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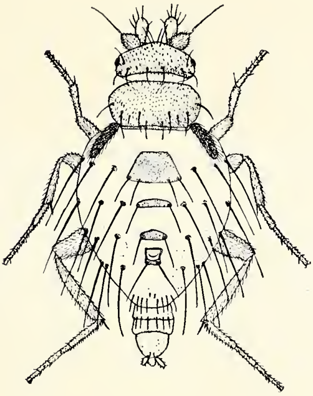

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Charles Albert Frost, about 1934-1935

PSYCHE

Vol. 70 March, 1963 No. 1

CHARLES ALBERT FROST

A Biographic Sketch and List of Publications

Charles Albert Frost was born in Monmouth, Maine, on August 28, 1872. He attended local schools and the University of Maine, where he graduated in 1895 with a bachelor's degree in civil engineering. He spent his working years as a civil engineer with the Waterworks Division of the Metropolitan District Commission, with responsibilities in and around Framingham, Massachusetts. He lived in Framingham for the last fifty years of his life, at 67 Henry Street. Here he built up a very important private collection of North American beetles. Its importance lay less in what he published than in the part it enabled him to play: in his wide knowledge, the extensive correspondence that he continued almost to the day of his death, and his very great helpfulness to other coleopterists. He was almost the last of the old-time, general students of Coleoptera, who knew the entire order, and who were members of a network of collectors and students interested in beetles who covered the whole of the United States and southern Canada. He was one of my first entomological friends (much older than I, of course), and a fine, intelligent, generous, useful man. He died at home on March 11, 1962, at the age of 89.

Mr. Frost has left his collection of beetles to the Museum of Comparative Zoology, Harvard University. It fills 116 Schmitt or similar boxes. There are at least 50,000 specimens and perhaps many more; some of the boxes are so crowded that it is difficult to count the specimens in them. The specimens are well mounted, well labeled, and clean, and a large proportion of them have been studied and identified either by Mr. Frost himself or by competent specialists with whom he corresponded. There are some holotypes, and many paratypes of other workers. The collection is especially strong in small beetles, which are hard to collect and mount, and which are very much needed to fill out the study series of North American Coleoptera at the museum. The specimens will be individually labeled "C.A. Frost Collection" and incorporated in the museum's main series of North American beetles.

P. J. Darlington, Jr.

PUBLICATIONS OF CHARLES ALBERT FROST

1908

Notes on *Attelabus rhois* and parasite. Psyche, **15**: 26-32.

1909

Notes on wood-boring Coleoptera. Ent. News, **20**: 298-299.

1910

A new species of *Chrysobothris* (Coleoptera) from Maine. Journ. N. Y. Ent. Soc., **18**: 43-45.

1912

Variations on *Orsodachna atra* — Coleoptera. Psyche **19**: 153-156.

New species Coleoptera of the genus *Agrilus*. Can. Ent., **44**: 245-252.

Collecting Coleoptera in a Maine sawmill yard. Can. Ent., **44**: 304-308.

Note on *Tricrania sanguinipennis* Say (Coleoptera). Psyche, **19**: 208.

1913

Notes on *Tomoxia bidentata* Say and *T. lineella* Lec. (Coleop.). Ent. News, **24**: 126-129.

Peculiar habits of small Diptera, *Desmometopa latipes* Meig. Psyche, **20**: 37.

1915

June collecting in Maine — (Coleoptera) Can. Ent., **47**: 141-145.

List of Coleoptera collected from Tanglefoot. Ent. News, **26**: 269-270.

Remarks on collecting at light, with a list of the Coleoptera taken. Psyche, **22**: 207-211.

1916

Inhabitants on an April mud puddle. Can. Ent., **48**: 214-215.

Collecting notes and random observations on the Maine Coleoptera. Can. Ent., **48** : 381-390.

1920

A day's beating. Can. Ent., **52**: 25-29.

Notes on the Coleoptera with descriptions of new species. Can. Ent., **52**: 229-232; 249-253.

A bibliography of the literature on the described transformations and food plants of North American species of *Agrilus* (Col.) (with H. B. Weiss). Can. Ent., **52**: 204-210, 220-223.

An addition to bibliography on *Agrilus* (Coleop.) (with H. B. Weiss). Can. Ent., **52**: 247.

1921

Additions to *Agrilus* bibliography (with H. B. Weiss). Can. Ent., **53**: 72.

1922

A new species of New England Coleoptera *Cantharis (Telephorus) andersoni,* sp. nov. Psyche, **29**: 4-6.

Occurrence of *Agrilus coeruleus* Rossi in America. Can. Ent., **54**: 96.

1923

New species of Buprestidae from the United States (Coleoptera). Can. Ent., **55**: 279-281.

1924

Agrilus viridis in Massachusetts. Bull. Brooklyn Ent. Soc., **19**: 27.

Chrysobothris virdigripennis in Canada. Bull. Brooklyn Ent. Soc., **19**: 34.

Dorytomus frosti Blatchley. Bull. Brooklyn Ent. Soc., **19**: 37.

Parallelina saucia. Bull. Brooklyn Ent. Soc., **19**: 34.

1928

Unusual occurrence of *Gyrinus*. Psyche, **35**: 31-32.
Collecting by the sounding water. Bull. Brooklyn Ent. Soc., **23**: 84-86.
Notes on the Coleoptera of 1925. Bull. Brooklyn Ent. Soc., **23** : 133-136.

1929

The unexpected acid test. Psyche, **36**: 59.
(Note on) *Geotrupes horni* Blanchard. Psyche, **36**: 111.
Note on *Lema palustris* Blatchley. Psyche, **36**: 215.
Anatrichis minuta Dej. Psyche, **36**: 282.
Rare beetle, rarer luck. Bull. Brooklyn Ent. Soc., **24**: 14.
Uncommon Coleoptera. Bull. Brooklyn Ent. Soc., **24**: 34.
An early Cerambycid. Bull. Brooklyn Ent. Soc., **24**: 154.
Rarity vs. secrecy. Bull. Brooklyn Ent. Soc., **24**: 156.
Cicindela tranquebarica horiconensis Leng. Bull. Brooklyn Ent. Soc., **24**: 219.
A synonym. Bull. Brooklyn Ent. Soc., **24** : 249.
Cryptocephalus tinctus Lec. Bull. Brooklyn Ent. Soc., **24**: 294.
Information wanted. Bull. Brooklyn Ent. Soc., **24**: 12.
What attraction? Bull. Brooklyn Ent. Soc., **24**: 11.

1930

Paratenetus crinitus Fall. Psyche, **37**: 176-177.
Cis frosti Drury. Bull. Brooklyn Ent. Soc., **25**: 41.
Ludius fulvipes Bland. Bull. Brooklyn Ent. Soc., **25**: 41.
Addicted to strong-waters. Bull. Brooklyn Ent. Soc., **25**: 46.
Epiphanis cornutus Esch. Bull. Brooklyn Ent. Soc., **25**: 53.
Stenus retrusus Casey. Bull. Brooklyn Ent. Soc., **25**: 53.
Uloma imberbis Lec. Bull. Brooklyn Ent. Soc., **25**: 101.
Orchestes testaceus Mul. Bull. Brooklyn Ent. Soc., **25**: 97.
Anthaxia aeneogaster Cast. Bull. Brooklyn Ent. Soc., **25**: 146.
Seeking a better climate. Bull. Brooklyn Ent. Soc., **25**: 146.

1931

Abstrulia tessellata Melsh. Bull. Brooklyn Ent. Soc., **26**: 6.
Donacia liebecki Schaeffer. Bull. Brooklyn Ent. Soc., **26**: 46.
Ischalia costata Lec. Bull. Brooklyn Ent. Soc., **26**: 35.

1932

Amalus haemorrhous Hbst. in Massachusetts. Bull. Brooklyn Ent. Soc., **27**: 184.
An interesting northern record. Bull. Brooklyn Ent. Soc., **27**: 188.
A touching tale of a quaking quag. Bull. Brooklyn Ent. Soc., **27**: 195.
Cicindela purpurea nigerrima Leng. Bull. Brooklyn Ent. Soc., **27**: 245.

1933

Hister semisculptus Leconte. Bull. Brooklyn Ent. Soc., **28**: 159.
Trotting the bogs with the wise bullfrogs. Bull. Brooklyn Ent. Soc., **28**: 233-234.

1935

Three species of beetles from Labrador. Can. Ent., **67**: 19.

1938

Boreaphilus americanus Notman. Bull. Brooklyn Ent. Soc., **33**: 58.
Silpha americanus Linn. Bull. Brooklyn Ent. Soc., **33**: 70.
Hoplia equina Leconte. Bull. Brooklyn Ent. Soc., **33**: 107.

1939

Occurrence of *Aphodius scrofa* Fabricius in western Maine (Coleop.: Scarabaeidae). Ent. News., 50: 30.

1941

Notes on *Notiophilus*. Bull. Brooklyn Ent. Soc., 36: 127-128.

1945

Notes on Maine Coleoptera for 1945. Psyche, 52: 177.

1946

Dichelonyx canadensis Horn. Psyche, 53: 20-21.
Notes on uncommon Coleoptera. Psyche, 53: 21.
Cicindela formosa generosa Dej. Psyche, 53: 30.
Polydrusus sericeus Schall. Psyche, 53: 51.

1947

Octhephilum fracticorne Payk. Bull. Brooklyn Ent. Soc., 42: 18.
Sphindidae and Cisidae (Coleoptera). Psyche, 54: 180.

1948

Gyrohypnus emmesus Grav. Bull. Brooklyn Ent. Soc., 43: 79.

1949

Tritoma dissimulator Crotch. Psyche, 56: 115.

1950

Chalepus bicolor Oliv. (Coleoptera). Psyche, 57: 92.

A NEW FAMILY OF WASPS[1]

By Howard E. Evans
Museum of Comparative Zoology

The classification of the aculeate Hymenoptera is considerably complicated by the existence of a number of small families of doubtful relationships, families such as the Plumariidae, Rhopalosomatidae, Sierolomorphidae, Sclerogibbidae, and Loboscelidiidae. To add still another family to this list is a dubious distinction, and to base such a family on twelve specimens may be considered a dubious procedure. Nevertheless these twelve specimens present such an unusual array of structural features that they can scarcely be ignored. Although some of these features are clearly specializations, others are so very generalized, for Aculeata, that there can be little question that this family is a relict of a very ancient stock of wasps. These wasps have the habitus of certain Scolioidea, and probably the family should be placed in that superfamily. However, because of the 13-segmented antennae in the female and the lack of closed cells in the hind wings, the family will fall in the Bethyloidea in most classifications. The name of the type genus, *Scolebythus,* is meant to imply a sharing of certain characteristics of both these superfamilies of primitive Aculeata *(scol* being a prefix derived from *Scolia, lebythus* an anagram of *Bethylus).* Further discussion of the relationships of the family is deferred until after the descriptive material. In the description of the family, I have numbered the more significant characters so that these can be referred to more readily later on.

Scolebythidae, new family

Small wasps (known species 7-10 mm. long), fully winged, without strong sculpturing, known from the female sex only. Head vertical, hypognathous (1); head broad below, rather thick, the temples strongly developed. Hypostomal carinae well separated from mouthparts, forming a very broad V, the arms of which reach the ventral condyle of the mandibles (2). Labial palpi short, but with four segments (3). Maxillary palpi with six segments, the segments slightly flattened and bearing some strong setae. Mandibles unusually short and broad, measuring from 1.5 to 2 × as long as broad at the base, the apex with four strong teeth in an oblique series (4). Clypeus

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[1] Published with the aid of a grant from the Museum of Comparative Zoology.

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exceedingly short, extending beyond the antennal sockets by less than the diameter of the latter; median basal portion of clypeus extending triangularly upward between the antennal sockets, nearly reaching the level of the top of the sockets (5). Face depressed laterad of each antennal socket for reception of the scape. Rims of antennal sockets slightly raised on upper side, the sockets opening obliquely downward, not overhung by ridges (6). Antennae with thirteen segments (7); scape much flattened, slightly curved; flagellum simple, covered with short, suberect setulae. Malar space well developed, at least a third as long as width of mandibles at their base. Ocellar triangle at or slightly below level of tops of eyes, vertex rounded off well above ocelli and eye tops; occipital carina present or absent. Pronotum short, with a short dorsal surface and a strong, nearly vertical anterior face, but the collar virtually absent, revealing an open, membranous space between the tops of the propleura (8); posterior lateral lobes of pronotum somewhat rounded, touching the tegulae. Proepisterna very large, produced strongly forward so that the head is well separated from the pronotum (9). Proepimera present at base of front coxae, completely set off by sutures from the proepisterna (10). Prosternum remarkably large (more than half as long along midline as length of front femur), diamond shaped, the entire venter of the prothorax forming a large flat surface with a Y-shaped suture (the suture separating the prosternum from the proepisterna) (11). Front coxae flattened, compressed against the sternum (12). Mesosternal region large and somewhat flattened; mesosternum simple, not produced backward over middle coxae (13). Middle coxae separated by an elevated median ridge of the metasternal region (14), these coxae also slightly flattened. Hind coxae contiguous, their sockets not separated by any sclerotized parts. Mesoscutum with both notauli and parapsidal grooves nearly complete; scutellum at the base with a pair of widely separated, transverse pits. Metanotum a narrow transverse band, sometimes concealed medially by the scutellum. Propodeum with a basal transverse area which is longer on the midline than the metanotum and which is set off from the remainder of the propodeum by a strong suture (15); propodeal disc with the slope low and even, without sculpturing or a strong posterior rim. Mesopleura large and convex, without sculpturing except for a vertical suture passing downward from the posterior lobes of the pronotum, marking off a small epicnemium (16). All femora moderately broadened and compressed; legs completely without spines but bearing some unusually long setae (17). Tibial spurs 1-2-2. Claws slender, simple except subdentate basally (18). Fore wing with a stigma and a closed marginal cell, also with one submarginal cell and one fully closed discoidal cell, the second (lower) discoidal cell being closed below and on the outer side by obsolescent veins (19); outer part of wing membrane devoid of veins and cells (except marginal cell), but having three strong, parallel, unbranched hyaline streaks (20). Hind wing without closed cells, with only two short veins at the base (21); anal lobe distinct, large, fully .3 as long as total length of hind wing (22). Abdomen large, its articulation with the propodeum rather broad; first tergite broad at base, its anterior face strongly concave, fitting against the propodeum (23). No constriction whatever between first and second abdominal segments; first sternite arcuately prolonged backward, overlying the second sternite (24). Apex of abdomen directed upward slightly, distinctly flattened dorsoventrally, the apical sternite in particular rather flat (25). Sting and sting-sheaths strongly developed. (Figs. 1-8).

Key to Genera

Occipital carina well developed; malar space short, less than half as long as width of mandibles at their base; apex of marginal cell on the wing margin; abdomen robust, the fifth sternite simple (Fig. 3) (Madagascar) *Scolebythus* new genus

Occipital carina absent; malar space well over half as long as width of mandibles at their base; apex of marginal cell curving away from wing margin; abdomen slender, the fifth sternite slightly swollen posteriorly, the swelling terminating behind in a polished, triangular area which is flanked by two groups of dense, appressed setae (Fig. 7) (Brazil) *Clystopsenella* Kieffer

Scolebythus new genus

Type and only known species: *S. madecassus* n. sp.

Scolebythus madecassus new species

Plate 2, figs. 1-4

Type: ♀, MADAGASCAR: Mandritsara (Wulsin coll.) (Mus. Comp. Zool., no. 30494).

Description. — Length 7 mm.; fore wing 6.3 mm. Body piceous, shining; legs and antennae wholly dark brown. Wings hyaline, with a faint yellowish tinge, fore wing with a weak apical fuscous band; costa, subcosta, and stigma dark brown, remaining veins amber to yellowish. Entire body covered rather sparsely with golden-brown setae, mostly rather short, but distinctly longer toward the tip of the abdomen and also on the tibiae. Head very slightly wider than high (Fig. 1). Clypeus with a broad but very short median lobe, the margin of which is slightly concave, paralleled by a series of setae. Front slightly alutaceous, with many very small punctures, barely impressed medially. Minimum distance between eyes 1.15 × height of an eye; inner orbits closest near the middle, weakly divergent above, strongly divergent below. Posterior ocelli situated on an imaginary line drawn between eye tops; width of ocellar triangle (including ocelli) 1.15 × ocello-ocular line; distance from posterior ocelli to occipital carina 1.5 × width of ocellar triangle. Basal enclosure of propodeum much longer than metanotum, its posterior margin obtusely angulate; enclosure as well as main part of propodeum with a median groove, especially strong behind. Front femora 2.7 × as long as wide; hind femora longer and somewhat more compressed, but of about the same proportions. Wings as shown in Fig. 2.

Remarks. — This species is known only from the type.

Genus *Clystopsenella* Kieffer

Clystopsenella Kieffer, 1911, Ann. Soc. Sci. Bruxelles, 35: 204.
Kieffer, 1914, Das Tierreich, 41: 555-556.

Type species: *C. longiventris* Kieffer, monobasic.

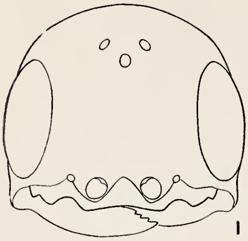
Kieffer included *Clystopsenella* in the subfamily Bethylinae of the Bethylidae, and in fact the wings do bear much resemblance to those of certain genera of that subfamily, especially *Eupsenella.* However, in virtually every respect *Clystopsenella* departs radically in structure from the Bethylinae, in fact from all Bethylidae, as discussed further below.

Clystopsenella longiventris Kieffer
Plate 2, figs. 5-8

Clystopsenella longiventris Kieffer, 1911, op. cit., p. 204 (♀, BRAZIL: St. Paul and Villanova; type and paratype in British Museum).

Description. — Length 7 mm.; fore wing 4 mm. Head testaceous, the vertex with three brownish streaks, one starting at the ocellar triangle and one at the upper end of each eye, all extending backward but not extending over the top of the vertex; mandibles testaceous, the teeth dark; first two antennal segments light brown, rest of antenna dark brown. Thorax wholly testaceous to pale castaneous, slightly darker on anterior face of pronotum, sides of mesoscutum, metanotum, pleura, and venter; legs wholly testaceous; abdomen pale castaneous, each segment with an indistinct paler apical band. Wings hyaline, weakly tinged with brownish along the veins, the veins and stigma brown. Head slightly wider than high. Clypeus with no evidence of a median lobe, but each side with a pair of rounded lobes which extend over the dorsal mandibular condyles (Fig. 5). Front shining, with a linear median impression which does not quite reach the anterior ocellus; punctures of front small, virtually absent above the ocellar triangle. Minimum distance between eyes 1.1 × height of an eye; inner orbits closest at the middle, weakly diverging above and below. Posterior ocelli situated well below an imaginary line drawn between eye tops; width of ocellar triangle 1.1 × ocello-ocular line; distance from posterior ocelli to top of vertex more than 1.5 × width of ocellar triangle. Basal enclosure of propodeum very short except medially, where it is roundly produced backward (Fig. 6); basal enclosure and propodeal disc barely impressed medially. Front femora about twice as long as wide; hind femora much flattened, measuring about 2.2 × as long as wide. Fore wing as figured by Kieffer, 1914, Fig. 195; marginal, submarginal, and first discoidal cell somewhat shorter than in *Scolebythus madecassus*, and the tip of the marginal cell turned away from the wing margin.

Remarks. — This description is drawn from the paratype, which is virtually identical to the type but in somewhat better condition. I have recently seen nine additional females of this species: eight from the Rio Caraguata, Matto Grosso, Brazil, collected by Fritz Plaumann in March, 1953; and one from Nova Teutonia, Santa Catarina, Brazil, taken by the same collector in December 1962 (collections of the Univ. of Kansas and Mus. Comp. Zool.). These specimens vary in size from 7 to 10 mm. (not counting the sting, which extends up to 3 mm. beyond the abdomen), the fore wing from 4 to 6 mm. In this series the body color varies from deep fusco-castaneous to piceous; it is nearly uniformly colored except that the abdomen tends to be slightly paler basally and apically and the less deeply colored specimens show evidence of markings on the vertex similar to those described above; the mandibles and legs are bright testaceous throughout the series. In these darker specimens the golden-brown body setae stand out strongly, particularly the long, rather dense setae on the apical tergite. Despite the darker color, I cannot believe that these specimens represent a different species, as structurally they are nearly identical to the types of *longiventris* (which were collected long ago and may have faded). One notes that in all nine specimens the basal enclosure of the propodeum tends to be subangulate behind rather than rounded as figured; and in three specimens the ocellar triangle is more compact than usual, the ocello-ocular line being subequal to or slightly greater than the width of the ocellar triangle.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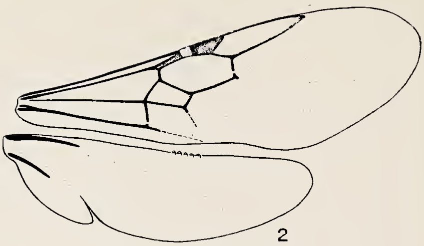
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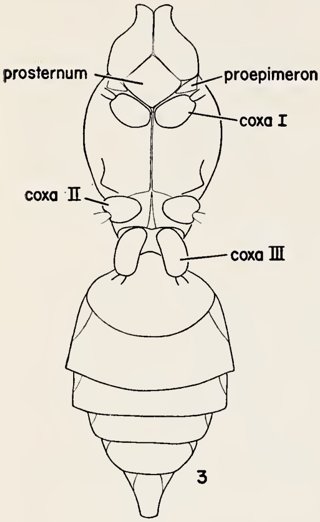

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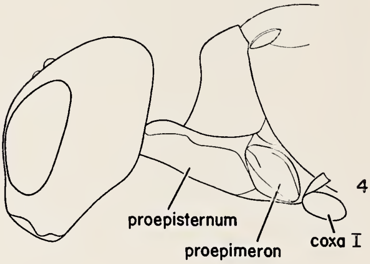

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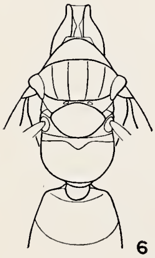
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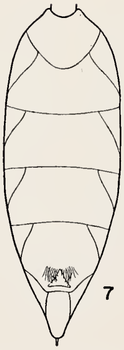
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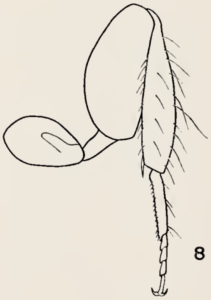
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EVANS — SCOLEBYTHIDAE

POSITION OF THE SCOLEBYTHIDAE

Characters relating them to the Scolioidea. — The superficial habitus of these wasps suggests that of certain of the Tiphiidae, some elements of which are presumed to be close to the ancestral stock of the Aculeata. Particular characters suggesting the tiphiids (more particularly the Anthoboscinae) are the broad, vertical head, the four-segmented labial palpi, the simple antennal orbits, the absence of a pronotal collar, the slightly separated middle coxae and contiguous hind coxae, the broadened and compressed femora and hairy legs, the closed marginal cell and tendency for unbranched streaks on the outer part of the wing membrane, and the broad first tergite. A simple mesosternum is found in the Scolioidea in the family Sapygidae, and the concave first tergite and general conformation of the abdomen also suggest the Sapygidae.

Characters relating them to the Bethylidae. — Antennae with thirteen segments in the female sex are the rule in the Bethylidae, but the antennae are normally 12-segmented in female Scolioidae. The simple mesosternum, slightly separated middle coxae, and contiguous hind coxae are characters which may be taken to relate these wasps to the Bethylidae as well as to certain Scolioidae. The most striking bethylid feature is the hind wing, which is very similar to that of most Bethylidae. The venation of the fore wings is unusual for a bethylid, but in itself would not rule out a relationship to *Eupsenella* and other Bethylinae. Most Bethylidae which have a relatively full venation have a series of complex, branching streaks on the outer part of the membrane.

In general, the resemblances to the Bethylidae are not impressive. The Aculeata were undoubtedly derived from ancestors with multiarticulate antennae, and it is possible that primitive Scolioidea went through a stage in which both sexes had 13-segmented antennae. These are small wasps, and one would expect reductions in wing venation. Many of the smaller scolioids exhibit various reductions in venation, but in no case are the wings as bethylid-like as in the Scolebythidae.

EXPLANATION OF PLATE 2

Figs. 1-4, ***Scolebythus madecassus*** n. sp. Fig. 1, anterior view of head, antennae omitted. Fig. 2, wings. Fig. 3, ventral view of thorax and abdomen, legs beyond coxae and sting and sting-sheaths omitted. Fig. 4, lateral view of head and prothorax.

Figs. 5-8, ***Clystopsenella longiventris*** Kieffer. Fig. 5, clypeus, mandibles, and antennal sockets. Fig. 6, dorsal view of thorax and base of abdomen. Fig. 7, ventral view of abdomen. Fig. 8, lateral view of hind leg.

Figures are drawn to various scales.

Unique and apparently primitive characters. — The prosternum of these wasps is of unusual interest. A large, flat, triangular or diamond-shaped prosternum occurs in a few sawflies (e.g. *Syntexis*) and a few parasitoids (e.g. *Spilochalcis*), but virtually all Aculeata have the prosternum much reduced and somewhat sunken, or even practically absent. The Sapygidae have a somewhat larger and less sunken prosternum than most Aculeata, but even here the resemblance to the Scolebythidae is not great. The free proepimeron is also most unusual. I find no evidence of this structure in most Aculeata examined, but in the Plumariidae the proepimeron is fairly well developed, although not quite so completely set off as in the Scolebythidae. The large first sternite of the abdomen, which extends arcuately backward and broadly overlaps the second sternite, is also unusual, as in most primitive Aculeata the first sternite is short and there is at least some evidence of the beginnings of a constriction at this point: this is true in such groups as the Anthoboscinae, the Sapygidae, and the Bethylidae. However, in the Plumariidae the condition is almost exactly the same as in the Scolebythidae.

Unique and apparently specialized characters. — Here I would include the broad mouth opening and powerful mandibles, the reduced clypeus, and the strong malar space; on the thorax the elongate proepisterna, perhaps the large prosternum, and the flattened coxae. These characters together surely make up a single adaptive complex, and give the anterior part of these insects a striking resemblance to that of certain parasitoids which attack wood borers (most particularly the Aulacidae). I feel there can be little question that the Scolebythidae attack wood-boring larvae, probably of beetles (since most Scolioidae and many Bethylidae attack beetle larvae). Probably they enter the burrows of the beetles to find their hosts. After I had come to these conclusions I sent specimens to Dr. J. G. Betrem for examination, and he expressed exactly the same opinion.

Summary of characteristics. — Of the 25 characters numbered in my diagnosis of the family on an earlier page, the following are primitive aculeate characters not necessarily relating these wasps to any other aculeate group: 3, 13, 14, 17, 18, 22. The following characters appear especially primitive and unlike other Aculeata: 10, 11, 15, 24 (but the Plumariidae possess 15 and 24, and 10 in some measure). The following are bethylid characters: 7, 19, 21 (but see discussion above). The following specializations make up an adaptive complex appearing to fit these wasps as parasites of wood-boring beetle larvae: 2, 4, 8, 9, 12, perhaps also 11. The remaining characters are shared with certain of the primitive Scolioidae such as the Anthoboscinae and Sapygidae: 1, 5, 6, 16, 20, 23, 25. Because of the preponderance of scolioid and primitive aculeate characters, I feel that this family unquestionably belongs in the Scolioidea. However, in artificial keys stressing wing venation and antennal segmentation, it may be desirable to key the family out with the Bethylidae.

Are the scolebythids female plumariids? Within the Scolioidea, the Scolebythidae appear to represent an isolated group; no less than 10 of the 25 characters considered are discussed above as in some measure "unique and apparently primitive" or "unique and apparently specialized". Yet several of these unusual features are shared, at least to some extent, with the Plumariidae. Since the Plumariidae are known from males only, and from South America and South Africa only, it is necessary to ask if the scolebythids may be female plumariids. I concede this possibility, but I think it unlikely for the following reasons. (1) The plumariids have closed cells in the hind wing, and the venation of the fore wing bears little resemblance to that of the scolebythids. (2) The prosternum of the plumariids is small and sunken. (3) The middle coxae of the plumariids are subcontiguous, and the legs very much longer than in the scolebythids. (4) There is little resemblance in the general configuration of the head and thorax, except in the several characters cited in the preceding paragraph. (5) *Plumarius* occurs chiefly in arid regions of Chile, Argentina, and Peru, and is surely not common, if it occurs at all, in Brazil. I am not aware that *Myrmecopterina,* the South African and only other known genus, has been found in Madagascar.

It may be argued that in several groups of Tiphiidae (most particularly the Methochinae and Brachycistidinae) the sexual dimorphism is nearly as great. It is greater, in fact, with respect to the wings, which are absent in the females of these tiphiids; in the scolebythids the wings of the female may merely have undergone much reduction in venation without much loss of size. The various apparent specializations of these wasps for attacking wood-borers might, of course, have evolved in the female sex only, just as only the female Brachycistidinae have become modified for living underground. However, at this stage of our knowledge it seems to me wiser to consider the scolebythids a distinct family than to place *Clystopsenella* in the synonymy of *Plumarius* and to consider the Madagascar specimen a female *Myrmecopterina,* an assignment that may prove to be very wide of the mark. The erection of a new family may serve as a challenge to workers to seek more data on these insects.

ACKNOWLEDGEMENTS

I have showed specimens of these wasps to several eminent hymenopterists and solicited comments from them. All of their suggestions have been considered carefully, and several have been incorporated into the above discussion. All agreed that these wasps are not bethylids, and the majority agreed that the erection of a new family was justified. These men were J. G. Betrem, J. C. Bradley, C. Jacot-Guillarmod, K. V. Krombein, C. F. W. Muesebeck, and O. W. Richards. I wish to express my thanks to all of these men.

Examination of the types of *Clystopsenella longiventris* Kieffer at the British Museum was made possible by a grant from the Permanent Science Fund of the American Academy of Arts and Sciences.

A NEW SPECIES OF *LIGYROCORIS* STAL WITH A KEY TO THE NORTHEASTERN SPECIES (HEMIPTERA: LYGAEIDAE)

By Merrill H. Sweet[1]
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In the course of current work upon the biology and ecology of the Rhyparochrominae of New England, a new species of *Ligyrocoris* was discovered. The species runs in Barber's (1921) key to the couplet separating *diffusus* (Uhler) from *sylvestris* (L.), but is distinct from either species. While the new species is closely related to these species, it is also quite close to *L. depictus* which is separated out in a different part of Barber's key.

These four closely related species are sympatric in New England, although they are markedly different in their overall distribution. The habitat preferences and life cycles of the species are quite different (Sweet, unpublished). The habitat of the new species described below is most unusual for the genus. The greater part of the type series was collected along the margin of a small pond where sedge clumps were standing in the water among occasional exposed rocks rather than in relatively dry fields or slope habitats where the other species occur. The species feeds upon the seeds of the sedge, *Carex stricta* Lam., and its life cycle is apparently adapted to that of the sedge, which fruits in late May and June. The insect becomes adult in mid-June and lays eggs until mid-July. The eggs remain in diapause over the summer and winter and hatch in May.

Ligyrocoris caricis n. sp.

Male: general body coloration black; posterior lobe of pronotum fuscous, becoming pale on humeral angles; connexivum and trichobothrial spots fuscous; acetabula, posterior margin of metapleuron and apex of scutellum pale; hemelytra patterned pale and brown; lateral margin of corium pale except for fuscous apex; at least apical half of clavus and corium brown, becoming dark at inner angle of corium; post median brown area (fascia) extending toward but not reaching lateral margin of corium; pale spots behind inner corial angles faint or absent; membrane infuscated with base, apex and veins pale; legs mostly flavescent; coxae, terminal tarsal segment, and ring on base of hind tibia fuscous; fore femora and apical portion of

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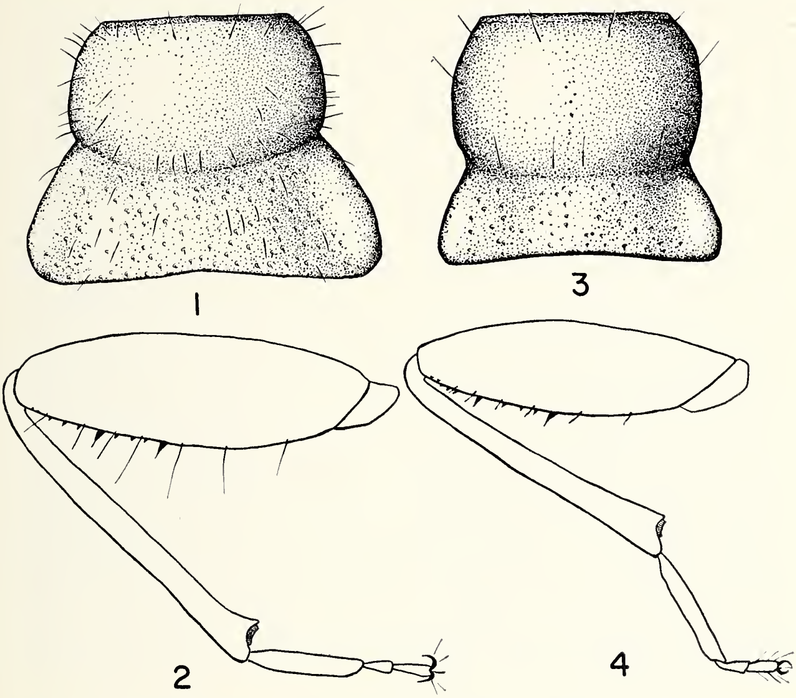
hind femora light brown; antennal segments one, two, and basal two-thirds of three flavescent, remainder fuscous; apex of tylus and entire labium brown, except fuscous apex of fourth labial segment; entire body clothed with fine, adpressed, shining hairs, densely so on head and abdomen, sparsely on hemelytra and thorax, pronotum nearly nude; long erect setae present on hemelytra and thorax, pronotum nearly nude; long erect setae present on entire dorsum, but with very few (ca. 10) on pronotum; head trichobothria one-third longer than other head setae; a few finer secondary head setae present behind eyes and ocelli and along meson; appendages with short fine semi-erect pale hairs. Head very finely punctate except on lorum and apex of tylus; hemelytra and entire thorax very finely granulose, dull; anterior lobe of pronotum, scutellum, thoracic pleura and sterna with fine sparse punctures; posterior thoracic lobe with scattered but definite punctures; hemelytra with three rows of punctures on clavus, two on corium along claval suture, and one lateral to radial vein, the rows becoming suffused posteriorly. Body small and slender for genus; *head* narrowed behind eyes, porrect; antennal segment one barely exceeding tylus; ocelli small, remote (.14 mm.) from eyes; eyes oval, not especially produced; postocular distance smaller than anteocular distance to apex of antenniferous tubercules; length of head .75 mm., width across eyes .96 mm., interocular distance .59 mm.; *pronotal* lobes distinctly but not incisively separated by transverse constriction (fig. 3); pronotal collar weakly differentiated from pronotum; anterior lobe rounded laterally and dorsally, and high and convex in profile; hind lobe with slightly raised and obtusely rounded lateral margins, hind margin slightly concave; pronotum length .96 mm., anterior lobe .63 mm., width across posterior lobe 1.11 mm., across anterior lobe .90 mm.; *scutellum* with weak posterior carina crossed by fine transverse grooves; length .77 mm., width .55 mm.; brachyterous, hemelytra narrow, membrane reaching tergum 7; lateral margin slightly sinuate at level of tip of scutellum; length of commissure .37 mm.; distance apex of clavus-apex corium .78 mm., apex corium-apex abdomen .74 mm.; hind wing three-fourths length of hemelytra; scent gland peritreme slightly raised, rounded, the coarsely granulose evaporatorium covering lower two fifths of metapleuron; parameres slender, pointed; posterior portion of pygophore slightly excavate; aedeagus similar to *L. sylvestris* (L.) (Ashlock 1957); abdomen with stridulatrum (stigose vittae) gently arching from sternum 2 to posterior margin of 4; plectrum on hind femora consisting of a field of 20 small tubercules; fore femora moderately incrassate, armed beneath with an inner distal row of spines consisting of two large spines each followed distad by three small spines, the outer row with two weak apical spines; length fore femora 1.18 mm.; length of hind tarsal segments I .63 mm., II and III .31 mm.; meso- and meta-tibia with three inner rows of spines; labium not exceeding mesocoxae, length of segments I .56 mm., II .59 mm., III .48 mm., IV .37 mm.; antennae relatively long, length of segments I .56 mm., II .94 mm., III .85 mm., IV 1.07 mm. Total length 4.81 mm.



Figs. 1-4. *Ligyrocoris.* 1, pronotum of *L. diffusus* (Uhler); 2, fore femora of *L. diffusus* (Uhler); 3, pronotum of *L. caricis* n. sp.; 4, fore femora of *L. caricis* n. sp.

Holotype: Male. Storrs, *Connecticut* (Pink Ravine) June 27, 1960 (M. Sweet). In United States National Museum. Type No. 66324.

Paratypes: Same locality as holotype. 9 males, 5 females, 3 nymphs. June 25, 27, July 11, 1960; June 27, 28, 1961. 2 females, 3 nymphs. Mt. Desert Island, *Maine* (Great Heath) July 8, 1955 (F. B. Shaw). In United States National Museum, Museum Comparative Zoology (Harvard), California Academy of Sciences, British Museum (Nat. Hist.), University of Connecticut, J. A. Slater, P. D. Ashlock, and author's collections.

From the other species of *Ligyrocoris sensu stricto, L. caricis* is readily distinguished by its relatively small size and narrow form. Like *diffusus, caricis* has an incomplete fuscous fascia on the hemelytra, smaller size, and the hind basal metatarsal segment only twice the length of the distal two combined. However, *caricis* appears to be more closely related to the larger species *depictus* and *sylvestris* for it shares with them a relatively narrow pronotum with very few erect setae, fore femora with short setae or none, a labium which only attains the mesocoxae, relatively long antennae, a similar pattern of spines on the aedeagal conjunctiva, and a brachypterous condition. *L. slossoni* Barb. differs in having a labium which attains the third abdominal segment and a complete fascia on the hemelytra.

It should be noted here that the fascia which Barber (1921) used as a major character to separate species is quite variable, and specimens of *depictus* will go to both sides of Barber's key on this character. Actually *depictus* is very closely related to *L. sylvestris* rather than to the very different *L. litigiosus* Barb. and other species which lack the fascia.

As all the species mentioned above are closely related, it is fortunate that the species concepts could be verified by mating experiments. In all four species, *caricis, diffusus, sylvestris,* and *depictus,* the males display a courtship "dance." When a female was approached by a male of a different species, she became extremely excited, and actively avoided the strange male so that cross-mating does not occur. This behavior is entirely different from the normal "reluctant response" of a female to a male of the same species. These behavior patterns will be discussed in detail in a later contribution.

Key to the Species of *Ligyrocoris* of the Northeastern United States

1. Pronotum with many (ca. 25 or more) erect setae (Fig. 1); fore femora with outer row of setae present and longer than basal width of fore tibiae (Fig. 2); labium reaching between hind coxae; labial segments II and III subequal (.70:.67 mm.); nearly always macropterous with membrane of hemelytra reaching beyond tergum 7 .... *diffusus* (Uhler)

Pronotum with few (ca. 10) erect setae (Fig. 3); fore femora without an outer row of short setae, if present (Fig. 4), length always less than basal width of fore tibiae; labium not reaching between metacoxae, usually just attaining mesocoxae; labial segment III shorter than II, often subequal to I (at most, II .81 mm., III .70 mm.); always brachypterous, membrane of hemelytra rarely reaching beyond tergum 7 2

2. Basal hind tarsal segment only twice combined length of distal segments (.67:.33 mm.); size small (length, 4.77 to 5.18 mm.); post median transverse fascia on corium not attaining lateral margin of corium; metapleura never inflated, invisible from above .... *caricis* n. sp.
   Basal hind tarsal segment nearly three times combined length of distal segments (.92:.34 mm.); size larger (5.16 to 7.47 mm.); post-median transverse fascia either present or nearly absent, but if evidently present then attaining corial margin; metapleura in male frequently inflated and visible from above 3
3. Post-median transverse fascia fuscous and broadly attaining lateral margin of corium; labial segment III longer than I (.70:.63 mm.); pale spot at mesal angle of corium faint or absent; basal and apical pale spots on membrane never confluent; fore femora usually fuscous .... *sylvestris* (Linnaeus)
   Post-median transverse fascia weak, ferrugineous, often absent; labial segment III shorter than I (.57:.67 mm.); pale spots at mesal angle of corium distinct; basal and apical pale spots on membrane usually confluent, fore femora usually light yellow brown .... *depictus* Barber

The above key does not include *L. obscurus, L. litigiosus, L. abdominalis, L. multispinus,* and *L. slossoni* which have a more southern distribution and are adequately separated in Barber's original keys, or Torre-Bueno's (1946) adaptation of it. As discussed by Ashlock (1957) the aedeagal spines will prove very useful in establishing group relationships in this genus, but they are of little value in distinguishing the species included in the above key.

ACKNOWLEDGEMENTS

I wish to express my grateful thanks to Dr. R. C. Froeschner (United States National Museum) for a loan of specimens and to Dr. James A. Slater (University of Connecticut) for allowing me to use his extensive collection and for critically reading the manuscript.

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AUSTRALIAN CARABID BEETLES XII. MORE *TACHYS*[1]

By P. J. Darlington, Jr.
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This is, in effect, a continuation of Part XI (Darlington 1962) of my series of short papers on Australian Carabidae. The present part deals with some additional groups of *Tachys*.

Tachys australis group

This is a group of small, rather convex, usually rufous (sometimes blackish), shining species, with 5 or more punctate dorsal striae on each elytron. Previously known species of the group are those named in couplets 47 through 57 in Sloane's key (1921, 199) to Australian *Tachys*, plus *Tachys yarrensis* Blackburn, which (I think) Sloane placed incorrectly.

Technical characters of the *australis* group (partly derived from Sloane's key, 1921, pp. 197-199) include upper surface not punctulate (except head in *pubifrons*); mentum 2-foveate at base; prothorax usually cordate, sometimes transverse (but if so, not notably wide across base); prothoracic angles without submarginal carinae; elytral margins behind humeri serrate and setulose (differently so in different species); 8th stria nearly entire or abbreviated anteriorly, formed anteriorly by a row of punctures, not bowed away from margin; elytron with 2 dorsal punctures; apical striole well developed, ending anteriorly about midway between suture and margin, with a strong puncture on its inner side behind middle of its length. Inner wings fully developed in most species but apparently dimorphic in *semistriatus* and reduced (or perhaps dimorphic) in *olliffi;* ♂ with 1 segment each front tarsus slightly dilated, slightly squamulose below; and ♂ with 1, ♀ 2 setae each side last ventral segment (♂♂ examined of all species except *yarrensis* and *olliffi,* of which my specimens are all ♀♀).

This group occurs throughout all or most of Australia including Tasmania, but is commonest in eastern and southeastern Australia. The members of the group live in damp or wet places, but I am not sure of the ecological limits of all the species. I have personally collected all of them except *olliffi,* but some of them were taken in flood debris so that I do not know their precise habitats. The group is not known to reach New Guinea (I have just completed what amounts

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to a revision of New Guinean *Tachys*) and seems to have no close relatives there or in the Orient. Some Oriental species are superficially similar, but quite different in technical characters: *e.g. Tachys ceylanicus* (Niet.) has a superficial resemblance to *australis* etc. but has the mentum without foveae, differently formed 8th striae, and 2 segments of the ♂ front tarsus widened and with squamules.

Although Sloane's key to the species of this group will separate them satisfactorily if used with care, he overlooked some striking and decisive characters that I shall use in the following key, which includes two new species.

Key to species of *Tachys australis* group

1. Elytra fully striate .... *yarrensis*
- Elytra not fully striate 2

2. Upper surface of head (but not rest of upper surface) extensively pubescent .... *pubifrons*
- Head not pubescent, except for usual fixed setae 3

3. Prothorax with extra marginal setae .... *seticollis*
- Prothorax with only usual 2 setae each side 4

4. Elytral margins fringed with long setae .... *punctipennis*
- Elytral margins with normal, short setae 5

5. Prothorax with lateral margins obsolete .... *semistriatus*
- Prothorax with lateral margins distinct 6

6. Prothorax rather wide (W/L 1.40 or more), sides not or scarcely sinuate posteriorly .... *bogani*
- Prothorax narrower, with sides sinuate posteriorly 7

7. Prothorax with sides long-sinuate (sinuation beginning well before base); color brown; very widely distributed in Australia .... *australis*
- Prothorax with sides short-sinuate; color usually blackish 8

8. Elytron 6-striate; wings fully developed; southwestern Australia .... *habitans*
- Elytron 5-striate; wings reduced; southeastern Australia .... *olliffi*

Tachys yarrensis Blackburn

Blackburn 1892, 20.
Sloane 1896, 357, 366.
——— 1921, 199.

Blackburn described this *Tachys* from Upper Yarra (River), (east of Melbourne), Victoria. Sloane (1896) records it from Mulwala, Urana, and Tamworth, New South Wales, "under logs and debris in very damp situations". I found 4 specimens in flood debris at Sale, southern Victoria, Oct. 1, 1957.

Blackburn and Sloane (1921) thought that this species lacked an apical striole, but I think the striole is present but incorporated in the striation. The apex of the 3rd stria is deeply impressed for a short distance, arcuate, and with a puncture beside it on the inner side as in other species of the *australis* group, with which *yarrensis* agrees in most significant characters.

Tachys pubifrons n. sp.

With characters of *australis* group as given above. A rather slender member of group; reddish testaceous; shining, without (or nearly without) reticulate microsculpture above but head punctulate and setulose as described below. *Head* .77 & .78 width prothorax; eyes moderate in size and prominence; antennae with segments 2 & 3 subequal, middle segments about 1½× long as wide; whole front depressed from behind level of eyes to clypeal suture, the depression including the frontal foveae, which are not individually distinct, and which do not extend to clypeus; front also irregularly punctulate and pubescent; mentum conspicuously 2-foveate at base. *Prothorax* cordate, width/length 1.36 & 1.33; base/apex .99 & .97; base/head .87 & .88; sides rounded anteriorily, strongly converging posteriorly, sinuate well before angles and then subparallel to angles (the sinuations occur about 1/7 of prothoracic length before angles); lateral margins poorly defined or partly obsolete; apex subtruncate with anterior angles rounded; base at most slightly and broadly lobed, slightly sinuate toward sides; basal angles sharply defined, approximately right; disc with anterior transverse impression and middle line vague, basal transverse sulcus moderately impressed but interrupted at middle, coarsely punctate. *Elytra* with humeri rounded but prominent; margins behind humeri finely serrate and setulose; each elytron 6-striate, with sutural stria entire, punctate anteriorly and groove-like posteriorly, and other striae formed of abbreviated rows of coarse punctures; stria 8 well impressed posteriorly, represented by a few punctures near middle, obsolete anteriorly; apical striole moderate, somewhat curved, ending about midway between suture and outer margin, with a coarse puncture on inner side well behind middle of its length; 3rd interval with 2 fixed punctures slightly before 1/3 and 2/3 of elytral length. Inner wings fully developed. Secondary sexual characters as given for group. Measurements: length *c.* 2.5 or slightly more; width *c.* 1.0 mm.

Holotype ♂ (M. C. Z. Type No. 30330) and 7 paratypes all from Termeil, southern New South Wales, October 1957, taken by myself. They were found under circumstances described under *Tachys lutus* (Darlington 1962, p. 120).

The outstanding structural character of this species is the modification of the front of the head, which is unique, so far as I know. It is nearly uniform in all 8 specimens, which include both sexes.

Tachys seticollis Sloane

Sloane 1896, 358, 366.
—— 1921, 199.

The type locality is King's Sound, North West Australia. My 4 specimens are from widely separated localities: Bogan River (S. of Nyngan) in interior New South Wales, and near Cardwell and near Cairns in eastern tropical North Queensland. They were taken in wet places but not by freely running water.

Tachys punctipennis (Macleay)

Macleay 1871, 116 *(Bembidium)*.
Sloane 1896, 366.

Sloane (1896) treats this as a synonym of *monochrous* (= *australis, v.i.*), but I think he probably misidentified *monochrous,* which is probably an earlier name for *flindersi.* I tentatively apply the name *punctipennis* to the present species (briefly characterized in the preceding key) because Macleay's superficial description seems to fit it and because it seems to be the commonest species of the group in South Queensland. I do not have it from the exact type locality, which is Gayndah, but I do have 28 specimens from other South Queensland localities including Brisbane and Jimna, and I have an additional series from the Richmond River near Wiangaree, northern New South Wales. I have also single specimens from 4 localities farther south in New South Wales, the 2 southernmost being Braidwood and Clyde Mt., 130 or 140 miles south of Sydney.

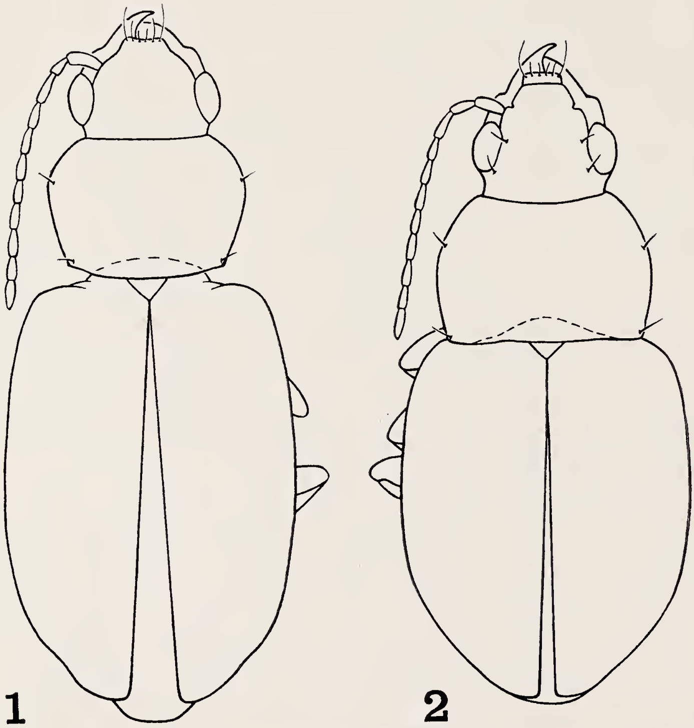
The outstanding recognition character of this species is the fringe of long setae on the elytral margins, combined with absence of extra setae on the prothoracic margins, but certain other characteristics of the species are noteworthy too. The lateral margins of the prothorax are partly obliterated in all specimens, being weak or obsolete behind the anterior marginal setae although more distinct in front of them. The inner wings are fairly long and more or less folded at tip, and in some individuals look fit for flight, but in other individuals the wings look so weak that I think they are probably flightless.

Tachys semistriatus Blackburn

Blackburn 1888, 41.
Sloane 1896, 358.
—— 1920, 151.
—— 1921, 199.

Blackburn originally found this species in several places in swampy ground near Port Lincoln, South Australia. I collected it along the lower Murray River between Murray Bridge and Meningie, South Australia; in southern Victoria (between Portland and Port Fairy; near the lower Gellibrand River; and near Winchelsea); and in southern New South Wales (Bodalla, in flood debris). Sloane (1920) records it from several localities in Tasmania.

Blackburn described the species as piceous, the elytra with a large obscure reddish mark on disc a little behind middle. Most of my specimens answer this description, except that the ground color is dark reddish rather than piceous. In some specimens the elytra have an actual pale area as described. In others, careful examination shows that the elytra are almost uniformly colored but translucent, and in these specimens the paler areas are not spots on the elytra but the pale tips of the inner wings seen through the elytra. The wings of this



Figs. 1-2. *Tachys*. 1, *T. bogani* new species; 2, *T. trunci* new species.

species are apparently dimorphic. In most specimens the wings are slightly reduced, not folded or only slightly folded or crumpled at tip, and evidently unfit for flight. However my 4 specimens from between Murray Bridge and Meningie and 1 from Winchelsea possess large, complexly folded, probably usable inner wings.

Tachys bogani n. sp.

With characters of *australis* group as given above. Form as figured (Fig. 1), slightly broader and more compact than usual in group; color reddish testaceous; shining, microsculpture absent above or nearly so. *Head* short, .79 & .76 width prothorax; eyes moderately large and prominent; antennae with segments 2 & 3 subequal, middle segments about 2× long as wide; frontal foveae sublinear, converging anteriorly, extending onto clypeus, partly and vaguely duplicated anteriorly by slight grooves outside the main sulci; mentum conspicuously bifoveate at base. *Prothorax* broad; width/length 1.41 & 1.40; base/apex *c.* 1.19 & 1.21; base/head 1.03 & 1.03; sides rounded anteriorly, nearly straight and rather strongly converging posteriorly, then slightly and briefly sinuate before basal angles; apex truncate, anterior angles rounded; base broadly lobed, slightly sinuate and then oblique toward sides; posterior angles well defined but obtuse; disc with anterior transverse impression and middle line almost obsolete; basal transverse sulcus sharply impressed but interrupted at middle, not punctate. *Elytra* with humeri prominent but rounded; width elytra/width prothorax 1.44 & 1.38; margins behind humeri slightly serrate and setulose; elytron 6-striate, with sutural stria entire, punctate anteriorly and groove-like posteriorly, and other striae formed by abbreviated rows of rather coarse punctures; stria 8 well impressed posteriorly, obsolete anteriorly; apical striole rather short, slightly curved, not quite parallel to sutural stria, with a strong puncture on inner side behind middle of its length; 3rd interval with 2 dorsal punctures before 1/3 and 2/3 of elytral length. Inner wings fully developed. Secondary sexual characters as described for group. Measurements: length *c.* 2.3; width *c.* 0.95 mm.

Holotype ♂ (M. C. Z. Type No. 30331) and 1 ♀ paratype both from Bogan River, south of Nyngan, New South Wales, October 1957, taken by myself probably by washing wet sand or debris beside pools in the bed of the Bogan River, which was not flowing at the time.

This species is distinguished from all others of the group by the virtually straight (scarcely sinuate) but converging sides of prothorax posteriorly.

Tachys australis Schaum

Schaum 1863, 90.
monochrous Schaum 1863, 90.
Sloane 1896, 357, 366.
—— 1921, 199.
flindersi Blackburn 1888, 41 (new synonymy).
Sloane 1896, 358, 368.
—— 1921, 199.
tersatus Broun 1893, 1110 *(Bembidium)* (new synonymy).

Schaum described this species under the heading *Tachys australis,* then on the same page erroneously used the name *monochrous* for it in the description. The two names are therefore absolute synonyms and the one used first, *australis,* should be recognized, as is done in the *Junk-Schenkling Catalogue.* Schaum's original specimen(s) were from Victoria, collected by Bakewell. I tentatively take as representing the species (but I do *not* mean to designate any kind of type or type locality) 3 specimens from Ferntree Gully, about 20 miles east of Melbourne, Victoria, collected Dec. 15, 1950, by W. L. Brown. Schaum's description calls for each elytron to have 6 dorsal striae formed by rows of punctures abbreviated apically. Revisers usually separate 6-striate and 5-striate individuals in this group of *Tachys* as different species, but the very short series from Ferntree Gully is by itself enough to show that this character is inconstant. Of the 3 Ferntree Gully individuals, one has the 6th stria represented by 4 punctures on the left elytron and 2 on the right; one, by one puncture on each side; and one, by no punctures on either side — that is, the last specimen is strictly 5-striate. Similar variation occurs in this species from some other localities. Failure of this character is one of the things that has persuaded me that *flindersi* (supposedly 5-striate) is synonymous with *australis* (supposedly 6-striate). Additional indications are that Schaum's and Blackburn's descriptions seem to fit this species and that the species is common and widely distributed and therefore likely to fall into the hands of early collectors. *"Bembidium" tersatum* Broun, of which I have 2 (♀♀) specimens from New Zealand received from A. E. Brookes and answering the original description, agrees with the present species in general appearance as well as technical characters. The inner wings are large and folded in this species and look fit for flight.

Blackburn collected his specimens (types of *flindersi*) near Port Lincoln and Adelaide, South Australia, on swampy ground and on the bank of the Torrens River. I have specimens from 22 localities, ranging from the middle part of the Cape York Peninsula (Iron

Range and Coen) south to Victoria (Ferntree Gully) and Tasmania (Arve River) and west through South Australia (several localities) to Western Australia (Wiluna). Sloane (1896, 368) records the species *("flindersi")* over an almost equally wide area including Central Australia. The presence of this species in New Zealand may be the result of introduction by man. It occurs under cover by standing or running water or in other wet places.

Tachys habitans Sloane

Sloane 1896, 358, 368.
—— 1921, 199.

This is apparently a common species in southwestern Australia. Sloane's original specimens came from the Darling Ranges, Bridgetown, and Pinjarra. I took a series in the general vicinity of Perth and southward, at Mundaring Weir, Rottnest Island, Margaret River, Bridgetown, and Pemberton. My 33 specimens are all fully winged.

Tachys olliffi Sloane

Sloane 1896, 376.
—— 1921, 199.

This may be the southeastern representative of the southwestern *habitans*. Sloane described it from Forest Reefs (which he says elsewhere is in the district of Orange), New South Wales. I have one specimen from Vermont, at Dandenong Creek, east of Melbourne, Victoria, collected September 16, 1951, by W. L. Brown, and one from Mt. Lofty, South Australia, collected in October, 1921, by F. E. Wilson. Both these specimens have more or less reduced wings and are evidently flightless, but the species may turn out to be dimorphic.

Tachys convexus and allied species

Tachys convexus Macleay is a convex, 4-maculate, 1-striate *Tachys*, with the basal sulcus of the pronotum 3-foveate at middle. It is characterized also in Sloane's key (1921) by stria 8 of elytron deeply impressed, with interval 9 convex; 2 fixed punctures on disc of elytron at position of third interval; apical striole present, with a fixed puncture on its inner side well back; prothorax with a transverse basal impression; humeri not specially modified; frontal sulci short; and (especially) posterior prothoracic angles reduced to small but prominent tubercles. Sloane (1921, 202-203), gives references and synonymy of the species. It is common and widely distributed especially in tropical Australia, living in damp, shady places by water. I have more than 100 specimens from eastern Queensland, from Cape York south to Brisbane, and it occurs also at Darwin and as far south as the Blue Mountains in New South Wales. It is not known to extend to New Guinea and has no close relatives there. Nevertheless an apparently distinct, related species occurs in a very small area near the tip of Cape York.

Tachys convexulus n. sp.

Form nearly as in *convexus* and with most characters of that species; convex, prothorax strongly narrowed behind and with dentiform subbasal posterior angles, and elytra broad and convex; color dark reddish, elytra 4-maculate (each with a posthumeral and subapical testaceous spot not very well defined), appendages testaceous; shining, without dorsal microsculpture or nearly so. *Head* .78 & .77 width prothorax; eyes large and prominent; antennae rather short, segment 3 slightly longer than segment 2, middle segments less than 2 × long as wide; frontal foveae short, not sharply defined; mentum not foveate at base, with simple tooth at middle. *Prothorax* rounded-cordate; width/length 1.21 & 1.20; strongly narrowed behind; base/apex .96 & 1.02; base/head .86 & .88 (base measured across subbasal tubercles); sides strongly rounded anteriorly, nearly straight and strongly converging posteriorly but interrupted by small right or acute tubercles of subbasal angles; apex truncate with anterior angles rounded; base subtruncate; lateral margins narrow, each with usual 2 setae about 1/3 from apex and on subbasal angles; disc very convex, with anterior transverse impression obsolete, middle line fine; transverse basal sulcus fine, *without conspicuous foveae at middle,* finely punculate. *Elytra* wide and convex (E/P 1.39 & 1.40), widest not far behind humeri; humeri prominent but rounded; margins ending inwardly about middle of elytral width, slightly sinuate behind humeri but not serrate or setulose; sutural stria entire except light or abbreviated anteriorly, other dorsal striae lacking; stria 8 deep, entire, bowed away from margin at and before middle; apical striole as described for *convexus;* dorsal punctures before 1/4 and not far behind 1/2 of elytral length. Inner wings fully developed. Male tarsi not visibly modified; ♂ with 1, ♀ 2 setae apex last ventral segment. Length 2.1-2.4; width 0.8-0.9 mm.

Holotype ♂ (M. C. Z. Type No. 30334) and 10 paratypes all from Bamaga, near the northern tip of Cape York, January 1958, taken by myself. They were, I think, washed from debris beside sluggish streams in shady places.

This species is smaller than *convexus* and slightly narrower but structurally similar except for the basal sulcus of the pronotum, which is conspicuously foveate in *convexus,* finely punctulate in *convexulus.* The two species are, I think, closely related but apparently distinct. The present new species seems to occur only in a very limited area, near but not quite on the tip of the Cape York Peninsula. It is within the range of *convexus,* which occurs at Lockerbie still farther north, almost on the actual tip of the Cape, but which I did not find at Bamaga. Only careful collecting, with detailed ecological notes, can show the relationships of these species to each other in nature. Two obvious possibilities are that *convexulus* may be a new species originating within the range of *convexus,* or that it may be an old species on the point of extinction.

Tachys, group unknown

Tachys trunci n. sp.

Form as figured (Fig. 2), oval, convex, compact; dark reddish piceous, each elytron with a partial transverse-oblique pale fascia about 3/5 from base, said fascia reaching neither margin nor suture, the inner end being further forward than the outer; appendages pale, maxillary palpi and outer part of antennae browner; very shining, without or almost without dorsal microsculpture (reticulations faintly indicated on front of head). *Head* .65 width prothorax; eyes moderate in size and prominence; antennae moderate, segments 2 and 3 subequal, middle segments less than 2× long as wide; frontal sulci linear, slightly diverging posteriorly, not crossing clypeus; mentum with two rather small foveae but not perforated, with median tooth. *Prothorax* transverse, strongly narrowed in front, slightly so behind; width/length 1.53; base/apex 1.43; base/head 1.39; sides broadly arcuate through most of length, slightly but broadly sinuate before base; apex subtruncate with anterior angles narrowly rounded; base somewhat sinuously subtruncate; basal angles well defined, approximately right, strongly carinate, the carinae curving inward anteriorly; side margins narrow, a little wider posteriorly, each with usual 2 setae about 2/5 from apex and near basal angle; disc very convex, *anterior transverse impression linear, deeply impressed, entire* (unusual in *Tachys*), middle line lightly impressed, not reaching base, basal transverse sulcus linear, faintly and finely punctulate, but interrupted and with a conspicuous fovea at middle. *Elytra* rather broadly oval; E/P 1.28; lateral margins apparently ending at or just inside of humeri (this detail not clearly visible without manipulating the single specimen, which I am unwilling to do); margin behind humeri vaguely (hardly distinctly) subserrate and setulose; stria 1 (sutural) deeply impressed and entire, very deep and curving outward at base; other discal striae almost absent, inner ones very faintly indicated in good light, but abbreviated at both ends, stria 8 rather lightly impressed, parallel to margin, subinterrupted or punctate anteriorly; apical striole rather short, nearer margin than usual, but turning inward near anterior end, with a seta-bearing puncture on its inner side well back; two dorsal punctures on position of 3rd interval near or slightly before 1/3 and 2/3 of elytral length. Inner wings probably fully developed but not examined. Lower surface essentially impunctate, not pubescent; prosternum impressed; mesosternal process not visible in the single specimen; tarsal claws slender, not serrate; ♂ with front tarsi apparently unmodified, 1 seta each side last ventral segment. Length *c.* 2.3; width 1.0 mm.

Holotype ♂ (M. C. Z. Type No. 30335) from west slope of Thornton Peak (Mt. Alexandra), near Daintree, North Queensland, December 1957, taken by my son (P. F. Darlington) on the trunk of a small tree in rain forest at probably about 3,000 ft. altitude. No other specimens were found.

This species is very different from any other known to me. In Sloane's key (1921) it would probably run to couplet 43, but it can hardly be related to any of the species there named (*ectromioides, atridermis,* etc.). Its arboreal habit suggests relationship to the *nanus* group of *Tachys* (which includes the Australian *brunnipennis* Macl.) and I have therefore compared it especially with the small, shining members of this group that occur in New Guinea (*acuticollis* Putz., *wallacei* Andr.), but the new species differs in having a shorter apical elytral striole, very different anterior pronotal impression, non-serrate claws, etc. It apparently does not fit in any Oriental group of the genus recognized by Andrewes (1925).

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FLORIDA SPIDERS IN THE *RUFUS* GROUP IN THE GENUS *PHILODROMUS* (ARANEAE: THOMISIDAE)

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The most useful means of classifying the North American species of *Philodromus* is to divide them into three groups according to carapace proportions, number of eye tubercles, and features of the external genitalia. The *aureolus* group (Dondale, 1961) and the *rufus* group (defined below) account for the majority of the species, while the remainder (e.g., *P. alascensis* Keyserling and *P. virescens* Thorell) comprise a small third (or possibly a third and fourth) group characterized in part by modifications in the tibial apophyses of the male palpus. In particular, the ventral apophysis is either in the form of a short, rounded lobe or entirely absent.

The *rufus* group can be defined briefly as follows: males rarely exceeding 3.5 mm in body length, and females rarely 4.5 mm; carapace usually longer than wide, and all the eyes except the anterior medians seated on small tubercles; ventral tibial apophysis of the male palpal tibia elongate, soft, and flattened; spermathecae of females situated anterior to rather than at, the genital groove.

The group presents a special challenge to the taxonomist because of the presence of several complexes of closely-similar forms. Some of these problems are discussed in this paper, particularly those involving the Florida peninsula and adjacent parts of the continent.

There are seven members of the *rufus* group in Florida. *P. placidus* Banks, *P. marxi* Keyserling, and *P. imbecillus* Keyserling range widely over North America and extend various distances into the Florida peninsula, although rarely south of approximately 28° north latitude. *P. montanus* Bryant and *P. floridensis* Banks are restricted to the southeastern United States. *P. peninsulanus* Gertsch and *P. bilineatus* Bryant are known only from the southern tip of Florida.

Philodromus placidus Banks

Synonymy. See Kaston (1948), Roewer (1954), and Bonnet (1958).

Description. See Kaston (1948).

Range. Alaska to Nova Scotia, south to Vancouver Island, Utah, Vera Cruz, and Florida.

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Florida Localities. Liberty County; Tallahassee; Leesburg; Trilby.

Comments. P. placidus appears to be a characteristic spider of coniferous trees. Both adults and immatures are recognized by the presence of a prolateral, dark, longitudinal band on patellae III and IV. Adult males have a coat of shiny scales on the abdominal dorsum, as do also the males of *peninsulanus, marxi,* and *imbecillus.*

Philodromus peninsulanus Gertsch

Figures 4, 9, 12, 18

Synonymy. See Roewer (1954) and Bonnet (1958).

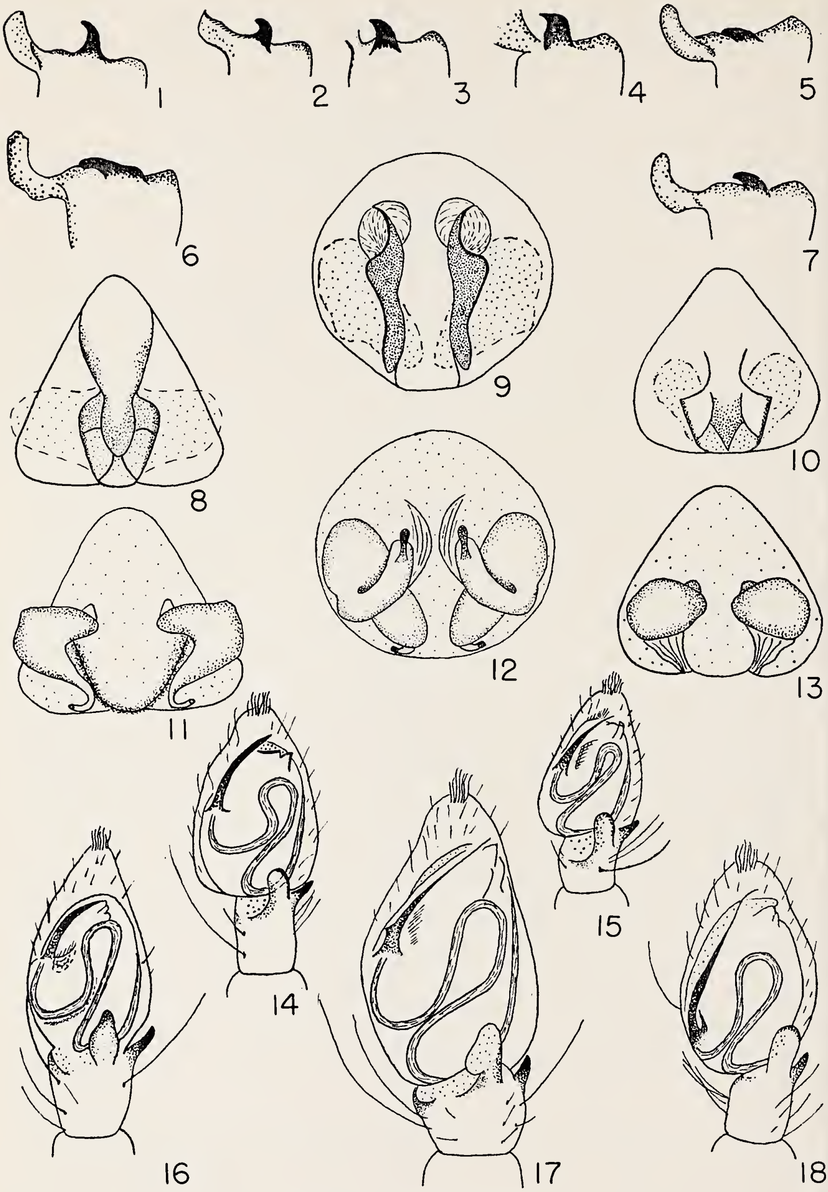
Description. Male: total length 3.20 mm; cephalothorax 1.60 mm long and 1.56 mm wide; femur II 2.28 mm long; ocular quadrangle 0.28 mm long and 0.49 mm wide. These measurements and the description that follows are taken from the type male. Carapace distinctly longer than wide, side margins abruptly constricted at the level of the posterior row of eyes; flattened in appearance, sloping gradually to the sides from the area of the dorsal groove; orange-yellow in color, with a thin white line at side margins and a pair of dusky, submarginal, longitudinal bands; pale median band indistinct, terminating anteriorly at the "cervical groove", which is marked by a white V. Eyes, except the anterior medians, seated on low, white tubercles. Legs orange-yellow. Dorsum of abdomen yellow-white, with a thin coat of shiny scales. Venter off-white.

Tibia of palpus slightly longer than wide, approximately the same thickness throughout; lateral apophysis shorter than the ventral, about as wide as long, with a short point on the lower corner (Fig. 4). Embolus slender and somewhat sinuate, arising proximally on the prolateral margin of the tegulum (Fig. 18).

Female: The female is described here for the first time. The following measurements are from a single female: total length 4.00 mm; cephalothorax 1.69 mm long and 1.64 mm wide; femur II 1.76 mm long; ocular quadrangle 0.28 mm long and 0.54 mm wide. Carapace similar in shape and color to that of the male. Legs and abdomen colored as in male, but without abdominal scales. Median plate of epigynum sinuous along the sides (Fig. 9). Spermathecae elongate (Fig. 12).

Range. The species is represented only by the type male and a female collected in Brevard County, Florida, both of which are in the American Museum of Natural History.

Comments. P. peninsulanus is similar to *P. placidus,* as noted by Gertsch (1934) in his diagnosis of the former, but in *peninsulanus* the femora are shorter and the ocular quadrangle wider. In color,



Dondale — Philodromus

peninsulanus is a yellow-orange spider with none of the dark body and leg patterns found in *placidus*. The relationship between these two species is, however, complicated by the existence of a third form with slightly different external genitalia. It occurs along the coastal plain of the southeastern United States in Mississippi, northern Florida, Georgia, and Long Island, New York and thus coincides with the southern part of the range of *placidus*. It is allopatric with *peninsulanus*, according to present knowledge. Its main characteristics are a shorter embolus than in either of the other two forms and a shorter and wider median epigynal plate and round spermathecae. Too few specimens of the three forms were available from the southeast to permit assessment of these differences.

Philodromus marxi Keyserling

Synonymy. See Kaston (1948), Roewer (1954), and Bonnet (1958).

Description. See Kaston (1948).

Range. Northeastern Mexico to Florida, north to Minnesota, northern New York, and Massachusetts.

Florida Localities. Liberty County; Quincy; Gainesville; Volusia County; Tarpon Springs; Tampa; Clearwater; Terreya State Park; Punta Gorda.

Comments. P. marxi can be distinguished from related forms by the basal origin of the embolus on the tegulum, the small, erect lateral apophysis on the male palpal tibia, and by the copulatory duct of females, which is wound once around the spermatheca. This species is almost identical to the type male of *P. undarum* Barnes (1953), and differs from it only in the shape of the lateral apophysis of the male palpal tibia. In *undarum* this apophysis is drawn out to a fine point, and is inclined toward the cymbium (Barnes, 1953, Fig. 14).

Philodromus imbecillus Keyserling

Synonymy. See Kaston (1948), Roewer (1954), and Bonnet (1958). *Philodromus emertoni* Bryant, 1933, Bull. Mus. Comp. Zool. Harvard College 74:184. New Synonymy.

EXPLANATION OF PLATE 3

Figs. 1-7. Lateral apophysis of male palpal tibia. 1. *P. satullus* (New Jersey). 2. *P. bil'neatus.* 3. *P. floridensis.* 4. *P. peninsulanus* (holotype male). 5, 6. *P. montanus* (Florida). 7. *P. montanus* (North Carolina).

Figs. 8-13. Epigynum of female. 8. *P. floridensis* (external view). 9. *P. peninsulanus* (external view). 10. *P. bilineatus* (external view). 11. *P. floridensis* (internal view). 12. *P. peninsulanus* (internal view). 13. *P. bilineatus* (internal view).

Figs. 14-18. Palpus of male, ventral view. 14. *P. floridensis.* 15. *P. bilineatus.* 16. *P. satullus.* 17. *P. montanus.* 18. *P. peninsulanus* (holotype male).

Description. See Kaston (1948).

Range. Southern British Columbia to Labrador, south to Arizona and, in the east, to Texas and Florida.

Florida Localities. Blountstown; Leon County; Gainesville; Enterprise; Newman Lake; Clara; Ona.

Comments. A study of Bryant's type series of *P. emertoni* from New Bern, North Carolina, deposited in the Museum of Comparative Zoology, indicates that *emertoni* is identical with southeastern specimens of *imbecillus.* Gertsch's (1934) synonymy of *emertoni* and *mineri* Gertsch is open to doubt, unless, of course, Gertsch considers *mineri* to be synonymous with *imbecillus. P. mineri* is a rare form known only from a male collected in the Michigan peninsula. It is very similar to *imbecillus,* but has the lateral apophysis of the palpal tibia longer and thinner, and the tibia itself more robust, than in most eastern specimens of that species.

Within the *rufus* group, *P. placidus, peninsulanus, marxi,* and *imbecillus* together form a distinct series based on the relative length of the male embolus and the corresponding length of the copulatory ducts in females. In *placidus* and *peninsulanus* the embolus arises at between one-quarter and one-half the distance from the base of the tegulum, and the female duct is short, with its point of communication with the spermatheca visible from the ventral side. In *marxi* the embolus arises at the base of the tegulum, and the female duct is long and makes a convolution about the spermatheca. The embolus of *imbecillus* attains the greatest length found in any of the species of *Philodromus;* it arises retrolaterally and nearly encircles the tegulum. The duct makes nearly two full turns around the spermatheca. In all of these forms a lobe arises at or near the point of communication between copulatory duct and spermatheca, and the males are clothed dorsally, at least on the abdomen, with shiny scales.

Philodromus montanus Bryant

Figures 5-7, 17

Synonymy. See Roewer (1954) and Bonnet (1958). *Philodromus mediocris* Gertsch, 1934, American Mus. Novitates *707:* 20. NEW SYNONYMY.

Description. Male: total length 2.80 mm; cephalothorax 1.33 mm long and 1.28 mm wide. These data are from Gertsch's (1934) original description of *P. mediocris.* Carapace longer than wide, less convex over the top than in *P. satullus* Keyserling; lateral areas orange-brown; pale median area as wide as the posterior eye row, narrowed behind; a white V at the "cervical groove"; eyes ringed with white, all except the anterior medians on low tubercles. Legs orange-yellow, paler below, with a well-defined prolateral black band from coxa to tibia on legs III and IV, and with fainter brown retrolateral bands. Width of the ocular quadrangle nearly twice the length. Abdomen diffuse reddish-brown, without definite markings; dorsum without scales; venter pale.

Tibia of palpus about as wide as long; lateral apophysis recumbent on the tibia (Figs. 5-7); ventral apophysis constricted at base, rounded apically (Fig. 17). Embolus about half the length of the tegulum, nearly straight, and with an angular projection on the prolateral side near its base.

Female. Unknown. Bryant's (1933) allotype female of *montanus* from the Black Mountains of North Carolina matches southern females of *satullus* in size, shape, color and in the epigynum, and is therefore believed to be of that species. Gertsch (1934) also included a female in his type vial from Lake City, Florida, although this was not included in his description of *mediocris,* and no characters were found for separation of this female from females of *satullus.* Further work is needed before the female of *montanus* can be properly diagnosed.

Range. Southeastern United States.

Florida Localities. Lake City; Gainesville.

Comments. P. montanus is very similar to the more widespread species *P. satullus,* but males of the two can be separated by the less convex carapace, the unusual embolus, and the recumbent lateral apophysis of the palpal tibia in *montanus* (compare Figs. 1, 16 with 5-7, 17). These species are apparently sympatric, males of *satullus* having been collected as far south as Georgia. The types of the southeastern species *P. inaequipes* Banks (1900), two females from Washington, D. C., appear also to be specimens of *satullus,* as they match females of the latter species in detail, but there remains the possibility that they are instead the females of *P. montanus.* The only description of the male of *inaequipes* (Bryant, 1933) definitely refers to *satullus.*

The synonymizing of *montanus* and *mediocris* is based on a comparison of the type males of both species. The type of *montanus* is in the Museum of Comparative Zoology, and of *mediocris* in the American Museum of Natural History, New York. The cotypes of *inaequipes* are also in the Museum of Comparative Zoology.

P. montanus is one of four forms that comprise a distinct series. In common with *satullus, floridensis,* and *bilineatus* it has a conspicuously wide ocular quadrangle and black-banded legs. The posterior lateral eyes in the members of the series are set on or very close to the carapace margin, and in *bilineatus* the anterior laterals are also on the margin. The embolus in males is relatively short as compared with that of the *placidus-peninsulanus-marxi-imbecillus* series, and the copulatory duct of females is correspondingly short and inconspicuous. Mature males lack shiny scales.

Philodromus floridensis Banks

Figures 3, 8, 11, 14

Synonymy. See Roewer (1954) and Bonnet (1958). *Philodromus deceptus* Gertsch, 1934, American Mus. Novitates *707*:21. NEW SYNONYMY.

Description. Male: total length 3.12 mm; cephalothorax 1.40 mm long and 1.39 mm wide; femur II 1.34 mm long; ocular quadrangle 0.25 mm long and 0.50 mm wide. The measurements were made from the type male of *deceptus;* no other males were available for study. Carapace depressed at the "cervical groove", which is marked with a white V, and highest behind the middle; lateral areas reddish-brown; pale median band as wide in front as the second row of eyes, narrowing posteriorly. Eyes set well apart, the posterior laterals situated at the carapace margins, all ringed with white, and, except the anterior medians, seated on low tubercles; a pair of short, longitudinal brown lines within the ocular quadrangle. Legs yellowish with irregular brown markings at middle of the femora and at the ends of most of the segments; a brown to black prolateral band extending from coxa to tibia, most noticeable on legs III and IV; fainter retrolateral bands on all legs. Dorsum of abdomen white to orange on anterior two-thirds, with a grey heart-shaped mark that is bordered with dark brown; four or five chevrons of various shades of brown to orange posteriorly, alternating with white. Venter pale with three narrow longitudinal bands that coalesce apically.

Tibia of palpus about one and one-half times longer than wide, nearly uniform in thickness throughout; lateral apophysis a short, curved hook (Fig. 3). Embolus short and curved, arising slightly distad of the middle of the tegulum (Fig. 14).

Female: total length 3.84 ± 0.39 mm; cephalothorax 1.55 ± 0.13 mm long and 1.50 ± 0.13 mm wide; femur II 1.71 ± 0.19 mm long; ocular quadrangle 0.29±0.02 mm long and 0.55±0.05 mm wide. These data are the means and standard deviations from a sample of 15 females. Carapace and abdomen generally paler than in the male. Median plate of epigynum U- or V-shaped, with a thickened, sword-shaped middle piece attached anteriorly and extending about two-thirds the length of the plate (Fig. 8). Spermathecae rather slender, situated anterior to the genital groove (Fig. 11).

Range. Southeastern United States and possibly northeastern Mexico.

Florida Localities. Royal Palm Park; Miami; Lake Worth; Dunedin; Leesburg, Lake County; Edgewater; Gainesville; St. Augustine; Blount's Ferry.

Comments. P. floridensis has been known heretofore only from Banks' (1904) type females, which were collected at Lake Worth, Palm Beach County, Florida. These specimens, which are deposited in the Museum of Comparative Zoology, have a rather unusual color pattern, and examination of the males of all known Florida species of *Philodromus* shows that the type male of *P. deceptus* Gertsch is the only one with the same pattern. The type male of *deceptus* is in the American Museum of Natural History, New York, and was collected at Gainesville, Florida.

P. floridensis can be separated from *P. satullus* and *P. montanus,* to which it is very similar, by the depressed "cervical groove" area, the placement of the posterior lateral eyes on the carapace margin, and larger size of *floridensis.* Although the body shape is quite distinct from that of *P. bilineatus,* which is an elongate, striped species, Bryant (1933), for some unspecified reason, indicated a female of *floridensis* as allotype of her new species *bilineatus.*

Philodromus bilineatus Bryant

Figures 2, 10, 13, 15

Synonymy. See Roewer (1954).

Description. Male: Measurements from two males were as follows: total length 2.40, 3.08 mm; cephalothorax 1.14, 1.16 mm long and 0.96, 1.04 mm wide; femur II 1.44, 1.40 mm long; ocular quadrangle 0.22, 0.21 mm long and 0.55, 0.52 mm wide. The first measurement given for each character is from the type male of *bilineatus.* Carapace roughly rectangular in dorsal view, much flattened; lateral areas yellow-orange, with a narrow white band along margin and a pair of orange-brown submarginal bands extending from the posterior lateral eyes to the posterior margin. Eyes ringed with white; lateral eyes of both rows placed on the carapace margins and seated on low tubercles. Legs orange-brown to yellow, III and IV with a narrow black prolateral band from coxa to tibia; all legs with indistinct brown retrolateral band; tibiae and basitarsi I and II each with three pairs of ventral spines, the distal pair on each segment apical and small; femora unarmed except for one prolateral spine near the middle of the segment on leg I. Abdomen elongate and narrow, tapering from front to rear; pale above and below, with a pair of submarginal brown bands along the sides.

Tibia of palpus about equal to patella in length, approximately uniform in thickness. Lateral apophysis a small, erect hook (Fig. 2). Ventral apophysis slightly longer than the lateral apophysis, rounded apically (Fig. 15).

Female: total length 3.82 ± 0.37 mm; cephalothorax 1.40 ± 0.07 mm long and 1.15 ± 0.07 mm wide; femur II 1.53 ± 0.12 mm long; ocular quadrangle 0.25 ± 0.011 mm long and 0.63 ± 0.015 mm wide. These data are the means and standard deviations from a sample of nine females. Shape and color as in the male. Tibiae I and II spined as in the male, but some specimens with one or two additional pairs of weak spines in the distal half. Basitarsal spination as in the male. Femur I with from none to four weak dorsal spines and one or two prolaterals. Abdomen colored as in the male, but not tapered. Median plate of epigynum U-shaped with a sword-shaped piece extending over it from in front (Fig. 10). Spermathecae oval, situated well in front of the genital groove (Fig. 13).

Range. Florida south of approximately 28° north latitude.

Florida Localities. Dunedin; Royal Palm Park; St. Petersburg; Mallet Key; Lake Placid; Fish Eating Creek, Glades County.

Comments. Gertsch (1933) erected the new genus *Tibellomimus*, the type of which was *T. lineatus* Gertsch, for this species. His publication was followed closely by Bryant's (1933), however, in which both sexes of the same species were described as *Philodromus bilineatus*. Gertsch later (1934) recognized the synonymy of the two species, but retained the genus *Tibellomimus*. Roewer (1954) correctly cited the species as *Philodromus bilineatus, lineatus* being preoccupied in the genus *Philodromus*. The basic arrangement of the eyes and structure of the external genitalia relate this species to the *rufus* group, while its nearly rectangular carapace and elongate, striped body appear to be superficial modifications.

Acknowledgements

The preserved specimens upon which this paper is based were borrowed from the American Museum of Natural History, New York, by kind permission of Dr. W. J. Gertsch, and from the Museum of Comparative Zoology, Harvard University, by kind permission of Dr. H. W. Levi.

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A MEGASECOPTERON FROM UPPER CARBONIFEROUS STRATA IN SPAIN[1]

By F. M. Carpenter
Harvard University

In 1962 Professor F. Stockmans, of the Institut Royal des Sciences Naturelles de Belgique, kindly sent me for study two insects from Upper Carboniferous deposits in Northern Spain. One of these (no. 94.837), from the Mine de Poleiro, is part of a cockroach tegmen, which cannot be placed with certainty even to family level. The other specimen (no. 97.587), from shales near the village of Magdalena, is a nearly complete, well-preserved wing of a megasecopterous insect. Since it shows interesting venational features and since there seems little chance of obtaining additional insects from this deposit in the near future, I have considered it advisable to publish a formal description of the fossil at this time. I am indebted to Dr. Stockmans not only for his courtesy in loaning me these specimens but for providing me with information about the geology and stratigraphy of the formation concerned.

Family **Anchineuridae,** new family

Differing from all other known families of Megasecoptera by having the cross veins numerous, irregular, and equally distributed over the wing area. The subcosta runs very close to the costal margin, terminating in the distal area of the wing; the costal margin is somewhat thickened and in the distal quarter of the wing, before the apex, the thickened area becomes much broader; the radius is parallel with the subcosta and close to it but not so near as Sc is to the costal margin. The radial sector has numerous branches, MA is free from Rs, and CuA is free from MP. The costal margin of the wing bears numerous, conspicuous, stout setae, especially prominent in the thickened region of the costa; the rest of the wing margin from the apical region along the posterior margin to the wing base bears a series of fine setae; some of the longitudinal as well as cross veins, especially the branches of Rs and associated cross veins, bear well-defined but short setae.

The closest relatives of this family seem to be the Aspidothoracidae, in which, however, the cross veins, although nearly equally distributed over the wing surface, are much fewer in number and are regular in formation. In the Anchineuridae the cross veins are irregularly

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Anchineura hispanica, n.sp. Photograph of holotype (× 3.5).

formed, often divided and branched, and in some areas forming a coarse reticulation.

Genus **Anchineura,** new genus

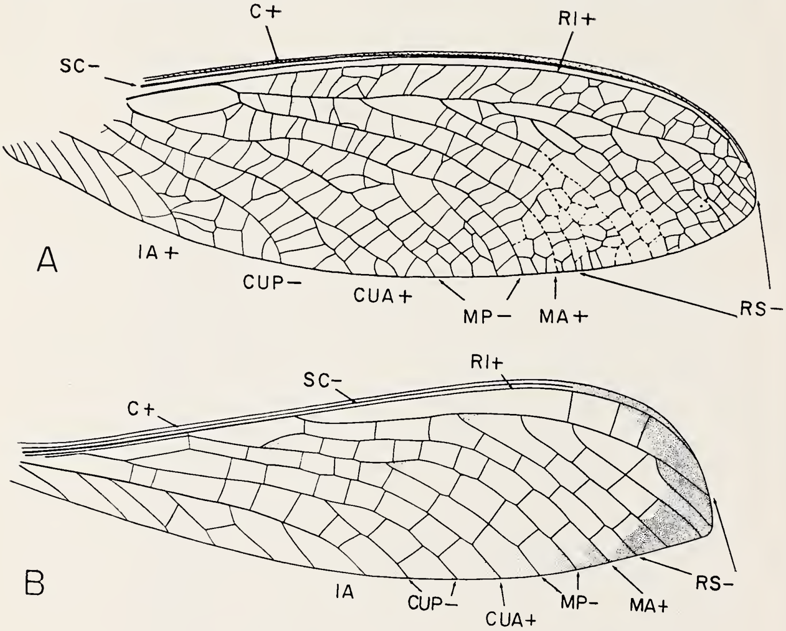
Rs is the most extensively branched longitudinal vein in the wing, having six main branches and numerous terminal ones. MA and CuA are unbranched and MP and CuP are branched.

Type species: *Anchineura hispanica,* new species.

Anchineura hispanica, n. sp.

Text figure 1A, plates 1, 2

Length of wing, 45 mm; maximum width, 13 mm. Costal margin slightly convex, apex broadly rounded, hind margin smoothly curved.



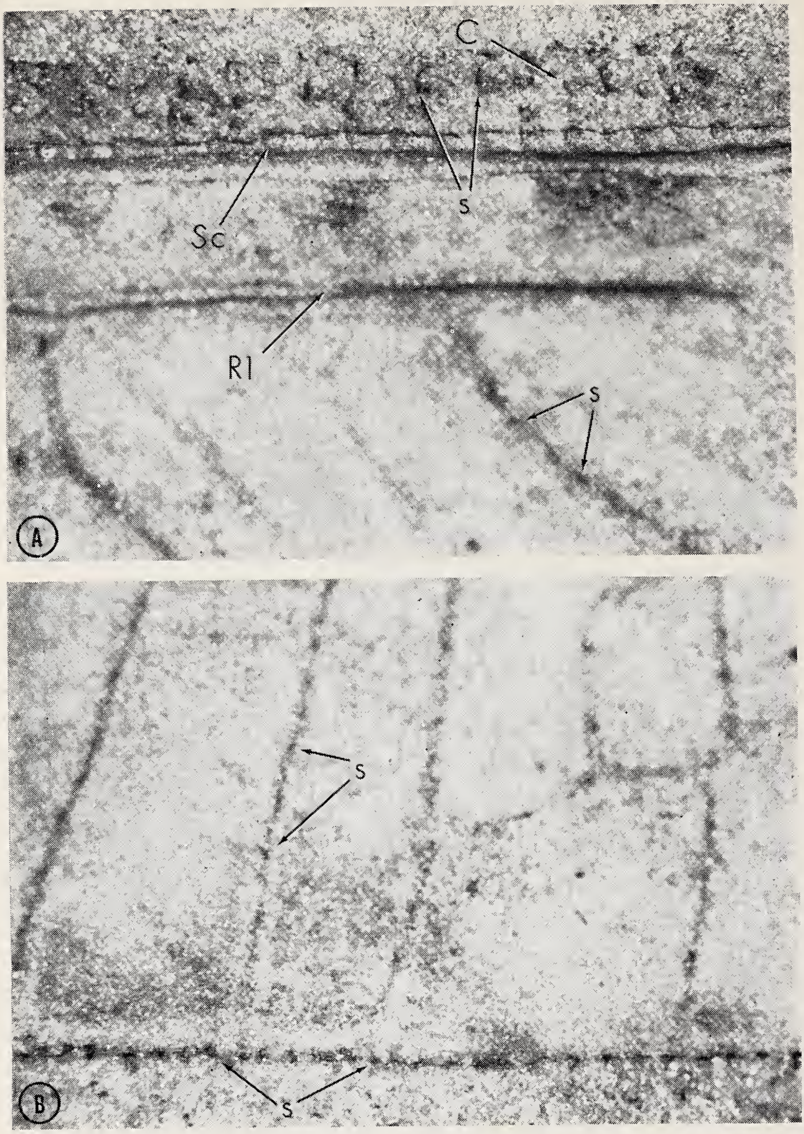
Text figure 1. A, *Anchineura hispanica,* n.sp. Drawing based on holotype. B, *Aspidothorax triangularis* Brongniart, from Commentry, France. Original drawing based on specimens in Museum National d'Histoire Naturelle, Paris. C, costa; Sc, subcosta; Rl, radius; Rs, radial sector; MA, anterior media; MP, posterior media; CuA, anterior cubitus; CuP, posterior cubitus; 1A, anal vein; +, convex veins; —, concave veins.

Rs arising about 1/4 of the wing length from the base, MA arising from M slightly basad of the origin of Rs. MA diverges slightly towards Rs and is joined to it by a cross vein at that point; MP has four terminal branches, one of which arises towards the base of MP, almost directly below the first cross vein joining MA with Rs. Fork of CuA rather shallow; 1A with several marginal branches. Other venational details, including the cross veins, are shown in text figure 1A.

Type: specimen no. 97.587, Institut Royal des Sciences Naturelles de Belgique; collected along route from La Magdalena to Barrios de Luna, north of the village of Magdalena, Spain, by Dr. F. Stockmans. The shales in which the insect was collected are of Stephanian age, probably belonging to the upper part of Stephanian B (Wagner, 1958, 1959). The type specimen is well-preserved (plate 1), except for the basal part of the wing, which is missing; the wing also shows clear signs of having been torn or broken at various places but most of these broken areas are very small and do not interfere with the interpretation of the venational pattern. One of the broken areas is along the anterior margin, not far from the level of the origin of Rs; here the wing margin is broken and the broken ends of the costal margin do not quite meet. That this is an actual break and not a normal part of the wing is clearly shown by the break which continues further towards the center of the wing as far as and slightly beyond Rs. The convexities and concavities of the wing are clearly shown in the fossil, although the wing was probably a very delicate one.

This unusually interesting insect shows, in the wing, some features of both Palaeodictyoptera and Megasecoptera. The cross veins and the main veins, apart from Sc and Rl, could very easily be those of a palaeodictyopterous insect. However, the anterior part of the wing, with Sc and Rl crowded towards the anterior margin, clearly shows megasecopterous affinites. So far as the preserved part of the wing is concerned, the main veins are suggestive of the venation of *Aspidothorax,* from Commentry, France (Stephanian). The relationship between MA and Rs is about the same; unfortunately the specimen of *hispanica* does not show the basal origin of CuA, although as it appears in the fossil it is very close to the stem of R and could very likely have continued basally parallel and close to R as it does in *Aspidothorax.*

The costal area of *hispanica* is similar to that previously noted in other Megasecoptera. In my account of *Actinohymen* from the Permian of Texas (Carpenter, 1962), I included a photograph of part of the costal margin of the wing, showing prominent setae or setal bases along the margin. The costal margin of *hispanica* has similar structures (fig. A, plate 5), especially in the thickened, distal part of the costa. As in *Actinohymen,* the setae are also present on some of



Carpenter — Anchineura

the main veins and cross veins. Most of them are short, robust spines, like those in certain Odonata (Fraser, 1942). In addition, *hispanica* has a fringe of short, stout setae extending along the distal and posterior margins of the wing (fig. B, plate 5). I have not previously observed a similar fringe in any Megasecoptera, although a weakly developed one does occur in some Palaeodictyoptera, as *Dunbaria.*

The presence of numerous irregular cross veins, reminiscent of those of most Palaeodictyoptera, in a wing which is otherwise typically megasecopterous is indicative of the assumed relationship between these two orders. I believe that *Anchineura* brings the Palaeodictyoptera and Megasecoptera closer together than any previously known fossil has done. This is not to imply that the Anchineuridae are in the direct line of evolution between these orders — much more information about these insects, especially body structures, needs to be known — but *Anchineura* provides some evidence for a relationship which was previously only assumed.

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EXPLANATION OF PLATE 5

Anchineura hispanica, n.sp. A, photograph of part of the costal area of wing (area labeled *a* on plate 4). B, photograph of part of the hind margin of wing (area labeled *b* on plate 4).

STUDIES ON THE CAVERNICOLE *PTOMAPHAGUS* OF THE UNITED STATES (COLEOPTERA: CATOPIDAE)[1]

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The cave beetles of the United States include members of the families Carabidae, Staphylinidae, Pselaphidae, Catopidae (=Leptodiridae), and occasionally Brathinidae, Tenebrionidae, Cryptophagidae, and Dermestidae. Troglobite species (obligate cavernicoles) are found among the carabids (Trechini, Agonini), pselaphids (Batrisini, Bythinini, and Speleobamini), and catopids (Ptomaphagini). In comparison with the cave carabids and cave pselaphids, which have been the objects of recent and continuing studies by American authors (see Barr 1960a for bibliography of cave trechines, Barr 1960b on agonine cave carabids, and Park 1960 on cave pselaphids), the cave catopids have received less attention. The most recent paper treating all known species of U. S. cave catopids is that of Jeannel (1949).

Although the essentially European subfamily Bathysciinae includes numerous highly modified troglobitic species, catopids in U. S. caves are represented only by a few members of the genus *Ptomaphagus* Illiger and rarely on occasional *Catops* or *Nemadus*. All U. S. species of *Ptomaphagus*, epigean or cavernicole, belong to the subgenus *Adelops* Tellkampf (type species: *Adelops hirtus* Tellkampf 1844, from Mammoth Cave, Kentucky). Twelve epigean species, 2 troglophile species, and 7 troglobitic species of *Adelops* have been described from the United States, and 3 more troglobitic species are described in the present paper. The cavernicole species thus comprise half of the number of species known at the present time. These inhabit caves of Missouri, Oklahoma, Arkansas, Iowa, Illinois, Kentucky, Tennessee, Alabama, and Georgia. Seven species of the *cavernicola* group are clustered in northeastern Alabama and adjacent parts of Tennessee and Georgia, but otherwise, the cave species are distinctly allopatric, indigenous to cave systems widely separated from each other, either by non-caverniferous regions or cave areas where *Adelops* has not been discovered.

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las, F.S.C., R. Oesch, Stewart Peck, Jack Reynolds, M. W. Sanderson, and H. R. Steeves, Jr. For assistance in collecting, I am indebted to Oscar Hawksley, Leslie Hubricht, Walter B. Jones, H. R. Steeves, Jr., and Frederick R. Whitesell. Dr. René Jeannel, Museum National d'Histoire Naturelle, Paris, kindly lent me the type of *P. laticornis* for examination.

Key to known Species of Cavernicole *Ptomaphagus* of the United States (Based on Jeannel 1949)

1 Elytral apex rounded in the male, obliquely truncate with external apical angle present in the female; pronotum with feeble or no transverse strigae (*hirtus* group) 2

1′ Elytral apex rounded or truncate in the male, acuminate in the female, external apical angle effaced; pronotum usually with prominent transverse strigae (*cavernicola* group) 4

2(1) Eyes reduced to a very small, pale areola; pronotal disc without transverse strigation or with strigae limited to region near the margins 3

2′ Eyes small but pigmented; pronotal disc lightly and irregularly transversely strigose; Oklahoma, Arkansas .... *shapardi* Sanderson

3(2) Antennal segment VIII half as long as wide; transverse strigae feebly developed near margins of pronotal disc; southern Illinois .... *nicholasi* n. sp.

3′ Antennal segment VIII three-fourths as long as wide; transverse strigae almost completely absent from pronotal disc; west-central Kentucky .... *hirtus* Tellkampf

4(1) Eyes reduced to a very small, pale areola, their diameter less than distance from anterior margin of eye to base of antenna; no functional wings; Alabama, Tennessee, or Georgia 5

4′ Eyes large and pigmented, their diameter greater than the distance from anterior margin of eye to base of antenna; functional wings present; Ozark region .... *cavernicola* Schwarz

5(4) Antennal segment III not longer than segment II 6

5′ Antennal segment III longer than segment II 10

6(5) Form oblong, less convex; pronotum narrow, its greatest width at the base 8

6′ Form shorter and convex; pronotum broad, its greatest width in front of the hind angles; elytra short and convex, briefly attenuate in the male; antennal segments IX and X not longer than wide 7

7(6) Transverse strigae of pronotum regular and distinct; antennae slender, reaching to anterior third of elytra when laid back; elytral apex evenly rounded in the male; Grundy and Franklin counties, Tennessee, to north-central Jackson Co., Alabama .... *hatchi* Jeannel

7′ Transverse strigae of pronotum irregular and dissociated, rather superficial; antennae thicker, reaching only to base of pronotum when laid back; elytral apex angular in male; Dade Co., Georgia .... *whiteselli* n. sp.

8(6) Antenna longer, easily reaching beyond base of pronotum; V, VI, and VII slender, VIII small but not transverse, almost as wide as long 9

8′ Antenna shorter, scarcely reaching the base of the pronotum; V and VI dilated, VII greatly enlarged, VIII very transverse (twice as wide as long); Madison Co., Alabama .... *laticornis* Jeannel

9(8) Color reddish-brown; body robust; VII and VIII enlarged; posterior pronotal angles relatively blunt; DeKalb and Wilson counties, Tennessee .... *hubrichti* Barr

9′ Color pale testaceous or rufotestaceous; body slender; VII and VIII not appreciably enlarged; posterior pronotal angles sharper; northeast Alabama .... *henroti* Jeannel

10(5) Size larger (2.8-3.5 mm); pronotum distinctly wider, the transverse strigae fine but distinct; elytral strigae very fine and superficial 11

10′ Size small (2.2-2.5 mm); pronotum narrower, with transverse strigae superficial and dissociated on the disc; elytral strigae deeper and more distinct; northeast Alabama .... *valentinei* Jeannel

11(10) Elytral apices subtruncate in the male; northeast Alabama .... *loedingi* Hatch

11′ Elytral apices rounded in the male; Franklin Co., Tennessee .... *fecundus* n. sp.

The above key is a tentative one, since there are probably several undescribed species of *Ptomaphagus* which occur in the caves of the United States. Most of these will be species which have pigmented eyes, will be most abundant in the twilight zone, and will key out near *P. cavernicola.* I have seen scattered material of this nature from caves in Florida, Texas, and Alabama.

hirtus group

Elytral apex rounded in the male, obliquely truncate in the female; transverse strigation of pronotal disc greatly reduced in some species.

Ptomaphagus (Adelops) hirtus Tellkampf

Adelops hirtus Tellkampf 1844: 313, fig. 106; type: Mammoth Cave, Kentucky. Hatch 1928: 169; 1933: 208. Jeannel 1931: 408.
Ptomaphagus (Adelops) hirtus: Jeannel 1936: 93, figs. 154-155; 1949: 99. Barr 1962: 282.

Common in Mammoth Cave, Kentucky, and known from caves in Hardin, Hart, Edmonson, Barren, and Warren counties, Kentucky, along the western Pennyroyal plateau and Dripping Springs escarpment. Troglobite.

Ptomaphagus (Adelops) shapardi Sanderson

Sanderson 1939: 121; type: Dresser Cave, Cherokee Co., Oklahoma (in coll. Illinois Nat. Hist. Surv. Div., Urbana). Jeannel 1949: 101.

Described from Dresser Cave, 5 miles north of Fort Gibson, Oklahoma, and reported from northwestern Arkansas (Sanderson, pers. comm.). The pronotal disc is transversely strigose, although less so than in most members of the *cavernicola* group, to which it was assigned by Jeannel (1949). In the sexual dimorphism of the elytral apex and in general form it seems closer to *hirtus* (and to the montane species *P. mitchellensis* Hatch, as suggested by Sanderson in the original description of *P. shapardi*). Small, pigmented eyes are present, the individual facets distinct. Troglophile?

Ptomaphagus (Adelops) nicholasi n. sp.

Length 2.3-2.7 mm; width 1.3-1.4 mm. Color dark brown to pale yellow testaceous. Form oblong, very convex, narrowing posteriorly. Eyes reduced to a small, pale areola. Antenna slender and elongate, extending to the anterior third of the elytra when laid back; segments I, II, and III subequal; IV, V, and VI each half as long as III, subequal; VII subconical, its apical diameter equal to its length; VIII very transverse, twice as wide as long, slightly narrower than VII; IX and X subquadrate and subequal; XI three-fourths as wide as long and subequal in width to X, attenuate in apical three-eighths. Pronotum 2/3 as long as wide, widest just before the base, slightly wider than elytra; hind angles a little less than right, acuminate; base entire, curved slightly back to the hind angles; disc with transverse strigae distinct only near the margins, strigae dissociated, indistinct, and very superficial medially. Elytra elongate, 3/4 as wide as long, subparallel, gradually attenuate to the apices, twice as long as pronotum; elytral apices rounded in the male, obliquely truncate with external apical angle in the female; strigae oblique to the suture. Described on five specimens, the holotype male (American Museum of Natural History), allotype female (AMNH), and three paratypes (coll. Barr), from Fogelpole Cave, Monroe Co., Illinois, 22 October 1961 (Bro. G. Nicholas, F.S.C., leg.).

This is the first troglobitic beetle to be described from the caves of southern Illinois. It seems most closely related, at least morphologically, to *hirtus*, from which it is readily distinguished by the transverse strigation at the margins of the pronotal disc and by the more transverse eighth antennal segment. The species is a morphological and geographic intermediate between *hirtus* and *shapardi* with respect to the pronotal strigation. The eyes, however, are very small and show no facets or pigmentation.

cavernicola group

Elytral apex either rounded or truncate in the male, acuminate in the female; transverse strigation of pronotal disc pronounced (except in *valentinei* Jeannel and *whiteselli* n. sp.).

Ptomaphagus (Adelops) cavernicola Schwarz

Schwarz 1898: 57; type: Marble (=Marvel) Cave, Stone Co., Missouri (U. S. Nat. Mus. #1424). Jeannel 1936: 92; 1949: 101.

The type of the species group has large, pigmented eyes and functional wings. It is apparently widely distributed in the Ozark region. My own material includes specimens from the following localities:

ARKANSAS. *Washington Co.:* Granny Dean Cave, near Black Oak. MISSOURI. *Benton Co.:* Flippen Cave, Lish Estes Cave, Luegenbeil Cave, Spring Cave. *Boone Co.:* Devils Icebox. *Camden Co.:* Carroll Cave. *Dallas Co.:* Cat Hollow Cave. *Franklin Co.:* Fisher Cave. *Laclede Co.* Mary Lawson Cave. *Stone Co.:* Marvel Cave (type loc.), Dillo Cave, Fairy Cave, Gentry Cave. IOWA. *Jackson Co.:* Hunter Cave, near Andrew.

In the caves, *P. cavernicola* is most abundant upon feces of bats or raccoons, or upon dead bat carcasses. Occasionally it occurs on wet, rotten wood. In Dillo Cave, Stone Co., Missouri, many larvae were collected from raccoon feces on 27 January 1958, and the species possibly reproduces throughout the year. *P. cavernicola* appears to be more tolerant of moisture and temperature fluctuations than its eastern troglobite relatives. In Marvel Cave large numbers were secured from dead bats (*Myotis grisescens* Howell) in the Waterfall Room, January 1958. A cold, dry current of air, blowing from a passage leading to a newly opened artificial entrance, was flowing over the bat carcasses. Although the species is known only from caves, this tolerance, in conjunction with the well developed eyes and wings, the retention of some pigment, and the comparatively extensive geographic distribution indicate that it is a troglophile.

Ptomaphagus (Adelops) hatchi Jeannel

Jeannel 1933: 252; type: Wonder Cave, Grundy Co., Tennessee (in Mus. Nat. Hist. Nat., Paris). Jeannel 1936: 93; 1949: 101.

Rather widely distributed in the caves of southeastern Grundy County (Crystal, Partin Spring, Trussell, Wonder) and eastern Franklin County (Crownover Saltpeter, Custard Hollow, Dry, Lost Cove, Wet, Ranie Willis), Tennessee, and in the caves of Crow Creek Valley in adjacent Jackson County, Alabama (Jesse Elliott, Talley Ditch). Troglobite.

Ptomaphagus (Adelops) whiteselli n. sp.

Length 2.8 mm; width 1.3 mm. Color dark brown, testaceous. Form oblong, very convex, narrowing posteriorly. Eyes reduced to a small, pale areola. Antenna rather short and thickened, extending to the base of the pronotum only when laid back; segment I longer and wider than II and III, which are subequal; IV, V, and VI subequal, cylindrical, a little shorter than III, three-fifths as wide as long; VII two-fifths longer than VI, subconical, the apical width 5/7 the length; VIII transverse, half as long as wide; IX and X subquadrate, 2 1/2 times as long as VIII; XI four-fifths longer than X, attenuate in apical four-ninths. Pronotum subequal in width to elytra, widest just before the base, 3/5 as long as wide; hind angles a little less than right, acuminate; base very shallowly emarginate medial to the hind angles; disc with transverse strigae superficial, irregular, and dissociated. Elytra elongate, subparallel, gradually attenuate to the apices, 2 1/2 times as long as pronotum; apex briefly and obliquely subtruncate in the male (female unknown); strigae oblique to the suture. Described from a unique male, the holotype (American Museum of Natural History), Sittons Cave, Dade Co., Georgia, 20 March 1959 (T. C. Barr, Jr., leg.).

This is the first troglobitic beetle to be described from the caves of northwestern Georgia. In the short, thickened antennae the species resembles *P. laticornis* Jeannel, from which it differs in the more robust body and longer 11th antennal segment. Since *P. whiteselli* is known from a single male and *P. laticornis* from a single female, the two species may not be satisfactorily compared at the present time. *P. whiteselli* may be distinguished from *P. hatchi,* which it resembles in convex form and in having the greatest width of the pronotum in front of the hind angles, by the irregular, superficial strigation of the pronotal disc, by the thicker, shorter antennae, and by the elytral apices of the male, which are more briefly subtruncate and less rounded. The apex of the aedeagus is smaller and narrower than in *hatchi.* Named in honor of Dr. Frederick R. Whitesell, University of the South, Sewanee, Tennessee.

Ptomaphagus (Adelops) laticornis Jeannel

Jeannel 1949: 102; type: Scott Cave, Madison Co., Alabama (in Museum National d'Histoire Naturelle, Paris).

Length 2.5 mm. Testaceous. Similar in body proportions to *P. henroti* but with shorter, thicker antennae, the club somewhat flattened. Segments V and VI are thickened, VI less than twice as long as wide; VII very large, as in *whiteselli;* VIII short and very transverse, half as wide as long; IX and X subquadrate; XI two-sevenths longer than X, attenuate in apical one-fifth. Known only from the unique female type, which I have seen. Troglobite. Sympatric with *P. henroti.*

Ptomaphagus (Adelops) henroti Jeannel

Jeannel 1949: 102; type: Aladdin Cave, Madison Co., Alabama (in Museum National d'Histoire Naturelle, Paris).

The smallest and most slender of our troglobitic *Adelops.* Known from the type locality and nearby Scott Cave, Madison County, and from Horseshoe and Blowing Caves, Fannin Cove, in nearby Jackson County, Alabama. Jeannel (1949) described *P. h. ellipticus* as a distinct race from Shelta Cave, Huntsville, Madison County, but only two specimens are known. I have seen only nominate *henroti.*

Ptomaphagus (Adelops) hubrichti Barr

Barr 1958: 170; type: Cripps Mill Cave, DeKalb Co., Tennessee (in American Museum of Natural History, New York).

Common in caves of southern DeKalb County, at the eastern edge of the Central Basin in Tennessee, and more recently collected in Hayes Cave, near Statesville, in eastern Wilson County, Tennessee. Distinguished from *henroti* by the more robust body form, the dilated 7th and 8th antennal segments, and the blunter posterior pronotal angles. Troglobite.

Ptomaphagus (Adelops) valentinei Jeannel

Jeannel 1933: 252; type: Sauta Cave, near Lim Rock, Jackson Co., Alabama (in Museum National d'Histoire Naturelle, Paris). Jeannel 1936: 93; 1949: 103.

A small, slender, troglobitic species with the 3rd antennal segment longer than the 2nd, the transverse strigation of the pronotal disc rather superficial and irregular. Known from the type locality, in Jackson County; from Cathedral Caverns and Guffey Cave, Marshall County; and from Twin Caves, near Brownsboro, Pitts Sinkhole, at the head of Big Cove, and Cave Spring Cave, near Berkeley, all in Madison County, Alabama. Jeannel (1949) described *P. v. jonesi* from Pitts Sinkhole and *P. v. longicornis* from Cave Spring Cave. I have not seen enough Madison County material to comment on the validity of these subspecies. *P. v. longicornis* is known from a single male. The few specimens from Twin Caves are doubtfully assignable to *P. v. jonesi.*

Ptomaphagus (Adelops) loedingi Hatch

Adelops lödingi Hatch 1953: 209, pl. 15, fig. 19; type: Shelta Cave, Huntsville, Madison Co., Alabama (U. S. Nat. Mus. #43763).
Ptomaphagus (Adelops) lödingi: Jeannel 1936: 93; 1949: 104.

A large troglobitic species characterized by the 3rd antennal segment being distinctly longer than the 2nd; the 8th segment is subquadrate; the strigation is superficial but quite distinctly transverse. Known from the type locality and Barclay and Simmons Caves, Madison Co., Alabama; and from Stewart, Tumbling Rock, and Ivey Bottom Caves, Jackson Co., Alabama. The two populations of *P. loedingi* are apparently allopatric, one in Madison County and the other in Jackson County. They may eventually be proven to be subspecifically distinct, although I have seen only 7 specimens from Jackson County and am reluctant to make a diagnosis on this basis.

The original spelling of the trivial name is altered in accordance with Art. 32 (c) (i) of the *International Code of Zoological Nomenclature,* adopted by the XV International Congress of Zoology.

Ptomaphagus (Adelops) fecundus n. sp.

Length 2.5-2.9 mm; width 1.3-1.4 mm. Color dark brown, testaceous. Form elongate and slender, narrowing posteriorly. Eyes reduced to a very small, pale areola. Antenna slender, elongate, attaining the basal 1/3 of elytra when laid back; segment I slightly thicker than segments II-V, which are subequal in diameter; segment I one and one-half times as long as II; segment II seven-eighths as long as III; IV-VII each about 4/5 as long as III; VII subconical, 1 1/4 times as wide as VI at the apex and 5/8 as wide as long; VIII subconical, 1 1/4 times wider than long; IX and X each 1/5 wider than long; XI as wide as X but 1/3 longer. Pronotum subequal in width to elytra, widest at the base, 2/3 as long as wide; hind angles acuminate, less than right, base very shallowly emarginate between the hind angles; disc with transverse strigae finely impressed and distinct. Elytra elongate, tapering, 2 1/3 times as long as pronotum; apices evenly rounded in the male, acuminate in the female with no external apical angle; strigae oblique to the suture; sutural angle narrow, its depth twice the distance between the apices. Aedeagus large and broad, as in *P. loedingi.* Described on holotype male and allotype female (both in American Museum of Natural History) and 94 paratypes, Caney Hollow Cave, Franklin Co., Tennessee, 9 May 1959 (T. C. Barr, Jr., leg.).

Abroad on the wet rock and mud floor among fragments of bat guano, the beetles were so numerous that it was difficult to traverse the cave without stepping on them. Caney Hollow Cave is located approximately 30 miles northeast of Huntsville, Alabama, at the margin of the Central Basin of Tennessee. The cave contains a perennial stream, is quite damp, and is inhabited by a large colony of bats (*Myotis grisescens* Howell), upon whose excrement the beetles feed.

P. fecundus is most closely allied to *P. loedingi,* from which it differs in having segment II of the antennae only 7/8 as long as III, instead of 7/9, and in having the elytral apices of the male rounded instead of subtruncate. *P. hatchi* inhabits the caves of eastern Franklin Co., Tennessee, at the base of the Cumberland Plateau. The Caney Hollow Cave is developed in Ordovician limestones immediately below the Chattanooga shale.

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STUDIES ON NORTH AMERICAN CARBONIFEROUS INSECTS. 2. THE GENUS *BRODIOPTERA*, FROM THE MARITIME PROVINCES, CANADA*

By F. M. Carpenter
Harvard University

Although few in number, the insects which have been found in the Upper Carboniferous strata of the Maritime Provinces of Canada are of exceptional interest. They occur in rocks which are well down in the Westphalian stage (Zone A) and are therefore only a little younger than the oldest insects known (Namurian). In 1957, Dr. M. J. Copeland of the Canada Department of Mines and Technical Surveys published an account of the arthropod fauna of the Upper Carboniferous rocks of these provinces and included descriptions of two species of the genus *Brodioptera,* which he placed in the Order Megasecoptera. Since Dr. Copeland's descriptions and illustrations are inadequate for our present needs of interpreting the relationships of these insects, I have found it necessary to make a study of this material. I am indebted to Dr. Copeland for arranging to have the type specimens loaned to me for this purpose.

One of the species which Copeland placed in *Brodioptera* is a member of the Order Megascoptera, as thought by him, although its affinities within the group are different from those which he assumed; the other species described in *Brodioptera* is not a megasecopteron at all but very clearly a member of the Order Palaeodictyoptera.

Order Megasecoptera

Family **Brodiopteridae,** new family

Anterior margin of wing very nearly straight proximally; hind margin apparently nearly straight or only slightly curved; the wing was almost certainly not petiolate, although the absence of the basal part of the hind margin permits the possibility of a slight narrowing in that region. Sc terminating on C, R1 straight at the base of the wing, not arched proximally; MA free from Rs, and Cu and CuA free from MP; one anal vein. Cross veins few and widely scattered.

This family is probably more closely related to the Sphecopteridae and the Corydaloididae than to any other known families of the order.

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*This research has been aided by a grant (NSF-G14099) from the National Science Foundation. The previous part of this series was published in Psyche, 67:98-110, 1961.

It is far removed from the family Brodiidae, within which it was placed by Copeland; it lacks the extreme petiolation characteristic of the Brodiidae, and more significantly, lacks the strikingly serrate costal margin, which is the outstanding feature of the brodiids. In the sphecopterids the subcosta terminates on the radius, the radial sector (at least in the fore wing) is anastomosed for a short distance with MA, and the cross veins are very regularly arranged, forming definite rows. In the corydaloidids the subcosta terminates in the costal area without definitely ending on either the costa or R1; and there is a brief anastomosis of MA with Rs and of CuA with M.

Brodioptera Copeland, 1957

Brodioptera Copeland 1957, Geological Survey of Canada, Mem. **286**: 53.

Wing venation: Sc terminating about two-thirds of the wing length from the base; Rs with several branches, MA, MP (apparently), CuA and CuP unbranched.

Type species: *Brodioptera cumberlandensis* Copeland.

Brodioptera cumberlandensis Copeland, 1957

Figure 1

Brodioptera cumberlandensis Copeland, 1957, Geol. Surv. Canada, Mem. **286**: 53.

Length of wing, 17 mm; maximum width, 4.5 mm.[1] Apex of wing rounded; Rs branched to form R2a, R2b, R3, R4+5; MA arising slightly distad of the origin of Rs; CuA arising much nearer the base of the wing. The arrangement of cross veins is shown in figure 1.

Type: no. 10390 (obverse and reverse), Geological Survey of Canada. This consists of a fairly well-preserved wing, lacking only the very base and a few small areas near the middle of the wing. Whether the wing is a fore or hind wing cannot be determined. The convexities and concavities of the veins are clearly indicated. The specimen was collected by Henry M. Ami, in 1899, in deposits at West Bay, Plarrsboro, Cumberland County, Nova Scotia. The deposit is stated by Dr. Copeland to belong to the Riversdale group and more specifically by Ami as probably of Joggins coalfield, of the Coal Measures.

This specimen is generalized so far as the absence of fusion of main veins is concerned but it is highly specialized in the reduction of branches on all veins accepting Rs, in the close proximity of Sc and R1 to the costal margin, and in the small number of cross veins. It is surprising to find a megasecopteron as specialized as this in the Rivers-

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[1] The dimensions are incorrectly indicated on p. 101 of Copeland's paper (1957).

dale group of strata, which is regarded as being about equivalent to Westphalian Zone A, just above the Namurian stage, in which the oldest insects (unquestionable) have been found.

Palaeodictyoptera

Family Dictyoneuridae Handlirsch[2]

I am placing the species described by Copeland as *Brodioptera amii*[3] in the family Dictyoneuridae, although I have doubts about its actually belonging within the limits of the family. The most distinctive characteristic of the Dictyoneuridae is the presence of an archedictyon over the wing surface. Unfortunately the specimen of *amii* shows no signs of either cross veins or an archedictyon, probably because of the coarse nature of the matrix in which the fossil is preserved. On the assumptions that true cross veins probably would show, if they were present, I am tentatively assigning the species to the Dictyoneuridae. Other characteristics of the family include the subcosta ending on the costal margin, well beyond the middle of the wing; Rl ending nearly at the apex, Rs with at least three branches; MA unbranched and arising as a distinct anterior branch of the media, CuA typically unbranched (though occasionally with a distal fork) and CuP with several branches. All of these features occur in the specimen of *amii*. The one characteristic of *amii* that has not previously been noted in the Dictyoneuridae is the presence of a definite cross vein joining the anterior media with the radial sector; such a vein, present in *amii*,

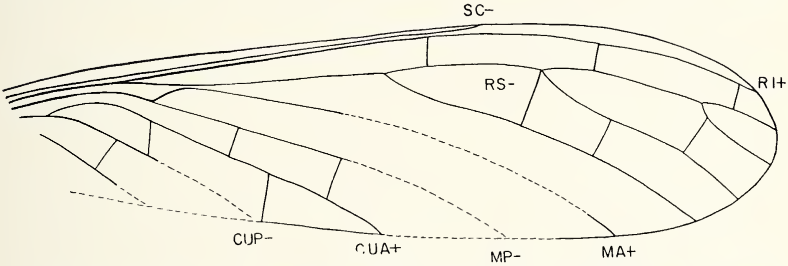

Figure 1. *Brodioptera cumberlandensis* Copeland. Original drawing, based on holotype. C, costa; Sc, subcosta; Rl, radius; RS, radial sector; MA, anterior media; MP, posterior media; CUA, anterior cubitus; CUP, posterior cubitus; 1A, first anal vein.

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[2] The name Stenodictyopteridae Brongniart used by some authors (e.g., Pruvost, 1919; Laurentiaux, 1953) for this family is invalid, since it is not based on a generic name.

[3] The name *amiae* was used by Dr. Copeland in error. He has informed me *(in litt.)* that the species was named for Dr. Henry M. Ami, the collector of the fossil, and that the name should accordingly have been *amii* instead of *amiae*.

may have been formed by an alignment of the sides of several of the cellules comprising the archedictyon. The wing on which *amii* is based is quite clearly a hind wing and although this is broader than the hind wings of any known dictyoneurids, the hind wings in several genera are markedly broader in the anal region than the fore wings. The greater differentiation in *amii* seems to me insufficient to eliminate it from the family on this basis alone. However, a distinct genus seems to be necessary for the fossil, since the genus into which it was placed by Copeland is a megasecopteron.

Schedoneura, new genus

Main veins of the wing with the general characteristics of the dictyoneurids: Sc and Rs extending almost to the apex, Rs arising just before the middle of the wing, with four branches; MA unbranched, joined to the base of Rs by a distinct cross vein; CuA unbranched; CuP very well developed, with six terminal branches; several anal veins.

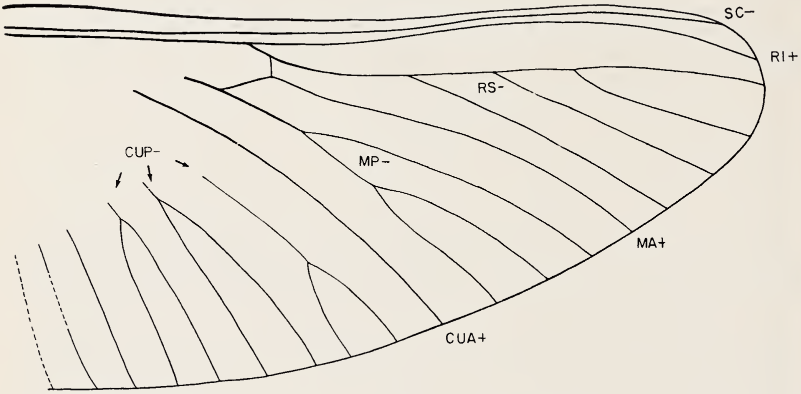

Figure 2. *Schedoneura amii* (Copeland). Original drawing, based on holotype. Lettering as in figure 1.

Type species: *Brodioptera amii* Copeland

Schedoneura amii (Copeland)
Figure 2

Brodioptera amii Copeland, 1957, Geol. Surv. Canada, Mem. **286**: 54, pl. 18, fig. 4-6.

Hind wing: length, 13.5 mm; maximum width, 6.5 mm.[4] Branches of Rs about equally spaced, the basal branches arising pectinately, the

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[4] The dimensions are incorrectly indicated on p. 101 of Copeland's paper (1957).

terminal ones forming a dichotomous fork. MA arises slightly basad of the level of the origin of Rs; MP with three branches; the six terminal branches of CuP are formed by bifurcation of three main branches, although their origin is not preserved in the fossil. The venational details are shown in text figure 2.

Type no. 10392 (obverse and reverse), Geological Survey of Canada. The specimen was collected by Henry M. Ami, in 1899, specifically at Howard's Mills, River Wallace, Cumberland County, Nova Scotia. This is placed by Dr. Copeland in the Riversdale group. The fossil consists of a moderately well-preserved wing, lacking only the base of the anal area and a part extending out towards the center of the wing from the base. The convexities and concavities of the veins are clearly shown but there are no indications of cross veins or of an archedictyon. The distal part of this wing is preserved on the counterpart; the rest of the wing is preserved in one piece.

As indicated above under discussion of the family relationships, the affinites of this fossil are not at all clear. That it is a palaeodictyopteron is obvious; however, the absence of an archedictyon or a cross venational system leaves us somewhat uncertain about its relationships. The main venational pattern, as indicated above, conforms to that of the Dictyoneuridae.

A DESCRIPTION OF THE MALE OF *SYMPHEROBIUS ARIZONICUS* BANKS (NEUROPTERA: HEMEROBIIDAE)

By Ellis G. MacLeod
Biological Laboratories, Harvard University

The genus *Sympherobius* Banks, 1904, is represented in the Nearctic Region north of Mexico by seventeen rather well-defined species. All but two of these were treated in detail by Carpenter (1940) in his revision of the Nearctic Hemerobiidae, while the remaining two species have been described more recently by Gurney (1948) and Nakahara (1960). Unfortunately, as the species *S. arizonicus* Banks and *S. pictus* (Banks) have been known only from females and as Nakahara's *S. stangei* was described from a single specimen lacking an abdomen, information concerning the taxonomically important structures of the male genitalia of these species has remained unknown. Recently Mr. John B. Ward of the University of Arizona has collected and forwarded for study a series of female specimens accompanied by males which he felt belonged to *S. arizonicus.* A comparison of Mr. Ward's specimens with the female type of this species shows the correctness of Mr. Ward's identification so it now becomes possible to supply a portion of the missing taxonomic information on our species of this genus. The author is indebted to both Mr. Ward and to Dr. F. M. Carpenter of Harvard University for the privilege of studying this material.

The following descriptions are based on specimens of *S. arizonicus* collected at Tuscon, Arizona, in November, 1961, and February, March, April and May, 1962. Male and female specimens of this species are being deposited in the Museum of Comparative Zoology, Harvard University, and in the U.S. National Museum, Washington, D. C.

Description of body pigmentation (based on three male and seven female specimens, all pinned) — Face with frons, clypeus and labrum tannish yellow and with a rather wide, dark brown interantennal mark extending about one-half way from lower rim of antennal fossae to epistomal sulcus; frontogenal and epistomal sulci brown, nearly black; genae medium to dark brown, this color extending as far anteriorily as the frontogenal sulci; vertex dark brown; antennae with scapes dark brown above, light tan beneath; pedicels and flagella nearly black. Pronotum nearly black with small area of light grey on lateral margins; meso- and metanota black; plurae medium brown; legs and abdomen brown.

The markings of the female holotype differ only in being somewhat lighter, which is due principally to the rather greasy condition of the specimen. The interantennal mark and the pale undersurface of the antennal scapes are both visible with only slight difficulty in the type. The wing venation and maculation of the new specimens depart in no significant regard from the condition found in the holotype and described and figured by Carpenter (1940) except that the gradates and other cross veins have a narrow fuscous margin, this being particularly evident with the two lower inner gradates and the MP-CuA cross vein.

Description of abdominal terminalia (based on three male and four female specimens, cleared and in glycerine) — Male abdomen (Pl. 6) with segments one through eight showing no unusual specializations. Ninth tergite ventrally produced and ending in a sharp posteroventrally projecting point; posterior and ventral margin with a darkly sclerotized rim; ninth sternite (Pl. 6, Fig. 1, 2, 6; IX) forming the usual subgenital plate characteristically present in *Sympherobius,* projecting a little beyond posterior margin of ectoprocts[1], broadly membranous dorsally, and appearing as a nearly equal-sided triangle when seen from above (Pl. 6, fig. 6).

Ectoprocts as in Pl. 6, fig. 1, 2, 3 (epr), consisting of a somewhat dumbell-shaped, darkly sclerotized central area bounded by a more transparent area anteriorly and posteriorly; the dorsally sclerotized portion with the usual callus cerci bearing about ten trichobothria, the ventrally sclerotized portion below the constriction much smaller and somewhat convex, this convex lobe continuing posteriorly and anteriorly into the unsclerotized areas of the ectoproct; anteriorly, this lobe is covered by numerous regularly arranged fine punctations in the nearly transparent cuticle before the sclerotized ventral portion of the ectoproct; a single very dark, posteriorly directed spine arises from a paler linear basal plate in the constricted region of the sclerotized area of the ectoproct. Gonarcus (Pl. 6, fig. 2, 4, 5 gs) narrowed posteriorly in lateral view with a large, ventrally directed portion (entoprocessus of Tjeder's terminology) near the anterior end; arcessus (Pl. 6, fig. 4, 5 ar) rather thick in lateral view, beset beneath with numerous small microtrichiae. Parameres (Pl. 6, fig. 6, 7 pa) fused for nearly their entire length, separate only posteriorly, with the tips of the anteriorly directed middle arms unexpanded and with the fused portion showing little or no indication of a tooth in lateral view.

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[1] The terminology used to describe the genital structures is that of Tjeder (1954).

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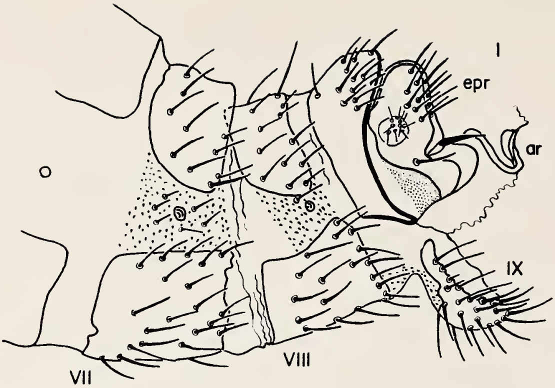

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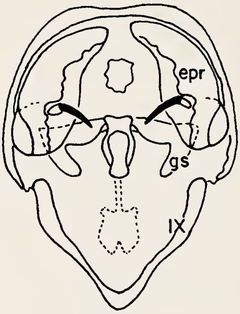

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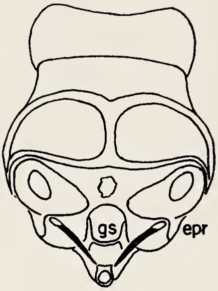

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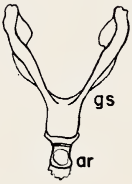

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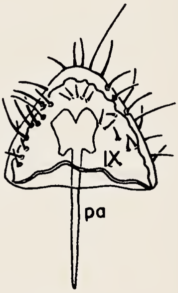

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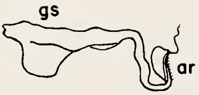

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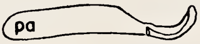

MACLEOD — SYMPHEROBIUS

Female abdomen of the usual type for *Sympherobius* with the subgenitale only slightly bifurcate posteriorly and with the small stylus of the gonopophysis lateralis twice as long as broad.

S. arizonicus clearly belongs to what Gurney (1948) has termed the *perparvus group* of Nearctic species which also includes *S. perparvus* (McLachlan), *S. killingtoni* Carpenter and *S. beameri* Gurney and which are all characterized by the presence of a single spine on the ectoproct and a close similarity in the form of the gonarcus and parameres. *S. arizonicus* differs from all of these in that the spine of the ectoproct is nearly straight and arises from a small linear basal plate from which the spine proceeds directly posteriorly rather than first arching dorsally. In addition, the other three species of this group have a rather triangular outline to the lateral wings of the gonarcus when seen in lateral view, while *S. arizonicus* has the wings of the gonarcus produced ventrally at the anterior end only and is abruptly narrowed posteriorly. The parameres of *S. arizonicus* are somewhat intermediate between *S. killingtoni* and *S. perparvus,* but lack the conspicuous tooth of the fused portion visible in lateral view. Gurney's Plates II and III should be consulted for a summary of these characters as found in the other three species of the *perparvus group.*

In terms of non-genitalic characters, the key of Carpenter (1940) will suffice for the proper identification of the males of *S. arizonicus* as the distinctive pattern of wing maculation is quite different from any of our other species, although coming closest to the maculation pattern of *S. killingtoni.*

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EXPLANATION OF PLATE 6

Sympherobius arizonicus Banks, ♂ terminalia. Fig. 1, lateral aspect of tip of abdomen. Figs. 2 and 3, postero-dorsal and dorsal aspects of tip of abdomen. Figs. 4 and 5, dorsal and lateral views of gonarcus. Fig. 6, dorsal view of ninth sternite with parameres within. Fig. 7, lateral view of parameres. Scale for all figures as indicated.

Abbreviations: ar, arcessus; epr, ectoproct; gs, gonarcus; pa, parameres VII-IX, abdominal segments seven-nine.

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The illustration on the front cover of this issue of Psyche is a reproduction of a drawing by Professor C. T. Brues of a myrmecophilous phorid fly, *Ecitomyia spinosa* Brues (Psyche, vol. 32, 1925, p. 306).

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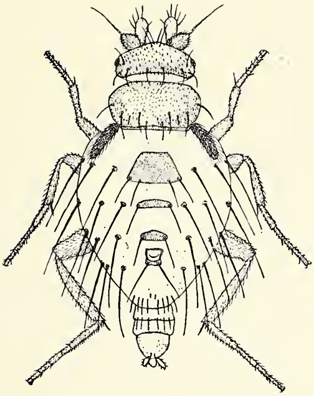

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PSYCHE

Vol. 70 JUNE, 1963 No. 2

THE VENOM AND POISON GLANDS OF *PSEUDOMYRMEX PALLIDUS* (F. SMITH)

BY MURRAY S. BLUM[1] AND PHILIP S. CALLAHAN[2]

In the United States, the small subfamily *Pseudomyrmicinae* is represented by several species which are known to sting severely. Probably the most common species in the southeastern area is *Pseudomyrmex pallidus* (F. Smith). As part of a program of study on ant venoms in our laboratories, this paper presents a characterization of the venom of this species, a description of its poison apparatus and a study of the reaction of human beings to its sting. In addition, the possible nature of the venoms produced by the *Formicidae* is discussed.

The Poison Gland

The poison gland of *Pseudomyrmex pallidus* is quite similar to that of *Solenopsis saevissima,* the imported fire ant, and the reader is referred to Callahan *et al.* (1959) for histological descriptions of the glands and sting of that species. As in the fire ant, the main gland of *Pseudomyrmex pallidus* is a rounded organ (Fig. 1D) consisting of glandular collecting ducts which branch into lateral ducts that reduce in size and lead to the secretory cells. The round gland is inserted into an invagination of the tunica propria (E) which forms the poison sac. The stored poison of the sac empties through a main collecting duct (F) into the base of the sting bulb (H). There are two extremely long (.49 mm) free poison glands (A) which lead by way of a single neck (C) to the convoluted poison gland (D). The collecting ducts of the free glands (B) unite at the neck. In proportion to the rest of the organ, the neck is considerably longer (.13 mm) and the gland narrower than in the fire ant. Dufour's gland (H) is extremely large in relation to the main poison gland, being .4 mm in length or 4/5 the length of the duct and sac of the

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main gland. In the fire ant it is only half the length of the duct and sac of the main poison gland.

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The make-up of the lancet of *Pseudomyrmex pallidus* is also quite similar to that of the fire ant with two important exceptions. The first is that the valve (Fig. 2D) is inserted quite far back at the posterior junction of the lancet body (G) with the ramus of the lancet (C), the ramus being almost at right angles to the lancet. In

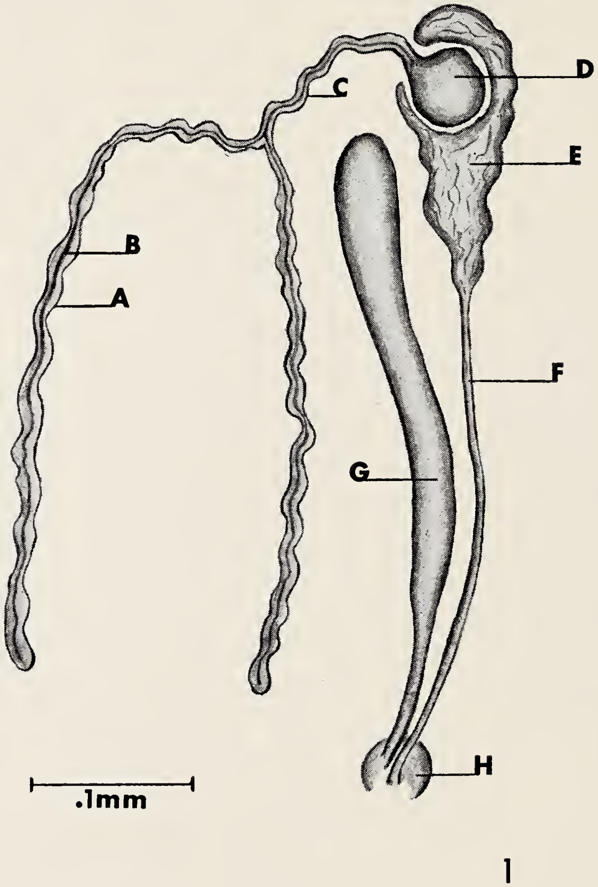

Figure 1. The poison glands of *Pseudomyrmex pallidus*. A, free poison gland; B, main collecting duct of free poison gland; C, neck of free poison gland; D, convoluted poison gland; E, tunica propria of poison sac; F, main duct of poison sac; G, Dufour's gland; H, base of sting bulb.

the fire ant the valve is inserted forward on the lancet body (See Fig. 8. Callahan *et al.* 1959) and the ramus makes more of a curve where it joins the lancet. Secondly, unlike the fire ant, the tip of the lancet of *Pseudomyrmex pallidus* is not barbed.

The Venom

The venom of *P. pallidus* was obtained by holding the isolated abdomen of the ant by the petiole and collecting the venom issuing from the everted sting in microcapillaries or in the depression of a microscope slide. As many as twelve small droplets may be obtained by this method, after which the sting is invariably withdrawn, although the poison vesicle may still contain substantial quantities of venom.

The venom is a water-clear liquid which consists of a single phase. On contact with the air, each droplet solidifies into clear plates which can be easily chipped off the glass. However, if the venom is collected directly in fine capillaries, it retains its fluidity. Examination of the poison gland and Dufour's gland reveals that both contain water-clear liquids. The substance in the poison vesicle solidifies on contact with the air to form plates identical to those formed by the venom issuing from the sting.

The solubility of the venom was determined by allowing it to issue while the tip of the sting was held under different liquids. The venom is insoluble in distilled water and forms opaque strands which suspend in the aqueous medium. In organic solvents such as methanol, chloroform, *n*-hexane and diethyl ether, the venom forms insoluble, clear plates similar to those obtained when it is exposed to air. The venom is very soluble in dilute acids.

The venom is alkaline when tested with various indicator papers as an aqueous suspension. When the poison vesicle is crushed on indicator papers it also gives an alkaline reaction but interestingly, the viscous contents from crushed Dufour's gland are neutral. The secretions of the two glands are further contrasted by the fact that the fluid in Dufour's gland is soluble in organic solvents whereas the poison vesicle contents are not.

The venom of *P. pallidus* is ninhydrin-positive, producing a dark purple coloration with this reagent. Paper chromatographic analysis of the venom did not reveal the presence of any free amino acids; the ninhydrin-positive material all remained at the origin. All these data are consistent with the conclusion that the venom of this pseudomyrmicine ant is a basic protein(s).

The small amount of venom available did not permit any further chemical characterizations.

The venom secreted from the sting of this ant is derived primarily, if not exclusively, from the true poison glands. Examinations of the poison glands of numerous ants from which venom had been collected frequently revealed that the poison vesicles were collapsed, whereas in every case Dufour's gland was distended with liquid. This was also the situation with glands from ants which had been allowed to sting human subjects. Although it is possible that traces of the secretion from Dufour's gland are secreted with the venom from the poison glands, it is quite evident that the biologically active secretion issuing from the sting of this ant essentially possesses the characteristics of the contents of the true poison glands.

Skin Responses of Humans to the Sting

Prior to stinging, the worker grips the skin with its mandibles and then arches the thorax upward so that the abdomen is bent underneath. The thorax and abdomen often form a sharply inverted v with a narrow angle between. This characteristic pose is a reflection of the elongate structure of these ants and probably provides the ant with sufficient leverage to drive the lancets into the skin. Although workers may sting for 30 seconds or more, multiple stings at one site were not frequently obtained.

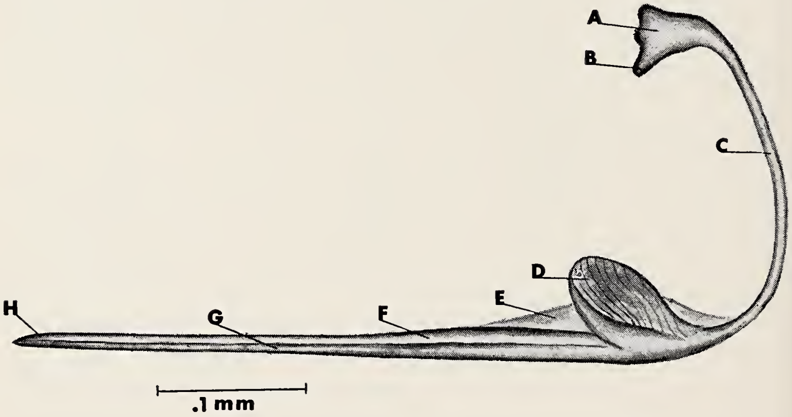

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Figure 2. The lancet of *Pseudomyrmex pallidus*. A, triangular plate (first valvifer); B, ventral apodeme of triangular plate; C, ramus of lancet (first valvula); D, valve of lancet; E, ligulate membrane; F, dorsal fin of lancet; G, main body of lancet; H, tip of lancet.

The skin response at the sting site is characterized by the immediate development of a flare, which reaches its maximum size in five to ten minutes. This is rapidly followed by the development of a wheal at the point where the lancets entered the skin. Within one hour the flare disappears and the area is marked only by the wheal which may persist for up to 24 hours. A dull pain is present after the ant has stung which becomes less intense within the first hour. A throbbing sensation is evident during this time which diminishes in intensity until by the end of the second hour very little discomfort is evident. Mild prurience is evident for at least 24 hours during which time a prominence develops at the site of the sting. This elevation is surrounded by a narrow red halo. After 48 hours, the puncture area is characteristically umbilicated and the depressed center is discolored, a condition which may persist for up to two weeks.

Discussion

One of the most significant characteristics about the venom of *P. pallidus* is that it is proteinaceous. Among the other stinging ants, only the myrmicine genus *Solenopsis* has been studied and it has been demonstrated that the venom is a non-protein (Blum *et al.* 1958; 1960). Thus, this pseudomyrmicine species is similar to vespid wasps and the honey bee in producing biologically active proteins in their poison glands whereas *Solenopsis,* a phylogenetically advanced myrmicine genus, differs in that its venom is non-proteinaceous.

The subfamily *Pseudomyrmicinae* is a relatively primitive one (Brown 1954) and it is tempting to speculate that proteinaceous venoms are characteristic of the more primitive subfamilies of ants. In support of this idea is the fact that the venoms of ponerine and doryline species that we have examined in our laboratories are proteinaceous. Along with the *Pseudomyrmicinae,* these families are more primitive than the *Myrmicinae.* In our laboratories, analyses of the venoms of the less highly developed myrmicines are now being carried out in order to determine whether or not this subfamily contains genera producing proteinaceous venoms as well.

It will of course be necessary to examine the venoms of many genera of ants in all subfamilies in order to determine whether or not proteins are limited to the phylogenetically less developed ones. It is well established that in the highly developed subfamily Formicinae, the poison glands produce the simple fatty acid formate, a considerable departure from the complexity of the proteinaceous or nitrogenous base-containing venoms found in *Pseudomyrmex* and *Solenopsis* respectively.

The function of the Dufour's gland secretion in *P. pallidus* is completely unknown. This gland is highly developed in this ant (Fig. 1) and contains at least as much material as the poison vesicle. The fact that this pseudomyrmicine species had a turgid Dufour's gland even after the poison vesicle had collapsed after secretion of the venom strongly indicates that the contents of Dufour's gland are secreted independently of the poison gland. In *P. pallidus* the Dufour's gland secretion is chemically very distinct from that of the poison gland. The fluid in Dufour's gland is a neutral non-protein which because of its high viscosity, is probably quite high boiling. In contrast, the poison gland contents consist of basic proteins which may not even be miscible with the secretion from Dufour's gland.

Wilson (1959) has demonstrated that in the myrmicine *Solenopsis saevissima* Dufour's gland produces the trail laying substance in this species. Callahan *et al.* (1959) demonstrated that the contents of Dufour's gland could be secreted independently of that of the poison glands. However, *P. pallidus* does not lay trails and indeed smears from Dufour's gland elicited no obvious responses from workers in a laboratory colony. Thus with the exception of the genus *Solenopsis,* the function of the Dufour's gland secretion in the *Formicidae* remains to be determined.

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OBSERVATIONS ON THE BALL-ROLLING BEHAVIOR OF *CANTHON PILULARIUS* (L.) (COLEOPTERA, SCARABAEIDAE)

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The present paper describes some aspects of the normal behavior of *Canthon pilularius* (L.) (*C. laevis* [Drury]) in the field and is the result of direct observations totalling about 57 hours, carried out in four field locations in Florida and Georgia in 1957 and 1961.

The approach of this study is neither ethological nor ecological, but taxonomic. That is to say, certain aspects of the normal behavior of the scarab were investigated and quantified with a view to using them as taxonomic characters in comparison with other related species and genera. My data on other species of the genus *Canthon* are not yet complete enough to present an interspecific analysis of the behavior of this genus, but are adequate for an intergeneric comparison with European representatives of the ball-rolling genera *Scarabaeus, Gymnopleurus,* and *Sisyphus,* which have been studied in detail by German investigators. Such a comparison is now in preparation by the author and will be published subsequently.

Previous literature gives the outlines of the life history of *C. pilularius* (Lindquist, 1935; Cooper, 1938; Ritcher, 1945; Miller, 1954), but there are no published observations describing the behavior sequences seen. Brief notes on the biology of about 25 other species of *Canthon, sensu stricto,* have been recorded in the literature (see von Lengerken, 1954, Pereira and Martínez, 1956, and Halffter, 1959, for discussions).

This species is commonly known in the United States literature as *Canthon laevis* (Drury). However, it has been known for some time that this is not the correct name. In a recent revision of the genus (Halffter, 1961) there is a review of the reasons showing why the name *pilularius* Linnaeus, 1758, is most probably correctly attributed to this species. Furthermore, Lane (1950) shows that even the name *hudsonias* Forster, 1771, has precedence over *laevis* Drury, 1773.

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Methods

The methods used consisted of sitting down and watching the activities of the scarabs after a quantity of human faeces or cow dung had been placed in a suitable location. Complete notes were taken describing the actions of the beetles involved, the rolling patterns were diagrammed in the field notebook, and pertinent data such as time in minutes, distances rolled (measured with a metric tape measure), terrain features, wind direction, sun position, etc. were recorded. The author always camped in the immediate area of observation so that he could be present for every phase of activity from beginning to end. Often several days were spent in the same spot, and it need hardly be mentioned that every hour of observation represents many additional hours of waiting. No special techniques were used and no experimentation was attempted. Beetles were marked with dabs of clear nail polish mixed with oil paints in different color combinations for identification; these markings were found not to last for more than a day or so because of the burrowing activity of the beetles.

The study was carried out near Arcadia, De Soto County, Florida, on 27 March, 1957, in the Osceola National Forest, Columbia County, Florida, on 7 — 11 June, 1957, near Brunswick, Glynn County, Georgia, on 13 — 14 June, 1957, and near Welaka, Putnam County, Florida, on 24 April — 6 May, 1961.

The illustrations (figs. 1 — 5) are traced exactly from photographs taken by the author and may be considered completely accurate in regard to the positions and the attitudes of the beetles and the general size and shape of the balls.

Distribution and Color Phases

Canthon pilularius (L.) is widespread in the eastern half of the United States from extreme south-eastern Wyoming, Kansas, Oklahoma, and northern Texas eastward. It is replaced in most of Texas and the Southwest by the closely related *C. imitator* Brown, which also occurs in Oklahoma, Arkansas, Louisiana, and Florida. In northern Florida east of the Apalachicola River and in southern Georgia a green or bronze phase of *pilularius* largely replaces the usual black one, while in most of peninsular Florida the species is largely represented by a blue-black phase which becomes intensely blue in the Keys. A more extensive discussion of the color phases will be found in Halffter (1961). The present observations are on all three color phases — green or bronze, black, and blue-black — and several instances of sexual pairing between all possible color combinations were observed, supporting the taxonomic evidence that there are no specific differences between them.

Morphology

The beetles are large (10 — 19 mm in length), broadly oval, and somewhat flattened (figs. 1 — 5). The head and legs are used extensively in the behavior described below and should therefore be briefly described. The head is strongly flattened and broad, with sharp edges, and is an excellent digging tool. The fore tibiae are strongly flattened and provided with teeth on the outer edges. The forelegs are used extensively in cutting and manipulating the dung and in patting the surface of the dung ball, as well as in digging. The middle and hind tibiae are very slender and a little curved and are used in rolling and guiding the dung ball. For a very detailed study of the morphology of the genus, see Halffter (1961).

The mouthparts have been described by several authors (Hardenberg, 1907; Mohr, 1930; Pereira and Martínez, 1956; Miller, 1961) and do not concern us here, particularly. The latter author showed that the molar surfaces of the mandibles are so constructed as to be capable of a very thorough grinding action. Beetles with a mandible removed were unable to feed.

There is no sexual dimorphism, other than in the forespur, and it is therefore not possible to determine the sex of a beetle without examining it closely. This complicates observation somewhat and means that a behavior sequence must be interrupted or allowed to be completed before the sex of the participants can be determined. This can be done by looking at the forespur (a lens is usually not necessary), which is bifurcate in the male and simply acute in the female.

Ecology

The autecology of this species has not been properly investigated (nor has that of any other American coprophage). It is common knowledge that the species feeds on cow dung in pastures, and my observations indicate that older dung is preferred. Decaying meat rarely attracts the beetles (Lindquist, 1935) and cadavers of small vertebrates may occasionally be made into balls and rolled off (Bragg, 1957[2]), as is commonly seen in some South American species of the genus (Luederwaldt, 1911). Human dung is readily taken, and many of the observations which follow are based on feeding behavior with human faeces.

Miller (1954) analysed the role of 17 species of coprophagous scarabs in the dispersal of human faeces in the same general geographical area in which this study was carried out. He found that *C. pilularius* made up 64% of the scarabs collected at human fecal traps in an open field in the daytime and that this species, because of its size, is potentially capable of removing more than 90% of the total exposed human dung removed by scarabs in the daytime, or 61% of the total at all times. This makes it by far the most important species of coprophage in this ecological situation (open fields). Tumble-bugs *(Canthon, sensu lato)* are not important in heavily overgrown situations, indicating the importance of the surrounding terrain.

The recent very fine studies of Landin (1961) on the ecology of Aphodiinae finally prove for this group what has long been suspected by students of the coprophages in general, namely, that it generally makes no difference what *kind* of dung is eaten by a given species, but only *where* it is deposited, that is, to what extent it will be affected by heat and desiccation. If the type of dung is important (as for instance in the cases of cow and horse dung), it is because its consistency or shape may influence temperature changes and evaporation rates (Landin, *op. cit.*).

In *C. pilularius* activity is at the highest level in the spring and is very much dependent on rains, the most intense activity being seen immediately after showers. Activity usually begins at about 0900 on warm days (when the shade temperature reaches about 90°F by 1100) and terminates at about 1700. During dry spells the beetles remain continuously inside cow droppings under the crust and I have not seen them spending this time in the soil. No studies have been made regarding optimal temperature and humidity limits for this species.

In the localities in which I observed this species the soil consisted

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[2] Bragg's observations on the rolling of decaying tadpoles were apparently made in central Oklahoma and therefore perhaps on the closely related *Canthon imitator* Brown.

entirely of white sand and was largely exposed, either on sand roads or open pastures.

Ball-rolling Behavior

The apparent function of the making and rolling of a ball of dung is to transport the dung away from the dropping and bury it to be eaten underground, where it is protected from desiccation. The dung ball serves as food either for the beetle rolling it or for the future larva. Reproductive activity is seen almost entirely during the spring months (March — May), after which adult feeding activity predominates. The behavior sequence in relation to the ball is significantly different depending on whether the dung ball is to serve as adult or larval food.

In the following account, the making and rolling of the food ball will be dealt with first. Quantitative or important statements are followed by a number in parentheses; this indicates the number of observations upon which the previous statement is based. This is to enable the reader to judge the relative reliability of a statement. Apparent discrepancies in these observation numbers are due to the fact that many fragmentary sequences were observed. Anthropomorphisms must be excused by the reader in the interest of avoiding lengthy circumlocutions.

The Food Ball

With regard to the food ball, both sexes behave the same way, acting individually. The sequence involved in the making, rolling, and burial of the ball is as follows: 1) Approaching the dung source, 2) cutting, 3) shaping, 4) rolling, and 5) burial of the ball. An additional section below is devoted to underground feeding.

The approach. When there is a wind, the beetles will approach a source of dung from down-wind, flying very low in zig-zags. At a certain moment, perhaps when the odor currents are encountered at a certain frequency, the beetle suddenly "cuts" its power and drops like a stone to the ground, often landing on its back. The point where it lands may be from three to 80 cm from the dung, usually 10 — 15 cm (5). The beetle then approaches on foot, moving jerkily with antennae outstretched. One beetle was seen to approach entirely on foot and was first spotted 150 cm away. The time it took for individual beetles to locate a given source of (human) dung after deposition varied from less than one minute to five hours and 30 min (23). Conversely, a given source of dung took from less than one minute to one hour and ten minutes to be first discovered by this species, the average being 23 min (6). Of course, these figures


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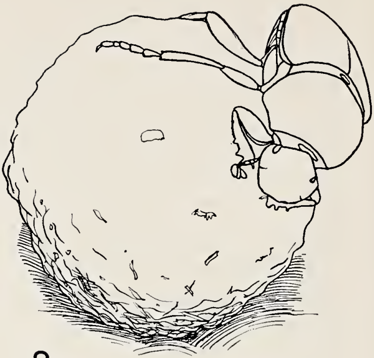
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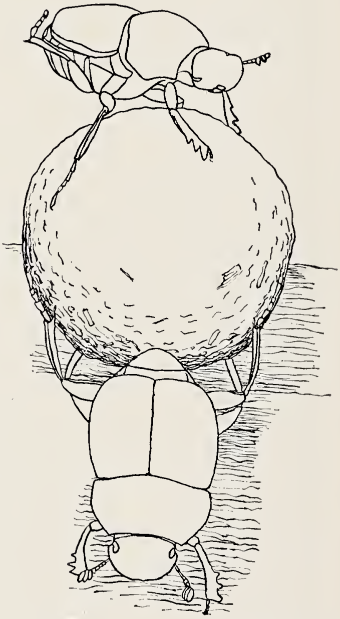
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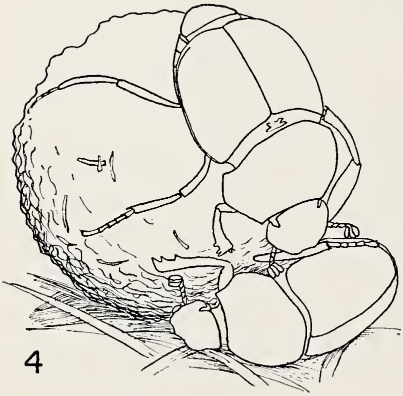
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depend a great deal on very variable factors such as the density and searching activity of the beetles and the amount of dung in a given area.

Cutting. Once a beetle has come up to a source of dung it begins immediately to start cutting a ball from the nearest portion. This process involves climbing on the dung and cutting a circular groove with the head and forelegs, the beetle pivoting in a circle. The dung is bunched up under the beetle with the forelegs and quickly acquires a ball-like shape (fig. 1). When the bunched dung is of a certain quantity, it is detached by reaching under and cutting the lump away at the base in a circle (fig. 3). At this point, if the quantity of dung in the lump is adequate, shaping begins. If it is not, the beetle, resting on the lump, reaches out with the forelegs and grasps small quantities of dung from the main pile (or sometimes from balls of other beetles) and adds them to the lump (fig. 1). I do not know how the beetle estimates the quantity of dung in the lump. The process of cutting takes 2 — 14 min, averaging 8.7 min (12).

Shaping. Once cut and detached, the crude lump is converted into a more or less perfect sphere. Before shaping, the detached lump may be rolled a short distance (3 — 30 cm) away from the main pile. The process of shaping involves patting the lump rapidly over and over with the underside of the fore tibiae acting alternately, with the beetle climbing over the surface of the ball (fig. 2) or lying to one side of it and rotating the ball slowly so that the entire surface is patted many times over. The head may also be used to trim lumps or fibers off the ball surface during this process. Occasionally, new material may be added to the ball during the shaping process also (2). For the food ball, the shaping process takes 2 — 7 min, averaging 4.2 min (15).

At this point the ball is made, the entire process (cutting and shaping) having taken 12 — 20 min and averaged 15.1 min (12). The food balls are often crude and not symmetrical, and measure 15 — 23

EXPLANATION OF PLATE 7

(All figures drawn from photographs taken by the author)

Fig. 1. Lone beetle adding more material to food ball during cutting process. Fig. 2. Lone beetle shaping food ball. Forelegs are used to pat surface of ball. Fig. 3. Male and female pair cutting brood ball. Beetle at right is severing ball at base. Fig. 4. Male and female pair shaping brood ball. Both beetles are going over surface of ball with forelegs. Fig. 5. Rolling completed brood ball. Male is below, pushing ball backwards over an obstacle. Female is above, balancing on moving ball. This relationship of the sexes during rolling is invariable. Note smooth contours of completed brood ball.

mm across their short diameter and 17 — 30 mm across their long, averaging 19.8 × 22.9 mm (11).

At one location (Brunswick, Ga.), I repeatedly noted a curious activity by eight of the 18 beetles observed. It occurred during the shaping process and involved rapidly rotating the ball in the sand, in a stationary position, for about two minutes with the result that the ball became coated with sand. As the ball acquires a sand coat on being rolled anyway, this observation cannot yet be explained.

Rolling. Once shaped, the ball is quickly rolled in a direction away from the dropping. Rolling is performed with the beetle head-downward behind the ball, pushing backward against the ground with the forelegs and steadying the ball with the middle and hind legs. The middle legs alternate between the ground and the ball and the hind legs are always in contact with the ball, alternately pushing against its surface with walking movements. When an obstacle is encountered the beetle will always attempt to push the ball over it rather than go around it (fig. 5). Frequent falls and tumbles occur, as a result of which the beetle may temporarily lose the ball. If this happens, the ball is searched for on foot in random patterns by the beetle, antennae outstretched. The procedure before resuming rolling after a tumble is always the same: the beetle climbs on top of the ball and turns so as to come down on the side of the ball necessary to resume rolling in the same direction in which it was rolling immediately before the tumble. Occasionally (2), the beetle will pause seemingly without reason, climb on the ball, turn around in either direction, and descend to resume rolling.

Once started in a given direction, the beetle will continue in this direction about half the time (13 of 23), although the actual course followed is quite zig-zag at best. The rest of the time there are pronounced changes in direction during rolling (enforced direction changes due to obstacles are not counted here). I have attempted to relate the direction in which a ball is *first* rolled away from the dropping to three possible environmental factors: the wind direction, the slope of the ground, and the position of the sun. In figures 6 — 10 I have indicated by dots the initial directions taken in relation to each of these three factors in turn, according to 70 observations on both food and brood balls in all localities. The number of dots indicates the number of times a ball was seen rolled at a given angle (to the nearest 45°) from the position or direction of the environmental factor indicated.

Chi-square calculations were made on each of the diagrams to ascertain the probability that the distributions obtained might have resulted by chance. Four class intervals were used for this, corresponding to four directions rather than the eight shown in the diagrams, since the numbers are too small to give meaningful results for eight class intervals. The chi-square figures and corresponding probabilities for three degrees of freedom are indicated in each diagram.

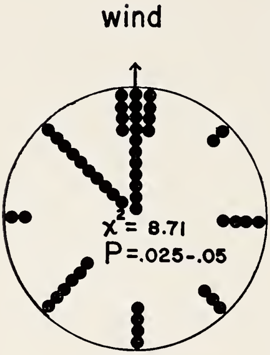
The diagrams and numbers may be interpreted as follows: If the distribution is significantly skewed when all observations are plotted in relation to the direction of one particular factor, we may expect that this factor overrides all others in governing the direction the ball is rolled. Such a factor is obviously the slope of the ground, the beetles rolling uphill ($P = <.005$) (fig. 8). Another strong factor appears to be the wind direction (balls rolled with the wind), but it is evidently not as overriding ($P = .025 — .05$) (fig. 6). When all observations are plotted in relation to the position of the sun, the resulting diagram is not very strongly skewed, having a relatively high probability of being a chance distribution ($P = .05 — .10$) (fig. 9). We may interpret this to mean that the sun position is the least influential of the three factors analyzed.

In order to pinpoint more accurately the influence of a single factor it is better to subtract observations which were also under the influence of other factors. It was possible to plot the directions in relation to the wind where the ground was level (minus the ground slope factor) (fig. 7), but this did not reveal a more significant relationship, for some reason. To have subtracted the sun factor as well would have left too few observations.

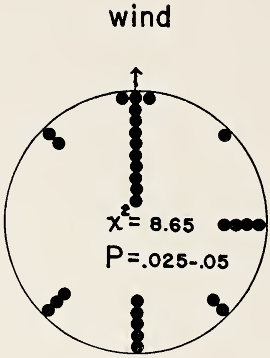
The situation with regard to the sun is quite different when we plot the observations obtained when the other factors played no part, that is, when there was no wind and the ground was quite flat. In these cases, the distribution is very significantly skewed, with 13 out of the 19 observations being either directly toward or directly away from the sun (fig. 10). The probability that this could have been brought about by chance is .005. It appears, therefore, that the sun is used in some way in guidance, providing more important factors do not intervene. More will be said on this matter in the discussion at the end of the paper.

The relation to the wind may be simply explained: the beetle approaches the dung from down-wind and therefore tends to work on the leeward side of the dropping. Once made, the ball is simply rolled away from the dropping, and this will automatically be more or less in the direction of the wind, other factors being equal. The

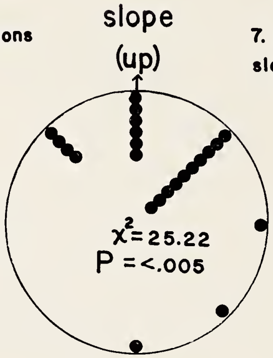
Directions Rolled in Relation to Three Environmental Factors



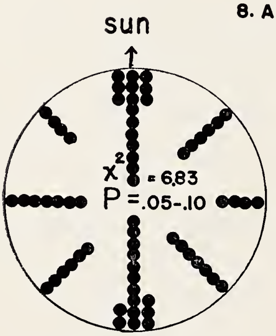
6. All observations



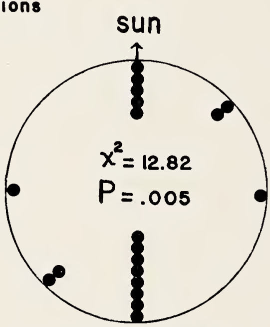
7. Minus ground slope factor



8. All observations



9. All observations



10. Minus ground slope and wind factors

Matthews — Canthon

tendency to uphill rolling may also be simply explained by the fact that it is difficult to roll a ball sideways or downward on a slope without losing control of it.

The length of time that a food ball is rolled before burial varies from two to 18 min and averages 9.5 min (16) (not "about an hour or more" as Lindquist states), and the distance rolled depends a great deal on terrain, of course; a heavily grassed or littered area impedes the progress of the beetle. The distance from the dropping that the food ball is rolled before burial varies from 15 to 830 cm, averaging 267 cm (19). This is not the straight-line distance, but that actually travelled by the beetle, as measured by tracing a line on the ground behind the beetle and measuring each twist and turn.

It is evident that almost any spot will do for burial and the beetle is not "seeking" an ideal spot. It is not clear what factors prompt the beetle to begin burial, as both the time and distance rolled are very variable.

Burial. When the time for burial has arrived the beetle will pause and dig a little in the soil under the ball. This is presumably to test the ground to see if it is suitable for burial. Usually (12 of 16), the very first spot tested is that where the ball is buried. Otherwise (4 of 16), one or two other spots are tested before the final burial place is chosen, the beetle resuming rolling after rejecting a spot. Burial takes place by pushing soil to the sides from under the ball in such a manner that the beetle sinks rapidly into the ground with the ball on top of it. The food ball is buried 1.5 — 4 cm below the surface, that is to say, at a very shallow depth (9). At Brunswick, Ga., where I measured soil temperatures at burial depth I found them to be only 1 — 9° C below the air temperature of 35° C (10).

Feeding. What happened after the food ball was buried was not directly observed, but some idea of the underground activity could be gained by unearthing different balls and beetles at varying intervals after burial. Fourteen such balls were dug up at intervals of 1:35 to 49:30 hrs after burial and indicated the following: The beetle may not begin to nibble at the ball up to 6:08 hrs after burial, but on the other hand it may have begun feeding at 1:35 hrs or earlier. The

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EXPLANATION OF PLATE 8

Figs. 6-10 represent the directions in which balls were seen rolled in relation to three different environmental factors in all localities, to the nearest 45° angle. Total of beetles observed is 70. Each dot represents one observation in the given direction. Chi-square and corresponding probability figures for three degrees of freedom are given in each diagram. Further discussion in text.

ball is entirely consumed in 26 — 30 hrs after burial. The beetle stays with the remains of the ball for some hours and sometime between 30 and 50 hrs it departs, leaving only coarse fibers and beetle excrement in the hole.

Feeding by adults is said to occur also directly on the dropping, without a ball having been previously made (Lindquist, 1935). I have not observed this in this species in the field, although this habit is common in a related species (*C. chalcites* [Haldeman]).

The Brood Ball

The behavior involved in the making and rolling of the ball destined to be converted into a brood pear[3] and serve as food for the larva is similar to that just described for the adult food ball but differs in a number of respects, the most important of which is the participation of both sexes in the making of a single ball. Although the importance of the male's role in this respect had been foreshadowed by comments in the literature on other species and genera (cf., e.g. Halffter, 1961, on *C. h. humectus* [Say]), I was surprised at the extent of the male's participation. The male plays the leading role in the making of the brood ball, and it is he exclusively who rolls, defends, and buries the ball, the female's role in these activities being purely passive.

The following account will deal in turn with the encounter of the sexes, the making of the ball, rolling and burial, robbery and combat, and underground activity.

The encounter of the sexes. I was able to observe the crucial moment of the meeting of the future pair only twice, and both of these instances are described in detail below. They are probably rather unusual in the lateness of the encounter in the behavior sequence, since in both cases the female only joined the male ball maker after the latter had completed the ball. More usually (11 of 13), the two members of the pair are seen cooperating in making the ball (figs. 3, 4). This means that the sexes meet and join early in the ball making process. From the two observed instances described below, it seems most probable that the male initiates the ball-making process and is subsequently joined by the female.

The first instance was observed near Brunswick, Ga., on 13 June, 1957. A large green male began making a ball (after trying to rob one from another male) at 1235. At 1310 he was still shaping the ball with very great care. At 1311 a small black female landed nearby and approached. She was met with hostility and repeatedly rebuffed

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[3] The term "brood pear" is a rendering of the German "Brutbirne" and is much more descriptive than the usual term "egg ball".

by the male, who used fighting movements to be described in the section on combat, but she persisted until the male accepted her presence. She climbed onto the ball and, since it was completed, it was rolled off at 1312 by the male, with the female clinging to it. The activities of this pair were followed for nine days in captivity and resulted in the formation of a brood pear containing an egg.

The other instance was observed near Welaka, Fla., on 6 May, 1961. A male was first seen making a ball with very great care and was observed for 20 minutes painstakingly patting the ball to a smooth sphere. During this time the beetle had to repulse no less than seven male intruders (the sex was checked in each case) apparently bent on robbing the ball. One intruder was chased some distance. The eighth intruder appeared when the ball was completed and about to be rolled off and was met with equal hostility, being rebuffed several times. It kept coming back, however, and was finally accepted, climbing onto the ball and being rolled off with it. On subsequent examination it proved to be a female.

These two observed instances of the moment of encounter are very much alike in that in both cases the male had completed the ball before he was joined by the female, and the male rebuffed the female several times before accepting her. Perhaps when the encounter occurs earlier, as it normally does, the male is less hostile.

The making of the ball. It will be noted from the first account above that the cutting and shaping of the brood ball by the male took 35 min, whereas cutting and shaping the food ball takes a maximum of 20 min. I also came across seven more pairs at work on the brood ball and watched them work for more than 20 additional minutes in all cases. It is evident, therefore, that a great deal more care is taken in making the brood ball, particularly in the shaping process. The interesting point is that a male beetle makes a *brood ball* even when he is all by himself, before being joined by the female. This is shown by the length of time spent in shaping the ball, and the experienced observer can always tell quite readily whether a food ball or a brood ball is being made by a lone beetle. I have seen ten males making brood balls alone, but no females. It seems most probable, therefore, that the male initiates the brood ball making process and is then joined by the female, who cooperates in both the cutting (fig. 3) and shaping (fig. 4) processes.

As may be imagined from the great deal of shaping that the brood ball undergoes, it is a much more perfect sphere than the food ball and has a much smoother surface (fig. 5), but there is no reason to believe that it contains any material different or more selected than the adult food ball. All the extra care appears to go into the surface layer. The brood ball measures 20 — 22 mm in diameter (10).

Rolling and burial. Unlike the food ball, which once shaped is rolled off more or less without interruption, the brood ball is often shaped several times during pauses in the rolling process. Shaping, as previously stated, is a cooperative act of the sexes and the female will often be seen continuing shaping even while the ball is being rolled. It is the male exclusively who rolls (17), the female merely walking head upward over the forward surface of the ball in time with its rotation, as on a tread mill (fig. 5). She does not help in the rolling process in any way that I could see, except perhaps as a counterweight. On the contrary, when the male has temporarily lost the ball after a tumble or is fighting off an attacker, the female will sometimes make off with the ball herself (3). In the three such cases observed the male soon caught up with the female rolling the ball and displaced her in the rolling position, whereupon the female climbed back onto the ball.

Table I. Data on dung balls made by *Canthon pilularius* (L.)

	FOOD BALLS			BROOD BALLS		
	Range	Average	N	Range	Average	N
Time for making ball (min)	12-20	15.1	12	>20-35	—	8
Size of ball (mm)	15-23 × 17-30	19.8 × 22.9	11	20-22 × 20-22	20.7 × 20.7	10
Time rolled (min)	2-18	9.5	16	3-23	9.3	10
Distance rolled (cm)	15-830	267	19	90-1060	414	14
Depth buried (cm)	1.5-4	2.6	9	6-10	7.6	9

The actual rolling process is the same as that described for the food ball. During the orientation pauses after a tumble, when the male roller climbs onto the ball, he comes into contact with the female but no longer displays any hostility toward her.

The distances that brood balls are rolled vary from 90 to 1,060 cm, averaging 414 cm (14), and are thus somewhat more than the distances recorded for the food balls, although the time spent rolling seems to average the same (table I).

The burying process is the same as that described for the food ball. The male does all the work, the female clinging passively to the ball and being buried with it. As the ball begins to disappear below the surface the female will dig down beneath it, presumably to ensure that she will not be left at the surface. The brood ball is buried 6 — 10 cm below the surface (9), two or three times as deep as the food ball. Subsequent activity underground is discussed below.

Since the encounter of the sexes is a chance one, there are many instances when the male, having completed a brood ball, is not joined by any female. In this case, he will roll the ball off anyway and bury it (8). One such ball was dug up 18 hrs later and was found intact, with the male next to it. This suggests that the beetle stays with the ball for a time without eating it, and then perhaps abandons it. Abandoned brood balls are not rare in a pasture.

Robbery and combat. Few attempts at ball robbery are observed during feeding activity later in the season, but during mating activity in the spring such attempts are extremely frequent and ball makers are under constant attack. In all instances checked (21), the attackers were males and the defenders also males. Since the female apparently never initiates ball making on her own, but joins a male already busy, she does not have to defend any balls and is not involved in combat. When the mating pairs have joined, the male of the pair is always the one called upon to repel attackers, the female usually sitting on the ball during the fight. In only one instance was I able to observe a successful robbery, the usurper making off with both the ball and the female of the other male.

The fighting movements involve primarily the head, which is used to butt, that is to say, to push upward and outward against the opponent. Each antagonist attempts to place the edge of its head under some part of the body of the opponent and then quickly jerk it upward. If successful, this procedure flips the opponent away and onto its back. The defender of a ball always has the advantage because it can use the ball to protect its underside by clinging closely to it, hence the small number of successful robberies. In addition to the head, all the legs are often used and the beetles may grapple together. Fights are of very brief duration and apparently do not result in any injury to the participants.

To summarize, the typical situation at a cow dropping during the reproductive season is as follows. A few males and pairs are making balls and several males are roving about trying to steal a ball rather than make one. These males are repulsed by the males of the pairs making balls, or the single male ball makers. One or two females may also be wandering around, presumably looking for mates. When one of these females comes upon a lone ball maker, she will probably be accepted, as we have seen. When she approaches a pair, the male of the pair will repel her (2). Ball rollers are also frequently attacked by roving males and violent fights may ensue.

Underground activity. When the soil is sufficiently compact to allow it, the ball and pair are in a definite chamber which is just large enough to hold the ball and the beetles. There is about 5 — 10 mm of space all around the ball. A definite passageway, which is left open, leads down at an angle from the surface. The nest is marked at the surface by a very low mound of loose soil, often very difficult to detect except to the experienced eye. As previously stated, the ball is buried 6 — 10 mm below the surface.

What occurs underground was investigated by digging up seven brood balls whose burial had been observed, at varying intervals after burial. In addition, 17 older brood pears were dug up in various pastures in Florida in April. Copulation apparently takes place a few hours after burial. Only one instance of this was observed; this was near Arcadia, Fla., on 27 March, 1957, 3:10 hrs after burial. The pair were unearthed *in coitu* next to the ball. On four other occasions the male was still present in the nest up to 21:35 hrs after burial. On the other two occasions investigated, 21 and 22 hrs after burial, the male was gone, the female being alone with the as yet unmodified brood ball. It seems therefore that the male's role, far more important than is usual among insects, is terminated at about this point. On all these occasions the brood ball had not been touched and was still spherical. Some time after the male departs the female must lay one egg into the ball and convert it into a pear. I have not observed this process and do not know when or how it occurs. In captivity, a ball made by a male in the manner described for brood balls, and rolled and buried with the female, was converted into a pear containing an egg in a period between four and ten days after it was buried.

Once converted into a pear, the ball is abandoned by the female and left unattended in the soil. I collected 17 such unattended brood pears in several pastures at Welaka, Fla., in April, 1961. Those broken open were found to contain either a first-, second-, or third-instar larva. The brood pear and larva have been described elsewhere (Lindquist, 1935; Ritcher, 1945). Lindquist gives the development intervals for each instar and gives the total development period from hatching to adulthood as 29 — 44 days in captivity. There is only one brood pear per nest.

Discussion of Sun Orientation

The observations presented above on the possible role of the position of the sun in guiding the direction of ball rolling merit some discussion in view of the considerable amount of experimental work done in Europe over the past ten years on this aspect of behavior in a geotrupine scarab, *Geotrupes sylvaticus* Panz. (see especially Geisler, 1961).

My observations above suggest that in the absence of stronger guiding stimuli *Canthon* tends to roll away from the dropping in a direction which is either directly toward or directly away from the position of the sun (i.e., at an angle of 0° or 180°) (fig. 10). By extensive experimentation Geisler (1961) was able to demonstrate definite "preference angles" (Vorzugswinkel) of travel in *Geotrupes* of 90°, 45°, and 0° angles from the position of the sun or the plane of oscillation of polarized light from the sky. Whether the preference angles are to the right or to the left of the sun depends on whether it is afternoon or before noon respectively. This is brought about by the use of the right eye in the morning and the left eye in the afternoon for orientation and makes east the preferred direction in the morning and west in the afternoon. The alternation of eye use and consequent complete reversal of preferred direction (bearing in mind the movement of the sun) enables the beetle to return in the afternoon to the place it left in the morning. *Geotrupes,* therefore, has a definite compass-true orienting ability — requiring an angle-true orientation plus a time sense ("built-in clock").

According to Wagner (1957), the sun plays an important part in orientation during ball rolling also, the beetles apparently using its position to maintain travel in a given direction, the most frequent direction being directly toward the sun. These observations were carried out in Mexico on "Geotrupinae" — however, this subfamily does not roll balls and it seems almost certain that a species of *Canthon* was involved.

The Geotrupinae are neither ball rollers nor primarily dung beetles, but it is possible that the light-compass orientation seen in *G. sylvaticus* occurs also in *Canthon* and other ball rollers. The exact adaptive purpose of this orienting ability is not clear either in *Geotrupes* or *Canthon,* but it will be remembered that after a tumble *C. pilularius* always climbs on top of the ball before resuming rolling.

This may possibly be to orient to the sun in order to continue rolling in the same direction as before.

Summary

The natural behavior in the field of the common Eastern tumblebug *Canthon pilularius* (L.) is discussed. Two types of dung balls are made: food balls and brood balls. The former are made, rolled, and buried by a single beetle of either sex to serve as food for itself, the latter are made, rolled, and buried by a male, accompanied by a female, to serve as food for a single larva.

Both types of balls are made, rolled, and buried similarly and involve a succession of separate processes. Time intervals and measurements are given for each phase of the behavior sequence. The brood ball is shaped much more carefully than the food ball and is a more perfect sphere; it is rolled farther and buried deeper.

The direction in which a ball is rolled away from the dropping was found to have some relationship to the slope of the ground, the wind direction, and the position of the sun, in that order of priority. Some discussion of sun orientation is presented.

The male is always the active partner in relation to the brood ball — he initiates ball making before the female joins him, he rolls the ball entirely, defends it from other males, and buries it unaided. The female cooperates only in making the ball and is otherwise passive.

The pair copulate soon after burial and the male seems to stay about 22 hours with the ball and female. The female stays several days longer to lay one egg in the ball and convert it into a brood pear, which is then abandoned and left unattended in the soil.

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DEFENSE MECHANISMS OF ARTHROPODS. XI. THE STRUCTURE, FUNCTION, AND PHENOLIC SECRETIONS OF THE GLANDS OF A CHORDEUMOID MILLIPEDE AND A CARABID BEETLE.[1]

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In the course of exploratory field studies on arthropods with defensive glands, we came across two species which emit a strong and persistent phenolic odor when handled. One is a carabid beetle (*Chlaenius cordicollis* Kirby), the other a chordeumoid millipede [*Abacion magnum* (Loomis)]. The fact that both animals produce repellent secretions is not surprising, since many other carabids and millipedes are well known for their defensive glands. But the particular phenolic odor possessed by these two species is unlike the odor of any other arthropod secretion that has been studied (for a summary of defensive secretions of arthropods see Roth and Eisner, 1962).

The purpose of this paper is to report on the nature of the two phenols involved, and to discuss the structure and mode of operation of the glands, as well as their defensive effectiveness. Both species were collected in the environs of Ithaca, N. Y. *Abacion* was from leaf litter in deciduous woods, and *Chlaenius* from beneath rocks near a creek bed. We had available for study ten specimens of *Abacion* and about two dozen *Chlaenius*.

I. Glandular Apparatus and Discharge Mechanism.

a. *Chlaenius*

Chlaenius has a pair of glands, the openings of which are visible as two tiny slits, situated submarginally on the hypopygium a short distance behind the terminal spiracles (Plate 9, fig. 1). When a live

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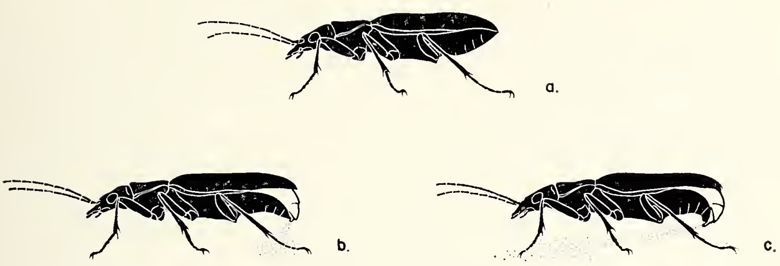
beetle is grasped gently by its front end, it can be induced to discharge one or more times simply by tightening the grasp intermittently or by pinching individual legs with forceps. When viewing such a beetle ventral side up with a stereomicroscope, it becomes evident that the secretion does not emerge as a liquid ooze, but is expelled from each opening as a jet of finely dispersed spray. At the moment of discharge there is seen to project from each glandular pore a short slender nozzle (Plate 9, fig. 1), from the tip of which the spray shoots forth. By prodding or pinching first one leg and then another, it becomes clear that the spray is not ejected in a fixed direction, but is aimed with some accuracy toward the particular appendage stimulated. Aiming is determined by the degree of flexion of the abdominal tip. When anterior legs are stimulated, the tip bends downward sharply, so that the projecting nozzles point forward almost horizontally. When middle or hind legs are stimulated, the bending is less pronounced, and the nozzles point downward at an angle (Text fig. 1). Also apparent was the fact that the discharge is not necessarily from both glands at once. When the stimulus is a unilateral one (e.g. the pinching of a leg) only one nozzle is seen to evaginate and spray, and this is invariably the one corresponding to the side of the body stimulated.



Text fig. 1. Diagrams of *Chlaenius,* showing how the beetle aims its spray by bending the tip of the abdomen. At *a,* the beetle is at rest; at *b,* the discharge is in response to stimulation of a hind leg; at *c,* the target is a stimulated middle or anterior leg.

Additional experiments were designed to determine more precisely the accuracy of aiming. The technique employed was the same as used previously with other arthropods that spray (Eisner, 1958a, 1958b, 1960a; Eisner et al., 1959, 1961). Individual beetles were attached to rods and placed on sheets of indicator paper impregnated with a chemical mixture that discolors in the presence of the secretion, thus enabling a visualization of the spray through the pattern of spots engendered on the paper. The mixture used as an indicator was an aqueous solution of ferric chloride and potassium ferricyanide. In the presence of secretion this mixture turns to an intense blue (the secretion acts as a reducing agent, causing formation of Prussian blue)[2].

Several beetles were subjected to traumatic stimulation, either by pinching single legs or antennae with forceps, or by touching various regions of the body with a hot probe. Any one such stimulus invariably induced a prompt aimed discharge (Plate 10, figs. 1-4). As expected, the discharge was always from one gland alone, providing the stimulus had been a unilateral one. Thus, stimulation of a leg or antenna of one side, was followed by an ejection from the gland of that side only. Similarly, when one side of the head or abdomen was touched with a hot needle, only the gland from the corresponding side discharged. But when the head was touched on both sides simultaneously, or when the abdomen was seized with broad-tipped forceps, then the discharge was a synchronous one from both glands.

Chlaenius cannot revolve its abdominal tip upward and around so as to spray upon its back. Touching the thoracic dorsum or elytra with a hot needle caused the animal to discharge forward under the abdomen in the usual fashion. Under such circumstances the traumatized region is likely to receive at best an incidental spattering of droplets.

A fair idea of the usual range of the spray can be obtained from figures 1-4 in Plate 10. Range is determined by the downward angle at which ejection occurs, hence the most anteriorly directed discharges are the farthest reaching. Maximum spray impact was within a radius of 10 cm., although occasional droplets nearly always surpassed this range, and sometimes reached as far as 50 cm. away.

The number of discharges that could be elicited from each gland of beetles that had remained undisturbed for two previous weeks ranged from two to four (five beetles tested). As a rule, the bulk of the secretion is expended with the first discharge; a much more scanty spray pattern is produced by the second discharge, and the third and fourth leave no more than a few scattered spots at close range.

Only three specimens were available for dissection, but this sufficed to establish the overall similarity of the glands to those of *Chlaenius velutinus* Duftschmid, briefly described and diagrammed by Dierckx (1899). The two glands are situated symmetrically on both sides of the midline in the posterior dorsal abdomen (Plate 11,

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[2] We are indebted to George M. Happ for suggesting the use of this particular indicator mixture.

fig. 2). Each consists of a racemose cluster of secretory cells (A), drained by numerous fine cuticular ductules that converge to merge into a single long and slender efferent tube (B). The tube leads to a capacious and strongly muscled storage reservoir (C), from which secretion is expelled *via* a short ejaculatory duct (D) that opens on the hypopygium.

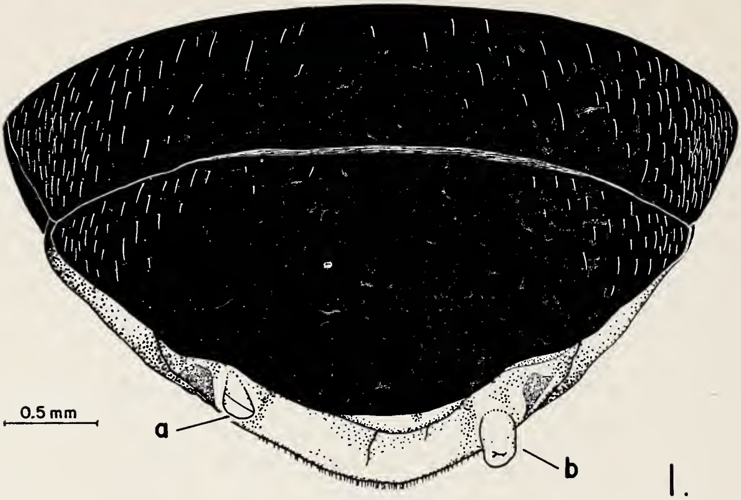
The opening itself is slit-like, the duct at this point being maintained closed under the spring-like action of an especially modified cuticular valve. Examination of a KOH-treated specimen consisting of cuticle alone confirmed the fact that closure of the orifice is maintained passively without muscle enforcement: the orifice was tightly collapsed, and could only be opened by prying with a glass needle.

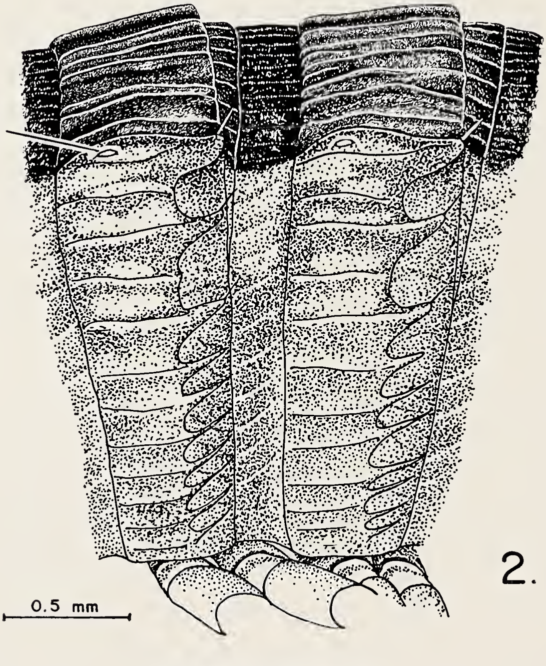
The ejaculatory duct is surrounded by circular muscles (Plate 11, fig. 4, C), but these do not extend the full length of the duct. The terminal portion is naked (E), and consists of only the cuticular intima and its surrounding epithelium. It is evidently this naked section that is extruded at the moment of discharge to form the spray nozzle. Two special muscles seem to effect nozzle extrusion. One of these is a broad and short sheet of fibers (A), originating on the hypopygial cuticle near the pore, and extending obliquely to the duct to merge with the duct's intrinsic circular muscles. Contraction of this muscle pulls on the duct, forcing its evagination. The second muscle (B) inserts on a cuticular flap at the edge of the pore and, after bending around the duct, extends to attach on the hypopygial cuticle. This particular muscle serves to force apart the cuticular valve that ordinarily closes the pore, thus enabling the nozzle to be extruded at the time of discharge. Without a gaping pore orifice, extrusion would be impossible and the tube would simply buckle.

b. *Abacion*

In this millipede, as in so many others that produce defensive secretions, the glands are distributed segmentally, one pair to each of most diplosegments. Only the first postcephalic segments and a few preanal ones lack glands. The openings of the glands are tiny pores situated dorsolaterally on the anterior half of the diplosegment, each on an elongate crest that protrudes from the tergum (Plate 9, fig. 2; Plate 12, fig. 3).

The ease with which a given *Abacion* may be induced to discharge varies greatly. Some discharge at once, the moment they are first picked up, but this is the exception. More often they will tolerate considerable prodding and even prolonged handling before the dis-





Defense Mechanisms

tinct phenolic odor finally becomes noticeable. But even the least responsive individual will eventually discharge when the stimulus is a more traumatic one, as for instance when legs are persistently pinched with forceps, or when the body is touched with a hot needle.

The secretion is not sprayed as in *Chlaenius,* but is discharged as discrete white droplets that ooze forth from the various glands and collect at the pore openings (Plate 12, fig. 2). The discharge is not from all glands at once, but is restricted to the glands of the region traumatized. Insufficient millipedes were available to study the precise pattern of discharge localization, or to determine in some detail the relative effectiveness of various types of traumatic stimuli. It seemed clear, however, that the first glands to discharge are those of the specific segments stimulated and that, with persistent stimulation at the same locus, the response tends to spread to adjacent segments, but never to more than a few on both sides of the area stimulated. Stimulation of the head — which lacks glands — results in an instantaneous ventral curling of the front end of the animal, so that the head is brought in close proximity to the first gland-bearing segments, which under these circumstances are ones that discharge. Once a millipede has been caused to discharge at a particular locus, subsequent discharges at other loci may usually be induced rather readily (e.g. by scratching with a cold needle), without resorting to the rather strong trauma (e.g. persistent pinching of legs, cautery) that is ordinarily required to evoke a first discharge. In all preceding respects, *Abacion* bears close resemblance to other millipedes whose discharge mechanism has been studied in some detail (Kafatos, 1961).

Each gland of *Abacion* consists of a spherical cuticular reservoir (Plate 12, figs. 3, 4), dorsolaterally situated in the posterior half of the diplosegment, and embedded within the thick multilayered somatic musculature. As evidenced from microscopic whole mounts of stained preparations, the wall of the reservoir consists of an outer glandular epithelium and an inner cuticular intima. There is no surrounding musculature: examination in polarized light—which ordinarily reveals even the most tenuous muscle fibers (Eisner, 1962)—served to confirm their absence.

EXPLANATION OF PLATE 9

Fig. 1. Ventral view of abdominal tip of *Chlaenius,* showing the slit-like gland opening as it appears at rest *(a),* and the nozzle *(b)* that projects from the opening at the moment of discharge (the nozzle was drawn from memory after observing beetles spraying under a microscope; its general proportions are probably accurate).

Fig. 2. Left lateral view of two diplosegments of *Abacion,* showing gland openings, one of them labelled *(p).*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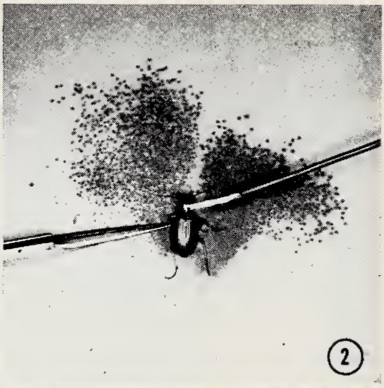
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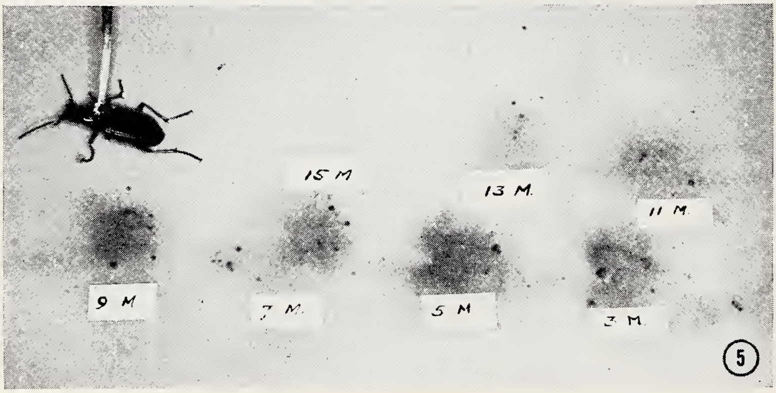
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DEFENSE MECHANISMS

The reservoir leads to the outside by way of a narrow duct, the terminal portion of which is occluded by a valvular infolding of the cuticular duct wall. A single muscle (Plate 12, fig. 4, A) inserts on this infolding, and extends to its origin on the body wall. It obviously serves to open the valve, clearing the duct lumen for the discharge.

In the absence of compressor muscles around the reservoir, there remains the question of how secretion is expelled. Perhaps compression is effected indirectly by the contraction of some of the somatic muscles that tightly surround the reservoirs. But it is also conceivable that the discharge is triggered by a rise in fluid pressure within the hemocoel, caused perhaps by a local telescoping of segments. These two possbilities need not be mutually exclusive.

II. Identification of the Phenolic Constitutents of the Secretions.

a. *m*-Cresol (*m*-methylphenol) in *Chlaenius*.

A total of ten glands were excised intact from beetles that had been freshly killed by freezing, and the secretion (a milky white emulsion) was aspiratd into fine glass capillaries as it emerged from the ejaculatory ducts, following compression of the reservoirs with forceps. The entire glandular apparatus was previously blotted dry with filter paper, thus minimizing the amount of extraneous fluid taken with this secretion. The capillaries were powdered in a small mortar and extracted with carbon disulfide. The solution was then dried over anhydrous magnesium sulfate, and concentrated by evaporation of the solvent in a stream of nitrogen. The infrared spectrum of the residual solution (Model 137 Perkin Elmer Infracord Spectrophotometer; 0.5 mm. liquid cells with KBr windows) was similar in all major respects to that of an authentic sample of *m*-cresol (Text fig. 2). The discrepancy in the region of C-H stretching (*ca.* 3.5 μ) and in the carbonyl region (*ca.* 5.8 μ) suggests that *m*-cresol is not the only component of the natural product.

The presence of *m*-cresol was confirmed by vapor phase chromatography (Aerograph Model 600 "Hy-Fi", using 3% neopentyl glycol

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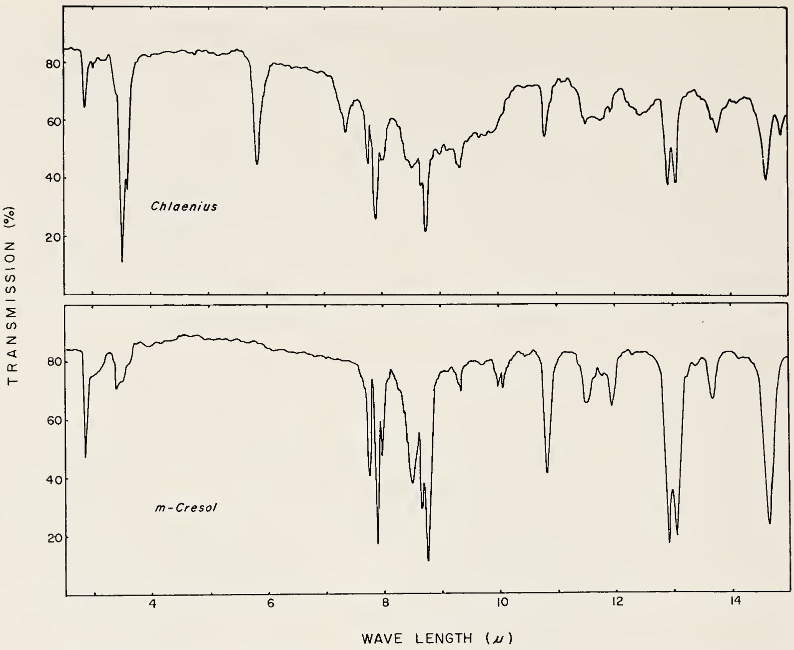
EXPLANATION OF PLATE 10

Figs. 1-4. Four consecutive discharges of *Chlaenius*, elicited by pinching with forceps individual pro- and metathoracic legs as shown. The spray pattern is registered on filter paper impregnated with a chemical indicator (see text, part I).

Fig. 5. An individual *Chlaenius*, after having been caused to discharge, was transferred from place to place on a sheet of indicator paper. As long as residual secretion remained on its body and feet, a conspicuous discolored zone developed around it at each locus (the dark spots within each zone are footprints). Transfer was at two-minute intervals; the times given are from the moment of discharge.



Text fig. 2. Infrared spectra (in carbon disulfide) of the secretion of *Chlaenius* and of authentic *m*-cresol.

sebacate on Chromosorb W, 80/100 mesh, at 166°C, with nitrogen as carrier gas). A dried carbon disulfide solution of the secretion yielded a major peak with retention time of 6.75 min., corresponding precisely to the single peak produced by authentic *m*-cresol. A complex second peak of short retention time in the chromatograph of the natural product indicated the presence of possibly several unknown minor constituents.

It might be added that the odor of *m*-cresol is indistinguishable from that of the *Chlaenius* secretion.

b. *p*-Cresol (*p*-methylphenol) in *Abacion*

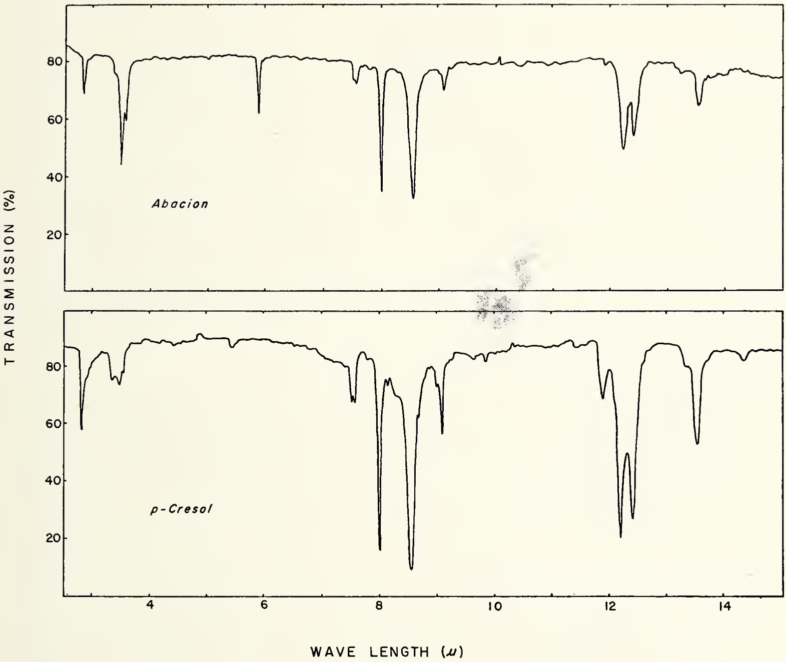
Secretion was obtained from two live millipedes by subjecting them to traumatic stimuli and taking up into capillary tubes the small droplets of secretion discharged at the gland openings. The analytical techniques employed were essentially those described above for *Chlaenius*. The infrared spectrum was found to be similar to that of an authentic sample of *p*-cresol (Text fig. 3), with the exception that the natural sample showed conspicuous bands at *ca.* 3.5 μ (C-H stretching) and at *ca.* 5.8 μ (carbonyl stretching), suggesting the presence of one or more minor components in the secretion.

The vapor phase chromatograph (same column as with *Chlaenius*, but run at 120°C) showed a main peak with retention time of 2.51 min., corresponding to the single peak obtained with authentic *p*-cresol. The secretion showed an additional complex peak of short retention time corresponding undoubtedly to the lesser constituents already suggested by the infrared spectrum.

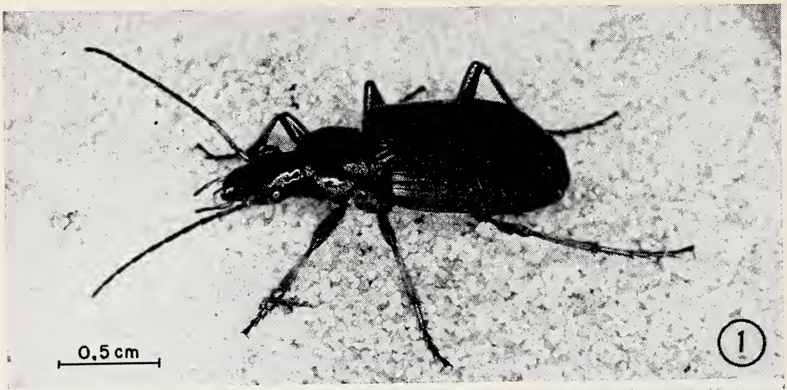
The odor of *p*-cresol, which differs slightly but unmistakably from that of *m*-cresol, is identical to that of the *Abacion* secretion.

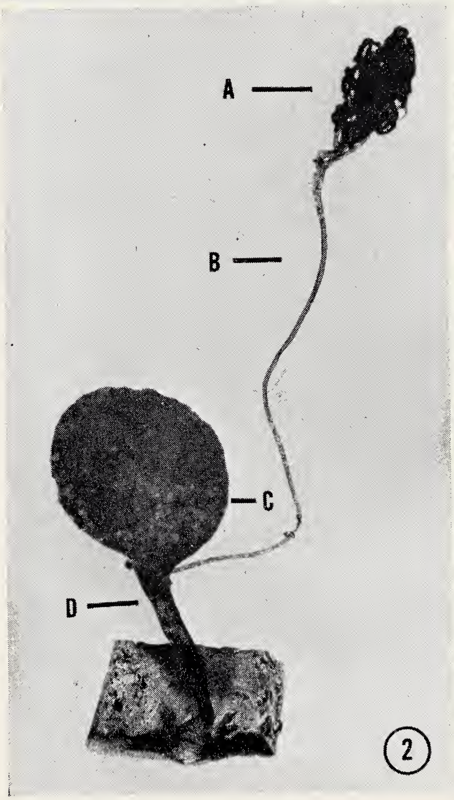
III. Repellent Effectiveness of the Secretions.

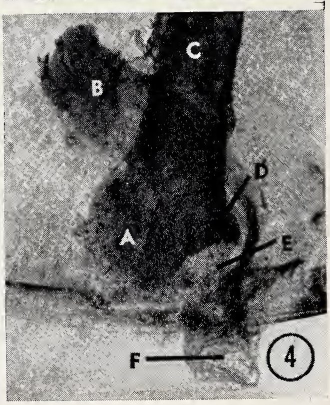
What follows are descriptions of laboratory encounters between individual *Chlaenius* or *Abacion* and a selected array of predators: ants [*Pogonomyrmex badius* (Latreille)], a collared lizard [*Crotaphytus collaris* (Say)], a blue jay [*Cyanocitta cristata* (Linnaeus)], and a grasshopper mouse [*Onychomys torridus* (Coues)]. The ants



Text fig. 3. Infrared spectra (in carbon disulfide) of the secretion of *Abacion* and of authentic *p*-cresol.







Defense Mechanisms

were from Ocean Beach Drive, S. C.; the blue jay was a laboratory-reared individual from Ithaca, N. Y., and the lizard and mouse stemmed from Arizona. Tape recordings were made of running commentaries delivered while witnessing the encounters, and these recordings provided the basis for the measurements of time intervals and other quantitative data given below. The scarcity of *Chlaenius* and *Abacion* limited the number of tests that were possible.

a. *Pogonomyrmex badius* (Latreille)

1. Versus *Chlaenius.*

The experimental conditions were similar to those that prevailed in tests with this same ant and certain other beetles, cockroaches and earwigs that also spray (Eisner 1958a, 1958b, 1960a). Individual beetles, affixed to rods, were placed one at a time just outside the nest entrance of a laboratory colony of *Pogonomyrmex.* The results were essentially the same with each beetle. The ants attacked immediately, converging upon the beetle in groups, grasping it with the mandibles while pointing their gasters forward in stinging position. Suddenly, within no more than a few seconds after initiation of the attack, the entire swarm dispersed. The ants fled aimlessly and quickly, pausing frequently for brief spells of intense cleansing activity. Their escape and cleansing behavior was identical in all major respects to that shown by this and other ants in response to arthropod secretions containing acids and quinones (Eisner, 1958a, 1958b, 1960a; Eisner et. al., 1961). Within one to several minutes after discharge, the ants seemed to have recovered completely, and had resumed their normal ambulatory pace. There were, however, no immediate new attacks. For 8 to 13 minutes after a discharge, the beetle remained invulnerable. Ants coming to within its immediate vicinity turned about abruptly and walked away, apparently repelled by residual secretion and its vapors. Some of this residual secretion must have

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EXPLANATION OF PLATE 11

Fig. 1. *Chlaenius cordicollis* Kirby.

Fig. 2. Excised gland of *Chlaenius. A,* racemose cluster of gland cells; *B,* efferent duct; *C,* reservoir; *D,* ejaculatory duct.

Fig. 3. Grasshopper mouse eating *Chlaenius* (for details, see text, part III).

Fig. 4. Terminal portion of ejaculatory duct and associated musculature of a *Chlaenius* gland. *A,* the short flat muscle that effects nozzle extrusion; *B,* the muscle that forces apart the terminal cuticular valve of the duct, thus freeing the lumen for nozzle extrusion; *C,* ejaculatory duct, invested by circular muscles; *D,* level at which circular muscles come to an abrupt halt; *E,* naked portion of ejaculatory duct; *F,* partly extruded spray nozzle (extrusion was apparently caused by shrinkage of muscles resulting from histological fixation).

been on the substrate where the beetle sprayed, but since shifting the beetle to a new position seemed in no way to increase its vulnerability, the repellent effect must have been due, in part at least, to secretion remaining on the beetle itself. One can demonstrate visually that this is the case, simply by causing a beetle to discharge, and then transferring him onto indicator paper, moving him from place to place as the minutes go by (Plate 10, fig. 5). At each locus the paper is seen to discolor, and even as late as fifteen minutes after discharge a positive test is still obtainable. *m*-Cresol evidently dissipates rather slowly, which is to be expected in view of its low vapor pressure: extrapolation from values given in the International Critical Tables (1928) yields *ca.* 0.1 mm at 25°C.

It follows from the preceding that a given *Chlaenius,* when under attack by ants (and ants are probably important natural enemies of many carabids), is not likely to be subjected to continuous assail and forced to deplete its secretion in a rapid sequence of discharges. *Chlaenius,* like so many other carabids, walks rapidly. Actual measurements made with two individuals released on a smooth horizontal surface, showed the rate of locomotion to range from 15 to 19 cm./s. (time was measured with a stopwatch; distance was determined by chalking a line behind the beetle as it scurried along, and then laying a string along the trail and measuring its length). In the *ca.* 10 min. of invulnerability that follows a discharge, a beetle is therefore free to walk about 100 m. before it is again subject to assail. Surely, this must suffice to outdistance many an arthropod predator, and in the case of ants, even a dense swarm of them. Of course, it remains to be seen whether the repellent effectiveness of the secretion against *Pogonomyrmex* is a true indication of its defensive potential against other ants, and against arthropods in general.

There is one other observation worth mentioning, concerning the defensive use of the beetle's mandibles. It was repeatedly noticed during the early stages of an attack, before *Chlaenius* had been induced to spray, that an ant venturing to within range of the beetle's mandibles was bitten. Although such ants did not seem to receive

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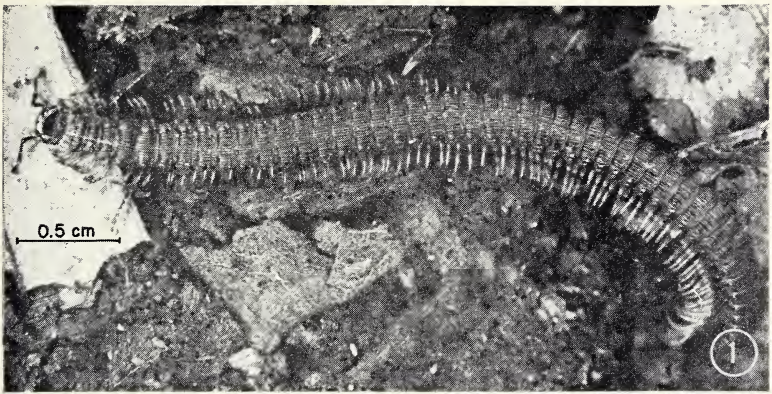
EXPLANATION OF PLATE 12

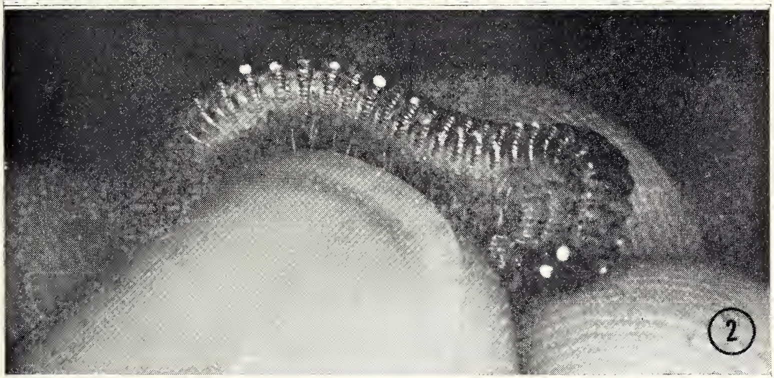
Fig. 1. *Abacion magnum* (Loomis).

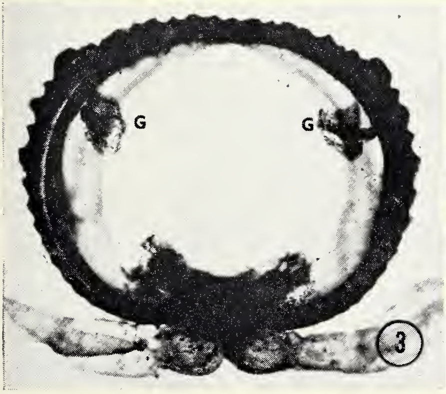
Fig. 2. *Abacion* discharging white droplets of secretion in response to handling.

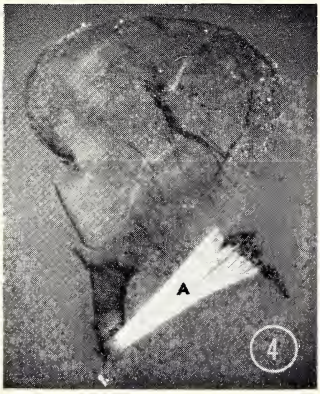
Fig. 3. Isolated segment of *Abacion,* treated with KOH and consisting of cuticle alone, showing the two glands *(G).*

Fig. 4. Excised gland of *Abacion,* seen in partly polarized light. Notice the strongly birefringent muscle (A) that controls the terminal cuticular valve of the efferent duct.









DEFENSE MECHANISMS

noticeable injury, they nevertheless desisted instantly from further assail and fled. *Chlaenius* is evidently endowed with a mechanical as well as a chemical weapon, and the former might be of particular importance at times when the beetle's secretion is temporarily exhausted.

2. Versus *Abacion.*

Three millipedes (3-5 cm. in length) were released individually near the entrance of a *Pogonomyrmex* nest, at a time when the ants were highly active and aggressive, as evidenced by the readiness with which they attacked and overcame mealworms (larvae of *Tenebrio molitor*) introduced as occasional controls. The millipedes walked amidst the swarming ants, and dozens of casual encounters between ants and millipedes were seen to take place, but in not a single instance did an ant attempt to bite or sting a millipede, nor did a millipede ever discharge. The reason for this was the remarkable fact that *Abacion* responded instantly to contact with an ant by coming to an abrupt halt, and remaining motionless thereafter until the ant departed or, more usually, until seconds after the ant's departure. While "death-feigning" in this fashion, the millipede evidently fails to evoke a full-fledged aggressive response from the ants. Time and again a millipede was released near the nest entrance, but it eventually always made its way to the safe outskirts of the nest, pausing intermittently during its escape whenever single ants or groups of ants scurried over its body, but never once being induced to discharge. When an ant contacted the millipede's head, and also apparently when the glandless postcephalic segments were touched, the millipede came to a halt with its front end coiled beneath the body, a response already noticed when the animals were stimulated by hand (see Ib above). Otherwise, when contact was with the body itself, the millipede simply halted without altering its stance.

In order to test for the actual repellency of the secretion, millipedes were first subjected to artificial traumatic stimuli locally applied, and then released with the ants. Under these circumstances, the ants never even contacted the millipede, but turned around and retreated as soon as they came to within close range. As was the case with *Chlaenius,* the millipedes remained repellent for considerable periods after a discharge. Invulnerability of several minutes was the rule, even when no more than a few adjacent glands had been activated [the vapor pressure of *p*-cresol, as estimated by extrapolation from values given in the International Critical Tables (1928), is as low as that of *m*-cresol, i.e. *ca.* 0.1 mm at 25°C].

Abacion is slower in its locomotion than *Chlaenius.* Six specimens

(3-5 cm. in length) whose ambulatory pace was measured (same technique as with *Chlaenius*) yielded values ranging from 2.6 to 6.0 cm./s. The distance that a given *Abacion* may be expected to cover unmolested after discharging is therefore considerably less than the 100 m. one can expect from *Chlaenius.* But *Abacion,* with its two glands per most body segments, has a rather formidable secretory supply not easily depleted, particularly since its glands are likely to be called into action only a few at a time rather than all at once (at least so long as small predators are involved that inflict localized rather than generalized injury). Small arthropod predators, and ants in particular, are probably among the chief natural enemies of *Abacion.* Considering its rich glandular endowment, and the proven effectiveness of "death-feigning", *Abacion* appears indeed to be a most admirably protected animal.

b. *Crotaphytus collaris* (Say)

Two tests were made, one with *Chlaenius* and one with *Abacion.* In the case of the millipede, the lizard eyed it almost continuously as it walked about the cage, but made no effort to seize it or even to approach it. One hesitates to attribute special significance to an isolated finding of this sort, but it should be mentioned that this particular lizard was confronted with no millipedes during its one year in captivity, and that its voraciousness at the time of the experiment was demonstrated by the readiness with which it caught and ate mealworms (larval *Tenebrio molitor*).

With the single *Chlaenius* the results were dramatically different. The lizard chased the beetle and caught it in its jaws, but instantly released it again, thereafter wiping its snout for several seconds in the substrate. Some secretion had evidently hit one eye, which remained closed for more than a minute. The beetle was uninjured (it smelled conspicuously of *m*-cresol when retrieved). The lizard showed no noticeable long range ill-effects.

c. *Cyanocitta cristata* (Linnaeus)

1. Versus *Chlaenius.*

Three beetles were offered, one after the other, within a period of 30 minutes. The results were the same in each case. The bird descended from its perch, and quickly pecked the beetle to death. Except for an occasional brief but violent shaking of the head, the bird betrayed no signs of discomfort. There was no question that the beetle had sprayed: the phenolic odor was clearly apparent, even from outside the cage.

With the dead beetle in its bill, the bird returned to its perch, and while holding the beetle against the perch with a foot, proceeded to dismember it with the bill. Except for the beetle's head and perhaps a portion of the thorax, no parts were swallowed. The discarded pieces were later pecked into various crevices and other hiding places in the cage [this behavior has been noted often when captive jays are offered noxious spray, e.g. meloid, coccinellid, and lycid beetles (Linsley et al., 1961; Eisner, unpublished)].

One wonders what would have happened had the secretion hit the bird's eyes. With other arthropods that spray, this has frequently been observed, and it invariably has an instantaneous repellent effect, leaving the bird partially incapacitated for a time with one or both eyes closed, or with the nictitating membranes being drawn back and forth over the eyeballs in a quick wiping action (Eisner et al., 1961, 1962, and Eisner, unpublished). Such birds usually avoid similar prey for at least several hours after an encounter. One might argue that the jay's eyes had really been hit by the *Chlaenius* spray, but that they were unaffected by it. It is doubtful, however, that *m*-cresol is harmless. What it does to a lizard's eye has already been described. To our own eyes, even the concentrated vapors are quickly irritating. Assuming, then, that the jay's eyes had indeed been missed, this brings to light what may well be a major shortcoming of the beetle's weapon: by aiming the spray against that portion of its body directly subjected to trauma, the beetle is likely to miss the eyes of a long-billed bird such as a jay, spraying instead the relatively insensitive bill. Other arthropods that have been tested (e.g. whipscorpions, *Calosoma*) also aim toward the body regions traumatized, but since their spray is of greater range and more broadly dispersed than that of *Chlaenius,* the probability is greater that the eyes of the bird receive at least a partial dousing (Eisner et al. 1961, 1962).

2. Versus *Abacion.*

The jay promptly pecked and killed the single millipede offered, carried the corpse to its perch, and then proceeded to treat it in the same way as *Chlaenius.* No parts were eaten, although a few pieces were malaxated in the bill before being dropped. Again as with *Chlaenius,* the discarded pieces were pecked into various hiding places.

d. *Onychomys torridus* (Coues)

1. Versus *Chlaenius.*

Two beetles were offered, with identical results in each case. The mouse pursued the beetle the moment it was introduced, quickly grasped it in its front paws, and with the beetle oriented in such a way that its rear was pushed into the sand, proceeded to eat it head first (Plate 11, fig. 3). Under these conditions most, if not all, of the secretion must have been ejected into the sand, sparing the mouse itself. The mouse betrayed no signs of discomfort and both beetles offered were devoured almost entirely. Only the legs and wings were discarded, as well as the tips of the abdomens, which presumably still contained the gland reservoirs. One might add that this same mouse, and others of the same species, have been seen to overcome and eat tenebrionid beetles of the genus *Eleodes* in exactly the same fashion (Eisner, 1960b, and unpublished). *Eleodes,* like *Chlaenius,* also sprays from the tip of its abdomen, although its secretion contains quinones rather than a phenol (Blum and Crain, 1961; Chadha et al., 1961b).

2. Versus *Abacion.*

The single millipede offered was promptly severed midway by the mouse's first bite. The mouse retreated instantly, scurrying about the cage with its muzzle intermittently pushed in the sand. Within seconds it returned to bite the millipede again, only to be repelled temporarily as before. This sequence of attack and retreat was repeated several times, until the mouse finally grasped several multisegmented portions of the millipede and ate them one by one. But most of the millipede was left uneaten. A strong odor of p-cresol permeated the cage. Grasshopper mice are known to pursue their prey relentlessly even in the face of repellent secretions (Eisner et al., 1961; Egoscue, 1960), and the persistent aggressiveness evidenced in this encounter was in no way unexpected.

IV. Irritant Effectiveness of the Secretions and Their Phenols.

The chemical evidence has shown (part II, above) that *m*-cresol and *p*-cresol are not the only components of the secretions. The possibility therefore exists that the unidentified lesser components contribute in an important way to the overall effectiveness of the secretion. Such possibility would not be without real precedent. For instance, the spray of the whipscorpion, *Mastigoproctus giganteus* (Lucas), contains a minor component that promotes the spread of the secretion over the cuticle of arthropod enemies, while at the same time accelerating the penetration of the poison (Eisner et al., 1961). The following experiments were aimed at determining whether the secretions of *Chlaenius* and *Abacion* are more effective as topical irritants to arthropods than pure samples of the phenols they contain. The arthropod used for the test was the cockroach *Periplaneta americana* (Linnaeus), and the technique was a slightly improved version of that employed previously for comparable purposes (Eisner et al., 1961).

In essence, the technique consists of applying the test substances topically to decapitated cockroaches, and timing the onset of the grooming reflexes that follow. The delay to onset of grooming is a criterion of the irritant effectiveness of the sample: the quicker the onset, the greater the irritability.

The droplets of sample were applied with a constant-volume micropipette (0.4 μl) to any one of three loci: the fifth abdominal sternite (on one side of the midline), a tarsus of a metathoracic leg, and a cercus. For each locus the grooming reflex induced is unmistakably distinct (Eisner, 1961). Each roach was tested three times, once at each locus, but the sequence of loci tested was not fixed, nor was the same sample necessarily used at each locus. Recovery of 15 to 20 minutes was allowed between consecutive tests on the same roach. Failure to induce a reflex within five minutes of application was considered a negative response (n. r.). Adult female roaches were used exclusively. The secretions were obtained by the same techniques as used for the chemical analyses (see part II, above).

TABLE I

○ *m*-cresol ▽ *p*-cresol
● *Chlaenius* secretion ▼ *Abacion* secretion
(n. r. = no response)

sternal reflex				tarsal reflex				cercal reflex			
○	●	▽	▼	○	●	▽	▼	○	●	▽	▼
4'22"	2'43"	2'17"	3'18"	1"	1"	1"	1"	1"	1"	1"	2"
n. r.	n. r.	n. r.	3'40"	1"		2"	2"	1"		1"	
n. r.	n. r.	n. r.	n. r.	1"		2"		2"		3"	
n. r.	n. r.	n. r.	n. r.	2"		4"		2"		4"	
n. r.	n. r.	n. r.	n. r.	6"		5"		4"		4"	

Table I. Sensitivity of *Periplaneta americana* to the secretions of *Chlaenius* and *Abacion,* and to the corresponding phenols. Sensitivity is expressed as the delay to onset of a grooming reflex (sternal, tarsal, and cercal) following topical application of a given sample. The times of delay for the three reflexes and four samples tested are given in the vertical columns. For full explanation see text, part IV.

The results are plotted in Table I. Unfortunately, with the actual secretions, the amount of material available sufficed for only relatively few tests. Still, some safe inferences can be made. First of all, as expected, the tarsi and cerci, with their relatively thin cuticle, are much more sensitive than the abdominal sternite: the reaction was always within seconds of application. By contrast, when application was to the sternite, there was in most cases no response at all, and in the few exceptions the reflex was delayed for at least two minutes. Evidently, when the cuticular barrier is a thick one, neither the secretions nor the pure phenols are very effective irritants. Moreover, none of the samples differed detectably in their activity.

The possibility still remains that the lesser components are of more than incidental significance (they might, for instance, act as emulsion stabilizers) but the present data offer no basis for further speculation.

V. Discussion

The protective function of the glands seems established, certainly as regards ants. The special adaptive refinements of the discharge mechanism, such as *Chlaenius'* ability to aim the spray, and *Abacion's* tendency to respond locally rather than from all glands at once, are by no means unique. Other carabids studied (*Brachinus, Calosoma*) also aim their spray (Eisner, 1958a; Eisner et al., 1962). In fact, aiming appears to be the rule rather than the exception among arthropods that spray (Roth and Eisner, 1962). Similarly, other millipedes studied thus far, and including juoids, spiroboloids, spirostreptoids, polydesmoids, and polyzenoids (Kafatos 1961; Eisner, unpublished), all share with *Abacion* the habit of restricting their discharge to the region stimulated.

The experiments with vertebrate predators were not nearly as conclusive as those with ants. There was only one instance of clear-cut prey rejection, involving the collared lizard and *Chlaenius,* and it is significant that the beetle survived the encounter uninjured. With the jay, the evidence clearly points to the unpalatability of *Chlaenius* and *Abacion,* but the prey was always killed before being rejected. Continued daily tests would have been desirable, since on the long run the bird might well have developed discriminatory tendencies. Similar long range experiments would have been justified with the grasshopper mouse, although with *Chlaenius* there is really no reason to anticipate eventual avoidance on the part of the mouse, since the beetle is subdued by a technique that evidently prevents effective employment of its weapon.

It may seem surprising to find a beetle and a millipede — two arthropods of widely distant phyletic positions — producing nearly identical secretions, but this situation is not without precedent. *p*-Benzoquinones, for instance, are known from the secretions of certain millipedes, phalangids, and representatives of several insectan orders (for summary, see Roth and Eisner, 1962). The aldehyde 2-hexenal is produced by some cockroaches (Chadha et al., 1961a; Roth et al., 1956) and certain Hemiptera (Blum, 1961; Waterhouse et al., 1961).

It is also not uncommon for relatively closely related forms to produce very different secretions. Millipedes and carabid beetles do in themselves illustrate this point. Among the millipedes, non-phenolic compounds that have been identified include hydrogen cyanide, benzaldehyde (Eisner, H. E., et al., 1962), and *p*-benzoquinones (reviewed in Roth and Eisner, 1962). Of the three carabid genera other than *Chaenius* that have been studied, one (*Calosoma*) produces a phenolic compound (salicylaldehyde; Eisner et al., 1962), but the other two do not: *Pseudophonus* secretes formic acid (Schildknecht and Weis, 1961); *Brachinus* sprays *p*-benzoquinones (Schildknecht, 1957).

These chemical similarities on the one hand, and dissimilarities on the other, illustrate some striking convergent and divergent trends in the evolution of arthropod secretions — trends that will some day have to be given the proper explanation they deserve. But this will have to await an understanding of the particular biochemical pathways by which the secretions are synthesized, and of the special relationships of these pathways to the fundamental biosynthetic machinery of the cell.

Summary

1. The carabid beetle *Chlaenius cordicollis* Kirby, and the chordeumoid millipede *Abacion magnum* (Loomis), produce defensive secretions which have been shown by infrared spectrophotometry and vapor phase chromatography to contain *m*-cresol (*Chlaenius*) and *p*-cresol (*Abacion*)

2. *Chlaenius* has two glands that open near the tip of the abdomen. It discharges its secretion as a spray, ejected from either one gland or from both, depending on whether the causative traumatic stimulus is unilaterally or bilaterally applied. The spray is not directed at random, but through bending of the abdominal tip is aimed with some accuracy toward the body region traumatized.

Abacion has a pair of glands per each of most diplosegments. The discharge is a liquid ooze, proceeding normally from only those glands close to the stimulus.

3. A brief account is given of the structure of the glands, as well as of their inferred mode of operation.

4. Experiments are described in which individual *Chlaenius* and *Abacion* were exposed to attacks by ants and several vertebrates.

With the vertebrates the results were variable, but with the ants the repellent effectiveness of the secretions was clearly established.

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A NEW GENUS OF THE TRIBE MESOSTENINI FROM CHILE (HYMENOPTERA, ICHNEUMONIDAE)*

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In my work on the Chilean Mesostenini it early became evident that the *Cryptus cyanipennis* of Brullé, one of the most striking and easily recognizable of the described mesostenines of temperate South America, is sufficiently distinct from other known forms to deserve separate generic status. I therefore give below a description of this new genus together with a brief discussion of its affinities and a redescription of the type species.

Xiphonychidion, new genus

Head transverse, temples strongly receding behind the eyes. Frons unarmed. Face gently convex between insertion of antennae and clypeus. Clypeus strongly convex, bluntly pyramidal in profile, the apical margin truncate, without a tooth. Antennae subequal to body in length, not at all thickened medially, subapical part of female antennae scarcely flattened below, white-annulate well beyond middle in both sexes. Epomia strong, with a little swelling above. Mesoscutum broadly convex, mat, with gross transverse foveolations arranged in roughly longitudinal series between which are much more finely sculptured areas; notaulus obsolete, not extending far beyond middle of mesoscutum, most clearly defined basally where it is a broad foveolate depression. Scutellum low, gently convex. Propodeum grossly and rather regularly rugoso-reticulate throughout, basal trans-carina complete; areola rather weakly to quite strongly delimited, smallish; apical trans-carina obsolete except medially, where it borders areola behind, forming very strong, blunt sublateral crests; spiracle long-elliptical. Wings dark-infumate with purplish reflections. Areolet very large, pentagonal, a little higher than wide, intercubiti straight, almost parallel, very slightly converging above; ramellus long and well-developed; nervulus postfurcal by about 1/3 its length; median part of mediella straight; nervellus broken at about its lower 1/3 in female, a little below middle in male; axillus far from anal margin of hind wing but distinctly closer to it than to submediella over most of its length. First abdominal segment rather slender; postpetiole moderately expanded, part behind spiracles about 1.0 times as long as wide

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in female and about 1.1 times as long as wide in male; spiracles well behind middle; a strong, bluntly-triangular lateral expansion subbasally; ventro-lateral carinae strong throughout; dorso-lateral carinae rather weak basad of spiracles; median dorsal carinae distinct from a little before to well beyond spiracles. Second tergite shining, with numerous minute setiferous punctures, emitting rather long, moderately-dense hairs. Succeeding tergites with rather long, thick, black, appressed hairs over most of their surface, giving a generally dull, velvety sheen at low magnification. Ovipositor about 0.4 times as long as the fore-wing, somewhat depressed above preapically, without a nodus, strikingly hooked downward at tip, the tips of the lower valves not at all enclosing the upper valve.

Type species: *Cryptus cyanipennis* Brullé

Xiphonychidion cyanipenne (Brullé), new combination

Cryptus cyanipennis Brullé, 1846, Histoire naturelle des insectes hyménopterès. 4: 188. female. Type, female. Chile: La Conception (lost).

Cryptus capensis Dalla Torre, 1902. Catalogus hymenopterorum 3: 564. Lapsus for *cyanipennis*.

Female: length of fore-wing 14-17 mm. Ovipositor 0.4 times as long as fore-wing.

First flagellar segment about 5.6 times as long as wide apically. Front with a few strong, somewhat irregular transverse wrinkles, smooth and shining below, becoming mat above. Prepectal carina strong, reaching or almost reaching subalarum. Metapleurum grossly rugulose. Hind femur about 4.7 times as long as deep at middle. Postpetiole smooth and shining with moderately dense, minute setiferous punctures and a shallow, anteromedian depression.

Dull black, the following more or less well-developed white marks: rather narrow post-median annulus on flagellum, frontal orbits narrowly, elongate spot at top of eye, narrow line on posterior orbit, spot at bottom of eye, and hind tarsomeres 3-4 (sometimes also base of 2). Wings deeply infumate, with purplish reflections.

Male: length of fore-wing about 12.5 mm. First flagellar segment approximately 3.4 times as long as wide apically.

Colored as in female.

Specimens examined: Five females and one male: Concepción, Chile, 1903 and 1904, P. Herbst. One female: Valparaiso, Chile, 2.XI, 1919, P. Herbst. One male: Penco, Chile, 1.1908, P. Herbst. All in collection of Museum of Comparative Zoölogy at Harvard University.

Xiphonychidion is a member of the *Trachysphyrus* Group of the subtribe Mesostenina of the tribe Mesostenini. Because of its large areolet, elongate propodeal spiracle, and almost straight mediella *X. cyanipenne* may be accounted a typical representative of this series of genera. From all described species, however, it differs conspicuously in the peculiar hooked-down ovipositor tip which indicates, perhaps, some rather special host. Otherwise, its closest approach is probably to *Trachysphyrus* Haliday to the vicinity of which it will run in Townes' key to the Nearctic genera (1962, Bull. U. S. Nat. Mus. 216, Pt. 3), differing, however, in its strongly convex clypeus, obsolete notauli, postfurcal nervulus, and in the prominent sub-basal triangular projection of the first abdominal segment.

The generic name is derived from the Greek *xiphos — sword, onyx (onychos)— claw,* and *idion,* a diminutive suffix. It refers to the characteristic ovipositor tip.

In conclusion I wish to express my thanks to Dr. H. K. Townes of the University of Michigan whose encouragement and vast knowledge are a constant help to me in my work on the South American Mesostenini. The synonomy given in this paper was kindly supplied by Dr. Townes from the manuscript of his projected *Catalogue and Reclassification of the Neotropical Ichneumonidae.*

STUDIES ON CARBONIFEROUS INSECTS FROM COMMENTRY, FRANCE: PART IV.
THE GENUS *TRIPLOSOBA*[1]

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Among the unusual insects described by Brongniart from the Commentry shales in France was a nearly complete, well-preserved specimen, apparently related to the mayflies. Now known as *Triplosoba pulchella* (Brongniart), the species has usually been considered as representing either a distinct order (Protephemerida) or the Order Ephemeroptera itself. In either case, the insect has held a unique position as the oldest representative of the mayfly line of evolution.

This fossil was well described by Brongniart and it has been discussed by Handlirsch (1906), Lameere (1917), Martynov (1923), Tillyard (1932), and Demoulin (1956). Aside from Brongniart, however, only Lameere based his account on an actual study of the fossil itself, the others mentioned depending on published descriptions, figures, or photographs.[2] Although there has been agreement on the general relationships of *Triplosoba,* much controversy has existed over the interpretation of its venation and consequently of its phylogenetic position within the palaeodictyopterous-ephemeropterous complex. Several of these authors, including Brongniart, have attempted to construct restorations of the complete insect, these also reflecting widely divergent views (see plate 13).

The present paper has been written with the hope of eliminating some of the uncertainties and confusion about the structure of *Triplosoba.* It is based upon my examination of the type specimen of *pulchella* in the Muséum National d'Histoire Naturelle in Paris. Study of this fossil was made on three separate occasions. The first examination was in 1938, although at that time only one counterpart, the poorer of the two, could be found in the Muséum collection. Following the publication of Demoulin's account of *Triplosoba* in 1956

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[1] The preceding part of this series, on the Caloneurodea, was published in Psyche 68:145-153, 1961. This study has been aided by a National Science Foundation grant.

[2] Demoulin's statement (1956, p. 1), that no new examination of the fossil had been made since Brongniart's description was published in 1893, is certainly an error. Lameere studied the fossil in 1914-15, the results being included in his 1917 summary of the Commentry insects. Demoulin, however, did not examine the specimen itself, but based his conclusions on photographs.

and learning that the other counterpart had subsequently been located in the Muséum, I made an examination of both counterparts in 1961, with special reference to the questions raised by Demoulin. Finally, in early 1963, during another visit to the Muséum, I made a final check on the specimen with reference to the drawings which accompany the present paper.[3] In the following account I have attempted to redefine the family Triplosobidae as well as the genus, using terminology consistent with that employed in my previously published papers on fossil mayflies.

Order Ephemeroptera

Family Triplosobidae Handlirsch, 1906

Fore and hind wings similar in form and venation; Rs having two intercalary veins and arising directly from R; MA free from Rs, unbranched. Abdomen slender, with prominent cerci and a median caudal filament.

Genus *Triplosoba* Handlirsch, 1906

Triplosoba Handlirsch, 1906, Foss. Ins.: 312 [*pro Blanchardia* Brongniart 1893: 325 (*non* Castleman, 1875)].

Since only one species of this genus is known, generic characters are assigned arbitrarily. It seems probable, however, that the branched condition of MP, the presence of IMP, and the unbranched CuA are features of generic significance.

Type species: *Blanchardia pulchella* Brongniart

Triplosoba pulchella (Brongniart)

Plate 14

Blanchardia pulchella Brongniart, 1893, Recherches Hist. Ins. Foss.:328, fig. 14; pl. 18, fig. 8, 9.

Triplosoba pulchella Handlirsch, 1906, Foss. Ins.: 312, pl. 32, fig. 6, 7; Handlirsch, 1911, Congr. Intern. Entom.: 183, pl. 8, fig. 12; Lameere, 1917, Mus. Nat. Hist. Natur., Bull., 23:103; Martynov, 1924, Rev. Russe Ent., 18:158, fig. 3; Tillyard, 1932, Amer. Journ. Sci., 23:101, fig. 1; Demoulin, 1956, Inst. Roy. Sci. Nat. Belgique, Bull., 32(14):1-8, fig. 1; pl. 1.

The type specimen is in the Institute de Paléontologie, Muséum National d'Histoire Naturelle, Paris. It consists of both counterparts, one represented (natural size) in Brongniart's figure 8, plate 18 of his 1893 monograph, the other in his figure 9; these illustrations are reproduced in the present paper, on plate 13, figure c, and plate 14,

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[3] In connection with this most recent visit, I am indebted to Professor J. P. Lehman, Director of the Institut de Paléontologie of the Muséum, for placing the Commentry fossils at my disposal.

figure a.[4] The fossil consists of a nearly whole insect, with outstretched but somewhat distorted wings. Subsequent to Brongniart's study of the fossil, as noted by Lameere (1917), specimen 18-8 was covered with shellac, which rendered the venation of that counterpart nearly invisible. The shellac was still on the fossil in 1938 when I examined the specimen, but it has subsequently been removed, so that the venational details are now discernible. The fore wing, not quite complete, is 21 mm. long; the hind wing, complete, is 21 mm. long and 7 mm. wide. The body length excluding cerci is 25 mm. In the following discussion I am using specimen 18-9 for reference, this being the better of the two counterparts and the one on which Demoulin based his interpretation.

WINGS. The *right fore wing* is incompletely preserved (fig. c, plate 14), lacking the very base, the apex, and the distal parts of the posterior margin; however, most of the rest of the wing is clearly preserved and it shows no distortion. Demoulin was convinced from his study of photographs of the fossil that the wing was very broad and nearly triangular (fig. a, plate 13); he also believed that he could see the veins of this wing extending much further distally than they were indicated in the figures of Brongniart. I have been unable to find any indications of such extensions of the veins in the fossil itself; there are faint surface markings on the rock which Demoulin may have noted in the photograph, but these are features of the rock's matrix; an examination of the specimen shows that similar markings are visible on various parts of the rock containing the fossil, some of this being clearly below the right hind wing of the photograph reproduced in Demoulin's paper. Such markings are also present on the rock a considerable distance away from the fossil itself. Consequently, although the apical and posterior margins of the fore wing are not preserved, there is, in my opinion, no evidence whatsoever that the wing was significantly broader than the hind wing or that it was nearly triangular in shape. Demoulin also believed that he could see in the photograph at the base of the fore wing a short submarginal costa and a precostal space. Neither Brongniart nor Lameere noted such a structure and I find none in the fossil. In this wing the stem of Rs can be followed clearly to its point of origin from R1 but the stem of MA is not preserved, a piece of the matrix being broken away at this point. However, one certainly gets the impression from the condition in the specimen that the basal part of MA is close to Rs, although the two veins are not in contact.

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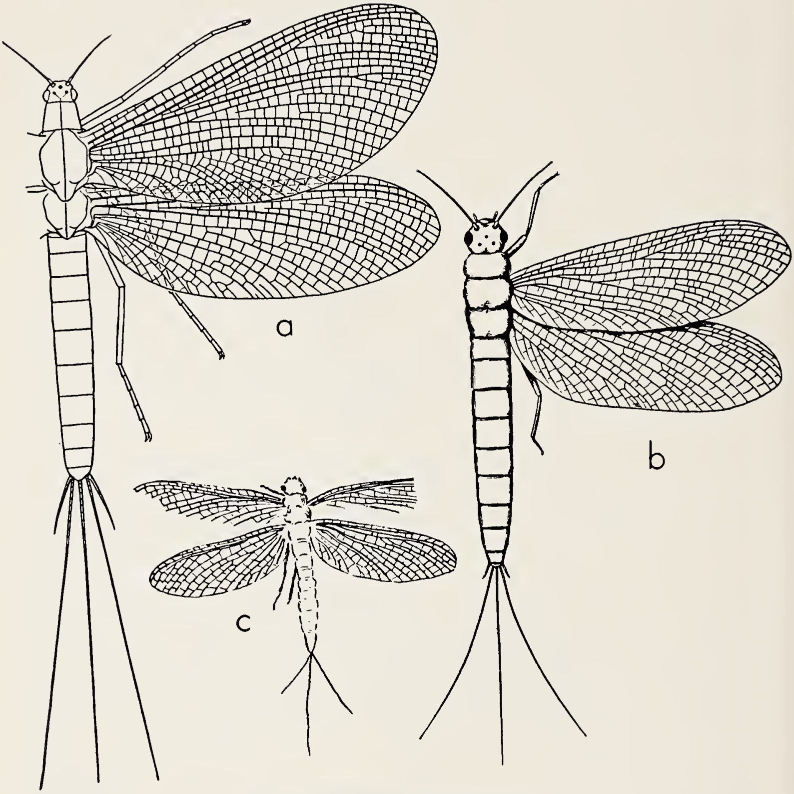
[4] For convenience of reference these counterparts are subsequently designated in the present paper as specimens 18-8 and 18-9.

The *left fore wing* (fig. b, plate 14) shows less of the wing area than the right, lacking the distal third and most of the entire hind margin; however, the basal part of the wing is clearly preserved and there seems little distortion in the preserved part of the wing. I could find no indication of the part of the hind margin suggested in Demoulin's paper nor of the submarginal costa and precostal space which he indicates in the left fore wing. It is of interest to note, incidentally, that the anterior margin of the wing near the base shows clear indications of serrations, comparable to those which have been seen in some Palaeodictyoptera. The origins of Rs and MA can easily be seen in this wing: Rs arises directly from R, without contact with MA, which can be seen to arise from the basal part of R, just a short distance basal of the origin of Rs. It is possible, of course, that the stem of M is actually parallel and in contact with R but it is not discernible in the fossil.

The *left hind wing* (fig. d, plate 14) is very nearly completely preserved, lacking only a short piece of the anterior margin towards the middle line of the wing; it shows no distortion. I could find no sign in the fossil of the precostal space and and submarginal costa shown in Demoulin's figure. Rs can be seen clearly arising from R, as in the two fore wings but the basal part of MA is very different in position from that in the other wings mentioned; basally it is more removed from Rs than in the fore wings and it appears to meet MP very close to the base of M itself. There is no visible connection between MA and R directly. The common stem M appears to be very close to R and may be in contact with it. The origins of CuA and CuP are not preserved; however, CuA shortly diverges away slightly from MP producing an unusually wide space and at about the same level CuP diverges towards CuA, the two latter veins being almost in contact at that point. CuA and CuP subsequently diverge as they approach the wing margin.

The *right hand wing* is the most poorly preserved of all, showing distortion and folding. The longitudinal veins are irregularly distributed over the wing area. The origins of Rs and MA are not preserved but the proximal parts of these veins seem to be remote from each other as in the other hind wing.

As can be seen from the foregoing remarks, I am in agreement with Brongniart and Lameere that the fore and hind wings of *Triplosoba* were very similar in form and in venation. I believe that Brongniart's drawing, figure 9 of plate 18, is reasonably accurate, although more cross veins are shown in his figure than are now discernible in the specimen. I think it is probable that the fore and hind wings differ



CARPENTER — TRIPLOSOBA

slightly in the origin of MA. As pointed out above, in both the fore wings the proximal part of MA is close to the proximal part of Rs and in the left fore wing MA can clearly be seen joining to R. In the hind wings, on the other hand, MA is quite remote from Rs proximally and in the left hind wing it appears to join MP very close to the stem of R. These differences were recorded by Brongniart not only in his figure (18-9) but in his description of the fossil, in which he states that although this vein in the anterior wing arises from the radius, in the posterior wing it arises from the very base of the wing. However, in his restoration of *pulchella* (fig. 14, p. 327), he does not show MA joining R in the fore wing although he does represent MA as being closer to R and Rs in the fore wing than in the hind wing. Handlirsch's figure (see fig. b, plate 13) of *Triplosoba* was taken from Brongniart's restoration in figure 14 rather than from his drawing of the fossil itself on plate 18; in the process Handlirsch apparently missed the difference between the fore and hind wings with respect to the origin of MA and its relationship to R and Rs. Similarly, Tillyard's drawing of a *Triplosoba* wing, adapted from Handlirsch, shows more nearly the condition of the hind wing but with the stem of M more remote from R than actually is the case. Demoulin's figure of the wing misses completely the difference in the position of MA with respect to Rs in the fore and hind wings; in fact, in his hind wing he shows MA actually closer to the base of Rs than it is represented in the fore wing.

Body. The body structure of *Triplosoba* is only vaguely preserved in the fossil. There is a suggestion of a head (which is interpreted by Demoulin as the prothorax), thorax and abdomen; three legs are indicated in the fossil, all of these being on the right side of the insect as preserved in counterpart 18-9. The segmentation of the legs is not clear and Demoulin's conclusion that the tarsi were five-segmented is unjustified. There is no question, however, as mentioned by Lameere (1917) that there are three caudal processes, the two cerci and the median filament. As shown in Brongniart's figure of 18-8 as well as in his restoration, figure 14, the median filament is much longer as preserved than it is in the cerci; this could of course be the result of the incomplete preservation of the latter. Demoulin has described and figured what he considers to be a gonostyle but actually the structure concerned is not part of the fossil; it is due entirely to an irregularity

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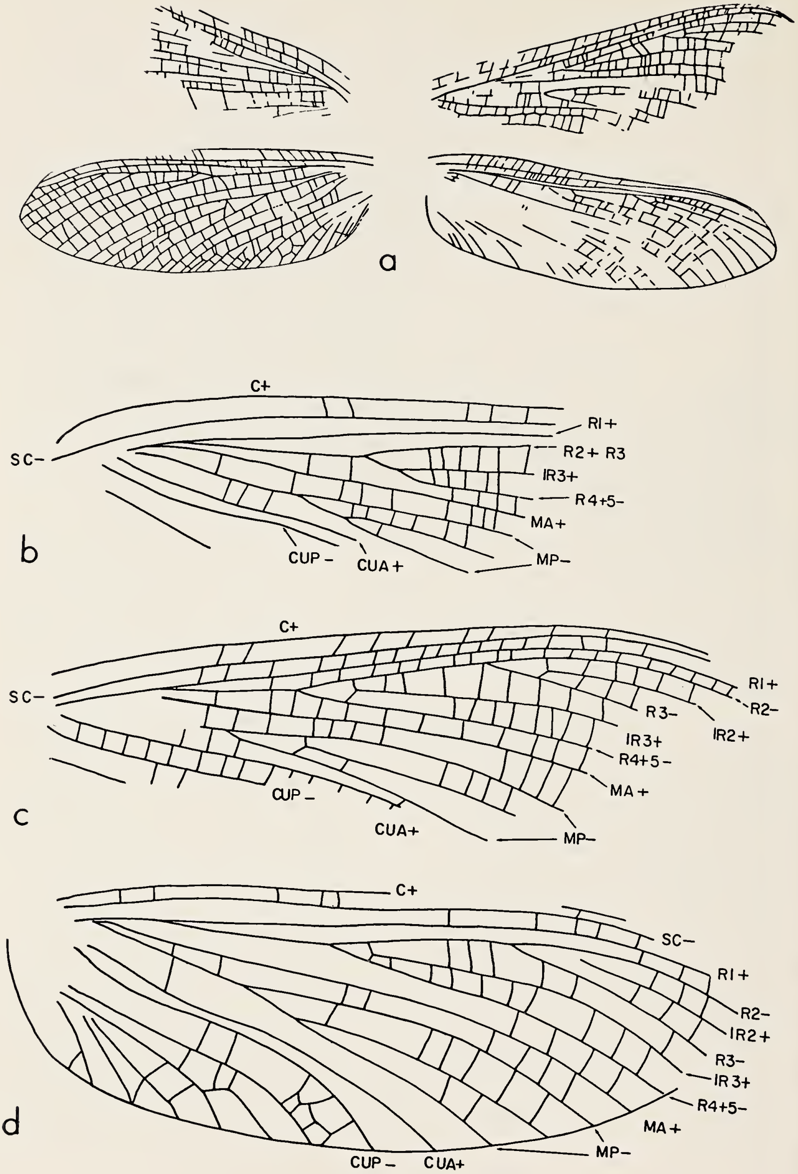
Explanation of Plate 13

Triplosoba pulchella (Brongniart). a) restoration of Demoulin; b) restoration of Handlirsch; c) Brongniart's figure of counterpart 18-8. For further explanation see text.



CARPENTER — TRIPLOSOBA

on the surface of the rock matrix as can be recognized easily from an examination of the fossil. Brongniart made no reference to such processes nor did Lameere. They were first shown by Handlirsch in his reconstruction but probably with no more reason than he showed ocelli, compound eyes, mouth-parts, antennae and tarsal claws, — none of which are even indicated in the fossil.[5]

PROBABLE RELATIONSHIPS OF TRIPLOSOBA

Triplosoba has nearly consistently been placed in the extinct Order Protephemerida, which was erected for it by Handlirsch in 1906. There are no other known genera of insects sufficiently close to *Triplosoba* to justify their inclusion in that order. However, the Permian Protereismatidae (and related families), which are accepted as true Ephemeroptera, tend to bridge the gap between *Triplosoba* and the Mesozoic and Recent mayflies. Inclusion of *Triplosoba* within the Ephemeroptera now seems more reasonable than it did in 1906, especially if it be placed in a separate suborder (Protephemerida). This is in fact the suggestion made by Demoulin, although I am not in accord with the reasons which he gives for that proposal, i.e., the supposed triangulization of the fore wing and the beginning of reduction of the hind wing. The most distinctive characteristic of *Triplosoba* (so far as we now know) is the independence of MA from Rs in both wings. In the hind wings MA is remote from Rs and seems to join MP directly near the base of the wing; in the fore wing MA is much closer to the base of Rs and actually coalesces with R without first joining MP. In all other Ephemeroptera, which may be regarded as comprising the suborder Euplectoptera, MA in both wings coalesces with Rs before diverging posteriorly and joining MP. In the Protereismatidae it diverges posteriorly again to meet MP but in Recent

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[5] I seriously question the usefulness of such reconstructions as these given by Handlirsch and Demoulin in which there is no differentiation between structures actually preserved in the fossil and those which are merely assumed by the author to have been present. Such reconstructions are, in fact, often misleading since they give the general impression that the details shown are actually preserved.

EXPLANATION OF PLATE 14

Triplosoba pulchella (Brongniart). All figures based on type counterpart 18-9. a) Brongniart's figure of counterpart 18-9; b) original drawing of left fore wing; c) original drawing of right fore wing; d) original drawing of left hind wing, C, costa; R1, radius; R2, R3, R4 + 5, branches of radial sector; IR2 and IR3, intercalary veins of radial sector; MA, anterior media; MP, posterior media, CuA, anterior cubitus; CuP, posterior cubitus; +, convex veins; —, concave veins.

families the origin of Rs (in the fore wing) has migrated basally to such an extent that this vein (Rs) is no longer attached to R, seeming to arise as a separate branch of M. So far as this trait is concerned, then, *Triplosoba* is more primitive than Protereismatidae or any other known mayflies. This is not to imply, of course, that the Triplosobidae were the ancestral stock from which the other Ephemeroptera arose; but they were also certainly a derivative of such a stock, having their own specializations.

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THE FEMALE OF *BERTRANA HIEROGLYPHICA* PETRUNKEVITCH (ARANEAE, ARGIOPIDAE)

By Arthur M. Chickering
Museum of Comparative Zoology

Four species of this very interesting genus are known at the present time. Keyserling (1884) established the genus and described the first known species from a group of females from Peras, Brazil. Two other species have been described from South America by Simon (1893); one of these was from Peru and the other from Para, Brazil. Dr. Petrunkevitch was the first to describe a male which was the only specimen in the genus collected at the Wilcox camp on the San Lorenzo River. I now have about five dozen specimens from various parts of Panama and the Canal Zone with both sexes well represented. I have thought it worth while to publish a description of the female with very brief attention paid to the male.

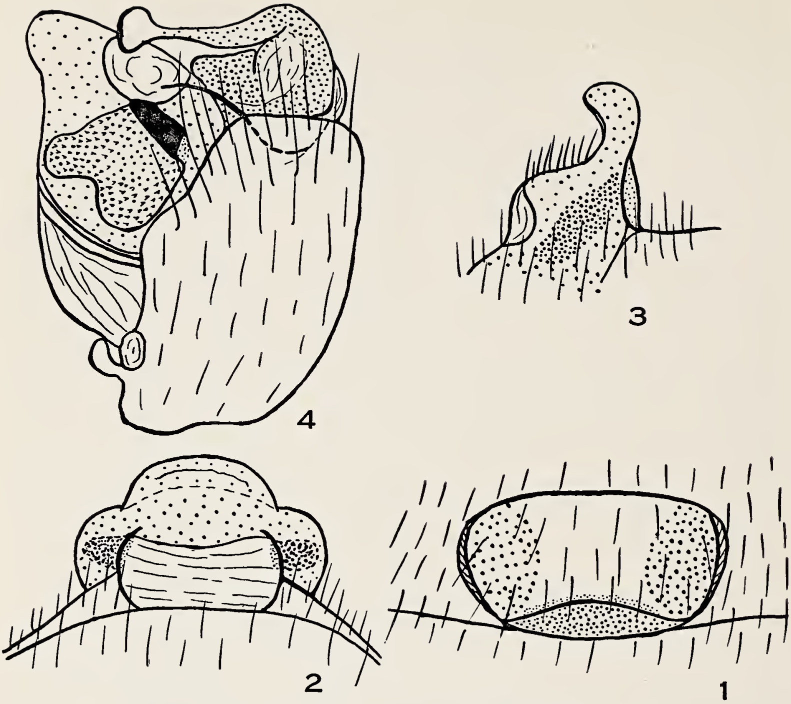
Genus *Bertrana* Keyserling, 1884

Bertrana hieroglyphica Petrunkevitch, 1925

Female. Total length 3.5 mm. Carapace 1.7 mm. long; .97 mm. wide opposite second coxae where it is widest; .44 mm. tall opposite second coxae where it is tallest; rises gently from PME to tallest region and then slopes directly to posterior border with a shallow concavity on the posterior declivity; lateral cephalothoracic grooves fairly distinct; with median fovea no more than a narrow groove; considerably overlapped by the globular abdomen.

Eyes. Eight in two rows. Viewed from above, anterior row strongly recurved, posterior row gently so. Viewed from in front, posterior row definitely procurved, anterior row slightly so; all measured by centers. Central ocular quadrangle wider in front than behind in ratio of about 5 : 4; wider in front than long in ratio of about 25 : 22. Ratio of eyes AME : ALE : PME : PLE = 8 : 6 : 7.5 : 6.5. AME separated from one another by about 1.5 times their diameter, from ALE by slightly more than their diameter. PME separated from one another by two thirds of their diameter, from PLE by slightly more than 5/3 of their diameter. Laterals separated from one another by about one third of the diameter of ALE. Height of clypeus equal to about three fourths of the diameter of AME.

Chelicerae. Basal segment about .49 mm. long; moderately robust; quite normal in general form; fang normal and regularly curved; the



Figs. 1-4. External Anatomy of *Bertrana hieroglyphica*. 1-3. Epigynum from below, in posterior view, and in profile from right side, respectively. 4. Tarsus of right palp of male.

promargin of the fang groove has three teeth the first of which is relatively large; the retromargin has a total of six teeth the first of which is relatively large, then three more smaller and close together follow together with two very small ones to complete the series; very minute tubercles may represent the two extremely small teeth which the author of the species considered to lie "between the two margins."

Maxillae and *Lip*. Essentially as described for the male except, of course, there is no "cone-shaped projection" extending laterally from the maxillae as in the male (see Petrunkevitch's Fig. 22, p. 113 and my later comments concerning the male palp).

Sternum. Rather strongly raised; sternal suture procurved; with fairly prominent, large tubercles opposite coxae 1-3 and between fourth coxae; scutiform in general; almost as wide between first coxae as long; bluntly rounded between fourth coxae which are separated by about two thirds of their width.

Legs. 1243. Width of first patella at "knee" .15 mm., tibial index of first leg 9. Width of fourth patella at "knee" .13 mm., tibial index of fourth leg 12.

(All measurements in mm.)

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
1.	1.34	.51	1.14	1.1	.45	4.54
2.	1.12	.44	.77	.86	.39	3.58
3.	.64	.28	.44	.48	.33	2.16
4.	1.08	.33	.75	.79	.35	3.30

Spines are so slender that they may be termed spinules. Trichobothria observed on tibiae and metatarsi; apparently not restricted to one dorsal unit on metatarsi as stated by the author of the species with respect to the male.

Abdomen. Essentially as described for the male. Total length of abdomen 2.4; almost as tall as long and with the same width in the middle.

Epigynum. Rather distinctive; features best shown in Figures 1-3.

Color in alcohol. Carapace yellowish with two large white patches near the middle, made by sub-chitinous deposits; with the usual black pigment surrounding the eyes. Sternum bright reddish. Chelicerae a light reddish brown; other mouth parts about the same but with whitish margins. The legs are colored essentially as described for the holotype male, but I have noted minor variations; first, second and fourth tarsi are black; the third tarsus is black in the distal half, yellowish in the proximal half. The anterior tibiae have a black and red distal transverse band. The abdomen is basically white dorsally and dorsolaterally with multiple hieroglyphic-like lines and bars of many different shapes and lengths; all of these are in red contrasted to the black hieroglyphs described in the male holotype. A great variation in the abdominal color pattern has been noted among the numerous specimens now available for study. Some of these have the hieroglyphs almost devoid of color; others have them in a mixture of red and black; still others run largely to black or red; this would also be true for males as well as females; the venter is basically yellowish with a superimposed reddish tint increasing in degree toward the center.

Male. The structure described by the author of the species as a "cone-shaped projection directed outward and upward" from the lateral margin of the maxilla is a tooth which I assume to be used in co-operation with the chitinized ridge on the base of the palpal femur, a structure found in many male argiopids. The second femur has the proximal prolateral groove and ridge corresponding to the hook on the first coxa. The main features of the palp are shown in Figure 4.

It has also been noted that, in some males, the pedal stripes described as black in the holotype are sometimes red in certain individuals.

Collection records. The female selected for detailed description is from the Canal Zone Experiment Gardens, August 18, 1954. I also have numerous specimens of both sexes from the locality just cited as well as from the C. Z. Forest Preserve, Summit, Balboa, Madden Dam region, and Barro Colorado Island, all in the Canal Zone. I also have specimens from Arraijan, Chiva, and Boquete, all in the Republic of Panama. All of these collections were made during July and August, 1936, 1939, 1950, and 1954.

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The illustration on the front cover of this issue of Psyche is a reproduction of a drawing by Professor C. T. Brues of a myrmecophilous phorid fly, *Ecitomyia spinosa* Brues (Psyche, vol. 32, 1925, p. 306).

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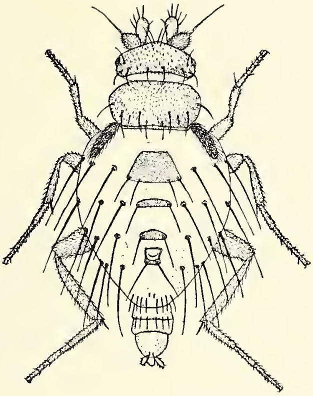

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FURTHER STUDIES ON THE HABITS OF *CRYPTOCERUS TEXANUS* SANTSCHI (HYMENOPTERA: FORMICIDAE)*

By Wm. S. Creighton[1]
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The observations presented in this paper were made on a colony of *Cryptocerus texanus* Santschi secured on December 19, 1961 at a station 21 miles north of Mathis, Texas. This colony was placed in small Janet nests and taken to the Southwestern Research Station of the American Museum of Natural History near Portal, Arizona. There it was observed for three and a half months. During this period Dr. Mont Cazier furnished much helpful information about the beetle larvae in whose burrows *texanus* lives and Mr. Martin Mortensen took the photographs included in this paper. I wish to thank Dr. Cazier and Mr. Mortensen for their help.

In 1954 Dr. R. E. Gregg and the writer published a study of the distribution and habits of *Cryptocerus texanus* (1). A large part of this study was concerned with the phragmotic activities of the *texanus* major. These responses as well as other activities discussed in the paper were shown by specimens in observation nests. Although the writer hoped to observe the activities of free nests of *texanus*, attempts to do so have met with no success so far. Nevertheless it has been possible to set up observation nests which permit the ants much greater freedom of action than did those used in our earlier study.

Before discussing these nests I wish to consider certain characteristics of *texanus* which largely determine its choice of nest sites. In common with a number of arboreal ants which occur in the southwest (species in the genera *Pseudomyrmex*, *Crematogaster*, *Leptothorax* and *Camponotus*) *texanus* does not construct its own nest passages. It may be too much to state that *texanus* is incapable of tunneling through the wood in which it lives, but there is abundant evidence to show that it does not ordinarily do so. Instead it utilizes burrows made by wood-

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Manuscript received by the editor January 28, 1963.

boring beetle larvae. The burrows most often selected are those of anobiids, bostrychids and some of the smaller buprestids. Under normal conditions each burrow consists of a long, slender, unbranched tube which opens to the outside at one end and terminates in a blind pocket at the other. The portion of the burrow just behind the opening curves inward but the rest of it roughly parallels the long axis of the branch. A branch whose diameter is 4 cm. or more may be traversed by several closely adjacent but completely separate burrows. This arrangement permits a number of beetle larvae to occupy the same branch without interference. By the time that the adult beetle emerges the branch is dead and the burrow is partially filled with detritus, which is mainly composed of small bits of cellulose that have passed through the gut of the beetle larva. The consistency of this material is similar to that of fine, tightly compacted saw-dust. This detritus must be removed before the ants can occupy the burrow, but its removal is not difficult and the process has little in common with the driving of a passage through sound wood. When the detritus has been removed what is left is a prefabricated burrow whose walls consist of hard, sound wood and whose entrance is of a size that can be occluded by the major. The branches in which *texanus* nests are largely or entirely devoid of bark. Branches which do not lose their bark are usually softened by dry rot. Such rotten branches often contain burrows but the ants seldom occupy them.

The behavior just discussed produces the problem of polydomy in *texanus*. A branch which has been extensively tunneled may contain several groups of *texanus* workers each living in a separate burrow. If it can be shown that only one of these groups contains a queen the probability is that the several burrows contain parts of a single, polydomous colony. But when each group contains one or more queens it is impossible to state whether one is dealing with several separate colonies or a single polydomous colony. The matter becomes even more complicated when several adjacent branches house groups of *texanus* workers. This was true of the population on which this study was based. The ants occupied burrows in the stubs of six dead branches, all attached to a single living branch of a live-oak (*Quercus virginiana* Nee). The total population of the six stubs consisted of approximately 275 individuals of which 23 were queens. Since the number of queens in each stub varied from two to five, it was impossible to say whether the six groups were separate colonies or parts of a single polydomous colony. As it was advantageous to have a number of equivalent groups for the work that was contemplated, it was decided to proceed on the latter assumption. The 18 queens which survived extraction were arranged in nine pairs and each pair was installed in a plaster observation nest with about twenty-five workers selected at random. No friction developed in any of the groups thus established and it was found that the groups could be reshuffled at will. It was not until much later, when some of the groups had been isolated for months, that they began to act as separate entities. Even then the groups would combine after a brief period during which an avoidance reaction was displayed. Since this combination was a voluntary response on the part of groups which could have nested separately, it seems probable that the original population was a single polydomous nest.

Through unusual good fortune one of the majors remained in the occluding position when the stub containing that portion of the colony was split open. The part of the stub which contained the nest opening and its adjacent nest passage was saved. The nest entrance was an oval with a long axis of 2.8 mm. and a short axis of 2.65 mm. With these proportions in mind it was easy to supply a branch containing a burrow whose entrance was of the proper size. After it was certain that this branch contained no other arboreal ants, it was placed on the floor of a two gallon aquarium together with one of the occupied Janet nests. The cover of the Janet nest was then removed and a glass top was sealed onto the aquarium with masking tape. The *texanus* workers at once began to explore the aquarium and soon abandoned the Janet nest for the burrow in the branch. With one exception the groups remained in the burrows. The one group which failed to do so had been given a branch which was rotten on the inside although it was sound to external appearances. When this group was given a sound branch they accepted it without further difficulty.

One interesting feature of the aquarium nests was that they offered natural conditions for nest occlusion. It is gratifying to report that the phragmotic responses described in our 1954 study are essentially the same as those of a major which is occluding a natural burrow entrance. In the main this is also true of the behavior of the minor but one interesting difference often occurred. In our earlier studies the minor always entered the nest by crawling over the dorsum of the crouching guard (Plate 1, figs. 1-3). As the glass top of the observation nest formed the roof of the passage, less traction was furnished by this glass roof than by the dorsum of the guard. But in a natural nest this is not true and the minors would often enter the nest by walking over the roof of the passage rather than over the dorsum of the guard. When this occurs the dorsal surface of the entering minor is very close to that of the crouching guard and may be in actual contact with it. Another advantage of the aquarium nests was that they permitted limited foraging. If free colonies of *texanus* forage as did those in the aquaria, then *texanus* forages only in the daytime. Foraging appears to be initiated by the morning increase in light intensity but it will not occur unless the temperature is 70°F. or higher. Much of the foraging was done by the medias and minors but the majors were not restricted to the nest. This led to another type of response when the major on guard at the nest entrance had to admit another major, for the usual crouching reaction of the guard will not furnish enough space to allow a major to enter. When this was necessary the guard came out of the nest entrance. The returning major then entered the burrow head first, after which the guard backed into the entrance and assumed the occluding position. In the aquarium nests the guard was not continually on duty. This may have been because no strange ants were present. The writer has observed the same behavior in *Camponotus (Myrmaphaenus) ulcerosus* Wh. (2), whose major assumes the phragmotic position only when other ants are in the vicinity of the nest entrance.

In our 1954 publication it was stated that *texanus* sometimes forages on the ground. This may be true but it is now clear that such foraging has not been conclusively demonstrated. The aquaria nests were kept supplied with fresh live-oak twigs and the ants constantly walked about on their leaves. Although *texanus* is not an agile ant, it is surprisingly sure-footed. Even so foraging workers would sometimes lose their balance and fall to the floor of the aquarium. When a worker lands on its back, as it often does, it rights itself in an unvarying fashion. Both the head and the gaster are lifted above the surface on which the ant is lying until the body forms an arc. Thereafter one of the hind legs is extended and the body is rocked until it turns on one side. In the scores of times that the ants were seen to regain their footing, the process never varied in the slightest particular. While the flattened dorsum of *texanus* undoubtedly makes it difficult to right the body from an inverted position, this will not explain why the righting reaction is so stereotyped. But this unvarying righting reaction can be explained if the ants have had occasion to right themselves so often that the most efficient method of righting has become an integral part of their behavior. This implies that the ants frequently fall from the trees in which they live, a view that is supported by their actions in the aquaria. For if the ants cannot always maintain their footing on leaves that are unaffected by wind, then every strong gust must displace some of the foraging workers of a free nest. The victims of such accidents undoubtedly return to the nest but to do so they have to traverse the ground at the base of the tree. It is easy to interpret this action as the return of a forager which, in a sense, it is. But when workers of *texanus* are found wandering on the ground at the base of a tree this does not constitute proof that the foraging has been terrestrial. The writer fell into this trap in 1954, for at that time it was not considered that the presence of *texanus* workers on the ground below a tree might be accidental.

While the nests in the aquaria showed many advantages they had one serious defect. It was impossible to see what was going on in the burrows. There seemed to be no reason why this defect might not be remedied if the ants could be made to accept "burrows" in which one side was closed with glass. Accordingly, small blocks of seasoned oak 10.5 x 3.5 x 2.5 cm were secured. A shallow groove about 7 cm. long was cut on one side of the block and at one end of this groove a hole was drilled to the opposite side of the block. By using a drill 3/32 of an inch (2.38 mm.) in diameter and by drilling at an angle to the surface, an oval nest opening 2.75 x 2.50 mm. was produced. While this was slightly smaller than the natural nest entrance, the size difference caused the ants no difficulty. After the oak block had been drilled the face with the "burrow" was placed against the front pane of the aquarium and the block was held in this position by a rim of paraffin. Light was excluded from the "burrow" by a piece of cardboard taped on the outside of the glass opposite the oak block. The ants had access to the "burrow" through the drilled hole which opened into the aquarium. The ants were much more hesitant to accept these passages than those in branches. In order to get them to enter the passage it was usually necessary to chill some members of the group to immobility and insert them through the nest opening. If the opening was plugged for several hours thereafter the workers inside the passage became accustomed to it and on their release would lead the remainder of the group into the passage. Once the ants had established themselves in the passage they seemed thoroughly satisfied with it. Some of the ants lived in the oak blocks for months.

One surprising fact was apparent as soon as the colony had established itself in the passage. Although the length of the passage was about 7 cm., the ants preferred to pack themselves tightly into the outer half of it. They would rarely go into the inner half of the passage and they would never stay there. As far as motility is concerned this packing is very awkward, for only individuals at either end of the mass can move freely. Those near the middle of the mass are usually unable to move at all. When the ants have formed this close-packed mass it is difficult to get them to move out of it. Illumination with a brilliant spot of light, unless long continued, will do no more than make the ants shift position slightly. This packing appears to be maintained continuously. For a period of several days the cardboard covers of the nests were replaced by pieces of red cellophane. The ants could thus be observed at any time without exposing them to light. Except for the egress and return of foragers the ants remained close-packed and quiescent during this entire period. The writer can offer no explanation for this behavior but it accords well with what has been noted when free colonies are exposed. From the standpoint of observation it is unfortunate, for it greatly increases the difficulty of keeping a close check on the brood.

Early in this study it became apparent that few of the feeding responses of *texanus* are normal when the ants are confined in Janet nests. Much the same conclusion had been reached in our 1954 study, when some of the colonies in Field nests had been kept alive for more than a year on a diet of maple syrup or honey mixed with egg yolk. But it was obvious that this food could not be obtained under natural conditions and equally obvious that the ants had little liking for such food even though they could subsist on it. Since no more acceptable food had been found, the Janet nests containing the Mathis colony were supplied with maple syrup or honey. The ants soon demonstrated that they preferred honey to maple syrup and honey became their sustaining diet during a period when they were given as wide a variety of small arthropods as could be secured. The arthropods were spiderlings, mites, collembolans, newly emerged mantids, nymphal coccids, membracids and bugs, termites, small beetles and the larvae of several species of arboreal ants. The reaction of the *texanus* workers to these arthropods varied. Some they attacked and cut to pieces, some they tried to discard and some they ignored. When the victims were cut to pieces the fluids which exuded from them were occasionally imbibed by the attacking *texanus* workers. But as soon as the victim had been immobilized or killed they rarely paid any further attention to it. This behavior was so strikingly different from that shown by most entomophagous species that, even admitting that it may have been abnormal, there was nothing about it to suggest that arthropods form a part of the diet of *texanus*. On the other hand this behavior could readily be regarded as a defense response which would rid the nest of an unwelcome intruder and later developments appear to confirm this veiw.

It was soon found that the ants would gorge themselves with honey until the posterior segments of the gaster were visibly distended to the rear. This response seems to have been due to a need for fluids and not to a fondness for honey. The presence of honey in the feeding chambers favored the growth of mould. To reduce mould growth to a minimum the nests were kept dry enough to prevent condensation and it is likely that the only fluids that the ants secured were those furnished by the food in the nests. Thus it seems correct to state that the conditions in the Janet nests were such that the ants were subjected to a sort of forcible feeding. The females also gorged themselves with honey and soon began to lay eggs. These were eaten by the workers almost as fast as the queens laid them. This obvious protein lack was corrected by giving the ants mantis eggs which had been sliced open. The ants would gorge themselves on the liquid contents of the mantis eggs and thereafter stopped eating their own eggs. As a result brood was produced, some of which was carried through to the pupal stage. It should be noted that both the egg-laying of the *texanus* queen and the development of her brood is slow, if one may judge from what happened in the artificial nests. The eggs were not laid at regular intervals but in bursts, during which three or four eggs were laid with comparative rapidity. Over an extended period the rate of egg-laying averaged out to one egg every forty-eight hours. At a temperature around 70°F. most of the eggs developed into larvae in 25 days. The larval period was about 55 days. Observations had to be discontinued before any of the pupae transformed to adults but, if the pupal period is as long as the larval period, the development of a *texanus* worker from egg to adult should have taken not less than four and a half months in the artificial nests. If this slow rate of brood development is true of free colonies of *texanus*, it is easy to appreciate why this species is pleometrotic. Unless several queens were present in each colony the production of adults could scarcely keep pace with the inevitable attrition of the foraging workers.

After the ants were installed in the aquaria nests they would not eat anything, not even the food on which they had gorged themselves while in the Janet nests. As already noted the *texanus* crawled over the oak leaves by the hour and occasionally drank from droplets of water that condensed on the walls of the aquaria. But for a period of several weeks they were not seen to swallow anything else. If the ants had died it would have been logical to conclude that they had starved, but they did not die. On the contrary they seemed to be in better shape than when they had been feeding on honey in the Janet nests. While the ants were in the Janet nests they had been given pieces of live-oak leaves on the chance that they might secure some nutricious secretion from them. The ants were definitely attracted to the leaf fragments and stripped off the small, stellate hairs which occur on the petiole and the lower surface of the blade. In the leaf of *Q. emoryi* Torr., the species mainly used in this study[2], the largest and most conspicuous stellate hairs are concentrated at the base of the blade where they form a dense, tangled mat at either side of the midrib. These matted hairs often shelter small mites and it was at first believed that the ants were stripping off the hairs to get at the mites. Further examination showed that this was untrue for, after removing the stellate hairs, the ants discarded both the hairs and the mites which were among them. This led to a series of efforts, all of which failed, to secure an extract from the hairs which would be acceptable to the ants. Instead of attracting the ants, such extracts usually repelled them. But this did not eliminate the possibility that the ants might somehow be securing food from the stellate hairs and their actions in the aquaria nests seemed to strengthen this possibility.

The oak twigs in the aquaria were sealed into small jars of water and usually remained fresh for ten days or more. During this period the buds on many of the twigs would unfold and small, new leaves would be displayed. If the ants were securing food from the stellate hairs, it might be expected that the hairs of the young leaves would be particularly attractive. It was, therefore, a surprise to discover that the ants paid much less attention to the young leaves than they did to the old ones. Subsequent events provided an explanation for this behavior, but its significance was not appreciated when it was first observed.

About March 8th choke-cherry trees near the laboratory began to leaf out and a day or two later willow bushes began to produce catkins. Twigs from these plants were substituted for the live-oak twigs in the aquaria largely, it must be confessed, as a desperation measure. As

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[2] It may be objected that *Q. emoryi* is unsuitable for this work since its range lies well to the west of that of *texanus*. Admittedly it would have been preferable to use the leaves of *Q. virginiana*, as most of the nests of *texanus* have been found in this oak. Although *texanus* could not nest in *Q. emoryi* under normal conditions, its western counterpart, *Cryptocerus rohweri* Wh. does so. On November 7, 1952, the writer took a small colony of *rohweri* that was nesting in *Q. emoryi* at Peña Blanca Springs, Santa Cruz Co., Ariz.

soon as the *texanus* workers began to forage over these twigs it was obvious that they were feeding. They spent much time licking the tips of some of the bud scales of the choke-cherry twigs. An examination of these showed that each of the inner scales possesses two oval nectaries at its tip. The nectaries produce a fluid which the ants collected. It is possible that nectar was also gathered from the willow catkins but the obvious thing that the ants took from these was pollen. Their liking for pollen was clearly demonstrated, for they would not only take it from the catkins but would also spend long hours picking up pollen grains that had fallen onto the sides and floor of the aquarium. When the pollen was collected from the sides of the aquaria the process was easy to observe but, despite much effort, the writer was never able to determine how the grains are initially picked up. It is probable that they are formed into clusters by the palps, for the mandibles appear to be closed throughout the process. When a number of grains have been formed into a cluster this is incorporated into a drop of liquid at the end of the hypopharynx. After a short period during which the pollen-filled drop is juggled about at the end of the hypopharynx, the drop is swallowed.

As the spring advanced other trees and shrubs came into bloom and as each did so twigs with blossoms were placed in the aquaria with the *texanus* workers. It was soon clear that not all pollen is equally acceptable to *texanus*. Although the ants crawled over blossoms of apples, plums and Oregon holly (*Mahonia* sp.) whose anthers were loaded with pollen, they paid no attention to the pollen or to the anthers which bore it. Conversely, they were strongly attracted to the pollen of the box elder (*Acer negundo* L.) and that of the live-oak *Q. emoryi*. The reaction of the ants to the live-oak catkins or to the box elder stamens was exactly that which they had shown with the willow catkins; pollen was collected directly from the catkins or anthers and also from other areas where it had settled. This last response suggested that under natural conditions the ants may secure much of their pollen supply not from the blossoms but from other parts of the plant. If they prefer wind-borne pollen, as seems to be the case, why might not their constant foraging over the surface of the leaves be a search for pollen grains adhering to the leaf? The difficulty in proving this lies in the fact that over most of the leaf the pollen grains are so widely scattered that their detection is difficult, even under high magnification. But a careful examination of the leaves of *Q. emoryi* showed that a considerable concentration of pollen grains is often present in the two tangled mats of stellate hairs at the base of the midrib. A great many dust particles are also trapped in these mats and earlier examinations had failed to distinguish between the dust particles and the pollen grains. But since pollen grains are often present in the basal hair mats on the leaves of *Q. emoryi,* the stripping of the hairs by the *texanus* workers becomes understandable. The hairs are removed in the process of extracting pollen grains from among them and after the pollen grains are extracted the hairs are discarded. Further, if a leaf contains no pollen grains the ants should not be overly interested in it. An excellent example of this had been furnished by the young oak leaves which unfolded in the aquaria. Since these leaves had developed in a sealed space they contained no pollen and as a result the ants paid scant attention to them. In addition, the pollen-gathering activities of *texanus* offer an explanation of their preference for nests in live-oaks. This preference was pointed out in our 1954 study but no attempt was made to account for it. Stellate hairs are present on the under surface of the leaves of most live-oaks. Their arrangement is highly variable. In *Q. hypoleucoides* Cam., the "silverleaf oak", these hairs give rise to the common name for the plant, since they form a dense, silvery, tomentose layer over the entire lower surface of the leaf. In *Q. emoryi,* as already noted, most of the stellate hairs are concentrated at the base of the blade. But whatever the arrangement, these hairs function with great efficiency as pollen traps, for they are sufficiently sticky to hold pollen grains with surprising tenacity. In one instance the leaves of *Q. hypoleucoides* were evenly coated with willow pollen over the entire lower surface. After the pollen had adhered to the stellate hairs no amount of shaking would dislodge it, but it is interesting to note that when these pollen coated leaves were placed in the aquaria the *texanus* workers completely cleared them of pollen in a few hours. It is even more interesting to consider the advantages of such a pollen trap to a pollen feeder. The catkins of live-oaks are produced in the spring and remain on the trees for a few days only. The period during which pollen can be taken directly from the catkins is, therefore, a comparatively brief one. Unless *texanus* could store pollen, and there is no evidence that it does so, it could not live on pollen taken directly from the catkins. This seemed so obvious that pollen was not even considered as a possible source of food in our 1954 study. But while *texanus* does not store pollen the leaves of live-oak trees do. Moreover, this storage is not selective but includes any wind-borne pollen. Thus when *texanus* nests in live-oak trees it is assured of a lasting supply of pollen trapped in the stellate hairs on the lower surface of the leaves.

Since *texanus* does not always nest in live-oaks it is clear that only a part of the picture has been presented here. The nectar-feeding activities of *texanus*, of which one instance was cited in this study, offer interesting possibilities for further investigation. If *texanus* feeds on nectar there is every reason to suppose that it will also feed on honey dew. This opens a wide range of possible food sources including the surface secretions of galls and the sugary exudates of coccids and aphids. But it now seems reasonably certain that *texanus* does not ordinarily augment its nectar-pollen diet with the tissues of other insects. This behavior is noteworthy, for many other ants which obtain the major part of their diet from plant sources (the harvesters and the honey ants) show no hesitation about feeding on the tissues of other insects as a supplementary item of diet. But the nectar-pollen diet of *texanus* is no more specialized than the ant itself. For the structure of *texanus*, like that of most of the members of the Cryptocerini, is highly specialized and it is not surprising that an ant with such advanced structural features should have an unusual and restricted diet.

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A NEW SPECIES OF *EURYGASTER* AND NOTES ON SOME LITTLE KNOWN SPECIES OF TURKISH PENTATOMIDAE (HEMIPTERA: HETEROPTERA)

By Niyazi Lodos[1]
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The species belonging to the genus *Eurygaster* Laporte are very important from the economic point of view in Turkey. *Eurygaster integriceps* Puton is one of the most harmful insects to wheat and barley, but in addition it also attacks rye, oat and other graminaceous plants. In Turkey it causes extensive damage especially in the eastern south provinces, the amount of injury caused varying from year to year and from place to place. In epidemic years the total amount of the losses in some areas can reach up to 90% if no control measures are used. *Eurygaster maura* (L.) and *Eurygaster austriaca* (Schrk.), found especially in Western Anatolia, cause damage approaching only 20% if no control measures are used, because their egg parasites are very active in this part of the country. A good knowledge of this genus is therefore very important to Turkish entomologists and agriculturists. While working at the University of Aegea, Izmir-Turkey, I paid special attention to these insects and collected many specimens whenever time was available. Amongst my material I find one new species which is described below.

Eurygaster chinai n. sp.

Plates 15 and 16

General shape: oblong-oval, subdepressed (fig. 1). General colour: reddish brown, except base of scutellum below pronotum which bears a narrow, blackish stripe transversally.

Structure (female): General shape of the head (fig. 2) subtriangular, about as broad between eyes as long, somewhat flattened on its surface except middle of tylus which is slightly prominent and regularly convex in front; lateral margins near eyes slightly sinuated and from eyes perceptibly narrowed and keeled; tylus long and somewhat broad, narrowed apically, truncate at the end; juga projecting slightly beyond end of the tylus, not in contact with each other, broadly rounded at apex; disc of head except margins finely and densely punctate. Antennae (fig. 3) brownish except fifth segment which is black-

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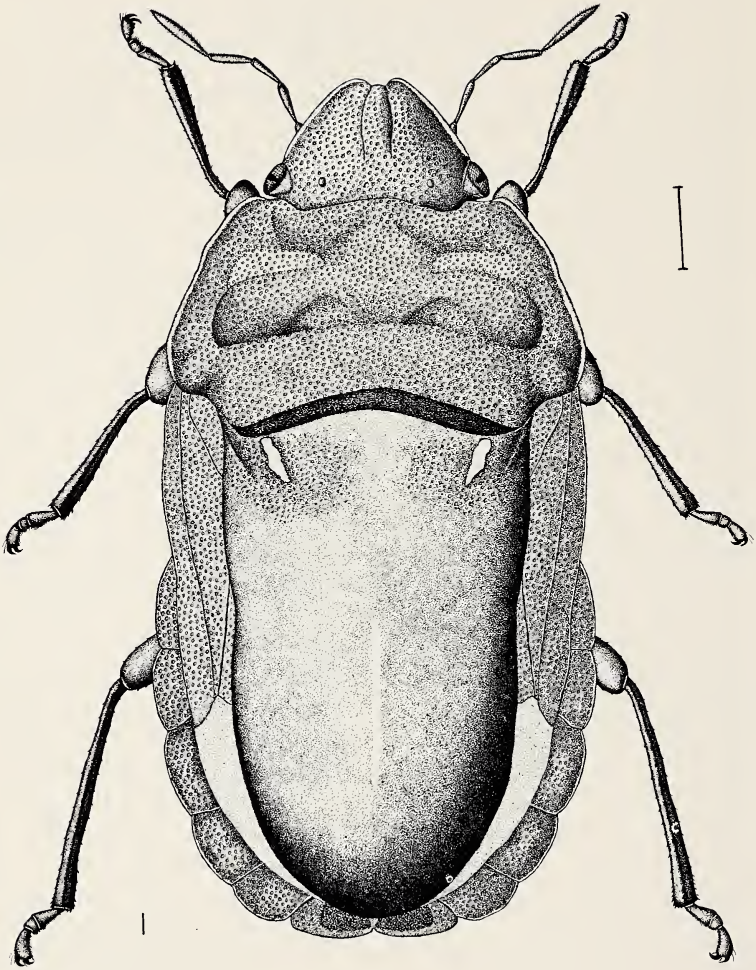
ish; first segment nearly clavate, almost equal to second; second somewhat cylindrical; third shortest and cylindrical; fourth shorter than fifth and second in length and cylindrical; fifth longest and pubescent; length of antennal segments I, II, III, IV, V ; 30, 30, 21, 28, 45. Eyes bright yellow except for middle which has a dark brown transverse stripe; inserted at posterior margin of the head, not prominent but also not contiguous with pronotum; ocelli brownish, inserted fairly far from base of head and somewhat prominent. Rostrum thick and nearly reaching to the middle of hind coxae, brownish except the last segment which is blackish.

Pronotum fairly broad, more than twice as broad as long in the middle and flattened (fig. 4), anteriorly nearly straight, a little broader than the eyes and head together, lateral margins slightly sinuate, humeral angles somewhat pointed, lateral margins slightly keeled, and pale in colour, without punctures; posterior margin of pronotum at base of scutellum concave; disc of pronotum finely and densely punctured; in middle of disc a large, long transverse prominence (fig. 1, 4, 5); in front of the prominence two somewhat low impressions; behind it, two somewhat strong impressions; cicatrices light yellowish, large, punctured finely and obscured. Scutellum nearly parallel at the sides and sinuate towards the middle, at the apex regularly rounded; distinctly shorter than abdomen; at each basal angle there is a strong narrowed impression; base of scutellum against pronotum with a blackish somewhat wide transverse stripe (fig. 1, 4); each basal angle with a whitish callus located some distance from the base of pronotum; colour of base of scutellum brownish, gradually paler toward apex; puncturations near and around of calli largest and gradually disappearing far from these areas; middle of scutellum an obscure longitudinal carina. Clavus very small and punctured. Corium somewhat strongly punctured, extending beyond middle of the scutellum, same colour as that of scutellum and other parts of the body; outer vein of the corium distinct and reaching nearly to the apex of corium. Membrane transparent, reaching just to apex of scutellum. Connexivum a little broader than thorax, darker than scutellum and other parts of body, surface irregular; finely and densely puncured, outer margins of each connexival segment distinctly rounded. Underside of head, sternum and acetabula strongly punctured. Venter light brownish, without or with only obscure punctures; underside of each connexival segment with a blackish spot near margin. Spiracles reddish. Female genitalia with a distinctive structure as seen in fig. 6. Valvifer I large, nearly triangular and each one has small blackish



Lodos — Eurygaster

stripe near distal end; paratergite 9 large and some distance from the margin of seventh sternal segment; valvifer II triangular. Legs light brown; tibiae almost straight and with a few very small and obscure spines; at the apex, spines become closer and with few hairs; tarsus normal for the genus, underside with thin, dense and short hairs; second tarsal segment shortest; third with a few hairs at apex; claws dark brown 3/4 from the base (fig. 2).

Size (female): length 12 mm.; maximum width across abdomen 7.2 mm., head: length 2.4 mm.; width 2.9 mm.; vertex 2.5 mm., pronotum: length 2.7 mm.; width 7 mm., scutellum: length 6.7 mm.; width 5 mm.

Holotype: female, Turkey, Izmir-Bornova, 14.V.1958 (N.Lodos), in the British Museum (Natural History).

Habitat: the type, a female was found by me by sweeping on wild graminaceous plants in a wooded hill formation. It seems to be a very rare species and the male is unknown.

This new species is related to *Eurygaster integriceps* Put. by external appearance but can easily be distinguished by its distinct prominence on the pronotum, shorter scutellum, distinctly rounded connexivum and particularly the structure of the female genitalia. I name this species after the outstanding British authority on the *Hemiptera,* Dr. W. E. China, who has helped me a great deal in my entomological work.

Solenostethium bilunatum (Lefebure)

Scutellera bilunulata Lefebure 1827, Mém. Soc. Linn. Paris, :102; pl. 5, f. 5.

This species was first recorded from Turkey by Fieber (1861) as *Coeloglossa ledereri* without specific location. Lethierry and Severin (1893) also listed it in the same way. Oshanin (1912) was the only one to express the locality more definitely as "Turkei (in Europa)" which at that time was Thrace. So far as is known *Solenostethium bilunatum* (Lef.) is a Mediterranean element which extends from Tunisia, Morocco, Algeria, Cyprus, Turkey and Syria. It is obvious that it could not have existed so far north as Oshanin states. Its northern range was not previously even as far north as Izmir (Turkey). This species has remained known to Turkey only from these early records until the present time.

The writer now is able to confirm the presence of this species in the Turkish fauna. I have collected 14 female and 11 male specimens at

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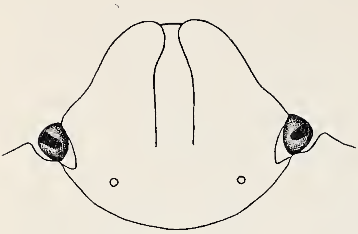
EXPLANATION OF PLATE 15

Fig. 1. *Eurygaster chianai* n. sp. female (holotype).



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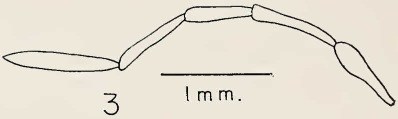

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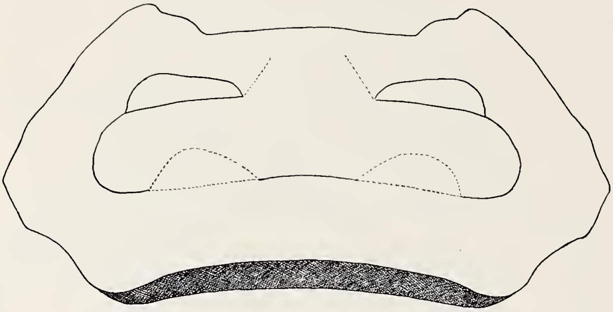

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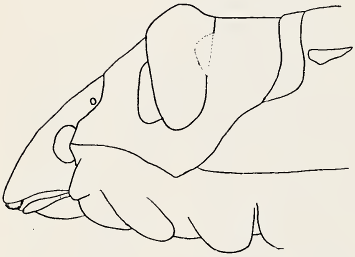

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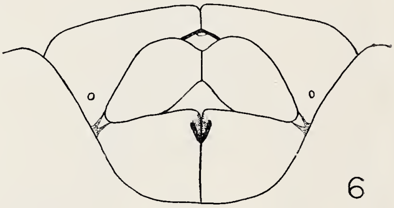

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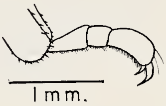

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Lodos — Eurygaster

Dalaman-Muğla (Turkey), 23.VI.1962, and some specimens at Köycegiz-Muğla (Turkey), 21.VI.1962. All these specimens were taken from *Paliurus spina-christi* Miller. These specimens are deposited in the personal collection of the author and the Aegean University, Faculty of Agriculture collection in Izmir (Turkey).

In 1861 Fieber described *Coeloglossa ledereri* from 7 specimens (male and female) and cited its distribution as Turkey and Syria without any specific locality. Fieber's description seems rather meagre, having some characteristics of *Solenostethium bilunatum* (Lef.) and some *Solenostethium ledereri* Fieb. These characteristics are based on the formation of clypeus, the colour of the dorsum of the insect and the existence of black spots on the head. *Solenostethium ledereri* Fieb. is now considered at the most as a colour form of *Solenostethium bilunatum* (Lef.) (Stichel 1960).

I have examined specimens from Dalaman which I collected at the same locality and discovered that while there are some different characteristics attributable to *Solenostethium bilunatum* (Lef.) and *Solenostetium bilunatum* f. *ledereri* Fieb., these different characteristics are not at all constant. Therefore, *Solenostethium bilunatum* f. *ledereri* Fieb. is here considered as a straight synonym (new synonymy).

Pausias martini Puton

Piezodorus martini Puton 1890, Rev. d'Ent., 9:227.

This species has only recently been included as a part of the Turkish fauna, although its geographic range includes Syria and Caucasia (Puton 1890, Oshanin 1912, Vidal 1949, Stichel 1960 and Linnavuori 1960). This distribution shows that it should also be found within the boundaries of Turkey. Wagner (1959) has recorded this species from Turkey for the first time. He reported if from Diyarbakir, which is in the south east of Turkey. The locality is some 200 km. from the northern border of Syria. The author is now able to establish the presence of this species on the Aegean sea coast in Western Anatolia. One male and 2 female specimens were collected from Karsiyaka-Izmir (Turkey), 10.VIII.1960, from a mulberry tree (*Morus alba* L.). Thus the range of this species is spread over a considerable part of Turkey.

EXPLANATION OF PLATE 16

Fig. 2-7. *Eurygaster chinai* n. sp. female (holotype); 2, dorsal view of the head; 3, antenna; 4, dorsal view of pronotum; 5, lateral view of pronotum; 6, female genitalia; 7, hind tarsus.

ACKNOWLEDGEMENTS

While preparing this work I used the collections and library of the British Museum (Natural History) and the laboratory and library of the University of Connecticut, Department of Zoology and Entomology. To these institutions the author expresses his sincere appreciation. My thanks are due to Dr. J. A. Slater for his kind help and the loan of literature. I also appreciate help received from Dr. W. E. China, especially for valuable opinions on the subject and for reading the typescript.

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A NEW SPECIES OF *CEPHALONOMIA* EXHIBITING AN UNUSUALLY COMPLEX POLYMORPHISM (HYMENOPTERA, BETHYLIDAE)[1]

By Howard E. Evans
Museum of Comparative Zoology

Polymorphism is well known in *Cephalonomia* and certain other genera of Bethylidae. Kearns (1934) has studied the phenomenon in *C. gallicola* (Ashmead), a species in which the females are always apterous, the males either apterous or macropterous. A different type of polymorphism occurs in *C. formiciformis* Westwood (Richards, 1939); in this species the females are either macropterous or brachypterous, the males always macropterous. In the related genus *Scleroderma,* most species appear to be dimorphic in both sexes, either fully winged or completely apterous (e.g., Bridwell, 1920). As compared to fully winged forms, brachypterous and apterous forms tend to exhibit reduction in eye size, ocelli, width of the head, and some of the sutures of the pterothorax. Thus apterous individuals may look very different from macropterous ones of the same species.

A few years ago Hugh B. Leech, of the California Academy of Sciences, sent me a series of a minute, polymorphic *Cephalonomia* which he reared from ciid-infested fungi collected in Baja California. More recently John F. Lawrence, of the University of California at Berkeley, has sent me examples of this same *Cephalonomia* from ciid-infested fungi collected in numerous localities in Oregon, California, Arizona, Baja California, and Nayarit. This wasp is quite distinct from any other North American *Cephalonomia,* its closest relative apparently being the Palaearctic *formiciformis,* which also attacks ciid beetle larvae in fungi. This new species, described below as *perpusilla,* differs from *formiciformis* in its smaller size and also in minor details of color and structure. It also differs from *formiciformis* and from all other bethylids, so far as I know, in that no less than six well-differentiated types of individuals can be discerned, each type differing in certain aspects of wing development, size of the eyes and ocelli, head shape, or other details. In brief, the males are either alate (i.e., macropterous) and broad-headed or apterous and narrow-headed, the females macropterous, micropterous (in either case narrow-headed, about like the apterous males), subapterous, or apterous (in these two

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TABLE ONE

Cephalonomia perpusilla: numbers of each form arranged by locality

Zone	Locality	Alate ♂♂	Apterous ♂♂	Alate ♀♀	Micropterous ♀♀	Subapterous ♀♀	Apterous ♀♀	Total
D	CALIFORNIA							
	Plumas Co., Twain	1	2	6	0	0	0	9
	Plumas Co., Canyon Dam	2	7	15	0	0	30	54
	Eldorado Co.	0	0	1	0	0	1	2
B	OREGON							
	Douglas Co.	0	0	1	0	2	0	3
	CALIFORNIA							
	Mendocino Co.	0	0	0	0	1	0	1
	Marin Co.	0	0	2	0	5	0	7
	Contra Costa Co.	0	0	1	0	1	0	2
	Fresno Co.	0	0	0	0	1	0	1
A	CALIFORNIA							
	Alameda Co.	0	0	0	5	0	0	5
	Santa Clara Co.	0	0	0	1	0	0	1
	Santa Cruz Co.	0	0	0	2	0	0	2
C	ARIZONA							
	Rustler Park	0	1	1	0	3	1	6
	Portal & vicinity	3	1	8	0	4	6	22
	Douglas	0	1	0	0	2	0	3
D^1	BAJA CALIFORNIA							
	San Jose Island	4	14	3	0	0	4	25
	Cerralvo Island	0	0	1	0	0	13	14
	El Triunfo	1	30	0	0	0	37	68
	NAYARIT							
	San Blas	7	6	3	0	0	8	24
	TOTALS	18	62	42	8	19	100	249

cases extremely narrow-headed). However, samples from any one locality do not in any case contain all six forms. Males appear dimorphic throughout the range, but the females appear to show geographic variation in morphism (Table I). This unusual situation is discussed further following the description of the six forms.

Cephalonomia perpusilla new species

Holotype. — ♂ (macropterous), Twain, Plumas Co., Calif., 6 Nov. 1960 (J. F. Lawrence, no. 720, *ex Polyporus versicolor* on *Acer* sp.).

Paratypes with the following data (see Table I for numbers of each sex and form from each locality). — OREGON: 10 mi. SW Camas Valley, Douglas Co., 24 Oct. 1962 (JFL, no. 1126, *ex Polyporus adustus*). CALIFORNIA: Mendocino Co., 2 mi. N Piercy, 26 Oct. 1962 (JFL, no. 1131, *ex Polyporus versicolor*) ; Plumas Co., Twain, 6 Nov. 1960 (JFL, no. 120, *ex Polyporus versicolor*) ; Plumas Co., Canyon Dam, 6 Sept. 1960 (JFL, no. 713, *ex Fomes pinicola*) ;

Eldorado Co., 2 mi. N Placerville, 18 May 1961 (JFL, no 823, *ex Polyporus versicolor;* coll. P. Wygodzinsky) ; Marin Co., San Geronimo, 16 April 1961 (JFL, no. 791, *ex Polyporus versicolor*) ; Marin Co., Alpine Lake, 8 July 1961 (JFL, no. 846, *ex Lenzites betulina*) ; Contra Costa Co., 1.5 mi. W Danville, 12 Aug. 1961 (JFL, no. 938, *ex Polyporus adustus*) ; Contra Costa Co., 14 mi. S Clayton, 18 June 1961 (JFL, no. 835, *ex Lenzites betulina*) ; Alameda Co., Oakland, 26 Dec. 1959 (JFL, *ex Polyporus versicolor*) ; Santa Clara Co., 16 mi SE Sveadal, 19 June 1960 (JFL, no. 605, *ex Polyporus adustus*) ; Santa Cruz Co., Ben Lomond, 25 Feb. 1962 (JFL, no. 994, *ex Fomes pinicola*) ; Fresno Co., Huntington Lake, 31 Aug. 1960 (JFL, no. 675, *ex Fomes annosus*). ARIZONA: Cochise Co., Rustler Park, 8 mi. W Portal, 8 Aug. 1961 (JFL, no. 924, *ex Fomes* sp.) ; Cochise Co., 5 mi. SSW Portal, 4 Aug. 1961 (JFL, no. 899) ; Cochise Co., 2 mi. SW Portal, 9 Aug. 1961 (JFL, no. 928, *ex Trametes hispida*) ; Southwestern Res. Sta., 5 mi. SW Portal, 5 Aug. 1961 (JFL, no. 902, *ex Ganoderma lucidum*) ; same locality, 7 Aug. 1961 (JFL, no. 916, *ex Trametes hispida*) ; Cochise Co., 15 mi. E Douglas, 5 Aug. 1961 (JFL, no. 906, *ex Trametes hispida*). BAJA CALIFORNIA: San José Island, 11 April 1962 (R. Moran, no. 9415, *ex Ganoderma* sp.) ; Cerralvo Island, 16 April 1962 (R. C. Banks, *ex Ganoderma* on *Ficus*) ; 0.7 mi. NW El Triunfo, 9 January 1959 (H. B. Leech, *ex* ciid in fungus). NAYARIT: San Blas, 28 December 1960 (JFL, no. 746; coll. P. DeBenedictis, *ex Ganoderma* sp.).

Holotype and paratypes to be deposited in the California Academy of Sciences; paratypes at the California Insect Survey, U. S. National Museum, Museum of Comparative Zoology, and collection of J. F. Lawrence.

Description of alate male. — Total length about 0.7 mm. to 1.1 mm. Head length .253-.336 mm.; head width .80-.88 × head length (mean .84). Wings long, extending beyond apex of abdomen; ocelli strongly developed. Body dark brownish-fuscous; antennae dark brown; legs dark brown except tarsi straw-colored to light brown, tibiae often with a faint pale annulation at base; wings hyaline. Mandibles with a strong apical tooth and three small additional teeth; clypeus truncate apically, its median area roundly elevated. Antennae inserted well below level of bottoms of eyes; first four segments in a ratio of about 7:3:2:2 or 7:3:1:1, apical segment large, 2.3-2.8 × as long as wide. Eyes prominent, weakly hairy, removed from base of mandibles by about .3 × their own height, removed from vertex crest by .7-1.0 × their own height. Minimum width of front

.65 × width of head, 1.3-1.45 × eye height. Head, and also thoracic dorsum, polished, weakly alutaceous, obscurely punctate. Scutellum with a straight transverse groove at base. Propodeum without a median carina or a transverse carina margining the disc behind; surface somewhat alutaceous, especially on the posterior slope and sidepieces. Fore wing with subcosta, prostigma, and stigma distinct, median and anal veins indicated by very faint, hyaline streaks. Abdomen relatively broad and short.

Alate males are remarkably similar from throughout the range. However, California and Arizona males average larger than those from Mexico, and there is relatively little overlap in size. In the three California specimens head length is .293-.320 mm. (mean .302). In the three Arizona specimens head length is .308-.336 mm. (mean .320). In the twelve Mexican specimens head length is .253-.294 (mean .281).

Description of apterous male. — Total length about 0.7 mm. to 1.0 mm. Head length .233-.320 mm.; head width .68-.77 × head length (mean .72). Tegulae normally developed, but wings completely absent; ocelli always present, although tending to be slightly smaller than in the alate males. Color as in alate males, except basal segments of antennae light brown in some specimens. Features of head as in alate males, except the head more parallel-sided, the eyes smaller and less protruding; minimum width of front .63-.68 × width of head, 1.50-1.65 × eye height; distance from tops of eyes to vertex crest always greater than height of eye. Transverse groove at base of scutellum weak, sometimes barely apparent.

One of apterous males from Plumas Co., California is unusually large (head length .32 mm., as compared to .296 for the next largest specimen, from Arizona). The smallest male is also from Plumas Co., California (head length .233 mm.), and in fact the mean head length is nearly the same for U.S. and Mexican males.

Description of alate female. — Total length about 0.9 to 1.3 mm. Head length .288-.370 mm.; head width .68-.76 × head length (mean .72). Wings long, extending well beyond apex of abdomen; ocelli well developed. Coloration as in male, except antennal segment two and sometimes adjacent segments tending to be lighter brown than remainder of antennae. Mandibles and clypeus as in alate males. Antennae inserted well below bottom of eyes, distinctly shorter than in male; first four segments in a ratio of about 15:5:2:2, segments three through eleven wider than long, apical segment about 1.6-2.0 × as long as wide. Eyes weakly convex, protruding slightly from sides of head, covered with short hairs; eyes removed from base of mandibles by about .3 their own height, removed from vertex crest 1.1-1.2 × their own height. Minimum width of front about .65 × width of head, 1.35-1.40 × eye height. Head and thoracic dorsum polished, obscurely alutaceous, barely punctate. Transverse groove at base of scutellum present but rather weak. Propodeum and wings as in alate male. Abdomen depressed, the sting visible in most specimens.

As in the males, alate Arizona females tend to be largest (mean head length .337), California females next (mean head length .330), Mexican females the smallest (mean head length .314). These differences are very slight, and there is a broad overlap in size in specimens from all these areas. It should also be noted that the three alate females from zones A and B in California (Table I) have a mean head length of .350, while those from zone D in California average smaller (mean head length .327), approaching the mean for the Mexican specimens.

Description of micropterous female. — Total length about 0.9-1.3 mm. Head length .336-.364 mm.; head width .71-.78 × head length (mean .75). Wings, .09-.11 mm. long, about twice the length of the tegulae, extending slightly beyond anterior margin of propodeum; ocelli distinct, fully as strong as in alate female. Dark brownish-fuscous; antennae brown, basal flagellar segments somewhat paler than the others; legs as described for alate males. Head differing from that of alate female only in having the eyes slightly smaller, removed from base of mandibles by about half their own height, minimum width of front about 1.6 × eye height. Scutellum separated from mesoscutum by a thin line, also with a weak transverse basal groove. Other features as in alate female.

It will be noted that the micropterous females, all of which are from the San Francisco Bay region (Zone A in Table I), are considerably larger than the average for the fully alate females. The mean head length is .346 mm., considerably more than even that of the Arizona alate females. Also, the mean of the head width/length ratio is .75, considerably above the .72 mean ratio for the fully alate females. This ratio is not plotted on Figure 2, since the number of specimens is so small that one cannot be certain that there is any real difference in this regard from the alate females.

Description of subapterous female. — Total length about 0.8-1.2 mm. Head length .267-.363 mm.; head width .61-.71 × head length (mean .655). Wings about .05-.07 mm. long, barely if at all longer than tegulae, usually reaching but scarcely exceeding anterior margin

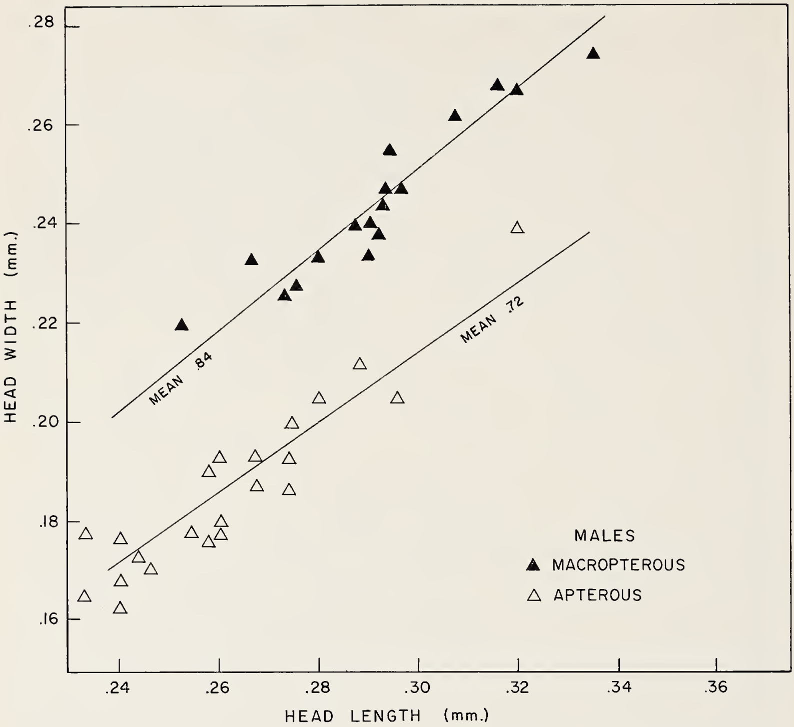

Fig. 1. Head width plotted against head length in the two forms of *Cephalonomia perpusilla* males.

of propodeum; ocelli present but small and weakly convex. Coloration as in micropterous female, head and thoracic dorsum polished and only very obscurely alutaceous. Sides of head subparallel except weakly converging anteriorly and posteriorly, eyes rather flat, not notably protruding from surface of head; eyes very small, weakly hairy, removed from base of mandible by .7 × their own height, removed from vertex crest by nearly twice their own height; minimum width of front 1.7 × eye height. Scutellum weakly separated from mesoscutum, with a very thin basal transverse groove.

Subapterous females occur only in Zones B and C (Table I). The one unusually large specimen (Fig. 2) is from Marin Co., Calif., but other relatively small specimens occur in this same sample. The smallest specimen is from Rustler Park, Ariz. The two females from Douglas Co., Oregon, are exceptional in having the head width/

length ratio .68 and .71, higher than in any other specimens, and in having the wings very slightly longer than usual. These are the only two of the 27 short-winged females which are somewhat intermediate between micropterous and subapterous, though in wing length they can be regarded as subapterous. The mean head width/length ratio is not plotted on Figure 2, as it is only slightly different from that for the apterous females.

Description of apterous female. — Total length 0.7-1.0 mm. Head length .253-.333 mm.; head width .61-.68 × head length (mean .64). Wings absent, but tegulae of nearly normal size; ocelli barely discernible, apparently absent in some specimens. Coloration and sculpturing as in subapterous female, head shape as in that form, the eyes even smaller; eyes removed from base of mandibles by .7-.9 × their own height, removed from vertex crest by 2.0-2.5 × their own height; minimum width of front 1.8-2.0 × eye height. Scutellum weakly separated from mesoscutum, with a barely perceptible basal groove.

As may be seen from Table I, apterous females occur in zones C (Arizona), D (Sierras of California), and D^1 (Mexico). Specimens from all three of these zones are exceedingly similar. Following the same trend as in the alate males and females, Arizona specimens average the largest, followed by California and Mexican specimens. The figures for head length are as follows: Arizona (zone C) .274-.333 (mean .297); California (zone D) .263-.304 (mean .290); Mexico (zone D^1) .253-.320 (mean .284).

Summary of sexual and morphic differences. — The males are readily separated from the females by the longer antennae, particularly the apical segment, which is more than twice as long as wide in the male, less than twice as long as wide in the female. In addition, the ocelli are well developed in both alate and apterous males, whereas subapterous and apterous females have the ocelli absent or barely discernible. Of course, in most females the sting is visible, and in many males the apices of the parameres can be seen.

Apterous males differ from alate males not only with respect to the wings, but also in having a decidedly more narrow head, smaller eyes, and slightly reduced ocelli. The difference in head shape of the two forms is particularly striking when the width is plotted against the length, as in Figure 1. It is interesting that the mean head width/length ratio for the apterous males is the same as that for the alate females (.72); that is, the lower line in Figure 1 is the same as the upper line in Figure 2.

As compared to the alate females, the micropterous females have

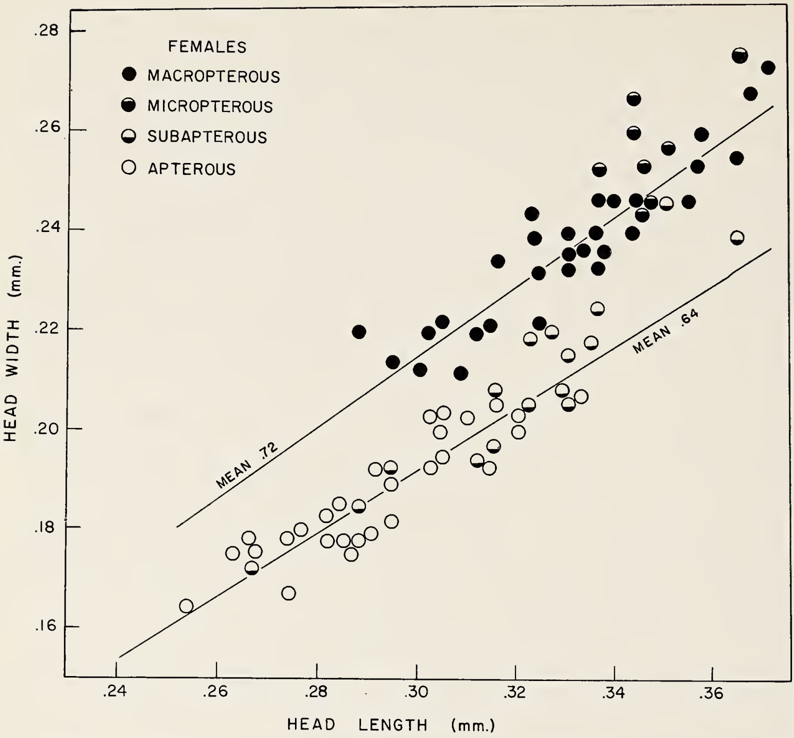

Fig. 2. Head width plotted against head length in the four forms of *Cephalonomia perpusilla* females.

the eyes very slightly smaller but the ocelli not noticeably reduced. The few available specimens (all from zone A, Table I) have the head, on the average, slightly wider than in the alate females, which is the opposite of what one would expect. As pointed out above, the mean head width/length ratio for the eight micropterous females is .75 (not plotted on Figure 1) while that for the many alate females is .72. It is probable that a larger sample would reveal no difference in this respect.

The subapterous females have the wings only slightly smaller than the micropterous females (about half to two thirds as long), a difference barely noticeable in these minute insects. Yet the head shape is different and the eyes and ocelli generally smaller in the subapterous females. Whereas the mean head width/length ratio is .75 in the micropterous females, it is only .655 in the subapterous females. There is, however, much variation in both these forms, so that in one subapterous female (from Douglas Co., Ore.) this ratio is the same (.71) as in one of the micropterous females (Santa Cruz Co., Calif.). However, there is considerable difference in wing length between these two specimens.

As compared to the subapterous females, the apterous females have a slightly smaller mean size, a mean head width/length ratio of .64, the eyes smaller and the ocelli so small they cannot be clearly discerned in many specimens. The wings are, of course, completely absent, although the tegulae are of nearly normal size. The line separating the mesoscutum and scutellum is very weak, the continuation of a trend begun in the subapterous females.

It may have been noted that there are, for most forms, fewer specimens indicated in Figures 1 and 2 than are listed in Table 1. This is a result of the fact that while wing length could be determined for all specimens, some specimens had the head missing or distorted to such an extent that accurate measurements could not be made. Also, not all specimens were measured in samples of one form from one locality of more than twenty.

Discussion. — That polymorphism for wing length occurs in both sexes of *Cephalonomia perpusilla* is not in itself surprising, for several different patterns of polymorphism are known to occur in this section of the family Bethylidae. That modifications in head shape and in size of the eyes and ocelli accompany modifications in wing length is also not surprising, since this has been reported for several polymorphic bethylids, and most aculeate Hymenoptera which are wingless also exhibit reduction in eye size and loss of the ocelli (e.g., female Mutillidae). It should be pointed out that the changes in head shape are not *merely* the result of decreased area and convexity of the eyes. In alate forms the whole side of the head is more bulging, presumably reflecting the much larger size of the optic areas of the brain, as compared to wingless and short-winged individuals. The apterous and short-winged forms of *Cephalonomia perpusilla* show only very slight reduction in thoracic structure, in contrast to other polymorphic species such as *Cephalonomia gallicola* and *Scleroderma immigrans,* in which the apterous individuals have the mesoscutum and scutellum completely fused and the tegulae absent.

What is unusual in *Cephalonomia perpusilla* is the presence of four distinct types of females. Although the two types with small wings differ only slightly in wing length, they nevertheless differ distinctly in head characters. The micropterous females are basically "alate" with respect to the head, although their wings are only about .1 mm. long, about half as long as the hind tibiae (in fully winged individuals the wings measure .8-1.0 mm.). In the subapterous females the wings are further reduced only slightly, being .05-.07 mm. long, roughly one third the length of the hind tibiae. Yet this slight reduction seems to influence head structure profoundly, as though wing reduction had crossed a narrow threshold below which reduction in the organs of vision was essential.

What is still more surprising is that the four types of females apparently never occur together (Table I). Although macropterous females occur throughout the range (except, so far as known, in zone A), micropterous females are known only from zone A, subapterous females only from zones B and C, apterous females only from zones C, D, and D^1. These zones are arranged somewhat concentrically, zone A being more or less in the center of the range, closed in by an elongate zone B, which is followed by zone D, comprising the more mountainous parts of the northern half of eastern California. Zone C (Arizona) is interposed between B and D^1 toward the south and is the only zone in which three types of females are known to occur; in the North, zones B and D are contiguous. Zone D^1 (Baja California and Nayarit) contains, like D, no short-winged females; nearly all females from this zone are apterous (7 alate females are known as compared to 62 apterous females). It looks very much as though the center of the range was the area of "greatest wingedness", and as one passes to the periphery in any direction the incidence of wing reduction increases.

It is tempting to erect hypotheses in an effort to explain this interesting situation. As I have noted, the closest relative of *perpusilla* appears to be the Palaearctic *formiciformis,* a species in which the males are always macropterous, the females macropterous or brachypterous in roughly a 1:1 ratio. Actually these short-winged females are more properly called micropterous, since the wings are scale-like and reach only to the anterior end of the propodeum; they are also like the micropterous females of *perpusilla* in lacking any substantial reduction in head width, eyes, and ocelli. Presumably the ancestor of *perpusilla* entered North America via the Bering land bridge and spread down the west coast, where selection favored smaller size and greater winglessness. The San Francisco Bay area may have served as a refugium and point of radiation for the species. As populations spread out from the center, selection favored still further reduction in the wings. Through changes in the genetics of wing inheritance, the males came to be winged or wingless in about a 1:3 ratio, the females winged or with wings reduced or absent in about a 1:3 ratio; furthermore the females came to show a distinct zonation with respect to wing-length types, the short-winged forms being entirely replaced by apterous forms at the periphery of the range. The actual figures are shown in Table I, where one notes with regret the absence of any records of males from zones A and B as well as far too few females to be sure of the present situation in the center of the range.

These 1:3 ratios suggest simple Mendelian inheritance, winglessness being dominant. I doubt very much if the situation is that simple. One notes, for example, that in the 69 available Mexican females, the winged : wingless ratio is 1:9. In the absence of careful sampling techniques and reared series, one simply cannot be sure what is happening. The genetics of *perpusilla* may not be radically different from that of *gallicola* as described by Kearns (1934), although clearly it is not quite the same for the characters of the female, since this sex is always apterous in *gallicola.*

One wonders if there is some particular selective advantage in wing dimorphism in these very small wasps. I have no new data bearing on this subject, but I suggest that this phenomenon may be related to the unusual mating behavior of these insects. Several persons have reported that in *Cephalonomia* and other gregarious Bethylidae the males emerge first and chew their way into the cocoons of the females (often their own sisters), fertilizing them before they emerge. This would result in much inbreeding unless males also flew about and mated with females elsewhere (since the females do mate again after emerging). The presence of two type of males, one fully winged and the other completely wingless, might be a mechanism for insuring that both inbreeding and outbreeding would occur. The same result would, of course, be achieved by alate males alone if they first mated with their sisters and then flew about and mated with other females, but there may be behavioral or ecological reasons why this is ineffective. It should be born in mind that these minute insects do not "fly" in the usual sense of the word. Their wings are slender and fringed with long setulae, and the venation reduced to a single short vein at the base of the fore wing. It seems quite certain that such insects are incapable of much sustained, directed flight, but after becoming airborne are merely wafted about by air currents. Since these wasps are restricted to fungi infested with ciid beetles, their available habitat is broken up into widely separated, strongly localized sites. The chances of a winged male alighting on (1) a fungus of suitable type, (2) infested with ciid beetles, (3) parasitized by this species of *Cephalonomia,* and (4) containing females ready for mating must be fairly small. Thus the presence of wingless males may assure that most females will be mated and capable of producing female offspring, while the winged males may represent a mechanism for providing for enough outbreeding to offset the serious effects of continued inbreeding.

These remarks will apply equally well to the females if one substitutes "finding the host" for "mating." That is, the presence of winged females throughout the range may be a mechanism for spread of the species into new areas containing the ciid hosts, although many winged females are doubtless wafted into unsuitable locations. Wingless females presumably attack ciids occurring in the same or neighboring fungi, and such females might eventually exhaust the available hosts; at the very least, a given growth of fungus will die out after a period of time. Thus the occasional fertilized, winged females which locate a new supply of ciid beetles may play an important role in the survival of the species, while the wingless females are responsible for localized build-ups in the population.

Having said all this, I must state that I consider it possible that genetics is not directly involved in the polymorphism of *Cephalonomia perpusilla.* Salt (1952) studied the ichneumonid wasp *Gelis corruptor,* in which the females are always apterous, the males either macropterous or micropterous, and found that on a large host the males develop into fully winged individuals but on a small host, providing meagre nourishment, the males develop into micropterous individuals. In an earlier paper, Salt (1937) showed that *Trichogramma semblidis* produced apterous males when reared on one host, alate males when reared on certain other hosts of equal size (or actually smaller); in this case it is the quality of food rather than its quantity which effects morphogenesis. The polymorphic forms of the chalcidoid wasp *Melittobia chalybii* have also been shown to be conditioned by trophic factors: the larvae produced from the first few eggs laid on the host feed on the blood, and develop into a short-lived form with much reduced wings; larvae produced from eggs laid after the first few days feed on other tissues and develop into "typical" adults (Schmieder, 1933). In this instance the short-winged forms develop much more rapidly and permit a rapid population build-up within the large host.

Clearly such mechanisms as these may have strong selective value even if their basis is not "genetic" in the usual sense. These morphs are comparable to the castes of social insects rather than to genetically determined morphs; they are, however, "fortuitous castes", depending upon the nature of the host rather than upon food provided by adults of the same species. Perhaps the term polyphasy is more applicable to such cases, and the term "phase" better than "morph".

In the case of *Cephalonomia perpusilla,* there is no way of knowing at the present time whether the various forms are determined genetically or as the result of the influence of hosts of different sizes and species. John F. Lawrence writes that most of the fungus samples from which these bethylids were reared contained several species of ciids (up to six). However, the samples from Mexico, all of which were from *Ganoderma* rather than the more usual *Polyporus* and *Fomes,* contained only one or two species of ciids, and these ciids were only 1 mm. long or less. Thus the smaller size and greater degree of winglessness of the Mexican material might reflect these smaller hosts. The rearing of this species in series from specific hosts would be difficult but not impossible, and it is the only way in which these questions can be answered.

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A PRELIMINARY REVIEW OF *ZELANOPHILUS* WITH DESCRIPTION OF A NEW AUSTRALIAN SPECIES (CHILOPODA : GEOPHILOMORPHA : GEOPHILIDAE)[1]

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The genus *Zelanophilus,* hitherto known only from New Zealand by a single species, *provocator,* is of special interest for several reasons. First, it is restricted, so far as we know now, to New Zealand and Australia yet is clearly similar in certain notable features to some equally bizarre genera known sporadically from the Indo-Australian area, e.g. *Tasmanophilus, Australiophilus, Sogophagus, Eucratonyx.* The suprageneric allocation of these and of some other evidently related genera has never been demonstrated convincingly. Secondly, *Zelanophilus* on the basis of some characters could be construed as occupying an almost annectent position between the Geophilidae (Geophilinae) and that section of the Schendylidae typified by *Escaryus.* A full discussion of the higher categorical considerations involved is beyond the scope of this paper but will be treated in a future publication whose supportive studies are still being undertaken. At this time I wish to clarify the identities of the genus and its type-species, *provocator,* and to describe a new species of the genus. It is of particular interest in that it is the second one known and extends the known distribution of *Zelanophilus (sensu stricto)* to Australia.

Like *provocator,* the new form exhibits the following especially significant, generically diagnostic characteristics. The teeth of the mandible are weakly but distinctly heterogenous. The first maxillary coxosternum is continuous centrally, not divided, and lacks lappets. The claw of the second maxillary telopodite is coarsely bristled (hispidate). A clypeal fenestra (clypeal area) is absent. Well-developed or vestigial *anterior* clypeal smooth areas (plagulae) are present. The labral sidepieces are in contact with each other or nearly so, i.e. the

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midpiece is apparently suppressed or weakly discrete and small: the sidepieces are fringed with a single row of long hyaline filaments. The pleurograms (chitin lines) of the prosternum are abortive, short, and concursive with the pleuroprosternal sutures. On the anterior part of the body each sternite has a large, single, posterior porefield; posteriorly on the body these divide in two. The anterior parunguis (of each pretarsus) is short and thin (not grossly hypertrophied as in *Eucratonyx* and *Sogophagus*). The coxopleural pores open singly and freely on all parts of the coxopleuron; they are not cavitate. The ultimate tarsus is bipartite; its pretarsus is strongly unguiform. The gonopods of both male and female are entirely separated from each other, and each is distinctly bipartite. Anal pores are present.

The two species differ from each other in the following notable, diagnostic characteristics.

Zelanophilus provocator: (1) Ventral porefields absent on 3-4 sternites anterior to the ultimate. (2) Final 4-5 sternites very densely clothed with fine setae. (3) First maxillary lappets absent. (4) First pedal tergite and those following on anterior quarter of body strongly bisulcate; the same tergites with extensive unpigmented areas. (5) First 4-6 spiracles very strongly and narrowly elliptical in shape. (6) Ultimate tergite much longer and narrower than that of *pococki.* (7) Central labral teeth deeply pigmented and as a group usually slightly separated from adjacent teeth. (8) Plagulae (smooth or lissate areas) of anterior clypeus typically large and prominent. (9) Pedal segments 67-77.

Zelanophilus pococki: (1) Ventral porefields present on all sternites except the ultimate. (2) Final 4-5 sternites' vestiture like that of those preceding, not contrastingly densely clothed with fine setae. (3) First maxillary lappets present. (4) First pedal tergite and those following on anterior quarter of body not sulcate or at most only very weakly so; the same tergites completely or nearly completely deeply pigmented. (5) First 4-6 spiracles round or nearly so, at most only very slightly, broadly elliptical. (6) Ultimate tergite much shorter and wider than that of *provocator.* (7) Central labral teeth weakly or not at all pigmented; as a group not separated from adjacent teeth. (8) Plagulae of anterior part of clypeus typically absent or at most very weak, small, and fragmented. (9) Pedal segments 59-73.

Zelanophilus provocator (Pocock)

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Australiophilus microtrichus Attems, Sonderabdruck, Ann. Naturhis. Mus. Wien, 55, p. 65, 1947. (New Synonymy: holotype seen).

Type-species: *Zelanophilus wheeleri* Chamberlin, 1920. (= *Zelanophilus provocator* (Pocock, 1891)). (Monobasic and by original designation).

Pocock based *provocator* upon two male specimens, each with 69 pedal segments, which the officers of the Challenger Expedition had collected at Wellington, New Zealand. His original description is composite, and he selected no lectotype. I have studied both specimens at the British Museum and find them to be conspecific with many non-typical specimens collected by Mr. P. M. Johns and his colleagues in New Zealand as well as with the typical series of *wheeleri* that I have studied at the Museum of Comparative Zoology, Harvard. I have selected one of Pocock's specimens as the lectotype and have labelled it accordingly. When I found the Pocock specimens, their heads and mouthparts had been removed and could not be located. None the less, the remaining body parts, in excellent condition, are quite sufficient for the confident identification of comparison material.

So far as is known, and excluding *ferrugineus*[2] from *Zelanophilus*, *provocator* is the sole species of the genus *(sensu stricto)* inhabiting New Zealand. The characters distinguishing it from *pococki*, Pocock's original description, and Archey's redescription of 1936 (p. 51) should readily facilitate its identification.

According to Archey (1936, p. 52), *provocator* is very common throughout South Island but his records showed that it is known from only a few localities on North Island. Thanks to Mr. Johns and his colleagues I am gradually acquiring considerable material from all

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[2] Dr. Archey (Rec. Auckland Inst. Mus., 2, p. 52, 1936) has included *ferrugineus* (Hutton, 1877) in *Zelanophilus*. I have examined one of Hutton's syntypes at the British Museum and a clearly conspecific specimen collected by Mr. Johns and have come to the tentative conclusion that the species, at least until more is known about the whole generic complex, is more advantageously placed in *Australiophilus* Verhoeff, with whose type-species, *longissimus*, it is almost certainly congeneric (New Combination). The nature and systematic location of the Hutton species will be discussed in a forthcoming publication.

parts of New Zealand, so that at a not distant time in the future it should be possible to issue an extensive list of localities for this and other New Zealand geophilomorphs.

Zelanophilus pococki[3] new species

Holotype: Female. Type locality: Australia, New South Wales, Hornsby; August 21, 1931; William Morton Wheeler, leg. Disposition: Myriapod Type Collection of the Museum of Comparative Zoology, Harvard University.

INTRODUCTORY. Total length: 67 mm. Pedal segments: 73. Body shape: Width essentially uniform from front to rear; however, the final 5-6 segments slightly narrowing. Color: Head and tergites approximately of anterior two-thirds of body yellowish-brown; without extensive unpigmented areas (cf. *provocator*); legs and underparts in general paler in color.

ANTENNAE. Length (unextended in balsam): 3.75 mm. Shape: Distally very slightly attenuate; not flattened. Vestiture (dorsal aspect): From 2nd to final article the setae decreasing gradually in length and increasing gradually in number. Ultimate article on lateral and mesal surfaces with an elongate patch of short, hyaline, robust specially-modified setae. CEPHALIC PLATE. Dimensions: Greatest length, 1.44 mm; greatest width, 1.32 mm. Shape: Sides slightly excurved; anterior and posterior margins straight. Setae short and sparse. Frontal suture present but obscure. Prebasal plate concealed. CLYPEUS. As limited laterally by paraclypeal sutures much wider than greatest length. Paraclypeal sutures: Sinuous; posteriorly passing toward but failing to join middle of labral fulcra (fulturae). Fenestra (clypeal area) absent. Immediately behind anterior margin of clypeus on each side of midline a very weak, fragmented, obscure plagula (lissate or smooth area). Well-defined, large prelabral plagulae present. Setae: Anterior third of clypeus across its entire width with numerous long setae randomly disposed; remaining two-thirds of clypeus glabrous; prelabral pair of setae absent. LABRUM. With prominent anterior alae, these completely separated from clypeus by a continuous suture. Sidepieces: Apparently contiguous centrally, the midpiece either incorporated into them or concealed by them; centrally-located teeth very slightly pigmented and shorter than the lateral filaments which are long, thin, and hyaline. Fulcrum: Massive;

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[3] Dedicated to Reginald Innis Pocock, late of the British Museum (Natural History), a pioneer student of the myriapods of the Australian area. Dr. Pocock's writings, though undertaken at a comparatively early time, still stand as outstanding examples of remarkable systematic intuition and discernment and unambiguous clarity of exposition.

strongly obliquely oriented to long axis of the head. MANDIBLE. Teeth fundamentally heterogenous; those of about 3/4 of the distal margin aciculate and hyaline, thinly filamentous; those remaining abruptly longer and more robust. FIRST MAXILLAE. Coxosternum: Medially continuous with division, diastema or suture; lappets absent. Telopodite: Distinctly bipartite; with a large, fleshy lappet, this largely concealed from ventral aspect. Dorsal surfaces of medial lobes and telopodites very densely clothed with minute setae. SECOND MAXILLAE. Isthmus anteroposteriorly very shallow but without diastema or division of any kind. Postmaxillary sclerite very extensive, extending anteromesally partly to occlude metameric pore opening. Telopodite: With prominent, strong dorsal and ventral basal condyles; articles inflate, robust, the 2nd and 3rd especially setose; terminal claw with numerous aciculate, long spines arising randomly on its distal half. PROSTERNUM. Much wider than long. Anterior denticles abortive, low, weakly-developed. Pleuroprosternal sutures arching obliquely laterad, complete, ending dorsolaterally. Pleurograms (chitin lines) abortive, short, concursive with pleuroprosternal sutures. PREHENSOR. When flexed not exceeding anterior margin of head. In general very robust and short. Tarsungula dark, its length about equal to outer length of trochanteroprefemur; dorsal and ventral edge of blade smooth, not serrulate; poison calyx very long, terminating in intercalary articles; poison gland terminating near base of trochanteroprefemur. Denticles: Mesodistal denticle of trochanteroprefemur low and blunt; femorid and tibiid each with a minute rounded denticle; tarsungula without a basal denticle. TERGITES. Basal plate anteriorly as wide as rear margin of cephalic plate, posteriorly as wide as first pedal tergite; color yellowish-brown except for very small unpigmented central area. Color: On anterior portion of body deeply yellowish-brown, thereafter gradually becoming paler; entirely without extensive unpigmented areas. Paramedial sulci: On anterior part of body essentially absent and pigmented (not unpigmented as in *provocator*); thereafter gradually becoming more apparent. Setae short and relatively numerous. SPIRACLES. All strictly circular except for first 2-3 which are very slightly subcircular. LEGS. Those of anterior third of body very robust and short, thereafter gradually becoming longer and more slender. Setae much longer and more numerous than in *provocator*. PRETARSI. Each unguis (claw proper) short and robust on anterior half of body, thereafter becoming longer and thinner. Each anterior parunguis thin and only about 1/3 as long as its unguis; each posterior parunguis so minute as easily to escape detection. STERNITES. Those of anterior third of body each with a deep anterocentral fovea and shallow longitudinal sulcus on posterior third; each much wider than long; carpophagus-structures absent. Setae short and relatively numerous (but final sternites not abruptly more densely setose than preceding sternites). Subcoxal and anterolateral porefields absent. Posterior porefields: Double on each sternite from first through the penult; those of anterior quarter of body very narrowly separated (often grossly appearing single); on posterior part of body the porefields clearly separating and becoming smaller. ULTIMATE PEDAL SEGMENT. Pretergite with pleurites fused without lateral sutures; much wider than preceding and succeeding tergites. Tergite: Sides parallel; rear margin evenly rounded; greatest length about 1.25 times greatest width. Presternite centrally divided. Sternite: Anterior margin straight; sides strongly convergent; length to width at midlength = 1 : 0.71. Coxopleuron: From dorsal aspect extending forward only to rear of penultimate segment; less swollen than in *provocator;* pores numerous, opening freely, piercing all sides. Ultimate leg: Only very slightly swollen (less so than in *provocator*); tarsus double, the two parts equal in length; pretarsus short, robust, strongly unguiform. POSTPEDAL SEGMENTS. Gonopods completely separated, unfused basally but contiguous; bipartite, the ultimate article conical. Anal pores lateral, concealed, large.

THE PARATYPES. All of the paratypes are Australian and are deposited in the British Museum (Natural History).

Paratype A: Male, 59 pedal segments, 44 mm; New South Wales; Number 1935.3.26.30. Paratype B: Female, 61 pedal segments, 38 mm; New South Wales, Dorrigo; Number 1936.3.3. Paratype C: Female, 73 pedal segments, 62 mm; New South Wales, Hornsby; Number 1925.7.10-11 (part). Paratype D: Female, 73 pedal segments, 53 mm; New South Wales, Hornsby; Number 1925.7.10-11 (Part). Paratype E: Female, 61 pedal segments, 51 mm; Hornsby; Number 1925.7.10-11 (part).

The paratypes do not differ significantly from the holotype except as noted above. The single male, Paratype A, differs from the females in having its ultimate legs distinctly more inflated and more densely pubescent; as in the females, its gonopods are separated and distinctly bipartite.

THE SPIDER GENERA *CEROCIDA, HETSCHKIA, WIRADA* AND *CRASPEDISIA* (ARANEAE: THERIDIIDAE)*

By Herbert W. Levi
Museum of Comparative Zoology, Harvard University

The four genera discussed in this paper are known only from tropical America. No species have been found in other parts of the world. All are small genera with one or two known species. The characters that distinguish the genera have been discussed in a previous paper (Levi and Levi, 1962), in which were illustrated the type species. For ease of comparison the type species are figured here again with some new drawings. Drawings of the expanded palpi are omitted.

A trip to examine the types was supported by a National Science Foundation Grant (G-4317) and the research and publication by a grant from the National Institutes of Health (E-1944). I wish to thank my colleagues who made rare specimens available to me: Prof. M. Vachon of the Muséum National d'Histoire Naturelle, Paris; J. Prószyński of the Polish Academy of Sciences, Warsaw; Dr. G. Owen Evans, Mr. E. Browning, K. Hyatt and D. Clark of the British Museum (Natural History); Mrs. D. L. Frizzell (Dr. H. Exline) and Dr. E. S. Ross of the California Academy of Sciences, San Francisco (CAS); Dr. W. J. Gertsch of the American Museum of Natural History, New York (AMNH) and Dr. O. Kraus of the Senckenberg Museum, Frankfurt (SMF).

Cerocida Simon

Cerocida Simon, 1894, Histoire Naturelle des Araignées, 1: 508. Type species by original designation and monotypy: *C. strigosa* Simon, 1894.

Cephalothorax with posterior stalk and raised reticulate pattern in both sexes (Fig. 6). Legs long, first patella and tibia as long or slightly longer than carapace. Abdomen small, higher than long; male with sclerotized rings around pedicel and spinnerets (Fig. 1). Colulus replaced by two setae, unlike the related *Helvibis,* which lacks setae.

Cerocida strigosa Simon
Figures 1-6

Cerocida strigosa Simon, 1894, Histoire Naturelle des Araignées, 1: 508, fig. 510. Female holotype from Venezuela in the Muséum National d'Histoire Naturelle, Paris, examined.

**Manuscript received by the editor February 19, 1963.*

Note. Since this specimen was presumably collected by Simon, the type locality can be narrowed to the limited northern areas of Venezuela, Caracas, and the states Aragua and Carabobo, through which Simon travelled.

Description. Carapace, sternum light brown; legs yellow-white; abdomen whitish; male darker than female and more heavily sclerotized. Carapace and sternum fused between coxae and around pedicel; both with a reticulate raised pattern and raised rings around pedicel. Female pedicel stalk slightly shorter than that of male (Fig. 6). Anterior median eyes two-thirds the diameter of posterior median eyes, their radius apart, almost touching laterals. Posterior median eyes of female one-third diameter apart, their radius from laterals. Posterior median eyes of male one-quarter diameter apart, one diameter from laterals. Chelicerae apparently with one large tooth on anterior margin. Abdomen higher than long with few long setae (Figure 1). Male abdomen with sclerotized ring around pedicel and sclerotized ring around spinnerets. Total length of female 1.5 mm. Carapace 0.80 mm long, 0.53 mm wide. First femur, 0.87 mm; patella and tibia, 0.92 mm; metatarsus, 0.57 mm; tarsus, 0.46 mm. Second patella and tibia, 0.66 mm; third, 0.50 mm; fourth, 0.71 mm. Total length of male 1.7 mm. Carapace 0.93 mm long, 0.55 mm wide. First femur, 1.06 mm; patella and tibia, 1.05 mm; metatarsus, 0.62 mm; tarsus, 0.46 mm. Second patella and tibia, 0.78 mm; third, 0.55 mm; fourth, 0.82 mm.

The genitalia are small, transparent (Fig. 3-5), and difficult to study in the few specimens available.

The descriptions and illustrations were made from British Guiana specimens.

Natural History. Specimens have been collected by sifting litter. This species is probably an ant mimic.

Record. British Guiana. Kartabo, 1924, 1 ♀, 1 ♂ (AMNH).

Hetschkia Keyserling

Hetschkia Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, 2(2):246. Type species by monotypy: *H. gracilis* Keyserling.

Carapace sclerotized, suboval with a posterior stalk in both sexes (Figs. 11, 12). Carapace of male wider than that of female. Abdomen suboval, without colulus.

The carapace shape distinguishes the genus from *Theridion,* the short embolus and female connecting ducts from *Helvibis.*

Hetschkia gracilis Keyserling
Figures 7-13

Hetschkia gracilis Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, 2(2):247, pl. 20, fig. 299, ♂. Male holotype from Blumenau, [Santa Catarina], Brazil in the Muséum National d'Histoire Naturelle, Paris, examined.

Description. Female. Carapace, sternum yellow. Legs yellow with tarsi brown and anterior side of each patella with a black spot. Abdomen whitish, unpigmented. Carapace sclerotized, slightly granulate, almost smooth. Sternum fused to carapace but with seam present above coxae. Carapace and sternum fused around pedicel (Fig. 7). Eyes subequal in size. Anterior median eyes one and one-half diameters apart, their radius from laterals. Posterior median eyes two diameters apart, one and one-half diameters from laterals. Abdomen spherical. Total length of female from São Paulo 2.2 mm. Carapace 1.20 mm long, 0.61 mm wide. First femur, 1.32 mm; patella and tibia, 1.21 mm; metatarsus, 1.19 mm; tarsus, 0.45 mm. Second patella and tibia, 0.90 mm; third, 0.62 mm; fourth, 0.90 mm.

Figures 12 and 13 were prepared from the holotype.

Records. Brazil. São Paulo: Botanical Gardens, São Paulo, 13-17 Jan. 1959, 2♀ (A. M. Nadler, AMNH). *Santa Catarina:* Blumenau, ♀ with ♂ holotype (MNHN).

Wirada Keyserling

Wirada Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, 2(2):25. Type species by monotypy: *W. punctata* Keyserling.

Carapace with eye region projecting and clypeus sloping back toward chelicerae. Carapace and sternum tuberculate (Figs. 18, 25, 26). Legs short; leg four about equal to leg one. Tarsi longer than metatarsi. Abdomen with a dorsal sclerotized shield, a large shield surrounds pedicel and a sclerotized ring around spinnerets (Figs. 24, 25). Colulus replaced by two setae.

The tuberculate carapace resembles that of *Crustulina; Wirada,* however, lacks the distal process on the palpal cymbium and lacks a large colulus. The relatively simple palpus and long tarsi make *Wirada* resemble spiders placed in the family Symphytognathidae. *Wirada* species, like members of the latter family, have tarsi longer

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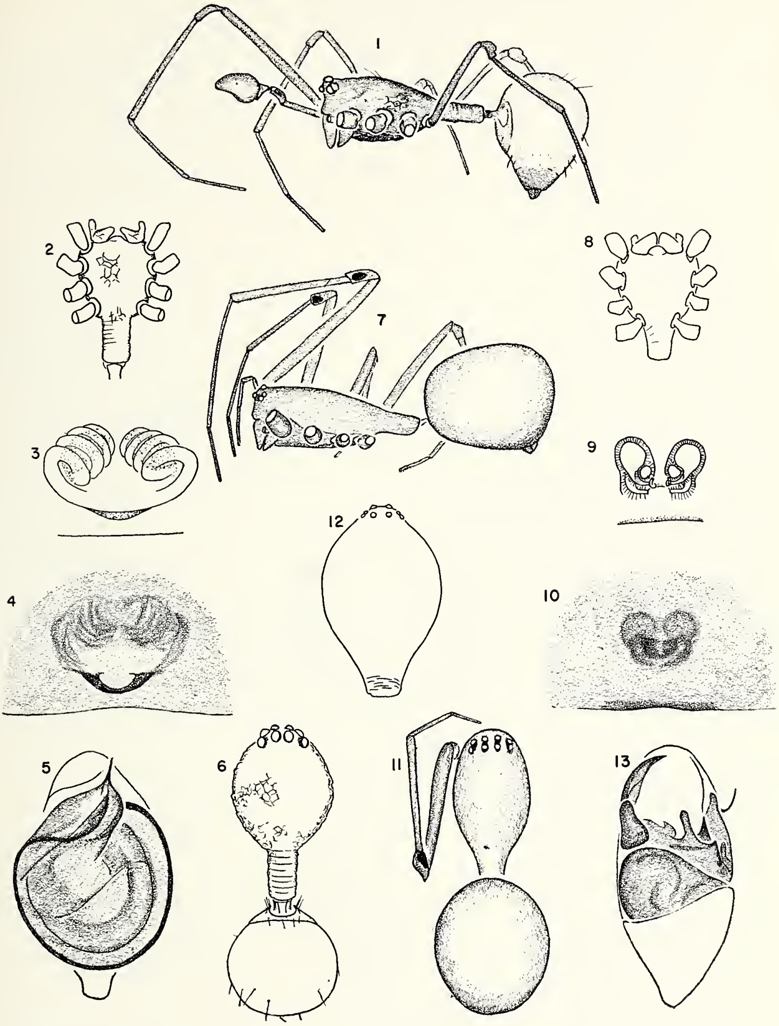
Explanation of Plate 17

Figs. 1-6. *Cerocida strigosa* Simon. 1. Male. 2. Male sternum and coxae. 3. Female genitalia, dorsal view. 4. Epigynum. 5. Left palpus. 6. Male.

Figs. 7-13. *Hetschkia gracilis* Keyserling. 7. Female. 8. Female sternum and coxae. 9. Female genitalia, dorsal view. 10. Epigynum. 11. Female. 12. Male carapace. 13. Palpus.



Levi — Cerocida and Hetschkia

than metatarsi, and may lack lungs, but lack teeth on the posterior margin of the chelicerae.

Wirada punctata Keyserling
Figures 14-18

Wirada punctata Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, 2(2):26, pl. 11, fig. 147, ♂. Male holotype from Montaña di Nancho, [? Cajamarca], Peru, 8000 m elev., in the Polish Academy of Sciences, Warsaw, examined.

Virada rugithorax Simon, 1894, Histoire Naturelle des Araignées, 1: 585, *nom. nudum;* 1895, Ann. Soc. ent. France, 64:148. Male holotype from San Esteban, [Carabobo], Venezuela in the Muséum National d'Histoire Naturelle, Paris, examined. NEW SYNONYMY

Description. Male. Sclerotized areas dark, rich red-brown. Legs and lightly sclerotized portions lighter; patellae and spinnerets lightest. Carapace and sternum heavily sclerotized with elongate dark tubercles (Fig. 18) that also cross clypeus. Eyes overhanging clypeus and clypeus receding above small chelicerae. Diameter of anterior median eyes more than twice that of posterior medians, one-third their diameter apart, almost touching laterals. Posterior medians slightly oval, more than three (longer) diameters apart, one diameter from laterals. Sternum wider than long. Chelicerae with one double tooth on anterior margin. Entire dorsum of abdomen covered by a shiny shield; venter by a smaller shield and a ring around spinnerets; abdomen of male flattened. Colulus with two setae. It is very possible that the specimen lacks lungs. Total length of male 1.4 mm. Carapace 0.58 mm long, 0.57 mm wide. First patella and tibia, 0.47 mm; second, 0.41 mm; third, 0.39 mm. Fourth femur, 0.57 mm; patella and tibia, 0.52 mm; metatarsus, 0.26 mm; tarsus, 0.30 mm.

Female. Carapace brown, area of anterior median eyes black. Sternum light brown, legs yellow-brown. Abdomen purplish brown, venter lighter; sclerotized areas red-brown. Carapace and sternum with elongate tubercles. Anterior median eyes larger than others, a little less than a diameter apart, their radius from laterals. Posterior median eyes two diameters apart, one diameter from laterals. Dorsum of abdomen with a circular scutum (Fig. 17). Venter with a semicircular shield anterior around the pedicel, a sclerite on each side of

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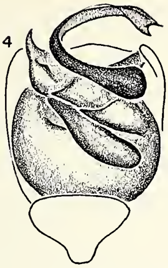
EXPLANATION OF PLATE 18

Figs. 14-18. *Wirada punctata* Keyserling. 14. Left palpus. 15. Female genitalia, dorsal view. 16. Epigynum. 17. Female. 18. Male.

Figs. 19-26. *W. tovarensis* Simon. 19. Male palpus, cleared. 20. Palpus. 21. Female genitalia, dorsal view. 22. Epigynum. 23. Male left chelicera, posterior view. 24. Male. 25. Male sternum and abdomen. 26. Male. (Abbreviations: E, embolus; M, medium apophysis; R, radix).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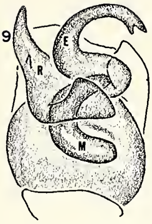
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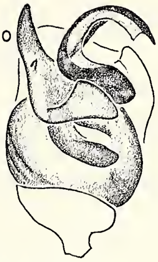
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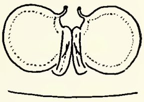
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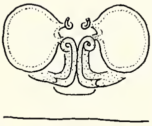
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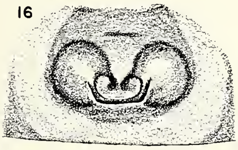
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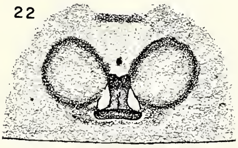
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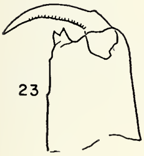
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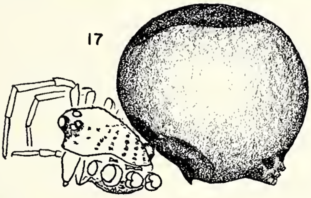
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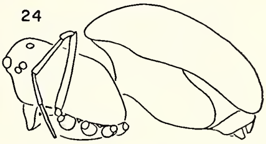
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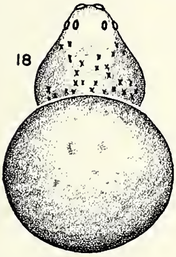
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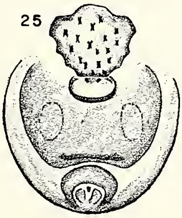
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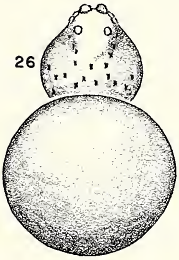
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LEVI — WIRADA

the epigynum, very small sclerites on the side and a broken ring of sclerites around spinnerets. Total length of female 1.5 mm. Carapace, 0.60 mm long, 0.52 mm wide. First patella and tibia, 0.41 mm; second, 0.38 mm; third, 0.35 mm. Fourth femur, 0.45 mm; patella and tibia, 0.44 mm; metatarsus, 0.22 mm; tarsus, 0.28 mm.

Epigynum (Fig. 16) with lip extending behind a slight depression. The female was not collected with the male and there is some doubt that it belongs to this species. Figures 14 and 18 were prepared from the holotype.

Record. Ecuador. Chimborazo: 48 km SW of Alausi, 2500 m, 14 Feb. 1955, 1 ♀ (E. I. Schlinger, E. S. Ross, CAS).

Wirada tovarensis Simon
Figures 19-26

Virada tovarensis Simon, 1894, Histoire Naturelle des Araignées, 1:585, *nomen nudum;* 1895, Ann. Soc. ent. France, 64:148. Male holotype from Colonia Tovar [Tovar, Aragua], Venezuela, 1888 (E. Simon), in the Muséum National d'Histoire Naturelle, Paris, examined.

Description. Sclerotized areas rich dark red-brown; areas between eyes of male yellowish; legs yellowish. Non-sclerotized areas on venter of abdomen whitish. Carapace and sternum of both sexes heavily sclerotized with elongate dark tubercles (Figs. 25, 26), and anterior portion of male carapace raised (Fig. 24). Diameter of anterior median eyes twice that of other eyes. Anterior median eyes of female one-quarter their diameter apart, one-quarter diameter from laterals. Posterior median eyes of female one and one-half diameters apart, one diameter from laterals. Anterior median eyes of male their radius apart, almost touching laterals. Posterior median eyes of male three diameters apart, one and one-half diameters from laterals. Chelicerae with a double tooth on anterior margin (Fig. 23), no teeth posterior. Both sexes with similar sclerotization of abdomen, completely covering dorsum, a smaller shield on venter and a sclerotized ring around spinnerets. The abdomen is flattened (Fig. 24), slightly thicker in female than in male. Male with first leg slightly longer than fourth; female with fourth leg slightly longer than first. Total length of female 1.0 mm. Carapace 0.55 mm long, 0.47 mm wide, 0.30 mm high. First patella and tibia, 0.32 mm; second, 0.31 mm; third, 0.26 mm. Fourth femur, 0.35 mm; patella and tibia, 0.39 mm; metatarsus, 0.18 mm; tarsus, 0.23 mm. Total length of male 1.0 mm. Carapace 0.47 mm long, 0.45 mm wide, 0.35 mm high in eye region. First femur, 0.39 mm; patella and tibia, 0.39 mm; metatarsus, 0.22 mm; tarsus, 0.27 mm. Second patella and tibia, 0.32 mm; third, 0.29 mm; fourth, 0.39 mm.

Record. Venezuela. Aragua: Tovar, 1 ♀ with ♂ holotype, 1888 (E. Simon, MNHN).

Craspedisia Simon

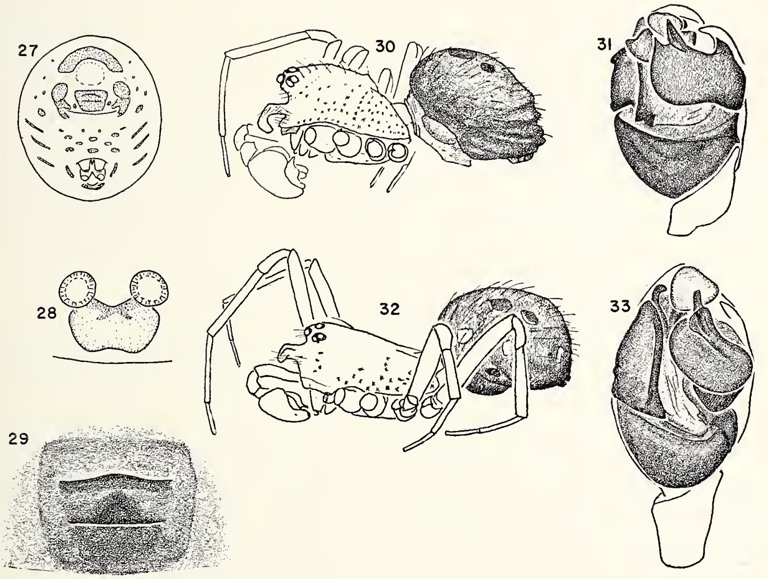
Craspedisia Simon, 1894, Histoire Naturelle des Araignées, 1:580. Type species by original designation and monotypy: *Umfila cornuta* Keyserling.

Carapace of female as in *Steatoda,* that of male with a projection on clypeus (Figs. 30, 32). Posterior extension of carapace covering pedicel. Chelicerae with a tooth on anterior margin. Abdomen suboval with a broken sclerotized ring around pedicel in both sexes; some sclerotized spots on venter. Colulus large.

The clypeal projection separates males from *Steatoda* and *Crustulina.* (Levi and Levi, 1962).

Craspedisia cornuta (Keyserling)
Figures 27-31

Umfila cornuta Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, 3:222, pl. 8, fig. 163, ♂. Male holotype from Neu Freiburg



Figs. 27-31. *Craspedisia cornuta* (Keyserling). 27. Female abdomen, ventral view. 28. Female genitalia, dorsal view. 29. Epigynum. 30. Male. 31. Left palpus.

Figs. 32-33. *C. spatulata* Bryant. 32. Male. 33. Palpus.

[Nova Friburgo, Est. Rio de Janeiro, Brazil], in the British Museum Natural History, examined. — Göldi, 1892, Mitt. Osterlande, neue Folge, 5:233.

Craspedisia cornuta, -Simon, 1894, Histoire Naturelle des Araignées, 1:580, fig. 587, ♂.

Description. Carapace, sternum orange; legs brown. Abdomen with dorsum black and venter white with a broad dark stripe between genital groove and spinnerets. Carapace of male punctate on sides (Fig. 30). Abdomen of male with four brown sclerotized spots on dorsum. Abdomen of female with scattered sclerotized spots on venter (Fig. 27). Eyes subequal in size. Anterior eyes one-quarter their diameter apart. Posterior median eyes one diameter apart, three-quarters diameter from laterals. Eyes of male smaller and slightly farther apart; anterior median eyes of males slightly larger than others. Chelicerae with two teeth on anterior margin in female; one fleshy tooth on anterior margin in male. Total length of female 3.1 mm. Carapace, 1.56 mm long, 1.32 mm wide. First patella and tibia, 1.20 mm; second, 1.07 mm; third, 0.98 mm. Fourth femur, 1.30 mm; patella and tibia, 1.40 mm; metarsus, 0.72 mm; tarsus, 0.58 mm. Total length of male, 2.9 mm. Carapace, 1.62 mm long, 1.30 mm wide. First femur, 1.10 mm; patella and tibia, 1.23 mm; metatarsus, 0.77 mm; tarsus, 0.57 mm. Second patella and tibia, 1.17 mm; third, 0.94 mm; fourth, 1.22 mm.

Records. Brazil. Est. Rio de Janeiro: Teresópolis, 900-1000 m (H. Sick, AMNH). *São Paulo:* Jabaquara, Cidade São Paulo, 700-800 m (H. Sick, AMNH). *Santa Catarina:* Nova Teutonia, 27° 11′ S, 52° 23′ W (F. Plaumann, SMF).

Craspedisia spatulata Bryant
Figures 32-33

Craspedisia spatulata Bryant, 1948, Bull. Mus. Comp. Zool., 100:373, figs. 47, 48 ♂. Male holotype from rain forest near Valle Nuevo, [near Constanza], Cordillera Central, 1800 m elev., Dominican Republic, in the Museum of Comparative Zoology, examined.

Description. Carapace, sternum, legs red-brown. Abdomen black, dorsum with three large white spots on the anterior, one on each side and a pair towards the posterior; sclerotized spots brown. Second specimen with two rows of three white spots and one median posterior spot. Anterior median eyes slightly larger than others, half their radius apart and a radius from laterals. Posterior median eyes one and one-third diameters apart and the same distance from laterals. Chelicerae with a fleshy tooth on anterior margin, none posterior. Carapace with some tubercles on sides. Sternum with some tubercles.

Tarsal comb indistinct. Abdomen with four dorsal sclerotized spots, the anterior pair the largest; venter almost two-thirds covered by epigastric shield. Total length of holotype, 2.2 mm. Carapace, 1.36 mm long, 0.94 mm wide. First femur, 0.95 mm; patella and tibia, 1.04 mm; metatarsus, 0.59 mm; tarsus, 0.43 mm. Second patella and tibia, 0.95 mm; third, 0.78 mm; fourth, 1.04 mm.

Record. Dominican Republic: Loma Rucilla Mountains, 1500-2400 m., Cordillera Central, ♂ paratype (P. J. Darlington).

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THE MALE OF *MECYNOMETA GLOBOSA* (O. P.-CAMBRIDGE) (ARANEAE, ARGIOPIDAE)*

By Arthur M. Chickering
Museum of Comparative Zoology

The female of this species was described from Guatemala by the elder Pickard-Cambridge in 1889. Apparently it was known only from that part of Central America until Dr. Petrunkevitch reported a female specimen from the Wilcox camp on the San Lorenzo River in Panama in 1925. Mr. Banks reported two females from the Panama Canal Zone in 1929. I now have in my collection about two dozen females from several localities in the Canal Zone and El Valle, Panama. Only three males have appeared in the collection and all were collected in 1934 and 1936. *Mecynometa* is an interesting genus with a total of seven species now known. Simon described a species from the African Congo; five species have been described from South America; *M. globosa* (O. P.-Cambridge) is now known from two countries in Central America. Because males have hitherto been unknown I have thought it worth while to describe one of these in this brief paper.

Mecynometa globosa (O. P.-Cambridge), 1889
(Figures 1-5)

Meta globosa O. P.-Cambridge, 1889
Argyroepeira globosa Keyserling, 1893
Mecynometa globosa Simon, 1894
M. globosa F. P.-Cambridge, 1903
M. globosa Petrunkevitch, 1911
M. globosa Petrunkevitch, 1925
M. globosa Banks, 1929
M. globosa Roewer, 1942
M. globosa Bonnet, 1957

Male. Total length 2 mm. Carapace about 1 mm. long; about .8 mm. wide between second and third coxae where it is widest; about .4 mm. tall; with median fovea a broad, shallow depression.

Eyes. Eight in two rows. Viewed from above, anterior row strongly recurved; posterior row only slightly so. Viewed from in front, anterior row almost straight; posterior row procurved, all measured by centers. Central ocular quadrangle as wide in front as behind; longer than wide in ratio of about 11 : 10. Ratio of eyes AME : ALE : PME : PLE = 7.5 : 6 : 7 : 5. LE somewhat angu-

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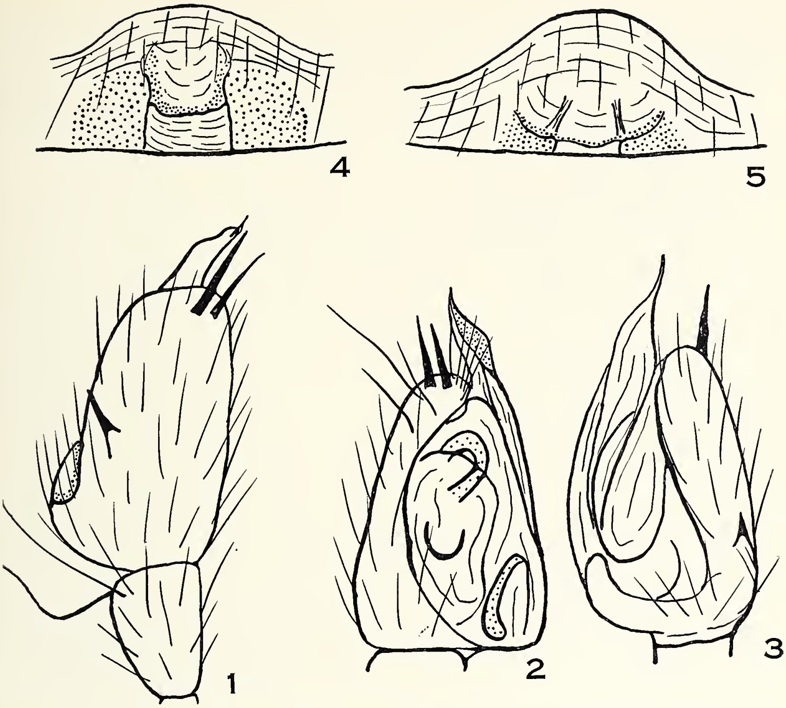
* *Manuscript received by the editor January 8, 1963.*



Figs. 1-5. External anatomy of *Mecynometa globose.* Fig. 1. Tarsus and tibia of left palp of male; dorsal view. Figs. 2-3. Two other views of same male palp. Figs. 4-5. Epigyna from two different specimens; as viewed from behind.

lar. AME separated from one another by about their diameter, from ALE by slightly more than their radius. PME separated from one another by slightly less than their diameter, from PLE by their diameter. Height of clypeus equal to a little less than the diameter of AME. A long, slender spinule lies ventral to the interval between AME and ALE on each side.

Chelicerae. Nearly vertical and parallel; moderately robust; basal segment about .8 mm. long; fang normal, regularly curved; fang groove with teeth but exact number and placement not determined because of fragility of specimen.

Maxillae. Parallel; fairly broad; quite normal in respect to the usual features; without special modifications.

Lip. Much broader than long; strongly rebordered; does not quite reach to middle of the maxillae.

Sternum. Broadly scutiform; broader than long in ratio of about 8 : 7; with numerous stiff bristles; not continued between fourth coxae which are separated by a little less than their width.

Legs. 1234. Width of first patella at "knee" .13 mm., tibial index of first leg 3. Width of fourth patella at "knee" .11 mm., tibial index of fourth leg 5.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
		(All measurements in mm.)				
1.	3.90	.48	3.97	4.42	1.04	13.81
2.	2.93	.44	2.55	3.06	.91	9.89
3.	1.43	.24	.84	1.10	.45	4.06
4.	2.41	.33	1.76	1.98	.59	7.07
Palp	.45	.09	.14	——	.44	1.12

Legs well supplied with relatively long hairs. The few spines are long and slender. Some of the curled hairs on the fourth femora have been broken off but there appear to be two rows of eight or nine in each row; these are in longitudinal rather than oblique rows as seen in *Leucauge* and extend nearly throughout the proximal half of the prolateral surface of the segment.

Palp. Both patella and tibia are short as shown in the table above. The cymbium has three unusual spines, two near the distal end and one near middle. The most important features are shown in Figures 1-3.

Abdomen. About 1 mm. long; only slightly overlapping the carapace; about .8 mm. wide near posterior end where it is widest; about .8 mm. tall; closely resembles the abdomen of the female.

Color in alcohol. Cephalothorax, legs, and mouth parts all yellowish white with variations. Grayish flecks occur on several parts but their distribution is too irregular for description. Abdomen: basically yellowish white; with many silvery flecks on the dorsolateral and lateral surfaces; the middorsal region is free from the silvery flecks; there is a relatively large silvery spot on each side on the posterior surface dorsal and lateral to the spinnerets, less conspicuous in the male than in the female but still distinctive; the whole posterior end is light grayish except for the silvery spots but is probably quite deeply colored in some males as in certain females in the collection; the venter is generally yellowish white with a conspicuous transverse spot near the middle which is composed of a group of bright silvery flecks.

Female. The fang groove has three relatively robust teeth on the promargin; the retromargin has four teeth, the first of which is relatively large, the other three smaller. The curled hairs on the fourth femora appear to be arranged in two longitudinal rows with twelve in each row. Published figures of the epigynum differ considerably. This has led me to make a rather careful examination of these organs on several specimens. I have noted considerable difference in the appearance of this organ in different individuals. Perhaps these differences can be attributed to variations in internal tension and degree of chitinization and development following the process of moulting. Figures 4 and 5 illustrate differences noted in two females among specimens in my collection.

Collection records. Both Pickard-Cambridges (1889-1903) and Keyserling (1893) gave Guatemala as the locality for the original specimens. In addition to the specimens reported by Petrunkevitch (1925) and Banks (1929) as cited in the introduction to this paper I can now report collection of the species as follows: numerous females from Barro Colorado Island, Frijoles, and the Canal Zone Experiment Garden, all in the Canal Zone; four specimens from El Valle, Panama. I also have a total of four males in the collection. One of these is from El Valle, Panama; the remaining three are from Barro Colorado Island, C. Z. The described male was taken in August, 1936. All specimens in my collection have been taken in July and August during my repeated collecting trips to the Canal Zone and other parts of Panama beginning in the summer of 1928.

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TWO NEW NORTH AMERICAN SPECIES OF *HYDROVATUS,* WITH NOTES ON OTHER SPECIES (COLEOPTERA: DYTISCIDAE)[1]

By Frank N. Young
Department of Zoology, University of Indiana

The North American species of *Hydrovatus* still present some of the most perplexing problems found among the water beetles. The western United States and Mexican species are particularly poorly known, and considerable work is needed before a satisfactory taxonomic treatment of the Nearctic fauna can be completed. Even in the eastern United States, several problems remain and new species may be found as characteristics for their separation are discovered.

The two new species described below were first recognized in mass collections from Payne Prairie south of Gainesville, Florida. Once their distinctiveness was realized other specimens were found either mixed with other species in the collection or in unsorted material. The series from Payne Prairie were sorted out from among approximately 5,000 specimens of other species of *Hydrovatus.*

After examining and dissecting specimens of the Palearctic *H. cuspidatus* Kunze in the British Museum (Natural History), I am convinced that I was completely in error in referring the Nearctic *pustulatus* Melsheimer and *compressus* Sharp to this species. *H. cuspidatus* and *clypealis* Sharp, although superficially similar to *pustulatus* differ in several important respects. Both, for example, have a ridge with cross striations on the anterior border of the hind coxae which probably functions as a stridulatory organ, and in both species the male genitalia are of an entirely different type from any of the American species. The parameres are complex, in *cuspidatus* (fig. 1) there is a distinct hook at the apex and in *clypealis* chitinous pieces curve in at the tip and membranous lobes project irregularly. The shape of the aedeagus is distinctive in both species.

In consequence, the American forms need to be reassigned as follows: *Hydrovatus pustulatus pustulatus* Melsheimer (fig. 10), new combination to replace *H. cuspidatus pustulatus* Melsh. (Young, 1956) and *H. pustulatus compressus* Sharp (fig. 9), new combination to replace *H. cuspidatus compressus* Sharp (Young, 1956).

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The relationship between *pustulatus* and *compressus* is still not completely determined, but the two apparently represent the extremes of a single species which varies geographically. Typical *pustulatus* decreases in size from north to south and possibly also to the east in North and South Carolina and Georgia. The largest specimens I have seen are from Wisconsin, Michigan, New York, Illinois, and Indiana. Specimens from Virginia, Tennessee, Arkansas, and northern Louisiana are smaller although very similar in other respects. Specimens from Cherokee County, Alabama; Mitchell, Lanier, Baker, and Decatur counties, Georgia; Houston County, Alabama; and Calhoun, Jackson, and Walton counties, Florida, apparently represent intergrades between typical *pustulatus* and the smaller, darker *compressus*. The latter apparently replaces *pustulatus* in the Atlantic and Gulf Coastal plain from Louisiana to North Carolina, although occasional specimens occur which have when teneral elytral markings of the type of *pustulatus*.

The male genitalia (fig. 3)[2] of the single type of *compressus* (in BMNH) is as far as I can see identical with those of *pustulatus* (fig. 2) and with those of numerous specimens examined from throughout the range. Specimens from southern Florida tend to be smaller and somewhat more coarsely punctate than the type of *compressus*, but in other respects agree with it perfectly. Specimens from North Carolina (Brunswick Co., Near Bishop, vii.25.1959, F.N. Young in University of Michigan Museum of Zoology) and South Carolina (Beaufort Co., Cambahee River marsh, vii.25.1959, F.N. Young in UMMZ) although variable are also very similar to the type of *compressus*. I have also seen a single female from the Bahamas (San Salvador Island, near Cockburn Town, iii.18.1953, E. B. Hayden in American Museum of Natural History) which probably also represents *compressus*.

Hydrovatus inexpectatus new species

Diagnosis: A small, pale *Hydrovatus* (fig. 4) similar in shape to the Brazilian *crassulus* Sharp (fig. 6), but differing from that species in the smaller size (1.89-2.15 mm in length) and the different structure of the clypeus. Body form less convex than any of the American species and with the sides of the elytra converging so gradually that they appear almost parallel-sided when viewed from above. Male

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[2] The genitalia of the type were unfortunately lost after the above figures were drawn. A specimen from Florida with genitalia intact and previously compared with those of the type has been deposited in the BMNH.

aedeagus unique (fig. 5) among the American species (male of *crassulus* unknown to me), the broadened tip suggesting some of the Old World species.

Holotype male: *Body form* irregularly elongate oval, the sides of the elytra when viewed from above less strongly arched than in most species and thus giving the appearance of being parallel-sided in the middle portion, gently converging posteriorly until the sides curve sharply in and then recurve to form the acuminate tip; in profile, body arched dorsally but somewhat flattened on pronotum; ventral profile less arched than usual, almost flat. Total length, 1.98 mm; greatest width, 1.29 mm; width at base of pronotum, 1.20 mm; width at apex of pronotum, 0.82 mm; length of pronotum at midline, 0.43 mm; length from base of prosternal process to apex of coxal lamina, 0.86 mm; width between eyes, 0.52 mm. *Head* distinctly microreticulate, the meshes impressed so that surface is only feebly shiny; meshes finer on clypeus than on front and vertex; punctation fine, sparse, and irregularly distributed; clypeus with distinct margin, the margin irregular and somewhat thickened at middle but not noticeably truncate and not sharply raised in middle (not as described for ♂ of *crassulus,* Zimmermann 1921: 191); antennal tubercles, feeble clypeal tubercles, and punctate clypeo-frontal grooves much as in *pustulatus* and other species, but clypeal tubercles somewhat more distinct; usual rows of punctures near eyes difficult to see because of the impressed microsculpture; arms of tentorium (?) vaguely visible through the thin integument running from antennal bases to converge on the front. *Pronotum* with impressed microreticulations much as on vertex of head; usual transverse anterior row of punctures and discal punctures coarser than punctures on head, the latter somewhat irregularly distributed but denser than on head; sides distinctly margined, the margins nearly straight with anterior angle acute; angle of pronotal margin with elytra when viewed from the side very obtuse. *Elytra* with impressed microreticulation as on head and pronotum but the meshes coarser and more regularly hexagonal; punctation coarse, deep, rather regularly distributed; punctures coarser than on pronotum, separated by from two to four times the diameter of a single puncture; intermediate series of punctures indistinguishable from others; elytral margins distinct, curved in profile, not visible from directly above; no distinct sulci on sides of elytra; tip moderately acute, somewhat deflexed. *Venter:* Prosternal process broadly triangular, the tip cephalad forming a minute ventral hook; disk of process microreticulate, the lateral (hind) angles irregularly minutely tuberculate; lateral borders indistinct. Hind coxae coarsely microreticulate and with large punctures separated by from one to two times the diameter of a single puncture. Abdominal sternites microreticulate, the meshes irregular and not deeply impressed; first visible sternite coarsely but shallowly and irregularly punctate; fused 2nd and 3rd sternites with a few coarse but shallow and scattered punctures on 2nd; last visible sternite pointed behind, the point deflexed. Anterior and middle tarsi moderately expanded; middle tibiae with a few large setigerous punctures on anterior face; antennae not evidently modified, not noticeably thicker than in female. *Coloration:* Head and pronotum light reddish yellow. Elytra darker, light reddish brown except along suture and sub-basal and postmedian fascia or spots which are lighter (lighter markings more evident in other specimens in series.) Venter light reddish yellow including legs and antennae. Male genitalia with parameres of usual type for American species but aedeagus distinctive (fig. 5) in lateral aspect acuminate to tip and feebly recurved; in ventral aspect broadened toward tip and spatulate.

ALLOTYPE FEMALE: Very similar to holotype; sex apparently determinable only by dissection. Clypeus not detectably different from that of male except that the clypeal tubercles are reduced. Microsculpture and punctation very similar to holotype. Color somewhat lighter on all parts. Total length 1.98 mm; greatest width, 1.20 mm; width at base of pronotum, 1.02 mm; width at apex of pronotum, 0.82 mm; length of pronotum at midline, 0.43 mm; length from base of prosternal process to apex of coxal lamina, 0.86 mm; width between eyes, 0.52 mm.

VARIATION: The paratype series varies somewhat in color — some specimens being slightly darker, particularly on the elytra, and some have light markings more distinct. The types may be slightly teneral.

TYPE LOCALITY: Holotype and allotype: FLORIDA: Alachua County, Payne Prairie south of Gainesville, vii.23.1960, F. N. Young (in UMMZ). Paratypes: 1 ♂ same data (U. S. National Museum); 1 ♂ same data (Museum of Comparative Zoology); 1 ♀ same locality, viii.21.1961 (California Academy of Science); 1 ♀ same locality, viii.21.1961 (BMNH); 1 ♀ same locality, viii.22.1961 (American Museum of Natural History); 2 ♀ FLORIDA: Dade County, Miami, ix.13.1960, blacklight trap, P. E. Briggs (Florida State Collection).

Hydrovatus platycornis new species

DIAGNOSIS: A medium sized, dark colored, and immaculate *Hydrovatus* (fig. 12) similar to the Mexican *concolor* Sharp (fig. 13) but differing from all the known American species in the flattened and widened intermediate antennal segments in the male (fig. 11). Larger and less attenuate behind than *pustulatus compressus* Sharp with which it has usually been found associated; smaller, more attenuate behind, and more finely punctate than *peninsularis* Young with which it was also associated. Male genitalia of same general type as in *pustulatus* but differing in shape of aedeagus and parameres. Although the antennal modification suggests some of the African species, the genitalia and other characters indicate relationship with the American group.

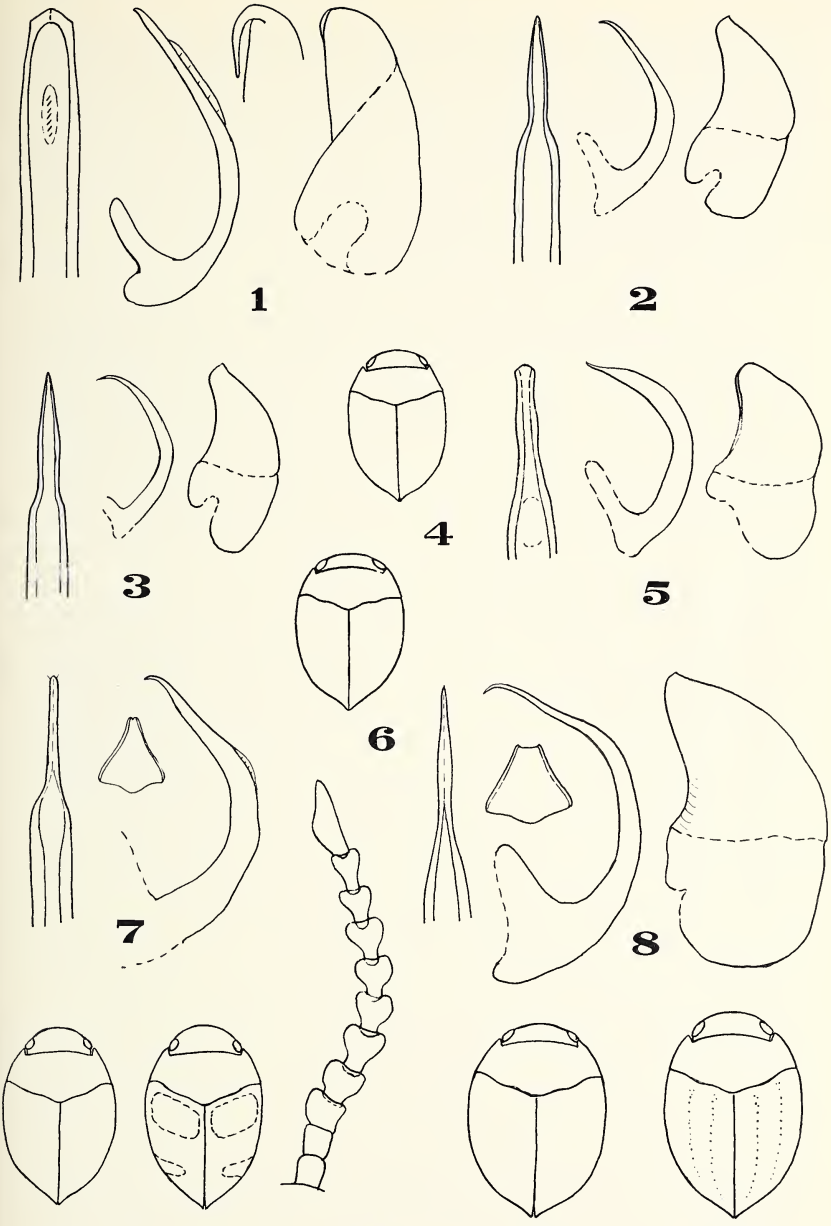
HOLOTYPE MALE: *Body form* broadly oval, less strongly attenuate behind than *concolor;* broadest at about basal third of elytra; dorsal profile convex, regularly curved; ventral profile not strongly arched;

EXPLANATION OF PLATE 19

(Scale: 1 mm = approximately 10 mm on figure at × 10; approximately 34 mm at × 40; approximately 46 mm at × 60.)

1. *Hydrovatus cuspidatus* Kunz., Corsica: Bastia, E. Reveliere (Sharp coll., BMNH). L-R. Ventral view of male aedeagus × 60; lateral view aedeagus × 60; inner face left paramere × 60; outer face right paramere × 60.
2. *H. pustulatus pustulatus* Melsh. Indiana: Monroe Co., Bloomington, x.20.1952, J. R. Munsee (UMMZ). L-R. Ventral view of male aedeagus × 60; lateral view of aedeagus × 40; outer face right paramere × 40.
3. *H. pustulatus compressus* Sharp. Louisiana: New Orleans (male type in BMNH). Same as 2
4. *H. inexpectatus* new species. Dorsal outline of holotype (UMMZ) × 10.
5. *H. inexpectatus* new species. Holotype (UMMZ). As in 2 and 3.
6. *H. crassulus* Sharp. Brazil. Dorsal outline of female cotype (BMNH) × 10.
7. *H. concolor* Sharp. Mexico: Mexico City, Höge. Male cotype (BMNH). L-R. Ventral view of aedeagus × 60; prosternal process × 40; lateral view of aedeagus × 60.
8. *H. platycornis* new species. Holotype male (UMMZ). L-R. Ventral view of aedeagus × 60; prosternal process × 40; lateral view of aedeagus × 60; right paramere × 60.
9. *H. pustulatus* compressus Sharp. Dorsal outline of male type (BMNH) × 10.
10. *H. pustulatus pustulatus* Melsh. Dorsal outline of male (same as fig. 2) × 10.
11. *H. platycornis* new species. Right antenna of holotype × 60.
12. *H. platycornis* new species. Dorsal outline of holotype × 10.
13. *H. concolor* Sharp. Same data as fig. 7. Holotype male (BMNH) × 10.

Note: The male genitalia of Dytiscidae are retracted into the body on the side. In copulation they are extruded outward, rotated, and projected forward and downward. The parts in the above figures are designated in relation to the copulatory position. Dashed or cross-barred areas are easily distorted membranous portions or portions broken in dissection. The dashed line across the parameres represents the base of the sheath into which the genitalia are withdrawn into the body.



YOUNG — HYDROVATUS

more strongly convex in dorsal profile, less strongly convex in ventral profile than *peninsularis,* much as in *pustulatus.* Total length, 2.49 mm; greatest width, 1.80 mm; width at base of pronotum, 1.60 mm; width at apex of pronotum, 1.02 mm; length from base of prosternal process to apex of coxal lamina, 1.10 mm; width between eyes, 0.69 mm. *Head* microreticulate much as described in *inexpectatus* but meshes somewhat less impressed, the surface appearing more shiny; clypeal tubercles reduced; clypeo-frontal grooves more closely and heavily punctate; punctures along inner margins of eye difficult to see, apparently not setigerous; clypeal margin distinct, feebly truncate at middle, and bordered behind by an indefinite groove; punctation fine, sparse, and irregularly distributed. *Pronotum* microreticulation coarser and more deeply impressed than on head but surface moderately shiny; punctation on disk coarse and dense compared with that on head, rather uniformly distributed but irregularly spaced; anterior row of coarse punctures not readily distinguished from discal punctation; punctation finer toward margins; sides distinctly margined, gently curved, anterior angles moderately acute; angle of pronotal margin with elytral obtuse but less so than in *inexpectatus,* about as in *pustulatus. Elytra* microreticulate about as on pronotum, meshes not deeply impressed, the surface moderately shiny; punctures coarser than on pronotum, more regular in size, and having a tendency to form irregular rows although not nearly as coarse nor with intermediate series of punctures forming such distinct rows as in *concolor;* humeri moderate, a feeble, punctate groove behind them above a feeble ridge; both groove and ridge more evidnt than in *pustulatus* but much less evident than in *concolor. Venter:* Prosternal process triangular with anterior end truncate; distinctly but narrowly margined at sides; disk punctate with inconspicuous microreticulations. Hind coxae and coxal lamina with very coarse, dense punctation, the punctures separated by less than the diameter of a single puncture and sometimes confluent; interspaces with irregular rugose sculpture but moderately shiny. First visible abdominal sternite and 2nd (fused with 3rd) with coarse punctures much as on coxae; interspaces with rugose sculpture representing the coarse, deeply impressed meshes of the microreticulation evident on other abdominal sternites; meshes of abdominal microreticulation elongate; last visible sternite acuminate behind, the tip deflexed. Anterior and middle tarsi moderately expanded, slightly more so than in female. Middle tibiae rather coarsely and densely punctate on anterior face, the punctures setigerous and irregular in shape. Antennae (fig. 11) with 3rd through 6th segments conspicuously broad and flat; the 7th and 8th broader and flatter than usual; the 11th modified, laterally excised. *Coloration:* Head and pronotum brownish yellow, pronotum somewhat darker on disk than at sides; elytra dark brown, lighter on lateral margins particularly toward apices, but without indication of any maculation. Venter and appendages nearly uniformly brownish yellow. *Male Genitalia* (fig. 8): Parameres of general type of pustulatus; tips less rounded than in *concolor* (fig. 7). Aedeagus flexulose at tip, finer and less abruptly narrowed than in *concolor.*

Allotype female: Similar to male except for unmodified antennae; sex doubtfully determinable by the narrower anterior and middle tarsi. Microsculpture and punctation very similar. Coloration throughout slightly darker than holotype. Total length, 2.40 mm; greatest width, 1.80 mm; width at base of pronotum, 1.55 mm; width at apex of pronotum, 1.02 mm; length of pronotum at midline, 0.69 mm; length from base of prosternal process to tip of coxal lamina, 1.10 mm; width between eyes, 0.69 mm.

Variation: The series before me varies slightly in color some specimens being darker and presumably more fully hardened than others. A series from Lanier County, Georgia, are particularly darker below than those from central Florida.

Type locality: Holotype and allotype: FLORIDA: Alachua County, Payne Prairie south of Gainesville, vii.23.1960, F. N. Young (in UMMZ). Paratypes, to be distributed to other museums: 8, same data as types; 27, same locality, viii.21-22, 1961. Alachua Co., San Felasco Hammock west of Gainesville, 2, x.5.1948; 1, ix.13.1950. Alachua Co., Lake Newnan east of Gainesville, 1, ix.27.1939. Gadsden Co., Chattahoochee, 2, vi.13.1954. Jackson Co., Cypress pond east of Marianna, 2, vi.14.1954. GEORGIA: Lanier Co., Pond south of Raysville, 15, vii.13.1960. All collected by F. N. Young.

The two species described above will run in my key (Young 1956) to couplet four but are immediately distinguishable from *davidis* J. Balfour-Browne by size, body form, elytral punctation, and genitalia and from *pustulatus* by the genitalia and characters given under the diagnoses.

I wish to express my thanks to Mr. J. Balfour-Browne and other members of the staff of the British Museum (Natural History) for their assistance and tolerance during my studies of the types of American aquatic beetles in that institution.

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CAMBRIDGE ENTOMOLOGICAL CLUB

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

The illustration on the front cover of this issue of Psyche is a reproduction of a drawing by Professor C. T. Brues of a myrmecophilous phorid fly, *Ecitomyia spinosa* Brues (Psyche, vol. 32, 1925, p. 306).

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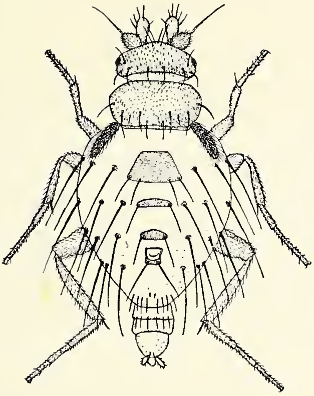

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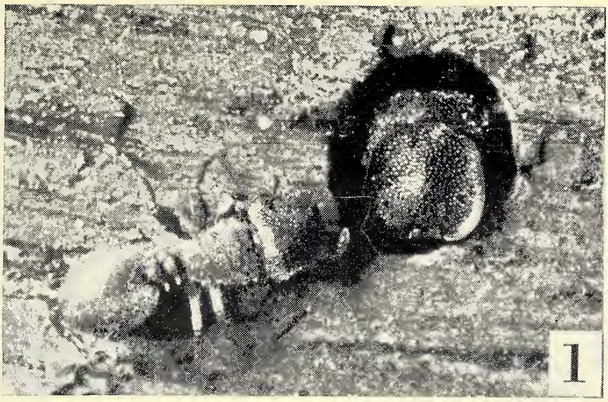

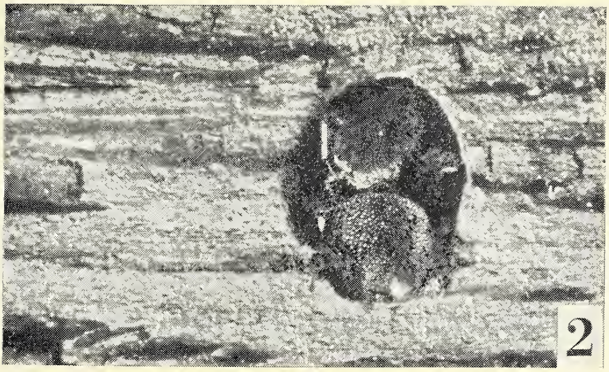

Creighton — Cryptocerus
Figures 1-3

PSYCHE

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A NEW GENUS AND SPECIES OF NEOTROPICAL HORSEFLY (DIPTERA: TABANIDAE)*

By G. B. Fairchild

Gorgas Memorial Laboratory, Panama, R. de P.

The Neotropical Tabanidae are remarkable for the number of bizarre forms which have developed, especially in the Tribe Diachlorini. Of the 146 generic names proposed at one time or another to include Neotropical Tabanidae, 65 were proposed for Diachlorini. The mortality rate among these names has been high, and conservative students of the family will probably recognize hardly half of these as useful. The proposal of another new genus in this fauna may thus appear somewhat foolhardy; nevertheless, the subject of this note presents a so far unique combination of characters which disturbs current ideas as to relationships within the Tribe.

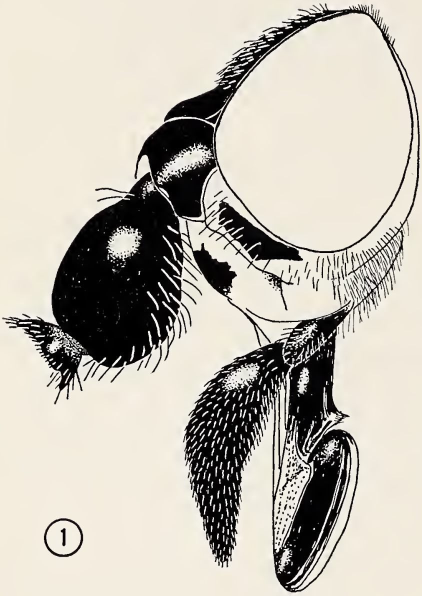
Querbetia gen. nov.

Eyes bare, apparently with green bands in life. Frons broad, less than twice as high as basal width, with basal callus as wide as frons. Vertex with vestiges of ocelli. Antennae with first segment very greatly inflated and shiny, second segment short and normal, third segment lacking in the only known specimen. Proboscis with theca and labella extensively sclerotized and shiny. Wing venation normal, the subepaulet or basicosta lacking strong setae. Abdomen with second segment narrowed, giving a wasp-waisted appearance. Legs without hind tibial spurs or hind tibial fringes. The name is an anagram of that of Dr. Joseph Bequaert and is masculine. Type and sole species of the genus, *Querbetia bequaerti* n. sp., described below.

Querbetia bequaerti n. sp.

A blackish wasp-like insect with greatly inflated and shiny subcallus and basal antennal segments, constricted abdomen and wings with anterior half black.

Manuscript received by the editor June 10, 1963.



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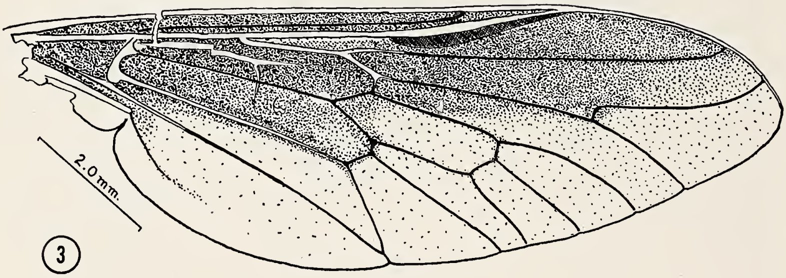

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Fairchild — Querbetia

Female. Length, 14 mm., of wing, 12 mm. Eyes bare. Efforts to revive the eye pattern were not wholly successful, but suggest that the eye was probably green with two narrow parallel transverse dark bands. Frons slightly higher than basal width, narrowed above. Callus black, rugose, nearly filling lower half of frons, and leaving but two small thinly yellowish pollinose triangular areas separating callus from the wholly black and shiny vertex. Vestiges of three ocelli are visible close to the lower margin of the shiny area of vertex. Subcallus greatly inflated, black and shiny, with a strong median groove dividing it into two hemispherical halves. Fronto-clypeus and genae thinly yellowish pollinose, with a roughly wineglass-shaped bare area in center of fronto-clypeus, and large bare patches on genae, both bare areas dark brown to black. First antennal segments enormously inflated, black and shiny with sparse long hairs at base and on ventral surface. Second segment black and shiny, not inflated, with a strong dorsal spur and numerous black hairs. Third segment missing. Palpi black, subshiny, black-haired dorsally, longer ventral hairs brownish yellow. Proboscis black, the theca and a broad basal strip of labella sclerotized, shiny.

Mesonotum blackish in ground color, subshiny to thinly grey pollinose, with the sides and humeral callosities reddish, and a pair of dull reddish dorsolateral stripes. Vestiture of sparse black hairs, with some reddish brown hairs accentuating the dorsolateral stripes. Pleura blackish brown, thinly grey pollinose, sparsely dark-haired. Scutellum black, with black and sparse pale hairs. Legs black, black-haired, the basal thirds of all tibiae yellowish white, white-haired, the tarsi yellow and yellow-haired. No hind tibial fringe. No spurs on hind tibiae. Wing as figured, the basicosta bare, the dark portions deep brownish black, the clear portions yellowish tinged.

Abdomen slender, the second segment slightly narrowed, the tergites dark brown, their posterior margins very narrowly yellowish. Vestiture of thin greyish pruinosity and sparse hairs, mixed black and yellowish, without noticeable pattern. Venter as dorsal surface, except that first four sternites are more densely white-haired, fifth and succeeding sternites dark reddish-haired.

Holotype female, Tingo Maria (Rio Huallaga) Peru, 700 M., Aug. 1947, leg. Weyrauch. In Museum of Comparative Zoology. The abdomen is intact, though detached and glued to a card below the

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EXPLANATION OF PLATE 20

Querbetia bequaerti, n. sp. Fig. 1. Head in side view. Fig. 2. Frons and basal antennal segments. Fig. 3. Wing.

specimen. One wing was also so glued, but has been mounted in Euparal on a microscope slide. The generic name is an anagram of that of Dr. Joseph Bequaert, to whom this remarkable genus and its included species are respectfully dedicated.

The relationships of this genus appear to be closest to *Acanthocera,* with which it agrees in general facies, wing pattern, shape of frons, etc., but from which it differs most markedly in the inflated subcallus and first antennal segments. The lack of terminal antennal segments in the only known specimen makes detailed comparison unprofitable. The only other genera of Neotropical Tabaninae with such inflated first antennal segments are *Bolbodimyia* Big. and *Oopelma* End. From *Bolbodimyia* the present genus differs in wasp-like fascies, different wing pattern, shiny areas on frontoclypeus and genae, lack of inflated tibiae or hind tibial fringe, normal venation (R 2 + 3 not bent abruptly forward), and presence of marked vestiges of ocelli. From *Oopelma* it differs in much greater size, *Oopelma* being a tiny Tabanid less than 7 mm. long, in not having the cross-veins prominently clouded, and in having shiny inflated palps and sclerotized theca and labella of the proboscis.

Oopelma appears to be an extreme development of tendencies foreshadowed in certain species of *Stenotabanus,* e.g. *St. liokylon* Fchld., which have the first antennal segments bare and shiny, though very little inflated. It would appear that development of the greatly inflated basal antennal segments has taken place independently in these three genera of *Diachlorini,* and is unlikely to be of phylogenetic significance.

ON SPERMATIC TRANSMISSION IN SPIDERS

By J. W. Abalos[1] and E. C. Baez[2]

Lister observed in 1678 that in copulation the male spider applies its palpi to the genital opening of the female, and since then the mechanics of sperm transmission has provided a fascinating problem for research. Formerly it was thought that there existed an internal communication between the organs of spermatogenesis and the palpi; careful studies have shown a total lack of such a connection.

In 1843, Menge described the construction by the mature male of a nuptial web into which (or directly into the web of the female) he deposits a drop of semen. The semen is produced in his abdominal reproductive organs, a pair of gonads with their respective deferent ducts meeting to form a terminal duct, opening at the midline of the body into a seminal vesicle in the epigastric furrow. This drop of semen is then taken up by the copulatory apparatus situated in the male palpi, which are transformed for this purpose into more or less complex organs, according to the spider family. Once the palpi are filled with sperm, the male is ready for mating.

Copulation is preceded by a courtship typical for each species and described by various authors. The male introduces the embolus of one palpus into the female epigynum, transferring the sperm into the seminal receptacle; immediately afterwards he repeats the operation with the other palpus. The deposition of the sperm in the nuptial web as described by Menge was later observed by various authors, among whom Montgomery (1903) suggested the term "sperm induction".

Various authors have tried to explain the origin of this double process (sperm induction and copulation). Alexander and Ewer (1957) summarize the literature and try to explain sperm induction, postulating a protoarachnid that, originally aquatic and later becoming terrestrial, was unable to return to the water and thus transformed fertilization to an internal process in agreement with its new habitat. Considering the reproductive process in those arachnid groups in which there is no direct contact of the respective genital openings (scorpions, pseudoscorpions, solpugids and some mites), the authors consider the different possibilities available to the protoarachnid, and arrive at the following conclusion: "From a comparative survey of the mating habits of those arachnids for which the facts are known,

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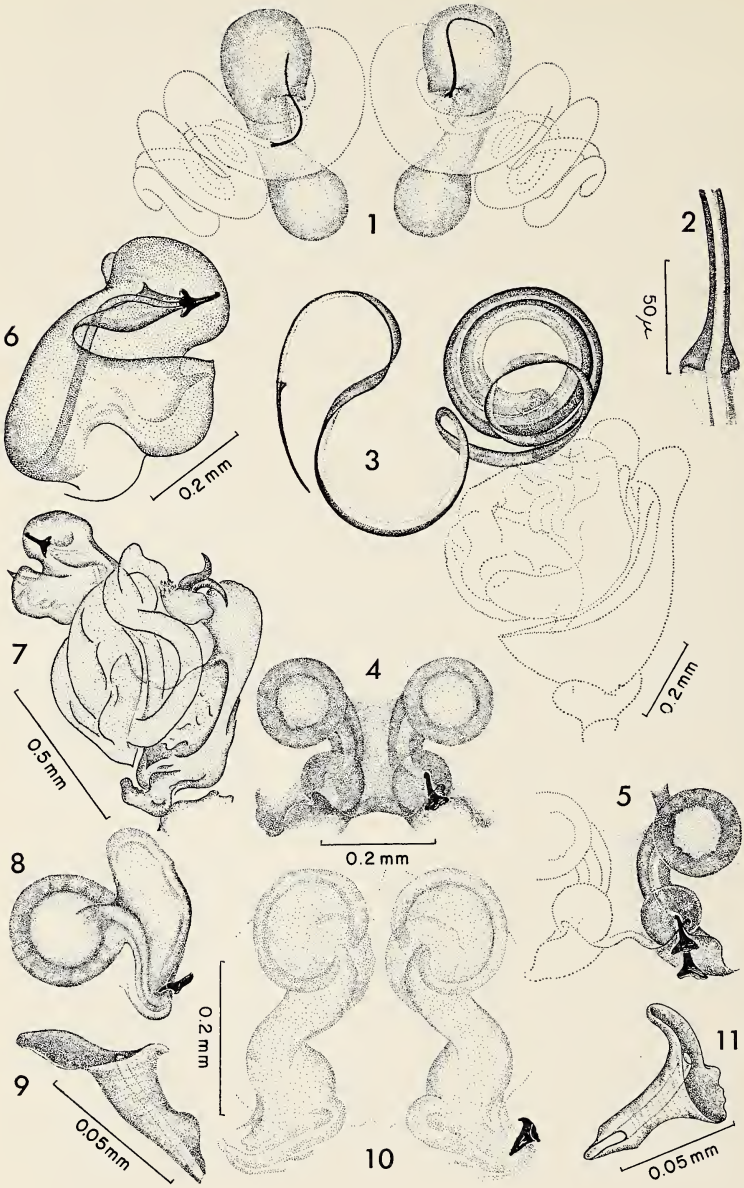

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it is suggested that the proto-spiders may have transferred the sperm to the female by way of a spermatophore which they deposited on the substratum. The pedipalps may initially have assisted in this operation or have merely held open the female genital aperture. It is further suggested that the loss of the spermatophore and retention of the pattern of deposition of the spermatic fluid are to be correlated with the evolution of web-spinning."

Equally numerous authors have studied the morphology of the palpi of male spiders, attempting to interpret the functions of its different components. The most important paper is one by Comstock (1910), who described palpi of varied complexity, the simplest being that of the cosmopolitan spider *Filistata hibernalis* in which the widened palpal tarsus forms a kind of bulb containing the coiled blind duct. The most complex structures are possessed by the *Argiopidae*. Since 1953, Levi has described in detail the male palpal apparatus in various theridiid genera and lately (1961) he has studied the evolution of the development of the palpal sclerites in this family. He supposes that in these spiders the simplest palpus is primitive and that the more complex ones indicate a higher degree of evolution.

As to the interpretation of the function of the different parts of the bulbs, authors do not agree with each other; some even believe that these organs have lost their function but still persist. Berland (1932) says: "During copula certain parts of the bulb have an important role; the accessory pieces, apophysis of the bulb, the tibia, and the patella, crest of the tarsus, etc., seem to be a completely unnecessary luxury; the attempts made to find a role for each of these parts rest upon the preconceived idea that each organ must have a function."

The different authors who have been interested in this subject do not provide a clear answer to the problem of exactly how the transmission of the sperm from the male palp to the female seminal receptacle is carried out. Equally it is not well established how sperm enters the bulb during sperm induction and how it is expelled during copulation.

EXPLANATION OF PLATE 21

Figs. 1-3. *Latrodectus geometricus*. Fig. 1. Seminal receptacle with male apical element. Fig. 2. Place of separation of apical element. Fig. 3. Complete embolus. -Baez del.

Figs. 4-11. *Metepeira* sp. Fig. 4. Seminal receptacle with male apical element. Fig. 5. Seminal receptacle with two apical elements. Figs. 6, 7. Location of apical element in the palpus — Argiopid species. Fig. 8. Seminal receptacle with apical element. Fig. 9. Apical element — *Metepeira candida*. Fig. 10. Seminal receptacle with apical element. Fig. 11. Apical element. -Baez del.

In the present paper we describe an element of the embolus of the male that in some spiders is retained by the female in her seminal receptacle after copulation. We have found this element in some members of the families *Theridiidae* and *Argiopidae.*

The following species of *Latrodectus* have been examined by us: *mactans, curacaviensis, geometricus* from Argentina, and *mactans* (=*hasselti*) from Australia. In all fertilized females we have found in each seminal receptacle (figs. 1, 20) one or more dark, sclerotized, flagelliform, slightly twisted pieces approximately 200 microns in length; with one end delicately pointed, the structure becoming progressively wider toward its other end. The center of this structure is found to contain a longitudinal transparent tube, circular in section, and opening laterally near the pointed end; at the opposite end the tube seems to be cut.

Adult virgin females, reared individually in the laboratory never contained these elements; nor did females collected in the field and maintained in isolation without ovipositing (fig. 21).

On examining unmated males we found the above mentioned element to be the tip of the embolus of the palpus (fig. 3). It is obvious that the transparent tube is the apical portion of what Comstock (1910) calls *ejaculatory duct,* and we shall refer to it here as the *apical element.*

We wish to emphasize that females that had laid fertile eggs always were found upon dissection to contain the apical element, either within the seminal receptacle, at their entrance, or near them in the ducts. If virgin females of *Latrodectus* were placed together with males that had not mated and had the emboli complete (as observed under the stereoscopic dissecting microscope), it was found that after mating the apical element was found in the seminal receptacle and was now lacking in the males, having broken off during sperm transmission.

When the apical element is found inside the seminal receptacle, the latter contains a granular seminal mass in which spermatozoa can be found. When the apical element is situated in the canals of the female, this seminal mass is found in the canal. We have never encountered the spermatic mass in females that did not also harbor the male apical element.

The blind end of the palpal tubes of males whose embolus is complete contain the seminal mass; males that lack the apical portion of the embolus (those that have copulated), show only sperm residues in the tubes.

Slide mounts of palpi of unmated males show distinctly the place where the embolus will separate (fig. 2); this is particularly conspicuous in *Latrodectus geometricus* as shown in figures 3 and 22.

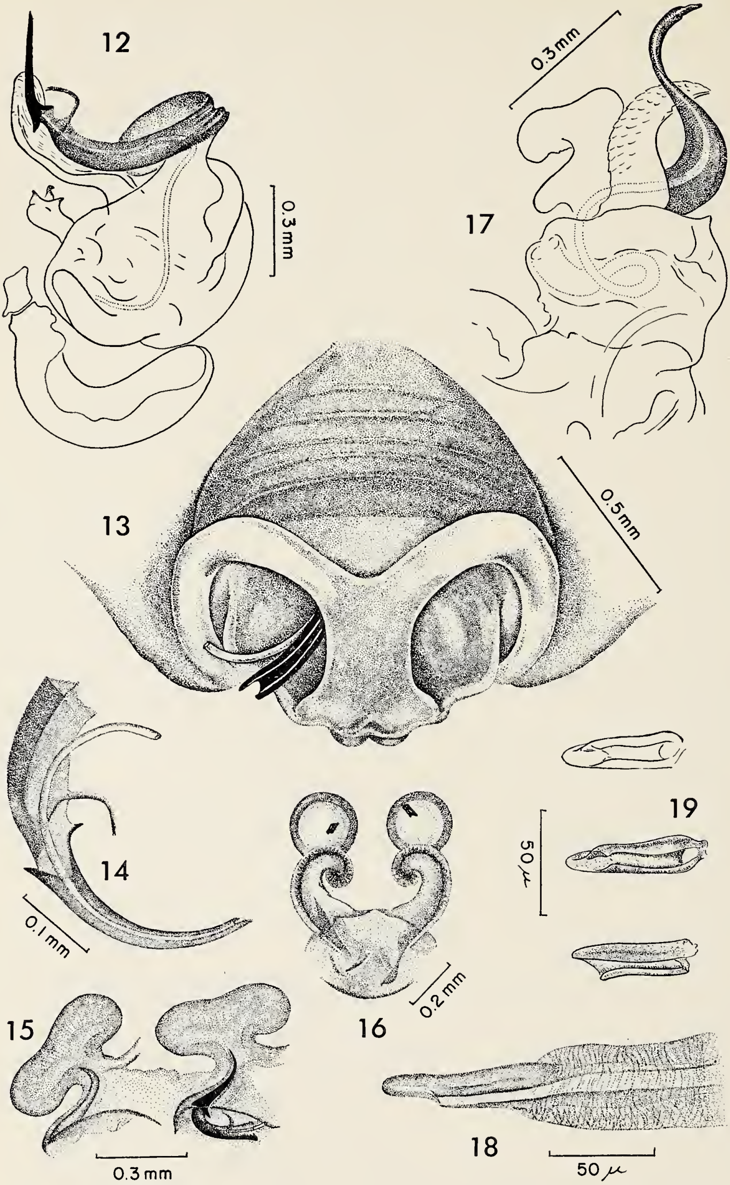
It should be emphasized that the phenomenon described is not the accidental breaking-off of the embolus at some place as mentioned by Dahl in 1902 (*fide* Levi, 1959), Smithers (1944), Levi (1959), and lately De Biasi (1962). We have frequently found such different sized parts of the embolus in the female ducts: however we stress that what we describe in the present paper is a well differentiated sclerite normally retained in the seminal receptacle of the female after the male withdraws its palpus. Recently Bhatnagar and Rempel (1962) have also observed in a species of *Latrodectus* a backward directed tooth which gets caught in the female genital organs, making the apical element break off.

The apical element of the embolus of the male of a *Metepeira* sp. is stouter and more conspicuous than that of *Latrodectus;* it is strongly sclerotized and its calyx-like shape (figs. 4, 23, 24) calls to mind a Morning Glory flower. Its size is 80 microns, and it has delicate transverse striae. The extreme apex is fish-hook shaped, this hook attaching it to the seminal receptacle; the entrance of the latter is situated directly on the epigynum and a connecting canal is lacking, matching the short male embolus. In some, two apical male elements have been found side by side (fig. 5). Unfertilized adult females have rarely been encountered; in them the potential resting place of the male element can be seen to have a cavity opening agreeing in form and dimensions with those of the apical element, including the place where the hook is to be inserted (fig. 4).

Fertilized females were always found to contain these male elements. The extreme apex of the embolus of unmated males consists of the well-differentiated organ described above, with its ejaculatory duct opening laterally at its distal end. (figs. 6, 7, 24, 25).

In *Argiope argentata* (Fabr.) the apical element is large and sclerotized, attaining a maximum length of 1 mm. Its shape is that of a curved arrow (fig. 26). The female connecting canal is short, sclerotized, funnel-shaped, with a double curve. Fitting into it, the apical element of the male adapts itself to the curvature of the duct. The male element found in the fertilized female shows an irregular zone of rupture from which the ejaculatory duct is separated, distinctly visible.

The ejaculatory duct opens apically. Slide mounts of the epigyna of fertilized females showed in some cases that in addition to correctly placed male elements, another pair was located in the atrium, indicating that copulation has been attempted or accomplished more than



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once. In the male, the apical element comprises a large portion of the embolus and no definite place of breaking exists (figs. 12, 27).

The epigynum and the seminal receptacles of other *Argiope* are similar to those of the foregoing species, and the male element is also very similar (fig. 14), though smaller (less than 0.5 mm) (figs. 15, 28).

The apical element of another undetermined species of Argiopidae is similar to that of *Metepeira* sp.; its shape is as in figures 8, 9. The element is strongly anchored in the seminal receptacle; more data are not available as it could not be removed without damage, and its position was not favorable for detailed observation. No additional females could be obtained, and the complete male apparatus is not known.

The situation is similar in *Metepeira candida* (Simon), where the apical element shown in figures 10 and 11 is anchored in the seminal receptacle.

In the theridiid, *Achaearanea tepidariorum* (C. L. Koch), the male apical element is found in the interior of the seminal receptacle (figs. 16, 29). The connecting canal of the female is short and sclerotized. The short, stout male embolus (figs. 17, 30) is abruptly narrowed near its conical apex, and at the constriction ends a delicately transversly striate region containing an internal tube of different structure (fig. 18). It is the portion beyond the striate region that remains in the seminal receptacle after mating; it is canaliculate (fig. 19) and its maximum length is 75 microns.

We are not yet able to interpret the function of the apical element, but suggest that in the above mentioned species, transfer of the seminal mass might be by spermatophore, supported by the apical element.

In other arachnid orders sperm transmission is by spermatophores. In solpugids, the male emits a sperm mass which he picks up and kneads with his chelicerae, introducing it subsequently into the female genital openings; this sperm-mass is called, by Millot and Vachon (1949) and other authors, spermatophore.

In some mites the male transfers a spermatophore to the female

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Explanation of Plate 22

Figs. 12-15. *Argiope argentata.* Fig. 12. Location of embolus in palpus. Fig. 13. Epigynum with male element in atrium. Fig. 14. Apical element. Fig. 15. Seminal receptacles with apical element.-Baez del.

Figs. 16-19. *Achaearanea tepidariorum.* Fig. 16. Seminal receptacles containing apical elements. Fig. 17. Embolus of male palpus. Fig. 18. Embolus tip. Fig. 19. Apical element showing several faces. -Baez del.


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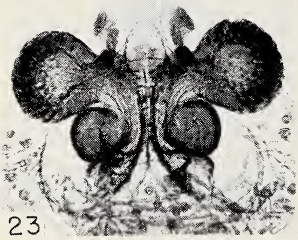
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with his chelicera. In pseudoscorpions, the male deposits a spermatophore on the ground, then pulls the female over it (Vachon, 1938). In scorpions, various authors have recently described almost simultaneously the complete mating act, in which a spermatophore is fixed by the male on the substratum (Angerman, 1955; Alexander, 1956, *fide* Alexander and Ewer, 1957). It has been reported for South American scorpions by Bücherl (1956), Matthiesen (1960) in species of *Tityus,* and Zolessi (1956) in *Bothriurus;* the male paraxil apparatus (sclerotized support of the spermatophore) was described for a representative of the family Bothriuridae by Abalos (1955), as an element of the internal anatomy of the male and without taking into account its possible function.

That all arachnids with indirect fertilization employ spermatophores permits us to expect a similar mechanism in spiders. Alexander and Ewer (1957) suggest that a spermatophore could have intervened in the sperm transmission of their hypothetical protoarachnid.

We do not believe that in the theridiids mentioned (16, 29) the apical element of the male palpus acts as a simple plug to prevent the loss of seminal liquid from the female reproductive organs. Nor can the flagellar element of *Latrodectus* act as a plug; it is much too slender to occlude the seminal receptacle or the ducts. However, the apical element of *Metepeira* species closely fits the entrance of the seminal receptacle, which, lacking a connecting canal, is almost open to the exterior. Here the element might assume the role of a plug.

In *Argiope argentata* and *Argiope* sp. the apical element (the posterior portion of which can be seen in fertilized females when the abdomen is inspected from below) is fixed by a granular mass that at the same time obstructs the access to the seminal receptacle (fig. 13). This mass recalls the *spermatocleutrum* of the scorpions; its presence indicates that fertilization has taken place.

EXPLANATION OF PLATE 23

Figs. 20-22. *Latrodectus geometricus.* Fig. 20. Seminal receptacle with apical element. Fig. 21. Seminal receptacles of virgin female. Fig. 22. Male palpus tip, with embolus.

Figs. 23-25. *Metepeira* sp. Fig. 23. Seminal receptacle with apical element. Fig. 24. Apical element of embolus extracted from seminal receptacle. 25. Male palpus with apical element of embolus.

Figs. 26-28. *Argiope argentata.* Fig. 26. Apical element of embolus extracted from seminal receptacle. Fig. 27. Embolus in the male palpus. Fig. 28. *Argiope* sp., seminal receptacles and atrium with several apical elements.

Figs. 29-30. *Achaearanea tepidariorum.* Fig. 29. Seminal receptacle with apical elements in its interior. Fig. 30. Embolus of palpus.

In additional families of spiders we have found evidence of such an apical element; but, lacking data for both sexes, we have not included these data in the present paper.

The breaking of the apical element of the male palpus is a mutilation that renders the male unable to carry out further matings. If the males of *Latrodectus* are not killed by the female after mating, they perish in a few days. Authors who have made detailed observations on the mating in different species of *Latrodectus,* i.e. Herms et al. (1935), D'Amour et al. (1936), Smithers (1944), Baerg (1945) and Shulov (1940), do not mention that copulation was repeated after it had been carried out with both palpi. Herms et. al. (1935) says "In the laboratory the males will readily mate a second time, but the females do not evidence such a tendency." Montgomery says "Promiscuous mating is general, a male impregnating a number of females, and a female receiving a number of males." However no concrete evidence is cited and we believe these two remarks might be the result of mistaken observations.

Of course, not all spiders have been observed to have an apical element. Montgomery (1909) describes in much detail the mating of a pair of salticids, *Phidippus purpuratus* Keyserling, and observes that the male carries out a new sperm induction every time the mating act is repeated. We ourselves have examined numerous specimens of common domestic salticids without being able to identify an apical element in the male palpus.

This paper is a partial result of research that one of us (Abalos) is carrying out on spiders of the genus *Latrodectus,* under a grant from the Argentine National Council for Scientific and Technical Research. Our thanks are extended to Dr. and Mrs. Levi for help with determinations and with the preparation of this paper for publication.

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FURTHER STUDIES OF THE BIOECOLOGY OF THE NEW ENGLAND TINGIDAE (HETEROPTERA)[1]

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I. INTRODUCTION

A. *Terrain and Vegetation*

Seasonal population trends for three species of *Corythucha* were followed by regular observations and timed collections made from their respective host plants at selected stations on an undeveloped tract of land belonging to Bradford Junior College. A rather full description of the vegetation and terrain is included here to serve as a reference to the general environmental features of these lace bug habitats and their surroundings during the period of these studies. The seasonal activities of the lace bugs were followed from April until October in 1957, 1958, and 1960.

An estimate made from a plan drawn by the city engineer (Haverhill, Massachusetts) indicates that approximately ten acres are included in the study area. Our college residence is located near the southwestern corner of this property, making the area exceptionally convenient for these studies. The land is generally low and poorly drained, despite a series of open ditches that have obviously been neglected for years. More than half of the land lies between 130′ and 135′ elevation, with a low point at 125′, where two of the ditches converge near the east corner of the tract and a high of 144′ above sea level on the west corner of our house lot. Because of the poor drainage, much of the land is swampy and in spring (or later in wet seasons) the water table is at, or even above, the ground surface wherever the elevation is below 132′. Within these narrow limits, the surface is somewhat irregular with a general east-southeast slope which determines the direction of the drainage.

Northeast of the study area a natural boundary, forty to fifty feet wide, is provided by a belt of mature trees. Beyond this narrow stand lies the open college athletic field. Roughly half of the field is well-cared for turf and the southeastern part supports various grasses with a scattered assortment of other herbs. This portion is usually cut over once or twice annually. The band of trees consists mostly

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[1] Acknowledgment is gratefully made of a Sigma Xi-Resa Research Fund Grant and Grant No. G5477 from the National Science Foundation, which made this series of studies possible.

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of oaks. White oaks predominate in the central portion where the elevation is between 131′ and 132′. Both to the northwest and to the southeast the land rises a little and black oaks replace the white oaks. Among the oaks some red maples, a few young elms, and such small trees as *Betula populifolia* Marshall, *Populus tremuloides* Michaux, *Prunus serotina* Ehrhart occur. Although undergrowth is sparse except under the white oaks where *Viburnum dentatum* L. grows lushly, such shrubs as *Vaccinium corymbosum* L., *Amelanchier,* an occasional *Cornus,* some *Rhus radicans* L., *Vaccinium angustifolium* Aiton, and *Gaultheria procumbens* L., along with a variety of herbaceous plants, provide some cover.

Southeast of the playing field and of the study area is a fairly extensive wooded tract. This mixed stand of hardwoods shows evidence of blow downs and fire damage. As a result, the stand is somewhat open above and a dense undergrowth of suckers and shrubs has been encouraged. Near the eastern corner of the study area is a fairly dense stand of gray birch and alders which merges with the woodland to the east and with a swampy area on the south. This small swamp spreads irregularly somewhat to the northwest. Through it runs the shallow brook that drains the tract. Much of the summer the black muck of its bed is exposed, but during the wetter seasons there is usually at least a trickle of water flowing along its course in an east-southeasterly direction.

South of the brook and swamp there is a gradual rise with patches of blackberries (*Rubus*) and scattered clumps of shrubby oak and wild black cherry suckers with intermingled patches of rank herbs, grasses, and even occasional areas carpeted with *Danthonia* and *Polytrichum* or other low-growing mosses. This rather open, shrubby growth merges with a denser cover of young hardwoods along the property boundary until such growth yields to the open lawn of a houselot on the south-southeast margin which bounds on that side a fairly level field on that corner of the college property. The field serves the neighborhood children as a playground and lies a few feet below the level of the road (Hyatt Avenue) which bounds the college tract on the south-southwest. On the west a ditch bounds this field and beyond it is a wild growth of naturalized garden roses, shrubs, and herbs mixed with native plants. Further west the land rises to road level and the site of a levelled house has groups of trees including *Acer negundo* L., *Juglans cinerea* L., neglected apples, pears, with broken fields between. Just beyond is our house which is surrounded by trees and lawn areas. Behind (or north) of these roadside conditions is a marshy field with rank grasses that merges west and north with a red maple - alder swamp which follows along the ditches towards the northwest and in part joins the swamp on the northeast. South and west of the dense young red maple growth and west of our house lie relatively large and open fields with some scattered clumps of alders and highbush blueberries. Along the west-northwest, private homes in a single row buffer this tract from a busy city thoroughfare (Kingsbury Avenue). Their back yards are hedged by wild shrubs and trees of species already noted. These bound the extensive fields just mentioned.

This is obviously a city area, presently (and for an extended period) much influenced by impinging humanity in a diversity of ways. Grass fires have been occasional and to reduce this hazard, the college has had the more open areas cut over with a heavy tractor-drawn rotary mower at irregular intervals. This has been frequent enough to maintain the fields and to set back the establishment of highbush blueberries and other woody plants. The normal ecological sequence is more or less continually interrupted tending to maintain conditions of constant change within rather narrow limits. Several mowing operations took place during the period of these studies without any apparent influence on the Tingid populations under observation. Thamnophilous species may actually benefit from the mowing since it slows the establishment of trees which would otherwise ultimately crowd out their host plants.

The negative results of two methods of collecting not previously recorded for Tingids deserve brief mention.

A light trap using a 60 watt incandescent bulb was hung about 9 feet high in an Ash-leaved Maple (*Acer negundo* L.) which grows on the edge of the lace bug study area and nearly 100 feet behind (N.E., i.e.) the garage. Lower limbs were trimmed from the tree and the light was visible for a considerable distance in all but the S.W. direction, which was unimportant because of the garage and grounds around the house. Several species of lace bugs (at least six) occur nearby. Alders, host of *Corythucha pergandei* Heidemann, grow under the branch tips of the maple and *Alnus* Station I was only about 100′ to the east. The light was operated one or two full nights each week. Usually an evening that promised to be seasonably warm was intentionally chosen. The insects captured were mostly moths, beetles, and Homoptera (mainly leaf hoppers). As anticipated, no lace bugs were attracted. The most spectacular catch was a young catbird that was released unharmed.

In another maple a few yards to the north, three Japanese beetle-type traps were hung about 6 - 8 feet from the ground. These traps, and the light trap as well, were provided with circular metal hoods (14″ in diameter) from bird feeders to keep the rain out. The hoods were very effective with the bait traps. Of the three, one was continuously supplied with the commercial Japanese beetle bait (geraniol), in one no bait was used, and in the third the substances listed below were used, usually for a week at a time. These traps were run from late July until mid-September or during the period when the lace bugs were assumed to be moving from overcrowded hosts to others and into the period when many were expected to be seeking hibernation sites. In spite of the fact that alders within a few feet of these traps were infested, only one lace bug turned up in the trap catches. The substances used were amyl acetate, amyl alcohol, orange oil, oil of thyme, oil of peppermint, methyl salicylate, saturate sugar solution, and molasses.

B. *Environmental Conditions*

During the 1958 and 1960 seasons, daily maximum and minimum temperatures were recorded and rainfall records were kept. In 1958 an attempt was made to take light readings at 9:00 a.m., 12:00 noon, and 3:00 p.m. Eastern Standard Time.

For a variety of reasons, fifty-six out of a total of 552 readings between April 15th and October 15th were missed . . . roughly 10%. Even if the light readings had all been taken, however, they would have little measurable significance. On a few occasions, for example, I actually recorded a variation of as much as 4500 foot candles in light readings taken just seconds apart. On the usual somewhat cloudy days in New England, this would be the expected situation. Consequently, without equipment for continuous recording of light intensities from dawn to dark, no critical evaluation can be satisfactorily determined. Furthermore, daily temperatures and rainfall records together serve as a good index of conditions controlling plant growth and incidentally, therefore, of conditions controlling the activities of such strictly phytophagous insects as the lace bugs. Temperature and rainfall data are, therefore, recorded graphically and any correlations between the tingid population cycles and such environmental factors will be evident.

The Taylor maximum-minimum thermometer was attached to a board and protected from the sides and from the top by masonite shields. Thus sheltered, it was mounted about 6 feet high on the trunk of a Mulberry tree (*Morus alba* L.) behind the house. Because of the buildings and several large trees nearby, the temperatures recorded were probably less extreme than they might have been

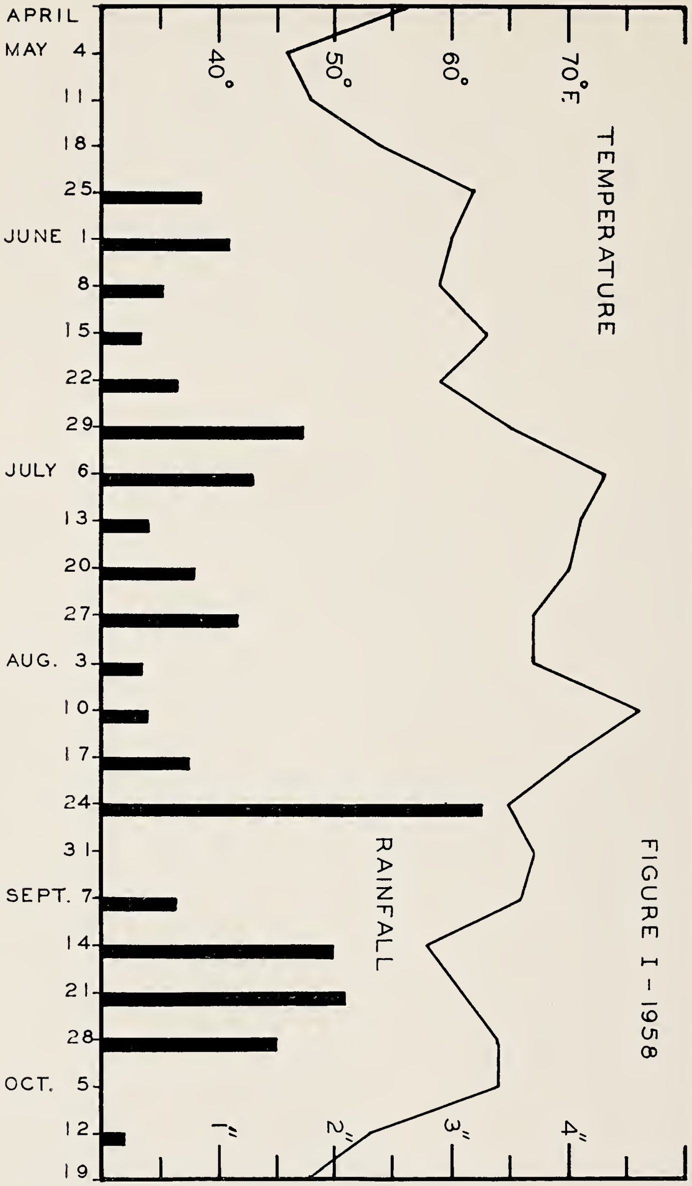

FIGURE I - 1958

in an open spot. The daytime high was a bit lower because of the shade and the night low somewhat higher because of the sheltering trees and buildings. Nevertheless, they are satisfactorily representative for the area and agreed reasonably well with those broadcast on the local weather reports.

The Victor rain gauge was mounted according to directions in an open area about 5′ high on a 4 x 4 post facing about due north. During both 1958 and 1960, the precipitation in the summer months was adequate and distributed sufficiently for the maintenance of plant growth. The gauge is evidently accurate since my readings on several occasions agreed with those announced by our local radio weatherman. The gauge was set up for operation on May 20, 1958. From then on daily records were kept throughout the two seasons without interruption. However, from August 14 to September 19, 1958 the aluminum cup that catches the rain disappeared and 37 days elapsed before another could be obtained. Therefore, the amount of rain collected during this interval was appreciably less due to the smaller diameter of the tube. Nevertheless, it was possible to compute approximate amounts for this period since I could compare the amount the gauge took without the catch cup with the amount reported locally for particular storms. This proved to be two-fifths on the few occasions checked and is considered sufficiently correct for this purpose.

The bar graphs in Figures I and II represent the total rainfall plotted on a weekly basis for the two seasons indicated. Maximum and minimum daily temperatures were averaged and also plotted on a weekly basis to give the temperature ranges shown in the same figures.

For ease of comparison, the same collecting technique described for population studies of *Corythucha cydoniae* (Fitch) and *C. pruni* O. & D. was again employed (Bailey, 1951, p. 78). This involved the use of small vials . . . 45 mm. deep and 10 mm. in diameter at the top opening . . . with plastic caps. Each vial was partially filled with alcohol and could be easily held against the leaf of the host plant while the lace bugs were flicked into it with a finger tip. Collecting time was limited to five minutes and labels with pertinent data were enclosed with each collection as it was made. Some of the

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Explanation of Figures I and II

The bar graphs represent total weekly rainfall in inches with the seasonal distribution indicated below. The curves above show maximum and minimum daily temperatures averaged and plotted on the same weekly basis for the period of lace bug activity during 1958 and 1960 respectively.

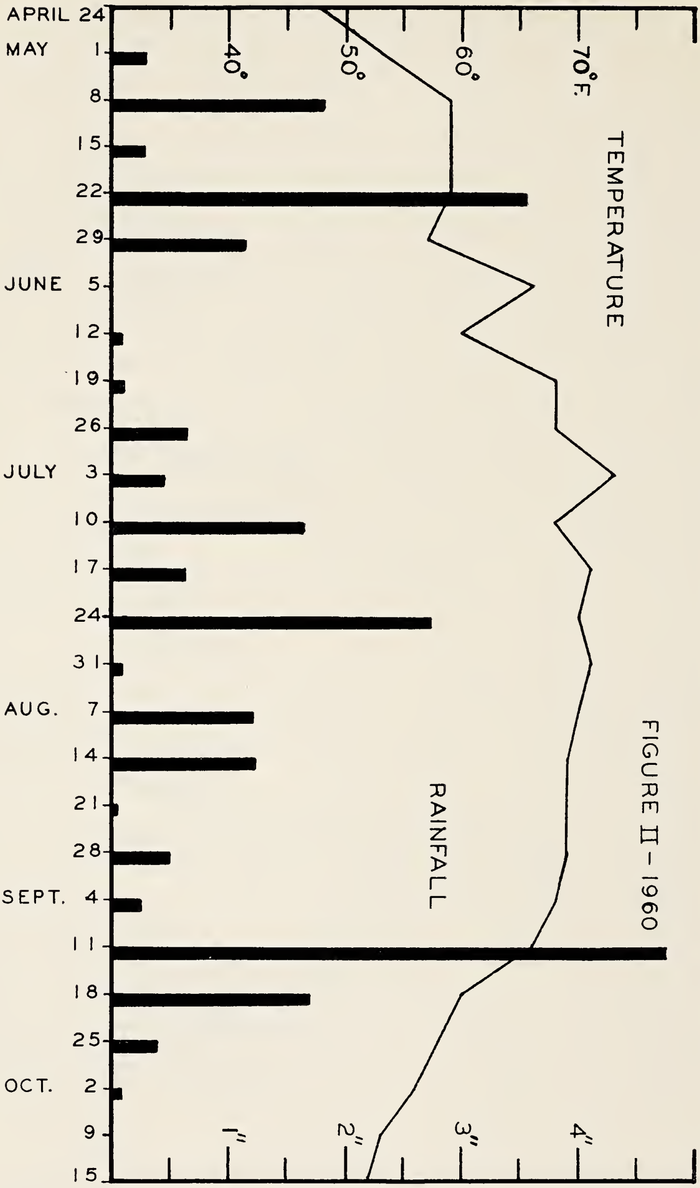

FIGURE II – 1960

limitations of this method were suggested in the report cited above. On the whole it gives very satisfactory results for these relatively sedentary arboreal and thamnophilous species when at least moderately abundant. When the host plant is small or the lace bug population somewhat sparse, the attrition from collecting alone could undoubtedly influence seasonal trends. Throughout the period of these studies there is no evidence that this was a significant factor.

During the 1957 season, pilot studies were made in the area described above to determine the number of species of Tingidae present and to tentatively locate host plant stations supporting sizeable lace bug populations. This initial survey revealed at least ten resident species. Of these, seven were in the genus *Corythucha* and one each in the genera *Corythaica, Acalypta,* and *Leptopharsa.* Collections were made at approximately weekly intervals. At the end of the season analysis of the field work indicated profitable population studies could be made for *Corythucha juglandis* (Fitch), *C. mollicula* O. & D., and *C. pergandei* Heidemann. These studies were, therefore, continued during 1958 and 1960. In the course of this work other observations were made and will be reported.

II. SEASONAL POPULATION TRENDS
and Other Notes Concerning the Willow Lace Bug (*Corythucha mollicula* Osborn and Drake)

Among the stations chosen as a result of the 1957 survey was a shrubby clump of *Salix* growing on the northeastern edge of the swamp and only five or six yards from the shelter belt of trees described above. This clump of willows is about 10′ tall and is surrounded by other willows, trembling aspens, young oaks and elms, gray birch, alders (some appreciably taller) with a lush undergrowth of such shrubs as wild roses, *Spiraea,* and *Viburnum* species, while such ferns as the Sensitive, Royal, Cinnamon, and Interrupted along with *Iris versicolor* L. and sedges grow rankly amongst them. On the edge of the woods the vegetation changes to include *Pteridium, Lysimachia,* along with various sedges, grasses, a small tangle of *Smilax herbacea* L. and other herbs which form a generally more open ground cover.

The host selected supported fair numbers of *C. mollicula* in 1957 and collections were started on May 21st. Such collections were made fairly regularly in 1957, but not strictly at weekly intervals as in 1958 and 1960. In 1957 no specimens were taken after August 20th.

Two observations made in 1957 were essentially confirmed by the field studies of subsequent seasons. First, although shrubby willows are common in the area, this particular plant was the only one found supporting a fair population of lace bugs continuously. Actually, after collecting more or less intensively there for five summers, I have discovered *C. mollicula* on only one or two other willow clumps located about 150 yards west of the chosen station. Although I collected this species in the area on several occasions, they were never sufficiently numerous on any other willow to serve my purpose.

Secondly, of the five tingid species that I have studied in this manner and others noted in the literature, *C. mollicula* has the shortest period of seasonal activity. Most of them disappear from the *Salix* by mid-August or even late July (note Figure V for 1960 season). *C. pergandei* Heidemann and other species may be collected on their respective hosts until late September or even into early October in favorable years. So far I have been unable to account for this. If *C. mollicula* hibernate early, I have yet to locate them. If they migrate to other willows (or another host species), I have yet to find the evidence. In 1958 ten adults were taken on their host on May 11th and a single specimen was found on September 7th, although none had been seen since August 3rd.

Since the figures are largely self-explanatory, comment will be minimal. Overwintering adults emerge from hibernation as soon as leaf development favors feeding. Usually by mid-May temperatures have made this possible. However, in some years (1957 graph) the peak may not occur until June. Graphs for the three years plainly reveal seasonal differences that largely reflect weather conditions. Maturation of the annual brood may show a peak as early as mid-June (1960 graph) . . . or possibly early July is more usual. From then on the number of adults taken tends to decline, often somewhat irregularly, until by early August (or early September at the latest) no more are found. Since eggs are laid over a period of several

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EXPLANATION OF FIGURES III, IV, AND V

These figures present graphically the population trends for *Corythucha mollicula* Osborn and Drake for each of the years specified. The curves are based on the actual numbers (indicated on the left) of adult lace bugs collected on the dates given below. The uppermost curve represents the totals of all population samples for the season. Differences in the seasonal distribution of females and of males in these same collections are shown by the middle and the lowermost graphs respectively.

Hibernating adults emerge from early to late May depending on the weather and temperature which also largely determine host plant leaf development. Maturation of the annual brood begins by early or . . . perhaps more commonly . . . by late June, depending on the same environmental conditions. By late July or, apparently less frequently, by early September (Figure IV) the host plant has been deserted for the year.

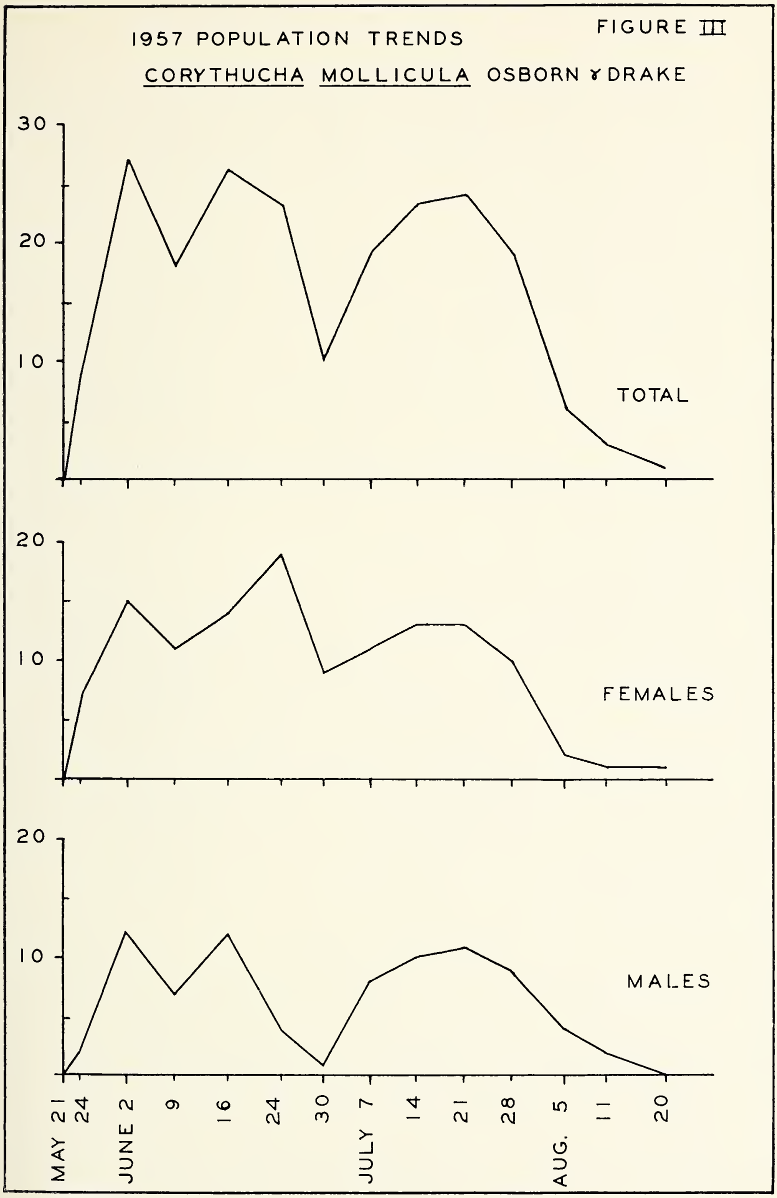
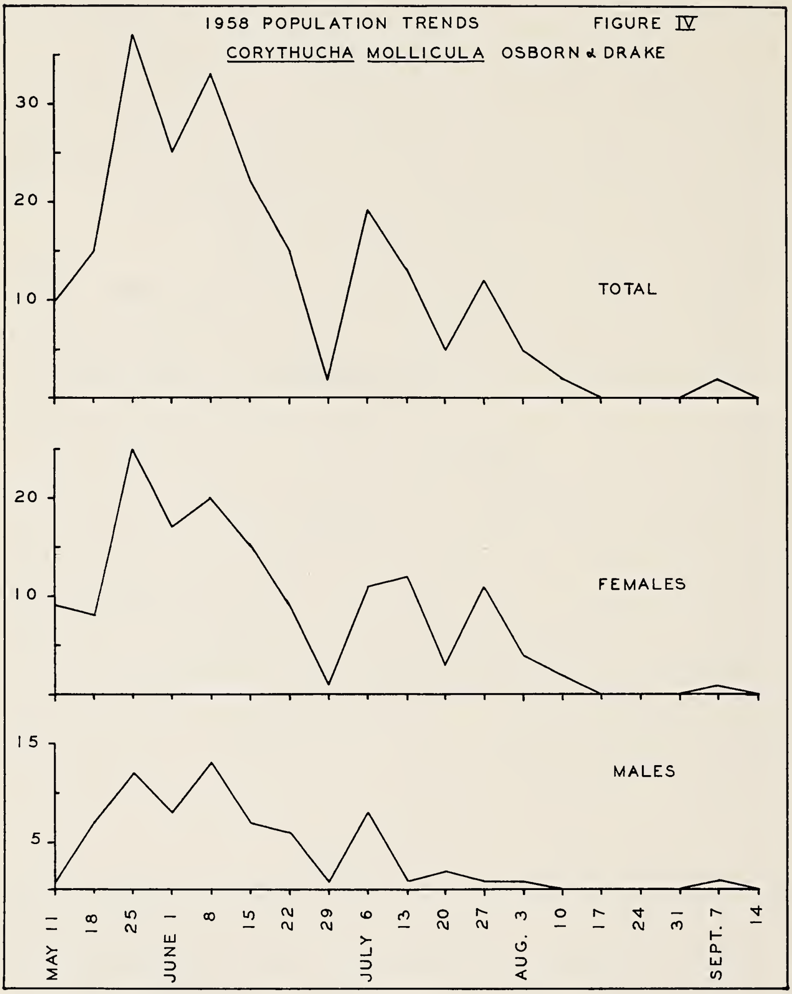
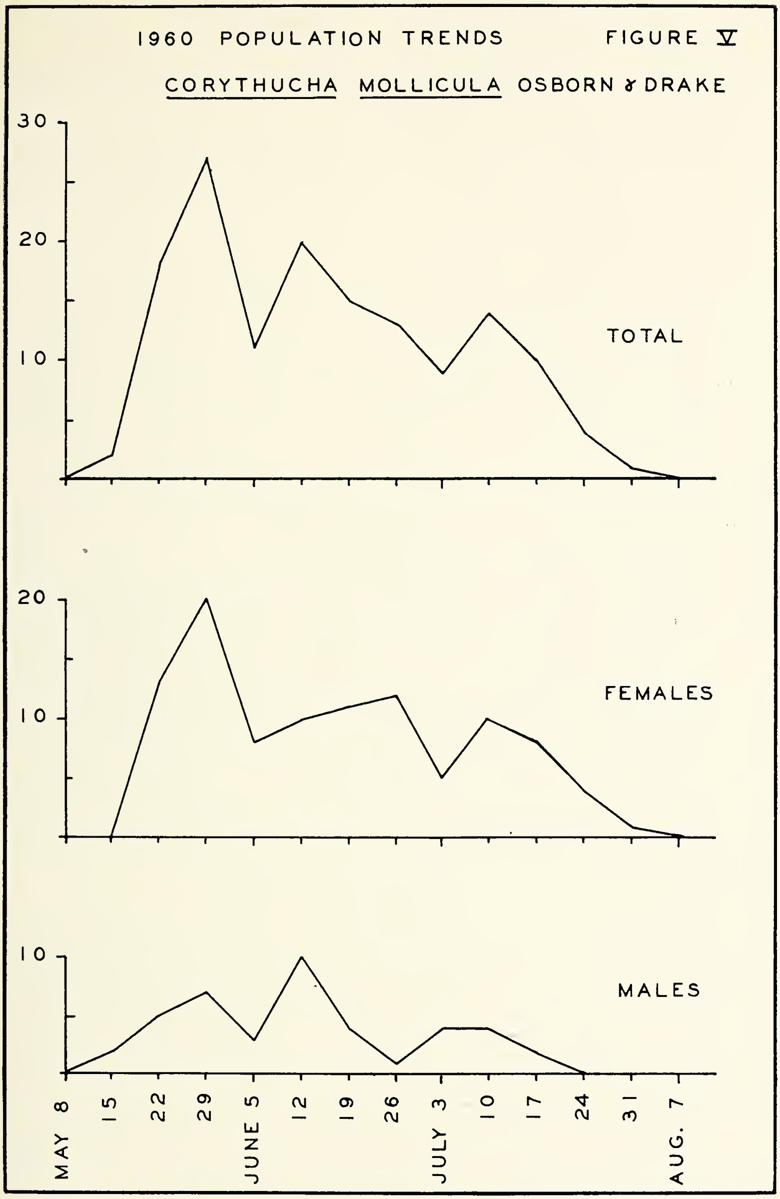


FIGURE III
1957 POPULATION TRENDS
CORYTHUCHA MOLLICULA OSBORN & DRAKE
30
20
10
TOTAL
20
10
FEMALES
20
10
MALES
MAY 21
24
JUNE 2
9
16
24
30
JULY 7
14
21
28
AUG. 5
11
20


1958 POPULATION TRENDS
FIGURE IV
CORYTHUCHA MOLLICULA OSBORN & DRAKE
30
20
10
TOTAL
20
10
FEMALES
15
5
MALES
MAY 11
18
25
JUNE 1
8
15
22
29
JULY 6
13
20
27
AUG. 3
10
17
24
31
SEPT. 7
14


1960 POPULATION TRENDS
FIGURE V
CORYTHUCHA MOLLICULA OSBORN & DRAKE
30
20
10
TOTAL
20
10
FEMALES
10
MALES
MAY 8
15
22
29
JUNE 5
12
19
26
JULY 3
10
17
24
31
AUG. 7

weeks, and since environmental factors regulate the time of incubation as well as the rate of nymphal development, there is a prolonged period during mid-summer when various nymphal instars may be found together and along with teneral adults. Nymphs were recorded from June 16 to August 20th in 1957.

Another notable detail is the fact that unlike *C. cydoniae* (Fitch) and *C. pruni* O. & D. (Bailey, 1951), the *C. mollicula* population yielded 349 ♀♀ and 171 ♂♂ for the three seasons, giving a ratio of slightly more than 2 to 1 in favor of the females.

Since the eggs of *C. mollicula* O. & D. have not been described the following data are provided. The preserved (ethyl alcohol) eggs of this species are approximately .6 mm. long by .2 mm. in diameter at the central bulge. They taper towards the rounded basal ends that are barely inserted into shallow, narrow, elliptical incisions which the females make in the tissues of the lower leaf surface. The operculum on the free, apical end resembles the cupule of an acorn in shape and even in pattern and color to some extent. The flange of the operculum is set down inside the collar-like opening of the egg shell. This opening is about .1 mm. in diameter. The operculum is circular with a flattened margin that looks somewhat alveolar. The center of the disc usually rises more or less sharply to a peak. The base of this little cone flares in a rather evenly diverging series of fine, radiating ridges. The shells are quite uniformly fuscous-amber and somewhat translucent except for the whitish alveolar rim of the operculum. The surface of the shell appears delicately reticulated when light strikes it from certain angles. These eggs are spaced closely, without touching, in circular or rather irregular patches on the underside of the willow leaf blade. The egg placement of this species bears no relationship to the leaf venation, which is not very prominent. The lower leaf surface is also sparsely hirsute. The axis of the egg is almost vertical to the leaf epidermis.

As the tables show, a leaf may bear as many as 420 eggs in four discrete patches. Since the willow leaves are relatively small (a pressed branchlet at hand is 23 cm. long and has 18 leaves, the largest of which has a blade 10 cm. long and 2.8 cm. in maximum width), and since the adult lace bugs of this species seldom occur in large numbers on a single leaf here, single egg clusters are more frequent. Probably the females normally lay one hundred or more eggs at a time. Disturbance during oviposition may account for small clusters and the occasional egg laid singly. Eggs were noted as early as May 24th in 1957 and as late as August 3rd in 1958.

The willows locally have regularly been quite heavily infested

Table I Eggs of *Corythucha mollicula* O. & D. on *Salix* leaves in Bradford, Mass., June 24, 1957

Leaf No.	Number of Eggs in Mass a.	b.	c.	d.	Total
1	177				177
2	173	71	114	62	420
3	53				53
4	253				253
5	106				106
6	91	3	178		272
7	34				34
8	72				72
9	63				63
10	133				133
11	117				117
					1700 eggs

Average: 154.5 eggs per leaf
106.25 eggs per mass

The majority of these eggs had already hatched and some were just hatching at the time of preservation.

Table II *Salix* leaves with eggs taken from the same station on June 15, 1958

Leaf No.	Number of Eggs in Mass a.	b.	c.	d.	Total
1	78				78
2	16	1			17
3	151				151
4	122				122
5	191				191
6	160				160
7	76				76
8	31				31
9	73	19			92
10	161	7	7	1	176
					1094 eggs

Average: 109.4 eggs per leaf
73 eggs per mass

with a small green chrysomelid beetle. Both the adult beetles and their grubs feed voraciously on the willow foliage. Both leaf #4 and #10 in the 1958 series showed considerable chrysomelid damage. Tingid eggs in some numbers seem to be destroyed incidentally by their beetle competitors.

In these collections two specimens had parasites attached. The first was collected on July 28, 1957 with a white ovoid mite about .2 mm. wide and .4 mm. long clinging to the right side of the body under the elytron and above the leg base. It was attached at the joint between the metathorax and the abdomen.

There was a female lace bug in the collection for June 8, 1958 with a grub-like, whitish parasite projecting from the right side of the abdomen. Dissection revealed that the parasite was about .7 mm. long and .2 mm. wide. It lay transversely in the abdomen of the host and about half of the parasite extended beyond the body wall of the lace bug in the pleural region. Lack of distinctive features made it impossible for me to identify.

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THE AMERICAN SPIDER GENERA *SPINTHARUS* AND *THWAITESIA* (ARANEAE: THERIDIIDAE)*

By Herbert W. Levi

Museum of Comparative Zoology, Harvard University

The two genera *Spintharus* and *Thwaitesia* are very similar. I have not combined them, however, because I expect that additional species may throw new light on the relationship. Both genera are close to *Episinus* in genitalic structure, general appearance, and in possession of a small spigot at the anterior pair of spinnerets (Levi and Levi, 1962).

Thwaitesia has never been revised. North American *Spintharus* has previously been revised (Levi, 1955). On reexamining a few specimens, I began to think that I had confused several species in my previous revision and that the specimens could easily be sorted out into three species. Reexamination of larger collections, however, reestablished my previous observation that the genitalia of *Spintharus* are variable and that there are at most two species. Evidence for this is presented in Figures 1 and 2.

A National Science Foundation Grant (G-4317) permitted the examination of many types, a grant from the National Institutes of Health (AI-01944) supported the research. I am thankful to the following colleagues who provided me with specimens or permitted examination of types under their care: Dr. W. J. Gertsch of the American Museum of Natural History (AMNH), Dr. H. Exline (Mrs. D. Frizzell) for specimens of her own collection and, with Dr. E. S. Ross, specimens from the California Academy of Sciences (CAS). Dr. J. Cooreman and J. Kekenbosch of the Institut Royal des Sciences Naturelles de Belgique (ISNB), Dr. A. M. Chickering whose collections are housed in the Museum of Comparative Zoology, Dr. G. Owen Evans, K. Hyatt, E. Browning of the British Museum (Natural History); Prof. M. Vachon of the Muséum National d'Histoire Naturelle, Paris (MNHN), Prof. G. C. Varley and E. Taylor of the Hope Department of Entomology, Oxford, and Dr. O. Kraus of the Senckenberg Museum, Frankfurt (SMF).

Spintharus Hentz

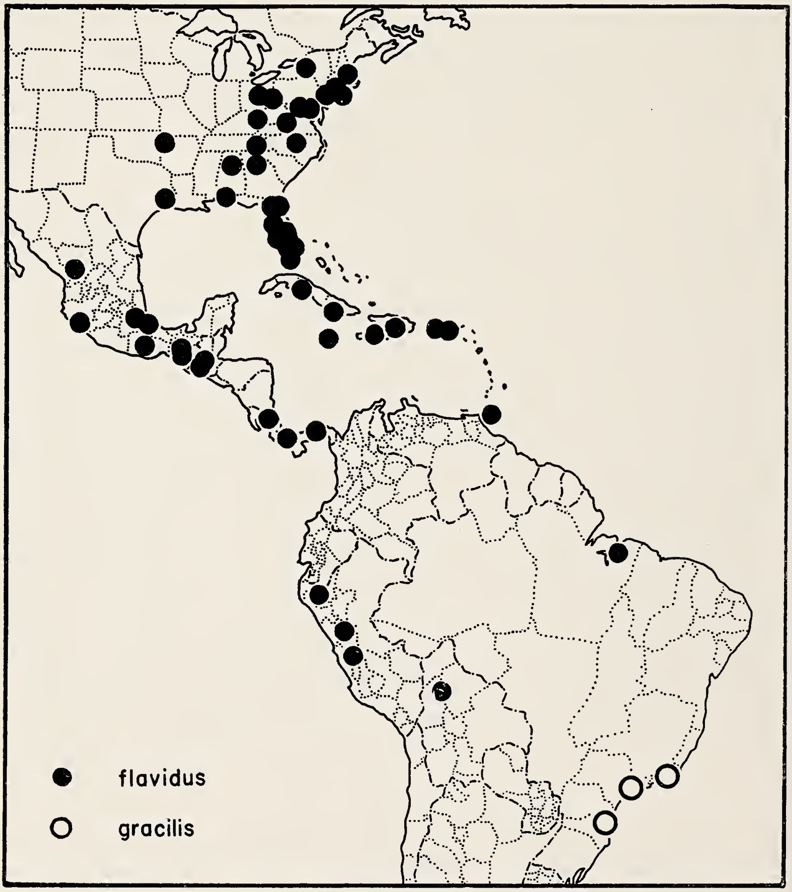
Spintharus Hentz, 1850, Jour. Boston Soc. Nat. Hist., 6: 284. Type species by monotypy: *Spintharus flavidus* Hentz.

**Manuscript received by the editor April 29, 1963.*

Description. Carapace nearly circular, weakly sclerotized. Posterior median eyes separated by about three diameters. Chelicerae small. Legs long, first patella and tibia 1.5-3.0 times carapace length. Abdomen longer than wide, widest anterior (Figs. 6, 7).

Diagnosis. Separated from *Argyrodes* by having two setae in place of colulus, from *Episinus* by having different abdominal shape, the abdomen being longer than wide, widest anterior, and by lacking horns in eye region and not having eyes on tubercles. Unlike *Thwaitesia, Spintharus* lacks silvery spots and has the posterior median eyes far apart.

Distribution. Known from only two American species.



Map 1. Distribution of *Spintharus* species.

Problems. The specimens of *S. flavidus* are variable in structure. They sometimes have an elevated eye region or humps on the anterior of the abdomen (Levi, 1955). Reexamining larger collections reestablished my previous observation that the genitalia of *Spintharus* are variable. Evidence is presented in Figures 1 and 2. Of interest is the much shorter embolus in the palpus of a North Carolina specimen (F) and in one series from Panama (R). A second series from the same Panamanian locality contained three individuals with emboli of variable length (Q). The ducts of the female epigynum also seem variable in length, but since their study means damaging specimens, this was not done. This might be advisable when more specimens are on hand.

Spintharus flavidus Hentz

Figures 1, 2K-U, W, 3-9

Spintharus flavidus Hentz, 1850, Jour. Boston Soc. Nat. Hist., **6**: 284, pl. 10, fig. 8, ♀. Types from Alabama, lost. — Levi, 1955(1954), Jour. New York Ent. Soc., 62: 79, figs. 46, 43-50, 52, 53, ♀, ♂.

Spintharus elongatus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, **1**: 178, pl. 8, fig. 108, ♀. Female type from Tambillo, [1850 m Cajamarca, prov. Jean] Peru in the Polish Academy of Sciences, Warsaw.

Spintharus lineatus O. P-Cambridge, 1896, Biologia Centrali-Americana, Araneidea, **1**: 190, pl. 23, fig. 11, ♂. Male holotype from Chichochoc [?], Guatemala in the British Museum.

Spintharus affinis O. P-Cambridge, 1896, *op. cit.* **1**: 190, pl. 24, fig. 2, ♂. Male holotype from Cobán, Guatemala in the British Museum.

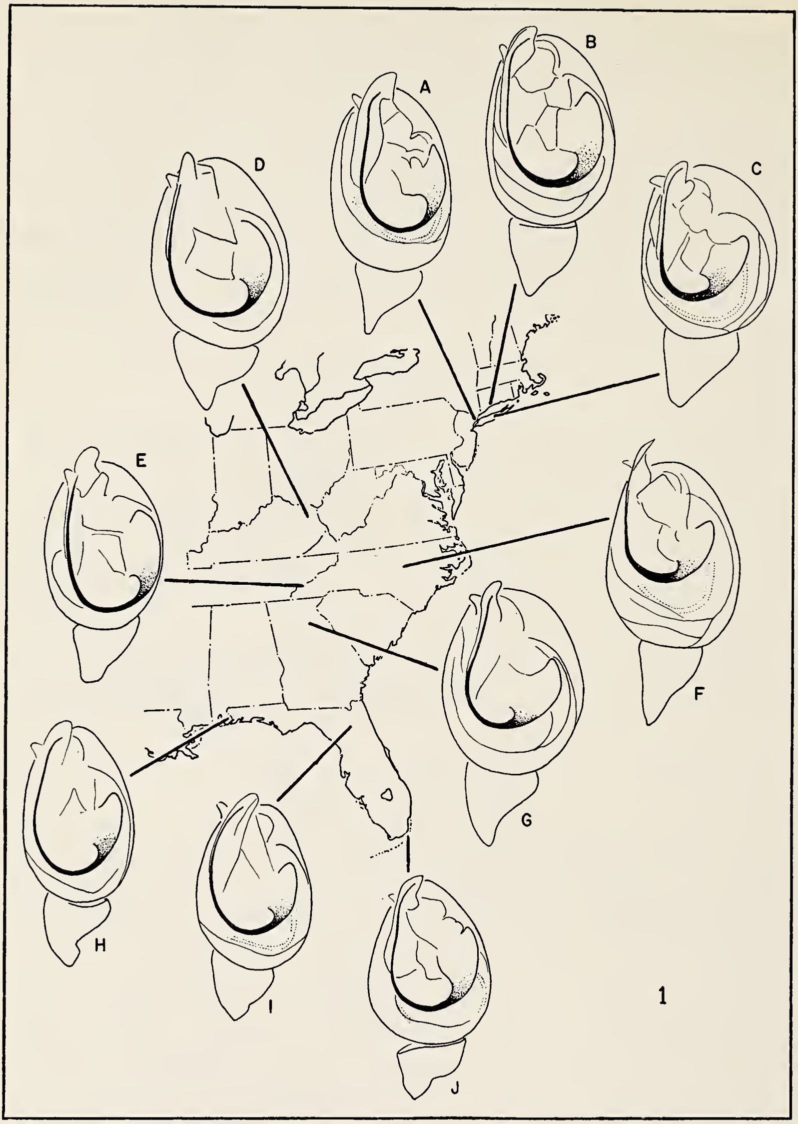
Spintharus hentzi Levi, 1955(1954), Journ. New York Ent. Soc., **62**: 83, figs. 47, 51, 54, 55, ♀. Female holotype from Trinidad, Lesser Antilles, in the American Museum of Natural History. NEW SYNONYMY.

Distribution. Eastern United States to Peru and northern Brazil (Map 1)

Additional records: United States. District of Columbia: Washington (N. Banks). *Tennessee.* Great Smoky Mtn. Natl. Park, Newfound Gap (P. J. Darlington). *Arkansas.* Washington Co.: S. of Prairie Grove (M. Hite). *Texas.* Hardin Co.: Saratoga (J. Bequaert); Old Hardin (A. Brady).

Mexico. Puebla: ? Tehiutlan (H. Wagner, AMNH). *Oaxaca:* Oaxaca (AMNH). *Costa Rica:* San Isidro del General, 600-1200 m (D. Rounds); San José (E. Schmidt, AMNH). *Panama.* El Volcán (A. M. Chickering); Boquete (A. M. Chickering). *Panama Canal Zone.* Forest Reserve (A. M. Chickering); Barro Colorado Isl. (many collections).

Cuba. Oriente: S. side of Pico Turquino (P. J. Darlington). *Las Villas:* Soledad (P. J. Darlington). *Jamaica:* John Crow Mtns. WSW of Ecclestown (A. F. Archer, AMNH); Claremont (P. Vaurie, AMNH). *Haiti:* La Visite (P. J. Darlington); NE of La



Levi — Spintharus flavidus

Hotte (P. J. Darlington). *Dominican Republic.* S of Santiago (P. J. Darlington); Loma Rucilla (P. J. Darlington). *Puerto Rico:* El Yunque (P. J. Darlington); Maricao Forest (P. J. Darlington). *Virgin Isl.* St. John (A. F. Archer, AMNH).

Peru. Huánuco: Tingo María (J. C. Pallister, AMNH). *Junín:* Pan de Azúcar, Río Tarma, 1400 m (A. M. Nadler, AMNH). *Brazil. Pará:* Belém (A. M. Nadler, AMNH). *Bolivia. Beni;* Rurrenabaque, 10 Nov. 1956, ♀ (L. Peña, ISNB).

Spintharus gracilis Keyserling

Figures 2V, 10-13

Spintharus gracilis Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, 2 (2): 244, pl. 20, fig. 298, ♀, ♂. Syntypes from Blumenau, [Santa Catarina], Brazil, in the British Museum, examined.

Spintharus flavidus, — Mello-Leitao, 1943, Arq. Museu Nacional, Rio de Janeiro, 37: 168, fig. 11, ♂, Not *S. flavidus* Hentz.

Description. Carapace of female yellow-white; eyes on black spots; male with a black band on each lateral margin. Sternum yellow-white. Legs yellow in female; male with some longitudinal black stripes and ends of femora and tibiae black, patellae black. Abdomen of female yellow-white, without pigment in alcohol; that of male with some gray pigment on sides. Lateral eyes of females two diameters of anterior medians, posterior medians one and one-half diameters of anterior medians. Eyes of male about sub-equal in size. Female with anterior median eyes one diameter apart, almost touching laterals. Posterior median eyes three and one-half diameters apart, touching laterals. Anterior median eyes of male one-third diameter apart, almost touching laterals. Posterior median eyes two diameters apart, one-third diameter from laterals. Total length of female 3.7 mm. Carapace 0.9 mm long, 0.8 mm wide. Abdomen 2.8 mm long, 0.9 mm wide. First patella and tibia, 1.6 mm; second, 1.0 mm; third, 0.7 mm. Fourth femur, 2.3 mm; patella and tibia, 2.0 mm; metatarsus, 2.4 mm; tarsus, 0.6 mm. Total length of male 2.3 mm. Carapace 0.8 mm long, 0.8 mm wide. First patella and tibia, 1.3 mm; second, 0.7 mm; third, 0.5 mm. Fourth femur, 1.7 mm; patella and tibia, 1.3 mm; metatarsus, 1.5 mm; tarsus, 0.5 mm.

Fig. 1. Variation in palpal structure of *Spintharus flavidus,* United States. A. Alpine, Bergen Co., New Jersey. B. New Haven, Connecticut. C. Long Island, New York. D. Olive Hill, Carver Co., Kentucky. E. Newfound Gap, Great Smoky Mountain Natl. Park, Tennessee. F. Raleigh, North Carolina. G. Athens, Georgia. H. Baldwin Co., Alabama. I. Gainesville, Florida. J. Tavernier, Monroe Co., Florida.

Records. Brazil. Guanabara: Paineiras, Cidade Rio de Janeiro, 22 Jan. 1949 (A. M. Nadler, AMNH). *São Paulo:* Jabaquara, Cidade São Paulo, 21 Dec. 1945 (H. Sick, AMNH); São Paulo, 13 Jan. 1959 (A. M. Nadler, AMNH).

Thwaitesia O. P.-Cambridge

Thwaitesia O. P.-Cambridge, 1881, Proc. Zool. Soc. London, **1881**: 766. Type species by monotypy: *T. margaritifera* O. P.-Cambridge, 1881 from Ceylon.

Description. Carapace nearly circular. Posterior median eyes separated by their diameter or less. Chelicerae small, without teeth. Legs long, first patella and tibia 2.0-3.5 times carapace length. Abdomen usually higher than wide with silvery spots. The genitalia are similar to those of *Spintharus.* Both have palpi with a large conductor and duct looping through the median apophysis (Levi and Levi, 1962).

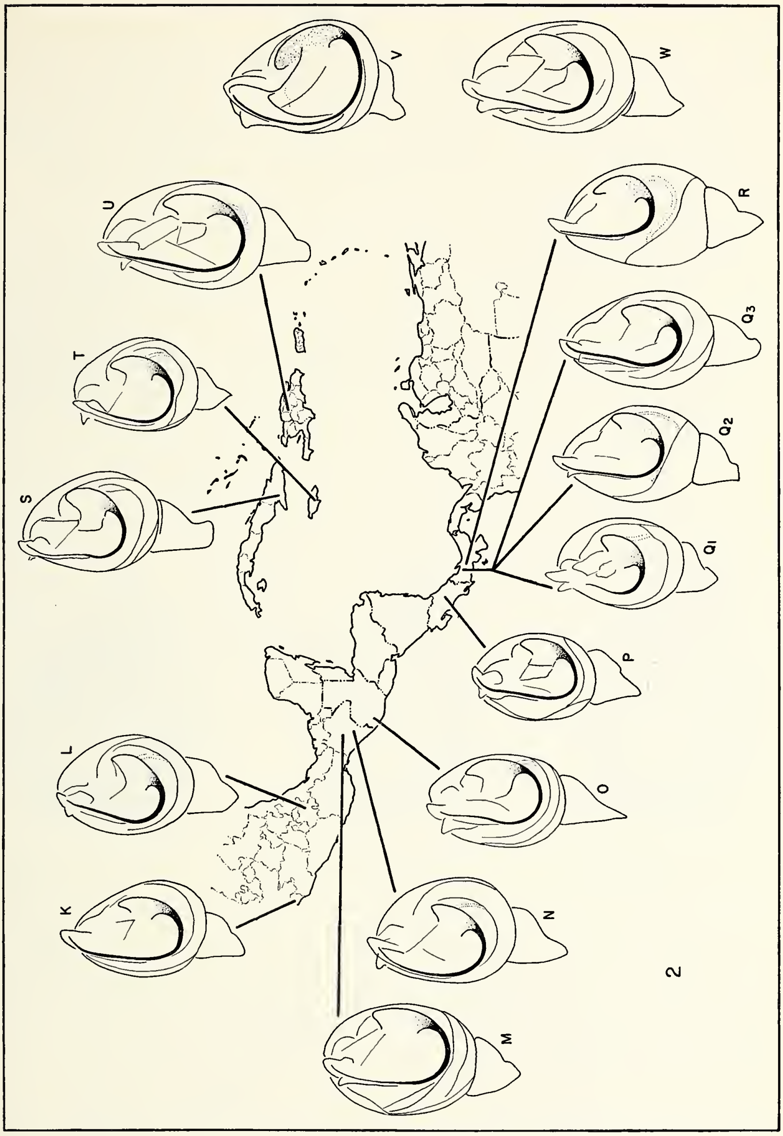
Diagnosis. Separated from *Argyrodes* by having two setae in place of colulus, from *Episinus* by different shape of abdomen (Figs. 14, 15), by lacking horns in eye region and not having tubercles. *Thwaitesia* differs from *Spintharus* by having the posterior median eyes closer together.

Distribution. Probably world-wide in tropics. Four species from America.

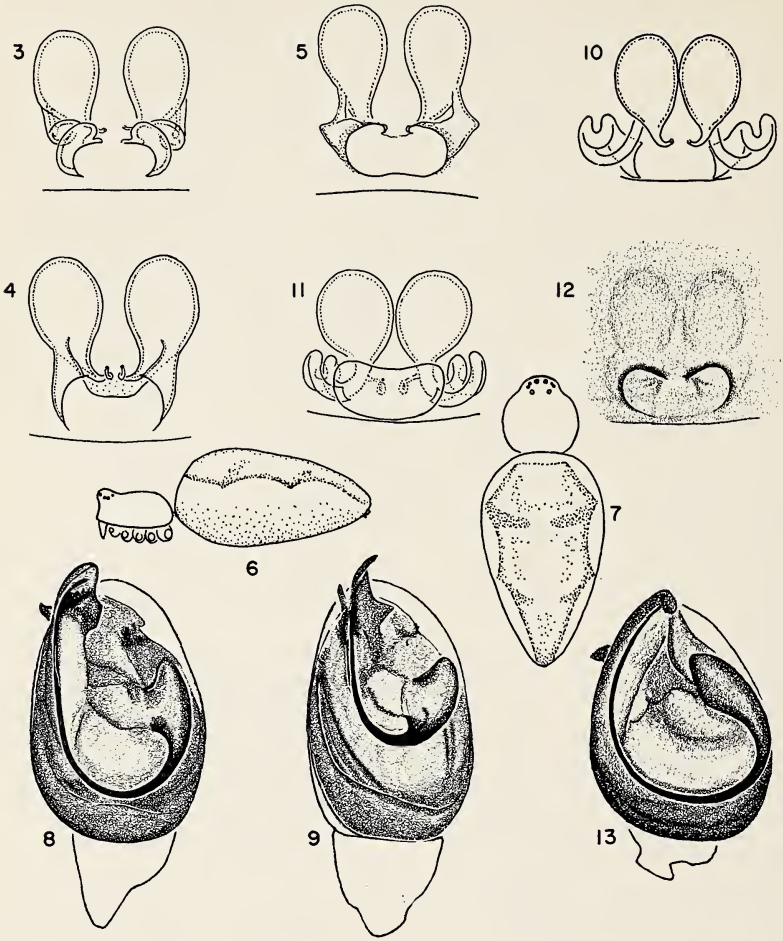
Problems. Two of the four American species are known from the type specimens only. The two other species, *T. affinis* and *T. bracteata* are widespread and probably have been confused with each other, a reason for not copying literature records. It is of interest that the species have not been collected in the same vicinity; they may have similar ecological requirements (Map 2).

In the American Museum of Natural History is a *Thwaitesia* with an epigynum similar to that of *T. bracteata* but with ducts parallel and seminal receptacles more anterior. The abdomen is low, subtriangular, widest anterior and without silvery spots. The specimen is from Minnehaha Springs, 700 m, Pocahontas County, West Virginia, July 1948 (K. W. Haller) and is believed to be exotic.

Figure 2. Variation in palpal structure of *Spintharus* south of the United States. K. Manzanillo, Colima, Mexico. L. Huauchinango, Puebla, Mexico. M. Las Casas, Chiapas, Mexico. N. Tenejapa, Chiapas, Mexico. O. Moca, Guatemala. P. San Isidro del General, Costa Rica. Q. El Volcán, Panama (one collection). R. El Volcán, Panama (second collection). S. Pico Turquino, Oriente, Cuba. T. Portland, Jamaica. U. Loma Rucilla, Dominican Republic. V. Rio de Janeiro, Brazil. W. Utcuyacu, Junín, Peru. (K-U, W are *S. flavidus;* V is *S. gracilis*)



LEVI — SPINTHARUS



Figs. 3-9. *Spintharus flavidus* Hentz. 3-5. Epigynum cleared. 3. (Washington, D. C.). 4. (Peru). 5. (Belém, Brazil). 6, 7. Female, without legs. 8, 9. Left palpus. 8. (Washington, D. C.). 9. (Panama).

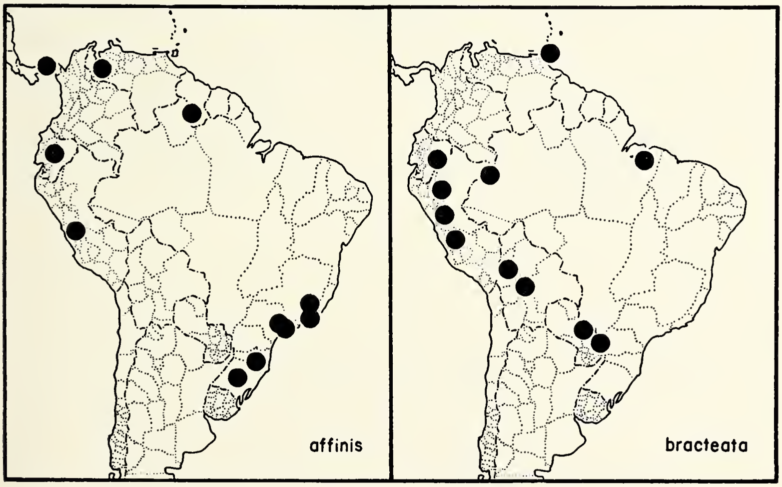
Figs. 10-13. *S. gracilis* Keyserling. 10. Female genitalia, dorsal view. 11. Epigynum, cleared. 12. Epigynum. 13. Palpus.

Thwaitesia affinis O. P.-Cambridge
Figures 14-19

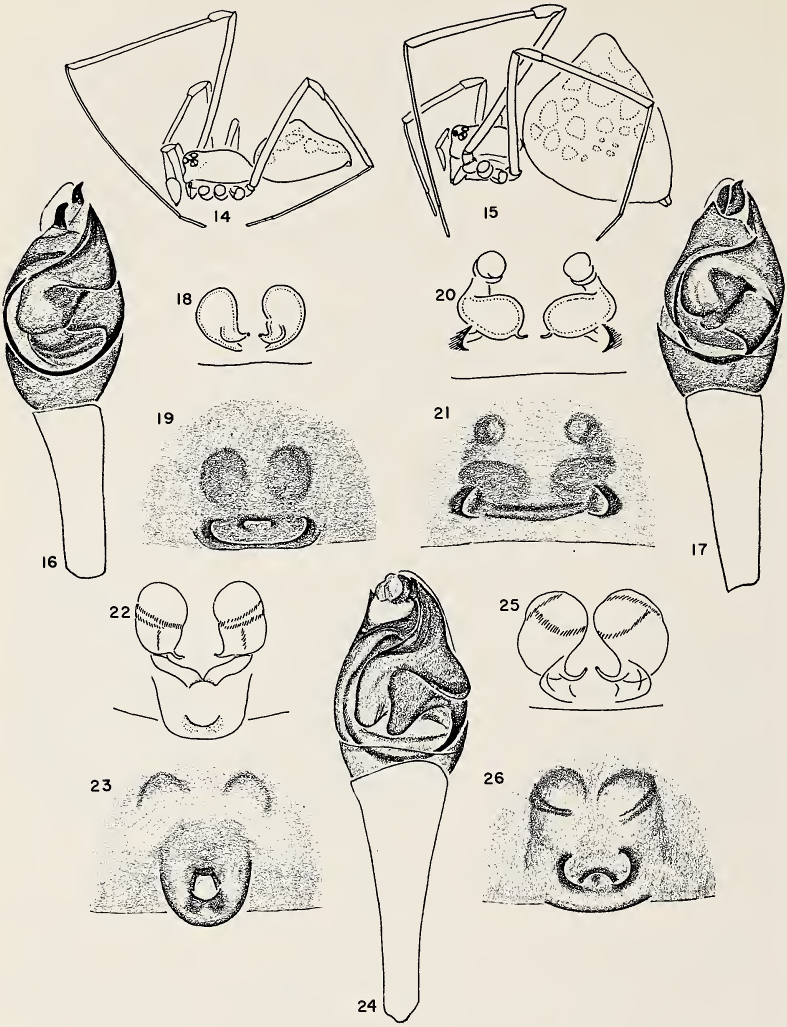
Thwaitesia affinis O. P.-Cambridge, 1882, Proc. Zool. Soc. London, 1882: 431, pl. 31, figs. 8a, ♀, ♂. Female, male syntypes from the Amazon, in the Hope Department of Entomology, Oxford, examined.

Thwaitesia adamantifera Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2(1): 164, pl. 7, fig. 101 (in part) ♀. Female lectotype here designated Maraynioc, [Junín], Peru in the Polish Academy of Sciences, Warsaw, examined. Male paratype from Minas Gerais [Brazil] in the O. P.-Cambridge collection in the Hope Department of Entomology, Oxford, examined. Female, male paratypes from Rio de Janeiro in the Keyserling collection in the British Museum, examined. NEW SYNONYMY.

Description. Carapace, sternum and legs yellowish. Distal ends of tibiae brown. Abdomen yellowish with silvery spots on dorsum. Carapace with clypeus projecting. Eyes subequal in size. Anterior median eyes one diameter apart, almost touching laterals. Posterior median eyes one diameter apart, two-thirds diameter from laterals. Abdomen subtriangular (Fig. 15), male not as high (Fig. 14). Epigynum with an oval depression wider than long, a pocket on each side and openings apparently in center (Fig. 19). Palpus as illustrated by Figures 16, 17. Total length of female 4.5 mm. Carapace, 1.6 mm long, 1.3 mm wide. First femur, 3.5 mm; patella and tibia, 3.6 mm; metatarsus, 3.9 mm; tarsus, 0.7 mm. Second patella and tibia, 2.1 mm; third, 1.2 mm; fourth, 3.2 mm. Total length of the male, 2.7 mm. Carapace, 1.1 mm long, 1.0 mm wide. First femur, 3.5 mm; patella and tibia, 3.5 mm; metatarsus, 3.9 mm; tarsus, 0.7 mm.



Map 2. Distribution of *Thwaitesia affinis* and *T. bracteata.*



LEVI — THWAITESIA

Second patella and tibia, 1.7 mm; third, 1.0 mm; fourth, 2.5 mm.

Records. Panama: Barro Colorado Isl.; Forest Reserve; Chilibre; Fort Davis; Arraiján; Summit; Fort Randolph; Fort Sherman; Madden Dam; (A. M. Chickering). Las Sabanas (N. Banks). *Venezuela. Mérida*: Timotes (SMF). *Ecuador.* Tungurahua, 2200 m (W. C. Macintyre). *Peru. Junín:* Maraynioc (Keyserling coll., BMNH). *British Guiana.* Rupununi Riv., near Mt. Makarapan (W. G. Hassler, AMNH). *Brazil. Minas Gerais:* Vicosa (Hambleton, AMNH). *Guanabara:* Sumaré, Rio de Janeiro (sev. coll.). *Est. Rio de Janeiro:* Teresópolis (H. Sick, AMNH); Petropolis (H. Sick, AMNH). *São Paulo:* Cidade São Paulo (sev. Coll.); Guapituba (N. L. H. Krauss, AMNH); Itú (A. M. Nadler, AMNH). *Paraná:* Rolândia (A. Maller, AMNH). *Santa Catarina:* Pinhal (A. Maller, AMNH); Nova Teutonia, lat 27° 11′ S, 52° 23′ W (F. Plaumann, SMF). *Paraguay.* Territ. Fonciere (E. Reimoser). *Alto Paraná:* Hernandarías, 25° S; 55° W (C. J. D. Brown).

Thwaitesia bracteata (Exline)

Figures 22-24

Thwaitesia adamantifera Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2(1): 164. In part from Soriano, Peru, not *T. affinis* O. P.-Cambridge.

Topo bracteatus Exline, 1950, Studies Honoring Trevor Kincaid, 1950: 114, pl. 1, figs. 1, 6, pl. 2, fig. 15, ♀. Female holotype from junction of Pastaza and Topo Rivers, Province Napo, Ecuador, in the Museum of Comparative Zoology, examined.

Description. Carapace, sternum, legs yellowish. Abdomen yellowish with silvery spots on dorsal portion. Anterior median eyes slightly larger than others. Anterior median eyes two-thirds their diameter apart, almost touching laterals. Posterior median eyes almost one diameter apart, their radius from laterals. The eyes of the male slightly smaller than those of female. Total length of female, from Peru, 4.3 mm. Carapace 1.7 mm long, 1.3 mm wide. First femur, 3.2 mm; patella and tibia, 3.4 mm; metatarsus, 3.7 mm; tarsus, 0.8 mm. Third patella and tibia, 1.3 mm. Total length of male, 2.9 mm. Carapace, 1.4 mm long, 1.2 mm wide. First femur,

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Figs. 14-19. *Thwaitesia affinis* O. P.-Cambridge. 14. Male. 15. Female. 16,17. Left palpus. 18. Female genitalia, dorsal view. 19. Epigynum.

Figs. 20, 21. *T. simoni* (Keyserling). 20. Epigynum, cleared. 21. Epigynum.

Figs. 22-24. *T. bracteata* (Exline). 22. Epigynum, cleared. 23. Epigynum. 24. Palpus.

Figs. 25-26. *T. splendida* Keyserling. 25. Epigynum, cleared. 26. Epigynum.

4.3 mm; patella and tibia, 4.4 mm; metatarsus, 5.0 mm; tarsus, 0.9 mm. Second patella and tibia, 2.2 mm; third, 1.4 mm; fourth, 3.4 mm.

Diagnosis. The palpus of *T. bracteata* has a longer tibia and a different tip than that of *T. affinis.* The depression in the epigynum is almost square and on a projection (Figs. 22-24).

Natural History: The type specimens were found on underside of a leaf.

Records. Trinidad. Port of Spain, 1913 (R. Thaxter). *Colombia. Amazonas:* Leticia (J. N. Layne). *Peru: Huánuco:* Tingo María, 8 Oct. 1946 (J. C. Pallister, AMNH); Monzón Valley, Tingo María (E. I. Schlinger and E. S. Ross, CAS). *San Martín:* Moyobamba, 20 Dec. 1949 (J. C. Pallister, AMNH); Mishqui-yacu, 20 km NE of Moyobamba, 1600 m, Aug. 1947 (F. Woytkowski, AMNH). *Ayacucho:* Soriano (K. Jelski, PAS). *Brazil. Pará:* Belém, Feb. 1959, ♀, ♂ (A. M. Nadler, AMNH). *Paraguay: Concepción:* Apa, 1909 (AMNH) *Alto Paraná:* Taquarazapa (AMNH). *Bolivia. Cochabamba:* El Palmar, Chapare, 900-1000 m, Sept. 1956, ♀ (L. Peña, ISNB). *La Paz:* Chulumani, 1700 m, Dec. 1955, ♀ (L. Peña, ISNB).

Thwaitesia splendida Keyserling
Figures 25-26

Thwaitesia splendida Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2(1): 166, pl. 8, fig. 102. Female holotype from "Neu Granada" [Colombia, Panama and Venezuela] in the British Museum, examined.

Thwaitesia simoni (Keyserling)
Figures 20-21

Hildbolda simoni Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2(1): 157, pl. 7, fig. 97, ♀. Female holotype from "Le Para" [Belém, Pará, Brazil], in the Muséum National d'Histoire Naturelle, Paris, examined. Keyserling wrote that this species came from "Boston"; it does not occur in North America and the label in the vial indicates a Brazilian locality.

Thwaitesia simoni, — Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29: 212.

The abdomen of this species is wider than high with silvery spots.

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MEXITERPES SABINUS, NEW GENUS AND NEW SPECIES, A MEXICAN TROGLOBITE (DIPLOPODA: TRICHOPETALIDAE)*

By Nell B. Causey

University of Arkansas, Fayetteville, Arkansas

This troglobitic milliped is of unusual interest because it is the type of a new genus and the first Mexican record of the family Trichopetalidae, which previously has been known from Nova Scotia to Louisiana, Oklahoma, and Colorado. If the genus has undergone speciation as related genera have, then additional species and subspecies will be found in other Mexican caves. Other millipeds from Mexican caves have been described by R. V. Chamberlin (1942).

I am indebted to the members of the Texas Speleological Survey for the specimen from which this species was described.

Genus **Mexiterpes,** new

Type-species: M. sabinus, n. sp. Monobasic.

Diagnosis. Depigmented, eyeless, medium-sized trichopetalids of 30 body segments that are nearest *Scoterpes.* Characterized by the gonopods and by the unmodified condition of all pregonopodal legs. Coxa of anterior gonopods bears one short branch on its distal margin; telopodite is thick and short as in *Scoterpes,* but is more complex, seems to lack a plumose branch, and has a short, ectal, setose branch. Posterior gonopods are short, slender, and consist of 4 articles; article 1 is coalesced with its homologue in midline, and there is no partition between them; all other articles are separated by partitions; a gland opening is on article 1 at base of telopodite; article 2 is elongated as is usual in the family; combined length of articles 3 and 4, which are not inflated, is a little less than length of article 2.

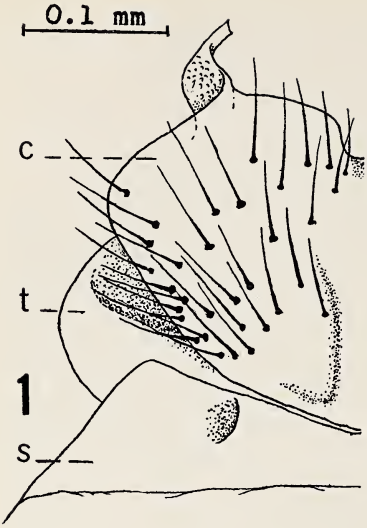
Mexiterpes sabinus, new species

Figures 1-3

Type locality. Mexico: San Luis Potosí: Sótano del Arroyo, which is near village of Los Sabinos and 8 miles north of Valles; 1 specimen was collected on silt in Big Room 3000 feet from entrance after intensive search 24 Nov. 1962 by James R. Reddell.

Deposition. Male holotype is in Museum of Comparative Zoology. Posterior gonopods are mounted on a slide; anterior gonopods are in a microvial.

**Manuscript received by the editor May 8, 1963.*



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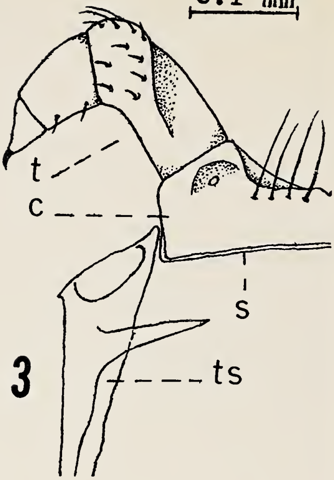

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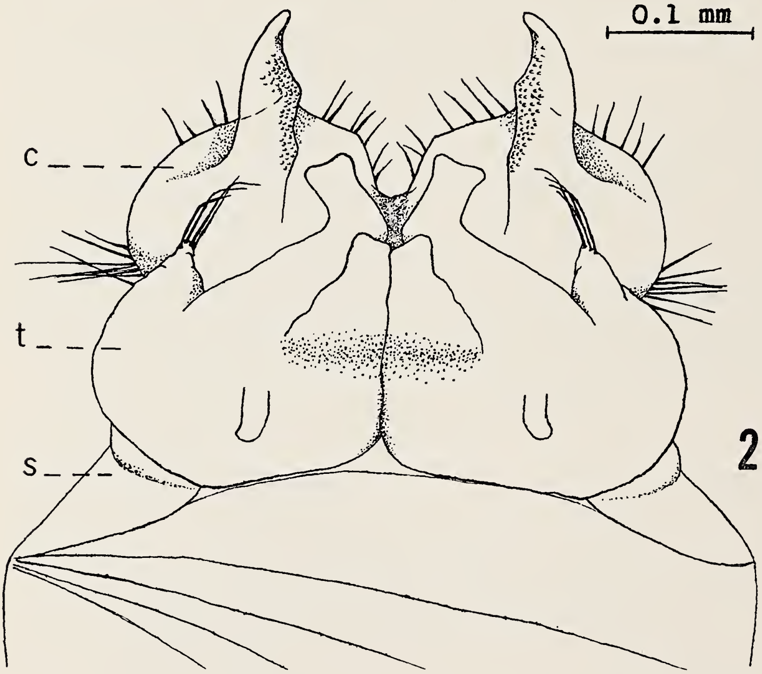

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Causey — Mexiterpes

Description of male holotype. Length is about 9 mm.; width is 0.9 mm. Body is white except for black gut contents. Length of antennae is 1.2 mm.; ratio of length of articles 1-7 is 2:4:5.6:6:8:3:2. Segmental setae are relatively coarse, attenuated, slightly curved, and in slightly oblique rows on ectal one-fourth of metatergites; their length is from ½ to ¾ the body width; no mucus droplets are on setae. Shoulders are prominent, with ectocephalic margin rounded and outermost seta on ectocaudal angle. No pregonopodal legs are modified; no tarsal setae are capitate. Legpairs 10 and 11 are unmodified except for the usual gland opening on coxae. Somatic characters that are not mentioned are as in species of *Scoterpes* and *Zygonopus.*

Figure 1 is an anterior view of right half of anterior gonopods and their sternum; no distinct partition is in midline of coxal region, which juts forward at base and is coarsely setose. Figure 2 is a caudal view of anterior gonopods; telopodite is wide, thick, coalesced to its homologue, and has 4 short branches on caudal surface; ectal branch bears 4 stout, curved setae; if there is a plumose branch, it is between coxa and telopodite; opening of sperm canal, which is probably on anterior surface of telopodite, was not observed. Figure 3 is an anterior view of right half of posterior gonopods; sternum is thin; tracheal pouches and spiracles are large; syncoxa is thick, lacks a partition in midline, has 10 stout setae on ventral margin, and has the usual gland opening at base of telopodite; terminal claw is minute.

Sternum of anterior gonopods will be described when more material can be obtained.

Family Trichopetalidae Verhoeff 1932

Species of the Trichopetalidae have either 28 or 30 body segments, are either pigmented or depigmented, and have conspicuous segmental setae. Ocelli are absent in troglobitic species; in epigean species, ocelli are arranged in a single series, in irregular lunate patches, or in triangular patches of up to 15. Male: Legpairs 10 and 11 have a gland opening on the coxae. Anterior gonopods are coalesced; coxal region is large, has one or more branches on the distal margin, and is distinctly divided from the telopodite, which is behind it and variously developed. Posterior gonopods consist of from 3 to 5 articles either

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EXPLANATION OF PLATE 27

Figs. 1-3. *Mexiterpes sabinus,* n. gen. and n. sp. 1, Anterior view of right anterior gonopod. 2. Posterior view of anterior gonopods. 3. Anterior view of right posterior gonopod. c, coxa; t, telopodite; ts, tracheal sac; s, sternum.

with or without a terminal claw; a partition between prefemur and femur is always present; partitions between other articles are either present or absent; coxa has a gland opening, which may be on a simple, rounded lobe; prefemur is elongated and more or less vertical; femur is usually swollen.

Species of the Conotylidae differ from the Trichopetalidae in that all have 30 body segments, all have ocelli, they tend to be larger, they are often darkly pigmented, segmental setae are sometimes shorter, and the coxae of legpair 11 of the male lack a gland opening. Anterior gonopods are not coalesced, are simpler, do not have the coxa and telopodite distinctly divided, and frequently are smaller than the coxal endites of the posterior gonopods. Posterior gonopods consist of 3 articles, lack a terminal claw, and there are partitions between all of the articles.

Troglobitic species of the Trichopetalidae outnumber the epigean species, possibly because of more zealous collecting in caves. *Flagellopetalum* is known by one collection of the type species in Illinois. *Scoterpes,* entirely troglobitic, is represented by many species and subspecies in Missouri, Kentucky, Tennessee, Georgia and Alabama. *Trichopetalum,* the most widely distributed genus of the family, is represented by five species (Chamberlin and Hoffman, 1958) from Nova Scotia to Oklahoma. Immature specimens from Louisiana and Colorado have been tentatively assigned to this genus. *Trigenotyla* is represented by two species in Arkansas and Oklahoma. *Craspedosoma flavidum* Bollman, which I have not seen, may go into this genus. *Tynopus* is known by a single collection of the type species from North Carolina; I have not examined it; the number of body segments is unknown. *Zygonopus,* entirely troglobitic, is in Virginia and West Virginia; the four species that I formerly assigned to it (Causey, 1960) are two species, of which one is composed of three subspecies. The following key to the genera emphasizes the ocelli too much and the gonopod structure too little.

KEY TO THE GENERA OF THE FAMILY TRICHOPETALIDAE BASED MAINLY ON THE MALE

1. About 8 ocelli are arranged in a bent series; length is about 4 mm. .... *Tynopus* Chamberlin
   Ocelli are either otherwise or are absent; length is up to 15 mm. 2
2. 28 body segments; with ocelli 3
   30 body segments; either with or without ocelli 4

3. About 5 ocelli are in a single curved series; body is lightly pigmented .... *Flagellopetalum* Causey
   Ocelli are in 2 or 3 irregular series; body is depigmented. .... *Trichopetalum* Harger
4. 14 or 15 ocelli are in a triangular patch; body is either pigmented or depigmented; prefemur of posterior gonopods is prolonged well beyond its articulation with the smaller femur .... *Trigenotyla* Causey
   No ocelli; body is depigmented; prefemur of posterior gonopods is not prolonged beyond its articulation with femur 5
5. Legpair 7 of male is greatly enlarged .... *Zygonopus* Ryder
   Legpair 7 of male is enlarged either slightly or not at all 6
6. Legpairs 3 through 7 of male have no special modification; a partition is between coxa and prefemur of posterior gonopods .... *Mexiterpes,* new genus
   One or more of legpairs 3 through 7 of male are modified; no partition is between coxa and prefemur of posterior gonopods .... *Scoterpes* Cope

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STUDIES ON CARBONIFEROUS INSECTS FROM COMMENTRY, FRANCE: PART V. THE GENUS *DIAPHANOPTERA* AND THE ORDER DIAPHANOPTERODEA

By F. M. Carpenter
Harvard University

This is the fifth in a series of studies based on the Carboniferous insects from the Commentry Basin, France.[1] It consists of an analysis of the genus *Diaphanoptera* Brongniart and a discussion of the Order Diaphanopterodea, which was erected by Handlirsch in 1919 to receive the genus. In more recent years, there have been described other Carboniferous and Permian genera which, although previously placed in the Order Megasecoptera, now appear to belong to the Diaphanopterodea. This group of insects, apparently having a combination of palaeopterous and neopterous characteristics, presents one of the most intriguing and puzzling problems in the geological history of the insects. Our unsatisfactory knowledge of the Commentry fossils has added to the difficulties.

Survey of Commentry Species

Diaphanoptera was established by Brongniart in 1893 to include two species, *D. munieri* Brongniart and *D. vetusta* Brongniart, both from the Commentry shales. The specimen of one *(munieri)* consists of a complete wing, and of the other *(vetusta)*, of the apical half of a wing. The genus was placed by Brongniart in the group of fossils he termed the "Megasecopterida", including *Aspidothorax, Sphecoptera, Psilothorax,* etc. In the same publication, Brongniart described a fossil, consisting of a whole but poorly preserved specimen with very long cerci, as *Anthracothremma scudderi,* placing it in another "family", the "Protephemerides", along with *Triplosoba* and *Homaloneura.* In his 1906 treatise, Handlirsch followed Brongniart's treatment of *Diaphanoptera,* but he removed *scudderi* from *Anthracothremma,* placing it in a new genus, *Pseudanthracothremma,* which he allocated to an *incertae sedis* category, the ordinal position being uncertain.

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[1] This research has been aided by a grant (NSF-G14099) from the National Science Foundation and by a previous grant from the Penrose Fund of the American Philosophical Society (1938). I am indebted to the authorities of the Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle in Paris for placing at my disposal the unique collections of Commentry insects in the Muséum, in 1938, 1961, and 1963; and to the authorities of the British Museum (Natural History) for allowing me to examine the Commentry fossils in that institution. The previous paper in this series was published in Psyche, vol. 70, pp. 120-128, 1963.

Shortly after this, Meunier described (1908) as *Diaphanoptera superba,* a specimen which showed all four wings held back over the abdomen; the venation was very clear but virtually no body parts were preserved. Meunier recognized that the affinites of this fossil were with Brongniart's species of *Diaphanoptera,* but he made no comments in his paper on the wings being flexed over the abdomen. Lameere, who examined the Brongniart and Meunier specimens in Paris, noted (1917) that *Pseudanthracothremma scudderi* is very close to, if not the same species as, *Diaphanoptera superba,* reaching this conclusion because of the general similarity of size and form of the two fossils, and the nature of the fragmentary venation known in *scudderi;* and that in both specimens of *superba* and *scudderi* the wings rest obliquely along the abdomen (i.e., neopterous-like), not perpendicular to the body (i.e., palaeopterous-like), as in all other Megasecoptera then known. Nevertheless, he continued to place *Diaphanoptera* in the Megasecoptera. Handlirsch, in his superficial revision of Palaeozoic insects (1919), established a new genus, *Diaphanopterites,* and a new family, Diaphanopteritidae, for Meunier's *superba.* Unfortunately, he did not see the fossil itself and his interpretation of it was based entirely on Meunier's incorrect drawing and on a small, published photograph. The flexed position of the wings led Handlirsch to remove these diaphanopterids from the Megasecoptera and to establish a new order, Diaphanopteroidea, for their reception.

As a result of my examination of the fossils mentioned above, I propose the following classification of the Diaphanopteridae from the Commentry shales.

Order Diaphanopterodea Handlirsch
  Family Diaphanopteridae Handlirsch (synonym: Diaphanopteritidae Handlirsch)
    Genus *Diaphanoptera* Brongniart (synonyms: *Diaphanopterites* Handlirsch; *Pseudanthracothremma* Handlirsch)
      munieri Brongniart (type-species)
      vetusta Brongniart
      scudderi (Brongniart)
      superba Meunier

The family Diaphanopteridae is also represented in Upper Carboniferous strata of the Soviet Union; other families apparently belonging to the Order Diaphanopterodea have been found in Upper Carboniferous and Permian beds of the Soviet Union and the United States. A discussion of the characteristics and relationships of the Diaphanopterodea will follow the detailed account of the Commentry fossils.

Family Diaphanopteridae Handlirsch

Diaphanopteridae Handlirsch, 1906, Foss. Ins.:313
[= Diaphanopteritidae Handlirsch, 1919; Denks., Akad. Wiss. Wien, *96*:65]

Fore and hind wings similar; Sc terminating on R1 slightly beyond mid-wing; MA diverging away from MP immediately after its origin and just touching or very nearly touching Rs before continuing as an independent, convex vein; CuA coalesced with the base of M. Several large, thickened, circular spots on membrane of both wings. Body structure little known; thorax and abdomen combined about as long as wings; abdomen slender; cerci very long, about twice as long as wings.

Text figure 1. *Diaphanoptera scudderi* (Brongniart), after Brongniart, 1893.

There seems to me no basis for accepting Handlirsch's family Diaphanopteritidae, which was erected for *Diaphanoptera superba* Meunier. The diagnosis given by Handlirsch for the family is very vague and his interpretation of the venation of *superba,* based entirely on Meunier's published photograph, is inaccurate.

In addition to the Genus *Diaphanoptera,* which is now known only from the Commentry shales, the family Diaphanopteridae is represented in the Upper Carboniferous strata of the Kuznetsk Basin (Asian RSFSR), Soviet Union, by *Philiasptilon maculosum* Zalessky (1931). Although only the distal half of a wing of this insect is known, its affinites with *Diaphanoptera* are obvious; two circular spots on the wing membrane correspond approximately in position to spots in *Diaphanoptera.*

The nature of the circular, cuticular thickenings on the wings of *Diaphanoptera* is by no means clear. Forbes (1943) identifies them as nygmata,[2] and, incidentally, considers *Diaphanoptera* to be a true neuropteron, closely related to the living genus *Corydalis.* However, cuticular thickenings occur in certain families of Palaeozoic insects which can hardly be regarded as endopterygotes, e.g., the Mischopteridae of the Megasecoptera, which are clearly Palaeoptera, and the Cacurgidae of the Protorthoptera, to cite only two examples. The spots in all these Palaeozoic forms are much larger than the nygmata of the endopterygote insects and there is certainly no reason to regard them as homologous structures. Forbes' figure of *Diaphanoptera* (1943) represents the spots as very small, like nygmata, although they are actually large (see plate 28).

Genus *Diaphanoptera* Brongniart

Diaphanoptera Brongniart, 1893, Recherches Hist. Ins. Foss.:308; Handlirsch, 1906, Foss. Ins.: 313; Lameere, 1917, Mus. Nat. Hist. Natur., Bull. 23:148.
Pseudanthracothremma Handlirsch, 1906, Foss. Ins.:324; Lameere, 1917, Mus. Nat. Hist. Natur., Bull. 23:148.
Diaphanopterites Handlirsch, 1919, Denkschr. Akad. Wiss. 96:66.

Hind wing very slightly broader distally than the fore wing and apex slightly more rounded. Rs with from 5 to 7 branches; R4 + 5 parallel with MA; MA unbranched; MP with from 4 to 5 branches; CuA unbranched; CuP branched.

Type-species: *Diaphanoptera munieri* Brongniart [Designation by Handlirsch, 1922].

The generic characteristics given above are somewhat arbitrary, since only one other genus, *Philasptilon,* is known in the family. The latter, represented by an incomplete wing, differs from *Diaphanoptera* in having R4 + 5 and MA converging distally; at the point of its origin R4 + 5 is much more remote from MA than it is further distally. The rest of the known venation of *Philasptilon* is very close to that of *Diaphanoptera.* I am following Lameere in considering *Pseudanthracothremma* a synonym of *Diaphanoptera;* it has flexed wings and very long cerci, and the few veins that can be seen in the fossil are like those of *Diaphanoptera. Diaphanopterites* is even more clearly a synonym. The distinguishing characteristics attributed by

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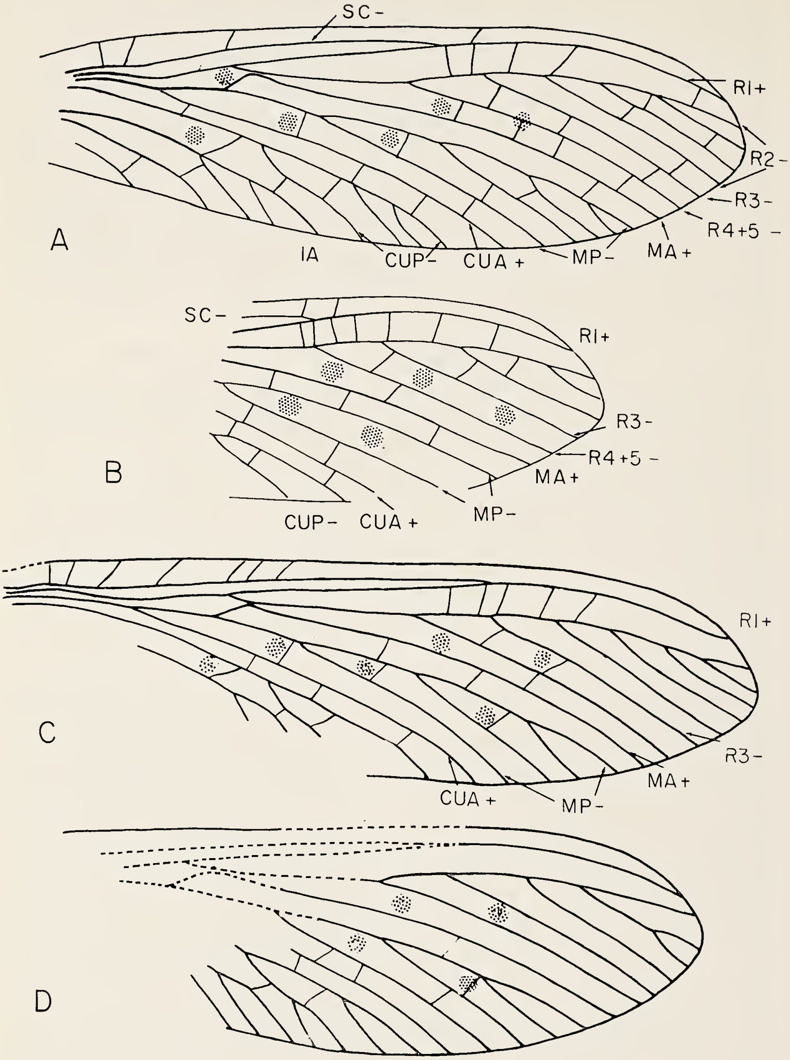
[2] The term nygmata is a modification (Forbes, 1924) of "nigmas" proposed by Navas in 1917 for small cuticular spots which occur on the wings of certain Trichoptera, Neuroptera and related Endopterygota and which grade into similar spots in other insects. Very little is known of their structure and nothing of their function. Martynov (1925) has published the only account of their histology, Martynova (1949) has investigated their presence and distribution in Permian Mecoptera, and Jolivet (1955) has studied the external structure of a variety of types. They have been regarded as probably either glandular or sensory structures.



CARPENTER — DIAPHANOPTERA

Handlirsch to the genus do not exist; Sc, for example, was described as extending to the wing apex, but it actually terminates just beyond mid-wing, as in *Diaphanoptera.*

Diaphanoptera munieri Brongniart
Plate 28, A

Diaphanoptera munieri Brongniart, 1893, Recherches Hist. Ins. Foss.:309, pl. 17, fig. 10; Handlirsch, 1906, Foss. Ins.:313, pl. 32, fig. 8; Lameere, 1917, Mus. Nat. Hist. Natur., Bull. 23:149.

This species was based on a single, well-preserved wing, 38 mm. long and 11 mm. wide; on the basis of the shape, I assume it is a hind wing. Its venation is shown in plate 32, fig. A, which is drawn directly from the type specimen in the Laboratoire de Paléontologie. All main veins are clearly preserved and their convexities or concavities distinct. Brongniart's figure of the wing, although very small, correctly represents the venation except in two areas: (1) The proximal parts of Sc and R1 are distinctly bent, as in other primitive Diaphanopterodea; and the stems of R and M are independent, not in contact, as suggested in Brongniart's drawing. (2) MA, distinctly convex, arises from M at about the level of origin of Rs and then diverges abruptly towards Rs. These two veins do not, however, quite coalesce, as is shown in Brongniart's figure; there is, in fact, a narrow space between them, even at the point of closest association. Handlirsch's figure of *C. munieri* (1906), crudely copied from Brongniart's work, shows the basal piece of MA as very weak and nearly transverse. This illustration, which is definitely incorrect, has been reproduced in various publications on wing venation and fossil insects (e.g., Comstock, 1918; Rohdendorf, 1962). Forbes' figure (1943), although based on Brongniart's, is somewhat altered, depicting a broader, more oval wing, and representing the base of MA by a broken line. Actually, the basal origin of MA and its divergence to and away from Rs are clearly preserved in the fossil.

Like the other diaphanopterids, *munieri* shows several large spots on the wing. Brongniart indicated six of these in his figure and I find this number in the fossil; but I believe he included one which is actu-

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Explanation of Plate 28
Diaphanoptera

A. Fore wing of *D. munieri* Brongniart (type).
B. Distal part of fore wing of *D. vetusta* Brongniart (type).
C. Fore wing of *D. superba* Meunier (type).
D. Hind wing of *D. superba* Brongniart (type).

All drawings original, based on specimens in Laboratoire de Paleontologie, Paris. Sc, subcosta; R1 radius; R2, R3, R4+5, branches of radial sector; MA, anterior media; MP, posterior media; CuA anterior cubitus; CuP, posterior cubitus; +, convex veins; —, concave veins.

ally not present and that he omitted one. The one which he omitted is located between CuP and 1A; the one which he shows most distally is, I believe, only an irregularity in the rock, not part of the wing; its appearance is very different from that of the others.

Diaphanoptera vetusta Brongniart
Plate 28, B

Diaphanoptera vetusta Brongniart, 1893, Recherches Hist. Ins. Fiss.:311; pl. 17, fig. 9; Lameere, 1917, Mus. Nat. Hist. Natur., Bull. 23:147.

This species was based on a well-preserved specimen, consisting of about the distal third of the wing, 20 mm. long and 10 mm. wide; the shape of the apex suggests a fore wing. Brongniart's drawing is essentially correct, except that the first branch of Rs has an additional fork, which he did not show. The species is probably distinct from *munieri* on the basis of the reduced (i.e., forked) MP and the less extensive Rs. Of particular interest are the wing spots, some of which differ in location from those of *munieri:* there are two between R3 and R4 + 5 and two between MP1 and MP2, instead of only one, as in *munieri.*

Diaphanoptera scudderi (Brongniart)
Text figure 1

Anthracothremma scudderi Brongniart, 1893, Hist. Ins. Foss.:329; pl. 18, fig. 10.
Pseudanthracothremma scudderi Handlirsch, 1906, Foss. Ins.:324.
Diaphanoptera scudderi Lameere, 1917, Mus. Nat. Hist. Natur., Bull. 23:149.

This species was based on a poorly preserved fossil, representing a whole insect, the wings (33 mm. long and 11 mm. wide) resting obliquely along the abdomen and the cerci extending fully twice the length of the body; suggestions of the thorax and two legs are present but are too vague to have morphological meaning. Brongniart's figure is essentially correct. The wing venation is so obscure that no satisfactory description or drawing of it can be made; however, the pattern, so far as it can be seen, is consistent with that of *Diaphanoptera.* There are faint indications of the wing spots but their disposition is not clear because of the confused venation.

Brongniart, not recognizing the affinities of this fossil with his *Diaphanoptera,* placed it in Scudder's genus *Anthracothremma,* which had been established for an "orthopteroid" species from North America. Brongniart assigned *Anthracothremma* to the "protephemerides", along with *Triplosoba.* Handlirsch (1906) correctly removed *scudderi* from *Anthracothremma,* erecting a new genus, *Pseudanthracothremma,* which he placed (1922) in Insecta *incertae sedis.* In the meantime, however, Lameere (1917), during his examination of the Commentry fossils in Paris, had noted the similarity of the specimen of *scudderi* to the type of Meunier's *Diaphanoptera superba* and even considered it a possible synonym of *superba.*

The significance of the specimen is that it shows that *Diaphanoptera* had very long cerci, similar to those subsequently found in other Diaphanopterodea.

Diaphanoptera superba Meunier
Plate 28, C, D; Plate 29

Diaphanoptera superba Meunier, 1908, Ann. Soc. Scient. Brux., 32:155; 1908, Mus. Nat. Hist. Natur., Bull. 14:173; 1909, Ann. Paleont. 4:141, pl. 2, fig. 4; Lameere, 1917, Mus. Nat. Hist. Natur., Bull. 23:148.
Diaphanopterites superbus Handlirsch, 1919, Denkschr. Akad. Wiss. 96:66.

The type and only known specimen of this species consists of a whole specimen, shown in ventral view (counterpart not preserved), the wings resting obliquely along the abdomen. The structure of the thorax and abdomen is only vaguely indicated; cerci, as well as other appendages and the head, are not preserved. The wings, however, are very clearly shown and except for the parts covered by the abdomen the venation can readily be worked out. Convexities and concavities are distinct. No satisfactory drawing of this fossil has been published. Meunier's bears little resemblance to the actual fossil, having subpetiolate wings and complete absence of Sc in the hind wing. Handlirsch's figure, based entirely on Meunier's very small published photograph, is misleading in almost all respects, showing anal lobes on the hind wings. This specimen is the most important of all those known in *Diaphanoptera.* The drawing in the accompanying figure includes only what can clearly be seen of the venation in the fossil, with some restored parts indicated by dotted lines. The specimen shows the basal curvature of Sc and R1, as well as the characteristically radiating arrangement of the costal cross veins. In most respects the venation is close to that of *munieri,* although CuP is less branched in the latter. The wing spots are somewhat different; *superba* lacks the one at the origin of Rs but has an extra one in the area between MP3 and R4 + 5; so far as they are preserved, the spots in the hind wing of *superba* are placed like those of the fore wing. There are no cerci visible in the specimen of *superba.* At the end of the abdomen there is a short projection or extension, which might be part of an ovipositor.

The Order Diaphanopterodea[3]

Handlirsch erected this order in 1919 for the family Diaphanopteridae. He gave two reasons for the ordinal separation of this family

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[3] Handlirsch's spelling of the ordinal name, Diaphanopteroidea, is unsatisfactory since the suffix "oidea" is ordinarily used for subordinal names. I have accordingly followed Rohdendorf's altered version (1962).

from the Megasecoptera, to which he had previously assigned it: first, the resting position of the wings (along the abdomen, as shown in the type of *superba*); and second, the presence of an anal lobe on the hind wing. The latter characteristic does not actually exist in the fossil — Handlirsch simply incorrectly interpreted the photograph of *superba* published by Meunier. But as to the resting position of the wings, there can be no question.[4]

The Order Diaphanopterodea has not generally been accepted by students of fossil insects, the Diaphanopteridae being placed in the Order Megasecoptera, as previously. In recent years, however, several families apparently related to the Diaphanopteridae have been described from Upper Carboniferous strata of the Soviet Union and North America. These fossils, which have in the past been included in the Megasecoptera along with *Diaphanoptera,* furnish evidence which supports the validity of the Order Diaphanopterodea. In 1961, during my visit to the Institute of Paleozoology at Moscow, I discussed the question of the Diaphanopterodea with the staff of the Institute (Drs. Rohdendorf, Martynova, Sharov, and their associates) and learned that they also were convinced of the validity of the Order Diaphanopterodea. In their subsequent publication, Osnovy (1962), the order is treated as consisting of twelve families. However, since this work includes no discussion of the reasons for recognizing the order or of the general question of its relationships, I am presenting here my own views on the order and an account of the puzzling morphological features of the insects in this group.

The following are the families which now appear to belong to the Diaphanopterodea, in addition to Diaphanopteridae:

1. Prochoropteridae Handlirsch, 1911 (emend. Carpenter, 1940) [Upper Carboniferous, North America]. The genus *Prochoroptera* Handlirsch is based on a single specimen showing the wings held over the abdomen, as in *Diaphanoptera,* and indicating vague outlines of the abdomen, which bears what appears to be the basal part of a large ovipositor. It was placed by him in the Megasecoptera in 1911 and again in 1919, although the Order Diaphanopterodea was therein erected for *Diaphanoptera* on the wing position. Haupt (1941) established the Order Palaeohymenoptera for *Prochoroptera* but gave no reasons for connecting the genus with the hymenopterous line of insects; like Handlirsch, he did not associate it with the Diaphanop-

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[4] Handlirsch (1919) treated this difference in wing position as ordinal only and not as indicating a major development in the evolution of insects. Martynov (1923) and Crampton (1924) were the first to propose independently the concept of the Palaeoptera and Neoptera (Archipterygota and Neopterygota of Crampton).

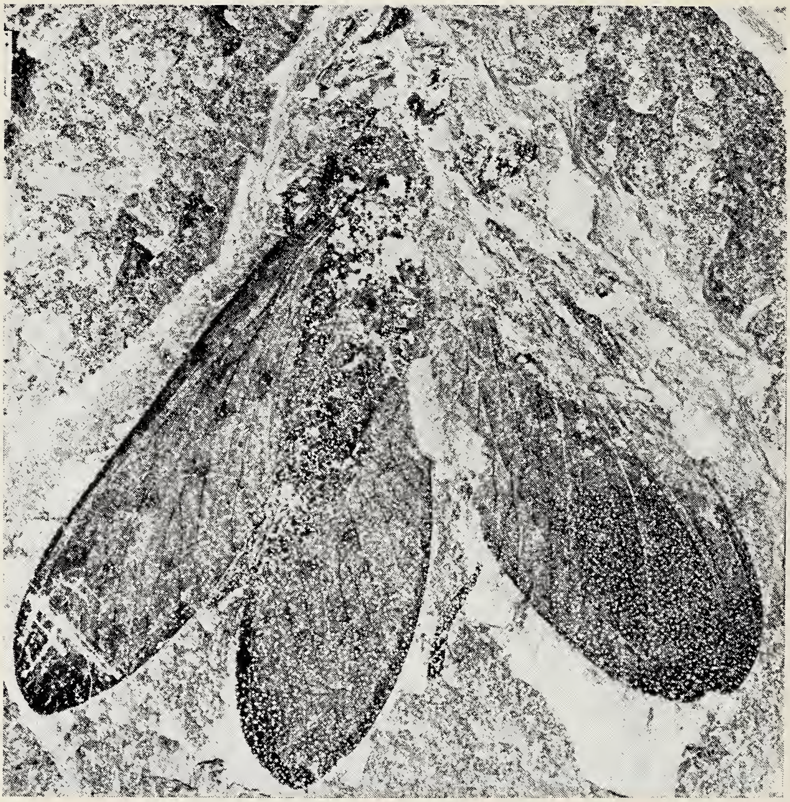
teridae. A second prochopterid, *Euchoroptera* Carpenter from Kansas (Stanton formation), was based on a single, whole specimen, the wings resting along the abdomen; in addition there is clear preservation of a rostrum (details not discernible), a large ovipositor and a pair of very long cerci, about twice the length of the insect's body.

2. Asthenohymenidae Tillyard, 1924 (emend. Carpenter, 1939) [Lower Permian, Kansas]. This was placed by Tillyard, along with the family Protohymenidae, in a new order, the Protohymenoptera, but was later transferred to the Megasecoptera. Additional material from Kansas (Carpenter, 1931, 1939) belonging to both these families showed that although the Protohymenidae were palaeopterous (their wings always being preserved in the outspread position), the asthenohymenids clearly rested with their wings over the abdomen, in an apparently neopterous position. These additional fossils also showed that the asthenomymenids possessed a well developed ovipositor, a pair of very long cerci, and a prominent beak.

3. Martynoviidae Tillyard, 1932 (emend. Carpenter, 1943) [Lower Permian, Kansas, Okla.]. Tillyard placed this family in the sialoid Neuroptera, although he noted some features suggesting the Protohymenoptera. Additional material, including the hind wings, showed that the martynoviids were close to the Prochoropteridae and Asthenohymenidae (Carpenter, 1947). The body structure and the resting position of the wings are unknown.

4. Elmoidae Tillyard, 1937 (emend. Carpenter, 1943, 1947) [Lower Permian, Kansas, Okla.]. This was assigned by Tillyard to the Neuroptera, although he recognized a possible relationship to the Protohymenidae and Asthenomymenidae. Additional genera, belonging to this family (Carpenter, 1947) from Lower Permian beds of Oklahoma, made the relationship to the Asthenohymenidae and Martynoviidae more clear. The body structure of the Elmoidae is unknown, but a whole specimen shows that the wings were held over the abdomen at rest.

Using as a basis the features of the five families considered above, we are able to assign the following characteristics to the members of the Order Diaphanopterodea: Fore and hind wings homonomous or nearly so, the hind wing at most slightly broader than the fore wing, never with an anal lobe; wings held over or along the sides of the abdomen at rest; head with a prominent beak or rostrum, the detailed structure unknown; cerci very long, fully twice the length of the body. The combination of the rostrum, flexed wings, and very long cerci is a unique one and certainly justifies ordinal distinction.



Photograph of *Diaphanoptera superba* Meunier, type specimen (original, × 6), in Laboratoire de Paleontologie, Paris. The fine white spots visible on wings and body are mineral in nature and also occur on much of the rock surface.

Within the order several evolutionary trends are recognizable, of which the following four are the most obvious (see plate 30) : 1. The costal area, starting as moderately broad (Diaphanopteridae, Elmoidae) becomes narrowed distally and eventually very narrow for its entire length (Asthenohymenidae). This change is correlated with the reduction of the subcosta, which clearly terminates on R1 in the Diaphanopteridae but in other families tends to end vaguely in the costal space. The cross veins in the costal space also disappear; in the Diaphanopteridae, Elmoidae, and Martynoviidae, these veins form a definite pattern in the proximal part of the wing, the more basal ones slanting towards the wing base, and the immediate ones following slanting towards the apex. Finally, the membrane between R1 and the costal margin tends to thicken, forming a weak pterostigmal area; this is not visible in the Diaphanopteridae but is in the martynoviids, the prochoropterids, and asthenohymenids. 2. The anastomosis of MA and Rs increases greatly. In the Elmoidae the anastomosis between these veins has not even started, but in the Diaphanopteridae it has clearly begun, and the Martynoviidae show a progressive increase which eventually leads to the near loss of the basal part of MA *(Phaneroneura)* and the ultimate loss in the Asthenohymenidae. 3. The stems of R, M and CuA have become coalesced in the more specialized members of the order. In even the most generalized of these families, the base of CuA has anastomosed with the stem of M, but this compound stem is free from the stem of R (Diaphanopteridae, Elmoidae) ; in the Martynoviidae and Asthenohymenidae, these two stems have fused. In the process of this change, a definite pattern of separation of R, M, and CuA has taken place, this pattern being already discernible in the Diaphanopteridae: R diverges anteriorly from CuA, the angle between them being bisected by the stem of M. This arrangement finally disappears with the loss of the stem of M. It is interesting to note that the basal parts of Sc, R, and M + CuA are arched in all but the most reduced families, this curvature beginning in the Diaphanopteridae and reaching its maximum development in the Martynoviidae and Asthenohymenidae.

In addition to the families mentioned above, several others, previously assigned to the suborder Paramegasecoptera of the Order Megasecoptera,[5] may also belong to the Diaphanopterodea. These are Parabrodiidae and Raphidiopsidae, from the Upper Carboniferous of the United States; and Kulojidae and Biarmohymenidae from Permian

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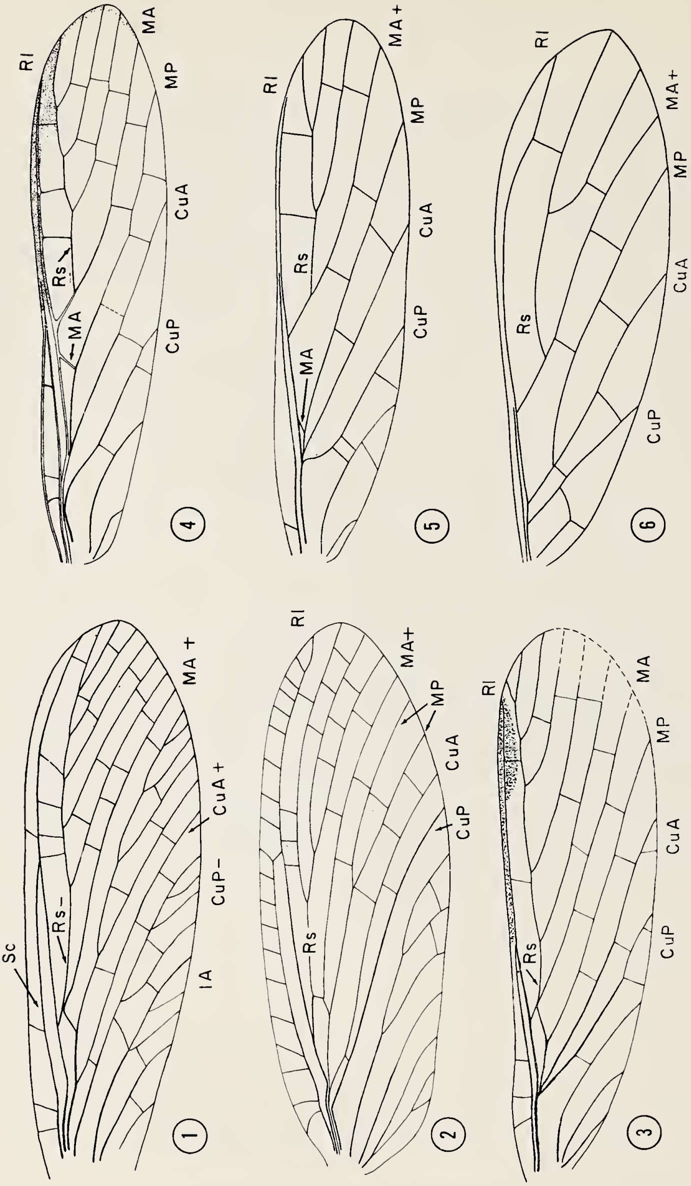
[5] The suborder Paramegasecoptera Carpenter was established (1954) for those Megasecoptera which rested with their wings held back over or along the abdomen.



Carpenter — Diaphanopterodea

beds in the Soviet Union. At present not enough is known about the structure of the members of these families to permit more definite assignment. The Permian family Kaltanelmoidae (Soviet Union), placed in the Diaphanopterodea by Rohdendorf (1962), is so little known and its known structure so peculiar that I doubt that it has affinites with the Diaphanopterodea. The Carboniferous family Sypharopteridae (United States), which is also placed in the Diaphanopterodea by Rohdendorf, definitely belongs to another section of the Insecta. Among its other peculiarities is the complete absence of MA, which occurs as a prominent convex vein in the Diaphanopterodea.

Relationships of the Diaphanopterodea

In my account of the Megasecoptera of the Wellington formation in Oklahoma (1947), I discussed in some detail the question of the possible relationships of this order, and in particular of those families in the diaphanopterid-asthenohymenid group. Much of what was presented there now pertains to the relationships of the Diaphanopterodea. However, two questions now arise in a different form. *First,* there is the question of the relationship between the Diaphanopterodea and the Megasecoptera (s.s.). Tillyard (1936) found it impossible to conceive of the separation of the Asthenohymenidae from the Protohymenoptera on an ordinal level. However, the evidence now strongly indicates that the similarities between these two families are entirely a matter of convergence. The coalescence of MA with Rs and of the stem of CuA with M is certainly in this category: a similar coalescence occurs in several unrelated orders of insects and a great many families within them. What is more important is the distinctive evolutionary trend within the Megasecoptera. The tendency for petiolation of the wings, for extreme and uniform narrowing of the costal space, the loss of costal cross veins, persistence of setae on the costal margin, the straightness of the stems of Sc, R, and CuA + M — all of these represent significant trends in the Megasecoptera not present in

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EXPLANATION OF PLATE 30
FOREWINGS OF DIAPHANOPTERODEA
(original drawings)

1. *Diaphanoptera munieri* Brongniart, U. Carb., France.
2. *Parelmoa revelata* Carpenter, L. Perm., Okla.
3. *Martynovia insignis* Tillyard, L. Perm., Kans.
4. *Eumartynovia raaschi* Carpenter, L. Perm., Okla.
5. *Phaneroneura martynovae* Carpenter, L. Perm., Okla.
6. *Asthenohymen apicalis* Carpenter, L. Perm., Okla.

the Diaphanopterodea. These, added to the difference in the resting position of the wings, require, in my opinion, ordinal separation.

Second, there is the more fundamental question of whether the *Diaphanopterodea* belong to the Neoptera or Palaeoptera, which for the purpose of this discussion are being regarded as monophyletic groups. Unfortunately, we do not know, and probably never will know, whether or not the mechanism of wing flexing in the Diaphanopterodea is the same as that in the Neoptera. One possibility, therefore, is that the Diaphanopterodea are true Neoptera. In this case, because of the long cerci and complete venation (including convex MA), they should be primitive members of the Neoptera — more primitive, in fact, than any other known order in the series (Protorthoptera, Perlaria, etc.). The difficulty with this theory is the presence of a definite rostrum in the Diaphanopterodea. It is hardly conceivable that the mandibulate trophi of the primitive Neoptera (Perlaria, etc.) were derived from such a specialized type. If the Diaphanopterodea were to be regarded as Neoptera, it would be necessary to assume that they were a specialized derivative of even more generalized Neoptera having mandibulate trophi.

A much more appealing view is that the Diaphanopterodea are direct derivatives of the Palaeodictyoptera and that they developed the wing flexing mechanism independently of the true Neoptera. The venation of the Diaphanopteridae could readily be derived from that of the Palaeodictyoptera and what is more important, the rostrum of the Diaphanopterodea is like that of the Palaeodictyoptera. Actually, the rostrum of *Stenodictya* (Laurentiaux, 1952), which I was able to study in Paris in 1963, is remarkably similar to that of the Asthenohymenidae.

Until evidence to the contrary is found, therefore, my view of the Diaphanopterodea is that they are phylogenetically members of the Palaeoptera which have developed a type of wing flexing independently of that of the true Neoptera; and that their closest relatives are the Palaeodictyoptera, from which they were probably directly derived.

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

The illustration on the front cover of this issue of Psyche is a reproduction of a drawing by Professor C. T. Brues of a myrmecophilous phorid fly, *Ecitomyia spinosa* Brues (Psyche, vol. 32, 1925, p. 306).

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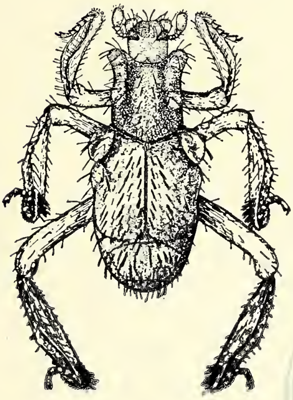

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CHEMICAL RELEASERS OF SOCIAL BEHAVIOR. II. SOURCE AND SPECIFICITY OF THE ODOR TRAIL SUBSTANCES IN FOUR ATTINE GENERA. (HYMENOPTERA: FORMICIDAE).[1]

By Murray S. Blum[2], John C. Moser[3], and A. D. Cordero[4]

The higher members of the tribe Attini characteristically lay persistent and extensive odor trails especially in many neotropical areas. Thus, in *Acromyrmex* and *Atta,* long columns of foraging workers are frequently present on the odor trails but in the less specialized attine genera, workers may forage either in files or singly. Weber (1958) has indicated that the workers in monomorphic genera forage singly, a behavioral characteristic which he offers as evidence for the primitive position of these attine genera.

Species in the genus *Trachymyrmex* appear to be intermediate, since they forage either singly or in columns. This, Weber concludes, indicates a transition to the well developed odor trails of the higher attines.

Since the Attini constitute a tribe of closely related genera which exhibit varying degrees of development of trail laying behavior, they are admirably suited for studies of odor trail laying.

The rôle of odor trail laying in the social biology of ants has been demonstrated clearly by Wilson (1962) using an artificial trail technique. Previous investigations had demonstrated that the trail substances of the myrmicine *Solenopsis saevissima* (Fr. Smith) (Wilson, 1959) and several Dolichoderinae (Wilson and Pavan, 1959) originated as glandular secretions. Employing similar techniques, Moser and Blum (1963) demonstrated that the odor trail substance of one attine, *Atta texana* (Buckley), was a product of the poison glands.

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[1] Based on research supported in part by U. S. National Science Foundation Grant No. G22074.

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It has now been possible to examine the glandular sources of the odor trail substances in four genera of the Attini and to determine their cross-specificities. The results of these studies are the subject of this paper.

TEST SPECIES

Based on morphology, behavior, and nest structure, Weber (1958) concludes that *Cyphomyrmex rimosus* (Spinola) is the most primitive of the attines. This species was selected as an ideal representative of the less specialized attine genera. Odor trail laying has not been noted in *C. rimosus*, which has been reported to forage singly. However, our own observations of the foraging behavior of workers from two colonies of this attine strongly indicate that this species lays odor trails. Both of the observed colonies were located in sandy soil at the base of trees (*Pinus* spp.) in Desoto National Forest near Gulfport, Mississippi. Each worker that emerged from the inconspicuous nest entrances moved slowly over the bark of the trees and made the same twists and turns as the workers that had preceded it. In two instances, pairs of workers emerged from the nest and moved with such complete synchrony that it seems very likely that odor trails were being followed.

The other attines examined were *Trachymyrmex septentrionalis* (McCook)[5], *Acromyrmex octospinosus* (Reich)[6], and *Atta cephalotes* (Linnaeus)[6]. In addition, odor trail species specificity studies were undertaken employing *Atta texana*[7].

SOURCE OF TRAIL SUBSTANCES

The sources of the odor trail substances were determined by using either a modification of the artificial trail technique of Wilson (1959) or the method of Moser and Blum (1963). For all species examined, preliminary experiments indicated that the odor trail substances originated in the abdomen. Three organs in the abdomen, the hind gut, the paired poison glands and Dufour's gland, are known to secrete their contents into the external environment. These organs were dissected out of workers, washed in saline, and applied as smears on 75 cm. sinusoidal trails drawn on pieces of 8½" x 11" paper.

The trail-treated papers were placed either on glass platforms adjacent to laboratory colonies or in metal trays. Groups of 10 ants from laboratory colonies were placed on the treated papers and a response was considered positive when a worker followed the trail to its

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[5] Collected at Baton Rouge, Louisiana.
[6] Collected at Alajuela, Costa Rica.
[7] Collected at Forest Hill, Louisiana.
[8] Collected at Barro Colorado, Canal Zone.

Table 1. Response of attine workers to artificial trails prepared from three abdominal glands.

		No. of Positive Responses *(Total Workers Responding in Parentheses)*		
Species	No. of Tests[9]	Hind Gut	Poison Gland (Plus Vesicle)	Dufour's Gland
Cyphomyrmex rimosus	8	0	8(69)	0
Trachymyrmex septentrionalis	10	1(3)	10(83)	0
Acromyrmex octospinosus	10	0	10(78)	0
Atta cephalotes	10	2(7)	10(90)	0

end after crossing it during a three minute observation period. Although the major workers of *Atta texana* are too excitable to be employed in the artificial trail test (Moser and Blum, 1963), the medium workers of *Acromyrmex octospinosus* and *Atta cephalotes* were found to be much more suitable than their minor workers for these tests. The results of these experiments are presented in table 1.

The poison glands are clearly the source of the odor trail substances in all four attine species. Ants frequently followed the artificial odor trails during the entire course of the observation period. When workers had run the entire length of the trail they would invariably overshoot and, often after milling around, they would encounter the artificial trail again and resume trail following.

SPECIES-SPECIFICITY OF THE ODOR TRAIL SUBSTANCES

Cross-species tests with artificial odor trails were made with the four attine species principally employing the circular trail technique of Moser and Blum (1963). Poison glands (and vesicle) were dissected out of freshly-killed or frozen workers and after rinsing in saline were crushed in 0.5-1.0 ml. of methylene chloride. Aliquots of 0.1-0.2 ml. of the methylene chloride solution of the poison gland contents were then applied with a pipette to a circle 6″ in diameter and the solvent was allowed to evaporate. Subsequently, 10 ants were introduced into the middle of the circle and the numbers of ants which, after encountering the circle, followed the circular trail for at least half its length were recorded.

As the data in table 2 demonstrate, the odor trail substances in the attine genera are not generic or species-specific. Although the artificial trails prepared from extracts of the poison glands of *Atta* and

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[9] Ten workers per replication.

Table 2. Numbers of workers responding to the poison gland secretion in the artificial test. Number of replications in parentheses.[9]

	Test Species				
	Cyphomyrmex rimosus	*Trachymyrmex septentrionalis*	*Acromyrmex octospinosus*	*Atta cephalotes*	*Atta texana*
Source Species					
Cyphomyrmex rimosus	74(8)	70(8)	—	—	56(8)
Trachymyrmex septentrionalis	52(6)	64(7)	30(4)	26(4)	66(8)
Acromyrmex octospinosus	—	48(6)	69(8)	31(4)	27(4)
Atta cephalotes	—	16(2)	77(10)	87(10)	50(6)
Atta texana	63(8)	54(6)	34(4)	—	33(4)

Acromyrmex sometimes produced a greater trail following response among all four genera than those obtained with *Trachymyrmex* and *Cyphomyrmex* extracts, no definite conclusions can be drawn from these results. The glands dissected out of *Atta* and *Acromyrmex* workers were generally larger than those obtained from the other two genera and conceivably they contained more odor trail substance. Even if all of the poison glands from all four genera were the same size, there would be no way of determining whether they all contained equal concentrations of the trail substances. Reliable quantitative experiments on the cross-generic activities of the attine odor trail substances must await isolation and identification of the pure pheromone(s).

The odor trail substances of the attines did not release trail following behavior in any non-attine species which were examined. Thus, no response was obtained with the odor trail laying ponerine *Termitopone laevigata* (Fr. Smith)[8], the dorylines *Eciton burchelli* (Westwood)[7] and *E. hamatum* Forel.[7], the myrmicines *Crematogaster lineolata* (Say)[5], *Monomorium minimum* (Buckley)[5], and *Solenopsis saevissima* (Fr. Smith)[5] or the dolichoderines *Conomyrma pyramica* (Roger)[5] and *Iridomyrmex pruinosus* (Roger)[5].

DISCUSSION AND CONCLUSIONS

Based on external morphological features, the genera of the tribe Attini have the most easily recognized phylogenetic relationships of any of the myrmicine tribes (Creighton, 1950). Thus *Trachymyrmex* can be shown to grade into *Atta* and into the genus *Cyphomyrmex* through the transitional genus *Mycetosoritis*. The interrelationships of the attine genera are further supported by ethological evidence which largely parallels the morphological conclusions (Weber, 1958).

Based on an examination of the glands associated with the sting in the attine genera *Cyphomyrmex, Trachymyrmex, Acromyrmex,* and *Atta,* it appears that at least some internal morphological characters may be quite similar throughout the tribe. In *Cyphomyrmex rimosus,* the most primitive of the attines, (Weber, 1958), the paired free arms of the poison gland are rather blunt structures which are enclosed in a large bulbous vesicle. The vesicle rapidly narrows down to an extremely fine duct which is attached to a very reduced sting. Dufour's gland is inserted near the base of the sting and is considerably smaller than the poison glands. Notwithstanding differences in size, the form and relative proportions of the poison and Dufour's glands in *Trachymyrmex, Acromyrmex,* and *Atta* are virtually identical to those of *Cyphomyrmex.* Indeed the sting-associated glands of a minor worker of *Atta cephalotes* are a veritable carbon copy of those found in a *Cyphomyrmex* worker. It thus appears that the gross morphology of the poison apparatus of workers in the most primitive attine *Cyphomyrmex,* has undergone little change during the evolution of this tribe. The gross form of the glands associated with the reduced sting form a distinctive attine structure which may be an excellent diagnostic character for this tribe.

The lack of generic specificity of the odor trail substances of the four attines must be regarded as further evidence for the close relationship of the attine genera. In spite of the fact that *Cyphomyrmex* and *Atta* stand at the phylogenetic extremes of the tribe Attini, the odor trail substance of *Cyphomyrmex* is capable of releasing trail following behavior in *Atta* and vice versa. It is interesting to contrast the lack of generic specificity in the attine odor trail substances with the great specificity of the odor trail substances in the myrmicine genus *Solenopsis.* In transposition experiments with species of *Solenopsis,* Wilson (1962) demonstrated the odor trail substances of three members of this genus were highly species-specific. In addition, the *Solenopsis* trail substances produced no trail following in four other myrmicine genera. Similarly, the odor trail substances of the Attini do not produce any response in any of the myrmicine genera that we tested. One possible explanation that is consistent with the lack of specificity of the trail substances among the attines is that the odor trail chemicals are identical or closely related in the different genera. If this is correct, then the biogenetic pathway for the synthesis of the odor trail compound(s) in *Cyphomyrmex* has been utilized by the more highly developed attine genera with little modification. It is thus possible that the Attini are closely linked by the natural products chemistry of their poison glands.

Since workers of the different attine genera follow each others' artificial trails in the laboratory, the question arises as to whether this occurs in the field. The tribe Attini is limited to the New World where most of the genera are sympatric. Weber (1958) has emphasized the fact that the attines are tolerant of one another as indicated by the fact that different genera forage beside one another, without any hostility. Furthermore, Weber notes that nests of genera such as *Cyphomyrmex* and *Trachymyrmex* are commonly found in the soil of the *Atta* mounds. These facts certainly emphasize the probability that under field conditions, the odor trails of different attine genera can frequently overlap. Indeed, strong trails of *Atta cephalotes* and *Acromyrmex octospinosus* crossed in at least two different places in a field that we observed at Alajuela, Costa Rica. In no instance were workers of either species observed to violate the other species' trail. When *Acromyrmex* workers were placed on the *Atta* trail, they invariably wandered off the trail almost at once and resumed trail following on their own trail when it was encountered. It does not seem unlikely that the persistent trails which attines follow over long periods contain secretions other than their odor trail substances which may render them more specific. Likely sources of trail additives are anal emissions which should present a considerable accumulation on a trail which is being utilized for extended periods. It is interesting to note that the odor trail of the formicine *Lasius fulginosus* (Latreille) is derived from an anal emission (Carthy, 1951). Whether attine odor trails maintain their specific identities among the tribal members because of supplemental secretions remains to be proven. However, in view of the non-specificity of the demonstrated odor trail substances among the Attini, it seems necessary to propose that additional chemical stimuli are present on the trails.

Nothing is known about the chemical nature of the attine odor trail substances. Preliminary examinations of the contents of the poison vesicles of the four attine genera indicate that all the secretions have similar physical properties. The vesicle contents are viscous, water-clear liquids which produce a strongly alkaline reaction with various indicator papers. When the poison vesicle is ruptured, its liquid contents immediately are converted into a semisolid mass. This latter property of the poison gland contents is certainly consistent with what is known about the general nature of the attine odor trail substances especially among the more highly developed genera. The persistent trails of *Atta* certainly reflect the presence of an odor trail substance(s) with a low vapor pressure. Assuming that the sting secreted odor trail substance similarly solidifies under field conditions, then the deposited compounds could be expected to be quite nonvolatile. That this is the case is indicated by the fact that artificial trails prepared from the poison glands (and vesicle) of *Trachymyrmex* were highly active when tested three weeks after their preparation. Furthermore, when poison glands of *Atta cephalotes* were crushed on microscope slides, the semisolidified secretion retained its original appearance for 28 days at room temperature (approximately 28°C.) and released strong trail following behavior in *Trachymyrmex* when artificial trails were prepared from chloroform extracts.

SUMMARY

In *Cyphomyrmex rimosus* (Spinola), *Trachymyrmex septentrionalis* (McCook), *Acromyrmex octospinosus* (Reich) and *Atta cephalotes* (Linnaeus), four attine genera representing the broad phylogenetic development of the tribe Attini, odor trail substances originate in the poison glands. These substances, when cross genera tested, were found to be non-generic specific. This fact is interpreted as further evidence for the close relationship of the attine genera.

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REMARKS ON *SCELIOTRACHELUS* BRUES AND ALLIED GENERA (HYMENOPTERA, PLATYGASTERIDAE)*

By Lubomír Masner
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In 1908 Brues (in Wytsman, Genera Insectorum) described a peculiar new genus *Sceliotrachelus* Brues from South Africa. At the same time he erected the new subfamily Sceliotrachelinae to comprise the single genus *Sceliotrachelus* Brues. Having some doubts on the phylogenetic relationships of this curious genus (and subfamily as well) Brues decided to place it in Scelionidae between the subfamilies Telenominae and Baeinae. He says: "The species upon which this genus is based is without doubt one of the most remarkable insects which I have ever seen. For some time I was undecided to what family it could be referred, but after much thought, I believe that it shows the greatest affinity to certain Telenominae or Teleasinae, although the relationship is by no means close. The large pronotum and the small mesoscutum are unique in this and related families, but the form and insertion of the antennae, and the configuration of the abdomen undoubtedly denote relationship to either the Ceraphronidae, Scelionidae or Platygasteridae". Brues established his new subfamily first of all on the large pronotum and on the morphology of the wings. Kieffer (1926) did not recognize the subfamily Sceliotrachelinae and included *Sceliotrachelus* Brues among the Platygasterinae (tribe Platygasterini). Contrary to Brues (1908) he emphasized that the shape of the scutellum in *Sceliotrachelus* Brues exhibits a close relationship with Chalcididae (!) rather than with families mentioned by Brues. So far as known to the author there is no study referring to this problem except for the two mentioned above.

The description (and the figure as well) does not give a clear idea of the relationships of the genus. We have had the opportunity of examining the male paratype of *Sceliotrachelus braunsi* Brues. Unfortunately, we cannot agree with either Brues or Kieffer regarding the position of this genus. After examining the paratype we have no doubt that *Sceliotrachelus* Brues belongs to the family Platygasteridae. There is no evidence of relationship either with the Scelionidae or even the Ceraphronidae. Kieffer's (1926) conjecture on the rela-

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tionship or similarity with the Chalcididae is evidently wrong. It is doubtful if Kieffer actually saw any specimens.

In 1959 Szabó established a new tribe within the Platygasteridae, the Amitini, to comprise the following genera: *Amitus* Hald., *Fidiobia* Ashm., *Pulchrisolia* Szabó and *Isolia* Förster. The genus *Sceliotrachelus* Brues exhibits a striking relationship with some of these genera (particularly with *Isolia* Förster.) so we are sure it should belong there. From the nomenclatorial point of view we are forced to change the name of the tribe as follows:

Sceliotrachelini Brues, 1908 — NEW STATUS
(= Amitini Szabó, 1959 — NEW SYNONYMY)

As Sceliotrachelini Brues was proposed originally as a subfamily of Scelionidae in 1908 it becomes automatically the new name of the group. The type genus is consequently *Sceliotrachelus* Brues.

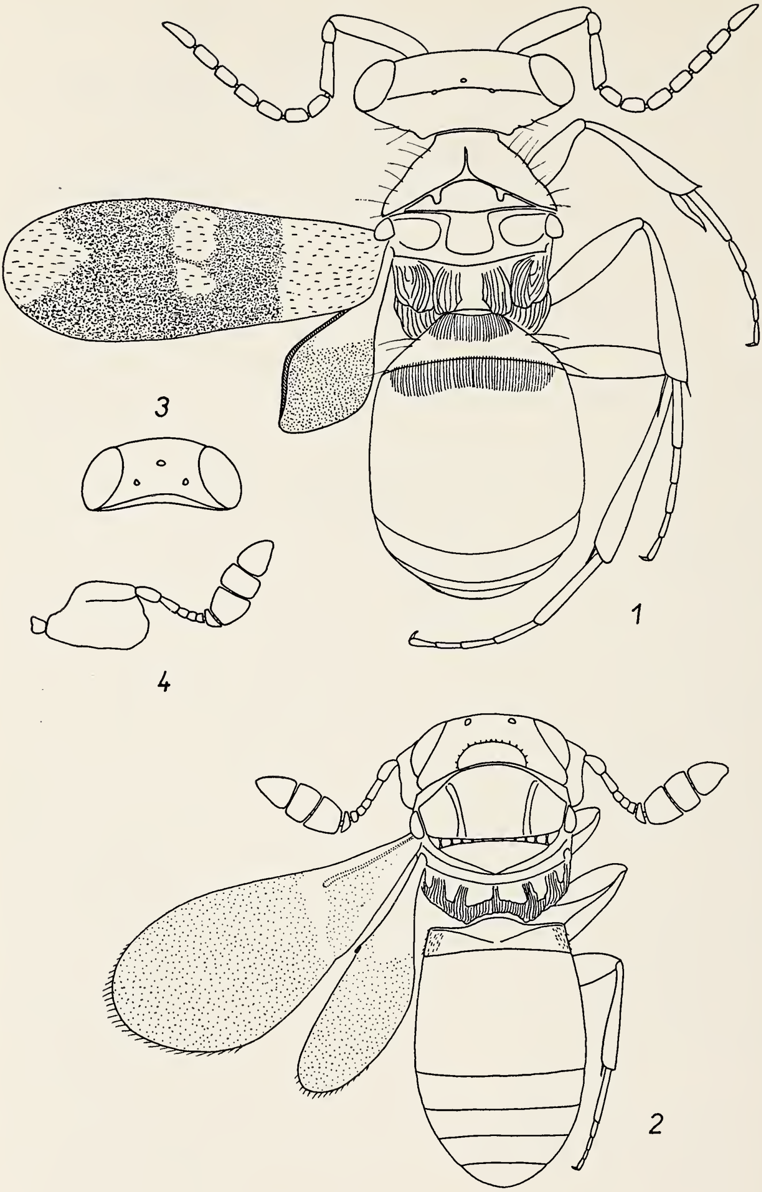
The tribe Sceliotrachelini, according to our conception, should belong to the subfamily Inostemminae. We suggest it to be the most apomorphous tribe of Inostemminae, where the subcostal vein is tending to disappear gradually. In *Fidiobia* Ashm. (in all species we have seen, except in brachypterous *F. pronotata* Szabó) there is a very short subcostal vein, knobbed apically. In *Platygastoides* Dodd, at least in P. *mirabilis* (the type of genus) the subcostal vein is still knobbed apically, but as a whole, the vein is tending to disappear (Fig. 2). In *Amitus* Hald. (= Zacrita Förster., *Passalida* Brèth.) there is sometimes a trace of vein but this is never knobbed apically. In *Isolia* Förster. and *Sceliotrachelus* Brues the fore wing is perfectly veinless. The typical character of Sceliotrachelini is the antennal club in the female, which is abrupt, massive and 3-jointed (in *Amitus* Hald. the club is rather solid, the sutures obsolete). The gaster in this tribe is very stout, resembling that of the subfamily Telenominae (Scelionidae), not carinated ventrally (there is no impressed submarginal ridge) at most slightly sharpened at sides.

The curious *Platygastoides* Dodd is included also in this tribe. It combines some characters of *Fidiobia* Ashm. and *Isolia* Förster. Figures 2, 3 and 4 illustrate this peculiar insect.

Genus *Sceliotrachelus* Brues

Sceliotrachelus Brues, 1908, in Wytsman, Genera Insectorum, 80:13.
Pulchrisolia Szabó, 1959, Ann. Hist. — Nat. Mus. Nat. Hung., 51:395 — NEW SYNONYMY.

The male paratype of *Sceliotrachelus braunsi* Brues was examined. Labels: "Algoa bay Capland, 11.10.96; *Sceliotrachelus braunsi* Brues, Paratype". Right wing and some legs torn off.



Masner — Sceliotrachelus

The description should be completed and corrected. There are no "tufts of long yellow hairs" on the propodeum which Brues compares with those of some myrmecophilous beetles (e.g. *Lomechusa* Gr.). There is a compact hyaline membrane, just as in *Isolia* Först., *Fidiobia* Ashm. and *Platygastoides* Dodd. Consequently, there is no reason to suggest that *Sceliotrachelus* Brues is a myrmecophilous insect. The long dense hairs are found on the base of first as well as second tergite of the gaster.

The figure in Brues (1908) is, as a whole, not very exact and therefore we prefer to give a detailed drawing of the insect here (Fig. 1).

Pulchrisolia Szabó becomes inevitably a synonym of *Sceliotrachelus* Brues. The holotype of *Pulchrisolia maculata* Szabó (a female from Shirati, East Africa) was examined and found to belong to *Sceliotrachelus* Brues. So far no more material is available. We prefer to keep both — *braunsi* Brues and *maculatus* Szabó — as independent species. The necessary nomenclatorial formality is as follows — *Sceliotrachelus maculatus* (Szabó, 1959) — **new combination** (= *Pulchrisolia maculata* Szabó, 1959).

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EXPLANATION OF PLATE 1

Fig. 1. *Sceliotrachelus braunsi* Brues, male paratype. Fig. 2. *Platygastoides mirabilis* Dodd, female. Fig. 3. *Platygastoides mirabilis* Dodd, female, head, Fig. 4. *Platygastoides mirabilis* Dodd, female, antenna.

NORTH AMERICAN WIDOW SPIDERS OF THE *LATRODECTUS CURACAVIENSIS* GROUP (ARANEAE: THERIDIIDAE)

By John D. McCrone[1] and Herbert W. Levi[2]

Our taxonomic knowledge on widow spiders was summarized in a previous study of *Latrodectus* (Levi, 1959). However, at the time it was known that there were several areas of difficulty: the Near East, where several species with similar genitalia occur; and northern Argentina, where one or two additional species are found (Abalos, 1962). Field and laboratory work in Curaçao, Lesser Antilles, and in Florida, as well as additional specimens, have provided many more data on the species called *L. curacaviensis* in the previous paper.

We wish to thank Drs. B. de Jong of Curaçao and Dr. I. Kristensen of the Caribbean Marine Biological Institute, Curaçao, for their hospitality and help in the field work on the island. We are also grateful to Dr. P. Wagenaar Hummelink, Dr. L. van der Hammen and Mr. P. J. van Helsdingen of the Natural History Museum, Leiden, for specimens collected in the Netherlands Antilles. Dr. A. R. Brady photographed the Abbot manuscript with the help of the staff of the British Museum (Natural History), Mr. J. Beatty provided specimens from Florida, and Mr. P. Dell gave technical assistance.

This investigation was supported in part by Public Health Service Research Grant AI-01944 from the National Institute of Allergy and Infectious Diseases and Public Health Service Research Grant GM 11206-01 from the National Institute of General Medical Sciences.

Descriptions and Nomenclature

The specimens considered to be *L. curacaviensis* in the previous paper belong to several species. Only females from the type locality of *L. curacaviensis* were examined; males are unknown from the type locality, and the species seems to have disappeared from the island of Curaçao. The specimens examined were collected by Hasselt over one-hundred years ago (Hasselt, 1860, 1887). The specimens considered to be *curacaviensis* from Argentina (Levi, 1959) also appear to belong to two or more species. The oldest name for the additional

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species is probably one given by Nicolet (1849), who named several *Latrodectus* from Chile.

Latrodectus curacaviensis (Müller)
Figures 1, 16, 17

Aranea curacaviensis Müller, 1776, p. 242. Female type from Curaçao, Netherland Antilles, lost.
Latrodectus curacaviensis, — Levi, 1959, p. 38 (in part).

Description of female specimen from Curaçao: Carapace light yellow-brown, slightly darker in thoracic depression and around margin. Sternum darker yellow-brown with a narrow median longitudinal lighter mark. Legs light yellow-brown; patellae, distal ends of femora, and tibiae slightly darker. Abdomen black with white marks (Fig. 16, 17) that are lighter around the edge than centrally, and presumably were red in the live animal. Carapace comparatively long. Total length 6.5 mm. Carapace 2.6 mm long, 1.4 mm wide. First femur 3.8 mm. Patella and tibia 4.2 mm, metatarsus 3.8 mm, tarsus 1.3 mm. Second patella and tibia 2.7 mm, third 1.9 mm, fourth 4.0 mm.

Latrodectus variolus Walckenaer (Northern Widow)
Figures 3, 8-13, 27

Latrodectus variolus Walckenaer, 1837, p. 648. Female lectotype here designated: Abbot manuscript figure 391, manuscript in the British Museum (Natural History) library.
Latrodectus curacaviensis, — Levi, 1959, p. 38 (in part; not *L. curacaviensis* Muller)

Note: Abbot manuscript figure 391 was chosen lectotype because Abbot described two ventral transverse bars on the specimen, a characteristic of the species (Fig. 27) that distinguishes it from *L. mactans,* which has an hour glass (Fig. 26). It presumably came from the Beaver Dam Creek area, Screven County, near where Abbot lived in the 1790's, in a part that used to be Burke County.

The comments to Abbot's figures are (in original spelling):

"191 Aranea Taken 28th May in the Oak Woods. very rare [♀]

194 Aranea Taken 15th May on Oak, in Oak Woods. Rare [juv. ♀]

195 Aranea Taken 23 Feb. under a Stone. It has a large angulated red spot beneath the Abdomen. It makes an irregular Web, under old Logs and Rails, not very common.

The bite of the Species of spider is accounted very poisonous [♀]

391 Aranea Taken 5th April on a small Pine Bush in the Oak Woods of Burke County. Beneath the abdomen is black with two transverse red Bars, Rare [juv. ♂]

396 Aranea Taken 30th June in a Dirt daubers Nest. very Rare [juv. ♂]"

Walckenaer's names for Abbot's figures and their probable disposition are:

Fig. 191 *Latrodectus formidabilis* Walckenaer, 1838, p. 647 [= *L. variolus*]; Fig. 194 *Latrodectus variolus* Walckenaer, 1838, p. 648; Fig. 195 *Latrodectus perfidus* Walckenaer, 1838, p. 647 [= *L. mactans*]; Fig. 391 *Latrodectus variolus* Walckenaer, 1838, p. 648; Fig. 396 *Latrodectus variolus* Walckenaer, 1838, p. 648.

Description of female from Torreya State Park, Liberty County, Florida: Carapace brownish black. Sternum, legs, abdomen, black. Dorsum often with a median longitudinal row of red spots. Venter with two transverse red bars (Fig. 27). Total length 11 mm. Carapace 4.2 mm long, 3.8 mm wide. First femur, 8.0 mm; patella and tibia, 9.8 mm; metatarsus, 8.3 mm; tarsus, 2.5 mm. Second patella and tibia, 5.0 mm; third, 4.2 mm; fourth, 7.3 mm.

Male from Torreya State Park: Carapace brown. Sternum dark brown. Legs: coxae dark brown; proximal portion of first femora, brown; patellae brown; other parts orange, except brown at distal ends of tibiae. Abdomen black, dorsum variable with two to three red spots in a median longitudinal line; sometimes orange lines going down sides from spots, and a line above spinnerets. Venter with two red transverse bars. Total length 6.7 mm. Carapace 2.7 mm long, 2.1 mm wide. First femur, 6.5 mm; patella and tibia, 7.6 mm; metatarsus, 7.3 mm; tarsus, 2.1 mm. Second patella and tibia, 4.2 mm; third, 2.7 mm; fourth, 5.9 mm.

Female from Dover, Massachusetts: Color as in Florida female. Abdominal dorsum with a median row of three to four spots above spinnerets. Lines on sides of spots. Venter with two transverse marks that, like the spots, were probably red in the live animal. Total length 9.2 mm. Carapace 3.2 mm long, 3.4 mm wide. First femur, 5.9 mm; patella and tibia, 6.0 mm; metatarsus, 5.5 mm; tarsus, 1.8 mm. Second patella and tibia, 3.9 mm; third, 2.6 mm; fourth, 5.2 mm.

Male from Vermont: Carapace, sternum and legs, brown. Abdomen black with four dorsal spots in a longitudinal median row and some spots on sides. Venter with two transverse marks probably red in live animal. Total length 6.5 mm. Carapace 2.9 mm long, 2.6 mm wide. First femur, 6.7 mm; patella and tibia, 6.9 mm; metatarsus, 7.0 mm; tarsus, 2.0 mm. Second patella and tibia, 4.2 mm; third, 3.0 mm; fourth, 5.6 mm.

Distribution. Southern Canada, United States, northern Florida, Texas to central California (records of *L. curacaviensis,* — Levi, 1958 except those of central and southern Florida).

Latrodectus bishopi Kaston (Red Widow)
Figures 2, 4-7, 21-22

Latrodectus mactans var. *bishopi* Kaston, 1938, p. 60. Male holotype from Lake Worth, Florida, in the American Museum of Natural History, examined.

Latrodectus curacaviensis, — Levi, 1959, p. 38 (in part, central and southern Florida records, not *L. curacaviensis* Müller).

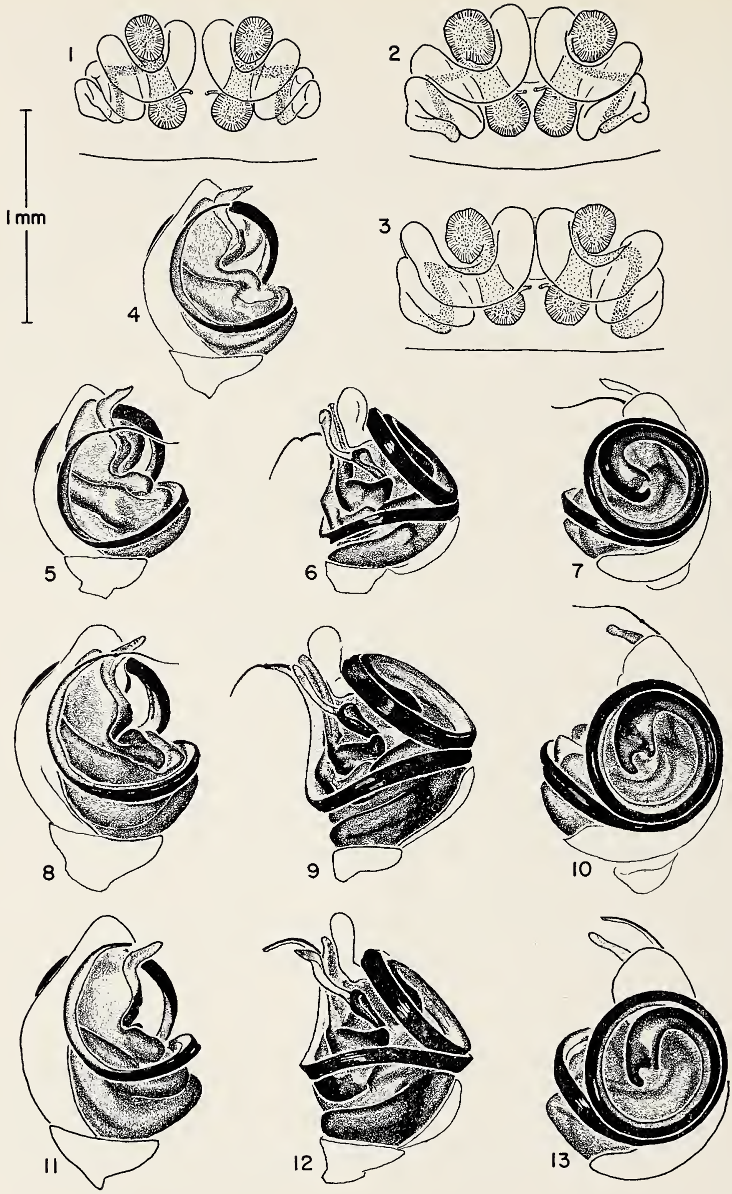
Description. Specimens from 18 km (11 mi.) south of Lake Placid, Highlands Co., Florida: Female. Carapace orange with dark rings around eyes. Sternum, legs orange. Abdomen black without any marks, or with median red dorsal spots, or red spots surrounded by a yellow border. Total length 8.5 mm. Carapace 3.4 mm long, 2.5 mm wide. First femur, 6.9 mm; patella and tibia, 6.9 mm; metatarsus, 6.8 mm; tarsus, 2.3 mm. Second patella and tibia, 4.2 mm; third, 2.9 mm; fourth, 5.5 mm.

Male: Carapace, sternum, legs, orange. Abdomen black, with a variable number of spots. Usually two to three median dorsal red spots in a longitudinal line and some light marks on the side. Line above spinnerets absent and venter black or with spots. Total length 4.2 mm. Carapace 2.1 mm long, 1.7 mm wide. First femur, 5.5 mm; patella and tibia, 5.9 mm; metatarsus, 5.9 mm; tarsus, 1.4 mm. Second patella and tibia, 3.5 mm; third, 2.2 mm; fourth, 4.4 mm.

Distribution. Central and southern Florida, in sand-pine scrub. (Central and southern Florida records of *L. curacaviensis,* — Levi, 1959).

Diagnosis

Latrodectus curacaviensis, L. variolus and *L. bishopi* differ from *L. mactans* by their genitalic structure: *L. mactans* has one more loop in the embolus of the palpus and one more loop in the connecting ducts of the internal female genitalia. All specimens of *L. mactans* from the eastern and southern United States have an hour-glass mark on the venter (Fig. 26) with the exception of some from southern Texas and Mexico. *Latrodectus variolus* usually has two transverse



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red bars on the venter (Fig. 27); the anterior bar may be triangular. Of the specimens examined only one male from South Carolina was found to have an hour-glass. Kaston (1948, figs. 101-104) noticed the reduction of the hour-glass in specimens which he thought were northern specimens of *L. mactans*. *Latrodectus bishopi* also lacks a complete hour-glass and may have two ventral spots, one or none (Figs. 21-22).

Males of *L. bishopi* and *L. variolus* are much larger than those of *L. mactans;* male from Torreya State Park had the carapace 2.7 mm long, first patella and tibia 7.6 mm; a male from Vermont, 2.9; 6.9. Males of *L. mactans,* though smaller, are variable. Comparative measurements from Brewster Co., Texas, 1.4; 3.7; from Silverhill, Alabama, 1.7; 4.3; from Savannah, Georgia, 2.1; 5.6; and from Punta Gorda, Florida, 1.7; 4.3.

Latrodectus curacaviensis, L. variolus and *Latrodectus bishopi* are allopatric in distribution and can be separated by the coloration of the carapace, sternum and legs: orange-red in *L. bishopi;* black in *L. variolus,* light brown in *L. curacaviensis* from Curaçao. The genitalia of the three species are surprisingly similar (Figure 1-13); however, among Florida specimens there seem to be slight differences in the shape of the hard sclerotized parts of the palpus. These differences are not seen between *L. bishopi* and New England specimens of *L. variolus*. *Latrodectus curacaviensis* seems to be smaller and more colorful (Figs. 16, 17) than the other two. It also has a comparatively long carapace. A similar pair of *Latrodectus* species is *L. mactans tredecimguttatus* (Rossi) and *L. pallidus* O. P. Cambridge in the Near East, differing in color and texture of the abdomen, but not in the structure of genitalia.

COLORATION

It is well known that juvenile widows are brighter colored, with streaks and marks, than the adults. It was completely overlooked in

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EXPLANATION OF PLATE 2

Figs. 1-3. Cleared dorsal view of epigyna. 1. *Latrodectus curacaviensis* (Müller) from Curaçao. 2. *L. bishopi* Kaston. 3. *L. variolus* Walckenaer from Torreya State Park, northwestern Florida.

Figs. 4-7. *Latrodectus bishopi* Kaston, left male palpus. 4. Mated individual. 5-7. Virgin individual. 4, 5. Mesal view. 6. Ventral view. 7. Ectal view.

Figs. 8-10. *Latrodectus variolus* Walckenaer, male palpus, virgin individual from Torreya State Park, northwestern Florida. 8. Mesal view. 9. Ventral view. 10. Ectal view.

Figs. 11-13. *Latrodectus variolus* Walckenaer, male palpus, mated individual from Vermont. 11. Mesal view. 12. Ventral view. 13. Ectal view. All figures are drawn at the same magnification.

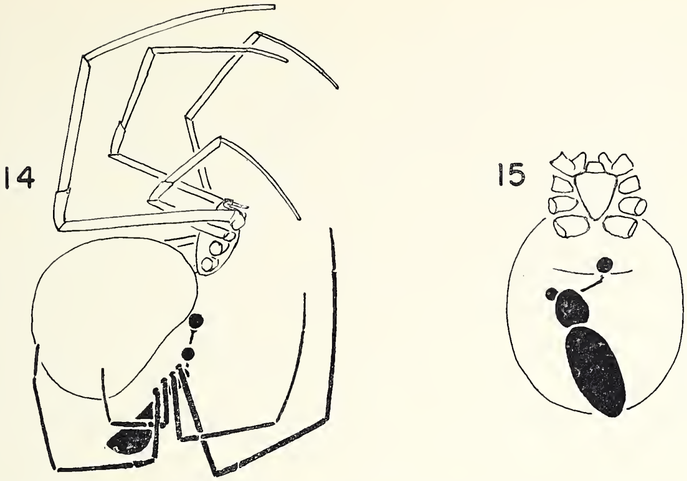
the previous paper that there is a striking correlation between total length of the spider and the coloration of different forms, the smaller ones being brighter colored, the largest ones dark. As shown below there is some variation among individuals in the number of molts undergone and it is possible that the brighter colored and smaller *L. curacaviensis* undergoes fewer molts than *L. bishopi* and *L. variolus,* and that the brightly colored populations of *L. mactans* in some parts of the world are made up of individuals that undergo fewer molts before maturity. Differences in the number of molts (4-9) of males with accompanying large differences in color and size in a laboratory culture of the araneid *Nephila madagascariensis* Vinson was reported by Gerhardt (1933).

Natural History

A trip was made to Curaçao in December, 1962, during the wet season. Despite a thorough search of the island, no *L. curacaviensis* were found. We had previously been advised by Drs. de Jong, a student of spiders and long time resident, that he had been unable to find the species, described in 1776 by Müller, and collected by Hasselt in 1860. Two factors may have led to its disappearance. First, the habitat probably has become less favorable. Thirty thousand goats roam the island and they appear to have placed a strong selection pressure on the vegetation, favoring plants with long spines and those that are poisonous. Shulov (1940) has reported that an area heavily infested with *L. pallidus* was almost freed of them by the grazing of cows and goats. Furthermore, on this densely populated island any woody plants are cut for fuel. Both of these ecological factors may have contributed to the increased dryness of the island. One *Latrodectus* collecting site of Hasselt was visited and was found to be moister than the island generally. Second, the introduced *L. geometricus* may have replaced *L. curacaviensis,* even though *L. geometricus* appears to be most abundant near Willemstad and human habitations.

Although they are very similar morphologically, *L. bishopi* and the Florida populations of *L. mactans* and *L. variolus* can easily be differentiated on the basis of their color, ecology and behavior.

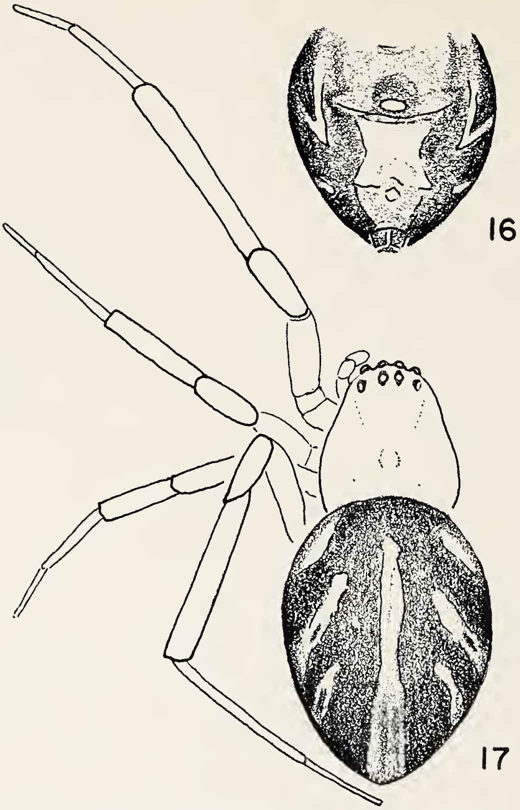
Latrodectus bishopi shows a very distinct habitat preference. It is completely restricted to inland, dune-like areas that support a plant association called sand-pine scrub (Fig. 23). The vegetation is xeromorphic and is dominated by the sand pine, *Pinus clausa.* Beneath the pines there is a dense growth of evergreen shrubs but little or no herbaceous ground cover. For a more complete description of the association see Laessle (1958).



Figs. 14, 15. *Latrodectus bishopi* Kaston, mating position. Male black, female in outline. Web supporting the spiders not shown.

Within the scrub, *L. bishopi* almost always makes its webs 30 cm or higher off the ground in the palmetto bushes, *Serenoa repens* and *Sabal etonia* (Fig. 24). The spider makes its web retreat by taking a frond of the palmetto and rolling it into a cone. The interior of the cone is lined with silk and the egg sacs are hung from the sides of the cone (Fig. 25). The egg sacs are light gray to white in color and have a fairly soft texture unlike those of *L. mactans* and *L. variolus,* which are brown and papery (Figs. 18-20). Often a mature male is found in the cone-shaped retreat with the female. There is little difference in the sizes of the sexes and a small silk partition usually separates them. The outer threads of the web spread from frond to frond of the palmettos and form a sheet-like pattern. The web is completely free of insect remains in contrast to those of *L. mactans* and *L. variolus,* which are heavily festooned with them. The reason for this may be that *L. bishopi* feeds only on very softbodied insects or ejects the remains from the web. The developing spiderlings remain in the parental web until they are half-grown whether the mother is still alive or not.

The courtship and copulatory behavior of *L. bishopi* have been observed in the laboratory in Cambridge. A male was placed with an adult female on 22 March 1963 at 7:00 A. M. Ten minutes later their legs were 1 cm apart and the male's abdomen jerked three times.



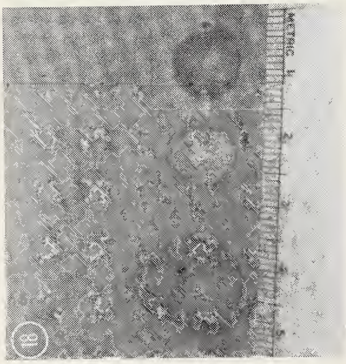
Figs. 16, 17. *Latrodectus curacaviensis* (Müller), female. 16. Ventral view of abdomen. 17. Dorsal view.

At 7:29, after climbing around, the male moved behind the female jerking the web, and using his long forelegs touched the first legs of the female with his and then climbed on the dorsum of the female's abdomen, facing in the opposite direction. The female kept completely still even though the male was climbing around her. The male vibrated his abdomen occasionally and sat behind the female touching her first leg with his. By 7:42 the male had moved below the female. The female was completely inactive while the male climbed around and boxed her epigynum. At 7:44 the male came to rest below the female's abdomen, facing in the same direction, and seemed to insert one or the other palpus in the epigynum while pulling the female's abdomen up slightly with his fourth leg. His abdomen continued to vibrate and he kept boxing the epigynum without quite touching it. At 7:50 the right palpus was inserted and withdrawn after four minutes. The male then rested behind the female, vibrating his abdomen. Soon he moved anteriorly and shook the web. At 8:02 he inserted the left palpus. Both animals were quiet, then the male moved its legs and shook both the web and the female. After 11 minutes the left palpus was withdrawn; it was pulled back about 2 mm while the embolus stretched like a pulled-out watch spring and then suddenly snapped back (apparently the distal portion broke off, see Abalos, et. al. 1963). The male again moved behind the female, boxed her epigynum, vibrated his abdomen and jerked the female. At 8:31 he seemed to introduce the right palpus again, then moved back, boxed her abdomen and palpated her sternum with his palpus. At 8:37 he inserted the right palpus again and pulled back slightly (Figs. 14, 15). After insertion all was quiet except that the male occasionally moved his legs and jerked the female. At 9:07, 30 minutes later, the palpus was withdrawn 3-4 mm with the embolus again stretching. Suddenly it snapped back and the male moved behind the female. At 9:13 he began boxing the epigynum and vibrating his abdomen. Alternately with boxing the epigynum he cleaned his palpi against each other and the chelicerae. After this the male moved 2 cm in front of the female. At 9:22 the glass was accidentally jarred and the male and female moved off in opposite directions.

Latrodectus variolus is found in mesic and xeric deciduous forests and is particularly abundant in Torreya State Park in northwest Florida. There the adults make their webs in trees, 3 to 20 feet off the ground (Fig. 28). They build dome-shaped retreats in the leaves at the ends of branches and the outer threads of the web radiate out from the retreat to the surrounding branches. The females and any egg sacs are usually found in the retreat. The webs contain many insect remains, primarily those of large flying insects such as cicadas.

During March and April large numbers of immature *L. variolus* are found at the bases of stumps in mixed forest litter. In the summer, however, the adults are found in the trees. The migration up into the branches has not been observed.

In Wisconsin, *L. variolus* has been collected from Baxter's Hollow in Sauk County and Wildcat Mountain in Vernon County. Both are natural undisturbed forest areas. On Wildcat Mountain a spider was found in a hollow stump. Michigan collecting labels of Dr. A. M. Chickering indicate localities in Ott Biological Preserve, in Calhoun County, Douglas Lake in Cheboygan County and dry hardwood and oak-hickory in Barry County.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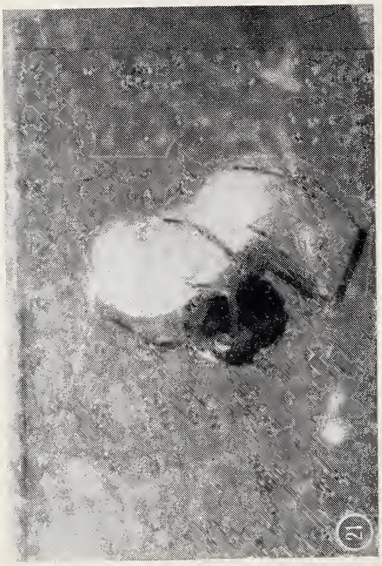
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Latrodectus mactans is sympatric with both *L. bishopi* and *L. variolus* in Florida. It has been found in the same sand-pine scrubs as *L. bishopi* and in Torreya State Park with *L. variolus*. In both places it makes its webs near the ground. It seems to prefer ground depressions around the bases of palmetto bushes in the sand-pine scrub, and debris and rocks in Torreya State Park. It readily invades disturbed areas.

The most striking difference between *L. mactans* and *L. variolus* is the difference in their rate of post-embryonic development. Both species spend almost exactly the same amount of time in the egg sac but after emergence there is a marked difference in the length of time and the number of molts to maturity.

Twelve *L. mactans* egg sacs and 10 *L. variolus* egg sacs were formed in the laboratory in St. Petersburg during the summer of 1963. The average length of time spent in the egg sac by *L. mactans* spiderlings was 29.3 ± 1.3 days (range 27-31) and the average length of time for *L. variolus* spiderlings was 29.3 ± 1.3 days (range 28-31).

Fifty of the spiderlings that emerged from an egg sac of *L. mactans* on 16 June 1963, and fifty that emerged from an egg sac of *L. variolus* on 19 June 1963, were taken for observation and rearing. Both egg sacs had been produced in the laboratory by individuals collected in northwest Florida. Each of the 100 spiderlings was placed in an individual, numbered container and these containers were then placed in an air-conditioned room where the temperature was kept reasonably constant around 24°C. The spiderlings received a plentiful supply of living fruit flies, *Drosophila melanogaster*. When the immature spiders were large enough, they were fed as many housefly maggots as they would take, until they reached maturity. Originally we had planned to feed them adult flies, but both species showed a decided preference for the maggots. At no time were the developing spiders given water; all fluid came from the food. It was our experience that the addition of water is unnecessary and may encourage mold, which inhibits growth or may be lethal. A record was kept for each developing spider of the number of molts and the duration of the stadia

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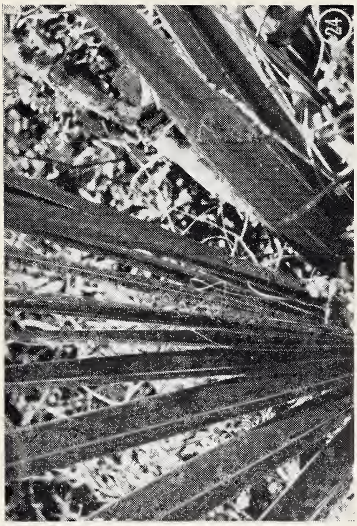
EXPLANATION OF PLATE 3

Fig. 18. Egg sacs (from left to right), *Latrodectus variolus, L. bishopi* and *L. mactans,* all Florida.

Fig. 19. Egg sac of *L. variolus.*

Fig. 20. Successive egg sacs of an individual female of *Latrodectus mactans tredecimguttatus* from Israel (in Florida laboratory culture; order unknown).

Figs. 21-22. *Latrodectus bishopi* Kaston, females. (Photograph by H. K. Wallace)



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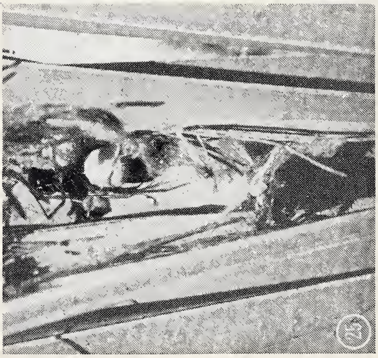

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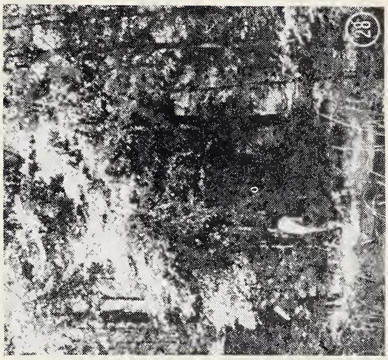

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passed through to maturity. The first post-emergence molt was considered the first molt. These data are summarized in Table I.

A total of 45 *L. mactans* and 44 *L. variolus* reached maturity. The sex ratio for *L. mactans* was 19 males to 26 females, for *L. variolus* 22 males to 22 females. A chi-square analysis at the 5% level of significance demonstrated that both these ratios are consistent with the hypothesis of a 1:1 sex ratio.

Male *L. mactans* passed through fewer molts to maturity (mode 4) than male *L. variolus* (mode 7). Male *L. mactans* matured in an average of 42.0 ± 7.8 days (range 32-58) while male *L. variolus* took much longer, 129.6 ± 7.5 days (range 122-135).

The same relationship held for the females. *Latrodectus mactans* females required from 5 to 8 molts (mode 6) to maturity, *L. variolus* females 7 or 8 molts (mode 7). Females of *L. mactans* averaged 63.8 ± 9.4 days (range 53-90) to maturity, while females of *L. variolus* averaged 152.6 ± 17.9 days (range 125-199). The discrepancy in number of instars suggests that the greater number of molts of *L. variolus* determines the very much larger size of the males, and also that the size variation and well-known variation in coloration of *L. mactans* males might be due to the different number of molts undergone.

SPECIES RELATIONSHIPS

Latrodectus bishopi and *L. variolus* are certainly distinct species, but the close similarity between the two in morphology and their allopatric distribution suggests that *L. bishopi* might have been derived from *L. variolus*. It is known that the sand-pine scrubs inhabited by *L. bishopi* arose in connection with islands that were present in the Florida area during the Pleistocene (Laessle, 1958). The literature (see Neill, 1957) records a number of species that are endemic to these scrubs or other south-central habitats in Florida. Many of these species are closely related to other species whose ranges extend only into northern Florida. Thus the conjecture can be made that *L. bishopi* differentiated from *L. variolus* on an isolated island or island group in the Pleistocene seas.

EXPLANATION OF PLATE 4

Figs. 23-25. Habitat of *L. bishopi*. 23. Florida scrub pine. 24. Web in palmetto. 25. Close-up of female with egg sac in palmetto.

Fig. 26. *Latrodectus mactans* (Fabricius) female from Tennessee.

Fig. 27. *Latrodectus variolus* Walckenaer, female from northern Florida. (Photograph by H. K. Wallace)

Fig. 28. Habitat of *L. variolus* in lower limbs of trees in northwestern Florida.

Table I.—Rate of development of *L. mactans* and *L. variolus*.

Species	No. of molts to maturity	No. of Individuals	Average No. of Days Elapsed to Each molt (Measured from Time of emergence from egg sac)							
			1*	2	3	4	5	6	7	8
L. mactans males	4	14	6.1	15.2	25.6	38.9				
	5	5	8.0	16.6	29.0	41.8	50.8			
L. variolus males	5	1	6	18	29	44	131			
	6	9	5.1	20.2	32.0	45.4	78.0	129.4		
	7	12	5.2	21.7	34.0	45.3	59.4	91.0	129.7	
L. mactans females	5	3	4.7	15.3	26.3	41.7	58.0			
	6	13	5.8	14.7	24.2	36.1	45.9	60.8		
	7	9	5.8	15.5	26.7	35.0	43.9	60.1	75.2	
	8	1	8	15	22	32	43	53	59	66
L. variolus females	7	18	6.4	20.2	31.3	44.7	67.3	109.2	152.4	
	8	4	6.3	18.3	27.5	41.5	56.3	81.5	120.0	153.5

*First molt after emergence from egg sac.

VENOMS

The results of a toxicological study of differences between the venoms of *L. mactans, L. variolus* and *L. bishopi,* and those of *L. mactans tredecimguttatus* from Israel and *L. geometricus,* will be published elsewhere (McCrone).

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THE ANATOMICAL SOURCE OF TRAIL SUBSTANCES IN FORMICINE ANTS[1]

By M. S. Blum[2] and E. O. Wilson[3]

Carthy (1951) showed that when workers of the formicine ant *Lasius fuliginosus* (Latreille) lay odor trails, they emit minute streaks of liquid that can be made visible to the naked eye by dusting with lycopodium power. By tracing food marked with edible charcoal, Carthy further proved that at least some of the liquid comes from the hind gut. He concluded that the trail substance is produced by the hind gut, probably as a component of the ingested gut contents rather than as a special secretion of the gut walls. In fact, this conclusion does not necessarily follow from the experimental results. It is equally possible that the critical trail substance is produced by another organ (e. g. the poison glands) and added to the anal streak. The necessity of considering such an alternative has been impelled by the discovery in recent years that the trail substances of certain non-formicine species are powerful attractants generated as glandular secretions in trace amounts (Wilson, 1963).

Nevertheless, even though Carthy's original evidence was not definitive, it now appears probable that his conclusion is basically correct. Using the artificial trail technique (Wilson, 1959), which allows a more certain identification of the anatomical source, we have been able to establish that in two other formicine species, *Myrmelachista ramulorum* Wheeler and *Paratrechina longicornis* (Latreille), the hind gut is the true primary source. Since no non-formicine ant species investigated thus far shares the character, the interesting possibility is raised that the hind-gut source is a unique evolutionary innovation of the Formicinae.

Procedure and Results

Myrmelachista ramulorum. The workers of this species form some of the longest and most conspicuous trail formations found in the Formicinae. At Mayaguez, Puerto Rico, where the species is abundant, it was noted that workers following trails frequently touched

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Table 1. Response of *Myrmelachista ramulorum* workers to artificial trails prepared from three abdominal organs.

Organ	*No. of workers tested*	*No. of workers responding*
Poison gland (plus vesicle)	180	6
Accessory gland	180	0
Hind gut	180	161

the tips of their gasters to the substrate. This indicated the possibility that the trail substance is secreted from some abdominal organ. In experiments conducted by Blum in 1963, artificial trails were made by streaking single organs and their contents onto a piece of paper in the form of a circle six inches in diameter. Groups of 20 living *ramulorum* workers were then quickly introduced onto the center of the circle and their movements followed. If an ant, upon encountering the circle, proceeded to follow it closely at least once through its entire circumference, a positive response was recorded. The principal terminal abdominal organs were tested in this fashion. The results of six replications are given in Table 1. They show clearly that the hind gut is at least a major source of the trail substance. In supplementary experiments, artificial trails prepared from the hind gut of *Myrmelachista* were also tested on workers of the following species: the myrmicines *Solenopsis geminata* (Fabricius) and *Pheidole fallax* Mayr, the dolichoderines *Tapinoma melanocephalum* (Fabricius) and *Iridomyrmex melleus* Wheeler, and the formicine *Paratrechina longicornis.* The results were all completely negative.

Paratrechina longicornis. This pantropical species is well known both for the efficiency of its recruitment trails and the length and complexity of its persistent trunk trails. In experiments conducted by Wilson at Bacolet, Tobago, in 1961, workers were first attracted in large numbers to sugar baits. Artificial trails were then led from the periphery of the feeding groups outward for a distance of 30 centimeters. A positive response was recorded if an ant followed the trail to at least its midpoint. Control experiments using trails of tap water produced entirely negative results. In the experimental trails, all of the major organs located in the posterior half of the abdomen were tested. The results are given in Table 2. They identify the hind gut as the primary immediate source of the trail substance.

Discussion

Our results do not disclose whether the pheromone is produced as a

Table 2. Response of *Paratrechina longicornis* workers to artificial trails prepared from four abdominal organs.

Organ	*No. of replications*	*No. of workers responding*	*Duration of response to nearest ½ min.*
Poison gland (plus vesicle)	8	0,0,0,0,0,0,0,1	½
Accessory gland	8	all 0	———
Hind gut	8	0,4,8,8,11,15, 31,37+	0,1½,½,2½,1, 2,7½,20+
Ovary	8	all 0	———
Control (water)	8	all 0	———

side product of digestion or as a special secretion of the gut wall. Examination of the freshly dissected gut wall under low power with a light microscope failed to reveal obvious glandular tissue that could serve as a possible source. But this is in itself quite inconclusive, since inconspicuous unicellular glands are known to abound elsewhere in the ant body. Also, the data do not reveal whether the trail substance is actually manufactured in the hind gut, or whether it is produced forward of the hind gut and passed — perhaps in precursor form — back with the gut contents. The solution of these questions awaits the development of a finer dissection technique than the one used in the present study.

These preliminary results have an important phylogenetic implication. All seven non-formicine genera on which similar experiments have been conducted (*Solenopsis, Pheidole, Tetramorium, Acromyrmex, Atta, Iridomyrmex, Monacis;* see Wilson, 1963) secrete trail substances from glands not associated with the hind gut. Moreover, the two formicine species reported here belong to widely different branches of the subfamily: *Myrmelachista* constitutes a tribe by itself within Emery's section Alloformicinae, while *Paratrechina* is a member of the tribe Lasiini of the section Euformicinae. No member of the third formicine section, the Heteroformicinae (consisting of the tribes Myrmecorhynchini and Myrmoteratini) has been investigated. It will be of interest to see whether trail-laying species in other formicine genera and tribes also use the hind gut as a primary source.

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THE AMERICAN SPIDERS OF THE GENERA *STYPOSIS* AND *PHOLCOMMA* (ARANEAE, THERIDIIDAE)*

By Herbert W. Levi
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Several new species have been discovered since publication only a few years ago of a paper on *Styposis* (Levi, 1960). One of these new species, *S. selis,* gives a clue to the relationship of the genus. The features characterizing *Styposis* are the ectally-facing embolus of the male palpus, and reduced or absent anterior median eyes. In only one other theridiid genus are there six-eyed species: *Comaroma* Bertkau, found in south-central Europe, Japan, and the western United States. However, the different structure of *Comaroma* genitalia and the large colulus suggest that the eye reduction evolved independently. The ectally-facing embolus is found also in one species of the genus *Pholcomma* (*P. hirsuta* Emerton, Levi 1957), members of which also frequently have the anterior median eyes reduced in size, and the colulus replaced by two setae; but, unlike most species of *Styposis, Pholcomma* species usually have denticles on the posterior margin of of the chelicerae. In our revision of theridiid genera (Levi and Levi, 1962) it was suggested that there might be species intermediate between *Styposis* and *Pholcomma.* However the female of *S. rancho* here described has the epigynum similar to that of some Chilean *Anelosimus* species, a theridiid genus of larger spiders. But the epigynum of *S. selis* from southern Brazil resembles that of the Chilean *Anelosimus,* and furthermore the complexity of the male palpus also suggests that it belongs to the species group of *Anelosimus* endemic in Chile. The chelicerae have teeth on the posterior margin, as in *Anelosimus* and *Pholcomma* species, a feature uncommon in the Theridiidae. But unlike Chilean *Anelosimus* (Levi, 1936), *S. selis* has only six eyes. Before the discovery of *S. selis,* it was thought that the ectally facing embolus in some Chilean *Anelosimus* (Levi, 1963), was a unique character, evolved independently. It is now evident that *Styposis* is intermediate between *Pholcomma* and the Chilean *Anelosimus,* the most abundant theridiid spiders in Chile, although *Styposis* generally lacks posterior teeth on the chelicerae. *Styposis clausis* has a rough cheliceral surface facing the fang and a carina ending in an indistinct tooth (Fig. 10).

Previously *Styposis* was known only from America; now a small

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specimen has been found in New Guinea, collected with a Berlese funnel in rain forest. The specimen is short-legged, pigmented and has eight eyes. It is the only *Styposis* specimen having habitat information.

The two species described here from South America are placed in *Pholcomma* tentatively, awaiting the discovery of males and additional specimens.

I would like to thank Dr. W. J. Gertsch of the American Museum of Natural History; Dr. A. Collart and J. Kekenbosch of the Institut Royal des Sciences Naturelles, Brussels; and Prof. M. Vachon of the Muséum National d'Histoire Naturelle, Paris (MNHN), for the loan of collections; and Prof. M. Birabén, director of the Museo Argentino de Ciencias Naturales, Buenos Aires, for the loan of a specimen from the La Plata Museum. This investigation was supported in part by Public Health Service Research Grant AI-01944, from the National Institute of Allergy and Infectious Diseases.

Key to American *Styposis* species

1a. With six eyes (1960, fig. 1; Fig. 8) 2

1b. With eight eyes or six eyes and pigment spots in place of anterior medians (1960, fig. 5, 10, 18, 24) 4

2a. First patella-tibia less than one and one-half times carapace length; southern Brazil .... *selis* sp. n.

2b. First patella-tibia more than twice carapace length 3

3a. Male with first patella-tibia more than three times carapace length (Fig. 12); epigynum with a transverse knob (1960, fig. 3); Panama .... *clausis* Levi

3b. Male with first patella-tibia two and one-half times carapace length; female unknown; Nicaragua .... *nicaraguensis* Levi

4a. Abdomen wider than long (1960, fig. 10); Panama .... *chickeringi* Levi

4b. Abdomen larger than wide or subspherical 5

5a. Carapace sclerotized, with reticulate raised pattern 6

5b. Carapace lightly sclerotized, smooth 7

6a. Carapace widest behind middle, rounded behind (1959, fig. 18); Nicaragua to Venezuela .... *flavescens* Simon

6b. Carapace widest in middle, drawn out behind with a short stalk (1960, fig. 24); Panama .... *scleropsis* Levi

7a. Posterior median eyes separated by their diameter (1959, fig. 27); southwestern United States .... *ajo* Levi

7b. Posterior median eyes their radius or less apart 8

Levi — Styposis

8a. Anterior lateral eyes separated by one diameter (1959, fig. 5); Venezuela .... *rancho* Levi
8b. Anterior lateral eyes separated by about one and one-half diameters (Fig. 1); Equador .... *colorados* sp. n.

Styposis colorados sp. n.

Figures 1-3

Holotype. Male from 35 km northwest of Santo Domingo de los Colorados, Pichincha, Ecuador, 22 Dec. 1958 (A. M. Nadler), in the American Museum of Natural History. The specific name is a noun in apposition after the type locality.

Description. Carapace, sternum, reddish brown. Legs grayish brown. Abdomen whitish. Diameter of anterior median eyes less than radius of other eyes. Anterior median eyes less than one diameter apart, touching laterals. Posterior median eyes their radius apart, almost touching laterals. Legs short. A small transverse, sclerotized plate anterior to spinnerets on venter. Between plate and spinnerets, two setae replace colulus. Total length 1.0 mm. Carapace 0.51 mm long, 0.47 mm wide. First femur, 0.52 mm; patella and tibia, 0.52 mm; metatarsus, 0.39 mm; tarsus, 0.25 mm. Second patella and tibia, 0.41 mm; third, 0.35 mm; fourth, 0.48 mm.

Diagnosis. The embolus is on the ectal side of the palpus as in other *Styposis* (Figs. 2, 3), but is easily visible, and the species is thereby distinguished from *S. rancho* in which the embolus is difficult to see.

Styposis selis sp. n.

Figures 4-9

Holotype. Male from Nova Teutonia, lat 27° 11'S, long 52° 23'W, Santa Catarina, Brazil, July 1955 (F. Plaumann) in the Institut Royal des Sciences Naturelles, Brussels. The specific name is an arbitrary combination of letters.

Description. Carapace, sternum, legs yellow; abdomen whitish with

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EXPLANATION OF PLATE 5

Figs. 1-3. *Styposis colorados* sp. n. 1. Male Carapace. 2. Left palpus, ventral view. 3. Left palpus, ectal view.

Figs. 4-9. *S. selis* sp. n. 4. Palpus. 5. Male. 6. Female genitalia, dorsal view. 7. Epigynum. 8. Female. 9. Left female chelicera, posterior view.

Figs. 10-12. *S. clausis* Levi. 10. Left Female chelicera, posterior view. 11. Palpus. 12. Male.

Figs. 13-14. *S. rancho* Levi. 13. Female genitalia, dorsal view. 14. Epigynum.

sclerotized part yellowish. Ducts and seminal receptacles black and showing through epigynum. Carapace of female longer than wide (Fig. 8), that of male almost circular and quite high (Fig. 5). Six eyes in two clumps touching each other. Posterior median eyes one diameter apart. Abdomen longer than wide. Abdomen of male with a lightly sclerotized ring around spinnerets. In female, first leg equals fourth in length; first leg longer than fourth in male. Total length of female 1.3 mm. Carapace 0.55 mm long, 0.50 mm wide. First femur, 0.48 mm; patella and tibia, 0.55 mm; metatarsus, 0.26 mm; tarsus 0.30 mm. Second patella and tibia, 0.43 mm; third 0.38 mm. Fourth femur, 0.48 mm; patella and tibia, 0.58 mm; metatarsus, 0.26 mm; tarsus, 0.31 mm. Total length of male 1.2 mm. Carapace 0.58 mm long, 0.54 mm wide. First femur, 0.54 mm; patella and tibia, 0.64 mm; metatarsus, 0.31 mm; tarsus, 0.32 mm. Second patella and tibia, 0.47 mm; third, 0.42 mm; fourth, 0.60 mm.

Diagnosis. The coiling of the heavily sclerotized ducts of the epigynum, and the *Anelosimus*-like palpus separate this species from *S. clausis.* The six eyes and small size separate the species from Chilean *Anelosimus.*

Records. ♀♀, ♂♂ paratypes collected with holotype, July 1955 and August 1957.

Styposis rancho Levi
Figures 13-14

Styposis rancho Levi, 1960, Psyche, *66*; 18, figs. 5-6, ♂. Male holotype from Rancho Grande, Venezuela, in the American Museum of Natural History.

Description of female. Coloration and eyes as in male. Abdomen subtriangular, as wide as long, widest anterior. Epigynum very transparent with dark ducts showing through (Fig. 14). The female has much longer legs than the male. Total length 1.6 mm. Carapace 0.71 mm long, 0.66 mm wide. First femur, 1.72 mm; patella and tibia, 1.80 mm; metatarsus, 1.30 mm; tarsus, 0.52 mm. Second patella and tibia, 1.30 mm; third, 0.67 mm; fourth, 1.03 mm.

Records. Venezuela. Distrito Federal: Caracas, Dec. 1887-Feb. 1888, ♀ (E. Simon, MNHN). *Aragua:* Tovar, Jan.-Feb. 1888, ♀ (E. Simon, MNHN).

Styposis clausis Levi
Figures 10-12

Styposis clausis Levi, 1960, Psyche, *66*: 15, figs. 1, 2, 4, ♀. Female holotype from Forest Reserve, Panama Canal Zone, in the Museum of Comparative Zoology.

Description of male. The animal is entirely yellow-white without pigment; abdomen whitish. Anterior lateral eyes more than one diameter apart. Posterior median eyes a little less than a diameter apart, touching laterals. Total length 1.7 mm. Carapace 0.69 mm long, 0.69 mm wide. First femur, 1.97 mm; patella and tibia, 2.22 mm; metatarsus, 1.64 mm; tarsus, 0.60 mm. Second patella and tibia 1.72 mm; third, 0.84 mm; fourth 1.11 mm.

The male differs from the female by having a narrower abdomen.

Records. Panama: El Valle, ♀, ♂, July 1936 (A. M. Chickering).

Key to American *Pholcomma* species

1a. Carapace yellow-white 2
1b. Carapace brown 3
2a. Male palpus with a spring-like coiled embolus (1957, figs. 35-37); epigynum with anterior depression (1957, figs. 32-33); Pennsylvania to North Carolina .... *barnesi* Levi
2b. Male palpus with a short embolus (1957, figs. 28-30); female unknown; North Carolina coast .... *carota* Levi
3a. Ducts anterior to seminal receptacles (1957, figs. 24-25); male palpus with embolus facing ectally (1957, figs. 19-21); eastern United States to Wisconsin, Mississippi, Florida .... *hirsutum* Emerton
3b. Ducts posterior of seminal receptacles; males unknown; South America 4
4a. Ducts, in ventral view, looping (Fig. 16); Catamarca, Argentina .... *micropunctatum* (Mello-Leitão)
4b. Ducts, in ventral view, straight (Fig. 18); Minas Gerais, Brazil .... *mantinum* sp. n.

Pholcomma hirsutum Emerton

Pholcomma hirsutum Emerton, 1882, Trans. Connecticut Acad. Sci., *6*:29, pl. 6, fig. 6, ♀, ♂. Two female, one male syntypes from New Haven, Connecticut in the Museum of Comparative Zoology, examined. — Levi, 1957, Trans. Amer. Micros. Soc., *76*:110, figs. 19-27, 48, map *(hirsuta)*.

Note. The gender of the generic name is neuter.

Pholcomma micropunctatum (Mello-Leitão)

Figures 15-16

Dipoena micropunctata Mello-Leitao, 1941, Rev. Mus. La Plata, n. s., 2:142, fig. 37, ♀. Female holotype from La Viña, Catamarca, Argentina in the Museo de La Plata, examined.

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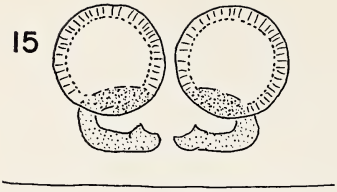

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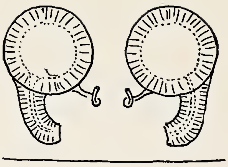

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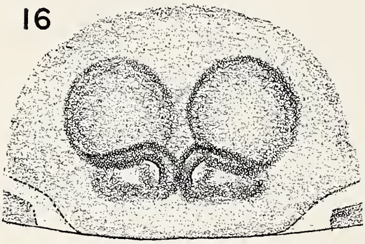

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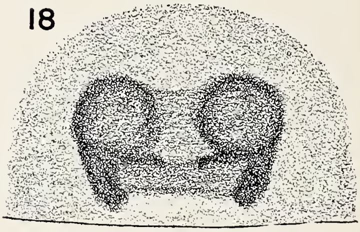

Figs. 15-16. *"Pholcomma" micropunctatum* (Mello-Leitão). 15. Epigynum cleared. 16. Epigynum.

Figs. 17-18. *"Pholcomma" mantinum* sp. n. 17. Epigynum cleared. 18. Epigynum.

Description. Sclerotized areas brown; abdomen gray with four white spots on anterior end of dorsum. Carapace, legs sclerotized. Carapace rather high. Eyes subequal in size. Anterior medians two-thirds diameter apart, touching laterals. Posterior median eyes one-third diameter apart, one-quarter from laterals. Chelicerae weak, pointed on both ends, without teeth. Fang large, curved, almost one-half total height of chelicerae. Abdomen with bases of setae sclerotized and some scattered small sclerotic spots. A sclerotic ring around pedicel and around spinnerets. Colulus with two setae. Total length 2.0 mm. Carapace 0.71 mm long. First patella and tibia 0.93 mm.

The male being unknown, placement of this species is uncertain. Since the female has only two seminal receptacles (Fig. 15) it cannot be a *Dipoena* and is probably not *Euryopis*. It differs from other *Pholcomma* by lacking teeth on the chelicerae. It is possible that the specimen lacks lungs and belongs to the family Symphytognathidae.

Pholcomma mantinum sp. n.

Figures 17-18

Holotype. Female from Diamantina, Minas Gerais, Brazil in the American Museum of Natural History. The specific name is an arbitrary combination of letters.

Description. The whole spider is brownish, the abdomen is lighter on venter. The carapace is sclerotized. The posterior median eyes are largest, the anterior median eyes smallest. The anterior median eyes are two-thirds their diameter apart, almost touching laterals. The posterior median eyes are almost touching, less than one-quarter diameter from laterals. The chelicerae are very small, the shape of an equilateral triangle, and lack teeth. The abdomen is suboval with setae coming from sclerotized round spots on dorsum. The sides seem folded and there is a sclerotized ring around the spinnerets. The colulus is replaced by two setae. Total length 1.5 mm. Carapace 0.62 mm long, 0.56 mm wide. Second patella and tibia 0.66 mm; third 0.56 mm. Fourth femur, 0.66 mm, patella and tibia, 0.88 mm.

The specimen is in poor physical condition.

Diagnosis. This specimen is quite close to *P. micropunctatum* (Mello-Leitão). The ducts of the genitalia are shorter (Figs. 17, 18). Along with *P. micropunctatum* this species may belong to the family Symphytognathidae; its placement in *Pholcomma* is tentative.

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The illustration on the front cover of this issue of Psyche is a reproduction of a drawing of a myrmecophilous staphylinid beetle, *Euxenister wheeleri* Mann, from Barro Colorado Island (Psyche, vol. 32, p. 173, 1925).

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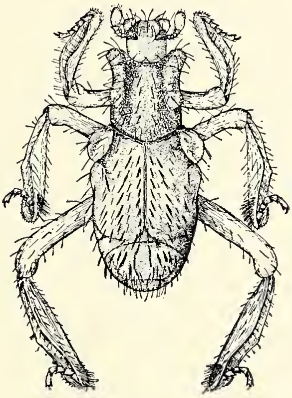

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Vol. 71 June, 1964 No. 2

THE FIRST FOSSIL TARDIGRADE: *BEORN LEGGI* COOPER, FROM CRETACEOUS AMBER*

By Kenneth W. Cooper
Dartmouth Medical School, Hanover, N. H.

In the summer of 1940, William M. Legg made a small but valuable collection of chemawinite, or Canadian amber, from sparse secondary deposits along beaches not far from the entrance of the Saskatchewan River into Cedar Lake, southeast of The Pas, Manitoba. His interest in this amber derived from the insects and other arthropods it is known to contain, for they are an extraordinary lot that very likely represent a Cretaceous fauna of some 60 to 80 million years ago (Carpenter *et al.* 1937; Holland 1951). The collection contained well over 200 zoological specimens, and its preliminary preparation and study was the subject of William Legg's unpublished undergraduate thesis in the Department of Biology at Princeton University (1942). Following his untimely death in 1953, the amber and prepared material that could be brought together was placed by his family in the collections of the Museum of Comparative Zoology at Harvard University. I had the pleasure of his friendship and of fostering his studies at Princeton; this brief study of one of the most remarkable of his specimens, and the specific name given to it, are dedicated to his memory.

Among the specimens that Legg classified in his sample are: Crustacea (copepod ?) 1, Araneida 10, Acarina 27, Thysanoptera 1, Corrodentia 3, Homoptera 43, Hemiptera 1, Trichoptera 2, Diptera Nematocera 59, Diptera Brachycera 5, Coleoptera 3, and Hymenoptera 25. Only one of these was identified by Legg with a form already described, and that is a forewing of the hymenopteron *Serphites paradoxus* Brues (in Carpenter *et al.* 1937). This wing is a remarkable specimen because (along with a head capsule, a thorax, several legs, and a second wing — all of different insects) it had been digested free from the amber by prolonged refluxation in a Soxhlet condenser, first with absolute ethanol, then ether, and finally dioxane.

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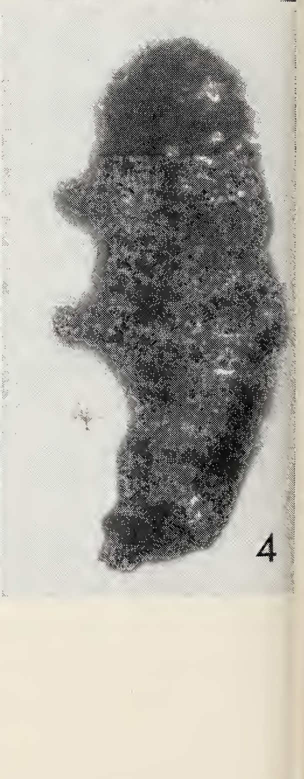
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Cooper — Beorn

Surprisingly, these specimens which had been liberated from the amber are hardly more friable or fragile than the exoskeletal remains of insects found in forest litter today.

In addition to the above, and 27 specimens of uncertain relationship, two fossils are of exceptional and general interest: a naked ciliate protozoan (Wichterman, 1953) and a tardigrade or "water-bear". The occurrence of aquatic and semiaquatic forms such as these, at first thought, may seem implausible at best. Yet Kirchner (1950) points out that large numbers of aquatic organisms have been discovered in Baltic amber in recent years, including Radiolaria, Volvocales, Cyanophyceae, corals with partially expanded polyps, and so on, and suggests that some ambers, at least, may have originated from the resin flows of swamp trees akin to cypress rather than to firs and pines. If the inclusions of chemawinite represent a swamp fauna, then the failure to find ants in the samples so far examined would have an explanation, and not require the assumption that they are of a more recent origin.

The water-bear is not to be placed in any known genus. The specimen itself lies within a small (6 × 7 × 3 mm) piece of deeply honey-colored, transparent chemawinite that is partially polished on two opposite, not parallel surfaces. Submersion in a bath of crown oil (refr. index 1.515), with illumination by reflected white light, permits its study in right dorso-lateral and left ventrolateral aspects at magnifications up to 300 diameters. A combination of transmitted and reflected light is sufficient to define the distal two-thirds of the claws of at least one of each pair of legs. The refractive index of chemawinite spans the range 1.535-1.537 (Walker 1934), and so the specimen was also studied, and all details checked, in 1, 2 dibromoethane (refr. index 1.538). Though helpful, the gain in image detail was too slight to merit prolonged use of this volatile, extremely toxic liquid. The tardigrade is placed in the genus

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EXPLANATION OF PLATE 6

Beorn leggi Cooper, figs. 1-5; fig. 6 — juvenile (? hetero)tardigrade (see text).

Figs. 1, 3 — right aspect of the specimen; figs. 2, 4 — left aspect; fig. 5 — legs II and III of fig. 3, enlarged. Scale = 100 microns. Silhouettes 1 and 2 were photographed by William Legg, and are reproduced from his thesis. Figs. 3 and 4 were photographed with the specimen immersed in crown oil, illuminated with a combination of reflected and transmitted light, and in positions similar, but not identical, to those of 1, 2 and of the text figures. None of the photographs have been retouched, but the claws in fig. 5 have been given emphasis by "dodging" during enlargement.

Beorn Cooper, n. gen.

(Fig. 1; Plate 6, Figs. 1-5)

Description: Mouth without discernible palps or other appendages, dorsally and laterally enclosed by a well-defined cuticular frontal element which caps and delineates the "head"; no cephalic appendages, no lateral cirrus, no clava, and no discernible eye-spots. Body naked; cuticle evidently regionally thickened dorsally, annulated by transverse lines of flexion, but not sclerotized into distinct exoskeletal plaques either dorsally or ventrally. Legs moderately long, telescopable; each leg with four claws (or 2 two-branched claws ?), and with a short, anterior, flattened, apical cuticular extension or spine, but without lateral or basal papillae.

Genotype: *Beorn leggi* Cooper, n. sp.

Origin of name: The name Beorn is that of the now storied magical bear of the Wilderland in the Third Age of Middle-earth. "Some say that he is a bear descended from the great and ancient bears of the mountains . . ." (J. R. R. Tolkien, 1937, The Hobbit).

Beorn leggi Cooper, n. sp.

(Fig. 1; Plate 6, Figs. 1-5)

Description: Of subaverage size: 0.3 mm long by 0.08 mm wide. Convex above, flattened ventrally. Cuticle of head without eyespots, of body smooth and without noticeable sculpture — at most very finely coriaceous; transversely crossed by four main furrows, or lines of flexion, which divide the body into five regions: P - the prostomial ("head") region, I - the first segment bearing leg pair-I ventrolaterally, II - the second segment bearing legs-II, III - the third segment bearing legs-III, and IV - the terminal segment bearing legs-IV. The relative proportions of the body regions just defined are: P (1) : II (1.3) : III (1.3) : IV (2+). Whereas each of the four major annular furrows encircles the body region, region-I has a short, transverse furrow just posterior to the middle, and regions-II and -III are each in turn divided dorsally by a secondary furrow just anterior to their midpoints; the lateral extensions of these secondary furrows fade just anterior to the base of the corresponding leg. In contrast, segment IV has a secondary furrow that extends ventrally but fades out dorso-medially.

Apically and anteriorly each leg has a short, scale-like projection of the cuticle, or perhaps flattened spine (that of leg-I being most prominent), and a cuff-like fold at midlength which strongly suggests that the leg may telescope. There are four claw-rays per leg, of which the middle two of each leg are the more dorsal. *If* the pairs of claws are joined at their bases to form an inner (cephalad) and an outer (caudad) compound branched claw, or "diplogriffe", then the major (dorsal) branch of the inner pair is the longest of all the four elements, and the major (dorsal) branch of the outer pair is the second longest claw of each leg[1]. Finally, the minor element of the inner pair of claws is larger than the minor ramus of the outer pair. Whether joined in pairs or not, the four unequal elements are obviously asymmetrically disposed with respect to the median plane of the leg.

Type: MCZ No. 5213, Museum of Comparative Zoology, Harvard University.

Type locality: One source of Legg's collection was the drift on Amber Beach, a shore that rims a small bay at the base and to the south of Oleson Point. This is in fact the site from which most of the collections of chemawinite have come. The second source, which he believed to have discovered, was the drift and debris along a beach lying due west of Oleson Point, and due south of the southern limit of the Chemawin Indian Reservation[2]. These beaches are near to one another and to the entrance of the Saskatchewan River into Cedar Lake, and their secondary deposits are probably of a common primary origin. Regrettably no record remains from which of the two beaches the piece containing *Beorn leggi* derived.

A second tardigrade: In addition to *Beorn leggi,* the amber specimen contains a second, juvenile tardigrade (fig. 1c, d; plate 6, fig. 6). This specimen is displayed in dorsal and ventral views. Though adequate to establish its identity as a tardigrade, it is very poorly preserved, curled on itself and shriveled. There is so little detail that can be made out reliably, it does not merit description. But if there be lateral cirrus and clava as the full ventral view hints (fig. 1D), it is a heterotardigrade, perhaps an echiniscoid as the *two* claws suggest which are visible from above on the left posterior leg. In any case it is evidently remote from *Beorn* in its affinities.

Relationships: Though certain morphological features of cardinal taxonomic importance cannot be made out in the specimen as it is now displayed, including stylets, buccal apparatus with its possible

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[1] The first three legs of the left side are displayed directly in end view in text fig. 1B, and legs 2 and 3 are similarly viewed in the photograph of fig. 4, plate 6; regrettably the optical images given by the refringent claw-rays of these legs are no more than bright beads of light at each focal level, and nothing can be made out by me of their union with the soles of the legs themselves.

[2] See sheet No. 63F, the The Pas Quadrangle, Department of Interior, Topographical Survey of Canada, 1927.

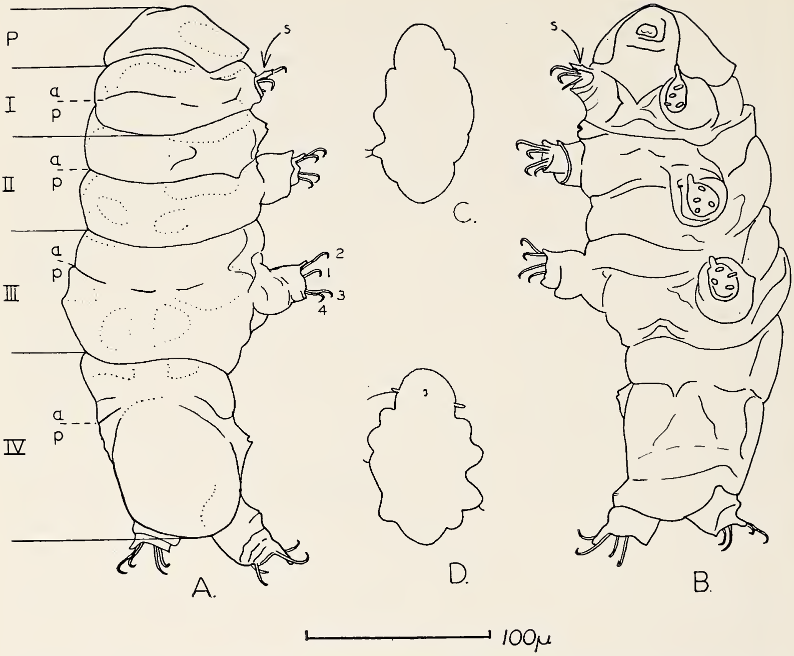

Fig. 1 A, B — *Beorn leggi* Cooper; C, D. — juvenile heterotardigrade (an echiniscoid?). Compare these camera lucida sketches with the photographs of plate 6. Scale represents 100 microns.

P — "head"; I, II, III, IV — body segments bearing legs; a, p — anterior and posterior halves of segments I, II, etc., each marked off by a dorsal furrow; IVa = "pseudosegmental region" of others; s — apical cuticular projection or spine; 1 + 2 — "inner" pair of claws, of which 2 is the dorsal element; 3 + 4 — "outer" pair of claws, of which 3 is the dorsal element; claw $2>3>1>4$, see text. Dotted lines represent wrinkles and depressions.

skeletal elements, presence or absence of cloaca, or gonopore and anus, or indeed whether there are 4 claws per leg or 2 two-rayed claws, *Beorn* can nonetheless be given ordinal assignment. Though this must be done chiefly by the negative process of exclusion, the absence of cephalic appendages, of a lateral cirrus, and of a clava, are sufficient to eliminate assignment to either the Mesotardigrada (1 genus; Rahm 1937) or to the Heterotardigrada (4 families, *ca.* 10 genera, see Marcus 1929, 1936). The remaining order, Eutardigrada, encompasses but two recognized families: Milnesiidae (= Arctiscidae; 1 genus : *Milnesium*) and Macrobiotidae (4 genera : *Macrobiotus, Hypsibius, Itaquascon,* and *Haplomacrobiotus*). The obvious lack of rostral and lateral palps, no less the morphology of the claws (regardless whether or not there are four, or but two, separate claw elements), eliminates the family Milnesiidae from further consideration.

If the claws of each leg of *Beorn leggi* are two in number, and if each is in turn two-rayed (that is, the individual claw is a "diplogriffe"), then it would be helpful to know whether basal lunules are present. But whether or not there are basal lunules, *Haplomacrobiotus* is eliminated as congeneric by the fact that the claws of each leg possess a total of 4 long rays in *Beorn,* and not 2 as in *Haplomacrobiotus.* Both the inequality of the rays, and the lack of rigorous symmetry of the claw rays about the median plane of the leg, and in lesser degree the sensible thickening of the dorsal cuticle in *Beorn,* set it apart from *Macrobiotus.* In these respects, and in its markedly subaverage size, *Beorn leggi* superficially calls to mind certain species of *Hypsibius.* The fossil form, however, differs sharply from the described species of both *Hypsibius* and *Itaquascon* (de Barros 1939) by the marked superiority in size of the major ramus of its *inner* (instead of outer) claws. Is *Beorn,* then, to be placed among the macrobiotids, more or less closely affined to *Itaquascon* and *Hypsibius?*

The family Macrobiotidae encompasses forms with strongly developed stylets and (aside from *Itaquascon*) a complicated internal buccal apparatus. Furthermore they possess gonoducts that enter the hindgut to create a "cloaca". All of these features are regrettably unascertainable in the fossil in its present state of preparation. But inasmuch as the legs of *Beorn* appear to be telescopable and provided with a distal, anterior, cuticular scale (or flattened spine), and as the pattern of the claws in any case departs from those known in the genera of living macrobiotids, it seems prudent to set the fossil form aside in a separate family, **Beornidae** (*n. fam.*), with no implication as to the possible nature of stylets, buccal apparatus, genital and anal orifices, and so on. Though telescopable legs are a feature otherwise known only in certain Heterotardigrada, it seems an insufficient character to justify creation of a new order. The Beornidae are therefore viewed tentatively as a third family of the order Eutardigrada.

At present it seems that the current major classification of the Tardigrada is not likely to be an enduring one. *Thermozodium* (Rahm 1937), for example, has a lateral cirrus but no clava, basal papillae on the legs, four peribuccal papillae, and pharyngeal skeletal elements, thus sharing cardinal features of Heterotardigrada and Eutardigrada alike. *Beorn* seems akin to eutardigrades, but possesses a telescopable leg. And within the Eutardigrada, *Itaquascon* bridges the Milnesiidae and Macrobiotidae (de Barros 1939). In a few words, these three genera blur the distinctions that, thirty years ago, provided the Tardigrada with a clean-cut suprageneric classification.

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ON NEOTROPICAL CARABIDAE (COLEOPTERA)

By Hans Reichardt*

In the course of the study of Neotropical Carabidae in the collections of the Museum of Comparative Zoology and the Departamento de Zoologia, a new species of *Galeritula* was recognized. It is described in order that the name will be available for use elsewhere. In addition new synonymies are established in some other genera of Neotropical Carabidae.

Genus *Otoglossa* Chaudoir.

Otoglossa Chaudoir, 1872, Ann. Soc. Ent. Belg., 15:158. Type: *O. tuberculosa* Chaudoir.

Heraldinium Liebke, 1927, Ent. Blaett., 23: 101-102. Type: *H. nevermanni* Liebke. NEW SYNONYMY.

Liebke, 1938, Fest. Emb. Strand, 4:42, 88.

Mateu, 1961, Ann. Mus. Civ. Stor. Nat. Genova, 72:163, 169.

Liebke described *Heraldinium* as belonging to the Odacanthini, and included it in his Odacanthini revision of 1938. Studying a series of specimens that proved to be *O. tuberculosa,* I found (1) that this species has all characters of *Heraldinium* but (2) is different from *nevermanni,* the only species assigned to *Heraldinium* by Liebke. A more careful study brought me to the conclusion that Liebke's genus belongs to the Lebiini, and must be considered a synonym of *Otoglossa.* This genus, as defined recently by Mateu (1961), included only *O. tuberculosa* Chaudoir and *subviolacea* Mateu, to which *nevermanni* (Liebke) must now be added.

Otoglossa tuberculosa Chaudoir
(Figs. 1-3)

Otoglossa tuberculosa Chaudoir, 1872, Ann. Soc. Ent. Belg., 15:158-159. Type: Minas, Brazil; Paris Museum.

Mateu, 1961, Ann. Mus. Civ. Stor. Nat. Genova, 72: 170. (see for additional references and synonyms).

To the localities given by Mateu, I add the following: from the Departamento de Zoologia: Ilha dos Buzios, São Paulo, 16.X.-4.XI. 1963, Exp. Dep. Zool. col.; Caraguatatuba (Reserva Florestal, 40 m.), São Paulo, 22.V.1962, Exp. Dep. Zool. col.; Barueri, São Paulo, K. Lenko col.; Ponta Grossa, Paraná, III. 1939, Camargo col.; from the Museum of Comparative Zoology: Nova Teutonia, Santa Catarina, F.Plaumann col.

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*Departamento de Zoologia da Secretaria da Agricultura, São Paulo. On a fellowship of the Organization of American States at Harvard University.

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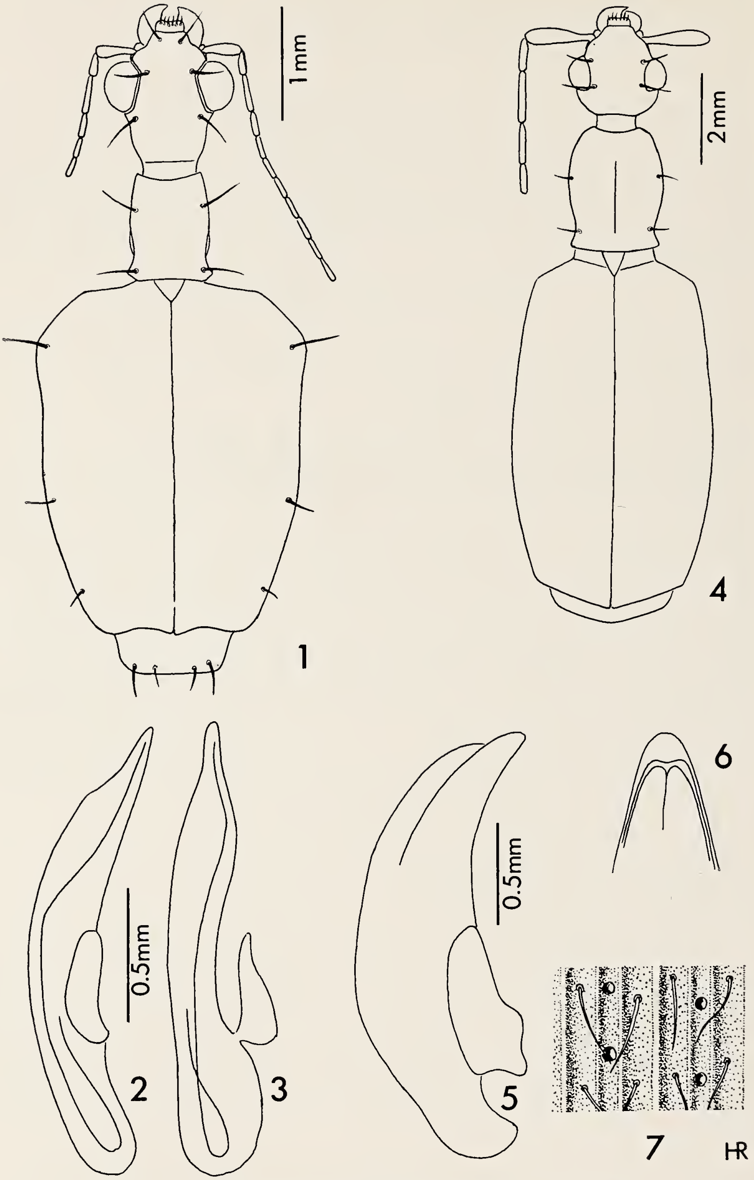

REICHARDT — CARABIDAE

Galeritula pilosa, n. sp.
(Figs. 4-7)

Description: dark brown, almost black, with lighter brown legs, antennae and mouthparts. Winged species.

Head slightly wider than long, with large prominent eyes; slightly rugose, with broad, poorly developed median carina; posterior half and sides of anterior half with long yellowish, almost erect hairs; two orbital setae. Pronotum longer than wide (length to width ratio: 1.2); as wide as head; anterior margin concave, posterior margin slightly emarginate; widest in the middle; more narrowed anteriorly; sides divergent after the constriction; surface convex, rugose; median sulcus almost erased; covered with long yellowish, backwards directed hairs; two pronotal setae. Scutellum triangular, punctured, with yellow hairs. Elytra twice as wide as pronotum, almost twice as long as wide (length to width ratio: 1.8); widest behind the middle; apex truncate; with nine carinae and two less developed carinulae between each two carinae; a row of deep punctures filling out the carinulae interspace; a row of long yellow hairs (more or less as long as interspace between two carinae) between each carina and carinula; interspaces transversely rugose; scutellar carina usually not joining the first carina (in the holotype the right one joins it). Legs (the holotype has the right middle femur bifurcated at apex), antennae, mouthparts and ventral side, very densely hairy.

Measurements: length 12.61-14.56 mm.; width 4.16-4.81 mm. (Holotype: 13 mm. × 4.16 mm.).

Types: Salobra, Mato Grosso, X. 1938, Exp. Instituto Oswaldo Cruz col. (Holotype ♂ and 4♂, 6♀, Paratypes; 1♀, Paratype, same locality, I.1955, no collector; all in the Departamento de Zoologia, São Paulo; 1♂ and 1♀, Paratypes, same data as Holotype, in the Museum of Comparative Zoology, Cambridge, Mass.

Notes: this species of *Galeritula* is well defined by its rather small size, and by the long yellowish hairs which cover it. Very similar to *G. palustris* (Liebke), of which 2♂ and 3♀ were collected together with *pilosa,* n. sp.; distinguished by its darker brown legs; by the different pronotal form; by the carinae, which are thicker than in *palustris,* and by the pilosity, which is much denser and longer in *pilosa,* n. sp.

EXPLANATION OF PLATE 7

Otoglossa tuberculosa Chaudoir: fig. 1, dorsal view; fig. 2, genitalia of ♂ from Nova Teutonia, lateral view; fig. 3, same genitalia, dorsal view; *Galeritula pilosa,* n. sp.: fig. 4, Holotype; fig. 5, lateral view of genitalia of Holotype; fig. 6, same genitalia, dorsal view; fig. 7, detail of elytral structure.

Trichognathus marginipennis Latreille

Trichognathus marginipennis Latreille, 1829, Regne Anim., 2. ed., 4:375. Type: Brazil.

Trichognathus cinctus Chaudoir, 1848, Bull. Soc. Nat. Mosc., 21(1):68. Type: Colombia. NEW SYNONYMY.

Trichognathus immarginipennis Steinheil, 1875, Col. Hefte, 13:96. Type: Muzo, Colombia. NEW SYNONYMY.

Having seen abundant material showing all possible grades of variation between typical specimens of the three described species, I consider these species as synonyms. Van Emden (1935, Rev. Ent., 5:314), pointed out that the great variation in these species, made it almost impossible to separate them, when larger series were studied. Liebke (1951, Beitr. Faun. Perus, 2:260) comes to almost the same conclusion, although he observes a geographic variation in the yellow elytral border. I cannot find geographic variation in this or any other character. In a series of specimens from Nova Teutonia, Santa Catarina, I found specimens which could be assigned to *"cinctus"* and to *"marginipennis"*, together with intermediate specimens; in another series from Dept. del Cuzco, Peru, all three "species" were represented; not only *"cinctus"* in Peru and *"marginipennis"* in Southern Brazil, as supposed by Liebke.

There is a fourth species of *Trichognathus* listed in the catalogues: *strangulatus* Lacordaire, which must be eliminated from this genus, since it was designated as type species of another genus *(Ancistroglossus)* by Chaudoir [1862, Bull. Soc. Nat. Mosc., *35*(4):307].

ANCHONUS DURYI IN SOUTHEASTERN POLYNESIA (COLEOPTERA: CURCULIONIDAE: HYLOBIINAE: ANCHONINI)[1,2,3]

By Elwood C. Zimmerman
Bishop Museum, Honolulu

It was with much surprise that I found a species of the American genus *Anchonus* Schoenherr, 1825, when collecting in southeastern Polynesia 30 years ago during the course of Bishop Museum's Mangarevan Expedition. I learned later that A. M. Adamson had found the species on Tahiti a few years before my visit there, and, more recently, N. L. H. Krauss found the weevil on Raiatea. I had intended to report upon the discovery soon after the return of the Mangarevan Expedition, but the pressure of other work delayed this note.

I am grateful to Prof. F. M. Carpenter, Harvard University, who most kindly prepared the photographs reproduced here.

Anchonus is a genus of more than 100 species and is spread widely over parts of Mexico, Central America, northern South America, the West Indies and extending to such outlying areas as the Cocos and Galapagos Islands and to Florida in the United States. The greatest numbers of species are in the West Indies and Central America. The weevils are flightless ground-dwellers, and they appear most often to be found beneath decaying wood or other vegetation on the ground.

I have identified the species found in southeastern Polynesia as *Anchonus duryi* Blatchley, heretofore recorded only from Florida in the United States. I suspect that the species of *Anchonus* recorded from Florida are introductions to that area and are possibly natives of the West Indies.

In Florida, this weevil has been found under masses of sea weed and driftwood on beaches. Such a habit may make possible its wide dispersal by man. I presume that the weevil was transported to southeastern Polynesia after it had concealed itself in cargo that may have been stored on the beach before being loaded aboard ship. It may have been carried to Tahiti by sailing ship many years ago.

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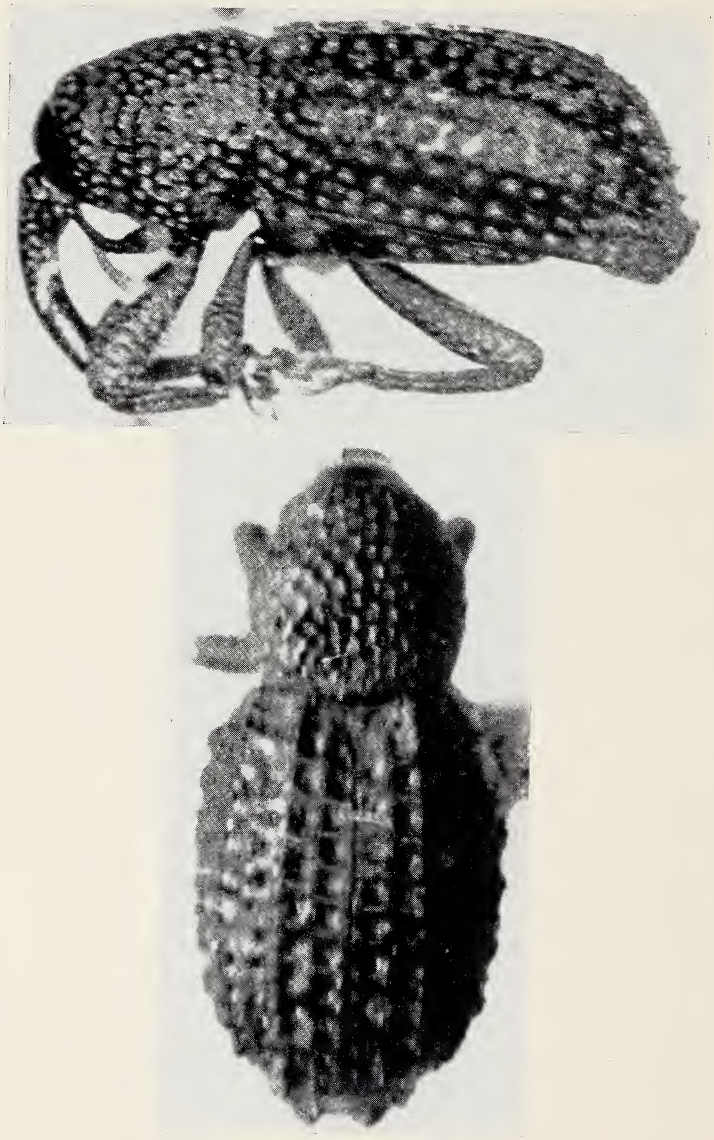
[1] A combined Pacific Entomological Survey and Mangarevan Expedition report.

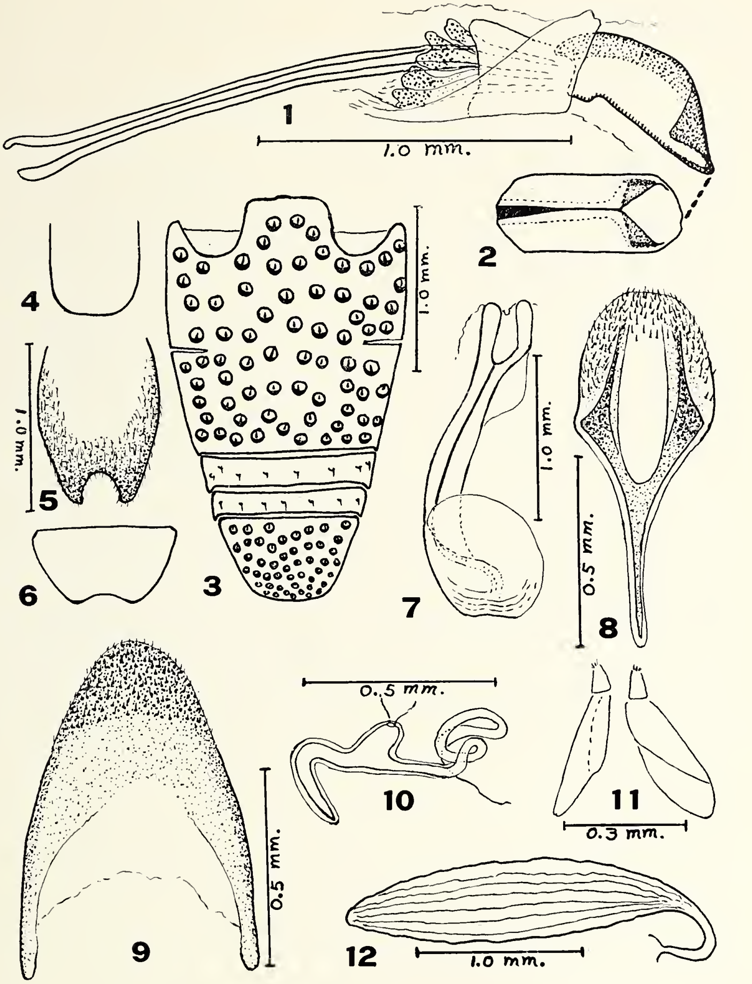
[2] Rhynchophora of Southeastern Polynesia, part 12.

[3] This is the fifth of a series of reports resulting from the project "Pacific Island Weevil Studies" made possible by National Science Foundation research grant G-18933. *Manuscript received by the editor May 1, 1964.*



EXPLANATION OF PLATE 8

Lateral and dorsal views of a female *Anchonus duryi* Blatchley from Raiatea, Society Islands. Length: 4.5 mm., excluding head. (Photographs by Prof. F. M. Carpenter.)



Figures 1-12: Anatomical details of *Anchonus duryi* Blatchley. 1, lateral view of aedeagus with phallobase ("tegumen") *in situ* (note lack of well-developed apodemes of phallobase); 2, dorsal view of apical part of aedeagus drawn to same scale as 1; 3, ventral view of abdomen of female; 4, outline of pygidium of male; 5, pygidium of female; 6, outline of ventrite five of male (compare shape of caudal margin with that of female); 7, urosternite ("spiculum gastrale") of male; 8, urosternite of female; 9, eighth tergite of female; 10, spermatheca (the convolutions vary); 11, lobes of ovipositor; 12, the single ovary (this is sclerotized and is unusual because it persists after digestion in KOH). The male specimen used for these drawings is from Tahiti; the female came from Florida, U. S. A.

This is one of a very few American Curculionidae that have become established on mid-Pacific islands.

Anchonus duryi Blatchley
Figures 1-12 and Plate 8

Anchonus duryi Blatchley, 1916, *Rhynchophora or Weevils of North Eastern America,* p. 521, fig. 114 (poor).

Distribution: Florida, U. S. A. (type locality), introduced to the Society and Gambier Islands in southeastern Polynesia. The following data from 26 specimens are new:

Society Islands. *Tahiti:* 15 specimens from Fautaua Valley, September 6, 1928, 11 of these 1 mile from the sea and at about 50 feet elevation and 4 at 2 miles from the sea at about 75 feet elevation (A. M. Adamson); 1 found beneath a log at Tiupi Bay, Papiari, March 21, 1934 (Zimmerman); 3 from the same place, April 12, 1934 (Zimmerman). *Moorea:* 1 from Faatoai Valley, about 200 feet elevation, September 23, 1934 (Zimmerman); 3 from beneath leaves in Tepatu Valley, between about 300 and 500 feet elevation, September 27, 1934 (Zimmerman). *Raiatea:* 1 from mountains near Uturoa, March, 1955 (N. L. H. Krauss).

Gambier Islands. *Mangareva Island:* 1 from between 100 and 500 feet elevation on the northeast slope of Mount Duff, May 23, 1934 (Zimmerman); 1 from near the convent at about 300 feet elevation, May 24, 1934 (Zimmerman).

THE STATUS AND AFFINITIES OF *DUVALIOPSIS* JEANNEL (COLEOPTERA: CARABIDAE)[1]

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The genus *Duvaliopsis* was established by Jeannel (1928) for a small group of endogenous, anophthalmous trechines from the Carpathian Mountains and the Transylvanian Alps of Romania, Czechoslovakia, and Poland. Although earlier authors had classified them with *Anophthalmus* Sturm, *Trechus* Clairville, or *Duvalius* Delarouzée (formerly considered a subgenus of *Trechus*), Jeannel (1928) clearly demonstrated their morphological similarity to *Trechoblemus* Ganglbauer and to North American cavernicole trechines of the genera *Pseudanophthalmus* and *Neaphaenops*. *Trechoblemus, Duvaliopsis, Pseudanophthalmus,* and *Neaphaenops* were placed in a "série phylétique de *Trechoblemus*", united by the common possession of certain characters: (1) the mentum is fused to the prementum; (2) the recurrent portion of the apical groove of the elytron is usually connected to or directed toward the 3rd longitudinal stria; (3) the copulatory sclerites (of which there are one or two) are placed laterally (anisotopic), rather than ventrally (isotopic), in the internal sac; and (4) the anterior tibiae are pubescent on the outer side.

Subsequent to 1928, additional genera in North America and Japan have been described which should probably be allied with this series (Valentine 1952, Yoshida and Namura 1952, Uéno 1956 and 1958, Barr 1960).

In the eastern United States, the largest and most widely distributed genus of cave beetles is *Pseudanophthalmus*, species of which are now known from Indiana, Kentucky, Tennessee, Alabama, Georgia, Ohio, Virginia, West Virginia, and Pennsylvania. Although found only in caves up to the present time, a few Virginia species have rudimentary eyespots, suggesting comparative recency of adopting a wholly subterranean mode of life. The absence of epigean trechines from North America which seem to share a relatively recent ancestry with *Pseudanophthalmus* and other cave genera has provoked considerable speculation on the history and evolution of the group. *Trechoides fasciatus* Motschulsky, from the Oligocene Baltic amber, could belong either to *Lasiotrechus* or *Trechoblemus* (Jeannel, 1928). This fossil demon-

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strates the presence of the series in Europe in the mid-Tertiary, but reveals nothing about the North American representatives. Morphologically, the closest known relative of *Pseudanophthalmus* is *Duvaliopsis.*

The Museum of Comparative Zoology, Harvard University, recently obtained part of the collection of Dr. Eduard Knirsch, Kolín, Czechoslovakia, which contains 44 specimens of *Duvaliopsis,* including all 8 forms treated by Jeannel in his monumental *Monographie des Trechinae* (1928). I am indebted to Dr. Philip J. Darlington, Jr., curator of entomology at the Museum of Comparative Zoology, for permission to undertake a study of these beetles.

When Jeannel (1928) established the genus *Duvaliopsis,* only 10 species of the North American *Pseudanophthalmus* were known, presenting a far narrower conception of the limits of the latter genus than is held today. The chief diagnostic characters of *Duvaliopsis* were said to be (Jeannel 1928): (1) punctures 3 and 4 of the marginal series ("fouets humeraux de la série ombiliquée") are closely applied to the marginal gutter; and (2) the transfer apparatus consists of a single copulatory piece in the form of a very long, concave spoon, bifid at the apex, the convex side facing the right side of the internal sac. *Pseudanophthalmus* differed in having: (1) punctures 3 and 4 of the marginal series farther from the marginal gutter than punctures 1 and 2; and (2) the transfer apparatus consisting of 2 pieces, not bifid.

In examining all 8 forms of *Duvaliopsis* known to Jeannel when he established the genus and in comparing them with most of the known species of *Pseudanophthalmus,* I am unable to find any consistently significant difference in the chaetotaxy of the humeral marginal set. In larger species of *Pseudanophthalmus,* especially those with moderately convex elytra, the 3rd and 4th punctures do appear farther from the gutter than the 1st and 2nd. As Jeannel himself very clearly explained (*Monographie,* III, p. 18), the relative positions of the umbilicate series are far from absolute, and are related to the hypertrophic enlargement of the external interstriae. Thus the alleged generic character would appear valid when a large, convex *Pseudanophthalmus* (e.g. *P. menetriesii* Motsch., the generotype) is compared with a *Duvaliopsis* (all of which are small and rather depressed), but would break down when the comparison is made with a small species of *Pseudanophthalmus* with depressed elytra.

The transfer apparatus of *Duvaliopsis* is indeed distinctive, but so are the many transfer apparatus types of the twenty-odd species groups of *Pseudanophthalmus.* The unusual length of the copulatory piece in itself is not diagnostic, since certain species of *Pseudanophthalmus*, e.g. the *gracilis* section of the *hubbardi* group, have equally long transfer apparatuses. Even the single copulatory piece is not peculiar, since *P. cumberlandus* Val. and its allies have but a single copulatory piece.

In conclusion, there appears to be no reason why *Duvaliopsis* should be maintained as a genus distinct from *Pseudanophthalmus*. Its distinctiveness is on the order of magnitude of the difference between various species groups of *Pseudanophthalmus*, and it is to this status which I propose it be relegated.

The study of the Knirsch material has suggested certain changes in the taxonomic arrangement proposed by Jeannel (1928). A revision is given below.

Pseudanophthalmus Jeannel

Jeannel 1920: p. 154; type species: *Anophthalmus menetriesii* Motschulsky.
SYNONYM: *Duvaliopsis* Jeannel 1928: p. 106; type species: *Anophthalmus bielzi* Miller.

bielzi group

(= *Duvaliopsis* Jeannel)

Size small (3.3-4.0 mm.), integument pubescent. Head rounded or slightly wider than long; eyes absent, their site indicated in some species by a small, oblique cicatrix; antennae about half the body length (except in *rybinkskii*). Pronotum transverse, 1/5 to 1/3 wider than long; margins arcuate in apical 1/2 to 2/3, then sloping evenly back to the hind angles with little or a very brief sinuosity; hind angles rather small, variable; disc with sparse, long pubescence. Elytra 3/5 as wide as long, subconvex or depressed; striae regular or irregular, deeply or shallowly impressed, finely punctulate (except in *bielzi*); first discal puncture at the level of the 4th marginal puncture, slightly anterior to it, or slightly posterior; apical recurrent groove highly variable, parallel or oblique to the suture, connecting with either the 3rd or 5th longitudinal stria, with or without a crochet, but always terminating well in advance of the apical puncture. Aedeagus usually arcuate and moderately slender, the basal bulb set off from the median lobe by a slight constriction, the apex attenuate with the tip reflexed (produced into the shape of a boot in *meliki*); transfer apparatus a single, elongate, spoon-shaped copulatory piece with its concave side facing the left side of the internal sac, its dorsal and ventral edges rolled and sclerotized and apically produced to give a bifid appearance; internal sac with moderate armature of small, blunt scales; parameres with 3 or 4 setae at their apices. Type species: *Anophthalmus bielzi* Seidlitz.

KEY TO SPECIES OF THE BIELZI GROUP[2]

1 Elytra with internal longitudinal striae deeply impressed, all striae more or less irregular; labrum with a rather deep, V-shaped emargination 2

Elytra with the internal longitudinal striae shallowly impressed and regular, finely punctulate; labrum shallowly emarginate 3

2(1) Elytra subconvex, striae deep and fairly regular, with little or no punctulation; humeri rounded, the prehumeral borders oblique to the median line (Romania: Transylvanian Alps) .... *bielzi* (Seidlitz)

Elytra depressed, internal striae moderately impressed, slightly irregular, and finely punctulate; humeri more angular, the prehumeral border nearly perpendicular to the median line (Czechoslovakia: Carpathians) .... *pilosellus* (Miller)

3(1) Antennae half as long as the total body length; segments VII-X thick, more than half as wide as long 4

Antennae 2/3 as long as total body length; segments VII-X slender, less than half as wide as long (Poland: Carpathians) .... *rybinskii* (Knirsch)

4(3) Humeral margin distinctly serrulate; head as long as wide 5

Humeral margin with serrulations obsolete; head slightly but distinctly wider than long (Romania: eastern Carpathians) .... *calimanensis* (Knirsch)

5(4) Aedeagus long and slender, the apex reflexed then curved downward in the shape of a boot (Romania: eastern Carpathians) .... *meliki* (Csiki)

Aedeagus robust, with a slender and briefly produced apex (Romania: Transylvanian Alps) .... *transylvanicus* (Csiki)

Most of the species are figured by Knirsch (1924) or Jeannel (1928), who also list the precise localities from which each is known.

Pseudanophthalmus bielzi (Seidlitz) new combination

Anophthalmus Bielzi Seidlitz 1867: p. 45.
Trechus (Duvalius) Bielzi: Knirsch 1925: p. 90.
Duvaliopsis Bielzi: Jeannel 1928: p. 109, figs. 1349-1352.

Pseudanophthalmus pilosellus (Miller) new combination

Anophthalmus pilosellus Miller 1868: p. 11.
Trechus (Duvalius) Bielzi pilosellus: Knirsch 1924: p. 65, figs. 3 and 8; Knirsch 1925: p. 91.

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[2] Includes only the Knirsch material; I have not seen *D. pilosellus beskidensis* Hliskowski 1942 (Ent. Listy 5: 17).

Duvaliopsis pilosellus: Jeannel 1928: p. 110, figs. 1354, 1346, and 1347.
Anophthalmus Bielzi Stobieckii Csiki: 1907: p. 574.
Trechus (Duvalius) Bielzi Stobieckii: Knirsch 1925: p. 91.
Duvaliopsis pilosellus Stobieckii: Jeannel 1928: p. 111.

Jeannel's key to species (*Monographie,* III, p. 108) is erroneous because *bielzi* is said to have angular humeri with the prehumeral border perpendicular to the median line. However, only in *pilosellus* are the humeri sharply angular and the prehumeral borders perpendicular. This is amply confirmed by Knirsch's long series of both *pilosellus* and *stobieckii.* I can find no taxonomically significant differences between these two supposed subspecies. The male genitalia are identical.

Pseudanophthalmus rybinskii (Knirsch) new combination

Trechus (Duvalius) Bielzi Rybinskii Knirsch 1924: p. 63; figs. 5 and 6; Knirsch 1925: p. 91.
Duvaliopsis pilosellus Rybinskii: Jeannel 1928: p. 111.

Pseudanophthalmus calimanensis (Knirsch) new combination

Trechus (Duvalius) Bielzi calimanensis Knirsch 1924: p. 65, figs. 4 and 7.
Duvaliopsis pilosellus calimanensis: Jeannel 1928: p. 111, fig. 1353.

These two species, *P. rybinskii* and *P. calimanensis,* are quite distinct from *pilosellus* in characters given in the key as well as in genitalic differences. Judging from strictly morphological criteria, they are probably more closely related to *meliki* and *transylvanicus* than they are to either *bielzi* or *pilosellus.*

Pseudanophthalmus meliki (Csiki) new combination

Anophthalmus Bielzi Meliki Csiki 1912: p. 537.
Duvaliopsis Meliki: Jeannel 1928: p. 114, figs. 1355, 1356, and 1357.
Trechus (Duvalius) pauperculus Knirsch 1925: p. 91.
Duvaliopsis Meliki pauperculus: Jeannel 1928: p. 114.

In the distinctive boot-shaped enlargement of the apex of the aedeagus, this species recalls a similar feature in *P. valentinei* Jeannel and *P. vanburenensis* Barr (Tennessee, U. S. A.). The other species of the *bielzi* group are possibly more closely related to each other than to *P. meliki,* but the transfer apparatus confirms their affinity with the latter species.

Pseudanophthalmus transylvanicus (Csiki) new combination

Anophthalmus Bielzi transylvanicus Csiki 1902: p. 52.
Trechus (Duvalius) transylvanicus: Knirsch 1925: p. 91.
Duvaliopsis transylvanicus: Jeannel 1928: p. 113.

In this species the head is as long as wide; the labral emargination is very shallow; the pronotum is 1 1/4 times as wide as long; the hind angles of the pronotum are acute, with a deep and very brief marginal sinuosity before them; the elytral humeri are clearly serrulate; the first discal puncture is at or behind the 4th humeral marginal puncture; and the apical recurrent groove is long and parallel to the suture, variably connected with the 5th or the 3rd longitudinal stria. The aedeagus of a topotype (Schuler Gebirge, Transylvanian Alps, Romania) in the Knirsch collection measures 0.86 mm. long, much larger and more robust than that of *pilosellus*. The apex narrows abruptly and is briefly produced. The copulatory piece measures about 1/3 of the total length of the aedeagus.

DISCUSSION

The realization that the *Pseudanophthalmus* found in caves of the eastern United States have their endogenous counterparts in the mountains of eastern Europe is primarily of zoogeographic interest. Like many disjunct distributions, this one suggests an earlier, broader distribution followed by intermediate extinction. Certainly the geographic extent of compatible trechine microenvironments would have been considerably broadened under the influence of a periglacial climate. The species of the *bielzi* group are now as closely restricted to the higher elevations (1200 meters and above, according to Jeannel, op. cit.) of the Carpathians and Transylvanian Alps as the American *Pseudanophthalmus* are restricted to caves. Both American and European species are presumably descended from winged, *Trechoblemus*-like ancestors.

Although the species of the *bielzi* group are not primarily cavernicolous, they are probably similar to forms which colonized North American caves during the Pleistocene interglacials. Endogenous *Pseudanophthalmus* have not been discovered in the eastern United States. I made a careful search of the high mountains of North Carolina and Tennessee in the summer of 1960, finding many *Trechus* (Barr 1962) but no *Pseudanophthalmus*. If we were to seek a close environmental parallel to the Carpathians and Transylvanian Alps in North America, however, we would have to look farther north, nearer to the terminal moraines of the Pleistocene glaciers. The few scattered peaks 4000 feet or higher in Virginia and West Virginia would bear careful search. A recent study of the *Pseudanophthalmus* of the Appalachian valley (Barr, in press) suggests that the cave species of that area have descended, with slight modification, from a smaller number of endogenous species. Each ancestral endogenous species is presumed to have occurred in the geographic area in which the caves are at present inhabited by closely similar, allopatric species or subspecies.

Similar patterns of speciation occur among *Pseudanophthalmus* of the *horni* group in the Bluegrass of Kentucky, where apparently two ancestral species colonized the caves. One species had a short aedeagus similar to that of *P. horni* Garman, while the other had a long, hooked aedeagus similar to that of *P. inexpectatus* Barr. A single ancestral species is postulated for the *tiresias* section of the *engelhardti* group, which occupies the Central Basin of Tennessee. Cave colonization and speciation does not seem to have been radically different in the Appalachian valley, the Bluegrass, and the Central Basin.

Patterns of trechine speciation are more difficult to explain in cave systems of the karst plains developed on Meramac and Chester limestones of the Interior Low Plateaus — specifically, the Mitchell plain of Indiana, the Pennyroyal plateau of Kentucky, and the Eastern Highland Rim of Tennessee. Here the networks of subterranean solutional openings are more extensive, and dispersal from one cave system to another takes place more readily. Here it is possible for abundant, mobile species to have (for cave trechines) fantastically extensive ranges, up to 75 miles long in *Darlingtonea kentuckensis* Valentine and 110 miles long in *Neaphaenops tellkampfii* Erichson. Here it is not uncommon for 3, 4, or even 5 species of troglobitic trechines to inhabit the same cave, a phenomenon best explained by multiple invasion.

But despite the special interest that American coleopterists may have in speculating that American *Pseudanophthalmus* descended from preadapted, montane, endogenous species like those of eastern Europe, the *bielzi* group itself deserves further careful study. With the possible exception of *P. pilosellus*, all the species are quite rare, so that morphological variation cannot be adequately subjected to statistical analysis. No useful taxonomic purpose is served by naming each local population a different subspecies, as has been done for certain European carabids (hundreds of names have been applied to *Carabus granulatus* and *C. cancellatus*, for example). It appears premature to apply the polytypic species concept to the *bielzi* group. However, extensive collecting, especially in Romania, would make possible a sound study of alpine speciation in the *bielzi* group, involving analysis of variation and comparison of existing geographic ranges with Pleistocene glacial patterns and inferred Pleistocene climatology. Few detailed studies of the flightless insects of the Carpathians have been made (Kaszab 1961). Such an investigation, while increasing the store of information on the role of the Carpathians and Transylvanian Alps as a

Pleistocene refugium, would also significantly broaden the base of our knowledge of cave colonization and speciation among trechines.

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FURTHER STUDIES OF THE BIOECOLOGY OF THE NEW ENGLAND TINGIDAE (HETEROPTERA)[1]

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Part III. Seasonal Population Trends of the Walnut Lace Bug, *Corythuca juglandis* (Fitch)

The area in which this study was made is described generally in Part I of this series, where the methods employed are also detailed (Bailey, 1963). There are two butternut trees (*Juglans cinerea* L.) near the Hyatt Avenue boundary of the College land. The smaller of the two is only about 20′ north of the roadside while the other is about 75′ from the street and approximately 60′ NW of the first butternut, which will be referred to as *Juglans* A. There is a grassy field between them.

Juglans A is only about 20′ tall with a low, spreading top. At its branch tips on the east is a tall white lilac (*Syringa vulgaris* L. var. *alba* West.) with a neglected pear tree (*Pyrus communis* L.) just beyond. By the roadside there is a red cedar (*Juniperus virginiana* L.) with a mulberry (*Morus alba* L.) growing beside it. These two trees are nearly as tall as *Juglans* A. Except for these four specimens, *Juglans* A stands in the open surrounded by a field except to the east where a tangle of shrubs and rank herbs prevails. The three main stems of *Juglans* A have the heartwood exposed on the west from the ground to a height of about ten feet. I have been told that this was the result of fire injury that occurred a few years before we moved here. In the eight years the tree has been under my observation (since the fall of 1956), the bark has grown in some from the sides of the wound but the exposed wood is now badly decayed. The somewhat stunted habit of *Juglans* A probably is due in part to this severe injury and to the heavy annual infestation by *Corythuca juglandis* (Fitch). Except on the west side, the lower branches are easily reached, making collecting convenient.

The second butternut, *Juglans B,* is tall and apparently vigorous. By estimate, its height is about 35′ and it dominates spreading ash-

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leaved maples (*Acer negundo* L.) growing under and around it to the south and east. Northwest is an old apple tree (*Pyrus malus* L.). Because of these surrounding trees, there are few branches of *Juglans* B accessible from the ground.

In the fall of 1956 large numbers of *Corythuca juglandis* (Fitch) were observed on *Juglans* A. This suggested the field work that was initiated the following spring and expanded to a study of local Tingid populations. During the 1957 season collections were taken from Juglans A at near weekly intervals from late May until early October. In 1958 and 1960, with assistance from the grants mentioned, regular weekly collections were made from both butternuts throughout the periods of lace bug activity.

For reasons not yet clear the infestation has been consistently heavier on *Juglans* A. Two conditions may have some bearing on this. As already noted, *Juglans* A has several leafy branches near the ground and there is a heavy sod of timothy (*Phleum pratense* L.) orchard grass (*Dactylis glomerata* L.) and other herbs beneath this tree. The clumps of grass culms and other low vegetation possibly provide a favorable shelter for overwintering lace bug adults. Just under *Juglans* B the ground is nearly bare because of heavier shade from the surrounding trees, and only on the east are a few branches within reach from the ground. Curiously, these two trees, with only a grassy field between them and the minor differences cited, support very different population concentrations of this lace bug as the graphs clearly show (Figures I-IV).

In 1957 seventeen collections were made and a total of 266 specimens taken. Of these 176 were females and 90 were males for a sex ratio of almost 2:1. Unlike the three season record for *C. mollicula,* however, (Bailey, 1963) totals for *C. juglandis* for the same three seasons are 1696 ♀♀ and 1505 ♂♂ — or a ratio of roughly 5:4 in favor of the females. With more collecting this would perhaps approximate even more closely a 1:1 relationship. Since the population trends for 1957 are otherwise similar to the subsequent studies, and because the interval between collections was not as regular that year,

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Explanation of Figures I, II, III and IV.

These figures present graphically the population trends for *Corythuca juglandis* (Fitch) on two specimens of *Juglans cinerea* L. for the two years specified. The curves are based on actual numbers (indicated on the left) of adult lace bugs collected on the dates given at the bottom of each figure. In each figure the uppermost curve represents the totals of all population samples for the season. Differences in the seasonal distribution of females and of males in these same collections are shown by the middle and the lowermost graphs respectively.


1958 POPULATION TRENDS
FIGURE I
CORYTHUCHA JUGLANDIS (FITCH)
ON JUGLANS A
110
100
90
80
70
60
50
40
30
20
10
TOTAL
50
40
30
20
10
FEMALES
60
50
40
30
20
10
MALES
MAY 17
25
JUNE 1
8
15
22
29
JULY 6
13
20
27
AUG. 3
10
17
24
31
SEPT. 7
14
21
28
OCT. 5
11

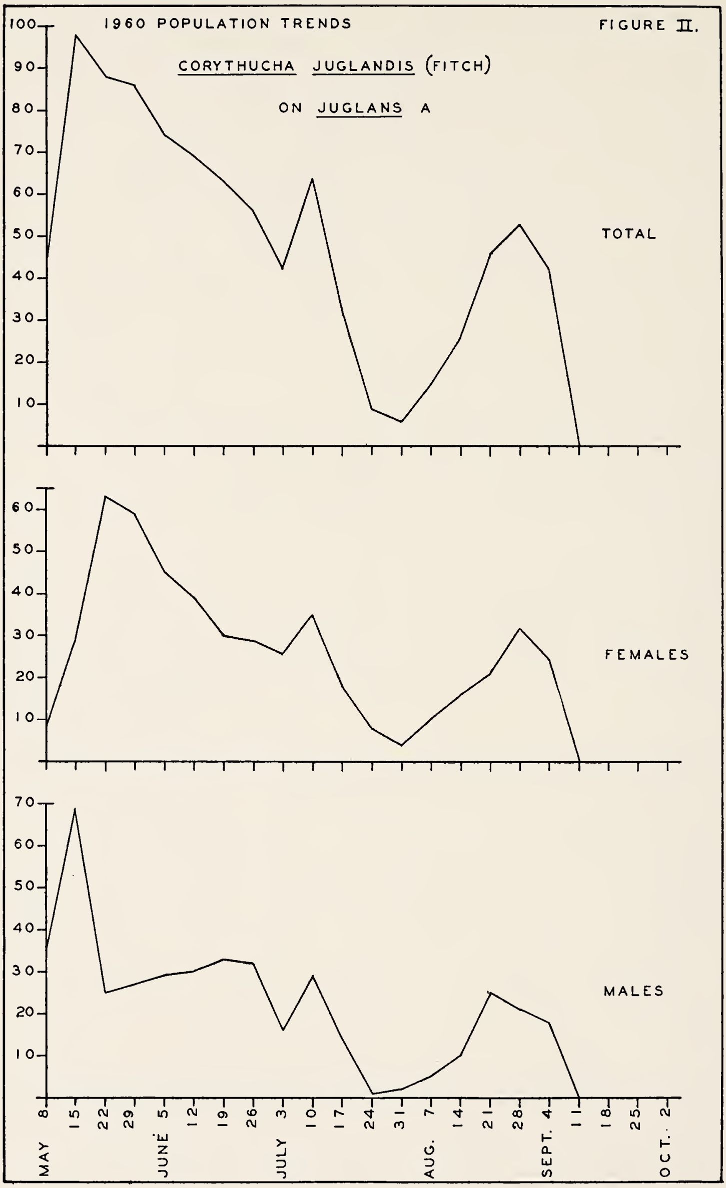

FIGURE II.

1960 POPULATION TRENDS
CORYTHUCHA JUGLANDIS (FITCH)
ON JUGLANS A
TOTAL
FEMALES
MALES
100
90
80
70
60
50
40
30
20
10
MAY 8
15
22
29
JUNE 5
12
19
26
JULY 3
10
17
24
31
AUG. 7
14
21
28
SEPT. 4
11
18
25
OCT. 2

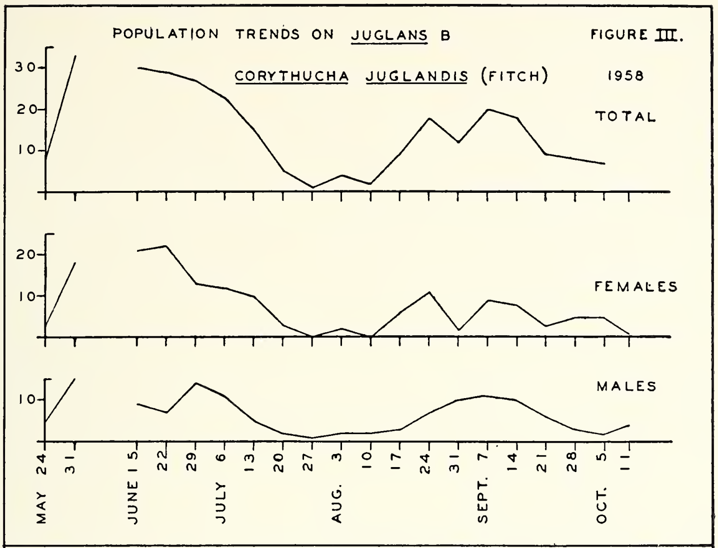

FIGURE III.

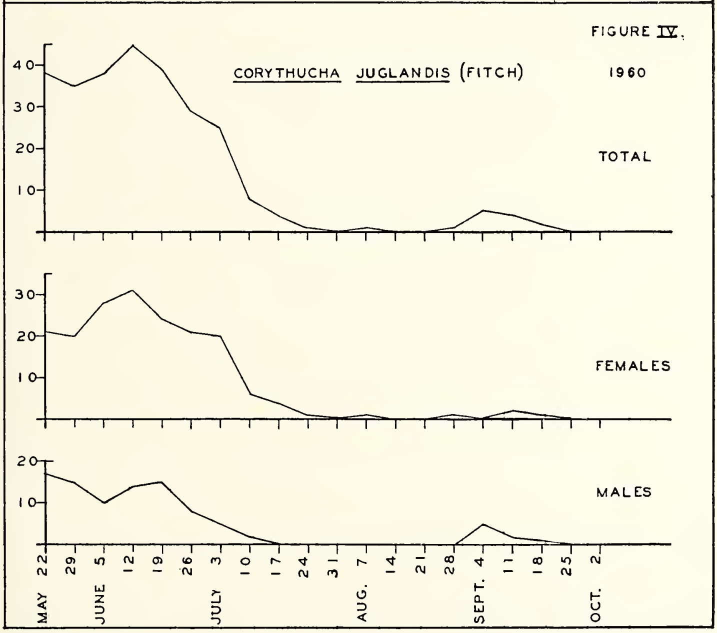

FIGURE IV.

only the collections from *Juglans* A and B in 1958 and 1960 are recorded graphically. In Part I of this series (Bailey, 1963) Figures I and II show the weekly rainfall and the weekly temperature averages for these two seasons.

Depending on climatic conditions this species is active from early May (May 8, 1960) into early October (October 11, 1958). On one occasion they were so abundant on *Juglans* A that 110 were collected in five minutes (September 7, 1958).

In 1957 a single leaf yielded 48 (31 ♀♀ and 17 ♂♂). Since the leaves of *Juglans* are large and pinnately compound, this is actually not a large number. At times, I am sure, the number on such a leaf would far exceed this. Usually these leaves consist of 15 leaflets (7-17 according to Fernald, 1950). These leaflets are oblong-lanceolate with acuminate tips and broadly rounded bases. The veins are prominent on the lower surface and both surfaces are covered with a velvety pubescence. An individual leaflet may be more than 12 cm. long and nearly 6 cm. wide. The entire compound leaf is often about 24 cm. wide by over 50 cm. long. The Tingids generally feed on the lower surface but may be seen infrequently on the upper side of the leaflet in heavy infestations.

Experimental marking of this species gave some promising results. On August 5, 1958, 100 specimens were marked with a yellow plastic paint by placing a dot on a hemielytron with a fine brush tip (or dry grass stem) while the insects were on the leaves of *Juglans* A. For several days thereafter marked specimens were seen on the host plant until as late as August 31st. Again on September 3rd more than 525 lace bugs on *Juglans* A were marked in the same manner with white paint to distinguish them from the earlier lot. Many of these were observed still feeding on the host on September 7th, and as late as September 21st marked specimens were easily located on the foliage. Although little collecting was done in 1959, a single marked specimen that had overwintered was recovered early in the season. At least under some conditions this plastic paint will adhere well and it is apparently non-toxic as used. Also, it is available in many colors and is sold inexpensively in small bottles. Further experimental use is indicated by the results of these preliminary efforts.

Figures I and II reveal an interesting contrast in the seasonal population trends of *Corythuca juglandis* (Fitch) on *Juglans* A in 1958 and 1960. In 1958 it was mid-May before leaf development and temperatures favored mass emergence of the hibernating lace bugs. Although temperature fluctuations were marked throughout the season, the lace bugs were active into early October. In 1960, however, emergence was about a week earlier and temperature changes were less marked, especially after early July. Although collections were attempted through October 2nd, no specimens were taken on *Juglans* A after September 11th. That fall the fringe of a hurricane brought strong winds and 4½ inches of rain in a storm that started on the 11th and lasted until the following evening. The night of the 17th there was a light frost. Most of the large butternut leaves were stripped off or badly tattered. The severe storm followed so soon by a frosty night sent most *C. juglandis* into hibernation nearly a month earlier than in 1958.

Lace bug numbers on *Juglans* B have been consistently small as Figures III and IV indicate. Somehow the collection for June 8, 1958 was misplaced or passed over when the data were being tabulated. This explains the break in the Figure III graphs. The storm and frost that drove the insects from *Juglans* A after September 11, 1960 did not as completely eliminate them from *Juglans* B which is somewhat more protected by the surrounding trees. On the basis of the few differences noted, it is difficult to understand why the populations on these two host plants should vary so much.

This species emerges from hibernation by early or mid-May, depending on host leaf development. By late June or early July the first brood is maturing and a second appears by mid-August or early September. In favorable seasons they may remain active into early October, but such a combination of weather conditions as occurred in early September 1960 may send most of them into hibernation a month earlier. Two annual broods are apparently usual in northeastern Massachusetts. In 1958 the second brood produced the greatest population concentration (see Figure I) while in 1960 the greatest population peak was produced by the emergence of overwintering adults (see Figure II).

It is also evident (Figures I and II) that males of this species are somewhat more numerous than the females at the beginning of the season. This was also true in 1957.

LITERATURE CITED

N. B. The names of cultivated and native plants mentioned in this paper are those used by L. H. Bailey and M. L. Fernald respectively.

The distribution and biology of *Corythuca juglandis* (Fitch) is fully reviewed and detailed references are given in my 1951 paper on the Tingoidea of New England.

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THE SPIDER GENERA *STEMMOPS, CHROSIOTHES,* AND THE NEW GENUS *CABELLO* FROM AMERICA

By Herbert W. Levi
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While examining types of theridiid spiders in European museums, I discovered that the genus *Theridiotis* Levi, 1954, is a synonym of *Chrosiothes* Simon. In the meantime, additional species have been found of *Chrosiothes,* and also of *Stemmops,* revised in 1955. In addition, in Simon's large collections from Venezuela, a theridiid spider was found that could not be placed in any known genus.

A National Science Foundation Grant (G-4317) made possible a trip to examine types. I am grateful also for the hospitality of Prof. M. Vachon of the Muséum National d'Histoire Naturelle, Paris; and Dr. G. Owen Evans, Mr. E. Browning and Mr. K. Hyatt of the British Museum (Natural History) in London. Without the unfailing help in the loan of specimens of Prof. Vachon, Dr. W. J. Gertsch of the American Museum of Natural History (AMNH), Dr. R. V. Chamberlin of the University of Utah (UU), and Mrs. D. Frizzell (Dr. H. Exline) of Rolla, Missouri, this paper would not have been possible. I would like to thank Fr. Chrysanthus who gave advice on Latin specific names. A National Institutes of Health Grant (AI-01944) facilitated completion of the paper.

Stemmops O. P.-Cambridge

Stemmops O. P.-Cambridge, 1894 (January), Biologia Centrali-Americana, Araneidea, 1: 125. Type species by monotypy *S. bicolor* O. P.-Cambridge. The name *Stemmops,* according to Bonnet (1958, Bibliographia Araneorum, 2: 4150), is of masculine gender.

Description. Eyes very large, close together, usually in a black area. Legs very strong and short. Fourth leg sometimes longer than first, fourth patella and tibia 1.5 to 1.6 times carapace length. Abdomen longer than wide; dorsoventrally flattened. Colulus replaced by two short setae. Abdomen usually with a light spot above spinnerets.

Diagnosis. Separated from other genera that bear two colulus setae by relatively large eyes, close together, and short stout legs. *Stemmops* is similar to the African *Coscinida* and differs only by having colulus setae. It is probable that *Coscinida* Simon, 1894, a name several months younger than *Stemmops,* has to be synonymized after more species have been examined (Levi and Levi, 1962).

Distribution. Stemmops is known only from America. Most species have been described and illustrated in a previous paper (Levi, 1955).

Key to *Stemmops*

1a. Males 2
1b. Females 9
2a. Embolus coiled (Fig. 9); Panama .... *servus* sp. n.
2b. Embolus not coiled 3
3a. Palpal embolus short, framed by outline of bulb or cymbium in ventral view 5
3b. Palpal embolus long, partly covering cymbium margin in ventral view 4
4a. Radix with a hook (1955, figs. 17, 18); Georgia, Gulf states, Mexico to Panama, Bahama Isl. .... *bicolor* O. P.-Cambridge
4b. Radix with a spine (1955, fig. 19); Mexico .... *lina* Levi
5a. Embolus filament thick; half as wide as area surrounded by embolus (1955, fig. 20); Yucatan, Tabasco, Honduras .... *cambridgei* Levi
5b. Embolus filament fine, one-third as wide as area surrounded by embolus (Figs. 1, 3, 6) 6
6a. Carapace sclerotized, brown; area between lateral and median eyes not black (Fig. 3); Minas Gerais, Brazil .... *vicosa* sp. n.
6b. Carapace soft, yellowish; area between lateral and median eyes black 7
7a. Distal portion of embolus almost straight, pointed distally (1955, fig. 22); eastern United States possibly to Panama .... *ornatus* (Bryant)
7b. Embolus describing a half circle, its tip pointing ectally (Figs. 1, 6) 8
8a. Area enclosed by embolus in ventral view longer than wide (Fig. 1) Venezuela .... *subtilis* (Simon)
8b. Area enclosed by embolus in ventral view subcircular (Fig. 6); Southern Mexico to Panama .... *questa* Levi
9a. Epigynum with triangular median dark area (Fig. 5); Minas Gerais, Brazil .... *vicosa* sp. n.
9b. Epigynum otherwise 10
10a. Epigynum with a median depression or dark marks (Figs. 15, 18) 11
10b. Epigynum otherwise, with an indistinct transverse lip (Fig. 12), Panama .... *servus* sp. n.
11a. A median dark mark (Fig. 15) or a median dark septum in

depression (1955, fig. 34); ducts with small loop anterior to seminal receptacles (1955, fig. 33; Fig. 14) 12

11b. Epigynum and ducts otherwise 13

12a. Duct loop anterior of seminal receptacles on their ectal side (Figs. 14, 15); Panama .... *mellus* sp. n.

12b. Duct loops anterior to seminal receptacles on their mesal side (1955, fig. 33); southern Mexico to Panama .... *questa* Levi

13a. Depression containing shadows of sclerotized areas (1955, figs. 32, 36) 14

13b. Depression otherwise 15

14a. Ducts looping anterior; seminal receptacles behind depression (1955, fig. 35); Georgia, Gulf states, Mexico to Panama, Bahama Isl. .... *bicolor* O. P.-Cambridge

14b. Duct barely anterior of seminal receptacles; seminal receptacles anterior to depression (1955, fig. 31); Yucatan, Tabasco, Honduras .... *cambridgei* Levi

15a. Depression bordered anterior (1955, fig. 30); eastern United States 16

15b. Depression bordered on sides or posterior 17

16a. Connecting ducts coiled (Fig. 17); anterior border of depression ventral to seminal receptacles (Fig. 18), Panama .... *orsus* sp. n.

16b. Connecting ducts not coiled, bent (1955, fig. 29); anterior border of depression posterior to seminal receptacles (1955, fig. 30); eastern United States .... *ornatus* (Bryant)

17a. Depression bordered on sides (1955, fig. 28); Tamaulipas .... *victoria* Levi

17b. Depression otherwise 18

18a. Duct coiled, heavily sclerotized (1955, fig. 26); Mexico .... *lina* Levi

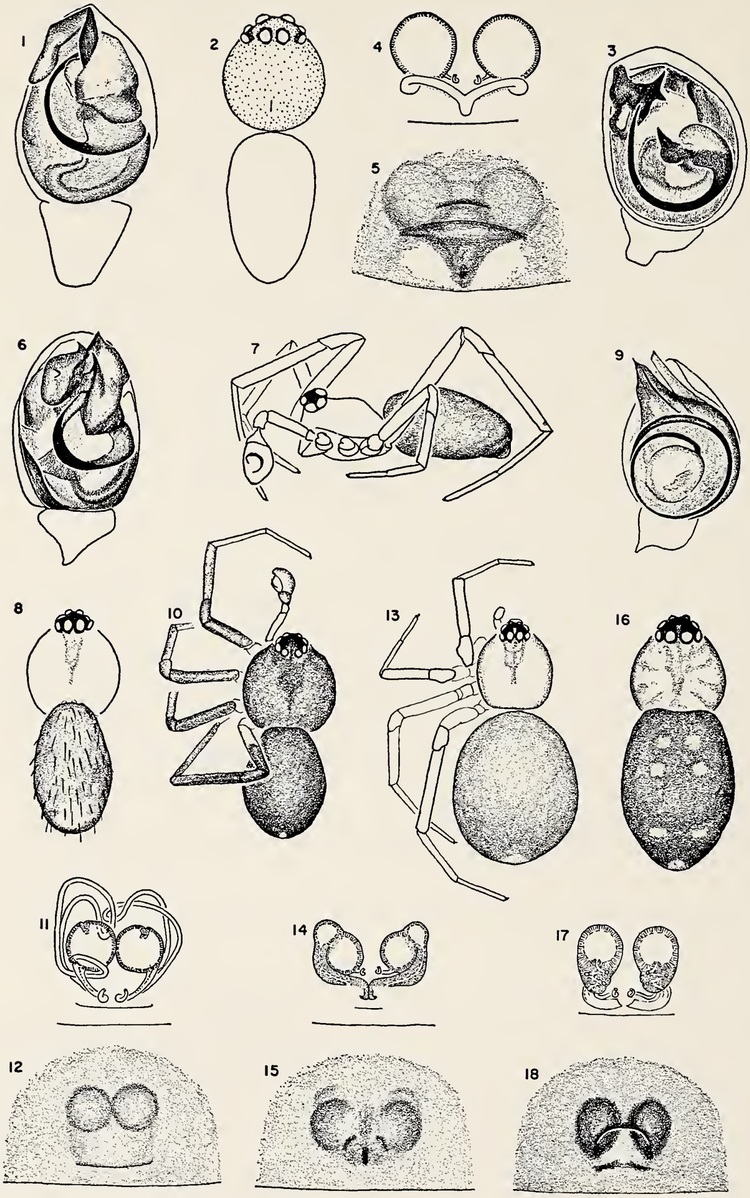
18b. Duct almost straight, lightly sclerotized (1955, fig. 23); Panama .... *cryptus* Levi

Stemmops bicolor O. P.-Cambridge

Stemmops bicolor O. P.-Cambridge, 1894, Biologia Centrali-Americana, Araneidea, 1: 125, pl. 17, fig. 5, ♂. Male holotype from Teapa, Tabasco, Mexico in the British Museum. — Levi, 1955, Ann. Ent. Soc. Amer., 48: 338, figs. 14, 17, 18, 35, 36, ♀, ♂.

Distribution. Georgia, Gulf states, Mexico, to Panama and Bahama Isl.

Additional records. Panama. Boquete (A. M. Chickering). *Panama Canal Zone.* Summit, (A. M. Chickering); Barro Colorado Island (A. M. Chickering); near Pedro Miguel (A. M. Chickering).



LEVI — STEMMOPS

Stemmops ornatus (Bryant)

Euryopis ornata Bryant, 1933, Bull. Mus. Comp. Zool. 74: 172, figs. 2, 3, ♂. Male holotype from Meridian, Lauderdale County, Mississippi in the Museum of Comparative Zoology.

Stemmops ornata, — Levi, 1955, Ann. Ent. Soc. America, 48: 341, figs. 16, 21, 22, 29, 30, ♀, ♂.

Distribution. New Jersey, Ohio, Missouri, Georgia to Mississippi.

Additional record. Missouri, Johnson Co.: Warrensburg, 29 June 1962, ♀ (W. Peck).

Stemmops subtilis (Simon), n. comb.
Figure 1

Coscinida subtilis, 1895, Ann. Soc. ent. France, 64: 137. Male holotype from San Estaban, [Carabobo], Venezuela in the Muséum National d'Histoire Naturelle, Paris, examined.

Stemmops vicosa sp. n.
Figures 2-5

Type. Male holotype from Viçosa, Minas Gerais, Brazil, 6 July 1933 (Hambleton), in the American Museum of Natural History. The specific name is a noun in apposition after the type locality.

Description. Carapace brown. Eyes ringed by black but otherwise little black between eyes. Sternum, legs yellow-brown. Abdomen whitish without pattern or marks, lighter above spinnerets in female. Carapace high and sclerotized. Eyes subequal in size. Anterior median eyes one-third diameters apart, touching laterals. Posterior median eyes slightly less than their radius apart, two-thirds diameters from laterals. Eyes of female slightly farther apart. Anterior margin of chelicerae without teeth. Abdomen of female subtriangular, of male slightly wider in front than behind (Fig. 2). Colulus replaced by two setae. Total length of female 1.6 mm. Carapace 0.54 mm long,

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EXPLANATION OF PLATE 9

Fig. 1. *Stemmops subtilis* (Simon), left palpus.

Figs. 2-5. *S. vicosa* sp. n. 2. Male. 3. Palpus. 4. Female genitalia, dorsal view. 5. Epigynum.

Figs. 6-8. *S. questa* Levi. 6. Palpus. 7-8. Male.

Figs. 9-12. *S. servus* sp. n. 9. Palpus. 10. Male. 11. Female genitalia, dorsal view. 12. Epigynum.

Figs. 13-15. *S. mellus* sp. n. 13. Female. 14. Female genitalia, dorsal view. 15. Epigynum.

Figs. 16-18. *S. orsus* sp. n. 16. Female. 17. Female genitalia, dorsal view. 18. Epigynum.

0.50 mm wide. First patella and tibia 0.60 mm; second 0.48 mm; third 0.39 mm. Fourth femur 0.59 mm; patella and tibia 0.71 mm; metatarsus 0.44 mm. Total length of male 1.4 mm. Carapace 0.52 mm long, 0.58 mm wide. First femur 0.65 mm; patella and tibia 0.66 mm; metatarsus 0.32 mm; tarsus 0.36 mm. Second patella and tibia 0.50 mm; third 0.39 mm; fourth 0.65 mm.

Diagnosis. Genitalic structure (Figs. 3-5), brown carapace and absence of black eye area separate this species from *S. bicolor* and others.

Record. ♀ paratype collected with ♂ holotype.

Stemmops servus sp. n.

Figures 9-12

Type. Male holotype from Forest Preserve, Panama Canal Zone, 29 Jan. 1958 (A. M. Chickering) in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Female with carapace yellow. dusky on sides, eye region black, sternum gray, legs yellow, abdomen gray with white spot above spinnerets. Male with carapace dark brown, sternum black, palpi colorless light. First and second coxae black, third and fourth yellow-white; all trochanters yellow-white; other leg segments black, except proximal half of fourth femora yellow-white. Abdomen black with white spot above spinnerets. Carapace subcircular. Anterior median eyes slightly smaller than others, about two-thirds their diameter apart, touching laterals. Posterior median eyes one diameter apart, touching laterals. Total length of female 1.2 mm. Carapace 0.5 mm long, 0.5 mm wide. First patella and tibia, 0.6 mm; second, 0.6 mm; third, 0.5 mm. Fourth femur, 0.6 mm; patella and tibia, 0.7 mm; metatarsus, 0.4 mm; tarsus, 0.3 mm. Total length of male 1.0 mm. Carapace, 0.5 mm long; 0.5 mm wide. First femur, 0.6 mm; patella and tibia, 0.7 mm; metatarsus, 0.4 mm; tarsus, 0.4 mm. Second patella and tibia, 0.5 mm; third, 0.4 mm; fourth, 0.7 mm.

The male and female have not been collected together. But the structure, particularly of the carapace and eye region, is very similar. The coloration, however, differs; the female is lighter.

Diagnosis. The coiled embolus of the palpus (Fig. 9) separates this species from other *Stemmops*. The epigynum (Fig. 12) has no distinguishing marks and the ducts could be found only under a compound microscope (Fig. 11).

Records. Panama Canal Zone: Forest Preserve, Jan., Feb. 1958, ♀ (A. M. Chickering).

Stemmops questa Levi
Figures 6-8

Stemmops questa Levi, 1955, Ann. Ent. Soc. America, 48: 340, figs. 33, 34, ♀. Female holotype from Chiapas, Mexico in the American Museum of Natural History.

Description. Male. Carapace yellow-white, eye region black, some median longitudinal gray pigment marks. Sternum, legs yellow-white. Abdomen gray with unpigmented yellow-white spot above spinnerets. Anterior median eyes slightly smaller than others, less than one-quarter diameter apart, touching laterals. Posterior median eyes less than one-quarter diameter apart, touching laterals. Total length 1.4 mm. Carapace 0.7 mm long, 0.5 mm wide. First patella and tibia, 0.9 mm; second, 0.7 mm; third, 0.6 mm. Fourth femur, 0.8 mm; patella and tibia, 1.0 mm; metatarsus, 0.5 mm; tarsus, 0.5 mm.

The embolus of the palpus is relatively short (Fig. 6).

The male described here has not been collected with the female, but seems to match the female in general appearance and particularly in eye arrangement.

Natural history. Found in leaf mold in Panama.

Distribution. Southern Mexico to Panama.

Additional records. Panama. Boca Toro, Changuinola Dist., 18 Jan. 1925, ♀ (F. R. Swift, AMNH). *Panama Canal Zone:* near Cocoli, 13 Jan. 1958, ♂ (A. M. Chickering); Forest Preserve, Jan., Feb. 1958, ♂ (A. M. Chickering); Experimental Gardens, 10-14 July 1955, ♀ (A. M. Chickering); Pedro Miguel, 25 Aug. 1954, ♀ (A. M. Chickering).

Stemmops mellus sp. n.
Figures 13-15

Type. Female holotype from Barro Colorado Island, Panama Canal Zone, June-July 1934 (A. M. Chickering) in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Carapace yellow-white, dusky on sides, with median dorsal gray marks. Sternum light with gray pigment and scattered small unpigmented spots. Legs yellow-white. Abdomen dorsum gray, light spot above spinnerets without pigment; venter without pigment, almost whitish. Carapace subcircular (Fig. 13). Anterior median eyes smaller than other eyes, their radius apart, touching laterals. Posterior median eyes less than a quarter of their diameter apart, touching laterals. Total length 1.7 mm. Carapace 0.6 mm long, 0.6 mm wide. First patella and tibia, 0.8 mm; second, 0.6 mm; third, 0.6 mm. Fourth femur, 0.8 mm; patella and tibia, 0.9 mm; metatarsus, 0.5 mm; tarsus, 0.4 mm.

Diagnosis. This species can be separated from *S. questa* by the internal female genitalia (Fig. 14) and by the dark marks on the anterior of the seminal receptacles in the epigynum. The dark marks are toward the lateral side of the seminal receptacles in *S. mellus* (Fig. 15) while they are median in *S. questa.*

Record. Two juvenile paratypes collected with type.

Stemmops orsus sp. n.

Figures 16-18

Type. Female holotype from Forest Preserve, Panama Canal Zone, 28 Feb. 1958 (A. M. Chickering) in the Museum of Comparative Zoology. The name is an arbitrary combination of letters.

Description. Carapace yellow, dusky on sides and in center; eye region black. Sternum dusky around edges; legs yellow. Abdomen black with three pairs of white dorsal spots and a spot above spinnerets (Fig. 16). Diameter of anterior median eyes almost half that of others. Anterior median eyes almost one diameter apart, touching laterals. Posterior median eyes one-quarter diameter apart, touching laterals. Total length 1.3 mm. Carapace 0.4 mm long; 0.4 mm wide. First patella and tibia, 0.5 mm; second, 0.4 mm; third, 0.4 mm. Fourth femur, 0.4 mm; patella and tibia, 0.6 mm; metatarsus, 0.2 mm; tarsus, 0.3 mm.

Diagnosis. Stemmops orsus differs from *S. lina* by having a transverse curved lip in the eyigynum (Fig. 18). It differs from *S. ornatus,* found in the eastern United States, by having the internal ducts coiled (Fig. 17).

Records. Panama. Boquete, 1-8 Aug. 1950, 2 ♀ paratypes (A. M. Chickering).

Chrosiothes Simon

Chrosiothes Simon, 1894, Histoire Naturelle des Araignées, 1: 521. Type species by original designation and monotypy: *C. silvaticus* Simon, 1894.

Theridiotis Levi, 1954, Trans. Amer. Micros. Soc., 73: 178. Type species by original designation. *Dipoena jocosa* Gertsch and Davis.

Description. Abdomen suboval, subtriangular or with humps on each side, and often with characteristic coloration. Venter black, particularly anterior and above pedicel. Two minute setae replace colulus. Legs sometimes noticeably thick, first or fourth the longest.

Longest patella and tibia one to two times carapace length. Male very much smaller than female.

Epigynum with an indistinct oval depression; connecting ducts in most species characteristically coiled. The male palpus has the conductor absent or minute; the cymbium is uniquely modified to hold tip of long embolus.

Diagnosis. The coloration, the coils of the internal genitalia, the superficially simple structure of the palpus, and the above mentioned modification of the cymbium separate this genus from the related *Episinus, Spintharus, Thwaitesia* and *Anelosimus.*

Distribution. The genus is known only from the Americas.

Misplaced species. Chrosiothes australis Simon, 1896, = *Anelosimus australis* (Simon). *C. porteri* Simon, 1900 = *Anelosimus australis* (Simon).

Key to species of *Chrosiothes*

1a. Abdomen with seven dorsal humps (Fig. 36), Mexico .... *litus*
1b. Abdomen with two or without humps 2
2a. Abdomen with humps or abdomen as wide or wider than long 3
2b. Abdomen without humps, longer than wide 8
3a. Abdomen width equal to length or wider than long 4
3b. Abdomen longer than wide 6
4a. Abdomen with anterior lateral humps (1954, figs, 10, 19); Texas, Tamaulipas .... *jocosus*
4b. Abdomen without humps, or humps anterior dorsal 5
5a. Palpal embolus as long as circumference of bulb (1954, fig. 6); female abdomen with transverse stripes (1954, fig. 22); Tamaulipas to Honduras .... *tonala*
5b. Palpal embolus shorter than bulb circumference (Fig. 19); female abdomen with two dark spots (Fig. 22); Arizona to Nayarit, Mexico .... *portalensis*
6a. Abdomen humps anterior (Fig. 39); California .... *iviei*
6b. Abdomen humps in middle or posterior of abdomen 7
7a. Abdomen widest in middle (Fig. 30); Jamaica .... *jamaicensis*
7b. Abdomen widest posterior (1954, figs. 11, 21); Texas, northern Mexico .... *minusculus*
8a. Abdomen widest in posterior half (1954, fig. 23); Veracruz, Mexico .... *wagneri*
8b. Abdomen widest anterior or in middle 9
9a. Abdomen suboval, rounded behind (1954, fig. 20); Utah, Colorado to central Mexico .... *chirica*

9b. Abdomen subtriangular, pointed behind 10

10a. Females 11

10b. Males 14

11a. Epigynum with small median depression, its width less than radius of seminal receptacle (Fig. 32); Est. Rio de Janeiro, Brazil .... *niteroi*

11b. Width of depression equal to shorter seminal receptacle diameter 12

12a. Depression bordered only anterior (Fig. 25); duct with only one loop (Fig. 24); Veracruz, Mexico .... *proximus*

12b. Depression bordered all around, or only on posterior (1954, figs. 34, 36) 13

13a. Dorsum of abdomen white with black spots; duct diameter near openings wider than duct near seminal receptacle (1954, fig. 35); Veracruz, Mexico to Costa Rica .... *goodnightorum*

13b. Dorsum of abdomen purplish, duct diameter of equal width (1954, fig. 37); Florida, Mexico to Ecuador .... *silvaticus*

14a. Cymbium outline subcircular in ventral view; embolus filament (except for tip) not supported by radix (1954, fig. 9); Veracruz, Mexico to Costa Rica .... *goodnightorum*

14b. Cymbium otherwise; at least distal third of embolus supported by radix 15

15a. Embolus long (1954, figs. 13, 14); Florida, Mexico to Ecuador .... *silvaticus*

15b. Embolus short (Fig. 23); Lesser Antilles .... *valmonti*

Chrosiothes jocosus (Gertsch and Davis), n. comb.

Map 1

Dipoena jocosa Gertsch and Davis, 1936, Amer. Mus. Novitates, **881**: 7, fig. 20, ♂. Male holotype from Austin, Texas in the American Museum of Natural History.

Theridiotis jocosa,—Levi, 1954, Trans. Amer. Micros. Soc., **73**: 180, figs. 1-5, 10, 19, 26, 27, ♀, ♂.

Distribution. Texas and Tamaulipas, Mexico.

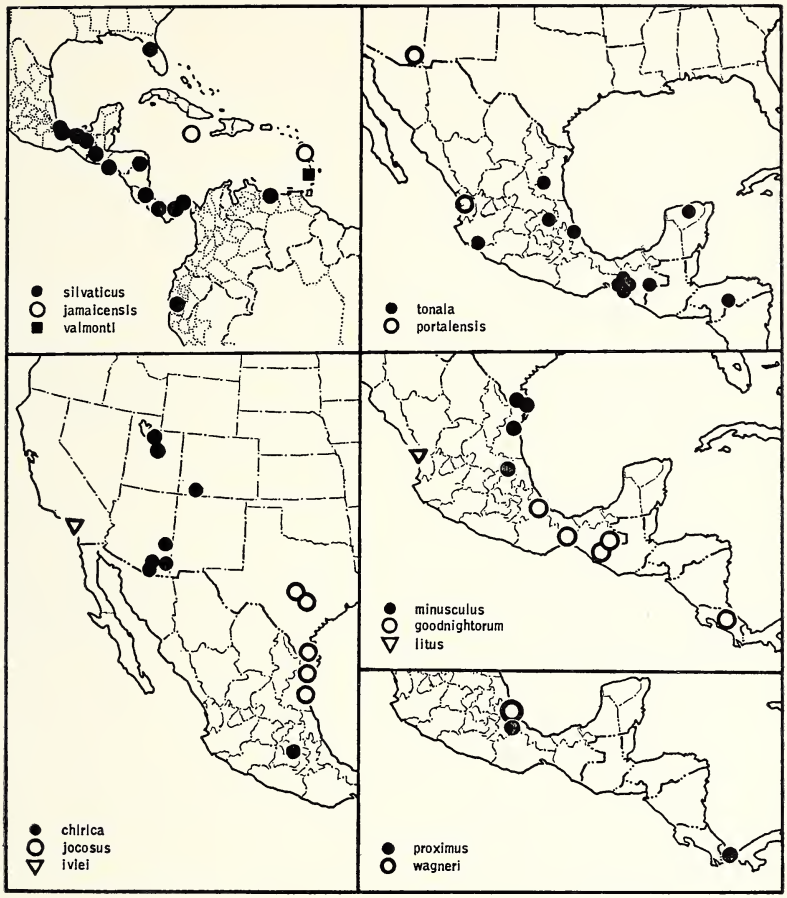
Chrosiothes minusculus (Gertsch), n. comb.

Map 1

Episinus minusculus Gertsch, 1936, Amer. Mus. Novitates, **852**: 9, fig. 9, ♂. Male holotype from five miles south of San Juan, Hidalgo County, Texas in the American Museum of Natural History.

Theridiotis minuscula,—Levi, 1954, *ibid.* **73**: 182, figs. 11, 16-18, 21, 28-29, ♀, ♂.

Distribution. Southern Texas; Tamaulipas, San Luis Potosí, Mexico.



MAP 1. Map of *Chrosiothes* species

Chrosiothes chirica (Levi), n. comb.

Map 1

Theridiotis chirica Levi, 1954, *ibid.,* 73: 184, figs. 7-8, 20, 30-31, ♀, ♂. Male holotype from Rustlers Camp, Chiricahua Mountains, Arizona in the American Museum of Natural History. The specific name is an arbitrary combination of letters as a noun in apposition.

Distribution. Utah, Colorado, Arizona to Distrito Federal, Mexico.

Additional records. Georgia: Okefenokee Swamp (AMNH), doubtful locality. *Utah:* Salt Lake Co.: 1-2 mi. up Mill Creek

Canyon, 21 Aug. 1941, ♀ (J. C. Chamberlin, UU). Emery Co.: Hughes Canyon (W. Ivie, UU).

Chrosiothes tonala (Levi), n. comb.
Map 1

Theridiotis tonala Levi, 1954, *ibid.*, 73: 185, figs. 6, 22, 32-33, ♀, ♂. Male holotype from Tonalá, Chiapas, Mexico in the American Museum of Natural History. The species is named after the type locality as a noun in apposition.

Distribution. Tamaulipas, Mexico to Honduras.

Additional records. Mexico. Colima: 16 km S of Colima, 1 Aug. 1954, ♂ (W. J. Gertsch, AMNH); Arméria, 1 Aug. 1954, ♀ (W. J. Gertsch, AMNH); Tecolapa, 31 July 1954, ♀, ♂ (W. J. Gertsch, AMNH). *Hidalgo:* Jacala, 1400 m alt., sweeping (R. Haag).

Chrosiothes goodnightorum (Levi), n. comb.
Map 1

Theridiotis goodnightorum Levi, 1954, *ibid.*, 73: 186, figs. 9, 24, 34-35, ♀, ♂. Male holotype from between Comitán and Ocotal, Chiapas, Mexico in the American Museum of Natural History. The species is named after the collectors.

Distribution. Veracruz, Mexico to Costa Rica.

Chrosiothes wagneri (Levi), n. comb.
Map 1

Theridiotis wagneri Levi, 1954, *ibid.*, 73: 188, figs. 12, 23, ♂. Male holotype from Papantla, Veracruz, Mexico in the American Museum of Natural History.

Distribution. Known only from Papantla, Veracruz.

Chrosiothes silvaticus Simon
Figure 26, Map 1

Chrosiothes silvaticus Simon, 1894, Histoire Naturelle des Araignées, 1: 521. Female holotype from Venezuela [probably Dist. Fed., Carabobo or Aragua and collected by Simon in 1888] in the Muséum National d' Histoire Naturelle, Paris, examined.

Theridion munifex O. P.-Cambridge, 1896, Biologia Centrali-Americana, Araneidea, 1: 203, pl. 24, fig. 8, ♀. Female holotype from Teapa, Tabasco, Mexico in the British Museum, examined. NEW SYNONYMY.

Euryopis probabilis O. P.-Cambridge, 1899, *ibid.*, 1: 295, pl. 39, fig. 1, ♀. Female holotype from Orizaba, Veracruz in the British Museum, examined.

Chrosiothes conservaticus Chamberlin and Ivie, 1936, Bull. Univ. Utah, biol. ser., 3(2): 32, pl. 10, fig. 81, ♀. Female holotype from Barro Colorado Island, Panama Canal Zone in the American Museum of Natural History, examined. NEW SYNONYMY.

Theridiotis probabilis, — Levi, 1954, Trans. Amer. Micros. Soc., 73: 187, figs. 25, 36, 37, ♀.

Theridiotis barrowsi Levi, 1954, *ibid.,* 73: 187, figs. 13-15, ♂. Male holotype from Hernando County, Florida in the American Museum of Natural History. NEW SYNONYMY.

The male and female have been collected at the same locality, Barro Colorado Island, and their similarity indicates that they belong together. Thus *T. barrowsi* Levi is a synonym of *C. silvaticus. Euryopis proxima* O. P.-Cambridge, which was thought to be a synonym of *E. probabilis* is, however, a separate species. Figure 26 was drawn from Simon's holotype. The internal genitalia are as in figure 37 in Levi, 1954.

Distribution. Florida, Mexico to Ecuador.

Additional records. Nicaragua: Musawas, Waspuc River, Oct. 1955, ♀ (B. Malkin, AMNH). *Panama Canal Zone.* Barro Colorado Island, numerous ♀, ♂ (W. J. Gertsch, AMNH; A. M. Chickering). Summit, July, Aug. 1950, ♀, ♂ (A. M. Chickering). *Panama:* Boquete, Aug. 1954, ♀ (A. M. Chickering); El Valle, July 1936, ♂ (A. M. Chickering). *Ecuador. Arenillas:* 20 km SE of Machala, 1 Nov. 1942, ♂ (E. L. Moore).

Chrosiothes proximus (O. P.-Cambridge), n. comb.

Figures 24-25

Euryopis proxima O. P.-Cambridge, 1899, Biologia Centrali-Americana, Araneidea, 1: 296, pl. 39, fig. 2, ♀. Female holotype from Orizaba, Veracruz in the British Museum, Natural History, examined.

Note. This species, which was considered in my previous paper to be the same as *C. silvaticus* Simon, is distinct. Though superficially similar, the connecting ducts of the internal genitalia are very short (Fig. 24) in *C. proximus.* The drawings were made from the holotype. I have some doubt that the type locality is correct, as large collections from Veracruz have not revealed additional specimens.

Records. Panama. El Volcan, Chiriquí, 20 March, 1936, ♀ (W. J. Gertsch, AMNH); Chiriquí, 1938, ♀ (R. V. Chamberlin, UU).

Chrosiothes valmonti (Simon), n. comb.

Figure 23

Dipoena valmonti Simon, 1897, Proc. Zool. Soc. London, p. 863. Male holotype from St. Vincent Island, Lesser Antilles in the British Museum, examined.

Chrosiothes jamaicensis sp. n.

Figures 27-30

Type. Female holotype from Liguanea, St. Andrew Parish, Jamaica, West Indies, October 1957 (A. M. Chickering) in the Museum of Comparative Zoology. The species is named after the island of the type locality.

Description. Carapace brown with irregular dusky marks in eye region, and on sides and middle; eyes on reddish areas. Sternum brown, gray on sides. Legs yellowish to brown with indications of dusky marks on venter. Abdomen with two humps (Fig. 30), dorsum black, white and mottled gray; venter black. Male is lighter yellowish with a wide median dorsal longitudinal band on carapace. Eyes subequal in size, laterals on slight tubercles. Anterior median eyes one diameter apart, almost touching laterals. Posterior eyes one diameter apart in female, one-third diameter in male, their radius from laterals in male. Total length of female 2.9 mm. Carapace 1.04 mm long, 1.00 mm wide. First femur 1.50 mm; patella and tibia 1.62 mm; metatarsus 1.47 mm; tarsus 0.65 mm. Second patella and tibia 1.04 mm; third 0.82 mm; fourth 1.50 mm. Total length of male 1.6 mm. Carapace 0.65 mm long, 0.57 mm wide. First femur 0.93 mm; patella and tibia 1.06 mm; metatarsus 0.88 mm; tarsus 0.48 mm.

Variation. The specimens from Dominica have a longer abdomen and higher humps.

Diagnosis. The female resembles *Episinus amoenus* Banks, but has very different internal genitalia (Fig. 28). The male is very different. The species has to be placed in the genus *Chrosiothes.* The palpus (Fig. 27) suggests that it is probably close to *C. wagneri* but the shape of the radix, the embolus supporting structure, differs.

Natural history. The species has been found under ledges on Dominica.

Records. Jamaica: 15 km W of Red Hills Road, St. Andrew Parish, Nov. 1957, 2 ♀ paratypes, (A. M. Chickering); Long Mountain, 5 Dec. 1955 (C. Underwood); Guanaboa Vale, St. Catherine Par., Nov.-Dec. 1957, ♀ paratype, (A. M. Chickering). *Dominica:* Jacks Walk above Roseau, July 1958, ♀ ♂ (S. Lazell, AMNH).

Chrosiothes niteroi sp. n.

Figures 31-33

Type. Female holotype from Niterói, Est. Rio de Janeiro, Brazil, in the Muséum National d'Histoire Naturelle, Paris (no. 9143). The specific name is a noun in apposition after the type locality.

Description. Carapace, sternum olive-gray. Legs yellow with narrow gray rings. Abdomen spotted with white, gray and black pigment on dorsum (Fig. 33); black on venter with many fine light yellow spots where pigment is lacking. Carapace slightly pointed between anterior median eyes. Eyes subequal in size. Anterior median eyes their radius apart, touching laterals. Posterior median eyes their radius apart, one-third diameter from laterals. Total length 1.8 mm. Carapace 0.68 mm long, 0.66 mm wide. First patella and tibia, 0.89 mm; second, 0.62 mm; third, 0.53 mm. Fourth femur, 0.85 mm; patella and tibia, 0.89 mm; metatarsus, 0.60 mm; tarsus, 0.47 mm.

Diagnosis. Chrosiothes niteroi has a much smaller depression in the epigynum (Fig. 32) than other *Chrosiothes.*

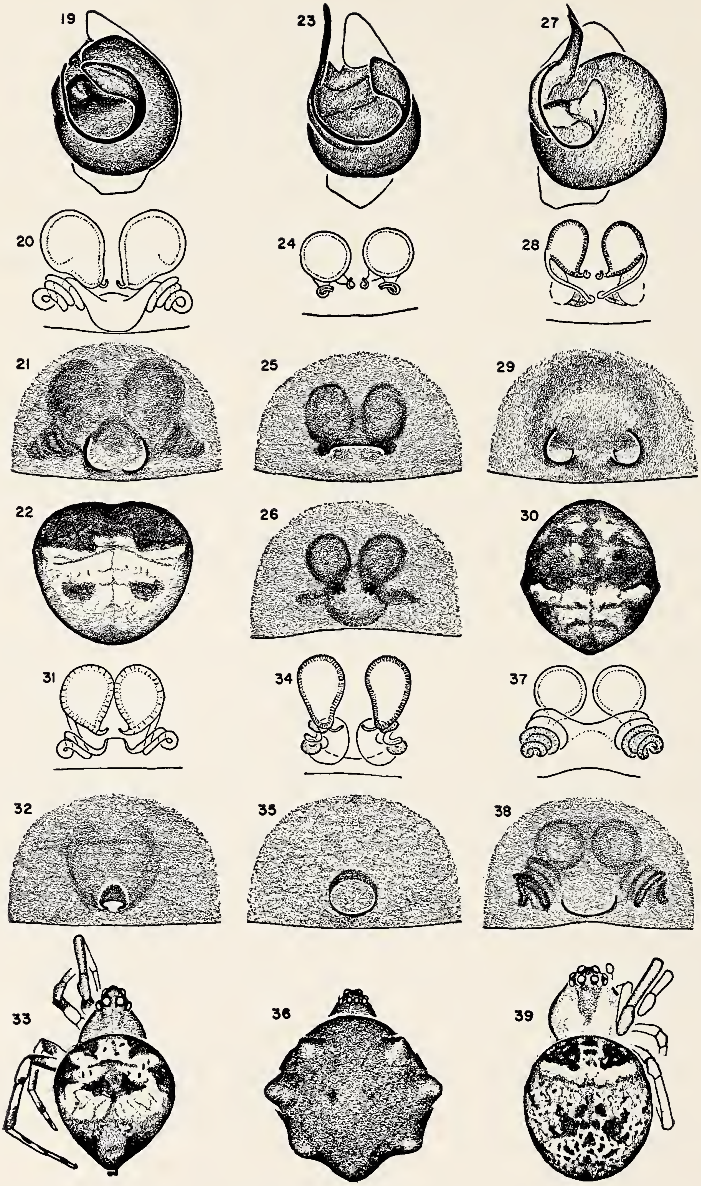
Chrosiothes iviei sp. n.
Figures 37-39

Type. Female holotype from Fish Springs, Salton Sea, Imperial County, California, 2-12 March 1941 (A. and W. Ivie), in the American Museum of Natural History. The species is named after its collector.

Description. Carapace yellowish with a dusky median band as wide as eye region in front, narrowing behind, and a narrow black border. Area around eyes reddish. Sternum yellow, dusky on sides. Legs yellowish with wide brown rings on distal ends of femora and tibiae. Abdomen white with dusky and black pattern (Fig. 39) on dorsum; venter white with irregular black streaks; black anterior and above pedicel. Eyes subequal in size. Anterior median eyes one diameter apart, less than one-quarter from laterals. Posterior eyes two-thirds their diameter apart. Abdomen suboval with slight lateral humps anterior (Fig. 39). Total length 2.0 mm. Carapace 0.75 mm long, 0.75 mm wide. First patella and tibia 1.06 mm; second 0.68 mm; third 0.57 mm. Fourth femur 1.17 mm; patella and tibia 1.06 mm; metatarsus 0.82 mm; tarsus 0.50 mm.

Diagnosis. The epigynum has no distinct structures (Fig. 38), but the ducts (Fig. 37) are slightly different from those of other species. The abdomen shape (Fig. 39) separates this species from *C. chirica.*

Record. California. Orange Co.: Laguna Beach, 27 July 1931, ♀ paratype, (W. Ivie, AMNH).



LEVI — CHROSIOTHES

Chrosiothes portalensis sp. n.

Figures 19-22

Type. Male holotype from Southwestern Research Station, 5 miles west of Portal, Cochise County, Arizona, 5-15 Aug. 1955 (W. J. Gertsch), in the American Museum of Natural History. The species is named after the type locality.

Description. Carapace light brown, gray on sides and head region, reddish around eyes. Sternum yellow-brown, black around margins. Legs yellow-brown; proximal ends of femora lighter. Dorsum of abdomen white, sometimes with a pair of indistinct gray spots; anterior of dorsum black (Fig. 22). Venter black or gray except for light area anterior to spinnerets. Eyes subequal in size, laterals on slight tubercles. Anterior median eyes of female one diameter apart, one-quarter diameter from laterals. Posterior median eyes their radius apart, two-thirds diameter from laterals. Eyes of male slightly closer together. Abdomen subtriangular with a pair of anterior humps on dorsum (Fig. 22). Total length of female 2.7 mm. Carapace 0.78 mm long, 0.85 mm wide. First femur 1.04 mm; patella and tibia 1.12 mm; metatarsus 0.65 mm; tarsus 0.41 mm. Second patella and tibia 0.78 mm; third 0.59 mm; fourth 0.92 mm. Total length of male 1.1 mm. Carapace 0.54 mm long, 0.52 mm wide. First femur 0.71 mm; patella and tibia 0.75 mm; metatarsus 0.45 mm; tarsus 0.32 mm. Second patella and tibia 0.57 mm; third 0.39 mm; fourth 0.58 mm.

Diagnosis. The shorter palpal embolus (Fig. 19) separates this species from *C. jocosus.* The shorter duct of the female (Fig. 20) and the different shaped abdomen (Fig. 22) separates it from *C. minusculus.*

Records. Arizona: ♀ paratype collected with holotype. *Nayarit.* 24 km N of Tepic, 25 July 1954, ♀, ♂, (W. J. Gertsch, AMNH).

EXPLANATION OF PLATE 10

Figs. 19-22. *Chrosiothes portalensis* sp. n. 19. Left palpus. 20. Female genitalia, dorsal view. 21. Epigynum. 22. Female abdomen, dorsal view.

Fig. 23. *C. valmonti* (Simon), palpus.

Figs. 24-25. *C. proximus* (O. P.-Cambridge). 24. Female genitalia, dorsal view. 25. Epigynum.

Fig. 26. *C. silvaticus* Simon, epigynum.

Figs. 27-30. *C. jamaicensis* sp. n. 27. Palpus. 28. Female genitalia, dorsal view. 29. Epigynum. 30. Female abdomen, dorsal view.

Figs. 31-33. *C.. niteroi* sp. n. 31. Female genitalia, dorsal view. 32. Epigynum. 33. Female.

Figs. 34-36. *C. litus* sp. n. 34. Female genitalia, dorsal view. 35. Epigynum. 36. Female.

Figs. 37-39. *C. iviei* sp. n. 37. Female genitalia, dorsal view. 38. Epigynum. 39. Female.

Chrosiothes litus sp. n.

Figures 34-36

Type. Female holotype from San Blas, Nayarit, Mexico, 6 August 1947 (C. M. Goodnight, B. Malkin) in the American Museum of Natural History. The specific name is an arbitrary combination of letters.

Description. Carapace, sternum, legs dark brown. Distal end of third and fourth tarsi yellow-white. Abdomen black with scattered small white pigment spots, most distinct on humps. Eyes subequal in size; anterior median eyes three-quarters diameter apart, almost touching laterals. Posterior eyes their diameter apart. Abdomen relatively flat, as wide as long with seven humps (Fig. 36). Total length 3.4 mm. Carapace 1.2 mm long, 1.2 mm wide. Third patella and tibia, 0.9 mm. Fourth femur, 2.0 mm; patella and tibia, 2.0 mm; metatarsus, 2.1 mm; tarsus, 0.8 mm.

The specimen described is damaged and lacks first and second legs.

Diagnosis. The seven humps of the abdomen (Fig. 36) readily separates *C. litus* from all other species of *Chrosiothes*.

Cabello gen. nov.

Type species. Cabello eugeni sp. n. *Cabello* is named after the city Puerto Cabello, Venezuela and the name is of masculine gender.

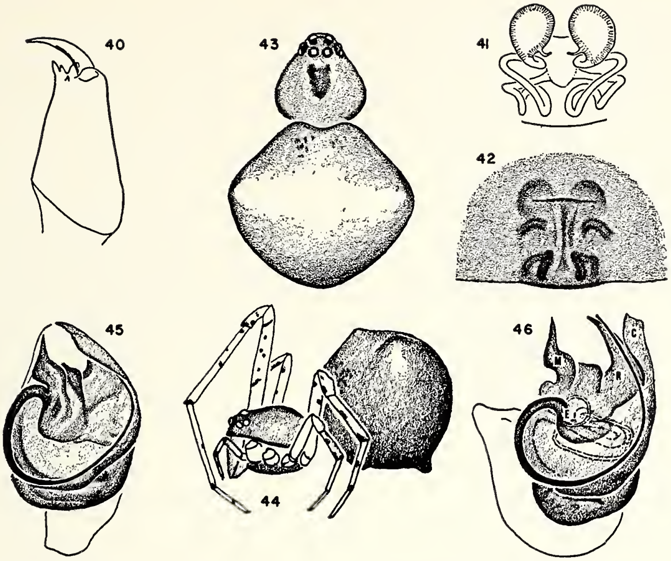
Description. Small theridiid spider with eight eyes, carapace as wide as long, first patella and tibia almost twice as long as carapace width. Chelicerae with two teeth on anterior margin, one posterior. Fourth leg with tarsal comb. Abdomen wider than long with two humps. Colulus lacking. Female genitalia with winding duct. Palpus has all sclerites: median apophysis, radix, conductor (Fig. 46).

Diagnosis. This genus differs from *Theridion* and *Achaearanea* in having the abdomen wider than long, with two humps, and in having the left embolus pointing counterclockwise. It differs from *Achaearanea* in having a radix in the palpus; from *Theridula* in having a more complex palpus with radix and median apophysis. It differs from *Chrosiothes* and *Episinus* by lacking a colulus.

Cabello eugeni sp. n.

Figures 40-46

Type. Male holotype from "Corosal, Puerto Cabello", Venezuela, 1888 (E. Simon), in the Muséum National d'Histoire Naturelle, Paris (no. 10959). Corosal was a coffee plantation on the north slope of Mt. Silla (Dist. Fed.), Puerto Cabello is in the state Cara-



Figs. 40-46. *Cabello eugeni* sp. n. 40. Left female chelicera, inside view. 41. Female genitalia, dorsal view. 42. Epigynum. 43-44. Female. 45-46. Left palpus. 46. Expanded (C, conductor; E, embolus; M, median apophysis; R, radix).

bobo. The specimens were marked as coming from both places. The species is named after its collector.

Description. Carapace yellow-white, reddish in eye region with a dusky median longitudinal band. Sternum whitish, gray on sides. Legs yellow-white with scattered black spots on anterior face. Abdomen with scattered white pigment spots, more dense on dorsum between humps. Some gray pigment on each side above spinnerets. Eyes subequal in size. Anterior median eyes one diameter apart, almost touching laterals. Posterior median eyes a little less than their diameter apart, one diameter from laterals. Eyes of male slightly farther apart. Chelicerae with two teeth on anterior margin, one on posterior (Fig. 40). Abdomen wider than long, quite variable in different specimens, but narrowest in males. Total length of female 2.0 mm. Carapace 0.71 mm long, 0.65 mm wide. First femur, 1.20 mm; patella and tibia, 1.23 mm; metatarsus, 0.91 mm; tarsus, 0.39 mm. Second patella and tibia, 0.80 mm; third, 0.52 mm; fourth, 0.82 mm. Total length of male 1.6 mm. Carapace 0.71 mm long, 0.63 mm wide. First femur, 1.43 mm; patella and tibia, 1.58 mm;

metatarsus, 1.16 mm; tarsus, 0.42 mm. Second patella and tibia, 0.98 mm; third, 0.58 mm; fourth, 0.81 mm.

Record. 2 ♀, 1 ♂ paratypes in the same collection as holotype.

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A FOSSIL ANT COLONY: NEW EVIDENCE OF SOCIAL ANTIQUITY*

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Biological Laboratories, Harvard University

The fossil remains which will be described below are of exceptional interest for two reasons: (1) they are the first ant fossils to be reported from Africa south of the Sahara and (2) they comprise what appears to be a fragment of a colony preserved as a unit, thus constituting the first fossil insect colony ever recorded. From the sample we have been able to make measurements of the worker polymorphism and certain deductions concerning the biology and social structure of an ant species as it lived in the lower Miocene over 30 million years ago.

We are indebted to the Trustees and Director of the Coryndon Museum for the opportunity to study this unique material, which was collected by Dr. and Mrs. L. S. B. Leakey in the Lower Miocene deposits of Mfwangano Island, Lake Victoria, Kenya. Professor A. E. Emerson first identified the specimens as ants, realized their potential significance, and forwarded them to us for examination. The research program of which the study became a part is currently supported by Grant No. GB 1634 from the National Science Foundation.

Oecophylla leakeyi Wilson and Taylor, new species
(Subfam. Formicinae, Tribe Oecophyllini)

Diagnosis. Distinguished from all other known species of the genus, living and fossil, by the large size of both worker subcastes; by the massive, cordate head of the major worker; and by the presence of well developed ocelli in the major worker. All of these characters are illustrated in Figure 2.

The mesosoma is stouter than in the two living species *(longinoda, smaragdina)* and in the Miocene species *sicula;* in this regard its structure is closer to the Eocene species *brischkei.* The petiole is not well enough preserved in any of the *leakeyi* specimens to permit a meaningful comparison with the same structure in other species. The gaster has the form typical of all other known members of the genus.

The *holotype* is the major worker head illustrated in Figure 2 and Plate 11. Its maximum width taken perpendicular to the long axis is

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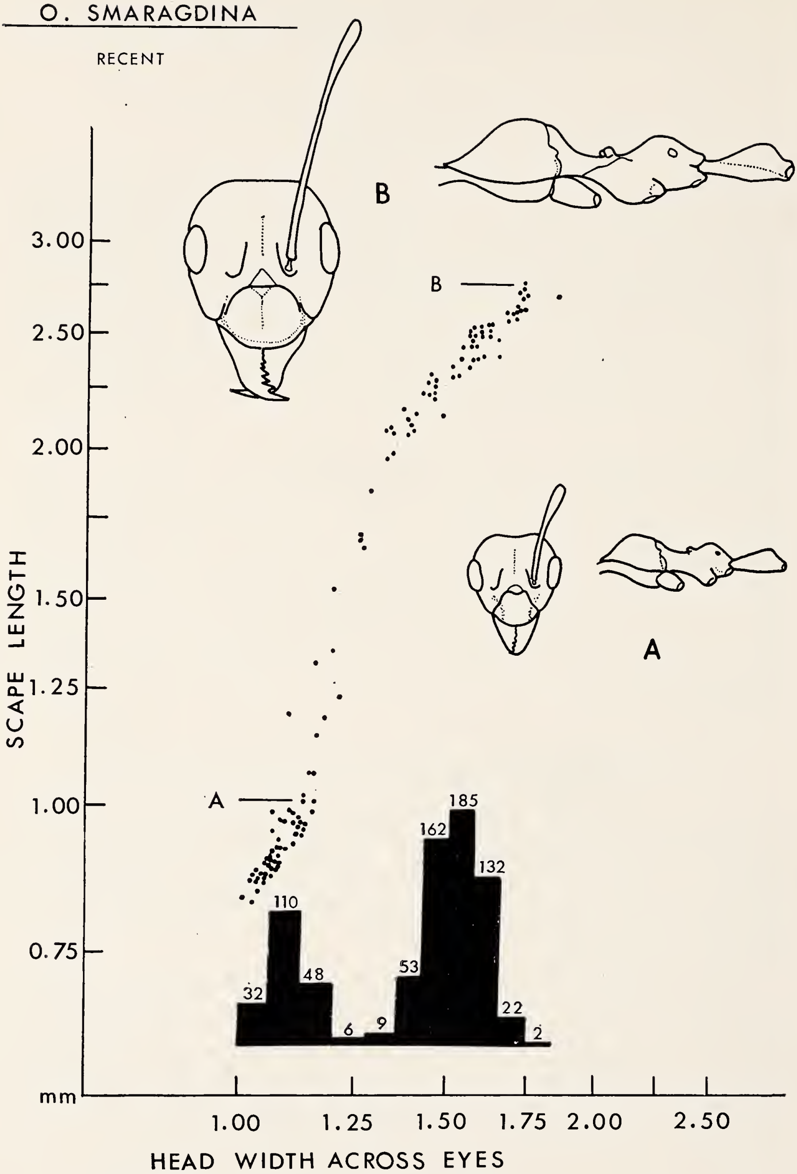


Figure 1. *O. smaragdina.* (For explanation see opposite page).

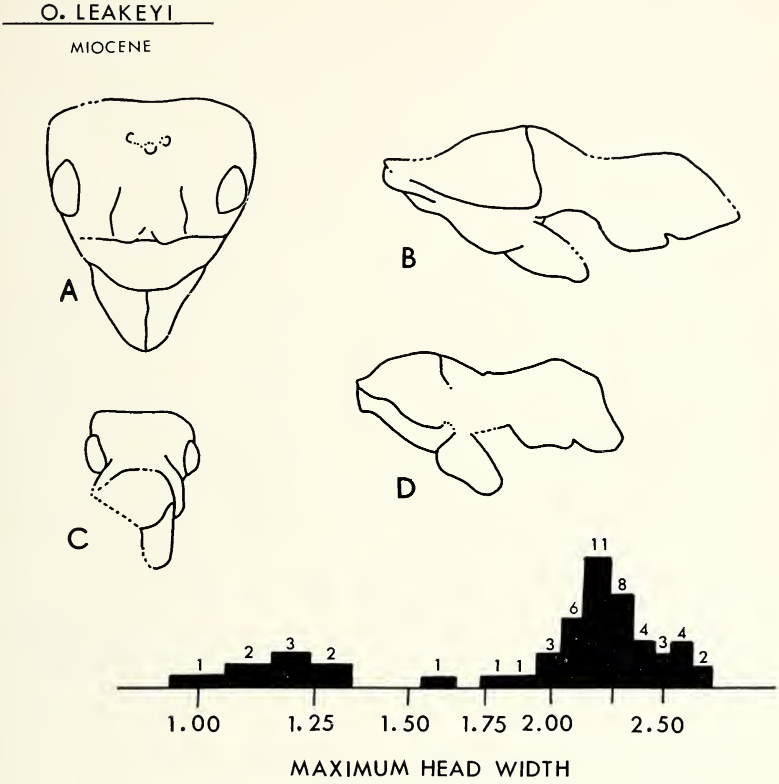


Figure 2. *O. leakeyi*

Figures 1-2. *The comparison of worker polymorphism in the Miocene Oecophylla leakeyi with that in the living O. smaragdina.* In Figure 1 (opposite page), the size frequency curve of a large random sample from a single colony of *O. smaragdina* from Assam is given in head width units plotted logarithmically. The mesosomas and petioles of selected minor and major workers are also shown, as well as the double logarithmic plot of the scape length against head width. (Modified from Wilson, 1953). In figure 2 (above) similar data from the fossil *leakeyi* colony are given in scale with Figure 1. Pupal worker head widths are used but are closely comparable to adult worker head widths. Scape length could not be measured in this material. A, head of holotype major worker (imaginal), B, mesosoma and petiole of a major worker (imaginal), C, head of a minor worker (pupal), D, mesosoma and petiole of a minor worker (imaginal).

2.36 mm.; its length, taken from the posteriormost level of the occiput to the anteriormost level of the clypeus, is 2.19 mm. This specimen agrees well in size and structure with the heads of entire worker pupae. There can be no doubt that it is from a worker specimen.

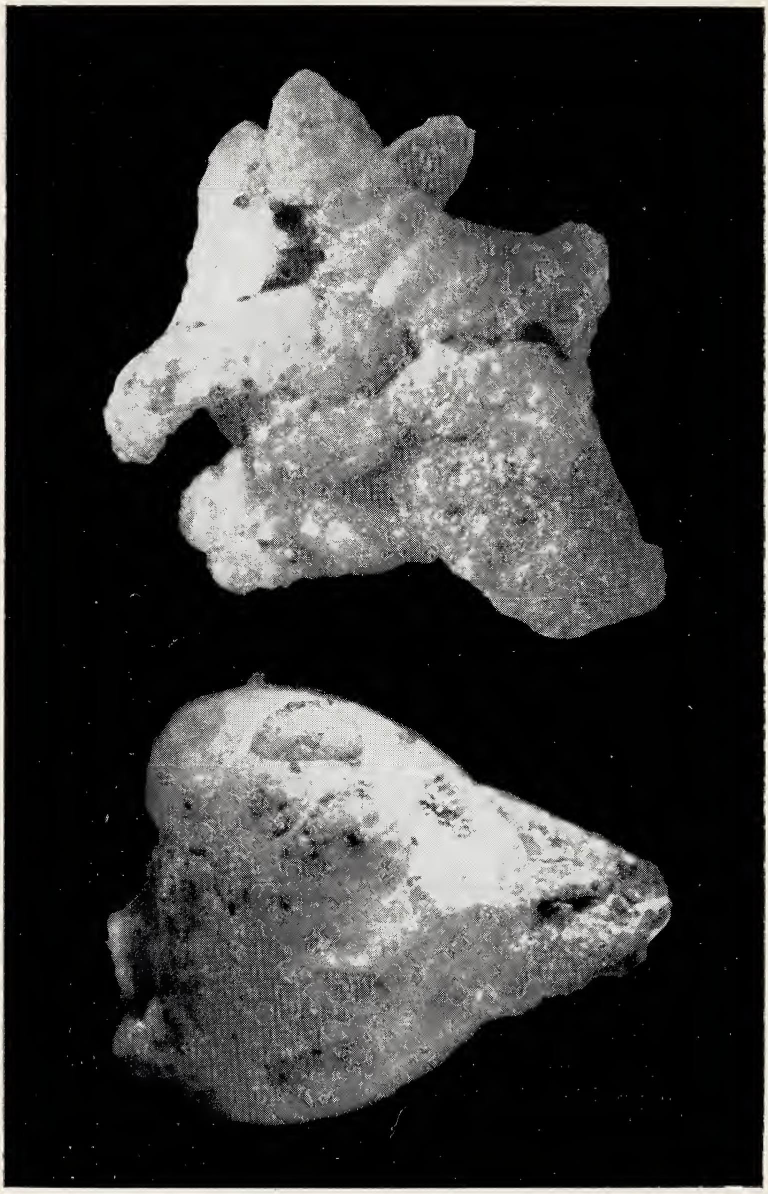
Material examined. A total of 438 specimens, including 197 larvae (perhaps including some prepupae), 105 worker pupae, 24 worker heads, 48 worker mesosomas, and 64 worker gasters. Even if the various worker body parts are assumed to have resulted from dismemberment of a smaller number of workers, the total number of individuals represented in the collection is at least 197 + 105 + 64 = 366. All of these pieces were collected together by Dr. and Mrs. Leakey in a volume of matrix about 2 feet square and several inches thick, in a Lower Miocene Deposit on Mfwangano Island, near Rusinga Island, in the Kavirondo Gulf neighborhood of Lake Victoria, Kenya. The geology of this and similar deposits in the area has been briefly reviewed by Chesters (1957). The holotype and some paratypes will be deposited in the British Museum (Natural History). Other paratypes will be placed in the ant collection of the Museum of Comparative Zoology, Harvard University, and in the Centre for Prehistory and Paleontology, Coryndon Museum, Nairobi, Kenya.

The Zoogeography of *Oecophylla*

The genus is represented by two living species: *O. smaragdina* (Fabricius) which ranges from India to the Solomon Islands and Queensland; and *O. longinoda* (Latreille), which occurs throughout most of tropical Africa. These are the famous "weaver ants" whose workers employ the mature larvae as shuttles to bind the nests together. The nests are always arboreal and consist of clusters of green leaves folded over and fastened together with larval silk. A single mature colony usually occupies many such nests scattered through one or more trees. The colonies are highly territorial, defending their trees against other ant species and larger invading animals. The workers are exclusively arboreal in their foraging, collecting varied insect prey and attending coccids. The two species are very similar in both morphology and behavior, but sufficient minor differences in morphology exist to justify their specific separation. Over most of their ranges both species are very abundant and highly adaptable. They occur in rain forests, groves of crop trees, and even shade trees along urban streets. The most complete and general studies of the biology of the genus are contained in the works by Ledoux (1950, 1954) on *O. longinoda.* Bhattacharya (1943) and Brown (1959) have reported on special aspects of the ecology and physiology of *O. smaragdina.* Variation and taxonomic relationships of the two species are discussed in the reviews of Emery (1921) and Wheeler (1922).

Oecophylla is well represented in Tertiary fossil deposits. *O. brishkei* Mayr, which closely resembles the modern forms, is moderately abundant in the Baltic amber, of Eocene age. It was represented by 50, or 0.4% of all of the 11,678 Baltic amber ants examined by G. Mayr and W. M. Wheeler jointly (Wheeler, 1914). A second, more divergent species, *O. brevinodis* Wheeler, was represented in the collections by a single specimen. Another species, *O. sicula* Emery, has been described from Upper Miocene deposits in Sicily. The species thus far mentioned form a morphocline in the increase of length of the legs, antennae and petiole, and the narrowing of the metathoracic constriction. This morphocline, which follows the geologic sequence, runs as follows: *brevinodis* → *brischkei* → *sicula* → *longinoda* (together with *smaragdina*). It seems reasonable to conclude that the species exhibit the approximate phylogenetic succession that must have occurred in the evolution of the modern species of the genus. *O. leakeyi* is a somewhat divergent member with reference to this succession, in its larger size and retention of ocelli in the major worker caste. It would appear to fall nearest to *brischkei* in the degree of mesosomal and appendage elongation. Two other species have been named on the basis of queens found in the Miocene shales of Europe: *O. obesa radobojana* (Heer) from Radoboj, Croatia; and *O. praechara* (Foerster) from Brunstatt, Alsatia. The precise relationships of these forms cannot be determined, although Mayr (cited by Wheeler, 1914) stated that *radobojana* cannot be distinguished from *smaragdina.* No New World fossils of *Oecophylla* are known, and the genus is notably absent from the rich Miocene collections from Florissant, Colorado, described by Carpenter (1930).

In sum, the picture that emerges of *Oecophylla* is that of a morphologically stable Old World genus that has persisted through most of the Tertiary with very little speciation. *Oecophylla* is related to at least two other relict, arboricolous Old World genera that date to the Eocene: *Dimorphomyrmex* and *Gesomyrmex.* Furthermore, it is not far distant from *Gigantiops,* a remarkable terricolous genus now limited to the South American rain forests. It seems appropriate to regard *Oecophylla* as both specialized and caught in an evolutionary cul-de-sac. We can speculate that its unique specializations have permitted it to remain abundant and widespread — but at the expense of blocking further significant evolution and speciation.



Wilson and Taylor — Fossil Ant Colony

The Polymorphism and Inferred Biology of *Oecophylla leakeyi*

There are good reasons to regard the Mfwangano Island material as a sample from a single colony, perhaps the contents of one nest preserved intact. In evidence is the fact that such a large number of specimens in all stages of development were recovered from a volume of roughly only one cubic foot of rock. Also, and equally important, many of the immature forms are beautifully preserved in clusters. A single group of newly hatched larvae are joined together in a typical "microlarval pile" (Plate 10). These groupings could have been preserved only if the colony had been subjected to a minimum of disturbance prior to fossilization.

When we measured the head widths of all of the adequately preserved pupal workers (the measurable adult workers were too few for our purposes) the results were startling. As shown in Figures 1 and 2 the size-frequency distribution is of essentially the same form as in the living species *O. smaragdina.* This particular distribution includes the following two important features: the separate distributions of the minor and major worker castes are nearly but not completely nonoverlapping, and the majors are *more numerous* than the minors. So far as is known, the *Oecophylla* type of distribution is peculiar to the genus among living ants (Wilson, 1953). The polymorphism in *O. longinoda* was shown independently by Weber (1949) and Ledoux (1950) to be correlated with a division of labor in which the majors do most of the foraging and nest defense and the minors serve more as nurses. The allometry of the living *Oecophylla,* involving a narrowing of the metathoracic constriction with increase in size (instead of the reverse), is also unusual if not unique among living ant species. The same kind of allometry is exhibited by *O. leakeyi.* Thus *O. leakeyi* possessed the same unusual and quite specialized features of worker polymorphism retained by the modern members of the genus. This first direct demonstration of the nature of polymorphism in an extinct ant species shows *Oecophylla* to be conservative not only in morphology but in basic social organization.

But this is not the end of the story. Further findings indicate that the *leakeyi* nest was arboreal, just as in modern species. Numerous larvae, pupae, and adults are attached directly to well preserved leaf frag-

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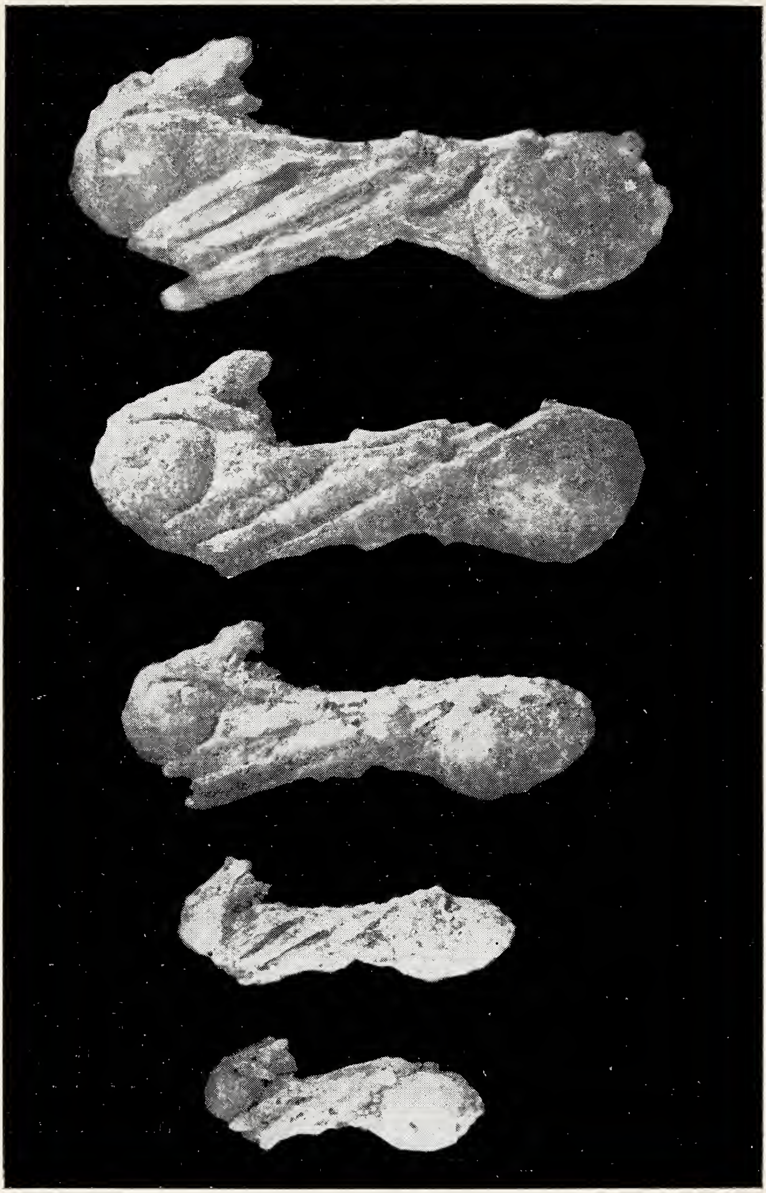
EXPLANATION OF PLATE 11

Left: head of holotype major worker, *O. leakeyi. Right:* fossilized microlarval pile of *O. leakeyi.* The maximum diameter of the larval pile is approximately 3.4 mm.



Wilson and Taylor — Fossil Ant Colony

ments. Also, the *leakeyi* pupae are not enclosed in cocoons, a negative character shared with the modern species of the genus. The absence of cocoons is a rare and probably derived character within the subfamily Formicinae (Wheeler, 1915). Cocoons are omitted by many of the diverse species of *Polyrhachis* that are arboreal and use silk produced by their larvae for nest construction. They are also omitted by certain twig-dwelling species belonging to such genera as *Camponotus (Colobopsis)* and *Gesomyrmex;* the latter genus is included on the basis of a single naked pupa recorded by Wheeler (1929). Cocoons are also lacking in two related terricolous genera, *Prenolepis* and *Paratrechina.* The great majority of formicine genera, however, are both terricolous and cocoon-makers. The absence of cocoons is, therefore, correlated, but not perfectly, with the arboricolous habit. Additional evidence favoring the proposition that the *leakeyi* colony was arboricolous is the very fact that the colony was preserved intact. It is very difficult to imagine how a subterranean or log-nesting colony could have been preserved as a unit; but it is much easier to imagine how an arboreal nest, especially the kind constructed by modern *Oecophylla,* could have broken off, dropped into the water, and been preserved with little further disturbance. The small ratio of workers to immatures suggests that the former were able to escape in part while the latter remained trapped inside the drowned nest.

Although the foregoing considerations are admittedly tenuous, something more definitive can be said about the habitat in which the *leakeyi* colony lived. The species was part of a rich arthropod fauna. The Leakeys *(in litt.)* found it in association with many hundreds of other soft-bodied insects of diverse orders, as well as arachnids. Very little of this interesting fauna has been studied. There is also abundant associated plant material. In a preliminary study of the Mfwangano and Rusinga Islands plant fossils, Chesters (1957) discerned a minimum of 17 families and 21 genera of which five are fern genera. The majority of the fossils represent living African tropical genera. "Much of the material awaiting detailed examination will probably prove to be unidentifiable owing to its mode of preservation as crystalline casts. But the report here published does give a representative picture of a Miocene flora closely akin to that of tropical Africa at the present day. . . . The large number of lianas suggests a gallery-type forest in which trees festooned with climbers overhung the water-course."

EXPLANATION OF PLATE 12

Fossil pupae of *O. leakeyi* of various sizes. The actual total length of the smallest specimen is about 4.0 mm.

SUMMARY

Oecophylla leakeyi Wilson and Taylor is described as a new species. It is from the Lower Miocene deposits of Mfwangano Island, Kenya, and is the first species of fossil ant described from Africa south of the Sahara. The type series, which contains worker subcastes, pupae, and larvae in all stages of development, is interpreted as comprising a colony fragment, the first ever recorded as a unit in the social insects. From statistical and morphological studies of the three-dimensional specimens it is concluded that the worker polymorphism conforms to the essential features that uniquely characterize the living *Oecophylla* species within the modern ant fauna. This constitutes direct evidence of the stability of a specific social system through a considerable period of time, i.e. 30 million years or longer. Other evidence is cited which suggests that the *leakeyi* colony also resembled the modern species of *Oecophylla* in that it nested arboreally in tropical rain forest.

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STUDIES ON CARBONIFEROUS INSECTS OF COMMENTRY, FRANCE: PART VI. THE GENUS *DICTYOPTILUS* (PALAEODICTYOPTERA)*

By F. M. Carpenter
Harvard University

The genus *Dictyoptilus* was established by Brongniart in 1893 for a single species, *renaulti,* based on two small wing fragments. It was placed by Brongniart in the series of Palaeozoic insects which he termed the "Sténodictyoptérides" and which he assigned to the "Primitive Neuroptera". Two very closely related species were subsequently described by Meunier (1908, 1910) in a new genus, *Cockerelliella.* Although the Meunier specimens are very well preserved, the published accounts of them by Meunier, Handlirsch, and Lameere have not included their venational details, which turn out to be very important for the determination of the phylogenetic position of *Dictyoptilus.* From a study of these fossils, made at the Laboratoire de Paléontolgie in Paris, in 1938 and 1961, I am convinced that *Dictyoptilus* is very close to the Permian genus *Eugereon* and should be included in the family Eugereonidae of the Order Palaeodictyoptera; that the venation of the hind wing of the Eugereonidae has been basically misinterpreted, the pattern being very different from that of the fore wing; and that the wings of *Eugereon* were actually long and slender, not short and broad, as formerly assumed. The reasons for these conclusions will be given after the descriptions of the Commentry fossils belonging to *Dictyoptilus.*

Family Eugereonidae Handlirsch, 1906

Eugereonidae Handlirsch, 1906, Foss. Ins., p. 388
Dictyoptilidae Lameere, 1917, Mus. Nat. Hist. Natur., Bull. 23:194

Fore wing: slender, costal margin very nearly straight, not arched; Sc long; Rs arising near wing base, with 4 or 5 main branches; stem of M arising independently at base, then aligned with R for a short distance before diverging away; M forking near the level of origin of Rs; MA unbranched; MP branched; Cu curving towards M + R at very base, then parallel to it before dividing; CuA diverging towards M shortly after its origin, unbranched; CuP forked; several

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anal veins arising from one stem. Cross veins numerous, forming a reticulation in some areas of wing.

Hind wing: shape apparently as in fore wing; Rs diverging away from Rl after its origin; base of M apparently independent of R, curved; MA arising at about level of origin of Rs, ending at the position of termination of CuA in fore wing; CuP forking into at least 4 terminal branches; CuA strongly curved.

Body structure (known only in *Eugereon*): head small, with slender haustellate beak [For details of body structures see Dohrn, 1867; Handlirsch, 1906].

This family is represented in the Commentry shales by the single genus *Dictyoptilus*.

Genus *Dictyoptilus* Brongniart

Dictyoptilus Brongniart, 1893, Recherches Hist. Ins. Foss.:390; Handlirsch, 1906, Foss. Ins.:66; Lameere, 1917, Mus. Nat. Hist. Natur., Bull., 23:103

Cockerellia Meunier, 1908, (non *Cockerellia* Ashmead, 1898), Ann. Soc. Sci. Brux., 32:154

Cockerelliella Meunier, 1909, Ann. Paléont., 4:132

Fore wing: long and slender, the length more than five times the width; posterior margin with two slight indentations, one near R5 and the other near the end of the posterior branch of MP2. Sc extending almost to wing apex, R1 terminating at very apex; Rs and MA arising at about the same level; Rs with five or more branches; MP dividing into MP1 and MP2 directly after its origin; CuA diverging towards M, as characteristic of the family, and either touching or not quite touching M; cross veins numerous; those in the costal and subcostal areas straight and unbranched; those in other areas straight or reticulate, forming a coarse, irregular network in many parts of the wing.

Hind wing: known only in *D. peromapteroides* (Meunier); shape apparently as in fore wing, with a slightly broader base; space between Rs and MA much broader than that between MA and MP.

Body unknown.

Type-species: *Dictyoptilus renaulti* Brongniart, 1893 (by monotypy).

The generic characteristics suggested above are tentative, since only one other genus, *Eugereon*, is known in the family, and since only the basal parts of the wings are known in that genus.[1] *Dictyoptilus*

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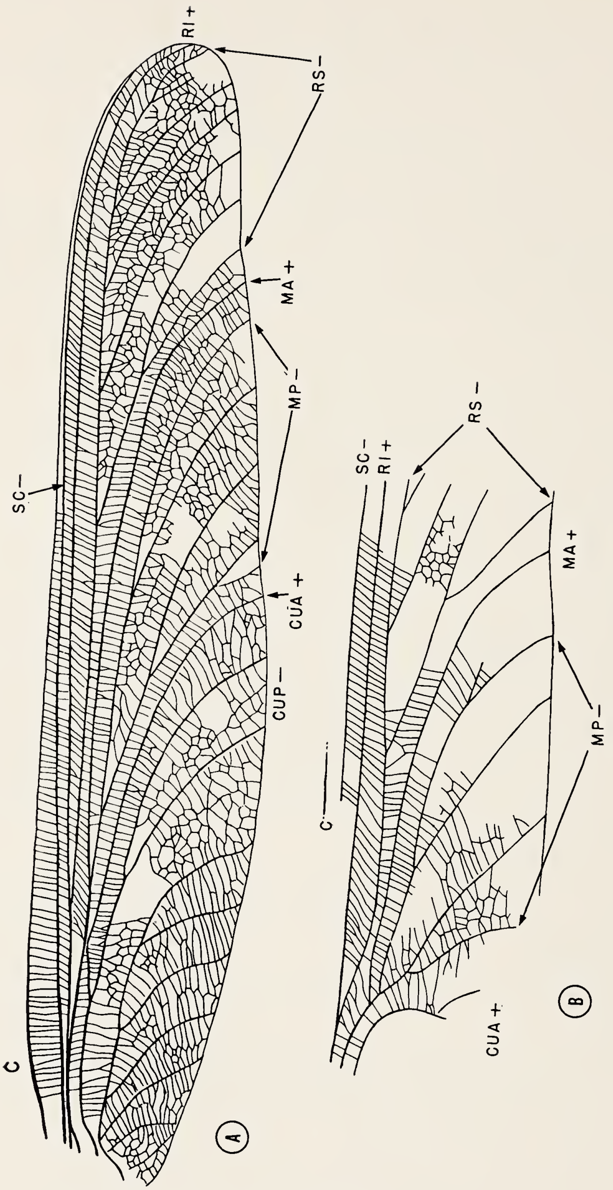
[1] The Commentry genus *Archaemegaptilus* Meunier (1908), which Lameere (1917) considered close to *Dictyoptilus*, seems to me to require family separation; the wing is relatively broad and lacks the basal divergence of CuA. The family Archaemegaptilidae, established by Handlirsch (1919, p. 13) for this genus, appears to be valid.



CARPENTER - DICTYOPTILUS

seems very similar to *Eugereon* on the basis of the parts of the wings known in both genera. The basal portions of the fore wings are, in fact, so much alike that generic distinction is not apparent; the hind wings, however, show a few differences, e.g. the area between Rs and MA in *Eugereon* is fully twice as wide as that of *Dictyoptilus.*

The type-species of *Dictyoptilus (renaulti)* is known only from two specimens, each consisting of the middle part of a fore wing. However, the venational pattern included is so much like that of the type-species of *Cockerelliella (peromapteroides)* that the generic synonomy given above seems obvious.

Dictyoptilus is at present known only from the Commentry shales, in France. Two species *(sepultus* and *peromapteroides)* have been described in addition to *renaulti.* These are quite clearly very close and might well belong to one species. However, since the specific names, which have already become established in the literature, provide convenient means of referring to individual specimens, I am treating them as distinct.

Dictyoptilus renaulti Brongniart

Dictyoptilus renaulti Brongniart, 1893, Recherches. Hist. Ins. Foss.: 391, pl. 22, figs. 13,14; Lameere, 1917, Mus. Nat. Hist. Natur., Bull. 23:103.

This species was based on the two specimens (herein designated 22-13 and 22-14) figured in Brongniart's *Recherches,* each representing middle portions of a wing. Specimen 22-14 was examined by me at the Museum National, but 22-13 could not be found in the collection. The former is presumably part of a fore wing, on the basis of its venation;[2] the venation of the hind wing beyond the basal part is unknown in *Dictyoptilus.*

Brongniart's figure of this fossil is correct, as noted by Lameere

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[2] Brongniart's figure shows a minute fragment of another wing *in front of* the wing of *renaulti,* which suggests that the latter was a hind wing. However the venation of specimen 22-14 is not like that of a hind wing, as known in *peromapteroides*; and the figures in Brongniart's *Recherches,* although generally accurate so far as the fossils are concerned, are often imaginary with respect to the presence of other fossils on the individual pieces of shale. See Carpenter 1943, p. 529-530.

EXPLANATION OF PLATE 13

Fig. A. *Dictyoptilus sepultus* (Meunier), original drawing of fore wing based on type in Laboratoire de Paléontologie, Paris. Fig. B. *Dictyoptilus peromapteroides* (Meunier) original drawing of hind wing based on type in Laboratoire de Paléontologie, Paris.

Lettering: c. costa; Sc. subcosta; RI. radius; RS, radial sector; MA anterior media; MP, posterior media; CuA, anterior cubitus; CuP, posterior cubitus; —, concave veins; +, convex veins.

(1917). The length of the specimen is 32 mm. and its width 19 mm. Comparing this fragment with the corresponding part of the complete wing of *D. sepultus* (Meunier), I estimate that the fragment is about 1/5 the total wing length, indicating that a complete wing of *reuaulti* would be about 160 mm. long.

Dictyoptilus sepultus (Meunier)

Plate 13, Fig. A; Plate 14

Cockerellia sepulta Meunier, 1910, Ann. Soc. Sci. Brux., 34:195; Meunier, 1910, Mus. Hist. Nat., Bull. 16:235, fig. 3.
Cockerelliella sepulta, Meunier, 1912, Ann. Paleont., 7:6; pl. 6, fig. 4, 4a.
Dictyoptilus sepultus, Lameere, 1917, Mus. Nat. Hist. Natur., Bull., 23:160.

This species is based on a single, excellent fossil, consisting of a complete fore wing; the veins and cross veins are very clearly preserved. In one counterpart (the obverse, with Sc concave) the distal third is missing but the rest is exceptionally clear; in the reverse, the basal quarter is missing but the distal portion is very well preserved. Figure A, plate 13, is a drawing of a complete wing, based on the two counterparts. The total wing length is 106 mm., which is about 50 mm. less than the wing length of *renaulti.* The wing of *sepultus* has a maximum width of about 20 mm. The venation presents no problems in homology, the convexities and concavities being strongly indicated. There are two noteworthy aspects of the venation, however. (1) M arises as an independent vein at the wing base, but shortly diverges anteriorly and continues in contact (but not anastomosed) with R for a short distance, forming a double vein; it then separates off as an independent vein. (2) Cu at its base is directed anteriorly but shortly runs parallel with R + M, and then divides into CuA (+) and CuP (−). CuA diverges anteriorly at this point, touching, but not anastomosing, with M before diverging away again. These unusual features are duplicated in *Eugereon,* as noted below.

Lameere (1917, p. 160) has stated that there is a small precostal space at the base of the wing. A slight thickening of the wing is visible at the base, but I am not convinced that it is actually a precostal area. Lameere also states that the subcosta terminates well before the wing apex, as it is shown in Meunier's figure (1910) and also in Handlirsch's (1919). Laurentiaux (1957) in an original figure shows Sc extending a little further than indicated in the previous figures. I am convinced from my study of the fossil (as well as of the type of *peromapteroides*) that Sc extends even further towards the apex; at any rate, it is still identifiable as a distinct vein up to that point (See plate 14).

Meunier's figure of this fossil (1910, p. 236) is unbelievably inaccurate. Handlirsch's illustration (1919, p. 12), although not so crudely done as Meunier's, is erroneous in several major respects, — i.e., short Sc, and the absence of the divergence on CuA. Laurentiaux's figure (1953, p. 423) is accurate in all important aspects, but shows a fork on the penultimate branch of Rs, instead of the terminal one.

As noted above, this species is very close to *renaulti,* but the difference in size is sufficient to retain the species as distinct.

Dictyoptilus peromapteroides Meunier
Plate 13, Fig. B

Cockerellia peromapteroides Meunier, 1908, Ann. Soc. Sci. Brux., 32:154; Meunier, 1907, Mus. Hist. Natur., Bull., 14:36, fig. 2.

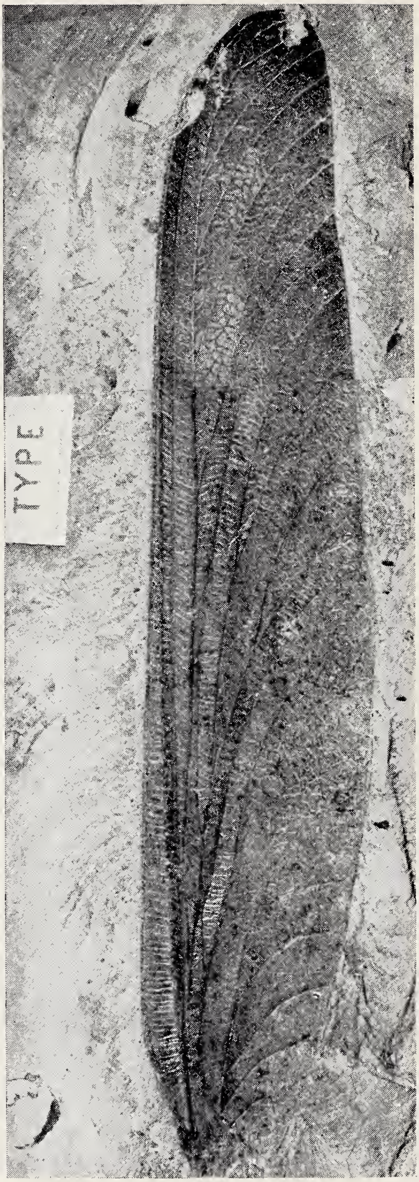
Cockerelliella peromapteroides, Meunier, 1909, Ann. Paléont., 4:132, pl. 1, fig. 3.

Dictyoptilus peromapteroides, Lameere, 1917, Mus. Nat. Hist. Natur., Bull., 23:159.

This species is based on a single specimen consisting of a nearly complete fore wing and the basal half of a hind wing; the preservation is satisfactory, although not so good as that of the type of *sepultus.* The fore wing as preserved is 130 mm. long and has a maximum width of 22 mm.; the complete length of the wing was probably about 140 mm. The venation of the fore wing seems to be very close to that of *sepultus*; in fact, it is difficult to find differences. The cross veins appear to be a little closer together than those of *sepultus* and the reticulation formed by the cross veins a little finer. The fore wing is about 25 mm. longer than that of *sepultus* and 30 mm. shorter than that of *renaulti.*

The type specimen of *peromapteroides* is especially interesting because of the presence of the hind wing, which is otherwise unknown in *Dictyoptilus.* Meunier's figure of the hind wing (1908, p. 36) is very misleading. Handlirsch's figure (1919, fig. 13), which was made by a tracing from Meunier's published photograph of the fossil, is better than Meunier's but misses many of the important features noted below. Lameere (1917) in his brief notes on *peromapteroides* makes no comment on the peculiarities of the venation of the hind wing.

The hind wing is preserved only to about the level of the middle of the fore wing; at this point it is clearly broken away. There is no indication that the hind wings were substantially shorter than the fore wing, as shown in Handlirsch's figure (1919); the distal part of the fragment of the hind wing measures 20 mm. in width, which is only 2 mm. less than the fore wing at that position. So far as is



Photograph of type of *Dictyoptilus sepultus* (Meunier). This is a composite picture, the basal two-thirds being the obverse and the distal third, the counterpart of the same specimen. Original photograph, × 1.4.

known at the present time, therefore, the hind wing was of the same length or nearly the same length as the fore wing. The accompanying drawing (Plate 13, fig. B) of the hind wing of *peromapteroides* was made from the type specimen in the Museum National in Paris in 1938 and was verified by checking with the specimen in 1961. The costal margin of the hind wing is not actually visible in the fossil; the basal part is covered up by the hind margin of the fore wing and beyond that point it is broken away; there is, at most, a faint indication of what might be a short piece of the margin just beyond the edge of the fore wing. The first vein which is clearly apparent in the wing is, therefore, the subcosta, which is preserved as a concave vein. Below that, the vein Rl is readily recognizable as a strong convex vein; its basal part is not preserved, being covered by the fore wing. Rs is very closely preserved as a concave vein but unlike Rs in the fore wing, it diverges posteriorly away from Rl and then turns towards Rl; the space between Rl and Rs is actually wider shortly after the origin of Rs than it is further along in the wing. In the part of the wing preserved, Rs gives rise, in a pectinate manner, to three concave branches, separated by several rows of cellules. Rs in the hind wing, therefore, differs from that in the fore wing by its more basal origin and earlier branching. The rest of the venation of the hind wing is even more different from that of the fore wing. The next vein, which is not obviously convex or concave, arises near the base and is slightly curved; it first gives rise to a strong convex vein, and beyond that it forks to produce two major branches, each in turn forking; this whole system is composed of concave veins. The convex vein I am identifying as MA, since it follows the distinctly concave Rs; the concave veins below that would appear to be MP. The next and only remaining vein preserved in the wing is a strongly curved, convex vein, apparently CuA; this is not preserved to its termination but the part that is present is almost semicircular. It is difficult to imagine what the distal portion of this hind wing was like; Rs was apparently extensively developed distally, no other main veins remaining. As noted above, there is no evidence that the hind wing was markedly shorter than the fore; the slight indentation of the hind margin corresponds to the first indentation of the fore wing margin. At any rate, it is obvious that the fore and hind wings in *Dictyoptilus* are remarkably different in venation — more so, in fact, than those of any other Palaedictyoptera known. The fore and hind wings of even those genera (as *Dunbaria*) which show differentiation of wing form, have a similar venation, except for the number and length of anal veins.

The Affinities of *Dictyoptilus*

As mentioned above, Brongniart, who did not accept Goldenberg's order Palaeodictyoptera, placed *Dictyoptilus* with several other genera, without formal family assignment, in his "Néuroptères Primaires". Handlirsch (1906) included the genus in the family Dictyoneuridae of the order Palaeodictyoptera. Of course, both Brongniart and Handlirsch knew the genus only by the small fragments representing the type-species, *renaulti.* In 1917 Lameere, who used a unique system of classification that virtually excluded extinct orders,[3] erected the family Dictyoptilidae for the genus and five other genera *(Archaemegaptilus, Peromaptera, Protagrion, Gilsonia,* and *Meganeura),* indicating that he was including the "Protodonates" in the Dictyoptilidae. That family along with two others (Dictyoneuridae, Fouqueidae) he included in a major division of the winged insects, the Odonatoptères. From this classification, it is apparent that Lameere regarded *Dictyoptilus* as more closely related to the obvious odonate types, such as *Meganeura,* than to the palaeodictyopterous types, such as *Dictyoneura* and *Stenodictya.* In his discussion of the group which he terms the Protodonates (1917, p. 186) Lameere gives as part of the evidence for this position of *Dictyoptilus* the presence of a precostal space at the base of the fore wing and he also points to similarities in venation between *Dictyoptilus* and such forms as *Protagrion,* which is, however, now placed in the Palaeodictyoptera (Carpenter, 1943). As noted above, I am not convinced that there is a true precostal space present in any of the specimens of *Dictyoptilus.*

Handlirsch in 1919, not accepting Lameere's synonomy of the genus *Cockerelliella* with *Dictyoptilus,* erected the family Cockerelliellidae, which he placed in the Palaeodictyoptera. He assigned *Dictyoptilus* to the family Dictyoneuridae, as previously. In his posthumously published paper of 1937, Handlirsch reviewed Lameere's classification, stating his conviction that the Dictyoptilidae of Lameere were a mixture of odonate and of true palaedictyopterous types. In this work he recognized the family Dictyoptilidae in the sense of his previous family Cockerelliellidae, placing it in the Palaeodictyoptera. In 1935 Lameere still put *Dictyoptilus* in the Odonoptères but within the Sténodictoides, thus separating it from the Odonata and Protodonata (Odonatoides).

From the above summary it is apparent that Handlirsch and finally Lameere were convinced that *Dictyoptilus* was most closely related

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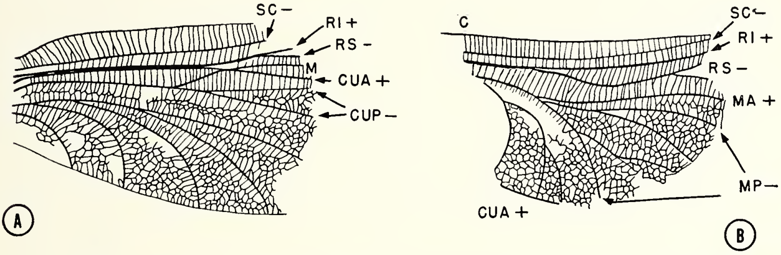
[3] The order Pseudohemiptera (=Protohemiptera) was the only extinct order recognized by Lameere.

to the primitive families (e.g., Dictyoneuridae) of the order Palaeodictyoptera. A different view has been advanced by Laurentiaux (1957), who associates it with the family Eugereonidae, which has included a single genus from the Permian of Germany, and which has become well known because of the presence of a haustellate beak. *Eugereon* was designated by Handlirsch (1906) the type-genus of a new order (Protohemiptera) but it has been included by most students of Palaeozoic insects in the Palaeodictyoptera. Lameere (1935), however, separated the group, which he termed the Pseudohemiptera, from the palaeodictyopterous families (including Dictyoptilidae) by superordinal lines. Laurentiaux (1953) has elevated the Palaeodictyoptera to a superorder and has recognized the Protohemiptera as an order within that complex. In addition to the Eugereonidae and Dictyoptilidae, Laurentiaux has included within the Protohemiptera the Protagrionidae (based on the monotypic genus *Protagrion*) and the Calvertiellidae (based on the monotypic genus *Calvertiella*). For reasons which will be apparent in the following discussion, I believe Laurentiaux is right in associating *Dictyoptilus* with *Eugereon* but I do not believe there is evidence to justify the inclusion of *Protagrion* and *Calvertiella* in the same complex.



Text-fig. 1. *Eugereon boeckingi* Dohrn. A. fore wing; B, hind wing. Original drawings based on photograph of type sent by Dr. Paul Guthörl, Lettering as in Plate 13.

A detailed study of the venation of *Dictyoptilus* indicates that this genus is actually closer to *Eugereon* than has been assumed even by Laurentiaux and, as I have mentioned above, I consider that the two belong to the same family. The basal part of the fore wing, for example, is strikingly similar to that of *Eugereon* (text-fig. 1); the stem of M arises precisely the same and forms a double vein with the stem of R, although in *Eugereon* the double vein is somewhat longer than it is in *Dictyoptilus*. The stem of Cu arises in the same fashion in both of these genera and CuA diverges anteriorly and touches the stem of M. The structure of MA and of MP is essentially the same in the two genera. The anal veins of *Dictyoptilus* are similar to those of *Eugereon* except that they are not quite so strongly curved near the base of the wing. However, it is when we compare the hind wings of these two genera that we find the similarities most striking. Rs, after its origin from Rl, diverges away the same way in the two genera and then gives rise to the first of the pectinate branches. The media is curved in both genera and produces the strongly convex MA and after a very short interval MP divides to form the two main concave branches. CuA appears in essentially the same form in both genera.

The close relationship between *Dictyoptilus* and *Eugereon* now seems obvious; the similarities of the fore wings might be due to convergence but the similarities of the remarkably specialized hind wings, even in minor venational details, make this explanation untenable. The affinities of these two genera have two interesting implications regarding *Eugereon.* Since the hind wing of *Dictyoptilus* is better and more extensively known than that of *Eugereon,* our previous interpretations (Handlirsch, 1906) of the venation of *Eugereon* now seem to require modification: the vein which has been interpreted as the media in the hind wing is actually the radial sector (Rs) and the former cubitus now turns out to be MA and MP. It might be noted in this connection that Handlirsch's figure of the hind wing of *Eugereon* (1906) shows the very beginning of a branch originating from the vein herein indicated as Rl. Since Rl very rarely carries branches in any insect (except distally), Handlirsch apparently identified this vein as the base of the radial sector, which would, of course, be consistent with his interpretation of the next vein as the media. However, no fork or branch of this vein (Rl) is shown by Dohrn in his original figure of *Eugereon* or by any of the other workers who have studied the fossil, and none shows in a photograph of the specimen sent to me by the late Dr. Paul Guthörl.[4] Furthermore, it is now obvious from the convexities and concavities preserved in the hind wing of *Dictyoptilus* that the subsequent vein (herein designated as Rs) is a concave vein and that all of its branches are concave; if this vein were the media, it should (in the Palaeodictyoptera) be convex or at any rate have a convex anterior branch (MA).

The second implication with respect to *Eugereon* is the shape of the wings. Although only the basal portions of the wings are preserved

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[4] The figure of *Eugereon* included in the Osnovy (B. P. Rohdendorf, 1961, figure 40B) shows the branch on Rl, but that illustration was copied from Handlirsch, 1906.

in the fossil, Handlirsch has presented a detailed restoration of the entire insect (1921), which shows the complete wing as curiously shaped, short and broad. Haupt (1949), basing his conclusions on the same unique specimen, has given another restoration, which shows equally strange but short wings[5]. Actually, of course, there is no evidence whatever for the peculiar shapes of the wings depicted by Handlirsch and Haupt. Indeed, from the similarity of *Dictyoptilus* to *Eugereon,* it now becomes virtually certain that the fore wing of *Eugereon* was long and slender as in *Dictyoptilus* and that the hind wing was similarly shaped.

Although the Eugereonidae, as conceived here, includes species in which the venational patterns of the fore and hind wings are markedly different, I see no reason for separating the group into a distinct order, as has been done by Laurentiaux. Very little is actually known about most genera of Palaeodictyoptera and as indicated by the history of *Dictyoptilus* and *Eugereon,* discussed above, when more information is obtained, it is usually quite different from what was expected. Attempts to divide the Palaeodictyoptera into suborders and superfamilies, as has been done by Rohdendorf (1961) or into orders, as has been done by Laurentiaux (1953) seems to me to be useless nomenclature in the present state of our knowledge of Palaeozoic insects. The evidence at hand suggest that the order Palaeodictyoptera was a very large and diverse group — far more diverse than we have realized — but still monophyletic. It seems highly probable on the basis of the history of other groups of animals that these early winged insects underwent a rapid, radial evolution, but until more structural details are known (e.g., *both* fore and hind wings, body structure, etc.), I believe we cannot untangle the numerous lines of evolution.

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[5] Both of these restorations are included in Haupt's paper (1949, page 33). The best published photograph of the actual specimen of *Eugereon* is included in Handlirsch, 1906, plate 38.

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The illustration on the front cover of this issue of Psyche is a reproduction of a drawing of a myrmecophilous histerid beetle, *Euxenister wheeleri* Mann, from Barro Colorado Island (Psyche, vol. 32, p. 173, 1925).

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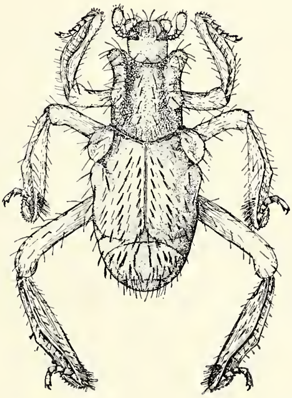

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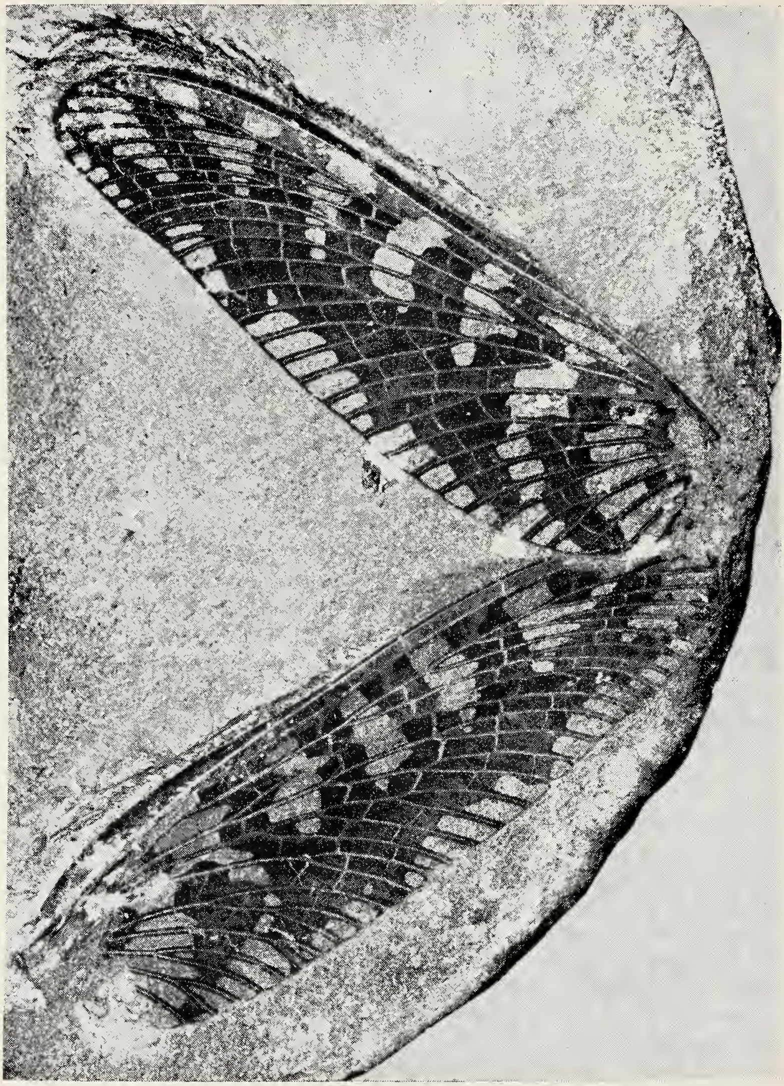

Homaloneura dabasinskasi, n.sp. Photograph of holotype (original). ×2. The fore wing is the lower of the two wings.

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STUDIES ON NORTH AMERICAN CARBONIFEROUS INSECTS. 3. A SPILAPTERID FROM THE VICINITY OF MAZON CREEK, ILLINOIS (PALAEODICTYOPTERA) *

BY F. M. CARPENTER
Harvard University

The Spilapteridae of the Order Palaeodictyoptera, although well represented in Carboniferous deposits of France (Commentry), Czechoslovakia (Moravia) and USSR (Asian RSFSR), has had only doubtful representation in Carboniferous strata of North America. Indeed, the only species that might possibly belong here is *Mcluckiepteron luciae* Richardson [Francis Creek shales of Illinois, near Mazon Creek] and its relationship to the family seems remote. Recently, I have had the opportunity of studying a new fossil from the same deposit; it is not only an unquestionable member of the family Spilapteridae but it seems to me to fall within the genus *Homaloneura,* already known from the Commentry shales in France. This fossil shows both fore and hind wings, with complete preservation of the venation as well as color markings, all in extraordinary detail.

I am deeply indebted to Mr. Walter Dabasinskas of Chicago for loaning me the fossil for study and for permitting me to prepare the fossil by removing the rock matrix which covered much of the wings. I am also grateful to Dr. Eugene Richardson of the Chicago Museum of Natural History for calling my attention to the existence of this fossil in Mr. Dabasinskas' collection and to Dr. Jarmila Kukalová, of Charles University in Prague (but currently visiting Harvard University), for the preparation of the excellent drawing on plate 16.

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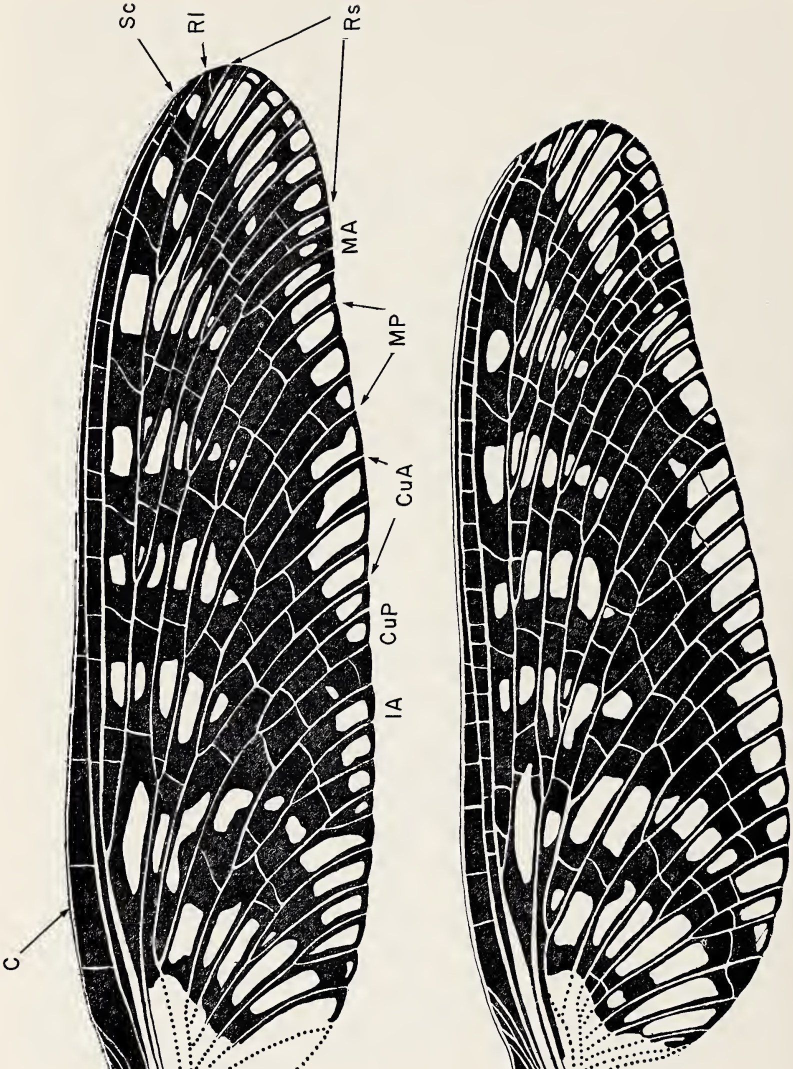
*This research has been aided by grant no. NSF GP-2038 from the National Science Foundation. The previous part in this series was published in Psyche 70:59-63.



CARPENTER — HOMALONEURA

ORDER PALAEODICTYOPTERA

Family Spilapteridae Handlirsch

Spilapteridae Handlirsch, 1906, Die fossilen Insekten p. 101.

The insects included in this family have distinct cross veins, which usually form definite rows; a true archedictyon is absent. The anterior margin of the wings (fore and hind) tends to be concave, often strongly so; the shapes of the fore and hind wings may be very similar (e.g., *Homaloneura)* but more often the hind wing has a broader cubital-anal region (e.g., *Dunbaria);* in such cases, although the cubitus and anal veins may have a few more branches than in the fore wing, the venation is essentially alike in the two wings. The radial sector has at least six terminal branches, both MA and MP have at least two branches, and CuA has several branches. The wings are commonly marked with bands or spots. The family is known from Upper Carboniferous strata to the Upper Permian. I consider the families Dunbariidae Handlirsch (1937), Doropteridae Zalessky (1946) and Neuburgiidae Rohdendorf (1961) to be inseparable from the Spilapteridae.

Genus *Homaloneura* Brongniart

Homaloneura Brongniart, 1885, Bull. Soc. Amis Sci. Natur. Rouen, 1885:50-68; 1893, Recherches pour servir a l'histoire des insectes fossiles des temps primaires, p. 316.
Homaloneurina Handlirsch, 1906, Die fossilen Insekten, p. 46.
Homaloneurites Handlirsch, 1906, ibid., p. 47.

Homaloneura belongs to that series of genera of the Spilapteridae in which the subcosta etxends nearly to the apex of the wings and in which there is no anastomosis of MA with Rs (or R) or of CuA with MP (or M). It is related to *Doropteron* (Permian, USSR), *Permiakovia* Martynov (Permian, USSR), *Neuburgia* Martynov (U. Carb., USSR) and *Dunbaria* Tillyard (L. Permian, Kansas). Unfortunately, our knowledge of even the wings of most of these genera is unsatisfactory; *Permiakovia* is known only from the hind wing and *Doropteron* and *Neuburgia* are known from the fore wings or parts of the fore wings. Some synonymy may eventually be necessary when more is known about these genera, but

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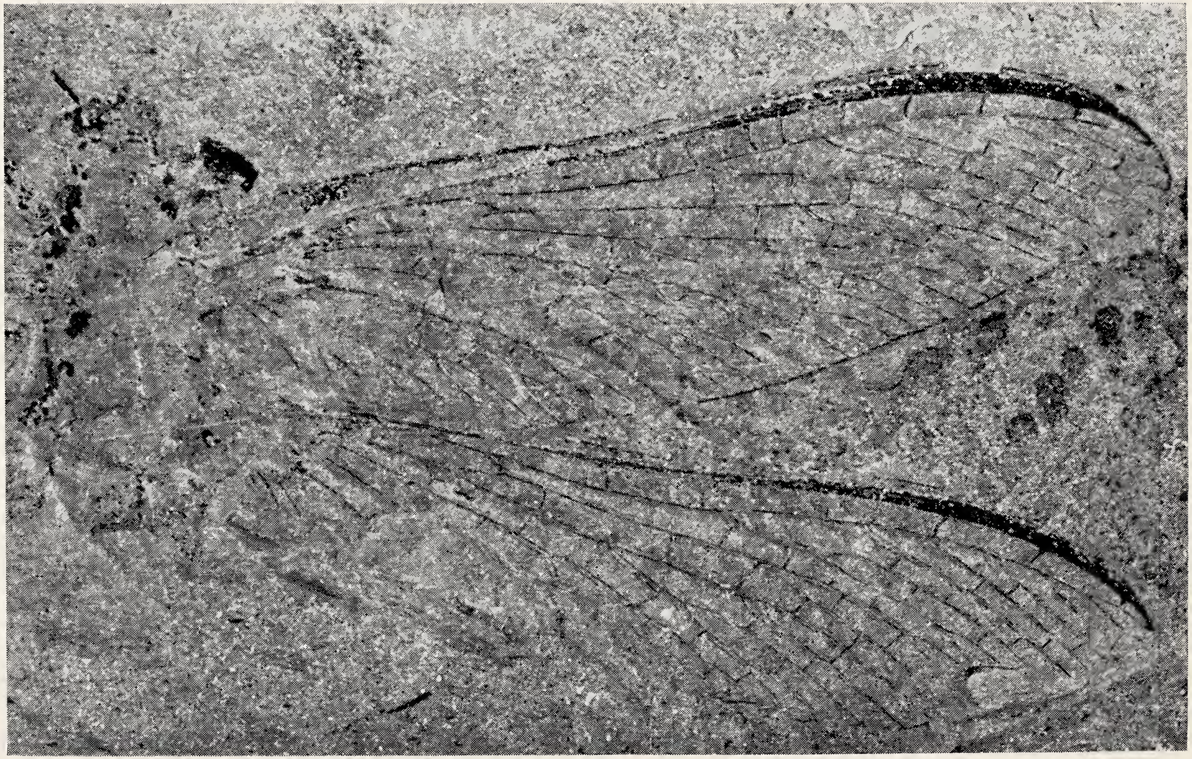
Explanation of Plate 16

Homaloneura dabasinskasi, n.sp. Fore and hind wings; original drawing of holotype by Dr. J. Kukalová. C, costa (+), Sc, subcosta (—), R1, radius (+), Rs, radial sector (—), MA, anterior media (+), MP, posterior media (—), CuA, anterior cubitus (+), CuP, posterior cubitus (—), 1A, first anal (+).



Carpenter — Homaloneura

Homaloneura, being the first of this series to be described, will remain valid. It is distinguished from the other genera of the Spilapteridae in having the concavity of the front margin of both fore and hind wings very slight and in having the anal region of the hind wing much less extensively developed than in the other genera in which the hind wing is known. *Homaloneura elegans* Brongniart was designated the type-species of the genus *Homaloneura* by Handlirsch in 1922; a photograph of the type specimen of *elegans* is given on plate 17 of the present paper.

Homaloneura dabasinskasi, n. sp.

Plates 15 and 16

Fore wing: length, 55 mm.; maximum width, 15 mm. Costal margin very slightly concave, apex of wing rounded, hind margin with two slight indentations, one near the posterior branch of MA and the other near the anterior termination of MP. Costal space broad in the basal half of the wing but narrowing abruptly towards the middle of the wing and continuing of uniform width for the rest of the wing until the termination of Sc, just before the apex; R and R1 nearly parallel to Sc; Rs arising about a quarter of the wing length from the base, dividing to form five main branches, about half of which fork once again; the branches of Rs tending to arise more dichotomously than pectinately; M arising from the base of the wing as an independent vein, forming MA and MP slightly distally of the origin of Rs; MA with three terminal branches; MP with four; Cu apparently arising independently from the wing base, forking very shortly into CuA (with four branches) and CuP (forked). The basal connections of the anal veins are not clearly preserved; the first of these terminates in three branches, the next three are forked. Cross veins distinct, arranged as shown in plate 16. The wing is distinctly marked with transverse bands and spots.

Hind wing: length, 50 mm.; maximum width, 18 mm. This is shaped like the fore wing except that the concavity of the costal margin is slightly more pronounced and the anal area is somewhat more rounded. The number of anal veins appears to be the same

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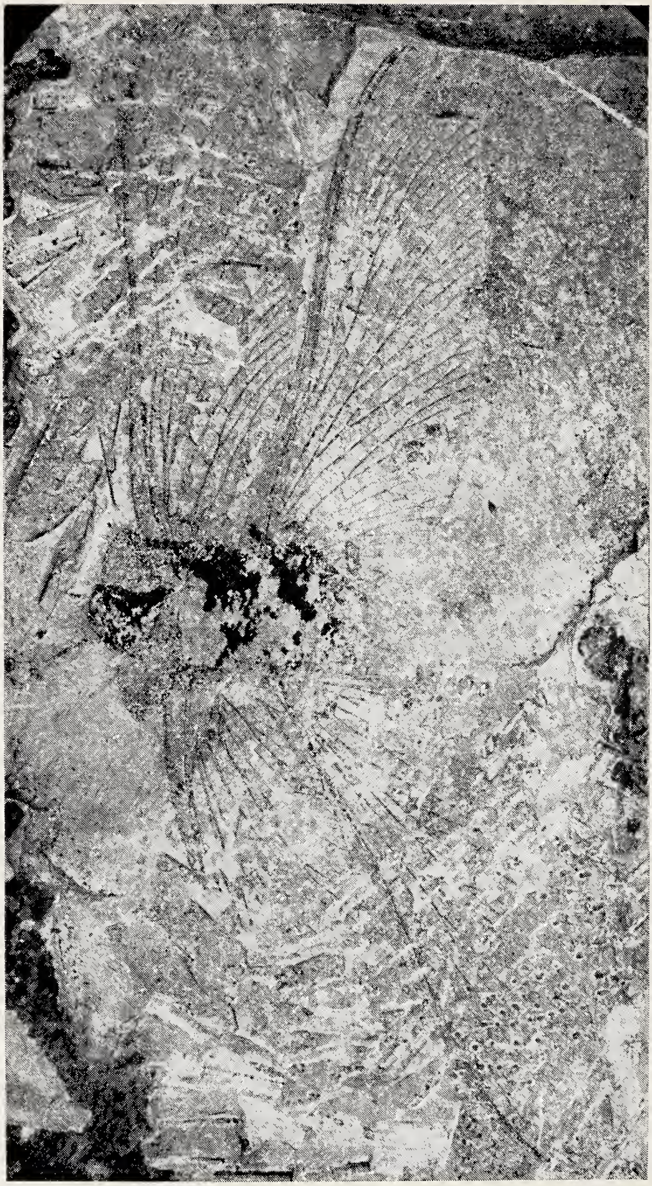
Explanation of Plate 17

Homaloneura elegans Brongniart, U. Carboniferous, Commentry, France. Photograph of type in Laboratoire de Paleontologie, Paris. (Original). × 4. Note the prothoracic lobes and the similarity of the wing venation to that of *H. dabasinskasi*. The posterior margin of the hind wing is incompletely preserved.



Carpenter — Homaloneura

in both wings. The venational pattern is basically as in the fore wing, with only slight differences in the positions of the branches, mainly those of the radial sector. The wing markings and cross veins are essentially as in the fore wing.

Holotype: collected by Mr. Walter Dabasinskas in June, 1960, in an ironstone nodule, found at the Greer Earthmoving and Mechanics School, Will County, Illinois, 4 miles north of Braidwood. The type is contained in Mr. Dabasinskas' collection and the species is named for him. This fossil is the most spectacularly preserved fossil insect which I have ever seen in a nodule from the Mazon Creek region and it is indeed one of the striking Carboniferous insects known to me. As can be observed in the photograph (plate 15) the fore wing is posterior in position to the hind wing and the apex of the fore wing rests near the base of the hind wing. That these two wings were derived from one side of the same specimen of an insect seems almost certain. The subcosta is concave in one wing and convex in the other; presumably, the wings broke away from the body as the insect rested in water and one of the wings turned over as well as rotating through 180° before coming to rest in the mud. The counterpart of the half of the specimen shown in plate 15 has the apex of the fore wing and basal region of the hind wing completely preserved.

A comparison of the wings of *dabasinskasi* with those of *H. elegans* and the other Commentry species shows enough differences to require a distinct species for the new fossil but not enough in my opinion to justify generic separation. The hind margin of the fore wing of *dabasinskasi* is somewhat more sharply curved basally than in the Commentry species. The wing markings of *dabasinskasi* are distinctly different from those of *elegans,* which has a dark, longitudinal stripe along R1 distally; but they are similar to those of another Commentry species, *H. ornata* Brongniart.

In addition to the features mentioned above as specific in nature, several other structures preserved in this new fossil deserve mention, since they may turn out to be common to all Spilapteridae and perhaps to other families of the Palaeodictyoptera. One of these is the series of fine ridges at the base of the costal area of both fore and hind wings (see plate 16). These do not appear to be veins in

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Explanation of Plate 18

Homaloneura bonnieri Brongniart, U. Carboniferous, Commentry, France. Photograph of type in Laboratoire de Paleontologie, Paris. (Original). × 2. Note the prothoracic lobes and the similarity of the hind wing to that of *H. dabasinskasi.*

this species and the more basal area cannot be considered as a precostal area, as it occurs in the Orthoptera or Protodonata. Since similar ridges or actual veinlets have been observed (Kukalová, 1960) in other Palaeodictyoptera *(Breyeria* and *Ostrava),* they may turn out to be characteristic of most Palaeodictyoptera. Another interesting structure present in *dabasinskasi* is the thickened basal stem of R. Examined under certain angles of illumination, the posterior edge of this stem *appears* as an independent vein extending almost from the base of M to the origin of Rs. Careful examination of the base of the wing, under various types of illumination, however, has convinced me that this apparent vein is actually the posterior edge of the stem of R. Similar widening of R can be seen in the Commentry specimens of *Homaloneura.*

To enable further comparisons of *dabasinskasi* with the described species of *Homaloneura,* I am including here (plates 17 and 18) photographs of the types of *H. elegans* Brongniart and of *H. bonnieri* Brongniart, which are contained in the Laboratoire de Paleontologie of the Museum National d'Histoire Naturelle, Paris. It is regrettable that the Illinois fossil does not show such body structures as the prothoracic lobes, which are visible in both of the Commentry fossils depicted.

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AUSTRALIAN CARABID BEETLES XIV. *PERIGONA**

By P. J. Darlington, Jr.
Museum of Comparative Zoology, Harvard University

This paper is a by-product of work on New Guinean *Perigona*, which forced me to identify the Australian species and compare them with the New Guinean ones. New Guinea, incidentally, possesses 14 species of the genus: 8 in *Perigona sensu stricto* and 6 in subgenus *Trechicus*. The only species common to Australia and New Guinea is probably the nearly cosmopolitan *nigriceps* Dejean.

The last key to Australian *Perigona* then known (3 species) is by Sloane (1903, Proc. Linn. Soc. New South Wales **28**, P. 635). One additional species has been recorded since then, but probably in error. It is *P. plagiata* Putzeys, which ranges from southeastern Asia and Japan to the Philippines and New Guinea. Csiki (1924, Ann. Mus. National Hungary **21**, p. 172) lists it from "New-South-Wales: Mt. Victoria (Biró, 1900)." However, I have seen (borrowed from the Hungarian National Museum) specimens with this label, and they were set with and exactly match specimens of the species collected in New Guinea by Biró. I feel sure that the supposed Australian specimens are wrongly labeled and are really from New Guinea. So far as I know, the species has not been found in Australia by other collectors.

The two subgenera of *Perigona* (see following key) differ in habits. *Perigona s. s.* usually occurs under bark of logs or in rotting logs; subgenus *Trechicus*, among leaves or in leaf mold on the floor of rain forest. *Perigona (Trechicus) nigriceps* (Dejean), however, occurs also in fermenting vegetation and some other plant materials and has been carried over the warmer parts of the world by commerce.

Key to Australian Species of *Perigona*

1. Three seta-bearing punctures of submarginal depression (at outer curve of elytron at 2/3 or 3/5 of elytral length) forming a straight line *(Perigona s. s.)* 2
— These punctures forming a triangle (subgenus *Trechicus*) 3
2. Length *c.* 7 mm.; color light brown, head dark, elytra yellow .... *tricolor*
— Length *c.* 4 mm.; reddish, head dark, elytral disc more or less (variably) dark .... *rufilabris*
3. Eyes large, forming *c.* right angles with neck; front of head and

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**Manuscript received by the editor May 14, 1964.*

neck plainly, nearly isodiametrically reticulate; color *either* pale with head and apex of elytra darker *or* irregularly reddish castaneous with paler suture but without well defined markings .... *nigriceps*

— *Either* eyes smaller (moderate in size), forming obtuse angles with neck, *or* front without distinct reticulate microsculpture, *or* color not as described above 4

4. Head relatively wider and prothorax narrower (head/prothorax .86 and .84 in measured specimens); head and prothorax dark, elytra yellow with variable darker discal cloud .... *dorsata*

— Head relatively narrower and prothorax wider (head/prothorax .70 and .73); color dark with margins of prothorax and elytra usually contrastingly pale (sometimes less contrasting) .... *picta*

Perigona (s. s.) tricolor (Castelnau)

Castelnau 1868, Trans. R. Soc. Victoria 8, p. 127 (*Siltopia*).
Sloane 1903, Proc. Linn. Soc. New South Wales 28, p. 635.

I do not know this species. Size alone is enough to separate it from all other Australian members of the genus. It is recorded from the Clarence River and Parramatta (Castelnau) and from Wiseman's Ferry on the Hawkesbury River (Sloane). All these localities are in New South Wales.

Perigona (s. s.) rufilabris (Macleay)

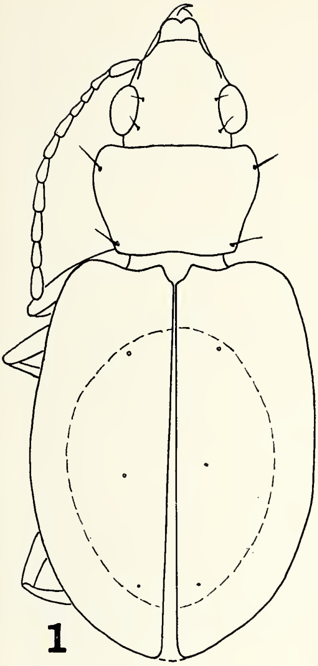
Macleay 1871, Trans. Ent. Soc. New South Wales 2, p. 114 (*Trechus*).
Sloane 1903, Proc. Linn. Soc. New South Wales 28, p. 635.
basalis Putzeys 1873, Ann. Mus. Civ. Genoa 4, p. 223.

Sloane has determined the synonomy given above. Macleay's specimen(s) were from Gayndah, South Queensland; Putzeys' (types of *basalis*), from "Queensland". I have the species from Kuranda, Longlands Gap, and Mt. Fisher (all on the Atherton Tableland in North Queensland), and from rain forest north of Dunoon in northern New South Wales.

Perigona (Trechicus) nigriceps (Dejean)

Dejean 1831, Species Général Coléoptères 5, p. 44 (*Bembidium*).
Csiki 1931, Junk-Schenkling Coleop. Cat., Carabidae,
Harpalinae 5, p. 897 (see for synonymy and references).
australica Sloane 1903, Proc. Linn. Soc. New South Wales 28, p. 635.

This is a nearly cosmopolitan species, carried by man, but it occurs also in natural habitats. I took a series at Lockerbie, on the tip of



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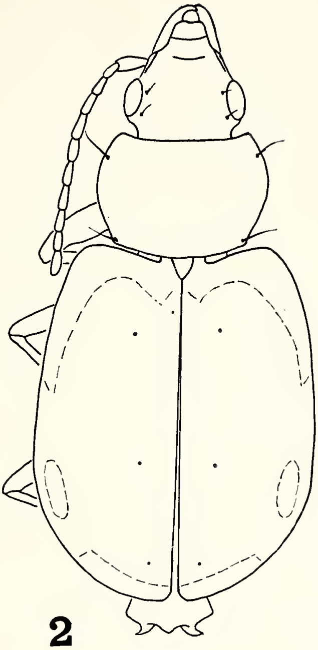

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Fig. 1 *Perigona dorsata* n. sp.
Fig. 2. *Perigona picta* n. sp.

Cape York, by washing thick accumulations of leaves and bird droppings from under a tree where a colony of birds had nested, and I have specimens from Lankelly Creek on the McIlwraith Range east of Coen half way up the Cape York Peninsula, and from Cairns, Kuranda, and Longlands Gap on the Atherton Tableland, North Queensland. Sloane's type of *australica* was from Mackay, Queensland. The species is to be expected anywhere in the warmer part of Australia.

Perigona (Trechicus) **dorsata** n. sp.

Figure 1

Form as figured (Fig. 1), almost as in *nigriceps* but slightly less broad; head black (except labrum and mandibles testaceous), pronotum dark reddish brown, elytra reddish testaceous with median dorsal cloud brown (suture pale); shining, slightly iridescent, reticulate microsculpture lightly impressed, *c.* isodiametric on head, probably fine and transverse on pronotum and elytra but not distinctly visible at 100×. *Head* .86 and .84 width prothorax (in ♂♀ measured); eyes large, forming *c.* right angles with neck; antennae with middle segments scarcely longer than wide; frontal sulci moderate, irregular, ending before mid-eye level; 2 setae over each eye. *Prothorax:* width/length 1.44 and 1.46; base/apex 1.01 and 1.05; disc with middle line distinct, transverse impressions vague, baso-lateral impressions slight; 2 pair lateral setae present. *Elytra* 2/3 wider than prothorax (E/P 1.68 and 1.66); impression behind puncture-triangle (near margin at 2/3 or 3/5 of elytral length) wide, flat-bottomed; discal striae indicated, first 2 or 3 slightly impressed, irregular but not distinctly punctate; intervals not or very sparsely punctulate, 3rd 3-punctate with anterior and middle punctures near 3rd stria and posterior one near 2nd stria. *Inner wings* fully developed. *Lower surface, legs,* and *secondary sexual characters* normal; ♂ front tarsi scarcely dilated, 3 segments briefly biseriately squamulose. *Measurements:* length *c.* 3-4; width *c.* 1.4 mm.

Holotype ♂ (M. C. Z. No. 30, 524) and 9 paratypes all from Kuranda, near Cairns, North Queensland, *c.* 1000 ft., Feb., 1958, taken by myself in piles of dead leaves under the heads of felled trees on the edge of rain forest. Also 1 specimen, not a type, from Rocky River, Cape York Peninsula, North Queensland, (late May or early June) 1958, also taken by myself.

See preceding key for distinguishing characters of this new species.

Perigona (Trechicus) picta n. sp.

Figure 2

Form as figured (Fig. 2), stouter than *nigriceps* or *dorsata,* with wider and more rounded prothorax and narrower head; piceous black, with prothorax (including apex and base) and elytra (base, sides, and apex) margined with testaceous, the pale color expanded inward on elytra before subapical curve, and dark color reaching margin of elytra at the curve and extending forward along actual margin; moderately shining, faintly iridescent, microsculpture absent or faint on head, apparently fine and strongly transverse on pronotum and elytra. *Head* .70 and .73 width prothorax (in ♂♀ measured); eyes smaller than in preceding species, partly enclosed by genae, forming obtuse angles with neck; antennae with middle segments slightly longer than wide; frontal sulci impressed, diverging posteriorly, almost reaching anterior supraocular setae. *Prothorax* rounded-transverse, with basal angles very obtuse; width/length 1.51 and 1.50; base/apex

1.10 and 1.13; disc with middle line distinct, transverse impressions vague, baso-lateral impressions slight and poorly defined; 2 pair lateral setae present. *Elytra c.* ½ wider than prothorax (E/P 1.50 and 1.53); submarginal channel behind puncture-triangle wide, flat-bottomed; discal striae impressed, irregularly subpunctate; intervals not or not much punctulate, 3rd 3-punctate as in *dorsata. Inner wings* fully developed. *Lower surface, legs,* and *secondary sexual characters* normal; ♂ front tarsi scarcely dilated, 3 segments inconspicuously biseriately squamulose. *Measurements:* length 2.8-3.2; width 1.3-1.4 mm.

Holotype ♂ (M. C. Z. No. 30, 525) and 14 paratypes from Longlands Gap, Atherton Tableland, North Queensland, *c.* 3000 ft., Feb. 1958, taken by myself by washing piles of dead leaves from under the heads of felled trees in rain forest. Five additional paratypes from Atherton, Atherton Tableland, North Queensland, Dec. 1957-Feb. 1958, taken by myself. And 2, not types, from Kuranda, near Cairns, *c.* 1000 ft., taken by myself.

This species is immediately distinguished from *nigriceps* and *dorsata,* above, by its broader form, more rounded prothorax, and narrower head with relatively smaller eyes, as well as by the usually sharply marked color pattern. The pattern is less well defined in the Kuranda specimens, which nevertheless show the structural characters of the species.

AN UNDESCRIBED SPECIES OF *MELANICHNEUMON* THOMSON FROM NEW JERSEY (HYMENOPTERA: ICHNEUMONIDAE)*

By Charles C. Porter
Biological Laboratories, Harvard University

Recent collecting in the vicinity of Metuchen, New Jersey, has produced an undescribed species of *Melanichneumon* Thomson belonging to Heinrich's subgenus *Vulgichneumon* and therein closely related both to *M. (V.) brevicinctor* (Say) and to *M. (V.) saevus* (Cresson). I therefore give below a description of both sexes of this new species.

Melanichneumon (Vulgichneumon) heleiobatos, n.sp.

TYPES: *Holotype:* female, Metuchen, New Jersey, June 28, 1964, in Museum of Comparative Zoology, Cambridge, Massachusetts. *Allotype:* male, Metuchen, New Jersey, June 29, 1964, Museum of Comparative Zoology, Cambridge, Massachusetts. *Paratypes:* four males, Metuchen, New Jersey, June 30, July 2, and July 3, 1964; one in Museum of Comparative Zoology, Cambridge, Massachusetts, three in the Porter Collection, Metuchen, New Jersey.

FEMALE: *Color:* black, shining, the following white: annulus, incomplete below, on flagellar segments 7 to 12 (in greater part); short, narrow mark on frontal orbit above; most of outer face of fore-tibia dully; a very large dorsal blotch on gastral tergites 6 and 7. Wings hyaline. *Flagellum:* moderately long and slender, very slightly attenuate toward apex; distinctly flattened below beyond middle; 31 segments, the first ± 18 times as long as wide apically. *Head:* temple profile narrowed, a little curved; cheek profile narrowed, about straight. Malar space subequal to basal width of mandible. *Thorax:* mesoscutum finely and densely punctate, extensively micro-aciculate between punctures, rather weakly shining; scutellum highly polished, with sharp, well separated punctures, the lateral carinae distinct for about one half its length; pleura conspicuously shining with abundant but generally discrete fine to rather large punctures, mesopleuron with subadjacent to adjacent punctures and some longitudinal wrinkling mainly in lower hind quadrant — otherwise generally with distinct polished interspaces between the punctures, area immediately

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Manuscript received by the editor August 18, 1964.

below subalarum with a few punctures and rather weak wrinkling. *Legs:* hind-coxa without a clearly defined scopa, finely and densely punctate beneath. *Propodeum:* areolation sharp and complete; area superomedia distinctly a little longer than wide, considerably narrowed anteriorly, its surface highly polished, with only vague wrinkling; the rather large, strong punctures of area superoexterna (sparser) and area dentipara mostly well separated by polished interspaces. *Gaster:* median field of postpetiole discrete, with weak longitudinal striation and a few scattered, large punctures; gastrocoeli distinct but rather small and shallow, thyridium defined; second and third tergites strongly and densely punctured, the rest much more sparsely and weakly so; narrow anterior band on second tergite between gastrocoeli with distinct longitudinal striation in addition to punctures. *Length:* ± 8.5 mm.

MALE: *Color:* black, the following white: maxillary palpi; mandibles except toward tips; clypeus; face; frontal orbits about to level of anterior ocellus; hind orbits on a little more than lower half of eye, broadly interrupted in malar space; most of scape beneath; collare in great part; pronotal ridge, broadly interrupted in front; scutellum except for a basal triangular area occupying about one-fourth its surface; subalarum except toward apex; outer face of fore femur toward apex and outer face of fore tibia dully; dullish area on outer face of mid-femur apically; most of gastral tergites six and seven conspicuously. Wings hyaline. *Flagellum:* 32 segments, bacilliform tyloides on segments 5 to 13. *Head:* malar space slightly less than half basal width of mandible. *Thorax:* generally as in female, punctation slightly finer and sparser, the surface a little more shining; scutellum with lateral carina distinct basally for about one-third its length. *Propodeum:* area superomedia no longer than wide, horse-shoe shaped, its surface highly polished with obscure wrinkling; areae superoexternae and dentiparae polished with rather large but weak punctures and obscure wrinkling. *Gaster:* gastrocoeli rather broad and short, distinctly wider than long, considerably stronger and deeper than in female; central portion of second tergite between and to some distance behind gastrocoeli longitudinally striate; second and third tergites rather strongly punctured, fourth and following less strongly so. *Length:* ± 9.5 mm.

VARIATION: the flagellum may have 33 or 34 segments; the lateral carinae of the scrutellum, in specimens before me, vary from being defined only at base to extending about half the length of the sclerite; area superomedia sometimes distinctly wider than long, its surface often more strongly wrinkled than described above — by no means coarsely so; punctures of areae superoexternae and dentiparae often strongly defined, but generally discrete with highly polished intervals. The white markings, which are constant in location, vary only slightly in extent.

AFFINITIES: The female holotype will run directly to the couplet containing *M. brevicinctor* (Say) and *M. saevus* (Cresson) in Heinrich's key (Heinrich 1962) to the eastern Nearctic species of the subgenus *Vulgichneumon* Heinrich.

From *M. saevus* (Cresson) it differs in the frontal orbits which are only white for a short distance above; in the flagellar annulus on segments 7 to 12 rather than 6 to 14 or 15; in lacking all white maculation on the collare, apex of pronotal ridge, and scutellum; by reason of the 31 segmented flagellum [38 or 39 segments in *saevus* (Cresson)]; in the area superomedia which is distinctly longer than wide, and in its smaller size ± 8.5 mm. as compared to 11-13 mm.

The female of *M. heleiobatos* displays also many points of distinction from that of *M. brevicinctor* (Say). As to color, there is the white line on the frontal orbit above, the black scutellum and black hind trochanters as compared to the black frontal orbits, wholly white scutellum, and white hind trochanter of *brevicinctor* (Say). Furthermore *heleiobatos* has a white macula on gastral tergites 6 and 7, *brevicinctor* (Say) only on 7. The lateral carinae of the scutellum, which in *brevicinctor* (Say) are only present at the extreme base, extend in *heleiobatos* almost half the length of the scutellum. The mesopleuron (and thoracic pleura in general) is much more shining and sparsely punctate than in *brevicinctor* (Say), where the surface is dull, closely punctured and extensively wrinkled, not only below but also above beneath the subalaum. The hind coxa is without a distinct scopa, whereas *brevicinctor* (Say) has a comparatively weak but easily visible and clearly delimited scopa. The surface of the areasuperomedia is smooth and polished with obscure wrinkles, while in *brevicinctor* (Say) it is completely reticulo-rugose. Likewise the areaesuperoexternae and dentiparae are more shining and less closely punctured in *heleiobatos*. Finally, in the females of *brevicinctor* (Say) examined, the area between the gastrocoeli has much less tendency to longitudinal striation than in the present species.

The male may at once be distinguished from all eastern Nearctic species of *Melanichneumon* Thomson with mostly black abdomen by three characters in combination: no white flagellar annulus, black legs, prominent white marks on gastral tergites 6 and 7.

From the male of *saevus* (Cresson) this species is moreover distinct in its completely white clypeus and face, 32 to 34 segmented antennal flagellum [as compared to 37 to 38 segments in *saevus* (Cresson)], and its smaller size ± 9 to ± 10 mm. as against 13 to 14 mm.

Heleiobatos is also very distinct from *brevicinctor* (Say) in the male. The white maculations are more extensive, *brevicinctor* (Say) being entirely black except for its white scutellum and mark on gastral tergite 7. In structure the most significant distinction concerns the gastrocoeli, which in *brevicinctor* (Say) are shallow and conspicuously longer than wide, whereas those of *heleiobatos* are a little wider than long and comparatively deep. The characters of scutellar carination and sculpture described for the female also apply in general for the male, although there are some specimens of *brevicinctor* (Say) in which the dorsal areae of the propodeum are almost as smooth as in many specimens of *heleiobatos*.

DERIVATION OF SPECIFIC NAME: *Heleiobatos* is a Greek adjective signifying "inhabitant of swamps".

TYPE LOCALITY: The type specimens were collected, all within a few yards of each other, at Metuchen, New Jersey, in a swampy area along the Lehigh Valley Railroad tracks just north of the bridge which carries the Reading Railroad across the Lehigh Valley.

The locality is along a very small stream draining a pond. It is overshadowed by *Salix discolor* and supports a moderately thick ground cover of various grasses and clumps of *Impatiens*. Like the abundant tenthredinid sawflies and such ichneumonid genera as *Cteniscus, Orthomiscus,* and *Smicroplectrus,* which are also found here, *M. heleiobatos* appears to be a species of particularly moist habitats. This is in contradistinction to its close relative, *M. brevicinctor* (Say), which occurs commonly in a wide range of habitats from woods to the margins of fields.

CONCLUSIONS: Unless it should turn out to be conspecific with some Palaearctic form, *M. heleiobatos* is an easily recognized new species distinct from its relatives by ample characters of color and structure. The association of sexes is, of course, only tentative, but appears logical both from characters displayed by the specimens themselves and from the fact that all examples were obtained within a very limited area where no other *Melanichneumon* of similar aspect has been taken.

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TAXONOMY AND PARATAXONOMY OF SOME FOSSIL ANTS (HYMENOPTERA-FORMICIDAE)[1]

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In current revisionary studies of the ant tribe Ponerini it has become necessary to re-examine the status of various fossils previously placed in the genus *Ponera*. This taxon dates to 1804 and consequently has an unusually complex conceptual and nomenclatural history. The included fossils require special treatment to unravel their part in the resulting snarl.

Thirty-six fossil ants have been placed as *Ponera* or *Ponera*-like by earlier authors but little confidence in the generic assignment of most of them is possible. Some are certainly ponerine, and occasional placement in tribe Ponerini is reasonable. Most species, however, cannot be satisfactorily placed, even to subfamily. The fact is that, to some authors, *Ponera* has served as a "catch-all" for small, possibly ponerine ant fossils, or wing impressions with venation similar to that of *Ponera*.

It is proposed here to review these species and to attempt their allocation into various categories: (1) Formicidae *incertae generis;* (2) Ponerinae *incertae generis;* (3) *Ponera;* (4) (?) *Ponera;* or (5) the form-genus *Poneropsis* Heer, 1867 — as redefined below. The result of sorting the fossil *"Ponera"* in this way has, I believe, some utility relative to evolutionary studies. Species are either placed definitely or reasonably certainly in a known taxon, rendered *"incertae"* at the level at which they *begin* to be uncertain in diagnostic features; or allocated to the phylogenetically meaningless limbo of the parataxon *Poneropsis*. My category "(?) *Ponera*" in general contains species equally well placed in *Ponera* or *Hypoponera*[2], although smaller members of other genera of tribe Ponerini may be included.

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[1] Based on research supported by the U.S. National Science Foundation, Grant No. GB 1634.

[2] Santschi's subgenus *Ponera* (*Hypoponera*) (1938, Bull. Soc. Ent. France, 43: 8-80) has recently been elevated to full generic status (Taylor, *mss.*). It contains the majority of the living species currently assigned to *Ponera*, and many of its species are superficially *Ponera*-like.

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The form-genus *Poneropsis* Heer.

In his study of the fossil Hymenoptera of Oeningen and Radoboj, Heer (1867) proposed the use of a formicid form-genus *Poneropsis,* which was defined as follows: ". . . Die fossilen Ameisen welche drei Cubitalzellen in den Oberflügeln und einen einknötigen Hinterleibsstiel, aber keine Einschnürung beim zweiten Hinterleibssegment haben. Sie stimmen im Flügelgeäder und dem einknötigen Stiel mit *Ponera* überein, daher ich sie früher dieser Gattung zugerechnet habe; in der Bildung des Hinterleibes weichen sie aber bedeutend von den *Poneren* ab, namentlich die Arten mit rundem, dickem Hinterleib." Heer's figures show that his "drei Cubitalzellen" are those now referred to as the first and second cubital cells, with the discoidal cell.

Sixteen species were allocated to *Poneropsis* at its inception, including some previously placed in *Ponera* by Heer (1849). No better placement of any of them is possible on the basis of the published data. There appears to be much species-level synonomy among these forms and judging from their size most do not seem close to *Ponera.*

Since the venational type specified for *Poneropsis* is convergently developed in many lines of ant evolution, this "genus" could conceivably contain wing impressions of members of almost every ant subfamily[3]. Moreover the convergent types cannot be separated on the basis of wing venation alone. Accordingly it is pointless to assign such wings indiscriminately to recent taxa to whch they might, at present, be referable. It is far better to assign them definitely to a parataxonomic form-genus which need not be considered in phylogenetic, paleo-zoogeographic, or other studies, rather than to place them randomly in a true taxonomic genus, with presumed affinities to other taxa, extinct or living.

It may be argued that this procedure offers little in comparison with a simple "Formicidae *incertae generis*" allocation. This is partly true, but since Heer's parataxon is available, use of it may as well be maintained, at least until a complete revision of fossil ants is possible. At that time the problem of the use of ant-wing form-genera will

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[3] For example, all the following recent genera possess wing venation of the "*Poneropsis*" type: *Gnamptogenys, Eciton, Pseudomyrmex, Messor, Aneuretus, Dolichoderus, Hypoclinea* (See figures of Brown and Nutting, 1950, and Wilson et.al., 1956). Extinct ants with this venation pattern include: *Trachymesopus succinea* (Mayr), *Aphaenogaster mayri* Carp., *Pheidole tertiaria* Carp., *Dolichoderus antiquus* Carp., *Iridomyrmex florissantius* Carp., *Liometopum microcephalus* Carp., and members of the genera *Protazteca* and *Elaeomyrmex* (see Wheeler, 1914 and Carpenter, 1930).

need careful consideration. We must consider the fact that *Poneropsis,* as defined here, contains wings all of which are at approximately the same evolutionary grade of venational reduction (Brown and Nutting, 1950), and that certain genera of ants can be excluded from it, as they never possess such venation. Under such terms we are actually designating fossils more precisely by placing them in *Poneropsis* rather than considering them simply as "Formicidae *incertae generis*". Moreover, and this is an important consideration, use of this parataxon allows convenient placement of such fossils in a single group easily referred to by those seeking examples of such venational types for other studies.

I propose the following redefinition of *Poneropsis.* The nomenclature used for wing veins is that of Brown and Nutting (1950).

Form-genus, *Poneropsis* Heer, 1867

Hymenopterous forewings, apparently belonging to family Formicidae, and either alone or attached to fossils otherwise unclassifiable, and of a type not known to be associated with remains yielding more satisfactory placement.

Two closed, fully separated, cubital cells (the 1st and 2nd) present. First discoidal cell always closed; second discoidal open or closed. Radial cell open or closed. The adventitious longitudinal vein Rsx, and the first radial cross vein (1r), or a stub of it, absent.[4] Second radial cross vein (2r) usually arising near the anterior base of the radio-medial cross vein (r-m), and always reaching the stigma at a point distal to the first quarter of its posterior border.[5] The second free abscissa of the median vein may be contracted, so that the posterior end of Rs + M2 lies adjacent to the anterior end of the (first) medio-cubital cross vein (m-cu); or fusion of elements in this area may cause the base of the former vein to lie distal to that of the latter. First abscissa of median vein (Mf1) lying proximal, distal, or adjacent to the anterior base of the cubital anal cross vein (cu-a) where it meets CuA.[6]

Specimens with a two-segmented petiole and *Poneropsis*-type wing

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[4] Wings referable to primitive ponerines and myrmeciines such as *Platythyrea, Myrmecia,* and some Amblyoponini are, therefore, excluded, (Brown and Nutting, 1950; Brown, 1960).

[5] This clause allows distinction of *Eoponera* Carpenter (1929) — see Brown and Nutting, fig. 6.

[6] As Brown and Nutting point out, it is possible that origin of Mf1 well proximal of cu-a is a key character identifying doryline ants. If this should prove to be so, the above diagnosis could be easily modified to preclude wings of fossil Dorylinae.

venation must be placed in the Myrmicinae or one of the other applicable subfamilies. If the node is one-segmented and other characters of the gaster (presence of sting, etc.) are visible, then placement to subfamily should be possible.

The many qualifications made to the simple basic diagnosis, "two closed cubital cells, and a single closed discoidal," allow inclusion in *Poneropsis* of virtually all known ants with these primary characters. I do not wish to imply that study of wing vein patterns, such as was pioneered by Brown and Nutting, should not be applied to ant fossils. These authors have shown, however, that extreme parallelism may take place in the details of venational reduction in the various ant subfamilies, with the result that amazingly similar wings may be produced in divergent lines. The various ranges specified in my diagnosis simply cover all stages in venational reduction known to show such parallelism in wings with two cubital cells and at least one closed discoidal cell.

With the possible exception of the feature discussed in footnote 6 of the diagnosis, no alternative condition in these venational characters, or combination of conditions, is currently known to diagnose unequivocally any ant taxon.

Ponera and Poneropsis species described by Heer (1849, 1867).

In 1849, Heer described nine extinct species in *Ponera* from the Miocene of Radoboj, Oeningen and Parschlung, Croatia. In his 1867 paper four of these were referred to the newly defined form-genus *Poneropsis,* and thirteen further specific or infraspecific forms were also described, all in *Poneropsis.*

I have been unable to justify any of the generic assignments in *Ponera,* and find that most of Heer's species, both of *Ponera* and *Poneropsis,* can be assigned to *Poneropsis* as defined above, thus conveniently disposing of them. Others, including some placed by Heer in *Poneropsis,* do not appear referable there on the basis of his figures, since the wing venation is too incompletely shown in the fossils or the wings appear to have had only a single cubital cell.

The history and present status of Heer's (1849) *Ponera* species is summarized in the following Table. The two species considered here to be "Formicidae *incertae generis*" were based on remains too incomplete to allow better allocation.

Mayr (1867) and Popov (1932) have both referred to some of these species, assigning them with or without query to *Ponera.* Repetition of Mayr's names serves no purpose; most of them were originally placed in *Poneropsis* (by Heer) and so Mayr's combinations do not constitute nomenclatural occupation in *Ponera,* since none of

Species placed in *Ponera* by Heer 1849	Species placed in *Poneropsis* by Heer 1867	Current assignment
affinis	*affinis*	Formicidae *incertae generis*
crassinervis	—	*Poneropsis*
croatica	—	*Poneropsis*
elongatula	*elongatula*	Formicidae *incertae generis*
fuliginosa (with subspecies *oeningensis* and *radoboj*)	*fuliginosa*	*Poneropsis*
globosa	—	*Poneropsis*
longaeva	—	*Poneropsis*
nitida	*nitida*	*Poneropsis*
ventrosa	—	*Poneropsis*

them are now considered to belong in the genus. Popov's citations are important, however, as he used some of the names originally assigned to *Ponera* by Heer, thus firmly establishing them in modern systematic nomenclature. Those involved are *croatica, crassinervis* (incorrectly spelled as *crassicornis*), *ventrosa, longaeva* and *globosa.*

All of the additional thirteen species described in *Poneropsis* in 1867 appear to be satisfactorily placed, except *elongata, anthracina, imhoff,* and *stygia* in which the wings are too incompletely preserved to allow allocation — they should be considered "Formicidae *incertae generis*".

A further species, *Ponera veneraria,* was described by Heer in his *Urwelt der Schweiz* (1865). This species was later transferred to *Poneropsis* in the 1879, second edition of the same work. On the basis of Heer's 1865 figure I concur with Handlirsch (1908) that this species is best placed as Formicidae *incertae generis.* The name was misspelled "*vernaria*" by Handlirsch.

Fossil *Ponera* described by authors other than Heer.

The following list, as far as I am aware, includes all ant fossils allocated to *Ponera* by authors other than Heer. This includes those which have since been placed elsewhere by previous authors, whose reassignments are discussed below with my own opinions on the proper placement of all the species listed here. The appropriate references may be obtained in the bibliography.

1. *Ponera atavia* Mayr, 1868: 72, figs. 66-69, female, male. Oligocene — Baltic Amber. Wheeler, 1914: 38, fig. 9. worker.
2. *Ponera brodiei,* Giebel, 1856: 173. This forewing fragment, originally described as an ant, *Formicium brodiei,* by Westwood (1854) has been subsequently placed in the Jurassic siricoid family Anaxyelidae (Maa, 1949).
3. *Ponera gracilicornis* Mayr, 1868: 72, worker, Baltic Amber.
4. *Ponera hendersoni* Cockerell, 1906, female. Miocene-Florissant.
5. *Ponera hypolitha* Cockerell, 1915: 483, plate 64, figs. 3-4, wing impression. Oligocene — Gurnet Bay, Isle of Wight.
6. *Ponera*(?) *leptocephala* Emery, 1891: 8, plate 1, figs. 3, 4, female. Miocene — Sicilian Amber.
7. *Ponera minuta* Donisthorpe, 1920: 85, plate 5, fig. 4, male (?). Oligocene, Gurnet Bay, Isle of Wight.
8. *Ponera rhenana* Meunier, 1917, wing impression. Oligocene — Bavaria.
9. *Ponera scitula* Clark, 1934, listed from Tertiary, Allendale, Australia by Oke (1957).
10. *Ponera succinea* Mayr, 1868: 72, female. Oligocene — Baltic Amber.
11. *Ponera*(?) *umbra* Popov, 1933: 17, fig. 1, female. Miocene — Kuban Caucasas.

Of these species only one, *P. atavia* Mayr, is considered here to be satisfactorily referred to *Ponera. P. succinea* Mayr was transferred to *Euponera (Trachymesopus)* — now *Trachymesopus* — by Wheeler (1914), on grounds which are entirely acceptable. *P. gracilicornis* Mayr is too large to be considered a *Ponera* (Wheeler, 1914), but Mayr's assignment of the species to the Ponerinae is probably dependable — the species is considered here as "Ponerinae *incertae generis*". (?)*P. leptocephala* Emery is best assigned with reservation to *Ponera.* This form is evidently close to *Ponera* or *Hypoponera,* but has very long legs and antennae, and the eyes appear to be placed exceptionally far back on the head. It may belong to a distinct genus as yet undiagnosed, but it would be premature to so assign it on the basis of Emery's description and figures. *P.*(?) *umbra* Popov also seems best assigned to (?) *Ponera.* It appears close to *Ponera* although it could equally well be a *Hypoponera* or a member of some other small genus of the tribe Ponerini.

I propose the following NEW COMBINATIONS in *Poneropsis: Poneropsis hypolitha* (Cockerell), and *Poneropsis rhenana* (Meunier), these are both wing impressions and cannot be assigned more satisfactorily at present. *P. minuta* is considered "Formicidae *incertae* *generis*"; no reason whatsoever was presented by Donisthorpe to justify its placement in *Ponera*, and no satisfactory diagnostic characters are given in his figure or description. *P. hendersoni* Cockerell has been shown by Carpenter (1930) to be referable to the extinct genus *Protazteca*. The recent Australian species, *Hypoponera scitula* (Clark) (NEW COMBINATION from *Ponera)*, was listed as a tertiary fossil from Allendale, Victoria, under the name *Ponera scitula*, by Oke (1957). I have not seen the specimens involved, but since they were determined by Clark, the assignment is presumably trustworthy.

Fossil names and their nomenclatural status.

According to the principle of homonomy certain of the specific names given above are no longer available for use in *Ponera*. The eleven names assigned by Heer in 1849 (see list, p. 138), and the ten species, excluding *brodei*, assigned by subsequent authors and listed above on page 139 are in this category, as is the specific name *veneraria* Heer (1865).

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NOTES ON THE NESTING BEHAVIOR OF *PHILANTHUS LEPIDUS* CRESSON (HYMENOPTERA, SPHECIDAE)*

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Several years ago Evans and Lin (1959) discussed the nesting behavior of four species of *Philanthus* which occur commonly in the northeastern United States. The four species were found to have many ethological similarities as well as several interesting differences. The larger species tend to take larger bees as prey, and certain of the species nest earlier in the season than others or seem to prefer more sloping earth in which to nest. The fact that there is much overlapping with respect to these slight ecological differences suggests that competition for prey and nesting sites has been of minor importance in the evolution of these species; this may in part be a consequence of the fact that populations of all four species appear to be kept well below their maxima by parasites. In point of fact, all of the major behavior differences between these four species appear "to represent mechanisms which have evolved as a response to parasite pressure": for example, differences in closure, in mound-leveling, and in burrow profile.

I am now able to add a fifth species to this picture without necessitating any change in these conclusions. *Philanthus lepidus* is a locally common species which occurs in much the same situations as the four studied earlier and preys upon much the same kinds of bees: in fact one common green "sweat bee", *Augochlorella striata,* has been found in the nests of all five species, and several others have been found to be used by three or four of them. The distinctive features of *P. lepidus,* as in the case of the other four species, appear to be associated with parasitism. In particular, this species prepares one or more "false burrows", which remain open at all times, although the true burrow is closed. False burrows have to my knowledge not been reported for other philanthine wasps, but they occur in certain species of at least two other subfamilies, as discussed further in the final section of this paper. It cannot be proved that these false burrows do, in fact, divert parasites in any important way, but there is now considerable circumstantial evidence that this is their function.

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Ecology. — I first encountered *Philanthus lepidus* in an area of extensive small sand dunes and blow-outs near Granby Center, Oswego Co., N. Y., on August 31, 1960. Here I found some thirty nests, mostly in two well separated aggregations about ten meters apart. Within each colony the nest entrances were separated at times by no more than 10 cm. Many of the nests were in depressions amongst ferns, and the soil was so full of roots as to make it very difficult to dig out the nests successfully. I spent only a few hours with these nests, as I was gathering data on *Bembix pruinosa* and on a species of *Tachytes* which nested in more open sand in the same locality. I noted no other philanthine wasps in the area on that date.

For the past several summers *P. lepidus* has nested in considerable numbers in a large, eroded sand bank near my home in Lexington, Massachusetts. Each year the species appears at the end of August and remains active well into September. In 1962, when most of my studies were made, I noted much activity on September 7, which was a cool day (73°F maximum), and on September 23 a few females were noted digging sluggishly at an air temperature of 60°F, after several nights of frost. On this date virtually all other solitary wasps had disappeared. Even *P. solivagus,* another species characteristic of the late summer, emerges and disappears one to two weeks before *lepidus.* However, the nesting cycle of the two species overlaps for two or three weeks at Lexington, and the nests of the two species are sometimes intermingled. However, in this particular sand bank *solivagus* occurs mostly near the top, in a moderately steep slope, while most nests of *lepidus* are near the bottom, in weakly sloping, firm sand eroded from above. In this very same place, *P. politus* is common in early summer, but I saw none nesting after mid-August. *P. gibbosus* also occurs in this sand bank, nesting in small numbers both in the *solivagus* and *lepidus* areas, but mainly in mid-summer.

Both males and females of *P. lepidus* visit the flowers of *Solidago* in considerable numbers. The males are otherwise rarely seen, though they do appear from time to time around the nests of the females, landing on the sand with their antennae extended rigidly and now and then pursuing females. I have taken males as late as September 14 at Lexington.

Nesting behavior. — From three to six hours are required to complete the burrow. Then sand is allowed to plug the entrance, and from time to time the wasp comes out and clears it away, sweeping it into a broad mound in front of the opening. Mounds of completed nests measure from 8 to 13 cm in length by 6 to 8 cm in width and 0.5 to 1.5 cm in depth. No true leveling movements occur at any time, but mounds may weather away after several days, particularly if there has been a heavy rain or strong wind.

Following completion of the burrow, but before making a cell or bringing in prey, the wasp digs a short, blind burrow on one side of the entranceway, sometimes one on each side. Whether these are dug before or after the initial closure of the true burrow was not determined. Thereafter these "false burrows" are never closed, but the true burrow is closed from the outside when the female is hunting, from the inside when she is inside the nest for more than brief periods. I obtained the impression that the wasps keep these false burrows "in repair", although they do not use them in any way. One female was seen to bring a bee into the true burrow, then emerge and enter a false burrow for a moment and come out and fly off.

I found no fresh nests without at least one false burrow. At Granby Center, N. Y., I took notes on four nests, three of which had one false burrow and one of which had two. These false burrows began 1-4 cm from the opening of the true burrow and started out at roughly a right angle to it, but often curved toward or away from the true burrow. They varied in length from 6.5 to 9 cm, and for the most part were at only a 15 to 30° angle with the horizontal (like the beginning portion of the true burrows) (Fig. 1).

In Lexington, Mass., I observed many nests with false burrows, but took measurements on only seven. Of the seven, four had one and three had two false burrows beside the entrance of the true burrow and forming a 45 to 90° angle with it; these varied in length from 1 to 3 cm (notably less deep than those at Granby Center). In addition, four of these nests had additional, very shallow false burrows (0.5-1.0 cm deep), not beside the nest entrance but farther back on the mount. One nest had a total of five false burrows, one of them with a double entrance (Fig. 3). Such nests presented a confusing picture of holes going in various directions, with the true nest entrance well concealed and discoverable only when the female arrived with prey.

Nest structure. — Diameter of both the true and false burrows is about 5 mm. As already mentioned, the top section of the true burrow is at only a 15 to 30° angle with the horizontal; after some 8 to 15 cm the burrow bends down sharply, attaining an angle of from

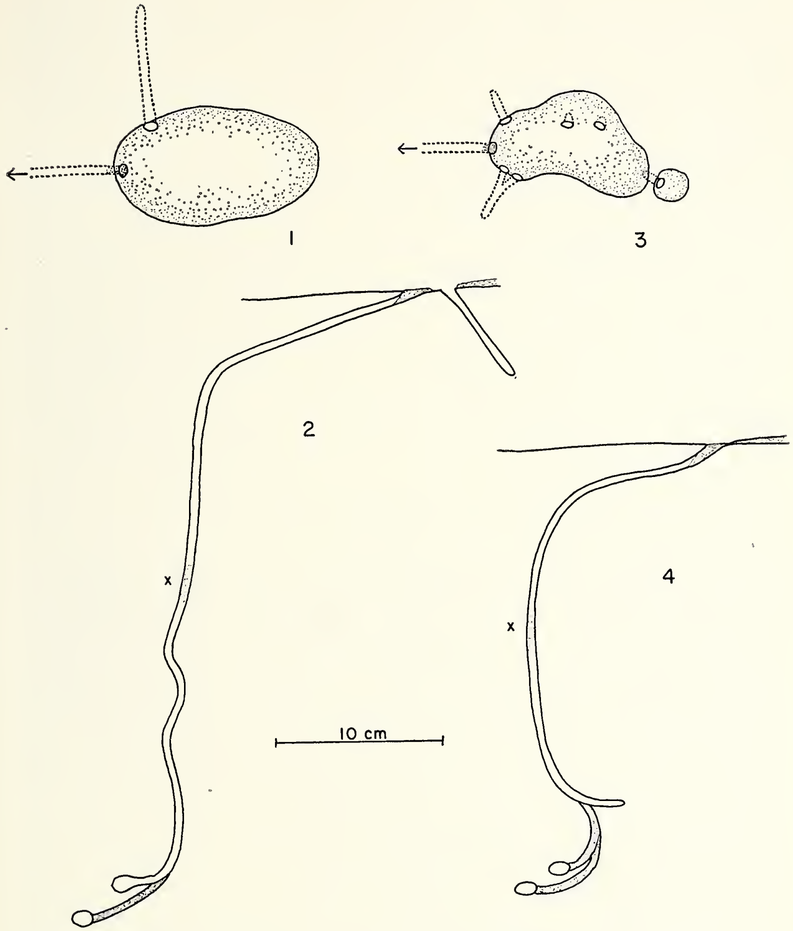

Fig. 1. Mound of nest no. 1674, Granby Center, N. Y., showing true burrow (left) and false burrow (top). Fig. 2. Same nest in profile; one bee was found in the burrow at *x*, several others in each cell. Fig. 3. Mound of nest no. 1848-3, Lexington, Mass., showing five false burrows, one with a double entrance. Fig. 4. Nest no. 1846, Lexington, Mass., in profile; eight bees were found in the burrow at *x*, several others in each cell; the false burrow was destroyed accidentally and hence is not shown here.

70 to 90° with the horizontal. In the one nest successfully excavated at Granby Center, the burrow was 48 cm long and reached a point 37 cm in vertical depth (Fig. 2). Two nests at Lexington both had burrows only 24 cm long, reaching depths of from 17 to 19 cm (Fig. 4). The initial burrow terminates blindly, and it is apparently only after several bees have been taken and stored in the burrow that the first cell is constructed.

I obtained no precise data on the duration of nests or the final number of cells per nest. Females evidently remain with a single nest for several days (at least three), but they prepare several nests in the course of the nesting season. I found no more than two cells in any of the nests excavated, but it seems very probable that the final number of cells in any one nest averages higher than this. The cells were found to be located at or slightly below the terminus of the burrow, at a vertical depth of 33-35 cm (Granby Center) or 24-26 cm (Lexington). The cells are small, about 10 mm long by 8 mm high; in the nests excavated the two cells were separated by only about 2 cm of soil.

As usual in philanthine wasps, the bees are stored in the burrow for a period before being introduced into a cell. In some cases they are stored about halfway down the burrow (9 to 17 cm deep), in some cases at the bottom of the burrow. One nest at Lexington had seven bees halfway down and one at the bottom. The stored bees are surrounded by a small amount of loose sand.

Provisioning the nest. — Bees are paralyzed at the site of capture and are carried to the nest beneath the body of the wasp, the middle legs providing the major grasp as usual in this genus. The wasps fly in to their nests low, only 10-15 cm above the ground. The nest entrance is opened by a few scrapes of the front legs and the bee carried directly in. Females watched over a period of time appeared to provision very slowly, bringing in bees at the rate of about one every half hour. Usually females remain within the nest for only 20-30 seconds, but occasionally they remain within for long periods of time, presumably digging a cell and introducing the bees into the cell. From 9 to 11 bees are provided per cell. The egg is laid longitudinally on the venter of one of the topmost bees in the usual manner of members of this genus (Evans and Lin, 1959, Fig. 9).

In both areas of study, *P. lepidus* preyed upon a considerable variety of small bees, all but one of the 69 specimens taken belonging to the family Halictidae. Individual nests always contained a mixture of species (from 3 to 7). Male and female bees were used in roughly equal numbers. Many of these same species of bees appear on the lists of prey taken by *P. solivagus, politus, gibbosus,* and *bilunatus* (Evans and Lin, 1959). The complete list follows (determinations made by myself, using the keys in Mitchell, 1960, in connection with specimens determined by Mitchell):

Species of prey	*Number taken*			
	Granby Center, N. Y.		Lexington, Mass.	
Andrenidae				
Pseudopanurgus andrenoides (Smith)	1 ♀			
Halictidae				
Augochlora pura (Say)				2 ♂♂
Augochlorella striata (Provancher)	1 ♀,	3 ♂♂	1 ♀,	1 ♂
Dialictus apertus (Sandhouse)				1 ♂
D. cressonii (Robertson)			1 ♀,	6 ♂♂
D. inconspicuus (Smith)			16 ♀♀,	1 ♂
D. laevissimus (Smith)		10 ♂♂		3 ♂♂
D. tegularis (Robertson)			7 ♀♀	
D. versans (Lovell)			1 ♀	
D. spp.	1 ♀,	2 ♂♂		5 ♂♂
Evylaeus divergenoides Mitchell				3 ♂♂
E. macoupensis (Robertson)				2 ♂♂
Halictus ligatus Say			1 ♀	
Total	3 ♀♀,	15 ♂♂	27 ♀♀,	24 ♂♂

Parasites. — Parasitic flies were much in evidence in both localities. In both areas several of the flies were captured as they pursued females laden with prey; all were determined by C. W. Sabrosky as members of the *Senotainia trilineata* complex (Sarcophagidae: Miltogramminae). Members of this complex are known to attack a wide variety of ground-nesting wasps. None of the six cells excavated contained maggots, and no maggots were noted on any of the bees found in storage in the burrows.

Provisioning females being pursued by Senotainia undertake a characteristic flight, hovering near the nest or flying slowly forward 3-6 cm high, sometimes to a distance of several meters from the nest. The fly usually follows just behind the wasp and slightly below. If unable to rid herself of the fly, the wasp may fly rapidly and deviously and may leave the area altogether, to return a few moments later, usually without the fly. Presumably the flies larviposit successfully on the prey at times, as described in the case of *P. solivagus* and these same flies by Ristich (1956), but I observed no cases of successful larviposition and, as already mentioned, found no maggots in the few nests excavated.

In Lexington, the mutillid *Dasymutilla nigripes* was very common. On several occasions females were seen entering the open false burrows, digging a bit, and then leaving. None were seen entering the true nest entrances. Shappirio (1948) observed this same species of mutillid entering nests of *P. gibbosus* at Washington, D. C. It seems very probable that this species is a parasite of several species of *Philanthus,* although no one has actually reared it from cells of these wasps.

Discussion. — False burrows are a characteristic feature of the nests of several nyssonine digger wasps (e.g., Tsuneki, 1943, Evans, 1957) and of at least one sphecine wasp (Tsuneki, 1963). There are now many observations of mutillid wasps and miltogrammine flies being attracted to these burrows, and bombyliid flies have been observed ovipositing in false burrows of certain species. There is no evidence whatever that these burrows play a role in orientation, resting, or storage of prey. Tsuneki and I are in agreement that their function must be to divert parasites, and in a paper in preparation I shall attempt to trace their evolution, in the Nyssoninae, from quarries used for soil for closure to ritualized false burrows serving a very different function. The occurrence of false burrows in the Philanthinae has not, to my knowledge, been recorded previously. They were found to occur in all nests in both areas of study, but they may not occur in all individuals throughout the range of this species (geographic variation in this feature was found to occur in *Bembix pruinosa* by Evans, 1957, and has since been found in certain other species). It is important that this behavior be recorded in all species in which it occurs, and in various localities.

In the case of *P. lepidus,* the false burrows would seem to afford no protection against *Senotainia,* which appeared to be the major enemies in both areas of study. Presumably the selection pressure was provided at a time and place when hole-searching miltogrammines, bombyliids, chrysidids, and mutillids were of major importance.

Otherwise the behavior of *P. lepidus* does not differ in any major way from that of *gibbosus* and *bilunatus,* which make similar nests, maintain an outer closure, and do not level the mound at the nest entrance. *P. lepidus* nests later in the season than those species, emerging slightly later even than *solivagus.* The latter is a larger species which preys mostly on larger bees, sometimes on wasps; in the area of study *solivagus* nested in a slightly different situation, although there was some intermingling of nests. That the five species of *Philanthus* common in the northeastern states have been only partially successful in "dividing up the sand + bee niche" probably means, as suggested earlier, that the populations of all five are kept fairly low by parasite pressure. All five have developed certain behavioral mechanisms apparently serving to reduce the incidence of parasitism, and in each case the mechanism is different, at least in part. In a given area, the species whose behavior patterns are most successful in combating the parasites most prevalent in that location may well inherit the bulk of the sand + bee niche.

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PAUSSID BEETLES IN MEXICO*

By P. J. Darlington, Jr.
Museum of Comparative Zoology, Harvard University

In America, paussids are rare insects, strictly confined to the tropics. Only one individual has been recorded from Mexico (Pallister 1954), so far as I know. Six additional Mexican specimens that are now before me are therefore of special interest. They represent three distinct species. All three species have been known before from South America or at least from Panama. All three may therefore have spread northward comparatively recently, perhaps since the Central American isthmus was completed late in the Pliocene. The accompanying sketch-map of southern Mexico (Fig. 1) shows the localities of the specimens in question. The actual northernmost record for any American paussid is still that of *Homopterus hondurensis* from northern Yucatan (Pallister). The new record of H. *(A.) praemonens* from 22 miles southeast of Jalapa, Vera Cruz, represents the farthest known advance of any paussid onto the continent of North America.

Although most or all paussids are probably myrmecophilous at least during some stage of their life history, the only actual record of an American species with ants is still apparently that of *Homopterus steinbachi* in a nest of *Dolichoderus bispinosus* (Darlington 1950, p. 48). Pallister's (1954) specimen of *H. hondurensis* from Yucatan was "swept from weeds and vegetation, about two feet from the ground, bordering a trail through deep forested jungle." Most or all other Mexican specimens, recorded now, were taken at light, including "black" light. They are of course all winged, and they evidently fly at night.

The recent, useful review of American paussids by Luna de Carvalho (1963) makes it unnecessary for me to cite references or discuss species in detail. The present short paper is in fact little more than a supplement to Carvalho's paper.

I am indebted to the following persons for loan of specimens: Drs. Jerry A. Powell, John A. Chemsak, George W. Byers, and Henry F. Howden.

Homopterus (Arthropteropsis) praemonens Kolbe

Previously known from Bolivia, Brazil, and San Salvador. New records: El Zapotal, 2 miles south of Tuxtla Gutiérrez, Chiapas,

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* *Manuscript received by the editor May 31, 1964*

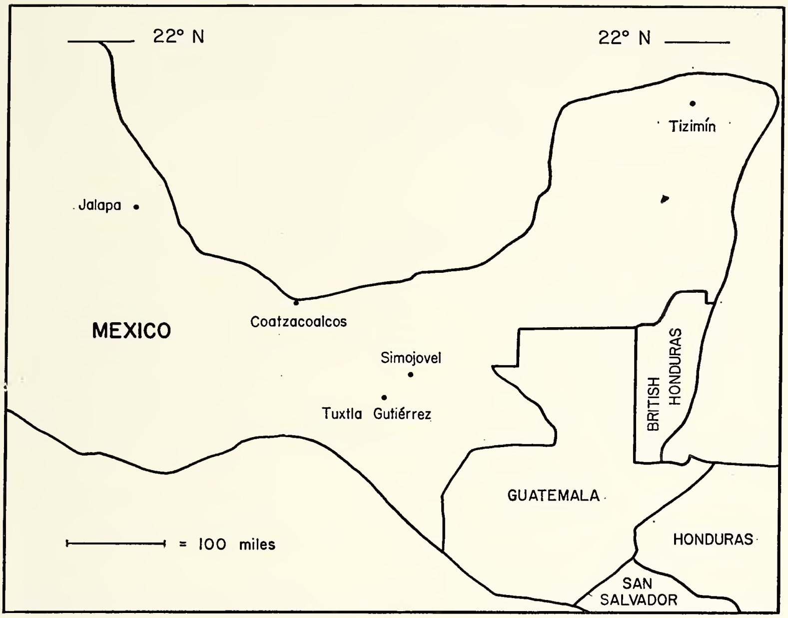

Fig. 1. Mexican localities at or near which paussids have been collected.

July 1, 1957, at light (J. A. Chemsak & B. J. Rannells, in collection of California Insect Survey, Berkeley); 22 miles southeast of Jalapa, Vera Cruz, 1100 ft., June 29, 1958 (University of Kansas Mexican Expedition).

Homopterus hondurensis Darlington

Previously known from Panama, Honduras, and about 40 miles east of Tizimín, nothern Yucatan (Pallister 1954). New records: El Zapotal, 2 miles south of Tuxtla Gutiérrez, Chiapas, July 1, 1957, at light (J. A. Chemsak and B. J. Rannells, in collection of California Insect Survey); Santo Domingo, 15 miles southeast of Simojovel, Chiapas, July 8-15, 1958, at light (J. A. Chemsak, 2 specimens, in collection of California Insect Survey and Canadian National Collection).

Homopterus steinbachi Kolbe

Previously known only from South America: Bolivia (the type), Colombia (Darlington 1950, p. 48), French Guiana, and Brazil

(Luna de Carvalho 1963). New records: Camp Sibun, 200 m., Cayo District, British Honduras, July 23, 1960 (E. Willing, in collection of California Insect Survey); 10 miles south of *Coatzacoalcos,* Vera Cruz, July 10, 1963, at black light (J. T. Doyen, in collection of California Insect Survey).

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The illustration on the front cover of this issue of Psyche is a reproduction of a drawing of a myrmecophilous histerid beetle, *Euxenister wheeleri* Mann, from Barro Colorado Island (Psyche, vol. 32, p. 173, 1925).

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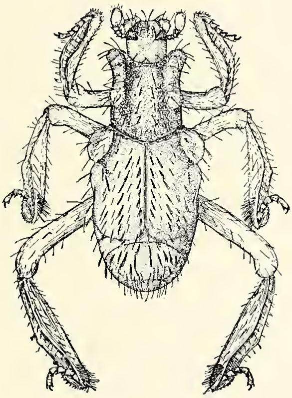

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REVIEW OF THE CALVERTIELLIDAE, WITH DESCRIPTION OF A NEW GENUS FROM PERMIAN STRATA OF MORAVIA (PALAEODICTYOPTERA)

By Jarmila Kukalová*
Charles University, Prague

The extinct order Palaeodictyoptera now includes some twenty families, which appear to represent many lines of evolution radiating in different directions. Most of them resemble the Ephemeroptera, at least superficially, more than any other order of living insects but a few show some features highly suggestive of the Odonata and Protodonata.

The most notable of the latter is the family Calvertiellidae, now represented by *Calvertiella* Tillyard from Lower Permian deposits near Elmo, Kansas, and by *Moraviptera* Kukalová from the very base of the Lower Permian strata in Moravia (Zbýsov). Recently, some remarkably preserved fossils belonging to a new genus were found in Moravia at the Obora locality. Since both fore and hind wings are preserved, they add a great deal to our knowledge of this group of Palaeodictyoptera. The present paper consists of a review of the Calvertiellidae and the description of the new genus *Moravia* from Czechoslovakia.

Calvertiella was originally (1925) placed by Tillyard in the family Protagrionidae within the order Protodonata, but this was before the Protodonata (as well as Odonata) were known to lack the veins MA and CuA. The family Calvertiellidae, established by Martynov in 1931, was transferred to the Palaeodictyoptera by

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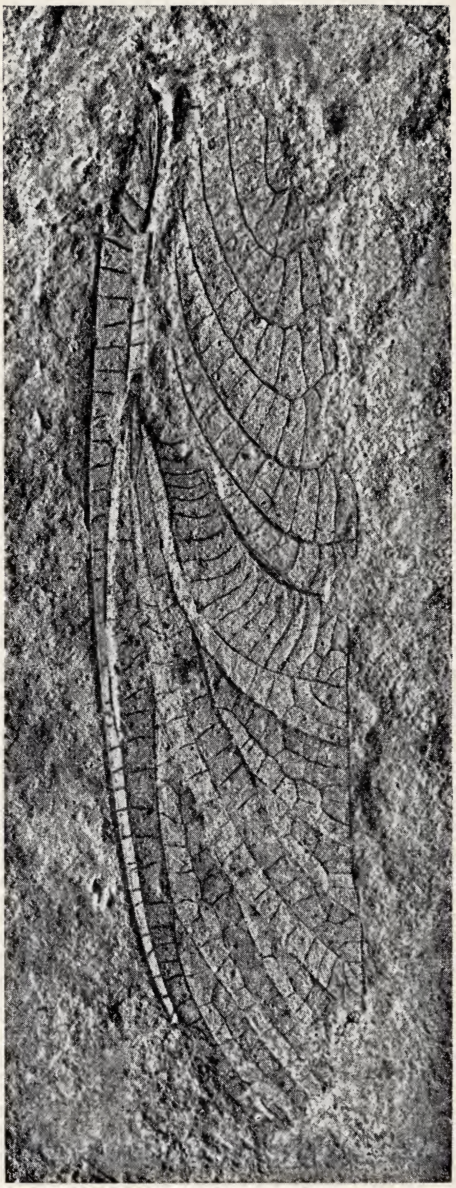
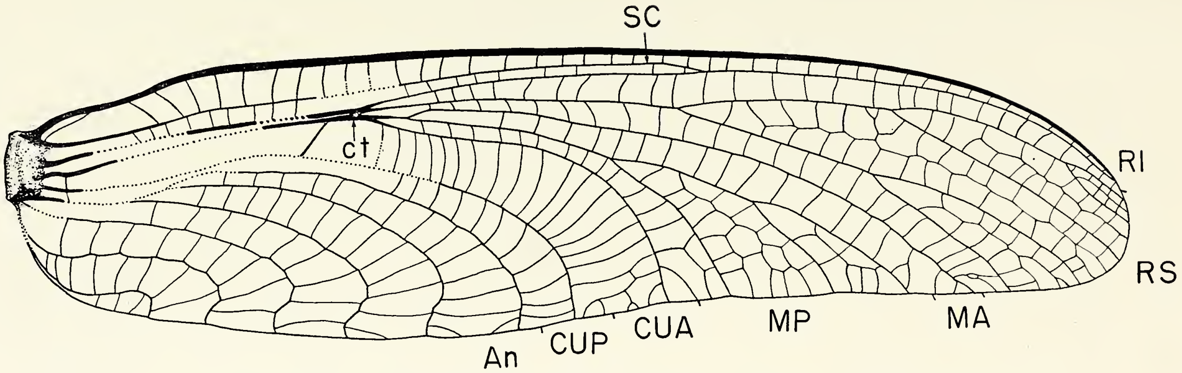
*Current address: Biological Laboratories, Harvard University.

This research has been aided by a National Science Foundation Grant, No. NSFGP - 2038. I am much indebted to Professor F. M. Carpenter, who made it possible for me to study the type of *Calvertiella* and who was very helpful in the preparation of this paper.



Calvertiella permiana Tillyard (reverse of holotype). Lower Permian of Kansas. Original photograph, × 5.



Text-figure 1. *Calvertiella permiana* Tillyard. Drawing of fore wing, based on obverse and reverse of the holotype. Lower Permian of Kansas. Original drawing.

Lettering: C, costa (+); Sc, subcosta (—); R, radius (+); Rs, radial sector (—); MA, anterior media (+); MP, posterior media (—); CuA, anterior cubitus (+), CuP, posterior cubitus (—); An, anal area (+); ct, cuticular thickening (+); (—) concave veins; (+) convex veins.

Handlirsch in 1937, along with the Protagrionidae. Since then, both families have been treated as Palaeodictyoptera.[1]

ORDER PALAEODICTYOPTERA GOLDENBERG

Family Calvertiellidae Martynov, 1931

Calvertiellidae, Martynov, 1931, Bull. Acad. Sci. URSS, 1:146 [Protodonata (Meganisoptera)]; Handlirsch, 1937, Ann. Naturh. Mus. Wien, 48:82 [Palaeodictyoptera]; Martynov, 1938, Trav. Inst. paleont., 7(4):41 [Protodonata]; Carpenter, 1943, Bull. Geol. Soc. Amer., 54:536 [Palaeodictyoptera]; Laurentiaux, 1953, Traité de paléont.:424 [Palaeodictyoptera]; Carpenter, 1954, Bull. Mus. Comp. Zool., 108:786 [Palaeodictyoptera]; Kukalová. 1955, Sborník Ústř. Úst. geol., 21:571 [Palaeodictyoptera]; Rodendorf, 1962, Osnovy paleont.:52 [Palaeodictyoptera].

DIAGNOSIS. The following diagnosis of the family is based on a study of the type of *Calvertiella permiana* Tillyard, 1925, as well as on the material from Moravia.

Fore wing: a very short convex veinlet present at the basal part of the costal area; Sc terminating on R1 slightly beyond mid-wing; Rs arising before the end of the first third of wing length, with 3-4 main branches; a cuticular thickening (ct)[2] between R and M, at about the level of the origin of Rs; stems of R and M independent at the wing base, but approaching each other near the point of origin of Rs; M forking near the level of the origin of Rs; MA unbranched, MP branched; stem of Cu independent, its branches simple and strongly curved towards posterior margin; CuA diverging towards M near the level of origin of Rs and fusing with it for some distance, or connected with it by means of a short, convex connecting vein; in its further course, CuA runs very near to the posterior branch of MP; area between CuA and CuP broad; 6 anal veins, at least the first 3 arising from one independent stem, all strongly arched, especially the proximal ones; cross veins more or less numerous, forming a reticulation in at least some areas of the wing; intercalary sectors more or less definitely indicated in the radial and medial areas.

Hind wing: broad basally and triangular in shape *(Moravia, n.g.)*; anterior margin concave; basal veinlets in costal area somewhat better developed than in the fore wing; Sc terminating much

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[1] For a discussion of the nomenclatural problems involving the name Protodonata see Carpenter, 1943 and 1954.

[2] Not known in *Moraviptera* because of poor preservation in the region of the origin of Rs.

as in fore wing; Rs arising slightly more basally than in the fore wing, with about 4 main branches; cuticular thickening as in fore wing; stem of M independent, forked near the level of origin of Rs; MA unbranched, MP branched; stem of Cu independent, dividing into two simple branches, arched strongly towards posterior margin; CuA diverging towards M as in the fore wing, and then continuing close to the posterior branch of MP; 4 anal veins, at least 3 arising from the base independently of each other, somewhat recurved; cross veins numerous, forming a reticulation over much of the wing; intercalary sectors in radial and medial area.

RELATIONSHIPS: The family Calvertiellidae clearly has a very specialized venation and seems far removed from most of the families of the order. This is shown by the short Sc, proximity of CuA and MP, the wide separation of CuA and CuP, the curved CuP, recurved anal veins (fore wing) and presence of intercalary sectors. Its closest relatives in the order seem to be the Eugereonidae (including Dictyoptilidae; see Carpenter, 1964, p. 104), which differ from Calvertiellidae in having Sc long and terminating on C, CuA more remote from the posterior branch of MP, CuP branched and less arched, area between CuA and CuP narrower, anal veins less arched, absence of intercalary sectors and of the cuticular thickening. The hind wing of Calvertiellidae is broader than that in the Eugereonidae and more triangular in shape.

It is interesting to find in the wings of the Calvertiellidae a short, simple or branched veinlet, which has now been noted in several families of Palaeodictyoptera (e.g. Breyeriidae, Kukalová, 1958; Spilapteridae, Carpenter, 1964). In *Calvertiella* it is a simple convex vein, but in the hind wing of *Moravia,* n.g., it is better developed, with a series of short veinlets. Although this vein may actually be a basal branch of the costa, since the area set off cannot reasonably be considered homologous with the precostal area of the Orthoptera, I have termed it the postcostal area (Kukalová, 1963). The vein seems more likely to be homologous with the costal brace of Ephemeroptera, resembling especially the Permian types.

Geological occurrence of family: Lower Permian of Kansas (USA) and Moravia (Czechoslovakia).

Genera included: *Calvertiella* Tillyard, 1925; *Moraviptera* Kukalová, 1955; *Moravia,* new genus (herein).

Genus *Calvertiella* Tillyard

Calvertiella Tillyard, 1925, Amer. Journ. Sci, 10:43; Tillyard and Fraser, 1938, Austral. Zool., 9(2):141-142; Fraser, 1957, Royal Zool. Soc. NSW:24.

DIAGNOSIS. Fore wing: long and slender, broadest before mid-wing; veins strong, wing membrane thin; anterior margin slightly concave near base, then almost straight; apex slightly directed posteriorly; posterior margin slightly concave at mid-wing; Sc terminating on R at about the end of the second third of the wing length; R1 long; Rs originating before the end of the first third of the wing length, forming three branches, the first forked; an oblique cuticular thickening (ct) running from the very base of Rs to M+CuA; M close to R before, and branching slightly beyond, the level of the origin of Rs; MA simple; MP giving rise to two branches; Cu dividing before the origin of Rs, CuA fused with M for a short distance, then closely following MP; CuP simple, arched strongly backwardly; 6 anal veins arising perhaps from a common stem, recurved and slightly sigmoidal; cross veins not dense, mostly simple, forming little reticulation; intercalary sectors distinctly formed.

RELATIONSHIP: *Calvertiella* differs from *Moraviptera* (probably a hind wing) in having CuA more remote from MP, a three branched MP and more regular cross veins. From *Moravia,* n.g., it differs in the more slender fore wing, with only three branched MP, the fusion of CuA with M for some distance, the absence of supporting cross veins near origin of R4+5, and in having far less dense cross venation and less reticulation.

Type-species: *Calvertiella permiana* Tillyard.

Calvertiella permiana Tillyard

Text-figures 1 and 4A; plate 19

Calvertiella permiana Tillyard, 1925, Amer. Journ. Sci., 10:43, figs. 1, 2A.

Fore wing, 27.5 mm long, 7 mm broad; about 4 times longer than broad. Intercalary sectors well indicated, convex, irregular reticulation almost absent; first branch of Rs with a long fork, the third very short; anal area gradually broadening in the distally, the wing being broadest shortly before the middle.

Tillyard was apparently not aware, when he prepared his account of this fossil, that some tearing and distortion of the wing had taken place in connection with its preservation in the fossil state. In the basal third of the wing, the costal and subcostal areas are broken and pushed posteriorly over the stems of R. At the same time, the anal area was broken and pushed anteriorly over the stem of A1. Careful removal of small pieces of matrix shows that all of the main veins have independent stems. The drawing in text-figure 1 depicts these veins restored to their normal positions. Clearing away of the matrix also revealed the complicated structure herein designated the cuticular thickening (ct, text-figure 4A). This does not resemble a vein but is a thick, cuticular band which extends from the stem of M + CuA to the origin of Rs. It is much more extensively developed in the genus *Moravia,* described below.

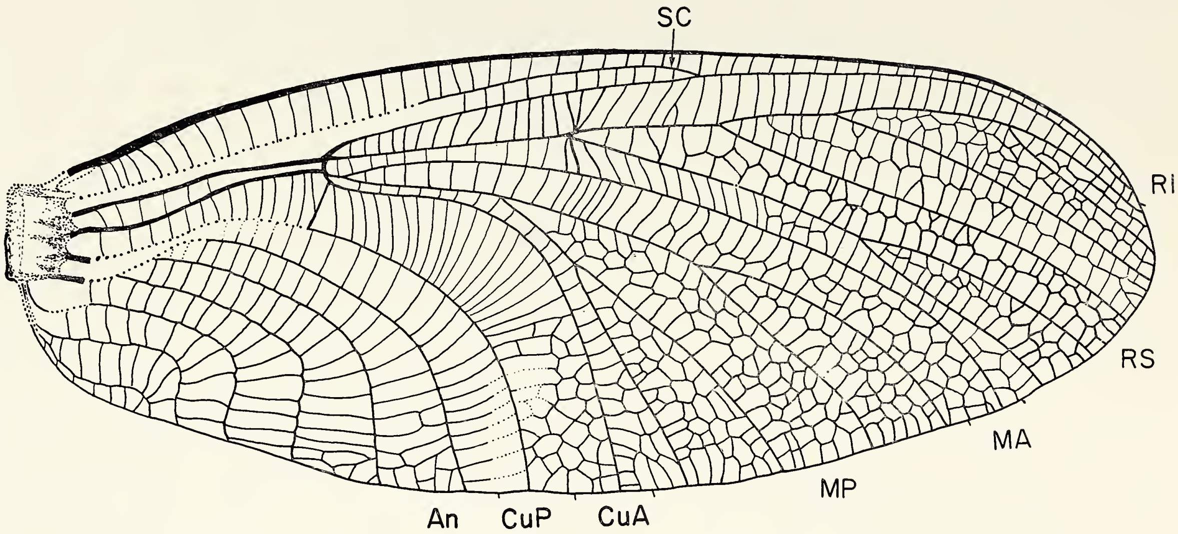
Holotype: No. 5007 (obverse and reverse), Peabody Museum, Yale University; collected in the Wellington Shales, Elmo, Kansas. I am indebted to the authorities of the Peabody Museum for the opportunity of studying this fossil.

Genus **Moravia,** new genus

Fore wing: broad, almost oval. Apex very broadly rounded; anterior margin convex; posterior margin even more convex; postcostal area very small and indistinct; Sc terminating on R1 before the end of the second third of the wing length; R1 long; Rs originating before the end of the first third of the wing length, with four branches, the first of them forked; cuticular thickening (ct) arched, starting from R at the point of origin of Rs, crossing the stem of M and continuing by a convex connecting vein between M and CuA; M approaching R before the origin of Rs, but not touching it, branching slightly behind the cuticular thickening; MA simple, MP forked three times; Cu dividing into CuA and CuP slightly before the level of the origin of Rs; CuA approaching close to M, connected with M and with the cuticular thickening by a short connecting vein; in its further course, CuA follows MP closely; area between CuA and CuP with many cross veins and a reticulation; curvature of the 6 anal veins becoming more pronounced proximally; cross veins numerous, simple, reticulated in the radial, medial and cubital areas; several cross veins radiating from Rs to R and to MA in the proximity of the origin of the first branch of Rs; intercalary sectors present in the radial area.

Hind wing: triangular, very broad basally; anterior margin slightly concave. Postcostal area larger than in the fore wing; Sc terminating on R somewhat beyond mid-wing. Rs originating at about the end of the first quarter of the wing length, giving rise to about four main branches, the first of them forked; cuticular thickening (ct) arched, starting from the very base of Rs and crossing M at the point where the short convex connecting vein between M and CuA is starting; stem of M approaching R before the origin of Rs, but not touching it, branching some distance beyond the cuticular thickening; MA simple, MP with 4 terminal branches; the stem of

Moravia convergens n.sp. (holotype, fore wing). Lower Permian of Czechoslovakia. Photograph by F. M. Carpenter, × 3.7.



Text-figure 2. *Moravia convergens* n.sp. Drawing of holotype (fore wing). Lower Permian of Czechoslovakia. Original. Lettering as in text-fig. 1.

Cu parallel with the stem of M, dividing well before the origin of Rs; CuA diverging towards M and connected to it by a short connecting vein; in its further course, CuA parallel with MP; both cubital branches sigmoidal, directed almost perpendicularly to the posterior margin; area between CuA and CuP not broadened; four anal veins, arising independently from the base, arched, rarely branched; cross veins numerous, forming a reticulation in radial, medial, cubital and anal areas; several supporting cross veins radiating from Rs to R1 and from Rs to MA in about the level of the origin of the first branch of Rs; intercalary sectors well developed in the radial area.

Moravia differs from *Calvertiella* in the broader and shorter fore wing; Sc is shorter, Rs gives off four main branches, the cuticular thickening is arched, M does not touch R, MP is forked three times, CuA does not fuse directly with M and the cross veins and reticulation are much more dense.

From *Moraviptera* Kukalová (1955)[4], which is apparently a hind wing, it differs in the broader wing, a broader area between MP and CuA and in presence of more numerous cross veins and a denser reticulation.

Moravia is in many features the most specialized of all the genera of Calvertiellidae, known so far. Its cuticular thickening is highly convex, and continues as a convex connecting vein, forming a transverse "bridge" between R and CuA. It may have had a function like the arculus in Recent Odonata. The function of the radiating cross veins near the origin of R4+5 was probably that of support.

Both fore and hind wing of *Moravia* are known. Coloration in the fore wing is absent, but in the hind wing there are irregular pigment spots. The wings differ also little in length, and their venational patterns are very similar. It is impossible to determine whether the fore and hind wings belong to one species, but they are here treated as such.

Stratigraphic occurrence: Lower Permian (Upper Autunian) of Czechoslovakia.

Type-species: *Moravia convergens* n. sp.

Moravia convergens n. sp.

Text-figures 2, 3, 4B, 4C; plates 20 and 21.

Fore wing: 38 mm long and 15 mm broad, about 2.5 times

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[4] In the figure of *Moraviptera reticulata* Kukalová, (1954, p. 548, fig. 3) the origin of Rs is not correctly shown; it arises directly from R, just before the forking of M.

longer than broad. Coloration completely absent; postcostal area short and indistinct; length of Sc slightly variable, as well as the length of the forks on Rs and MP, the width of area between MP and CuA, and the curvature of the anal veins.

Hind wing: about 43 mm long and 20 mm broad, about 2.1 times longer than broad; triangular in shape. Postcostal area broad and long, with a series of short branches directed towards costa; irregular colored spots concentrated mainly in the posterior half of the wing; fork on the first branch of Rs relatively broad, as well as the fork on MP; area between CuA and CuP not very wide, but area between CuP and 1A broad; anal veins arising mostly independently from the base, curving slightly backwards; first two anal veins simple, the third one with a long fork, the fourth simple; reticulation dense, filling the area between CuP and 1A and the anal veins.

Holotype (fore wing): No. 1/1965, Department of Palaeontology, Charles University, Prague; collected by Anna Havlatová in Lower Permian shales (Upper Autunian), Obora, Moravia, Czechoslovakia.

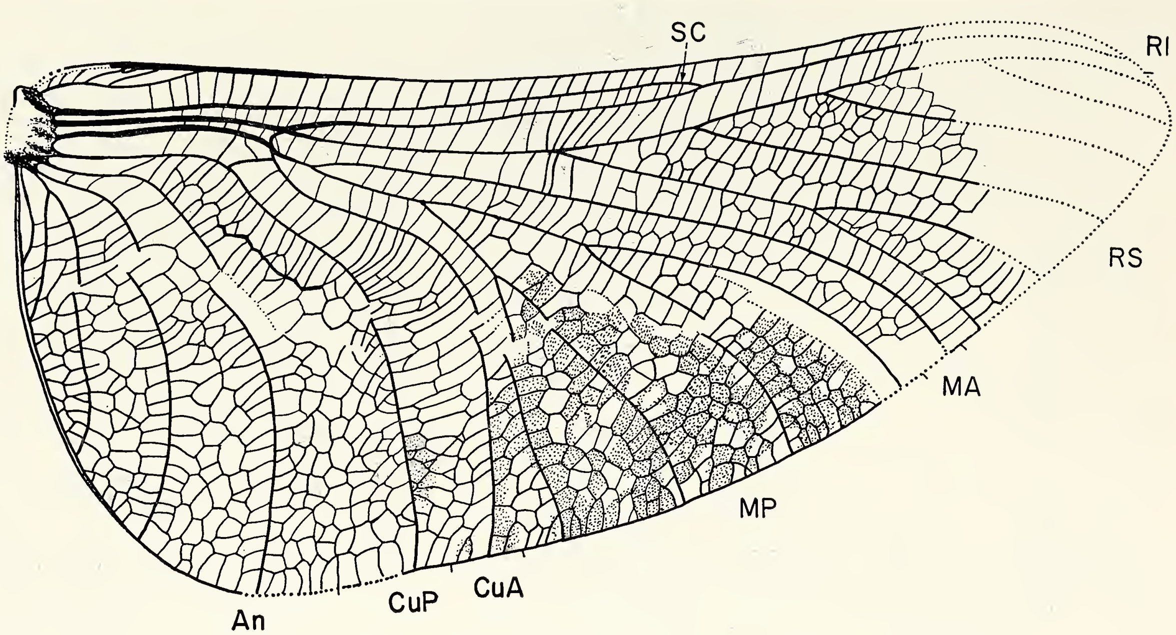
Paratype (hind wing): No. 3/1965; collected by Jarmila Kukalová, at the same locality.

Another specimen of a fore wing (No. 2/1965), showing the basal part of the wing especially clearly, also collected at the Obora locality. Its venation is very similar, even in detail, to that of the holotype.

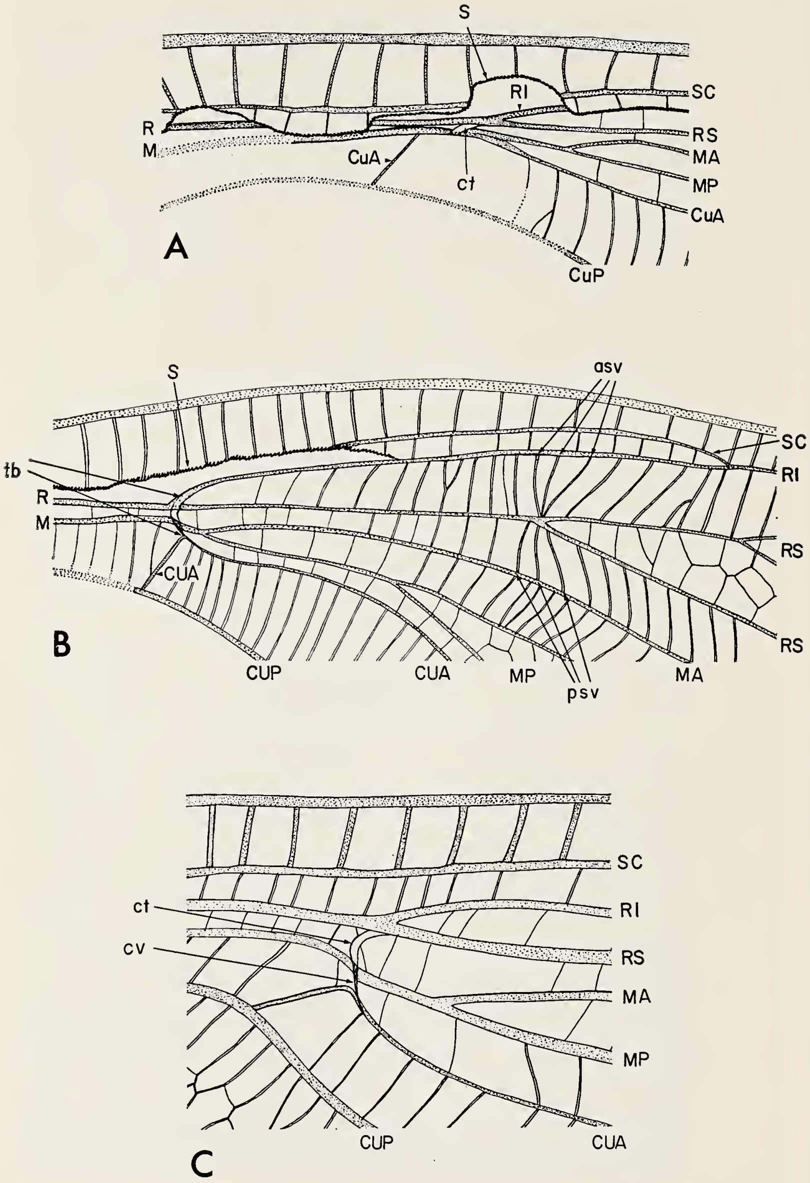
The holotype specimen was apparently distorted in preservation in much the same way as the type of *Calvertiella.* The wing is broken along Sc and the costal area has shifted towards R, while the anal area is drawn anteriorly across the stems of Cu and A. Nevertheless, the independent nature of the stems of the main veins can be seen. In text-figure 2, the veins have been restored to their original positions. The dotted lines representing the stems of Cu and A have been restored on the basis of those clearly preserved in specimen No. 2/1965.

Discussion: One of the remarkable features of *Moravia* is the peculiar cuticular thickening, which conceivably acts as a support between R and M at a point where most of the veins of the wing actually diverge. It is clearly developed in *Calvertiella* (see text-figure 4A), although very short — probably because of the close proximity of R and M + CuA at this point. It is more extensive in the fore wing of *Moravia convergens,* and much more so in the hind wing. In both wings the cuticular thickening is slightly curved

Moravia convergens n.sp. (paratype, hind wing). Lower Permian of Czechoslovakia. Photograph by F. M. Carpenter, × 4.



Text-figure 3. *Moravia convergens* n.sp. Drawing of paratype (hind wing). Lower Permian of Czechoslovakia. Original. Lettering as in text-fig. 1.



Text-figure 4

and seems to lead into the base of R1, at least in the fore wing, where it is more convex. It continues posteriorly, seeming to cross M, and finally joins the angle of CuA, which is directed anteriorly. This cuticular arch is herein designated the *transverse bridge* (tb) and its posterior portion, the *connecting vein* (cv). It is highly probable that this whole structure functioned in much the same way as the arculus complex in the Odonata. Very different veins are involved in the Odonata, which lack MP and CuA.

The presence of the several radiating cross veins near the origin of R4+5 is another notable feature of *Moravia convergens*. As can be seen in text-figure 4B, one group of three veins (asv) runs from Rs to R1, and the second group (psv) from Rs to MA just below the last group; the cross veins between MA and MP are much closer together than are the others. This structure also looks much like a supporting or strengthening device and recalls to mind the subnodal complex of the Odonata, although the locations of the two sets of structures are very different.

The enlarged anal area of the hind wing of *M. convergens*, as well as the triangular shape of the wing, also recalls the Odonata and, indeed, makes it difficult to realize that this insect, possessing all main veins including MP and CuA, was a palaeodictyopteron, not an odonate. Moreover, the similarities of the Calvertiellidae to the Eugereonidae make it nearly certain that the Calvertiellidae were haustellate, with a long and highly specialized beak.

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Text-figure 4. Details of venational structures in Calvertiellidae:

A. Oblique cuticular thickening (ct) in *Calvertiella permiana* Till.

B. Arched "transverse bridge" (tb), anterior supporting cross veins (asv) and posterior supporting cross veins (psv) in *Moravia convergens* n.sp. (fore wing).

C. Arched "transverse bridge", composed of cuticular thickening (ct) and convex connecting vein (cv) in *Moravia convergens* n.sp. (hind wing). Lettering as in text-fig. 1. S = broken edge of wing.

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THE HABITS OF *PHEIDOLE* (*CERATOPHEIDOLE*) *CLYDEI* GREGG (HYMENOPTERA: FORMICIDAE)

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Although the subgenus *Ceratopheidole* has been recognized for almost three-quarters of a century, virtually nothing is known about the habits of the species included in it. The present study is based upon four nests of *Ph.* (*C.*) *clydei* Gregg. Three of these were situated in Deep Canyon on the grounds of the Desert Research Center of the University of California. This spectacular and forbidding canyon, cut into the eastern slopes of the Santa Rosa Mountains, is about seven miles southeast of Palm Desert, California. The fourth nest was at Horse Tanks in the Castle Dome Mountains of Arizona. It is probable that the Deep Canyon colonies would have gone unnoticed had not a lucky series of events led to their discovery. Mr. Charles Musgrove of the Entomology Division of the Citrus Research Station of the University of California showed me a single minor worker which Professor William Ewart, also of that Division, had taken in Deep Canyon while sweeping for thrips. Dr. Ewart was good enough to point out to me bush from which the minor of *clydei* had come. Even with this advantage it was some time before the Deep Canyon nests were found, for their placement is most unusual.

Gregg's original description of *clydei,* published in 1950 (1) was based upon a small series of minor workers taken by C. P. Stroud near Carizozo, New Mexico. Since these were strays it was impossible for Dr. Gregg to give any nesting data for *clydei.* Later, however, he published on specimens of both major and minor castes (2) which the writer had taken from a nest at Split Mountain in the Anza Desert State Park, California. Certain features of this nest were so peculiar that both Gregg and I hesitated to accept it as a normal nest of *clydei.* It was situated in crevices beneath a weathered lamina of stone which had partially split off from the top of a large boulder that was buried in the sand of the canyon floor. The crevices were fully three feet above the sand and there was not the slightest indication that any of them extended into it. It is now clear that the only abnormal thing about the Split Mountain colony was that the boulder selected as a nest site was far smaller than usual.

The three colonies of *clydei* found in Deep Canyon were in

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crevices on the tops of enormous boulders twelve to fifteen feet high and twenty to thirty feet across. The base of each of these boulders was embedded in the gravel and sand of the canyon floor and the back face of each was buried in a mass of rubble that formed the bottom of a talus slope extending downward from the steep canyon wall. It may be seen that the crevices in which *clydei* was living were at least twelve feet above the canyon floor and even further removed from the talus slope at the rear of the boulder. The nests appeared to be completely isolated from any contact with soil although, since it was impossible to determine the extent of the crevices, there was a remote chance that they might extend through the boulder to the soil at its base or to the talus slope at the rear. The action of the foragers made this seem unlikely, for if there had been any soil connection at the bottom or rear of the boulder heavily laden minors would scarcely have struggled to the top of the boulder when returning to the nest with food. But the character of the nest at Horse Tanks definitely ruled out any chance of a connection with the soil. This nest was situated on the face of a ledge which overhung the pool or "tank" at its base. The ledge was about twenty-five feet high and so nearly vertical that it could not be climbed. All that could be done was to watch the ants until they went out of sight up the ledge. But it was plain that there could be no connection with soil here, for the ledge was a part of a basin of solid stone in which the pool lay. Thus it seems clear that *clydei* customarily nests in the crevices of large boulders or ledges and not in the soil.

The writer knows of no other North American species of *Pheidole* which behaves in this fashion. While several species of *Pheidole* (*grallipes, subdentata, hyatti,* etc.) will sometimes nest in the crevices between separated layers of stone, these crevices are always filled with soil and the nest passages run into the soil in which the layers of stone are buried. Such nests are not isolated from the soil, as are those of *clydei.* This peculiar nesting response of *clydei* is not easy to explain. The writer at first believed that *clydei* selected nest sites that would protect it from flash floods, which are heavy and destructive both in Deep Canyon and in the Split Mountain area. There is enough truth in the above view to make it dangerous, for the elevated position of the *clydei* nests undoubtedly puts them above flash flood levels. But this view fails to take account of the fact that *clydei* might secure equally good flood protection, as do most of the ants which live in Deep Canyon, by nesting in the talus slopes above the flash flood levels. The protection afforded by nests in rock crevices may be of another sort. In several of the areas where *clydei* occurs the environmental conditions are extreme enough to tax the hardiest xerophiles. This is shown by the fact that few of them can survive in these areas. Competition for food in such areas is severe and considerable advantage must derive from a type of nest that no predator could enter except through a fixed and easily guarded opening.

As soon as the nests of *clydei* were found, observations were begun on its foraging activities. The observations were made in late March and early April. At that time the ants were foraging mainly in the period between 9:00 A. M. and 1:00 P. M. The nests were in shade until 8:30 A. M. but there was a thirty minute period after the sunlight reached them when no foragers emerged. About 1:00 P. M. foragers ceased to emerge from the nest but during the next hour or so many foragers returned to it. Observations made after dark showed nothing that could be regarded as foraging, although minors could be brought out of the nest if the entrance was sufficiently illuminated. It appears that all the foraging is done by the minors. The majors leave the nest only to assist the minors in dealing with some large item of food when this has been brought close to the nest entrance. While the minors obviously follow scent trails they do not forage in columns for the foragers are well separated. Except for one minor, who brought in the withered anther of a flower, all material brought to the nest during the period of observation consisted of arthropods or their disarticulated remains. Much of this was too fragmentary for identification but on several occasions entire arthropods were brought in. There were two dead spiders, two dead majors of *Ph. grallipes*, one dead fly, one dead geometrid larva and one living termite nymph. No seeds were ever brought in, although there were a number of plants in the area which had gone to seed. On the basis of these observations it may be concluded that *clydei* is not a harvester but carnivorous. But, like many xerophiles, it appears to be an opportunist where food is concerned. Since the only way to get the ants out of the nest was to bait them out and since I wished to set up artificial nests, I spent considerable time at first looking for suitable insect bait. Later I discovered that sugar cookies or cheese crackers worked just as well. On one occasion a bit of sugar cookie about the size of a quarter was inadvertently left at the entrance of one of the nests at the conclusion of the observations. The following day there was no trace of it and the members of the colony which had acquired this prize were so full or so busy with their bits of cookie that they did not begin foraging again until the next day.

As already noted the major of *clydei* has a secondary role in foraging activities. When entire arthropods are brought in by the minors they may be too large to take into the nest without dissection. The majors are very efficient at this for they have powerful mandibles and use them effectively. But their main function seems to be to guard the nest entrance. They stand so close to the nest entrance that it is often possible to see them and they savagely attack any object thrust into the nest entrance. This attack consists of locking the jaws on the intruding object and the major will often hold on so firmly that it can be pulled out of the nest. It appears that a cluster of majors is normally present just inside the nest entrance and it is easy to appreciate why this would make the nest virtually impregnable to any intruder. For, since the walls of the nest are solid rock, the guarding majors cannot be outflanked.

Despite the fact that the minors of *clydei* occasionally bring in living victims I believe that this species is best regarded as a scavenger. This view is based on the lack of pugnacity in the minor. Experiments with this caste in artificial nests showed that the minor of *clydei* is slow to attack other insects and equally slow to defend itself when attacked by them. Since I had observed foraging minors of *clydei* entering termite passages it was a surprise to find that when termites were introduced into the artificial nests they usually killed the minors of *clydei* even when the latter outnumbered them. It seems safe to assume that most of the termites or termite remains brought back to the nests of *clydei* are dead or moribund individuals secured by stealth rather than by predation. This behavior is entirely unlike that of the species of *Pheidole* which are carnivorous and predatory. Dr. Gregg and I have shown (3) that *Ph. titanis,* which conducts well-organized forays against termite nests, has a minor that is fully as pugnacious as the major. Both castes participate in the foray and, when this is successful, both castes return to their nest with live termites in their jaws.

In conclusion I wish to point out a suggestive feature in the response of *clydei* to elevation. The insect is now known from five stations. These show little latitudinal difference since all five occur in an east-west band less than a hundred miles wide of which Lat. 33° is the approximate center. Yet the elevational range shown by these five stations is striking. It is given below:

STATION	ELEVATION
Carizozo, New Mexico	5429 feet
Windy Point, Sta. Catalina Mts., Ariz.	7100 feet
Horse Tanks, Castle Dome Mts., Ariz.	1200 feet
Deep Canyon, Sta. Rosa Mts., Calif.	1200 feet
Split Mountain, Anza Desert, Calif.	500 feet

It may be added that *clydei* is not confined to the 1200 foot level in Deep Canyon. Dr. Evert Schlinger of the Entomology Division of the Citrus Research Station has written me that he has taken several colonies of *clydei* at higher elevations there. Few xerophilic ants possess such a large elevational tolerance, but those which can equal it or come anywhere near it are commonly encountered over large areas. This suggests that *clydei* may be much more abundant than has been supposed and that its "rarity" is mainly the result of an unusual nesting habit which has kept it out of the hands of collectors.

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TWO NEW SPECIES OF THE GENUS *ACCOLA* (ARANEAE, DIPLURIDAE)*

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Museum of Comparative Zoology

Up to the present time six species of the Genus *Accola* Simon have been described from parts of South America, Central America and the West Indies. One of these, *A. spinosa* Petrunkevitch, has been known from both sexes since 1945; two of the others described by Simon are known only from immature specimens; the remaining three species are known only from females, which have very few distinguishing features. Dr. Petrunkevitch (1929) described a mature female of the genus *Accola* from Puerto Rico and considered it to belong to the species he originally described from Panama. Since the publication of my brief paper on *A. spinosa* Petrunkevitch (1945) and of the description of a male for the first time, I have collected a considerable number of specimens of this genus, from Panama, Jamaica and Puerto Rico. It is now quite clear that the Puerto Rican species is not the same as the species common in Panama and that the species from Jamaica appears to be quite different from other known species. Dr. Petrunkevitch stated that the Puerto Rican species had been taken with a sweeping net but I have taken all of my numerous specimens from debris of one kind or another by shaking or sifting. In order to bring our knowledge of this genus up to date I have thought it worth while to publish descriptions of these new species, both containing males and females. The types will be deposited in the Museum of Comparative Zoology at Harvard University. Female paratypes will also be deposited in the American Museum of Natural History and in the Museum of the Institute of Jamaica, Kingston, Jamaica, W. I.

At this time I wish to express my appreciation to the National Science Foundation for Grant No. GB-1801, which made it possible for me to collect in the West Indies and Panama for seven months. The grant also provides assistance for a period of study on my collections in the Museum of Comparative Zoology. My gratitude and appreciation are also again expressed for the priviledge of working in the Museum of Comparative Zoology at repeated intervals over a period of many years. Publication and library privileges together with continued encouragement from directors and staff members have been indispensable for the continuation of my studies.

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Genus *Accola* Simon, 1889

Accola petrunkevitchi sp. nov.

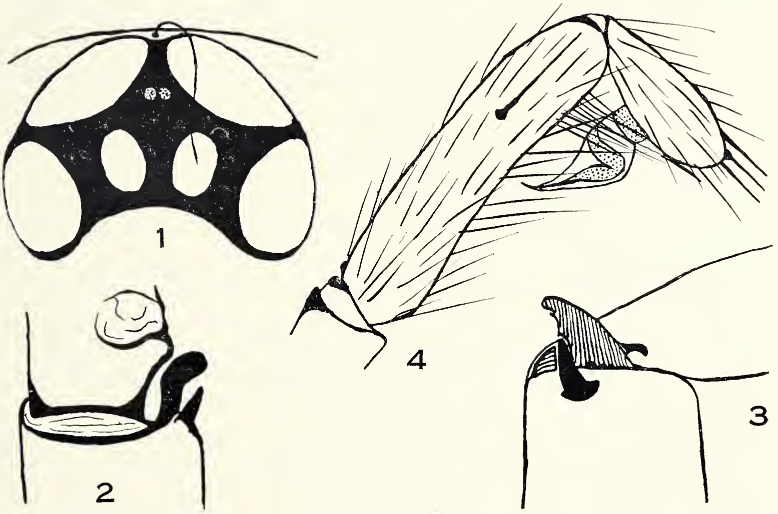
Figures 1-4

Accola spinosa,-Petrunkevitch, 1929. Not *A. spinosa* Petrunkevitch, 1925.

The species is named after Dr. Alexander Petrunkevitch, noted arachnologist, former teacher, and always a source of inspiration.

Male holoype. Total length from clypeus to posterior end of abdomen 3.9 mm; from anterior border of porrect chelicerae to posterior end of abdomen 4.16 mm. Carapace 1.69 mm long; 1.3 mm wide opposite second coxae where it is widest; .39 mm tall and, therefore, about three-tenths as tall as wide; cephalic part rises gently from ocular tubercle to dorsal fovea; opposite third coxae the posterior declivity begins and declines to broad posterior border; dorsal fovea a well defined pit opposite interval between second and third coxae; dorsal striae only moderately well indicated; broad posterior end supplied with a row of long, stiff, erect bristles; numerous stiff bristles over surface largely removed by handling.

Eyes. Eight in two rows essentially as in *A. spinosa* Pet. except that AME are very minute and, apparently, in close contact medially (Fig. 1); all on a moderately well developed tubercle.



Figures 1-4, *A. petrunkevitchi*, n. sp.

Fig. 1. Eyes of male, seen from above. Fig. 2. Spines and associated parts at articulation of left first tibia and metatarsus of male, seen from above. Fig. 3. The same as seen in prolateral view. Fig. 4. Left palpal tibia and tarsus of male; prolateral view.

Viewed from above, posterior row strongly recurved, anterior row strongly procurved. Some irregularity in form and size of corresponding eyes has been noted among paratypes. Ratio of eyes AME : ALE : PME : PLE = 1 : 10 : 5.5 : 8.5. AME darkened and difficult to measure with accuracy; all others white. AME appear to be in contact medially; well separated from ALE. PME separated from one another by about one third of their width, from PLE by about their width. PLE separated from one another behind by slightly more than their length. Width of clypeus equal to one fourth of the long diameter of ALE. Long diameters of eyes used for measurements unless otherwise stated.

Chelicerae. Paraxial, parallel, porrect as usual in the genus; fairly robust; clothed with a thick coat of stiff, procurved bristles. Fang long, slender, evenly curved; promargin of fang groove with eleven teeth, the last five considerably longer than others, together with several long, slender hairs; the retromargin has a well developed scopula of long, slender hairs.

Lip and *Sternum.* Essentially as described for *A. spinosa* Pet.

Legs. 4123. Tibial index of first leg 10; of fourth leg 12.

(All measurements in mm.)

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
1.	1.41	.84	1.25	.99	.81	5.30
2.	1.13	.66	.88	.88	.66	4.21
3.	1.10	.55	.77	.95	.62	3.99
4.	1.50	.66	1.28	1.32	.79	5.55
Palp	.92	.55	.88	——	.48*	2.63

* Not including terminal spines.

Spines. In general the legs are well supplied with ordinary spines; legs one and two with many fewer than legs three and four. Detailed statement of number and position of ordinary spines not regarded as necessary for adequate description of the species. Special spines at articulation of first tibia and metatarsus as shown in Figures 2 and 3 should be noted. Numerous trichobothria have been noted but many are broken off from handling and the specific number and placements have not been determined.

Palp. Essential features shown in Figure 4. Coxa with a rudimentary maxillary lobe bearing a chitinized ridge which, in one view, appears like a small tooth.

Abdomen and *Color in alcohol.* Both essentially as described for *A. spinosa* Pet.

Female allotype. Dr. Petrunkevitch (1929) gave a description of what was probably a mature female of this species and for this reason only those features which are not in agreement with that description will be given here. Total length from anterior border of porrect chelicerae to posterior end of abdomen 5.07 mm. Ratio of eyes AME : ALE : PME : PLE = 1? : 9 : 5 : 8. AME asymmetrically placed and so darkened that measurement is difficult. Not only procumbent hair on carapace but also long, stiff bristles arranged in somewhat irregular rows. Promargin of fang groove with twelve teeth; retromargin with a row of minute nodules at distal end. Fourth coxae separated by nearly one half their width. From genital groove anteriorly the abdomen is thickened, considerably raised and more strongly chitinized thus accentuating the genital area but yet without a definite epigynum.

Type locality. The male holotype is from a university farm a short distance east of the campus of the University of Puerto Rico at Mayaguez, P. R.; taken January 15, 1964. The allotype female was taken in a woody area near the Nuclear Center just east of the same university campus, January 27, 1964. I now have more than thirty specimens belonging to this species. Nearly all of these were collected in the vicinity of Mayaguez, P. R. or at the El Yunque Biological Station where the species appeared to be quite common. Three of the specimens are mature males but all of the rest are females or immature individuals and all were taken from various types of debris during the months of January and February, 1964.

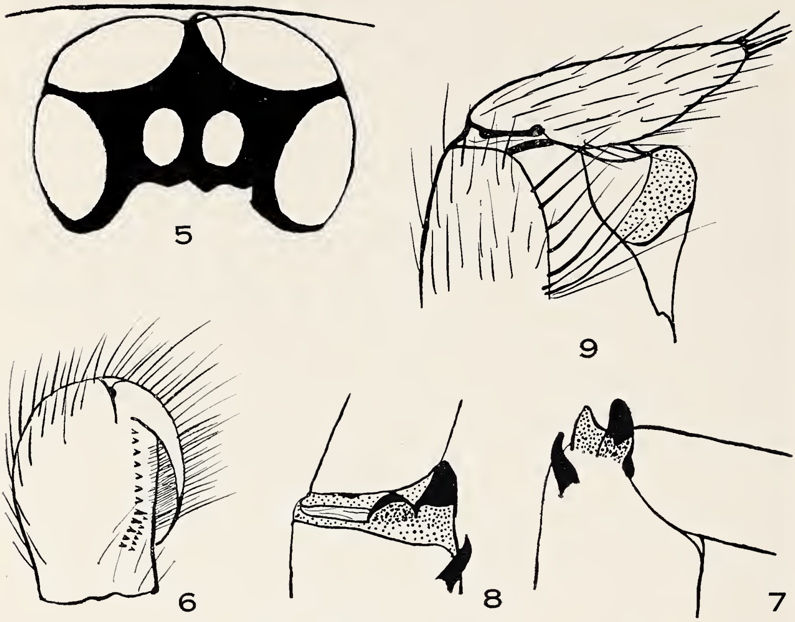
Accola lewisi sp. nov.

Figures 5-9

This species is named after Mr. C. Bernard Lewis, Director of The Institute of Jamaica, Kingston, Jamaica, W. I.

Male holotype. Total length from anterior border of porrect chelicerae to posterior end of abdomen 3.33 mm. Carapace 1.34 mm long; 1.04 mm wide opposite second coxae where it is widest; .26 mm tall and, therefore, about one fourth as tall as wide. Other features essentially as described for *A. petrunkevitchi* sp. nov.

Eyes. In this species I have been unable to find any indication of the AME as found in the other two species directly known to me. Viewed from above, posterior row strongly recurved as usual. All eyes white. Ratio of eyes ALE : PME : PLE = 7.5 : 3.5 : 6.5 (considerable irregularity in shape noted). ALE separated from one another by slightly more than one fourth of their diameter. PLE separated from one another behind by about 1.5 times their diameter (Fig. 5). PME separated from one another by slightly more than one fourth of their diameter. Long diameters are always used for



Figures 5-9, *A. lewisi,* n. sp.
Fig. 5. Eyes of male: dorsal view. Fig. 6. Left chelicera of female, seen from below. Fig. 7. Spines at articulation of left first tibia and metatarsus of male; prolateral view. Fig. 8. The same as seen from above. Fig. 9. Left palpal tibia and tarsus of male; prolateral view.

measurements unless otherwise stated. Width of clypeus equal to slightly less than one half the diameter of ALE.

Chelicerae. Promargin of fang groove appears to have eleven teeth of moderate size; the retromargin has a row of about six very small, slender and closely crowded teeth opposite the last four or five promarginal teeth. Otherwise essentially as described for *A.* petrunkevitchi sp. nov.

Lip and *Sternum.* Essentially as described for *A. spinosa* Pet.

Legs. 4123. Tibial index of first leg 9, of fourth leg 11.

(All measurements in mm)

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
1.	1.19	.75	1.10	.66	.55	4.25
2.	.95	.55	.66	.62	.53	3.31
3.	.88	.44	.57	.70	.44	3.03
4.	1.19	.55	1.02	.99	.66	4.41
Palp	.81	.55	.68	—	.35	2.39

Spines. Essentially as described for *A. petrunkevitchi* sp. nov. Detailed statement of number and position of ordinary spines not regarded as essential for adequate description of the species. The special spines at the articulation of the first tibia and metatarsus (Figs. 7-8) should be noted.

Palp. Essential features shown in Figure 9. Measurements of segments shown in table. There are close similarities among all three species well known to me but, nevertheless, there are specific differences and these, I think, can best be shown by drawings.

Abdomen. Somewhat distorted but essentially as described for *A. spinosa* Pet. (Chickering, 1945).

Color in alcohol. Also essentially as described for *A. spinosa* Pet.

Female allotype. Total length from anterior border of porrect chelicerae to posterior end of abdomen 4.42 mm. Carapace 1.43 mm. long, 1.11 mm. wide opposite second coxae where it is widest, .46 mm. tall and, therefore, about two fifths as tall as wide.

Eyes. Essentially as in male.

Chelicerae. Promargin of fang groove with a row of twelve small teeth (Fig. 6); the retromargin with a row of six minute teeth nearly opposite the last four promarginal teeth; retromarginal teeth well developed.

Lip and *Sternum.* The sternum is abruptly raised a short distance medial to the border thus making what appears to be a depressed border surrounding this part of the body except for the portion contiguous to the lip. Otherwise essentially as in male.

Legs. 4123. Tibial index of first leg 11, of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
1.	1.10	.66	.90	.67	.55	3.88
2.	.88	.53	.60	.55	.53	3.09
3.	.88	.47	.53	.65	.50	3.03
4.	1.06	.55	.97	.90	.62	4.10

Spines. Present in small numbers on legs one and two; present in large numbers on legs three and four. Detailed statement of numbers and positions of spines regarded as unnecessary for adequate description of the species.

Abdomen. Essentially as described for *A. spinosa* Pet. (Chickering, 1945).

Color in alcohol. Essentially as I have described for other species with which I am directly acquainted.

Type locality. The male holotype and the female allotype were both taken in St. Catherine Parish, Jamacia, W. I. two miles west of the junction of Red Hills Road and the highway to Spanishtown on October 1, 1957. One male paratype was taken in St. Andrew Parish, two miles north of Papine on May 19th, 1956 (C. C. Hoff). I have numerous females and immature individuals from many localities in Jamaica, W. I., and I believe all of these have been taken from debris of some kind.

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WEST INDIAN CARABIDAE X.
THREE MORE SPECIES FROM JAMAICA, INCLUDING A NEW CAVE *COLPODES**

By P. J. Darlington, Jr.
Museum of Comparative Zoology, Harvard University

The following three species are additions to the list of Jamaican Carabidae recorded in my earlier papers (Psyche Vol. *48,* 1941, pp. 10-15; and Occasional Papers of the Museum of the Institute of Jamaica No. 8, 1953).

Colpodes cavicola n. sp.

Form of a slender *Agonum (Platynus),* but with long head and long, slender appendages; brownish piceous, margins of prothorax and elytra not paler, legs brownish piceous, antennae and palpi paler brown; moderately shining, elytra not much duller than head and prothorax; upper surface almost impunctate, with microsculpture lightly impressed, isodiametric on front of head, transverse on pronotum and elytra. *Head* rather elongate, .84 and .83 width prothorax (in ♂♀ measured); eyes rather large, moderately prominent; genae slightly shorter than eyes, oblique, not swollen; neck constriction indistinct; front convex, with normal, parallel impressions anteriorly; posterior supraocular setae present, between posterior edges of eyes; anterior supraocular setae absent; antennae long and slender but otherwise normal; mentum with an acute tooth. *Prothorax* subquadrate; about as long as wide (but appearing longer), width/length 1.02 and 1.02 (in ♂♀ measured); base about 1/10 wider than apex; apex slightly, broadly emarginate; base almost truncate; sides broadly, irregularly arcuate especially near middle of length, nearly straight and converging anteriorly, and nearly straight, converging, and usually slightly and broadly sinuate posteriorly; posterior angles narrowly rounded; lateral margins moderate, slightly wider posteriorly; both pairs lateral setigerous punctures lacking; disc normal and normally impressed; basal marginal line entire, apical one interrupted at middle. *Elytra* about 2× wide as prothorax, long, almost subparallel; humeri prominent but broadly rounded, with basal margin entire and scarcely angulate at humeri; sides almost straight and slightly diverging to about middle of length, then arcuate to weak subapical sinuations; apices bluntly angulate or narrowly rounded about

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opposite ends of 2nd striae; striae rather lightly impressed, vaguely punctulate; internals flat or slightly convex, 3rd normally 3-punctate. Inner wings fully developed; metepisterna long. Body below with fine punctures on sides of mesosternum, otherwise impunctate; abdomen not pubescent. Tibiae not grooved on outer edges; hind tarsi slender, basal segments grooved above on outer side, less so on inner side; 4th hind-tarsal segment with very long outer lobe and much shorter inner one; 5th hind-tarsal segment without accessory setae. External sexual characters normal. Length 9.5-11.0; width 3.2-3.7 mm.

Holotype ♂ (M. C. Z. Type No. 29,463) and 6 paratypes (2 in M. C. Z., 4 in Museum of the Institute of Jamaica) all from St. Clair Cave, St. Catherine, Jamaica, 5 March 1954, collected by C. B. Lewis and R. P. Bengry.

This is a distinct, well defined species. It differs from all previously known Jamaican *Colpodes* in lacking *both* pairs of lateral prothoracic setae, and it has a unique combination of other specific characters. It is perhaps a distinct member of the Jamaican *vagepunctatus-macer-subovalis* group, beginning to be specialized for life in caves. However, the specialization has not yet gone far. The brownish rather than black color and the long, slender appendages may be adaptations to life in caves; but the eyes are not much reduced and the wings are still fully developed. Another, somewhat similar (but probably not related) agonine, more highly modified for life in caves, is *Speokokosia corneti* Alluaud of the Grotte de Kokosi in the Congo in tropical Africa. In *Speokokosia* the eyes are much reduced, the wings have atrophied, and more depigmentation has occurred. In time, the Jamaican *Colpodes* may be expected to evolve in this direction.

Callida caymanensis Darl.

Entomologist's Monthly Magazine, 83, 1947, 210.

One specimen is before me from Crossroads, St. Andrew, Jamaica, 24 Nov. 1954, T. H. Farr. This is the first Jamaican record for the species — but when I described it, from the Cayman Islands, I suggested that it might prove to be Jamaican.

Pentagonica vittula Darl.

Memorias de la Sociedad Cubana de Historia Natural, 13, 1939, 100.

Three specimens now before me constitute the first records of this species from Jamaica. It was previously known only from Hispaniola. Two of the specimens are from Upper Mt. View, St. Andrew, Jamaica, 19 Nov. 1954, C. B. Lewis; and the other is from Beverly Hills, St. Andrew, 23 Dec. 1954, R. P. Bengry.

THE STRUCTURE OF THE PROTELYTROPTERA, WITH DESCRIPTION OF A NEW GENUS FROM PERMIAN STRATA OF MORAVIA*

By
F. M. Carpenter, Harvard University
and
Jarmila Kukalová, Charles University, Prague[1]

The extinct order Protelytroptera was established by Tillyard in 1931 for a series of elytrophorous insects from Lower Permian deposits near Elmo, Kansas. Additional genera from the same strata were subsequently described by Carpenter (1933, 1939). Apart from one little-known species (*Uralelytron martynovi* Rohdendorf) from the Russian Permian and the controversial Protocoleidae from the Upper Permian of Australia, nothing more has been known of the order.[2] This meager record has given the general impression that the order was a small one, not very diversified, and unusually restricted geographically.

A very different view of the order now results from the discovery of Permian representatives in collections from Moravia (Czechoslovakia) and Australia which are being studied by one of the present authors (Kukalová); they show a diversity of wing and body structure that has not previously been expected in this order. A full treatment of the Moravian and Australian material will be published elsewhere. The present paper consists of an account of what is now known about the wing and body structure of the members of this extinct order. A description of one of the Moravian fossils is included, since it gives information about the hind wing and body of a new family; also included are the results of a restudy of some specimens from the Elmo locality, in particular types which are in the Museum of Comparative Zoology at Harvard University and the Peabody Museum at Yale University.

Family Protelytridae Tillyard

Protelytridae Tillyard, 1931, Amer. Journ. Sci. 21:235; Carpenter, 1933, Proc. Amer. Acad. Arts Sci. 68:465-473.

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*This research has been aided by grant no. NSF GP-2038 from the National Science Foundation.

[1] Current address: Biological Laboratories, Harvard University.

[2] The poorly known species, *Arctocoleus ivensis* Martynov and *Bardocoleus insignis* Zalessky, from Permian deposits in Russia, may also belong to the Protelytroptera.

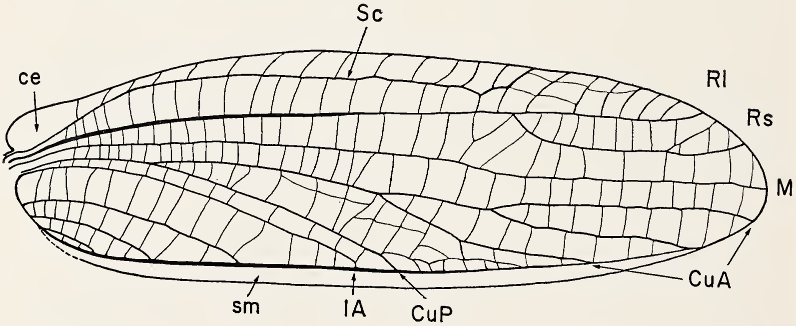
This is the only family of which the hind wing and body structure have been known. These have already been described (Carpenter, 1933) but the reconstructed figure of the whole insects, including only those details which are actually known, is included here for comparison with other families (Text-figure 2).

Family Archelytridae Carpenter

Archelytridae Carpenter, 1933, Proc. Amer. Acad. Arts Sci. 68:477.

This family is still known only by the type specimen of *Archelytron superbum* Carpenter, from the Elmo deposit. However, new specimens of related Protelytroptera from Moravia require a modification of our concept of this family and of the actual structure of the elytron. At the time of the description of *Archelytron,* no Protelytroptera were known which had cross veins on the elytra. In the original account of *A. superbum,* it was stated that cross veins were absent but that the surface of the elytron was rough and under oblique light appeared to have a series of short ridges between the veins over the entire elytron. Since the elytra of several new genera from the Permian of Moravia have numerous and distinct cross veins, we are convinced that the supposed ridges in *Archelytron* are also cross veins. Revised definitions of the family Archelytridae and the genus *Archelytron* now seem necessary.

The family Archelytridae appears to have the following characteristics: elytron only slightly convex; costal expansion weakly developed; stems of main veins independent; Sc long, well developed, terminating on costa about two-thirds wing length from the base;



Text-figure 1. Drawing of elytron of *Archelytron superbum* Carpenter (holotype). Original. ce, costal expansion; Sc, subcosta; R1 radius; Rs, radial sector; M, media; CuA, anterior cubitus; CuP, posterior cubitus; 1A, first anal vein; sm, sutural margin.

Sc, R1, CuP, 1A unbranched; CuA usually with three branches; CuP markedly concave for its entire length; sutural margin well developed, its termination well before the apex; cross veins numerous but weakly developed over the entire wing; most cross veins simple, some forked or connected by transverse veinlets. Hind wing unknown.

Genus *Archelytron* Carpenter

Archelytron Carpenter, 1933, Proc. Amer. Acad. Arts Sci: 68:477.

Costal margin of elytron strongly convex; Sc weakly developed at the base but well formed distally; Rs originating well beyond middle of wing; CuA and CuP diverging in basal fifth of wing, CuA forked dichotomously near the middle of the wing, the anterior branch forking again at about the level of the origin of Rs; CuP and the anal veins sub-parallel; few cross veins connected.

Type-species: *Archelytron superbum* Carpenter

Archelytron superbum Carpenter
Text-figure 1

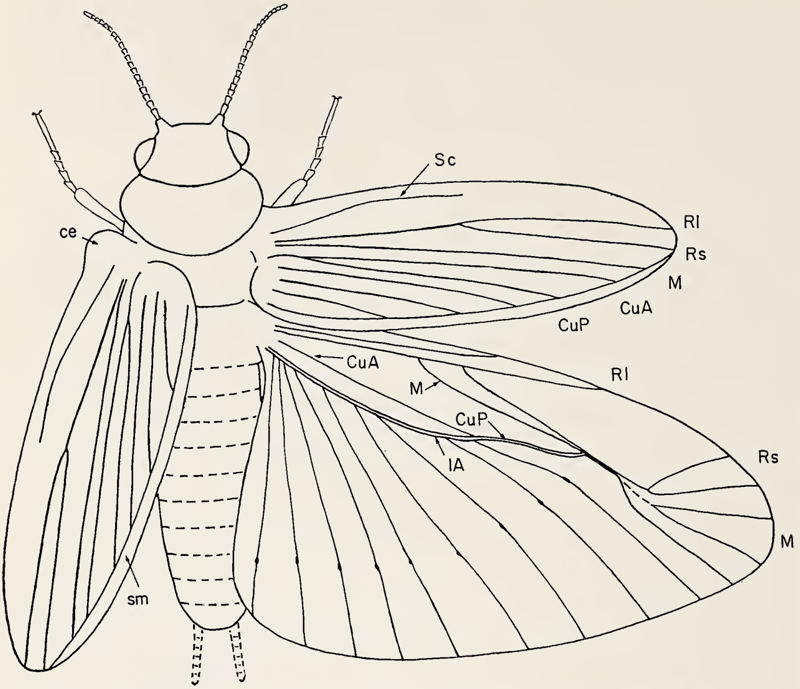
Archelytron superbum Carpenter, 1933, ibid.: 477, fig. 22.

The specific description originally given is correct with the exception of the reference to cross veins, as noted above. In addition, it should be pointed out that the oblique vein connecting M to Rs in the original figure of *Archelytron* is almost certainly a cross vein (a possibility that was mentioned in the original description) instead of part of a branch of M.

Apachelytridae, new family

Related to the Archelytridae. Fore wing: almost flat and thin, weakly tegminous rather than elytrophorous; costal expansion well developed and distinct; Sc prominent, probably long; main veins arising independently from the wing base; CuP strongly concave; CuA and CuP arising much as in Archelytridae; CuA with several terminal branches; sutural margin wide (length unknown); cross veins numerous and well developed over wing, mostly regular and simple.

Hind wing: anal fan large, as in Protelytridae; stem of M independent of R; M forked into M1 and M2 near mid-wing; M1 independent of Rs, twigged at wing apex; M2 diverging posteriorly and coalesced with CuA to its termination; base of Cu free from the stem of M: 1A (convex) fused with CuP distally; 2A (con-



Text-figure 2. Reconstructed drawing of *Protelytron permianum* Tillyard, based on specimens in the Museum of Comparative Zoology (Harvard University) and the Peabody Museum (Yale University), and showing in solid lines only those details actually preserved. The abdominal segmentation and cerci, indicated by broken lines, are unknown in *Protelytron* (Carpenter, 1933). Lettering as in text-figure 1.

cave) parallel with 1A and somewhat close to it. 1A without branches; anal veins radiating to form the anal fan; several branches arising from 2A; some cross veins over most of remigium, absent in anal fan.

Body structure: head with small eyes, pronotum nearly square, with posterior corners rounded, resembling a small pronotal disc; fore legs short, hind legs much longer, with well developed femora; tarsal segmentation unknown; abdomen apparently with seven normal segments, others more modified; cerci short, with distinct segmentation.

This family is differentiated from the Archelytridae by having a more distinct costal expansion and by having the cross veins of the elytra more regular and more numerous, with almost no branching.

Apachelytron, new genus

Elytron: costal margin convex; Sc well developed, apparently extending well beyond mid-wing; Rs arising in the distal part of the wing, with several branches; Cu dividing into CuA and CuP remote from the wing base; CuA forking below origin of Rs, each division with several branches; CuP nearly straight; about 4 anal veins, all simple; cross veins well developed over all the wing, mostly straight, except in the region of Rs; no anastomosis of cross veins.

Hind wing: Rs arising well beyond mid-wing, with all its branches distal and directed towards anterior margin; CuA diverging before fork of M; CuA + M with several cross veins directed posteriorly to CuP + 1A; cross veins present between 1A and 2A.

Type-species: *Apachelytron transversum,* n. sp.

Apachelytron transversum, n. sp.

Text-figure 3; plate 22

Length of right fore wing (elytron), 6 mm.; width, 2.2 mm.; length of right hind wing, 7 mm. Since only one specimen is known and since the venation in the Protelytroptera is unusually variable (Carpenter, 1936), the specific characteristics designated are necessarily arbitrary. In this category we consider the following: Rs forked, each of the main branches dividing again at least once; CuA1 with fewer terminal branches than CuA2. Other details are shown in text figure 2.

Type: specimen no. 47/1964, Department of Paleontology, Charles University, Prague, Czechoslovakia. Collected by A. Havlatová in Lower Permian (Autunian) clayey shale, near Obora, Boskovice Furrow, Moravia, Czechoslovakia. The type specimen is remarkably well preserved, as shown in plate 1. Although the insect as a whole is seen in ventral view, there seems to be slight twisting of the abdomen.[3] Not enough of the head is clear to permit an estimate of the size and shape. The pronotum is partially preserved; it appears to be about as broad as long, with the posterior angles more rounded

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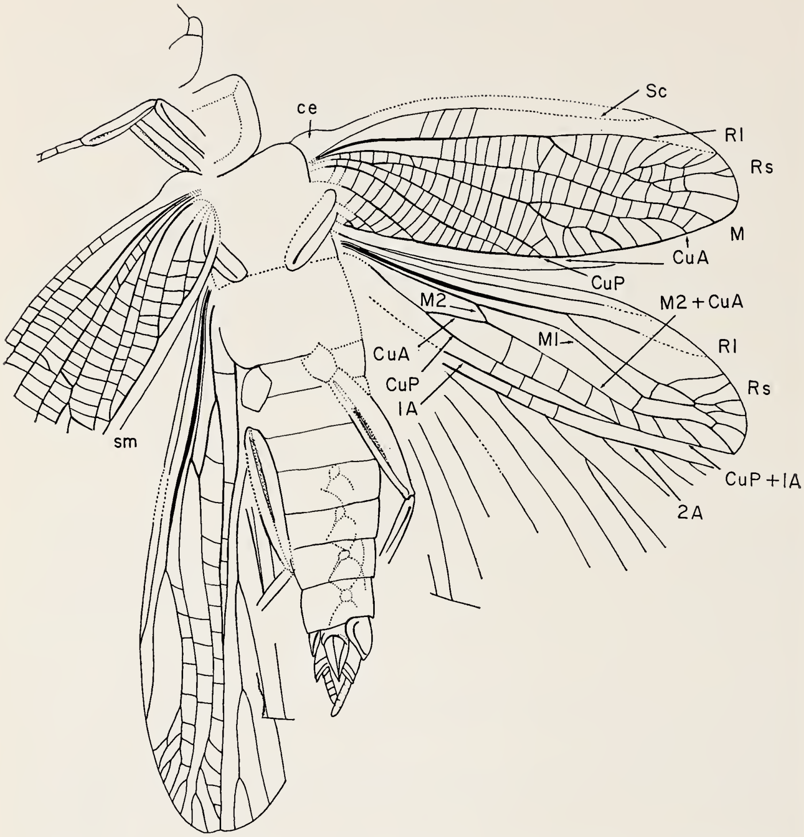
[3] This fossil shows a type of distortion not uncommon in specimens found in the clayey shale of the Obora locality; the distortion probably results from small rock movements associated with post-Paleozoic folding in the Boskovice Furrow sediments. The effect of this is to cause, in the specimen of *A. transversum,* an elongation of the wings along the longitudinal axis of the body; as can be seen in figure 2, the left hind wing is considerably longer than the right one. It is quite likely that the right fore and hind wings, which are nearly at right angles to the body, are distorted by having a somewhat greater width than in the original insect.



Text-figure 3. Drawing of holotype of *Apachelytron transversum*, n.sp. Lettering as in text-figure 1.

than the anterior ones. The meso- and metathoracic segments are large and about square. The fore legs are short and unmodified; two tarsal segments are visible but more were undoubtedly present. The hind legs are much longer, the femur being long and quite thick. The abdomen shows seven normal segments; the remaining ones are apparently modified to form a complex of small sclerites and processes. Clearly identifiable are the two short cerci, consisting of about five segments. Two conspicuous lateral sclerites are also discernible, although these are not seen in the same position, since one is much larger than the other; they appear to be derived from the eighth segment. Between the latter plates are a pair of short, tapering structures, almost certainly constituting a small ovipositor.

Neither elytron is quite complete, but only two important details are missing: the point of termination of Sc and the distal part of the sutural margin. In all probability both of these were as described for *Archelytron.* In both elytra one cross vein between M and CuA is slightly oblique, but this is not heavier than the others and seems almost certainly not a branch of M.

The hind wing seems only slightly longer than the fore wing; the subcosta is distinctly longer than in *Protelytron;* Rs arises after the mid-wing, much later than in *Protelytron;* the stem of M, although not fused with R, as in *Protelytron,* is very close to it, especially proximally. The anastomosis of CuA and M is very different from the structure of these veins in *Protelytron* and the fulcrum of the latter is completely absent, although it is suggested by the convergence of Rs, M and CuA distally. Another striking difference between *Protelytron* and *Apachelytron* is in the configuration of CuP, 1A and 2A. In *Protelytron* CuP and 1A are very close together and parallel and 1A gives off a long series of radiating anal veins. In *Apachelytron* CuP and 1A are remote proximally, though fused distally; and 2A gives rise to the radiating anal veins.[4] It is apparent that more differences exist between the hind wings of *Protelytron* and *Apachelytron* than between the elytra.

Family Blattelytridae Tillyard

Blattelytridae Tillyard, 1931, Amer. Journ. Sci. 21:249; Carpenter, 1939, Proc. Amer. Acad. Arts Sci., 73:60.

This family, which now includes several species of *Parablattelytron,* one of *Permelytron* (probably inseparable from *Parablattelytron)* and the type-species of *Blattelytron,* has been known up to the present time only by elytra. The venation of the elytra shows much individual variation in the degree of development of the veins (Carpenter, 1939, p. 62); the family is characterized so far as the elytra are concerned by the obsolescent nature of the veins of the elytra and probably also by the absence of Rs. One specimen of *Parablattelytron subincisum* Tillyard, collected at the Elmo locality in 1958, is nearly complete, showing the hind wings as well as parts of the body and the elytra. Since this has not previously been described, it is considered here in order to permit comparison with the complete specimens of *Protelytron* and *Apachelytron.*

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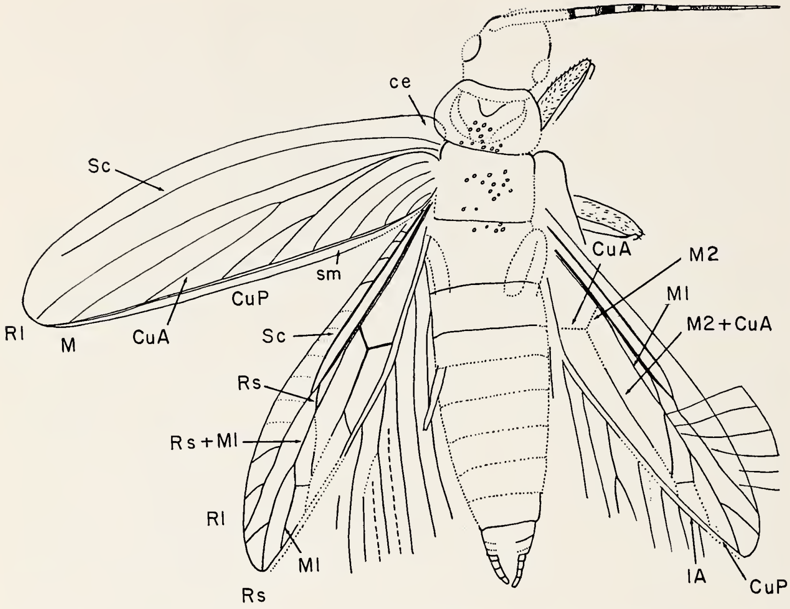
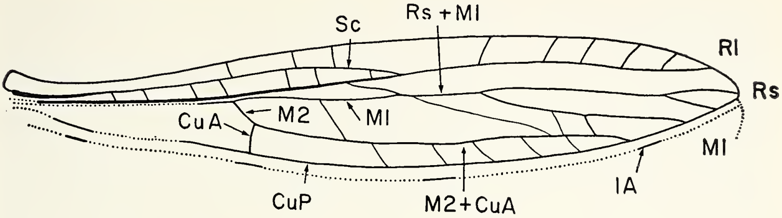
[4] A somewhat similar variation in the origin of the anal veins forming the fan of the hind wing occurs in the Blattaria.



Text-figure 4. Drawing of *Parabattelytron subincisum* Tillyard, based on specimen no. 5827, Mus. Comp. Zool. Lettering as in text-figure 1.

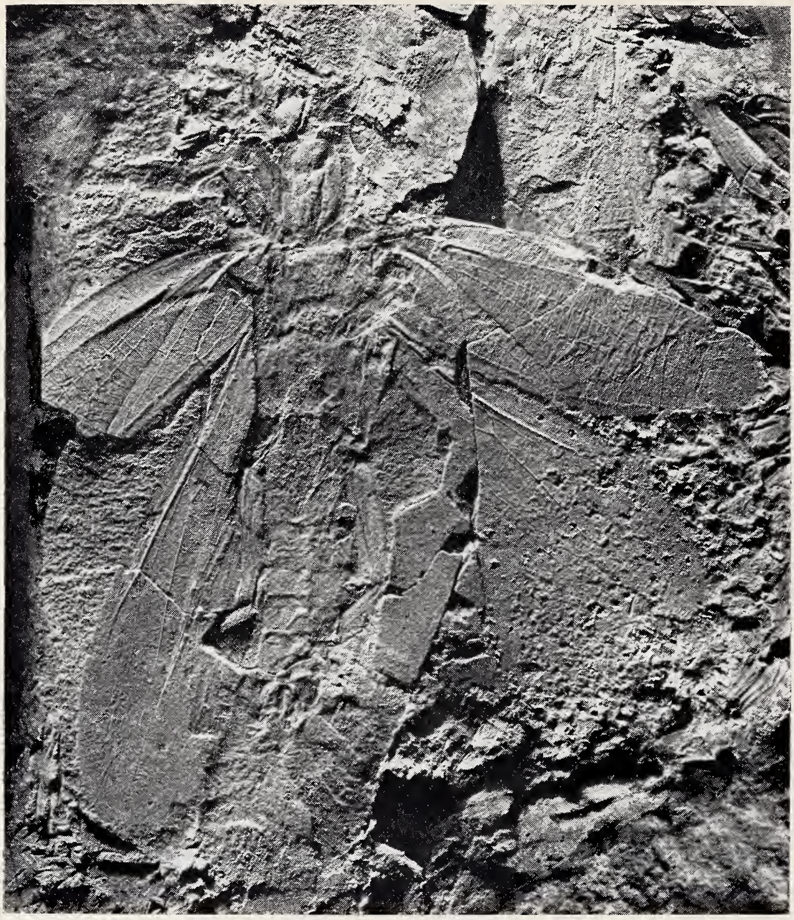
The venation of the elytron of this specimen (text-figure 4) is typical of that of well preserved specimens of *Parablattelytron:* the veins are about as long as in the Protelytridae but are very faint and fade out in their distal portions. The remigia of both hind wings are preserved but the anal fans are represented only by the more basal parts of the radiating anal veins. The subcosta of the hind wing terminates on R1, instead of on the costal margin as in the hind wings of *Protelytron* and *Apachelytron.* R1 continues for a considerable distance beyond the end of Sc, finally terminating on the costal margin not far from the probable apex of the hind wing; weakly developed but distinct cross veins are present in the costal area along the length of Sc as well as along R1 beyond the end of Sc; Rs arises from R just before the termination of Sc and anastomoses for a short distance with M; thees two veins separate before terminating at the apex of the wing; M arises from the base of the wing as an indepedent vein and continues very close to R until near mid-wing (as in *Apachelytron),* when it forks into M1 and M2; M1 continues in a nearly straight line, diverging only slightly from



Text-figure 5. Drawing of specimen (hind wing) of Blattelytridae from Obora, Moravia (Lower Permian), no. 6/1965, Department of Palaeontology, Charles University, Prague. Lettering as in text-figure 1.

R, then anastomosing with Rs; M2 diverges posteriorly abruptly after its origin and anastomoses with CuA, which is directed anteriorly away from the stem of Cu; these two veins, together with their fused portions, form a very distinct "Y" vein, which terminates on CuP well before the apex; Cu arising as an independent vein from the base; 1A also arising from the base, close to CuP, and continuing parallel to it and very close to it for its entire length to the apex of the wing; a series of radiating anal veins extends from 1A, forming the anal fan. As shown in text-figure 3, the remigia of the right and left sides are slightly different in shape; the hind wing on the right probably has more distortion than that on the left, as indicated by the presence of some of the anal veins across the tip of the remigium.

The body structure of this specimen of *Parablattelytron* is only moderately well preserved; the abdomen is suggested by an outline in the matrix, although the terminal segments, with a pair of cerci (length, 1.2 mm.), are distinct; the distance from the point of attachment of the elytra to the end of the abdomen is about the length of the elytra, indicating that the abdomen as a whole was covered by the elytra when they were folded back over the body. The pronotum is much broader than long, with a slightly concave anterior margin. The thoracic nota are irregularly rough in appearance and seem to bear short, truncate tubercles. Only the femora of the front and middle legs are preserved, these bearing short setae. The head is only vaguely indicated but it is distinctly smaller and narrower than in *Protelytron* and *Apachelytron.* One antenna, clearly preserved, is 4 mm. long, relatively broad at the base but tapering abruptly; about 17 segments are visible but there were probably



Photograph of holotype of *Apachelytron transversum.* n.sp. Original. × 7.5.

several more in the basal part, which is not preserved. The proximal segments show distinct signs of alternation of color.

The family Blattelytridae is apparently represented in the Lower Permian deposit in Moravia. One specimen from this locality consists of a remigium of a hind wing (text-figure 5), the venation of which is so nearly like that of *Parablattelytron* that we consider its family assignment almost certain. Up to the present, however, no elytra have been found in the Moravian deposit which can be associated with this hind wing.

Family Megelytridae Carpenter

Megelytridae Carpenter, 1933, Proc. Amer. Acad. Arts Sci. 68:476

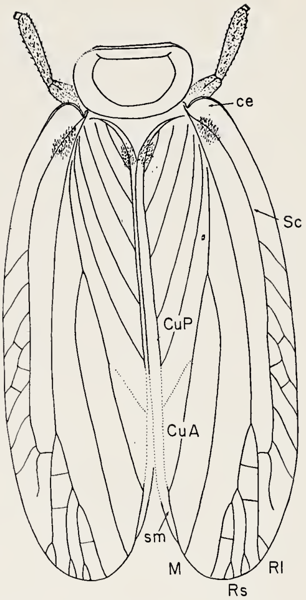
This family is still known only by the type specimen of *Megelytron robustum* Tillyard, from the Elmo locality. Examination of this fossil (Peabody Museum, Yale University) in the light of the additional and related Protelytroptera now at hand, convinces us that the sutural margin is present and that the venational pattern is quite different from its representation in Tillyard's figure. The fossil is actually very poorly preserved and the venational details can be ascertained only with great difficulty. The family may now be characterized as follows: elytron thin, only slightly convex; costal expansion not developed as a distinct lobe; costal area uniformly broad; R very strong; Rs arising in distal part of wing, branched; M and CuA apparently unbranched; CuA and M coalesced basally, separating just before mid-wing; several indistinct, oblique veinlets in the costal area and weak, widely spaced cross veins in other regions of the wing; elytron with a dense cover of fine hairs. The hind wing is unknown.

Megelytron robustum Tillyard

Text-figure 6

Megelytron robustum Tillyard, 1931, Amer. Journ. Sci. 21:247.

A drawing of the type specimen is given in text-figure 6. The fossil consists of the two elytra folded back over the body; the pronotum and two of the fore legs are preserved. This is the only specimen so far described which shows the position of the elytra at rest. As indicated in the drawing, the sutural margins of the elytra overlap. The venation is very poorly preserved and both Tillyard (1931) and Carpenter (1933) were misled by the appearance of a coarse reticulated network in the distal part of the elytron, as well as by the apparent existence of weak veins in the anal region. Re-



Text-figure 6. Drawing of holotype of *Megelytron robustum* Tillyard (holotype). Original. Lettering as in text-figure 1.

examination of this fossil has convinced us that the supposed reticulation and some weak veins in the elytron are only impressions of parts of the hind wing venation. The vein which Tillyard identified as M in his figure is clearly a hind wing vein; this is also true of the peculiar veins which he shows in the anal region of the elytron. Use of ammonium chloride covering on the fossil has indicated the difference between the veins which are actually part of the elytron and those which show through from the hind wing below. The venation of the elytron, as it now seems with reasonable certainty, is shown in the accompanying figure (text-figure 5).

In addition to having the small clusters of setae in the region of the base of the subcosta and the inner angle of the anal area, the elytra of *Megelytron* are covered with fine hairs; no other elytra of Protelytroptera which have been described have shown hairs so distinctly and so dense, although a punctation or some other type of sculpturing is usual. The type specimen of *Megelytron* also shows a pronotal disc which resembles that in *Parablattelytron.* The leg segments, apparently the femora and tibiae, are not distinctive except for the presence of a fine hair covering and several rows of coarse setae.

General Characteristics of the Order Protelytroptera

The present indications are that the order Protelytroptera was a large and varied group of insects during the Permian times. The general characteristics which have been applied to this order (Carpenter, 1933) now require considerable modification as a result of even the relatively few additional species which have been studied in the past few years. The following account summarizes these characteristics as we now know them.

In what are almost certainly the more primitive forms, the fore wings are tegminous or almost flat, the costal expansion only slightly enlarged and the sutural margin either completely missing (Elytroneuridae) or at most not fully developed (Archelytridae). The thinner types of fore wings often have cross veins (Archelytridae, Apachelytridae), eventually with the addition of diverse kinds of sculpture (Protocoleidae). In others, presumably more highly specialized species (e.g., Protelytridae and Blattelytridae), the fore wings are convex and strongly sclerotized, forming true elytra. The sculpturing in these is in the form of either an indistinct rugosity or conspicuous reticulation, often arranged in complicated patterns. The veins of such elytra have few branches and are always indistinct, even to the degree of being obsolescent (Carpenter, 1933). The hind wing is known in three families, the Protelytridae, Blattelytridae and Apachelytridae. In all of these a well developed anal fan is present, this being made up of radiating anal veins. The remigium is distinctly narrow. Differences in the venational patterns of the remigium of these three families are very striking. In the Protelytridae, Rs, M and apparently Cu and 1A coalesce to form a strongly sclerotized plate, which Tillyard has designated the fulcrum and which he considered comparable to a similar structure in the Dermaptera. This was, in Tillyard's opinion, developed in connection with the evolution of the folding of the hind wings. The reduction of the main veins in the hind wing is undoubtedly a specialization relating to wing folding. In the other two families, the hind wing is much less modified; neither one has a fulcrum, although in the Apachelytridae the distal parts of the veins are in close association in the general region where the fulcrum in the Protelytridae occurs. In the Blattelytridae, on the other hand, the hind wing does not show even this trend. It is surprising that in the Blattelytridae, which have the more highly specialized elytra, the hind wings are much less specialized than those of the Protelytridae. There seems to be little question on the basis of the evidence which Tillyard has given (1931) that the remigium of the protelytrid hind wing was capable of transverse folding at the level of the fulcrum; the hind wing is distinctly longer than the fore wing and the presence of the "hinges" on the anal veins, in line with the fulcrum, is indeed strong evidence. On the other hand, it is doubtful that the hind wings of the Blattelytridae were capable of transverse folding; indeed, the hind wings, as they are known to us in this family, are not as long as the front wings and could, therefore, have been completely covered by the elytra in the resting position without the transverse folding. In the case of the family Apachelytridae, the hind wing is slightly longer than the elytra but there are no signs of "hinges" on the veins and the fulcrum is not developed. The condition of the wings and wing venation strongly indicates that these three families are not part of a single evolutionary line within the order but represent three radiating lines. It is especially interesting to note in the Apachelytridae CuP and 1A are not close together or parallel, as they are in the other two families.

The body structure of the Protelytroptera is not sufficiently known to permit any general conclusions about lines of evolution within the order. The head apparently was relatively small with prominent eyes. The antennae prominent, relatively thick basally; known only in the Protelytridae and the Blattelytridae, they are about half the length of the fore wing. The prothorax apparently included a small pronotal disc. The prothoracic legs were apparently short, with five tarsal segments; the hind legs were much longer apparently with well developed femora and five tarsal segments, also. The abdomen terminated in a pair of short but distinctly segmented cerci; the females (Apachelytridae) apparently possessed a short ovipositor.

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CONTROL OF REPRODUCTION IN FEMALE COCKROACHES WITH SPECIAL REFERENCE TO *NAUPHOETA CINEREA*.
II. GESTATION AND POSTPARTURITION.

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In Part I (Roth, 1964) of this paper I presented the results of a study on the reproductive behavior during the first preoviposition period of 4 species of cockroaches that incubate their eggs internally. *Nauphoeta cinerea* (Olivier) was the principal species used, but some experiments were conducted on *Leucophaea maderae* (Fabricius), *Pycnoscelus surinamensis* (Linnaeus), and *Diploptera punctata* (Eschscholtz).

In both *N. cinerea* and *L. maderae* receptivity can be correlated with the beginning of yolk deposition in the oöcytes. Yolk deposition in cockroaches is dependent upon corpus allatum hormone (Scharrer, 1946; Engelmann, 1957a, 1959; Roth and Stay, 1961, 1962b). Since allatectomized females mate (Roth and Barth, 1964), receptivity is determined by some event, presumably in the brain, which occurs at about the same time as onset of activity of the corpora allata; it was suggested that the neurosecretory system is involved in acceptance of the male by the female.

Females of *N. cinerea* become sexually receptive and mate at an average age of 4 days; females that are starved from emergence mate at the same age as fed individuals. Females of *L. maderae* also undergo a precopulatory period before they become receptive, and mate at an average age of 9 days. In this species more than 50% of the females that are starved from emergence do not mate (Roth, 1964). Thus, in virgin females starvation affects receptivity in *L. maderae* but not in *N. cinerea* (Roth, 1964).

Once a virgin *N. cinerea* mates, she becomes unreceptive and will not mate again during the first preoviposition period. Mechanical stimulation caused by the firm insertion of the spermatophore in the bursa copulatrix inhibits the female's sexual feeding response on the male's tergum (Roth, 1962, 1964). Whereas insertion of the spermatophore renders the female unreceptive it increases the activity of the corpora allata resulting in rapid development of the oöcytes. There appears to be a synergistic action of nutrition and mating stimuli in controlling the rate of oöcyte development because both stimuli are usually required in *N. cinerea* and *L. maderae* for activating the corpora allata to their fullest extent so that the oöcytes mature at their maximum rate (Roth, 1964).

In *N. cinerea,* the growth of the oöcytes remain inhibited during most of the gestation period (Roth and Stay, 1962b). The female remains sexually unreceptive during gestation and will not mate. She may or may not mate again after parturition (Roth, 1962). Obviously, a pregnant female, or one that has given birth, differs physiologically from a virgin female or one that has mated but not yet oviposited. This report concerns the control of, and factors affecting sexual receptivity and oöcyte development during gestation and after parturition.

MATERIALS AND METHODS

Nauphoeta cinerea was the principal species used, but several experiments were also performed on *L. maderae,* and the bisexual and parthenogenetic strains of *Pycnoscelus surinamensis* (Roth and Willis, 1961). The insects were reared and maintained on Purina dog chow or laboratory chow. Methods for testing receptivity, determining corpus allatum activity, operating on females, and laboratory conditions are given in Roth (1964).

To determine the effect of uterine pressure on oöcyte development, artificial oöthecae made of glass rods or beads were inserted in the brood sacs after the oöthecae were removed manually. To reduce the size of the oötheca, various numbers of eggs were removed from the females of *N. cinerea* as oöthecae were being formed (Roth and Hahn, 1964). Other techniques are described in their appropriate sections in the text. Numbers following ± are standard errors of mean values. Unless otherwise indicated, parturition refers only to birth of the first litter.

RESULTS AND CONCLUSIONS

Mechanism of inhibition of the oöcytes during gestation

The growth of the oöcytes during gestation in *N. cinerea* is shown in figure 1. Gestation may last 35-50 days. After 35 days of pregnancy, the oöcytes in different individuals may vary considerably in length. Many females may have oöcytes that contain large amounts of yolk prior to or at the time of parturitition.

When the oöthecae are removed from pregnant females, the oöcytes mature prematurely, indicating that an inhibitory influence

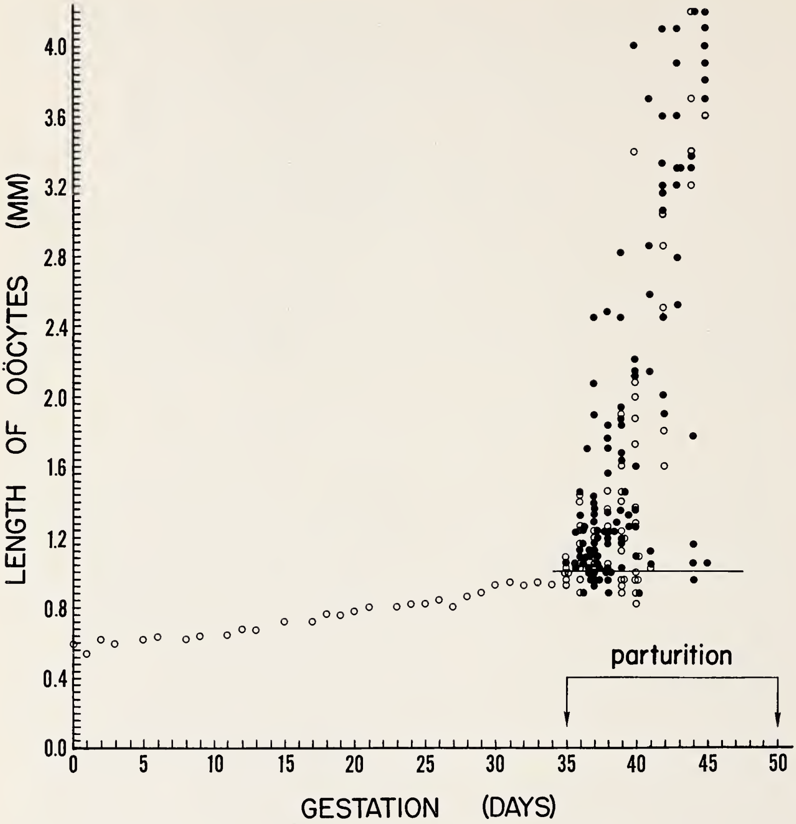


Fig. 1. Oöcyte development during pregnancy in *N. cinerea.* All points from 0 - 34 days are mean values of 5 - 9 individuals (N = 197); standard errors are not indicated but were ± 0.04 mm. or less for all of these measurements. Each point beyond 35 days of pregnancy represents the oöcytes of one female. Open circles = females were still carrying oöthecae when dissected. Solid circles = females dissected at the time of parturition or within 24 hr. after giving birth. The horizontal line is drawn at 1 mm. which is about the minimum size of the oöcytes that contain yolk.

on the corpora allata has been removed. The older the uterine eggs when removed, the less time is required to ovulate again (fig. 2). Roth and Stay (1959, 1961, 1962a, b) concluded that mechanical stimuli resulting from the oötheca in the uterus inhibit the corpora allata during pregnancy. Engelmann (1964) believes that in *L. maderae* the corpora allata are inhibited by a substance

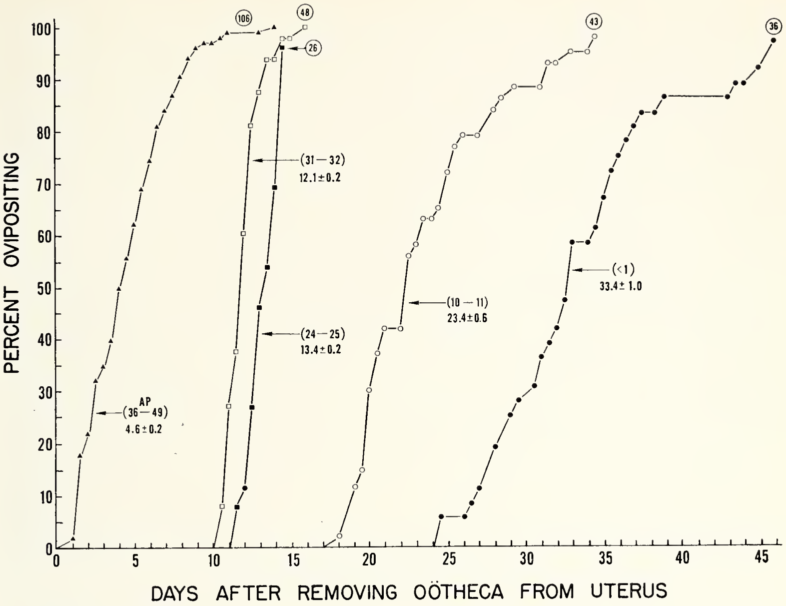


Fig. 2. Relationship between the age of the oötheca at the time it was removed from the uterus of *N. cinerea* and the time required to form a new egg case. Numbers in circles = number of insects used for each curve. Numbers in parentheses = number of days females were pregnant when their oöthecae were removed. AP = after parturition; 36-49 represents the range (days) of gestation in these females. Numbers under parentheses = mean number of days ± standard error, to form a new oötheca. The per cent ovipositing is expressed as accumulative data.

released by the egg case or brood sac, acting on neurones in the nerve cord and brain.

To determine if a chemical agent or mechanical stimulation prevents the growth of oöcytes in *N. cinerea* during pregnancy, glass tubes were inserted in the uteri of females after their oöthecae were removed at 3 different periods of gestation. The results (figs. 3,4) show that with glass oöthecae, the oöcytes did not develop as rapidly as they did in females in which no tubes were inserted in the uteri, indicating that the corpora allata were inhibited by the artificial egg cases. When oöthecae were removed about 24 hours after oviposition, females oviposited again on an average of 33 days; when oöthecae were removed 10 - 11 days after oviposition, the average time taken to oviposit again was 23 days (fig. 2). In both groups of females

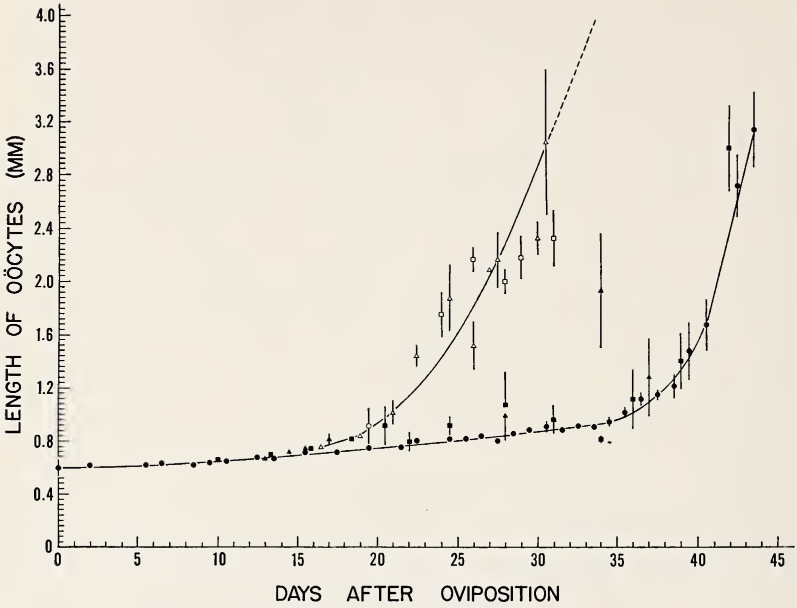


Fig. 3. Effect of distention of the uterus on inhibition of the corpora allata during early gestation in *N. cinerea.* Solid circles = Carrying oöthecae (controls). Five to 18 females per point (N = 276). Open squares = oöthecae removed <24 hr. after ovipositing; no glass tube inserted in uteri. Five to 16 females per point (N = 65). Solid squares = Oöthecae removed <24 hr. after ovipositing, glass tube (3 - 3.5 mm. × 10 - 11 mm.) inserted in uteri. Four to 10 females per point (N = 99). Open triangles = Oöthecae removed 10 - 11 days after ovipositing; no glass tube inserted in uterus. Three to 12 females per point (N = 65). Solid triangles = Oöthecae removed 10 - 11 days after ovipositing; glass tube (3 - 3.5 mm. × 10 - 11 mm.) inserted in uteri. Four to 10 females per point (N = 42). Vertical bars are one standard error but only one-half the error is indicated where they overlapped; no bars indicate standard errors of ± 0.02 mm. or less. A single curve is drawn through open triangles and open squares (see text for explanation).

the average time to oviposit again *after the initial* oviposition was about 33 days and for this reason in figure 3 (△ and □), a single curve is drawn through the points for females whose oöthecae were removed about 24 hours, and 10 - 11 days after oviposition. Eventually, inhibition of the corpora allata ceased in females with glass tubes in the uteri and the oöcytes developed. This also occurs in normal pregnant females in late gestation (fig. 1). Inhibition may

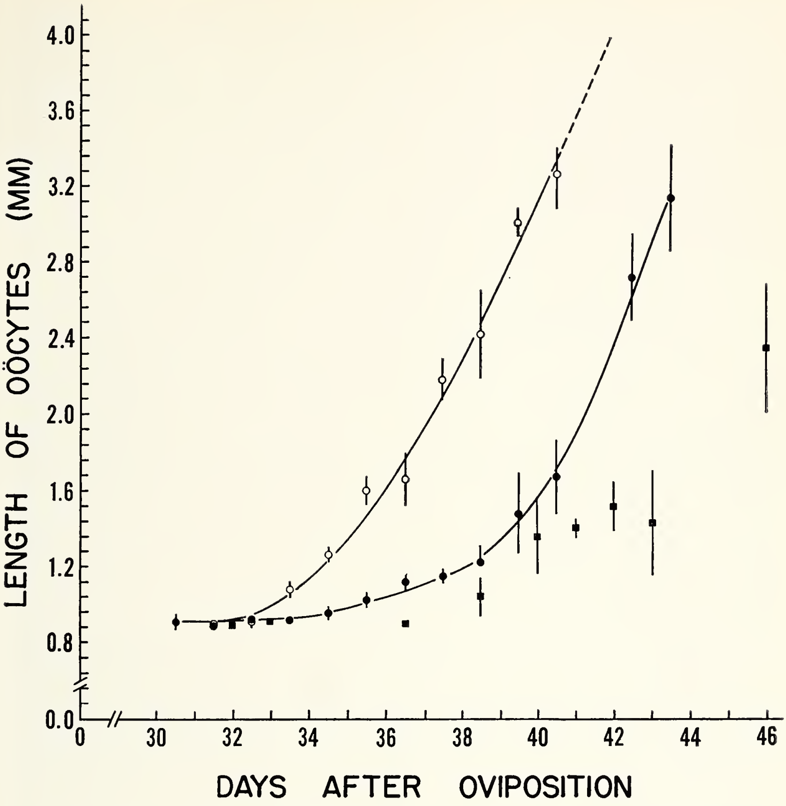


Fig. 4. Effect of distention of the uterus on inhibition of the corpora allata during late gestation in *N. cinerea*. Solid circles = Carrying oöthecae (controls). Ten to 18 females (N = 143) used for each point. Open circles = Oöthecae removed 30 - 31 days after oviposition; no tube inserted in uteri. Ten females (N = 100) used for each point. The average time required to oviposit again, when the oöthecae were removed at 31 - 32 days of pregnancy, was 12 days (fig. 2) or 43 - 44 days after the initial oviposition. Solid squares = Oöthecae removed from females 30 - 31 days after oviposition and glass tubes (4.1 - 4.3 mm. × 10 - 11 mm.) inserted in the uteri. Five to 16 females (N = 92) used for each point. Vertical bars are one standard error but only one-half the error is indicated where they overlapped; no bars indicate standard errors of ± 0.02 mm. or less.

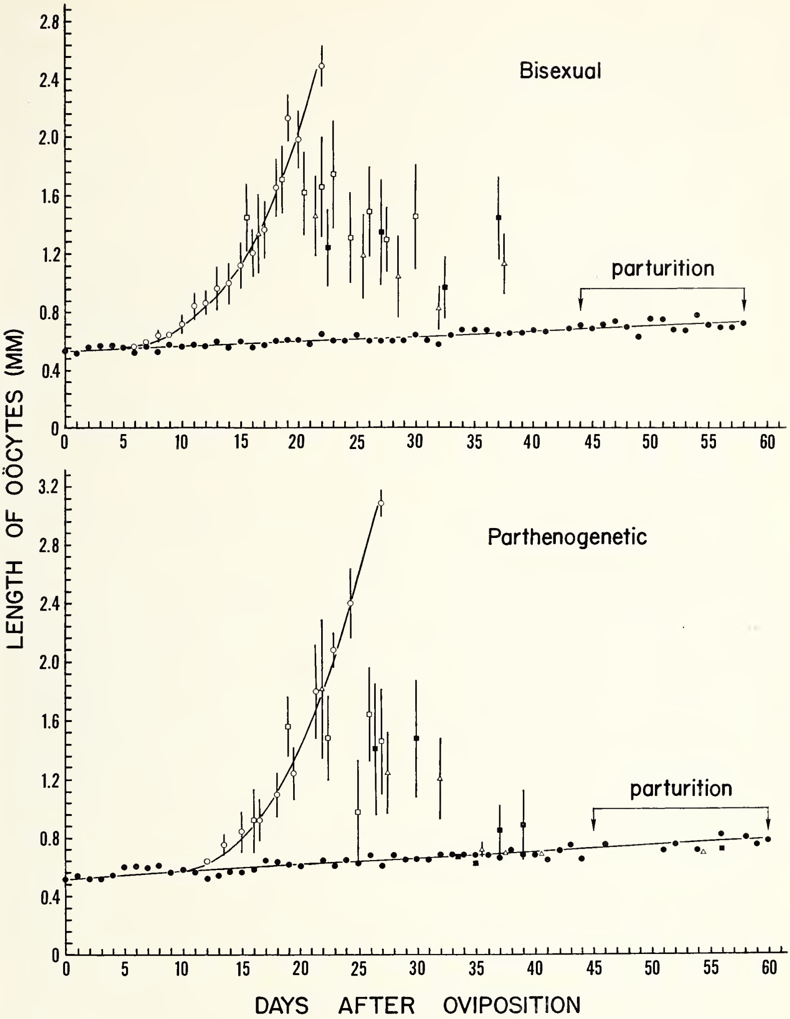
cease earlier in some females with glass inserts than in females carrying oöthecae (fig. 3).

The effect of different degrees of uterine stretching, using glass rods, and glass beads of 3 different diameters, was investigated in

2 strains of *P. surinamensis.* The artificial oöthecae were inserted into the uteri of females after their oöthecae were removed <24 hr. after ovipositing. The results are shown in figure 5 and table 1. The oöcytes of some females with bead inserts developed as rapidly as in females without beads. In the bisexual strain, the largest bead, and consequently the greatest uterine streching, was more effective than the two smaller beads in inhibiting the corpora allata. In the parthenogenetic strain, 4.0 mm. beads were about as effective as 4.5 mm. beads (table 1). The bead experiments were conducted for a maximum of 56 days in the parthenogenetic strain and for 37 days in the bisexual strain. In the glass rod experiments, females were sacrificed from 27 - 100 days after the rods were inserted in the uteri. Inhibition was virtually complete in all females (table 1), their oöcytes ranging in size from 0.58 - 0.88 mm. long ($\bar{x}$ = 0.74 ± 0.01 mm.). Of 68 bisexual strain females that had rods inserted in their uteri, only 3 females had well-developed oöcytes when examined on the 17th, 25th, and 36th days. The other 65 females had oöcytes that were virtually completely undeveloped when examined 24 - 71 days after the rods were inserted; their oöcytes ranged from 0.54 - 0.95 mm. and averaged 0.71 ± 0.01 mm. in length.

It was of interest to determine if reduction in size of the oötheca would influence the size of the ovarian oöcytes at parturition. There are an average of 33 eggs in the oötheca of *N. cinerea* (Willis *et al.,* 1958). The results of reducing the number of eggs in the oötheca are shown in figure 6. The oöcytes of females that had carried small oöthecae were not larger than the oöcytes of the control females.

Fig. 5. Effect of distention of the uterus with glass beads on inhibition of the corpora allata during gestation in two strains of *P. surinamensis.* Solid circles = Carrying oöthecae (controls). Each point represents one female or is an average value of 2 - 5 females. Bisexual — N = 107; parthenogenetic — N = 75. Open circles = Oöthecae removed <24 hr. after ovipositing; no glass beads inserted in uteri. Bisexual — 9 - 16 females per point (N = 189); parthenogenetic — 4 - 14 females per point (N = 96). The 3 remaining symbols were females whose oöthecae were removed <24 hr. after oviposition and glass beads of the following approximate diameters were inserted in the uteri; open squares = 3.5 mm. Bisexual — 7 - 11 females per point (N = 86); parthenogenetic — 5 - 8 females per point (N = 36). Open triangles = 4.0 mm. Bisexual — 8 - 15 females per point (N = 65); parthenogenetic — 3 - 10 females per point (N = 48); solid squares = 4.5 mm. Bisexual — 10 - 13 females per point (N = 44); parthenogenetic — 6 - 9 females per point (N = 49). Curves are drawn through solid and open circles only. For the points indicating females with bead inserts, vertical lines are one standard error of mean values; no vertical lines indicate standard errors of ± 0.02 mm. or less.



If small oöthecae, and, consequently, less stretching of the uterus (principally lengthwise), were less effective than normal-sized egg cases in inhibiting the corpora allata, one would expect the oöcytes to be larger at parturition. Since the small oöthecae are considerably reduced in length, the results suggest that in *N. cinerea:* 1) transverse rather than longitudinal stretching of the uterus, and 2) the gradual increase in size of the uterine eggs, even in oöthecae with

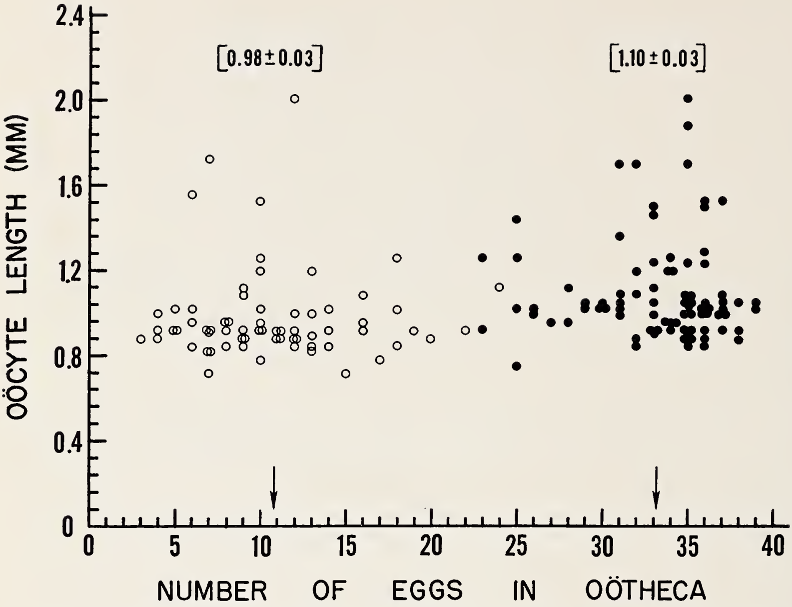


Fig. 6. Effect of reducing the number of eggs in the oötheca on the size of oöcytes at parturition in *N. cinerea.* Open circles = number of eggs in oöthecae reduced manually (N = 66). Solid circles = number of eggs in oöthecae not reduced manually (controls; N = 84). Each circle represents one female. Arrows indicate the average number of eggs in the oöthecae for the 2 groups of females. Numbers in brackets are the mean lengths ± standard errors of the oöcytes for both groups. Oöcytes were measured <24 hr. after parturition. Gestation period for the females whose oöthecae were artificially reduced in size averaged 60 days and for the control group 58 days. (Room temperature.)

very few eggs, are important in inhibiting the corpora allata during pregnancy.

Mechanism of inhibition of receptivity during gestation

Pregnant females of *N. cinerea* are unreceptive and do not respond to the courting male (Roth, 1962). Eight pregnant females had their ventral nerve cords transected <24 hr. after ovipositing. They were exposed to males for 1 - 2 hr. trials daily to determine if they would mate. Six females mated in 2 - 8 days after cord transection; one mated 18 days after transection. The spermatophores were attached to the surface of the oötheca, usually in the vestibule, because

TABLE 1 — Effect of inserting glass beads and rods in the uteri on oöcyte development in bisexual and parthenogenetic strains of *P. surinamensis*

Approximate size (mm.) of glass beads and rods inserted in uteri*	N	Treated females whose oöcytes developed as rapidly as in females without glass inserts**		Females in which growth of oöcytes was retarded or completely inhibited by glass inserts**					
				Partially inhibited		Completely inhibited§		Totals	
		Bisexual Strain							
		N	%	*N*	%	*N*	%	*N*	%
Beads¶									
3.5	86	38	44	11	13	37	43	48	56
4.0	65	22	34	7	11	36	55	43	66
4.5	44	6	14	11	25	27	61	38	86
Rods									
3-3.5 × 7.5-10	68	1	1	12	18	55	81	67	99
		Parthenogenetic Strain							
Beads¶									
3.5	36	23	64	2	6	11	30	13	36
4.0	48	7	15	6	12	35	73	41	85
4.5	49	5	10	5	10	39	80	44	90
Rods									
3-3.5 × 7-9	64	0	0	2	3	62	97	64	100

* Size of beads refers to diameter, and of rods to diameter and length.

** Based on the range in variation of oöcyte development in females whose oöthecae were removed and no beads were inserted.

§ For the bead experiments, oöcytes were 0.75 mm. or less; up until the fortieth day of pregnancy the maximum oöcyte length of females carrying oöthecae was 0.75 mm. in the bisexual strain and 0.71 mm. in the parthenogenetic strain.
For the rod experiments, oöcytes were 0.78 mm. or less until the 58th day (maximum gestation period) and later in the bisexual strain. For the parthenogenetic strain, oöcytes were 0.85 mm. or less until 60 days; this was the maximum size of the oöcytes at parturition.

¶ Data for the bead experiments are taken from females used in fig. 5.

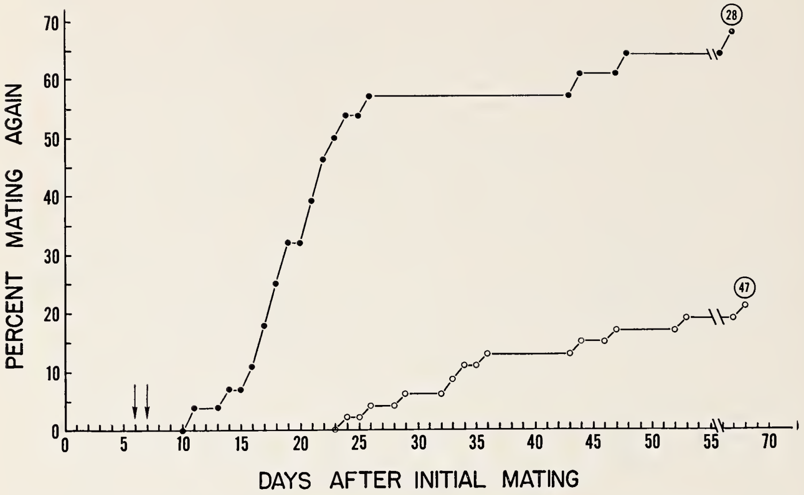


Fig. 7. Effect of ovariectomy on subsequent return of receptivity of females of *N. cinerea*. Open circles = ovariectomized only. Solid circles = ovariectomized; glass tube inserted in uterus on the sixth or seventh days (arrows) after mating; tubes then removed 3 - 10 days after being inserted and the females kept with males until they mated. Numbers in circles indicate the number of females used. Per cent mating is expressed as accumulative data.

the egg case blocked the bursa copulatrix. Thus in mated females, as in virgin females that oviposit (Roth, 1964), the mechanical presence of the oötheca inhibits receptivity.

Ovariectomized (ovaries removed in last nymphal stage) females of *N. cinerea* mate within 3 - 6 days after emergence. When kept with males continuously only about 20% of ovariectomized females mated again and this occurred over about a 2-month period (fig. 7). Thus, either the lack of ovaries or oötheca in some way prevented return of receptivity. Sixteen pregnant females had their oöthecae and ovaries removed 12 - 13 days after oviposition; eleven (69%) mated 7 - 17 days after the operation, showing that the presence of the ovaries themselves were not needed for the return of receptivity. *N. cinerea* nymphs were ovariectomized and the resulting adults were mated 3 - 6 days after emergence. After the spermatophores were dropped (6 - 7 days after copulation), glass tubes (about 4.3 mm. × 10 mm.) were inserted into the uteri; the posterior ends of the tubes extended beyond the abdomen and were cemented to the last abdominal segment to prevent their being extruded. After re-

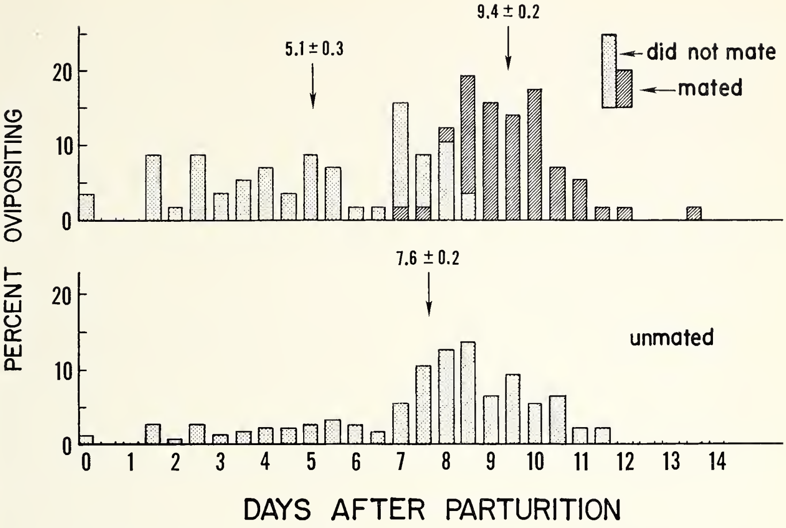


Fig. 8. Relationship between receptivity and subsequent oviposition, and the effect of mating following parturition on oviposition in *N. cinerea.* Top: Females that did or did not mate when exposed to males from time of, or <24 hr. after, parturition. (N = 57 for each group). Bottom: Females that were not mated after parturition. (N = 181). All females had mated previously only once, as virgins, prior to the first oviposition. Gestation period for all females ranged from 36 - 48 days. Arrows and numbers indicate the mean days ± standard errors to oviposit for each of the three groups.

maining in the uteri for 3 - 10 days, the tubes were removed and the females were placed with males continuously. About 70% of the females treated in this manner eventually mated and these generally became receptive earlier than ovariectomized females that had not had artificial oöthecae inserted (fig. 7). These results suggest that the prerequisites for the return of receptivity in the normal period of time in mated females are 1) the presence of an oötheca (uterine stretching) for at least a short time and then 2) the absence of the oötheca (removal of stretch stimuli).

Receptivity of females after parturition, and the effect of mating on oöcyte deevlopment

Females of *N. cinerea* may or may not mate again after they give birth (Roth, 1962). If not mated after parturition, females averaged about 8 days to oviposit (fig. 8, bottom). The time required for oviposition by females which did or did not mate when exposed to males after parturition is shown in figure 8 (top). Females which mated oviposited *later* than those that did not mate, indicating that the females which were receptive afer parturition had comparatively smaller oöcytes (see below) and therefore took longer to oviposit than the unmated females. This apparent lack of stimulation of mating differs from that produced by mating during the first preoviposition period where firm insertion of the spermatophore results in an increase in the rate of development of the oöcytes (Roth, 1964).

In *L. maderae,* mating after parturition also does not accelerate oöcyte maturation (Engelmann, 1960a). *Leucophaea maderae* differs from *N. cinerea* in that the time taken to oviposit after parturition in females that do or do not mate is essentially the same; 14.5 ± 0.5 days and 15.4 ± 0.3 for mated and unmated females respectively (table 9), whereas *N. cinerea* females that do not mate oviposit sooner than mated females. The difference between these species apparently is due to the fact that in *L. maderae* the corpora allata are inhibited during the entire gestation period and the oöcytes of females at parturition are more or less the same size and do not contain yolk (see fig. 7 *in* Roth and Stay, 1962b); in *N. cinerea* the oöcytes at parturition may vary considerably in size (figs. 1, 6).

At high (26°-28°C.), fairly constant insectary temperatures, the number of *N. cinerea* which have yolk in the oöcytes at or prior to parturition was greater than females maintained at usually lower, markedly fluctuating, room temperatures (fig. 9, bottom). Females which become receptive after parturition generally mate within 24 hr. Figure 9 (top) shows the lengths of the oöcytes about 24 hr. after parturition of females that did and did not mate when they had access to males. The females with comparatively small oöcytes

Table 2 — Relationship between length of gestation period and receptivity following parturition in *N. cinerea*

Gestation period (days)	Number used and percent mating*	
	N	%
35 - 36.5	28	79
37 - 38.5	69	75
39 - 40.5	31	36
41 - 42.5	28	11
43 - 44.5	36	19
45 - 46.5	16	25
47 - 50	13	0

* Females kept with males until they mated or oviposited.

TABLE 3 — Effect of starvation and delayed exposure to males on receptivity of *L. maderae* following parturition

Treatment after parturition¶	Number used and percent mating		Days to mate after exposure to males (Mean ± S. E.)
	N	%	
With food and males	25	92	1.2 ± 0.2
With food but isolated from males for 7-8 days, then starved and exposed to males	26	23	*
Starved and isolated from males for 7-8 days, then with food and males	24	92**	1.4 ± 0.4

¶ Food for all groups was lab chow; all groups had been fed during gestation.

* The 6 females that mated did so immediately or within a few hours after being with males; their oöcytes averaged 2.84 ± 0.35 mm. Fifteen of the 20 females that did not mate oviposited 16.1 ± 0.4 days after parturition (the exact time to oviposit of 5 females was not known).

** The oöcytes of the females that mated averaged 1.51 ± 0.10 mm.

mated, whereas females whose oöcytes were fairly large shortly after parturition tended to be unreceptive. This relationship was true for females which had two litters and had mated once or twice prior to the second parturition. Of 58 females that mated once, prior to the first oviposition, and were then exposed to males after having the second litter, only 9 (16%) mated again, and their oöcytes measured 1.19 ± 0.06 mm. within 24 hr. after mating. The mean oviposition time after parturition for the 49 (84%) females that did not mate was 4.1 ± 0.3 days. Sixty-three females were mated twice (once prior to the first oviposition and once after giving birth to the first litter) and were exposed to males after the second parturition. Thirty-two (51%) mated again and the oöcytes of these females were 1.17 ± 0.04 mm. long within 24 hr. after mating. The 31 (49%) females that were unreceptive and did not mate oviposited in 5.6 ± 0.6 days, again indicating that their oöcytes were well developed at the time of parturition; females that mate oviposit on an average of 9 days after giving birth (fig. 8, top).

An analysis of the histories of 221 females that did or did not mate after parturition showed that females with longer gestation periods tended to be sexually unreceptive after they gave birth, whereas those with shorter gestation periods usually mated again (table 2). These results again show that after parturition, receptivity can be correlated with relatively small oöcytes because females with longer gestation periods usually have large oöcytes at parturition. It appears that if the oöcytes begin to mature several days before the female gives birth, she will tend to be sexually unreceptive after parturition.

If large oöcytes are an indicator of nonreceptivity following parturition, then females that are receptive at parturition should become unreceptive if isolated from males for several days after giving birth because an additional mating is not necessary for continued development of the oöcytes. The effect on receptivity of isolating females from males for various periods of time after parturition and then placing them with males until they mated or oviposited is shown in figure 10. There was a marked decline in receptivity of females after they had given birth, the longer they were isolated from males. The oöcytes of 30 females that mated after being placed with males 2 - 6 days after parturition averaged only 1.40 ± 0.06 mm., indicating that in these females the oöcytes were relatively small at parturition. The largest oöcytes of all the females that mated following a delay in exposure to males was 2.21 mm. (she mated 6 days after parturition).

Females of *L. maderae* usually mate within a day or two after parturition and mating after parturition is not required to mature the oöcytes. As in *N. cinerea,* delayed exposure to males also results in a loss of receptivity in fed females (table 3).

Return of receptivity of females after removing the oöthecae from the uteri

Roth (1962) found that the elapsed time for the return of receptivity following removal of the oöthecae was shorter when the egg case was removed late rather than early in gestation; in that experiment the actual ages of the oöthecae when removed from the uteri were unknown. The return of receptivity in females which had their oöthecae removed at several known periods following oviposition is shown in table 4 and figures 11 and 12 (done under different temperature conditions). More than 50% of the control females became receptive within a few hours after giving birth (fig. 11, AP). The time required for the return of receptivity in the experimental animals varied and depended on how long the females had been pregnant when their oöthecae were removed. The younger the oöthecae when removed, the longer it took for the return of

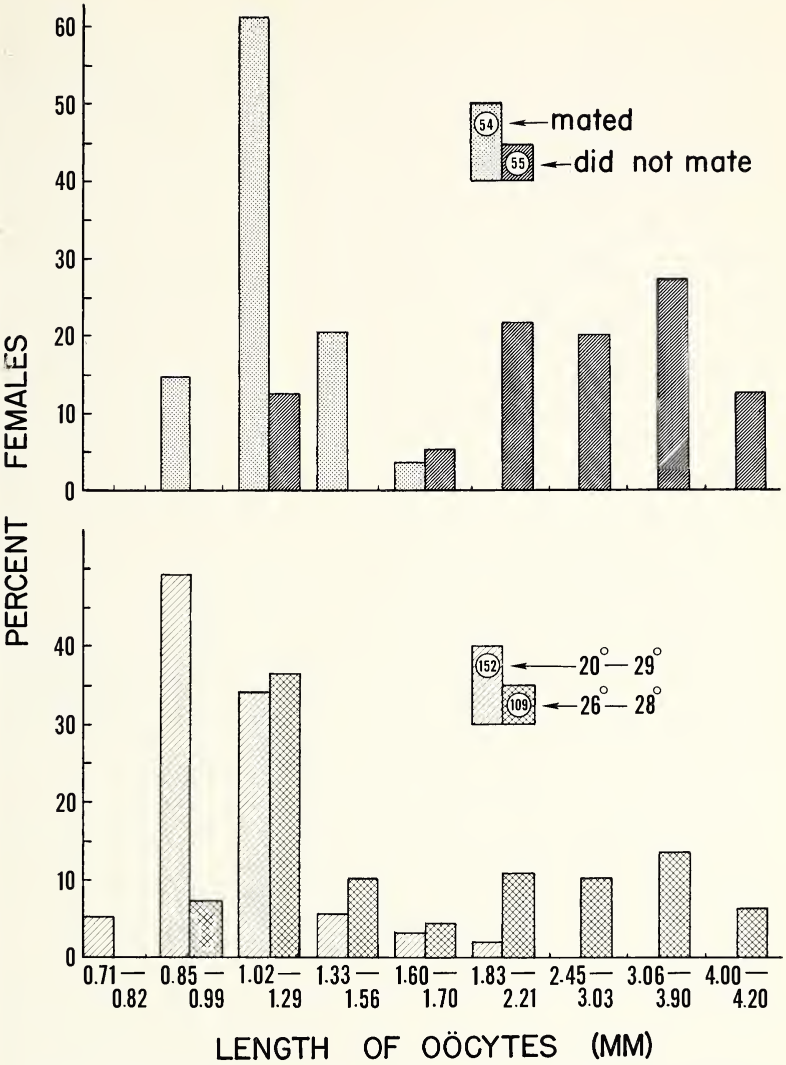


Fig. 9. Relationship between receptivity and size of oöcytes following parturition in *N. cinerea*. Top: Females exposed to males from time of parturition and given <24 hr. to mate. Oöcytes measured within 24 hr. after parturition (27 ± 1° C.). Bottom: Oöcytes measured at the time of parturition or <24 hr. after the females had given birth. Females maintained during gestation at 2 different room conditions. (Numbers in circles in top and bottom histograms indicate the numbers of insects used for each group).

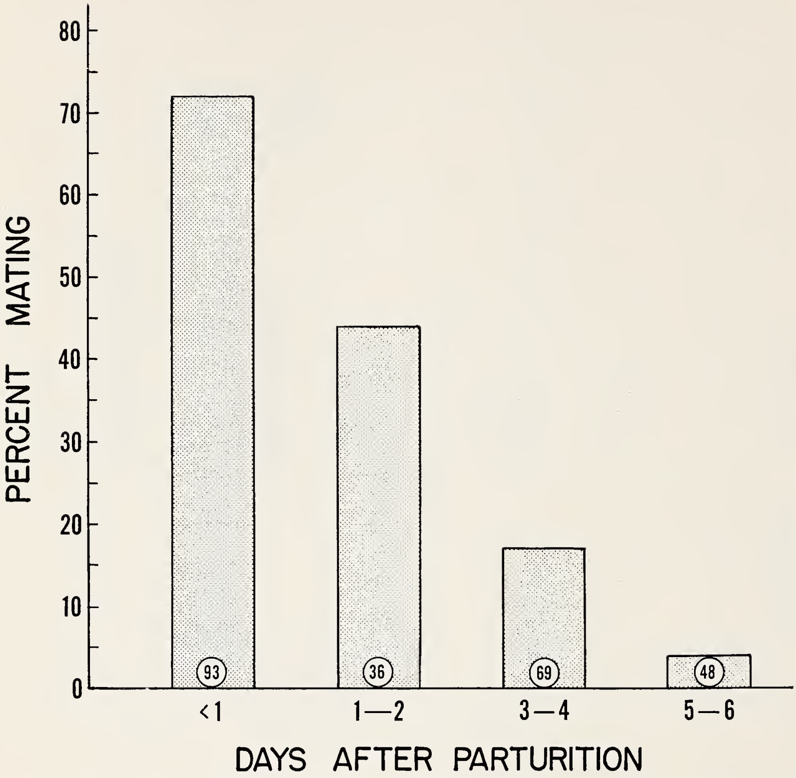


Fig. 10. Effect of delayed exposure to males on receptivity of females following parturition in *N. cinerea*. The axis of abscissas indicates the days after parturition the females were placed with males. Numbers in circles indicate the numbers of females used. Gestation period 35 - 50 days. Females fed during gestation and after parturition.

receptivity. The results were similar whether females which had their oöthecae removed 1 - 2 days after ovulation were exposed to males for 1 hr. daily, or were exposed to males continuously (fig. 11, cf. □ and △). Note the similarity between figures 2 and 12 (both done under similar conditions). The same relationship holds for the return of receptivity as for the time taken to oviposit following removal of the oöthecae at various periods of pregnancy. Virgin females differ from mated individuals in that receptivity returns sooner when the oötheca is removed from the uterus (figs. 11, 12; table 4).

TABLE 4 — Receptivity of virgin and mated *N. cinerea* females whose oöthecae were removed at different periods of pregnancy

Age (days) of oöthecae when removed from uteri	Days after removal of oöthecae females mated, and length (mm.) of oöcytes (Mean ± S. E.)					
	Mated			*Virgins*		
	Days	*Oöcytes*	*N*¶	*Days*	*Oöcytes*	*N*¶
<1 - 1	17.7 ± 0.4	1.05 ± 0.03	62	6.5 ± 1.0	0.91 ± 0.01§	33
5 - 10	9.3 ± 1.0	1.06 ± 0.07*	6	5.0 ± 0.7	0.88 ± 0.05	9
11 - 12	8.0 ± 0.3	1.08 ± 0.05	24	—	—	
11 - 13	—	—	—	3.3 ± 0.5	0.92 ± 0.04	5
13 - 16	6.6 ± 0.5	1.30 ± 0.20	6	—	—	—
14 - 19	—	—	—	4.2 ± 0.3	1.00 ± 0.01	3
17 - 23	5.7 ± 0.8	1.21 ± 0.17*	7	—	—	—
25	3.5 ± 0.04	1.06 ± 0.02	25	—	—	—
31 - 32	2.2 ± 0.2	1.08 ± 0.02	22	—	—	—

¶ Refers to the number of females used in determining values in the *Days* column; unless indicated by footnotes, the number used to determine oöcyte length was the same. The oöcytes were measured <24 hr. after mating.

§ Based on 15 females that mated 7 - 17 days after ovipositing. The oöcytes of 39 virgin females that mated 1 - 24 days (room temperature; see fig. 10) after the oöthecae were removed <1 day after oviposition, measured 0.82 ± 0.02 mm.

* Based on 3 females.

Histograms showing the frequency distributions of the lengths of the oöcytes at the time of mating of the females used in figure 11 are given in figure 13. Except for females whose oöthecae were removed 1 - 2 days after oviposition, the greatest percentage of females mated when their oöcytes were 0.99 - 1.09 mm. long and contained yolk. The basal oöcytes of females whose oöthecae were removed 1 - 2 days after oviposition are about 0.51 mm. long and smaller than the oöcytes of females whose oöthecae are removed at 21 - 26 days or 51 - 54 days after ovulation, or at parturition. There is an increase in the length of the oöcytes during gestation, even though the corpora allata are inactive during most of the gestation period as indicated by absence of yolk in the oöcytes. When the oötheca is removed just after ovulation, a certain amount of time elapses before the oöcytes attain the length of those of females whose oöthecae were removed near the middle or about the end of the gestation period. Many females that mated after their oöthecae were removed 1 - 2 days after oviposition, had oöcytes that did not contain yolk; but their colleterial glands usually contained some secretion. However, not all of the colleterial gland secretion is used during the first oviposition so that its presence in the gland after parturition cannot be used as an indicator of corpus allatum activity.

Effect of mating stimuli on return of receptivity

Females were mated to castrated males. After oviposition their oöthecae were removed at different periods of gestation, and the females were placed with males and checked daily for spermatophores. The return of receptivity (table 5) of these females that lacked sperm in the spermathecae was similar to that found in normally mated females (cf. table 4); the longer the oöthecae had been in the uterus when it was removed, the quicker the females regained receptivity. Ten females (room temperature) were allowed to mate to completion and had their spermatophores removed 1 - 2 min. after mating so that no sperm entered the spermathecae (Roth, 1964). After ovipositing (oöthecae were aborted and never had been in the uteri, or were removed <24 hr. after oviposition) they were exposed to males (2♂♂ : 1♀) for 1 hr. daily to determine when receptivity would return. Six of the females mated in 16 - 28 days ($\bar{x} = 21.2 \pm 1.9$) and their oöcytes averaged 0.99 ± 0.04 mm. long. The return of receptivity in these females was similar to that of normally mated females rather than virgin females whose oöthecae were removed (cf. table 4). These experiments show that

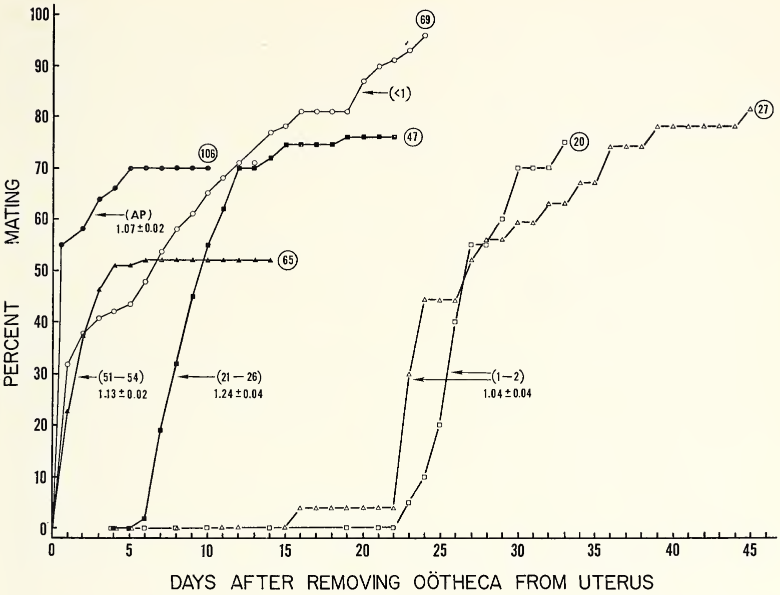


Fig. 11. Relationship between age of oötheca when removed from the uterus and recovery of receptivity in *N. cinerea.* Numbers in circles = numbers of insects used. Numbers in parentheses = number of days females were pregnant when their oöthecae were removed from the uteri. Numbers under parentheses = mean length (mm.) ± standard errors of the oöcytes, measured at the time of mating (except for females represented by open squares; the oöcytes of these females were measured <24 hr. after mating). (AP) = females that gave birth normally; fifty-five per cent of the females mated <24 hr. after parturition and these are plotted at 0.5 day. The females of this group that failed to mate oviposited 6 - 10 days after parturition. Open circles = virgin females; all other groups had mated prior to ovipositing. Open squares = each of the females in this group were confined with 2 males continuously until they mated; females examined daily for spermatophores. The females in all other groups were tested for receptivity once a day for one hr. (2♂♂ : 1♀) and were removed when they mated. The per cent mating is expressed as accumulative data. (Room temperature.)

1) prolonged loss of receptivity during gestation can be induced by mating stimuli, *i.e.,* the firm insertion of the spermatophore in the bursa copulatrix, and 2) the absence of sperm in the spermathecae does not influence the return of receptivity after the first oviposition.

Males produce small spermatophores if they mate more than once with brief intervals between matings (Roth, 1964) and it is probable

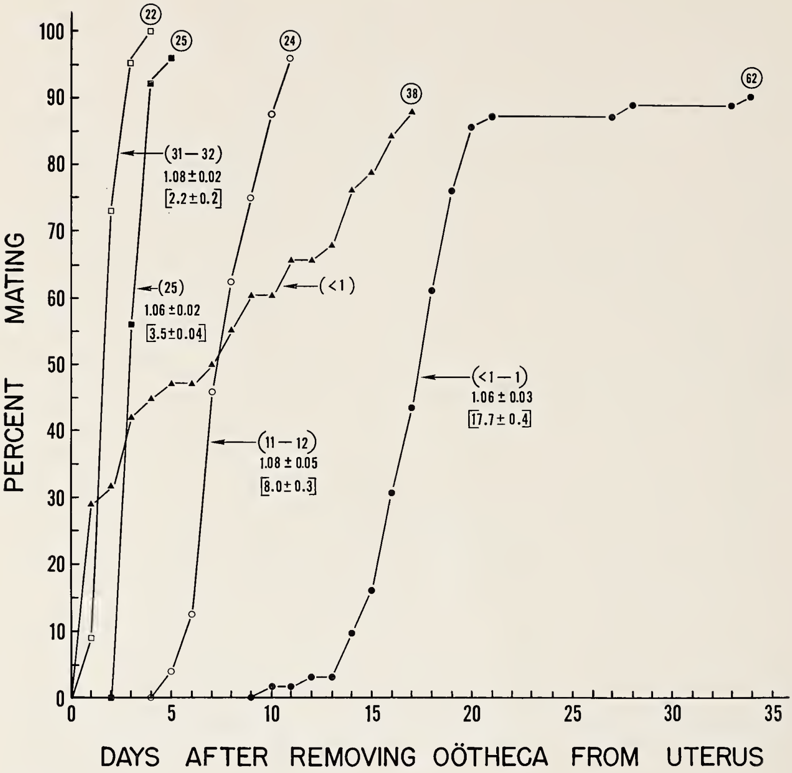


Fig. 12. Relationship between age of oötheca when removed from the uterus, and recovery of receptivity in *N. cinerea*. Numbers in circles = number of insects used. Numbers in parentheses = number of days females were pregnant when their oöthecae were removed. Numbers under the parentheses = mean length (mm.) ± standard error of the oöcytes measured <24 hr. after mating. Numbers in brackets = mean days ± standard error for return of receptivity. Solid triangles = virgin females; all other groups had mated prior to ovipositing. All females with males continuously until they mated; females examined daily for spermatophores. The per cent mating is expressed as accumulative data.

that fewer sperm are present in the smaller consecutively formed spermatophores. One experiment was performed to determine the oviposition behavior and subsequent receptivity of females that were mated to males that had mated consecutively; in all cases a spermatophore was transferred. Of 150 females mated to virgin males, only 2 (1%) aborted their oöthecae prematurely and the eggs were unfertilized. Six (10%) of 61 females mated to males that had mated previously within an hour aborted unfertilized eggs; thirteen (81%) of 16 females that were mated to males that had mated twice within a few hours aborted their oöthecae. Subsequent receptivity, following parturition of females that were mated to virgin males or males that mated twice consecutively, was the same. Of 132 females mated to virgin males, 117 (89%) were receptive after parturition; 52 (93%) of 56 females that had mated males, which mated twice consecutively, were receptive; only 3 females (the others aborted unfertilized eggs) mated to males that mated 3 times consecutively, gave birth to normal sized litters, and these females mated again following parturition. Consecutive matings may affect female oviposition behavior because no sperm, or an insufficient amount of sperm enter the spermathecae from spermatophores formed during the second and third matings. However, if sperm are present and the eggs are fertilized, the mating behavior of females, following parturition, is the same whether they are mated to virgin males or males that mated 2 or 3 times consecutively; the spermatophores produced by the latter males presumably had fewer sperm.

Effect of starvation on receptivity of females

Thirty-six females were given food and water for 24 hr. only on the sixteenth day of pregnancy. After parturition (gestation averaged 39.0 ± 0.6 days) they were exposed to males and lab chow. Thirty-four (94%) eventually mated and their oöcytes were 0.96 ± 0.01 mm. long <24 hr. after mating. At parturition, the oöcytes of females starved during pregnancy are smaller than those in females that feed during gestation. In starved females, presumably the corpora allata do not become reactivated in late gestation, as they do in fed individuals (cf. fig. 1). It was shown earlier that after parturition receptivity could be correlated with the size of the oöcytes; unreceptive females were those whose oöcytes were relatively

TABLE 5 — Receptivity of females, mated to castrated males, which oviposited and whose oöthecae were removed after various periods of time

Age (days) of oöthecae when removed from uteri	Days after removal of oöthecae females mated (Mean ± S. E.)	Oöcytes (mm.) (Mean ± S. E.)*	N
16 - 18	6.3 ± 0.7	1.21 ± 0.06	5
19 - 21	3.6 ± 0.4	1.04 ± 0.02	10
33,34	2.5 ± 0.5	1.02 ± 0.07	2

* <24 hr. after mating.

TABLE 6 — Effect of nutrition on receptivity following parturition in *N. cinerea*

Diet		Number used and percent mating		Days after parturition to mate (Mean ± S.E.)
During gestation	after parturition	*N*	%	
lab chow	lab chow*	60	85	0.7 ± 0.1
lab chow	starved	105	76	0.7 ± 0.1
starved§	lab chow*	60	98	2.8 ± 0.2¶
starved§	starved	128	23	3.5 ± 0.4

* Females that were fed were exposed to males and food <24 hr. after parturition.

§ Given 9-10 days to mate after parturition.

¶ The oöcytes of these females were 0.94 ± 0.02 mm. long measured <24 hr. after mating.

large at the time the females gave birth. Therefore, one would expect that inanition during gestation, and subsequent feeding following parturition would affect female receptivity. The results of experiments to determine the effect of nutrition on receptivity in *N. cinerea* are shown in table 6 and figure 14. A high percentage (85 and 76%) that were fed during gestation, and were then starved or fed, mated again. In marked contrast, only 23% became receptive again if they were starved during and after gestation; in other experiments, as high as 40% of similarly starved females were receptive (fig. 16). It should be noted that the females were starved in groups; some females died and were partly or completely eaten during the night before they could be removed from the containers. This may have increased the percentage of females that became receptive again. However, in spite of this source of error, it is evident that starvation during gestation markedly reduced the number of females that regained their receptivity, provided the females were not fed after parturition.

N. cinerea females that are fed during gestation and become receptive after parturition, usually mate within a day after giving birth; this is true whether or not the females are fed after parturition (table 6). However, females which are starved during gestation and are then exposed to males and food after parturition become receptive more slowly; 80% mated within 4 days after giving birth whereas a comparable percentage of females fed during gestation did so <24 hr. after parturition (fig. 14). Only 23% of the females starved during gestation and after parturition mated within a 9 - 10 day period and these averaged 3.5 ± 0.4 days to mate (table 6). When, after 9 - 10 days, the remaining females were

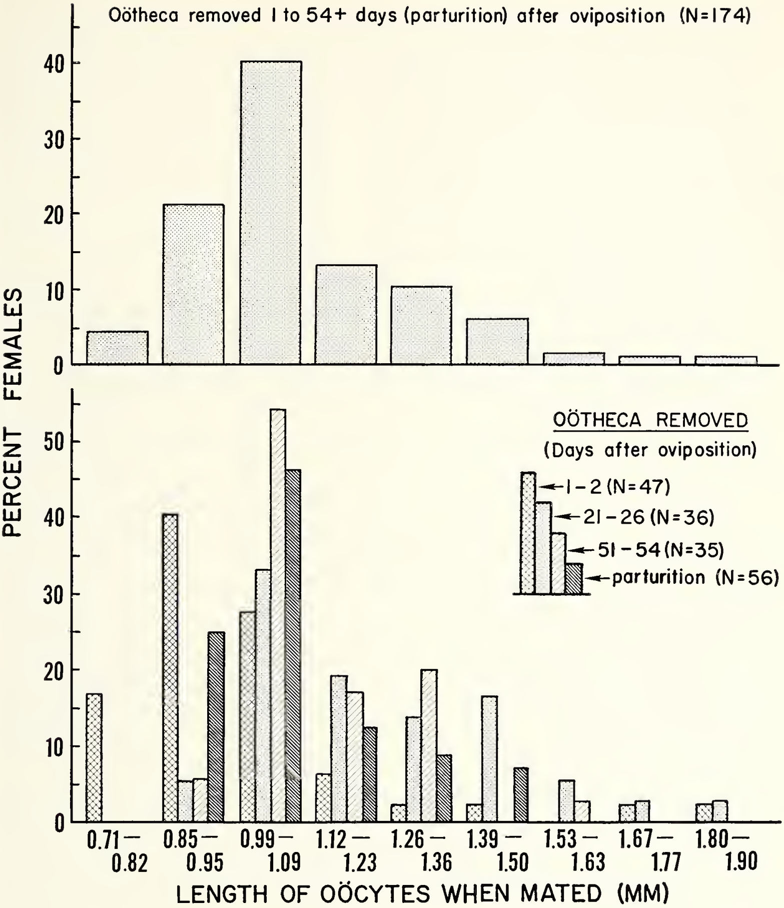


Fig. 13. Frequency distribution of lengths of oöcytes of females of *N. cinerea* that mated after their oöthecae were removed from the uteri. The parturition group was females that gave birth normally. The top histogram is a combined summary of all the groups shown in the figure below. (Room temperature.)

exposed to food for only 2 hr., the number of females that mated increased rapidly within the next 5 days (fig. 14); the oöcytes of females that mated after this meal were 0.88 ± 0.01 mm. long (N = 20). An additional increase in mating occurred when the remaining females were fed again *ad libitum* (fig. 14); the oöcytes of 10 of these females were only 0.86 ± 0.02 mm. long. The

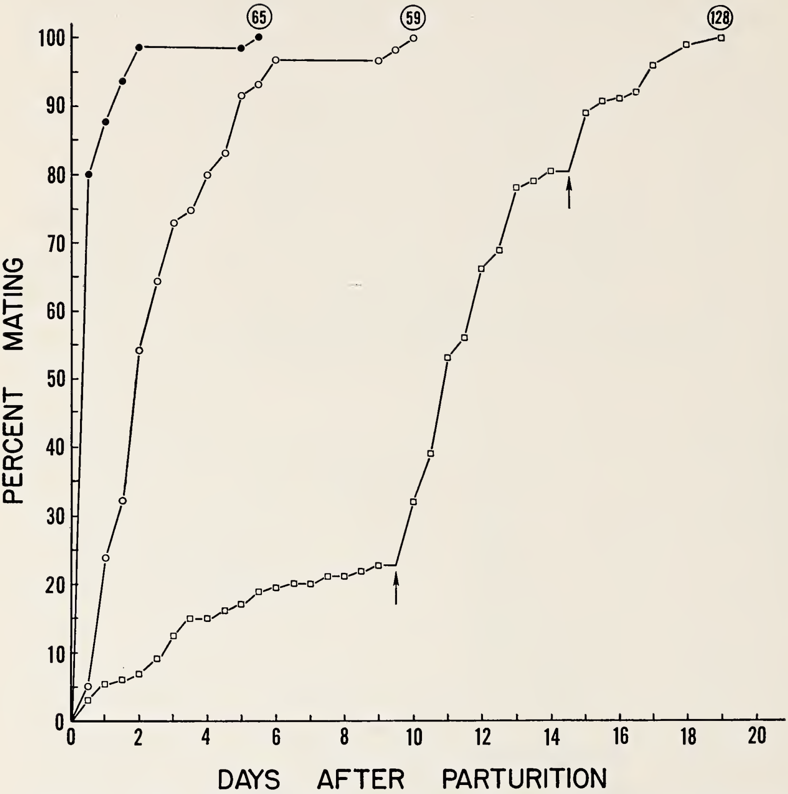


Fig. 14. Effect of starvation on receptivity of *N. cinerea* following parturition. Solid circles = Females fed during gestation and after parturition; average days to mate after parturition was 0.7 ± 0.3. Open circles = Females starved during gestation, then exposed to males and food after parturition; 59 of 60 females mated; average days to mate after parturition was 2.8 ± 0.2. Open squares = Females starved during gestation and for 9 - 10 days after parturition, then fed; average days to mate prior to feeding was 3.5 ± 0.4. First arrow = remaining females (i.e., those that did not mate) fed for 2 hr. only; average days to mate after feeding was 2.0 ± 0.1. Second arrow = remaining females fed *ad libitum;* average days to mate after second feeding was 1.7 ± 0.3; 128 out of 136 females mated. Food was lab chow. Numerals in circles = number of insects (based only on females that mated).

oöcytes of the females that mated after being fed for 2 hr. and then *ad libitum* did not contain yolk so that return of receptivity could not be correlated with corpora allata activity using oöcyte yolk as an indicator.

Females that were starved during gestation and fed after parturition but were not mated again, oviposited in 11 - 25 days ($\bar{x} = 15.5 \pm 0.2$; fig. 15, bottom). Females starved during gestation were exposed to males for 2 - 4 hours within 2 days after parturition and the oöcytes of receptive (those that mated) and non-receptive individuals were measured. Non-receptive females had oöcytes that averaged 0.83 ± 0.01 mm. ($N = 44$) whereas the oöcytes of receptive females averaged 0.94 ± 0.01 mm. long ($N = 16$). The oöcytes were slightly larger in the receptive females, but receptivity could not be correlated with the presence of yolk in the oöcytes of all cases. Females, starved during gestation, were exposed to males for 2 - 4 hrs. within 2 days after parturition, and those that mated were separated from their partners before a spermatophore was transferred, thus insuring that there would be no effect of spermatophore stimuli on rate of oöcyte development (Roth, 1964). After being given food *ad libitum,* receptive females usually oviposited sooner than nonreceptive individuals (fig. 15, top). These results suggest that even though yolk was not present in the oöcytes of many of the receptive females, their endocrine system was more active than nonreceptive individuals.

Effect of starvation and isolation from males on receptivity

Females that were fed during and after gestation became unreceptive if they were isolated from males for several days after giving birth (fig. 10). Since receptivity can be correlated with the presence of small oöcytes, and starvation during gestation or after parturition affects the rate of oöcyte development, one would expect starved females to behave somewhat differently from fed individuals. Starved females, whose oöcytes develop slightly or not at all, should remain receptive for longer periods of isolation from males. The receptivity of starved females is shown in figure 16. As found previously (fig. 10) there was a marked decline in receptivity, of females fed during and after gestation, after 3 - 6 days of isolation from males (fig. 16A, lined bars). Females fed during gestation but starved after parturition also became nonreceptive with isolation but to a lesser extent than the fed group; about 29 - 36% were still receptive after 3 - 6 days of isolation (fig. 16A, stippled bars). About 40% of the females starved during gestation and after parturition were receptive (fig. 16B, stippled bars). Even after 5 - 6 days of isolation from males, 38% were still receptive. This is to be expected since in these females there is little or no oöcyte develop-

TABLE 7 — Effect of partial and complete inanition on receptivity of *N. cinerea* whose oöthecae were removed at different periods of gestation

Days pregnant when oöthecae were removed	Conditions, number used, per cent mating, and days (Mean ± S. E.) to mate after removing the oöthecae								
	With food continuously		Days	With food until oöthecae were removed		Days	Starved during entire experimental period		Days
	N	%		*N*	%		*N*	%	
5 - 6	27	85	11.1 ± 0.5	40	45	11.7 ± 0.7	28	36	12.7 ± 1.0
10 - 11	28	96	9.4 ± 0.4	17	100	9.0 ± 0.3	25	52	10.0 ± 0.4
24 - 26	49	92	3.5 ± 0.2	37	97	3.7 ± 0.3	24	42	5.7 ± 0.4
31 - 32	40	100	2.3 ± 0.1	27	100	2.2 ± 0.2	27	48	3.3 ± 0.3

ment following parturition if starvation is continued. More than 25% were still receptive after 9 - 10 days isolation from males and food. In the experiments with females starved during gestation and after parturition, only data from individuals that lived at least 5 days after being placed with males was used. However, starved females that mate after being isolated for several days after parturition do so almost immediately on being placed with males. The results with females starved during gestation but fed after parturition differed markedly from females fed during and after gestation. Ninety-eight per cent were receptive and this did not change even after 5 - 6 days isolation from males (fig. 16B, lined bars). Sixty-five per cent were still receptive after 7 - 8 days isolation and this dropped to 20% only after 9 - 10 days of isolation. In all females that mated, the oöcytes averaged less than 1.5 mm. long (fig. 16A, B).

Females of *L. maderae* which feed during and after gestation also become unreceptive if they are isolated from males; and as in *N. cinerea,* starvation after parturition prolongs receptivity (table 3).

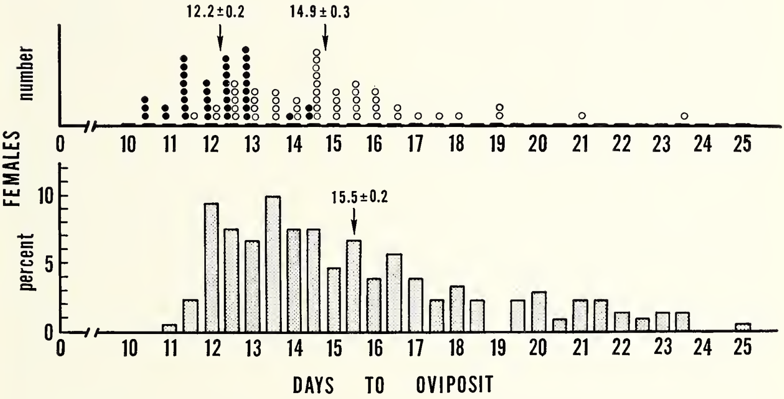


Fig. 15. Receptivity and oöcyte development following parturition in *N. cinerea* starved during gestation. Top: Females exposed to males and food after parturition. Solid circles = receptive females. Open circles = non-receptive females. Each circle represents one female. Days to oviposit calculated from time of exposure to food. Bottom: Females that were not exposed to males after parturition. (N = 213). Days to oviposit calculated from time of parturition; females were given food within a day after giving birth. Numbers above the arrows indicate the average number of days ± standard errors taken to oviposit by the various groups of females.

Effect of partial and complete starvation on receptivity after removing the oöthecae from the uteri

The time taken for return of receptivity, after the oötheca is removed from the uterus, varies with the length of the gestation period at the time of removal of the egg case (figs. 11, 12). The effect of partial and complete inanition on return of receptivity following removal of the oötheca is shown in table 7. Females fed for 10 - 11, 24 - 26, and 31 - 32 days before having their oöthecae removed behaved like control females that were fed lab chow continuously. However, only 45% of the females fed for 5 - 6 days only, mated. There was a marked drop in the number of females that mated (36 - 52%) in all 4 groups of females starved during the entire experimental period. The females that were fed for only 5 - 6 days behaved like completely starved females. Regardless of the extent of feeding or starvation, time taken to mate after removing the oöthecae was similar or only slightly delayed in females starved during the entire experiment. The lengths of the oöcytes of the females that did not mate, in the groups with 52% or less receptive, are shown in table 8. The oöcytes, in practically all of these nonreceptive females, were undeveloped and lacked yolk.

Effect of starvation and mating, following parturition, on oöcyte development in females fed during gestation

Females of *N. cinerea* fed during gestation were fed or starved after giving birth. These females were not mated again, and the time taken to oviposit was determined. The results in table 9 show that the average number of days taken to oviposit was about the same for both groups (8.5 and 9.2 days for the fed and starved groups, respectively). However, 13% of the starved females took 11.5 - 15 days, whereas only 1% of the fed group required 11.5 days to oviposit and none took longer. Starvation following parturition had only a slight or no effect on the rate of oöcyte development if females were fed *ad libitum* during gestation. Females that mated after parturition and were either fed or starved during their second preoviposition period did not oviposit sooner than comparably treated nonmated females (table 9); in fact, the mated females took slightly longer to oviposit. Thus, when females have access to food during the entire gestation period, the oöcytes mature at a rapid rate if fed or starved after parturition and an additional mating after the female gives birth does not affect this rate of development. The

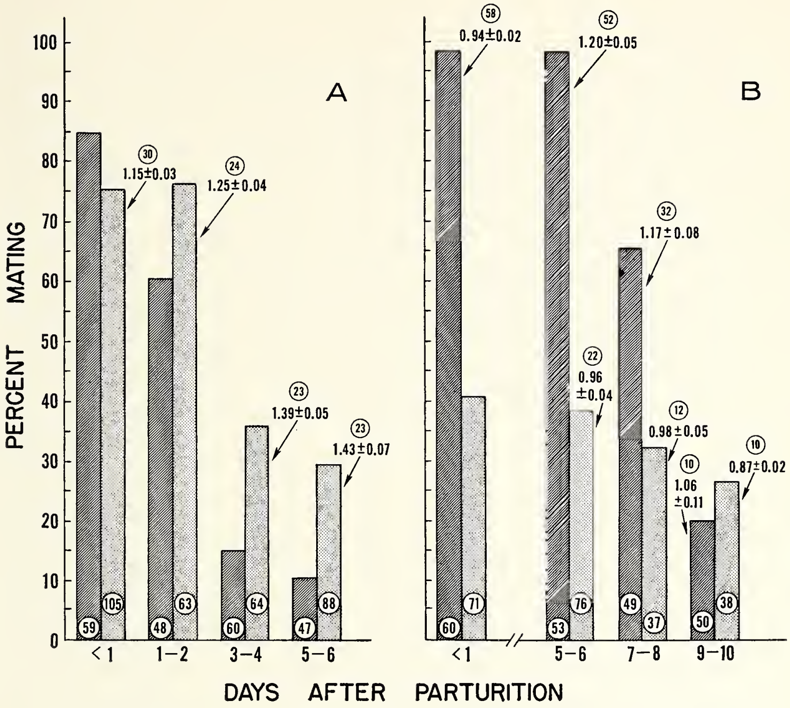


Fig. 16. Effect of starvation and delayed exposure to males on receptivity of females following parturition in *N. cinerea.* A — Fed during gestation. B — Starved during gestation. The axis of abscissas indicates the days after parturition females were placed with males. Lined bars = fed after parturition. Stippled bars = starved after parturition. Numerals in circles within the bars = number of females used. Numerals opposite the bars = length of oöcytes (mm.) ± standard errors of females that mated, measured at the time of, or <24 hr. after copulating; numerals in circles outside the bars = number of females whose oöcytes were measured. Gestation period of all the females was 35 - 40 days. Females fed during gestation and those starved during gestation but fed after parturition were kept with males until they mated or oviposited. Females starved during gestation and after parturition were allowed up to 10 days after parturition to mate.

slightly longer period taken for mated females to oviposit in these experiments probably indicates that the females that became receptive and mated had smaller oöcytes than the unmated females at the time of parturition.

L. maderae differs from *N. cinerea* in that starvation after partu-

Table 8 — Oöcytes of females of *N. cinerea* that did not mate when exposed to males*

Conditions	Days pregnant when oöthecae were removed	Dissected (days after removing oöthecae)	Number of females with or without yolk in oöcytes		Oöcytes (mm.) (Mean ± S. E.)
			With	Without	
With food until oöthecae were removed	5 - 6	17 and 22	3	—	1.77 ± 0.38
			—	19	0.80 ± 0.01
Starved during the entire experiment	5 - 6	18 and 22	0	18	0.81 ± 0.02
	10 - 11	18	0	12	0.72 ± 0.03
	24 - 25	14	0	14	0.78 ± 0.01
	31 - 32	15	0	14	0.82 ± 0.01

* Females used in table 7.

TABLE 9 — Effect of mating and starvation, following parturition, on oöcyte development in *N. cinerea* and *L. maderae* that were fed during gestation

Treatment after parturition	Number of females used, per cent ovipositing, and days after parturition to oviposit (Mean ± S. E.)					
	N. cinerea			*L. maderae*		
	N	%	*Days*	*N*	%	*Days*
Starved						
Not mated§	180	100	9.2 ± 0.2	19	5**	—
Mated	71	78*	12.0 ± 0.3	17	0¶	—
Fed						
Not mated	145	94	8.5 ± 0.1	27	100	15.4 ± 0.3
Mated	48	100	10.3 ± 0.2	21	100	14.5 ± 0.3

§ Based mainly on females used in figure 15 that were exposed to males but did not mate.

* Females that did not oviposit were dissected 19 - 21 days after parturition. Three still retained their spermatophores and had oöcytes 0.92 ± 0.04 mm. long; eleven had extruded the spermatophores and their oöcytes were 1.98 ± 0.16 mm.

** The oöcytes of females that did not oviposit were 1.70 ± 0.22 mm. long, 21 - 31 days ($\bar{x} = 25$) after parturition.

¶ Females that did not oviposit were dissected 20 - 27 days ($\bar{x} = 24$) after parturition and mating. Eight still retained their spermatophores and had oöcytes 1.20 ± 0.06 mm. long; nine had dropped their spermatophores and their oöcytes were 2.01 ± 0.28 mm. long.

rition, in females fed during gestation, inhibits oöcyte development; mating does not result in oöcyte development in these starved *L. maderae* (table 9).

Effect of nutrition and mating, following parturition, on oöcyte development in females starved during gestation

The effect of exposing females, which were starved during gestation, to food for various periods of time following parturition is shown in table 10. If not mated, only 6 and 10% of the females oviposited when given food for 0 and 1 day. Mating similarly treated females did not increase the percentage ovipositing. When fed for 2 and 3 days, the number ovipositing increased to 22 and 39%, respectively, and mating further increased the number ovipositing to 53 and 69%. Mating had no effect on the percentage ovipositing after the females had access to food for 5 days; however, after this amount of feeding as high as 68% of the nonmated females oviposited. Seventy-one to 100% of the females oviposited if they were fed for 6 - 12+ days (table 10). The average time taken to oviposit was very similar in all the females that oviposited regardless of the length of time they had access to food. Also, the time taken to oviposit by the mated females was the same as the nonmated females only the percentage of females ovipositing differed in the groups fed for 2 and 3 days.

The oöcytes of the females that were starved after parturition and were not mated again averaged only 0.77 ± 0.02 mm. (13 of the 29 females were dissected). The oöcytes of the remaining 6 nonmated females, from all groups, which did not oviposit ranged from undeveloped to practically mature, the latter occurring in the small number of individuals that were fed for 8 - 10 days before being starved. Thirty-seven (41%) of the females had oöcytes that were less than 1 mm. long and lacked yolk. Twenty-eight (31%) had oöcytes in various stages of resorption.

The oöcytes of the 20 mated females that did not oviposit averaged 0.98 ± 0.08 mm. after they were starved continuously after parturition; all still retained their spermatophores when dissected. In the remaining groups, the 56 mated females that did not oviposit had oöcytes that varied considerably in size 25 days after parturition. Thirty-one (55%) still retained their spermatophores and their oöcytes averaged 1.19 ± 0.09 mm. The 25 females that had dropped their spermatophores had oöcytes that averaged 1.84 ± 0.13 mm. long. Forty-four nonmated females which were fed for 2, 3,

TABLE 10 — Effect of nutrition and mating, following parturition, on oöcyte development in *N. cinerea* that were starved during gestation

Days with food after parturition¶	Number used and per cent ovipositing		Days to oviposit after parturition**
	N	%	
0	31	6	13.5 ± 0.5
0 (M)	23	13	16.0 ± 0.6
1	21	10	15.0 ± 0.5
1 (M)	6	0	
2	23	22	16.8 ± 0.7
2 (M)	49	53	16.1 ± 0.5
3	31	39	16.4 ± 1.3
3 (M)	28	61	15.7 ± 0.5
5	25	68	17.1 ± 0.6
5 (M)	43	63	16.8 ± 0.6
6	24	71	15.4 ± 0.5
8	27	74	17.6 ± 0.8
10	32	91	16.9 ± 0.4
12	62	100	17.3 ± 0.4
12+§	215	99	15.5 ± 0.2
12+ (M)§	15	100	16.8 ± 0.6

¶ Food was Purina lab chow. (M) = mated on the day food was removed; all other females were not mated again after parturition.

** Time allowed for the females that were not fed after parturition was 13 - 20 days (not mated) and 16 - 22 days (mated). All other groups were given 25 days to oviposit after parturition at which time females that did not oviposit were dissected and their oöcytes were measured.

§ Fed until oviposition.

and 5 days (comparable to the mated groups) had oöcytes 1.23 ± 0.08 mm. long. The larger size of the oöcytes in mated females that dropped their spermatophores is indicative of a higher concentration of corpus allatum hormone than that found in the females that failed to drop their spermatophores or in those that were not mated.

The results show that when females are starved during gestation and not mated after parturition, exposure to food for at least 5 days is required for more than 60% of the individuals to oviposit. The stimulus afforded by mating has little or no effect on oöcyte development if the females are starved continuously, or if given food for only 1 day after parturition; the mating stimulus did increase the percentage of females that oviposited if the females were first fed for 2 or 3 days after parturition.

Effect of partial and complete starvation, and mating, on oöcyte development following removal of the oöthecae at different periods of gestation

Given an adequate diet during gestation and after parturition, an additional mating did not affect the rate of oöcyte development. If oöthecae were removed during gestation, the oöcytes matured prematurely. A series of experiments were performed to determine the effect, if any, of partial and complete starvation and mating on oöcyte development in *N. cinerea* after their oöthecae were removed at different periods in gestation. The results are shown in tables 11 and 12. Practically all females that were fed continuously oviposited. Mating increased the rate of oöcyte development, only in females whose oöthecae were removed 5 - 6 and 10 - 11 days after oviposition; mated females oviposited on an average of 3 or 4 days earlier than nonmated individuals. Partial starvation (those starved only after their oöthecae were removed) markedly reduced the number of nonmated females that oviposited. Virtually all females that were fed for 5 - 6 and 10 - 11 days only, and then had their oöthecae removed and were starved, failed to oviposit if they were not mated again. The percentage of ovipositing females that were starved after their oöthecae were removed 25 - 44 days after ovulation, was lower than those fed during the entire experiment. Partial starvation also slightly retarded the rate of oöcyte development (as indicated by time of oviposition) in females whose oöthecae were removed prior to parturition. Mating increased the percentage of females that oviposited in the 4 similar groups whose oöthecae were removed 5 - 32 days after oviposition. Of 110 females starved throughout the experiment, only 8 (7%) oviposited after their oöthecae were removed 5 - 32 days after oviposition. Of these 110 females, 24% (including the 8 that oviposited) had yolk in their oöcytes when dissected (table 12). Of the 46 females in the comparable mated group that were starved during the whole experimental period, 18 (39%) oviposited and an additional 16 females had yolk in their oöcytes; thus, 74% had yolk in their oöcytes after mating. Of the 28 females that did not oviposit, 16 (57%) still retained their spermatophores when dissected, indicating insufficient amount of corpus allatum hormone to affect the spermathecal glands whose secretion facilitates extrusion of the spermatophore (Engelmann, 1960a; Roth and Barth, 1964).

TABLE 11 — Effect of partial and complete inanition, and mating, on oöcyte development in *N. cinerea* following removal of the oöthecae at different periods of gestation

Days pregnant when oöthecae were removed	Number used and per cent ovipositing				Days (Mean ± S. E.) to oviposit after:		
					removing oötheca		
	Not mated		Mated*		Not mated	Mated	Mating
	Fed during entire experiment						
	N	%	*N*	%			
5-6	55	94	23	96	27.6 ± 0.4	23.0 ± 0.4	12.0 ± 0.3
10-11	43	100	26	100	23.4 ± 0.6	20.5 ± 0.3	11.0 ± 0.3
24-25	26	96	20	100	13.4 ± 0.2	13.8 ± 0.4	10.2 ± 0.2
31-32	48	100	18	100	12.1 ± 0.2	12.3 ± 0.2	9.8 ± 0.1
44-46 (NB)§	32	100	—		10.4 ± 0.4	—	—
	Fed until oöthecae were removed, then starved						
5-6	25	0	18	22	—	25.9 ± 1.5	16.9 ± 1.5
10	18	6	16	81	27	22.6 ± 0.6	13.9 ± 0.6
25-26	24	75	32	91	18.9 ± 0.4	16.3 ± 0.3	12.5 ± 0.3
31-32	28	57	25	76	15.7 ± 0.4	13.8 ± 0.4	11.7 ± 0.4
38-44	34	79	—		14.8 ± 0.6	—	—
44 (NB)§	12	100			10.7 ± 0.5	—	—
	Starved throughout experiment						
5-6	29	7	10	30	< 31 ¶	26.7 ± 1.7	18.2 ± 1.1
10-11	26	0	13	54	—	26.4 ± 1.4	16.9 ± 1.0
24-25	23	17	10	10	< 26 ¶	< 27 ¶	—
31-32	32	6	13	54	< 25 ¶	15.6 ± 0.4	12.5 ± 0.4

* After removing the oöthecae; all females had mated prior to the first oviposition.

§ (NB) = normal birth.

¶ Exact time unknown.

TABLE 12 — Oöcyte development in females of *N. cinerea* that did not oviposit*

Days pregnant when oöthecae were removed	Dissected - days after:		Length (mm.) of oöcytes (Mean ± S. E.)				Number of mated females with spermatophores:	
	removing oöthecae	mating	With yolk	N	Without yolk	N	in	out
		Fed until oöthecae were removed, then starved						
Not mated								
5-6	35	—	1.30 ± 0.25	3	0.82 ± 0.01	22		
10	30	—	1.35 ± 0.09	9	0.85 ± 0.02	8		
Mated								
5-6	30,33	13-23	2.14 ± 0.32	5	0.87 ± 0.02	9	7	7
			Starved throughout experiment					
Not mated								
5-6	31	—	1.25 ± 0.04	5	0.82 ± 0.01	22		
10-11	25	—	1.17 ± 0.02	3	0.78 ± 0.02	23		
25-26	24,26	—	1.11 ± 0.01	3	0.84 ± 0.02	16		
31-32	21,23	—	1.60 ± 0.24	7	0.83 ± 0.01	23		
Mated								
5-6	33-34	17-23	2.46 ± 0.67	4	0.87 ± 0.02	3	4	3
10-11	32	20-24	2.72	1	0.78 ± 0.02	5	4	2
25-26	27	19-24	1.95 ± 0.24	6	0.78 ± 0.00	3	6	3
31-32	20-22	13-20	2.35 ± 0.46	5	0.85	1	2	4

* Females used in table 11.

These experiments show that partial or complete starvation affected the resumption of oöcyte development when the oötheca was removed from the uterus at different periods in gestation. In partially fed females the effect was greatest (fewer females oviposited and developed yolk), the shorter the exposure to food (i.e., when the oöthecae were removed 5 - 6, or 10 days after oviposition and the females were then starved). In totally starved females the effect was about the same, regardless of when the oöthecae were removed; 0 - 17% oviposit. In both partially and completely starved females, mating had a stimulating effect and increased the percentage of females that oviposited and had yolk deposited in the oöcytes.

DISCUSSION

During gestation the female remains unreceptive, apparently because mechanical stimuli resulting from the oötheca in the uterus prevents the receptivity center from being reactivated. Thus, if the nerve cord is transected in a pregnant female, the inhibitory signals from the uterus are interrupted, the receptivity center becomes activated and after a few days the female mates again in spite of the fact that she is carrying an oötheca. The return of receptivity in females whose oöthecae are removed at different periods in gestation usually, but not always can be correlated with onset of corpus allatum activity, as indicated by yolk deposition in the oöcytes. However, *N. cinerea* mate even if they are allatectomized <6 hr. after emergence or have their inactive corpora allata removed during pregnancy; the latter females mate after parturition (Roth and Barth, 1964). Roth and Barth suggested that some event, possibly the release of neurosecretion, which occurs at about the same time as onset of corpus allatum activity, determines whether or not the female will accept the courting male.

Engelmann (1960b) observed that some females of *L. maderae* do not mate (but their oöcytes mature) even though they have access to males. He concluded from his observations that ". . . the corpus allatum hormone must be present in low titer to stimulate the responsiveness of the female. A high titer of the hormone has no effect since, from a total of 80 females, none mated that had oöcytes exceeding a size of 1.46 mm. Apparently as soon as a certain titer is surpassed, the female does not accept the male any more." Since in Engelmann's experiment the females had constant access to males, his conclusion that females will not mate when corpus allatum hormone is high is not warranted because these nonreceptive females did not mate even when their hormone concentration was low. In addition, virgin allatectomized *L. maderae* do mate if they are exposed to courting males (Roth and Barth, 1964); presumably the corpus allatum hormone concentration is very low or nonexistent in these females.

There may be a decided difference in oöcyte size at mating in *N. cinerea* during the first preoviposition period as compared with that following parturition. Although virgin females usually mate when their oöcytes first begin to show yolk deposition, they remain receptive (if isolated from males) even though their oöcytes continue to grow (Roth, 1964). This is also true in *L. maderae* (Roth and Stay, 1962b). Receptivity of females of *N. cinerea* following parturition differs in that those with well developed oöcytes at the time of parturition, or those isolated from males for 2 or more days after giving birth (and consequently have large oöcytes) are or become unreceptive. Virtually all females of *L. maderae* become receptive shortly after birth. In this species the oöcytes do not contain yolk at parturition (Roth and Stay, 1962b). However, *L. maderae* is similar to *N. cinerea* in that females usually become unreceptive if they are not given access to males a week after parturition. If, as suggested, neurosecretion is responsible for receptivity, it appears that the concentration of the hormone is critical only after parturition but not during the first precopulatory period (i.e., in the virgin female). Perhaps a high titer of neurosecretion does not inhibit receptivity in the virgin female but may prevent mating after parturition in once-mated females. It has already been shown in *N. cinerea* (Roth, 1964) that the effect of a particular reproductive stimulus may vary depending on the period in the reproductive cycle in which it occurs; for example, uterine stretching inhibits mating and oöcyte development after oviposition (i.e., during gestation) but is not effective when exerted during the first preoviposition period.

Ovariectomized virgin females of *N. cinerea* mate a few days after emergence but most of them do not become receptive again even 2 months after the initial mating; this is longer than the time required for normal gestation. In *Leucophaea* ovariectomy results in hypertrophy of the corpora allata and, as a result, the normal cyclical activity of the corpora allata (i.e., active during preoviposition and inactive during gestation) does not occur (von Harnack and Scharrer, 1956). The oötheca in the uterus is undoubtedly largely responsible for the cyclical activity of the corpora allata (Engelmann, 1957a, Roth and Stay, 1959, 1962b). It is possible that the neurosecretory system of the brain also continues to be active in ovariectomized females, and, if it controls receptivity it may explain our results with mated *N. cinerea* females whose ovaries were removed. Continued neurosecretory activity and the resulting high titer of hormone may tend to inhibit female receptivity for an abnormally long period. When oviposition is simulated by inserting glass tubes in the uteri of mated ovariectomized females and the inserts are removed after a few days, more females become receptive much more quickly than mated ovariectomized females that were not subjected to this treatment. Perhaps the insertion of the glass tubes resulted in stimuli that inhibited the neurosecretory system, thus preventing an increase in hormone titer. Upon removal of the artificial oötheca, the system is reactivated and the female mates. Thus, the results suggest that some center must first undergo a period of inactivity, induced by the oötheca in the uterus, for receptivity to return rapidly after parturition, or after removal of the egg case.

The hypothesis that a low concentration of a hormone activates and a high titer inhibits a receptivity center could also explain why some females are unreceptive after parturition. These would be the individuals whose neuroendocrine systems become active in late gestation. Theoretically, these females should have become receptive in late gestation since they would have gone through a period when their hormone titer was sufficiently low to induce receptivity. That they do not mate in late gestation may be explained by the mechanical stimulation, resulting from the oöthecae in the uteri, which suppresses mating behavior. That the same females do not mate even after parturition may be explained by assuming that the hormone titer has increased beyond the critical concentration necessary to induce receptivity. A high hormone titer would also explain why females become unreceptive after being isolated from males for several days after parturition. Nutrition may act as a "trigger" stimulus to the neuroendocrine system (de Wilde, 1961). This could account for the prolongation of receptivity when females are starved during gestation and after parturition; presumably the absence of nutritional stimuli prevents the accumulation of neurosecretion and its consequent inhibition of receptivity.

Females of *D. punctata* usually mate just after they emerge from the last nymphal skin, when they are still white and teneral. If isolated from males at emergence, the females tend not to mate (Stay and Roth, 1958). The mechanism governing this behavior is unknown. It cannot be correlated with increased activity of the corpora

TABLE 13 — Influence of mating and nutrition on oöcyte development during the first and second preoviposition periods

Treatment	Oöcyte Development				
	First preoviposition period*		Second preoviposition period**		
			Fed during gestation		Starved during gestation
	N. cinerea	*L. maderae*	*N. cinerea*	*L. maderae*	*N. cinerea*
Fed					
Not mated	Slow, incomplete or complete	Slow, incomplete or complete	Rapid	Rapid	Rapid
Mated	Rapid¶	Rapid	Rapid	Rapid	Rapid
Starved					
Not mated	Slight	None	Rapid	None	Usually none
Mated	Rapid	None	Rapid	None	Usually none

* From Roth (1964).

** All females were mated during the first oviposition period. Subsequent mating or non-mating (first column) refers to treatment after the females gave birth.

¶ Also means that the oöcytes mature and are oviposited.

allata since these endocrines remain inactive in most virgin females and the oöcytes fail to develop (Engelmann, 1959; Roth and Stay, 1961).

The influence of mating and nutrition on oöcyte development in most females during the first and second preoviposition periods is compared and summarized in table 13. If females of *L. maderae* are starved during the first preoviposition, their oöcytes fail to develop even if the individuals are mated. In virgin *N. cinerea* the oöcytes develop only slightly if the females are starved but mating results in sufficient stimulation (via the brain) of the corpora allata so that the oöcytes mature in about the same time as fed-mated controls. In fed females of both species, mating and feeding stimuli act synergistically to activate the corpora allata to their fullest extent so that the oöcytes mature at their maximum rate (Roth, 1964).

After parturition, the oöcytes in normally fed individuals of *N. cinerea and L. maderae* mature rapidly and mating does not increase the rate of maturation. The effect of starvation following parturition, in females fed during gestation, differs between the 2 species. In *N. cinerea* the oöcytes mature rapidly even though the females are starved and not mated again. In marked contrast, the oöcytes of *L. maderae* are inhibited after parturition if the females are starved and an additional mating does not affect this inhibition. In *N. cinerea* mating has a stimulating effect on oöcyte development if females are starved during gestation and are then given food for 2 and 3 days only, after parturition (table 10). However, mating has no effect if the females starved during gestation continue to be starved, or are given food for only one day after giving birth. These results are in accord with the hypothesis (Roth, 1964) that mating stimuli are effective in further stimulating the corpora allata only if the corpora allata have reached a certain level of activity, or if activating stimuli to the corpora allata have begun to occur as a result of nutritional factors. This hypothesis also would explain the results obtained when oöthecae were removed from the uteri at different periods of gestation and the females were then starved (table 11).

The corpora allata of cockroaches which incubate their eggs internally are inhibited during pregnancy and the oöcytes increase only in length and usually yolk is not deposited (Roth and Stay, 1962b). However, in *Diploptera punctata* (Eschscholtz) (Engelmann, 1959; Roth and Stay, 1961) and *N. cinerea* (Roth and Stay, 1962b), the corpora allata may become active a few days before parturition and yolk is deposited in the oöcytes while the female still has an oötheca in the uterus. Engelmann believed that in *L. maderae* inhibition of the corpora allata during pregnancy was due to a humoral factor from the eggs in the oötheca (Engelmann, 1957a, b), and mechanical stimulation of the genital apparatus by the egg case, plus a "nonspecific" substance from the uterine eggs (Engelmann, 1960a). More recently (Engelmann, 1964) he suggests that inhibition is caused by a specific or nonspecific agent released by the egg case or the brood sac; this agent acts on neurones in the ventral nerve cord and brain which influence regions in the brain that in turn inhibit the corpora allata. Roth and Stay (1959, 1961, 1962a, b) concluded that mechanical stimuli alone resulting from the stretched uterus could account for inhibition of the corpora allata during pregnancy.

The experimental inhibition of the corpus allatutm by introducing glass oöthecae in the uteri of *N. cinerea* and *P. surinamensis* does not support Engelmann's last hypothesis. Engelmann (1964) concluded from his observations on *L. maderae* that the insertion of an artificial oötheca into the uterus reduces the female's food intake. Since fasting or reduced food consumption inhibits the corpora allata and egg development, he questions the conclusion, based on the insertion of an artificial oötheca, that inhibition of the corpora allata by the oötheca is exclusively by a nervous pathway. Although this may be the case in *L. maderae,* the oöcytes in *P. surinamensis* that have wax oöthecae inserted in their uteri, mature after nerve cord transection (see figs. 13A, B, *in* Roth and Stay, 1962b) and do not mature if the nerve cord is intact. It is true that in most pregnant females of *N. cinerea* the oöcytes do not mature if their oöthecae are removed very early in gestation and the individuals are then starved (tables 11, 12). However, the oöcytes of females which have their oöthecae replaced by a glass tube <24 hr. after oviposition eventually develop almost to maturity like normal pregnant controls (fig. 3); this would not have occurred if the glass oöthecae had prevented feeding. The lack of oöcyte development during pregnancy in *N. cinerea* and *P. surinamensis* can be explained by the hypothesis that mechanical stimulation alone, resulting from the presence of the oötheca in the uterus, inhibits the corpora allata.

Roth and Stay (1962a, b) have suggested that pressure changes resulting from the increasing size of the oötheca in the uterus tend to prevent or retard adaptation of mechanoreceptors, or the central nervous system, so that the corpora allata are inhibited during most of the gestation period. In *Blaberus craniifer* Burmeister, *Byrsotria* *fumigata* (Guérin) and the bisexual strain of *Pycnoscelus surinamensis* with unfertilized eggs in the uterus, the oötheca does not increase markedly in size because the eggs do not develop, inhibition of the corpora allata ceases prematurely, and consequently the oöcytes develop in spite of the presence of the egg case (Roth and Stay, 1962b). The earlier return of corpora allata activity in some females of *N. cinerea* with glass tubes in the uteri (figs. 3, 4) may be due to the fact that there is no change in size of the uterus. A glass oötheca might be likened to the presence of unfertilized eggs in the brood sac. In both strains of *P. surinamensis* the glass rods were more effective inhibitors than the beads. Perhaps the shape of the insert, in this species, influences the degree of inhibition; the shape of a glass rod is more like an oötheca than is a bead.

During normal pregnancy, the length of time the corpora allata are inhibited differs between *P. surinamensis* and *N. cinerea.* Inhibition frequently ceases shortly before parturition in *N. cinerea* and only after parturition in *P. surinamensis.* The species difference might account for the greater effectiveness of glass rods in inhibiting the corpora allata in *P. surinamensis.*

SUMMARY

During gestation in *N. cinerea* the mechanical presence of the oötheca inhibits sexual receptivity. The prerequisites for the return of receptivity in the normal period of time, after oviposition or parturition, are: 1) the presence of an oötheca (i.e., uterine stretching for at least a short period, and then 2) the removal of the oötheca (i.e., the stretch stimuli).

Return of receptivity can usually be correlated with the beginning of yolk deposition in the oöcytes. But the corpora allata do not control receptivity since allatectomized females mate. As shown for the first preoviposition period, return of receptivity after parturition is correlated with some event that occurs at about the same time as onset of corpus allatum activity. Some center, perhaps affected by the neurosecretory system in the brain, controls receptivity by controlling the response of the female to the male's pheromone.

Females of *N. cinerea* which mate after giving birth have small oöcytes; females which do not mate have large oöcytes. After parturition, in *N. cinerea* and *L. maderae,* the oöcytes mature rapidly, and the females become unreceptive, if they are isolated from males for several days. The data suggest that a high hormone (neurosecretion?) titer, after parturition, may inhibit receptivity.

Given an adequate diet during gestation and after parturition, an additional mating does not increase the rate of oöcyte development in *N. cinerea* and *L. maderae.* The oöcytes of pregnant females of *N. cinerea* starved during and after gestation, usually do not develop after parturition. Mating increases the percentage of females which mature their oöcytes if *N. cinerea* females that were starved during gestation are first fed for 2 or 3 days after giving birth. The combined effects of mating and nutrition on oöcyte development are in agreement with the hypothesis that mating is effective in stimulating the corpora allata only if these endocrine glands have first reached a critical level of activity.

During pregnancy, mechanical stimuli resulting from the oötheca in the uterus inhibit the corpora allata and consequently the oöcytes remain undeveloped for almost the entire *(N. cinerea)* or entire *(P. surinamensis)* gestation periods.

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

The illustration on the front cover of this issue of Psyche is a reproduction of a drawing of a myrmecophilous histerid beetle, *Euxenister wheeleri* Mann, from Barro Colorado Island (Psyche, vol. 32, p. 173, 1925).

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