymnopolybia) testacea*

This nest was collected on July 22, 1968, in rain forest at Fazenda Taperinha, 40 km east of Santarém, Pará, Brazil (2°26'S, 51°11'W). It was discovered where it had fallen onto a footpath. The nest had been suspended about ten meters above the ground beneath a large, woody spathe of an "inaja" palm (*Maximiliana regia* Mart.). This inverted spoon-shaped structure, nearly a meter in length, had

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Fig. 4. The nest of *Stelopolybia testacea* as it lay on the ground when discovered. The supporting spathe, to the left and rear, arches over the combs, which lie stacked face up. The topmost comb, number 11, is folded back upon itself. There are numerous adult wasps on the spathe and combs.

Fig. 5. *S. testacea* nest reconstructed, as it would appear from beneath if the nest were *in situ*. The base of the spathe is at the right. The semi-cylindrical form of the nest is most pronounced in the older combs, at the top of the illustration. About 1/8 natural size.



formed a natural roof over the nest, but the base of the spathe had so rotted that the weight of the nest caused it to break (Fig. 4). The nest had lain on the ground for more than a week, but the adults had not abandoned it. The fall had torn the nest away from the spathe, but the combs lay stacked on top of one another in the normal position relative to one another, so the nest could be roughly reconstructed (Fig. 5).

The nest was constructed of fine-textured carton of a uniform tan color. The cells averaged 5.9 mm in diameter (measured between midpoints of opposite walls) and opened on the convex sides of the combs. The silken caps of the pupal cocoons were slightly domed, and were not covered with bits of carton. The bottoms of the cells were convex, giving the backs of the combs a mammillated surface.

There were twelve combs, each hanging vertically from an edge by several pillars, and not surrounded by an envelope. The combs were constructed as concentric semi-cylinders around a vertical axis at one side of the spathe. Each comb was connected to adjacent combs by many pillars (Fig. 6). The comb nearest the central axis was the smallest and apparently was the first to have been built. Between combs 5 and 8 were three combs. Two of them, labelled 6 and 7, were at the proximal end of the nest (end nearest the base of the spathe; see Fig. 5). The third, called 7a, filled up most of the remaining space at the distal end of the nest. A vertical discontinuity between the right and left sides of combs 4 and 5 (Fig. 8) suggests that these two combs were initially composed of separate right and left portions which were fused as they were enlarged toward one another. A similar situation seemed to have occurred in the case of combs 6, 7 and 7a, except that 7a and 7 (or 6) were never fused. The size and brood contents of each comb are given in Table I.

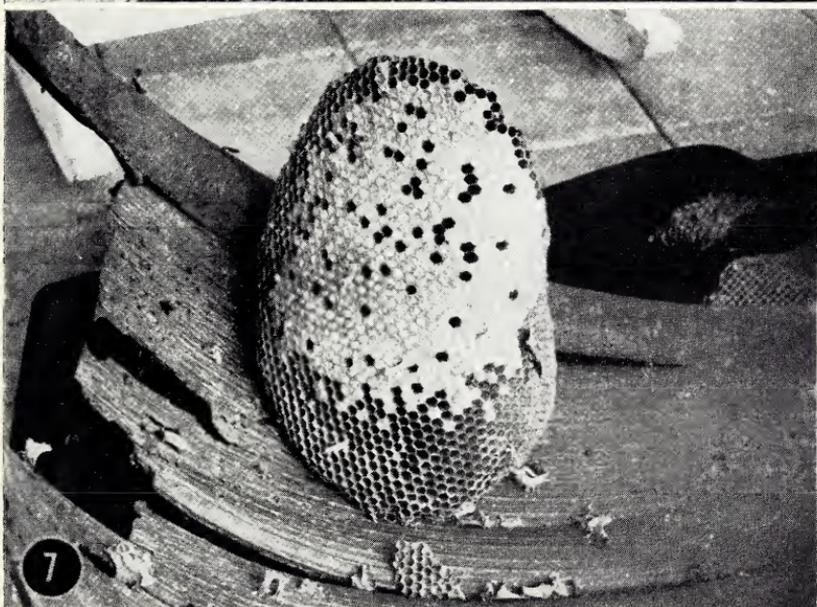
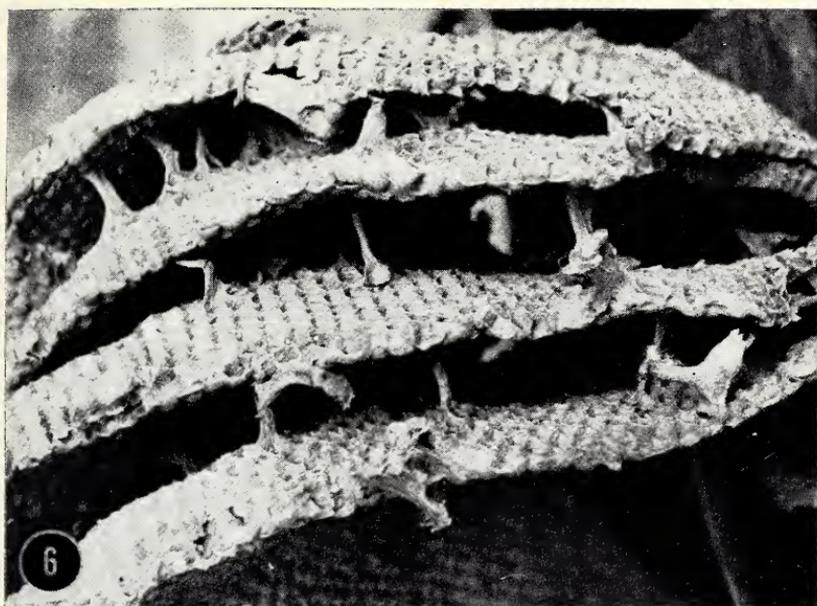
The presence of a meconium in a cell indicated that the cell had produced an adult. No attempt was made to determine the presence of more than one meconium in a used cell. Within a given comb the brood decreased in age from the center outwards. Comb 8

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Fig. 6. Combs 4-7 of the *S. testacea* nest showing how they are interconnected by numerous pillars. About 1/2 natural size.

Fig. 7. Comb 3 of the *S. testacea* nest in position on the spathe, combs 4-11 removed. The white caps of the pupal cocoons cover most of the central cells.

In Figs. 7-9 the combs are shown in an upside down position; that is, the edge from which each comb is suspended from the spathe is at the bottom of the figure. The proximal end of each comb is to the right.



showed this most clearly (Fig. 9). In comb 3 (Fig. 7), since the empty cells peripheral to the pupae had meconia, at least one complete generation of brood had been produced by this comb, and the pupae present belonged to a second generation. Since combs 1 and 2 were probably older than 3, it can be assumed that comb 1 had produced two complete generations and that the pupae of comb 2 were vestiges of the second generation. Comb 4 was then probably of approximately the same age as 3, and its pupae were of the second generation. Comb 5 had probably contained larvae of the second generation before the nest fell. Comb 7a was probably only slightly younger than 5, and had larvae of the second generation. Combs 6 and 7 had not produced any adults. Either they were constructed after 5, 7a and 8, or they were constructed in sequence and not used. Since the cells peripheral to the masses of capped cells in combs 8 and 9 (Fig. 9) were free of meconia, the pupae of these combs must have been of the first generation. Combs 10 and 11, free of meconia and with low cell walls, may have been empty or may have contained first-generation eggs and young larvae before the nest fell.

The entire nest contained an estimated 27,600 cells, and of these approximately 3,000 contained pupae. The nest was at least two-plus developmental units old, and possibly older. That is, it is possible that combs 1 through 7a had produced more than two generations of brood, and that comb 7a may have produced at least one full generation before combs 8 through 11 were even constructed.

It is interesting that nearly all the brood were in pupal stages, and that eggs and younger larvae were totally lacking. It may be that the fall of the nest caused the adults to remove the younger brood in order to devote all their efforts to rearing the older brood to maturity. Or it is possible that the fall of the nest had nothing to do with it, and that the colony was mature and was getting ready to swarm. In Panama, Rau (1933) collected an apparently mature colony of *Stelopolybia pallipes* var. *bequaerti*, the brood of which

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Fig. 8. Combs 5, 6 and 7 of the *S. testacea* nest in position on the spathe, with combs 7a-11 removed. The discontinuity in the rows of cells runs up the middle of comb 5. Combs 6 and 7 are nearly the same size and cover the right side of comb 5.

Fig. 9. Comb 8 of the *S. testacea* nest. The brood decreases in age from center outward. The empty cells in the center had all produced adults, and at the time the nest was collected adults were emerging from the innermost capped cells (note torn cell caps), indicating that these contained the oldest pupae. Newly-emerged adults can be seen resting on the comb.

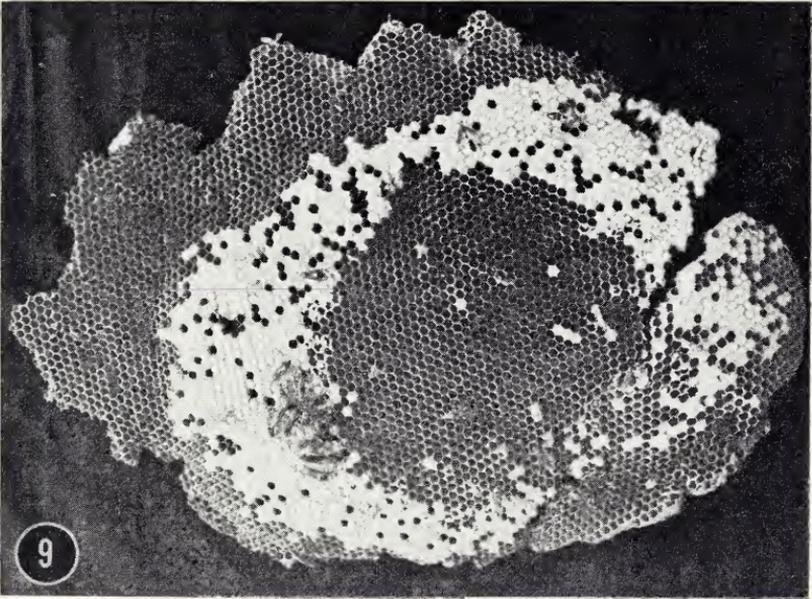
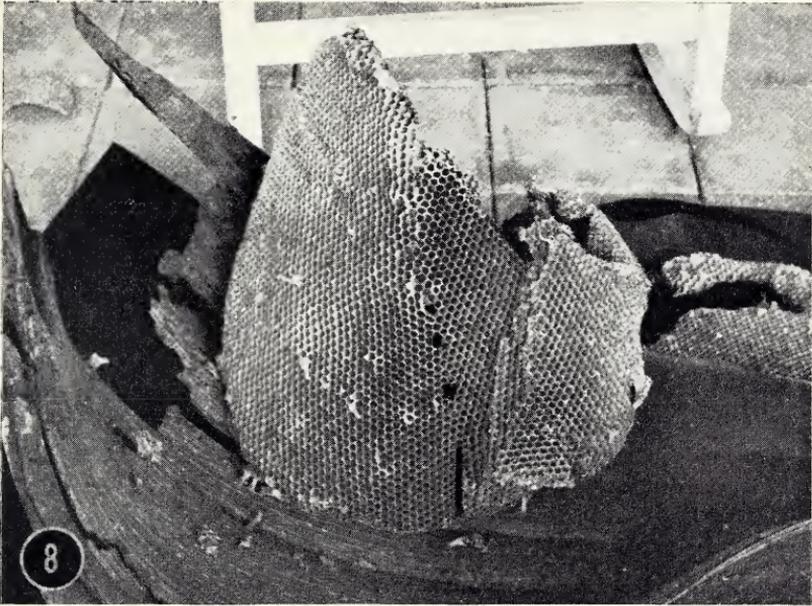


TABLE I

Comb	Dimensions (in cells)		Est. no. of cells	Brood	Meconia
	width	length			
1	26	16	300	none	most cells
2	40	40	1200	a few pupae in center	most cells
3	41	50	1500	large mass of pupae and a few mature larvae in center	most cells
4	80	60	3600	large mass of pupae and a few mature larvae in center	most cells
5	80	60	3600	none	most cells
6	35	40	1100	none	none
7	35	40	1100	none	none
7a	60	45	2100	none	most cells
8	90	36	2500	ring of pupae	most cells inside ring, none outside ring
9	90	36	2500	large mass of pupae and a few mature larvae in center	none
10	85	55	3700	none	none
11	100	55	4400	none	none

were almost all pupae. Rau concluded that the colony was about to swarm.

The *S. testacea* colony was collected at night, when all the adults were presumably on the nest, and very few escaped during collection, so the 6,466 adults taken represent close to the total population of the colony at the time. However, due to the disruption caused when the nest fell, it is possible that the population before the fall was significantly greater.

A sample of 1,626 wasps was examined and found to comprise 115 males (7.1%) and 1511 females (92.9%). During the day after the nest was collected one male and three females emerged from combs 3 and 4, and one male and 32 females emerged from combs 8 and 9. This indicates that males are reared in both younger and older portions of the nest. During the four days following collection of the nest a total of 422 adults emerged from all combs, and of these 20 (4.7%) were males and 402 (95.3%) were females.

The fourteen species of *Stelopolybia*, all neotropical, fall into two subgenera, *Angiopolybia* and *Gynnopolybia*. The nests of two of the three species of subgenus *Angiopolybia* have been described (see

Richards and Richards, 1951, and the references they cite), and both are stelocytтарous, rectinidal and calyptodomous, meaning the combs are suspended horizontally one below the other by pillars and are surrounded by an envelope.

The nests of six of the eleven species of subgenus *Gymnopolybia* are known, though adequate descriptions seem to exist for only four. All are stelocytтарous and gymnodomous, that is the combs are suspended by pillars and are not surrounded by an envelope. They are built in hollow trees or other sheltered places. The architecture of the *S. (G.) testacea* nest described here most closely resembles that of *S. (G.) pallipes* and *S. (G.) cajennensis*, which build semi-cylindrical interconnected combs hung vertically by their edges (Richards and Richards, 1951, and cited references). *S. (G.) vicina* and *S. (G.) meridionalis* hang their combs horizontally, each one suspended from the one above by many paper pillars (R. von Ihering, 1904).

The marked curving of the combs around a vertical axis seems to be the rule in *S. pallipes*, *cajennensis* and probably *testacea* as well. The effect is to stiffen the combs, making them much less likely to bend along a horizontal axis. Such a configuration may have been evolved to reduce nest damage due to wind when the nests are constructed in exposed situations, as was the nest of *S. testacea*.

As far as I am aware, the 6,466 adults of this colony make it the most populous colony of *Stelopolybia* ever collected, and it is among the largest colonies of any neotropical wasp. The above-mentioned colony of *S. pallipes* var. *bequaerti* collected by Rau had 1965 adults, and Richards and Richards (1951) describe taking a nest of *S. fulvo-fasciata* in Guyana with 1409 adults (many more escaped). Eight colonies of *S. pallens* collected by Richards and Richards in Guyana contained between 25 and 390 adults each. The largest colony of any New World polistine wasp on record is one of *Brachygastra mellifica* collected near Brownsville, Texas, with about 15,000 individuals (Schwarz, 1929). Naumann (1968) reported seeing a colony of the same species with about 10,000 adults (no locality was given). Richards and Richards report taking a nest of *Protopolybia pumila* in Guyana with 7,087 individuals.

These figures, of course, do not necessarily indicate maximum mature colony size. If the colony was collected during the day, many foragers may have been gone from the nest. In many cases in the literature a good portion of the adult population escaped during collection and were not counted. More fundamentally, the popula-

tion size depends upon the age of the colony. For these reasons the figures cited can be used as only a very approximate guide to the mature size of a "typical" colony of each species.

*Note on a parasite of Stelopolybia testacea*

On the second day following collection of the *S. testacea* nest, a parasite emerged from one of the capped cells of comb 8. It has been tentatively identified<sup>2</sup> as *Nomadina cisandina* (Schulz) (Hymenoptera, Trigonalidae). It superficially resembled its host in form and color except that it was slightly smaller in size, had a relatively smaller head, and lacked the black markings on the gastral segments. The empty pupal skin of the *S. testacea* host remained between the cocoon of the parasite and the wall of the paper cell. The cap of the cell appeared normal and was evidently spun by the *S. testacea* larva. It is interesting that the adult parasite emerged from a section of comb from which adult *S. testacea* were emerging at that time. A second adult parasite of the same species was found on the nest several days later.

Other species of Trigonalidae are known to be parasitic on social Vespidae. Bertoni (1911) has recorded *Seminota marginata* from species of *Apoica* and *Polistes*, and *S. depressa* from *Polistes*. Clausen (1929) has recorded *Nomadina cisandina* from *Polybia*, *Seminota mejicana* from *Parachartergus*, and *Pseudogonalos hahni* and *Bareogonalos canadensis* from *Vespa*.

Acknowledgements

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<sup>2</sup>By I. H. H. Yarrow, British Museum (Natural History).

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SIBLING SPECIES IN THE *EURYDICE* GROUP OF  
*LETHE* (LEPIDOPTERA: SATYRIDAE)

BY RING T. CARDÉ,<sup>1</sup> ARTHUR M. SHAPIRO,<sup>1</sup>  
AND HARRY K. CLENCH<sup>2</sup>

INTRODUCTION

We have uncovered a pair of sibling species in the comparatively well-known butterfly fauna of eastern North America: the common Grass Nymph or Eyed Brown, *Lethe eurydice* of recent authors, is actually two species, which are extensively sympatric.

Curiously, the distinctness of these two has been known since at least 1936, when W. D. Field discovered and characterized them as subspecies. He assigned names to them which we now know to be inapplicable. This was corrected in 1947 by R. L. Chermock, who named the presumably more southern "subspecies" *appalachia*. Neither of these authors was aware that the "subspecies" are sympatric.

The present investigation was first suggested when one of us (Clench) found both forms flying in the same area near Leesburg, Mercer Co., Pennsylvania in 1966. The conspicuous habitat difference between them implied that two species might be involved. In 1968 another of us (Shapiro) found the same situation in western and central New York and (with Cardé) investigated the immature stages and biology of the insects. The results of this study are partly reported elsewhere (Shapiro and Cardé, 1970).

Independently of us, C. F. dos Passos and his correspondents simultaneously made the same discovery. Several of the conclusions contained in the resulting paper (dos Passos, 1969) appear erroneous. Since the taxonomic situation is very complex, we here review the whole subject, nomenclatorially, morphologically, and distributionally.

In brief, we recognize two species in this group, as follows:

(1a) *Lethe eurydice eurydice* (Johansson), widely distributed from Labrador to Great Slave Lake and south to Delaware and Illinois, occurring in open marshes and sedge meadows.

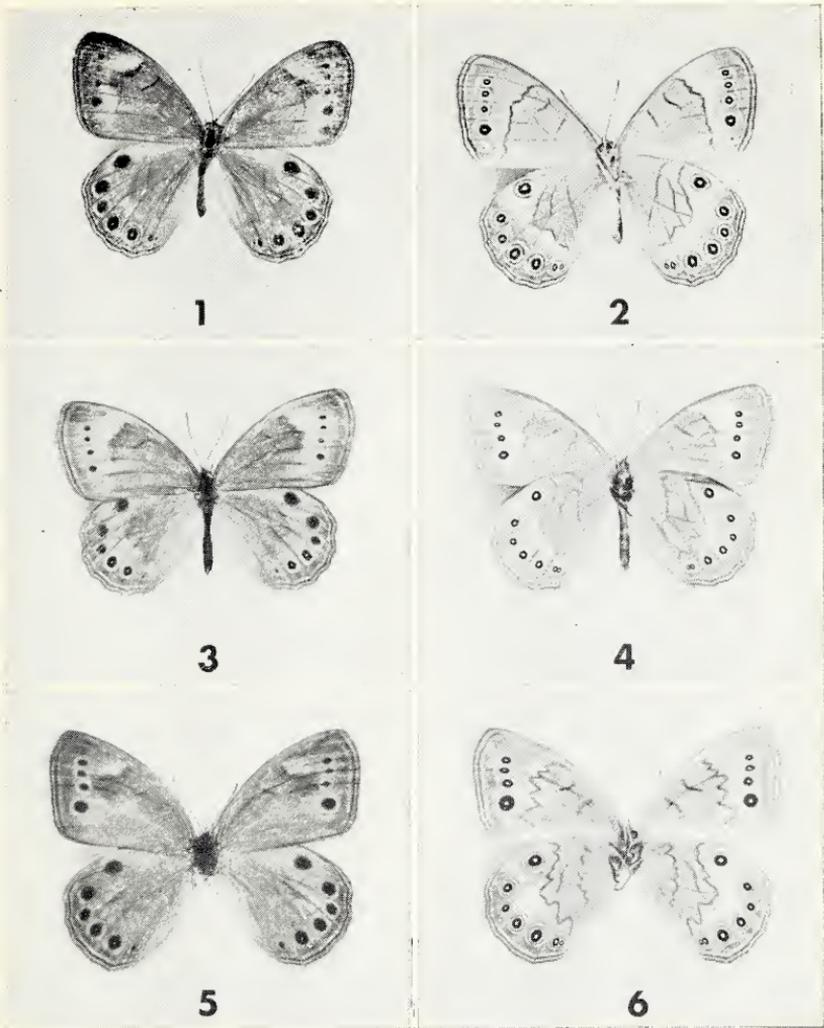
(1b) *Lethe eurydice fumosa* (Leussler), scattered in small isolated colonies (many now extinct) in sedgy permanent marshes in the

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<sup>1</sup>Department of Entomology and Limnology, Cornell University, Ithaca, N.Y. 14850.

<sup>2</sup>Section of Insects and Spiders, Carnegie Museum, Pittsburgh, Pa. 15213

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Figs. 1-2. *Lethe appalachia* male, McLean Bogs Reserve, Tompkins Co., New York. Figs. 3-4. *Lethe eurydice* (male) neotype, Morris Arboretum, Philadelphia Co., Pennsylvania. Figs. 5-6. *Lethe eurydice fumosa* male, Sarpy Co., Nebraska.

prairie regions from Minnesota and South Dakota to Indiana, Nebraska and Colorado.

(2) *Lethe appalachia* R. L. Chermock, widely distributed from Maine to northern Florida, westward to South Dakota and Alabama, broadly sympatric with *L. e. eurydice* but occurring primarily in swamp forest, shrub swamps and forest-edge ecotones.

These forms have had a particularly extensive history in earlier literature, involving not just the above names but several others as well, as may be seen below.

#### TAXONOMY

In reviewing the taxa of the *Lethe eurydice* group, we have given the synonymies in strict chronological order, following the practice of some of the older authors. We hope this practice will add historical perspective to the discussions of these intricate synonymies.

The distributional data and maps (figs. 21, 22) were based on material examined in the following institutional collections: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); United States National Museum, Washington, D.C. (USNM); Carnegie Museum, Pittsburgh (CM); Cornell University, Ithaca, New York (CU); New York State Museum, Albany (NYSM); and Hope Department of Entomology, Oxford University, England (Oxon.). Also the following private collections: Robert H. Whittaker (RHW); David J. Horn (DJH); Arthur M. Shapiro (AMS). A few reliable printed or other records, based on specimens not seen, are given separately, along with a few which are queried.

The sexes of *Lethe* are very similar and may at times be difficult to determine in a superficial examination. We have therefore listed only the localities and dates of material examined. In the case of large series, only a range of dates may be given.

The characters differentiating the three entities recognized in this paper are summarized in Table 1 and in the accompanying section of the text. A brief summary of the most conspicuous characters of each is given following its taxonomic history.

#### *Lethe eurydice eurydice* (Johansson)

*Papilio eurydice* Johansson 1763, Amoen. Acad. 6: 406; type locality Philadelphia [Pennsylvania]; type formerly in the De Geer collection (Stockholm, Sweden), now lost; neotype designated below.

*Papilio canthus* Linnaeus 1767, Syst. Nat. (12th ed.): 768; type locality "in America septentrionali;" no type exists (replacement name for *Papilio eurydice*).

- ? *Papilio canthus*: Fabricius 1775 (*partim*), Syst. Ent.: 486.  
*Argus canthus*: Scopoli 1777, Introd. Hist. Nat.: 432.  
*Satyrus canthus*: Godart 1821, Encycl. Meth. 9: 465, 493.  
*Neonympha canthus*: Westwood 1851, in Doubleday, Westwood, and Hewitson, Gen. Diurn. Lep. 2: 375.  
*Neonympha cantheus* (*nec* Godart 1821, see below): Morris 1860, Cat. Lepid. N. Amer.: 10.  
*Hipparchia boisduvallii* Harris 1862, Ins. Inj. Veg. (Flint ed.): 305, fig. 128; type locality "this State" (Massachusetts), type now lost; no neotype designated.  
*Debis canthus*: Herrich-Schaeffer 1865, Correspbl. Zool.-Min. Ver. Regensburg 19: 72.  
*Pararge canthus*: Butler 1868, Cat. Satyridae Br. Mus.: 123.  
*Euptychia canthus*: Kirby 1871, Syn. Cat. Diurn. Lep.: 55.  
*Pararge boisduvallii*: Edwards 1872, Synopsis N. Amer. Butt.: 26.  
*Argus eurydice*: Scudder 1872, Syst. Rev. Amer. Butt.: 6.  
*Satyrodes eurydice*: Scudder 1875, Bull. Buffalo Soc. Nat. Sci. 2: 243.  
*Satyrodes canthus*: Smith 1884, Bull. Brooklyn Ent. Soc. 6: 119.  
? *Satyrodes canthus* ab. *bowveri* F. H. Chermock 1927, Bull. Brooklyn Ent. Soc. 22: 118; type locality Port Hope, Ontario; type not located, stated by dos Passos to be in Carnegie Museum, but not found. (Infrasub-specific name with no standing in nomenclature.)  
*Satyrodes eurydice transmontana* Field 1936, J. Ent. Zool. (Pomona) 28: 22; type locality Compton, Quebec; no type designated.  
*Satyrodes eurydice transmontana* f. ♀ *rawsoni* Field 1936, J. Ent. Zool. (Pomona) 28: 22; type locality Bloomfield, Michigan; type deposited in U. S. National Museum. (Infrasubspecific name with no standing in nomenclature.)  
*Lethe* (*Enodia*) *eurydice*: R. L. Chermock 1947, Ent. News 58: 29.

The descriptions of both *eurydice* [Johansson and *canthus* Linnaeus are too scanty to restrict on internal evidence to either of the sympatric northeastern species, both of which occur at the type locality (Shapiro, 1970a). If that locality (Philadelphia) is accurate, there can be no doubt that Johansson's description applies only to a member of this group, even though no mention is made of eyespots on the forewing above (an objection to this usage, raised by Harris, 1862 and Edwards, 1897). No type of *eurydice* or *canthus* (which was proposed explicitly as a replacement name for *eurydice* and hence has the same type) exists in the British Museum (Natural History) or in the De Geer collection at the Naturhistoriska Riksmuseet, Stockholm.

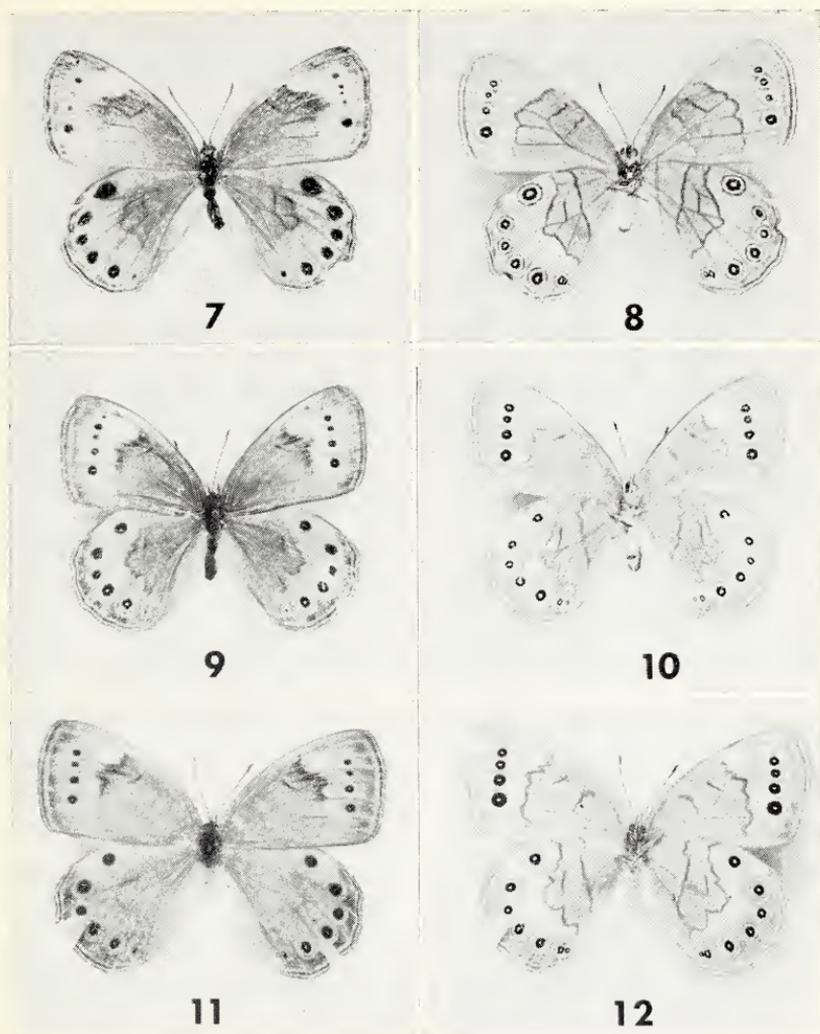
When *appalachia* (see below) was described as the southern subspecies of *eurydice*, the latter name became firmly associated with the assumed "northern" subspecies whose color and pattern were contrasted with *appalachia* by Chermock. It seems desirable to

stabilize the nomenclature by preserving this usage through a neotype designation. This removes the possibility that a specimen of Chermock's *appalachia* might eventually be selected as neotype of *eurydice*, leaving the familiar "northern" insect's name in question. The only Philadelphia specimens of *eurydice* auct. with full data which we have found were collected by one of us (Shapiro). Several of these were placed in the United States National Museum two years ago, and we designate one such specimen the neotype of *Papilio eurydice* Johansson.

*Neotype*. — A male deposited in the U.S. National Museum bearing the manuscript label "eurydice ♂/Morris Arboretum/Phila. Co. Pa./29 June 1967/A. M. Shapiro" (fig. 1). We have added a label identifying the specimen as the neotype of *Papilio eurydice* Johansson. The U.S.N.M. also contains a second specimen with the same locality and collection date.

*Taxonomic History: the Euptychia names*. — The taxonomy of *L. eurydice* is complicated by confusion with *Ypthimoides* (= *Euptychia*) *argulus* (Godart). This problem was not noted by dos Passos, and is reviewed here.

Fabricius (1775) reworked the description of *canthus*, adding "immaculatis" to the upperside diagnosis and altering various details. The "immaculatis" may have been by inference from the lack of reference to spots in the earlier descriptions, but it seems more likely that Fabricius was working from some other insect he confused with the Linnean one. In 1779 Cramer described and figured a species from Surinam as *Papilio argante*. This name is a junior homonym of *Papilio argante* Fabricius 1775 (now *Phoebis argante*, Pieridae). Fabricius synonymized *argante* Cramer to *canthus* (Fabricius, 1781), improperly emending it to *arganthe* in synonymy. (*Arganthe* is not available as a replacement name because it was proposed in synonymy.) He repeated this usage in 1787 and 1793. His own descriptions of "*canthus*" do not fit Cramer's figure well. Godart (1821) recognized that three species were included in the Fabrician concept "*canthus*" and attempted to end the confusion by redescribing the true *canthus* (translating Linnaeus), and naming two new entities, *argulus* and *cantheus*. Godart's *argulus* is a replacement name for the preoccupied *argante* and is the oldest valid name for this taxon. *Cantheus* is a renaming of the entity Fabricius first thought was *canthus*, theretofore without a valid name. The identity of this animal cannot be determined if, as appears, Fabrician specimens of "*canthus*" do not exist.



Figs. 7-8. *Lethe appalachia* female, McLean Bogs Reserve, Tompkins Co., New York. Figs. 9-10. *Lethe eurydice eurydice* female, McLean Bogs Reserve, Tompkins Co., New York. Figs. 11-12. *Lethe eurydice fumosa* female, Sarpy Co., Nebraska.

Butler (1868) described *Euptychia perfuscata* and subsequently (1869) synonymized it to *argante*. We have not seen his specimens (which should be in the British Museum), nor any specimen definitely determinable under any of these names. The most recent discussion of *argulus* is by Weymer (1907, p. 202). The leading North American authority on *Euptychia* and its allies, L. D. Miller, advises us (*in litt.*) that he does not know the species, but from Cramer's description and figure would place it near *Yphthimoides grimon*. The partial synonymy of *argante* = *argulus* is thus:

*Papilio argante* Cramer 1779 (*nec Papilio argante* Fabricius 1775), De Uitlandsch. Kapell. 3: 19, pl. 204; type locality Surinam; type not investigated.

‡ *Papilio canthus* (*nec* Linnaeus 1767): Fabricius 1781 (*partim*), Spec. Ins. 2: 64 (*arganthe* in synonymy); 1787, Mant. Ins. 2: 31; 1793, Ent. Syst. 3(1): 157.

*Satyris argulus* Godart 1821, Encyl. Meth. 9: 463, 488; type locality Surinam; type never existed (replacement name for *argante*).

? *Euptychia perfuscata* Butler 1868, Cat. Satyridae Br. Mus.: 18; type locality Para, Brazil; type probably in British Museum, not investigated.

? *Euptychia argante*: Butler 1869, Cat. Diurn. Lep. Fabr. Br. Mus. 13.

*Cantheus*, which is the unknown animal Fabricius confounded first with *canthus* and then with *argante*, usually appears in the synonymy of *eurydice* = *canthus*, but its only proper claim there is its mistaken use in synonymy by Morris (1860). We have removed *cantheus* Godart from the synonymies of the other entities and regard it as a *nomen dubium*, presumably a species of *Euptychia sens. lat.* Its synonymy is:

‡ *Papilio canthus* (*nec* Linnaeus 1767): Fabricius 1775 (*partim*), Syst. Ent.: 486; 1781, Spec. Ins. 2: 64; 1787, Mant. Ins. 2: 31; 1793, Ent. Syst. 3(1): 157.

*Satyris cantheus* Godart 1821, Encyl. Meth. 9: 465, 493; type locality "l'Amerique septentrionale"; type not investigated, probably never existed.

Godart's description of *cantheus* erroneously cites Fabricius, "Species Insectorum" for "Mantissa Insectorum." The name is misspelled "cautheus" in the heading on page 465.

*Taxonomic History: other names.*—Gosse (1841) attributes the name *Hipparchia transmontana* to Say, but it does not appear in any extant work by that author. It usually appears in the synonymy of *eurydice* attributed to Gosse 1840. Apparently Gosse believed it was described elsewhere, since his "description" (1840, p. 247) is

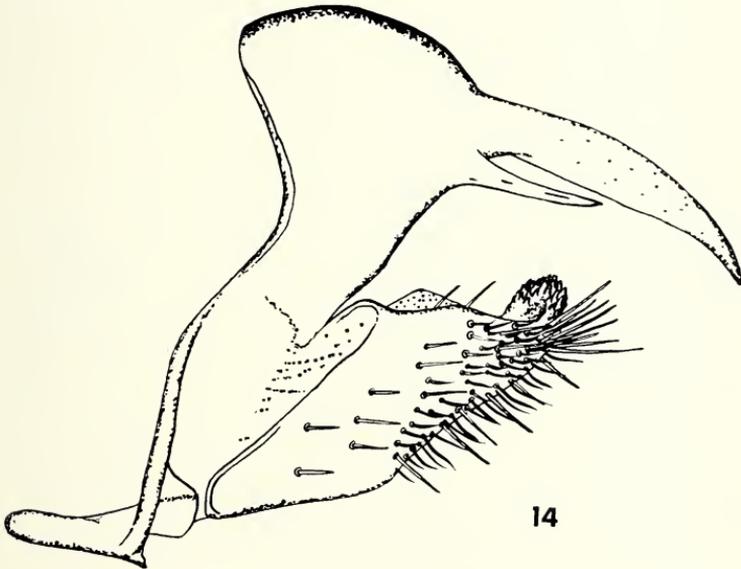
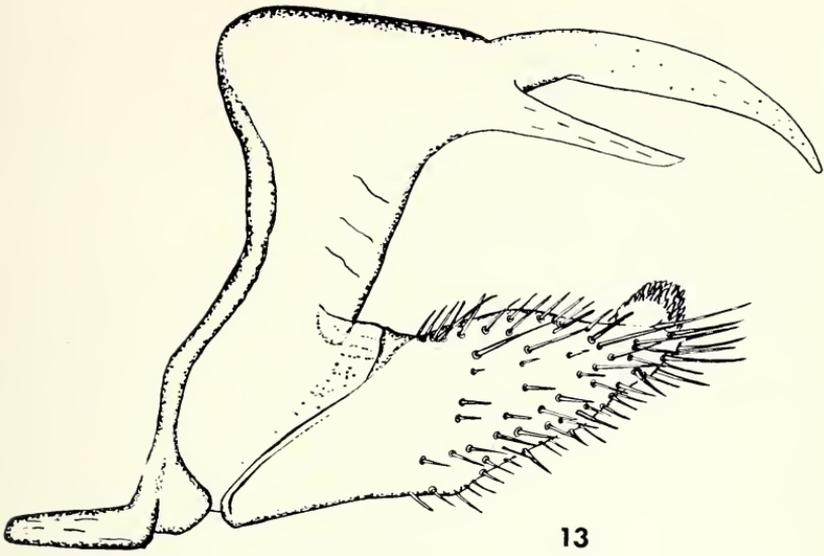


Fig. 13. Male genitalia of *Lethe appalachia*.

Fig. 14. Male genitalia of *Lethe eurydice eurydice*.

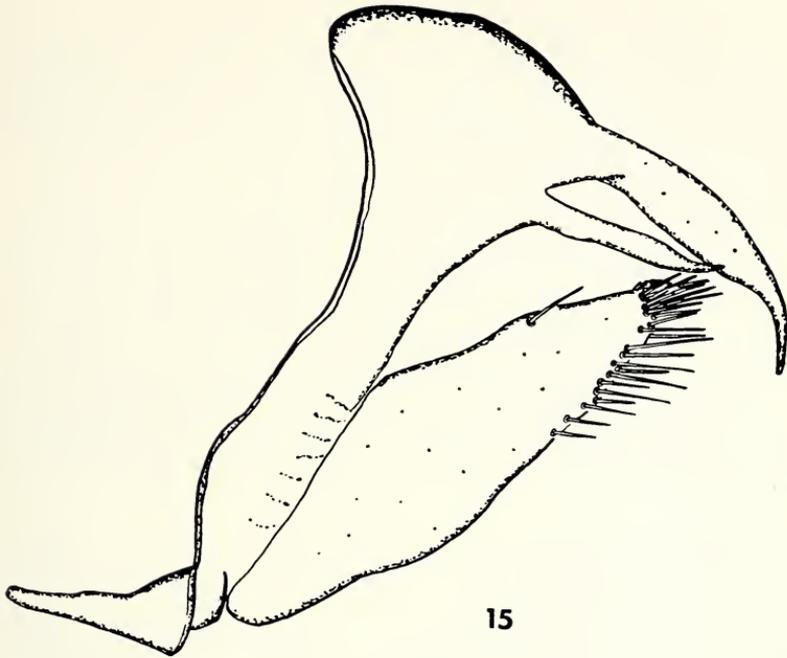
inadequate to associate it with any biological entity. It could apply to any of several Quebec Satyridae, which are not exhausted by the other species enumerated in the text. His statement that "this is likewise described by the American naturalists as very rare, and is found only beyond the Rocky Mountains . . ." makes no sense when applied to any species of *Lethe*. We regard this as a *nomen nudum* and have omitted it from the synonymy.

Field (1936) resurrected *transmontana* as the northern subspecies of *eurydice*, describing it adequately and giving as the type locality Gosse's base at Compton, Quebec. This is the oldest valid publication of the name, which should thus be credited to Field 1936. This subspecific distinction was grounded in confusion over the entities now called *eurydice* and *appalachia*. Observing differences between northern *eurydice* and specimens from near the type locality, Philadelphia, which he took as typical of that taxon but which were really *appalachia*, Field felt that a subspecific name was warranted. This is clear from his article, particularly the citation of Clark's (1932) figures of Beltsville, Maryland *appalachia* which Field (like Clark) calls typical *eurydice*. Thus *transmontana* becomes a junior subjective synonym of *eurydice*. We can see no subspecific differences among eastern populations of *eurydice* as here restricted. Field's female form *rawsoni* is based on specimens faded in life; such specimens occur throughout the range of *eurydice*. The name is infrasubspecific and therefore has no formal standing.

The name *boisduvallii* was attributed by dos Passos (1964) to Morris (1862), an error corrected later (dos Passos, 1969). Morris published the name in synonymy, spelled *boisduvalli*. The first valid publication was in the posthumous (1862) edition of Harris's "Insects Injurious to Vegetation," edited by Flint. The editor's preface makes clear that the name should be attributed to Harris. It was emended to *boisduvalii* by Scudder (1889) in synonymy; this spelling is used by Forbes (1960) and dos Passos (1964). Dos Passos (1969) has further emended it to *boisduvali*. Although not the preferred form, the double "i" is acceptable in taxonomy as the genitive of the Latinized name, i.e. "Boisduvalius." While Boisduval spelled his name with only one "i" and there is no orthographic reason to double it in forming the Latin genitive, the fact that the

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Fig. 15. Male genitalia of *Lethe eurydice fumosa* (valve in slightly different position than valves of figs. 13 and 14). Fig. 16. Ventral view of *Lethe appalachia* valve. Fig. 17. Ventral view of *Lethe eurydice eurydice* valve. Fig. 18. Ventral view of *Lethe eurydice fumosa* valve.



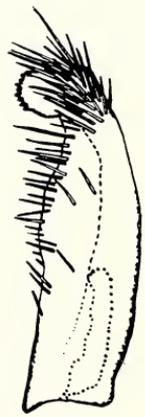
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16



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18

name is spelled *boisduvallii* in both the text and index of Harris (1862) indicates that the double "l" was the form used in the Harris manuscript, and this is confirmed by its use in Morris's (1862) citation from that manuscript. Unfortunately, then, *boisduvallii* is technically a "correct original spelling" and cannot be emended under the Code.

*Summary of Characters.*—*Lethe eurydice eurydice* is relatively pale, pinkish brown above, somewhat yellowish beneath, with the postmedial line deeply indented beneath on all wings. The male valve is strongly 4-sided when viewed laterally, and the tegumen is dorsally rounded. The larva appears superficially to have dark side-stripes on the head capsule, extending from near the tip of the horns to the ocelli. These and other characters are discussed more completely under the headings "Diagnostic Characters" and "Biological Differences," after the taxonomic treatment of *Lethe appalachia*, below.

*Distribution* (fig. 21).—Material examined:

DELAWARE: New Castle Co.: Blackbird, vii.62-65 (AMS); Kent Co.: Smyrna, vii.62-65 (AMS)

PENNSYLVANIA: Philadelphia Co.: Morris Arboretum, vi.29.67 (AMS) (USNM), Tinicum Wildlife Preserve, vi-viii.60-68 (AMS), George's Hill, no date (P. Laurent) (ANSP); Montgomery Co.: Cheltenham Twp., Horsham Twp., Montgomeryville, vi-viii.58-68 (AMS), Pennsburg, vi.21-66 (AMS) (USNM); Bucks Co.: Buckingham, East Rockhill, Ivyland, Chalfont, Trevoise, vi-viii.58-68 (AMS), Bristol, vi.27.67 (AMS) (USNM); Chester Co.: vic. Downingtown, vi-viii.58-68 (AMS); Susquehanna Co.: vii.22-31.? (CM); Lackawanna Co.: Scranton, vii.4.05 (M. Rothke) (CM); Elk Co.: Medix Run, vii.16.64 (H. K. Clench) (CM); Beaver Co.: New Brighton, vii.?03 (W. C. Wood coll.) (AMNH); Mercer Co.: 2 mi. SE Leesburg, vii.11.66 (H. K. Clench) (CM), North Liberty, viii.3.60, viii.9.59 (J. Bauer) (CM); Allegheny Co.: Nadine, vii.29.24 (CM); Erie Co.: Presque Isle, no date, vii.7.26, vii.?40 (CM)

NEW JERSEY: Camden Co.: Westville, Haddon Heights, Atco, Magnolia, vi-viii.58-68 (AMS); Burlington Co.: Mt. Holly, Whitesbog, vi-viii.58-68 (AMS); Gloucester Co.: Woodbury, Glassboro, vi-viii.58-68 (AMS); Atlantic Co.: Da Costa, vi-viii.58-68 (AMS); Mercer Co.: Pennington, Washington's Crossing State Park, Dutch Neck, vi-viii.58-68 (AMS); Ocean Co.: Lakehurst, New Egypt, vi-viii.58-68 (AMS); Middlesex Co.: Jamesburg, vii.8.32 (A.S. Pin-

kus) (AMNH); Union Co.: Elizabeth, vii.13.? (O. Buchholz) (AMNH); Sussex Co.: Arlington, vii.13.18 (O. Buchholz) (AMNH), Hopatcong, no date (C. Palm) (AMNH), "Sussex Co." vii.1.43, vii.6.41 (O. Buchholz) (AMNH).

NEW YORK: New York Co.: West Farms, no date (J. Angus) (AMNH); Queens Co.: Flushing, vii.27.18 (E. L. Bell) (AMNH); Kings Co.: East New York, vii.?03 (W. C. Wood) (AMNH); Suffolk Co.: Calverton, v.26.25, vii.14.29 (R. Latham) (CU), Orient, vi.2.38 (R. Latham) (CU); Richmond Co.: Staten Island, no date (Barnes coll.) (USNM), "S.I." no date (USNM); Rockland Co.: Spring Valley, vii.20.68 (E. L. Rittershausen) (AMS); Orange Co.: 1 mi. E Monroe, vii.21.68 (E. L. Rittershausen) (AMS); Westchester Co.: Somers, no date, viii.9.16, vii.31.26 (W. C. Wood) (AMNH), Bedford, no date (R. B. Dominick), vii.17.37 (A. C. Frederick), vii.16-18.37 (all AMNH), Lake Wacabuc, vii.14.10 (AMNH); Sullivan Co.: Lava, vi.?? (Barnes coll.) (USNM); Albany Co.: Karner, vii.11.03 (J. Cook) (Oxon.), Albany, vii.24.27, vii.25.32 (A. C. Frederick) (AMNH), vii.7.28 (A. C. Frederick) (CU); Otsego Co.: Cooperstown, vii.27.24 (B. Smith) (CU); Cortland Co.: 2.7 mi. W Willet, viii.2.68 (AMS), McGraw, vi.8.14 (Engel coll.) (CM); Tompkins Co.: McLean, vic. Tompkins Co. Airport, Cayuga Inlet Valley, Michigan Hollow, Ringwood Hollow, Wilseyville, vi-ix.67-69 (AMS); Schuyler Co.: Texas Hollow, vii-viii.68 (AMS), Watkins Glen, vii.19-68 (AMS); Yates Co.: Potter Swamp, vi.14.15 (CU); Oswego Co.: Minetto, vi.22.38 (W. T. M. Forbes) (CU); Livingston Co.: Lakeville, vii.18.27 (E. A. Maynard) (NYSM); Clinton Co.: Plattsburgh, vii.2.96, vii.19.93 (G. H. Hudson) (NYSM); Columbia Co.: Ghent, viii.?.31 (AMNH); Saratoga Co.: Saratoga Lake, vii.8.28 (A. C. Frederick) (AMNH); Jefferson Co.: Wellesley Island, viii.13.68 (L. L. Pechuman) (AMS), Thousand Islands, vii.12.09 (AMNH), Clayton, no date (J. H. Stebbins) (AMNH); Cattaraugus Co.: Crystal Lake, vii.6.30 (J. G. Franclemont) (CU); Erie Co.: Chafee, vi.18.32 (J. G. Franclemont) (CU), Buffalo, no date (C. V. Riley coll.) (USNM); Lewis Co.: vii.18.76 (W. W. Hill) (USNM), vii.15.47 (C. P. Kimball) (AMNH); Monroe Co.: vii.2.48, vii.23.46 (C. P. Kimball) (AMNH); Ontario Co.: Fishers, vii.30.48 (C. P. Kimball) (AMNH); Orleans Co.: Oak Orchard Swamp, vii.16.68 (AMS); Genesee Co.: Oak Orchard Swamp, vii.16.68 (AMS); County undetermined: "NY," no date (G. D. Hulst coll.) (AMNH), "vic. NYC" no date (S. L. Elliot) (AMNH)

CONNECTICUT: Tolland Co.: Rockville, no date (Engel coll.) (CM); Litchfield Co.: Litchfield, vii.1.94, vii.15.94 (L. B. Woodruff) (AMNH); Windham Co.: Putnam, vii.21.50 (A. B. Klots) (AMNH); County undetermined: "Ct." no date (G. D. Hulst coll.) (AMNH)

MASSACHUSETTS: Worcester Co.: Winchendon, vii.3.? (J. A. Grossbeck) (AMH), Princeton, no date (W. T. M. Forbes) (CU); Middlesex Co.: Wayland, vii.7.21 (CU); Silver Hill, vic. Lincoln, vii.7.23 (figured by Clark, 1932, pl. 1, figs. 5, 6); County undetermined: "Mass." no date (Barnes Coll.) (USNM)

NEW HAMPSHIRE: Cheshire Co.: Dublin, 1899 (A. H. Thayer) (Oxon.), West Rindge, vii.15.60, vii.10.61 (DJH); Coos Co.: Jefferson, vii.15-21.? (Engel coll.) (CM), vii.7.32 (G. & J. Sperry) (AMNH), Shelburne, vii.4-10.01 (USNM), White Mts., no date (H. Edwards) (AMNH); Grafton Co.: Franconia, no date (A. T. Slosson) (AMNH); Sullivan Co.: Claremont, 1908 (USNM); County undetermined: "N.H." no date (H. Edwards coll.) (AMNH)

VERMONT: Windham Co.: Stratton, vii.21.37 (H. Kahl) (CM); Rutland Co.: Mt. Killington, 4000', viii.17.40 (AMNH); County undetermined: vic. Sandgate, vii.13.49 (A. B. Klots) (AMNH)

MAINE: Piscataquis Co.: Greenville, vii.21-29.19 (F. Haimbach) (CM), Sebec Lake, vii.24-31.? (Barnes coll.) (USNM); Hancock Co.: Bar Harbor, vii.3.38 (A. E. Brower) (USNM), North Bluehill, vii.21.23 (AMNH), Mt. Desert, vii.?.? (W. C. Wood) (AMNH), vii.13.33 (O. Buchholz) (AMNH); Kennebec Co.: Augusta, vii.23.38 (A. E. Brower) (USNM), vii.22.50 (A. E. Brower) (AMNH); Penobscot Co.: Orono, no date (M. Fernald) (CU), Bangor, no date (Engel coll.) (CM), vii.10.89 (E. A. Smyth) (USNM), Passadumkeag Bog, vii.1-7.? (W. Sweadner coll.) (CM), vii.12.34 (A. E. Brower) (AMNH), vii.2.33 (L. P. Grey) (USNM), South Lincoln, vii.15.50 (L. P. Grey) (AMNH), Lincoln, no date (L. P. Grey) (AMNH), (J. C. Hopfinger) (USNM), vii.10.40 (J. C. Hopfinger coll.) (USNM); County undetermined: "Maine," no date (E. A. Smyth) (USNM)

OHIO: Stark Co.: Waynesburg, vii.21.29, vii.4.30 (AMNH)

MICHIGAN: Allegan Co.: Douglas Lake, vii.10.30 (H. C. Will) (CM); Livingston Co.: Pinckney, vii.9.? (CM), vii.9.39, vii.23.39 (AMNH), George Reserve, Pinckney, vii.23.38, vii.31.38 (G. W. Rawson) (USNM), "Livingston Co." vii.9.32 (G. W. Rawson) (USNM); Branch Co.: no date (B. Stroup) (CU); Otsego Co.:

Sturgeon River, 5 mi. E Vanderbilt, vii.8.55 (Klots & Rindge) (AMNH), 7 mi. E Vanderbilt, vii.7.55 (F. H. Rindge) (AMNH), Lake Otsego, vii.7.55 (F. H. Rindge) (AMNH), Pigeon River, 11 mi. E Vanderbilt, vii.8.55 (Klots & Rindge) (AMNH); Cheboygan Co.: vii.6.52, vii.19.52 (H. V. Daly) (AMNH); Emmett Co.: 6 mi. W Pellston, vii.9.55 (Klots & Rindge) (AMNH), Petoskey, vii.8.13, vii.8.14 (J. J. Lichter) (AMNH), Galloway Lake, North Levering, vii.9.55 (Klots & Rindge) (AMNH); Huron Co.: Hume Twp. Arboretum, vi.28.52 (H. V. Daly) (AMNH); Schoolcraft Co.: Thompson, vii.10.55 (Klots & Rindge) (AMNH); Oakland Co.: New Hudson, vi.20.27 (G. W. Rawson) (USNM), Bloomfield, viii.4.29 (G. W. Rawson) (AMNH), viii.12.28 (G. W. Rawson, paratype of *rawsoni* Field) (USNM), viii.4.29 (G. W. Rawson) (USNM); Washtenaw Co.: Willis, vii.30.39 (AMNH), Sharon, vii.2.44 (G. W. Rawson) (USNM); County undetermined: "Michigan" vii.8.90 (AMNH), Green Oak, vi.25.33 (G. W. Rawson) (AMNH), Calvin, vii.3.90 (AMNH), "Snow I., Lake Michigan," no date (CM)

INDIANA: Steuben Co.: vi.16.03 (AMNH); Lake Co.: Hessville, vii.4.08 (E. Beer) (USNM)

ILLINOIS: Lake Co.: "NE Lake Co." viii.24.30 (H. M. Bower) (AMNH); Cook Co.: Chicago, vii.6.13 (J. D. Gunder coll.) (AMNH)

MINNESOTA: Ramsey Co.: St. Paul, no date (Barnes coll.) (USNM); County undetermined: "Minn." no date (AMNH)

WISCONSIN: Douglas Co.: 2 mi. E Maple, vii.11.55 (Klots & Rindge) (AMNH); Milwaukee Co.: Milwaukee, vii.10.08, viii.5.17 (H. M. Bower) (AMNH); Waukesha Co.: Dousman, vii.14.16, vii.20.19 (H. M. Bower) (AMNH); Dane Co.: Madison, no date (E. T. Owen coll.) (USNM); County undetermined: "Wis." no date (A. T. Slosson) (AMNH), (E. T. Owen coll.) (USNM)

NOVA SCOTIA: Cape Breton, viii.?.49 (G. Macmillan) (CM); Cape Breton National Park, viii.?.54 (H. Dietrich) (CU)

NEW BRUNSWICK: Bathurst, viii.5-6.51 (A. B. Klots) (AMNH)

QUEBEC: Dunlop Rd., Gatineau Provincial Park, vii.6.52 (F. H. Rindge) (AMNH); Montreal, vii.1.29 (J. C. Hopfinger coll.) (USNM); "Quebec" vii.3.35 (J. C. Hopfinger coll.) (USNM)

ONTARIO: Ottawa, bred (W. H. Edwards) (CM), vii.23.97 (M. Holmes) (Oxon.); Toronto, viii.9.24 (R. N. & F. A. Dixey) (Oxon.), vii.19.15, vii.20.18 (H. V. Andrews) (CM); Bancroft, vii.1-7.? (W. Sweadner coll.) (CM); Spider Lake, Georgian Bay,

vii.22.14 (G. K. Jennings) (CM); Point au Baril, vii.21.35 (E. D. McDonald) (CU); Don Valley, Toronto, vii.8.57 (J. C. E. Riotte) (AMNH); Sudbury, vii.7-10.59, vii.7-10.60 (J. C. E. Riotte) (AMNH), vii.7.60 and vii.12.58 at UV lights (J. C. E. Riotte) (AMNH); Gravenhurst, Muskoka Dist., iv.7.18 (!) (AMNH); Geraldton, Ashmore Twp., vii.16.55 (Klots & Rindge) (AMNH); Grand la Cloche, vi.27.41, vii.1.41 (O. Buchholz) (AMNH); Leamington, Essex Co., vi.?.90 (E. A. Smyth coll.) (USNM); "Ont." no date (Blackmore coll.) (USNM)

MANITOBA: Aweme, vii.15.07 (CM), vii.19.08 (Barnes coll.) (USNM); Riding Mts., vii.11.38, vii.9.39, vii. 2-3.40 (C. S. Quelch) (AMNH), vii.17.38 (J. F. May) (AMNH), vii.11.38 (G. W. Rawson) (USNW); Transcona, vii.19.48 (C. S. Quelch) (AMNH); Birtle, vii.7.44, vii.19.44 (J. Dennis) (AMNH); Telford, White-shell Provincial Park, vii.24.55 (Klots & Rindge) (AMNH)

ALBERTA: Rivercourse, near Lloydminster, vii.6.41 (R. J. Fitch) (CU)

Other records: Dos Passos (1969) erroneously records *eurydice* from "south to Colorado and east of the Rocky Mountains to Georgia and Florida." The Colorado records represent *L. e. fumosa* (see below). At present the southernmost record of true *L. e. eurydice* is northern Delaware.

Scudder (1889) records *L. eurydice* from Rupert's Fort, Quebec (east shore Hudson's Bay); Mingan, Labrador; and Great Slave Lake, NWT. All of these are plotted on the map.

The western distribution of *eurydice* is unclear. Puckering and Post (1960) record it from Cass, Cavalier, Dickey, Grand Forks, and Pembina Cos., North Dakota. These are entered on the map. We have seen no South Dakota records. However, Leussler (1938), who was well acquainted with *L. e. fumosa*, reported typical *eurydice* in Sioux Co., northwestern Nebraska. This record seems to require special confirmation, and has not been plotted.

The "*eurydice*" reported from Monroe Co., Tennessee (Mather, 1961) was *appalachia* (W. Reinthal, pers. comm.). The latter species was found at Jackson, Tenn. by Roeber (Mather and Mather, 1958).

#### *Lethe eurydice fumosa* (Leussler)

*Satyrodes canthus* n.v. *fumosus* Leussler 1916, Ent. News 27: 99, pl. iv, figs. 1, 2; type locality Sarpy County, Nebraska; type reportedly deposited in Ohio State University, not seen.

*Lethe fumosus*: dos Passos 1969 (*partim*), J. New York Ent. Soc. 77: 120.

*Taxonomic History.*—Described from 17 males and 8 females, all labeled "Omaha" by Leussler, as are various later topotypes. Although it was described as a "variety," the geographic nature of *fumosa* was clearly expressed.

The Greek noun *λήθη* is feminine and retains its gender in the Latinized form *Lethe*. Both the species names in this group are also feminine. We have adopted the spelling *fumosa* to make this subspecies agree in gender, as provided by the Code.

*Summary of Characters.*—*Lethe eurydice fumosa* resembles *L. eurydice* in most respects, but the males and some females are darker above. The four eyespots on the forewing are consistently graded in size, from the smallest on top to the largest at the bottom; this is especially obvious beneath. The male valves have far fewer setae than in *L. e. eurydice*. The early stages are unknown.

*Distribution* (fig. 21).—Material examined:

NEBRASKA: Sarpy Co.: "Omaha" vi.28.13, vii.1.15 (R. A. Leussler) (cotypes) (ANSP); vii.12.13, vi.14.13, vi.27.14 (cotype), vii.7.17 (R. A. Leussler) (USNM); vi.27.14 ("topotype"), vii.5.13, vi.28.13, vi.26.15 (cotype), vii.7.17 (R. A. Leussler) (AMNH); vi.27.14 (paratype), vii.1.16 (figured by Holland, pl. 63, fig. 11) (R. A. Leussler) (CM); County undetermined: "Nebraska," no date (J. Angus coll.) (AMNH)

IOWA: Dickinson Co.: Lake Okoboji, vi.25.21 (R. A. Leussler) (USNM); Hancock Co.: 1 mi. W Klemme, vii.24.60 (L. D. Miller) (CM); Poweshiek Co.: Grinnell, vii.4.81 (AMNH); County undetermined: "Ia." no date (H. Skinner) (CM)

WISCONSIN: Kenosha Co.: Twin Lakes, vi.1-4.11 (A. Kwiat) (USNM); County undetermined: "Wis." no date (E. T. Owen coll.) (USNM)

MINNESOTA: Hennepin Co.: Lake Minnetonka, no date (USNM), St. Anthony Park, vii.15.91 (USNM)

INDIANA: County undetermined: Tremont, vii.24.48 (O. Buchholz) (AMNH)

SOUTH DAKOTA: Brookings Co.: Volga, no date (P. C. Truman) (CM)

COLORADO: Larimer Co.: Loveland, no date (W. H. Edwards coll.) (CM); County undetermined: "Colo." no date (David Bruce) (CM), "Colorado" no date (E. T. Owen coll.) (USNM), "Colorado" no date (H. S. Burnett) (USNM)

Bruce collected *fumosa* at Estes Park, Larimer Co., Colorado (Edwards 1897, p. 197). The identities of the Indiana, Minnesota, and Wisconsin specimens noted above were not checked by the genitalia, and are somewhat uncertain.

*Lethe appalachia* R. L. Chermock

*Lethe (Enodia) eurydice appalachia* R. L. Chermock 1947, Ent. News 58: 29; type locality Conestee Falls, North Carolina; type in R. L. Chermock collection, not seen.

*Lethe fumosus appalachia*: dos Passos 1969, J. New York Ent. Soc. 77: 121.

*Taxonomic History.* — Unmistakable figures of *appalachia* appear in three older works under other names. None of these has any taxonomic significance. Boisduval and Le Conte (1829) figure a male *appalachia* with an ambiguous female as *Satyryrus canthus* (pl. 60). Edwards (1897) figures a female *appalachia* (pl. 26, figs. 3, 4) with a normal male *eurydice* (figs. 1, 2) as *Satyrodes canthus*, along with a dark male which is probably also *eurydice* but might be *fumosa* (fig. 5). Denton (1900) figures an ambiguous specimen (p. 217), an *eurydice* (p. 218), and an *appalachia* (p. 219), all as *Neonympha canthus*.

Dos Passos (1969) erred in sinking *appalachia* to "*fumosus*." There is no evidence for his statement that "*fumosus* and *appalachia* occur at opposite ends of a cline."

Dos Passos lists ab. *boweri* F. H. Chermock under *appalachia*. It cannot be identified to species by the description, and the type has not been found; it is not in the Carnegie Museum, where dos Passos recorded it. We have placed *boweri* provisionally in the synonymy of *eurydice* because that species is considered more likely from the type locality, Port Hope, Ontario. However, a specimen of *appalachia* with no ocelli on the forewings above, labeled "Bowie, Md./ v-29-45/DDT experiment," is in the U.S. National Museum. At any rate, the name is clearly infrasubspecific and has no standing.

*Summary of Characters.* — *Lethe appalachia* differs from both subspecies of *eurydice* in being grayish or mousy brown above (blackish when fresh) and somewhat purplish or lilac-tinged beneath; the postmedial lines rounded, with only slight indentations. The male valve is less clearly 4-sided in lateral view, and the tegumen is dorsally flattened. The larval head capsule bears side-stripes not reaching below the bases of the horns.

*Distribution* (fig. 22). — Material examined:

FLORIDA: Jefferson Co.: Monticello, x.4.14 (paratype) (AMNH)

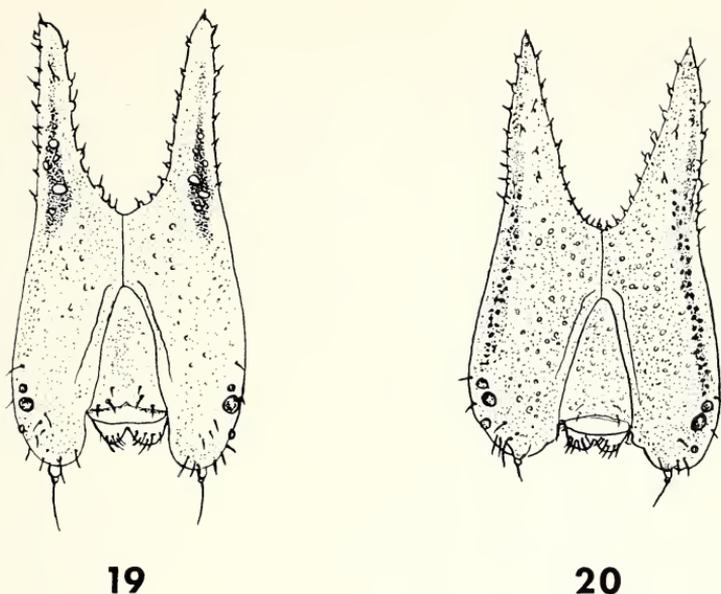


Fig. 19. Larval head capsule of *Lethe appalachia*.

Fig. 20. Larval head capsule of *Lethe eurydice eurydice*.

SOUTH CAROLINA: Jasper Co.: Coosawhatchie, vii.26.36 (R. B. Dominick) (paratype) (AMNH); Clarendon Co.: ix.?.89 (E. A. Smyth) (USNM) (see Smyth, 1890)

NORTH CAROLINA: Mitchell Co.: vii.?.92 (O. Buchholz) (AMNH); Transylvania Co.: Conestee Falls, vii.1-7.?, vii.15-21.? (CM)

VIRGINIA: Amherst Co.: 1936 (J. Bauer) (CM); Prince George's Co.: New Bohemia Swamp, viii.22.67 (J. Bauer) (CM); Nansmond Co.: Dismal Swamp, vi.19.40 (CM); Giles Co.: Little Meadows, vii.25-26.40 (L. Carr) (paratypes) (USNM); Montgomery Co.: viii.20.98 (E. A. Smyth) (USNM); Fairfax Co.: Vienna, vii.19.38 (A. H. Clark) (paratype) (USNM); Wythe Co.: Speedwell, viii.11.38 (A. H. Clark) (paratype) (USNM); Grayson Co.: Long's Gap, viii.11.38 (A. H. Clark) (paratype) (USNM); County undetermined: Glen Carlyn, viii.12.? (A. N. Caudell) (paratype) (USNM)

DISTRICT OF COLUMBIA: Washington, vii.17.29 (G. W. Rawson) (USNM), vi.29.29 (paratypes) (USNM), vi.17.29 (paratype) (figured by Clark, 1932, pl. 1, figs. 3,4) (USNM)

MARYLAND: Prince George's Co.: Hyattsville, vi.20.39 (G. W.

(Rawson) (USNM), Bowie, v.29.45 (USNM), Beltsville, vii.15.28 (paratype) (USNM); Calvert Co.: Mutual, vi.21.36 (G. W. Rawson) (USNM)

DELAWARE: New Castle Co.: Christina, vii.64 (AMS)

PENNSYLVANIA: Crawford Co.: Hartstown, vii.4.21 (H. Kahl) (CM), viii.8-14.? (CM); Mercer Co.: North Liberty, viii.3.60 (J. Bauer) (CM), 2 mi. SE Leesburg, vii.11.66 (H. K. Clench) (CM); Butler Co.: Slippery Rock, vii.4.31 (W. Sweadner) (CM); Fayette Co.: Dunbar, vii.6.31 (CM); Westmoreland Co.: Powdermill Nature Reserve, vi-viii.56-68 (H. K. Clench) (CM); Chester Co.: Exton, vii-viii.59-68 (AMS); Montgomery Co.: Horsham Twp., Cheltenham Twp., Enfield, vi-viii.59-68 (AMS); Delaware Co.: Chadd's Ford, vii-viii.62-66 (AMS); Philadelphia Co.: Mt. Airy, v.28.? (P. Laurent) (AMNH), Tincum Wildlife Preserve, Eastwick, vii-viii.58-68 (AMS)

NEW JERSEY: Cape May Co.: Woodbine, vi-viii.59-67 (AMS); Camden Co.: Westville, viii.6.92, viii.14.92 (P. Nell) (CM), vi.12.? (P. Laurent) (CM) (AMNH); Burlington Co.: Warren Grove, Wading River, vii-viii.64-68 (AMS); Gloucester Co.: Wenonah, viii.21.10 (CM); Ocean Co.: Cassville, viii.17.10 (AMNH); Morris Co.: Green Village, vii.30.? (C. Rummel) (CM), vii.15.? (C. Rummel) (ANSP), "Morris Co." vii.21.50 (P. Ehrlich) (AMNH), vii.9.30, vii.6.41, vii.18.50 (O. Buchholz) (AMNH); Union Co.: vi.16.40 (O. Buchholz) (AMNH); Somerset Co.: Orange Mts., vi.14.?, viii.20.31 (O. Buchholz) (AMNH); Bergen Co.: Ramsey, viii.?.17 (AMNH); Passaic Co.: Paterson, vii.17.? (J. A. Grossbeck) (AMNH); Sussex Co.: Springdale, vii.9.49 (P. Ehrlich) (AMNH), vii.10.49 (N. W. Gillham) (AMNH), Lake Lackawanna, vii.9.49 (P. Ehrlich) (AMNH), Stanhope, vii.28.33 (C. Rummel) (AMNH), Hopatcong, no date (C. Palm) (AMNH), "Sussex Co." vii.9.30, vii.6.41, vii.1.43, vii.18.50 (O. Buchholz) (AMNH); County undetermined: "N.J." (Neumoegen coll.) (USNM), "N.J." (C. Palm) (AMNH)

NEW YORK: New York Co.: West Farms, no date (J. Angus) (AMNH), Bronxville, vii.9.11, vii.22-23.11 (L. B. Woodruff) (AMNH), Bronx, bred (E. Gerstenkorn) (AMNH); Suffolk Co.: Riverhead, vii.7.49, vii.8.49, vii.17.52, vii.5.53, viii.11.53 (R. Latham) (CU), Orient, vi.30.41, viii.2.49, vi.17.52 (R. Latham) (CU), East Hampton, vi.14.49 (R. Latham) (CU), Greenport, viii.1.20, ix.1.51, ix.6.28 (R. Latham) (CU), Calverton, vii.8.30 (R. Latham) (CU), Brookhaven, vii.5-13.65 (RHW);

- Queens Co.: Flushing, vii.27.18 (E. L. Bell) (AMNH); Westchester Co.: Bedford, vii.7-9.34, vii.17.37 (R. B. Dominick) (AMNH), Somers, no date (W. C. Wood) (AMNH), Crugers, vii.16.12 (AMNH); Dutchess Co.: Fishkill, ix.7.65 (DJH); Sullivan Co.: Lava, no date (Barnes coll.) (USNM); Albany Co.: Albany, vii.24.27 (A. C. Frederick) (AMNH), Karner, vii.7.70 (Lintner) (USNM), vii.20.79 (W. W. Hill) (NYSM), vii.11.03 (J. Cook) (Oxon.); Tompkins Co.: McLean, vii.18.91 (local collection, CU), viii.7.25, vii.27.29, viii.1.25 (CU), vii.18-21.68 (AMS), Sapsucker Woods, viii.7.68 (AMS); Schuyler Co.: Texas Hollow, viii.3.68 (AMS); Orleans Co.: Oak Orchard Swamp, vii.16.68 (AMS); Genesee Co.: Batavia, vii.16.87 (CU); Cattaraugus Co.: Allegany State Park, vii.21.40 (A. R. Shadle) (USNM); Franklin Co.: Paul Smith's, vii.?03 (A. P. Hunt) (Oxon.); County undetermined: "New York" (H. Edwards coll.) (AMNH)
- CONNECTICUT: New Haven Co.: Sound View, vii.16-21.34 (A. H. Clark) (USNM); Litchfield Co.: Sharon, vii.14-21.40, vii.?41 (L. J. Sanford) (AMNH) (one figured by Klots, 1951, pl. 10); Fairfield Co.: Stamford, vii.22.37 (J. G. Thorndike) (AMNH); Hartford Co.: Avon, viii.1.03 (R. C. Williams) (CM), vii.18.22 (R. C. Williams) (ANSP)
- MASSACHUSETTS: Suffolk Co.: Newton Highlands, no date (W. Baines) (USNM); Hampden Co.: Wilbraham, viii.?94 (CU); Bristol Co.: Swansea, vii.18-22.34 (E. T. Learned) (ANSP)
- RHODE ISLAND: Providence, vii.10-20.? (H. Engel) (CM), North Scituate, 1912 (G. H. & J. L. Sperry) (AMNH)
- NEW HAMPSHIRE: Coos Co.: Jefferson, vii.7.32 (G. H. & J. L. Sperry) (AMNH), "White Mts." no date (W. H. Edwards) (CM)
- MAINE: Penobscot Co.: Bangor, no date (CM)
- QUEBEC: "Quebec," vii.3.35 (J. C. Hopfinger coll.) (USNM)
- ILLINOIS: Cook Co.: Chicago, vii.6.13 (J. D. Gunder coll.) (AMNH)
- INDIANA: Lake Co.: Hessville, vii.4.08 (E. Beer) (USNM); County undetermined: "Indiana," no date (E. A. Smyth coll.) (USNM)
- MICHIGAN: Huron Co.: Hume Twp. Arboretum, vi.28.52 (H.V. Daly) (AMNH); Cass Co.: Wakelee, viii.3.58 (L. J. Sanford) (AMNH); County undetermined: "Michigan," no date (AMNH)
- MINNESOTA: Hennepin Co.: Lake Minnetonka, viii.?86 (AMNH)
- WISCONSIN: County undetermined: "Wis." no date (E. T. Owen coll.) (USNM)

SOUTH DAKOTA: Brookings Co.: Volga, no date (Ehrman coll.) (CM)

MISSOURI: St. Louis Co.: St. Louis, vii.10.? (CM)

We regard the South Dakota and Missouri records of *L. appalachia* as somewhat dubious, but they are shown on the map.

Other records: The following are probably accurate, although the specimens have not been seen. They are included on the map:

GEORGIA: Thomas Co.: Linton Lake, viii.9.67, viii.29.67; Fulton Co.: Atlanta (Harris Trail), vii.29.60, viii.20-26.61; De Kalb Co.: Avondale Estates, vi.16.44; Union Co.: Copper Creek State Park, vi.6.58, vii.16.61, vi.18.62, vii.18.62, viii.22.59; White Co.: Cleveland, vi.13.57 (all from L. Harris, unpublished MS, p. 244)

MINNESOTA: Anoka Co.: Bald Eagle Lake, 1966 (Masters, 1967)

INDIANA: Steuben Co.: Hogback Lake, vii.17.42 (Price and Shull, 1969)

TENNESSEE: Madison Co.: Jackson (Mather and Mather, 1958)

ALABAMA: Tuscaloosa Co.: vic. Tuscaloosa (Chermock, 1949)

MICHIGAN: Montcalm Co.: Sidney, vii.26.50 (F. Rutkowski)

PENNSYLVANIA: Fayette Co.: Markleysburg Bog, 2 mi. N Markleysburg (H. K. Clench)

#### DIAGNOSTIC CHARACTERS

*Color and Pattern.*—*Lethe e. eurydice* and *L. e. fumosa* differ subtly but consistently from *L. appalachia*. Nearly all specimens can be assigned to the correct species by color and pattern alone. The most useful characters separating the two species are the ground color above and beneath, and the waviness of the postmedial line beneath. The two subspecies of *eurydice* differ most consistently in the relative sizes of the forewing ocelli. All of the observed differences are given in Table 1.

We have not seen a truly fresh specimen of *L. e. fumosa*. Leussler (1916) describes the ground color of fresh specimens as "a very dark smoky grey . . . even a blackish appearance." This sounds very much like the color of newly emerged *appalachia*. Old specimens of the two are very different, however: *fumosa* males are an even, somewhat purplish or reddish brown, while *appalachia* is grayish or mousy brown. Some female *fumosa*, particularly from Colorado, are nearly identical in color to nominate female *eurydice*, but the ground color of the males is nearly always distinctive. A few male *eurydice* from the northeast are dark purplish brown when

fresh, and fade to an even dark reddish brown. Their spot-sizes are normal and they lack the *fumosa* tendencies to "high angledness" of the forewing and blind and rimless ocelli above. A specimen of this dark form of nominate *eurydice* is probably represented by Edwards' figure 5 (1897, pl. 26).

Specimens of the three taxa are shown in figs. 1-12.

*Male Genitalia.* — Chermock (1947) and dos Passos (1969) reported no genitalic differences between *L. e. eurydice* and *L. appalachia*. However, we have found that they do differ slightly but significantly. The tegumen of *appalachia* is flattened dorsally, while that of *eurydice* (both subspecies) is rounded. The valves of *appalachia* are shorter and narrower dorso-ventrally, and from the side appear less quadrilateral than those of the *eurydice* subspecies. The male genitalia of *L. e. eurydice* and *L. e. fumosa* are substantially similar, but differ from each other and from *appalachia* in the density and arrangement of setae on the valves. See Table 1 and figs. 13-18.

*Female Genitalia.* — There seem to be no useful characters here. Some minor differences in the sclerotization of the genital plate were found among all three taxa.

*Early Stages.* — The larvae of *L. e. eurydice* and *L. appalachia* from central New York differ consistently in the maculation and tubercles of the head capsule. In *L. e. eurydice* the red side stripes become darker below the bases of the horns, extending to the ocelli. The darker part of the stripe consists of small, heavily pigmented, regularly arranged tubercles on a less heavily pigmented ground. In *L. appalachia* the stripe does not extend below the horn, and its lower end contains several large, pale, irregularly placed tubercles which contrast with the red ground (figs. 19, 20).

The early stages of *L. e. fumosa* are completely unknown.

#### BIOLOGICAL DIFFERENCES

*Developmental Rate.* — Larvae of *L. e. eurydice* and *L. appalachia* from McLean, N.Y. reared *ex ovo* at 24°C on late summer photo-periods showed developmental differences. *Eurydice* larvae invariably entered diapause in the third or fourth instar. *Appalachia* larvae usually developed without diapause, the entire life cycle requiring about 60 days. *Lethe appalachia* is at least double-brooded in its southern range; apparently it has the potential to breed continuously

Table 1. Differences separating taxa of the *Lethe eurydice* group. Color terminology follows Kornerup and Wanscher (1963) and Ridgway (1912).

character	<i>L. e. eurydice</i>
<b>I. COLOR AND PATTERN</b>	
postmedial line of forewing beneath	projects marginad into teeth at M <sub>3</sub> , Cu <sub>2</sub>
postmedial line of hindwing beneath	projects marginad into teeth at Cu <sub>1</sub> , Cu <sub>2</sub>
ground color beneath (fresh males)	red-haired (6C4) = wood brown
ground color beneath (fresh females)	greyish orange (5B5) = clay color
ground color above (fresh males)	sunburn (6D5) = snuff brown
ground color above (fresh females)	clay (5D5) = Saccardo's umber
color between ocelli and subterminal line beneath	darker than ground, tinged with orange
color marginad of postmedial line on hindwing beneath	lighter than ground, yellowish especially in M <sub>3</sub>
contrast between discal and limbal areas on forewing above	moderate to strong
rings around ocelli above	usually strong
ocelli of forewing beneath	variable, subequal, 4 usually largest
ocelli 4, 5 on hindwing above	usually pupilled
apex of forewing	tending to be "low angled" <sup>d</sup>
<b>II. MALE GENITALIA</b>	
valve shape	4-sided in lateral view
valve costa	inner lip larger
valve setae	valve tip heavily armed; many setae on sacculus
tegumen	dorsally rounded
<b>III. LARVAL HEAD CAPSULE</b>	
red stripe	top of horns to ocelli
tubercles in red stripe	red, small, regularly arranged
<b>IV. HABITAT</b>	open sedge marshes

<sup>a</sup>only old specimens seen

<sup>b</sup>fades in life to Van Dyke brown (6F6) = bistre

<sup>c</sup>fades in life to brown (6E5) = brownish olive

*L. e. fumosa**L. appalachia*

as in <i>L. e. eurydice</i>	smoother, only slightly wavy
as in <i>L. e. eurydice</i>	smoother, only slightly wavy
cinnamon (6D6) = Rood's brown greyish orange (5B5) = clay color	dark blonde (5D4) = buffy brown topaz (5C5) = avellaneous
cocoa brown (6E6) = cinnamon brown <sup>a</sup>	teak (6F5) = mummy brown <sup>b</sup>
sahara (6C5) = sayal brown <sup>a</sup> as in <i>L. e. eurydice</i>	teak (6F5) = mummy brown <sup>c</sup> paler, not orange-tinted
as in <i>L. e. eurydice</i>	lighter than ground, with violet iridescence
slight (♂) to moderate (♀)	moderate to strong
weak to strong usually 4>3>2>1 frequently unpupilled "high angled" in ♂♂ only	weak to strong usually 1 and 4 largest frequently unpupilled frequently "high angled" (both sexes)
as in <i>L. e. eurydice</i>	less 4-sided; short; narrower dorso-ventrally
as in <i>L. e. eurydice</i>	inner lip smaller
few setae on valve tip or sacculus	some setae distally and on sacculus
as in <i>L. e. eurydice</i>	dorsally flattened
unknown	horns only
unknown	irregular, large, pale
permanent marshes within prairie region	swamp forest, shrub swamp, forest- edge ecotones

<sup>a</sup>"high angled": ratio of length of forewing (base to apex):  
outer margin < 1.5.

(without diapause) elsewhere as well. So far as is known, *eurydice* is single-brooded everywhere. Larvae of both species turn from yellow green to straw yellow when in diapause, and are capable of changing color in either direction overnight.

A usually small emergence of fresh *eurydice* occurs in some localities in New York, New Jersey and Pennsylvania in the first half of August, four to five weeks after the principal emergence. Males of this late "brood" are frequently of the dark form noted above. It is very unlikely that these butterflies are descendants of those which emerged a month earlier. There may be a genetic basis for the emergence times; a bimodal emergence of *Hyalophora cecropia* (L.) (Saturniidae) was recently reported by Sternburg and Waldbauer (1969), with no genetic data. We do not believe the late *eurydice* are identical with *fumosa*, but the slight possibility exists that they represent another sibling species, unrecognizable in the adult except by its flight period and a statistical color difference. We have not obtained ova from these insects.

*Food Plants.* — Dos Passos (1969) speculates that a food plant difference between *L. eurydice* and *L. appalachia* is likely. However, our observations suggest that both are sedge-feeders and that neither is species- or group-specific within *Carex*. Female *appalachia* occur near sedges in shrub swamp or forest habitats where observation is difficult. One oviposition was seen in the field, on *Carex lacustris* Willd. (Cyperaceae) at Texas Hollow, Schuyler Co., N.Y. Other sedges commonly associated with this species in New York, all of which were completely acceptable in the laboratory, are *Carex gracillima* Schwein., *C. lanuginosa* Michx., and *Scirpus georgianus* Harp. Wild hosts of *L. e. eurydice* in central New York include *C. lacustris*, *C. stricta* Lam., *C. rostrata* Stokes, and *C. trichocarpa* Michx. All of these sedges were fully acceptable to both species, as are some dozen other species tested (mostly undetermined). We reared both species from egg to adult on *Carex torta* Boott. Neither species would accept any of the following grasses (Gramineae): *Festuca ovina* L.; *Elymus riparius* L.; *Brachyelytrum erectum* (Schreb.) Beauv.; *Muhlenbergia schreberi* Gmel.; *Agrostis alba* L.; *Phalaris arundinacea* L.; *Leersia oryzoides* (L.) Sw.; *Echinochloa crus-galli* (L.) Beauv. (*B. erectum* and *P. arundinacea* are wild food plants of *Lethe portlandia anthonon* A. H. Clark, and *M. schreberi* is acceptable in the laboratory; Shapiro and Cardé, 1970.)

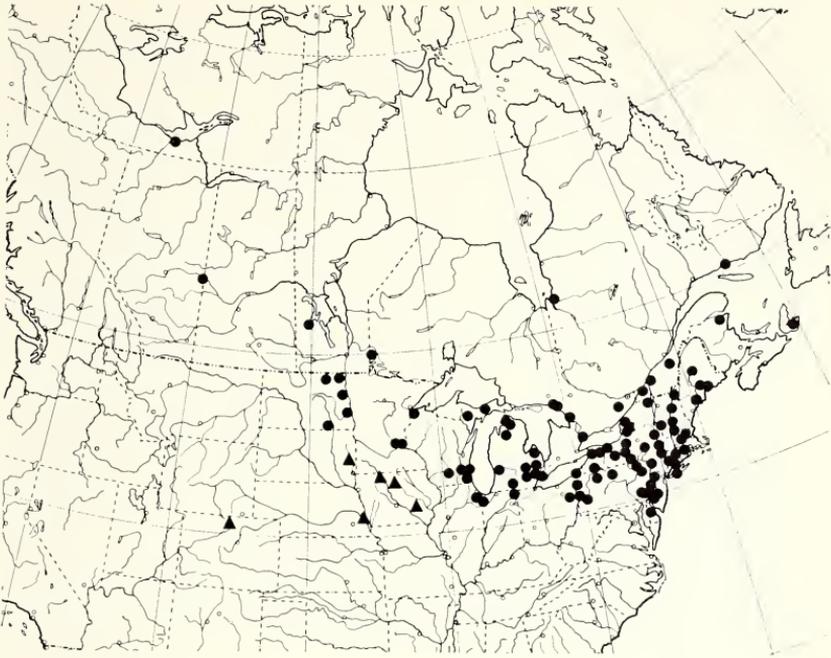


Fig. 21. Distribution of *Lethe eurydice eurydice* (solid circles) and *Lethe eurydice fumosa* (solid triangles).

*Adult Behavior.*—The most striking difference between *L. e. eurydice* and *L. appalachia*, and the one leading to the discovery of their sympatry, is their differential habitat selection (Shapiro and Cardé, 1970). At the McLean Bogs Reserve, Tompkins Co., New York, these two species are frequently found flying within a few feet of each other, but do not mix. The preference of *L. appalachia* for shaded habitats often results in its association with *L. p. anthedon* upland or *L. p. portlandia* on the Coastal Plain. We have found *L. e. eurydice* only in relatively open sedge marshes or, rarely, in drier meadows; it never enters dense shrub swamp or woods. We have seen *L. eurydice* and *L. p. anthedon* in copula in their usual habitats, once each (3 p.m. and 3:30 p.m., respectively).

#### DISCUSSION

Although the term "sibling species" has been in the literature for nearly thirty years and the concept is even older, it still seems necessary to point out that excessive dependence on morphological



Fig. 22. Distribution of *Lethe appalachia*.

differences can hinder the recognition of such biologically interesting species as those of the *Lethe eurydice* group. Despite abundant museum evidence of sympatry, these species went unrecognized for twenty years after Chermock (1947) was unable to find genitalic differences between them.

As usually happens with sibling species, recognition on biological grounds has led to discovery of morphological characters hitherto overlooked. These, however, are of a magnitude which would not be considered diagnostic of species in most groups of Lepidoptera. In fact, the genitalia seem to be among the most conservative characters in *Lethe*. Chermock found only very minor genitalic differences between *L. portlandia* and *L. creola* Skinner in the other American species group, and circumstantial evidence suggests that *portlandia* itself is really a pair of (largely allopatric) sibling species. Many Asiatic *Lethe* we have examined also show only slight differences among themselves and from their close American relatives. We consider it likely that what we are calling *Lethe eurydice fumosa* may also prove specifically distinct when its biology

— particularly the early stages — becomes better known. Similar cases recently uncovered in the Lepidoptera include the tortricid moths *Archips argyrospilus* and *A. mortuanus*, which differ only in sex attractant and in some characters of the last-instar larva (Roelofs and Comeau, 1969), and the papilionid butterflies *Papilio zelicaon* and *P. gothica*, said to differ consistently only in host-plant specificity but to behave as species in genetic tests (Remington, 1968). The *Holomelina aurantiaca* complex (Arctiidae), often thought to consist of two species, actually includes at least ten, exceedingly similar in genitalic morphology, color and pattern, but differing in chromosome number (Cardé, unpublished).

The seemingly inevitable problem with sympatric sibling pairs such as *Lethe eurydice* and *appalachia* is to account evolutionarily for the "elegant" manner in which they coexist. The view that reproductive isolating mechanisms and ecological differences evolve in response to deleterious hybridization and competition in secondary sympatry (Brown and Wilson, 1956) is now very widely accepted. It was recently challenged by Ehrlich and Raven (1969), who proposed that isolating mechanisms usually develop during the genetic differentiation of allopatric populations under different selective regimes. This is in effect a reformulation of the view of most nineteenth- and early twentieth-century evolutionists. Attempting to explain the ecological relationship of a given set of sibling species requires consideration of the following points:

1. The apparent absence of ecological interaction (e.g., competition) or gene flow between presently sympatric populations does not rule out such events in the past, nor for competition, in the future. Furthermore, intermittent large-scale gene flow between normally allopatric populations, associated with fluctuations in population sizes, has probably been an important component of speciation (Brown, 1957). Such fluctuations could also result in episodes of competition between otherwise non-competing species.
2. Biogeographical evidence may offer important clues to episodes of prior sympatry or allopatry in the evolution of species differences (*cf.* Mengel, 1964).
3. In the absence of evidence for character displacement, it cannot be assumed that biological differences which appear to prevent competition evolved in response to the adverse effects of competition.

The ecological differences among the American species of *Lethe* can be resolved into two parts: that involving the *eurydice* group alone and that concerning the *eurydice* and *portlandia* groups. The

species *eurydice*, *appalachia*, and *portlandia* (in the broad sense, including *anthon*) divide neatly into "non-competing" pairs: the two sedge feeders (*eurydice* and *appalachia*) differ in habitat; the two woodland species (*appalachia* and *portlandia*) differ in larval food plant. (Similarly, in sexual behavior, *eurydice* and *appalachia* are essentially non-territorial; *portlandia* is strongly territorial.)

*Lethe* and the genera closely related to it are hypothesized to have originated in southeast Asia (Miller, 1968), a region with many forest-dwelling, grass- (mostly bamboo-) feeding representatives of both the *eurydice* and *portlandia* groups. It seems reasonable that the ancestors of both these groups migrated to North America via the Bering land bridge in the Arcto-Tertiary forest, and were forced southward by the events of the Pleistocene.

With the vast majority of the many Asian *Lethe* feeding on grasses, the evolution of sedge feeding in North America by the ancestor of the *eurydice* group is a tempting hypothesis. Evolution of this trait by proto-*eurydice* independent of competition with proto-*portlandia* or by character displacement in sympatry with it are both possibilities. T. Shirôzu (pers. comm.) informs us that *Lethe marginalis* Motschulsky, which seems to be a member of the *eurydice* group, feeds on non-bamboo grasses and on sedges in Japan, as does *Kirinia epaminondas* Staudinger, formerly placed in *Lethe*. *Ninguta* ("*Lethe*") *schrenckii* Menetries is an obligate sedge feeder.

On the other hand, the speciation of *eurydice* and *appalachia* may have occurred when one of the Pleistocene glaciations isolated some populations of proto-*eurydice* in prairie to the west of populations in the eastern Austral forests. Virtually the entire range of *eurydice* was glaciated, and the distribution is therefore of recent origin. The same can be said for the northern portions of the ranges of *appalachia* and *portlandia*, but the southern portions are characteristic of many organisms which presumably survived the Wisconsin (and earlier glaciations) in the southeast. The lack of recorded relict populations of *eurydice* south of Pennsylvania in the Appalachians, if not due to inadequate collecting, suggests that the species did not have a Wisconsin refugium in the forested Austral Zone of the southeast; its habitat preference and developmental rate support this interpretation. (We do know of species of Hesperiidæ, e.g. *Euphyes bimacula*, with ranges and biologies substantially similar to *L. eurydice*, which have relict populations in the southeast; Shapiro, 1970b.) Its most probable refugium, then, was in glacial Transition Zone somewhere west of the Appalachians. The existence of *L. e. fumosa* also supports

a prior western distribution for *eurydice*, but does not help in dating it. We have no grounds for estimating evolutionary rates in this group; all that can be said now with some confidence is that *eurydice* and *appalachia* were more likely allopatric than sympatric in the Wisconsin (and *appalachia* and *portlandia* more likely sympatric).

The critical evidence concerns character displacement. We have found no morphological character displacement in sympatric *vs.* allopatric populations of *Lethe eurydice* and *L. appalachia*. One of us (Clench) believes he has observed behavioral character displacement between them in Pennsylvania, within the area of general sympatry; in certain localities where only one species occurs, it appears that the habitat selection is not so rigorous as elsewhere. This needs additional study and quantification. Another geographic area also bears close investigation in this connection. Specimens of *eurydice* from southeastern New York (Orange, Rockland, and Westchester Counties) are somewhat anomalous, tending to vary in color and pattern (but not genitalia) toward *appalachia*. We have seen very few specimens from outside this small area which we would hesitate to classify to species by color and pattern. The area is completely surrounded by normal, sympatric, well-differentiated populations of both. It is thus critical to determine the ecology of these anomalous insects. Should *appalachia* be rare or absent, and *eurydice* occupying its niche at least in part, one would have a powerful argument for character displacement as the origin of the habitat difference. (There is a chance of natural hybridization due to man's extensive disturbance of *Lethe* habitats in southeastern New York.)

There are, then, two basic questions: Did the behavioral and food plant differences between the American *eurydice* and *portlandia* groups evolve independently, or largely as a result of competition? Did the sharp habitat selection between *eurydice* and *appalachia* in close sympatry evolve in isolation, or was it intensified by behavioral character displacement?

On the first point, any evolutionary scenario will require much more comparative data on the Asiatic species than is readily available. Only a comprehensive revision, identifying the closest relatives of the American species and comparing their biologies, will allow a convincing argument.

On the second point, field studies in areas of allopatry will be critical. It should be noted that while we suspect the *eurydice* - *appalachia* habitat difference may have evolved to prevent competition

for larval food, it also may function, and have evolved, as a reproductive isolating mechanism. Greater knowledge of mating behavior in this group (Shapiro and Cardé, 1970), as well as more information on the southeastern New York populations, may be able to distinguish the correct hypothesis.

Our current state of knowledge does not allow us to choose between independent evolution and character displacement in accounting for the differences between the American *eurydice* and *portlandia* groups. But character displacement is an attractive hypothesis for the *eurydice* - *appalachia* habitat selection difference.

#### ACKNOWLEDGMENTS

We wish to thank William D. Field of the U.S. National Museum and Dr. Alexander B. Klots of the American Museum of Natural History for their advice and cooperation; Dr. Michael Emsley for the loan of specimens of *Lethe eurydice fumosa* from the Philadelphia Academy of Natural Sciences; N. D. Riley of the British Museum (Natural History) and Dr. T. Nyholm of the Naturhistoriska Riksmuseum (Stockholm) for aiding in the search for the early types; Dr. Lee D. Miller for information on *Euptychia* spp.; Lucien Harris, Jr. and Frank Rutkowski for field notes and unpublished locality data; Edward L. Rittershausen for specimens from southeastern New York; Dr. Takashi Shirôzu, Kyushu University, Japan, for data on Asiatic *Lethe*; and Dr. Peter A. Hyypio for determining species of sedges. Dr. John G. Franclemont of Cornell University provided invaluable assistance in the taxonomic research. Mrs. Adrienne R. Shapiro assisted in color determinations and in the preparation of the manuscript. Dr. John Burns made several helpful suggestions.

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THE MALE GENITALIA OF BLATTARIA. II.  
*POECILODERRHIS* SPP.  
(BLABERIDAE: EPILAMPRIINAE).\*

BY LOUIS M. ROTH  
Pioneering Research Laboratory  
U. S. Army Natick Laboratories  
Natick, Massachusetts 01760

Although the males of most species currently assigned to *Epilampra* lack tergal glands, there are several with dorsal abdominal modifications (Roth, 1969a) which are presumably involved in sexual behavior. The presence or absence of tergal glands and the differences in the genitalia of these two groups of *Epilampra* warrant their being placed in different genera.

MATERIALS AND METHODS

The material used in this study were all museum specimens which were softened and had their genitalia removed after slitting the lateral margins of the terminal abdominal segments. The genitalia were treated with 10% KOH, cleared and mounted in Permunt. In the illustrations, the hooked right phallomeres are mounted ventral side up, and phallomeres L1 and L2d are mounted dorsal side uppermost.

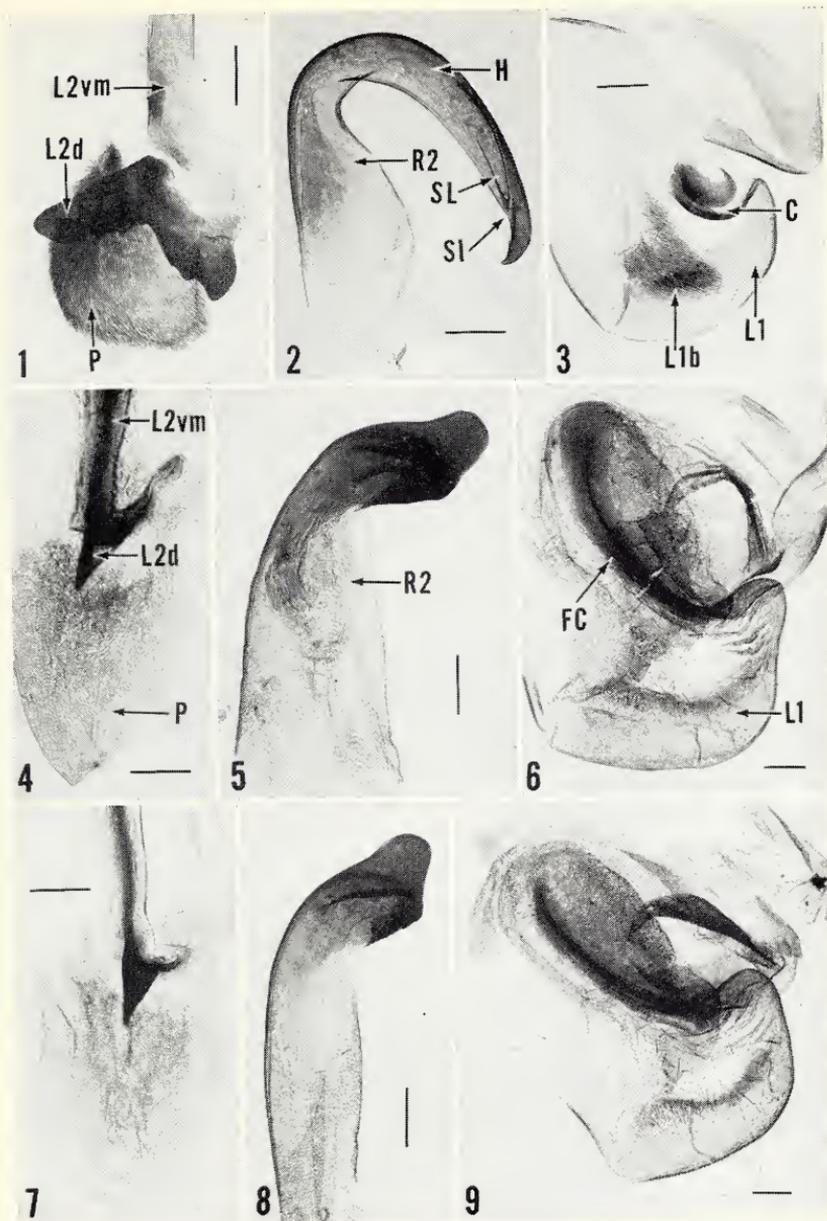
The source of each of the specimens illustrated is given, using the following abbreviations: (AMNH) = American Museum of Natural History, New York; (ANSP) = Academy of Natural Sciences, Philadelphia; (BMNH) = British Museum (Natural History), London; (L) = Zoological Institute, Lund, Sweden; (MCZ) = Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; (USNM) = United States National Museum, Washington, D.C.

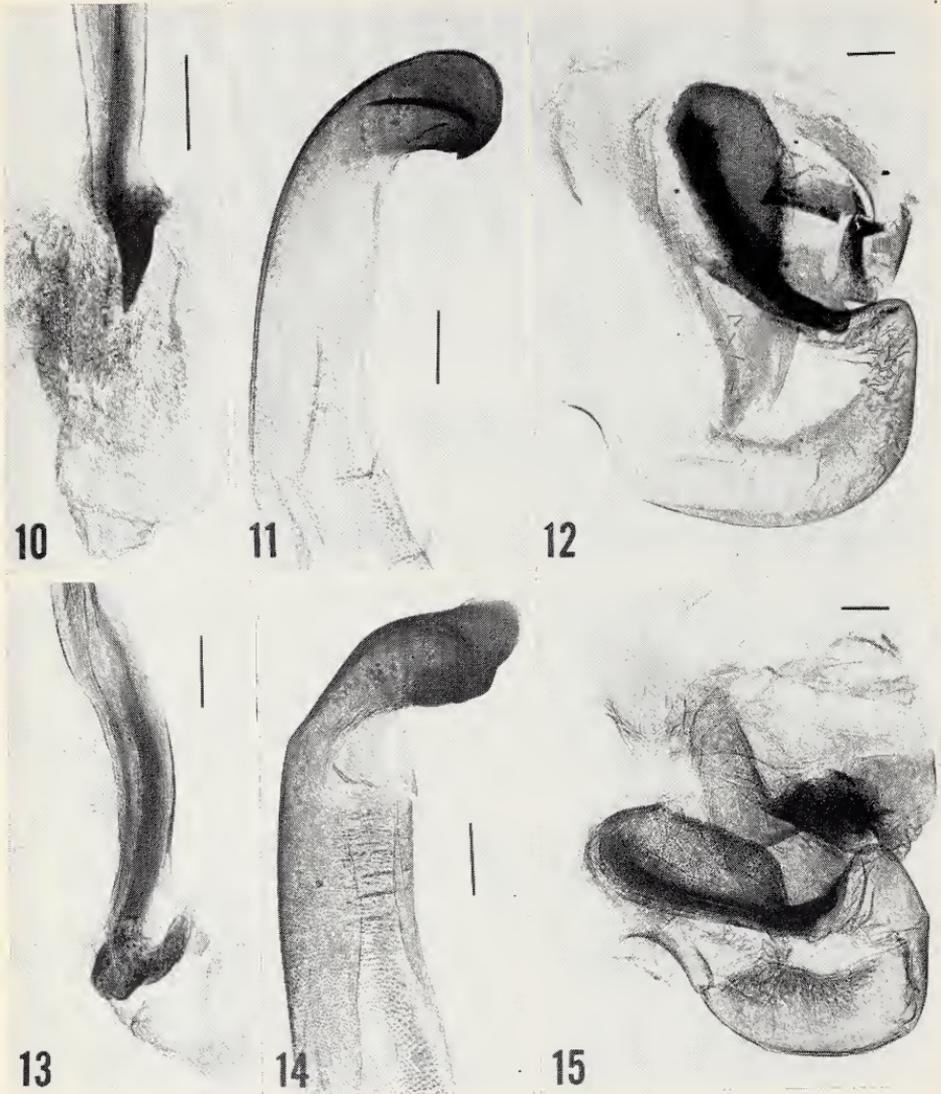
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\*Manuscript received by the editor January 15, 1970.

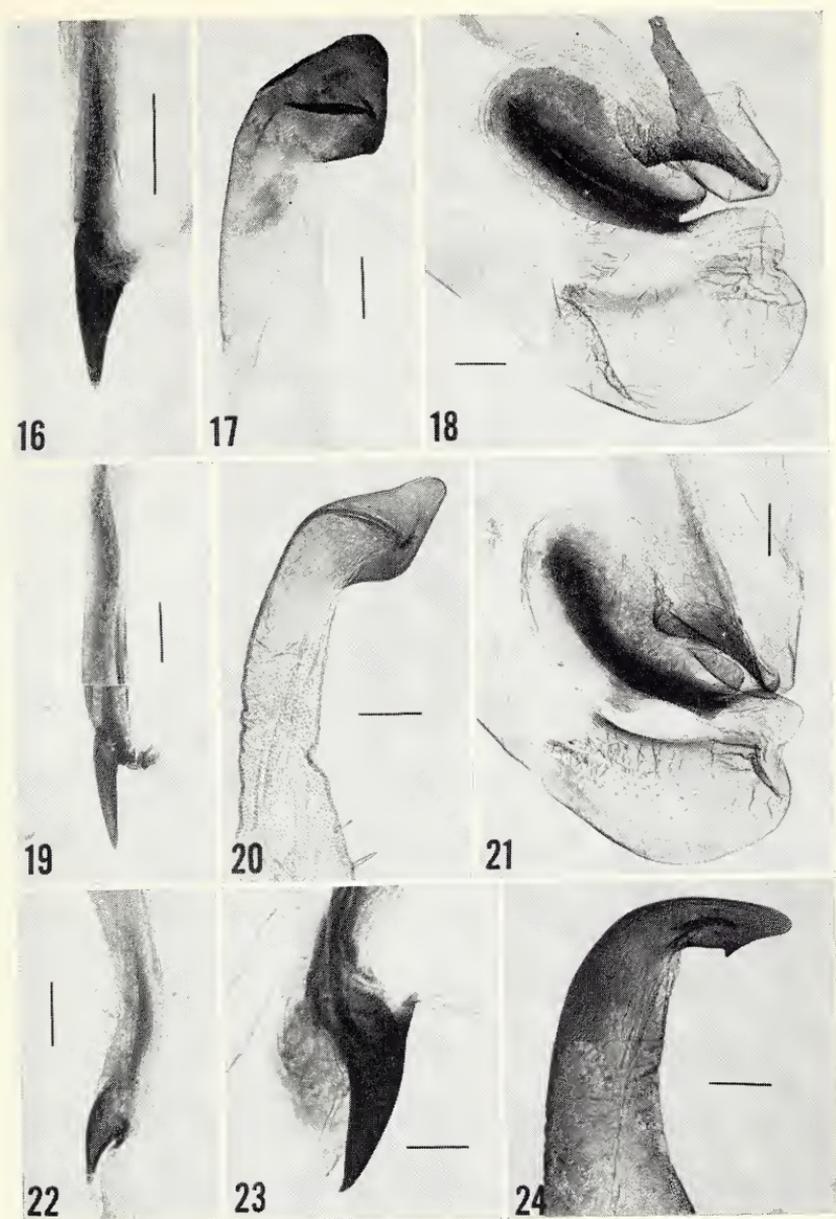
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Figs. 1-9. 1-3. *Epilampra maya* Rehn. (158, USNM). Boston Quarantine (det. Roth). 4-9. *Poeciloderrhis proxima*. 4-6. (22, MCZ). Brazil (det. Roth). 7-9. (20, BMNH). Brazil, Rio de Janeiro, Itatiaya (det. Roth). AL = accessory lobe; H = hook; L1 = first sclerite of left phallomere; L1b = setal brush of L1; L2vm = median sclerite (L2 ventromedial); L2d = dorsal sclerite of L2; P = prepuce; R2 = hooked sclerite of right phallomere; C = cleft of L1; FC = fused cleft of L1; SI = subapical incision of R2; SL = subapical lobe. (scale = 0.2 mm).

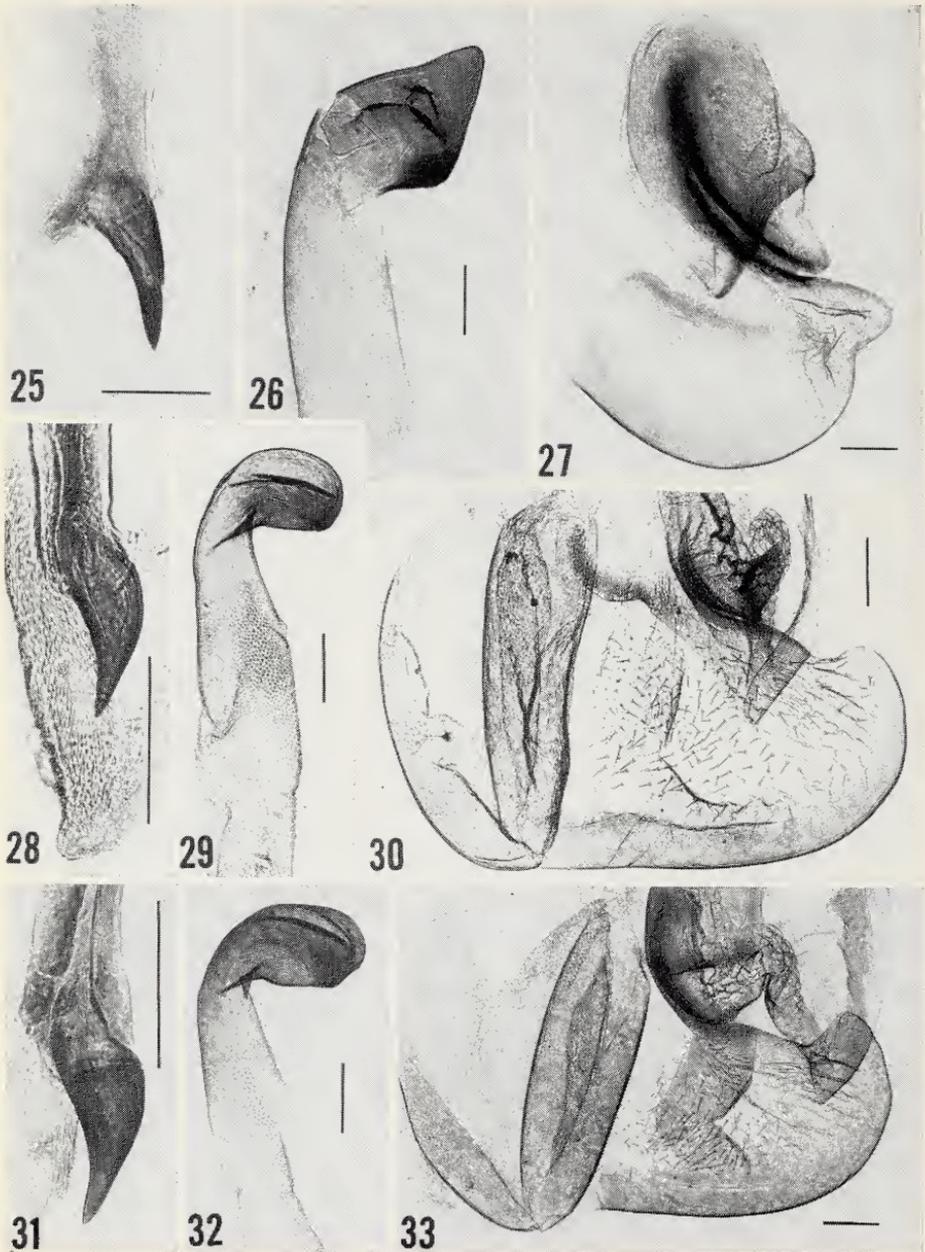




Figs. 10-15. *Poeciloderrhis* spp. 10-12. (1501, L). *P. proxima*. Ornsköldsvik, Sweden; tergal glands in Figs. 48, 49. (Adventive) (det. Princis). 13-15. (58, USNM). *P. verticalis*. Serra Caraça, Matto Grosso, Brazil; adult and tergal glands in Figs. 50-52. (det. Gurney). (The tip of L2d was inadvertently cut off.) (scale = 0.2 mm).



Figs. 16-24. *Pocilloderphis* spp. 16-22. *P. ferruginea*. 16-18. (110, ANSP. São Paulo, Brazil (det. Roth). 19-21. (31, AMNH). Corupa, Hansa Humbolt, St. Catharina, Brazil. (det. Roth). 22. (167, USNM). St. Catharina, Nova Teutonia, Brazil (det. Roth). 23-24. (45, ANSP). *P. atriventris*. (det. Hebard). (scale = 0.2 mm).



Figs. 25-33. *Poeciloderrhis* spp. 25-27. (12, BMNH). *P. ferruginea*. Rio de Janeiro, Organ Mts. near Tijuca, Brazil. (det. Princis). 28-33. *Poeciloderrhis* sp. A. 28-30. (72, MCZ). Annapolis, Goias, Brazil; tergal gland in Fig. 40. (det. Roth). 31-33. (109, ANSP). "Vlannopolis", Goias, Brazil. (det. Roth). (scale = 0.2 mm).



Figs. 34-39. *Poeciloderrhis* spp. 34-36. (9, BMNH). *P. atriventris*; tergal glands in Figs. 43-44. (det. Hebard). 37-39. (183, USNM). *P. catharina*. (Type of *Audreia catharina* Shelford. St. Catharina, Brazil; adult in Figs. 41-42.) (scale = 0.2 mm).

Geographical collection data, and the specialists who identified the specimens, if known, follow these abbreviations. The number preceding the abbreviations refers to the number assigned the specimen and its corresponding genitalia (on a slide) which were deposited in the museums indicated.

#### RESULTS AND DISCUSSION

In a previous paper on *Epilampra*, Roth and Gurney (1969) followed McKittrick's (1964) terminology. In her figure 128 (p. 180) of the male genitalia of *Epilampra azteca* Saussure there are 2 structures below L2vm (median sclerite of left phallomere) one of which she labeled L2d (dorsal sclerite of left phallomere). In most *Epilampra* there is a sclerotized plate which lies at the base of L2vm (but separated from it by a thin membrane) (Fig. 1) and Roth and Gurney (1969) named this structure L2bp (basal plate of L2). However, I have studied the male genitalia of a large number of Blaberidae and believe that L2bp is actually L2d and what we and McKittrick (1964) called L2d in *Epilampra* is in reality a modified prepuce. In *Blaberus* (Princis, 1946; Roth, 1969b) and other Blaberinae (Roth, unpublished observations) the prepuce has characteristic spines associated with it and partly surrounds the virga (L2d) (See Fig. 121 in McKittrick 1964).

Stål (1874) without mentioning any species proposed the name *Poeciloderrhis* for American *Epilampra* and separated them from the genus *Epilampra* (which he considered Asiatic-Australian) on the differences of front femoral spines. Kirby (1903) split the old genus *Epilampra*, proposing *Heterolampra* for an Australian species, retained Burmeister's *Epilampra* for American species with *E. brasiliensis* (Fab.) as type species, and selected *E. verticalis* Burm. (a species of Brazil and Argentina) as the type of *Poeciloderrhis* Stål. In his 1904 catalogue Kirby listed *Poeciloderrhis* as valid, with *verticalis* as type; he also included under this genus, *proxima* Brunner, *bivittata* Saussure, and *maculifrons* Stål. In the Genera Insectorum fascicle on Epilamprinae, Shelford (1910) listed *Poeciloderrhis* as a synonym of *Epilampra*, as does Princis (1967a) in his catalogue.

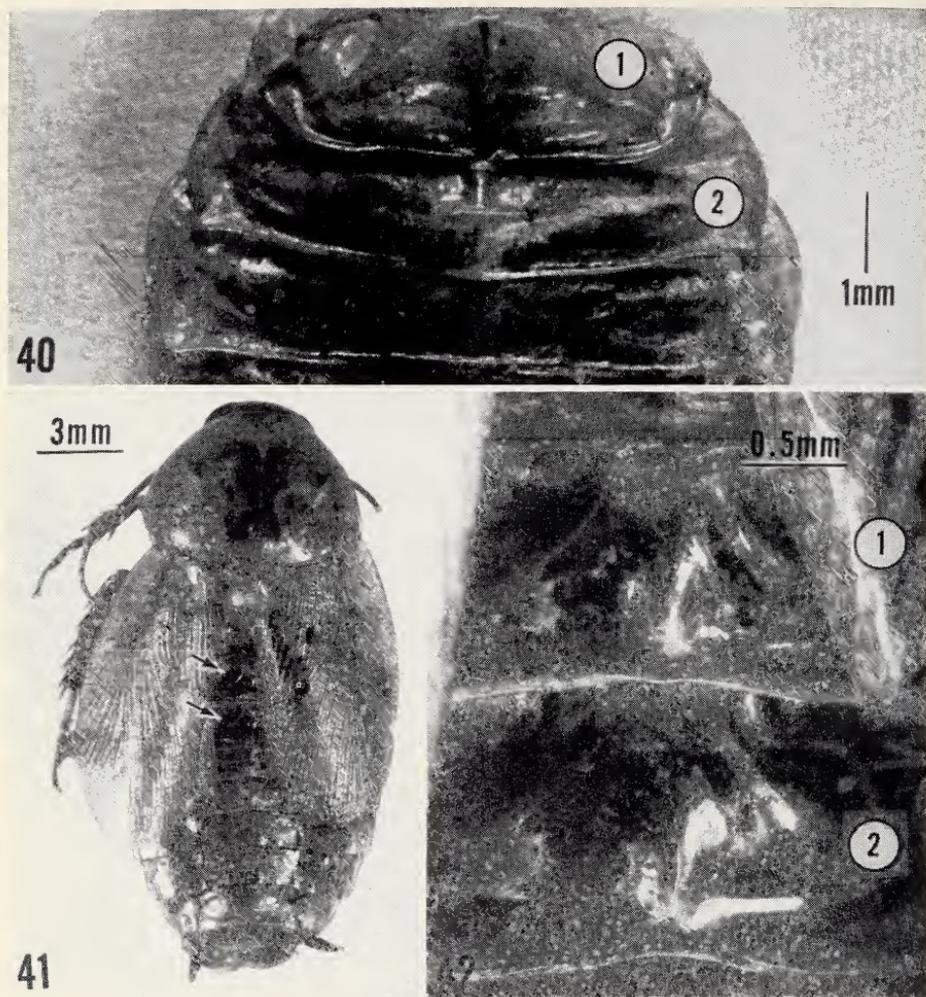
The species of *Epilampra* in which males have tergal glands have markedly different genitalia than the species which lack these modifications. *Epilampra verticalis* Burmeister has tergal glands on segments 1 and 2 and since this species is the type of *Poeciloderrhis* I use this generic name to represent tergal modified species of *Epilampra*.

The male genitalia of species of *Epilampra* (lacking tergal glands) consist of 3 principal phallomeres (Roth and Gurney, 1969) which may vary sufficiently in shape to distinguish species and species groups (Roth, 1970). All 3 phallomeres of *Epilampra* differ basically from *Poeciloderrhis* (cf. Figs. 1-3 and 4-6). The two genera may be separated in the following key:

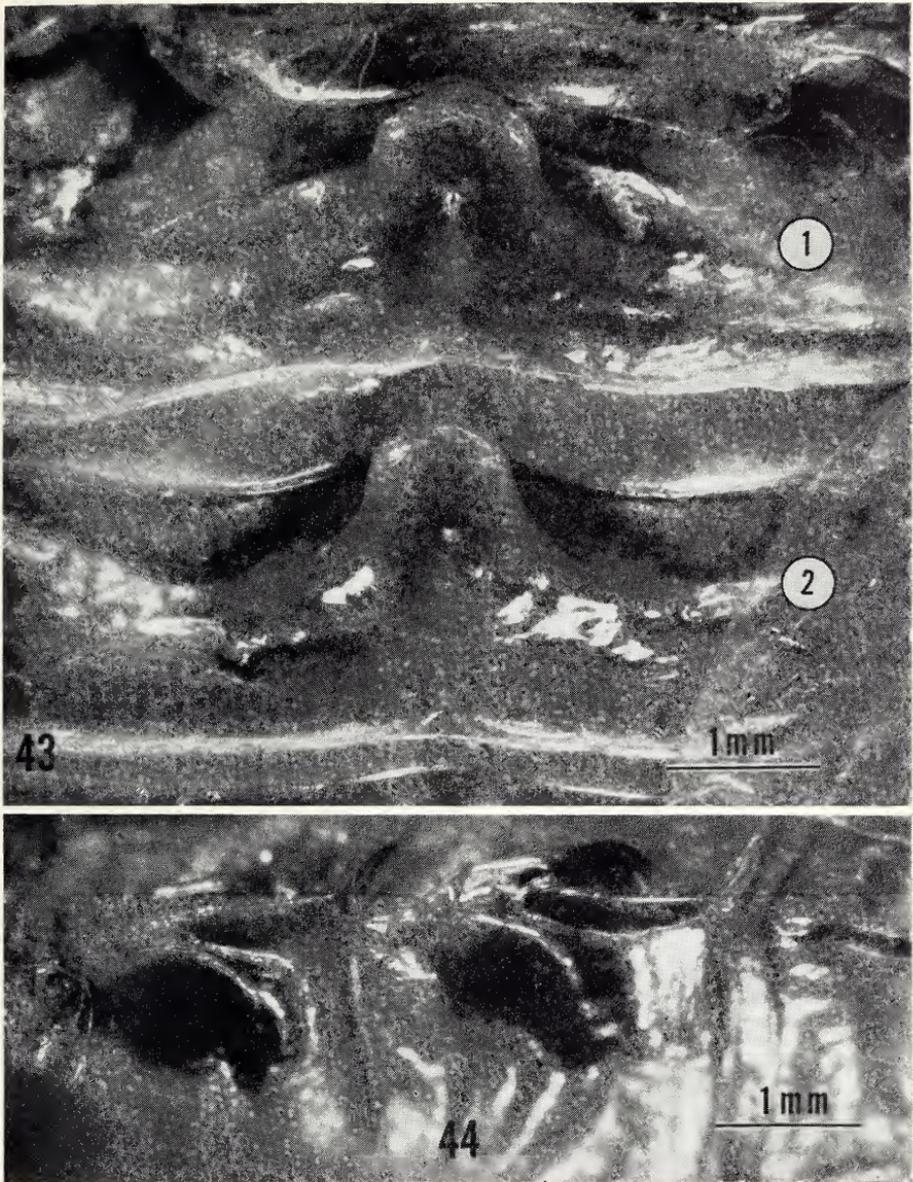
1. Males without tergal modifications on segments 1 and 2. L2d and L2vm separated from each other, and the prepuce usually distinctly outlined and setose (Fig. 1). Hooked portion of R2 usually relatively slender and tapering (sometimes broadened in the middle by a flange), with a subapical incision, and subapical lobe (Fig. 2). L1 with or without a setal brush (Fig. 3), and cleft not fused together. .... *Epilampra* spp.
2. Males with tergal glands on abdominal segments 1 and 2 only. L2d pointed and fused solidly to L2vm; prepuce membranous, not clearly defined by dense setae (Figs. 4, 7, 10, 13, 16, 19, 22, 23, 25, 28, 31, 34, 37). R2 short and stout, without apical incision (Figs. 5, 8, 11, 14, 17, 20, 24, 26, 29, 32, 35, 38). L1 without a setal brush and the sclerotized cleft fused together (Figs. 6, 9, 12, 15, 18, 21, 27, 30, 33, 36, 39). ....  
..... *Poeciloderrhis* spp.

The tergal glands on segments one and two of *Poeciloderrhis* show greater differences between species than do their genitalia and the following key characters may be used to distinguish the forms discussed in this paper:

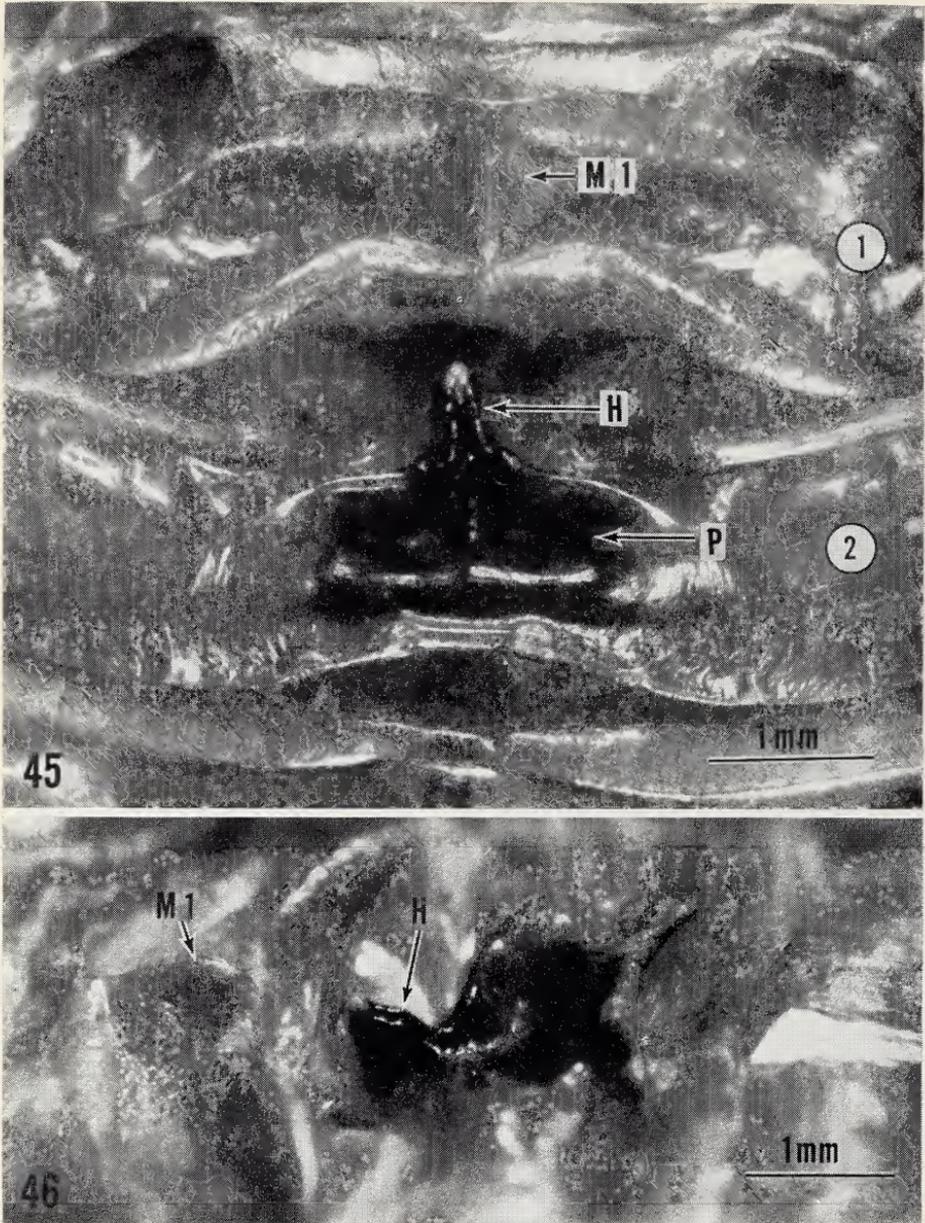
1. Glands without sclerotized horns or deep depressions on either segments one and two. Segment 1 with a low median ridge flanked on each side by raised mounds bearing setae. Segment 2 with a transverse elevation bearing setae; medially, a small vertical ridge anterior to the elevation (Fig. 40). .... sp. *A*.  
Modifications include medial knobs on segments 1 and 2, or a sclerotized horn on segment 2 only. .... 2.
2. Broad, anteriorly rounded, relatively flat medial knobs on segments 1 and 2. .... *catharina* (Shelford) (Figs. 41, 42).  
..... *atriventris* (Saussure) (Figs. 43-44).  
Segment 2 with a black sclerotized horn arising from a deep depression. .... 3.
3. Deep sclerotized pit behind the black horn on segment 2; horn relatively short and stout. Segment 1 with a well defined medial mound, bearing fine short setae (Figs. 45-46). ....  
..... *ferruginea* (Brunner).



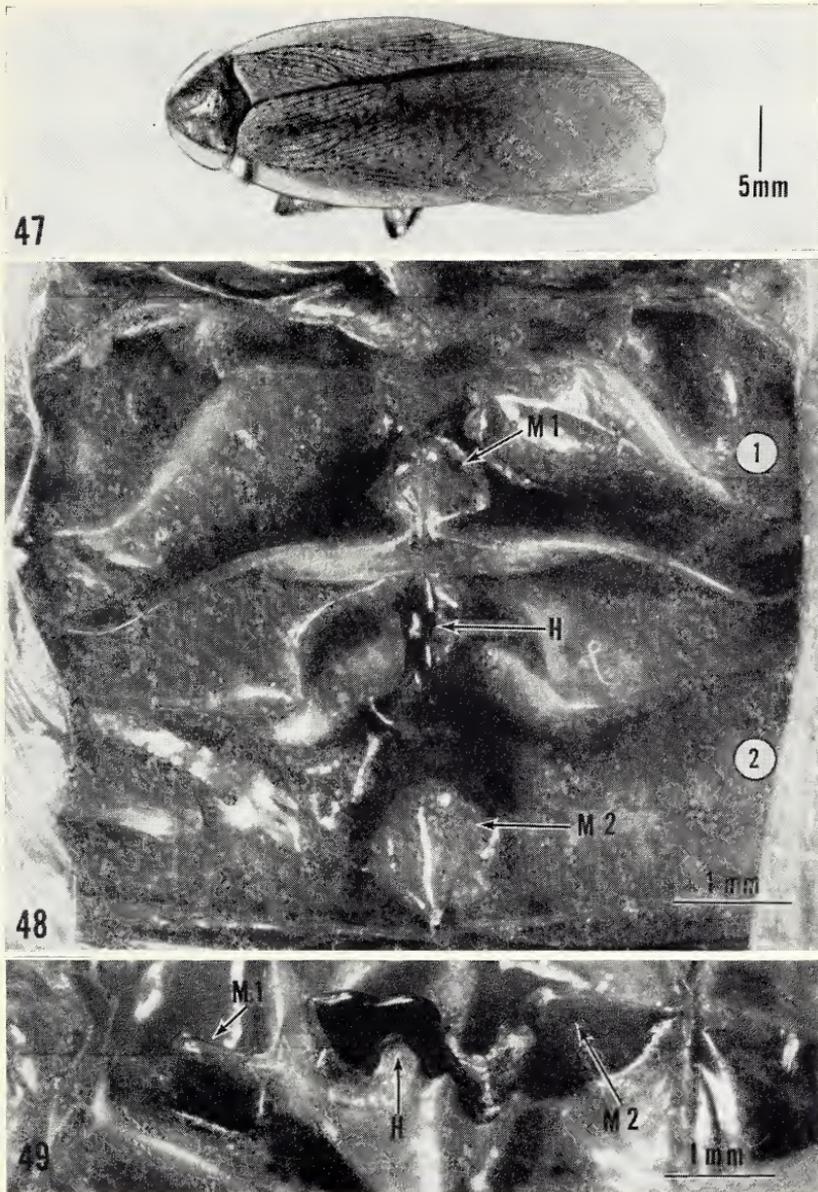
Figs. 40-42. *Poeciloderrhis* spp. 40. (72, MCZ). *Poeciloderrhis* sp. A. Tergal modifications on segments 1 and 2 (circled numbers). Annapolis, Goiás, Brazil (det. Roth). (genitalia in Figs. 28-30). 41-42. (183, USNM). *P. catharina*. The tergal glands are indicated by arrows (Fig. 41) and circled numerals (Fig. 42). (Type of *Audreia catharina* Shelford, St. Catharina, Brazil; genitalia in Figs. 37-39).



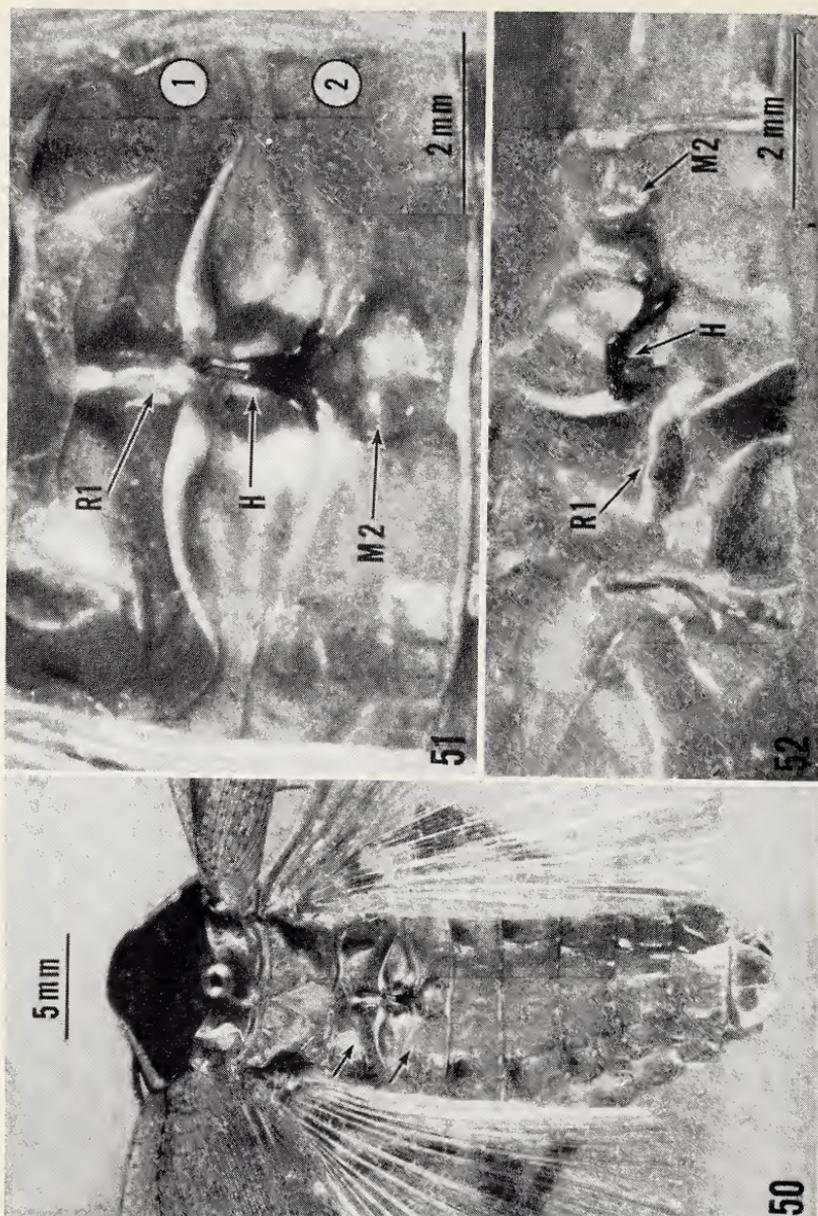
Figs. 43-44. *Poeciloderrhis atriventris*. Tergal glands on segments 1 and 2 (circled numbers). (9, BMNH). Dorsal (Fig. 43) and lateral (Fig. 44) views; genitalia in Figs. 34-36). (det. Hebard).



Figs. 45-46. *Pociloderrh's ferruginea*. Tergal glands on segments 1 and 2 (circled numbers). (166, USNM). St. Catharina, Nova Teutonia, Brazil. Dorsal (Fig. 45) and lateral (Fig. 46) views. (det. Roth). M1 = pyramidal shaped, setose mound on segment 1; H = sclerotized horn on segment 2; P = pit.



Figs. 47-49. *Poeciloderphis proxima*. 47. (22, MCZ). Brazil. (det. Roth). 48-49. (1501, L). Tergal glands on segments 1 and 2 (circled numbers). Ornsköldsvik, Sweden (adventive). Dorsal (Fig. 48) and lateral (Fig. 49) views; genitalia in Figs. 10-12. (det. Princis). M1 = pyramidal shaped mound on segment 1; H = sclerotized horn on segment 2; M2 = pyramidal shaped mound on segment 2.



- Pyramidal shaped elevation on segment 2, behind a slender horn, which is elongate, hook shaped, directed anteriorly, and reaches the posterior margin of segment 1. .... 4.
4. Anterior margin of segment 2 roundly indented, semicircular in outline. Medial moundlike elevation on segment 1 similar in shape though smaller than the one found behind the horn on segment 2 (Figs. 48-49). .... *proxima* (Brunner).
- Anterior margin of segment 2 not as deeply excavated nor as clearly semicircular in outline. Raised medial ridge on segment 1 not pyramidal in shape but more or less uniform in height for its entire length (Figs. 50-52). .... *verticalis* (Burmeister).

The subgenital plates of *Poeciloderrhis* males are highly asymmetrical and more or less similar in shape (see Fig. 8, in Princis, 1967b). *Epilampra cribrata* Burm. has tergites 1 and 2 modified (Princis, 1967b) and therefore is a *Poeciloderrhis*.

The status of the genus *Audreia* Shelford has been questionable and was based principally on a reduction in wings and tegmina in both sexes. It will be reported on elsewhere. The genitalia of *Audreia catharina* Shelford are obviously typical of species of "*Epilampra*" which have tergal glands and I therefore place it in the genus *Poeciloderrhis*. The tergal glands and genitalia of *catharina* are closer to *atriventris* than they are to the other species of the genus.

There may be some question as to the identity of *verticalis* and *proxima*. These are species which have lateral pale markings of the pronotum (Figs. 47, 50). The genitalia of *proxima* shown in Figs. 4-6, came from a specimen (Fig. 47) determined by Rehn as *verticalis*; however, its tergal gland was similar to the specimen determined by Princis as *proxima* (Figs. 48, 49). I have seen a third species belonging to this complex (pale, lateral pronotal coloration) whose tergal glands differed from the species here considered to be *proxima* and *verticalis*. In the final analysis, only type males can solve questions of identity in these similar appearing species.

*Epilampra* is in the tribe Epilamprini (McKittrick, 1964). Because of the morphologic (tergal glands, subgenital plate) and genital differences between *Epilampra* and *Poeciloderrhis* I suggest that the latter genus be assigned to the Poeciloderrhini.

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Figs. 50-52. *Poeciloderrhis verticalis*. (58, USNM). Serra Caraça, Matto Grosso, Brazil; genitalia in Figs. 13-15. The tergal glands are indicated by arrows (Fig. 50), and circled numbers (Fig. 51, dorsal). Fig. 52 is a lateral view. (det. Gurney). R1 = medial ridge on segment 1; H = sclerotized horn on segment 2; M2 = pyramidal shaped horn on segment 2.

## SUMMARY

Based on differences in male genitalia, and the presence or absence of tergal glands, species of *Epilampra* are divided into 2 genera. Species in which the males have tergal glands on segments 1 and 2 are placed in the genus *Poeciloderrhis* Stål. Species with males lacking glandular modifications on the tergites are restricted to the genus *Epilampra* Burmeister. *Poeciloderrhis* is placed in the tribe Poeciloderrhini.

## ACKNOWLEDGEMENTS

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A NEW THRIPS-HUNTING *MICROSTIGMUS*  
FROM COSTA RICA  
(HYMENOPTERA: SPHECIDAE, PEMPHREDONINAE)

BY ROBERT W. MATTHEWS  
Department of Entomology  
University of Georgia, Athens, Ga. 30601

In the two years since the discovery (Matthews, 1968a, b) of the first social member of the Sphecidae, *Microstigmus comes* Krombein, which preys on Collembola, I have received a number of additional preserved nests of this genus from the same Costa Rican locality. Two of these, collected by Miss Robin M. Andrews and Dr. Daniel H. Janzen, are quite distinctive and have proven to be those of a new species whose prey is Thysanoptera. O. W. Richards has very graciously consented to describe this new species; I have added notes on the unique prey and distinctive nest structure.

***Microstigmus thripoctenus* O. W. Richards, new species**

*Female.* Pale testaceous; disc of metanotum, propodeum just above petiolar attachment, distal end of petiole, two oval spots on gastral tergite 2 and sometimes a central spot on tergite 1, blackish suffused. Antennal segment 12 sometimes darker. Tips of mandibles piceous. Most of prothorax, tegulae, coxae, trochanters and narrow bases of femora, white. Wings hyaline-iridescent, venation very pale, pterostigma with a large dark distal spot. Eyes evidently green in life. Length ca. 2.5 mm.

Head between eyes nearly as broad as mesoscutum, with eyes clearly broader than distance between outer edges of tegulae. Antennal scape not extending quite halfway to median ocellus; segment 2 clearly longer than 3, about two and a half times as long as broad, 3 almost one and a half times as long as broad, 3-11 very gradually decreasing in length, penultimate segments hardly more than quadrate, 12 a little longer than 2 but considerably thicker. Head smooth and shining, area above antennae with a fine reticulation; clypeus transversely rather convex, ventral margin feebly emarginate and like the outer edge of mandibles with very long pale hairs. Ocelli in a triangle somewhat narrower than equilateral. Oculo-malar space considerably wider than long. Ventral tooth of mandibles long, four times as long as the subtruncate dorsal one, but both

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teeth shorter than in some of the other species. Transverse keel of pronotum very strong but surface otherwise smooth. Mesoscutum shining with some feeble subcoriaceous sculpture in front half, surface with rather close, short stout pale bristles, recurved backwards. Scutellum strongly raised from in front and behind to a sharp transverse keel. Metanotum with a well-marked transverse keel just behind the front margin, a central longitudinal keel with a weaker keel on each side. Propodeum with a number of strong keels, mostly transverse or longitudinal, defining about twelve large rectangular or polygonal areas. Mesopleuron generally smooth but with a system of irregular keels, especially one curving well in front of mid coxa, two irregularly sinuous ones leading upwards from near it, and a keel defining a prepectal area, distinctly below but only feebly above.

*Male.* Rather smaller and paler than the female. Gaster without dark marks. Face from a little way below median ocellus, most of scape, much of side of pronotum, front part of mesopleuron, much of femora, white. Head wider, oculo-malar space longer, but not quite quadrate. Antennae very similar though with one more segment, segment 3 if anything shorter. Distal part of gaster somewhat distorted but tergite 7 apparently not emarginate, with rather long bristles on each side; sternites with much longer apical bristles than female; sternite 7 triangular but with a short, straight apical truncation, a little upcurved, with numerous long bristles beneath.

Holotype ♀, 2♀-1 ♂ paratypes, Costa Rica, Prov. Puntarenas, Osa peninsula, 2½ miles S.W. Rincón, 08°42' N, 83°29' W, 16 Feb., 1969, ex nest (*R. Andrews*). One paratype from nest in same locality 26 Feb. 1968 (*D. H. Janzen*). Holotype and two paratypes deposited in U. S. National Museum, Type No. 70759; other paratype in British Museum.

*Discussion.* There are more species of *Microstigmus* than is usually supposed; as a result several references to the type of the genus, *M. theridii* Ducke, 1907, cannot be accepted without reserve. The British Museum, however, has a female from Ducke's original series from Tefe.

Pate (1937) gives a key to the genera of Pemphredonini including the Neotropical *Microstigmus*. A key to the described species was given by Richards (1932); since then, only *M. comes* Krombein (1967) has been described. The species of *Microstigmus* fall into two groups; those like the present one in which the third antennal segment is less than twice as long as broad and segments

4-11 are hardly longer than quadrate and those more like *M. theridii* in which the third segment is fully twice as long as broad and the remaining segments are also clearly longer than broad.

In the present group three species have been described and I know of no others. These are *M. wagneri* du Buysson, 1907, described from near Tijuca, State of Guanabara, Brazil; *M. guianae* Rohwer, 1923, (= *hingstoni* Richards, 1932) from Guyana (not British Columbia as stated by Rohwer) and *M. myersi* Turner, 1927, from Trinidad. *M. wagneri* has the apical portion of the clypeus considerably produced, a little upturned, and separated from the proximal part by a shallow depression. The mesoscutum is finely rugose. In color it is brownish-black, with head, pronotum, mesoscutum and metanotum reddish, legs testaceous. The nest is said to resemble that of *M. theridii*. *M. guianae* is testaceous with a few brown markings. The mesoscutum is clathrately sculptured. The nest is made of fibre and rotten wood with a pedicel 6 cm long. *M. myersi* is a brown species and the metanotum is hardly convex. The mesoscutum is smooth. The nest is said to resemble that of *M. theridii* but to include some small mud pellets.

#### BIOLOGICAL NOTES

*Nest Construction.* In the same Costa Rican rain forests<sup>1</sup> where *Microstigmus comes* occurs so abundantly, the two nests of *M. thripoctenus* were obtained at heights of 4 and 7 feet above ground. One was found hanging beneath a palm frond tentatively identified as being of the genus *Geonoma*, and the other was suspended from the 12 cm long leaf of an unidentified vine. Both nests hung firmly from the approximate center of the leaf midrib (Fig. 1). Their pedicels, measuring 22 mm (Janzen nest) and 45 mm (Andrews nest) in length, increased in thickness toward the nest proper, from 0.2 mm in diameter at the point of attachment to 0.8-1.0 mm just above the nest entrance.

At first glance, both nest bags appeared somewhat like greyish shriveled pears, but close examination revealed 5 distinct pouch-like lobes about the periphery of the lower half of each. One nest bag proper measured 11 mm long by 10 mm at greatest width (Janzen); the other was 12 mm long by 7 mm at its widest point (Andrews). The nest entrance, situated to one side of the pedicel attachment, was shielded in both nests by a distinctly protuberant hood-like overhang. Such a hood is never present in *M. comes* nests.

<sup>1</sup>See Matthews, 1968b, for a more nearly complete habitat description.

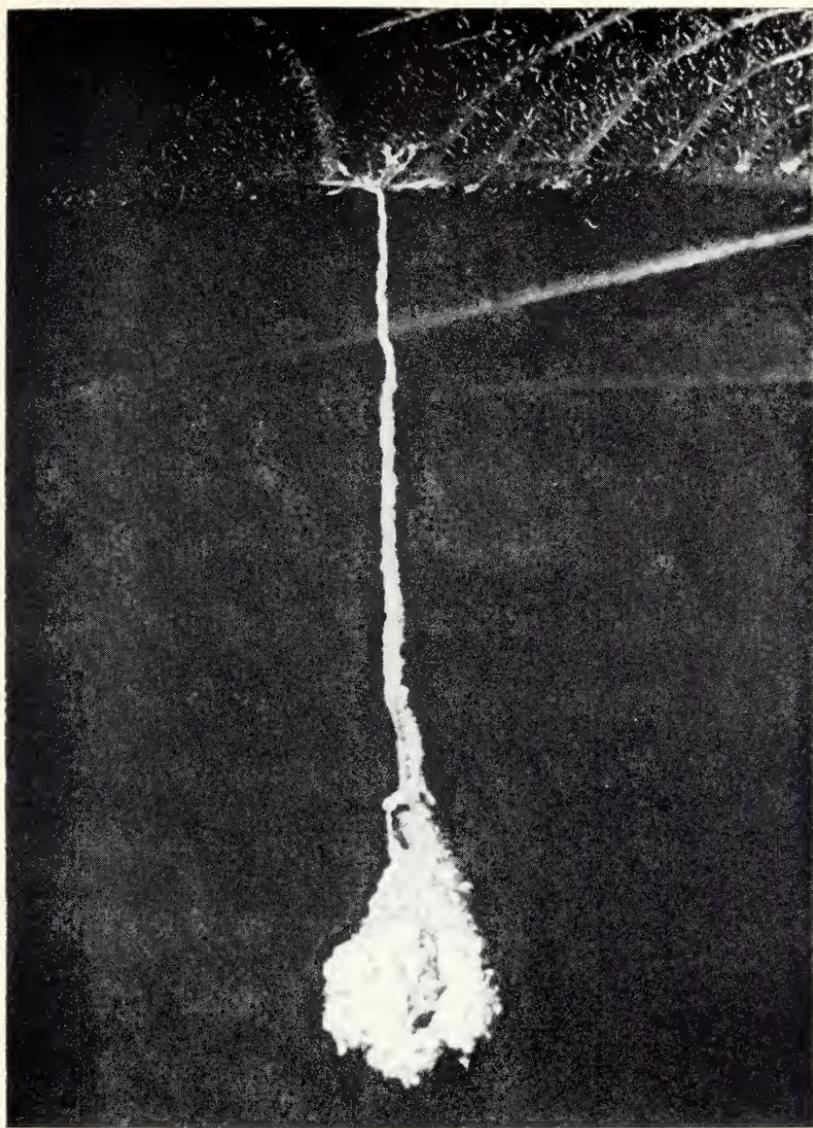


Fig. 1. Nest of *Microstigmus thripoctenus* O. W. Richards. (Photo by Daniel H. Janzen.)

Relatively coarse and irregular chips of punky wood form the basic construction material for the nests. The particles, varying from grey to brown or black and resembling sawdust when dry, are securely bound up in a silken matrix. The entire nest interior, including the cells, is also coated with a silk-like material. Little or no unincorporated nest material remains in the bottom of the nest. In general construction, the nest of *M. thripoctenus* bears a resemblance to that of *M. guianae* which is also made of rotted wood pellets and has a straight, non-spiraled pedicel (see photo in Howes, 1925, p. 276). The nest of another undescribed species from Ecuador is also similar in appearance.

Because the two nests were suspended from different plants, it appears that *M. thripoctenus* does not exhibit the host plant specificity so characteristic of *M. comes*. Neither, as one might suspect from this, does *M. thripoctenus* appear to derive its nest material from the host leaf in the manner of *M. comes*; the leaf undersurface bears no evidence of a scraped area in the vicinity of the nest attachment. And although the nests of both species are coated with a silk-like material, *M. thripoctenus* females have only sparsely scattered hairs on the apical tergite where *M. comes* exhibits its well developed setal brush.

*Cell Contents.* Upon dissection, each nest was found to contain six pocket-like cells, each corresponding to one of the pouch-like lobes (with the extra cell in the center). As with *M. comes*, the cells were mass provisioned, and no two cells were at the same stage of development. Three cells of the Andrews nest contained pupae: one fully pigmented female, one male with cinnamon eyes, and one completely white female. All were oriented with head in the bottom, anus at the cell opening. The remaining three cells of the nest contained a prepupa, a small larva with 171 thrips, and an incompletely provisioned cell containing 58 thrips with no evidence of egg or larva. The Janzen nest, which was less complete, contained one newly emerged adult with freshly expanded wings and, in another cell, a pupal female. A third cell contained a shriveled egg or young larva with 70 thrips. Of the remaining cells, one contained a dozen thrips and two were empty.

The Andrews nest was collected at night when all adults were presumed to be present. It yielded three females and one male. The other nest, collected during the day, contained no adults except for the newly emerged female still in her cell. In the absence of further data, the social status of *M. thripoctenus* must remain un-

certain, although the presence of three females in one nest seems indicative of some degree of social cooperation, which may perhaps be similar to that of *M. comes*.

*Prey.* Use of Thysanoptera as prey has not previously been reported for the genus *Microstigmus*; those species for which prey records are known (*M. comes*, *M. theridii*) use Collembola for provisioning their cells. However, it seems possible that *M. wagneri* and *M. guianae* may also be found to utilize thrips, for they share similar morphological characteristics with *M. thripoctenus*. Other Sphecidae known to prey on thrips include members of the genera *Spilomena* and *Ammoplanus*, pemphredonines which, so far as known, nest in various pre-formed cavities.

All of the over 300 thysanopterans in the Andrews nest were immature individuals, belonging to apparently 4 species (differences may be in stadium rather than taxon). The largest individual measured nearly 1 mm long, but most were about 0.5 mm in length. With but two exceptions, the 82 thrips from the Janzen nest were also immatures, belonging to 3 or more apparent species. Kellie O'Neill of the U.S. National Museum determined the Janzen nest prey as species of Thripidae and identified the two adult females as *Leucothrips* sp. and *Bradinothrips* n. sp. In her letter, she states that the prey "belong to groups of minute, pale, solitary leaf feeders that jump readily and are difficult for humans to capture." Indeed, she added, *Bradinothrips* was previously known only from a unique individual collected in British Guiana.

Within the *M. thripoctenus* nests, the prey appeared to be piled loosely in the cell bottoms rather than packed in compact masses like the Collembola of *M. comes*. Since several specimens were dislodged from their cells during shipment, exact prey counts per cell were not possible. However, the 171 individuals that remained in one cell of the Andrews nest seems an extraordinary number; by contrast, the most Collembola present in any of 22 *M. comes* cells examined was 58.

#### SUMMARY

The new sphecid wasp, *Microstigmus thripoctenus* O. W. Richards, is described and its relationships to other species of *Microstigmus* discussed. Its 11-12 mm long bag-like nest is suspended on a straight pedicel from the underside of leaves in the Costa Rican rain forest. Constructed of punky wood chips bound together in a silken matrix, the nest has a hood-like overhang above

the entrance and a bottom half with lobes roughly corresponding to the cells within. The six cells are mass provisioned with Thysanoptera (*Leucothrips* and *Bradinothrips*), a new prey record for the genus, with as many as 171 individuals found in one cell. One male and 3 female wasps were present in one nest collected at night.

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DURATION OF COPULATION IN  
*POANES HOBOMOK*  
(LEPIDOPTERA: HESPERIIDAE)  
AND SOME BROADER SPECULATIONS\*

BY JOHN M. BURNS  
Museum of Comparative Zoology, Harvard University

Many aspects of diurnal lepidopteran reproductive biology are still poorly known. Duration of copulation—an awkward phrase which, for convenience, is here symbolized  $T_f$ — can readily be determined in various species but rarely has been. It is of interest not only as a behavioral element of possible taxonomic value but also as a highly critical time in the life cycle: copulation is, of course, required for insemination; but copulating individuals, being mutually occupied and encumbered, must often be more vulnerable to predation than separate ones are. Since the act of copulation is vital for contributing genetic material to the succeeding generation but is not performed without risk, one may ask, What fraction of adult life is, on an average, spent copulating? Answers depend on knowing such attributes as  $T_f$  and mating frequency, as well as adult longevity for each sex.

Progress has recently been made in gathering comparative data on mating frequency by counting spermatophores dissected from reproductive tracts of wild females and in interpreting these data (Burns 1966, 1968; Shields 1968; Pliske, in prep.). On the other hand,  $T_f$  has received scant attention. Scattered observations include the following. An interspecific copulation involving pierid butterflies, *Colias interior* ♂ × *C. eurytheme* ♀, lasted 67 minutes (Ae 1956). Among crosses of *C. eurytheme* carried out to study the genetics of an intricate enzyme polymorphism (Burns and Johnson 1967), the two that were timed gave  $T_f$ s of 55 and 75 minutes. In *Danaus plexippus*, a nymphalid butterfly, "It is not known for what length of time the male and female remain . . . united, but on one occasion such a pair was found an hour and a half later on the same tree and in the same position" (Urquhart 1960). A related species, *D. gilippus*, copulates for a period of about one to (usually) several hours (Brower, Brower and Cranston 1965). Indeed, timed copula-

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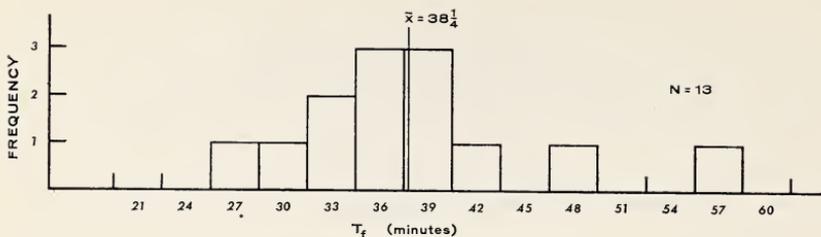


Fig.1. Frequency distribution of  $T_f$  in *Poanes hobomok*.

tions in this species have ranged from a low of 100 minutes to a high of 12 ( $\pm 3$ ) hours (T. E. Pliske, personal communication). A pyrgine skipper butterfly, *Erynnis tristis*, copulated for a little less than one hour (Shields 1968).

Data reported below were obtained in the course of genetically analyzing sex-limited wing-color dimorphism in a hesperiine skipper, *Poanes hobomok* (Burns, unpublished). All material used in this work came from southern New England: Rockfall and Portland, Middlesex County, Connecticut; vicinity of Mt. Tom, north of Holyoke, Hampden County, Massachusetts; and Jacksonville, Windham County, Vermont. Although, in nature, *P. hobomok* is univoltine and spring-flying, a second generation was forced in late summer by laboratory rearing. On sunny days in August and September at Middletown, Connecticut, reared virgins were placed in outdoor screen cages, large enough (60" long  $\times$  28" wide  $\times$  39" high) to permit flight, and were continuously watched. Copulations were timed from beginning to end, with the result shown in Table 1.

The  $T_f$ s are normally distributed around a mean of 38  $\frac{1}{4}$  minutes (fig. 1). In view of their considerable length, the  $T_f$ s are remarkably consistent.

Males of *P. hobomok* are monomorphic but females are dimorphic: one female morph (light) is similar in facies to the male whereas the other (dark) is not. Seven experimental crosses involved light females and six, dark ones. Female color-pattern did not significantly affect  $T_f$ . Nor did the time of summer at which crosses occurred, later crosses not being significantly longer than earlier ones.

In general,  $T_f$ , like so many behavioral phenomena, is best approached statistically, with due regard, however, for prevailing weather conditions. Casual observations suggest that cloudiness and lower temperatures tend to prolong  $T_f$ , which is not surprising. Presumably it cannot be shortened indefinitely because of the logistics of spermatophore production.

Taken together, the meager data assembled here from four unrelated genera suggest, first, that  $T_f$  will tend to be a normally distributed variable (in any particular species population and under similar environmental conditions); and, second, that it will vary widely from some groups of species to others. In the series *Poanes* : *Erynnis* : *Colias* : *Danaus*, mean  $T_f$ s run a gamut from 38 minutes to nearly one hour to roughly 66 minutes to several hours.

The excessively long  $T_f$  of *D. gilippus* may relate to the fact that individuals of this species are often distasteful to vertebrate predators that can learn to leave them alone. Similarly, it may be on this account that danaines can afford to mate so very many times (see Burns 1968; Pliske, in prep.). But inedibility does not explain *why* they mate so long or so much. Although it has been suggested that the high number of matings may partly derive from increased longevity conferred by distastefulness (Pliske, in prep.), far more than this must be involved because danaines will mate several times in what, for a butterfly, can only be considered rapid succession. For example, three pairs of *D. plexippus* in separate small outdoor cages at San Antonio, Texas, were seen to mate once or (usually) twice each day over a four-day period (R. O. Kendall, personal communication). The question remains open. A correlation noted, in *D. gilippus*, between high mating frequency and a low population density associated with great mobility (Burns 1968) hints at directions for future inquiry.

Until we have hard longevity data for these relatively long-lived danaine butterflies, we cannot be precise about the proportion of

Table 1. Duration of copulation in 13 crosses of *Poanes hobomok*.

Cross No.	Date of Cross	Female Morph	$T_f$ (min.)
63×A	VIII-20-1963	dark	38
63×B	VIII-21-1963	light	39
63×C	VIII-22-1963	dark	37 1/2
63×D	VIII-23-1963	dark	38 1/4
63×E	VIII-23-1963	dark	27 1/2
63×F	VIII-23-1963	light	30
63×G	VIII-28-1963	light	56
63×H	IX- 1-1963	light	36 1/2
63×I	IX- 3-1963	light	49
64×A	VIII-18-1964	light	37
64×B	VIII-24-1964	dark	41
64×C	VIII-27-1964	dark	34 1/2
64×E	IX- 2-1964	light	32

adult life actually given over to copulating. Unfortunately, data on longevity in the field are more laboriously got than are those on mating frequency and  $T_f$ . Yet *all* this information, from a variety of diurnal Lepidoptera, is needed for sound comparative analysis of evolutionarily critical features of reproductive biology.

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NEW SPECIES OF *ERIGONE*  
(ARANEAE, LINYPHIIDAE)  
FROM PANAMA AND THE WEST INDIES\*

BY ARTHUR M. CHICKERING  
Museum of Comparative Zoology

In the course of my collecting activities for many years in Central America and the West Indies I have accumulated a considerable number of the small Linyphiidae assigned to the Micryphantinae or frequently given independent family status (Micryphantidae). Among those are numerous interesting genera not well known from the Neotropical Region. Recently I have been able to separate out from the collection a number of specimens which I believe to represent new species of the genus *Erigone* which is well known in North America. Descriptions of these are given in the following pages of this paper for the consideration of those who later continue the study of this genus. I feel certain that careful collecting in Central America and the West Indies will yield numerous additional species. Cuba, Haiti and the Dominican Republic should be especially productive. More careful collecting and matching of males and females is much needed. My own studies of the genus have, thus far, produced only a very small number of known females although other specimens have been under suspicion.

Grants GB-1801 and GB-5013 from the National Science Foundation have furnished financial aid for several collecting trips in Central America, the West Indies and Florida together with my continued research in the Museum of Comparative Zoology for nearly five and one half years. As I have repeatedly acknowledged in my published papers, I am deeply grateful for the help and encouragement received from members of the staff of the Museum of Comparative Zoology extending over a period of many years.

Genus *Erigone* Audouin, 1826

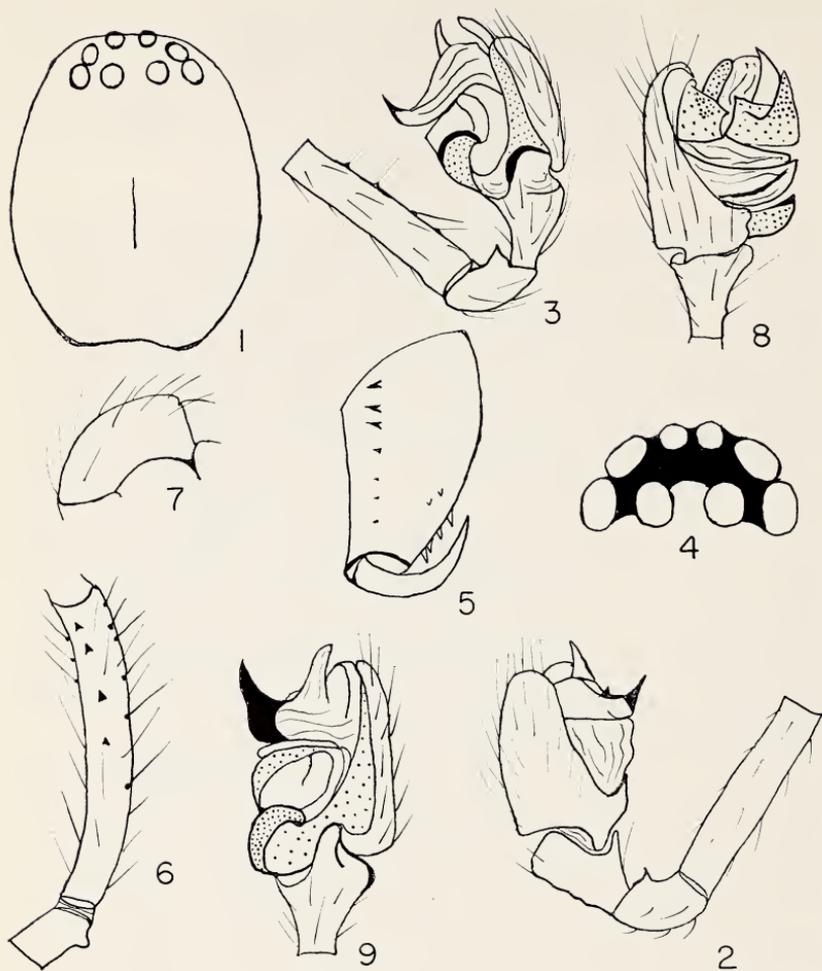
*Erigone antegona* sp. nov.

Figures 1-3

*Holotype.* The male holotype is from the Panama Canal Zone, Forest Preserve, January 29, 1958. The name of the species is an arbitrary combination of letters.

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\*Manuscript received by the editor August 13, 1969.



Figs. 1-3. *Erigone antegona* sp. nov. Fig. 1. Carapace and eyes from above. Figs. 2-3. Left palp of holotype; prolateral and retrolateral views, respectively. Figs. 4-9. *Erigone aptuna* sp. nov. Fig. 4. Eyes from above; tipped backward slightly. Fig. 5. Right chelicera from in front. Fig. 6. Left palpal femur and trochanter; nearly ventral view. Fig. 7. Right palpal patella of holotype; retrolateral view. Figs. 8-9. left palpal tibia and tarsus; prolateral and retrolateral views, respectively.

*Description.* Total length 1.06 mm. Carapace 0.6 mm long; 0.45 mm wide opposite second coxae where it is widest; about 0.22 mm tall at beginning of very gradually declining posterior declivity opposite interval between first and second coxae; broadly rounded in front (Fig. 1); with a fairly well defined median thoracic groove; without teeth along ventral margin. Eyes: eight as usual in the genus; viewed from above, both rows moderately recurved; viewed from in front, both rows moderately procurved. Ratio of eyes AME : ALE : PME : PLE = nearly 5 : 7 : 8 : 8. AME separated from one another and from ALE by a little less than their diameter. PME separated from one another by nearly their diameter and from PLE by about their radius. Laterals separated only by a line. Central ocular quadrangle wider behind than in front in ratio of about 11 : 7; wider behind than long in ratio of about 11 : 9. Height of clypeus equal to a little more than four times the diameter of AME. Chelicerae: with three or four teeth in basal half of anterior surface (right and left sides differ somewhat); with three low and minute cusps along medial margin; fang groove well supplied with teeth but exact number not determined because of fragility of holotype and lack of paratypes. Maxillae: robust; moderately convergent; without special modifications except that there appear to be a few obscure cusps. Lip: short; less than half as long as maxillae; deeply excavated in basal half. Sternum: scutiform; widest in anterior quarter; quite convex; obtusely truncated and extended between fourth coxae which are separated by a little less than half their width. Legs: 1423 in order of length; slender spines as usual in the genus. Palp: obscurely distinctive; the trochanter has a moderately well developed ventro-lateral projection; the femur has a series of four or five small ventral cusps each with a bristle; the patellar apophysis is much reduced; the tibia appears to be quite distinctive but its parts are so intimately related to corresponding parts of the tarsus that representation in a drawing is difficult; essential parts of the tarsus represented in Figures 2-3. Abdomen: considerably smaller than cephalothorax and without special modifications; essentially typical of males of the genus. Color in alcohol: Carapace dark brown with gray streaks radiating from the middle line of the thoracic region; with a moderate amount of black pigment in ocular region; sternum dusky brown; legs and mouth parts yellowish with dusky streaks; abdomen a dark, dusky brown, nearly black.

*Diagnosis.* This species with its reduced palpal patellar apophysis

seems to belong in the group to which *Erigone barrowsi* Crosby and Bishop and *Erigone dentimandibulata* Keyserling belong. Its independent status as a new species is more or less clearly indicated by the body features and by the characters of the male palp.

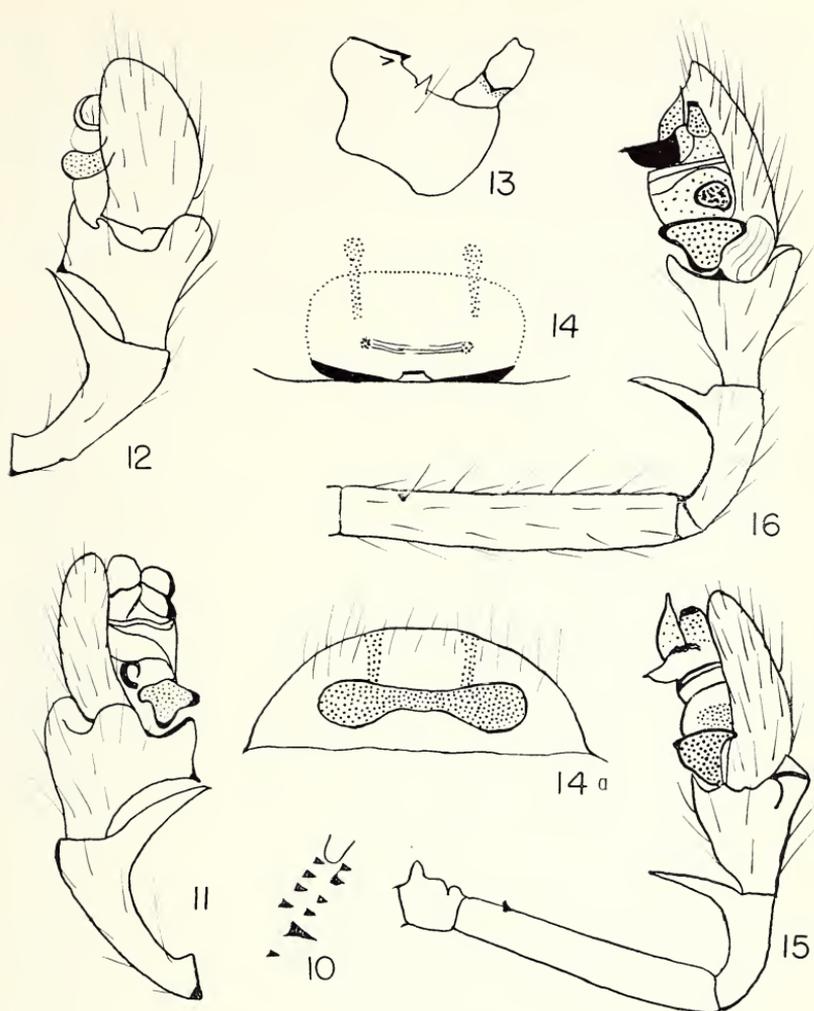
*Records.* The female is unknown and there are no male paratypes.

### *Erigone aptuna* sp. nov.

Figures 4-9

*Holotype.* The male holotype is from the Panama Canal Zone, Barra Colorado Island, August 15, 1954. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.28 mm. Carapace 0.66 mm long; 0.54 mm wide; about 0.29 mm tall shortly behind PME where it is tallest; no serrations observed along ventral margin; general features typical of the genus. Eyes: eight in two rows as usual; viewed from above, anterior row definitely recurved, posterior row slightly so. Ratio of eyes AME : ALE : PME : PLE = 4 : 6.5 : 6 : 6.5 (slight irregularities noted). AME separated from one another only by a broad line and separated from ALE by a little more than their radius; separated from PME by nearly their diameter (Fig. 4). ALE and PLE contiguous to one another. PME separated from one another by about two-thirds of their diameter and from PLE by a little less than their radius. Central ocular quadrangle wider behind than in front in ratio of 7 : 4; wider behind than long in ratio of nearly 7 : 6. Clypeus somewhat extended forward; with height nearly equal to three times the diameter of AME. Chelicerae: vertical; nearly parallel; with teeth on anterior surface essentially as shown in Figure 5 but there appear to be fewer teeth on the left than on the right; with teeth along the fang groove but exact number not determined because of fragility of holotype and lack of paratypes; no lateral striations observed. Maxillae: convergent; essentially typical of the genus except that conspicuous teeth appear to be absent and with only small cusps present. Lip: short; with swollen anterior border as usual in the genus. Sternum: convex; only a little longer than wide; extended between fourth coxae which are separated by nearly their width. Legs: 1=423 in order of length; with slender spines, bristles, hairs and trichobothria. Palp: trochanter with the usual ventral protuberance; femur with inconspicuous teeth and cusps (Fig. 6); patella short and with a short, sharply pointed apophysis (Fig. 7); tibia more or less typical of males of the genus; tarsus complicated and obscurely distinctive (Figs. 8-9). Abdomen:



Figs. 10-12. *Erigone bereta* sp. nov. Fig. 10. Right cheliceral teeth along fang groove. Fig. 11. Right palp of holotype; retrolateral view. Fig. 12. Idem; dorso-prolateral view. Figs. 13-16. *Erigone autumnalis* Emerton. Fig. 13. Left maxilla of male from Panama Canal Zone. Fig. 14. Epigynum of female from Panama; seen from below. Fig. 14a. Idem; from behind with posterior border lifted. Fig. 15. Left palp of male from Trinidad, W. I.; retrolateral view. Fig. 16. Left palp of male from Puerto Rico; retrolateral view.

quite typical of males of the genus and without special modifications. Color in alcohol: carapace a very light yellowish brown with a very narrow median gray stripe and irregular radiating grayish lines; with a moderate amount of black pigment in the ocular area; sternum light grayish; legs and mouth parts yellowish with variations; abdomen a light grayish on the dorsum and lateral sides and with more gray color irregularly distributed on the venter.

*Diagnosis.* This species appears to be more or less closely related to *Erigone tamazunchalensis* Gertsch and Davis from Mexico but differs from that species in details of the male palp.

*Records.* The female is unknown and there are no male paratypes.

### ***Erigone bereta* sp. nov.**

Figures 10-12

*Holotype.* The male holotype is from Corozal, Panama Canal Zone, May 25, 1964. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.65 mm. Carapace 0.81 mm long; 0.58 mm wide opposite second coxae where it is widest; cephalic region considerably raised much as in *Erigone dentigera* O. P.-C.; thoracic portion very gradually slanted to posterior border; ventral margin with a series of small teeth beginning opposite first coxae; with a moderately well defined median, longitudinal, thoracic groove. Eyes: eight in two rows as usual; with chitin raised and with distortion of eyes; apparently both rows are curved essentially as described for *Erigone antegona* sp. nov. Ratio of eyes AME : ALE : PME : PLE = nearly 7 : 10 : 9 : 8. AME separated from one another by slightly less than their diameter; separated from ALE by slightly more than their diameter. PME separated from one another by about seven-ninths of their diameter and from PLE by about two-thirds of their diameter. Laterals as usual, separated only by a line. Central ocular quadrangle wider behind than in front in ratio of about 4 : 3; wider behind than long in ratio of about 6 : 5. Height of clypeus nearly equal to four times the diameter of AME. Chelicerae: well extended to expose fang, fang groove and teeth; fang somewhat irregularly curved; fang groove with six promarginal teeth of which the fifth is the largest and four retromarginal teeth, all small (Fig. 10); front surface of each chelicera with five teeth along the lateral margin with the first very small and others much larger and hooked; apparently each chelicera also has two or

more very minute cusps each with a bristle and irregularly distributed; the only striations observed are on the front surface and those are irregular and probably not used for stridulation. Maxillae: of typical shape; each with several small cusps four of which are grouped closely together with the others more widely distributed. Lip: short as usual; with basal half excavated. Sternum: of usual form; only very moderately convex; extended between bases of fourth coxae which are separated by slightly less than their width. Legs: 1=423 in order of length; patellae three and four each with a very slender dorsal distal spine; tibiae three and four each with a single slender, dorsal spine near proximal end; true spines not observed elsewhere. Palp: essential features of patella, tibia and tarsus shown in Figures 11-12; the patellar apophysis is extremely well developed; the tibia is quite distinctive; the femur has a series of minute cusps on its ventral surface and a weakly developed cusp at its base on the proteral surface. Abdomen: a swelling appears in the middle of the venter just anterior to the genital groove; otherwise essentially typical of males of the genus. Color in alcohol: carapace brownish with darker streaks; sternum dusky brown; mouth parts yellowish brown; legs yellowish; abdomen yellowish on dorsum but grayish laterally and ventrally.

*Diagnosis.* This species appears to be closely related to *Erigone autumnalis* Emerton. It differs from that species, however, in respect to the details of the palp, chelicerae and maxillae.

*Records.* The female is unknown and there are no male paratypes.

### *Erigone autumnalis* Emerton

#### Figures 13-16

*Erigone autumnalis* Emerton, 1882: 58. The male and female types from Boston, Mass. and New Haven, Conn. are in the Museum of Comparative Zoology. Emerton, 1902: 151; 1930: 165; Keyserling, 1886: 171; Banks, 1895: 87; 1899: 189; 1910: 31; 1911: 447; Crosby, 1905: 314; Bryant, 1908: 36; Petrunkevitch, 1911: 232; Comstock, 1912: 373; 1940: 387; Crosby and Bishop, 1928: 19; Jones, 1936: 70; Kaston, 1938: 180; 1948: 191; Roewer, 1942: 726; Bonnet, 1956: 1757.

The group of specimens now considered to belong in Emerton's species were for some time considered to represent four new species. A thorough restudy of the entire lot has now convinced me that they must be regarded as presented here. The appearance of the terminal structures in the male palpal tarsus differs considerably depending upon the way they are viewed and the degree of expansion at the time

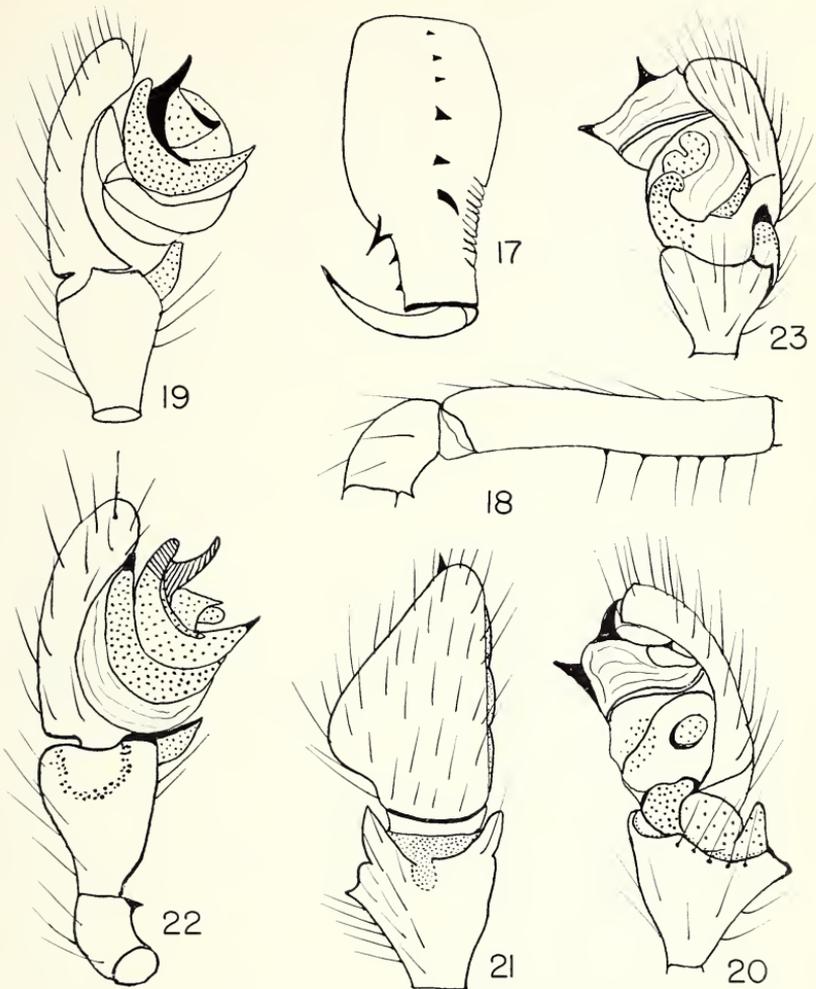
of death. I now have in my collection specimens from the mountainous regions of Panama as well as from several locations in the Panama Canal Zone. I also have a male from Trinidad, W. I. and a male from Puerto Rico, W. I. The species has previously been reported from Bermuda and Cuba. The species seems to be the most abundant of any member of the genus from the region under consideration. Drawings are offered of specimens from Panama, Trinidad, W. I. and Puerto Rico, W. I.

***Erigone digena* sp. nov.**

Figures 17-23

*Holotype.* The male holotype is from the Panama Canal Zone, Gatun, February 27, 1958. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.69 mm. Carapace 0.88 mm long; nearly 0.64 mm wide; nearly 0.4 mm tall in cephalic region where it is tallest; posterior declivity beginning opposite second coxae is somewhat steeper than in *E. antegona* sp. nov. and *E. bereta* sp. nov. Eyes: eight as usual in the genus; viewed from above, posterior row moderately recurved and anterior row more definitely so. Ratio of eyes AME : ALE : PME : PLE = nearly 5 : 6.5 : 6 : 6 (some variation noted among available paratypes); lateral eyes somewhat protuberant and PLE somewhat angular. AME separated from one another by about one third of their diameter and from ALE by about their radius. PME separated from one another by about two-thirds of their diameter and from PLE by about the same distance. Laterals contiguous to one another as usual. Height of clypeus nearly equal to eight-thirds of the diameter of AME. Central ocular quadrangle wider behind than in front in ratio of nearly 5 : 4; and about as wide behind as long. Chelicerae: essentially typical of males of the genus; teeth along lateral margin and near the fang groove essentially as shown in Figure 17. Promargin of fang groove apparently with four teeth and retromargin with three. Maxillae: with few very small cusps and each with a bristle; otherwise essentially typical of males of the genus. Lip: essentially typical of males of the genus. Sternum: moderately convex; almost as wide just behind first coxae as long; extended between fourth coxae which are separated by about two-thirds of their width. Legs: 1423 in order of length; trichobothria observed but not placed accurately. Palp: the trochanter has a ventral tooth; the femur has a series of small cusps on the ventrolateral surface; the patella has a short apophysis near the distal



Figs. 17-23. *Erigone digena* sp. nov. Fig. 17. Left chelicera of holotype from in front. Fig. 18. Left palpal femur and patella; retrolateral view. Fig. 19. Left palpal tibia and tarsus of holotype; prolateral view. Fig. 20. Idem; retrolateral view. Fig. 21. Idem; nearly dorsal view. Fig. 22. Palpal patella, tibia and tarsus of male from Jamaica, W. I.; prolateral view. Fig. 23. Palpal tibia and tarsus of male from Puerto Rico, W. I.; retrolateral view.

end; the tibia and tarsus seem to be quite distinctive (Figs. 18-23). Abdomen: typical of males of the genus; without special modifications. Color in alcohol: carapace yellowish brown with cephalic region much darker; chelicerae nearly like carapace; sternum dusky gray against a yellowish brown background; legs generally yellowish; abdomen yellowish in general with the dorsum showing a faintly indicated median longitudinal gray stripe and with faintly indicated grayish, narrow, transverse bars; the posterior end is a darker grayish with the venter a varied grayish and yellowish. The color pattern is quite variable among the paratypes available for comparison.

*Diagnosis.* This appears to be another species closely related to *Erigone tamazunchalensis* Gertsch and Davis from Mexico but I believe that the rather distinctive features of the palp definitely establish it as a new species.

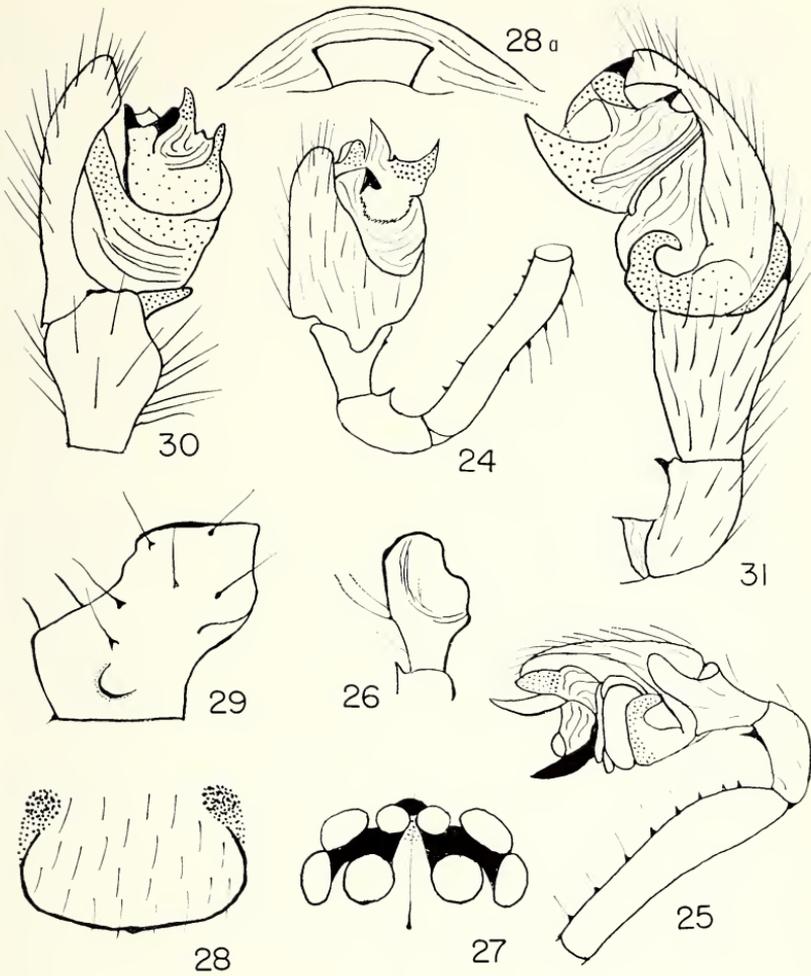
*Records.* In addition to the male holotype, my collection now includes ten males from the Panama Canal Zone as follows: Barro Colorado Island, August, 1950 and July-August, 1954; Summit, August, 1954; Summit Gardens, July, 1954; Pedro Miguel, January, 1958; Gatun, February, 1958. A male from Jamaica, Trelawney Parish, Glastonbury, November, 1957 and two males from the vicinity of the campus of the University of Puerto Rico at Mayaguez, January 29, 1964 are also placed here following a period during which they were regarded as representing another new species.

### ***Erigone dipona* sp. nov.**

Figures 24-28a

*Holotype.* The male holotype is from Boquete, Panama, August 4-11, 1954. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.17 mm. Carapace 0.6 mm long; nearly 0.49 mm wide; with cephalic region steeply raised where it is nearly 0.33 mm tall; with a moderately well defined median longitudinal thoracic groove. Eyes: eight as usual in two rows; viewed from above, posterior row gently recurved and anterior row more definitely recurved. Ratio of eyes AME : ALE : PME : PLE = 7 : 11 : 11 : 10. Outlines of eyes very obscure. AME very narrowly separated from one another, apparently by somewhat less than their radius; separated from ALE by slightly more than this distance and separated from PME by a little less than their diameter. PME separated from one another by a little less than two-thirds of their



Figs. 24-28a. *Erigone dipona* sp. nov. Fig. 24. Left palp of holotype; nearly prolateral view. Fig. 25. Idem; retrolateral view. Fig. 26. Left palpal tibia; nearly dorsal view. Fig. 27. Eyes of described female paratype; from above. Fig. 28. Epigynum of described female paratype; from below. Fig. 28a. Idem; lifted to show posterior surface. Figs. 29-31. *Erigone tepena* sp. nov. Fig. 29. Right maxilla; posterior surface. Fig. 30. Left palpal tibia and tarsus of holotype; prolateral view. Fig. 31. Left palpal patella, tibia and tarsus of holotype, retrolateral view.

diameter and from PLE by nearly their radius. ALE and PLE contiguous as usual. Height of clypeus nearly equal to three times the diameter of AME. Chelicerae: general shape typical of males of the genus; a series of teeth along near the lateral sides are, apparently, differently arranged on the right and the left; the right chelicera has a series of three teeth fairly clearly delineated in a row below the clypeal margin and probably two or three very minute cusps below those; on the left chelicera there may be three teeth but they are out of line; in place of the usually more or less conspicuous tooth near the promarginal row of teeth along the fang groove appears a group of minute cusps. Maxillae: typical of males of the genus except that teeth appear to be absent. Lip: as usual in the genus. Sternum: convex as usual; about as wide as long; extended between fourth coxae which are separated by a little less than their width. Legs: 1 = 423 in order of length; other features typical of the genus. Palp: trochanter with a small, ventral protuberance; other features essentially as shown in Figures 24-26. Abdomen: typical of males of the genus. Color in alcohol: carapace a light yellowish brown with few darker streaks and with a moderate amount of black pigment in ocular area; sternum a light grayish brown; mouth parts yellowish brown with variations; legs yellowish with some variations; abdomen a light grayish brown dorsally and quite grayish laterally and ventrally where there are several darker areas and lines especially anterior to the genital groove.

*Female paratype.* Total length 1.27 mm. Carapace 0.61 mm long; 0.42 mm wide; about 0.22 mm tall; not as steeply raised in cephalic region as in male holotype but posterior declivity is quite steep. Eyes: essentially as shown in Figure 27; ratio of eyes AME : ALE : PME : PLE = 3 : 5 : 5 : 4.5. ALE somewhat angular. AME barely separated from one another; separated from ALE by nearly half their radius and from PME by nearly their diameter. PME separated from one another by nearly seven-tenths of their diameter and from PLE by half their radius. ALE and PLE contiguous as usual. Height of clypeus nearly equal to four times the diameter of AME. Chelicerae: general features typical of females of the genus; fang groove probably with five teeth on each margin. Maxillae and lip: general features typical of females of the genus. Sternum: convex as in male; longer than wide in ratio of about 16 : 13; otherwise essentially as in male. Legs: 1423 in order of length but with only small difference in lengths of first and fourth. Spines on palp but no claw observed. Abdomen: typical of females

of the genus; epigynum somewhat distinctive (Figs. 28-28a). Color in alcohol: carapace, legs and mouth parts yellowish with variations; sternum light grayish; abdomen yellowish white in general but slightly grayish especially on the venter.

*Diagnosis.* This is another species which seems to be closely related to *Erigone tamazunchalensis* Gertsch and Davis from Mexico but the features of the male palp, chelicerae and eyes establish it as a new species.

*Records.* Four paratype males and nine paratype females are in the collection and all are from Boquete, Panama, August 4-11, 1954. Although there can be no certainty, the resemblance of these females to the holotype male seems to warrant their inclusion in this species.

### ***Erigone tepena* sp. nov.**

Figures 29-31

*Holotype.* The male holotype is from the vicinity of the School of Agriculture, St. Catherine Parish, Jamaica, W. I., November 23, 1957. The name of the species is an arbitrary combination of letters.

*Description.* Total length 2.09 mm. Carapace 0.97 mm long; about 0.77 mm wide; nearly 0.33 mm tall in cephalic region where it is tallest; with a well defined median thoracic groove; no serrations observed along ventral margin; general features quite typical of the genus. Eyes: eight in two rows as usual in the genus; seen from above, posterior row slightly recurved; anterior row quite definitely recurved; seen from in front, anterior row gently procurved and posterior row rather strongly so. Ratio of eyes AME : ALE : PME : PLE = 11 : 13 : 14 : 13. Slight differences noted between right and left sides and in contours. AME separated from one another by nearly their radius; separated from ALE by slightly less than their radius and from PME by nearly three-fourths of their diameter. PME separated from one another by nearly two-thirds of their diameter and from PLE by slightly less than that distance. Central ocular quadrangle wider behind than in front in ratio of nearly 17 : 14; slightly wider behind than long. Height of clypeus equal to a little less than three times the diameter of AME. Chelicerae: with three minute cusps followed by two small teeth of medium size all in a row in the proximal two-thirds of each chelicera near the lateral side and with a well developed tooth near the promarginal row of four or five teeth; the retromargin of the fang groove has several teeth but the exact number not determined because

of fragility of the holotype. Maxillae: essentially as represented in Figure 29. Lip: considerably wider than long; with a conspicuous distal border. Sternum: typical of males of the genus as observed in this study. Legs:  $1=423$  in order of length; with few true spines but with many bristles and several trichobothria. Palp: trochanter with a rather poorly developed protuberance; femur with small cusps; other important features essentially as shown in Figures 30-31. Abdomen: typical of males of the genus. Color in alcohol: carapace very light yellowish brown; very little black pigment in ocular area; mouth parts nearly like carapace with variations; sternum very light grayish; abdomen nearly white with faint reticulations.

*Diagnosis.* This is another species which seems to be closely related to *Erigone tamazunchalensis* Gertsch and Davis and other species like *Erigone dipona* sp. nov. included in this study. Its status as a new species is, I believe, established on the basis of the features of the palp, chelicerae and maxillae.

*Records.* The female is unknown and there are no male paratypes. Two males and a female collected in the same locality and on the same day probably represent another new species. The male, intended to be the holotype of a new species, had its left palp lost because of a defective tube and the other male is dismembered. The female is in good condition but its relation to the two kinds of males is so uncertain that it has been laid aside awaiting further study.

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A regular meeting of the Club is held on the second Tuesday of each month October through May at 7:30 p.m. in Room B-455, Biological Laboratories, Divinity Ave., Cambridge. Entomologists visiting the vicinity are cordially invited to attend.

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The illustration on the front cover of this issue of *Psyche* is a line-cut photograph of a phasmatid (*Pseudophasma*) from Costa Rica, designed by Carl F. Moxey.

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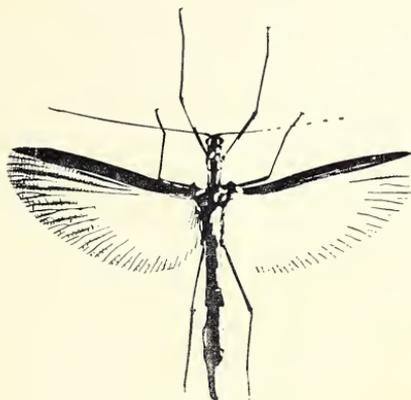
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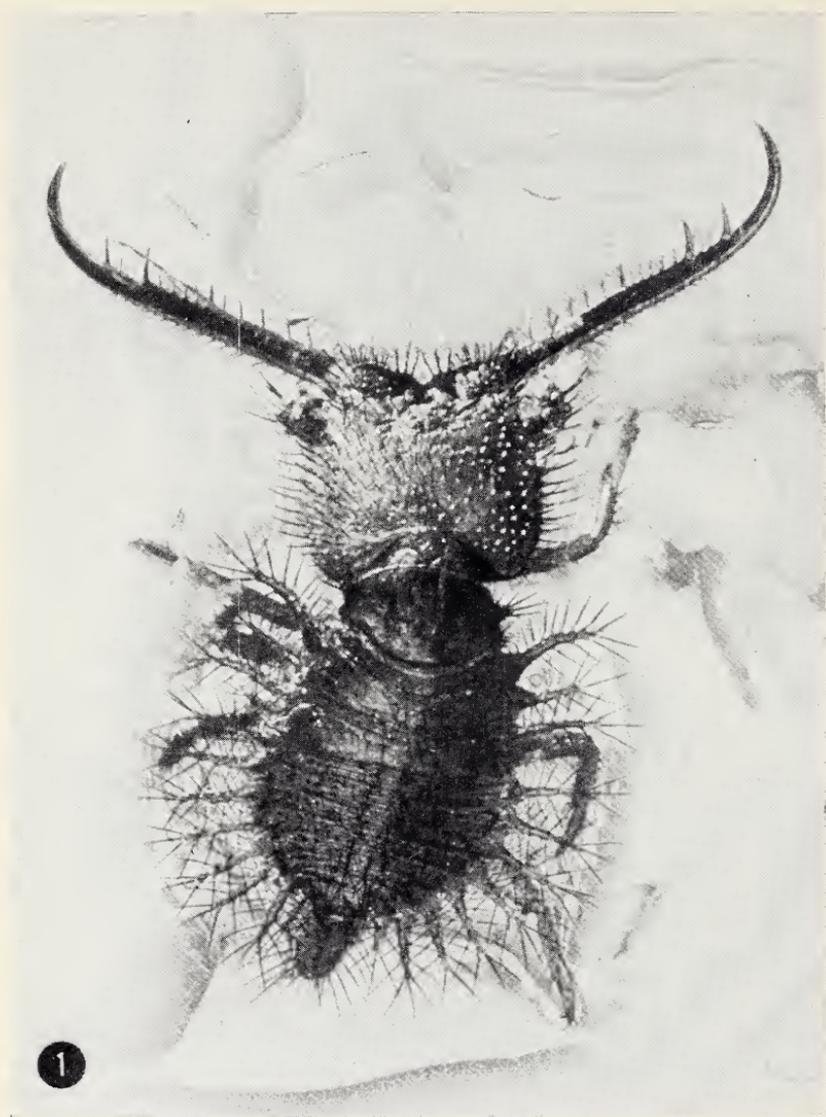


Fig. 1. *Neadelphus protae* n. sp. Dorsal aspect of holotype.

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## THE NEUROPTERA OF THE BALTIC AMBER. I. ASCALAPHIDAE, NYMPHIDAE, AND PSYCHOPSIDAE<sup>1</sup>

BY ELLIS G. MACLEOD<sup>2</sup>

### INTRODUCTION

Along with the related Megaloptera and Raphidiodea, fossils representing the Neuroptera (Planipennia) are known from the Permian of Russia (Martynova, 1962), Australia (Riek, 1953), and Kansas.<sup>3</sup> Several of these early fossils, such as those of the Palaemerobiidae and Permithonidae, have a decidedly modern aspect and by the mid-Mesozoic the living families Chrysopidae (Adams, 1967), Nymphidae (Adams, 1958), and Psychopsidae were already in existence. Other than the Baltic amber, Tertiary deposits have yielded a disappointingly small number of Neuroptera. Among these the Chrysopidae are relatively the most numerous, although in fact they are actually represented by only a small number of fossils from the Florissant shales of Colorado and a few additional specimens from Europe.

Both the Megaloptera and Raphidiodea are known from the Baltic amber (Hagen, 1856; Carpenter, 1956) from a very limited number of specimens, whereas the Neuroptera are much more com-

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<sup>2</sup>Department of Entomology, University of Illinois, Urbana, Illinois.

<sup>3</sup>The two insects described as planipennian Neuroptera from the Lower Permian of Kansas by Tillyard (1932, 1937) are now considered as having quite different affinities. One of them, *Permobiella perspicua* Tillyard, is now recognized as belonging to the Caloneuroidea (Martynov, 1938a, 1938b; Carpenter, 1943a); and the other, *Permoberotha villosa* Tillyard has been assigned to the Glosselytroidea (Martynova, 1962), which is regarded by Carpenter (1964) and Sharov (1966) as closely related to the Neuroptera. The collections of the Museum of Comparative Zoology do, however, contain a specimen from this deposit which I regard as a true neuropteran.



mon and present a gratifying diversity of forms. Hagen (1856), completing the work of Pictet and Berendt, gave the first thorough account of this fauna with a description of seven species which he placed in five Recent genera. Although he referred these species to the single, all-inclusive subfamily "Hemerobiden", his material actually represented the currently recognized families Coniopterygidae, Hemerobiidae, Nymphidae, Osmylidae, and Neurorthidae. In addition, as noted below, he described two larvae which he felt belonged to this order. Other than this early account, only Krüger (1923) has restudied these insects as a unit, although Enderlein (1910) described additional amber Coniopterygidae. Krüger's unillustrated work dealt with most of the species described from adults by Hagen and he recorded, for the first time, adults of the Berothidae and Psychopsidae. Krüger's account is rather disappointing since he considered virtually no structures other than the wing venation and in only a limited way did he attempt to assess the relationship of the amber species to the taxa of the present day.

Based largely on the Haren Collection of Baltic amber in the Museum of Comparative Zoology, Harvard University, but supplemented by important additional pieces from a number of European Museums, it has been possible to assemble a total of fifty-seven specimens for the present study, which represents by far the most extensive collection of Tertiary Neuroptera available at this time. This assemblage includes adult forms of the families Berothidae, Coniopterygidae, Hemerobiidae, Neurorthidae, Osmylidae, Psychopsidae, and Sisyridae as well as larvae of the Psychopsidae and of the Ascalaphidae and Nymphidae.

The only really surprising omission from the list of represented families is that of the Chrysopidae,<sup>4</sup> which I am convinced must certainly have been a component of the fauna of the amber forest. As noted below, a larval chrysopid was very likely described by Hagen (1856), although the present whereabouts of this specimen is unknown. Almost equally surprising, in view of their apparent

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<sup>4</sup>Although recorded as known from the Baltic amber by both Handlirsch (1906) and Bachofen-Echt (1949), no specimen definitely referable to the Chrysopidae has ever been described. Handlirsch has simply repeated the strictly bibliographic listing of Scudder (1891), which in turn is obviously based on an early misidentification by Berendt (1845). Hagen (1852) also noted the presence of a chrysopid from the amber, but no such specimen was listed or described in his works of 1854 and 1856. In all probability Bachofen-Echt's erroneous notation is also derived from these same old sources.

present scarcity, is the relative abundance of the interesting family Neurorthidae, which is represented by twenty-four of the specimens in the collection.

Although the Lower Oligocene horizon represented by this amber is too recent to throw much light on such critical areas of our ignorance as that concerning the phylogenetic relationships of the families of the Neuroptera, the amber fauna does illuminate interesting areas relating to the phylogeny of several of the living genera and to the zoogeography of the order. These findings will be noted in connection with the specific discussions of the families involved. The present paper will treat the families Ascalaphidae, Nymphidae, and Psychopsidae. Although I feel that these groups do form an important phylogenetic unit (MacLeod, 1964 and below), a more practical reason for this grouping is that they are all represented by larval specimens. In the case of the Psychopsidae, adults are also present in the collection.

*Acknowledgements.* It is to Professor F. M. Carpenter that I owe the most profound debt of gratitude, since it was he who first suggested that I undertake this project and who has done the yeoman's work of gathering together the material for study. In addition, he has provided me with a continuing source of intellectual stimulation and with badly needed assistance in preparing the photographic illustrations for this paper. His enthusiasm and friendship have in a very real way opened the difficult doors of insect palaeontology to me.

In addition to the basic collection contained in the Museum of Comparative Zoology, the following individuals and institutions have loaned important specimens, or have otherwise provided aid and advice, and their assistance is gratefully acknowledged: Professor R. Dehm, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; Dr. W. Hennig, Staatliches Museum für Naturkunde, Stuttgart; Dr. H. Jaeger, Institut für Paläontologie und Museum der Humboldt Universität, Berlin; Dr. S. Larsson, Universitetes Zoologiske Museum, Copenhagen; and Dr. H. Weidner, Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg. Finally, I must acknowledge the good counsel of Mr. Carl Moxey of the Biological Laboratories, Harvard University, who provided a learned supplement to my imperfect knowledge of Greek mythology, and Mrs. Alice Prickett, staff artist of the School of Life Sciences, University of Illinois, whose skill produced most of the line drawings.

## THE NEUROPTEROUS LARVAE OF THE BALTIC AMBER

Without formally naming them, Hagen (1856) provided detailed descriptions of two larval specimens which he felt belonged to the Neuroptera. The first of these, designated as "Larva Hemerobii", was described as possessing long, scimitar-shaped jaws, a broad head, and round, strongly constricted setigerous tubercles on the thorax. The remains of a trash packet, consisting of stellate plant hairs, was noted to be present in the vicinity of the larva. It has proved impossible to learn of the present whereabouts of this larva and this is unfortunate since it is quite likely that this specimen is a chrysopid, a family, as noted above, otherwise curiously unrepresented in the Baltic amber. Hagen suggested that this "Larva Hemerobii" might possibly belong to one or another of his several species of amber Hemerobiidae, but our knowledge of present-day hemerobiids rules this out as their larvae are now known to be non-trash carrying forms lacking tubercles and with unspecialized setae. The idea that hemerobiid larvae were trash carriers was wide-spread in the last century and for its time Hagen's suggestion, though incorrect, was reasonable. I have seen several specimens of trash-carrying coleopterous larvae from several amber collections, and it might seem possible that Hagen misidentified one of these as a neuropteran. The mouthparts of these beetle larvae, however, are small and typically coleopterous, whereas Hagen describes the jaws of his larva as ". . . etwa noch einmal so lang als der Kopf, säbelförmig mit scharfer Spitze, glatt und zahnlos, und zangenförmig gestaltet wie bei Hemerobius und Chrysopa." Various species of Ascalaphidae, Myrmeleontidae, and Nymphidae are also known to construct dorsal trash packets, but the larvae of none of these families really have globular, strongly constructed tubercles and, of course, all have toothed mandibles.

Hagen's second larval specimen, designated by him simply as "Larva", has been located in the portion of the Berendt collection now residing in the Museum of Humboldt University, Berlin. It is a member of the Psychopsidae, a family which at the time was unknown to Hagen in the larval stage. This specimen is redescribed below.

In addition to these specimens, larvae, apparently of a myrmeleontoid facies, were mentioned on a number of occasions in the early literature dealing with the Baltic amber (Berendt, 1830, 1845; Burmeister, 1832; Hope, 1834). Upon study, it emerges that only Berendt claimed to have actually seen such a specimen,

the notations of Burmeister and Hope being obviously secondary sources. Such a larva was, curiously, not mentioned by Hagen and, aside from the later bibliographic compilations of Scudder (1886, 1891), which do not note that the earlier references pertained to a larva, this larval type was not mentioned again until 1910. In that year Klebs, again without formal description, mentioned the existence of this type of larva in his extensive personal collection and, without reaching any final conclusions, discussed the opinions of several persons whom he had contacted as to whether it was an ascalaphid or a myrmeleontid. Klebs' collection was subsequently acquired by Albertus University, Königsberg (Andrée, 1937), while, as noted above, portions of Berendt's collection are now located in Berlin; however, a recent search of the remains of these collections has failed to produce any specimens on which these records might have been based. Both Handlirsch (1906, 1925) and Bachofen-Echt (1949), again apparently misled by the earlier references of the nineteenth century, have also dutifully recorded the existence of a myrmeleontid from the amber.<sup>5</sup>

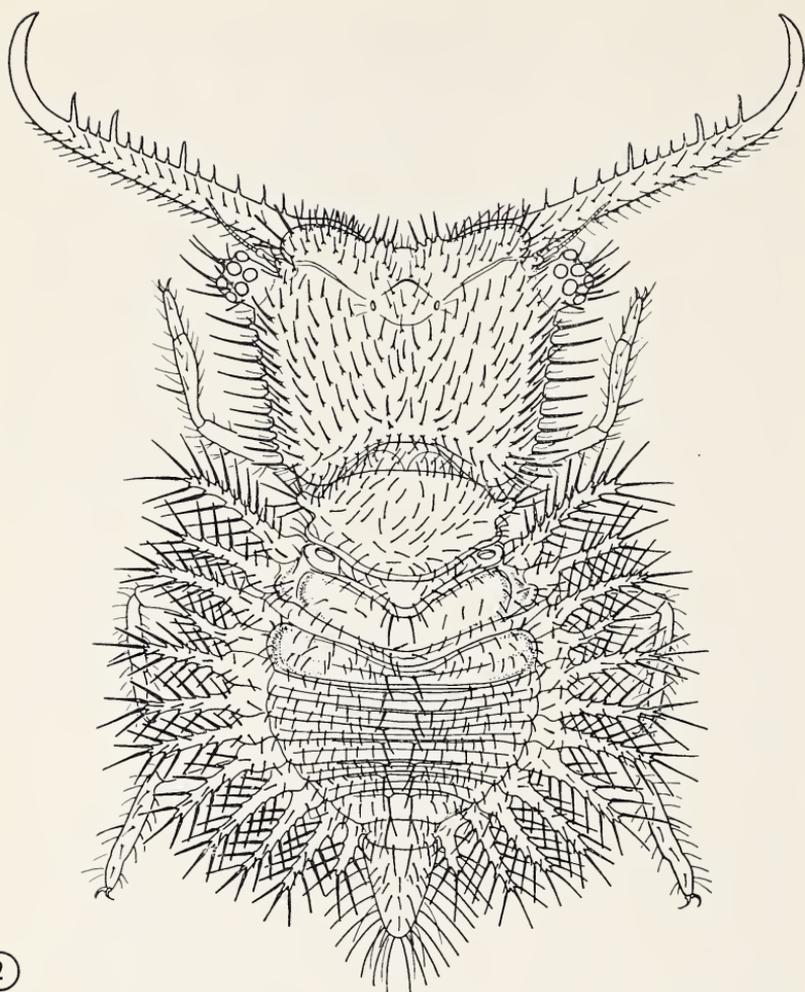
Weidner (1958) has finally given a formal description of a myrmeleontoid larva and his specimen has been available to me for restudy. In addition, a magnificent specimen of an ascalaphid larva from the Hagen Collection of the Museum of Comparative Zoology will also be described. As noted below, it is possible that this latter specimen is the one which was once owned by Klebs.

#### FAMILY ASCALAPHIDAE SCHNEIDER, 1845

The present distribution of this small family includes all major zoogeographic regions, although there is a pronounced concentration of the major taxa in the tropical and subtropical regions of the New and, particularly, the Old World. Two fossil ascalaphids, both adults, have been described from Tertiary deposits of Europe: *Ascalaphus proavus* Hagen (1858), from the brown coal near Linz, West Germany, and *A. edwardsi* Oustalet (1870) from Saint-

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<sup>5</sup>Like Scudder, the listings of both Handlirsch and Bachofen-Echt suggest that they are based on adult fossils. Handlirsch, however, is clearly citing the old reports of Berendt (1830, 1845) and Burmeister (1832) which deal with a larval specimen. Handlirsch and Bachofen-Echt have introduced additional confusion by claiming not one myrmeleontid species from the amber, but three. The three "species" of Handlirsch's account trace back to the three early papers just noted, all of which deal with a single (larval) specimen. Bachofen-Echt has simply repeated Handlirsch's error.



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Fig. 2. *Neadelphus protae* n. sp. Dorsal aspect of holotype. The body, which is slightly curved in the specimen, is here depicted as straightened out.

Gerand le Puy, France. Both of these deposits are referred to Upper Oligocene horizons. Navás (1913) has erected a new genus for each of the fossil species, *Borgia* and *Ricartus* respectively, but this treatment, as well as their original assignment to *Ascalaphus*, has no present value as the fossils have never been restudied in the light of the modern classification of the family. Weidner (1958) described a larva from the Baltic amber which he felt was an ascalaphid. My study of this specimen had indicated that it is actually a nymphid and it is dealt with below under that family.

The collection of the Museum of Comparative Zoology contains a beautifully preserved small larva which is without question an ascalaphid. Because this specimen provides the earliest geological record for a member of this family, a formal description of the larva is presented here.

### **Neadelphus** new genus

(figs. 1-4)<sup>6</sup>

*Description.* Head capsule: quadrate, parallel-sided, with cordate postero-lateral margins; surface generally smooth, raised bases of setae imparting only a slightly rugose texture to surface. Ocular tubercles large, prominent, approximately parallel-sided, each with the usual seven stemmata, six visible in dorsal view, the seventh located ventrally. Antennal tubercle very small. Jaws very long and slender, nearly straight for most of their length, with the three true teeth of the medial mandibular surface beyond the mid-point of the mandible. Labial palpi short, slender.

Body: prothorax approximately elliptical, with a bilateral pair of small, globular setigerous tubercles antero-laterally; prothoracic spiracles only slightly produced as a low cone, elliptical in outline. Meso- and metathorax broader and shorter, each with two elongate setigerous scoli on each lateral margin, the posterior member of each pair distinctly smaller than the anterior one. Legs as in fig. 4, the tarsi quite distinct from the tibiae on the pro- and mesothoracic segments, the metathoracic tarsi fused to their tibiae and showing no indication of a line of fusion.

Abdominal segments I-VIII with a bilateral pair of elongate, unflattened, setigerous scoli, the pairs located on segments I-VII

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<sup>6</sup>The specimen upon which these descriptions are based has previously been illustrated, as a color photograph, on p. 21, of the volume of the *Life Nature Library* entitled *The Insects* (1962. New York: Time Inc.).

subequal in length, the pair on segment VIII much shorter; with no trace of a ventral series of scoli. Only abdominal spiracles I-II visible in fossil, these located ventrally, directly beneath base of corresponding scoli (fig. 4, sp 1, sp 2). Posterior margin of ninth sternum lacking short, stout, "digging" setae.

Head and body covered with short black setae which are longer along the lateral margins of the head capsule, down the midline of the thorax and abdomen and, particularly, on the scoli; longer setae narrowly lanceolate in shape.

Type species, the following—

### ***Neadelphus protae*** new species

*Description.* Setae along lateral margins of head only moderately elongated; central mandibular tooth the largest of the three, distinctly nearer the anterior tooth than the posterior tooth, the posterior tooth the smallest; right antenna with 14 sub-segments distal to the scape, the left antenna with 12.

Maximum width of head capsule immediately behind ocular areas — 1.40 mm. Body length from anterior-most clypeal margin to tip of IX abdominal segment — 3.6 mm.

Holotype: No. 5848, in the Haren Collection of Baltic amber of the Museum of Comparative Zoology. The name for this insect is derived from the Greek Phaëthon myth and translates literally as "Protæ's new brother".

The specimen, undoubtedly a first-instar larva, is contained in a nearly square block of pale-yellow amber with all important taxonomic details easily visible. The block has been mounted on an oblong piece of glass by some previous owner. This glass bears a label with the printed notation "Coll. Dr. Klebs", to which someone has added in india ink "N27-". To this I have added the MCZ type number in blue ink and a new label with the designations "*Neadelphus protae* MacLeod" and "Holotype". It seems certain that this was the larva mentioned by Klebs in 1910, and it is possible that the references to a larva from the early nineteenth century also pertain to this specimen. The route by which it finally reached the Haren Collection is not known.

*Generic diagnosis and discussion.* The cordate posterior margins of the head capsule and large ocular tubercles with seven stemmata combined with the distinct fusion of the tibia and tarsus of the metathoracic leg show, without question, that this larva belongs to the Ascalaphidae.

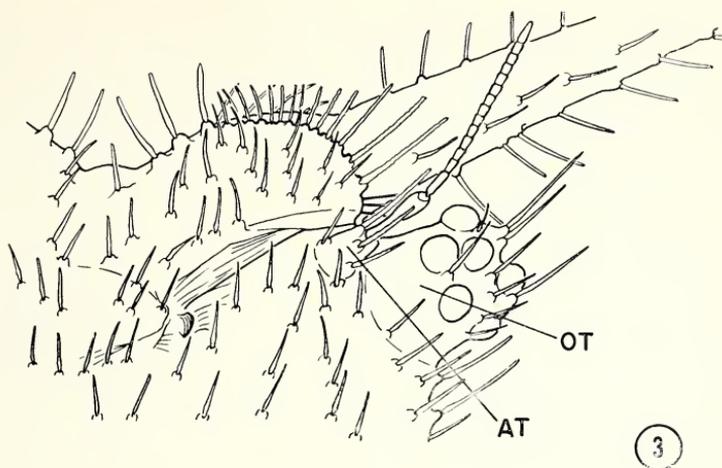
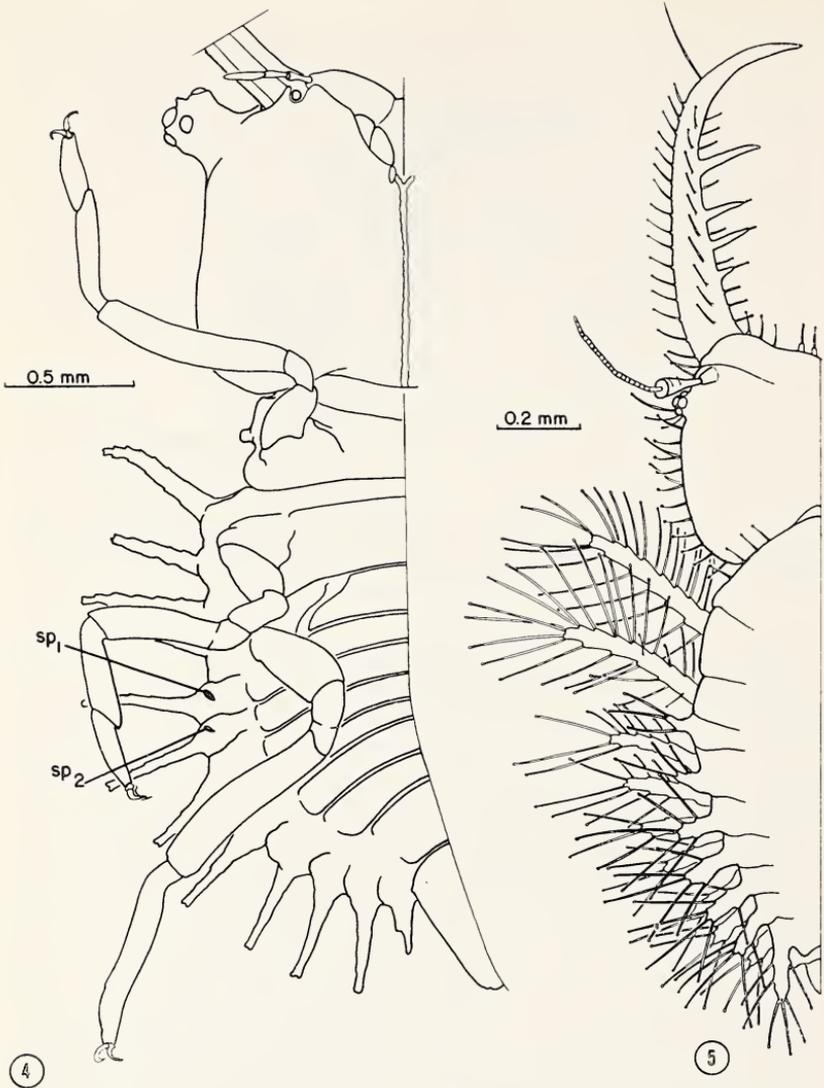


Fig. 3. *Neadelphus protae* n. sp. Detail of ocular tubercle (OT), antennal tubercle (AT) and antenna, jaw base, and chaetotaxy of holotype, dorsal view.

From the time of Hagen's pioneering synthesis of 1873, a number of different types of larval ascalaphids have been described (summarized in MacLeod, 1964 and MS in preparation). A careful reading of this literature, however, reveals few cases in which larvae have been associated with their adults either through rearing or by hatching from eggs laid by a captive female. Most often these associations have been made by a loose, deductive process of elimination from a list of the species which are known as adults from the general area from which the larva was obtained. In view of the continuing poor state of our knowledge concerning the distribution of the species of the Ascalaphidae, this procedure is of no real value. Larval-adult associations which I believe to be reliable have only been achieved for the genera *Ascalaphus*, *Helicomitus*, *Pseudoptynx*, *Suhpalacsa*, and *Ululodes*, all of which belong to the subfamily Ascalaphinae. One might add to these the description by Froggatt (1902) of the rearing of a species now placed in the genus *Acmonotus*, but his unillustrated account is too general to be of any present use. In addition to the genera just noted, I can add to the list of associated forms the larvae of the genus *Ascaloptynx*, representing the subfamily Ascaloptynginae, which I have reared. For strictly nomenclatorial reasons, the larvae of the genera *Neulatus*



Figs. 4, 5. Larvae of Nymphidae and Ascalaphidae.

Fig. 4. *Neadelphus protae* n. sp. Ventral view of holotype showing position of first two abdominal spiracles (sp1, sp2) and leg segmentation, setae omitted.

Fig. 5. Larvae of ?*Pronymphes mengineanus* (Hagen), dorsal view, showing details of lateral scoli; setae of dorsal head capsule and of body proper omitted.

and *Sodirus*, which Navás (1913) erected for two unassociated larval forms, must also be noted here. Although long experience with Navás' taxonomic methods teaches one to anticipate novel procedures, I am hard put to understand this particular action since I believe that there is every reason to anticipate the discovery that these larvae produce adults which belong to long-established genera.

By comparison with these larvae and with a number of additional, unassociated forms available to me for study or described by previous workers, *Neadelphus* appears to differ by the following combination of characters: 1) the quadrate, parallel-sided head capsule; 2) the relatively narrow, produced jaws which are curved only near their tips and which bear the three mandibular teeth distal to the midpoint of the jaw; 3) the elongate, unflattened shape of the twelve pairs of lateral scoli which are unaccompanied by the development of small, additional anterior or ventral scoli or tubercles on the abdominal segments; 4) the ventral position of the first two pairs of abdominal spiracles (and presumably of the remaining six posterior pairs). Various larvae of living species show one or a few of these features, but none show this unique combination. With particular respect to the larval-based genera *Neulatus* and *Sodirus*, *Neadelphus* differs in the form of its prominent, parallel-sided ocular tubercles. These are small and distally narrowed in *Neulatus* and rather short and hemispherical in *Sodirus*. In addition, this latter genus has flattened scoli and a small tubercle on several of the abdominal segments, immediately anterior to the scoli, which are features lacking in *Neadelphus*.

The ventral location of all eight pairs of abdominal spiracles, which *Neadelphus* shares with several living genera including *Ululodes*, is presumably a generalized feature derived from the lateral position of these openings in unflattened ancestral nymphids. Such additional features of *Neadelphus* as the cylindrical shape of the scoli and the non-falcate development of the jaws, though also shared with some living forms, are probably additional examples of generalized character states. In contrast, the presence of only a dorsal series of abdominal scoli must be considered as a specialization from the nymphid double series (see below). Thus, in this respect, the Oligocene *Neadelphus* appears already specialized by comparison to several living larval forms which retain a trace of the ventral series of scoli either as short projections beneath the main dorsal series on abdominal segments I and II (as in an un-

associated larva which I have seen from Tanzania), or perhaps as the small tubercles anterior to the main scoli on abdominal segments III-VII (as in *Ascaloptynx* and several unassociated forms from Central and South America which I have studied). Other than these general observations, I do not believe that the inadequate state of our knowledge of the larvae of this family permits any more definite taxonomic assignment of *N. protae* at this time.

#### FAMILY NYMPHIDAE RAMBUR, 1842<sup>7</sup>

This phylogenetically important family is presently confined to the Australian Region where a small number of species, classified into six genera, are known. The group is obviously of great antiquity as the very closely related Nymphitidae is known from Triassic strata of Russia (Martynova, 1949) and the species *Mesonymphes hageni* Carpenter from the Bavarian Jurassic is already so similar to the living forms that Adams (1958) concluded that it should be included in the Nymphidae itself.

The only apparent Tertiary record of the family<sup>8</sup> has been an adult specimen described from the Baltic amber by Hagen (1856) as *Nymphes mengeanus* and redescribed as representing a new genus, *Pronymphes*, by Krüger (1923). This specimen, originally from Menge's collection, retained only the basal portion of the wings and was missing its abdomen. Krüger's reexamination of the specimen provided a few additional details and corrected several minor errors in Hagen's drawing of the wings. Krüger noted that the specimen was at that time contained in the collections of the Danzig Provincial Museum and, as it has proven impossible to locate, it may not have survived World War II. My redescription of the genus *Pronymphes* is, then, derived from the accounts of Hagen and Krüger and may require future corrections.

I will also here redescribe the larval specimen which Weidner (1958) has treated as a member of the Ascalaphidae. For reasons to be given shortly, I am convinced that the specimen is actually a nymphid, which I will tentatively refer to *Pronymphes*.

<sup>7</sup>In my treatment of this family I am tentatively following the conclusions of Adams (1958) who presented important reasons against the separation of the Myiodactylidae from their close relatives in the Nymphidae. I have previously suggested (1964 and MS in preparation) that a fuller knowledge of the structure and ecology of the larvae of this group may force a reevaluation of this idea.

<sup>8</sup>Bachofen-Echt (1949) notes seven species as having been described from the Baltic amber. I am unable to determine the origin of this error.

*Pronymphes* Krüger

*Pronymphes* Krüger, 1923, Stett. Ent. Zeit. 84: 75-80.

Type species (by original designation): *Nymphes mengineanus* Hagen. Bachofen-Echt, 1949, Der Bernstein und seine Einschlüsse, p. 136.

*Description.* Wings narrowly elongate. Fore wing: costal space narrow, not abruptly widened at base, costal crossveins unforked; Rs+MA originating near base of wing, fused for a rather long distance before separation of MA; MP deeply forked at a level which is distinctly proximal to separation of MA from Rs, the two branches of MP running nearly parallel, the posterior branch separate from CuA; basal branches of Cu running close together and nearly parallel, CuA unforked in portion preserved, CuP with pectinate branches to hind margin of wing, lacking crossveins between branches basally, perhaps with a series of irregular crossveins distally.

Hind wing: costal space and crossveins as in fore wing; origin of Rs+MA much further distal than in fore wing; MP deeply forked to base of wing, MP<sub>2</sub> with wide fork slightly distal to origin of Rs+MA; Cu very short, with only a few pectinate branches to hind margin of wing, unconnected by crossveins.

*Discussion.* The elongate, narrow form of the wings of *Pronymphes* is quite unlike the short, broad wings with abrupt basal dilations of the costal space to be found in the living genera *Myiodactylus* and *Nymphidrion* and I believe that these genera bear no close phylogenetic relationship to the fossil genus. There are such additional differences in venational details as the unforked MP in the fore wing of *Myiodactylus* to reinforce this conclusion. The wings of the species of *Osmylops*, though somewhat narrower in proportion to their width, are still distinctly broader than those of *Pronymphes* and the costal space of *Osmylops* also has a pronounced dilation near the base.

In terms of their overall similarity in wing shape and venation, *Pronymphes* is obviously close to the living genera *Nymphes*, *Austronymphes*, and, particularly, *Nesydrion*. Unfortunately, attempts to infer the probable details of the interesting phylogenetic interrelationship of these four genera, from which I believe their phenetic similarities derive, will be somewhat frustrated until specimens showing the complete wings of *Pronymphes* are discovered. It is especially critical to learn the detailed structure of CuA in the fore wing and, particularly, whether this vein was forked or not. Certain similarities



Fig. 6. Larva of ?*Pronymphes mengeanus* (Hagen), dorsal view.

and differences between *Pronymphes* and these living genera are, however, obvious.

Thus, in the fore wing, the rather far distal separation of MA from Rs is a feature common to all of these genera, while *Pronymphes* shares the deep, basal fork of MP in this wing with both *Nymphes* and *Nesydrion*. In both *Nymphes* and some of the species of *Nesydrion* this forking is distal to the separation of MA from Rs but in other species of *Nesydrion* the fork of MA is as far proximal as it is in *Pronymphes*. *Austronymphes* differs from the other three genera in having MP unforked in the fore wing. The three living genera show various stages in the evolution of the prominent fork of CuA in the fore wing, which is characteristic of all the higher myrmeleontoid families, with this fork nearly marginal in *Nesydrion*, just proximal to the middle of the wing in *Austronymphes* and far proximal to mid wing in *Nymphes* where it is closer to the base than the fork of MP or the separation of MA from Rs. The exact development of this important venational feature cannot yet be determined in *Pronymphes*, although it is obvious that if a fork of CuA was present it certainly was considerably more distal than in *Nymphes* and, probably, *Austronymphes*. The rather distal point of origin of Rs+MA in the hind wing of *Pronymphes* is quite like the condition of this vein in *Nesydrion* and this feature contrasts sharply with the distinctly more basal origin of this vein in all other living genera of the family. Finally, in the weak, submarginal development of the fork of MP<sub>2</sub> in the hind wing, *Pronymphes* is similar to the condition found in *Austronymphes* and *Nesydrion* and quite distinct from *Nymphes* where a deep fork is developed which mimics the appearance of the fork of CuA of the fore wing.

Krüger, who was also impressed with the similarity of *Pronymphes* and *Nesydrion*, felt that these genera could be differentiated by the fact that the fork of CuA of the fore wing is at about the level of the separation of MA from Rs in *Nesydrion*, while in *Pronymphes* no such fork in CuA is developed at this level. The fore wing of *Pronymphes* is preserved for only a very short distance beyond this region and if, with the discovery of additional specimens, a fork in CuA is found to be present just distal to the region preserved in Hagen's specimen, I doubt if a generic distinction will be possible. Krüger suggested that there were additional differences to be found in the hind wings of *Pronymphes* and *Nesydrion*, although he did not stipulate what these might be. I am unable to discover any important differences in the hind wings of these two genera. It will

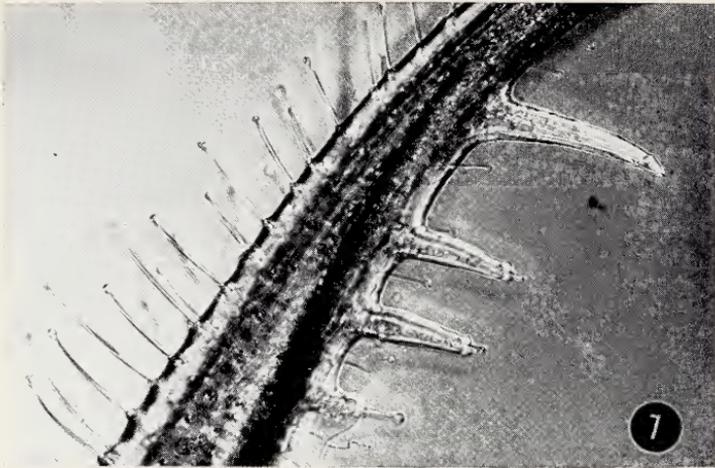


Fig. 7. Detail of left jaw of larva of ?*Pronymphes mengeanus* (Hagen) showing the small setae at the tips of the three proximal mandibular teeth and the globular tips of additional setae. Setae elsewhere on the body proper have these same modified tips. (Photographed with a Zeiss compound microscope using Nomarski interference contrast optics.)

be interesting to see if the larvae of the species of *Nesydrion*, when they are discovered, will throw any light on this question when they are compared to the presumptive larva of *Pronymphes* described below.

*Pronymphes mengeanus* (Hagen)

*Nymphes mengeanus* Hagen, 1854, Verhandl. zool. bot. Ver. Wien 4: 228. (*Nomen nudum*).

*Nymphes mengeanus* Hagen, 1856, in Berendt, Die im Bernstein befindlichen organischen Resten der Vorwelt 2: 85-86, Pl. 8 (fig. 15). Type specimen stated to be in the Danzig Provincial Museum by Krüger (1923), not examined. Hagen, 1866, Stett. Ent. Zeit. 27: 453; Scudder, 1891, Bibliog. of Fossil Ins., p. 354; Handlirsch, 1906, Die fossilen Insekten, p. 908.

*Pronymphes mengeanus*, Krüger, 1923, Stett. Ent. Zeit. 84: 75-80; Weidner, 1958, Mitt. Geol. Staatsinst. Hamburg 27: 67.

?*Pronymphes* sp. (Larva)

(figs. 5-7)

Ascalaphidarum Genus, species, Larva (Planipennia), Weidner, 1958, Mitt. Geol. Staatsinst. Hamburg 27: 64-67.

*Description.* Head: somewhat quadrate, with broadly rounded occipital margins which are not, however, cordate; surface some-

what rugose; clypeal margin with two bilateral pairs of setae with large, blunt bases. Ocular area not borne on raised tubercle. Antenna arising from small antennal tubercle; scape large, prominent, dilated distally, diameter much larger than remainder of antenna. Jaws longer than head, curving inwardly for distal one-third of length; with four apparent teeth on medial surfaces of each mandible, the three proximal teeth with a seta at tip (fig. 7). Undersurface of head with the usual myrmeleontoid specializations of maxillae and labium (MacLeod, 1964). Anterior margin of postlabium very broad; divided pieces of prelabium (apparent basal palpmere) subequal in length to basal palpmere; second palpmere  $\frac{3}{4}$  length of basal palpmere, distal palpmere lanceolate, about as long as basal palpmere. Maximum head width 0.65 mm.

Body: thorax with an elongate, finger-like scolus at sides of meso- and metathorax. All legs with tibia and tarsus unfused. Abdominal segments I-VII each with two lateral scoli on each side, placed to form a dorsal series along edges of terga and a ventral series along edges of sterna; scoli of dorsal series shortest anteriorly, gradually increasing in length posteriorly; those of ventral series longest anteriorly, gradually decreasing in length posteriorly (fig. 5). Scoli of both thorax and abdomen simple tubular projections, not pedunculate.

Both head and body, including scoli, clothed with smooth-sided setae of varying lengths, many with globular tips (figs. 5, 7).

Judging from its size, the specimen is almost certainly in its first larval stadium. The material studied comprises a thin, triangular piece of clear yellow amber, numbered "25", from the collection of the Geologisches Staatsinstitut of Hamburg, Germany. The piece also contains a thysanuran and a small nematoceros dipteran.

*Discussion.* The few known larvae of the living species of Nymphidae have been poorly described and as a result the exact features by which they differ from those of other families of the Myrmeleontoidea have remained rather vague. Tillyard (1926) figured a form identified as *Osmylops pallidus* Banks which he may have reared and this illustration has been widely copied. Although the larva of *Nymphes myrmeleonoides* Leach has apparently been known to several Australian entomologists (Froggatt, 1902; Tillyard, 1926; Gallard, 1935) it has never been properly described.<sup>9</sup>

<sup>9</sup>Froggatt has given a poor figure of the larva of what is probably this species as fig. 36 in his book *Australian Insects* (1907) under the misidentification of *Porismus strigatus*, a member of the Osmylidae!

In connection with a general study of the larvae of the Neuroptera (MacLeod, 1964), I have examined the known larvae of the Nymphidae, including authentic material of *Nymphes* hatched from eggs from a captive female, and larvae identified as *Osmylops* and *Nymphidrion* from Tillyard's collection. The results of this more general study are now in preparation for publication, but the relevant information relating to the unique features of larval nymphids will be noted here.

Nymphid and nemopterid larvae differ from other members of the Myrmeleontoidea in the lack of any fusion of the tibia and tarsus in any of their legs. In contrast, other myrmeleontoids have these segments fused in the metathoracic leg. In addition to a single scolus on each side of the meso- and methathorax, nymphids characteristically have two elongate lateral scoli on each side of the first seven abdominal segments, either arranged above each other as in the larva described here and in *Nymphes*, or else with these tubercles placed one behind the other as in the very flattened type of larva figured by Tillyard as *Osmylops*. In contrast, wherever elongate scoli are developed on the abdomen in the larvae of the Ascalaphidae and Myrmeleontidae these are present dorsally on segments I-VIII (figs. 1, 2)<sup>10</sup> and if any portion of a ventral series is present, as they are in a few ascalaphids, these are confined to the first two abdominal segments. As noted above, in a few ascalaphid larvae from the New World there is, in addition to the usual scoli on the first eight abdominal segments, a very small setigerous tubercle on segments III-VII just anterior to the scolus of the segment. The known larvae of the Nemopteridae lack any real traces of scoli.

The larvae of the Ascalaphidae, Stilbopterygidae, and most Myrmeleontidae also differ from those of the Nymphidae in the shape of the ocular area formed by the aggregated lateral stemmata. This area is produced into a distinctly raised ocular tubercle (fig. 3, OT) in these three families (secondarily reduced only in some specialized myrmeleontids), rather than having the stemmata organized as a nearly sessile lateral group as occurs in the Nymphidae. With respect to this feature, the larvae of the Nemopteridae are similar to nymphids.

Nymphid larvae have been presumed to differ from those of the

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<sup>10</sup>Actually most myrmeleontids (and *Stilbopteryx*) have only setigerous swellings on the abdomen and elongate scoli do not occur; however, a few generalized Myrmeleontidae have moderately developed scoli and, with their somewhat quadrate heads, they look surprisingly like ascalaphids.

Myrmeleontidae and Ascalaphidae in their possession of a single mandibular tooth, as opposed to three or four in these other two families. All ascalaphid larvae with which I am familiar do have three mandibular teeth, but the number varies from one to four in the Myrmeleontidae (MacLeod, 1964). In addition, this generalization is now further weakened by the very large setal bases along the inner surface of the mandible in the larva of ?*Pronymphes* sp. which approximate true teeth very closely. In my opinion the size of these bases in this fossil larva, combined with Baba's (1953) experimental demonstration that such enlarged setal bases are the probable precursors of the true mandibular teeth, robs this character of whatever residual value it might have had in identifying nymphid larvae. Very likely the number of teeth in the larvae of this family has varied during its evolutionary history.

The amber larva is quite similar to the larva of the living *Nymphes myrmeleonoides* in such important regards as its unspecialized body shape, in the somewhat rugose texture of the cuticle of the head, in the presence of distinct dorsal and ventral rows of lateral scoli on the abdomen, and in the vestiture of setae with globular tips. Differences, probably of generic importance, occur in the details of the lateral abdominal scoli, which are longer and, in the dorsal series, distinctly pedunculate in *N. myrmeleonoides*. In addition, *N. myrmeleonoides* shows no traces of tooth-like, enlarged setal bases along the medial mandibular surface.

#### FAMILY PSYCHOPSIDAE HANDLIRSCH, 1906

Of the living families of Neuroptera, the family Psychopsidae is among the earliest to appear in the fossil record, since species, apparently little different from some recent forms, are known from Mesozoic horizons as old as the Upper Triassic of Australia (Tillyard, 1922; Riek, 1956) and the Jurassic of Russia (Martynova, 1949). Apparently related species, presently classified as the families Kalligrammatidae, Osmylopsychopsidae, and Prohemerobiidae, are also known from Triassic and Jurassic strata and there appears to have been a rather extensive radiation of this group in the early Mesozoic from which only the approximately two dozen species of living psychopsids remain as descendants. Other than Krüger's (1923) description of a species from the Baltic amber, Tertiary records of this family have seemed to be lacking. Carpenter (1943b), however, concluded that Cockerell's species *Polystoechotes piperatus* (Cockerell, 1908) from the Oligocene (Florissant) of Colorado is probably a psychopsid

and my recent restudy of this specimen has substantiated this view, so a rather wide Tertiary distribution of these insects is indicated.

At the present time the family is restricted to southern Africa, Asia (Burma, China, Formosa), and Australia. In the most recent revision, Kimmins (1939) treated the living species as representing eight genera which are distinguished principally on the basis of rather small differences in such details as the pattern of anastomoses between M and Cu in the fore wing, the pattern of maculation of the wings, and in the relative widths of the fore and hind wings.

In the Baltic amber the family has, until now, been known only from the single specimen described as *Propsochopsis helmi* by Krüger (1923), although as noted above one of Hagen's larval specimens turns out to have been a psychopsid. A total of six specimens, including two larvae, is available for the present study. The four adults seem to fit Krüger's description of *Propsochopsis* and although these specimens show a number of similarities to several living genera, the differences between the living and fossil forms are sufficient to retain Krüger's generic name. I shall here redescribe, and somewhat redefine, *Propsochopsis* based on Krüger's account and on the new material now available.

*Propsochopsis* Krüger

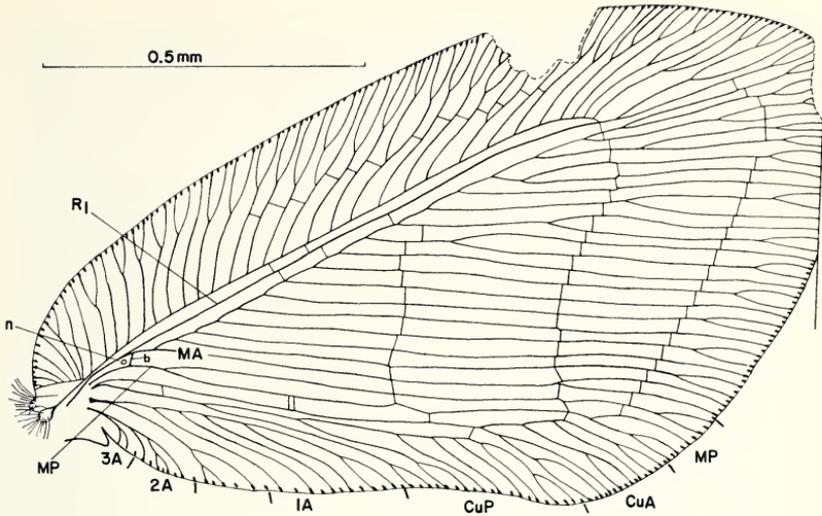
(figs. 8-11)

*Propsochopsis* Krüger, 1923, Stett. Ent. Zeit. 84: 84.

Type species (by original designation): *Propsochopsis helmi* Krüger. Ander, 1942, Lunds Univ. Arsskr. N.F. Avd. 2, 38:15, map 2; Bachofen-Echt, 1949, Der Bernstein und seine Einschlusse, p. 136; Tjeder, 1960, South African Animal Life 7:206.

*Description.* Head lacking ocelli, but vertex with three raised, wart-like protuberances bearing long setae, the median protuberance smaller than the lateral two; head with a trace of a median sulcus posteriorly. Pronotum about as long as broad, anterior margin nearly straight, rounded at lateral corners. Male: prothoracic tibiae not swollen; ectoprocts posteriorly produced (figs. 10, 11); mediuncus elongate. Female: ninth gonocoxites with a stylus.

Fore wing (figs. 8, 9): 30-40 costal veinlets, mostly single forked, a few twice or unforked. Rs with 12-18 branches, mostly unforked before marginal twiggings. Basal piece of MA (fig. 8, b) oblique, fusing with stem of R for a very short distance and separating from stem of Rs near its base; a nygma present in small cell basad of basal piece of MA (fig. 8, n). MP (fig. 8, MP) with basal fork



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Fig. 8. Left fore wing (drawn as right fore wing) of paratype ♀ of *Propsychoopsis lapicidae* n. sp.

Abbreviations: 1A, 2A, 3A — 1st, 2nd, 3rd anal veins; b — basal free piece of MA; CuA, CuP — anterior, posterior cubitus; MA, MP — anterior, posterior median; n — nygma; R<sub>1</sub> — anterior branch of radius.

far proximal and with no additional forkings before vicinity of wing margin, the two main forks connected to each other only by cross veins, the posterior fork not touching or anastomosing with CuA. Cu forking very near wing base; CuA with several series of dichotomous forkings slightly proximal to marginal forks; CuP with several pectinate forkings nearer wing base. 1A well developed, with a number of pectinate branchings; 2A and 3A smaller, with fewer branches. Costal space with an interrupted series of gradate veins; three series of gradate veins elsewhere on wing, the outer series somewhat interrupted or nearly complete; elsewhere only a few irregularly spaced cross veins between Sc and R<sub>1</sub>, between R<sub>1</sub> and the axis of R<sub>s</sub>, and between the branches of MP and Cu. Pattern consisting of a series of distinct, separated dark spots and with a paler, more diffuse series of separate and fusing irrorations scattered uniformly over wing; transverse fasciate patterns absent.

Hind wing: slightly fewer costal veinlets than in fore wing,

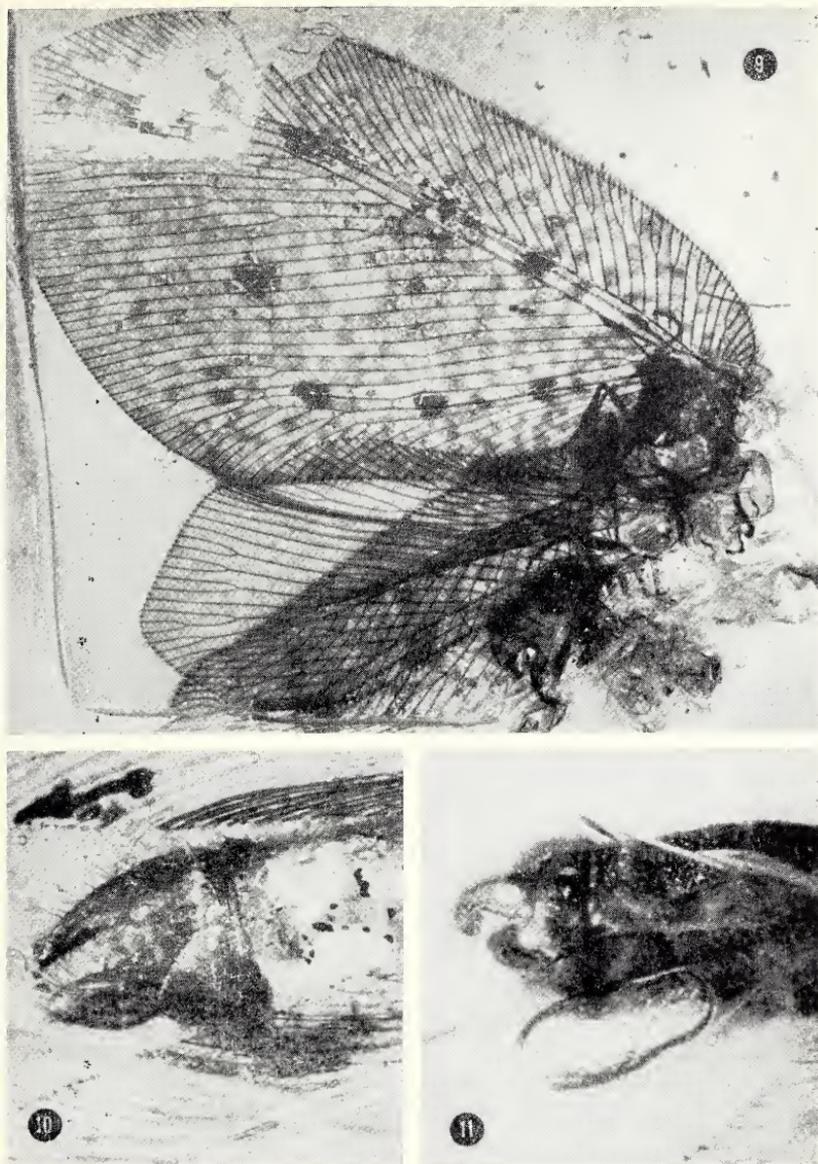
mostly once forked; 8-12 branches to Rs, unforked before terminal branchings at margin; free basal piece of MA longitudinal but not sinuate, not fusing with R but connected to base of Rs by a short cross vein; MP forking somewhat more distally than in fore wing, at about the level of first forking of Rs beyond cross vein to MA, without further branches before forks at margin; Cu forked very near wing base, neither CuA nor CuP with further forks until just before margin. Cross veins present only as an interrupted costal gradate series and two somewhat interrupted gradate series behind vena triplica. Wing membrane nearly clear, with a very faint irrorated pattern, lacking the darker spottings of fore wing and without any trace of a circular dark mark distally behind the terminal anastomosis of the vena triplica.

*Discussion.* The species of *Propsochopsis* possess a number of features which, by comparison to the Mesozoic fossils and to the magnificent living *Megapsychoys illedgi* (Froggatt)<sup>11</sup> of Australia, I judge to be somewhat generalized. These include the retention of all three raised vertex protuberances, the lack of any anastomoses between the branches of MP or between the posterior branch of MP and CuA in the fore wing, the longitudinal orientation of the free basal piece of MA in the hind wing, and in the relatively broad hind wing. In this combination of features *Propsochopsis* is unique.

Various living genera retain one or more of these generalized character states, and I would judge that *Propsochopsis* is only slightly more unspecialized than several of these living groups and is clearly more specialized than *Megapsychoys*. Thus *Silveira* possesses the full complement of three vertex tubercles and the two lateral tubercles are retained in *Balmes*, *Cabralis*, and *Notopsychops*. In the strictly Australian *Magallanes* and *Psychopsis*, at most only a small vestige of these structures remains and in *Wernzia* they are totally absent. In the fore wing, some degree of fusion between the branches of MP or between MP and CuA occurs in all living genera of the family (including *Megapsychoys*) with the exception of *Balmes*, *Magallanes*, and *Wernzia*, and in this last genus MP<sub>2</sub> and CuA usually touch at a point and in some specimens are actually fused for a short distance. With respect to the orientation of the basal piece of MA in the hind wing, only *Notopsychops* (and

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<sup>11</sup>The ensuing discussion is derived from an examination of species of all living genera with the exception of *Megapsychoys*. My knowledge of this insect is based on the account of Tillyard (1918a).



Figs. 9-11. Adults of *Propsychoopsis* spp.

Fig. 9. Paratype ♀ (MCZ) of *Propsychoopsis lapicidae* n. sp. illustrating venation and maculation pattern of fore wing.

Fig. 10. Holotype ♂ (Berlin Mus.) of *Propsychoopsis lapicidae* n. sp. showing detail of ectoprocts, latero-dorsal view.

Fig. 11. Holotype ♂ (Berlin Mus.) of *Propsychoopsis hageni* n. sp. showing detail of abdomen and ectoprocts, latero-ventral view.

possibly *Megapsychops*, Tillyard's account does not mention or figure this vein) retains a longitudinal orientation of this vein although in *Magallanes*, *Silveira*, and *Wernzia* it is distinctly oblique in its placement. In *Psychopsis* the transverse orientation of the basal piece is so pronounced that it resembles a cross vein and in *Balmes* it is absent altogether. Finally, a number of living forms retain relatively broad hind wings, although a reduction in width has occurred in the species of *Silveira* and in the Australian *Balmes gallardi* Tillyard.

Contrary to Krüger's belief in a close similarity between *Propsychoopsis* and *Psychopsis*, I believe that the species of this latter genus are the quite specialized products of a long, isolated evolutionary history of their own and are only distantly related to the living species outside of Australia and to *Propsychoopsis*. In addition to the specialized structural features of *Psychopsis* noted above, the complex, colorful, and very beautiful transverse fasciate patterns of the fore wing and the large dark spot behind the terminal anastomosis of the vena triplica of the hind wing of these species should also be noted. Both of these features are shared with *Megapsychops* and the hind-wing spot also occurs in *Magallanes* and *Wernzia*. These patterns are quite unlike the mottled, splotched, or irrorated wing patterns of the living species outside of the Australian Region and of *Propsychoopsis*.

In its pattern, small size, unspecialized condition of MP and CuA in the fore wing and in its broad hind wing, *Propsychoopsis* approaches the Asiatic species of *Balmes* very closely, although, as I have noted, *Balmes* shows the specializations of the loss of the median vertex tubercle and the base of MA in the hind wing neither of which are found in *Propsychoopsis*. The African genera *Notopsychoops* and *Silveira* show the more generalized state of these two features, but these genera have such additional specializations as anastomoses between the branches of MP (or between MP<sub>2</sub> and CuA in *Notopsychoops*) and, in *Silveira*, a reduction in the width of the hind wing. Barring the discovery of additional fossils or annectant living forms, I do not believe that a more precise conclusion as to the phylogenetic relationship between *Propsychoopsis* and the living species is now possible.

The four adult specimens now before me clearly comprise two species. I am, however, unable to identify either of these as Krüger's *P. helmi* from his very general description and, as I have been unable to locate his type specimen for restudy, I am describing each

of these as new. Following these descriptions I will present a general account of the two larval specimens.

*Propsochopsis helmi* Krüger

*Propsochopsis helmi* Krüger, 1923, Stett. Ent. Zeit. 84: 84-85. Type specimen stated to be in the Danzig Museum, not examined.

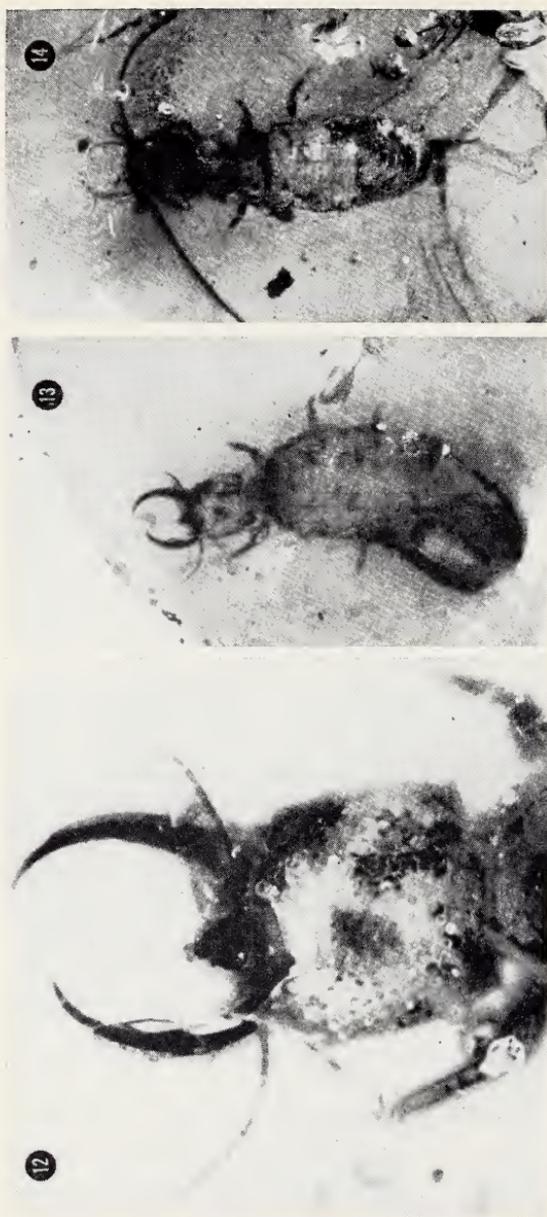
*Discussion.* Krüger mentions the presence of about 40 costal cross veins and about 25 cross veins in each of the cells between Sc and R<sub>1</sub> and between R<sub>1</sub> and R<sub>s</sub>. All of these counts are higher than in the specimens now at hand and it is possible that these characters may provide the means of subsequently identifying *P. helmi* when additional material is discovered. These particular venational features, however, are quite variable and new material could also show these characters to have no taxonomic importance in *Propsochopsis*. Krüger made no mention of any wing pattern in his description, but as he seldom mentioned any features other than the venation in his treatment of any species, living or fossil, his omission in this case is probably of no significance.

***Propsochopsis lapicidae* n. sp.**

(figs. 8-10)

*Description.* Antenna with about 30 flagellomeres distal to pedicel. Fore wing with 33-35 costals proximal to end of vena triplica; 16-17 branches to R<sub>s</sub> (not including MA); terminal (outer) gradate series complete; with a pattern (fig. 9) of two large spots along length of Cu and a third across MP distally, with additional similar-sized dark spots in the middle of the discal gradate series and along vena triplica, elsewhere smaller, paler spots and blotches. Hind wing with 10-11 branches to R<sub>s</sub>, two gradate series; membrane patterned with faint irrorations. Male genitalia (fig. 10) with the ectoprocts produced posteriorly, presenting a rounded triangular outline in lateral view; mediuncus (arcessus of Tjeder, 1960) elongate, parallel sided basally, then tapering to a long triangular point.

Holotype, male: right fore wing with 33 costal veinlets, 17 branches to R<sub>s</sub>; length approximately 13 mm (tip missing); right hind wing with 10 branches to R<sub>s</sub>. The specimen is oriented with all four wings spread in a thin piece of yellow amber which, except for one rounded corner, is rectangular in shape. This insect was apparently subject to some decay before complete entombment, as the ventral half of the head and thorax, including the legs, are missing. In addition much of the tip of the left fore wing is gone



Figs. 12-14. Larvae of ?*Protophyopsis* sp.

Fig. 12. Detail of head, dorsal view, of Berlin larval psychosid.

Fig. 13. Berlin larval psychosid.

Fig. 14. MCZ larval psychosid. The small projections visible at the sides of the thorax and abdomen are dolichasters.

along with a small piece of the right fore wing tip. The type is contained in the amber collection of the Institut für Paläontologie und Museum der Humboldt Universität, Berlin. The specimen is in mineral oil in a vial along with its original labels reading "Fam. Megaloptera" and "Hemerobius resinatus" in black ink and "B-8" in blue ink to which I have added my determination label. Paratypes comprise one male and one female in the collection of the Museum of Comparative Zoology.

This species is named in honor of Professor F. M. Carpenter of Harvard University, whose concern and efforts, extending over many years, are primarily responsible for the development of the collection of fossil insects of the Museum of Comparative Zoology.

### **Propsochopsis hageni** n. sp.

(fig. 11)

*Description.* 29 flagellomeres distal to pedicel. Fore wing with 28 costals proximal to end of vena triplica; 13 branches to Rs (not including MA); terminal (outer) gradate series interrupted; pattern indistinct, but consisting at least of faint irrorations. Hind wing indistinct. Fore wing length — 12 mm. Male (fig. 11): 9th tergite with a pronounced lobe postero-ventrally; ectoprocts very narrowed posteriorly and curving ventro-medially; mediuncus with a broad trapezoidal base from which the remaining portion extends as an elongate ligulate structure with a blunt, triangular tip.

Holotype, male: from the amber collection of the Institut für Paläontologie und Museum der Humboldt Universität, Berlin. The type specimen is contained in a flat block of dark orange amber and is preserved in mineral oil along with labels reading "Fam. Megaloptera" and "Hemerobius resinosus" in black ink and "B-7" in blue ink along with my determination label. I have seen no additional specimens of this species.

This species is named in honor of Hermann Hagen whose thread of life is so richly interwoven with the Neuroptera, the Baltic amber, and the Museum of Comparative Zoology.

*Discussion.* *P. hageni* differs strikingly from *P. lapicidae* in the form of the ectoprocts which in lateral view are quite narrow with a distinct medioventral curvature in *P. hageni* in contrast to their broader, rounded triangular outline in *P. lapicidae*. The mediunci of the two species are also quite distinct, the tip having a ligulate shape, in dorsal view, in *P. hageni* rather than the produced, triangular shape seen in *P. lapicidae*. Comparable differences between

the male genitalia of closely related species of living psychopids occur in *Silveira* judging from Tjeder's (1960) revision of these species. It is possible that additional material may show other important differences in such non-sexual features as the fore wing pattern and may reveal whether the apparent difference in the degree of development of the terminal gradate series of the fore wing is real or not.

The two psychopid larvae are rather poorly preserved and show no important differences from each other. As noted above, Hagen's specimen is now contained in the Museum of Humboldt University, Berlin, while the second specimen is from the collection of the Museum of Comparative Zoology. As our knowledge of the taxonomy of the larvae of this family is so scanty, being confined to the brief accounts of Froggatt (1902, 1907), Gallard (1914, 1922, 1923), and Tillyard's more extensive study of 1918b, there is no real reason for referring the amber larvae to the amber genus, and I do so here only as a bookkeeping measure.

*?Propsochopsis* sp. (Larvae)

(figs. 12-14)

"Larva". Hagen, 1854, *Verhandl. zool. bot. Vereins Wien* 4: 228; 1856, in Berendt, *Die im Bernstein befindlichen organischen Resten der Vorwelt* 2: 90; Scudder, 1891, *Index Fos. Ins.*, pp. 330, 337; Handlirsch, 1906, *Die foss. Ins.*, p. 909.

*Description.* Head capsule: nearly quadrate in dorsal view, widest at about level of antennal bases, narrowing somewhat anteriorly to jaw bases and much more gradually posteriorly to distinct occipital corners, beyond occipital corners head abruptly constricted to form short tubular section anterior to cervix; anterior margin with a distinct, triangular labrum-like projection between jaw bases; ventral surface (best seen in Berlin specimen) with sclerites of maxillary bases and labium small, confined to anterior portion of head capsule; surface of head capsule covered with small papillae, imparting a rugose texture to cuticle. Appendages: antennae slender, with flagellomeres much longer than wide, length of antennae about equal to jaws; jaws smoothly curved throughout length, straight-line length from base to tip slightly shorter than length of head capsule; labial palpi short, slender, segmentation indistinct but with at least three palpimeres.

Body: widest at methathorax (approximately twice as wide as head in Berlin specimen, narrower in MCZ specimen), parallel

sided for abdominal segments I-IV then narrowing gradually to tip of abdomen; prothorax much narrower than remainder of thorax, somewhat trapezoidal in shape, widest posteriorly, dorsal surface with dolichasterine setae which are somewhat more slender than elsewhere on body (best seen in MCZ specimen); meso- and meta-terga with small, triangular, smooth latero-dorsal sclerites (pinacula of Tillyard, 1918b) above corresponding coxae, each bearing a few small dolichasters, these sclerites equal sized on the two segments (not visible in Berlin specimen); body surface posterior to prothorax (and ventrally on prothorax) covered with numerous small, broad, cup-shaped dolichasters; legs rather short, stout (tips missing in Berlin specimen).

Head width — 0.98 mm (both specimens); head length (base of labral extension to level of occipital corner) — 1.0 mm (both specimens); total length from tip of closed jaws to tip of abdomen — 6.1 mm (MCZ specimen).

*Discussion.* While recognizing his larva as a neuropteran, Hagen was understandably perplexed as to its relationships and after rejecting any association with the Coniopterygidae, Hemerobiidae, and Sisyridae, he left open the possibility that it might be a nymphid or perhaps an unusual osmylid. Larvae of living species of the Psychopsidae were not described until the early years of this century, so Hagen's perplexity is quite understandable.

Hagen indicated some concern over the apparent shortness of the legs of his specimen and suggested the possibility that they had been mutilated. The amber piece containing his specimen was evidently once a faceted bead as it has a nearly circular outline and has been pierced through the center. In addition, traces of facets are still visible around its circumference. The original bead was not a single unit, however, as two separate pieces of amber have been joined together and, probably in preparation for this joining, the piece containing the larva was planed down to the point where portions of the legs and the ventral surface of the body were removed. The composite bead itself has been subsequently ground down, probably so as to better examine the larva, and the double piece now has the form of a round flat disc. The portions of the legs remaining in Hagen's specimen, and the intact legs of the MCZ specimen, show that the legs of these amber larvae are normally proportioned for psychopsids.

Judging from the size of the amber specimens they are both second-instar larvae. They differ in no important regard from a

series of unidentified, field-collected larvae of one or more living Australian species which I have studied, and it would be difficult to separate the amber specimens from these living forms. Although the mature-sized larvae of my Australian series have heads which are distinctly longer than broad, the smaller larvae of this series, presumably second-instar, have more quadrate head capsules like the two amber specimens. Whether this is a feature of taxonomic importance or is simply a reflection of a pattern of ontogenetic allometry occurring in the Psychopsidae cannot now be known.

Tillyard (1918b) reports that the larvae of Australian forms are to be found in the deep crevices of the bark of living trees of a number of species and that they are especially frequent in the vicinity of sap flows where they presumably seize, as prey, other insects visiting the fermenting sap. Similar habits in the larvae of the amber species should have made them especially liable to entrapment in the resin which produced the amber and this perhaps accounts for the capture of the larvae discussed here.

Recent classifications of the families of living Neuroptera have usually treated the Psychopsidae as belonging to the same superfamily as the Hemerobiidae (Withycombe, 1925; Tillyard, 1926; Handlirsch, 1936; Killington, 1936; Riek, 1970), although Withycombe and Riek realized that such a classification of this odd family was an oversimplification. The Psychopsidae and its close Mesozoic relatives have also been placed in the Hemerobioidea by Martynova (1962) in her classification of the fossil forms. In Tillyard's final statement on the question (1932) he considered the Psychopsidae to comprise a very specialized side branch of their own.

I have elsewhere (1964 and MS in preparation) noted that the larvae of the Psychopsidae are structurally of the same, unique form as are those of the families of the Myrmeleontoidea, complete to such details as the very unusual specializations of the tentorium, maxillae, and labium. It would seem that these specializations rule out any close evolutionary relationship of the Hemerobiidae, or its true allies, to the Psychopsidae. Future attempts to trace the origins of the Psychopsidae and its Mesozoic relatives, or the origins of such phylogenetically important myrmeleontoids as the Nymphidae, must take these distinctive features of larval morphology into account.

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STRIDULATION IN  
*ACANTHOPHRYNUS CORONATUS* (BUTLER)  
(AMBLYPYGI, TARANTULIDAE)

BY WILLIAM A. SHEAR<sup>1</sup>

In April, 1965, during a visit to the vicinity of San Blas, Nayarit, Mexico, I collected a living specimen of *Acanthophrynus coronatus* (Butler), the largest known species of the amblypygid family Tarantulidae. The specimen lived in captivity for over a year, despite several escapes, and fed voraciously on moths and other soft-bodied insects. The usual predatory sequence consisted of repeated light taps on the prey with the whip-like first legs, the left and right legs acting alternately, followed by a sudden lunge, too quick for the eye to follow in detail, with pedipalps spread wide. The prey was caught and impaled on the spines of the pedipalps, and torn to bits by alternating movements of the chelicerae. During these cheliceral movements, a faint sound could be heard.

When prodded into its defensive posture, the specimen raised its body high off the substrate, spread its palps wide, rocked up and down, and rubbed its chelicerae together with reciprocating circular movements. A loud, rattling hiss resulted, sounding very much like the warning of a small rattlesnake.

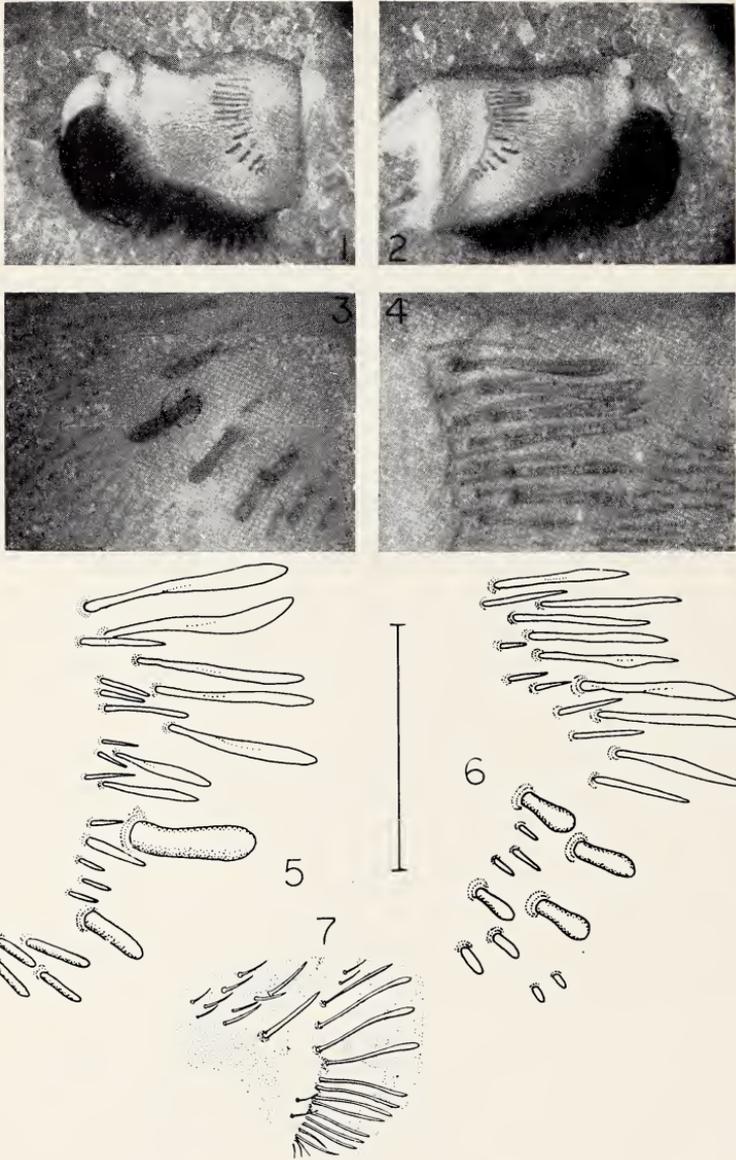
In May, 1966, the specimen molted for the first time in captivity, and failed to survive. Upon examination, the newly molted corpse proved to be that of a mature male. Recently, I examined the specimen in detail. The inner surface of each chelicera (Figs. 1, 2) bears a stridulating lyre consisting of a row of short, apically expanded spines (Fig. 4) and a plectrum of even heavier spines (Fig. 3). There are some differences in the arrangement and number of these spines between the right (Fig. 1) and left (Fig. 2) chelicerae of the specimen.

I examined three other males of *Acanthophrynus coronatus* in the collection of the Museum of Comparative Zoology. All had the stridulating apparatus, though there were differences in specimens from different localities. Figure 5 shows the apparatus of a specimen from San Marcos, Jalisco, Mexico, and Fig. 6 that of a specimen

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<sup>1</sup>Department of Biology, Concord College, Athens, W. Va. 24712. Work done while supported by a Richmond Fellowship at Harvard University, at the Museum of Comparative Zoology.

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Figs. 1-6. *Acanthophrynus coronatus*. Figs. 1-4. Specimen from San Blas, Nayarit. Fig. 1. Inner face of right chelicera. Fig. 2. Inner face of left chelicera. Fig. 3. Plectrum of right chelicera. Fig. 4. Lyre of left chelicera. Fig. 5. Specimen from San Marcos, Jalisco, stridulating apparatus of left chelicera. Fig. 6. Specimen from Mazatlan, Sinaloa, stridulating apparatus of left chelicera. Fig. 7. *Musicodamon atlanteus*, stridulating apparatus of left chelicera (after Fage, 1939), same orientation as Figs. 5 and 6. Scale line = 5 mm for Figs. 1 and 2, 2.1 mm for Figs. 3-6. Fig. 7 not to scale.

from Mazatlan, Sinaloa, Mexico. Differences between the left and right chelicerae of these specimens were similar to those illustrated for the San Blas specimen (Figs. 1, 2). Two females from Apatzingan, Michoacan, and a single female from Mazatlan (American Museum of Natural History) were also examined, and found to have the stridulating apparatus essentially as described for the males. The Michoacan females more closely resembled the male from San Marcos, Jalisco, than the Mazatlan specimens.

Fage (1939) described *Musicodamon atlanteus* from Morocco, which has a similar stridulatory apparatus, though the spines are arranged quite differently (Fig. 7). Some mygalomorph spiders stridulate, using spines on the inner faces of the chelicerae (Millot, p. 610).

The stridulating apparatus is absent or replaced by a group of much weaker spines in the following species that were readily available for examination: *Phrynus operculatus* Pocock, *Tarantula palmata barbadensis* Pocock, *T. fuscimana* (C. L. Koch), *T. marginemaculata* (C. L. Koch), *Phrynichus bacillifer* (Gerstaecker) and *Hemiphrynus raptor* Pocock. I also examined a few specimens of undetermined species from India, Ceylon, Africa, South America and Indonesia, and failed to find any anatomical evidence for stridulating abilities. Fage (1939) stated that he examined material of all species in the very complete collection of the Paris Museum and was unable to find evidence of a stridulating apparatus on any species except *M. atlanteus*. Thus it appears that *Acanthophrynus coronatus* is the second example to be discovered of a stridulating whip-scorpion.

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## DEFENSIVE BEHAVIOR OF HONEY BEES TOWARD ANTS<sup>1</sup>

BY HAYWARD G. SPANGLER AND STEPHEN TABER, III  
Entomology Research Division, Agr. Res. Serv., U.S.D.A.  
Tucson, Arizona 85719

Honey bees (*Apis mellifera* L.) often exhibit a unique behavior pattern in the presence of ants. We observed this behavior pattern and obtained evidence that it is induced by odors from the ants. Although the response was not limited to odors known to be produced by ants, its primary function is probably a defense against them.

*Iridomyrmex* is a genus of ants commonly associated with honey bee colonies, and the Argentine ant, *I. humilis* (Mayr), which occurs in the southeastern United States and in California, is a frequent pest (Newell and Barber, 1913). This ant lays scent trails. No alarm pheromone has been identified from it although Blum (1969) reported that one was released by crushing the gaster. Newell and Barber (1913) and Wilson and Pavan (1959) reported that disturbed workers of *I. humilis* did not release sufficient quantities of volatile substances to be detected by human observers, but we have detected a faint odor from workers crushed between fingers. In contrast, disturbed workers of *I. pruinosus analis* (Andre) emit a strong odor which to the human observer resembles 2-heptanone, an alarm pheromone isolated from *I. pruinosus* (Roger) (Blum et al., 1963) and also from the mandibular glands of older honey bees (Shearer and Boch, 1965; Boch and Shearer, 1967).

We studied the response of bees to two species of ants to determine whether the defensive behavior of honey bees might be initiated by odorous substances and alarm pheromones from an odorous ant (*I. pruinosus analis*) and also by ants which were comparatively odor free (*I. humilis*).

### THE DEFENSIVE BEHAVIOR PATTERN

Honey bees in a hive frequently were observed being approached by ants (*I. pruinosus analis*) running about on the landing board

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<sup>1</sup>This work was done in cooperation with the Arizona Agricultural Experiment Station.

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near the hive entrance. When the worker bees and ants approached each other, the bees initiated a characteristic behavior pattern that consisted initially of turning the posterior of the bees directly toward the ant. If the ant was directly ahead of the bee when detected, the rotation of the bee often approached 180°. During or immediately following this rotation, the bee fanned its wings vigorously. Also, simultaneously with the completion of rotation, the bee frequently kicked its hind legs rearward so they often struck the ant. The kicking action combined with air currents from the fanning wings often dislodged and moved the ant. This behavior pattern, repeated successively by a number of bees, effectively prevented the ants from entering the colony. Ants placed inside a bee colony on top of the brood comb frames were ordinarily removed from the colony in less than one hour. There was no evidence of the venom fanning behavior described by Maschwitz (1964).

#### CONDITIONING AS A FACTOR IN THE DEFENSIVE BEHAVIOR PATTERN

We conducted the following tests to determine whether bees that had not had recent or any contact with ants would respond with defensive behavior to ants or to an alarm pheromone. Twelve colonies were selected and arranged into groups of two each in a bee yard at Tucson, Arizona. These colonies were not opened for three days before testing.

Combs with honey were placed in locations where large numbers of worker *I. pruinosus analis* readily crawled into them to imbibe. Then the combs with the adhering ants were inserted in the brood nest in one of each group of two test hives. Three hours later, an observer who was unaware of which hives had been exposed to ants placed two  $3 \times 150$ -mm dowels on the tops of the brood frames in each of the 12 hives. One end of one of the dowels had been used to crush workers of *I. pruinosus analis*; the other dowel had no ant odor. The observer then counted the number of bees exhibiting defensive behavior patterns towards the dowels in each hive during a three-minute period. The entire procedure was repeated one week later, with the ants placed in the colonies that had not received them in the previous test. No defensive reactions to the control dowels were observed. A total of 379 responses to the dowels with crushed ant odor was observed in colonies previously conditioned to ants and 293 in colonies not preconditioned. When the data from both tests were lumped, the results (mean  $\pm$  standard error) indicated no significant change in the number of defense

responses by bees that had just previously contacted ants ( $31.6 \pm 5.6$ ) and those that had not ( $24.4 \pm 5.4$ ).

Other tests were conducted at a mountain apiary where *I. pruinosus analis* was not found. Dowels dipped  $\frac{1}{8}$  inch into 2-heptanone were placed on top of the brood combs. The bees immediately responded with the defensive behavior pattern. Thus previous experience with ants was not essential for the response.

#### COMPOUNDS RELEASING DEFENSIVE BEHAVIOR

To determine if the bees were responding to the odors of the ants, we tested several alarm and defensive secretions of ants by the same method. The bees responded with defensive behavior to the following compounds:

Compound	Ant	Reference
Benzaldehyde	<i>Veromessor pergandei</i> (Mayr)	Blum et al., 1969
2-heptanone	<i>Iridomyrmex pruinosus</i> (Roger)	Blum et al., 1963
Citral	<i>Acanthomyops claviger</i> (Roger)	Regnier and Wilson, 1968
Formic acid	<i>Formica</i> spp.	Wheeler, 1910

Other odorous compounds not known to be present in any ant (Blum, 1969) were selected and tested in the same manner, and all tested were found to release a positive response. These compounds were as follows:

Acetic acid	2-6 Dimethyl -4-heptanone
Propionic acid	Propanol
Acetic anhydride	Butanol
Propionic anhydride	

The bees also responded to both methyl and ethyl alcohols, but this response was reduced. Therefore, bees almost certainly respond to chemicals not found in ants in the same manner as they respond to those found in ants or to the ants themselves.

#### RESPONSES TO ANTS PRODUCING HIGH-ODOR AND LOW-ODOR

Because *I. humilis* can be a serious pest to bees and has a comparatively low level of odor to humans and because no alarm pheromones have been isolated from it, we suspected that the low odor might be the reason it can invade bee colonies with little

resistance. The previous tests had already shown that the bees readily responded to *I. pruinosus analis* and to 2-heptanone, an alarm pheromone of *I. pruinosus*.

*I. humilis* workers were obtained and placed on the wooden top bars of several brood combs. The responses of the bees to these ants were reduced both in frequency and vigor from the responses to *I. pruinosus analis*; the ants generally moved freely about beneath the bees. Occasionally a bee would detect one of these ants, usually by contacting it with its antenna. The bee then went through the described behavioral response, turning its body, fanning its wings, and kicking with the rear legs. Comparatively few of the bees which detected *I. humilis* turned a full 180 degrees. When *I. humilis* workers were crushed on wooden dowels which were also laid on the tops of brood frames, some response was noted, but again it was sharply reduced.

#### DISCUSSION

Honey bee workers responded readily to several compounds that are not associated with ants and to several that are. This defensive behavior pattern enables the bees to rid their colony of harmful pests so the response appears to be a defense mechanism against ants. It is unlikely that the compounds tested which are not associated with ants would enter a colony under normal conditions, and strong foreign odors in a hive would frequently, if not usually, result from the presence of ants.

Bees are successful in keeping practically all small odoriferous Dolichoderine, Formicine and Myrmicine ants out of their colonies. The fact that honey bees are apparently less able to detect and respond to ants which have little demonstrable odor indicates that the odors of the ants play a key role in their detection. Therefore, Argentine ants, *I. humilis*, which are probably nearly odorless to honey bees, have been able to invade and damage bee colonies and often cause colonies to abscond. Were the bees able to detect these ants as readily as they detect others, they would doubtless rid their colonies of them.

Boch et al. (1970) described the behavior of honey bees exposed to 2-heptanone at the hive entrance as "short jerks forward and in reverse." Thus, 2-heptanone can apparently release more than one type of response. They also reported evidence to support previous suggestions that the primary alarm pheromones of the honey bee are associated with the sting and that 2-heptanone may be more impor-

tant in some other function. Simpson (1966) reported that the mandibular gland secretion repelled honey bees when it was added to a dish of sucrose syrup. This repellency probably depends on the content of 2-heptanone in the mandibular glands (Butler, 1966).

Our study provides no evidence that the worker bees release their mandibular gland secretion when they detect ants. When the ant or odorous compound was removed, the defensive behavior stopped, and the bees resumed normal activity. This defensive response of honey bees toward ants described here may illustrate a situation where one species of insect appears to emit an alarm pheromone acting as a "Kairomone" (Brown et al., 1970) which releases defensive behavior for another species, and may also indicate that honey bees can react in several different ways to the same compound.

#### SUMMARY

Honey bees respond to ants and certain chemicals by turning away from the ants or chemicals, fanning the wings, and kicking the rear legs. This activity is believed to be a defense against ants invading the nest. Argentine ants are probably successful pests of bees because they apparently have a low level of odor.

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*HOPLITIS ANTHOCOPOIDES*,  
A EUROPEAN MASON BEE  
ESTABLISHED IN NEW YORK STATE  
(HYMENOPTERA: MEGACHILIDAE)

BY GEORGE C. EICKWORT<sup>1</sup>

*Hoplitis anthocopoides* (Schenck) (new combination for *Osmia anthocopoides* Schenck, 1853) was discovered in Albany County, New York State, in the summer of 1969 (Fig. 1). This bee is a common inhabitant of Central Europe and is found as far north as Scandinavia and as far south as Greece. In Europe, the bee is usually known as *Osmia spinolae* Schenck (e.g., Dalla Torre, 1896; Friese, 1926) or as *Osmia caementaria* Gerstaecker (e.g., Schmiedeknecht, 1884-85; Friese, 1923; Blüthgen, 1930). However, *spinolae*, the oldest name for the species, is preoccupied in *Osmia*, and the name *caementaria* is younger than *anthocopoides*, which has been rarely used in recent literature (e.g., Hedicke, 1930). Most European authors do not recognize *Hoplitis* as a separate genus and place *anthocopoides* and its relatives in *Osmia*.

*Hoplitis anthocopoides* is similar to *H. adunca* (Panzer), the type species of *Hoplitis* Klug and its synonym, *Ctenosmia* Thomsen. The species is thus a member of the nominate subgenus, which previously was restricted to the Old World. The subgenus (as *Ctenosmia*) was briefly described by Schmiedeknecht (1884-85).

Description

New York specimens fit the species descriptions of Gerstaecker (1869), Schmiedeknecht (1884-85), and Blüthgen (1930), and have been compared with European specimens by Dr. E. Staněk and are conspecific. The following notes, emphasizing the characters used by Michener (1947) to describe the American subgenera of *Hoplitis*, will distinguish *H. anthocopoides* from other American *Hoplitis*:

*Female*: Length 8.5-10.5 mm. Integument black. Pubescence generally white; scopa yellowish-white; metasomal (gastral) terga 1-5 with narrow white apical hair bands, often interrupted medially. In fresh specimens, dorsal pubescence light ochraceous. Head and thorax distinctly and closely punctate, punctures usually separated by less than their diameter. Clypeus (Fig. 2) strongly convex,

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<sup>1</sup>Department of Entomology and Limnology, Cornell University, Ithaca, New York 14850.

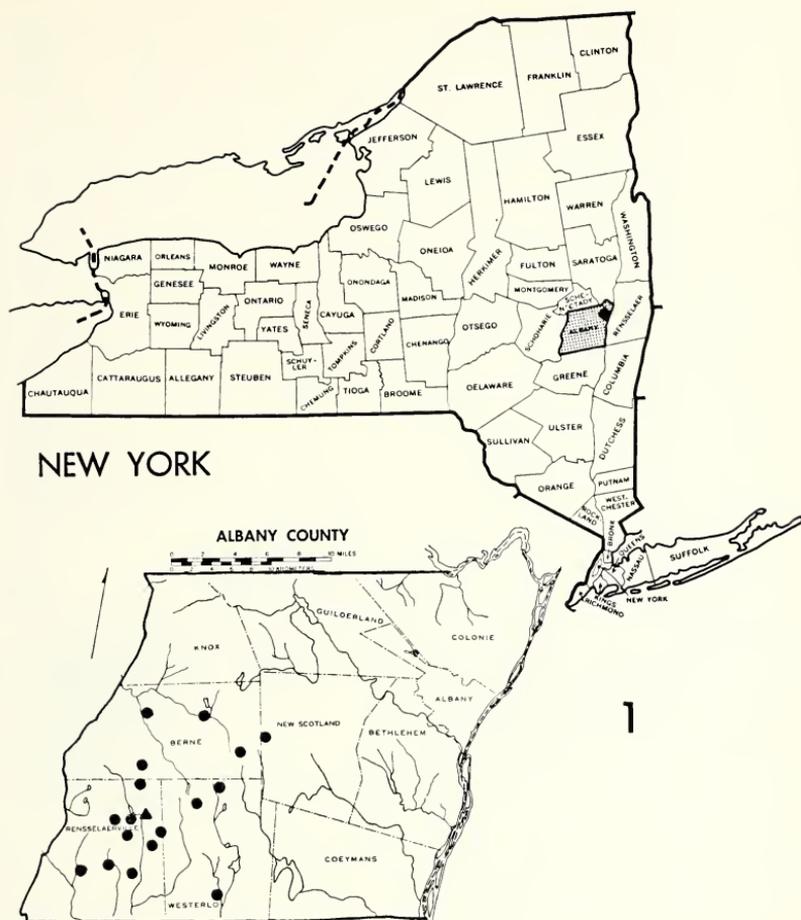


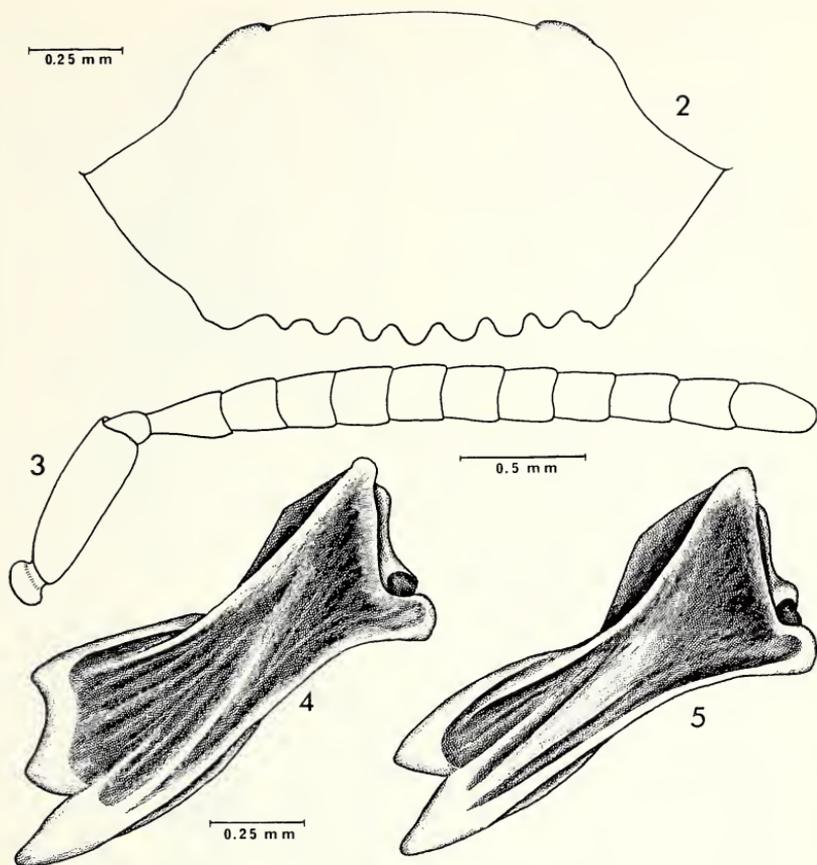
Fig. 1. Range of *Hoplitis anthocopoides* in New York State in 1969. Albany County shaded in state map, enlarged below. Circles, peripheral and important central collections of *H. anthocopoides*; triangle, Rensselaerville; diamond on state map, City of Albany.

closely and distinctly punctate to apex, apical margin truncate, crenulate, and only slightly projecting over base of labrum. Inner margins of eyes slightly convergent below; genae subequal in width to eyes in lateral view. Mandibles (Fig. 4) tridentate, long, narrowed medially. Mouthparts long; length of galea subequal to width of head; second segment of labial palp 1.5-1.7 times length of segment 1; third segment of maxillary palp longest, fifth segment slender. Antennae with flagellar segment 1 much longer than pedicel and subequal in length to segments 2 plus 3. Thorax robust, metanotum on posterior surface so that anterior part is lower than convexity of scutellum. Wings papillate distally. Metasoma (gaster) rather broad, length from dorsal margin of anterior concavity of first tergum 1.0-1.3 times maximum width, punctures not distinct; terga 1-5 without impunctate margins. Anterior surface of tergum 1 shallowly concave, impunctate, with longitudinal sulcus, sharply delimited from dorsal surface. Last visible (sixth) tergum concave in lateral view, impunctate rim slightly raised and shining; last visible (sixth) sternum unmodified.

*Male:* Length 8.0-10.0 mm. Pubescence long, white in older specimens, in young specimens dorsally and laterally more orange than in females. Clypeus with long hairs. Mandibles (Fig. 5) bidentate. Antennal scape (excluding basal bulb) 2.6-2.7 times longer than broad; pedicel mostly exposed; first flagellar segment 1.35-1.45 times as long as segment 2; flagellomeres flattened but segments not otherwise modified; terminal flagellomere rounded (Fig. 3). Posterior coxae unmodified. Metasomal tergum 6 laterally toothed, apical margin irregularly sinuate medially; tergum 7 projected to rounded truncate apex, with small teeth laterally (Fig. 6). Metasomal sterna 2-5 with low, transverse, submarginal swellings and without median projections; sternum 6 (Fig. 7) with bilobed median apical projection bearing dense patches of erect setae; sterna 7 and 8 as in Figures 8 and 9. External genitalia as in Figures 10 and 11.

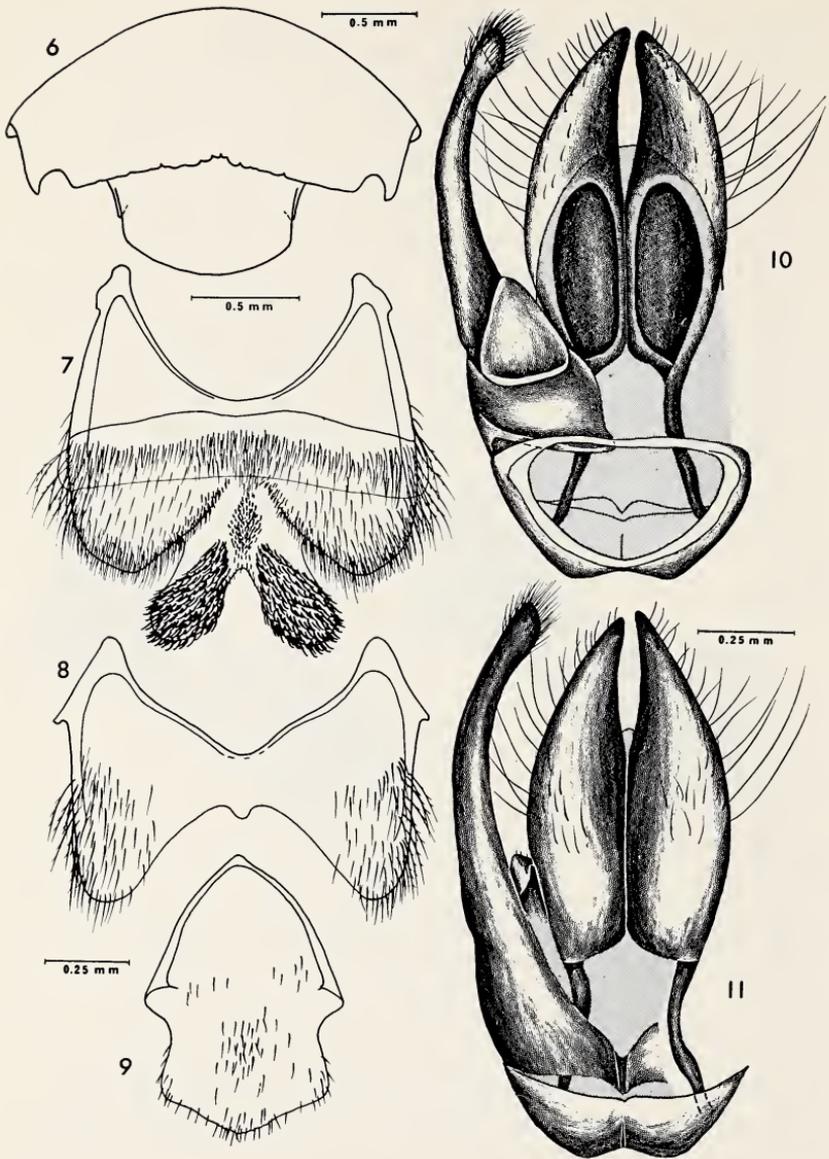
#### Position among the American subgenera of *Hoplitis*

Michener (1947) has revised the American subgenera and species of *Hoplitis*. In an account of the megachiline bees of California, Hurd and Michener (1955) revised Michener's key to the American subgenera, synonymizing 2 subgenera and including 2 taxa previously considered to be separate genera. In a numerical study of the American species in the *Hoplitis* complex of genera, Michener and



Figs. 2-5. *Hoplitis anthocopoides*. 2, clypeus of female; 3, antenna of male; 4-5, left mandibles, lateral view (4, female; 5, male).

Sokal (1957) removed 2 subgenera, *Hoplitina* and *Acrosmia*, from *Hoplitis* and placed them in the genus *Proteriades*. Michener (1968) has recently synonymized *Anthocopa* s.l. with *Hoplitis* s.l. If the subgenera of *Anthocopa* are now to be considered as subgenera of *Hoplitis*, there are currently 11 subgenera of native *Hoplitis*: *Andronicus*, *Monumetha*, *Dasyosmia*, *Cyrtosmia*, *Alcidamea*, *Formicapis*, *Robertsonella*, *Atoposmia*, *Hexosmia*, *Eremosmia*, and *Isosmia*. The Old World *Hoplitis* are more abundant and diverse than their American counterparts, and the genus is probably of Old World



Figs. 6-11. Metasomal structures of male *Hoplitis anthocopoides*. 6, terga 6 and 7; 7, sternum 6; 8, sternum 7; 9, sternum 8; 10-11, external genitalia (10, ventral view; 11, dorsal view).

origin (Michener, 1947). However, only one native American subgenus, *Alcidamea*, also contains Old World species. The genus is absent in the Neotropical region south of Mexico.

The above subgenera (except *Isosmia*, which was described as a subgenus of *Anthocopa* by Michener and Sokal, 1957) can be distinguished by means of the subgeneric keys to *Anthocopa* and *Hoplitis* in Hurd and Michener (1955). *Hoplitis* (*Hoplitis*), based on *anthocopoides*, runs to couplet 8 of Hurd and Michener's key to *Hoplitis* based on males, if the second alternative of couplet 6 is changed to read:

Seventh tergum produced to a pointed or truncate apex; antennae modified; scape often thickened, the flagellum flattened and the last segment often pointed; clypeus with the usual long hairs ..... 7

The remainder of the key should be changed as follows:

- 8(7) Antennal pedicel almost completely hidden in concavity at end of scape when antennae are in normal position; last antennal segment bent and drawn out to a point ..... *Alcidamea*  
 Antennal pedicel at least partly exposed; last antennal segment rounded, or if pointed as in *Alcidamea*, posterior coxae each with broad ventral tooth ..... 9  
 9(8) Seventh metasomal tergum produced to median point or tridentate; posterior coxae each with broad ventral tooth; Western ..... *Dasyosmia*  
 Seventh metasomal tergum produced to subtruncate apex (Fig. 6); posterior coxae unmodified; Northeastern ..... *Hoplitis* s.s.

In Hurd and Michener's (1955) key to subgenera of *Hoplitis* based on females, *Hoplitis* s.s. runs to couplet 7. The remainder of the key, excluding *Acrosmia* (now in *Proteriades*), can be changed as follows:

- 7(5) Mandibles short and broad, not narrowed medially and apices much narrower than eye; first flagellar segment of antennae subequal to pedicel ..... *Alcidamea*  
 Mandibles longer and narrowed medially (Fig. 4) or apices nearly as broad as eye; first flagellar segment longer than pedicel ..... 8  
 8(7) Clypeal margin not crenulate, impunctate; apices of mandibles nearly as broad as eye; Western ..... *Dasyosmia*  
 Clypeal margin crenulate (Fig. 2), punctate to apex; apices of mandibles much narrower than eye; Northeastern .... *Hoplitis* s.s.

Position among New York species of *Hoplitis*

Mitchell (1962) lists 6 native species of *Hoplitis* that are known from or might be expected to occur in New York State. Most are less robust and smaller than *H. anthocopoides*; only *H. cylindrica* (Cresson) and *H. truncata* (Cresson) typically overlap it in size. In Mitchell's key to the species of *Hoplitis* based on females, the second alternative of couplet 4 should lead to (*Hoplitis* s.s.) as well as to (*Alcidamea*), and should direct the user to 6a.

Couplet 6a may be inserted to follow 6 as follows:

- 6a(4) Apical margin of clypeus crenulate (Fig. 2); first flagellar segment of antennae subequal to 2 plus 3; mandibles long, narrowed medially (Fig. 4) . (*Hoplitis* s.s.) *anthocopoides* Schenck  
 Apical margin of clypeus not crenulate; first flagellar segment of antennae shorter than 2 plus 3; mandibles short and broad, not narrowed medially (*Alcidamea*) ..... 7

In Mitchell's key to the males, couplet 4 should be modified as follows:

- 4(2) Small (8 mm or less); antennae filiform, median segments narrow and elongate; abdominal tergum 7 simple, broadly rounded (*Robertsonella*) ..... 5  
 Larger (8 mm or more); antennae modified, median segments not much longer than broad; abdominal tergum 7 produced to pointed or truncate apex ..... 7

*Hoplitis anthocopoides* then runs to couplet 8, which should be changed as follows:

8. Clypeus with appressed tomentum; margins of abdominal sterna 1 and 2 with slender median spines .....  
 ..... (*Monumetha*) *albifrons* Kirby  
 Clypeus with long erect pubescence; margins of abdominal sterna 1 and 2 without spines ..... 9  
 9. Apical segment of antennae curved, tapering to a point; pedicel nearly concealed by scape ..... (*Alcidamea*) *truncata* Cresson  
 Apical segment of antennae straight, rounded; pedicel largely exposed (Fig. 3) ..... (*Hoplitis* s.s.) *anthocopoides* Schenck

## Distribution and Biology

In Europe, *Hoplitis anthocopoides* collects pollen exclusively from 2 species of blue-flowered Boraginaceae, *Echium vulgare* Linnaeus

and occasionally *Anchusa officinalis* Linnaeus. Both plants have been introduced into eastern North America, where *Echium*, known as viper's bugloss or blueweed, has become a common weed on disturbed sites with poor rocky or sandy soil. In the area southwest of Albany, New York, *Echium* is found principally along roadsides, on gravel beds along streams, in slate quarries, and in overgrazed pastures. I observed that the female bees collect pollen only from *Echium vulgare* (*Anchusa* was not found there); moreover, both sexes visit only *Echium* for nectar.

This oligotrophy allowed us to accurately plot the range of *H. anthocopoides* by examining roadside stands of *Echium*, whose distinctive appearance can be easily recognized from a slowly moving automobile. Peripheral and important central collections of the bee are indicated by circles on the Albany County map in Figure 1. All of these sites are on the Helderberg Plateau, an extension of the Catskill Mountains largely covered by second-growth woodlands and pastures. The bee is most abundant to the southwest of Rensselaerville (center of operations for this study, indicated by a triangle in Fig. 1), where extensive rocky pastures provide both nest sites and abundant *Echium*. To the north, the Helderberg Plateau drops precipitously to the Mohawk River valley, where *Echium* is almost completely absent. To the south, the plateau descends more gradually to the Catskill Creek valley, where *Echium* is also scarce. *Hoplitis anthocopoides* was represented by few specimens in most peripheral collecting sites, sometimes only by a single male, despite intensive searching. The bee was not found in patches of *Echium* beyond the indicated range and was also consistently absent from some patches within its range boundaries. The extent of the range towards the Hudson River in the east, and especially towards Schoharie County in the west, may not be accurate since I was not able to cruise many roads in those areas before the end of the bee's flight season.<sup>2</sup> However, a collecting trip through Schoharie County to Otsego County during flight season produced no *H. anthocopoides* at apparently suitable stands of *Echium*.

In Europe, *H. anthocopoides* is well known for the mortar-and-pebble nests it builds on the surfaces of boulders (see especially Gerstaecker, 1869; Torck, 1913; Friese, 1923; and Jøker, 1942).

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<sup>2</sup>Note added in proof: In 1970 *H. anthocopoides* was found throughout most of Albany County, east to the Hudson River, and west 10 miles into Schoharie County. This range extension probably represents previously established populations in areas not searched in 1969.

These nests are constructed very similarly to those of the famous European mason bees of the genus *Chalicodoma*, and I propose that we also use the vernacular name "mason bee" to refer to *H. anthocopoides* and related *Hoplitis* (*Hoplitis*) with similar habits. My study of its nesting behavior in New York will be presented in a future paper.

None of the native American *Hoplitis* whose biologies have been investigated are mason bees. All but one species build rows of cells, one above the other, in tubular holes in dead stems or tree trunks (reviewed by Michener, 1947, and Hurd and Michener, 1955). The one exception, *H. (Dasyosmia) biscutellae* (Cockerell), has been recorded as nesting in soil by Linsley and MacSwain (1943) and reusing mud-dauber (*Sceliphron*) nests by Stephen, Bohart, and Torchio (1969). However, some American *Osmia* build exposed nests on rock surfaces (Stephen, Bohart, and Torchio, 1969), including at least one species at Rensselaerville.

Freshly emerged males and females of *H. anthocopoides* were first seen on June 14. Adults are common to the latter part of July, when they taper off, and are rare after August 1. The last adult was seen on August 19.

#### Discussion

Megachilid bees have frequently been transported long distances by man, probably because their nests are often concealed in the stems and crevices of plants and other articles of commerce. In the United States, 5 Old World species other than the mason bee have been introduced in historical times (Mitchell, 1962; Jaycox, 1967). *Megachile rotundata* (Fabricius) and *M. concinna* Smith are now both widespread in this country, and the former species has been semi-domesticated for alfalfa seed production in the Pacific Northwest. *Megachile concinna* presumably reached this country from the West Indies after World War II, and had probably reached the West Indies from Africa in the early 19th century. *Megachile apicalis* Spinola has been recorded several times from eastern North America but may not be established. *Chalicodoma lanata* (Fabricius) was apparently introduced into the West Indies with the slave trade, and has recently been found in southern Florida. The most recent introduction has taken place around Ithaca, New York, about 120 miles from the range of *H. anthocopoides*, where the European *Anthidium manicatum* (Linnaeus) was first collected in 1963 (Jaycox, 1967). This species is common in the Ithaca area and

is extending its range (L. Pechuman, personal communication). In addition, 4 other North American megachilid bees, *Osmia coerulescens* (Linnaeus), *O. inermis* (Zetterstedt), *O. nigriventris* (Zetterstedt), and *Megachile centuncularis* (Linnaeus); also occur in the Old World (Mitchell, 1962), and may have been accidentally introduced by man before records were kept.

All of the introduced megachilids except the mason bee are polylectic, although they show preferences for certain flowers and frequently visit plants of European origin (Hurd, 1954; Stephen and Torchio, 1961; Pechuman, 1967). *Hoplitis anthocopoides* is the first oligolectic bee of any family to accidentally follow its host plant to the United States. The host is a widespread and common weed and the nest sites are abundant and rarely used by native bees. There is little doubt that *H. anthocopoides* will extend its range over much of eastern North America. Since even vanguard mason bees can be easily detected on roadside stands of viper's bugloss, its range extension can be followed more exactly than that of any other introduced species. I urge entomologists in the Northeast to be on the watch for the mason bee.

#### Summary

*Hoplitis (Hoplitis) anthocopoides* occupied a 25 mile diameter range in the Helderberg Plateau of Albany County, New York, in 1969. It is the first species of the nominate subgenus to occur in the Western Hemisphere. The bee is described and distinguished from other American *Hoplitis*, and Hurd and Michener's key to the American subgenera and Mitchell's key to the Eastern species of *Hoplitis* are modified to include *H. anthocopoides*. The mason bee builds exposed mortar-and-pebble nests on surfaces of rocks and visits only the introduced weed *Echium vulgare* for pollen and nectar.

#### Acknowledgments

I am grateful to the Edmund Niles Huyck Preserve of Rensselaerville, New York, which awarded a summer research fellowship to my wife and myself and provided the facilities which made this study possible. I thank Dr. Eduard Staněk of Uherský Brod, Czechoslovakia, for providing an unpublished description of *H. anthocopoides* and many helpful comments, and for comparing New York specimens with European ones. The Cornell University insect collection provided European specimens of "*Osmia caementaria*" that first enabled me to identify the bee. I thank Dr. LaVerne L.

Pechuman and Dr. John G. Franclemont of Cornell University for critically reading the manuscript. Finally, I express my appreciation to my wife, Kathleen, who aided in collecting the bees, provided constant encouragement, and offered suggestions on the manuscript.

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STEATODA FULVA (THERIDIIDAE), A SPIDER  
THAT FEEDS ON HARVESTER ANTS\*

BY BERT HÖLDOBLER

Harvard University, Biological Laboratories  
Cambridge, Massachusetts 02138

In his revision of the spider genera *Crustulina* and *Steatoda* H. W. Levi says of the *Steatoda fulva*-group [*Steatoda fulva* (Keyserling); *S. medialis* (Banks); *S. pulcher* (Keyserling)]: "Virtually nothing is known of the natural history of these three species" (1957, p. 387). The present paper places on record some preliminary observations on the feeding behavior of *Steatoda fulva*, which were made during the course of field experiments with ants in April 1970 near the campus of the University of South Florida, Tampa.

The study area, a field of 135 m<sup>2</sup>, contained 54 nests of the harvester ant *Pogonomyrmex badius* (Latreille). The nests were uniformly distributed throughout the area. They are excavated in the soil; the nest opening is located in the center of a flat sand crater (Fig. 1). On 10 occasions webs of *Steatoda fulva* were found in front of the nest entrance. Observations throughout the day showed that the webs were probably built and occupied only during the afternoon. The webs were attached to dry grass stems around the nest entrances and contained from 2-6 trapped ant workers when found (Fig. 2). The fact that *Steatoda fulva* is able to build its web so close to the nest entrance is surprising because the ants are constantly running in and out of the nest and react aggressively to any foreign animal. However this is understandable when one compares the activity of the ants on a hot day with the timing of the spider's predatory behavior. During April the *Pogonomyrmex* began to open the nests about 8 AM. Movement to and from the nest soon increased, reaching its maximum between 11:00-12:00 AM, then decreased and by 14:00 had ceased almost completely. Generally nests became active again about 15:00, reaching a second maximum about 17:00. The ants returned to their nests before sunset and outside activity had ceased by 19:00 (Fig. 3). Apparently it is during the early afternoon, when temperatures are high and the ants are inactive, that *Steatoda fulva* is able to approach the nest entrance. Ant nests that are blocked by a spider's web show no

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\*Manuscript received by the editor, August 3, 1970.



Fig. 1. Nest crater of a *Pogonomymex badius* nest.



Fig. 2. Web of *Steatoda fulva* in front of the entrance of the *Pogonomrmex* nest. Five captured ants and the spider are in the web.

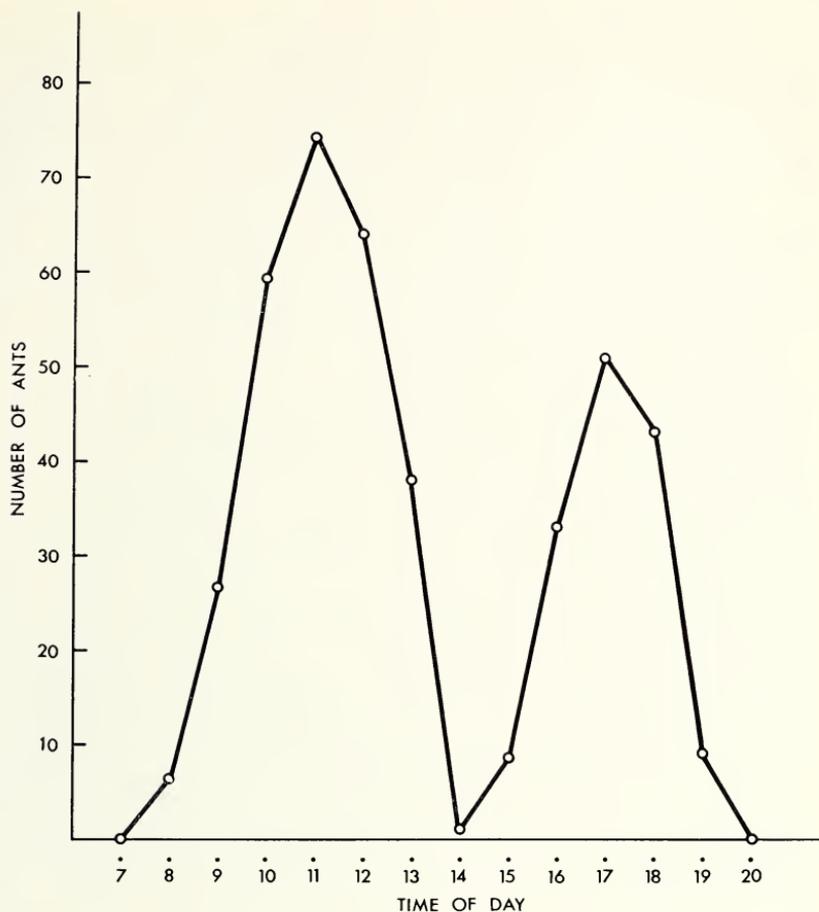


Fig. 3. Activity of *Pogonomyrmex badius* at the nest entrance on April 11, 1970, near Tampa, Florida. Abscissa: average number of ants passing through nest entrance during 5 one minute observation periods. Ordinate: time of day.

late afternoon activity. On one occasion a nest was observed soon after the web was erected. The first few ants to come out of the nest were captured in the silk. They struggled and probably discharged the mandibular gland alarm secretion (Wilson, 1958) as they elicited help from nestmates. However even giant soldiers were unsuccessful in their attempts to remove the cobweb and

finally shrank back from the sticky silk. After about 30 minutes the ants began to close the entrance from within. No more ants emerged. Up to this point the spider remained in one corner of its web. As soon as the ants withdrew into the nest, the spider wrapped its captives with more silk and then began to suck them out, one after another (Fig. 4).

The entrance of the ants' nest remained closed. After three days a new entrance was found about 1 m from the previous one. It would seem therefore that the spider can prey only once at a given entrance. Further observations on other harvester ant hunting *Steatoda fulva* were essentially the same.

As mentioned before, we found *Steatoda fulva* with *Pogonomyrmex badius* on 10 occasions. Once a *S. fulva* was seen at the entrance of the fungus growing ant *Trachymyrmex septentrionalis* (McCook). However this exception seemed to be an accident as this very small *Trachymyrmex* nest opened within a *Pogonomyrmex* nest crater and the entrances were only 15 cm apart. Thus it might be that the spider, attracted by the *Pogonomyrmex* nest area, chose the wrong entrance.

Clearly, it would be most interesting to investigate the signals by which the spider locates its prey and the nest entrance. Pilot experiments in an olfactometer arena have shown that hungry spiders orient towards a slight air current which carries the odor of *Pogonomyrmex* workers rather than an odorless air current. It is not yet known whether the spider reacts to only specific ant odors, but it is remarkable that the distribution of *Steatoda fulva* (Levi, 1957) coincides very well with the range of the genus *Pogonomyrmex* (Cole, 1968).

The related *Steatoda albomaculata* (De Geer) [= *Lithypantes albomaculatus*] also often feeds on ants (Levi, 1957).

#### ACKNOWLEDGEMENTS

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Fig. 4. *Steatoda fulva* eating captured *Pogonomymex badius*.

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ERRATUM. — In my paper on "A New Flightless *Dolichoctis* (Coleoptera: Carabidae) from Sumbawa," in *Psyche*, Vol. 76, No. 4, pages 387-389, the name *terrestris* in the next to the last line on page 388 is a *lapsus calami*. This name should be struck out and the name *pedestris* substituted. — P. J. Darlington, Jr., Museum of Comparative Zoology.

STUDIES OF THE MEXICAN SUBGENUS *PLATYNELLA*  
CASEY (COLEOPTERA: CARABIDAE: AGONINI)<sup>1</sup>

BY THOMAS C. BARR, JR.

Department of Zoology, University of Kentucky, Lexington

Studies of the Mexican cave carabids of the genus *Mexisphodrus* (Barr, 1965, 1966) led me to a comparison of its species with *Bolivaridius*, described as a genus of sphodrines by Straneo (1957), and *Platynella*, described as a subgenus of *Anchomenus* by Casey (1920). It is probable that neither *Bolivaridius* nor *Mexisphodrus* are "true" sphodrines in the final analysis, since both have the simple right paramere of subtribe Agoni rather than the elongate ones characteristic of the European and Asiatic sphodrines. *Mexisphodrus* does have a sharply truncate, triangular prosternal base similar to that of the sphodrines, but *Bolivaridius* does not. However, the truncate prosternum is also found in a number of other Mexican and Central American "*Colpodes*", and *Mexisphodrus* is perhaps best regarded as allied with other American species.

*Mexisphodrus tlamayaensis* (Barr, 1966), a winged species with a predilection for caves (San Luis Potosi, Tamaulipas, Veracruz), should probably be excluded from *Mexisphodrus* until a thorough study of the American colpodines has been made; it has the truncate prosternum and colpodine tarsi of *Mexisphodrus* but not the same habitus. Described as piceous in color, it acquires a dark, bluish-black pigment in some habitats, and is doubtless related to some of the species described as *Colpodes* by Chaudoir.

*Platynella* and *Bolivaridius* share the same generally somber color, vestigial wings, and elongate, subconvex form of *Mexisphodrus*, but lack the truncate prosternum and the bilobed 4th metatarsal segment of the latter. The descriptions of these two groups are surprisingly similar, not only to each other but also to the description of *Anchomenus montezumae* Bates (1878). Thanks to my colleague, Dr. Candido Bolívar y Pieltain, Instituto Politecnico Nacional, Mexico City, I was able to examine topotypes of *Bolivaridius tolucensis* and a paratype of *B. ovatellus*, and to compare them with two specimens of *Anchomenus montezumae* lent to me from the Biologia Centrali-Americana collection by Dr. R. B. Madge, Commonwealth Institute of Entomology, British Museum. Casey's types and associated speci-

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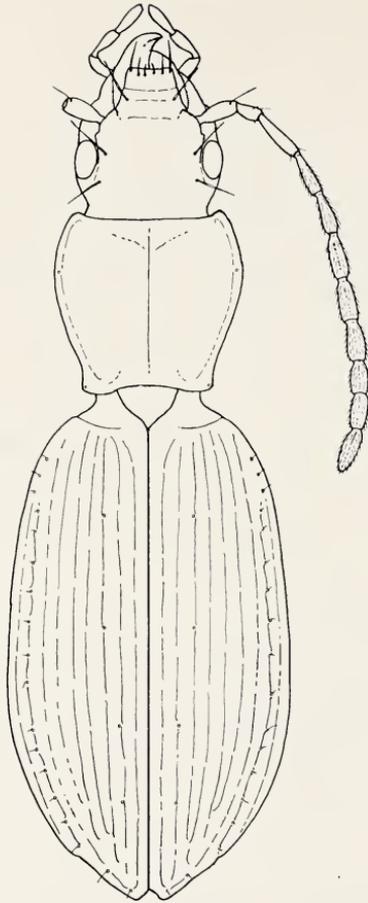


Fig. 1. *Agonum* (*Platynella*) *montezumae* (Bates), length 11.6 mm. Esperanza, Puebla.

mens of *Platynella* were studied at the United States National Museum. Dr. George E. Ball, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada, lent me eight specimens from his extensive collection of Mexican carabids and made valuable comments on an early draft of this paper. Senor Jorge Hendrichs S., Mexico City, clarified the locations of the older collecting sites.

It is now evident that *Bolivaridius* is a junior synonym of *Platynella*, and that *B. ovatellus* is a synonym of *Anchomenus* (*Platynella*)

*districtus* Casey. *A. montezumae* is closely similar to *A. districtus*, and should be transferred to *Platynella*. In the present unsatisfactory state of classification of Mexican and Central American agonines, I believe it is best to leave *Platynella* a subgenus of *Agonum*, in the widest sense.

### *Agonum* Bonelli

#### Subgenus *Platynella* Casey

Casey, 1920, p. 23; no type designated, *Anchomenus* (*Platynella*) *districtus* Casey herewith designated.

*Bolivaridius* Straneo, 1957, p. 81; type species, *B. toluensis* Straneo, by original designation. NEW SYNONYMY.

*Description*: Length 9-14 mm; color piceous or dark purplish piceous to ferruginous; form subconvex, legs long and slender; microsculpture of head isodiametric, of pronotum transverse, of elytra, which are dull shining, intensely isodiametric, subgranular. Eyes small to moderate, tempora distinctively inflated behind eyes. Pronotum with sides feebly rounded in apical  $1/4$  to  $1/3$ , then oblique and very feebly sinuate to the obtuse, sometimes minutely denticulate hind angles, margins moderately to strongly reflexed; pronotum  $3/4$  as long as wide to nearly as long as wide; base trisinate, rounded behind the angles; anterior angles moderate to very prominent; with two pairs of slender, fragile setae in pronotum margin, probably always present in life but apparently easily broken off in dried specimens. Elytra with apices briefly and individually produced, rounded, or bluntly angular; umbilicate series on 8th stria with about 15-17 punctures; usually with four minute, non-setiferous discal punctures on 3rd interval, the first two touching either the 3rd or 2nd stria, the posterior two touching the 2nd stria, first two absent in one species (*toluense*). Antenna rather short, with outer seven segments gradually and progressively compressed, dense pubescence beginning on apical  $3/4$  of fourth segment. Tarsi with 4th segment not lobed on any of the legs, glabrous above, setose beneath, including 5th segment of metatarsus; tarsi strigose or smooth above, according to species (strigose in three of the seven known species). Mentum tooth prominent, truncate at the tip. Base of prosternum not sharply truncate. Metathoracic wings vestigial, more or less micropterous. Aedeagus with small basal bulb and small proximal orifice, median lobe arcuate and swollen, apex pointed and briefly attenuate, distal orifice large and opening asymmetrically to the left, the complexly folded internal sac protruding; internal sac with numerous small spines but without

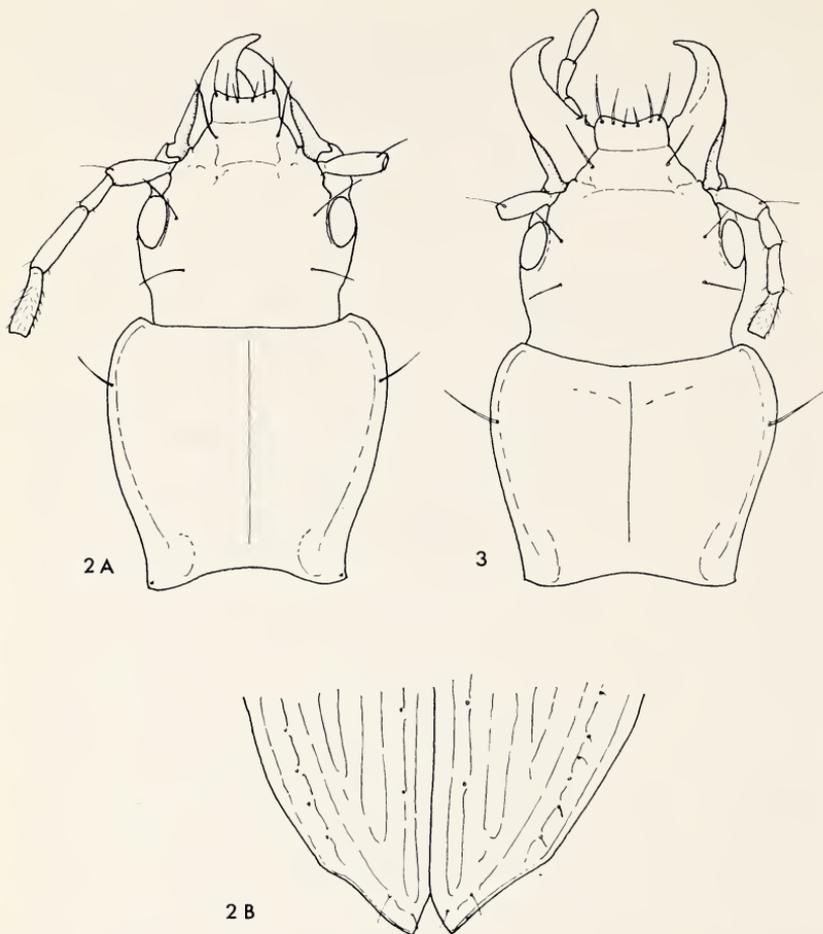


Fig. 2. *Agonum (Platynella) districtum* (Casey). Zempoala, Morelos. A. Head and pronotum. B. Apices of elytra.

Fig. 3. *Agonum (Platynella) toluicense* (Straneo), head and pronotum. Nevado de Toluca, Mexico.

conspicuous sclerites; parameres conchoid, the right smaller. Type species of subgenus: *Anchomenus (Platynella) districtus* Casey (1920, p. 24), here designated.

*Discussion:* *Platynella* appears to be limited to the central highlands of Mexico, along the Sierra Volcanica Transversal from Michoacan to Veracruz. I have not studied Casey's four species with

smooth tarsi (Casey, 1920, pp. 24-26) except to note that they are apparently valid species and probably belong in *Platynella* rather than in some other subgenus. Three of them — *logicus*, *morelosensis*, and *infidus* — were described from Huitzilac (= "Tres Marías"), Morelos, and were presumably collected by Wickham at the same time he collected *districtus*. These three species closely resemble *districtus* in superficial appearance and body proportions. *Platynella baroni* Casey, a more aberrant species, was described from "Guerrero" without indication of the precise locality. The species with strigose tarsi may be differentiated by the following key.

Key to Species of *Agonum* (*Platynella*) with Strigose Tarsi

1. Pronotum nearly as long as wide; third interval of elytron with four minute punctures ..... 2  
 Pronotum 3/4 as long as wide; third interval of elytron with two minute punctures against 2nd stria in apical third .....  
 ..... *tolucense* Straneo
- 2(1). Eye diameter less than length of scape; pronotum margins strongly reflexed; apices of elytra angulate .....  
 ..... *districtum* Casey
- Eye diameter and scape length subequal; pronotum margins moderately reflexed; apices of elytra less produced and not sharply angulate ..... *montezumae* Bates

*Agonum* (*Platynella*) *districtum* (Casey), new combination

Figures 2A, 2B, 5

*Anchomenus* (*Platynella*) *districtus* Casey, 1920, p. 24, type from Tres Marías (=Huitzilac), Morelos, Mexico, in U. S. National Museum.  
*Bolívaridius ovatellus* Straneo, 1957, p. 82; type from Zempoala National Park, Morelos (Huitzilac township), Mexico, in coll. Bolívar, Instituto Politécnico, Mexico. NEW SYNONYMY.

Length of five specimens 11.3-12.1 mm; one of Straneo's specimens was recorded as 14 mm long. Color dark ferruginous, dull shining. Pronotum more than 0.9 as long as wide, greatest width in apical fourth, very shallowly sinuate in basal fourth, margins strongly reflexed; with a pair of anterior marginal setae, the posterior absent in some specimens but probably merely broken off. Eycs small, their diameter less than the length of the scape; tempora behind the eyes longer than eye diameter. Elytra with four discal punctures, apices angulate, sharper than in the two following species. Aedeagus of a paratype of *ovatellus* 1.85 mm long, basal bulb rather long with moderately prominent keel, median lobe arcuate, apex slender and produced.

*Distribution*: Known only from three localities. *Morelos*: Huitzilac (known as Tres Marias until 1930, according to J. Hendrichs, *in litt.*); Zempoala National Park (Bolívar, May, 1940, in coll. Bolívar, I.P.N., Mexico). *Michoacan*: "1.1 mi. S. Angahuan, cornfield, edge of lava flow, 7300'", August 14, 1967 (Ball, Erwin, and Leech, in coll. G. Ball, University of Alberta, Edmonton, Alberta, Canada). At Zempoala, which is about 7 kilometers west from Huitzilac, the beetles occurred in a forest of *Abies* and *Pinus* at an elevation of 2800-3000 meters. The village of Huitzilac, located at kilometer 53 on the Mexico City-Cuernavaca highway, is near an old volcano (Tres Cumbres) with three peaks which overlooks the valley of Cuernavaca east of the village. The Wickham specimens in the Casey collection were probably collected around this mountain.

*Agonum (Platynella) montezumae* (Bates), new combination  
 Figures 1, 4A, 4B, 4C

*Anchomenus montezumae* Bates, 1878, p. 593; type from vicinity of Mexico City, in British Museum (Natural History).

*Platynus montezumae*: Bates, 1882, p. 92, pl. 4, fig. 24.

*Laemostenus (s. str.) montezumae*: Csiki, 1931, p. 812.

Length of six specimens 9.3-13.6, mean 11.6 mm. Color and general form as in *districtum* but a little more slender, humeri more sloping away from the base. Eyes larger, their diameter equal to either length of scape or length of tempora behind. Pronotum similar but margins much less strongly reflexed. Elytral apices feebly produced, rather blunt, not sharply angulate as in *districtum*. Aedeagus of a specimen from Esperanza (Puebla) 1.60 mm. long, a little smaller and less arcuate than in *districtum*, basal bulb not distinctly narrower than median lobe.

*Distribution*: The three localities from which Bates (1882) reported this species are (1) "near the capital (Flohr)"; (2) "Cumbre del Pelado, San Antonio de Arriba (Salle)", approximately kilometer 37 on the Mexico City-Cuernavaca highway (J. Hendrichs, *in litt.*); and (3) "Esperanza (Höge)", presumably in the state of Puebla. I have seen specimens from the last two localities. Professor Ball's material (in coll. G. Ball, University of Alberta, Edmonton, Alberta, Canada) includes three specimens from "Tlachichuca, Puebla, 8300'", May 29, 1966 (Ball and Whitehead); and two specimens from the Cofre de Perote, "N. slope 10.0 mi. S. Las Vigas, 9600'", August 24, 1967 (Ball, Erwin, and Leech). The Tlachichuca "specimens from the vicinity of Mt. Orizaba were collected in a cornfield" (G. E. Ball, *in litt.*).

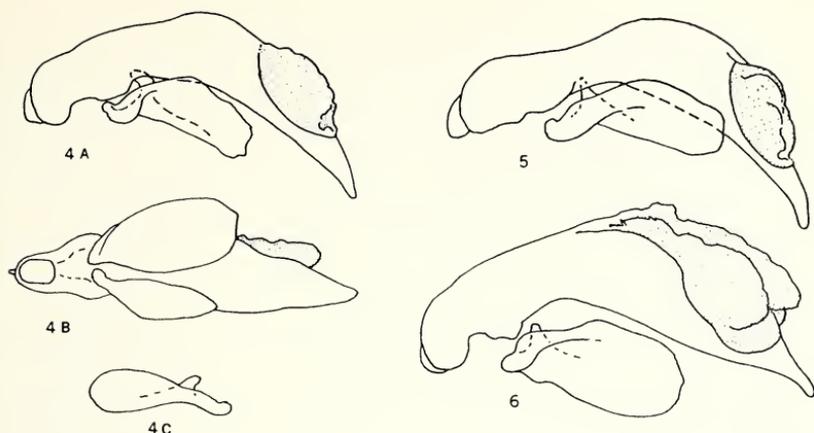


Fig. 4. Aedeagus of *A. (P.) montezumae* (Bates), length 1.60 mm. A. Left lateral view. B. Ventral view. C. Right paramere.

Fig. 5. Aedeagus of *A. (P.) districtum* (Casey), length 1.85 mm, left lateral view.

Fig. 6. Aedeagus of *A. (P.) toluense* (Straneo), length 1.95 mm, left lateral view.

*Agonum (Platynella) toluense* (Straneo), new combination  
Figures 3, 6

*Bolivariidius toluensis* Straneo, 1957, p. 81; type from the Nevado de Toluca, state of Mexico, Mexico, in coll. Bolívar, I. P. N., Mexico.

Length of six specimens 10.6-11.5, mean 11.0 mm. Color rather pale piceous, elytra dull shining, pronotum shining (microsculpture locally obsolescent, leaving small patches on disc). Eye diameter less than either length of scape or length of the tempora behind. Pronotum transverse, only  $\frac{3}{4}$  as long as wide. Elytra depressed, with only the two posterior discal punctures present, on third interval against 2nd stria; apices rounded. Aedeagus of a topotype 1.95 mm, larger than in the other two species.

*Distribution:* Known only from the Nevado de Toluca, in the state of Mexico, where it is reported to be moderately abundant at altitudes of 4100-4300 meters.

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THE MALE GENITALIA OF BLATTARIA.  
III. BLABERIDAE: ZETOBORINAE.

BY LOUIS M. ROTH  
Pioneering Research Laboratory  
U. S. Army Natick Laboratories  
Natick, Massachusetts 01760

In this paper I shall illustrate and characterize the male genitalia of 9 genera of blaberids which belong in the subfamily Zetoborinae. These genera are *Capucina* Saussure, *Lanxoblatta* Hebard, *Phortioeca* Saussure, *Phortioecoides* Rehn, *Schistopeltis* Rehn, *Schizopilia* Burmeister, *Tribonium* Saussure, *Zetobora* Burmeister, and *Zetoborella* Hebard. Princis (1960) includes *Tribonoidea* Shelford in this subfamily but I have been unable to obtain a male of the one species in this genus.

The male genitalia of most species of Blaberidae are characterized by the presence of three phallomeres: a median sclerite, a sclerite on the left, and a retractable hook on the right side. This led McKittrick (1964, p. 72) to conclude that "The male genitalia are extraordinarily uniform throughout the Blaberidae." She also stated (1964, p. 35) that "The male genitalia differ slightly in hook shape and the configuration of the posterior tip of the median sclerite within the Blaberidae, but otherwise show little variation within that group," and on p. 110 "The great uniformity of blaberid male genitalia precludes drawing many conclusions regarding subfamily relationships, except in the case of the Blaberinae and Panesthiinae." "The great uniformity" of the male genitalia of Blaberidae is generally true only for the usual presence of three distinct phallomeres; in certain genera one or more of the phallomeres may be greatly reduced and even absent (e.g. R2 in *Panchlora*). However, the shapes of the phallomeres, especially the retractable hook (R2), prepuce, and L2d are often so distinctive that they may show subfamily, tribal, generic, species Group characteristics, and in some genera may be used for specific determination (Roth and Gurney, 1969; Roth, 1969, 1970).

MATERIALS AND METHODS

The technique for preparing the genitalia has been described in previous papers (Roth, 1969, 1970). The source of each of the specimens illustrated is given, using the following abbreviations: (ANSP) = Academy of Natural Sciences, Philadelphia; (BMNH) = British

Museum (Natural History), London; (CUZM) = Copenhagen University, Zoological Museum, Denmark; (MCZ) = Museum of Comparative Zoology, Harvard University; (N) = Natick culture, U. S. Army Natick Labs., Massachusetts; (USNM) = United States National Museum, Washington, D.C.

Geographical collection data, and the names of specialists who identified the specimens, if known, follow these abbreviations. The number preceding the abbreviations refers to the number assigned the specimen and its corresponding genitalia (on a slide) which are deposited in the museums indicated.

### RESULTS AND DISCUSSION

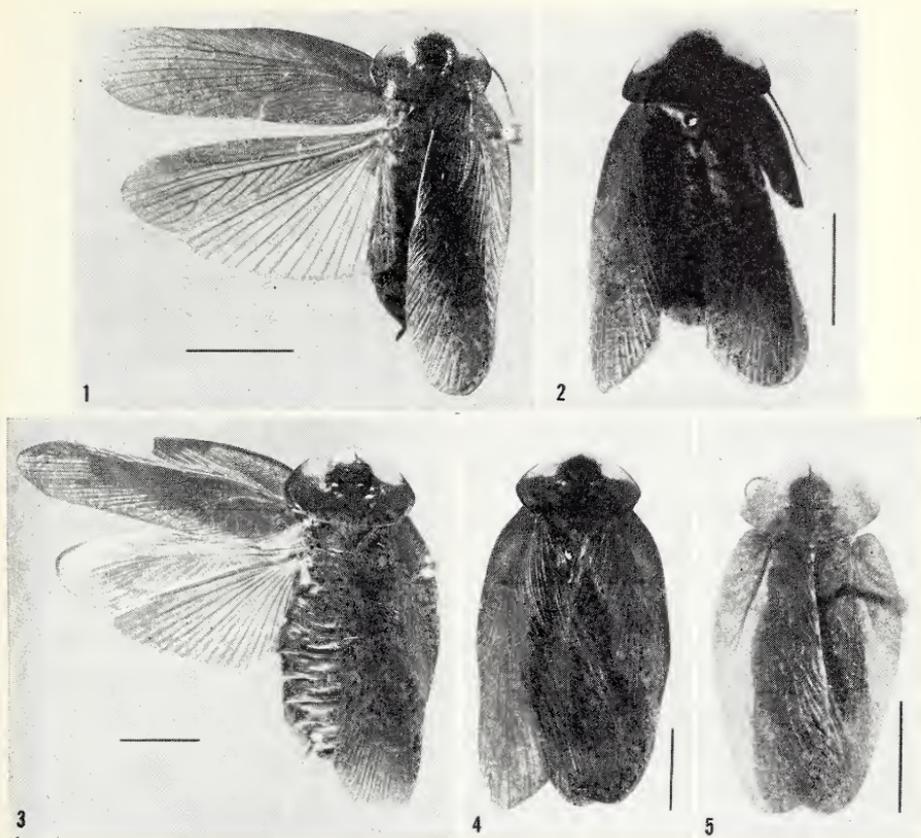
The basic features of the 3 phallomeres of the male genitalia of Zetoborinae are as follows: R2 (hooked right phallomere) is well developed and usually has a subapical incision (Fig. 32). The preputial membrane has a heavily sclerotized area (L2d) which extends dorsally or dorsolaterally to the right of L2vm (Fig. 28); L2d is flattened in the preparations and it should be remembered that it usually extends dorsally. L1 is very well developed and various areas are darkly sclerotized (Fig. 30).

Based on the degree of development of L2d and shape of L2vm, the Zetoborinae may be divided into 3 Tribes as follows:

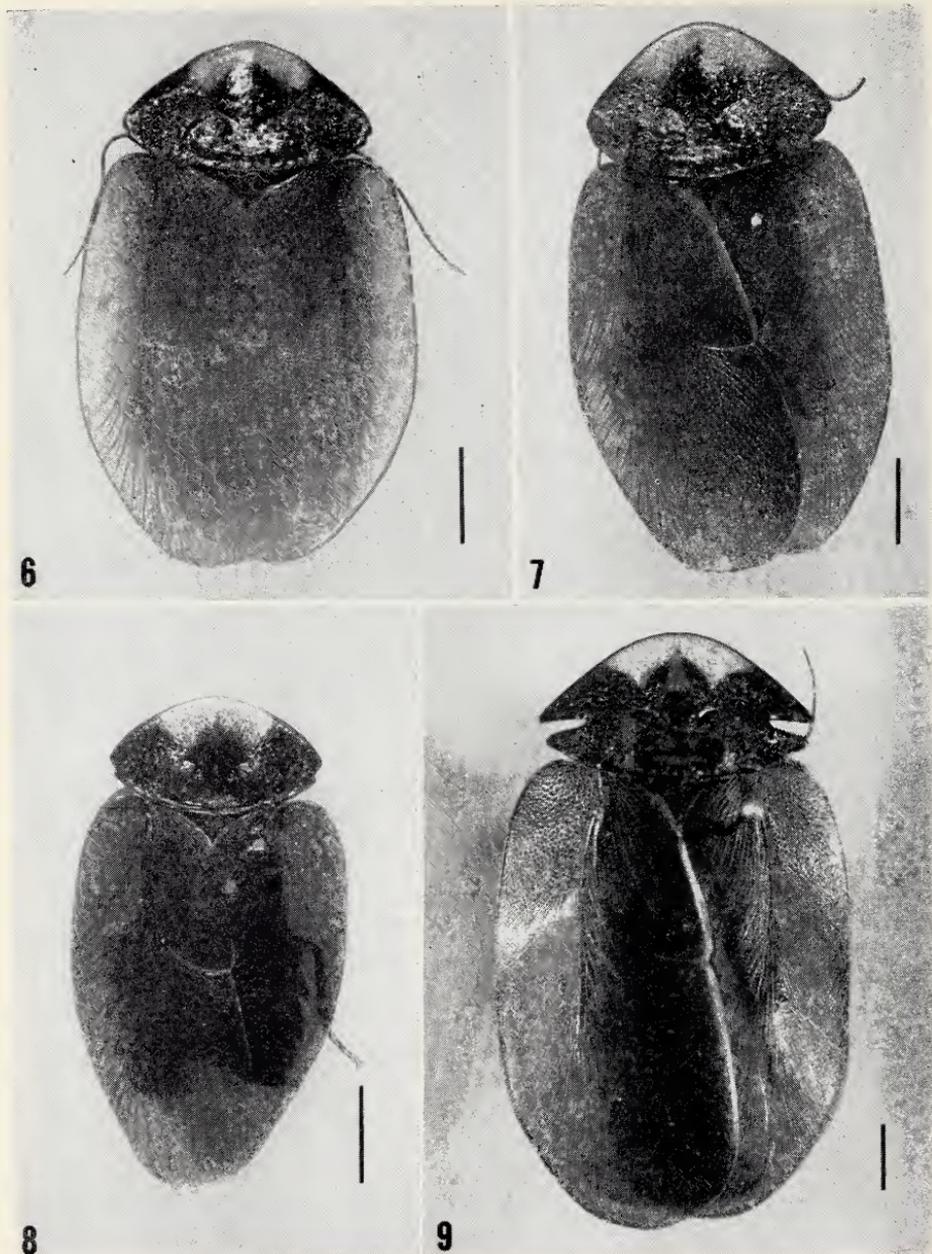
1. Zetoborini (*Zetobora* and *Phortioecoides*, Figs. 1-5, 22-39). L2d is least developed in this tribe and is a thin sclerotization of the preputial membrane which extends dorsally (Figs. 22, 25, 27, 28, 31, 34, 37). The subapical incision of R2 is clearly defined (Figs. 23, 29, 32, 35, 38). L1 is very similar in all the species in this tribe (Figs. 24, 26, 30, 33, 36, 39).

Hebard (1921, p. 245) stated that "The differences shown by the forms recognized by us as *Tribonidium* [= *Zetobora*] *monasticum*, *transversum*, and *amplum*, may indicate full specific distinction, geographic racial differentiation or, indeed, mere individual variation in a single exceptionally plastic species." The male genitalia of the above 3 species (Figs. 22-26, 28-36) are so similar that they are of little help in distinguishing the various species of *Zetobora*.

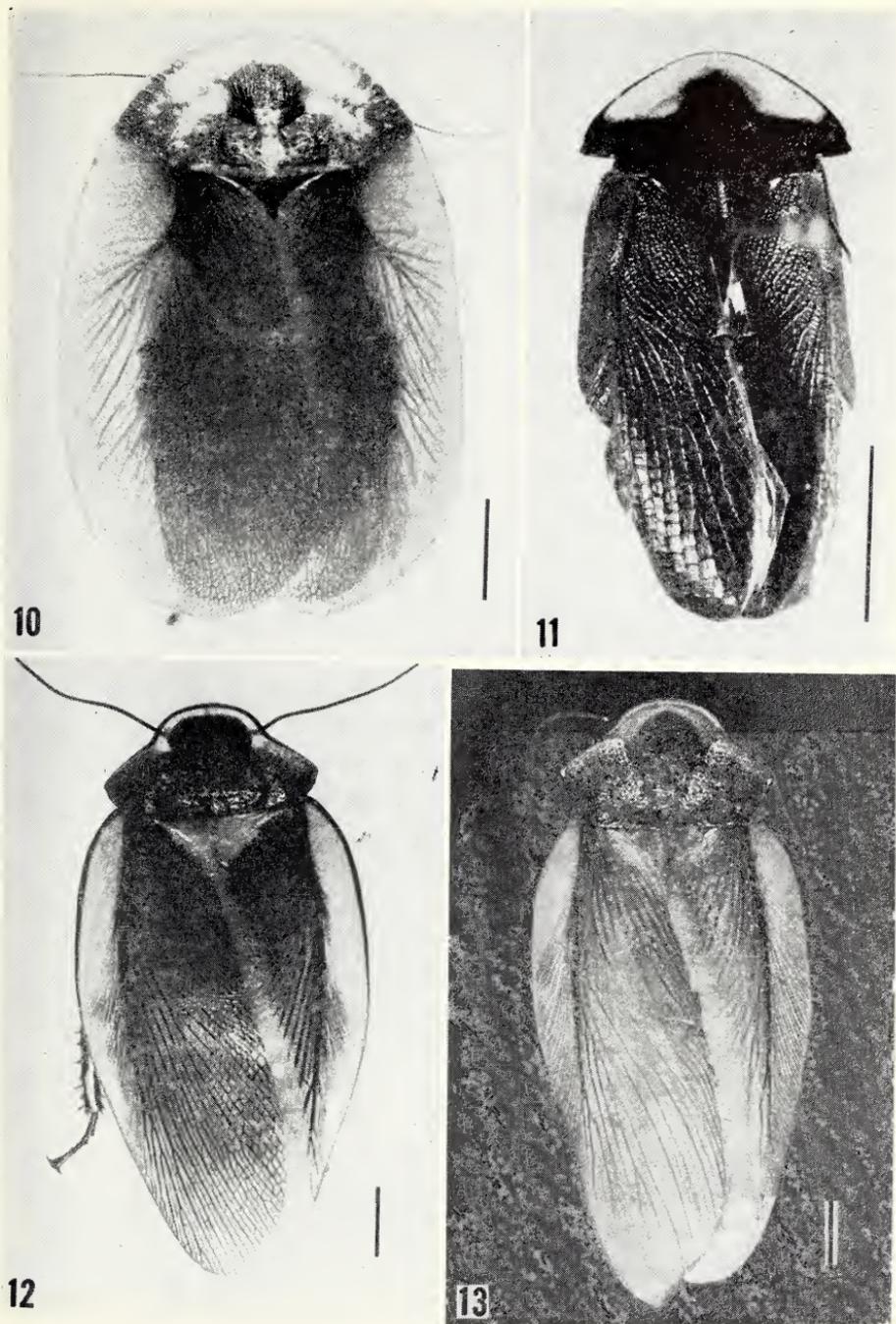
Rehn (1937) placed *Phortioecoides* in the Panchlorinae. Princis (1961) followed Rehn and placed it in the Panchloridae. Princis' Panchloridae is based principally on the shape of the subgenital plate in the male. However, the subgenital plate of the type male of *Phortioecoides guarani* Rehn (the only species of the genus) is not at all like that of *Panchlora*. Also the genitalia of *Panchlora* are



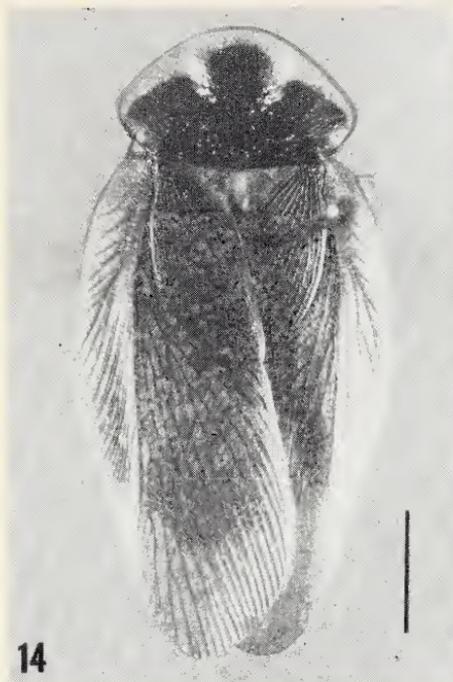
Figs. 1-5. 1. (105 ANSP). *Zetobora signaticollis* Burm. Curityba, Brazil (det. Hebard). 2. (6 BMNH). *Zetobora transversa* (Brunner). Rio de Janeiro, Brazil. 3. (106 ANSP). *Zetobora ampla* (Hebard). Paratype. Montagnes Des Orgues, Prov. de Rio Janeiro, near Tijuca, Brazil. 4. (7 BMNH). *Zetobora monastica* Sauss. 5. (113 ANSP). *Phortioecoides guarani* Rehn. Paratype. Horqueta, Paraguay—40 Km east of Rio (57°W, 23°N). (scale = 5 mm.)



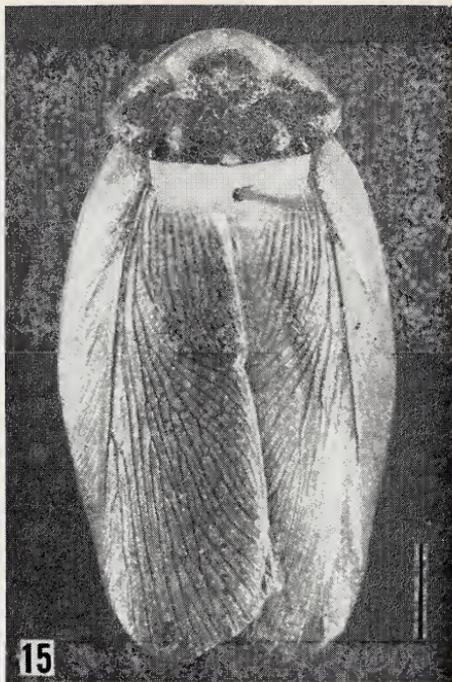
Figs. 6-9. 6. (5 ANSP). *Lanxoblatta lata* (Shelford). Muzo, Boyacá, Colombia (det. Hebard). 7. (4 ANSP). *Lanxoblatta frater* Hebard. Paratype. Antioquia, Colombia. 8. (2 ANSP). *Lanxoblatta emarginata* (Burm.). La Forestière, Haut Maroni, French Guiana (det. Hebard). 9. (97 ANSP). *Schizophilia fissicollis* (Serv.). La Forestière, Haut Maroni, French Guiana. (det. Hebard). (scale = 5 mm.)



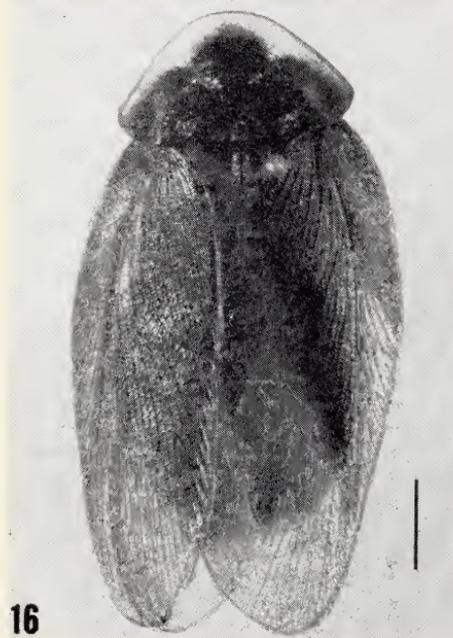
Figs. 10-13. 10. (N.) *Capucina patula* (Walker). Costa Rica (det. Gurney). 11. (102 ANSP). *Zetoborella gemmicula* Hebard. Topotype. St. Jean du Maroni, French Guiana. 12. (N.) *Phortioeca phorasoides* (Walker). Panama. (det. Gurney). 13. (98 ANSP). *Phortioeca peruana* Sauss. Marcapata, Peru. (scale = 5 mm.)



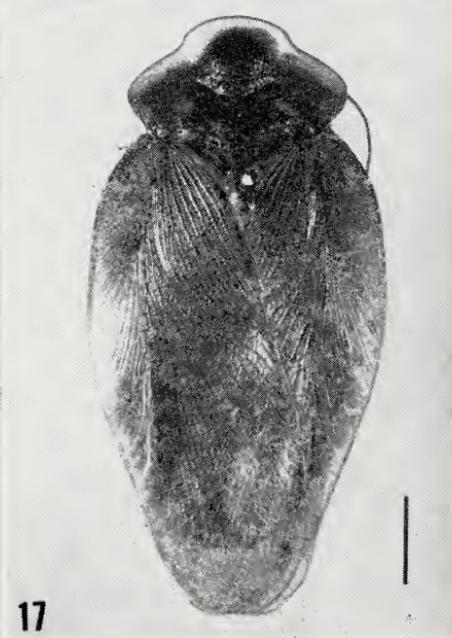
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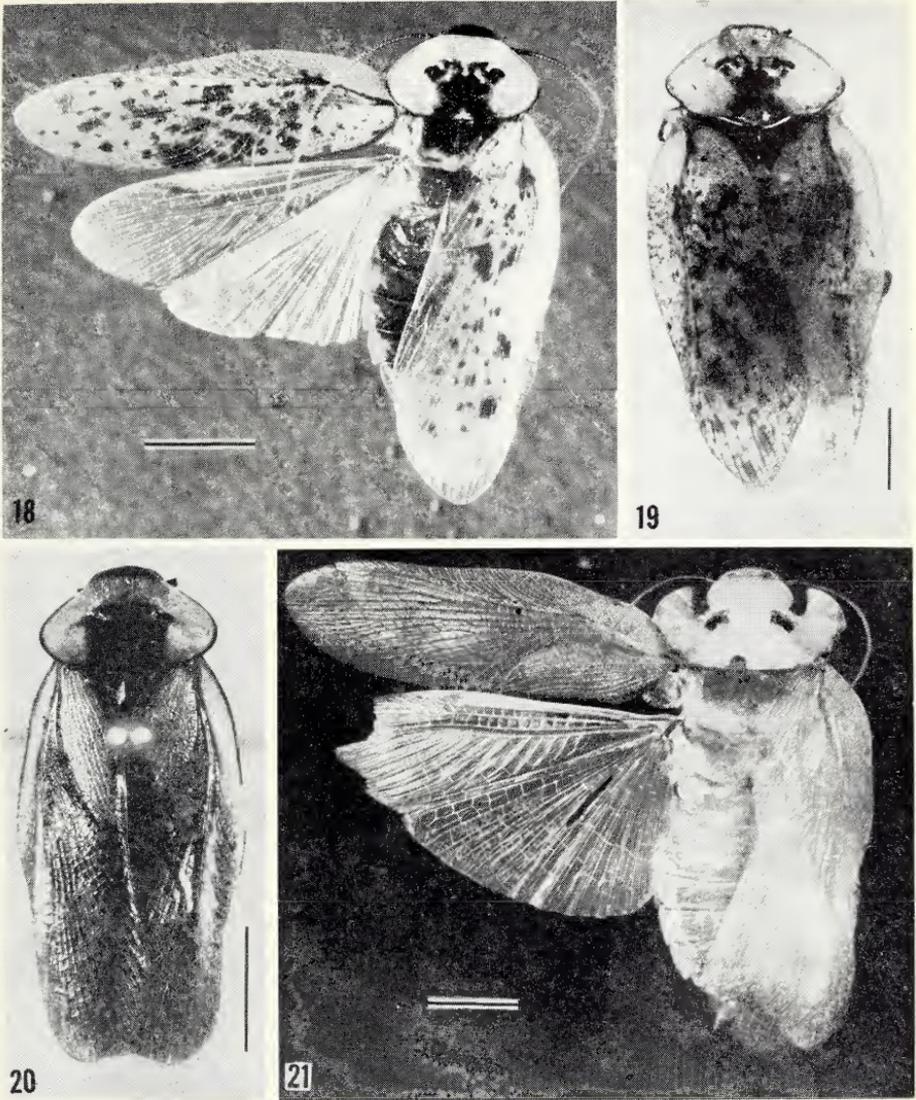


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Figs. 14-17. 14. (101 ANSP). *Phortioeca nimbata* (Burm.). St. Jean du Maroni, French Guiana. 15. (100 ANSP). *Phortioeca apolinari* Hebard. Paratype. Villavicencio, Colombia. 16. (2 CUZM). *Phortioeca verrucosa* (Sauss.). Riacho del Pra. (det. Princis). 17. (5 BMNH). *Phortioeca maximiliani* (Sauss.). Cahabon, Vera Paz, Mexico. (scale = 5 mm.)



Figs. 18-21. 18. (104 ANSP). *Tribonium conspersum* (Guérin). Nova Teutonia, Brazil. 19. (103 ANSP). *Tribonium colombicum* Hebard. Paratype. "New Grenada" (= Colombia). 20. (73 MCZ). *Tribonium* sp. Brazil. 21. (115 ANSP). *Schistopeltis peculiaris* Rehn. Holotype 5244. Porto Velho, Rio Madeira, Brazil. (scale = 5 mm.)

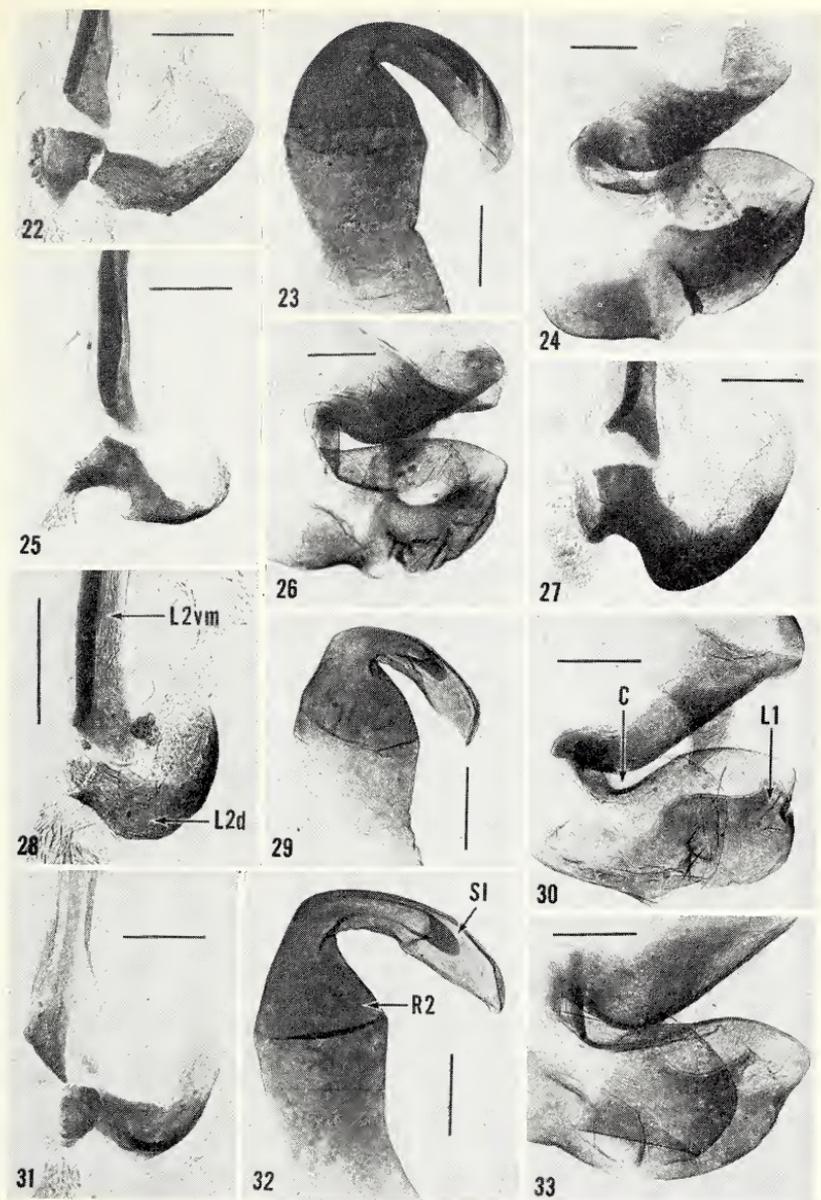
greatly reduced and poorly developed or sclerotized. Most *Panchlora* lack an L2d and R2, and L1 is usually represented by a weakly sclerotized cleft.

In erecting the genus *Phortioecoides*, Rehn (1937, p. 234) stated that it is "Related to *Phortioeca* Saussure, *Capucinella* Hebard, and *Capucina* Saussure, showing certain features of agreement with each, but differing from each one by combinations of characters." The genitalia of *Capucinella* (L2d and R2) show none of the typical characters of Zetoborinae; the genus probably belongs in the Epilamprinae. The shape of L2d of *Phortioecoides* (Fig. 37) more closely approaches that of *Zetobora* (Figs. 22, 27, 28) and I place *Phortioecoides* closer to this genus than to *Capucina*.

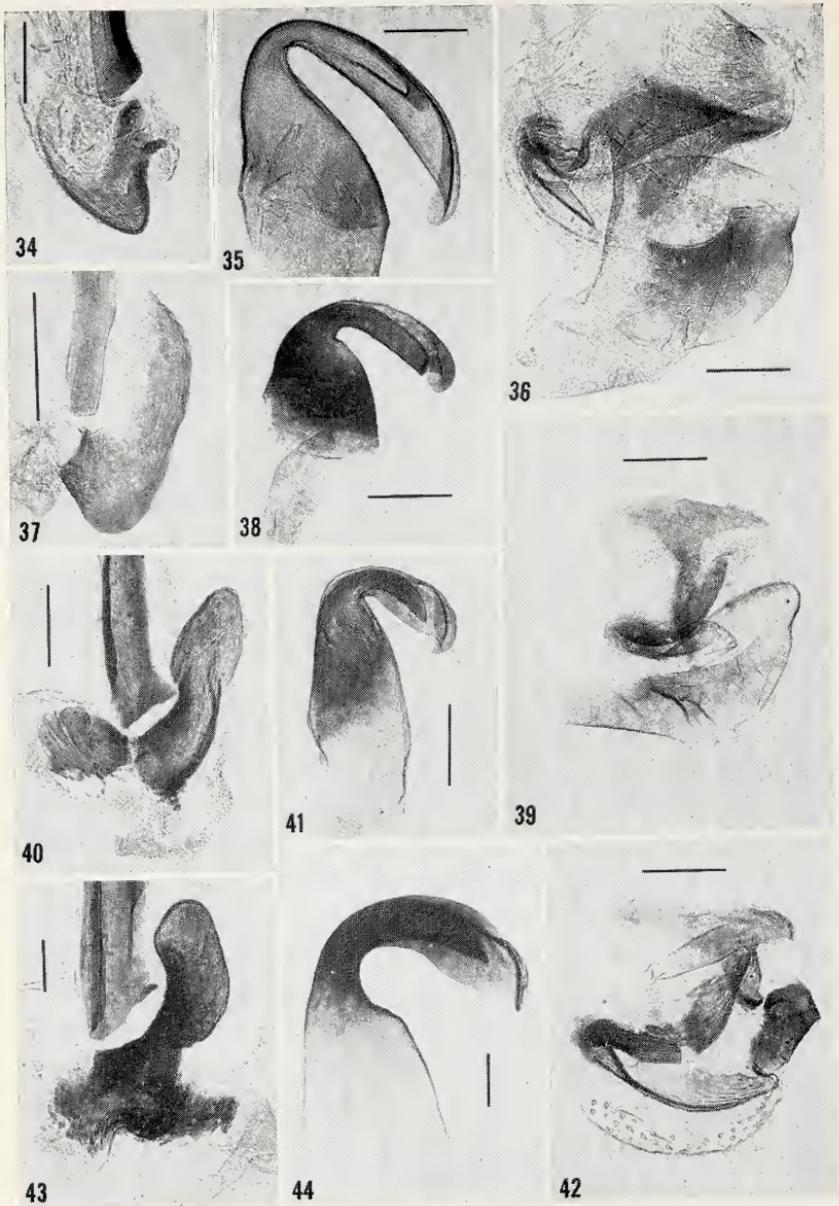
2. Phortioecini (*Capucina*, *Lanxoblatta*, *Phortioeca*, *Schizopilia*, and *Zetoborella*, Figs. 6-17, 40-98). L2d (Figs. 40, 43, 45, 48, 50, 51, 54, 57, 60-62, 63, 66-70, 72, 75, 78, 81, 84) is considerably more developed and robust than in the Zetoborini, and reaches its greatest development in certain species of *Phortioeca* (Figs. 87, 90, 93, 96-98). R2 has a well defined subapical incision (Figs. 41, 44, 46, 52, 55, 58, 64, 71) except for several species of *Phortioeca* (Figs. 73, 76, 79, 82, 85).

Hebard (1921, p. 210) compared *Zetoborella* with *Zetobora* spp. The genitalia of *Zetoborella* (Figs. 40, 41) are closer to other members of the Phortioecini (e.g. Figs. 43-46) than to *Zetobora*.

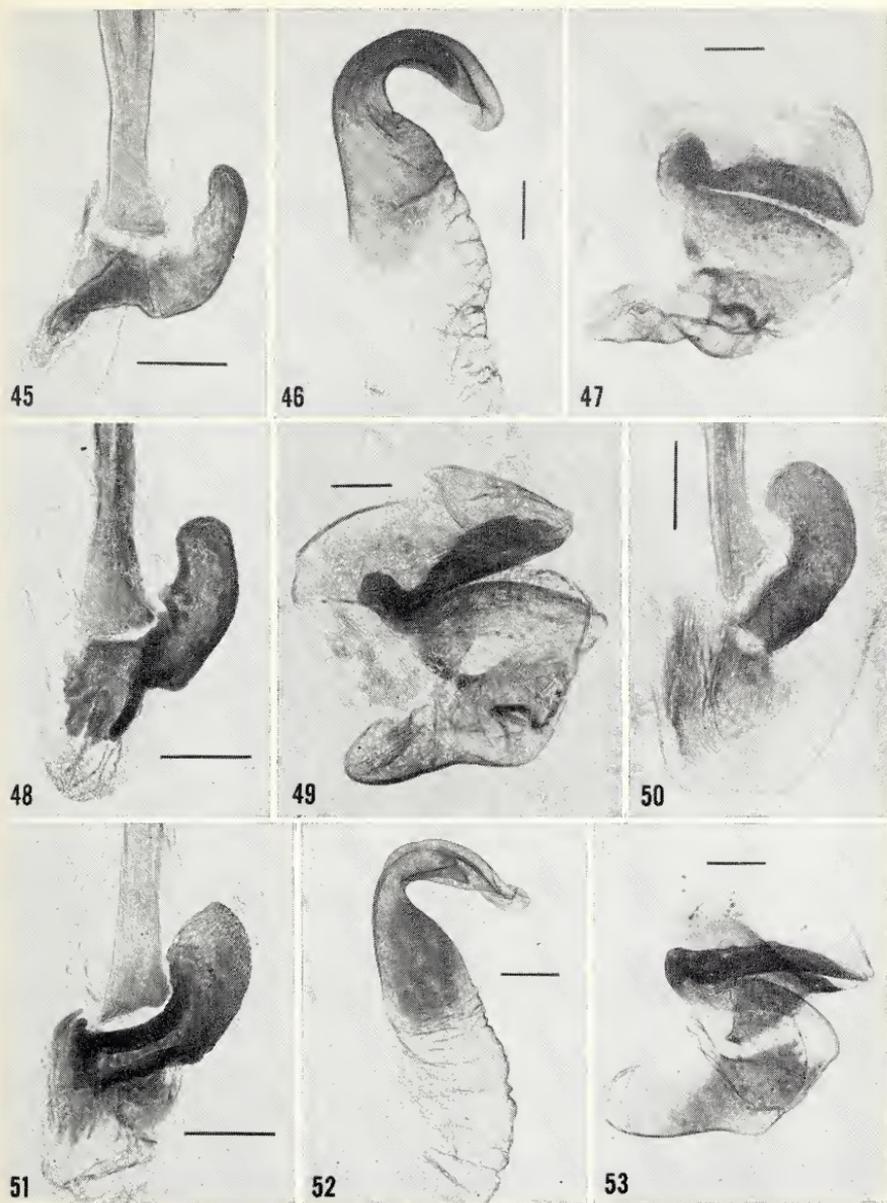
*Capucina patula* (Fig. 10) was placed in the Panchlorinae by McKittrick (1964) and in the Laxtinae by Princis (1960). The Laxtinae of Princis is not recognized by McKittrick and she has assigned several of the genera in this grouping to other subfamilies. Princis (personal communication) regards his subfamily Laxtinae ". . . as provisional. Further study will probably show that it is not at all a homogeneous group and must be sooner or later split up." McKittrick used proventricular and female genitalic characters in placing *Capucina* in the Panchlorinae. However many of the character differences she used in comparing ovipositors and proventriculi seem to be very subtle, and I believe the male genitalia offer characters which show more clear cut relationships in the Blaberidae than do the proventriculus or ovipositor. Miller (1969) found that the morphological diversity of the proventriculus in 9 subfamilies of Blaberidae ". . . often defied the most dedicated efforts to group them into subfamilies." The male genitalia of *Capucina* are so similar basically to those of other members of the *Phortioecini* that I do not hesitate to assign this genus to the Zetoborinae.



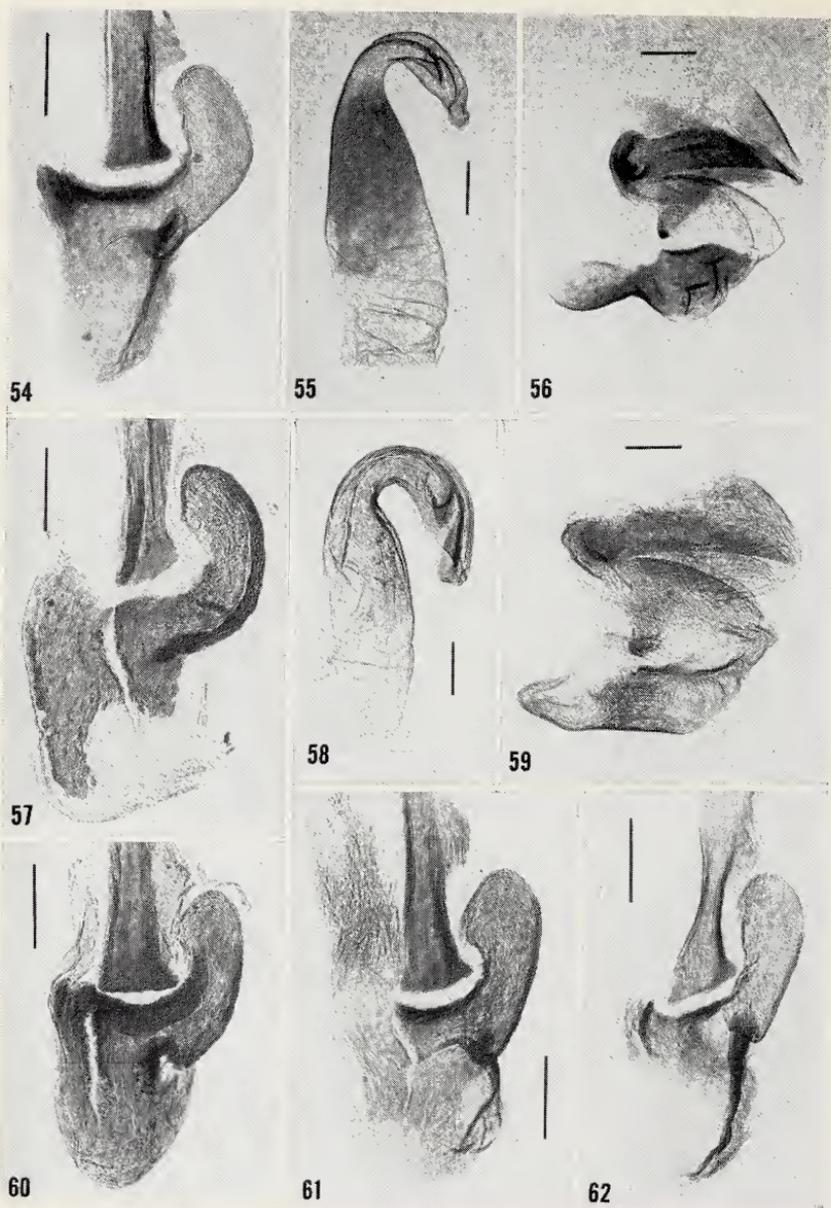
Figs. 22-33. 22-24. (179 USNM). *Zetobora signaticollis*. Santo Amaro, São Paulo, Brazil. (det. Gurney). 25-26. (180 USNM). *Z. signaticollis*. Santo Amaro, São Paulo, Brazil. 27. (181 USNM), *Zetobora* sp. Serra Caraça, M. G. Brazil. 28-30. (6 BMNH), *Zetobora transversa*. (from adult shown in Fig. 2). 31-33. (7 BMNH). *Zetobora monastica*. (from adult shown in Fig. 4). L1 = first sclerite of left phallosome; C = cleft of L1; L2vm = median sclerite (L2 ventromedial); L2d = dorsal sclerite of L2; R2 = hooked sclerite of right phallosome; SI = subapical incision of R2. (scale = 0.2 mm.)



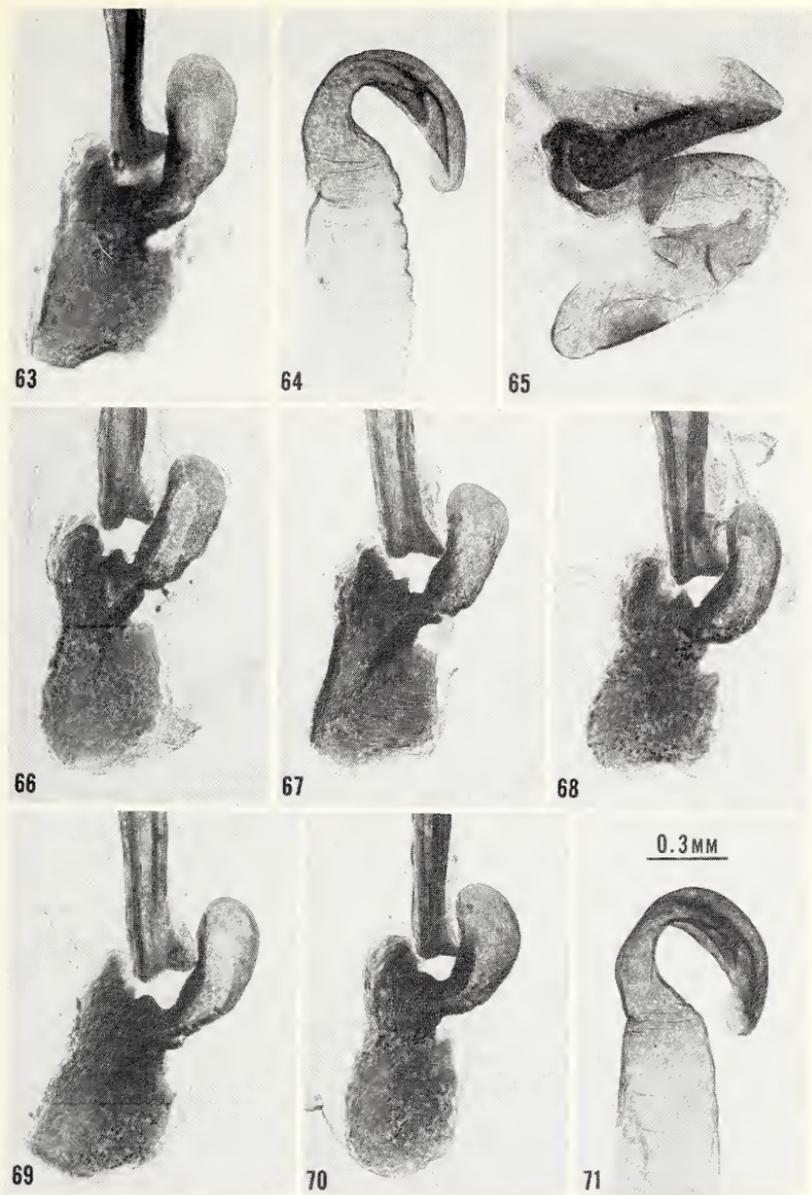
Figs. 34-44. 34-36. (106 ANSP). *Zetobora ampla*. (from adult shown in Fig. 3; Fig. 34 is a ventral view). 37-39. (113 ANSP). *Phortioecoides guarani*. (from adult shown in Fig. 5). 40-42. (102 ANSP). *Zetoborella gemmicula*. (from adult shown in Fig. 11). 43-44. (97 ANSP). *Schizopilia fissicollis*. (from adult shown in Fig. 9). (scale = 0.2 mm.)



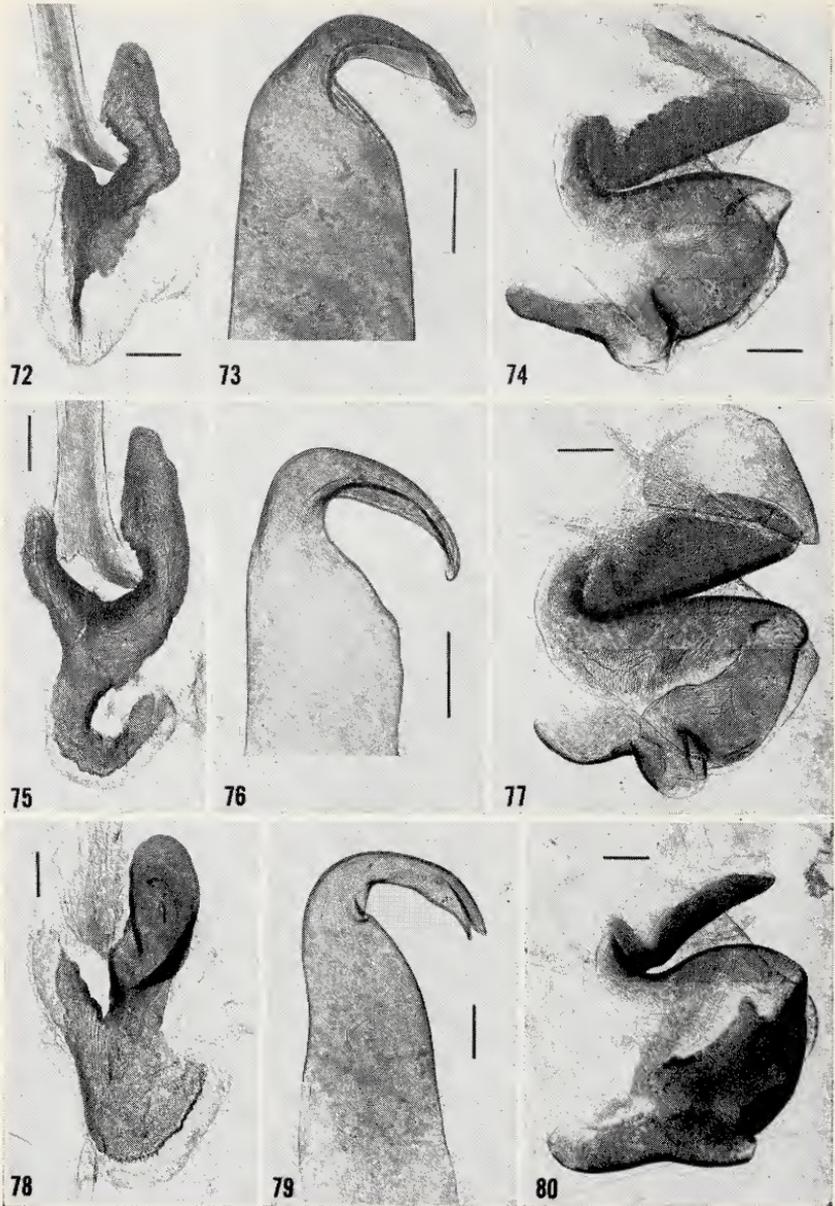
Figs. 45-53. 45-49. *Lanxoblatta frater*. 45-47. (3 ANSP). Paratype. Antioquia, Colombia. 48-49. (4 ANSP). (from adult shown in Fig. 7). 50. (1 ANSP). *Lanxoblatta lata*. Muzo, Boyacá, Colombia. 51-53. (N). *Lanxoblatta emarginata*. From laboratory colony originating in Flores, Manaus, Amazonas, Brazil. (scale = 0.2 mm.)



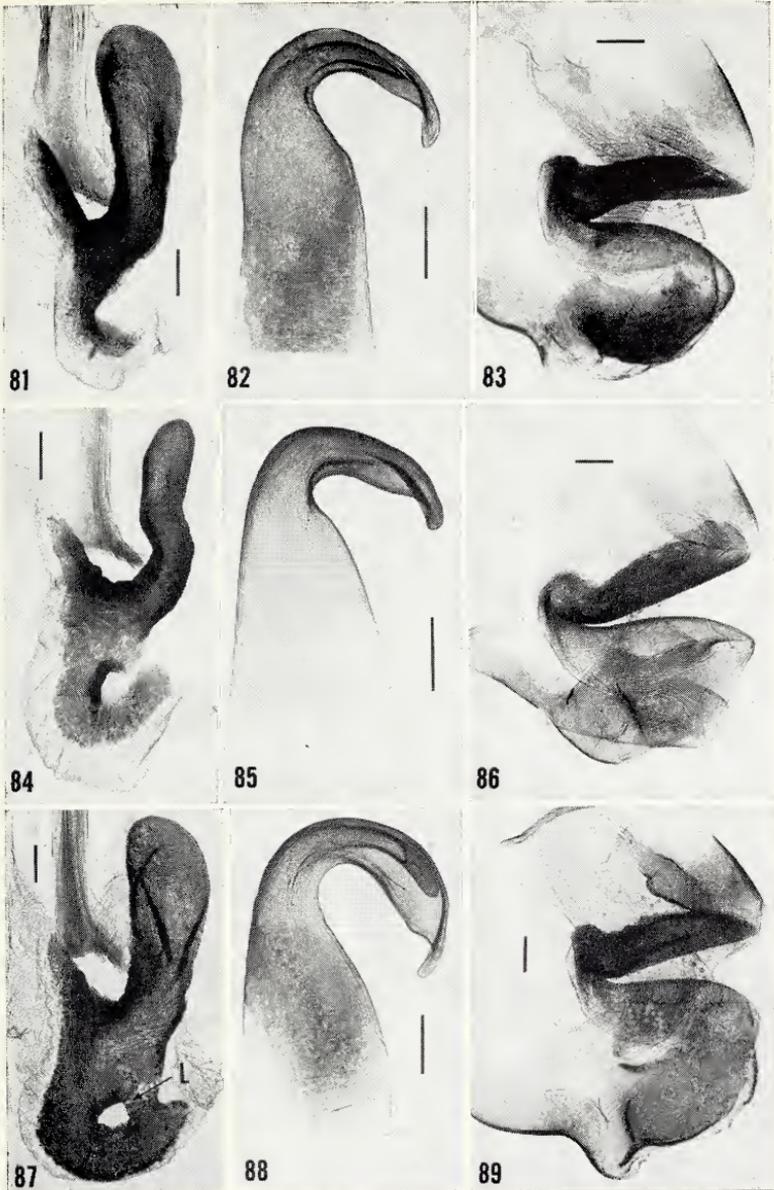
Figs. 54-62. *Lanxoblatta emarginata*. 54-56. (2 ANSP). (from adult shown in Fig. 8). 57-59. (9 MCZ). Ecuador. 60. (10 MCZ). Probably Brazil. 61. (6 ANSP). St. John du Maroni, French Guiana. 62. (7 ANSP). Antioquia, Colombia. (scale = 0.2 mm.)



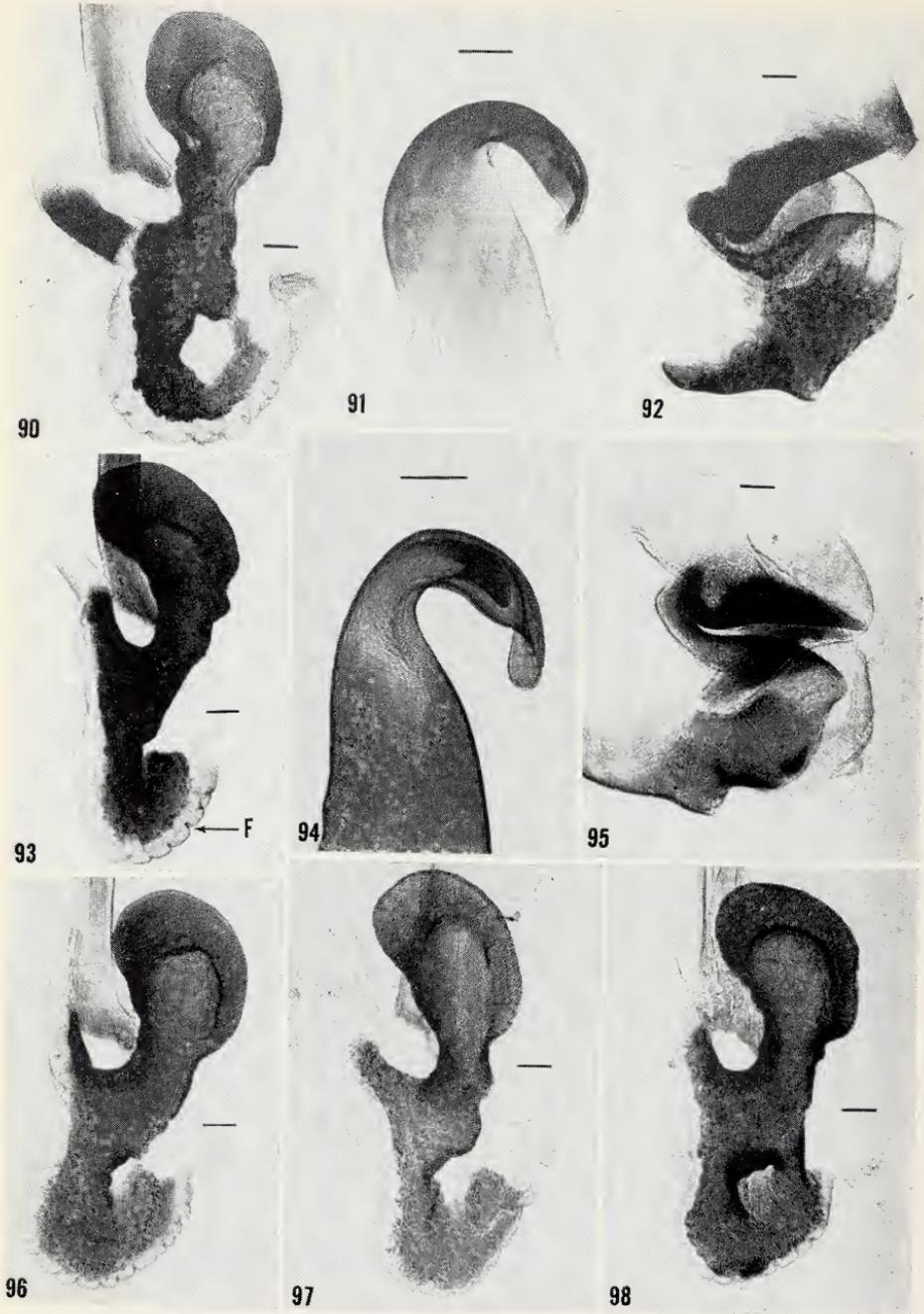
Figs. 63-71. *Capucina patula*. (N). From a laboratory culture originating in Costa Rica. (all to scale shown in Fig. 71).



Figs. 72-80. 72-77. *Phortioeca nimbata*. 72-74. (101 ANSP). (from adult shown in Fig. 14). 75-77. (107 ANSP). La Forestière, Haut Maroni, French Guiana. 78-80. (5 BMNH). *Phortioeca maximiliani*. (from adult shown in Fig. 17). (scale = 0.2 mm.)



Figs. 81-89. 81-83. (100 ANSP). *Phortioeca apolinari*. (from adult shown in Fig. 15). 84-86. (2 CUZM). *Phortioeca verrucosa*. (from adult shown in Fig. 16). 87-89. (98 ANSP). *Phortioeca peruana*. (from adult shown in Fig. 13). L = lacuna in sclerotized basal area of L2d. (scale = 0.2 mm.)



Figs. 90-98. *Phortioeca phoraspoides* (Walker). 90-92. (99 ANSP). Muzo, Colombia (det. Hebard). 93-98. (N). Laboratory culture originating from Panama. F = fringe around preputial membrane. (scale = 0.2 mm.)

In *Phortioeca peruana* (Fig. 87) and *P. phorasoides* (Fig. 98), the sclerotization of the preputial membrane, which forms the base of L2d, may be incomplete leaving a lacuna or window. However, it is clear that this character is variable (Figs. 90, 93, 96-98) and cannot be used for specific determination. In *P. phorasoides* the rounded margin of the preputial membrane which surrounds the sclerotized base of L2d has more or less uniformly spaced indentations (Fig. 93) which are absent in other species of *Phortioeca* examined.

Based on the shape of R2, *Phortioeca nimbata*, *maximiliani*, *apolinari*, and *verrucosa* can be grouped together. In these species the curved hook portion of R2 is relatively narrow and its subapical incision is poorly developed or absent (Figs. 73, 76, 79, 82, 85). *Phortioeca peruana* and *P. phorasoides* both have stouter and more robust R2's and the subapical incisions (Figs. 88, 94) are distinct.

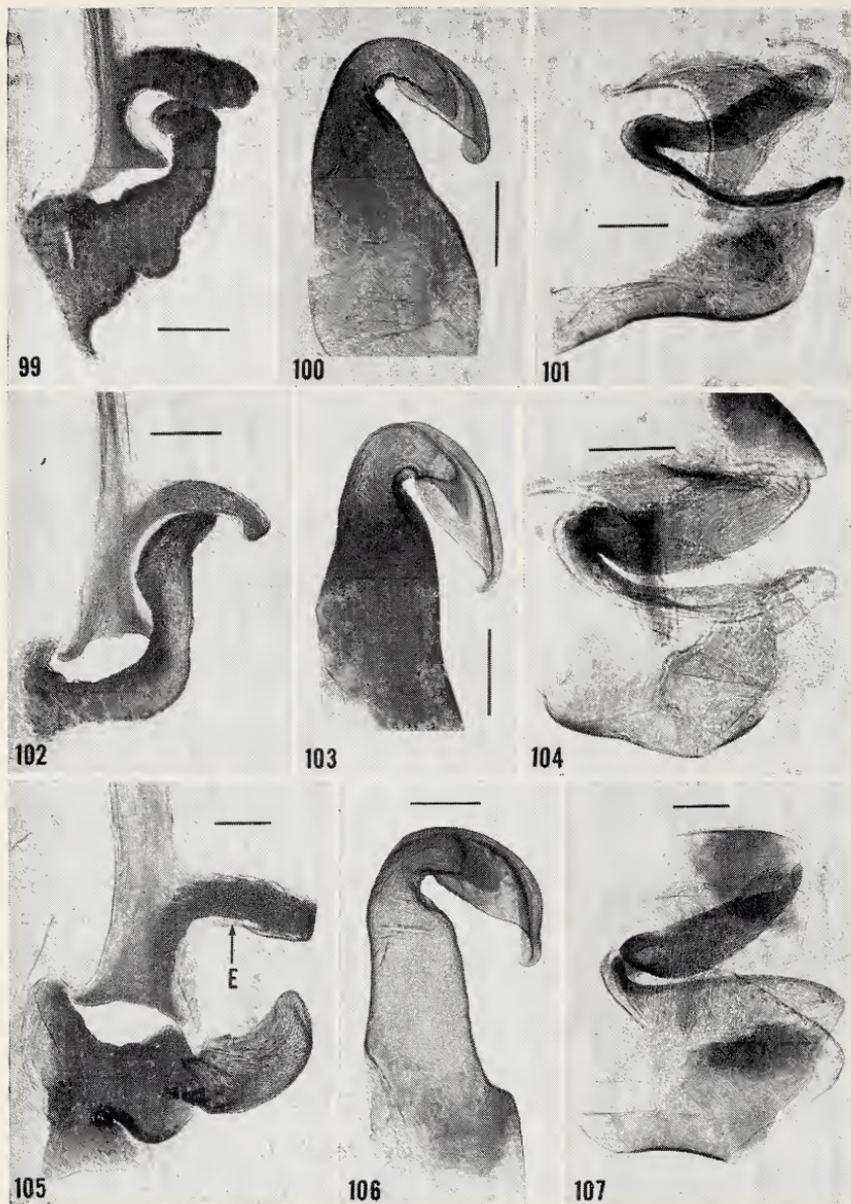
Rehn (1932) stated that the genera *Zetobora*, *Lanxoblatta*, *Zetoborella*, and *Schizopilia* ". . . are clearly derivatives of a single phylum," whereas *Schistopeltis* and *Tribonium* ". . . typifies a distinct and clearly marked phylogenetic series." In general the male genitalia tend to support Rehn's hypothesis. However, I have separated *Zetobora* from the other 3 genera of his grouping because of the relatively poorly developed L2d.

3. *Triboniini* (*Tribonium* and *Schistopeltis*, Figs. 18-21, 99-113). In this tribe, L2vm has a well developed posterior arm or extension (Fig. 105) which extends dorsally (laterally in the photographs because of flattening) and L2d extends upward and curves towards this outgrowth (Figs. 99, 102, 105, 108, 111). The subapical incision of R2 is clearly defined and occurs at about the middle of the hook (Figs. 100, 103, 106, 109, 112).

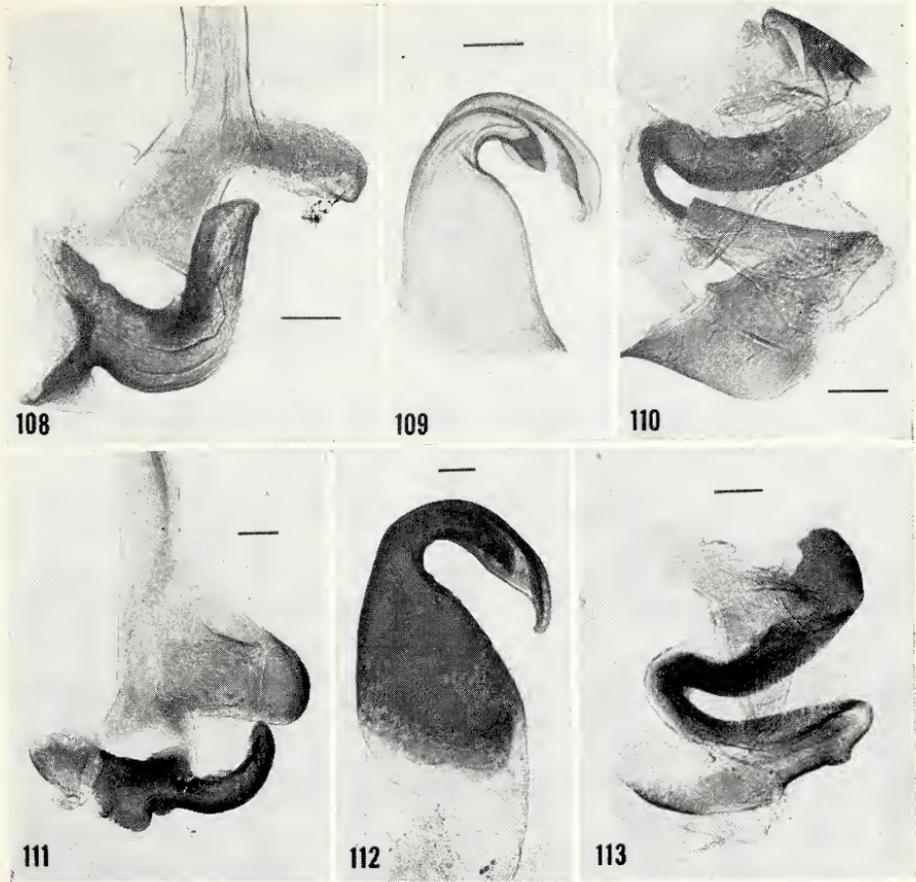
#### SUMMARY

Based on the shape of L2vm and L2d of the male genitalia, 9 genera of Zetoborinae are divided into 3 tribes as follows:

1. Zetoborini (*Zetobora* and *Phortioecoides*).
2. Phortioecini (*Capucina*, *Lanxoblatta*, *Phortioeca*, *Schizopilia*, and *Zetoborella*).
3. Triboniini (*Tribonium* and *Schistopeltis*).



Figs. 99-107. 99-101. (103 ANSP). *Tribonium colombicum*. (from adult shown in Fig. 19). 102-104. (104 ANSP). *Tribonium conspersum* (from adult shown in Fig. 18). 105-107. (1 CUZM). *Tribonium* sp. E = dorsal extension of L2vm. (scale = 0.2 mm.)



Figs. 108-113. 108-110. *Tribonium* sp. 108. (73 MCZ). (from adult shown in Fig. 20). 109-110. (31 MCZ). 111-113. (115 ANSP). *Schistopeltis peculiaris*. (from adult shown in Fig. 21). (scale = 0.2 mm.)

## ACKNOWLEDGEMENTS

I thank the following for the loan of Museum material: Dr. M. G. Emsley and Dr. N. D. Jago, Academy of National Sciences, Philadelphia; Dr. Ashley Gurney, U. S. National Museum, Washington, D.C.; Dr. D. R. Ragge, British Museum (Natural History) London; Dr. S. L. Tuxen, Zoological Museum, Copenhagen. I collected living specimens of *Lanxoblatta emarginata* during Phase C of the Alpha Helix expedition to the Amazon in 1967. I thank the National Science Foundation for support on the Amazon expedition under Grant NSF-GB-5916. I thank Mr. Samuel Cohen for taking the photographs.

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THE CATOPINAE (COLEOPTERA; LEIODIDAE)  
OF PUERTO RICO\*

BY STEWART B. PECK

Museum Comparative Zoology, Harvard University  
Cambridge, Massachusetts 02138

Only three species of Catopinae have been reported from the Greater Antillean Islands: *Dissochaetus portoricensis* Hatch 1933 from Puerto Rico; *Ptomaphagus (Adelops) darlingtoni* Jeannel 1936 from Cuba; and *Proptomaphagus apodemus* Szymczakowski 1969 from Cuba. These three species are known from a total of four specimens.

In December-January 1966-1967 I had the opportunity to collect in Puerto Rico and to begin field studies on the evolution and distribution of West Indian Leiodidae. This paper reports on the Puerto Rican collections. Seventeen days were spent in the field. Twelve collecting visits were made to 11 caves along the north slope of the island. Carrion (rotted liver) and yeast baited pitfall traps were set in the moist forests of the eastern and central parts of the Island. The collecting stations yielding Catopinae are shown in fig. 1. Collected were 230 *Dissochaetus portoricensis* and 60 specimens of a new species of *Proptomaphagus*. Additional information is given for Cuban *Proptomaphagus*.

*Dissochaetus portoricensis* Hatch 1933

Fig. 9

Type: 1 female, El Yunque, Puerto Rico, alt. 2950', Feb. 1900, L. Stejneger leg., in U. S. National Museum. I have seen the type.

Up to now the species was known only from the single type female. The collection of several males allows additional description.

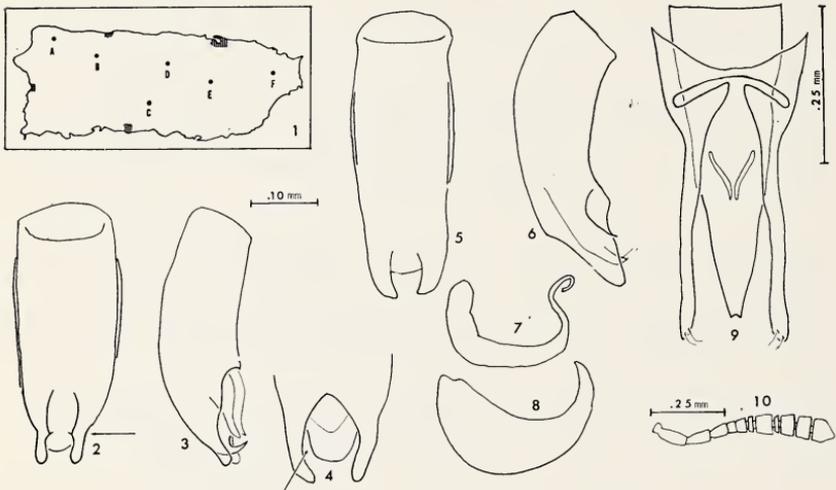
Males. Total length 2.1-2.3 mm., noticeably smaller than females (total length 2.6-2.8 mm.). Aedeagus elongate, narrowing gradually to tip, small notch at tip. Parameres long and thin, slightly reaching beyond tip of aedeagus, armed with two apical hairs. Both narrow and straight in side view. Internal sac with two thin chitinized pieces. Ligulae lacking.

Zoogeography. The species seems to belong to the *spinipes* group

\*Manuscript received by the editor, May 6, 1970.

of Jeannel (1936) which mostly inhabits South America. The two known Lesser Antillean *Dissochaetus* (*granadensis* Jeannel 1936 of Granada and *smithi* Jeannel 1936 of St. Vincent) are in this group, and suggest initial colonization of Puerto Rico either directly from South America or indirectly by way of the Lesser Antilles. However, the possibility cannot be excluded of the beetles having reached Puerto Rico either directly or by way of other Greater Antillean Islands from Central America or Mexico. The *Dissochaetus* of these later three groups are yet too poorly known to evaluate the faunal relationships.

Collections. Puerto Rico. Luquillo Experimental Forest, (El Yunque area), 26.xii.1966-1.i.1967, S. Peck, carrion trap, 1 male, 1 female. Toro Negro Forest, Cerro Dona Juana, 28.xii.1966-4.i.1967, S. Peck, 1000m, yeast bait trap, 16 females; carrion bait trap, 1 male, 23 females; carrion bait traps, 900m, 10 males, 170 females; carrion bait trap, 600 m, 3 males, 5 females.



Figures 1-10. Fig. 1, collecting sites on Puerto Rico yielding Catopinae. (A). Cueva de los Alfaros. (B). Empalme Cave. (C). Toro Negro Forest. (D). Cueva de Corozal. (E). Aguas Buenas Cave. (F). Luquillo Forest, (El Yunque). Fig. 2, dorsal surface aedeagus *Proptomaphagus darlingtoni*. Fig. 3, lateral surface aedeagus *P. darlingtoni*. Fig. 4, dorsal surface of tip of aedeagus *P. apodemus*. Fig. 5, dorsal surface aedeagus *P. puertoricensis*, Fig. 6, lateral surface aedeagus *P. puertoricensis*. Fig. 7, spermatheca of *P. puertoricensis*. Fig. 8, spermatheca of *P. apodemus*. Fig. 9, dorsal surface aedeagus *Dissochaetus portoricensis*. Fig. 10, antenna *P. puertoricensis*.

Ecology. The species is appreciably more abundant in the less wet forests of the Island's center. Two hundred and twenty eight specimens were collected in five traps in the moist Toro Negro forests of the center of the Island, while only two specimens were collected in 9 traps in the wet eastern montane Luquillo forest.

Genus *Proptomaphagus* Szymczakowski

Diagnosis. Mesothoracic episternum not reaching coxal cavity. Metathoracic epimeron clearly transverse. Male portarsi not expanded. Flattened protibia with row of short equal spines along outer margin. Bilobed aedeagal apex, orifice central on ventral surface.

Zoogeography. The genus is most closely related to *Ptomaphagus* (with 23 species limited to the Indo-Malayan region). When Szymczakowski (1969) described *Proptomaphagus* and the Cuban species *apodemus* he pointed out the possible ancient significance of this disjunct distributional relationship. His views are not weakened by the addition of the following Puerto Rican species and the following transfer of *Ptomaphagus* (*Adelops*) *darlingtoni* to this genus.

Additional evidence is now available on the source of the original West Indian colonization of *Proptomaphagus* or its ancestor. The genus occurs on the island of Hispaniola (I have seen one female of a possibly undescribed species in the MCZ collections). I did not find it in two weeks of field work in Jamaica in 1968. The genus occurs in Mexico (I found an undescribed edaphobitic species in a cave in the Mexican state of San Luis Potosi in 1969). It has not been found in Central America. I found none in field work in 1965 in Panama and Costa Rica or in 1969 in Guatemala, and none are in Dybas' extensive 1959 Panama collections in the Field Museum. This pattern of occurrence on three Greater Antillean Islands and in Mexico and absence from Jamaica and Central America suggests initial derivation from Mexican lands, and not Central American lands by way of Jamaica.

***Proptomaphagus puertoricensis* new species**

Figs. 5-7, 10

Holotype. Male (deposited in Museum Comparative Zoology, Harvard University, MCZ type #31886). Puerto Rico; Toro Negro Forest, Cerro Dona Juana, 28.xii.1966-4.i.1967, S. Peck, carrion trap, 900 m elev. Female allotype and 6 paratypes, same data.

Diagnosis. Very similar to *P. apodemus* and *P. darlingtoni* of Cuba in external appearance. Differing mostly in shape of internal male and female genital structures. The male aedeagus of *puertoricensis* when seen in lateral view has higher and broader lateral extensions at its posterior (fig. 6), than *darlingtoni* (fig. 3) and *apodemus*. The aedeagus of *puertoricensis* in dorsal view is wider and shows more regularity in the external outer surfaces at its posterior (fig. 5) than in *darlingtoni* (fig. 2) or *apodemus* (fig. 4). The female spermatheca of *puertoricensis* is more slender (fig. 7) than *apodemus* (fig. 8).

Description of holotype. Length 1.70 mm, width 0.85 mm. Color reddish brown. Shape elongate oval, convex. Pubescence short and thick. Head width 0.55 mm. Eyes large, antero-posterior diameter 4 times wider than distance between eye and antennal insertion.

Antennal club flattened, segments as in fig. 10.

Pronotum convex, width 0.83 mm, length 0.48 mm, widest at point  $\frac{3}{4}$  along length, posterior margin even. Distinct transverse striae. Hind margin slightly sinuous, hind angles drawn out.

Elytral length 1.20 mm, width 0.85 mm. Narrowing at front, sides slightly curved; apex truncate, slightly concave; sutural angle rounded. Striae distinct, oblique.

Fully developed flight wings.

Mesosternal carina low.

Aedeagus tubular, broad, straight, with ventral orifice, bilobed lateral projections at apex.

Female paratype like male holotype, with thin, curved, spermatheca.

Collections. Puerto Rico: Cueva de los Alfaros, Barrio Mora, near Isabela, 4 July 1958, M. W. Sanderson, 100 on bat guano (Illinois Natural History Survey collection). Empalme Cave, Bayaney, near Arecibo, 7.i.1967, S. Peck, 15. Cueva de Corozal, Corozal, 6.i.1967, S. Peck, 5 in cave carrion trap. Aguas Buenas Cave, Aguas Buenas, 30.xii.1966, S. Peck, 26 on fruit bat guano. Aguas Buenas Cave, river passage, 13 Feb., 1968, B. Fenton, 10 on dead bat (in Canadian National Collection, Ottawa). Toro Negro Forest, Cerro Dona Juana, carrion baited pitfall traps, 28.xii.1966-4.i.1967, S. Peck, 600 m. elev., 2; 900 m, 8; 1000 m, 2; yeast baited pitfall trap, 900 m, 1. Luquillo Experimental Forest, carrion pitfall traps, 26.xii.1966-1.i.1967, S. Peck, 300 m, 2; 500 m,

1. El Yunque and vicinity, 16-17 July 1958, M. W. Sanderson, beating and sweeping, 1 (Illinois Natural History Survey collection).

Ecology. Most of the cave collections were from bat guano, found in association with their larvae, and not far from the cave entrance. It would seem that the lowland cave populations may now be at least partially isolated from the montane forest populations since the clearing and destruction of much of the lowland forest for agricultural purposes. I visited Cueva de los Alfaros where Sanderson found the beetles abundant, and found none. The Cerro Dona Juana forest collections were from traps in moist closed-canopy forest with a good ground cover of herbaceous plants. Floor litter was abundant at higher elevations. The beetles are more abundant in the Cerro Dona Juana forest. Four carrion and one yeast baited trap in the Cerro Dona Juana forest caught 13 beetles, compared with 3 beetles from 6 carrion and 3 yeast traps in the Luquillo forest. A possible explanation for the lower catch in the montane Luquillo rain forest is that it may be too wet.

*Proptomaphagus darlingtoni* (Jeannel), new combination

Figs. 2, 3.

*Ptomaphagus (Adelops) darlingtoni* Jeannel 1936: 92.

Type: 1 male (MCZ number 22521). Cuba, Cienfuegos, Soledad, x.28.1926, Darlington. "Wash. gravel bar small brook in woods".

Examination and dissection of the type show it to be a male (not a female as Jeannel stated, because of the narrow pro-tarsomeres, a female character in other *Catopinae*), and to have an aedeagus very similar to *P. apodemus*.

The similarity of the two species is very striking. The only available characters to separate them are the smaller size of *darlingtoni* (1.6 mm) compared to *apodemus* (2.0-2.2 mm), and a few minor details of the aedeagus. The aedeagus of *darlingtoni* is smaller and has a greater constriction at the base of the lateral lobes (arrow in fig. 2), than *apodemus* (fig. 4), the aedeagus tip is broad in *darlingtoni* between the lateral lobes and narrow in *apodemus* so that a space shows along the lobes in their interior side (arrow in fig. 4).

There is a possibility that *darlingtoni* and *apodemus* are conspecific. Only further collecting will show if the differences are distinct between populations, or only extremes of variation within populations. The two localities are 130 km from each other, and on opposite sides of the Island.

I believe the species is still known only from the type. I discount the records of Jeannel and Henrot (1949: 98) of the species from San Jose and Reventazon in Costa Rica. These specimens must be reexamined. Their identity will influence future zoogeographic conclusions.

*Proptomaphagus apodemus* Szymczakowski

Fig. 8

Described from two males from Humbolt Cave, Punta Caguanes, Las Villas Province, Cuba. Through the kindness of Ing. Fernando de Zayas, Academy of Sciences, Havana, Cuba, I have had the opportunity to examine two additional males and two females.

The female specimens allow me to illustrate the female spermatheca (fig. 8) and compare it to that of *P. puertoricensis*. In *apodemus* it is swollen at one end, and gradually curves and constricts to a point at the other end. The spermatheca of *darlingtoni* is unknown.

The specimens came from "Cueva Caguanes", May 1958, F. de Zayas collector. They are either from the type cave populations, or from another cave very near by.

Acknowledgements

I wish to thank Miss Margaret Starr, formerly of the Inter-American University of Puerto Rico, for her assistance in the field work. Milton Sanderson graciously provided specimens from the Illinois Natural History Survey, Urbana. The field work was supported by Evolutionary Biology Training Grant GB3167 of the National Science Foundation, Prof. Reed C. Rollins, principal investigator, Harvard University.

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THE PREDATORY BEHAVIOR OF TWO WASPS,  
*AGENOIDEUS HUMILIS* (POMPILIDAE) AND  
*SCELIPHRON CAEMENTARIUM* (SPHECIDAE),  
ON THE ORB WEAVING SPIDER  
*ARANEUS CORNUTUS* (ARANEIDAE)<sup>1</sup>

BY WILLIAM EBERHARD<sup>2</sup>

Museum of Comparative Zoology, Harvard University

The nesting habits of many wasps have been studied, but much less is known of how they locate and capture their prey. Many wasps in the families Pompilidae and Sphecidae prey on orb weaving spiders, and knowledge of their predatory behavior is crucial to an understanding of the biology of orb weavers. This paper describes the hunting behavior of two species of wasp, *Agenoideus humilis* (Pompilidae) and the mud dauber *Sceliphron caementarium* (Sphecidae) which were observed preying on the orb weaver *Araneus cornutus* during July and August, 1968, and discusses the significance of their behavior for the spiders.

There was a dense population of the spider *Araneus cornutus* on the windows and shingled walls of a cottage on Lincoln Pond in the Huyck Preserve, Rensselaerville, New York. Spiders spun orbs in the early evening and sat at the hubs during the night, then (except for a few younger individuals) left the orbs and crouched in retreats during the day. The retreats were usually approximately tubular, silk-lined, and often had silk just beyond the mouth. Although most of the retreats around the cottage were in cracks beneath shingles, the spiders were especially plentiful around windows from which lights showed at night, and there were a number of retreats at the edges of window panes (there were 15 30×15 cm panes/window) and in the corners of window frames. Retreats like these, which

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<sup>1</sup>This is part of a thesis done under the direction of Dr. H. W. Levi and submitted to the Department of Biology of Harvard University, in partial fulfillment of requirements for the PhD degree. The work was done in 1968 while I held a Summer Fellowship from the E. N. Huyck Preserve, Inc.; I thank the directors and staff of the Preserve for making it possible for me to do this work in such pleasant surroundings. I thank Dr. H. E. Evans for encouragement and for identifying the wasps, and Mary Jane Eberhard, Robert Jeanne, and William Shear for helpful comments on the manuscript. Specimens of the species observed are deposited in the Museum of Comparative Zoology, Cambridge, Mass.

<sup>2</sup>Present address: Depto. Biología, Universidad del Valle, Cali, Colombia.

were not hidden from view, were made of silk, often approximately tubular, and usually open at both ends. The dark-colored spiders contrasted with the white woodwork as they rested in these retreats, and were thus easy to locate visually. Spiders in the field were usually impossible to see because their retreats were generally in curled leaves or under flakes of bark.

When sufficiently disturbed during the day, the spiders dropped out of their retreats. Sometimes they stopped before they reached the ground, hung motionless at the end of their trail lines for a short while, then climbed back to their retreats; other times they descended to the ground. Although they often began to crawl as soon as they landed on a flat surface, they usually remained motionless with their legs pulled tight against their bodies when they landed on irregular surfaces such as grass or leaf litter.

#### Predatory behavior of *Agnoideus humilis*

*Agnoideus humilis* is relatively rare in the northeastern U.S. (Evans and Yoshimoto 1962) but was not hard to find around the cottage on Lincoln Pond, and has previously been collected there by both Kenneth Cooper in 1952 and Robert Matthews in 1967 (unpublished reports to the Trustees of the E. N. Huyck Preserve, Inc.). Evans and Yoshimoto summarize the literature on the biology of this species, noting that it is often found near buildings. It has been recorded preying on orb weavers in the araneid genera *Neoscona*, *Araneus*, and *Conepeira*, but there are no records of its predatory behavior.

Females of *A. humilis* were observed hunting for spiders on the walls and windows of the cottage. Typically, a wasp walked along the surface of the wall until she encountered a crack between two shingles, then walked up the crack and under the overlapping shingle, often staying out of sight for 30 seconds or more. The wasps did not investigate every crack they encountered, and often passed two or three before walking up one. They usually showed no obvious reaction when they encountered silk in them. Occasionally a wasp bent her abdomen forward beneath her so that the tip was near her head as she entered a crack.

Four complete wasp-spider encounters were observed. One involved a spider resting in a horizontal retreat at the top edge of a window pane. The wasp, after passing within two cm of another spider in a retreat, encountered some silk about two cm below the retreat and climbed directly to it. She touched the side of the

retreat, climbed around to one end, curled her abdomen forward under herself, and moved in. Almost immediately the spider fell backwards out the other end, descended to the floor (these observations were made on a porch), and began to crawl away. The wasp flew out of sight for about 30 seconds (perhaps disturbed by my presence, see below), then came back (I assume it was the same wasp), flew to the spot directly below the retreat where the spider had landed, and ran around quickly in that area. I could not discern any pattern in the search except that the wasp quickly began searching farther and farther from the original area. By the time the wasp had returned, the spider was about 0.5m away and climbing along the wall under the edge of the second row of shingles. The area of the wasp's hunt quickly expanded to include the wall, and after about 15 seconds she moved straight toward the spider which was about 1 m away now. She grabbed the spider with her legs and stung it once on the ventral side of its cephalothorax as soon as she reached it. The spider showed no defense against the wasp's attack. It stopped moving as soon as it was stung, and the wasp grabbed it near the base of one leg with her mandibles and began drawing it up the wall.

Wasps with spiders always moved backwards, dragging the spider behind them, and several wasps showed strong tendencies to drag their spiders upward. This behavior was probably preparation for a flight with the spider. One wasp was observed flying with a spider, and judging from the angle of its flight as it came to earth, it must have climbed at least 10 m up a tree that was 15-20 m from the site where it landed.

Each wasp dragging a spider paused periodically, released her grip on the spider and flew around for a short while, then returned and dragged the spider onward. When I moved the spider a short distance while a wasp was gone on one of these short excursions, the wasp returned to the spot where she had left the spider and ran around quickly (again I could see no pattern) in that area. When she re-encountered the spider she stung it on the ventral side of its cephalothorax. This experiment was repeated several times, and even though the wasp encountered the spider from a different direction each time, she always stung it in the same region. The stinging was evidently released by the change in the spider's position, since wasps did not sting spiders which had not been moved. This behavior may normally occur when a wasp fails to completely paralyze a spider with her first sting.

Two wasps were observed attacking spiders which had evidently been driven from their retreats and were hanging at the ends of threads. Each wasp flew close to (and probably hit) the spider, then immediately flew to the floor directly beneath the spider and ran around quickly. In both cases this first encounter caused the spider to descend only part of the way to the floor, and after a short time the wasp flew back up and buzzed the spider again. The quickness with which these wasps searched the floor below following their encounters with spiders suggests the wasps in the case reported above may have been disturbed.

One wasp's encounter with an *A. cornutus* exuvium was also observed. The skin hung near one entrance of an empty retreat, and when she encountered it the wasp inserted her sting into it two or three times.

Two spiders escaped after a wasp encountered them. There was a strong ( $> 15$  kmph) wind blowing when one of them left its retreat and hung on a thread as a wasp entered. The wasp flew down to the spider, but as the spider let out more thread, a gust of wind blew it around the corner of the house. The wasp did not follow it, but landed on the wall. Another spider was at the mouth of its retreat in the crack between two shingles as a wasp approached, and dropped out just as the wasp walked up the crack. The wasp walked on under the overlapping shingle, stayed out of sight for about 15 seconds, then walked on. After about a minute, the spider climbed back up its thread to its retreat.

In summary, spiders were always attacked while they were on surfaces, and those not on surfaces (on a thread) were driven to them and then attacked. The wasps used their superior speed and an ability to locate the ventral surface of the spider's cephalothorax to sting the spiders into paralysis. The wasps probably did not use vision to locate spiders in their retreats, but probably did use it to locate spiders which had fallen from their retreats and perhaps to locate the general area in which to search for retreats. Tactile or perhaps chemical stimuli from the skin of a spider released stinging behavior.

These observations of the predatory behavior of *A. humilis* differ dramatically from the description of the predatory behavior of *A. sericeus* (= *Pompilus sericeus*) by Soyer (1950). He saw these wasps hunting the orb weavers *Araneus diadematus* and *Zygiella x-notata*, but claimed that the wasps, by flying about until they fell into an orb and then searching sites to which the web threads led, used the spider's web to find its retreat. The observations above

indicate that *A. humilis* did not use cues from the orb to locate the spiders. Although these differences may be due to differences in the species, it seems more likely that Soyer misinterpreted some of the behavior he observed.

#### Predatory behavior of *Sceliphron caementarium*

*Sceliphron caementarium* is much larger than *A. humilis* (length about 25 mm vs. about 8 mm). This species has been recorded stocking its tubular mud cells with spiders in the families Araneidae, Thomisidae, Salticidae, Oxyopidae, Anyphaenidae, Clubionidae, Mimetidae, Theridiidae, and Lycosidae (Muma and Jeffers 1945). In general, they take spiders commonly found on plants (Rau 1935, Muma and Jeffers 1945).

Two individuals of *S. caementarium* were observed searching for *A. cornutus* on and near the windows of the cottage, and 18 wasp-spider encounters were seen. *S. caementarium* appeared to use different signals than those used by *A. humilis* to locate spiders. The wasps hovered near the windows, alighting occasionally and sometimes walking across a pane or two, then flying on. They apparently oriented visually before landing since they almost always lit either on small dark spots which contrasted with their background (the white trim of the cottage) or in corners of window panes. Occasionally they lit on dark objects (usually masses of dead ephemeropterans) suspended by spider threads. The contrast between a spot and its background appeared to be more important in determining its attractiveness to a wasp than its shape, as the wasps often landed on dark spots bearing little resemblance to a spider crouching in its retreat. These wasps encountered only the spiders which were resting on the white woodwork of the house.

There were *A. cornutus* orbs on and near the windows, and the wasps sometimes flew into them as they hunted, but the wasps were strong and heavy enough that they quickly freed themselves. Their hunting behavior was never noticeably altered by such an encounter, indicating that they do not use the presence of an orb as a cue signaling the presence of a spider.

Memory of previous captures probably influenced the choice of a site for hunting: after depositing a spider in her nest (about 5 m away), one wasp resumed hunting at the same edge of the same window pane where that spider had just been captured. The intensity of hunting activities at a given site also may be influenced by previous experience at that site. Two windows which were examined only

cursorily or not at all during intermittent searches for weeks prior were searched very thoroughly on one day when at least three spiders were captured there. About two weeks later, hunting intensity had returned to the level previous to the burst of captures.

The wasps may also establish hunting routes. One individual visited a series of four windows in the same order four times, each time after depositing a new spider in her nest. She caught all the spiders on the third and fourth windows, and the later visits to the first two windows were very brief.

When a wasp encountered a silken retreat with a spider in it she immediately pulled and tore at the silk in the side of the retreat with her mandibles. After a few tugs by the wasp, the spider usually left the retreat at the end farthest from the wasp and descended on a thread. Spiders usually remained inside vertical retreats longer when the wasp was attacking from below, leaving the top end hesitantly. One spider moved to the bottom of the retreat where a wasp was pulling, moved back up to the top end, and, when the wasp moved to the top along with it, dropped out the bottom.

The wasps pursued the spiders as they struggled out of their retreats and as they fell. Several times a wasp captured a spider just as it fell from the retreat and stung it as she flew away. On three occasions the spider fell to a windowsill and the wasp attacked it there. In each case the wasp grasped the spider with her mandibles and front pair of legs and curled her abdomen forward beneath her body and stung it. On one occasion a wasp stung a spider four times, the last three times on the ventral side of its cephalothorax. Several other times a wasp stung a spider as she flew, then landed and stung it at least once more.

On two occasions a spider dropped out of its retreat and hung on a line some distance below (once after it hit the windowsill and crawled off that). In one of these cases, the wasp captured the spider as it hung, and bent her abdomen forward and stung it as she flew away. In the second case, she landed on the windowsill after seizing the spider and bent her abdomen forward and sideways to sting it.

Usually a wasp paused for several seconds after stinging a spider, and on at least four occasions, the wasp's mouth was pressed against the mouth region of the spider during this pause. On one occasion the spider was rotated so that its mouth region was next to that of the wasp. The wasps may have been ingesting fluids from their victims' mouths during these pauses.

Twice a wasp captured and then discarded a very small spider. Both spiders, which were less than half the size of the wasp's head, were captured at the bottoms of their retreats, stung in midair, then dropped as the wasp resumed hunting. There were a number of individuals of *A. cornutus* on the windows where the wasps hunted which were too large (i.e. larger in diameter than the wasp's mud cell), but no encounters with these individuals were observed. Sometimes the wasps appeared to avoid their retreats.

Occasionally hunting wasps paused and flattened themselves on a flat, light-colored surface in the sunlight. These pauses probably functioned to elevate the wasp's body temperature. The predominantly black coloration of *S. caementarium* (and *A. humilis*) may function to speed this process, but this is not certain since many wasps which do not obviously need to collect heat are also black.

Wasps attempted to sting three different empty spider skins which hung near empty retreats. Thus the stinging behavior of *S. caementarium* is probably released by the stimuli of contact with the surface of the spider, just as it is in *A. humilis*. This response would be highly adaptive for both wasps when they hunt for spiders which are difficult to see after they drop into litter below the retreat and assume cryptic postures. Apparently contact with arthropod cuticle of all kinds will not release stinging; once a *S. caementarium* landed on a phalangid (daddy-long-legs), but immediately flew on; the phalangid remained motionless.

The wasps did not capture all spiders they encountered. Twice a wasp failed to react when a spider fell from the retreat she was tearing at. Another relatively small spider was blown some distance as it descended on a thread, and the wasp did not follow it. Two other times, a spider did not leave when a wasp pulled at its retreat, and after several tugs, the wasp moved on. Both of these retreats were exceptional. One was under a large mass of dead ephemeropterans and spider silk and the wasp pulled at this mass rather than the retreat. The wall of the other was unusually strong because it was quite thick and made of thick fibers spun by a relatively large spider.

The observations above are not in complete agreement with published observations of *S. caementarium* predatory behavior. The Peckhams (1905) also saw this species (= *Pelopaeus caementarium*) hunting *Araneus cornutus* (= *Epeira strix*) on the side of a house, but recorded that the wasps walked along the wall and pried into nooks and crannies rather than hovering nearby and landing on dark

spots. They also recorded that the wasps only seldom followed spiders which fell from their retreats. These differences may be due to differences in cues learned by individual wasps.

#### Discussion

The hunting behaviors reported above illustrate selective pressures on *A. cornutus* and other orb weavers. A spider at the hub of an orb in the daylight is probably relatively safe from attacks by predators not strong and heavy enough to escape easily from its web, but it is very vulnerable to attacks by large, visually orienting, versatile predators such as *S. caementarium*. On the other hand, many insects fly only during the day, and it is certainly advantageous for the spider to use its web during the day. Devices such as stabilimenta found in webs of *Cyclosa*, *Argiope*, *Uloborus*, and others (Gertsch 1949) which obscure the spider's outline, a "stopping mesh" next to the orbs of *Nephila*, *Metepeira*, *Argiope*, *Araneus*, and others (McCook 1889), and signal threads leading to the web from the hiding place of *Zygiella*, *Hyptiotes*, *Araneus*, and others (McCook 1889) may all function to hinder attacks by relatively large predators while allowing the spider to capture prey caught in the web during the day.

A spider off its web is relatively safe from larger predators because it can crawl into places too small for them, and also relatively safe from smaller substrate-bound predators because it can escape by falling and hanging on a thread. A spider in a retreat is probably only especially susceptible to wasps which are relatively good fliers, which are about its own size, which hunt by crawling into tight spots, and whose behavior can cope with the spider's escape behavior. A larger wasp can attack an orb weaver in its retreat only if it can drive or lure the spider from the retreat. The wasp can only drive the spider from its retreat if it can find it, and if the retreat is not in a sheltered spot. It can probably only lure it out with relatively complicated behavior like that of *Belanogaster junceus* (?) which hovers next to the hub of the web and taps it with its antennae and perhaps its front legs to lure the spider to the hub (MacNulty 1961).

It is possible that wasp predation has been a selective force influencing web site selection, as the observations above indicate that *S. caementarium* might be less likely to encounter well-scattered webs in cool places.

*Araenus cornutus* appears to have two effective close range defenses against wasp attacks: a quick unobserved exit from its retreat, and

cryptic coloration and posture when it lands below. Both of these tactics may help explain why some orb weavers such as *Zygiella litterata* (Kaston 1948) and *Singa haemata* (Nielson 1931) build retreats with two open ends, and why some such as *A. cornutus* are cryptically colored even though they are normally hidden during the day. The behavior of *A. humilis* and *S. caementarium* indicate that while there may be selective pressure on orb weavers to hide themselves, there is probably little or no pressure to hide their webs, at least from these species.

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THE NYMPH OF  
*WILLIAMSONIA LINTNERI* (HAGEN)  
(ODONATA: CORDULIIDAE)

BY HAROLD B. WHITE, III<sup>1</sup> AND RUDOLF A. RAFF<sup>2</sup>

The genus *Williamsonia* (Davis 1913) is composed of two little-known species: *lintneri* (Hagen 1878) and *fletcheri* (Williamson 1923). Both are rather similar with respect to their early flight season and their habitat preference. *Williamsonia lintneri* is recorded in the literature from only four northeastern states of the U.S.A.: Massachusetts, Rhode Island, New York, and New Jersey. *Williamsonia fletcheri* has a larger and more northern distribution which includes the states of Maine, Massachusetts, New York, and Michigan, and four provinces of Canada: Manitoba, New Brunswick, Ontario, and Quebec. Of *Williamsonia lintneri*, Howe (1923) commented:

"The dates, as will be seen, range from April 1 to June 4 (sic) and undoubtedly the reason *Williamsonia lintneri* has been overlooked is because of its early flight season when collectors are not alive to the presence of Odonata in the field. . . . I always find it a woodland species inhabiting the neighborhood of cold bogs and brook runs. . . . Its larva is unknown."

In his description of *Williamsonia fletcheri*, Williamson (1923) quoted similar comments from a letter of J. H. McDunnough, collector of the type specimens near Ottawa, Ontario.

"This species is one of the earliest to occur in our locality and nearly all the specimens I took were more or less teneral and were taken in a small spruce grove close to a sphagnum bog which contained several open pools of water, in which I presume the nymphs lived."

Both Howe and Williamson were interested in obtaining a nymph of *Williamsonia* but neither succeeded. In the early 1930's Dr. James G. Needham of Cornell University offered five dollars and a copy of his book (Needham and Heywood 1929) to anyone at Harvard University who could produce a nymph of *Williamsonia*.<sup>3</sup> Apparently the prospect of wading in cold bogs in the early spring

<sup>1</sup>James Bryant Conant Laboratory, Harvard University, Cambridge, Massachusetts 02138.

<sup>2</sup>Biology Department, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139.

<sup>3</sup>This story was related to us by Dr. Floyd Werner, University of Arizona, who was a graduate student at Harvard at the time of Dr. Needham's offer.

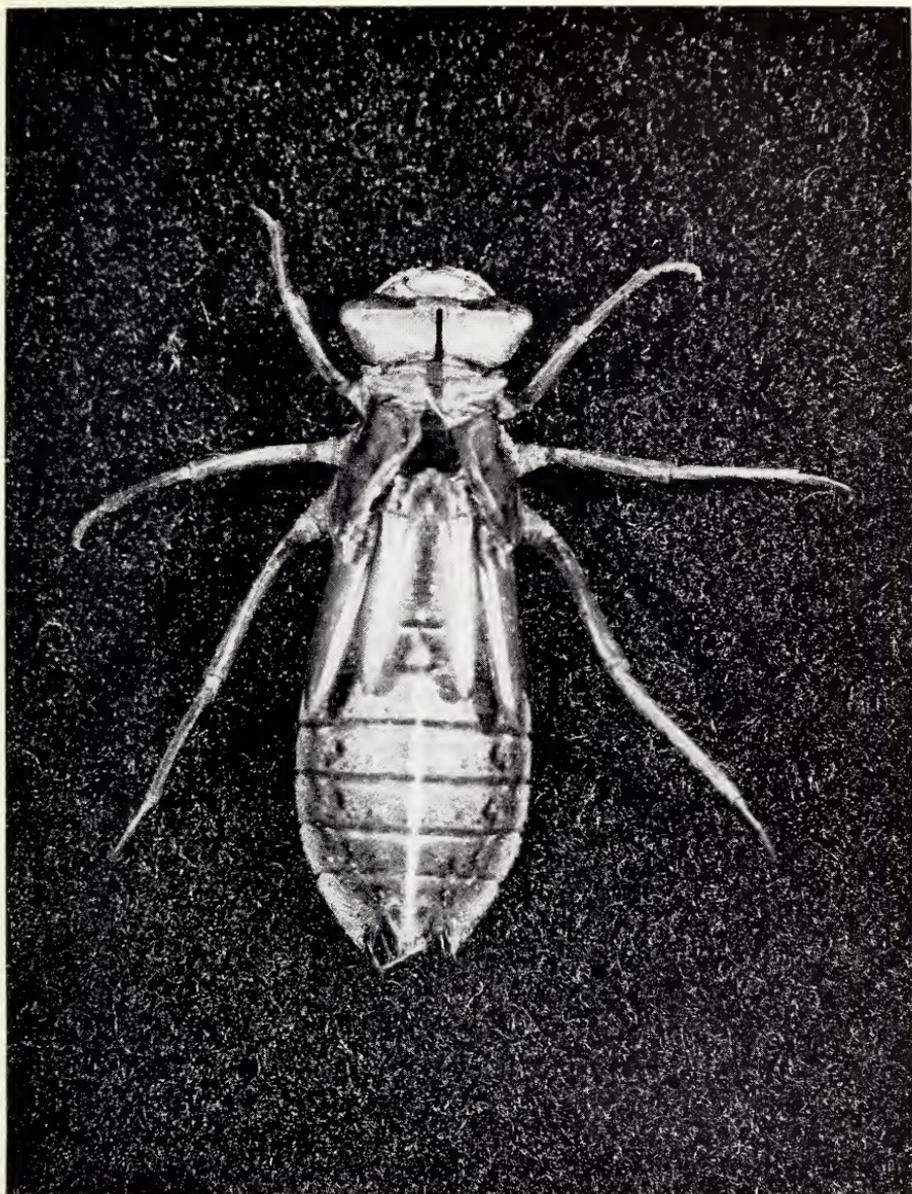


Figure 1. Dorsal view of an exuvia of *Williamsonia lintneri*, male.

searching for an unknown nymph was not worth the reward even during the Depression, for the search was never made. Since that time few serious attempts to collect the nymph have been made. With the exception of a few predominantly tropical genera whose ranges extend into extreme southern United States or northern Mexico, *Williamsonia* is the last genus of Nearctic Odonata for which the nymph heretofore has been undescribed.<sup>4</sup> In this paper we describe the nymph of *Williamsonia lintneri*.

During May for the past three years we have frequently collected adults of *lintneri* in the vicinity of a 40-hectare bog adjacent to Ponkapoag Pond in the Blue Hills of eastern Massachusetts (42° 12'N, 71° 06'W). Our observations of the adults range from 30 April to 26 May. Although we rarely observed adults in the bog, their close association with the woodlands bordering the bog suggested that the bog, not the pond, was the habitat of the nymph. Dredging at several locations within the bog was unsuccessful; however, the flushing of a teneral adult from its site of emergence on 2 May 1970 led to the discovery of twelve exuviae and a full grown nymph which emerged three hours after its capture. The exuviae were shown to be *lintneri* by comparison to the exuvia of the reared nymph.

The nymph and exuviae were collected adjacent to a log path where it crosses an overgrown channel 275 m from the bog margin. Here, in contrast to most other parts of the bog, the water is deep and remains year-around despite fluctuations created by summertime irrigation of a nearby golf course. Highbush blueberry (*Vaccinium corymbosum*), swamp laurel (*Kalmia polifolia*), leather leaf (*Chamaedaphne calyculata*), and Atlantic Coast White Cedar (*Chamaecyparis thyoides*) form dense thickets on both sides of the channel while the channel itself is choked with sphagnum, water arum (*Calla palustris*), and other water plants.

All of the exuviae of *Williamsonia lintneri* were found within 15 cm of the water surface on emergent vegetation. Over half (7) of the exuviae were clustered within a two square meter area where young shoots of marsh grass were particularly dense. The teneral adults observed in the bog and the emergence of the reared nymph suggest that emergence takes place about midday. The fact that all but three of the exuviae collected in the area mentioned above were collected on or before 3 May indicates that the peak emergence

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<sup>4</sup>Dr. Minter J. Westfall, Jr., personal communication.

period was over by that time. On 3 May the surface water temperature was 15°; 60 cm below the surface the temperature was 10°.

In association with *lintneri* were nymphs of *Libellula quadrimaculata* L., *Sympetrum rubicundulum* (Say), and *Chromagrion conditum* (Hagen). In addition an exuvia of *Leucorrhinia hudsonica* (Selys) was found in the same area. Later in the year this portion of the bog is inhabited by the above species as well as *Gomphaeschna furcillata* (Say), *Nannothemis bella* (Uhler), *Leucorrhinia proxima* Calvert, and a large population of *Nehalennia gracilis* Morse.

*Williamsonia lintneri* (Hagen)

*Specimens examined* — An exuvia from a nymph which emerged in captivity and twelve exuviae collected 2 May - 9 May 1970 at Ponkapoag Bog, Blue Hills Reservation, Norfolk County, Massachusetts.<sup>5</sup>

*Description* — Body length 17-18 mm, width of the abdomen 7.5 mm. In general appearance the nymph is light brown in color and practically devoid of prominent setae except on the hind margin of abdominal segment 9 and on the hind tibiae. The dorsum of the abdomen is speckled with small spots of darker pigmentation and a narrow stripe of lighter pigmentation extends down the dorsal ridge (Figure 1). The wing sheaths extend to the base or middle of abdominal segment 6. Dorsal spines are present on abdominal segments 3 through 9. In profile (Figure 2) they are rather small and project posteriorly. Lateral spines are present only on abdominal segment 9 where they form about one-third of the lateral margin of that segment. Setae along the posterior margin of segment 9 are about twice as long as the lateral spines.

There are seven antennal segments. There are no dorsal horns on the head. The labium is as shown in Figure 3. Premental setae (terminology of Corbet 1953) usually number 12 + 12 but a range from 11 + 11 to 12 + 12 was observed. The even spacing of the 8 palpal setae on each palpus is interrupted slightly between

<sup>5</sup>Of these specimens seven have been distributed to the following institutions and investigators: Florida State Collection of Arthropods, Gainesville, c/o Dr. Minter J. Westfall, Jr.; Royal Ontario Museum, Toronto and The Canadian National Collection, Ottawa, c/o Dr. Philip S. Corbet; The U. S. National Museum, Washington, D. C., c/o Dr. Oliver S. Flint, Jr.; The University of Michigan Museum of Zoology, Ann Arbor, c/o Mrs. Leonora K. Gloyd; G. H. and A. F. Beatty, State College, Pennsylvania; and the Museum of Comparative Zoology, Harvard University, c/o Dr. Howard Evans.

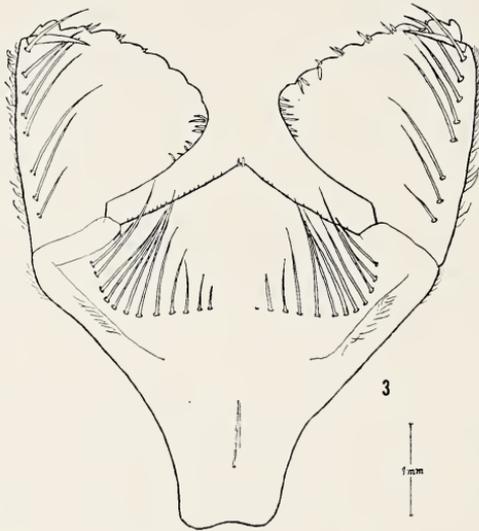
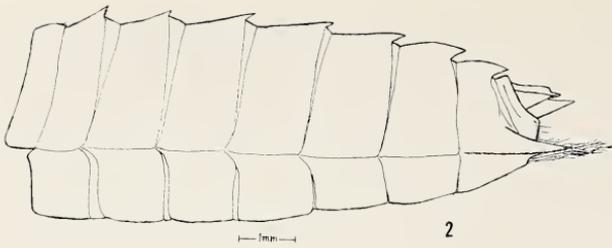


Figure 2. Lateral view of an exuvia of *Williamsonia lintneri*, male, showing dorsal spines on abdominal segments 3 through 9 and the conspicuous setae on segment 9.

Figure 3. Labium of the nymph of *Williamsonia lintneri*.

the third and fourth setae from the proximal end. The distal margin of the palpus possesses seven or eight crenulations which become progressively deeper near the movable hook. Each crenulation except that nearest the movable hook usually bears two spiniform setae of unequal length. The inner margin of the palpus near the apex has about ten irregularly placed spiniform setae, which are directed inward. The legs are uniform in color with relatively few setae except on the middle and hind tibiae. The setae on the hind tibiae are arranged in two rows with the posterior one being more prominent.

*Discussion* — When Davis (1913) erected the genus *Williamsonia*, he noted the difficulties previous investigators had had in assigning *Williamsonia lintneri* to the already established genera. Certain characters of wing venation in particular were quite distinct while others suggested affinity with the Libellulidae. The nymph of *Williamsonia lintneri* also differs from those of other corduliid genera and consequently gets lost in the keys of Needham and Westfall (1955, p. 349) and of Gloyd and Wright (1959). In general appearance the nymph of *Williamsonia lintneri* somewhat resembles that of *Dorocordulia lepida* (Hagen); however, it is easily distinguished from that species and the nymphs of all other corduliid genera by the combined presence of dorsal hooks on abdominal segments 3 through 9 and lateral spines on abdominal segment 9 only.

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The illustration on the front cover of this issue of *Psyche* is a line-cut photograph of a phasmatid (*Pseudophasma*) from Costa Rica, designed by Carl F. Moxey.

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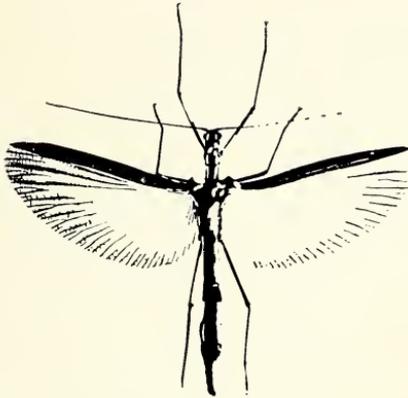
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The June, 1970, Psyche (Vol. 77, no. 2) was mailed January 29, 1971.

A NEW GENUS OF PONERINE ANTS  
FROM WEST AFRICA  
(HYMENOPTERA: FORMICIDAE) WITH  
ECOLOGICAL NOTES

BY WILLIAM L. BROWN, JR.<sup>1</sup>, WILLIAM H. GOTWALD, JR.<sup>2</sup>,  
AND JEAN LÉVIEUX<sup>3</sup>

During work in recent years in the Ivory Coast, one of us (Jean Lévieux) has collected 4 colonies and colony-fragments of an extraordinary small ponerine ant belonging to a new genus apparently related to *Amblyopone*, but having the petiole separated from the postpetiole by a deep vertical constriction. The formal description of this genus and species is offered below.

The characterization is greatly enhanced by scanning electron micrographs (Plates I, II) taken by Prof. Howard E. Hinton of the University of Bristol, England, for whose generosity we are most grateful.

**Apomyrma** genus nov.

Worker: Habitus in life and to the naked eye much that of a very small, slender, shining *Amblyopone*. Also reminiscent of *Leptanilla*.

Head oblong, depressed, parallel-sided, with rounded corners (like that of many female pristocerine Bethyridae), anterior corners of head unarmed. Eyes and ocelli lacking. Antennae 12-segmented, scapes very short and clavate, funiculus robust, with an indistinct 4-merous club. Antennal sockets round, impressed, completely exposed, the frontal carinae extremely reduced and indistinguishably fused with the reduced median portion of the clypeus to produce a small, subtriangular tumulus or convex platform that trails a brief septum posteriad scarcely beyond the level of the posterior socket

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<sup>1</sup>Department of Entomology, New York State College of Agriculture at Cornell University, Ithaca, New York 14850, USA.

<sup>2</sup>Department of Biology, Utica College of Syracuse University, Utica, New York 13502, USA.

<sup>3</sup>Laboratoire de Zoologie, École Normale Supérieure, Paris V, France. Research and publication aided by grants nos. 5574X and 24822 from the U. S. National Science Foundation to William L. Brown, Jr., principal investigator. Research of Jean Lévieux supported in large part by the Centre National de Recherche Scientifique de France.

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rims (see Fig. 5). Clypeus, except for the small raised median portion, impressed, very narrow and not distinctly demarcated behind, its anterior border shallowly but broadly concave, unarmed. The basal part of the labrum forms a straight line within the clypeal concavity, and bears a row (actually backed by a second row) of peg-like teeth that seem at first sight to spring from the clypeal margin. These teeth fill the narrow space between the clypeus and the normally closed mandible. Mandibles short, gently curved, and linear, with bidentate apex and a few blunt, spaced teeth on apical half of inner border. Labrum broader than long, sides converging distad; apex broadly emarginate; extensor surface with two irregular rows of peg-like teeth (or modified hairs) on basal half. Maxilla simplified from form of *Amblyopone pallipes* (see Gotwald, 1969), without galeal comb, and galeal crown smoothly continuing the dorsal galeal margin; maxillary palpus 2-segmented. Labium apparently without paraglossal lobes; setae of subglossal brushes tapered to apices; labial palpi 2-segmented.

Truncus (= alitrunk, = thorax + propodeum) long and slender, consisting of a convex, immarginate pronotum into which is flexibly fitted a slightly longer oblong portion consisting mainly of propodeum, meso- and metathorax; mesonotum reduced to a narrow, depressed transverse strip largely covered by posterior edge of pronotum except when pronotum is flexed downward. Propodeal dorsum almost flat (weakly convex), immarginate but with pleura perpendicular; declivity strongly convex, immarginate and unarmed, overhanging lower part and orifice. Bulla of metapleural gland conspicuously outlined through cuticle, subcircular; propodeal spiracle contiguous with it anteriorly. Coxae nearly the same size (anterior coxa largest); femora short and strongly incrassate toward their middle; tarsi short, slender at base but gradually becoming thicker to near their apices. Tibial spurs 1, 2, 2, the middle and posterior legs each with one large, broadly pectinate inner spur and a smaller, more slender, sparsely pectinate outer one. Metatarsus of anterior legs strongly

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Plate 1. *Apomyrma stygia*, worker of the small kind (type nest series), scanning electron micrographs by H. E. Hinton. A, head and part of truncus in oblique lateral view,  $\times 43$ . B, head in oblique dorsal view,  $\times 49$ . C, dorsal view of pronotum and adjacent structures,  $\times 104$ ; note reticulation of cervix and striation of mesonotum. D, back of head and cervix, dorsal detail,  $\times 248$ . E, lateral view of pronotum and adjacent structures,  $\times 83$ . F, oblique dorsal view of posterior part of dorsal pronotum, mesonotum, and propodeal dorsum, looking caudad,  $\times 104$ .

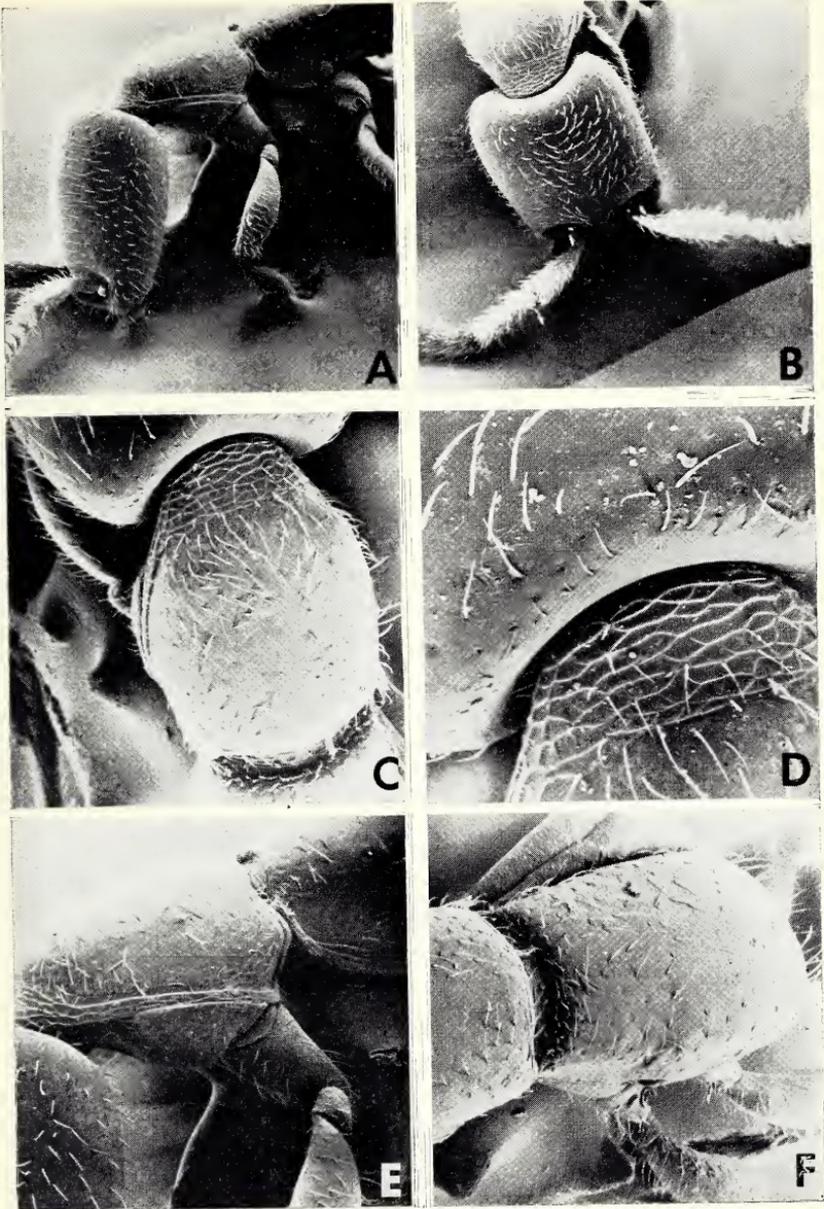


PLATE 1

curved, opposing the large pectinate tibial spur; other metatarsi straight, weakly clavate. Tarsal claws small, slender, simple.

Petiole with a massive subcubical node, a brief, slender, but distinct anterior peduncle, and a very short posterior peduncle. Both anterior and posterior faces of the node are vertical, and the petiole is connected to the gaster only by the narrowly strangulated connection of the posterior petiolar peduncle to the short anterior peduncle of the first gastric (postpetiolar) segment. Postpetiole (first gastric segment = true abdominal segment III) reduced in size, only slightly broader than petiole; much smaller than the following segment, and showing a very slight beginning of constriction from the latter (constriction a little more distinct in the queen). Sternum of postpetiole especially reduced, only weakly convex and with only a suggestion of bilateral anteroventral processes on either side of a shallow anteromedian impression. Second gastric (IV abdominal) segment the longest, widest and deepest of the gaster; larger than the remaining apical segments taken together; these taper to a rounded apex from which issues a very long, slender, curved sting. Postpetiolar tergum and the terga of all succeeding segments of gaster easily and cleanly separable from sterna.

Entire body shining, smooth, with abundant small, distinct, spaced punctures on dorsum of head, becoming fewer and smaller on truncus and remainder of body; legs and antennal funiculae becoming more densely and finely punctulate apicad; cervix and a few other areas on sides of truncus and node loosely reticulate.

Entire body (except lower sides of truncus) and appendages covered densely (more sparsely on underside of petiole and gaster) with short, fine, pointed hairs.

Color ferruginous yellow; mandibles and appendages lighter yellow.

Queen, alate: Like the worker in general form of body, but more robust overall. Eyes well-developed, pigmented and moderately convex, with about 10 facets across the greatest diameter, situated

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Plate 2. *Apomyrma stygia*, same worker as in Plate 1, scanning electron micrographs by H. E. Hinton. G, posterior part of truncus, oblique lateral view,  $\times 86$ . H, petiole and associated structures, lateral view,  $\times 87$ . I, closer view of propodal-petiolar articulation, showing details of sculpture and of spiracles,  $\times 203$ . J, lateral view of hind tibial apex, showing coarsely pectinate smaller spur lying over larger, broader, more regularly and finely pectinate medial spur,  $\times 203$ . K, portions of the 3 apical segments of an antenna, showing reclinate peg-like sensilla and finer setae,  $\times 428$ . L, end of front tarsus, showing a tarsal claw,  $\times 473$ .

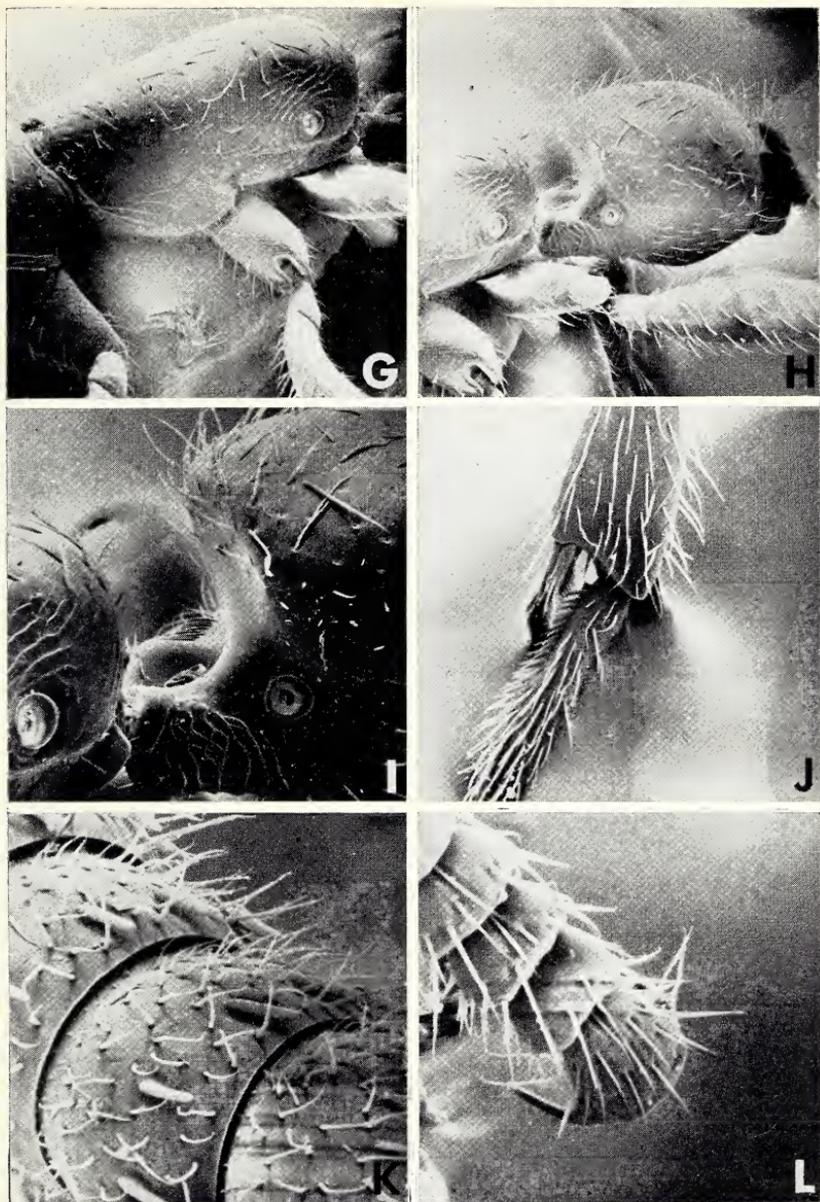


PLATE 2

far back, at about the posterior quarter of the head length. Ocelli developed, situated between compound eyes. Pterothorax well developed but nearly flat, continuing the nearly straight (very feebly convex) dorsal profile of the truncus as seen from the side. Scutum, prescutellum (= axillary area) and scutellum all developed, flat, the scutum without recognizable notauli or parapsidal furrows. Wings delicate, hyaline, microtrichiate.

The second and third free abscissae of Rs are wanting, creating a large cubital cell; Mf<sub>4</sub> is completely lacking, and there is even a small gap left at its former origin at the angle between Mf<sub>3</sub> and r-m, so that the cubital cell is not completely closed at its posterodistal corner (Fig. 7). Rs narrowly recurved into costal margin about halfway between pterostigma and wing apex, thus enclosing a fairly long radial cell; except for Rs, apical half of wing membrane without veins. Hind wing narrow, acutely rounded, venation restricted to R + Sc, which fades out before reaching midwing; hamuli small and weak, 5 in number in the specimen counted; no anal lobe.

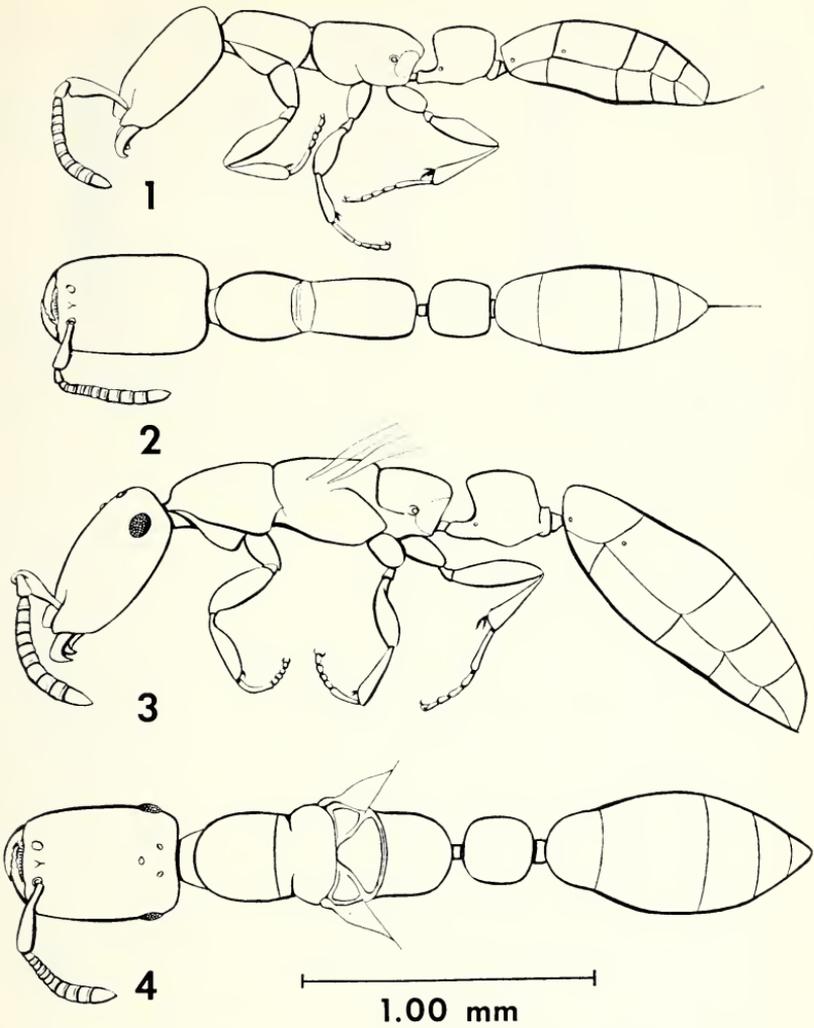
Petiolar node and gaster a little wider than in worker, and the incipient constriction between postpetiole and succeeding segment a bit more distinct. Form of body, sculpture, pilosity and color otherwise much as in worker (the pilosity may be slightly more abundant and a bit longer.)

Type species, by present designation:

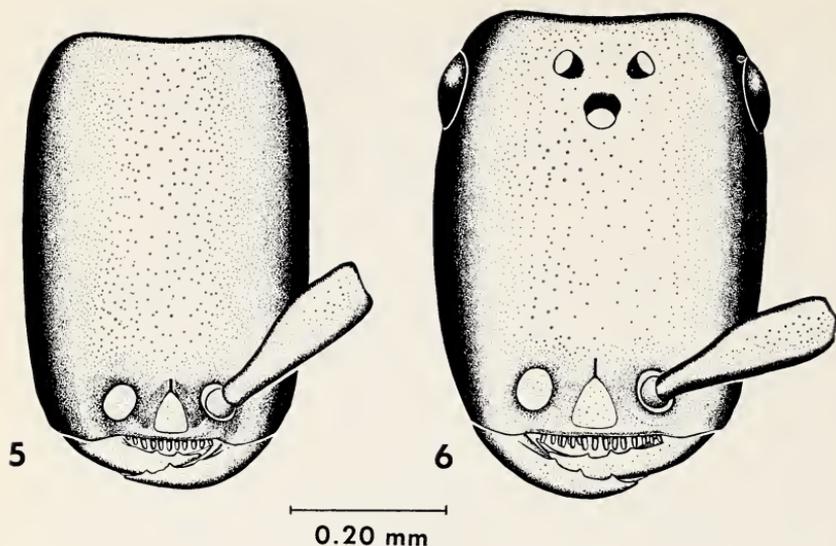
### *Apomyrma stygia* species nov.

Worker, small form, composite description — total length (TL) 2.0 - 2.2 mm, head length (HL) 0.46-0.50 mm, head width (HW) 0.32-0.34 mm, cephalic index (CI) 68-70, scape length 0.20-0.22 mm, hind femur length 0.22-0.24 mm, length of trunk (WL) 0.59-0.69 mm, length of petiole with anterior and posterior peduncles 0.27-0.28 mm, length of petiolar node 0.20-0.21 mm, width of node 0.18-0.20 mm, length of postpetiole (first gastric segment) 0.16-0.19 mm, width of postpetiole 0.23-0.26 mm. Length of hairs about 0.01-0.04 mm, mostly 0.02-0.03 mm. Hairs mostly erect, many inclined at different angles. The distribution of superficially reticulate areas on the cervix and lower sides of pronotum, on coxae, on sides of propodeum around spiracle, and on anterior sides of petiolar node are shown well in the scanning electron micrographs (Plates I, II). The SEM also shows the sunken, narrow mesonotum to be transversely striolate.

Worker, large form (from nest AA 315 N1) — TL 3.0-3.1



Figures 1-4, *Apomyrma stygia* sp. n., small form, worker and queen, habitus drawings, pilosity omitted. Fig. 1, worker, lateral view. Fig. 2, worker, dorsal view. Fig. 3, queen, lateral view, wings omitted. Fig. 4, queen, dorsal view, wings omitted.



Figures 5-6, *Apomyrma stygia* sp. n., small form, heads in dorsal view, pilosity omitted. Fig. 5, worker. Fig. 6, queen.

mm, HL 0.62-0.65 mm, HW 0.47-0.50 mm (CI 76-77), scape L 0.29-0.30 mm, hind femur L 0.35-0.36 mm, WL 0.91-0.96 mm, petiole L 0.38-0.41 mm, petiolar node L 0.27-0.29 mm, petiolar node W 0.30-0.32 mm, postpetiole L 0.25 mm, postpetiole W 0.42 mm.

Distinctly more robust than small form; head, truncus, petiolar node, postpetiole and rest of gaster all relatively wider. Color darker, medium ferruginous. Punctures on head a little more numerous and much more distinct, at least in part because of the darker ground color. Otherwise, the large form is very similar to the small form, and probably is no more than a size variant of the same species showing slight allometric tendencies.

Queen, alate small form (holotype), from nest of 17 June, 1968 — TL 3.0 mm, HL 0.57 mm, HW 0.43 mm, (CI 75), scape L 0.26 mm, hind femur L 0.32 mm, forewing L 1.95 mm, WL 0.95 mm, petiolar node L 0.27 mm, petiolar node W 0.30 mm, postpetiolar node L 0.19 mm, postpetiolar node W 0.26 mm, greatest diameter of compound eye 0.11 mm.

Queen, dealate small form, from nest AA 318 N<sub>1</sub> — TL 2.7 mm, HL 0.54 mm, HW 0.41 mm (CI 76), scape L 0.24 mm, hind

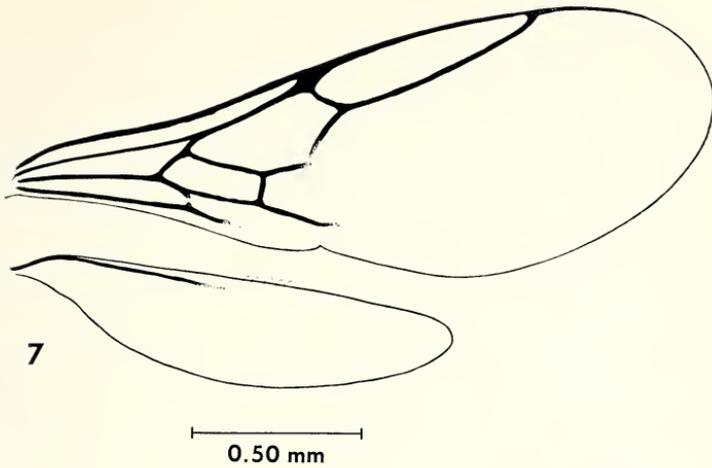
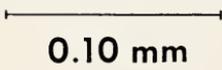
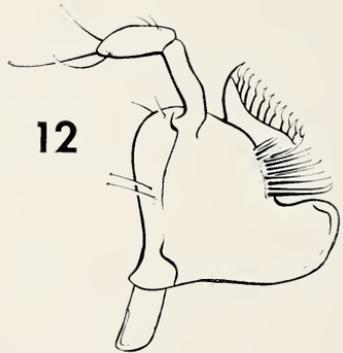
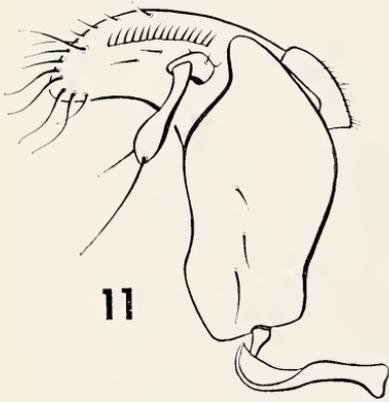
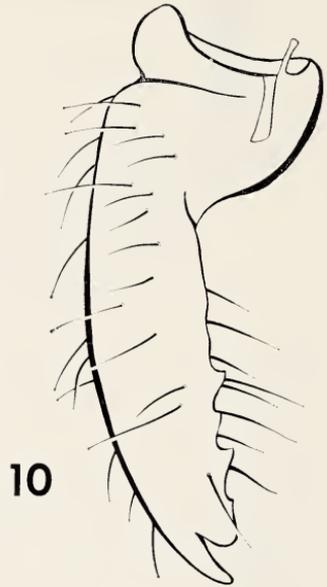
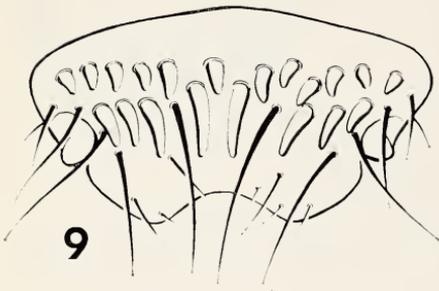
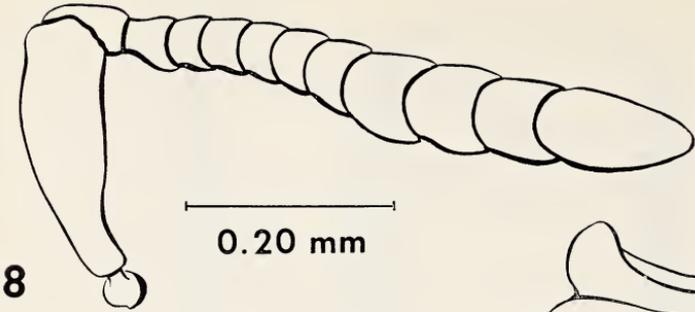


Figure 7, *Apomyrma stygia* sp. n., small form, wings of queen.

femur L 0.30 mm, WL 0.94 mm, petiolar node L 0.24 mm, petiolar node W 0.27 mm, greatest diameter of compound eye 0.095 mm.

Ergatoid — Two specimens from the type nest are intermediate between winged queens and workers from this nest series in size, and wings or wing stumps are absent. The mesonotum is reduced to a subquadrate piece. Compound eyes are present but smaller than in winged queens; 3 ocelli are present.

Male, pharate adult: removed from cocoon, which is similar in size and color to the small-form worker cocoons with which it was mixed in type nest. Pupal skin partly removed by needle. Total length (TL) about 2.8 mm, HL about 0.4 mm, WL about 1.1 mm. The specimen is still pale, with compound eyes in the purple stage (greatest diameter 0.24 mm), and only the first faint flush of tannish pigmentation showing, mainly on truncal dorsum. Numerous fine brownish points probably indicate the presence of an abundant fine pilosity. Details of smaller mouthparts cannot be made out, since the parts are still soft and transparent, but the mandibles are vestigial, small and triangular, with rounded apices, separated by nearly the whole width of the labrum. Details of middle front of head also obscure, but from what can be seen, not much different from the worker here. Antennae 13-segmented, with very short scape, funicular segments varying from about as broad as long to longer than broad; apical segment longest. Truncus as in Fig. 19; wings not yet unfolded. Petiole short, much higher and broader than long,



thick-squamiform, with a free steep, flat anterior face, but attached over nearly its entire posterior face to the next gastric segment (postpetiole). This petiole is an axially-compressed version of the usual amblyoponine pattern. Gaster not unusually long, tapering gradually toward apex; genitalia not distinct, and represented in Fig. 19 only as a rough approximation. The integument, as far as it is developed, seems relatively smooth and featureless overall, though, as mentioned above, the punctulation is apparently rather dense.

Pupae, worker, queen and male, enclosed in white cocoons, about 2.0 to 2.6 mm long in the small form and 3.1-3.5 mm in the large form, with conspicuous black meconial spot at one end.

Larvae to be described separately by George C. and Jeanette Wheeler in a paper accompanying this one.

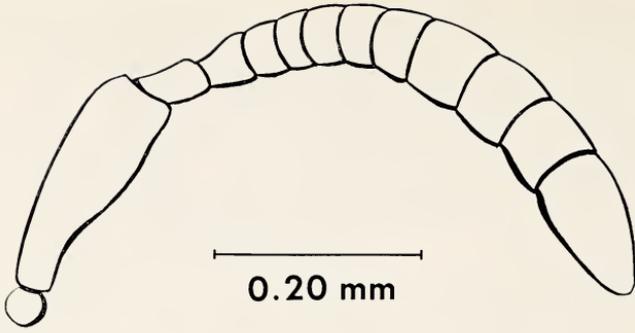
The type nest and 3 additional samples all came from the vicinity of Lamto Field Station of the University of Abidjan, south-central Côte d'Ivoire. Lamto is off the main highway 50 km or so south of Toumodi, the nearest town of any size. The holotype and some paratypes are deposited in the Musée Nationale d'Histoire Naturelle, Paris. Other paratypes are placed in the Museum of Comparative Zoology at Harvard University, the British Museum (Natural History), the Muséum d'Histoire Naturelle of Geneva, Switzerland, and elsewhere.

### Bionomics

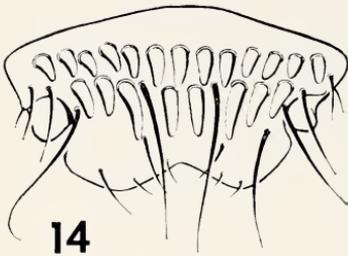
So far, *Apomyrma stygia* has been found only in the vicinity of Lamto. This is a region where savanna of the "Guinean" type interdigitates with the gallery forest of the Bandama River and its tributaries. *A. stygia*, which almost certainly is completely subterranean (except possibly for nuptial flight or promenade), is found here only by digging in the soil of the gallery forest and the "unburned" savanna. Unburned savanna has been spared the passage of fire for at least 6 years, with the result that thick vegetation renders the microclimate at the surface similar to that of the humus level in the gallery forest. Up to the present, extensive digging in

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Figures 8-12, *Apomyrma stygia* sp. n., small form, antenna and mouthparts of queen. Fig. 8, antenna. Fig. 9, labrum, external view. Fig. 10, right mandible, dorsal view. Fig. 11, left maxilla, external view; the maxillary comb has been drawn as seen through the transparent galea. Fig. 12, labium with left labial palpus, lateral view.



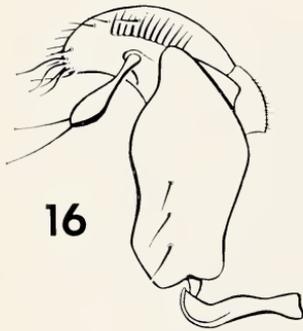
13



14

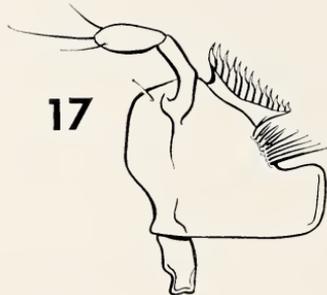


15



16

0.10 mm



17

the annually-burned savanna (by Lévieux) has failed to turn up any samples of the new species, either as colonies or as single foraging workers. *Apomyrma* and the 5 or 6 *Amblyopone* species also found here constitute a remarkable and unexpected cryptic soil faunule, some members, perhaps all, of which belong to a centipede-feeding guild. This assemblage was revealed only by systematic large scale excavation and sifting of the soil in the course of intensive studies of savanna ant ecology conducted since 1962 at Lamto.

Like the *Amblyopone* species at Lamto, *Apomyrma stygia* is probably best considered as an invader of the savanna via the gallery forest from the more extensive rain forest belt to the south. So far, excavations like those completed at Lamto have not been made in the rain forest proper, and have been made only to a limited extent in gallery forest. *Apomyrma*, like many of the other subterranean predatory ponerines, moves deep (30 cm or more) into the soil during the dry season (October to April), but during the rainy season it comes up to within 10 cm of the surface.

The 4 nests of *A. stygia* were all found during April-June 1968. Nos. AA 315 N1 and AA 318 N1 (both May 1968) were taken in sandy alluvial soil of the gallery forest of the Bandama River. The soil surface in each case, while tree-shaded, was bare of herbage. AA 315 N1, a nest of nest fragment of the large form consisting of 12 workers and a single dealate queen, was taken about 10 cm deep, and was found in the same meter quadrat as *Amblyopone* sp. near *normandi*. AA 318 N1, 15 workers and a dealate queen, was found about 15 cm beneath the surface and in the same meter quadrat as a colony of *Amblyopone mutica*.

The type nest (without code number) was taken 17 June 1968; it and AA 285 N8 came from unburned savanna with dark clayey "terre noire" soil bearing a cover of the grass *Loudetia simplex* growing about 1 m high. The nest contained about 75 workers, 6 alate and 15 dealate queens, 2 ergatoids, and a few pupae and pharate adults of queens, males and workers, plus a few larvae of different sizes.

The type nest was 15-20 cm in diameter and 2 cm high, containing the brood, most of the adults, and cut-up remains of a geophilomorph

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Figures 13-17, *Apomyrma stygia* sp. n., small form, antenna and mouthparts of worker. Fig. 13, antenna. Fig. 14, labrum, external view. Fig. 15, right mandible, dorsal view. Fig. 16, left maxilla, external view; the maxillary comb has been drawn as seen through the transparent galea. Fig. 17, labium with left labial palpus, lateral view.

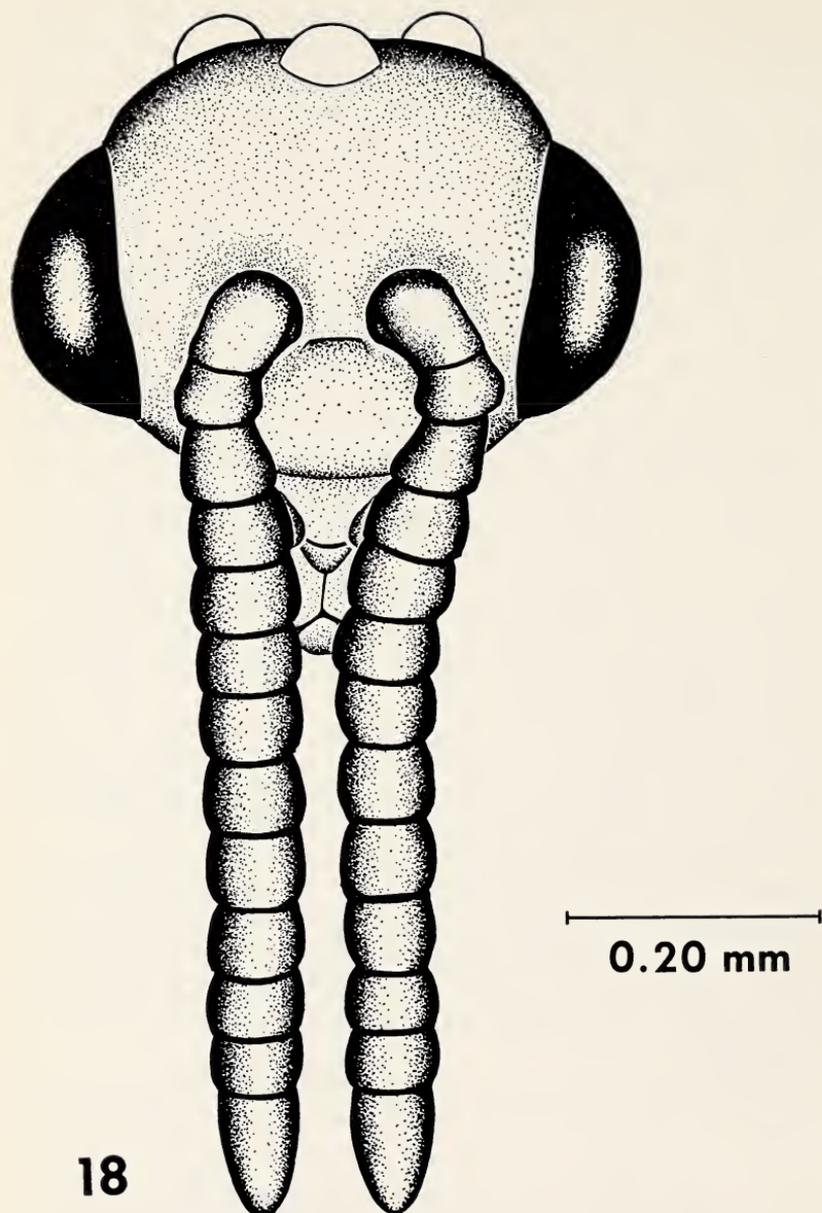
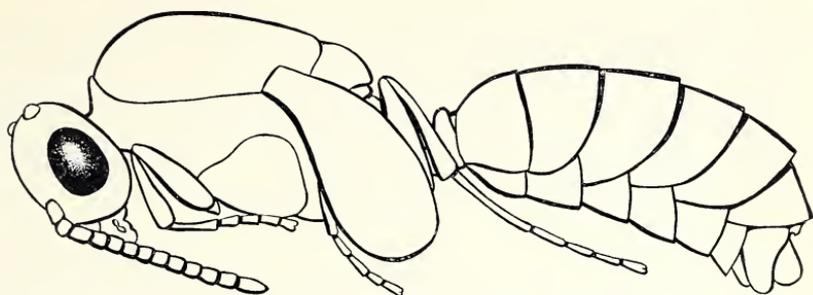


Figure 18, *Apomyrma stygia* sp. n., small form, head of pharate male in dorsal view, pilosity omitted.



19



1.00 mm

Figure 19, *Apomyrma stygia* sp. n., small form, pharate male, habitus drawing, lateral view, pilosity omitted.

centipede determined by M. Demange of the Musée Nationale d'Histoire Naturelle, Paris, as belonging to genus *Schendylurus*. This suggests that *Apomyrma*, like a larger new species of *Amblyopone* found at Lamto, is a specialist predator of geophilomorph chilopods. Of course, direct observations on feeding are needed.

The colony did not occupy more than a part of the cavity, and it seems likely that the workers merely touched up a pre-existing hollow of some sort. From the main chamber ran several passages in different directions. Their diameter (less than 3 mm), their position and lengths, as far as one could follow them, resembled the paths of vanished grass roots. After finding this nest, the soil was dug carefully for a meter around it and to a depth of 30 cm, but no more specimens were found.

AA285 N8, found 16 April 1968, consisted of about 32 workers and a dealate queen from a small pocket about 20 cm deep.

The occurrence of winged sexual adults and pupae in mid-June suggests that *Apomyrma* has a nuptial season in late June, a little later than that assumed for *Amblyopone* species at Lamto.

#### Taxonomic position

This species is without much doubt related to *Amblyopone*. The

head and truncus, while modified from the general amblyoponine form, nevertheless do not depart from it radically, and the extreme posterior placement of the queen's eyes is a "super-amblyoponine" character. However, the very deep constriction between the petiole and postpetiole, and the strong reduction (but without significant post-constriction) of the postpetiole, are traits that do set *Apomyrma* off very strongly from *Amblyopone*. For a time, our instincts wavered in the direction of setting up a separate new tribe. In the end, the impressions of the collector (Léviex), and his observation that *Apomyrma* follows the generalized amblyoponine habit of preying upon chilopods, pushed us to the conclusion that the new genus is really basically an amblyoponine. Larval characters (see following paper) confirm this placement. This conclusion also tends to follow the good rule of taxonomic parsimony, so we foreswore the establishment of a new tribe, even though the morphological definition of tribe Amblyoponini thereby loses most of its former sharpness based upon the lack of constriction between petiole and postpetiole. Actually, this character is partly transgressed by some species of the Australian genus *Onychomyrmex*, and an African morphocline including *Amblyopone muticum* also shows one kind of approach toward the constriction of the posterior part of the petiole in that genus.

#### APPENDIX

##### Details of worker-female mouthparts

Labrum (Figs. 9 and 14): Distal margin emarginate but without medial cleft; numerous slender, tapering setae inserted on the distal two-thirds of the external surface; two rows of stout peg-like setae inserted on the proximal half of the external surface.

Mandible (Figs. 10, 15): Internal margin not distinctly divided into basal and masticatory components; provided with 1 apical and 1 subapical teeth, 3 to 4 denticles proximad of subapical tooth; numerous setae inserted on the dorsal and lateral surfaces and on the ventral surface of the internal margin.

Maxilla (Figs. 11, 16): Maxillary palpus 2-segmented. Stipes subrectangular but drawn into a blunt point distally; usually 3 setae inserted on the proximal external face; lateral shoulder evident but smoothly rounded; external surface without conspicuous sculpturing. Galea typically formicoid in shape, with well developed maxillary comb; galeal crown inconspicuous and bearing numerous setae; 3 to 4 setae approximate a galeal comb in position of insertion but

not in individual shape. Lacinia subquadrate with a rounded gonia and a pointed apex; lacinial comb reduced but continuous.

Labium (Figs. 12, 17): Labial palpus 2-segmented; premental shield lightly sclerotized and bearing only a few setae; subglossal brushes moderately developed, all included setae pointed; paraglossae and paraglossal sensory pegs absent.

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WHEELER, G. C. AND J. WHEELER

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THE LARVA OF *APOMYRMA*  
(HYMENOPTERA: FORMICIDAE)

BY GEORGE C. WHEELER AND JEANETTE WHEELER<sup>1</sup>

Recently Dr. W. L. Brown sent us for study the larvae of a new genus of ponerine ants from Ivory Coast collected by J. Lévieux. The adults of the genus are described in the previous article in this issue. Our descriptions of the larva follow:

Genus *APOMYRMA* Brown, Gotwald & Lévieux

Body elongate, terete, moderately slender and with the thorax slightly curved ventrally. Body hairs numerous, short, simple and generally distributed except on the intersegmental membranes. No spinules on the integument. Cranium transversely subelliptical in anterior view. Antennae with 2 minute sensilla each. Labrum narrow, elongate-parabolic, with the base dilated; with a few spinules on the posterior surface. Mandibles elongate and very slender; basal  $\frac{1}{4}$  abruptly dilated laterally; remainder slightly curved medially and posteriorly; apical tooth small; 2 small acute medial teeth; anterior surface smooth. Maxillary palps peg-like. Labial palps low rounded elevations. Maxillae, labium and hypopharynx without spinules.

The larva of *Apomyrma* resembles most closely those of *Prionopelta* (Wheeler and Wheeler 1952: 120, 141; 1964: 447, 460) in the tribe Amblyoponini, but differ as follows:—

CHARACTER	<i>Apomyrma</i>	<i>Prionopelta</i>
anus	terminal	subterminal
head size	small (body length: head length=15)	large (body length: head length=8)
cranium shape	transversely sub- elliptical	subcircular
antennae	2 sensilla	3 sensilla
labrum	narrow and elongate- parabolic	broad, transversely subrectangular and feebly bilobed
mandible base	abruptly dilated laterally	dilated basally
mandible blade	slightly curved medially	straight

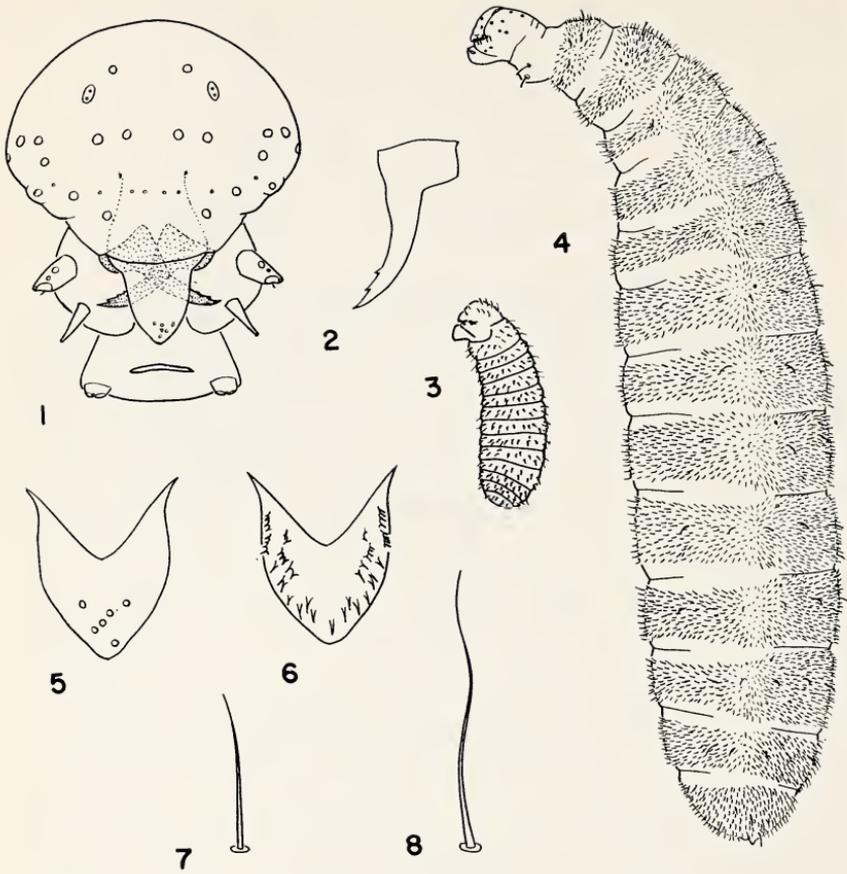
<sup>1</sup>Desert Research Institute, University of Nevada System, Reno, Nevada.  
*Manuscript received by the editor October 22, 1970.*

appearance of maxillae and labium	seemingly very large and flaring due to constriction at bases and to narrow labrum	seemingly normal
spinules on maxillae and labium	none	present
maxillary palp	a stout peg	bootee-shaped

*Apomyrma stygia* Brown, Gotwald & Lévioux

Length (through spiracles) about 2.3 mm. Moderately slender; abdomen elongate-ellipsoidal; posterior end narrowly rounded; thorax slightly curved ventrally, its diameter decreasing rapidly toward the anterior end; anterior half of prothorax forming a nearly hairless "broken" neck. Anus terminal with 2 lips, the posterior lip larger. Spiracles minute. Eleven differentiated somites. Integument apparently without spinules. Body hairs numerous, very short (0.02-0.06 mm long), the longest in a transverse band around the middle of each somite. Head small; cranium transversely subelliptical in anterior view; breadth equal to length; due to the narrowness of the labrum and the constriction of their bases, the maxillae and labium appear prominent and flaring. Head hairs few [all hairs broken on our material]. Antennae small, slightly raised, each with 2 minute sensilla. Labrum narrow and elongate-parabolic, with the base dilated; anterior surface with 6 irregularly placed sensilla; ventral border with 4 sensilla; posterior surface without sensilla but with a few relatively long spinules, isolated distally and in short arcuate rows basally. Mandibles feebly sclerotized; basal  $\frac{1}{4}$  abruptly dilated laterally, distal  $\frac{3}{4}$  narrow, slightly curved medially and posteriorly into an apical tooth; with 2 small acute subapical teeth on the medial border; anterior surface smooth. Maxillae lobose; apparently without spinules; palp a stout peg with 5 sensilla (1 large and encapsulated, 1 bearing a long peg); galea slender and digitiform. Labium about half as wide as head; apparently without spinules; palp a low knob with 3 sensilla; opening of sericteries wide. Hypopharynx apparently without spinules.

*Very Young Larva.* Length (through spiracles) about 0.7 mm. Subcylindrical, slightly attenuated anteriorly and slightly curved ventrally. Anus terminal, without lips. Apparently without integumentary spinules. Body hairs very few, simple, very short (0.004-0.012 mm long), in a band around the middle of each somite. Head



Figs. 1-8. *Apomyrma stygia*. 1. Head in anterior view (only bases of head hairs shown),  $\times 284$ . 2. Left mandible in anterior view,  $\times 520$ . 3. Very young larva in side view,  $\times 42$ . 4. Mature larva in side view (reconstruction),  $\times 42$ . 5. Anterior surface of labrum,  $\times 625$ . 6. Posterior surface of labrum,  $\times 625$ . 7 and 8. Two body hairs,  $\times 1065$ .

hairs few, simple, short (0.01 mm long). Antennae small, with 2 sensilla each. Labrum small; subparabolic in anterior view; breadth twice the length; with 4 ventral sensilla; apparently without spinules. Mandibles small; feebly sclerotized; subtriangular in anterior view; with 2 minute subapical teeth on the medial border. Maxillae large and lobose; apparently without spinules; palp a cluster of 5 sensilla; galea represented by 2 sensilla. Labium large; half as wide as head; apparently without spinules; palp a cluster of 4 sensilla. Hypopharynx apparently without spinules.

Material studied: numerous larvae from Ivory Coast, courtesy of Dr. W. L. Brown.

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THE *RAVILLA* GROUP OF THE ORBWEAVER GENUS  
*ERIOPHORA* IN NORTH AMERICA  
(ARANEAE: ARANEIDAE)\*

BY HERBERT W. LEVI

Museum of Comparative Zoology, Cambridge, Mass. 02138

The contradicting synonymies presented in the two recent catalogs of spiders (Roewer, 1942; Bonnet, 1955) reflect the confusion in names and species of *Eriophora* in the literature. Comstock (1940) indicates that specimens of *Eriophora* have been found as far north as Oregon. Presumably this error can be traced to the use of the George Marx collection by McCook and Keyserling. The Marx collection, housed in the U.S. National Museum, has unreliable locality labels. No recent collections of *Eriophora* from central and northern California have been seen.

The object of this revision was to find the differences among species of these very large, common orbweavers of the southern United States. The types of the old names were examined in hope of providing the stability and unversality required of animal names. Only adult specimens that I have myself examined were used for mapping ranges. Unfortunately, South American collections of Araneidae in North American museums are unsorted and only a few specimens provided records for the southern limits of the distributions.

Dr. M. H. Robinson of the Smithsonian Tropical Research Institute, Panama Canal Zone, called my attention to his immediate need of an *Eriophora* revision to make it possible for him to publish his behavior observations. I take this opportunity to thank Dr. J. G. Sheals and Mr. D. Clark for the hospitality extended when I worked at the British Museum (Natural History), and to thank Mr. Clark for numerous favors. Collections were made available by Dr. W. J. Gertsch and Dr. J. A. L. Cooke of the American Museum of Natural History, Dr. M. Grasshoff of the Senckenbergischen Naturforschenden Gesellschaft, Frankfurt, Dr. J. Prószyński, Polish Academy of Sciences, Warsaw, Dr. D. C. Robinson and Mr. C. E. Valerio of the biology department of the University of Costa Rica, San José, Dr. H. V. Weems, Florida State Museum, Gainesville, Prof. H. K. Wallace, University of Florida. Additional specimens were made available by Dr. L. van der Hammen, Natural History

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Fig. 1a. *Eriophora fuliginea* feeding on a bat. On the left are two web parasites belonging to the genus *Argyrodes* (Theridiidae). Photograph taken in the Panama Canal Zone by Dr. R. Akre.

Museum, Leiden, Dr. M. Moritz, Zoologisches Museum der Humboldt Universität, Berlin, Prof. R. D. Schiapelli and Mrs. B. G. dePikelin, of the Museo Argentino de Ciencias Naturales, Buenos Aires, Mr. D. Bixler and Dr. R. E. Leech. This investigation was supported in part by Public Health Service Research Grant AI-01944 from the National Institute of Allergy and Infectious Diseases, and published with a grant from the Museum of Comparative Zoology.

At present I consider *Paravixia* a synonym of *Eriophora*. However, the species customarily included in *Paravixia* are not included in this paper. They are much less common and most are South American, the most northern ones coming from Mexico. Collections from these areas have not been sufficiently sorted and few specimens are available. The publication of this paper is necessitated by the immediate need for names and means of identification of these common species.

*Eriophora* Simon

*Eriophora* Simon, 1863, Histoire Naturelle des Araignées, ed. 1, p. 261.

New subgenus of *Epeira* (= *Araneus*). The type of *Eriophora* is *Epeira ravilla* C. L. Koch as designated by F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, vol. 2, p. 461. The gender is feminine.

All *Eriophora* species differ from *Araneus* by having a paramedian apophysis in the palpus (PM in Figs. 2, 4).

The female has the second leg almost the same length as the first (Fig. 1b); the third is always shortest. The median eyes are separated by about their diameter or less. The clypeus width is less than the diameter of the anterior median eyes. The abdomen shape varies from bluntly pointed anteriorly, acutely pointed posteriorly, and widest in the anterior third, to almost spherical (Fig. 32). The posterior of the abdomen is generally high above the spinnerets (Figs. 22-24). There are often posterior or dorsal tubercles on the abdomen: In *E. ravilla* there is one posterior to another; in *E. edax* (Figs. 42-44) there is always one distinct tubercle and often more. The venter has a median black patch (Figs. 16, 31).

The lateral eyes of males are on a short stalk, the medians on a projection. The small chelicerae are long, attenuated and concave anteriorly, providing space for the large palps. The first coxae of males have a hook on the distal margin (absent in *E. nephiloides*). The second tibiae are modified, most so in *E. ravilla* (Fig. 8), only swollen in *E. nephiloides*. The fourth coxae have a row of transverse macrosetae in *E. edax* (Fig. 48) and thin setae in *E. nephiloides* (Fig. 58). An unusual character is the presence of two strong macrosetae on the fourth trochanter of males (Figs. 7, 48) (except in *E. nephiloides*, which has only some weak setae).

Juvenile specimens of *Eustala* and *Eriophora* are often confused.

*Genitalia.* The epigynum is very small in *E. nephiloides*; in most other species it has a relatively long scape. The scape is attached to the anterior of the base and bends backward; in *Verrucosa* and in species previously considered to belong to *Paravixia*, it is attached ventrally. In *E. ravilla* and *E. fuliginea* the scape breaks off, probably in mating, and about half the females of these two species in collections lack the scape. It does not break off in the other two species, though *E. edax* may very rarely have the tip of the scape broken off. The base of the epigynum contains the seminal receptacles (SR in Figs. 5, 6). The shape of the seminal receptacles probably differs in different species, as reflected by the proportions of the base; this possibility was not pursued because the base is so

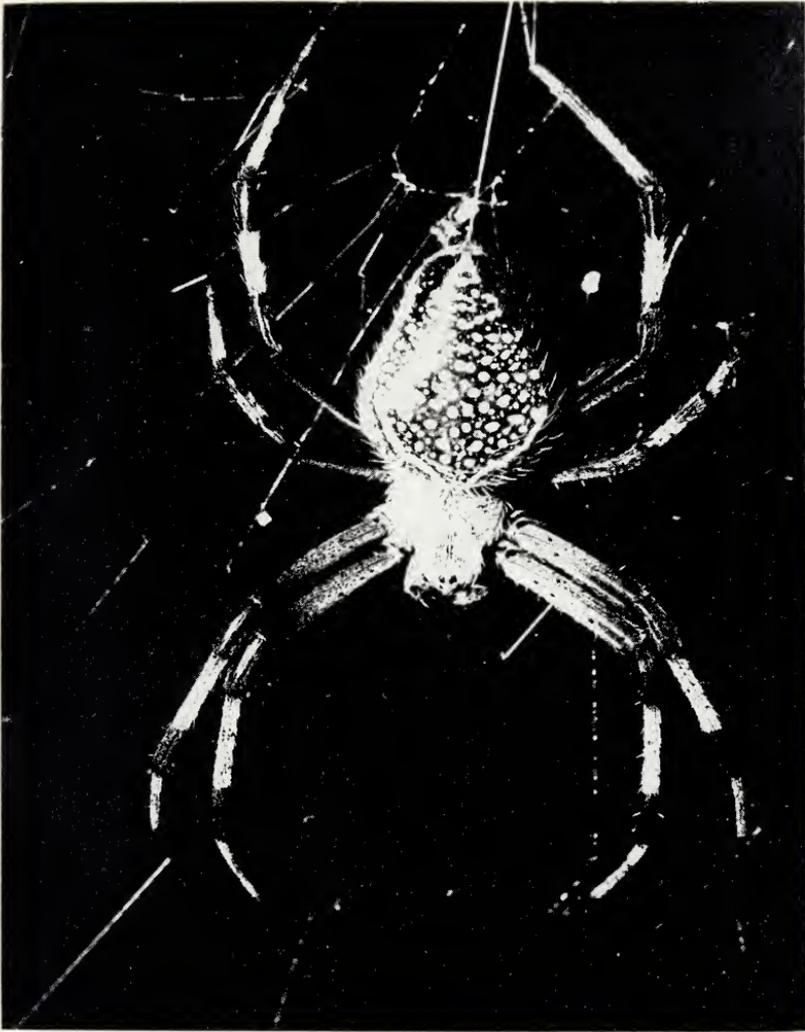


Fig. 1b. *Eriophora nephiloides*. Photograph taken at Barro Colorado Island, Panama Canal Zone by Dr. M. H. Robinson.

heavily sclerotized that the character would be almost useless for separating species. The openings are ventral, under the scape (Fig. 5). The openings are bordered posteriorly by a triangular piece (Figs. 5, 14). There are no sclerotized basal lamellae as in some species of *Araneus* and *Verrucosa*.

The patella of the palpus has two macrosetae of which one may be much longer than the other.

The palpus of *Eriophora* was first described by Comstock (1910, 1912, 1940). In all species of *Eriophora* the palpus is similar in structure. The radix (R of Figs. 2-4), stipes (I) and median apophysis (M) are elongated compared to *Araneus*, but the tegulum (T) is compact (Figs. 2-4). As a result, the median apophysis has shifted laterally from the ventral position it occupies in *Araneus*, and if viewed from the mesal side seems to be behind the embolus (E in Fig. 4). A separate piece, called the paramedian apophysis (PM) by Comstock, is present. In *Verrucosa*, which has a similar palpus, the piece is not separate, but is an extension of the proximal end of the conductor. Perhaps because parts of the bulb are elongated, the cymbium (Y) is very narrow and canoe-shaped. Unlike *Araneus*, *Eriophora* has little distal hematodocha (DH) and the terminal apophysis (A) and embolus (E) are on a complex V-shaped structure that has only limited articulation with the stipes (I). A spur of the terminal apophysis is probably homologous to the sub-terminal apophysis of *Araneus*. If there is a tip that breaks off the embolus in mating, it must be small. None was seen, but emboli were not examined under a compound microscope.

Data from the collections indicate that throughout the range of the genus (except possibly the most northern parts), adult males can be found throughout the year and there is no definite season of maturity as in the species related to *Araneus diadematus*.

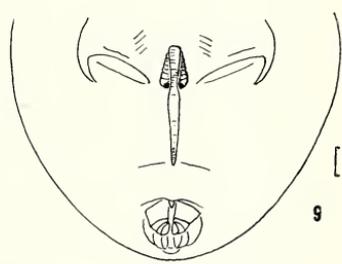
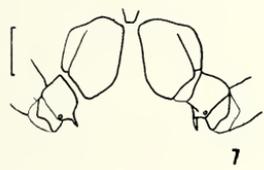
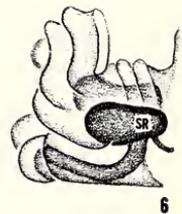
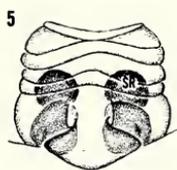
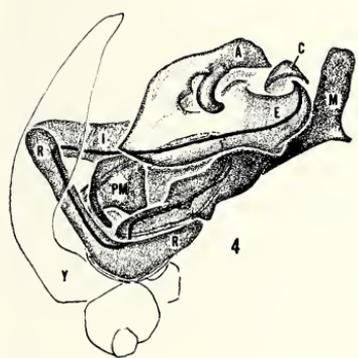
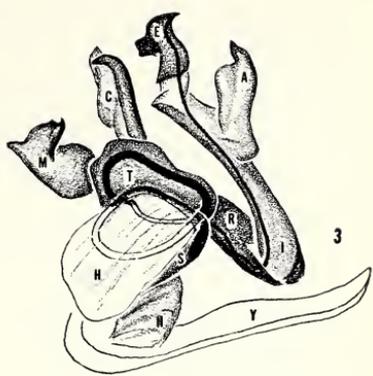
*Web.* The web of *E. fuliginea* (according to M. H. Robinson, personal communication) has an open hub and usually is very asym-

Figs. 2-6. Structure of *Eriophora* genitalia, diagrammatic. 2-4. Left palpus. 2. Expanded, mesal. 3. Expanded, lateral. 4. Contracted, mesal. 5-6. Base of epigynum.

Figs. 7-9. *Eriophora ravilla* (C. L. Koch). 7. Male, fourth coxae and trochanters, ventral view. 8. Male, left second tibia and tarsus, ventral view. 9. Female, abdomen with epigynum, ventral view.

*Abbreviations:* A, terminal apophysis; C, conductor; D, sperm duct; DH, distal hematodocha; E, embolus; H, basal hematodocha; I, stipes; M, median apophysis; PM, paramedian apophysis; P, paracymbium; R, radix; S, subtegulum; SR, seminal receptacle; T, tegulum; Y, cymbium.

*Size Indicators:* 1 mm.



metrical. The hub is in the upper third of the web. The web may be as large as 1.6 to 2 m in diameter. The spider occupies a retreat to the side.

*Distribution.* There are specimens of *Eriophora* species in collections from New Guinea, New Caledonia, New Zealand and Australia. One species belonging to the genus has recently been described from South Africa.

Key to North American species of the *ravilla* group of *Eriophora*

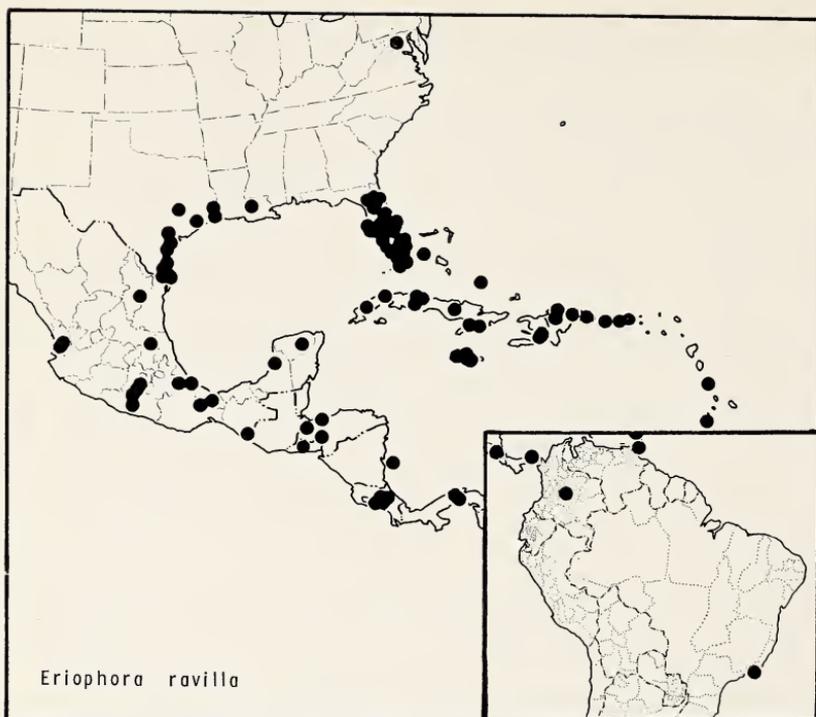
- |  |                    |
|--|--------------------|
| 1a. Males .....  | 2                  |
| 1b. Females .....  | 5                  |
| 2a. Fourth coxa with a transverse row of 3 macrosetae (rarely, only 2 in northern specimens) (Fig. 48) .....   | <i>edax</i>        |
| 2b. Fourth coxa without a transverse row of macrosetae (Figs. 7, 34) .....   | 3                  |
| 3a. Median apophysis of palpus short, framed by other structures (Fig. 49) .....   | <i>nephiloides</i> |
| 3b. Median apophysis of palpus long, extending beyond other structures (Figs. 10, 25, 35) .....  | 4                  |
| 4a. Median apophysis with a spur (Figs. 2, 10); tip of embolus drawn out, recurved (Fig. 11) .....   | <i>ravilla</i>     |
| 4b. Median apophysis without a spur (Fig. 25); tip of embolus with a flap on its side (Fig. 26) .....  | <i>fuliginea</i>   |
| 5a. Carapace, coxae yellow, sternum black; epigynum of minute size (Figs. 51, 54) .....  | <i>nephiloides</i> |
| 5b. Coloration otherwise; epigynum of normal proportions .....   | 6                  |
| 6a. Posterior of dorsum of abdomen with a distinct hump (Fig. 42); scape of epigynum usually with a keel, sometimes circular in cross section, rarely broken off (Fig. 37) ..... | <i>edax</i>        |
| 6b. Posterior of dorsum with only a slight hump or none at all (Figs. 22-24); epigynal scape without a keel or often broken off (Figs. 12, 27) .....                             | 7                  |
| 7a. Base of epigynum wrinkled (Fig. 13) .....  | <i>ravilla</i>     |
| 7b. Base of epigynum not wrinkled, but flat shield-shaped (Fig. 28) .....  | <i>fuliginea</i>   |

*Eriophora ravilla* (C. L. Koch)

Map 1; Figures 7-24

? *Epeira circulata* Walckenaer, 1841, *Histoire Naturelle des Insectes Aptères*, vol. 3, p. 79. Female syntypes from America lost and also Abbot illustrations no. 170, 363 from Georgia. The Abbot manuscript is at the British Museum, Natural History. A copy of it in the Museum of Comparative Zoology was examined. *Nomen dubium*.

- Epeira ravilla* C. L. Koch, 1845, Die Arachniden, vol. 11, p. 73, fig. 890, ♀. Female holotype from Mexico in Royal Collection in Berlin, lost, likely destroyed. However, a specimen from Veracruz, Mexico, in the L. Koch collection in the British Museum, Natural History, with the label probably by C. L. Koch saying *E. ravilla*, examined. McCook, 1893, American Spiders, vol. 3, p. 161, pl. 5, figs. 7, 8, ♀, ♂.
- ? *Epeira septima* Hentz, 1847, J. Boston Soc. Natur. Hist., p. 470, pl. 30, fig. 9, ♀. The types from Alabama and North Carolina have been destroyed. *Nomen dubium*.
- Eriophora ravilla*,—Simon, 1864, Histoire Naturelle des Araignées, 1st ed., p. 261. F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, vol. 2, p. 465. Roewer, 1942, Katalog der Araneae, vol. 1, p. 866. Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 1785.
- Epeira nicaraguensis* Keyserling, 1885, Verhandl. Zool. Bot. Ges. Wien, vol. 34, p. 523, pl. 13, fig. 31, ♀. Female holotype from Nicaragua in the Museum of Comparative Zoology, examined. Keyserling, 1893, Spinnen Amerikas, vol. 4, p. 214, pl. 10, fig. 159, ♀. NEW SYNONYMY.
- Epeira balaustina* McCook, 1888, Proc. Acad. Natur. Sci. Philadelphia, p. 198. Female syntypes from Florida, Swan Island, Caribbean, and San Domingo, lost; the type locality is here restricted to [tropical] Florida. McCook, 1893, American Spiders, vol. 3, p. 155, pl. 4, fig. 2, ♀. NEW SYNONYMY.
- Epeira bivariolata* O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, vol. 1, p. 27, pl. 6, fig. 15, juv. Types from Guatemala in the British Museum, Natural History, lost. *Nomen dubium*. Keyserling, 1892, Spinnen Amerikas, vol. 4, p. 100, pl. 5, fig. 74, ♂. McCook, 1893, American Spiders, vol. 3, p. 160 (in part), pl. 5, fig. 5, ♀, ♂.
- Epeira variolata* O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, vol. 1, p. 46, pl. 6, fig. 14, juv. Juvenile syntypes from Guatemala in the British Museum, Natural History, lost.
- Eriophora balaustina*,—Banks, 1909, Rep. Centr. Exp. Sta. Cuba, p. 161.
- Epeira minax* O. P.-Cambridge, 1893, Biologia Centrali-Americana, Araneidea, vol. 1, p. 112, pl. 15, fig. 1, ♀. Three female syntypes from Acaguizotla, Guerrero, Mexico, in the British Museum, Natural History, examined. NEW SYNONYMY.
- Eriophora minax*,—F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, vol. 2, p. 464, pl. 44, fig. 3, ♀. Roewer, 1942, Katalog der Araneae, vol. 1, p. 867. Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 1784.
- Aranea nicaraguensis*,—F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, vol. 2, p. 519. Roewer, 1942, Katalog der Araneae, vol. 2, p. 848.
- Eriophora circulata*,—Comstock, 1912, Spider Book, figs. 108-111, 538; 1940, Spider Book, rev. ed., figs. 108-111, 538. Probably not *Epeira circulata* Walckenaer.
- ? *Araneus perfoliatus* Franganillo, 1936, Los Aracnidos de Cuba, p. 70. Specimen in Cuban Academy of Sciences, Havana, with numbered code lacking key. *Nomen dubium*.
- ? *Araneus anuncinatus* Franganillo. 1963, Los Aracnidos de Cuba, p. 71. Specimen disposition, see above. *Nomen dubium*.
- Araneus nicaraguensis*,—Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 549.



Map 1. Distribution of *Eriophora ravilla* (C. L. Koch)

*Note.* *Walckenaer's* (1841) description of *Epeira circulata* suggests the pattern illustrated by Fig. 20, but the specimen is lost and Abbot's illustration, fig. 170 made from a Georgia spider, also resembles this pattern. However, this species is not usually found as far north as Georgia. Chamberlin and Ivie (1944, Bull. Univ. Utah, Biol. Ser., vol. 7, no. 5, p. 105) interpreted the description to be an *Eustala*. Also I have not seen any other specimens with this pattern from the southeastern United States. It seems best not to use this doubtful name. The illustration of *Epeira septima* Hentz fits this species, the description may be a composite. Hentz reported the species from Alabama, where it occurs, and North Carolina, where it does not occur. Archer (1940) considered *E. septima* a synonym of *Araneus trifolium*.

In the L. Koch collection in London there are two specimens labeled *E. ravilla*, one from Cuba, and one from Veracruz, Mexico. Since the type locality is Mexico, I assume the Veracruz specimen

might be the lost type, and that L. Koch received the specimens from the elder Koch. The one from Cuba is *Eriophora edax*. McCook (1893) first suggested that *balaustina* might be *ravilla* of C. L. Koch.

*Description.* Female from Florida. Carapace red-brown with white hairs. Chelicerae dark brown. Sternum and coxae red-brown. Legs red-brown with femora darker and with white hairs and white setae. Dorsum of abdomen dark gray to black. Venter with a triangular black mark on gray with some white pigment surrounding it between epigynum and spinnerets. The triangular mark is pointed posteriorly. Anterior median eyes largest, posterior medians 0.6 diameters of anterior medians, laterals radius of anterior medians. Anterior median eyes one diameter apart, posterior medians two-thirds diameters apart. Abdomen is suboval, slightly pointed anteriorly and on sides. Total length 17 mm. Carapace 6.8 mm long, 5.8 mm wide. First femur, 7.6 mm; patella and tibia, 9.6 mm; metatarsus, 6.0 mm; tarsus, 1.7 mm. Second patella and tibia, 8.6 mm; third, 4.7 mm; fourth, 7.8 mm.

Male from Cuba. Coloration almost like that of female. Legs banded. Abdomen dark gray. Carapace with a deep longitudinal thoracic groove. Eye proportions like those of female. The second tibia is illustrated in Fig. 8. Abdomen oval, widest anteriorly. Total length 10 mm. Carapace 5.3 mm long, 3.7 mm wide. First femur, 6.8 mm; patella and tibia, 9.0 mm; metatarsus, 6.3 mm; tarsus, 1.4 mm. Second patella and tibia, 6.8 mm; third, 4.0 mm; fourth, 5.8 mm.

*Variation.* Females measure total length, 12-24 mm. Some females are almost white, others nearly black. Some have an irregular asymmetrical longitudinal white pigment patch which may be a narrow line or widest anteriorly just over the heart area. Males are 9-13 mm in total length. In some the legs lack banding. The abdomen is white to dark gray. Puzzling is the coloration (Fig. 20) having two dark-bordered, slightly sclerotized humps, one after another. All but one with this coloration were juveniles, the only adult being from Veracruz, Mexico.

*Diagnosis.* Females are readily told from *Eriophora fuliginea* by the wrinkled base of the epigynum (Figs. 13-15), males by the spur on the median apophysis (Fig. 10).

*Natural History.* The species has been collected in live oak trees of scrub at a salt marsh in Levy County, Florida and on a hammock above dense undergrowth in Dade County, Florida. In Alachua

County, Florida, H. K. Wallace (personal communication) observed a pompilid wasp [*Poecilopompilus interruptus* (Say)] attacking a spider while in the web and on the ground.

*Distribution.* Gulf coast, Florida, Central Mexico, and West Indies to South America.

*Border records.* *Maryland.* Bethesda, 6 August 1943, ♀ (J. M. Davis). *Grenada:* near St. George's. *Brazil.* Rio de Janeiro, [1865-1866], ♂ (Thayer Exped.).

*Eriophora fuliginea* (C. L. Koch), new combination

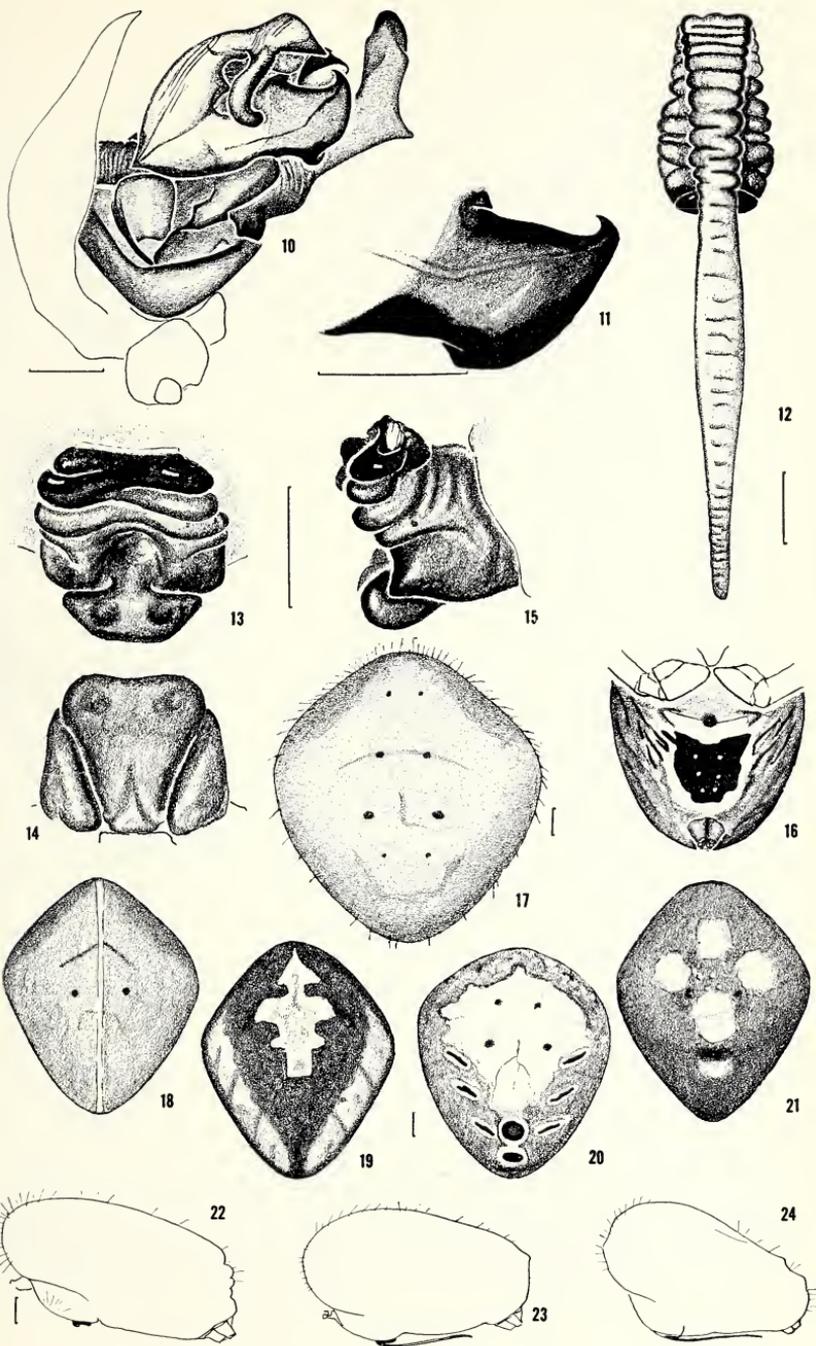
Map 2; Figures 1a, 25-34

- Epeira fuliginea* C. L. Koch, 1893, Die Arachniden, vol. 5, pl. 58, fig. 375, ♀. Three female syntype specimens from Brazil were in the Bavarian collection in Munich, presumably destroyed. — Taczanowski, 1873, Horae Soc. Entomol. Ross., vol. 9, p. 129.
- Epeira hispida* C. L. Koch, 1845, Die Arachniden, vol. 11, p. 71, fig. 889, ♂. Male type from Brazil in the Zoologisches Museum, Humboldt Universität, Berlin; examined. NEW SYNONYMY.
- Epeira ursina* Keyserling, 1865, Verhandl. Zool. Bot. Ges. Wien, vol. 15, p. 822, pl. 19, figs. 3-5, ♀. Female holotype from [the Spanish Colony] New Granada, in the British Museum, Natural History, examined. Keyserling, 1893, Spinnen Amerikas, vol. 4, p. 229, pl. 11, fig. 170, ♀. NEW SYNONYMY.
- Epeira trapezoides* Karsch, 1879, Stettiner Entomol. Z. vol. 40, p. 107. Female holotype from Santa Marta, Colombia, in the Zoologisches Museum, Berlin, examined. NEW SYNONYMY.
- Epeira messalina* Hasselt, 1888, Tijdschr. Entomol. 31: 181, pl. 6, figs. 1, 2, ♀. Female holotype from Surinam, in the Natural History Museum, Leiden, examined. NEW SYNONYMY.
- Epeira purpurascens* O. P.-Cambridge, 1889, Biologia Centrali-Americana, vol. 1, p. 33, pl. 7, figs. 4, 5, ♀, ♂. Female syntypes from Bugaba, Panama, in the British Museum (Natural History), examined. Keyserling, 1893, Spinnen Amerikas, vol. 4, p. 226, pl. 11, fig. 168, ♀, ♂ [*purpurescens*]. NEW SYNONYMY.
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- Araneus purpurascens*, — Simon, 1897, Proc. Zool. Soc. London, p. 873.

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Figs. 10-24. *Eriophora ravilla* (C. L. Koch). 10. Male, left palpus, mesal view. 11. Embolus. 12. Epigynum. 13-15. Base of epigynum. 13. Ventral. 14. Posterior. 15. Lateral. 16. Female, ventral view of abdomen. 17-21. Female, dorsal view of abdomen. 17. (Florida). 18. (Texas). 19. (Nayarit). 20. (Veracruz). 21. (Nicaragua). 22-24. Female, lateral view of abdomen. 22. (Jamaica). 23. (Nayarit). 24. (Veracruz).

*Size Indicators:* Figs. 10-15, 0.5 mm. Figs. 17-24, 1 mm.





Map 2. Distribution of *Eriophora fuliginea* (C. L. Koch)

*Eriophora purpurascens*.—F. P.-Cambridge, 1903, *Biologia Centrali-Americana*, vol. 2, p. 463, pl. 43, figs. 14, 15, ♀, ♂. Roewer, 1942, *Katalog der Araneae*, vol. 2, p. 867. Bonnet, 1955, *Bibliographia Araneorum*, vol. 2, p. 1784.

? *Araneus fuligineus* var. *rhomboidalis* Franganillo, 1936, *Los Aracnidos de Cuba*, p. 67. The Franganillo collection is in the Cuban Academy of Sciences, Havana, but with a numbered code and without a key to the numbers. *Nomen dubium*.

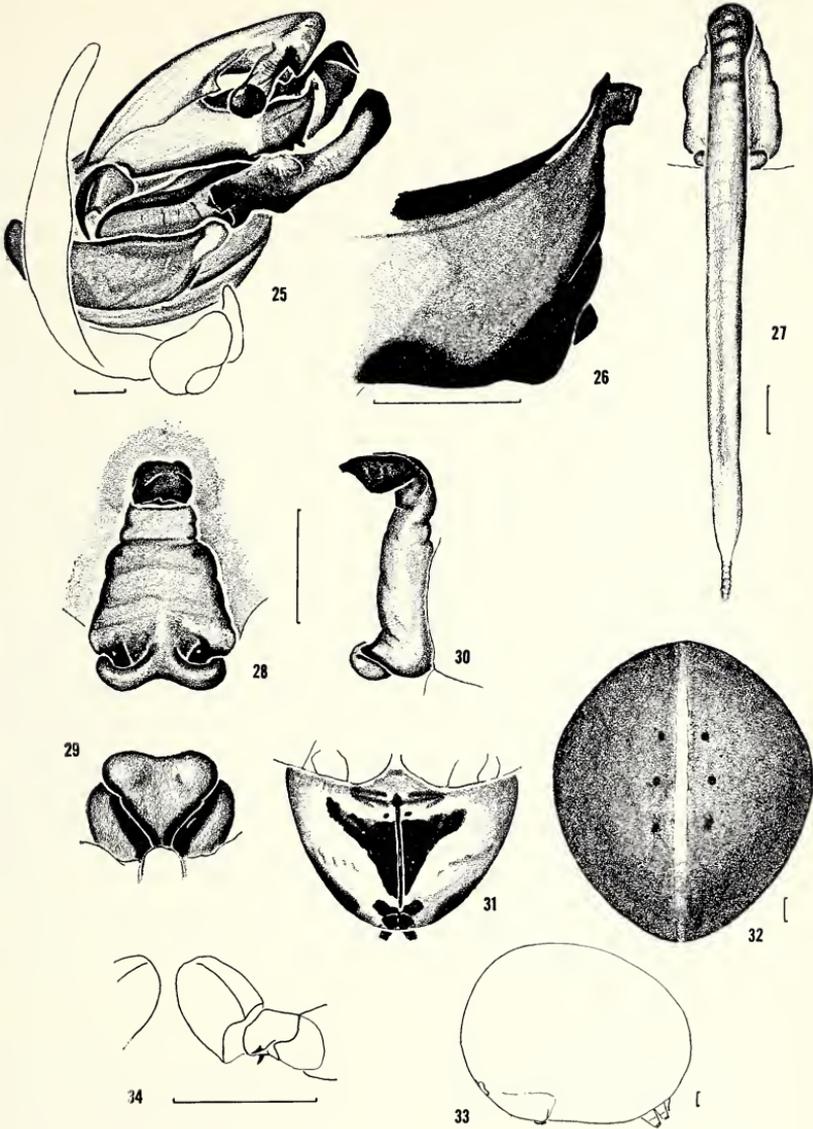
? *Araneus fuligineus* var. *sanguineus* Franganillo, 1936, *Los Aracnidos de Cuba*, p. 68. Specimen deposition, see above. *Nomen dubium*.

*Aranea fuliginea*.—Roewer, 1942, *Katalog der Araneae*, vol. 2, p. 842.

*Aranea ursina*.—Roewer, 1942, *Katalog der Araneae*, vol. 2, p. 855.

*Araneus ursinus*.—Bonnet, 1955, *Bibliographia Araneorum*, vol. 2, p. 626.

*Note.* There are no specimens of *Epeira fuliginea* in the Staatssammlungen des Bayerischen Staates, Munich, according to Dr. Egon Popp. Presumably these were specimens collected by the Spix and Martius expedition to equatorial Brazil. The oldest specimens



Figs. 25-34. *Eriophora fuliginea* (C. L. Koch). 25. Male, left palpus, mesal view. 26. Embolus. 27. Epigynum. 28-30. Base of epigynum. 28. Ventral. 29. Posterior. 30. Lateral. 31-33. Female, abdomen. 31. Ventral. 32. Dorsal. 33. Lateral. 34. Male, fourth coxa and trochanter.

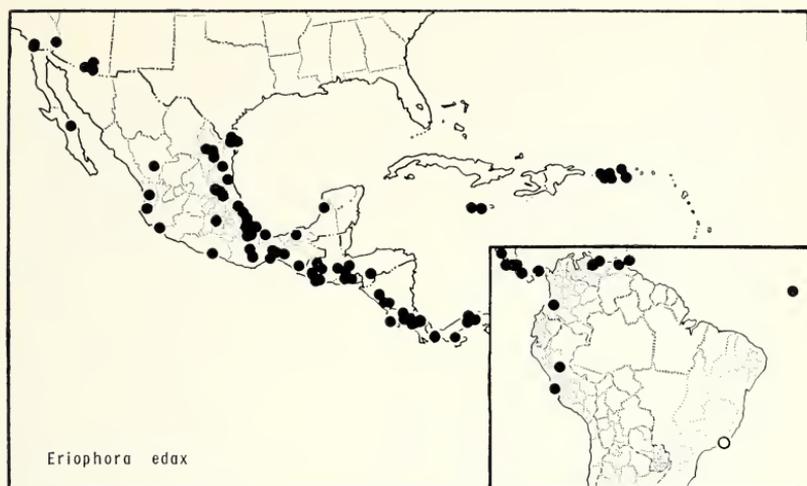
Size Indicators: Figs. 25-30, 0.5 mm. Figs. 31-34, 1 mm.

of this species examined bearing this name are those of Taczanowski in the Polish Academy of Sciences, Warsaw. The Franganillo names may refer to this species or *E. ravilla*.

*Description.* Female from Panama Canal Zone. Carapace, sternum, and legs brown. Carapace with some long white hairs from thoracic groove toward sides of head and shorter ones on the anterior margin. Dorsum of abdomen black with a well defined narrow longitudinal white line. Area on venter between epigynum and spinnerets with a triangular black mark pointing posteriorly, and a white pigment spot on each side anterior of the spinnerets (Fig. 31). The dorsum of abdomen is sparsely covered by long white hairs. The anterior median eyes are largest, the posterior medians about 0.8 diameters of anterior medians, laterals about 0.7 diameters. The anterior median eyes are a little more than one diameter apart, the posterior medians about two-thirds diameters apart. The abdomen is subtriangular, rather high above spinnerets. Total length, 18 mm. Carapace 8.3 mm long, 6.8 mm wide. First femur, 10.0 mm; petella and tibia, 12.3 mm; metatarsus, 8.7 mm; tarsus, 2.6 mm. Second patella and tibia, 12.4 mm; third, 6.7 mm; fourth, 10.5 mm.

Male from Panama Canal Zone. Coloration like that of female but lighter. Sternum light brown. Distal segments of legs light with some dark spots at origin of setae. The carapace has a deep longitudinal thoracic groove with two short posteriorly directed branches. The anterior median eyes are largest, the posterior medians 0.7 diameters of anterior medians, the anterior laterals 0.6 diameters and the posterior laterals 0.5 diameters of anterior median eyes. The anterior median eyes are one and one-half diameters apart, the posterior medians about two-thirds their diameter apart. Total length, 14 mm. Carapace 7.2 mm long, 6.0 mm wide. First femur, 8.0 mm; patella and tibia, 10.5 mm; metatarsus, 7.8 mm; tarsus, 2.2 mm. Second patella and tibia, 9.6 mm; third, 5.5 mm; fourth, 8.0 mm.

*Variation.* The total length of the female varies between 14-30 mm. The total length of adult males 12-16 mm. The largest come from the northern Amazon region. The dorsal white line on the abdomen may be absent. The dorsum sometimes has white patches instead of a line and sometimes the sides of the abdomen have white pigment patches. Most specimens, however, do have the longitudinal line. Some females have a dorsal posterior hump on the abdomen as large as that of *E. edax*. The length of the scape of the epigynum



Map 3. Distribution of *Eriophora edax* (Blackwall)

seems quite variable. Sometimes it extends as far as the anterior spinnerets, sometimes it is shorter, depending perhaps on the size of the abdomen. One male from Panama had a hump as well as two macrosetae on the posterior edge of the fourth coxae. (All Panamanian *E. edax* had three or four macrosetae.)

*Diagnosis.* This species differs from *Eriophora ravilla*, the epigynum of which also has a flat scape, by the shield-shaped base of the epigynum (Figs. 28-30). In *Eriophora ravilla* the base of the epigynum has annuli, in *Eriophora fuliginea* it does not. The median apophysis (Fig. 25) of the male differs in lacking the spur present in *Eriophora ravilla*. The distal edge of the median apophysis has a flat edge and the shape of the embolus with a flap near the tip is characteristic (Fig. 26).

*Natural History.* The spider is known to be nocturnal and has been observed occasionally to feed on bats, probably *Myotis nigricans*, that become entangled in the large web (Fig. 1a) (personal communication of M. H. Robinson).

*Distribution.* Honduras, Trinidad to western Peru and southeastern Brazil (Map 2).

*Border Records.* Honduras: Tela. Peru. Junín: Amable María (K. Jelski). Brazil. Rio de Janeiro.

*Eriophora edax* (Blackwall)

Map 3; Figures 35-48

*Epeira edax* Blackwall, 1863, Ann. Mag. Natur. Hist. ser. 3, vol. 11, p. 30.

Female and male syntypes from Rio de Janeiro, Brazil, lost, probably destroyed.

*Eriophora edax*,—F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, vol. 2, p. 464, pl. 44, figs. 1, 2, ♀, ♂. Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., vol. 30, p. 325, figs. 205-207, ♀, ♂.*Aranea edax cauca* Strand, 1915, Arch. Naturgesch., vol. 81, p. 111. Juvenile holotype from Popayan or Cauca, Colombia in the Senckenberg Museum, Frankfurt, examined. NEW SYNONYMY.

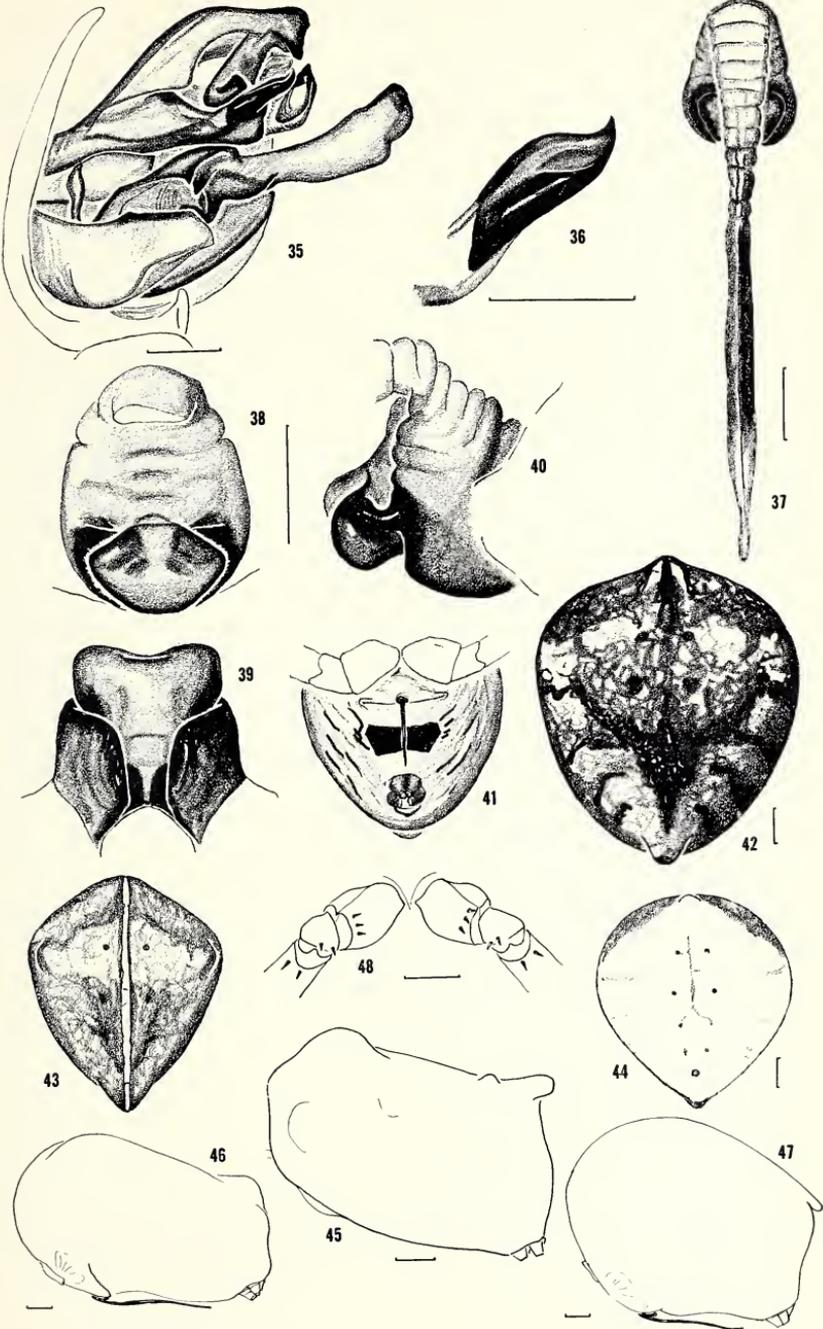
*Note.* Blackwall's rather detailed description matches specimens of this species. The unusual macrosetae in a line across the fourth coxa of males are mentioned by Blackwall. The proportions given by Blackwall fit. The Blackwall types are not known to exist. There are no recent collections of this species from Rio de Janeiro (open circle Map 3) but there are some from the east side of the Andes in the Amazon basin in Peru. Thus the recognition of the Blackwall name is not in doubt. Strand's specimen is a characteristic specimen, a juvenile, of this species.

*Description.* Female from Arizona. Carapace yellow-brown with a median longitudinal dark brown band and irregular brown spots. Clypeus dark brown, as is median eye area not including the posterior median eyes but including the anterior lateral eyes. Labium and endites dark brown, distally white. Sternum marbled brown. Coxae brown, bordered by dark brown. Legs banded with narrow bands, more distinct on venter. Abdomen with black and white pigment on dorsum (Figs. 41-47). Venter with a black mark wider than long, surrounded by white. Spinnerets dark brown. Anterior median eyes largest, posterior medians the radius of anterior medians in size, anterior laterals 0.8 diameters of anterior medians, posterior lateral eyes the radius of anterior medians. Anterior median eyes less than one diameter apart, posterior median eyes a little more than one diameter apart. The abdomen has a median dorsal hump and a smaller hump anteriorly. Total length 14 mm. Carapace 6.2 mm

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Figs. 35-48. *Eriophora edax* (Blackwall). 35. Male, left palpus, mesal view. 36. Embolus. 37. Epigynum. 38-40. Base of epigynum. 38. Ventral. 39. Posterior. 40. Lateral. 41-47. Female, abdomen. 41. Ventral. 42-44. Dorsal view. 42. (Arizona). 43. (Veracruz). 44. (Loreto, Peru). 45-47. Lateral view. 45. (Arizona). 46. (Puerto Rico). 47. (Veracruz). 48. Male, fourth coxae and trochanters.

*Size Indicators:* Figs. 35-40, 0.5 mm. Figs. 41-47, 1 mm.



long, 5.0 mm wide. First femur, 5.8 mm; patella and tibia, 8.0 mm; metatarsus, 4.7 mm; tarsus, 1.6 mm. Second patella and tibia, 6.9 mm; third, 4.0 mm; fourth, 6.5 mm.

Male from Arizona. Carapace and sternum light brown. Legs only indistinctly banded. Dorsum of abdomen evenly covered with white pigment and tiny black spots at the base of setae. Venter with area between genital groove and epigynum white. Carapace with a deep longitudinal groove. Eye sizes almost like those of female. Anterior median eyes slightly more than their diameter apart, posterior median eyes slightly more than their diameter apart. Abdomen subtriangular with a distinct posterior hump. Total length 11 mm. Carapace 5.8 mm long, 4.4 mm wide. First femur, 5.8 mm; patella and tibia, 7.2 mm; metatarsus, 4.7 mm; tarsus, 1.4 mm. Second patella and tibia, 6.4 mm; third, 3.6 mm; fourth, 5.4 mm.

*Variation.* Some specimens have the cephalothorax red-brown and abdomen almost black; other have the cephalothorax yellowish-brown and the abdomen white or yellow-brown. The abdomen may have a folium-like patch (Fig. 42) or may be almost completely white as in a specimen from Peru (Fig. 44). The posterior dorsal hump is distinct in all specimens. But there may be two posterior humps in a row and other humps. The keel of the epigynum scape is less distinct in some specimens from Central and South America but the shape of the base of the epigynum stays about the same. No specimens were seen in which the scape was torn off, but in some the tip had broken off. Northern males, from Mexico and the United States, may have only two macrosetae on the fourth coxa while those examined from Central and South America all had three or four macrosetae. Females ranged from 12-16 mm in total length, males from 8-12 mm in total length.

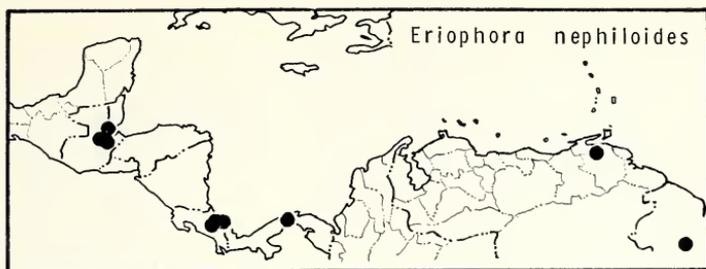
*Diagnosis.* The keel of the epigynal scape (Fig. 37), the large projecting median sclerite of the base of the epigynum (Figs. 38-40), and the cylindrical embolus of the male palp (Fig. 36) and usually the macrosetae across coxa (Fig. 48) and the large posterior hump of the abdomen (Figs. 45-47) can be used to separate specimens of *E. edax* from those of *E. fuliginea*.

*Distribution.* From southern Texas, Arizona and southern California to Peru and Brazil (Map 3).

*Eriophora nephiloides* (O. P.-Cambridge)

Map 4; Figures 1b, 49-58

*Epeira nephiloides* O. P.-Cambridge, 1889, *Biologia Centrali-Americana*, Araneidea, vol. 1, p. 32, pl. 7, figs. 1, 2, ♀. Female syntypes from Panzos,



Map 4. Distribution of *Eriophora nephiloides* (O. P.-Cambridge)

Dolores, Cubilguitz and [?] Menché, Guatemala in British Museum, Natural History, examined.

*Araneus nephiloides*,—Simon, 1895, Histoire Naturelle des Araignées, vol. 1, p. 811.

*Aranea nephiloides*,—F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, vol. 2, p. 511, pl. 48, fig. 22, ♀.

*Eriophora nephiloides*,—Banks, 1909, Proc. Acad. Natur. Sci. Philadelphia, p. 210. Roewer, 1942, Katalog der Araneae, vol. 1, p. 867. Bonnet, 1955, Bibliographia Araneorum, vol. 2, p. 1784.

*Description.* Female from Panama Canal Zone. Carapace yellowish-white, dusky in the center and including head region. Sternum dark brown. Coxae yellow-white. Legs yellow-white, banded brown. Dorsum of abdomen white, sides yellow-white with a black edge toward dorsal white spot. Venter of abdomen with a black rectangle longer than wide, bordered by white. The pigment covers almost the entire area between epigynum and spinnerets. Anterior median eyes slightly larger than others, posterior medians 0.9 diameters of anteriors, laterals about 0.8 diameters of anterior medians. Anterior medians one and one-half diameters apart, posterior medians more than one diameter apart. Abdomen longer than wide, widest in anterior half, sometimes pear-shaped, quite variable. Total length, 16 mm. Carapace 6.1 mm long, 5.2 mm wide. First femur, 8.9 mm; patella and tibia, 10.5 mm; metatarsus, 8.2 mm; tarsus, 2.3 mm. Second patella and tibia, 10.0 mm; third, 5.3 mm; fourth, 8.6 mm.

Male from Panama Canal Zone. Carapace darker than that of female. Sternum with dark border only. Legs are not banded. Dorsum of abdomen all white, ventral abdominal black band may be wider than long or as wide as long. Anterior median eyes largest, posterior medians about 0.8 diameters of anterior medians, laterals about the radius of anterior medians. Anterior median eyes slightly more than one diameter apart, posterior medians slightly more than

one diameter apart. Coxae not modified. Second tibia is thick but not otherwise modified. The abdomen is longer than wide, widest in anterior half and has long hair. Total length 5 mm. Carapace 2.5 mm long, 2.3 mm wide. First femur, 2.9 mm; patella and tibia, 3.8 mm; metatarsus, 2.5 mm; tarsus, 0.8 mm. Second patella and tibia, 3.3 mm; third, 1.6 mm; fourth, 2.6 mm.

*Variation.* The female varies from 11-22 mm total length. The abdomen may be quite variable in markings and color (Figs. 55, 56) and also the white dorsal patch is variable in shape. In some specimens the white patch appears spotted.

*Diagnosis.* The short median apophysis (Fig. 49) and the striking coloration of the female and small epigynum (Figs. 51-54) with unsclerotized scape separates this species from others. This species appears to be close to *Epeira musiva* (Hasselt) but differs by the epigynum.

*Natural History.* According to M. E. Robinson (personal communication), this species unlike *E. fuliginea* is mainly diurnal. The carapace in the living animal is brilliant emerald green.

*Distribution.* Guatemala to Guiana (Map 4).

*Records.* *Guatemala* (syntypes). *Costa Rica.* Limón, Río Toro Amarillo; Calle Angeles, 5 km S. de Univ.; Guápiles. *Panama Canal Zone.* Barro Colorado Isl. *Venezuela.* Caripito. *Guiana.* Tukeit [Falls], 1911 (Lza.).

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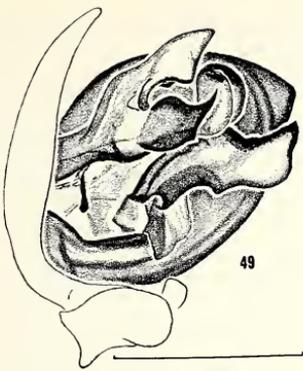
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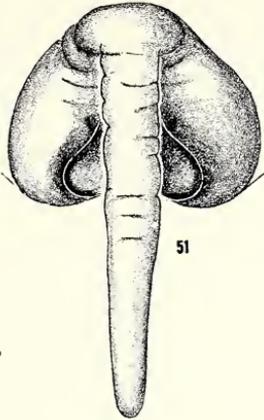
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Figs. 49-58. *Eriophora nephiloides* (O. P.-Cambridge). 49. Male, left palpus, mesal view. 50. Embolus. 51-53. Epigynum. 51, 52. Ventral. 51. (Syntype, Guatemala). 52. (Panama Canal Zone). 53. Posterior view (syntype, Guatemala). 54-55. Female, abdomen. 54. Ventral view. 55. Dorsal view (Panama). 56. Female, dorsal view, appendages removed (Panama). 57. Female, abdomen, lateral view. 58. Male, fourth coxa and trochanter.

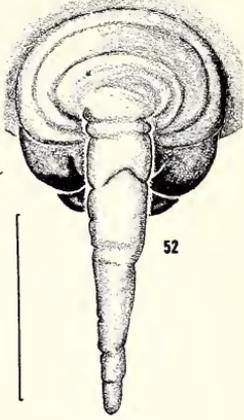
*Size Indicators:* Figs. 49, 51-53, 0.5 mm. Fig. 50, 0.05 mm. Figs. 54-57, 1 mm.



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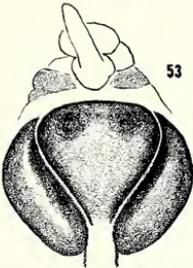
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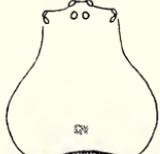
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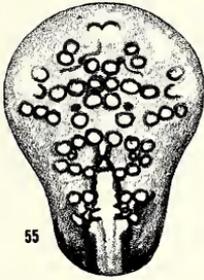
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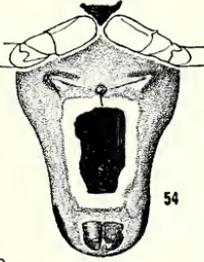
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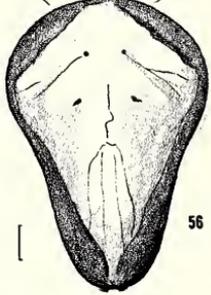
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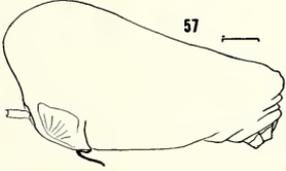
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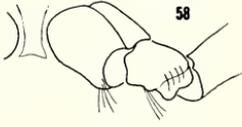
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A NEW GENUS OF ANT-MIMICKING SPIDER WASPS  
FROM AUSTRALIA  
(HYMENOPTERA, POMPILIDAE)\*

BY HOWARD E. EVANS  
Museum of Comparative Zoology

Australia has a rich fauna of spider wasps (Pompilidae), but aside from numerous species descriptions by R. E. Turner, Frederick Smith, and others, it is almost totally unstudied. There would be little excuse for further species descriptions if it were not for two factors: (1) one of these species was figured in the recent book *The Insects of Australia*, where it was identified as simply "brachypterous Pepsini," although it is such an unusual wasp that one is immediately curious as to its proper position in the classification; and (2) these are among the most striking ant mimics known, and furthermore each of the two known species appears to mimic one particular species of ant.

Ant mimicry is not wholly unknown in the Pompilidae. I regard some of the pale-bodied, banded-winged North American *Ageniella* as generalized ant mimics (e.g. *A. conflicta* Banks). Here the wing pattern creates the appearance of a wingless insect with several body constrictions, such as an ant. It is probable that some of the apterous and brachypterous Ctenoceratini of Africa are ant mimics, although Arnold (1932) suggests that some may mimic mutillids.

In the present instance there seems little question that ant mimicry is involved, and it is possible to name the model in each case. The one figured in *The Insects of Australia*, here described as *Iridomimus spilotus*, is mounted on a card point on the same pin as a worker *Iridomyrmex rubriceps* Forel.<sup>1</sup> Although I know nothing of the circumstances under which this was collected, the striking resemblance of the pompilid and the ant suggests that whoever collected them took them in close proximity and was impressed by this resemblance.

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\*Published with the aid of a grant from the Museum of Comparative Zoology at Harvard College.

<sup>1</sup>Ant determinations are by Dr. R. W. Taylor, Division of Entomology, C. S. I. R. O., Canberra, Australia. Dr. Taylor found that this specimen compared favorably with a syntype of what has been called *Iridomyrmex gracilis* var. *rubriceps* Forel, but he thinks it probable that *rubriceps* should be regarded as a full species, perhaps not closely related to *gracilis*.

Manuscript received by the editor November 13, 1970.

They are similar in size and both are yellowish with a darker metasoma; in both there is a metallic sheen to the anterior part of the body, but the pompilid differs in having a black spot on the vertex and one on the pronotum. The pompilid has very long, slender, smooth legs; there is a constriction in the middle of the mesosoma exactly paralleling that in the *Iridomyrmex* worker; and the wings are so small as to escape immediate notice. The resemblance between the two is indeed striking.

The second species (like the preceding known from one specimen) was collected by myself in a sandy blow-out in South Australia. This was an area in which a somewhat larger species of *Iridomyrmex*, *viridiaeneus* Viehmeyer,<sup>2</sup> was abundant, and these ants were conspicuous because of their metallic bluish bodies. When I first observed the pompilid (described below as *Iridomimus violaceus*) I had no suspicion that it was not simply another worker ant of this species. Something about its gait warned me that it was not, and close inspection showed that it had minute, stalked wings and that it lacked a nodose petiole. In size, color, and general form of the mesosoma it was an almost perfect copy of a worker *Iridomyrmex viridiaeneus*.

Why should female pompilids with a well-developed and presumably painful sting mimic ants? *Iridomyrmex purpureus* and certain other species of this genus are known to produce methylheptenone and iridodial from anal glands; it is believed that the former serves as a defensive secretion while the latter may be an adherent, retarding the loss of more volatile components when discharged on a predator (Pavan and Trave, 1958; Cavill and Robertson, 1965). Thus these relatively abundant and conspicuous ants may be avoided by many or all predators. Presumably the pompilids hunt and nest in situations where one particular species of *Iridomyrmex* is prevalent, and it proved selectively advantageous for them to assume a common Müllerian mimetic pattern with the ant. There may, of course, have been selection for flightlessness first (we do not know what kind of spider these pompilids prey on), and if so it would be particularly advantageous for them to compensate for their inability to escape by assuming an ant-like form. It is curious that these wasps

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<sup>2</sup>Dr. R. W. Taylor found my specimens to compare favorably with a syntype. This form has been considered a variety of the meat ant, *Iridomyrmex purpureus* Smith, but Taylor believes it is probably distinct. He states that it is probable that *I. viridiaeneus* and *rubriceps* are fairly closely related within *Iridomyrmex*.

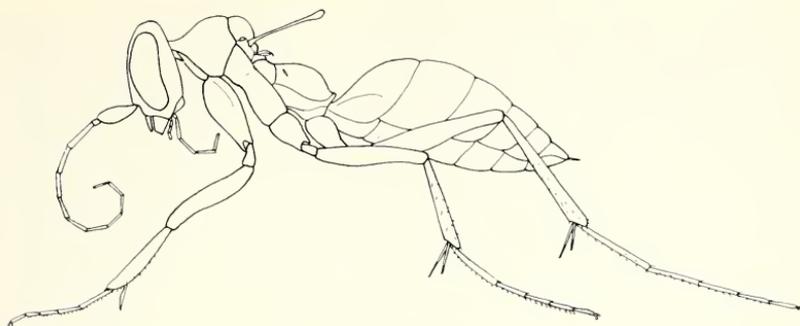


Fig. 1. *Iridomimus violaceus* new species, holotype (setae omitted).

appear to be so rare. I have scanned the collections of Pompilidae in all the major museums of Australia, but I have been unable to find additional specimens of these or related species.

### **Iridomimus**, new genus

Type species: *Iridomimus violaceus*, new species.

*Generic diagnosis* (females only; males unknown). — Front wings in the form of a stalk much longer than the terminal, expanded portion, the latter with or without one or two short veins, these wings not extending beyond the base of the second metasomal tergite; hind wings minute, not surpassing the postnotum. Postnotum transversely striate, unusually long, approximately as long as the very short scutellum and metanotum combined; thoracic profile markedly constricted at the postnotum and at the mesopleura, so that the mesosoma appears to form two separate nodes both in dorsal and lateral views; mesoscutum also unusually small; pronotum large, rounded, constricted behind, with no evidence of a furrow extending laterad from the collar; mesopleura slender, the transverse furrow weak to virtually absent, located only a short distance from the top. Legs very slender and with only a few short spines, front tarsus with no evidence of a pecten, middle and hind tibiae with a few weak spines along the shaft and a few short apical spines which are somewhat splayed out; claws dentate. Second sternite of metasoma with a transverse furrow, apical tergite strongly setose but without thick bristles. Head without unusual features, clypeus transverse, truncate, antennae long and slender, base of mandibles slightly separated from bottoms of eyes; eyes convergent above, their inner margins not at all emarginate; ocelli well developed.

*Generic relationships.*—The head and metasoma bear a close resemblance to those of members of the genus *Priocnemis*, and I would regard this genus as a derivative of a *Priocnemis*-like stock which has undergone many modifications of the thorax as a result of loss of flight and the evolution of ant-mimicry. Although the few spines at the apices of the tibiae are somewhat splayed out (as in Pompilinae), this condition is approached by several other genera of Pepsinae, and I would not hesitate to assign this genus to that subfamily and to the tribe Cryptocheilini, which is very well represented in Australia.

***Iridomimus violaceus*, new species**

*Holotype.*—♀, SOUTH AUSTRALIA: Port Germein, 28 October 1969 (H. E. Evans) [to be deposited in the Australian National Insect Collections, CSIRO, Canberra].

*Description.*—Length 7.5 mm; fore wing 1.5 mm. Body and basal parts of legs black, with strong reflections of violet and (especially on the metasoma) dark blue-green; tarsi and antennal flagellum brownish. Head, thorax, and propodeum with sparse, fairly long setae; coxae and to a lesser extent the femora with pale setae. Clypeus  $3 \times$  as wide as high; first four antennal segments in a ratio of about 23:9:30:27, segment three  $4.6 \times$  as long as its apical width; middle interocular distance  $.53 \times$  transfacial distance; upper interocular distance  $.64 \times$  lower interocular distance; postocellar and ocello-ocular distances subequal; temples, in lateral view, not nearly as wide as eye. Pronotum smoothly rounded; mesoscutum strongly humped; propodeum smoothly rounded; fore wings reaching to about the middle of the propodeum, spatulate, evidently supported by a single vein; hind wings scale-like, about  $3 \times$  as long as wide. Apical tarsal segments without spines beneath, but other tarsal segments with short spines in several rows beneath; tibiae smooth, with scattered short spines. (See Fig. 1).

***Iridomimus spilotus*, new species**

*Holotype.*—♀, NORTHERN TERRITORY: Powell Creek, June, 1947 (no collector given; on a card point, an additional card point bearing a worker ant, *Iridomyrmex rubriceps* Forel). [Australian National Insect Collections, CSIRO, Canberra].

*Description.*—Length 6 mm; fore wing 2.3 mm. Head, mesosoma, and first metasomal segment predominantly pale ferruginous; ocellar area covered with a black spot, from which dark streaks

pass to the eye tops; pronotum with a central black spot, this spot with a bluish sheen; both dark and light areas of the front and vertex with a violet sheen; metasoma beyond basal segment fuscous, with weak violet reflections; antennae dusky ferruginous, legs also of this color but femora rather strongly infuscated above; fore wings fuscous, the apical 0.1 contrastingly white. Body clothed with a delicate silvery to cinereous pubescence, but with no erect setae except for a few on the clypeus and on the front coxae. Clypeus  $2.5 \times$  as wide as high; first four antennal segments in a ratio of about 15:5:19:18, segment three  $4 \times$  as long as its apical width; middle interocular distance  $.58 \times$  transfacial distance; upper interocular distance  $.78 \times$  lower interocular distance; ocellar triangle compact, ocello-ocular distance nearly twice the postocellar distance; temples, in lateral view, somewhat more than half as wide as the eyes. Pronotum rounded gently, not as convex as in *violaceus*, mesoscutum small and nearly flat, not nearly as prominent as in that species; propodeum elongate, gently arched. Fore wings reaching to base of second metasomal tergite, in the form of a long, linear stalk which slightly exceeds in length a slightly expanded apical portion in the base of which a reduced venation can be observed (including, apparently, a small stigma and short radial vein; hind wings slender, pointed, reaching to the anterior margin of the propodeum. Legs very slender, spined much as in *violaceus*, but the middle tibiae slightly more strongly spinose and the apical tarsal segments with one or two weak spines beneath.

*Remarks.*— This specimen was figured in *The Insects of Australia*, p. 930, fig. 37.28B. This line drawing, by T. Binder, is small but essentially correct in all details. When it was drawn the specimen was apparently complete, but it is now lacking most of the hind legs.

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THE MALE GENITALIA OF BLATTARIA. IV.  
BLABERIDAE: BLABERINAE\*

BY LOUIS M. ROTH  
Pioneering Research Laboratory  
U. S. Army Natick Laboratories  
Natick, Massachusetts 01760

In this paper I shall illustrate and use male genitalic structures to show the probable relationships of the following 21 genera of *Bionoblatta* Rehn, *Blaberus* Serville, *Blaptica* Stål, *Brachycola* Serville, *Byrsotria* Stål, *Eublaberus* Hebard, *Hemiblabea* Saussure, *Hiereoblatta* Rehn, *Hormetica* Burmeister, *Hyporhichnoda* Hebard, *Minablatta* Rehn, *Monachoda* Burmeister, *Monastria* Saussure, *Oxycercus* Bolivar, *Parahormetica* Brunner, *Petasodes* Saussure, *Phoetalia* Shelford, *Sibylloblatta* Rehn, and *Styphon* Rehn.

Princis (1960) placed most of the above genera in 2 subfamilies (Blaberinae and Brachycolinae) of Blaberidae. He also included *Cacoblatta* Saussure and *Mesoblaberus* Princis in the Blaberinae but I have not seen any males of species belonging to these genera. *Anchoblatta* Shelford, which Princis (1960) included in the Brachycolinae with a (?) and listed under this subfamily in his 1963 Catalogus, has male genitalia characteristic of the Panchlorinae and I have assigned it to this subfamily (Roth, 1971).

McKittrick (1964, p. 34) stated "The Blaberinae are the largest subfamily in this complex [Blaberoid Complex], and it forms a peculiarly diverse group made up entirely of tropical and subtropical New World forms. It includes here both the Blaberinae and Brachycolinae of Rehn (1951) and Princis (1960). Because of overlapping characteristics, any subdivision at this level would necessarily be arbitrary. As may be seen in tables VI [♀ genitalia] and VII [proventriculus], there are no clear divisions within the group, only distinct trends." Previous studies (Roth, 1969, 1970a, 1970b) have indicated that the male genitalia of species of Blaberidae possess excellent characters for showing subfamily, tribal, generic, and species group characteristics, and in the present study this was found to be true for the Blaberinae.

I shall follow McKittrick in assigning all of the genera she studied

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\*Manuscript received by the editor April 8, 1970.

to the subfamily Blaberinae. The genera *Hyporhcnoda*, *Phoetalia*, and *Oxycercus*, which were placed in subfamilies other than the Blaberinae by McKittrick and Princis, have male genitalia characteristics of members of Blaberinae and I include them in this subfamily.

#### MATERIALS AND METHODS

The technique for preparing the male genitalia is given in Roth (1969). Unless otherwise indicated in the explanation of figures, the 2 phallomeres L2d (Fig. 41) and L1 (Fig. 43) were mounted dorsal side up and the genital hook R2 (Fig. 42) is oriented ventral side uppermost. The source of each of the specimens illustrated is given using the following abbreviations: (AMNH) = American Museum of Natural History, New York; (ANSP) = Academy of Natural Sciences, Philadelphia; (BMNH) = British Museum (Natural History), London; (CUZM) = Copenhagen University, Zoological Museum, Denmark; (L) = Zoological Institute, Lund, Sweden; (LEM) = Lyman Entomological Museum, Macdonald College, Quebec, Canada; (N) = U. S. Army Natick Labs., Natick, Mass.; (USNM) = United States National Museum, Washington, D. C. Geographical collection data and the names of specialists who identified the specimens, if known, follow these abbreviations. The number preceding the abbreviations refers to the number assigned the specimen and its corresponding genitalia (on a slide) which are deposited in their respective museums.

#### RESULTS AND DISCUSSION

The male phallomeres which have proved useful in studies of Blaberidae are a retractable hook on the right side (R2) (Fig. 42); a median sclerite (L2vm) which may or may not be solidly attached to a sclerite L2d (L2 dorsal); and lying below or partly surrounding L2d is a membrane, the prepuce, which almost always bears spines of various sizes and shapes (Fig. 41). The phallomere (L1) on the left side, has a heavily sclerotized cleft (Fig. 43) and a well defined membranous lobe which overlaps the cleft area; because of its transparency this membrane is difficult to see in most of the photographs.

Rehn and Hebard (1927, pp. 257-258), in discussing the Blaberinae, concluded that there are ". . . at least three lines of development or phyla, which are as follows:

1. *Archimandrita*, *Blaberus*, *Eublaberus*

2. *Blaptica*, *Byrsotria*, *Hemiblabera*, *Aspiduchus*, *Monachoda*
3. *Monastria*, *Petasodes*

The first group is well defined, although relationship with *Byrsotria* is evident . . . The second group is well defined from the first, but whether *Monachoda* should be considered the maximum differentiation of the second group, or a less highly modified member of the third one, is a matter of opinion." The above linear arrangement was the one preferred by Rehn and Hebard.

Princis' (1963) arrangement of some of the genera in the Blaberinae follows Rehn and Hebard, but several additional genera were included.

Brachycolinae: *Brachycola*, *Hormetica*, *Parahormetica*, *Sibylloblatta*, *Bionoblatta*

Blaberinae: *Archimandrita*, *Blaberus*, *Mesoblaberus*, *Eublaberus*, *Blaptica*, *Byrsotria*, *Hemiblabera*, *Aspiduchus*, *Monachoda*, *Monastria*, *Minablatta*, *Petasodes*, *Cacoblatta*, *Hiereoblatta*, *Styphon*

McKittrick (1964) studied 11 genera of Blaberinae and "for convenience" arranged them in the following tribes:

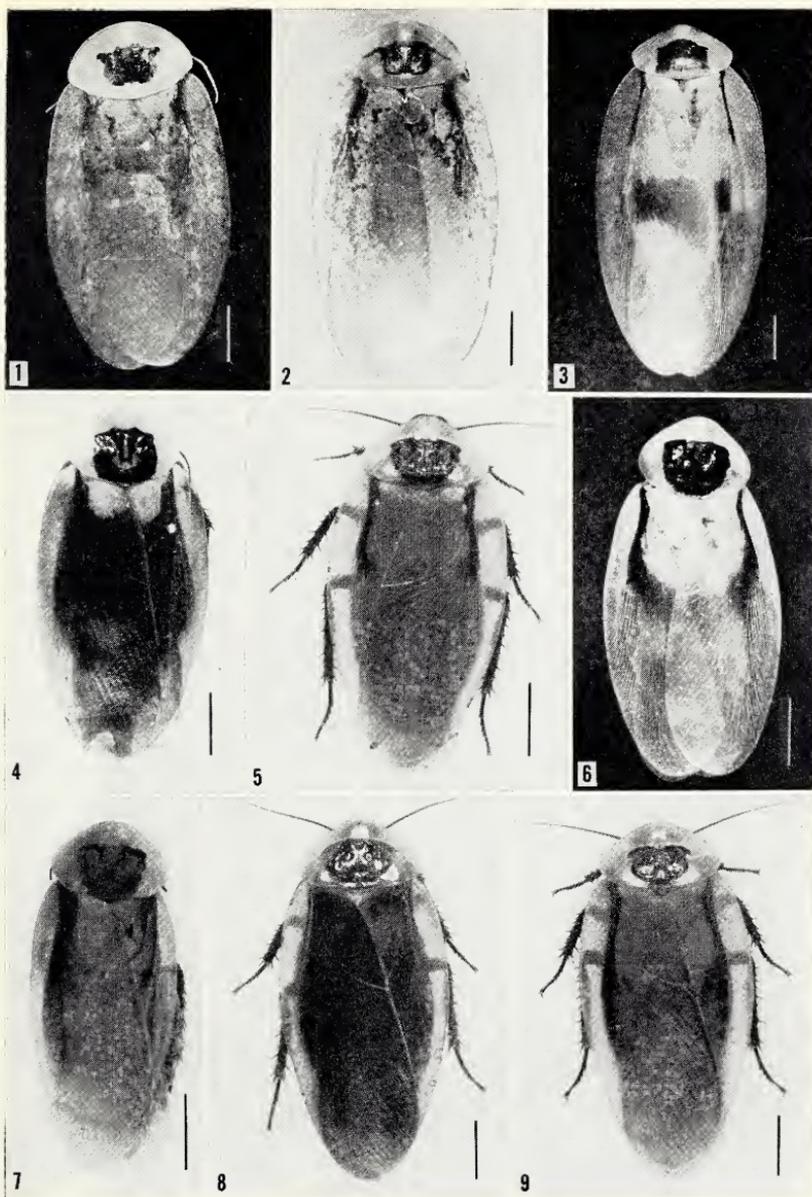
1. Blaberini: *Archimandrita*, *Blaberus*, *Blaptica*
2. Brachycolini: *Brachycola*, *Hormetica*, *Parahormetica*, *Petasodes*
3. Byrsotriini: *Byrsotria*, *Eublaberus*, *Hemiblabera*
4. Monastrini: *Monastria*

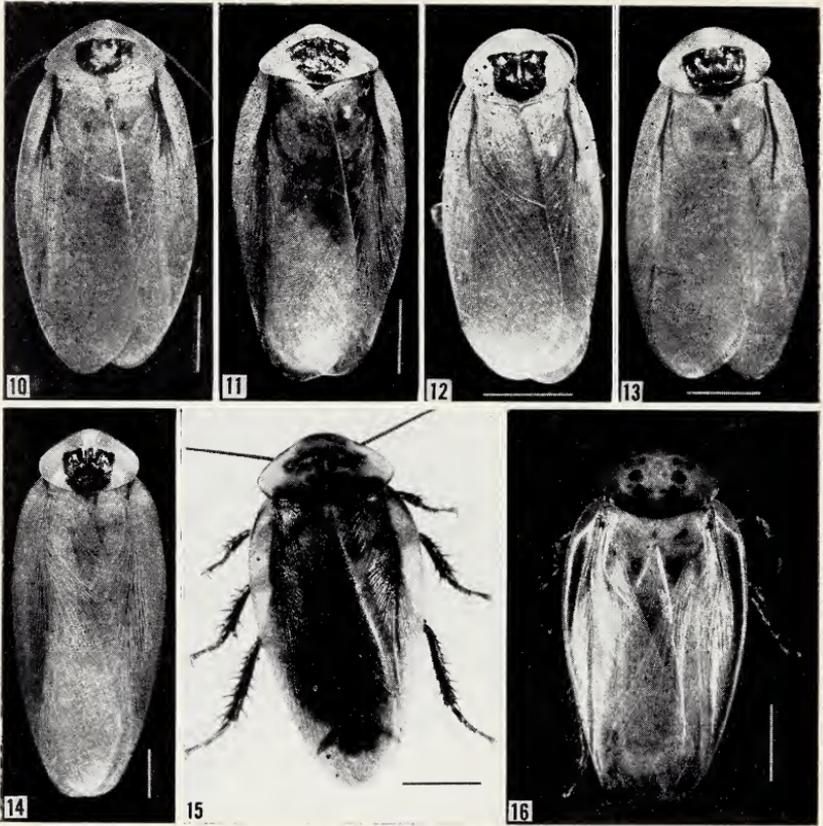
Male genitalic characters support the separation of genera of Blaberinae into 3 (Blaberini, Monastrini, and Brachycolini) rather than 4 tribes; and the genitalia of *Petasodes* indicate that it does not belong in the Brachycolini as suggested by McKittrick. The present study tends to support Rehn and Hebard's arrangement, especially with regard to the placement of *Petasodes*.

1. Blaberini: *Archimandrita*, *Aspiduchus*, *Blaberus*, *Blaptica*, *Byrsotria*, *Eublaberus*, *Hemiblabera*, *Hyporhynchoda*, *Minablatta*, *Styphon* (Figs. 1-117).

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Figs. 1-9. 1. (11 ANSP). *Archimandrita marmorata* (Stoll). San Marcos, Nicaragua. 2. (61 USNM). *Archimandrita tessellata* Rehn. San José, Costa Rica (det. Rehn). 3. (18 USNM). *Blaberus giganteus* (L.). St. Jean, French Guiana (det. Roth.). 4. (5 USNM). *Blaberus craniifer* Burmeister. Key West, Florida (det. Roth.). 5. (N). *Blaberus discoidalis* Serville. Panama (det. Roth.). 6. (516 L). *Blaberus boliviensis* Princis. Guayaquil, Ecuador (det. Princis). 7. (514 L). *Blaberus anisitsi* Brancsik (det. Princis). 8. (N). *Blaberus atropos* (Stoll). Trinidad (det. Roth.). 9. (N). *Blaberus parabolicus* Walker. Puraquequara, Rio Negro, Amazonas, Brazil (det. Roth.). (scale = 10 mm).





Figs. 10-16. (19 ANSP). *Blaberus brasilianus* Saussure. Natal, Brazil. 11. (23 ANSP). *Blaberus scutatus* Saussure (paratype of *B. scutata* var. *obscura* S. and Z.). 12. (8 ANSP). *Blaberus minor* Saussure. Argentina (det. Hebard). 13. (14 ANSP). *Blaberus fusiformis* Walker. Santa Cruz de la Sierra, Bolivia (det. Hebard). 14. (32 ANSP). *Blaberus colosseus* (Illiger). Fyzabad, Trinidad (det. Roth). 15. (N). *Eublaberus posticus* (Erichson). Panama (det. Roth). 16. (N). *Eublaberus distanti* (Kirby). Trinidad (det. Roth). (scale = 10 mm).

To a considerable extent the male genitalia of the genera placed in the Blaberini, show distinct trends (as do the female genitalia and proventricular characters used by McKittrick). It is difficult to separate them into the 2 tribes Blaberini and Byrsotriini which McKittrick used and I have combined them into the Blaberini. However, certain of the genera show closer relationships to one another than to others and therefore I have arranged them in generic groups.

In the Blaberini, L2d is solidly joined to L2vm, and may or

may not be hookshaped. The prepuce is a flexible membrane bearing characteristic spines. When flattened, the margins of the preputial membrane often extend beyond the outline of L2d and the preputial spines are readily visible.

The genera may be arranged as follows:

Generic Group 1. *Archimandrita* (Figs. 1, 2), *Blaberus* (Figs. 4-14), *Blaptica* (Figs. 26, 27, 29).

I have reported on the genus *Blaberus* in a recent paper (Roth, 1969) and for this reason have illustrated R2 (Fig. 42) and L1 (Fig. 43) for only one of the species. However, for the sake of completeness I have included the L2d for the known species (Figs. 41, 44-55); these structures allow the separation of 3 species groups of *Blaberus*:

*Giganteus* Group: L2d is recurved dorsally and slightly to the right, often forming a hooklike structure. Extending dorsally and laterally on the left, about where L2vm and L2d are joined, is a tumorlike outgrowth. Spines on the preputial membrane are relatively small. (*Blaberus giganteus*, Figs. 3, 41-43; *B. cranifer*, Figs. 4, 44).

*Atropos* Group: L2d is not hookshaped and the tumorlike outgrowth on the left side is absent. Truncate or rounded elevations are usually present only on the left side and are generally much larger and more robust than spines on the right. The preputial spines are often arranged in a single row on the left, and a single or sometimes double or partially double row on the right; spines on the right usually more numerous than on the left. (*Blaberus discoidalis*, Figs. 5, 47; *B. boliviensis*, Figs. 6, 49; *B. anisitsi*, Figs. 7, 48; *B. atropos*, Figs. 8, 45; *B. parabolicus*, Figs. 9, 46).

*Brasilianus* Group: L2d not hookshaped and tumorlike outgrowth absent as in the *Atropos* Group. Anterior elevations not greatly enlarged on the left side and about the same size as those on the right. Preputial spines numerous, usually present on the left and right sides and often occur in more than a single row. (*Blaberus brasilianus*, Figs. 10, 50; *B. scutatus*, Figs. 11, 52; *B. minor*, Figs. 12, 51; *B. fusiformis*, Figs. 13, 53; *B. colosseus*, Figs. 14, 54-55).

There is considerable intraspecific variation in the male genitalia of *Blaberus* spp. often making specific determination of certain species difficult. However, the species group separations are reasonably clear cut.

In *Archimandrita* spp. (Figs. 32, 35, 38), L2d is not hookshaped, but otherwise this sclerite and the associated preputial fringe of spines are closest to the *Giganteus* Group of *Blaberus*.

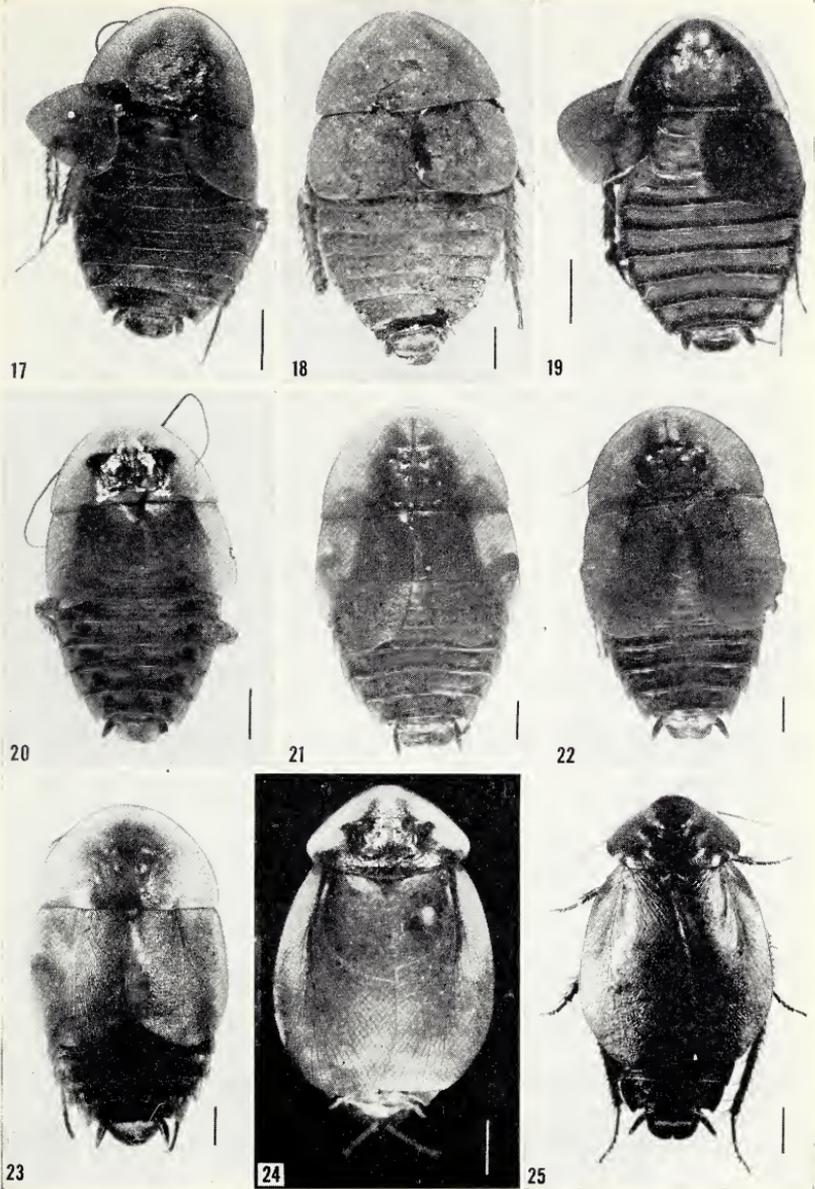
In the genus *Blaptica* the preputial spines are small and occur in multiple rows in *obscura* (Fig. 56) and *dubia* (Fig. 62) but are reduced in number and arranged in a single row in *interior* (Fig. 59). According to Hepper (1965), *Blaptica pereyrai* Hepper is near *B. dubia*, but Hepper noted that the preputial spines of *pereyrai* are fewer in number than in *dubia*. The number of spines shown in Hepper's (1965) figure 11 closely approximate those found in *B. interior*. The number of preputial spines in species of *Blaberus* is variable (Roth, 1969) and this is probably also true for the genus *Blaptica*.

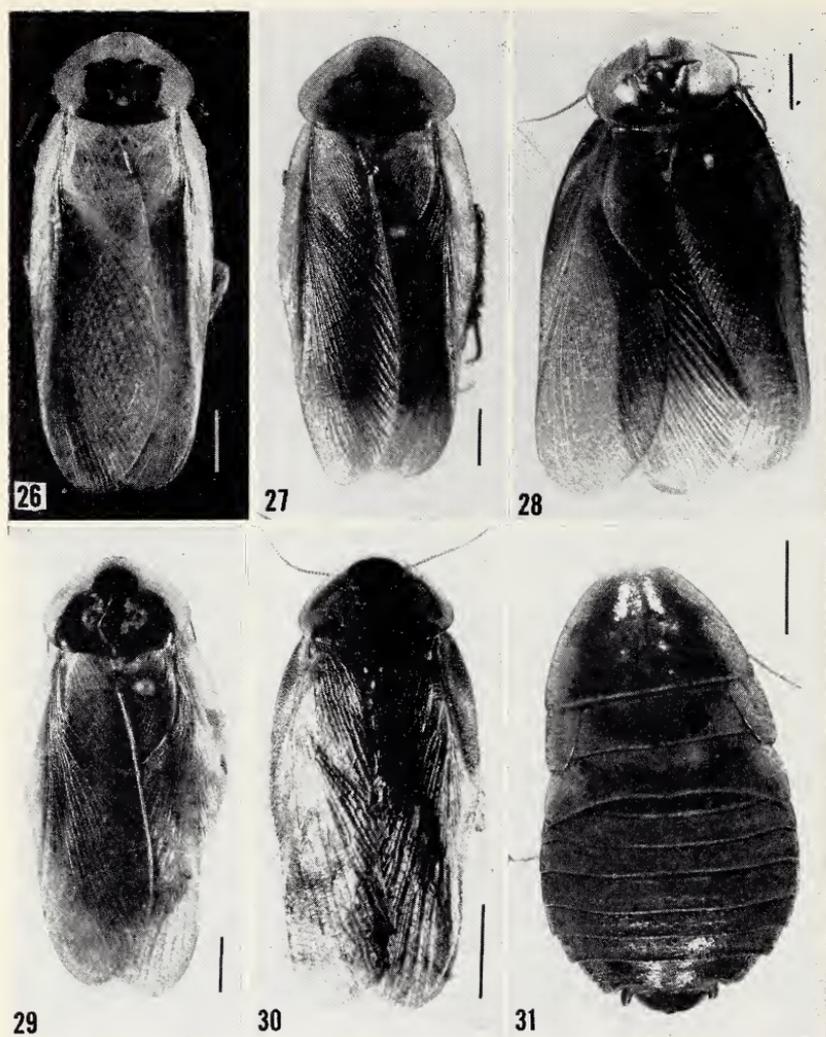
Rehn (1930, p. 62) stated that *Styphon* ". . . is a distinctive genus occupying an isolated position and not closely related to any of the other previously known genera." The genus is found in the Dutch Leeward Islands and Rehn (1930, p. 67) further stated "It is most unexpected to find on these semiarid islands off the north coast of South America an entirely unrecognized genus which has no known close relative on the adjacent mainland. The genus *Parahormetica*, which is in some respects the nearest relative, is an inhabitant of regions widely removed in South America." The L2d and prepuce of *Styphon* (Fig. 64) indicate a closer relationship to *Blaptica* (Fig. 59) than to *Parahormetica* (Figs. 199, 202, 203); the latter is a member of the Brachycolini (see below).

Generic Group 2. *Aspiduchus* (Figs. 21-23), *Byrsotria* (Figs. 24, 25), *Eublaberus* (Figs. 15-16), *Hemiblabera* (Figs. 17-20).

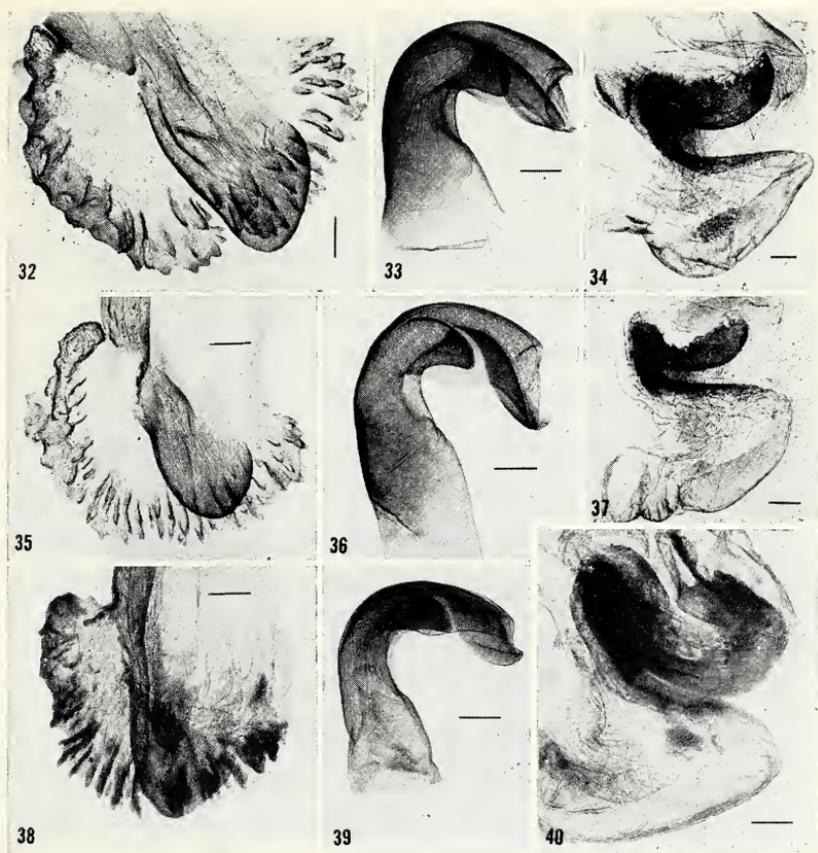
In this group L2d is strongly hookshaped. The genera *Aspiduchus* (Figs. 97, 100, 103, 106), *Byrsotria* (Figs. 75, 78, 81), and *Hemiblabera* (Figs. 84, 87, 90, 93, 96) all have very similar L2d's and the preputial spines are somewhat elongated and arranged principally in a single row. Bonfils' (1969, p. 132) drawing of the L2d and

Figs. 17-25. 17. (24 ANSP). *Hemiblabera granulata* Saussure. Antigua, West Indies. 18. (50 USNM). *Hemiblabera* sp. probably *tenebricosa* Rehn and Hebard. Rojo Jeco, Mt. Samana, San Domingo (det. Gurney). 19. (26 ANSP). *Hemiblabera brunneri* (Saussure). Puerto Rico (det. Rehn). 20. (16 MCZ). *Hemiblabera pabulabor* Rehn and Hebard. Andros Island, Bahamas (det. Gurney). 21. (16 ANSP). *Aspiduchus cavernicola* J. W. H. Rehn. Paratype. Barrio Monte, Cabo Rojo, Puerto Rico. 22. (15 ANSP). *Aspiduchus borinquen* J. W. H. Rehn. Paratype. Corozal, Puerto Rico. 23. (29 AMNH). *Aspiduchus borinquen*. Corozal, Puerto Rico. (det. by J. A. G. Rehn as *A. deplanatus*; J. W. H. Rehn (1951) synonymized Rehn and Hebard's *deplanatus* with *borinquen*). 24. (25 ANSP). *Byrsotria cabrerai* Rehn and Hebard. Matanzas Province, Cuba (det. Rehn). 25. (N.) *Byrsotria fumigata* (Guérin). (det. Roth). (scale = 5 mm)





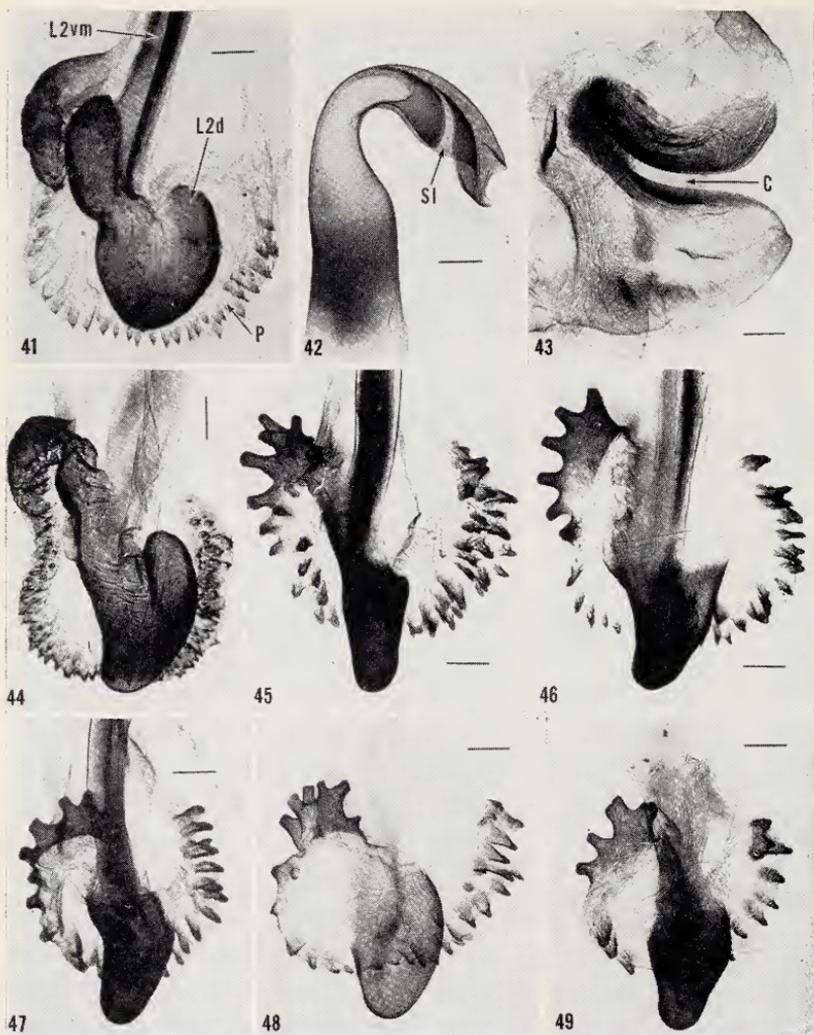
Figs. 26-31. 26. (20 ANSP). *Blaptica interior* Hebard. Formosa, Argentina. (det. Rehn). 27. (22 ANSP). *Blaptica obscura* Saussure and Zehntner. São Leopoldo, Rio Grande do Sul, Brazil (det. Rehn.) 28. (64 USNM). *Minablatta bipustulata* (Thunberg). Viçosa, Minas Geraes, Brazil (det. Rehn). 29. (21 ANSP). *Blaptica dubia* (Serville). Buenos Aires, Argentina (det. Hebard). 30. (N). *Hyporhcnoda litomorpha* Hebard. Panama. (det. Gurney). 31. (6 ANSP). *Styphon bakeri* Rehn. Paratype, Curaçao, Dutch West Indies. (scale = 5 mm).



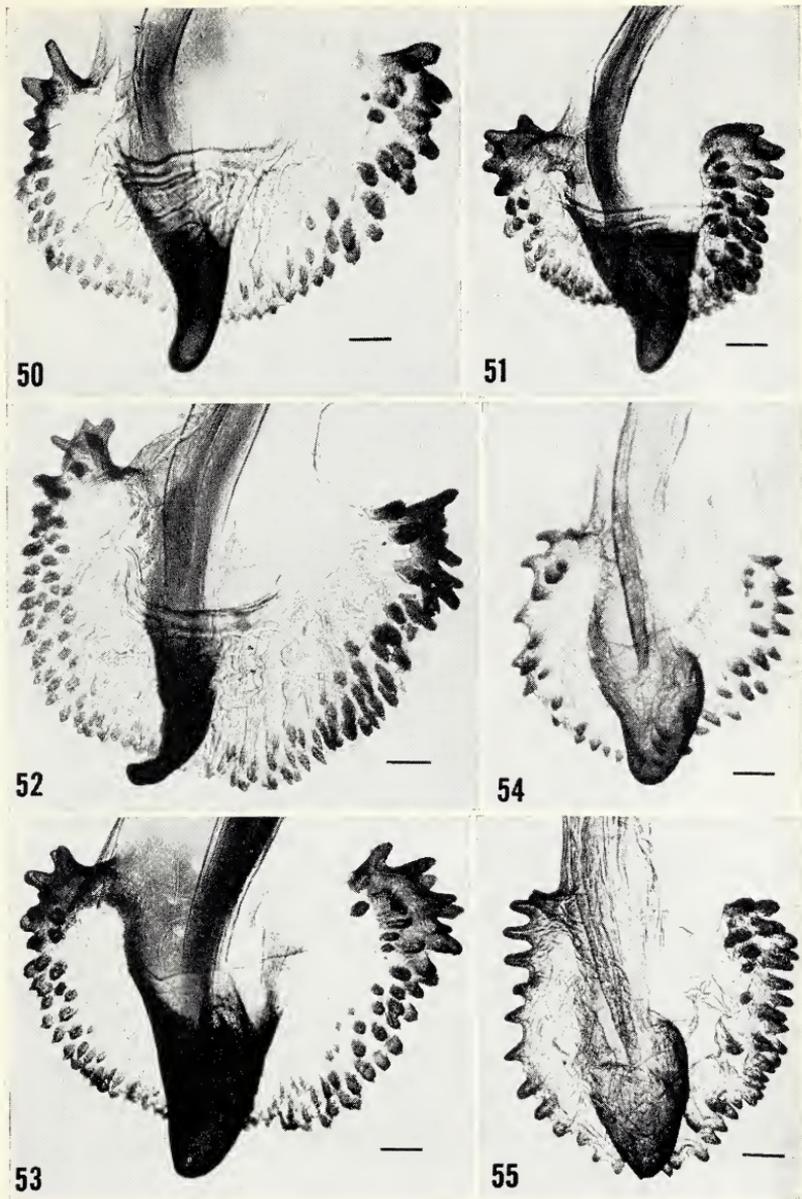
Figs. 32-40. 32-34. (62 USNM). *Archimandrita tessellata*. Canal Zone, Panama (det. Hebard). 35-37. (61 USNM). *A. tessellata*. (from specimen shown in Fig. 2). 38-40. (11 ANSP). *Archimandrita marmorata*. (from specimen shown in Fig. 1). (scale = 0.3 mm).

prepuce of *Hemiblabera tristis* Bonfils shows these structures to be similar to other members of the genus.

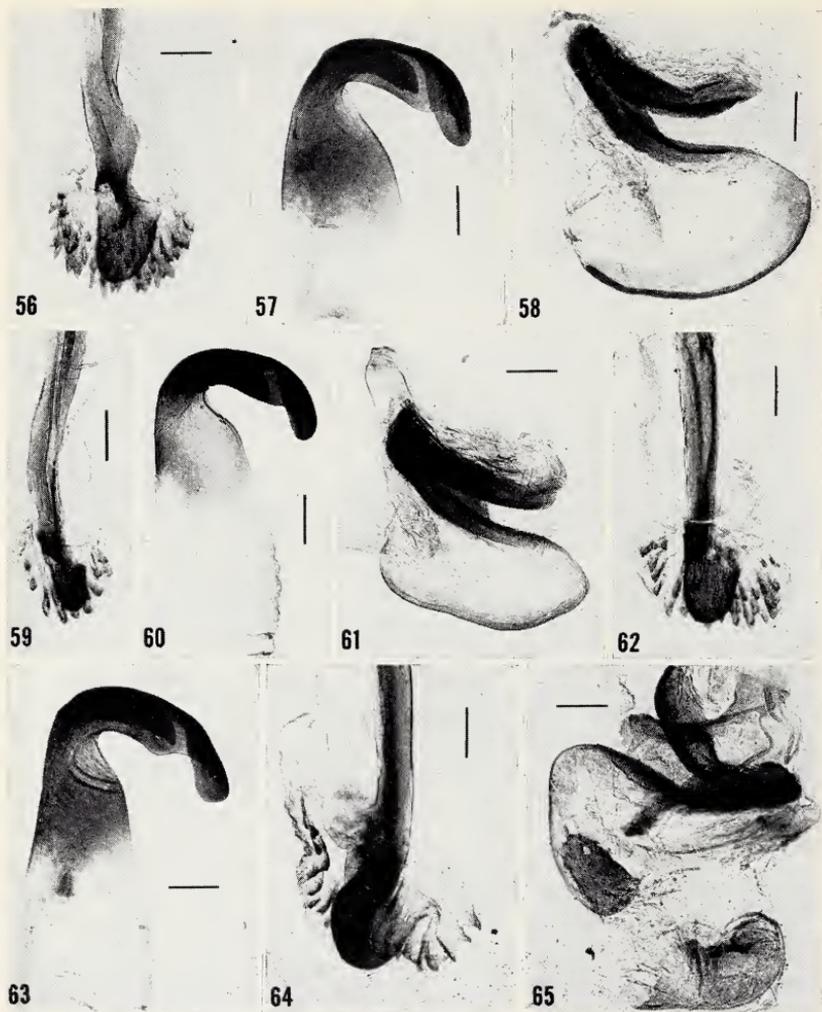
Rehn and Hebard (1927, p. 268) stated that *Hemiblabera* ". . . clearly occupies a position intermediate between *Byrsotria* and *Aspiduchus*, . . . The species *brunneri* has a distinct tendency toward *Byrsotria*, while conversely *H. pabulator* and *granulata* exhibit more of an approach toward *Aspiduchus*." The male genitalia are basically too similar to support Rehn and Hebard's



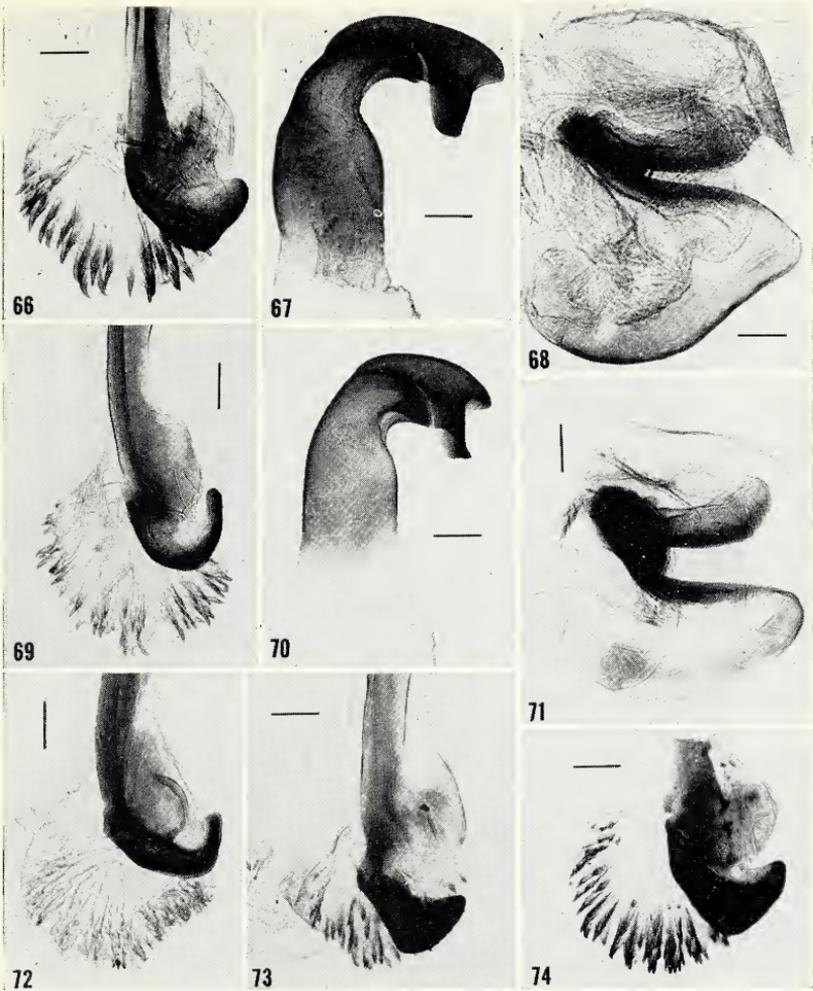
Figs. 41-49. 41-43. *Blaberus giganteus*. 41. (1 AMNH). Caripito, Venezuela. (L2d = dorsal left phallomere; L2vm = ventromedial left sclerite; P = prepuce.) 42-43. (27 ANSP). Muzo, Colombia. (det. Roth). (SI = Subapical incision of hooked right phallomere R2; C = Cleft of left phallomere L1). 44. (46 USNM). *Blaberus craniifer*. Cordoba, Mexico. (det. Roth). 45. (34 USNM). *Blaberus atropos*. Charleston Quarantine (? Colombia) (det. Roth). 46. (6 AMNH). *Blaberus parabolcus*. San Martin, Peru (det. Roth). 47. (N). *Blaberus discoidalis*. Panama (det. Roth). 48. (514 L). *Blaberus anisitsi*. (from specimen shown in Fig. 7). 49. (516 L). *Blaberus bolivicensis*. (from specimen shown in Fig. 6). (scale = 0.3 mm).



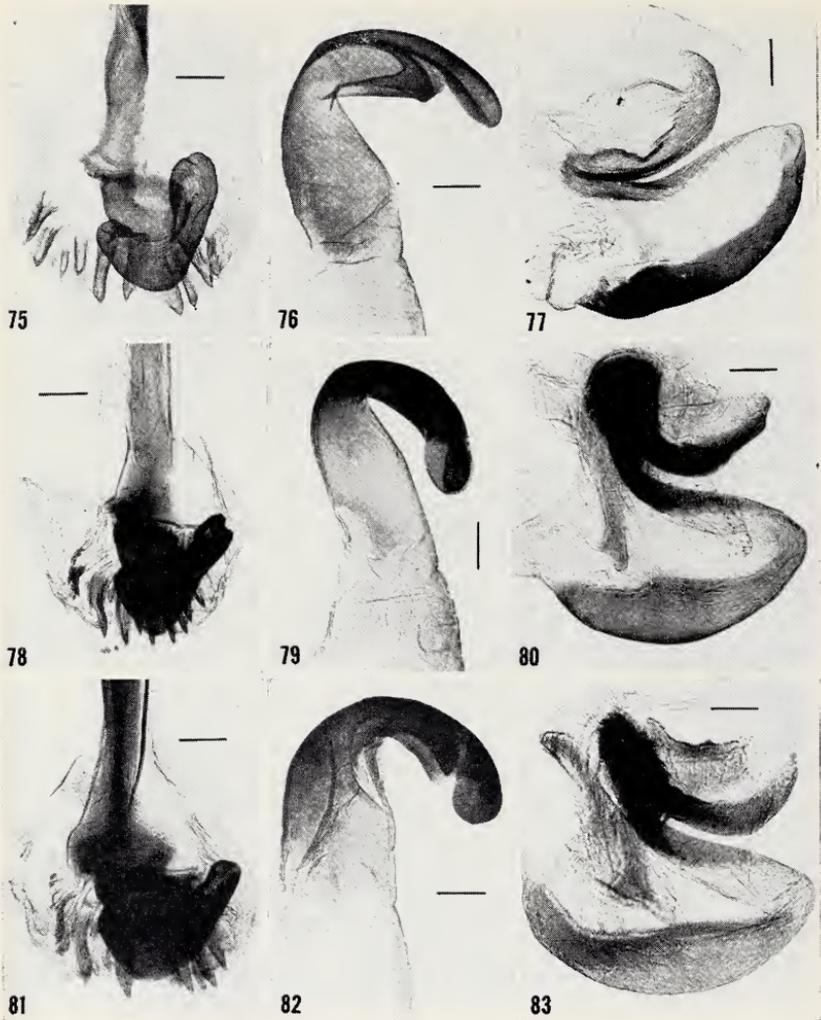
Figs. 50-55. 50. (19 ANSP). *Blaberus brasilianus*. (from specimen shown in Fig. 10). 51. (62 ANSP). *Blaberus minor*. Paraguay. 52. (23 ANSP). *Blaberus scutatus*. (from specimen shown in Fig. 11). 53. (56 ANSP). *Blaberus fusiformis*. Provincia Sara, Dept. Vera Cruz, Bolivia. 54-55. *Blaberus colosseus*. 54. (1 USNM). Trinidad (det. Roth). 55. (30 ANSP). Caparo, Trinidad (det. Hebard). (scale = 0.3 mm).



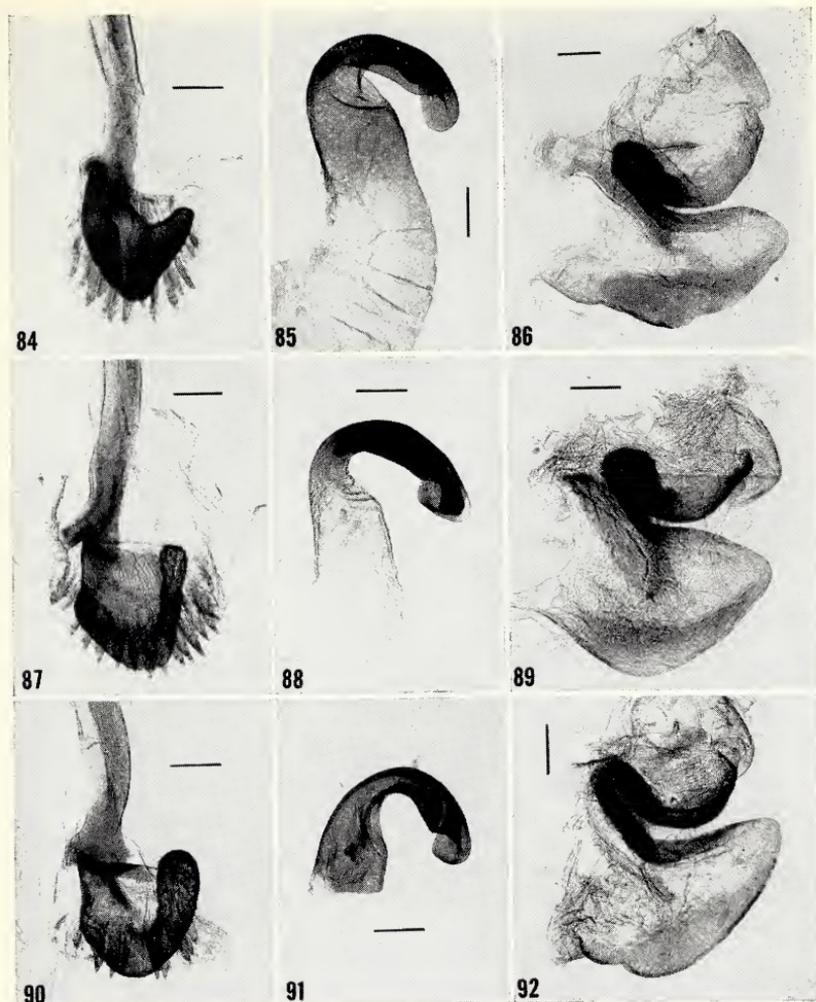
Figs. 56-65. 56-58. (22 ANSP). *Blaptica obscura*. (from specimen shown in Fig. 27). 59-61. (20 ANSP). *Blaptica interior*. (from specimen shown in Fig. 26). 62-63. (21 ANSP). *Blaptica dubia*. (from specimen shown in Fig. 29). 64-65. (6 ANSP). *Styphon bakeri*. (from specimen shown in Fig. 31). (Fig. 65 is a ventral view.) (scale = 0.3 mm).



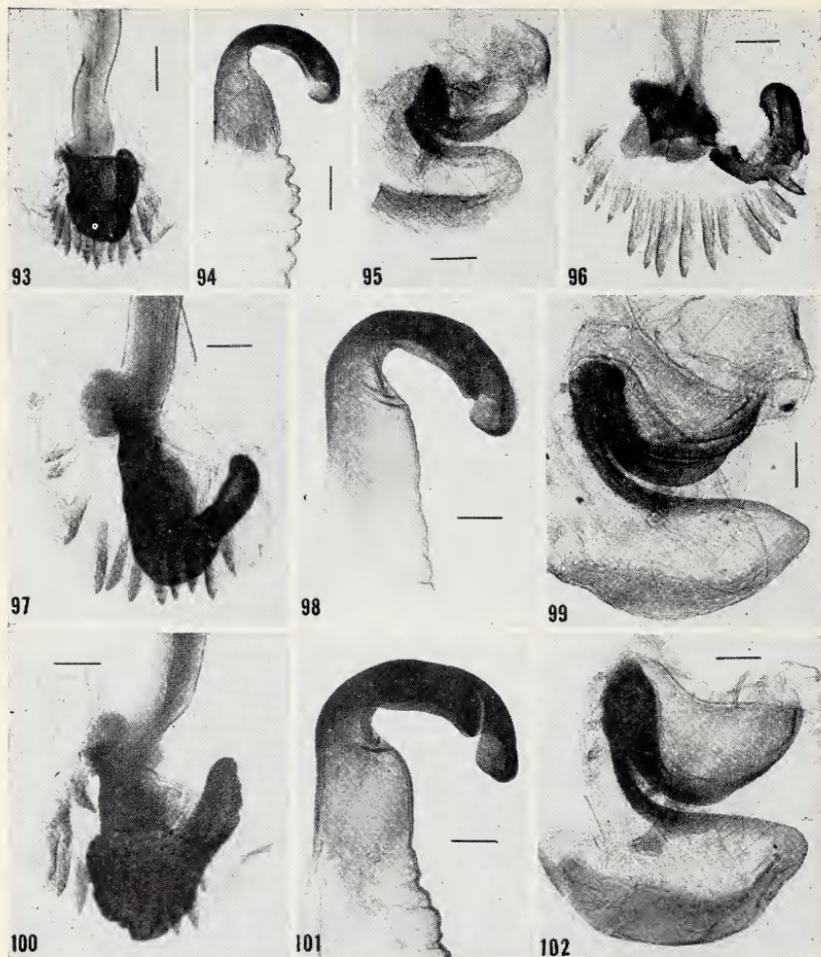
Figs. 66-74. 66-68. (19 MCZ). *Eublaberus posticus*. (Type 16074 of *Blabera femorata* Scudder). Napo or Marañón. 69-71. (27 AMNH). *Eublaberus distanti*. Moyobamba, San Martín, Peru. (det. Roth). 72. (N). *Eublaberus distanti*. Trinidad. (det. Roth). 73. (N.) *Eublaberus posticus*. Panama. (det. Roth). 74. (4 BMNH). *Eublaberus* sp. Para, Brazil. (det. Roth). (scale = 0.3 mm).



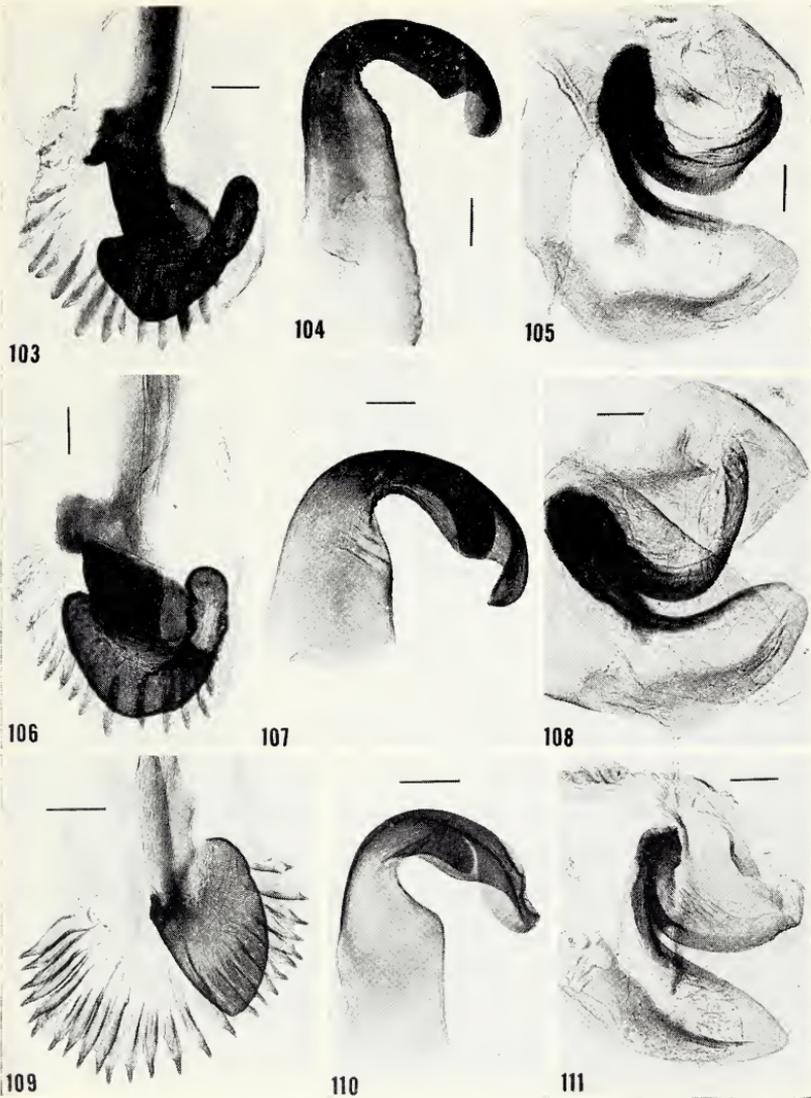
Figs. 75-83. 75-77. (N). *Byrsotria fumigata* (det. Roth). 78-80. (25 ANSP). *Byrsotria cabrerai*. (from specimen shown in Fig. 24). 81-83. (15 MCZ). *B. cabrerai*. Coast below Pico Turquino, Cuba. (det. Gurney). (scale = 0.3 mm).



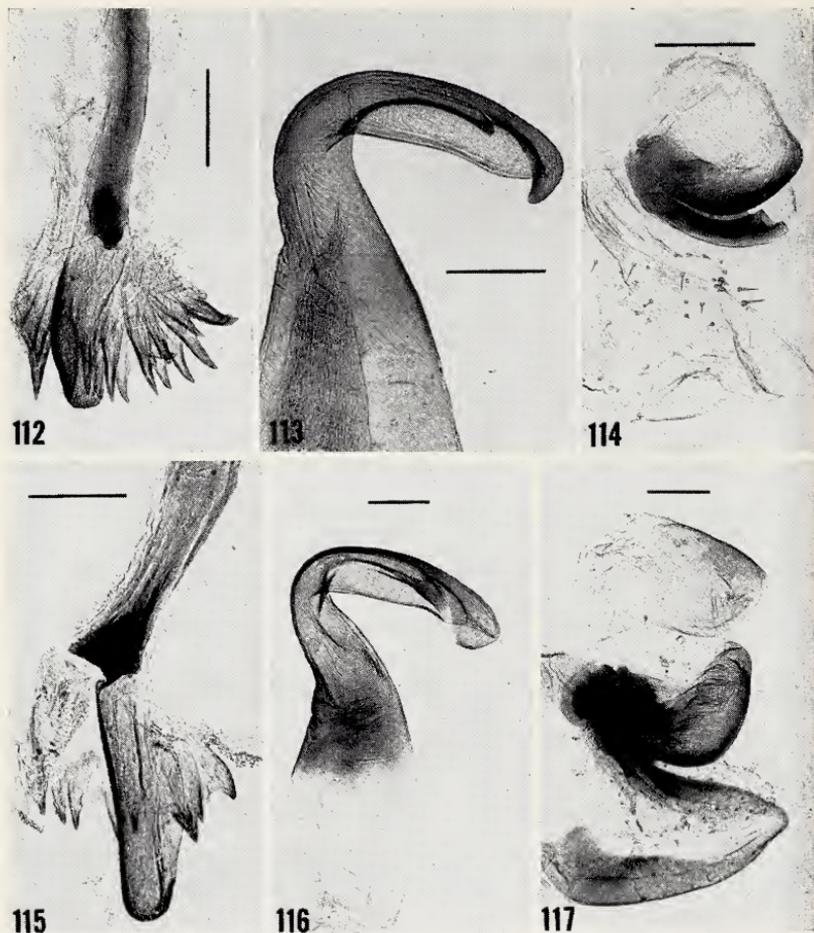
Figs. 84-92. 84-86. (13 ANSP). *Hemiblabea pabulator*. Paratype. Nassau, Bahamas. 87-89. (16 MCZ). *H. pabulator*. (from specimen shown in Fig. 20). 90-92. (24 ANSP). *Hemiblabea granulator*. (from specimen shown in Fig. 17). (scale = 0.3 mm).



Figs. 93-102. 93-95. (26 ANSP). *Hemiblabea brunneri*. (from specimen shown in Fig. 19). 96. (50 USNM). *Hemiblabea* sp. probably *tenebricosa*. (from specimen shown in Fig. 18). 97-99. (15 ANSP). *Aspiduchus borinquen*. (from specimen shown in Fig. 22). 100-102. (16 ANSP). *Aspiduchus cavernicola*. (from specimen shown in Fig. 21). (scale = 0.3 mm).



Figs. 103-111. 103-108. *Aspiduchus borinquen*. 103-105. (30 AMNH). Corozal Cave, Puerto Rico. (misidentified by Rehn and Hebard as *deplanatus*). 106-108. (29 AMNH). (from specimen shown in Fig. 23). 109-111. (64 USNM). *Minablatta bipustulata*. (from specimen shown in Fig. 28). (scale = 0.3 mm).



Figs. 112-117. 112-114. (177 USNM). *Hyporhcnoda reflexa* (Saussure and Zehntner). Turrialba, Costa Rica (det. Gurney). 115-117. *Hyporhcnoda litomorpha* Hebard. Panama (det. Gurney). (scale = 0.3 mm).

suggestion about the relationship of species of *Hemiblabera* to *Byrsotria* and *Aspiduchus*.

Rehn and Hebard (1927, p. 278) in erecting the genus *Aspiduchus* stated that it ". . . is apparently related on one hand to *Hemiblabera* Saussure, and on the other to *Monachoda* Burmeister." The male genitalia of *Aspiduchus* (Figs. 21-23) indicate a close relationship to *Hemiblabera* (Figs. 17-20) but less so to *Monachoda* (Figs. 142, 144, 145) which I place in the Monastriini (see below).

Rehn's (1951, p. 7) drawings of the L2d's of *Aspiduchus cavernicola* (Fig. 100) and *A. borinquen* (Figs. 97, 103, 106) show relatively small differences. It is doubtful that the male genitalia can be used to distinguish between these 2 species.

In *Eublaberus* spp. the preputial spines occur in more than a single row (Figs. 66, 69, 72-74). These spines are more slender and less sclerotized in *E. distanti* (Figs. 69, 72) than in *E. posticus* (Figs. 66, 73), as noted by Princis (1950). Hebard (1920, p. 116) states that *Eublaberus* is closely related to *Blaberus*. However L2d is more distinctly hookshaped in *Eublaberus* than it is in most species of *Blaberus* and for this reason I place it in the second generic group.

Generic Group 3. *Hyporhcnoda* (Fig. 30), *Minablatta* (Fig. 28).

In this group L2d is not hookshaped. Rehn (1940) stated that *Minablatta* is related to *Blaptica* and *Eublaberus* but is probably more closely related to the former. The absence of a hookshaped L2d in *Minablatta* (Fig. 109) places the genus closer to *Blaptica*. However, the elongated preputial spines, occurring in a single row in *Minablatta* (Fig. 109) show a similarity to the spines found in *Aspiduchus* (Fig. 106), *Byrsotria* (Fig. 75), and *Hemiblabera* (Fig. 96).

*Hyporhcnoda* has been placed in the Epilamprinae by Hebard (1920), Princis (1960), and McKittrick (1964). However, the prepuce of the male has a fringe of spines (Figs. 112, 115) which is characteristic of the Blaberinae. Spines are not found on the prepuce of any genera belonging to the Epilamprinae; nor have I seen these spines in males other than Blaberinae, representing more than 90 genera of Blaberidae. In *Hyporhcnoda* the apex of L2vm is more darkly pigmented than L2d so that the junction of the 2 sclerites is readily discernible.

2. Monastriini: *Hiereoblatta* (Fig. 126), *Monachoda* (Figs. 123-125), *Monastria* (Figs. 121-122), *Petasodes* (Figs. 118-120).

In this tribe the apex of L2vm is solidly joined to a relatively broad L2d. In *Monastria* (Figs. 127-138), the prepuce (Figs. 127, 130, 133, 136, 138) is almost entirely covered by rows of small, closely packed spines and extends well below the posterior margin of L2d. In *Monachoda* (Figs. 139-150), *Hiereoblatta* (Figs. 151-153), and *Petasodes* (Figs. 154-162) the prepuce extends little or not at all beyond the margin of L2d and many of the preputial spines (considerably fewer in number than in *Monastria*) are usually hidden under L2d. In *Petasodes reflexa* (Fig. 160) there is a marked reduction in number of preputial spines and these are very lightly sclerotized.

McKittrick (1964) placed *Petasodes* in the Brachycolini, but all the members of this tribe have L2d clearly separated from L2vm by a membrane (see below). Rehn's (1937, p. 241) statement that *Hiereoblatta* is related to *Monastria* is justified by the similarities in male genitalia. However, the shape of L2d and the preputial spines hidden under it in *Hiereoblatta* (Figs. 148, 151) indicate a closer relationship to *Monachoda* (Figs. 142, 144, 145) than to *Monastria* (Figs. 127, 130, 133, 136, 138).

Brachycolini: *Bionoblatta*, *Brachycola*, *Hormetica*, *Oxycercus*, *Parahormetica*, *Phoetalia*, *Sibylloblatta* (Figs. 163-211).

This tribe is clearly differentiated from the Blaberini and Monastriini in that L2d is not solidly attached to L2vm, but is separated from it clearly by a membrane. The spines on the prepuce vary in size from relatively large in *Phoetalia* (Figs. 175, 178) to small in *Parahormetica* (Figs. 199, 202, 203), *Oxycercus* (Fig. 206), *Bionoblatta* (Fig. 209), *Sibylloblatta* (Figs. 195, 198), and *Brachycola* (Fig. 193).

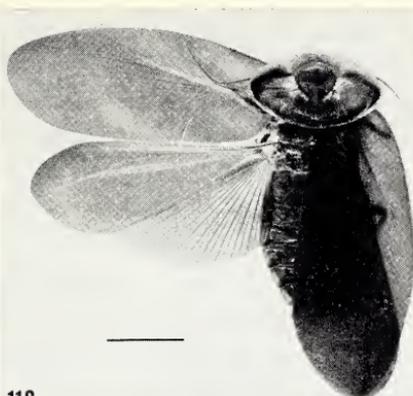
Princis (1960) placed *Phoetalia* in the Epilamprinae and McKittrick (1964) assigned it (as *Leurolestes*) to the Diplopterinae. The male genitalia of *Phoetalia* are not characteristic of either of these

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Figs. 118-126. 118. (17 ANSP). *Petasodes dominicana* (Burmeister). Rio de Janeiro, Brazil (det. Hebard). 119. (7 ANSP). *Petasodes moufeti* (Kirby). São Paulo, Brazil. (det. Hebard). 120. (18 ANSP). *Petasodes reflexa* (Thunberg). 46 m. south of Bahia, Brazil. (det. Rehn). 121. (10 ANSP). *Monastria biguttata* (Thunberg). Rio de Janeiro, Brazil (det. Hebard). 122. (963 L). *Monastria similis* (Serville). Misiones, Argentina (det. Princis). 123. (42 CUZM). *Monachoda latissima* Brunner. Bahia, Brazil. 124. (6 MCZ). *Monachoda burmeisteri* Saussure. 125. (21 BMNH). *Monachoda grossa* (Thunberg). 126. (964 L). *Hiereoblatta cassidea* (Eschscholtz). Lages, Brazil (det. Princis). (scale = 10 mm).



118



119



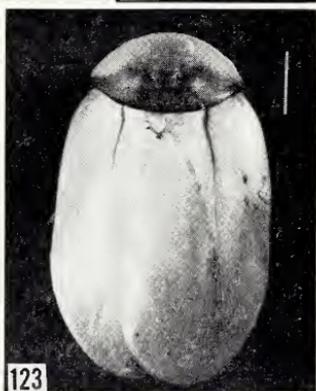
120



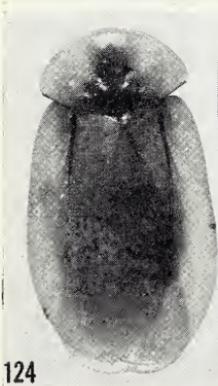
121



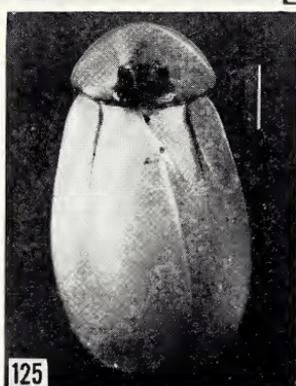
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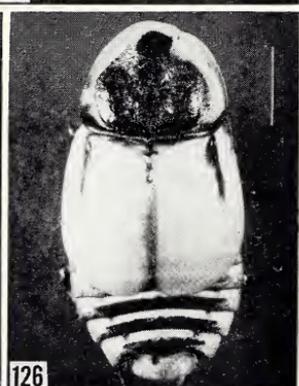
123



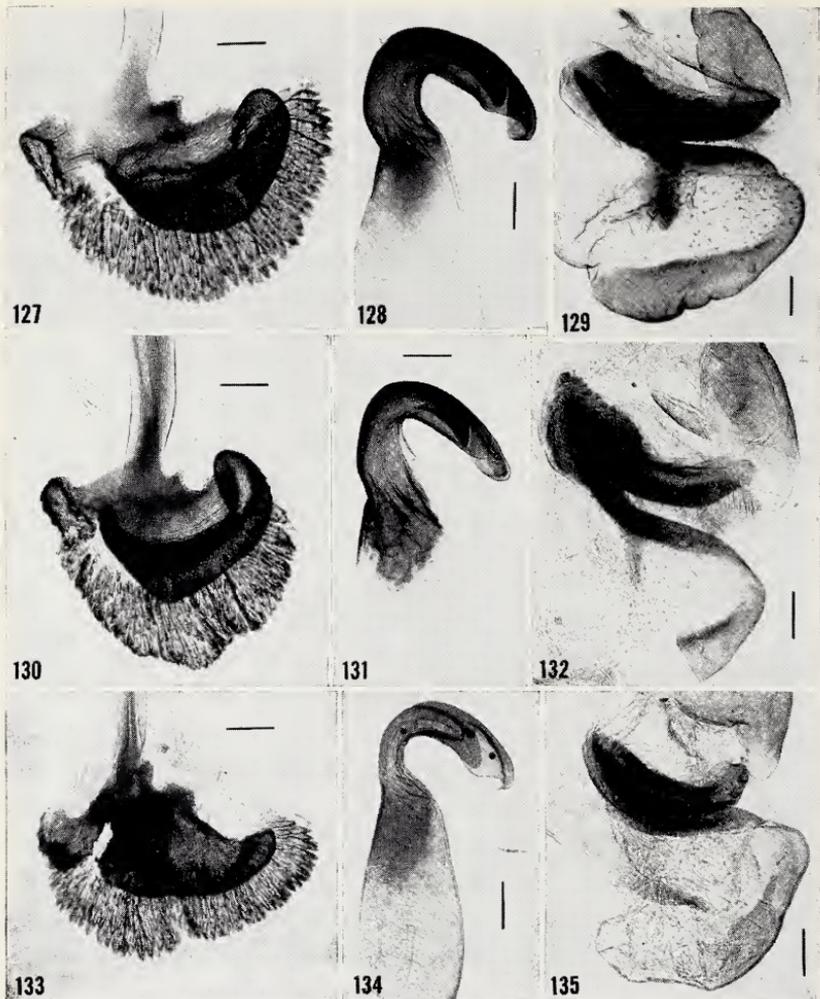
124



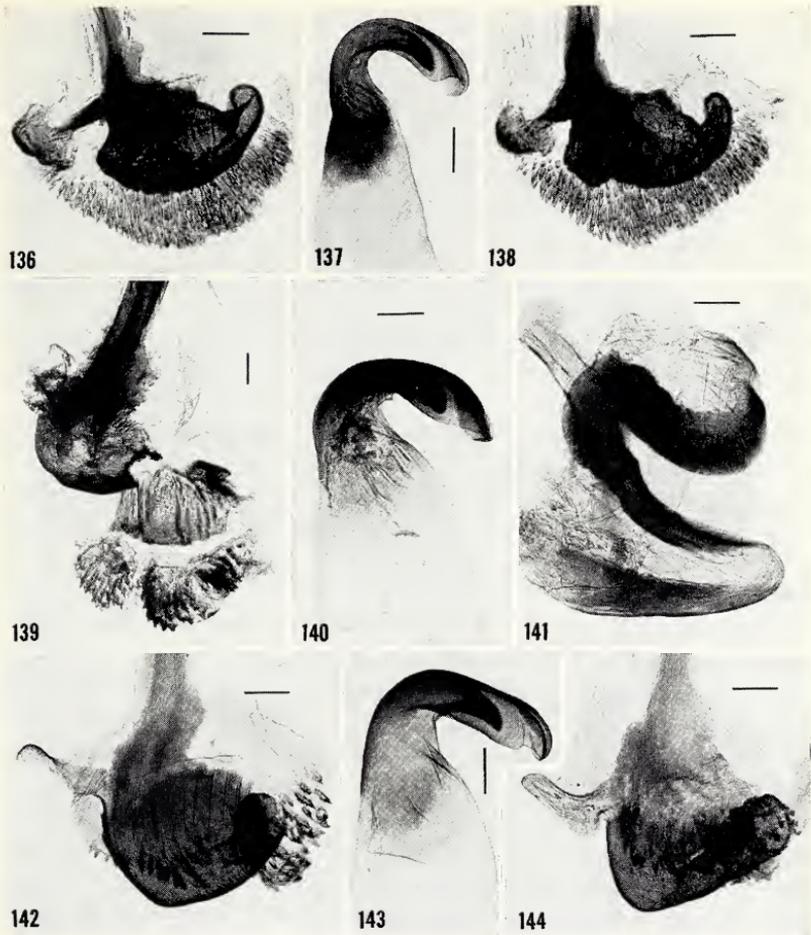
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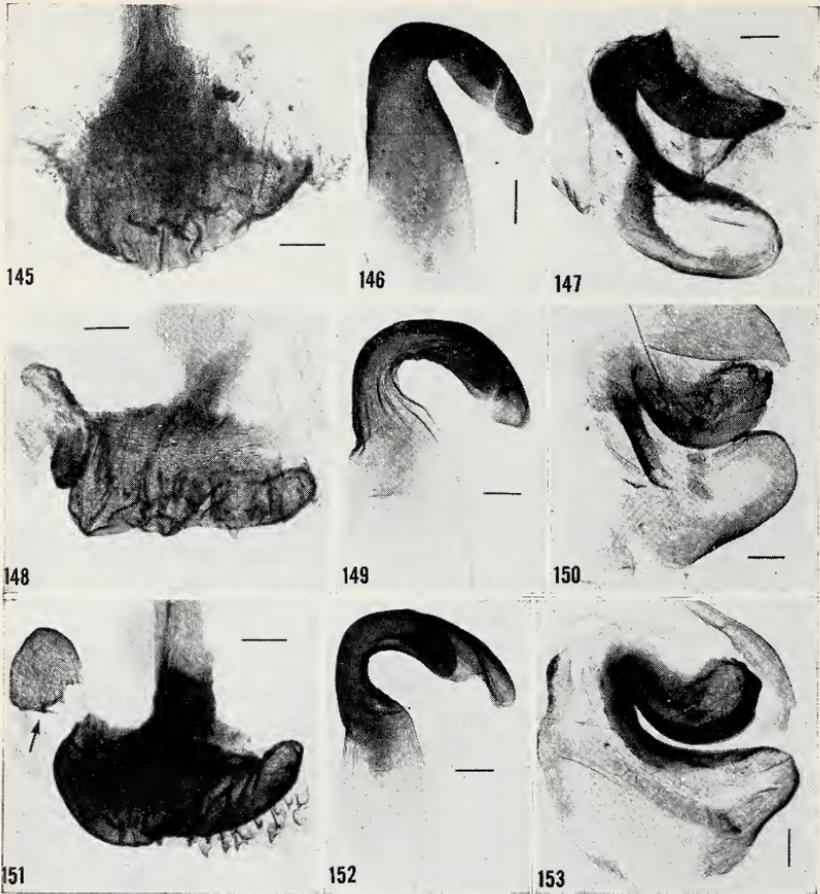
126



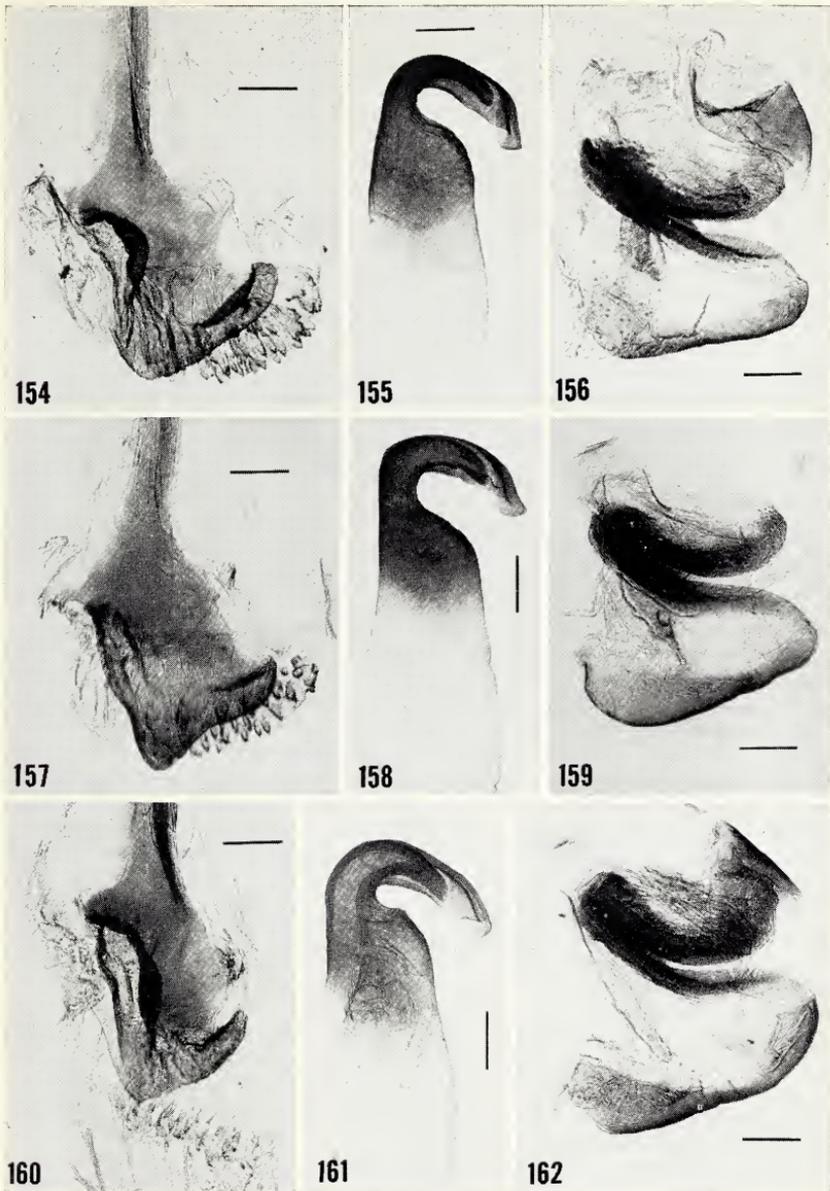
Figs. 127-135. 127-129. (963 L). *Monastria similis* (from specimen shown in Fig. 122). 130-132. (52 USNM). *Monastria* sp. possibly *similis*. São Paulo, Brazil (det. Gurney). 133-135. (10 ANSP). *Monastria biguttata*. (from specimen shown in Fig. 121). (scale = 0.3 mm).



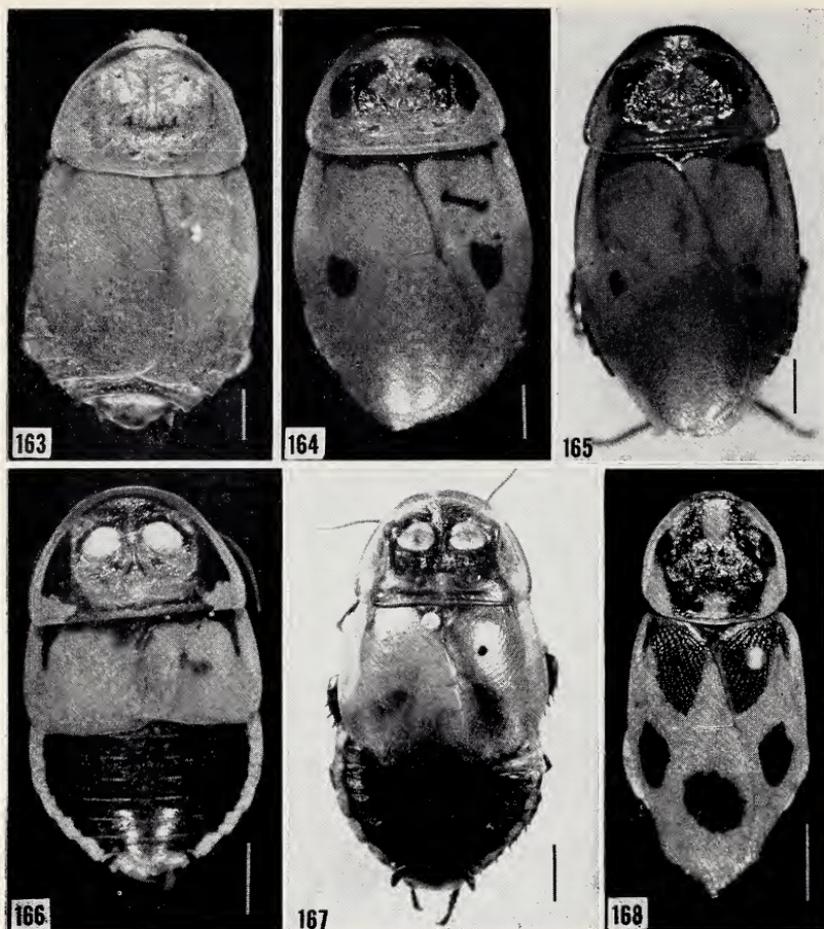
Figs. 136-144. 136-138. (12 MCZ). *Monastria biguttata*. Brazil. 139-141. (6 MCZ). *Monachoda burmeisteri*. (from specimen shown in Fig. 124). The ventral surface of L2d (Fig. 139) was cut away and pulled downward to show the preputial spines. 142-144. (2 LEM). *Monachoda grossa*. 143-144. (21 BMNH). *Monachoda grossa*. (from specimen shown in Fig. 125). (scale = 0.3 mm).



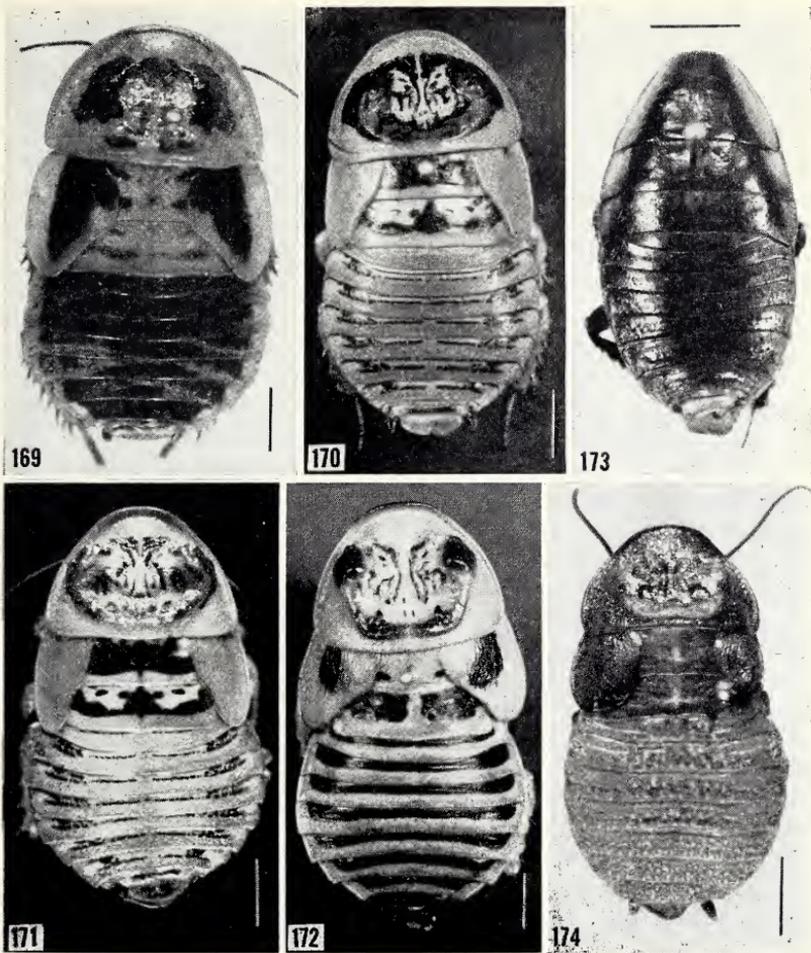
Figs. 145-153. 145-147. (42 CUZM). *Monachoda latissima*. (from specimen shown in Fig. 123). 148-150. (964 L). *Hiereoblatta cassidea*. (from specimen shown in Fig. 126). 151-153. (120 ANSP). *Hiereoblatta cassidea*. Paratype of *Monastria semialata* Saussure. Capivary, Santa Catharina, Brazil (from specimen Fig. 23 in Rehn, 1937). A piece of L2d (arrow, Fig. 151) is torn away from the main body of the sclerite. (scale = 0.3 mm).



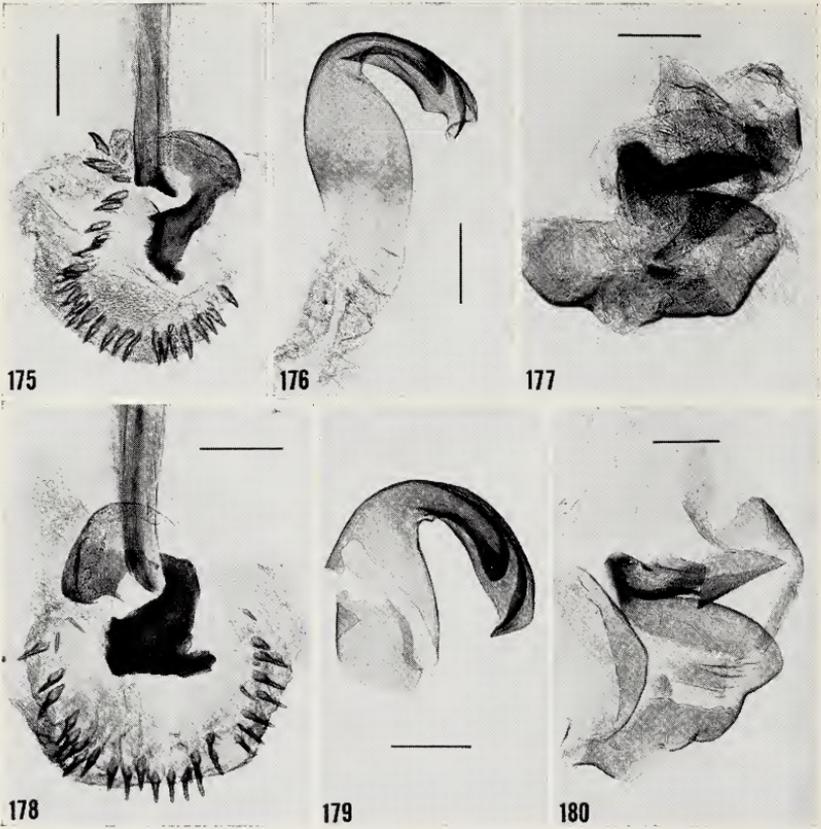
Figs. 154-162. 154-156. (17 ANSP). *Petasodes dominicana*. (from specimen shown in Fig. 118. 157-159. (7 ANSP). *Petasodes moufeti*. (from specimen shown in Fig. 119). 160-162. (18 ANSP). *Petasodes reflexa*. (from specimen shown in Fig. 120). The prepuce has been pulled down so that the lightly sclerotized spines are visible. (scale = 0.3 mm).



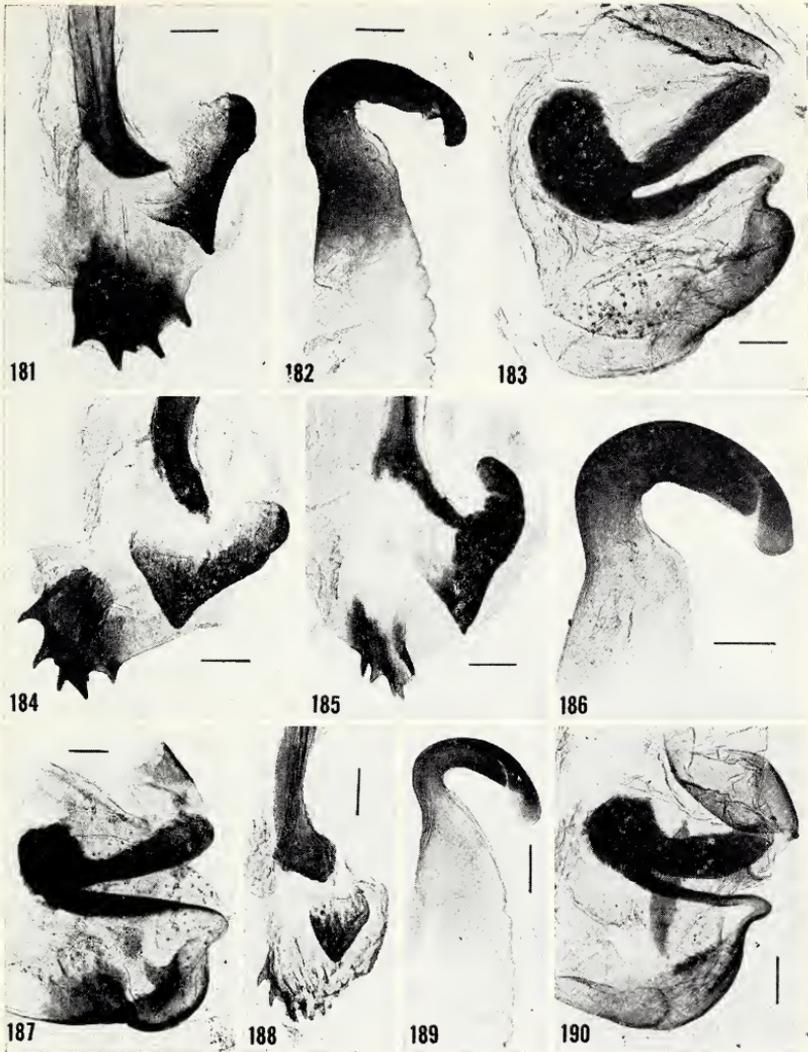
Figs. 163-168. 163. (1 ANSP). *Hormetica laevigata* Burmeister. São Paulo, Brazil (det. Rehn). 164. (2 ANSP). *Hormetica apolinari* Hebard. Susumuco, Colombia (det. Hebard). 165. (14 MCZ). *Hormetica apolinari*. Villavicencio, Colombia (det. Roth). 166. (4 ANSP). *Hormetica subcincta* (Walker). Villavicencio, Colombia (det. Hebard). 167. (44 CUZM). *Hormetica verrucosa* Brunner. Colombia. 168. (5 ANSP). *Brachycola sexnotata* (Thunberg). 92 Km from Rio de Janeiro, Brazil (det. Rehn). (scale = 5 mm).



Figs. 169-174. 169. (5 MCZ). *Sibylloblatta panesthoides* (Walker). Type 1621 of *Hormetica advena* Scudder. Belmont, Massachusetts (adventive). 170. (961 L). *Parahormetica bilobata* (Saussure). Lages, Brazil (det. Princis). 171. (3 ANSP). *Parahormetica bilobata*. Minas Geraes, Brazil (det. by Hebard as *P. tumulosa* Brunner a synonym of *bilobata*). 172. (962 L). *Parahormetica cicatricosa* Saussure. Brazil (det. Princis). 173. (972 L). *Oxycercus peruvianus* Bolivar. Carpapata, Peru (det. Princis). 174. (49 USNM). *Bionoblatta itatiayae* (Miranda Ribeiro). Serra do Itatiaya, Brazil (det. Gurney). (scale = 5 mm).



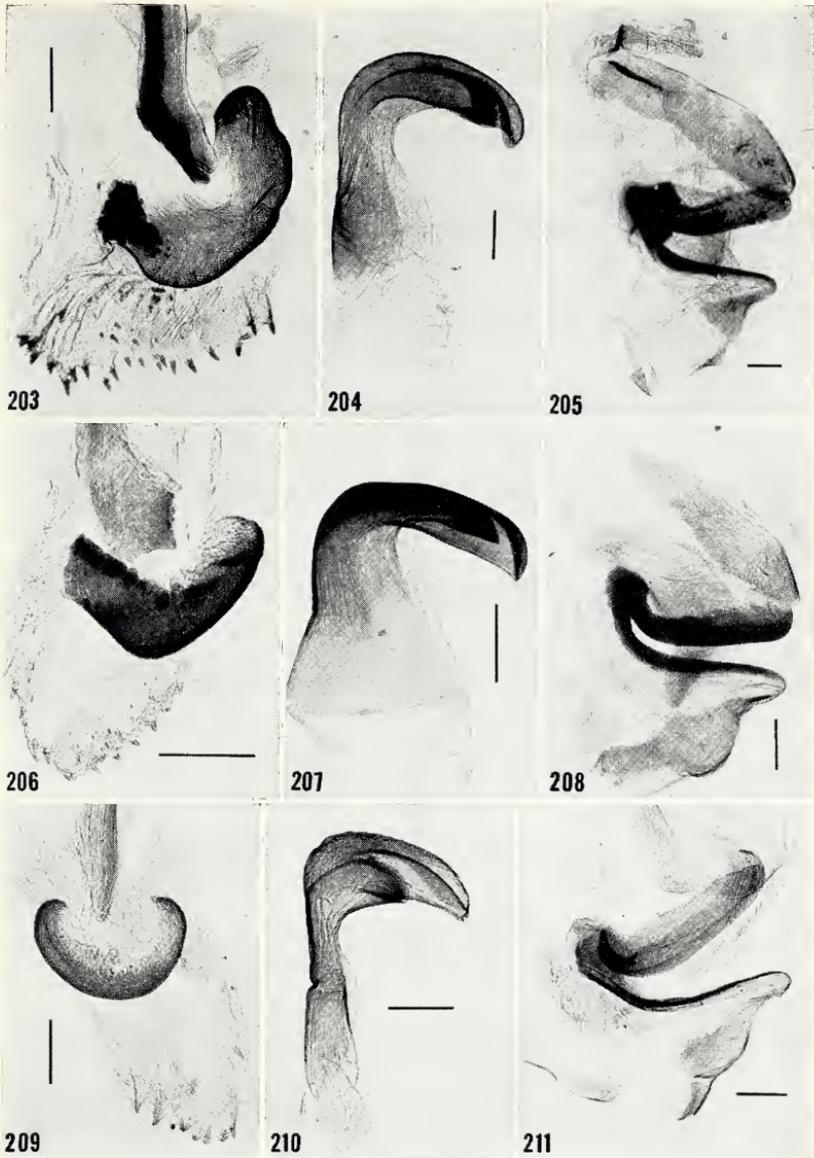
Figs. 175-180. 175-177. (57 MCZ). *Phoetalia pallida* (Brunner). Point Antonio, Jamaica. 178-180. (38 BMNH). *Phoetalia circumvagans* Burmeister. (scale = 0.3 mm).



Figs. 181-190. 181-183. (14 MCZ). *Hormetica apolinari*. (from specimen shown in Fig. 165). 184. (2 ANSP). *Hormetica apolinari*. (from specimen shown in Fig. 164). 185-187. (44 CUZM). *Hormetica verrucosa*. (from specimen shown in Fig. 167). 188-190. (4 ANSP). *Hormetica subcincta*. (from specimen shown in Fig. 166). (scale = 0.3 mm).



Figs. 191-202. 191-192. (1 ANSP). (from specimen shown in Fig. 163). 193. (5 ANSP). *Brachycola sexnotata*. (from specimen shown in Fig. 168). 194. (20 MCZ). *Brachycola sexnotata*. 195-197. (1 LEM). *Sibylloblatta panesthoides*. England (adventive) (det. McE. Kevan). 198. (5 MCZ). *Sibylloblatta panesthoides*. (from specimen shown in Fig. 169). 199-201. (961 L). *Parahormetica bilobata*. (from specimen shown in Fig. 170). 202. (3 ANSP). *Parahormetica bilobata*. (from specimen shown in Fig. 171). (scale = 0.3 mm).



Figs. 203-211. 203-205. (962 L). *Parahormetica cicatricosa*. (from specimen shown in Fig. 172). 206-208. (972 L). *Oxycercus peruvianus*. (from specimen shown in Fig. 173). 209-211. (49 USNM). *Bionoblatta itatiayae*. (from specimen shown in Fig. 174). (scale = 0.3 mm).

two subfamilies and the fringe of preputial spines (Figs. 175, 178) place it in the Blaberinae. Hebard (1917) who placed *Leurolestes* (= *Phoetalia*) in the Epilamprinae noted that the male's subgenital plate had ". . . features comparable to those found in *Blaberus* [Blaberinae]." McKittrick (1964, p. 34) concluded that "The Zetoborinae are closely related to the Brachycolini . . ." This is supported by the similarity in shape of L2d of certain species of Brachycolini (especially *Phoetalia*, Figs. 175, 178) with those found in many males of Zetoborinae (Roth, 1970b); however, there are no preputial spines in the Zetoborinae.

Hebard (1919, p. 128) grouped *Hormetica apolinari* and *H. verrucosa* together based on the black markings on the tegmina. The preputial spines of *apolinari* arise from a heavily sclerotized region (Figs. 181, 184) and though this region and the spines are reduced in *verrucosa* (Fig. 185) the shapes of their L2d's indicate a close relationship. The L2d and preputial spines are much reduced in *Hormetica subcincta* (Fig. 188), and show a resemblance to these structures in *Brachycola* (Fig. 193). *Hormetica laevigata* (the genotype) is unique in lacking preputial spines (Fig. 191) and is the only member of the Blaberinae I have seen in which these spines are completely absent (except for rare aberrant specimens of *Blaberus* spp., Roth, 1969). The fringelike indentations of the preputial membrane of *H. laevigata* are reminiscent of this membrane in *Phortioeca phorasoides* (Walker) (Roth, 1970b), though the indentations are broader in the former species. Hebard's (1921, p. 151) conclusion that *Hormetica* and *Parahormetica* are closely allied as indicated by Brunner is supported by the present study. Rehn (1937, p. 248) concluded that the genus *Sibylloblatta* was a member of endemic neotropical Brachycolae (*Hormetica*, *Parahormetica*, *Brachycola*, *Styphon*, and *Bion* [= *Bionoblatta*]). The male genitalia of *Styphon* (Fig. 64) are clearly those of Blaberini, but the other genera grouped together by Rehn are Brachycolini. Rehn (1937, p. 252) placed *Bionoblatta* (Figs. 209-211) between *Hormetica* and *Parahormetica* but closer to *Parahormetica* (Figs. 199-201), and much less closely related to *Brachycola* (Figs. 193-194) than to either of the other 2 genera. The marked reduction in preputial spines does indicate a close relationship to *Parahormetica* (e.g. *P. bilobata*, Figs. 199, 202), but also to *Oxycercus* (Fig. 206). The hook R2 of *Bionoblatta* (Fig. 210) differs somewhat in shape from this phallomere in other species of the tribe and the subapical incision extends beyond the middle of the hook; in the other genera

the subapical incision is found closer to the tip of the hook (e.g., Fig. 207). Princis (1960) placed *Oxycercus* in the Laxtinae, a subfamily which McKittrick did not recognize and which Princis considers provisional (Roth, 1907b). The L2d and prepuce of *Oxycercus* (Fig. 206) are clearly those of Brachycolini and near *Parahormetica* (Fig. 203). Caudell's record of *Oxycercus peruvianus* from Peru is an error (Proc. U. S. Nat. Museum, 44: p. 350: 1913). I examined his specimen at the USNM and found it to be a species of *Parahormetica*.

#### SUMMARY

Based on male genitalia, 21 genera of Blaberinae are assigned to 3 tribes as follows:

Blaberini: *Archimandrita*, *Aspiduchus*, *Blaberus*, *Blaptica*, *Byrsotria*, *Eublaberus*, *Hemiblabera*, *Hyporhichnoda*, *Minablatta*, *Styphon*.

Monastriini: *Hiereoblatta*, *Monachoda*, *Monastria*, *Petasodes*.

Brachycolini: *Bionoblatta*, *Brachycola*, *Hormetica*, *Oxycercus*, *Parahormetica*, *Phoetalia*, *Sibylloblatta*.

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THE *TETRAGONODERUS* GROUP OF *CHLAENIUS*  
(COLEOPTERA: CARABIDAE) IN THE  
INDO-AUSTRALIAN ARCHIPELAGO

BY P. J. DARLINGTON, JR.  
Museum of Comparative Zoology

The two new *Chlaenius* here described belong to a zoogeographically interesting group of the genus characterized by exceptionally short, subtransverse mandibles. The group may be called the *Chlaenius tetragonoderus* group. *C. tetragonoderus* Chaudoir itself occurs from the southeastern corner of Asia (Burma) to Celebes and the Philippines, with subspecies in the Moluccas (Louwerens 1956) and the Palau Islands (Darlington 1970); it is recorded also from Timor (Louwerens 1953). The group is represented in New Guinea and northeastern Australia by *maculiger* Castelnau (Darlington 1968, 2-5), on the Mariana Is. in Micronesia by a very distinct endemic species (*marianensis* Darlington 1970), and on Timor and the Solomons by new species described below. It will be seen that the group has differentiated mainly in the Indo-Australian archipelago and western Pacific Islands. It is in fact the only group of the genus that has differentiated over so wide an area of the islands. Its success on islands may be due partly to its habitat. Many *Chlaenius* live in wet places, but *tetragonoderus* and *maculiger* (which I have collected in the Philippines and New Guinea respectively) and presumably the other species of the group apparently live away from water, on the ground in rain forest, and need not depend on finding permanent fresh water when they reach a new island.

Key to *Chlaenius* of *tetragonoderus* group

1. Elytra duller with intervals closely punctate with punctures of moderate size, the punctures not or not much sparser toward base of inner intervals; elytra often spotted ..... 2  
— Elytra more shining; elytral punctation *either* much sparser toward base of inner intervals *or* coarser (with pronotum more coarsely punctate too); elytra not spotted ..... 4
2. Head and pronotum submetallic (greenish or bluish); legs usually pale; length *c.* 10-12 mm (3 subspecies) ..... *tetragonoderus*  
— Head and pronotum not metallic; legs dark ..... 3
3. Prothorax narrow (width/length 1.21 and 1.22); pronotum closely punctate throughout; length *c.* 12 mm ..... *timorensis*

- Prothorax wider; pronotum with sparsely punctate areas near middle; length *c.* 12-14 mm ..... *maculiger*
4. Elytral punctures of moderate size but sparser especially toward base of inner intervals; length 11.2-12.7 mm ..... *greensladei*
- Elytral (and pronotal) punctures very coarse; length *c.* 10 mm ..... *marianensis*

### *Chlaenius timorensis* n. sp.

Fig. 1

*Description.* Form as in Fig. 1, rather depressed; brownish-black, appendages dark; entire upper surface moderately punctate and with fine, moderately long pubescence, the punctation being closer on head; surface between punctures shining on head, faintly transversely microreticulate on pronotum, dull and heavily *c.* isodiametrically reticulate on elytra. *Head* 0.69 and 0.71 width prothorax; mandibles short, subtransverse, very strongly arcuate; antennae with segments 3 and 4 subequal (3 slightly longer), pubescent from segment 4; mentum with large apically rounded tooth. *Prothorax:* width/length 1.21 and 1.22; base/apex 1.28 and 1.20; lateral margins narrow, very weakly reflexed posteriorly, each with seta near base but none near middle; base with hair fringe, not margined; apex not distinctly margined; disc depressed, with middle line distinct, transverse impressions obsolete, baso-lateral impressions weak, sub-linear, running into slight longitudinal impressions anteriorly; surface of disc nearly evenly punctate with rather close, nearly uniform punctures of moderate size. *Elytra* subparallel; width elytra/prothorax 1.42 and 1.43 (approximate); base margined, margins rounded at humeri; subapical marginal interruptions present; striae fine finely impressed, intervals slightly convex, finely multipunctate, the punctures not forming regular rows. *Lower surface:* prosternal process rounded, margined at sides but margin weak or interrupted at apex; much of lower surface including part of proepisterna rather finely punctate, but abdomen nearly smooth (with some sparse minute *punctules* at middle). *Inner wings* fully developed. *Legs* normal; 5th hindtarsal segments with *c.* 4 accessory setae each side below. *Secondary sexual characters:* ♂ front tarsi rather widely dilated, with 2nd segments *c.* 1/3 wider than long; ♂ with 1 seta each side last ventral segment; ♀ unknown. *Measurements:* length *c.* 12; width *c.* 4.6 mm.

*Types.* Holotype ♂ (British Mus.) and one broken ♂ paratype (M. C. Z., Type No. 31,676) both from "G<sup>ng</sup> Leo," Timor, 2000-4000 ft. (*c.* 600-1200 m), Nov., Dec. (Doherty).

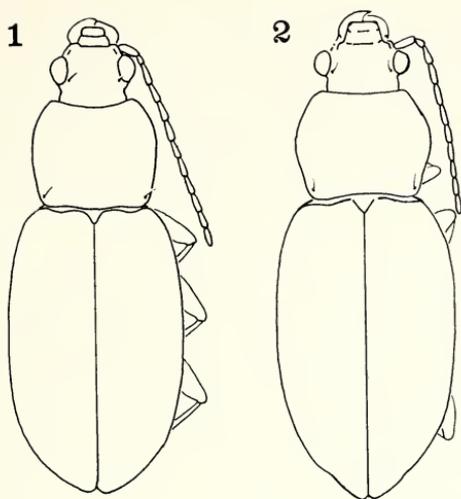


Fig. 1. *Chlaenius timorensis* n. sp., holotype.

Fig. 2. *Chlaenius greensladei* n. sp., holotype.

*Notes.* The very short, subtransverse mandibles, as well as other characters of this insect, place it in the *Chlaenius tetragonoderus* group. The present new species differs from the others of the group as indicated in the preceding key.

### ***Chlaenius greensladei* n. sp.**

Fig. 2

*Description.* Form as in Fig. 2, rather depressed; black, appendages dark; rather shining, pubescence very short, virtually obsolete except at sides of elytra; head with punctures fine, close, of mixed sizes; pronotum with punctures close and of mixed sizes laterally, slightly more sparse in areas near middle; elytra with punctures not dense, sparser on inner intervals anteriorly; reticulate microsculpture between punctures absent on head, fine and light on pronotum and elytra. *Head* 0.67 and 0.68 width prothorax; details *c.* as in preceding species (*timorensis*). *Prothorax:* width/length 1.33 and 1.32; base/apex 1.27 and 1.23; other details *c.* as in preceding species (*timorensis*) except punctation of disc sparser especially near middle and punctures of mixed sizes. *Elytra:* width elytra/prothorax 1.30 and 1.31; striae deeper than in preceding (*timorensis*); intervals convex, irregularly rather sparsely punctate, the punctures sparser anteriorly on inner intervals. *Lower surface:* prosternal

process rounded, weakly margined; much of lower surface (somewhat variably) punctate but abdomen with only sparse minute punctules at middle. *Inner wings* fully developed. *Legs* normal; 5th hind tarsal segments with *c.* 4 accessory setae each side below. *Secondary sexual characters*: ♂ front tarsi rather widely dilated with 2nd segments nearly  $\frac{1}{3}$  wider than long; ♂ with 1, ♀ 2 setae each side last ventral segment. *Measurements*: length 11.2-12.7; 4.3-4.7 mm.

*Types*. Holotype ♂ (British Mus.) from Mt. Austen, Guadalcanal, Solomon Is., Aug. 15, 1966 (P. J. M. Greenslade), at m(ercury) v(apor) light, Field No. 21778; and paratypes as follows. One ♀, Kukum, Guadalcanal, Solomon Is., April 1965 (Greenslade), at m. v. light, Field No. 16780 (M. C. Z., Type No. 31,677); 1 ♂ (U. S. N. M.), Bougainville, Solomon Is., Jan. 1944 (A. B. Gurney); 1 (broken) ♂ (M. C. Z.), Munda, New Georgia, Solomon Is., Feb. 1945 (L. A. Conwell).

*Measured specimens*. The ♂ holotype and ♀ paratype from Guadalcanal.

*Notes*. The characters distinguishing this species from other members of the *tetragonoderus* group of *Chlaenius* are given in the preceding key. The present species differs also in having exceptionally short dorsal pubescence.

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NEW SPECIES OF *GRAMMONOTA*  
(ARANEAE, LINYPHIIDAE) FROM  
PANAMA AND COSTA RICA\*

BY ARTHUR M. CHICKERING  
Museum of Comparative Zoology

Numerous species of the genus *Grammonota* Emerton, 1882, have been recognized from North and Central America as far south as Costa Rica. Two species of this genus were reported from Costa Rica by Bishop and Crosby in 1932. Kraus (1955) did not report this genus from El Salvador, and it has not been reported from Panama as far as I have been able to determine. Many specimens belonging to this genus have appeared in my collections from Panama during the past forty years and the present seems to be a convenient time to put these on record. The frequency with which members of this genus have appeared in my collections from Panama indicates, I believe, the need for more careful collecting throughout the Neotropical region.

Grants GB-1801 and GB-5013 from the National Science Foundation have furnished aid for several collecting trips in Central America, the West Indies and Florida together with my continued research in the Museum of Comparative Zoology, Harvard University, for nearly five and one half years. As I have so frequently done in the past, I am again acknowledging the very gracious help and encouragement received from members of the staff of the Museum of Comparative Zoology extending over a period of many years.

Genus *Grammonota* Emerton, 1882

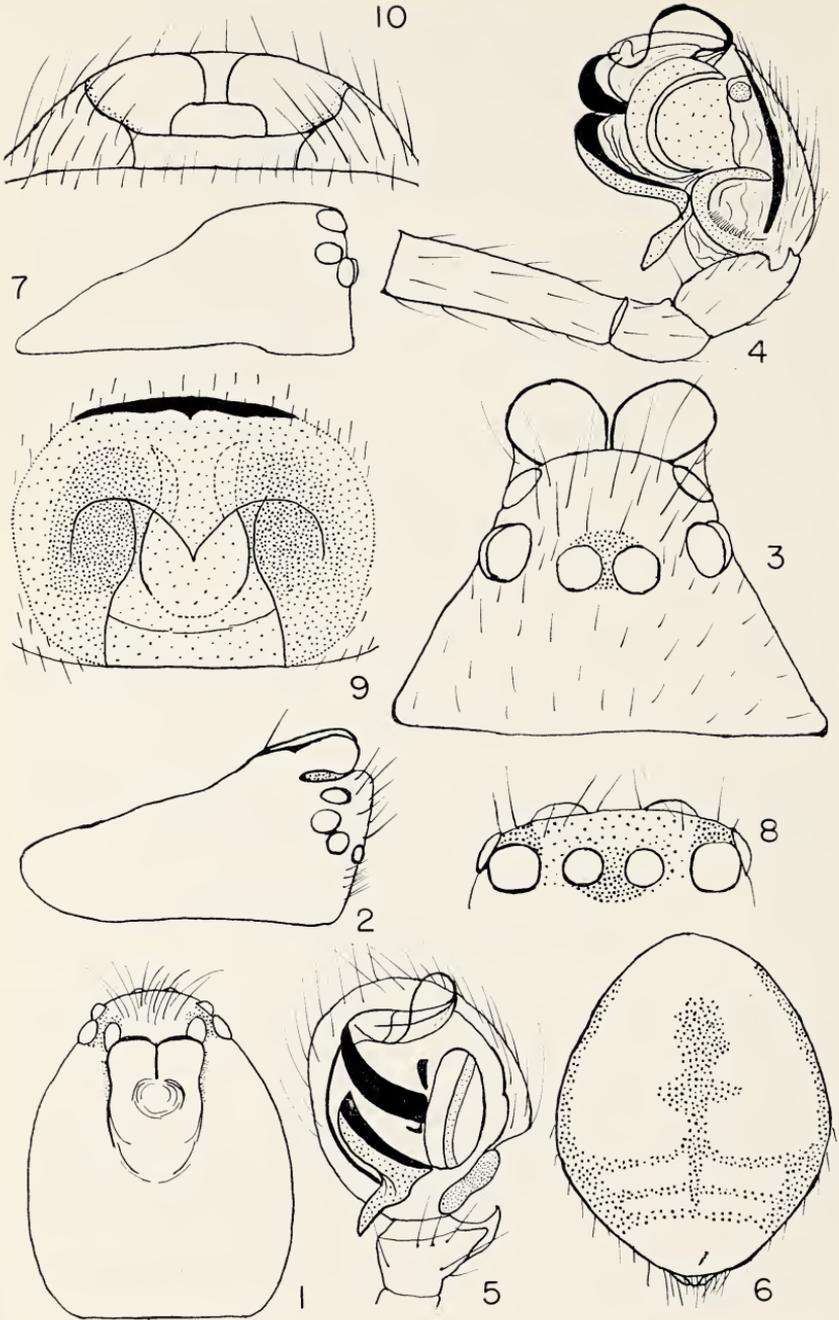
***Grammonota tabuna* sp. nov.**

Figures 1-10

*Holotype.* The male holotype is from Gatun, Panama Canal Zone, January 30, 1958. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.8 mm. Carapace about 0.92 mm long (overlapped by anterior border of abdomen); 0.77 mm wide opposite second coxae where it is widest; with an obscure longitudinal thoracic groove; cephalic region considerably raised and strongly modified by a pair of conspicuous lobes (Figs. 1-3); below each lobe is a

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lateral pit and between the bases of the lobes there is a median dorsal depression. Eyes: eight in two rows; viewed from above, anterior row strongly recurved and posterior row only slightly so; viewed from in front, rows as shown in Figure 3. Ratio of eyes AME : ALE : PME : PLE = nearly 12 : 12 : 14 : 13. AME narrowly separated from one another; separated from ALE by about two-thirds of their diameter. PME separated from one another by about 2.5 times their diameter; separated from PLE by less than their radius. ALE and PLE contiguous. Height of clypeus equal to slightly less than three times the diameter of AME. Chelicerae, maxillae and lip all apparently typical of the genus; cheliceral fang groove with six teeth along promargin and five along retromargin (taken from male paratype). Legs: 4123 in order of length; true spines seem to be absent. Palp: essential features shown in Figures 4-5. Abdomen: typical of the genus; with no important modifications. Color in alcohol: carapace light yellowish-brown with variations; slightly grayish along ventral margins; with a moderate amount of black pigment in ocular area; sternum, mouth parts and legs nearly the same as the carapace with variations; sternum with a thin, grayish margin; abdomen with a median, dorsal, irregular gray stripe extending from near the base to meet three irregular, narrow, transverse bars in the posterior third; these transverse bars connect laterally with an irregular, dorsolateral stripe reaching forward nearly to the base (Fig. 6); on each side of the group of spinnerets there is a narrow gray stripe; the venter is yellowish-white. Considerable variation in color pattern has been noted among the paratypes; the gray abdominal areas may be almost lacking in some specimens.

*Female paratype.* Total length 2.2 mm; carapace about 0.92 mm long (overlapped by anterior border of abdomen); 0.77 mm wide opposite second coxae where it is widest; nearly 0.33 mm tall (Fig. 7). Eyes: arrangement quite different than in male; viewed from above, anterior row definitely recurved and posterior row very slightly so; seen from in front, eyes essentially as shown in Figure 8. Ratio of eyes AME : ALE : PME : PLE = nearly 11 :

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Figures 1-10. *Grammonota tabuna* sp. nov. Figs. 1-2. Carapace of male holotype; from above and right lateral view, respectively. Fig. 3. Eyes and cephalic lobes of holotype from in front. Fig. 4. Left palp of holotype; retrolateral view. Fig. 5. Left palpal tarsus and tibia of holotype; ventral view. Fig. 6. Abdomen of holotype; dorsal view. Fig. 7. Carapace of female paratype; right lateral side. Fig. 8. Eyes of female paratype from in front. Figs. 9-10. Epigynum of female paratype; from below and from behind, respectively.

16 : 15 : 15 (small irregularities in outlines make exact measurements difficult). AME separated from one another by nearly two-fifths of their diameter and separated from ALE by nearly three-fifths of their diameter. PME separated from one another by slightly less than their diameter; separated from PLE by nearly one-third of their diameter; laterals contiguous to one another. Chelicerae, maxillae, lip and sternum essentially as in male. Legs: 4123 in order of length as in male; few true spines present but with many stiff bristles. Abdomen: in general, typical of females of the genus; epigynum quite distinctive, with essential features shown in Figures 9-10. Color in alcohol: very similar to that of male but with gray areas somewhat reduced; sternum slightly grayish; abdomen as in male except that the grayish stripes on each side of the spinnerets are extended forward a short distance and somewhat widened.

*Diagnosis.* This species appears to be most closely related to *Grammonota texana* (Banks) and *Grammonota gigas* (Banks) but I regard it as representing a new group in the genus. Here the cephalic lobes are separated from the eyes, advanced forward and separated from the ocular region by a deep cleft. The form of the cephalic lobes, position of the eyes, features of the male palp and the female epigynum definitely establish it as a new species.

*Records.* The described female paratype was taken with the male holotype. The collection now contains numerous males and females from the following localities in the Panama Canal Zone: Barro Colorado Island, Gamboa, Frijoles, Madden Dam Area, Naval Station near Coccoli, Fort Clayton, Pedro Miguel, Gatun, Summit Gardens and Forest Preserve. All of these were taken during my visits to this region in 1950, 1954 and 1958. In July and August, 1965 I collected more than two dozen of this species in the vicinity of Turrialba, Costa Rica.

### ***Grammonota lutacola* sp. nov.**

Figures 11-15

*Holotype.* The female holotype is from Boquete, Panama, July, 1939. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.94 mm. Carapace 0.71 mm long; 0.55 mm wide opposite interval between second and third coxae where it is widest; nearly 0.22 mm tall; posterior declivity very gradual to posterior border; apparently with a recurved shallow depression representing the median thoracic fovea. Eyes: eight in two rows as usual; viewed from above, anterior row definitely re-

curved and posterior row only slightly so (Fig. 11). Central ocular quadrangle only slightly wider behind than long and wider behind than in front in ratio of nearly 13 : 11. Ratio of eyes AME : ALE : PME : PLE = nearly 5 : 5.5 : 5.5 : 5. AME separated from one another by nearly four-fifths of their diameter and from ALE by a little less than that distance. Lateral eyes contiguous. PME separated from one another by a little more than their diameter and from PLE by slightly less than their diameter. Clypeus slanted forward from AME; height nearly equal to 2.5 times the diameter of AME. Chelicerae, maxillae and lip apparently all essentially typical of females of the genus. Sternum: convex; longer than wide in ratio of nearly 7 : 6; with very narrow lateral extensions between coxae; posterior end obtusely truncated between fourth coxae which are separated by nearly five-fourths of their width. Legs: 12 = 43 in order of length; with numerous slender spines. Abdomen: robust fairly typical of females of the genus; with no special modifications (Figs. 12-13); epigynum essentially as shown in Figures 14-15. Color in alcohol: with a rather distinctive color pattern; carapace brownish in general but with many variations; a darker, irregularly angular spot occupies the center of the dorsal area; the lateral sides are also darker; with considerable black pigment in ocular area. The sternum is a rich, dark brown; legs and mouth parts yellowish with variations. Abdomen: the ground color is light yellowish; the dorsum has a very irregular, central, brownish area (Fig. 12); there is a large, anterior, lateral brownish area (Fig. 13); nearly the whole ventral region is irregularly brownish, darker around the bases of the spinnerets. Considerable variation in the color pattern has been noted among the paratypes but the basic pattern remains in all.

*Diagnosis.* This species appears to be closely related to *Grammonota electa* Bishop and Crosby from Turrialba, Costa Rica, 1932, but this relationship must remain uncertain until the genus is much better known in the Neotropical Region.

*Records.* Six females are in the collection and all are from Boquete, Panama; all were taken in August 1-8, 1950.

### ***Grammonota dalunda* sp. nov.**

Figures 16-19

*Holotype.* The male holotype is from Summit Gardens, Panama Canal Zone, July 29, 1954. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.6 mm. Carapace nearly 0.73 mm long; nearly 0.6 mm wide opposite second coxae where it is widest; about 0.18 mm tall; only slightly raised in cephalic area; median thoracic pit present but obscure; with no lobes or humps. Eyes: eight in two rows as usual in species in which the cephalic region is not modified by lobes or humps; viewed from above, posterior row straight, anterior row quite strongly recurved. Central ocular quadrangle wider behind than in front in ratio of nearly 3 : 2; slightly wider behind than long (Fig. 16). Ratio of eyes AME : ALE : PME : PLE = 7.5 : 11 : 11 : 10. AME separated from one another by a little less than their diameter and from ALE by a little more than their radius; separated from PME by a little less than 1.5 times their diameter. Lateral eyes contiguous. PME separated from one another by nearly four-fifths of their diameter and from PLE by a little more than their radius. Clypeus moderately porrect; height nearly equal to 3.5 times the diameter of AME. Chelicerae: vertical; parallel; typical of the genus in general; fang groove with several teeth along margins but exact number not determined because of fragility of holotype and lack of paratypes. Maxillae and lip essentially typical of the genus. Sternum: moderately convex; about as wide as long; extended just to bases of fourth coxae which are separated by a little more than their width. Legs: 1423 in order of length; with numerous long slender spines. Palp: essential features shown in Figures 17-18. Abdomen: typical of males of the genus; without special modifications. Color in alcohol: carapace light yellowish with vaguely outlined and indistinct grayish areas and with a moderate amount of black pigment in ocular area. Sternum yellowish. Legs and mouth parts light yellowish. Abdomen: yellowish with vaguely outlined, narrow, light grayish, transverse lines on dorsum and with a pale yellowish venter.

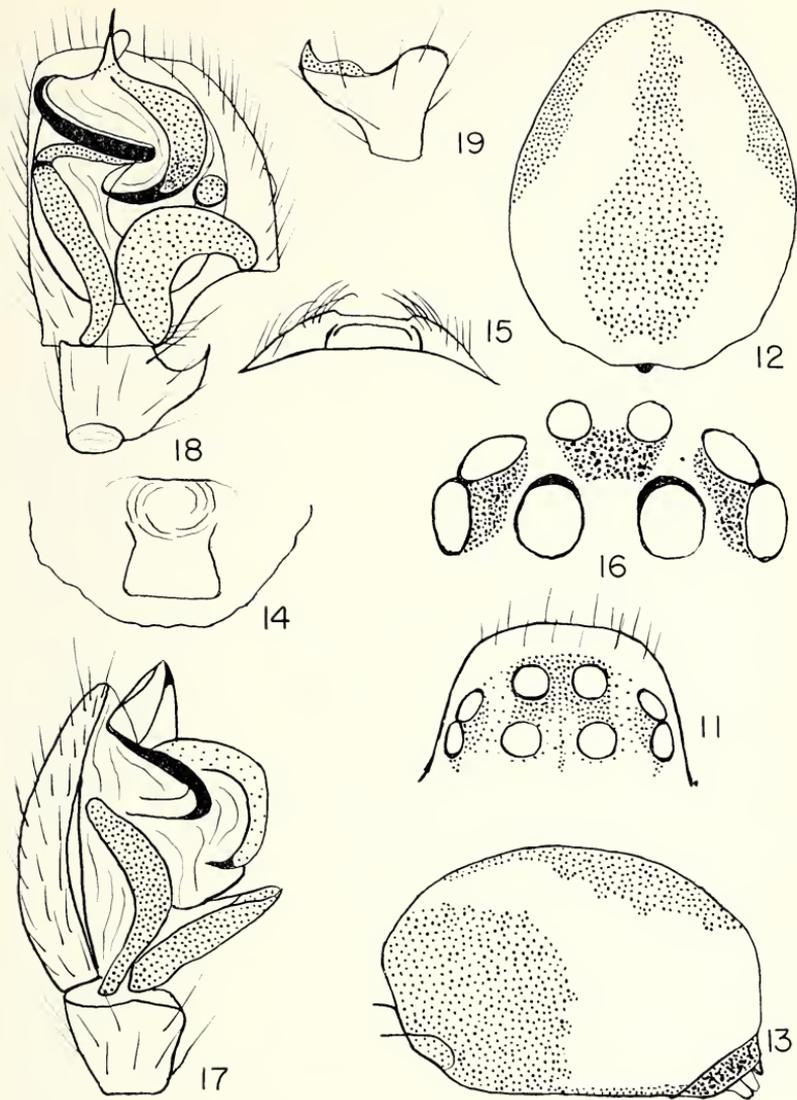
*Diagnosis.* This species seems to be closely related to several known species such as *Grammonota suspiciosa* and *Grammonota nigrifrons* described by Gertsch and Mulaik from Texas in 1936 and reported from Mexico in 1937 by Gertsch and Davis. I believe that the palpal features definitely establish it as a new species.

*Records.* The female is unknown and there are no male paratypes.

### **Grammonota innota** sp. nov.

Figures 20-26

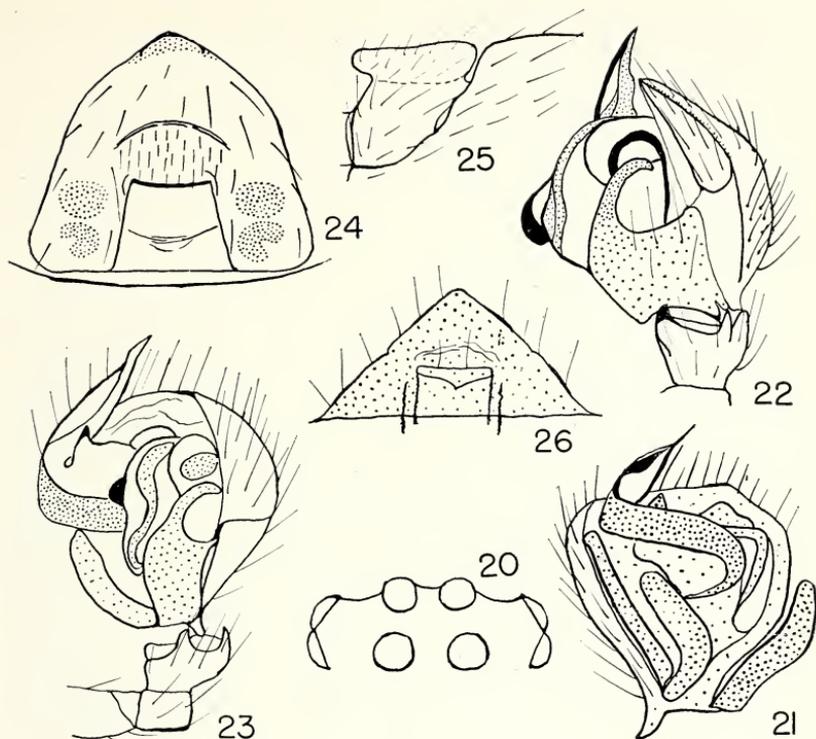
*Holotype.* The male holotype is from Barro Colorado Island, Panama Canal Zone, February 6, 1958. The name of the species is an arbitrary combination of letters.



Figs. 11-15. *Grammonota lutacola* sp. nov. Fig. 11. Eyes of holotype from above. Figs. 12-13. Abdomen of holotype; dorsal and left lateral views, respectively. Figs. 14-15. Epigynum of holotype; from below and behind, respectively. Figs. 16-19. *Grammonota dalunda* sp. nov. Fig. 16. Eyes of holotype from above. Figs. 17-18. Left palpal tibia of holotype; prolateral and ventral views, respectively. Fig. 19. Left palpal tibia of holotype; dorsal view.

*Description.* Total length 1.58 mm. Carapace 0.63 mm long; 0.57 mm wide opposite second coxae where it is slightly wider than it is opposite third coxae; nearly 0.26 mm tall; without definite lobes or humps in cephalic area. Eyes: eight in two rows; viewed from above, anterior row gently recurved and posterior row straight (Fig. 20). Central ocular quadrangle wider behind than in front in ratio of nearly 7 : 5; slightly wider behind than long. Ratio of eyes AME : ALE : PME : PLE = nearly 8 : 11 : 10 : 9.5. AME separated from one another by a little less than their diameter and from ALE by slightly more than 1.5 times their diameter. Laterals contiguous as usual. PME separated from one another by a little less than their diameter and from PLE by about six-fifths of their diameter. Height of clypeus nearly 4.5 times the diameter of AME. Chelicerae: moderately robust; vertical; parallel; fang evenly curved; fang groove probably with five small teeth along promargin and four along retromargin. Maxillae: convergent; typical of the genus. Lip: very short; twice as broad as long. Sternum: very convex; nearly as broad as long; extended between fourth coxae which are separated by their width. Legs: 1243 in order of length; long and slender as usual in the genus; with numerous slender spines. Palp: essential features shown in Figures 21-23. Abdomen: typical of males of the genus; without special modifications. Color in alcohol: carapace brown with darker streaks and vague, small, angular spots; near the middle of the dorsum there is an elongate, angular, darker spot with fine dark streaks reaching toward the posterior eyes. Legs and mouth parts yellowish brown with variations; the sternum is dark brown; abdomen brown with small light colored irregular spots. There is considerable variation in color pattern among the available paratypes.

*Female paratype.* Total length 1.8 mm. Carapace about 0.66 mm long (considerably overlapped by abdomen); 0.61 mm wide opposite second coxae where it is widest; nearly 0.26 mm tall. Eyes: eight as usual in females of the genus; very similar to those of male holotype. Clypeus quite porrect; height nearly equal to three times the diameter of AME. Chelicerae, maxillae and lip all essentially typical of females of the genus and without special modifications. Sternum: quite convex; about as wide as long; extended between fourth coxae which are separated by nearly 1.3 times their width. Legs: 41 = 23 in order of length; with numerous slender spines. Abdomen: typical of females of the genus in general. Epigynum: essentially as represented in Figures 24-26. Color in alcohol: considerably lighter than in the male but otherwise essentially as in that sex. The color pattern



Figs. 20-26. *Grammonota innota* sp. nov. Fig. 20. Eyes of holotype from above. Fig. 21. Left palpal tarsus of holotype; ventral view. Figs. 22-23. Left palpal tibia and tarsus; retrolateral and ventro-retrolateral views, respectively. Fig. 24. Epigynum of female paratype from below. Fig. 25. Idem; right lateral view. Fig. 26. Idem; posterior view with posterior portion lifted; second paratype.

is quite variable among the available paratypes as was noted among the males.

*Diagnosis.* This species seems to be most closely related to the group of species including *Grammonota suspiciosa* Gertsch and Mulaik and *Grammonota nigrifrons* Gertsch and Mulaik described from Texas, 1936 and reported from Mexico in 1937 by Gertsch and Davis.

*Records.* The described female paratype was taken with the holotype. Beginning in July, 1934, this species has appeared in my collections during each of my seven periods of field work in the Panama

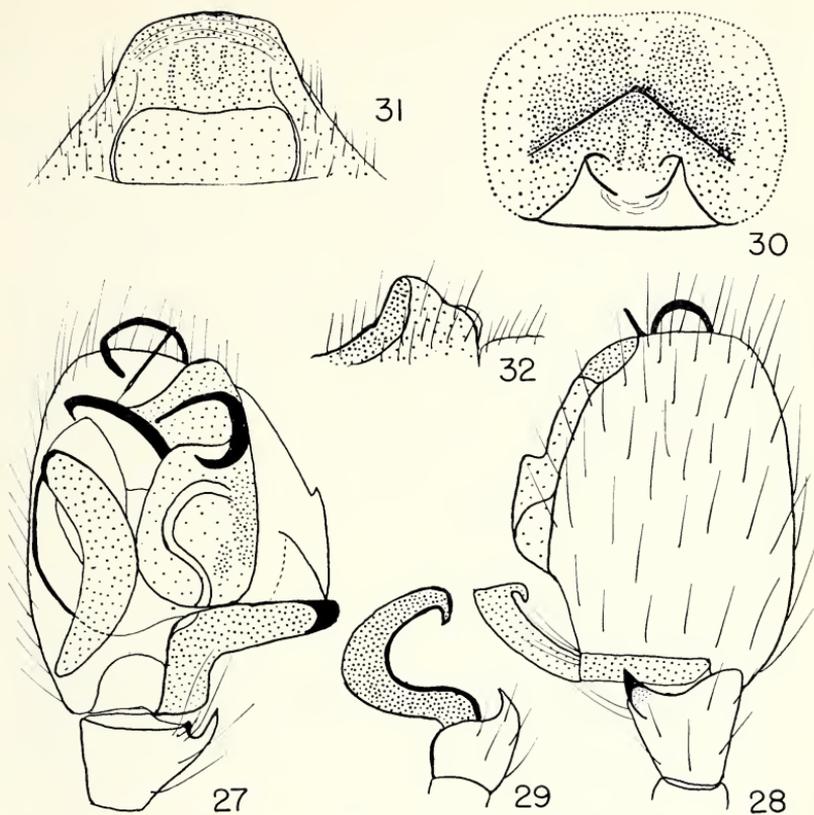
Canal Zone ending in May, 1964. All of these have been collected on Barro Colorado Island or in the Madden Dam region.

**Grammonota secata** sp. nov.

Figures 27-32

*Holotype.* The male holotype is from Barro Colorado Island, Panama Canal Zone, January 15, 1958. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.65 mm. Carapace 0.73 mm long; 0.65 mm wide opposite interval between second and third coxae where it is widest; about 0.28 mm tall in cephalic region where it is tallest; without cephalic lobes or humps. Eyes: eight in two rows; nearly typical in general in those species without cephalic modifications; viewed from above, anterior row gently recurved and posterior row slightly procurved. Central ocular quadrangle nearly as long as wide behind; wider behind than in front in ratio of nearly 17 : 10. Ratio of eyes AME : ALE : PME : PLE = nearly 4 : 7 : 7 : 7 (long diameters always used when eyes are oval). AME separated from one another and from ALE by nearly five-eighths of their diameter. Laterals contiguous. PME separated from one another by five-sevenths of their diameter and from PLE by a little less than this distance. AME separated from PME by a little less than the diameter of the latter. Height of the clypeus slightly less than four times the diameter of AME. Chelicerae, maxillae and lip all typical of the genus and without observed modifications. Sternum: convex; slightly wider than long opposite interval between first and second coxae; extended between fourth coxae and squarely truncated; fourth coxae separated by about seven-fifths of their width. Legs: 2143 in order of length; several long, slender spines observed but exact number and placement not recorded. Palp: essential features shown in Figures 27-29. Abdomen: typical of males of the genus; with no special modifications observed. Color in alcohol: carapace light yellowish-brown with faint darker streaks; with considerable very dark brown pigment in ocular area; sternum very light grayish; legs and mouth parts yellowish with variations; palpal tarsus yellowish-brown with many variations; abdomen light yellowish in general; a narrow, indefinite, median, grayish stripe extends along the dorsum from base for about half the length of this part of the body; about five or six narrow, transverse, grayish bands cover the posterior half of the dorsum; faint grayish patches occur on the lateral sides and the



Figs. 27-32. *Grammonota secata* sp. nov. Figs. 27-28. Left palpal tibia and tarsus: nearly ventral and dorsal views, respectively. Fig. 29. Left palpal tibia and paracymbium; nearly retrolateral view. Figs. 30-32. Epigynum of described female paratype; from below, from behind and right lateral side, respectively.

venter also shows small, grayish patches especially in front of the genital groove. The color pattern varies considerably among the numerous paratypes.

*Female paratype.* Total length 1.76 mm. Carapace considerably overlapped by abdomen; very similar in general to that of male. Relationships of eyes only slightly different from those of male. Chelicerae, maxillae and lip essentially typical of females of the genus. Sternum: convex; nearly as wide as long; extended between fourth coxae which are separated by nearly four-thirds of their width. Legs also essentially as in male. Abdomen: quite typical of females of the genus. Essential features of the somewhat unusual epigynum shown in Figures 30-32. The color pattern of the described female paratype is like that of the male holotype except that the gray abdominal bands and irregular spots are somewhat clearer. The color pattern also varies considerably among the numerous female paratypes.

*Diagnosis.* This species seems to have the same fundamental relationships with previously known species as I have already recorded for *Grammonota innota* sp. nov.

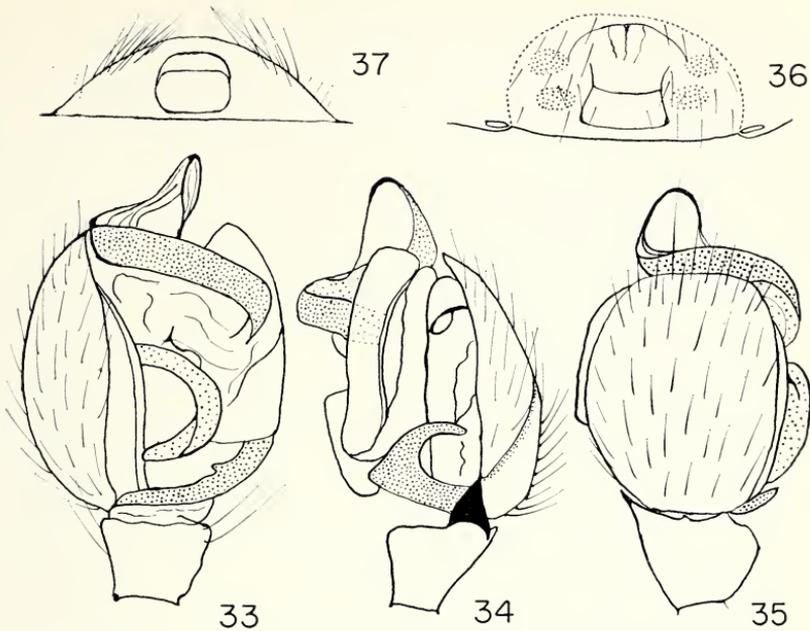
*Records.* The described female paratype was taken in the same locality and on the same day as the male holotype. Numerous specimens of both sexes are in the collection from Barro Colorado Island, Madden Dam region, Summit Gardens, Canal Zone Forest Preserve, Summit, Pedro Miguel, and the vicinity of Paraiso all in the Panama Canal Zone. The species has been collected during my visits to this region in 1936, 1939, 1950, 1954 and 1957-1958. It seems to be quite abundant on Barro Colorado Island.

### **Grammonota teresta** sp. nov.

Figures 33-37

*Holotype.* The male holotype is from Summit, Panama Canal Zone, August 23, 1950. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.56 mm. Carapace 0.59 mm long; 0.5 mm wide opposite second coxae where it is widest; only about 0.13 mm tall; without lobes or humps on cephalic region. Eyes: eight as usual in species without cephalic lobes or humps. Viewed from above, anterior row strongly recurved, posterior row slightly so. Ratio of eyes AME : ALE : PME : PLE = nearly 3 : 4 : 4.5 : 4. Height of clypeus nearly four times the diameter of AME. AME separated from one another by about their diameter and from ALE by slightly less than this distance. PME separated from one



Figs. 33-37. *Grammanota teresta* sp. nov. Figs. 33-35. Left palpal tibia and tarsus of holotype; prolateral, retrolateral and dorsal views, respectively. Fig. 36. Epigynum of female paratype from below. 37. Idem; posterior view with posterior border lifted.

another and from PLE by slightly more than their diameter. Laterals barely separated. Chelicerae: essentially typical of males of the genus; several teeth along both margins of the fang groove but exact number difficult to determine; those on retromargin very minute and restricted to a region near the base of the fang; those on promargin relatively large and well extended along fang groove, observed on paratype male. Maxillae and lip essentially typical of the genus; lip more than twice as wide as long. Sternum: convex as usual; longer than wide in ratio of nearly 9 : 8; extended between fourth coxae which are separated by 1.2 times their width. Legs: 12 = 43 in order of length; long, slender and with numerous long, slender spines. Palp: essential features shown in Figures 33-35. Abdomen: typical of the genus; without special modifications. Color in alcohol: carapace dark brown with darker radial stripes; just anterior to the thoracic pit there is a darker, irregular, central spot; eye region with considerable black pigment added to the basic brown color; sternum brown, darker along margins; legs light brownish with variations;

coxae and trochanters whitish; palp and other mouth parts yellowish-brown with variations; abdomen brownish in general; dorsum with a broken, irregular, herringbone pattern; venter brownish with a pair of narrow, irregular, yellowish stripes widely separated.

*Female paratype.* Total length 1.72 mm, including somewhat extended spinnerets. Carapace about 0.66 mm long; 0.52 mm wide; otherwise essentially as in male. General features very close to those of male. Epigynum: essential features shown in Figures 36-37. Color in alcohol: essentially as in male except that there is a small, dorsal, white spot on the abdomen near the posterior end. The female paratype resembles the male so closely that a detailed description is regarded as unnecessary.

*Diagnosis.* This species appears to be closely related to *Grammonota sclerata* Ivie and Barrows apparently known only from Florida. I believe the features of the male palps and the female epigynum establish it as a new species.

*Records.* The described female paratype was taken with the holotype. Numerous males and females are in the collection from the following named localities in the Panama Canal Zone beginning in July, 1936; Barro Colorado Island, Forts Davis, Randolph and Sherman, Frijoles, Summit Gardens, vicinity of Paraiso, Canal Zone Forest-Preserve. The species has also been collected in Panama outside of the Canal Zone in the vicinity of Arraijan, August, 1936, and in the region around Boquete, August, 1936, July, 1939, and August, 1954.

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THE NATURAL HISTORY OF THE FUNGUS GNATS  
*LEPTOMORPHUS BIFASCIATUS* (SAY)  
AND *L. SUBCAERULEUS* (COQUILLET)  
(DIPTERA: MYCETOPHILIDAE)<sup>1</sup>

BY WILLIAM G. EBERHARD

Museum of Comparative Zoology, Harvard University<sup>2</sup>

Although there are many species of Mycetophilidae (or Fungivoridae) and some that are quite common, little is known about the natural history of most species. The literature on the genus *Leptomorphus* is typically scanty: there are no descriptions of any activities of adults, and only brief descriptions of the general habitat and activities of eggs, larvae, and pupae of one species, *L. walkeri* (Edwards 1925, Brocher 1931, Madwar 1937). This report, which includes observations on all life stages of *Leptomorphus bifasciatus* and *L. subcaeruleus*, is the first study of the natural history of these species.

Most of the observations were made during the summer of 1968 near Rensselaerville, N.Y., at the E. N. Huyck Preserve, and a few additional notes were made on individuals found near West Chesterfield, New Hampshire. *Leptomorphus subcaeruleus* was found near West Chesterfield, and both this species and *L. bifasciatus* (with *L. subcaeruleus* most common) occurred on the Huyck Preserve. I discerned no difference in the habits of the two species, and adult males and females of both species were found at the same time at several sites in the Huyck Preserve. Specimens of larvae, pupae, and adults of both species have been deposited in the Museum of Comparative Zoology in Cambridge, Massachusetts.

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<sup>2</sup>Present address Depto. Biología, Universidad del Valle, Cali, Colombia.  
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## Precopulatory behavior of males

Male flies searched out female pupae<sup>3</sup> which were suspended on silk threads, then hung under them (Fig. 1) until the adult emerged. They flew in a characteristic bobbing pattern as they searched for pupae hanging under the bottom surfaces of logs. Usually, as they flew along the length of the log, they bobbed up until they hit the bottom of the log with their front legs, which they carried raised over their heads, then flew down and onward. Sometimes they swung back and forth from one side of the log to the other as they flew along under it. They made frequent darting flights to other objects in the vicinity where they occasionally landed and paused.

Although the bouncing flight appeared erratic, the pattern is probably controlled. A male which was confined in a cage which had pupae fastened to the roof with long pins was able to touch pupae over and over without running into pins.

The males' responses to pupae they encountered are listed below in order of increasing attention to the pupa.

1. no change in flight pattern
2. hover near pupa momentarily, back off
3. (often preceded by hovering) touch pupa, back off
4. touch pupa, stop flying and cling to it, move about under it, fly off
5. same as 4 except end by hanging immobile under pupa with ventral side of thorax pressed against the dorsal surface of the pupal thorax (Fig. 1)

Encounters with a given pupa did not always elicit the same reaction, even from the same male.

The males probably used either visual cues or tactile cues from their front legs (or both) while locating pupae during bobbing flight. The males usually mounted a pupa with their anterior ends at the pupa's anterior end and their longitudinal axes parallel to that of the pupa. Without exception, the anterior end of a pupa hung below the rest of its body, and this position appeared to be the cue used by males in positioning themselves: a pupa which was hung so the posterior end was the lowest was repeatedly mounted backwards.

Males hung persistently only under pupae of females about to

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<sup>3</sup>It is possible that the males were actually responding to pharate adults still within the pupal cuticle rather than to actual pupae. Observations were not made on this point, so the term "pupa" below should not be construed to exclude this possibility.



Fig. 1. A male *L. subcaeruleus* clinging to a pupa.

emerge. Only five of more than 40 pupae observed in nature had males hanging under them. All five of these pupae were females, and four of them produced adults within one day (the average pupal life is about four days). The fifth died. Males often mounted young or male pupae again and again only to climb off each time, but seldom dismounted from mature female pupae. Males also consistently ignored some unsuitable pupae but repeatedly touched and mounted other unsuitable pupae nearby.

There was brisk competition among males for suitable pupae. Males flying near a male hanging under a pupa often bumped against the resident male as they flew by; three extended fights over pupae were observed; and an additional male was found hanging on the back of a newly emerged female which was mating with another male. In each of two fights observed from the beginning, one male

was hanging immobile under a pupa and a second male approached, bumped against the resident male, and clung to the pupa. Both males held the pupa or the pupal thread with their front and middle legs, and buzzed their wings and pushed each other with their hind legs and abdomens. Each male appeared to be attempting to dislodge the other. Two of the fights ended when both males fell from the pupa, separated, and flew away; the other ended when the intruder, which was smaller than the resident, left.

Although combatants left the pupa when they were dislodged, they sometimes remained in the vicinity. One defeated male rested on a leaf about one meter from the pupa for about a minute, then hung under a pupa about 20 cm from the first. Another contested pupa was revisited within 15 minutes by a male of the same size and color pattern as one of the contestants. After another suspected fight (two males flew from the vicinity of a single pupa as I approached), males of the same sizes and color patterns as the fleeing males reappeared within 15 minutes, and one of them spent more than an hour flying in the vicinity in an apparent search for the pupa. This pupa was in a spot particularly difficult for a male flying in normal searching patterns to reach.

### Mating

Complete mating sequences were observed twice, once in nature when a waiting male mated with a female emerging from her pupal skin, and once in captivity when both animals were flying in a cage. In the first case, the female's thorax and head (the lowest parts of her body) were cradled against the ventral surfaces of the male's thorax and coxae as she emerged from her pupal skin, and he maintained this contact by lowering his body as she emerged. As she came free from the skin, the female drew her legs free from the pupal cuticle, then extended them perpendicular to her body axis just as other emerging adults did (below). However, in contrast to others, her abdomen came completely free from the pupal cuticle very quickly, and for a moment she lay just above the male, their bodies both horizontal. Almost immediately he curled the tip of his abdomen over the tip of hers (he had curled his over the tips of her wings twice before her abdomen emerged) and pressed it against the ventral surface of the tip of her abdomen, then lowered his abdomen until they were both nearly vertical, and gently turned her  $180^\circ$  on her longitudinal axis with his legs. This brought her legs against his legs and the pupal skin, and she clung to them weakly. Both animals remained nearly motionless in this position (Fig. 2)

for about three hours. Then after a few twitches by the female, they separated, and both hung for several moments under the pupal skin.

The other observed mating involved two individuals placed in a cage after being captured *in copulo* under a pupal skin and then kept separated for several hours. In the course of several minutes of flying around the cage, the male brushed against the female several times as she sat on the floor, and each time she started and moved away. One time, however, she did not move away when the male landed on her back. He immediately curled the tip of his abdomen over hers, engaged it against the ventral surface of the tip of hers, and then dismounted and turned 180° to face away from her. They both rested on the floor for over an hour, then separated. On another occasion a male attempted to mate with another female (a virgin) in the same situation, but was unsuccessful. Although she allowed him to land on her back, she did not let him press the tip of his abdomen against the ventral surface of hers: whenever he curled the tip of his abdomen over hers, she moved her abdomen to the side or pressed it against the surface she was on.

It is not clear how often copulation occurs between two free-flying individuals in nature. It may be difficult for males to locate, recognize, and couple with free-flying females, but the smoothness with which the one male mounted, locked, and then turned and dismounted suggests that this type of mating may occur naturally.

### Eggs

Oviposition by both virgin females in captivity and presumably mated females in nature appeared to be nearly identical. Eggs were laid singly rather than in clusters. The female walked quickly over the surface on which the egg would be laid, pausing occasionally and rubbing the tip of her abdomen rapidly back and forth on the surface. Egg laying did not always accompany these pre-oviposition movements. The female bent her abdomen forward underneath her body so that the tip was nearly under her thorax as she laid an egg. Usually she deposited some clear fluid just before laying the egg, and this dried and remained visible around the margins of eggs laid on glass in the laboratory. In captivity, some eggs lacked this fluid, and some deposits of the fluid lacked eggs. The maximum number of eggs laid by a female in captivity was 110. Each egg was oval, about 0.8 mm long, and covered with tiny points apparently similar to those on the eggs of *L. walkeri* (Brocher 1931). Eggs found in



Fig. 2. A newly emerged female (right) and a male *L. bifasciatus* mating under the female's pupal skin.

nature were on the undersurface of a log where there were larvae and pupae present, and in cracks between the edges of bracket fungus sporophores and tree trunks.

### Larvae

The larvae found during the study period (1 July-1 Sept., 1968) varied from 3 to 19 mm in length. They were similar to the larva of *Leptomorphus walkeri* described by Madwar (1937), with a sclerotized head capsule and 12 fleshy body segments. As in *L. walkeri*, the labrum bore eight prominent papillae, and each maxilla also carried one large papilla. Madwar termed these structures "sensory papillae", and Brocher (1931) called them teeth ("dents"), but lines of silk were seen emerging from these papillae during spinning activity, so *spigot* seems a more logical name.

The 12 fleshy segments behind the head capsule were all moist. The color of their cuticle ranged from nearly transparent to light brown in different individuals, with markings of darker brown. The heart was just under the dorsal surface, and in a nearly fully grown larva a peristaltic beat originated at the posterior end and moved forward about 50 times/minute. The larvae were always found upside down under more or less horizontal surfaces such as the undersides of fallen logs or bracket fungus sporophores. Each larva was on the bottom surface of a sheet of silk it had spread under the supporting object. The sheets were relatively flat, and often 1 mm or more below indentations in the supporting surface. There was always a dendritic network of slime trails on the silk, and the larvae were always on one of these trails (Fig. 3).

Larval sites had several features in common. There was almost always (one exception in more than 60 cases) an open space of more than 3 cm (usually much more) between the larva and the nearest surface below; the sites were always at least slightly moist; and the silken<sup>4</sup> sheets were nearly always built under fungal sporophores. The larvae were found under several types of sporophores, including both brackets (probably *Fomes*) and others which spread along the surfaces of rotten logs.

Many of the sporophores occupied by larvae appeared to be perennial, having a soft, moist, and evidently sporulating layer during part of the study period, but were dry and evidently not releasing

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<sup>4</sup>The material has not been chemically analysed, and is called silk because it is formed in threads and is white.



Fig. 3. A *L. subcaeruleus* larva on its silk sheet. Note the slime trails and the areas where the larva fed recently (arrow).

spores at other times. Although pupae, pupal skins, fragments of silken sheets, and (occasionally) dead larvae were found under apparently dormant bracket sporophores, living larvae were found only under active brackets. Sporophores on the undersurfaces of fallen logs sometimes had large "dormant" areas adjacent to active areas, and larvae were always under only the active areas.

The silken sheets under which the larvae lived often contained large numbers of tiny specks barely visible to the naked eye. When pieces of sheet which had specks in them were placed on a sterile nutrient medium (Wort agar), fungus grew, but no fungus grew when the same medium was inoculated with pieces of speckless sheet spun by captive larvae on surfaces which lacked fruiting fungi. Thus the specks which were common in sheets in nature were probably fungal spores.

Undisturbed larvae under sheets of silk were observed in only four activities: resting motionless, moving across the sheet, eating holes in the sheet, and laying silk. Larvae spent the majority of their time both day and night motionless.

The larvae could move forward and backward, in each case by

means of peristaltic contractions which originated in the trailing segment(s) and moved toward the leading end. A band of slime was laid on the silk when one of the fleshy segments came in contact with it, so as the larva moved forward, it left a slime trail behind it. A dendritic network of slime trails extended to all parts of the sheet, and the larvae always followed trails as they moved about. A peculiar method of turning around (also noticed in the mycetophilids *L. walkeri* by Madwar 1937, *Platyura nigricornis* by Mansbridge and Buxton 1933, and *Sciophila* sp. by Osten Sacken 1886) enabled them to remain on a slime trail at all times without constructing any circular trails: they turned the head  $180^{\circ}$ , and crawled back along themselves, advancing all segments simultaneously so that the head moved along the back or side in what had been the posterior direction while the tail continued to move forward until the turn was complete (see Fig. 4e). The function of the slime trails is not clear.

While spinning and feeding, the larvae moved their anterior four segments without moving the rest of the body. Larvae ate holes in their sheets by moving their heads slowly in arcs in front of themselves. The sheet was broken where the head touched it, and the portion inside the cut was ingested as the head swung. A part of the head capsule (the mandibles?) moved rapidly as the silk was cut. The rapidity with which the silk disappeared suggests the larvae probably used a silk-digesting enzyme. The alimentary canals of several dissected specimens were full of spores but contained no visible traces of any other solid matter, indicating that the larvae usually ingest nothing other than their sheets and their contents and rapidly digest the silk.

Usually a larva immediately filled each hole it made in the sheet, swinging its head and segments 1-4 rapidly from side to side in a complicated pattern (see below). A new mat of silk lines running in several directions across the hole in the sheet was produced by these spinning movements. The new lines were almost always attached to the edges of the hole in the sheet rather than to the surface of the fungus. Silk eating was always preceded by a semicircular sweep (see description of spinning movements below), and was always followed by spinning activity. Semicircular sweeps were not always followed by eating, however, and larvae on sheets often spent periods of time spinning but not eating.

A larva often concluded a series of spinning movements by placing its anterior end against the sheet and moving its whole body back-

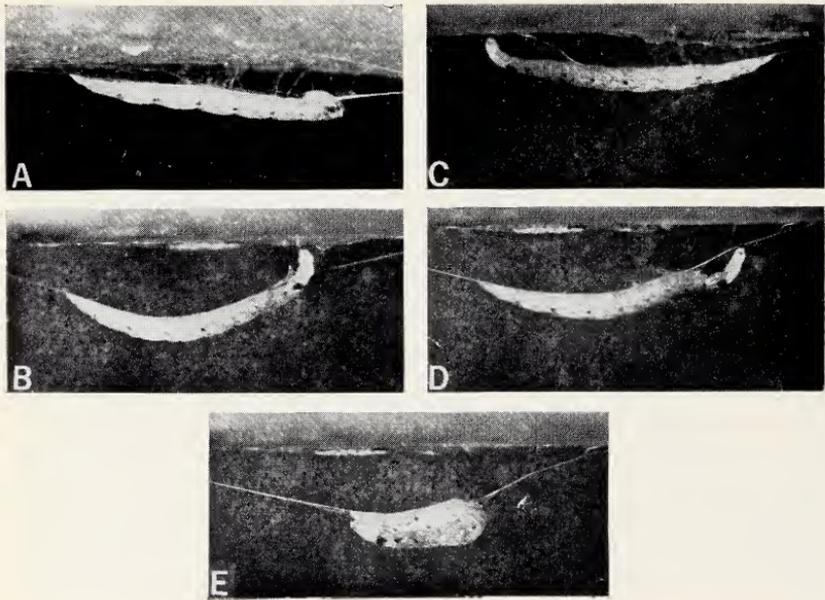


Fig. 4. Construction of the pupal line. Activities illustrated are swinging (*a*), cutting (*b*), tapping (*c*), trimming (*d*), and turning around (*e*).

wards, leaving a slime trail extending all the way to the end of the new silk. Larvae left overnight on a new surface often constructed long dendritic networks of silk trails, each with a slime trail running down the middle.

The larvae were apparently able to perceive vibrations in their sheets, but either fled from or did not respond to the struggles of animals such as sminthurid collembolans caught in the sheet. They usually appeared to sense the presence of another larva before contact was made, and often moved away as another approached, but occasionally when they met head to head, larvae fought. Their heads locked, and they swung from side to side in wide arcs, sometimes quite violently. After a few swings they disengaged, and one or both backed away.

#### Construction of the pupal line

Before pupating, the larvae always suspended themselves on a line under or near the surface where they had been feeding. The process of construction of this line was nearly identical in each of four cases observed in captivity.

Larvae maintained apparently normal activity until just before they began to construct the pupal line. When four larvae were placed on a log in an observation chamber, two individuals which were to pupate 12 hours later could not be distinguished on the basis of the rate or type of their activity from the two which did not pupate.

A series of probing movements (observed only once but probably performed in each case) immediately preceded line construction. The larva extended the anterior half of its body downward, perpendicular to the log's surface, and waved it from side to side. It repeated this behavior several times, each time after raising itself back to the log's surface and moving forward a centimeter or so. This probing behavior may be used to select appropriate pupation sites, informing the larva of any objects close below it. Pupae were never found where any such object could interfere with them as they swung on their lines.

The construction of the pupal line took about 40 minutes. The larva first added silk to a long, relatively straight trail, and cut the silk along the edges of this trail, leaving only the central portion intact. It laid silk with bursts of a swinging motion which was less complex than the silk-laying movements described below. The larva's head moved from the slime trail to one ventrolateral surface of segment 5 or 6 (abdominal segment 2 or 3) of its body (Fig. 4a), back to the trail, and then to the other side. Bursts of swinging often lasted 15 seconds or more, and the larva inched forward following each burst.

Larvae often cut silk just after moving forward: the head bent to the side of the trail, and moved slowly (usually forward) in a line nearly parallel with the trail. The threads encountered by the head were severed, and the central portion of the trail was progressively freed from the log's surface and sagged down under the larva's weight (Fig. 4b).

At the ends of the trail, where the pupal line would be anchored to the log, the larva spent periods of up to 40 seconds in another activity, tapping its head rapidly against the wood (Fig. 4c). The taps were occasionally interrupted by swinging silk-laying movements. These swings occurred only singly and infrequently early in a burst of tapping, but occurred more often and in longer bursts toward the end. Tapping sometimes covered a relatively large area, and the pupal line was often split near its end, with each smaller line running to a different area of attachments. This pattern probably

functions to anchor the pupal line more securely by allowing an increased area of attachment.

One other kind of behavior occurred on portions of the trail which hung free of the log. The larva drew its head slowly along the line (Fig. 4d), moving its mouthparts rapidly and apparently either packing the strands together or eating away some strands of silk. These "trimming" movements often resulted in a perceptible thinning of the line.

The four types of behavior — swinging, cutting, tapping, and trimming — were interspersed throughout most of the construction of the pupal line. Cutting and tapping were more frequent during the early stages, and most of the trimming which occurred during this time was done as the larva backed slowly away from a tapping (attachment) site. The larvae were able to turn around on the pupal line by crawling back on themselves just as they did while on their sheets (Fig. 4e), and occasionally ceased work at one end of the line, turned around, and began different behavior somewhere else on the line.

When the line was completely or nearly completely free from the sheet, the larva positioned itself near the center and made final spinning movements which lasted two to three minutes. These movements differed from the swinging movements of line construction only in that the silk was now laid from the pupal line to a dorsal section of the larva's body. The head swung farther and farther over the back, eventually crossing the dorsal midline of segments 5 and 6 with each swing. This behavior produced a small collar of silk which anchored the larva's body to the pupal line (arrow in Fig. 5a). Larvae inched themselves forward along the line as they spun the collar; the distances they moved varied, and thus the number of segments anterior to the collar and free of the pupal line varied.

The larva trimmed the line near its head for a short time after fastening itself into position on the pupal line, but soon the head movements diminished, and the segments anterior to the collar sagged away from the line and hung below the rest of the body. Segments 4-12 began a series of contractions, and segments 1 and 2 (thoracic segments 1 and 2) swelled. The contractions occurred approximately every 15 seconds at first, but soon slowed considerably. As segment 1 expanded, it began to engulf the head capsule, and the larva flexed the capsule ventrally during the contractions so that its ventral surface lay against the ventral surface of segment 1 (Fig. 5a).

About an hour after the collar was completed, the body contractions, still accompanied by movements of the head, had decreased in amplitude and slowed to about one every seven minutes.

The contractions and subsequent changes in body form apparently follow construction of the pupal line and collar regardless of the larva's situation. One larva fell off its line as it constructed a collar, and although it began to lay a trail of silk soon after it landed, its anterior end was swollen and it was nearly immobile 30 minutes later.

Although most pupae found in nature were under or near sites where larvae had apparently fed, the positions of some pupae suggested that larvae sometimes moved several centimeters from their feeding sites before pupating. In one case, seven of eight pupae found on a fallen beech tree were under bare bark at the bottom-most surface of the log, several centimeters from the nearest fungal sporophores (brackets on the side of the log). Pupae were also usually oriented so that their longitudinal axes were nearly parallel to the longitudinal axes of the logs they were under. The axes of 17 of 21 pupae were more nearly parallel than perpendicular to the axes of the logs they were under. The cues used to achieve these orientations and the functions of the positioning are not known.

Larvae often pupated soon after being brought into the laboratory, and it appeared that cues from the environment may sometimes induce them to pupate prematurely. In one typical case, 24 bracket fungus sporophores inhabited by larvae were removed from beech trees and pinned to cardboard boxes in the laboratory. Within two days the sporophores became noticeably drier, and eight of the largest larvae constructed pupal lines and pupated. None of the other larvae pupated, and all except two which were on surfaces particularly well sheltered from air movement were dry and dead in the midst of their sheets after five more days. On the other hand, some larvae kept on portions of sporophores in a cool (about 15°C) and moist environment in captivity only pupated after more than a week. Results like these suggested that once a larva reaches a certain size or maturity, it will pupate if its food source dries up.

#### Pupation

Larvae remained suspended for about 24 hours before they pupated. At the end of this period, segments 1 and 2 swelled even more, so that the line dividing them became less distinct and the head capsule was nearly completely engulfed (Fig. 5 c, d). Hints of ridges also

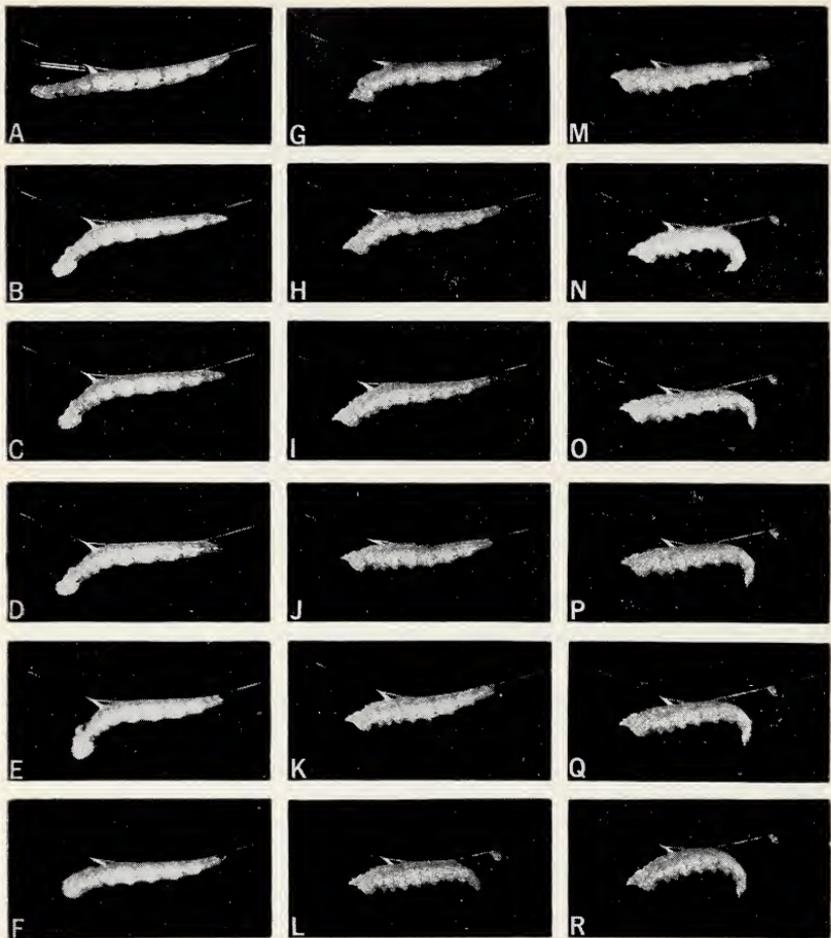


Fig. 5. Pupation. Pictures *a*, *b*, *c*, and *d* were taken 20, 2,  $\frac{1}{2}$ , and  $\frac{1}{4}$  hour respectively before picture *e*. Strong contractions had just started when *e* was taken, and each subsequent picture was taken 30 seconds later. Arrow in *a* marks collar of silk spun by larva.

appeared along the dorsal and lateral midlines of more posterior segments (Fig. 5 a-d). About 40 minutes before the transformation to pupal body-form occurred, the posterior tip of the larva's body began to darken and shrink in circumference (Fig. 5 a-d).

The transformation to the pupal body-form took only about five minutes. It was observed twice in nature and twice in captivity. Contractions of muscles in segments posterior to segment 3 accompanied the transformation. In two cases there were preliminary contractions causing the body to arch away from the log. Then, in all cases, powerful peristaltic contractions in the posterior end of the body caused it to thin, straighten, and lengthen. These were presumably contractions of circular muscles, and, like the contractions following collar construction, probably served to increase the internal fluid pressure and cause the cuticle to give in weaker places and expand into the form of a pupa.

Almost immediately after the contractions began, segments 1 and 2 swelled even more and the head capsule disappeared within them. After less than a minute, the anterior end suddenly assumed a new shape, with two small "horns" (which would house parts of the antennae) protruding (Fig. 5 g). About one minute later the cuticle just anterior to the last two and one half segments began to appear loose, and wrinkled during each contraction. Suddenly the rest of the body broke away from these segments, and they were left stuck to the pupal line while the new posterior end of the animal hung free (Fig. 5 l). The contractions continued, and the new tip extended straight behind the body during each contraction (Fig. 5 m). After another two minutes, the contractions had shifted the whole animal forward so that the new posterior tip could no longer touch the discarded segments. The contractions were substantially weaker by six minutes after the beginning of the transformation, and the new posterior tip no longer extended straight behind during each contraction but hung below the line in the characteristic pupal attitude (Fig. 5 q). The contractions continued for several more minutes, but rapidly became weaker and more infrequent, and soon the new pupa hung motionless.

#### Emergence of the adult

The pupa dried within a few hours after pupation and remained motionless until an adult emerged about four days later. The pupal lives of five individuals kept in captivity at room temperature lasted from three and one half to five days ( $\pm 6$  hours).

The complete process of emergence from the pupal skin was

observed twice, and portions of the process were observed several other times. All emergences (except that of a female attended by a male — see above) were nearly identical. First the pupal skin covering the dorsal surface of the thorax and head split, and the adult began to emerge through this hole. The insect was nearly motionless during this process, and its forward movement through the pupal skin probably resulted from peristaltic contractions of its abdomen. About eight minutes after the head and thorax first began to emerge, the legs, which by now were nearly free, began to twitch. The fly gradually pulled them forward and out of the pupal skin, then extended them horizontally so they were perpendicular to its longitudinal axis. The wings came free about four minutes later; at first they were soft and slightly bent, but they soon straightened and began to harden. After about 15 minutes, the entire animal was free from the pupal cuticle except for the terminal segments of its abdomen which were just inside the skin and supported the animal as it hung facing downward. While the fly hung in this position, the diameter of its abdomen decreased, and its new cuticle hardened. After about two hours the fly seized the pupal skin with its legs and swung its abdomen free of the skin. Undisturbed individuals hung motionless in this position for an additional hour or so before flying away.

The mechanism by which the flies supported themselves with the tips of their abdomens while they hardened was clarified when one fly fell completely free from its pupal skin unusually early. The last two segments of its abdomen were flexed dorsally so they formed a right angle with the rest of the abdomen. Apparently this crook at the tip of the abdomen is wedged tightly enough in the anterior end of the pupal skin that the weight of the fly's entire body is supported.

### Discussion

The observations of pupation indicate that the larval cuticle is not shed prior to pupation, that the last two and one half segments of the larva are discarded, and that the larval head capsule is engulfed by the pupa during pupation — all phenomena apparently undescribed in other Diptera (Imms 1964). It appears that the larval head capsule may migrate the length of the pupa after being engulfed. Head capsules appeared to be emerging from the ventral surfaces of abdominal segment #8 of some preserved pupae, and were on this surface, completely free of the pupa in others which

were darker and thus apparently older. More work is clearly needed to establish the details of this remarkable metamorphosis.

It remains possible that the larval cuticle was shed during pupation but was so thin that its movement was not observed; indeed the swelling of the anterior segments prior to pupation suggests a rupture of the larval cuticle. A search for signs of larval cuticle on pupae did not yield clear evidence of its presence: pupal cuticle did have the same number and pattern of spiracles as the larva's, but seemed to lack the rows of dark denticles near segmental boundaries on the ventral surface which were quite prominent in larval cuticle.

Other mycetophilids are generally thought to shed their larval skin during pupation (Osten Sacken 1886), but masses of material occur near the posterior tips of the abdomens of the pupae of several species, including *Ceroplatus* sp. (Malloch 1917), *Macrocera anglica* (Madwar 1935), *Leptomorphus walkeri* (Edwards 1925, Madwar 1937), *Speolepta leptogaster* (Madwar 1937), *Mycetophila cingulum* (Madwar 1937), and *Mycomya limbata* (Lindner 1949). Although in some cases (e.g. *Macrocera anglica*) this material apparently is the larval cuticle (Madwar 1935), the details of the pupa's position within its cocoon indicate that the material may not be larval cuticle in at least two of the other cases. Threads are attached to lateral projections along the sides of the pupa of *Ceroplatus* sp. (Malloch 1917) and *Mycomya limbata* (Lindner 1949). As Malloch points out, any silken attachments the larva might make to itself would be shed with the larval cuticle, and it is difficult to imagine how the pupa could be suspended in such a way if the larval cuticle is shed. It thus seems possible that the larval skin is not shed in these species, and that the mass of material behind the pupa is a discarded portion of the larva's body.

The selective advantages of some aspects of *Leptomorphus* pupation are not clear. Ingestion of the head capsule and the possible failure to shed the larval skin may be involved in maintaining silk attachments to the pupa, and thus in suspending it on a thread. Suspending the pupa may in turn be advantageous at least in females because it makes the pupa more easily found by flying males. The contents of the discarded larval segments and the function of discarding them are not known. Active larvae defecated repeatedly, and their feces were a much lighter brown than the discarded body section,

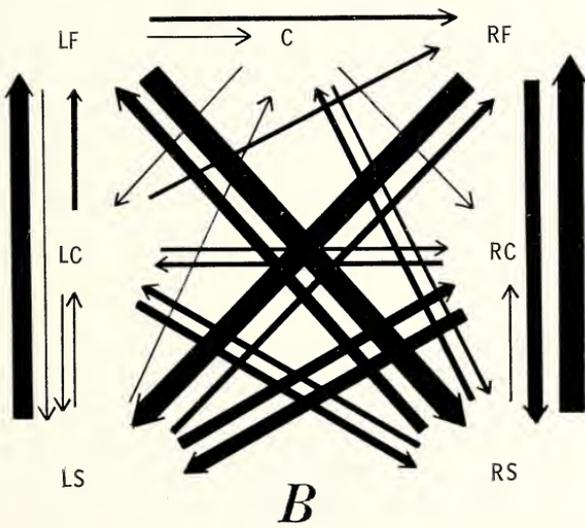
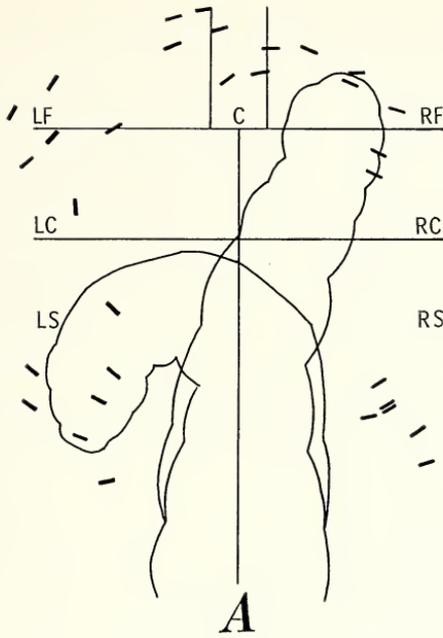
indicating that disposal of this section does not represent elimination of waste from the digestive tract.

*Leptomorphus walkeri*, the only other member of this genus whose natural history has been described, appears to be similar to the species of this study. The form of the eggs and the sites at which they occur are nearly identical to those described above (Brocher 1931). The larvae are also associated with fungi (Edwards 1924, Brocher 1931), usually on the undersurface of the fungus (Brocher 1931). They probably also build silk sheets: Edwards (1924) notes that they build a "web", and Brocher (1931) reports that they lay networks of silk trails which they use to support themselves under the fungi, but Madwar (1937) claims that they construct only slime tubes. Brocher found that larvae sometimes ate silk from old trails, and his brief description of silk-laying movements indicates they are at least roughly similar to those of *L. subcaeruleus* and *L. bifasciatus*. The larval food has not been established, although Madwar (1937) speculated that larvae fed on "microscopic bits of fungus" dislodged when the head tapped against the fungus. The pupae are suspended on threads (Brocher 1931, Madwar 1937), at least sometimes at sites with open spaces below (Brocher 1931).

These observations indicate that the larvae of *L. subcaeruleus* and *L. bifasciatus* normally feed on spores caught in their sheets: they were almost always found under spore-shedding structures of fungi; they constructed sheets of silk which collected spores; they periodically ingested these sheets and their contents; and their alimentary tracts contained large quantities of spores. Other mycetophilid larvae, in the genus *Ceroplatus*, apparently subsist on spores caught in sheets of slime (Madwar 1937, Stammer 1937), but are carnivorous at times (Mansbridge 1933). Several *Leptomorphus* larvae were found during this study which were not near fruiting fungi, and one dead larva was partially eaten by two other larvae in captivity, indicating that these species of *Leptomorphus* may also be carnivorous at times.

---

Fig. 6. Spinning motions of *L. subcaeruleus* larvae. The attachments made by one larva in a typical series of swings are represented by dark bars in *A*. The sequences of successive attachments during four typical series of swings by two individuals are shown in *B*. The frequency with which an attachment in one zone (labelled in *A*) was followed by an attachment in another zone is indicated by the width of the arrow running from the first to the second zone.



The only other mycetophilid species in which the larvae have been described pupating while hanging on threads in exposed places are *Arachnocampa luminosa* (Hudson 1950, Richards 1960), and *Speolepta leptogaster* (Edwards 1924). Competition between males for female pupae has been recorded in *A. luminosa*. Males of this species commonly rest on female pupae, and at least in some situations where there are dense populations, there are often several males clinging to a female pupa which is about to produce an adult (Richards 1960). In contrast to *L. subcaeruleus* and *L. bifasciatus*, which probably use tactile or chemical cues to discriminate mature female pupae from others, *A. luminosa* males probably use vision: female pupae luminesce when touched, and glow especially brightly when the adult is about to emerge (Richards 1960). Emerging adults of this species sometimes hang from the pupal cuticle by the tips of their abdomens for several hours (Hudson 1950), and may use the same mechanism to support themselves as the species in this study.

There is probably selection in *Leptomorphus bifasciatus* and *L. subcaeruleus* favoring males which are able to find, recognize, and hold mature female pupae, and also selection favoring females which pupate at easily located sites. Males which are larger, and thus perhaps more successful in fights, and which copulate long enough to insure the female is fully sclerotized and able to avoid the advances of other males might also be favored. These types of selection probably do not occur in many other Mycetophilidae, since most of the genera in the subfamilies Ditomyiinae, Bolitophilinae, Diadocidiinae, Ceroplatinae, and Mycetophilinae pupate within fungi, under ground, or in cocoons in cracks (Edwards 1924, Madwar 1937). The adults of at least some species, including *Phronia* sp. and *Mycetophila* sp. (Colyer and Hammond 1951) form swarms where mating may occur.

### Summary

The larvae of *Leptomorphus bifasciatus* and *L. subcaeruleus* live on sheets of silk which they build under fungal sporophores, and apparently subsist on fungal spores caught in these sheets. Pupation occurs while the animal is suspended on a line constructed by the larva, and involves discarding the last two and one half segments of the larval body, but possibly not the larval cuticle. Adult males search for pupae, and rest on female pupae which are about to produce adults. There is brisk competition between males for such pupae. The selective advantages of some of these habits are dis-

cussed, and comparisons are made with the natural history of other mycetophilids.

#### APPENDIX

##### Details of larval spinning behavior

The spinning behavior of *Leptomorphus subcaeruleus* larvae was complex, and it is likely that an evolutionary series of behavior may eventually be established between this species and others whose spinning behavior is less elaborate. The following description, derived from study of 24f/sec. movies of two *L. subcaeruleus* larvae laying trails on the undersurface of clean saranwrap, will hopefully serve as a basis from which to start such a study.

Silk laying involved three steps repeated over and over: the larva swept slowly once or twice in an often nearly semicircular arc in front of itself with its outstretched head, laid silk by swinging its head quickly from side to side, placed its anterior end against the silk and moved forward, and swept slowly again. Larvae usually tapped their heads on the surface on which they moved several times during one of the slow sweeps, but occasionally a larva did not touch the surface at all. No silk was laid during sweeping activity since there were no lines running in the direction of the semicircular sweeps on glass slides on which larvae had moved. Sweeping motions were much slower than swinging movements: one larva averaged about 0.7 seconds for sweeps of about 120°, but took only 0.04-.08 seconds to swing approximately the same distance while spinning silk. Larvae usually modified sweeping motions (often by repeating the sweep) when they encountered an object such as another larva's body during a sweep. It appears that sweeping is a type of exploratory behavior, probably functioning to guide the animal as it moves.

Direct observations of active larvae and examinations of glass slides on which they had moved showed that silk was spun during the swinging movements following sweeps. Eight or (often) fewer equally spaced threads of equal diameters were laid down with each pass of the larva's head, indicating that silk from the spigots on the labrum was laid during swinging. Additional threads with smaller diameters were also laid. The threads were attached to the slide near the edges of the silk trail, and the attachments appeared to consist of unpolymerized thread material: each line, whose diameter was uniform between attachments, spread out into a long "puddle" at each attachment.

In photographing spinning behavior, a movie camera was focussed in the plane of the saranwrap under which the larvae moved, and in analysing the films, I assumed that the movie frames with the larva's head in focus represented moments when the larva was making an attachment, while those with it out of focus represented moments when the head was lifted away from the surface and moving toward the next attachment site. This assumption is supported by the fact that attachments of lines laid on glass slides occur in the same areas as the presumed attachments in the movies.

As illustrated in Fig. 6a, attachments were not restricted to certain areas, but were spread along the sides and in front of the larva. Their distribution was not uniform however: they nearly always occurred near the edges of the spinning area, and were less common in the central portion of the area than in the anterior and posterior portions. The attachments in the central portion were usually made in the later part of a sequence of swings.

There were discernible patterns in the sequences of attachments, but there were also many variations on these patterns. The most common patterns, illustrated in Fig. 6b, included movements from the anterior to the contralateral posterior zone (e.g. RF to LS), and the posterior zones to both ipsi- and contralateral anterior zones (e.g. LS to LF, LS to RF). Larvae often made series of attachments to alternate sides, but also made series of attachments on the same side. The functional significance of these patterns is not known.

The result of the variety of sequences of attachments and the dispersion of attachment points was that a larva laid lines running in many different directions each time it executed a series of swings. Another result was that there were usually no large holes in the array of newly laid threads. The variation in site and sequence of attachments may serve to eliminate holes in the sheet, and thus to prevent loss of spores through these holes.

The variation in movements and the dispersion of attachments may be the product of regular patterns of spinning behavior, but such patterns were not noticed in this short study.

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The illustration on the front cover of this issue of *Psyche* is a line-cut photograph of a phasmatid (*Pseudophasma*) from Costa Rica, designed by Carl F. Moxey.

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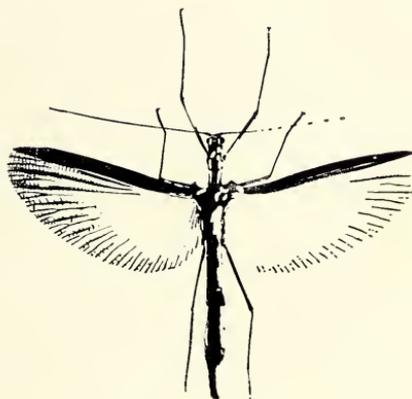
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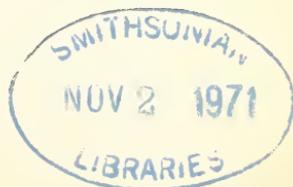
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## RECRUITMENT TRAILS IN THE HARVESTER ANT *POGONOMYRMEX BADIUS*

BY BERT HÖLLDOBLER AND E. O. WILSON  
Harvard University, Biological Laboratories  
Cambridge, Massachusetts 02138

### INTRODUCTION

*Pogonomyrmex* is the most abundant and specialized genus of harvester ants in North America. The workers mainly collect seeds for food, but they also carry dead insects into their nests. In view of the great abundance of these ants in many parts of the United States (Cole 1968), the ease with which they can be cultured in the laboratory, and their considerable economic importance, surprisingly little has been learned to the present time concerning their communicative behavior. Most attention has been focused on alarm behavior. Wilson (1958) discovered that alarm responses are released in workers of the Florida Harvester Ant (*P. badius*) by a pheromone produced in the mandibular gland of the ant. This behavior ranges, according to the stimulus intensity and duration, from mild attraction to attack and prolonged digging in the soil. In 1966 McGurk *et al.* identified the pheromone as 4-methyl-3-heptanone and also detected it in *P. barbatus*, *P. californicus*, *P. desertorum*, *P. occidentalis* and *P. rugosus*. Although in many ant species chemical trails laid down by worker ants are the essential signals for the initiation of mass foraging behavior in nestmates (see review by Wilson 1971), they have not yet been implicated (or even suspected) in *Pogonomyrmex*. This article reports the discovery and subsequent analysis of such a recruitment system in *Pogonomyrmex badius*.

### MATERIALS AND METHODS

Field work was conducted in Tampa, Florida, in an open field near the campus of the University of South Florida. Laboratory experiments at Harvard University utilized three large colonies of *Pogonomyrmex badius* housed separately in two sand-filled terraria

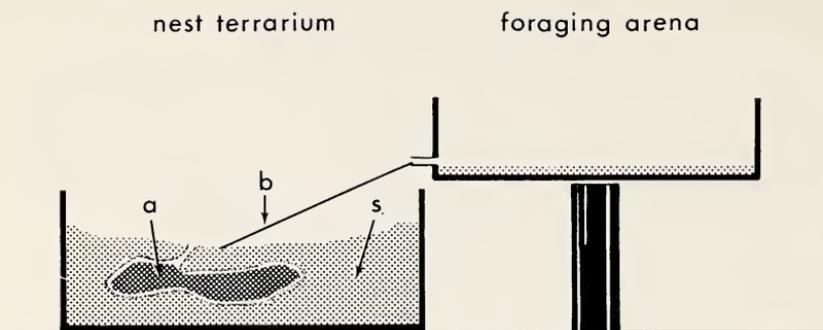


Fig. 1. Laboratory nest arrangement. *a* = nest chambers; *b* = bridge; *s* = sand.

(75 × 30 × 30 cm). These colonies had been kept in the insectary for three years, since the early spring of 1967. Their good health was attested by the fact that they continuously reared large quantities of brood, and each year produced winged males and females. Each nest terrarium was connected with a foraging arena 70 cm in diameter (Fig. 1). This combination provided an excellent arrangement for laboratory pheromone tests and orientation experiments that simulated natural conditions. Additional methodological details will be given with the description of the individual experiments.

## EXPERIMENTS AND RESULTS

### *Description of the food alarm behavior*

We have noted that when individual workers of *P. badius* attack large, active insect prey in the vicinity of the nest, they discharge the alarm pheromone 4-methyl-3-heptanone from their mandibular glands. The pheromone both attracts and excites other workers within distances of ten centimeters or so, with the result that the prey is more quickly subdued. This observation led to the question: Do workers also employ a directed food alarm when they encounter a food source several meters distant from the nest entrance? The following laboratory experiments were designed to find an answer to this question.

In the center of the foraging arena (Fig. 1) a freshly killed cockroach (*Nauphoeta cinerea*) was offered. The first ant to discover the prey was marked; all other scouting ants were then removed. After several unsuccessful attempts to transport the cockroach, the scout ant typically ran toward the arena exit near

the nest. At this time its locomotory behavior changed markedly. The abdomen was bent downward and the tip dragged over the ground with the sting fully extruded (Fig. 2). Almost invariably within seconds after the ant had entered the nest, a group of 10-15 nestmates ran out and took the precise course of the scouting ant over the bridge to the foraging arena (Fig. 3). It is noteworthy that the recruited group often included the big soldier caste, because this caste is seldom seen making individual foraging excursions. Before the first recruited group arrived at the food source, the original recruiting ant usually also returned to the food in the arena, following its own trail and reinforcing it with the extruded sting. At this time it was closely followed by other ants (Fig. 3). After a few more minutes a number of ants finally assembled around the prey (Fig. 4). Small dissected pieces were then carried

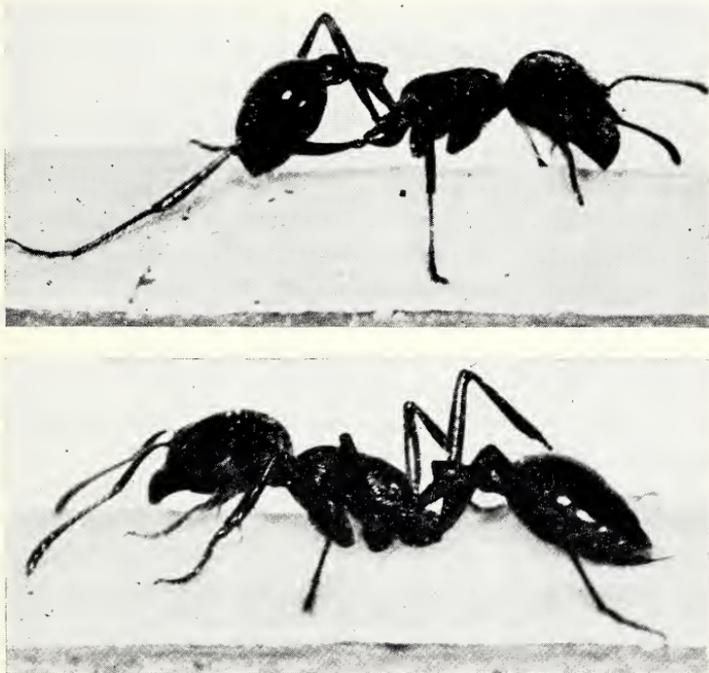


Fig. 2. *Above*: A foraging *Pogonomyrmex badius* worker passes over the bridge to the arena. During this searching phase the ant only occasionally touches the surface with the tip of its abdomen. *Below*: After discovering a source of food, the scouting ant returns to the nest, dragging the tip of the abdomen over the surface with sting extruded.

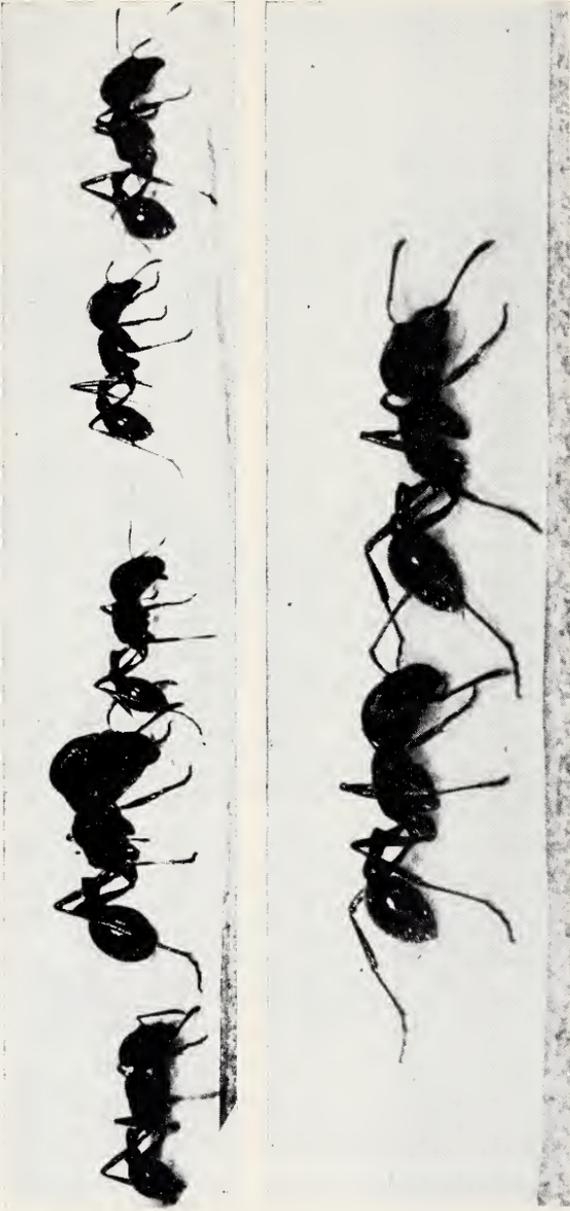


Fig. 3. *Above*: Recruited ants pass over the bridge to the arena while carefully scanning the surface with their antennae. *Below*: The recruiting ant returns to the arena, reinforcing its trail with its extruded sting and closely followed by nestmates.

home by individual ants, some of which extruded their stings and touched them to the surface (Fig. 5). Simultaneously, another group of ants, mostly belonging to the smaller caste, ran with extruded stings back and forth between the nest and the prey, apparently reinforcing the recruitment trail. A freshly killed cockroach usually caused a much stronger recruitment alarm than oat flakes. Moreover, when all of the oat flakes were offered at one spot, the recruitment activity was more intense than if the same number of flakes were scattered over the whole arena. Fig. 6 gives the quantitative data from representative experiments in which ants were placed in the three feeding circumstances.

Our observations on the recruitment behavior strongly suggest that chemical signals are involved. The next series of experiments tested this hypothesis:

1) In one series the ants were counted as they passed over the bridge after a recruiting ant had returned on it from the arena to the nest. In a second series the old bridge was replaced with a new one immediately after the recruiting ant had passed over it, and again the number of ants running to the arena was recorded. The number of ants passing over the bridge in the second series proved to be far smaller than in the first series (Table 1).

	Number of ants that passed over the bridge after a recruiting ant returned to the nest.	Number of ants that passed over a new bridge, which replaced the old one after a recruiting ant returned to the nest.
M $\pm$ sd	17.8 $\pm$ 5.3	1.7 $\pm$ 1.9
Range	12 — 28	0 — 5

Table 1. During a 5 minute period all ants that passed over the bridge to the arena were counted (see Fig. 1). The data are derived from 8 replications of each of the two experiments.

2) If the arena was rotated after the recruiting ant had left the arena, thus removing the trail from the arena entrance, or if the surface was covered with a new layer of sand, the recruited ants no longer oriented accurately to the source of food.

The results of these experiments left little doubt that *P. badius* utilizes special chemical recruitment and orientation signals. We next conducted a search for the anatomical source of the recruitment pheromone.

#### *The source of the recruitment pheromone*

In preliminary experiments we learned that *P. badius* workers



Fig. 4. *Above:* A scouting ant discovers a cockroach in the arena. *Below:* About 10 minutes later she has recruited 10-15 ants, which are now assembled around the prey.

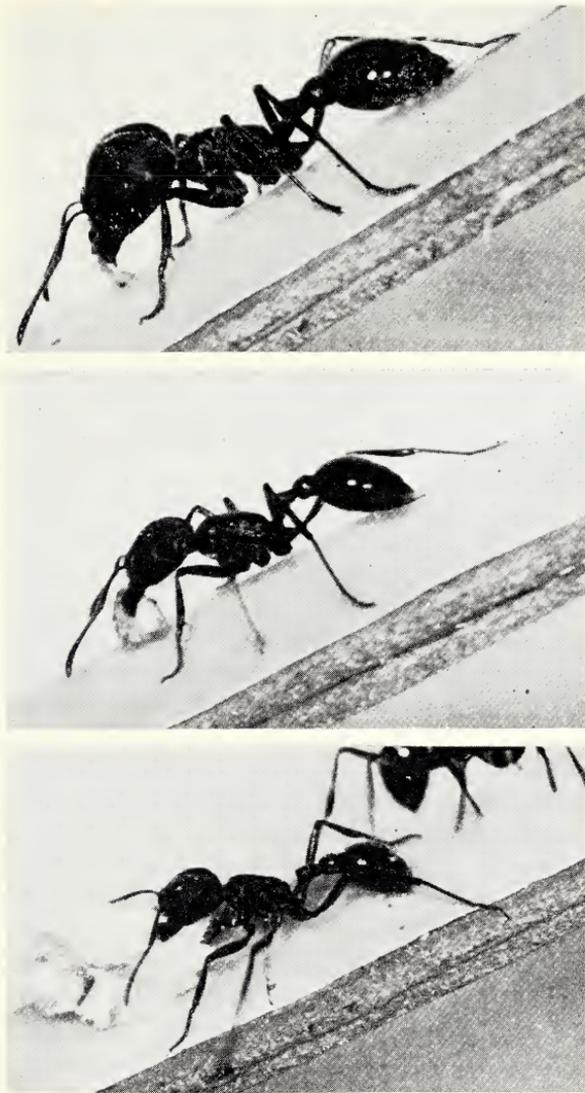


Fig. 5. Recruited foragers return to the nest transporting food. *Above*, "soldier" (very large worker) with extruded sting and carrying cockroach fragment; *middle*, smaller worker with extruded sting, carrying cockroach fragment; *below*, smaller worker with oat flake, no sting extruded.

are too excitable and discharge the mandibular gland pheromone too readily to permit reliable assays of the trail pheromone on small groups of workers separated from their colony. For this reason we designed the test to utilize the undisturbed laboratory nest arrangement. The nest terraria are so large that artificial test trails 50 cm in length could be laid beginning at the nest entrance. Furthermore such trails could be laid over the paper bridge, and into the arena.

The extrusion of the sting by recruiting *Pogonomyrmex* workers suggests that the trail pheromone is produced in one of the glands associated with the sting apparatus. This would not be surprising in view of the fact that other members of the subfamily Myrmicinae produce trail pheromones either in Dufour's gland [*Solenopsis* (Wilson 1959), *Pheidole* (Law *et al.* 1965)], or in the true poison gland [*Atta* (Moser and Blum 1963), *Tetramorium* (Blum and Ross 1965), *Monomorium* (Blum 1966)].

To test the effectiveness of different abdominal gland secretions, the hindgut, the poison gland (with vesicles), and the Dufour's gland were first dissected out of workers. For each replication the organs of a kind from three workers were washed in distilled water and then crushed in 0.5 ml of benzine. Aliquots of 10  $\mu$ l of the benzine solution of the gland secretions were then applied with a syringe along a 50-cm-long artificial trail drawn away from the nest entrance. During the next five minutes a count was taken of all the ants—except those carrying sand—that left the nest entrance and followed the trail to the end (Fig. 7). The data obtained (Table 2) show clearly that the poison gland has the strongest recruiting power. Since the ants also followed the artificial poison gland trails through each twist and turn, we conclude that the poison gland secretion serves both as a releaser of recruitment behavior and as an orientation cue. However, in a separate study Hölldobler (1971) found that the Dufour's gland secretion of *P.*

	Poison Gland			Dufour's Gland			Hindgut		
	N	M	Range	N	M	Range	N	M	Range
Colony I	6	77.3	39-120	9	11.3	5-27	9	5.1	1-12
Colony II	8	97.9	38-187	10	8.2	3-18	8	5.1	0-17
Colony III	7	81.6	32-157	9	15.5	5-29	9	6.1	0-12

Table 2. Artificial trails composed of benzine solutions of different abdominal gland secretions were drawn for distances of 50 cm from the nest entrance. During the next 5 minutes all the ants that followed the trails to the end were counted. The number of replications (*N*) and the mean and range of the number of responding workers are given.

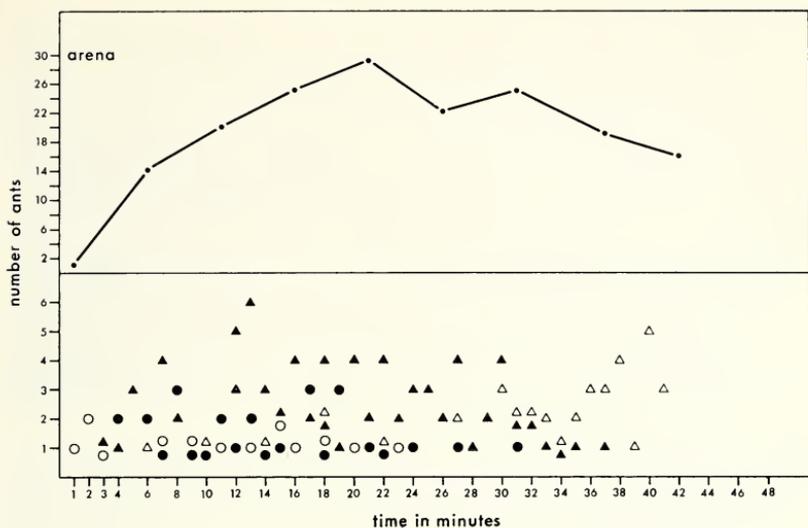


Fig. 6a. The progress of recruitment and foraging activity at insect prey (the cockroach *Nauphoeta cinerea*). Above: Total number of ants in the arena. Below: Ants returning to the nest. O = sting extruded, no food; ● = sting extruded, with food; solid black triangle = sting not extruded, with food; △ = sting not extruded, no food.

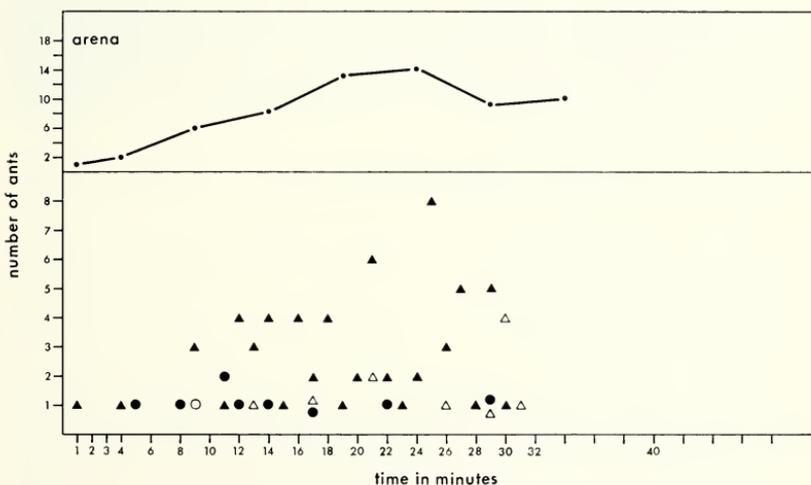


Fig. 6b. The progress of recruitment and foraging activity at oak flakes at one spot. Details as in caption of fig. 6a.

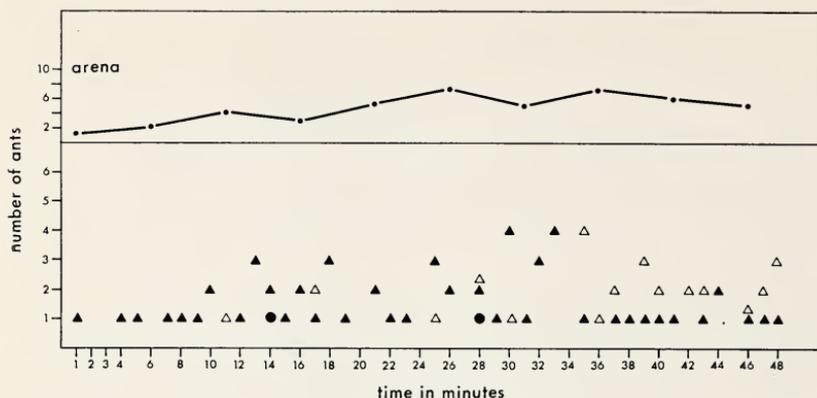


Fig. 6c. The progress of recruitment and foraging activity at oak flakes widely dispersed. Details as in caption of fig. 6a.

*badius* attracts homing ants. His orientation experiments indicated that the Dufour's gland secretion serves as a special chemical homing signal, since homing harvester ants closely follow artificial Dufour's gland trails. These results raise the following question: Is the Dufour's gland secretion used as an orientation cue for recruited ants as a supplement to the poison gland material? The following experiments were devised in an attempt to disentangle these two functions.

An artificial poison gland trail was laid from the nest entrance over the bridge to the opening of the arena. In the arena the artificial poison gland trail was continued while an artificial trail made from the Dufour's gland substance was simultaneously drawn at an angle of about  $45^\circ$  to the poison gland trail. In a second series the artificial poison gland trail was stopped at the arena entrance and then continued in one direction with a Dufour's gland trail and in another

	Poison Gland	Dufour's Gland	Dufour's Gland	Hindgut
N	5	5	5	5
M $\pm$ sd	70.8 $\pm$ 24.4	20 $\pm$ 10.4	46 $\pm$ 11.3	6 $\pm$ 3.5
Range	46-109	9-36	31-60	2-10

Table 3. In the arena a poison gland trail and a Dufour's gland trail (*left*) or a Dufour's gland trail and a hindgut trail (*right*) were offered simultaneously. During the next 5 minutes the ants which followed the trails were noted. The number of replications (N) as well as the mean and range of numbers of responding workers are given. The differences in response to the two trails are significant at the following levels: *left*,  $p < 0.005$ ; *right*,  $p < 0.002$ .

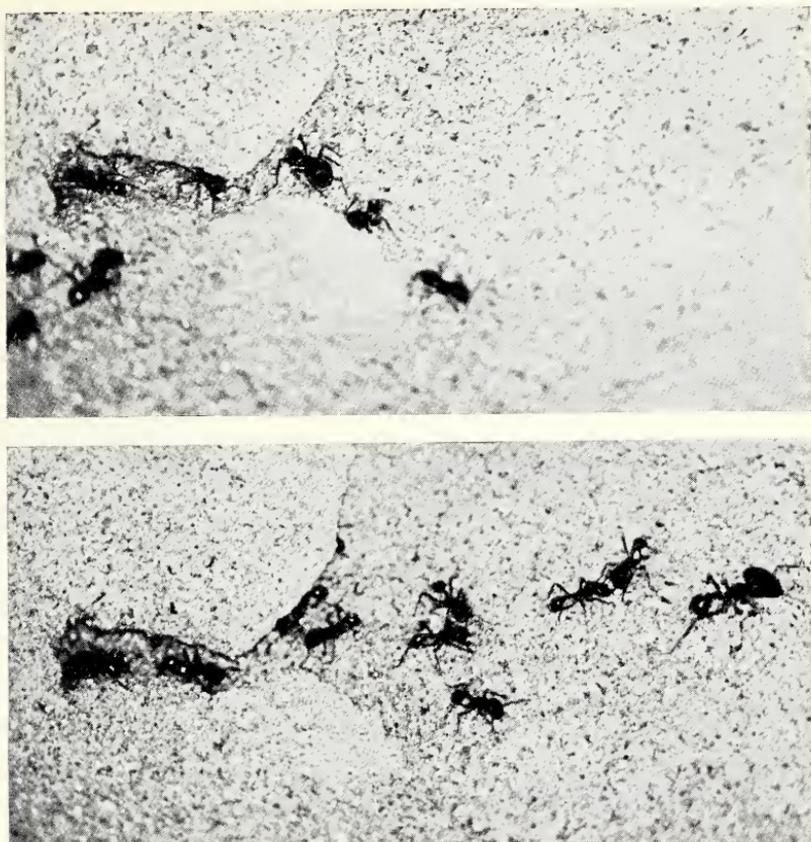


Fig. 7. *Above*: Activity at the nest entrance before a poison gland trail was laid. *Below*: Immediately after a poison gland trail was laid from left to right.

direction ( $45^\circ$ ) with a hindgut trail. In both series all ants which entered the arena during the next five minutes and which followed one or the other of the two trails were counted. The results (Table 3) indicate that the poison gland trail is much more attractive to recruited foragers than the Dufour's gland trails. However, if the poison gland trail substance is discontinued and replaced by a Dufour's gland trail, the recruited ants tend to follow the latter. Therefore it may well be that the Dufour's gland secretion also serves as an additional orientation cue in recruitment trails. This problem draws additional interest from the fact, demonstrated by

the experiments to be described next, that the Dufour's gland trails are longer lasting than the poison gland trails.

In the arena a Dufour's gland trail and a poison gland trail were drawn simultaneously, beginning at the entrance to the bridge and deviating at an angle of  $45^\circ$ . Then after ten minutes in the first series and 25 minutes in the second series, a poison gland trail was laid from the nest entrance over the bridge to the arena entrance, stimulating ants to run immediately into the arena. A record was kept of the trail chosen by each ant as it continued on its course. The results, presented in Table 4, reveal that after 10-15 minutes the poison gland trail was still more attractive, but after 25-30 minutes significantly more ants followed the Dufour's gland trail. We conclude that the poison gland evaporates more rapidly relative to its threshold concentration than does the Dufour's gland secretion.

	10-15 Minute Interval		25-30 Minute Interval	
	Poison Gland	Dufour's Gland	Poison Gland	Dufour's Gland
	$p < 0.3$		$p < 0.002$	
N	6	6	8	8
M $\pm$ sd	$39.2 \pm 12.8$	$12 \pm 6.5$	$7.4 \pm 3.2$	$26.5 \pm 6.07$
Range	26-58	8-19	3-12	19-38

Table 4. A poison gland trail and a Dufour's gland trail were offered simultaneously in the arena. After 10 minutes (*left*) and after 25 minutes (*right*) the ants were induced to approach the two trails, and their choices were recorded during a period of 5 minutes. The number of replications (*N*) and the mean and range of numbers of responding ants are given.

#### *Recruitment trails in other Pogonomyrmex species\**

Subsequent field and laboratory studies have revealed that recruitment behavior of the kind just described for *Pogonomyrmex badius* also occurs in other members of the genus (*P. occidentalis*, *P. rugosus*, *P. barbatus*, *P. maricopa*, *P. californicus*). In *P. maricopa* and *P. californicus* the change in the locomotory behavior of trail laying ants is particularly clear. In ordinary locomotion workers of these species hold their abdomen upwards (Fig. 8a). But when entering a new area (for example a new bridge in Fig. 1) they repeatedly touch the surface with the abdominal tip (Fig. 8b). A successful scouting ant on the other hand returns to the nest with the abdomen completely lowered and dragging the extruded sting over the surface (Fig. 8c). With the nest arrangement illustrated in Fig. 1 we were able to show that in the first case the ants apparently set orientation marks, whereas in the second case they lay

\*Note added in proof.

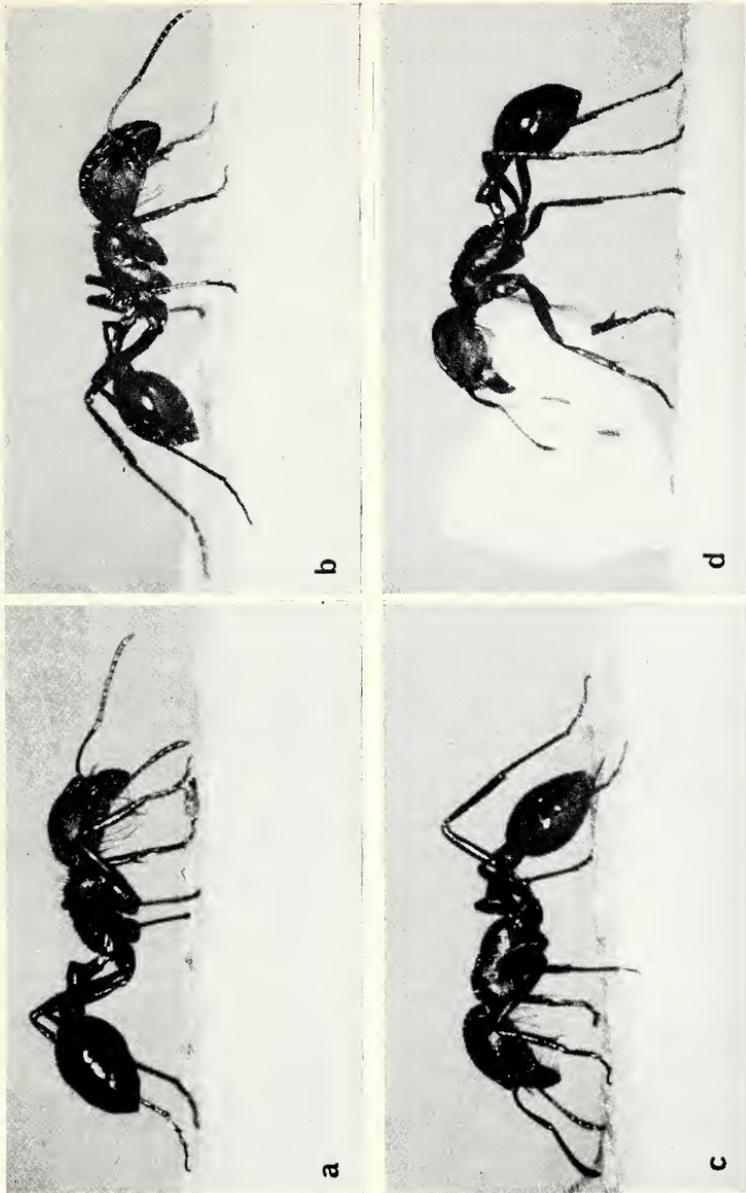


Fig. 8. *a*. *Pogonomyrmex californicus* with normal position of the abdomen. *b*. Marking a new bridge. *c*. Laying a recruitment trail. *d*. Carrying an oak flake on "tip-toes."

a recruitment trail. Artificial poison gland trails have the strongest recruitment effect. The available data do not allow us to suggest a species specificity of the recruitment pheromone. Nevertheless, a specificity may well be accomplished by additional chemical orientation cues.

#### SUMMARY

Since individual harvesting ants (*Pogonomyrmex badius*) usually collect scattered seeds, casual observations in the past have seemed to indicate a foraging system based on individual initiative and orientation. But in the experiments described here and elsewhere (Hölldobler 1971), we have proved that *P. badius* uses recruitment pheromones released from the poison gland and orientation or homing pheromones released at least in part from the Dufour's gland. Recruitment of nestmates is initiated when scouting workers encounter food sources too large to retrieve in a single homeward trip. Although the poison gland pheromone is distinctly more effective in recruitment, the possibility exists that the Dufour's gland pheromone can play a supporting role, especially in the establishment of longer-lasting foraging trails.

#### ACKNOWLEDGEMENTS

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# FOSSIL INSECTS FROM NEW MEXICO<sup>1</sup>

BY F. M. CARPENTER

Biological Laboratories, Harvard University

Several years ago Dr. Charles B. Read, of the U. S. Geological Survey, kindly sent me a fossil insect which he had collected in the Sandia Formation (Pennsylvanian age) in New Mexico. Although recognizing the specimen as a member of the extinct order Palaeodictyoptera, I deferred publication on it with the hope that additional insects might subsequently be found in the same deposit. So far none has been, but about a year ago Dr. Sergius Mamay, also of the U. S. Geological Survey, sent me five insects which he had found at an exposure of the Madera Formation in New Mexico. Since these are also of Pennsylvanian age, I decided to publish this account of both the Sandia and the Madera specimens. As on many previous occasions, I am deeply indebted to Dr. Read and to Dr. Mamay for the opportunity of studying these fossils.

The Sandia Formation is considered to be of Lower Pennsylvanian age, probably equivalent to the Pottsville (see Keroher, 1966; Bates and others, 1947; Read and Wood, 1947). So far as I am aware the specimen collected by Dr. Read is the only insect which has been found in the Sandia Formation. This fossil, however, is of unusual interest, since it belongs to the palaeodictyopterous family Eugereonidae, which is otherwise known only from the Upper Carboniferous of France and Portugal, and the Permian of Germany.

The Madera Formation is also referable to the Upper Pennsylvanian period but is somewhat younger than the Sandia and may possibly belong to the uppermost Pennsylvanian (Mamay, personal communication; Read and others, 1944; Bates and others, 1947; Read and Wood, 1947). The collection made by Dr. Mamay from an exposure of this formation is of exceptional interest. All insects are very well preserved and four of the five specimens have body structures present. This is an unusual occurrence and it takes on even greater significance in view of the systematic positions of the fossils concerned. One of the species seems to be a member of the palaeodictyopterous family Lycocercidae, which has previously been found only in the Upper Carboniferous of France and Germany; another is a member of the extinct order Caloneurodea, which has

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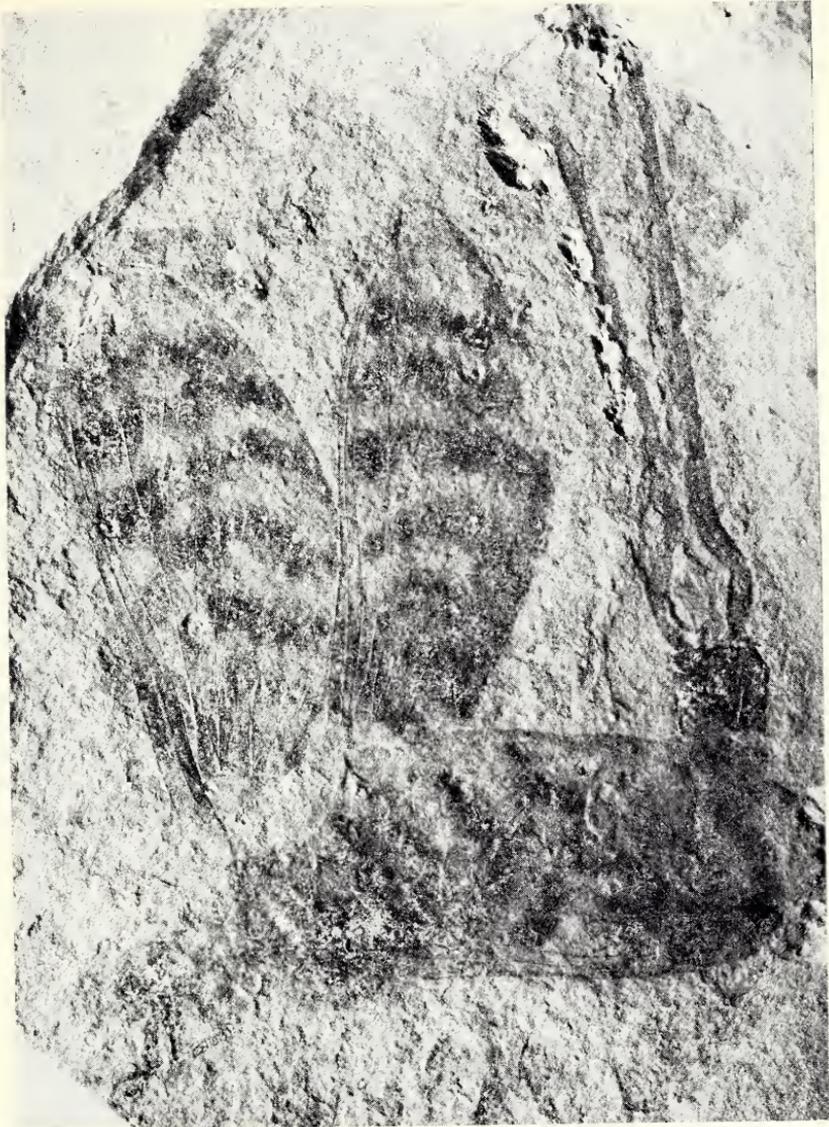


Fig. 1. *Madera mamayi*, n.sp. Photograph of holotype (Madera Formation, New Mexico).

only one previous record from Pennsylvanian deposits of North America, although it is well represented in Upper Carboniferous beds of Europe. The third specimen belongs to the order Thysanura, which has not previously been reported from North American deposits older than the Tertiary; since this specimen is very incompletely preserved, a formal description of it is not being presented at this time. The two remaining specimens are cockroaches, one consisting of a fore wing (tegmen) and the other of a whole insect except for the tegmina; the latter specimen is discussed briefly below but neither of these blattarians is being formally described here.

ORDER PALAEODICTYOPTERA  
Family Lycocercidae

As characterized by Kukalová (1969), the members of this family have MA and CuA unbranched, MP and CuP branched, and the cross veins fine, numerous and more or less irregular. The family has not previously been reported from any deposit in North America, although I have in my possession a representative of the family from the vicinity of Mazon Creek (Francis Creek Shales) in northern Illinois (Pennsylvanian Period).

Genus *Madera*, new genus<sup>2</sup>

This genus contains species which are much smaller than those in *Lycocercus*; the fore and hind wings are relatively broad, compared to those of *Lycocercus*; MA in both pairs of wings arises at about the level of the origin of Rs, and CuP consists of two long branches, without marginal forks.

Type species: *Madera mamayi*, new species.

I have placed this genus in the Lycocercidae mainly on the basis of the unbranched MA and CuA, a feature which seems to be consistent and reliable, as pointed out by Kukalová (1969). This single condition of MA and CuA actually occurs in several families but all of them except Lycocercidae possess peculiar characteristics absent in *Madera*. My first thought on examining this new species of *Madera* was that it was related to the genus *Eubleptus*, which contains species of about the same size. However, with the presence in *Eubleptus* of a branched MA and a forked CuP, the Eubleptidae are clearly members of that complex of Palaeodictyoptera in which these two veins are branched. In shape, the wings of *Madera*

<sup>2</sup>The name of the genus is derived from that of the village of La Madera, New Mexico, and is considered feminine.

recall those of some of the Spilapteridae but they have no other characteristics of that family. A separate family may eventually be needed for *Madera*; for the present it seems advisable to place it in the family Lycocercidae rather than to add another family to the long list of those in the Palaeodictyoptera which are monospecific and based upon unique specimens.

***Madera mamayi*, n. sp.**

Figures 1 and 2

Fore wing: length, as preserved, 15 mm (estimated wing length 15.5 mm); width of fore wing, 5.5 mm. Hind wing: length, 14 mm; width, as preserved, 5 mm. Fore and hind wings with six conspicuous transverse bands of dark pigmentation, as shown in the photograph, Figure 1. The venational details are included in Figure 2; the number of branches on Rs and MP differs slightly in the fore and hind wing but this is only consistent with what has previously been noted in other Palaeodictyoptera.

The prothorax and fragments of some of the legs are preserved in this specimen but not well enough to allow me to make out details. The terminal portion of the abdomen is also preserved; this clearly terminates in a pair of conspicuous cerci, which are bow-shaped

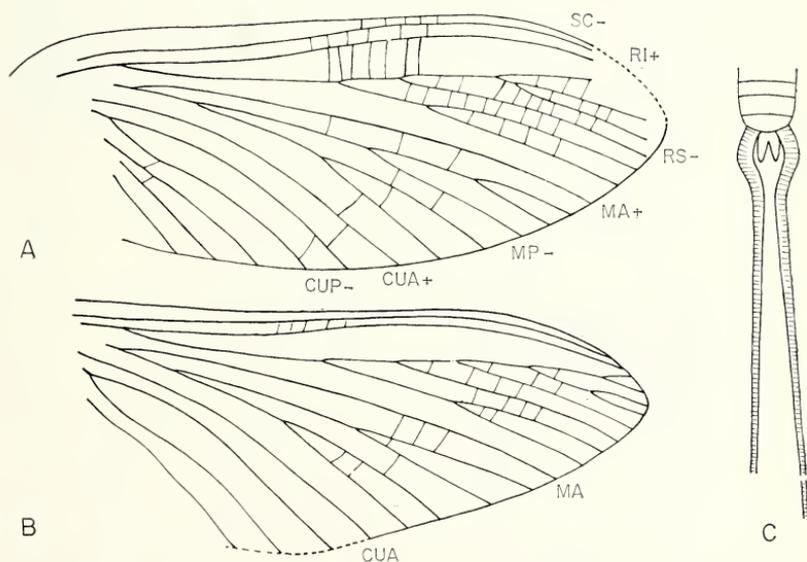


Fig. 2. *Madera mamayi*, n.sp. Drawing of fore wing (A), hind wing (B) and terminal portion of abdomen and cerci (C).

shortly beyond their origin (Figure 3). The cerci as preserved are 17 mm long but they are clearly broken off at this point and were therefore longer in the original insect. Between the cerci there is a pair of short, stout processes, faintly but clearly preserved (length 1.5 mm). The species is named for Dr. Sergius Mamay, who has sent me many fine specimens of Paleozoic insects during the past decade.

Holotype: No. 170365 U. S. National Museum; collected by Dr. Sergius Mamay in May, 1969, at an exposure of the Madera Formation in the Manzano Mountains, southeast of Albuquerque, New Mexico.

The type specimen consists of a nearly complete insect, with the two right wings outstretched and the two left wings superimposed (see Figure 1). The head is completely missing but there are remnants of the prothorax and of the anterior legs; the main part of the abdomen is not present but the last several segments and the cerci can be seen very clearly.

This insect has many interesting features. With a wing expanse of about 32 mm, it is among the smallest Palaeodictyoptera known. The species of *Lycocercus* were much larger, with wing expansions of from 140 mm to 150 mm. The transverse banding on the wings, although strikingly preserved, is not uncommon in the Palaeodictyoptera, including the species of *Lycocercus*. The form of the cerci is especially interesting, the marked bowing being very distinct. This curvature of the cerci has been seen or at least suspected in several species of Palaeodictyoptera, from both Upper Carboniferous and Permian deposits. The type specimen of *Lycocercus goldenbergi*, although preserved in a side view, shows a similar curvature (see Kukulová, 1969, Fig. 32). Two faintly preserved but dis-

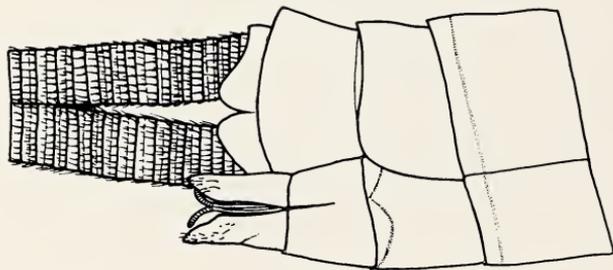


Fig. 3. *Dunbaria fasciipennis* Tillyard (Lower Permian of Kansas; from original drawing by Dr. Kukulová, based on type specimen in Peabody Museum, Yale University).

tinct processes extend beyond the end of the abdomen between the cerci; their exact nature is not clear but they are probably homologous to similar structures observed in the spilarpterid *Dunbaria fasciipennis*, from the Lower Permian of Kansas (Figure 3)<sup>3</sup>. Presumably these processes are ventral to the cerci.

#### Family Eugereonidae

The type genus of this family, *Eugereon*, is known only from the Lower Permian of Germany but *Dictyoptilus* and *Peromaptera* are known from the Upper Carboniferous of Commeny in France, and *Valdeania* is known from the Upper Carboniferous of Portugal (Kukalová, 1969). The fore wings in this family were long and narrow, with a dense pattern of cross veins, often forming a coarse network; the hind wings were at least considerably shorter and had a modification of the venation basally.

I have assigned the specimen from the Sandia Mountains in New Mexico to this family, placing it in the following new genus.

#### Genus *Sandiella*, new genus<sup>4</sup>

Fore wing similar to that of *Dictyoptilus* but with a much coarser reticulation of the cross veins and without the rows of regular cross veins, mainly unbranched, between the radial sector and R1, and between R1 and Sc; the subcosta terminates well before the apex of the wing rather than almost at the apex as in *Dictyoptilus*. The hind wing is unknown.

Type species: *Sandiella readi*, n. sp.

#### *Sandiella readi*, n. sp.

##### Figure 4B

Fore wing: length, as preserved, 40 mm; estimated complete length, 60 mm; width, 10 mm. Rs with seven main branches (branching probably variable within the species); MP with four branches, as in *sepultus*; cross veins numerous, irregular, and forming a coarse reticulation over most of the wing. Venational details are shown in Figure 4B. The species is named for Dr. C. B. Read, who, over a period of years, has sent me many fine Paleozoic insects.

Holotype No. 170364, U. S. National Museum, collected by Dr. C. B. Read in 1941 in the Sandia Formation on an exposure on the north side of Santa Fe Creek in the eastern suburbs of the city of

<sup>3</sup>I am indebted to Dr. Jarmila Kukalová for permission to use this unpublished figure of *Dunbaria*. (See also Kukalová, 1971).

<sup>4</sup>The name of the genus is derived from that of the Sandia Mountains in New Mexico and is considered feminine.

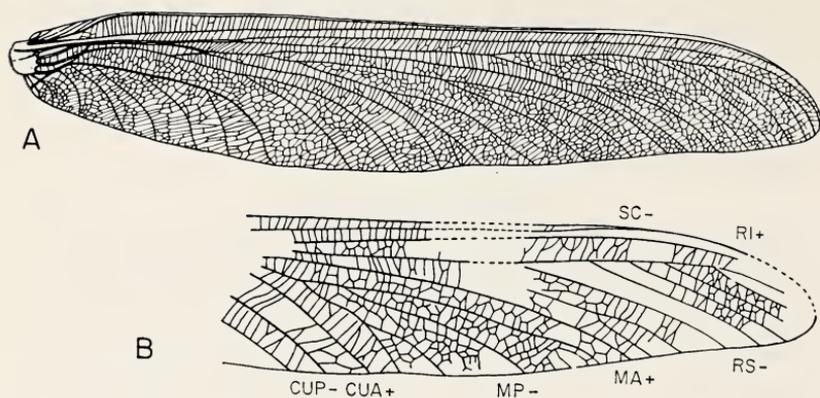


Fig. 4. A. *Dictyoptilus sepultus* (Meunier), drawing of fore wing (Upper Carboniferous of Commentry, France; from Kukulova, 1969).

B. *Sandiella readi*, n.sp., drawing of fore wing (Sandia Formation, New Mexico).

Santa Fe, New Mexico (locality no. 8941, Geological Survey). The type specimen consists of the apical three-quarters of a fore wing, moderately well preserved; the details of venation and of the cross veins have been worked out by the application of alcohol and glycerine to the specimen.

The similarity of the preserved part of this wing to the fore wing of *Dictyoptilus* is very striking (see Figures 4A and 4B). It is becoming increasingly clear that the apparently local distribution of the families of Palaeozoic insects has been largely the result of the distribution of collecting patterns. The families were probably just as widely distributed as most families of insects at the present time.

#### ORDER CALONEURODEA

##### Family Permobiellidae Tillyard

This family, which has previously been found only in the Lower Permian deposits of Kansas, is characterized by having the subcosta terminating at about mid-wing, by having three branches on the radial sector and by having CuA and CuP close together proximally but diverging distally. Only the genus *Permobiella* Tillyard, with its type species *perspicua* Tillyard, is known (Carpenter, 1943).

The fossil from New Mexico appears to belong to this family. It clearly has the relatively short subcosta and the three-branched radial sector. CuA and CuP are close together proximally but since CuP is not preserved distally, its terminal relationship to CuA is unknown. The general venational pattern of the specimen from New

Mexico is very similar, so far as can be seen in the type specimen, to that of *Permobiella*. There is one other genus of the Caloneurodea which has the short subcosta, this being *Anomalogramma* from the Lower Permian of Kansas. However, Rs in this insect has only two very short branches and the anal veins are quite differently formed.

#### Genus *Pseudobiella*, new genus

This includes species similar to those of *Permobiella* but with the cross veins normal or relatively weak, instead of very strongly convex, as in *Permobiella*. Both fore and hind wings are marked by several strongly contrasting transverse stripes, unlike those of *Permobiella*, which are without markings of any kind. Since the basal portion of the wing of *Permobiella* is unknown, it might be noted here that four anal veins are distinctly preserved in the hind wing of *Pseudobiella fasciata*; three anal veins are preserved in the fore wing, which, however, lacks the more basal region.

Type species: *Pseudobiella fasciata*, n. sp.

#### *Pseudobiella fasciata*, n. sp.

Figures 5 and 6A, 6B

Fore wing: length, as preserved, 11 mm (estimated complete length, 11.5 mm); width, 2.5 mm. Hind wing: length, as preserved, 10 mm (estimated complete length, 11 mm); width, 2.5 mm.

Holotype: No. 170366, U. S. National Museum; collected by Dr. Sergius Mamay in May, 1969, at an exposure of the Madera Formation in the Manzano Mountains, southeast of Albuquerque, New Mexico.

As can be seen from the photograph (Figure 5), this specimen consists of all four wings and parts of the body (the head, antennae and thorax); the abdomen is completely missing. The venation is clear where it is preserved at all and the nature of its preservation is very unusual. The veins are distinct in those portions of the wings that were originally heavily pigmented but they are completely absent from the parts of the wings that were presumably hyaline or unpigmented. The symmetry of hyaline areas of all the wings shows that this is not just an apparent distribution of pigment but that it reflects the original color pattern of the wing. The left fore wing, as preserved in the fossil, extends to one side but the other three wings are aligned more or less in an overlapping position over the abdomen. Since these wings rest at slightly different angles, I was



Fig. 5. *Pseudobiella fasciata*, n.sp., photograph of holotype (Madera Formation, New Mexico). A, antenna; H, head; P, prothorax; M, mesothorax; L, prothoracic legs.

able, by using photographic enlargements and colored ink, to trace out the veins belonging to each of the three wings. This has resulted in a composite picture of a fore wing (based on two wings, one of which is isolated from the others) and a composite picture of the two hind wings. Of course, technique cannot restore the portions of the wing which are missing in the unpigmented areas. However, it is possible, because of the simplicity of the venational pattern, to restore with confidence the general venational pattern in the missing areas.

The fore wing margin is very slightly concave, the wing being broadest beyond the termination of the subcosta; in contrast, the anterior margins of wings of most Calaneurodeia are straight or

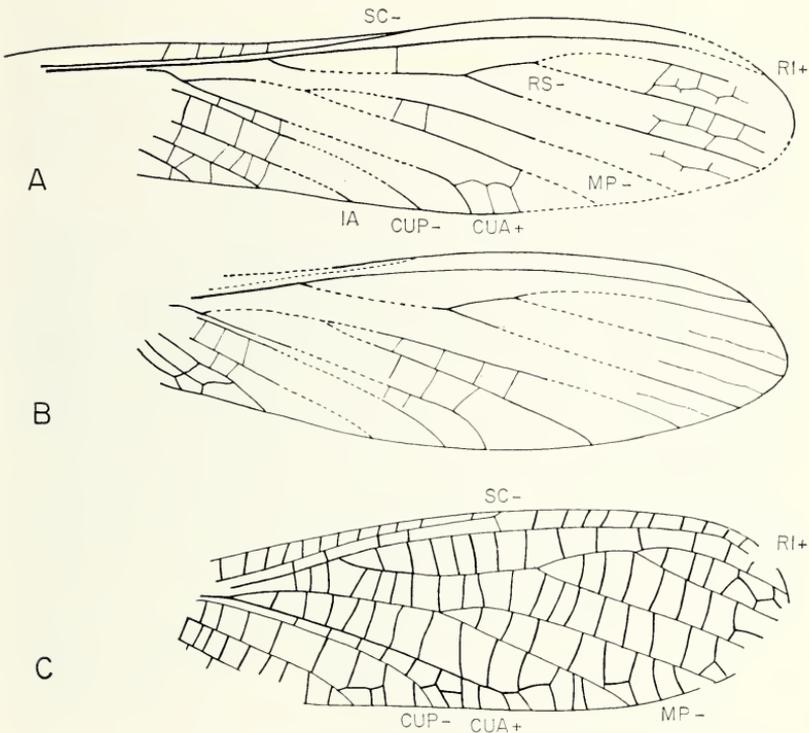


Fig. 6 (A) and (B) *Permobiella fasciata*, n.sp, drawing of fore (A) and hind (B) wings.

(C) *Permobiella perspicua* Tillyard (Lower Permian of Kansas; original drawing based on type specimen, Peabody Museum, Yale University and other specimens in the Museum of Comparative Zoology).

nearly so, although the wing of *Pseudogramma* (Permian, USSR) is slightly concave towards the base. The radial sector of *P. readi* arises well before the end of Sc, as in *Permobiella*; only its basal stem is preserved in that region but it is distinct again at about the level of the termination of the subcosta. The forking of Rs is very clear, forming three terminal branches, as in *Permobiella*. Between the branches of Rs and between  $R_4 + 5$  and MA there is an alignment of cross veins, forming a weak, irregular vein which extends only a short distance back from the wing margin. Similar irregular veins are found in some Caloneuroidea previously described, such as *Permobiella*, *Caloneurella* and *Apsidoneura*. M and CuA are anastomosed towards the base of the wing, as in other Caloneuroidea; the forking of M is not preserved but the two branches are preserved beyond the middle of the wing. CuA has the characteristic form of that of other Caloneuroidea; between it and  $MP_3 + 4$  there are a couple of large cells formed by cross veins, very similar to those in *Permobiella*. CuP is close to CuA, and the anal veins are more remote from each other. The cross veins are preserved only in pigmented portions of the wing; they are almost as numerous as those in *Permobiella*.

The hind wing, although about the same size as the fore wing, seems to have a somewhat different shape; the anterior margin is slightly arched. The venational pattern is basically like that of the fore wing, including the presence of the irregular secondary veins between the branches of the radial sector. An additional anal vein is visible in one of the hind wings.

The venational pattern of the wings, with restoration of some of the missing portions, is shown in Figures 3 and 4.

Several body structures are preserved in the fossil. The abdomen, however, is completely absent in the half of the specimen which was collected; it probably was included in the counterpart. The mesothorax (Figure 5, M) and metathorax are clearly preserved, the mesothorax being somewhat the larger (1.5 mm length and width as compared with 1.2 mm for the metathorax). These are almost circular, as they are preserved in the specimen. The prothorax (P) has been broken away from the mesothorax and rests to the right side of the mesothorax (as preserved); attached to the prothorax are portions of two front legs (L). The prothorax is 1 mm wide and .7 mm long. The head (H) is in the normal position with respect to the rest of the insect; it is 1 mm long and 1.3 mm wide. Two slight bulges on each side may represent the

eyes. One antenna (A) is preserved for a length of 6.5 mm but quite clearly this is not the complete antenna, since it ends abruptly in the matrix. The other antenna is preserved only for a short distance from the head. It is probable that the antennae were at least as long as the fore wings.

The few body parts preserved in this specimen are consistent with those known in the Caloneuroidea.

#### ORDER BLATTARIA

Two specimens of roaches were collected by Dr. Mamay in the Madera formation. One of these consists of an isolated fore wing and the other of a nearly complete insect, lacking the two fore wings. Because of the difficulty of making taxonomic assignments of Paleozoic roaches, I am not describing these specimens formally.

The second specimen, however, is of interest because it shows

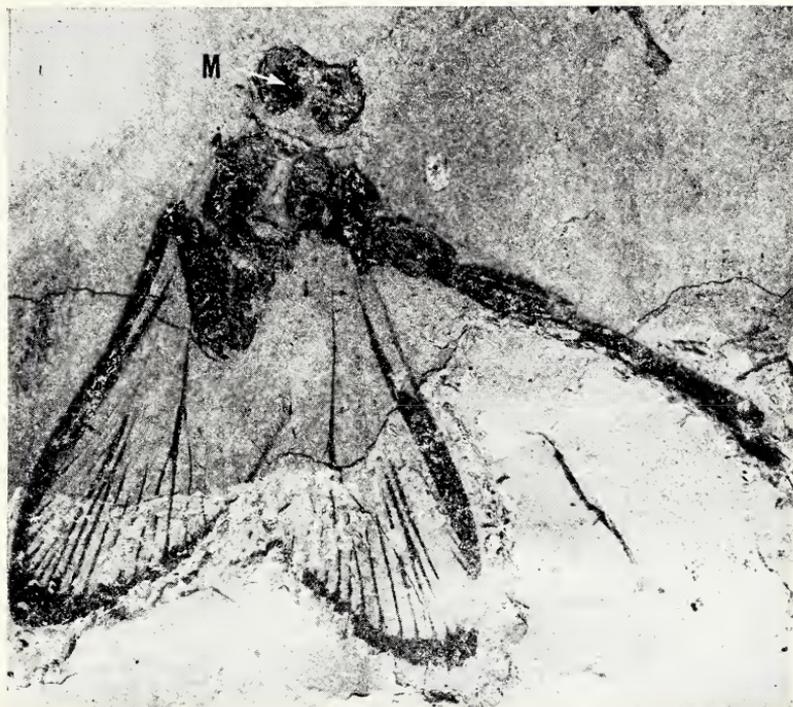


Fig. 7. Photograph of a roach (*Blattaria*) from Madera Formation, New Mexico. M, mesothorax.

the hind wings, which are very little known in Paleozoic roaches. As shown in the photograph (Figure 7), the specimen shows part of the thorax, apparently a middle and hind leg, and the two hind wings, the length of the complete hind wing being 20 mm. The thorax has obviously been crushed and distorted but the mesothorax (M) can readily be distinguished, the former showing scars of the dorsoventral muscles. However, one can distinguish a fairly large coxa, small trochanter and large femur and tibia; the segmentation of the tarsus is not preserved. The hind wing is of interest because of the preservation of most of the veins. The venational pattern is similar to that of the hind wing which Tillyard described as belonging to the genus *Pycnoblattina* Sellards, from the Lower Permian of Kansas, although the Madera specimen shows a somewhat shorter subcosta. The posterior margin of the hind wing is clearly preserved to the level at which the anal fan presumably extended. This specimen indicates, as noted previously by Tillyard, that the anal area was very small in at least some of the Paleozoic roaches, in contrast to its development in most Recent Blattaria.

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BIOLOGICAL NOTES ON TWO SPECIES OF  
*SERICOPHORUS* FROM AUSTRALIA  
(HYMENOPTERA: SPHECIDAE)

BY ROBERT W. MATTHEWS AND HOWARD E. EVANS<sup>1</sup>

*Sericophorus* is a genus of robust, often iridescent bee-like wasps belonging to the larrine tribe Miscophini. The genus is endemic to Australia and Tasmania and possibly extends into New Guinea, where one male has been taken (A. S. Menke, *pers. comm.*). Riek (1970) reports 14 species from Australia. Males are unusual in that the antennae typically consist of only 12 segments instead of the 13 found in most male sphecid wasps.

The only previous biological observations on members of this genus are those by Rayment (1955a, b). His papers include miscellaneous notes on at least six species occurring in Victoria, Western Australia, and New South Wales, and present the main behavioral features of the genus. Unfortunately, the rambling conversational style adopted by Rayment makes it difficult to sort out the facts in his reports, and indeed, it is often unclear as to which species his discussions refer. Numerous fragmentary observations, such as the occurrence of two adults in the same nest of *S. sydneyi* Rayment (1955b, pp. 75-76) and *S. victoriensis* Rayment (1955a, p. 137, presumed subterranean mating in *S. viridis roddi* Rayment (1955b, p. 74), and apparent territoriality in *S. sydneyi* females (1955b, p. 75) were not confirmed in the present very incomplete studies. We did, however, confirm two unusual behavior patterns reported by Rayment: hunting in the early morning hours and capture of only male flies. Rayment found this to be true in *S. teliferopodus* Rayment, and we found it to be the case in *S. viridis* Saussure.

Our observations concern two forms not previously studied, *S. viridis* Saussure and *S. relucens* Smith. Included also is the first detailed larval description for the genus, and notes on a parasitic nyssonine wasp, *Acanthostethus portlandensis* (Rayment).

*Sericophorus viridis* Saussure

With one exception, all of our notes on *S. viridis* were made on

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<sup>1</sup>Respectively, Department of Entomology, University of Georgia, Athens, Georgia 30601, and Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. Research supported by the National Science Foundation, U. S. A., Grant No. GB 8746.

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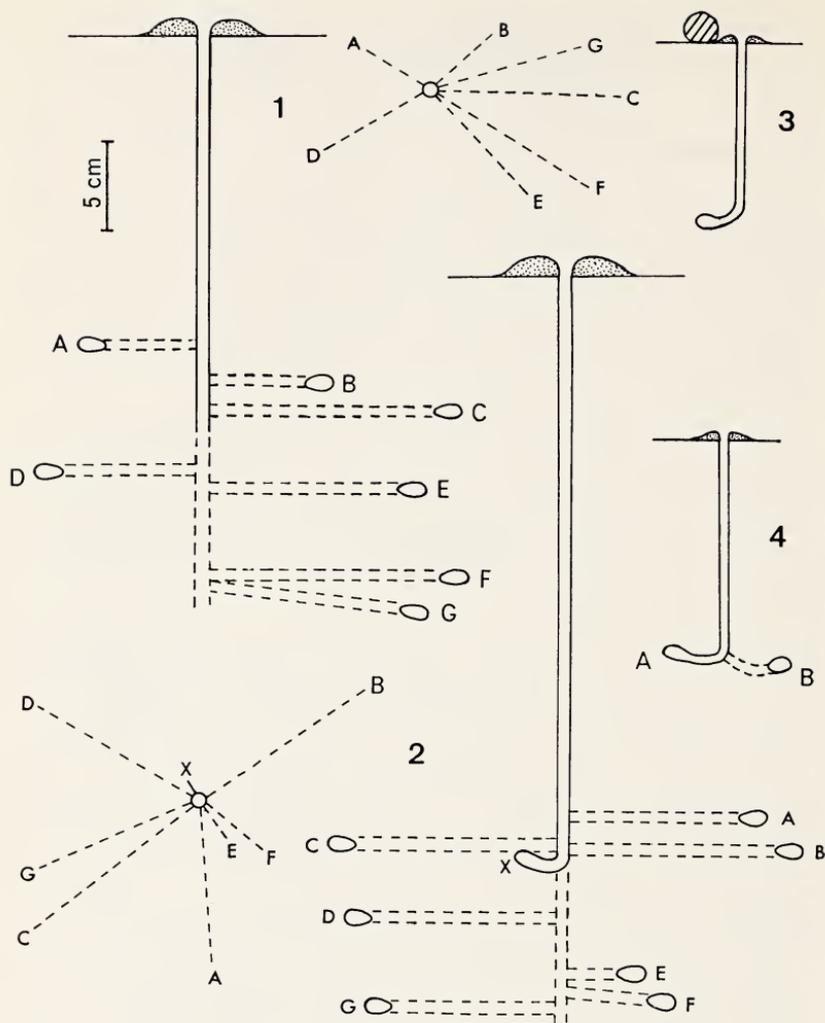


Fig. 1. *S. viridis*, no. A 258, shown in profile (left) and plan (right). Cells B and E contained eggs, cell F a cocoon. Contents of the other cells were molded. Fig. 2. *S. viridis*, no. AM 144, shown in plan (left) and profile (right). Eggs or fresh flies were present in cells A, B, C and D. The contents of cell E were molded; cell F contained a half-grown larva and cell G a cocoon. The blind end of the burrow is indicated by an X. Fig. 3. *S. relucens*, no. AM 133, in profile. Fig. 4. *S. relucens*, no. AM 152, in profile; both cells contained fresh flies.

a large colony nesting on the lower slopes of Black Mountain, Canberra, A. C. T., behind the C. S. I. R. O. Entomology buildings. The soil containing nests was a sandy loam of rather firm and uniform consistency forming a layer from 15 to 40 cm deep overlying coarse gravel and small rocks. Possibly these areas were parts of former stream channels on the mountain, since a few meters away the soil graded rather abruptly into loamy to hard clay, which characterized most of the lower slopes of Black Mountain.

This wasp was extremely successful in this area and active nests were found from mid-December through April. Nests were concentrated in three more or less contiguous areas. On 13 February 1970, the largest of these nesting aggregations contained 88 active nests, concentrated in an area of about  $8 \times 2$  meters along the fence bordering the Botanical Gardens. This area had been harrowed for a fire break earlier in the summer and lacked vegetational cover. The smaller aggregations were estimated to contain 40-50 active nests, and were in adjacent areas having a sparse herbaceous cover. Inter-nest distances were variable, but on several occasions active nests were noted within 5 cm of one another.

*Nesting Behavior.* — Nineteen nests were excavated by the authors between 6 January and 18 April, 1970 (note numbers A 193, A 221, A 251, A 252, A 259-261, A 306, AM 141-144, AM 153, AM 217). Representative nests are illustrated in Figures 1 and 2. Females dig a more or less vertical main shaft from 10-50 cm deep (ave. 21.3 cm), and construct up to 23 cells (ave. 5.6) at depths of 10-50 cm. Cells are placed in a radiating pattern, each at the end of a more or less horizontal lateral burrow extending 1-14 cm (ave. 7.0 cm) from the main tunnel. Cells are elliptical and more or less horizontal, measuring about  $9 \times 18$  mm. The lateral tunnels leading to the cells are approximately perpendicular to the main shaft or inclined slightly upwards. A single cell is excavated at the end of each lateral tunnel, and after provisioning and oviposition, the tunnel is completely refilled. In some nests (e.g., note AM 144) the first made or oldest cells were apparently deepest and more recent cells closest to the surface. However, in one 7-celled nest the freshest flies and eggs were in the deepest cells (A 260), and in some nests the newer cells appeared to be interspersed at various depths between older cells (e.g., A 261).

Nests are made conspicuous by the accumulation of a prominent rim-like mound, 6-8 cm across and 0.5-2.0 cm deep, surrounding the 7-8 mm diameter entrances (Fig. 9). These buff-colored mounds contrasted strikingly with the grayish soil surface, and were easily



Table 1 (Continued)

Prey species	<i>Sericophorus</i> species
<b>MUSCIDAE</b>	
<i>Musca domestica</i> Linnaeus	
<i>M. vetustissima</i> Walker	
<i>M. fergusoni</i> Johnston & Bancroft	
<i>Helina caerulescens</i> Stein	
<i>H.</i> sp. A	
<i>H.</i> sp. B	
<i>H.</i> sp. C	
<b>SARCOPHAGIDAE</b>	
<i>Boettcherisca peregrina</i> (Robineau-Desvoidy)	
<i>Parasarcophaga misera</i> (Walker)	
<i>Taylorimyia iota</i> (Johnston & Tiegs)	
<b>PLATYSTOMATIDAE</b>	
<i>Duomyia</i> sp.	
	<i>chalybaeus</i>
	<i>cliffordi</i>
	<i>relucens</i>
	<i>sydneyi</i>
	<i>telferopoulos</i>
	<i>victoricensis</i>
	<i>viridis</i>
	<i>o. roddi</i>
	1-V
	2-V
	8-VI
	*-VI
	*-VIII
	1-X
	*-VI
	10-VII
	*-VII
	1-III
	2-IV
	1-X
	3-X
	1-IV
	7-III,
	5-IV
	1-III

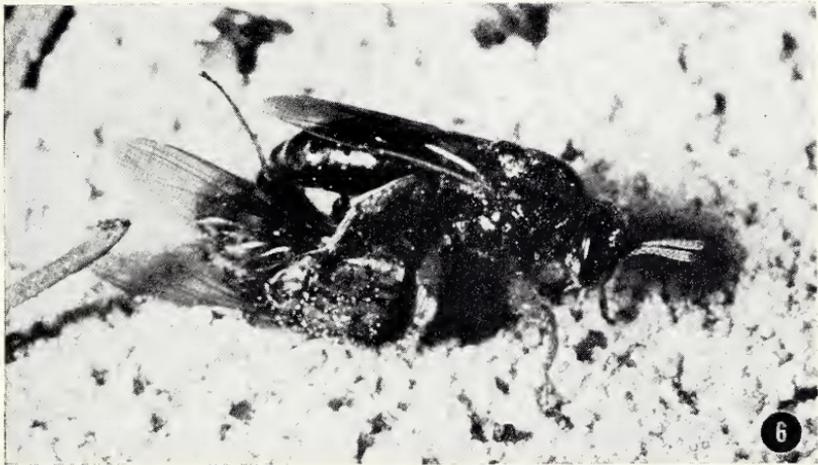
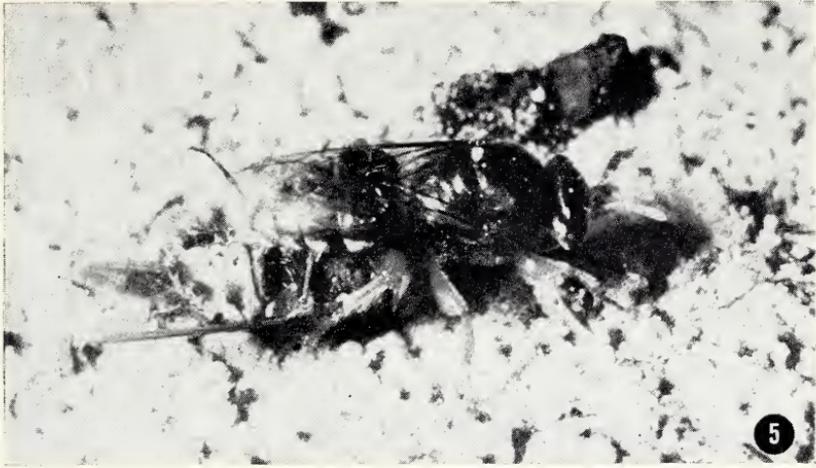
\*Prey names used by Rayment were checked by Dr. D. H. Colless and corrected as follows (Rayment's name in parentheses): *Lucilia cuprina* (= *L. argyricephala*), *Musca fergusoni* (= *M. convexifrons*), *Calliphora stygia* (= *Neopollenia stygia*).

located. Brief observations of digging behavior indicated that the soil is pushed out a load at a time, the females emerging abdomen first, with a pellet of soil held ventrally between the curved tip of the abdomen and the hind legs. At the nest entrance the soil is thrust out, apparently by the hind legs, and simply accumulates as a rim about the entrance, with no leveling being done. Apparently most digging is done at night or in the very early morning, for when we checked the colony early on days following heavy rains, numerous freshly made mounds were always present.

The Black Mountain colony exhibited a very decided preference for a single blowfly species, *Calliphora tibialis* Macquart (Table 1). The constancy over the entire nesting season to this one species was remarkable, and indeed, the only nest from a different locality (Note A 193, Cotter Reserve, A.C.T.) also contained exclusively *C. tibialis*. The only exceptions at the Black Mountain colony were a single individual of *C. sternalis* Malloch found in a nest excavated on 7 January (early season) and 7 individuals of *C. accepta* Malloch, all taken on the same day (4 March) near the end of the nesting season, when *C. tibialis* populations may have been declining.

By visiting the colony at different times of the day we were able to establish that most, if not all, provisioning occurred during the first hour after the morning sun first hit the tops of the trees. On 26 February, a completely clear morning, much provisioning occurred between 6:20 and 6:50 a.m. On 28 February the sun was behind clouds until 6:55; no provisioning was noted between 6:00 and 6:55, but after that time, until 7:45, many flies were brought in. The temperature at 6:00 was 58° F; during the period of provisioning it was undoubtedly a few degrees higher than this, but no other Hymenoptera whatever were observed to be active at this time. Indeed, there was no considerable amount of Hymenoptera activity in this area until about 9:00. Yet *Sericophorus viridis* appears specially adapted for performing under these conditions of cool temperatures and long shadows. Only one instance of prey carriage was recorded after 8:00, a situation in striking contrast to the behavior of the following species, *S. relucens*. Similar early morning hunting was also reported, however, for *S. teliferopodus* in Victoria, and according to Rayment (1955b) this species also preyed exclusively on blowflies, utilizing only the males. This led us to inquire as to the sex of our sample, and Dr. D. H. Colless reports that in fact all of the nearly 100 blowflies we recovered from nests of *S. viridis* were males.

This puzzling behavior is more understandable if one considers



Figs. 5-6. Two views of female *Sericophorus viridis* with prey. These females have landed on the ground near their nests and will shortly proceed to them. Note that the fly is held well back, beneath the abdomen of the wasp, the hind legs embracing the back of the fly's thorax. In most cases the fly is venter-up, as in Fig. 5; carriage of the fly sideways (Fig. 6) is exceptional.

the biology of the blowflies that are used as prey. Dr. K. R. Norris informs us (*in litt.*) that the males of *Calliphora tibialis* resemble those of some of the carrion calliphorids in exhibiting intense activity from just before dawn until at most an hour afterward. Each male selects a perch from which it flies off periodically to challenge passing insects. Dr. Norris believes that this may be an instance of territoriality, as males often appear on the same perch time after time and may engage in aerial combat with neighboring males. The females, on the other hand, do not exhibit this behavior and are usually to be found on the ground or moving about from place to place. Thus the males would be especially available to a wasp capable of attacking in the early morning hours, especially if the males challenged approaching *Sericophorus*.

It is possible, too, that there is a selective advantage in the wasps' use of males. The females are ovoviviparous, and might deposit maggots in the cells which could destroy the wasp egg or larva, as sometimes occurs in *Bembix* (Evans, 1957, p. 77). *C. tibialis* happens to be specific to earthworms, so it is improbable that its maggots would attack wasp larvae. However, it is probable that other calliphorids are used in numbers at other times and places, and these may be capable of doing so.

The hunting activities of *Sericophorus* must have a tremendous impact on the host fly populations. Estimating conservatively, over 50,000 male *C. tibialis* are captured and entombed by the colony behind C. S. I. R. O. in a single season (i.e., 100 active nests  $\times$  100 days  $\times$  5 flies per day per wasp)! Such an apparent high degree of host specificity is possible only when the prey are continuously available and themselves maintain relatively large populations.

During transport, the fly is held venter up and grasped near its wing base by the wasp's hind legs only (Figs. 5, 6). The sting was never observed to be used for holding the fly. The wasps' flight is swift and noiseless, the females reappearing suddenly. Typically the prey-laden wasp lands on the edge of her nest mound and quickly plunges into the open entrance; rarely she lands on the ground nearby and walks to her nest. Walking is done in a somewhat jerky manner, the wings held flat over the body, with no flicking. During the period of active provisioning, several trips for prey are made in rather rapid succession, with little time spent in the nest between trips. Whereas in *S. victoriensis* two or more adults are reported to utilize the same nest (Rayment, 1955a), this was never observed in *S. viridis*. The females appear to spend the

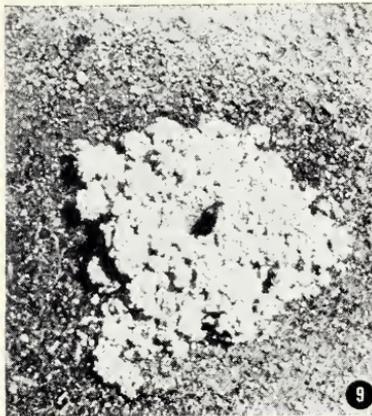
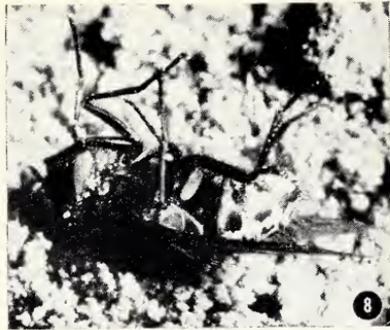
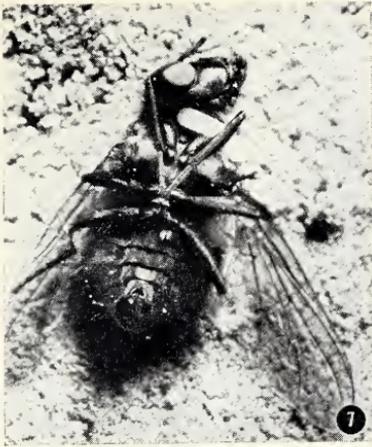


Fig. 7. Egg of *Sericophorus viridis* on prey, a male *Calliphora tibialis*. Fig. 8. Egg of the parasitic wasp, *Acanthostethus portlandensis*, on a *Calliphora tibialis* from a nest of *Sericophorus viridis*. Fig. 9. Typical nest entrance of *S. viridis*, Canberra, A. C. T. Fig. 10. Nest entrance of *S. relucens*, AM 122, near Peak Hill, N. S. W. Debris from *Eucalyptus* inflorescences has accumulated on the lee side of a stick; a nail used as a nest marker is above the nest.

night within their nests, the entrances closed from within. However, during the day our impression was that about half of the nests in the colony were left open at any given time.

No final closing behavior was observed. However, while the lateral tunnels leading to the individual cells are always refilled following provisioning, the main vertical nest shaft is apparently never filled in, and the mound remains to be eventually eroded by the elements. Possibly the female constructs a simple plug in the entrance of completed nests, as we occasionally observed the entrances of formerly active nests to be plugged with debris, mostly short pieces of grass stems and other dried plant parts. Whether these apparent final closures were the work of the wasps or the elements is unknown. However, related miscophine wasps in the genus *Solierella* often close the burrow with assorted debris, including seeds, small twigs, leaves, and sand grains (Kurczewski, 1967). We occasionally noted unidentified spiders occupying former nests, and Rayment (1955a, b) reports that certain pompilid wasps sometimes utilized the abandoned *Sericophorus* burrows.

A brief description of two nests of *S. viridis roddi* Rayment (a subspecies of doubtful validity) from Cheltenham, N.S.W., is reported by Rayment (1955b); these nests appear similar in form to those of the Black Mountain colony. Also, Rayment reported that males were observed flying over a different *S. viridis roddi* colony at Tallong, N.S.W., in the early summer and were often seen to enter closed nests. On the basis of these observations, he suggests that mating may take place below ground. As we did not discover the Black Mountain colony until the nesting season was well under way, and never noted evidence of males, we are unable to add any information on this aspect of their biology.

*Egg and Larval Development.*—Prey are placed in the cell head in first, usually venter up, and are strung out more or less in a row. The flies are dead or profoundly paralyzed, and remain relaxed but wholly immobile for several days. In 17 cells containing eggs, the number of flies per cell averaged 5.6 (range 3-9).

The egg is laid on the first fly placed in the cell (occasionally apparently on the second fly), i.e., the fly at the end of the cell farthest from the main nest shaft. Cells are mass provisioned, but apparently the egg is not laid until after the full complement of flies has been placed in the cell, as on several occasions excavated nests were found having cells with one or more flies present but containing no egg. As in the species studied by Rayment (1955a, b),

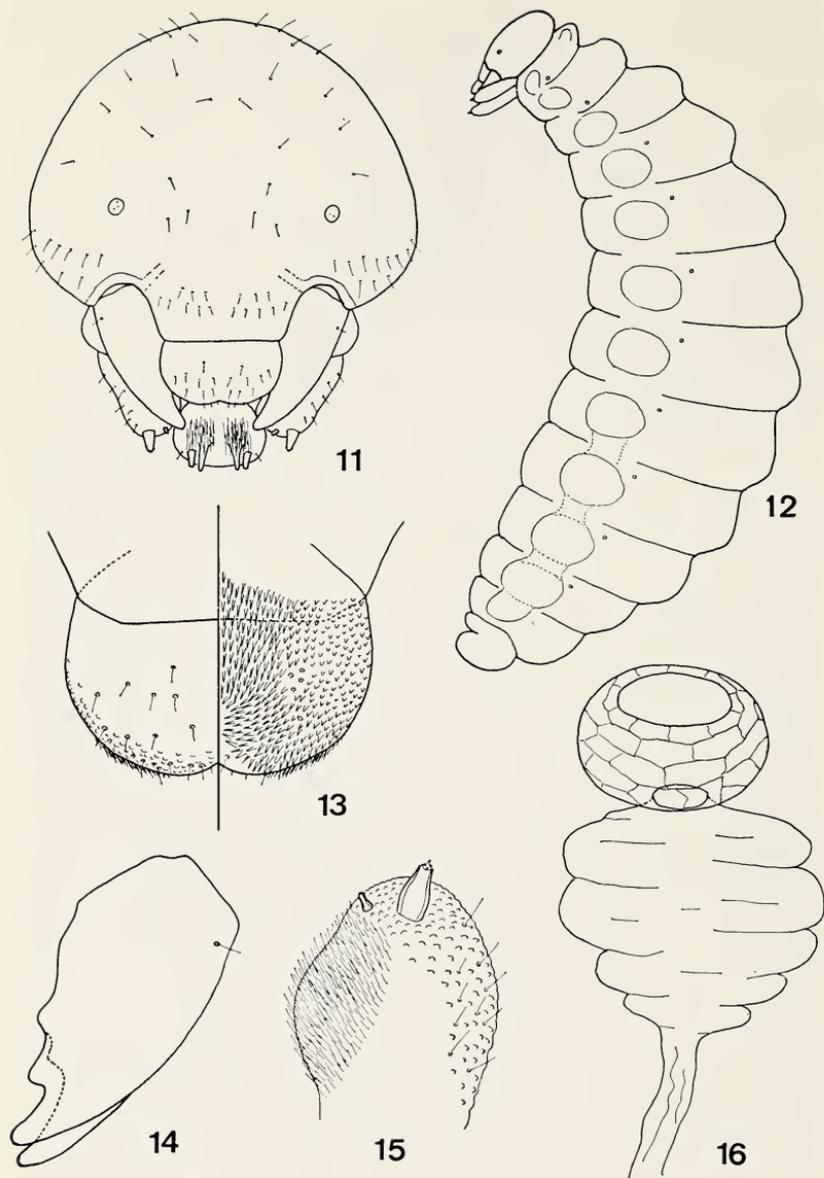
the egg is attached ventrally and more or less transversely on the prothorax just anterior to the fore coxae and slightly off center to one side (Fig. 7). According to Rayment, one anterior leg of the egg-bearing fly is sometimes dislocated or raised; however, this was not observed in *S. viridis*.

Eggs are whitish and sausage-shaped, measuring 2.5 mm long by 0.5 mm wide at the middle. No data were obtained on time required for egg hatch or larval development; however, Rayment (1955b) gives the incubation period for *S. teliferopodus* eggs as between 4 and 6 days, with larval development requiring about 12-14 days. Normally only one or possibly two new cells appeared to be stocked each morning, a rate possibly determined by availability of mature eggs in the females' ovaries. The most cells in a single nest that contained eggs was three.

*Larval characters.*—The following description is based on two fully grown, non-diapausing larvae from Canberra (note nos. A 260, AM 217). Notes on several diapausing larvae removed from cocoons follow the description.

Body length 9.5 mm; maximum width 3.3 mm. Robust, more tapered anteriorly than posteriorly; dorsal profile somewhat serrate, each segment somewhat expanded posteriorly, without distinct division into annulets; terminal segment rounded beyond the broad, ventral anal opening; pleural lobes prominent, rounded protuberant, the thorax without prominent accessory lobes although prothorax with prominent pleural lobes and with small latero-dorsal swellings (Fig. 12). Spiracles small, lightly pigmented; atrium lined with weak, irregular hexagons; opening into subatrium simple, unarmed; subatrium swollen, of irregular shape (Fig. 16). Integument mainly smooth, but entire venter minutely spinulose; each segment with a few very short setae dorsally, the pronotum with somewhat more setae than following segments (about 20, these about the same length as the head setae).

Head 1.2 mm wide, 1.1 mm high (not including labrum and mouthparts) (Fig. 11). Parietal bands and coronal suture absent; top and sides of head roughened by many small convexities; antennal orbits small, subcircular, each bearing three minute sensilla; head setae sparse but moderately long, the longest ones measuring about 60  $\mu$ ; clypeus with a double row of setae. Labrum weakly emarginate medially, its surface with numerous strong setae, median apical margin also with a few setae; margin with only a few, weak sensory cones, rather roughly spinulose laterally; epipharynx covered with



Figs. 11-16. *Sericophorus viridis* Saussure, mature non-diapausing larva. Fig. 11. Head, anterior view. Fig. 12. Body, lateral view. Fig. 13. Labrum (left) and epipharynx (right). Fig. 14. Mandible, dorsal aspect. Fig. 15. Maxilla, mesal margin at left. Fig. 16. Spiracle.

long spinules, medially and apically, these tending to converge toward the midline; extreme sides of epipharynx with only short, sparse spinules (Fig. 13). Mandibles approximately twice as long as their basal width, terminating in five teeth, the basal two smaller than the apical three; base of mandibles with a single seta (Fig. 14). Maxillae directed mesad, their inner margin somewhat lobed, strongly spinulose; palpi large, about 80  $\mu$  in length; galeae very much smaller than palpi, only about 25  $\mu$  in length (Fig. 15). Apical portion of labium circular, bearing two patches of long spinules on its oral surface; palpi about 70  $\mu$  long, slightly exceeded by the spinnerets.

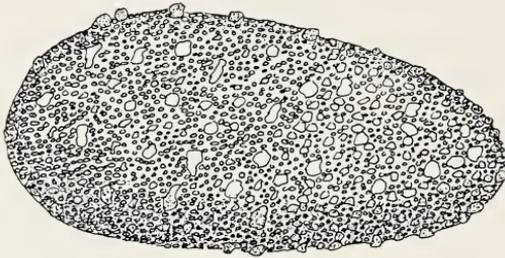
In larvae removed from cocoons after passing their meconium, the body is much more compact, the segments being shortened but with very strong pleural lobes and transverse dorsal elevations; the anterior part of the body is curved strongly and pressed against the venter, the head being invisible or nearly so. Head features are unchanged except that the maxillae and labium are somewhat flattened and the spinnerets difficult to detect.

The larvae agree well with the characters of the Larrinae as defined by Evans (1958, 1964). In features of the epipharynx, *Sericophorus* approaches *Liris* most closely, and there is good agreement in general form of the body and head with that genus. In the artificial key to sphecid larvae (Evans, 1959, p. 171) the larva of *Sericophorus* runs reasonably smoothly to *Motes* (i.e., *Liris*). However, the described larvae of *Liris* have a much more hirsute body and a non-emarginate labrum. There is a reasonably close resemblance to the larvae of such genera of Miscophini as *Lyroda* and *Plenoculus*, but those genera have more finger-like prothoracic lobes and a different arrangement of generally much shorter spinules on the epipharynx. The larvae of these four genera show no really important differences and do not reflect the major differences in nesting behavior among them.

*Cocoon.* — Cocoons measure 12-14 mm long by 5.5-6.5 mm maximum width; they are rounded at both ends but very slightly more tapered toward one end than the other (Fig. 17). The walls are composed of soil particles glued together to form a thin, brittle case; there is no silken lining and there are no evident pores in the walls (as there are in *Bembicini*). The soil grains are evidently fastened together with viscid strands of silk. The walls of the cocoon are relatively smooth on the inside, quite rough on the outside.

*Natural Enemies.* — The nyssonine wasp, *Acanthostethus port-*

*landensis* (Rayment) was common in the nesting area throughout the season. It was often observed to investigate, and sometimes to enter, open nests, and actively patrolled the nesting area throughout the day. With the exception of some miltogrammine flies noted on one occasion but not collected, no other parasites were observed in the nesting area.



## 17

Fig. 17. Cocoon of *Sericophorus viridis*, anterior end at right.

Of 17 cells with *Sericophorus* eggs (and several more incompletely provisioned cells), only one contained evidence of parasitism (note AM 143). This cell contained 8 flies with the egg of *Sericophorus* on the fly deepest in the cell. However, a somewhat smaller egg, presumably that of *Acanthostethus*, was found on the fourth fly in the cell, tucked ventrally just posterior to the left hind coxa and well concealed between it and the base of the fly's abdomen (Fig. 8). The parasite egg measured 1.3 mm long and 0.5 mm wide at the middle. Attempts to rear the parasite in a tin failed.

Rayment (1953, 1955a) first discovered this interesting wasp entering nests of *S. victoriensis*, and his account of its behavior is essentially the same as we have observed, although he failed to find its eggs or immature stages. He also mentioned the presence of several unidentified mutillids and the bombyliid *Systoechus* sp. in the vicinity of the *Sericophorus* nests.

In our nests, mold was an important mortality factor. For example, in the largest nest excavated, viable offspring were found in 14 cells (11 cocoons, 2 larvae, 1 egg), but an additional 9 cells were overgrown with mold. Another seven nests excavated on the same day (4 March 1970) contained a total of 50 cells of which 27 had been destroyed by mold.

*Sericophorus relucens* Smith

According to Rayment (1955b), *S. relucens* is one of the commonest and most widely distributed *Sericophorus* species in Australia. However, in contrast to nests of the gregarious *S. viridis*, nests of *S. relucens* were never found in abundance. Indeed, all were discovered when the female was observed to return suddenly to a spot and disappear into the ground. The largest number of nests found in a given locality was three at 8 miles north of Peak Hill, N.S.W. (AM 112-114) on 11 December 1969. Here *S. relucens* nested in a flat area of rather coarse and moderately packed sand, at the base of eroded slag heaps of an abandoned mining operation. Other wasps nesting here included *Bembix lamellata* Handlirsch, *B. raptor* Smith, *Bembecinus hirtulus* (Smith), and *Cerceris minuscula* Turner. Additional single nests were found about 2 m above flood level on the west bank of the Murrumbidgee River at Pine Island Reserve, 10 miles south of Canberra, A.C.T., on 10 January 1970 (AM 152) and on the south bank of Baker's River, 5 miles S. Machay, Qld., on 2 May 1970 (AM 232).<sup>2</sup> Both were in moderately friable loamy sand with sparse vegetation. Nests of *Bembix trepida* Handlirsch, *Bembecinus hirtulus* (Smith), and *Prionyx globosus* (Smith) occurred in the same general area at Pine Island Reserve, and *Bembecinus egens* (Handlirsch) and *Bembix raptor* nested commonly at the Mackay site.

*Nest Structure.* — The five excavated nests were of typical sericophorine form, consisting of a vertical main shaft 8-13 cm long and one or two cells at the end of short 2-3 cm long lateral tunnels from the bottom of the main burrow. Typical nest profiles are illustrated in Figures 3 and 4. The relatively inconspicuous mounds or tumuli encircling the nest entrances measured 2.5-3.0 cm across. Those of the Peak Hill nests were marked by accumulated piles of wind-blown plant debris, consisting mostly of dried *Eucalyptus* inflorescence parts (Fig. 10). All of the Peak Hill nests were situated adjacent to sticks which littered the soil surface and appeared to act as miniature windbreaks.

The most cells found in any nest was two, and it seems likely that this is the maximum number per nest made by this species. Supporting this was the fact that no cells containing mature larvae or cocoons were ever found; cells always contained fresh flies. Typically both cells were situated at about the same depth and on opposite sides

<sup>2</sup>Specimens were collected at all three localities and found to compare very favorably with the type specimen of *relucens* Smith, which we studied in the British Museum (Natural History).

of the main burrow (Fig. 4), an architecture similar to that of *S. teliferopodus* (Rayment, 1955b).

Unlike *S. viridis*, females of *S. relucens* were observed to return to the nests with prey throughout the day, a behavior similar to the daytime hunting reported for *S. sydneyi* and *S. victoriensis* (Rayment, 1955a, b). The wasps' flight is silent, and upon returning they plunge quickly and without hesitation into their open nest entrances. The sample of prey removed from the eight excavated cells included 13 species belonging to four families (see Table 1), a much broader range than that taken by *S. viridis*. The strongest preference appeared to be shown for the sarcophagid, *Taylorimyia iota* (Johnston and Ties), which comprised 7 of the 10 flies in the Pine Island Reserve nest, and 5 of the 18 flies from the Peak Hill nests. Interestingly, two individuals of *Calliphora tibialis* (the major prey of *S. viridis*) were found in one nest from the Peak Hill colony.

In contrast to the all male prey taken by *S. viridis* (and indeed the prey of all the species studied by Rayment), *S. relucens* prey samples included a small proportion of female flies (5 of 18 from Peak Hill, 3 of 10 from Pine Island Reserve; all 5 from Mackay were males). However, none of these females belonged to the Calliphoridae, although calliphorids comprised 1/3 of the total prey sample. Certainly the matter of prey selection by *Sericophorus* is worthy of further investigation, particularly as it is related to time of hunting and the reproductive characteristics of the preferred prey.

The flies are strung out in a row in the cell, head in first and usually venter up. Three cells which were apparently complete (i.e., situated at the ends of filled lateral tunnels), were accidentally broken into during excavations, but no eggs or larvae were subsequently recovered. Nevertheless, the number of prey in these cells (6, 7 and 7) is probably representative of the normal prey complement per cell for *S. relucens*.

*Natural Enemies.*—No parasites were recovered from the nests, but the mutillid *Ephutomorpha mackayensis* André. was common at the Peak Hill site, and one female was observed walking around the entrance of one of the *Sericophorus* nests (AM 114).

#### ACKNOWLEDGEMENTS

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Colless (all other families), both of the above address. We are also indebted to Drs. Colless and Norris for information on the sex and biology of the flies used as prey. Specimens of the prey, wasps and associated parasites have been deposited in the Australian National Insect Collection, Canberra, and in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U. S. A. These bear our note numbers as referred to in the text.

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SECONDARY SYMMETRY OF ASYMMETRIC  
GENITALIA IN MALES OF  
*ERYNNIS FUNERALIS* AND *E. PROPERTIUS*  
(LEPIDOPTERA: HESPERIIDAE)

BY JOHN M. BURNS

Museum of Comparative Zoology, Harvard University

The form of the genitalia is extraordinarily useful for distinguishing species in many animal groups, and nowhere more so than in the Lepidoptera. Indeed, in various genera—including some of those in Evans' (1953) "Erynnis Group" of American pyrgine hesperiids—the genitalia have become asymmetric so that the number of potential, taxonomically valuable characters is about doubled. Asymmetry of this kind was first described a century ago (Scudder and Burgess 1870) in males of *Erynnis*, where it is very pronounced.

Out of 12,000 specimens whose genitalia I have examined in the course of microevolutionary studies of *Erynnis* (Burns 1964 and unpublished), two individuals have genitalia so deviant yet so harmoniously formed as almost to suggest new species. Both are males of *Erynnides*, a subgenus in which the valvae (or claspers) are characterized as "always highly asymmetric" (Burns 1964: 24); however, both "show striking secondary symmetry of the genitalia, in which the left valva is not its distinctive self, but instead, a mirror image of the right valva" (Burns 1964: 9). These variants belong to two of the species—*Erynnis funeralis* and *E. propertius*—that were described as new by Scudder and Burgess (1870) solely on the basis of morphologic differences in the asymmetric genitalia of males.

In figs. 1-4, the symmetric valvae of the "half-wrong" variants are directly compared with their standard asymmetric counterparts. The secondarily established symmetry is extremely good in *E. funeralis* (fig. 2) but rather less exact in *E. propertius* (fig. 4) in which, for example, the distal ends of the ventral processes do not agree in detail. Clearly, there is no reversion here to some ancestral symmetric condition: in both *E. funeralis* (cf. figs. 1 and 2) and *E. propertius* (cf. figs. 3 and 4), the right valva in the symmetric variant precisely retains its modern shape, and it is this shape that the left valva duplicates.

Both variants appear to have stemmed from developmental quirks. Experimental analyses of insect morphogenesis (see e.g. Ursprung

1963) suggest the following general explanation. In the course of differentiation, cells destined to produce the left valva were damaged; and the organism regulated with a contribution from corresponding cells of the right side. These were already determined for right valval morphology. But, in their new location on the left, they made a structure that assumed the proper functional orientation. Thus a mirror image of the right valva emerged.

Regulation of this kind, detectable when it overturns asymmetry, would never reveal itself in most species because the genitalia are symmetric from the beginning.

#### ACKNOWLEDGEMENTS

I thank M. P. Kambysellis and J. H. Postlethwait for reading the manuscript, and R. G. Gillmor for drawing the figures. This work was supported in part by grants from the National Science Foundation (GB 5935) and the William F. Milton Fund of Harvard University.

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Figures 1-4 follow

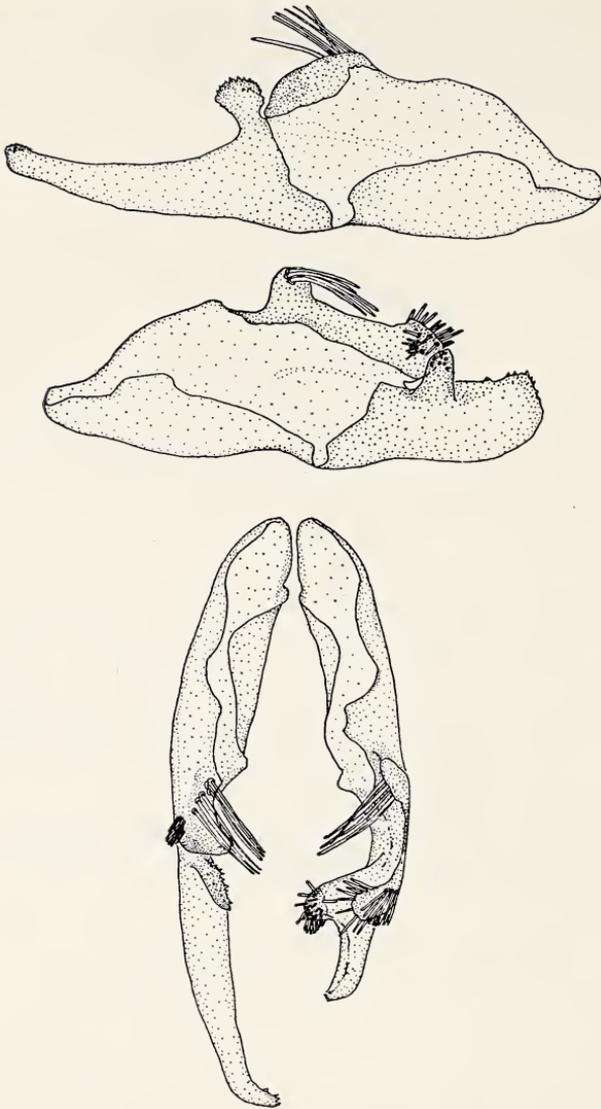


Fig. 1. Normal asymmetric male genitalia of *Erynnis funeralis*. *Top*: Medial view of left valva. *Middle*: Medial view of right valva. *Bottom*: Dorsal view of both valvae. (Specimen from Southwestern Research Station of the American Museum of Natural History, Cave Creek Canyon, 5400 ft., Chiricahua Mountains, Cochise County, Arizona, VII-4-1958, J. M. and S. N. Burns.)

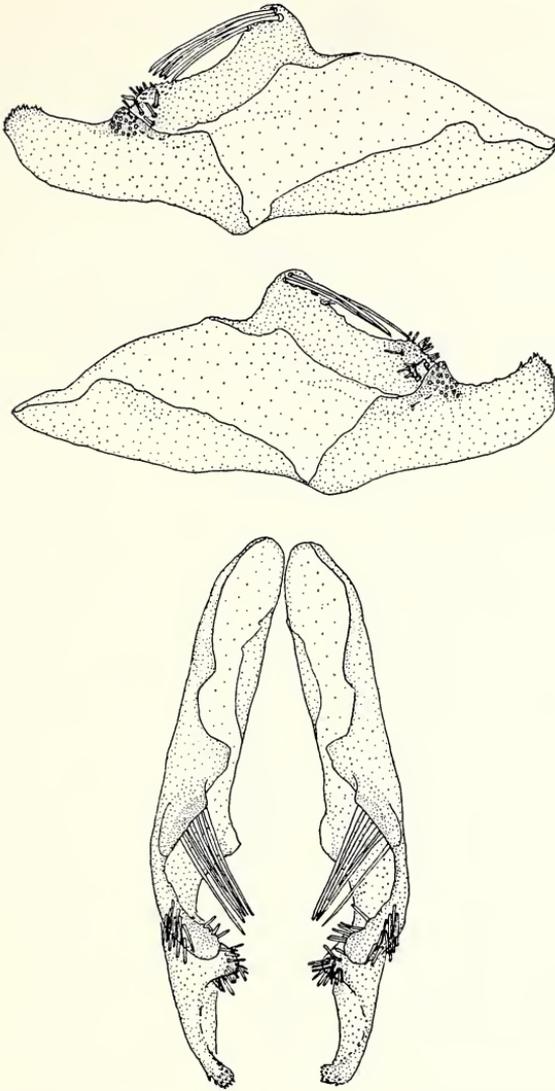


Fig. 2. Abnormal symmetric male genitalia of *Erynnis funeralis*. Arranged as in fig. 1. (Specimen supposedly from "Fla." [no date, no collector].)

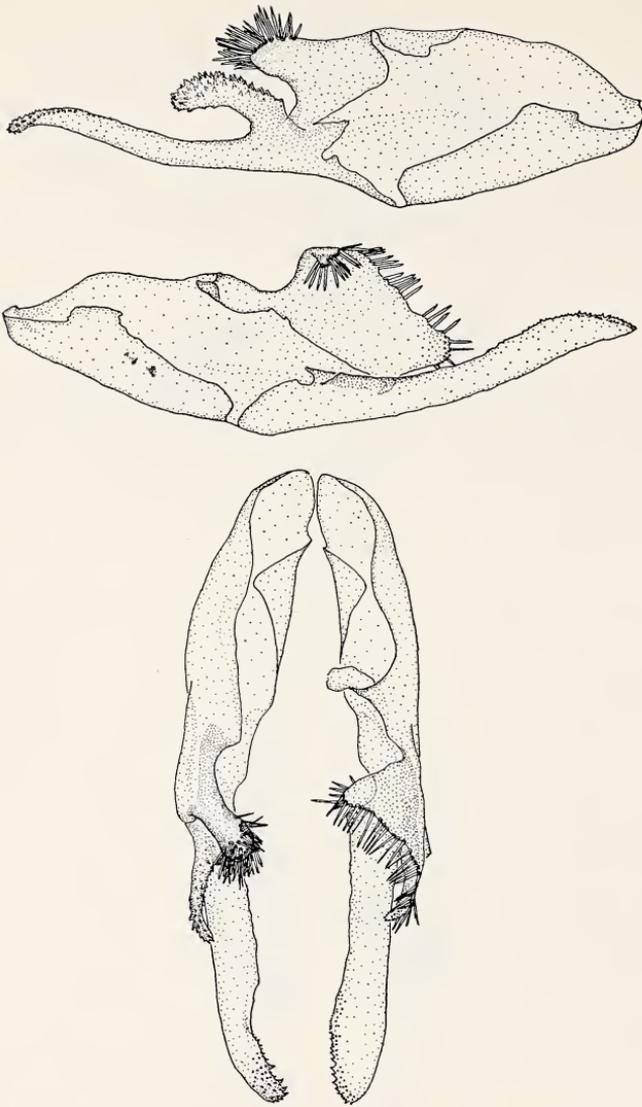


Fig. 3. Normal asymmetric male genitalia of *Erynnis propertius*. Arranged as in fig. 1. (Specimen from Arroyo Seco, Monterey County, California, V-23-1958, D. D. Linsdale.)

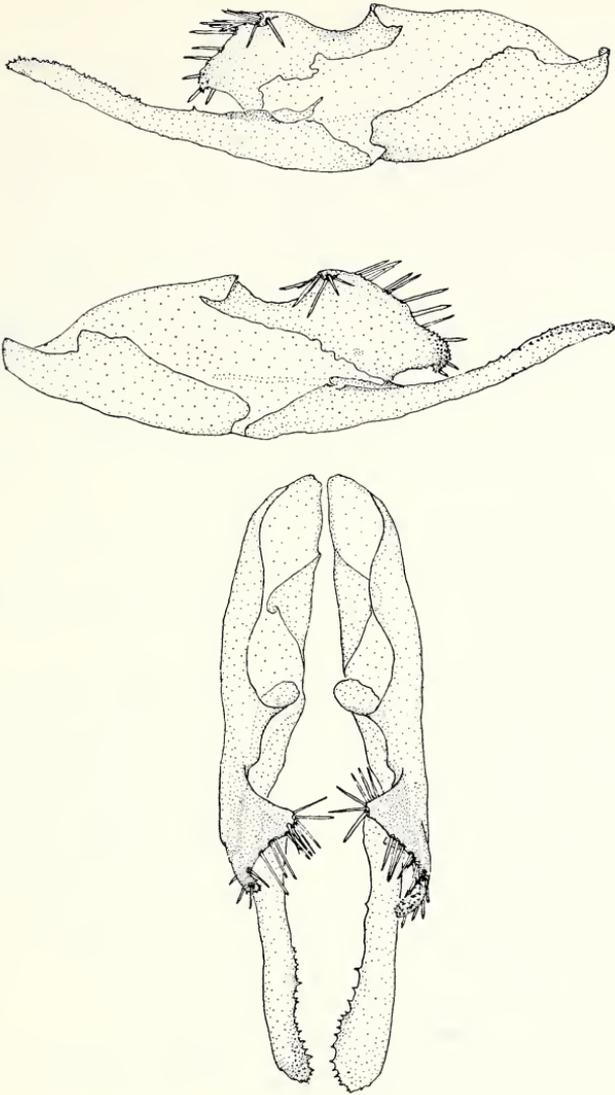


Fig. 4. Abnormal symmetric male genitalia of *Erynnis propertius*. Arranged as in fig. 1. (Specimen from Victoria, British Columbia, IV-19-1903 [no collector].)

THE MALE GENITALIA OF BLATTARIA. V.  
*EPILAMPRA* SPP.  
(BLABERIDAE: EPILAMPRINAE).

BY LOUIS M. ROTH

Pioneering Research Laboratory  
U. S. Army Natick Laboratories  
Natick, Massachusetts 01760

"The genus *Epilampra* is one of those assemblages which have developed within the tropics of both hemispheres a vast number of species, often quite distinct, again closely related and difficult to distinguish. With a general type of coloration the fluctuations of which make definite and exact characterization difficult, if not at times virtually impossible, it combines a uniformity of development in numerous other features, that in general in the family are sufficiently varied to prove of value to the systematic student. To add to the uncertainty of a situation difficult at best, we find many of the published descriptions almost valueless to aid in the recognition of these forms. As a whole the genus is one of the most difficult, obscure and generally unsatisfactory to study in the entire Blattidae." (Rehn and Hebard, 1927, p. 209).

Princis (1967) lists 60 species of *Epilampra* all of which are found only in the New World. At least five of these species [*atriventris* (Saussure), *cribrosa* (Burmeister), *ferruginea* (Brunner), *proxima* (Brunner), and *verticalis* (Burmeister)] have males with tergal glands, and their genitalia are so distinctly different from the males which lack tergal glands that I (1970) have placed them in the genus *Poeciloderrhis* Stål. This study of about 30 of the remaining 55 species of *Epilampra* listed by Princis (1967) shows that the male genitalia are useful not only for specific determinations of many species, but they may also indicate species relationships.

MATERIALS AND METHODS

The technique of preparing slides of genitalia has been described in earlier papers (Roth, 1969b, 1970).

The source of each of the specimens illustrated is given, using the following abbreviations: (AMNH) = American Museum of Natural History, New York; (ANSP) = Academy of Natural Sciences, Philadelphia; (BMNH) = British Museum (Natural History), London; (CUZM) = Copenhagen University, Zoological Museum, Denmark; (L) = Zoological Institute, Lund, Sweden; (MCZ) =

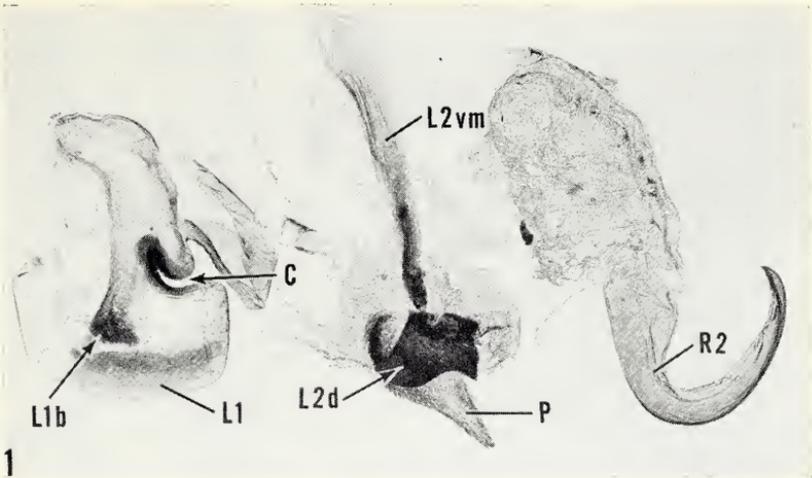


Fig. 1. Male genitalia (dorsal view) of *Epilampra abdomeningrum* from Tapurucuara, Rio Negro, Brazil. (C = cleft of L1; L1 = first sclerite of left phallomere; L1b = setal brush of L1; L2vm = median sclerite L2 ventromedial); L2d = dorsal sclerite of L2; P = prepuce; R2 = hooked sclerite of right phallomere).

Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; (N) = U. S. Army Labs., Natick, Mass.; (USNM) = United States National Museum, Washington, D.C. Geographical collection data, if known, follow these abbreviations. The number preceding the abbreviations refers to the number assigned the specimen and its corresponding genitalia (on a slide) which were deposited in the museum indicated. These numbers are used in the text where the identifications of certain species are discussed.

If known, the taxonomists who identified the species are given. In several cases these specialists of the *Blattaria* disagreed in their determinations, emphasizing the difficulty in identifying species of *Epilampra* from literature descriptions. Unfortunately male type material was not always available so that several questions still remain unresolved. In spite of this drawback the results point up the value of using male genitalia in the taxonomy of a difficult genus.

#### RESULTS AND DISCUSSION

The phallomeres characteristic of *Epilampra* male genitalia are shown in Figure 1.

Prepuce—Usually distinctively shaped with a definite marginal outline and often covered by microtrichia (Fig. 1, P).

L2d—This sclerite (Fig. 1, L2d) is always separated from L2vm (Fig. 1) by a membrane, and may or may not be clearly separated from and lie above the prepuce. In some species (e.g. *Mexicana* Group) most of L2d is a sclerotized and integral part of the prepuce.

R2 (retractable genital hook, Fig. 1, R2) — A subapical incision is often found on the ventral surface (Fig. 18, SI).

L1 — A deep lateral curved incision or cleft is present (Fig. 1, C) and a setal brush (Fig. 1, L1b) may or may not be found on the dorsal surface.

Rehn and Hebard (1927, p. 210) without specifying the characters used, tentatively erected 5 species Groups for *Epilampra*, primarily for West Indian species. These Groups and the species included were:

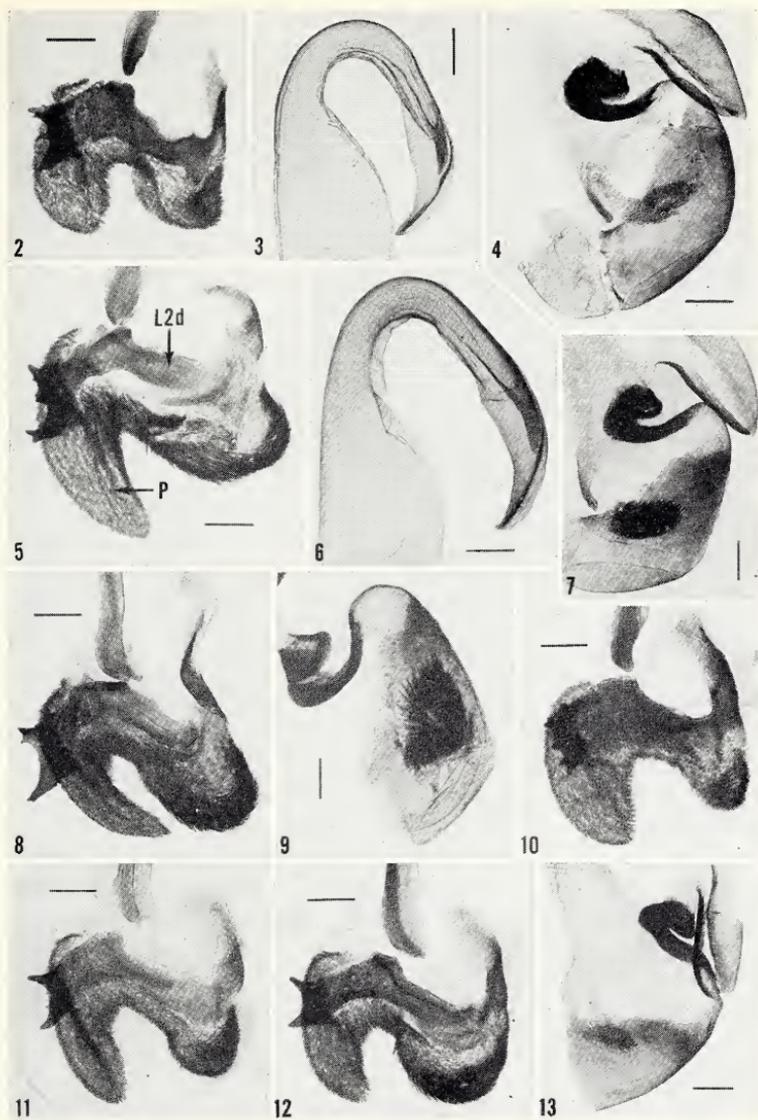
1. *Cubensis* Group: — *cubensis* Bolivar.
2. *Mexicana* Group: — *insularis* Bolivar, *tainana* Rehn and Hebard.
3. *Abdomennigrum* Group: — *abdomennigrum* (De Geer), *mona* Rehn and Hebard.
4. *Burmeisteri* Group: — *gundlachi* Rehn and Hebard, *burmeisteri* (Guérin), *wheeleri* Rehn, *haitensis* Rehn and Hebard, *sabulosa* Walker.
5. *Grisea* Group: — *quisqueiana* Rehn and Hebard.

Rehn and Hebard (1927) indicated that other species would probably fall into these groups. The male genitalia do not support the placement of a number of the above species in the groups erected by Rehn and Hebard. Based on genital characters I suggest the following species groups of *Epilampra*: *Mexicana*, *Abdomennigrum*, *Burmeisteri*, *Sodalis*, *Shelfordi*, *Heusseriana*, and *Yersiniana*.

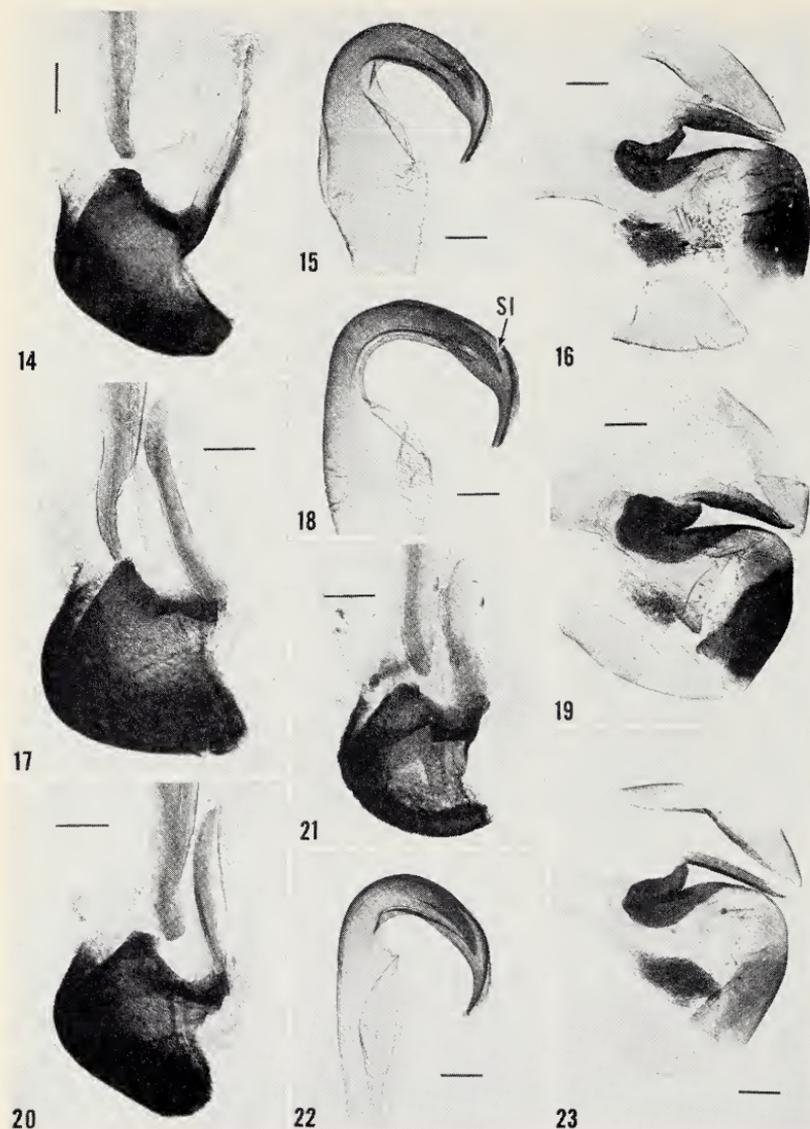
#### *Mexicana* Group

[*Epilampra mexicana* Saussure (Figs. 2-13); *E. fallax* Saussure and Zehntner (Figs. 14-23); *E. conferta* Walker (Figs. 24-43)].

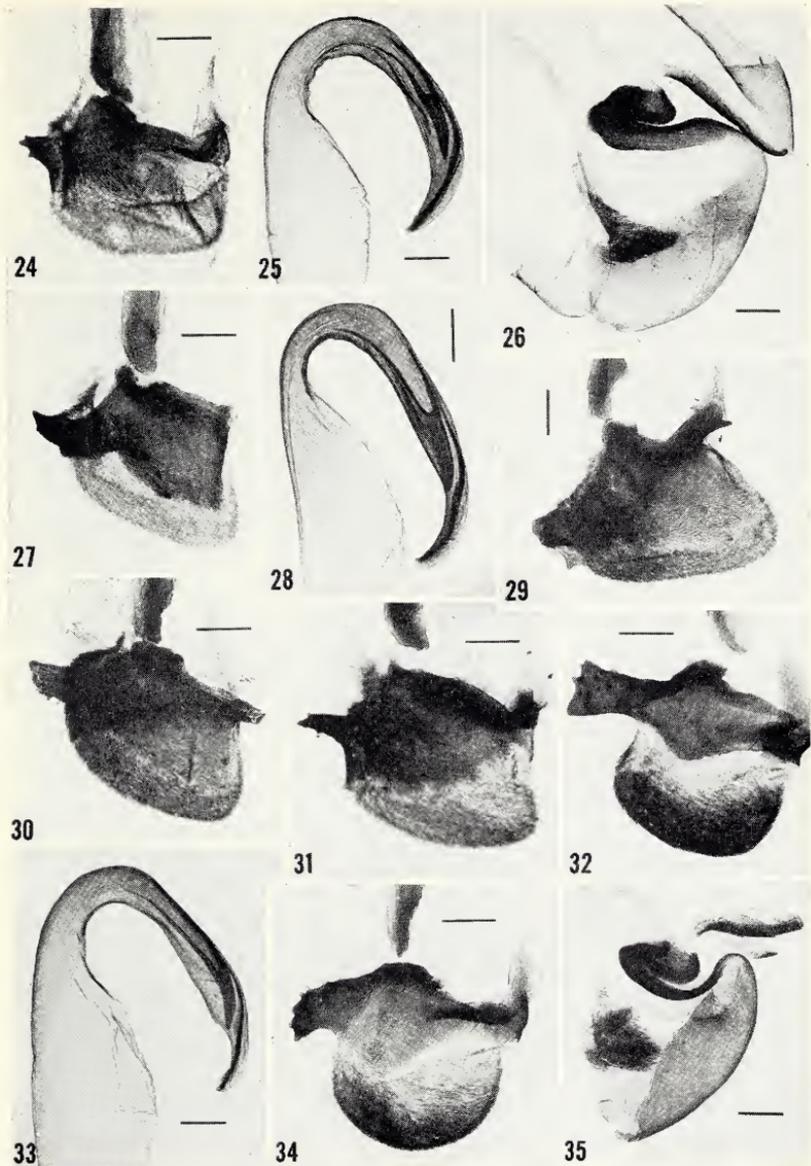
This group includes species in which most of L2d is a flattened sclerotized plate which is an integral part of, and does not lie above, the prepuce (Fig. 5). In *mexicana* only a small part of L2d on the left side is separated from and lies above the prepuce, and on the right side the L2d tapers and extends upward toward the L2vm (Figs. 2, 5, 8, 10, 11, 12). In *fallax* the lateral extension of the right side of L2d is quite long (Figs. 14, 17, 20, 21). In some *conferta* the L2d extends well beyond the left side of the prepuce (Figs. 24, 27, 29-32, 34) and the extension on the right may vary considerably in length. The prepuce of *mexicana* is deeply notched and is readily distinguished from the other members of the group.



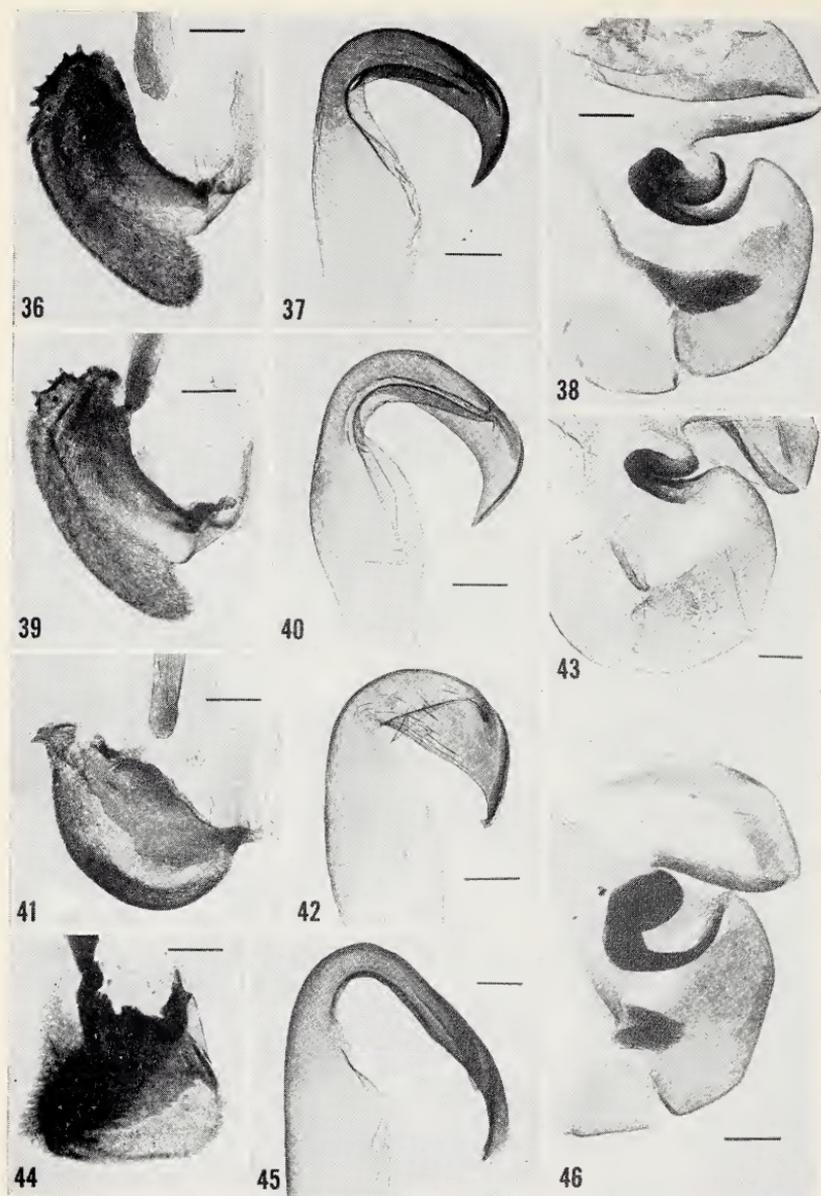
Figs. 2-13. Cockroach male genitalia. *Epilampra mexicana*. 2-4. (63 USNM). Guatemala. 5-7. (109 USNM). Turrialba, Costa Rica. 8-9. (106 USNM). Turrialba, Costa Rica. 10. (111 USNM). Chis. Soyalo, [Rt. 195, Km 24], Mexico. (2-10, det. Gurney). 11. (52 ANSP). Central Mexico. 12-13. (110 USNM). Ver. Rio Tacolopan, [Rt. 195, Km 24], Mexico. (11-13 det. Roth). (L2d = dorsal sclerite of L2; P = prepuce). (scale = 0.2 mm)



Figs. 14-23. Cockroach male genitalia. *Epilampra fallax*. 14-16. (51 ANSP). Sapucay, Paraguay (det. Roth). 17-18. (66 USNM). Santa Catarina, Brazil. (det. Albuquerque). (SI = Subapical Incision). 19-20. (73 USNM). Santa Catarina, Brazil. (det. Albuquerque). 21-23. (103 USNM). Rio Lujer, Buenos Aires, Argentina (det. Albuquerque). (in Fig. 21 the prepuce is collapsed). (scale = 0.2 mm)



Figs. 24-35. Cockroach male genitalia. *Epilampra conferta*. 24-26. (134 USNM). El Valle, Panama (det. Princis). 27-28. (136 USNM). Barro Colorado Island, Panama. (det. Princis). 29. (135 USNM). Barro Colorado Island, Panama. (det. Roth). 30. (50 ANSP). Chiriqui, Panama. (labeled *stigmosa* in pencil). 31. (105 USNM). San Isidro del General, Cattaño, Costa Rica (det. Princis). 32-33. (132 USNM). Napo, Santa Cecilia, Rio Aguatico, Ecuador. (det. Roth). 34-35. (133 USNM). Same locality as 32-33. (det. Roth). (scale = 0.2 mm)



Figs. 36-46. Cockroach male genitalia. 36-38. (4 CUZM). *E. conferta*. Callanga, Peru. (det. Princis). 39-40. (121 USNM). *E. conferta*. Callanga, Dept. of Cusco, Peru. (det. Roth). 41-43. (67 USNM). *Epilampra* sp. Rio Blanco or Ecuador. (det. as *E. mexicana* by Albuquerque). The setal brush in Fig. 43 is very lightly pigmented and difficult to see in the photograph. 44-46. (168 USNM). *Epilampra* sp. Cundinamarca, Colombia. (scale = 0.2 mm)

In species of the *Mexicana* Group, R2 (Figs. 3, 6, 15, 18, 22, 25, 28, 33, 37, 40, 42, 45) has a subapical incision, and a setal brush (Figs. 4, 7, 9, 13, 16, 19, 23, 26, 35, 38, 43, 46) occurs on L1.

Princis (1958, p. 63) synonymized *Epilampra stigmosa* Giglio-Tos with *Epilampra conferta* Walker. The specimens determined by Princis (Figs. 24-28, 31) as *conferta* are similar to a specimen, in the Philadelphia Academy collection, which was labeled (in pencil) *E. stigmosa* (Fig. 30). However, the *E. conferta* identified by Hebard, Albuquerque, and Rehn (Figs. 229-237) have entirely different genitalia from Princis' *conferta* (Figs. 24-28, 31, 36-38). The type of Walker's *conferta* (Brazil) is a female, whereas Giglio-Tos' type of *stigmosa* is a male.

According to Gurney (personal communication) "*E. stigmosa* G.-T. was based on 4 males from Ecuador. Giglio-Tos also described *E. josephi* from 2 males from S. Jose, Ecuador (*stigmosa* was from the valley of Santiago, Ecuador); they apparently were similar to *stigmosa* for the most part. . . . No. 76 [*conferta*, det. Albuquerque] (Figs. 235-237), seems rather small to be *conferta*, judging from Walker's description (though type is a female), but size may be quite variable. I would be inclined to use the name *stigmosa* for No. 132 [Figs. 32-33], No. 134 [Figs. 24-26], and No. 136 [Figs. 27-28], and perhaps No. 105 [Fig. 31], but am more uncertain about No. 76 [Figs. 235-237] being *conferta*. . . . No. 105 [Fig. 31] has the face darker than 132, et. al., the interocular space is wider, and the ventral surface of the abdomen is much darker; however, if the genitalia agree this may be just variation."

It is apparent that Gurney is not convinced that *stigmosa* and *conferta* are the same species. However, for the present, I am following Princis' conclusions. It is highly probable that more than one species is involved here which are very similar in external appearance. The problem may be partly solved by examining the male genitalia of the type of *stigmosa*. Unfortunately the Type of *conferta*, as indicated above, is a female. The prepuce and L2d of *conferta* specimens from Ecuador (Figs. 32, 34) differ somewhat from these structures in specimens from Panama and Costa Rica (Figs. 24, 27, 29, 30, 31) and from specimens from Peru (Figs. 36, 39). The R2 (Figs. 37, 40) of Peruvian males are noticeably stouter than the genital hooks (Figs. 25, 28) of Panamanian specimens. *Epilampra conferta* may well be a complex of sibling species.

The genitalia of two undetermined or questionably determined species belonging to this group are shown in Figures 41-46. One specimen from Ecuador, determined by Albuquerque as *E. mexicana*

is not this species, according to Princis (personal communication) and its genitalia (Figs. 41-43) are distinctly different from those of *mexicana* (cf. Figs. 2-13).

#### *Abdomennigrum* Group

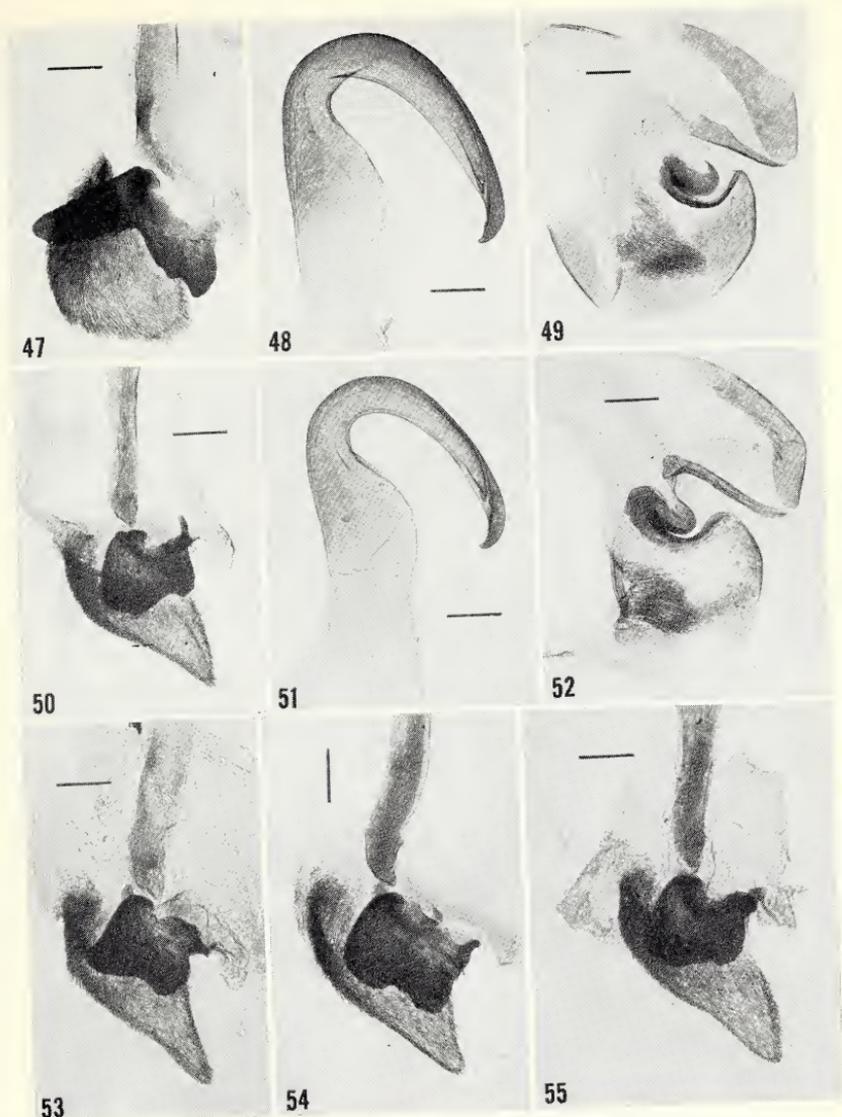
[*Epilampra abdomennigrum* (De Geer) (Figs. 50-55); *E. maya* Rehn (Figs. 47-49); *E. sagitta* Hebard (Figs. 59-67); *E. taira* Hebard (Figs. 56-58); *E. grisea* (De Geer) (Figs. 68-96); *E. jorgenseni* (Rehn) (Figs. 97-113); *E. berlandi* Hebard (Figs. 114-117); *E. guianae* Hebard (Figs. 119-127)].

In this group L2d is a thick, black, variably shaped sclerite, which lies above the prepuce. The presence of a setal brush on L1 distinguishes it from the following *Burmeisteri* Group. The size of the setal brush is inter- and intraspecifically variable and sometimes the area covered by the setae is small, or the setae are lightly sclerotized (Figs. 58, 99) and difficult to see. The hook (R2) has a subapical incision in all the species listed in this Group.

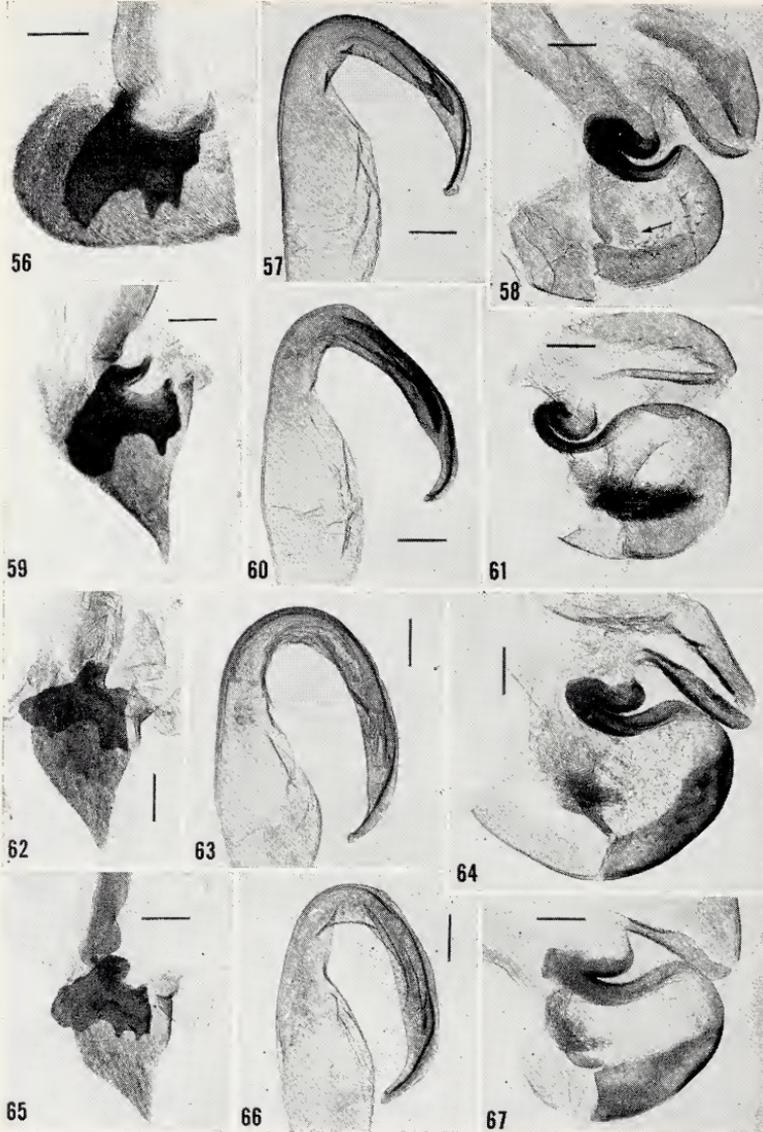
*Epilampra maya* (Figs. 47-49), until recently considered a synonym of *E. abdomennigrum* (Figs. 50-55), was shown to be a valid species by Roth and Gurney (1969). They illustrated the genitalia of a large number of individuals of both species to show the extent of variation which occurs in the phallomeres. *Epilampra abdomennigrum* is found in South America, Trinidad, and the West Indian Islands of Grenada and St. Lucia, but whether it occurred in Puerto Rico was uncertain (Roth and Gurney, 1969). The Puerto Rican record reported here (Figs. 50-52) suggests that Rehn and Hebard (1927, p. 228) were probably correct in regarding Sein's (1923) record of *wheeleri* in Puerto Rico as actually being *abdomennigrum*. *Epilampra maya* occurs in Central America and Mexico. The male taken in Boston Quarantine (Figs. 47-49) had Jamaica as the locality but it is possible that the specimen boarded ship in a Central American port.

Rehn (1902) stated that *E. maya* is closely related to *E. conspersa* and *E. azteca* and that it is separated from the latter by the shape of the supraanal plate. *E. maya* is very close to *abdomennigrum* with which it has been confused, and the genitalia of *azteca* (Figs. 247-249) are decidedly different and I have placed it in the *Burmeisteri* Group.

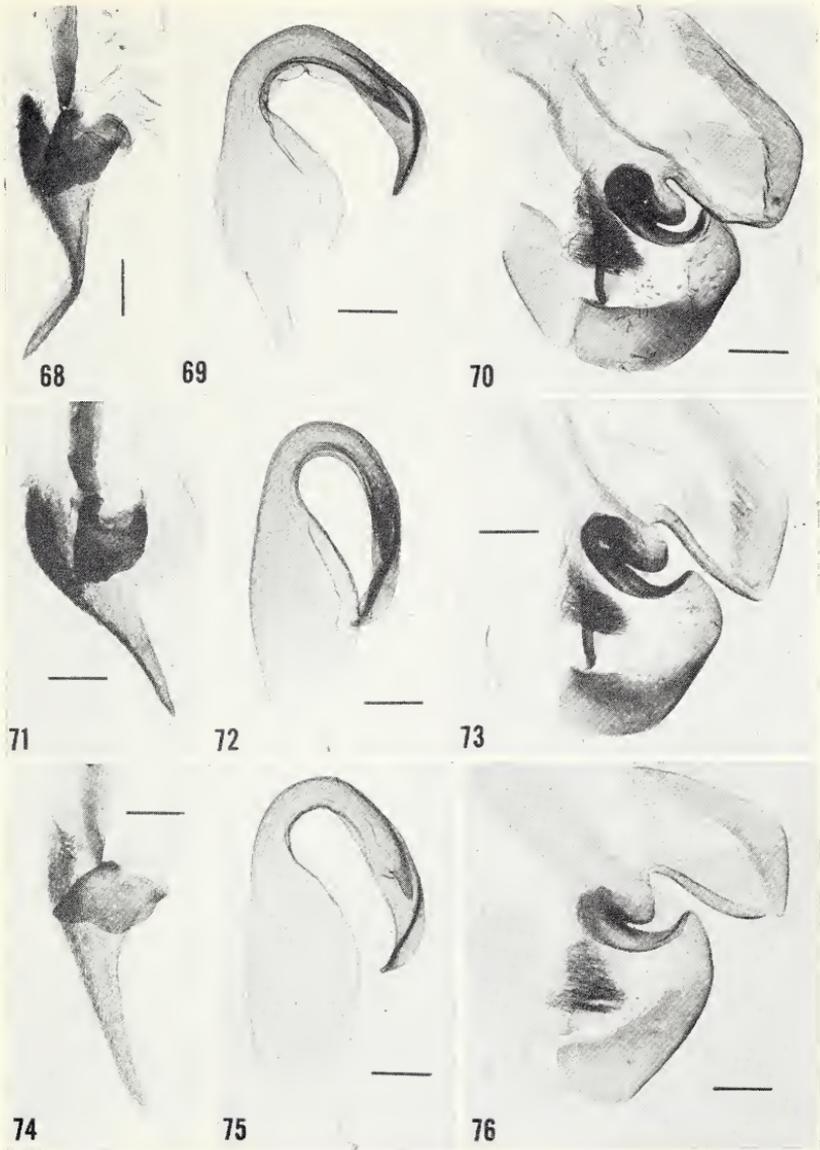
Hebard (1929, p. 366) stated that *E. sagitta* is near (by markings) *E. columbiana* and *E. opaca*. However, the shape of L2d and prepuce of *sagitta* (Figs. 59, 62, 65) appear to be closer to those of *abdomennigrum* (Figs. 50, 53-55) than to *columbiana* (Figs. 208-219) and



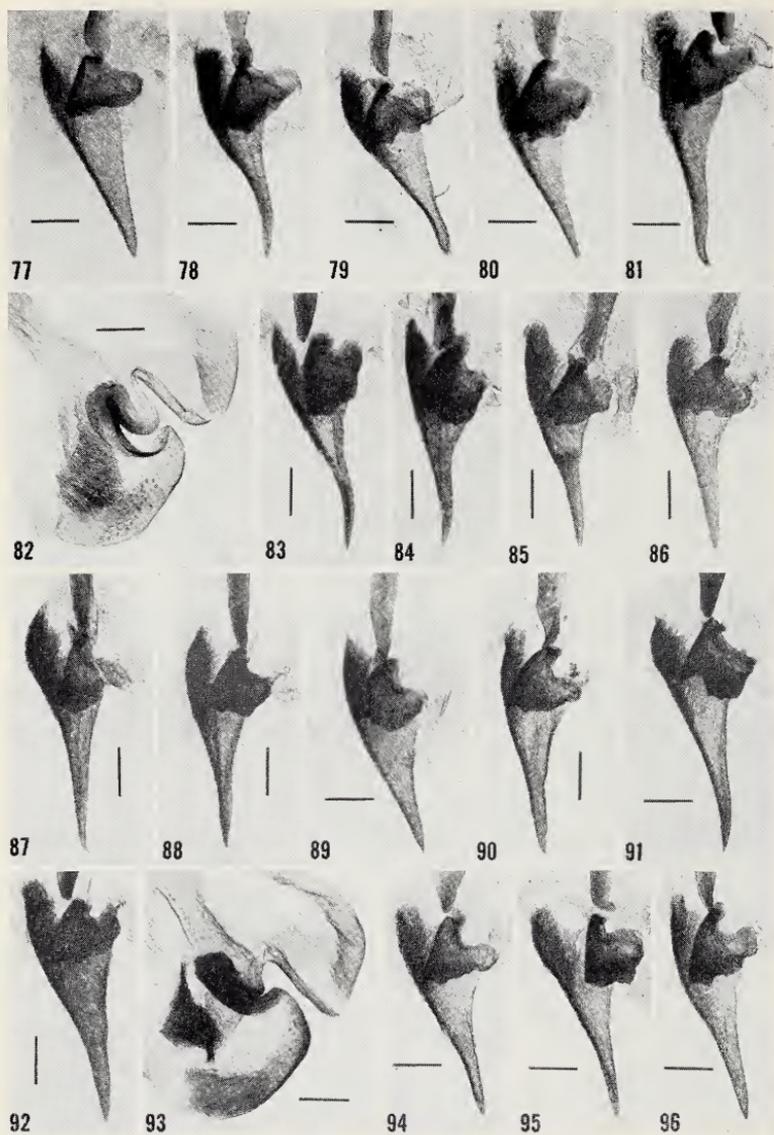
Figs. 47-55. Cockroach male genitalia. 47-49. (158 USNM). *Epilampra maya*. Boston Quarantine (det. Roth). 50-55. *Epilampra abdomennigrum*. 50-52. (101 USNM). Puerto Rico (det. Roth). 53. (71 MCZ). British Guiana. 54. (163 USNM). Essequibo River, British Guiana (det. Roth). 55. Le Moule, Guadeloupe (det. Bonfils). (scale = 0.2 mm)



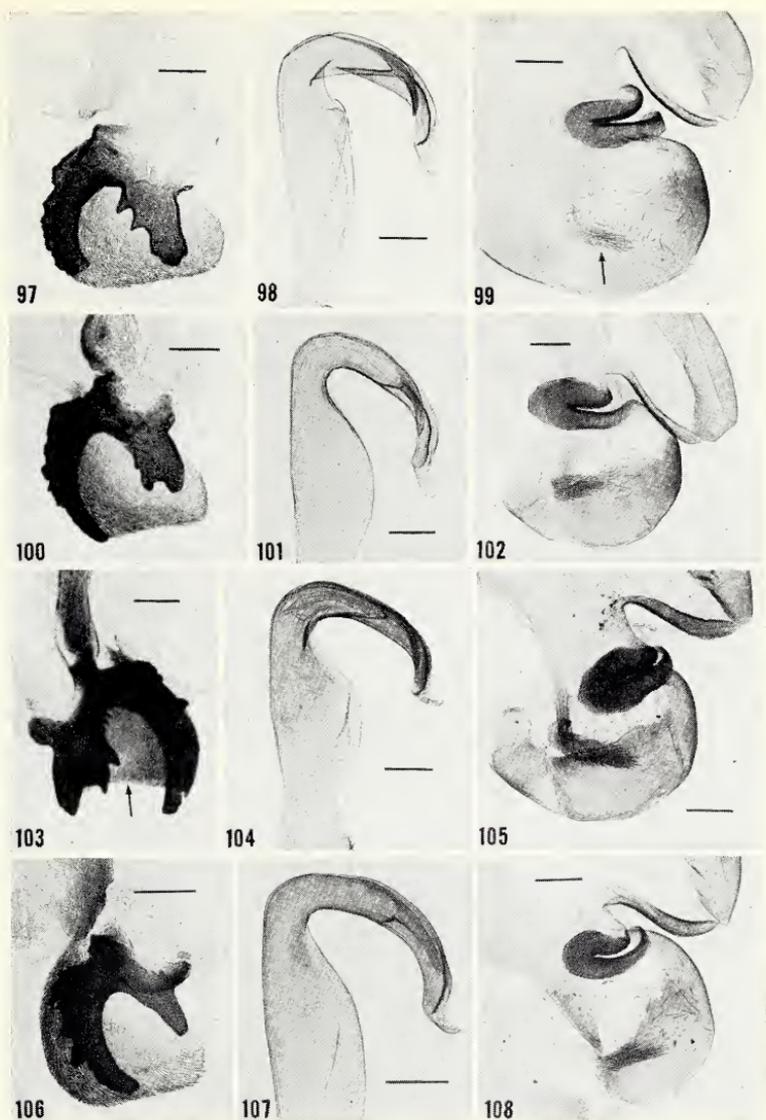
Figs. 56-67. Cockroach male genitalia. 56-58. (83 USNM). *Epilampra taira*. Surinam (det. Gurney) (arrow in 58 indicates setal brush). 59-67. *Epilampra sagitta*. 59-61. (74 USNM). Amapá, Brazil (det. Albuquerque; confirmed by Princis). 62-64. (182 ANSP). Type 1135. Teffe, Amazonas, Brazil. 65-67. (N). Flores, Manaus, Brazil (det. Roth). (scale = 0.2 mm)



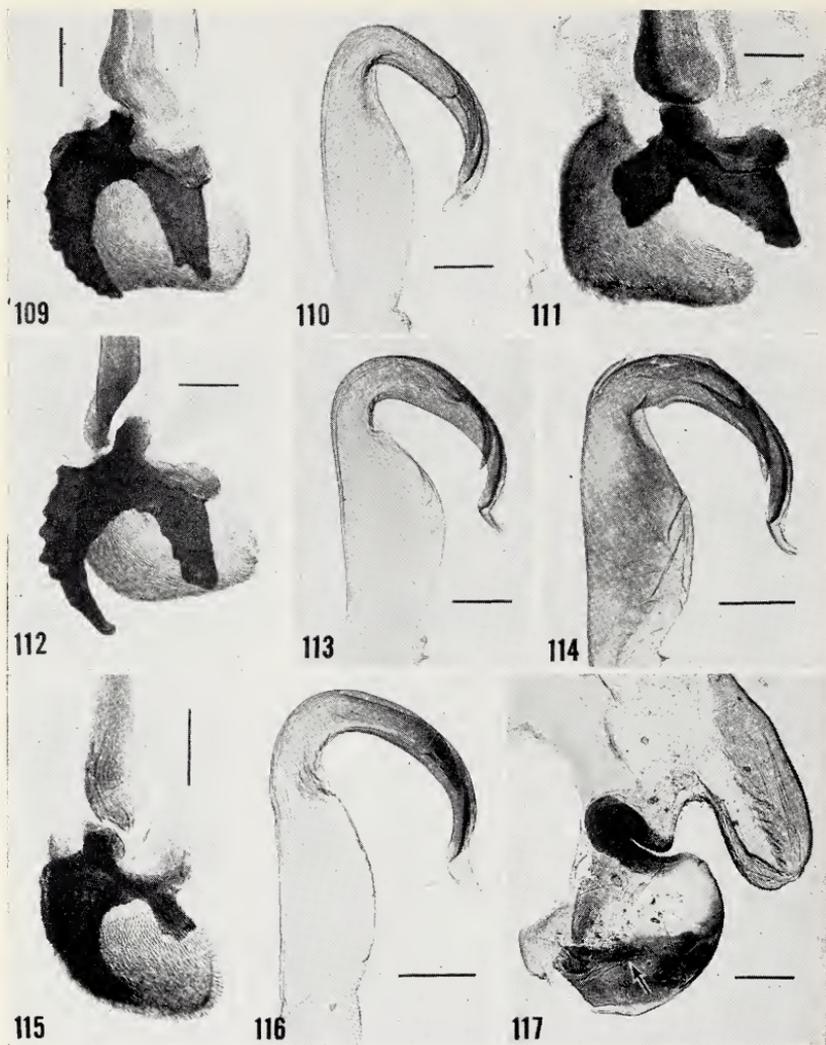
Figs. 68-76. Cockroach male genitalia. *Epilampra grisea*. 68-70. (42 ANSP). Bartica, British Guiana (det. Hebard). 71-73. (34 AMNH). Surinam (labeled *E. lucifuga* Rehn, a synonym of *grisea*). 74-76. (157 USNM). Rosario, Lake Rogagua, Bolivia (det. Roth). (scale = 0.2 mm)



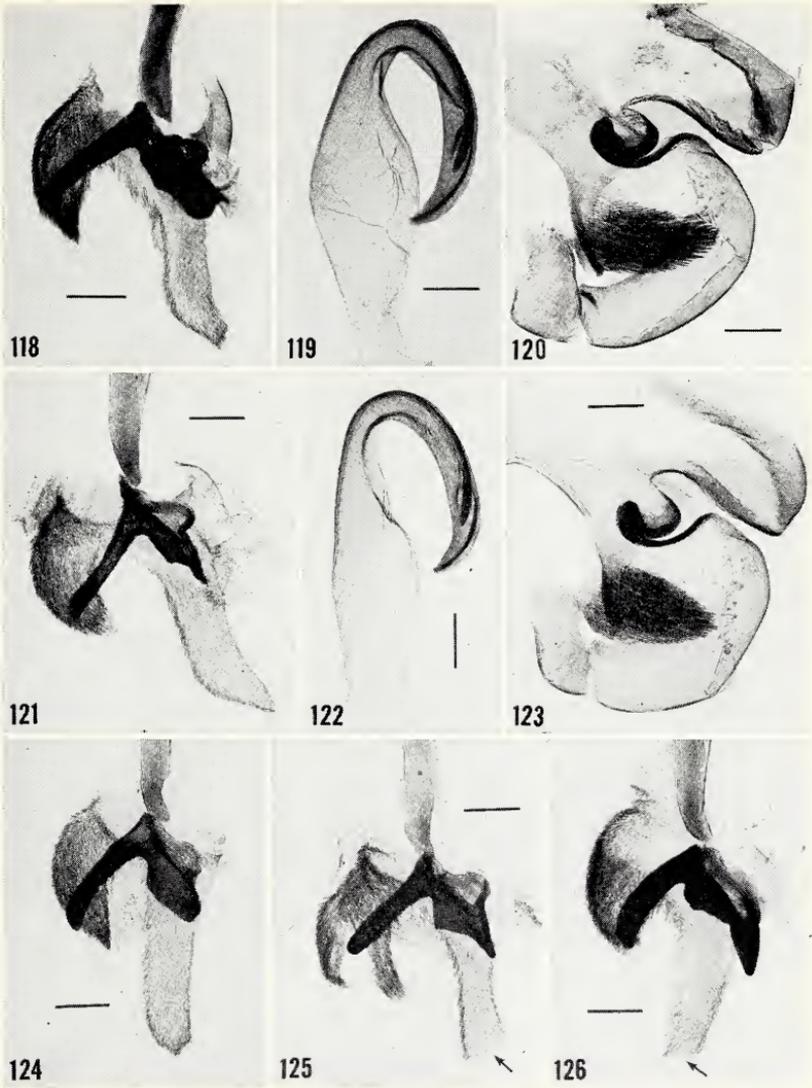
Figs. 77-96. Cockroach male genitalia. *Epilampra grisea*. 77. (169 USNM). Trinidad, British West Indies. 78. (93 USNM). Lelydorp, Sumatraweg, Surinam. 79. (94 USNM). Surinam. 80. (96 USNM). Popogaimama Creek, Surinam. 81-82. (156 USNM). Blancaflor, Beni, Bolivia. 83-93. (N). 83-85. Flores, Manaus, Brazil. 86. Adolpho Ducke Forestry Preserve, about 60 Km. from Manaus, Brazil. 87. Puraquequara, Rio Negro, Amazonas, Brazil. 88-89. Moura, Rio Negro, Amazonas, Brazil. 90-93. Tapurucuara, Rio Negro, Amazonas, Brazil. 94. (107 USNM). 95. (108 USNM). At Plant Quarantine, Miami, Florida; with some bromeliads, possibly from Peru. 96. (65 USNM). At Miami, in plane, probably from South America. (all det. Roth). (scale = 0.2 mm)



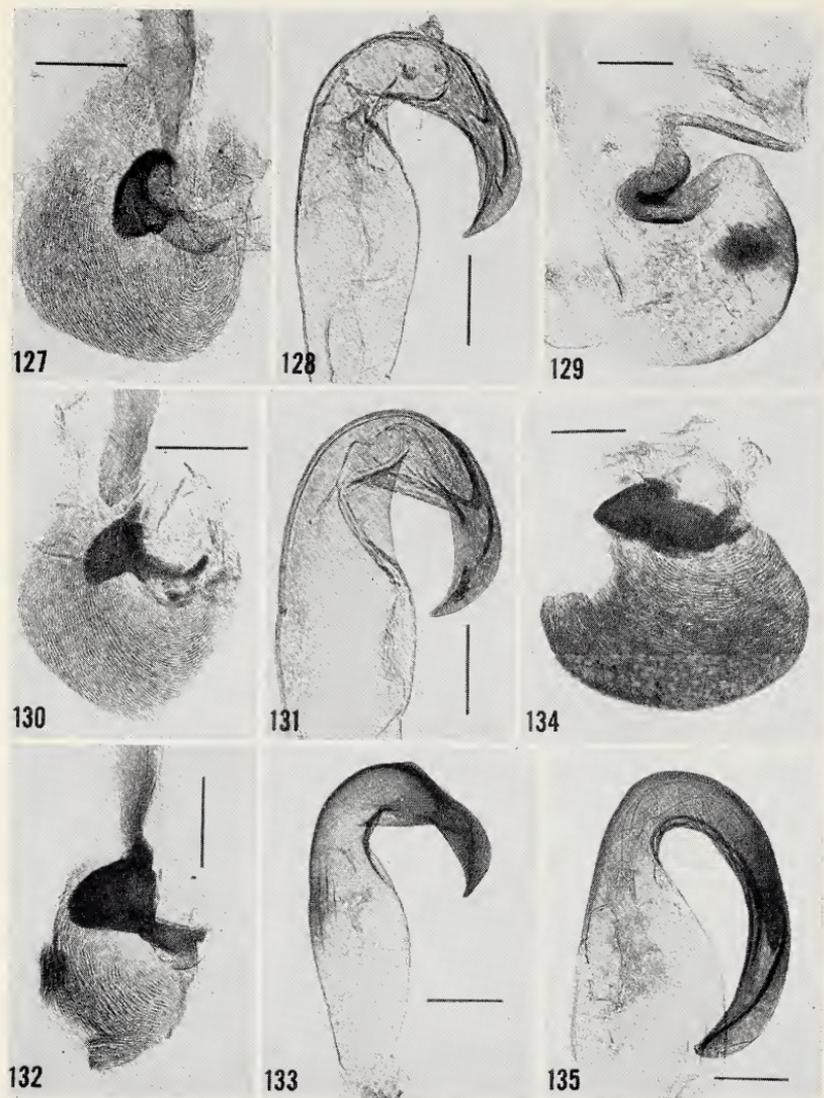
Figs. 97-108. Cockroach male genitalia. *Epilampra jorgensei*. 97-105. Paratypes of *Epilampra stigmatiphora* Rehn (= *E. jorgensei*). Misiones, Argentina. 97-99. (86 ANSP). (arrow in 100 indicates setal brush). 100-102. (96 ANSP). 103-105. (48 ANSP). (Fig. 103 is a ventral view; part of the prepuce (arrow) in this specimen is missing). 106-109. (164 USNM). Between Coronel Oveido and Asuncion, Paraguay (det. Roth). (scale = 0.2 mm)



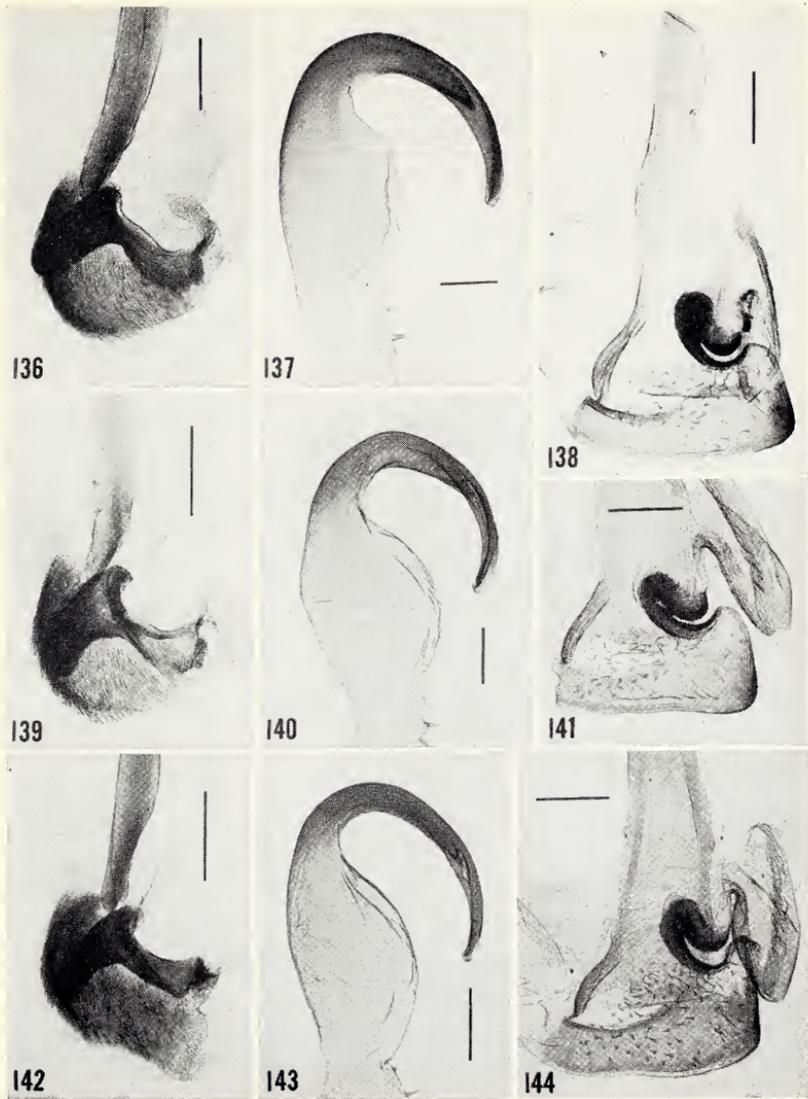
Figs. 109-117. Cockroach male genitalia. 109-113. *Epilampra jorgenseni*. 109-110. (94 ANSP). Paratype of *Epilampra stigmatiphora* Rehn (= *E. jorgenseni*). Misiones, Argentina. 111. (95 ANSP). Misiones, Argentina (det. Rehn). 112-113. (81 ANSP). same data as figs. 109-110. 114-117. *Epilampra berlandi*. 114. (47 ANSP). Provincia Sara, Bolivia (det. Hebard). 115-117. (83 ANSP). Paratype. Icaño, Santiago del Estero, Argentina. (arrow in 117 indicates setal brush). (scale = 0.2 mm)



Figs. 118-126. Cockroach male genitalia. *Eplampra guianae*. 118-120. (35 ANSP). Paratype. Rockstone, British Guiana. 121-123. (91 USNM). Surinam. 124. (90 USNM). 125. (89 USNM). Brokopondo, Surinam. 126. (92 USNM). Surinam. (tips of prepuce (arrows) in figures 125 and 126 missing). (121-126, det. Roth). (scale = 0.2 mm)



Figs. 127-135. Cockroach male genitalia. 127-133. *Epilampra burmeisteri*. 127-129. (26 MCZ). Cuba (labeled *E. carai-bea* S. and Z., which is a synonym of *burmeisteri*). 130-131. (24 MCZ). Yunque de Baracoa, Oriente Province, Cuba (det. Gurney). 132-133. (39 ANSP). Cuba (det. Rehn). 134-135. (21 MCZ). *Epilampra tainana*. Mountains north of Imias, Oriente Province, Cuba (det. Gurney). The L1 of *tainana* was lost in preparation of the slide and the species is tentatively placed in the *Burmeisteri* Group; all other Cuban *Epilampra* belong to this Group. (scale = 0.2 mm)



Figs. 136-144. Cockroach male genitalia. *Epilampra quisquiana*. Paratypes. 136-138. (37 ANSP). 139-141. (84 ANSP). San Lorenzo, Province of Samaná, Dominican Republic, Hispaniola. 142-144. (82 ANSP). San Francisco Mountains, Province of Santo Domingo, Dominican Republic. (scale = 0.2 mm)

*opaca* (Figs. 178-195) which I place in the *Burmeisteri* Group because of the absence of a setal brush on L1.

The prepuce of *E. taira* (Fig. 56) is relatively broad and extends well beyond the margins of the L2d. These structures resemble those of *E. opaca* but the right side of the prepuce of *opaca* is more extended and pointed (Fig. 178).

The prepuce of *E. grisea* is greatly elongated, tapers to a point posteriorly, and shows remarkably little variation (Figs. 68, 71, 74, 77-81, 83-92, 94-96) over a wide geographical range. Based on Princis' (1967) catalogue, new geographical records for this species are Bolivia (Figs. 74-76), Trinidad (Fig. 77), and possibly Peru (Fig. 95).

The L2d of *E. jorgenseni* is unusual in being very large and deeply indented. The left side of the L2d tends to follow the contour of the underlying prepuce (Figs. 97, 100, 103, 106, 109, 112). One of the specimens (det. Rehn) apparently has an aberrant shaped L2d (Fig. 111). The genitalia of *E. berlandi* (Figs. 115-117) are very similar to those of *jorgenseni* and support Hebard's (1921, p. 283) claim that the two species are closely related. The Paraguayan record for *jorgenseni* (Figs. 106-108) is new.

The prepuce of *E. guianae* is unique for this group, and is deeply notched (Figs. 118, 121, 124-126); in this respect the prepuce is reminiscent of that of *mexicana* (Figs. 2, 5, 8, 10-12), though the general shape is different between these 2 species. The prepuce of one unusual specimen of *guianae* has 2 indentations in the prepuce (Figs. 125).

#### *Burmeisteri* Group

[*Epilampra burmeisteri* (Guérin) (Figs. 127-133); *E. tainana* Rehn and Hebard (Figs. 134-135); *E. quisqueiana* Rehn (Figs. 136-144); *E. sabulosa* Walker (Figs. 145-150); *E. wheeleri* Rehn (Figs. 151-156); *E. gundlachi* Rehn and Hebard (Figs. 157-162); *E. haitensis* Rehn and Hebard (Figs. 163-165); *E. hamiltoni* (Rehn) (Figs. 166-168); *E. bromeliadarum* (Caudell) (Figs. 169-171); *E. exploratrix* (Gurney) (Figs. 359-361); *E. gatunae* (Hebard) (Figs. 172-174); *E. fugax* (Bonfils) (Figs. 175-177); *E. opaca* (Walker) (Figs. 178-195); *E. substrigata* Walker (Figs. 196-207); *E. columbiana* Saussure (Figs. 208-219); *E. latifrons* Saussure and Zehntner (Figs. 299-301); *E. basistriga* Walker (Figs. 220-228); *E. thunbergi* Princis (Figs. 238-243); *E. castanea* Brunner (Figs. 244-246); *E. azteca* Saussure (Figs. 247-280); *E. crossea* Saussure (Figs. 293-298)].

This Group is essentially similar to the *Abdomennigrum* Group

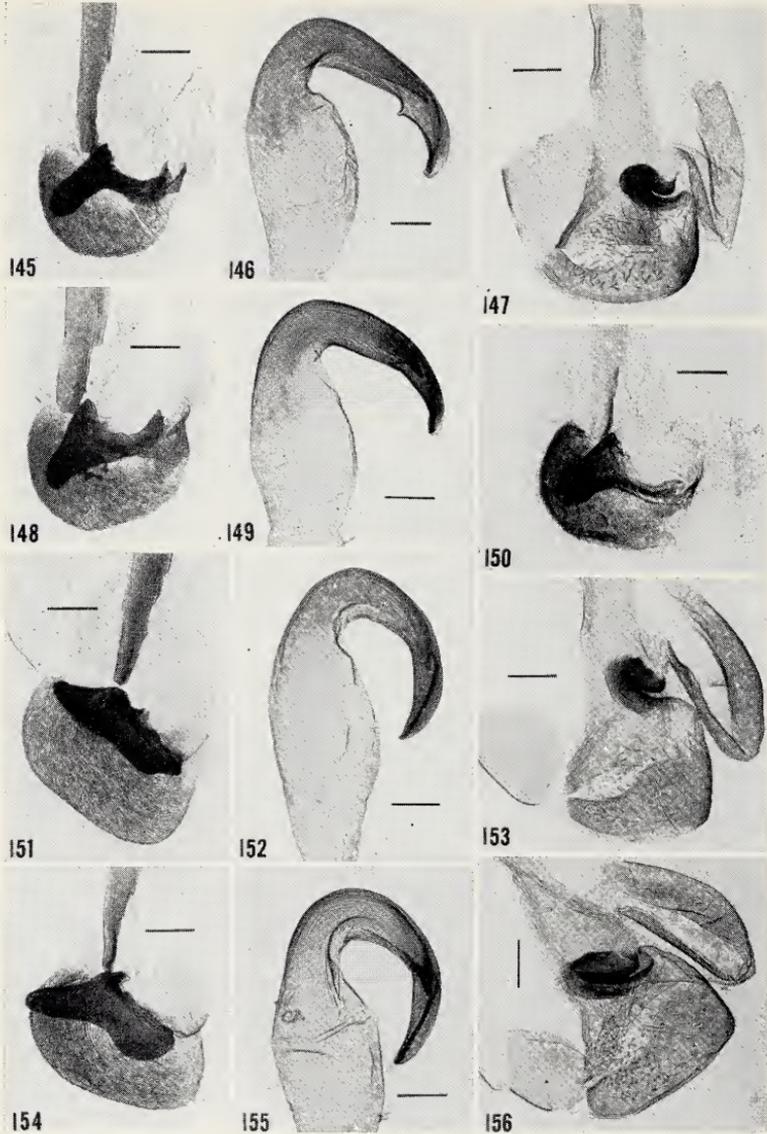
but is separated from it by the absence of a setal brush on L1. R2 usually has a subapical incision but a few species lack this character. The prepuce is usually well defined but in a few species it is markedly reduced.

The *Burmeisteri* Group includes the largest number of species of *Epilampra* and may be further divided into subgroups based on the relative sizes, shapes, and extent of development of L2d and the prepuce. Although not all of the species will fit readily into the following subgroups many of them do show a close relationship and I believe an attempt at sub-divisions is worthwhile.

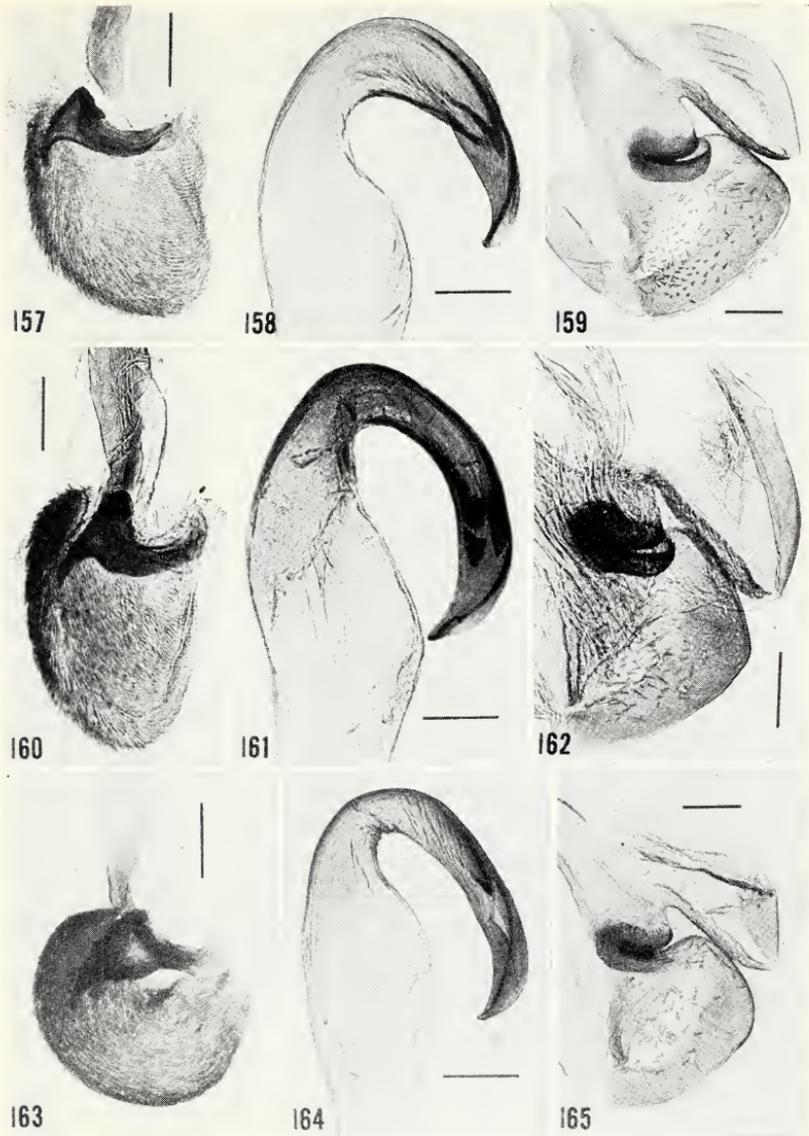
Subgroup A: (*burmeisteri*, *tainana*, *quisqueiana*, *sabulosa*, *wheeleri*, *gundlachi*, *haitensis*, *hamiltoni*, *bromeliadarum*, *gatunae*, *fugax*): In this subgroup the area of L2d is relatively small in relation to, and covers only a small anterior part of the prepuce. In *burmeisteri* (Figs. 127, 130, 132), *quisqueiana* (Figs. 136, 139, 142), and *sabulosa* (Figs. 145, 148, 150) the L2d is roughly divided in 2 parts, the left half usually being larger and sometimes more darkly pigmented than the right half. Rehn and Hebard (1927, p. 233) compared *quisqueiana* with *grisea* and *substrigata*. The prepuce and L2d of *quisqueiana* are closest to *sabulosa* and differ noticeably from those of *substrigata* (Subgroup B, Figs. 196, 199, 202-203, 205-206) and *grisea* (*Abdomennigrum* Group, Figs. 68, 71, 74).

*Epilampra gundlachi* has been confused with *burmeisteri* (Rehn and Hebard, 1927, p. 223), but the male genitalia of these 2 species are distinctive (cf. Figs. 157-159 and 127-129). According to Rehn and Hebard (1927, p. 228), the nearest relative of *haitensis* is *wheeleri*. However, the L2d of *haitensis* (Fig. 163) is closer to *gundlachi* (Figs. 157, 160) than it is to *wheeleri* (Figs. 151, 154); note the pointed spur on the left side of L2d in *gundlachi* and *haitensis*, and its absence in *wheeleri*.

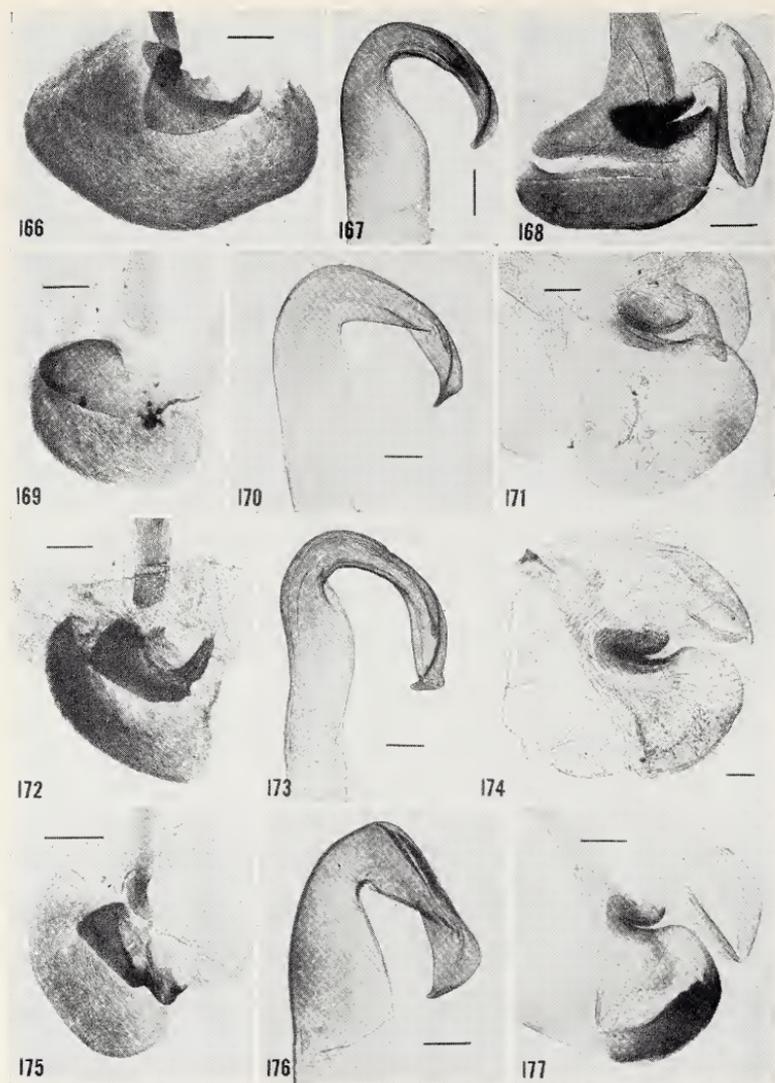
For almost 50 years the status of the genus *Audreia* Shelford has been in question. Hebard (1920, p. 92-93) stated "First steps only have as yet been taken to separate properly the generic units related to *Epilampra*, in which partial to complete reduction in organs of flight has occurred. At the present time, as was the case with Shelford in 1910, insufficient material is at hand to allow a proper revision to be made. A number of species are before us which must be assigned to this genus as characterized by Shelford, but which indicate the presence of at least four distinct groups, though females alone of the majority of species are represented. Larger series and male examples will be needed before it can be determined whether these



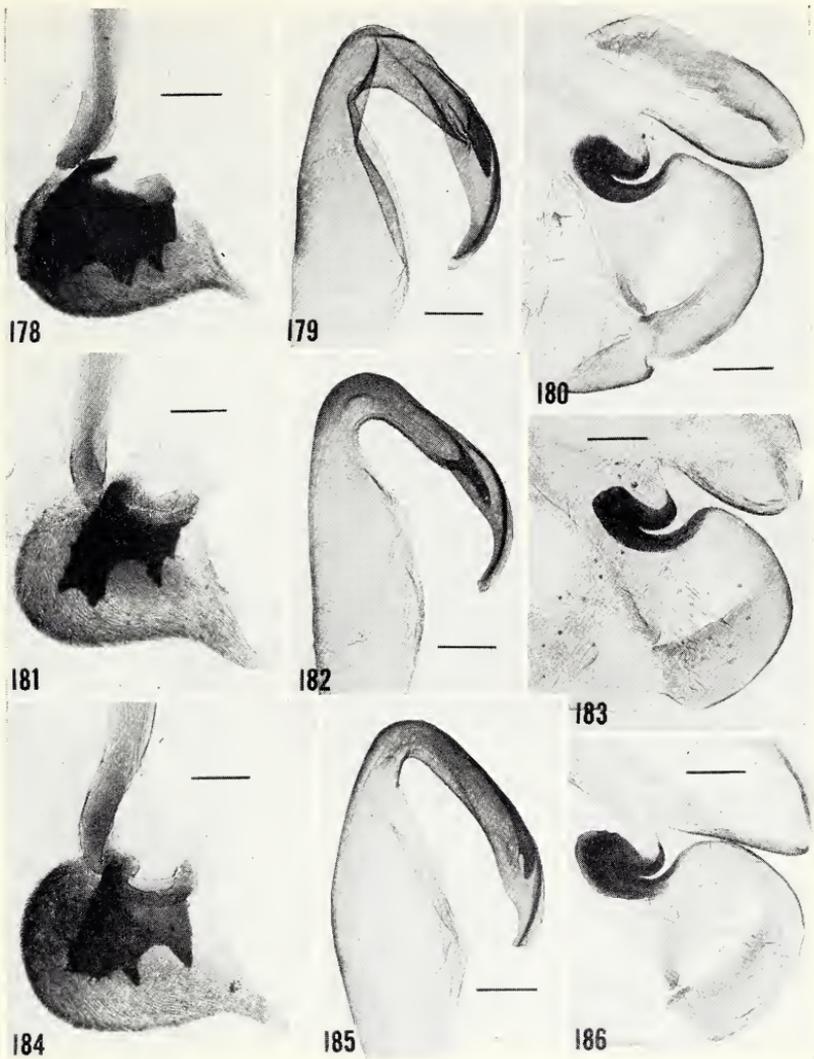
Figs. 145-156. Cockroach male genitalia. 145-150. *Epilampra sabulosa*. 145-147. (33 AMNH). La Moriniere, Haiti (det. Rehn). 148-149. (53 ANSP). Bourdon, Haiti (det. Rehn). 150. (149 ANSP). Porto Prince, Haiti. 151-156. *Epilampra wheeleri*. 151-153. (32 AMNH). Adjuntas, Porto Rico (det. Rehn; from specimen shown in figure 8 in Rehn and Hebard, 1927). 154-156. (102 USNM). El Yunque, Porto Rico (det. Roth). (scale = 0.2 mm)



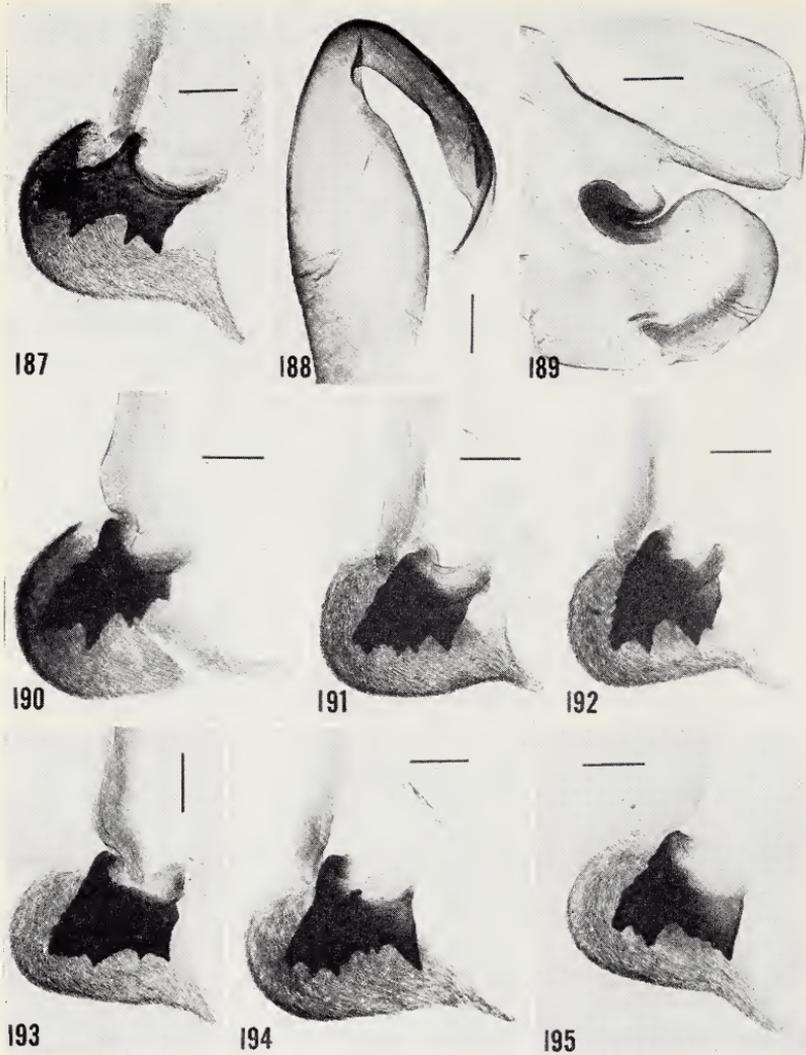
Figs. 157-165. Cockroach male genitalia. 157-162. *Epilampra gundlachi*. 157-159. (97 USNM). Cayamas, Cuba (det. Hebard). 160-162. (23 MCZ). Mountains north of Imias, Oriente Province, Cuba (det. Gurney). 163-165. (69 USNM). *Epilampra haitensis*. Port-au-Prince, Haiti (det. Albuquerque). (scale = 0.2 mm)



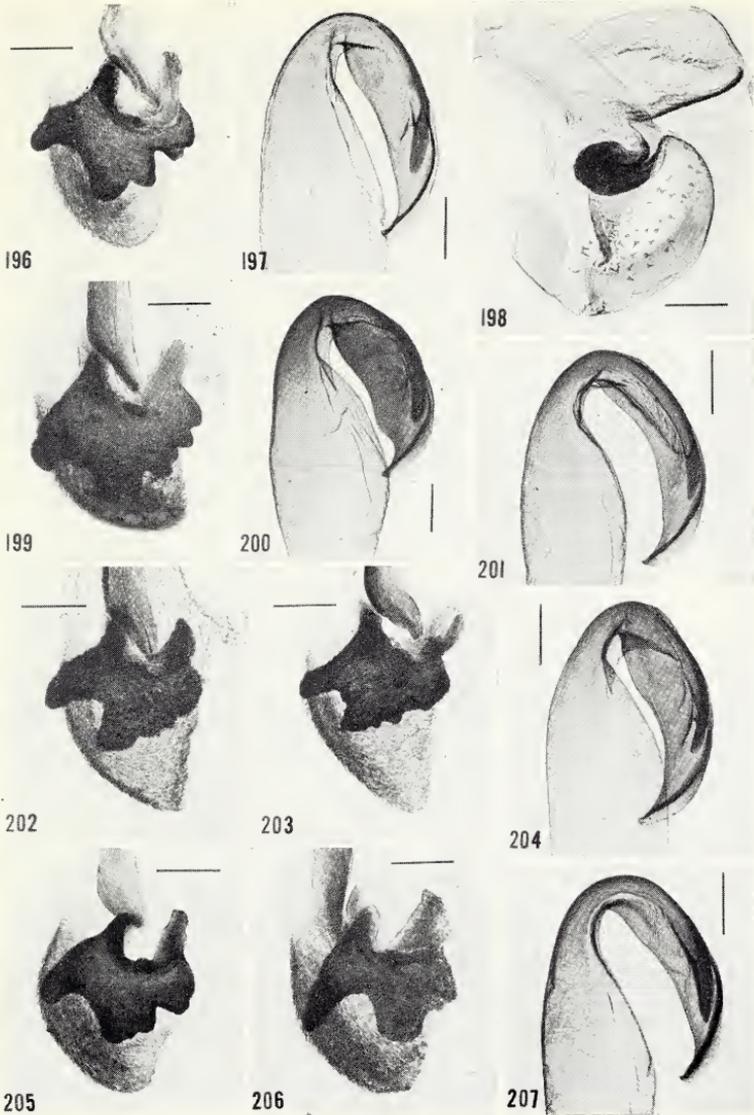
Figs. 166-177. Cockroach male genitalia. 166-168. (175 USNM). *Epilampra hamiltoni*. Pico, Turquino, Cuba (det. Gurney). 169-171. *Epilampra bromeladarum*. Panama. (det. Huber). 172-174. (184 USNM). *Epilampra gatunae*. Pozo Azul, San José, Costa Rica (det. Gurney). 175-177. *Epilampra fugax*. Paratype of *Audreia fugax* Bonfils. Saint Francoise Anse-a l'Eau, Guadeloupe. (scale = 0.2 mm)



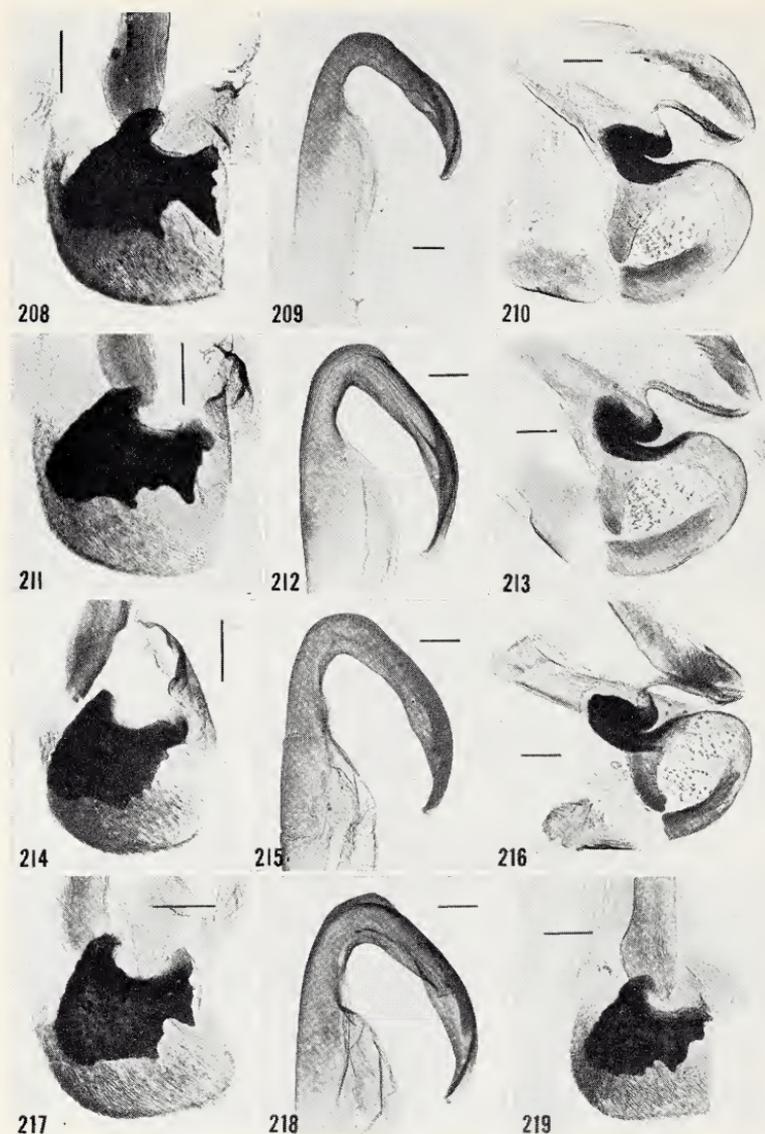
Figs. 178-186. Cockroach male genitalia. *Epilampra opaca*. 178-180. (38 ANSP). St. Jean du Maroni, French Guiana (det. Hebard). 181-183. (17 CUZM). Essequibo, British Guiana (det. Princis). 184-186. (80 USNM). Amapá, Brazil (det. as near *berlandi* by Albuquerque, and as *sagitta* by Princis). (scale = 0.2 mm)



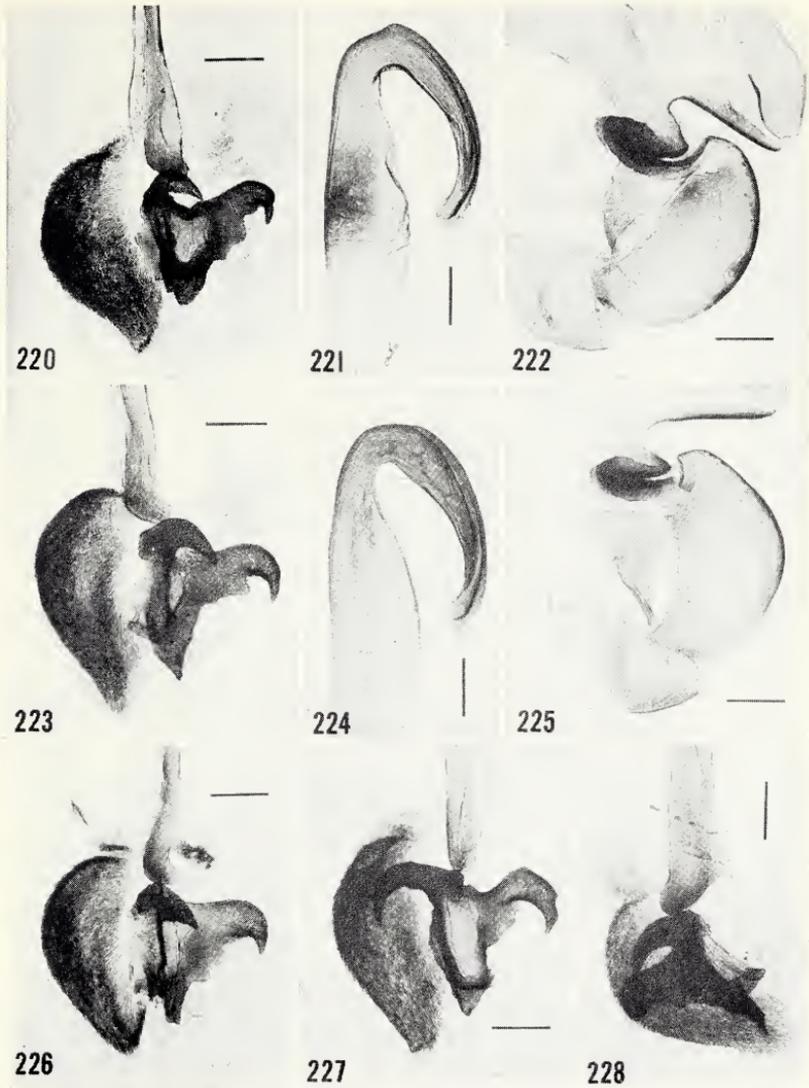
Figs. 187-195. Cockroach male genitalia. *Epilampra opaca*. 187-189. (70 USNM). Amapá, Brazil (det. as near *berlandi* by Albuquerque). 190. (88 USNM). Brownsberg, Wakti-basoe Creek, Surinam (det. as *sagitta* by Princis). 191-193. (125, 127, and 126 USNM). Napa Santa Cecilia, Rio Aguarico, Ecuador. 194-195. (89 and 87 ANSP). Provincia Sara, Dept. Santa Cruz, Bolivia, (all det. Roth). (scale = 0.2 mm)



Figs. 196-207. Cockroach male genitalia. *Epilampra substrigata*. 196-198. (129 USNM). Napo Santa Cecilia, Rio Aguarico, Ecuador (det. Roth). 199-200. (46 ANSP). Villavicencio, Colombia (det. Hebard). 201-202. (68 USNM). Anabern, Colombia (det. Albuquerque). 203-204. (71 USNM). Territ. Amazonas, San Fdo. Atabapo, Venezuela (det. Albuquerque). 205. (128 USNM). Napo Santa Cecilia, Rio Aguarico, Ecuador. (det. Princis). 206-207. (79 USNM). Territ. Amapá, Brazil (det. Albuquerque). (scale = 0.2 mm)



Figs. 208-219. Cockroach male genitalia. *Epilampra columbiana*. 208-210. (49 ANSP). 211-213. (138 USNM). Barro Colorado Island, Panama (det. Roth). 214-216. (98 USNM). Sierra Campana, Panama (det. Gurney). 217-218. (137 USNM). Barro Colorado Island, Panama (det. Roth). 219. (154 USNM). La Campana, Panama (det. Roth). (scale = 0.2 mm)



Figs. 220-228. Cockroach male genitalia. *Epilampra basistriga*. 220-222. (78 USNM). Piracicaba, São Paulo, Brazil (det. Gurney). 223-225. (104 USNM). Brazil (det. Albuquerque). 226. (114 USNM). South of São Paulo, Brazil. 227. (90 ANSP). Guaraja, São Paulo, Brazil (det. by Hebard as *E. delicata* Hebard, a synonym of *basistriga*). 228. (77 USNM). Same locality as figures 220-222; L2d is turned on its side (det. Roth). (scale = 0.2 mm)

groups represent distinct genera, or are simply striking divisions in the genus *Audreia*, comparable to the many striking divisions in the genus *Epilampra* as at present defined. . . . Whether the tegmina and wings are reduced, truncate, lateral and lobiform, or absent, are features which in the Blattidae are known to be often utterly worthless from a generic standpoint. . . . Without the sexes of each species, we do not feel in a position to characterize *Audreia* more definitely than has been done in the meager description given by Shelford."

A few years later Rehn and Hebard (1927, p. 204) commented further on the genus *Audreia* stating that it ". . . is composed of a small number of species described from the tropics and subtropics of both hemispheres, the majority, however, tropical American. The species much resemble certain forms referred to the genus *Epilampra*, but all possess reduced or subquadrate tegmina in both sexes, these subquadrate or distally emarginate in most of the forms . . . . Until the genus *Epilampra* as a whole is critically studied, and our knowledge of the extent to which brachypterism occurs in that assemblage is more complete, it is unwise to do other than follow Shelford's use of the generic name *Audreia*. We can say, however, that the genus *Calolampra*, to which a number of the species now placed in the more recently described *Audreia* were originally referred, is well distinct from *Audreia* of Shelford. The West Indies possess two species which can logically be assigned to *Audreia*, one from higher mountains of eastern Cuba, the other from Blue Mountains of Jamaica. The possibility that these may be members of an ancient relic fauna forces itself upon one, although the converse argument that tegminal reduction has been brought about by adjustment to a peculiar and restricted montane environment cannot be ignored."

The male genitalia of *Calolampra carinulata* Saussure, the species which Hebard (1920, p. 92) selected as the type for the genus *Audreia* Shelford show 2 distinct differences from the genitalia of most species of *Epilampra*. The hooked right phallomere (Figs. 348, 351) lacks a subapical incision and is relatively stout. The hook from the specimen shown in Fig. 348 tends to resemble the hook of *E. sodalis* (Fig. 309) but is shorter. The L2d of *A. carinulata* (Figs. 347, 350) is a flattened sclerotization of the preputial membrane; the remainder of the prepuce is shapeless. In most *Epilampra*, the prepuce has a well defined shape and is densely covered by microtrichia. The L1 of *A. carinulata* lacks a setal brush (Figs. 349, 352).

The genitalia of 5 other species of *Audreia* (Figs. 166-177) differ from those of *A. carinulata*, and are similar to the genitalia of certain other species of *Epilampra*. Rehn and Hebard (1927, p. 205) stated

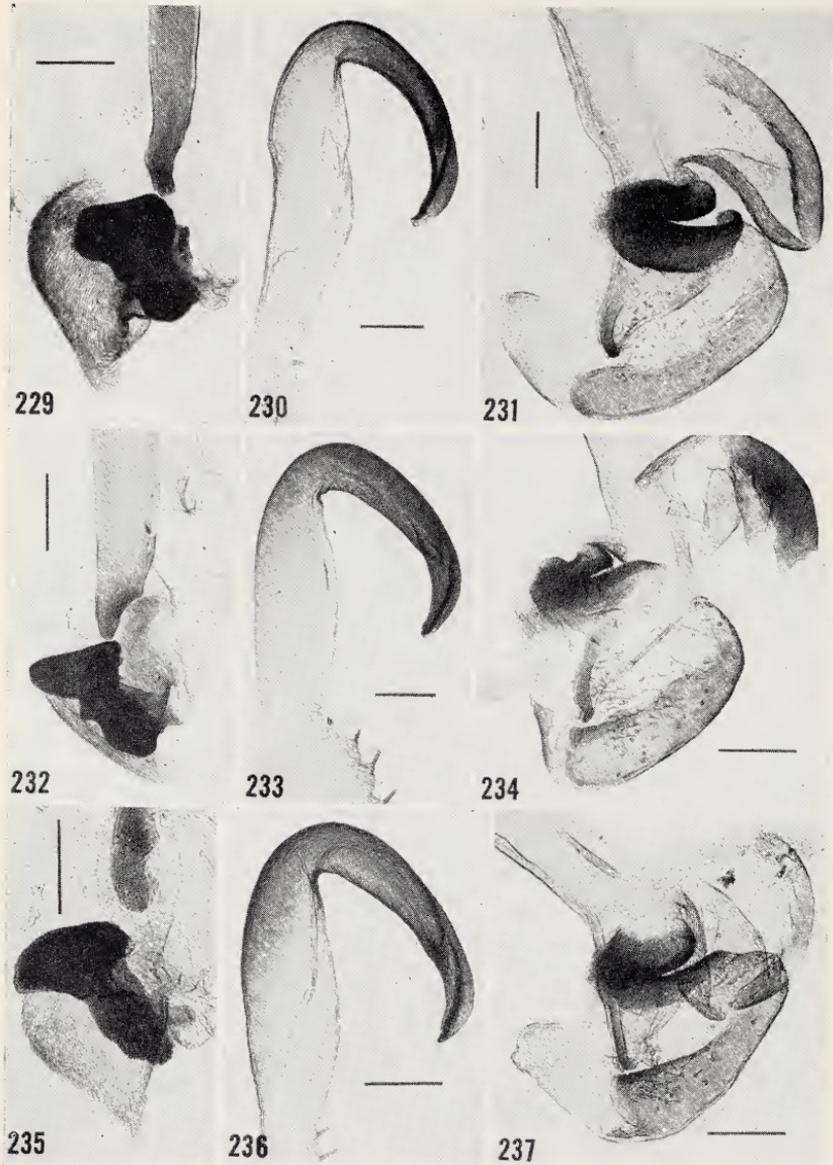
that *Audreia hamiltoni* “. . . is clearly congeneric with *carinulata* (Saussure) of Central America, the genotype, as selected by Hebard, although it has a number of features of difference.” However, the L2d and prepuce of *hamiltoni* (Fig. 166), *bromeliadarum* (Fig. 169), *gatunae* (Fig. 172), *fugax* (Fig. 175), and *exploratrix* (Fig. 359) are so typical of *Epilampra* that I assign them to this genus. The R2 of *fugax* (Fig. 176) lacks a subapical incision; this incision is present in the other 4 species of “*Audreia*” (Figs. 167, 170, 173, 360) but is much reduced in *bromeliadarum* (Fig. 170), *gatunae* (Fig. 173), and *exploratrix* (Fig. 360). The L1's (Figs. 168, 171, 174, 177, 361) of all 5 species lack a setal brush as do the other members of the *Burmeisteri* Group.

Princis (1967) lists 9 species of *Audreia*, two of which (*A. cicatricosa* Rehn, and *A. jamaicana* Rehn and Hebard) I have not seen. It is possible that these species are also *Epilampra*. Princis included *Epilampra heusseriana* under *Audreia* but its genitalia (Figs. 302-307) are basically those of *Epilampra* and I have placed it in a separate group (see below). The male of *Audreia catharina* Shelford has tergal glands on tergites 1 and 2. Its genitalia are basically similar to species of “*Epilampra*” that possess tergal glands and I placed it in the genus *Poeciloderrhis* (Roth 1970).

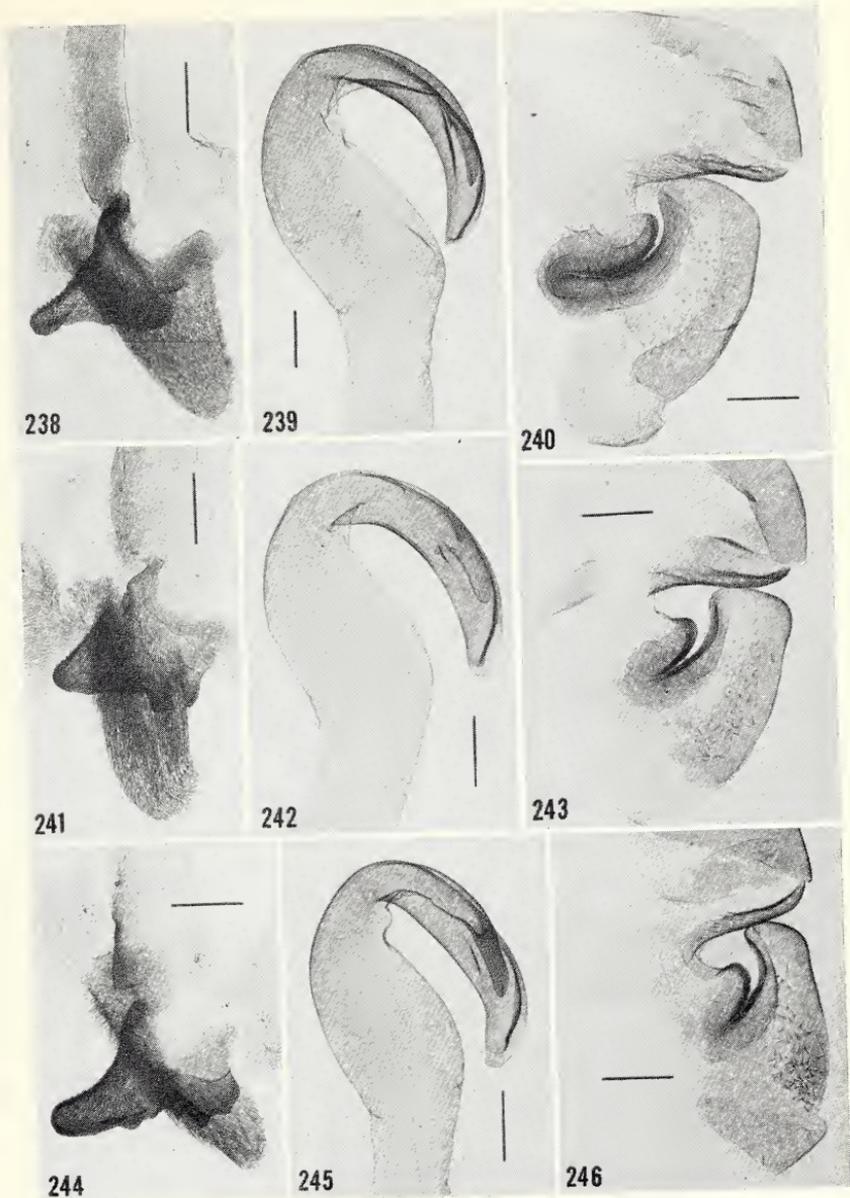
For the present I suggest that the genus *Audreia*, as represented by *carinulata*, be retained until a more detailed study is made of other morphological characters of this species.

Subgroup B: (*opaca*, *substrigata*, *columbiana*, *latifrons*, *basistriga*, *thunbergi*, *castanea*): The species in this subgroup have a relatively large L2d which overlies a considerable area of the prepuce.

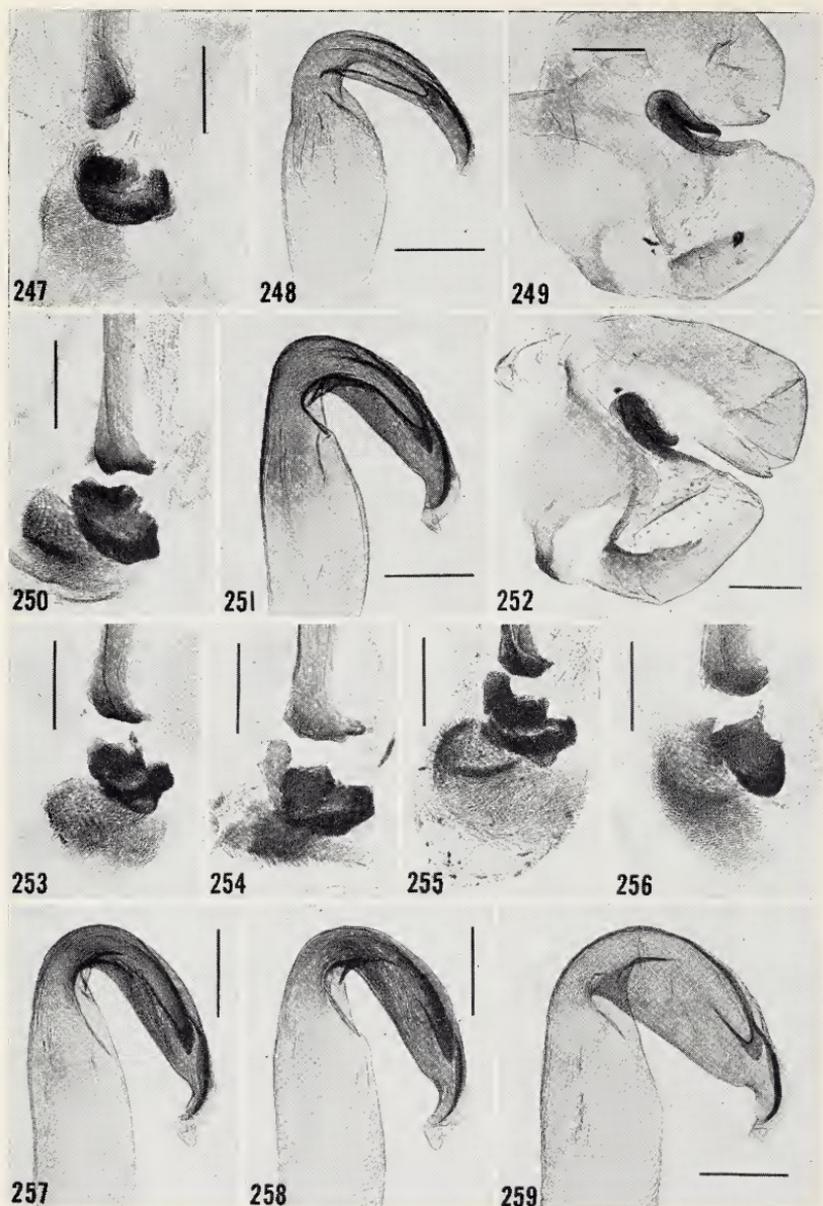
According to Princis (1958, p. 62) Walker's *E. opaca* is a synonym of his *E. substrigata*. Princis (personal communication) examined the types of *opaca* and *substrigata* “. . . and could not find any noteworthy differences. Hebard had never seen the types and he thought them to be two different species. I supposed that Hebard's records from French Guiana [*opaca*] could be correct, whereas his record of *substrigata* from Colombia evidently relates to another species. This was, however, a pure speculation of mine.” The genitalia of Hebard's *substrigata* from Colombia (Figs. 199-200) clearly differ from those of specimens he considered to be *opaca* from French Guiana (Figs. 178-180). Princis' *substrigata* (Fig. 205) is similar to Hebard's *substrigata* specimens (Fig. 199). The genitalia of a specimen from British Guiana at the CUZM, determined as *opaca* by Princis (probably before he considered it to be a synonym of *substrigata*) are similar (Figs. 181-183) to Hebard's *opaca* (Figs. 178-180).



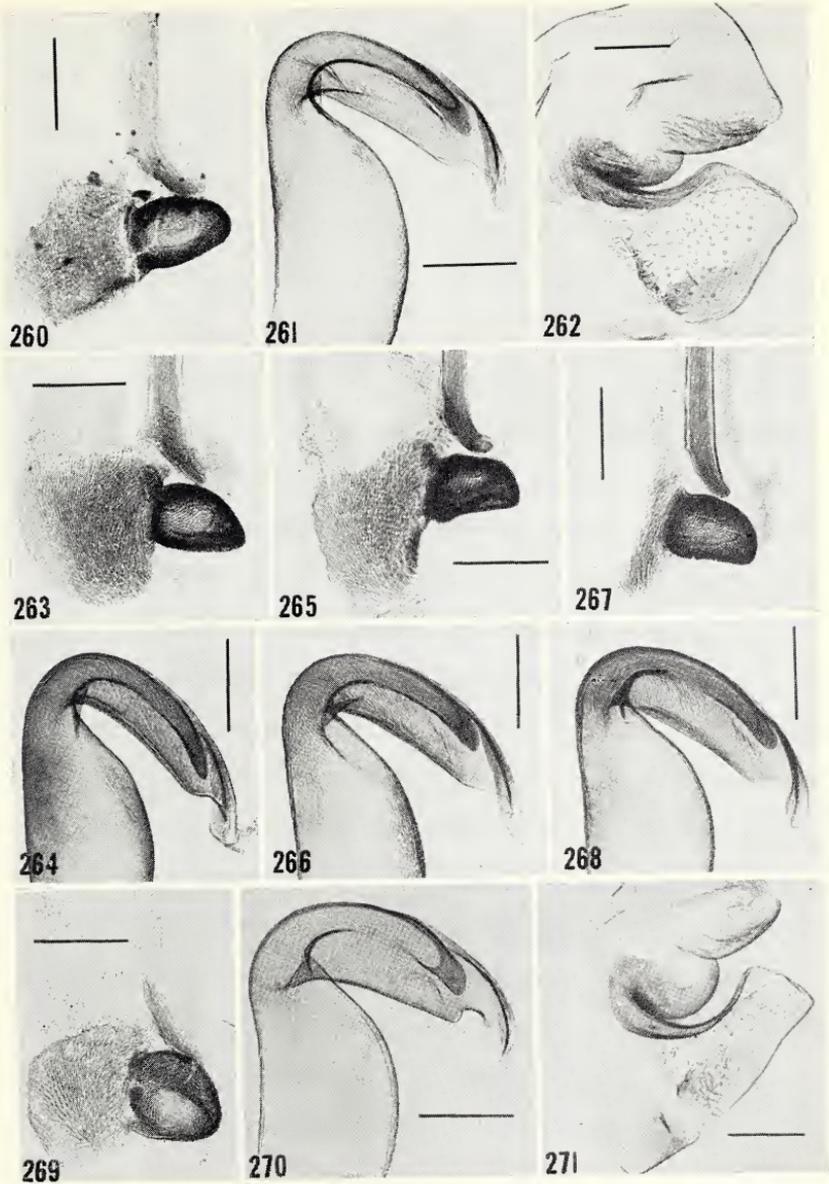
Figs. 229-237. Cockroach male genitalia. *Epilampra* sp. 229-231. (44 ANSP). Provincia Sara, Dep. Santa Cruz, Bolivia (det. as *E. conferta* by Hebard). 232-234. (43 ANSP). Parintins, Pará, Brazil (det. as *E. conferta* by Rehn). 235-237. (76 USNM). Serra do Navio, Territ. Amapá, Brazil (det. *E. conferta* by Albuquerque; recorded in Albuquerque and Gurney, 1962, p. 242). (see discussion on page 443). (scale = 0.2 mm)



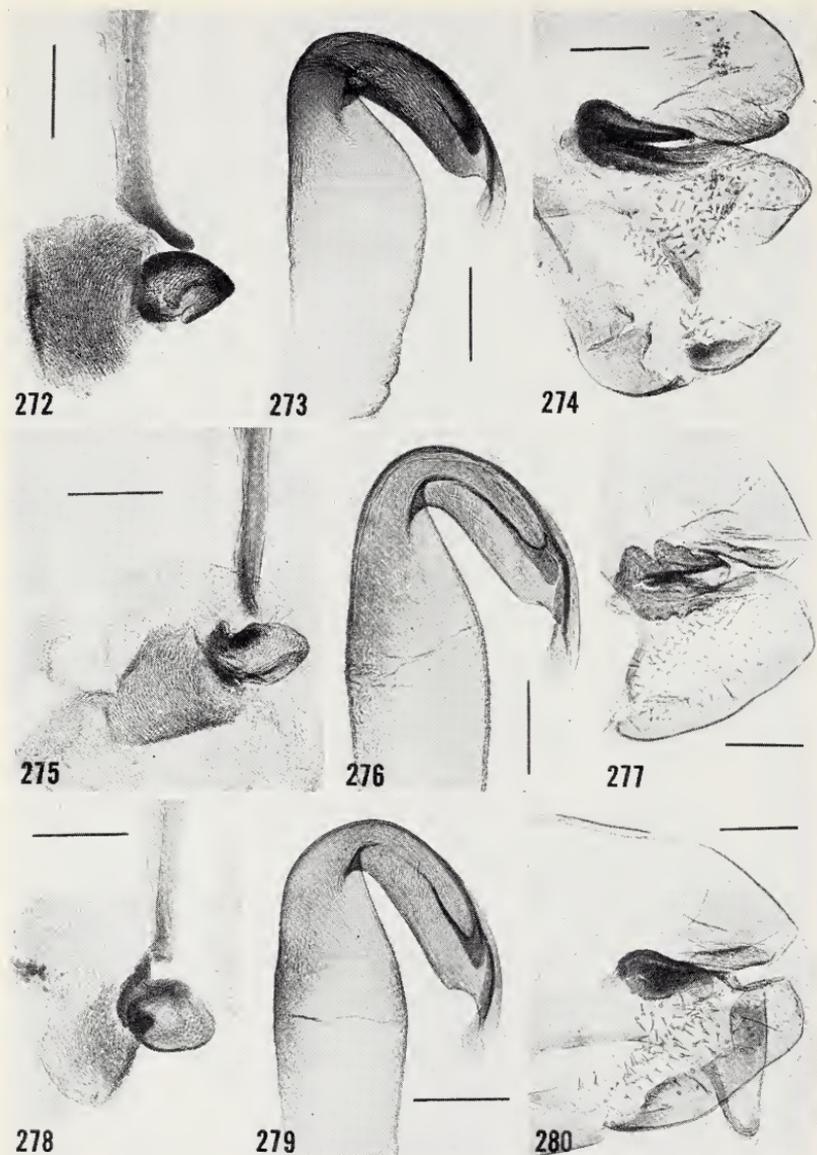
Figs. 238-246. Cockroach male genitalia. 238-240. (18 CUZM). *Epilampra thunbergi*. Rio de Janeiro, Brazil (det. Princis). 241-243. (11 BMNH). *E. thunbergi*. Theresopolis, Santa Catarina, Brazil (det. Princis; this specimen was determined as *E. testacea* Brunner by Hebard). 244-246. (18 BMNH). *Epilampra castanea* (det. Princis; this specimen was determined as "*Epilampra*" *puncticollis* Walker by Hanitsch). (scale = 0.2 mm)



Figs. 247-259. Cockroach male genitalia. *Epilampra azteca*. 247-249. (171 USNM). Palenque, Chiapas, Mexico (det. Roth). 250-252. (41 ANSP). Pozo Azul, Costa Rica (det. Hebard). 253-254. (141, 140 USNM). Barro Colorado Island, Panama (det. Roth). 255. (144 USNM). Cerro Campana, Panama (det. Roth). 256. (20 CUZM). Taboga, Panama (det. Princis). 257-259. (143, 142, 140 USNM). Barro Colorado Island, Panama (det. Roth). (scale = 0.2 mm)



Figs. 260-271. Cockroach male genitalia. *Epilampra azteca*. 260-262. (84 USNM). Wakti-basoe Creek, Brownsberg, Surinam. 263-264. (86 USNM). Phedra, Surinam. 265-266. (87 USNM). Same data as Figs. 260-262. 267-268. (85 USNM). Same data as Figs. 260-262. (260-268 det. Gurney). 269-271. (13 BMNH). Trinidad (very light specimen labeled "extreme recessive color"). (det. Hebard). (scale = 0.2 mm)



Figs. 272-280. Cockroach male genitalia. *Epilampra azteca*. 272-274. (75 USNM). Territory Amazonas, Mt. Marahuaca, Venezuela (det. Albuquerque). 275-277. (131 USNM). Napo Santa Cecilia, Rio Aguarico, Ecuador (det. Roth). 278-280. (130 USNM). Same data as Figs. 275-277. (det. Roth). (scale = 0.2 mm)

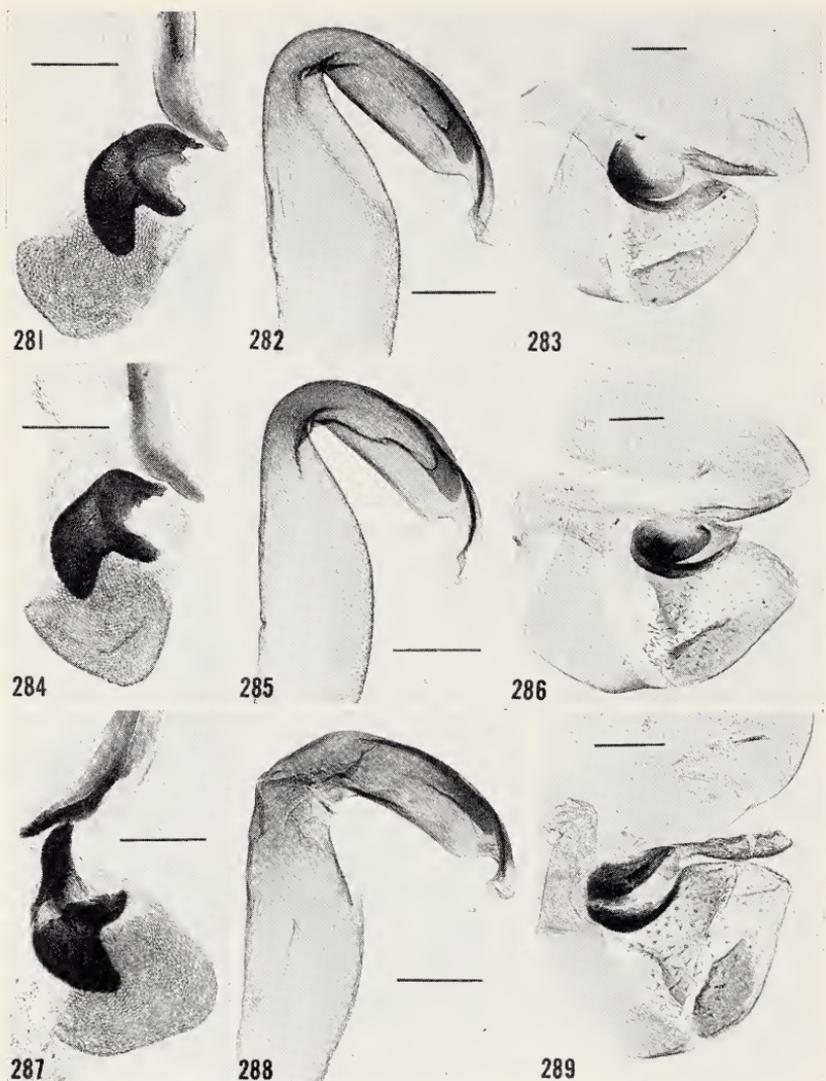
Gurney (personal communication) commented that "Judging from Hebard's descriptive remarks about *substrigata* Walker, he, Albuquerque, and Princis apparently have correctly identified it, but unfortunately there is no type locality for it, and the types of both it and *opaca* Walker are females . . . On the other hand, the type locality of *opaca* is Demerara, British Guiana, so Hebard may have had it from his French Guiana collections."

For the present I am considering *opaca* and *substrigata* to be distinct. In addition to the marked differences in L2d and prepuce of these 2 species, the hook (R2) of *substrigata* (Figs. 197, 200, 201, 204, 207) is usually distinctly wider than that of *opaca* (Figs. 179, 182, 185, 188). Hebard (1926, p. 201) stated that *E. opaca* ". . . may prove to be a synonym of the Brazilian *E. maculicollis* (Serville), and the Ecuadorean *E. stigmosa* Giglio-Tos may fall in the same synonymy. Numerous distinct, though easily confused, species are known to belong to this group and, until a better concept of the distribution and individual variation within these is formed, we believe it best to use the name *opaca*." According to Princis *stigmosa* is a synonym of *E. conferta* (see discussion under *Mexicana* Group).

Hebard (1921, p. 136) stated that *substrigata* is closely related to *grisea* ". . . though separable by numerous features." The genitalia of *substrigata* relate it more closely to *columbiana* (Figs. 208-219) and *opaca* (Figs. 178-186), than to *grisea* (Figs. 68-76).

The difficulty in identifying some of these species is shown by the fact that two specimens (Figs. 184-186, 187-189) determined as closely related to "*berlandi*" (cf. Figs. 115-117) by Albuquerque and Gurney (1962, p. 243) are similar to Hebard's *opaca*. Princis determined one of these specimens (Figs. 184-186) as well as one from Surinam (Fig. 190) as *E. sagitta*. Gurney examined these specimens and in the absence of a careful study of types and genitalia felt that external features suggested the occurrence of more than one species. There can be little doubt that the genitalia of the Type of *E. sagitta* (Figs. 62-64) and what is here considered to be *opaca* are distinctly different. In *sagitta* L1 has a setal brush (Figs. 61, 64, 67) (*Abdomennigrum* Group) and the tip of the prepuce is directed more posteriorly (Figs. 59, 62, 65). In *opaca* there is no setal brush on L1 (Figs. 180, 183, 186, 189) (*Burmeisteri* Group) and the tip of the prepuce is directed laterally (Figs. 178, 181, 184, 187, 190-195).

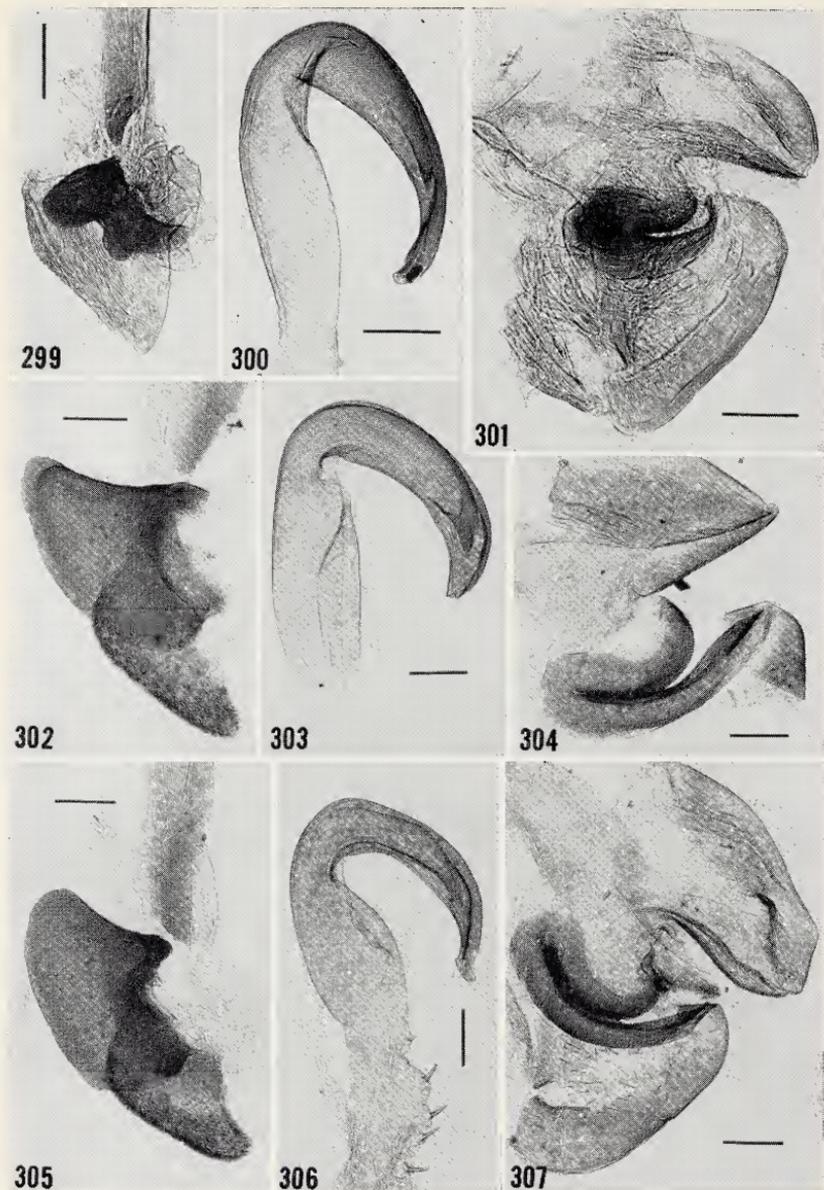
Hebard (1920, p. 98) stated that *E. columbiana* ". . . is extremely close to *E. mexicana* Saussure and may eventually prove to be a geographic race of that insect." These are unquestionably distinct spe-



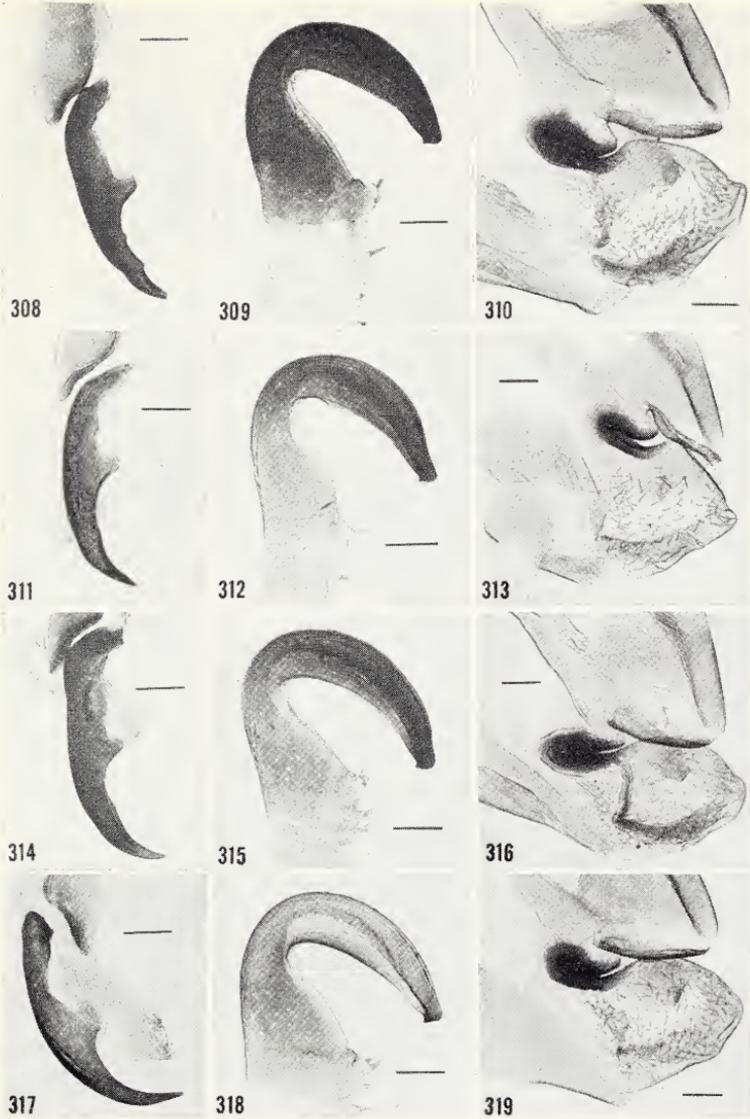
Figs. 281-289. Cockroach male genitalia. *Epilampra* sp. D. 281-283. (115 USNM). Turrialba, Costa Rica. 284-286. (133 USNM). Same data as Figs. 281-283 (281-286 det. as *E. azteca* by Princis). 287-289. (139 USNM). Cerro Campana, Panama (det. Roth). (scale = 0.2 mm)



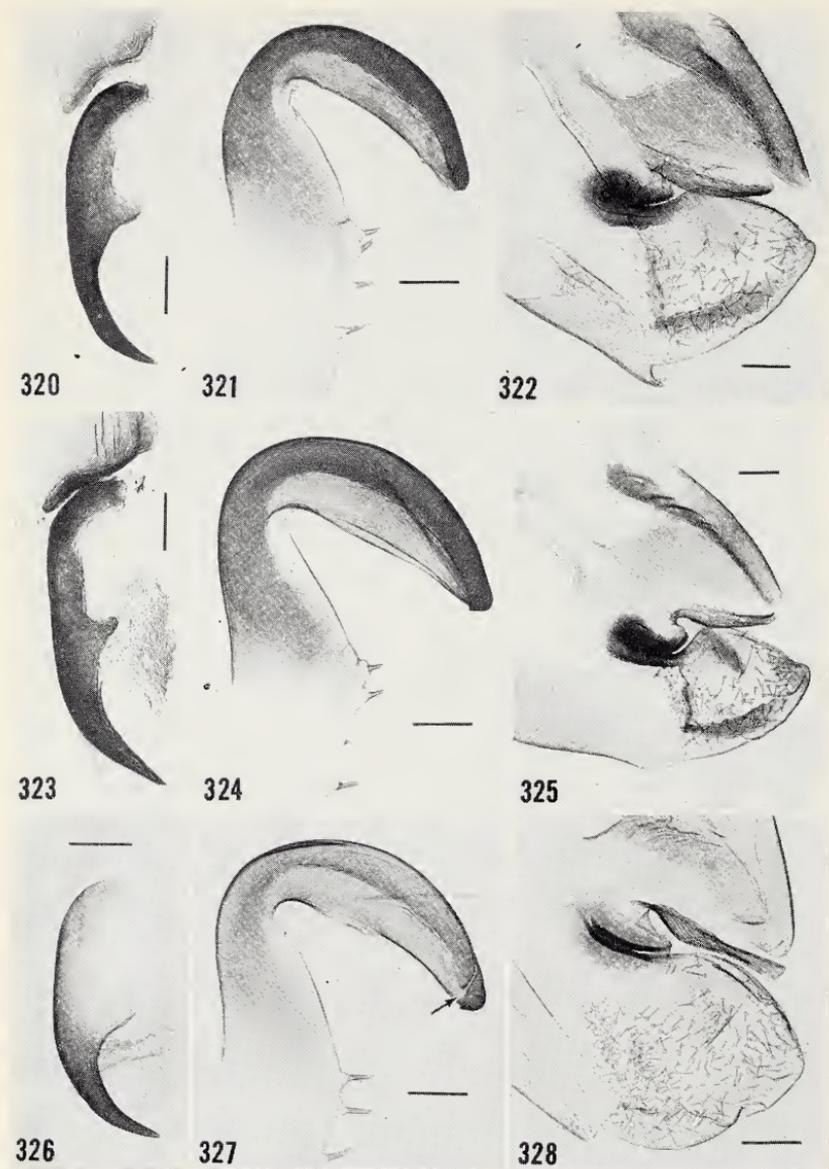
Figs. 290-298. Cockroach male genitalia. 290-292. (178 USNM). *Epilampra azteca*. Holotype of *E. colorata* R. S. Albuquerque and Gurney. Rio Felicio, Amapá, Brazil. 293-298. *Epilampra corseae*. 293-295. (40 ANSP). St. Jean du Maroni, French Guiana (det. Hebard). 296-298. (85 ANSP). Pará, Brazil. (scale = 0.2 mm)



Figs. 299-307. Cockroach male genitalia. 299-301. (25 MCZ). *Epilampra latifrons*. Pernambuco, Brazil. (det. Rehn). 302-307. *Epilampra heusseriana*. 302-304. (151 USNM). Cerro Montevideo. (det. Albuquerque). 305-307. (160 USNM). Rio Grande da Sul, Brazil (det. Roth). (scale = 0.2 mm)



Figs. 308-319. Cockroach male genitalia. *Epilampra sodalis*. (all Paratypes of *Epilampra cinnamomea* Hebard. St. Jean du Maroni, French Guiana. 308-310. (36 ANSP). 311-313. (93 ANSP). 314-316. (80 ANSP). 317-319. (91 ANSP). (scale = 0.2 mm)



Figs. 320-328. Cockroach male genitalia. 320-328. *Epilampra sodalis*. 320-322. (92 ANSP). St. Jean du Maroni, French Guiana (Paratype of *E. cinnamomea* Hebard). 323-325. (48 USNM). Surinam (det. Roth). 326-328. (88 ANSP). Pará, Brazil (det. Rehn; arrow in Fig. 327 points to a thin line representing the subapical incision). (scale = 0.2 mm)

cies and their genitalia are so different that by my criteria I place them in different groups. The shape of the L2d of *E. columbiana* (Figs. 208, 211, 214, 217, 219) is distinctly fishlike and it is easily distinguished from *mexicana* (Figs. 2, 5, 8, 10, 11, 12).

The L2d and prepuce of *E. latifrons* (Fig. 299) are very similar to those of *abdomennigrum* (Figs. 50, 53-55); the L1 of *latifrons* lacks a setal brush (Fig. 301), whereas these setae are present in *abdomennigrum* (Fig. 52).

The unique tarsal-clawlike shape of the L2d of *basistriga* (Figs. 220, 223, 226-228) distinguishes this species from any other *Epilampra*. Hebard (1929, p. 369) believed that *E. delicata* (Fig. 227) (= *basistriga*) seemed to be near *E. berlandi*, and *E. jorgenseni* and apparently even more closely related to *Audreia catharina*; this conclusion is not supported by genitalia. *E. berlandi* (Figs. 114-117) and *jorgenseni* (Figs. 97-113) are in the *Abdomennigrum* Group; and Shelford's *Audreia catharina* with genitalia (Figs. 37-39 in Roth 1970) completely different from those of *Epilampra* is now in the genus *Poeciloderrhis*.

Two species, *E. thunbergi* (Figs. 238-243) and *E. castanea* (Figs. 244-246) are apparently closely related; the R2's (Figs. 239, 242, 245) and L1's (Figs. 240, 243, 246) are especially similar. Hebard apparently had misidentified one of these specimens (Figs. 241-243) of *thunbergi* as *E. testacea*. Princis (1949, p. 65) discussed *thunbergi* (Type: ♂?, without abdomen) and compared it with *grisea* and also stated that *E. substrigata* Walker may prove to be a synonym of *thunbergi*. The genitalia of *grisea* (Figs. 68-96) and *substrigata* (Figs. 196-207) are distinctly different from Princis' *thunbergi* (Figs. 238-240). Hebard (1929, p. 365) stated that what he considered to be *testacea* [= *thunbergi*] (Figs. 241-243) was closely related to *guianae* (Figs. 118-126); but this conclusion is not supported by the genitalia which are markedly different.

The specimen of *E. castanea* was recorded by Hanitsch (1931, p. 385) as *Epilampra puncticollis*. *E. puncticollis* is now in *Rhabdoblatta*, a genus not found in the New World (Princis, 1967). This specimen is from the Fry Collection in BMNH and Hanitsch in reporting it commented that "No particulars are available concerning the specimens from the late Mr. Alexander Fry's collection. Some of the material seems Malayan, but the rest is almost certainly Neotropical." Fry lived at one time in Rio de Janeiro and this specimen most probably came from there.

Subgroup C (*azteca*, *crossca*): The prepuce is usually poorly developed or indefinitely outlined; if the prepuce is clearly outlined, its surface sculpturing is scalelike.

The genitalia of *E. azteca* from different localities suggest that two species and possibly three may be included in this taxon. In specimens from Mexico (Fig. 247), Costa Rica (Fig. 250), and Panama (Figs. 253-256), L2d is irregular in outline and lies above the prepuce; the prepuce is irregular in outline and some portions tend to blend into the surrounding membrane. The L2d in specimens from Trinidad (Fig. 269), Surinam (Figs. 260, 263, 265, 267), Venezuela (Fig. 272), and Ecuador (Figs. 275, 278), is knoblike in shape and appears to be an outgrowth of the prepuce.

The L2d in two specimens from Costa Rica (Figs. 281, 284) (det. as *azteca* by Princis), and one from Panama (Fig. 287) differs distinctly from the *azteca* just discussed; the prepuce is more clearly defined and its scalelike surface sculpturing also differs from the other *azteca*. This is probably an undescribed species and I am tentatively calling it *Epilampra* sp. *D.* Gurney (personal communication) has commented on *E.* sp. *D.* and states “. . . they (Nos. 113, 115, 139) are very much like *azteca* from Central America (Nos. 140, 141, 143, 144) but differ in face markings. However, No. 131 from Ecuador is darker in general, has darker and larger face markings, and the ventral surface of the abdomen is mostly blackish, unlike 115 et al. The type of *azteca* is a male from Mexico because, though Cuba and Mexico were both mentioned originally, Cuba was eliminated as type consideration by comments in the *Biologia*. We have a male from “Mexico” which in face markings is more like the Princis det. specimen than like 140, et. al., so perhaps Princis is right. Consulting the type of *azteca* should solve the problem.”

According to Albuquerque and Gurney (1962, p. 244), *E. colorata* is related to the “*maculifrons*” Stål group. The genitalia (Figs. 290-292) of the Type of *colorata* are very similar to those of *E. azteca* from Central America (e.g. Figs. 250-252). Gurney (personal communication) re-examined the Type and stated that *colorata* is quite likely a synonym of *azteca*. The Type is smaller than many *azteca* but probably within the normal size range. With Gurney's concurrence I consider *colorata* a synonym of *azteca*.

The prepuce of *E. crossea* (Figs. 293, 296) has no distinctive shape and is simply a membrane covered with microtrichia.

#### *Heusseriana* Group

[*E. heusseriana* Saussure (Figs. 302-307)]

At present, only *E. heusseriana* belongs to this group. The L2d (Figs. 302, 305) of *heusseriana* is unusually large in relation to the prepuce. R2 has a subapical incision (Figs. 303, 306) and L1 lacks a setal brush (Figs. 304, 307).

The battleaxe-shaped L2d is continuous with a sclerotized portion of the prepuce and is not separated from the prepuce by a thin clear membrane (as is usual in the *Abdomennigrum* and *Burmeisteri* Groups). In the *Mexicana* Group, L2d is not a distinct sclerite lying above the prepuce but is a flat sclerotization lying on the same plane as the prepuce.

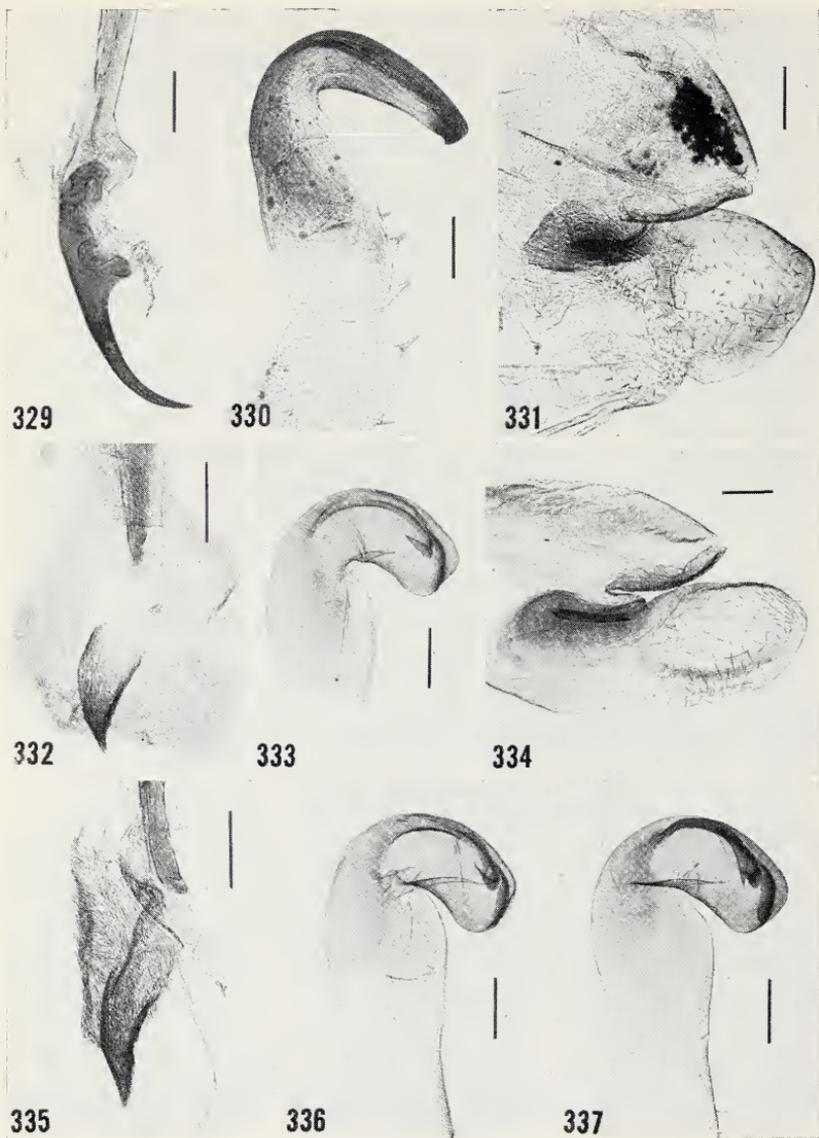
There has been some question about the placement of *Epilampra heusseriana* Saussure. According to Hebard (1921) this species “. . . has been assigned to the genera *Calolampra* and *Audreia*, due mainly to the fact that the type female had short truncate tegmina. Though this is true for the female sex, the male before us is seen to have fully developed organs of flight, and shows no characters which would warrant its being placed other than in the genus *Epilampra*.” Princis (1967) lists *heusseriana* under *Audreia* apparently following Albuquerque (1964). The male genitalia of *heusseriana* are typical of many other *Epilampra* and tend to support Hebard's placement of the species.

#### *Sodalis* Group

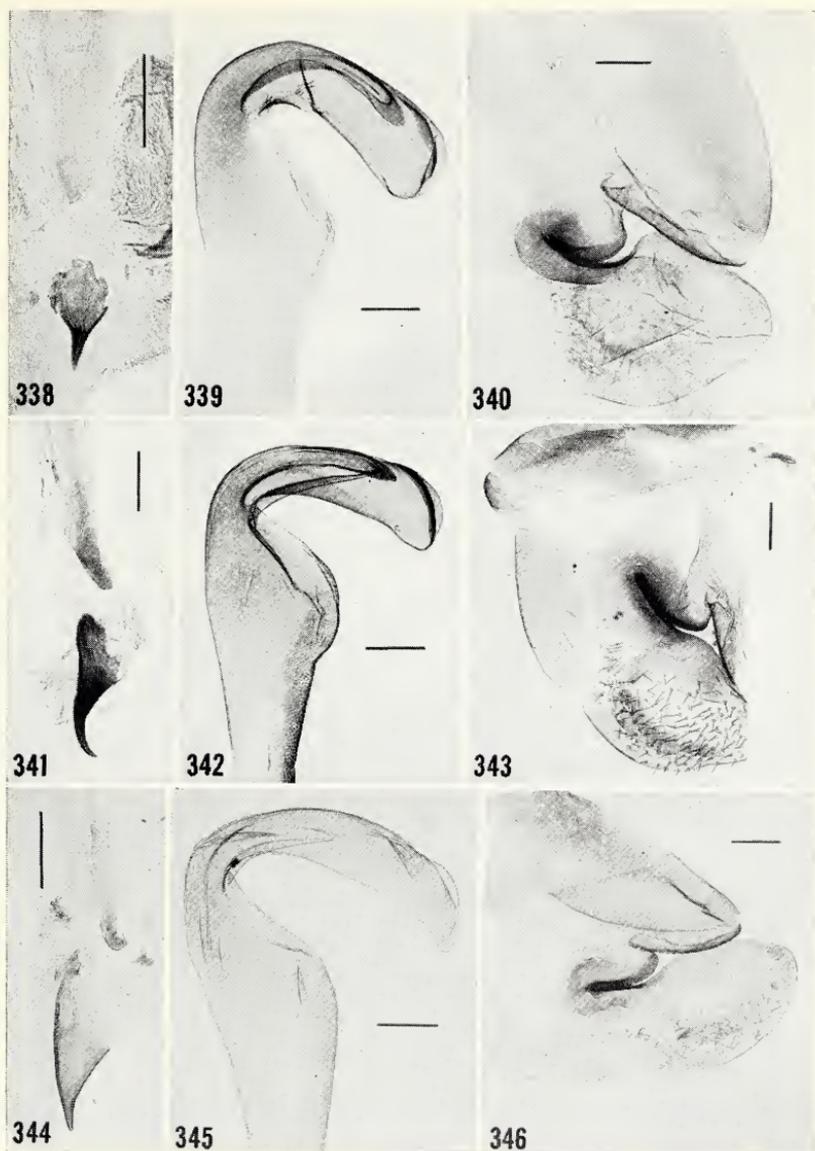
[*Epilampra sodalis* Walker (Figs. 308-328)]

In this group which includes *E. sodalis* and possibly several undetermined species, there is no distinctive prepuce and L2d is a single more or less clawlike sclerotization. In a recent paper I indicated that the male of *E. sodalis* had tergal modifications on segments 3 and 4 (Roth, 1969a, p. 202, Table 10, footnote b). I have examined males of *E. cinnamomea* Hebard, which Princis synonymized with *sodalis* Walker (Princis, 1958, p. 16), and found that the males lack tergal glands. I also examined Walker's Type ♀ of *sodalis* and concur with Princis that *cinnamomea* is a synonym of this species. The male genitalia of *sodalis* (Figs. 308-328) are distinctive; L2d resembles a single tarsal claw, and R2 is rather stout with a subapical “incision” represented by a fine line which is best seen in a lightly sclerotized specimen (Fig. 327, arrow).

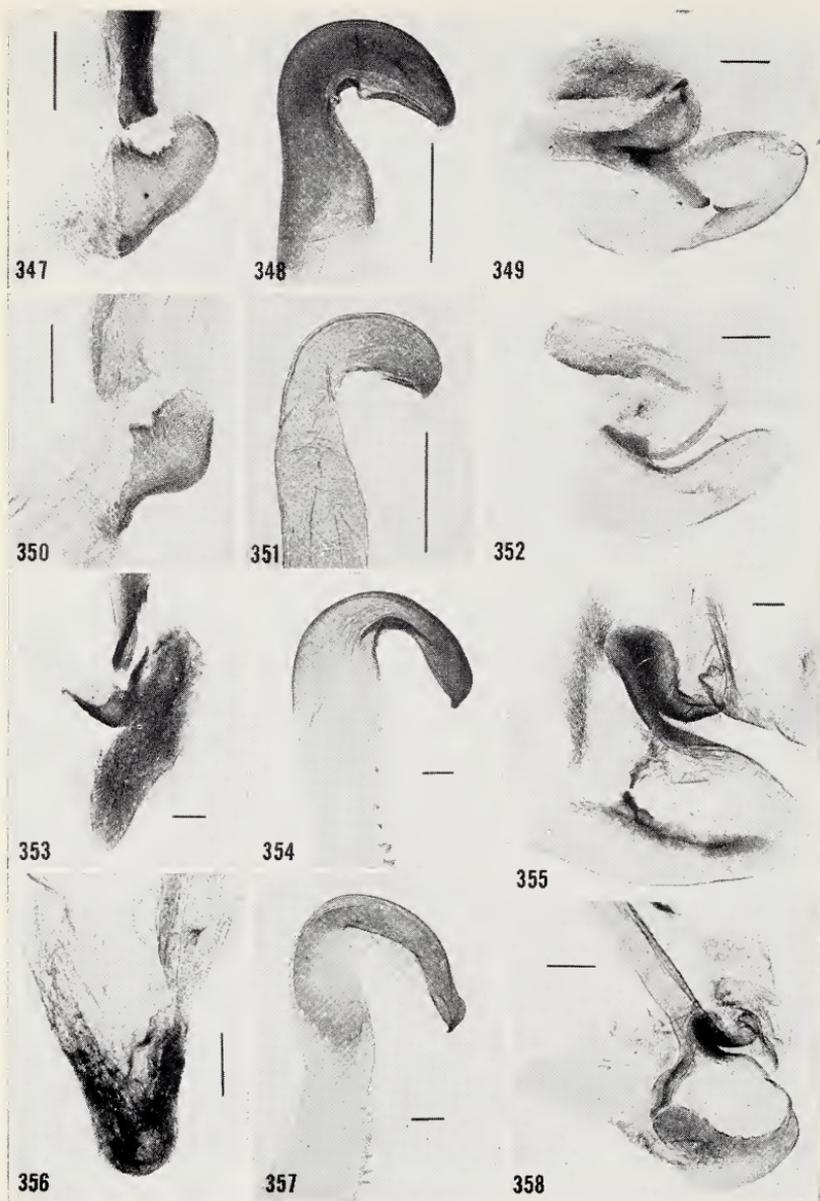
The genitalia (Figs. 329-331) of the specimen previously reported by me as *sodalis* (Roth, 1969a) (here designated as *Epilampra* sp. *A*) are only subtly different from those of *sodalis*; L2d (Fig. 329) and R2 (Fig. 330) are slightly more slender in sp. *A*. However, there is a striking difference in the pronotal markings of these two species. In *sodalis* the microspots are all small and more or less the same size whereas in sp. *A* there are distinctly large spots, interspersed among small ones. These two forms are probably sibling species. Species *A* is the only *Epilampra* I know in which male tergal



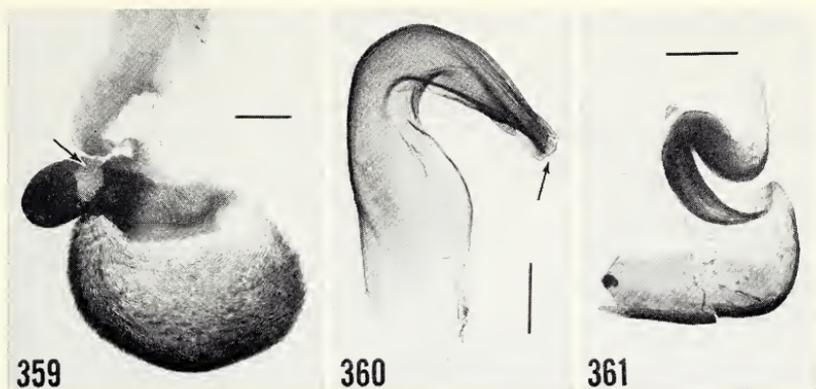
Figs. 329-337. Cockroach male genitalia. 329-331. (182 USNM). *Epilampra* sp. A. Tapurucuara, Rio Negro, Brazil. 332-337. *Epilampra* sp. C. 332-334. (152 USNM). Camp Rangel, Arague, Venezuela. 335-336. (55 USNM). Same data as Figs. 332-334. 337. (112 USNM). Ar. Rancho Grande, Venezuela. (scale = 0.2 mm)



Figs. 338-346. Cockroach male genitalia. 338-343. *Epilampra* sp. B. 338-340. (10 BMNH). Pancina, Vera Paz. 341-343. (72 USNM). Territ. Amazonas, Mt. Marahuaca, Venezuela (det. as *E. sodalis* by Albuquerque). 344-346. (153 USNM). *Epilampra* sp. (near sp. B). Taken at Hoboken Quarantine (Venezuela?). (scale = 0.2 mm)



Figs. 347-358. Cockroach male genitalia. 347-352. *Audreia carinulata* (Saussure). 347-349. (176 USNM). La Palma, Costa Rica. (det. Rehn). 350-352. Volcan Barba, Costa Rica. (det. Fisk). 353-355. (81 USNM). *Epilampra yersiniana*. São Paulo Rio Cubatão, Brazil (det. Princis). 356-358. (181 ANSP). *Epilampra shelfordi*. Type 5345. El Coredo, Cauca, Colombia. (scale = 0.2 mm)



Figs. 359-361. (108 MCZ). Cockroach male genitalia of *Epilampra exploratrix* (Gurney). Holotype 25559 of *Audreia exploratrix* Gurney. Buenos Aires, Trinidad Mts., Santa Clara Province, Cuba. (the left side of L2d [Fig. 359, arrow] was torn due to pressure of the coverslip, and the tip of R2 [Fig. 360, arrow] was accidentally cut off). (scale = 0.2 mm)

modifications are found on segments 3 and 4; the genitalia do not conform with those of *Pociloderrhis* whose species (formerly in *Epilampra*) have tergal glands on segments 1 and 2 (Roth, 1970).

Two or three other species may belong to this group. *Epilampra* sp. B. (Figs. 338-343) has a very small clawlike L2d (Figs. 338, 341) and its R2 (Figs. 339, 342) differs markedly from *sodalis* (cf. Fig. 327); Albuquerque misidentified this species (Figs. 341-343) as *sodalis*. Princis determined one of these specimens as *E. columbiana* but its genitalia (Figs. 338-340) are quite different from specimens which I and Gurney (personal communication) consider to be *columbiana* (cf. Figs. 208-219). Another specimen, *Epilampra* sp., is very near sp. B. (Figs. 344-346); it has an L2d (Fig. 344) slightly different in shape from the other two specimens and its R2 (Fig. 345) is more elongate. In *Epilampra* sp. C (Figs. 332-337), L2d (Figs. 332, 335) is not heavily sclerotized but is a hollow, membranous, pointed extension of the preputial membrane and is covered by microtrichia. Its R2 (Figs. 333, 336, 337) is noticeably shorter than that of sp. B (cf. Figs. 339, 342).

#### *Yersiniana* Group

[*Epilampra yersiniana* Saussure (Figs. 353-355)]

In *E. yersiniana* the prepuce, when flattened, extends obliquely to the right of L2d (Fig. 353). The hook (R2) lacks a subapical in-

cision and its tip is nipple shaped (Fig. 354). The setal brush of L1 extends vertically behind the darkly sclerotized cleft region (Fig. 355).

Though originally described as an *Epilampra*, *yersiniana* has been placed in the genus *Hedaia* (by Saussure, Finot, Kirby, Hebard, and Rocha e Silva Albuquerque) and was listed by Kirby as a *Rhabdoblatta* (Princis, 1967). Princis (1967) listed the species under *Epilampra* and stated (personal communication) that "*Hedaia* is a Malagassy genus and I do not believe that it occurs in South America. Probably a new genus is required [for *yersiniana*]."

#### *Shelfordi* Group

[*Epilampra shelfordi* Hebard (Figs. 356-358)]

*E. shelfordi* is the only species belonging to this group. It is unique in that L2d is absent and the preputial membrane is in the form of a rounded hollow cylinder (Fig. 356) covered with microtrichia. The R2 lacks a subapical incision (Fig. 357). No setal brush is present on L1 (Fig. 358). According to Hebard (1919, pp. 106-107), *E. shelfordi* ". . . belongs to an apparently exclusively South American group of the genus . . . To this group belong *E. conspersa* and *E. agathina*, of which single specimens are at hand. More material may show these forms to be generically distinct."

#### SUMMARY

The male genitalia of species of *Epilampra* are not only useful for specific determinations but can also be used to show species relationships. Thirty-six species of this genus have been divided into the following Groups and Subgroups:

1. *Mexicana* Group:—*mexicana*, *fallax*, *conferta*.
2. *Abdomennigrum* Group:—*abdomennigrum*, *maya*, *sagitta*, *taira*, *grisea*, *jorgenseni*, *berlandi*, *guianae*.
3. *Burmeisteri* Group
  - a. Subgroup A:—*burmeisteri*, *tainana*, *quisqueiana*, *sabulosa*, *wheeleri*, *gundlachi*, *haitensis*, *hamiltoni*, *bromeliadarum*, *gattunae*, *fugax*, *exploratrix*.
  - b. Subgroup B:—*opaca*, *substrigata*, *columbiana*, *latifrons*, *basisstriga*, *thunbergi*, *castanea*.
  - c. Subgroup C:—*azteca*, *crossea*.
4. *Heusseriana* Group:—*heusseriana*.
5. *Sodalis* Group:—*sodalis*.
6. *Yersiniana* Group:—*yersiniana*.
7. *Shelfordi* Group:—*shelfordi*.

Genitalic differences indicate that *E. opaca* is a distinct species and not a synonym of *E. substrigata*.

The male genitalia of 5 species of *Audreia* (*hamiltoni*, *bromeliadarum*, *exploratrix*, *gatunae*, and *fugax*) are so characteristic of *Epilampra* that I have transferred them to this genus.

*Epilampra colorata* is synonymized with *E. azteca*.

#### ACKNOWLEDGEMENTS

I thank the following for the loan of museum material: Dr. M. G. Emsley and Dr. N. Jago, formerly with the Philadelphia Academy of Natural Sciences, Dr. A. B. Gurney, U. S. National Museum, Washington, D.C., Dr. Karl Princis, Zoological Institution, Lund University, Sweden, Dr. Jerome G. Rozen, Jr., American Museum of Natural History, New York, Dr. S. L. Tuxen, Zoological Museum, Copenhagen, Dr. David R. Ragge, British Museum (Natural History), London, Dr. Ivan Huber, Dr. J. Bonfils, and Dr. P. R. Castillo.

In addition I collected several species of *Epilampra* during Phase C of the Alpha Helix expedition to the Amazon in 1967. I thank the National Science Foundation for support on the Amazon expedition under Grant NSF-GB-5916.

I am grateful to Dr. K. Princis and Dr. A. Gurney for determinations and Mr. Sam Cohen for taking the photographs.

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THE GENUS *OONOPS* (ARANEAE, OONOPIDAE)  
IN PANAMA  
AND THE WEST INDIES. PART 1

BY ARTHUR M. CHICKERING  
Museum of Comparative Zoology

This is the sixth paper in the series planned for publication on the various genera in the Family Oonopidae in Central America and the West Indies. The genus *Oonops* appears to include many more species than any other genus now believed to occur in the region under study at the present time. For this reason the treatment of the genus in this region will be divided into two or three separate papers. The present one will include all species at present known to occur in Panama, Trinidad, W. I. and Curaçao, Netherlands Antilles.

Again, I am taking this opportunity to express my appreciation for the continued aid and encouragement extended to me by the staff of the Museum of Comparative Zoology, Harvard University, over a period of many years. Grants GB-1801 and GB-5013 from the National Science Foundation have aided me in carrying on extensive collecting activities in Panama, Costa Rica, Florida and the West Indies during the years 1963-1968 and in continuing my studies in the Museum of Comparative Zoology during this period.

All types described in this paper together with my entire collection of specimens treated here will be deposited in the Museum of Comparative Zoology, Harvard University.

Genus *Oonops* Templeton, 1835

The type species is *Oonops pulcher* Templeton, 1835, by monotypy, based upon both males and females from Belfast, Ireland. Simon was the first to describe species belonging to this genus in the Western Hemisphere. Between 1891 and 1907 Simon described several species from St. Vincent, B. W. I., Brazil, Venezuela and Argentina. Since that time several additional species have been described from Bermuda, Florida, Dominican Republic, Puerto Rico, Texas, Mexico, Panama and Brazil. Dr. Petrunkevitch had one species from Panama in 1925 and in 1951 I recognized two additional species from the same region. Since 1951 the specimens assigned to this genus have been increasing with each of my collecting trips in Panama and other nearby regions.

As in my treatment of the genus *Stenoonops* (1969) I must con-

fess that I am well aware that some uncertainties still exist in my treatment of this genus. However, I feel compelled to recognize a total of fifteen species from Panama, Costa Rica, Trinidad, W. I. and Curaçao, Netherlands Antilles. Eleven of these species are regarded as new. The list of species recognized in this paper may be given as follows: *Oonops amacus* sp. nov.; *Oonops anoxus* sp. nov.; *Oonops donaldi* Chickering; *Oonops itascus* sp. nov.; *Oonops ornatus* sp. nov.; *Oonops pallidulus* (Chickering); *Oonops persitus* sp. nov.; *Oonops reticulatus* Petrunkevitch; *Oonops sativus* sp. nov.; *Oonops sicorius* sp. nov.; *Oonops tectulus* sp. nov.; *Oonops tenebus* sp. nov.; *Oonops trapellus* sp. nov.; *Oonops vestus* sp. nov.; *Oonops zeteki* Chickering. Several specimens have been left unplaced in any species because of their uncertain status. One species in the above list is from Curaçao, Netherlands Antilles, six are from Trinidad, W. I. and the remaining eight are from Panama and Costa Rica.

In addition to the general family characteristics, the features of the genus *Oonops* as observed in this study may be stated as follows: the size varies from about 1.2 mm to 2.26 mm with females usually somewhat larger than the corresponding males. The carapace is usually of moderate height with both height and general shape varying somewhat among the species; a few species have the carapace considerably more highly raised. There are six eyes in two rows in a fairly compact group; the posterior row is usually quite definitely recurved and somewhat wider than the anterior row and usually occupies most of the width of the carapace at that level. There are only small differences in the size of the three pairs of eyes. The chelicerae probably bear minute teeth on each margin of the fang groove but these are often difficult to observe. The maxillae and lip are usually conservative and without special modifications but there are occasional exceptions to this rule. The legs are moderately long and slender and have spines at least on the third and fourth legs but the spination is quite variable among the recognized species and often difficult to determine. The sternum is convex, only a little longer than wide; usually without special modifications but occasionally shows weakly developed lobes and grooves. The legs are most commonly 4123 in order of length but there is some variation in the order in certain species. The male palp usually has rather distinctive tarsal features but other segments are not highly modified. Abdomen: a dorsal scutum is absent; typically two obscure ventral scuta are discernible in the anterior third of the venter but in some species these are so indistinct that clear representation in drawings

is practically impossible; similar difficulties are encountered in respect to the epigynal areas of females and frequently these cannot be clearly represented in figures; small, subsurface, dark colored structures usually show more or less clearly just anterior to the bases of the spinnerets much as in *Stenoonops*.

*Oonops reticulatus* Petrunkevitch

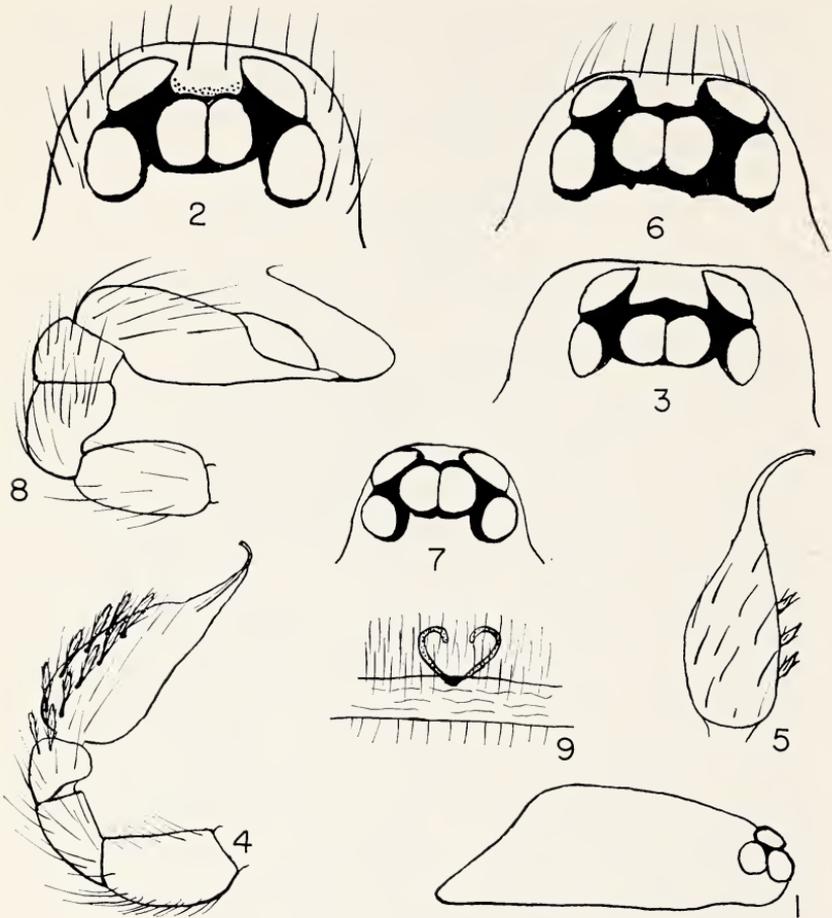
Figures 1-2

*Oonops reticulatus* Petrunkevitch, 1925: 98. The female holotype was from Panama City, Panama, but is now unavailable for study. Roewer, 1942: 278; Bonnet, 1958: 3192.

*Oonopoides bryantae*, — Chickering, 1951: 224, figs. 12-13.

No figures accompanied the original description and the female holotype was sectioned for the study of internal anatomy and, of course, was unavailable for examination in 1951 when I had but one male in my collection. Figure 1 shows the carapace of the male in profile and Figure 2 shows the eyes of the female; these specimens are from Corozal and Balboa, Panama Canal Zone, respectively. In both original descriptions cited above it was stated that true spines were lacking on the legs. Repeated examinations have now convinced me that there are actually true spines on the appendages although they are difficult to distinguish from numerous spiniform bristles and hairs. The ventral scuta in females are faintly outlined but the epigynal area is so indefinite and, apparently, variable in appearance that it seems impossible to provide reliable drawings of this region. The color pattern is highly variable among the specimens now assigned to this species; reticulation is very clear in some specimens but obscure in others; in some individuals the purplish color is subdivided into a series of irregular spots separated by yellowish areas.

*Records.* Two males are now in the collection from Corozal, Panama Canal Zone, January 4, 1958; a third male was collected in the vicinity of Turrialba, Costa Rica, Aug. 10, 1965. More than a dozen females from several localities in the Panama Canal Zone were taken in 1950, 1954, 1958, 1960 (W. J. Brown) and 1964; and also in Turrialba, Costa Rica, July-August, 1965. Two females from El Volcan, Panama, August, 1950 belong in this genus but their specific status is uncertain at present. It seems probable, however, that they will eventually be regarded as representing a new species.



Figs. 1-2. *Oonops reticulatus* Petrunkevitch. Fig. 1. Carapace of male; right lateral side. Fig. 2. Eyes of female from above. Figs. 3-6. *Oonops ornatus* sp. nov. Fig. 3. Eyes of male from above. Fig. 4. Left palp of male holotype; prolateral view. Fig. 5. Left palpal tarsus of holotype; dorsal view. Fig. 6. Eyes of female from above. Figs. 7-9. *Oonops tectulus* sp. nov. Fig. 7. Eyes of male holotype from above. Fig. 8. Left palp of male holotype; prolateral view. Fig. 9. Epigynal area of described female paratype from below.

***Oonops ornatus* sp. nov.**

Figures 3-6

*Holotype.* The male holotype is from Boquete, Panama, August 4-11, 1954. The name of the species is a Latin adjective suggested by unusual palpal tarsal decorations.

*Description.* Total length about 1.94 mm including extended spinnerets. Carapace about 0.81 mm long; 0.68 mm wide opposite second coxae where it is widest; about 0.32 mm tall; only slightly arched from PME to beginning of steep posterior declivity; shape of carapace in profile very similar to that of *O. reticulatus*; surface smooth and shining; with coarse, dark bristles along median and ocular regions; posterior border slightly overlapped by abdomen; no median thoracic groove or pit observed. Eyes: six as usual in a moderately compact group; posterior row occupies about seven-tenths of width of carapace at that level and is definitely recurved. Ratio of eyes ALE: PME : PLE = nearly 9 : 7 : 8 (some irregularities noted and pigment is somewhat irregularly distributed thus making it difficult to measure with the desired accuracy). ALE separated from one another by nearly their long diameter (Fig. 3); subcontiguous to PLE and separated from PME by nearly one fourth of their long diameter. PME contiguous to one another and separated from PLE by nearly half their radius. Clypeus very narrow with exact height obscure. Chelicerae: vertical, essentially parallel; apparently without special modifications. Maxillae distally narrowed and probably obscurely modified but details not determined. Lip: somewhat longer than wide; without special modifications. Sternum: very convex; longer than wide in ratio of about 12 : 11; obtusely rounded posterior end extended between bases of fourth coxae which are separated by about 1.3 their width; surface smooth and shining; only faintly grooved; with numerous long, stiff, dark, spiniform bristles; widest between second coxae but nearly as wide between first coxae. Legs: 4123 in order of length; it is difficult to distinguish between stiff, spiniform bristles and true spines but, as in *O. reticulatus*, after repeated examinations I have decided that we must recognize numerous, transparent spines on the legs; trichibothria are fairly prominent but their exact numbers and placement have not been determined. Palp: essential features shown in Figures 4-5; the distal end of the tarsus and the unusual, feathery hairs on the prolateral surface of the cymbium are the most distinctive features. Abdomen: regularly ovoid in shape; spinnerets essentially typical of the genus; the region anterior to the genital groove appears

to be slightly suggestive of an epigastric scutum but its outlines are very indistinct. Color in alcohol: carapace and legs above are a definite yellow color; sternum, mouth parts and lower surfaces of the legs are a lighter yellowish; abdomen light purplish brown with a distinct, irregular reticulation dorsally and laterally; the cardiac region is nearly white through the first quarter; the venter is nearly white; some variation in color pattern has been noted on the two paratype males.

*Females.* Several specimens are, apparently, either immature or dismembered to such an extent that an adequate description is regarded as impossible. These females are probably correctly matched with the males, however, because of color pattern, general anatomical features, the eyes (Fig. 6) and the decorative feathery hairs on the palps.

*Diagnosis.* The peculiar color pattern, the eyes and other general anatomical features seem to indicate a rather close relationship with *Oonops reticulatus* Petrunkevitch. The distinct features of the male palp definitely establish this as a new species.

*Records.* One paratype male was taken with the holotype and another male was taken in the same locality in August, 1950. Five or six damaged or immature females were also taken in the vicinity of Boquete, Panama, August 4-11, 1954.

### **Oonops tectulus** sp. nov.

Figures 7-9

*Holotype.* The male holotype is from St. Augustine, Trinidad, W. I., April 9, 1964. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.43 mm, exclusive of the somewhat extended spinnerets. Carapace 0.66 mm long; 0.48 mm wide opposite interval between second and third coxae where it is widest; 0.20 mm tall; gently arched from PME to beginning of only moderately steep posterior declivity; surface smooth and shining except posterior declivity where there are very fine transverse corrugations; with a sparse supply of moderately long hairs mostly removed by handling; with no evidence of a median thoracic groove or pit. Eyes: six as usual in a moderately compact group; posterior row occupies nearly entire width of carapace at that level and is rather strongly recurved. Ratio of eyes ALE : PME : PLE = nearly 6 : 6.5 : 6. ALE separated from one another by nearly three-fourths of their long axis; subcontiguous to PME and slightly further removed from PLE

(Fig. 7). PME contiguous to one another for nearly one-third of their circumference and subcontiguous to PLE. Height of clypeus apparently equal to nearly one-fourth of the long axis of ALE but transparency makes accurate measurement difficult. Chelicerae: parallel; apparently without special modifications. Maxillae and lip: apparently typical of the genus. Sternum: convex; scutiform; with a deep excavation at junction with lip; only slightly longer than wide between second coxae where it is widest but nearly as wide between first coxae; only slightly lobed and not noticeably grooved; with a sparse coating of stiff bristles; squarely truncated between fourth coxae which are separated by eight-fifths of their width; second and third coxae nearly globose; first and second coxae somewhat more elongated. Legs: 4123 in order of length; slender, transparent spines are present especially on the third and fourth legs but these could easily be regarded as spiniform bristles. Palp: all segments short and broad except the tarsus which terminates in a long, lash-like embolus (Fig. 8). Abdomen: ovoid; with a weakly chitinized epigastric scutum and a narrow, transverse scutum just posterior to the genital groove; openings to book lungs and tracheal spiracle obscure. Spinnerets as usual in the genus with posterior pair the longest. Color in alcohol: carapace a medium brownish with three pairs of obscure more or less radiating streaks along lateral sides; with a conspicuous, somewhat diamond-shaped figure on the posterior declivity subdivided in the middle; only a moderate amount of black pigment in the ocular region; legs, mouth parts and sternum yellowish with variations. Abdomen: dorsum and lateral sides purple with cardiac region nearly white and with dentate margins; purple areas obscurely subdivided into angular areas; venter purplish except for the scutal areas which are yellowish streaked with purple; a light yellowish median stripe extends posteriorly three-fourths of the distance from the genital groove to the spinnerets which are yellowish.

*Female paratype.* Total length 1.61 mm. Carapace 0.66 mm long; 0.51 mm wide opposite second coxae where it is widest; 0.17 mm tall; very slightly arched from PME to beginning of posterior declivity; otherwise essentially as in male. Eyes: ratio of eyes  $ALE : PME : PLE = 7.5 : 6.25 : 7$ . ALE separated from one another by nearly three-fifths of their long axis. Clypeus appears to be practically eliminated because the ALE are set so low on the front of the carapace; otherwise essentially as in male. Chelicerae, maxillae and lip: all essentially as in the male holotype and without special modifications. Sternum: excavation at base of lip much less

than in male; sternal suture gently procurved; otherwise essentially as in male. Legs: 4123 in order of length as in male; slender, transparent spines seem to be present on legs as in male but it is difficult to distinguish between spiniform bristles and very slender spines. Abdomen: essentially as in male except that the scuta are even less distinct than in that sex; the epigynal area is very obscure but appears to exhibit a few faintly indicated distinctive features (Fig. 9); the female paratypes generally show no epigynal features of distinction. Color in alcohol: the conspicuous mark on the posterior declivity of the male is much less distinct here in the female; the purple areas on the abdomen are lighter in color and the reticulation is much clearer than in the male; otherwise essentially as in the male; considerable variation of the color pattern has been noted among the paratypes.

*Diagnosis.* This species also seems to be closely related to *Oonops reticulatus* Petrunkevitch. The features of the eyes, the obscure features of the epigynal area in the female paratype and, especially, the palpal tarsal features of the male establish it definitely as a new species.

*Records.* The described female paratype was taken on the same day and in the same locality as the male holotype. Several paratypes of both sexes, some immature, were collected in the same general locality April 5-8, 1964.

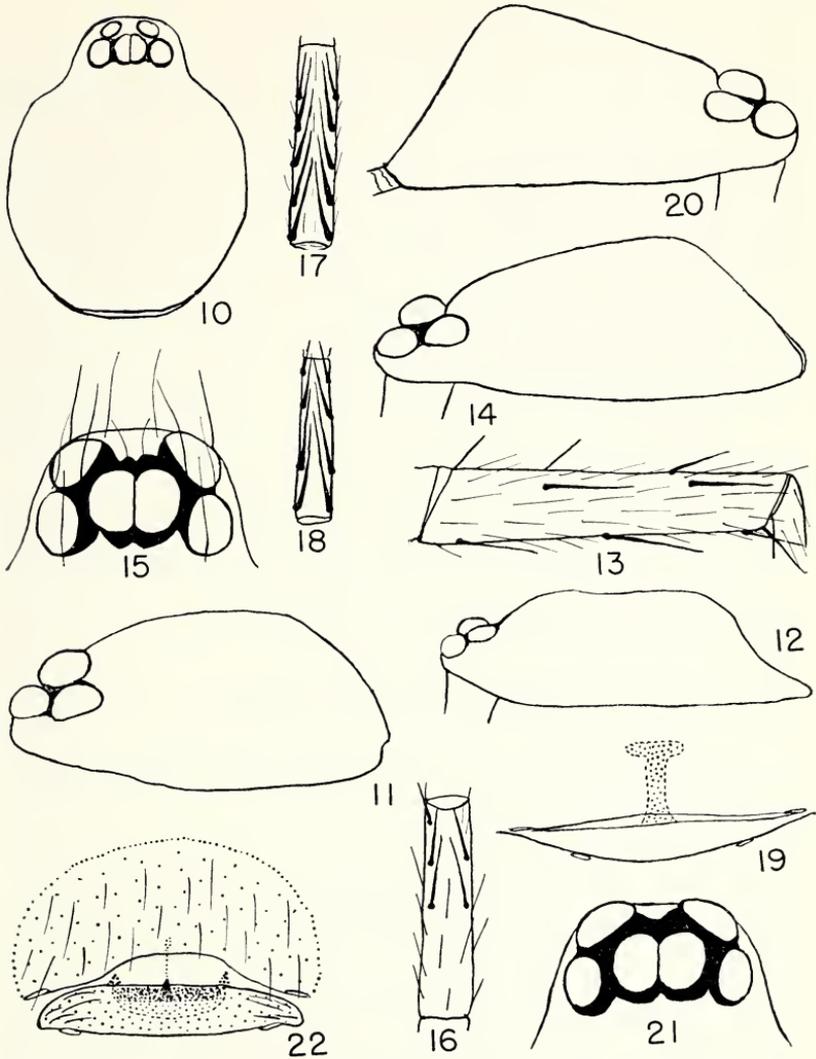
### *Oonops zeteki* Chickering

#### Figures 10-11

*Oonops zeteki* Chickering, 1951: 229, fig. 17. The holotype female from Barro Colorado Island, Panama Canal Zone was taken in a Berlese funnel, July 1943-March 1944 by Dr. James Zetek and is now in the Museum of Comparative Zoology, Harvard University.

The posterior row of eyes is only slightly recurved in this species and the carapace has a somewhat different shape than usual (Figs. 10-11). The pedal spines are conspicuous and the epigynal area is without observed distinctive features.

One additional female taken on Barro Colorado Island by Dr. Zetek in a Berlese funnel in 1946 and another female taken in the same locality August 16, 1954 are definitely placed in this species. Three females taken in Summit Gardens, Panama Canal Zone, July 24, 1954 were for a time placed in this species but now their status is uncertain. The male remains unknown.



Figs. 10-11. *Oonops zeteki* Chickering. Fig. 10. Carapace from above. Fig. 11. Carapace; left lateral view. Figs. 12-13. *Oonops pallidulus* (Chickering). Fig. 12. Carapace; left lateral view. Fig. 13. Left fourth tibia; dorso-proximal view. Figs. 14-19. *Oonops persitus* sp. nov. Fig. 14. Carapace of holotype; left lateral view. Fig. 15. Eyes of holotype from above. Figs. 16-18. First femur, tibia and metatarsus, respectively from below. Fig. 19. Epigynal area of holotype from below. Figs. 20-22. *Oonops amacus* sp. nov. Fig. 20. Carapace of holotype; right lateral view. Fig. 21. Eyes of holotype from above. Fig. 22. Epigynal area from below.

*Oonops pallidulus* (Chickering)

Figures 12-13

*Oonopinus pallidulus* Chickering, 1951: 222, figs. 10-11. The female holotype from Barro Colorado Island, Panama Canal Zone is in the Museum of Comparative Zoology, Harvard University.

In 1951 I had only the female holotype. Since that date numerous specimens, believed to belong here, have been added to the collection. Identification is often difficult, however, because of the obscurity of some important features especially of the epigynal area which seems to vary in appearance in different specimens. Repeated examinations have convinced me that spines are present on the legs (Fig. 13) but they are very inconspicuous as compared to those occurring on the legs of *Oonops persitus* sp. nov. for example. It now seems probable that I also have this species recorded from Jamaica, W. I. but the final decision in this matter must await more careful study of the available specimens. The male remains unknown.

*Records.* I now have about nineteen females assigned to this species. All of these have been collected in the Panama Canal Zone on Barro Colorado Island, in Summit Gardens or in the Canal Zone Forest Preserve on the following dates: July-August, 1954; January-February, 1958 and in May, 1964.

*Oonops persitus* sp. nov.

Figures 14-19

*Holotype.* The female holotype is from Barro Colorado Island, Panama Canal Zone, July 1-2, 1939. The name of the species is an arbitrary combination of letters.

*Description.* Total length, exclusive of the somewhat extended spinnerets 2.13 mm; including the spinnerets total length is 2.24 mm. Carapace nearly 0.77 mm long (somewhat overlapped by abdomen); nearly 0.66 mm wide opposite interval between second and third coxae where it is widest; nearly 0.33 mm tall; considerably raised and gently arched from just behind PME to beginning of fairly steep posterior declivity (Fig. 14); surface smooth and shining; with a row of five or six long, slender spinules along median region and with few hairs elsewhere. Eyes: six as usual in a moderately compact group; seen from above, posterior row recurved and occupies nearly the full width of the carapace at that level (Fig. 15). Ratio of eyes ALE : PME : PLE = nearly 8.5 : 8 : 8. ALE separated from one another by slightly less than their long axis; separated from PME by nearly three-eighths of their long axis and from PLE by less than one-eighth of their long axis. PME contiguous for nearly

one-third of their circumference and separated from PLE by a little more than one-eighth of their long axis. Height of clypeus equal to slightly less than one half the the long axis of ALE. Chelicerae: fairly robust; vertical; parallel; with no observed special modification. Maxillae and lip apparently quite typical of females of the genus; without observed special modifications. Sternum: moderately convex; nearly as wide as long; surface smooth and shining; without grooves or definite lobes; posterior end broadly rounded opposite bases of fourth coxae which are separated by nearly their width. Legs: 4213 in order of length; with conspicuous spines; first leg with spines as shown in Figures 16-18 (taken from paratype to avoid injury to holotype); some irregularities of spination noted among paratypes; second leg essentially as in first; third and fourth legs with several spines on femora, tibiae and metatarsi but much less conspicuous than on first and second legs; palp with several slender, inconspicuous spines. Abdomen: ovoid; widest about one-third from base to posterior end; six spinnerets typical of the genus with posterior pair the longest; with no evidence of a collulus; epigastric and narrow ventral scuta barely discernible; epigynal area obscurely distinctive (Fig. 19). Color in alcohol: carapace, sternum, legs and mouth parts yellowish with some variation; considerable black pigment in ocular area; abdomen light yellowish in general; with dorsal and lateral regions clearly reticulated into irregular polygons; on each side just in front of the anterior spinnerets there is a group of four or five minute more deeply colored yellowish bodies believed to represent the dark subsurface bodies typically seen in the same position.

*Diagnosis.* This species is believed to be closely related to *Oonops pallidulus* (Chickering). The conspicuous pedal spines, relative position of the eyes, shape of the carapace and the epigynal area seem to establish it as a new species.

*Records.* Ten female paratypes are in the collection from the following localities in the Panama Canal Zone: Summit, July, 1950; Barro Colorado Island, July-August, 1954; Summit Gardens, August, 1954; Canal Zone Forest Preserve, July, 1954 and December 1957.

### ***Oonops amacus* sp. nov.**

Figures 20-22

*Holotype.* The female holotype is from Simla, Trinidad, W. I., April 18, 1964. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.91 mm, exclusive of the somewhat extended spinnerets. Carapace 0.74 mm long; 0.60 mm wide opposite posterior border of second coxae where it is widest; 0.33 mm tall opposite anterior border of third coxae where it is tallest; rises considerably from PME to beginning of steep posterior declivity (Fig. 20); surface smooth with a moderately well developed coat of erect, light colored hair; without a definite median thoracic fovea. Eyes: six in two rows in a fairly compact group; posterior row occupies nearly nine-tenths of width of carapace at that level and is moderately recurved (Fig. 21). Ratio of eyes ALE : PME : PLE = 8 : 8.5 : 7. ALE separated from one another by nearly five-eighths of their diameter, separated from PME by a little less than one-fourth of their diameter and barely separated from PLE. PME contiguous to one another for one-third of their circumference and separated from PLE by a fairly broad line. Height of clypeus probably about equal to the radius of ALE; clypeus with numerous spiniform bristles. Chelicerae: vertical; parallel; without special modifications. Maxillae and lip: apparently typical of the genus; close observation prevented by folded, fragile legs. Sternum: scutiform; convex; as wide as long; posterior end bluntly rounded and extended halfway between fourth coxae which are separated by slightly more than their width. Legs: 4213 in order of length; spines quite well developed but they are less conspicuous than in *Oonops persitus* sp. nov.; first tibia with about five pairs of ventral spines with some irregularities; first metatarsus with about four pairs of ventral spines also with some irregularities and with differences between right and left; second tibia with spines nearly like those on first tibia; about the same for the second metatarsus; third and fourth legs also with numerous spines on tibiae and metatarsi; palp with numerous slender spines especially on the tarsus; no claw observed on palpal tarsus. Abdomen: broad ovoid; with two rather weakly outlined ventral scuta as shown in Figure 22; spinnerets essentially typical of the genus; epigynal area obscure but apparently somewhat distinctive (Fig. 22). Color in alcohol: carapace, legs, sternum and associated parts all yellowish with variations; black pigment in ocular area essentially as shown in Figure 21; abdomen white with grayish, irregular, small spots showing through from within; scuta yellowish with variations; on the venter just anterior to the base of the spinnerets are two clusters of very small dots.

*Diagnosis.* Although relationships among species in this genus are very difficult to establish, this species appears to be closely related

to *Oonops pallidulus* (Chickering). The relative position of the eyes, the pedal spines, the shape of the carapace and the features of the epigynal area all seem to establish this as a new and distinct species.

*Records.* One female paratype was taken with the holotype; one female, on loan from the American Museum of Natural History, New York City, was taken in Arima Valley, Trinidad, W. I. 800-1200 ft. elevation, February 10-22, 1964 (Wygodzinsky & Rosen). The male is unknown.

*Oonops donaldi* Chickering

Figure 23

*Oonops donaldi* Chickering, 1951: 226, figs. 14-16. The holotype male from Barro Colorado Island, Panama Canal Zone is in the Museum of Comparative Zoology, Harvard University.

Only one male from Barro Colorado Island, Panama Canal Zone, June, 1950 has been added to the collection since the holotype was collected in 1936. Two females taken with this male appear to be immature and unfit for description.

*Oonops itascus* sp. nov.

Figures 24-26

*Holotype.* The male holotype is from Simla, Trinidad, W. I., April 23, 1964. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.58 mm. Carapace 0.69 mm long; 0.57 mm wide opposite second coxae where it is widest; about 0.3 mm tall; rises immediately behind PME and continues a gradual rise to highest point opposite interval between third and fourth coxae and then descends steeply to posterior border; similar to that of *Oonops donaldi* Chickering in profile; with no evidence of a median thoracic pit or groove; with a sparse covering of dark hairs; surface smooth and shining. Eyes: six as usual in a compact group; posterior row recurved and occupies nearly the entire width of the carapace at that level (Fig. 24). Ratio of eyes ALE : PME : PLE = nearly 7 : 8 : 7. ALE separated from one another by nearly five-sevenths of their diameter; subcontiguous to PME and slightly separated from PLE. PME contiguous to one another and subcontiguous to PLE. Height of clypeus nearly equal to radius of ALE. Only a few inconspicuous bristles in ocular area. Chelicerae, maxillae and lip: all appear to be typical of the genus and without special modifications. Sternum: convex; scutiform; slightly the

widest between second coxae but nearly as wide between first coxae; surface without grooves, smooth and shiny; almost as wide as long; bluntly rounded at posterior end which extends midway between fourth coxae which are separated by nearly 1.5 times their width. Legs: 4213 in order of length; long and slender; true spines appear to be present on all legs; these are long, slender and transparent; many spiniform bristles and hairs are also present; fourth femur nearly as long as abdomen. Palp: very distinctive; the femur is much inflated; the patella is short and curved; the tibia is without special modifications; the tarsus with its bulb and associated structures is curiously modified (Fig. 26). Abdomen: ovoid; without special modifications; epigastric and ventral scuta faintly outlined. Color in alcohol: ocular area with a moderate amount of black pigment; cephalothorax, legs and mouth parts yellowish with varia-

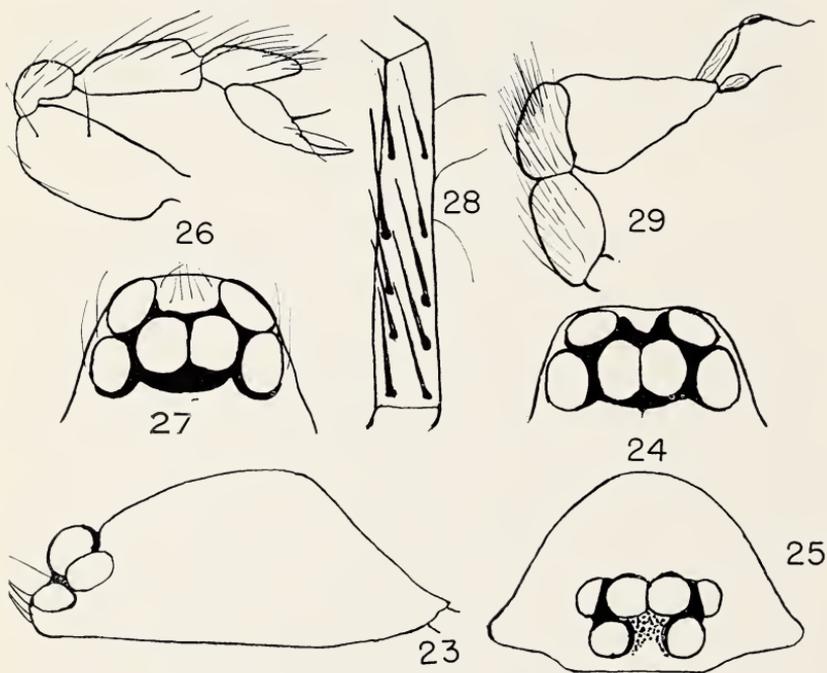


Fig. 23. *Oonops donaldi* Chickering; carapace of male; left lateral side. Figs. 24-26. *Oonops itascus* sp. nov. Figs. 24-25. Eyes of male holotype from above and from in front, respectively. Fig. 26. Left male palp; prolateral view. Figs. 27-29. *Oonops trapellus* sp. nov. Fig. 27. Eyes of male holotype from above. Fig. 28. Left second tibia; ventral view. Fig. 29. Left palp of male holotype; prolateral view.

tions; palps medium brown; abdomen very light yellowish, nearly white with several irregular, small, darker spots just anterior to the spinnerets on the venter.

*Diagnosis.* It is difficult to relate this species closely to any known species but its eyes, shape of the carapace and pedal spines seem to place it fairly close to *Oonops donaldi* Chickering. I believe that the features of the palp definitely establish it as a new species.

*Records.* Two male paratypes were taken in the same locality and on the same day as the holotype. The female is unknown.

### ***Oonops trapellus* sp. nov.**

Figures 27-29

*Holotype.* The male holotype is from Simla, Trinidad, W. I. April 19, 1964. The name of the species is an arbitrary combination of letters.

*Description.* Total length nearly 1.75 mm (body somewhat curled). Carapace 0.79 mm long; 0.59 mm wide opposite interval between second and third coxae where it is widest; 0.32 mm tall opposite third coxae where it is tallest; rises from PME to highest point and then descends steeply to posterior border with a slight concavity about the middle of the declivity; in profile it appears much like that of *Oonops itascus* sp. nov.; surface smooth with a sparse covering of dark hairs. Eyes: six as usual; posterior row rather strongly recurved and occupies nearly entire width of carapace at that level (Fig. 27). Ratio of eyes ALE : PME : PLE = nearly 9 : 8.5 : 8. ALE separated from one another by nearly their diameter; separated from PME by a fairly broad line and are subcontiguous to PLE. PME contiguous to one another for fully one fourth of their circumference and separated from PLE by a fairly broad line. Height of clypeus obscure but probably somewhat less than the radius of ALE; pigment in ocular area with a reddish tint. Chelicerae: apparently typical of the genus; without special modifications. Maxillae: parallel; distal end probably divided but details undetermined because of fragility of holotype and scarcity of paratypes for dissection. Lip: apparently as usual in the genus, without special modifications. Sternum: scutiform; convex; not noticeably lobed or grooved; only slightly longer than wide between second coxae where it is widest but nearly as wide between first coxae; appears to be firmly united to lip; bluntly terminated just before bases of fourth coxae which are separated by considerably more than their width. Legs: 4213 in order of length; spines quite conspicuous

especially on first and second legs (Fig. 28). Palp: essential features shown in Figure 29; tarsal features quite distinctive. Abdomen: ovoid; without special modifications; epigastric and ventral scuta barely indicated. Color in alcohol: carapace light yellowish with pigment in ocular region as shown in Figure 27; legs like carapace above but lighter below; sternum very light yellowish and mouth parts essentially the same with some variations; abdomen nearly white.

*Diagnosis.* This species appears to be closely related to *Oonops itascus* sp. nov. from Trinidad, W. I. with relationships as indicated. The features of the palpal tarsus definitely establish it as a new species.

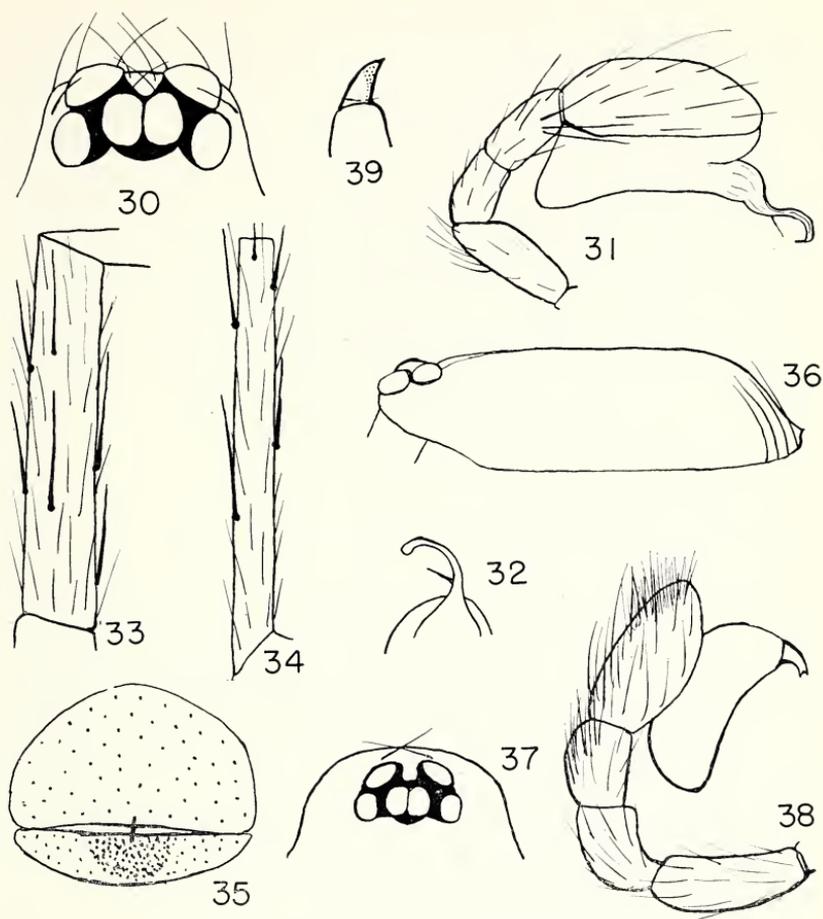
*Records.* One male paratype was taken with the holotype. The female is unknown.

### **Oonops anoxus** sp. nov.

Figures 30-35

*Holotype.* The male holotype is from Barro Colorado Island, Panama Canal Zone, May 17, 1964. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.76 mm exclusive of the extended spinnerets; including these organs, total length is 1.91 mm. Carapace 0.79 mm long; 0.56 mm wide opposite second coxae where it is widest; nearly 0.30 mm tall; gently raised just behind PME and then nearly level along midline to beginning of moderately steep posterior declivity; surface smooth and shining; with a moderately well developed coat of dark hairs; with no evidence of a median thoracic groove or pit. Eyes: six as usual in a moderately compact group (Fig. 30); posterior row recurved and only a little wider than anterior row; posterior row occupies a little more than four-fifths of the width of the carapace at that level. Ratio of eyes ALE : PME : PLE = nearly 8.5 : 8 : 7. ALE separated from one another by slightly more than half their long axis; separated from PME by a little less than one-fourth of their long axis and from PLE by a narrow line. PME contiguous to one another for nearly one-third of their circumference and separated from PLE by nearly one-sixth of their long axis. Height of clypeus equal to nearly three-eighths of the long axis of ALE. Chelicerae, maxillae and lip all apparently quite typical of the genus; with no special modifications observed. Sternum: rather strongly elevated; longer than wide in ratio of nearly 5 : 4; slightly lobed along margins; rounded posterior



Figs. 30-35. *Oonops anoxus* sp. nov. Fig. 30. Eyes of male holotype from above, Fig. 31. Left palp of male holotype; prolateral view. Fig. 32. Tip of left palpal tarsus; ventral view. Figs. 33-34. Fourth tibia and metatarsus, respectively; prolateral views. Fig. 35. Epigynal area of female paratype from below. Figs. 36-39. *Oonops sativus* sp. nov. Fig. 36. Carapace of paratype male; left lateral side. Fig. 37. Eyes of male holotype from above. Fig. 38. Left palp of male holotype; prolateral view. Fig. 39. Tip of left palpal tarsus; nearly dorsal view.

end extended between fourth coxae which are separated by nearly their width; with a cluster of stiff bristles at posterior end and at each of the slightly indicated marginal lobes. Legs: 4123 in order of length; first and second legs seem to be without spines but third and fourth legs bear several spines especially on tibiae and metatarsi (Figs. 33-34). Palp: femur of moderate length; patella and tibia short and without special modifications; tarsus inflated and with embolus and accompanying spinule as shown in Figures 31-32; the position of the spinule seems to vary among the paratypes. Abdomen: ovoid in general; spinnerets slender and elongated; epigastric and narrow ventral scuta weakly outlined. Color in alcohol: carapace, sternum, legs and mouth parts yellowish with variations; black pigment in ocular region essentially as shown in Figure 30; abdomen nearly white in general but on the venter just anterior to the spinnerets are two groups of minute, brownish spots closely crowded together; the scuta are light yellowish.

*Female paratype.* Total length, exclusive of the extended spinnerets, 1.98 mm; including the spinnerets total length is 2.14 mm. Carapace 0.85 mm long; 0.64 mm wide opposite second coxae where it is widest; 0.33 mm tall; otherwise essentially as in male holotype. Eyes: six as usual in the genus. Ratio of eyes ALE : PME : PLE = nearly as in male; PME quite elongated and others with some irregularities in outline; ALE separated from one another by nearly their radius and separated from PME and PLE by a broad line. PME contiguous to one another for nearly one-third of their circumference and separated from PLE by a broad line. Height of clypeus nearly equal to one-fourth of the diameter of ALE. Chelicerae, maxillae and lip apparently typical of females of the genus. Sternum: essentially as in male. Legs: 4123 in order of length as in male holotype; spines apparently as in male but somewhat less obscure than in that sex; palpal spines numerous, especially on the tarsus. Abdomen: typical of females of the genus in general; spinnerets much extended, especially the posterior pair; epigynal area obscurely distinctive (Fig. 35).

*Diagnosis.* After repeated consideration I have concluded that I must regard this species together with four additional species as constituting a group somewhat clearly separated from others treated in this paper. The male palpal tarsus is closely similar to that of *Oonops chilepensis* Chamberlin and Ivie, 1936 from Mexico. No minute spine was apparently seen near the base of the embolus in the Mexican species, however, and no mention was made of many other important features in that species.

*Records.* The described female paratype was taken with male paratypes on Barro Colorado Island, Panama Canal Zone, May 20-21, 1964. The specimens now assigned to this species were for some time considered to represent two different species but are now placed together. Males are now in the collection from the following localities: Balboa, Panama Canal Zone, August, 1936; Boquete, Panama, August 4-11, 1954; Panama Canal Zone Forest Preserve, Jan. 8, 1958 and Panama Canal Zone Summit Gardens, May 1964. Nineteen females are in the collection from Boquete, Panama, Aug. 4-11, 1954; some of these are probably immature and their status uncertain; one additional female and immature females are in the collection from Barro Colorado Island, May 20-21, 1964.

***Oonops sativus* sp. nov.**

Figures 36-39

*Holotype.* The male holotype is from Simla, Trinidad, W. I., April 16, 1964. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.3 mm. Carapace 0.59 mm long; 0.46 mm wide opposite interval between second and third coxae where it is widest; nearly 0.15 mm tall; lower than usual in the genus as observed in this study (Fig. 36); nearly level medially from PME to beginning of moderately steep posterior declivity; with a sparse supply of dark bristles and with a series of eight to ten long, slender spines along lateral margins of the posterior declivity and contiguous ventral border of the carapace; with no definite median fovea. Eyes: six as usual in a compact group; posterior row very moderately recurved and occupies only about half the width of the carapace at that level. Ratio of eyes ALE : PME : PLE = nearly 5 : 4 : 3.5. ALE separated from one another by a little more than their radius; separated from PLE by one-fifth of their diameter and from PME by a slightly greater distance. PME contiguous to one another for nearly one third of their circumference and subcontiguous to PLE. Clypeus obscure but probably somewhat less than diameter of ALE in height. Black pigment in ocular area essentially as shown in Figure 37. Chelicerae: vertical; parallel; moderately long and slender; without special modifications. Maxillae: moderately long and slender; slightly convergent; narrowed distally. Lip: nearly as wide at base as long; appears to be firmly united to sternum. Sternum: convex; with many stiff, dark bristles some of which are erect; not notably lobed; surface quite smooth; longer than wide

in ratio of nearly 4 : 3; bluntly terminated between bases of fourth coxae which are separated by a little more than their width; first and second coxae somewhat elongated; third coxae globose; fourth coxae moderately elongated. Legs: 4123 in order of length; long and slender spines are present on third and fourth legs but probably not on first and second; what have usually been designated as spini-form bristles might, by some araneologists, be regarded as very slender spines. Palp: femur of moderate length, not inflated; patella and tibia short; tarsus quite distinctive (Figs. 38-39). Abdomen: slender ovoid; with a rather coarse coat of dark hair somewhat concentrated at base; spinnerets typical of the genus; region of epigastric scutum appears to be lightly chitinized. Color in alcohol: carapace a medium dark yellowish with fine brownish streaks and dots from ocular region along broad lateral regions thus making a rather distinctive color pattern; legs yellowish above but somewhat lighter below; sternum and mouth parts like legs above with variations; abdomen nearly pure white.

*Female paratype.* Total length 1.63 mm. Carapace 0.61 mm long; 0.45 mm wide opposite posterior border of second coxae where it is widest; about 0.17 mm tall; otherwise essentially as in male. Eyes: ratio of eyes ALE : PME : PLE = 4.5 : 4 : 3.5; otherwise essentially as in male holotype. Chelicerae, maxillae and lip all essentially as in male holotype. Epigynal area appears to be completely lacking in distinctive features. Color in alcohol: almost exactly as in male holotype except that the brownish streaks and dots on the carapace are less conspicuous than in the male.

*Diagnosis.* This is the second of five species grouped together because thus far I have been unable to relate it closely to any other known species. The features of the ocular area, the shape of the carapace and the features of the male palp seem to establish it as a new species.

*Records.* The described female paratype was taken on the same day and in the same locality as the holotype. Several paratypes of both sexes were taken in the vicinity of Simla, Trinidad, W. I., in April, 1964.

### **Oonops sicorius** sp. nov.

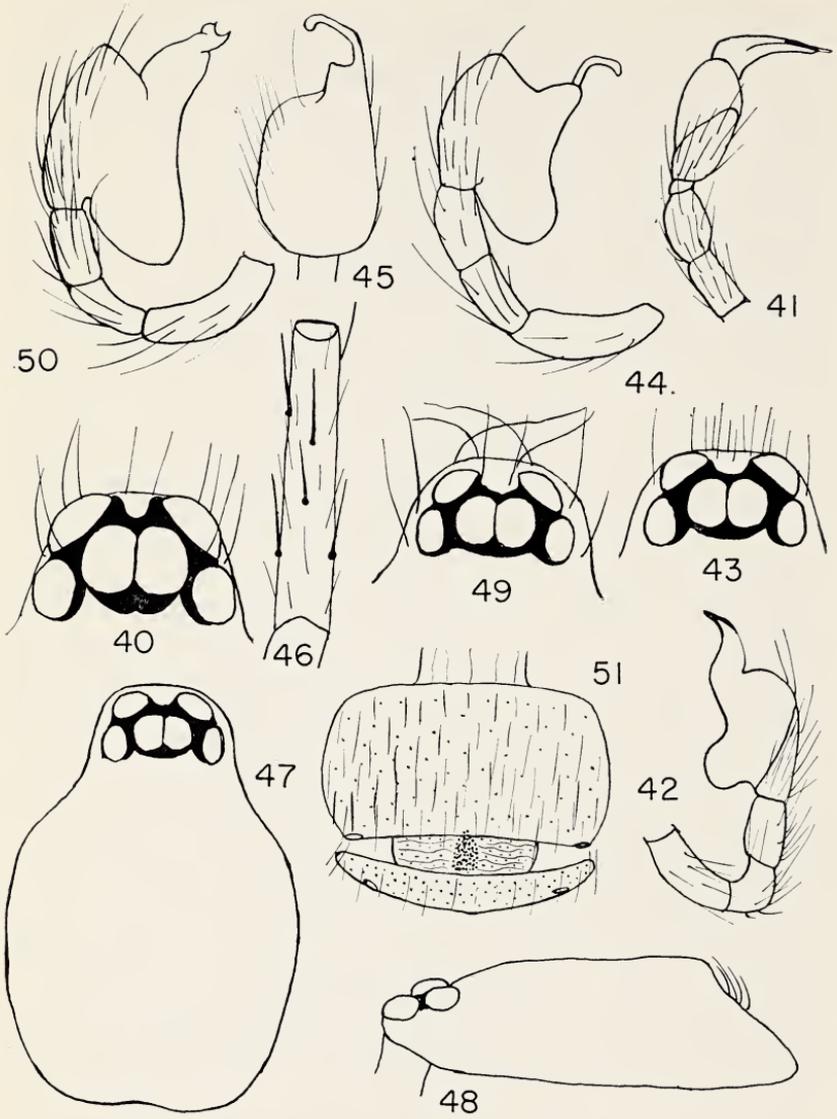
Figures 40-42

*Holotype.* The male holotype is from Fuik (Oostpunt), Curaçao, Nederlands Antilles, December 26, 1962; collected by Dr. and Mrs. H. W. Levi and B. de Jong. The name of the species is an arbitrary combination of letters.

*Description.* Total length 1.19 mm, exclusive of the extended spinnerets; including the spinnerets total length is 1.32 mm. Carapace 0.55 mm long; 0.45 mm wide opposite second coxae where it is widest; 0.26 mm tall; only slightly arched and only moderately raised from PME to beginning of steep posterior declivity opposite interval between second and third coxae; surface smooth with a moderate number of dark, stiff bristles. Eyes: six as usual and in a moderately compact group; posterior row moderately recurved and occupies practically the entire width of the carapace at that level (Fig. 40). Ratio of eyes ALE : PME : PLE = nearly 7 : 6.5 : 6. ALE separated from one another by nearly one-half their long axis; separated from PME only by nearly one-tenth of their long axis and nearly contiguous to PLE at one point. PME contiguous to one another for about one-fourth of their circumference and separated from PLE by a line. Apparently the clypeus is practically eliminated because the ALE are placed so low and because the margin of the carapace turns dorsally between these eyes. Chelicerae and lip appear to be typical of the genus and without special modifications. Maxillae: these appear to be divided distally to form tooth-like terminations; fragility of the holotype and lack of paratypes prevents more detailed observation. Sternum: strongly elevated; nearly as wide as long; surface smooth and shining; with numerous bristles the most conspicuous of which are clustered opposite the coxae and at the bluntly rounded posterior end between the bases of the fourth coxae which are separated by about their width. Legs:  $4I=23$  in order of length; no spines have been observed on first and second legs; the third and fourth legs bear a few spines; trichobothria have been observed on tibiae and metatarsi. Palp: all segments except the tarsus appear to be quite typical of males of the genus and without special modifications; the tarsus appears to be quite unusual among species studied in the preparation of this paper (Figs. 41-42). Abdomen: ovoid; 0.61 mm long, exclusive of the extended spinnerets; 0.37 mm wide; no scuta visible; spinnerets essentially typical of the genus. Color in alcohol: abdomen nearly white; all other parts light yellowish except the black pigment in the ocular area.

*Diagnosis.* It is difficult to relate this species directly to other species within the genus but it seems to belong with *Oonops anoxus* sp. nov. together with three other species as indicated in the appropriate descriptions. The features of the palp definitely establish it as a new species.

*Records.* There are no male paratypes and the female is unknown.



***Oonops tenebus* sp. nov.**

Figures 43-46

*Holotype.* The male holotype is from the Panama Canal Zone Forest Preserve, February 14, 1958. The name of the species is an arbitrary combination of letters.

*Description.* Total length, exclusive of the extended spinnerets, 1.39 mm; including the spinnerets total length is 1.49 mm. Carapace 0.68 mm long; 0.54 mm wide opposite second coxae where it is widest; nearly 0.26 mm tall; with no median thoracic groove observed; nearly level along median region from just behind PME to beginning of steep posterior declivity. Eyes: six as usual in a moderately compact group (Fig. 43); seen from above, posterior row recurved and occupies a little more than five-sixths of width of carapace at that level. Ratio of eyes ALE : PME : PLE = nearly 7.25 : 7 : 6. ALE separated from one another by nearly six-sevenths of their long axis; separated from PME by nearly two-sevenths of their long axis and nearly contiguous to PLE. PME contiguous to one another for about one-fourth of their circumference and separated from PLE by nearly one-fifth of their long axis. Clypeus difficult to observe but its height appears to be nearly three-sevenths of the long axis of ALE. Chelicerae: vertical; parallel; with no special modifications observed. Maxillae: convergent; considerably longer than lip; with no special modifications observed. Lip: essentially typical of the genus. Sternum: fragile, folded legs prevent the usual close observation; moderately elevated; longer than wide in ratio of nearly 4 : 3; extended just to bases of fourth coxae which are separated by nearly their width; with no lobes or grooves observed. Legs: 4123 in order of length; apparently only very few spines on first and second legs; third and fourth legs with numerous spines especially on tibiae and metatarsi (Fig. 46). Palp: femur of moderate length; patella and tibia short; tarsus inflated and with obscurely distinctive features (Figs. 44-45). Abdomen: essentially typical of

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Figs. 40-42. *Oonops sicorius* sp. nov. Fig. 40. Eyes of male holotype from above. Figs. 41-42. Left palp of male holotype; nearly dorsal and nearly retrolateral views, respectively. Figs. 43-46. *Oonops tenebus* sp. nov. Fig. 43. Eyes of male holotype from above. Fig. 44. Left palp of male holotype; prolateral view. Fig. 45. Left palpal tarsus of male holotype; nearly ventral view. Fig. 46. Right fourth tibia of holotype; dorsal view. Figs. 47-51. *Oonops vestus* sp. nov. Figs. 47-48. Carapace of male paratype; from above and left lateral side, respectively. Fig. 49. Eyes of holotype from above. Fig. 50. Left palp of male holotype; prolateral view. Fig. 51. Epigynal area of described female paratype from below.

the genus; epigastric scutum barely discernible. Color in alcohol: carapace, legs, mouth parts and sternum all light yellowish with variations; considerable black pigment in ocular area; abdomen very light yellowish, almost white with faintly indicated reticulations; epigastric scutum faintly outlined.

*Diagnosis.* This is the fourth species which I have come to regard as worthy of a separate grouping. It is regarded as being more or less closely related to *Oonops anoxus* sp. nov. but greater clarity on this question must await further study of the genus. The features of the palp together with other features mentioned in the description seem to establish it quite definitely as a new species.

*Records.* Two male paratypes are in the collection from the Panama Canal Zone Forest Preserve, January, 1958 and Summit Gardens, Canal Zone, May, 1964. Two females were collected on the same day and in the same general locality as the male holotype; one of these may be the female of this species but it is not described here because of the uncertainty involved.

### *Oonops vestus* sp. nov.

Figures 47-51

*Holotype.* The male holotype is from Simla, Trinidad, W. I., April 25, 1964. The name of the species is an arbitrary combination of letters.

*Description.* Total length, exclusive of the somewhat extended spinnerets, 1.54 mm. Carapace 0.73 mm long; 0.54 mm wide opposite interval between second and third coxae where it is widest; nearly 0.26 mm tall opposite third coxae where it is tallest; rises gradually but only moderately from PME to beginning of steep posterior declivity (Figs. 47-48); with no definite median fovea; with numerous stiff hairs in ocular region and shorter dark hairs over lateral and posterior surfaces. Eyes: six as usual in a fairly compact group (Fig. 49); posterior row rather strongly recurved and occupies nearly four-fifths of width of carapace at that level. Ratio of eyes ALE : PME : PLE = nearly 7 : 6.5 : 6. ALE separated from one another by nearly five-sevenths of their long axis, subcontiguous to PLE and PME; PME contiguous to one another for more than one-fourth of their circumference and separated from PLE by nearly one-fourth of their long axis. Clypeus very narrow; height probably about equal to one-fourth of the long axis of ALE. Chelicerae, maxillae and lip apparently typical of the genus and without observed special modifications. Sternum: convex; smooth and

shining; with numerous stiff, dark colored hairs; posterior end with a tuft of stiff, dark colored hairs; nearly as wide as long; blunt posterior end extended somewhat between fourth coxae which are separated by nearly their width. Legs: 4123 in order of length; first and second legs with few spines but with many coarse hairs and bristles; third and fourth legs with several long, slender, transparent spines somewhat difficult to distinguish. Palp: with distinctive features essentially as shown in Figure 50; only tarsus with special modifications. Abdomen: ovoid; epigastric scutum slightly chitinized; typical in general of males of the genus. Color in alcohol: cephalothorax, legs and mouth parts yellowish with some variations; abdomen nearly white with three pairs of small, greenish spots on the venter just anterior to the spinnerets.

*Female paratype.* Total length 1.89 mm. Carapace 0.77 mm long; 0.55 mm wide; nearly 0.26 mm tall; otherwise essentially as in male. Eyes: ratio of eyes ALE : PME : PLE = nearly 6 : 6 : 5; otherwise essentially as in male. Chelicerae, maxillae, lip, sternum, legs and spines all essentially as in male; details regarded as unnecessary with paratype. Abdomen: essentially as in male except for the epigynal area and related scuta; with a weakly outlined epigastric scutum; just behind this scutum is a narrow, chitinized band apparently representing the ventral scutum; epigynal area obscurely distinctive (Fig. 51). Color in alcohol: essentially as in male in general; the dark, subsurface spots just anterior to the spinnerets are brownish in color.

*Diagnosis.* This is the last of the group of five species whose relationships to already known species has been difficult to determine. I believe that the features of the ocular area, the shape of the carapace, the features of the male palp and the epigynal area of the female establish it as a new species.

*Records.* The described female paratype was taken in the same locality and on the same day as the male holotype. A male and a female collected by Dr. N. A. Weber in Trinidad, W. I. but with no date indicated are now in the collection. In April, 1961 I collected three males and ten females in the vicinity of Simla, Trinidad, W. I.

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