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Volume 82

1975

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No. 1

MEGASECOPTERA FROM THE LOWER PERMIAN OF MORAVIA*

BY JARMILA KUKALOVA-PECK

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The Megasecoptera are separated from the closely related Paleozoic Order Palaeodictyoptera by having nearly homonomous, elongate, petiolate (or basally narrowed) wings; usually a simple venation; and Sc and R crowded towards the costal margin. The body structures in both orders are virtually identical, so far as known. The relationship of these groups gives the impression of being like that between dragonflies and damselflies within the Order Odonata, rather than that between two different orders (Kukalova-Peck, 1973). Only recently has the wing attachment to the body in both groups been studied (Kukalova-Peck, 1974), revealing evidence which justifies the recognition of Megasecoptera as a distinct order. The Palaeodictyoptera have been found to retain many features of the primitive paleopterous wing base, such as the fully developed subcostoanal axillary plate. In the Megasecoptera, however, the subcostoanal axillary plate is missing and the axillary sclerites are highly specialized and largely fused. The morphology of the axillary region in Megasecoptera is unique within the Paleoptera and shows once again the potential for extraordinary diversity in the paleopterous orders.

The Lower Permian locality of Obora in Moravia (Czechoslovakia) has recently yielded twelve specimens of Megasecoptera, referred here to six new families: Caulopteridae, Hanidae, Arcioneuri-

*This study has been supported in part by grant no. GB 39790 from the National Science Foundation (F. M. Carpenter, Principal Investigator, Harvard University) and in part by a publication grant of Carleton University, Ottawa, Canada. I am deeply indebted to Dr. Frank M. Carpenter for critical review of the manuscript and for his manifold support of my work.

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dae, Ancopteridae, Engisopteridae and Alectoneuridae, in addition to the families Bardohymenidae and Moravohymenidae, already reported in a previous paper (Kukalova-Peck, 1972). One of the new species, *Hana lineata*, with a wing about 100 mm long and only 8.3 mm wide, represents an extreme case of specialization of wing shape within the Insecta. Further evidence of the close relationship in wing venation between Megasecoptera and Palaeodictyoptera is now revealed. The postcostal vein, homologous with the "costal brace" in the Ephemeroptera and present in most Palaeodictyoptera, is recognizable in the family Engisopteridae. Intercalated sectors, which also occur in several families of the Palaeodictyoptera, as well as in all dragonflies and mayflies, are present in five of the new genera described below. Also, some of the new species have relatively broad subcostal areas and a richly branched venation very reminiscent of the Palaeodictyoptera.

The Upper Carboniferous (Westphalian) families Frankenholziidae (Germany), Mecynopteridae (Belgium) and the new family Dictyoneurellidae (France) (described below), all of which were previously considered palaeodictyopterous, are apparently related to the newly described families mentioned above and to the primitive family Anchineuridae (Upper Carboniferous, Spain) of the Order Megasecoptera. They are herein referred to that order.

Besides the adults, three nymphal forms are described: *Cauloptera colorata*, *Arcioneura juveniles*, and *Alectoneura europaee*. The nymphal wings are easily distinguished from the adult wings, which are held at right angles to the body, by the characteristic bend in the proximal third of the wing length. This bend determined the oblique-lateral position of the wing pads in the living nymphs, as described by Carpenter and Richardson (1968) in the completely preserved early stage of the megasecopteran nymph of *Mischoptera douglassi*. However, in all isolated nymphs from Obora the angle of the bend is more obtuse than in *Mischoptera douglassi*. This fact together with the larger size and good sclerotization of the venation (the sclerotization being weak in *douglassi*) implies that the nymphal wings from Obora belonged to late, possibly the ultimate, instars. There is no evidence as to whether or not a subimago stage was present in Megasecoptera. In the Palaeodictyoptera, parts of a shed cuticle have been found attached to a female of *Lycocercus goldenbergi* (Kukalova, 1969, p. 449, fig. 32), including a smaller and less sclerotized ovipositor than that of the adult. It is therefore conceivable that the related Megasecoptera, which clearly descended from the Palaeodictyoptera, had adult molts.

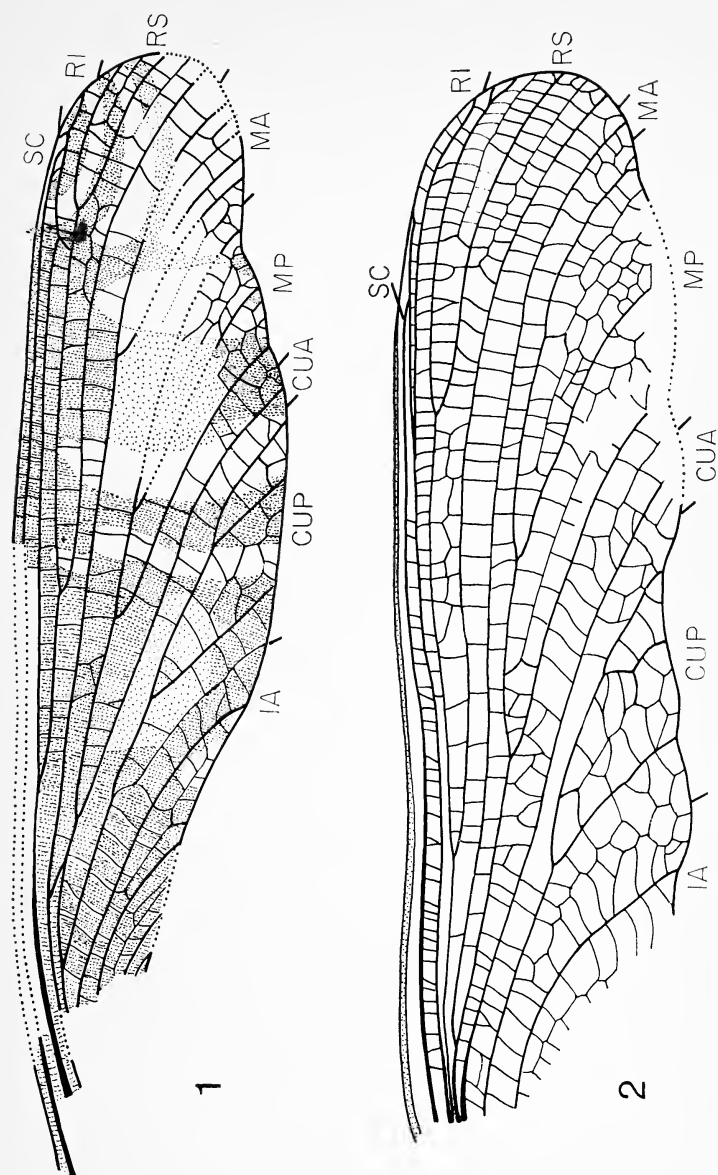


Fig. 1. *Cauloptera colorata* n.sp., specimen 24/1974. Wing fragment, length 38 mm, width 9 mm. Holotype.

Fig. 2. *Ancoptera permiana* n.sp., specimen 30/1974. Wing fragment, length 36 mm, width 9.8 mm. Holotype.

Family **Caulopteridae**, new Family

Nymphal wing: petiolate, broadened beyond mid-wing, narrowed in the apical third; posterior margin undulated. Sc long; stems of R and M not coalesced in the basal third; Rs diverging from R1 before mid-wing; MA and MP branched; MP anastomosed with CuA for a short distance; CuA simple, CuP sending off several branches; 1A with a series of branches. Cross veins numerous, irregular, forming intercalated sectors.

This family differs from the Anchineuridae in the petiolation of the wing, the branched MA and the coalesced MP and CuA.

Although the shape of the wing in the family Caulopteridae and in the following three families is specialized and typical for Megaseoptera, the venation is reminiscent of that in the Palaeodictyoptera. If the proximal, narrow part of the wing has not been preserved, the megaseopterous character of such a fragment would be obscure. This seems to be true for several incompletely preserved wings previously considered palaeodictyopterous, discussed below.

At present this family includes only the following genus:

Cauloptera, new genus

Nymphal wing: moderately slender, with a broad lobe in the third quarter of the wing length; posterior margin undulated beyond mid-wing only within the mp area. Sc, R1 and Rs equally distant from each other, close to, but not crowded towards the costal margin; Rs with 2 long branches; MA with several short branches.

The generic name is derived from the Greek words *kaulos* and *ptera* (petiole + wings) and is considered neuter plural.

Type species: *Cauloptera colorata*, n.sp.

Cauloptera colorata, n.sp.

Figure 1

This species is based on a detached, well-preserved wing pad of a late nymph; the base is narrowed, perhaps petiolate; the basal third is missing.

Nymphal wing: length (estimated) about 41 mm, width 9 mm. Broadened part of the wing forming a smooth, broad lobe; undulations in the mp area shallow; apex comparatively broad and rounded.

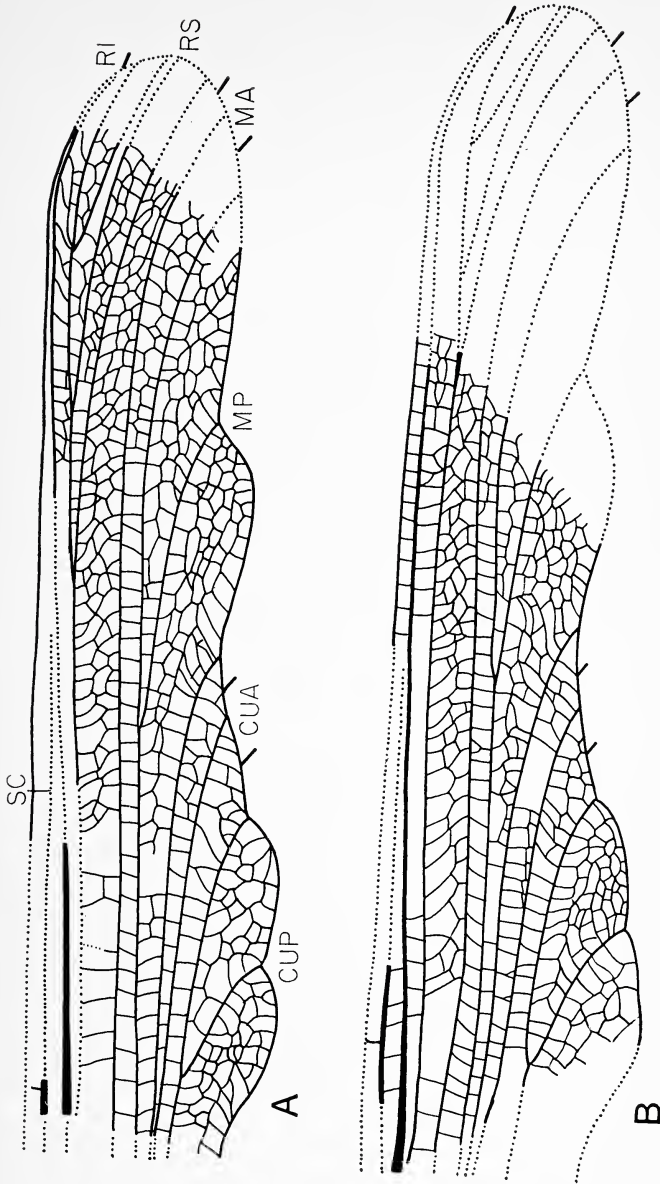


Fig. 3. *Hana flia* n.sp., specimen 25/1974. A. Fore wing fragment, length 45 mm, width 9 mm; B. Hind wing fragment, length 38 mm, width 11 mm. Holotype.

Sc terminating on R1; Rs originating before mid-wing; MA sending off 3 branches; MP with 2 branches; CuA simple, CuP with 2 branches; 1A with a series of about three branches; intercalated sectors mostly short. Wings dark-colored, with irregular light bands becoming crescent in the apical area.

Holotype: No. 24/1974; wing fragment, length 38 mm, width 9 mm; obverse. Paleontological Institute of Charles University, Prague, Czechoslovakia.

Family **Hanidae**, new family

Wing: petiolate, broadened at about mid-wing, narrowed in cua area; posterior margin deeply undulated. Venation simplified; Sc terminating shortly beyond mid-wing; stems of R and M not coalesced in the basal third; Rs diverging from R1 about mid-wing; MA and CuA simple, MP and CuP with few branches; MP anastomosed with CuA for a short distance; 1A simple. Archedictyon and irregular cross veins present. Intercalated sectors absent.

The family Hanidae differs from the related family Caulopteridae in the more deeply undulated posterior margin, in the short Sc, the simplified venation, the presence of the archedictyon and in the absence of the intercalated sectors.

The large, elongate, extremely narrow wings of Hanidae, with an intricate outline, are among the most unusual wings within the Paleoptera. The preservation of a primitive archedictyon, which in other families becomes reduced to cross veins by Westphalian time, is a remarkable example of mosaic evolution in Paleozoic Paleoptera.

Type genus: *Hana*, new genus.

Hana, new genus

Wing: very long and narrow; posterior margin forming several prominent lobes in the median and cubital areas. Sc distant from anterior margin in the basal half of the wing; Rs with about 3 short branches; 1A following closely the posterior margin. Wing membrane with a dense covering of tubercles.

This genus is represented by two species: *H. filia*, based on the distal half of a wing, and *H. lineata*, n.sp., based on the proximal half of a wing. The genus is named for my daughter Hana, who has been very helpful to me in the field work.

***Hana filia*, n.sp.**

Figures 3-6a

This species is based upon beautifully preserved distal halves of the fore and hind wings, in normal positions (see reconstruction of the outlines, fig. 6a). The hind wing is somewhat longer and broader at the end of the anal area than the fore wing. The venation is almost identical in the wings, though the first branch of Rs originates more markedly distally in the hind wing. In both wings, the costal margin is proximally broken away; in the fore wing, the posterior part of the wing is superimposed over R. Both wings are restored to the original widths in figure 3.

Besides the holotype, a small fore wing fragment (specimen no. 26/1974, fig. 4), and a hind wing fragment (specimen no 27/1974, fig. 5) were found, showing a coloration and a lobation of the posterior margin remarkably similar to that of the holotype.

Wings: length of the fore wings about 84 mm, width 10.5 mm; length of the hind wing about 88 mm, width 12 mm. Posterior margin deeply incised at the end of all branches of CuP and MP₂; Rs originating before mid-wing, Rs branches originating in the distal quarter of the wing; MA and CuA simple; MP with 2 branches, CuP probably with 1 short branch; archidictyon and cross veins strong, conspicuous. Wing membrane covered with numerous prominent tubercles and with extensive, irregularly outlined dark areas; hind wings darker than fore wings.

Holotype: no. 25/1974 (fore wing fragment, length 45 mm, width 9 mm; hind wing fragment, length 38 mm, width 11 mm; obverse and reverse); specimen no. 26/1974 (fore wing fragment, length 33 mm, width 9.5 mm; obverse and reverse); specimen no. 27/1974 (hind wing fragment, length 19 mm, width 8.4 mm; obverse and reverse). Paleontological Institute of Charles University, Prague, Czechoslovakia.

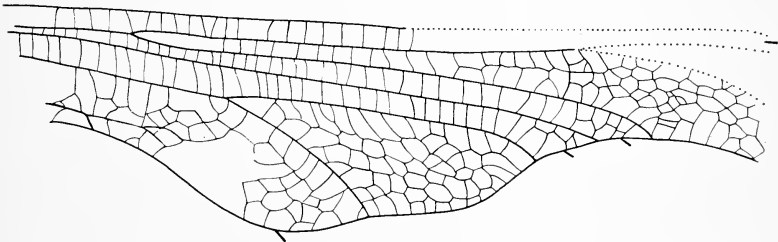


Fig. 4. *Hana filia* n.sp., specimen 26/1974. Fore wing fragment, length 33 mm, width 9.5 mm.

Hana lineata, n.sp.

Figures 6b and 7

This species is based upon the proximal half of the longest and narrowest wing known in the Megasecoptera (see reconstruction, fig. 6b). The subcostal area is proximally partially superimposed across R. In figure 7 the venation is shown restored to its normal position.

Wing: length about 96 mm, width 8.3 mm. Posterior margin convexly bent at the end of all branches of CuP; Rs originating beyond mid-wing; first branch of MP long, starting before mid-wing; CuP with a series of 3 short branches; archidictyon and cross veins similar to those of *flia*, but finer. Wing membrane densely covered with small tubercles. A few dark spots occur in the subcostal area.

This species differs from *flia* in its narrower wings, finer membrane and its series of 3 CuP branches.

Holotype: no. 28/1974 (wing fragment, length 58 mm, width 8.3 mm; reverse). Paleontological Institute of Charles University, Prague.

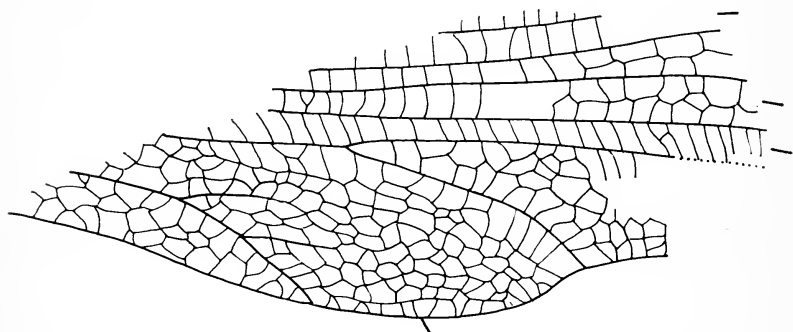


Fig. 5. *Hana flia* n.sp., specimen 27/1974. Hind wing fragment, length 19 mm, width 8.4 mm.

Family Arcioneuridae, new family

Nymphal wing: petiolate, narrow, broadened at about mid-wing; posterior margin undulated. No coalescing veins; Sc short; Rs diverging from R1 well before mid-wing; MA and MP with several branches; CuA and CuP with few short branches. Cross veins numerous, forming intercalated sectors.

This family differs from the Caulopteridae in the shorter Sc and in lacking the coalesced MP and CuA. Type genus: *Arcioneura*, new genus.

Arcioneura, new genus

Nymphal wings: very long and narrow. RI close to the costal margin in the distal half of the wing; Rs with about 2 long branches; MA with a series of short branches; MP forming a long branched fork. Cross veins almost regular.

The generic name is derived from the Greek words *arkios* and *neura* (certain + veins) and is considered neuter plural.

Type species: *Arcioneura juveniles*, n.sp.



Fig. 6. Hanidae, reconstruction of the specialized wing outline. A. *Hana filia* n.sp., fore and hind wing in natural position. Fore wing, length about 84 mm, width 10.5 mm. B. *Hana lineata* n.sp. Wing, length about 96 mm, width 8.3 mm.

Arcioneura juveniles, n.sp.

Figure 8

This species is based upon a detached wing of a nymph, bent typically into oblique-lateral position in the basal third. The slight angle of the bend and the advanced sclerotization of veins and cross veins indicate that the nymph was close to the adult stage.

Nymphal wing: length about 19 mm, width 2.6 mm. Sc terminating shortly beyond mid-wing; Sc much closer to R and RI than to the costal margin; Rs detaching from RI at the end of the basal third, the first branch of Rs starting shortly beyond mid-wing; MA sending off 4 branches, MP probably 3 times branched; CuP with 1 branch; 1A probably simple.

Holotype: no. 29/1974 (almost complete wing, length 18.3 mm, width 2.6 mm; reverse). Paleontological Institute of Charles University, Prague.

Anconeura, new genus

Wings: very long and narrow; posterior margin undulated beyond mid-wing. R1 close to the costal margin; Rs with about 4 long branches, sometimes forked; MA with a series of short branches; MP with a long, branched fork; CuA forked. Cross veins irregular.

Anconeura differs from *Arcioneura* by its larger wings, which have more numerous branches on Rs and CuA. The generic name is derived from the Greek words *ankos* and *neura* (curve + veins) and is considered neuter plural.

Type species: *Anconeura havlatai*, n.sp.

Anconeura havlatai, n.sp.

Figure 9

This species is monotypic, based upon an adult wing with a well preserved, long, petiolate base. Distally from mid-wing, the wing is broken into several dislocated pieces. In figure 8, the venation is shown restored to its normal pattern.

Wing: length about 41 mm, width 5.7 mm. Wing broadest shortly beyond mid-wing; posterior margin with 4 undulations; at its proximal end the petiole broadens for its attachment to the thorax. Rs originating at about the end of the basal third, the first branch of Rs starting before mid-wing; MA sending off 3 branches; MP probably branched 4 times; CuA probably branched 5 times; CuP with 1 branch. 1A close and parallel with the posterior margin, with one branch.

Holotype: no. 23/1974 (almost complete wing, length 40 mm, width 5.7 mm; obverse). Paleontological Institute of Charles University, Prague.

The species is named for Karel Havlata of Prague, who has collected hundreds of specimens of insects in the Obora beds.

Family **Ancopteridae**, new family

Wings: elongate; almost equally broad beyond mid-wing; posterior margin undulated. Sc somewhat shortened; stems of R and M not coalesced in the basal third; Rs diverging from R1 much before mid-wing; MA and CuA simple, MP and CuP branched. Cross veins numerous, forming conspicuous intercalated sectors.

The family Ancopteridae differs from the related family Dictyoneurellidae (Westphalian, France), and Anchineuridae (U. Carboniferous, Spain) in the presence of the undulated posterior margin,

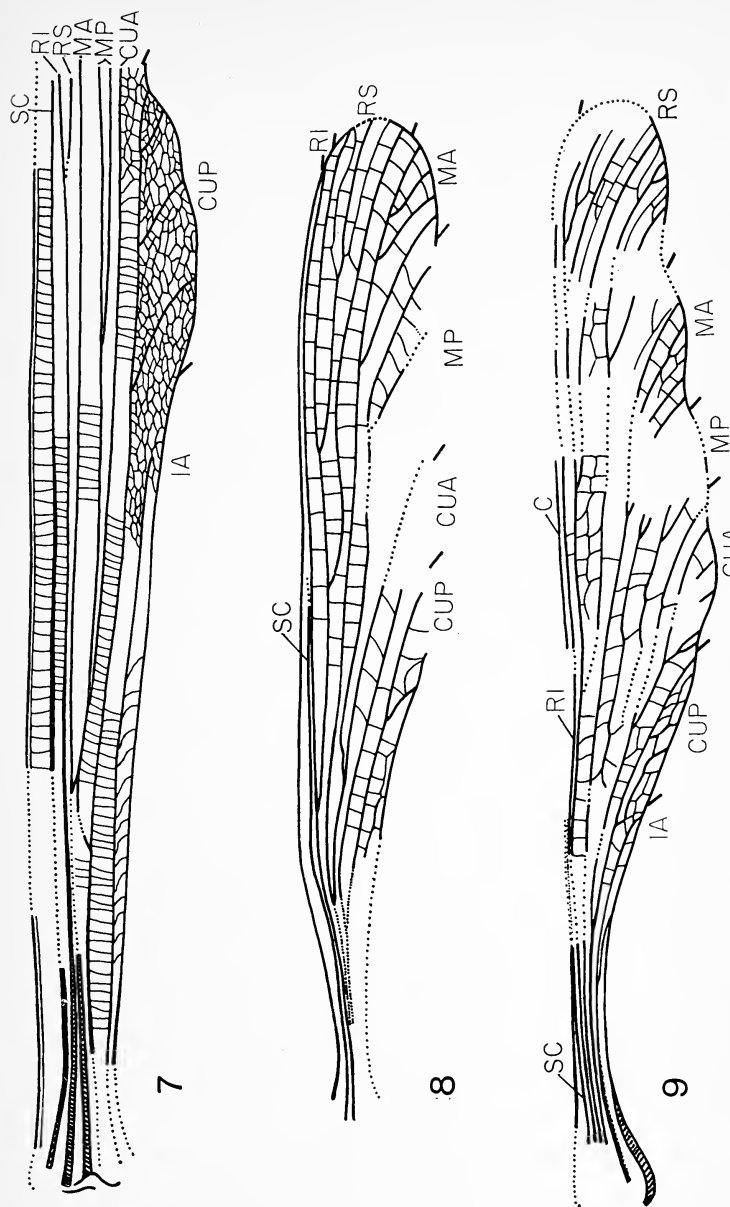


Fig. 7. *Hana lineata* n.sp., specimen 28/1974. Wing fragment, length 58 mm, width 8.3 mm. Holotype.
 Fig. 8. *Arcioneura juvenales* n.sp., specimen 29/1974. Wing, length 18.3 mm, width 2.6 mm. Holotype.
 Fig. 9. *Arcioneura havelatai* n.sp., specimen 23/1974. Wing, length 40 mm, width 5.7 mm. Holotype.

in the longer Rs and in the branching of the main veins, which generally arise much more basally. From the Arcioneuridae it differs in the longer Sc, in the simple MA and CuA; from the Caulopteriidae in the simple MA and the absence of coalescence between MP and CuA.

Type genus: *Ancoptera*, new genus.

Ancoptera, new genus

Wings: long but only slightly narrow, with broadly rounded apex; posterior margins with only shallow undulations. C broad, flattened; Sc and R1 crowded towards the costal margin in the distal third, but well remote from it proximally; Rs with 2 long branches; stem of R, stem of M and CuA touching each other in the proximal third of the wing; mp area large.

The generic name is derived from the Greek words *ankos* and *ptera* (curve + wings) and is considered neuter plural.

Type species: *Ancoptera permiana*, n.sp.

Ancoptera permiana, n.sp.

Figure 2

This species is based upon a well preserved adult wing, with the narrowed basal part missing. The long anterior branch of R1 is probably only an individual variation. Besides the holotype, another specimen (no. 31/1974, fig. 10) was found, this being the distal part of a wing. In this wing fragment, the apical part is more pointed and the Rs branches are much shorter than in the holotype. The veins and cross veins are surrounded by dark-colored, narrow bands, as in *Dictyoneurella*. Specimen no. 31/1974 probably belongs to a separate species, but because of the small size of the fragment it is referred here to *Ancoptera* sp.

Wing: length about 43 mm, width, 9.8 mm. Posterior margin with 4 undulations in the distal part of the wing, Rs diverging from R1 at about the first fifth of the wing length; first branch of Rs originating much before mid-wing; MP with a series of 3 branches; CuP forming a wide fork, mp-cua area and cup-anal area are wide. Intercalated sectors long and regular.

Holotype: no. 30/1974 (wing fragment, length 36 mm, width 9.8 mm; obverse and reverse); specimen no. 31/1974 (wing fragment, length 31.5 mm, width 10.7 mm; reverse). Paleontological Institute of Charles University, Prague.

Family **Engisopteridae**, new family

Wings: narrow, but not petiolate, almost uniformly broad in distal half; posterior margin not undulated. Postcostal vein present; Sc terminating shortly before mid-wing, subcostal area relatively broad; Rs short; ma area large and rich in long branches, mp area narrow; CuA simple, CuP with long branches. Cross veins numerous, intercalated sectors present.

This family differs from the Arcioneuridae in the broader wings, the presence of the postcostal vein, the shorter Rs, and larger ma and cup areas. From the primitive family Archineuridae it differs in its relatively broad subcostal area, short Sc and Rs and in the more nearly parallel arrangement of median and cubital branches.

The family Engisopteridae has several characteristics of venation which are among the most primitive known in the Megaseoptera: the relatively broad subcostal area with a series of Sc branches, the postcostal vein, and the generalized, richly branched venation (except for a simple CuA). These particular features are palaeodictyopterous in character, and they are more primitive than their structure in Anchineuridae.

The postcostal vein, which I consider homologous with the "costal brace" of Ephemeroptera, is present in almost all Palaeodictyoptera. In addition to the Engisopteridae, the vein has been found in the Mischopteridae (Carpenter & Richardson 1968, fig. 1, 2), in both adult and nymphal wings. It is probable that this inconspicuous vein has been overlooked in several other families. The postcostal veins are completely reduced in families with a convexly bent Sc at the very base, as in Protohymenidae or Alectoneuridae.

Engisoptera, new genus

Wings: more or less elongate-oval in shape, narrowed across the anal area. C, Sc and R1 equidistant from each other in the distal half of the wing; Sc terminating on C; Rs very remote from R1, sending off 2 short branches; MA, MP, and CuP branches originating very anteriorly. Cross veins almost regular.

The most conspicuous character of this new genus is the branches of the main veins originating very anteriorly in the wing. A similar branching pattern is present in the hind wings of some Palaeodictyoptera.

The generic name is derived from the Greek words *engys* and *ptera* (near + wings) and is considered neuter plural.

Type species: *Engisoptera simplices*, n.sp.

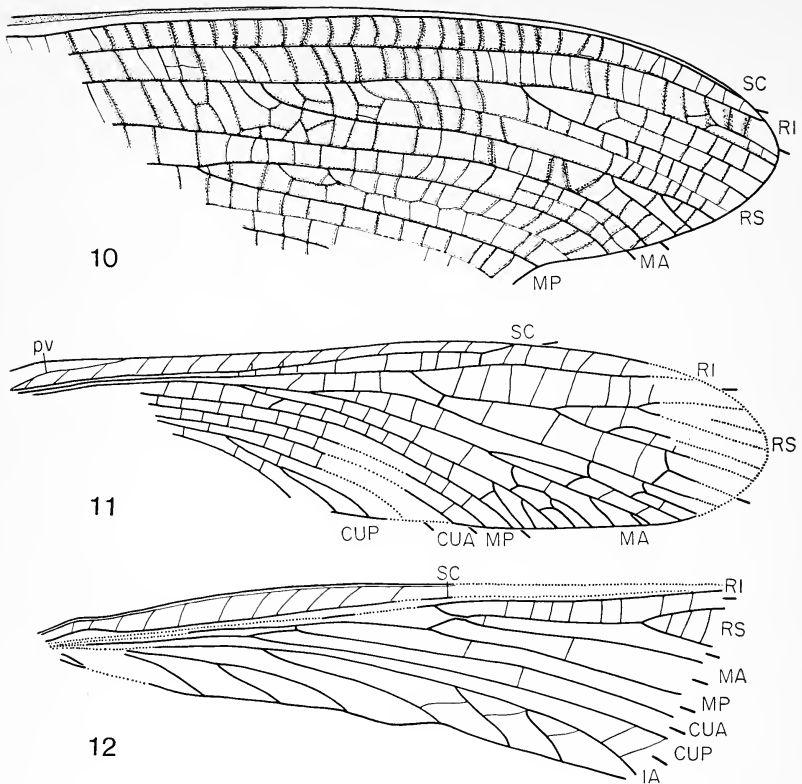


Fig. 10. *Ancoptera* sp., specimen 31/1974. Wing fragment, length 31.5 mm, width 10.7 mm. Original.

Fig. 11. *Engisoptera simplices* n.sp., specimen 32/1974. Wing fragment, length 18 mm, width 4 mm. Holotype. pv = postcostal vein.

Fig. 12. *Alectoneura europaea* n.sp., specimen 33/1974. Wing fragment, length 12.8 mm, width 3.3 mm. Holotype.

Engisoptera simplices, n.sp.

Figure 11

This species is based upon a detached, very delicate wing with the anal area and the apical area missing.

Wing: length about 20 mm, width 4 mm. Rs diverging from RI shortly beyond mid-wing, rs area small, triangular; MA with 2 long branches, the distal one twice branched; MP with a single, long parallel branch; CuP with a series of several relatively long branches. Intercalated sectors almost regular, well-pronounced.

Holotype: no. 32/1974 (wing fragment, length 18 mm, width 4 mm; obverse). Paleontological Institute of Charles University, Prague.

Family **Alectoneuridae**, new family

Wings: very narrow in the proximal third but not petiolate, broadest beyond mid-wing. Venation simplified; Sc terminating before the apical third; stems of R and M not coalesced in the basal third; Rs diverging from R1 before mid-wing; MA adjoining or coalescing with Rs for a short distance. 1A with a series of long branches. Cross veins few.

The venation of Alectoneuridae is very close to that of Mischopteridae. However, the shape of the wing is less specialized in lacking the petiole, and the anal area has a more generalized venation. The basal part of the wing, including the convex basal bend of the subcosta, is very reminiscent of the Protohymenidae (Kukalova-Peck, 1974).

The Alectoneuridae combines morphological features of two groups of families, which originated from common ancestors: Mischopteridae, Sphecopteridae, Carbonopteridae, Ischnoptilidae, Corydaloididae, Foririidae on one side; and Aspidothoracidae, Scytohymenidae, Aspidohymenidae, Vorkutiidae, Bardohymenidae, and Protohymenidae on the other side. The family Alectoneuridae probably descended from the ancestors of both groups and has a morphologically intermediate position similar to that of the Moravohymenidae (Kukalova-Peck 1972, p. 256).

Type genus: *Alectoneura*, new genus.

Alectoneura, new genus

Wing: C and Sc convexly bent before the base; subcostal area relatively broad in the proximal half of the wing, with a series of Sc branches; M dividing into MA and MP at the level of the origin of Rs; anal area relatively broad and long, reaching beyond mid-wing.

In its venation, *Alectoneura* recalls *Psilothorax* (Mischopteridae); and in the structure of the basal part of the wing, *Protohymen* (Protohymenidae). The broad subcostal area, with a series of numerous subcostal branches and the relatively large anal area with richly branched 1A, are the characters typical for primitive Megaseoptera with generalized venation.

The generic name is derived from the Greek words *alecto* and *neura* (indescribable + veins) and is considered neuter plural.

Type species: *Alectoneura europaea*, n.sp.

Alectoneura europaea, n.sp.

Figure 12

This species is based upon a single wing, which is slightly bent at the end of its basal quarter. The wing might have belonged to a subimago of a species like *Sphecoptera elegantissima*, since all other wings in all related families are straight in the basal part. In this case, the deep concavity of the posterior margin at the 3rd branch of 1A would probably become less pronounced in the adult wing. In the holotype, the very fine wing membrane has split along the veins and become slightly superimposed posteriorly over other parts of the membrane. In figure 12, the venation is restored back into normal position.

Wing: length of the fragment 12.8 mm, width 3.3 mm. Anterior margin broadly bent in the basal quarter; posterior margin slightly undulated at about the middle of the anal area; Sc close to R along its whole course; Rs and MA adjoining for a short distance; first branching of Rs broadly dichotomous; M and Cu branches almost parallel and probably simple; CuA soon after its origin connected with M by a short cross vein; 1A with 4 long branches; 2A short, simple. Cross veins near the posterior margin sigmoidal, almost parallel with the longitudinal axis.

Holotype: no. 33/1974 (obverse and reverse). Paleontological Institute of Charles University, Prague.

THE PROBLEM OF RECOGNIZING GENERALIZED MEGASECOPTERA

Before this new material from Moravia was made known, megasecopteran wings were readily separated from those of the Palaeodictyoptera by the crowding of Sc and R towards the costal margin, the basally narrowed wings, and the simplified venation (Carpenter, 1963). However, with the presence of a rather broad subcostal area in Ancopteridae, Alectoneuridae, Engisopteridae and Hanidae, and the richly branched venation in Caulopteridae, Arcioneuridae and Engisopteridae, the recognition of primitive Megasecoptera becomes more difficult. This is true especially for fragmentary wings, in which the proximal, narrow part may not be preserved.

For identifying Megasecoptera with a generalized venation, the most reliable criteria are as follows: long, nearly homonomous wings; a narrow anal area; at least a partial crowding of Sc and R towards the costal margin; and the wing conspicuously broad at about mid-wing but narrowed both proximally and distally. An irregular and

not very dense cross venation, coarse archedictyon, and incomplete intercalated sectors are often present. However, each single feature mentioned above occurs randomly in the Palaeodictyoptera and should be carefully considered if found separately.

Keeping in mind the similar features of primitive megaseopterous and palaeodictyopterous venation, I believe that the following species, based upon fragments and previously considered to belong to the Palaeodictyoptera, need to be reconsidered for possible inclusion within the Megaseoptera.

Dictyoneurella perfecta Laurentiaux, 1949 (Westphalian, northern France) is probably megaseopterous because of the shape of the wing, which is broadest at the middle, and narrowed both proximally and distally; and because of the general resemblance to Anchineuridae and Ancopteridae. This species is herein referred to a new family, **Dictyoneurellidae**, characterized by having a simple lobe on the posterior wing margin, and a primitive venation that lacks coalescence of veins, a relatively broad subcostal area, simple MA and CuA, richly branched MP and CuP, and irregular cross veins forming intercalary sectors.

The family Frankenholtiidae, based on *Frankenholtzia culmani* Guthörl, 1962 (Lower Westphalian D, Germany) is in all probability megaseopterous, since the wing is broadest at mid-wing and narrows distally and proximally. It differs from the Arcineuridae by having broader wings, a broad lobe on the posterior margin and by less abundant cross veins [The vein marked by Guthörl, 1962, fig. 3, as Sc is in reality R1, R is Rs, and A is CuP].

The family Mecynopteridae, based on *Mecynoptera splendida* Handlirsch, 1904 (Westphalian C, Belgium), is almost certainly megaseopterous, because Sc and R1 are crowded towards the costal margin and the wing is elongate. It is related to the Upper Carboniferous Anchineuridae and Dictyoneurellidae and to the Lower Permian Ancopteridae, all characterized by the presence of irregular cross veins and intercalated sectors. *Mecynoptera tuberculata* Bolton, 1921, is a wing fragment too small to be referred to any particular genus; and *Merlenbachia grimaldi* Waterlot, 1934, classified by its author in the Mecynopteridae, is a wing fragment of dubious systematic position, and may even be neopterous.

Saurodictyum abnormis Guthörl, 1939 (Westphalian D, Germany) is very probably megaseopterous, because of the typical narrowing of the wing towards the base, almost into a petiole. Very likely it represents a separate family with primitive venation and a dense archedictyon, and rather broad subcostal area. Unfortunately, the

venation of the holotype is misinterpreted in the original figure (Guthörl, 1939, fig. 1), and the type specimen, which was deposited in a private collection, is not accessible for study. Hence, this species is referred to the Megasecoptera, family uncertain.

Orthocosta lithomantidoides Waterlot, 1934 (Westphalian C, Belgium) is based upon a small wing fragment. Because of the shape of the posterior margin and the irregular cross venation, with incompletely developed intercalated sectors, I believe it belongs to the Megasecoptera, though of uncertain family position. *Orthocosta splendens* Bolton, 1912, on the other hand has a loose "palaeodictyopterous" type of reticulation and is referred here to the Palaeodictyoptera, uncertain family position.

Palaeopalara gracilis Handlirsch, 1904, and *Antracopalara falcipennis* Handlirsch, 1904 (Westphalian C, Belgium) are small wing fragments with megasecopterous wing shape. Both species are here referred to the Megasecoptera, families uncertain.

Since it seems clear that the most primitive Megasecoptera merge fully in the wing venation pattern with the Palaeodictyoptera, we must accept the fact that some little-known species cannot be identified to either order with certainty.

The following is a summary of my present concept of the relationships of the species mentioned above:

Order Megasecoptera

Family Dictyoneurellidae Kukalova-Peck (herein described)

Dictyoneurella perfecta Laurentiaux, 1949

Family Frankenholtiidae

Frankenholtzia culmani Guthörl, 1962

Family Mecynopteridae

Mecynoptera splendida Handlirsch, 1904

Family uncertain

Saerodictyum abnormis Guthörl, 1939

? genus *lithomantidoides* Waterlot, 1934

Palaeopalara gracilis Handlirsch, 1904

Antracopalara falcipennis Handlirsch, 1904

? genus *tuberculata* Bolton, 1921

Order Palaeodictyoptera

Family uncertain

Orthocosta splendens Bolton, 1912

Order uncertain

Merlenbachia grimaldi Waterlot, 1934

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HYDROGEN CYANIDE PRODUCTION IN NORTH AMERICAN AND AFRICAN POLYDESMOID MILLIPEDS¹

BY HANS E. EISNER,² WILLIAM F. WOOD,³
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A diversity of substances has been isolated from the defensive secretions of millipeds, including hydrogen cyanide, benzaldehyde, phenols, 1,4-benzoquinones, quinazolinones, and nitrogen-containing terpenes (references in Altman and Dittmer, 1973; Duffield *et al.*, 1974; Meinwald *et al.*, 1975; Smolanoff *et al.*, 1975; Wood, 1974; Wood *et al.*, 1975). Hydrogen cyanide, the first of these compounds identified (Guldensteeden-Egeling, 1882), has been reported from over a dozen European and New World species, all members of the suborder Polydesmida (Barbetta *et al.*, 1966; Blum and Woodring, 1962; Blum *et al.*, 1973; Casnati *et al.*, 1963; Davenport *et al.*, 1952; Duffield *et al.*, 1974; Eisner *et al.*, 1963; H. E. Eisner *et al.*, 1963; Hall *et al.*, 1969; Monteiro, 1961). We have demonstrated hydrogen cyanide production in four additional polydesmoid species, strengthening the view that cyanogenesis may be of widespread, if not general, occurrence within the suborder. Three of the species, *Apheloria trimaculata*, *A. kleinpeteri*, and *Pseudopolydesmus branneri*, stemmed from the U. S. A. (the first species was from Clifton Forge, Virginia; the other two from Roanoke, Virginia); the fourth species, *Astrodesmus laxus*, was from Africa (Mombasa, Kenya). The animals were tested for cyanogenesis by manipulating them and gently squeezing them, while at the same time holding beside their bodies strips of filter paper impregnated with benzidine acetate-copper acetate reagent (Feigl, 1966). In all instances the papers turned blue, indicating release of hydrogen cyanide vapor from their glands. In single individuals of each of the North American species, cyanogenetic output was assayed quantitatively (see accompanying table), using the technique previously developed in our laboratories (H. E. Eisner *et al.*, 1967).

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TABLE
CYANOGENETIC OUTPUT OF MILLIPEDS

Species	Sex and Body Weight of individual	Cyanogenetic Output ($\mu\text{g}/\text{individual}$)
<i>Apheloria trimaculata</i>	♂ (769 mg)	16
<i>A. kleinpeteri</i>	♀ (1053 mg)	27
<i>Pseudopolydesmus branneri</i>	♂ (199 mg)	32

Cyanogenesis in polydesmoid millipeds involves simultaneous release of hydrogen cyanide and aldehyde from stored cyanohydrin (Eisner *et al.*, 1963). The aldehyde has been shown to be benzaldehyde in several species (Barbetta *et al.*, 1966; Blum *et al.*, 1973; Blum and Woodring, 1962; Casnati *et al.*, 1963; Duffield *et al.*, 1974; H. E. Eisner *et al.*, 1963; Monteiro, 1961; Weatherston and Gardiner, 1973). We made no effort to isolate the aldehyde in the three North American species, but found evidence that *Astrodesmus latus* produces benzaldehyde. Gas-liquid chromatography of a sample of secretion from this milliped, obtained by wiping the discharged fluid from the gland openings with pieces of filter paper, showed a peak of identical retention time to that of authentic benzaldehyde. Some polydesmoid millipeds have ancillary phenolic components in their secretion (Blum *et al.*, 1973; Duffield *et al.*, 1974; Monteiro, 1961). We did not attempt to isolate such components in our species, although the secretion of *Pseudopolydesmus branneri* had a phenolic odor.

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MUTUALISTIC ASSOCIATION
BETWEEN ANTS AND SOME HOMOPTERA
— ITS SIGNIFICANCE IN COCOA PRODUCTION*

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During my field collections of ants in some cocoa farms on Ondo Road in Western Nigeria, I have come to observe that certain species of ants are associated with scale insects (Coccidae), mealybugs (Pseudococcidae) and aphids in a way which suggests that the association must be mutually beneficial. Although a great deal has been done by many workers to determine experimentally the nature of this association (Strickland, 1951; Nixon, 1951; Way 1954), there seems to be so much variation in the degree of the ant-Homoptera association that many questions still remain unanswered. Further, many claims by previous workers need to be substantiated, particularly as these claims in some instances are contradictory. In this paper I present an account of the ants and Homoptera that were observed in association on the cocoa farm in West Nigeria, an analysis of this association, and a discussion of the effects of the association on the cocoa crops. Although there are records of ant-Homoptera association for Ghana and some other parts of West Africa (Strickland, 1951; Leston, 1970), these are the first such records, as far as I am aware, for Nigeria.

The following is a list of Homoptera attended to varying degrees by ants:

Family Pseudococcidae

- Planococcoides* sp. nr. *njalensis* (?)
- Phenacoccus hargreavesi* (Laing)
- Planococcus citri* (Risso)
- Ferrisia virgata* (Cockerell)
- Dysmicoccus brevis* (Cockerell)

Family Coccidae

- Gascardia* sp.

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Family Margarididae

Icerya purchasi (immature stages)

Family Diaspididae

Aspidiotus destructor (Signoret)*Aonidiella replicata* (Lindinger)

Family Aphidae

Toxoptera aurantii (Boyer de Fonscolombe) (alate and apterous, all immature stages)

Family Flatidae (?)

Genera and species undetermined (all immature states)

The following genera of ants were found associated with mealybugs (Family Pseudococcidae) listed above:

Subfamily Myrmicinae

Crematogaster spp. — workers only(subgenus *Sphaerocrema*) *C. striatula*, *C. luctans*, *C. leneri*, *C. boxi*.(subgenus) *Crematogaster* group.(subgenus) *Atopogyne* group — *Crematogaster africana*.*Pheidole* spp. (*megacephala* being the most notorious).*Macromischoides*, *Atopomyrmex*, *Cataulacus*, *Monomorium*, *Meranoplus*, *Xiphomyrmex*, *Tetramorium* and *Solenopsis*.

Subfamily Formicinae

Oecophylla, *Acantholepsis*, *Polyrachis* and *Camponotus*.

Subfamily Ponerinae

Platythyrea

The mealy bugs found in association with ants can be divided into two groups — those for which the association is obligatory and those for which it is facultative. *Planococcoides njalensis*, alone in the first group, is regularly attended by ants. The obligate nature of this association is not surprising; since the mealybugs have very short legs and are ovoviparous, they most probably depend on the ants for transportation from tree to tree. The other mealybugs on the above list are facultative and are only sometimes found with ants. They have longer legs and all are oviparous.

Gascardia sp. (Coccidae) is regularly attended by *Oecophylla longinoda*, *Crematogaster africana* and *Macromischoides aculeata*. On the other hand, the association of *Icerya purchasi* (Margarididae), *Aspidiotus destructor* and *Aonidiella replicata* (Diaspididae) with the same ants is facultative.

Table 1a.

Oecophylla and *Crematogaster* (*Cr.*) Interaction

	<i>Oecophylla</i>			Ratio
	Present	Absent	Total	
<i>Cr.</i> Present	6	211	217	1:35
<i>Cr.</i> Absent	243	1010	1253	1:4
Chi-squared (X^2) = 36.3 significant at $P < 0.001$				

Table 1b.

Macromischoides (*Macr.*) and *Oecophylla* Interaction

	<i>Oecophylla</i>			Ratio
	Present	Absent	Total	
<i>Macr.</i> Present	9	105	114	1:12
<i>Macr.</i> Absent	240	1125	1365	1:4.5
Chi-squared (X^2) = 14.55 significant at $P < 0.001$				

Table 1c.

Crematogaster (*Cr.*) and *Macromischoides* Interaction

	<i>Macromischoides</i>			Ratio
	Present	Absent	Total	
<i>Cr.</i> Present	2	433	435	1:216
<i>Cr.</i> Absent	114	1139	1253	1:10
Chi-squared (X^2) = 96 significant at $P < 0.001$				

There are five forms exhibited by ant-Homoptera 'mutualism' and these have been exhaustively discussed in a review by Way (1963). 'Mutualism' is defined as "an association between ants and other insects which is mutually beneficial without necessarily implying obligate dependence or interdependence" (Way, 1963). These forms include: (i) adaptation of the Homoptera related to the association with ants; (ii) benefits derived by the Homoptera; (iii) benefits derived by the ants in form of contribution of the Homoptera to the food of the ants; (iv) specificity in the ant-Homoptera association; (v) ant-Homoptera association in relation to their natural control.

However, one aspect of this mutualistic association, which is incidental but nevertheless significant for the host plant carrying the ants and the Homoptera, is the capacity of some of the Homoptera to transmit fungal and viral diseases to the host plant.

Laboratory tests have confirmed that all the mealybugs have been found to transmit strains of virus diseases (Thresh *et al.*, 1959) but *Planococcoides njalensis* is now considered the most important vector, especially of the virulent types of swollen shoot virus (Leston, 1970). Workers of *Crematogaster* spp. and *Macromischoides* have been observed actively carrying up cocoa trees particles of soil which they use in building their nests. During the rainy season this sort of activity will no doubt help to spread fungal spores of the black pod disease (*Phytophthora palminivora*).

There is therefore some contrast in the roles played by ants in the entomological problems of cocoa crops. Predaceous ants like *Oecophylla*, *Crematogaster* and *Macromischoides* more or less determine the composition of the insect spectrum. An extensive survey of cocoa farms in Nigeria for these three also confirms Leston's (1970) work in Ghana that each cocoa farm carries a mosaic of these dominant species in which the three species are more or less mutually exclusive (see Tables below).

These tables show that the coincidence of *Oecophylla* and *Macromischoides* (Table 1b) is occasional, that of *Oecophylla* and *Crematogaster* (Table 1a) very rare and that of *Macromischoides* and *Crematogaster* (Table 1c) extremely rare. Leston (1970) claimed that up to fifty percent of Ghana's cocoa trees are permanently protected by *Oecophylla* from *Distantiella* (mirid) damage in some areas. There is little doubt that both *Macromischoides* and *Crematogaster* are negatively correlated with mirid (*Distantiella* and *Salbergella*) population densities (Adenuga, unpublished report). On the other side of the scale is the fact that these ants increase the damage to cocoa crops because they encourage the establishment of viral and fungal homopterous vectors by actively transporting them and to a limited extent offering them protection against their natural parasites and predators. In addition, *Macromischoides* does direct damage, although minor, to cocoa leaves by stripping them to build its nest.

A decision as to whether or not to encourage the establishment of these ants in cocoa farms will depend on whether mirid infestation is more or less important than fungal and viral diseases of cocoa in a particular locality.

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PREDATOR AVOIDANCE BEHAVIORS AND
WEB DEFENSIVE STRUCTURES IN THE
ORB WEAVERS *ARGIOPE AURANTIA*
AND *ARGIOPE TRIFASCIATA*
(ARANEAE, ARANEIDAE)*

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INTRODUCTION

Many spiders spend virtually all of their lives on orb webs. Orb weavers are known from all continents except Antarctica, as well as many island groups. In addition to a cosmopolitan distribution, individual species are locally abundant in a variety of habitats. The diversity of this assemblage is also quite pronounced with 2500 species of Araneidae, 150 species of Uloboridae and over a dozen species of Tetragnathidae recognized (Levi and Levi, 1968). Since the uloborids are not closely related to the other two orb-weaving families, the ability to construct orb webs probably evolved independently (Kaston, 1966). It is generally conceded that the orb web is a highly developed type of spider web (Kaston, 1964) which allows exploitation of aerial food sources (insects and other invertebrates), not readily available to other spiders, with a minimum of wind damage to the web. Despite the apparent success of this web type, it allows exposure of its occupant not only to the exigencies of the abiotic environment but to predators and parasites as well. Orb weavers fall prey to wasps (Muma and Jeffers, 1945; Kurczewski, 1963; Kurczewski and Kurczewski, 1968a, 1968b and Dorris, 1970), birds (Robinson and Robinson, 1970 and Royama, 1970) and other spiders (Enders, 1974). Vertebrate predators such as frogs, toads and lizards may be locally important.

While predator avoidance behaviors have been examined in several animal groups (Tinbergen, 1969 and Eibl-Eibesfeldt, 1970), no formal study has been completed on spiders. Several earlier spider workers (Bristowe, 1941 and Comstock, 1940) noted that web flexing, dropping from the web, color changes and other behaviors were elicited when spiders were disturbed. Gertsch (1949) listed some escape responses of the line weaver *Pholcus phalangioides*

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(Fuesslin) and Savory (1964) discussed web flexing, dropping from the web and death feigning as reflex responses. Robinson and Robinson (1973) ascribed a defensive function to movement by *Nephila maculata* (Fabricius) up the web, sometimes onto nearby vegetation. Eberhard (1970) was able to relate dropping from the retreat by *Araneus cornutus* (Clerck) to attack by predatory wasps.

This study identifies some of the components of predator avoidance behavior in *Argiope aurantia* Lucas and *A. trifasciata* (Forskål), which are known as the black and yellow garden spider and banded garden spider respectively. The frequency of occurrence of various components is determined for both species; response variation with instar and direction of approach by a predator model is assessed. In addition, specific aspects of web architecture, barrier webs and stabilimenta, are examined and the possible relationships to predator avoidance behaviors are discussed.

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METHODS

During the spring of 1974 a field study of mortality factors and migration characteristics of the orb weaver *Argiope aurantia* was initiated in an overgrown, abandoned pasture 2 mi. west of Glendale, Loudon County, Tennessee. While engaged in this research, I frequently observed encounters between the two *Argiope* species, *aurantia* and *trifasciata*, and salticid spiders, *Phidippus audax* (Hentz) and *P. clarus* (Keyserling). Some attacks by the salticids were successful, some resulted only in leg losses by *Argiope* and some were unsuccessful. Due to the brevity of these encounters I rarely observed complete sequences. Thus, in order to obtain quantitative evidence concerning the nature of predator avoidance in *Argiope*, an artificial predator was employed. For the purposes of this study, a standard-sized lead pencil with rubber eraser (roughly the cross-sectional diameter of the salticids) was used to simulate an invertebrate predator. Spiders were approached with the eraser end of a pencil from either the ventral surface, in which case the hub of the web near the eye region was touched or from the dorsal surface. When approached dorsally either the eye region or to a lesser extent

(<5%) the abdomen was touched. I positioned myself approximately 0.5-1.0 m either directly behind or directly in front of the web depending on the direction of model presentation to be used. In employing this model the assumption was made that all spiders tested, regardless of instar and species, recognized the model as a predator. Data on construction of barrier webs or "tangles" and the nature of stabilimenta were gathered throughout the summer in an attempt to assess possible anti-predator functions. The chi-square test and Cox and Stuart test for trend were used in the statistical analyses. The taxonomy of *Argiope* follows Levi (1968).

THE WEB

The orbs of *A. aurantia* and *A. trifasciata* are "typical" araneid webs, consisting of foundation lines, radii, spirals, a free zone and a hub. Neither species constructs a retreat. The spider is normally located at the hub in a head-down position. The web is inclined slightly from the vertical and there may be several stabilimenta bands in or near the hub (fig. 1). Up to two barrier webs (fig. 2) may be associated with each orb web.

BARRIER WEBS

Barrier webs or "tangles" were frequently constructed by *A. trifasciata* and to a lesser extent by *A. aurantia*. Essentially a barrier web is an irregular non-viscid silk mesh connected to the orb web and nearby vegetation or other supports. There can be up to two such tangles, with the primary barrier web positioned behind the dorsum of the spider. The secondary barrier, which is nearly always smaller, is located on the other side of the orb (fig. 2). In early instar *A. trifasciata* the primary barrier web is quite cone-like with the orb forming the base of the "cone". A small gap is left at the bottom of the orb and the cone through which the spider may drop if disturbed. Since these barriers are connected to the outer edge of the orb, disturbances (vibrations) are transmitted to the spider. It is generally thought (Comstock, 1948; Gertsch, 1949 and Marples, 1969) that they serve some defensive function. My experience with these two species confirms this observation. In paint marking spiders on the dorsum I have often accidentally touched the barrier web, alerting the spider and making it more difficult to mark. In addition to an early warning function, the barrier webs, particularly the primary barrier, constitute a physical obstacle to invertebrate predators. Such barriers reduce the direct points of entry that predators might

otherwise employ. This is not to suggest that barrier webs are impenetrable; they are easily penetrated, but in the process the occupant is forewarned.

Barrier webs do not act as prey catching structures *per se* though they may slow down grasshoppers and other relatively strong prey and thereby facilitate capture. Twenty prey items (leaf-hoppers and flies) were tossed onto the primary barrier webs of 20 different *A. trifasciata*. In 19 of 20 cases the prey were either ignored or the spider plucked strands of the orb with no subsequent action. In one instance the prey, a leafhopper, struggled to a point very close to the margin of the tangle and the orb web where it was successfully attacked. In the capture the spider did not completely leave the orb web at any time. Incidental field observations during the summer are in close agreement with the results of this test.

The occurrence of barrier webs changes markedly with the instar of *A. trifasciata* (Table 1). With the increase in secondary barrier webs, the primary webs are made less cone-like and the mesh progressively coarser. Adult males rarely build complete webs since they generally abandon the web building habit upon reaching maturity and begin the search for females. When the male locates a female or penultimate female web site, he remains on the barrier web until mating can take place. Mating occurs generally within a few days, sometimes within a few hours after the female adult molt. Female

TABLE 1.

Barrier webs and stabilimenta of all field instars of *A. trifasciata*

	Instar	Number of webs ¹	Primary barrier web	Secondary barrier web	Stabilimenta: mean number bands/web \pm S.E.
	2	300	300	0	0.00 \pm 0.000
	3	200	200	0	0.00 \pm 0.000
	4	36	36	0	0.11 \pm 0.053
	5	20	20	0	0.25 \pm 0.104
	6	34	34	1	0.38 \pm 0.095
Juvenile ♀	7	39	39	17	1.02 \pm 0.107
Penultimate ♂	7	102	102	41	0.76 \pm 0.064
Juvenile ♀	8	95	95	48	1.40 \pm 0.063
Penultimate ♀	9	39	39	27	1.72 \pm 0.097
Adult ♀	10	29	1	0	0.38 \pm 0.126
		894	866	134	

¹Represents minimum number of webs examined with no more than one web/spider counted.

A. trifasciata virtually cease construction of barrier webs one to two weeks after becoming adults. The omission of barrier webs by mature adult females may relate to the increased size and strength of the female (size increase is quite rapid at this time), to decreased activity of salticids, to the need to maximize food intake before cold weather (both sides of the orb are available as catching surfaces rather than one side or parts of two sides), to nerve degeneration or some other factor(s). No data are available at this time to determine the relative importance of these various factors.

It is interesting to compare the use of barrier webs by the two *Argiope* species. *A. aurantia* is the larger of the two and it achieves its larger size in a relatively short time. Larger size probably deters some salticid and other attacks by invertebrate predators. I did not observe such attacks on penultimate and adult *A. aurantia* while they were a frequent occurrence on juvenile *A. trifasciata* at the same time. *A. aurantia* construct fewer barrier webs and this activity is restricted primarily to the mid-instars. *A. trifasciata* is smaller, matures more slowly and constructs barrier webs throughout most of its life (Table 1). Since the primary barrier excludes some prey as well as predators, the inter-relationship between spider size, predator avoidance behavior, food intake and web architecture must be complex. Factors controlling the building of barrier webs need to be determined in order for the niche relations of these two closely related, sympatric species to be properly evaluated.

STABILIMENTA

Stabilimenta, the white zigzag lines of silk which form discrete bands in or near the hub of the orb of several spider species, are a common feature in *Argiope* webs. These structures vary considerably in form and relative size both between *A. aurantia* and *A. trifasciata* and within each species. Since I found stabilimenta to possess some defensive value to these spiders, their structure and frequency of occurrence are discussed here.

A. aurantia build extensive disc-shaped stabilimenta as early and mid-instars (fig. 1). Up to 7 individual bands were often found in webs but never more than this and usually less (Table 2). A Cox & Stuart test for trend (Conover, 1971) revealed a significant decrease ($p < 0.05$) in the number of bands occurring from mid-instar to adult female. This trend is apparent in Table 2. Older spiders construct a thinner "patch" of silk at the hub in place of distinct stabilimenta bands. Adult females make this patch as well as an accompanying linear band below the hub. I also compared adult

TABLE 2.

Barrier webs and stabilimenta of *A. aurantia*¹

	N	Mean number of bands \pm S.E.	Barrier webs
Early & mid-instars (study area)	61	4.789 \pm 0.218	9
Penultimate & adult ♀'s (study area)	28	2.429 \pm 0.196	0
Older adult ♀'s (study area)	29	1.828 \pm 0.100	0
Older adult ♀'s (Knox Co., Tenn.)	50	1.740 \pm 0.085	0

¹Thin "patch" was not assigned a value and thus was not used in calculations.

female webs in my study area to those of a population near Stock Creek Boat Dock in Knox County, Tenn. The results of a t-test showed no significant difference ($p < 0.05$) in the number of bands in these two populations. It is interesting that Reed, *et al.*, (1969) found "no obvious pattern or change in complexity" in laboratory-reared *A. aurantia*. Whether this difference is due to selection pressures or possibly some cue(s) existing in field situations that do not exist in the laboratory is not known.

The stabilimenta of *A. aurantia* can conceal the spider. Concealment of the spider's state (especially when molting) is probably advantageous. Both *Argiope* species molt at the hub during the day and are completely defenseless during this process. Concealment of the true size of the spider may also be a deterrent to the invertebrate predator since larger orb weavers can ward off and maybe even kill a smaller attacker. It is even possible that stabilimenta conceal attack-eliciting stimuli from certain predators.

A. trifasciata constructed substantially fewer bands in their webs than *A. aurantia* (Tables 1 & 2). A Cox & Stuart test for trend indicated a significant increase ($p < 0.05$) in the number of bands with instar of *A. trifasciata* (20 individuals of each instar were selected at random prior to testing). These results differ from Comstock (1948) who found that juvenile *A. trifasciata* built extensive disc-shaped stabilimenta. The reasons for these differences are not known, but I suspect that extensive use of barrier webs and the increase in stabilimenta bands may be related to heavy predation pressure by salticids.

Stabilimenta can also function as physical shields. The heavy silk bands reinforce the hub and make direct penetration more difficult. This is readily demonstrated by forcing a pencil or similar object through the hub of webs with and without such stabilimenta.

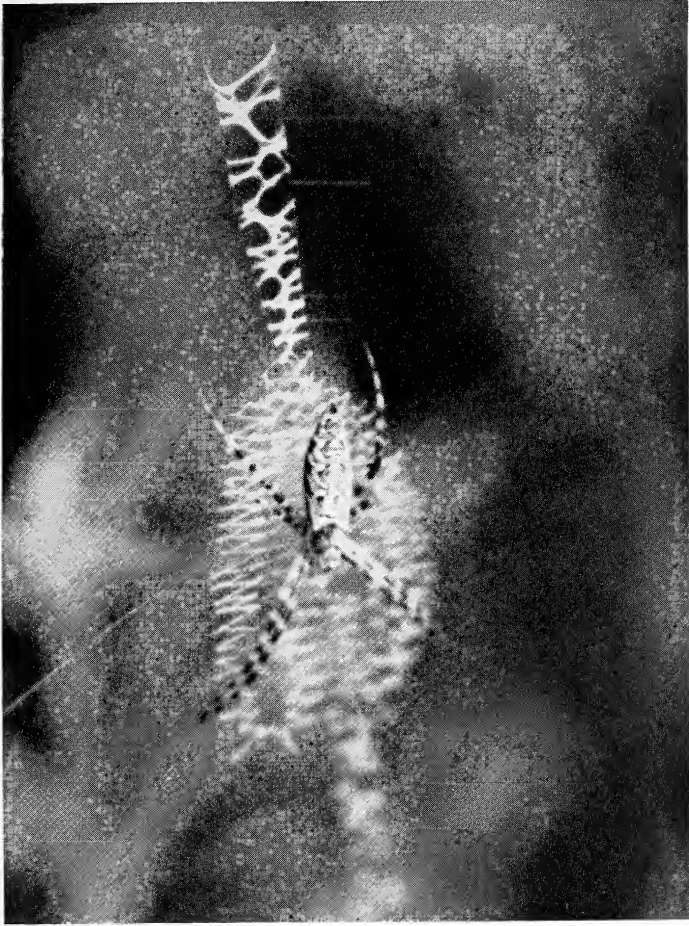


Figure 1. *Argiope aurantia* and its stabilimentum. Note light color of spider.

PREDATOR AVOIDANCE COMPONENTS

All descriptions of predator avoidance components apply equally to *A. aurantia* and *A. trifasciata*. There are differences in relative usage of these components (discussed in next section) and their combination in behavioral sequences.

Web Flexing

Web flexing is accomplished when the spider sets the web in motion along its short axis by rapid extension and retraction of the legs. Spider and web thus swing back and forth parallel to the ground surface, since the long axis of the web is oriented more or less perpendicular with respect to the ground. Web flexing adds another dimension to the predator's attempt at attack, that of motion. Obviously, contact is more difficult to establish and maintain when the spider and web are in motion. In one encounter of a salticid and an



Figure 2. Juvenile *A. trifasciata* with barrier webs. Note primary barrier behind dorsum of the spider; arrow is pointing to spider's dorsum.

A. aurantia, the salticid lost its grip on the *Argiope's* web and body (?) after web flexing was commenced; the salticid (a juvenile *P. audax*) fell onto the sticky spirals of the orb weaver's web where it became entangled and was treated as a prey item (i.e. wrapped, bitten and fed upon). Web flexing might also distract the potential predator and temporarily conceal the exact location of the orb weaver.

Stilting

Stilting results when the spider straightens all four pairs of legs and thus moves the sternum and venter further away from the hub surface (fig. 3). The abdomen is often tilted dorsally as well; the spider when viewed from the ventral side appears smaller because of the reduced surface area exposed. This response might also change the sign stimulus to a shape the predator does not readily recognize (Riechert, personal comm.), but additional testing will be required before this is known.

Dropping from web

Dropping or jumping from the web rarely occurred in the testing. During the trials it was never followed by leaving the web site though I have observed this behavior in certain field situations. When a web is approached rapidly and it or the vegetation to which it is attached is severely disturbed, the spider may jump from the web and actively leave the site. When dropping or jumping from the web did occur under test situations and when it was normally observed in the field, a dragline was secured to the hub before the spider dropped into the vegetation. Spiders then took up a position underneath a blade of grass, a leaf or along a plant stem where they remained for periods of less than one minute to over an hour (*A. aurantia* N = 6, \bar{x} time = 3 min. 02 seconds; *A. trifasciata* N = 35, \bar{x} time = 3 min. 11 seconds). Return to the hub was always via a direct, rapid climb up the dragline to the hub where a head-down position was assumed. If the vegetation near the spider or the spider itself was touched it immediately went back to the hub. Leaving the web is certainly an escape response and hiding underneath the vegetation is probably best applied against visual predators. Rapid return to the hub, especially when the vegetation is lightly disturbed, would facilitate escape if the predator was no longer in visual contact. Returning directly to the hub immediately places the spider at the center of its web. This may be advantageous since the orb weaver is back at the center of its auxiliary information gathering system, the web, and because most predator avoidance options are available at the hub.

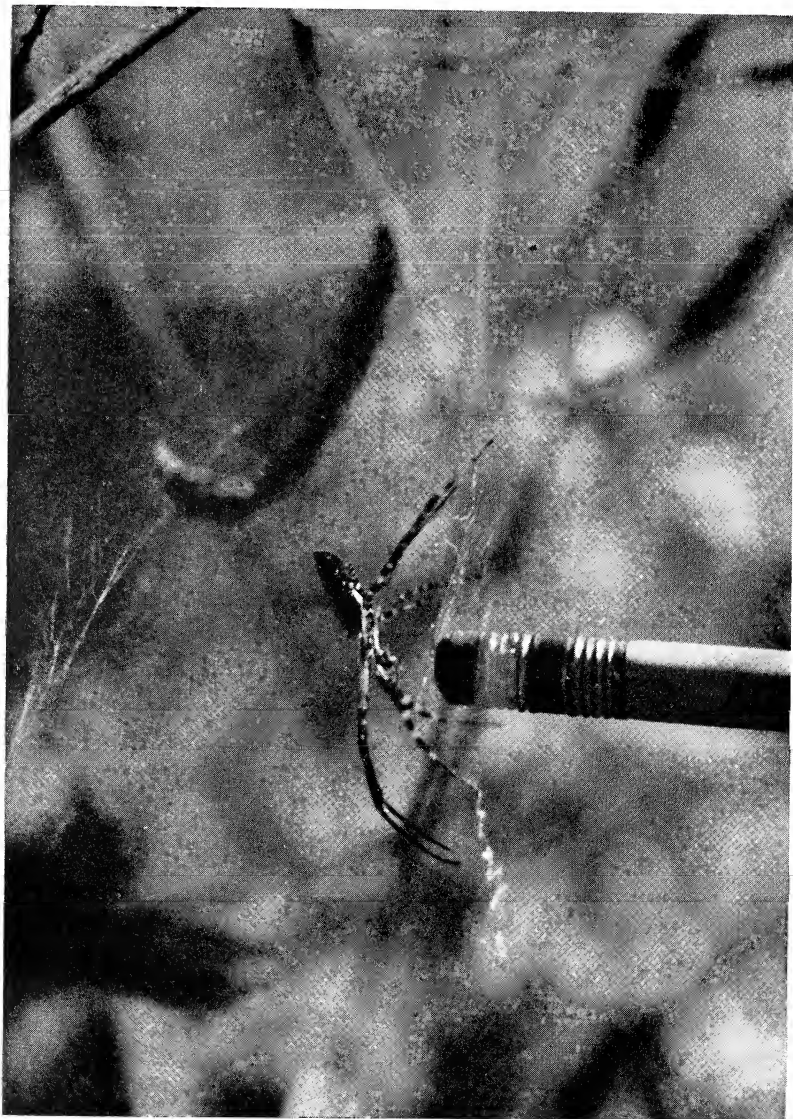


Figure 3. *Argiope trifasciata* stilting. Note extension of legs and distance of body away from hub surface.

Switching sides of the web

Switching sides of the web is accomplished when the spider moves between the radii in the "free zone" to the other side of the hub. It may be followed by web flexing, stilting, or web flexing later followed by stilting (fig. 4B). This response results in the interposition of the web as a physical barrier between the orb weaver and a potential predator.

Moving away from hub

When moving away from the hub the spider moves directly away from the point of contact: when its eye region is touched, the spider moves up the web and if the abdomen is touched, it moves down the web. Although one component was often immediately followed by another in a single response sequence, individual components were usually easy to identify. One exception is when the spider leaves the hub while simultaneously flexing the web; it is often impossible to tell which is the initial response. In statistical analyses and graphic presentations (figs. 4, 5 and 6) web flexing is treated as the initial response. This particular behavioral sequence is unusual in another way. Generally web flexing was initiated by rapid spider movement which resulted in considerable web movement and a large amplitude of web displacement. The response gradually subsided with web amplitude decreasing as web and spider movement slowed. In the hub leaving-web flexing sequence, however, the spider sometimes slowly returned to the hub while web flexing continued. Upon reaching the hub or shortly thereafter all motion quickly ceased. An observer has to watch closely to detect spider movement toward the hub; this behavior probably serves to distract the predator and then hide the orb weaver.

Rebuff

Rebuff, as used here, should not be confused with elements of the predatory behavior of these species (see Harwood, 1974). It is here defined as actively repulsing (pushing away) the model by using any of the legs of pairs I or II and/or briefly grasping the model with these legs. Biting was never observed although chelicerae were sometimes opened and fangs exposed. This may be an intention movement and/or threat posture.

Body flatten

In a few instances when spiders were approached dorsally, they would simply depress their bodies away from the model and flatten against the hub.

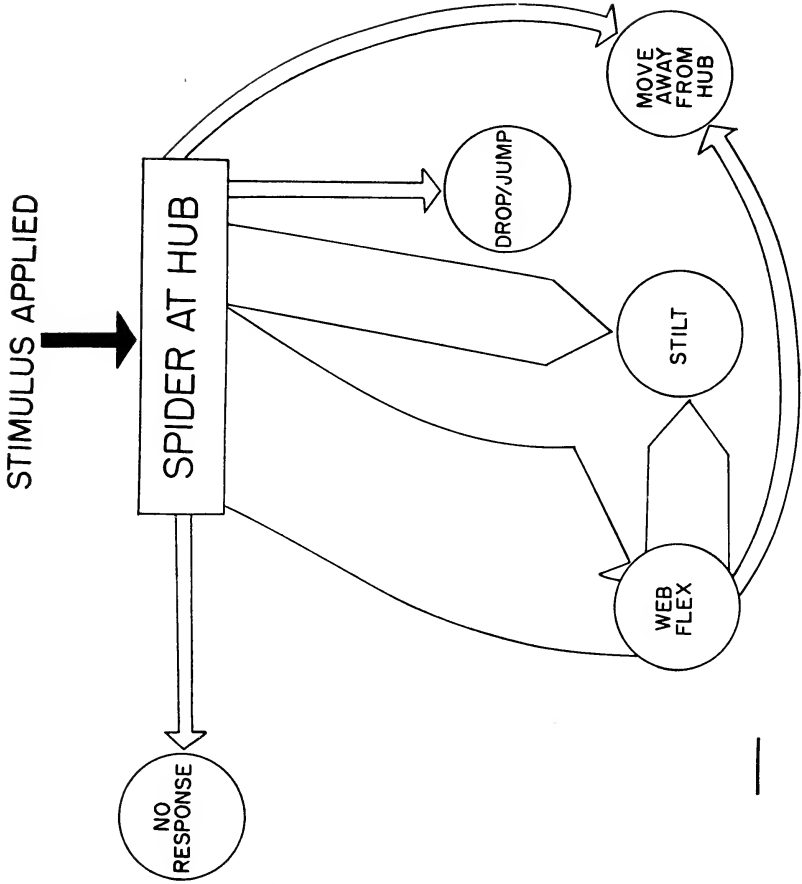


Figure 4A. *Argiope aurantia* behavioral components elicited by presentation of predator model: Ventral approach. [Note: in figures 4, 5 and 6 the width of the arrows is proportional to frequency of response; scale line = 20%.]

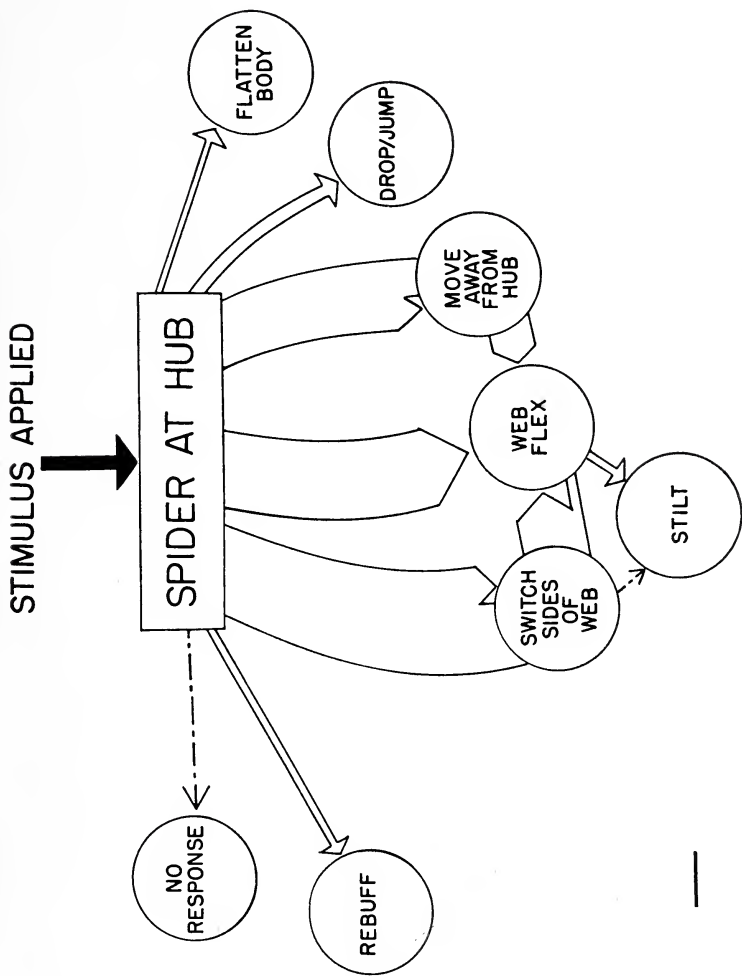


Figure 4B. Same as figure 4A: Dorsal approach.

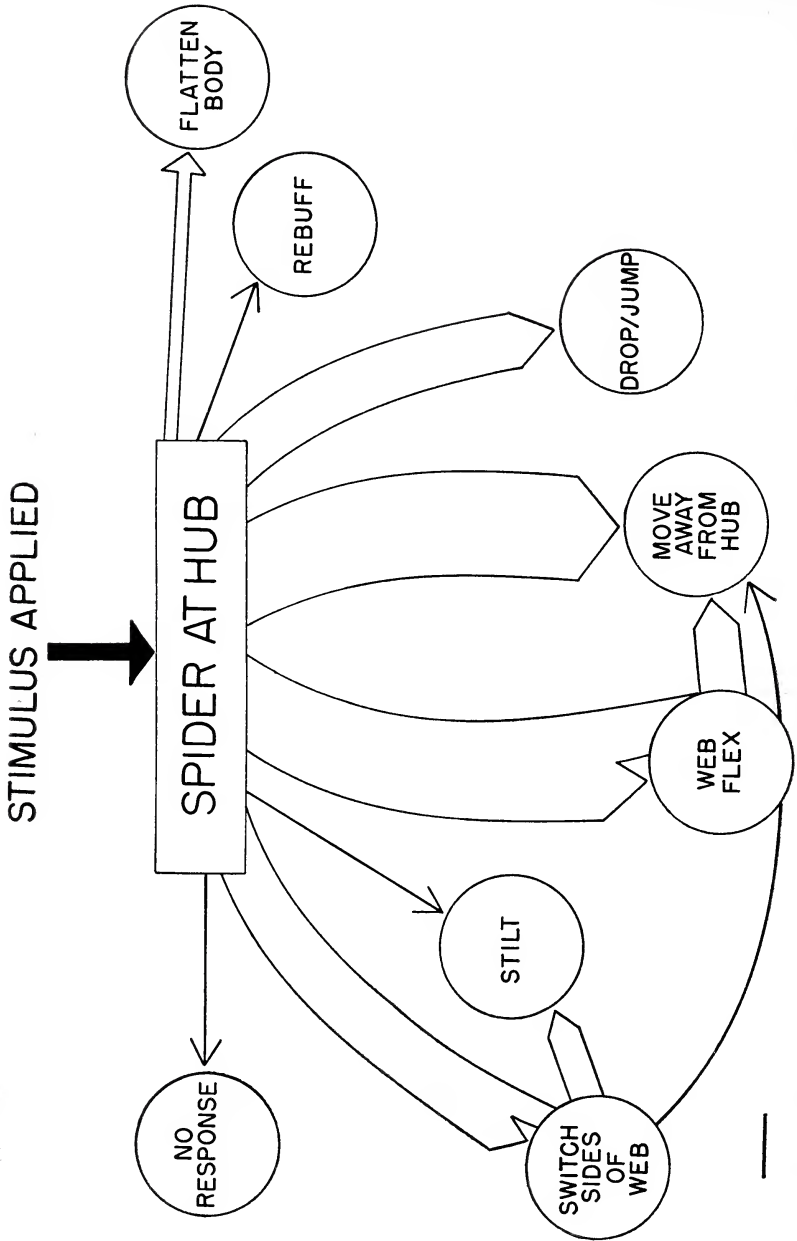


Figure 5A. Response components of juvenile female *A. trifasciata* to dorsal presentation of predator model.

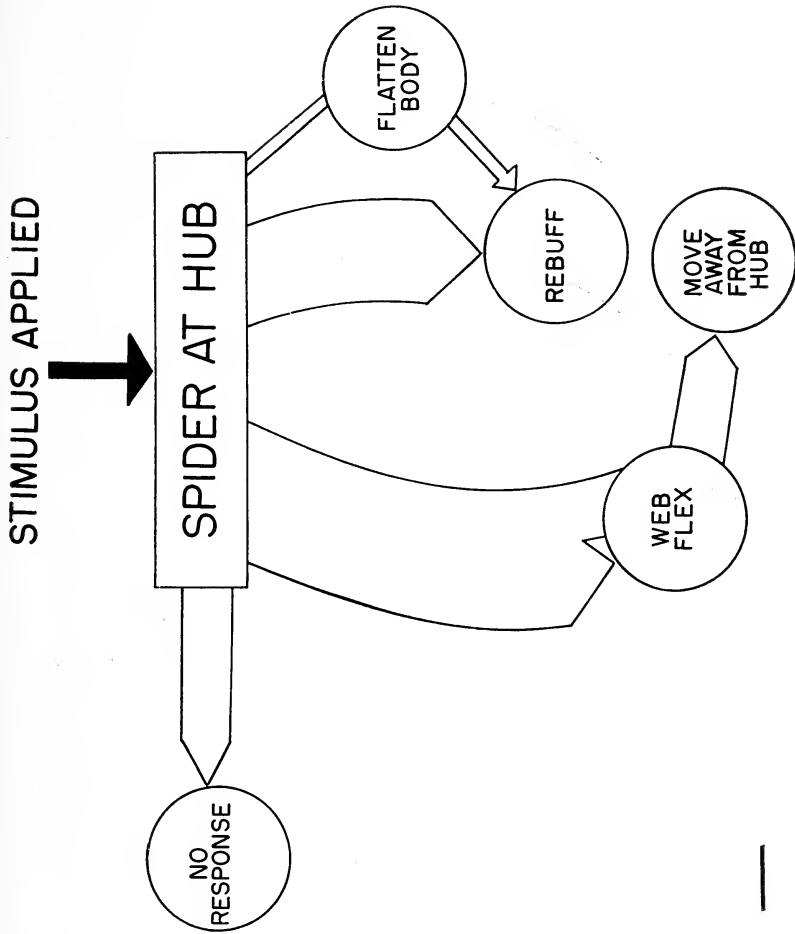


Figure 5B. Response components of adult female *A. trifasciata* to dorsal presentation of predator model.

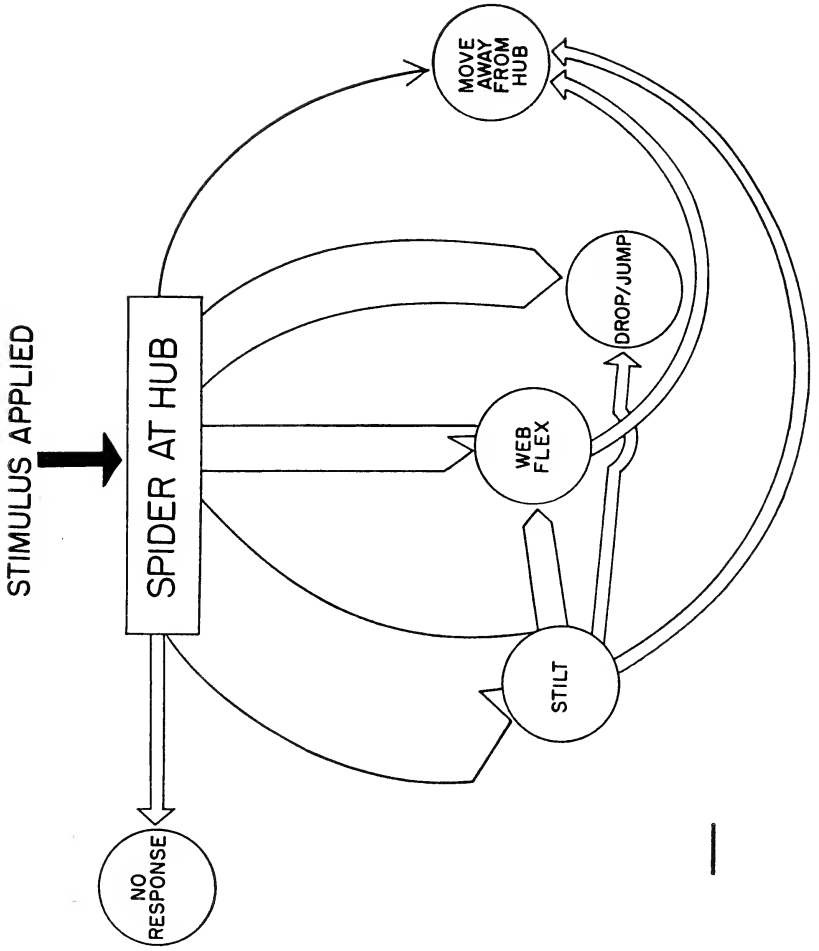


Figure 6. *A. trifasciata* behavioral components elicited by ventral presentation of predator model.

At times no response was observed even with repeated presentation of the model.

DIFFERENCES IN COMPONENT USE

Any insect or arachnid that approaches an orb web falls into one of four categories: (1) potential prey, (2) potential predator or parasite, (3) potential mate and (4) "neutral" (unpalatable prey, too large or strong an animal for the spider to subdue, etc.). An orb weaver that responds incorrectly may fail to obtain sufficient food, may be killed or may fail to mate. While this study does not identify the specific cues involved in these decisions, one would not expect all spiders of the same species or the same individual at different times to respond identically to a standard stimulus. The various response components are analyzed below under a variety of conditions to delineate their use.

Dorsal vs. ventral model presentation

A. aurantia and *A. trifasciata* were tested separately for differences in response components elicited by dorsal vs. ventral presentations of the simulated predator. A chi-square test (Conover, 1971) was employed in the analyses and unless otherwise stated this is the test used throughout the paper. The response of *A. aurantia* differed significantly ($n = 94$, $\chi^2 = 41.23$, $p < 0.001$) with dorsal and ventral presentations (fig. 4). Stilting and web flexing followed by stilting accounted for over 50% of the above variability. They occurred with substantially greater frequency than expected when the model was presented ventrally. Switching sides of the web followed by web flexing occurred more often than expected on dorsal presentations. *A. trifasciata* also exhibited a significant difference ($n = 181$, $\chi^2 = 102.84$, $p < 0.001$) in response components. Stilting again proved to be primarily a response to ventral presentations of the model. Web flexing, moving away from the hub and rebuff occurred much more often than expected when spiders were touched dorsally (figs. 4 and 5). It should be mentioned that the majority of responses (>95%) occurred after the model touched either the web or the spider with less than 5% occurring on the actual approach. Due to the small number of responses to the actual approach of the simulated predator these data are included, without distinction, in the various statistical tests. Also, the term "presentation" refers to both approach and touch responses.

aurantia vs. *trifasciata*

The responses of *A. aurantia* and *A. trifasciata* to dorsal presentations and of *A. aurantia* and *A. trifasciata* to ventral presentations were analyzed separately. The two species differed significantly ($n = 138$, $\chi^2 = 33.1$, $p < 0.005$) from one another in their respective responses to dorsal presentations of the simulated predator. Switching sides of the web and this component followed by web flexing occur more frequently in *A. aurantia* than *A. trifasciata*. *A. trifasciata* either failed to respond or rebuffed the model with greater frequency than expected (compare figs. 4B and 5B). Responses to ventral presentations of the model were also significantly different ($n = 138$, $\chi^2 = 38.3$, $p < 0.005$) for the two species. Differences in web flexing accounted for over 75% of this variability and differences in this component alone were sufficient to produce a significant difference ($p < 0.005$) between the responses of the two species. *A. aurantia* web flexed significantly more often than *A. trifasciata*.

Component differences of instars

Since behavioral responses may change with the age or instar of the spider due to maturation, learning, perceptual abilities or other factors, juvenile instars 4, 5 and 6 and adult female (instar 10) *A. trifasciata*, were examined for possible differences in predator avoidance. When the simulated predator was presented dorsally there was a significant difference ($n = 61$, $\chi^2 = 41.4$, $p < 0.005$) in response components. Dropping and moving away from the hub were primarily juvenile responses while rebuff and failure to respond were adult responses (fig. 5). Juvenile responses also contained more components than adult responses. It should be noted that adult female *A. trifasciata* are large enough to ward off the salticid species common in the area, since the salticid populations are primarily represented by eggs and juveniles at this time; male salticids have died and females spend much of their time guarding eggsacs and young. This may account for some of the differences observed. Data were insufficient to compare ventral presentations statistically, but the relative frequencies of occurrence of various components are shown in fig. 6.

Both species are thus capable of a broad array of responses that enable them to escape predation on their relatively exposed webs. These responses may also be important in avoiding predatory wasps and other predators and parasites. It is not claimed that the responses discussed here represent the complete repertoire of the two species.

As previously mentioned, leaving the web site does occur in some instances. I have also observed "death feigning" by one adult female *A. aurantia* when I rapidly approached her web. The individual dropped into the vegetation and all legs were drawn in close to the body. The spider's venter was exposed as it lay on its back and the spider remained motionless for several minutes. No color change such as that reported for *Gea heptagon* (Hentz) (Sabath, 1969) was detected.

RESPONSE THRESHOLD

The response threshold is operationally defined here as the number of stimulus applications (model presentations) needed to elicit a response of any kind (one component or a sequence of components) by the spider. If 10 stimulus applications failed to produce a response, "no response" was recorded.

Dorsal vs. ventral model presentations

Intuitively it would seem that a spider approached from the ventral side would be safer from predators since the web constitutes a physical barrier. Response threshold, in addition to response components, thus might differ with orientation of model presentation. When this parameter was tested for *A. aurantia* and *A. trifasciata*, they exhibited significantly different response thresholds to ventral vs. dorsal presentations of the model (*A. trifasciata* $n = 189$, $x^2 = 11.1$, $p < 0.05$; *A. aurantia* $n = 95$, $x^2 = 17.2$, $p < 0.005$). Both species were more responsive to the dorsal than the ventral model presentations.

aurantia vs. trifasciata

I found no significant difference in response thresholds ($n = 284$, $x^2 = 10.5$, $p < 0.05$) between the two species. Thus, while predator avoidance behaviors are utilized to different extents, the readiness to respond apparently does not differ in these two species.

Age differences

A. trifasciata instars 4, 5, 6, 7 and adult females were tested for differences due to age. No significant difference ($n = 176$, $x^2 = 48.8$, $p < 0.05$) among instars was revealed.

Differences to repeated model presentations

Finally I wanted to know if there were differences in the response thresholds in individuals undergoing successive trials. I applied four series of model presentations to the same individual with a 30 second pause at the end of each response sequence. There was no significant

difference in either *A. aurantia* ($n = 18$ spiders, $\chi^2 = 5.04$, $p < 0.05$) or *A. trifasciata* ($n = 8$ spiders, $\chi^2 = 4.03$, $p < 0.05$) for dorsal or ventral model presentations. The spiders apparently exhibited neither habituation to the stimulus nor increased sensitivity under these test conditions.

RESPONSE DURATION

Since the duration of several response components could vary with the particular test situation, I analyzed the variability of the web flexing response in this context since it is an easily measured component. Response levels were grouped into four categories: 0-10, 11-30, 31-120 and >120 seconds. These levels were chosen such that the expected values would be large and the test thereby more rigorous (Conover, 1971). Response duration of web flexing to dorsal vs. ventral presentations of the model were not significantly different ($p < 0.05$) for either *A. aurantia* ($n = 56$) or *A. trifasciata* ($n = 45$). The mean web flexing duration was 39.71 ± 10.52 and 44.27 ± 12.72 seconds respectively, for the two species. Thus the apparent variability existed in the ranges of response duration, but was not associated significantly with the test situation.

DISCUSSION

In this study, barrier webs and stabilimenta were found to complement the predator avoidance behaviors of *A. aurantia* and *A. trifasciata*. It is interesting that these two closely related species with sympatric populations should also employ barrier webs and stabilimenta to such markedly different extents. Recall that *A. aurantia* switched sides of the web with much greater frequency when approached dorsally or touched on the dorsum than *A. trifasciata*. This behavioral difference may be related to the more extensive use of stabilimenta by this species. *A. trifasciata*, on the other hand, has a thinner hub which more easily permits viewing the spider, and use of other predator avoidance behaviors or web structures, such as barrier webs, may better enhance survival. It is also noteworthy that *A. aurantia* web flexed to a significantly greater extent when the simulated predator was presented ventrally than *A. trifasciata*. Web flexing, in addition to adding motion to the potential predator's attack problem, might give the stabilimentum some shock value. Web flexing and the stabilimentum may act synergistically as a threat stimulus. Salticids are known to respond to a wide variety of shapes and patterns (models) as though they were prey items. If the models

are not distinguished as other salticids, then they are considered potential prey, with size of the prey being the primary discriminant (Drees, 1952 as reported by Land, 1972). Since the stabilimentum can conceal the spider's size by obscuring its outline (fig. 1) and if salticids do respond to the stabilimentum or parts of this structure rather than the orb weaver when web flexing is commenced, it is easy to see how a threat stimulus situation could arise. Of course, web flexing would rapidly change the apparent size of the stabilimentum and in some instances the spider also. This may explain why *A. aurantia* with their extensive stabilimenta web flex more when approached ventrally than *A. trifasciata*. The differences in *A. aurantia* and *A. trifasciata* are more easily understood when elements of web architecture are also considered.

The diversity of orb weaving species is immense and has already been discussed, but the variability in the structure of orb webs is also extensive (Levi, 1974). I believe considerable insight into spider defensive strategies can be gained by comparison of web architecture, predator avoidance behaviors and predation pressures in this and other spider genera. It may be more than coincidental that species of six genera (*Argiope*, *Cyclosa*, *Gasteracantha*, *Gea*, *Nephila* and *Uloborus*) known to construct stabilimenta or other web decorations are diurnal. Of course one way in which a stabilimentum might function to conceal a spider is for it, rather than the spider, to be conspicuous and daylight is presumably necessary for a stabilimentum to be visible. This is not to say that stabilimenta in different species function in precisely the same manner or that they might not possess other functions but diurnality for these six genera is a striking fact. Neither do these species build identifiable retreats which could provide some measure of protection from predators. Several species, particularly in the genus *Argiope*, are also a silver color which would tend to blend with a stabilimentum. *A. aurantia* and *A. trifasciata* individuals undergo color change during their lives and are silver-colored when stabilimenta are extensive.

SUMMARY

The orb weavers *A. aurantia* and *A. trifasciata* utilize numerous behavioral responses complemented by both barrier webs and stabilimenta as defenses against predation. Barrier webs alert the spider to the presence of a potential predator; primary barrier webs are constructed by all instar *A. trifasciata* except older adult females. *A. aurantia* build fewer such structures. Stabilimenta function to con-

ceal the orb weaver and when the spider web flexes the stabilimentum may become a threat stimulus. *A. aurantia* construct more extensive stabilimenta than *A. trifasciata*.

Web flexing, stilting and web flexing followed by stilting predominate as responses to ventral presentations of a simulated predator. Switching sides of the web, web flexing, switching sides followed by web flexing and moving away from the hub are main responses to dorsal presentations. Predator avoidance components are used differentially by the two species for both dorsal and ventral model presentations, by each species for dorsal vs. ventral model presentations and by various instars of one species, *A. trifasciata*. Juvenile responses contain more components than adult responses and adult female *A. trifasciata* are more prone to rebuff or ignore the model than juveniles. Response thresholds differ significantly only with dorsal vs. ventral presentations of a simulated predator for both species. No significant differences in response thresholds exist between species and among instars of a species. Neither species becomes habituated or more sensitive to repeated model presentations. Web flexing response duration is not significantly different for either species when the simulated predator is presented dorsally vs. ventrally. Behavioral components and web architecture are believed to work together in the defensive strategies of these two orb weaving species.

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THE SYSTEMATIC POSITION OF *GLYPHOLOMA*
JEANNEL, WITH A NEW SYNONYMY
(COLEOPTERA: SILPHIDAE, STAPHYLINIDAE)*

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INTRODUCTION

In 1962 R. Jeannel described *Glypholoma pustuliferum*, a new genus and species of an interesting small beetle from southern Chile for which he created a new tribe in the family Silphidae. A similar-looking beetle from southern Argentina was more recently described by O. Scheerpeltz as *Lathrimaeodes pustulipenne*, a new genus and species of the staphylinid sub-family Omaliinae. The two species have apparently not been compared to one another or otherwise mentioned in the literature. Since neither author gave detailed reasons for the placement of his genus, and neither mentioned several characters that are now considered essential to such placement, the systematic position of these genera may be considered unsettled.

A small series of specimens which agrees with the descriptions of both of the above species is in the collection of the Museum of Comparative Zoology. Based on an examination of these specimens and on the information given in the original descriptions, I would here like to present evidence for the synonymy of the two names, to expand upon the published descriptions, and to reconsider the relationships of the genus. This paper is also intended as an initial contribution to a revision of the classification and phylogeny of Staphylinoidea.

SYNONYMY AND DISTRIBUTION

A careful comparison of the description and figures of *Glypholoma pustuliferum* by Jeannel (1962) with the more detailed description and photograph of *Lathrimaeodes pustulipenne* by Scheerpeltz (1972) leaves no doubt that the two species are extremely closely allied. The agreement is so complete that there is nothing to suggest that more than one species is involved. *G. pustuliferum* was recorded from Chile Chico (type locality) and Rio Murta at about 46°30'S latitude

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in the southern Andes of Aisén Province, Chile; and from the vicinity of Punta Arenas and Boqueron in the Magellan Strait area, Magallanes Province, Chile, at about 35°30'S latitude. Habitat data were not given, but these localities are within the *Nothofagus* forest zone. *L. pustulipenne* was recorded from 27 sites in the vicinity of El Bolsón, Rio Negro Province, and El Puelo and El Turbio, Chubut Province, Argentina, all at about 42°S latitude on the east slope of the southern Andes. The large series were found between 220 and 1170 meters, nearly all by sifting ground litter in forests of *Nothofagus*, *Libocedrus* and other trees. The *pustulipenne* localities are thus little more than half as far removed from the *pustuliferum* type locality as the Magallanes records of the latter species, and in the same mountain range. Because of the relative completeness of the original descriptions and the distinctiveness of the species, I have not felt it necessary to examine type material, but believe that the combination of morphological agreement and apparent continuity of habitat of the two nominal species is sufficiently strong evidence of conspecificity to formally synonymize the two names. *Lathrimaeodes pustulipenne* Scheerpeltz hence becomes a junior synonym of *Glypholoma pustuliferum* Jeannel (NEW SYNONYMY).

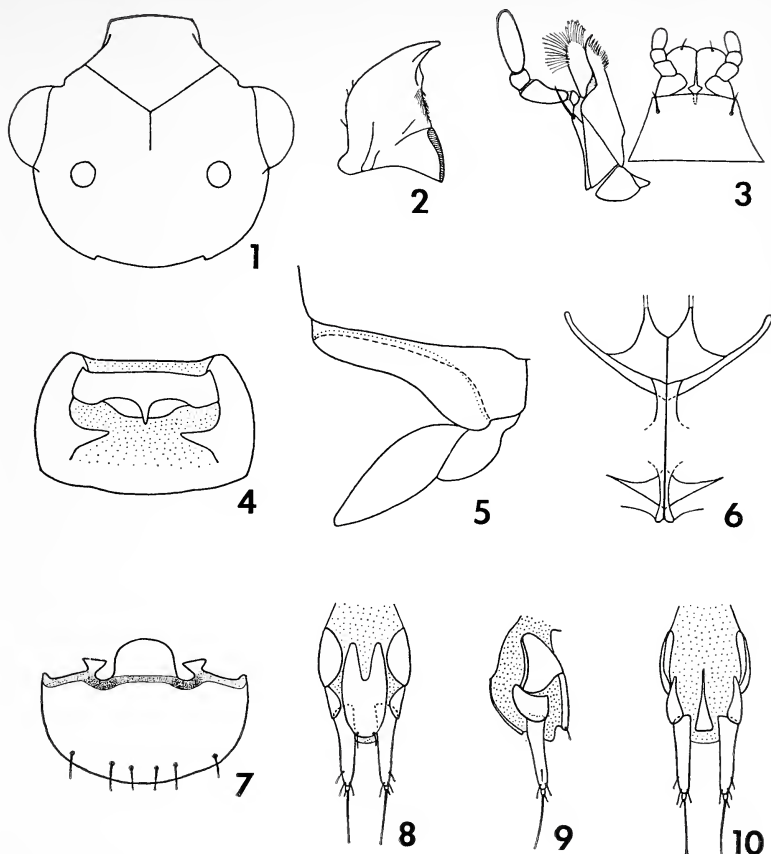
In addition to the material recorded in the original descriptions, which should be consulted for complete collection data, six specimens labeled "Punta Arenas, Chile, Feb. '06, R. Thaxter" are in the Museum of Comparative Zoology. The following descriptive notes and illustrations have been taken from these specimens.

PARTIAL REDESCRIPTION

Each of the original descriptions provides a habitus illustration and sufficiently treats the external characteristics of the species for recognition purposes. Here I would like to describe or illustrate several features of systematic importance that were covered incompletely or not at all in those descriptions.

Head capsule shaped as in Fig. 1, with a transverse V-shaped sulcus in the frontal region. This sulcus is the external indication of an internal ridge connecting the anterior attachments of the tentorium. From the middle of this sulcus a faint sulcus runs a short distance posteriorly. Mandible (fig. 2) with a well developed molar lobe at base. Maxilla and labium as in fig. 3.

Prothorax with coxal cavities as in fig. 4. Hind coxa strongly excavate (fig. 5), the postero-ventral edge produced into a thin plate capable of covering more than half of the femur in repose. Metendo-



Figs. 1-10. *Glypholoma pustuliferum* Jeannel.

1. Head capsule, dorsal view. 2. Right mandible, ventral view. 3. Labium and right maxilla, ventral view. 4. Prothorax, ventral view, legs removed. 5. Right metacoxa and femur, ventral view (dotted line = extent of coxal cavity, dashed line = postero-dorsal edge of coxa). 6. Metendosternite, dorsal view. 7. Eighth abdominal sternite, ventral view. 8.-10. External female genitalia (membranous areas stippled); 8., dorsal; 9., left lateral; 10., ventral view. Not drawn to scale.

sternite as in Fig. 6, the dorsal flange of the stalk flaired out into membrane at the middle. Elytra covering all of the first four abdominal tergites, the fifth tergite partially exposed. Folding pattern of hind wing similar to that illustrated for *Anthobium* (= *Eusphalerum*) *sorbi* by Forbes (1926: fig. 33), the first transverse fold being a hinge in which the costal margin is turned about 90°.

Tergites of abdominal segments 2 and 3 sclerotized to some degree, those of fourth and following segments more strongly so. Tergites 4 and 5 each with a pair of patches of short, pale, mesally-directed setae, the patches together covering most of the surface of the tergite. Sternite 8 with complex anterior modification as in fig. 7. Inter-segmental membranes of abdomen with rectangular plates arranged in a brick-wall-like pattern.

Male genital segment and aedeagus as illustrated by Jeannel (1962: figs. 10, 11), except that both figures are ventral rather than dorsal views as stated. Pleurites of genital segment narrowly connected anterior to tergite. Parameres of aedeagus in repose in abdomen facing dorsally. Female external genitalia as in figs. 8-10.

DISCUSSION

Jeannel considered *Glypholoma* to be closely allied to the silphid tribe Pterolomini. He differentiated it from that tribe by the structure of the maxillary palpus, with a very short third segment, and by what he considered a very unusual aedeagus. Scheerpeltz placed the genus in the Omaliinae and considered it closely related to *Lathrimacum* (= *Anthobium* of current usage). He separated it from *Anthobium* by the absence of a nuchal sulcus and by the longer and differently sculptured elytra.

In considering the placement of the two long-controversial genera *Brathinus* and *Canioleum*, Hammond (1971) has reviewed and augmented the characters of the Omaliinae that are useful in distinguishing them from other Staphyloidea. *Glypholoma* has all 11 of the mentioned features. The three characters that will immediately exclude *Glypholoma* from association with Pterolomini and allied tribes of Silphidae are: 1) the hinging of the costal margin of the hind wing during folding, whereas the costal margin is folded back on itself in primitive Silphidae as illustrated for *Necrophilus hydrophiloides* by Forbes (1922: fig. 27); 2) the anterior modification of the eighth sternite, whereas Silphidae have at most a simple median projection; and 3) the structure of the aedeagus with a large lightly sclerotized basal bulb, short median lobe and small median foramen,

whereas in Pterolomini and allies the aedeagus is a large heavily sclerotized tubular structure without basal bulb and with a large median foramen. The characteristically modified eighth sternite is restricted, according to Hammond, to the staphylinid subfamilies Proteininae and Omaliinae and the genus *Empelus* which probably belongs near those subfamilies. The two additional characters of *Glypholoma* that specifically place it in the Omaliinae are the presence of a pair of ocelli on the vertex of the head, and the presence of paired setal patches on abdominal tergites 4 and 5.

Within the Omaliinae the general habitus, palpal and tarsal structure and nearly all other features indicate a close relationship of *Glypholoma* to *Anthobium* and related Holarctic genera such as *Mathrilaenum*, *Camioleum*, *Deliphrum* and *Olophrum*, as originally proposed by Scheerpeltz. Hammond (op. cit.) has pointed out that this generic group is badly in need of worldwide revision and that the generic concepts will probably change when this is done. At the present time I can only point out what appear to be three exceptional features of *Glypholoma* that may be unique in the Omaliinae, based on the literature and on examination of the omaliine genera in the Museum of Comparative Zoology. These are: 1) the pustules on the elytra referred to by both original authors; 2) the excavate hind coxae, also found in *Empelus*; and 3) the Y-shaped sulcus on the head capsule.

The distribution of the last-mentioned character merits special attention. To my knowledge Y-shaped sulci have been previously reported only in the staphylinid tribe Tachyporini among Staphylinidae (Blackwelder 1936), but are much more widespread. In addition to all genera of that tribe and *Glypholoma*, I have confirmed them in: Staphylinidae — *Trigonurus* spp. (Piestinae) and *Habrocerus magnus* (of uncertain position, not a true *Habrocerus*); Silphidae — *Nicrophorus* spp. (Silphinae) and *Pelatinus latus* and *Lyrosoma opaca* (Agryrtinae); Leiodidae — *Catopocerus* spp. (Catopocerinae), several genera of Agryrtodini (Catopinae), and an unidentified Tasmanian genus of Neopelatopini (Leiodinae). Such sulci are well-known features of many members of the related superfamily Hydrophiloidea. They have been considered absent from Histeroidea, the third group of Staphyliniformia (Crowson 1974), but are found in *Sphaerites politus* (Sphaeritidae) and at least some species of the histerid genera *Bacanius* and *Idolia*. Consideration of the origin and functional significance of this structure is beyond the scope of the present work. However, this widespread distribution among what many would consider primitive members of the three related super-

families, and absence from clearly derivative forms, suggests that the presence of the Y sulcus is an ancestral feature of Staphyliniformia. In *Glypholoma* it is therefore probably best interpreted as a primitive condition which has been lost in other Omaliinae.

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I wish to thank P. M. Hammond for calling my attention to the description of *Lathrimaeodes*, and T. F. Hlavac and J. F. Lawrence for reading and commenting on the manuscript.

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A REVIEW OF THE DISTRIBUTION AND HABITATS
OF NORTH AMERICAN *BRATHINUS*
(COLEOPTERA; STAPHYLINIDAE; OMALIINAE)*

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The genus *Brathinus*, with one Japanese species and three in the United States and Canada, has been considered either as the basis for the monogeneric family Brathinidae (such as in Arnett, 1963), or as belonging to the Staphylinid subfamily Omaliinae (such as in Hatch, 1957, and Crowson, 1967). Hammond (1971) has reviewed the question, has presented a series of eleven morphological characteristics of the Omaliinae possessed by *Brathinus*, and has concluded that *Brathinus* belongs in this subfamily. In addition, he provides a key to the species, illustrations of the male genitalia of the American species, and comments on the rarity of distribution and habitat data. The purpose of this paper is to provide additional habitat data and to contribute to an understanding of the distribution of the North American species.

The data are drawn mostly from my own records and collecting, and from material in the collections of the California Academy of Sciences, San Francisco (CAS), the Canadian National Collection of Insects, Ottawa (CNC), the Field Museum of Natural History, Chicago (FMNH), the Illinois Natural History Survey, Urbana (INHS), the Museum of Comparative Zoology, Harvard University (MCZ), and the United States National Museum, Washington, D. C. (USNM). In the following records, the locality and habitat data are given first, then, when available, the month of collection in lower case Roman numerals, the number of specimens, and the abbreviation of the collections containing the material.

Brathinus nitidus Leconte 1852

The species ranges (map 1) from Newfoundland and Nova Scotia westwards to the Lake Superior Region, and south along the Appalachians to northern Alabama. It is associated with cool riparian and bog habitats, usually in shaded situations, in moss or wet plant roots or under stones, and especially in the spray zone of waterfalls. C. Lindroth (in Hammond, 1971) observed the beetles emerging

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from earthworm-like holes in damp soil on the banks of a Newfoundland river. Most of the more southerly records of the species are from caves, where the beetles are probably seeking the cooler, more moist, and darker conditions. In caves, the beetles seem to be able to survive quite well in the dark zone as well as in the twilight zone, but the association with caves is only a facultative (troglophilic) one, in spite of the cavernicolous characteristics of the beetles' thin cuticle and reduced pigmentation.

Barr (1968: 81) indicated that there was a cave-specialized (troglobitic) brathinid in lava tube caves in southeastern Idaho, but this is the leiodid (*sensu lato*) *Glacicavicola bathyscioides* Westcott (1968) which has converged to look remarkably like *Brathinus* (Peck, 1970, 1973, 1974). The omaliine characters cited by Hammond aid in separating *Glacicavicola* from this subfamily of staphylinids.

Adults have been collected in February and from May through November, but are most often taken in the summer months. At least in the southern Appalachians and in caves the beetles may pass the winter as adults.

I have seen the following material:

CANADA. Newfoundland. Mountains east of Codroy, vii, 1, MCZ. Steady Brook, vii, 2, CNC.

Quebec. Comté Brome. Knowlton, vi, 1, CNC. Comté Gaspé-Est. Gaspé, vi, 23, CNC. Comté Gaspé-Ouest. Mont Albert, viii, 1, CNC. Comté Montmorency. Lac J. Cartier, Parc des Laurentides, vi, 1; viii, 2, CNC. Mare-du-Sault, Parc des Laurentides, viii, 3, CNC. County unknown. Pt.-aux-Saumons, vii, 1, CNC. Ste-Mathilde, vi, 1, CNC.

UNITED STATES. Alabama. Dekalb County. Fort Payne, Manitou Cave, 1 (Univ. Alabama Museum Natural History). Limestone County. Spence Cave, along cave stream in gravel, viii, 4, SBP. Madison County. New Hope, Cave Spring Cave, x, 3, INHS. Marshall County. Kirkland Cave, along stream, ix, 1, SBP. Natural Bridge Cave, along stream, xi, 1, SBP. Morgan County, 3.5 mi SE Fayette, forest litter at cave entrance, v, 1, SBP.

Kentucky. Carter County. Carter Caves State Park, Bat Cave, along stream, vii, 1, SBP. Elliott County. Tar Kiln Cave, along stream, v, 1; viii, 3, SBP. Jackson County. Station Camp Creek, in wet gravels, v, 1, SBP. Powell County. Betsy Cave, vii, 1, FMNH.

Maine. Grafton, v, 1, MCZ.

Michigan. Keweenaw County. Eagle Harbor, vi, 7, USNM. Marquette County. Huron Mountains, viii, 18, USNM. Marquette, vii, 2, USNM.

New Hampshire. Ammonoosuc River shores, vii, 3, MCZ. Fabyans, Ammonoosuc River, 2, MCZ. Franconia, 12, MCZ. Mount Madison, 1, FMNH. Mount Pleasant, ix, 1, MCZ. Mount Washington, 3500-5000 feet, vii, 3; viii, 11; ix, 3; no date, 1; CNC, MCZ. Rumney, vi, 1, MCZ. White Mountains, in woods, 3, MCZ; no other data, 3, CNC, USNM.

New Jersey. Fort Lee, 14, MCZ, USNM. State label only, 3, USNM.

New York. Jefferson County. Watertown, Ice Labyrinth Cave, on damp silt floor, x, 4, SBP. Ulster County. Olivera, vi, 6, USNM, CAS. Westchester County. Peekskill, v, 32, CAS, CNC, FMNH, MCZ, USNM; xii, 1, MCZ. County unknown. Pike, vii, 11, CAS, FMNH, MCZ; Slide Mountain, Catskills, vi, 6, USNM. State label only. 3, CAS, MCZ.

Tennessee. Cumberland County. Mill Cave, flood debris at base of dome at far wall of upper entrance, vii, 1, SBP. Grundy County. Monteagle, Wonder Cave, vi, 1, USNM; ii, 1, CAS. Hamilton County. Lookout Mountain, v, 2, USNM, INHS. State Label only, 7, INHS.

Virginia. Scott County. Flannery Cave, Rye Cove, along stream, xi, 1, SBP.

Vermont. Stowe, vi, 2, USNM.

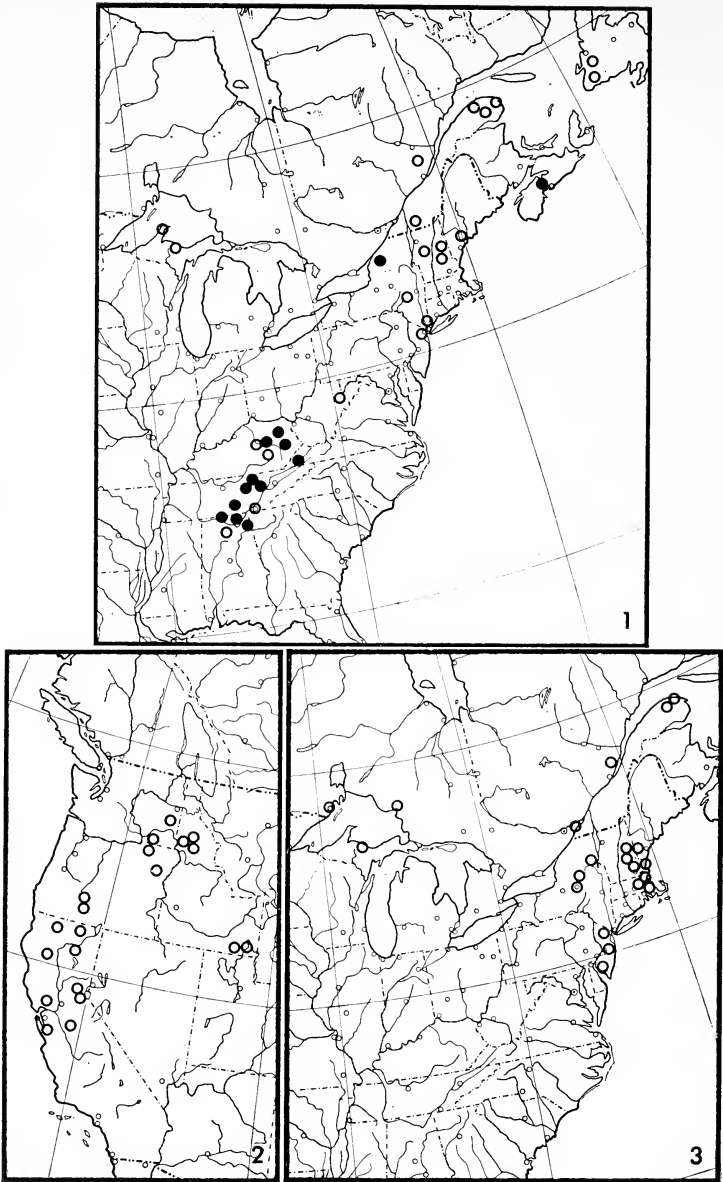
West Virginia. Tucker County. Blackwater Falls State Park, wet moss mats at falls base, vi, 1, SBP.

The species is also reported from an unspecified locality in Nova Scotia by Hammond (1971) and from Frenchman's Cave, St. Croix, Hants County, Nova Scotia (Calder and Bleakney, 1967).

Dr. T. C. Barr, Jr. (in litt.) reports the species from the following additional localities: Kentucky. Jessamine County. Spring on upper Clear Creek. Tennessee. Overton County. Mill Cave; and a sinkhole near Obe Lee Cave. Putnam County. Terry Cave.

Dr. M. W. Sanderson (in litt.) reports taking the species in northern Illinois, but the specimens cannot be located.

Larvae of *Brathinus* are not reported, but a larva associated with the Mill Cave (Cumberland County, Tennessee) population was taken by Barr, and examined by M. W. Sanderson who found it to have omaliine characteristics. I have tried to obtain more larvae from this and other cave populations but have been unsuccessful.



Maps 1-3. Map 1. Distribution of *Brathinus nitidus*. Open circles are above-ground localities. Dark circles are cave localities. Map 2. Distribution of *Brathinus californicus*. Map 3. Distribution of *Brathinus varicornis*.

Brathinus varicornis Leconte 1852

The species ranges (map 3) from Quebec and Ontario southward to Michigan and through the northeastern states to New Jersey. The habitat notes are fewer for this species but they suggest cool riparian or swampy-boggy situations.

Adults have been collected from May through October.

I have seen the following material:

CANADA. Ontario. Michipicoten River, viii, 5, MCZ, USNM. Thunder Bay, I, CNC.

Quebec. Comté Charlevoix-Est. St. Fidèle, vi, I, CNC. Comté Gaspé-Ouest. 6 mi S Riviere-a-Claude, 1000 feet, vii, I, CNC. Parc Gaspesie, Lac Cascapedia, 1700 feet, vii, 2, CNC. Comté Vaudreuil. Rigaud, vi, I, CNC.

UNITED STATES. Maine. Bethel, vi, viii, x, II, MCZ. Kittery Point, II, MCZ.

Massachusetts. Brookline, ix, I, MCZ. Framingham, treading and sifting wet leaves in wooded swamp, vi, 6; v, 6, CAS, CNC, FMNH, MCZ, USNM. Lexington, vi, I, MCZ. Natick, dead grass in swamp, x, I, MCZ. Newton, x, I, MCZ. Wakefield, I, MCZ. Wayland, grass in water, vi, I, MCZ.

Michigan. Marquette, vii, 4, MCZ, USNM. "L.S.", perhaps meaning Lake Superior, I, MCZ.

New Hampshire. Exeter, swamp treading, 2, MCZ. Farmington, viii, 5, MCZ. Rumney, vi, 2, MCZ. Mt. Washington, ix, I, MCZ.

New Jersey. Bridgeton, v, 3, USNM, FMNH. Hilldale, ix, I, MCZ. Monmouth Junction, x, 4, USNM. No other data, v, 4, CAS.

New York. Essex County. Newcomb, Huntington Forest, from *Sphagnum* in swamp, vii, I, W. R. Suter collection. Herkimer County. Thendara, from *Sphagnum* in swamp, vi, 5, W. R. Suter collection.

Leonard (1926) cites the species from Utica, New York.

Hatch (1957: 53) cites all material from the Pacific Northwest under this name but they are undoubtedly referable to the following species.

Brathinus californicus Hubbard 1894

The species ranges (map 2) from the San Francisco area of California northward along the coastal and interior mountains through Oregon to Washington and Idaho. The species is associated with damp moss, and cool, mountain-streamside situations.

Adults have been collected from April through August.

I have seen the following material:

UNITED STATES. California. El Dorado County. Emigrant Gap, v, 1, CAS. Lake Tahoe, vii, 28, FMNH, USMN. Tahoe City, 2, CAS. Modoc County. Cedar Creek, E slope Cedar Pass, 5300 feet, viii, 3, CAS. Napa County. No other data, 12, CAS. Santa Clara County. San Jose, iv, 1, CAS. Shasta County. Burney Falls, vi, 2, CAS. Siskiyou County. Shasta Retreat, 2416 feet, vii, 1, CAS. Sisson, vii, 8, CAS, CNC, MCZ, USNM. No other locality data, vii, 20, CAS, FMNH, MCZ, USNM. Stanislaus County. Adobe Creek, 22 mi W Patterson, iv, 3, CAS. Trinity County. Butler Creek, 12 mi SE Hyampom, 3450 feet, in aggregation with *Stenus* under loose bark of *Abies* log by creek, vii, 130, CAS.

Idaho. Latah County. Moscow, Cedar Mt., v, 2, MCZ. County unknown. Willow Flat, Cub River Canyon, Wasatch Mts., 1, FMNH.

Oregon. Baker County. Pine Creek, near Baker, on debris partly in swift stream, vi, 16, FMNH. Klamath County. 6 mi S Ft. Klamath, Crooked Creek, treading creek-side grass, vi, 9, CNC. 9 mi NE Bly, Deming Creek, 5000-5800 feet, treading moss under Alders, vi, 8, CNC. Umatilla County. Meacham, v, 13, USNM.

Washington. Whitman County. Palouse, x, 2, MCX. Walla Walla County (?). Kooskoosie, vi, 1, USNM.

Hatch (1957: 53) adds the following localities from which I have not seen material: Idaho; Deary, Elk River, and Franklin County. As noted above, these and other localities of Hatch were listed under the name *B. varicornis*, not *californicus*. In discussing this species, Hammond (1971: 68) gives east Wisconsin as part of the range, but this is a misinterpretation of the symbol "e Wn." used by Hatch to signify eastern Washington.

Zoogeographic Considerations.

The distribution of the genus is disjunct, occurring in Japan and temperate North America. This is not an uncommon distribution disjunction. It is shown in many plant genera (Li, 1952), is generalized as an Asian-American distribution type by Thorne (1972), and, except for the presence of *B. californicus*, is an example of the east Asian-eastern North American disjunct pattern of Darlington (1957: 417), based on vertebrates. From my observations, and data provided by Hammond on *B. oculus* Lewis of Japan, I suggest the following distributional-evolutionary history.

The genus had a continuous distribution from Asia through Beringia into and across North America in the Tertiary. The ancestral species *nitidus-californicus* may have been limited to North America, but ancestral *varicornis-oculatus* ranged from Asia across Beringia to eastern North America. With the progressive deterioration of climates in the Pliocene, the Beringian distributional link of this second ancestral species was broken, and the Asian population evolved into *oculatus*, and the North American populations into *varicornis*. The western North American populations of *varicornis* were eliminated by fluctuating Pleistocene climates, and the species became restricted to eastern North America. The range of ancestral *nitidus-californicus* was formerly across North America, but it became broken into two, in the mountains of eastern and western North America, during the fluctuating climatic events of the Pleistocene. Population separation and subsequent speciation into *nitidus* and *californicus* was facilitated by a dry-warm central continental climate in the Sangamon Interglacial or during an earlier interglacial. Later dispersal and expansion of ranges southwards was during the Wisconsin glacial. This is especially true for the expansion of *nitidus* south along the Appalachians. Both *nitidus* and *varicornis* have expanded northwards into formerly glaciated lands since deglaciation. Their southern limits may be contracting as warmer and drier interglacial conditions return. *B. nitidus*, because of its preadaptation for cool and moist conditions, is now favoring caves in the southeast because they can serve as climatic refugia (Barr, 1968: 80).

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HISTOLOGY AND FUNCTION OF THE VENOM GLAND SYSTEM IN FORMICINE ANTS¹

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The hymenopterous venom apparatus characteristically is associated with two sac-like structures, one of which is responsible for venom production and storage. The venom components generally include one or more filaments, a gland-like area and venom reservoir. According to Blum and Hermann (1969), the filaments in some hymenopterous insects apparently function in part in the pick-up of venom precursors and the transference of these compounds to the adjacent convoluted gland. Venom synthesized in the convoluted gland moves to the venom sac where it is stored until it is used.

In a brief investigation of these venom components in formicine ants, we realized that the general picture reported by Blum and Hermann (1969) varied slightly in different aculeates. The venom components in formicines are uniquely arranged and facilitate a detailed study of the cells throughout the structures that are responsible for venom production and storage.

METHODS

The venom components of several formicine species were examined carefully and found to be identical in structure. *Camponotus pennsylvanicus* was chosen to represent the group.

The convoluted gland was unraveled by pulling the entire gland from the sac and pulling on the proximalmost end of the tube on the basal side of the gland. In this way the length of the tube composing the convoluted gland, the point of junction between gland and sac and the point of junction between gland and filaments were determined.

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Venom components were embedded in toto, sectioned at 7μ and stained with Delafields hematoxylin and eosin y and Mallory's triple stain. Longitudinal sections were valuable in examining the cellular differences between the venom components.

MTT (3-(4,5-dimethyl-thiazolyl-2)-2,5-diphenyl tetrazolium bromide, a tetrazolium salt with a high redox potential, was employed as an easily reduced electron acceptor, as outlined by Blum and Hermann (1969). This colorless compound is converted to a purplish-black formazan when reduced. Since the formazan formed by MTT chelates with certain metals to form non-crystalline deposits, cobalt ions were added to the reaction mixture, resulting in the formation of a metallic cobalt-formazan complex.

RESULTS AND DISCUSSION

Venom is forced from the large reservoir through an acidpore (Acp, Fig. 1 A) in formicine ants. A sting is wanting (Hermann and Blum, 1968). Most of the sac is entirely surrounded by relatively sparse circular muscle, which assists in the evacuation of venom. Abundant muscles surrounding the base of the sac are chiefly responsible for the rapid movement of venom out of the sac (Mus, Fig. 2 A).

The venom reservoir (PS, Fig. 1 B) is large, covered by a simple squamous epithelium (RW) and lined internally by a well defined intima. There are no cells incorporated in the reservoir that have a glandular function.

The convoluted gland is an extremely long tube, averaging 376 cm (15 in.) in length. It attaches to the venom reservoir near the latter structure's apex (#1, Fig. 1, C; Jct, Fig. 1 C) and is tightly coiled outward so that the filaments appear to extend from the base of the gland.

Two filaments branch from the single tube (#2, Fig. 1 C) and meander through fatty tissue in the hemocoel. Upon a general examination of the reservoir it appears that the filaments extend from the base of the venom reservoir (Fig. 1, B). The junction between convoluted gland and venom reservoir is hidden beneath the convoluted gland. After dissection the branches of the filaments come together at the base of the convoluted gland (#2, Fig. 1, C) but the basal region of the duct that forms the convoluted gland attaches to the reservoir near the latter structure's apex (#1, Fig. 1, C).

Cellularly, the filaments are very well developed glands themselves (FF, Fig. 2 C), the cells being large and supporting large nuclei.

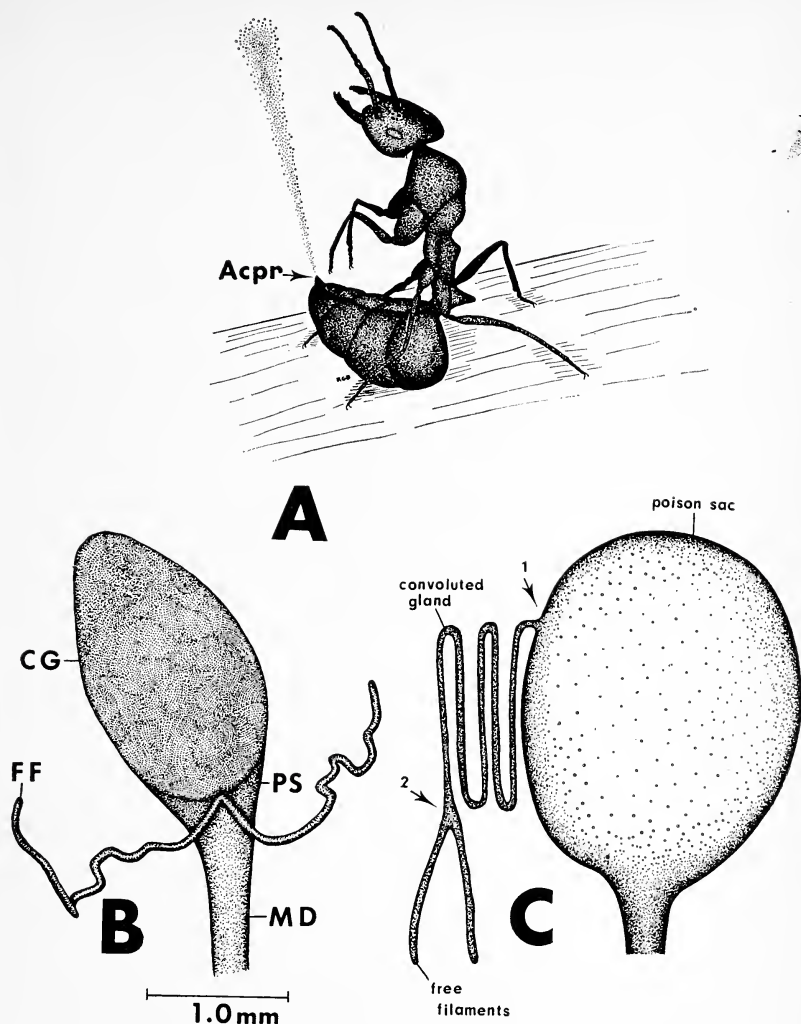


Fig. 1-A. Defensive attitude of formicine ants when venom is evacuated through the acidopore. B—Venom sac, showing its component parts in formicine ants. C—Diagrammatic drawing of the venom components and how they attach to one another in formicine ants. Acpr, Acidopore. CG, Convoluted gland. FF, free filamentous glands. PS, Poison sac (venom reservoir. 1, Junction between convoluted gland and venom reservoir. 2, Junction between single and branching ducts of filamentous gland.

Each filament is made up of two or three cells in transverse section. The lumen in the filaments is well defined (Lu). Since the filaments do possess well defined gland cells that probably have an important part in venom synthesis, it is appropriate to call them filamentous glands rather than free filaments as has been done in the past.

Originally, these filaments were called acid glands because it was believed that they produce an acid venom. This may be the case in the Formicinae but hymenopterons in other subfamilies of the Formicidae and in other aculeate families generally produce a basic venom. These filaments clearly are glandular in function, and they react significantly with tetrazolium salts in tests for enzymatic activity. Blum and Hermann (1969) reported faint reactions in the filaments of *Pogonomyrmex badius* (Latreille) with malate and α -glycerophosphate. Although formazan deposition was apparent only in the distal part of the filaments in that investigation it is now believed that reactions to produce formazan probably occurred throughout the filaments but were difficult to see in the thinner basal region.

It is in the filaments or possibly in the associated fatty tissue that the beginnings of venom production probably occur. Fatty tissue in insects is a general center for intermediary metabolism. The citric acid cycle operates in the fat body. It can incorporate a wide variety of precursors into fat, protein and glycogen, and it functions much like a vertebrate liver in transmitting amino acids and making them available for anabolic processes in other tissues, in this case the filamentous glands and distal convoluted gland. An involvement with amino acids, which subsequently are built into venom proteins, takes place in non-formicine hymenopterons while other compounds would be utilized in formicines in the production of formic acid.

At the point of junction between the filaments and convoluted gland (#1, Fig. 1 C; Jnct, Fig. 2 C) the cellular composition of the convoluted gland is similar to that of the filaments. However, cell type changes shortly beyond the attachment so that the convoluted gland is composed of polygonal cells with smaller nuclei and more internuclear cytoplasm (Fig. 2D). This cellular change indicates that the filaments are quite active as glands themselves and that much of the chemical change of venom precursors already has occurred before they reach the convoluted gland. The cellular composition remains much the same throughout the apical half of the convoluted gland. We have called this the cortex (Cor, Fig. 2 E) since there appears to be considerable glandular activity and hence continued production of venom components.

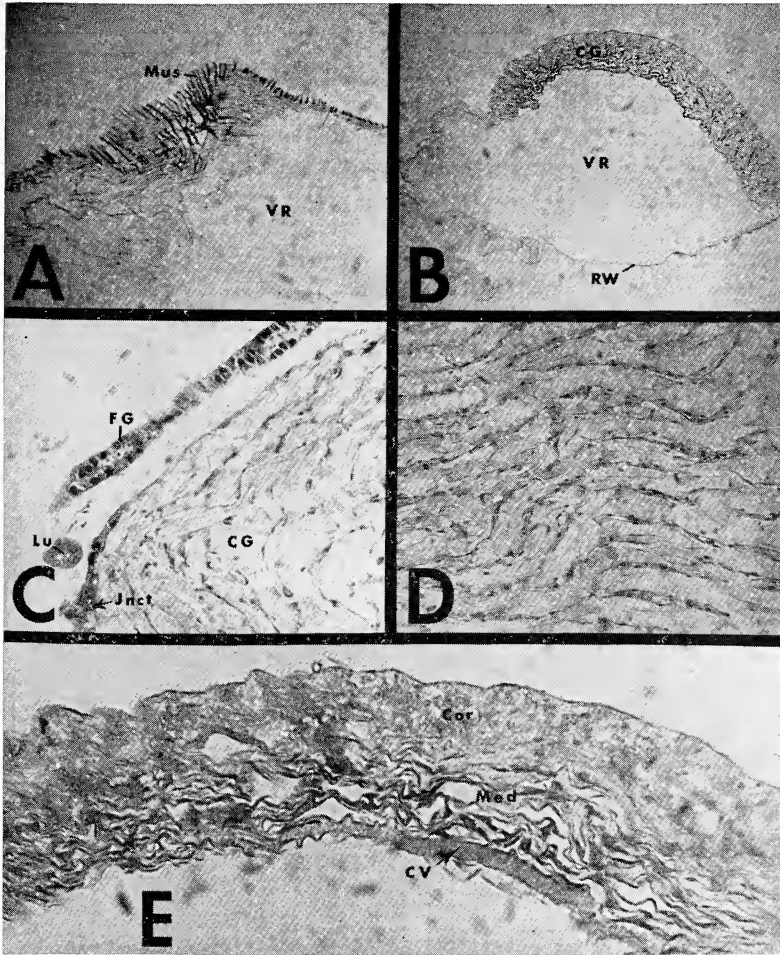


Fig. 2. Sections through the venom components of *Camponotus pennsylvanicus*. A — Oblique section, showing periodic transverse muscle in the basal region of the venom sac. B — Transverse section, showing the reservoir and convoluted gland. C — Horizontal section, showing filament and point of attachment on the convoluted gland. D — Horizontal section through the convoluted gland, showing the arrangement of polygonal cells along collection ducts. E — Transverse section through convoluted gland, showing a well-defined cortex and medulla. The large ducts adjacent to the venom reservoir are filled with venom. CG, Convoluted gland. Cor, Cortex of convoluted gland. CV, Collected venom. FG, Filamentous gland. Junct, Junction between filamentous gland and convoluted gland. Lu, Lumen of filamentous gland. Med, Medulla of convoluted gland. Mus, Muscles transversely arranged around venom sac base. RW, Reservoir wall. VR, Venom reservoir.

The basal half of the convoluted gland is chiefly composed of ducts lined with squamous cells and a strongly refringent intima (Med, Fig. 2 E). We have termed this region the medulla since it clearly functions in the collection of venom synthesized in the filaments and distal convoluted gland. The strongly developed intima probably is necessary for the protection of the remaining cellular components that link the convoluted gland with the reservoir. Formic acid is the chief constituent of formicine venom. The basal ducts in the medulla have an increasingly large lumen. Adnate to the venom sac a large supply of venom collects to flow into the reservoir. There appears to be no control of the venom flow from the medulla duct to the reservoir. No valves, dilator or occlusor muscles could be found.

Based on an examination of the venom components in most of the other formicid subfamilies, it appears that the venom components of hymenopterous insects other than the Formicinae have a similar composition cellularly, regardless of the arrangement between the glandular and reservoir regions. The convoluted gland in non-formicine hymenopterans is inside the reservoir. However, the basic connections between reservoir, convoluted gland and filamentous glands are similar; the venom components of all hymenopterans have been modified from a simple invagination of the integument.

Since fatty tissue functions in the storage of a diverse array of compounds and it is the site for intermediary metabolism, it is reasonable to assume that venom synthesis begins at this point. The filamentous glands, being closely associated with the fat, pick up venom precursors and change them considerably before they get to the convoluted gland. Venom synthesis is completed in the distal region of the convoluted gland, the proximal portion functioning only in the collection of venom and the transportation of it to the venom reservoir.

SUMMARY

The cells of the filaments, convoluted gland and venom reservoir vary considerably. The filaments are more glandular in function than previously expected. The convoluted gland clearly is part glandular (cortex) and part collecting duct (medulla). The movement of venom from the medullar region of the convoluted gland is unaided by a special release mechanism. In its release from the venom reservoir, venom is forced out through the acidopore by circular muscles most abundantly found near the base of the reservoir.

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OCCUPANCY BY *HYLAEUS* OF SUBTERRANEAN HALICTID NESTS (HYMENOPTERA: APOIDEA)¹

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Hylaeus (Colletidae) is well known to nest in various preformed cavities. It is most commonly reported in hollow stems (Stoekert, 1933; Malyshev, 1936; Michener, 1965; Stephen et al., 1969) but also may occupy cynipid wasp galls (Stoekert, 1933; Laroca, 1971) and dead wood (Perkins, 1899; Michener, 1965). However, nest sites are not limited to plant materials. Smith (1855) reported cells in hollow pieces of "flint stone"; Ferton (1932), in earthworm burrows; and Perkins (1899), in ground. The present paper concerns nests of *H. bisinuatus*² in burrows of a halictine bee in an earthen bank; this is the first record of *Hylaeus* occupancy of nests of another hymenopteran.

H. bisinuatus has also been found in North America nesting in soda-straw traps and nail holes (R. R. Snelling, pers. comm.) and in Europe in hollow briar (*Rubus*) stems (Stoekert, 1933). Thus this species evidently has behavior which is flexible enough to enable it to nest in a variety of preformed holes in a wide geographical area.

In early July to early August, 1974, six nests of *H. bisinuatus* were found among those of *Lasioglossum* (*Dialictus*) *zephyrum* (Halictidae: Halictinae) in a nesting aggregation in vertical banks of the Kansas River, near Eudora, Douglas County, Kansas. Although the *Lasioglossum* nest aggregation is enormous, extending for about 1 km up and down the river, all the *Hylaeus* nests were found in about 10 square meters where the bank faces northwest.

The burrows occupied by *H. bisinuatus* were obviously former nests of *L. zephyrum*. In two nests vacant cells of *L. zephyrum* were near those used by *H. bisinuatus*; abandoned cells of *L. zephyrum* probably would have been found in all nests by following main burrows farther into the soil. Cells of *Hylaeus* were constructed in cells of the *Lasioglossum* still having the shape and wax-like lining

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²*H. bisinuatus* (Förster, 1871), described from Europe, is a senior synonym of *H. stevensi* (Crawford, 1913), described from North America, where it is probably adventive (R. R. Snelling, pers. comm.).

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characteristic of the halictine. The longitudinal axes of the burrows and cells of the nests were horizontal as is typical for nests of *L. zephyrum* in vertical banks (Batra, 1966). Burrows and nest entrances were similar in size to those of *L. zephyrum*. Thus there is no evidence that the *Hylaeus* did any nest excavation; it appears to have merely used available nests for its own purposes. Furthermore there is no evidence that the *Hylaeus* entered occupied *Lasioglossum* nests, although this possibility exists.

All six *Hylaeus* nests were discovered after their entrances had been closed, each with a sheet of a cellophane-like material flush with the surface of the soil bank. The sheets had striations radiating from their centers and small openings along their margins. A female of *H. bisinuatus* was discovered licking across a nest entrance already closed by a "cellophane" sheet. Evidently she was finishing the closure. She revolved around the entrance 3 times in 18 minutes while she licked 22.5 times per minute ($n = 2$ min) across the sheet; during this time she took occasional rests of several seconds each. During each lick the tip of her proboscis moved from her midventral area to a point in front of her head.

For identification she was captured before she finished the closure and two days later (on 5 July) her nest was examined (Fig. 1). All three of the cells in her nest were provisioned with a soft yellow material, most likely a mixture of pollen and nectar as is used by

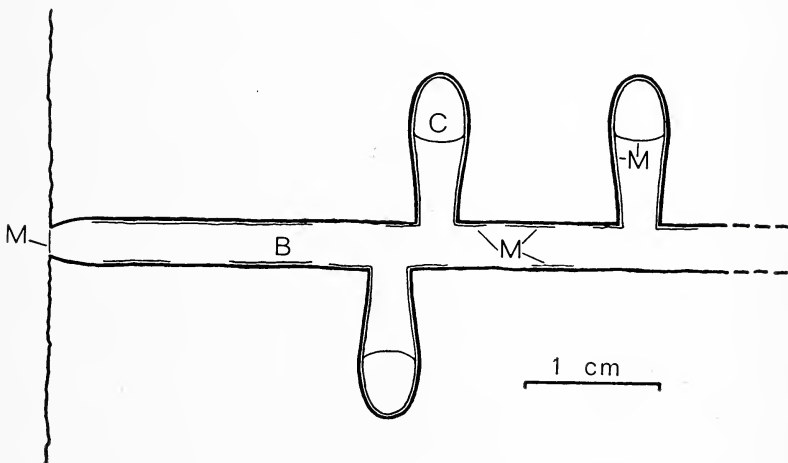


Fig. 1. Top view of a nest of *Hylaeus bisinuatus* made in a nest of *Lasioglossum zephyrum*; B, main burrow; C, *Hylaeus* cell inside *Lasioglossum* cell; M, cellophane-like membrane secreted by the *Hylaeus*.

other *Hylaeus*, and each contained a larva. One larva became a prepupa on 6 July, a pupa on 7 July, and an adult female on 14 July; the other larvae were small and died.

Nests had from 1 to 3 *Hylaeus* cells ($\bar{x} = 1.7$, $n = 6$ nests), each in a different *Lasioglossum* cell (Fig. 2). Both *Hylaeus* cells which were measured were 5 mm long and 3.5 mm in maximum diameter and at the ends of *Lasioglossum* cells. The walls of the cells had old wax-like lining deposited by *L. zephyrum* (Batra, 1966). *H. bisinuatus* laid down two other cell linings to form its cells: (1) a very thin "cellophane" layer visible under a microscope (30X) only when light strikes it at a certain angle and (2) a slightly thicker "cellophane" layer over the first one. This thicker layer also covered walls of lateral burrows and parts of main burrows. A sheet of what appeared to be this same second layer closed off each cell and with the unaided eye the halictine cells appeared to be constricted where such a sheet was placed. Complete removal of the cellophane-like material, however, shows the unmodified form of the halictine cell.

H. bisinuatus used cells of *L. zephyrum* that were 0.8 to 4.5 cm ($\bar{x} = 3.3$ cm, $n = 6$ nests) from the nest entrances. Since *L. zephyrum* constructs cells this close to the surface of a soil bank only in spring or early summer, the *Hylaeus* must have used early-season *Lasioglossum* cells made in the year of this study or possibly in the previous year.

ACKNOWLEDGMENTS

I thank Mr. Roy R. Snelling of the Los Angeles County Museum of Natural History for identifying *Hylaeus bisinuatus*. He and Drs. Charles D. Michener and William J. Bell and Ms. Marjorie R. Chabot made important suggestions regarding this note. It is a byproduct of National Science Grant GB-38502 (W. J. Bell and C. D. Michener, coprincipal investigators).

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1,4-BENZOQUINONES IN AFRICAN MILLIPEDS¹

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The defensive glands of millipeds have been the subject of considerable recent chemical and biological investigation. Compounds identified from the secretions have included hydrogen cyanide, acetate esters, aldehydes, phenols, 1,4-benzoquinones, quinazolinones, and nitrogen-containing terpenes (references in Eisner *et al.*, 1975). The most widespread of these components are the 1,4-benzoquinones which have been found in the secretion of species of the orders Julida, Spirobolida, and Spirostreptida. We here report the isolation of 1,4-benzoquinones from three species of Spirostreptida from Africa: *Archispirostreptus tumuliporus*, *Peridontopyge conani*, and *P. rubescens*.

The millipeds were collected in Senegal, in the region of Kaolack (Sine-Saloum), where they are known to damage agricultural crops, particularly peanuts. *Peridontopyge conani* and *P. rubescens* can be especially abundant. At the beginning of the rainy season the millipeds swarm over the soil surface in large numbers in search of food and mates.

The animals were shipped live to Ithaca, N. Y., where they were "milked" of secretions on arrival. Individual animals were handled and tapped gently with a small metal mallet, until the golden-brown secretion oozed from their glands. The effluent was soaked up in pieces of filter paper, and transferred to carbon disulfide. Examination of the secretion from the two species of *Peridontopyge* by gas-liquid chromatography (6 ft. column, 15% SE-30, 200°C) revealed the presence of a single component. Comparison with an authentic sample (gas-liquid chromatography, infrared spectroscopy, proton magnetic resonance spectroscopy) showed this component to be 2-methyl-3-methoxy-1,4-benzoquinone.

The secretion from *A. tumuliporus* was shown by gas-liquid chromatography to contain two components, which by chromatographic and spectroscopic comparison with authentic samples were shown to

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be 2-methyl-3-methoxy-1,4-benzoquinone and 2-methyl-1,4-benzoquinone. Gas-liquid chromatography indicated the presence of a third minor component, present as a shoulder on the downward side of the 2-methyl-1,4-benzoquinone peak.

Individual milkings from males and females of the three species showed no qualitative sexual differences in quinone content, although the ratio of the two quinones in *A. tumuliporus* showed considerable individual variability.

The two quinones here identified are the most common ones found in millipeds (references in Eisner *et al.*, 1975). Fifteen spirostreptoid species have been previously studied. Of these, eight resemble *Archispirostreptus tumuliporus* in that they produce both quinones (*Archispirostreptus gigas*, *Cambala hubrichti*, *Collostreptus fulvus*, *Dorotogonus annulipes*, *Orthoporus flavior*, *O. punctilliger*, *Prionopetalum frundsbergi*, *P. tricuspis*) (Eisner *et al.*, 1975; Perissé and Salles, 1970; Wood, 1974). One species resembles *Peridontopyge conani* and *P. rubescens* in that it produces 2-methyl-3-methoxy-1,4-benzoquinone only (*Orthoporus conifer*) (Eisner *et al.*, 1965). Five species, including two other *Peridontopyge*, produce only 2-methyl-1,4-benzoquinone (*Auglonopygus aculeatus*, *Peridontopyge aberrans*, *P. vachoni*, *Spirostreptus multisulcatus*, *Rhapidostreptus (Spirostreptus) virgator*) (Barbier, 1959; Barbier and Lederer, 1957). One species produces the unsubstituted quinone, 1,4-benzoquinone (*Spirostreptus castaneus*) (Barbier and Lederer, 1957).

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LIFE HISTORY OF THE FISHFLY,
NIGRONIA FASCIATUS
(MEGALOPTERA: CORYDALIDAE)

BY DONALD C. TARTER,¹ WILLIAM D. WATKINS²
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The objective of this study was to describe certain aspects of the life history of the fishfly, *Nigronia fasciatus* (Walker), in a small, woodland stream in Cabell County, West Virginia. Some investigators, including Tarter and Watkins (1974), Evans (1972), Neunzig (1966) and Cuyler (1965), have reported taxonomical and distributional information on this fishfly. The egg masses, eggs, and first-instar larvae of *N. fasciatus* were described by Baker and Neunzig (1968), and the mature larva by Cuyler (1965) and Neunzig (1966).

The genus *Nigronia* Banks 1908 includes two recognized species in North America, *N. fasciatus* (Walker) and *N. serricornis* (Say). *N. fasciatus* was originally described by Walker (1853) as *Chauliodes fasciatus*. It has been collected in New York, Pennsylvania, Ohio, Glen Echo, D. C., Maryland, Illinois, Missouri, Arkansas, and Mexico (Davis, 1903). In West Virginia, Tarter and Watkins (1974) reported *N. fasciatus* from eight major drainages in 15 counties. The larvae are most often found under rocks and logs in small, woodland streams.

MATERIALS AND METHODS

Hisey Fork, a small, woodland stream in Cabell County, West Virginia, is the study area. The stream flows northeast for 7.4 km and empties into Fourpole Creek near Huntington, West Virginia. The average gradient is 45 m/km. The stream is about 1 m wide throughout its length, and the water depth is about 0.1 m. The substrate consists of sand, coarse rubble and large boulders. The riparian woodland is composed of beech *Fagus grandifolia* Ehrh., yellow poplar *Liriodendron tulipifera* L., oak *Quercus* spp., and hickory *Carya* spp.

This study was initiated in September 1972 and continued until August 1973. To study the life history of *N. fasciatus*, the year was

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divided into four seasons; fall (Sept.-Nov.), winter (Dec.-Feb.), spring (Mar.-May), and summer (June-Aug.). Usually a single collection was made during the middle month of each season. Larval fishflies were collected from under rocks (8-50 cm in diam) and in logs throughout Hisey Fork by handpicking with forceps. Generally, the larvae occurred about 1 per 20-30 meters of stream length. They were placed in boiling water to prevent shrinkage and stored in 70 per cent ethanol.

Size-frequency distributions of head widths, arranged in 0.2 mm groups, were employed each season to determine the size classes of *N. fasciatus* larvae. Also, 211 larval head widths, measured with a dial vernier caliper (nearest 0.1 mm), were used as an index of growth.

Data regarding larval food habits were determined by foregut analysis. The foreguts were excised and the contents sorted into various taxonomic categories under a dissecting microscope. The number of specimens in each taxon was counted and recorded for each foregut. The following calculations were made seasonally: (1) the percentage of foreguts in which a particular taxon occurred (percentage frequency of occurrence) and (2) the average number of specimens in all foreguts containing that particular taxon.

Fecundity in the adult fishfly *N. fasciatus* was determined by direct counts of ovarian eggs. Both ovaries of 10 adults were removed and a total of 6802 eggs were counted. The regression of fecundity on total length was calculated and a coefficient of correlation determined.

Water temperature was measured with a thermometer placed near the bottom. Determinations of total alkalinity, total hardness as CaCO_3 and pH were carried out in the laboratory with a Hach chemical kit, Model DR-EL. Dissolved oxygen concentration was measured in the field with a Hach chemical kit, Model AL-36-WR.

RESULTS AND DISCUSSION

Stream Environment. — During the study period, water temperature ranged from 5.6 to 18.3 C, winter and summer, respectively. The average pH value was 7.7 (range, 7.0-8.0). The waters usually were supersaturated with dissolved oxygen which ranged from 9 to 13 mg/l (\bar{x} = 11 mg/l). Total alkalinity concentrations ranged from 45 to 85 mg/l, winter and summer, respectively (\bar{x} = 68 mg/l). The average total hardness concentration was 163 mg/l; the range was 120 (spring) to 210 (summer) mg/l.

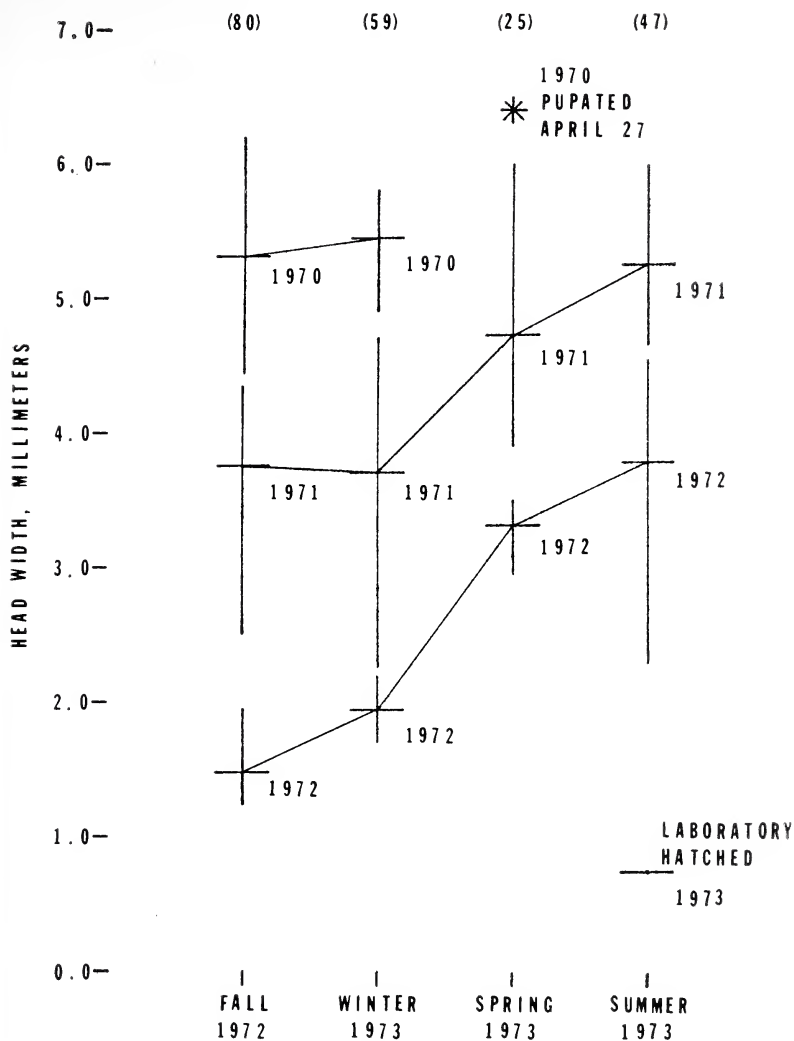


Figure 1. Seasonal size-frequencies of *N. fasciatus* larvae from Hisey Fork, Cabell Co., W. Va. Number of larvae is given in parentheses, and size classes are marked with year of hatching.

Larval Food Habits. — The following food categories were identified in the foreguts of larval fishflies from Hisey Fork: Isopoda, Diptera, Ephemeroptera, Megaloptera, and Trichoptera. Of the 181 foreguts examined, 170 (93.9%) contained food and 11 (6.1%) were empty. The highest percentage of empty foreguts (8.9%) occurred in fall.

Of the identifiable food materials, the isopod *Asellus militaris* (Hay) ranked first in percentage frequency of occurrence in all seasons. It ranged from 22.9 per cent in summer to 56.0 per cent in spring. The largest number (27) and the highest average (1.2) of isopods occurred in fall.

Larvae of the caddisfly *Cheumatopsyche* sp. ranked second to isopods in percentage frequency of occurrence in summer (14.3), fall (19.7) and winter (18.0). Pupation and emergence could be responsible for their lowest frequency (8.0%) in spring. In fall, the highest average (1.1) and greatest number (15) of larval caddisflies occurred in the diet of the fishfly.

A limited number of mayfly naiads, *Ephemerella coxalis* McDunough, entered the diet in the spring and summer. The naiads ranked second (20.0%) to isopods in percentage frequency of occurrence in spring.

Chironomid larvae were consumed in winter, where they occurred with a frequency of 10.3 per cent. They ranked behind isopods and caddisflies as a food source for larval fishflies.

Some cannibalism was found in all seasons. It reached the highest frequency of occurrence (11.4%) in summer, where four *N. fasciatus* larvae were consumed.

Digested and unidentified materials comprised a high percentage frequency of occurrence in fall (55.0), winter (46.1) and summer (51.4). In spring, they were found in 24 per cent of the foreguts.

Minshall (1967) reported that larvae of *N. fasciatus* from Morgan's Creek, a woodland springbrook in Meade County, Kentucky, consumed *Gammarus*, *Asellus*, *Ectopria* and unidentified amorphous materials. The guts of most larvae were partially full, and the consumed material was of indeterminate nature.

Larval Development. — The larval population of *N. fasciatus* consisted of three size classes (Fig. 1). In the youngest size class (1973, year of hatching), laboratory hatched larvae in June measured 0.75 mm in head width (Fig. 2 and Table 1). The smallest larva in the stream measured 1.3 mm in head width and was collected in fall (29 November 1972). The method of collection precluded getting large numbers of the youngest size class from the

Table 1. Seasonal head widths (mm) of larval size classes of *N. fasciatus*, Hisey Fork, Cabell Co., W. Va.

Size Classes (Year of Hatching)	Fall	Winter	Spring	Summer
1970	$\bar{x} = 5.3$ (4.5-6.2) N = 41	$\bar{x} = 5.5$ (4.9-5.8) N = 27	PUPATED	—————
1971	$\bar{x} = 3.8$ (2.5-4.4) N = 35	$\bar{x} = 3.7$ (2.5-4.7) N = 30	$\bar{x} = 4.7$ (3.9-6.0) N = 20	$\bar{x} = 5.3$ (4.7-6.0) N = 22
1972	$\bar{x} = 1.5$ (1.3-2.0) N = 4	$\bar{x} = 2.0$ (1.7-2.2) N = 2	$\bar{x} = 3.3$ (3.0-3.5) N = 5	$\bar{x} = 3.8$ (2.3-4.6) N = 15
1973	—————	—————	—————	$\bar{x} = 0.8$ (0.8) N = 10

stream. The mean head width of larvae at the end of the first year of development (1972) was 3.8 mm (Table 1 and Fig. 2). After the 2nd year of development (1971), the mean head width was 5.3 mm (Table 1 and Fig. 2). At the end of the 3rd year (1970), just prior to pupation, the mean head width was 5.5 mm (Table 1 and Fig. 2).

Larval head width demonstrated seasonal changes in growth (Fig. 2). The greatest growth rate (69.7%) of the larval population, occurred from winter to spring in the 1972 size classes. This development coincided with the greatest seasonal changes in water temperature, 5.6 C and 16.0 C, winter and spring, respectively.

Pupal Stage. — One pupa was collected in the spring (April 27). It was found under a flat rock (ca 45 cm in diam) in an earthen cell 30 cm from the stream. Based on field observations of the first adult, pupation lasted approximately 21 days.

Neunzig (1966) reported that *N. fasciatus*, in Nature Trail Creek, North Carolina, started pupation around May 5 and reached a peak the following week. The pupae were located under moss in earthen cells about 6-12 inches from the creek. Minshall (1968) noted that *N. fasciatus* from Morgan's Creek, Kentucky, pupated in the early spring (April).

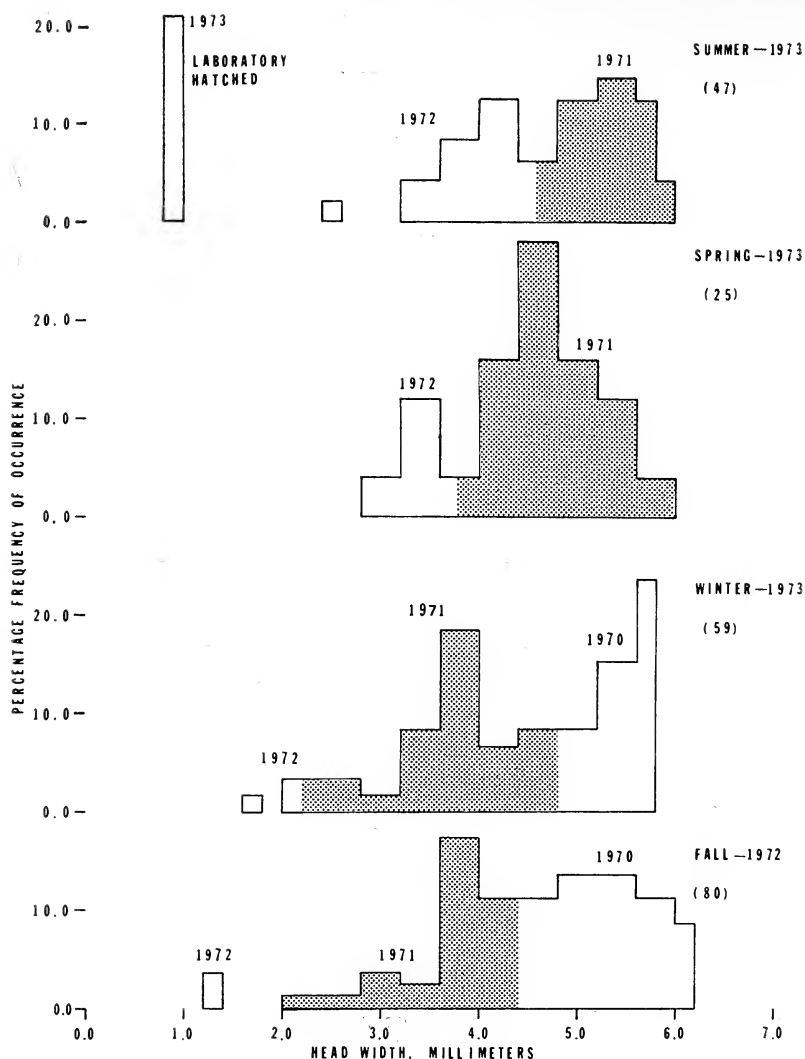


Figure 2. Seasonal variation of the head width in *N. fasciatus* larvae in Hisey Fork, Cabell Co., W. Va. Vertical lines = ranges, horizontal lines = means.

Adult Stage.—The first adult fishfly was collected near the stream on May 16. In one hour 13, 8 and 3 adults were observed on May 20, 22, and 25, respectively. On different occasions, several wings of adult fishflies were found scattered along the stream bank. Apparently, birds or other predators had fed upon the adults. No wings or fishflies were found after May 25. The approximate flying season for *N. fasciatus* was 10 days.

Oviposition was observed in the field on May 20 and 22. Females oviposited their entire egg mass on the underside of leaves 4-6 m above the stream between 1300 and 1600 hours. Several leaves with egg masses were brought to the laboratory and suspended over water. Hatching occurred in 14 days and first-instar larvae (1.5-2.0 mm, body length) fell into the water and crawled underneath rocks.

There was high correlation ($r = 0.95$) between the numbers of eggs produced and the total length of female fishflies. The following equation was calculated to express this relationship.

$$Y = -2800.0 + 93.9X$$

where Y = the number of eggs, and
X = total length, mm

Ovarian egg counts of 10 females showed a range from 275 to 1134 eggs per female ($\bar{x} = 680$).

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OBSERVATIONS ON BREEDING BEHAVIOR OF
PACHYDIPLAX LONGIPENNIS
(ODONATA:LIBELLULIDAE)*

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INTRODUCTION

Pachydiplax longipennis Burmeister is a medium sized dragonfly found throughout the United States. Clifford Johnson (1962) has described the general pattern of breeding behavior of this species in North Carolina, Virginia and Texas. In this paper I report my observations of three populations of this species in Massachusetts. While territorial and mating behavior is similar to that described by Johnson, I am able to extend his findings in some areas. In addition, I describe the coloration of this species in ultraviolet light and speculate as to the behavioral significance of the high reflectancy of areas of blue pruinescence.

METHODS

Observations were made at three ponds near Boston, Massachusetts, during the period June-August, 1974. *Pachydiplax longipennis* was relatively abundant at each pond. Observations were made throughout the daily activity period and under a variety of weather conditions.

Initial observations were made at Pickman Pond at the Concord Field Station of Harvard University in Bedford from June 13-July 18. This is a shallow man-made pond of about 1.5 hectares. The banks are thickly vegetated with bushes and sedges; the surrounding vegetation has been mapped by Maguire *et al.* (1973). Water depth within 2 m of the shore was typically 20-50 cm. Fallen branches and emergent vegetation, such as water lilies, lined the periphery. In early July, studies were conducted at a second shallow, artificial pond in Lexington (Five Fields: ca. 0.5 hectares), where the lack of dense fringing vegetation facilitated detailed observations. The pond was bordered on two sides by grassy banks and overhung by trees (mostly *Acer rubrum*). Emergent vegetation included

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arrow head (*Sagittaria latifolia*). Observations were made daily until August 8, by which time the water had dropped to such a level that few emergent perches suitable for *Pachydiplax longipennis* remained. On August 12, observations were commenced at a third shallow, artificial pond off Shade Street in Lexington. This 1.2 hectare pond was completely surrounded by trees (*Acer rubrum* and *Alnus* sp.) and emergent sticks and logs suitable for perches were plentiful.

At the Five Fields pond, attempts were made to study behavior by marking males. These attempts were largely unsuccessful due primarily to failure to relocate marked individuals. Thereafter, identifications of individuals were made by recording natural variations.

Some preliminary studies were made of the ultraviolet reflectant properties of the blue-grey abdominal pruinescence. With the collaboration of Robert E. Silberglied (Department of Biology, Harvard University) ultraviolet patterns were examined, using a 35mm single-lens-reflex camera with Zeiss F.4, 60mm Ultraviolet Objektiv lens, Zeiss UV 366 filter (=Wratten 18A), Bowens Texturelight electronic flash, Kodak Tri-X Pan film, and Acufine developer.

Although most of my observations confirm those of Johnson (1962), I found that there was a difference in male perching behavior. These and some additional observations are reported below.

MALE-MALE INTERACTIONS

From the time of their arrival (approx. 10 a.m.) until their departure (approx. 4 p.m.), the males observed defended a defined territory as described by Johnson (1962). The "threat display" (Johnson, 1962) was also frequently seen. Following this display, I observed that the two males engage in further agonistic behavior. One male pursues the other in a horizontal direction with abdomen raised while the leading insect flies with abdomen lowered (Fig. 1a). The two may repeat this behavior several times, exchanging positions and/or reversing direction after flying a distance of 1-2 meters. (They may alternatively resume the "threat display." Occasionally this may involve only one male if the other has returned to a perch.) After a variable duration (usually less than a minute) this pursuit behavior is discontinued and the males may begin a third behavior, as Johnson (1962) noted. Then, as I observed, the male who does succeed in getting the lower position, flies upwards, forcing the other up with him as much as 15 meters into the air at an angle of 50-80

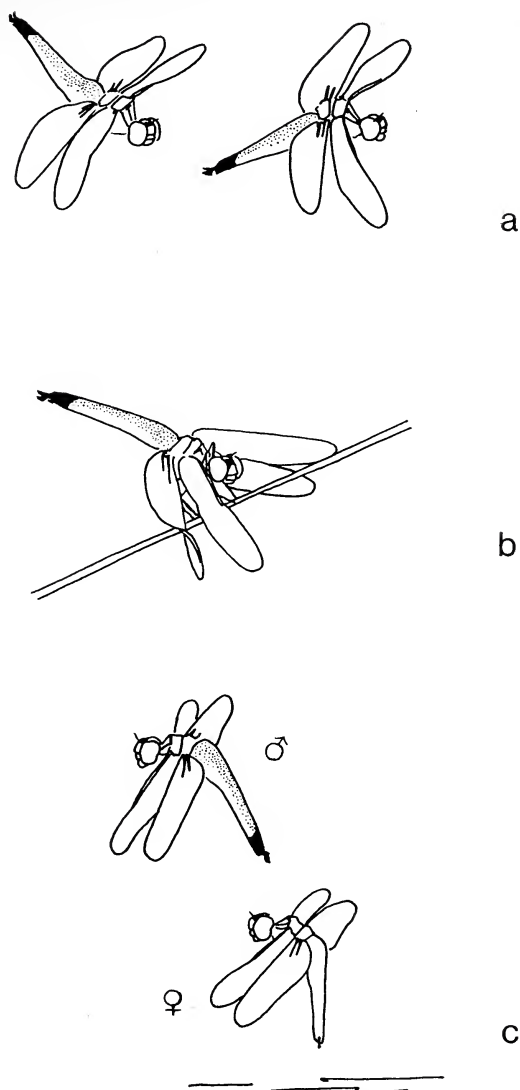


Figure 1. *Pachydiplax longipennis*: a, male-male chasing behavior; b, male perching position; c, male-female precopulatory position.

degrees. Immediately, one male returns directly to defend the territory while the defeated male returns many seconds later to rest or does not return to the area at all. Unfortunately, the flight speed was so great, and the distance so far, that I was unable to determine which male claimed the territory, or whether either regularly did, but I would hypothesize that the lower and therefore faster male usually dominates. As Johnson (1962) stated, this is the final step in establishing territorial dominance between two males. At any time one male may abandon this territorial dispute and retreat out of the area leaving it for the remaining male. In further agreement with Johnson (1962), I observed that the original owner often retains the territory. Such disputes generally last from 5 to 50 seconds and terminate with territorial possession and perch display by the dominant male.

PERCHING POSITION

The perching position of *Pachydiplax longipennis* is probably determined by several factors including wind, sun intensity, air temperature, the kind of perch, and the behavior of other dragonflies. Under typical summer daytime conditions when the wind speed is low, a male in an open situation exposed to full sunlight, usually aligns his body along the length of the perch. He raises his abdomen only a few degrees and brings his wings forward (Fig. 1b). Every 10 to 60 seconds he leaves his perch to patrol but returns directly if undisturbed by intruders. Very rarely did any male raise his abdomen to the extent illustrated by Johnson (1962: Fig. 2). On windier days, males keep their wings fully outstretched and at right angles to the prevailing wind. Only on hot calm days, when the air temperature rose above 30°C, did perching males raise their abdomens higher.

My observations, coupled with Johnson's (1962), suggest that male perching behavior is influenced by at least four factors including thermoregulation, aerodynamics, predator avoidance, and territorial display. It is interesting to note that whereas Johnson (1962) and Williamson (1900) reported that males generally perch with their abdomens directed upwards, this behavior was rarely seen in Massachusetts populations. Johnson and Williamson's observations were made on sunny days, at stations where daytime temperatures are typically 2-4°C higher than those prevailing in Massachusetts. This suggests that this behavior may be temperature dependent. As male-male territorial interactions were otherwise fully developed in the Massachusetts populations, I suspect that the abdomen orienting

behavior may be primarily thermoregulatory in function rather than purely for territorial display as concluded by Johnson (1962).

MATING AND OVIPOSITION

Pachydiplax females were infrequently seen at the three ponds. During July and August only 25 matings were closely observed. Females appeared between 1300 and 1500 hours (E.S.T.) on warm sunny days and courtship commenced immediately. A territorial male, upon seeing a female within his territory, would fly directly to a position above her. Hovering a few centimeters above her he would raise his abdomen in a manner similar to that seen in the threat display. (But in a position that makes it difficult for the female to see this display.) He then flaps his wings rapidly in an unusually wide arc. A receptive female will permit the male to align his body directly above hers. The male then descends and the female rises up slightly while lowering her abdomen and presenting her head (Fig 1c). In rapid sequence he clasps her with his abdominal appendages and they go into copula. Copulation occurs in flight and is brief, lasting 10-40 seconds. Its duration appears to depend, in part, on the number of previous inseminations received by the female, but only by collecting data could this speculation be verified. The pair then separate and the male returns directly to his display perch. On three occasions the male was seen to transfer sperm to his genitalia during this short postmating flight. Typically, the female also rests for 5-10 seconds on a nearby perch before searching for oviposition sites.

Oviposition was observed as illustrated by Needham and Westfall (1955). I found that the male defended the female from interference by other males only as long as she remained within his territory. The flight of these defending males was more directed and intense than that seen in male-male interactions. Nonetheless, in a few cases, when many males were present and/or when the female strayed out of her mate's territory, his fervent defense was inadequate and oviposition prevented. A behavior, marked in *Libellula incesta* Hagen but less common in *P. longipennis*, occurred when unmated males attempted to grasp the female while her head was exposed during oviposition. The female was usually knocked, tumbling, into the water. *L. incesta* females, being stronger fliers, would attempt to evade such attacks; *P. longipennis* females usually retreated to the trees until male excitement diminished. In addition to interference from other males, frogs presented a major threat to females ovipositing near the edge of the ponds.

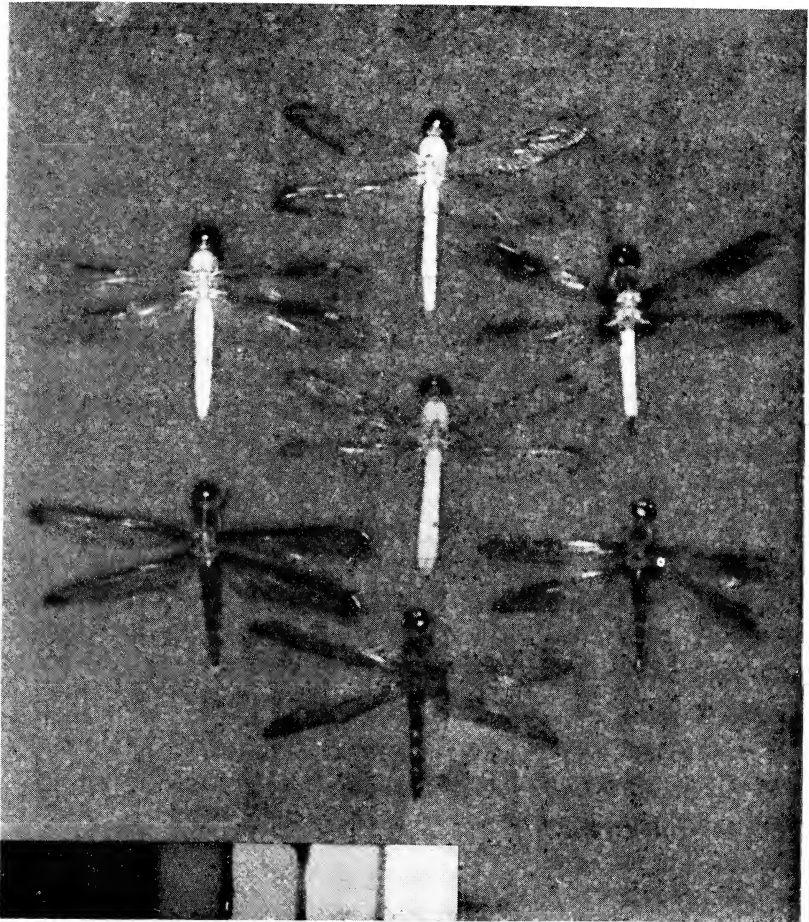


Figure 2. Three species of libellulids illuminated under 300-400 nm U.V. light. Percent reflection indicated in lower left corner: from left to right, 1%, 2.5%, 5.0%, 16.0%, > 25.0%.

INTERSPECIFIC BEHAVIOR

Pachydiplax longipennis males are unusually aggressive dragonflies when compared with other Libellulids. They react with particular ferocity to three larger sympatric species whose pruinosity color is similar to the grey-blue color of *Pachydiplax longipennis*. The first, *Libellula cyanae* Fabricius, most common at Pickman and the Five Fields ponds has a slightly darker pruinescence, covering the entire adult male body. *Libellula incesta*, common only at the Shade Street pond, has a much darker, almost black, pruinescence. The third, *Erythemis simplicicollis* Say, has the same color as *Pachydiplax longipennis*, covering a teneral green on the dorsal surface of the abdomen and synthorax. It occurred at all three of these ponds. *Libellula incesta* and *L. cyanae* sometimes occupy perches and enter the territory of *Pachydiplax longipennis*. *Erythemis simplicicollis* usually preferred to perch on an exposed log or rock, situations rarely used by *P. longipennis*. Despite its smaller size, *P. longipennis* would display and chase all three of these species that entered its territory.

Other dragonflies commonly present at these ponds included: *Plathemis lydia*, *Sympetrum rubicundulum*, *Leucorrhina intacta*, *Gomphus furcifer*, *Perithemis tenera*, *Libellula pulchella*, *L. luctosa* and *Ladonia julia*. *P. longipennis* males generally ignore them, presumably because of their different appearance.

COLORATION

Coloration patterns of recently dead males (killed by chilling) were compared in visible and ultraviolet light. It was found that the blue pruinose areas on the abdomen though dull under visible light have marked reflectivity in the ultraviolet. Highly reflective pruinescent areas were also found in males of *Libellula cyanae*, *L. incesta* and *Erythemis simplicicollis* (see Fig. 2), but were absent in females of these species.

Some odonates, including a libellulid, have been shown by physiological methods to be UV-sensitive (Goldsmith and Bernard, 1974: Table 5). Why is it that these, more stationary, libellulids have pruinescence in similar areas while in others it is a different color, located in different areas or absent all together? Species such as *Libellula pulchella* have only white pruinescent spots on their wings and are much more mobile than *P. longipennis*. In light of these preliminary findings, the possible role of ultraviolet patterns in odonate behavior deserves careful attention.

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BIOLOGY OF *POLISTES ANNULARIS*
(HYMENOPTERA: VESPIDAE)
I. SPRING BEHAVIOR

BY HENRY R. HERMANN¹ AND TOBIAS F. DIRKS²

Although the social biology of several polistine wasps has been discussed in considerable detail by Bequaert (1923), Eberhard (1969), Evans and Eberhard (1970), Isely (1922), Pardi (1948), Rabb (1960), Rau (1931, 1933, 1939) and Spieth (1947), relatively little has been reported on *Polistes annularis* L. (Rau, 1940). *P. annularis* is the most common paper wasp around the Athens area. It is pleometrotic (=polygynic=cooperative cofounding) (Bequaert, 1923; Rau, 1940; Reuter, 1913; Wasmann, 1910) in its behavior and in being such is an excellent subject for the study of dominance reactions in social insects.

We began our studies on this species in the spring of 1970, and we collected detailed information on all of the life stages and seasonal activity through June of 1971. Additional data was collected on occasion through the active season of 1974. Our findings differ in some respects from those of Rau (1940), who studied *P. annularis* in the midwest, and Rabb (1970), who investigated polistine species in the Raleigh, N. C., area. The predominant polistine species in Rabb's area were *P. exclamans* and *P. fuscatus*.

Because we have collected a considerable amount of information, we have decided to consider each phase of the seasonal history of *P. annularis* separately and publish this information in series form. The serial reports will be three in number, dealing with behavioral periods of the 1) Spring, 2) Summer and 3) Fall-Winter-Spring. The present report, the first of the series, deals with Spring behavior. We previously reported on the anatomy and function of the venom apparatus and sternal glands in this and other vespid species (Hermann and Dirks, 1974; Hermann and Krispyn, 1975; Hunt and Hermann, 1970) and on the cohibernation of five polistine species (Hermann, Gerling and Dirks, 1974).

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MATERIALS AND METHODS

A large barn on the edge of Athens, Ga., was selected as the main site for investigation because it harbored one of the best populations of *P. annularis* in the area (Fig. 1). Although several polistine species nested there, *P. annularis* was the predominant species with *P. hunteri* and *P. exclamans* next in abundance. Abandoned houses and other barns also were investigated, as well as nests in shrubs and bushes.

Cofounding females were marked on the thoracic dorsum with rapid drying model paints of various colors and combinations of colors. Marking was most often done at night with no aggressive occurrences. Similar marking of workers was more difficult.

Cofounding females were watched daily, their presence and absence from the nest being recorded. Any new arrivals from one nest to another could be spotted immediately due to the different colors used in marking. All of the behavioral characteristics were observed repeatedly on numerous nests to assure that they were routine in the life of *P. annularis*.

Dominance reactions were carefully investigated on separate nests where each cofoundress could be marked differently. Upon behaviorally determining the dominant cofoundress (queen) the wasps of a number of nests were taken and dissected for an investigation of their reproductive systems (Dirks and Hermann, 1975a).

Observations on nest size increase and immature stages were made at night since the nest could be approached with ease during early colony development, prior to the emergence of workers. Also, much of the information on the number of adults on a nest and the identity of females on a nest was obtained at night.

RESULTS AND DISCUSSION

P. annularis clearly demonstrates seasonal colonial changes while its relative, *P. canadensis*, apparently shows no seasonal synchrony in the foundation and termination of colonies in tropical areas where no temporal changes occur (Eberhard, 1969).

PRE-NESTING AGGREGATIONS

In the beginnings of nest establishment by *P. annularis*, certain behavioral characteristics are carried over from a pre-nesting or post-hibernation period (Hermann and Dirks, 1975). The fertilized females from the previous year show strong tendencies to aggregate into groups of individuals having similar origins (sibling relationship).

Although they form aggregations, each adult wasp is an individual which functions almost independently from other wasps in the aggregation (i.e., no individual forms a "nucleus" as with the queen honey bee). This independence remains to some extent throughout colony life, although each wasp on a nest influences and is influenced by the other co-foundresses of the colony.

In addition, the establishment of dominance hierarchies begins during the pre-hibernation period in late fall (at the end of the nesting period) and continues through the post-hibernation period of early spring (Hermann and Dirks, 1975). These hierarchies later are instrumental in determining nest duties (division of labor among colony cofoundresses). Dominant females remain at the "parent site" and because of this struggle for dominance some of the cofoundresses are forced to disseminate. Each dominance hierarchy has, within its own structure, characteristic behavioral patterns that are present regardless of colony size.

DOMINANCE HIERARCHIES

Each colony of these pleometrotic females commences under the pressure of dominance establishment. Such establishment often involves up to eight or ten females (cofoundresses) which are all making an attempt to become the dominant queen of the colony (alpha individual of Pardi, 1948). Although single *Polistes canadensis* females have been reported by Eberhard (1969) to most often initiate a nest alone, similar to the fashion demonstrated by *P. fuscatus*, Rau (1933) has described colony founding by several *P. canadensis* nestmates (siblings) that were chased from their original nest. The females of *P. annularis*, a close relative of *P. canadensis*, readily initiate their nests with a number of females. However, like with *P. canadensis*, additional females often join the *P. annularis* nest after initiation (Rau, 1940).

A colony usually benefits by having a number of cofoundresses rather than a single queen, but maximum efficiency is not achieved because of dominance struggles. As an example, by April 15, 1971, nest #18 occupied by a single queen had 6 cells. On the same date nests #16 and #17 with multiple queens (2 and 5 respectively) had 11 and 13 cells respectively; the number of cells, however, is not in proportion to the number of cofoundresses present. If the number of cofoundresses could be directly correlated with the cells present in a nest, we would expect nest #16 to have 12 cells on April 15 and nest #17 should have 18 on the same date. In addition,

with proper division of labor among cofoundresses we would expect an even higher number of cells. This is not the case; there is a loss in efficiency due directly to dominance reactions on the nest, which we will discuss later. Larger nests also are produced in colonies by both *P. fuscatus* and *P. canadensis* when foundress associations are large.

Bequaert (1923) and Isely (1922) reported similar findings in their investigations of *P. pallipes* and *P. metricus* respectively, although an efficiency loss was not as apparent in colony founding by either of these species. Rau (1940) found highly significant differences in cell numbers of single versus multiple cofoundresses in his studies of *P. annularis*.

COFOUNDRRESS CHARACTERISTICS

Several anatomical and behavioral characteristics are demonstrated by each cofoundress. Each such female 1) is a fertile producer of diploid eggs (Dirks and Hermann, 1975a); she attempts to establish her dominance by 2) demonstrating unilateral aggressiveness toward other cofoundresses (i.e., biting, over-under posture, stinging); and 3) she is capable of rigid gastral movements, known as abdomen (tail) wagging (Eberhard, 1969).

Insemination the previous fall or in the following spring (Hermann, Gerling and Dirks, 1974) appears to be quite successful in this species. All of the females examined on nests in the early days of colony establishment were found to be fertile and all were found to be depositing eggs (Dirks and Hermann, 1975a). However, in the struggle for dominance, a significant amount of oophagy persists until a more stable nest is established.

OOPHAGY AND COOPERATIVE EGG DEPOSITION

Recognition of oophagy is facilitated by the deposition of eggs near the cell surface after the wasp has ingested an egg. As the cells of a nest are elongated the eggs are deposited further and further from the cell base. The finding of eggs deposited a considerable distance from the cell base during the period of early nest building is a definite sign of oophagy. Oophagy will continue in an early colony until about the time that larvae appear.

Each cofoundress seems to demonstrate oophagy. Likewise, in an early examination of reproductive systems, it was found that every female on a nest in the beginning stages of colony founding was depositing eggs (Dirks and Hermann, 1975). Hence, after oophagy

Table 1. Average data from *P. annularis* nests with multiple cofoundresses, 1970.*

Date	# of Cofoundresses	# of cells present	# of capped cells	# of workers
April 16	3	13.33	0	0
17	2.33	14	0	0
18	2.33	16	0	0
22	2.33	21	0	0
23	2.33	24	0	0
26	2.0	24	0	0
May 1	2.0	32.33	0	0
13	2.33	41.5	0.33	0
20	2.33	44.33	8	0
22	2.33	46	11.33	0
27	2	50.67	16	0
June 16	2	80	14	16***
17	1**	—	13.5	13.5

*Nests #17, 19 and 20.

**Initial loss of first cofoundresses and emergence of workers.

***First emergence of workers, leading to interactions between new workers and colony cofoundresses.

by a female she immediately deposits her own egg, thus resulting in a very inefficient waste of time and energy on the part of colony building. According to Eberhard (1969) only one egg-laying female of *P. canadensis* was ever present on a nest at any one time. Consequently, differential oophagy was not observed in this species.

Such an efficiency loss in the early colonies of *P. annularis* is recognized by the slow process of cell building in the early stages of nest construction in which several cofoundresses are involved. As dominance is established by the dominant queen, subordinate cofoundresses put more time into colony duties (become workers or beta individuals) and the building of cells increases.

Table 1 illustrates an average of 3 *P. annularis* nests in which there are only about 2 cofoundresses per nest. Whenever there are only 2 or 3 cofoundresses present dominance is established at an early stage of nest development and there is not as evident an efficiency loss as we find on larger nests.

A decrease in colony activity was reported for *P. canadensis* by Eberhard (1969) although it apparently did not represent a loss in efficiency. During a five-week period of early nest founding there were no new cell building and no observed oviposition. Eggs and larvae also developed at a reduced rate.

AGGRESSIVENESS TOWARD COFOUNDRASSES

Unilateral aggressiveness is evident even before colony initiation. Much like the behavior of *P. gallicus* (L.) (Pardi, 1948), there is a lack of equivalence between females, certain females apparently showing dominant characteristics from the start. Likewise, a female that appears dominant never loses her dominant position on the nest. Females attack each other in the pre-hibernation and early post-hibernation clusters (Hermann and Dirks, 1975). Such aggressiveness may involve a rapid darting of one female toward another. In many cases, aggressive attacks result in the entanglement of a wasp's legs with those of the other wasp and the subsequent falling to the ground by these individuals while attempting to bite and sting.

On occasion, we have found individuals that were stung, although most encounters merely result in some establishment of dominance by one of the fighting pair without bodily harm. Both wasps most often take flight after such an encounter and either return to the cluster (in the case with the dominant wasp and often the subordinate one also), or retreat to a new location. As with *P. canadensis* (Eberhard, 1969), subordinate cofoundresses that actually were attacked by the dominant female often left the colony. Subordinate *P. canadensis* females that remained on the nest became idle residents; however, subordinate *P. annularis* females became workers (beta individuals of Pardi, 1948).

We believe that the females remaining in these clusters are the ones that commence a pleometrotic colony while the most subordinate females (the ones that fly away from the clusters) often establish small colonies as single queens, sometimes later to be joined by other cofoundresses. In most cases, females that initiated their nest building alone never completed their nest; the nests never got to be larger than a few cells and the nests eventually were abandoned.

During colony initiation, subordinate females that initiate their own colonies singly are occasionally replaced by new dominant females that arrive after a small nest with several cells has been constructed. On occasion, we have even seen *P. annularis* queens replaced by a *P. exclamans* queen (possible beginning of an allometrotic association), although colony life ceases to function when there is such an aggregation of two species.

In other cases, nests with single or multiple foundresses may pick up additional females that come from other nests. In the latter case, these females either come from nests that they were chased from or from a nest of sibling females (females that originated from the same

nest the year before). Several nests in our study area had sibling wasps that originated from the same nest the year before.

There was an extensive exchange of wasps between some of the nests that were established by sibling females. Wasps occasionally were also found to join females on unrelated nests. During the exchange of wasps on nests, acceptance of these females by the original females usually was the case, although there is more exchange among sibling than unrelated wasps. Apparently, there is not much exchange of wasps between the nests of *P. canadensis* (Eberhard, 1969).

Unilateral aggressiveness continues to a lesser degree in later stages of colony building. Usually, the dominant queen demonstrates a dominant posture over her peers and upon approaching these peers she often moves rapidly toward them in a jerky aggressive manner.

CHARACTERISTICS OF A DOMINANT FEMALE

Once dominance is established by a single female, certain behavioral and anatomical changes occur in her and in the subordinate females. Anatomically, the reproductive system of the dominant female increases in size and she is able to increase her egg production. Simultaneously, the reproductive system of the subordinate females atrophies and they commence functioning as workers (Dirks and Hermann, 1975a; Pardi, 1948).

Behaviorally, the dominant female begins to "tail wag," a phenomenon not well understood at this time. Tail wagging may be demonstrated by a number of individuals on a nest or just by the dominant female. Workers also have been seen tail wagging on numerous occasions. When several cofoundresses all tail wag it always is the dominant female that is outstanding in her demonstration of it.

Tail wagging produces several results: 1) it points out the dominant female and the subsequent subordinates; 2) it helps maintain a position for the tail wagging female in the dominance hierarchy; 3) it appears to increase nest activity either audibly or visually; 4) it indicates that workers really do enter into dominance reactions with fertile cofoundresses and other workers.

The dominant female checks the cells periodically, and thus she investigates the larvae and deposits eggs in the new cells. This female also is responsible for most of the "smearing" (Hermann and Dirks, 1974). She spends much of her time on the face of the nest during the day but at night she may either be on the face or on the nest pedicel.

Subordinate females check the cells periodically but do not deposit eggs in them. They feed the larvae material brought in by them or by other cofoundresses. They also "smear" to some degree, although most of this is done by the queen (Hermann and Dirks, 1974).

It is obvious at this stage that the subordinate cofoundresses become workers (beta individuals, Pardi, 1948), in spite of the fertile condition of their spermatheca. They are subordinate to a single dominant queen (alpha individual). The establishment and maintenance of a well defined dominance hierarchy takes as long as two and a half months, until the first emerging workers arrive.

The emergence of workers further complicates the dominance hierarchy since workers begin competing with the subordinate cofoundresses for dominance and the workers evidently put the cofoundresses under extensive pressure at this time (about June 16, Table 1); with the appearance of the first workers, the subordinate cofoundresses leave the nest, never to return, leaving only the dominant queen and workers (new beta individuals) on the nest. Workers begin to "tail wag" to some degree and "smear," behavior normally demonstrated by the queen or cofoundresses. The leaving of the subordinate cofoundresses is a strong indication of their extremely subordinate position in the colony. It appears that once a cofoundress becomes subordinate it will be dominant to no wasp, except those already subordinate to her, including a worker. The queen (dominant cofoundress) usually remains on the nest through August but leaves the nest permanently long before cold weather. According to Pardi (1948), the queen (representing the alpha individual on the nest during most of the nest life) shows a lower dominance frequency upon growing old but maintains supremacy on the nest until later in the season. Rau (1939) indicated that his observations of *P. annularis* colonies likewise revealed first the arrival of workers and a subsequent departure of subordinate cofoundresses.

Pardi (1948) reported that after the eclosion of *P. gallicus* workers and the elimination of auxiliary females (if the queen dies), a worker that is in the beta position on the nest begins to dominate its siblings and soon begins to deposit eggs. Rau (1931) also mentions egg deposition by workers when the queen is lost. Pardi does not mention the pressures of the dominance hierarchy as being put on colony cofoundresses, thus resulting in their permanent departure from the nest.

The build up and atrophy of colony life encompasses approximately five months. This is much the same as the cycle found in colonies of *P. canadensis* (Eberhard, 1969). Colony enlargement ceases when

the queen leaves the nest. Loss of the queen occurs in April for *P. canadensis* and in late August for *P. annularis*.

SELECTION OF A NEST SITE

P. annularis females most often select a nest site near or on the nest site from the previous year. In the Athens area this is on and in buildings. Very little nesting occurs in trees, shrubs or bushes. Of the nests found in shrubs and bushes, none appeared to last through a complete season. After their posthibernation aggregating and mating they go to or near the nest site occupied by the nest from which they emerged. If the old nest still remains, they may begin construction of a new nest near the old nest or on rare occasions even on the face of the old nest. If the old nest has been removed, the new nest most often is started directly on the old pedicel or on the exact spot that the old nest occupied. Never is the old nest used again.

The reasons for not using the old nest are several. The old nest is often torn and dirty. These problems, however, could be handled by repair and cleaning. Probably the most important consideration is that many of the nests are parasitized by late summer and the parasites sometimes overwinter in the nest. The old nests, thus, would have built-in parasites which would be highly detrimental to a colony. Also many nests have overwintering moths that prey on the immature stages of polistine wasps.

COLLECTION OF WOOD FIBER

From the beginning of nest establishment, the dominant queen remains on the nest most of the time while her cofoundresses collect wood and build the nest. Wood is collected most often from old buildings by scraping surface wood off with the mandibles. This wood pulp is mixed with saliva and added to the nest in a characteristic way (Eberhard, 1969). As dominance is established and workers emerge, the functions of wood gathering and nest building are assumed by them.

COLLECTION OF FOOD

As in wood gathering and nest building, the dominant queen devotes very little time to the collection of food. On nests with only 2 or 3 cofoundresses, the dominant female may leave on occasion but as dominance is better established she ceases functioning away from

the nest. Food supplied to an early nest usually is the function of the subordinate cofoundresses. When workers emerge they assume this duty.

Rabb (1960) put together an extensive list of prey collected by workers of *P. annularis*. It included 16 families of Lepidoptera and a few records of prey from the orders Diptera, Hemiptera, Homoptera, Hymenoptera and Orthoptera, as well as a few spiders. About 20% of the wasps returning to the nest had some type of prey while most returned with liquid.

Rabb also reported that 85% of the prey collected was gotten from wooded areas while the remaining prey was taken in fields. This is in contrast to the collecting of some other polistine species (e.g., *P. fuscatus* and *P. exclamans*) that collect most of their prey in fields.

COLONY PROTECTION

Nests and the inclusive immature stages are protected in a number of ways: 1) repellent compounds are routinely smeared on the nest pedicel (Hermann and Dirks, 1974); 2) adult wasps rest in a characteristic defensive fashion at night; 3) a defensive posture is readily assumed by females when a nest is approached; 4) along with a defensive posture the prothoracic legs and possibly the antennae and wings are moved in such a way as to represent a warning mechanism; 5) darting at small intruders is occasionally seen; 6) adult wasps, especially workers, will aggressively attack an intruder.

Defensive Smearing — Hermann and Dirks (1974) have reported smearing by a number of polistine wasps and the possibility of smearing by all vespids. Smearing is accomplished by the rubbing of the gastral sternites on the structure to be smeared (usually the nest pedicel). The glands that produce the repellent compounds are found inside the hemocoel immediately above gastral sternites 6 and 7. The glands consist of numerous unicellular structures, each joined to the sternite base by a single filamentous duct. The sternite has a dispenser brush to facilitate the smearing process.

The smearing compounds evidently are volatile since smearing takes place periodically throughout the day. Detection of the compounds or lack of them appears to be accomplished with the antennae. Double smearing appears to occur often and may be the result of detecting more of the smearing compound on one side of the pedicel than the other. Occasionally, the pedicel is worked with new wood fiber. The mandibular gland may play a role here in adding a different and possibly a synergistic repellent compound to the nest base.

Although smearing has been seen in only a few species of the Polistinae, sternal glands and sternal brushes have been found in many vespids. It is possible that *Vespula* species smear on the structures to which their nest adheres.

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THE COMPARATIVE UTILIZATION OF
CULTIVATED AND WEEDY UMBELLIFER SPECIES
BY LARVAE OF THE BLACK
SWALLOWTAIL BUTTERFLY, *PAPILIO POLYXENES*

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INTRODUCTION

For many years, much of the emphasis in agriculture and plant breeding has been placed on increasing overall production (Allard 1960). This is because man is almost totally dependent on plants for his food. The things he eats come directly from plants or indirectly from herbivorous animals. Plants are also the major source, directly or indirectly, of most clothing, fuel, drugs, and construction materials.

The impact of insects on plants cannot be overemphasized. For example, some insects can be very successful in the biological control of weeds (Holloway 1964). Insects also have a great impact on the evolution and ecology of plants through their destruction of seeds, young seedlings, or the plants themselves (Breedlove and Ehrlich 1968, Janzen 1969, 1971). The relationships between the insect and the plants that we observe today are based upon millions of years of co-evolution. During the course of this evolution, plants have developed various mechanisms to resist insect attack. The majority of plant defenses can be classified as physical or chemical defenses (Stahl 1888). Plant physical defenses may include thickened cuticle (Tanton 1962, Feeny 1970) or hairs, spines, and thorns on the epidermis (Johnson 1953, Pearson 1958, Bernays and Chapman 1970), which interfere with the insects feeding. The high silica content of some plants or the crystalline materials in the leaves of many conifer species add a further physical barrier to insect attack (Merz 1959, Pathak 1969).

Plants have also evolved a great array of chemical defenses, the so-called secondary substances. These include the alkaloids, glycosides, tannins, flavenoids, terpenoids, essential oils, and saponins, to name a few (Fraenkel 1969, Whittaker and Feeny 1971). Stahl (1888) advanced the idea that these compounds evolved in plants as

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a defensive mechanism against insect and vertebrate herbivores, pathogens, and perhaps competitors. This view has been supported, as far as insects are concerned, by Dethier (1954, 1970), Thorsteinson (1960), Ehrlich and Raven (1965), Jermy (1966), Whittaker and Feeny (1971), and Erickson and Feeny (1973). Much of the interaction between insects and these secondary substances is sensory in nature, and such substances may inhibit or deter feeding (Thorsteinson 1960, Gill and Lewis 1971), or may prove toxic to non-adapted larvae (Taylor 1959). Some plant species even synthesize and accumulate sterols which mimic insect molting secretions (Williams 1970). These phyto-ecdysones have been found in numerous fern species and prevent molting in insects feeding on such species (Whittaker and Feeny 1971).

These secondary chemicals are not the only chemical means that plants have evolved to protect themselves from insect attack. Plant proteins are often deficient in some individual amino acids necessary for insect growth and development (Lord 1968, Boyd 1970). The nutritional quality or adequacy of the food plant is of utmost importance to a phytophagous insect (Friend 1958, Legay 1958). Aphids (Auclair et al. 1957), beetles (Allen and Selman 1955, 1957), butterflies and moths (Hovanitz and Chang 1962, Feeny 1970), grasshoppers (House 1959, Dadd 1961), flies (Chapman 1969), and other insects (Gilmour 1961, Levinson 1962), have all been shown to exhibit quite variable feeding responses which in turn influence larval development, mortality, fecundity and fertility, when reared on different host plant species or on the same host plants grown under differing conditions or ages. Gordon (1959) has suggested that nutrient deficiencies in plants ". . . may be a result of natural selection of inedibility." The interaction between the nutritive adequacy of leaves and secondary chemistry has been demonstrated for oak trees and oak leaf tannins (Feeny 1968, 1969, 1970).

Agriculturists and plant breeders have become aware of the problems that increased yield and palatability of crop species present in terms of the plant's inherent defensive mechanisms (Snelling 1941, Painter 1951, Allard 1960, Briggs and Knowles 1967). The oldest record of inherent plant resistance to insect herbivores was by Havens (1792) in which he recognized the Hessian fly resistance of the Underhill variety of wheat. However, scarcely 200 papers have dealt with this subject in the 148 year period from 1792 to 1940 (Snelling 1941). Generally, as plants species were domesticated and cultivated, various morphological and physiological changes

occurred (Polunin 1960). Cultivated plant species are often larger in size, have larger seeds or seed sets, have more rapid and uniform seed germination, lose defensive structures such as hairs, thorns, or spines, and display improved palatability and nutritive content compared to their corresponding wild relatives.

The domestication of plants involves more than simply modifying the genetics of a species, because reciprocal adaptations between the domesticated (cultivated) species and the domesticator (man) are required. The domestication and cultivation of plants is in sorts a two way street; it may bring about ecological, social, and/or genetic changes in man as man has brought these changes to the plants. Selection for increased yield or increased productivity of the edible part of a crop species does not necessarily mean an increase in primary production. Above a certain point, increased yield must come at the sacrifice of some other adaptive use of energy (Cody 1966). As an example, generally increasing the yield of wheat decreases the amount of straw which is a fundamental part of the plant's self-productive maintenance equipment (Odum 1971). Is it then possible, when breeding for increased palatability, yield, or nutritive content in cultivated plant species, to alter or decrease the inherent defensive mechanisms of the plants involved, be they physical, chemical, or both?

The purpose of this study is to examine this question in detail, utilizing the oligophagous butterfly, *Papilio polyxenes*, whose larvae feed on a variety of cultivated and wild or weedy species of the carrot family, the Umbelliferae (Chittenden 1909, Forbes 1960, and others). Many umbellifer species upon which these larvae feed, have been cultivated for centuries, primarily for spices and condiments for prepared foods (Buttery et al. 1968, French 1971, Kasting et al. 1972), and for medicinal or toxic drugs (Muenscher 1951, Kingsbury 1964). Umbellifer plants are a major source of various vitamins (especially vitamin A) and minerals essential for proper growth in man (Lewis and Rubenstein 1971) as well as insects (Fraenkel 1953, Dadd 1957). Through studies of larval growth efficiency and food plant utilization, comparisons as to the relative adequacy of each host plant species, cultivated versus wild, can be determined.

METHODS AND MATERIALS

Eggs of *P. polyxenes* were taken from the second generation of a culture founded from wild insects taken near Ithaca, New York and reared in the laboratory on carrot (*Daucus carota*). A minimum of 15 and a maximum of 20 eggs were placed on each of 32 umbellifer

species: 10 species of cultivated umbellifer and 22 species of wild or weedy umbellifers found in the Central New York area. The larvae were maintained on these species throughout larval development. Mature and uninjured leaves of the wild species were gathered in the field each day and the leaves of the cultivated umbellifers were collected from greenhouse reared plants. All leaves were sealed in plastic bags and offered to the larvae within 2 hours. Leaves were replaced and feces collected every 24 hours to prevent bacterial or fungal development. The larvae were reared in clear plastic boxes (9 × 12 × 4 inches) (Tri-State Plastic Molding Co., Henderson, Ky.), in a climatically controlled chamber with the following parameters: temperature 22° day, 18° night, approximately 55% humidity, and a 16-8 LD photoperiod.

For the purposes of examining larval energy and nutrient utilization, a minimum of 8 and a maximum of 10 newly molted 4th instar larvae were placed individually in glass petri dishes (Pyrex, 100mm × 15mm) lined on the bottom with a piece of Whatman No. 1 filter paper. The ideal utilization study would, of course, encompass the entire life cycle as the efficiency of food utilization by the early instars is certainly of interest. The nutritional adequacy of the food plant material can be judged only by its ability to support growth in successive instars. There were, however, 2 reasons for utilizing only 4th instar larvae in this experiment. Since larvae of *P. polyxenes* consume approximately 0.1% of the total food ingested during larval development during the 1st instar, these minute quantities of food ingested and digested lead to exceptionally high error values and are therefore inaccurate. Similar results were obtained for the 2nd and 3rd instars where the percentage of the total food consumed during larval development was 0.6% (L2) and 2.8% (L3). The ultimate instar was not included for the purposes of the energy utilization experiments due to a pre-pupal clearing of the gut in which a larva may lose up to 40% of his maximum wet weight within a 5 minute period. Once this occurs, there is no way to estimate the maximum larval weight which is necessary for various calculations to determine larval food utilization efficiencies. During the 4th instar, approximately 10 to 15% of the total food ingested during larval development is consumed. These larger amounts lead to more accurate weights which significantly reduce the statistical error.

All the individual larvae were placed in the same controlled temperature room, except for the period of time each day during which new food was offered to the larvae and the feces collected. The

experimental larvae were fed the same leaves as the maintained cultures. These randomly collected leaves were split along the midrib, one half weighed and offered to the larvae and the other half weighed and used to determine the percent dry matter in the leaf material (Waldbauer 1960, 1964).

Besides the percent dry matter in the leaf material, the calorific and nitrogen content of the leaf material, the larvae, and the feces were determined. Calorific values of the larval food plants, feces, and larvae were determined by means of a Phillipson non-adiabatic microbomb calorimeter (Gentry and Wiegert Inst. Inc., Aiken, S.C.) (Phillipson 1964). The lyophilized leaf material, feces, and larvae were subjected to 3 replications for the determination of calorific values. The organic nitrogen content of the leaf material, the feces and the larvae, were determined either by the Kjeldahl method for total nitrogen (Williams 1964) or the microKjeldahl method (McKenzie and Wallace 1954). A minimum of 3 replicate samples was obtained for the larvae and the feces, as well as each host plant species.

The dry weight of food ingested by the larvae was estimated following the techniques of Waldbauer (1960, 1964), and Waldbauer and Fraenkel (1961) except that plant material was lyophilized instead of oven-dried. The dry weight of the food utilized or assimilated was assumed to be the dry weight of the food ingested minus the dry weight of feces. An additional group of larvae were reared along with the experimental larvae, and these were sacrificed to determine the dry weights, and thus, the percentage of dry matter of the larvae. Indices of food utilization were determined following the methods of Waldbauer (1960, 1964, 1968). Many terms have been used both by ecologists and by physiologists to describe various measures and indices of food utilization and efficiency. Relationships between many of these terms are discussed by Kozlovsky (1968) and Waldbauer (1968).

As an index of digestibility, the ratio of the amount of food assimilated to the amount of food ingested, referred to as the 'Assimilation Efficiency' (Clark 1946, Odum 1957, Odum 1971), or the 'Coefficient of Digestibility' (Waldbauer 1964, 1968, House 1965), was used. In practice, this measure is only an approximation since the numerator (as determined by the usual gravimetric procedure) does not quite represent the amount of food actually assimilated (Waldbauer 1968). This slight error is due to the presence of metabolic wastes in addition to the undigested food in the feces (Lafon 1951). For this reason Waldbauer (1968) has suggested

'Approximate Digestibility' as a less ambiguous term to describe this measure. However, Hiratsuka (1920) and Waldbauer (1964) point out that the uric acid content of the phytophagous insects is relatively low and that the difference between true and measured assimilation efficiencies is negligible.

The efficiency with which ingested food is converted to biomass is calculated by dividing the dry weight of food ingested into the dry weight gained by the larva during the instar. This index, referred to by the physiologists as the 'Efficiency of Conversion of Ingested Matter' (Waldbauer 1968) and by ecologists as the 'Ecological Growth Efficiency' (Gerking 1962, Odum 1971), is an overall measure of an animal's ability to utilize for growth the food ingested.

The efficiency with which digested food is converted to biomass is calculated by dividing the dry weight of food assimilated into the dry weight gained by the larva during the instar. This index, referred to by Waldbauer (1968) as the 'Efficiency of Conversion of Digested Matter' and by Gerking (1962) and Odum (1971) as the 'Tissue Growth Efficiency', decreases as the proportion of digested food metabolized for energy and maintenance of physiological functions increases (Waldbauer 1968).

In his classic work on accessory growth factors, Hopkins (1912) pointed out that absolute quantities cannot be used to compare the intake of food by animals growing at different rates. Valid comparisons could only be made on the basis of the rate of intake relative to the mean weight of the animal during the feeding period. Waldbauer (1964, 1968) working on this basis proposed the 'Consumption Index' calculated in this experiment as:

$$\frac{\text{dry weight of food ingested}}{\text{duration of feeding period}} \times \text{mean dry weight of the animal during feeding period}$$

The mean weight of the animal is most accurately calculated from the area under its growth curve as determined by integration. A weighted average of daily weights will give an almost identical value if the growth curve is smooth (Waldbauer 1964). Such three variable equations are at times difficult to discuss, being included in the present work only for later comparison with other insect species (see Waldbauer 1968). From the equation, if 2 individual larvae ingest the same total amount of food, with the larva on the less nutritiously adequate food plant taking a great deal of time and gaining little biomass and the other larva on a more acceptable food plant gaining

a great deal of biomass in a short time, the respective consumption indices may in fact be identical.

A more useful index for the growth rates of an individual larva is the mean dry weight added to larval biomass per day. This measure gives the investigator a much more accurate estimation as to the growth potential of the various umbellifer food plants.

For the purposes of food utilization and efficiency determinations, the experiment was concluded when the larvae molted into the ultimate instar. The larvae were then reared through to the adult stage on the same experimental plants that they fed upon before and during the utilization experiments. All resulting adult females were then utilized in various host plant selection experiments.

The data are generally presented as a mean and standard error for the larvae in any particular host plant treatment group. The various experimental parameters were subjected to one way analysis of variance (Guenther 1965, Snedecor and Cochran 1967) to determine differences among the various treatment groups. A typical T-test for 2 independent samples of unequal sizes utilizing a pooled variance (Guenther 1965) was used for analysis of the differences between cultivated and wild umbellifer species. Linear regression analyses were performed and the significance of the correlation coefficients was tested using a table of critical 'r' values (Snedecor and Cochran 1967). All statistical procedures were completed with the aid of a programmable calculator (Olivetti programa 101 or microcomputer P602).

RESULTS

Various plant parameters differed greatly between cultivated (domesticated) and wild (weedy) species of Umbelliferae offered to the swallowtail larvae (Table 1). The dry matter content of the leaf material was significantly lower ($P < 0.01$) at a mean of approximately 12.25% for the cultivated umbellifers than the wild umbellifer species which had a mean of about 21% dry matter. In terms of caloric content, no significant difference ($P < .3$) was found between the cultivated species, at a mean of about 4.11 cal/mg dry weight, and the wild occurring species, at a mean of about 4.13 cal/mg dry weight. The nitrogen content of the leaf material was significantly higher ($P < 0.05$) in the cultivated species, averaging approximately 1% higher than the wild species in terms of total nitrogen. This value becomes significant when converted to protein content, as 1% nitrogen equals approximately 6.25% protein (Lord 1968).

Table 1. Dry weight, calorific values and nitrogen content of various species of Umbelliferae offered to the larvae of the eastern black swallowtail, *Papilio polyxenes*, during the 4th instar.

Plant species	Mean percent dry material in leaves \pm SE ^{1,2}	Mean calories per milligram dry weight of leaf material \pm SE ^{1,3}	Mean percent of nitrogen in leaf material \pm SE ^{1,4}
Cultivated species			
<u>Anethum graveolens</u> Dill	8.58 \pm 0.15 N = 20	4.00 \pm 0.11	5.48 \pm 0.27
<u>Apium graveolens</u> Celery	15.90 \pm 0.48 N = 28	3.94 \pm 0.21	3.57 \pm 0.10
<u>Carum carvi</u> Caraway	15.10 \pm 0.37 N = 34	4.31 \pm 0.10	4.81 \pm 0.16
<u>Coriandrum sativum</u> Coriander	11.63 \pm 0.36 N = 36	4.36 \pm 0.07	4.93 \pm 0.31
<u>Daucus carota</u> Carrot	8.96 \pm 0.29 N = 42	4.05 \pm 0.22	5.31 \pm 0.09
<u>Foeniculum vulgare</u> Fennel	7.64 \pm 0.16 N = 16	4.01 \pm 0.09	5.45 \pm 0.31
<u>Ligusticum scoticum</u> Scotch lovage	15.27 \pm 0.68 N = 29	4.11 \pm 0.26	2.80 \pm 0.17
<u>Pastinaca sativa</u> Parsnip	16.00 \pm 0.27 N = 33	4.44 \pm 0.37	5.12 \pm 0.40
<u>Petroselinum crispum</u> Parsley	8.83 \pm 0.21 N = 24	4.03 \pm 0.17	5.52 \pm 0.19
<u>Pimpinella anisum</u> Anise	14.65 \pm 0.37 N = 37	3.83 \pm 0.09	2.83 \pm 0.07
Wild species			
<u>Aegopodium podagraria</u> Goutweed	21.87 \pm 0.22 N = 22	4.42 \pm 0.13	4.60 \pm 0.31
<u>Aegopodium varigatum</u> Goutweed	20.73 \pm 0.31 N = 39	4.30 \pm 0.22	3.03 \pm 0.11
<u>Aethusa cynapium</u> Fools parsley	11.56 \pm 0.23 N = 39	4.06 \pm 0.17	3.68 \pm 0.23

Table 1. Continued.

Plant species	Mean percent dry material in leaves ± SE ^{1,2}	Mean calories per milligram dry weight of leaf material ± SE ^{1,3}	Mean percent of nitrogen in leaf material ± SE ^{1,4}
<u>Angelica atropurpurea</u> Angelica	25.22 ± 0.41 N = 25	4.25 ± 0.06	5.12 ± 0.09
<u>Angelica triquinata</u> Angelica	18.49 ± 0.65 N = 36	4.27 ± 0.19	4.56 ± 0.33
<u>Cicuta bulbifera</u> Bulb bearing water hemlock	18.17 ± 0.42 N = 17	4.15 ± 0.17	3.64 ± 0.08
<u>Cicuta maculata</u> Water hemlock	19.20 ± 0.62 N = 27	4.19 ± 0.19	3.67 ± 0.25
<u>Coelopleurum lucidum</u>	18.23 ± 0.66 N = 42	4.13 ± 0.23	3.21 ± 0.07
<u>Conium maculatum</u> Poison hemlock	20.98 ± 0.55 N = 53	4.31 ± 0.21	3.44 ± 0.15
<u>Cryptotaenia canadensis</u> Honestwort	16.96 ± 0.50 N = 16	4.07 ± 0.11	4.25 ± 0.29
<u>Daucus carota</u> Carrot	19.73 ± 0.36 N = 24	3.95 ± 0.21	3.04 ± 0.06
<u>Heracleum maximum</u> Cow parsnip	24.66 ± 0.69 N = 24	3.97 ± 0.11	4.71 ± 0.10
<u>Heracleum sphondylium</u> Cow parsnip	23.67 ± 0.72 N = 34	4.10 ± 0.23	3.61 ± 0.27
<u>Imperatoria ostruthium</u> Masterwort	21.99 ± 0.96 N = 24	4.13 ± 0.17	4.26 ± 0.31
<u>Levisticum officinale</u> Lovage	20.48 ± 0.23 N = 26	3.98 ± 0.27	3.70 ± 0.16
<u>Pastinaca sativa</u> Parsnip	19.34 ± 0.36 N = 20	4.19 ± 0.23	5.12 ± 0.07
<u>Pseudotaenidia montana</u> Mountain pimpernel	31.41 ± 0.49 N = 23	4.01 ± 0.16	1.54 ± 0.07
<u>Sium suave</u> Water parsnip	7.38 ± 0.21 N = 27	4.06 ± 0.31	3.80 ± 0.13

Table 1. Continued.

Plant species	Mean percent dry material in leaves ± SE ^{1,2}	Mean calories per milligram dry weight of leaf material ± SE ^{1,3}	Mean percent of nitrogen in leaf material ± SE ^{1,4}
<u>Taenidia intergerrima</u> Yellow pimpernel	24.31 ± 0.64 N = 30	3.97 ± 0.13	2.81 ± 0.20
<u>Thaspium barbinode</u> Meadow parsnip	30.79 ± 0.58 N = 28	3.93 ± 0.23	2.22 ± 0.19
<u>Zizia aptera</u> Heart shaped alexanders	19.80 ± 0.73 N = 27	4.31 ± 0.17	3.21 ± 0.22
<u>Zizia aurea</u> Golden alexanders	23.53 ± 0.16 N = 18	4.25 ± 0.19	4.23 ± 0.11

¹The significance values of the 'T' statistic with 30 df are: 0.05 = 2.042, 0.01 = 2.750.

²T = 5.666

³T = 0.422

⁴T = 2.349

The larvae reared on the 32 umbellifer species all ingested approximately the same total amount of food, averaging about 144 dry weight mg, during the 4th instar ($P < .3$) (Table 2). Generally, all larvae completed the 4th instar in about 3 days ($P < .3$), thus the rate of food consumed also did not vary significantly ($T = 0.247$, $P < .4$). The proportion of ingested food which was digested and assimilated ('Approximate Digestibility') averaged approximately 53% for the larvae reared on the cultivated umbellifer species and about 47% for the larvae reared on the wild umbellifer species ($P < 0.05$). The efficiency with which ingested food was converted to larval biomass ranged from approximately 25% for the larvae reared on the cultivated umbellifer species to approximately 19% for the larvae reared on the wild umbellifer species ($P < 0.05$).

The efficiency of conversion of digested food into larval biomass did not vary significantly between the two groups of plants tested and averaged approximately 45% in all cases ($P < .2$) (Table 3). Individual larvae gained on the average approximately 10 dry wt. mg more on cultivated umbellifer species than the larvae reared on wild umbellifer species, during the 4th instar ($P < 0.05$). This

figure converts to approximately 80 wet wt. mg which for a normal 4th instar caterpillar comprises about 20% of its maximum net weight. In terms of the consumption index, or the rate, corrected for larval weight, at which food enters the gut, both groups of larvae were ingesting at approximately the same rate ($P < .1$), although larvae reared on wild umbellifer species did display a slightly higher consumption (Table 3). In terms of larval weight gained per day, the larvae reared on the cultivated umbellifer species gained about 11.6 dry wt. mgs per day whereas larvae reared on the wild species averaged on the whole about 8.7 dry wt. mgs per day ($P < 0.05$).

DISCUSSION

One of the major concerns of modern ecology is the description and explanation of the energetic relationships between and within various communities. A knowledge of the food and energy utilization of insects is thus of particular importance to ecology since insects exert a substantial influence and impact on almost all terrestrial communities. Energy utilization studies and their ecological significance have been extensively reviewed (Englemann 1966, Phillipson 1966, and others).

Adaptive nutritional differences in host plants must be sought on a quantitative level and meaningful comparisons of food utilization and nutrition will not emerge until quantitative studies are carried out (Erickson 1972). The determination of absolute requirements for dietary constituents depends upon the measurement of food or nutrient intake. Differences in food utilization efficiency can be demonstrated only by measuring intake and growth. Measurement of the food intake and the utilization of this food elucidates to a great degree the physiological processes occurring in an insect since patterns of utilization may be different although food sources are similar in their ability to support growth. For instance, low food intake may be offset by a high utilization of ingested or digested food and a very high food intake may well lead to a very low efficiency in the utilization of ingested or digested food.

In this experiment, the larvae of the black swallowtail, *P. polyxenes*, display a marked differential growth rate when reared on cultivated versus weedy umbellifer species. Larvae reared on cultivated umbellifer species gained approximately 25% more weight during the 4th instar than larvae reared on the wild or weedy umbellifer species (Table 3). Since the larvae were generally from the same genetic background and were reared under similar conditions,

Table 2. The utilization of food by 4th instar larvae of the black swallowtail *P. polyxenes*, when reared on various species of cultivated and wild umbellifer food plants (Mean \pm SE). Common names of plant species can be found in Table 1.

Plant species	Total food ingested (mg) ^{1,2}	Duration of 4th instar (Days) ^{1,3}	Approximate digestibility ^{1,4}	Efficiency of conversion of ingested matter ^{1,5}
Cultivated species				
<u>Anethum graveolens</u>	112.91 \pm 8.26	3.06 \pm 0.17	55.86 \pm 2.09	37.04 \pm 2.86
<u>Apium graveolens</u>	196.14 \pm 5.48	2.99 \pm 0.06	64.94 \pm 0.89	21.45 \pm 0.57
<u>Carum carvi</u>	147.74 \pm 3.86	2.90 \pm 0.03	54.74 \pm 0.77	27.88 \pm 0.36
<u>Coriandrum sativum</u>	191.09 \pm 4.70	2.97 \pm 0.02	46.33 \pm 0.98	22.88 \pm 0.66
<u>Daucus carota</u>	150.63 \pm 5.92	3.55 \pm 0.09	55.07 \pm 2.00	29.99 \pm 0.96
<u>Foeniculum vulgare</u>	117.90 \pm 12.15	3.07 \pm 0.19	56.49 \pm 2.02	31.97 \pm 1.70
<u>Ligusticum scoticum</u>	120.95 \pm 5.07	2.98 \pm 0.01	48.11 \pm 1.53	14.05 \pm 0.81
<u>Pastinaca sativa</u>	145.15 \pm 6.16	3.33 \pm 0.07	49.64 \pm 0.70	25.23 \pm 0.23
<u>Petroselinum crispum</u>	129.82 \pm 5.76	3.47 \pm 0.06	57.99 \pm 2.86	31.04 \pm 1.48
<u>Pimpinella anisum</u>	123.96 \pm 6.21	3.07 \pm 0.17	43.55 \pm 1.48	14.20 \pm 0.93
Wild species				
<u>Aegopodium podagraria</u>	154.21 \pm 5.43	2.82 \pm 0.05	48.02 \pm 2.58	21.14 \pm 1.23
<u>Aegopodium variegatum</u>	170.92 \pm 4.61	2.93 \pm 0.06	52.40 \pm 1.13	24.81 \pm 0.61
<u>Aethusa cynapium</u>	168.15 \pm 6.24	2.97 \pm 0.01	47.16 \pm 1.06	18.52 \pm 1.74
<u>Angelica atropurpurea</u>	186.69 \pm 13.14	2.86 \pm 0.06	60.15 \pm 3.57	18.65 \pm 1.41
<u>Angelica triquinata</u>	86.38 \pm 6.39	3.09 \pm 0.26	42.63 \pm 1.33	29.51 \pm 1.35
<u>Cicuta bulbifera</u>	122.37 \pm 9.82	2.86 \pm 0.23	47.68 \pm 3.87	14.80 \pm 0.72

Table 2. Continued.

Plant species	Total food ingested (mg) ^{1,2}	Duration of 4th instar (Days) ^{1,3}	Approximate digestibility ^{1,4}	Efficiency of conversion of ingested matter ^{1,5}
<u>Cicuta maculata</u>	157.38±14.29	2.69±0.09	46.27±2.56	20.32±1.60
<u>Coelopleurum lucidum</u>	118.70± 3.39	2.91±0.06	45.80±1.22	14.58±0.58
<u>Conium maculatum</u>	133.23±13.34	3.28±0.12	49.43±3.82	18.40±0.96
<u>Cryptotaenia canadensis</u>	100.58± 7.32	2.88±0.19	46.43±3.89	18.29±2.12
<u>Daucus carota</u>	136.33±13.99	3.20±0.09	51.48±3.02	13.99±0.65
<u>Heracleum maximum</u>	221.30±15.81	2.97±0.04	70.03±1.77	11.86±0.84
<u>Heracleum sphondylium</u>	217.62±14.37	2.97±0.04	67.64±1.37	13.91±0.49
<u>Imperatoria ostruthium</u>	142.90± 8.96	3.48±0.07	45.16±1.20	18.36±0.57
<u>Levisticum officinale</u>	120.57± 9.27	3.67±0.13	39.85±1.06	17.09±1.07
<u>Pastinaca sativa</u>	88.42± 9.19	3.02±0.01	52.40±2.68	18.51±1.31
<u>Pseudotaenidia montana</u>	152.55±14.63	4.62±0.26	22.41±2.65	14.05±1.34
<u>Sium suave</u>	118.37± 4.55	3.15±0.02	49.11±0.90	31.08±1.14
<u>Taenidia integerrima</u>	142.56±15.64	2.84±0.09	45.13±4.10	16.88±1.51
<u>Thaspium barbinode</u>	161.70± 6.03	4.41±0.26	28.10±2.12	14.42±1.88
<u>Zizia aptera</u>	138.73± 4.77	2.91±0.06	44.20±1.87	29.11±0.74
<u>Zizia aurea</u>	140.04± 9.55	2.69±0.07	34.50±1.33	19.29±0.80

¹The significance values of the 'T' statistic with 30 df are: 0.05 = ±2.042, 0.01 = ±2.750.

²T = 0.079

³T = 0.058

⁴T = 2.103

⁵T = 2.615

Table 3. The utilization of food by 4th instar larvae of the black swallowtail, *P. polyxenes*, when reared on various species of cultivated and wild umbellifer food plants (Mean \pm SE). Common names of plant species can be found in Table 1.

Plant species	Efficiency of conversion of digested matter ^{1,2}	Larval wt. gain (mg) ^{1,3}	Consumption index ^{1,4}	Larval wt. gain (mg dry wt./day) ^{1,5}
Cultivated species				
<u>Anethum graveolens</u>	69.03 \pm 4.93	40.64 \pm 2.47	1.53 \pm 0.10	13.66 \pm 1.26
<u>Apium graveolens</u>	33.27 \pm 0.98	41.97 \pm 1.12	2.65 \pm 0.08	14.11 \pm 0.56
<u>Carum carvi</u>	50.99 \pm 1.05	41.10 \pm 0.76	2.12 \pm 0.03	14.17 \pm 0.25
<u>Coriandrum sativum</u>	49.41 \pm 1.15	43.57 \pm 0.95	2.55 \pm 0.08	14.66 \pm 0.38
<u>Daucus carota</u>	54.04 \pm 2.76	45.03 \pm 1.78	1.62 \pm 0.06	12.66 \pm 0.30
<u>Foeniculum vulgare</u>	57.38 \pm 4.32	36.59 \pm 2.43	1.75 \pm 0.15	12.17 \pm 1.13
<u>Ligusticum scoticum</u>	29.36 \pm 1.97	17.15 \pm 1.22	3.39 \pm 0.13	5.77 \pm 0.41
<u>Pastinaca sativa</u>	50.91 \pm 0.80	36.61 \pm 1.54	2.00 \pm 0.05	11.04 \pm 0.53
<u>Petroselinum crispum</u>	54.40 \pm 4.12	40.64 \pm 3.19	1.54 \pm 0.09	11.66 \pm 0.82
<u>Pimpinella anisum</u>	32.52 \pm 1.63	17.84 \pm 1.86	3.36 \pm 0.23	5.92 \pm 0.76
Wild species				
<u>Aegopodium podagraria</u>	45.65 \pm 4.55	32.67 \pm 2.33	2.77 \pm 0.26	11.66 \pm 0.93
<u>Aegopodium variegatum</u>	47.44 \pm 1.15	42.30 \pm 0.90	2.38 \pm 0.09	14.45 \pm 0.38
<u>Aethusa cynapium</u>	39.29 \pm 1.43	31.17 \pm 1.83	2.99 \pm 0.11	10.49 \pm 0.59
<u>Angelica atropurpurea</u>	32.69 \pm 3.25	33.98 \pm 2.33	2.97 \pm 0.23	11.92 \pm 0.80
<u>Angelica triquinata</u>	69.23 \pm 2.29	25.59 \pm 2.32	1.74 \pm 0.20	8.28 \pm 0.12
<u>Cicuta bulbifera</u>	33.12 \pm 2.68	17.76 \pm 1.63	3.48 \pm 0.36	6.36 \pm 0.63

Table 3. Continued.

Plant species	Efficiency of conversion of digested matter ^{1,2}	Larval wt. gain (mg) ^{1,3}	Consumption index ^{1,4}	Larval wt. gain (mg dry wt./day) ^{1,5}
<u>Cicuta maculata</u>	45.29±4.67	31.04±2.48	2.92±0.19	11.46±0.66
<u>Coelopleurum lucidum</u>	31.76±1.52	17.32±0.87	3.37±0.10	5.78±0.45
<u>Conium maculatum</u>	39.53±3.58	23.79±1.65	2.41±0.12	7.33±0.60
<u>Cryptotaenia canadensis</u>	42.31±5.38	17.76±1.89	2.88±0.30	6.60±1.02
<u>Daucus carota</u>	28.00±2.30	19.05±2.15	3.23±0.20	5.98±0.68
<u>Heracleum maximum</u>	17.14±1.50	25.64±1.69	4.11±0.25	8.65±0.60
<u>Heracleum sphondylium</u>	20.67±0.99	29.84±1.34	3.99±0.19	10.05±0.46
<u>Imperatoria ostruthium</u>	40.82±1.50	26.22±1.76	2.40±0.06	7.53±0.50
<u>Levisticum officinale</u>	41.65±1.92	20.73±2.41	2.33±0.09	5.69±0.66
<u>Pastinaca sativa</u>	36.01±3.12	16.20±1.82	2.43±0.15	5.36±0.60
<u>Pseudotaenidia montana</u>	64.05±5.15	21.32±2.38	2.10±0.04	4.67±0.59
<u>Sium suave</u>	63.45±2.75	36.82±1.96	1.62±0.04	11.71±0.66
<u>Taenidia integerrima</u>	40.18±4.63	23.21±1.75	2.96±0.27	8.23±0.68
<u>Thaspium barbinode</u>	51.53±5.33	23.02±2.51	2.24±0.13	5.37±0.81
<u>Zizia aptera</u>	66.86±3.70	40.37±1.67	1.96±0.08	13.86±0.47
<u>Zizia aurea</u>	56.66±3.67	26.60±1.23	2.90±0.10	9.88±0.33

¹The significance values of the 'T' statistic with 30 df are: 0.05 = ±2.042, 0.01 = ±2.750.

²T = 1.019

³T = 2.814

⁴T = 1.937

⁵T = 2.510

these different growth rates could be due to a variety of factors within the various host plant species. A particular host plant species may be deficient in certain nutrients necessary for proper larval growth and development or may contain various secondary chemicals which deter or inhibit larval feeding or physiologically interfere with the digestion, the assimilation and/or the utilization of food by the larvae.

If the larvae reared on the wild umbellifer species gained less weight because of a behavioral deterrence or inhibition of feeding, a reduction in the total food consumed or in the consumption indices would be observed. However, all larvae on the 32 treatment groups ingested approximately the same total amount of food ($P < .3$), and consumed this food at approximately the same rate ($P < .1$) (Tables 2, 3). It thus appears that the observed reduction in growth rate was not due to a purely behavioral response to repellent substances in the leaf material.

Any physiological effect that would significantly reduce larval growth and development would become evident in either the reduced digestibility of the food or in a reduction of the efficiency of conversion of ingested food to larval biomass. In terms of the overall digestibility of the food, cultivated umbellifer species are significantly ($P < 0.05$) more digestible for the larvae than the weedy umbellifer species (Table 2). Along with this, the efficiency with which larvae utilize ingested matter for the production of biomass is significantly higher ($P < 0.05$) for larvae reared on cultivated umbellifer species (Table 2). It was also found that a strong correlation exists between the dry weight gained per day by the larvae and the digestibility of the food ($r = .586$, 30 df.) and the efficiency of conversion of ingested matter ($r = .711$, 30 df.). It thus appears that some interference to the digestive processes is occurring in larvae reared on the weedy umbellifer species. This could be due to the action of secondary chemicals, either qualitative, quantitative, or both on the gut lining. This interference with digestion in the gut by the action of plant secondary chemicals has been previously established (Erickson and Feeny 1973).

Once the food material has passed through the gut, all larvae, be they reared on cultivated or wild umbellifers, utilize it for biomass production to the same degree (Table 3). A non-significant correlation exists between the efficiency of conversion of digested matter and the amount of weight gained per day ($r = .248$, 30 df.) and the efficiency of conversion of digested matter and the approximate digestibility ($r = .258$, 30 df.). This suggests that once the food is

assimilated through the gut wall, there is no further effect on its utilization, which supports the supposition of interference with digestion occurring in the gut of the larvae reared on weedy umbellifer species.

Besides the apparent interference with digestion found in larvae reared on wild or weedy umbellifer species, are there any nutritional differences between the cultivated and wild plant species that may influence overall food utilization? Among the 32 umbellifer species tested, no significant difference was found in the caloric content of the leaf material offered to the larvae (Table 1). Thus, in terms of calories all leaves presented to the larvae were of equal value.

It has been suggested that the water content of the host plant would greatly affect the utilization efficiencies. A strong significant difference ($P < 0.01$) exists between cultivated and weedy umbellifer species, with the cultivated species being much higher in water content than the weedy species. A definite negative correlation exists between plant dry matter content and the amount of larval weight gained ($r = .466$, 30 df.) and plant dry matter content and the utilization of ingested matter ($r = .711$, 30 df.). It has been shown in this laboratory, that by varying the water content of leaf material, the utilization of food by the cecropia moth, *Hyalophora cecropia*, is greatly affected (J. M. Scriber, in preparation). This effect was shown in lengthened development times for larvae reared on plants with low water content in which the total food consumed increased but the consumption rate remained relatively constant. In our experiment however, larval developmental times as well as total food consumed did not vary significantly but larval food utilization was affected by the digestibility and the efficiency of conversion of ingested food into larval biomass. It appears from the correlations found that the dry matter content of the umbellifer leaves may have some influence on the larval utilization efficiencies to an unknown degree.

The importance of nitrogen for larval growth and development cannot be overemphasized. Friend (1958), House (1961, 1962), and Dadd (1973) have discussed the qualitative requirements of proteins and amino acids for larval development. There appears to be an optimal nitrogen level, which varies from species to species, that produces maximal larval growth (Dadd 1961, House 1959, Vanderzant 1958). If nitrogen is a limiting factor for larval growth in this species as has been shown for other lepidopterous larvae (Erickson 1972), larvae reared on plant species containing higher

nitrogen levels should develop at a faster rate and gain more larval biomass. A highly significant difference ($P < 0.05$) exists in the nitrogen content between cultivated and weedy umbellifer species (Table 1). In terms of larval growth rates, a significant correlation exists between the weight gained per day and the nitrogen content of the plant ($r = .701$, 30 df.). Cultivated umbellifer species contain approximately 1% more total nitrogen than weedy umbellifer species, which in terms of protein content means an increase of approximately 6.25% (Lord 1968). This increase in nitrogen protein content would allow larvae to gain more weight per unit of food, thus utilizing their ingested food more efficiently.

The differential growth rates displayed by larvae reared on cultivated and weedy umbellifer species is most likely due to a variety of factors. Cultivated umbellifer species generally appear to be more digestible and more nutritionally adequate for larvae of *P. polyxenes*. Is it possible that through the long history of the domestication and cultivation of plants that man has developed plants more digestible and nutritionally adequate for insects as well as for himself? Organisms have a limited amount of energy to spend and will be selected to partition this energy in different ways depending upon changing environments and physiological conditions (Cody 1966). Any activity of an organism, or more precisely, the energy expenditure for that activity, can be viewed only in relation to all other demands for energy. Wild or weedy umbellifer species are under a constant selection pressure, always adapting to new predators, be they arthropod, vertebrate, or pathogen. Domesticated and cultivated species have been carefully and artificially selected for increased palatability, yield, and nutritional quantities possibly at the expense of the plant's own defenses. Thus, in producing plants more edible and nutritionally adequate for man, agriculturists have unintentionally made these plants more edible and nutritionally adequate for the insect herbivore. Has man, in a sense, chained himself to the plant, having to provide for the plant's defense through the use of insecticides or through other biological control mechanisms?

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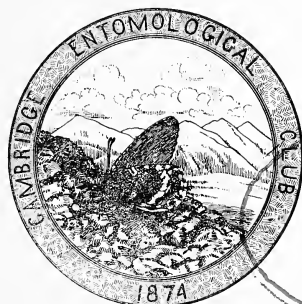
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THE NORTH AMERICAN CERYLONIDAE (COLEOPTERA: CLAVICORNIA)¹

BY JOHN F. LAWRENCE² AND KARL STEPHAN³

INTRODUCTION

The Cerylonidae are a family of small to minute beetles (usually 2 mm. or less) which occur most commonly in forest litter and under bark. At present, there are about 40 genera and over 300 described species known from all of the major zoogeographic regions. Crowson (1955) first recognized the Cerylonidae as an independent clavicorn family, including the cerylonines and murmidiines, as well as *Euxestus* and its allies; but these groups have been treated as tribes of the heteromerous family Colydiidae by both Hetschko (1930) and Arnett (1968). In their world generic revision of the family, Sen Gupta and Crowson (1973) added *Anommatus* Wesmael, *Abromus* Reitter, and *Ostomopsis* Scott, while transferring *Eidoreus* Sharp (= *Eupsilobius* Casey) to the Endomychidae. The present paper consists of a revision of the 10 genera and 18 species of Cerylonidae occurring in America north of Mexico. With respect to the composition of the family and that of its major subordinate groups, we have followed the classification presented by Sen Gupta and Crowson; the interrelationships among the subgroups, however, are still obscure, so we have treated the Euxestinae, Anommatinae, Metaceryloninae (not North American), Murmidiinae, Ostomopsinae, and Ceryloninae as independent subfamilies.

The following abbreviations have been used in keys and descriptions: PL — pronotal length, PW — pronotal width, EL — elytral length, EW — elytral width, and TL — sum of PL and EL. The word "length" refers to the total length, including the head, and is

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not equivalent to TL. The word "ventrite" has been used for each of the five visible abdominal sternites; thus the first and last ventrite refer to abdominal sternites three and seven, respectively. Descriptions of pronotal and elytral punctation should be used with caution, since the apparent diameters of punctures may vary considerably with the angle of light.

A complete family definition and comparisons with related or similar groups have been provided by Sen Gupta and Crowson (1973). A brief summary will be given here. Adult Cerylonidae may be characterized as follows: 1) antennal insertions exposed; 2) antennal club compact, rarely with more than 2 segments; 3) corporotentorium with median anterior process; 4) procoxae small and rounded, with concealed lateral extensions; 5) mesocoxal cavities broadly closed outwardly by the sterna and joined by a straight line; 6) trochanters not or only weakly heteromeroid (obliquely attached to femur); 7) tarsal formula 4-4-4 (or rarely 3-3-3), the segments simple (or rarely the first lobed), with simple claws; 8) hindwing without a closed radial cell and with one anal vein, or with the first anal running into the subcubital fleck; 9) abdominal ventrites free, the first distinctly longer than the second; 10) aedeagus of the clavicorn type, lying on its side when retracted, often with a reduced tegmen. In addition, the majority of cerylonids are glabrous, and many have reduced antennal segmentation, aciculate maxillary palps, femoral lines, and a crenulate hind margin on the last ventrite.

Several of the above characters are shared with other families of the cerylonid series (Crowson, 1955), namely, the Sphaerosomatidae, Endomychidae, Coccinellidae, Corylophidae, Discolomidae, Mero-physiidae, and Lathridiidae. The broadly closed middle coxal cavities, characteristic tentorium, more or less compact antennal club rarely more than 2-segmented, and simple tarsi will distinguish the cerylonids from most of the above groups. Corylophids have similarly closed mesocoxal cavities, but the tentorium is reduced, the antennal club is 3-segmented and relatively loose, and the second tarsal segment is often lobed. Although cerylonids were formerly included in the family Colydiidae, members of the latter group are easily distinguished by having the basal three or four ventrites connate, the aedeagus of the pseudotrilobe type, and the trochanters strongly heteromeroid or the antennal insertions concealed.

Cerylonid larvae are elongate or oval in shape, without or with weakly developed frontal sutures, and with 0, 2, or 3 ocelli on each side of head. The antennae are relatively short, with the sensory

appendix longer than the terminal segment, the tarsungulus bears a single seta, and the spiracles are annular. In the more generalized forms, such as *Anommatus*, *Murmidius*, and the Euxestinae, the head is prognathous or somewhat inclined, and the mouthparts are of the normal clavicorn type, with a chewing, mola-bearing mandible and a short, blunt mala. In the Ceryloninae, however, the head is strongly hypognathous or opisthognathous, and the mouthparts form a highly modified piercing apparatus, in which both mandible and the mala are elongate and blade-like.

The flat, onisciform larvae of *Murmidius ovalis* (see Böving and Craighead, 1931; Halstead, 1968; Sen Gupta and Crowson, 1973) resemble those of the Discolomidae and certain Corylophidae. Discolomid larvae, however, have only 2-segmented maxillary palps, those of the Corylophidae have the labrum and clypeus fused, and both lack the characteristic bundles of long, barbed setae along the sides of the body. The larvae of *Euxestus* and *Hypodacne* bear a resemblance to certain Languriidae, especially *Cryptophilus*, in the form of the tergal processes, surface granulation and setation, and in the single tarsungular claw, but the latter group may be distinguished by the presence of a mandibular prostheca, bicameral spiracles, and 5 or 6 ocelli on each side of the head. Cerylonine larvae are similar in form to some of the smaller Endomychidae, but they are easily recognized by the modified piercing mouthparts.

Because of their small size, most cerylonids are collected by mass sampling techniques, and little is known of their food habits or life histories. The most frequented habitats for the group are leaf litter and rotten wood, especially cambium. Species of *Cerylon*, *Philothermus*, and *Myhocerus* are usually collected under bark, while those of *Lapethus* appear to be equally common in leaf litter and forest debris. A number of species have been recorded from ant nests: *Hypodacne punctata* is known from *Camponotus* galleries; *Aculanathus mirabilis* Oke has been associated with *Amblyopone* in Australia; and two species of *Lapethus* have been collected in large numbers in the refuse deposits of the leaf-cutting ant *Atta mexicana*. *Elytrotetrantus chappuisi* (Jeannel and Paulian) is known from a mole-rat nest, while *Euxestus erithacus* Chevrolat was found breeding in bat guano in a Jamaican cave. Adults and larvae of certain Neotropical *Philothermus* have been taken in polypore fungi, but there were never more than a few individuals. Finally, *Murmidius ovalis* is known to feed on stored products of man.

Almost nothing has been recorded on the actual type of food material taken in by cerylonids. Several gut dissections were made

by one of us, but the particles were often impossible to identify. The larval gut contents of the *Euxestus* from bat guano contained a variety of hyphal sections and spores, while numerous darkly-pigmented spores of a single type were found in the adult proventriculus of a *Philothermus* collected under pine bark in Mexico. The proventriculus of *Cerylon castaneum* collected on dried mushrooms from a tree was filled with sculptured basidiospores, while that of the same species taken under conifer bark contained sections of hyphae, as well as spores. Those forms with piercing-sucking mouthparts have been assumed to be predators (Besuchet, 1972), but as yet there is no direct evidence supporting this hypothesis (*see below*).

Perhaps the most interesting feature of the subfamily Ceryloninae is the occurrence of piercing-sucking mouthparts in all known larvae and in adults of over 50 species in at least six genera. This condition may have evolved twice in the larval forms and several times in the adults (*see below*). The most highly specialized type of piercing apparatus in adult cerylonids occurs in the genus *Cautomus* and has been described and illustrated by Besuchet (1972). In this group, the labrum-epipharynx and the labium together form an elongate, tubular beak, in which are contained four pairs of stylets, each set consisting of a mandible and its lacinia mandibularis (prostheca), a galea, and a lacinia. The molar area of the mandible is absent, while both the mandibular apex and the prostheca are long and blade-like. The maxillary stylets are extremely long and thin and are attached to a basal fulcrum which allows them to be protracted; the lacinia bears fine recurved teeth and the galea is provided with hairs at the apex. Finally the pharynx is enlarged, forming a pharyngeal pump. This type of condition also occurs in *Axiocerylon* and its relatives, in the New World *Ceryloncautomus*, and in a few species of *Lapethus*. Although the mechanics have not been studied, it is obvious that this represents a piercing-sucking organ similar to those found in various Diptera and Hemiptera.

Besuchet (1972) also discussed the transition from normal chewing mouthparts found in *Cerylon* to those in *Cautomus* through forms such as *Ectomicrus*, which exhibit an elongation of the labrum, mandibular apex, galea, and labium. The same type of intermediate condition may be found in species of *Lapethus* (figs. 11-12) and in certain *Philothermus*. In most of these species, the labrum and labium are somewhat elongate, the galea and lacinia are both stylet-like, the mola is usually present, and the mandibular apex retains two

or three small teeth, which appear to interlock with those of the opposite mandible. This type of mandible resembles that found in Collembola, and it may function in a similar way, with the apical teeth pulling hyphae or strands of wood into the mouth, where they are acted upon by the mola (Folsom, 1899; Macnamara, 1924). The maxillary lobes, although very long and stylet-like, have numerous fine hairs which may serve to gather spores or other particles into the mouth cavity. These mouthparts are somewhat similar to those found in the rhyphiine Corylophidae (Paulian, 1950). In *Rhypobius* and its relatives, the maxilla has a single stylet, the mandible is divided, with a basal fulcrum and a long hooked apex, and both are enclosed within the head cavity when not in use.

The larvae of cerylonines have two different types of feeding mechanism. In *Philothermus* and *Lapethus*, the labrum and labium form a tubular beak, while the mandible and the mala are both modified into long, blade-like stylets. In addition, the pharynx is enlarged and a pair of salivary glands extend back into the thorax for a distance equal to the head length. These, like the *Cautomus* adults, have a well-developed piercing-sucking apparatus. The larval head, however, is strongly hypognathous, and not prognathous like that of the adult. The second type of feeding apparatus is found in the larvae of *Cerylon*. Here the head is opisthognathous with the labium short and fused to the thorax, and the mandibular and maxillary stylets completely enclosed within the head and apparently attached to a heavily sclerotized internal framework. This condition is remarkably similar to that found in the entognathous apterygote insects, such as the Diplura, Protura, and Collembola (Tuxen, 1959).

As mentioned above, the actual food source of these small and uncommon insects is often difficult to ascertain, and this is especially true for those species ingesting fluids, if this is the case. Although it would be an obvious conclusion that those cerylonids with piercing beaks are predators on small arthropods and nematodes, it is also possible that the beaks penetrate wood or fungal hyphae or that these substances are digested extra-orally. Another possibility is that spores or other objects less than 5 or 6 microns in length are moved into the labral-labial tube by suction or by the action of the setiferous galea; the apical openings of those beaks examined were at least 8 microns wide. Another matter to consider is the normal position of the head. In most of the adults with piercing beaks, the head is somewhat prognathous, so that predation would be possible on active prey species of various sizes. Most cerylonine larvae, however, are

strongly hypognathous, while that of *Cerylon* is opisthognathous with entognathous stylets. It is less likely that either larval type would be predaceous. It is hoped that observations on living specimens will provide more information on the feeding habits of both larvae and adults.

The evolution of piercing-sucking mouthparts has occurred at least two more times in the Coleoptera. Leiodid beetles of the genus *Myrmecholeva* Lea, which occur with ants in Australia, have a relatively robust, piercing beak and prognathous head, and they may be predators on ant larvae. The maxillary stylets are well-developed and blade-like in this group, but the mandibles are much shorter than the beak and do not appear to function as piercing organs. In the family Eucinetidae, members of an undescribed genus from the New World are extremely small (less than 1 mm.) with a hypognathous head and a labral-labial beak with an opening of about 5 microns; the mandibles in these insects are even further reduced, but the maxillary stylets are very long and fine. A detailed comparison of piercing-sucking feeding mechanisms in beetles will be included in a paper now in preparation by J. F. Lawrence and T. F. Hlavac.

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Key to the Genera of North American Cerylonidae

1. Frontoclypeal suture present; terminal segment of maxillary palp at least $2 \times$ as long as and more than $0.5 \times$ as wide as segment 3, which is shorter than or subequal to segment 2; last ventrite not or very finely crenulate. 2
- Frontoclypeal suture absent; terminal segment of maxillary palp aciculate, shorter than and less than $0.5 \times$ as wide as segment 3, which is longer than segment 2; apex of last ventrite always strongly crenulate (fig. 1). 7
2. Procoxal cavities closed behind; length at least 2 mm.; body oval and highly convex, with smooth, even, lateral edges and no antennal cavities. *Hypodacne* LeConte
- Procoxal cavities open behind; length less than 1.5 mm.; without other characters in combination. 3
3. Prothorax without antennal cavities; lateral edges of pronotum crenulate or serrate; metasternum and first ventrite without femoral lines; tarsi 3-segmented; body more elongate, TL/EW more than 1.75. 4
- Prothorax with antennal cavities; lateral edges of pronotum smooth; metasternum and first ventrite with femoral lines; tarsi 4-segmented; body round or oval in outline, TL/EW less than 1.75. 5
4. Lateral margins of pronotum crenulate; eyes absent; body elongate, TL/EW about 2.5; elytra with 7 rows of punctures bearing very short, fine hairs; procoxal cavities very narrowly separated, the intercoxal process depressed and less than $0.2 \times$ a coxal width. *Anommatus* Wesmael
- Lateral margins of pronotum serrate; eyes present; body oblong, TL/EW less than 2.0; elytra with 10 rows of punctures bearing longer, suberect hairs; procoxal cavities more widely separated, the intercoxal process not depressed and at least as wide as one coxa. *Ostomopsis* Scott
5. Antennal cavities of prothorax dorsal, easily visible from above (fig. 21); antennae 10-segmented; body strongly convex and elytral punctation seriate. *Murmidius* Leach
- Antennal cavities of prothorax ventral, not visible from above; antennae with less than 10 segments; body flattened or elytral punctation confused. 6
6. Body distinctly flattened; antennae 9-segmented; elytral punctation seriate; mesosternum truncate anteriorly; metasternal suture present. *Mychocerus* Erichson

- Body strongly convex; antennae 8-segmented; elytral punctation confused; mesosternum rounded anteriorly; metasternal suture absent. *Botrodes* Casey
- 7. Prothorax with large, ventral, antennal cavities, situated laterally and formed primarily from the hypomera; metasternum and first ventrite with femoral lines; antennae 8-segmented. *Lapethus* Casey
- Prothorax without antennal cavities, or with smaller, mesal cavities, formed entirely from the prosternum; metasternum and abdomen without femoral lines; antennae 10- or 11-segmented. 8
- 8. Prosternum raised mesially and excavate laterally, forming two shallow antennal cavities; labrum acute at apex, beak-like; length less than 1.3 mm.; antennae 10-segmented, with a 1-segmented club. *Ceryleautomus* Sen Gupta and Crowson
- Prosternum without antennal cavities; labrum not acute; length more than 1.3 mm. 9
- 9. Procoxal cavities open behind or narrowly closed, the postcoxal bridge at apex less than 0.25 \times as wide as cavity (fig. 9); intercoxal process of prosternum not widened behind; mesosternum concave; antennae 11-segmented with a 2-segmented club; lateral margins of pronotum visible for their entire lengths from above. *Philothermus* Aubé
- Procoxal cavities broadly closed behind, the postcoxal bridge more than 0.5 \times as wide as cavity (fig. 10); intercoxal process of prosternum strongly widened posteriorly; mesosternum flat or slightly convex; antennae 10-segmented with 1-segmented club; lateral margins of pronotum not visible for their entire lengths from above. *Cerylon* Latreille

Euxestinae Grouvelle

As used here, this group is equivalent to the tribe Euxestini described and delimited by Sen Gupta and Crowson (1973), and including the Cycloxenini and Tachyoryctidiini of Jeannel and Paulian (1945). Sen Gupta and Crowson admitted that those characters shared by the Euxestini, the Anommatini, and the Metacerylonini of Heinze (1944) are, for the most part, primitive for the family, and that all three tribes might be given subfamily rank. Of the eight known genera, only one, *Hypodacne*, occurs in America north of Mexico. The genus *Euxestus* Wollaston, however, includes a widely distributed Neotropical species which might be expected to occur in southern Florida (see below).

Hypodacne LeConte

Hypodacne LeConte, 1875: 170. Type species, by monotypy, *H. punctata* LeConte.

Euxestus, of authors (not Wollaston).

Sen Gupta and Crowson resurrected LeConte's name for a group of species, usually included in *Euxestus*, which have simple tarsi, lacking the characteristic ventral lobe on the first tarsal segment. In addition to the North American *H. punctata*, several Australian and New Zealand species are included.

Hypodacne punctata LeConte
(Fig. 20)

Hypodacne punctata LeConte, 1875: 171. Type locality: Eastern United States. Holotype, No. 6763 M.C.Z.

This species is easily distinguished from other North American cerylonids by the highly convex and oval body, which is longer than 1.5 mm., widely separated and posteriorly closed procoxal cavities, distinct frontoclypeal suture and characteristic antennal club, and the lack of pronotal antennal cavities, femoral lines on the abdomen, and crenulations on the last visible ventrite. The related *Euxestus erithacus* Chevrolat occurs in the Greater Antilles and might be found in southern Florida, but that species is smaller in size and bears a distinct ventral lobe on the first tarsal segment, a feature absent in *Hypodacne*.

Distribution. Known from scattered localities throughout eastern North America, from southern Ontario to Florida and west to Kansas and Texas.

Biology. According to Stephan (1968), this species occurs in the galleries of carpenter ants (*Camponotus*) in southern Ontario. Specimens were observed crawling on walls of carpenter ant galleries in oak, elm, and beech. The larva of *H. punctata* is unknown, but that of the Australian species, *H. bivulneratus* (Lea), was described by Sen Gupta and Crowson (1973: 381) from specimens collected in leaf litter and decayed wood.

Anommatinae Ganglbauer

This subfamily includes the two Palaearctic genera *Abromus* Reitter and *Anommatus* Wesmæl, the latter of which has been introduced into North America. Ganglbauer (1899) originally considered this tribe to be related to cerylonids, but Crowson (1955)

placed the group in his Merophysyiidae. Sen Gupta and Crowson (1973) recognized its affinities to the Cerylonidae, and especially the Euxestinae, after the description of the *Anommatus* larva by Dajoz (1968).

Anommatus Wesmael

Anommatus Wesmael, 1835: 338. Type species, by monotypy, *A. terricola* Wesmael [= *A. duodecimstriatus* (Müller)].

This genus is native to Europe, where it is represented by 49 species. It has been recently revised by Dajoz (1965).

Anommatus duodecimstriatus (Müller) (Fig. 23)

Lyctus duodecimstriatus Müller, 1821: 190. Type locality: Odenbach, Germany. (For complete synonymy, see Dajoz, 1965.)

This species may be distinguished by the elongate form, distinct frontoclypeal suture, apparently 1-segmented antennal club, 3-segmented tarsi, and the lack of eyes or wings. It superficially resembles the eyeless colydiid *Aglenus brunneus* (Gyllenhal), which differs by having a 3-segmented antennal club, 4-segmented tarsi, and hidden antennal insertions.

Distribution. Fairly widely distributed in Europe and extending at least to Turkey and Algeria. Recorded also from Madeira, St. Helena, South Africa, Chile, Tasmania and North America (Cooper, 1962). North American specimens collected at Rochester, New York (Cooper, 1962; Peck, 1972); Cincinnati, Ohio (Dury, 1928); and Lake Forest, Lake Co., Illinois (W. Suter, Nov. 7, 1959).

Biology. Adults have been collected from litter and damp soil under railroad ties, under stones, around grass roots, and from grass cuttings. The Illinois specimen was taken in a tree hole. Larvae have been found in soil at the base of a tree and in leaf mold (Dajoz, 1968; Sen Gupta and Crowson, 1973). No males have been found in North America, and Cooper (1962) and Peck (1972) have postulated that our populations may be parthenogenetic.

Murmidiinae Jacquelin DuVal

This corresponds to the Murmidiinae of Sen Gupta and Crowson, except for the exclusion of *Ostomopsis* (see *Ostomopsinae* below). The group may be characterized by the presence of a frontoclypeal

suture and prothoracic antennal cavities, and it includes the three genera *Murmidius*, *Mychocerus*, and *Botrodus*, all of which are represented in North America. Casey (1895) also included the Lapethini and the Eupsilobiini, with the single genus *Eupsilobius*. According to Sen Gupta and Crowson (1973), the Lapethines should be transferred to the Ceryloninae, while *Eupsilobius* Casey, a junior synonym of *Eidoreus* Sharp, should constitute a distinct subfamily of Endomychidae.

Murmidius Leach

Murmidius Leach, 1822: 41. Type species, by monotypy, *M. ferrugineus* Leach [= *Murmidius ovalis* (Beck)].

Ceutocerus Germar, 1824: 85. Type species, by monotypy, *C. advena* Germar [= *Murmidius ovalis* (Beck)].

This genus contains five Neotropical species and five from the Old World. One of the latter, *M. ovalis*, has been introduced in stored products to many parts of the world, including North America. Hinton (1942b) provided a key to the Old World species.

Murmidius ovalis (Beck)

(Fig. 21)

Histor ovalis Beck, 1817: 7. Type locality: Bavaria.

Murmidius ferrugineus Leach, 1822: 41.

Ceutocerus advena Germar, 1824: 85.

This species may be distinguished by its small size (1.2-1.4 mm.), oval, convex body with seriate elytral punctation, dorsal antennal cavities, 10-segmented antennae with a 1-segmented club, and 4-segmented tarsi.

Distribution. Cosmopolitan. In North America, recorded from Alaska, California, Kansas, Illinois, Ontario, New York, Maryland, District of Columbia, Louisiana, and Florida.

Biology. Usually associated with stored products and often found in granaries and warehouses. Reported from fruits and seeds, Indian corn, rice, wheat, flour, hay, straw, gall-nuts, oak-galls, ginger, and pepper, and also collected in dead leaves and cut grass (Hinton, 1945; Halstead, 1968). The larva, which is flat and onisciform, with barbed setae, has been illustrated by Boving and Craighead (1931) and Halstead (1968), while the last author figured the pupal cocoon and gave additional information on life history and development.

Mychocerus Erichson

Mychocerus Erichson, 1845: 292. Type species, by monotypy, *M. ferrugineus* Erichson.

This New World genus contains five species, two of which occur in America north of Mexico. The described Seychelles species, *M. alluaudi* Grouvelle, was transferred to *Lapethus* by Hinton (1936). Grouvelle (1895) also included *Philothermus gibbulus* Reitter (1876), without giving his reasons; although Reitter's type has not been seen, the description of *gibbulus* could hardly apply to a species of *Mychocerus*. The species of *Mychocerus* may be distinguished by the small size and flattened form, 9-segmented antennae with a 1-segmented club, anteroventral antennal cavities, and seriate elytral punctation. The literature is somewhat confused as to the type species for this genus. In the original description, Erichson mentioned that three species were included in his genus, but he named one from Cuba, "*M. ferrugineus* Nob." Since the genus was described in the same paragraph, this must constitute the species description as well, and thus *M. ferrugineus* is the only included species and the type. We have not seen the Cuban species, but we are assuming that it is congeneric with *M. depressus*, which LeConte (1869) placed in *Mychocerus*, and which is usually considered the type.

Key to the North American *Mychocerus*

1. Sides of pronotum gradually converging near apex, not angulate; lateral lines of mesosternum subparallel for most of their lengths, abruptly converging anteriorly, each line posteriorly forming an abrupt angle (about 120°) with the metasternal line (fig. 2); apical edge of prosternum slightly emarginate; size smaller, length usually less than 1 mm.; eastern North America. *M. depressus* LeConte
- Sides of pronotum abruptly converging near apex, so that the lateral edge is more angulate; lateral lines of mesosternum converging from base to apex, each line posteriorly forming a wider angle (about 150°) with the metasternal line (fig. 3); apical edge of prosternum more deeply emarginate; size larger, length usually more than 1 mm.; Arizona and northern Mexico. *M. arizonensis*, n. sp.

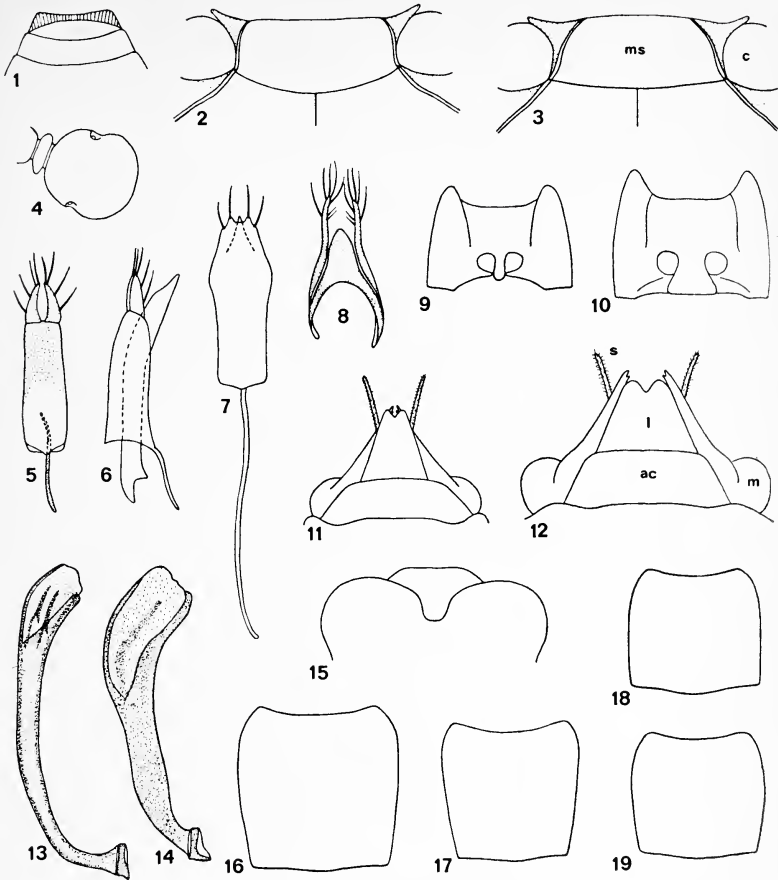


Fig. 1. *Cerylon unicolor* (Ziegler), fifth ventrite, posteroventral view. Fig. 2. *Mychocerus depressus* LeConte, mesosternum and portion of metasternum. Fig. 3. *Mychocerus arizonensis*, n. sp., same (ms = mesosternum; c = coxa). Fig. 4. *Ostomopsis neotropicalis*, n. sp., antennal club. Fig. 5. *Mychocerus arizonensis*, tegmen, dorsal view. Fig. 6. *M. arizonensis*, aedeagus, lateral view. Fig. 7. *Ostomopsis neotropicalis*, tegmen, dorsal view. Fig. 8. *Philothermus occidentalis*, n. sp., tegmen, dorsal view. Fig. 9. *P. occidentalis*, prothorax, ventral view. Fig. 10. *Cerylon unicolor* (Ziegler), prothorax, ventral view. Fig. 11. *Lapethus striatus* (Sen Gupta and Crowson), anterior portion of head, dorsal view. Fig. 12. *Lapethus discretus* Casey, same (ac = anteclypeus, l = labrum, m = mandible, s = maxillary stylet). Fig. 13. *Cerylon conditum*, n. sp., aedeagus, lateral view. Fig. 14. *Cerylon distans*, n. sp., same. Fig. 15. *Cerylon castaneum* Say, male, clypeus and labrum. Fig. 16. *Cerylon conditum*, male, pronotum. Fig. 17. *C. castaneum*, male, pronotum. Fig. 18. *C. unicolor*, female, pronotum. Fig. 19. *C. unicolor*, male, pronotum.

Mychocerus arizonensis, New Species

This species may be distinguished from either *M. depressus* or *M. pilifer* Lewis (1888: 241) by the larger size and by the shape of the pronotum, which is more abruptly narrowed apically. From *M. depressus* it also differs in the form of the mesosternal lines.

Description. Length 1.1-1.3 mm. Color reddish-brown; vestiture of short, fine, decumbent, yellow hairs, which are barely visible under 25 \times magnification. Antennae with segments 4-6 distinctly serrate, the club about 1.35 \times as long as wide. Pronotum about 0.48 \times as long as wide, sides subparallel for basal three-fourths, abruptly converging apically, the apical angles produced and subacute; lateral margins distinct and slightly elevated, especially towards base; disc slightly convex; punctation somewhat irregular, coarser than in *M. depressus*. Elytra about 1.15 \times as long as wide and 3.0 \times as long as pronotum, widest at apical fourth; rows of punctures lightly impressed and not distinct, the punctures smaller than those of *M. depressus*, intervals shiny, but with a fine reticulation. Apical edge of prosternum distinctly concave; mesosternal lateral lines gradually converging anteriorly, each line posteriorly forming an angle of about 150 $^{\circ}$ with the line of the metasternum (fig. 3). Aedeagus about 0.6 \times as long as abdomen, parameres longer and narrower than those of *M. depressus*, about 3 \times as long as wide at base (figs. 5-6).

Types. Holotype, 3 mi. NW Arivaca, Pima Co., ARIZONA, Dec. 21, 1969, under bark of mesquite (K. Stephan) [No. 32239 M.C.Z.]. Paratypes: ARIZONA: Pima Co.: 11, same data as holotype; 5, same locality, Jan. 25, 1970, under bark of mesquite (K. Stephan) [KS, MCZ, USNM]. Four other specimens were collected at East Stronghold, Cochise Co., Arizona, April, 1972 and 1973, by K. Stephan, and a single specimen was collected 10 mi. SE Alamos, Sonora, Mexico, Oct. 1972 (D. Chandler).

Distribution. Southeastern Arizona and southern Sonora, Mexico. In Arizona, known from low elevations in the extreme southern part of the state and from higher elevations in the Chiricahua Mountains.

Biology. Individuals from the lowland Arizona population were taken under dry mesquite bark and were not associated with running wounds. Those from the montane locality were collected under oak bark.

Mychocerus depressus (LeConte)

(Fig. 22)

Murmidius depressus LeConte, 1866: 376. Type locality: Washington, D.C. Holotype, No. 6829 M.C.Z.

This is the smallest cerylonid in our fauna, seldom exceeding 1 mm. in length. It is very similar to *M. arizonensis*, but may be distinguished by the smaller size, more gradually narrowed pronotal apex, subparallel mesosternal lines which form a more abrupt angle with the lines on the metasternum, and shorter, broader parameres (about twice as long as wide at base). The pronotal punctation in *M. depressus* is finer than that of *arizonensis*, while the elytral punctures are larger and more distinct. According to Lewis (1888), the Guatemalan species, *M. pilifer*, is about the same size, but has a differently shaped pronotum and less distinct elytral punctation.

Distribution. Known from scattered localities in eastern North America, from southern Ontario south to Florida and west to eastern Texas.

Biology. Adults have been collected under fungus-infested bark of oak, and also under bark of beech and hickory. The larva is unknown.

Botrodus Casey

Botrodus Casey, 1890: 319. Type species, by monotypy, *B. estriatus* Casey.

This New World genus contains only two described species, *B. estriatus*, discussed below, and *B. dufau* Grouvelle from Guadeloupe.

Botrodus estriatus Casey

Botrodus estriatus Casey, 1890: 320. Type locality: Columbus, Texas. Holotype, No. 48336 U.S.N.M.

This species resembles a small lapethine with respect to its oval and highly convex body, confused elytral punctation, and ventral, rather than dorsal antennal cavities. Its relationship to *Mychocerus* and *Murmidius* is indicated by the presence of a frontoclypeal suture, murmidiine mouthparts (galea and lacinia not elongate, terminal segment of maxillary palp not aciculate), and *Mychocerus*-like aedeagus. The species may be distinguished from the other murmidiines by the anteriorly rounded mesosternum, 8-segmented antennae, and lack of metasternal suture.

Distribution. Known only from Florida and Texas.

Biology. Habitat and immature stages unknown.

Ostomopsinae Sen Gupta and Crowson

This monotypic subfamily is considered to be a tribe of Mirmiidiinae by Sen Gupta and Crowson (1973), but its relationship to the latter group is somewhat unclear. It is here treated as an independent subfamily.

Ostomopsis Scott

This genus was described by Scott (1922: 250-253, pl. 19, fig. 11) for the Seychelles species *O. solitaria*, and has been redescribed and illustrated by Sen Gupta and Crowson (1973: 400-402, figs. 43-49) on the basis of new material from New Caledonia and Florida. There is little to add to the generic description provided by the latter authors, except that the hind edge of the pronotum has a raised margin and the scutellum is transverse. Also the antennal club is broader than their illustration suggests, and it appears to be pinched in the middle due to the presence of lateral sensillae (see fig. 4).

Species of *Ostomopsis* may be distinguished from other Cerylonidae by the frontoclypeal suture, internally and externally open procoxal cavities, and 3-segmented tarsi, and the lack of femoral lines, antennal cavities, and a transverse line on the vertex. *Ostomopsis solitaria* Scott is known only from the Seychelles, but specimens appearing to be conspecific have been seen from New Caledonia and the Loyalty Islands. The Neotropical species described below extends the range of the genus into the New World.

***Ostomopsis neotropicalis*, New Species**
(Fig. 24)

This species may be distinguished from *O. solitaria* by the smaller size (less than 1.10 mm.), somewhat more elongate body, and narrower, less explanate, pronotal margins with more irregularly serrate edges.

Description. Length 0.95-1.10 mm. Color yellowish-brown; vestiture of dense, suberect, yellowish hairs, which are about three-fifths as long as scutellar base, intermixed, especially at sides, with much longer hairs exceeding scutellar base in length. Antennal club (fig. 4) about as long as wide and twice as wide as the segment preceding it. Pronotum about 0.60 × as long as wide, widest at posterior third, sides weakly rounded, apical angles slightly produced and acute; lateral margins moderately broad and explanate, but less so than in *O. solitaria*, the edges coarsely and irregularly serrate; disc slightly

convex, slightly flattened mesially, punctation moderately coarse and dense, the interstices shiny. Scutellum transverse. Elytra about 1.42 \times as long as wide and 2.50 \times as long as pronotum; sides weakly rounded, almost parallel basally, the margins somewhat explanate, with finely, but sparsely and irregularly serrate edges; punctures of two types: large, somewhat rectangular ones, closely packed in regular rows, and very fine ones occurring in the intervals, both types bearing suberect hairs. Aedeagus about as long as abdomen; tegmen (fig. 7) with fused parameres and very long median strut; median lobe about as long as tegmen, very narrow, with long basal struts.

Types. Holotype, Fairchild Trail, Barro Colorado Island, CANAL ZONE, Jan. 28, 1959, berlese sample, B-180, heart of old palm on ground (H. S. Dybas) [FM]. Paratypes: MEXICO: San Luis Potosi: 2, 8 mi. N. Huichihuayan, June 20, 1941 (H. S. Dybas) [FM]. Veracruz: 1, Cordoba, Aug. 4, 1969, berlese sample, B-173, tropical evergreen forest (S. & J. Peck) [MCZ, on slide]. CANAL ZONE: 1, same data as holotype [JL].

Distribution. Florida and northern Mexico, south to the Isthmus of Panama. We have been unable to locate the specimen from Florida mentioned by Sen Gupta and Crowson, although we are assuming that it is conspecific with the Mexican and Central American specimens.

Biology. Possibly associated with rotten palm wood. Specimens of *O. solitaria* from New Caledonia and the Loyalty Islands were collected under bark.

Ceryloninae Billberg

This subfamily includes all of the remaining cerylonids, which are characterized by the lack of a frontoclypeal suture and the presence of relatively long and slender maxillary lobes, aciculate maxillary palps, and a distinctly crenulate margin on the last ventrite. The last feature, which may be present but much less obvious in certain murmidiines, is actually a series of vertical ridges on the inflexed margin of the ventrite (fig. 1); these form an interlocking mechanism with a corresponding series beneath the elytral apices. All known cerylonine larvae and adults in at least six genera have evolved highly modified, piercing mouthparts, with an elongate, pointed labrum, and mandibular and maxillary stylets (see p. 134).

Although there is little argument concerning the limits of the subfamily, whose distinguishing features are primarily derived, the interrelationships among the included genera and the limits of cer-

tain of these genera (*Cerylon*, *Philothermus*, *Lapethus*) are far from being understood. Sen Gupta and Crowson (1973) divide the group into three tribes: Lapethini, Cerylonini, and Aculagnathini. Members of the first group are distinguished by the oval or globose form and the presence of lateral antennal cavities on the anteroventral portion of the pronotum; three genera are included at present, but two of these are synonymized below. The remaining genus *Lapethus* is closely related to certain Cerylonini, and the larvae are more similar to those of *Philothermus* than the latter are to the larvae of *Cerylon*.

The Aculagnathini are a diverse group which have one feature in common — the possession of piercing mouthparts. In the Indo-Australian genus *Cautomus* and its relatives, the prosternum is raised in the middle, so that a shallow antennal cavity is formed on either side, and the dorsal surface of the body is relatively simple. The Asian and African *Axiocerylon*, *Dolosus*, and *Thyroderus*, on the other hand, are characterized by having the prosternum produced forward to form a chin-piece, which fits against the clypeus to conceal the mouthparts, and by the possession of deep antennal cavities, clytral ridges, and pronotal grooves. In both of the above groups, the labrum tapers to a sharp point, and a tube is formed to contain the mandibular and maxillary stylets (*see* p. 134). In the New World, *Cerylcautomus floridensis* resembles the *Cautomus* group in having shallow median antennal cavities and an acute labrum, but this species differs in the 1-segmented (instead of 2-segmented) antennal club. In Central America and the West Indies, a number of undescribed forms have been seen which resemble *C. floridensis* in most respects, but which vary considerably in the development of those characters considered to be diagnostic of the *Cautomus* group or of aculagnathines in general. In one case, the antennal cavities are absent and the labrum is elongate but not acute or tube-like, while in another the antennal cavities are well-developed but the mouthparts are not at all of the piercing type. Finally, the South American *Glyptolopus* resembles a large member of the *Axiocerylon* group, but the characteristic chin-piece and antennal cavities are absent, the antennae are 3-segmented, and the labrum is not acute. The great variation within this tribe, the existence of a number of forms with intermediate types of mouthparts, both within the tribe and within cerylonine genera, such as *Ectomicrus*, and the occurrence of piercing beaks in the lapethines and in cerylonine larvae, all suggest that the Aculagnathini may be polyphyletic and that the diagnostic piercing type of mouthparts may have arisen independently in

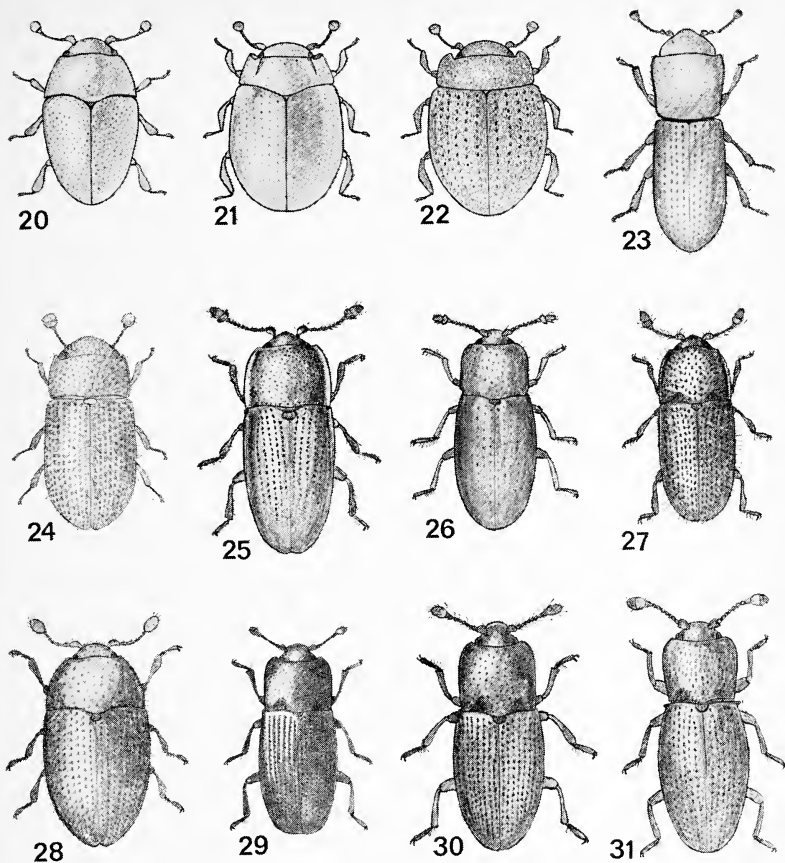


Fig. 20. *Hypodacne punctata* LeConte. Fig. 21. *Murmidius ovalis* (Beck). Fig. 22. *Myhocerus depressus* LeConte. Fig. 23. *Anommatus duodecimstriatus* (Müller). Fig. 24. *Ostomopsis neotropicalis*, n. sp. Fig. 25. *Philothermus glabriculus* LeConte. Fig. 26. *P. occidentalis*, n. sp. Fig. 27. *P. puberulus* Schwarz. Fig. 28. *Lapethus discretus* Casey. Fig. 29. *Cerylon distans*, n. sp. Fig. 30. *C. unicolor* (Ziegler). Fig. 31. *C. californicum* Casey. [Not drawn to same scale].

several phyletic lines. A more detailed analysis of the group and the related Cerylonini, based on characters unrelated to the feeding apparatus, may shed more light on the problem.

The Cerylonini include the remaining dozen or so cerylonine genera which have not been placed in the above tribes, and these also form a diverse assemblage. The large genera *Cerylon* and *Philothermus* are discussed below, while the smaller exotic groups are covered in Sen Gupta and Crowson (1973), Hinton (1942a), and Heinze (1944).

Philothermus Aubé

Philothermus Aubé, 1843: 93. Type species, by original designation, *P. montandoni* Aubé.

There has been considerable confusion concerning the constitution of this genus, and both Heinze (1944) and Sen Gupta and Crowson (1973) have attempted to clarify its limits and to distinguish the included species from those of *Cerylon*. The latter authors have defined the group primarily on the basis of prosternal characters and have included a number of forms with 10-segmented antennae and a 1-segmented club. Among these are members of the genus *Ectomicrus* Sharp (1885) and a group of African *Cerylon*-like forms. Although *Ectomicrus* was synonymized with *Philothermus* by Reitter (1890), Heinze (1944) found several characters to distinguish it, in addition to the 1-segmented antennal club. The African forms mentioned (at least *P. camerunense* Sen Gupta and Crowson) have well-developed femoral lines on the abdomen and appear to have more in common with *Philothermopsis* than *Philothermus*, in spite of tarsal differences. As presently conceived, *Philothermus* includes about 50 species, which are characterized by having a more or less elongate form, 4-segmented tarsi, no prothoracic antennal cavities, procoxal cavities open or narrowly closed behind, and the prosternal process not or only slightly widened and more or less rounded at apex. In addition, most of the species have 11-segmented antennae with a 2-segmented club and no femoral lines on the first ventrite. In North America, the genus is represented by a California and a Florida endemic and a widespread eastern species.

Key to the North American *Philothermus*

1. Body more elongate, PL/PW more than 0.82 and EL/EW more than 1.58; each elytron with 7 rows of punctures (not

- counting that along lateral edge); lateral margins of pronotum narrow; procoxal cavities narrowly closed behind; California. *occidentalis*, n. sp.
- Body shorter and broader, PL/PW less than 0.82 and EL/EW less than 1.58; each elytron with 8 rows of punctures; lateral margins of pronotum broad and explanate; procoxal cavities open behind; eastern North America. 2
2. Elytral vestiture consisting of numerous erect hairs, which are usually much longer than the diameter of an elytral puncture; pronotal punctation coarser and denser, the punctures usually separated by less than the diameter of one; lateral margins of pronotum distinct crenulate and lateral margins of elytra visible from above almost to apex; Florida. *puberulus* Schwarz
- Elytral vestiture consisting of very short hairs, which are shorter than a puncture diameter, and a few scattered longer hairs; pronotal punctation finer and sparser, the punctures usually separated by more than the diameter of one; lateral margins of pronotum relatively smooth and lateral margins of elytra visible from above only for anterior half. *glabriculus* LeConte

Philothermus glabriculus LeConte

(Fig. 25)

Philothermus glabriculus LeConte, 1863: 69. Type locality: Pennsylvania. Lectotype, ♂, No. 6827 M.C.Z. (selected by J. F. Lawrence, April, 1975).

This species may be distinguished from the Floridian *P. puberulus* by the larger size (1.9-2.3 mm.) and somewhat broader form, shorter elytral hairs, finer and sparser pronotal punctation, and relatively smooth and even lateral pronotal margins. The western *P. occidentalis* is more elongate, with narrower pronotal margins and closed procoxal cavities. This is probably the most common cerylonid in eastern North America and it may occur with *Cerylon unicolor*, which is easily distinguished by the much narrower form and 1-segmented antennal club.

Distribution. Widespread throughout eastern North America from southern Ontario and Maine, south to northern Florida and west to Oklahoma and Texas.

Biology. Adults have been taken under the bark of *Acer*, *Carya*, *Fagus*, *Pinus*, *Quercus*, *Tsuga*, and *Ulmus*. Also taken under boards, in rotten logs, sawdust piles, malt traps, leaf litter, tree holes, and forest debris.

Philothermus occidentalis, New Species
(Fig. 26)

This species is characterized by the elongate body, narrow pronotal margins, 7 rows of elytral punctures, narrowly closed procoxal cavities, slightly expanded pronotal process, deeply concave mesosternum, and elongate metasternum.

Description. Length 1.8-2.2 mm. Color reddish-brown; vestiture of short, erect hairs, which are visible under $25\times$ magnification. Pronotum about $0.85\times$ as long as wide, widest at basal fourth, sides slightly converging to rounded apical angles; disc moderately convex, lateral margins narrow and somewhat irregular, the edge slightly crenulate at base; punctation fairly coarse and dense, punctures near center about $0.2\times$ as large as scutellar base and usually separated by less than a diameter; interstices smooth and shiny, with scattered very fine punctures. Elytra about $1.67\times$ as long as wide and $2.25\times$ as long as pronotum, widest at anterior third, each elytron with 7 rows of punctures (not counting marginal row), the punctures about as large as those on pronotum, deeply impressed, and fairly closely and irregularly spaced, intervals slightly convex, smooth and shiny, with scattered, very fine punctures. Prosternal process slightly narrower than a coxal diameter, very slightly expanded posteriorly and broadly rounded at apex; coxal cavities narrowly closed behind (fig. 9). Mesosternal concavity fairly deep, without a median carina, the process truncate at apex. Metasternum slightly longer than first ventrite. Aedeagus (fig. 8) with long, narrow parameres; median lobe about $0.75\times$ as long as abdomen.

Types. Holotype, Mather, Tuolumne Co., CALIFORNIA, June 15, 1969, sifting conifer debris (K. Stephan) [No. 32242 M.C.Z.]. Paratypes: CALIFORNIA: El Dorado Co.: 1, Blodgett Forest, July 24, 1972 (D. S. Chandler) [OSU]; 1, Lake Tahoe, 11.7 (Hubbard & Schwarz) [USNM]; 1, same, July 17-21, 1917 (H. C. Fall) [MCZ]; 1, Pollock Pines, May 21, 1970 (R. Belmont) [DSC]; 1, no specific locality, Aug. 7, 1970 (F. Andrews) [FA]. Mariposa Co.: 1, 10 mi. NW Yosemite, 6000', July 21, 1946 (H. P. Chandler) [CAS]. Placer Co.: 4, Forrest Hill, Mar. 1898 (E. C. VanDyke) [CAS]. Shasta Co.: 1, Hat Creek R. S., 3000', June 23, 1947 (H. P. Chandler) [CAS]; 1, Viola, June 18, 1972 (D. P. Levin) [KS]. Trinity Co.: 1, Trinity Center, June 15, 1972 (D. S. Chandler) [OSU]. Tuolumne Co.: 16, Mather, June 15, 1969, sifting conifer debris (K. Stephan) [KS, MCZ, USNM]; 1, Strawberry Valley, Aug. 6, 1912 (E. C. VanDyke) [CAS].

Distribution. Mountains of northern California and south in the Sierra Nevada at least to Mariposa County.

Biology. The Mather series was sifted from conifer debris together with *Cerylon californicum*.

Philothermus occidentalis is not very closely related to its eastern congeners, as evidenced by the prosternal and mesosternal characters, as by the elongate parameres, which are extremely reduced in both *puberulus* and *glabriculus*.

Philothermus puberulus Schwarz
(Fig. 27)

Philothermus puberulus Schwarz, 1878: 361. Type locality: Tampa, Florida. Holotype, No. 4512 U.S.N.M.

This species is easily distinguished from *P. glabriculus* by the vestiture of numerous, long, erect hairs and the distinctly crenulate lateral pronotal margins. It is also smaller in size (1.6-1.9 mm.) and somewhat more elongate, with coarser and denser pronotal punctation.

Distribution. Georgia, Florida, and the Greater Antilles. Reported by Hinton (1936) from Mexico, Guatemala, and Panama.

Biology. Adults collected under bark of *Pinus* and in a berlese sample from a swamp floor.

The Neotropical distribution of this species must remain tentative until a complete revision is undertaken, since there appears to be a complex of tropical species related to *P. puberulus*. Specimens from Cuba, Puerto Rico, and Hispaniola appear to be conspecific with the Floridian population, but most of the specimens we have examined from Mexico and Central America are not the same species. Horn (1878) also reported this species from Arizona, but we have seen no specimens to verify this record.

Cerylcautomus Sen Gupta and Crowson

Cerylcautomus Sen Gupta and Crowson, 1973: 439-441. Type species, by original designation, *C. floridensis* Sen Gupta and Crowson.

This genus was based on a single Floridian species and several unnamed forms from Jamaica, Hispaniola, Puerto Rico, Trinidad, and British Guiana. All members of the genus have at least vaguely defined antennal cavities, similar to those in *Cautomus*, located laterally on the prosternum (not on the hypomera) and defining a median, raised, prosternal plate. In addition, the procoxal cavities are open

behind, the antennae are 10-segmented with an elongate, 1-segmented club, and the labrum is elongate and narrowed, or sometimes acute, at the apex.

Cerylcautomus floridensis Sen Gupta and Crowson

Cerylcautomus floridensis Sen Gupta and Crowson, 1973: 441, figs. 205-213. Type locality: Chaires, Leon Co., Florida. Holotype, Field Museum.

This species is easily distinguished from other North American cerylonines by the small size (less than 1.25 mm.) and elongate form, 10-segmented antennae with a 1-segmented club, prosternal antennal cavities, and acute labrum.

Distribution. Known only from northern Florida.

Biology. Recorded from an old sawdust pile (more than 20 years old) at the edge of a cypress swamp. Other members of the genus have been extracted with Berlese funnels from forest litter and rotten logs.

Lapethus Casey

Lapethus Casey, 1890: 317. Type species, by monotypy, *L. discretus* Casey.

Lytopeplus Sharp, 1895: 494. Type species, by monotypy, *L. compactus* Sharp.

Brachylon Gorham, 1898: 256. Type species, by monotypy, *B. breve* Gorham.

Lapecautomus Sen Gupta and Crowson, 1973: 409. Type species, by original designation, *L. dybasi* Sen Gupta and Crowson. New Synonymy.

Sharp originally placed *L. compactus* in a separate genus because of the widely separated pro- and mesocoxae and the coadaptation of the pro- and mesosternum. Hinton (1936) pointed out that the differences were only a matter of degree and that certain *Lapethus*, such as *L. sharpi* Champion, displayed an intermediate condition; on this basis he synonymized *Lytopeplus* with *Lapethus*. Sen Gupta and Crowson, however, recently resurrected *Lytopeplus*, stating that the only difference between species of the genus and those of *Lapethus* is the slight closure of the procoxal cavities in the former. After examining a number of lapethines from Mexico and Central America, we are of the opinion that the features diagnosing *Lytopeplus* represent a general trend towards compaction throughout the group, and that these compact forms are not necessarily members of a single phyletic line. Likewise, the condition represented in the three described

species of *Lapecautomus* — piercing beak with mandibular and maxillary stylets — is one which occurs throughout the subfamily in both larvae and adults, so that a group, even at the generic level which is defined on the basis of this feature alone, may well be polyphyletic. Within the genus *Lapethus* (in the broad sense), there is a general trend towards the elongation of the labrum, and in most forms examined it is somewhat elongate and deeply emarginate at the apex, as in *L. discretus* (fig. 12). In *Lapethus* (= *Lapecautomus*) *striatus*, the labrum is even more elongate than in *discretus*, but it is still emarginate at the tip (fig. 11). In *L. dybasi*, however, the apex is pointed. A similar trend may be found in the mandibles and maxillae. With respect to other characters not involved in the piercing apparatus, the three species presently included in *Lapecautomus* do not appear to be closely related and may well be derived from two or more stocks of typical *Lapethus*. *Lapecautomus mexicanus*, for instance, is a globose, highly convex form, which is almost impunctate and glabrous, and which has the type of pro- and mesosternum characteristic of a *Lytopeplus*. In contrast, *L. striatus* is more elongate and flattened, with distinctly seriate elytral punctation, erect vestiture, and a raised lateral pronotal margin; in all these respects it resembles the type of *Lapethus*, *L. discretus*. For these reasons, we recognize the single genus *Lapethus*, and we suggest that the evolution of compact, globose forms and forms with piercing mouthparts represent two independent trends occurring in more than one lineage.

The genus *Lapethus*, as here delimited, contains about 25 described species, and a number of undescribed forms have been seen, especially in the New World. The group is primarily tropical, and the North American species are restricted to humid areas along the Pacific coast and in the mountains of the Southeast.

Key to the North American *Lapethus*

1. Pronotal punctation very fine and sparse, the punctures usually separated by at least two diameters; eyes reduced consisting of about 10 facets; labrum slightly longer than broad at base; size smaller, TL less than 1.75 mm.; Great Smoky Mountains and vicinity. *striatus* (Sen Gupta and Crowson)
- Pronotal punctation coarser and denser, the punctures usually separated by less than a diameter; eyes normal, with more than 30 facets; labrum slightly shorter than broad at base; size larger, TL more than 1.75 m.; California. *discretus* Casey

Lapethus discretus Casey
(Fig. 28)

Lapethus discretus Casey, 1890: 318. Type locality: Near Humboldt Bay, Humboldt Co., California. Holotype, No. 48835 U.S.N.M.

This species is characterized by the oval, somewhat flattened form, reddish color, distinctly seriate elytral punctation, fine, erect hairs easily visible under 10× magnification, distinct lateral pronotal margins, 8-segmented antennae with a 1-segmented club, and large anterolateral antennal cavities on the underside of the pronotum. The procoxal cavities are fairly narrowly separated and distinctly open behind, while the prosternal process is parallel-sided and strongly rounded at apex. *Philothermus glabriculus* is superficially similar but more elongate and parallel sided, with different antennae and no antennal cavities. The species may be distinguished from the related *L. striatus* by the larger size (2.0-2.3 mm.), coarser and denser pronotal punctation, shorter labrum, and fully developed eyes and wings.

Distribution. Pacific Coast, from western Washington (King County) to central coastal California (Santa Cruz County) and the Sierra Nevada (Tuolumne and El Dorado Counties).

Biology. Collected in the Sierra Nevada by sifting rotten conifer logs in the red rot stage.

Lapethus striatus (Sen Gupta and Crowson), New Combination

Lapecautomus striatus Sen Gupta and Crowson, 1973: 412, fig. 178. Type locality: Below Ramsay Cascades, 3500', Great Smoky Mts. National Park, Sevier Co., Tennessee. Holotype, Field Museum.

This species is smaller than *L. discretus* (1.5-1.7 mm.), with the pronotum more finely and sparsely punctate, the eyes reduced to about 10 facets, and the wings completely absent. The labrum is also longer and narrower at the apex, and the mouthparts are more highly modified for piercing.

Distribution. Known only from the cove forests of the Great Smoky Mountains, Tennessee, and the nearby Joyce Kilmer Forest, North Carolina.

Biology. Adults have been collected in samples of leaf litter under *Rhododendron* and in mixed hardwood and *Tsuga* forest.

Cerylon Latreille

Cerylon Latreille, 1802: 228. Type species, by subsequent monotypy (Latreille, 1810: 431), *Lyctus histerooides* Fabricius.
Aphardion Gozis, 1886: 11.

This genus is distinguished by the broadly closed procoxal cavities and apically expanded prosternal process (fig. 10) and by the 10-segmented antennae with a 1-segmented club. In addition, the body is usually elongate and more or less parallel-sided, and the tegmen is reduced to a small ring at the base of the median lobe (figs. 13-14). Although the mouthparts in *Cerylon* are less modified than in *Philothermus* or *Lapethus*, the elongate, rigid body form, with complete posterior coxal closure, the extremely reduced tegmen, and the highly modified larval head all appear to be derived characters. There are about 75 species, but a number of them may have to be transferred to other genera with further study. The majority of species occur in the Holarctic, Ethiopian, and Oriental regions, while the group is poorly represented in the New World tropics and Australia. In North America, the genus is represented by two widely distributed, primarily northern and eastern species, and three western endemics.

Key to the North American *Cerylon*

1. Intercoxal process of mesosternum twice as wide as a mesocoxal cavity; prosternal process slightly concave; basal impressions of pronotum large and distinct; clypeus shallowly emarginate in both sexes; Arizona. *distans*, n. sp.
- Intercoxal process of mesosternum barely wider than a mesocoxal cavity; prosternal process flat or slightly convex; basal pronotal impressions obscure or absent. 2
2. Elytral vestiture distinct, easily visible at 10× magnification; size larger, length usually 3.0 mm. or more; elytral intervals flat or slightly convex; clypeus deeply notched in male; California. *californicum* Casey
- Elytral vestiture consisting of very short hairs, which are barely visible at 50× magnification; size smaller, length usually less than 2.7 mm. 3
3. Sides of pronotum (figs. 18-19) subparallel or slightly diverging for three-fifths of their lengths, strongly converging apically; antennal segment 3 more than 1.5 × as long as 4; body less elongate, TL/EW usually less than 2.42; clypeus shallowly emarginate in both sexes; widespread in the east and on the Pacific coast. *unicolor* (Ziegler)

- Sides of pronotum (figs. 16-17) slightly to strongly diverging for at least three-fourths of their lengths; antennal segment 3 less than $1.5 \times$ as long as 4; body more elongate, TL/EW 2.45 or more; clypeus deeply notched in male (fig. 15). 4
- 4. Sides of pronotum (fig. 17) strongly diverging for four-fifths of their lengths; elytral intervals flat; body usually smaller and more elongate (length usually less than 2.3 mm. and TL/EW greater than 2.50); northern part of continent. ... *castaneum* Say
- Sides of pronotum (fig. 16) slightly diverging for three-fourths of their lengths; elytral intervals convex; body usually larger and less elongate (length usually more than 2.3 mm. and TL/EW less than 2.50); Arizona and New Mexico. *conditum*, n. sp.

Cerylon californicum Casey

(Fig. 31)

Cerylon californicum Casey, 1890: 316. Type locality: Lake Tahoe, California. Holotype, No. 48834 U.S.N.M.

This is the most distinctive of the North American *Cerylon* because of its large size (3 mm. or more) and obvious vestiture. The body is also much stouter and more convex than in other species, although the elytral intervals are almost flat. It resembles *C. castaneum* and *C. conditum* in having a more elongate pronotum and deeply notched clypeus in the male, but both of those species are smaller, flatter, and subglabrous.

Distribution. Extending from southern Oregon into northern California and south in the Sierra Nevada to Tulare County.

Biology. Collected by sifting moist coniferous forest litter in July at medium elevation in the Sierra Nevada. *Philothermus occidentalis* was collected in this same habitat.

Cerylon castaneum Say

Cerylon castaneum Say, 1827: 259. Type locality: Canada. Neotype, ♂, No. 32238 M.C.Z. (designated by J. F. Lawrence, April, 1975).

Cerylon clypeale Casey, 1897: 636. Type locality: Kansas. Holotype, ♂, No. 48833 U.S.N.M. New Synonymy.

Cerylon sticticum Casey, 1897: 636. Type locality: Iowa City, Iowa. Holotype, ♀, No. 48832 U.S.N.M. New Synonymy.

Individuals of this species are the narrowest, flattest, and usually the smallest of the North American *Cerylon*. They may occur with *C. unicolor*, from which they may be distinguished by the apically expanded pronotum, elongate and flattened body, and deeply notched clypeus in the male (figs. 15 & 18).

Distribution. Northern and eastern North America, from south-eastern British Columbia and central Alberta to southern Quebec and Maine, and south to Texas and the Carolinas. More commonly collected in the northern part of the range.

Biology. Collected under bark of *Acer*, *Fagus*, and *Picea*, and in the following fungi: *Pleurotus* sp., *Fomes fomentarius*, *Phellinus igniarius*, and *Bjerkandera adusta*. Larvae collected in July in New Hampshire, under bark of hardwoods.

The name *Cerylon castaneus* has usually been associated with the species called *C. unicolor* in this paper, and in most collections these two names are confused, Casey's *clypeale* and *sticticum* being applied to specimens with expanded pronotum and notched clypeus. In Say's description, the point is made that the thorax is widely and slightly indented at base, each side of middle. This could refer to the basal narrowing of the pronotum, but it may also refer to discal impressions. Specimens under the name *castaneum* in the LeConte collection are definitely of the type with apically expanded pronotum and notched clypeus in the male, and we are considering this as Say's species. The first specimen in the series has an orange disc (referring to southern states) and it is a female. Two other specimens have faded discs, so that the locality is uncertain. A fourth specimen bears the label "Can." and is a male. Since the species is much more common in the northern part of the continent, we have chosen this last specimen as Neotype.

***Cerylon conditum*, New Species**

This species is in the size range of *C. distans*, but differs from that species by the more elongate pronotum, more approximate mesocoxae, and notched clypeus in the male. *Cerylon unicolor* is usually smaller, and less elongate, without the notched clypeus in the male, while *C. castaneum* differs in having the pronotum strongly expanded apically and the elytral intervals flat.

Description. Length 2.2-2.7 mm. Color dark reddish-brown; vestiture of very short, erect hairs, barely visible under 50 \times magnification. Antennae about 0.75 \times as long as pronotal width; segment 3 1.25 \times as long as 4; club 1.3 \times as long as wide. Clypeus slightly emarginate in ♀, deeply notched in ♂. Pronotum (fig. 16) 0.95 \times as long as wide, sides subparallel or slightly diverging, for basal three-fourths, converging apically to rounded angles; disc very slightly convex at middle, slightly sloping anterolaterally, with 2

broad and very shallow basal impressions; punctation relatively uniform, slightly finer at apex, punctures near center elongate, about $0.2 \times$ as long as scutellar base, and usually separated by less than a diameter; interstitial microsculpture distinct, consisting of longitudinal, sinuate rugulae. Scutellum finely granulate. Elytra about $1.67 \times$ as long as wide and $2.50 \times$ as long as pronotum, widest at anterior third; striae fairly deeply impressed, their punctures distinctly separated from one another; intervals moderately convex, shiny, and finely punctate. Prosternal process flat, about $1.5 \times$ as wide as a coxal diameter. Mesosternal process about $1.3 \times$ as wide as a coxal diameter, broadly rounded at apex. Metasternum $1.2 \times$ as long as first visible abdominal sternite. Aedeagus (fig. 13) about $0.8 \times$ as long as abdomen.

Types. Holotype, ♂, and allotype, ♀, Santa Catalina Mts., 8000', Pima Co., ARIZONA, June 16, 1968, under bark of conifer (K. Stephan) [No. 32240 M.C.Z.]. Paratypes: ARIZONA: Apache Co.; 1, Chuska Mts., 8500' Aug. 31, 1974, under bark of conifer (J. Lawrence, K. & B. Stephan) [KS]; 1, Springerville, Oct. 15, 1972 (K. Stephan) [KS]. Cochise Co.: 20, Chiricahua Mts., 8500', June 29, 1968, May 4, Aug. 3, 1969 (K. Stephan) [MCZ, KS]. Graham Co.: 12, Graham Mts., May 18, 1969 (K. Stephan) [KS]; 3, same 9200', Apr. 25, 1971 (K. Stephan) [KS]; 1, Hospital Flat, Mt. Graham, 9000', Aug. 6, 1949 (F. Werner and W. Nutting) [UAZ]. Pima Co.: 2, Santa Catalina Mts., 7000', May 5, 1968 (K. Stephan) [KS]; 44, same 8000', June 16, Sept. 7, Sept. 29, 1968, Apr. 12, 1969 (K. Stephan) [CAS, FM, MCZ, KS, USNM]; 1, same, Marshall Gulch, Aug. 1, 1959 (F. Werner) [UAZ]; 4, same, Mt. Bigelow, 8300', Aug. 11, 1968, under bark, (W. Suter) [WS]; 1, same, Aug. 27, 1974, under bark of conifer (J. Lawrence) [MCZ]; 4, same, Mt. Lemmon, May 16, June 13, 1970 (K. Stephan) [KS]. Santa Cruz Co.: 1, Santa Rita Mts., 6000', Dec. 8, 1968 (K. Stephen) [KS]. NEW MEXICO: San Miguel Co.: Las Vegas Hot Springs, 15.8 (Barber & Schwarz) [USNM].

Distribution. Mountains of Arizona and New Mexico, usually above 6000 ft.

Biology. Adults collected under the bark of conifer logs, especially those from which bark beetles have emerged. The beetles are usually found near the butt end in moist fungus-infested areas. Often taken in the same situations with *C. distans*.

***Cerylon distans*, New Species**

(Fig. 29)

The widely separated mesocoxal cavities will separate this species from all others in North America. In addition, the pronotum is much shorter and broader than in *C. conditum*, which also differs in having the clypeus notched in the male. The general form is similar to *C. unicolor*, in which the mesocoxae are more approximate, the size smaller, and the pronotal impressions shallower.

Description. Length 2.4-3.0 mm. Color dark reddish-brown to black; vestiture of very short, erect hairs, not visible under $50\times$ magnification. Antennae relatively short, about $0.6\times$ as long as pronotal width; segment 3 $1.4\times$ as long as 4; club only slightly longer than wide. Clypeus slightly to moderately emarginate, but never notched. Pronotum about $0.87\times$ as long as wide, sides subparallel for basal three-fourths, converging apically to rounded angles; disc moderately convex at middle, steeply sloping anterolaterally, with 2 broad and moderately deep basal impressions; punctuation variable, coarser at base than apex, punctures near center about $0.2\times$ as long as scutellar base and usually separated by less than a diameter; interstitial microsculpture very lightly impressed or absent, with scattered fine punctures. Scutellum transversely rugulose. Elytra about $1.6\times$ as long as wide and $2.35\times$ as long as pronotum, widest at middle; striae deeply impressed, their punctures elongate and subconfluent; intervals moderately convex, shiny, and finely punctate. Prosternal process slightly concave, about $1.8\times$ as wide as a coxal diameter. Mesosternal process $2\times$ as wide as a coxal diameter, truncate at apex. Metasternum $1.35\times$ as long as first visible abdominal sternite. Aedeagus (fig. 14) about $0.6\times$ as long as abdomen.

Types. Holotype, ♂, and allotype, ♀, Chiricahua Mts., 8500', Cochise Co., ARIZONA, May 4, 1969, under bark of conifer (K. Stephan) [No. 32241 M.C.Z.]. Paratypes: ARIZONA: Apache Co.: 3, Chuska Mts., 8500', Aug. 31, 1974, under bark of conifer (J. Lawrence, K. & B. Stephan) [KS, JL]. Cochise Co.: 24, Chiricahua Mts., Sept. 18, Aug. 6 (B. Malkin) [FM]; 1, same, June 23 (Hubbard & Schwarz) [USNM]; 3, same, July, 1936, from pine (E. S. Ross) [CAS]; 2, same, 5000', June 19, 1971 (K. Stephan) [KS]; 21, same, 8500', May 4, 1969 (K. Stephan) [FM, JL, USNM, KS]; 1, same, Aug. 3, 1969 (K. Stephan) [KS]; 1, Rustler Park, June 17, 1973, under bark (D. S. Chandler) [DSC]; 1, same, 8300', Sept. 16, 1962 (B. Malkin) [FM]; 8, same, 8400', June 13,

1956, pine (H. & A. Howden) [HH]; 8, Huachuca Mts., July (J. Knull) [OSU]. Coconino Co.: 3, Flagstaff, Hopk. U.S. 5007g,j, *Pinus ponderosa* (Webb) [USNM]; 1, same, July 7 (Barber & Schwarz) [USNM]; 1, Williams, May 27 (Barber & Schwarz) [USNM]; 1, same, (Hubbard & Schwarz) [USNM]; 3, same, (Wickham) [CAS, USNM]. Graham Co.: 16, Graham Mts., May 18, 1969, under bark of conifer (K. Stephan) [MCZ, KS]. Pima Co.: 1, Santa Catalina Mts., Sept. 26, 1907, Hopk. U.S. 5603g, *Pinus ponderosa* (J. L. Webb) [USNM]; 1, same, July 1, 1936 (E. S. Ross) [CAS]; 2, same, June 1, 1938 (Van Dyke) [CAS]; 8, same, 7000', May 12, 1968, under bark of conifer (K. Stephan) [KS]; 2, same, Apr. 5, 1969 (K. Stephan) [KS]; 23, same, 8000', May 12, May 23, Sept. 7, Oct. 20, Nov. 10, 1968, June 29, 1971 (K. Stephan) [KS]; 3, same, 8500', Oct. 4, 1971 (K. Stephan) [KS]; 9, same, Bear Canyon, Dec. 14, 1968, Jan. 25, Mar. 29, 1970 (K. Stephan) [KS]; 1, same, Bear Canyon, Mt. Lemmon Hwy., 6000', June 16, 1970 (D. S. Chandler) [DC]; 5, same, Mt. Lemmon, near Observatory, Mar. 1965, (M. L. Lindsey) [UAZ]; 11, same, Rose Canyon, Apr. 1965 (M. L. Lindsey) [UAZ]. Santa Cruz Co.: 1, Santa Rita Mts., 6000', Dec. 8, 1968 (K. Stephan) [KS]; 2, same, 7000', Apr. 20, 1969, under bark of conifer (K. Stephan) [KS].

Distribution. Mountains of Arizona, usually above 5000 ft.

Biology. Collected in the same situations as *C. conditum*, under the bark of old conifer logs, usually in moist, fungus-infested areas of the cambium.

Cerylon unicolor (Ziegler)

(Fig. 30)

Latridius unicolor Ziegler, 1845: 270. Type locality: Carolina. Holotype, ♀, No. 6825 M.C.Z.

Cerylon angustulum LeConte, 1863: 69. Type locality: Georgia Lectotype, ♂, No. 6824 M.C.Z. (designated by J. F. Lawrence, April, 1975). New Synonymy.

Cerylon simplex LeConte, 1857: 39. Type locality: San Jose, California. Lectotype, ♂, No. 6826 M.C.Z. (designated by J. F. Lawrence, April, 1975). New Synonymy.

Cerylon sylvaticum Casey, 1897: 635. Type locality: Coeur d'Elene, Idaho. Holotype, No. 48821 U.S.N.M. New Synonymy.

This is the most commonly collected *Cerylon* in eastern North America and on the Pacific Coast. It may be distinguished from *C. castaneum*, with which it is sympatric throughout much of its range, by the shape of the pronotum, the slightly emarginate clypeus

in the male, and the less flattened form. *Cerylon distans* is larger, with more widely separated mesocoxae, while *C. conditum* is usually larger and more elongate, with a notched clypeus in the male. In California, this species is easily distinguished from *C. californicum* by the much smaller size, less distinct vestiture, and less robust form. *Cerylon unicolor* is the only species in which there appears to be pronounced sexual dimorphism in prothoracic shape, the sides in the female being parallel basally and convergent apically, while those in the male are slightly divergent at the base (figs. 18-19).

Distribution. Northern and eastern North America and the Pacific Coast. Extending from southern British Columbia, south through Washington, Oregon, Idaho, and California as far as Los Angeles County on the coast and Fresno County in the Sierra Nevada; east across southern Canada and the northern United States to southern Ontario and Maine; south on the Atlantic Coast to northern Florida, and west to the 100th meridian.

Biology. Adults collected under the bark of *Carya*, *Fagus*, *Liriodendron*, *Picea*, *Pinus*, *Platanus*, *Populus*, *Liquidambar*, *Salix*, and *Tsuga*. Also in rotten logs, leaf mold, at sap, in an ear of corn, at light, at malt traps, and in various fungi, including *Phellinus gilvus* and *Bjerkandera adusta*. Larvae found under bark of hardwood logs in Arkansas.

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STATUS OF THE GENERA
UNGLA AND *MALLADA* NAVÁS*
(NEUROPTERA: CHRYSOPIDAE)

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This paper is the first in a series treating results of an examination of Navás material in several museums, and deals with two genera whose status has been problematical. One of these proves to be a striking example of a composite specimen, or "humbug".

A recent trend in chrysopid systematics is toward division of the genus *Chrysopa*, based primarily upon characters of the male genitalia. It appears that despite conservatism in wing and body characters, the genitalic structures exhibit considerable divergence. Furthermore, non-genitalic characters are by no means absent; for example, I estimate that at least 80% of the species of *Suarius* can be assigned to that genus on the basis of these characters, as discussed below. A problem arises from the plasticity of the genitalic structures. The principal generic criterion is the particular combination of tignum, gonosaccus, pseudopenis, or gonapsis present (plus whatever venational and female genitalic characters may be available). Any of these structures appears subject to reduction or loss by species within a taxon, with consequent high probability of erroneous assignment. Until a better understanding of evolutionary trends is achieved and additional characters are found, a period of nomenclatorial instability is to be expected. In my view, the inconvenience and confusion thus inevitably generated is amply justified by the pressing need to subdivide the genus *Chrysopa*, in which most species reside, into workably small fragments.

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Genus *Suarius* Navás 1914a: 73

=*Ungla* Navás 1914b: 224. New synonymy (subjective); type species, *U. annulata* Navás (by original designation).

Suarius is regarded as a distinct genus by Hölzel, 1970. Frequently species can be assigned here without reference to genitalic structures, on the basis of some combination of a series of rather variable characters: short pronotum with arcuate anterior margin, tarsal claws with a very wide notch and small basal expansion, short body and wing setae, coloration often predominately brownish, blackish, or yellowish, costal margin often narrow. Usually the zig-zagging of veins comprising pseudomedia not strong, so that 2 or 3 sections of psm consist of crossveins and the apical pseudo-medial veins (apparent crossveins) are strongly inclined (Fig. 1A). Basal inner gradate crossvein ends on psm in the hind wing at least, in nearly all New World species. Frequently, enough of these characters are present to result in a distinctive habitus, reminiscent of a *Pimachrysa* or small *Nodita*.

The male genitalia consist of gonarcus, with mediuncus (=arcesus), gonocoxites (=entoprocessi), frequently with gonosetae and gonocristae, never with gonopsis or tignum; eighth and ninth sternites fused, microtholi occasionally present. The condition of media and generalized male genitalia preclude derivation of this genus from *Chrysopa* s. str. or *Mallada*.

Ungla was based upon *U. annulata* Navás, known from a single specimen, and distinguished by its unusual foreleg. Navás states (translation mine), "The peculiar form of the anterior leg with long and thin tibial spurs and claws, a thing which is not seen in any other genus of chrysopids; the same with the elongate tarsus, is characteristic of this new genus". N. Banks' card file (unpublished) contains a note which succinctly expresses the suspicion long shared by me and others: "leg of a myrmeleontid". The type specimen indeed proves to be a *Suarius argentinus* with a single grotesquely oversized myrmeleontid leg loosely clasped among its own, undoubtedly acquired during the final struggle in the killing bottle. As the genus *Ungla* was based upon the composite nature of the unique specimen of the type species, the name must be rejected under the provisions of Article 1 of the International Code. Furthermore, *Suarius* was published earlier and has priority. According to C. Courtoy (pers. comm.) the number of the "Annales de la Société scientifique de Bruxelles" containing the description of *Suarius* was published either in December 1913 or January 1914; the entire

volume was published prior to August 1914. *Ungla* was not published until October 1914.

This common species proves to have several synonyms:

Suarius argentinus (Navás) 1911, new combination

Figure 1

Hypochrysa argentina Navás 1911: 267, "Chaco de Santiago del Estero, Bords du Río Salado, Env. d' Icaño, E.-R. Wagner 1903, September. *Hypochrysa argentina* Nav." Tjeder's lectotype label is also present. Female, in Paris Museum (examined).

Synonyms:

Chrysofa argentina, Tjeder 1971: 112 (lectotype designation, re-description).

Ungla annulata Navás 1914b: 224. New synonymy. "Huasan (R.A.), 11-1912, *Ungla annulata* Nav., Navás S. J. det., Typus." Female, in Navás collection, Colegio del Salvador, Zaragoza, Spain (examined).

Chrysofa graciana Navás 1919: 301, 1927: 21. New provisional synonymy. "Alta Gracia, II-918, Bruch, *C. lanata* v. *graciana*." Male, in the Museum de la Plata, Buenos Aires (seen). Although careful examination of the type was not possible, two females in the Paris Museum identified by Navás, and from the same locality, are *S. argentinus*.

REDESCRIPTION

Head markings variable. Clypeus often black-bordered; genae with dark mark varying from brown dot to black extending from eye to mandibular articulation and anterior tentorial pit. A brown X-mark between antennae; anterior forks often separate or absent; posterior portion borders antennal fossae. Red-brown vertex stripes appear continuation of X mark posteriorly, but include hypodermal red. Dorsal antennal fossa with transverse punctate red-brown mark; may extend over entire space, often absent. Scape with lateral brown stripe and dorsal mark, which may be apical spot or wide diffuse stripe which extends partially or entirely to base of scape, or is absent. Pedicel dark-annulate, flagellum pale or light brown. Palpi tan or black, pale at joints.

Male genitalia. Ectoprocts short (Fig. 1B), broad, rounded, without apodeme hinged on 8+9 sternite. Apex of sternite 8+9 rounded, about half as wide as base of sternite 8, with normal setae at posterior margin; no microtholi. Gonarcus (Fig. 1C,D) broadly arcuate, with lateral blunt spinose entoprocessus; mediuncus lightly sclerotized, with blunt tip. Gonosaccus double, with stout, pale, hollow setae. Gonocristae absent.

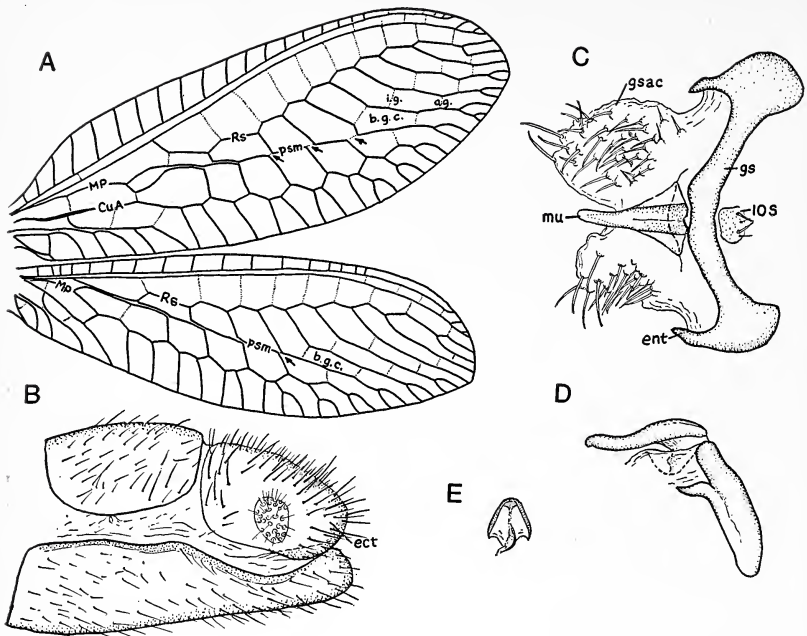


Figure 1. *Suaris argentinus*. A. Wing venation, showing portions of pseudomedia consisting of crossveins (arrows) and inner gradate series ending on a branch of Rs in the forewing, on psm in the hindwing. Crossveins in discal area of wing indicated by dots; overlap of veins forming psm shown by double lines. Male genitalia: B, apex of abdomen, lateral; G, gonarcus and mediuncus, dorsal, gonosaccus everted; D, same, lateral; E, hypandrium internum.

Abbreviations: bgc — basal gradate cell, CuA — cubitus anterior, ect — ectoproct, ent — entoprocessus, ig — inner gradate crossvein, gs — gonarcus, gsac — gonosaccus, MA — media anterior, MP — media posterior, mu — mediuncus, o.g. — outer gradate crossveins, 10S — tenth sternite.

Female genitalia (see Tjeder, 1971). Seminal bursa small, opening ventrally directly into the spermatheca; bursal glands slender, dorsal.

This species is recognizable by the heavy wing veins, alternately black and white, conspicuous crossveins beneath stigma, and head markings. The short ectoprocts, without hinge, are unusual, but also occur in *S. squamosus* (Tjeder) from Africa, *S. confraternus* (Banks) 1913 n. comb. (*Chrysopa*), from Argentina, and several undescribed species. The type of *U. annulata* differs slightly from that of *S. argentinus* in having the stigmas opaque pale yellow (probably an artifact of preservation) and having an irregular longitudinal dark stripe in the dorsal antennal fossa. *C. venulosa* Navás 1918 and *C. nervulosa* Navás 1924 are probably *S. argentinus*; I have not seen the types.

Material examined — the following are in my collection: R. Argentina, Santiago del Estero: Choya, Oct.-Nov. 1961, 13 females, 3 males; Fernandez, Feb. 1957, 11 females, 2 males; El Pinto, Dec. 1956, 2 females. La Rioja: Patquía, 600m., Dec. 1957, 1 female, 2 males.

Genus *Mallada* Navás 1925:24

Mallada basalis is conspicuously dimorphic sexually, the males having heavy elongate stigmas, and Sc and Rs fused in the hindwing. These features were noted by Navás, who based his genus *Mallada* upon the thickening of the stigmas. The type species of *Mallada*, by original designation, *M. stigmatus*, is a synonym of *M. basalis*. The type species of *Anisochrysa*, *A. paradoxa*, was also synonymized with *M. basalis* by Adams (1959: 25). *Anisochrysa* is therefore a junior objective synonym of *Mallada*.

Most species of *Mallada* can tentatively be assigned by venational characters. The inner gradate series in larger species with numerous veins extends basad parallel to psm, hence does not converge on psm, and the basal inner gradate crossvein does not end on psm, but on a branch of Rs, resulting in a y-formation. A similar configuration, as shown in Fig. 1A, forewing, occurs also in other genera such as *Suaris*, but is rare in *Chrysoperla* and *Chrysopa*, s. str. Psm in *Mallada* only very infrequently includes a crossvein (the only example of which I am aware is *M. venosellus* (Tjeder 1966, Fig. 1643), but commonly includes 1 to 3 crossveins in *Suaris*.

Mallada, named after the Spanish naturalist, D. Lucas Mallada, is masculine, necessitating changes in many terminations. It con-

tains numerous Old World species (Tjeder, 1966, Hölzel, 1970) but is not so important in the New World, where it is represented in North America by *M. perfectus* (Banks, 1895), (*Chrysopa*), n. comb., *M. luctuosus* (Banks, 1911), (*Chrysopa*), n. comb., and two undescribed species.

Navás referred *M. stigmatus*, *delmasinus* and *verticalis* to this genus. Their synonymy follows.

Mallada basalis (Walker), new combination

Chrysopa basalis Walker 1853: 239.

Synonyms:

Anisochrysa paradoxa Nakahara 1955: 145; Adams 1959:25.

Mallada stigmatus Navás 1925:24; Banks 1937:285. New synonymy.

Type: "Formosa, Taihorin, III-10. H. Sauter S.G. *Mallada stigmatus* Nav., P. Navás S.J. det., Type." Male, Berlin Museum (examined).

Mallada delmasinus Navás 1935:57; Esben-Petersen 1937: 57. New synonymy. Type: "Museum Paris, Iles Marquises, P. Simeon Delmas 1924, *Mallada delmasinus* Nav., Navás S.J. det., Type", male. Eleven additional specimens with the same data in Paris Museum (examined).

It is interesting that in 1927 Navás noted the sexual dimorphism in describing *C. delmasi* (female) and *C. delmasi* var. *densata* (male) from precisely the same locality and collector as material of *M. delmasinus*; the former species was synonymized with *M. basalis* by Esben-Petersen in 1937.

Another new synonym of *M. basalis* is *C. jolyana* Navás 1910: 194. The type, in the Paris Museum, is labeled "Port Sandwich, Nouv-Hebrides, Ile Maillicols, Dr. Joly 1903"; "*Chrysopa jolyana* Nav. (in Navás' hand)". It is a teneral female; the specimen I described (Adams 1959:27) is male, with the incompletely developed sclerotization of the genitalia typical of teneral specimens.

Suaris figuralis (Banks), new combination

Chrysopa figuralis Banks 1915: 626. Type: "Chosica, Peru 2800'. 10-VI, Parish, col." Mus. Comp. Zool., Harvard, Type 11984. male (examined).

Synonym:

Mallada verticalis Navás 1929: 19. New synonymy. Type: "Museum Paris, Perou Merid., Arequipa, Dr. E. Escomel 1922, *Mallada verticalis* Nav., P. Navás S. J. det., type" (examined). A single faded and wrinkled female, probably from alcohol, appears the same as the relatively common *S. figuralis*. Probably the specimen was assigned to *Mallada* because the stigma has been rendered opaque by preservation.

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ONTOGENY OF DISPLAY IN IMMATURE
SCHIZOCOSA CRASSIPES (ARANEAE: LYCOSIDAE)

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Most studies dealing broadly with behavioral ontogeny in spiders have been concerned with orb-weaving (Witt and Baum, 1960; LeGuelte, 1969; Peters, 1969; Reed, Witt, Scarboro and Peakall, 1970). However, relatively little attention has been directed to the ontogeny of display. Immature lycosid spiderlings do not exhibit the complex stereotyped displays typical of adult wolf spiders during courtship (Rovner, 1968) or agonistic encounters (Aspey, 1974, 1975). Crane (1949) reported that several species of immature salticid spiders occasionally performed abortive displays, but she considered such displays exceptions to the rule. Rovner (1968) looked unsuccessfully for courtship display in penultimate male *Lycosa rabida*; the tendency to court did not appear until several days after the final molt. The first study of display ontogeny in spiders was that of Dijkstra (1968, in Koomans et al., 1974), which was expanded by Koomans, van der Ploeg and Dijkstra (1974) who observed a characteristic "leg wave behavior" in a variety of sub-adult *Pardosa* spp. This behavior was observed from the second instar to the adult molt in *P. lugubris* and *P. nigriceps*, and decreased in frequency with concomitant increases in courtship.

In considering the functional significance of leg wave behavior, Koomans et al. (1974) suggested that courtship replaced the behavior in adult males, while in adult females, the behavior was probably replaced by specific reactions to courtship. Dijkstra (1968, in Koomans et al., 1974) observed similar leg movements in juvenile *P. amentata*, but the behavior was not restricted to courtship situations. Van der Ploeg (personal communication) has observed leg waving in immature *P. purbeckensis* in the field. Similarly, I had observed (Aspey, 1974) that both male and female *Schizocosa crassipes* (Walckenaer) exhibit a characteristic leg wave display as juveniles.

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In extending the generality of leg waving display among immature lycosids, this study describes the ontogeny of leg wave display among immature *S. crassipes* and suggests a biological significance for the behavior.

METHODS

The subjects were 64 immature *S. crassipes*. Thirty-two spiders (16 males and 16 females) were collected during early May, 1971-73, as antepen- or penultimate instars from Stroud's Run State Park, Athens Co., Ohio, USA. The remaining spiderlings were reared from laboratory-mated adults. These spiderlings were observed from egg case emergence (considered the second instar) until approximately 1 wk after dispersal from the female. For most spiderlings, one additional molt (to the third instar) occurred in the laboratory, but too few animals survived beyond this time to continue observations. However, observations continued until the final molt for those spiders collected as antepen- and penultimate instars in the field. Data are reported only for those individuals for whom sex was correctly established at the antepen- or penultimate instars.

Six antepen- and penultimate spiderlings of each sex collected from the natural habitat and 12 laboratory-maintained spiderlings were isolated in covered clear plastic containers ($12.5 \times 7.0 \times 7.0$ cm). One-half of these spiders were visually isolated, while the remaining containers were adjacent and allowed the spiders visual access to one another. Ten antepen- and penultimate spiderlings of each sex collected from the field were socially housed (sexes separate) in glass terraria ($26 \times 19 \times 22$ cm) fitted with plastic covers.

Two groups of laboratory-maintained spiderlings (10 per group) were observed during their second and third instars. In order to observe these animals under the above conditions, spiderlings were brushed off the female's abdomen with a camel hair brush. Ten individuals were then placed in an observation chamber identical to the one in which socially grouped antepen- and penultimate instars were maintained. At the conclusion of each observation period the spiderlings were returned to the female and allowed to regroup. After dispersal from the female began, two groups of 10 individuals were transferred to separate observation chambers until the third instar, at which age observations were terminated.

The frequency (i.e., bouts per 30 min) and duration of leg waving were recorded for 30 min daily with a manually activated Ester-

line-Angus event recorder (chart speed of 15.2 cm/min). Total observation time varied according to whether the subject reached sexual maturity or died at a previous instar. The temporal patterning of leg waving from six laboratory-maintained spiders during the antepen- and penultimate instars was also recorded. Protocol was whispered into the microphone of a tape recorder. These recording instruments were placed on a separate table from the observation chambers to minimize the effects of machine vibration.

Vestigial-winged *Drosophila melanogaster* were offered as food to each spiderling once weekly, and a constant water supply was available. The spiderlings were maintained and observed under relatively constant temperature (22-26°C) and humidity conditions (55-62% RH).

RESULTS

Leg waving display in immature *S. crassipes* consisted of the simultaneous raising and lowering of the first and second ipsilateral legs. Leg waving was generally performed at a steady and smooth rate, and not alternated from side to side during a leg waving bout. Spiderlings showed no preference for either the right or left side during leg waving. Although leg waving occurred nearly as often per 30 min during all instars, no consistent temporal patterning was evident until the antepen- and penultimate instars, at which time leg waving became increasingly stereotyped and sexually differentiated.

Leg waving was observed only five times in the 24 socially isolated spiderlings. Four of these instances were limited to those spiders having visual access to one another, while only one visually isolated spiderling exhibited leg waving. The five observations of leg waving occurred in females once each at the second, third, and antepenultimate instars, and in males twice during the penultimate instar.

Although leg waving was rarely observed in socially isolated spiderlings regardless of age or sex, socially grouped spiderlings of both sexes at all the developmental stages studied exhibited leg waving. With regard to the frequency of leg waving as a function of age, no differences were evident in the average frequency of leg waving/30 min among the four developmental stages (second instar: 19.7 ± 9.6 SD; third instar: 21.2 ± 6.3 SD; antepenultimate instar: 19.8 ± 5.1 SD; penultimate instar: 22.2 ± 6.7 SD). Considering

leg waving as a function of sex, antepen- and penultimate males exhibited higher average frequencies of leg waving/30 min (27.2 ± 7.0 SD) than females (12.4 ± 4.0 SD) (Mann-Whitney $U = 18, p < 0.02$).

Of the 10 males and 10 females collected from the natural habitat and grouped separately by sex, nine males and four females reached sexual maturity. Cannibalism among these spiders was directly observed on two occasions; the remaining deaths may have been due to other causes. In the two groups of 10 laboratory-maintained juveniles, two individuals from each group reached the fourth instar. Among these spiders cannibalism was also directly observed on two occasions.

Among socially grouped antepen- and penultimate males, bouts of leg waving lasted an average of 7.3 ± 2.1 (SD) sec, and consisted of the legs being waved 3-27 times ($\bar{x} \pm$ SD: 16.0 ± 4.7) in succession at a rate of approximately 2 waves/sec. With increasing age, film analysis revealed that the foreleg was lifted higher off the substratum (20 - 25° in the second and third instars) until an arc 40 - 50° relative to the substratum was reached in the antepen- and penultimate instars. The second ipsilateral leg that accompanied the foreleg during leg waving was lifted only 5 - 25° relative to the substratum. The legs were raised and lowered almost simultaneously, with the foreleg occasionally leading.

Among socially grouped antepen- and penultimate females, bouts of leg waving lasted an average of 4.1 ± 2.0 sec, and consisted of the legs being waved 1-10 times ($\bar{x} \pm$ SD: 3.0 ± 2.2) in succession at a rate of approximately 1 wave/sec. Although females exhibited leg waving more slowly and less frequently than males, the behavioral topology of leg waving was indistinguishable between the sexes. Bouts of leg waving alternated with variable periods of immobility or locomotion, and depended on the behavior of conspecifics.

The circumstances under which leg waving occurred did not seem to change with age. A spiderling initiated leg waving in response to a darting front approach by a conspecific when it approached to within two or three body lengths. In response to one or several bouts of leg waving, the approaching spider turned away and/or retreated. On the four occasions when cannibalism was observed, the cannibalized spiderling was approached from the posterior; leg waving was not observed to occur in response to these posterior approaches.

DISCUSSION

Observations on the ontogeny of display in *S. crassipes* provide an interesting contrast with those of Koomans et al. (1974) for *Pardosa* spp., although certain similarities exist. For example, in both sexes of the *Pardosa* species, the pattern of leg wave behavior was generally the same at all developmental stages, with the frequency decreasing rapidly at the adult molt. In *S. crassipes* leg waving patterns become increasingly stereotyped with age, but the frequency did not vary with age or decrease as the final molt neared. Blinded *Pardosa* showed relatively little leg wave behavior, similar to the lack of leg waving exhibited by socially isolated *S. crassipes*. Although both sexes of *Pardosa* spp. and *S. crassipes* exhibited leg waving, antepen- and penultimate male *S. crassipes* displayed significantly more than females. Of further interest were the findings that bouts of leg waving by males lasted longer and consisted of more waves than those exhibited by females. These findings, coupled with the observation that more males than females reached sexual maturity among socially grouped spiderlings, suggested that leg waving serves a communication function that becomes more sexually differentiated with age. This idea is consistent with Aspey's (in preparation "a," "b," "c") research that only adult males exhibit the highly complex agonistic display which serves to maintain dominance-subordination relations and preserve inter-individual distances.

The decrease in leg wave behavior concurrent with increased courtship by adult male *P. lugubris* and *P. nigriceps* suggested to Koomans et al. (1974) that the behavior was replaced by courtship. Analogously, leg wave behavior in adult females could be replaced by specific reactions to courtship. In immature *S. crassipes* leg waving may be homologous with the similar ipsilateral Prolonged Wave in adult males (Aspey, 1974, in preparation "a"). Although Prolonged Wave occurred infrequently in adults relative to the frequency of immature leg waving among socially grouped spiderlings, both behaviors occurred under similar circumstances (i.e., one spider approaching another from the front). These behaviors seemed to have similar behavioral consequences, that of increasing distance between two individuals and thwarting approaching conspecifics.

Koomans et al. (1974) suggested that since leg wave behavior is similar in most *Pardosa* species observed, it may serve as a signal in agonistic encounters between individuals of different sympatric species, as well as between conspecifics. Just as one of the functions of courtship is the suppression of predatory tendencies, experimentally

demonstrated in jumping spiders by Drees (1952), a similar inhibition of agonistic responses may also be the role of leg wave behavior.

Leg waving probably is a mechanism to space spiders living in dense populations; this would minimize cannibalism and competition for food supplies. Observations on immatures and adults support this idea. The only occasions during which observed cannibalism occurred among immatures was during a posterior approach when leg waving did not occur. The probability of cannibalism is likely minimized during a face-to-face encounter when the approached spider exhibits leg waving, and the approaching spider subsequently retreats.

Although immature *S. crassipes* exhibit the various locomotory and contact behaviors of reproductively mature adults (Aspey, 1974, in preparation "a"), adult-like foreleg movements and postures are not observed until sexual maturity. The complex, stereotyped agonistic display of adult male *S. crassipes* serves to determine dominance-subordinance relations (Aspey, in preparation "b"), as well as space the animals according to a specific inter-individual personal distance (Aspey, in preparation "c"). The prominent tibial brushes of adult males, coupled with foreleg movements, probably serve as visual signals to indicate the presence of male conspecifics. However, with immatures, tibial brushes are lacking, and leg waving is probably the only visual signal available; it may serve a generalized spacing function for immatures of both sexes until the various adult behaviors develop. Thus immature leg waving may be considered a mechanism to space spiderlings, with the added consequence that cannibalism is minimized and spiders are selected against that do not exhibit and/or respond appropriately to leg waving.

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DESCRIPTION OF THE DEVELOPMENTAL STAGES
OF THE MITE PREDATOR, *OLIGOTA OVIFORMIS*
CASEY, WITH NOTES ON THE OSMETERIUM
AND ITS GLANDS (COLEOPTERA: STAPHYLINIDAE)

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Oligota oviformis was described by Casey in 1893. Quayle (1912, 1913) called attention to the fact that both larvae and adults were predaceous on spider mites and consequently beneficial in orchards where mites were a pest. Quayle partially outlined the life history of *O. oviformis* but was unable to induce pupation. Ewing (1914) and Essig (1926) reviewed Quayle's work. Badgley and Fleschner (1956) were able to induce pupation by providing a floor of sand in which pupation took place. However, little detailed description of the early stages was provided. A brief account of the osmeterium of the larva and its protective opercula was given by Badgley and Fleschner. The osmeterium is of particular interest as its occurrence appears to be widespread among the Aleocharinae, although it has been misinterpreted (Badgley and Fleschner, 1956).

Larva of *Oligota oviformis* Casey

Length 2.1 mm (mature larva). Body elongate, subcylindrical, tapered at each end; integuments soft, not chitinized, without distinct sclerites; pale testaceous with the opercula of the osmeterium piceous, darkest along the posterior margin of eighth tergite, osmeterium bright orange. *Head* oval, about as wide as long, with a single ocellus on each side behind the antennal fossae. Epicranial suture absent. Antennal fossae located at sides of head outside the bases of the mandibles. Antennae three-segmented; first segment about as long as wide; second segment narrower than first, a little more than twice as long as wide, with two long setae near the middle and a modified "acorn seta" without obvious articulation at base; third segment about half as wide as second and a little more than twice as wide, with two long setae at apical third and a shorter

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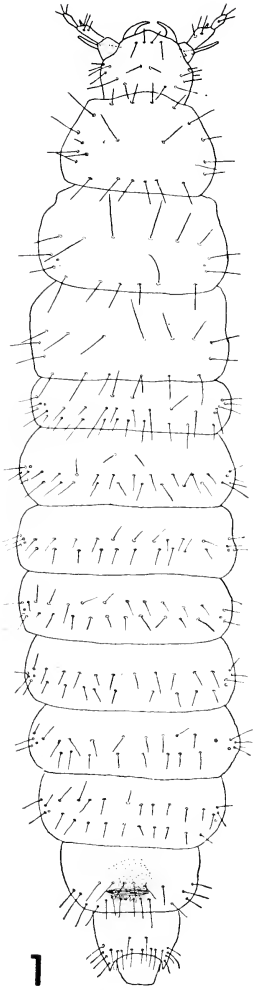
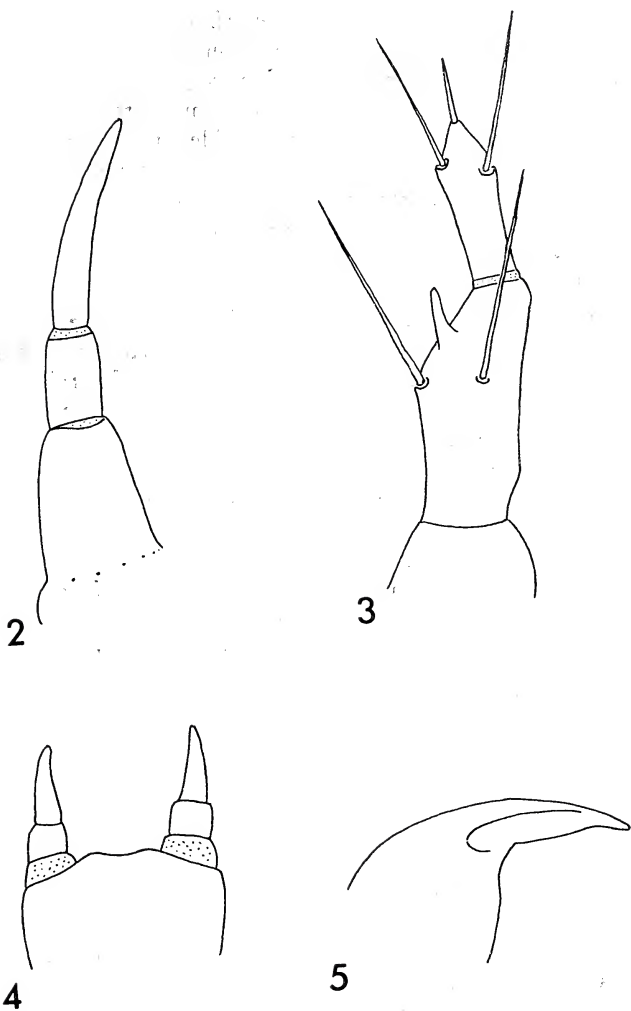


Figure 1. *Oligota oviformis*. Larva, dorsal aspect.



Figures 2-5. *Oligota oviformis*, larva. Fig. 2, maxillary palpus. Fig. 3, antenna. Fig. 4, labium. Fig. 5, right mandible.

stout seta at pointed apex. Mandibles simple, stout at base, narrowed in apical two-fifths, arcuate externally, pointed at apex. Maxillary palpus three-segmented; first segment somewhat longer than wide, narrowed to apex; second segment a little narrower than apex of first, almost twice as long as wide, nearly parallel sided; third segment narrower at base than apex of second, almost four times as long as wide, gently arcuate, gradually pointed to apex. Labial palpus two-segmented; first segment about as long as wide; second segment narrower than first, a little more than twice as long as wide, slightly arcuate, gradually narrowed and pointed to apex. *Pronotum* wider than head, narrowed in front, wider than long, with a row of four setae along front margin, a pair of setae on disc, four setae along lateral margin, two setae in sub-lateral series and six setae along posterior margin. *Mesonotum* about as long and a little wider than pronotum, with no setae at anterior margin, six transversely arranged on disc, two in the lateral series and six in the basal series. *Metanotum* about the same size and shape as mesonotum with chaetotaxy the same. *Abdomen*. First abdominal segment about as wide as metanotum and half as long as metanotum; without setae at anterior margin; with two transverse rows of discal setae, the first of two setae and the second of ten setae, with ten setae along the posterior margin and three or four irregularly placed setae at each side. Second abdominal segment about as wide as first and almost as long as metanotum; with setae arranged almost as on first segment except the setae are moved forward so that there are two discal series of eight setae each and none along the posterior margin. Third through seventh segments very similar in all respects to second except the seventh is narrower than the sixth and the two anterior setae are lacking on all but the first two segments. Eighth segment narrower than seventh but about as long; with two dark conjointly oval opercula in the middle near the posterior margin, divided longitudinally so that the anterior operculum is the largest; with chaetotaxy as on seventh segment. Ninth segment narrower than eighth, about as long as wide; with two discal setae and about eight or ten setae along the posterior margin; the outer apical angle produced on each side in a pointed fleshy urogomphus which apparently has no basal articulation and is unsegmented. Pseudopod produced between and beyond urogomphi. Spiracles present at the outer margins of the mesothorax and the first seven abdominal segments with much the appearance of empty hair follicles.

Three specimens, Carlsbad, San Diego County, California, 17 September 1970, on avocado leaves, Horace G. Johnson collector.

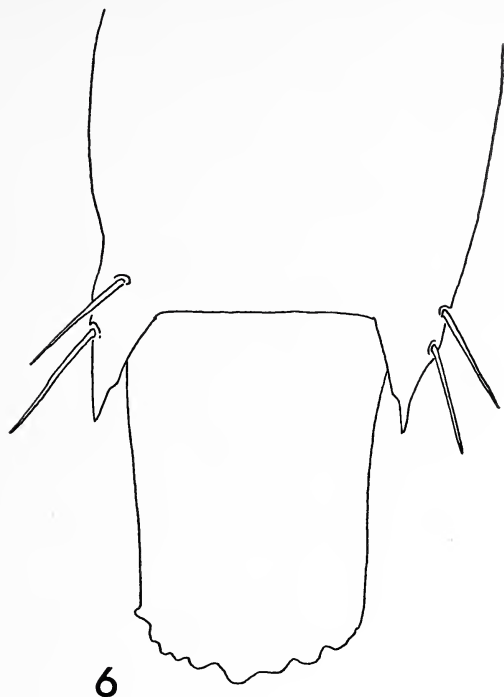


Figure 6. *Oligota oviformis*, larva. Pseudopod and urogomphi.

The larva of *Oligota oviformis* is similar to that of *O. flavicornis* Boisduval and Lacordaire as described and illustrated by Paulian (1941). The two species differ in that in *O. oviformis* the "acorn seta" of the second antennomere is almost as long as the third segment and has no distinct articulation at its base whereas Paulian's illustration of *O. flavicornis* shows two very small "acorn setae" with distinct articulations at the base. In *O. oviformis* the urogomphus is an extension of the eighth segment without articulation or segmentation. In *O. flavicornis* it is distinctly two-segmented.

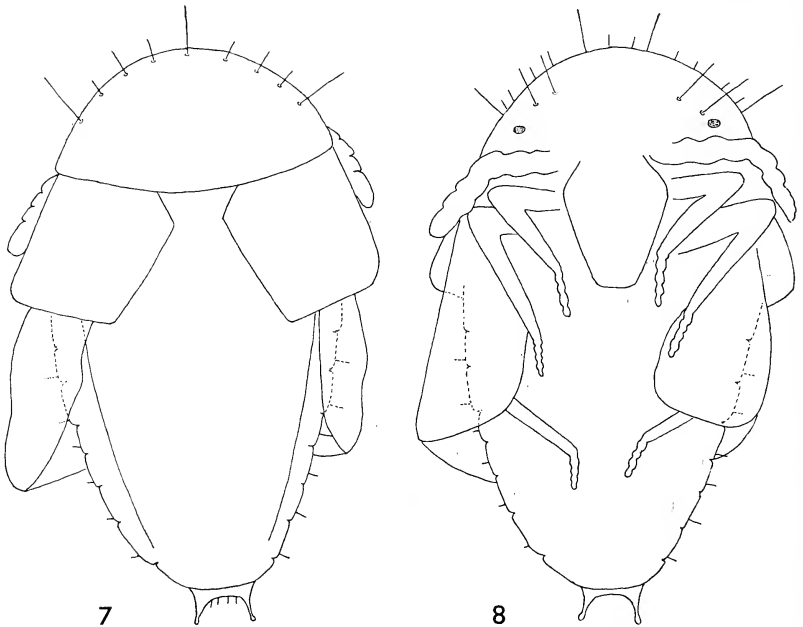
Pupation takes place in a cocoon in which the pupa is quite loose. The cocoon is formed of sheets of silk to which grains of sand adhere. In one instance the cocoon was formed in part of several sheets of silk extending like short walls perpendicular to the axis of the pupa.

Pupa of *Oligota oviformis* Casey

Pupa exarate, pale yellow, ovoid, about one and one-half times as long as wide, not chitinized in any part, without tubercles. Head ventrally reflexed so that none of it is visible from above; with a single dark eye spot on each side; with two long setae above each eye spot. Pronotum hemispherical, wider than long; with a row of setae along the anterior margin, the two outer and the middle setae distinctly longer than the other six. Elytra each about as long as wide, about as long as pronotum, with outer apical angles broadly rounded and inner apical angles narrowly rounded. Wings as seen from below almost twice as long as elytra. Abdomen apparently eight-segmented as viewed along the side margins of the paratergites; segmentation of tergites and sternites indistinct; segments two through seven each with a short seta on each side of side margin; eighth segment with a diaphanous bidentate process at apex each tooth of which is swollen at tip.

Three specimens reared from larvae collected at Riverside, Riverside County, California, 22 April 1975, lemon leaves, Ian Moore collector.

This is the first description of a pupa of a member of this genus.



Figures 7 and 8. *Oligota oviformis*, pupa. Fig. 7, dorsal aspect. Fig. 8, ventral aspect.

The Osmeterium

The eighth abdominal tergite of many larvae of the subfamily Aleocharinae bears in its center near the posterior margin a dark tumid area of distinctive texture which has usually been called a gland. Paulian (1941) referred to it as a silk gland. Badgley and Fleschner (1956) disclosed that in *O. oviformis* it is a cover for an osmeterium. They stated, "This black spot consists of two heavily pigmented, chitinized plates, with a transverse slit between them. The plates appear to act as a protection for an inner bladder-like organ called an osmeterium. It apparently acts as a protective device, quite possibly giving off an offensive odor, as does the osmeterium of certain lepidopterous larvae." When a larva was prodded with a camel's hair brush the two opercula parted and the bright orange osmeterium protruded from one to two seconds. The osmeterium appeared to be about as long as wide. According to Paulian (1941) the following genera possess this structure: *Alianta*, *Antarctophytosus* (= *Halmaeusa*), *Bolitochara*, *Gyrophaena*, *Lomechusa*, *Microglotta*, *Oligota*, *Phloeopora* and *Thectura*. Moore (1956) confirmed its presence in *Diaulota*, *Liparocephalus* and

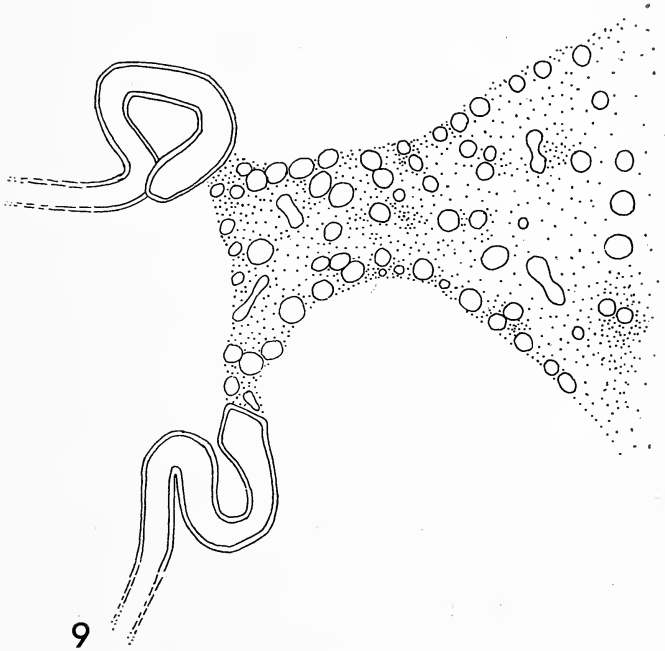


Figure 9. *Oligota oviformis*. Larva. left pair of osmeterial glands.

Phytosus. Paulian (1941) reported it absent in *Aleochara*, *Atheta* and *Cyphea*.

Osmeterial Glands

Through the transparent integuments of the larvae of *O. oviformis* there are visible on each side of the area of the osmeterium a pair of tubular coiled structures which appear to be connected to the osmeterium by convoluted material. These would seem to be glands so it may be reasonable to call them osmeterial glands. If the osmeterium gives off an offensive odor these could be its source.

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THE LYNX SPIDER GENUS *OXYOPES* IN MEXICO AND CENTRAL AMERICA (ARANEAE:OXYOPIDAE)¹

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INTRODUCTION

This is the second in a projected series of papers on the Neotropical Oxyopidae. In this study 16 species of *Oxyopes* are recorded from Mexico and Central America. Of these, 11 are predominately Mexican and Central American, four are more abundant in America, north of Mexico, and one is widely distributed throughout Mexico, North and Central America. Numerous specimens from Mexico and Central America were examined during this study. Collections available from the Museum of Comparative Zoology and the American Museum of Natural History provided an abundance of specimens from certain areas, such as the Panama Canal Zone. However, some regions of Mexico and Central America are poorly collected. Additional specimens came from field studies during several summers in Mexico (1969-71), Costa Rica (1972), and Panama (1972).

Named species of *Oxyopes* from Mexico and Central America were often inadequately described and figured and there was some confusion as to the correct names of several species, males and females having been separately described. In addition, little was known of the geographic ranges nor was there any clear concept of the evolutionary relationships of Neotropical *Oxyopes* to each other or to their North American relatives.

Certain species of *Oxyopes* are extremely abundant in areas of grassy or herbaceous vegetation. For example, *O. salticus* and *O. flavus* constituted as much as 20% of the total number of spiders taken in sweeping vegetation (0.5-1 m in height) in some coastal areas of Guerrero and Veracruz. Judging from their abundance, these spiders are evidently important predators of insects within these habitats. The species of *Oxyopes* observed were all active during the day. They ran swiftly over the plants where they occurred and when disturbed exhibited characteristic erratic leaps which allow them to be immediately recognized in the field. Although *Oxyopes* do not actively pursue their prey by sight, they are much

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more active than thomisids, and exhibit a general "searching" behavior when observed. Long spines on the legs, another field characteristic of lynx spiders, are apparently used to subdue prey. Much remains to be learned about prey capture and other forms of behavior.

The systematic findings in this work are based largely upon morphological studies and distributional data. Ecological and behavioral information has been incorporated where available. Members of the *O. acleistus* species group and the *O. tridens* group are distinguished as much by their ecology as their morphology. Species in the former group are found in areas of moderately luxuriant herbaceous vegetation, while species of the latter group have been found chiefly in rather dry, rocky areas with relatively scanty vegetation. Color patterns of the two species groups generally reflect their surroundings. Species of the *O. tridens* group are generally black and white, fitting well the rather drab, gray backgrounds where they occur. Members of the *O. acleistus* group blend more appropriately with their background coloration of green, and are often deceptively iridescent in sunlight. Members of the *tridens* group have a more robust fourth pair of legs, presumably fitted for saltatory locomotion in a more open habitat.

Systematic studies, such as this one, often provide a foundation for more detailed investigations into the biology of organisms. I hope that this paper will not only fill the need for a basic morphological revision, but stimulate further investigations of the ecology and behavior of *Oxyopes*.

ACKNOWLEDGMENTS

To fully acknowledge help with this paper, I must trace its inception back to a study begun in 1963 while I was a student at the Museum of Comparative Zoology, Harvard University. The major thrust of this early work resulted in the publication of a monograph on the Oxyopidae of North America, north of Mexico (Brady, 1964). A grant from the Evolutionary Biology Committee, Biological Laboratories, Harvard University, made possible a three week visit to the British Museum (Natural History) in the summer of 1963. Here several of the type specimens of *Oxyopes* of F.O.P.-Cambridge were examined and drawn for the first time (Figs. 80-83, 84-87, 96, 97).

The initial writing and preparation of this paper for publication began in 1973. The types of F.O.P.-Cambridge were examined

again. I appreciate the courtesy of Mr. F. R. Wanless, Department of Zoology (Arachnida), British Museum (Natural History) for making this possible

I am especially grateful to Dr. H. W. Levi of the Museum of Comparative Zoology, Harvard University, who has loaned specimens, offered helpful criticism, and aided in other ways the preparation of this publication. Special acknowledgement is due to the late Dr. A. M. Chickering whose collections, now housed in the Museum of Comparative Zoology, provided a wealth of material. I am also indebted to Dr. W. J. Gertsch and Dr. N. I. Platnick for the loan of specimens from the American Museum of Natural History.

During the 1972-73 academic year I was appointed Visiting Professor in the Department of Zoology, University of Florida at Gainesville. For facilities and various courtesies there, I wish to thank Dr. Brian K. McNab, who was then Acting Chairman. For their helpfulness and encouragement of research, I would like to especially thank Dr. Jonathan Reiskind, Dr. H. K. Wallace, and Dr. John Anderson also of the University of Florida.

Special thanks are due to my wife Sara who has aided in proof reading and accepted my long absences during the preparation of this paper.

A 1974 Summer Faculty Grant from Hope College aided in preparation of this paper. National Science Foundation Grant GB-13925 helped to defray expenses connected with this study and permitted its publication.

METHODS

Measurements. All measurements listed are in millimeters. When available ten specimens of each sex were measured. The purpose of this was to give some idea of the variation to be expected within a species population. Measurements are presented in tabular form to facilitate comparisons and aid in their use.

Collection Records. Collection records for Mexico and Central America only are listed. Records north of Mexico are in earlier publications. Localities are listed geographically from north to south and from east to west. The number of specimens collected at each locality is indicated; the lower case "o" representing immature specimens.

Drawings. Epigyna and palps were drawn after they were scraped free of hair and large setae removed. Internal genitalia of the female were drawn after clearing in clove oil.

SPECIES GROUPS OF *OXYOPES*

The 16 species of *Oxyopes* reported from Mexico and Central America in this paper can be combined into five distinct groups. These species groups are based primarily upon the shape or form of the body (morphology), color pattern, relative lengths of legs, and structure of the male and female reproductive organs. For the sake of completeness, five species of *Oxyopes* recorded only from north of Mexico are included in the discussion below.

Acleistus Group. This species group may be arbitrarily subdivided into two subgroups: one containing *chiapas*, *summus*, *occidens*, and *aglossus*; the other containing *tibialis*, *acleistus*, *bifidus*, and *bifissus*. In the first sub-group only *aglossus* is not recorded from Mexico or Central America. All of the second group are found in Mexico. In light of comparative morphology, genitalic structure, color patterns, and geographical distribution, a dendrogram representing the relationships of the eight species in this species group is shown in Diagram 1.

Important considerations in grouping species in Diagram 1 were as follows: (1) *chiapas* and *summus* have similar internal female genitalia (compare Fig. 33 to Fig. 31) and the male palpi are alike (compare Figs. 92, 93 to Figs. 90, 91); (2) *occidens* and *aglossus* are similar in coloration (compare figs. 7, 8 to figs. 9-12 of Brady, 1964), female reproductive organs (compare figs. 23, 24 to figs. 21, 22 of Brady, 1964), and male palpi (compare figs. 33, 34 to figs.

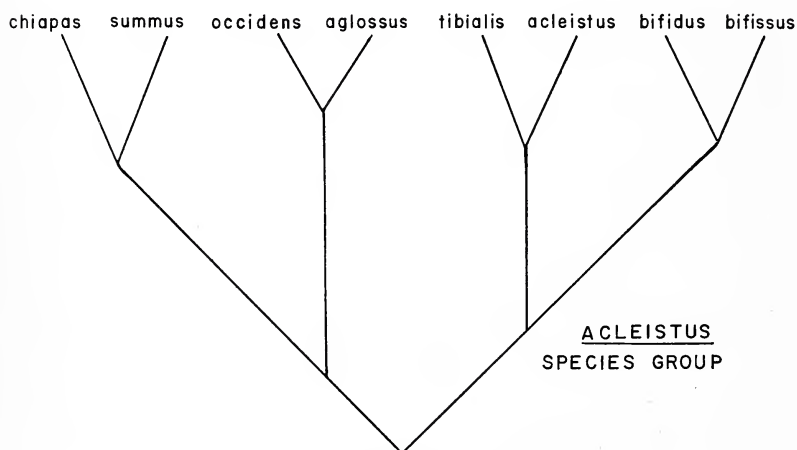


Diagram 1.

39, 40 of Brady, 1964); (3) *tibialis* and *acleistus* are much alike in color pattern (compare Figs. 5, 6 with figs. 1-6 of Brady, 1964), female reproductive organs (compare Figs. 35, 36 with figs. 13-20 of Brady, 1964), and male palpi (compare Figs. 94-97 with figs. 35-38 of Brady, 1964); (4) *bifidus* and *bifissus* have similar color patterns (compare Figs. 1, 2 with Figs. 3, 4) internal female genitalia (compare Figs. 25, 27 with Fig. 37) and male palpi (compare Figs. 78-81 with Figs. 84-89).

It should be stressed that these are observations that lend credibility to Diagram 1 as it is conceived. The relationships of the species is actually much more complex. For example, it appears that *tibialis* may be near the ancestral stem of both *acleistus* and *aglossus-occidens*, although it shows more similarities to the former species. The diagram is a simplification of relationships. This is certainly a case where additional specimens subjected to numerical analyses of multiple characters might yield important information about relationships.

Tridens Group. This species group may also be arbitrarily subdivided into two subgroups: one containing *apollo* and *artemis*; the other *cougar*, *lynx*, *tridens*, *pardus*, *panther*, *ocelot*, *cornutus*, and *felinus*. In the first subgroup only *apollo* has been found in Mexico. In the second subgroup *pardus* and *lynx* are represented by unique specimens (Brady, 1964), and *cougar* is recorded only from the southeastern United States (Brady, 1969).

Utilizing comparative morphology, genitalic structure, color patterns, and distribution patterns, a dendrogram representing the hypothetical relationships of the eight species in the second subgroup is shown in Diagram 2. The well developed tibial apophyses and palpal sclerites of *O. apollo* and *O. artemis* males, as well as strongly developed fourth legs in both sexes, place them near the eight species in Diagram 2. There is considerable resemblance in color among the species of the *tridens* group that I have seen in the field. This is not so apparent in preserved specimens. Members of this group are not often taken in sweep-nets, but seem to frequent rather dry areas with scanty, low-growing vegetation. Some are found at high elevations. When more information is available, this group may be as well defined ecologically as morphologically.

Important considerations in grouping species in Diagram 2 were as follows: (1) *cougar*, *lynx*, *tridens*, *pardus*, and *panther* have well-developed tibial apophyses on the male palpi; (2) *cougar* and *lynx* have very similar palpi (compare figs. 9, 10 of Brady, 1969, with figs. 66, 67 of Brady, 1964); (3) *tridens* and *pardus* have similar

palpi (compare figs. 70, 71 and figs. 68, 69 of Brady, 1964); (4) *tridens* and *panther* have color patterns (compare figs. 62, 63 of Brady, 1964 with figs. 5, 6 of Brady, 1969 and Figs. 15, 16) and epigyna alike (compare figs. 53-55 of Brady, 1964 with figs. 16, 17 of Brady, 1969 and Figs. 45, 46). It is possible that *panther* is the female of *pardus*.

Also (1) *ocelot*, *cornutus*, and *felinus* have predominant black and white color patterns, but they lack prominent tibial apophyses. *Oxyopes felinus* has a small knob on the tibial segment (Figs. 102, 103), (2) the male palpi (Figs. 100-105), as well as the epigyna and internal genitalia (Figs. 39-44) of these three species are much alike. *Oxyopes ocelot* is the most distinctive of the three.

Color patterns in *Oxyopes* seem to be a conservative feature and are useful in determining relationships. It should be pointed out, however, that color is often altered by scraping off hair during handling and to a lesser extent by preservation in alcohol. Also, one needs an adequate sample of specimens to determine the color pattern norm, because of individual variation within a population and geographic variation within the species. The structure and arrangement of male palpal sclerites and apophyses as well as external and internal structure of the female genitalia are the most reliable criteria for determining species relationships. Because of a need for more specimens from certain critical areas in Mexico and Central America the proposed dendrograms must be considered strictly tentative as based on the available material.

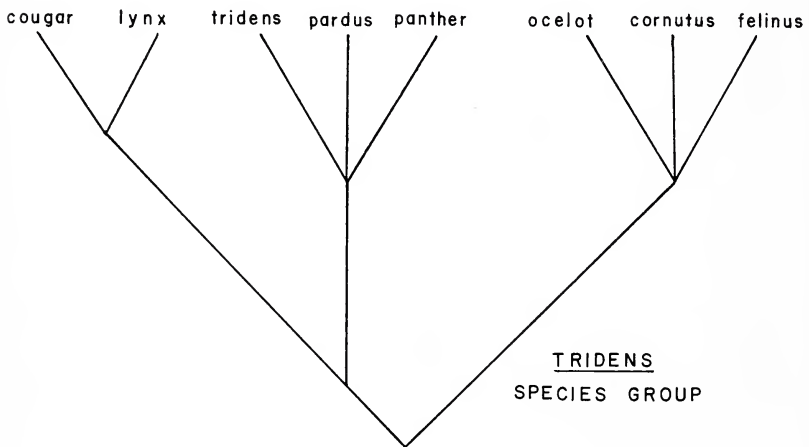


Diagram 2.

The remaining three species of *Oxyopes* found in Mexico and Central America are *O. scalaris*, *O. salticus*, and *O. flavus*. They are different from all other species found in this region. In context with the other species they would constitute distinct monotypic species groups.

Oxyopes scalaris is essentially a temperate species whose southern limit of range extends into the northern Mexican plateau (Map 4). *Oxyopes salticus* is found in the United States and occurs throughout Mexico and Central America (Map 3). *Oxyopes flavus* does not occur north of Mexico (Map 4).

UNIDENTIFIABLE SPECIES

Nathan Banks (1898) described *O. acutus* based upon several young males from La Chaparos, Sierra Laguna, and Hermosillo, Mexico and an adult female from Baja California. The female which is figured by Banks, is *O. scalaris* Hentz. One of the immature males is labelled as a type in the collection of the Museum of Comparative Zoology. The color pattern of this specimen matches that of several species in the *O. tridens* complex. *Oxyopes acutus* has appeared only as an entry in faunal lists in the zoological literature. The name has not been associated with any specimens since the original description by Banks. For that reason and because of the difficulty in accurately determining the species that the immature type represents, I think it best to consider *O. acutus* as a *nomen dubium*.

The type female of *O. actophilus* described by Chamberlin (1924) has apparently been lost. The description, based upon an immature female type, is not adequate enough to determine the species with any accuracy. Therefore, I think that *O. actophilus* is also best considered a *nomen dubium*.

KEY TO SPECIES OF *OXYOPES*

FEMALES

- | | |
|---|---------------|
| 1a. Leg I longer than leg IV. | 2 |
| 1b. Leg IV longer than leg I. | 9 |
| 2a. Body length 7.2 mm or less. | 3 |
| 2b. Body length greater than 7.2 mm. Color yellow with black markings. Pattern as in Figures 13, 14. Epigynum as in Figures 47-54. | <i>flavus</i> |

- 3a. Distinct mid-ventral stripes on femora I-II. 6
- 3b. No distinct mid-ventral stripes on femora I-II. 4
- 4a. Thin vertical black stripes beginning under AME and continuing to subdistal region of chelicerae as in Figure 3. 5
- 4b. No thin black stripes as in Figure 3. Russet brown, dark brown, or gray in general appearance (figs. 89, 90, 97-99 of Brady, 1964). *scalaris*
- 5a. Found in Arizona, Baja California. Probably limited to Sonoran Desert region (figs. 7, 8, 23, 24 of Brady, 1964).
..... *occidens*
- 5b. Found south of Sonoran Desert region (Map 1). Figures 3, 4, 37, 38. *bifissus*
- 6a. Epigynum with an anteriorly directed scape (Fig. 24). Color pattern as in Figures 11, 12. *salticus*
- 6b. Epigynum without an anteriorly directed scape. Color pattern not as above. 7
- 7a. Found in northeastern Mexico (Map 1). Color pattern as in figure 1-6, epigynum as in figures 13-20 of Brady, 1964.
..... *acleistus*
- 7b. Not found in northeastern Mexico. Occurring westward or southward of *acleistus*. 8
- 8a. Color pattern as in Figures 1, 2. Epigynum as in Figures 25-30. *bifidus*
- 8b. Color pattern as in Figures 5, 6. Epigynum as in Figures 35, 36. *tibialis*
- 8c. Color pattern as in Figures 7, 8. Epigynum as in Figures 33, 34. *chiapas*
- 8d. Color pattern as in Figures 9, 10. Epigynum as in Figures 31, 32. *summus*
- 9a. Color pattern as in Figures 15, 16. Epigynum as in Figures 45, 46. *panther*
- 9b. Color pattern as in Figures 17, 18. Epigynum as in Figures 41, 42. *ocelot*
- 9c. Color pattern as in Figures 19, 20. Epigynum as in Figures 43, 44. *cornutus*
- 9d. Color pattern as in Figures 21, 22. Epigynum as in Figures 39, 40. *felinus*
- 9e. Color pattern as in figures 45, 46 of Brady, 1964. Epigynum as in figures 53, 55 of Brady, 1964. *acleistus*

KEY TO SPECIES OF *OXYOPES*

MALES

- 1a. Leg I longer than leg IV. 2
- 1b. Leg IV longer than leg I. 10
- 2a. Body length 5 mm or less. 3
- 2b. Body length greater than 5 mm. Color yellow with black markings. Pattern as in Figures 76, 77. Palpus illustrated in Figures 106, 107. *flavus*
- 3a. Distinct mid-ventral black stripes on femora I-II. 6
- 3b. No distinct mid-ventral stripes on femora I-II. 4
- 4a. Thin vertical black stripes beginning under AME and continuing to subdistal region of chelicerae as in Figures 57, 59. 5
- 4b. No thin black stripes as in Figures 57, 59. Russet brown, dark brown, or gray in general appearance (figs. 87, 88, 106, 107 of Brady, 1964). *scalaris*
- 5a. Found in Arizona, Baja California. Probably limited to Sonoran Desert region (figs. 25, 26, 33, 34 of Brady, 1964). *occidens*
- 5b. Found south of Sonoran Desert region (Map 1). Figures 57-60, 84-89. *bifissus*
- 6a. With a well-developed retrolateral tibial apophysis as in Figures 94-97. 9
- 6b. Without a well-developed retrolateral tibial apophysis as in Figures 94-97. 7
- 7a. Tarsus of palpus deeply concave, and with a brush of stiff hairs on the ventral surface of the patella. Color pattern as in Figures 73-75. Palpus as in Figures 98, 99. *salticus*
- 7b. Tarsus of palpus not deeply concave, and without a brush of stiff hairs on the ventral surface of the patella. 8
- 8a. Palpus illustrated in Figures 78-81. *bifidus*
- 8b. Palpus illustrated in Figures 90, 91. *summus*
- 8c. Palpus illustrated in Figures 92, 93. *chiapas*
- 9a. Found in northern Mexico and northward (Map 1). Palpus illustrated in figures 35-38 of Brady, 1964. *acleistus*
- 9b. Found in southern Mexico and southward (Map 1). Palpus illustrated in Figures 94-97. *tibialis*
- 10a. With a conspicuous apophysis on the patella of the palpus (figs. 70, 71 of Brady, 1964). *tridens*

- 10b. With a small apophysis on the patella of the palpus (figs. 74, 75 of Brady, 1964) or without a patellar apophysis. 11
- 11a. With a small apophysis on the patella of the palpus as in figures 74, 75 of Brady, 1964. Color pattern as in figures 72, 73 of Brady, 1964. *apollo*
- 11b. Without an apophysis on the patella of the palpus. 12
- 12a. Palpus illustrated in Figures 100, 101. *ocelot*
- 12b. Palpus illustrated in Figures 102, 103. *felinus*
- 12c. Palpus illustrated in Figures 104, 105. *cornutus*

SPECIES DESCRIPTIONS

Oxyopes acleistus Chamberlin

Map 1.

Oxyopes acleistus Chamberlin, 1929, Ent. News, 40:19, fig. 3, ♀. Female holotype from Sanford, Seminole Co., Florida, in the American Museum of Natural History, examined. Roewer, 1954, Katalog der Araneae 2(a):330. Bonnet, 1958, Bibliographia Araneorum, 2(4):3223.

Oxyopes aureus Brady, 1964, Bull. Mus. Comp. Zool., 131(13):457, figs. 1-4, 13-17, 27, 28, 35, 36, ♂ ♀. Female holotype from Bentsen State Park, 6 mi. SW of Mission, Hidalgo Co., Texas, in the Museum of Comparative Zoology. NEW SYNONYMY.

Discussion. After seeing both individual and geographic variation of the epigynia of *O. bifidus* (Figs. 25-30), I am led to believe that the differences between *O. aureus* and *O. acleistus* are, at best, subspecific. The fact that the color patterns and the male palpi of these two species are much alike supports this position. After seeing the variance of certain taxonomic characters within some Mexican and Central American species, I am impressed with the similarities between *O. aureus* and *O. acleistus*. Therefore, I consider them conspecific here.

See Brady, 1964, pages 454-460 for figures, measurements, color descriptions, diagnoses, notes on natural history, and collection records north of Mexico.

Distribution. Florida, Louisiana, Texas and northern Mexico. (Map 1).

Records. MEXICO, *Tamaulipas*. Rio Gualoliejo near Forólón, 16 April 1939, ♂ oo (LID, B. Brown). *San Luis Potosí*. Huichihuyan, 19 May 1952, ♂ (MAC, WJG, RS); 10 mi. N of Valles, 23 July 1945, (A. M. Dame). *Nuevo León*. Horsetail Falls, 7 July 1972, ♀ ♀ (ARB).

Oxyopes occidens Brady

Map 1.

Oxyopes occidens Brady, 1964, Bull. Mus. Comp Zool., 131(13):464, figs. 7, 8, 23-26, 33, 34, ♂ ♀. Male holotype from Sabino Pond, Sabino Canyon, Santa Catalina Mtns., Pima Co., Arizona, in the Museum of Comparative Zoology.

Discussion. For figures, measurements, color descriptions, diagnosis, notes on natural history, and collection records north of Mexico, see Brady (1964), pages 464-467.

Distribution. Arizona, Baja California (Map 1).

Record. MEXICO. *Baja California.* San José del Cabo, 1896, ♀ (NB).

Oxyopes bifidus F.O.P.-Cambridge

Figures 1, 2, 25-30, 55, 56, 78-81. Map 1.

Oxyopes bifidus F.O.P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, Araneidea, 2:344, pl. 32, figs. 20, 20a, ♂. Male holotype from Acapulco, Guerrero, Mexico, in British Museum (Natural History), examined. Roewer, 1954, Katalog der Araneae, 2(a):331. Bonnet, 1958, Bibliographia Araneorum, 2(4):3225.

Discussion. *Oxyopes bifidus* is one of the most common and widespread species of *Oxyopes* in Mexico and Central America. The epigyna of this species is remarkable for its variation in structure (Figs. 25-30). This variation is also characteristic of *O. acleistus*, a member of the same species group (see Brady, 1964, figs. 13-20).

Measurements. Ten females and ten males.

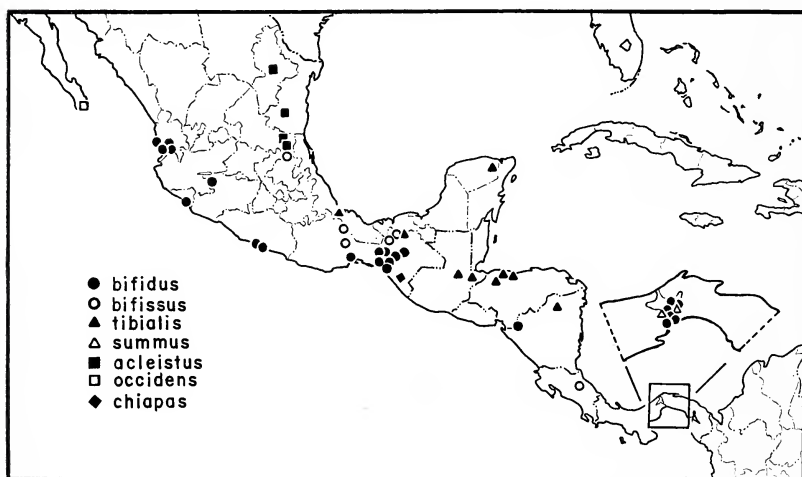
FEMALES: Mean		Range	Mean	Range
Clypeus	.518	.45-.58	Femur I	2.42 2.1-2.8
AME	.343	.30-.38	Patella-Tibia I	3.01 2.7-3.7
ALE	.625	.55-.68	Metatarsus I	2.44 2.2-2.8
PLE	1.148	1.00-1.25	Tarsus I	.99 .8-1.3
PME	.623	.55-.68	Total Length I	8.86 7.8-10.4
Carapace Width	1.78	1.6-2.0	Patella-Tibia II	2.72 2.4-3.1
Carapace Length	2.37	2.1-2.7	Patella-Tibia III	2.06 1.7-2.4
Total Length	5.58	4.8-6.6	Patella-Tibia IV	2.40 2.2-2.8
			Total Length IV	8.05 7.2-9.4

MALES:	Mean	Range		Mean	Range
Clypeus	.423	.38-.53	Femur I	2.31	2.1-2.6
AME	.313	.30-.35	Patella-Tibia I	2.97	2.7-3.2
ALE	.565	.53-.65	Metatarsus I	2.81	2.5-3.2
PLE	1.015	.95-1.15	Tarsus I	1.21	1.0-1.5
PME	.555	.53-.63	Total Length I	9.31	8.4-10.5
Carapace Width	1.62	1.5-1.9			
Carapace Length	2.12	2.0-2.5	Patella-Tibia II	2.66	2.4-3.1
Total Length	4.30	4.0-5.0	Patella-Tibia III	1.97	1.8-2.3
			Patella-Tibia IV	2.30	2.0-2.6
			Total Length IV	7.88	7.2-9.0

Color. Female. Face and chelicerae cream to pale orange, lighter along lower edge of clypeus. Darker brownish vertical stripes as in Figure 1. Eye region dark brown or black, overlaid with white appressed hair.

Carapace cream to pale orange with darker brown markings as illustrated in Figure 2.

Dorsum of abdomen white to yellow medially, the cardiac area translucent; bounded on each side by brown as in Figure 2. Venter with broad, dark brown median stripe from epigastric furrow to base of spinnerets; bounded by lighter cream to yellow.



Map 1.

Legs cream to yellow. Dark median stripe on ventral surface of femora I and II.

Labium and endites yellow to pale orange. Sternum cream to pale yellow.

Color. Male. Face and chelicerae yellow to pale orange with darker brown stripes as illustrated in Figure 55. Eye region dark brown to black. Cymbia of palpi dark brown to black.

Carapace yellow to pale orange with faint indications of more dusky markings as shown in Figure 56.

Dorsum of abdomen with median area cream to pale yellow, bordered laterally by dark brown as in Figure 56. Venter with broad median brown stripe from genital area to base of spinnerets. Lateral areas pale yellow, mottled with darker color.

Legs yellow. Ventral surface of femora I and II with a dark median stripe.

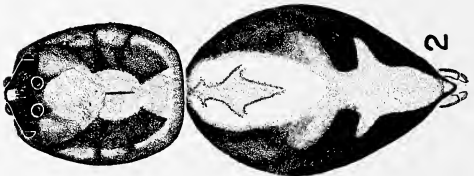
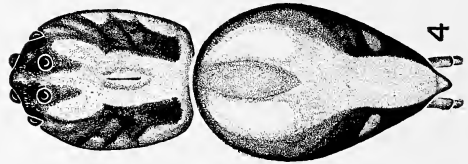
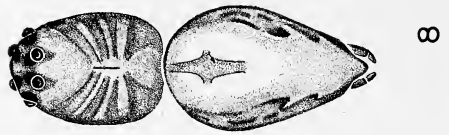
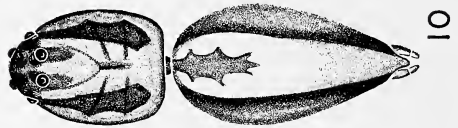
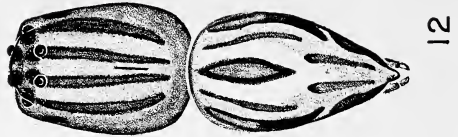
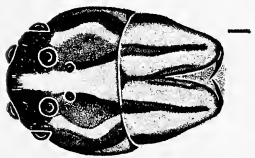
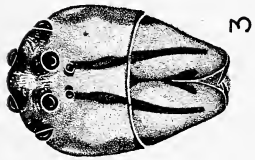
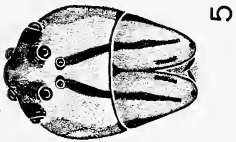
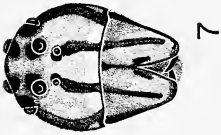
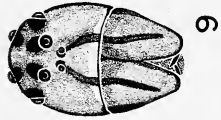
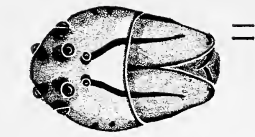
Labium and endites pale orange. Sternum yellow.

Diagnosis. *Oxyopes bifidus* is most closely related to *O. bifissus* as evidenced by coloration and morphology. The male palpi are very similar (compare Figs. 78-81 with Figs. 84-89), but distinct. The two species are easily separated by epigynal structure (compare Figs. 25-30 with Figs. 37-38). Preliminary collecting indicates that these two species are largely allopatric, *O. bifidus* occurring in western Mexico and Central America and *O. bifissus* in eastern Mexico with one record from Costa Rica.

Natural History. *Oxyopes bifidus* was collected in Panama and Costa Rica by sweeping tall grass and herbaceous vegetation. *Oxyopes salticus* was present in these same habitats in much greater numbers than *O. bifidus*. No differences were noted in the microhabitats of these two species.

Distribution. Western Mexico to Panama (Map 1).

Records. MEXICO. *Nayarit.* Compostela, 12-13 July 1972, ♂ : 3 ♀ ♀ : 0 (ARB, AJ); 6 mi. E of Las Varas, 13 July 1972, 400 (ARB); San Blas, 14 Sept. 1957, ♂ ♂ (RD); 20 mi. S of Tepic, 4 Aug. 1956, ♀ (WJG, VDR); Tepic, 6-7 Aug. 1955, ♂ (BM). *Guerrero.* Acapulco, ♂ (HHS), Pie de las Cuesta, 8 mi. W of Acapulco, 29 June 1941, ♀ (LID). *Colima.* Boca de Pascuales, 10 Jan. 1943, ♀ (FB). *Michoacan.* 25 mi. E of Mazamitla, 2 Aug. 1956, ♂ ♀ 0 (WJG, VDR). *Oaxaca.* Tehuantepec, 26 Aug. 1947, ♀ (HMW). *Chiapas.* Arriaga, 1-2 Sept. 1947, ♂ ♂ ♀, Chiapa, 6 Sept. 1947, ♂, Cintalapa, 17 Sept. 1947, 3 ♀ ♀, Las Cruces, 18 Sept. 1947, ♂, Río de las Flores, 15 Sept. 1947, 4 ♀ ♀ : 0, 16 Sept. 1947, ♀ (HMW); Tonalá, Aug. 1909, ♂ ♂ ♀ ♀ 0 (AP).



1mm

NICARAGUA. San Marcos, ♂ (CTB).

PANAMA. Arraiján, 6-9 July 1950, ♀♀, Chilibre, 8 July 1950, 5 ♀♀ (AMC). Canal Zone. Balboa, 1-14 Mar. 1954, ♂, Feb.-Aug. 1957, ♂♂ (WEL); Chiva, 23 July 1954, ♀oo (AMC); Cocoli, 3 Dec. 1956, ♀, 26 Jan. 1958, ♀ (WEL); Experimental Gardens, 12-13 July 1954, ♂♂♀, 12 Aug. 1954, ♀, Forest Reserve, 10-12 Aug. 1939, ♀, 23 July 1950, ♂, 30 July 1950, 4♂♂:0, 25-28 July 1954, 3♂♂:7♀♀:00, 24 Dec. 1957, ♂:9♀♀:0, 21-22 Jan. 1958, 7♂♂:19♀♀:1300, 29 Jan. 1958, ♂:3♀♀, Madden Dam, 8 July 1950, ♂, Miraflores Locks, 3 July 1958, ♂, Pédro Miguel, 31 Dec. 1957, ♀ (AMC); Summit, Jan. 1947, ♂ (NLHK), 7-10 July 1950, ♂♀, 21-29 July 1950, 4♂♂:3♀♀, 16-17 Aug. 1950, 3♂♂:♀, 23-28 Aug. 1950, 3♂♂:♀♀, 17 Aug. 1954, ♀ (AMC).

Oxyopes bifissus F.O.P.-Cambridge

Figures 3, 4, 37, 38, 57-60, 84-89. Map 1.

Oxyopes bifissus F.O.P.-Cambridge, 1902, *Biologia Centrali-Americana*, Arachnida, Araneidea, 2:344, pl. 32, figs. 21, 21a, 22, ♂♀. Male holotype from Teapa, Tabasco, Mexico, in British Museum (Natural History), examined. Roewer, 1954, *Katalog der Araneae*, 2(a):331. Bonnet, 1958, *Bibliographia Araneorum*, 2(4):3225.

Oxyopes calcarifer F.O.P.-Cambridge, 1902, *Biologia Centrali-Americana*, Arachnida, Araneidea, 2:344, pl. 32, fig. 24, ♂. Male holotype from Costa Rica, in British Museum (Natural History), examined. NEW SYNONYMY.

Discussion. *Oxyopes calcarifer* F.O.P.-Cambridge is undoubtedly the same species as *O. bifissus* as evidenced by a comparison of the male holotypes (compare Figs. 84, 85 with Figs. 86, 87).

Figs. 1-2. *Oxyopes bifidus* F.O.P.-Cambridge, female from Compostela, Nayarit, 12 July 1972. 1. Face view. 2. Dorsal view.

Figs. 3-4. *Oxyopes bifissus* F.O.P.-Cambridge, female from Tamaunchale, San Luis Potosi, 19 April 1963. 3. Face view. 4. Dorsal view.

Figs. 5-6. *Oxyopes tibialis* F.O.P.-Cambridge, female from Musawas on Waspuac River, Nicaragua, 10-31 Oct. 1955. 5. Face view. 6. Dorsal view.

Figs. 7-8. *Oxyopes chiapas* new species, female from La Zacualpa, Chiapas, Aug. 1909. 7. Face view. 8. Dorsal view.

Figs. 9-10. *Oxyopes summus* new species, female from Gamboa, Panama Canal Zone, 24 July 1959. 9. Face view. 10. Dorsal view.

Figs. 11-12. *Oxyopes salticus* Hentz, female from Horsetail Falls, Nuevo Leon, 7 July 1972. 11. Face view. 12. Dorsal view.

Measurements. Ten females and ten males.

FEMALES: Mean			Range			Mean			Range		
Clypeus	.463	.40-.55	Femur I	2.21	2.0-2.4						
AME	.363	.33-.43	Patella-Tibia I	2.70	2.4-2.9						
ALE	.673	.63-.75	Metatarsus I	2.18	2.0-2.4						
PLE	1.223	1.10-1.38	Tarsus I	.91	.8-1.0						
PME	.680	.60-.78	Total Length I	8.00	7.3-8.6						
Carapace Width	1.77	1.5-2.0	Patella-Tibia II	2.56	2.3-2.8						
Carapace Length	2.31	2.0-2.6	Patella-Tibia III	2.05	1.9-2.3						
Total Length	5.27	3.9-6.5	Patella-Tibia IV	2.24	2.1-2.5						
			Total Length IV	7.37	6.5-8.1						
MALES: Mean			Range			Mean			Range		
Clypeus	.335	.28-.45	Femur I	2.06	1.9-2.4						
AME	.320	.30-.40	Patella-Tibia I	2.64	2.4-3.0						
ALE	.590	.55-.70	Metatarsus I	2.40	2.2-2.8						
PLE	1.063	.95-1.30	Tarsus I	1.10	.9-1.3						
PME	.590	.55-.70	Total Length I	8.19	7.4-9.4						
Carapace Width	1.61	1.5-1.9	Patella-Tibia II	2.44	2.2-2.8						
Carapace Length	2.09	1.9-2.5	Patella-Tibia III	1.88	1.7-2.2						
Total Length	4.20	3.7-5.3	Patella-Tibia IV	2.05	1.8-2.4						
			Total Length IV	6.98	6.2-8.0						

Color. Female. Face and chelicerae yellow to pale orange with darker brownish or black stripes as illustrated in Figure 3. Eyes surrounded with black, overlaid with white spatulate-shaped hair. Lower edge of clypeus white to pale cream.

Carapace yellow to pale orange with dark brown hairs forming pattern as illustrated in Figure 4.

Dorsum of abdomen white to pale yellow, bordered by dark brown as in Figure 4. Venter white to pale yellow, speckled with brown.

Legs yellow to pale orange with irregular dusky spots, most conspicuous ventrally.

Labium cream to pale orange. Endites cream to pale orange, outlined with dark brown, Sternum white to pale yellow, with dark brown margin.

Color. Males of *O. bifissus* occur in two color phases. The darker of these forms is described first, then the lighter phase.

Dark male. Face and chelicerae dark brown with vertical black stripes as in Figure 57. Eye region dark brown with iridescent scales. Cymbia of palpi dark brown to black. Distal ends of chelicerae lighter.

Carapace with median area light brown, bordered by dark brown to black as shown in Figure 58.

Dorsum of abdomen light brown in center to dark brown along sides as in Figure 58; overlaid with iridescent scales. Spinnerets yellow to light orange-brown. Venter dark brown to black with pale lines originating at corners of epigastric furrow and continuing to base of spinnerets. Median area heavily clothed with iridescent scales. Scales impart a green or pink iridescence in preserved specimens.

Legs yellow to light orange-brown. Longitudinal black line along retrolateral surface of femora I.

Labium and endites dark brown to black with pale distal ends. Sternum brown.

Light male. Face and chelicerae orange-brown with vertical black stripes as indicated in Figure 59. Distal ends of chelicerae pale yellow. Eye region with a few iridescent scales. Cymbia of palpi dark brown.

Carapace light orange-brown, darker along sides as shown in Figure 60.

Dorsum of abdomen white to pale cream, overlaid with iridescent scales, bounded by darker brown as in Figure 60. Spinnerets orange-yellow. Venter white to pale cream spotted with brown.

Legs cream to pale yellow.

Labium and endites pale yellow-orange. Sternum pale yellow.

Diagnosis. *Oxyopes bifissus* is similar to *O. bifidus* in form and coloration. The male palpi of these two species are much alike, but distinct (compare Figs. 84-89 with Figs. 78-81). The two species can be readily distinguished by their epigyna (compare Figs. 37, 38 with Figs. 25-30).

Distribution. Eastern Mexico to Costa Rica (Map 1).

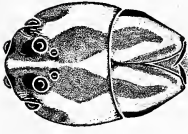
Records. MEXICO. *San Luis Potosí.* Tamazunchale, 19 Apr. 1963, ♂♂ ♀ (WJG, WI). *Veracruz.* La Buena Ventura, July 1909, ♀ (AP). *Oaxaca.* Palomares, July 1909, 12♂♂ : 5♀♀ : 1500 (AP). *Chiapas.* Pichucalco, 17 July 1947, ♂♀ (CG, MG). *Tabasco.* Teapa, ♂♀ (HHS), 16 July 1947, ♂♀ (CG, MG). COSTA RICA. ♂ (Rogers).



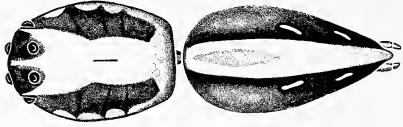
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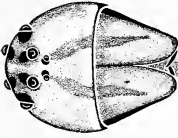
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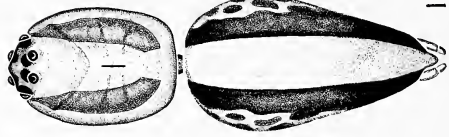
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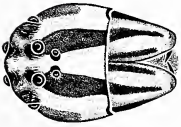
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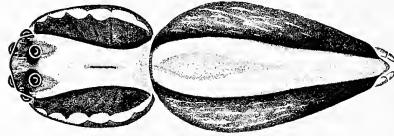
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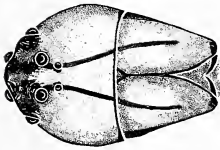
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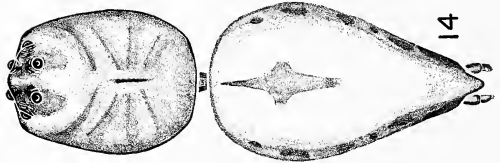
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16



13



14

1mm

Oxyopes tibialis F.O.P.-Cambridge

Figures 5, 6, 35, 36, 61, 62, 94-97. Map 1.

Oxyopes tibialis F.O.P.-Cambridge, 1902, *Biologia Centrali-Americana*, Arachnida, Araneidea, 2:344, pl. 32, figs. 23, 23a, ♂. Male holotype from Guatemala, in British Museum (Natural History), examined.

Oxyopes transversus F.O.P.-Cambridge, 1902, *Biologia Centrali-Americana*, Arachnida, Araneidea, 2:345, pl. 32, fig. 28, ♀. Female holotype from Teapa, Tabasco, Mexico, in British Museum (Natural History), examined. NEW SYNONYMY.

Discussion. *Oxyopes transversus* of F.O.P.-Cambridge (1902) is almost certainly the female of *O. tibialis*. Collections from four different localities contain representatives of both sexes taken together. Size, coloration, and morphological features lend support to this synonymy.

Measurements. Ten females and ten males.

FEMALES: Mean			Range			Mean			Range		
Clypeus	.503	.48-.55	Femur I	2.32	2.1-2.6						
AME	.325	.30-.38	Patella-Tibia I	2.80	2.5-3.2						
ALE	.628	.60-.68	Metatarsus I	2.30	2.0-2.6						
PLE	1.120	1.05-1.20	Tarsus I	.92	0.9-1.0						
PME	.623	.60-.68	Total Length I	8.33	7.4-9.3						
Carapace											
Width	1.75	1.7-2.0	Patella-Tibia II	2.60	2.3-3.0						
Carapace			Patella-Tibia III	1.99	1.8-2.3						
Length	2.32	2.2-2.6	Patella-Tibia IV	2.26	2.0-2.6						
Total			Total Length IV	7.52	6.7-8.6						
Length	5.62	4.6-6.4									

Figs. 13-14. *Oxyopes flavus* Banks, female from Iquala, Guerrero, 27 Oct. 1947. 13. Face view. 14. Dorsal view.

Figs. 15-16. *Oxyopes panther* new species, female from Palos Colorados, Durango, 5 Aug. 1947. 15. Face view. 16. Dorsal view.

Figs. 17-18. *Oxyopes ocelot* new species, female from Arcelia, Guerrero, 2 Nov. 1947. 17. Face view. 18. Dorsal view.

Figs. 19-20. *Oxyopes cornutus* F.O.P.-Cambridge, female from 8 mi. SW of Colima, Colima, 10 May 1963. 19. Face view. 20. Dorsal view.

Figs. 21-22. *Oxyopes felinus* Brady, female from SW of Acaponeta, Nayarit, 15 May 1963. 21. Face view. 22. Dorsal view.

MALES:	Mean	Range		Mean	Range
Clypeus	.445	.38-.50	Femur I	2.24	2.1-2.4
AME	.313	.30-.33	Patella-Tibia I	2.87	2.6-3.2
ALE	.583	.55-.65	Metatarsus I	2.58	2.4-2.8
PLE	1.043	.98-1.13	Tarsus I	1.18	1.1-1.3
PME	.583	.55-.65	Total Length I	8.86	8.0-9.5
Carapace Width	1.69	1.6-1.8	Patella-Tibia II	2.58	2.3-2.8
Carapace Length	2.19	2.0-2.3	Patella-Tibia III	1.93	1.6-2.1
Total Length	4.63	4.1-5.0	Patella-Tibia IV	2.16	2.0-2.4
			Total Length IV	7.30	6.6-7.9

Color. Female. Face and chelicerae pale yellow to light yellow-orange with dark stripes from AME to subdistal region of chelicerae as in Figure 5. Eyes with black nacelles, overlaid with white spatulate hair.

Carapace cream to light yellow-orange, with broad dark submarginal stripes as in Figure 6.

Dorsum of abdomen with cardiac area translucent, accented by white. Median area white to pale yellow, outlined by mottled brownish yellow anteriorly and dark brown posteriorly as in Figure 6. Spinnerets pale yellow. Venter with broad, mottled brown or solid brown median stripe from epigastric furrow to base of spinnerets.

Legs yellow. Femora I-III with mid-ventral dark lines.

Labium and endites yellow to light yellow-orange. Sternum cream to pale yellow.

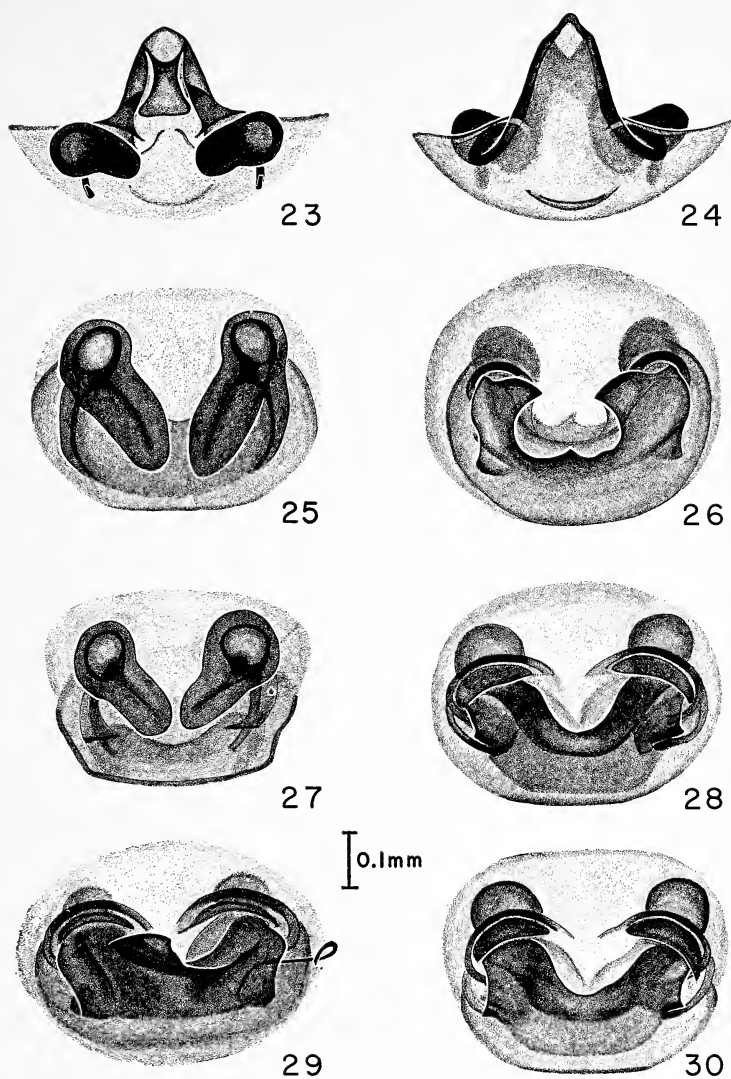
Color. Male. Face and chelicerae with black reticulate pattern and indistinct vertical stripes as in Figure 61. Some specimens dark brown to black without stripes apparent. Cymbia of palpi black. Eyes with black nacelles.

Carapace yellow to yellow-orange in some; dark brown with lighter yellow surrounding thoracic groove in others.

Dorsum of abdomen brown mottled with cream to yellow, giving overall gray-brown appearance. Spinnerets yellow. Venter with same mottled appearance as dorsum, with a wide median brown stripe from epigastric furrow to base of spinnerets.

Legs yellow with median ventral stripe on femora I-III.

Labium brown with light yellow distal end. Endites brown with light yellow inner margins and distal ends. Sternum yellow.



Figs. 23-24. *Oxyopes salticus* Hentz, female from Horsetail Falls, Nuevo Leon, 7 July 1972. 23. Internal genitalia. 24. Epigynum.

Figs. 25-26. *Oxyopes bifidus* F.O.P.-Cambridge, female from Compostela, Nayarit, 12 July 1972. 25. Internal genitalia. 26. Epigynum.

Figs. 27-30. *Oxyopes bifidus* F.O.P.-Cambridge, females from Rio de las Flores, Chiapas, 15 Sept. 1947. 27. Internal genitalia. 28-30. Epigyna.

Diagnosis. *Oxyopes tibialis* is closest to *O. acleistus* as it is understood in this paper. Color patterns of these two species are alike (compare Figs. 5, 6 to figs. 1-6 of Brady, 1964), and the male and female reproductive organs are similar. The two species can be distinguished by comparing the epigynum of *O. tibialis* (Figs. 35, 36) to that of *O. acleistus* (figs. 13-20 of Brady, 1964). In males, the tibial apophysis of *O. tibialis* (Figs. 94-97) is larger than that of *O. acleistus* (figs. 35-38 of Brady, 1964) and their palpal sclerites differ.

Distribution. Southern Mexico and Central America (Map 1).

Records. MEXICO. Veracruz, Tuxtilla, 23 July 1946, ♂ (HMW). Tabasco. Teapa, 4 ♀♀ : 0 (HHS). Campeche. San Jose, Dec. 1946, ♂ (HMW). Yucatan. Colonia Yucatan, 13-19 Aug. 1952, ♂ ♀ (JP, DP).

GUATEMALA. Los Amates, 1908, 4 ♂♂ : ♀ : 300 (Kellerman), Panzós, 14-17 July 1947, ♀ (CV, PV).

HONDURAS. La Ceiba, 19 Dec. 1916, ♀ (Dyer); Lancetilla, July 1929, ♂ : 3 ♀♀, Progress, 6 July 1929, ♂, Tela, 26 July 1929, 3 ♂♂ : 5 ♀♀ (AMC).

NICARAGUA. Musawas, Waspuc River, 30 Sept. 1955, ♂, 10-31 Oct. 1955, ♀ (BM).

Oxyopes chiapas new species

Figures 7, 8, 33, 34, 63, 64, 92, 93. Map 1.

Holotype. Male from La Zacualpa, Chiapas, Mexico, Aug. 1909, (A. Petrunkevitch), in American Museum of Natural History. The specific name is a noun in apposition after the type locality.

Measurements. Five females and two males.

FEMALES: Mean			Range	Mean	Range
Clypeus	.475	.43-.50	Femur I	2.19	2.0-2.3
AME	.305	.30-.33	Patella-Tibia I	2.72	2.6-2.8
ALE	.600	.58-.63	Metatarsus I	2.26	2.2-2.3
PLE	1.075	1.05-1.13	Tarsus I	.88	.9
PME	.600	.58-.63	Total Length I	8.06	7.8-8.3
Carapace Width	1.63	1.6-1.7	Patella-Tibia II	2.50	2.4-2.6
Carapace Length	2.22	2.1-2.3	Patella-Tibia III	1.93	1.9-2.0
Total Length	5.19	5.0-5.4	Patella-Tibia IV	2.18	2.1-2.3
			Total Length IV	7.31	7.0-7.6

MALES:

Clypeus	.40, .43	Femur I	2.0, 2.3
AME	.30, .30	Patella-Tibia I	2.6, 2.8
ALE	.55, .55	Metatarsus I	2.5, 2.7
PLE	.98, 1.00	Tarsus I	1.1, 1.2
PME	.55, .55	Total Length I	8.2, 9.0
Carapace Width	1.5, 1.6	Patella-Tibia II	2.4, 2.7
Carapace Length	2.0, 2.1	Patella-Tibia III	1.8, 2.0
Total Length	4.1, 4.3	Patella-Tibia IV	2.0, 2.3
		Total Length IV	—, 7.7

Color. Female. Face and chelicerae pale cream to yellow with vertical black stripes from AME to subdistal ends of chelicerae as in Figure 7. Eye nacelles black, overlaid with white hair.

Carapace pale yellow.

Dorsum of abdomen white to cream with brown along sides as in Figure 8. Spinnerets pale yellow. Venter with broad cream colored stripe outlined with brown, extending from epigastric furrow to base of spinnerets. Lateral areas white.

Legs cream to pale yellow. Brown stripe on ventral surface of femora I and II in one specimen.

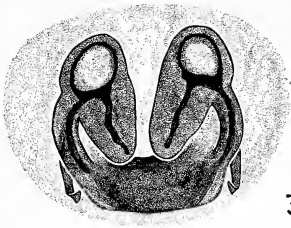
Labium brown. Endites pale yellow. Sternum cream.

Color. Male. Face and chelicerae pale yellow to yellow-orange. Black vertical stripes from AME to subdistal region of chelicerae as in Figure 63. Eye region black. Iridescent spatulate hairs between PME. Cymbia of palpi dark brown to black.

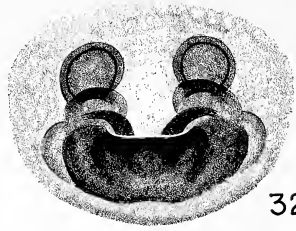
Carapace yellow to yellow-orange. Some purplish iridescence in one male.

Dorsum of abdomen with cardiac area translucent gray, surrounded by white pigment with lateral areas dark brown to black as in Figure 64. Other male with dorsum entirely black. Venter with dark patch over genital area. Dark median stripe from epigastric furrow to base of spinnerets. Spinnerets yellow. Other male with venter entirely black.

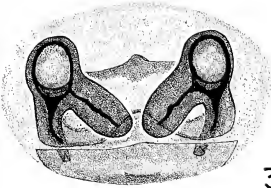
Legs yellow. Faint stripe on ventral surface of femur I in one male.



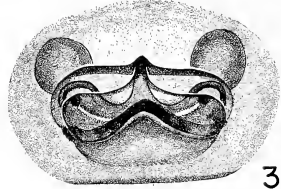
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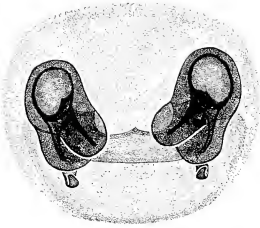
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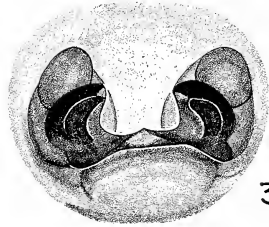
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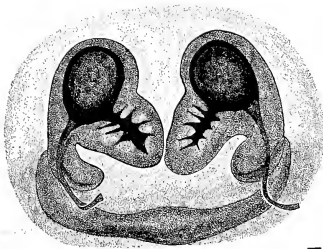


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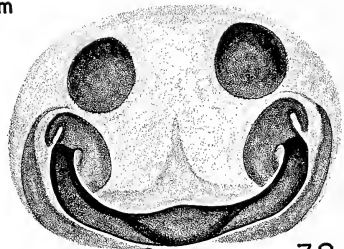


36

0.1mm



37



38

Labium and endites yellow to yellow-orange. Sternum yellow.

Diagnosis. *Oxyopes chiapas* is related to other members of the *acleistus* species group based upon its color pattern and genital structure. It is probably closest to *O. summus*, but is easily distinguished from this species and all others by the structure of the female genitalia (Figs. 33, 34) and the male palpus (Figs. 92, 93).

Record. MEXICO. *Chiapas*. La Zacualpa, Aug. 1909, ♂♂ : 5 ♀♀ :00 (AP).

Oxyopes summus new species

Figures 9, 10, 31, 32, 65, 66, 90, 91. Map 1.

Holotype. Male from Summit, Panama Canal Zone, 21-29 July 1950, (A.M. Chickering), in Museum of Comparative Zoology. The specific name is a noun in apposition after the type locality.

Measurements. Seven females and four males.

FEMALES: Mean		Range		Mean	Range
Clypeus	.440	.43-.48	Femur I	1.96	1.8-2.1
AME	.310	.30-.33	Patella-Tibia I	2.44	2.3-2.6
ALE	.608	.58-.63	Metatarsus I	1.96	1.8-2.1
PLE	1.065	1.03-1.13	Tarsus I	.80	.7-.9
PME	.578	.55-.60	Total Length I	7.16	6.7-7.7
Carapace Width	1.56	1.4-1.7			
Carapace Length	2.09	1.9-2.2	Patella-Tibia II	2.24	2.1-2.4
Total Length	4.87	4.2-5.5	Patella-Tibia III	1.68	1.6-1.8
			Patella-Tibia IV	1.97	1.8-2.1
			Total Length IV	6.55	6.0-7.1

Figs. 31-32. *Oxyopes summus* new species, female from Gamboa, Panama Canal Zone, 24 July 1954. 31. Internal genitalia. 32. Epigynum.

Figs. 33-34. *Oxyopes chiapas* new species, female from La Zacualpa, Chiapas, Aug. 1909. 33. Internal genitalia. 34. Epigynum.

Figs. 35-36. *Oxyopes tibialis* F.O.P.-Cambridge, female from Musawas on Waspuc River, Nicaragua, 10-31 Oct. 1955. 35. Internal genitalia. 36. Epigynum.

Figs. 37-38. *Oxyopes bifissus* F.O.P.-Cambridge, female from Tamazunchale, San Luis Potosi, 19 April 1963. 37. Internal genitalia. 38. Epigynum.

MALES:	Range		Range
Clypeus	.30-.38	Femur I	1.7-2.0
AME	.28-.30	Patella-Tibia I	2.2-2.7
ALE	.50-.55	Metatarsus I	2.0-2.4
PLE	.90-1.00	Tarsus I	.8-.9
PME	.50-.55	Total Length I	6.8-8.0
Carapace Width	1.3-1.6		
Carapace Length	1.7-2.1	Patella-Tibia II	2.0-2.4
Total Length	3.5-4.2	Patella-Tibia III	1.4-1.7
		Patella-Tibia IV	1.6-2.0
		Total Length IV	5.6-6.7

Color. Female. Face and chelicerae pale orange-yellow, lighter cream along lower edge of clypeus. A pair of black lines from AME to subdistal region of chelicerae as in Figure 9. Eye nacelles black.

Carapace pale orange-yellow with darker brown submarginal stripes as in Figure 10.

Dorsum of abdomen with a broad median white stripe from base to spinnerets, outlined with dark brown. Sides mottled with brown as in Figure 10.

Venter with a broad median black stripe from epigastric furrow to base of spinnerets, mottled with cream in center. Median stripe flanked by pale cream.

Legs yellow with mid-ventral black line on femora I and II. Line faintly visible on femora III.

Labium and endites cream to pale yellow with lighter distal ends. Sternum ivory to cream.

Color. Male. Face and chelicerae pale orange-yellow; lighter along lower edge of clypeus. Two black lines from AME to subdistal end of chelicerae as in Figure 65. Eye tubercles black.

Carapace pale orange-yellow with few scattered dusky hairs. Faint iridescent sheen of green and purple.

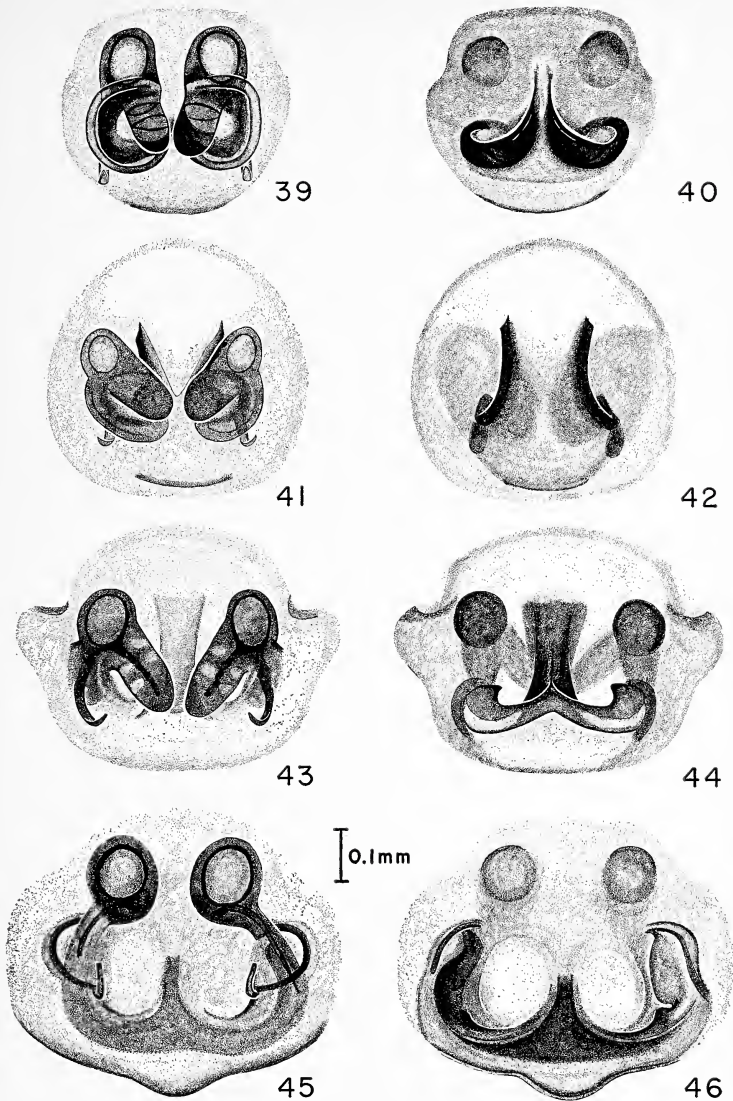
Dorsum of abdomen with a broad white stripe from base to tips of spinnerets, bordered laterally by mottled light brown extending along sides as in Figure 66.

Venter with wide black median stripe from genital area to base of spinnerets, bounded by pale yellow.

Legs yellow with mid-ventral black stripe on femora I-III.

Labium pale yellow with brownish tinge. Endites pale yellow. Sternum cream.

Diagnosis. *Oxyopes summus* is placed in the *acleistus* species group because of its leg formula of I-II~IV-III. Although its dorsal



Figs. 39-40. *Oxyopes felinus* Brady, female from SW of Acaponeta, Nayarit, 15 May 1965. 39. Internal genitalia. 40. Epigynum.

Figs. 41-42. *Oxyopes ocelot* new species, female from Arcelia, Guerrero, 2 Nov. 1974. 41. Internal genitalia. 42. Epigynum.

Figs. 43-44. *Oxyopes cornutus* F.O.P.-Cambridge, female from 8 mi. SW of Colima, Colima, 10 May 1963. 43. Internal genitalia. 44. Epigynum.

Figs. 45-46. *Oxyopes panther* new species, female from Palos Colorados, 25 mi. W of Durango, 5 Aug. 1947. 45. Internal genitalia. 46. Epigynum.

color pattern is like some members of the *tridens* group, the stripes on the face are more like the *acleistus* group. Finally the epigynum (Figs. 31, 32) and male palpus (Figs. 90, 91) are similar to members of the *acleistus* group (*O. chiapas*, for example), but these reproductive organs readily separate *summus* from related species. Its color pattern is also distinctive for the *acleistus* group.

Natural History. All of the specimens of *O. summus* collected by Chickering were included in the same vials with specimens of *O. salticus*. *Oxyopes salticus* were much more numerous. Presumably *O. summus* occurs in the same or an adjacent habitat.

Distribution. Costa Rica and Panama.

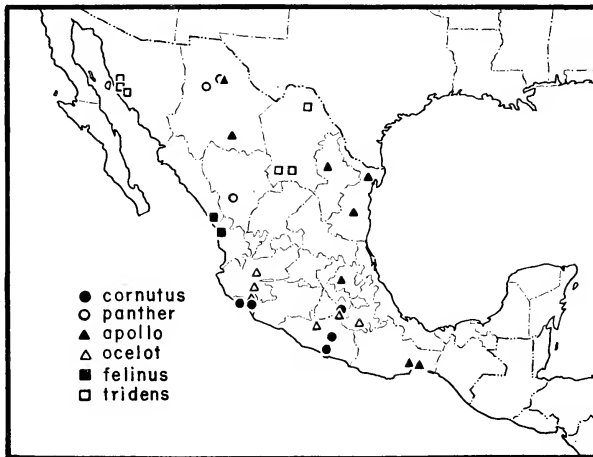
Records. COSTA RICA. Guanacaste. La Irma, 15 Aug. 1973, ♀, (ARB, RJW).

PANAMA. Canal Zone. Naval Air Station near Cocoli, 13 Jan. 1958, ♀, Gamboa, 24 July 1952, ♀, 1 July 1958, ♀, 2 mi. N of Paraiso, 21 Jan. 1958, ♀, Pédro Miguel, 31 Dec. 1957, ♂ ♂ ♀, Summit, 21-29 July 1950, ♀, 23-28 Aug. 1950, ♂ :3 ♀ ♀ (AMC).

Oxyopes apollo Brady

Map 2.

Oxyopes apollo Brady, 1964, Bull. Mus. Comp. Zool., 131(13):467, figs. 41, 42, 47-50, 72-75, ♂ ♀. Male holotype from Encino, Brooks Co., Texas, in the American Museum of Natural History. Brady, 1969, Psyche, 76(4):428.



Map 2.

Discussion. *Oxyopes floridanus* of Brady, 1964 was recognized as the same species as *O. apollo* in a review of the *apollo* species group (Brady, 1969). The reasons for synonymy are discussed in that paper.

For illustrations, measurements, color descriptions, diagnoses, notes on natural history, and collection records north of Mexico, see Brady (1964), pages 467-471 and Brady (1969), pages 428-431.

Distribution. Tennessee, Missouri, Arkansas, south through Oklahoma and Texas, west to Arizona and south through Nuevo Leon and Chihuahua to Oaxaca.

Records. MEXICO. *Tamaulipas.* San Pedro, May 1936, ♂ : 8 ♀♀ (W. A. Green), Santa Teresa, 15 May 1952, 3 ♀♀ : 0 (MAC, WJG, RS). *Nuevo Leon.* N of Monterey, 8 Aug. 1942, ♂. *Chihuahua.* 50 mi. S of Villa Ahumada, 11 June 1939, ♂ ♀♀ 0 (AMD, LID). *Hidalgo.* 10 mi. N of Ixmiquilipan, 5 July 1941, ♂ (AMD). *Oaxaca.* Jalapa, 28 Aug. 1947, ♂, Tuchtenan, 30 Aug. 1947, ♂ ♂ : 9 ♀♀ : 0 (HMW).

Oxyopes tridens Brady

Map 2.

Oxyopes tridens Brady, 1964, Bull. Mus. Comp. Zool., 131(13):472, figs. 45, 46, 53-55, 62, 63, 70, 71, ♂ ♀. Male holotype from Mercury, Nye Co., Nevada, in the American Museum of Natural History.

Discussion. For illustrations, measurements, color description, diagnosis, notes on natural history, and collection records north of Mexico, see Brady (1964), pages 472-474.

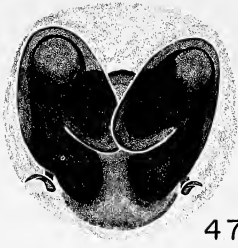
Records. MEXICO. *Coahuila.* La Gloria, 24 Aug. 1947, ♀ (WJG); 20 mi. E of San de las Colonias, 5 July 1936, ♀ (AMD, LID). *Chihuahua.* Samalayuca, 25 June 1947, ♂ (WJG). *Sonora.* El Desemboque, 1-10 Sept. 1953, ♂, 25 km S of El Desemboque, 11 Aug. 1953, ♀ (BM); 10 mi. S of Hermosillo, 16 June 1939, ♀ (AMD, LID).

Oxyopes felinus Brady

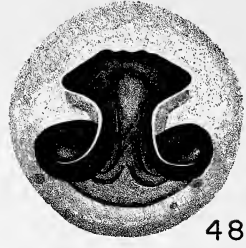
Figures 21, 22, 39, 40, 69, 70, 102, 103. Map 2.

Oxyopes felinus Brady, Bull. Mus. Comp. Zool., 131(13):476, figs. 56, 57, 64, 65, ♂. Male holotype from Molino Basin, Santa Catalina Mtns., Pima Co., Arizona, in the Museum of Comparative Zoology.

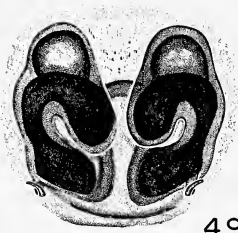
Discussion. The female of *O. felinus* is described here for the first time. A male from Mexico is also described and illustrated for comparison to the holotype.



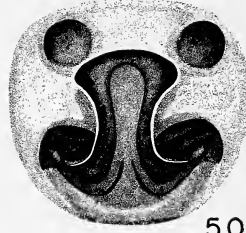
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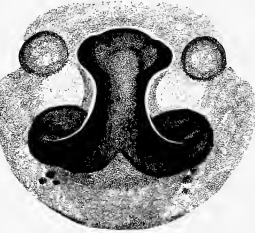
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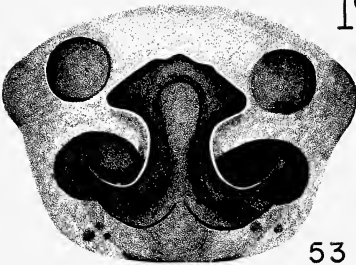


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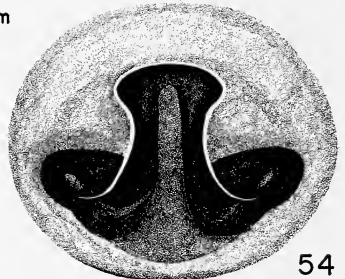


52

0.1mm



53



54

Measurements. Seven females and four males.

FEMALES: Mean			Range			Mean			Range		
Clypeus	.460	.43-.50	Femur I	1.66	1.6-1.8						
AME	.290	.28-.30	Patella-Tibia I	1.94	1.9-2.0						
ALE	.525	.50-.55	Metatarsus I	1.70	1.6-1.9						
PLE	.965	.93-1.00	Tarsus I	.73	.7-.8						
PME	.510	.48-.55	Total Length I	6.04	5.8-6.4						
Carapace Width	1.48	1.4-1.6									
Carapace Length	1.98	1.8-2.1	Patella-Tibia II	1.79	1.6-1.9						
Total Length	4.96	4.3-5.7	Patella-Tibia III	1.35	1.2-1.5						
			Patella-Tibia IV	1.97	1.8-2.1						
			Total Length IV	7.12	6.8-7.6						

MALES:			Range			Range		
Clypeus		.43-.45	Femur I		1.7			
AME		.28-.30	Patella-Tibia I		2.0-2.2			
ALE		.50-.53	Metatarsus I		2.0-2.1			
PLE		.93-.98	Tarsus I		.8-.9			
PME		.48-.53	Total Length I		6.5-6.8			
Carapace Width		1.4-1.5						
Carapace Length		1.9-2.0	Patella-Tibia II		1.8-2.0			
Total Length		4.2-4.4	Patella-Tibia III		1.4-1.5			
			Patella-Tibia IV		2.0-2.1			
			Total Length IV		7.2-7.6			

Color. Female. Face and chelicerae white to cream with wide dark brown stripes from ALE to distal end of chelicerae as in Figure 21. Eye region dark brown to black overlaid with white spatulate-shaped hair.

Figs. 47-48. *Oxyopes flavus* Banks, female from Iquala, Guerrero, 27 Oct. 1947. 47. Internal genitalia. 48. Epigynum.

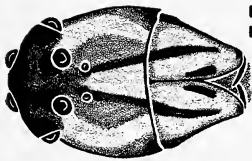
Figs. 49-50. *Oxyopes flavus* Banks, female from Tonalá, Chiapas, Aug. 1909. 49. Internal genitalia. 50. Epigynum.

Fig. 51. *Oxyopes flavus* Banks, epigynum of female from Alamos, Sonora, 7 Aug. 1956.

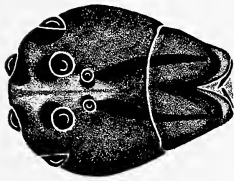
Fig. 52. *Oxyopes lingulifer* F.O.P.-Cambridge = *O. flavus*, epigynum of female holotype from Costa Rica.

Fig. 53. *Oxyopes flavus* Banks, epigynum of female from Valles, San Luis Potosí, 19 July 1956.

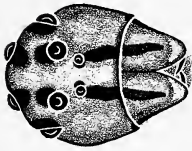
Fig. 54. *Oxyopes flavus* Banks, epigynum of female syntype from Sierra San Lazaro, Baja California.



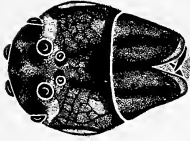
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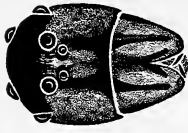
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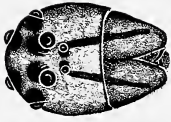
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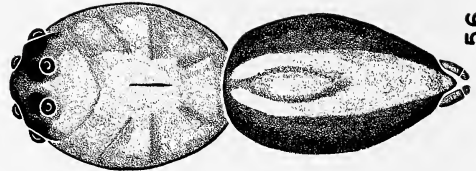
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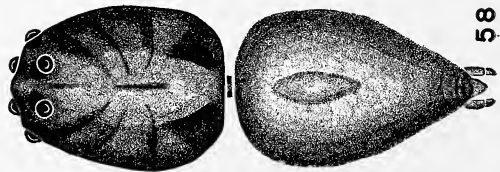
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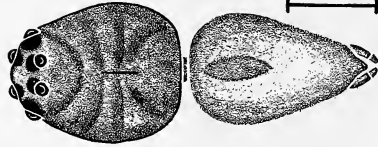
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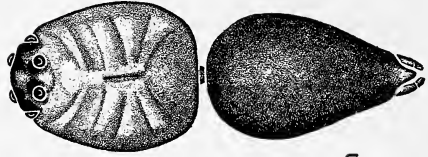
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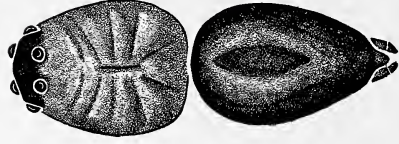
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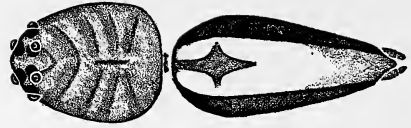
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62



64



66

Carapace cream to golden yellow with broad dark brown submarginal stripes as in Figure 22.

Dorsum of abdomen with cardiac area translucent cream, outlined with brown. Median area white to cream with lateral areas darker, mottled with dark brown or black against white as in Figure 22. Venter with dark brown median stripe, divided longitudinally into three narrower stripes, bounded on its edges by white or cream. Sides mottled brown and cream.

Legs yellow. Distal ends of femora and tibia with irregular dark markings. A pair of dark ventro-lateral stripes on femora I-III.

Labium brown with lighter yellow anterior end. Endites yellow. Sternum yellow with brown splotches near base of femora.

Color. Male. Face and chelicerae orange-brown with the central area of the face black and lateral areas thickly clothed with white hair as in Figure 69 or face orange-brown with two broad vertical black stripes from ALE to subdistal region of chelicerae. Eye region black.

Carapace yellow-orange with wide dark brown submarginal stripes as in Figure 70.

Dorsum of abdomen with white median longitudinal stripe from base to tip of spinnerets, bordered by dark brown to black as in Figure 70. Venter with broad median black stripe beginning over genital area and continuing to base of spinnerets. Black stripe outlined in cream or pale yellow, darker mottled brown along sides. Metallic sheen from transparent appressed hairs.

Legs yellow with dusky ventral surface.

Labium dark brown. Endites dark brown with distal ends yellow. Sternum yellow with dusky patches near base of coxae.

Figs. 55-56. *Oxyopes bifidus* F.O.P.-Cambridge, male from Compostela, Nayarit, 12 July 1972. 55. Face view. 56. Dorsal view.

Figs. 57-58. *Oxyopes bifissus* F.O.P.-Cambridge, male from Tamazunchale, San Luis Potosi, 19 April 1963. 57. Face view. 58. Dorsal view.

Figs. 59-60. *Oxyopes bifissus* F.O.P.-Cambridge, male from Palomares, Oaxaca, July 1909. 59. Face view. 60. Dorsal view.

Figs. 61-62. *Oxyopes tibialis* F.O.P.-Cambridge, male from E of Tela, Honduras, 26 July 1924. 61. Face view. 62. Dorsal view.

Figs. 63-64. *Oxyopes chiapas* new species, male holotype from La Zacualpa, Chiapas, Aug. 1909. 63. Face view. 64. Dorsal view.

Figs. 65-66. *Oxyopes summus* new species, male holotype from Summit, Panama Canal Zone, 21-29 July 1950. 65. Face view. 66. Dorsal view.

Diagnosis. *Oxyopes felinus* has the over-all black and white color pattern of other members of the *tridens* group. It does not have a strongly developed patellar apophysis, such as that found in *O. tridens* and *O. pardus*, but has a small protuberance on the patella. *Oxyopes felinus* is most closely related to *O. cornutus*, resembling this species in color and male and female reproductive organs. It can be distinguished from *O. cornutus* by reference to the epigyna (compare Figs. 39, 40 with Figs. 43, 44) and the male palpi (compare Figs. 102, 103 with Figs. 104, 105).

Distribution. Arizona, Sinaloa, Nayarit (Map 2).

Records. NORTH AMERICA. *Arizona.* Pima Co.: Molino Basin, Santa Catalina Mtns., 12 July 1962, ♂ (ARB).

MEXICO. *Nayarit.* SW of Acaponeta, 15 May 1963, 3 ♂♂ : 7 ♀♀ :900 (WJG, WI). *Sinaloa.* Rosario, 15 May 1963, ♂ (WJG, WI).

Oxyopes cornutus F.O.P.-Cambridge

Figures 19, 20, 43, 44, 67, 68, 82, 83, 104, 105. Map 2.

Oxyopes cornutus F.O.P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, Araneidea, 2:343, pl. 32, fig. 16, ♂. Male holotype from Tierra Colorado, Guerrero, Mexico, in British Museum (Natural History), examined.

Discussion. The female of *O. cornutus* is described here for the first time and the male redescribed.

Measurements. Ten females and eight males.

FEMALES: Mean			Range			Mean		Range	
Clypeus	.505	.43-.58	Femur I	2.12	1.8-2.4				
AME	.308	.30-.33	Patella-Tibia I	2.50	2.2-2.8				
ALE	.603	.55-.68	Metatarsus I	2.31	2.0-2.8				
PLE	1.083	.98-1.20	Tarsus I	.84	.8-.9				
PME	.580	.53-.65	Total Length I	7.76	7.0-8.9				
Carapace Width	1.66	1.5-1.9	Patella-Tibia II	2.29	2.1-2.7				
Carapace Length	2.23	1.8-2.7	Patella-Tibia III	1.65	1.4-1.9				
Total			Patella-Tibia IV	2.42	2.1-2.8				
Length	5.80	4.7-7.2	Total Length IV	8.66	7.5-9.9				

MALES:	Mean	Range		Mean	Range
Clypeus	.438	.35-.50	Femur I	2.14	1.9-2.3
AME	.290	.25-.30	Patella-Tibia I	2.62	2.4-2.9
ALE	.560	.50-.63	Metatarsus I	2.61	2.3-2.9
PLE	1.023	.93-1.15	Tarsus I	1.02	.9-1.1
PME	.550	.50-.60	Total Length I	8.40	7.5-9.2
Carapace Width	1.59	1.5-1.7			
Carapace Length	2.10	1.9-2.4	Patella-Tibia II	2.36	2.2-2.6
Total Length	4.80	4.3-5.3	Patella-Tibia III	1.64	1.5-1.8
			Patella-Tibia IV	2.34	2.2-2.5
			Total Length IV	8.39	7.6-8.9

Color. Female. Face and chelicerae white with a pair of wide dark brown stripes from ALE to subdistal ends of chelicerae as illustrated in Figure 19.

Carapace with median area white, bounded by wide dark brown submarginal stripes, with white at margins as in Figure 20.

Dorsum of abdomen with median white stripe outlined in black, becoming dark brown laterally. Two pairs of white marks posteriorly as in Figure 20. Venter with median area dusky, bounded by pale cream, becoming darker (light brown) laterally.

Legs yellow to light brown, overlaid with dark hair. Femora with dark stripe along antero-ventral surface.

Labium and endites yellow. Sternum cream to pale yellow.

Color. Male. Face with dark brown or black median area bounded by white and chelicerae with vertical black stripes as in Figure 67. Eye region black. Cymbia of palpi black.

Carapace with broad median white stripe bounded by wide submarginal stripes, with the margins of the carapace white as in Figure 68.

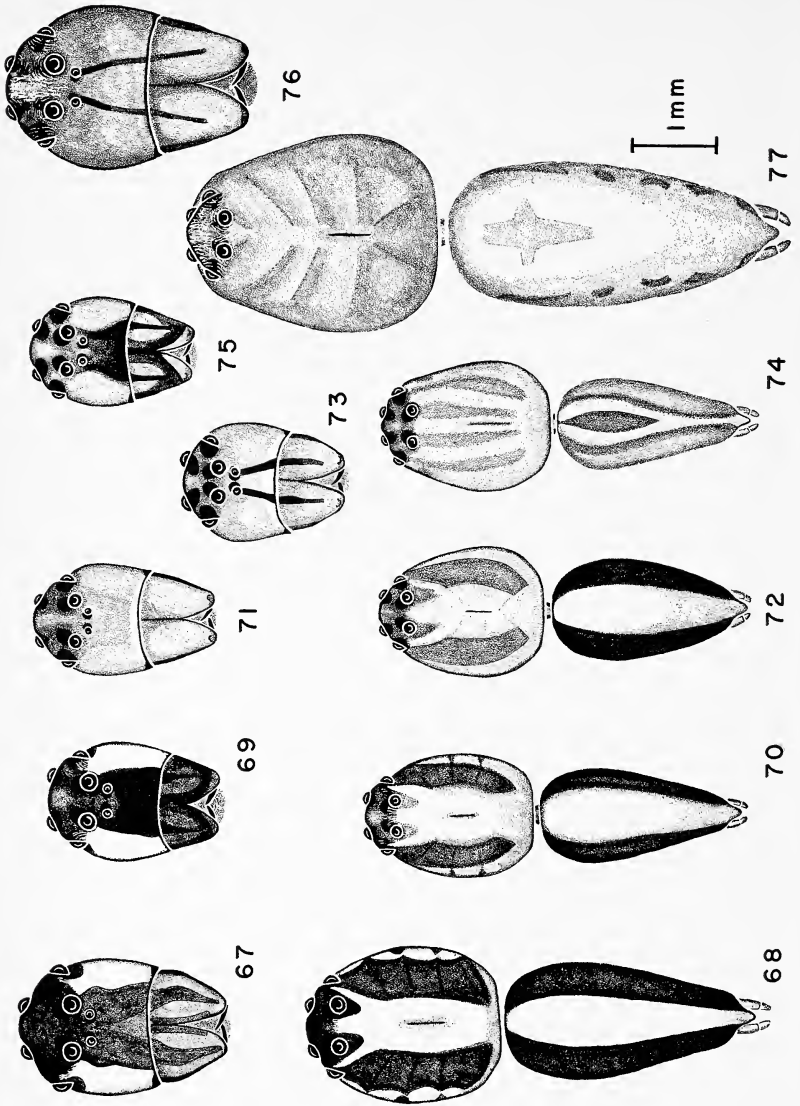
Dorsum of abdomen with a median stripe bounded by black as in Figure 68.

Venter with dark brown median stripe outlined in pale cream to yellow and becoming darker laterally.

Legs yellow to brown, overlaid with dusky hair, without distinct darker markings.

Labium and endites pale yellow. Sternum cream to pale yellow.

Diagnosis. *Oxyopes cornutus*, particularly the male, has a black and white color pattern similar to *O. tridens* and *O. pardus*. The male of *O. cornutus* lacks a patellar apophysis such as that found in



O. tridens and *O. pardus*. *Oxyopes cornutus* appears to be most closely related to *O. felinus* in male palpal structure and female epigynal structure. It can, however, be readily separated from *O. felinus* by comparing the male palpi (compare Figs. 104, 105 with Figs. 102, 103) and female epigyna (compare Figs. 43, 44 with Figs. 39, 40).

Natural History. *Oxyopes cornutus* is not as well represented in collections as *O. salticus* or *O. bifidus*. It is apparently not often taken by sweeping vegetation. A number of these spiders were observed as they were running and jumping over a rock slide in Zopilote Canyon, 10 mi N of Zumpango del Río. This was an old rock slide with sparse, grassy vegetation growing among the rock rubble. The over-all background color of this substrate was gray, and the black and white pattern of *O. cornutus* blended well with this particular habitat. The spiders became conspicuous only when they moved. Specimens from the rock slide were collected by hand since there was not enough vegetation to employ a sweep net.

The occurrence of *Oxyopes cornutus* in a rather dry, rocky habitat with little vegetation fits well with what is known of the biology of the *tridens* species group so far as I've observed. Members of this group appear to have an ecological niche quite distinct from members of the *acleistus* group which occur in considerable numbers in grassy and herbaceous vegetation.

Distribution. Colima, Guerrero, and Morelos (Map 2).

Records. Colima. 8 mi. SW of Colima, 10 May 1963, ♂♂ : 4 ♀♀ :00 (WJG, WI); 7 mi. SE of Manzanillo, 16 July 1972, ♂ (AJ). Guerrero. Tierra Colorado, ♂ (HHS), 22-23 July 1972. 3 ♂♂ : ♀♀ :1000 (ARB); 10 mi. N of Zumpango del Río, 23 July 1972, ♂♂ ♀♀ :400 (ARB, AJ). Morelos. Acatlipa, 10 Aug. 1946, ♀♀ (CG, FB).

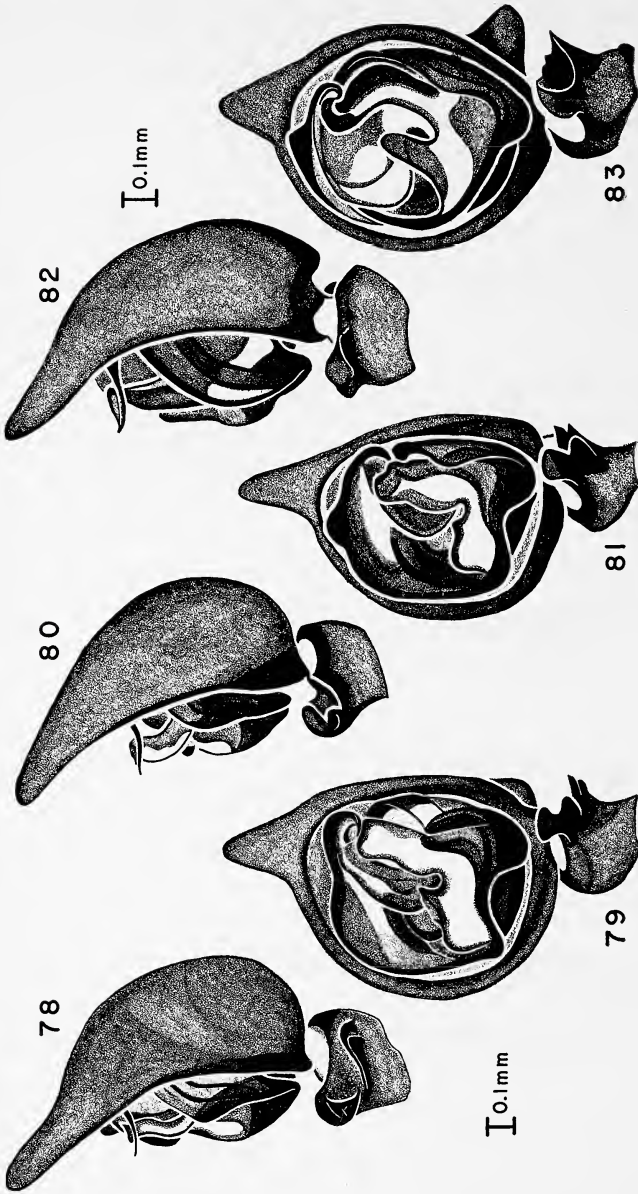
Figs. 67-68. *Oxyopes cornutus* F.O.P.-Cambridge, male from 8 mi. SW of Colima, Colima, 10 May 1963. 67. Face view. 68. Dorsal view.

Figs. 69-70. *Oxyopes felinus* Brady, male from SW of Acaponeta, 15 May 1963. 69. Face view. 70. Dorsal view.

Figs. 71-72. *Oxyopes ocelot* new species, male holotype from W of Lake Sayula, Jalisco, 3 Aug. 1956. 71. Face view. 72. Dorsal view.

Figs. 73-75. *Oxyopes salticus* Hentz, males from Veracruz, Veracruz, 30 July 1972. 73. Face view. 74. Dorsal view. 75. Face view, indicating variation in color pattern.

Figs. 76-77. *Oxyopes flavus* Banks, male from Tierra Colorado, Guerrero, 23 July 1972. 76. Face view. 77. Dorsal view.



Oxyopes panther new species

Figures 15, 16, 45, 46. Map 2.

Oxyopes sp. Brady, 1969, Psyche, 76(4):437, figs. 5, 6, 16, 17, ♀. Female from 12 mi. W of Portal, Cochise Co., Arizona, 13 July 1968, in the Museum of Comparative Zoology.

Holotype. Female from 12 mi. W of Portal, Cochise Co., Arizona, 13 July 1968, (L. D. Mikelson) in the Museum of Comparative Zoology. The specific name is a noun in apposition after the Panther.

Discussion. In an earlier paper on the *apollo* species group I illustrated and described an unknown female *Oxyopes* from Portal, Arizona (Brady, 1969). Since the females of *O. pardus*, *O. lynx*, and *O. felinus* were unknown at that time, I thought it best not to assign a distinctive name to a single female specimen that belonged to the same species group. During the present study four additional females of this same species were found in collections from Mexico. Although the male is still not known, I have decided to name the females in order that they can be identified. The actual relationship of these five females to *O. pardus* will be determined only when males and females are found in association.

Measurements. For measurements of the holotype see Brady, 1969. The range for the four Mexican females is given below.

Measurements. Four females.

FEMALES:	Range		Range
Clypeus	.55-.58	Femur I	1.9-2.2
AME	.30-.33	Patella-Tibia I	2.1-2.5
ALE	.53-.58	Metatarsus I	2.0-2.2
PLE	1.00-1.08	Tarsus I	.8-1.0
PME	.53-.58	Total Length I	6.8-7.8
Carapace			
Width	1.7-1.9	Patella-Tibia II	2.1-2.4
Carapace		Patella-Tibia III	1.6-1.9
Length	2.2-2.5	Patella-Tibia IV	2.4-2.8
Total		Total Length IV	8.4-9.8
Length	5.9-7.2		

Figs. 78-79. *Oxyopes bifidus* F.O.P.-Cambridge, male from Compostela, Nayarit, 12 July 1972. 78. Left palpus, retrolateral view. 79. Left palpus, ventral view.

Figs. 80-81. *Oxyopes bifidus* F.O.P.-Cambridge, male holotype from Acapulco, Guerrero. 80. Retrolateral view. 81. Ventral view.

Figs. 82-83. *Oxyopes cornutus* F.O.P.-Cambridge, male holotype from Tierra Colorado, Guerrero. 82. Retrolateral view. 83. Ventral view.

Scale on the left is for Figs. 78-79.

Scale on the right is for Figs. 80-83.

Color. Female from Mexico. Face and chelicerae pale cream to yellow, overlaid with white appressed hair. Brown stripes from AME to subdistal region of chelicerae as in Figure 15. Eye nacelles black, covered with white hair.

Carapace yellow, overlaid with white spatulate-shaped hair. Wide dark brown submarginal stripes as in Figure 16.

Dorsum of abdomen with broad median white stripe outlined with brown; brown mottled with white along sides as in Figure 16. Venter with a wide mottled brown and yellow median stripe from epigastric furrow to base of spinnerets. This stripe surrounded by pale cream laterally.

Legs yellow, shaded with brown.

Labium pale yellow, with brown along sides. Endites and sternum pale yellow.

Diagnosis. On the basis of morphological characteristics, color pattern, and the structure of the female genitalia *O. panther* belongs close to *O. tridens*. Since the female of *O. pardus*, another closely related species, is unknown, it is difficult to establish its relationship to *O. panther*. As has been suggested previously (Brady, 1969), *O. panther* may be the female of *O. pardus*. Until we have males and females collected together, it will be impossible to reach a decision. *Oxyopes panther* is easily distinguished from *O. tridens* by its epigynum (compare Figs. 43, 44 and figs. 16, 17 of Brady, 1969 with figs. 53-55 of Brady, 1964).

Natural History. One note of interest is that *O. panther* has not been found below 6,000 feet in elevation. Altitudes are listed for specimens in the records below.

Distribution. Arizona, Chihuahua, and Durango (Map 2).

Records. NORTH AMERICA. *Arizona.* Cochise Co.: 12 mi. W of Portal, 6,000 ft. (1,830 m), 13 July 1968, ♀ (L. D. Mikelson).

MEXICO. *Chihuahua.* W summit of Primavera near Gallego, 7,000 ft. (2,135 m), 2 July 1947, ♀ (WJG); NE summit of San José Babicora, 7,700 ft. (2,350 m), 3 July 1947, ♀ (WJG). *Durango.* Palos Colorados about 25 mi. W of Durango, 8,000 ft. (2,440 m), 5 Aug. 1947, ♀ (WJG).

***Oxyopes ocelot* new species**

Figures 17, 18, 41, 42, 71, 72, 100, 101. Map 2.

Holotype. Male from W side of Lake Sayula, Jalisco, Mexico, 3 Aug. 1956, (W. J. Gertsch, V. D. Roth), in the American Museum of Natural History. The specific name is a noun in apposition after the Ocelot.

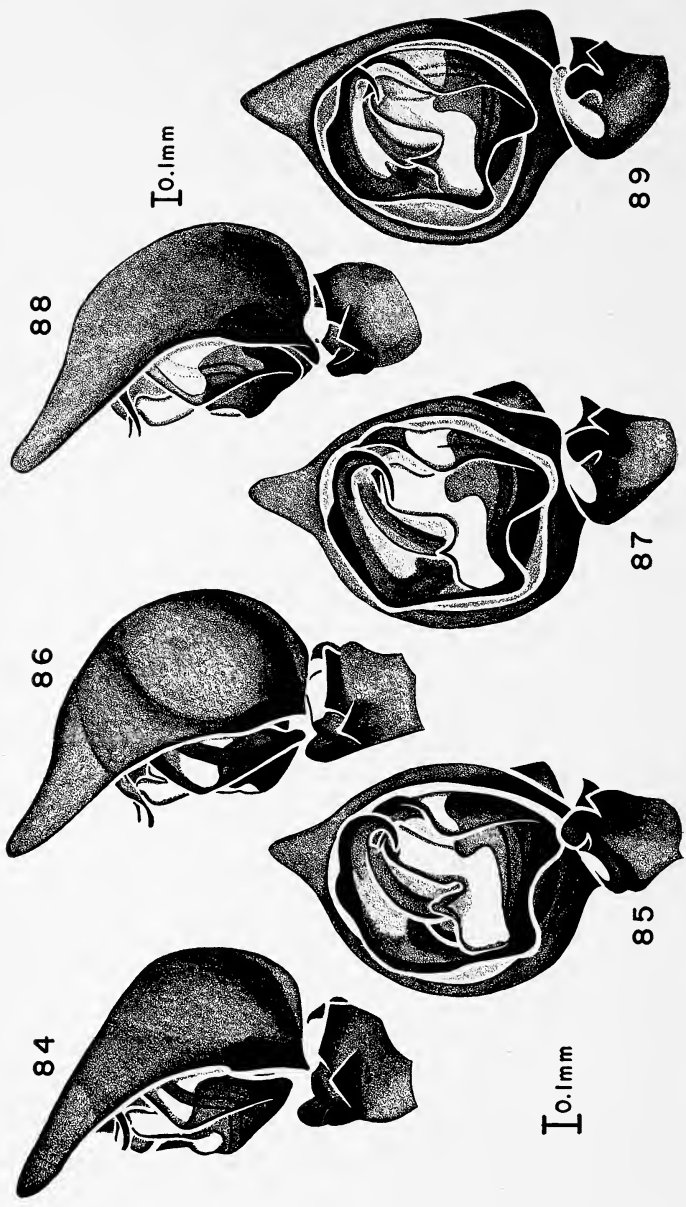
Measurements. Seven females and ten males.

FEMALES:			Mean	Range	
Clypeus	.530	.45-.65	Femur I	1.90	1.6-2.2
AME	.320	.30-.33	Patella-Tibia I	2.26	2.0-2.6
ALE	.540	.50-.58	Metatarsus I	2.00	1.7-2.3
PLE	.990	.93-1.05	Tarsus I	.79	.7-.8
PME	.540	.50-.58	Total Length I	6.96	6.0-7.8
Carapace Width	1.66	1.5-1.9	Patella-Tibia II	2.10	1.8-2.4
Carapace Length	2.26	2.0-2.6	Patella-Tibia III	1.62	1.4-1.8
Total Length	5.90	4.9-6.9	Patella-Tibia IV	2.49	2.2-2.8
			Total Length IV	8.76	7.9-9.7

MALES:			Mean	Range	
Clypeus	.445	.43-.48	Femur I	1.77	1.6-2.0
AME	.285	.25-.33	Patella-Tibia I	2.21	2.0-2.5
ALE	.480	.45-.53	Metatarsus I	2.10	1.9-2.4
PLE	.883	.80-.98	Tarsus I	.86	.8-1.0
PME	.478	.45-.53	Total Length I	6.94	6.3-7.8
Carapace Width	1.47	1.3-1.6	Patella-Tibia II	2.01	1.9-2.3
Carapace Length	1.97	1.8-2.2	Patella-Tibia III	1.51	1.4-1.7
Total Length	4.20	3.6-4.6	Patella-Tibia IV	2.26	2.0-2.5
			Total Length IV	7.97	7.3-8.8

Color. Female. Face and chelicerae yellow to yellow-orange with faint darker vertical stripes from AME to subdistal region of chelicerae as in Figure 17. Eye nacelles black. Lower edge of clypeus lighter, pale yellow.

Carapace pale yellow to yellow with a pair of wide brown submarginal stripes as in Figure 18.



Dorsum of abdomen dark brown with a wide median white stripe as in Figure 18. Sides of abdomen pale yellow with irregular brown spots. Venter with a wide brown stripe from epigastric furrow to base of spinnerets, outlined by white or pale yellow.

Legs yellow to yellow-orange with mid-ventral black stripe on femora I and II.

Labium pale yellow, brownish along sides. Endites pale yellow. Sternum cream to pale yellow.

Color. Male. Face and chelicerae pale yellow to light orange without darker markings, with lower edge of clypeus cream as in Figure 71. Palpi light to dark brown.

Carapace yellow to pale yellow-orange with darker brown submarginal stripes as in Figure 72.

Dorsum of abdomen with broad white median stripe bordered by dark brown to black as in Figure 72. Venter with wide median brownish stripe from epigastric furrow to base of spinnerets, bordered by lighter cream.

Legs pale yellow with mid-ventral black lines on femora I-II.

Labium and endites pale yellow. Sternum cream to pale yellow.

Dark Male. A single darker colored male has the face and chelicerae orange brown without distinct darker markings. Cymbia of palpi black.

Carapace yellow-orange with dark brown submarginal stripes.

Dorsum with broad white median stripe overlaid with darker scale-like hairs. Venter with median stripe dark brown to black.

Diagnosis. *Oxyopes ocelot* has the well-developed fourth pair of legs and the broad median white stripe of the abdomen flanked by black that is characteristic of the *tridens* species group. The face is not strongly marked as in other members of the group, however. The palpal organ of the male and to a lesser extent the epigynum of this species place it closest to *O. cornutus*. *Oxyopes ocelot* is distinguished from this species by its coloration and the distinctive male palpus (compare Figs. 100, 101 to Figs. 104, 105) and female epigynum (compare Figs. 41, 42 with Figs. 43, 44).

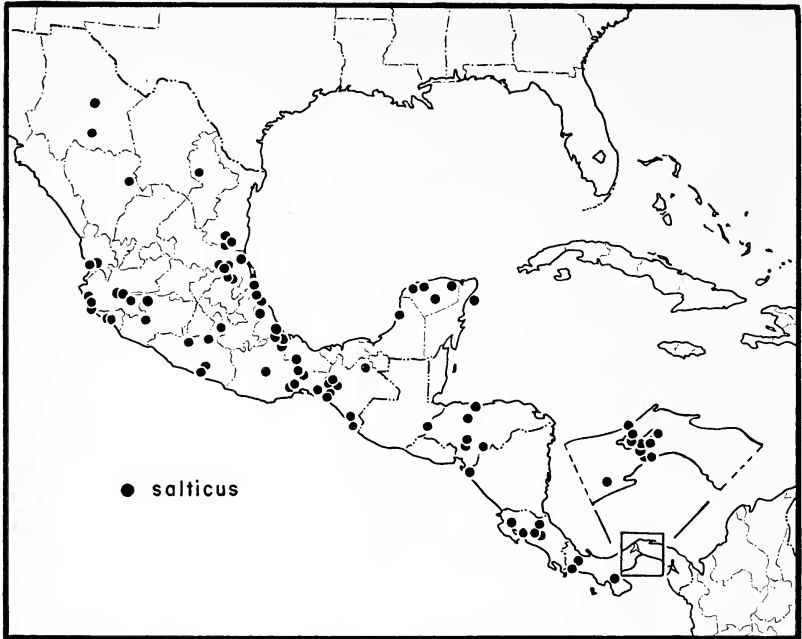
Figs. 84-85. *Oxyopes calcarifer* F.O.P.-Cambridge = *O. bifissus*, male holotype from Costa Rica. 84. Retrolateral view. 85. Ventral view.

Figs. 86-87. *Oxyopes bifissus* F.O.P.-Cambridge, male lectotype from Teapa, Tabasco. 86. Retrolateral view. 87. Ventral view.

Figs. 88-89. *Oxyopes bifissus* F.O.P.-Cambridge, male from Compostela, Nayarit, 12 July 1972. 88. Left palpus, retrolateral view. 89. Left palpus, ventral view.

Scale on the left is for Figs. 84-87.

Scale on the right is for Figs. 88-89.



Map 3.

Distribution. Puebla, Morelos, Jalisco, Colima, and Guerrero. (Map 2).

Records. *Puebla.* Acatlan, 24-27 Sept. 1946, ♀ (HMW). *Morelos.* Alpoyecá, 28 July 1956, ♂ (WJG, VDR). *Jalisco.* Guadalajara, 19 Sept. 1957, ♂ (RD); La Venta, 19 July 1953, ♂ (Albert Robinson, Jr.); W side of Lake Sayula, 3 Aug. 1956, ♂♂ (WJG, VDR). *Colima.* 20 mi. N of Colima, 2 Aug. 1956, ♀ (VDR, WJG). *Guerrero.* Arcelia, 2 Nov. 1947, 5♂♂:4♀♀:0 (HMW).

Oxyopes scalaris Hentz

Map 4.

Oxyopes scalaris Hentz, 1845, Boston Jour. Nat. Hist., 5:196, pl. 17, fig. 4, ♀. Female syntypes from North Carolina, lost; *ibid.*, 1875, Occ. Pap. Boston Soc. Nat. Hist., 2:47, pl. 7, fig. 4, pl. 19, fig. 120, ♀. Roewer, 1954, Katalog der Araneae, 2(a):334. Bonnet, 1958, Bibliographia Araneorum, 2(4):3241. Brady, 1964, Bull. Mus. Comp. Zool., 131(13): 484, figs. 87-90, 97-99, 106, 107, ♂♀.

Discussion. For a list of synonyms, measurements, illustrations, color descriptions, natural history, and records north of Mexico see Brady, 1964, pages 484-495.

Diagnosis. *Oxyopes scalaris* is unlike any other Mexican or Central American species of *Oxyopes*, although it clearly falls within the limits of the genus. The closest relatives of *O. scalaris* appear to be certain European species, such as *O. ramosus* or *O. heterophthalmus* (Brady, 1964).

Oxyopes scalaris can be easily recognized by the epigynum (figs. 97-99 of Brady, 1964) and the male palpus (figs. 106, 107 of Brady, 1964).

Distribution. Canada to northern Mexico.

Records. MEXICO. *Chihuahua*. 25 mi W of Camargo, 13 July 1947, ♂, Huejotitlan, 20 July 1947, ♀, Matachic, 6 July 1947, ♀ (WJG).

Oxyopes salticus Hentz

Figures 11, 12, 23, 24, 73-75, 98, 99. Map 3.

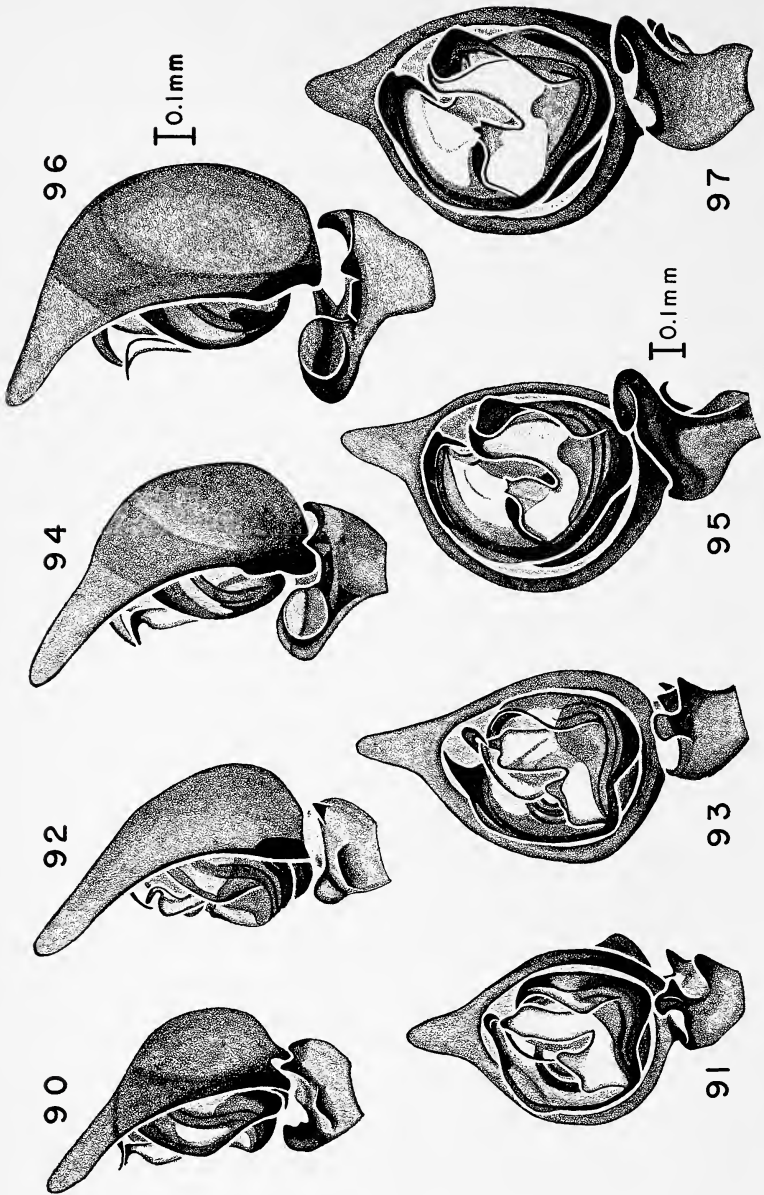
Oxyopes salticus Hentz, 1845, Boston Jour. Nat. Hist., 5:196, pl. 16, fig. 10, ♀. Female syntypes from North Carolina and Alabama, lost. Hentz, 1875, Occ. Pap. Boston Soc. Nat. Hist., 2:47, pl. 6, fig. 10, ♀. Roewer, 1954, Katalog der Araneae, 2(a):333. Bonnet, 1958, Bibliographia Araneorum, 2(4):3240. Brady, 1964, Bull. Mus. Comp. Zool., 131(13):478, figs. 80-86, 91-96, 104, 105, ♂ ♀.

Oxyopes luteus Blackwall, 1862, Ann. Mag. Nat. Hist. 10(3):350, ♂ ♀. Female holotype from Brazil in the University Museum, Oxford, England.

Oxyopes varians Taczanowski, 1873, Hor. Soc. Ent. Ross., 10:95, ♀ ♂. Female holotype from French Guiana in Instytut Zool. Polska Akademia Nauk, Warsaw, Poland.

Oxyopes gracilis Keyserling, 1877, Verh. Zool.-Bot. Ges. Wien, 26:698, pl. 2, figs. 63, 64, ♀. Syntypes from New Granada (Panama, Ecuador, Peru, Colombia, Venezuela) in the British Museum (Natural History), examined. F.O.P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, Araneidea 2:343, pl. 32, figs. 14, 14a, 14b, 15, 15a, 15b, ♂ ♀. Brady, 1964, Bull. Mus. Comp. Zool., 131(13):479, figs. 102, 103, ♂.

Discussion. In 1963 I examined large numbers of *O. salticus* from North America southward to Brazil. I noted a slight difference in the structure of the male palpus in specimens from central Mexico southward (Brady, 1964). Because of this difference (compare figs. 102, 103 to figs. 104, 105 of Brady, 1964) I decided to retain the name *O. gracilis* Keyserling for populations from central Mexico to Brazil. Having collected *O. salticus* in Mexico and Central America and examined numerous specimens from that area and South America, I have concluded that the slight differences in the male palpi between *O. salticus* and *O. gracilis* are simply a



reflection of geographic variation. Therefore, I now consider *O. gracilis*, *O. luteus*, and *O. varians* to be junior synonyms of *O. salticus*. This decision has been influenced by the considerable amount of variation seen within local populations of *Oxyopes* in Mexico and Central America.

Measurements. Ten females and ten males.

FEMALES: Mean			Range			Mean			Range		
Clypeus	.438	.38-.53	Femur I	2.20	1.9-2.6						
AME	.310	.30-.35	Patella-Tibia I	2.79	2.3-3.4						
ALE	.510	.48-.58	Metatarsus I	2.21	1.8-2.8						
PLE	.940	.85-1.05	Tarsus I	.95	.8-1.1						
PME	.508	.48-.58	Total Length I	8.16	6.9-9.9						
Carapace											
Width	1.64	1.4-1.9	Patella-Tibia II	2.58	2.1-3.2						
Carapace			Patella-Tibia III	2.00	1.6-2.4						
Length	2.27	2.0-2.6	Patella-Tibia IV	2.38	2.0-2.8						
Total			Total Length IV	7.76	6.6-9.2						
Length	5.34	4.4-6.0									
MALES: Mean			Range			Mean			Range		
Clypeus	.395	.33-.45	Femur I	2.13	1.8-2.4						
AME	.293	.28-.30	Patella-Tibia I	2.73	2.3-3.0						
ALE	.473	.43-.50	Metatarsus I	2.54	2.0-2.8						
PLE	.870	.75-.93	Tarsus I	1.18	1.0-1.3						
PME	.473	.43-.50	Total Length I	8.58	7.1-9.3						
Carapace											
Width	1.64	1.4-1.8	Patella-Tibia II	2.50	2.0-2.7						
Carapace			Patella-Tibia III	1.95	1.6-2.1						
Length	2.18	1.8-2.4	Patella-Tibia IV	2.26	1.9-2.4						
Total			Total Length IV	7.73	6.5-8.4						
Length	4.46	3.7-4.8									

Figs. 90-91. *Oxyopes summus* new species, male holotype from Summit, Panama Canal Zone, 21-29 July 1950. 90. Left palpus, retrolateral view. 91. Left palpus, ventral view.

Figs. 92-93. *Oxyopes chiapas* new species, male holotype from La Zacualpa, Chiapas, Aug. 1909. 92. Retrolateral view. 93. Ventral view.

Figs. 94-95. *Oxyopes tibialis* F.O.P.-Cambridge, male from E of Tela, Honduras, 26 July 1929. 94. Retrolateral view. 95. Ventral view.

Figs. 96-97. *Oxyopes tibialis* F.O.P.-Cambridge, male lectotype from Guatemala. 96. Retrolateral view. 97. Ventral view.

Scale on left, below is for Figs. 90-95.

Scale on right, above is for Figs. 96-97.

Color. Female. Face and chelicerae cream to pale yellow. Black stripes beginning under AME and continuing down chelicerae as in Figure 11. A black dash and a spot below this in cheek area. Eye nacelles black, overlaid with white hair.

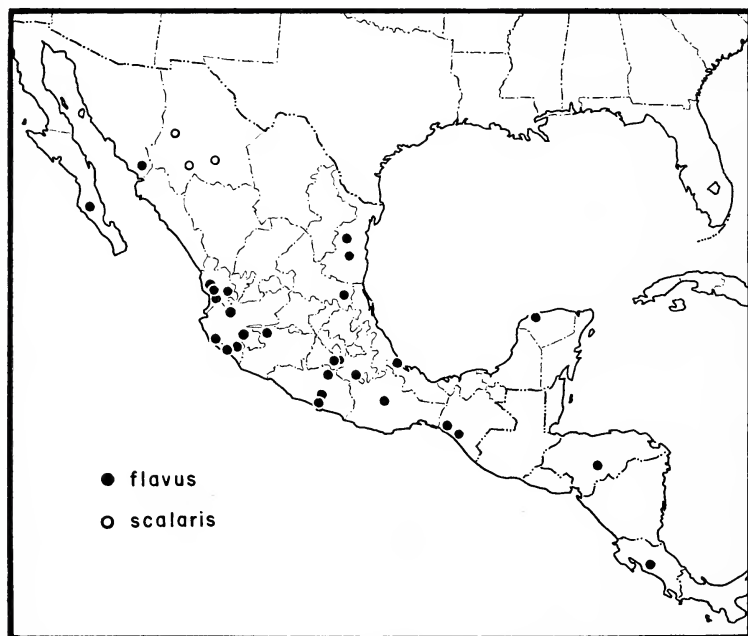
Carapace cream to pale yellow with four gray stripes as indicated in Figure 12. Gray stripes formed of appressed hairs, which are rubbed away in some specimens.

Dorsum with median area white with darker brown outlining cardiac area. White, pale yellow-orange, and brown spatulate hairs forming pattern illustrated in Figure 12. Venter with wide, dark brown median stripe beginning at epigastric furrow and continuing to base of spinnerets. Brown stripe is sometimes mottled.

Legs cream to pale yellow with black stripe on ventral surfaces of femora I-III.

Labium and endites cream to pale yellow. Sternum ivory to pale yellow, with four pairs of black spots at periphery.

Color. The male of *O. salticus* occurs in at least two different forms or morphs with some specimens intermediate. Two commonly occurring patterns are described below.



Map 4.

Light Male. Face and chelicerae cream to pale yellow with vertical black stripes as indicated in Figure 73. Cymbia of palpi dark brown to black. Eyes with black nacelles overlaid with iridescent scale-like hairs.

Carapace pale yellow to light yellow-orange. A few faint dusky markings contributed by spatulate-shaped hairs as in Figure 74.

Dorsum of abdomen cream to pale yellow, dusky laterally and along sides of abdomen. Scale like hairs providing a metallic green or pink sheen. Cardiac area outlined as in Figure 74. Venter with broad median brown stripe from epigastric furrow to base of spinnerets. The stripe outlined in white, with dusky color laterally.

Legs cream to pale yellow without stripes or dusky markings in most specimens. Mid-ventral black stripe on femora I and II of some.

Labium cream to pale yellow. Endites cream to pale yellow, outer margins darker brownish. Sternum yellow.

Dark Male. Face black between AME to clypeus and chelicerae with black markings as shown in Figure 75. Cymbia of palpi black.

Carapace pale yellow to light yellow-orange, with four longitudinal dusky stripes.

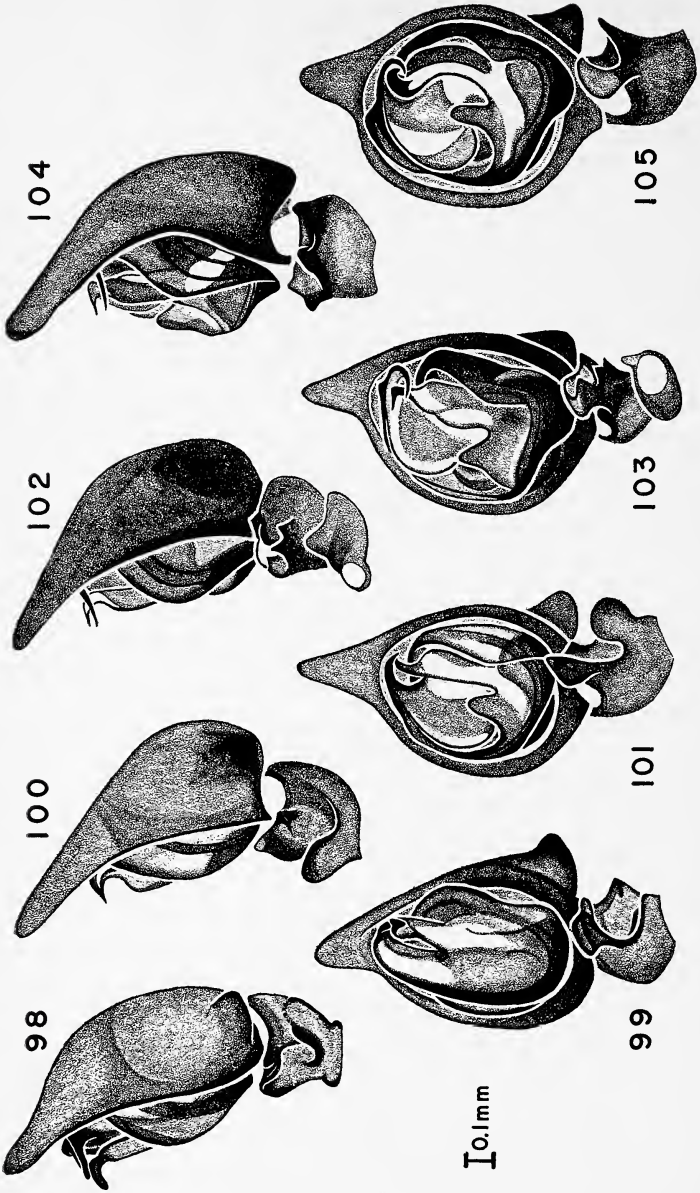
Dorsum of abdomen iridescent, mostly dark gray-brown to black. Venter dark gray-brown to black with white lines outlining median stripe conspicuously seen in lighter forms.

Legs cream to pale yellow. Patellae-tibiae and femora of palpi with black markings dominating lighter color.

Labium and endites black with distal ends pale cream. Sternum yellow with black periphery.

Diagnosis. *Oxyopes salticus* resembles members of the *acleistus* group with mid-ventral black stripes on the femora and vertical black lines on the face. It can be immediately distinguished by the peculiar shape of the epigynum (Figs. 23, 24) and the characteristic palpus of the male (Figs. 98, 99). The male palpus has a stout conical projection on the cymbium and a stout brush of short, stiffened bristles (not figured) on the ventral surface of the palpal tibia. *Oxyopes salticus* should be placed in a separate species group to reflect its relationship to other Mexican and Central American species.

Natural History. *Oxyopes salticus* is one of the most common spider inhabitants of tall grass and herbaceous vegetation and is found throughout Mexico and Central America wherever this type of vegetation occurs. The local abundance of these spiders gives evidence of their role as one of the important predators of insects



occurring in these habitats. For further notes on the biology of *O. salticus* see Brady (1964), pp. 481-482.

Distribution. North America (see Map 3 of Brady, 1964), Mexico, Central America, Lesser Antilles, and South America.

Records. Common throughout Mexico and Central America (Map 3).

Oxyopes flavus Banks

Figures 13, 14, 47-54, 76, 77, 106, 107. Map 4.

Oxyopes flavus Banks, 1898, Proc. Calif. Acad. Sci., 1(3):278, pl. 7, fig. 28, ♀. Female syntypes from Sierra San Lazaro, Baja California, Mexico, (G. Eisen, F. H. Vasilit), in Museum of Comparative Zoology, examined.

Oxyopes lingulifer F.O.P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, Araneidea, 2:345, pl. 32, fig. 28, ♀. Female holotype from Costa Rica, (Rogers), in British Museum (Natural History), examined. NEW SYNONYMY.

Discussion. The specimens from Sierra San Lazaro upon which Banks (1898) based the name *O. flavus* are at one extremity of the range of this species and the female holotype of *Oxyopes lingulifer* is from Costa Rica at the other end of the known range. Most of the other specimens are from in between (see Map 4). The epigynum of Cambridge's holotype (Fig. 52) seems to be quite different from that of *O. flavus*. An investigator might consider them distinct species. However, the epigyna of the specimens from geographic areas between these specimens show considerable variation (Figs. 47-51) and even specimens from the same locality may be different in this respect. Therefore, the type specimens of *O. flavus* and *O. lingulifer* are considered to be geographic variants of the same species. This species illustrates very well the greater amount of geographic and individual variation encountered in Mexican and Central American species when compared to their North American relatives.

Figs. 98-99. *Oxyopes salticus* Hentz, male from Veracruz, Veracruz, 30 July 1972. 98. Left palpus, retrolateral view. 99. Left palpus, ventral view.

Figs. 100-101. *Oxyopes ocelot* new species, male holotype from W side of Lake Sayula, Guerrero, 3 Aug. 1956. 100. Retrolateral view. 101. Ventral view.

Figs. 102-103. *Oxyopes felinus* Brady, male from SW of Acaponeta, Nayarit, 15 May 1963. 102. Retrolateral view. 103. Ventral view.

Figs. 104-105. *Oxyopes cornutus* F.O.P.-Cambridge, male from 8 mi. SW of Colima, Colima, 10 May 1963. 104. Retrolateral view. 105. Ventral view.

Measurements. Ten females and ten males.

FEMALES:					
	Mean	Range		Mean	Range
Clypeus	.708	.63-.80	Femur I	3.39	2.9-3.9
AME	.398	.35-.45	Patella-Tibia I	4.28	3.7-4.9
ALE	.648	.58-.70	Metatarsus I	3.54	3.0-4.0
PLE	1.153	1.05-1.25	Tarsus I	1.36	1.2-1.5
PME	.648	.58-.70	Total Length I	12.58	10.9-14.4
Carapace Width	2.38	2.1-2.7			
Carapace Length	3.10	2.7-3.6	Patella-Tibia II	4.05	3.5-4.7
Total Length	8.47	7.2-9.2	Patella-Tibia III	3.11	2.6-3.6
			Patella-Tibia IV	3.56	3.1-4.1
			Total Length IV	11.59	9.9-13.4

MALES:					
	Mean	Range		Mean	Range
Clypeus	.548	.48-.65	Femur I	3.02	2.4-3.5
AME	.318	.30-.35	Patella-Tibia I	4.02	3.1-4.5
ALE	.558	.50-.63	Metatarsus I	3.70	2.6-4.3
PLE	1.000	.95-1.05	Tarsus I	1.69	1.3-2.1
PME	.553	.50-.60	Total Length I	12.44	9.4-14.4
Carapace Width	2.07	1.8-2.3			
Carapace Length	2.62	2.3-2.8	Patella-Tibia II	3.69	2.7-4.2
Total Length	5.98	5.1-6.6	Patella-Tibia III	2.82	2.4-3.2
			Patella-Tibia IV	3.16	2.8-3.6
			Total Length IV	10.46	9.1-12.0

Color. Female. Face and chelicerae cream to yellow with thin black stripes from AME to distal third of chelicerae as in Figure 13. Lighter color along lower edge of clypeus. Eye region overlaid with white appressed, spatulate-shaped hairs.

Carapace cream to yellow with faint lines radiating from thoracic groove as in Figure 14.

Dorsum of abdomen white to pale yellow, with cardiac area translucent. Mottled with darker colors along sides as in Figure 14. Venter with a broad median dark brown to black stripe from epigastric furrow to base of spinnerets; median stripe outlined by white, becoming darker yellowish laterally.

Legs cream to pale yellow.

Labium and endites cream to yellow. Sternum cream to pale yellow.

Color. Male. Face and chelicerae cream to yellow with black stripes from AME to distal third of chelicerae as in Figure 76. Eye region black overlaid with white spatulate-shaped hairs.

Carapace cream to yellow with dusky markings as in Figure 77.

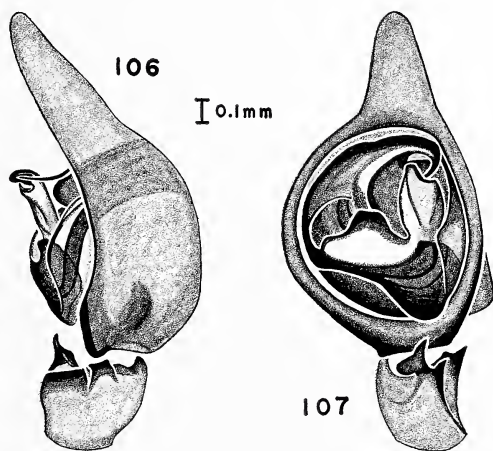
Dorsum of abdomen white to cream with darker brown marks along sides as in Figure 77. Venter with wide dark brown or black stripe from genital area to base of spinnerets. Median stripe bounded by white with yellow along sides.

Legs pale yellow to yellow without darker markings or a few scattered black spots, especially on ventral surfaces.

Labium, endites, and sternum cream to yellow.

Diagnosis. Although sharing certain characteristics with other members of the genus *Oxyopes*, *O. flavus* is the most divergent member of this group in Mexico and Central America. It is easily distinguished from all other *Oxyopes* by the bright yellow color contrasted with black markings in living specimens, by its large size, and by the distinct epigynum (Figs. 47-54) and palpus (Figs. 106, 107).

Natural History. *Oxyopes flavus* was collected in areas of relatively tall (3 ft. or 1 m) herbaceous vegetation by sweeping. It was relatively abundant in certain habitats where an hour's sweeping by one person would turn up about 20 specimens in the net.



Figs. 106-107. *Oxyopes flavus* Banks, male from Tierra Colorado, Guerrero, 23 July 1972. 106. Left palp, retrolateral view. 107. Left palp, ventral view.

Distribution. Mexico, mostly along the coastal regions, to Costa Rica (Map 4).

Records. *Tamaulipas.* 15 mi. S of Ciudad Victoria, 2 July 1936, ♂ (AMD, LID); Villagran, 19 July 1956, 5 ♂♂ (VDR, WJG). *San Luis Potosi.* Valles, 19 July 1956, ♂:3 ♀♀ (WJG, VDR). *Sonora.* Alamos, 7 Aug. 1956, ♀ (VDR, WJG). *Nayarit.* Compostela, 23 mi. S of Tepic, 12 July 1972, 400 (ARB); San Juan Peyotan, 1-3 Aug. 1955, ♂ ♀♀ (BM); Tepic, 2-7 Aug. 1947, 3 ♂♂:♀ 0 (CG, MG, BM); 20 mi. N of Tepic, 5 Aug. 1956, ♂ (WJG, VDR). *Veracruz.* Tierra Colorado, 26 July 1956, ♀ (WJG, VDR). *Puebla.* Acatlan, 24-27 Sept. 1946, ♀ (HMW). *Jalisco.* Cihuatlan, 15 July 1972, 800 (ARB, AJ); Barranchitas, 31 mi. W of Tequila, 13 July 1972, 0 (ARB); W side of Lake Sayula, 3 Aug. 1946, ♂ (WJG, VDR). *Morelos.* Cuernavaca, Aug. 1955, ♀ (NLHK); 13 mi. E of Cuernavaca, 14 Aug. 1954, ♀ (RD). *Colima.* 20 mi. N of Colima, 2 Aug. 1956, ♂ (VDR, WJG); 7 mi. SE of Manzanillo, 16 July 1972, 300 (ARB). *Michoacan.* 25 mi. E of Mazamitla, 2 Aug. 1956, ♂:3 ♀♀:00 (WJG, VDR). *Guerrero.* La Garita near Acapulco, 19 Aug. 1943, ♀ (D. Peleaez, M. Correa); Iguala, 27 Oct. 1947, 3 ♀♀ (HMW); Tierra Colorado, 22-23 July 1972, 8 ♂♂:2500 (ARB). *Oaxaca.* Oaxaca, 13-20 Oct. 1947, ♀ (BM). *Chiapas.* Los Amates, 6 July 1955, ♀ (CV, PV); Tonalá, Aug. 1909, ♂:3 ♀♀ (AP). *Yucatan.* Dolores Otero, 13 July 1952, ♀ (JCP, DLP); Progreso, 25 July 1952, ♂ ♀ (JCP, DLP).

HONDURAS. Tegucigalpa, 1 July 1948, ♂ (Clarke).

COSTA RICA. ♀ (Rogers).

LIST OF COLLECTORS

AJ	A. Jung	LID	L. I. Davis
AMC	A. M. Chickering	MAC	M. A. Cazier
AMD	A. M. Davis	MG	M. Goodnight
AP	A. Petrunkevitch	NB	N. Banks
ARB	A. R. Brady	NLHK	N. L. H. Krauss
BM	B. Malkin	PV	P. Vaurie
CG	C. Goodnight	RD	R. Dreisbach
CTB	C. T. Baker	RJW	R. J. Wolff
CV	C. Vaurie	RS	R. Schrammel
DLP	D. L. Pallister	VDR	V. D. Roth
FB	F. Bonet	WEL	W. E. Lundy
HHS	H. H. Smith	WI	W. Ivie
HMW	H. M. Wagner	WJG	W. J. Gertsch
JCP	J. C. Pallister		

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GENUS *EREMOPSOCUS* McLACHLAN: DISTINCTION
FROM *CERASTIPSOCUS* KOLBE AND REVIEW OF
SPECIES (PSOCOPTERA: PSOCIDAE)*

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During investigation on the systematics of *Cerastipsocus* and its close relatives, I have experienced difficulty in assigning species between the two genera *Eremopsocus* and *Cerastipsocus*. In this paper, I attempt an unequivocal definition of these genera. I also include diagnoses of the species placed by the new definition in *Eremopsocus*, and a reconsideration of geographic variation in the type species, *E. infumatus* McLachlan. The subgenera of *Eremopsocus* are also re-evaluated. One new species is described.

Measurements (Table II) were made on whole specimens either pinned or temporarily mounted in glycerine. They are in mm and have an error of ± 1.04 microns. Abbreviations used with the measurements are explained as follows: f_1, f_2 = lengths of first and second flagellomeres; Fw = forewing length; F = length of posterior femur; T = length of posterior tibia; t_1, t_2 = length of first and second posterior tarsomeres; t_1ct = number of ctenidia on posterior first tarsomeres; IO/D = least distance between compound eyes in dorsal view divided by greatest antero-posterior diameter of eye in dorsal view; PO = greatest transverse diameter of compound eye in dorsal view divided by greatest antero-posterior diameter of the eye in same view.

Characters of *Eremopsocus* and distinction from *Cerastipsocus*. — *Eremopsocus* McLachlan (1866) was erected for a single large Brazilian species, *E. infumatus*, with fuscous wing membranes. This species was reported to have incrassate flagellomeres in the male only, those of the female being slender. This antennal character, alone, was held to separate the genus from *Psocus*, which was then used in a very broad sense.

Pearman (1933) correctly aligned *Eremopsocus* with its close relatives by placing it in subfamily Cerastipsocinae of Family Psocidae. Pearman's material, from Venezuela, showed incrassate flagellomeres in both sexes, and on that account, he designated a distinct subspecies, *E. infumatus venezuelensis*.

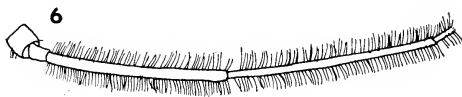
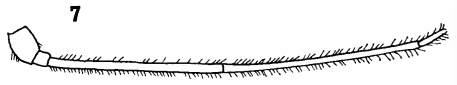
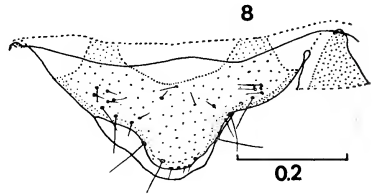
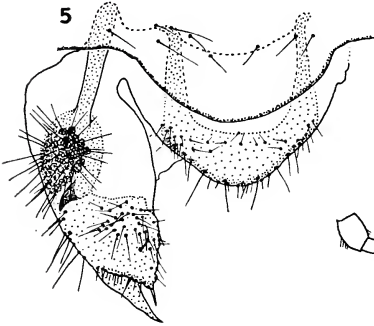
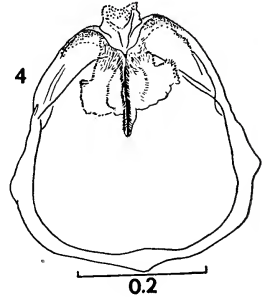
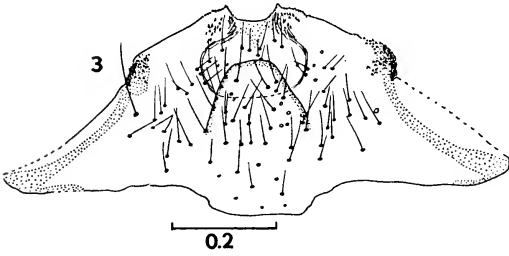
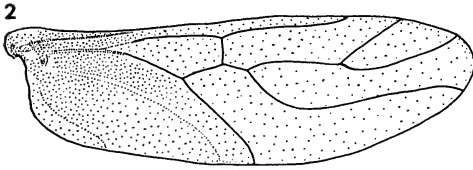
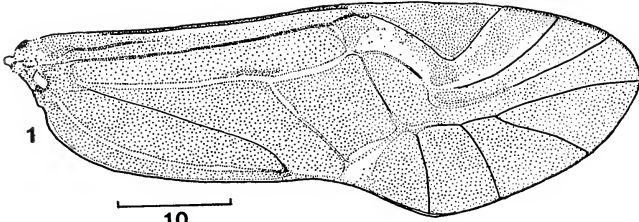
*Manuscript received by the editor August 15, 1975.

I have examined 15 adult specimens of this species from two localities in central Brazil, and I find that all individuals of both sexes have antennae incrassate. I believe that McLachlan's observation was incorrect and that the error arose from his having had more than one large, fuscous-winged *Cerastipsocine* species in his material. There are several such species in Brazil. Those with slender flagellomeres in both sexes are currently assigned to *Cerastipsocus*. The argument for McLachlan's having had a mixture of species is strengthened by another of his observations: that males have wings shining, while females have them dull. Pinned specimens in the series of *E. infumatus* which I studied have the wings shining in both sexes while pinned specimens of *Cerastipsocus fuscipennis* (Burmeister) received in the same shipment from a nearby locality in Brazil have the wings dull. I conclude that the flagellomeres of both sexes of *E. infumatus* are incrassate and that Pearman's Venezuelan subspecies has no validity.

Pearman (1933) described the genitalia of both sexes of *E. infumatus*. The hypandrium is symmetrical and bears an apically rounded lobe in the middle of the disc; distally, it bears a pair of blunt, posteriorly-directed prongs. This hypandrium differs from that of the type of *Cerastipsocus* (*C. fuscipennis* [Burmeister], designated by Roesler [1944], not *C. venosus* [Burmeister], erroneously designated by Smithers [1967]).

In *C. fuscipennis*, there is no trace of a rounded lobe in the middle of the disc and distal prongs are absent. This type of hypandrium has been illustrated for *C. cubanus* Enderlein (Mockford, 1974: 164, Fig. 118) and *C. venosus* Burmeister (Chapman, 1930, pl. XIII, Fig. 9). *C. beaveri* New (1972: 207, Fig. 32) is much the same but its hypandrium has a pair of short, laterally directed distal prongs.

The distinctive hypandria of the types of *Eremopsocus* and *Cerastipsocus* provide useful character complexes for distinguishing between these two genera. Unfortunately, these complexes do not correlate with the distribution of incrassate and slender flagellomeres in the species as currently assigned in these two genera. Thus *E. reductus* (Banks) has the flagellomeres developed as in *E. infumatus* but the hypandrium as in *C. venosus*, completely lacking a lobe in the middle of the disc and without distal prongs (personal observation). *C. crassicornis* (Kolbe) in which the male has only the first flagellomere incrassate and the flagellomeres of the female are slender has the hypandrium developed as in *E. infumatus* (personal observation).



It is my opinion that the hypandrium in these insects presents more information than the relative widths of flagellomeres and that the two genera can best be recognized on the basis of type of hypandrium. This opinion is strengthened by the fact that no intermediate type of hypandrium has been found, whereas flagellomeres of different species show varying degrees of incrassation.

In order to test this opinion further I have searched for additional characters showing essentially two states in the assemblage of species under consideration and noted how their states are distributed. The following characters were found:

(1) shape of posterior clunial margin of male in region of base of epiproct: slightly protruding and bilobed (Fig. 8) or decidedly protruding and not at all bilobed (Fig. 5);

(2) presence (Fig. 5) or absence of a protuberance immediately distad of sense cushion on paraproct in male;

(3) relative length of stem of dark T-shaped mark of female subgenital plate (stem of vase-shaped figure extending into distal process of plate): either more than twice as long as broad or scarcely longer than broad to much shorter than broad.

The following species were examined (assigned to genera according to current usage): *Cerastipsocus bogotanus* (Kolbe), *C. crassicornis* (Kolbe), *C. cubanus* Enderlein, *C. fuscipennis* (Burmeister), *C. ochraceocristatus* Enderlein, *C. sivorii* Ribaga, *C. trifasciatus* (Provancher), *C. venosus* (Burmeister), two undetermined species of *Cerastipsocus*, *Eremopsocus infumatus* McLachlan, and *E. reductus* (Banks).

The data are summarized in Table I. From this table, the following correlations are seen:

1. Incrassate flagellomeres correlate with hypandrial type of *E. infumatus*. The notable exception is *E. reductus*, while *C. cubanus* shows slight incrassation.

EXPLANATION OF FIGURES 1-8

Fig. 1. *Eremopsocus crassicornis* (Kolbe) ♂, forewing, scales in mm.
 Fig. 2. *E. crassicornis* (Kolbe) ♂, hindwing. Fig. 3. *E. crassicornis* (Kolbe) ♂, hypandrium. Fig. 4. *E. crassicornis* (Kolbe) ♂, phallosome.
 Fig. 5. *E. crassicornis* (Kolbe) ♂, epiproct, left paraproct, and adjacent clunial margin, scale of Fig. 3. Fig. 6. *E. crassicornis* (Kolbe) ♂, antenna (scape to base of f_3), scale of Fig. 1. Fig. 7. *E. crassicornis* (Kolbe) ♀, antenna (scape to base of f_3), scale of Fig. 1. Fig. 8. *Cerastipsocus venosus* (Burmeister) ♂, epiproct, base of right paraproct, and adjacent clunial margin.

Table I. Some character states of *Cerastipocus* and *Eremopocus* species assigned to genera by traditional criteria.

	<i>Cerastipocus bogotanus</i>	<i>C. crassicornis</i>	<i>C. cubanus</i>	<i>C. fuscipennis</i>	<i>C. ochraceo-cristatus</i>	<i>C. stivorii</i>	<i>C. trifasciatus</i>	<i>C. venosus</i>	C. sp. #1 ¹	C. sp. #2	<i>Eremopocus infumatus</i>	<i>E. reductus</i>
Flagellum incrassate (+) or not (-)	-	+	+	-	-	-	-	-	+	-	+	+
Hypandrium with (+) or without (-) central lobe of disc	-	+	-	-	-	-	-	-	+	-	+	-
Clunial margin bilobed (bl) or protruding and simple (pr)	bl	pr	pr (slight)	bl	bl	bl	bl	bl	pr	bl	pr	pr (slight)
Presence (+) or absence (-) of protuberance distad of δ para-proctal sense cushion (rounded)	+	+	-	-	-	-	-	-	+	-	+	-
Long (L) or short (S) stem of T-shaped mark of δ subgenital plate (see text)	S	L	S	S	S	S	S	S	L	S	L	S

¹This species is described in this paper as *Eremopocus nigripes* n. sp.

2. The protruding male clunial margin tends to correlate with the *E. infumatus* hypandrial type, while the bilobed male clunial margin tends to correlate with the *C. venosus* hypandrial type. This correlation is better than indicated on the table. In *E. infumatus*, *C. crassicornis*, and *C. sp. no. 1*, the protrusion is a thickened lip, while in *C. cubanus* and *E. reductus* it is only a thin rim, as in those species with the bilobed margin.

3. The protuberance distad of the male paraproctal sense cushion tends to correlate with the *E. infumatus* hypandrial type and absence of the protuberance with the *C. venosus* hypandrial type. Again, the correlation seems better than the table suggests, as the protuberance in *E. infumatus*, *C. crassicornis*, and *C. sp. no. 1* is small and decidedly pointed, while that in *C. bogotanus* is low, larger, and rounded.

4. The long stem of the T-shaped mark of the female subgenital plate shows complete correlation with the *E. infumatus* hypandrial type and the shorter stem with the *C. venosus* hypandrial type.

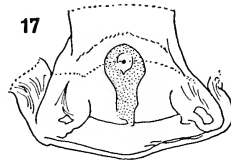
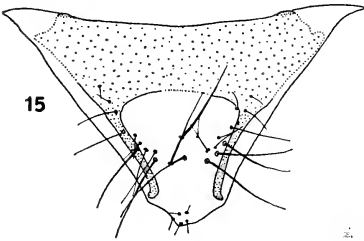
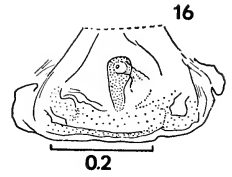
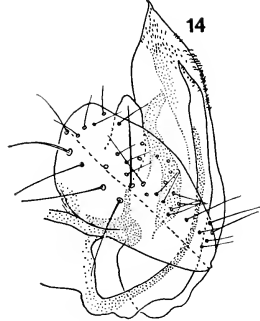
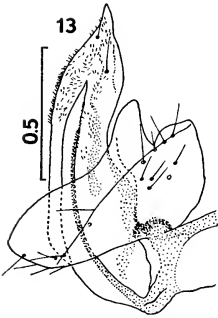
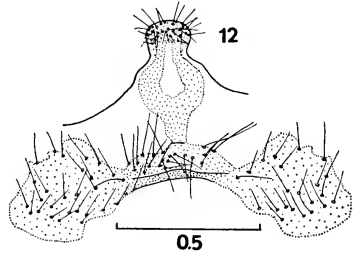
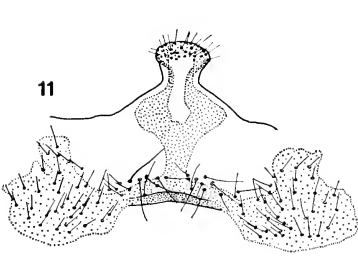
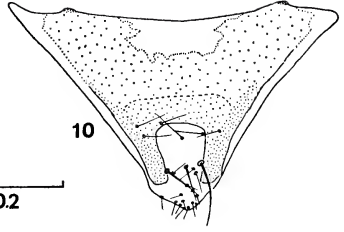
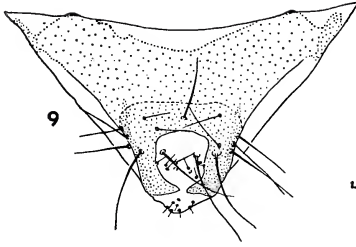
From the above correlations, I conclude that the genera *Eremopsocus* and *Cerastipsocus* may be differentially defined as follows:

Eremopsocus. — Antennae incrassate at least in male; hypandrium with central lobe of disc; male clunial margin protruding above epiproctal base as a rounded, thickened lip; a pointed protuberance distad of male paraproctal sense cushion; stem of T-shaped mark of female subgenital plate more than twice as long as broad.

Cerastipsocus. — Antennae incrassate or not; hypandrium lacking central lobe of disc; male clunial margin bilobed before base of epiproct or slightly protruding above epiproctal base but never developed as a decidedly protruding, thickened lip; generally lacking a protuberance distad of male paraproctal sense cushion, or with a low, rounded protuberance; stem of T-shaped mark of female subgenital plate little longer than broad to much shorter than broad.

Assignment of species to *Cerastipsocus* and *Eremopsocus*. — I can affirm, either through examination of specimens or by existing published descriptions, the generic assignment of the following species according to the above definitions:

Cerastipsocus. — *C. fuscipennis* (Burmeister) (type species), *C. beaveri* New, *C. bogotanus* (Kolbe), *C. cubanus* Enderlein, *C. ochraceocristatus* (Enderlein), *C. reductus* (Banks), new combination, *C. sivorii* (Ribaga), new combination, *C. trifasciatus* (Provancher), *C. venosus* (Burmeister).



Eremopsocus. — *E. infumatus* McLachlan (type species), *E. crassicornis* (Kolbe) new combination, *E. nigripes* n. sp. (heretofore referred to in this paper as *Cerastipsocus* sp. no. 1).

Several species traditionally assigned to *Cerastipsocus* are unassignable by the above definition, and I hope to review that genus and assign these species in the near future.

Subgenera of *Eremopsocus*. — Roesler (1944) assigned *Syngonosoma* Kolbe, *Dinopsocus* Banks, and *Podopteroocus* Banks as subgenera of *Eremopsocus*. These assignments were presumably made on the basis of incrassate flagellomeres alone. As I have shown that this character is not a reliable guide to relationships, it seems advisable to retain the old-world genera *Dinopsocus* and *Podopteroocus* at least until their external genitalia are known. The type of *Syngonosoma* being South American, it seems likely that this genus may be a synonym (not a subgenus) of *Eremopsocus* as was suggested by Enderlein (1911) and Pearman (1933), but it will be necessary to examine material of the type species in order to confirm this suggestion. Of the species listed in *Eremopsocus* by Smithers (1967), only the type species can be retained with certainty.

Systematics of *Eremopsocus* species. — In this section the species now assigned to *Eremopsocus* are diagnosed, the description of *E. infumatus* is augmented, a detailed description of *E. crassicornis* is presented and *E. nigripes* n. sp. is described. A key to the species is included.

Eremopsocus infumatus McLachlan

E. infumatus McLachlan, 1866: 348.

E. infumatus venezuelensis Pearman 1933: 159.

Diagnosis. — First four flagellomeres incrassate in both sexes, the basal two decidedly so, the next two somewhat less. Female subgenital plate with a single row of long setae along cross-piece of T-shaped mark (the row double to the sides and single in middle on specimen examined).

EXPLANATION OF FIGURES 9-17

Fig. 9. *Eremopsocus crassicornis* (Kolbe) ♀, epiproct. Fig. 10. *E. nigripes* n. sp. ♀, epiproct. Fig. 11. *E. crassicornis* (Kolbe) ♀, subgenital plate, scale of Fig. 12. Fig. 12. *E. nigripes* n. sp. ♀, subgenital plate. Fig. 13. *E. crassicornis* (Kolbe) ♀, gonapophyses. Fig. 14. *E. nigripes* n. sp. ♀, gonapophyses, scale of Fig. 9. Fig. 15. *E. infumatus* McLachlan ♀, epiproct, scale of Fig. 9. Fig. 16. *E. crassicornis* (Kolbe) ♀, spermapore sclerite. Fig. 17. *E. nigripes* n. sp. ♀, spermapore sclerite, scale of Fig. 16.

Pearman's description (1933) is augmented as follows: Measurements (Table II). Lateral prongs of hypandrium joined along their length to sides of hypandrium by semimembranous cuticle. Female epiproct (Fig. 15) with postero-lateral sclerotized strips turning slightly outward at their distal ends.

Material examined. — Brazil: Goiás: Jatai, October, 1972 1 ♀ F. M. Oliveira; 20 Km. north of Sao Joao da Alianca, April 14, 1956, 1 ♂, 13 ♀, F. S. Truxal.

Eremopsocus crassicornis (Kolbe), new combination

Cerastis crassicornis Kolbe, 1883: 70.

Cerastipsocus crassicornis (Kolbe), Smithers, 1967: 96.

Diagnosis. — See diagnosis of *E. nigripes* n. sp.

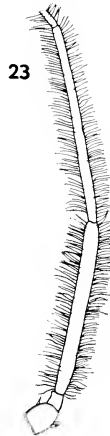
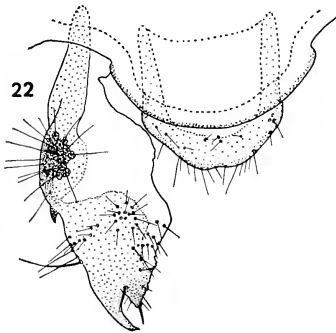
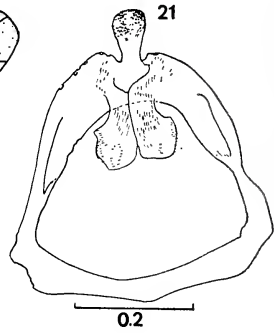
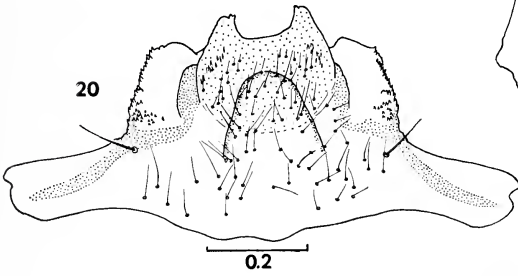
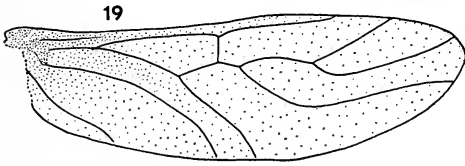
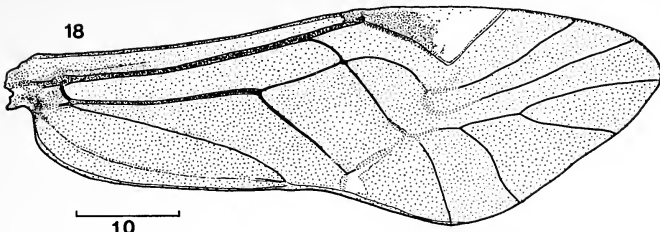
Male. — Measurements (Table II).

Morphology. — Antenna with basal flagellomere (Fig. 6) decidedly incrassate, second less so, third slightly incrassate basally; all flagellomeres densely beset with upright hairs. Compound eyes small (see Table II). Hypandrium (Fig. 3) with pair of short distal prongs; these and distal ends of lateral thickenings beset with minute denticles. Discal lobe and regions to its sides and base bearing setae. Phallosome (Fig. 4) a closed ring with truncate distal process, the process and weakly-sclerotized region to its sides bearing minute denticles. Paraproct (Fig. 5) with a long distal spur and a short spur distad of sense cushion. Epiproct and posterior clunial margin as in Fig. 5.

Color (in alcohol). — Compound eyes and inner rims of ocelli black. Head deep orange-brown with faint clypeal striations. Maxillary palpi dark brown. Antennal scape and pedicel dark chestnut brown; flagellum black. Mesonotal lobes deep to medium chestnut brown, their borders and thoracic pleura orange-brown. Forewing membrane (Fig. 1) uniformly fumose-brown except colorless in base of areola postica and nearly so in basal region of cell R₁ from behind stigmasac nearly to apex of pterostigma. Pterostigma brown

EXPLANATION OF FIGURES 18-24

Fig. 18. *Eremopsocus nigripes* n. sp. ♂, forewing. Fig. 19. *E. nigripes* n. sp. ♂, hindwing. Fig. 20. *E. nigripes* n. sp. ♂, hypandrium. Fig. 21. *E. nigripes* n. sp. ♂, phallosome. Fig. 22. *E. nigripes* n. sp. ♂, epiproct, left paraproct, and adjacent clunial margin, scale of Fig. 20. Fig. 23. *E. nigripes* n. sp. ♂, antenna (scape through base of f₃), scale of Fig. 18. Fig. 24. *E. nigripes* n. sp. ♀, antenna (scape through base of f₃), scale of Fig. 18.



outlined in white. Veins of forewing white except following brown: short segment of Rs before its fork, short segments of M before M-Cu1a junction, R₂ + 3, except its extreme base, R₄ + 5 in its distal two-thirds, M₁, M₂, M₃, Cu1a beyond junction with M. Hindwings (Fig. 2) uniformly pale fumose-brown. Coxae, trochanters and femora orange-brown; tibiae and tarsi duskier. Membranous portions of abdomen ringed with slender white stripes on a purplish-brown background (subcuticular pigment). Terminal abdominal segments medium to dark brown.

Female. — Measurements (Table II).

Morphology. — Flagellomeres slender (Fig. 7). Subgenital plate (Fig. 11) with pigmented area roughly T-shaped as in *E. infumatus* but with narrow region of stem of T shorter and setae distad of cross-piece shorter and not forming a distinct row, being interrupted in middle. Gonapophyses (Fig. 13) with first valvula acuminate distally, bearing a few minute spines on its edges; second valvula tapering distally and spinulose over distal third; third valvula with basal, more sclerotized region bearing setae (this region shown folded over rest in figure), remainder membranous, distal lobe straight. Ninth sternum and spermapore as in Fig. 16. Epiproct (Fig. 9) with clear region surrounded by approximately quadrate frame of heavier sclerotization, the frame and clear area bearing setae of various lengths.

Color. — Same as in male.

Material examined. — Brazil: Prov. Minas Gerais: Sao Joao del Rei, Coll. Sello, 1 ♂ (holotype); Santa Catarina: Nova Teutonia, November, 1970, Coll. F. Plaumann, 14 ♂, 23 ♀. Uruguay: Depto. de Treinta y Tres: Rio Olimar Chico, 25 Km. WSW Treinta y Tres, 11 April 1963, Coll. J. K. Bouseman, 8 ♂, 2 ♀.

***Eremopsocus nigripes*, new species**

Diagnosis. — Differing from *E. infumatus* in having only the first two flagellomeres incrassate and only in the male. Differing from *E. crassicornis* in having first two male flagellomeres decidedly more incrassate and having in both sexes posterior vertex of pterostigma angular, forming approximately a right angle, rather than rounded. Differing from the described fuscous-winged neotropical *Cerastipsocus* species in which external genitalia not known: from *C. ocellaris* (Kolbe), *C. moestus* (Kolbe), *C. pallidinervis* (Kolbe), *C. vetustus* (Kolbe) in having pterostigma deep and with decidedly angular posterior vertex.

Male. — Measurements (Table II).

Table II. Measurements (in mm) head ratios, and ctenoidal counts for three species of *Eremopsocus*. Abbreviations are explained in text.

	f_1	f_2	Fw	F	T	t_1	t_2	t_{1ct}	IO/D	FO
<u>E. infuratus</u> ♂	1.82	1.92	5.72	1.23	2.29	0.53	0.30	19	2.56	0.81
<u>E. infuratus</u> ♀	1.91	1.94	7.11	1.33	2.61	0.51	0.32	21	3.10	0.69
<u>E. infuratus</u> ♀	1.70	1.78	7.25	1.40	2.62	0.54	0.29	19	3.07	0.78
<u>E. crassicornis</u> ♂	1.43 ⁿ	1.58	4.79	1.02	2.00	0.50	0.30	21	3.01	0.81
<u>E. crassicornis</u> ♂	1.70	1.89	5.21	1.15	2.26	0.55	0.34	25	3.05	0.81
<u>E. crassicornis</u> ♀	1.65	1.95	5.94	1.32	2.21	0.48	0.35	18	3.27	0.78
<u>E. crassicornis</u> ♀	2.08	2.24	6.45	1.45	2.80	0.59	0.32	23	3.27	0.88
<u>E. nigripes</u> ♂	1.66	1.89	5.60	1.30	2.45	0.55	0.30	21	2.86	0.78
<u>E. nigripes</u> ♂	1.58	1.86	5.33	1.09	2.32	0.52	0.26	19	2.95	0.85
<u>E. nigripes</u> ♀	1.62	1.66	5.66	1.14	2.18	0.46	0.28	18	3.35	0.76
<u>E. nigripes</u> ♀	1.90	1.61	6.85	1.44	2.80	0.59	0.30	20	3.29	0.79

Morphology. — Basal flagellomere (Fig. 23) more incrassate than in *E. crassicornis*, second about the same, third to tip slender. All flagellomeres beset with upright hairs. Compound eyes small (see Table II). Hypandrium (Fig. 20) with distal prongs somewhat longer than in *E. crassicornis*; these and sides of hypandrium, to extreme base beset with minute denticles. Discal lobe and regions to its sides and base bearing setae. Phallosome (Fig. 21) symmetrical, with somewhat flattened base; the inset, spatulate distal process larger than in *E. crassicornis* and bearing minute denticles. Paraproct (Fig. 22) as in *E. crassicornis*. Epiproct and posterior clunial margin as in Fig. 22. The latter differing from that of *E. crassicornis* in having sides slightly indented.

Color (in alcohol). — Compound eyes and inner rims of ocelli black. Head yellow deepening to burnt orange on vertex with a spot of medium orange-brown in front of ocellar interval; clypeal striations faintly indicated by orange-brown mottling. Maxillary palpi pale brown on basal two segments, becoming darker distally on second; third segment dark brown, distal segment black. Antennal scape pale brown, rest of antenna black. Mesonotal lobes orange peripherally, deep orange-brown in a broad central band running length of mesonotum. Thoracic pleura violet. Forewing membrane (Fig. 18) uniformly fumose-brown except small region in base of areola postica extending distally along vein $Cu1a$; pterostigma and narrow *stigma* white mottled in base with fumose brown. Veins of forewing fumose brown except following: $R1$ colorless from posterior apex of pterostigma to wing margin; Rs pale brown at and immediately before and in its junction with $Cu1a$, colorless immediately beyond junction; $Cu1a$ colorless before and immediately beyond junction with M ; $Cu1b$ colorless. Hindwing (Fig. 19) uniformly pale fumose brown. Coxae, trochanters, and femora yellow; tibiae and tarsi black. Membranous portions of abdomen (note variation below) longitudinally striped with purple bands: a broad band along each side including spiracles, a narrower band along dorsal mid-line; an incomplete band ventrally from hypandrium, widest in 7th segment, narrowing to its anterior end in third segment; abdomen creamy white between purple bands. Terminal abdominal segments largely dark brown, paler on poorly sclerotized portion.

Female. — Measurements (Table II).

Morphology. — Flagellomeres slender (Fig. 24). Subgenital plate (Fig. 12) with narrow region of stem of T-shaped pigmented area shorter than in *E. infumatus*; setae distad of cross-piece of T

shorter and forming a continuous subquadrate region. Lamp-globe shaped pigmented region distad of narrow portion of T-stem not as broad as in *E. crassicornis*. Gonapophyses (Fig. 14) with second valvula not as long from broadest region to tip as in *E. crassicornis*; inner lobe of third valvula relatively longer. Epiproct (Fig. 10) with heavily sclerotized sides of distal clear area not decidedly pointing medially at their distal ends. Spermapore plate (Fig. 17) much as in *E. crassicornis*.

Color (in alcohol).—As in male except no spot of medium orange-brown before ocelli and three faint purple lines radiating from each compound eye medially.

Variation.—Some individuals lack the longitudinal purple bands of the abdomen but have, instead, transverse purple bands, one per segment, each band dividing into two at the spiracle on each side and continuing ventrally as two narrow bands which dissipate before reaching the ventral mid-line. These individuals have the dark pigmentation of the mesonotum more diffuse and, in males, the dark pigmentation of the pterostigma and *stigmaesum* more dispersed. I can detect no morphological difference between these and the form described above. The two forms were apparently collected together.

Holotype ♂, allotype ♀, 3 ♂ paratypes and 2 ♀ paratypes, Brazil: Santa Catarina: Nova Teutonia, November, 1970, Coll. F. Plaumann. Types will be deposited in the United States National Museum, Washington, D. C.

Other material examined.—(all from Nova Teutonia, Santa Catarina, Brazil, Fritz Plaumann collector). Same data as holotype, 12 ♂, 13 ♀, October, 1971, 4 ♂, 4 ♀; December, 1971, 2 ♂, 1 ♀.

Key to the Species of *Eremopsocus*

- 1a. First four flagellomeres incrassate in both sexes. Female subgenital plate with a single row of long setae along cross-piece of T-shaped mark *E. infumatus* McLachlan
- 1b. At most first two flagellomeres incrassate, and these only in male. Female subgenital plate with scattered setae bordering cross-piece of T-shaped mark, these not forming a single row 2
- 2a. Pterostigma with angular posterior apex. Veins in basal half of forewing, especially M + Cu1 brown, not contrasting sharply with wing membrane. First male flagellomere decidedly incrassate (Fig. 4) *E. nigripes* n. sp.

- 2b. Pterostigma with rounded posterior apex. Veins in basal half of forewing, especially M + Cu₁ white, contrasting strongly in well colored individuals with fumose wing membrane. First male flagellomere only slightly incrassate
 *E. crassicornis* (Kolbe).

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BEHAVIOR DURING SWARM MOVEMENT IN
STELOPOLYBIA AREATA
(HYMENOPTERA: VESPIDAE)

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INTRODUCTION

When a colony of bees or wasps leaves an old nesting site and moves to a new one it is faced with the problem of coordinating the movement of the individuals of the swarm so that all arrive at the new site. Scout honeybees (*Apis mellifera*) communicate the distance and direction of the new site by means of the same waggle dance used to communicate information about food sources (von Frisch, 1967). Martin G. Naumann has observed swarm movement in several species of Neotropical social wasps and has described behavior that suggests that scent marks are used to guide swarm members to a new site (Naumann, 1975).

The purpose of this paper is to present the author's own observations on behavior associated with swarm movement in *Stelopolybia areata*. The study was conducted during February 1973 at the Estación de Biología 'Los Tuxtlas' near San Andres Tuxtla, Veracruz, Mexico.

BEHAVIOR ASSOCIATED WITH SWARM MOVEMENT

The colony in which the behavior was observed had been constructing a new nest two meters up in a bush along a small arroyo in a cow pasture. On the morning of February 4 the adult population of several thousand was found to have abandoned the nest and to have settled on a twig of a large tree about 10 meters distant. The cause of the absconding was not certain, but several army ant (*Eciton* sp.) workers on the ground below the nest suggested that the nest may have been raided by a swarm of these ants earlier in the morning.

On the afternoon of the 4th and on each of the following three afternoons the swarm moved to a new site, providing an opportunity to observe its behavior. Data pertaining to each move are summarized in Table 1. The following description of the behavior of the wasps is extracted from the four days' observation.

Table I. Movement by a swarm of *Stelopolybia areata* on four successive days.

Date	Time	Direction	Distance	Terrain crossed	Height of bivouac	Characteristics of new site
4/II	1530	WSW	72m	along fence, then across tall grass and weeds	4m	tangle of lianas on trunk of large tree.
5/II	1730	NW	77m	tall 2nd growth, across arroyo into pasture	5m	split in trunk of dead tree.
6/II	1615	W	100m	pasture; across brushy arroyo	7m	tangle of lianas at top of small tree.
7/II	1650	NNW	70m	tall 2nd growth, along dirt road; across road into partially logged forest	8m	small twig near edge of crown of large tree.

In the mornings activity of the swarm was relatively low, though at least some wasps could always be seen flying within a meter or two of it. Observations of the swarm with a 60× telescope during these hours indicated that much of the activity was due to the arrival and departure of foragers. The approach of a forager would cause several wasps on the swarm to reach out toward the movement with their forelegs, while waving the antennae. When a forager landed she would immediately fold her wings, then often regurgitate liquid to these waiting workers. This behavior is identical to that observed on nests of the species. After such food exchanges the forager often disappeared into the midst of the swarm. The number of wasps engaged in foraging seemed to rise and fall with the appearance and disappearance of the sun in partly cloudy weather.

Though data collected from other colonies at the same time of year suggest that 5-12% of the swarm population should have been queens (Jeanne, 1973), no queens were ever visible on the surface of the swarm. Their morphological distinctiveness from workers (Jeanne and Fagen, 1974) should have made them discernible had they been there. It is likely that queens remained near the center of the swarm.

Toward midday workers could be seen flying about vegetation away from the swarm. As the afternoon wore on, these became more and more evident, and more so in a particular direction away from the swarm. These wasps seemed attracted to prominent objects in the environment — fenceposts, tall weeds or shrubs in the pasture, or leaves near the tips of twigs in tall second growth. In many instances they merely hovered a few centimeters from the object (“hovering”), but often they landed and walked about slowly with the head down and gaster up, antennating the surface over which they moved (“landing”).

During the course of an afternoon activity at the swarm varied. Several times rapid increases in activity were observed during which great numbers of wasps took off and flew about in a large, diffuse cloud. During these times the numbers hovering at and landing on vegetation within 10-20 meters of the swarm often increased conspicuously. Within minutes, however, many of these wasps returned to the swarm and the activity dropped to its previous level.

As early as 1430 (February 7), two hours and twenty minutes before the swarm began to move on that day, a new kind of behavior was observed. Some of the workers landing on the upper parts of conspicuous objects walked rapidly over the surface, dragging the gaster continuously (“dragging”). The wings were usually buzzed, though sometimes this was interrupted with brief periods during which the wings were merely outstretched. The distance walked was usually in the range of 10-15 cm, taking 2-3 seconds, though there was much variation. At the end of a run the worker immediately took off.

Close observation of these individuals indicated that either the apical margin of the 5th (penultimate) sternite or the basal portion of the 6th was in contact with the substrate. Neither the tip of the gaster nor the sting made contact. The exposed surfaces of the fifth and sixth sternites are more or less uniformly covered with short hairs, and don't appear markedly different from other sternites in this regard. The basal portion of the 6th sternite, normally overlapped by the 5th, is hairless and quite smooth. In workers this region is noticeably more convex than in queens. Though it was not possible to confirm during observation, it may be this basal region that is in contact with the substrate.

Later in the afternoon the frequency of dragging increased, though not steadily. Often several workers could be seen performing it in a small area within a few minutes, then none would be seen for 15 or 20 minutes. By midafternoon the activities of hovering about, land-

ing on, and dragging the gaster over objects were very obviously concentrated in one direction away from the swarm. This was invariably the direction the swarm would take when it moved. On one occasion I was able to trace these activities to 60 meters in the direction the swarm would take nearly an hour later.

Meanwhile, changes could be observed in behavior at the swarm. The level of general activity was greater over that of the morning hours. Foragers could still be seen coming and going and exchanging with wasps in the swarm, but a new kind of activity was also occurring with increasing frequency. From time to time a worker landed on the swarm or on the substrate at the edge of the swarm and ran agitatedly among the wasps. During these runs the wings were buzzed and the gaster was held low, possibly touching the substrate, though this could not be confirmed, and frequently the gaster was wagged from side to side. Often the running wasp bumped into others, but without stopping. Sometimes, but not always, such behavior was followed by a noticeable increase in flight activity of the swarm as a whole.

Such periods of heightened activity, both at the swarm and away from it, occurred with increasing frequency until the swarm finally began to move. This usually began quite suddenly as more and more wasps began to take off and fly in large arcs at increasing distances from the swarm. Within five minutes all but a few hundred wasps had left the old site and were on their way toward the new one.

During movement of the swarm workers were frequently seen dragging on prominent objects; this was performed by wasps moving both to and from the new swarm site. Many wasps passing a given landmark, however, did not land, but merely hovered a few centimeters downwind of it before flying on in the direction of the new swarm site. Others landed and walked over the surface of the object with their gasters raised.

The moving swarm was so diffuse that it would not catch the attention of a person unaware of what was happening, even if he were standing in the path of movement. The passage of all the wasps past a point along the path took longer than 30 minutes.

The path followed by the swarm was usually a straight line, though on the first day it followed a row of fence posts south for the first 30 meters, then turned WSW toward the new site. Here there was only low grass along the direct route. Evidently the fence posts provided more suitable landmarks even though they did not lead directly to the new site. The path may be quite wide. On

one occasion I observed wasps landing on and dragging their gasters over objects as far apart as 10 meters along a line perpendicular to the direction of swarm movement.

On two occasions an attempt was made to determine when queens moved by netting samples of wasps as they passed a point along the route. Beginning at 1735 on 5 February the numbers of workers (queens in parentheses) netted in successive three-minute intervals were: 10 (0), 9 (0), 8 (0), 3 (2), 4 (2), 5 (0), 1 (1), 2 (1), 6 (1), 4 (0). On 6 February beginning at 1615 the results were 0 (0), 1 (0), 2 (0), 2 (0), 1 (1), 5 (1), 7 (0), 3 (0), 1 (0). The scanty results reflect the difficulty of netting wasps due to the diffuse nature of the moving swarm. Though sample sizes are small, the results suggest that queens do not begin moving to the new site until 10 or 15 minutes after the first workers begin to move.

The swarm could be followed only by moving from one dragging site to the next. It was possible to first roughly localize the new swarm site by noticing the point beyond which no wasps were observed dragging. Pinpointing the site was sometimes difficult, because of the rather wide path that was followed by the wasps. This was especially true in dense vegetation, where there were many possible sites available. It was usually possible to find the swarm by searching for unusually dense aggregations of flying wasps. Upon arrival of the bulk of the population at the new site the swarm usually settled down fairly quickly. This behavior made it much easier to locate the swarm in the new site while wasps were still arriving, rather than later. On some occasions arriving wasps seemed to overshoot their goal and could be seen searching beyond the new site. In one case several wasps were seen hovering about the tip of a dead tree some 11 meters beyond the newly settled swarm.

DISCUSSION

The behavior described herein is very similar to what Naumann has observed in *Polybia catillifex*, *P. oecodoma*, *Stelopolybia myrmecophila*, *Leipomeles dorsata*, and *Angiopolybia pallens* (Naumann, 1975). As Naumann concluded, it strongly suggests involvement of a trail pheromone. The dragging behavior could well function to deposit scent marks on prominent objects along the swarm route. Following swarm members may then pick up the scent by hovering downwind of such marks or by landing on marked objects and inspecting them with their antennae.

What is needed now is an experimental investigation of the whole matter, testing 1) whether such a scent trail is indeed produced and followed, 2) how the swarm is finally stimulated to begin moving, and 3) how individuals recognize the new site when they arrive.

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Without the cooperation of Dr. Antonio Lot Helgueras in making available the facilities of the Estación de Biología Tropical "Los Tuxtlas" this study would not have been possible. Mr. Mark Winston assisted in the field. Dr. E. O. Wilson provided helpful comments during the preparation of the manuscript. This work was supported by National Science Foundation Grant GB-33619 to the author and H. E. Evans.

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ADDITIONAL NOTES ON THE ORB-WEAVER
GENERA *ARANEUS*, *HYPSOSINGA*, AND *SINGA*
NORTH OF MEXICO (ARANEAE, ARANEIDAE)*

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INTRODUCTION

After my first *Araneus* study was published in 1971 I was informed by W. J. Gertsch and V. Roth that the males of *A. illaudatus* are found with females of my newly described *A. pima*. However, owing to the great size difference and abdominal pattern difference, I remained stubbornly unconvinced that they could belong to the same species until spiderlings from an egg-sac raised by P. Witt grew up into female *A. pima* and male *A. illaudatus*. This persuaded me but raised some new questions, as the hand-reared males are larger, the females smaller, than in wild populations (see below).

While establishing this synonymy (in Levi, 1971), I take this opportunity to report on an additional new species of *Araneus* from the Southwest (Levi, 1973), as well as to report range extensions from the American Museum *Singa* and additional *Araneus* collections and from the R. V. Chamberlin (University of Utah) collection, now again available. I will publish later on a number of tiny new species of *Araneus*, most collected as provisions by wasps.

I would like to thank W. J. Gertsch, V. Roth, N. Platnick, of the American Museum of Natural History, S. Frommer, F. Enders and P. Witt for specimens, E. Mayr and Lorna R. Levi for reading the manuscript. National Science Foundation Grant BMS 75-05719 supported the researches and publication.

SIZE VARIATIONS

For unknown reasons, size differences between sexes and among individuals of the same sex within populations are much greater in orb-weavers in the superfamily Araneoidea than in other spiders, although adult size variations are common in arachnids. These differences, due to variation in the number of instars before maturity, have been commented on by others (e.g. Gerhardt, 1929, 1930; Probst, 1972 in *Isometrus* scorpions).

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Since large differences in size may be accompanied by allometric differences it often becomes very difficult to decide whether a large and a small female belong to the same species. Also, the large and small specimens have differences in numbers of macrosetae.

In addition, in the Araneidae there are often large differences in size between the sexes as the dwarfed males mature already after only a few molts, sometimes after fewer than half the number in females. Larger males, having undergone more molts, may resemble females more than they resemble smaller males (Gerhardt, 1929).

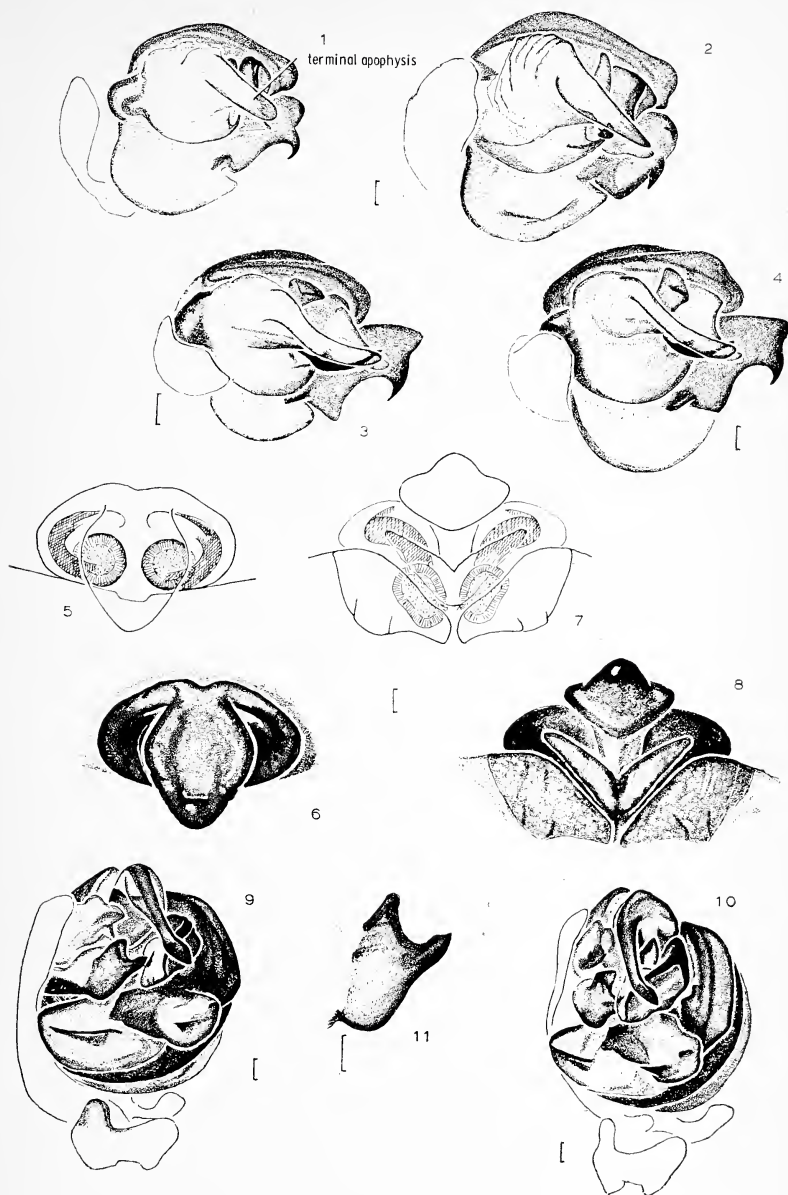
Oddly, the smallest female and one of the larger males of *A. illaudatus* came out of the same egg-sac, hand-raised in P. Witt's laboratory in North Carolina. This poses the question, to what extent the variable number of instars is environmentally determined? The egg-sac came from a building of the Southwestern Research Station near Portal, Arizona, where males are usually small and females large.

According to older literature the minute size of many male orb-weavers prevents suitors from being mistaken for prey by the large female. This idea, which originated with Charles Darwin and Friedrich Dahl (Gerhardt, 1929), is not convincing to me. In Gerhardt's experiments neither large nor small males were attacked. It is much more likely that the differences in size, especially in warm climate spiders, is a secondary by-product of selection for different rates of ontogeny. A quick maturation of males, etc. is an adaptation against inbreeding. The tiny males mature after a few molts, perhaps months before sibling females undergo their 8 to 11 instars, and are forced to look for mature females from earlier broods or even from a different generation. [Witt (personal communication) reports that in his cultures of *Araneus diadematus* males mature long before females.] But then why do small males come in various sizes (as in *A. illaudatus*), and why do hand-raised females vary in size? Is there genetic polymorphism for rate of development?

Figs. 1-4. Left palpus, apical view. 1. *Araneus gemmoides* Chamberlin and Ivie. 2. *Araneus gemma* (McCook). 3, 4. *Araneus illaudatus* (Gertsch and Mulaik). 3. (Portal, Arizona). 4. (hand-raised specimen, Portal, Arizona).

Figs. 5-11. *Araneus abigeatus* new species. 5-8. Epigynum. 5. Ventral view, cleared. 6. Ventral view. 7. Posterior view, cleared. 8. Posterior view. 9-11. Left palpus. 9. Mesal. 10. Ventral. 11. Embolus in mesal view.

Size indicators, 0.1 mm.



Araneus illaudatus (Gertsch and Mulaik)

Figures 3, 4

Aranea illaudata Gertsch and Mulaik, 1936, Amer. Mus. Novitates, no. 863, p. 19, figs. 36, 37, ♂. Male holotype from Edinburg, Texas in the American Museum of Natural History, examined.

Araneus pima Levi, 1971, Bull. Mus. Comp. Zool., vol. 141, p. 176, plates 1, 4, figs. 218-232, ♀, ♂, map 8. Female holotype from Madera Canyon, Santa Rita Mountains, Pima Co., Arizona in the American Museum of Natural History. NEW SYNONYMY.

Araneus illaudatus,—Levi, 1971, Bull. Mus. Comp. Zool., vol. 141, p. 176, figs. 238-240, ♂ (not figs. 233-237, ♀ which is *A. abigeatus*, n. sp.).

Note. Some *A. illaudatus* males had shorter embolus caps than others. The distribution maps (Levi, 1971) of *A. illaudatus* and *A. pima* should be combined.

Diagnosis. Males of the three similar species can be separated by the length of the terminal apophysis in apical view. *Araneus gemmoides* Chamberlin and Ivie has the shortest, widest terminal apophysis (Fig. 1) and largest palpal tibia (1971, figs. 199-200). *Araneus gemma* (McCook) has a pointed, curved terminal apophysis, widest at the base (Fig. 2). *Araneus illaudatus* has a long curved terminal apophysis, the sides more or less parallel (Figs. 3, 4).

Size ranges. Total length of females varied 11.5 to 27 mm. The smallest female was hand-raised from Chihuahua Mts., Arizona and another collected at Gateway, Oregon, both 11.5 mm. Total length of California females in mm: 14, 17, 22; Utah: 13, 23; Arizona, Fort Grant: 22; Huachuca Mts.: 18, 18, 18, 20, 23; Chihuahua Mts.: 13, 19, 21, 22, 23; Santa Rita Mts.: 18, 20, 24; Grand Canyon: 15; Texas: 14, 18; Mexico, Chihuahua: 18. Not all females were measured, only one from each collection. There appears to be no geographic pattern.

Total length of males 2.9 to 7.9 mm. Measurements of males in mm: Utah, Watson: total length 4.2, carapace 1.9 long, 1.5 wide; Arizona, Santa Rita Mtns.: total length 7.9, carapace 4.1 long, 3.0 wide; Chihuahua Mts.: total length 2.9 to 3.9 mm, carapace 1.6 to 1.9 long, 1.2 to 1.6 wide, three specimens; Texas: total length 3.6 to 4.0 mm, carapace 1.9 to 2.0 long, 1.3 to 1.5 wide, two specimens; specimen from Chihuahua Mts. hand-raised in North Carolina: total length 6.6 mm, carapace 3.6 long, 2.8 wide (Fig. 4). All males were measured; the 6.6 mm and 3.8 mm males are illustrated in Figures 3, 4.

***Araneus abigeatus* new species**

Figures 5-11

Araneus illaudatus,—Levi, 1971, Bull. Mus. Comp. Zool., vol. 141, p. 176, figs. 233-237, ♀, epigynum and abdomen; not figs. 238-240, ♂.

Holotype. Female from Rustler Camp, Chiricahua Mts., Cochise Co., Arizona, 9 Sept. 1950 (W. J. Gertsch) in the American Museum of Natural History. The name *abigeatus* is a Latin verb for cattle stealing, rustling.

Description. Female. Carapace dark brown, marbled on lighter brown with some light setae. Sternum dark brown, coxae light. Legs banded brown on yellow-white with some white-tipped setae. Dorsum of abdomen with a median longitudinal line of white spots and four pairs of dark brown chevrons, the posterior pair fused in middle on dark brown speckled background (1971, fig. 236). Venter with a black band from epigynum to spinnerets, and a pair of white spots side by side. Spinnerets dark brown. Eyes subequal in size. Anterior median eyes slightly more than their diameter apart. The abdomen has a pair of anterior dorsal humps. Total length 11.0 mm. Carapace 3.7 mm long, 3.5 wide. First femur, 4.5 mm; patella and tibia, 5.5; metatarsus, 3.7; tarsus, 1.4. Second patella and tibia, 5.0 mm; third, 2.9; fourth, 4.9.

Male. Coloration similar to that of female, except carapace more uniform light brown. Thorax with a longitudinal groove. Eye size and spacing as in female. First coxa with a hook, second femur with groove. Second coxa with a small posterior, proximal tubercle, no spur. Second tibia swollen with macrosetae on venter. Total length 7.0 mm. Carapace 3.8 mm long, 3.2 wide. First femur, 5.0 mm; patella and tibia, 6.5; metatarsus, 3.6; tarsus, 1.3. Second patella and tibia, 5.0 mm; third, 2.9; fourth, 4.5.

Diagnosis. The constricted neck of the scape of the epigynum covering a large hollow space (Figs. 6, 8) separates this species from *Araneus illaudatus*. The internal genitalia (Figs. 5, 7) are heavily sclerotized and were cleared but not macerated as only few specimens were available.

The male will key out to *A. washingtoni* in Levi (1971) but the palpus is similar to that of *A. nordmanni*. The palpus has a terminal apophysis prong similar to that of *A. nordmanni* but differs by the shape of the shorter embolus (Fig. 11) and shape of conductor (Figs. 9, 10).

Records. Known from type locality only. Paratypes collected on 25 Aug. 1952, 1 ♀ (B. Malkin), 23 Aug. 1968, 1 ♀ (V. Roth), 4 Aug. 1973, ♀, ♂ (S. Frommer).

Araneus washingtoni Levi

Additional Record. Ontario: Batchawana, ♂.

Araneus santarita (Archer)

Additional Record. Arizona: Cochise Co.: Upper Cave Creek, Chiricahua Mts. (V. Roth).

Araneus pratensis (Emerton)

Additional Records. Ontario: Thessalon. *Mississippi:* Wilkinson Co.: Centreville.

Araneus mammatus (Archer)

Additional Record. New Mexico: Santa Fe Co.: Hyde Memorial State Park, 8 miles northeast of Santa Fe.

Araneus mariposa Levi

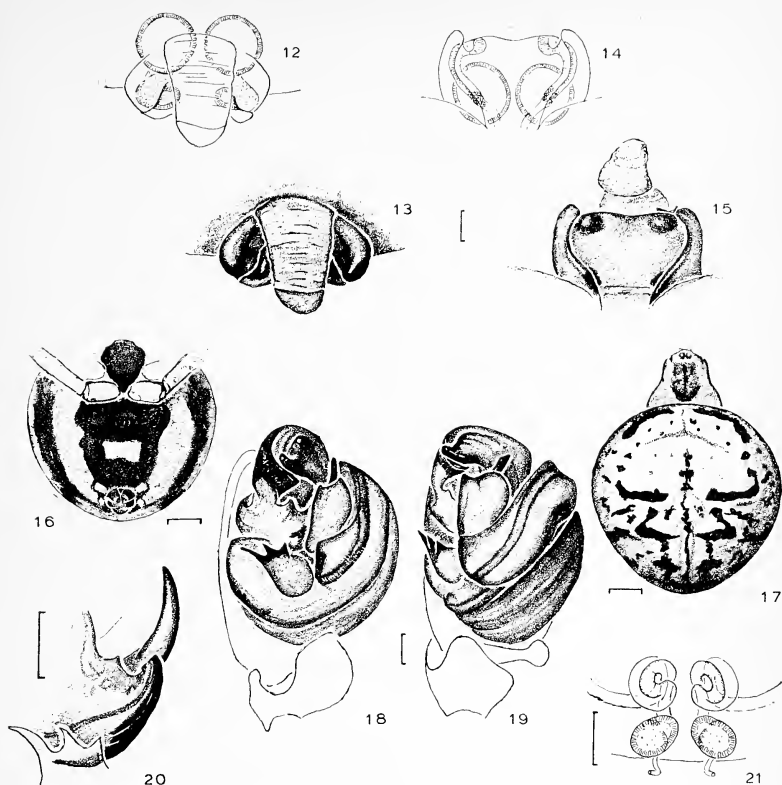
Additional Record. Oregon: Jackson Co: Sams Valley to Dead Indian Spring, 2 ♀ (J. Schuh).

***Araneus apache* n. sp.**

Figures 12-20

Type. Male holotype with a female paratype from Rustler Camp, Chiricahua Mts., 9 Sept. 1950 (W. J. Gertsch) in the American Museum of Natural History.

Description of female paratype. Carapace yellow-white with a wide median longitudinal brown band pointed posteriorly toward thoracic depression. Sternum brownish black. Legs with dark bands. Coxae yellow-white. Dorsum of abdomen with transverse marks as in Figure 17. Venter brownish black with transverse white mark behind epigynum (Fig. 16). Posterior median eyes subequal to anterior medians. Anterior laterals 0.8, posterior laterals 0.9 diameters of anterior medians. Anterior median eyes 1.4 diameter apart, 1.6 from laterals. Posterior median eyes slightly less than their diameter apart. The height of the clypeus is less than diameter of anterior median eyes. Abdomen is almost round, dorso-ventrally slightly flattened. Total length 7.5 mm. Carapace 3.1 mm long, 2.4 wide. First femur, 3.2 mm; patella and tibia, 4.2; metatarsus, 3.0; tarsus, 1.0. Second patella and tibia, 3.4 mm; third, 2.0; fourth, 3.0



Figs. 12-20. *Araneus apache* new species. 12-15. Epigynum. 12. Ventral view, cleared. 13. Ventral view. 14. Posterior view, cleared. 15. Posterior view. 16. Female abdomen, ventral. 17. Female carapace and abdomen, dorsal. 18-20. Left male palpus. 18. Subventral view. 19. Ventral view. 20. Embolus, subventral view.

Fig. 21. *Hypsosinga pygmaea* (Sundevall), dorsal view of genitalia.

Size indicators, 0.1 mm, except Figs. 16, 17, 1.0 mm.

Males. Males are less distinctly marked than females. The eye size ratios and distances are about the same as those of female. The first coxa has a hook, the second tibia has macrosetae but is not swollen. Total length 4.0 mm. Carapace 2.3 mm long, 1.9 wide. Second patella and tibia, 3.0 mm; third, 1.7; fourth, 2.5.

Variation. There is little variation in size of the few specimens available. The dorsum is much lighter in some individuals than in others; and in the pale specimens, the median carapace band and the dark spots on the abdomen barely show. All, however, have a dark sternum.

Diagnosis. This species is close to *Araneus pегnia* (Walckenaer), but males differ by having three prongs on the median apophysis (Fig. 18) rather than two and in details of the shape of other distal palpal structures (Figs. 18-20). Females differ from those of *A. pегnia* by having a wider scape (Fig. 13) and also a brownish black sternum and brownish black venter of the abdomen surrounding a transverse white mark (Fig. 16). Males differ from those of *A. thaddeus*, which have a similar three-pronged median apophysis, by the very differently shaped embolus (Fig. 20), bearing a worm-shaped lamella. Such an embolus lamella is present in *A. pегnia* also, but is not illustrated in Levi (1973, figs. 436, 437).

The species keys out to 3, *A. pегnia* and *A. thaddeus*, in my key to females of smaller species of *Araneus* (Levi, 1973, p. 488) and to 3 *A. thaddeus* in my key to males of smaller species of *Araneus* (Levi, 1973, p. 489).

Note. This is not *A. montanus* Archer. The holotype of *A. montanus* was re-examined and is *A. thaddeus* as synonymized before (Levi, 1973). Females of *A. apache* I had previously placed in *A. pегnia*. *Araneus pегnia* does not seem to occur in southeastern Arizona; it is found in California and Sonora (Levi, 1973, map 6).

Records. Paratypes from *Arizona*. Cochise Co.: Chiricahua Mts., 29 Aug. 1938, ♂ (R. H. Crandall). Graham Co.: Pinecrest, Graham Mt., 13 Sept. 1950, 2 ♀ (W. J. Gertsch), Shannon Camp, Graham Mt., 13 Sept. 1950, 5 ♀ (W. J. Gertsch). Pima Co.: Santa Catalina Mts., 5 Sept. 1938, 2 ♀ (R. H. Crandall).

Singa keyserlingi McCook

Additional Records. *New Jersey.* Ocean Co.: Lakehurst. Burlington Co.: Lebanon State Forest. *Minnesota.* Goodhue Co.: Lake Pepin. Carlton Co.: Carlton.

Singa eugeni Levi

Additional Records. *New York.* Kings Co.: Bergen Beach (Brooklyn). *New Jersey.* Atlantic Co.: Oceanville. *North Carolina.* Carteret Co.: Beaufort.

Hypsosinga pygmaea (Sundevall)

Figure 21

Theridion pygmaea Sundevall, 1831, Kongl. Svenska Vet. Akad. Handl. p. 121. Type from Sweden, assumed lost.

Singa variabilis Emerton, 1884, Trans. Connecticut Acad. Sci., vol. 6, p. 322, pl. 34, fig. 16, pl. 37, figs. 19-21, ♀, ♂. Five syntypes from New Haven, Connecticut in the Museum of Comparative Zoology. NEW SYNONYMY.

Singa pygmaea, — Wiehle, 1931 in Dahl, Tierwelt Deutschland, vol. 23, p. 47, figs. 64, 65, ♀, ♂. Roewer, 1942, Katalog der Araneae, vol. 1, p. 875. Locket and Millidge, 1953, British Spiders, vol. 2, p. 155, figs. 102c, 103b, 104b, ♀, ♂.

Hypsosinga variabilis, — Levi, 1972, Psyche, vol. 78, p. 242, figs. 44-57, ♀, ♂, map 2.

Note. Mr. G. H. Locket recently lent me British specimens of this species and they turned out to be the same as our common *H. variabilis*. There are only minor, probably geographic, differences.

Distribution. The distribution of this species is holarctic. The synonymy of *H. variabilis* with *H. pygmaea* was overlooked previously.

Additional American Records. *Nova Scotia.* Berwick. *Tennessee.* Lake Co.: Reelfoot Lake. *Georgia.* Chatham Co.: 3 mi. southeast of Savannah. *Nebraska.* Loup Co.: Taylor. *Wyoming.* Yellowstone Natl. Park: Yellowstone Lake. Grand Teton Natl. Park: Moran. *Utah.* Salt Lake Co.: Salt Lake City. *Cuba.* Pinar del Río: Viñales.

Hypsosinga funebris (Keyserling)

Cercidia funebris Keyserling, 1893, Spinnen Amerikas, vol. 4, p. 37, pl. 2, fig. 32, ♀. Female holotype from Crescent City, Florida, Marx collection of the United States National Museum kept in the American Museum of Natural History, examined.

Araneus singaeformis Scheffer, 1904, Entomol. News, vol. 15, p. 259, pl. 77, figs. 4-6, ♀. Female syntypes from Wallace County, Kansas in the Museum of Comparative Zoology.

Hypsosinga singaeformis, — Levi, 1972, Psyche, vol. 78, p. 246, figs. 58-71, ♀, ♂. Map 3.

Additional Records. *Alberta.* Medicine Hat. *Maine.* Acadia Natl. Park: Mt. Desert Island. *Connecticut.* South Meriden. *New Jersey.* Ocean Co.: Lakehurst. *Tennessee.* Bedford Co.: Shelbyville. *Minnesota* Carlton Co.: Barnum. *Texas.* Kerr Co.: Kerrville. Hildalgo Co.: Edinburg. *Utah.* Salt Lake Co.: Alta. *California.* Monterey Co.: Monterey.

Hypsosinga alberta Levi

Additional Record. *Yukon Territory.* South shore, Atlin Lake, willow, heath, dwarf shrubs, 20 Aug. 1974, ♀ (D. E. Bixler).

Hypsosinga groenlandica Simon

Additional Record. *Yukon Territory.* Herschel, 24 July 1971 (W. R. M. Mason). *Utah.* Cache Co.: Franklin Basin, 16 July 1975, 1 ♀ (G. F. Knowlton).

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NESTING BEHAVIOR OF
LARROPSIS CHILOPSIDIS AND *L. VEGETA*
(HYMENOPTERA: SPHECIDAE: LARRINAE)

BY DARRYL T. GWYNNE AND HOWARD E. EVANS¹

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In their revision of the genus *Larropsis*, Bohart and Bohart (1966) reported prey records for only two of the 25 described species. *L. divisa* (Patton) had been observed preying on immature camel crickets, *Ceuthophilus* sp., by Williams (1913), who also presented notes on nesting behavior; and R. M. Bohart himself had taken *L. flicornis* Rohwer with an adult camel cricket of the genus *Ammobaenetes*. A detailed study of the nesting behavior of *Ancistromma distincta* (Smith), a member of a closely related genus (often ranked as a subgenus of *Larropsis*), was published by Evans (1958a). The present paper adds to the limited knowledge of *Larropsis* biology by reporting observations on the nesting behavior of *L. chilopsidis* (Cockerell and Fox) and *L. vegeta* (Fox). These two species are very similar structurally, live in sand dune habitats, and exhibit virtually identical nesting behavior.

METHODS

Behavioral data were collected by following individual females as they walked over the sand surface searching for burrows of their camel cricket prey. Observations were read into a Sony cassette tape recorder and were later copied into a field notebook. Burrows were excavated to determine nest dimensions and to locate cells and prey. Cell contents were kept in rearing tins with moist sand.

Voucher specimens of both species of *Larropsis* and their prey and parasites have been placed in the collection of Colorado State University.

¹Part of a study of the comparative behavior of solitary wasps, supported by the National Science Foundation, grant GB 43790.

Manuscript received by the editor December 10, 1975.

OBSERVATIONS ON *L. CHILOPSIDIS*

According to Bohart and Bohart (1966) this species is distributed from Chihuahua, Mexico, north to southern Colorado and east into Texas. Our observations were made during late June and early July 1975 in sand dunes bordering the Rio Grande valley, at the La Joya Waterfowl Preserve, 20 miles north of Sorocco, New Mexico. At this locality, females were commonly observed in the dunes during the morning and again during late afternoon; during the heat of midday they were rarely seen. Their activity consisted mainly of walking in sinuous patterns over the sand and investigating small depressions and burrow entrances in the sand surface. In contrast to some Larrinae, females did not flicker their wings while hunting. Often they dug with the front legs and occasionally they entered holes in the sand. Most females were followed by one or more satellite flies hovering 6-8 cm behind (Table 1). We captured several of these flies and found that two species were involved: *Senotainia rufiventris* (Coquillett) and *S. (?) flavicornis* (Townsend) (Sarcophagidae, Miltogramminae) (det. R. J. Gagné) (Table 1). *L. chilopsidis* females appeared to spend a great deal of time searching, as evidenced by the many hours we spent following them before one was observed to locate her prey. All *L. chilopsidis* observed preyed on *Ammobaenetes phrixocnemoides* (Caudell) (Gryllacrididae, Rhaphidophorinae), a sand treader camel cricket (4 records).

Table 1. Records of satellite flies observed following female *Larropsis* species.

Number of flies per ♀	Number of females	
	<i>L. chilopsidis</i>	<i>L. vegeta</i>
0	11	7
1	15	1
2	1	0
3	0	0
4	1	0

Observation A.—The first interaction between female and prey was observed at 0920 on 27 June. The wasp was seen moving over the sand surface and digging briefly in various places. She flushed a sand treader camel cricket from just beneath the surface. The cricket jumped approximately 1.5 m but the wasp did not follow. We recovered the cricket and threw it at the wasp, which seized it

and held on while the prey still jumped around. The wasp stung the prey several times, preventing further movement. After a short period the wasp grasped the antennae of the cricket and started to pull it. However, the cricket was twice the length of the wasp and doubtless weighed several times as much, and after a few seconds she stopped trying to move it and began to feed at the ventral side of the neck region. After 30 seconds she abandoned the prey and resumed her searching behavior. She did not return to the cricket, which after one hour was collected for identification.

Observation B.—Another wasp was observed at 0905 on 28 June, moving up a 20 degree slope in the dunes, straddling a paralyzed cricket and holding it by the antennae, beating her wings rapidly to gain additional traction up the slope. After moving 0.5 m, she left the prey briefly and walked up the slope investigating several holes before she resumed dragging the prey. A satellite fly hovered around the wasp and prey and at one point perched briefly on the cricket. After dragging the prey another 0.5 m the wasp once again left it and moved about the sand surface for about 2 minutes. She returned quickly and carried the prey into an open hole. No satellite flies followed her to the hole.

At 0942 the wasp was observed to reappear at the mouth of the burrow, digging at the sides of the hole. As she moved toward the surface she turned, and sand from the burrow gradually filled the burrow behind her. At 0943 she flew away, leaving the top 1 cm of the burrow unfilled. She made no attempt to use sand from the dune surface to fill the hole. The burrow was evidently that of a cricket, possibly the one she had captured. It was dug into a slope of about 20 degrees and was steep for the first 15 cm (about 30-35 degrees with the surface); the first 11 cm was filled with sand and the next 4 cm was open. Beyond this the burrow had been filled and was impossible to trace. The cell with the paralyzed cricket was located 28 cm below the sand surface and 40 cm from the burrow entrance. The prey was positioned on its back and bore the *Larropsis* egg as well as a small satellite fly larva (Fig. 1).

Observation C.—At 1735 on 28 June a wasp was seen entering a burrow. About 1.5 min later she emerged 15 cm from the burrow mouth and immediately dug herself back in. Both times she entered the ground she had to dig for 15-20 seconds in order to get through the loose surface sand. At 1915 the wasp had not emerged from the burrow. At 0830 on the following day we excavated the area around the filled burrow and found a female camel cricket 19 cm deep and 35 cm from the burrow mouth. An egg was present on the cricket, which had completely recovered from paralysis.



Fig. 1. Paralyzed *Ammobaenetes phrixocnemoides* bearing the egg of *Larropsis chilopsidis* (broad arrow points to the egg, slender arrow to the maggot of *Senotainia* sp. directly behind it).

Observation D.—At 0900 on 30 June a *Larropsis chilopsidis* female, followed by a satellite fly, was observed digging for about 30 seconds before entering a burrow. The fly perched on a small twig, about 3 cm from the burrow mouth, as the wasp entered. The fly then flew to the burrow mouth but soon returned to her perch; she continued to show interest in the hole and several times moved between it and various perches. This alternated with bouts of flying in 0.5 m circles around the burrow. At one point the perched fly oriented to a passing harvester ant, *Pogonomyrmex* sp., which was about the same size and color as female *L. chilopsidis*. At 0912 the fly was still present but seemed to show less interest in the burrow, and by 0930 it had left the area.

At 1000 the wasp had not emerged from the burrow so the mouth was covered with an insect net. Upon returning to the area at 1400 we found the dead wasp in the net, evidently a victim of the intense afternoon heat. The nest, which was located on level ground about 0.5 m from a large shrub, was excavated that afternoon, but the filled burrow was impossible to trace. Cell and prey were located 31 cm from the burrow entrance. The female camel cricket prey, which had an egg attached, was apparently just recovering from paralysis, as it was able to walk slowly.

Egg and Larva.—The egg of *L. chilopsidis* is 2.0-2.2 mm long and about 0.4 mm wide ($N=3$). It is laid transversely between the front and middle coxae of the prey, with one end pressed against one of the front coxal cavities (Fig. 1). This is exactly the same egg position described for *Ancistromma distincta* (Evans, 1958a). In two observations (C and D) the prey seemed to recover from paralysis about 6-8 hours after being stung. The egg from observation C hatched in 44 hours, which is comparable to the 2 days reported for *A. distincta* by Evans. The larva, however, died soon after hatching. The egg from interaction B failed to hatch. As mentioned above, a satellite fly had been observed landing on the prey in this instance. In the cell a single fly larva was observed immediately behind the wasp egg; it was 1 mm in length and positioned at one end of the egg, between it and the right middle coxa of the prey (Fig. 1). By 6.5 hrs after the egg was laid it had been completely consumed by the fly larva. Sixteen hours later the larva had entered the body of the cricket, which was dead. By the morning of 4 July (6 days after the egg had been laid) the maggot pupated, leaving only the legs, head, and end of the cricket abdomen unconsumed. The puparium was brick red in color and measured 2×5 mm.

OBSERVATIONS ON *L. VEGETA*

Females of this species are about the same size as those of *L. chilopsidis* (approximately 15 mm) but are much darker in color, almost black. Bohart and Bohart (1966) reported the species from the central Great Plains in Wyoming, Colorado, western Nebraska, northern Arizona, and the base of the Texas panhandle. Our observations were made near Hasty, in southeastern Colorado, in early July 1975.

The behavior of this species appears almost identical to that of *L. chilopsidis*. Although one female *L. vegeta* was followed by a satellite fly (not identified), the majority were not (Table 1). Only one interaction between wasp and prey was observed. At 1000 on 5 July, a female was observed digging on the surface of a dune. She located a burrow and entered. We excavated the burrow about 5 minutes later; as it had not been filled it was easy to trace to the cell. The burrow formed an angle of about 10 degrees with the flat sand surface. It was straight for 34 cm, where the wasp and paralyzed prey were found about 15 cm below the surface. The prey was an immature female sand treader camel cricket, *Daihiniella* sp. The wasp had not yet laid an egg on her prey.

DISCUSSION

Both *Larropsis chilopsidis* and *L. vegeta* females obtain their prey by searching the sand surface for sand treader camel cricket burrows. Apparently they use olfactory cues to locate active burrows. Support for this hypothesis comes from an observation made after removing a cricket prey and egg of *L. chilopsidis* from the cell. A searching female walked into the hole we had dug out and showed much interest in the empty cell, digging in the area for several seconds.

Very little is known about the biology of sand treader camel crickets. There are several genera in the group (Tinkham, 1942), all characterized by a "sand basket" of spurs on the upper distal end of the posterior tibiae. An *Ammobaenetes phrixocnemoides* kept in the laboratory was observed to remove sand from its burrow by moving backwards, pushing sand behind it with the aid of the sand baskets. These insects are nocturnal and dig a simple, oblique burrow in which they pass the day (Tinkham, 1942). A searching female *Larropsis* is therefore more likely to find her prey deep in the burrow.

Our observations suggest that both species normally find and sting their prey underground, where the cricket has little opportunity to escape. In observation A (*L. chilopsidis*) the wasp had evidently

encountered a cricket near the sand surface, where it was able to escape by leaping away from the wasp. Even though searching *Larroopsis* females are usually followed by satellite flies, they normally successfully avoid these parasites by capturing their prey underground. *Senotainia* species will not enter burrows and will larviposit only on exposed prey outside the burrow (Evans and West Eberhard, 1970, p. 61). This was revealed when a satellite fly was observed to follow a *L. chilopsidis* female as she entered a camel cricket burrow. Although the fly appeared to show much interest in the burrow mouth she did not enter but perched nearby for about 20 minutes (observation D). A satellite fly was successful in larvipositing on the prey in the single observation (B) where the female had stung the prey outside the burrow. In this case the cricket had presumably escaped from the wasp and had been chased, subdued, and eventually dragged back to its burrow.

Both of the species studied do not dig their own nests but utilize burrows of their prey, thus conserving the energy required to dig a nest. Use of pre-existing cavities for nesting is common in the subfamily (Larrinae) to which *Larroopsis* belongs, having been reported in such genera as *Liris* (Steiner, 1962), *Lyroda* (Evans, 1964), *Ancistromma* (Evans, 1958a), and *Larra* (Williams, 1913, 1928; Smith, 1935). *Ancistromma distincta* females do some digging, but usually take advantage of natural cavities in the rocky soil of their nesting habitat. Species of *Larra* evidently locate their mole cricket prey in their burrows using olfactory cues, then attack the prey and lay their egg in the host's burrow, much in the manner of *Larroopsis* species. However, the position in which the egg is laid is quite different in the two genera, *Larra* spp. laying the egg just back of the base of a hind leg, *Larroopsis* spp. between the front and middle legs. These different egg positions are undoubtedly adaptive and are related to the fact that mole crickets dig with their front legs, sand treader camel crickets with their hind legs. Mole crickets attacked by *Larra* recovered quickly from paralysis and resume normal activities until killed by the developing wasp larva; thus it is to the advantage of the wasp larva that it be coiled posteriorly and not in a position to interfere with digging by the host. Sand treader camel crickets attacked by *Larroopsis* spp. also recover from paralysis within a few hours and appear to be able to resume normal activities. One cricket, which we dug up some 15 hours after it was stung (observation C, *L. chilopsidis*), leaped from the excavated cell, and it was only when we captured the insect and found the wasp's egg that we were able to be sure it was the prey. However, we have no actual evidence that the crickets are able to dig their way out of the cells into which they are packed by the wasps.

These traits (temporary paralysis and use of the host's burrow as a nest) are often regarded as primitive, since they resemble the condition in structurally generalized wasps such as *Scolioidea* (Evans, 1958a,b). However, they might equally well be derived traits, suited to the ecology of their prey, and likely to reduce the success of satellite flies.

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NOTES ON THE LIFE CYCLE AND
MYRMECOPHILOUS ADAPTATIONS OF
CREMASTOCHEILUS ARMATUS
(COLEOPTERA: SCARABAEIDAE)

BY GARY D. ALPERT¹ AND P. O. RITCHER²

INTRODUCTION

Adult cetonine scarabs of the genus *Cremastocheilus* are known for their association with ant colonies (Wheeler, 1908). The genus consists of approximately 40 species and has been recorded only in North America north of the Isthmus of Tehuantepec (Howden, 1971). Twenty-three species have been collected with 11 different genera of ants, yet their true relationship with the host ants remains unknown. Cazier and Statham (1962) and Cazier and Mortenson (1965) have summarized current knowledge of the genus based largely on their own studies of adult bionomics of several species from Arizona. The only information, however, on the development of the immature stages of this genus is a few scattered notes that the larvae of some species do occur in ant nests (Mann, 1911; Wheeler, 1908a; Windsor, 1964; and Ritcher, 1966).

This is the first account of the life history and development of *C. armatus* Walker, a western species (Fig. 1) occurring with different species of *Formica* ants from British Columbia to California and Nevada (Potts, 1945). The major host ant, *F. obscuripes* Forel, is one of the most common mound building ants in western North America. A very pugnacious and aggressive ant, *obscuripes* builds large mounds of soil and vegetation containing 50,000 or more individuals (King and Walters, 1950). How *armatus* survives from egg to adult within these nests was the object of field and laboratory studies.

METHODS

The following account is a synthesis of results obtained in western and central Oregon from 1957 to 1961 and eastern and western Washington from 1970 to 1975. All four study areas were charac-

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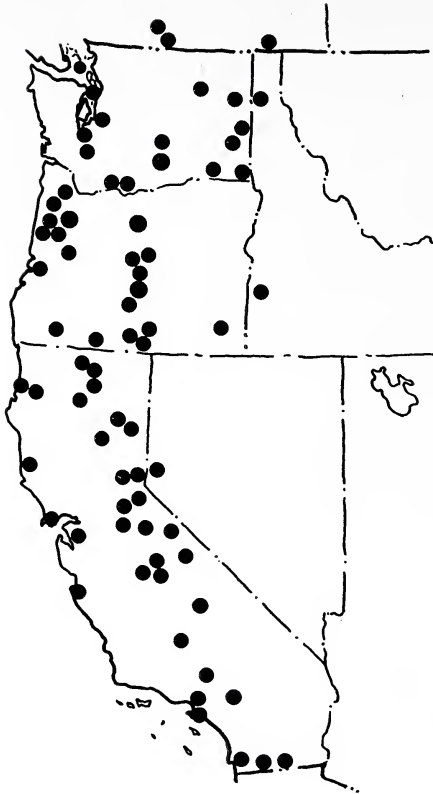


Figure 1. Distribution of *Cremastocheilus armatus* based on field collections and museum specimens.

terized by regions of high host ant density and the presence of a large population of *armatus* adults and immatures. Nest material was sorted, beetles were counted, and observations made on interactions with ants. All nest material was replaced to minimize the adverse impact of the sampling technique. The sex of the adult was identified in the field and later verified under a dissecting microscope. The sex was determined by evident geometrical differences of the last ventrite and the pygidium.

Adults and larvae were kept in the laboratory for many months with and without host ants. Larvae were most successfully reared in containers filled with original ant nest material. Adults were kept in closed containers at below room temperatures during the winter and were fed ant larvae the following spring.

LIFE HISTORY

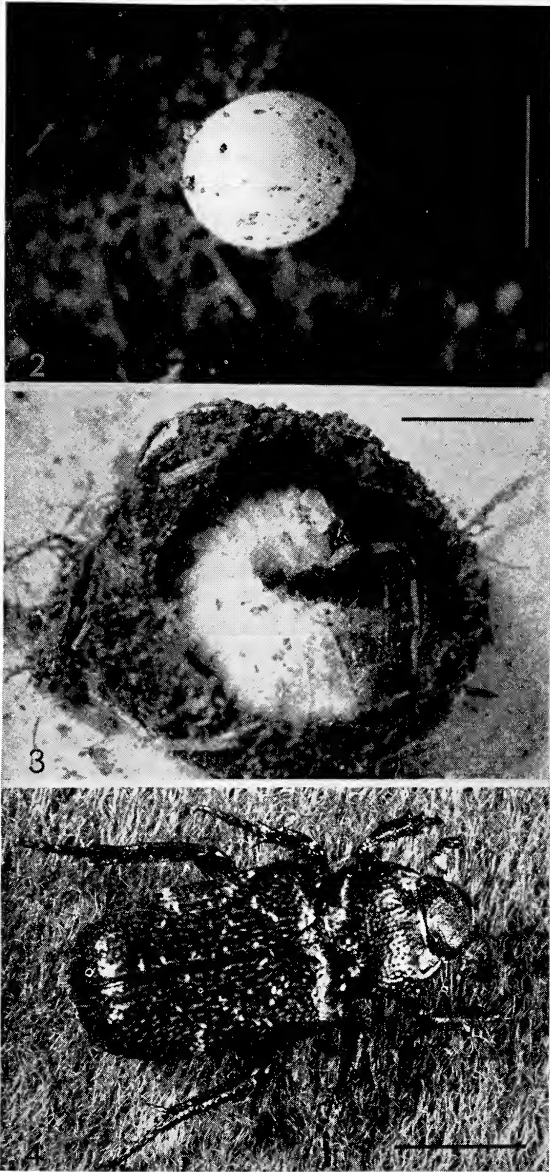
During the month of May, females laid eggs scattered throughout the outer soil edges of the ant nest. Here rich deposits of vegetative debris had accumulated and ant activity was low. Under laboratory conditions females laid a total of 3 to 12 eggs each. The broadly oval white eggs (Fig. 2) hatched after two weeks. First larval instars were collected until the middle of June. Second instars were found from June until the middle of July, and third instars were collected from the middle of June to the middle of August. The pupal stage lasted two more weeks, indicating that under field conditions development from egg to adult occurred in less than 4 months.

Most ant nests contained fewer than 30 larvae, although several nests contained well over 200. Second and third instars were gregarious, feeding within the vegetative debris just below the soil surface. Late third instars were darkened posteriorly due to the large number of fecal pellets retained in the abdomen. When uncovered, the larvae were quickly seized and bitten by many ants. They escaped the ants by rapidly burrowing down through the nest material. Late third instars left the outer soil edges and moved inward towards the center of the thatch mound to pupate. This took place during the hotter days of July when the ants were not very active in the upper mound area.

In the dry twig area above the ants' brood chamber larvae constructed elliptical earthen cases within which they pupated (Fig. 3). Easily damaged when newly formed, several of these pupal cases soon dried and hardened together into a protective clump. Adults eclosed during the late summer days and a few could be found on the surface of ant mounds at this time (Fig. 4).

As colder weather approached, the beetles moved deeper within the nest, often ending up a meter or more below the soil surface. Here the adults overwintered surrounded by dormant ants (Fig. 5). Periodic collections of overwintering adults revealed that within a few minutes at room temperature the beetles became active, even if temperatures outside the nest were below 10° C. Females often laid several eggs within a few days at room temperature but none of the eggs laid during the winter period hatched.

The following spring the adults moved back up to the outer areas in the mound. Most of the adults were collected within 3 centimeters of the nest surface at this time. Flight was so rapid at temperatures above 24° C. that mark and recapture methods were unsuccessful in determining the flight range. During this same period adult beetles



Figures 2-4. Developmental stages of *Cremastocheilus armatus* (2) Egg. (3) Late third larval instar inside earthen case. (4) Adult. (Scale: fig. 2 = 2mm; figs. 3 and 4 = 4mm).

readily fed on ant larvae and pupae. As many as 85 pairs (male and female) of adult *C. armatus* were collected in the outer nest galleries. Although they were not *in copula*, the females later laid fertile eggs. No mating was ever observed in the nest or in the laboratory. Data from museum collections indicate a peak of flight activity during April and May, the time during which mating may occur. Gravid females normally laid their eggs below the surface at the periphery of the nest.

Host records for *armatus* are probably incomplete (Table 1). *F. obscuripes* is the most common host but dispersal flights may introduce these beetles into a wide variety of ant nests. In western Oregon adults were collected from *Formica fusca* mounds, although immature stages were never found there. Larvae have been collected and reared from rich garden soil in western Oregon (Ritchee, 1966) indicating that under certain circumstances the immature stages may not have an obligatory relationship with ants.

Table 1. Host records for *Cremastocheilus armatus*

Host	Locality	Collector	Life-Stage	Reference
<i>Formica obscuripes</i>	E. Wash.	Mann	adult/larvae	Mann (1911)
	W. Wash.	Alpert	adult/larvae	New Record
<i>Formica fusca</i>	W. Oregon	Ritchee	adult	New Record
<i>Formica subpolita camponoticeps</i>	British Columbia	Howden	adult	Cazier (1962)
<i>Formica integra tahoensis</i>	E. Oregon	Ritchee	adult/larvae	Ritchee (1966)
<i>Formica integroides subnitens</i>	British Columbia	Ayre	adult	Cazier (1962)

LARVAL DEFENSE

To examine escape behavior, larvae were removed from the ant nests and placed in a series of containers with one to several ants. The normal feeding position of the larva is a C-shaped curve with the head and anal area closing off the ventral region from attack. The

ants readily attempted to bite the larvae but were unable to grasp a larva firmly with their mandibles from a dorsal approach because the dorsal surface was too convex. If however an ant came into contact with the head or ventral region there was a very rapid strike response from the larva. The larva struck at the ant with its mandibles as it coiled more tightly into the C-shape. A dark fluid was released from between the larval mandibles at the time of the strike. As the larva wriggled to escape, several wet fecal pellets were expelled which had a deterrent effect on aggressive ants. There was also a strong, unpleasant odor associated with the mandibular and anal secretions.

The above reaction was repeated until the mandibles made contact with and crushed the body of the ant. When this happened the ant immediately released its grasp of the larva and within a few seconds it collapsed. Movement was usually limited to tremors of the appendages until death occurred. Occasionally a beetle larva was fatally injured by attack from too many ants. The mandibular strike was most effective when a minor worker ant was attacked by a third instar larva.

ADULT DEFENSE

When first attacked, the beetle assumed a characteristic death feigning posture with all its legs out and slightly up at the sides. In the laboratory this position was seldom held for less than 5 minutes and showed little habituation. The ants grasped the beetles by their legs and pronotal projections and dragged them randomly about, eventually releasing their hold. Host ants regularly attacked beetles on the mound surface but as the beetles burrowed down into the thatch, most of the ants were removed. Beetles were able to penetrate the mound surface in less than one minute. In addition the beetle's heavily sclerotized integument, retractible antennae, and concealed mouth parts also represent adaptations for survival in ant nests.

If the beetle was violently disturbed or turned over by the ants, a droplet of viscous fluid was released from the anal opening. This fluid had an offensive odor and was effective in repelling the ants. When an ant came into physical contact with this fluid, it became agitated and spent considerable time grooming. Defensive secretions have been documented for other myrmecophiles (Hölldobler, 1970; Blum et. al., 1971) and their discovery in other species of *Cremastocheilus* is expected.

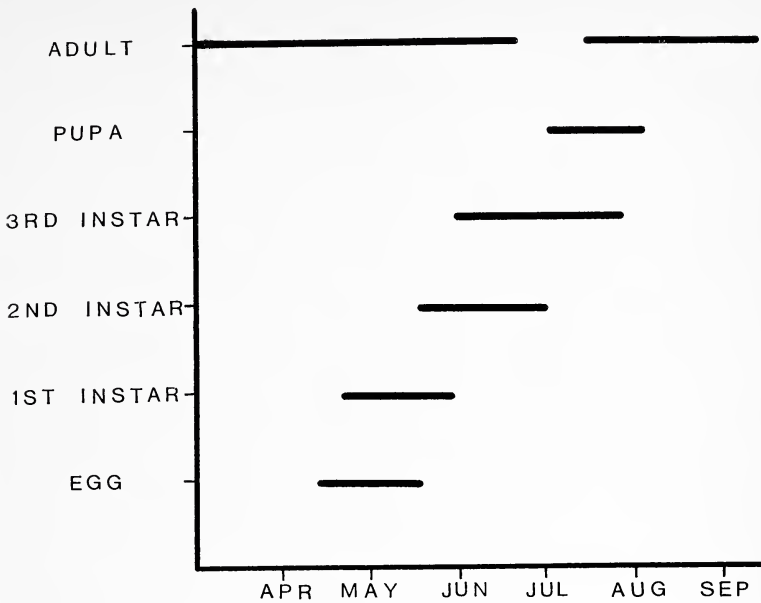


Figure 5. Seasonal distribution of the developmental stages of *Cremastocheilus armatus* collected from *Formica obscuripes* ant mounds.

PREDATION

During the spring adult beetles were predaceous on both ant larvae and pupae. In the field beetles were found feeding on larvae near the brood chamber while at the same time beetles in the outer galleries were motionless, suggesting that individuals moved into the center of the nest to feed and returned to the periphery when satiated. In the laboratory predation increased when beetles were deprived of food for over one month and when containers were darkened. It was not unusual for several beetles to feed on one ant larva at the same time.

Unlike other scarabs, *Cremastocheilus* has an unusual cupshaped mentum which prevents ants from contacting the beetle's mouth parts. When feeding, a beetle lowered its mentum and pierced an ant larva with its sharp maxillae. The mandibles are greatly reduced and aid in the transport of fluid. Feeding lasted from 10 to 30 minutes as the beetle slowly pumped the ant larva dry. Beetles were not disrupted from feeding even when covered with attacking ants.

C. armatus has fed on the larvae and pupae of the carpenter ant, *Camponotus* sp. in the laboratory (J. T. Doyen, pers. comm.). The larvae and pupae of other species of non-host *Formica* sp. have also been consumed. This lack of specificity may account for those species of ants that serve as alternate hosts, and for the wide distribution of *armatus*.

TRICHOMES

Hölldobler (1971) has shown that myrmecophiles have the ability to communicate in the same chemical language as their hosts. Trichomes are tufts of hairs that serve to increase the ability of well-integrated ant guests to communicate chemically. They are located on the ventral surface of highly modified anterior and posterior pronotal projections of *Cremastocheilus* adults. The pronotal projections have been cited as being modified to fit the mandibles of ants and to contain glands which emit a stimulating and attracting odor (Wheeler, 1908). It has been proposed that these beetles are brought into the nest and held captive by the ants because of this odor (Cazier and Mortenson, 1965).

The role of trichomes in the relationship of *C. armatus* to its host, *F. obscuripes*, is unknown. The ants do not appear to be specifically attracted to trichome areas nor are the beetles held captive by the ants. *C. armatus* is usually found unattended by ants within the nest, and is attacked by ants when on the nest surface.

ACKNOWLEDGEMENTS

The writers extend their appreciation to J. T. Doyen and J. A. Chemsak, U. C. Berkeley for their valuable field and laboratory data. J. T. Doyen also provided data concerning predation on *Camponotus* sp. larvae and pupae, including the suggestion that body fluid was being pumped from the prey. H. F. Howden, Carleton Univ., Canada identified the *Cremastocheilus*, and D. R. Smith, U. S. N. M. identified the ants. We also thank Terri Alpert and Don Frechin for their help in collecting field data.

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BIOLOGICAL NOTES ON *OCYPUS OLENS*,
A PREDATOR OF BROWN GARDEN SNAIL,
WITH DESCRIPTIONS OF THE LARVA AND PUPA
(COLEOPTERA: STAPHYLINIDAE)¹

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INTRODUCTION

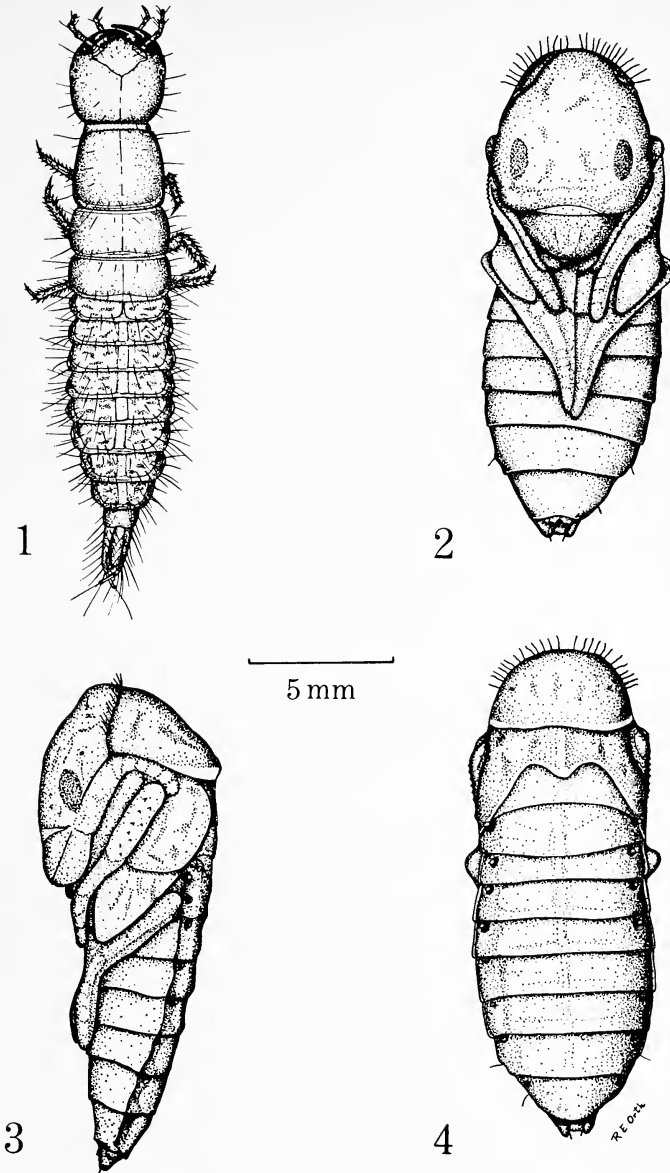
In a recent article by Orth, Moore, Fisher, and Legner (1975) laboratory studies of the snail eating habits of an adult specimen of *Ocypus olens* Müller were reported. Since then there has been opportunity to conduct similar studies of several larvae of the same species. The egg remains unknown. These larvae readily consumed snails, thus also demonstrating a potential for snail control. This view is further encouraged in the Riverside garden of one of the authors (I. Moore) which has a well established population of *O. olens* but a very low population of *Helix aspersa* Müller (brown garden snail). Other nearby gardens where *O. olens* appears not to be established have much higher population densities of *H. aspersa*.

The host snail employed in our laboratory studies was *Helix aspersa*. In California this snail has long been considered a major agricultural and suburban pest with an omnivorous diet which includes living and decaying vegetables, flowers, ground cover, citrus leaves and fruit as well as paper labels and cardboard cartons and cadavers of its own species.

The rove beetle *Ocypus olens*, sometimes referred to as the devil's coach horse, is a large (to 32 mm) black staphylinid indigenous to Europe. In North America it is known only from California where it was first recorded in southern California in 1931 (Orth, et al., 1975). Since that time distributional records extend about six hundred miles to the north.

In California both *Ocypus olens* and *Helix aspersa* seem to prefer cultivated or landscaped habitats. In the field we have seen and collected *O. olens* only in areas disturbed by man. This beetle therefore would seem to pose no threat to California's native land snails, which are generally found in the undisturbed hillsides, mountains, and deserts.

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Figs. 1-4. *Ocybus olens* Müller. Fig. 1, larva; Fig. 2, venter of pupa; Fig. 3, side of pupa; Fig. 4, dorsum of pupa.

MATERIALS AND METHODS

The larvae used in this study were from the garden of the Ian Moore residence in Riverside. Repeated attempts for over a year to obtain larvae of *Ocypus olens* at that site had failed until 4 April 1975 when 5 large larvae ranging in size from 21 to 25 mm were found beneath oleander plants. Under these plants was a dense accumulation of decomposing leaves from the oleanders as well as from neighboring trees. The habitat was very moist as a result of recent rains. The 5 *O. olens* larvae were underneath or within this material. One of the larvae was injured with a trowel and consequently died. The remaining four were brought to the laboratory for biological studies.

In the laboratory each beetle larva was housed in a circular 16 oz. plastic food container with a wire screen lid. Room temperature was maintained at $23^{\circ}\text{C} \pm 1^{\circ}$. The substrate within the containers consisted of $1\frac{1}{4}$ to $1\frac{1}{2}$ inches of moist soil from the collecting site. A loose mulch of dead leaves approximately $\frac{1}{2}$ inch in depth was added on top of the soil. Two *Helix aspersa* whose shells measured about 10 to 12 mm were placed in each unit. Small amounts of lettuce were added as food for the snails and also to induce them to come down from the top or side of the container where they would be more vulnerable to staphylinid attack. As snails were killed fresh hosts were added so there were never more than two living snails per observation unit.

BIOLOGY

The larvae of *O. olens* were fed an exclusive diet of *Helix aspersa* for a period of 2 to 3 weeks. During this period larvae consumed from 2 to 8 snails each. Attack and feeding usually occurred at night. Generally, the shells were left intact. However, some of the smaller shells showed various degrees of destruction from the body whorl to the apex. Attack by an adult beetle resulted in more severe mutilation of the shell.

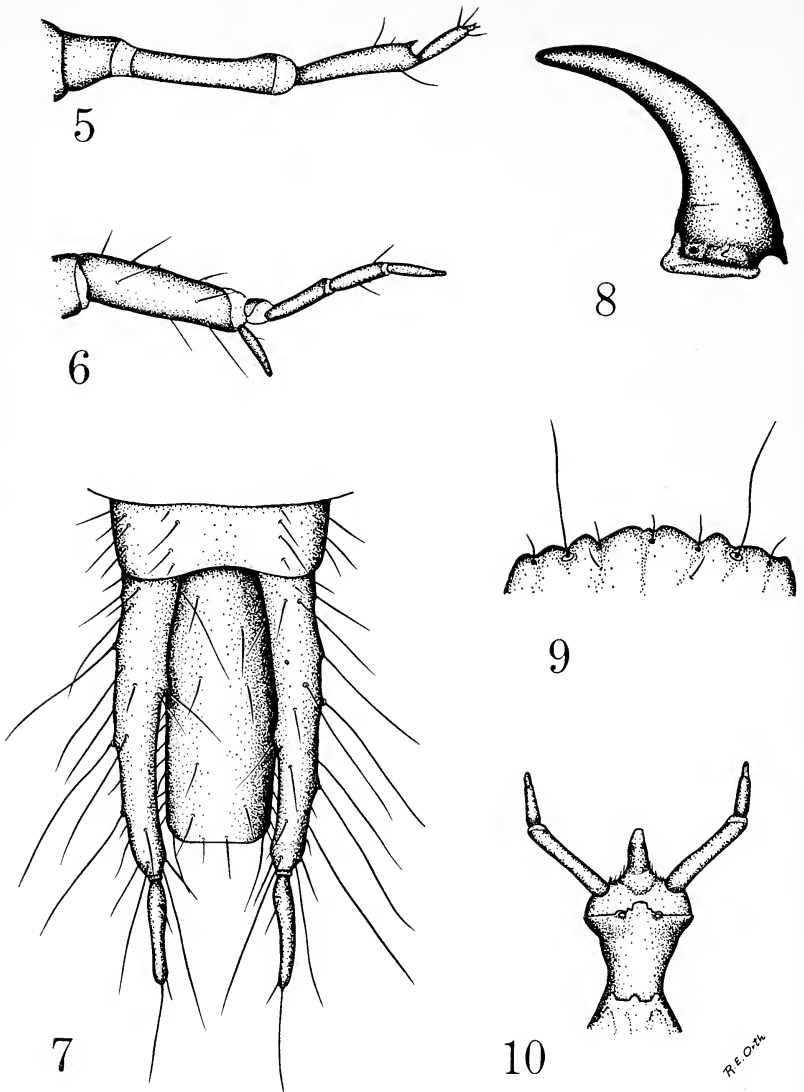
Once feeding was completed the mature larvae then burrowed through the substrate to the bottom of the unit and formed individual cells which were elliptical in shape, approximately 2.5 cm long, and 1.6 cm high and flat on the bottom as a result of the container shape. Had the substrate been deeper the larvae probably would have burrowed to a greater depth as all cells were tight against the bottom of the unit.

Once the larvae were housed within the cells they remained inactive without visual physical change for a period of about 10 days. Pupation then took place. Visual observations were facilitated by the clear plastic containers.

The newly transformed pupae were testaceous and about 18 mm in length. They changed rapidly from testaceous to piceous 9 to 14 days after pupation. The pupa illustrated was removed from the substrate and held in a covered petri dish which contained dampened filter paper to preserve moisture. This greatly facilitated the drawings and observations. Eighteen days after pupation it appeared ready for emergence. However, for reasons not understood, the specimen in the petri dish and those that remained in the plastic containers failed to emerge. An additional mature larva (29 mm) was brought into the laboratory 30 May 1975. Shortly thereafter, without any laboratory feeding, it burrowed to the bottom of the unit. It then pupated but it too failed in its final development.

MATURE LARVA OF *OCYPUS OLENS* (Müller)

Length 21.0 mm. Body elongate, somewhat convex, subparallel, tapered to apex of abdomen; piceous with the appendages paler; foreparts shining, abdomen finely densely reticulate and dull. Head oval, very slightly wider than long; with four ocelli grouped in a compact square at each side behind the base of the mandible. Clypeus with nine short blunt teeth, the center one smallest (another specimen lacked the center tooth), the next two very broad, occupying about two-fifths of the width of the clypeus. Antennal fossa located at front of the head slightly basal to and between the base of the mandible and the clypeus. Antenna four-segmented, first segment short, almost as wide as long; second segment a little narrower than first, about four times as long as wide; third segment narrower and shorter than second, four times as long as wide, with a minute "acorn seta" at apex; fourth segment a little more than half as long and about half as wide as third, about four times as long as wide. Mandibles arcuate, acute at tip, without internal teeth. Maxillary palpus five segmented; first segment short, stout, not forming a complete ring, possibly representing the galea; second segment more than three times as long as wide; third segment a little shorter and a little narrower than second; fourth segment shorter and hardly more than half as wide as third; fifth segment one-third as long and one-half as wide as fourth, tapered to pointed apex. Mala cylindrical, narrower than second segment of maxillary palpus and about half as



Figs. 5-10. Larva of *Ocybus olens* Müller. Fig. 5, antenna; Fig. 6, maxilla; Fig. 7, urogomphus and pseudopod; Fig. 8, mandible; Fig. 9, anterior margin of the clypeus; Fig. 10, labium.

long, without setae. Labial palpus three-segmented; first segment four and one-half times as long as wide, cylindrical; second segment a little narrower than first and about one-third as long; third segment narrower than second, about one-third as long, pointed. Ligula cylindrical, about as wide as first segment of labial palpus and less than half as long. Pronotum a little wider than long, about as wide as head; with three setae each side along anterior margin; five each side along posterior margin; two discal setae each side; three large and several small setae in the lateral series. Anterior face of protibia with a row of six or seven closely placed setae at distal edge which are less than one-third the length of the major setae near them. Mesonotum and metanotum of about equal size and shape, each about as wide as pronotum and about half as long; each with about twelve setae each side along the anterior margin, about eight setae along the posterior margin, with several lateral setae and no discal setae. Abdominal segments of about equal length, diminishing in width so that the abdomen is tapered; each tergite on each side, with about five setae along the anterior margin, five in a transverse row along the disc and five along the posterior margin. Spiracles prominent on all abdominal segments. Pseudopod cylindrical, more than twice as long as wide. Urogomphus two-segmented, first segment about half as wide and slightly longer than pseudopod, second segment about half as wide as first segment and about one-third as long.

One specimen Riverside, Riverside County, California, 11 March 1972, Ian Moore collector.

PUPA OF *OCYPUS OLENS* (Müller)

Length 18.0 mm. Elongate, piceous with the mesonotum and metanotum paler, heavily chitinized, surface minutely reticulate and dull. Head longer than wide, ventrally reflexed so that it is not visible from above, with a large dark eye spot each side, without tuberculi or setae. Antennae curved over legs, reaching to the tibio-femoral joint of the middle leg. Pronotum about as long as wide, arched, with a row of stout setae at the front margin divided into two series by a gap in the center which is more than twice as wide as the distance between the other setae; twelve setae on the right side and thirteen on the left. Mesotibia with a row of nine tubercles along the posterior edge and an adjacent row of six tubercles. Metatibia with a row of five small tuberculate hooks with their apices hooked distally. Elytra reaching to mid point on mesotibia. Apices of wings extending posteriorly from apex of elytra to about

the same length as elytra. Abdomen eight segmented; first four segments with prominent raised spiracles each side; last four segments with small spiracles each side; seventh and eighth sternites with a stout seta projecting laterally each side so that it is visible from above. Urogomphus short, blunt.

One specimen collected at Riverside, Riverside County, California, 4 April 1975 by R. E. Orth, reared to mature larva which pupated and died 13 May 1975.

DISCUSSION

It has been demonstrated in the laboratory that the larvae as well as the adults of *Ocypus olens* are predaceous on brown garden snails. In order to pursue biological control field studies with *O. olens* as a possible agent for control of *Helix aspersa*, insectary production of the beetles in large numbers will be necessary. Therefore further biological investigations are planned. An objective of critical importance to this total effort is to learn why fully formed and healthy looking pupae did not transform to the adult stage. We speculate that perhaps in the observations thus far completed optimum temperature, moisture, or even light were not provided.

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USURPATION AND DOMINANCE BEHAVIOR
IN THE POLYGYNOUS SOCIAL WASP
METAPOLYBIA CINGULATA
(HYMENOPTERA: VESPIDAE: POLYBIINI)¹

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INTRODUCTION

Usurpation is facultative intraspecific social parasitism. The term "usurpation" was first proposed by Yoshikawa (1955) to denote the process in which a female social insect invades a colony of the same species, kills or dominates the resident reproductive female and assumes her reproductive role. It has been postulated that usurpation behavior represents the first step in the evolution of the more advanced classes of interspecific social parasitism in wasps (Taylor, 1939; Wilson, 1971). However, usurpation behavior remains poorly studied relative to interspecific social parasitism and has been described in detail only twice (Janet, 1903; Yoshikawa, 1955). Detection of usurpation requires the observation of marked colonies and this probably accounts for the paucity of data related to usurpation.

With reference to energy management, usurpation is an aggressive analogue of the cleptoparasitic reproductive strategy employed by many solitary wasps, flies, and scarab beetles. The usurping queen gains a nest and often a worker force to aid in rearing her own offspring. Hence there is an obvious selective advantage to usurpation which is presumably opposed by the probability of being killed by the resident queen or worker wasps. However, it is not clear what the stimuli involved in illiciting usurpation actually are. The loss of a nest or the failure to gain the alpha position in a dominance hierarchy are obvious possibilities.

Previous observations of usurpation have not included data on the prior behavior of the usurping females and have been confined to temperate monogynous species. There have been no reports of usurpation or social parasitism in polygynous wasps such as the Polybiini in spite of an a priori higher expectation of cheating and deception in polygynous systems relative to monogynous systems.

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Moreover, dominance behavior has been poorly studied in polygynous wasps. Herein, a set of observations on an instance of usurpation in a tropical polygynous wasp, *Metapolybia cingulata* (Hymenoptera: Vespidae: Polybiini) and the dominance interactions that preceded usurpation seem worthy of a separate presentation.

MATERIALS AND METHODS

The observations presented here were made during a three month study of *Metapolybia cingulata* in western Ecuador.

A group of colonies were modified to permit close observation and were marked for identification in the manner described by Forsyth (1976). The two colonies discussed in this report were relatively small and young. Colony C initially contained 27 adults and a comb area of 110×85 mm. Colony F initially contained 55 adults and a comb area of 120×80 mm. On the basis of cell reusage, colony F was older than colony C.

Metapolybia cingulata, like most polybiines, lacks strongly differentiated morphological castes, and it is usually necessary to dissect females to conclusively distinguish workers from queens (Richards and Richards, 1951). However, there are differences in queen and worker behavior which allows one to categorize individuals; for example, workers groom queens but not each other. The observations presented here were derived from a continuing long term study in which the reproductive roles were inferred behaviorally rather than by dissection.

OBSERVATIONS

Strong dominance interactions were first observed in colony C on June 28. Two females were involved which are designated DDT and YA. DDT was a young female which had eclosed on June 20. YA had been present in the colony since the initiation of the study on May 23. DDT was very attractive to the workers who frequently groomed her, particularly about the abdomen. YA was much less frequently groomed, but clearly occupied a dominant role. She frequently postured in the aggressive wing-spread position and was often the recipient of trophallaxis.

On June 28 I observed YA approach DDT and grab with her forelegs the head of DDT. DDT broke the hold and moved away. Shortly after, while DDT was being groomed, YA again approached and attempted to bite the abdomen of DDT. DDT responded with an abdominal stinging motion (sting retracted) but was physically

knocked from the nest by YA. After DDT returned, aggressive interactions of similar nature were again initiated by YA, but these were not successful in displacing DDT.

There were two basic forms of aggressive contact. In the milder form, both individuals stood grasping each other face to face with their abdomens pointing towards each other and would vigorously antennate each other. In more extreme interactions, YA would attempt to bite the abdomen of DDT, who would make stinging motions and then break away.

On June 29 YA was absent from the nest. Colony C was exchanging workers with other colonies at this time (Forsyth, 1976). However, YA was not present at any of these colonies and after several days was presumed dead. DDT was behaving in a queen-like manner, being the only wasp receiving extensive grooming and trophallactic donations.

On July 3 a routine check of colony F revealed the presence of YA. This was unexpected as colony F was not exchanging workers with colony A and non-interchanging colonies are generally hostile to foreign wasps. At this time, YA was behaving as a worker sitting quietly on the comb and regurgitating when solicited.

YA subsequently became more active working on the comb. By July 6, YA was exhibiting wing-spreading behavior. On July 7th, I found an individual from colony B with one wing chewed in two. Dissection revealed this to be a young reproductive female. YA was very active and aggressive. YA continued to be a resident in colony F until July 13. Shortly after this, colonies C and F were destroyed by nearby construction work. Dissection of some wasps salvaged from colony B revealed at least one reproductive female to be present.

DISCUSSION

One interpretation of these observations is that the failure of an older queen (YA) to dominate a younger reproductive (DDT) led it to abandon colony C, invade colony F and displace one of the resident queens.

Metapolybia cingulata is known to exchange workers between related colonies (Forsyth, 1976). However, in this instance a non-interchanging and presumably unrelated colony was the object of usurpation. In unrelated colonies the invading female should be opposed by not only the resident queen, but also by the workers who will "prefer" to rear related offspring. Clearly, there is some subtle deception process involved in this particular usurpation. In a small

monogynous system such as *Polistes*, usurpation may be accomplished by simple mechanical domination of both workers and reproductives by the invading female. In this case, in which there are many resident workers, usurpation cannot proceed simply by aggression. It is probable that the invasion is accomplished by deception based on colony odor. The usurping female was not at either colony for several days. This may have allowed loss of colony odor and facilitated her acceptance into the colony.

The dominance behavior and aggression described previously may have broader significance than simply the triggering of usurpation. Inter-queen competition appears to be pronounced in small colonies to the extent that it may alter the social structure. Most small *Metapolybia cingulata* colonies rapidly become effectively monogynous (Forsyth, in prep.). Eberhard (1973) has reported this phenomenon in *M. docilis* and *M. aztecoides*. She found that monogyny was produced by worker persecution of all reproductive females but one. My observations suggest that monogyny in small colonies may also be the result of inter-queen aggression. Polygyny develops when colonies become large (Forsyth, in prep.). In a proximate sense, the occurrence of many reproductive females in the large colonies may simply reflect the ineffectiveness of dominance in large colonies. In an evolutionary context, the importance of inter-queen dominance will vary as a function of colony level selection pressures and inbreeding, a relationship yet to be quantified in the field.

ACKNOWLEDGEMENTS

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NOTE ON *BITTACUS VALIDUS* IN BALTIC AMBER.
In my reviews of Tertiary Mecoptera (1931, 1954), I expressed doubt that *Bittacus validus*, preserved in Baltic amber and described by Hagen in 1856, was actually a mecopteran. Recently, Dr. Hermann Jaeger, of the Paläontologisches Museum (Humboldt-Universität) in Berlin, sent me Hagen's type specimen for study. It turns out to be a caddisfly, showing clearly the characteristic mouthparts, hairy wings, and looped anal veins. Unfortunately, other structural features are so poorly preserved in the specimen that generic determination within the Trichoptera will probably prove impossible. For the present, at any rate, it seems advisable to list the insect as (Trichopteron) *validus* Hagen. [Reference: Carpenter, F. M., 1931, Journ. N. Y. Ent. Soc., 39: 412; 1954, Psyche, 61: 36. Hagen, H. A., 1856, Berendt, Bernst. befindl. organ. reste vorw., 2(1):91] — F. M. Carpenter, Harvard University.

STARTLE BEHAVIOR IN AN ASCALAPHID (NEUROPTERA)

BY THOMAS EISNER¹ AND PHILLIP A. ADAMS²

According to van der Weele (1908), male Ascalaphidae of the genera *Byas* and *Haploglenius* have a peculiar hinged flap covering the pronotum. The flap is more or less developed in different species, and in some conceals a bright pronotal patch. No mobility or function was ascribed to the flap. On November 17, 1968, while blacklighting at the Smithsonian Tropical Research Station, Barro Colorado Island, Canal Zone, one of us (T.E.) had occasion to observe the response to manipulation of a male of *Haploglenius luteus* that had come to rest at the light. Every time the insect was poked or seized, it abruptly exposed its patch, which in this species is brilliantly white-pruinose and contrasts sharply with the drab remainder of the body (Figs. 1-3). We suggest that this "flashing" behavior is defensive in function. Whether it merely startles predators or serves also as reinforcement of distastefulness cannot be said, since nothing is known about the palatability of *Haploglenius* (some ascalaphids have a bad stench and may be distasteful). The startling function need not be the only, or for that matter primary, function of the flap. Since the device is restricted to one sex, it probably serves also for signalling purposes in courtship.

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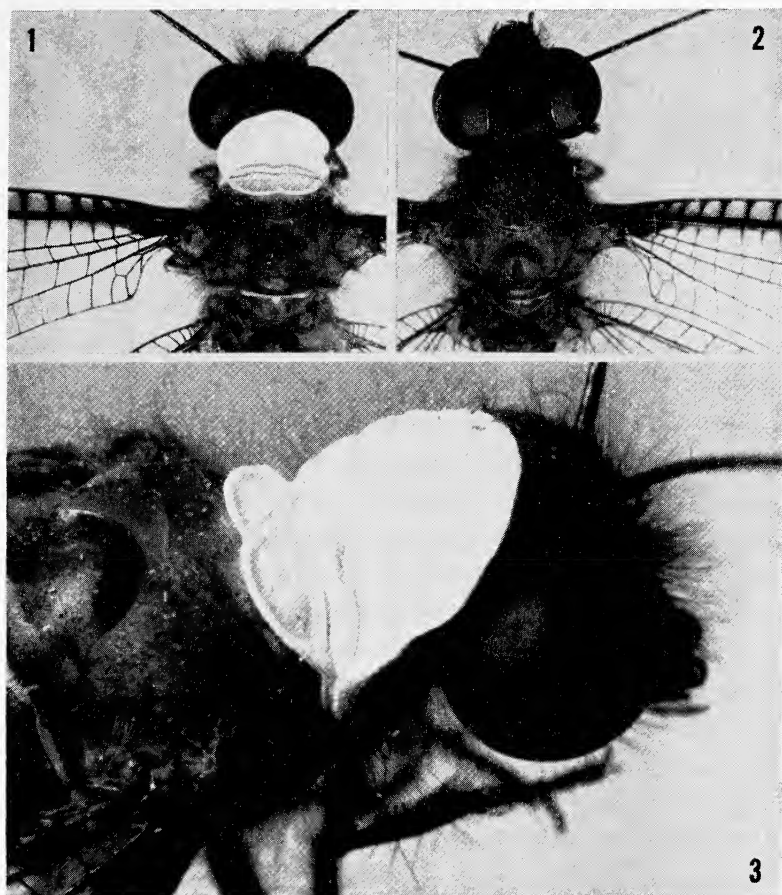
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Figs. 1-3. *Haploglenius luteus* (δ), with the thoracic patch exposed as in the startle display (fig. 1, 3), and concealed beneath the pronotal flap as it ordinarily is in the undisturbed animal (fig. 2).

MIXED NESTS OF *CONOMYRMA INSANA* AND
C. FLAVOPECTA — EVIDENCE OF PARASITISM
(HYMENOPTERA: FORMICIDAE)¹

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Ants of the dolichoderine genus *Conomyrma* are abundant in Florida. The nests are in the ground with the usually single nest opening surrounded by a rather uniformly constructed crater approximately 7 to 18 cm in diameter. Open areas in sandy soil with little vegetation are usually preferred as nesting sites. The ants often forage in full sunlight and move rapidly and seemingly erratically. Further information on the general biology of the ants is given by Nickerson et al. (1976).

Two common species occur in Florida. We have, for the present, identified these species as *Conomyrma insana* (Buckley) and *C. flavopecta* (M. R. Smith), following the revision of Snelling (1973) and the identification criteria given by Creighton (1950). The 2 species differ in color, morphology, and biology. *C. insana* is nearly uniformly dark, greyish black, has a broad, straight, or slightly concave occipital border, and has a distinct declivity on the mesonotum seen in profile, while *C. flavopecta* is light yellowish brown, with the head and apex of gaster weakly to moderately infuscated, the occipital border rounded or straight only medially, and the mesonotum in profile evenly convex without trace of a declivity. Colony structuring differs markedly in the 2 species as shown by Nickerson et al. (1976). *C. insana* exists in enclaves of multiple nests with much traffic between the nests, transfer of brood, food exchange, and many queens localized together in only 1 of many nests, while in *C. flavopecta* there is no traffic between the nests or food exchange and a single queen per nest. These consistent data are postulated by Nickerson et al. (1976) as solid evidence that colonies of *C. insana* are polydomous whereas colonies of *C. flavopecta* consist only of a single nest. Thus the differences between the 2 taxa in all respects are striking, and the evidence that 2 distinct species are involved seems unequivocal.

¹Florida Agricultural Experiment Station Journal Series 6080.

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Reactions between the 2 species in the field are entirely inimical (observations of the writers). When workers of the 2 species meet (in accidental meetings as far as we can judge), the *C. insana* worker usually holds its ground and may open its mandibles, while the *C. flavopecta* worker almost immediately breaks contact and runs rapidly and erratically away. We term this reaction "panic retreat" paralleling the terminology of Wilson and Regnier (1971) who distinguish between "panic alarm" and "aggressive alarm" reactions in ants. Movements during panic retreat are more rapid and erratic than during normal foraging. In contrast, accidental or other contacts between *C. insana* workers never, in our observations, lead to antagonistic or panic retreat reactions. Chance encounters between 2 foraging *C. flavopecta* workers can either be non-antagonistic or can initiate panic retreat (sometimes both workers displaying this behavior) according, we presume, to whether the meeting is between workers of the same colony or from 2 different colonies.

With these uniformly different behavioral patterns, it has been rather surprising to discover on several occasions and places in Florida mixed colonies of the 2 species. The specific records for these mixed nests are as follows: Highlands Co., Archbold Biological Station, Lake Placid, 18 April 1973, J. C. Nickerson; Polk Co., Winter Haven, Camp's citrus grove, 19 April 1973, J. C. Nickerson; Polk Co., Winter Haven, Camp's citrus grove, 13 April 1974, J. C. Nickerson; Alachua Co., Gainesville, Depot Road, 30 April 1974, J. C. Nickerson; Alachua Co., Gainesville 15 May 1974, Wm. F. Buren; Alachua Co., Gainesville, 10 April 1975, J. F. Carroll; Alachua Co., Gainesville, 23 May 1975, Wm. F. Buren; Wakulla Co., Medart, 20 June 1975, D. P. Wojcik.

In all of the mixed nests, workers of both species were observed participating in normal activities as nest-mates (foraging, casting out soil particles, moving together in the nest burrows, brood tending, etc.) without antagonism. The mixed nests were never a part of an established enclave of unmixed *C. insana* nests but could be as close as 10 m from such an enclave or could be 1 of a number of separate nests in a field in which all or most of the other *Conomyrma* nests were unmixed *C. flavopecta*. We interpreted these observations and records as an indication that temporary parasitism might be occurring in these ants.

Temporary parasitism is very well known in ants, especially in the subfamilies Formicinae and Myrmicinae (see excellent reviews by Wheeler 1910 and Wilson 1971). In the subfamily Dolichoderi-

nae, species of the genus *Bothriomyrmex* are temporary parasites on species of *Tapinoma* (Santschi 1906, Wilson 1971). Several species of the genus *Azteca* are also suspected of being temporary parasites because they have microgynous queens (Wheeler 1910) and therefore cannot be expected to employ the usual claustral method of colony establishment. There has been no previous suspicion that parasitism was occurring in *Conomyrma*, however.

Most of the material in the next 3 paragraphs has been reviewed by Wilson (1971), but we touch on this briefly again in order to introduce our lines of thought.

In many temporary parasitic ants, adoption of the parasitic queen by a host colony appears difficult and not too often successful. Mixed nests of these species and their hosts are rare or uncommon. Nevertheless, the parasitic species may become locally abundant by the process of colony fission (hesmosis) to form an enclave of closely spaced interconnected nests. Further adoption of newly mated parasitic queens, additional to the original parasitic queen, seems a logically necessary step in the growth of such an enclave. Colony "towns" of such ants often have been noted by observers. In the case of the allegheny mound building ant, *Formica exsectoides* Forel, enclaves of up to 1700 individual nests have been recorded (Wheeler 1901). Nickerson (unpublished) has studied localized enclaves of an estimated 200 to 400 nests of *Conomyrma insana* at Tall Timbers Research Station north of Tallahassee, Fla.

Queens of temporary parasitic species are all modified in lesser to greater degree. In many species this modification is shown merely by modest enlargement of the head and reduction of the gaster in relation to the thorax. In other examples the mandibles may be strongly modified to form falcate, piercing organs, or the whole insect may be very small (microgynous) in relation to the workers and/or may have various other characteristics such as modified pilosity or integument (Wilson 1971). Myrmecologists familiar with a number of these modified females can often guess that a species is a temporary parasite merely by examination of the queens. In contrast, females of free living species which practice the normal claustral method of new colony formation almost uniformly have voluminous gasters and relatively small heads with mandibles, pilosity and integument not modified from the norm for the genus.

The actual step by step methods by which the parasitic queens attempt to gain adoption by host colonies has been observed for only a few of the temporary parasitic species (reviewed by Wilson 1971).

The details of the behavior appear to vary considerably but the general patterns and results are quite similar. The newly mated parasitic queen approaches the host colony, is "discovered" by the host workers, and then according to the particular species, either adopts so-called "conciliatory" reactions to these workers, or else fights with them and "intimidates" them. In either case, if she is successful and not killed by the host workers, she enters the host colony and gradually is accepted and finally adopted as the colony queen. During this process the host queen is eliminated by various methods. In most cases this appears to be by assassination, the parasitic queen killing the host queen by strangulation, cutting off her head, or other means according to the particular species. The adopted parasitic queen then begins to lay eggs. The host workers care for the parasitic brood as they would for their own, and the newly reared parasitic workers work side by side with the host workers in a mixed nest until normal attrition of the host workers in time leaves the parasite in an unmixed colony. There is no reported evidence that the host workers are ever subjected to overt suppression by the parasitic workers or treated as anything but nest-mates.

As stated above, the mixed nests of *C. insana-flavopecta* found in Florida and the localized enclaves of *C. insana* appeared to us to give presumptive evidence that temporary parasitism followed by hesmosis was occurring in these ants. Further evidence may be given by the morphology of the queens. In queens of *C. insana* the head is large, wider than the thorax, while the gaster is rather small and slender in alate queens. In *C. flavopecta* queens, however, the head is of moderate size, about equal in width to the thorax, and the gaster is large and voluminous in both alate and dealate queens. The morphological modifications of the *C. insana* queens therefore seem to be similar to the modifications already known for many temporary parasitic ants.

The existence of incipient nests is excellent evidence that a species has the normal claustral type of new colony establishment. Incipient nests of *C. flavopecta* have been found several times at Gainesville, Fla. by the senior author whereas no incipient nests of *C. insana* have been found in Florida even with intensive search over a period of several years by Nickerson (unpublished). Two incipient nests of *C. flavopecta* excavated by the senior author consisted of a single *C. flavopecta* queen and less than 20 nanitic workers (all specimens not captured for accurate count) in each nest. Incipient nest craters of *C. flavopecta* are very small (radius less than 2 cm) and are

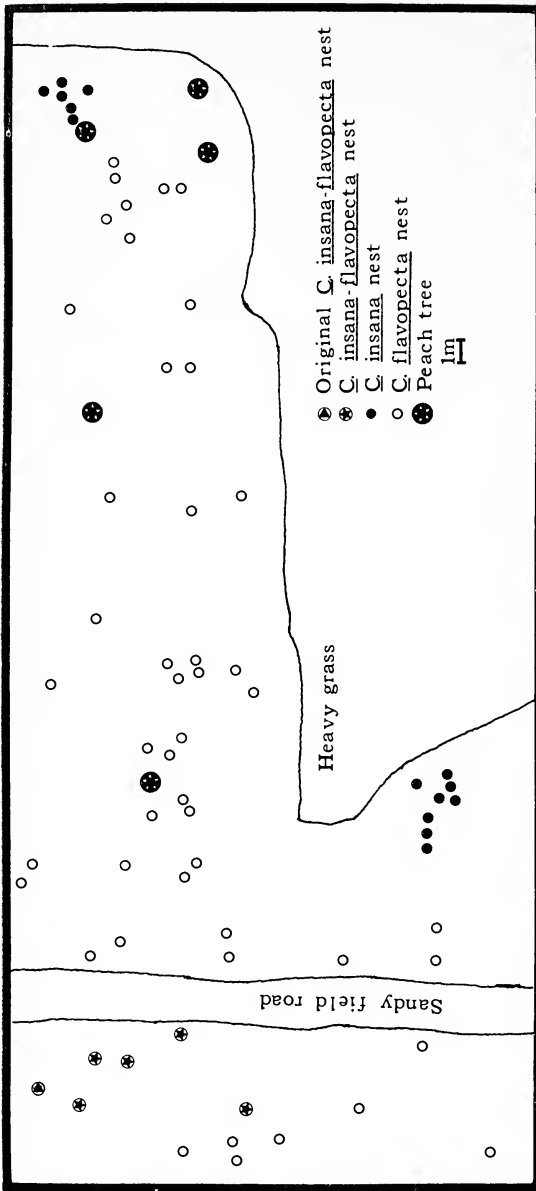


Fig. 1. Condition of study area 1 June to 10 June 1975, showing (1) location of original excavated *Conomyrma insana-flavopecta* nest, (2) additional mixed *C. insana-flavopecta* nests found several days after excavation, (3) small, localized enclaves of *C. insana* nests, and (4) scattered occurrence of *C. flavopecta* nests.

flattened and lunate rather than complete. The nest openings are very small (approximately 1.5 mm) compared to other *Conomyrma* nests and are blocked with soil diurnally. The tiny workers only forage nocturnally. We suspect the small, blocked nest entrances and nocturnal foraging habits may be adaptations which allow these incipient colonies to coexist near larger nests of their own species without excessive competition. In full sized nests of *C. flavopecta* the workers usually forage diurnally and the nest entrances are sometimes blocked nocturnally.

In the interest of keeping a permanent record of the mixed nest phenomenon and in seeking other data, 1 of these nests, found in the experimental farm area at the University of Florida on 23 May 1975, was excavated and collected as thoroughly as possible. Three hundred twenty-six *C. flavopecta* workers and 726 *C. insana* workers were collected from this nest and have been deposited as a voucher series in the Florida State Collection of Arthropods, Gainesville. A single dealate queen also was captured in the nest, and in confirmation of our hypothesis, was a queen of *C. insana* rather than *C. flavopecta*. All pupae (approximately 75) mature enough to identify (by head shape) were *insana* rather than *flavopecta* and all callow workers found (36) were also *insana*.

The data suggest that *C. insana* is a temporary parasite of *C. flavopecta*. The modus operandi for the adoption of the parasitic queen, elimination of the host queen, formation of the mixed nest, and eventual maturation to an unmixed *insana* nest must be similar in a general way to numerous other temporary parasitic ant species. The findings that a *C. insana* queen was the only queen found in the mixed nest and that only brood of *C. insana* and young adults of *C. insana* were present strongly suggests that the *C. flavopecta* queen had already been eliminated.

Distributional patterns of the ants at the Gainesville location are shown in Figs. 1 and 2. All unmixed *C. insana* nests appear to be clustered into localized enclaves, whereas the unmixed *C. flavopecta* nests have a more scattered but probably not random spacial arrangement. Small peach trees present in the study area do not appear to influence the distribution patterns. No *Conomyrma* nests were found in an area of high, dense grass, however.

The distribution of the mixed *C. insana-flavopecta* nests needs explanation which we cannot give at this time. The original mixed nest in the study area was found on 23 May 1975. It was excavated and collected on 27 May. On 1 June to 10 June the area was

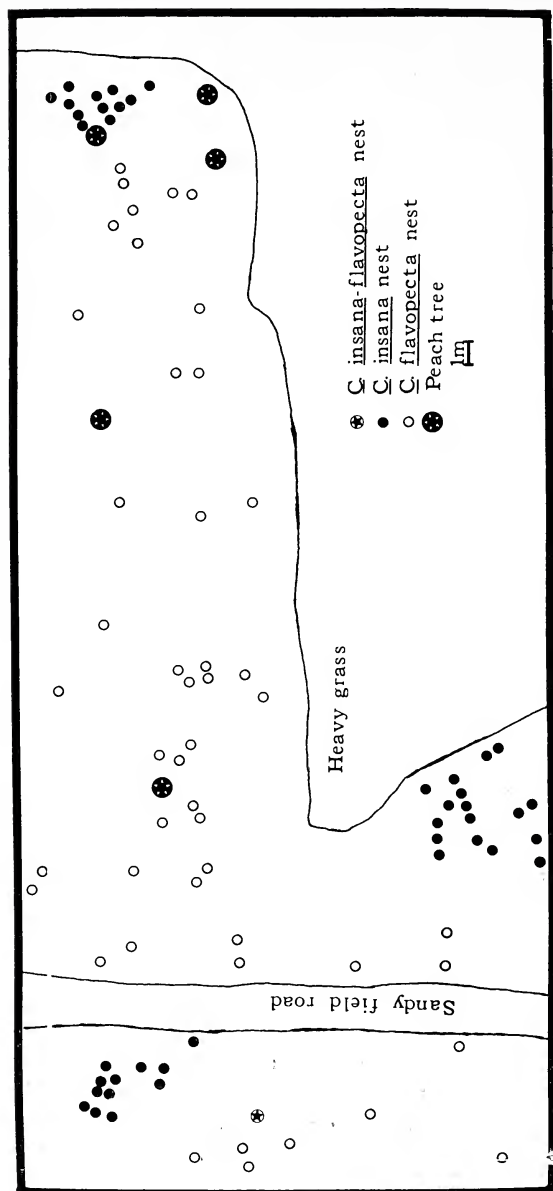


Fig. 2. Condition of study area on 26 June 1975 showing growth of the *C. insana* enclaves and appearance of a new enclave of *C. insana* in the same area as the previously present mixed nests, while the unmixed *C. flavopecta* nests appear to have remained unchanged.

mapped and the distribution of the 3 types of nests determined as shown in Fig. 1. Although the ratio of *C. insana* to *C. flavopecta* workers in the original mixed nest was about 7 to 3, the ratios of *C. insana* to *C. flavopecta* in the mixed nests observed at the time of mapping was about 20 to 1, judging from the workers appearing at the nest entrances (no further nests were excavated, however). The area was mapped again on 26 June (Fig. 2). Although the unmixed *C. flavopecta* population appears stable, obvious changes occurred in the *C. insana* population. The numbers of individual nests in the unmixed *C. insana* enclaves increased, there was a new enclave of unmixed *C. insana* in the area formerly occupied by the mixed nests, and only 1 mixed nest could still be found, this one with an estimated 100 to 1 *insana* to *flavopecta* ratio.

The speed of the change over from the mixed nests to the new unmixed *C. insana* enclave was surprising to us and we have no unequivocal explanation for this phenomenon. Although we observed no overt actions of the *C. insana* workers against *C. flavopecta* in the mixed nests, the death rate or attrition of the latter may be greater than normal for reasons we do not understand. We also have no certain explanation for the clustering of the mixed nests in one small part of the study area. Perhaps the process of hesmosis begins to occur even while the nests are still mixed. Obviously one or more additional *C. insana* queens were present in these mixed nests, because the new *C. insana* enclave proceeded in its development even after the *C. insana* queen found in the original nest was removed.

This is the first report of temporary social parasitism in the genus *Conomyrma*. It may be noted that mixed nests of *Conomyrma* have been recorded (as *Dorymyrma*) previously by Wheeler (1901) who gave the remarks of Forel upon finding mixed nests of ants identified as *Dorymyrma pyramicus* var. *niger* Pergande and *D. pyramicus* var. *flavus* McCook near Faisons, North Carolina. Forel attributed these mixed nests to a queen of each taxon fortuitously associating together when first founding a new colony. Such a chance association of 2 species of females has never been confirmed for any ants as far as we are aware, although reported in older literature (Forel 1874, Wheeler 1901). In the Forel colonies all alates found were identified as *niger* except for 1 male which Forel identified as *flavus* on the basis of color. In the absence of any positive statement, we assume no dealate queens were found to confirm Forel's hypothesis.

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THE INTERNATIONAL UNION FOR THE STUDY OF SOCIAL INSECTS has announced the publication of the proceedings of the Symposium held in September, 1975, on "Pheromones and Defensive Secretions in Social Insects." Orders for this publication [250 pages] should be sent to Dr. R. Brossut, Université de Dijon, Laboratoire de Zoologie, Boulevard Gabriel, 21000 Dijon, France. Price, including postage: regular mail, \$15; air mail, \$16.50.

THE PHENOLOGY OF *HEXACENTRUS MUNDUS*
(F. WALKER) AT WAU, PAPUA NEW GUINEA
(CRTHOPTERA, TETTIGONIIDAE)

BY MICHAEL H. ROBINSON¹ AND THANE PRATT²

INTRODUCTION

When at Wau, Morobe District, Papua New Guinea, during 1970-1971, the senior author was impressed by the very distinctive nature of the stridulation of a common tettigoniid *Hexacentrus mundus* (F. Walker). No attempt was made to study the species at this stage but it was encountered frequently during other researches and males appeared to be stridulating throughout the entire year. Phenological studies of the spiders at Wau (Robinson & Robinson, 1973; Robinson, Lubin & Robinson, 1974) showed that adult spiders of several species were active and reproducing throughout the year and gave rise to the suggestion that tropical arthropods may be less seasonal at middle altitudes than they are in the lowlands. Nearly all the sparse data on the phenology of tropical insects come from lowland study areas (see review in Robinson, Lubin & Robinson *ibid.*). We therefore decided to census the number of singing male *H. mundus* that were audible from three line transects located at around 1066 meters altitude. We carried out this survey, weekly, for one year (January 1974 to December 1974). We originally chose to census *H. mundus* because its song sounded unique among the orthopteran stridulations at Wau; it turned out to be a lucky choice since the insect is almost certainly predatory and therefore more interesting for comparisons with the spider data that are already available from this locality. Stridulation is essentially a sexual activity and the census should provide an index of reproductively active individuals. It showed that males were active in every one of the months of the year.

MATERIALS AND METHODS

The species

The species was identified by Prof. I. J. Cantrall, Museum of Zoology, Ann Arbor, Michigan, to whom we are most grateful.

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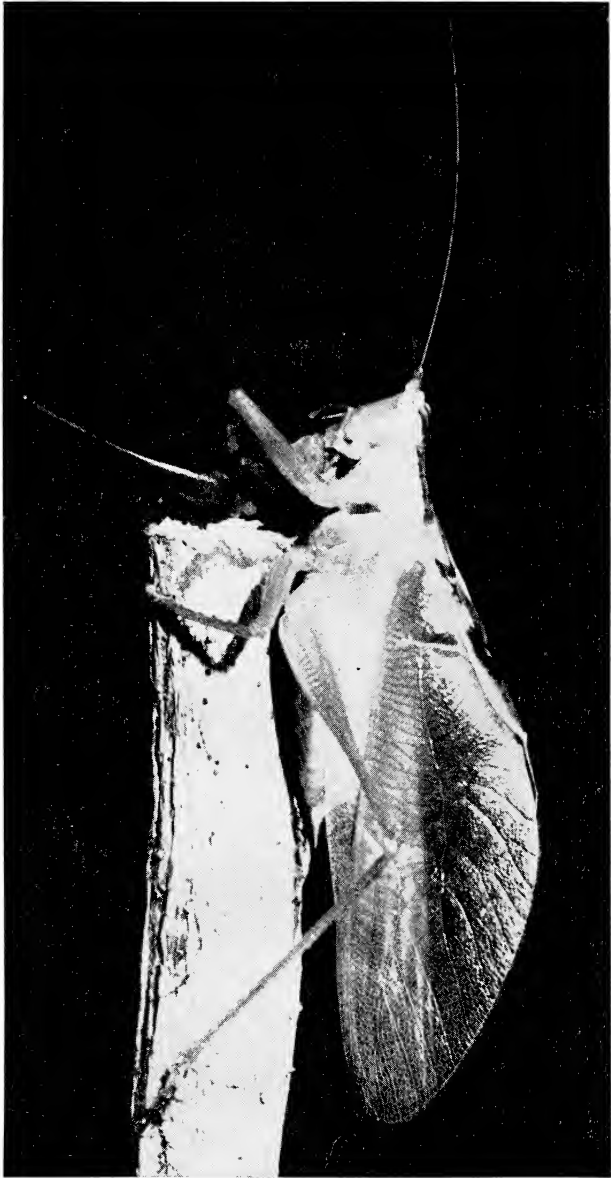


Figure 1. Male of *Hexacentrus mundus* feeding on small acridiid. Note that the prey is being held down by an anterior leg. Length ca. 60 mm.



Figure 2. Female of *Hexacentrus mundus*; compare the tegminal outline with that of the male shown in Figure 1. Length ca. 70 mm.

Figures 1 and 2 show the general appearance of male and female adults. The insect is grass green in color at all developmental stages and there is a quite distinct sexual dimorphism in the general shape of the resting adult. The dimorphism largely derives from a difference in the shape of the tegmina. Both sexes have large, widely spaced and projecting compound eyes, as have most predatory katydids. The tibiae of the anterior legs have rows of strongly developed spines with which the animal holds and restrains live prey (see Figure 1). As far as we were able to determine the insect has no specialized cryptic or mimetic posture (unlike some of the other tettigoniids at Wau; see Robinson, 1973).

We originally considered the possibility that the species was predatory after an examination of its morphology. Later we found an adult male eating a large jumping spider that was obviously not carion. This was the only instance we saw of predation in natural conditions (we never saw the species eating plant material at any stage). In captivity the insect caught and ate a variety of living insects and was particularly adept at catching calliphorid flies. These were caught if they settled close to the resting katydid; we did not see any stalking behavior. The katydid made a rapid forward lunge and then trapped the flies against the substrate beneath the spinous anterior tibiae. We saw nothing that was homologous to a mantid (or reduviid) strike, i.e., the anterior legs were not extended and then rapidly folded around the prey in a pincer grip. Figure 1 shows a male *Hexacentrus* feeding on an acridiid nymph which was caught after it had been left (by us) in a damaged condition in front of the katydid.

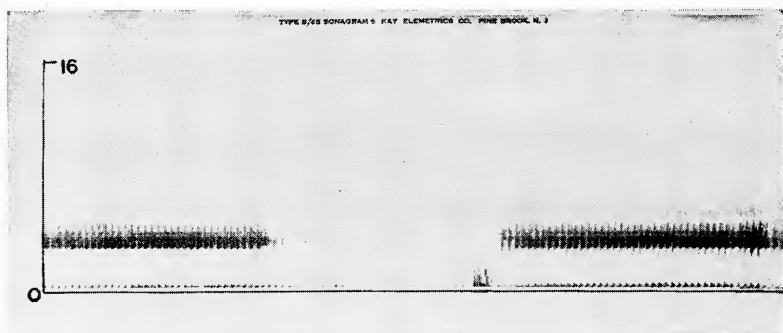


Figure 3. Sonagram of interrupted stridulation. Frequency range 0-16 KHz. Time base 0.6 seconds.

During the day the insect responded to the movements of flies by orienting towards them. The impression gained was that the animal was responding to visual stimuli. If feeding occurs principally at night (when stridulation occurs), visual prey detection seems less likely. We do not know that the animal is active only at night. In captivity it certainly feeds by day and in the wild it assumes positions, by day, on vegetation from which it could capture prey.

The stridulation

The males stridulate at night from the upper surface of leaves in secondary growth and in forest- and roadside-edge clearings. The stridulation is bisyllabic, "metallic," and repeated over long periods of time. Figure 3 shows sonographic representation of the sound. It is based on a recording made at $1\frac{7}{8}$ inches per second on a Uher 3000S tape recorder. Some harmonics are visible, but the frequency range of the principal stridulation is clearly visible in the sonagram.

Striduating males stand with their tegmina partly opened, i.e., the two tegmina are not touching along their posterior margins (which normally lie along the midline of the body when the insect is not in flight or singing).

The song of *Hexacentrus mundus* has all the characteristics of a *calling song* as defined and described by Dumortier (1963).

The census

The census was carried out on one day per week between 2000 and 2100 hours, between 1.5-2 hours after nightfall, irrespective of the weather conditions. Locations of the transects involved are shown diagrammatically in Figure 4. They were always censused in the same order, I, II, and III. The technique was very simple. One of us simply walked along each transect to the end and back (transects I and III) or around twice (transect II), counting all the singing *Hexacentrus* that were audible on the two journeys. Individuals that were singing during both journeys were scored once only. From January to August (inclusive) the census was carried out by M.H.R.; T.P. carried out the remainder of the year's study.

The transects differed in vegetational structure. Transect I was along an unpaved road flanked by uncut verges (1-1.5 meters wide) and bordering coffee plantations for most of its length (100 meters). Transect II (ca. 200 meters) was around the outer perimeter of a garden which abutted coffee plantation around the entire length except for the short stretch of road shown in Figure 4. Transect III (100 meters) was along a footpath connecting House 4 with the

Table 1. Census results.

	Transects			Average of all transects		Transects			Average of all transects
	I	II	III			I	II	III	
January	2	2	1		July	4	1	1	
	2	2	-			3	2	0	
	3	2	1			2	1	2	
	4	3	1			3	1	2	
Monthly totals;	4	3	1						
averages	15	12	4	6.2		12	5	5	5.5
February	4	2	1		August	2	1	1	
	4	3	-			1	-	1	
	3	1	1			2	1	1	
	4	1	1			2	1	1	
Monthly totals;	15	7	3			1	-	-	
averages	3.7	1.75	0.75	6.25		8	3	4	3.0
March	2	1	2		September	3	2	1	
	4	3	3			3	1	4	
	2	2	2			2	1	4	
Monthly totals;	4	2	2			5	2	5	
averages	12	8	9	7.25		13	6	14	8.25
April	3	2	1		October	3	1	3	
	4	2	2			5	2	4	
	3	2	2			4	2	3	
	3	2	1			4	3	4	
Monthly totals;	2	3	1			1	-	-	
averages	15	11	8	6.6		17	8	14	7.8
May	3	3	1		November	4	2	5	
	2	2	1			4	2	7	
Monthly totals;	5	5	2			4	2	3	
averages	12	6	15	6.0		12	6	15	11.0
June	3	1	2		December	4	1	2	
	4	2	1			-	-	-	
	2	-	1						
Monthly totals;	1	2	2						
averages	10	5	6	5.25		4	1	2	3.5
	2.5	1.25	1.25			2.0	0.5	1.0	

main building complex of Wau Ecology Institute. This footpath passed through coffee plantation edge for approximately one third of its length. The remainder of this transect ran through tall grass. All three transects were equally exposed; transects I and II were surrounded by trees and bushes.

RESULTS

The weekly census totals and monthly averages are shown in Table 1. Three month's censuses are incomplete. May is for only two weeks (MHR was absent from Wau), November is based on three weeks, and December is based on two weeks only (TP left

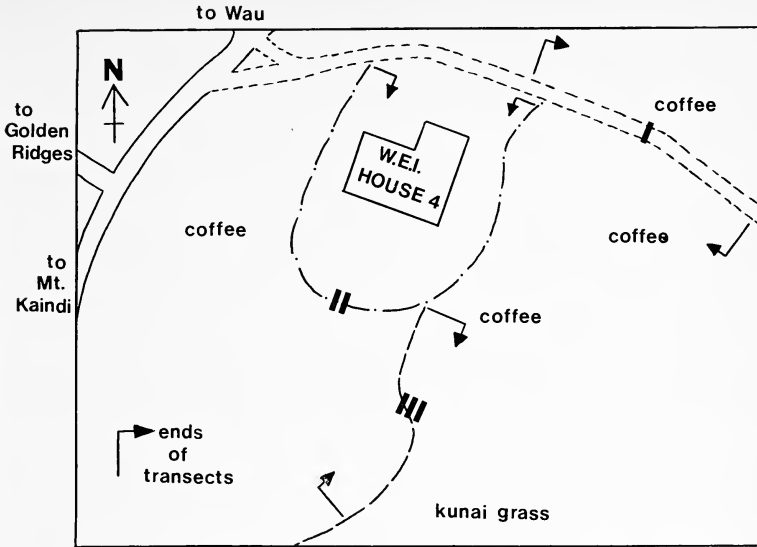


Figure 4. Sketch map of the location of the transects.

Wau; MHR left in September). We have graphed the monthly averages for each transect and the average for the combined monthly totals and these are shown in Figure 5.

DISCUSSION

The sampling system that we used was not only simple but arbitrary. We did not attempt to determine whether the results were influenced by the weather conditions obtaining during the census period. We would guess that we were sampling a fairly high proportion of the males within earshot of the transects but that this proportion did not remain the same, necessarily, from census to census. We got the impression that fewer insects were singing on cold clear moonlit nights. Dumortier (1963; 638-9) lists a number of climatic variables that may affect insect song (either as exciters or inhibitors). For these reasons we would not place too much reliance on the magnitude of the variations in the census results. The direction of the variations may reflect some general trends, since the lowest counts occur towards the middle of the Southern Hemisphere winter when rainfall and temperatures at Wau are low (see Robinson, Lubin & Robinson, 1974: 132-3).

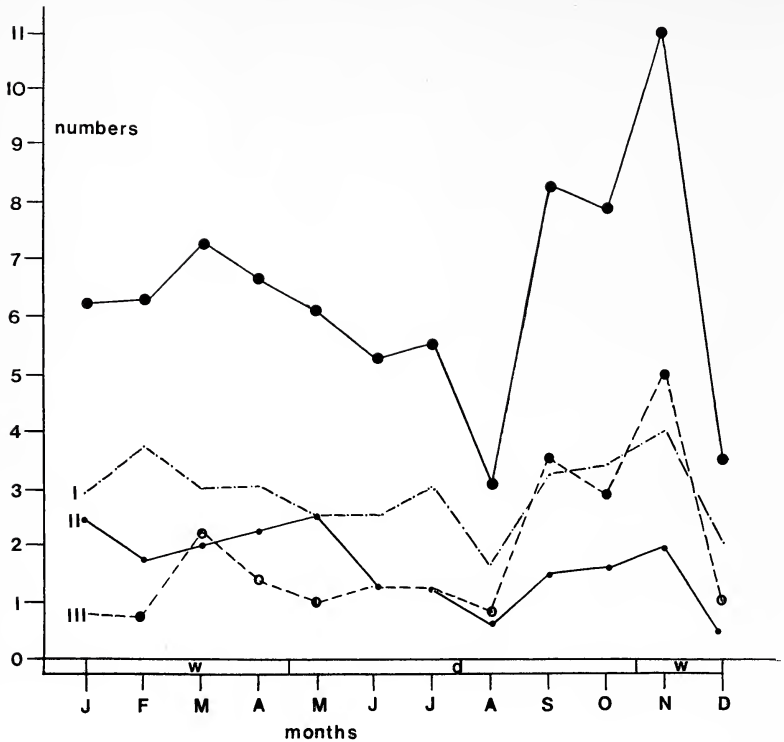


Figure 5. Graph of monthly average number of male *Hexacentrus mundus* stridulating on transects I, II, and III. Average for all transects marked A.

The most important conclusion that we draw from our data is that they are a reliable indication of year-round activity by a moderately large carnivorous insect. We strongly suspect that katydids in temperate regions will prove to be markedly seasonal in singing activity, reflecting the fact that adults are not present throughout the year. It would further seem probable that in temperate regions the larger the insect the shorter the portion of the year "occupied" by adults and we would expect that large katydids would be more seasonally restricted (as adults) than smaller species. (This should be generally true of temperate region arthropods that do not possess a pupal stage or cannot otherwise spread their development over more than one year, assuming it takes longer to reach a larger adult size, and that the overall period of each year available for active life is more or less equally restricted for all arthropods living under-

the same climatic regime.) Fulton's (1951) data for 19 species of North American orthopterans show that most of these sing at some stage during the period June to November.

If largish insects such as *H. mundus* exist on a year-round basis, as secondary consumers, it is possible that primary consumers may be similarly (relatively) aseasonal. Sustained coexistence (Robinson, Lubin & Robinson, 1974: 158) of organisms over long periods of the year may be a situation with a high potential for generating species diversity. Thus, at the simplest level, it is possible to visualize the evolution of a predator specializing in large orthopterans only in a situation where, as at Wau, large orthopterans are present on a year-round basis.

ACKNOWLEDGMENTS

The work was carried out at Wau Ecology Institute, which supported T.P. in part. We are grateful to Dr. J. L. Gressitt for use of the facilities at Wau. Donald Windsor prepared the sonagram.

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SLOWED MOTION ANALYSIS OF
SOUND PRODUCTION IN THE
GRASSHOPPER *ARPHIA SULPHUREA*
(ACRIDIDAE: OEDIPODINAE)

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From the time of the classic studies by Pierce (1948) and Pasquinely & Busnel (1955), there have been many attempts to slow the movement of insects visually so that the sounds they produce can be analyzed biomechanically. Usually these efforts have been directed towards "elytral" stridulation (Bailey, 1970; Bailey & Broughton, 1970; Morris & Pipher, 1972) by the use of photographic stroboscopy and oscillography of potentials from electrodes or sensors on the moving parts or in the muscles governing the movements. Also the Hall-effect has been used to plot oscillographically the movements and acoustic signals simultaneously. This has been effected in an insect as small as *Chorthippus mollis* by means of permanent magnets attached to the moving femur, which in turn produces a changing voltage in a Hall-generator fixed on the back of the insect between the wings (Elsner, 1970, 1974a). Miniature magnetometers of this type have been used in human vocalization movements also (Hixon, 1971). Other workers have reported routine use of television tape systems with simultaneous sound recording and/or sound visualization (review: Wussow *et al.*, 1974).

All of the methods so far mentioned have disadvantages. 1) It is difficult to adjust a stroboscope if motions are non-cyclical, very brief in duration or variable in frequency or velocity. 2) Electrodes and magnetic sensors may restrict or disturb normal behavior of small organisms. Also, simultaneous recording of both femora in motion using the Hall-effect apparatus has not proved feasible (Elsner, 1974a). 3) The nature of the television trace mechanism causes a time delay distortion between the upper and lower portions of the picture when the tape is stopped for analysis. A single video field represents more than 16 msec which is unsuitable for analysis of motions taking less than 50 msec to complete (Steinberg & Willey, 1974; Wussow *et al.*, 1974). However, for gross motion studies, the television tape system is the least expensive and most useful of all compound methods.

An alternative method, ptenocinematography,¹ is capable of fine resolution of visual-acoustical signals. Walker *et al.* (1970) showed that motion pictures of actions and the oscillograms of sounds produced by those acts can be synchronized by using a two-lens system of an ultra-high-speed motion picture camera to show the generation of stridulations by tree crickets (*Oecanthinae*). I wish to present here an independently developed method which uses a similar principle for analysis of femoro-tegminal stridulations of the grasshopper *Arphia sulphurea*. The basic behavior patterns of *A. sulphurea* have been described in detail by Otte (1970). I have published an abstract of the methods (Willey, 1971).

MATERIALS AND METHODS

Arphia sulphurea was reared in captivity from eggs produced by females collected in an abandoned gravel and limestone quarry in the village of Oconomowoc Lake, Waukesha County, Wisconsin. Figure 1 diagrams the arrangement of the photorecording equip-

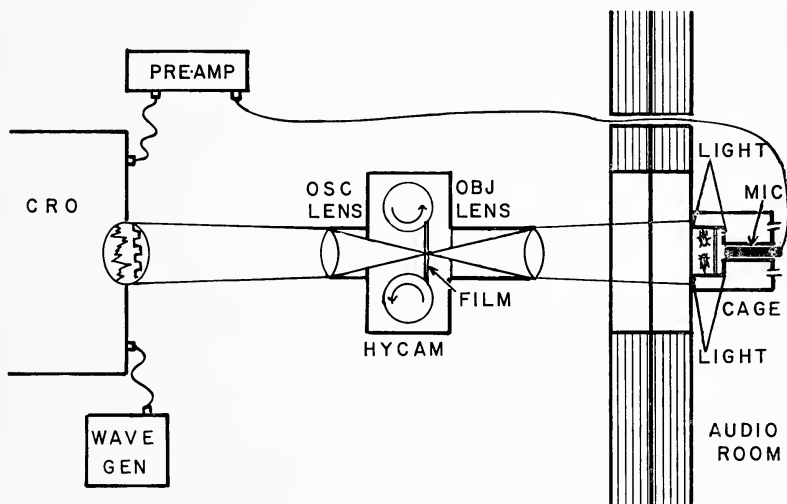


Fig. 1. Schema of equipment arranged for ptenocinematography, top view. CRO = cathode-ray oscilloscope, OSC = oscillo-lens, MIC = microphone. Three movie lights were used in addition to the two on either side of the cage, one was attached to the HYCAM above the objective lens.

¹Pteno- (derived from the Greek term for *rapid, high velocity*), a prefix to be preferred to the awkward "ultra-high-speed motion photography" and other phrases.

ment. The basic principle is the superposition of images from two lens systems, one from the moving specimen and one from an oscillographic trace, on the same film frame as it passes the lens openings. The insects were placed in a water-cooled cage (Fig. 2) against the observation window within a double-walled audiometric room (Industrial Acoustics Corporation). The camera (HYCAM, Red Lake Laboratories) was positioned outside the room on the opposite side of the window. An Angenieux 12:120 mm zoom lens faced the insects and was equipped with a 1-diopter enlarging lens. The ultra-high-speed 16 mm camera is capable of speeds up to 11,000 16 mm pictures per second, but only 800 pps was used in the present study. An 8-sided revolving prism coupled with a 1/2.5 shutter is driven by the film advance mechanism. The prism and shutter are in the light path of the front lens only, and this system imposes a minimum aperture of F 4.2 on the objective. The rear lens (Pentax, F. 1.8, automatic) which faces the oscilloscope is inserted into the through-the-lens viewing aperture in the camera back. A two-way prism directs the oscillographic image through the *back* of the film onto the emulsion. (Film with minimum anti-halation backing is desirable, q. v.)

The Tektronix 502-A oscilloscope (CRO) has a dual-beam cathode-ray tube (CRT) with a phosphor coating (P 11) which has the least persistence, greatest resolution and greatest photosensitivity ratio for the film speeds used. The trace is viewed on the CRT as a standing wave with only vertical amplification, and the advancing film, moving horizontally in the same direction as a normal oscillogram, acts as that in a kymograph camera. It is possible to burn the CRT phosphor when the screen is on full intensity, therefore full intensity is used only for the few seconds of filming. The calibrating grid should be removed from the screen for filming. A light-tight sleeve connects the oscillo-lens and the CRT. Beam orientation and focus are important. The upper trace should be inverted so that the normal positive peaks of both traces point to the center of the screen (therefore, the film track) — especially if one wishes to have the traces at the sides of the finished film rather than superimposed over the specimen. A timing trace of 1600 Hz (later calibrated at 1560 Hz in the pictures here) was produced by a Precision model E-310 signal generator using the square-wave mode, its 0.5 cm displacement was a calibration for the amplitude of the other trace.

The acoustic signals were received by a Sennheiser 404 directional condenser microphone situated directly behind the grid in the water-

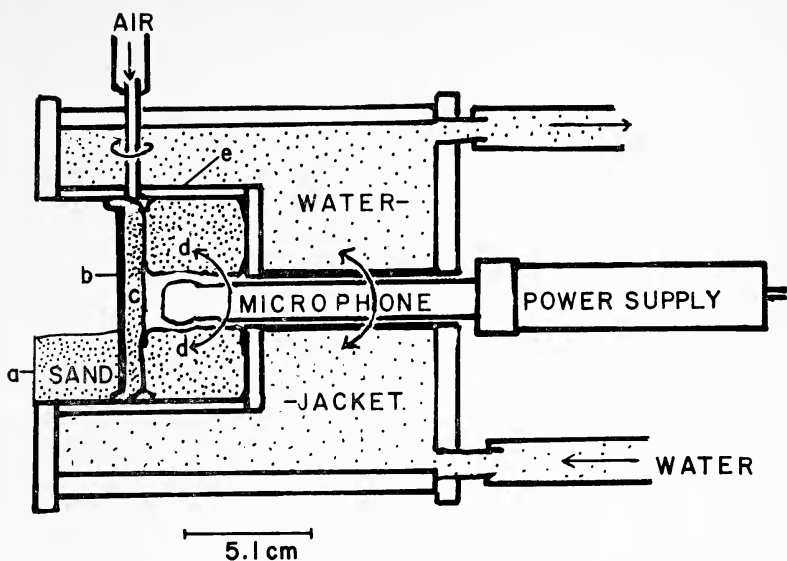


Fig. 2. Schema of the water- and air-cooled observation cage, sagittal section. In practise, the water flow was discontinued during filming, but not more than five minutes at a time. (a) Tape dam, (b) wire mesh screen (nine grids/cm²), (c) plastic foam wind-screening, (d) glass wool acoustical packing, (e) opal plastic cylinder.

cooled cage (Fig. 2). The distance was only 2 or 3 cm and therefore time delay due to speed of sound in air was negligible. Figure 9 illustrates the maximum calculated delay (0.1 msec, frame duration of 1.2 msec, shutter speed of 0.5 msec). Electronic delay also can be considered negligible. The microphone was protected from the noise of the air stream in the cage by a glass wool material which effectively dampened the acoustical components of the air stream. This is the same material used in the audiometric room to silence the ventilation system. The microphone, powered by mercury batteries totalling 7.5 V, was connected to the CRO by means of a 20 ft (6 m) extension cord and Acoustic Designs ADM 667 pre-amplifier.

The subjects were illuminated by three General Electric Company MG-1 movie lights with 500W mini-lamps. One light was attached to the camera outside the audiometric room and was used at full intensity for front lighting; the other two lights were used inside the room to side-light the insects (Fig. 2). The inside cylinder of the cage is of white opal plastic to diffuse the incoming side light.

The side lights were reduced by a rheostat to 60% intensity for the present experiment because the greater intensity resulted in compulsive phototropism (in the sense of Verheijen, 1958) and a disturbed dorsal light reflex by the insects, effectively inhibiting any social interactions.

Kodak RAR 2485 Instrumentation film (on thin Estar-base) has a reversal exposure index (E. I.) of 1600 and a photosensitivity rating of 10,000 in response to the activated P 11 CRT phosphor coating. Eastman-Kodak MS 857 developer minimizes graininess if development is forced only one F-stop (to E. I. 3200), comparing favorably with Tri-X film of 320 E. I. using standard exposures and D-19 developer. With the present system the correct exposure for the CRT trace was with the oscillo lens open (F 1.8) and CRT beams at full intensity at 0.65 m. For the subjects I had to open the front lens $1\frac{1}{2}$ to 2 F-stops over the reading on the calibrated Hycam exposure meter (Pentax $1^\circ/21^\circ$).

Angles and displacements of moving organs were analyzed on a Vanguard motion analyzer (model M16C), and the tapes were analyzed with a Kay Electric Co. model 675 audiospectrograph (Missilyzer) and a Tektronix model R5030 oscilloscope and C-70 camera. The secondary emission electron photomicrographs of the stridulatory file were produced by a Cambridge scanning electron microscope using standard mounting and gold shadowing techniques.

RESULTS AND ANALYSIS

Arphia sulphurea and *A. conspersa* have five acoustical signals which Otte (1970) and Willey & Willey (1969) have discussed in detail. Of these, I have filmed the chirps (ordinary stridulation) produced during contra- and ipsesexual courtships and the flutter-rasps (femur-shaking with wing-striking) during male-to-male interactions. Only the chirps will be discussed in this paper and are known to be produced by rubbing a ridge on the medial surface of

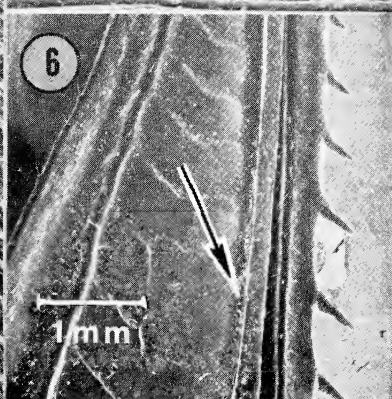
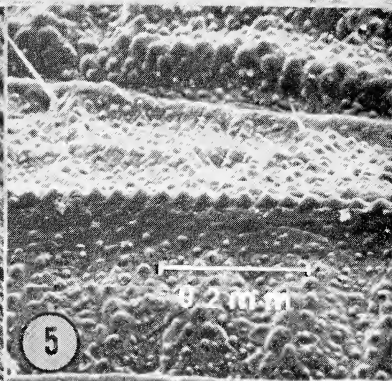
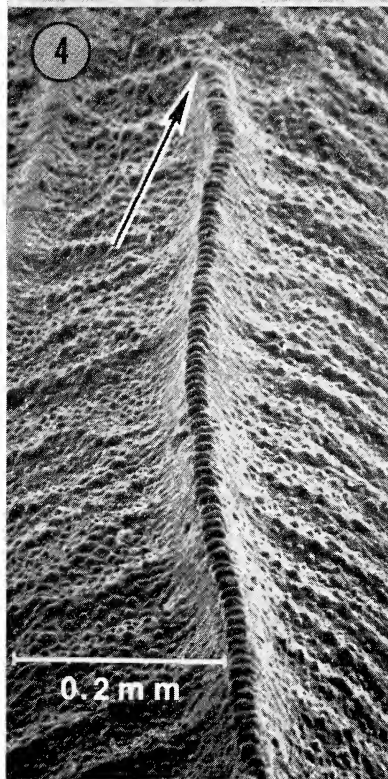
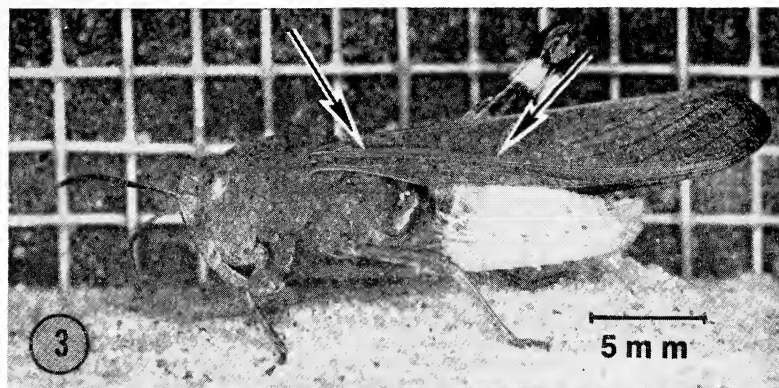
Fig. 3. Lateral view of *Arphia sulphurea* showing position of intercalary vein dorsal to the long median vein.

Figs. 4-6. Secondary emission electron photomicrographs of the stridulatory apparatus of *A. sulphurea* male seen in Fig. 3.

Fig. 4, oblique view of intercalary vein from 20° above the surface of the tegmen, arrow points to the basal origin of the vein, $127\times$.

Fig. 5, lateral view about 19° from horizontal plane of the tegmen, $100\times$.

Fig. 6, vertical view of medial surface of the right mesothoracic femur, arrow points to the area of the femoral ridge which contacts the tegminal file, $20\times$.



the femur against a row of pegs on a longitudinal intercalary vein of the tegmen or fore-wing. There are 39 ± 0.88 (S.E.) pegs per mm in the file, which averages 6.74 ± 0.17 mm in length.² However, the mechanism for production of the flutter-rasp still is unknown.

The acoustical properties of the chirp in *A. sulphurea* have been illustrated by Otte (1970, p. 22) and the present study confirms his report for the usual recording conditions (Fig. 7b). The signal rises in frequency from 2 KHz to 6-8 KHz with a duration of about 50 msec. The oscillograms also confirm the frequencies reproduced in the sonagrams. Even tape recordings made under conditions for ptenocinematography are only 50 to 75 msec in duration. Faint peaks sometimes isolated from the higher amplitude signals have been interpreted in the past as sounds made during the upstroke. Comparison of Figs. 7 through 48 will show this interpretation to be partly correct. However, the entire movement recorded by the motion picture camera takes 110 to 140 msec, during nearly all of which time some sound is produced. It is clear that most of the sound produced on the upstroke is of such low amplitude and frequency that it is not reproduced by the audiospectrograph, nor by an oscilloscope which is regulated to trigger only on the higher amplitude sounds. Whether the upstroke is informationally important is unknown, but doubtful, since it is so variable in duration.

The definitive chirp, however, is made on the downstroke. Figures 8 through 48 make it clear, from measurements and photographs of side and rear views, that the jagged peaked appearance of the chirp is not due to pulsed changes in the velocity of movement, for the femora move rapidly in a single sweep to the resting position. On the other hand, the femora are forced to move in tandem, since the pressure necessary to produce the chirp causes the femoro-tibial joints to overlap the midline and displace one another. It would be interesting to record the first chirps of a young male to determine the ontogeny of this metachronous movement. The net result of the movement of the two femora is to produce pulses of sonic amplification modulated by irregular low amplitude interference as the discrete pulses produced by the two files phase together and then go

²The pegs are smaller and more numerous per mm in the anterior (proximal) part of the file. The mean = 42.2 ± 0.71 (S.E.) pegs in the second mm from the proximal end and 35.8 ± 0.68 in the second mm from the distal end of the file. This difference is highly significant statistically ($t = 6.51$, $df = 18$, $p \ll 0.005$, $n = 10$ animals). Further studies are underway to determine the functional significance of this asymmetry.

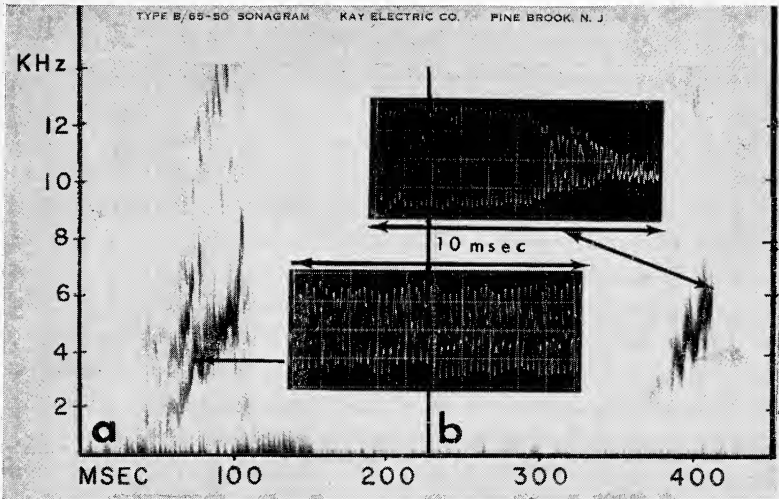
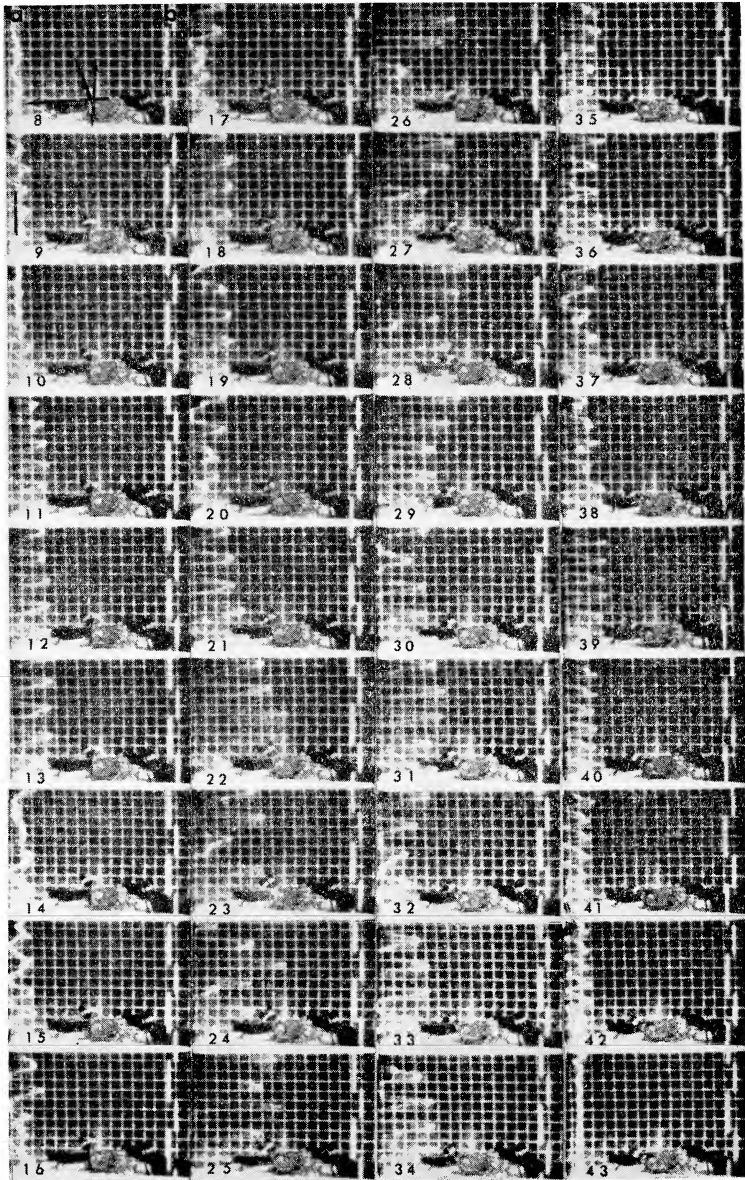


Fig. 7. Audiospectrograms of representative unitary chirps by *A. sulphurea* and the respective oscillograms (inserts). (a) Chirp recorded under ptencinematographic conditions in water-cooled cage, audiometric room, 35°C, Sennheiser 404 microphone at 2 cm with 6 m extension cord. (b) Chirp recorded under usual conditions of laboratory analysis (microphone 10 cm from insect, 33°C, 20 × 30 cm wire cage in quiet room). Protocol: Audiospectrograms—0 db input and output levels, 38.1 cm/sec; record level +2 to 3 VU, 0.8 sec per revolution; print level -10 VU, filter band width 600 Hz. Oscillograms—vertical = 10 V per division, horizontal = 1 msec. Arrows point to the 10 msec portions of the sonagram from which each oscillogram was derived.

into antiphase, cancelling each other. The sonagrams show that the greatest amplitude (darkest and thickest portion of the trace) always falls in frequency, and the oscillogram in Figs. 22 and 31 shows this. The faintest portions of the downstroke sonagram are not clear because the period of antiphase is only fractions of a millisecond (Figs. 14, 26, and perhaps 32). The frequencies are variously modulated in other frames between Figs. 13 and 39. The oscillogram in Figs. 10 to 13 definitely is the result of the movement of the left femur only. However there is some modulation irregularity in the trace from Fig. 39 to Fig. 43, which could be the result of continued unobserved motion of the left femur or some other sound. Figure 43 is typical of the background noise, whereas Fig. 8 is typical of the 40 frames during the upstroke, i.e., wavering non-regular traces of low frequency and amplitude.



Because the femora often are out of phase and modulate one another, one can not merely count spikes of sound and numbers of pegs on the calculated route of the femur along the stridulatory file. However, the distance travelled during the 10° change in the angle of the left femur between Figs. 10 and 13 (incl.) equals about 0.6 mm at file level. Since about 22 pegs occur in 0.6 mm of file and 19 spikes appear in the frames mentioned, each acoustical spike \cong one peg struck.³ Such calculations depend on the file being perpendicular to the femoral ridge, and parallel to the direction of stroke. Figures 3 and 4 show the convex curve of the file which would parallel rather accurately the path of the femoral rotation. Of course a one-legged male could solve the problem of interfemoral modulation. Motion pictures of such males in ideal positions for analysis have not yet been produced.

Elsner (1974a) has published an elegant study of stridulations in several gomphocerine species, in which he also is impressed with the

³The correct spike count is from the calculated beginning of the synchronized oscillogram with the image exposure to the end of the calculated synchronization (see Fig. 9). With each frame \equiv 1.2 msec, the calculated frequency of 19 spikes per 4.1 msec synchronized oscillogram corresponds to an average spike frequency of about 4650 Hz. Probably the file was first contacted by the left femur some distance posterior to the file's proximal end. These calculations are at variance by more than $10\times$ with those of Pierce (1948, p. 250-254) who studied living specimens of *A. sulphurea* in eastern New England. He reported spike frequencies of the "insect at rest" of 360 Hz with a harmonic frequency of 7900 Hz. It is problematical whether this sound was the chirp or one of the other signals.

Fig. 8 through 43. Ptenocinematographic sequence from the last frame of the upstroke (Fig. 8) and the entire downstroke of a unitary chirp filmed at 800 (± 10) pictures per sec. Entire sequence is graphed in Fig. 44.

Fig. 8, (a) oscillogram of sound, (b) oscillogram of 1600 Hz square wave (later calibrated at 1560), black arrows are along axes of measurement (right, left femoral axes, dorsal line of tegmen). Background grid, woven metal screening \equiv 3 squares per cm. Amplitude of oscillogram \equiv 50mV/cm, square wave \equiv $\frac{1}{2}$ cm.

Fig. 9, line at left illustrates the calculated synchrony of the audio oscillogram with the open shutter of the objective system (shutter speed is 0.5 msec duration).

Fig. 11 to 13, note regularity of oscillogram as left femur begins downstroke first and then the sonic (and perhaps mechanical) interference as the right femur begins the downstroke, the femoro-tibial angle is kept closed throughout. Fig. 22 shows probable sonic amplification as the femora move into phase. Finally, as left femur stops moving (Fig. 39), the sound of the right femur approximates the regular wave form and amplitude of Figs. 11 to 13. Refer to Fig. 44 for angle measurements and time relationships of the entire motion.

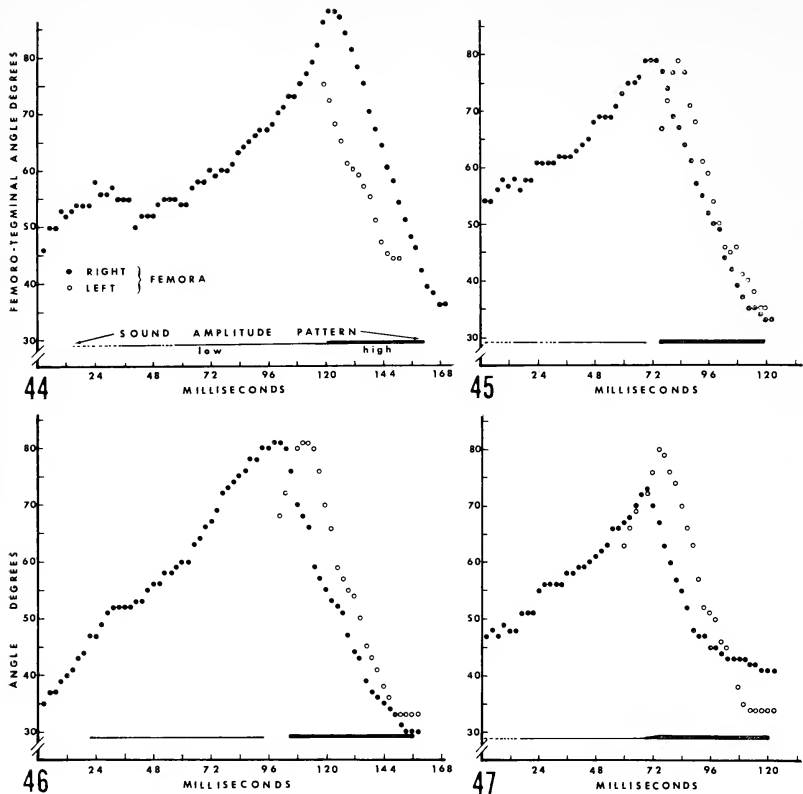


Fig. 44 through 47. Graphs of four unitary stridulations in lateral view during an interaction between two males, one attempting courtship (illustrated, the other responding with the male interaction "rasp" or "femur-shake with wing-striking" (not illustrated). The frames of Fig. 44 are partly reproduced in Figs. 8-43 and the angles relative to the tegmina dorsal line are drawn in Fig. 8. Alternate frames were measured, the abscissa points are frame numbers converted to msec. The far (left) femur could only be measured when out of synchrony with the near (right) femur, i. e., on the downstroke. Note: a) either femur can lead on the downstroke, lagging behind the other by 20 to 30° and 12 to 24 msec; b) high amplitude sound occurs only on the downstroke; and c) total silence occurs if both femora pass one another at angles above 70° (see Fig. 48), but if one femur fails to complete the full upstroke, the sound is not interrupted.

phase shift of right and left hind femora. In these grasshoppers which produce several clearly defined amplitude-modulated (AM) pulses per stroke by each femur, phase shift serves to blur or erase the amplitude-modulation which each femur alone is producing. His careful analysis shows, however, that this AM-erasure is due not to a sloppy coordination of the two femora, but rather that the proprioceptors of the two legs produce a feedback which precisely times the movements to the msec. He postulates that the main signal is a *frequency modulated* (FM) pulse series superimposed on the combined AM system, ranging between 250 Hz to 8 KHz. Elsner suggests that there may be discrete frequencies in this range which would activate specific groups of sensory cells or neuronal circuits in a manner already known in locusts. If we reexamine Figs. 8-43 of the present paper, even the single AM-pulsed chirp of *Arphia sulphurea* has a rather regular, though weak, FM signal which peaks several times at about 10 KHz in addition to the carrier frequency of about 5 KHz (average). This FM signal would appear in a sonagram as a faint octave overtone merging with the instrumental artifact (see Willey & Willey, 1969), perhaps indistinguishably. Nevertheless, one of the earliest determinations of an insect's acoustic sensitivity was performed on *A. sulphurea* by Wever (1935) who showed that the maximum sensitivity of the tympanal organ was reached at 10 KHz — a result which makes the oscillographically observed FM signal more biologically significant.

I present the following hypothesis: that the necessity to place the femora out of phase, because the femoro-tibial joints overlap the midline, also allowed a metachronous mechanism to develop which could control the frequency modulation of the signal. *Arphia sulphurea* and other oedipodines are at the least modified end of the spectrum and show perhaps how the more elaborate gomphocerine signal systems began.

TECHNIQUE RECOMMENDATIONS

The technique of superimposing synchronizable, visually transduced signals on a high-speed film of a moving structure is elegant, but expensive. However, good preparations are permanent and can be analyzed over and over for new permutations. I advise one to copy the best sections by means of an internegative, before they are viewed in a standard projector or motion analyzer. A careful check through a *clean* 16 mm movie editor is the maximum handling the original should receive. Then the original should be filed away

using proper film storage procedures, a positive made from the inter-negative and then the internegative should be filed. Analysis should be conducted with the positive — if possible one should pay extra to get an “answer print” in which very little of the original resolution is lost. Insist on the processor’s retaining the *side numbering* of the original; every twentieth frame is numbered in sequence, a very useful reference for frame-by-frame analysis. A professional movie processor will advise customers on special applications, including A & B answer prints for an exhibit, film titling and/or optical vs. magnetic sound track.

Improved techniques of filming could include 1) use of high intensity strobe lights flashing at a rate synchronized by the shutter-pulse signal of the camera and at a speed higher than the flicker-fusion frequency of the insect’s eyes. This would reduce the heat generated, but on the other hand there seems to be an upper limit to the frequency of stroboscopic flashing and resulting light intensity which allows the insects so far examined to behave normally. Other improvements in technique would include 2) a system allowing easy attachment of a mini-oscilloscope to the camera, thereby allowing easy movement of the camera relative to those of the subjects. A less expensive dual-trace mini-CRO is on the market (Tektronix 212) and is quite satisfactory for speeds up to 2000 pps. Also 3) use of reflective paints at anatomical points of reference, and 4) combination with some other techniques now in use, including telemetry (especially magnetometers with Hall-generators), probe microphones, electrode pickups, etc. superimposed and synchronized on the film frame.

The versatility and precision of ptenocinematography with synchronized oscillography for analysis of animal behavior is not equalled by any other method and, as one becomes familiar with the technique, the expense of film will decrease. The maximum initial investment and maintenance are probably equal to that of the least expensive electron microscope, if one needs to purchase an audiometric room and all ancillary facilities.

This technique is most useful for biomechanical studies where precise synchronization and micro-timing is necessary, i.e., where movements take less than 50 msec, as in the vibratory stridulations of many grasshoppers (Otte, 1970; Willey & Willey, 1969). Otherwise, videotape systems can approximate a 60 pps cinema system and, combined with simultaneous or *ex post facto* oscillography of the recorded sounds (Wussow *et al.*, 1974; Steinberg & Willey, 1974), would be as useful and less expensive.

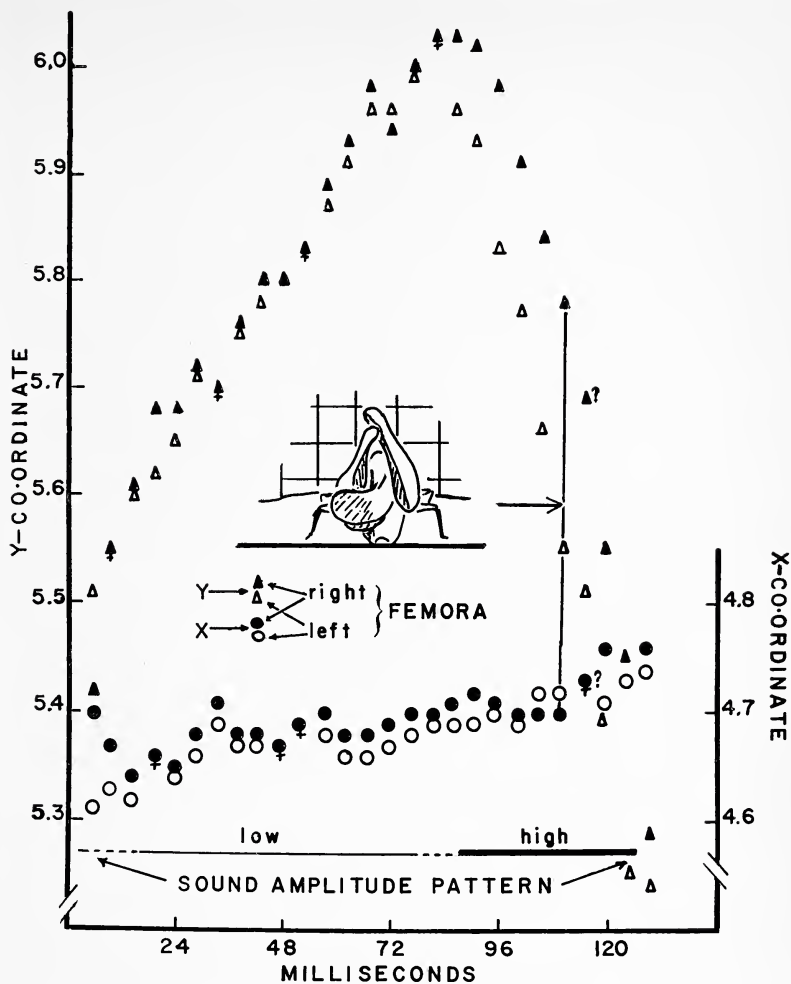


Fig. 48. Posterior view of stridulation movement made while male turns around in cage, pressing the wing-tips against the glass (insert). X and Y coordinates of the medial points of the femoro-tibial joints were measured instead of angles which could not be discerned readily. Angle of view is about 10° from the horizontal. Y-coordinates (+ triangle) approaching unity or overlapping represent parallel motion in the plane of the stroke, X-coordinates approaching unity or overlapping represent convergent motion at right angles to the plane of rotation, i.e., toward the midline. Note that the greatest Y-separation of the two femoral tips coincides with convergence in the X-dimension, i. e., the femoral tips overlap the midline and must displace one another if any pressure is to be placed on the tegminal file, imposing the asynchrony of downward motion observed in Figs. 44-47.

CONCLUSIONS

Analysis of micromovements during insect communication is crucial to understanding the external effects of internal neuromuscular systems and would be a desirable part of electrode implantation experiments as those performed by Elsner & Huber (1973) and Elsner (1974b). In addition, the comparative behavioral analysis is much enhanced if the motion is precisely linked with the signal presented. As Walker *et al.* (1970) have pointed out and demonstrated (Walker & Dew, 1972), if the motions are similar and produced by the same neuromuscular mechanisms (but the acoustic signals differ between taxa) then those taxa probably have some common lineage. I think this may be truer of insects which call to prospective mates from hidden positions than the Oedipodinae which seem to have a system of visual semaphores (colored hind-femora, tibiae, and/or abdomens) presented simultaneously with the acoustic signals in close visual communication (Willey & Willey, 1969). Thus careful analysis of oedipodine signals may reveal — as Otte (1970, 1972) and Steinberg & Willey (1974) indicate — that the acoustic signals often are a *lingua franca* among closely related as well as relatively unrelated taxa, advertising sex, physiological state, and "mood". Motion or color variation may be the species-specific component. We are not yet in a position to postulate rules of phylogeny as far as the oedipodine grasshoppers are concerned.

SUMMARY

The unitary stridulation (chirp) of a band-winged grasshopper species has been analyzed by ultra-high-speed motion photography (ptenocinematography), audiospectrography, and scanning electron microscopy. By means of a two-lens system, oscillographic traces of the sounds were synchronized with a motion picture of these sounds: at 0.5 msec per picture. This was sufficient to determine that the downstroke of the hind femora, pressing against the tegminal stridulatory file, produced the definitive signal previously recorded audiospectrographically and oscillographically by other authors. The oscillographic spike frequency was proved to be at a 1:1 ratio with the number of pegs struck by the femoral scraper. The right and left hind femora move in synchrony on the upstroke and produce a very weak and irregular series of acoustical spikes; however the two femora pass out of phase to produce the high amplitude and higher velocity downstroke (>4650 Hz per femur). Mechanically, this

phase shift is caused by the necessity of the femoro-tibial joints to overlap the mid-point of the dorsum in order to produce enough pressure on the file. Functionally, it is postulated that this system produces a frequency modulation which allows an FM signal of $\cong 10$ KHz to be pulsed periodically during the downstroke—a frequency long ago proved to be also at the greatest sensitivity of the tympanal receptor of this species.

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A REVIEW OF THE NEW WORLD ONYCHOPHORA
WITH THE DESCRIPTION OF A
NEW CAVERNICOLOUS GENUS
AND SPECIES FROM JAMAICA*

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Few animals are as avidly sought and as rarely found by invertebrate zoologists in the American tropics as are onychophorans. Yet, attempting to determine any specimens which one is fortunate enough to find can be a frustrating experience because of the scattered and incomplete literature.

In December 1972, while engaged in a survey of the invertebrate cave fauna of Jamaica, I discovered an eyeless and depigmented onychophoran. At that time, I knew that the only other known species of cave-adapted (troglotic) onychophoran, *Peripatopsis alba* Lawrence 1931, was from one cave in South Africa. To evaluate the status of the Jamaican troglotic species I undertook a review of the literature of New World Onychophora, and an examination of some 300 specimens in the collections of the Museum of Comparative Zoology (Harvard University) and the Institute of Jamaica. As a result, I have concluded that a summary of the literature on the systematics and distribution of New World onychophorans would be of interest, with the description of the new genus and species.

General treatments of Onychophora morphology, anatomy, and biology are those of Cuenot (1949), Zacher (1933), Kaestner (1968), Barnes (1968) and the references cited in these and other invertebrate texts.

The only systematic treatment of the Onychophora of the world is that of Bouvier (1905, 1907). Sedgwick (1908) reviewed the classification but did not formally add to it. Cuénot (1949) and Brues, Melander and Carpenter (1954) characterize the families and subfamilies of the world. No work unites what is known of all New World species. Brues (1911) presented a key for some species from the Caribbean and surrounding mainlands, adapted from Bouvier. Clark (1913a) revised the American species on a generic level, and (1913b) gave an annotated list of species. Keys for the West Indian species are available only for the Islands of Hispaniola (Brues, 1935) and Jamaica (Arnett, 1961). Clark and Zetek

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(1946) gave a key for species known from the Canal Zone and adjoining regions.

Distribution has been discussed by many, including Brinck (1956), Brues (1923) and Clark (1913a, 1913b, 1915a, b). The circum-tropical distribution of the family Peripatidae and the generally south temperate distribution of the family Peripatopsidae have led several authors to speculate that these distributions have been achieved through a Gondwana or continental drift mechanism (for instance, Cuénot, 1949; Hutchinson, 1928). However, although continental drift may be a fact, onychophoran distributions have not necessarily been controlled by it alone, and active, dynamic biological factors were probably more important in forming the distributions (Brinck, 1956; Darlington, 1965).

Since the summary papers by Bouvier and Clark, several species have been described and others have been placed in synonymy. The following key to the genera and list of species unites this dispersed literature and hopefully will provide a basis for encouraging further studies.

Key to the families and genera of New World onychophorans

- 1a. Sexual opening between last pair of legs (Fig. 1); Peripatopsidae, Peripatoidinae; south-temperate distribution in southern and central Chile. *Metaperipatus*
- 1b. Sexual opening between penultimate pair of legs (Fig. 2); Peripatidae, Peripatinae. 2
- 2a. Nephridial tubercles (urinary papillae) of fourth and fifth legs indenting proximal margin of third creeping pad band on leg, usually dividing third pad into two segments (Fig. 3); four or five creeping pads; four foot papillae, 2 on each side of foot. *Oroperipatus*
- 2b. Not the above combination; nephridial tubercles of fourth and fifth legs perhaps connected to third pad and indenting its proximal margin, but opening in space between third and fourth creeping pads, usually indenting fourth pad or rarely dividing fourth pad into two segments (Figs. 4, 7); usually four (rarely five or three) creeping pads (Fig. 4); three or four foot papillae. 3
- 3a. Four foot papillae (three anterior and one posterior, or rarely two anterior and two posterior) (Fig. 4); El Salvador.
..... *Heteroperipatus*
- 3b. Three foot papillae (two anterior and one posterior, Fig. 7). ... 4

- 4a. Twenty-four transverse dorsal folds to each segment, only slightly distinct because of numerous anastomoses and irregularities in grooves which separate them; 37 to 41 pairs of legs; Jamaica. *Plicatoperipatus*
- 4b. Twelve transverse dorsal folds to each segment, separated by continuous grooves except at level of legs where some grooves usually bifurcate; 36 or fewer pairs of legs. 5
- 5a. Eyeless; 22 or 23 pairs of legs; Jamaica. *Speleoperipatus*
- 5b. With eyes; 27 to 36 pairs of legs. 6
- 6a. Primary papillae of dorsal surface with a quadrangular base separated by straight grooves parallel with axis of body, dorsal body folds apparently divided by grooves; accessory papillae usually small and few in number. *Macroperipatus*
- 6b. Primary papillae of dorsal surface with a rounded base, dorsal body folds usually appearing undivided; accessory papillae with diverse degrees of development. 7
- 7a. Primary papillae of dorsal surface with great size differences in all ages, some very predominant, cylindrical, the other conical, smaller, usually three of the smaller or accessory papillae between two of the larger ones; the primary papillary tubercles separated by rather broad intervals where the accessory papillae occur; crural tubercles in male usually present on more than two pregenital pairs of legs. *Peripatus*
- 7b. Primary papillae of dorsal surface all of one type; in medium or large specimens these papillae intergrading through all sizes, while in small specimens some are conspicuously larger, papillae closely set though with occasional accessory papillae between them; crural tubercles in male present on only the two pregenital pairs of legs. *Epiperipatus*

I find it difficult to separate the last two genera with certainty. They have been used commonly as subgenera of *Peripatus sensu lato* and this might be a better arrangement in view of their lack of external distinctness. A study of the integumentary papillae with a scanning electron microscope (Peck, in preparation) might help to clarify the utility of these characters in *Peripatus* and *Epiperipatus*. Froehlich (1962) noted the need for a thorough review and revision of the complicated taxonomy of the New World onychophorans. This should be based on internal as well as superficial external characters. There is probably as much future work in the detection of synonyms as there is in finding and describing new species. As long ago as 1913, Clark (1913b) stated that "it is

astonishingly easy to make mistakes in their determination." This is still true, partly because no key to the species exists. It was beyond the intent of this study to prepare one.

In the following list, references to Bouvier (1905, 1907) and Clark (1913a, 1913b, 1915a) are not individually given because they apply to almost all species. Also, dates and literature citations to descriptions of Bouvier (1905, 1907) and earlier are not given, because they may be found in these works. The word "seen" indicates specimens from the Museum of Comparative Zoology and the Institute of Jamaica on which some data are based. All new records reported here are based on specimens of the Museum of Comparative Zoology. A history of synonymy of each species is not given because the intention of the list is only to report presently accepted species and their documented localities.

Family Peripatopsidae

Metaperipatus Clark, 1913a

Type species. *Peripatus blainvillei* Blanchard, 1847. By original designation and by monotypy.

Distributed only in southern and central Chile.

M. blainvillei (Blanchard). Southern Chile. Loncoche; Pucón; Palguin; San Carlos; Chiloé Island; Corral; Volcán Villarica; Enero, in Cordillera Peluda in Valdivia Prov.; Contulmo, in Cordillera Nahuelbuta separating Mallerco and Arauco Provinces; Buchoco valley between Lake Lanalhue and sea; south of Cañete, 10 km from Contulmo. Bouvier, 1928; Claude-Joseph, 1927, 1928; Gravier and Fage, 1925; Johow, 1911.

M. costesi (Gravier and Fage), 1925. Chile: Prov. Colchagua; Marga Marga near Santiago; "central Chile." Gravier and Fage, 1925.

M. umbrinus (Johow), 1911. Chile, near Zapallar, on coast of Aconcagua Prov., at 32°33'20" S. lat. Johow, 1911.

Family Peripatidae

Epipeperipatus Clark, 1913a

Type species. *Peripatus edwardsii* Blanchard, 1847. By original designation.

Distribution. From Santarem, Brazil, through French Guiana, Surinam, Guyana, Trinidad, Tobago, and Grenada and westward in South America to Central America and north through Nicaragua

to Guatemala and possibly British Honduras (Belize).

E. barbouri (Brues), 1911. Grenada: Grand Etang, 2000 ft. seen. Carriacou (?), seen. Tobago: Scarborough. Brues, 1911, 1914; Clark, 1937.

E. biolleyi (Bouvier). Honduras: San Juan Pueblo. Brues, 1925. British Honduras: near Benque Viejo (?), seen. Costa Rica: "La Estrella"; Parismina; San José; Surubres, near San Maeto; fruit farm near Siquirres, 6.vi.1930, Waldeck, 1, new record; Turrialba, 6.vii.1956, C. Gans, 4, new record; Turrialba, 25.vii-15.viii.1965, A Chickering, 6, new record; Talamanca, no other data, 4, new record; Orotina, 30 Aug. 1920, E. R. Dunn, 2 in hollow tree 6 ft. above ground, new record. Panama: El Ceremeño. Brues, 1911; Clark, 1937; Clark and Zetek, 1946; Picado, 1911.

E. brasiliensis brasiliensis (Bouvier). Brazil: Santarém. Venezuela: Mérida. Bouvier, 1908.

E. brasiliensis vagans Brues, 1925. Canal Zone: Barro Colorado Island, seen; Las Cascadas, seen; Fort Sherman, seen; Río Chinilla, seen; Balboa. Panama: San Pablo, seen; Río Tapia, seen. Brues, 1925; Clark and Zetek, 1946.

E. edwardsi (Blanchard). Brazil: Rio Guamá, Belém do Pará; Pôrto Cachoeira, Rio Doce, Espírito Santo State. French Guiana: Cayenne. Surinam: Paramaribo. Trinidad (?). Venezuela: Haute Sarare; Bas Sarare; Mérida; Valencia; Caracas, seen. Colombia: Santa Marta Mts., seen; Cincinnati Coffee Plantation in Santa Marta Mts., seen. Panama: Panama Station; Darién; El Cermeño; Balboa. Canal Zone: Barro Colorado Island, 3.viii.1925, C. W. Dodge, 1, new record; Barro Colorado Island, 17-19.iii.1967, Patterson exp., 3, new record. Arnett, 1961; Bouvier, 1906; Brues, 1914, 1925; Clark and Zetek, 1946; Froehlich, 1968.

E. evansi (Bouvier). Guyana: east bank of Demerara River.

E. imthurmi (Sclater). Surinam: Paramaribo, seen. French Guiana: Cayenne; Haut Carsevenne. Guyana: Essequibo; Georgetown (Demerara); Maccasseema on Pomeroon River; Hoorubea on Demerara River; Dunoon; Wakapa; Issororo. Trinidad. Colombia: Santa Marta, Cincinnati Coffee Plantation, 3000 ft., seen. Brues, 1914, 1925; Clark, 1915b; Froehlich, 1968.

E. isthmicola (Bouvier). Costa Rica: San José; Cachí; Santa Clara, Colombiana Farm, seen; Hamburg Farm, 1.iii.1930, F. Nevermann, one on dry wood under loose bark, new record; Guápiles, 7 Aug. 1920, E. R. Dunn, 4, new record; Navarro, 22 Aug. 1920, E. R. Dunn, 8, new record; Zent, 22-30 July 1920, E. R. Dunn, 6, new record. Brues, 1925.

E. lewisi Arnett, 1961. Jamaica: John Crow Mts., 10 mi. SW Priestmans River; 5 mi. SW Priestmans River, 1500 ft.; 1 mi. WSW Ecclesdown; all in Portland Parish, seen.

E. nicaraguensis (Bouvier). Nicaragua: Matagalpa; San Benito.

E. simoni (Bouvier). Brazil: Pará; Breves, on Marajó Island. Venezuela: Caracas. Clark, 1913c; Clark and Zetek, 1946.

E. trinidadensis trinidadensis (Stuhlmann). Trinidad: Port of Spain, seen; Maraval Valley, seen; Laventille, seen; Simla, 15.iv. 1964, A. M. Chickering, 1, new record; Simla, 1960, C. Carter, 1, new record. Brues, 1914.

E. trinidadensis broadwayi Clark, 1913. Tobago, seen. Clark 1913c.

E. tucupi Froehlich, 1968. Brazil: Pará.

E. vespucci Brues, 1914. Colombia: Santa Marta Mts., Cincinnati Coffee Plantation, 2300 ft., seen.

Heteroperipatus Zilch, 1954a

Type species. *Heteroperipatus engelhardi* Zilch, 1954a. By original designation and by monotypy.

Known only in El Salvador and Panama.

H. engelhardi Zilch, 1954. El Salvador: Finca El Carmen, Volcán San Vicente, 1100-1300 m, in litter-filled grooves in coffee plantation.

H. clarki (Dunn), 1943. New combination, suggested by Zilch, 1954a. Panama: Azuero Peninsula.

Macroperipatus Clark, 1913a

Type species. *Peripatus torquatus* von Kennel, 1883. By original designation.

Distribution. Rio de Janeiro north to French Guiana, Guyana and Trinidad, west to Panama, and north to Veracruz, Mexico; and on Hispaniola and Jamaica.

M. acacioi Marcus and Marcus, 1955. Brazil: Minas Gerais, Ouro Preto, 1100 m. Froehlich, 1968.

M. geayi (Bouvier). French Guiana; on the Brazilian border. Colombia: Sierra Nevada de Santa Marta, seen; Sierra Nevada de Santa Marta, Cincinnati Coffee Plantation, seen. Panama: La Chorrera. Canal Zone: Barro Colorado Island, seen; Pedro Miguel; Balboa. Costa Rica; Osa Peninsula, Rincón, 10.viii.1966, S. B. Peck, 1 under log at 400 ft., new record. Brues, 1925; Clark, 1913b; Clark and Zetek, 1946.

M. guianensis (Evans). Guyana: east bank of Demerara River.

M. insularis insularis Clark, 1937. Haiti: between Jacmel and Tronin.

M. insularis clarki Arnett, 1961. Jamaica: Portland Parish, 5 mi. SW Priestmans River, 1500 ft., seen.

M. ohausi (Bouvier). Brazil: near Rio de Janeiro; Petrópolis.

M. perrieri (Bouvier). Mexico: Veracruz.

M. torquatus (von Kennel). Trinidad: Port of Spain, seen; Maraval Valley, seen. Brues, 1914.

Oroperipatus Cockerell, 1908

Type species. *Peripatus lankesteri* Bouvier, 1899. Believed to be by subsequent designation of Clark, 1913a. Original paper unavailable.

Distribution. The Pacific slope of tropical America from Tepic, Mexico, southward through Colombia, Ecuador, and Peru to Sorata, Bolivia, and in western Brazil.

O. balzani (Camerano). Bolivia: Coroico and Chulumani states.

O. belli (Bouvier). Ecuador: Durán, on Guayas River.

O. bimbergi (Fuhrmann), 1913. Colombia: Amagatal, 900-1800 m; Guaduas, 800 m. Fuhrmann, 1914.

O. bluntschli Fuhrmann, 1915. Peru: Río Samiria, 120 m. Zilch, 1954b.

O. cameranoi (Bouvier). Ecuador: Cuenca; Sigsig.

O. corradoi (Camerano). Ecuador: Quito; Balzar; Guayaquil. Panama: El Ceremeño. Canal Zone: Barro Colorado Island, seen; Ancon. Venezuela: Falcón State, Paují Acosta District, H. G. Kugler, 1.xi.1945, 5, new record. Brues, 1925; Clark, 1914a, 1914b; Clark and Zetek, 1946.

O. ecuadoriensis (Bouvier). Ecuador: Bulim.

O. eiseni (Wheeler). Brazil: Rio Purus. Panama: El Cermeño; Panama City. Mexico: Tepic. Clark and Zetek, 1946; Fuhrmann, 1914.

O. goudoti (Bouvier). Mexico.

O. intermedius (Bouvier). Bolivia: Sorata.

O. koepckeii Zilch, 1954b. Peru: western side of Andes, 35 km from Olmos, toward Jaén, 1400 m.

O. lankesteri (Bouvier). Ecuador: Paramba, near Quito.

O. multipodes (Fuhrmann), 1913. Colombia, Río Amagá. Fuhrmann, 1914.

O. omeyrus Marcus, 1952. Peru: San José de Lourdes, on Río Chirinos, 1000 m; Sahuayaco, between Abancay and Marcos, Urubamba valley, 800 m. Zilch, 1954b.

- O. (?) peruanus* (Grube). Peru. Marcus, 1952; Zilch, 1954b.
O. peruvianus Brues, 1917. Peru: Tabaconás, near Huancabamba, 6000 ft., seen. Zilch, 1954b.
O. quitensis (Schmarda). Ecuador: high regions.
O. soratanus (Bouvier). Bolivia: Sorata.
O. tuberculatus (Bouvier). Colombia: Popayán.
O. weyrauchi Marcus, 1952. Peru: Yurac on Río Aguaytia, 300 m. Zilch, 1954b.

Peripatus Guilding, 1825, *sensu stricto* of Clark, 1913a

Type species. *Peripatus juliformis* Guilding, 1825. By monotypy.

Distribution. West Indian Islands of Jamaica, Haiti, Puerto Rico, Vieques, St. Thomas, Antigua, Monserrat, Barbados, Guadeloupe, Dominica, and St. Vincent, and in South America in Brasil and from the mountains of western Venezuela westward to Colombia and north of Panama and Costa Rica.

P. antiguensis Bouvier. Antigua: Barlar, near Warburton. Monserrat. Clark, 1929.

P. bavayi Bouvier. Guadeloupe.

P. bouvieri Fuhrmann, 1913. Colombia: Boca del Monte, near Bogotá; Cundinamarca Dept., above Aguadita, wet forest with ferns, 26.iii.1967, W. Brown, 1, new record. Fuhrmann, 1914.

P. brolemanni Bouvier. Venezuela: Tovar, near Mérida; Raxto Casselo; Puerto Cabello.

P. dominicae dominicae Pollard. Dominica: Laudat; Prince Rupert; Roseau, seen.

P. dominicae barbadensis Froehlich, 1962. Barbados: St. John, Codrington College.

P. dominicae basilensis Brues, 1935. Haiti: Mount Basil, 4000 ft., seen. Dominican Republic: Mt. Diego de Ocampo, 3500-4000 ft., seen; north slope Loma Rucilla, 8000 ft., seen; north of Loma Rucilla, 6000-7000 ft., seen; Constanza, 3000-4000 ft., seen; Vic Valle Nuevo, 7000 ft., seen. Brues, 1935; 1939.

P. dominicae darlingtoni Brues, 1935. Haiti: Massif de la Hotte, between Camp-Perrin and Mafin, 3000 ft., seen.

P. dominicae haitensis Brues, 1913. Haiti: Furcy (type locality); La Visite, La Selle Plateau, seen. Brues, 1935.

P. dominicae lachauxensis Brues, 1935. Haiti: Étang Lachaux, Massif de la Hotte, under 1000 ft., seen.

P. evelinae (Marcus), 1937. Brazil: between Canra Brava and Nova Roma, near border of Goiás and Minas Gerais. Froehlich, 1968.

P. heloisae Carvalho, 1941. Brasil: Rio Tapirapé, near confluence with Rio Araguaia. Carvalho, 1942.

P. juliformis Guilding. St. Vincent.

P. juliformis danicus Bouvier. Virgin Islands: St. Thomas. St. Croix. St. John: along trail from Centerline Road to Cinnamon Bay, in litter in dry north-facing gully, 3.i.1967, S. Peck, 1, new record. Brues, 1925; Clark, 1937.

P. juanensis Bouvier. Puerto Rico: Arecibo; Utuado; Vieques Island; El Yunque, May 1938, Darlington, 3000 ft., 1, new record; Manatí, 2.vi.1943, F. Mora, Indoors, 1, new record; Toro Negro Forest Preserve, trail up Cerro Doña Juana, 28.xii.1966, S. Peck, 6 on *Fomes* woody fungi bract on log on ground, 600 m, new record, specimens lost. Clark, 1913b; 1913c.

P. manni Brues, 1913. Haiti: Furcy; La Visite, La Selle Plateau, 5000-7000 ft., seen. Brues, 1935.

P. ruber Fuhrmann, 1913. Panama: Chiriquí Prov., Lino, near Boquete, 4100-4500 ft. Costa Rica: Rancho Redondo. Guatemala: Puerto Barrios (?). The record of *P. (Epipeperipatus) biolleyi* var. *betheli* Cockerell 1913 from Puerto Barrios appears to be *P. ruber* according to Clark and Zetek (1946). Clark, 1941b; Fuhrmann, 1914.

P. sedgwicki Bouvier. Venezuela: Caracas, seen; San Esteban; La Moka; Las Trincheras; La Guayra.

P. swainsonae Cockerell. Jamaica: Bath; Savanna la Mar; localities in Hanover, Portland and Trelawny Parishes, from 400 to 1500 feet, seen. Andrews, 1933; Arnett, 1961; Brues, 1911; Lynn, 1936.

Plicatoperipatus Clark, 1913a

Type species. *Peripatus jamaicensis* Grabham and Cockerell, 1892. By original designation and by monotypy.

Known only from Jamaica.

P. jamaicensis (Grabham and Cockerell). Jamaica: Portland, Manchester, St. Thomas, Trelawny, St. Ann, and Westmorland Parishes, seen. Andrews, 1933; Arnett, 1961; Brues, 1911; Lynn, 1936.

Speleoperipatus new genus

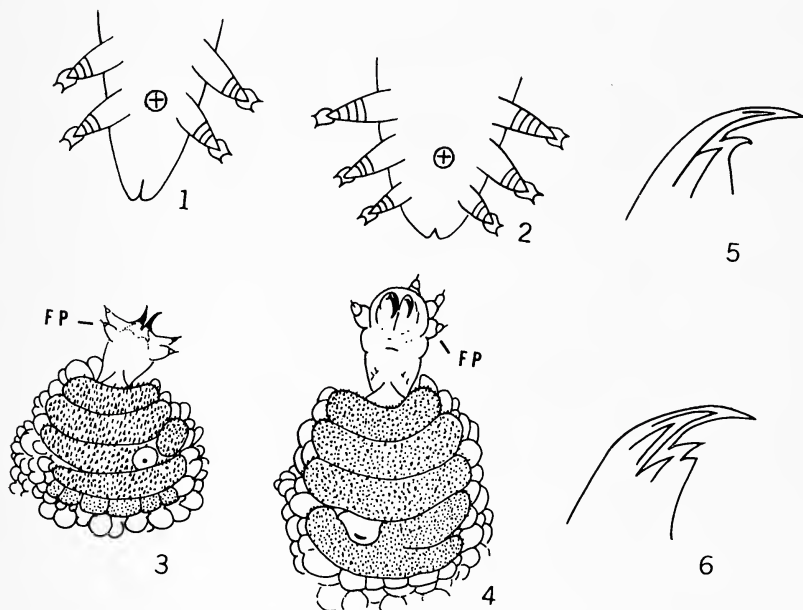
Description. Peripatidae, Peripatinae, with 22 or 23 pairs of legs; three foot papillae (two anterior and one posterior); legs four and five with urinary papillae broadly attached to and indenting creeping pad three, pad four crescent-shaped; no fifth pad.

Type species. *Speleoperipatus speleus*, new species.

Speleoperipatus speleus new species

Holotype deposited in invertebrate collections of the Museum of Comparative Zoology, Harvard University. Type locality: Jamaica, Clarendon Parish, Pedro River, Pedro Great Cave. Type data: 20 December 1972, S. B. Peck. Paratypes: all from same locality; one, 25 March 1973, R. Norton and R. Zimmerman (deposited in Peabody Museum, Yale University); two, 17 August 1974, S. Peck and family, in Museum of Comparative Zoology.

Description. Eyes absent, no trace remaining. Depigmented; specimens in life pale, almost white, with a slight greenish-yellow cast (Fig. 8). Legs and "antennae" not appreciably elongated. Holotype 34 mm long, with 22 pairs of legs. Paratypes: One 27 mm



Figures 1-6. 1. Location of genital opening in Peripatopsidae, Peripatoidinae. 2. Location of genital opening in Peripatidae, Peripatinae. 3. Ventral surface of left fourth leg of *Oroperipatus koepckeii* (after Zilch, 1954b) showing urinary papilla dividing the third band of the creeping pads, and four foot papillae (fp). 4. Ventral side of right fourth leg of *Heteroperipatus engelhardi* (after Zilch, 1954a) showing urinary papilla between creeping pads three and four, indenting pad four, and three anterior and one posterior foot papillae (fp). 5. Outer blade of right mandible of *Speleoperipatus speleus*. 6. Inner blade of right mandible of *S. speleus*.

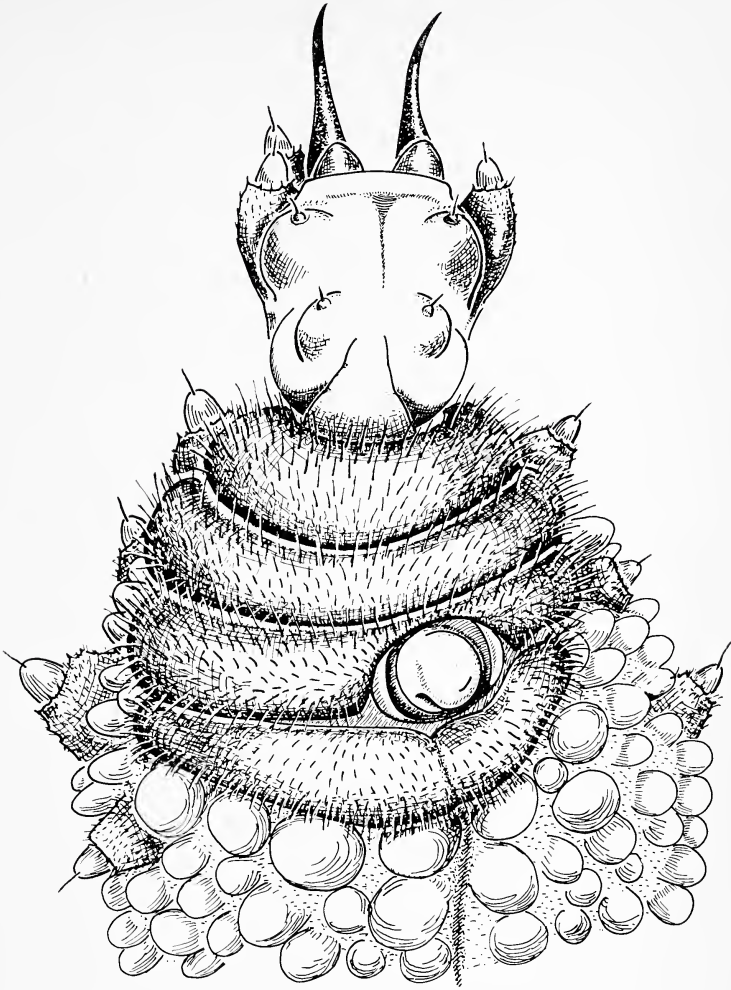


Figure 7. Left fourth leg of *Speleoperipatus spelaeus*.

long, with 23 legs on the left side and 22 on the right; a second 34 mm long with 22 pairs of legs, and the third 34 mm long with 23 pairs of legs. Widths 2 to 3 mm depending on preservation. All legs with four creeping pads; pad three broadly connected to urinary papillae in legs four and five; pad four crescent-shaped; all feet with two anterior and one posterior papilla (Fig. 7).

Each body segment with 12 skin folds; folds neither diverging nor fusing along lateral side above the legs. The skin papillae with round bases but of varying sizes and shapes; lateral papillae with more elongate and straight-sided tip, tips shorter and more rounded on dorsal papillae; one to three but usually two small papillae between major papillae.

Mandible (Figs. 5, 6) outer blade with long thin main tooth and a short thin accessory tooth; inner blade with long, thin main tooth and two thin shorter accessory teeth. No small sawlike teeth below a diastema on outer or inner blade.

Type locality description and observations. The type locality cave is 1500 feet long, at 1700 feet elevation, 0.6 air miles SE of the village of Pedro River, in northeastern Clarendon Parish. The cave is a large diameter, relatively simple, moist tunnel with large deposits of calcium carbonate dripstone and bat guano, and an air temperature of 21.5°C. All specimens were found near the middle of the cave in the "Three Ways" section (see map in Fincham and Ashton, 1967). One was found in the open on wet decomposed guano before, and the other three specimens in the chamber after, the low crawlway leading to Three Ways. In 1974, one specimen was sighted while it was partially exposed, feeding on an immature, blind *Nelipophygus* roach (Blatellidae), with most of its body hidden in a small hole at the side of a ceiling pocket. The second 1974 specimen was found hidden under a loose clay-guano flake formed by the drying of a formerly flooded section of the cave floor. Four people searched this chamber thoroughly for an hour in 1974 for more specimens but found none. A rich invertebrate fauna of potential prey exists in the cave. When touched, all specimens ejected a viscous, sticky fluid for 2-3 cm from their oral papillae.

Cave adaptation. The eyeless and depigmented conditions of the species are usually associated with troglobitic (cave-evolved) species, but are not limited to such species. These characters are also encountered in forest litter-evolved species, and many litter inhabitants in the past were certainly ancestral to presently troglobitic species (Barr, 1968). The legs and antennae of *Speleoperipatus* may be somewhat elongated (Fig. 8) as a specialization for cave life, but measurements (in life) of the appendages of this and epigeic species are not available for comparison.

The general region of Jamaica from which *Speleoperipatus* comes is known to have several species of seemingly troglobitic invertebrates (personal observations), all of which have been derived from litter-inhabiting ancestors. But collecting in forest litter in Jamaica is

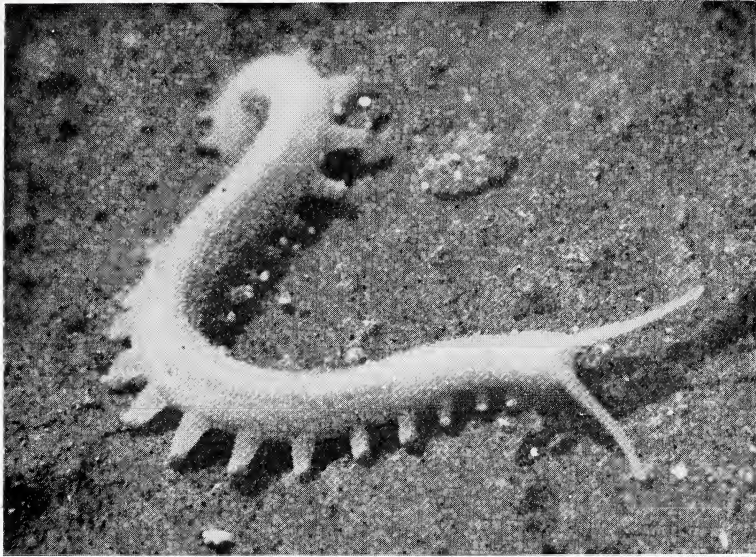


Figure 8. *Speleoperipatus spelaeus* in life.

inadequate so it is not known with certainty that the seemingly troglotic species live only in caves. In my field work on Jamaican cave faunas, I have made some 70 visits to some 50 caves in search of their invertebrates, and Russell M. Norton has made some 20 visits to some 20 caves (many of the same caves in which I have collected). Since many of the other troglotic species have been encountered in many of these caves over much of Jamaica and *Speleoperipatus* has not, it is possible that this genus may now be limited to a single cave system. And since it may exist only in small numbers, future collecting of it should be restrained, in order to preserve this unique genus from extinction.

Discussion. The genus and species is close to both *Epiperipatus* and *Peripatus* (s.str.) in its skin papillae; and to these and *Macroperipatus* in the number of feet papillae (2 anterior and 1 posterior in all these genera), and four foot creeping pads (as in all these genera). However, the new genus differs from these genera in having some four fewer (at least) pairs of legs, and in the mandibles.

In some respects, the new genus and species resembles *Typhloperipatus williamsoni* Kemp (1914) from the Himalaya foothills of eastern India (near Rotung, on the Dihang River, Assam, near Tibet). Both are eyeless, and the latter has only 19 to 20 pairs of

legs. The latter species was taken abundantly in leaf litter in scrub-jungle at from 1200 to 2000 feet elevation. However, eyelessness and loss of legs are characters that can be convergently acquired, and the two genera are presently placed in different subfamilies, based on the number of foot papillae (three and more in Peripatinae of the New World and equatorial Africa, and only two in the Eoperipatinae (containing *Eoperipatus* and *Typhloperipatus* in the Indo-Malaysian area). Kemp (1914: 491) lists other features uniting *Typhloperipatus* with New World genera more closely than with Malaysian *Eoperipatus*, but this relationship should be reviewed.

A low number of legs may be a primitive feature in the Peripatidae. In comparison to the 22 or 23 pairs in *S. spelaeus*, 23 (to 27) pairs occur in *Mesoperipatus tholloni* of equatorial Africa, and 23 (to 29) pairs occur in some species groups of *Oroperipatus*. However, in all other New World genera, 27 pairs seems to be the lowest number.

In conclusion, the genus *Speleoperipatus*, because of its intermediate characteristics involving Asian and African as well as New World genera, seems to have originated from an ancient lineage of onychophorans in which the characters were not as well segregated as they are at present. In this case, *Speleoperipatus*, *Mesoperipatus* and *Typhloperipatus* of the Peripatidae can be regarded as relicts of earlier more widespread groups. The eyelessness of *Typhloperipatus* shows that this feature can be associated with species that do not live in caves. *Speleoperipatus* may thus have become eyeless before it entered a cave habitat, but until it is found in a non-cave habitat (such as forest litter or talus slopes), it should be considered as a troglobitic cave-limited species. It is worth noting, in closing, that the two families of the Phylum have once each, and independently, entered and permanently occupied a cave habitat and may have become restricted to, and specialized for, this cave habitat.

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Dr. Herbert Levi, Museum of Comparative Zoology, permitted study of the specimens in the collections under his care. The manuscript was reviewed by Henry Townes and Herbert W. Levi.

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GROOMING THROUGH THE REPRODUCTIVE
CYCLE IN MALE *SINELLA COECA*
(COLLEMBOLA: ENTOMOBRYIDAE)*

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INTRODUCTION

Pheromones function in several roles important in insect reproduction: location of associate, species recognition, sex recognition, and as aphrodisiacs. The receptors that detect most sex pheromones are located on the antennae and mouth parts. Grooming behaviors free these sensory surfaces of foreign materials permitting their optimal functioning.

Collembola are commonly very abundant in leaf litter and soil ranging up to 200,000 per m² (Hale, 1967). They contribute by their food processing and locomotion to soil genesis and the maintenance of soil fertility. Their abundance is due not to a large diversity of species, but to a high reproductive potential (Kuhnelt, 1961).

Reproduction utilizes indirect sperm transfer via stalked spermatophores. In *Sinella curviseta* Brook (Family Entomobryidae) spermatophore deposition by males is stimulated by a female sex pheromone (Waldorf, 1974a). Under ideal conditions, *Sinella curviseta* females can deposit an average of 45 eggs every 8 days for 3 months (Waldorf, 1971; Niiijima, 1973). Both sexes in this species release gametes during specific intervals that alternate with nonreproductive periods (Waldorf, 1971). Males and females molt twice between successive reproductive intervals.

Although reproduction has not been described in *Sinella coeca* (Schott), preliminary work suggested that the frequency of cleaning might vary with the reproductive condition of the individual (Waldorf, 1974b). These data demonstrate a difference between the sexes in the frequency of grooming, with males grooming more often. In addition, the frequency of grooming in females depends on the reproductive condition of the female.

This study examined the frequency of grooming in *Sinella coeca* males in a sequence of reproductive conditions. Since females with

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eggs groom more often than other females (Waldorf, 1974b), I expected males depositing spermatophores to exhibit a higher rate of grooming.

METHODS

Mass cultures of *Sinella coeca* were maintained as previously described (Waldorf, 1971). Animals were held at room temperature (25-26°C) in constant light. Brewer's yeast was provided as food and replaced as the supply became contaminated with fungal growth.

Ten pharate males were isolated in individual plastic-capped glass vials. The vials with an inner diameter of 22.0 mm contained a moist plaster of paris-charcoal substrate and food. Each male was observed for five minutes every 12 hours for 10 days. With the observer wearing a fiber mask to reduce disturbance of the animals, observations were begun 12 hours after isolation. Records were made of number of bouts of antennal grooming, total number of bouts of grooming and total seconds grooming. For the latter an electric second counter was activated by a depression switch. In addition, exuvia were removed and their presence recorded, and observations of spermatophore deposition behavior were noted.

Table 1. The lengths of reproductive and nonreproductive instars in male *Sinella coeca* in days at 25-26°C.

	Reproductive instar	Nonreproductive instar
Instar length	5.4	3.1
SD	1.006	.512
No. of males	10	9

RESULTS

Spermatophore deposition behaviors occur in *Sinella coeca* only in alternate instars. The lengths of the two types of instar (Table 1) differ significantly ($t = 6.62$, $df 17$; $P < .005$). The reproductive instars average 5.4 days, one and $\frac{3}{4}$ times the length of the non-reproductive ones.

The percentages of the males exhibiting spermatophore deposition behavior through the reproductive instar appear in figure 1. The maximum occurred early in the instar with all males depositing spermatophores spontaneously 24-36 hours after ecdysis. There is a

gradual decline until 6 hours prior to the next ecdysis when no males exhibited this behavior.

Neither the number of bouts of cleaning nor the lengths of these differed in reproductive as compared with nonreproductive males. The averages, considering all grooming, are presented in Table 2. Similarly, there are no differences in antennal grooming as a function of reproductive condition.

The average frequencies of grooming through the instars are illustrated in figure 2. The patterns in reproductive and nonreproductive males are essentially the same. Both groom most frequently 12-18 hours after ecdysis. Thereafter a lower rate is more or less constant until 70-75% of the instar has elapsed. This declines to near zero before ecdysis. Of the 11 pharate males observed in previous experiments, only one performed one antennal cleaning.

Table 2. The average number of bouts of grooming in 5 min. and their average duration in male *Sinella coeca* in the reproductive and nonreproductive instars.

	No. of bouts per animal			Length of bouts (in sec)		
	\bar{x}	n	SD	\bar{x}	n	SD
Reproductive instar	1.3	10	.518	25.93	98	15.86
Nonreproductive instar	1.3	10	.441	23.43	49	10.48

DISCUSSION

The pattern of alternate reproductive and nonreproductive instars observed in *Sinella coeca* characterizes both sexes of *Sinella curviseta* (Waldorf, 1971) and some members of the genera *Orchesella*, *Tomocerus* and *Isotoma* (Poggendorf, 1956; Mayer, 1957; Joose and Veltkamp, 1970). Similarly, reproductive instars are longer in males of *S. curviseta* (Waldorf, 1971) and *Orchesella cincta* L. (Poggendorf, 1956) than nonreproductive ones. Although not enough data are available to draw a conclusion, this pattern might apply generally within the family Entomobryidae.

The experimental observations of isolated males provided estimates of the frequency of spontaneous grooming. The data indicate that the rate of spontaneous grooming does not vary between types of instar but does vary within instars.

Fluctuations in response to female (or male) associates might be superimposed on the basic pattern (fig. 2). An example of the effect

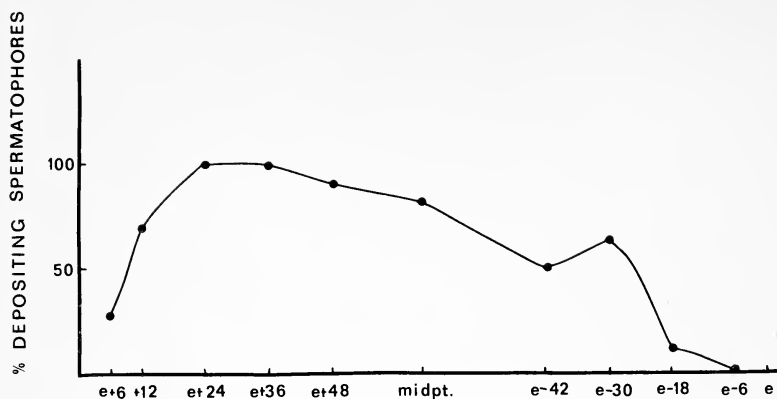


Figure 1. The percentages of males depositing spermatophores through the reproductive instars. Ages are given in hours relative to ecdyses (e) at the onset and conclusion of the instar.

of association has been reported in *Sminthurides aquaticus* Bourlet (Mayer, 1957). Males of this springtail clasp the antennae of females and are carried about by the females. Such males groom more than unattached males.

The previous finding (Waldorf, 1974b) that *Sinella coeca* males groom more frequently than females is possibly explained by the positive correlation reported by Jander (1966). She found higher rates of grooming in animals that exhibited more locomotor activity. *S. coeca* males are more active than females.

This correlation receives further support from comparison with *Sinella curviseta* males. *S. coeca* males groomed their antennae about 1.8 times in 5 min. This contrasts with .4 antennal cleanings observed on the average in five min (at the same temperature) in the less active *S. curviseta* males ($n = 10$; $SD = .70$).

My earlier data (1974b) on variation in grooming in *S. coeca* females, although less precise, was similar to the pattern in males shown in figure 2. In that experiment the category termed newly ecdysed females (ecdysis (e) to e + 22 hours) exhibited moderate frequency of grooming; females with eggs (e + 24 to e + 44 hours) exhibited the highest frequency of cleaning; and, other females (>e + 24 hours in nonreproductive instars and >e + 44 hours in reproductive ones, assuming these occur) exhibited the lowest. Since these females were observed at 23°C (in contrast to 25-26°C for males in the present experiment), the hours cannot be compared exactly.

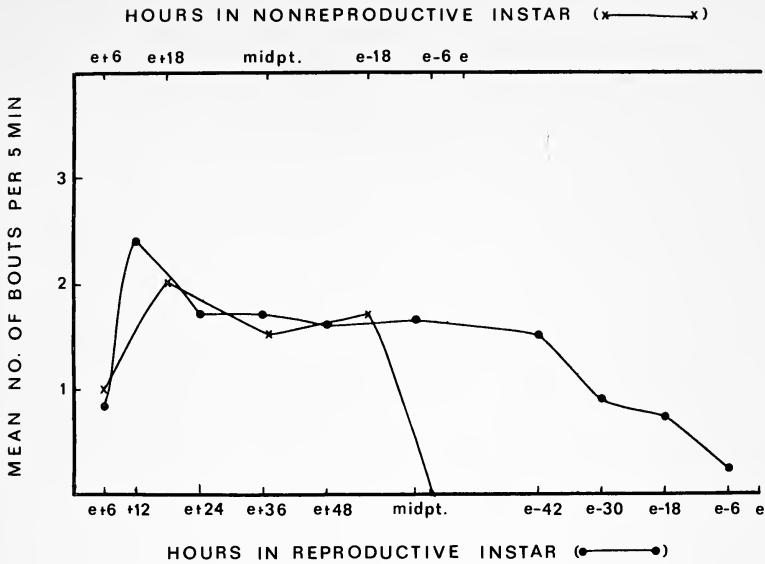


Figure 2. Average number of bouts of grooming behavior in 5 min through the reproductive and nonreproductive instars. Ages are given in hours relative to ecdyses (e) at the onset and conclusion of the instars.

Lepidocyrtus cyaneus Tullberg cleans its antennae twice in five minutes and its legs an average of 1.3 times (Pedigo, 1967). These compare with 1.8 times for antennae and a smaller value for leg grooming in male *Sinella coeca*. These rates are remarkably similar, perhaps indicating equal rates of locomotor activity in the two species. However, if *Lepidocyrtus* males are more active than females, those frequencies might be averages of the higher rate of grooming in males with the lower one in females.

The location in instars of the maximum grooming rate is of interest. In *S. curviseta*, females pick-up and utilize sperm only during about the first 20 hours of the reproductive instars (Waldorf, 1971). During this interval females release a volatile sex pheromone that increases male spermatophore deposition (Waldorf, 1974a). Further Joosse (1975) reports that certain events synchronize molting in natural populations of species of Entomobryidae. Consequently, if *Sinella coeca* females are similar to *S. curviseta* ones, the maximum spontaneous grooming in males might often coincide with the presence of the female sex pheromone.

In *Orchesella cincta* males, spermatophore deposition occurs typically only in the first half of the reproductive instar (Joosse, Brugman and Veld, 1973). The maximum number of males of *Sinella coeca* exhibit spontaneous spermatophore deposition in the first half of the instar. If reproduction in *S. coeca* females resembles that in *S. curviseta* and synchronization of molting occurs, *S. coeca* females probably have access to an abundance of spermatophores.

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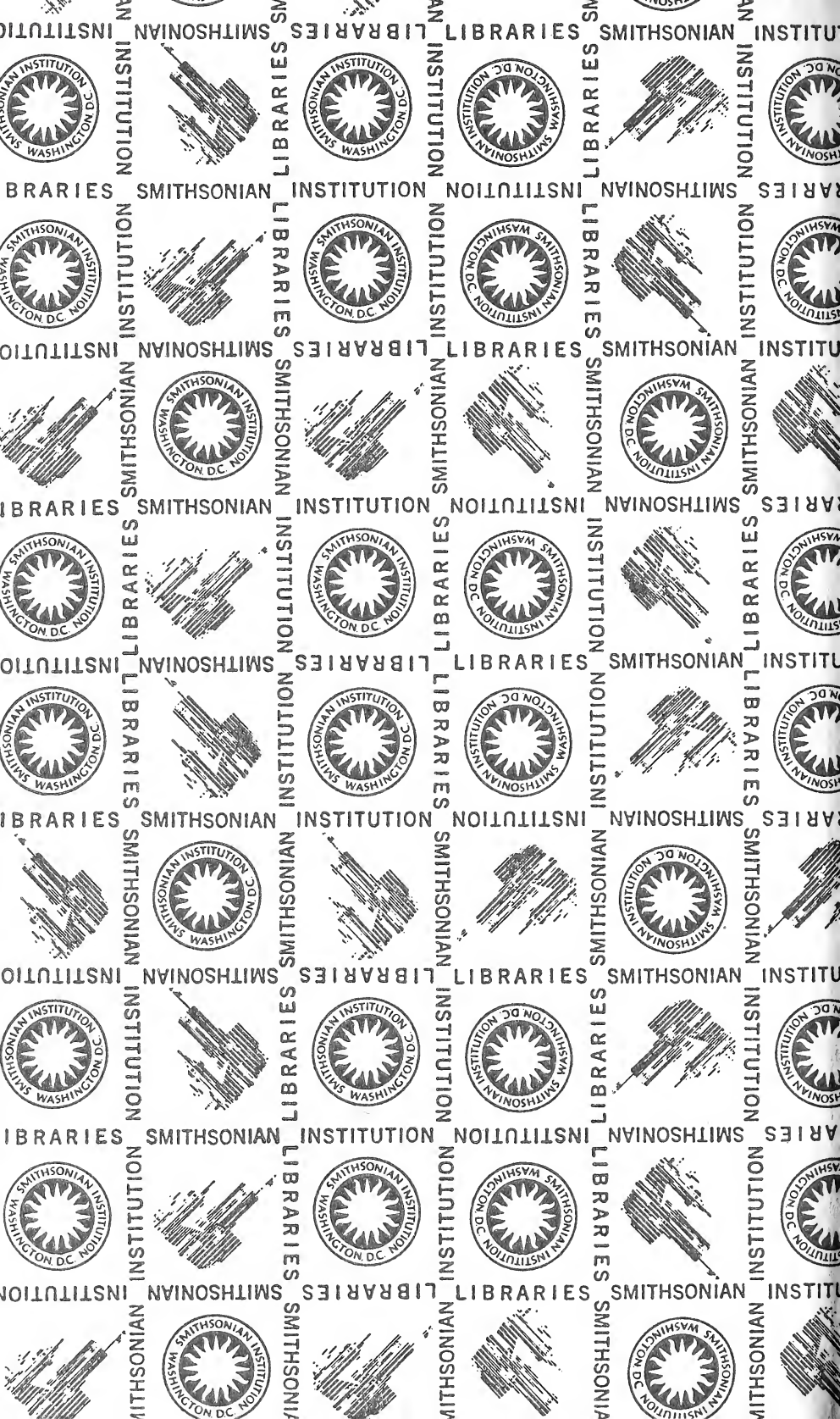
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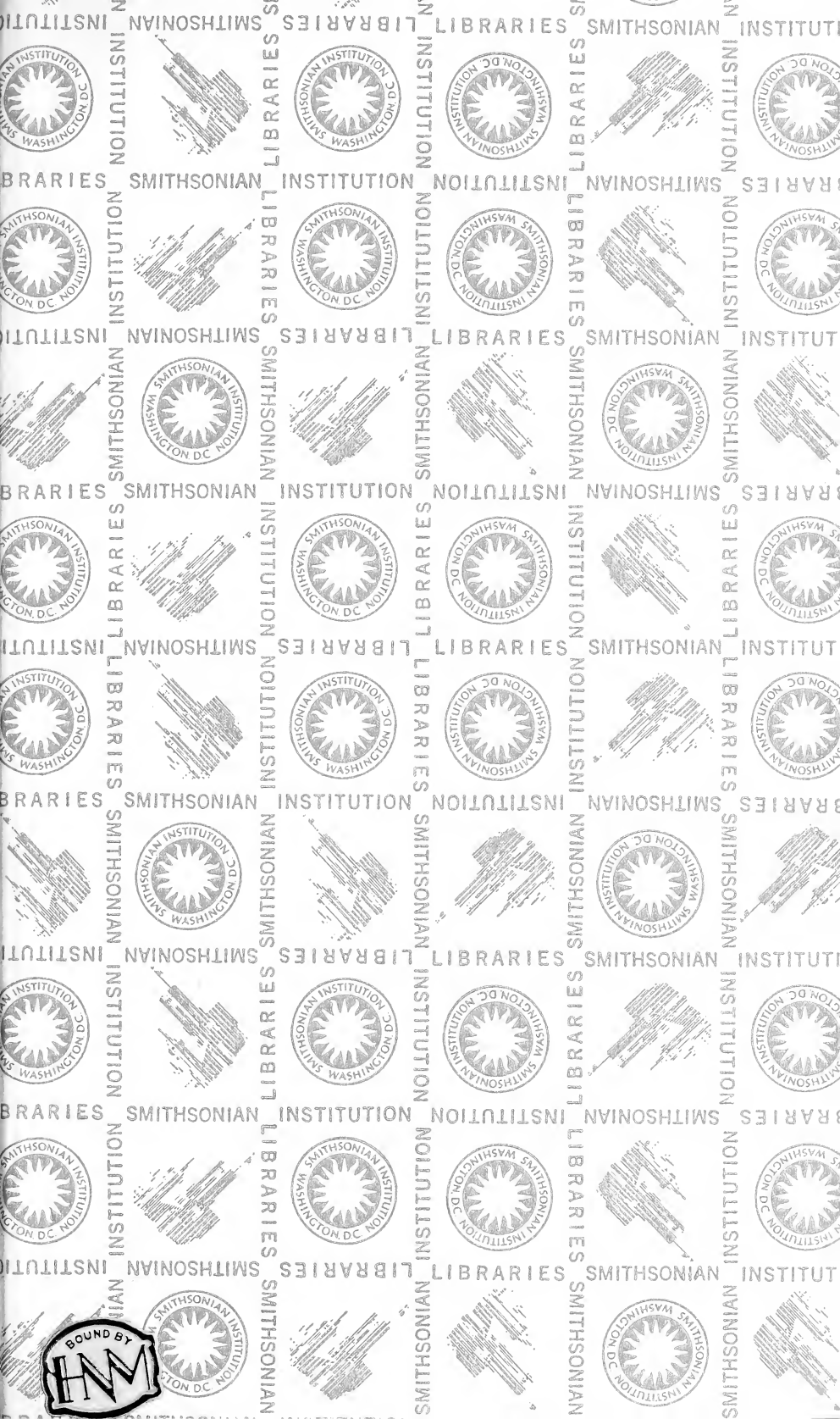
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