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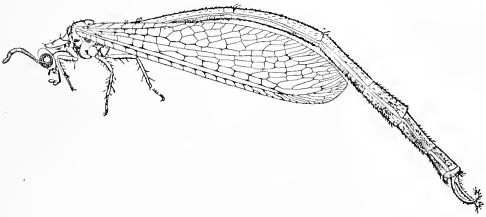

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PSYCHE

Vol. 76 March, 1969 No. 1

A REVIEW OF THE SPECIES OF *SCARITES (ANTILLISCARIS)*, (COLEOPTERA: CARABIDAE) WITH NOTES ON THEIR MORPHOLOGY AND EVOLUTION

By T. F. Hlavac[1]

Museum of Comparative Zoology, Harvard University

Recently, through the courtesy of Prof. R. A. Howard, Director of the Arnold Arboretum at Harvard University, the Museum of Comparative Zoology received a shipment of Coleoptera from the Luquillo Mountains of Puerto Rico, collected on "W. Peak" by R. A. McClain. Included in this material was a single specimen of the largest carabid in the Greater Antilles, representing a new species of *Scarites (Antilliscaris)*, 35 mm in length. This behemoth is superficially different from but shares a unique set of characters with two known species of the subgenus from the mountains of Puerto Rico. The presence in the depauperate Puerto Rican montane carabid fauna of three species of *Scarites* raises questions about the ecology and evolution of these beetles. These questions have been approached through study of the comparative functional morphology of *S. (Antilliscaris)* and other *Scarites* subgenera and through preliminary observations and experiments on one adult collected during a recent trip to Puerto Rico.

Banninger (1949, p. 146) proposed the subgenus *Antilliscaris* for *Scarites darlingtoni* Banninger, *S. mutchleri* Banninger (both orig-

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[1] I wish to thank Dr. P. J. Darlington, Jr., for suggesting this study, for advice and encouragement during its progress and for reading the manuscript. I am grateful to Dr. John F. Lawrence for reading the manuscript and for many helpful suggestions. Field facilities at the El Yunque Biological Station of the University of Puerto Rico were provided through the courtesy of Dr. Eric G. Matthews.

Field work on Puerto Rico was supported by NSF Grant GB 7346 to the Committee on Evolutionary Biology of the Department of Biology at Harvard University.

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

inally considered to be of uncertain systematic position, 1939, p. 148) and for *S. danforthi* Darlington. Banninger incorporated the new subgenus into his earlier key to the subgenera of *Scarites* (1937, pp. 123-128) and provided a key to separate the species.

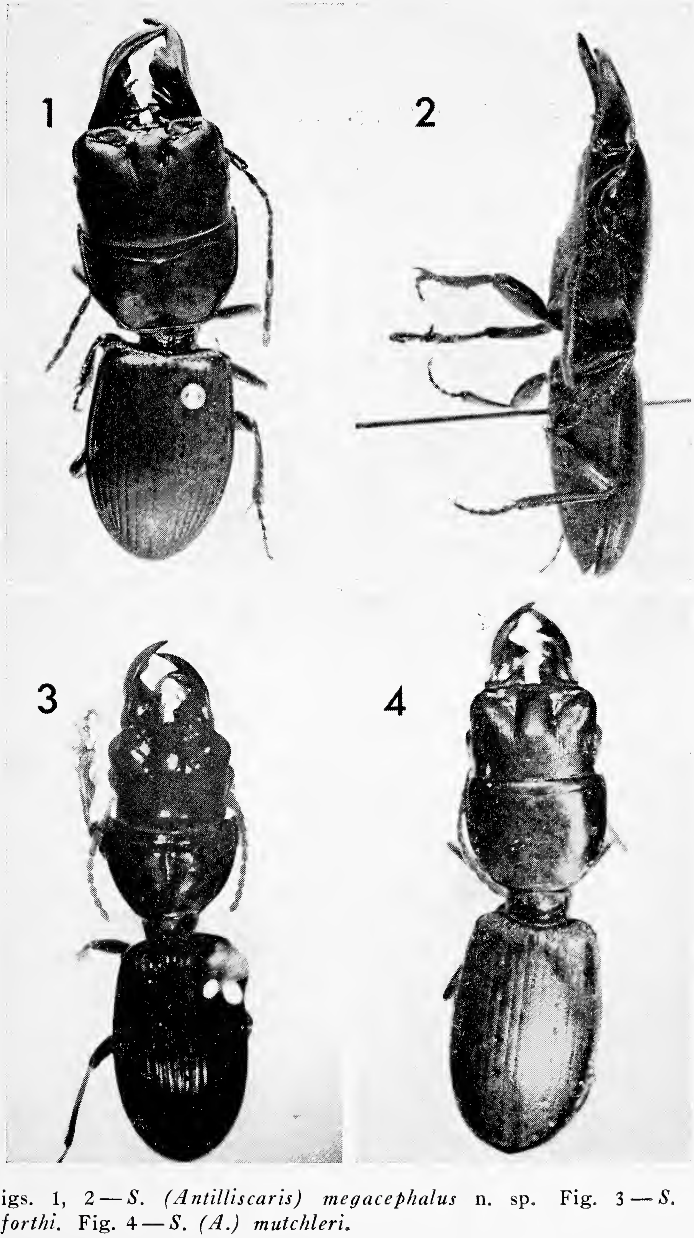
Scarites subgenus *Antilliscaris* Banninger 1949, p. 136

Diagnosis: head: large, 37-59% of length of elytra. *Mandibles:* median carnassal regions large, basal molar area small with complex of interdigitating cusps, dorsal surface smooth. *Eyes:* small, height 30-50% of height of mandible. *Antennae:* long to very long for a *Scarites*, segment 4 similar to apical segments, dorsal and ventral setose areas with rough microsculpture and pair of narrow lateral glabrous regions without setae, sides flattened but not as distinctly as in segments 5-11. Segment 3 circular in cross section with apical ring of setae as well as a number on the apical 2/3 of the dorsal surface and a few setae, including some very large ones on the ventral surface (Fig. 13). Frontal plate grooved. *Pterothorax:* metasternum and metepisternum short, L/W of episternum 0.87-1.3, elytra fused together and to mesanotum, wings reduced, shorter than metanotum in *mutchleri*. Lateral edge of mesotibia with one large spine. *Metepimeron:* slender, pleural suture very faint externally; epimeron-elytra interlocking mechanism absent.

Distribution: montane rain forests of Puerto Rico.

Key to the species of *S. (Antilliscaris)* and to *S.* (?) *darlingtoni* Banninger

1. Mandibles with series of striations on dorsal surface (Fig. 7) .... *darlingtoni*
1′ Mandibles: dorsal surface smooth (Figs. 6, 10, 11) 2
2. Elytral intervals 1, 3, 5 and 7 with setiferous punctures. Dorsal surface of head with 15 setiferous punctures. Antennae short, extending about to posterior border of prothorax, L/W of segments 6-10 less than 1.1 (Fig. 8) .... *danforthi*
2′ Only elytral interval 3 with setiferous punctures. Dorsal surface of head with 6 or fewer setiferous punctures 3
3. Antennae extending to mesocoxae, L/W of segments 6-10 between 1.3 and 1.6 (Fig. 9). Slight impression at posterior end of scrobe. Lateral margin of pronotum with 5-6 pairs of setiferous punctures, L/W 0.80. Total length 12-18 mm .... *mutchleri*
3′ Antennae extending to first abdominal sternite, L/W of segments 6-10 between 1.8 and 2.3 (Figs. 11, 12). Deep pit at posterior end of scrobe. Lateral margin of pronotum with 3 pairs of seti-



Figs. 1, 2 — *S. (Antilliscaris) megacephalus* n. sp. Fig. 3 — *S. (A.) danforthi*. Fig. 4 — *S. (A.) mutchleri*.

ferous punctures, L/W 0.54. Total length 30-35 mm. .... *megacephalus* n. sp.

Scarites (Antilliscaris) mutchleri Banninger

Scarites mutchleri Banninger 1939, p. 149, replacement name for *montanus* Mutchler 1934, not *montanus* Banninger, 1932.

Scarites montanus Mutchler 1934, p. 1.

Type: American Museum of Natural History, seen; type locality: Puerto Rico, Luquillo Mtns., El Yunque, 1800 ft.

Description (diagnostic characters only). With the characteristics of the subgenus *Antilliscaris*. Forms as in Fig. 4. *Head:* antennae long, extending to about middle of peduncle, apical segments intermediate between *danforthi* and *megacephalus*, L/W of segments 4-10 between 1.3 and 1.9 (Fig. 9). *Vertex:* 3 pair of setae, clypeal, supraorbital and a pair halfway between the two and closer together than either. Lateroclypeus and antero-lateral halves of vertex with a series of irregular striations. Without a large depression behind the eye and a deep pit at the posterior end of scrobe. *Prothorax:* lateral grooves narrow but distinct with 5 or 7 pairs of setiferous punctures, posterior angles small. *Sternum:* 6-8 setiferous punctures clustered in front of the intercoxal spine, the latter with 6-8 setae. *Elytra:* surface dull, anterior margin with dense band of coarse tubercles in addition to the tubercles associated with setiferous punctures. *Lateral groove:* dense concentration of tubercles, 7-8 setiferous punctures on third interval. Striae lightly impressed. *Pterothorax:* mesasternum, 2 setiferous punctures; metasternum 6-7 setiferous punctures. *Abdomen:* 1st and 2nd intersegmental sutures normal.

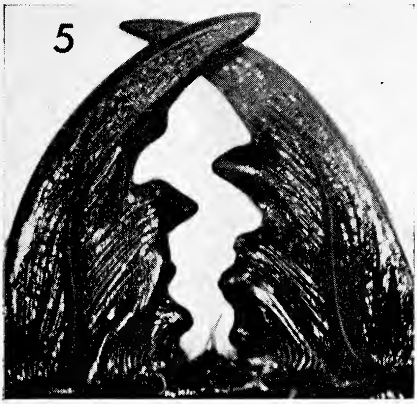
Measurements. Head: length 2.7-3.1 mm, width 3.6-4.0, length/width 0.75-0.77. *Mandible:* length 2.3-3.0. *Prothorax:* length 3.1-3.5, width 4.0-4.6, length/width 0.77-0.76. *Elytra:* length 6.9-7.9, width 4.2-4.8, length/width 1.64-1.64. Total length (including peduncle) 15.4-18.0 mm. *Measurements reported:* extremes in total length of the four specimens measured. *Specimens examined:* holotype and three others (M.C.Z.). A specimen, currently alive, about 12 mm in total length, has not been examined critically.

Distribution: El Yunque, 1800 ft. to summit (3493 ft.).

Larva: Three presumably second instar *Scarites* were collected on El Yunque, one in a decayed log in cloud forest c. 2200 ft., and two others under rocks along a forest trail c. 3200 ft. Based on size (head capsule of preserved larve 1.9 mm wide) these larvae are probably *mutchleri.*

Scarites (Antilliscaris) megacephalus n. sp.

Holotype: a male M.C.Z. No. 31710. *Type locality:* Puerto



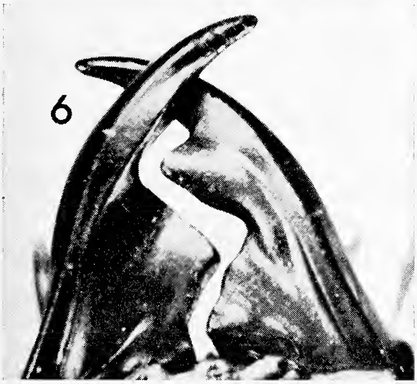


Fig. 5 — Mandibles, *S. (s. s.) substriatus.* Fig. 6 — Mandibles, *S. (A.) mutchleri.* Fig. 7 — Mandibles, *S.* (?) *darlingtoni.* Fig. 8 — Antennal apex, *S. (A.) danforthi.* Fig. 9 — Antennal apex, *S. (A.) mutchleri.*

Rico, Luquillo Mountains, top of West Peak, 3447 ft., May or June 1968, W. C. McClain Coll. *Paratype:* M.C.Z.; Sex ?, El Yunque *c.* 3200 ft., Feb. 1969, L. H. Herman Jr., B. C. and T. F. Hlavac collectors. This fragmented specimen, missing the antennal flagella, maxillae, several legs and the apical abdominal segments, was collected dead under a stone along a forest trail.

Description (diagnostic characters only). With the characteristics of the subgenus *Antilliscaris* (form as in Figs. 1, 2). *Head:* very large as compared to the relatively squat pronotum and elytra. Antennae very long, extend to first abdominal sternite, length/width of segments 4-10 between 1.8-2.3 (Fig. 12). *Vertex:* pair of clypeal and supraorbital setiferous punctures. With a deep, broad depression behind the eye and a deep puncture at the posterior end of the scrobe. Lateroclypeus and antero-lateral halves of vertex with series of irregular situations. *Prothorax:* lateral grooves narrow but distinct with 3 pairs of setiferous punctures (4 on left side of paratype). Sternum without setiferous punctures, intercoxal spine with 12. *Elytra:* surface dull. *Anterior:* margin with small number of minute tubercles about 1/3 the width of those associated with punctures; 1 pair of setiferous punctures in third interval, striae strongly impressed. Mesasternum with 2 setiferous punctures, metasternum with 4. *Abdomen:* lateral portions of 1st and 2nd intersegmental sutures broadened and deepened to form a large fossa, sutures separating other segments slightly enlarged laterally.

Measurments of holotype and paratype: Head: length 7.5-7.1 mm, width 9.5-7.2 length/width 0.79-0.98; *Mandible:* length 7.0-5.7; *Prothorax:* length 5.5-5.0, width 10.1-8.1, length/width 0.54-0.62; *Elytra:* length 13.0-12.5, width 9.3-7.9, length/width 1.4-1.58; *Total length (including peduncle):* 35-30 mm.

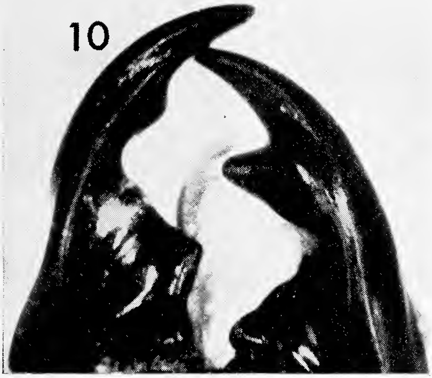
Distribution: known only from the type series.

Scarites (Antilliscaris) danforthi Darlington

Scarites danforthi Darlington 1939, p. 80.

Type: M.C.Z. No. 23,501 seen; type locality: Puerto Rico, Maricao forest, *c.* 3000 ft.

Description (diagnostic characters only). With the characteristics of the subgenus *Antilliscaris*, form as in Fig. 3. *Head:* antennae, relatively short, extend to posterior margin of prothorax, apical segments squat, L/W of segments 4-10 less than 1.1 (Fig. 8). Vertex with 15 setiferous punctures including 2 pair of supraorbitals. Lateroclypeus and anterolateral halves of vertex without series of irregular situations. Without a large depression behind eye and deep pit at posterior end of scrobe. *Prothorax:* lateral groove indistinct near



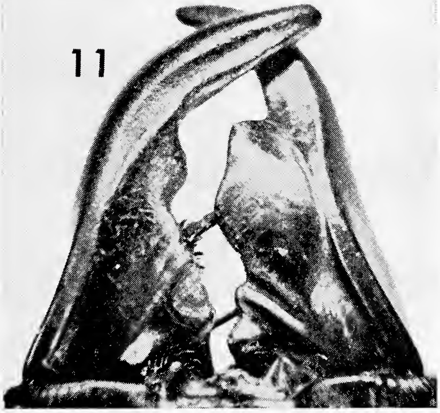


Fig. 10 — Mandibles, *S. (A.) danforthi*
Fig. 11 — Mandibles, *S. (A.) megacephalus* n. sp.
Fig. 12 — Antennal apex, *S. (A.) megacephalus* n. sp.
Fig. 13 — Antennal segments 3, 4, 5, *S. (A.) megacephalus* n. sp.

middle, with 5 pairs of setiferous punctures, posterior angles very small. *Sternum:* about 20 setiferous punctures clustered about the midline, intercoxal spine with 10-12 setiferous punctures. *Elytra:* surface shiny. *Anterior margin:* small number of minute tubercles 1/3 the width of the tubercles associated with setiferous punctures, 4 or 5 setiferous punctures in first interval, 7 or 8 in third, 6, 7, or 8 in fifth, and 5, 6, or 7 in seventh, striae lightly impressed. *Pterothorax:* mesasternum 8 setiferous punctures, metasternum 6 setiferous punctures. *Abdomen:* lateral parts of 1st and 2nd intersegmental sutures broadened and deepened to form a large fossa, other sutures enlarged laterally.

Measurements of holotype and paratype. Head: length 2.5-3.0 mm, width 3.1-3.5, length/width 0.81-0.86. *Mandibles:* 2.2-2.6. *Prothorax:* length 2.7-3.0, width 3.9-4.0, length/width 0.69-0.67. *Elytra:* length 6.7-6.7, width 4.0-4.0, length/width 1.68-1.68. Total length (including peduncle) 14.6-16.0.

Distribution: known only from the type series.

Scarites (subgenus?) *darlingtoni* Banninger

Scarites darlingtoni Bann. 1935, p. 159.
Scarites (Antilliscaris) darlingtoni Bann. 1949, p. 137.
Type: M.C.Z. No. 21,797, seen. Type locality: N. Haiti, Mt. Basil, *c.* 4700 ft.

Description (diagnostic characters only). *Head:* large, 43% of the length of the elytra. Mandibles (Fig. 7) heavily worn in type, with striate dorsal surface and relatively small molar area. *Eyes:* 50% of the height of the mandible. *Antennae:* absent in type. Lateroclypeus and antero-lateral halves of vertex with series of irregular striations. *Vertex:* pair of clypeal and supraorbital setiferous punctures. Without depression behind eye and large puncture at posterior end of scrobe. *Prothorax:* lateral grooves distinct with 7 or 8 setiferous punctures. *Sternum:* without setiferous punctures but with 17 on intercoxal spine. *Elytra:* surface polished. Anterior margin with small number of tubercles about 1/3 the width of those associated with punctures. Lateral groove rugose. 8 setiferous punctures in third interval, striae impressed. *Pterothorax:* reduced, elytra fused together and to mesanotum, wings shorter than the metanotum. Metepisternum and metepimeron absent in type, L/W about 1. Mesasternum without setae and metasternum with 6. *Abdomen:* intersegmental sutures normal.

Measurements of holotype: Head: length 4.0 mm, width 5.1, length/width 0.78. *Mandible:* length 3.0. *Prothorax:* length 4.0, width 5.6, length/width 0.72. *Elytra:* length 9.5, width 6.3, length/

width 1.50. Total length (including peduncle) 21.8. *Specimen examined:* holotype.

Comments: known from the appendageless fragments of two specimens. I regard it as of uncertain subgeneric position for three reasons. The structures containing the major diagnostic characters of *Antilliscaris,* antennae and metepimeron, are absent in the available material. A major similarity between *Antilliscaris* and *darlingtoni* is the reduction of the flight mechanism. Flightlessness and, *in extenso,* large-scale reorganization of the flight mechanism occur with high frequency among montane carabids (Darlington 1943), which argues against uniting *darlingtoni* with *Antilliscaris* in the absence of other evidence. Furthermore, there is a gap between *Antilliscaris* and *darlingtoni* in the dorsal surface of the mandibles (Figs. 5, 6, 7, 10, 11).

DISCUSSION

Several character states in *Antilliscaris* range from atypical to unique for a *Scarites s. l.* Many of these differences are found in the locomotory system or are peripheral to it. This raises questions about associated behavioral and ecological differences. In an attempt to list some of the possible answers to these questions, particular configurations of *Antilliscaris* are contrasted with *S. (s. s.) substriatus* Haldemann and *subterraneus* Fabricius. This is not done because I feel that these 2 species are closely related to *Antilliscaris,* but because both fly and burrow (Hlavac, 1967) and can be used as a base line in interpreting the morphology of *Antilliscaris.*

ANTENNAE: The antennae of *Antilliscaris* are unusual in three respects: in length, in the setation of the 4th segment and in the relative narrowness of the lateral glabrous areas. An increase in the size of the antennae can be documented in terms of elongation of individual segments, as expressed by length/width, and in terms of increase relative to body size. The ranges of length/width of segments 6-10 is 0.9-1.1 in *danforthi,* 1.35-1.55 in *substriatus,* 1.3-1.6 in *mutchleri,* and 1.8-2.3 in *megacephalus.* The antennae reach the procoxae in *substriatus,* the posterior margin of the prothorax in *danforthi,* and middle of the peduncle in *mutchleri* and the first abdominal sternite in *megacephalus.* As compared to *substriatus,* the antennae of *danforthi* are longer and the individual apical segments are much wider. Assuming that there are no major differences between the relative widths of the first segment in the above species, then a measure of width of the antennal apex can be expressed as width of an apical segment/width of segment 1. Using width of the 8th segment in this ratio, the figures are 0.72 for *substriatus* and *megacephalus,* 0.93 for *mutchleri* and 1.1 for *danforthi.*

To summarize, the antennae of all *Antilliscaris* are longer than *substriatus*. The apical segments are broad in *danforthi*, elongate in *megacephalus*, with *mutchleri* and *substriatus* intermediate.

In *substriatus*, 28% of the antennae extends beyond the mandible. When burrowing the antennae are held agaist the head wall causing the apical segments to curve in a broad U. In *megacephalus* 50% of the antennae extends beyond the mandible. If this species burrows the antennae would be doubled over while the animal is working. Short antennae are characteristic of the many diverse taxa of burrowing Coleoptera which have independently evolved a pedunculate body form. The long antennae of *Antilliscaris* and particularly *megacephalus* strongly suggests that these beetles do not burrow.

Captive *substriatus* and *subterraneus* and many geophilious carabids apparently do not react visually to prey; olfactory and/or tactile reactions have been observed upon physical contact. While patrolling a burrow system, the antennae of *subterraneus* are held parallel to the long axis; the maximum sweep width is limited by the diameter of the burrow. On the surface, they are held approximately 45° from the long axis. If only short range olfactory and tactile stimuli are used to recognize prey, then finding it will be a function of the distance travelled and the width of the band through which the sensory equipment move. On the surface, long antennae are clearly adaptive in increasing the width of the search band, and may partially explain the condition in *Antilliscaris*.

There is a gap in the setation and microsculpture of the first 4 segments as contrasted to segments 5-11 in all subgenera except *Antilliscaris* and *Typhloscaris* from the mountains of E. Africa. In most subgenera, segments 1-4 have few or no setae and are circular in cross section, while segments 5-11 are flattened laterally and have a dense covering of setae and rough microsculpture except for a glabrous, asetose median stripe. Segment 4 of *Antilliscaris* is intermediate in shape between segments 3 and 5 and has the surface organization of the apical segments.

The surface of the apical segments is divided into two distinct structural and, probably, functional areas. As seen in lateral view, a pair of setose bands with rough microsculpture extend along the dorsum and venter of the apical segments; they are united near the distal end of the 11th segment (Figs. 8, 9, 12). Between the setose bands is an asetose median band with smooth microsculpture. Members of the genus *Scarites* differ widely in the distribution of these two surface types; in *S. (Antilliscaris)* the median band is 25-30% of the width, but 55% in *substriatus*.

The elongate and/or broad apical segments and the state of the 4th segment in *Antilliscaris* represent an increase in surface area of antennal apex over *substriatus*. Due to differences in distribution of surface types, there is a large increase in setose areas, which can be interpreted as an intensification of the functions served by this region.

EYES: The eyes of *Antilliscaris* are small, 30-50% the height of the mandible, vs. 100% in *substriatus*, and are nearly circular except in *danforthi* where the posterior border is nearly straight. Smith (1964, p. 116) stated that the eyes of flightless carabids are not reduced, except for cave inhabiting species; this is clearly not the case for montane *Scarites* or for the montane carabid fauna of New Guinea (P. J. Darlington Jr., personal communication). Eye reduction in *Scarites* seems to have come about either from a reduction in diameter *(Antilliscaris)* or from diameter reduction and shortening the anterior posterior axis, giving the eyes of *S. (Typhloscaris)* and *S. (Taeniolobus) cubanae* Banninger a peculiar slit-like appearance.

MANDIBLES: The mandibles of scaritine carabids are structurally complex and can be divided into three functional regions, an apical and 2 medial carnassal areas and a basal molar part. *Antilliscaris* and *Scarites s. s.* represent extremes in the relative sizes of the latter 2 of these areas (Figs. 14, 15). In an unworn specimen of *substriatus* (Fig. 5) the apical carnassal is 34%, the median carnassals 26% and the molar 40% of the total length (perpendicular distance between apex and base); while in *Antilliscaris* (Figs. 6, 10, 11) the apical carnassal ranges from 24-34% the median carnassals from

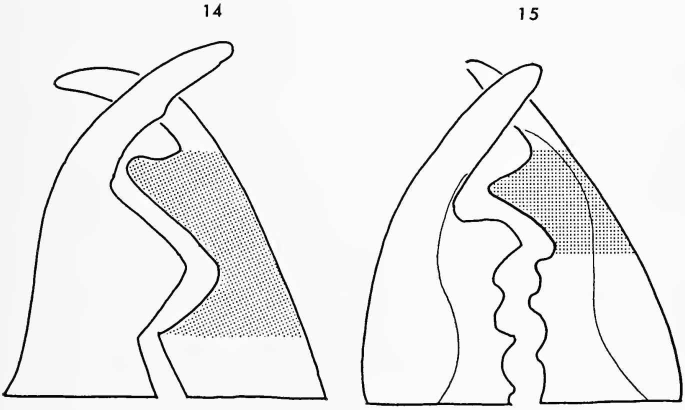


Fig. 14. — Mandibles, *S. (Antilliscaris)*. Fig. 15 — Mandibles, *S. (s. s.)*. Medial carnassal areas shaded.

45-59% and the basal molar part ranges from 17-21% of the total length. In *Antilliscaris* then, the median caranassals are twice as large and the molar area half the relative size of the corresponding areas of *substriatus.*

If it can be assumed that these structural differences correlate with behavioral differences, then the condition in *Antilliscaris* may reflect 3 types of such differences. The mandibles of *substriatus* and *subterraneus* are used to loosen material from the head wall of the burrow, in mating and, of course, in feeding. Some substrate loosened by the protibia is compressed further and compacted into a part of the stable burrow system by the vertex of the head and pronotum (Hlavac, 1967, and unpublished observations). The smaller molar area in *Antilliscaris* could indicate either that these animals burrow through a less dense, more easily compacted, substrate than *Scarites s. s.* or that they do not burrow at all. Secondly, the differences in mandible morphology may reflect differences in feeding behavior (see comments on body form, below) or mating.

FLIGHT MECHANISM: *Antilliscaris* represents an extreme point in the atrophy of the flight mechanism. The fused elytra are immovably joined to the mesathorax at two points, the posterior part of the mesatergum is tucked around and closely pressed against the anterior contours of the elytral cavity and secondly, the elytral hinge mechanism is solidly fused to the anterior part of the mesatergum.

The volume enclosed by the metathorax is reduced; externally, this is seen most clearly by comparing the relative size of the lateral portion of the sternum and the L/W ratio of the episternum in flying and wingless species. In *substriatus* the narrowest lateral part of the sternum is about half the mid-line length and the L/W of the episternum is about 4, whereas in *mutchleri* the lateral portion is 20% of the mid-line length and the L/W of the episternum is about 1. The central part of the sternum is also shortened in *Antilliscaris* but less dramatically; the mid-line in *substriatus* is equal to the length of tthe first 3 1/2 abdominal sternites while in *mutchleri* it is equal to the length of the first 2 2/3 abdominal segments. The vestigial wings of *mutchleri* are very small (.375 × .100 mm) and circular in cross section in a specimen examined in fluid.

In the Scaritini there are usually 3 lateral elytra-thorax and abdomen interlocking mechanisms. (Hlavac, unpublished observations.) The anterior lateral edges of the elytra fit into grooves on the dorsal rim of the mesepisternum, mesepimeron and metepisternum (Fig. 17). The dorsal part of the metepimeron slopes inwards; the elytra curve slightly outwards at this point and rest on top of the flat surface of the epimeron. An internal elytral carina extends from just behind the level of the epimeron to the elytral apex and is enlarged posteriorly forming the internal plica. The carina rests against the edge of the infolded abdominal sternites.

Antilliscaris differs from all other subgenera of *Scarites* examined, including many flightless species, in that the dorsal part of the metepimeron is in the same plane as the episternum and the dorsal groove extends along the epimeron, i. e. the elytra-epimeron interlocking mechanism is absent, becoming part of the elytra-episternum device (Fig. 18).

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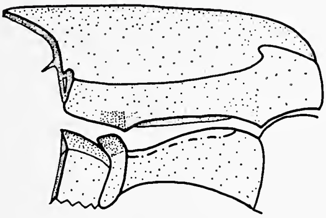

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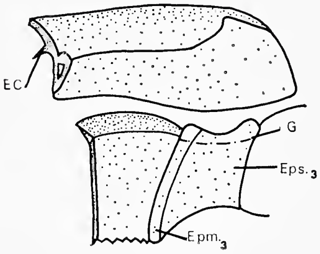

Fig. 16 — Elytra-metathorax interlocking mechanism *S. (s. s.) substriatus*

Fig. 17 — Elytra-metathorax interlocking mechanism, *S. (Antilliscaris)* (EC, internal carina of elytra; Epm$_3$, metepimeron; Eps$_3$, metepisternum; G, metapleural groove)

In burrowing and substrate dwelling Coleoptera, the elytral interlocking mechanisms maintain the structural integrity of the elytra-body joint against the forces generated in moving through a dense material. Lack of an integral portion of this mechanism in *Antilliscaris* can be explained in two, non-mutually exclusive manners. If the ancestral stock were not a highly adapted burrower (see below), then loss of epimeron-elytra joint could be due to neutral selection pressure for structural integrity. Or, secondly, after becoming flightless, the primary interlocking mechanism becomes the fusion of the elytra to each other and to the mesothorax; loss of epimeron-elytra joint represents post-adaptational adjustment; there is no need to assume a change in selection pressure for structural integrity.

BODY FORM: *S. (A.) megacephalus* and *S. (s. s.)* substriatus represent extremes in body proportions with *mutchleri* and *danforthi* intermediate. The outline of *megacephalus* can be derived from that of *substriatus* by shortening the pterothorax and abdomen (Elytra L/W from 1.8 to 1.4 in *S.* and *A.* respectively) and the prothorax

(L/W from 0.7 to 0.5) and by increasing the size of the head until it is 1.36 the length of the prothorax (0.82 in *substriatus*) and until the length of head and mandibles is 1.1 the length of the elytra (0.6 in *substriatus*).

A partial explanation of the shortening of the elytra is the atrophy of the flight mechanism. Differences in size between the head and prothorax can be looked at in terms of differences in muscle volume, i. e., a relative decrease in volume in the prothorax and a relative increase in the head. The prothorax houses most of the muscle volume responsible for its movement as well as that which moves the head and proleg (Larsen, 1966, p. 140), while the head encloses muscles responsible for the movement of its appendages. Ventrodorsal rotation of the head and prothorax are principal actions in burrowing, decrease in muscle volume for performing these actions indicates a shift in or absence of burrowing behavior. The large head implies a large mandibular adductor muscle and this along with the large carnassal areas of the mandibles could be an adaptation for seizing and breaking open large prey objects.

ECOLOGICAL SHIFT: Of the eight known montane species of carabids on Puerto Rico listed below, three are *Scarites*, and, with *Oxydrepanus coamensis* Mutchler, scaritines make up 50% of the known carabid fauna. On Jamaica, an island of similar size (4500 sq. mi. vs. 3400 for P. R.) 17 montane restricted species are known, nine of which are *Colpodes*; there are no *Scarites* (Darlington, 1941). As currently known, the montane biota of Puerto Rico is unique in the Greater Antilles in not having a large number of ecologically variable *Colpodes*. The size range of Puerto Rican species is 2.0 to 35 mm with the following distribution:

1-5 mm, 4 spp.,	*Oxydrepanus coamensis* Mutchler, 2 mm;
	Bembidion portoricense Darlington, 3.5 mm;
	Perigona microps Darlington, 2.9 mm;
	Phloeoxena portoricensis Darlington, 4.5 mm.
5-10 mm, 1 sp.,	*Colpodes estriatus* Darlington, 4.0-6.7 mm.
10-20 mm, 2 spp.,	*Antilliscaris danforthi*, 14.6-16.0 mm;
	Antilliscaris mutchleri, 12.0-18.0.
30+ mm,	*S. (A.) megacephalus*, 30-35 mm.

Antilliscaris is thus the largest carabid taxon, is at the apex of the size pyramid and is doubtless one of the top predators among ground invertebrates in this habitat.

It is useful to look at the mountains of Puerto Rico as habitat islands and to analyze the large *Scarites* fauna in the manner of MacArthur and Wilson (1967). In harmonic continental biotas, the large number of carabid species occupy three locomotory adaptive zones: arboreal (several tribes), ground in the broadest sense including soil surface and leaf litter (most tribes and species) and burrowing (primarily the Scaritini). All terrestrial zones available to a beetle are exploited by the Carabidae. Breadth of adaptation for the family and high local diversity (see Darlington 1943 for data) is the result of adaptive radiation and species packing via competition. The energetics of food searching differs between the zones. If the energy expended by a ground species in searching a unit area is taken a base point, then both arboreal forms, which fly and climb vertical surfaces, and burrowers producing a new section of burrow expend more. In the absence of competition from related taxa, as in the mountains of Puerto Rico for a large carabid, if ecological shift occurs in a new colonizer it should be in the direction of increased efficiency of search behavior.

The burrowing mechanism of Scaritine carabids consists of many interrelated morphological and behavioral adaptations. Evidence that several structures and proportions differ from a known burrow producer is presented above and can be interpreted as indicating a reorganization of the burrowing mechansm for a ground surface existence.

The steps taken by a species after colonizing a depauperate habitat island are: initial adaptation, ecological shift, loss of dispersal power, speciation, and adaptive radiation (MacArthur and Wilson 1967, Chap. 7). Speciation and loss of dispersal power have occurred in *Antilliscaris*; there is evidence for ecological shift. That an adaptive radiation has occurred in *Antilliscaris* is an exciting possibility and should stimulate further field work.

BEHAVIOR: A specimen of *S. (A.) mutchleri* is currently being observed. While a full report of its behavior is planned, the following observations are germane at this point. The beetle has not constructed an elaborate burrow system under conditions where *substriatus* and *subterraneus* would (Hlavac 1967). Daylight hours are spent under retreats or in concealment burrows, about 2 body lengths long, dug in areas where the soil has not been highly compressed. During the night, this animal has eaten food placed on the surface and fallen into a small pitfall trap in the center of the container 24 nights out of 37. These fragmentary data are consistant with the hypothesis of ecological shift.

BIOGEOGRAPHY: The factors responsible for the high frequency of wing atrophy in montane carabids have been analyzed by Darlington (1943). He pointed out (1939, pp. 79-80) that mountains over

5000 ft. high on Cuba, Jamaica, and Hispaniola have endemic montane species that had become -winged on the spot. Noting that three -winged stocks on the mountains of Puerto Rico (*Antilliscaris, Oxydrepanus* and *Colpodes estriatus* Darl.) were closely related to forms known only from the mountains of Haiti, he concluded that each had reached Puerto Rico from Haiti after becoming flightless, and that mountains lower than 4000 ft. in the Antilles "are too low to induce wing atrophy among Carabidae." *S. darlingtoni* was here held to be closely related to the known species now in *Antilliscaris*. While I consider this species to be *incertae sedis* at the subgeneric level, the evidence for so doing (see systematic treatment) is not overwhelming, and this decision mainly reflects caution. In any case, questions as to the point of origin and the site of wing atrophy remain.

Long distance dispersal of montane forest-floor-inhabiting, flightless carabids to another suitable montane environment must be a rare event. Such species have all "bad" attributes that preadapt a species to be "good" colonizers (MacArthur and Wilson 1967, p. 81). Flightless carabids are rare in the tropical lowlands (Darlington 1943, pp. 44, 49-50) and would be severely selected against in areas subject to flooding. A +winged hydrophilic lowland species has many "good" preadaptations for colonization, such as occupation of an unstable habitat including many coastal sites with the potential for high population densities in hydric environments and, of course, the ability to fly.

With 3 montane spp. of *Scarites* on Puerto Rico, additional collecting on Haiti should turn up new species if the area species curve is remotely applicable to montane scaritine faunas (but see comments on ecological shift). When more data becomes available, I propose that the following model be tested. Major colonizing *Scarites* is a +winged form which burrows in a variety of shore and lowland habitats. It disperses to similar habitats on neighboring islands and subsequently invades the montane zone where –wings and flight mechanism atrophy occur along with ecological shift. Evidence for this interpretation could be obtained from detailed analysis of widely distributed +winged lowland forms. *Colpodes estriatus* Darlington and its allies probably represent a distinct genus (Darlington 1939, p. 95). Then, of the three taxa represented in the mountains of Puerto Rico and Hispaniola by a –winged species one, *Oxydrepanus*, is widely distributed in the lowlands of the Greater Antilles; *O. rufus* (Putz.) is known from Cuba, Jamaica and Florida, and *O. micans* Putz. from Hispaniola and Puerto Rico; both species

+winged. A second montane species, *O. reichoides* Darl., occurs on Hispaniola.

The sophisticated taxonomy necessary to separate monophyletic from polyphyletic origins of –wings in closely related lower categories does not now exist for *Scarites.* Until a more refined systematics becomes available, I think it heuristic and economical to view the biogeography of *Antilliscaris* in light of the model presented above.

PRELIMINARY EVOLUTIONARY DIAGNOSIS: From an assumed lowland, winged and burrowing ancestor, *Antilliscaris* has entered the montane rain forests of Puerto Rico, become flightless, undergone an ecological shift from burrowing to ground crawling, and speciated.

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STUDIES ON NEOTROPICAL POMPILIDAE (HYMENOPTERA)
V. *AUSTROCHARES* BANKS*

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In the previous paper of this series (Evans, 1968), I described several cases of dual sex-limited mimicry in the genus *Chirodamus* and mentioned that certain species of *Austrochares* also exhibit this phenomenon. Since the situation is somewhat different from that prevailing in *Chirodamus,* and since I had previously stated (1966) that *Austrochares* as originally conceived by Banks (1947) was diphyletic, it seems desirable to clarify this matter further. *Austrochares* was based upon *gastricus* Spinola and properly includes this species and four others; this genus is closely related to *Episyron, Poecilopompilus,* and *Sericopompilus.* The remaining species placed in the genus by Banks are much more closely related to *Anoplius* and *Pompilus* and are properly assignable to the genus *Dicranoplius* Haupt (1950). I hope to review *Dicranoplius* in the next paper of this series.

The cases of dual mimicry occur in *Austrochares* as here restricted, and not in *Dicranoplius.* As in the instances of dual mimicry I described in *Chirodamus,* the females belong to a Müllerian mimetic complex principally involving solitary wasps, while the males appear to be Batesian elements in a large mimetic complex centering around certain social wasps. Both complexes happen to be different than in *Chirodamus,* but I assume that similar selection pressures have been operative. The females evidently spend most of their time on the ground hunting for spiders and have evolved a color pattern of black and rufous like that of a great many solitary wasps occurring in the same situations (e.g. *Dicranoplius satanus*) (Figs. 2, 4), while the males spend most of their time flying in low vegetation in company with the workers of various social Vespidae.

In this instance the model of the males is undoubtedly *Polybia occidentalis* Olivier and its complex of sibling species (partially resolved by Richards, 1951). Bequaert (1944) speaks of *occidentalis* (that is, of the complex) as "the most common social wasp of tropical America". The males are black except for conspicuous yellow spots on the scutellum and metanotum, a yellow margin on the pronotum,

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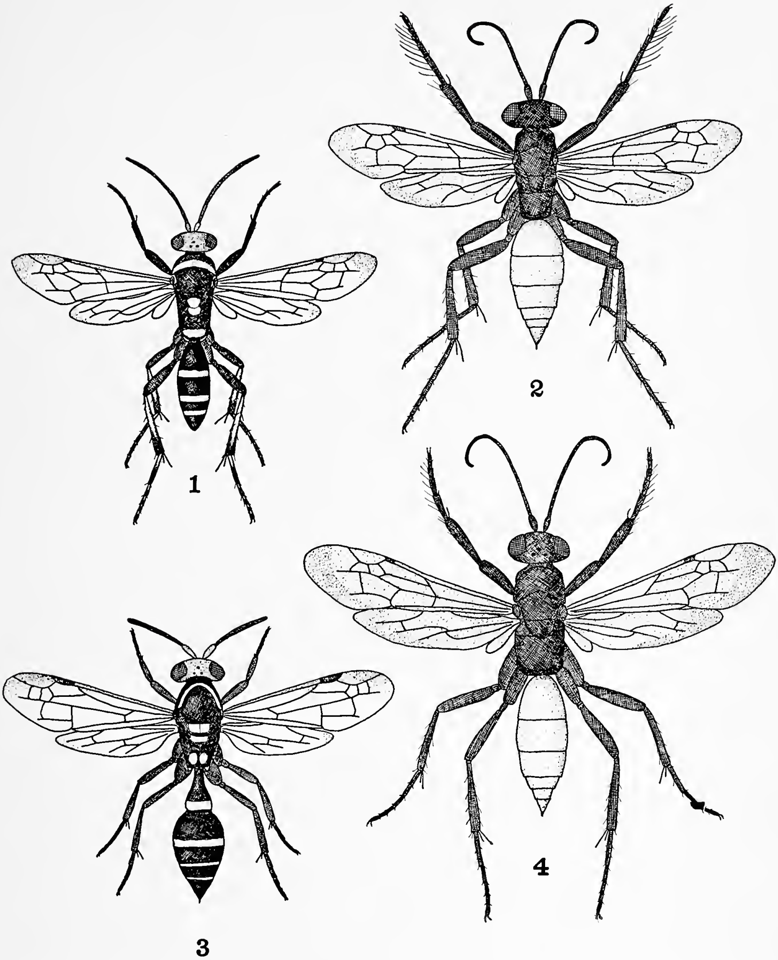


Figures 1-4. Dual mimicry in *Austrochares gastricus* (Spinola): male and female in upper two figures, models in lower two figures. Fig. 1. *A. gastricus* male, Potrerillos, Mendoza, Argentina. Fig. 2. *A. gastricus* female, same locality. Fig. 3. *Polybia parvula ruficeps* Schrottky (Vespidae), female, La Rioja, Argentina. Fig. 4. *Dicranoplius satanus* (Holmberg) (Pompilidae), female, Cacheuta, Mendoza, Argentina.

and transverse yellow bands on the abdomen (both models and mimics). Males of *Austrochares gastricus* in western Argentina also often have a partially or wholly rufous head (Fig. 1), as in *ruficeps* Schrottky (Fig. 3), a member of the *Polybia occidentalis* complex which is common in that area. Still others have reduced pronotal and abdominal banding, as in *scutellaris* White, another member of this complex. Since various members of the *occidentalis* complex range all the way from Mexico to Patagonia, the complex may provide models for several species of *Austrochares* of more restricted range, and it appears that *gastricus,* at least, is polymorphic in color, using at least three members of the complex as models. Similar color patterns also occur in several species of *Mischocyttarus* and other social Vespidae. Obviously the problem is complex and worthy of much more study.

One of the most interesting aspects of mimicry in *Austrochares* is that only three of the five species have males which share the color pattern of social wasps; the remaining two are not sexually dimorphic in color. The two which are not dual mimics (*elsinore* and *chilensis*) occur in areas where members of the *Polybia occidentalis* complex are rare or absent (coastal Peru and Chile), while the three species which have mimetic males occur in areas of great abundance of *occidentalis* and related species. Actually only *mexicanus* and *gastricus* are known to be dual mimics, since *exiguus* Banks is known only from the type male. However, the close resemblance of this male to that of *mexicanus* and *gastricus* leads me to believe that the female will also prove to be similar to those species.

The case of *Austrochares gastricus* is especially interesting. This species has been regarded by Banks and others as occurring in both Argentina and Chile, but several authors have remarked that no Argentinian males have ever been found (although Chilean males are common enough). Only Brèthes (1913) hit upon the truth when he suggested that Holmberg's "male" species *autrani* might go with *gastricus* or a similarly colored species. I regard *autrani* as in fact the male of *gastricus,* a species occurring east of the Andes and showing strong mimetic dimorphism. The Chilean *"gastricus"* is here described as a new species, which is not dimorphic. The association of *autrani* with *gastricus* is supported by the fact that both sexes bear a strong resemblance to *mexicanus,* the two sexes of which were associated several years ago. Banks (1947) assigned the males of two of the species of *Austrochares* to *"Batazonus",* i.e., *Poecilopompilus,* but they do not belong there. Most species of *Poecilopompilus* mimic social wasps (in both sexes), but none appear to have *Polybia occidentalis* as a model.

It is possible that the all-black species *elsinore* is the most primitive member of this complex, for it is remarkably like an *Episyron,* differing chiefly in the total absence of squamose pubescence. On the other hand, it may be a species derived from a *chilensis*-like or *gastricus*-like ancestor, the black color of both sexes being selected for within its range (arid portions of coastal Peru) because of the absence of the usual models and the presence of all-black models in this area.

In summary, the coloration of the five species of this genus may tentatively be described as mimetic in the following manner:

	Wholly black (like many solitary wasps	Black with rufous abdomen (like many solitary wasps)	Black and yellow (resembling *Polybia occidentalis* complex)
elsinore	Females & males		
chilensis		Females & males	
mexicanus		Females	Males
exiguus		(Females?)	Males
gastricus		Females	Males (polymorphic, resembling several members of complex)

Genus AUSTROCHARES Banks

Austrochares Banks, 1947, p. 423 (type species: *Pompilus gastricus* Spinola, original designation). — Evans, 1966, p. 200.

Generic characters. — Clypeus not or barely wider than lower interocular distance, apical margin truncate, upper margin strongly sinuate, with notches at the anterior tentorial pits; eyes of female strongly convergent on the upper third; ocellar triangle broad and rather flat. Scutellum and central part of metanotum convex; postnotum constricted medially and before the spiracles, slightly arcuately expanded between these constrictions; legs strongly spinose, front tibiae spinose for most of their length, front tarsus of female with a strong pecten; claws of both sexes bifid, inner ray truncate; pulvillar pad small, the comb weakly developed. Wings as figured by Evans, 1966, fig. 16, the second recurrent vein arising more than half way from base of subdiscoidal vein to wing margin, anal vein of hind wing meeting media at or slightly beyond origin of cubitus. Male genitalia with the basal hooklets double, parameres slender, aedoeagus with a few small setae (genitalia differing in no important ways from those of *Poecilopompilus* and *Episyron*). Female with only a few thin setae at apex of abdomen.

Key to Species

Females

1. Wholly black, pubescence mostly dark and with strong bluish reflections; spines of tarsal comb very short (Peru) .... *elsinore* Banks

   Abdomen rufous, pubescence brownish to silvery, without strong bluish reflections; spines of tarsal comb very long 2

2. Hind tibiae and tarsi and middle tarsi mostly rufous; entire body covered with conspicuous silvery pubescence (Mexico) .... *mexicanus* Dreisbach

   Middle and hing legs wholly black; pubescence finer and over most of head and thorax somewhat brownish 3

3. Head rather thick, the temples, as seen from above, about as wide as the eyes (Fig. 8) (Chile) .... *chilensis* n. sp.

   Head thin, the temples not nearly as wide as the eyes (Fig. 9) (Argentina, southern Brazil) .... *gastricus* (Spinola)

Males

1. Coloration similar to that of female, the head and thorax black, the abdomen either black or rufous; legs black 2

   Coloration very different from that of female, black or black and ferruginous, scutellum and metanotum spotted with yellow, and usually with other yellow markings on the body; legs annulated with yellow 3

2. Abdomen black; slope of propodeum low and even; digiti with short setae (Fig. 7) (Peru) .... *elsinore* Banks

   Abdomen rufous; propodeum, in lateral view, strongly convex, with a somewhat flattened declivity, digiti with longer setae (Fig. 5) .... *chilensis* n. sp.

3. Tibiae black, more or less marked with yellow; clypeus black, rarely yellow on extreme sides; a robust species (Argentina and southern Brazil) .... *gastricus* (Spinola)

   Tibiae mainly rufous, with yellow markings; clypeus broadly yellow on the sides; more slender species 4

4. Posterior rim of propodeum and a broad band on first tergite yellow; digiti of genitalia somewhat acute apically; length 6.5 mm, fore wing 5.5 mm (northern Brazil) .... *exiguus* (Banks)

   Posterior rim of propodeum and first abdominal tergite mostly or wholly black; digiti rounded apically; length 7 to 9.5 mm, fore wing 6.5-8.5 mm (Mexico) .... *mexicanus* Dreisbach

Austrochares elsinore Banks

Austrochares elsinore Banks, 1947, p. 426 [Type: ♀, PERU: Lima, 21 May 1920 (Cornell Univ. Exped.) (Cornell Univ., No. 2547)].

Female. — Length 10-11 mm; fore wing 9-10 mm. Black, except inner orbits with a small pale spot and outer orbits with a pale streak; pubescence with strong bluish reflections; propodeum with a few short hairs on the sides; wings moderately fumose, violaceous. Clypeus 2.2 × as wide as high; middle interocular distance .63 × transfacial distance; upper interocular distance .73 × lower interocular distance, the vertex arched gently above the eye tops; postocellar line slightly exceeding ocello-ocular line; antennae slender, third segment subequal to upper interocular distance. Propodeum with the slope low, posterior third with a flat declivity; fore tarsus with three slender comb-spines, the apical one .5-.7 × as long as second segment. Anal vein of hind wing reaching media well beyond origin of cubitus; third submarginal cell of fore wing trapezoidal, narrowed by about half above.

Male. — Length 8 mm; fore wing 7 mm. Color of body, wings, and pubescence as in female except marks on inner and outer orbits larger and apical tergite with a small white spot; propodeum with a few inconspicuous short hairs. Clypeus 2.0 × as wide as high; middle interocular distance .62 × transfacial distance; inner orbits strongly divergent from bottom, then abruptly convergent on upper third, upper and lower interocular distances equal; ocello-ocular line slightly exceeding postocellar line; antennae slender, segment three 2.1 × as long as wide, .6 × upper interocular distance. Slope of propodeum low and even; wing venation as in female. Abdomen slender, fusiform; genitalia with the parameres nearly straight, parapenial lobes very slender, curved, digiti clothed with very short setae (Fig. 7).

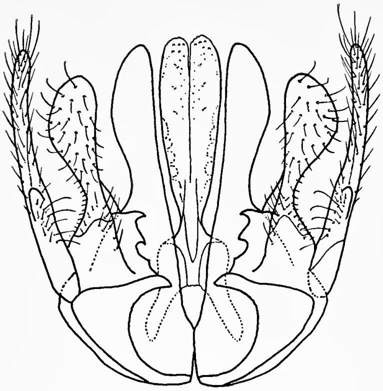
Distribution. — Known only from Lima, Peru. The male bears data identical to those of the type except that it was collected 8 May 1920; it is labeled as a paratype, but it is not really a paratype, as Banks makes no mention of this specimen. A female paratype [Mus. Comp. Zool.] also bears the same data except that it was collected 21 May 1920.

Austrochares chilensis new species

Pompilus gastricus Spinola, 1851, p. 380 [in part]. — Reed, 1894, pp. 611, 615. — Banks, 1947, p. 424 [in part].

Holotype. — ♀ CHILE: Pudahuel, Prov. Santiago, 29 Jan. 1951 (L. Peña) [Mus. Comp. Zool., no. 31678].

Description of female type. — Length 12 mm; fore wing 9.5 mm.



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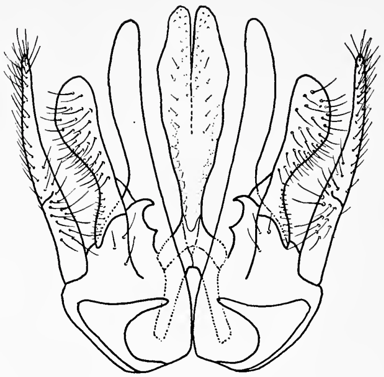

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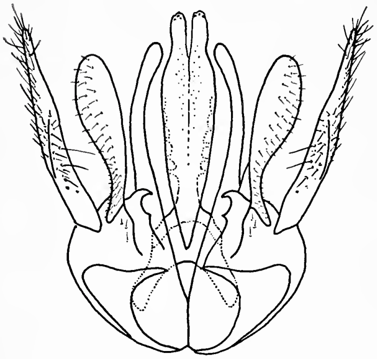

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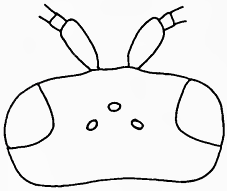

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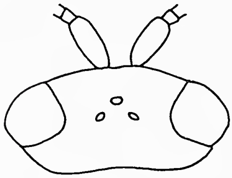

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Fig. 5. Male genitalia of *Austrochares chilensis* n. sp., ventral aspect. Fig. 6. Same of *A. gastricus* (Spinola). Fig. 7. Same of *A. elsinore* Banks. Fig. 8. Head of female *A. chilensis* n. sp., dorsal aspect. Fig. 9. Head of female *A. gastricus* (Spinola), dorsal aspect.

Head, thorax, legs, and antennae black, abdomen wholly ferruginous; wings lightly infuscated except fore wing more clouded on apical two-thirds and especially in a band along outer margin; pubescence of head and thorax dark, somewhat violaceous; propodeum with numerous rather long setae. Clypeus 2.5 × as wide as high; middle interocular distance .63 × transfacial distance; upper interocular distance .80 × lower interocular, vertex arched above eye tops; postocellar and ocello-ocular lines subequal; head thick behind eyes, the temples, in dorsal view, nearly as wide as the eyes (Fig. 8). Antennae slender, segment three .75 × upper interocular distance. Propodeum convex, with a somewhat flattened declivity on posterior half; front tarsus with a comb of long, somewhat flattened spines, four on the basitarsus, the apical one 1.7 × as long as second tarsal segment. Anal and cubital veins of hind wing interstitial; third submarginal cell of fore wing narrowed by two-thirds above.

Allotype. — ♂, same data as type [MCZ].

Description of male allotype. — Length 9 mm; fore wing 8 mm. Color exactly as in female, pubescence and pilosity also as in that sex. Clypeus 2.2 × as wide as high; middle interocular distance .62 × transfacial distance; upper interocular distance subequal to lower interocular distance; postocellar and ocello-ocular lines subequal. Antennae slender, segment three 2.5 × as long as wide, about half as long as upper interocular distance. Propodeum strongly convex and with a somewhat flattened declivity, as in female; wing venation also as in that sex. Abdomen robust, slope of the first tergite higher than in *elsinore;* subgenital plate tectiform, broadly rounded apically; genitalia as shown in figure 5, differing from those of *gastricus* in the shape of the aedoeagus and in the slightly broader parapenial lobes.

Paratypes. — CHILE: 1 ♀, *Santiago* [Mus. Comp. Zool]; 2 ♀♀, 1 ♂, Valparaiso, Dec., Jan. (Herbst, Faz) [Mus. Comp. Zool., Cornell Univ.]; 9 ♂♂, Hacienda Illapel, Coquimbo, Nov. (Peña) [Mus. Comp. Zool.]; 1 ♀, Angol, Dec. [Cornell Univ.]; 3 ♂♂, Los Angeles, Bio Bio, Feb. [Mich. State Univ.].

Variation. — The available females vary but slightly in size (fore wing 9.5 - 11 mm). In one specimen the clypeus is only 2.3 × as wide as high, and in two there is a small fifth comb-spine on the basitarsus. The males also show but little variation in size (fore wing 8-10 mm) and no noteworthy variation in color or other features.

Remarks. — There can be no question that the name *gastricus* properly applies to the species occurring east of the Andes; although Spinola describes the species in the *Historia de Chile,* he remarks as follows: "El tipo de esta especie es una hembra del Brasil que M. Klug me habia enviado con el nombre que le he conservado. Los individuos de Chile que le he juntado, me han parecido enteramente semejantes a este tipo por su talla, por sus formas y por sus colores."

Professor U. Parenti, of the Museum at the Universita di Torino, Italy, has sent me two females from the Spinola collection which presumably represent those which Spinola had before him. One, labelled simply "Brasil", is here designated lectotype of *gastricus* on the basis of the remarks quoted above. Since there are no specimens in the Berlin Museum clearly from the Klug or Spinola collections, it seems probable that this is the true type. The second specimen, labeled "Chili, Gay" has broad temples and clearly belongs to *chilensis* n. sp., while the female from Brazil has narrow temples characteristic of *gastricus* as here interpreted.

Austrochares gastricus (Spinola)

Pompilus gastricus Spinola, 1851, p. 380 [Type: ♀, BRAZIL (no further data) (Univ. Torino; see comments above)]. — Taschenberg, 1869, p. 65 [♀, Mendoza, Argentina]. — Burmeister, 1872, p. 238. — Holmberg, 1881, p. 143 [♀; ♂ misidentified]. — Berg, 1881, p. 71 [♀, Carhué, La Pampa, Argentina]. — Brèthes, 1909, p. 460 [Mendoza, Argentina].

Pompilus autrani Holmberg, 1903, p. 499 [♂, Chaco, Argentina]. New synonymy.

Pompilus annuliventris Brèthes, 1909, p. 460 [♂, Chacras de Coria, Potrerillos, Argentina]. Synonymy with *autrani* by Brèthes, 1913.

Psammochares autrani: Brèthes, 1913, p. 117 [♂, Mendoza, Argentina].

Batazonus autrani: Banks, 1947, p. 381 [♂, Mendoza, Argentina].

Austrochares gastricus: Banks, 1947, p. 434 [in part; ♀♀ from Mendoza and San Ignacio, Argentina].

Female. — Length 8-12 mm; fore wing 7-11 mm. Body color as in *chilensis;* wings rather heavily infuscated; pubescence of head and thorax brownish, somewhat violaceous, sometimes somewhat silvery on front; propodeum with erect setae which may be dark or rather pale. Clypeus 2.3-2.5 × as wide as high; upper interocular distance .70-.80 × lower interocular; postocellar and ocello-ocular lines subequal; third antennal segment .78-.90 × upper interocular distance; head distinctly thinner than in *chilensis,* as seen from above contracted immediately behind eyes, the temples not nearly as wide as the eyes. Features of thorax and abdomen as in *chilensis.* (Figs. 2, 9).

Male. — Length 7-9.5 mm; fore wing 6.5-9 mm. Body black, with pale yellow markings as follows: inner and outer orbits, scape beneath, posterior margin of pronotum, center of scutellum and metanotum, sometimes a band on propodeum, bands on tergites 2-4 and often an interrupted band on 1, spots on apical two tergites; middle and hind tibiae with pale streaks, all spurs pale, and all tarsi annulated with pale yellow; flagellum ferruginous, especially below, and specimens from western Argentina (Salta, Mendoza) often with the head partly or wholly ferruginous; wings hyaline, most specimens with a dark tip on the fore wing; pubescence mostly silvery, erect setae on propodeum and elsewhere pale (Fig. 1). Clypeus 1.9-2.0

× as wide as high; third antennal segment 2.0-2.4 × as long as wide; other head features as in *chilensis.* Propodeum short, strongly convex in profile. Subgenital plate similar to that of *chilensis;* genitalia as shown in figure 6.

Distribution. — Argentina south to Rio Negro; also southern Brazil. Actually the only Brazilian specimens I have seen are the type and a female from Goias, collected in October 1962 at Jatai. I have seen many specimens from Argentina (58 ♀♀, 33 ♂♂), from the provinces of Salta, Tucumán, La Rioja, Cordoba, Mendoza, Rio Negro, and Buenos Aires; it is also recorded from La Pampa and Chaco.

Variation. — Common variation in color of the male is summarized in the above description. A few males have the abdominal banding reduced, and some have the prothoracic band and the markings on the legs reduced; two males from Mendoza are all black except for the large scutellar-metanotal spot and some yellow on the outer orbits. These males may mimic a different member of the *occidentalis* complex (*scutellaris* White?) just as the red-headed males (also prevalent in Mendoza) may mimic *ruficeps* Schrottky.

Austrochares exiguus (Banks) new combination

Batazonus exiguus Banks, 1947, p. 380 [Type: ♂, BRAZIL: Vista Alegre, Rio Branco, 6 Sept. 1924 (J. Bequaert) (Mus. Comp. Zool., no. 26781)].

This species is still known only from the type, which differs but slightly from *mexicanus* and from the more extensively maculated males of *gastricus.* The late R. R. Dreisbach made a balsam mount of the genitalia some years ago, but the genitalia were mutilated and cleared too long in potash, so it is difficult to prepare a sketch or to make a detailed comparison with related species. The genitalia appear to be much like those of *gastricus* except that the aedoeagus is more slender and parallel-sided, the digiti more acute apically.

Austrochares mexicanus Dreisbach

Austrochares mexicanus Dreisbach, 1966, in Evans, 1966, p. 201 [Type: ♀, MEXICO: Minatitlan, Veracruz, 26 Aug.-1 Sept. 1961 (Dreisbach) (Mich. State Univ.)].

This species is known from a short series of both sexes from the type locality and one female from Chiapas. I have seen no additional specimens since the description. The differences from related species are adequately summarized in the keys; the genitalia (Evans, 1966, fig. 38) differ only slightly from those of *gastricus.* The males undoubtedly mimic Mexican members of the *Polybia occidentalis* complex, while the females bear a strong resemblance to such common pompilids as *Sericopompilus neotropicalis* and *Anoplius apiculatus.*

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EGGCASE CONSTRUCTION AND FURTHER OBSERVATIONS ON THE SEXUAL BEHAVIOR OF THE SPIDER *SICARIUS* (ARANEAE: SICARIIDAE)*

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The eggcase of *Sicarius* is unique among spiders. Its masonry wall resembles in texture the nests of mud dauber wasps. And, unlike other spider eggcases, it is buried in sand, attached to stones. We do not know of any other masonry construction by spiders, or of other buried eggsacs. Some spiders incorporate sand grains and detritus into their webs or their trapdoors. The European theridiid *Achaearanea saxatile* (C. L. Koch) makes a thimble-shaped retreat for herself and her silken eggsac (Pötzsch, 1963), and covers the thimble with large sand grains and little stones. The colonial European zodariids, *Zodarion germanicum* (C. L. Koch) and *Z. elegans* Simon, build retreats under stones. Each semispherical retreat is covered by sand grains from the surroundings, and pieces of bark and spruce needles are woven into the wall. The retreat is used by the spider and the eggsac is hung up in it. As far as I know, the building of the retreat has not been observed. Wiehle (1953) illustrates a row of large setae in front of the zodariid spinnerets and peculiar branched setae that cover the legs and tarsi. These setae are perhaps used for handling the detritus.

The unusual *Sicarius* eggcase was first noted by Simon (1899)[1]. Although we have two species of *Sicarius* in culture the possibility of watching eggsac construction seemed at first remote because the only eggcase made in the laboratory appeared to have been constructed while the spider was covered by sand.

Sicarius belongs to a small family of little-studied spiders, distributed in the southern hemisphere and related to the more widespread Loxoscelidae and Scytodidae. Any behavior observations are of phylogenetic interest. The several species of *Sicarius* inhabit deserts and bury themselves in the sand (Reiskind, 1966.) The burying, the material of the eggcase and the burying of the eggcase are probably adaptations to avoid extreme heat. The spiders presumably evolved

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[1] Birabén (1939) reported and described the egg cases for Argentinian species.

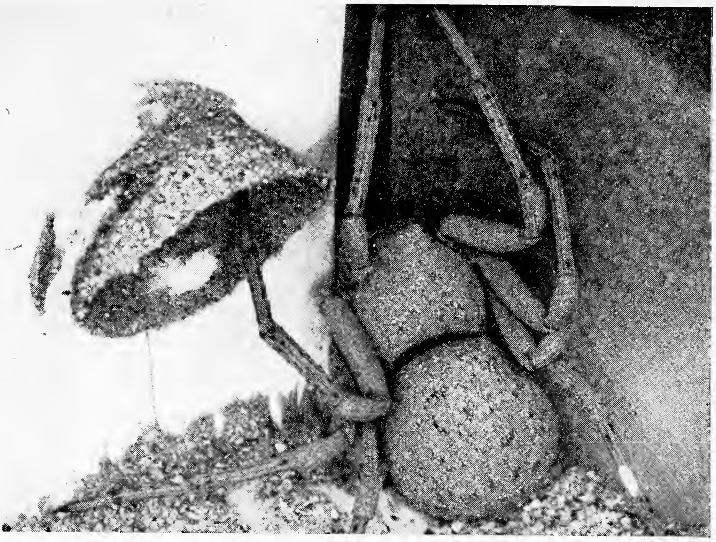

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Fig. 1. *Sicarius* "sp. 1" female with the foundation of the eggcase. The basal disc still has a bare spot, while the upper rim has been built up. On the left side are some foundation attachments not used. The sand next to the spider on the ground has been scraped away to the bottom of the container, while in later photographs sand has been thrown back into this area by the spider. The total length of the spider is 18 mm. The photograph was taken on 13 June.

Fig. 2. Female *Sicarius* rocking her abdomen in the sand. The abdomen is held at an unusual angle to the prosoma while picking up fine sand particles. The photograph was taken later on 13 June.

in desert areas and from there a few species have invaded neighboring savannah land. The sparing use of silk (Fig. 10) may also be an adaptation to the periodically sparse food supply and protein intake of desert inhabitants.

Here two observations are reported. During the first the spider was left undisturbed; during the second, to facilitate photography and observation, the spider's work was interrupted.

The spider under observation belongs to *Sicarius* sp. "no. 1," originating in Tucumán Province, Argentina. The female is the same individual reported on in the previous paper (Levi, 1968.)

On 5 April 1968, at 8 A.M. a basal masonry disc was found on the paper lining of a vertical side of the plastic polystyrene container. One edge was 5 mm high, the opposite rim missing. From time to time the female scratched in the sand on the bottom of the container, throwing sand grains underneath her abdomen and sometimes rocking her abdomen from side to side. At 10 A.M. the spider was clinging to the upper rim of the disc tapping the lower rim with the tip of her abdomen, but it could not be seen whether spinnerets were involved or the anal tubercle. The mouth was definitely not used. At 8 P.M. (20 h) the disc was complete but the lower rim still lacking. On 6 April in the morning, no change was noticed; the spider had not worked during the night. On 7 April, in the morning, the upper wall was higher, about 1 mm high, and strongly concave. The lower rim was only slightly raised above the basal disc. The spider was buried. At 5 P.M. (17 h) the spider was seen clinging to the cup, not moving; at 8 P.M. (20 h) the female had moved slightly and a yellowish clump of eggs was seen inside the cup. The female now attached silk threads criss-cross over the top of the cup. She touched her spinnerets to the rim of the cup then drew a thread to the center and returned to the rim. Light seemed to disturb her and she stopped working. At 4:30 A.M. on 9 April, the lid was plastered over and the spider was slowly digging in the sand. At 7 A.M. the female was still digging, but in a different place; after digging a few strokes she stopped for a long time. At 8:30 A.M. the female was found buried, but not in the place where she had been digging.

Although it could not be seen exactly how the sand was incorporated into the wall of the cup, the mouthparts were not used. It is of interest that the eggcase was started on 5 April and finished on 9 April, over a time span of four days, the female interrupting her work at intervals to return later. The construction of the eggsac of most spiders observed is started and completed within several hours. The eggcase was not constructed within the sand, but the base of the lower rim was about 5 mm above the level of the substrate. The eggcase was made 9 months after first mating in July, 1967. This period is generally much shorter in other spiders: days, or at most weeks.

On 4 June 1968, a smudge mark was again observed on the vertical paper wall. On 5 June, in the morning a foundation was present (Fig. 1). The spider container was moved and placed in light on a work desk for easier observation. Perhaps as a result of this disturbance the spider did not resume work until the night of 12-13 June. The cup was slowly built up and its walls, as well as the mud lining, seemed complete on the morning of 14 June. Interrupting her building on 13 June, the spider was observed to mate again. (Since construction of the first eggsac the spider had crossed the cardboard partition into the compartment of the male.) It was seen that the masonry construction material is made by incorporating sand with silk. The spider, jumping down from the eggcase, throws sand back with the first two legs as if beginning to bury herself (Reiskind, 1966.) However, instead of jumping into the depression, the spider bends her abdomen down so far that the pedicel shows, and pushes her abdomen into the pile of sand thrown up, rocking slowly from side to side (Fig. 2). The spider then moves up to the rim with a disc shaped load of sand around the spinnerets (Fig. 3) and pulls threads out of the spinnerets with the usual abdominal motions up and down (away from the rim and approaching it) and at times sideways, incorporating sand grains. From the motion it was assumed that silk is used to incorporate the sand into the wall.

The timing in one rapid sequence was as follows: at 10 A.M., spider jumps down on the sand; 15 sec later, she throws sand with her front legs; 5 sec she rocks abdomen in sand for 10 sec; all motion stops for 55 sec; spider jumps with load of sand up to the rim of the eggcase, and after sitting quietly, continues construction on the rim. 1 min 35 sec after jumping up, she jumps down again, turns, throws sand, rocks her abdomen, rests, and jumps up to the rim. She first touches the rim with palps. Temporarily in throwing back sand, the spider removed all sand to the bare plastic bottom under the eggcase, but later she replaced the sand. The male once emerged from the sand, put his long legs over the female, then backed up and away.

On 14 June, 9 P.M. (21 h) the rim seemed finished and perfectly circular (Fig. 4.) The next observation was made at 3 A.M., 15 June. The eggs must have been laid, as the eggcase was finished covered by the lid (Fig. 5). At 6 A.M. the female walked around in the sand,

Fig. 3. Female *Sicarius* incorporating fine sand particles, held in a disc around spinnerets, into the eggcase wall with silk. Notice the difference in grain size of the substrate and the material picked up. Photograph taken minutes after Fig. 2.

Fig. 4. Eggcase ready to receive the eggs. The rim is now circular and smooth. Photograph taken 14 June at 21 h.

Fig. 5. The finished eggcase. The edge of the cap overhangs the walls. Photograph taken before the eggcase was buried, 15 June.

Fig. 6. The eggcase has disappeared under the sand thrown over it. The line between 2nd and 3rd left legs of the spider is the same as the one in Fig. 5 above and to the right of the eggcase.

digging, but did not fit herself into the hole. This observation corresponded with that of the first eggcase construction. But now with strong movements of the first and second legs, the spider began throwing sand 10 cm back, toward the eggcase. The sand noisily struck against the paper lined plastic wall of the container. It was first thought that this action was to fill the hole in the sand under the eggcase, the hole produced by throwing sand back for the eggcase construction. But the spider continued changing her position around the eggcase, always remaining about 10 cm away, throwing sand toward the eggcase. The accuracy was not great and often the sand was thrown at an angle 45° off. But the spider must have been able to determine the direction of the eggcase from her changing position. The throwing back of sand reminded one of a dog digging a hole. The motions were those illustrated by Reiskind (1966, Fig. 1). By 11:30 A.M. the eggcase was buried under several cm of sand (Fig. 6) and the female dug herself into the sand and disappeared.

From the start to completion it took the spider 11 days — perhaps prolonged because of the disturbance. However, the spider continued construction and did not start out anew as might have been expected. Four days after completing the work the female was found dead on the sand surface. The cause of death is unknown. It may have been dehydration resulting from frequent disturbance.

Preserved *Sicarius* were examined under the microscope. Unlike juveniles and males, adult females have their spinnerets almost hidden by a crown of long setae many layers thick. Only the posterior spinnerets show (Figs. 7, 8). (*Sicarius* lacks the large colulus characteristic of the related *Loxosceles.*) Under the microscope the setae were found to be feathered (Fig. 9) and about 1 mm long. A needle run through these setae became dusty. To test the assumption that these setae can pick up sand mechanically, one female preserved in alcohol was dried and the spider's abdomen was rocked in the sand. No sand grains were picked up at all — only dust, the particles about 1/10 the diameter of sand particles. And, indeed, the particles in the wall of the eggcase were all much smaller than the majority of the sand grains in the spider's container. The setae around the spinnerets sift out the right size particles from the sand thrown back by the female. The sand grains were later measured and found to be 0.2 - 0.4 mm in diameter. Some of the fine particles that washed off the female, preserved in alcohol after she died, measured 0.02 - 0.06 mm diameter. Some of these particles may have come from setae on other parts of the female's body to which dust clings readily, giving the animal the color of the background. The difference in grain size

Fig. 7. Setae surrounding spinnerets that hold sand, seen from the side. At upper right is the genital groove.

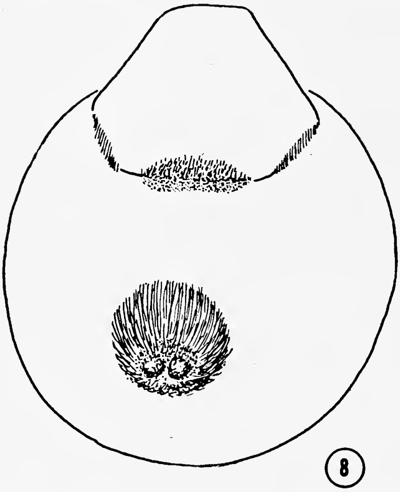


Fig. 8. Diagram of venter of female *Loxosceles* abdomen showing the long setae around and almost completely covering the spinnerets. The genital groove also has dense hair.

of the particles in the eggcase and the sand can be seen in Figs. 3 and 4.

The first eggcase had a hole near the top rim on the morning of 16 August, 1968, more than four months after its construction (Fig. 11). The intervening summer had been unusually hot with many days over 30° C. There were 2 young on the sand and during the course of the day one after another climbed sideways out of the hole, jumped to the sand (Fig. 12-14) and shortly after, buried themselves using the same motions as the adults (Reiskind, 1966). In an attempt to photograph the slow exodus of the young, the eggcase was carefully broken off, and placed on the sand. The egg case broke off cleanly, but since it did not have a back, some young spilled out and others left rapidly, one after another, through the tiny hole. Several that left in a hurry still had their molted skins clinging to the abdomen

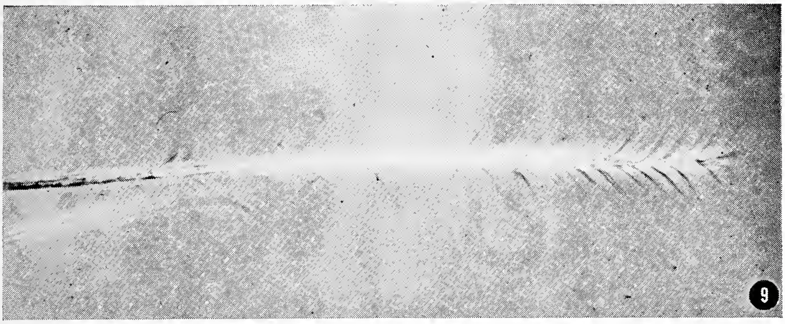
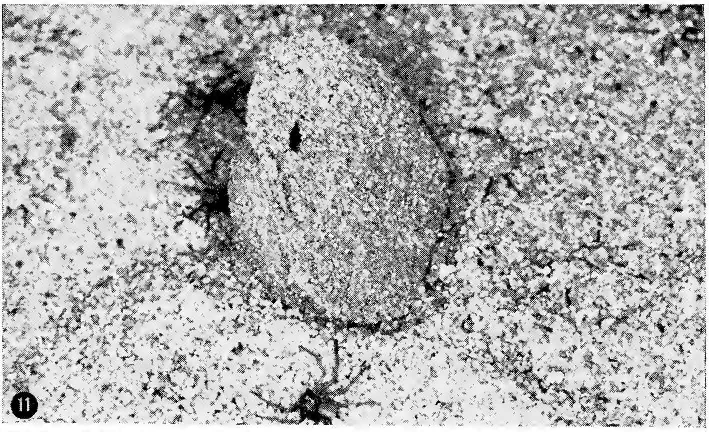
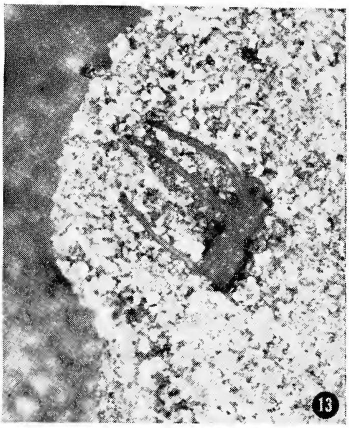


Fig. 9. A seta removed showing the branches to which dust particles cling. The seta is about 1 mm long; the section shown is about 0.5 mm long, photographed with phase microscopy.

Fig. 10. A portion of the basal disc of the eggcase. Only very few threads are used to hold the sand together.





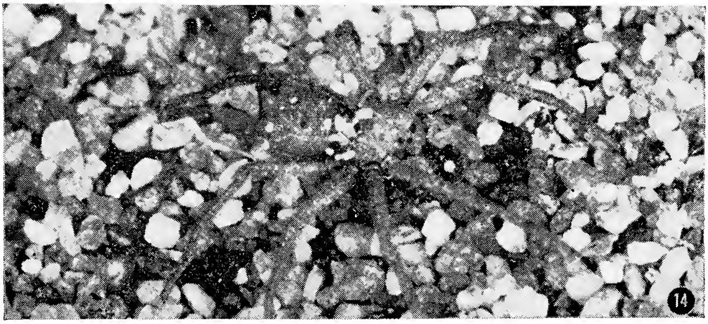


Fig. 11. The eggcase after the young have started to emerge. To facilitate photographing, the eggcase was removed from its attachment to the wall and placed on sand. The hole is near the upper edge. Several young, each about 2.5 mm long, are seen on the sand.

Fig. 12. One after another the young spiderlings emerge from the hole. The legs appear first.

Fig. 13. The body moves sideways through the hole.

Fig. 14. The young already have some sand grains clinging to their bodies. This individual left the eggcase when it was taken off the wall, and still has an exuvium attached to the abdomen.

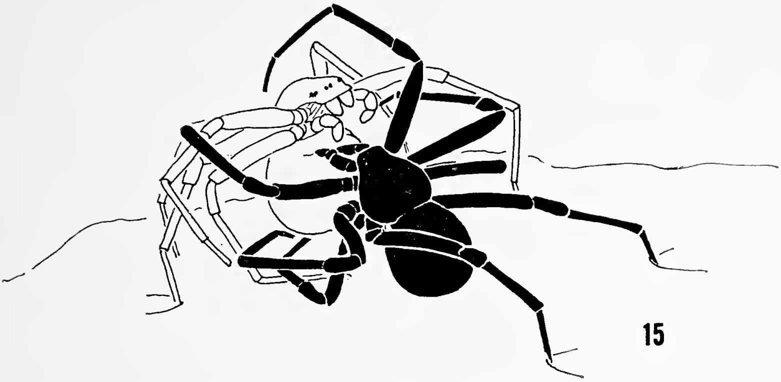


Fig. 15. *Sicarius* sp. mating on 13 June. The male has been illustrated black, the female white. The drawing was made from a photograph.

(Fig. 14). Some that had left the eggcase in the morning were feeding on drosophila flies by early afternoon. The young, about 2.5 mm long, at first looked skinny, but soon filled out. By the following day no more young were seen to emerge. The plastic cage was jarred to make the spiderlings emerge from the sand, and about forty spiderlings were counted. The eggcase was examined. In it were 10 shrivelled eggs that had not hatched and numerous exuviae. Many exuviae had an egg membrane attached. Apparently the young left the eggs, molted, and then made the hole and emerged. The eggcase had no silk lining but under the lid a few silk threads crossed. Apparently, after the cup was finished (Fig. 4) and filled with eggs, the eggs were secured by a few silk strands before the lid was constructed. The silk strands might also support the masonry lid. The contents of the second eggcase proved to be infertile and did not hatch.

During construction of the eggcase, on June 13 at about 4 P.M. (16 h) the female was observed mating. The constancy of mating position within spider families was discussed in a previous paper and the pair observed mating was the same one photographed mating previously (fig. 1, Levi, 1968). During the first matings observed, the female had been turned over with her abdomen in horizontal position, in the mating observed now, perhaps because of obstructions, the abdomen was vertical, the cephalothorax of the female still bent, but now horizontal over the male and the male was at an angle near vertical to the female (Fig. 15). The differences in positions of different matings of the same pair were as great as those puzzling differences observed by Dabelow (1958) in individuals of *Scytodes thoracica* coming from different parts of Europe.

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ECOLOGIC AND SPATIAL DISTRIBUTION OF *PYRGUS OILEUS* AND *PYRGUS PHILETAS* (LEPIDOPTERA: HESPERIIDAE) AT THEIR NORTHERN DISTRIBUTIONAL LIMITS

By John M. Burns[1] and Roy O. Kendall[2]

Introduction

In the course of his studies of the world hesperiid fauna, Evans (1937, 1949, 1951, 1952, 1953, 1955) was — as he himself stated (1949: xi) — much influenced by Mayr (1942) and therefore applied the polytypic species concept freely in postwar publications. Limited mainly to material in the British Museum (Natural History), Evans worked with fragmentary distribution data — especially for the western hemisphere — and often did not fully digest the data he had. (In view of the number of New World species to be treated and the uncertain but certainly brief time that remained to him, this is no surprise.) As a result, he frequently grouped in a single species morphologically related forms that struck him as approximately allopatric.

An extreme example of such lumping is Evans' (1953: 211) polytypic species *Erynnis juvenalis* embracing five subspecies — *propertius* (Scudder and Burgess), *meridianus* Bell, "*plautus* (Scudder and Burgess)," *juvenalis* (Fabricius), and *clitus* (Edwards) — each originally designated as a species. Detailed analyses (Burns 1960, 1964, in prep.) have shown that this transcontinental assemblage is far more accurately described as two distinct superspecies — one western and one eastern — that are *sympatric* in central North America from northern Arizona, New Mexico, Texas, and Oklahoma to at least the transverse Volcanic Cordillera of southcentral Mexico. Each superspecies comprises a pair of allopatric species: *E. propertius* and *E. meridianus*, on the one hand; and *E. juvenalis* (which includes *clitus*) and *E. telemachus* Burns (which succeeds *plautus* sensu Evans), on the other. [*E. plautus* (Scudder and Burgess) is really a synonym of *E. juvenalis* (Fabricius).] Submergence of these four species in a single one, in the manner of Evans, obscures rather than clarifies evolutionary relationships (see Burns 1964).

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A number of apparently hasty couplings of this kind have been uncritically repeated in the current synonymic list of Nearctic Rhopalocera (dos Passos 1964). Examples may be found in such genera as *Erynnis*, *Pyrgus*, *Staphylus*, *Cogia*, *Amblyscirtes*, and *Panoquina*. Thus Evans' interpretations receive empty endorsement and wider dissemination when, in fact, they require re-examination.

Pyrgus oileus and *P. philetas* are separate species

Evans (1953: 222) erroneously set *Pyrgus philetas* Edwards as a subspecies of *Pyrgus oileus* (Linnaeus), and dos Passos (1964: 19) echoed this action. MacNeill (1962: 101) meanwhile emphasized their distinctness: "The two species are broadly sympatric in Mexico and I have taken them together at several widely separated localities on the mainland [as opposed to peninsular Baja California, where only *P. philetas* is known]." More recently, Freeman (personal communication) also has found these two forms coexisting in mainland Mexico.

Central to any taxonomic interpretation is the fact that, even with spatial and temporal coexistence, *P. oileus* and *P. philetas* differ in diverse characters of facies and morphology. These include (*1*) color-pattern of the wings — particularly (*a*) the ventral surface of the secondary, which, in *philetas*, is characteristically blanched and much less marked by sharp contrasts than it is in *oileus*; and also (*b*) the dorsal surface of the male primary, which, in the proximal third of space 1b, almost always has 1 or 2 white spots in *philetas* that are virtually or (in nearly all individuals) quite lacking in *oileus*; (*2*) the density, length, and orientation of white hair-like scales on the dorsal surface of the male primary — these scales are abundant, exceedingly long, and directed obliquely distad-and-caudad in *oileus*, but are less common, short, and directed chiefly distad (not caudad) in *philetas*; and (*3*) the genitalia in both sexes (figs. 1-4). These distinguishing characters are various and complex enough that control of them by a single genetic switch mechanism is unlikely in the extreme. One may safely conclude that *P. oileus* and *P. philetas* are not polymorphic variants.

Genitalia differences are so pervasive and conspicuous, and so adequately shown in figs. 1-4, as scarcely to warrant verbal comment. Yet it may be worth directing specific attention, *in males* (figs. 1 and 2), to the relative lack of spines on the valvae in *oileus*, the medial extension of the anterodorsal part of the distal process of the valvae in *philetas*, the longer saccus and adjacent longer valval articulation in *oileus*, the median keel and flanking concavities of the dorsal surface of the uncus in *oileus* (giving the effect of a "double scoop") as opposed to the simple convex dorsal uncus surface in *philetas*, the more heavily dentate gnathos in *philetas*, and the more delicate apex of the aedeagus in *philetas;* and, *in females* (figs. 3 and 4), to the highly distinctive sclerotization around the ostium bursae in the two species, the much larger wrinkled membranous sac ventral to the ostium bursae in *oileus*, and the very different proportions and configurations of the major sclerotization (sterigma) between the ostium bursae and the ovipositor lobes in the two species.

Virtual allopatry in the United States

Despite extensive Mexican sympatry, it appears that, in the southern United States, where these related but distinct species reach their northern distributional limits, they are practically allopatric. They seem, moreover, to be ecologically segregated — *P. oileus* to moister and typically (though *not* exclusively) coastal-plain environments, and *P. philetas* to drier interior ones.

The United States distribution of these species can be summarized at two levels as follows. In broad view, *P. oileus* ranges from Florida to central Texas, and *P. philetas* from central Texas to Arizona. On state by state inspection, *P. oileus* is clearly widespread and common in the Florida Keys and in peninsular Florida, extending as far north, at least, as Gainesville, Alachua County; and it is known also from Escambia County bordering the Gulf of Mexico in the western tip of Florida adjacent to Alabama (Kimball 1965: 52). Although it is not yet reported from either Alabama or Louisiana, Mather and Mather (1958: 93) recorded the capture of 1 male in 1957 at Bay St. Louis, Hancock County, Mississippi; and, in 1960, with the aid of M. and E. Roshore, they collected a total of 6 males and 4 females from four localities in Jackson County, Mississippi. Both Hancock and Jackson counties border the Gulf of Mexico. (All 11 Mississippi specimens have been examined by Burns.) *Pyrgus oileus* occurs primarily in southern sections of east and central Texas; but a single female has been reported from as far north as North Little Rock, Arkansas (Freeman 1945: 61). *Pyrgus philetas* ranges from central, southcentral, and west Texas to southern New Mexico and southern and middle Arizona. Not known from California, it conceivably could be found in the extreme southeastern part of that state.

Narrow sympatry in Texas

Since Texas is the only one of the United States in which *P. oileus* and *P. philetas* meet, we have, for several years, in the course of other

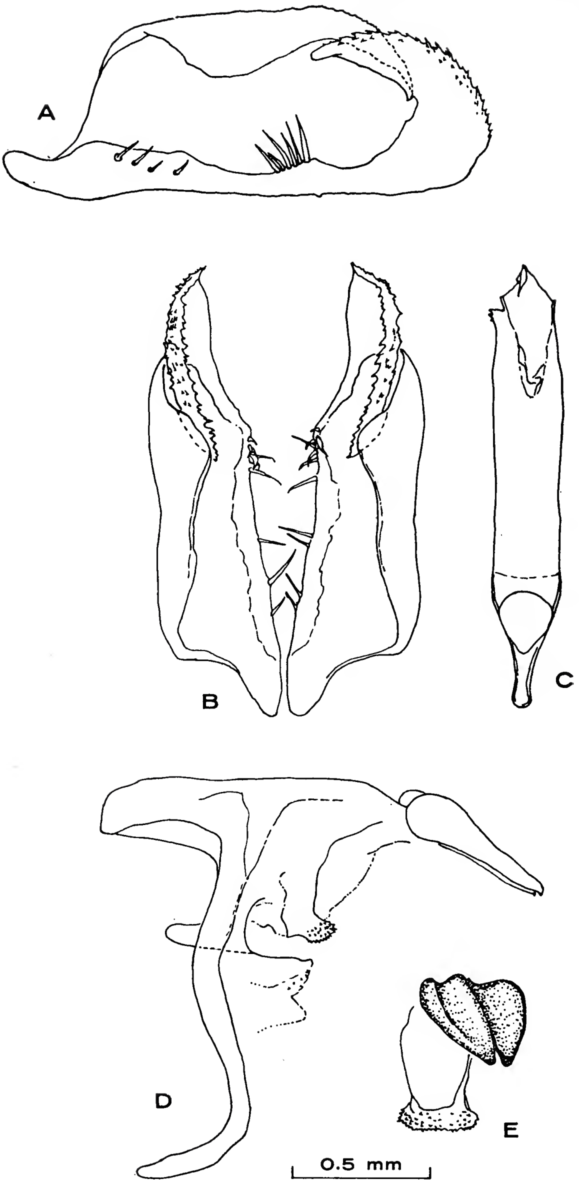


Fig. 1. Male genitalia of *Pyrgus oileus*. A. Medial view of right valva. B. Dorsal view of both valvae. C. Dorsal view of aedeagus. D. Left lateral view of uncus, tegumen, gnathos, vinculum, and saccus. E. Left dorsolateral view of uncus and gnathos. [A, drawn from one male, and B to E, from another; *both* from Houston, Harris County, Texas, VIII-12-1957 (J. M. and S. N. Burns).]

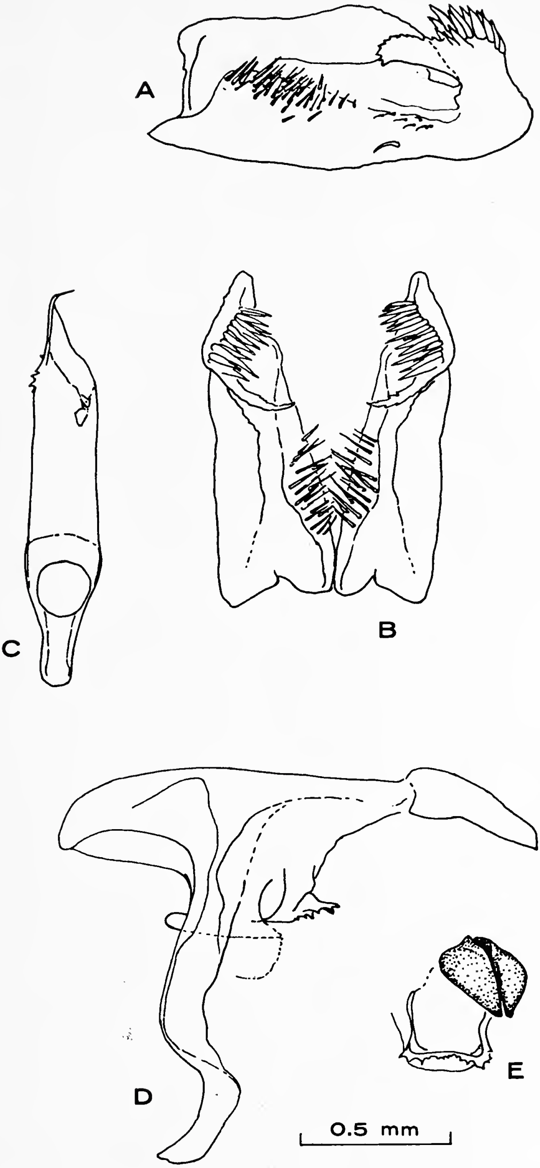


Fig. 2. Male genitalia of *Pyrgus philetas*. A to E as in fig. 1. [A, drawn from male from Nameless Road in NW Travis County, Texas, VI-3-1967 (J. M. Burns); B to E, from male from Palmetto State Park, Gonzales County, Texas, IV-6-1967 (J. M. Burns).]

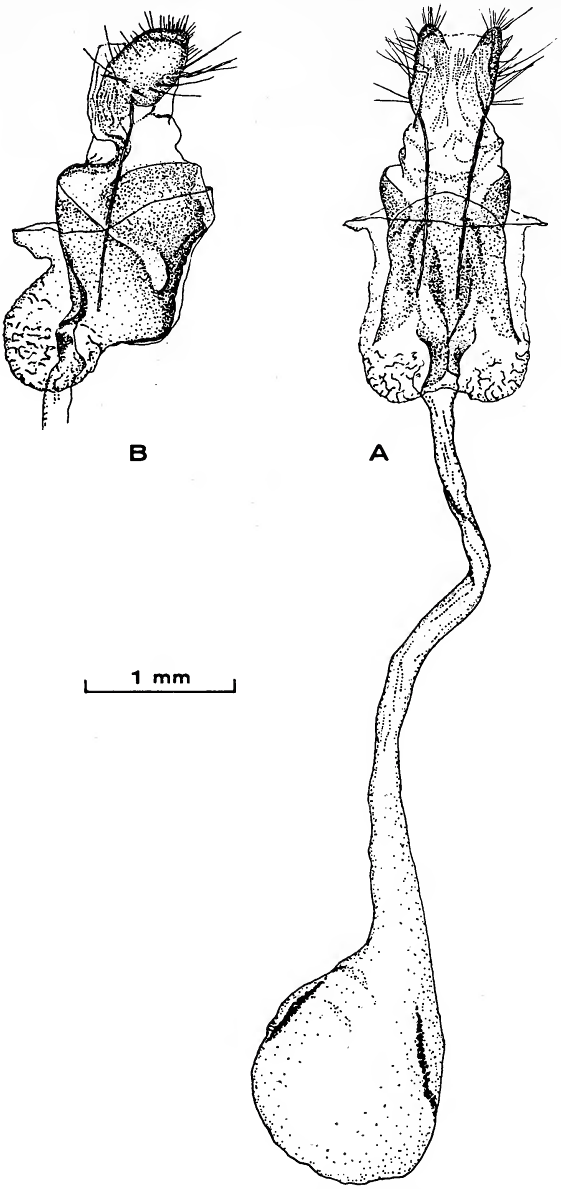


Fig. 3. Female genitalia of *Pyrgus oileus*. A. Ventral view of bursa copulatrix, sterigma, and ovipositor lobes. B. Right lateral view. [A and B, drawn from female from Houston, Harris County, Texas, VIII-12-1957 (J. M. and S. N. Burns).]

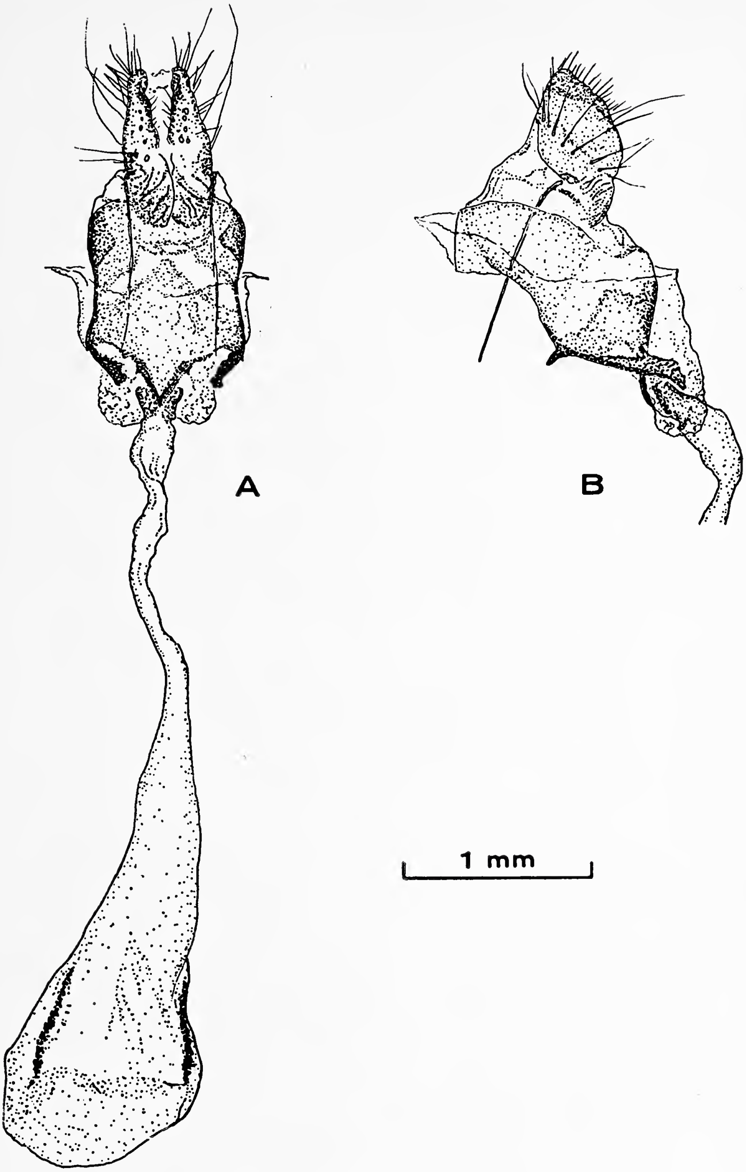


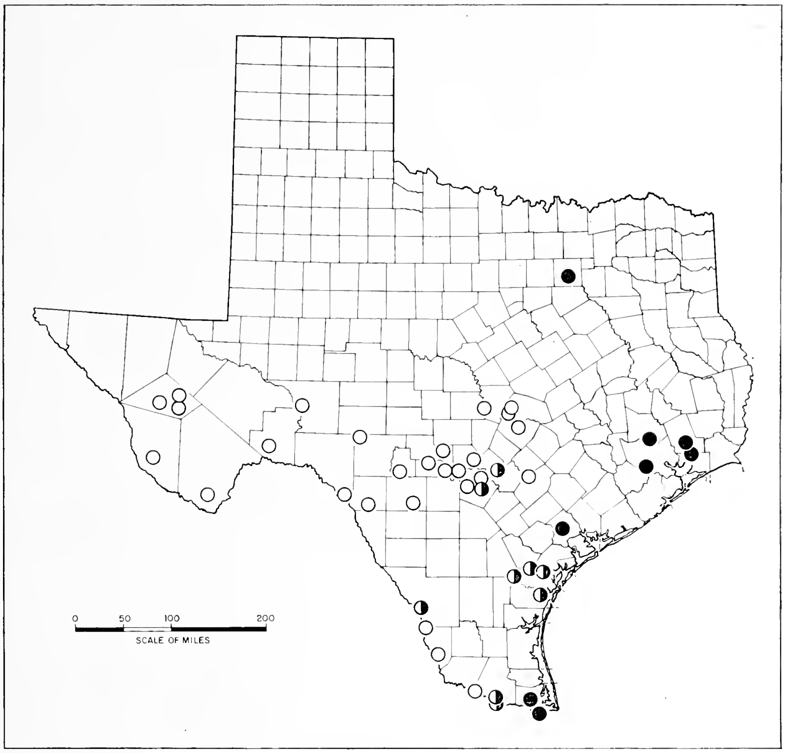
Fig. 4. Female genitalia of *Pyrgus philetas*. A. Ventral view of bursa copulatrix, sterigma, and ovipositor lobes. B. Left lateral view. [A and B, drawn from female from Welder Wildlife Foundation Refuge, Sinton, San Patricio County, Texas, X-13-1963 (J. W. Tilden).]

field studies, accumulated data on the spatial distribution of these skippers in Texas and have paid special attention to the critical zone of junction. As happens for so many east-west species pairs, *central* Texas is where the action is (see Remington 1968 for a recent summary and general discussion). We find the two species sympatric and synchronic at several points (fig. 5) — and find no evidence whatsoever of hybridization between them (either with or without introgression).

P. oileus is apparently common and resident in coastal regions of Texas and sporadic at interior localities in east and eastcentral Texas. *All* peripheral interior records derive from only one to a few specimens caught *late* in the year: Dallas, 1♂, IX-17-1948 (H. A. Freeman); 1♂, X-16-1949 (H. A. Freeman); New Braunfels, 3♂, X-8-1967 (J. F. Doyle III, R. Jameson, M. A. Rickard); San Antonio, 1♂, X-20-1945 (H. A. Freeman). This, along with the lateness of the lone Arkansas record (1♀, IX-10-1929, H. A. Freeman), suggests a fluctuating northern and western distributional limit that expands substantially in favorable years. The dots representing *P. oileus* in Chambers, Liberty, and Victoria counties (fig. 5) are based on larval collections reported by Bottimer (1926: 797) but are the *only* records (of either species) appearing in fig. 5 that are *not* taken from adult specimens examined by one or both of us.

Although Freeman (1951: 21) reported *P. philetas* only from far western (Marathon) and far southern (Laredo, Pharr) Texas, we find it resident through much of the central part of the state; and we believe that our present picture (fig. 5) is still incomplete. At middle latitudes in central Texas, the eastern distributional limit is *roughly* the eastern edge of the Edwards Plateau (marked by the Balcones Escarpment). Even there, however, in the vicinity of Austin, New Braunfels, and San Antonio, *P. philetas* is not rare; and correspondence is inexact, as evidenced by the occurrence of *P. philetas* early in the year in fresh condition in Gonzales County, 29 miles southeast of the Balcones Escarpment. Between Austin and San Antonio, the escarpment shifts rapidly from a north-south to an east-west orientation and extends westward from San Antonio. In southcentral Texas, then, *P. philetas* departs widely from the Edwards Plateau, ranging east to Corpus Christi and south to the Rio Grande. Altogether, its eastern limit is a fairly straight line falling between the 97th and 98th meridians.

Every instance of sympatry of *P. oileus* and *P. philetas* is in central and especially southcentral Texas between the 97th and 100th meridians. In this narrow zone we have found these species sympatric —



	J	F	M	A	M	J	J	A	S	O	N	D
Pyrgus oileus	1	5	2	12	7	13	10	28	6	43	10	1
Pyrgus philetas	0	3	4	10	6	13	6	11	14	35	12	2

Fig. 5. Spatial and temporal distribution of *Pyrgus oileus* (dots) and *Pyrgus philetas* (circles) in Texas. Half dots indicate known points of sympatry. The more interior and northern records of *P. oileus* probably represent transient populations (see text). Temporal distribution is crudely expressed in a month by month tally of all dated specimens examined.

and sometimes also *precisely* synchronic — at New Braunfels, Comal County (3 *oileus*, 4 *philetas*); San Antonio, Bexar County (1 *oileus*, 24 *philetas*); U.S. highway 181 x Papalote Creek, Bee County (1 *oileus*, 1 *philetas*); Lake Corpus Christi State Park, San Patricio County (1 *oileus*, 3 *philetas*); Welder Wildlife Foundation Refuge, San Patricio County (14 *oileus*, 6 *philetas*); Corpus Christi, Nueces County (2 *oileus*, 1 *philetas*); Pharr, Hidalgo County (9 *oileus*, 10 *philetas*); Santa Ana National Wildlife Refuge, Hidalgo County (3 *oileus*, 3 *philetas*); and Laredo, Webb County (2 *oileus*, 1 *philetas*).

Table 1 summarizes by county and by sex the 156 specimens of *P. oileus* and 128 specimens of *P. philetas* that we have examined from Texas and indicates the kinds of samples on which the symbols plotted in fig. 5 are based.

Table 1. Texas specimens of *Pyrgus* examined.

County	*Pyrgus oileus*		*Pyrgus philetas*	
	♂♂	♀♀	♂♂	♀♀
Bandera			6	
Bee	1			1
Bexar	1		12	14
Brewster			7	
Burnet			1	
Cameron	62	38		
Comal	3		4	1
Crockett			1	
Dallas	2			
Edwards			1	
Gonzales			1	
Harris	8	8		
Hidalgo	8	5	3	11
Jeff Davis			2	2
Kendall			4	2
Kerr			14	7
Kinney			7	
Montgomery	1			
Nueces	1	1	1	1
Presidio			1	
Real				1
San Patricio	10	5	6	3
Terrell			1	
Travis			5	1
Uvalde			1	1
Val Verde			1	
Webb	2		1	1
Williamson			1	
Zapata			1	
N =	99	57	82	46

Temporal distribution in Texas

Both species are multivoltine and occur almost throughout the year (see fig. 5, bottom) wherever a suitably mild climate prevails. Even where they are sympatric, there is no temporal displacement of these two related populations.

Discussion

Reproductively isolated populations recently evolved from a common ancestor may remain allopatric, not because of competitive exclusion or the persistence of an old extrinsic barrier to distribution, but because, in the course of inevitable ecologic differentiation, they have specialized in ways that put new restrictions on their distribution. If a potential distribution-limiting factor varies abruptly in the space between them, allopatric sister populations may become finely adjusted to distinct modes of that factor and thereafter be geographically segregated by this very adaptation. Should such a condition persist, even widely diverging populations would continue to replace each other geographically like subspecies of a polytypic species or species of a superspecies, without long qualifying as either. It would be most unreasonable to insist that ecologic divergence of sister populations to a patently non-competitive, *coexisting* state be the sole admissible evidence of complete speciation.

The mutual geographic replacement of *P. oileus* and *P. philetas* in the United States suggests competitive exclusion and suggests that they may be more closely related than their sympatry in Mexico and their level of morphologic divergence indicate. But competitive exclusion is probably not involved. Along its eastern margin through central Texas, *P. philetas*, as noted above, stops almost on a line; yet it regularly encounters *P. oileus* only along the southern part of this line, and there there is some overlap. Rather than limiting each other, *P. oileus* and *P. philetas* are more likely limited — directly or indirectly — by humidity, an abiotic factor that decreases rapidly from east to west in central Texas. Direct limitation could stem, of course, from physiological adaptation of *P. oileus* to moister and *P. philetas* to drier conditions; indirect limitation could take the form of different larval foodplants that are, in turn, directly limited by humidity. *P. oileus* and *P. philetas* are limited northward at similar latitudes. Altogether it appears that these species, which are substantially sympatric southward, gradually sort themselves out geographically in response to humidity as they approach their northern temperature limits.

Various explanations for the phenomenon of neatly allopatric sister species have recently been considered by, for example, Mayr (1963: 81-82), Remington (1968), and Selander (1969: 215-219). Mayr feels that interpretations — like the one offered here for *P. oileus* and *P. philetas* — involving differences in adaptation to sharply breaking variables of the environment, probably apply in a majority of cases. Remington and Selander, in dissimilar contexts, both emphasize interpretations involving competitive exclusion, though Selander implies that competitive exclusion may be pertinent in a minority of cases. There is general agreement that persistent allopatry of closely related species often poses intricate evolutionary problems that are hard to analyze and interpret with confidence.

SUMMARY

Pyrgus oileus and *P. philetas*, though closely related, are incontestably different species — some current opinion to the contrary notwithstanding. Sympatric in part of Mexico, these morphologically distinct, multivoltine species become allopatric toward their northern distributional limits in the southern United States. There, *P. oileus* of eastern, moister environments and *P. philetas* of western, drier environments approach each other or meet in central Texas, and overlap slightly in space (and fully in time) in southcentral Texas, without hybridizing. Although competitive exclusion could be suggested, it appears more likely that these species are limited (either directly or indirectly) by an abiotic factor, humidity.

Acknowledgements

We thank F. H. Rindge and W. D. Field for access to *Pyrgus* material in their care at the American Museum of Natural History and the United States National Museum, respectively; B. and K. Mather for lending Mississippi specimens of *P. oileus*, H. A. Freeman for lending peripheral Texas specimens of *P. oileus*, and J. W. Tilden for lending all specimens of *P. oileus* and *P. philetas* in his collection; and R. G. Gillmor for drawing the genitalia figures. This research was supported in part by National Science Foundation grant GB 5935 to J. M. Burns.

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A DESCRIPTION OF *POCOBLETUS CORONIGER* SIMON (ARANEAE, LINYPHIIDAE)*

By Arthur M. Chickering

Museum of Comparative Zoology

More than thirty years ago I began finding this species in my collections from localities in the Panama Canal Zone. For many years they were regarded as representatives of a new genus. During a period of work in the Museum National d'Histoire Naturelle in Paris in 1958 Dr. H. W. Levi made sketches of the type specimens of *Pocobletus coroniger* Simon and later identified my specimens from Panama. In 1894 Simon gave a brief definition of the genus *Pocobletus* and in a footnote he gave a very brief description of both sexes of *Pocobletus coroniger* and included the species in his general treatment of the Argiopidae. No figures were given with the description. Because of the uncertainties regarding the status of the species it now seems worth while to prepare a series of figures together with what I hope will be regarded as an adequate description of both sexes of this interesting species. As a basis for this description I have selected a male from Summit, Panama Canal Zone, August, 1950 and a female from Barro Colorado Island, Canal Zone, February, 1958. Other specimens from localities in the Canal Zone have also been used to supplement data derived from these two specimens.

Pocobletus coroniger Simon, 1894

Figures 1-9

Pocobletus coroniger Simon, 1894: 688, 705. The male and female syntypes are in the Museum National d'Histoire Naturelle, Paris. F. P.-Cambridge, 1903: 426; Petrunkevitch, 1911: 267; 1928: 124; Roewer, 1942: 595; Bonnet, 1958: 3729.

Male. Total length 1.65 mm. Carapace about 0.74 mm long; about 0.61 mm wide opposite second coxae where it is widest; about 0.4 mm tall; general form essentially as shown in Figure 1; anterior projection bearing eyes; ventral margin smooth; apparently with an obscure median pit shortly below the beginning of posterior declivity. Eyes: eight in two rows; anterior row moderately recurved; posterior row very slightly recurved; both rows as viewed from above (some variations in relative positions of eyes and rows have been noted

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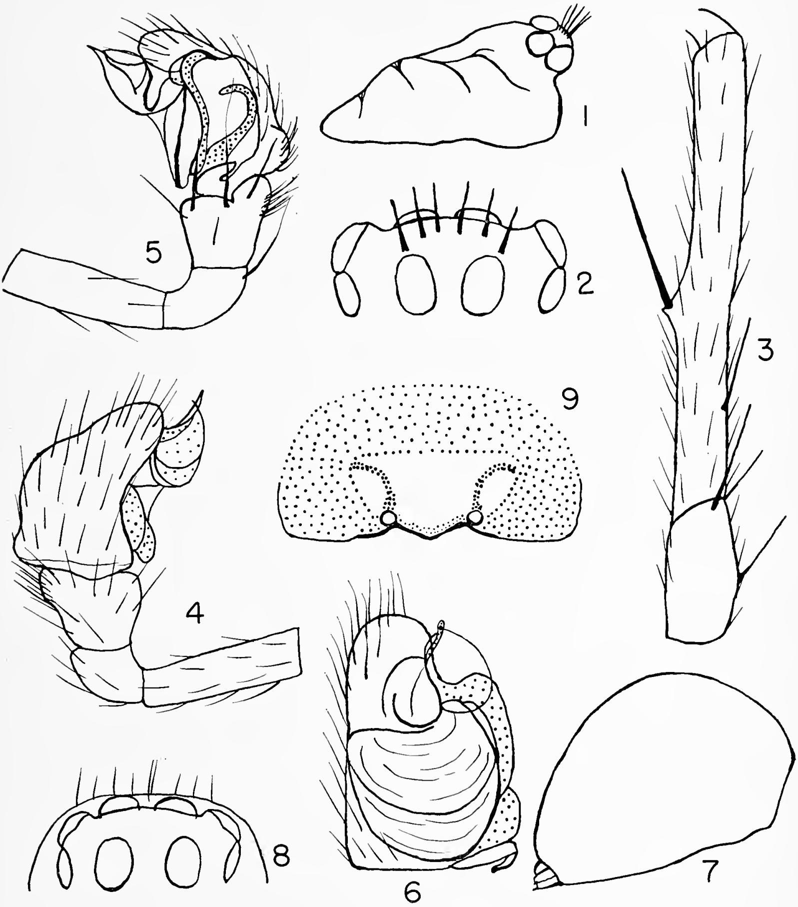
among the numerous available specimens). Ratio of eyes AME : ALE : PME : PLE = 5 : 7 : 8 : 6 (irregularities in outlines of eyes make it difficult to be accurate in measurements); AME separated from one another by about their radius and from ALE by slightly more than this distance; PME separated from one an-



Figures 1-9. *Pocobletus coroniger* Simon. Fig. 1. Carapace of male; right side. Fig. 2. Eyes of male from above. Fig. 3. First right patella and tibia of male; dorso-prolateral view. Figs. 4-5. Left palp of male; prolateral and retrolateral view, respectively. Fig. 6. Left palpal tarsus of male; ventral view. Fig. 7. Right lateral side of male abdomen. Fig. 8. Eyes of female from above. Fig. 9. Epigynum from below.

other by slightly less than their radius and from PLE by their radius; ALE and PLE contiguous; long diameters always used for measurements; all eyes on a forward projection of the cephalic region of the carapace. Height of clypeus equal to nearly three times the diameter of AME. Six robust spines are placed above AME (Fig. 2). Chelicerae: moderately robust, vertical, slightly divergent; fang normal, evenly curved; fang groove, as observed in dissested specimen, has a tooth of moderate size on each margin near base of fang and a pair of small teeth on each margin near the medial end of fang groove; on the posterior surface of each chelicera there is a cluster of small cusps a little above the middle; some variations in respect to teeth have been noted among the numerous specimens available for comparison and even between right and left sides in the same specimen. Maxillae: nearly three-fourths as broad as long; only slightly convergent. Lip: short, broad, only about one-third as long as maxillae. Sternum: very convex; scutiform; about as broad as long; bluntly terminated between fourth coxae which are separated by their width. Legs: 1243 in order of length; in general long and slender; with few slender spines; distinctive spines of first patella and tibia as shown in Figure 3. Palp: all segments except tarsus without special modifications; tarsus complicated (Figs. 4-6). Abdomen: general form as shown in Figure 7; without special modifications. Color in alcohol: carapace brownish with variations; lateral sides of thoracic region with irregular, darker, radiating bands; a somewhat irregular, central V-shaped darker area extends from the beginning of the posterior declivity toward the ocular region. Chelicerae, maxillae, lip and sternum brown with small irregular dots. Legs yellowish with darker areas. Abdomen: with a highly decorative color pattern; the anterior two thirds of the dorsal surface is yellowish with several irregular white spots; the posterior third of the dorsal surface is darker brownish surrounded by numerous irregular white inter-connected spots; ventro-laterally on each side there is an irregular white band composed of several iregular white spots; the venter is brown with a pair of small light spots somewhat behind the middle. The color pattern is difficult to describe accurately and, moreover, much variation has been noted among the numerous specimens available for comparison.

Female. Total length 1.58 mm. Carapace 0.57 mm long; about 0.53 mm wide; about 0.33 mm tall; general form essentially as in male; ocular region less prominent than in male. Eyes: ratio of eyes AME : ALE : PME : PLE = 5 : 7 : 8 : 6.5; AME separated from one another by a little less than their radius and from ALE by about their radius; PME separated from one another and from PLE by about their radius; ALE and PLE contiguous. Height of clypeus equal to about 1.5 times the diameter of AME; the robust spines in the ocular area, so prominent in the male, are absent here (Fig. 8). Chelicerae, maxillae, lip and sternum essentially as in male as far as observed. Abdomen: as in male in all major features except the epigynum shown in Figure 9. Color in alcohol: color pattern also essentially as in male except that it tends to be somewhat clearer than in that sex; the contrast between light and dark areas is greater than in the male but there is also considerable variation among available specimens.

Records. In addition to the specimens selected for moderately detailed description I also have in the collection more than fifty specimens taken in the following named localities in the Panama Canal Zone: Chilibre, Barro Colorado Island, Canal Zone Forest Preserve, Frijoles, Gamboa, Madden Dam Region, Pedro Miguel, Summit Gardens, Summit. A male and two females have recently been added to the collection from Turrialba, Costa Rica, August 4, 1965.

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CARBON DIOXIDE, A RELEASER FOR DIGGING BEHAVIOR IN *SOLENOPSIS GEMINATA* (HYMENOPTERA: FORMICIDAE)*

By Walter Hangartner

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The behavior of ants digging through sand or clay in the direction of trapped nestmates has been described by Belt (1874) and Lafleur (1940). Wilson (1958) showed that in *Pogonomyrmex badius* (Latreille) this behavior pattern is released by a volatile substance originating from the mandibular glands. Later, McGurk et al. (1966) identified the responsible compound as 4-methyl-3-heptanone. At the same time, Blum and Warter (1966) isolated 2-heptanone from *Conomyrma pyramica* (Roger) and described its function as the releaser of alarm and digging behavior. Spangler (1968) reported that not only whole workers, but also amputated parts as well as larvae and pupae of *Pogonomyrmex occidentalis* (Cresson) attract workers of this species and release digging behavior. Forrest (1963) studied *Lasius flavus nearcticus* and four species of *Acanthomyops* and found that workers also dig to free ants of another species but attack them as soon as they are released.

During studies on a colony of *Solenopsis geminata* (Fabricius), I noticed that returning foragers started to remove a plug of cotton used to block the entrance of an artificial nest immediately after its mounting, even if the position of the entrance was rotated through 180°. During most of these actions, they used their mandibles to chew away small pieces of the obstacle. The purpose of the present paper is to report on the finding that this behavior is released by the carbon dioxide produced by the ants trapped inside the nest.

Material and Method

During the whole experimental period, the same colony of *Solenopsis geminata* was used. This colony consisted of several thousand workers, a queen, large piles of brood and a few hundreds of winged males and females which were all kept in a Wilson nest (Wilson, 1962a). To examine the digging behavior toward trapped nestmates, workers or other objects were trapped in the vial shown in Figure 1. A hole 6 mm in diameter was punched through the top of the plastic

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*Manuscript received by the editor March 16, 1969

stopper and blocked again by gluing a piece of an index card (Oxford, 7182 B) to it. The bottom of this stopper was perforated with a needle approximately 50 times, which allowed volatiles produced inside the vial to penetrate but at the same time prevented contact between the trapped ants and the cardboard. A capillary (i.d. 1 mm) was efficient enough to supply the trapped ants with the necessary oxygen, and a layer of moist cotton guaranteed the essential humidity. The control bottle was prepared in the same way but contained only moist cotton. The test- and the control-tube were presented simul-

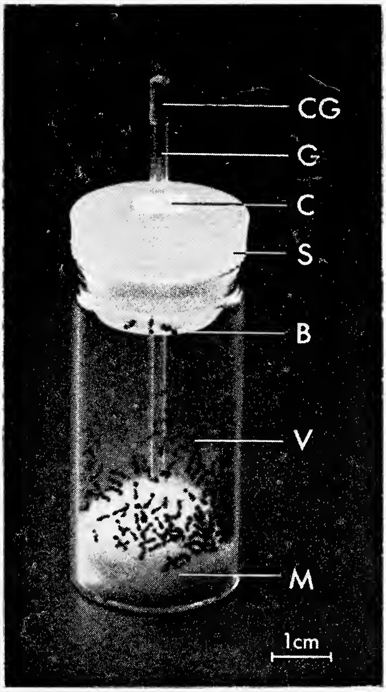

Figure 1. Arrangement used to measure the digging activity of *Solenopsis geminata* released by trapped nestmates.

V	Glass vial
S	Plastic-Stopper
C	Cardboard blocking a hole (6 mm) punched through the top of the stopper
B	Perforated bottom of the stopper
G	Glass capillary (gas exchange)
CG	Copper gauze
M	Moist cotton.

taneously on top of the nest and left there for 20-22 hours. Because the cardboard covering the hole on top of the stopper was the only material the ants could remove in attempting to reach the trapped workers, all their digging activity was directed towards these areas. After each test, the pieces of cardboard were therefore removed and the "damage" done to them by the digging ants examined. The following scoring system was used to quantify the findings:

0 : No visible chewing marks on the surface of the cardboard
1 : Superficial chewing marks
2 : Heavy chewing marks
3 : Only a transparent film of cardboard remains at the site of digging
4 : The diameter of the hole dug is < 1 mm
5 : The diameter of the hole dug is > 1 mm
6 : The diameter of the hole dug is > 2 mm
7 : The diameter of the hole dug is > 3 mm

If the ants worked on more than one place, the different scores were added. Each test was repeated at least five times.

RESULTS

Fifteen to thirty minutes after the bottles were placed on top of the nest, some workers could be observed palpating the surface of the cardboard-seal on the test-tube with their antennae. Others just rested on this place for a few minutes, their antennae slightly raised. Suddenly, a single ant started to work on the cardboard with its mandibles, rather hesitating at first, but gradually with more vigor. When one individual became involved in such activity, it soon was joined by at least another ant, and occasionally I noticed up to ten workers chewing at the same spot. The digging ants sometimes were replaced by other nestmates after various times, or they continued working until a hole was punctured. Very often, however, they abandoned this behavior before an opening was created, leaving only chewing-marks of different intensities.

Table 1. Result of the digging behavior released by trapped workers, females, males or brood (larvae and pupae approx. 1:1). The mean activity is based on eight repetitions.

Trapped individuals	Average digging response	Range
200 workers	5.6	5-6
15 winged females	5.0	2-8
20 winged males	4.6	2-6
200 larvae & pupae	4.6	2-6
Control	0.4	0-3

The first experiment showed that the behavior pattern just described can be released by trapped workers, females, males, and even brood (Table 1). The positive result obtained with brood indicates that the "rescue" activity can be initiated by something more than stridulation of the trapped individuals, the mechanism in leaf-cutting ants (Markl, 1967). Stridulation can also be ruled out by trapping dead ants which have been killed by chilling just before the experiment. In series A, the dead workers were presented intact, whereas in series B, they were homogenized, transferred to a small piece of cotton and trapped in this way. In both cases the small pieces of cardboard were replaced after 20 hours and the experiment stopped after 44 hours.

Figure 2 shows that the homogenized ants release a stronger digging activity than the intact ones and that this activity increases with

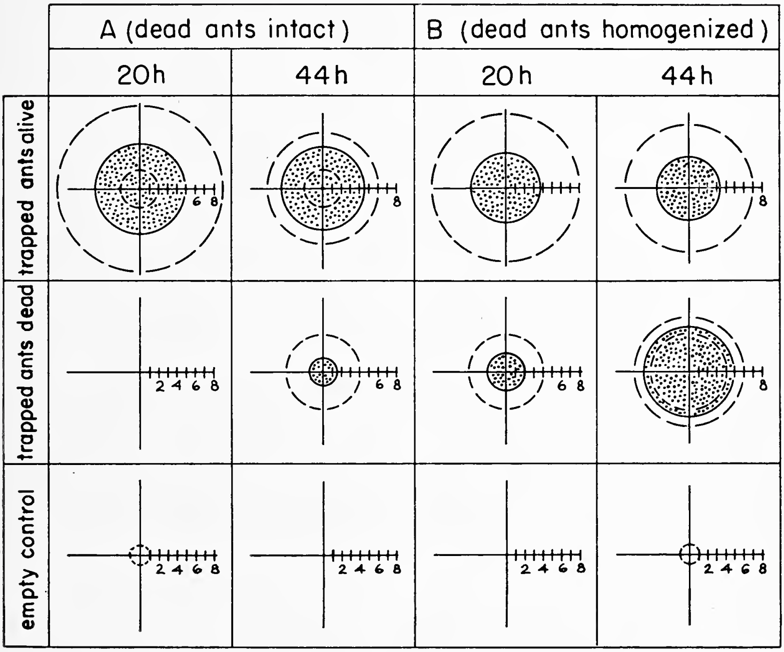

Figure 2. Comparison of the digging activity released by living and dead ants recorded after 20 and 44 h, respectively. Series A: Dead workers intact, Series B: Dead workers homogenized. The radius of the stippled areas represents the average digging response and the radius of the dashed circles indicates the range of the 10 experiments performed.

increasing decomposition time of the dead ants. There are at least 2 possible explanations to this phenomena:

1. The chemical releaser for digging behavior is produced somewhere inside the ant's body and, therefore, requires some time to diffuse to the surface of a dead worker to become active. This diffusion time is reduced if the workers are homogenized.

2. The responsible pheromone is a product of decomposition. Decomposition starts slower in intact ants, because an uninjured integument represents a certain barrier for external factors which induce or accelerate the decomposition process.

The first explanation is weakened by the fact that I did not succeed in localizing a gland responsible for the production of a pheromone. The second explanation, on the other hand, is slightly supported by the following finding: In *Solenopsis saevissima*, products of decomposition accumulate in the body of dead workers no sooner than 24 hours (Wilson et al. 1958). That is about the period during which I could not observe any digging behavior toward trapped *geminata*-corpses (see Fig. 2). Looking therefore for volatile products of decomposition that are also emitted by the living ants and brood, it seemed reasonable to suspect a substance such as carbon dioxide.

To obtain initial information about the value of this prediction, a small plastic container holding 0.5 ml of 1 M NaOH was introduced into the space between top and bottom of the stopper (cf. Fig. 1). A second stopper was prepared in the same way, but the container was filled only with 0.5 ml distilled water. Each stopper was used to seal a vial containing 150 workers. A third bottle did not contain ants and its container was empty. Table 2 shows that the presence of NaOH — a powerful absorbent for CO_2 — actually influences the digging behavior negatively. It reduces the average digging response to almost the same low level as found in the control.

Table 2. Effect of NaOH on the digging behavior of ants toward trapped nestmates. Number of repetitions: 10.

Number of trapped ants	Contents of inserted container	Average digging response	Range
150	0.5 ml H_2O dist.	3.6	1-6
150	0.5 ml 1 M NaOH	0.5	0-2
0 (control)	empty	0.1	0-1

This result supports the CO_2-hypothesis, but is not absolutely conclusive, because Sodium hydroxide could absorb other volatiles beside CO_2. In an attempt to get a more direct proof, I performed the following experiment: 5 bottles were prepared in the way shown in Figure 1 except that they did not contain any ants. They were then connected with U-shaped pieces of glass tubing (i.d. 1.5 mm) as demonstrated on top of Figure 3. After the whole system has been placed on a Wilson nest, a slow CO_2-stream (3.5 cm^3/min) was pressed into one end of the tubing. Due to loss of CO_2 through the cardboard and perhaps tiny leaks in the stoppers, only traces of this gas left the opening at the other end. I, thereby, got a more or less continuous gradient from a relatively high CO_2-concentration (vial 1) to a relatively low concentration (vial 5). Simultaneously I employed a second system of the same design, but compressed air was used instead of CO_2 (control). In 20 hour-intervals, the cardboard on each stopper was replaced by a new one. The results of five repetitions can be taken from Figure 3 (bottom).

It is evident that a relatively low concentration of CO_2 is able to release the same behavior pattern as do trapped workers. However, the efficiency of this releaser decreases with increasing concentration. It might be of interest to notice that ants which punctured the cardboard of vial 3 died or were at least anesthetized after penetration into the interior of the stopper, whereas this effect could not

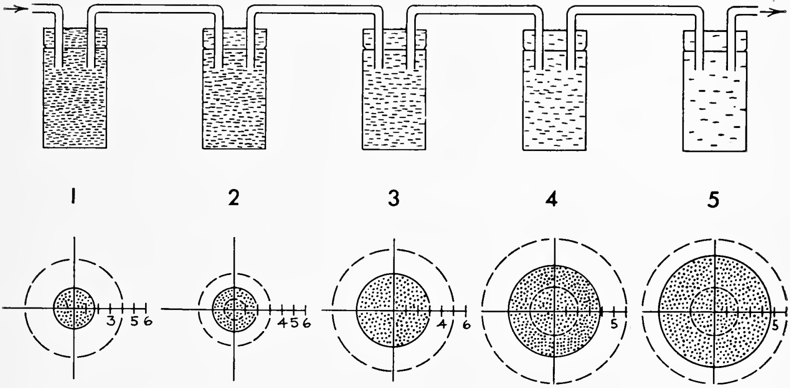

Figure 3. Arrangement (top) and results (bottom) of the experiment to test the effectiveness of CO_2 as a releaser for digging behavior. The density of the dashes represents the relative concentration of carbon dioxide inside the vials, and the arrows show the direction of the gas flow. The radius of the stippled circle areas represents the average digging response and the dashed circles indicate the range of five experiments.

be observed in either vial 4 or 5. This means that only concentrations of carbon dioxide which are harmless for these animals act as a highly efficient digging stimulus. No positive result could be registered in the control experiment, which indicates that pure air is completely inactive as a releaser of digging behavior.

If the CO_2 produced by trapped workers of *Solenopsis geminata* is the only substance responsible for the release of the described behavior, members of this species should also dig toward locked up ants of other species. I therefore trapped 150 workers of *Solenopsis geminata*, 150 workers of the closely related fire ant *Solenopsis saevissima* (Myrmicinae) and 30 workers of *Acanthomyops interjectus*, belonging to a different subfamily (Formicinae). The control-vial was empty. The 4 tubes were presented to the *geminata*-colony simultaneously, and the results are shown in Table 3.

All three species released digging behavior that is definitely above the control. The relatively small activity toward *Acanthomyops interjectus* is probably due to the fact that *Acanthomyops* species produce volatiles which have a strong repellant effect against members of other ant species (Regnier and Wilson, 1968 and pers. commun.).

Table 3. Results of the digging behavior of *Solenopsis geminata* released by trapped workers of *Solenopsis geminata*, *Solenopsis saevissima* and *Acanthomyops interjectus*. (Mean and range of ten repetitions).

Trapped species	Average digging response	Range
S. geminata	4.1	1-6
S. saevissima	5.0	0-10
A. interjectus	2.8	0-6
Control	0.1	0-1

Discussion

CO_2 is well known to attract the blood-feeding sexes of haematophagous arthropods (Reeves, Wiesinger, Carcia, Fallis and Smith, Nelson, Wilson et al., Kato et al., De Foliart and Morris, Thompson, in Anderson and Olkowski, 1968). Lacher (1964) found receptor cells on the antennae of workers and males of the honey bee which respond specifically to CO_2. Lacher (1964) and Boeck et al. (1965) speculated that this CO_2-response may serve the colony in controlling the concentration of carbon dioxide in the interior of the hive. Such a function, however, remains without proof. In the myrmecine ant *Solenopsis saevissima*, Wilson (1962b) demonstrated that carbon dioxide acts as a weak attractant that finally leads to settling. Because the same behavior could be observed during these studies on *Solenopsis geminata*, I consider the digging activity released by CO_2 as a by-product of attraction enabling the ants to get closer to the source of the stimulus. This interpretation is supported by the observation that if there is no hindrance between the workers and the source of CO_2, the ants are merely attracted to the place where the concentration is most convenient; no digging behavior can be observed in such a case.

The results presented in this paper offer a possible explanation to all the observations of digging behavior toward trapped ants as cited in the introduction. This of course does not mean that the same mechanism works in all ant species. The finding that single individuals of *Pogonomyrmex badius* or even parts of a worker release digging behavior (Spangler, 1968) indicates that this species is extremely sensitive to CO_2, or it could also be that other chemical stimuli are involved. The whole surface of the ant's body as well as larvae and pupae could be contaminated by 4-methyl-3-heptanone, the compound identified as releaser for alarm and digging behavior (McGurk et al., 1966).

Because CO_2-concentrations up to 1-2% were demonstrated in the interior of ant nests (Poitier and Duval, 1929; Raffy, 1929), this simple molecule could accomplish the following functions in a *Solenopsis geminata* colony:

1. It acts as a pheromone to control settling inside the nest (Wilson, 1962b).
2. It diffuses through the nest entrance and serves as an orientation aid, at least in the near vicinity of the nest. [Wilson (1962b) concluded that fire ant workers are able to move up CO_2 gradients.]
3. It acts as a "rescue"-pheromone in case groups of ants are trapped following a major cave-in.
4. The CO_2 produced by large piles of brood attracts the workers necessary to take care of the larvae and pupae.

Although there may exist other or stronger stimuli which control these behavior patterns, CO_2 at least plays an important supportive role.

SUMMARY

Workers of *Solenopsis geminata* are attracted to low concentrations of CO_2 and try to dig through all obstacles in order to get close enough to the source of this chemical stimulus.

ACKNOWLEDGEMENTS

Thanks are due to Dr. E. O. Wilson and Mr. J. M. Reichson for their reading of the manuscript. The author is also grateful to Miss N. K. Lind, who offered many useful suggestions.

This work was supported by Grant No. GB7734 of the U. S. National Science Foundation (Dr. E. O. Wilson sponsor) and a grant from the Swiss National Science Foundation.

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NOTES ON AMERICAN THERIDIID SPIDERS

By Herbert W. Levi

Museum of Comparative Zoology, Harvard University

About 195 species of theridiid spiders are known from north of Mexico, about 800 in all the Americas. Among them are our commonest spiders but also numerous rare species. This is the first addition to my revisions of spiders of this family. Similar additions will be made periodically as it becomes necessary to report on new species, describe the other sex of species known from only males or females, record habitat notes of rare species and make corrections.

For their assistance I want to thank Miss M. E. Galiano of Buenos Aires, Mr. V. D. Roth of the Southwestern Research Station of the American Museum of Natural History, who collected specimens of rare Arizona species, and Dr. W. J. Gertsch, who made me aware of an error in my revision of the genus *Tidarren* and facilitated the loan of *Latrodectus mactans hesperus*. This research is in part supported by Public Health Research Grant AI-01944 from the National Institute of Allergy and Infectious Diseases.

Theridion arizonense Levi

Figures 1-4

Theridion arizonense Levi, 1957, Bull. Amer. Mus. Natur. Hist. 112: 49, figs. 137, 138, ♀. Female holotype from Rustler's Camp, Chiricahua Mountains, Cochise County, Arizona, in the American Museum of Natural History.

This species has heretofore only been known from the female.

Description of male. Carapace yellowish with a gray line around carapace and a wide median gray band. Sternum gray all around. Legs dusky gray, darker distally. Dorsum of abdomen gray with pairs of white spots posteriorly, sides yellowish, venter gray. Eyes subequal in size. Anterior median eyes one and one-quarter diameters apart, their radius from laterals. Posterior median eyes less than a diameter apart, one diameter from laterals. Total length, 2.2 mm. Carapace, 1.1 mm long, 1.0 mm wide. First femur, 2.3 mm; patella and tibia, 2.5 mm; metatarsus, 2.3 mm; tarsus, 0.8 mm. Second patella and tibia, 1.6 mm; third, 0.9 mm; fourth, 1.5 mm.

The embolus of the palpus (Fig. 4) appears to be partly covered by a lamella like that of *T. lawrencei*. The shape of the radix (Fig. 3) and ducts within the tegulum (Fig. 4) differ.

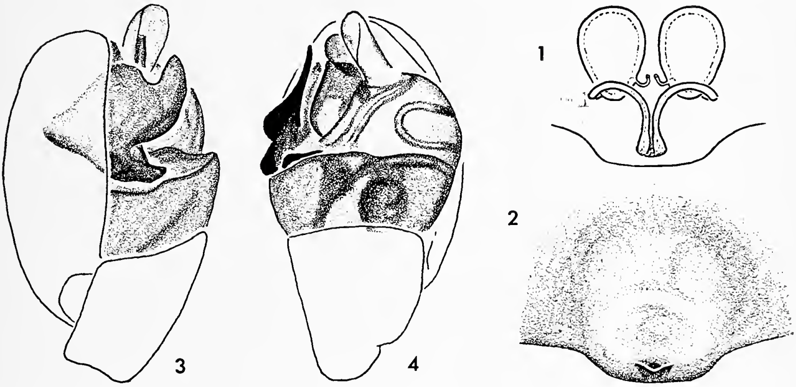
Record. Arizona: Rustler's Camp, Chiricahua Mtns., Cochise Co., 24 June 1963, ♂ (D. Futuyma).

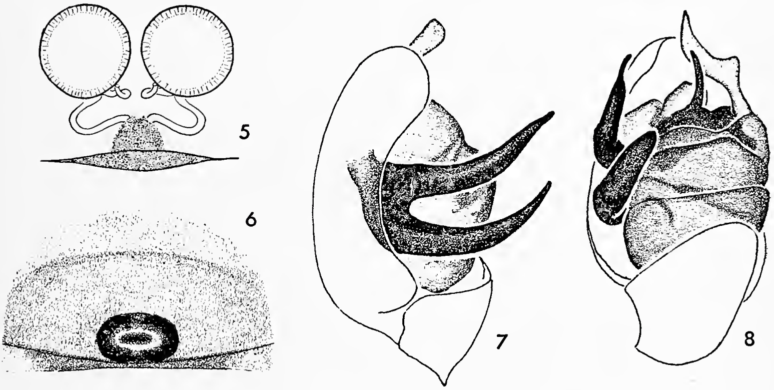
Theridion cochise Levi
Figures 5-8

Theridion cochise Levi, 1963, Bull. Mus. Comp. Zool., 129: 553, figs. 123, 124♂. Male holotype from Southwestern Research Station, Portal, Cochise County, Arizona, in the American Museum of Natural History.

This species has heretofore only been known from the male.

Description of female. Carapace, sternum and legs bright yellow.





Figs. 1-4 *Theridion arizonense* Levi. 1. Female genitalia, dorsal view. 2. Epigynum. 3,4. Left palpus. 3. Mesal view. 4. Ventral view.

Figs. 5-8 *Theridion cochise* Levi. 5. Female genitalia, dorsal view. 6. Epigynum (from slightly posterior). 7,8. Left palpus. 7. Mesal view. 8. Ventral view.

Abdomen whitish with some indistinct gray dorsal spots. Anterior median eyes one diameter apart, less than one diameter from laterals. Posterior median eyes one diameter apart, one and one-half diameters from laterals. Total length, 3.8 mm. Carapace, 1.4 mm long, 1.35 mm wide. First patella and tibia missing; second, 2.3 mm; third, 1.7 mm; fourth, 2.5 mm.

The epigynum (Fig. 6) is similar to that of *Theridion morulum* O.P.-Cambridge, but the dark area and openings are smaller. The opening is in the center of a dark depression.

Record. Arizona: Cochise County, South Fork, 13 July 1963, ♀ (V. Roth).

Theridion myersi Levi

Theridion myersi Levi, 1957, Bull. Amer. Mus. Natur. Hist. **112**: 31, figs. 95-98, ♀ ♂. Male holotype from Fort Myers, Lee Co., Florida, in the American Museum of Natural History.

This rare species was known only from Florida; Monterrey, Nueva León; Tamaulipas and Ixtepex, Oaxaca, Mexico, without information about its habitat. I collected an adult male under coral stones on the side of the highway. 18.III.1964, on Bahia Honda Key, Monroe Co., Florida.

Theridion melanosternum Mello-Leitão, emend.*

Figures 9-12

Theridion melanosternon Mello-Leitão, 1947, Arq. Mus. Paranaense 4: 237, figs. 4, 5 ♀. Female holotype from Bariquí, Curitiba, Brazil in the Inst. Defeso do Patrimonio Natural in Curitiba, examined by M. E. Galiano in 1968.

The types of the species were deposited in the Museu Paranaense. The museum no longer exists and the specimens are now kept in the Instituto de Defeso do Patrimonio Natural, Secretaria de Est. dos Negocios da Agricultura, Curitiba, Paraná, Brazil. It was never possible for me to examine the specimen. Miss Maria Elena Galiano paid a visit to this institution and made drawings for me of the type of *Theridion melanosternum.* The specimen is labeled *Theridium nigristerni.* Mello-Leitão gave total length 3.6 mm, and first patella and tibia 4.7 mm. The long legs and epigynum (Fig. 10-11) resemble those of *Theridion longipedatum* Roewer (=*T. longipes* Keyserling), described from Santa Fé de Bogota (a locality where the specimen presumably was bought or traded and not where it was found). However the measurements Keyserling gives are total length, 5.3 mm and first patella and tibia, 5.2 mm.

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*The specific name is here emended to have a correctly latinized ending,

Tidarren haemorrhoidale (Bertkau)

Theridium haemorrhoidale Bertkau, 1880, Mém. Cour. Acad. Roy. Sci. Lett. Belgique **43**: 78. Female holotype from Rio de Janeiro, lost. The description fits the widespread species believed to occur from the southern United States to Argentina and Chile.

?*Theridion maculosum* Keyserling, 1884, Die Spinnen Amerikas **2**(1): 30, pl. 1, fig. 14 ♀. Female holotype from Venezuela ["Caracas" on specimen], in the Institut Royal des Sciences Naturelles de Belgique, Brussels; examined, but in very poor physical condition.

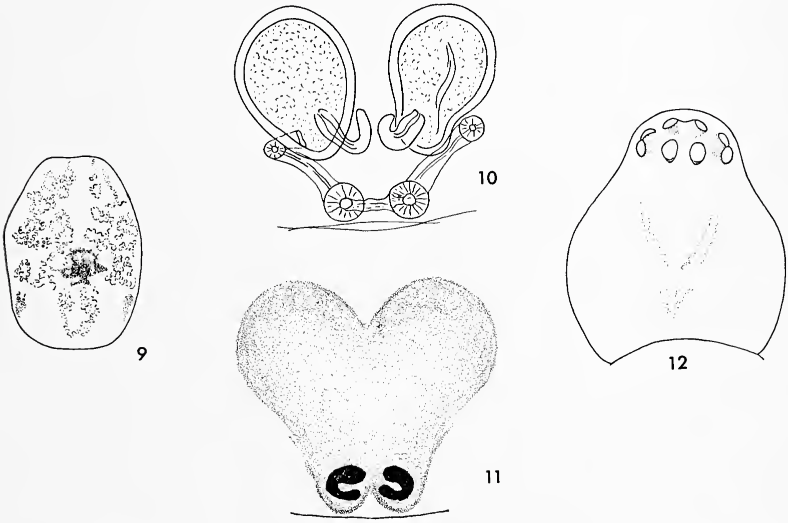
Theridium elevatum Banks, 1897, Canadian Entomol. **29**: 195. Female holotype from Brazos County, Texas, in the Museum of Comparative Zoology; examined. Name preoccupied by *T. elevatum* Thorell 1881.

Theridium fordulum Banks, 1909, Proc. Acad. Natur. Sci. Philadelphia **61**: 203. Female holotype from Chiral Paraíso, Costa Rica, in the Museum of Comparative Zoology; examined.

Theridium texanum Banks, 1910, Bull. U.S. Natl. Mus. **72**: 20. New name for *T. elevatum* Banks.

Theridion minor Chamberlin and Ivie, 1934, Bull. Univ. Utah, Biol. Ser. **2**(4): 10, 24-25, ♀. Female holotype from Tallahassee, Leon Co., Florida, in the collection of the University of Utah.

Tidarren fordum: — Levi, 1956, J. New York Entomol. Soc. **63**: 73, figs. 49-57, 61-64, ♀, ♂, map. 1967, Bull. Mus. Comp. Zool. **136**: 28, map. Not *Theridion fordum* Keyserling.



Figs. 9-12 *Theridion melanosternum* Mello-Leitão. 9. Abdomen. 10. Female genitalia, dorsal view. 11. Epigynum. 12. Carapace. (9, 10, 12 illustrated by M. E. Galiano, 11 after Mello-Leitao.)

Note. Recently I indicated that I had examined the type of *Theridion fordum* Keyserling (Levi, 1967, Bull. Mus. Comp. Zool. *136:* 28). This was not the case. Dr. W. J. Gertsch first made me aware that the type might not be the species I thought. Through the courtesy of Dr. J. G. Sheals and Mr. D. Clark the specimens were examined. Keyserling indicated that the specimen described came from Bogota, but that specimens from other parts of South America were at hand. The vial from Bogota contained two specimens: a mature female clearly belonging to *T. sisyphoides* (Walckenaer) and a juvenile specimen belonging to the other species for which the name *T. haemorrhoidale* is now used. The mature female was designated lectotype of *T. fordum.* The name *Theridion fordum* thus becomes a synonym of *T. sisyphoides.* All other specimens labelled by Keyserling as *T. fordum* belong to *T. haemorrhoidale.* The possibility exists that *T. haemorrhoidale* is a group of species having a similar epigynum. Particularly North American specimens are quite variable. However there are few males in collections and the females do not readily fall into groups. All intergradations occur.

Latrodectus variolus Walckenaer

Latrodectus variolus Walckenaer, 1837, Histoire Naturelle des Insectes Aptères, 1: 648. Female lectotype is Abbot manuscript figure 391, in the British Museum (Natural History) library. — McCrone and Levi, 1964, *Psyche* 71: 13.

Latrodectus mactans hesperus Chamberlin and Ivie, 1935, Bull. Univ. Utah, Biol. Ser. 3(1): 15. Figs. 1, 4, 6-14, 21, 22-23, ♀, ♂. Female holotype and male paratype from Salt Lake City, in the Univ. Utah collection now kept at the American Museum of Natural History; examined. NEW SYNONYMY.

Latrodectus curacaviensis: — Levi, 1959. Trans. Amer. Microscop. Soc. 78: 38 (in part).

In a recent paper Kaston (1968, Entomol. News *79:* 113) indicated that he considered *L. hesperus* different from *L. mactans* and *L. variolus* but gave no evidence for this statement. He indicated "that at least the common black widow of the west must be called *hesperus*." There is no indication whether he refers to the northern one common in British Columbia to northern California and considered *Latrodectus variolus,* or the one of southern California believed to be *Latrodectus mactans.*

The type of *L. m. hesperus,* was unavailable to me in 1957. I have recently examined both the female holotype and male paratype and have found them to be *L. variolus.* The female has a complete, unbroken "hourglass" on her venter. The name had previously been synonymized with *L. mactans* (Levi, 1959).

That the western form of *L. variolus* is the same as that of the east and southeast has to be assumed until we have contrary evidence based on modern species concepts. Such evidence might be significant morphological difference combined with differences in habits without intermediates by two populations separated geographically indicating reproductive isolation. This has not been found. Or better evidence might be the presence of two allopatric species with a region of overlap, in which two noninterbreeding populations can be found side by side. This also has not yet been demonstrated.

Vol. 76

A NEW GENUS OF MICRODONTINE FLIES (DIPTERA: SYRPHIDAE) WITH NOTES ON THE PLACEMENT OF THE SUBFAMILY[1]

By F. Christian Thompson[2]

I discovered the following new genus of Syrphidae while reviewing the Neotropical Microdontinae. I had planned to put aside its description until my study of the subfamily was finished. However, publication of a second species assignable to it by van Doesburg (1966) has necessitated publishing a name now for this genus so that it can be included in the Catalog of South American Diptera.

Paragodon, new genus[3]

Very small (4-5 mm.) microdontine flies. Face simple (slightly produced in *paragoides*); cheeks absent, eyes bordering on the oral opening; eyes dichoptic in both sexes; occiput evenly developed. Antennae short, about one-half as long as face; aristae short and thickened.

Thorax about as long as broad; pleura bare except mesopleura pilose and metapleura with microscopic pile; scutellum without apical spines and fringe; metasterna undeveloped and bare; metathoracic spiracles without hair fringes. Legs simple, with no basal setal patches on the femora and with cicatrices only on the hind femora. Wings without the spurious vein, with all apical crossveins straight.

Abdomen oval, lateral margins slightly emarginate and rolled under ventrally, with 1st sternite bare and 1st spiracles without hair fringes. Genitalia simple; ejaculatory apodeme simple, apical portion not triangularly flared; ejaculatory sac not sclerotized; ejaculatory process single, short, not posteriorly fused to ejaculatory hood; ejaculatory hood with anterior ventral portion elongate; sustentacular apodeme present, double, fused anteriorly to base of ejaculatory

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[1] Contribution no. 1392 from the Systematics and Morphology Research Laboratory, Department of Entomology, University of Massachusetts. Published with the aid of a grant from the Guy Chester Crampton Research Fund of the University of Massachusetts.

[2] 10 Edmunds Road, Wellesley Hills, Massachusetts, 02181. Personal Contribution no. 6.

[3] The name *Paragodon* is formed by adding the first part of *Paragus* to the last part of *Microdon*, thus indicating these flies' resemblance to *Paragus* and their phylogenetic affinity to *Microdon*.

Manuscript received by the editor April 20, 1969

hood, and connected posteriorly by membrane to dorsal infolded surface of penis sheath; cerci elongate.

Type-species: *Paragodon paragoides*, new species

Paragodon forms the plesiomorphic (primitive) sister group to the rest of the Microdontinae. It is the only known microdontine fly with a simple ejaculatory apodeme and sac. All other Microdontinae have an apical triangularly flared portion to the ejaculatory apodeme which fits into a strongly sclerotized cup-shaped sac (Fig. 8). The other primitive (plesiomorphic) characters which *Paragodon* displays are: 1) short antennae; 2) underdeveloped and bare metasterna; 3) lack of basal setal patches on the femora; 4) lack of a spurious vein; 5) lack of an appendix on the third vein (R4+5); 6) presence of a double sustentacular apodeme; 7) single, free ejaculatory process. The lack of cheeks on the head and the reduced thoracic pile are specialized (apomorphic) conditions. The isolated phylogenetic position of *Paragodon* suggests a number of interesting questions. What will the larvae be like? Will they be found in ant's nests like all other microdontine flies? And could *Paragodon* possibly be the adults of Wheeler's *Nothomicrodon*?

Since *Paragodon* appears to be the most primitive microdontine fly known, a general review of the characteristics and position of the subfamily seems in order.

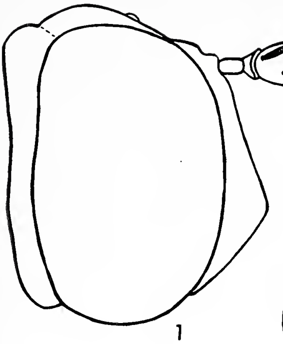
Subfamily Microdontinae

A small (350+ species) group of diverse syrphid flies.

Adults: Head: Face simple except slightly produced on the lower part in *Microdon (Rhopalosyrphus)*, pilose; facial grooves (anterior tentorial pits) reduced to pits; eyes dichoptic in both sexes; antennae usually long, longer than one-half as long as face except shorter in *Paragodon* and *Paramicrodon*, with first segment usually longer than broad except shorter in *Paramicrodon delicatula* Hull; aristae bare.

Thorax: Humeri always pilose, proanepisterna bare, anterior mesoanepisterna pilose except bare in *Microdon (Cerioimicrodon)*, scutellum without ventral hair fringe; plumula not differentiated from subalar; postmetacoxal bridge always present and complete. Legs: femora and usually tibiae with cicatrices. Wings: with first posterior cell (R5) closed and usually obtuse, with apical crossvein (upper turned portion of M1+2) recurrent or straight except directed outward in *Microdon (Aristosyrphus)*, with stigmatic crossvein (sc+r), with anterior crossvein (r+m) before middle of discal cell (2nd M1+2) and without radial sector bristles.

Abdomen: Males with four preabdominal segments, 1st abdominal



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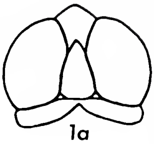

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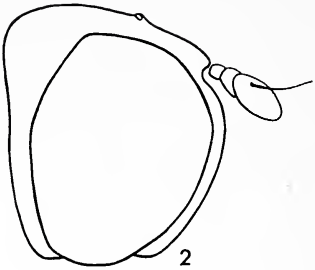

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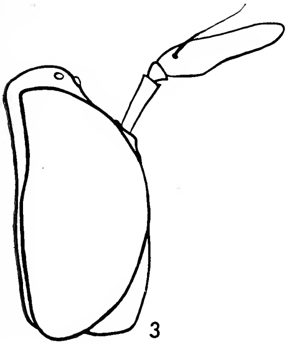

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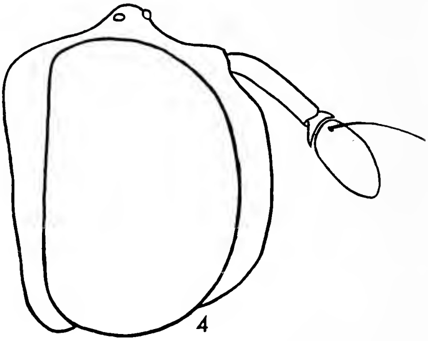

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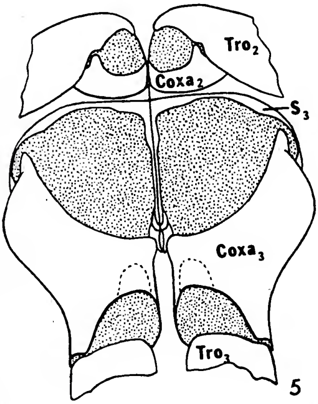

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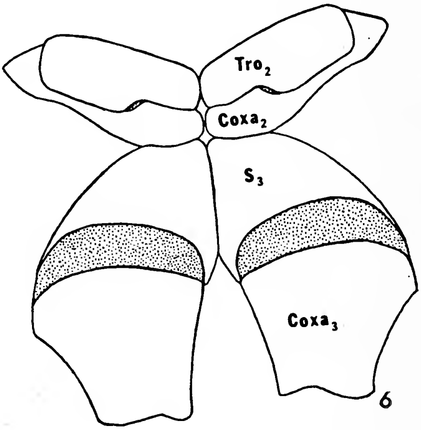

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spiracles embedded in metathoracic epimera. Genitalia: chitinous box usually spherical and without external lobes; ejaculatory process tubular and elongate; ejaculatory hood elongate, surrounding ejaculatory process, enclosing basal portion of the chitinous box, articulating dorsally with 10th sternite and ventrally with sustentacular apodemes; penis sheath without lobes, with posterior dorsal surface infolded and elongate posteriorly, where it is connected by membrane to the sustentacular apodemes when present; sustentacular apodeme usually present, absent or reduced in the specialized forms *Mixogaster* and *Microdon (Aristosyrphus)*, double, fused anteriorly to form a broad curved plate articulating with ventral end of ejaculatory hood and connected posteriorly by membrane to dorsal infolded surface of penis sheath; ejaculatory apodeme triangularly flared apically except in *Paragodon*; ejaculatory sac sclerotized and usually well-developed except in *Paragodon*.

Larvae: The larvae are exclusively scavengers in ants' nests and can be separated from other syrphid larvae by the following characteristics: 1) lack of body segmentation (Heiss, 1938); 2) lack of segmental spines (Heiss, 1938); 3) absence of cibarial ridges (also in Syrphinae) (Hartley, 1963); 4) presence of sclerotised labial lips (Hartley, 1963); 5) mandibles of a different form than the normal saprophagous types (Hartley, 1963); 6) opening of puparium by three pieces, two dorsal lateral pieces, and one ventral piece instead of two dorsal pieces (Lundbeck, 1916). Some of these characteristics may not be of subfamilial value since the larvae of only *Microdon s. s.* have been studied in detail. The larvae of *Mixogaster* have been described by Greene (1955) and Carrera and Lenko (1958) and appear to agree with the above. However, the existence of larvae like *Nothomicrodon* Wheeler (1924) (which may not be a syrphid) suggests that there may be much greater variability in the larval form than presently known.

Type-genus: *Microdon* Meigen

The genera I include in the Microdontinae are the same as those listed by Hull (1949) except *Spheginobaccha* is excluded. *Spheginobaccha* does not have a postmetacoxal bridge and lacks the specialized structures of the male genitalia. *Indascia* Keiser does belong to the

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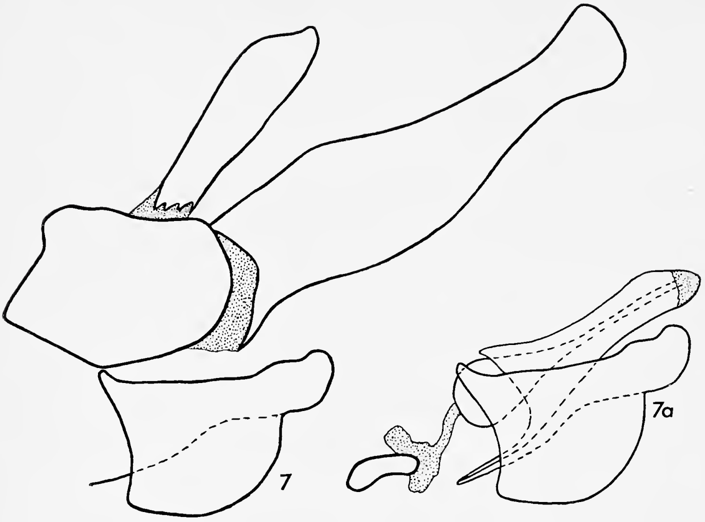
Figs. 1-4, lateral view of heads; la, ventral view; 5-6, ventral view of metasterna and surrounding parts. Fig. 1, *Paragodon paragoides*, n. sp., male (HT); 2. *Paramicrodon delicatula* Hull, male (LT); 3. *Microdon (Ubristes) triangularis* Curran, female; 4. *Microdon (Rhoga)* sp. A, female; 5. *Mixogaster cubensis* Curran; 6. *Microdon (Rhopalosyrphus) guntherii* Arribalzaga. HT-Holotype, LT-Lectotype.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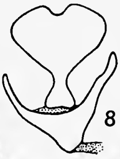
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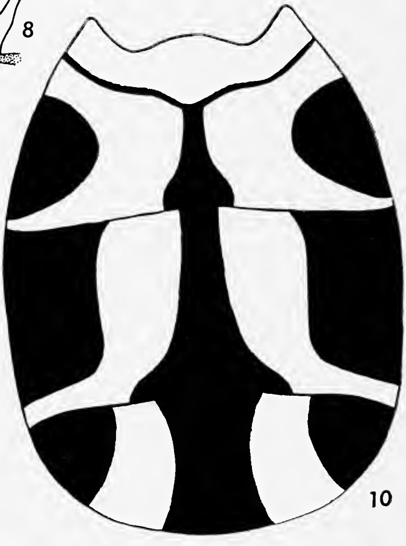
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Microdontinae, not to the Cheilosinae as supposed by its author (Keiser, 1958).

Since Rondani (1856-57) first divided the Syrphidae into supergeneric groups, most authors have accepted the Microdontinae as a distinct and separate group. However, Williston (1886), Goffe (1952), and Wirth *et al* (1965) have treated it as a tribe in one or another subfamily. Williston placed the "tribe" Microdontini in the Syrphinae, and Goffe and Wirth *et al* have placed it in the Milesinae (Sphixinae Goffe). The relative ranking of a group depends on its position in the phylogeny of the whole group, so when one finds a group given two different rankings by different workers one expects to find differences in their phylogenies of the group. This is the case with the Microdontinae. Hull (1949) has placed the Microdontinae with the Eumerinae and Nausigasterinae in his first phylogenetic dichotomy of the Syrphidae; whereas Goffe (1952) considers the microdontines to have diverged long after the Syrphinae.

These different views of the phylogeny of the Syrphidae can best be illustrated and compared by Hennig-type diagrams. The following diagrams (see text figure) illustrate the interpretations of Goffe (1952), Wirth *et al* (1965), and myself; I follow Hull (1949) except that I exclude the Eumerinae and Nausigasterinae from the *Microdon* line. Plan 1, my arrangement, clearly indicates that the Microdontinae should be considered the first divergence in the phylogeny of the family. Only one character state (#8) could be used to place the microdontine divergence second. If the reduction of preabdominal segments in the male (character #8) is not convergent in the Microdontinae and Pipizini, then the Microdontinae would have to be considered to have arisen after the Syrphinae (Plan 2).

Plan 2 explains Goffe's (1952) groupings. However, it is difficult to follow Goffe's "phylogenetic reasoning", which seems inconsistent with the modern "synthetic" theory of evolution and systematics. This plan creates more convergences than it solves. It seems to me more logical to consider the *reduction* of a character — in this case reduction of the abdominal segments in the male — as due to convergence than to suppose the development of a highly complex character such as aphidophagous larvae to be convergent.

Fig. 7, lateral view of male genitalia with axial system removed; 7a, lateral view of penis sheath and axial system; 8, ejaculatory apodeme and sac; 9-10, dorsal view of abdomen. Fig. 7, *Paragodon paragoides*, n. sp. (HT); 8. *Microdon (Cerioimicrodon) petiolatus* Hull (HT); 9, *Paragodon paragoides*, n. sp. (HT); 10, *Paragodon minutula* van Doesburg (after van Doesburg, 1966).

Wirth *et al* (1965) *have* used the larval state to define the first phylogenetic divergence and thus to define subfamilies of the syrphids (Plan 3). This arrangement too creates more problems than it solves. Placing the syrphine before the microdontine divergence leaves no synapomorphic characters for the Milesinae and creates even more convergences than Plan 2.

In short, Plan 1 seems to offer the most logical illustration of the relationship of the Microdontinae to the other syrphids. However, much is still to be learned about the phylogeny of the Syrphidae, and my placement of the Microdontinae must be accepted only as the best possible *present* arrangement. The strongly plesiomorphic nature of the subfamily suggests that the microdons might best be considered as a separate family (as Martin (1968) has done with the Leptogasteridae). However, regardless of the phylogenetic position of the microdontine flies, they should be clearly recognized as a subfamily equivalent to the Syrphinae and Milesinae.

No other groups have been derived from the microdontine line. Hull (1949) included the Eumerinae[4] and Nausigasterinae[4] in the microdontine divergence. However, these groups belong to the milesine line and are probably derived from a myoleptine ancestor. Eumerinae and Nausigasterinae could not have evolved from the Microdontinae for a number of reasons. Both of these groups lack a number of the specialized characteristics of the Microdontinae which one would expect to find in any derived group; for example, they lack 1) a complete postmetacoxal bridge, 2) the dorsal infolding of the penis sheath, 3) the double sustentacular apodeme or its absence, and 4) other genitalic characters. It is also highly unlikely that the phytophagous larvae of Eumerinae and the saprophytic larvae of Nausigasterinae could have evolved from a specialized larval form like *Microdon* which lacks segmentation and segmental spines and possesses specialized mouthparts.

PROVISIONAL KEY TO THE NEW WORLD GENERA AND SUBGENERA OF MICRODONTINAE

1. Abdomen petiolate; metasterna undeveloped, reduced to a thin line and bare (Fig. 5) .... *Mixogaster* Macquart
   Abdomen usually not petiolate; if petiolate then metasterna well-developed, not reduced and usually pilose (Fig. 6) 2

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[4] The use of these groups as subfamilies follows Hull (1949); I presently regard these two groups as forming one tribe with *Merodon*, *Alipumilio* and *Psilota* under the Milesinae.

2. Pteropleura bare .... *Paragodon* Thompson
   Pteropleura pilose 3
3. Antennae short, less than one-half as long as face; first antennal segment never more than twice as long as broad (Fig. 2) .... *Paramicrodon* de Meijere
   Antennae long, always longer than one-half as long as face; first antennal segment always much more than twice as long as broad (Figs. 4 & 5) .... *Microdon* Meigen .... 4[5]
4. Apical cross-vein angled outward on anterior one-half (Fig. 11) .... *Aristosyrphus* Curran
   Apical cross-vein not so, straight or slightly curved inward 5
5. Barrette (dorsal portion of hypopleura) bare 6
   Barrette pilose .... *Rhopalosyrphus* Giglio-Tos
6. Hind tibiae with distinct brushes of pile[6] 7
   Hind tibiae without brushes 8
7. Occiput uniformly developed, collar-like (Fig. 4) .... *Rhoga* Walker
   Occiput not uniformly developed (Fig. 3) .... *Ubristes* Walker
8. Anterior mesopleura bare; abdomen petiolate, petiole as long as thorax or longer; face slightly bulging below .... *Cerioimicrodon* Hull
   Anterior mesopleura pilose; abdomen usually not petiolate; if petiolate, then petiolate short and face not bulging below .... *Microdon* Meigen

Key to the species of *Paragodon*

1. Face with medial brown stripe; hind tibiae black .... *paragoides,* new species (Mexico)
   Face without medial brown stripe; hind tibiae whitish yellow .... *minutula* van Doesburg 1966 (Surinam)

Paragodon paragoides, new species

Face slightly produced medially, yellowish, with a diffuse medial brown stripe; thorax and abdomen brownish with yellow spots; legs black except front four tibiae and all tarsi orange.

Male. Head: face yellowish white except for diffuse medial brownish area, with white pile; front and vertex brownish black with pale pile; occiput black, grayish pollinose, with pale pile. Face narrower at oral opening than width of vertex, widest at base of

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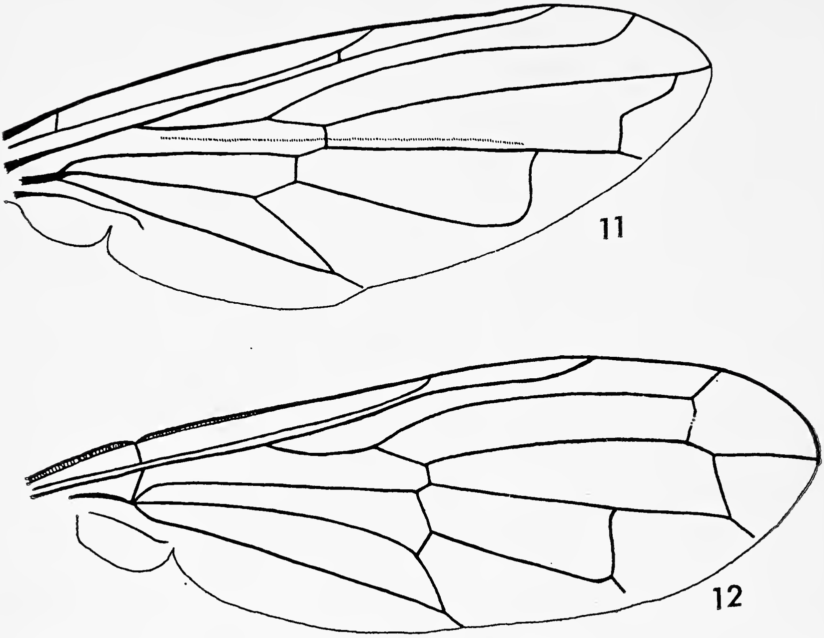
[5] On the whole the separation of *Microdon* into subgenera, couplets 4-8, is not satisfactory. I do not recognize these subgenera as anything more than distinctive species groups.

[6] Not all *Ubristes* types have distinct brushes of pile.



Figs. 11-12, wings; 11, *Microdon (Aristosyrphus) primus* Curran; 12, *Paragodon paragoides*, n. sp. (HT).

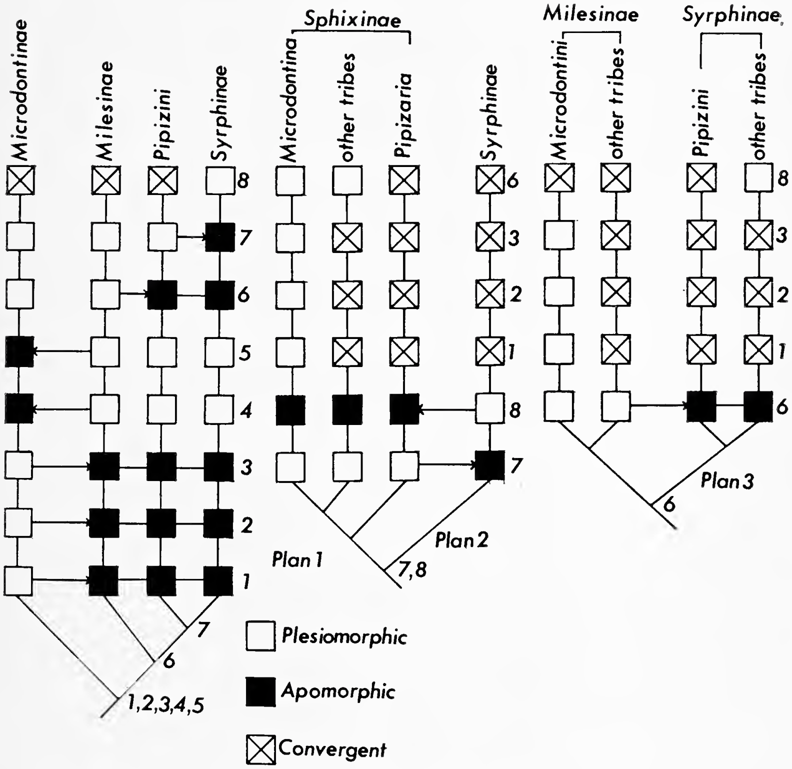
antennae, and slightly produced between oral margin and antennal bases; front wider than face. Antennae short, about one-third length of face; first two segments black with black pile; third segment pointed apically, light brown, with small round sensory pit near middle on ventral portion. Aristae short, about as long as third segment, thick, light brown. Antennal ratio: 2:1:6.

Thorax: brownish black except for humeri, postalar calli and dorsal surface of stenopleura dirty white; thoracic pile yellow except for transverse J-shaped spot of black pile above each wing base. Wings grayish, almost completely microtrichose, with bases of first and second basal cell bare; wing venation as figured (Fig. 12). Halteres yellow. Squamae gray with dark margins. Legs black except as follows: tips of femora, front four tibiae, and all tarsi orange; with pile dark except for light pile on front four tibiae.

Abdomen: Dorsum with black and yellow pattern as figured (Fig. 9); venter yellow; abdominal pile appressed black on black areas and pale yellow on yellow areas. Genitalia: as figured (Fig. 7, 7a); brown.

Holotype — male: Mazatlan, Sinaloa, MEXICO; 16 August 1964, at sea level; J. F. McAlpine, collector; holotype in Canadian National Collection, Ottawa.

Discussion: Paragodon paragoides is distinct from *minutula* van Doesburg, the only other known species of *Paragodon.* Besides the key characters and abdominal patterns (Figs. 9, 10), *paragoides* shows the following differences from *minutula*: 1) face produced forward in middle (Fig. 1); 2) sides of face not parallel, converging to oral margin; 3) third antennal segment three times as long as first, not equal; 4) an appendix present on second vein (connected to third vein on one side); 5) with spurs on first and second posterior cells.



Explanation of Argumentation plans. Apomorphic character states: 1, Single sustentacular apodeme; 2, complex faces; 3, absence of cicatrices on legs; 4, dorsal infolding of penis sheath; 5, lack of segmentation and segmental spines in the larvae; 6, carnivorous larvae; 7, bare humeri; 8, four preabdominal segments in the male.

The nomenclature used in describing the genitalia of the male is that of Metcalf (1921).

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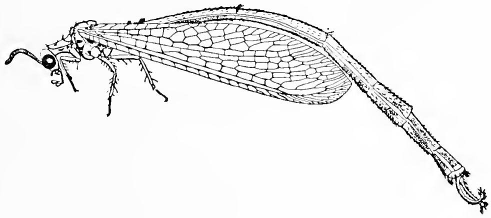

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PSYCHE

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A REVISION OF THE NEOTROPICAL DACETINE ANT GENUS *ACANTHOGNATHUS* (HYMENOPTERA: FORMICIDAE

By William L. Brown, Jr.[1] and Walter W. Kempf[2]

Introduction

At the time it was last reviewed (by M. R. Smith in 1944), *Acanthognathus* contained three species: *ocellatus, lentus* and *brevicornis,* known from Central America and a few localities along the eastern edge of South America. In the present paper we are able to add three distinctive new species—one from the heart of Amazonia, one from the Pacific Slope of Colombia, and one from Southeastern Brasil; and a male of the genus is described for the first time. We present fragmentary observations on living colonies of *A. rudis* and *A. ocellatus* to confirm M. R. Smith's surmise that the genus is predaceous, at least to some extent on Collembola.

Acanthognathus is a very distinctive genus within the tribe Dacetini, to which it clearly belongs, and within which it is one of the two most primitive living genera (Brown and Wilson, 1959). The other primitive member is *Daceton,* containing a single spectacular species confined to hylaean South America (Wilson, 1962). Though *Daceton* and *Acanthognathus* workers share a number of primitive characters (antennal segments 11; palpal segments 5, 3; compound eyes large; antennal scrobes absent; humeri armed), they are very different in size, habitus, and choice of nest site, and thus may have diverged a long time ago. *Acanthognathus* has the aspect of a genus that has begun a shift from epigaeic to cryptic foraging. Its retention of large eyes, multisegmented antennae and palpi, and long mandibles suggests that much of its foraging must still be done in the open,

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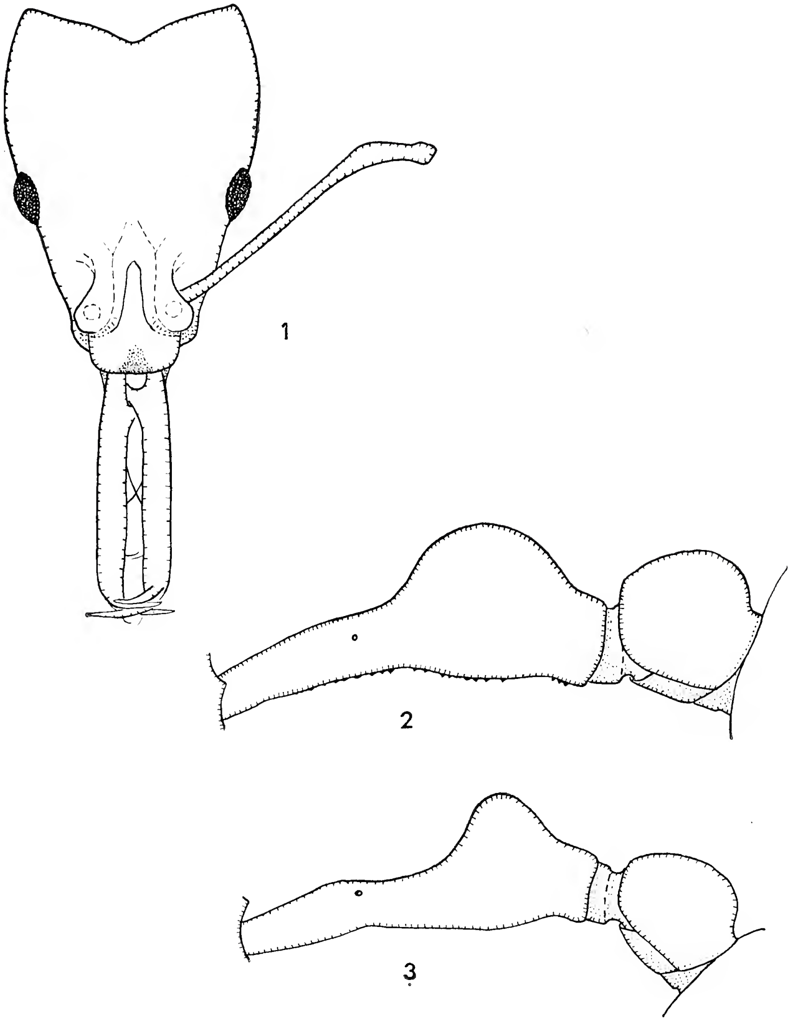


Figures 1 - 3. *Acanthognathus* spp., workers from type series in outline, sculpture and most pilosity omitted. Fig. 1, *A. rudis* sp. n. from type locality (Jardim Botanico, Agua Funda, São Paulo), dorsal view of head and mandibles. Fig. 2, *A. rudis* (Guararema, São Paulo), petiole and postpetiole from side. Fig. 3, *A. stipulosus* sp. n., holotype petiole and postpetiole in side view. Fig. 1 drawn by Brown, Figs. 2 and 3 by Kempf and Brown.

even though its nests tend to be cryptically situated in the ground or rotten wood. Like most or all *Orectognathus,* the related Australian genus, its species probably forage mainly at night.

Acanthognathus

Acanthognathus Mayr, 1887:578. Type species *Acanthognathus ocellatus,* monobasic.

Acanthognathus: Emery, 1922, Gen. Insect., 174c:317-318.— M. R. Smith, 1944:150-152, key to spp.— Brown, 1948:125, in generic key.— Brown and Wilson, 1959:281-283, phylogeny, biology.

Worker: Size small (TL 3.5-4.6 mm). Habitus of strumigeniform Dacetini, i.e., with head much longer than broad, more or less depressed dorsoventrally, and much narrowed and drawn out anteriad, with a deep posterior excision (Figs. 1, 11); mandibles greatly elongate, narrow and linear, straight or nearly so, each with 3 spiniform apical teeth. Somewhat beyond the midlength of each mandible, there is often a small welt or convexity on the inner margin, whence issues a long, fine hair, the trigger hair, which lies flat against the margin when the mandible is closed, but which stands erect when the mandible is open, pointing straight forward, and serving as a tactile range-finder. Preapical teeth or denticles also occur on the mandibles of some species. Near the base of each mandible a long, slender basal process arises from its ventral surface and runs obliquely basoventrad, crossing its opposite number when the mandibles are closed (Fig. 1); the apices of these processes are split into a pair of short acute teeth, by means of which they engage one another when serving as props to hold the mandibles widely open. (The basal processes have also been observed by Moeller and ourselves to be used in carrying brood in *rudis* and *ocellatus,* with mandibles opened widely.)

Frontal lobes form small convex shields over the antennal insertions. Eyes large, near or slightly in front of middle of sides of head, only moderately convex, normally with 40 to 70 or more facets. Clypeus narrowly bell-shaped, flat, with long posterior lobe inserted between frontal lobes. Antennae long and slender, 11-segmented (Figs. 1,4,11), with the scapes oddly bent and usually constricted near apex. Small antennal segments III through IX in a rigid straight line, and may sometimes be fused internally, corresponding (as Santschi has already pointed out) to the long segment III in the Australasian genus *Orectognathus.* Antennal scrobes lacking. Occipital area deeply and broadly concave, set off from vertex by a sharply rounded angle.

Maxilla with 5, labium with 3 segments in each palpus. Labrum reduced to a small piece shaped like an inverted V.

Truncus strongly constricted and deeply impressed at metanotal groove; pro- and mesonotum fused together; humeral angles distinct and often more or less toothlike. Propodeum armed with a pair of slender oblique spines; declivity flat or weakly concave, smooth, at most feebly carinate on sides; inferior propodeal plates small, subacutely angled to rounded; propodeal spiracles circular, situated close under the bases of the spines, directed posterolaterad; atrum of metapleural gland with dark borders visible through integument, large, elliptical, oblique. Petiole with a long, slender, anteriorly tapered peduncle in front, a distinct, at least discally smooth and shining node, and a short posterior peduncle (Figs. 2-4). Postpetiole rounded, not very different in width from petiolar node, smooth and shining, at least on summit. No spongiform tissues on nodes or elsewhere. Gaster broadly oval, smooth and shining. Legs long and slender, femora moderately incrassate in apical half; no spurs on middle and posterior tibiae; claws slender, simple. Sting slender, rigid, with very acute tip; exsertile, functional.

Sculpture ranging from almost entirely smooth and shining (*teledectus*) to rugulose and opaque over dorsum of head and truncus (*rudis*), with at least some coarse but shallow, round tuberculate fossae on the head, and often a few on promesonotum as well. The tubercles of these fossae often each bear a single, short, slender, curved or reclinate clavate hair, these clavate hairs also more or less generally distributed over scapes, mandibles, femora and tibiae, promesonotum, propodeal spines, posterodorsal faces of both nodes, and sometimes underside of head. Short fine erect or reclinate hairs on mandibular apices, funiculi of antennae, tarsi and gastric apex; gastric dorsum also with very sparse, fine, short appressed hairs. Color prevailingly ferruginous.

Queen: Similar to worker in size and proportions, but with 3 ocelli, larger compound eyes, and the usual differences due to the prenuptial presence of well-developed wings and thoracic flight sclerites. Scutellum prominent and convex, propodeal spines well-developed and acute, but stouter than in worker.

Male (known only for *A. rudis*, Figs. 5-10): Habitus dacetine, but slender; node long and low; sculpture mostly smooth and shining with fine punctures. Mandibles reduced to minute rounded lobes, each with a single acute tooth; separated by labrum, which is larger than mandibles and has a lobe at each free corner, just above the

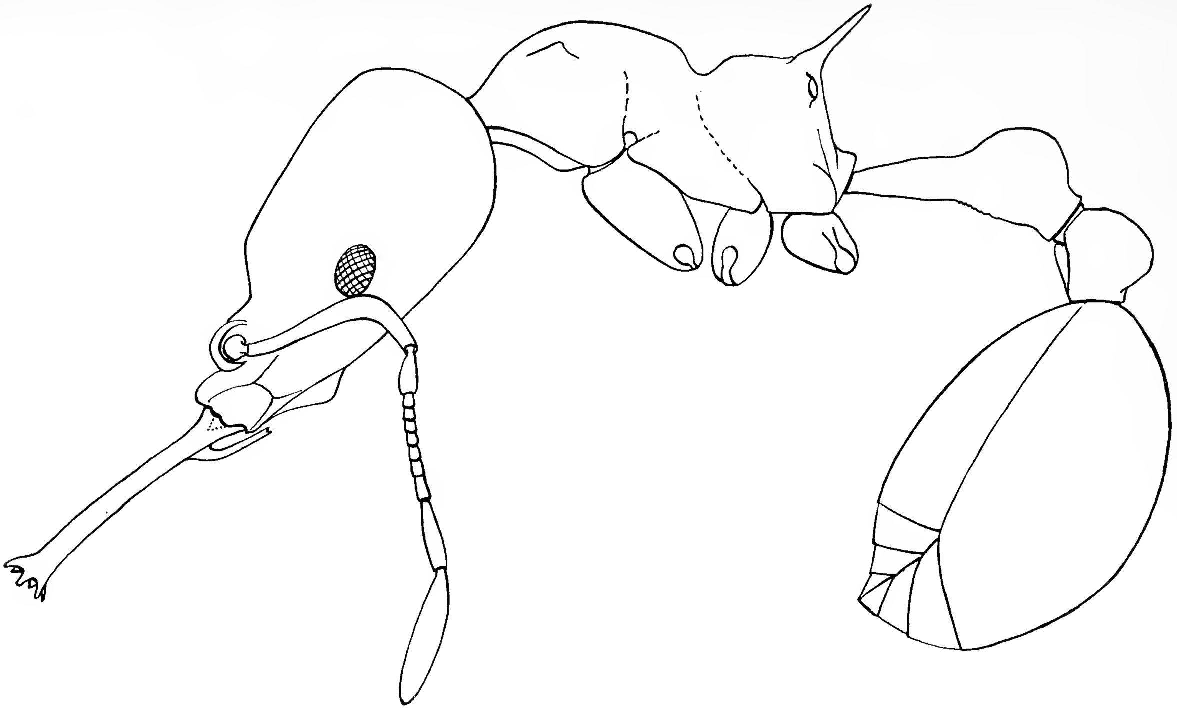


Fig. 4. *Acanthognathus rudis* sp n., worker from type series (Bocaiuva, parana), side view, pilosity and sculpture omitted. Drawn by Kempf.

slightly projecting, single-segmented labial palpi. Maxillary palpi not seen in undissected mouth-parts, presumably reduced to a single small segment. Antennae long, 12-segmented; scape and pedicel subequal in length, each about twice as long as broad; flagellum filiform, only very slightly thicker at apex than at base. Compound eyes large and strongly convex, placed near the front of the sides and occupying about half the sides. Ocelli prominent, raised, surrounding a prominent indentation in the vertex.

Truncus well-developed, mesonotum with weak parapsidal furrows and notauli, the latter incomplete, not or at least not distinctly fused behind. Pronotum and propodeum unarmed, rounded; inferior propodeal plates present.

Wings long, densely microtrichiate; apical margin of fore wing and apical and hind margins of hind wing with a wide fringe of fine hairs.

Legs slender, long; tarsal claws simple, short, fine; tibiae of middle and hind legs without apical spurs.

Genitalia (Figs. 8-10) formed on the same plan as *Strumigenys;* aedeagus valves subtruncate apically, cuspis of volsella slender; mesal face of paramere broadly excavated opposite volsella. Hypopygium elongate-triangular, with concave sides tapering to a narrowly rounded apex.

Pilosity abundant and widely distributed, consisting of short, fine soft brown hairs, mostly decumbent, but erect on propodeum. Color dark brown to probably blackish in fully-colored specimens; appendages pale.

Larva: To be described separately by G. C. and J. Wheeler.

DISTRIBUTION, ECOLOGY AND BEHAVIOR

As now known from definite records, *Acanthognathus* ranges from Honduras in the north to Rio Grande do Sul in the south. It seems very likely that its range reaches into northeastern Argentina and to Bolivia, and it would not be surprising to find the genus in southern Mexico. Two of the new species described here extend the records into the Amazonian heartland and to Trans-Andean Colombia, while a new collection of *A. ocellatus* is the first for the genus from Trinidad.

The great increase in collections of *Acanthognathus* in recent years is due in large part to the rise in use of the Berlese funnel and similar methods of extraction of forest soil and litter, as well as to more intensive collecting in rotting twigs and similar microhabitats on the floor of tropical forests. All of the samples for which we have ecological data came from moist or wet forest of the tropical or subtropical type. Nests of isolated (possibly nest-founding) dealate queens of *brevicornis, lentus, ocellatus* and *rudis* have usually been taken in rotten twigs or small pieces of rotting wood in forest litter. The colonies are small, often with only 10-20 or fewer adult workers, and no nests with more than about 30 workers have been seen. Usually there is a single dealate queen per nest, though two have been found in a nest of *A. rudis* from São Paulo. The nests resemble greatly those of certain long-mandibulate *Strumigenys,* as already noted by Mann (1922), and like *Strumigenys,* the *Acanthognathus* workers and queen move slowly and often curl up to play dead when jarred.

An observation of Moeller, repeated by Emery (1922) and others, showed that workers use the basal processes of the mandibles to carry their brood. We have been able to confirm this activity for *A. ocellatus* and *A. rudis* in captive colonies. We have also observed these same two species to capture, by means of a snap of the mandibles, entomobryid Collembola that were placed in the artificial nest with them. A colony of *A. ocellatus* from Cerro Campana, Panama, fed a newly-captured entomobryid to a larva, after the fashion of *Strumigenys.* Limited tests of other small, soft-bodied arthropods were tried with both *ocellatus* and *rudis,* and though none of these was captured or even approached, the trials were too few to establish the breadth of prey specificity. Foraging workers of these two species, and the holotype of *A. teledectus* before its capture in the leaf litter, held their mandibles open to about 180° when threatened or when approaching prey. This is apparently accomplished by locking together the apices of the opposed basal processes, but the details are not altogether clear, especially the role, if any, of the labrum in the process. As with *Strumigenys,* the sting is employed to quiet struggling prey.

A worker of *A. ocellatus* taken by Markl on Trinidad is accompanied by the note, "at night," indicating what the relatively large eyes suggest— that foraging is epigaeic, perhaps subarboreal, and largely crepuscular or even nocturnal. The similar Australasian genus *Orectognathus* appears to follow this foraging pattern.

The Species

Acanthognathus comprises six known species, of which five are very distinct, and one, *A. lentus,* is kept separate from *A. ocellatus* with doubt for the time being.

The descriptions and measurements (Table I) utilize some abbreviations kept standard in recent works on ants, particularly the tribe Dacetini. HL is the length of the head in full-face (dorsal) view, including occipital lobes and the entire clypeus. HW is the maximum measurable width of the head in full-face view. CI is cephalic index, or HW/HL × 100. ML is the exposed length of the closed mandibles beyond clypeal margin, measured in full-face view. SL is the chord length of the antennal scape; SI (scape index) is SL/HW × 100. MI is the mandibulo-cephalic index, or ML/HL × 100. SMI, scape-mandibular index, is SL/ML × 100. All measurements are in millimeters, and have an approximate error of ± 0.01 mm.

Abbreviations for the main collections in which deposit has been made are: (MCZ) Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, USA; (USNM) United States National Museum, Washington, D. C. 20560, USA; (WWK) Collection of W. W. Kempf, including the Collection of Thomas Borgmeier, Caixa Postal 5,650, São Paulo, S. P., Brasil; (DZSP) Departamento de Zoologia, Caixa Postal 7172, São Paulo, Brasil. Other collections are given in full. The species are listed in alphabetical order.

Acanthognathus brevicornis

Acanthognathus brevicornis M. R. Smith, 1944: 150-152, worker, dealate queen. Type loc.; Barro Colorado Island, Panama Canal Zone. Holotype worker and paratype queen in USNM; paratype queens in MCZ.— Kempf, 1964:67, worker from Nova Petropolis, Rio Grande do Sul, Brasil.

Worker and queen: Distinguishable from the similar *A. ocellatus* (see below) by 2 main characters:

1. Scapes shorter than those of other species of the same size; scape length (chord) about equal to head width in the worker, less in the queen (see Table I). Scape length markedly less than mandible length in both worker and queen; all other species have scapes as long as or longer than mandibles, except *A. teledectus* with its extraordinarily long mandibles.

2. Mandibles (0.86 mm long in holotype worker, *teste* Smith) with noticeable submedian welt on inner borders and 2-5 irregular, separated low denticles or minute tubercles in the space between the welt and the apical teeth on each mandible. No other species has these denticles so far as known.

In addition, the sculpture of *A. brevicornis* is more strongly effaced, more shining than in *A. ocellatus,* but not as much so as in *A.*

teledectus. The *brevicornis* fossae on head and alitrunk tend to be smaller, shallower and more widely spaced, with interspaces correspondingly broader, smoother and more shining.

Male unknown.

Material examined (in addition to type series— 1 worker and 3 queens from Panama Canal Zone): BRASIL: State of Rio Grande do Sul: Nova Petropolis, September 1959, F. Plaumann leg., 1 worker (WWK); Morro Reuter, December 1964, F. Plaumann leg., 1 dealate queen (WWK). State of Pará: Utinga Forest Tract, near Belém, 9 August 1962, P. F. Darlington leg., dealate queen from hollow rotten twig on rain forest floor (MCZ).

Acanthognathus lentus

Acanthognathus lentus Mann, 1922:34-35, fig. 16, worker, queen. Type loc.: Progreso, Honduras. Syntypes in MCZ, USNM, WWK.

Worker and queen: Measurements and proportions given in Table I, closely overlapping those of *A. ocellatus,* fossae of dorsum of head larger and more crowded, with some rugulae present between them even on the posterior half, weakly shining; extreme posterior corners of cephalic dorsum smooth and shining. Otherwise very similar to *A. ocellatus.*

A. lentus probably is only a local sculptural variant of *A. ocellatus.* The scanty material available does not yet wholly bridge the difference, but a Trinidad specimen of *ocellatus* (q.v.) shows a tendency to do so.

Male unknown.

Mann's description is sketchy, and there is apparently a confusing deletion of several lines coming near the middle of the last printed line on his p. 34. His artist's figure is also not very faithful in portraying mandibular apices and head sculpture.

Material examined: Only a few workers from the type series, collected by Mann in rotten wood (MCZ, USNM).

Acanthognathus ocellatus

Acanthognathus ocellatus Mayr, 1887: 579, worker. Type loc.: Brasil, "St. Catharina."— Mann, 1916: 452, pl. 5, "fig. 38" (*recte* 39), queen, from Belém, Pará, Brasil.— M. R. Smith, 1944: 150, in key. Type worker currently in Museo Civico di Storia Naturale, Genoa, Italy, but properly belongs in Naturhistorisches Museum, Vienna, Austria; not seen by authors (discussed below).

Worker: If there is an "average" or "typical" member of the genus, this is it. Head more convex dorsally than in *A. rudis;* posterior excision in full-face view evenly semicircular (rather than

TABLE I

Standard measurements and indices of *Acanthognathus* samples by species and caste.

SPECIES	HL	HW	CI	ML	MI	SL	SI	SMI	Sample
*_brevicornis_ worker (SE Brasil)	93	67	72	83	89	67	100	81	1
brevicornis queens	84-101	61-75	71-74	81-86	84-98	56-67	89-97	69-78	4-3
*_ocellatus_ workers	80-91	56-65	69-72	64-72	79-85	70-77	116-125	100-109	6-5
ocellatus queen	88	67	76	70	80	73	109	104	1
lentus workers	84-92	60-66	70-72	70-74	80-83	74-80	121-123	105-108	3-1
rudis workers	86-98	62-69	68-73	55-68	63-73	70-80	106-123	111-127	14-5
rudis queen	87	63	72	58	67	70	111	121	1
stipulosus worker (type)	80	56	70	59	74	64	114	108	1
teledectus worker (type)	100	59	59	121	121	75	127	62	1

*Does not include measurements of holotype worker; for this see descriptions of these species.

Figure under "Sample" indicates (first) number of specimens included, and (second), number of localities represented; thus, 14-5 means that 14 specimens were measured from 5 localities. For abbreviations, see p. 94.

V-shaped); posterior lobes very narrowly rounded. Mandibles slender and more than ¾ the head length (see Table I), with low welts or convexities developed on their inner margins beyond mid-length, but no preapical denticles. Compound eyes normally broad-elliptical, only weakly convex, with about 34-45 facets, greatest diameter 0.11-0.13 mm. One (Trinidad) specimen has the left eye abnormally small (diameter 0.08 mm, only about 9 facets), whereas the opposite eye is nearly normal in size and facet number.

The petiole is quite slender, especially as viewed from the side, and its node is a bit lower than in *A. rudis;* petiolar node widths of the available sample (n = 5) are 0.16-0.19 mm, modal at 0.17; while for *A. rudis* the width is 0.17-0.20 mm, modal at 0.18.

The fossae of the sculpture are crowded on the anterior part of the cephalic dorsum, but are mostly well-separated on the posterior half of the head, with smooth or nearly smooth, shining interspaces. The fossae themselves have broad, shining bottoms. In the Trinidad worker, the posterior fossae are more often contiguous, and longitudinal rugulae begin to appear between some of them, making transition toward the doubtfully distinct *A. lentus.* Sculpture of the truncus variable; rugulose-punctulate, with interspersed small fossae; sides of mesonotum usually smooth and shining, with scattered indistinct fossae, as is sometimes also the anterior part of the propodeal dorsum. Reticulo-punctulate sculpture of petiolar node confined to lowest parts of the sides (usually occupies most of side of node in *A. rudis*). Pilosity abundant on head and promesonotum, but not as abundant as in *A. rudis.* Color light to medium reddish-ferruginous, appendages lighter and more yellowish, gaster sometimes feebly infuscated.

Queen (dealate) from Belém, Brasil. Greatest diameter of compound eye 0.19 mm; petiolar and postpetiolar nodes relatively larger than in worker from same nest (petiolar node 0.20 mm wide). Propodeal teeth stout, but still long and acute. Mesonotum with crowded distinct fossae, contiguous and nearly so; interspaces and fossae smooth or nearly smooth, shining; scutum and scutellum with median longitudinal carinula. Mesopleura smooth and shining, sides of pronotum rugose-fossulate, sides and dorsum of propodeum in part finely rugulose-punctulate. Otherwise differing from the worker by the usual caste characters.

Male unknown.

ASSIGNMENT OF THE NAME

Acanthognathus ocellatus was described by Mayr (1887) from a single worker taken by Hetschko in "St. Catharina," southern Brasil. Since that time *Acanthognathus* has been collected rather frequently in southeastern Brasil, and until recently, it was assumed that all of these collections belonged to *A. ocellatus*. This assumption was based partly on the fact that the accumulating samples all clearly belonged to a single endemic southeastern species, and partly on Santschi's confident determination of 1922, by which he attached the name *ocellatus* to the commonly-collected species and gave a crude figure of the worker head over this name. His sample came from the vicinity of Rio de Janeiro.

Borgmeier had early doubts concerning the identity of this form, as seen from some labels on specimens in his collection that read, "*Acanthognathus* sp. nov." Borgmeier's opinion must have arisen when he compared his specimens of this form with Mayr's original description of *A. ocellatus,* for the match is a poor one. Mayr gives the length of the mandibles in *ocellatus* as 0.9 mm, and the head length as 1.0 mm, which yields a mandibulo-cephalic index (MI) of 90, whereas MI in the common species runs from 63 to 73 in the sample available. More significant even than this is Mayr's description of the cephalic sculpture of *ocellatus* as, "*. . . . nicht dicht mit sehr grossen, kreisrunden, flachen und sehr seichten Punkten besetzt, jeder punkt hat in der Mitte eine sehr kleine kegelige Erhöhung, welche ein Haar tragt; die Zwischenraume zwischen den Punkten, wie auch die Punkte selbst sind glatt und glanzend . . .*" The commonly-collected form, on the contrary, has dense, finely rugulose-punctulate, opaque sculpture within and between the numerous small circular fossae over the entire cephalic dorsum behind the eyes. It therefore seems clear that the southeastern Brasilian form called "*A. ocellatus*" (at least since 1922) cannot belong to that species, and we here describe it as a new species, *A. rudis* (below).

The problem remained as to what the original *A. ocellatus* really was. Unfortunately, the unique type specimen is missing from the place where one would expect to find it in the Mayr Collection in Vienna, and it was presumed lost. In recent years (Kempf, 1964), the rare species *A. brevicornis* has been found in the state of Rio Grande do Sul, neighboring Santa Catarina to the south. This species conforms to the *ocellatus* description in size and cephalic sculpture, but the promesonotum of *brevicornis* is smooth and shining, with a few scattered, feeble fossae, whereas Mayr described *ocellatus* as having "*Der ganze Thorax grob und verworren gerunzelt mit eingestreuten solchen haartragenden Punkten, wie sie am Kopfe* *vorkommen.*" Furthermore, in *brevicornis* the antennal scapes do not reach the posterior margin of the head at any point, whereas according to Mayr the scapes *"überragt sehr wenig die Hinterecken des Kopfes . . . ."* in his *ocellatus* type. It seemed unlikely that *brevicornis* and *ocellatus* were synonymous.

Of the forms represented among the *Acanthognathus* samples known at the present time, there is one that agrees reasonably well with Mayr's description of *ocellatus*. This is the form reported under this name by Mann (1916) from what it now Belém, at the mouth of the Amazon. This same species is now known also from Trinidad, Panama and Costa Rica (see below), and we believe that it ranges southward from the Amazon in Brasil, but that in this area it is probably even rarer and more local than it is northward. In particular, it does not occur at the same south Brasilian localities as the apparently much more common *A. rudis,* which inhabits only subtropical wet forests on the plateaus and mountain ranges that take up much of the region. Mayr's Santa Catarina ants were sent him by the collector Hetschko, whose base was the hot lowland town of Blumenau. Thus, it seems to us likely that the main reason this species — the real *ocellatus* — has not been collected again in 80 years is simply that no one has collected for cryptobiotic ants in the Bluemenau area or in other suitable hot lowland localities along the south Brasilian coast.

To the above reasoning, we can now add that the type of *A. ocellatus* has finally been located. It resides, probably ever since its loan to Carlo Emery, in the Museo Civico di Storia Naturale "Giacomo Doria" in Genoa. Dott. Delfa Guiglia, First Conservator of that institution, has kindly sent us information on the critical characters of the single worker specimen; this will have to serve in place of its loan for our standard measurement and examination.

According to Dott. Guiglia's first letter, dated 8 December 1968, the presumed type bears the label, *"Acanthognathus ocellatus* Mayr — St. Catharina." It is not labeled as type, but like us, Dott. Guiglia believes that it "is certainly the type." Her characterization, very slightly paraphrased: Dorsum of the head with large, shallowly impressed, well defined punctures, about 0.03 mm in diameter and papillate in the middle. Narrow spaces between these punctures smooth and rather shining, without any trace of reticulation. Anterior third of head with shallow longitudinal furrow in the middle."

The first measurements sent were mostly only taken to the nearest tenth of a millimeter, and therefore lack sufficient precision for our purposes. In answer to our further request, in her second letter, dated 29 December 1968, Dott. Guiglia graciously sent measurements of SL and ML taken to 4 decimal places of a millimeter. Rounded to 3 decimal places, which is nearer the limits of precision of standard stereomicroscopes, these are: SL 0.772, ML 0.755 — dimensions close to those listed for the other samples of *A. ocellatus* and not so close to those for the known samples of *A. brevicornis*. In order to differentiate further against *A. brevicornis*, we queried Dott. Guiglia about the presence of preapical denticles on the mandibles, and she replied emphatically in her second letter that "indistinct denticles on the inner mandibular margins before the apices [do] *not* exist."

While we recognize the danger of not actually examining the specimen in this case, it does seem hardly likely from the weight of the evidence that the *ocellatus* type can belong to any species but the one to which we here attach the name.

Material examined: COSTA RICA: Puerto Viejo de Sarapiquí, Heredia Prov., 30 July 1965, D. H. Janzen leg., 1 worker (MCZ). PANAMA: Cerro Campana, Prov. Panamá, ca. 800 m, 17 Jan. 1960, G. B. Fairchild and W. L. Brown, Jr. leg., 6 w and 1 dealate queen with brood, from rotten twig in wet montane forest (MCZ, WWK and elsewhere). Barro Colorado I., Canal Zone, 9 July 1956, C. W. and M. E. Rettenmeyer leg., 1 w, berlesate, dirt from bivouac of *Eciton vagans*. TRINIDAD: Simla, Arima Valley, 12 Jan. 1966, H. Markl leg., 1 w taken "at night" (MCZ). BRASIL: Belém, Pará, 1914, W. M. Mann leg., 1 w and 1 dealate queen (MCZ).

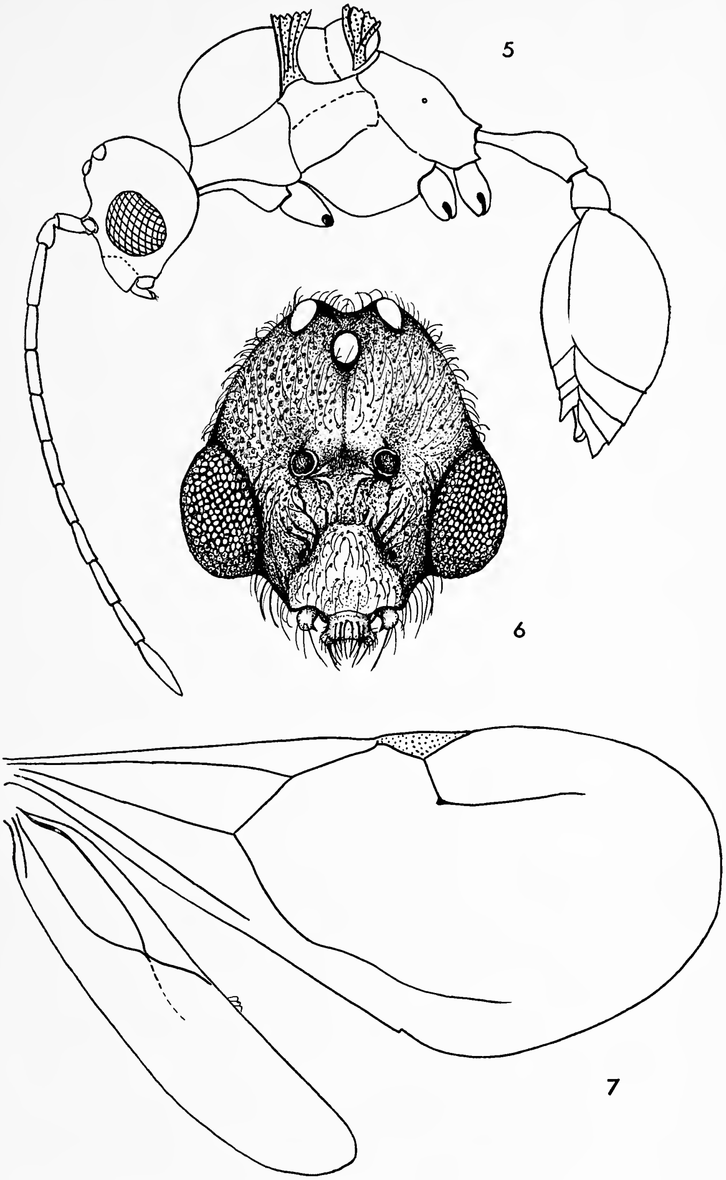
Acanthognathus rudis sp. nov.

(Figs. 1, 2, 4-10)

Acanthognathus ocellatus (not of Mayr): Santschi, 1922: 353-354, fig. 2, worker from State of Rio de Janeiro, Brasil. — Borgmeier, 1927:120, record from State of Rio de Janeiro.— Kempf, 1958:553-554, record from Guararema, S. Paulo.— Brown and Wilson, 1959:282, fig. 3, worker.— Kempf, 1964:67, records from states of Rio Grande do Sul, Santa Catarina, Paraná, São Paulo and Rio de Janeiro.

Holotype worker: TL 4.2, HL 0.93, HW 0.65 (CI 70), ML 0.68 (MI 73), WL 0.86, petiole L in dorsal view 0.55, postpetiole L 0.20 (W 0.20), gaster L 0.97, greatest diameter of compound eye 0.13, scape L (chord to basal collar) 0.76 mm. Standard measurements of a selection of specimens from the type series are listed in Table I.

This species is so well known (under the name *ocellatus*) that Figs. 1, 2, and 4, and the measurements and indices, plus mention



Figures 5-7. *Acanthognathus rudis* sp. n., male from type nest series (Agua Funda). Fig. 5, side view. Fig. 6, full-face view of head, antennae omitted. Fig. 7, wings, microtrichiae omitted. Figs. 5 and 7 drawn by Kempf, Fig. 6 by Ruth Ann DeNicola.

of a few outstanding features, should suffice to characterize it. Note the rather V-like outline of the posterior excision of the head. Head slightly more depressed, less convex above, than in *A. ocellatus.*

The outstanding trait is the fine, nearly opaque, densely rugulose-punctulate sculpture of head and truncus. Among the rugules are crowded numerous small piligerous fossae, especially on the dorsum of the head, but these are clearly visible only in certain lights. Sides of truncus finely punctulate-rugulose, except for the lowest part of the mesothorax, which is smooth and shining. The hairs are abundant, particularly on head and promesonotum, but also present on nodes, short and inclined, slender but blunt, often feebly flattened or clavate toward their apices, those on the head directed anteriad. Pilosity otherwise as described for the genus.

Humeral angles obtuse, not strongly projecting. Propodeal teeth diverging, very feebly curved as seen from above.

The mandibles lack preapical armament, and there is not even a distinct welt at the site of the trigger hair, though a formation extending internally to the base of the hair can be seen within the transparent cuticle of the inner mandibular margin.

Petiole with a low, rounded node (Fig. 2), the lower anterior slope with a low median carina; node obout 0.22 mm long and 0.18 mm wide; postpetiole subglobular. Petiole and postpetiole densely and finely reticulo-punctulate and opaque, except for the almost completely smooth, shining nodal summits.

Color light reddish ferruginous; nodes and gaster yellowish ferruginous; but the gaster with the middle third shading into a broad brownish-red transverse band; appendages yellow to straw.

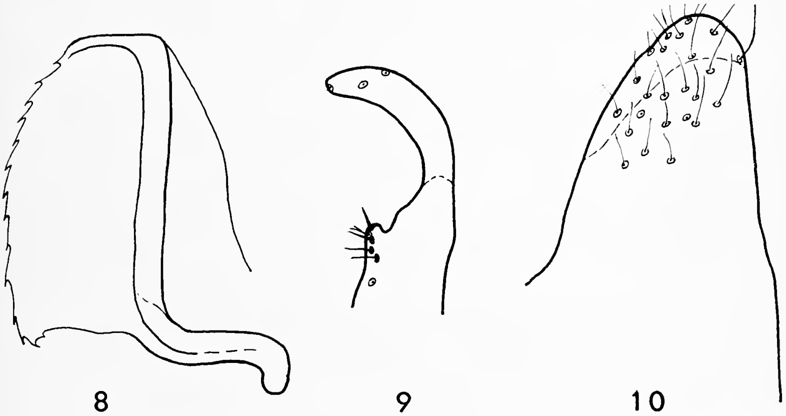
Paratype variation is slight on the whole (see Table I). Workers from Boraceia, S. Paulo State, have the upper as well as lower mesopleura largely smooth and shining. Color varies from light to medium ferruginous.

Queen: Measurements of a queen from the type locality are given in Table I. Her distinguishing specific characters correspond in the usual way to those of the worker. Mesonotum with crowded, slightly vermiculate longitudinal rugulae, interspersed with small fossae. Pronotum and propodeum transversely rugulose. Mesopleura with the upper half rugulose or smooth; lower half mostly smooth and shining.

Male from the type nest series: TL 2.8, HL 0.52, HW without eyes 0.45, with eyes 0.54, L antenna 2.0, ML 0.05, WL 0.90, L forewing 2.55 mm.

See Figs. 5-10. Smooth and shining, with small punctures abundant on head, a few rugae around the antennal insertions. Mesonotum finely and indistinctly longitudinally striolate-punctulate, sericeous-opaque. Color brown to piceous, head darkest (specimens may not be fully colored). Legs and mouthparts yellowish-tan.

Type material: all from Brasil; states are given in capital letters. Holotype (WWK) a worker from a small nest with queen and brood taken in a fragment of rotten wood found lying beside a brook in a moist, shaded gully in the forest reserve of the Jardim Botanico, environs of the city of São Paulo, SAO PAULO, February 1967, W. L. Brown leg. This colony was kept for observation, and eventually yielded two adult males, the only ones so far recorded for the genus. Paratypes, in addition to workers, queen and males from the type nest (MCZ, WWK), are the following (states listed south to north): RIO GRANDE DO SUL: Tainhas, April 1959, F. Plaumann leg., 1 w[orker] (WWK 3250). SANTA CATARINA (all Plaumann leg.): Chapecó, June, August 1960, 2w (WWK s/n and 4618); Ibicaré, July 1959, 1 q(ueen) (WWK 3126) and September 1960, 2 w, (WWK 3621); Nova Teutonia, July 1952 2 w, October 1953 2 w 1 q, June 1957 1 w 2 q, July 1957 1 q, February 1959 1 w, July 1959 1 w (WWK 3100); February 1960 1 w (WWK 3780), June 1960 1 w (WWK 3956); July 1961 1 w (WWK 3379); January 1963 1 w (WWK 3744); June 1963 1 w



Figures 8 - 10. *Acanthognathus rudis* sp. n., male genitalia from one of the specimens from the type nest series. Fig. 8, aedeagus. Fig. 9, volsella. Fig. 10, paramere, with dashed line indicating apical extremity of excavated portion. Drawn by Brown.

1 q (WWK 3709); Seara, July 1958 3 w (WWK 2687). PARANÁ: Bocaiuva, May 1963, F. Plaumann leg. 2 w (WWK 3999); Palmeira, May 1964, F. Plaumann leg. 1 w (WWK 4015); Volta Grande, April 1949, Hertel leg. 5 w (MCZ, WWK). SAO PAULO: Barueri, December 1958, K. Lenko leg. 8 w (No. 708); Guararema, December 1957, W. W. Kempf leg., 11 w, 1 q (WWK 2102, MCZ, Cornell); Jardim Botanico, Agua Funda, São Paulo, September 1958, K. Lenko leg. 8 w (No. 608); August 1962, and February 1967, W. L. Brown leg. 4 nests and partial nests from rotten wood, workers, queens and males (MCZ, WWK and elsewhere); Serra da Cantareira, cavity in small stump, with *Pheidole* sp., January 1959, W. W. Kempf and Vitor dos Santos leg., 4 w, 1 q (WWK 2915). Boraceia, Municipio de Salesopolis, February 1967, nest in rotten twig in litter, R. H. Crozier leg. 4 w (MCZ) RIO DE JANEIRO: Parque Nacional do Itatiaia, December 1955, T. Borgmeier leg. 1 w.

Acanthognathus stipulosus sp. nov.

(Fig. 3)

Holotype worker: Measurements and indices given in Table I. A small-sized, slender species resembling *A. ocellatus* and *A. brevicornis.*

The character that immediately sets this species off from the rest is the shape of its petiole (Fig. 3). Set on a long, gently curved peduncle, the node is compressed anteroventrally, and is sharply rounded above in side-view profile. Seen from above, the anterior peduncle is about 3½ times as long as the node, and the posterior peduncle about half as long; the node itself is about 0.10 mm long and 0.18 mm wide, with a convex anterior face and a flat, sloping posterior face; the anterior peduncle widens gradually behind the spiracles to receive the node. Seen from behind, the node is somewhat like a *Formica* petiole in outline, with broadly rounded crest, bulging sides and narrower ventral portion. Postpetiole about 0.16 mm long, 0.17 mm wide, subcircular as seen from above, with straight anterior margin.

Also the following characters:

(1) Mandibles relatively shorter than in *ocellatus,* their preapical borders unarmed except for an almost imperceptible "submedian welt."

(2) Humeral teeth triangular, strongly projecting, rendering the promesonotum very slightly broader than long (cervix excluded).

Sculpture of promesonotum consisting of about 8 slightly wavy costulae running anteriad from the metanotal groove and fanning out to meet 2-3 short transverse costulae on the anterior pronotum; costulae and interspaces shining; cervix smooth and shining.

(3) Propodeal dorsum gently convex, smooth and shining discad; spines long and nearly straight as seen from side, but slightly divergent with apices incurved as seen from above; moderately elevated.

(4) Head smooth and shining, with spaced but large and distinct round fossae over the dorsum, each centrally tuberculate and bearing an inclined, short, white clavate hair. Sides of alitrunk loosely rugose, shining; rest of body and most parts of appendages smooth and shining.

(5) Color reddish ferruginous, gaster darker, reddish-brown; legs, mandibles and antennae pale straw yellow, middle and posterior femora each with a broad subapical brownish band.

Holotype (MCZ) a unique taken in rain forest near the quarry at the high falls (Cachoeira Alta) of a branch of the Rio Tarumã, northeast of Manaus, Amazonas, Brasil; 28 August 1962, W. L. Brown, Jr., leg. The worker was taken from a leaf litter berlesate.

This is the first record of the genus from the middle Amazonian region. It must be uncommon, for it was taken only once out of many Berlese funnel extractions from the Manaus area.

Acanthognathus teledectus sp. nov.

(Fig. 11)

Holotype worker: Measurements and indices in Table I. A large species, distinguished by the very narrow head and extremely long mandibles. In addition, the following character states:

1. Each mandible with 2 long and 1 short spiniform preapical teeth, also a well developed convex lamelliform welt beyond midlength, giving rise to a fine erectile trigger hair.

2. Clypeus very narrow.

3. Alitrunk slender, humeral angles low, obtuse, not strongly projecting. Propodeal dorsum flat; spines approximately straight, only slightly diverging, not quite as long as the distance between the centers of their bases, only slightly elevated.

Petiole and postpetiole formed much as in *rudis,* but relatively more slender (petiolar node 0.16 mm wide); node as seen from above oval, slightly longer than broad, and about half as long as its anterior peduncle. Postpetiole about 0.19 mm long and 0.18 mm wide, narrower anteriad.

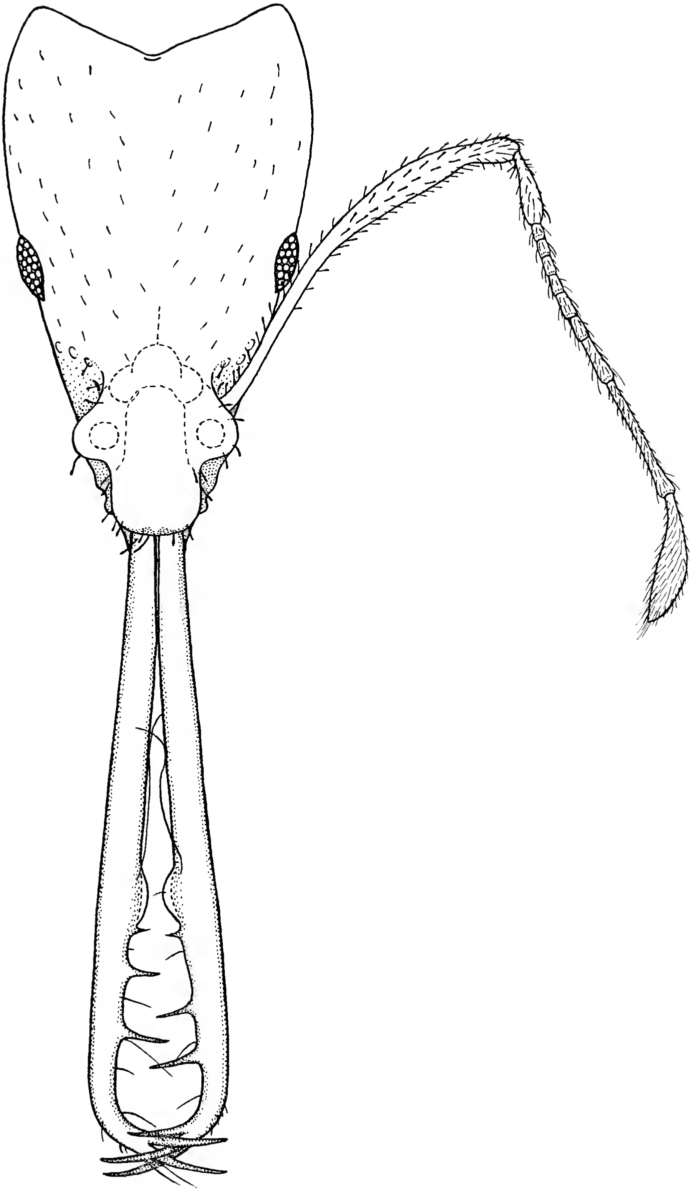


Figure 11. *Acanthognathus teledectus* sp. n., holotype worker (Bajo Calima, Colombia), dorsal view of head with mandibles and left antenna. Drawn by Margaret Menadue.

5. Body prevailing smooth and shining. A few indistinct fossae persist on anterior part of head, especially in the region in front of the eyes. Parts of lower sides of alitrunk, also petiolar peduncles in front and behind minutely and densely punctulate.

6. Clavate pilosity very sparse on clypeus, cheeks, mandibles, upper vertex, humeral angles, spines and posterior faces of both nodes, and more abundant on antennal scapes, legs and underside of head.

Color light ferruginous; antennae, legs and gaster lighter, more yellowish.

Holotype (MCZ) a unique taken in lowland rain forest on the property of Carton de Colombia (a paper-manufacturing firm) in Bajo Calima, Municipio de Buenaventura, Departamento de Valle, Colombia. The collection was made near the then principal logging road on 16 March 1967, at Kilometer 10 northward from the company's headquarters, R. B. Root and W. L. Brown, Jr., leg. The specimen was found, alive and with the incredible mandibles opened to approximately 180°, in thin humus immediately below a layer of leaf litter 1 cm. thick. No more specimens could be found in the vicinity.

This is the first member of the genus found in trans-Andean South America. The extremely long, heavily-armed mandibles and smooth integument distinguish it at once from the other known species.

Key to the Species of *Acanthognathus*, Based on Workers and Females

1. Mandibles decidedly longer than head proper, each with 2 or 3 long spiniform teeth before the apex (Fig. 11); dorsum of head smooth and shining (Colombia: Pacific lowlands) .... *teledectus*

Mandibles not longer than head proper, preapical inner borders unarmed, or at most with low irregular denticles and/or welts (Fig. 1); dorsum of head sculptured, at least with numerous distinct round fossae on the disc, intervals smooth or rugulose .... 2.

2. Petiole with very long, slender peduncle, about 3× as long as its node, which is short and transverse as seen from above (Fig 3; Amazonia: near Manaus) .... *stipulosus*

Petiolar peduncle slender, but less than twice as long as its node, which is oval and at least as long as broad as seen from above (Fig. 2) .... 3.

3. Antennal scapes short, chord less than 90% as long as manidibles seen in dorsal view; preapical area of inner mandibular border with (usually 2 or more) irregular denticles (Panama and Brasil: Para and Rio Grande do Sul) .... *brevicornis*

   Antennal scapes with chord about as long as, to much longer than, the mandibles as seen in dorsal view; inner mandibular borders without preapical denticles, though a submedian welt may be present .... 4.

4. Mandibles shorter (MI 60-75; Figs. 1, 4); dorsum of head completely, densely and rather finely rugulose, with interspersed fossae numerous, small and crowded, so that the surface, including the area around the eyes, is essentially opaque (SE Brasil, fairly common in wet forest in plateaux and uplands) .... *rudis*

   Mandibles longer (MI>75); dorsum of head loosely sculptured and more or less shining, fossae large and shallow, with smooth spaces or simple longitudinal rugulae between some rows; at least a strip bordering each eye mesially nearly smooth, shining .... 5.

5. Fossae on posterior half of dorsum of head smaller, mostly separated by flat, smooth spaces (Central America, Trinidad and southward locally in Brasilian lowlands to S. Catarina) .... *ocellatus*

   Fossae on posterior half of dorsum or head large, mostly contiguous or separated by single, simple longitudinal rugulae (Honduras; may be only a coarsely-sculptured variant of *ocellatus*) .... *lentus*

Acknowledgements

We are grateful for assistance that made this study possible. Brown was aided by U. S. National Science Foundation Grants G-23680, GB-2175 and GB-5574; Kempf received support from the Conselho Nacional de Pesquisas do Brasil. Dott. Delfa Guiglia gave us information on the type of *A. ocellatus*, and various collectors, listed under each species treatment, have sent us their valuable samples. Dr. Howard E. Evans (MCZ) has taken the trouble to mail us loans of material.

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THE LARVA OF *ACANTHOGNATHUS* (HYMENOPTERA: FORMICIDAE)

By George C. Wheeler[1] and Jeanette Wheeler[2]

In 1953 Brown divided the tribe Dacetini into four subtribes: Dacetiti, Orectognathi, Epopostrumiti and Strumigeniti. After studying the larvae of eight dacetine genera (*Daceton*, *Orectognathus*, *Epopostruma*, *Mesostruma*, *Alistruma*, *Clarkistruma*, *Strumigenys* and *Smithistruma*) representing all four subtribes, we concluded (1954) that the larval similarities and differences confirmed the grouping of the adults. But now, alas, our study of the larva of *Acanthognathus* forces us to revise our conclusion.

Genus *Acanthognathus* Mayr

Thorax and first abdominal somite strongly curved ventrally, remainder of abdomen straight; diameter increasing from head to mesothorax, decreasing slightly through metathorax and abdominal somite I, then increasing rapidly to abdominal somite V. Posterior end broadly rounded. Anus with a small posterior lip. Body hairs short to long, moderately numerous. Of three types: (1) bifid with the branches long, on the dorsal surface; (2) nearly straight, with the distal half finely denticulate, on the ventral surface and a few in a transverse row around the middle of each thorax somite and abdominal somites IX and X; (3) anchor-tipped, with long flexuous shaft, four in a row across the dorsum of each abdominal somite I-VIII. Antennae small, each with three sensilla. Head hairs moderately numerous, moderately long, denticulate. Mandibles long and narrow.

Acanthognathus rudis Brown and Kempf*

Submature. Length (through spiracles) about 2.6 mm. Thorax and first abdominal somite strongly curved ventrally, remainder of abdomen straight. Diameter increasing from the head to mesothorax, decreasing slightly through metathorax and first abdominal somite, then increasing rather rapidly to a maximum at abdominal somite V.

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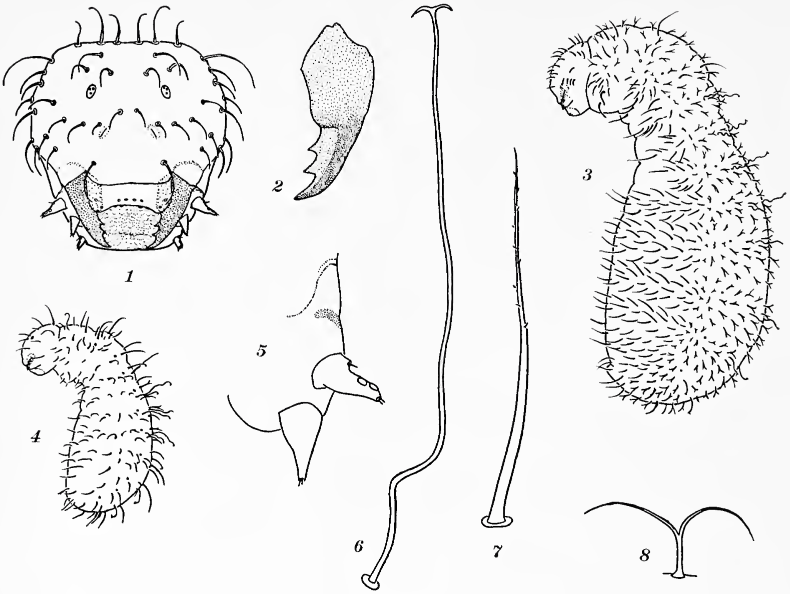
*See previous article, this issue.

Posterior end broadly rounded. Anus ventral and with a small posterior lip. Spiracles small; the mesothoracic the largest. Integument of ventral surface of thorax and first three abdominal somites with minute spinules in transverse rows. Body hairs short to long, moderately numerous. Of three types: (1) about 0.09 mm long, bifid with the branches long, alveolus and articular membrane lacking, on the dorsa of all somites; (2) 0.09-0.22 mm long, nearly straight, distal half finely denticulate, on the ventral surface of each somite and a few of the longest in a transverse row around the middle of each thoracic somite and abdominal somites IX and X; (3) 0.19-0.26 mm long, with flexuous shaft and a small anchor-tip, four in a transverse row across the dorsal surface of each abdominal somite I-VIII, the shaft becoming shorter and straighter posteriorly. Cranium subhexagonal in anterior view and with the occipital border straight. Antennae small, with three sensilla each bearing a minute spinule. Head hairs moderately numerous, 0.08-0.11 mm long, with numerous minute denticles. Labrum twice as broad as long, bilobed due to a median impression of the ventral border; anterior surface of each lobe with seven sensilla on and near the ventral border; ventral border with short rows of minute spinules; middle of posterior surface densely spinulose, the spinules minute and in long subparallel subtransverse rows, four sensilla near each ventrolateral corner. Mandibles large, heavily sclerotized; narrowly subtriangular in anterior view; lateral portion thick and ending in a long sharp-pointed apical tooth, which is curved medially; medial portion of apical half thin and blade-like, with two sharp pointed subapical teeth. Maxillae short and lobose; no spinules seen; palp a slender peg on a broad base, with two apical, two lateral and one basal sensilla, the lateral encapsulated, the others bearing a spinule each; galea a slender subcone with two apical sensilla, each of which bears a spinule. Labium with numerous minute spinules in short arcuate rows; palps short and peg-like with two apical two lateral and one basal sensilla; with an isolated sensillum between each palp and the opening of the sericteries; the latter a transverse slit in a depression. Hypopharynx spinulose, the spinules minute and in short arcuate rows.

Very Young Larva. Length (through spiracles) about 0.67 mm. Generally similar to the submature larva, except in the following details: — Body hairs mostly long, sparse. Of four types: (1) 0.04-0.13 mm long, slightly curved to flexuous, with many minute denticles, the longest with alveolus and articular membrane; (2) about 0.23 mm long, with flexuous shaft and small anchor-tip, four in a row across the dorsum of each abdominal somite II-V; (3) 0.07-



Figs. 1-8. *Acanthognathus rudis*. 1. head in anterior view, x74; 2. left mandible in anterior view, x155; 3. submature larva in side view, x22; 4. very young larva in side view, x22; 5. left maxilla in anterior view, x206; 6-8. three types of body hairs on submature larva, x260.

0.18 mm long, on abdominal somites VI-IX, with a recurved small anchor-tip; (4) 0.04-0.07 mm long, bifid, with a slightly curved shaft, a few on the dorsum of each abdominal somite. Integument of abdominal somites IX and X and of the ventral surface of the thorax and first three abdominal somites with minute spinules in short transverse rows. Cranium transversely subelliptical in anterior view.

Material studied: 18 larvae from Brazil, collected by K. Lenko, courtesy of Dr. W. W. Kempf.

Brown placed *Acanthognathus* in the Dacetiti along with *Daceton*, because the adults have ten funicular segments; but the larva of *Daceton* stands apart from all other known dacetine larvae with respect to body shape, abundance of body hairs and lack of medial mandibular teeth, whereas the larva of *Acanthognathus* shares most of the tribal characters (Wheeler and Wheeler 1954 p. 122). The only significant character shared with *Daceton* is head hairs moderately numerous instead of sparse.

The larva of *Acanthognathus* is perhaps most closely related to

Alistruma: both share body shape, postanal lip, mandibular blade and conical galea, in addition to most of the tribal characters. The next would be *Clarkistruma* with which it shares body shape and mandibular blade.

In our key to the genera (1960 p. 109) *Acanthognathus* would come under group D but would not fit the key below that. It would be in a rubric by itself, because the profile is aphaenogastriform, the mandibles are podomyrmiform and hooked hairs are present.

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NEW DATA ON ANTILLEAN SCARABAEINE BEETLES, AND TWO NEW SPECIES FROM HISPANIOLA

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The author has recently been able to examine material in the Museum of Comparative Zoology (MCZ) collected by Dr. P. J. Darlington, Jr., in Cuba in the 1920's and 1936, and Hispaniola in 1934 and 1938. The canthonines among this material were previously on loan to another specialist and could not be examined during the author's preparation of his revision of the Scarabaeinae of the Antilles (Matthews, 1966). Included are three undescribed species of *Canthochilum* from Hispaniola, where the genus was previously thought to be absent. Two of these species are here described, and the opportunity is taken to note some new distribution records and corrections, make some nomenclatorial changes, comment on some type material in European and Australian museums recently visited, and discuss some new generic names proposed by Vulcano and Pereira (1966).

Species and genera for which new data are available are discussed below in the same order as in the author's revision (Matthews, 1966).

Onthophagus albicornis Palisot, 1805.

A previously unrecorded locality for the subspecies *albicornis* Palisot is: Cap Haitien, on the north coast of Haiti. For the subspecies *capitatus* Laporte, 1840: N.E. foothills La Hotte, Grande Rivière, Ennery, Mt. Trou d'Eau, Diquini, St. Marc, Manneville, N. of Dessalines, and Camp Perrin, all in Haiti. This shows that *capitatus* occurs northward along the west coast of Haiti at least as far as Dessalines, while *albicornis* (widespread in the Dominican Republic) occurs westward along the north coast of Haiti. The two must meet somewhere on Cap St. Nicolas, and specimens collected there will decide whether we are dealing with two subspecies or two species. Intermediates have still not been seen.

Oniticellus cubiensis Laporte, 1840.

The type series of this species could not be found in the Paris

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Museum (nor could any Laporte material), but two specimens from Cuba are present in the Laporte de Castelnau Collection in the National Museum of Victoria, Melbourne. In view of the apparent loss of Laporte types in Paris, it is well to point out the availability of the Melbourne collection in cases of doubt. Since no specific specimens were designated as holotypes in Laporte's day, the Melbourne specimens could in some cases be designated lectotypes. Not all Laporte species are represented in the Melbourne collection, as this was his "secondary" series kept after the "primary" one was sold (Horne and Kahle, 1937). A quick survey uncovered 23 of Laporte's own species in the subfamily Scarabaeinae alone.

Uroxys productus Arrow, 1933.

As previously noted (Matthews, 1966:55), although the origin of the type is unknown, this name was given to a species from Guadeloupe by Paulian (1939) and the present author followed this usage, assuming that Paulian had compared the specimens directly. However, on examining the type of *U. productus* Arrow in the British Museum the author found enough differences between it and the description of the Guadeloupe specimens previously seen (Matthews, 1966:54-55) to cast doubt on the identity of the latter with *productus*. He would have let the matter go until direct comparison was possible between *productus* and a Guadeloupe specimen, except that in the meantime Balthasar (1966) redescribed the Guadeloupe species under a new name, unaware that a species of *Uroxys* had already been recorded from Guadeloupe and that it had been given the name *productus* Arrow. The introduction of a new name in the literature forces an immediate decision, even though the information at hand is inadequate. In view of the above-mentioned doubts regarding the conspecificity of the Guadeloupe species and *productus* (which concern mainly the depth and punctuation of the elytral striae and some other minor features), it is best for the moment to give the Guadeloupe species Balthasar's new name and to return the name *productus* to a species of unknown origin, represented by the unique type in the British Museum. Final determination of the problem must await a direct comparison between a Guadeloupe specimen and this type. The following synonymy is therefore suggested, subject to change:

Uroxys guadeloupensis Balthasar, 1966

Uroxys guadeloupensis Balthasar, 1966, Entomol. Blätter 62:182-183.
Uroxys productus auct. (*nec* Arrow, 1933, Ann. Mag. Nat. His., Ser. 10,

11:389); Paulian, 1939, Psyche 46:141; Paulian, 1947, Coléoptères des Antilles 1:32; Matthews, 1966, Mem. Am. Entomol. Soc., no. 21, p. 54.

Genus *Canthochilum* Chapin, 1934.

Simultaneously with the appearance of the author's revision (Matthews, 1966) there appeared another revision of the Autillean Canthonina by Vulcano and Pereira (1966), based largely on the MCZ material. In the latter work, the authors restrict the name *Canthochilum* to its type species from Puerto Rico (*oakleyi* Chapin), erect another monotypic genus *Chapincanthon* for the Puerto Rican *hispidum* Chapin, and place the three remaining species they recognize, from Puerto Rico, Cuba, and Hispaniola, in the new genus *Antillacanthon.*

The separation of *Canthochilum* sensu stricto is based on a supposed sclerite (or "piece") separating the lateral lobe of the metasternum from the mid coxa (Vulcano and Pereira, 1966:136, fig. 57). This piece is in fact not a sclerite but the widened margin of the mid-coxal cavity and therefore part of the metasternum itself, from which it cannot be separated (compare Matthews, 1965:460, fig. 15, msc). Some species of *Uroxys* have a similar widened mid-coxal margin.

The separation of *Chapincanthon* is based on the covering of clavate hairs which hold a layer of soil on *C. hispidum,* its posterior elytral tubercles, its reduced hind wings, and a number of additional features which are actually shared with other species.

The features mentioned, while unusual, are considered by the present author to be superficial modifications superimposed on a basic plan which is common to all of the species of *Canthochilum.* This basic plan, or generic conception, has been presented before as the description of the genus (Matthews, 1966:60; Zayas and Matthews, 1966:2) and need not be repeated here.

Therefore, the present author considers *Antillacanthon* Vulcano and Pereira and *Chapincanthon* Vulcano and Pereira to be subjective synonyms of *Canthochilum* Chapin.

Among the Cuban and Hispaniolan *Canthochilum* examined by Vulcano and Pereira (1966) were a number of then undescribed species to which they assigned the names *histeroides* Harold, 1868, and *gundlachi* Harold, 1868. In fact, these two species were not represented in the MCZ material subsequently examined by the author. This material contains some Cuban species recently described by Zayas and Matthews (1966) and the three undescribed Hispaniolan species discussed below.

When writing his revision, the author (Matthews, 1966) believed that *Canthochilum* either did not exist on Hispaniola, or was "reduced to as-yet-undiscovered pockets", since he did not get it during his five-day visit there. In this he proved to be wrong on all counts. Not only does it occur there, but there are at least three species, one of which is fairly widespread. Furthermore, the "pockets" were not undiscovered, but had been sampled by Dr. P. J. Darlington in 1934 and 1938 (this material was not previously available to the author).

Two of the species are described below. The third cannot be named at present as it is represented by only half a specimen, and while this actually presents enough characters for diagnosis, it is not desirable to establish a fragment as a holotype. The following descriptions are diagnostic and do not repeat generic characteristics or those not previously found to be useful in separating species.

Canthochilum darlingtoni, new species.

Description.-Oval, feebly convex, piceous to fuscous (one teneral specimen yellow), shiny, antennae and legs fuscous. Head.- Clypeal margin with four small teeth and an angulation at clypeo-genal suture. Dorsal ocular areas large, separated by a distance equal to 3 times their width (fig. 1). Head surface entirely smooth, uniformly very finely and sparsely punctate. Thorax.- Pronotum entirely smooth, shiny, uniformly very finely and sparsely punctate. Elytra moderately convex, intervals absolutely flat and extremely finely punctate, shiny. Striae indistinct, not at all impressed, very finely punctate except for 8th stria, which is coarsely punctate. Lateral carina alongside 7th stria extending for about ¾ of elytral length, not continued as a ridge posteriorly. Fully winged. Underside impunctate, faintly shagreened. Meso-metasternal suture obtusely angulate in the middle. Inner mid-coxal margin on median lobe of metasternum narrow, curving inward anteriorly to meet mesometasternal suture at a very obtuse angle. Outer mid-coxal margin uniformly narrow, paralleling edge of coxal cavity. Fore tibiae with distal edge straight, perpendicular to inner edge (fig. 2). Abdomen.- Sternites of approximately equal length along mid-line. Pygidium entirely margined, the disc convex, smooth and very finely punctate. Aedeagus with parameres triangular, basal piece with flattened ventral extension (fig. 4). Total length.- 3.0 — 4.2 mm.

Sexual dimorphism.- Major males have a widened prothorax, which thus has its lateral margins almost parallel; minor males and females have the lateral edges converging anteriorly. All males have a somewhat sinuate inner margin of the fore tibiae and blunt fore spurs (fig. 2), while the hind femora are widened and the hind tibiae slightly more curved (fig. 3).

Type.- Sánchez, Dominican Republic, July 1938, P. J. Darlington, MCZ.

This species is most closely related to the Cuban *C. histeroides* (Harold) with which it shares the number of clypeal teeth, shape of the fore tibiae, widened male fore spur and pronotum, and smoothness of dorsal surfaces. It differs in not having the middle teeth of the clypeus very slender as in that species, in having the inner midcoxal margin curving inward anteriorly, in size, the Cuban species being somewhat larger, and above all in the shape of the aedeagus, which is entirely different (compare fig. 4 here with fig. 75 in Matthews, 1966:68). The aedeagus is quite similar to that of the Cuban *C. pijirigua* Zayas and Matthews (Matthews, 1966:68, fig. 73), which is entirely different externally, while the sexual dimorphism in the fore and hind legs is a feature shared only with Puerto Rican species.

The 30 specimens which form the basis for this description were determined as *histeroides* Harold by F. S. Pereira. However, in their description under this name, Vulcano and Pereira (1966:147-151) do not mention or cite these Hispaniolan specimens and give the distribution as Puerto Rico only, although on their map (op. cit.:116) they indicate it to occur on Hispaniola as well. Not mentioned or indicated is the fact that Cuba is the type locality of the name. Apparently, their detailed description of *"histeroides"* is based on specimens of the Puerto Rican *C. taino* Matthews only. The type of *histeroides* in Paris has been examined by the author, as previously reported (Zayas and Matthews, 1966).

The author is pleased to name this species after Dr. P. J. Darlington, Jr., its collector.

Paratypes.- DOMINICAN REPUBLIC: Sánchez [Province of Samaná, on the northeast coast], July 1938, P. J. Darlington, 27 specimens (MCZ); Mt. Quita-Espuela [Province of Duarte],

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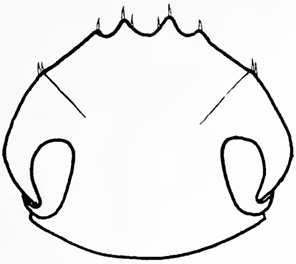
EXPLANATION OF PLATE 1

Figs. 1-4, *Canthochilum darlingtoni* n. sp. Fig. 1, outline of head in dorsal view; fig. 2, right fore tibia and tarsus in dorsal view; fig. 3, left hind femur, tibia, and tarsus in ventral view; fig. 4, aedeagus from side. Figs. 5-7, *Canthochilum ciboney* n. sp. Fig. 5, outline of head in dorsal view; fig. 6, right front tibia in dorsal view; fig. 7, aedeagus from side, membranes stippled. Fig. 8, unnamed Haitian species of *Canthochilum,* aedeagus from side.



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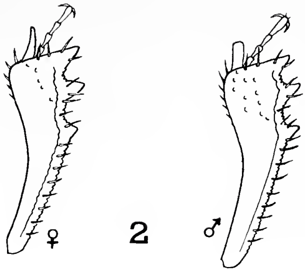

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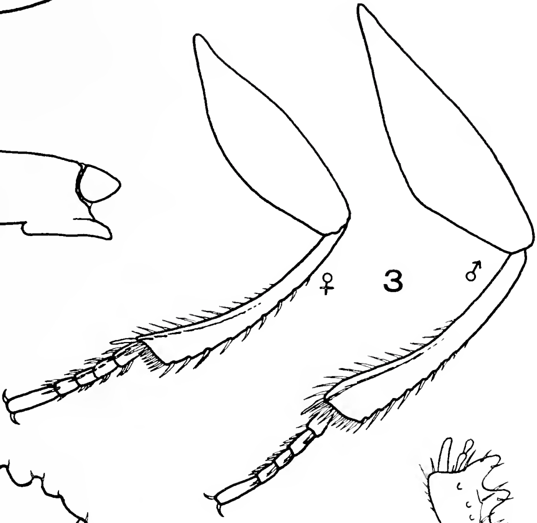

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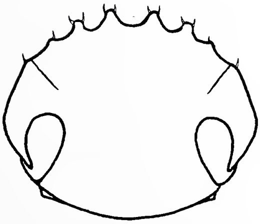

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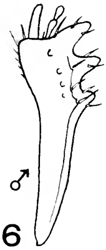

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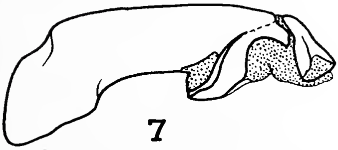

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8

MATTHEWS — CANTHOCHILUM

2—3,000 ft, July 1938, P. J. Darlington, 1 specimen (MCZ); Villa Altagracia [Province of San Cristóbal, low elevation], July 1938, P. J. Darlington, 1 specimen (MCZ).

Canthochilum ciboney, new species.

Description.- Oval, feebly convex, piceous, shiny, antennae and legs rufous. Head.- Clypeal margin with six small teeth and an additional tooth at clypeo-genal suture (the so-called "octodentate" condition). Dorsal ocular areas large, separated by a distance equal to 3 times their width (fig. 5). Head surface entirely smooth, shiny, uniformly moderately punctate. Thorax.- Pronotum entirely smooth, shiny, uniformly very finely punctate. Elytra moderately convex, intervals flat and finely shagreened, impunctate. Striae distinctly impressed and remotely punctate. Lateral carina alongside 7th stria extending for about ¾ of elytral length, not continued as a ridge posteriorly. Fully winged. Underside impunctate, slightly shagreened. Meso-metasternal suture obtusely angulate in the middle. Inner mid-coxal margin on median lobe of metasternum broadening anteriorly, meeting meso-metasternal suture at a moderately obtuse angle. Outer mid-coxal margin uniformly narrow, paralleling edge of coxal cavity. Fore tibiae with distal edge angulate, bending outward at insertion of first tooth (fig. 6). Fore spur blunt. Abdomen.- Last sternite longer than others along mid-line, as long as previous two combined. Pygidium entirely margined, the disc flat, smooth and finely punctate. Aedeagus with parameres unequally sclerotized, basal piece distally excavated with posteriorly directed projection (fig. 7). Total length.- 4.0 mm.

Sexual dimorphism.- Probably confined to the fore spur, which is blunt in the unique male, and perhaps the prothorax, which is nearly always slightly widened anteriorly in the males of this genus. The legs show no dimorphic modifications.

Type.- Mt. Trou d'-Eau, Haiti, 19 November 1934, P. J. Darlington, unique male, MCZ.

This species is most closely related to the Cuban *C. pijirigua* Zayas and Matthews, especially the latter's "form 1" (Matthews, 1966:71), from which it scarcely differs externally, being only a little more finely punctate and more pronouncedly octodentate. However, the aedeagus is entirely different (compare fig. 7 here with fig. 73 in Matthews, 1966:68) and unlike that of any other species examined.

The single known specimen was determined as *Antillacanthon gundlachi* (Harold), a Cuban species, by Vulcano and Pereira

(1966:143-144) and described in detail by them under that name. The type of *gundlachi* has been examined by the present author. It is also octodentate, but has a much coarser dorsal punctuation, the punctures of the pronotum especially running together to form grooves. Furthermore, it has a pair of low transverse ridges on the head, absent in *ciboney*, and the elytral intervals are more convex. The aedeagus of *C. gundlachi* has not been examined.

The two described species of Hispaniolan *Canthochilum* may be told apart at a glance by the shape of the head (figs. 1 and 5), also the distal edge of the fore tibiae (fig. 2 and 6), the shagreening of the elytra and deeper striae in *ciboney*, the latter's lengthened last sternite, and, of course, the male genitalia.

In keeping with a previous tradition in describing species of this genus, the new species is given an Amerindian name and is dedicated to the Ciboney tribe, which occupied part of Hispaniola and Cuba.

The third Hispaniolan species of *Canthochilum* in the MCZ material is represented by the hind body of a single male. It is a typical *Canthochilum*, judging by the sternal plates, lateral elytral carinae, and aedeagus, but is clearly different from either *darlingtoni* or *ciboney* in having the elytral intervals more strongly shagreened, the striae coarser, the elytra a little more flattened, and the aedeagus quite different, with slender parameres and a trilobed projection on the basal piece (fig. 8). The aedeagus is unlike that of any Cuban or Puerto Rican species known. The total length of the beetle is estimated at 3.3 mm.

Material examined.- Etang Lachaux, S.W. peninsula of Haiti, under 1,000 ft, 26-27 October 1934, P. J. Darlington, ½ specimen, MCZ.

New localities for previously known species of *Canthochilum* are as follows.

Canthochilum anacaona Zayas and Matthews, 1966

Mountains north of Imias, eastern Oriente, Cuba, 3-4,000 ft, 25-28 July 1936, P. J. Darlington, 1 specimen, MCZ. Previously known from the Yunque de Baracoa and Sierra de Cristal, also in extreme eastern Oriente but on different mountain ranges.

Canthochilum tureyra Zayas and Matthews, 1966

Pico Turquino, Oriente, Cuba, south side 1-3,000 ft, June 1936, P. J. Darlington, 1 specimen, MCZ. Previously known from Loma del Gato, some 50 miles to the east on the same south coast mountain range, where it was also collected by Darlington (3-7 July 1936, c. 3,000 ft, 3 specimens, MCZ).

Canthochilum hispidum hispidum Chapin, 1935

A fine series of 98 specimens was collected on Cerro Doña Juana, Toro Negro State Forest, Puerto Rico, on 28 December 1966 by Mr. S. Peck of Harvard University at 900 m (7 specimens) and 1,000 m (91) elevation, using rotten liver as bait (MCZ). Although the present author set excrement traps in this area, he did not get *C. hispidum* here (getting it about 7 mi to the west on Cerro de Punta). The present series shows sufficient variation not to be clearly ascribable either to the subspecies *hispidum* Chapin or *serropunctae* Matthews, and indicates that we are probably dealing with a cline running from east to west on the Cordillera Central at altitudes of about 3-4,000 ft. Consequently, it is here proposed to eliminate the subspecies *serropunctae* Matthews as a formal category and recognize only two subspecies: *hispidum* Chapin, 1935, showing clinal variation on the Cordillera Central, and *iunceanum* Matthews, 1965, occupying isolated mountain ranges in the east (Sierra de Cayey and Sierra de Luquillo).

The fact that these specimens came to liver bait supports previous indications (Matthews, 1965:458) that this species is partly necrophagous.

The total number of described species of *Canthochilum* now stands at 15, plus one unnamed species on Hispaniola and one subspecies on Puerto Rico, as follows.

CUBA.- Eight species. Described by Harold, 1868: *gundlachi* and *histeroides;* by Zayas and Matthews, 1966: *anacaona, baracutey, cemi, guayca, pijirigua,* and *tureyra.*

HISPANIOLA.- Three species. Described herein: *darlingtoni* and *ciboney*, plus one unnamed.

PUERTO RICO.- Five species. Described by Chapin, 1934, 1935: *andyi, hispidum,* and *oakleyi;* by Matthews, 1965, 1966: *borinquensis, taino,* and the subspecies *hispidum iunceanum* and *h. serropunctae,* of which only the former is now considered valid.

The total known taxa of Scarabaeinae from Hispaniola has now been raised from the previous three genera and six species (Matthews, 1966) to four genera and nine species (one unnamed) by the new recordings of *Canthochilum,* possibly ten species if *Onthophagus albicornis* and *capitatus* prove to be specifically distinct (see above).

Genus *Canthonella* Chapin, 1930

This genus was recently redescribed in detail and its affinities discussed by Halffter and Martínez (1967). They showed that the genus *Ipselissus* Olsoufieff, of Brazil and Northern Argentina, is extremely closely related to *Canthonella,* sharing even the very unusual form of the male genital capsule. *Canthonella,* therefore, is not as isolated taxonomically as the present author believed and is not of direct Holarctic origin in the Hemisphere. *Canthonella* and *Ipselissus* may be imagined to be now-localized relicts of a once-widespread Neotropical genus.

Less easy to explain is the similarity of both these genera to the genera *Sauvagesinella* Paulian of Southwestern Australia and *Nesovinsonia* Martínez and Pereira of Mauritius, described by Halffter and Martínez (op. cit.) and previously hinted at by the present author (Matthews, 1966:76). The genus *Sauvagesinella* needs to be redescribed in detail, a task which the present author will accomplish in his current revision of the Australian Scarabaeinae, during which affinities with Neotropical groups will also be examined.

Canthonella pygmaea (Harold, 1869).

The lost type of *Canthon pygmaeus* Harold was found by the author quite by accident in an unmarked box in the Paris Museum. This box contained numerous American canthonine specimens, including a number of unique types, removed from the René Oberthür collection, probably by R. Paulian. The other types found will be reported on by G. Halffter and A. Martínez in their current revision of the American Canthonina.

The type of this name belongs in fact to the Cuban species which has gone under the name previously (Zayas and Matthews, 1966; Matthews, 1966) and therefore presents no surprises. It bears the label, in Harold's own handwriting: "*pygmaeus* typ. Harold". It has now been placed in the Collection Générale near the types of *histeroides* and *gundlachi* (now in *Canthochilum*).

Vulcano and Pereira (1966:120-122) cite *Canthonella pygmaea* as occurring in Puerto Rico and Hispaniola, as well as Cuba. The Hispaniolan specimen on which they base this record has been examined by the present author and found to be *Canthonella constans* Matthews (mentioned below). The two supposed Puerto Rican specimens have not been seen by the author, but a total of 184 specimens of *Canthonella,* collected from all over the island of Puerto Rico, has been examined and all are *C. parva* Chapin. If the two specimens cited by Vulcano and Pereira are indeed *pygmaea,* then it is likely that they have been mislabelled. This species is exclusively Cuban, as far as we know.

Canthonella constans Matthews, 1966.

New locality record: Cloudforest, vicinity Valle Nuevo, Dominican Republic, August 1938, c. 6,000 ft, P. J. Darlington, 1 specimen, MCZ. This is very nearly, or perhaps exactly, the same location where the author collected his series, which was at 11 km south of Constanza, 5,700 ft, October 1964. Valle Nuevo itself is 21 km south of Constanza.

The same specimen was cited by Vulcano and Pereira (1966:122) as *Canthonella pygmaea.* The two species are quite different (see Matthews, 1966, key pp. 76-77, etc.).

Canthon perseverans Matthews, 1966.

The British Museum collection has two specimens of this Grenadan species, found among the unclassified material and labelled "Trinidad". They were entered as part of the Fry Collection in 1905. Doubting that this species actually occurs in Trinidad, the author checked under the specimen numbers in the Fry Collection catalogue and found that this material had been collected in "Trinidad *and Grenada*". This was not indicated on the specimen labels, and there can be no doubt that the two specimens of *C. perseverans* were collected on Grenada, to which island this species seems to be an exclusive endemic.

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A SYNOPSIS OF THE CAVE MILLIPEDS OF THE UNITED STATES, WITH AN ILLUSTRATED KEY TO GENERA*

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Museum of Comparative Zoology, Harvard University

INTRODUCTION

The taxonomy of the Class Diplopoda is presently in a chaotic and undeveloped state, even in an area so well-studied for most organisms as the United States. Attempts by the uninitiated to identify collections of even the most common forms of millipeds are usually thwarted by the lack of keys and revisions in the literature, and specialists in this group are frequently swamped with requests for determinations from ecologists, museums, general collectors and speleobiologists. Cave explorers have made a great contribution to our knowledge of the milliped fauna of the United States, with the result that the hypogean forms are usually better known than epigean ones.

At least in the United States, it seems unlikely that additional representatives of new families and genera of millipeds will be discovered in caves, and therefore the time seems ripe for a synopsis of our knowledge of troglobitic diplopods. Causey (1960b) summarized the features characterizing a milliped as a troglobite, though all sorts of gradations may be obtained within a given family from troglobite through troglophile to cave accidental. In general, pigmentation and the number of ocelli, if these are usually present in the family, are reduced in troglobites. The antennae and legs are longer in proportion to their thickness than in related epigean species and the body segments themselves may be elongated and narrowed. Calcification of the cuticle is often reduced. The dorsal ornamentation so characteristic of many of the families of millipeds is usually suppressed, though in at least one case (*Pseudotremia*, Cleidogonidae), some highly cave-adapted species are more ornamented than epigean ones. Troglobitic millipeds are frequently a little larger than their epigean relatives, though in some cases (*Pseudotremia*; *Cambala*, Cambalidae) troglobites are much smaller. *Speostriaria* (Striariidae) and *Tetracion* (Order Callipodida, family name uncertain) are the giants of their respective families in North

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America; in the Trichopetalidae, *Scoterpes* (to 8 mm) is larger than *Trichopetalum* (4-5 mm).

Troglobitic millipeds undoubtedly evolved under a combination of two major factors: their preadaptation for the cave habitat as a part of the humus fauna, and the climatic fluctuations of the Quaternary. This will be further discussed in a forthcoming revision of the Conotylidae.

Zoogeographically, the troglobitic millipeds present an interesting picture. *Pseudotremia*, which I am currently revising in connection with a larger study of the family Cleidogonidae, has more than 40 species in the Appalachian region from Alabama north to Indiana and northeast West Virginia. These fall into three groups: those which are clearly troglobitic, with, in some cases, a virtual absence of pigment and ocelli; a group of troglophiles, lightly pigmented and with 25-30 ocelli in each eyepatch; and a small number of very large epigean species with dark pigment and 35 or more ocelli in each eyepatch. The epigean species are mostly found at higher elevations, or associated with known glacial relict areas. The troglobites, for reasons not presently clear, are separated into two groups, one in an arc from extreme northwest Georgia and northeast Alabama through central Tennessee and Kentucky to Indiana, and a second enclave in western Virginia and eastern West Virginia. Endemism is remarkably high; two caves only a mile apart and in the same stream valley in DeKalb Co., Tennessee, have different species of *Pseudotremia.*

In contrast to this pattern of a widespread genus with highly endemic species are two other kinds of situations. A single species, *Cambala speobia*, ranges over an area of 2500 square miles in the Edwards Plateau in Texas; *Antriadesmus fragilis* is known only from a single cave in a well-collected area.

The ecological postion of cave millipeds is uncertain. Like all troglobites, they are ultimately dependent upon importation of food into the cave ecosystem from the outside. The most frequent ecological note with collections of troglobitic millipeds indicates that the specimens were found on rotting wood. I have examined the foreguts of individuals of five species of *Pseudotremia* and found that wood tracheids were the only identifiable remains. I have also observed a West Virginia species of *Pseudotremia* feeding on paper, candle wax, raccoon feces and a dead salamander. *Tetracion jonesi* Hoffman can be baited with carrion; a related epigean genus, *Abacion,* is at least partly carnivorous. In turn, cave millipeds may serve as food for cave crickets and salamanders; I have seen *Pseudotremia* specimens taken from the stomach of the cave salamander, *Eurycea lucifuga.*

The identification of millipeds is founded mostly on the shape of the male gonopods, modified legs found on the seventh segment of mature males. Classifications have been based on these structures to the extent that even some related families cannot be separated if only females and immature specimens are available. The gonopods are often small and retracted into pockets in the body; dissection is usually necessary to identify species. An attempt is made here to present a key to genera based on nonsexual characters that can be observed under low magnification. However, adults should be used; adult males can be recognized by the prominent reduced and specialized legs on the seventh segment, and females have slightly protruding genital valves at the base of the second legs (Figs. 2, 8, 10). With some experience, most specimens can be placed in the appropriate genus. Following the key are notes on the described species in each genus. The identification of species is still a matter for the specialist, most of whom are eager to do such work. Complete references are to be found in the checklist of Chamberlin and Hoffman (1958).

This study was based entirely on specimens, both types and general material, in the Museum of Comparative Zoology. I thank Dr. H. W. Levi for his cooperation and help, and Mr. Stewart Peck for many unpublished data.

Key to Genera

1a. Adults with no more than 20 segments .... Order POLYDESMIDA, 5.

1b. Adults with 28 or more segments .... 2.

2a. Body of 28 or 30 segments; each segment with six prominent macrosetae .... Order CHORDEUMIDA, 10.

2b. Body of more than 30 segments; segments without macrosetae, or with more than six .... 3.

3a. Body segments with elaborate and regular surface sculpturing of raised ridges or pyriform lobes; the largest of these bearing the pores of the repugnatorial glands (Figs. 1, 2) .... 4.

3b. Segments with no more than a few low striations, mostly lateral; repugnatorial pores inconspicuous (Fig. 14) .... Order JULIDA, Family Nemasomatidae, 20.

4a. First segment overlapping the head; gland openings on rounded lobes; ocelli usually in a single row, or absent (Fig. 1) .... Order SPIROSTREPTIDA, Family Cambalidae, *Cambala.*

4b. First segment not overlapping the head; gland openings on flat-topped ridges; ocelli usually in a triangular group (Fig. 2) .... Order CALLIPODIDA, Family ?, *Tetracion.*

5a. Dorsal surface set with rows of small, seta-bearing knobs, three to five rows per segment; 20 segments (Figs. 3, 4) .... Family Vanhoeffenidae, 7.

5b. Dorsal surface of each segment with distinct polygonal areas, each with a small seta; or quite smooth; 19 or 20 segments .... 6.

6a. Nineteen segments; dorsal surfaces with polygonal areas (Fig. 5) .... Family Polydesmidae, *Brachydesmus.*

6b. Twenty segments; each segment smooth .... Family Nearctodesmidae, *Ectopodesmus.*

7a. Segmental setae in five rows .... *Speorthus.*

7b. Segmental setae in three rows .... 8.

8a. Paranota (lateral "wings" on each segment) small, rounded (Fig. 3) .... *Antriadesmus.*

8b. Paranota of each segment prominent, sharply produced backward .... 9.

9a. Last segment triangular, slightly curved ventrad; Nevada .... *Tidesmus.*

9b. Last segment truncate, not curved (Fig. 4) Texas .... *Speodesmus.*

10a. Head partially concealed by the hoodlike first segment; last segment three-lobed; body with 10-12 more or less prominent ridges that run the length of each segment (Fig. 12) .... Family Striariidae, 16.

10b. Head completely exposed; last segment not lobed; body without ridges as described above, though other surface sculpturing may be present .... 11.

11a. Dorsal surface of segments with a heavy pattern of tiny, sharp ridges; macrosetae inconspicuous (Fig. 9) .... Family Tingupidae, *Tingupa.*

11b. Dorsal surface of segments smooth, except for six seta-bearing tubercles, or with rough granulations or knobs, but never sharp, tiny ridges (Figs. 8, 10, 13) .... 12.

12a. Segmental setae not on prominent knobs, body with nearly smooth margins when seen dorsally[1] .... Family Caseyidae, 17.

12b. Segmental setae on prominent knobs and/or shoulders .... 13.

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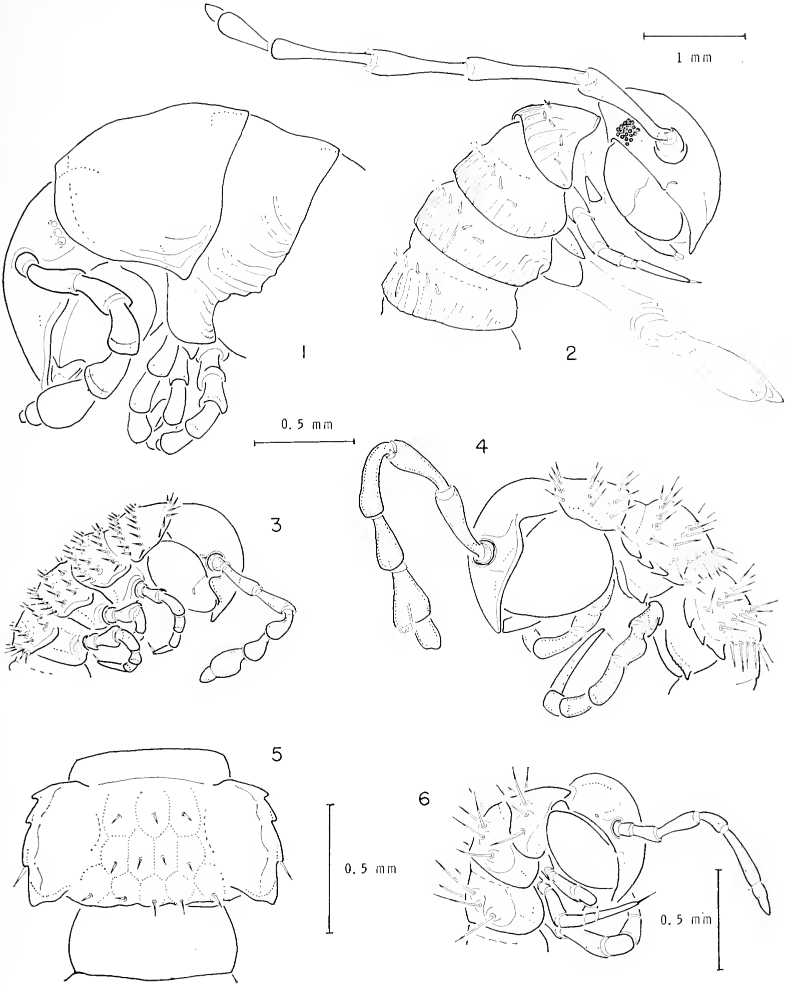
[1] Specimens of the eastern genus *Cleidogona* will key out here; see notes on Cleidogonidae.

13a. Dorsal surface of segments coarsely granular or with irregular large tubercles; lateral shoulders prominent on midbody segments (Figs. 10, 11, 13) .... Family Cleidogonidae, *Pseudotremia.*
13b. Dorsal surface smooth between the seta-bearing knobs .... 14.
14a. Pigmented specimens from Idaho caves, with more than 10 ocelli .... Family Idagonidae, *Idagona.*
14b. If from caves in Idaho, then not pigmented and with less than 10 ocelli; if pigmented, then from other localities .... 15.
15a. Ocelli in a triangular patch or two subparallel rows; adults usually longer than 12 mm; antennae long, reaching posteriad to the sixth or seventh segment (Fig. 8) .... Family Conotylidae.
15b. Ocelli in a crescent-shaped or right-angled row, or completely absent; adults usually less than 9 mm long; antennae short, reaching posteriad to third segment .... Family Trichopetalidae, 18.
16a. Body pigmented; to 20 mm long .... *Striaria.*
16b. Body white except for ocelli; to 30 mm (Fig. 12) .... *Speostriaria.*
17a. Without ocelli .... *Speoseya.*
17b. With 12-14 ocelli .... *Opiona.*
18a. Twenty-eight segments; with ocelli .... *Trichopetalum.*
18b. Thirty segments; no ocelli .... 19.
19a. Segmental setae nearly as long as segments are wide; Missouri, Illinois, Kentucky, Tennessee, Alabama, Georgia (Fig. 7) .... *Scoterpes.*
19b. Segmental setae little more than one-half as long as segments are wide; Virginia, West Virginia; eastern Kentucky (Fig. 6) *Zygonopus.*
20a. Sixty to 80 segments (Fig. 13) .... *Zosteractis.*
20b. Thirty-five to 45 segments .... *Ameractis.*

NOTES ON GENERA

ORDER POLYDESMIDA

None of the members of this order have ocelli, and if they undergo several molts in a cave, they may also become depigmented. However, except for *Ectopodesmus*, all known true troglobites in this order are no more than 20 mm long. All troglobitic polydesmids known to me are also narrower than surface forms; the width of *Ectopodesmus* is only about 1/10 its length. The large, heavily pigmented members of the families Polydesmidae and Xystodesmidae



Figs. 1-6. Lateral and dorsal views of anterior ends and body segments of cave millipeds. Fig. 1. *Cambala minor.* Fig. 2. *Tetracion jonesi,* female with ovipositor. Fig. 3. *Antriadesmus fragilis.* Fig. 4. *Speodesmus echinourus.* Fig. 5. Dorsal view of midbody segment of *Brachydesmus superus.* Fig. 6. *Zygonopus packardi.*

are frequently accidental in caves in the Appalachians, but in the midwestern region, the Family Euryuridae is more common.

Family Polydesmidae

The limit between this family and the one which follows is not well drawn, and a thorough study is needed to determine which of our North American genera belong here or in other families. At present, none of the North American Polydesmidae seem to be truly troglobitic, and only one genus is significant as a troglophile.

Genus *Brachydesmus* Heller

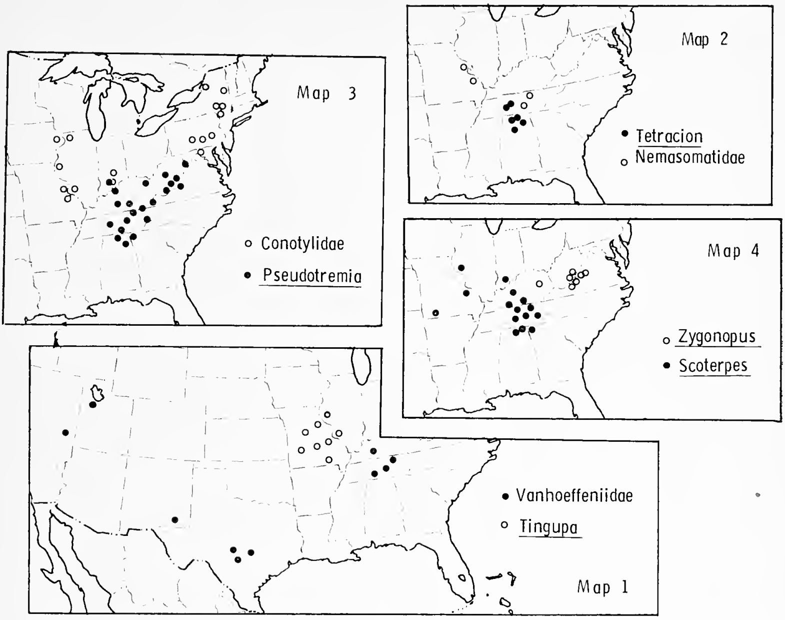
Some of the numerous European members of this genus are true troglobites, but the species which American diplopod systematists for the present assign to the genus are at most troglophilic. *Brachydesmus pallidus* Loomis (1939) has been recorded from caves in Virginia and West Virginia, but it is a synonym of *B. superus* Latzel (Fig. 5; holotype of *pallidus* in Museum of Comparative Zoology, examined) a European epigean and troglophilic species common in cultivated areas of the United States.

Polydesmus cavicola Packard (1877) was placed arbitrarily in *Brachydesmus* by Chamberlin and Hoffman (1958), who noted that the type was not known to exist. A careful search of the collections of the Museum of Comparative Zoology resulted in the rediscovery of the female holotype. It has 20 segments and three rows of prominent setigerous tubercles, and is thus excluded from *Brachydesmus*. The general appearance would place it in the 'Family' Vanhoefeniidae (it will key to *Tidesmus* in the key above), in which case it will probably require a new generic name, but the systematics of the small North American polydesmoids are so confused that I hesitate to add yet another name to the list. It seems clear, however, that the genus *Brachydesmus* is not well represented in North America.

Family Vanhoeffeniidae Attems

Map 1

Chamberlin and Hoffman (1958) and Loomis (1960) have both pointed out that the use of this family name is questionable. However, it is generally agreed (Loomis, 1960) that the following genera belong together, whatever the family name might finally become. Causey (1959b) states that *Antriadesmus* is troglophilic rather than troglobitic, but no surface collections of this genus are known to me. It is easily confused with the humicolous surface form *Chaetaspis*, of which it may indeed be a synonym. Undoubtedly numerous spe-



Maps of selected localities of cave milliped collections in the United States. Map 1. Distribution of *Tingupa pallida* and troglobitic and troglophilic members of the Family Vanhoeffeniidae. Map 2. Distribution of the genus *Tetracion* and troglobitic members of the Family Nemasomatidae. Map 3. Distribution of the genus *Pseudotremia* (includes some epigean records) and troglophilic members of the Family Conotylidae. Map 4. Distribution of the genera *Scoterpes* and *Zygonopus*.

cies remain to be discovered, particularly in the Southwest and Pacific regions.

Genus *Antriadesmus* Loomis

Fig. 3

Three species of this genus are known from the Appalachian region. All are about 6.5 mm long and can be separated only by the form of the male gonopods, and for the present, the collection locality. *Antriadesmus fragilis* Loomis (Fig. 3) was described from females (Loomis, 1953) collected in White's Cave, Mammoth Cave National Park, Kentucky; subsequently Loomis (1960) illustrated the male gonopod, and noted that the species occurs nowhere else in the entire Mammoth Cave complex. Causey (1959b) described *A. mollis* from Cumberland Caverns, Warren Co., Tennessee, and *A. debilis* from Walker Spring Cave, Wayne Co., Tennessee.

Genus *Speodesmus* Loomis

Fig. 4

Causey (1959a) has already noted the remarkable loose-jointed appearance of the members of this genus, due to the elongated legs and body segments. They are undoubtedly troglobites. The two known species can only be separated by reference to the male gonopods. Both are found in caves of the Edwards Plateau of Texas. *Speodesmus echinourus* Loomis (Fig. 4) is known from caves in Kerr and Hays Counties (Loomis, 1939; Causey, 1959a); *S. bicornourus* Causey from Beck's Ranch Cave, Williamson Co. (Causey, 1959a). Both species are considerably larger than the preceding genus, being 12-20 mm long, and they have much more prominent paranota, the posterior angles of which are drawn out posteriad.

Genus *Speorthus* Chamberlin

The single species of this genus, *S. tuganbius* Chamberlin, was described incompletely and without illustration (Chamberlin, 1952), but Loomis (1960) subsequently located and illustrated the male holotype. Although *tuganbius* is only 8 mm long, the gonopods look very much like those of *Speodesmus*, and it is quite likely that this name is a synonym of *Speodesmus*. It is known only from the types, collected in 1924 in Carlsbad Caverns, New Mexico.

Genus *Tidesmus* Chamberlin

It is clear from the description given by Chamberlin (1943) of the type species, *T. episcopus*, an epigean species, that *Tidesmus hubbsi*, described in the same paper, is not a member of that genus, and perhaps not even a member of the same family. The illustrations of the gonopods of *episcopus* are quite similar to those of members of the genus *Phreatodesmus* (Loomis, 1960). Thus *Tidesmus*, the older name, may eventually become the proper name of the species now grouped under *Phreatodesmus*. Only a study of the type material, now unavailable, will solve this kind of problem, common in diplopod taxonomy. But for the present, I will only note that *Tidesmus hubbsi* was described from the cave of Cave Valley, Lincoln Co., Nevada.

Family Nearctodesmidae Chamberlin and Hoffman

Genus *Ectopodesmus* Hoffman

The single species of this genus, *E. remingtoni* Hoffman, was originally described from an unnamed cave 1.7 miles north of Grafton, Jersey Co., Illinois[2] (Hoffman, 1962). Subsequent collections have shown it to be not uncommon in many of the caves of western Illinois, particularly in Adams, Pike, and Monroe Counties (S. Peck, pers. comm.). Its closest relatives occur in the Pacific Northwest, thus presenting another instance of the close faunistic correspondence between the Ozark-Appalachian system and the Pacific coast mountain ranges. The case of *E. remingtoni* is remarkably similar to that of the antrodiaetid spider genus *Atypoides*, with a single species in Missouri and Illinois and two in California and Oregon (Coyle, 1968). Missouri caves should be thoroughly searched for nearctodesmids.

ORDER SPIROSTREPTIDA

Family Cambalidae

The criteria for the establishment of genera in this family are as yet uncertain. Loomis (1938) recognized several genera, most of them from the western United States, without resorting to details of the gonopod structure. More recently, Hoffman (1956) established the genus *Troglocambala,* for specimens from Turk's Cave, Conecuh Co., Alabama, separated from *Cambala* by the three-jointed telopodite of the anterior gonopods. Causey (1964) implied without explanation that this genus was a synonym of *Cambala*, but established at the same time the genus *Mexicambala*, also a troglobite, based on specimens from Cueva de la Parra, San Luis Potosi, on differences of a similar quality. Until a thorough study reveals the true relationships of species in this family, it is my opinion that both these genera should be regarded as synonyms of *Cambala.*

Genus *Cambala* Gray

Fig. 1

In the eastern United States, both *Cambala annulata* (Say), a large (up to 45 mm long), black species, and *C. minor* Bollman (Fig. 1), a small (up to 20 mm long) brown species are troglophilic. The status of *C. minor* and a few other names based on similar forms is uncertain. Specimens from widely scattered caves in Alabama, Tennessee, Kentucky and West Virginia which I have recently examined show small but constant differences in the gonopods, ocelli number, and pigmentation. Careful study will probably reveal that more than one species is involved.

Cambala loomisi (Hoffman) has already been mentioned; it is the type species of *Troglocambala.* In Texas, the caves of the Edwards

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[2] Now known as Grafton Cave.

plateau have several species that are perhaps troglobitic; *C. reddelli* Causey is known from Culbertson, Wheeler, and Childress Counties, *C. speobia* (Chamberlin) from a long list of counties in central and southwest-central Texas (Causey, 1964).

ORDER CALLIPODIDA

Hoffman and Lohmander (1964) use this name for the order usually called Lysiopetalida in this country. The family name of the North American genera is uncertain.

Genus *Tetracion* Hoffman

Map 2; Fig. 2

Tetracion is represented by two species, *T. jonesi* Hoffman (Fig. 2), in the Tennessee River drainage in northeastern Alabama, and *T. tennesseensis* Causey (1959a) in Warren and Grundy Counties, Tennessee, in the Cumberland River drainage. Hoffman (1956) described two subspecies of *T. jonesi* from widely separated caves. Since that time, large series of specimens collected by carrion baiting in caves from the intervening localities have come into the collections of the Museum of Comparative Zoology. I have studied this material in detail and have come to the conclusion that the distinction between *T. j. jonesi* and *T. j. antraeum* cannot be maintained, because of the indistinct gradation between the two type localities. Relatively few specimens of *T. tennesseensis* have been collected, but it seems distinct in range and in structure, being somewhat smaller than *T. jonesi.*

ORDER CHORDEUMIDA

According to Causey (1960b), fully 80% of the troglobitic millipeds of North America fall in this order. Its members are easily distinguished from all others by the presence of six prominent macrosetae on each segment.

Family Conotylidae Cook

Map 3; Fig. 8

Two genera with troglophilic members occur in the eastern United States. *Conotyla* has two species known primarily from caves, *C. bollmani* (McNeill) of Indiana (Fig. 8), and *C. blakei* (Verhoeff) of New York, Pennsylvania and Maryland. *Austrotyla specus* (Loomis) is a troglophile of Missouri, Illinois, and Iowa. *Conotyla pectinata* Causey, of northern Illinois, represents a third distinct troglophilic genus, and *Conotyla humerosa* Loomis, a fourth genus containing the only real troglobites of the family. The details of these generic assignments and their names will appear in my forthcoming revision of the family. There are numerous epigean species.

Family Idagonidae Buckett and Gardner

Genus *Idagona* Buckett and Gardner

Idagona westcotti has been described in detail by Buckett and Gardner (1967) from material collected in two caves in Clark and Butte Counties, Idaho. However, the family is closest to the Conotylidae, which is completely unrelated to the Cleidogonidae, rather than near both these families, as they suggest. The affinities of the Conotylidae and related families are primarily Asian, while the Cleidogonidae are a uniquely American group. Superficially, members of the Idagonidae cannot be distinguished from conotylids, but the outline of a segment (Buckett and Gardner, 1967, Fig. 4) shows that *Idagona* is somewhat deeper-bodied than the sympatric conotylids.

Family Trichopetalidae Verhoeff

Two genera, *Scoterpes* and *Zygonopus*, are the most modified troglobitic millipeds of North America. Causey (1963) gives a key to all known genera of the Trichopetalidae.

Genus *Trichopetalum* Harger

Members of this genus seem to have remarkably wide distributions, especially for such fragile humus-dwelling animals. Close study of geographic variation may show that numerous species are involved. *Trichopetalum* is generally considered troglophilic, though one species, *T. subterraneum* Causey, is known only from Slack's Cave, Scott Co., Kentucky (Causey, 1967).

Genus *Scoterpes* Cope

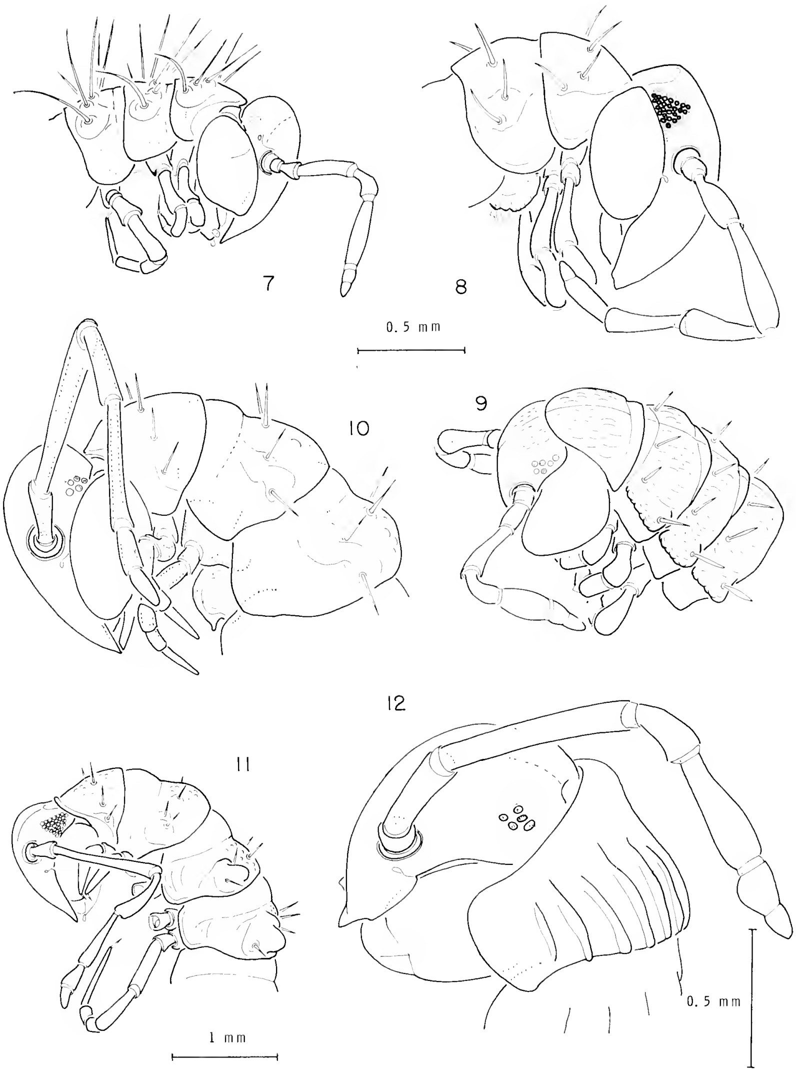
Map 4; Fig. 7

Causey (1960b) has identified 27 taxa in this genus, most of them as yet unnamed, presumably differing in details of the male gonopods. Because of their small size (to 8 mm) they are frequently overlooked by collectors, but are now known to occur in many caves in Missouri, Illinois, Kentucky, Tennessee, Alabama, and Georgia. Chamberlin and Hoffman list the four described species, of which one (*S. austrinus* Loomis) is illustrated here (Fig. 7).

Genus *Zygonopus* Ryder

Map 4; Fig. 6

Zygonopus is found in caves in eastern West Virginia (*Z. packardi*



Figs. 7-12. Lateral views of anterior ends of cave millipeds. Fig. 7. *Scoterpes austrinus*. Fig. 8. *Conotyla bollmani*. Fig. 9. *Tingupa pallida*. Fig. 10. *Pseudotremia nodosa*. Fig. 11. *Pseudotremia hobbsi*. Fig. 12. *Speostriaria shastae*.

Causey, Fig. 6) and adjacent western Virginia. A single Kentucky record is questionable. *Zygonopus* seems more distinct from *Trichopetalum* than is *Scoterpes*, and the two genera probably had independent origins. Despite a recent revision by Causey (1960a), the status of the four described species remains uncertain: ". . . the four species I formerly assigned to it [*Zygonopus*] . . . are two species, of which one is composed of three subspecies (Causey, 1963b)."

Family Caseyidae Verhoeff

This family is poorly known, but probably has many species in the Pacific Northwest and California. Causey (1963a) has done much to clarify the anatomy of the gonopods. The relationship of this family to the small, eastern Family Underwoodiidae needs study.

Genus *Speoseya* Causey

Speoseya grahami Causey, the only known species of this genus, is about 10 mm long and is known from caves in Calaveras Co., California (Causey, 1963a).

Genus *Opiona* Chamberlin

Opiona siliquae Causey (1963a), from Fault Rock Cave, Mendocino Co., California, is about the same size as *Speoseya grahami*, but has ocelli. Two additional epigean species of this genus are known from Washington and British Columbia (Chamberlin and Hoffman, 1958).

Family Cleidogonidae Cook

This is a very large family, distinguished by its large, well-defined genera and relatively wide range (from Ontario to Guatemala). Members of the genus *Cleidogona* are sometimes found in the Appalachian region as accidentals or troglophiles,[3] and will key out as caseyids in my artificial key, but the two groups are not sympatric — no caseyids occur in the eastern United States.

Genus *Pseudotremia* Cope

Map 3; Fig. 10, 11, 13

Dearolfia Loomis (1939) is a synonym of this genus. *Pseudotremia* is the most widespread and abundant genus of American cave millipeds, and has troglobitic, troglophilic and epigean members. Examination of several large collections and of all type material, including

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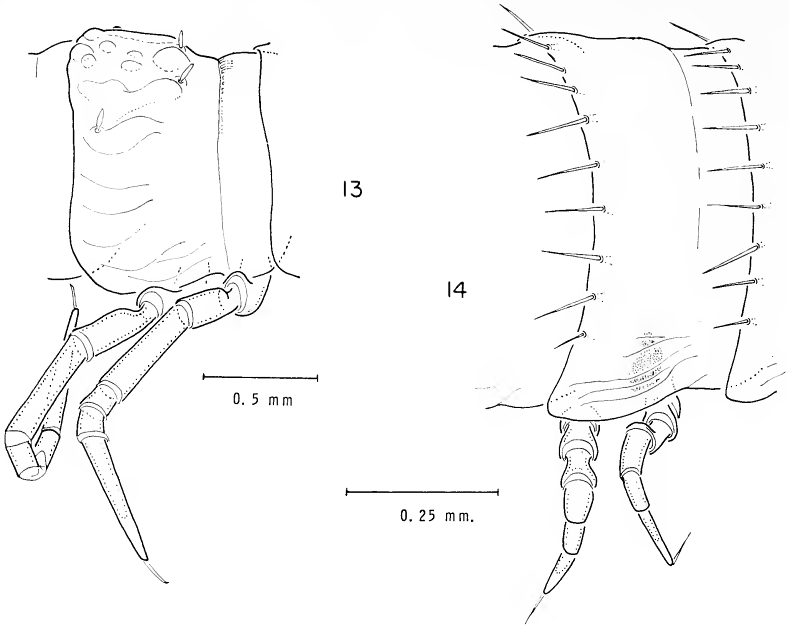
[3] There are numerous undescribed troglobitic *Cleidogona* spp. in Mexico.



Figs. 13-14. Lateral views of midbody segments of cave millipeds. Fig. 13. *Pseudotremia nodosa.* Fig. 14. *Zosteractis interminata.*

that of Packard's species, recently found in the Museum of Comparative Zoology, has shown that there are at least 45 taxa represented. many of them known only from single caves.

The appearance of the true troglobites is strikingly different from that of the other species; the troglobites are usually almost completely without pigment, less than 20 mm long, with depigmented and reduced ocelli (represented in some cases by only the cuticular lenses) and strongly knobbed segments (Figs. 10, 13). In a series of increasingly larger epigean forms, the lateral shoulders of the segments become more prominent, but the dorsum is not as knobby (Fig. 11). Strenuous efforts should be made to collect males wherever this genus is discovered. They are easily separated from the females by the prominent sclerotized gonopods on the seventh segment.

Family Tingupidae Loomis

Epigean members of this family are known from California, Utah, and Arizona.

Genus *Tingupa* Chamberlin

Map 1; Fig. 9

Tingupa pallida Loomis is the only known troglobite in this genus. It occurs in Missouri and Illinois and is about 5 mm long (Loomis, 1939, 1943, 1966).

Family Striariidae Bollman

Epigean species of the Striariidae are widely distributed, but seem to be concentrated in the Pacific Northwest. Two genera are known from caves.

Genus *Striaria* Bollman

Striaria columbiana Cook has been reported from Allen's Cave, Front Royal, Virginia (Loomis, 1939, footnote on p. 186), and *S. eldora* Chamberlin was described from Crystal-Cosumnes Cave, Eldorado Co., California (Chamberlin, 1953). Both may be troglophiles, though *S. columbiana* might better be regarded an accidental for the time being.

Genus *Speostriaria* Causey

Fig. 12

Speostriaria resembles *Striaria* but is nearly half again as large (30 mm long), depigmented, and has fewer ocelli (Fig. 12). The single species, *S. shastae* (Causey), is known only from Samwel Cave, Shasta Co., California (Causey 1958, 1960c).

ORDER JULIDA

Family Nemasomatidae Bollman

Map 2; Fig. 14

Hoffman (1964) has done much to clear up the status of the American members of this family, but hesitated to include *Zosteractis*, usually placed in the family Zosteractiidae. Study of holotype material (Museum of Comparative Zoology) indicates that his inference (1964) was correct, and *Zosteractis* is herewith included in the family Nemasomatidae.

Genus *Zosteractis* Loomis

Fig. 14

The single species of this genus, *Z. interminata* Loomis, (Fig. 14) is known from caves in Missouri and Illinois (Loomis, 1943; Causey, 1960d). It is about 20 mm long, but only slightly more than 0.5 mm wide.

Genus *Ameractis* Causey

Ameractis satis Causey has been recorded from White, Overton, Putnam and Hamilton Counties, Tennessee (Hoffman, 1964; Causey, 1959b). It is only half the length of *Zosteractis interminata* and has fewer segments.

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THE FAMILY OONOPIDAE (ARANEAE) IN FLORIDA*

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During my study of the family Oonopidae (Araneae) in Central America and the West Indies I have also become interested in this family as it exists in the State of Florida. In February, March and April, 1968, I had an opportunity to collect spiders in Florida as a part of my study of this group of animals with the support of the National Science Foundation Grant No. GB-5013. In addition to my own collection I have had helpful loans from the American Museum of Natural History and the University of Florida in Gainesville. Dr. W. J. Gertsch has also made it possible for me to examine the types of *Ischnothyreus barrowsi* Chamberlin and Ivie, 1935 and *Stenoonops minutus* C. and I., 1935, now being placed on semipermanent loan from the University of Utah to the American Museum of Natural History. Oonopidae from Florida and the West Indies now a part of the collections in the Museum of Comparative Zoology have also been very helpful in this study.

As usual, my entire collection of this family will be deposited in the Museum of Comparative Zoology. All types described from specimens on loan from the American Museum of Natural History will be deposited in that institution.

My appreciation and gratitude are again expressed for the continued aid and encouragement in the pursuit of my studies extended by the staff of the Museum of Comparative Zoology. My thanks are also extended to Dr. W. J. Gertsch, recently retired from the staff of the American Museum of Natural History and to Dr. Howard V. Weems, Jr., Florida Department of Agriculture, Gainesville, Florida, for the loan of very helpful collections. Grants GB-1801 and GB-5013 from the National Science Foundation have made it possible for me to continue my studies in the Museum of Comparative Zoology and on several collecting expeditions for nearly six years.

As a result of my study of the Oonopidae of Florida as indicated above I have been able to identify seven different genera. Among these I have been obliged to recognize five different species of the

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genus *Opopaea*. It seems highly probable that diligent collecting in the habitats preferred by members of this family will yield additional genera and species not yet recorded in the state.

Key to the known genera of Oonopidae in Florida

1a. Genera with dorsal abdominal scutum *(Ischnothyreus, Opopaea, Triaeris* 2

1b. Genera without a dorsal abdominal scutum *(Heteroonops, Oonops, Orchestina, Stenoonops)* 4

2a. Abdomen with dorsal and ventral scuta strongly chitinized and covering nearly the entire abdominal surface .... *Opopaea*, p.

2b. Abdomen with scuta covering only a relatively small portion of the abdominal surface and not so strongly chitinized .... *(Ischnothyreus, Triaeris)* 3

3a. ALE nearly contiguous to one another; PME contiguous to one another and to PLE; males with dark brown palps and a basal hook on the cheliceral fang .... *Ischnothyreus*, p.

3b. ALE fairly well separated; PME contiguous but more or less well separated from PLE .... *Triaeris*, p.

4a. PME moved far forward between ALE thus making an anterior row of four eyes .... *Orchestina*, p.

4b. PME not moved forward as given above; forming a somewhat recurved row with PLE .... *(Heteroonops, Oonops, Stenoonops)* 5

5a. Legs without conspicuous spines; venter of abdomen with a moderately well outlined epigastric scutum and with a narrow ventral scutum just posterior to the genital groove .... *Stenoonops*, p.

5b. Legs with more or less conspicuous spines; venter of abdomen with weakly outlined scuta .... *(Oonops, Heteroonops)* 6

6a. Palpal patella with a conspicuous prolateral bulge bearing robust spines; palpal femur and tibia also with conspicuous spines (Figs. 29-31) .... *Heteroonops*, p.

6b. Palpal patella without notable distortion; palpal segments without conspicuous spines .... *Oonops*, p.

SPECIES WITH DORSAL ABDOMINAL SCUTUM

Genus *Ischnothyreus* Simon, 1893

Ischnothyreus peltifer (Simon)

Ischnaspis peltifer Simon, 1891: 562. The female holotype from St. Vincent, B. W. I. is in the British Museum (Natural History), examined.

Ischnothyreus peltifer Simon, 1893: 298; (not the male p. 299 fig. 264). Petrunkevitch, 1911: 127; 1928: 88; 1929: 66; Bryant, 1940: 266; Roewer, 1942: 287; Chickering, 1951: 219; 1968: 80; Bonnet, 1957: 2309.

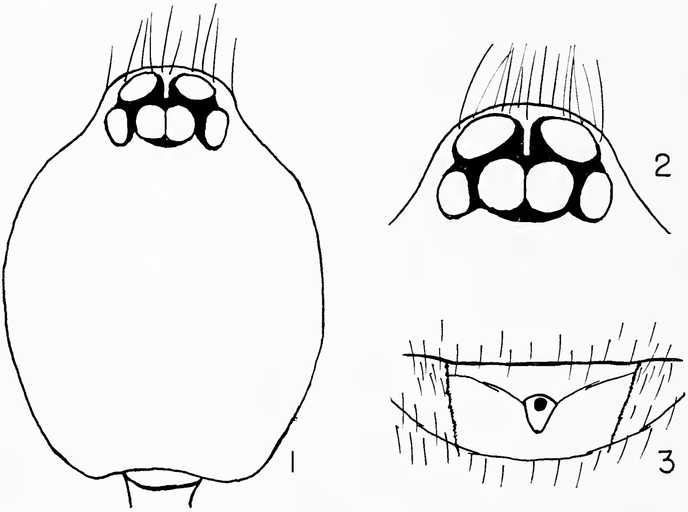
Ischnothyreus barrowsi Chamberlin and Ivie, 1935: 9, fig. 7. The female holotype from Marco Island, Florida has been in the University of Utah but is now being placed in the American Museum of Natural History on semipermanent loan, examined. New Synonymy.

Dysderina antillana Bryant, 1942: 234; 1948: 340. The female holotype from the Virgin Islands is in the Museum of Comparative Zoology, examined.

As I have shown in a recent publication (1968), this species is now well known from Costa Rica, Panama, many of the West Indies and now, also the State of Florida. I am, however, sceptical about its reported distribution in extensive areas of Asia and Africa. During my period of field work in Florida in the month of March (1968) I collected a few specimens of both sexes in avocado groves in the vicinity of Homestead. Further careful collecting will probably show that the species is well distributed through at least the southern parts of the state.

Genus *Opopaea* Simon, 1891

There is considerable confusion in the literature regarding the characters used for separating the genus *Opopaea* from the genus *Gamasomorpha*. I am not at present prepared to attempt a clarification of this confusion and in view of this fact I am placing *Gamasomorpha floridana* Banks along with four other species in the genus



Figures 1-3. *Opopaea bandina* sp. nov. Fig. 1. Carapace from above. Fig. 2. Eyes from above. Fig. 3. Epigynal area from below.

Opopaea. This decision appears to be in accord with the treatment given several species by Petrunkevitch (1929), Gertsch (1936), Bryant (1940), Chickering (1951), and Sumon (in part, 1965).

Key to the known males of *Opopaea* in Florida

1a. Species with palpal patella greatly inflated as shown in Figures 5-8 .... *O. brasima*, p.
1b. Species with palpal patella not greatly inflated .... *(O. calona, O. lutzi)* 2
2a. Species with palpal tarsus terminating in a pair of long, slender processes (Embolus and conductor) .... *O. lutzi*, p.
2b. Species with palpal tarsus terminating in a pair of short processes turned at right angles .... *O. calona*, p.

No satisfactory key has yet been devised to aid in the separation of the five known kinds of females from Florida.

Opopaea bandina sp. nov.

Figures 1-3

Holotype. The female holotype is from Pinellas Co., Largo, Florida, Nov., 1964. Collected by Mrs. Lorna R. Levi. The name of the species is an arbitrary combination of letters.

Description. Total length exclusive of the somewhat extended spinnerets 1.58 mm; including the spinnerets total length is nearly 1.67 mm. Carapace 0.56 mm long; 0.44 mm wide opposite second coxae where it is widest; about 0.20 mm tall; gently raised just behind PME and then nearly level along midline to beginning of steep posterior declivity opposite interval between third and fourth coxae; very finely rugulose as usual along lateral surfaces; with numerous short hairs. Eyes: six as usual in a compact group; posterior row only moderately recurved. Ratio of eyes ALE: PME: terior row only moderately recurved. Ratio of eyes ALE : PME : PLE = 12 : 10 : 9.5. ALE separated from one another by about one fourth of their diameter (some irregularities in outlines noted); separated from PME and PLE by broad lines. PME contiguous as usual and separated from PLE by a broad line. With a moderate amount of black pigment in ocular area. Height of clypeus nearly equal to radius of ALE. Folded fragile legs make it difficult to observe closely the chelicerae, maxillae, palps and lip but apparently all are typical of females of the genus. Sternum: quite typical of the genus; longer than wide in ratio of about 4 : 3; with marginal lobes and grooves moderately developed; posterior end squarely truncate, viewed directly from below; extended between bases of fourth coxae which are separated by nearly twice their width. Legs: 41-23 in order of length; no spines observed; only hairs, bristles and trichobothria. Abdomen: typical of the genus in general; dorsal scutum covers about ten-elevenths of dorsal surface; ventral and epigastric scuta cover nearly four-fifths of ventral surface; with rather wide lateral surfaces bare of scuta. Epigynal area obscurely distinctive (Fig. 3). Color in alcohol: quite typical of the genus. This species appears to be more or less closely related to *Opopaea recondita* Chickering.

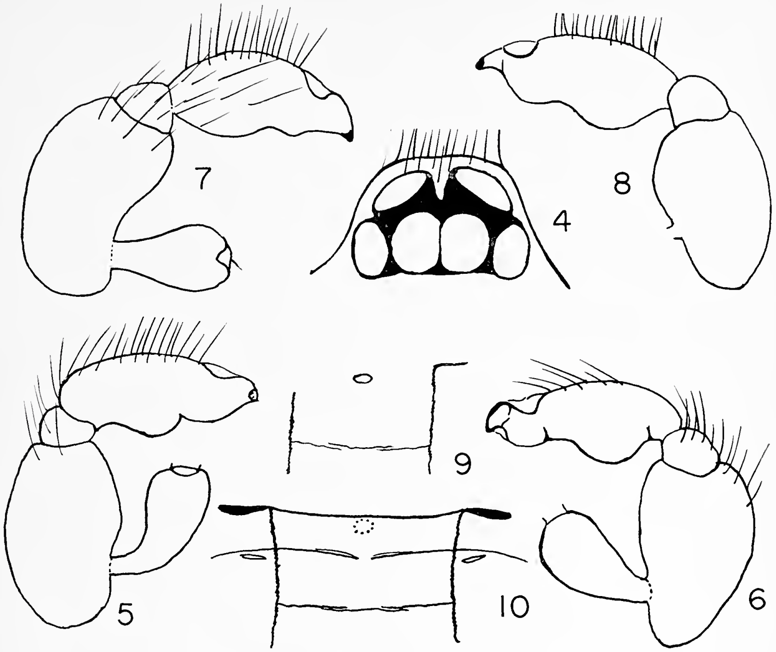
Records. One female paratype taken with the holotype. One female assigned to this species is from "Alachua Co., Florida, Science Hall bookcase"; no further data given but assumed to have been taken at the University of Florida, Gainesville. Two females from Edgewater, Florida, February 1939 (C. A. Frost) filed in Museum of Comparative Zoology as *Gamasomorpha floridana* Banks. Four females on loan from the American Museum of Natural History from the following localities: Lake Placid, Archbold Research Station, Nov. 23, 1952; December 8, 1959 and October 1, 1962 together with De Soto City, October 5, 1962 (all four just noted collected by A. M. Nadler).

Opopaea brasima sp. nov.

Figures 4-10

Holotype. The male holotype is from Kendall, Florida, Mar. 1953; collected by A. M. Nadler. The name of the species is an arbitrary combination of letters. The holotype will be deposited in the American Museum of Natural History, New York City.

Description. Total length 1.3 mm Carapace 0.55 mm long; 0.44 mm wide opposite second coxae where it is widest; nearly 0.22 mm tall; nearly flat along midline from slightly behind PME to beginning of steep posterior declivity; posterior border recurved; lateral and posterior surfaces finely rugulose; with numerous black hairs. Eyes: six as usual in a compact group; viewed from above, posterior row only gently recurved. Ratio of eyes ALE : PME : PLE = 13 : 11 : 10. ALE separated from one another by nearly half their radius. PME contiguous to one another and separated from PLE by a line. Height of clypeus nearly equal to two-thirds of the diameter of ALE. Chelicerae, maxillae and lip apparently quite typical of the genus. Sternum: moderately convex and moderately lobed along lateral margins; with marginal bristles curved medially; only a little longer than wide; nearly squarely terminated between bases of fourth coxae which are separated by about their width. Legs:



Figures 4-10. *Opopaea brasima* sp. nov. Fig. 4. Eyes of holotype from above. Figs. 5-6. Left palp of holotype; prolateral and retrolateral views, respectively. Fig. 7. Left palp of male from Homestead; prolateral view. Fig. 8. Left palp of male from Haines City; retrolateral view. Fig. 9. Genital area of male holotype. Fig. 10. Epigynal area of described female paratype.

4123 in order of length; no true spines observed; many hairs and spiniform bristles. Palp: essential features shown in Figures 5-8; femur short and moderately inflated; patella strongly inflated; tibia very short; tarsus with distinctive features obscure and difficult to observe clearly; a slight change of position greatly alters appearance. Abdomen: typically flattened; dorsal scutum covers entire dorsal area; ventral and epigastric scuta cover entire ventral surface back to bases of normal spinnerets; the expected sclerite at base of spinnerets shows dorsal to posterior border of ventral scutum; genital area very similar to that of *Opopaea calona* sp. nov. (Fig. 9). Color in alcohol: essentially as recorded for other species in the genus *Opopaea.*

Female paratype. Total length 1.67 mm. Carapace 0.59 mm long; about 0.46 mm wide opposite posterior borders of second coxae;

nearly 0.23 mm tall. Eyes: essentially like those of male holotype except that the posterior row appears to be straight or very slightly procurved, measured by posterior borders. Ratio of eyes ALE : PME : PLE = 10 : 10 : 9; PME plainly longer than wide (long diameters always used for measurements); posterior row occupies about three-fourths of width of carapace at that level. Chelicerae, maxillae, palps and lip all appear to be typical of females of the genus. Sternum and legs appear to be essentially like those of male holotype. Abdomen: scuta essentially as in male except that a larger area at posterior end of the abdomen is left uncovered on both dorsal and ventral sides. The epigynal area is very obscure but is, never-the-less, quite distinctive (Fig. 10). Color in alcohol: essentially as in male with minor differences.

Records. The described female paratype was taken 2 mi. southeast of Marathon, Florida, December 15, 1962 (Wilton Ivie). Numerous males and females have been on loan from the American Museum of Natural History as follows: Punta Gorda, January 1946 (Stowell Rounds); Alachua Co., Science Hall, Dec. 6, 1948; Key West, Dec. 1950 (A. M. Nadler); 2-5 mi. so. of Florida City, April 1, 1957 (R. Forster and W. J. Gertsch); 2 mi. southeast of Marathon, Dec. 15, 1962 (Wilton Ivie). I collected this species at Haines City, Feb. 28 and at Homestead, March, 1968. The male described as the allotype of *Gamasomorpha floridana* Banks by Miss Elizabeth Bryant apparently belongs in this species. Early in the study of this group of specimens three different species seemed to be present. Careful examination of all of them have finally convinced me that they all belong in a single species as presented here.

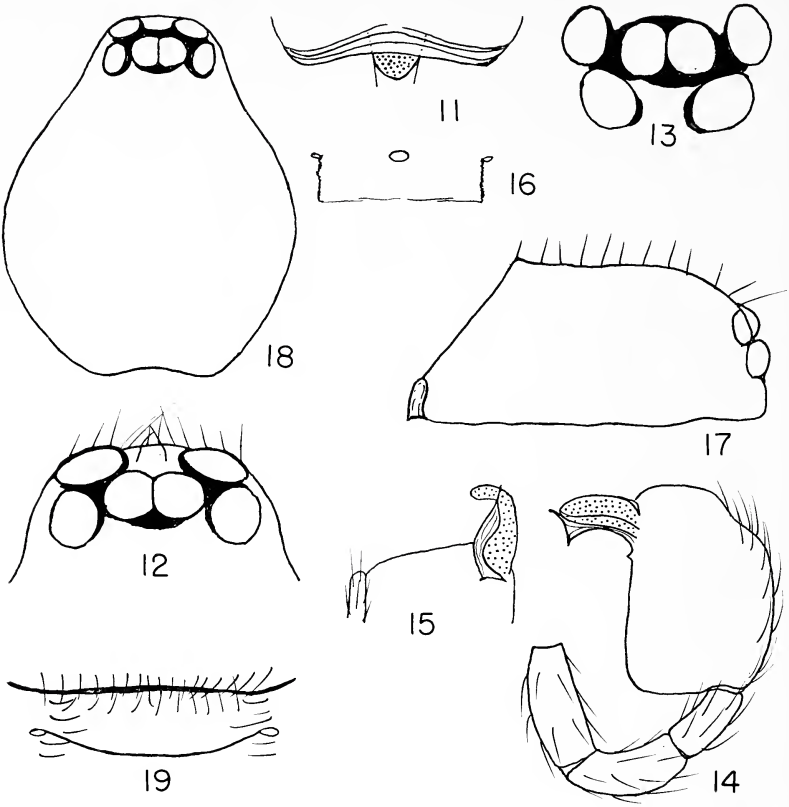
Opopaea calona sp. nov.

Figures 11-19

Holotype. The male holotype is from Florida. The label reads: Science Hall, October 15, 1947. Another vial on loan from the American Museum of Natural History states that Science Hall is in Alachua Co. It is assumed, therefore, that this specimen was taken in Science Hall at the University of Florida in Gainesville. It will be deposited in the American Museum of Natural History, New York City. The holotype has the abdomen separated from the cephalothorax but is in good condition for description.

Description. Total length nearly 1.54 mm. Carapace 0.66 mm long; 0.49 mm wide opposite second coxae where it is widest; about 0.23 mm tall; raised somewhat just behind PME and then slightly arched to slightly raised portion just at beginning of steep posterior declivity; just beneath posterior border there is a strongly chitinized conical projection not seen in any other species studied (Fig. 11); general form as in Figures 17-18 of female; surface nearly smooth and shiny with no median thoracic pit or groove. Eyes: six in two rows and in a compact group as usual; posterior row rather strongly recurved (Figs. 12-13) and occupies nearly three-fourths of width of carapace at that level. Ratio of eyes ALE : PME : PLE = 12.5 : 10 : 11. ALE separated from one another by nearly three-fourths of their diameter and only slightly separated from PME and PLE. PME contiguous for nearly their length and narrowly separated from PLE. Clypeus only slightly porrect; with height nearly equal to five-sixths of diameter of ALE. Chelicerae apparently as usual in the genus. Maxillae moderately convergent, slender and apparently without special modifications. Lip apparently as usual in the genus. Sternum: quite convex; nearly as wide as long; posterior end slightly bilobed and extended just to bases of fourth coxae which are separated by nearly twice their width; with a sparse supply of stiff bristles; only slightly lobed and grooved along margins. Legs: 41=23 in order of length; no true spines observed on legs or palps. Palp: general features shown in Figures 14-15; only tarsus inflated; features of tarsus appear to be unique since no structures like these closely adherent and so difficult to follow have been seen in collections available to me for study. Abdomen: dorsal scutum covers all of dorsal surface except a small area just above the anal tubercle; ventral and epigastric scuta cover all of venter except a narrow area just anterior to nearly semicircular sclerite at base of spinnerets; genital area as shown in Figure 16; dorsal and epigastric scuta nearly meet dorsal to base of pedicel but diverge posteriorly so that a lateral area of considerable size is left uncovered. Color in alcohol: carapace, sternum and scuta all a clear yellowish brown; legs yellowish; black pigment in ocular area essentially as shown in Figures 12-13; abdominal areas not covered by scuta a clear white.

Female paratype. 1.61 mm. Carapace about 0.7 mm long; about 0.53 mm wide opposite second coxae where it is widest; about 0.3 mm tall; somewhat overlapped by anterior end of abdomen; otherwise essentially as in male (Figs. 17-18). Eyes essentially as in male. Chelicerae, maxillae and lip essentially as in male with minor differences. Sternum as in male. Second legs missing but apparently all legs essentially as in male. Female palp as usual in females of the genus. Abdomen: the three recognized scuta cover almost the entire abdominal surface with very little exposure of the uncovered white surface; the epigynal area appears to be more or less distinctive



Figures 11-19. *Opopaea calona* sp. nov. Fig. 11. Posterior border of carapace from above; with conical extension of posterior border lying over the pedicel. Figs. 12-13. Eyes of male holotype from above and from in front, respectively. Fig. 14. Left male palp; retrolateral view. Fig 15. Tip of left male palpal tarsus; nearly ventral view. Fig. 16. Genital area of male holotype. Fig. 17. Carapace of described female paratype; right lateral view. Fig. 18. Carapace of female from above. Fig. 19. Epigynal area of female paratype from below.

(Fig. 19) and seems to indicate a close relationship with species such as *Opopaea lutzi* Pet. where the male palp has no greatly inflated patella such as occurs in species like *Opopaea timida* Chick. and numerous others to be treated later.

Records. No male paratypes have been found in the collection. The female, regarded as the described female paratype of this species, is from Valparaiso, Florida, April 1946 (Edwards).

Opopaea floridana (Banks)

Figures 20-21

Gamasomorpha floridana Banks, 1896: 57. The female holotype from Punta Gorda, Florida is in the Museum of Comparative Zoology, examined. Banks, 1904: 122; 1910: 5; Petrunkevitch, 1911: 126; Roewer, 1942: 286; Bryant, 1945: 199, not the male described as the allotype; this specimen was misidentified and is now placed with *Opopaea brasima* sp. nov.; Comstock, 1948: 309; Bonnet, 1957: 1930.

Two specimens are in the type vial; one is somewhat injured with cephalothorax and abdomen detached; the other is in good condition and has been used in this study. As indicated above, I cannot accept the male described as the male of this species. Several features seem to me to separate it very definitely from Banks' species.

Female holotype. Total length 1.85 mm. Ratio of eyes ALE : PME : PLE = nearly 7 : 6 : 5. ALE separated from one another by a little more than their diameter (Fig. 20); separated from PME and PLE by a broad line. PME contiguous as usual and separated from PLE by nearly one half their width. The epigynal area (Fig. 21) seems to indicate that this species is closely related to *Opopaea lutzi* Pet. I am inclined to the belief that when the male of this species is definitely identified it will be found to belong to the group in which the palpal patella is not greatly inflated nor with the palpal tibia so much diminished (*Opopaea lutzi* Pet. and *Opopaea calona* sp. nov.)

Opopaea lutzi Petrunkevitch

Figures 22-27

Opopaea lutzi Petrunkevitch, 1929: 61, figs. 42-50. The male holotype from Desecheo Island, Puerto Rico is probably in the American Museum of Natural History, New York City. Bryant, 1940: 267; Roewer, 1942: 288; Bonnet, 1958: 3197.

In addition to the holotype male Dr. Petrunkevitch also had an immature specimen taken with the holotype and a male and two immature specimens from Dorado, Puerto Rico. Miss Bryant (1940) had both sexes from Cuba. The species is now believed to be widely distributed in Central America and the West Indies as I hope to show in a later paper on this genus. I now have on loan from the American Museum of Natural History two females from Florida; one is from Crandon Park, Dade Co., November 27, 1952 (A. M. Nadler) and the other is from Kendall, Dade Co., November 26, 1965 (A. M. Nadler). I have in my personal collection several specimens of both sexes from Homestead, Florida, March, 1968. The species seemed to be abundant in leaf litter in avocado groves on West Mowry St; I also have both sexes taken from litter in an open field near the avocado groves just mentioned. Although the basic pattern of the parts associated with the epigynal area remain consistent the arrangement of the folds, grooves, etc. varies considerably among the specimens available for study.

Genus *Triaeris* Simon, 1891

Triaeris stenaspis Simon

Triaeris stenaspis Simon, 1891: 561. The type females from St. Vincent, B. W. I. are in the British Museum (Natural History). Simon, 1892: 443; 1893: 302; Petrunkevitch, 1911: 130; 1928: 88; Roewer, 1942: 290; Bryant, 1948: 342; Bonnet, 1959: 4684; Chickering, 1969 (in press).

Triaeris patellaris Bryant, 1940: 268. The type female from Cuba, W. I. is in the Museum of Comparative Zoology. Chickering, 1951: 243.

In a brief paper on the genus *Triaeris* in Central America and the West Indies now in press I have shown that *T. stenaspis* Simon is now known to be widely distributed in Costa Rica, Nicaragua, Panama and many of the West Indies with one record from Miami, Florida. I now believe that I have additional records from Fort Myers, January 1934 (W. M. Barrows) and also from Miami, Brickell Hammock, November 30, 1961 (F. M. Mead). The male is still unknown.

SPECIES WITHOUT A DORSAL SCUTUM

Genus *Heteroonops* Dalmas, 1916

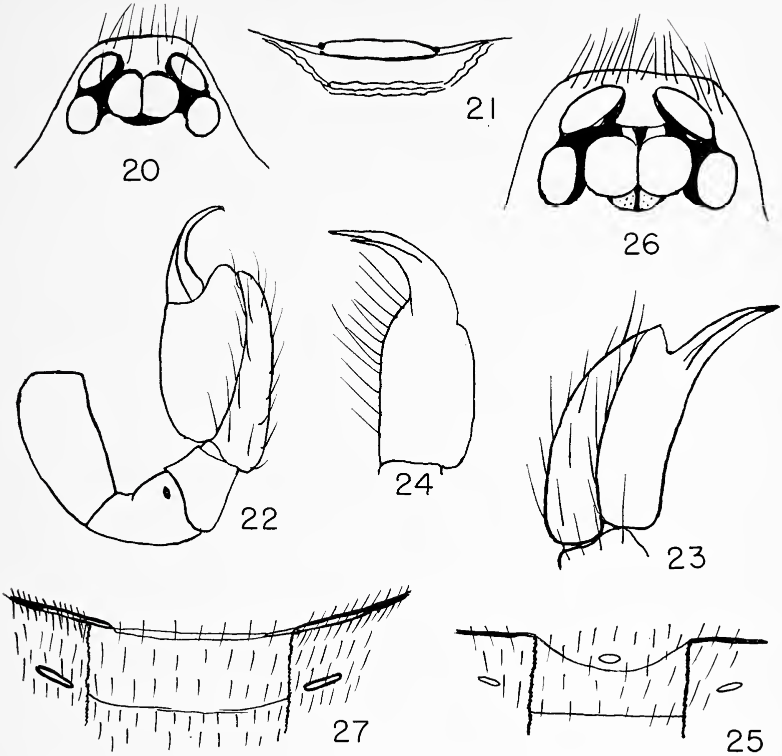
Heteroonops spinimanus (Simon)

Figures 28-32

Oonops spinomanus Simon, 1891: 563, fig. 6. The female holotype from St. Vincent, B. W. I. is in the British Museum (Natural History). Simon, 1893: 294; 1892: 445; Petrunkevitch, 1911: 128; 1929: 67, figs. 53-57; Gertsch, 1936: 8.

Heteroonops, spinimanus,—Dalmas, 1916: 203, 217; Bryant, 1940: 205; Roewer, 1942: 276; Bonnet, 1957: 2185.

Simon had only the female. Dr. Petrunkevitch had what he considered to be "several males and females" from Puerto Rico. Miss Bryant recorded the species from Cuba. Dr. Gertsch was the first to record it from Florida. The species is now believed to be widely



Figures 20-21. *Opopaea floridana* (Banks). Fig. 20. Eyes of female from above. Fig. 21. Epigynal area from below. Figures 22-27. *Opopaea lutzi* Petrunkevitch. Fig. 22. Left palp of male; retrolateral view. Figs. 23-24. Left male palpal tarsus; prolateral and nearly ventral views, respectively. Fig. 25. Genital area of male from below. Fig. 26. Eyes of female from above. Fig. 27. Epigynal area of female from below.

distributed in the northern parts of South America, at least in the southern parts of Central America, in many of the West Indies and at least in Florida in the United States. I am not certain that the species should be separated from the genus *Oonops* but for the present I am leaving it where Dalmas placed it.

I am also uncertain concerning the male of the species described by Dr. Petrunkevitch. I have not yet been able to identify the male with any degree of certainty among the numerous species of *Oonops* now awaiting final treatment. The eyes of the female are represented in Figure 28. There is a moderately well outlined epigastric scutum and a narrow ventral scutum. The epigynal area is quite distinctive (Fig. 32) with some variation in its appearance among numerous available specimens. The palp of the female is quite distinctive in respect to the shape of the patella and the conspicuous spination on several segments (Figs. 29-31).

In a collection of Oonopidae from the American Museum of Natural History I have found females from the following localities in Florida: Royal Palm Park, Feb. 26, 1936; Leesburg, Lake Co., March 1-11, 1954 (M. Stratham); Lake Placid, Archbold Biol. Sta., Oct. 1, 1962 (A. M. Nadler); Ochopee, Everglades, December 27, 1963 (Jean and Wilton Ivie). Dr. Gertsch (1936) reported the species from Newnan's Lake, near Gainesville and also stated that Dr. H. K. Wallace had females from localities in Alachua Co. In my personal collection from Florida in 1968 I have females from Homestead, March; Everglades National Park, March; Tallahassee, Tall Timbers Research Station, April.

Genus *Oonops* Templeton, 1834

Oonops floridanus (Chamberlin and Ivie)

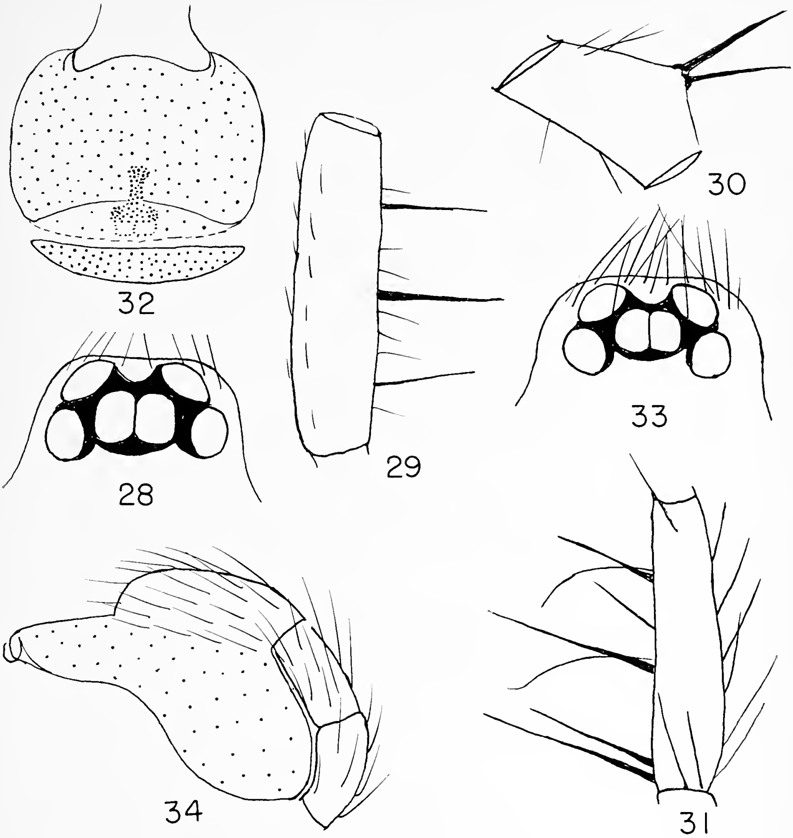
Figures 33-34

Oonopinus floridanus Chamberlin and Ivie, 1935: 9, figs. 8-9. The holotype male and female paratype have been in the Museum of the University of Utah, Salt Lake City but are now being transferred to the American Museum of Natural History, New York City. Roewer, 1942: 276.

Oonops floridanus, — Gertsch, 1936: 9; Bonnet, 1958: 3190.

Dr. Gertsch correctly recognized that this species belongs in the genus *Oonops*. The original description stated that there were no spines on the legs; actually there are many long slender, more or less transparent spines somewhat difficult to observe.

I did not collect this species during my period of field work in Florida in 1968 but I have had numerous specimens of both sexes on loan from the American Museum of Natural History and the University of Florida collected by H. A. Denmark, R. M. Baranowski, Drs. W. J. Gertsch and R. R. Forster, Dr. Wilton Ivie and Dr. F. E. Lutz. These collections have been made in numerous localities throughout the State of Florida and seem to indicate that this species is one of the most abundant in the family. Figure 33 represents the eyes of the male as seen from above; Figure 34 represents the left palpal patella, tibia and tarsus of a male as seen in retrolateral view. The epigynal area of females is extremely obscure and appears to be quite variable in appearance and for this reason no figure of this region has been prepared.



Figures 28-32. *Heteroonops spinimanus* (Simon). Fig. 28. Eyes of female from above. Fig. 29. Right palpal femur; retrolateral view. Fig. 30. Right palpal patella; dorsal view. Fig. 31. Right palpal tibia; dorso-prolateral view. Fig. 32. Epigynal area of female. Figures 33-34. *Oonops floridanus* (C. and I.). Fig. 33. Eyes of male from above. Fig. 34: Left palpal patella, tibia and tarsus; retrolateral view.

Several immature specimens of *Oonops* are in the collections but I have been unable to place them with any certainty.

Genus *Orchestina* Simon, 1882

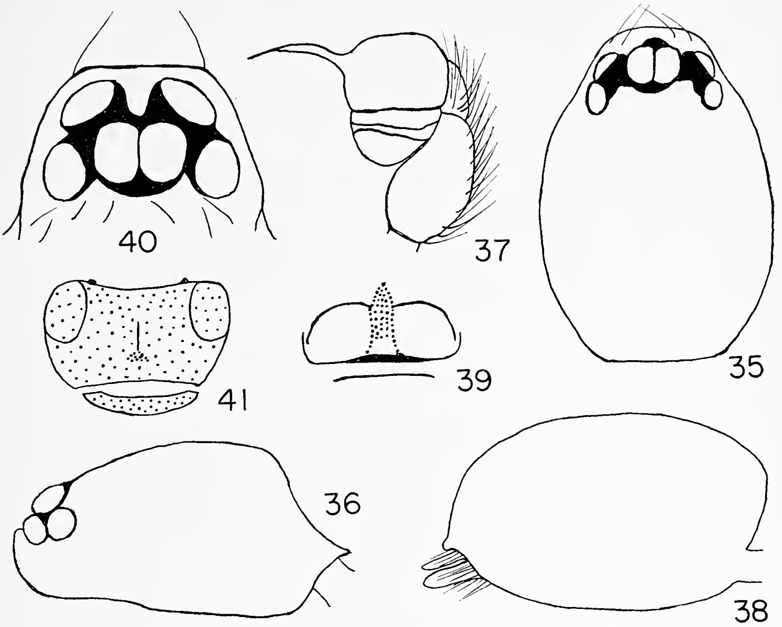
Orchestina nadleri sp. nov.

Figures 35-39

Holotype. The male holotype is from Key West, Florida, December 31, 1950 (A. M. Nadler). The species is named after the collector.

Description. Total length about 1.0 mm (body bent and very fragile). Carapace 0.46 mm long; about 0.33 mm wide opposite interval between second and third coxae where it is widest; about 0.24 mm tall opposite third coxae where it is tallest (Fig. 36); surface smooth with few hairs. Eyes: six as usual; with PME moved forward to make a row of four with ALE (Fig. 35); four posterior eyes in a strongly recurved row occupying about seven-ninths of width of carapace at that level. Ratio of eyes ALE : PME : PLE = about 8.5 : 12 : 10 (long diameters always used for measurements). ALE separated from one another by slightly more than twice their diameter; well separated from PME and nearly contiguous to PLE. PME contiguous for nearly one-third of their circumference and separated from PLE by nearly their width. Clypeus somewhat porrect and with height a little more than width of PME. Chelicerae vertical and apparently without special modifications. Maxillae convergent; nearly meeting in front of lip which is somewhat diamond-shaped with posterior angle fitting into a median sternal groove not seen elsewhere. Sternum: scutiform; somewhat convex; without marginal lobes; bluntly terminated opposite bases of fourth coxae which are well separated. Legs: 41=23 in order of length; fourth coxae somewhat enlarged; fourth femora elongated and enlarged as usual in the genus; probably lacking true spines but with numerous hairs, bristles and trichobothria. Palp: parts so fragile that no attempt has been made to remove it for the usual more complete examination. Figure 37 shows the essential features of the left palpal tibia and tarsus in retrolateral view. Abdomen: as usual in the genus. Color in alcohol: cephalothorax, legs and mouth parts light yellowish; abdomen almost white except for an area around the posterior end which appears light purplish gray.

Female paratype. Total length about 1.43 mm. Carapace about 0.55 mm long; about 0.44 mm wide; dorsal surface injured thus preventing determination of height. Eyes, mouth parts, sternum and legs all appear essentially as in male with minor variations. Ab-



Figures 35-39. *Orchestina nadleri* sp. nov. Fig. 35. Carapace of male holotype from above. Fig. 36. Carapace of male; left lateral view. Fig. 37. Left male palpal tibia and tarsus; retrolateral view. Fig. 38. Abdomen of female paratype; right lateral view. Fig. 39. Epigynal area of female paratype. Figures 40-41. *Stenoonops minutus* C. and I. Fig. 40. Eyes of female from above. Fig. 41. Epigynal area of female.

domen: general form essentially as shown in Figure 38; the epigynal area is only very dimly outlined but it seems to be distinctive (Fig. 39).

Records. There are no male paratypes. The described female paratype is from Key West, Florida, December 29, 1950 (A. M. Nadler). A second female belonging to the genus Orchestina is in very poor condition. From what can be observed, however, I have tentatively concluded that it represents another species and this suggests that more thorough collecting in the State of Florida would be likely to yield additional interesting species. Two immature specimens from Torreya State Park, Liberty Co., Florida, on loan from the University of Florida, seem to be close to the genus Orchestina but their condition precludes precise treatment.

The male holotype had apparently been selected and named by Dr. W. J. Gertsch for description but was never completed. I have merely accepted the specimens and proceeded with the description as given above.

Genus *Stenoonops* Simon, 1891

Stenoonops minutus Chamberlin and Ivie

Figures 40-41

Stenoonops minutus Chamberlin and Ivie, 1935: 8, figs. 1-2, 14. The male holotype from Tampa, Florida, August 26, 1933, formerly in the Museum of the University of Utah is now being transferred to the American Museum of Natural History, New York City, examined. Roewer, 1942: 280; Bonnet, 1958: 4156.

The authors of this species had only the male holotype. A female from Newnan's Lake, Gainesville, Fla., March 23, 1957 (Gertsch and Forster) has been selected for description as follows:

Female. Total length 1.43 mm exclusive of the somewhat extended spinnerets; including the spinnerets total length is 1.54 mm. Carapace about 0.6 mm long; about 0.43 mm wide opposite second coxae where it is widest; about 0.22 mm tall; very slightly arched along midline from PME to beginning of moderately steep posterior declivity nearly opposite third coxae; with few short hairs; lateral surfaces very finely granulate; no median thoracic pit or groove observed. Eyes: six as usual in two rows; viewed from above, posterior row recurved (Fig. 40). Ratio of eyes ALE : PME : PLE = nearly 7 : 6 : 5. ALE separated from one another by a little more than their radius; separated from PLE by nearly their radius and from PME by a broad line; PME contiguous for about one fourth of their circumference and separated from PLE by a broad line. Height of clypeus nearly equal to the radius of ALE. Some irregularities noted in shapes of eyes; long diameters always used for measurements. Chelicerae, maxillae and lip all as usual in the genus as far as observed. Sternum: convex; about seven-ninths as wide as long; widest just behind second coxae; plainly lobed and grooved along margins as usual in the genus; margins with curved black hairs; posterior end rounded and terminated just opposite bases of fourth coxae which are separated by nearly six-fifths of their width. Legs: 41=23 in order of length; only slight differences in lengths; no true spines observed; trichobothria present but number and placement undetermined. Abdomen: ovoid as usual in the genus; epigastric and ventral scuta together with epigynal area weakly outlined (Fig. 41); spinnerets as usual in the genus. Color in alcohol: as usual in the genus with minor variations; carapace and sternum somewhat lighter than in *S. nitens* Bryant from St. Croix, U. S. Virgin Islands but otherwise very similar.

Records. On loan from the American Museum of Natural History: two males and five females from Newnan's Lake, Gainesville, Florida, March 28, 1957 (Gertsch and Forster); two males from Torreya State Park, Florida, April 4, 1957 (Gertsch and Forster); one female from Myakka River State Park, December 26, 1963 (Jean and Wilton Ivie). One male in the Museum of Comparative Zoology from Welaka, Florida, May 9, 1949 (A Van Felt) probably belongs here but both palps are missing. Another female from Dunedin, Florida, 1927 (W. S. Blatchley) filed in the Museum of Comparative Zoology as *Gamasomorpha floridana* Banks is also placed here with some uncertainty because of its obscure features.

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REVISIONAL STUDY OF THE ORDER PALAEODICTYOPTERA IN THE UPPER CARBONIFEROUS SHALES OF COMMENTRY, FRANCE. PART I[1]

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The Upper Carboniferous shales in Commentry, France, are of incomparable significance for the study of insect evolution. The excellent preservation of the fossils and the diversity of insect groups represented make the Commentry fossils basic to any understanding of Palaeozoic insects and early insect evolution.

Almost all of the Commentry insects are contained in the Institut de Paléontologie in the Muséum National d'Histoire Naturelle, Paris, this constituting the largest assemblage in the world of Upper Carboniferous insects. A very few Commentry specimens are in the British Museum (Natural History) in London and in the Manchester Museum (Stirrup Collection), Manchester, England.

The Commentry shales are part of a small coal basin, situated on the north side of the large Carboniferous furrow of the Massif Central. The fossiliferous layers are of fresh water origin and are allochthonous, apparently deposited by streams in delta-like, detritic sediments along the shore of a lake. During his early study on stratigraphy and sediments (1880-1890), based on surface outcrops of the Commentry beds, Fayol assembled the greater part of the collection of fossil insects. This remarkable collection was turned over to Charles Brongniart (grandson of the palaeobotanist, Adolphe Brongniart), who was then an assistant in the Zoological Laboratory of the Muséum and who was interested in both geology and entomology. Brongniart's studies were brought out in a single major work, "Recherches pour servir à l'histoire des insectes fossiles des temps primaires", published in 1893. This was a pioneer work in the study of fossil insects. Although his classification of the insects is now seriously out-dated, Brongniart demonstrated in his illustrations and his descriptive accounts an exceptional ability for observa-

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tion. The collection at the Muséum has not been subjected to extensive restudy until recent years. Even Handlirsch, in connection with his monograph of fossil insects in 1906-1908 and his revision of Palaeozoic insects in 1919, made no examination of the Commentry fossils in the Muséum. Many additional Commentry insects were found and placed in the Muséum subsequent to Brongniart's death in 1899. Most of these were studied and described by Fernand Meunier in a series of superficial and confusing papers (1907-1921). Professor Aug. Lameere of Belgium, however, did make a careful study of both the original Brongniart material and the specimens later accumulated; his most significant account (1917) dealt with corrections in morphological details and systematics given by Brongniart and Meunier; his observations were remarkably good, although the complete absence of illustrations make the use of his revision somewhat difficult.

In 1935 Professor F. M. Carpenter, realizing both the significance of the Commentry insects and the lack of reliable information about them, decided to make a systematic study of the collection in the Paris Museum in connection with his investigations on Permian insects. He visited the Muséum first in 1938, making photographs of all the type specimens, as well as drawings of specimens of some families. Following three other visits to the Muséum (1961, 1962 and 1966), he published accounts revising the Commentry Protodonata, Megasecoptera, Diaphanopterodea, Ephemeroptera, and Caloneurodea. In 1967, realizing the extent of the fossils in the Commentry collection still remaining to be studied, he encouraged me to work on the large order Palaeodictyoptera, a group having more representation in the Commentry collection than in all other collections in the world combined. He turned over to me all the photographs and notes which he had previously made, and he obtained financial support from the Scientific Research Society (Sigma Xi) and the National Science Foundation for my visits to the Museum in Paris (1966, 1967) and my work in his laboratory at Harvard University. I am deeply indebted to Professor Carpenter for his assistance, without which the preparation and publication of these studies would not have been possible.

During my stay at the Institut in Paris, I was enabled, through the courtesy of the Director, Professor J. P. Lehman, to restudy all specimens of Palaeodictyoptera in the Muséum collection. Dr. J. Sornay of the Institut also kindly gave me great assistance with the collection. Unfortunately, some of the specimens previously present could not be found in 1966 or 1967, the only record of them being the photographs made by Professor Carpenter during his stay in Paris before the beginning of World War II. Although photographic documentation, especially of fossil insects, can be very misleading, I decided finally to include figures based on the photographs of these missing specimens, since they provide at least some basis for evaluating the original figures and descriptions given by Brongniart or Meunier. It is still my hope that the missing types will turn up so that more definitive figures can be made later.

For practical reasons, this revisional study will be published in three parts, as follows:

Part 1. Spilapteridae (including Lamproptiliidae), Fouqueidae, Mecynostomatidae, fam. nov.
Part 2. Homoiopteridae, Lycocercidae (including Apopappidae), Graphiptilidae (including Rhabdoptilidae), Breyeriidae, Eugereonidae (including Peromapteridae, Dictyoptilidae), Archaemegaptilidae, Megaptilidae (including Lithoptilidae).
Part 3. Dictyoneuridae (including Stenodictyidae).

The first two parts will be entirely systematic, but the third will include, in addition to the systematic account of the Dictyoneuridae, a discussion of the morphological features of the Palaeodictyoptera.

Since the Commentry insects in the Paris Institut have not been given catalogue numbers, I have followed Professor Carpenter's procedure of referring to Brongniart's specimens by plate and figure numbers as they appeared in his monograph (1893, thesis edition); thus, 17-7, refers to the fossil shown in his figure 7, of plate 17.

Family Spilapteridae Brongniart

nom. correct. Handlirsch, 1906: 101, *pro* Spilapterida Brongniart, 1893: 334.

Spilapteridae, Handlirsch, 1906: 101; Lameere, 1917: 102; Handlirsch, 1919: 20.
Lamproptiliidae, Handlirsch, 1960: 109; Lameere, 1917: 102; Handlirsch, 1919: 21. New synonymy.
Dunbariidae, Handlirsch, 1937: 81.
Doropteridae, G. Zalessky, 1947: 64.
Neuburgiidae, Rohdendorf, 1961: 72.

Type Genus: *Spilaptera* Brongniart, 1893.

This family, the largest in the order Palaeodictyoptera, was established by Brongniart as a subfamily and subsequently raised to family level by Handlirsch in 1906. Within the order, this family not only has the most extensive fossil record but also the longest range

(Namurian C to Lower Permian) and wide geographical distribution (North America, Europe and Asia).

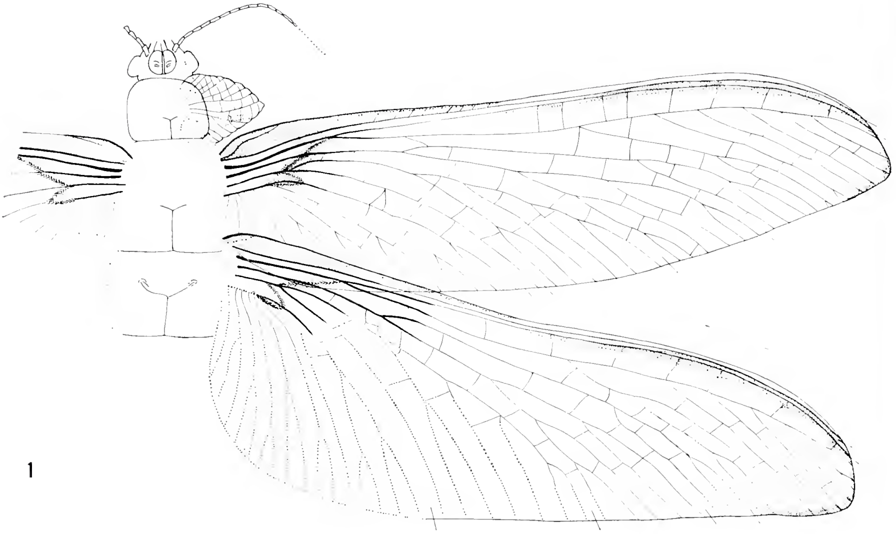
Unlike many other Palaeodictyoptera with a tendency to reduce the hind wings, the Spilapteridae and related families always have well-developed hind wings, which are markedly broadened in the basal half. The wing venation is very uniform throughout the family and seems to have been continued into the Lower Permian with relatively little change. The detailed branching of the veins, however, is highly variable, even within a single individual. As a result, any classification based upon details of branching of the veins is very questionable.

This study of the Commentry Palaeodictyoptera has brought to light a great deal about the structure of the wings and the body. In the wings transverse structures apparently concerned with strengthening the membrane have turned out to be very characteristic of some genera; since they were diverse, being either cuticular thickenings, oblique cross veins, or oblique, pigmented stripes, they are useful in classification. Many details of body structures not previously noted were observed; these included the fine structures of the antennae, the clypeus, and the prothoracic lobes. To some extent, their variability within the Palaeodictyoptera is now known. As a result of this more precise and extended knowledge of the structure of the Spilapteridae, I have found it necessary to make some taxonomic changes. *Lamproptilia* Brongniart, which is known from fore and hind wings, has a typical spilapterid venation, differing from other genera of the family only in the relatively broad fore wings, the convex curvature of the posterior margin of the hind wing, and the color pattern. None of these features seem to justify more than generic separation. Several generic changes also seem necessary: *Compsoneura* Brongniart, originally referred to the Spilapteridae, is herein placed with some doubt in the family Fouqueidae. *Apopappus guernei* (Brongniart), also originally placed in the Spilapteridae, is now put in the Lycocercidae. The new genus *Tectoptilus* is based on *Becquerellia grehanti* Brongniart. The new species, *Homaloneura lehmani*, is based upon one of Brongniart's specimens (17-15), which he erroneously thought was the reverse of his type of *Homaloneura ornata.*

The following are the characteristics which now seem to be valid for the Spilapteridae: wings about equal in length and similar in venation, but the hind wings broader basally; supporting structures often present in basal third of the wings; precostal strip present; anterior margin of wings more or less concave. Sc long, R simple or with terminal branches; Rs with 3-10 pectinate branches; both MA and MP with at least two branches, usually more; CuA with several branches, CuP with few branches or even simple; several anal veins. Cross veins mostly simple and not very numerous. The wings are often marked with broad transverse bands or with spots. Body structures: Head small, broad, with large projecting eyes and a large striated clypeus. Beak long; antennae long, with many long segments. Prothoracic lobes with radiating veins and with cross veins, but sometimes heavily sclerotized with the venation reduced or very weak. Metathorax usually somewhat longer than the mesothorax. Legs short, cursorial. Abdomen relatively slender, the females with ten visible segments and a short ovipositor; cerci in both sexes long and robust. Males of at least some genera with terminal claspers. Posterior-lateral angles of the abdominal tergites small and not projecting.

The family Spilapteridae differs from all other families in the order, excepting the Homoiopteridae (including Rochlingiidae and Thesoneuridae), Mecynostomatidae, Fouqueidae, and Eubleptidae, in having MA and CuA branched. Of these four families, the Homoiopteridae show no close relationship to the spilapterids; Mecynostomatidae, on the contrary, might have been derived from spilapterid ancestors. The Fouqueidae are very close to the Spilapteridae on the basis of their venation, which differs only in the tendency to have fewer branches on MA and more branches on CuP; they have been recognized as a distinct family mainly on the presence of a very dense coarse pattern of cross veins. It might turn out, as explained further below, that the Fouqueidae will be inseparable from the spilapterids. The Eubleptidae are apparently closely related to the Spilapteridae (Carpenter, 1965, p. 180); the family includes smaller species than those found in the Spilapteridae and is further characterized by having a less developed CuA and the presence of an archedictyon combined with cross veins.

The following Commentry genera are herein included in the family Spilapteridae: *Spilaptera* Brongniart, *Homaloneura* Brongniart, *Becquerelia* Brongniart, *Palaeoptilus* Brongniart, *Epitethe* Handlirsch, *Tectoptilus* gen. nov., *Spiloptilus* Handlirsch, and *Lamproptilia* Brongniart. Genera which appear to belong in the family, although not occurring in the Commentry shales, are the following: *Severinopsis* Kukalova, 1958 (Namurian C, Czechoslovakia); *Mcluckiepteron* Richardson, 1956 (Westphalian, Illinois); *Neuburgia* Martynov, 1931 (Stephanian, Kuznetsk); *Dunbaria* Tillyard, 1924 (Lower Permian, Kansas); *Oboria* Kukalova, 1958 (Lower Per-



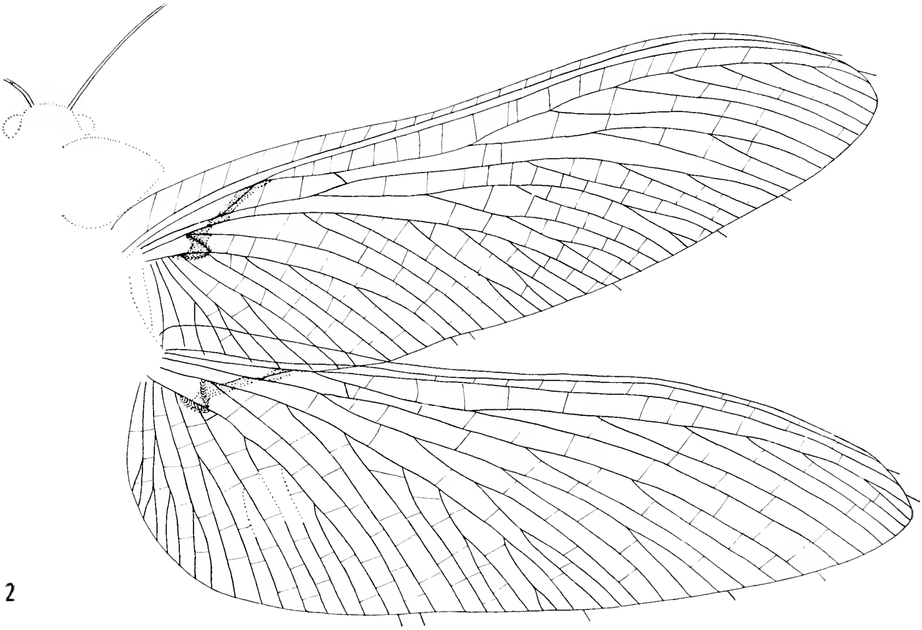


Figure 1. *Homaloneura elegans* Brongniart; specimen 17-11. Holotype.
Figure 2. *Homaloneura elegans* Brongniart; specimen 17-12.

mian, Czechoslovakia); *Doropteron* G. Zalessky, 1946 (Lower Permian, Ural, USSR); *Permiakovia* Martynov, 1940 (Lower Permian, Ural, USSR); *Abaptilon* G. Zalessky, 1946 (Stephanian, Kuznetsk). The genus *Homaloneura* occurs in the Westphalian of Illinois as well as in the Commentry shales (Carpenter, 1964, p. 117ff).

Genus *Homaloneura* Brongniart

Homaloneura Brongniart, 1885: 66; Brongniart, 1893: 316; Handlirsch, 1906: 107; Lameere, 1917: 148; Carpenter, 1964: 119.

Homaloneurina Handlirsch, 1906: Lameere, 1917: 148; Handlirsch, 1919: 20.

Homaloneurites Handlirsch, 1906: 107; Lameere, 1917: 147; Handlirsch, 1919: 20.

Type species: *Homaloneura elegans* Brongniart, 1885(OD).

Although Brongniart originally erected *Homaloneura* for a single species *(elegans)*, he added five more species in 1893: *bonnieri, punctata, joannae, ornata,* and *bucklandi.* In 1906, Handlirsch formed two new genera, their type species being two of those described by Brongniart: he established *Homaloneurina* for *bonnieri* and *Homaloneurites* for *joannae.* Both of these genera were rejected as unnecessary by Lameere (1917), a view which is undoubtedly correct and which is followed here. An additional species, *lehmani,* is described below; this is based upon Brongniart's specimen 17-15, which Brongniart erroneously considered to be the reverse half of the type specimen of *ornata.*

The basic venational pattern within *Homaloneura* is uniform, and many morphological features seem to have appeared independently among the species. It is usual for the species of *Homaloneura* to have cuticular thickenings, supporting cross veins, and color bands in the basal third of both pairs of wings. These structures presumably strengthen transversely the thin wing membrane. Among palaeopterous insects, they are most pronounced in the Odonata, but they occur in other orders as well. In the Palaeodictyoptera, they are most spectacularly represented by the Calvertiellidae (Kukalova, 1964). The strengthening structures in the wings of *Homaloneura* were noted originally by Brongniart (1893, p. 318), but neither Handlirsch nor Lameere made mention of them. In *Homaloneura elegans, bonnieri, parva,* and *dabasinskasi,* the cuticular thickening is a conspicuous V-shaped ridge with its apex on A1. In *ornata, joannae,* and *lehmani,* the cuticular ridge is directly on A1, strengthening it for a short distance where it abruptly bends toward the posterior margin. Present in all species is a long, oblique, strong cross vein, running from M to R, usually at the point of origin of Rs. In *elegans* and *bonnieri*, there is additional strengthening by means of a dark colored band running obliquely from A1 to R.

The body structures of *Homaloneura* were figured very roughly by Brongniart, and, with the exception of the prothoracic lobes and legs, they were not mentioned by Lameere. Actually, most of these structures are visible only under glycerin or glycerin-alcohol, but with the use of this clearing solution, the specimens of *Homaloneura* have contributed a great deal to our knowledge of the morphology of the Palaeodictyoptera. Most important is the presence of a large, bulging clypeus, with transverse ridges, best preserved in *H. lehmani*, which I first noted when I examined this specimen under glycerin in 1966. The structure of the clypeus is surprisingly like that of some Homoptera, such as the Cicadidae, and it undoubtedly indicates that in the Palaeodictyoptera a cibarium was present, much as in the true bugs. This was presumably developed in connection with the sucking beak. In the specimen of *lehmani*, the sheath of the beak is bent to one side, but the stylets are close together, not separated.

Another definite morphological feature of the species of *Homaloneura* is the prothoracic lobes. These were presumably homologous with wings, but in any event, they show longitudinal veins as well as cross veins, and they are attached to the prothorax along a short, cuticular ridge, corresponding to the articular region of the meso- and metathoracic wings. The prothoracic lobes are cordate and more or less sclerotized, the veins showing no convexities or concavities. The lobes were somewhat higher on the thorax than the meso- and metathoracic wings, and there was apparently some space between them and the front wings in many species. The size of the lobes varies in the species of the genus. In those species in which the lobes were large, they apparently overlapped to some extent the fore wings. Since there is no indication of articular plates at the base of the lobes, active movement of the lobes in these Palaeodictyoptera is eliminated. There is a possibility, however, that these lobes might have functioned as vanes in directing the flowing or movement of air in relation to the moving of the front wings.

The abdomen in *Homaloneura* was relatively narrow. Brongniart was of the opinion that only nine abdominal segments existed in the genus Homaloneura (1893, p. 316). This conclusion was apparently based on a specimen of *ornata*, the only Commentry specimen with the abdomen completely preserved, in which segments 1-3 are shorter than the following ones, and in which the posterior margin of the second segment is very indistinct. There are actually ten segments visible in this specimen.

In *H. ornata,* as well as in many other Palaeodictyoptera, the lateral parts of each tergite are separated by a longitudinal line from the main portion of the sclerite. The structural significance of this is not clear. Carpenter (1969, p. 306) suggests that they might be the actual ventral margins of the tergites, their impressions resulting from the flattening of the abdomen during preservation. On the other hand, they might be homologous with the so-called "lateral lamellae" of some mayfly nymphs, the function of which is apparently uncertain.

Description of Genus

Wings equal in length, or the hind pair a little longer. Wing membrane with variable color markings (transverse bands spots, longitudinal stripes). Hind wing always broader in the proximal half, but similar in venation to the fore wing. Cuticular thickenings and r-m cross vein present. R without terminal branches, Rs pectinate; MA and MP forked several times; CuA with several branches, CuP simple or weakly forked. Cross veins not very numerous.

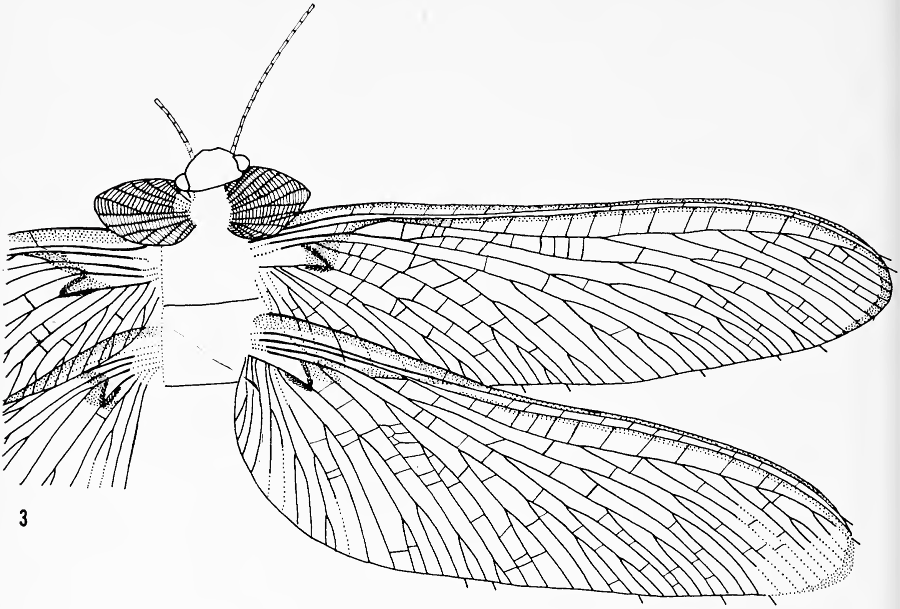
Head about as broad as the prothorax; eyes large, projecting; clypeus large, oval, with median ridges and transverse striations; beak long; antennae long, thin, with long segments. Prothorax narrower than and about half as long as the mesothorax; prothoracic lobes cordate, with about ten veins, sometimes branched, and numerous cross veins; in some species the lobes are strongly sclerotized and the venation is not visible. Meso- and metathorax almost equal in length; legs short and weak. Abdomen relatively narrow, shorter than the wings. Ovipositor short, cerci in the females robust, densely covered by hair; their structure in males is unknown.

Species of *Homaloneura* present in the Commentry shales: *H. elegans* Brongniart, 1885; *H. bonnieri* Brongniart, 1893; *H. punctata* Brongniart, 1893; *H. bucklandi* Brongniart, 1893; and *H. lehmani* sp. nov. The genus is also represented in the ironstone nodules of Illinois (Westphalian) by *H. dabasinskasi* Carpenter, 1964.

Homaloneura elegans Brongniart
Figures 1 & 2

Homaloneura elegans Brongniart, 1885: 66, pl. 3, fig. 2; Brongniart, 1893: 318, pl. 17, figs. 11-12, pl. 18, fig. 1; Handlirsch, 1906: 108, pl. 12, fig. 2; Lameere, 1917: 147; Handlirsch, 1919: 20.

The photograph of the type specimen was first published by Brongniart in 1885 and his figure (17-11), in 1893. Brongniart referred



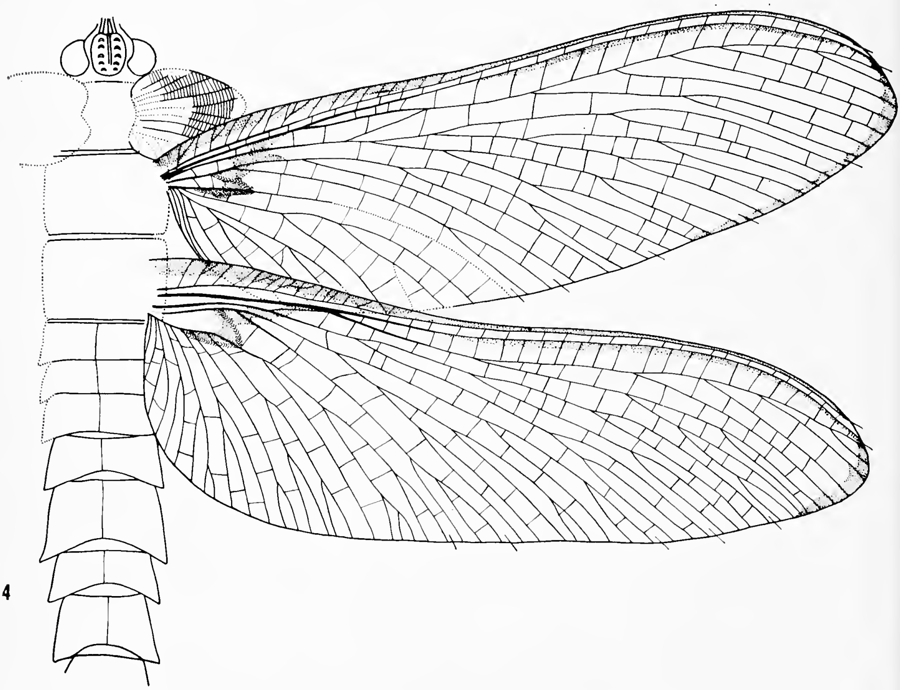


Figure 3. *Homaloneura bonnieri* Brongniart; specimen 17-17. Holotype.
Figure 4. *Homaloneura bonnieri* Brongniart; specimen 17-18.

to the same species specimen 17-12. Both obverse and reverse of 17-11 are in the Museum, but only the badly preserved obverse of specimen 17-12 could be found. Fortunately, Dr. Carpenter put at my disposal a good photograph of the reverse, which he made in 1938, so that a drawing of specimen 17-12 could be worked out very satisfactorily, also. The following account is based on the type specimen.

Wings slightly unequal, the hind pair being a little longer. Wing membrane very thin. Dark stripes following costa, subcosta, apical margin, and supporting structures. Cuticular thickening V-shaped. Dark band extending from cuticular thickening obliquely to R; a cross vein, rs-ma, running obliquely in the opposite direction. Fore wing: length 33 mm, width 9.3 mm. Anterior and posterior margins almost parallel for about two-thirds of wing length. Apical part narrowed, apex pointed, directed posteriorly. Rs with about 6-7 branches; MA pectinate, with 2-3 branches; CuP simple. Anal area with about ten branches, sometimes forked. Cross veins few, almost regular, arranged in two rows parallel with the posterior margin. Hind wing: length 34 mm, width 12 mm.

Body structures: Head length 1.5 mm, width 1.4 mm. Eyes of average size, projecting. Clypeus almost rounded. Antennae about 12 mm long, composed of equal, cylindrical segments. Prothorax half as long as mesothorax, almost square; prothoracic lobe: length 4.7 mm, width 4 mm, margin slightly undulated, veins about 11 in number, cross veins not numerous. Mesothorax about 1.4 times longer than metathorax. Fore legs very short, length of femur about 3 mm.

In his description (1893), Brongniart mentions the V-shaped cuticular thickenings and suggests the possibility that they were stridulatory organs, which seems probably incorrect.

Homaloneura elegans is related to *bonnieri* by its thin wing membrane, similar color pattern and wing venation. It differs in its smaller size, shape of wings, and the much less dense cross venation of the prothoracic lobes.

Homaloneura bonnieri Brongniart
Figures 3 & 4

Homaloneura bonnieri Brongniart, 1893: 322, 323, text fig. 12, pl. 17, figs. 17-18; Lameere, 1917; 148.

Homaloneurina bonnieri Handlirsch, 1906: 107, pl. 11, fig. 26; Handlirsch, 1921: 135, fig. 63.

Brongniart based this species upon two specimens, 17-17 and 17-

18. Since he gave a much more nearly complete figure of specimen 17-17, I am designating it as the lectotype specimen. Handlirsch (1906) established the genus *Homaloneurina* for *bonnieri* without giving any reasons; Lameere (1917) was undoubtedly right in synonymizing this genus with *Homaloneura*, *bonnieri* being very close to the type species of the genus.

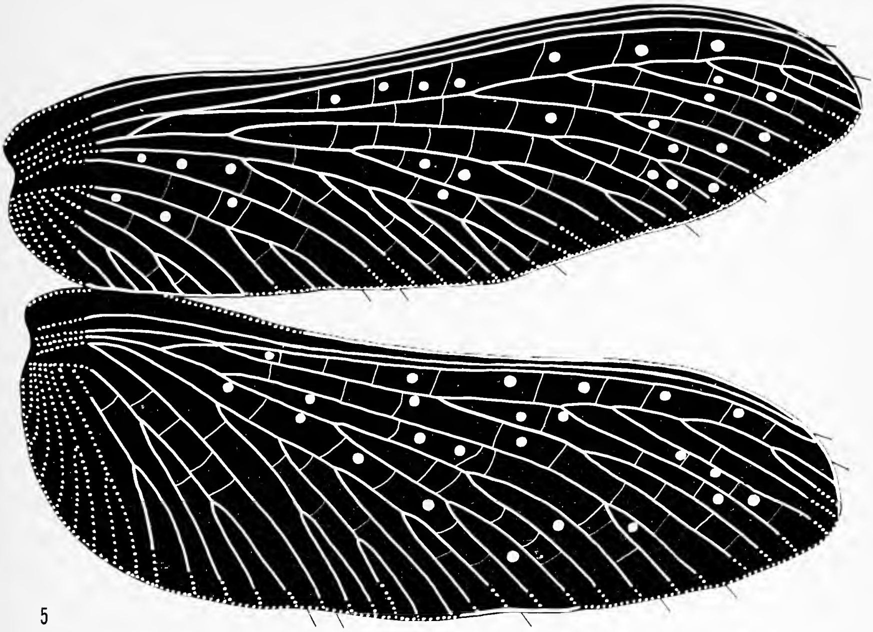
The type specimen 17-17 shows four rather damaged wings, but I found that the right fore wing could be fully restored by additional preparation and the use of glycerin. Specimen 17-18, which had been badly damaged, I was able to work out much more completely after removal of all the pieces of matrix. Reconstructions of *bonnieri* have been attempted twice — by Brongniart (1893, p. 323, text-fig. 12) and by Handlirsch (1921, p. 135, fig. 63). In both reconstructions, not one restored morphological feature is correctly shown.

Specimen 17-18 differs from the type specimen 17-17 in having much larger eyes and in the more convex apical part of the anterior margin of the fore wing, as well as in the more extensively branched MA. Nevertheless, I prefer to consider this to be *bonnieri* because the large eyes could be due to peculiarities of preservation or to difference in sex, and the other differences mentioned could be due to individual variability. The following account is based upon the type specimen only (17-17).

Wings equal in length, the hind pair slightly broadened basally. Wing membrane very thin; dark stripes following costa, subcosta, and supporting structures. Cuticular thickening V-shaped. Dark band extending from cuticular thickening obliquely to R. Fore wing: length 43 mm, width 12 mm. Anterior and posterior margins almost parallel. Apex rounded, directed slightly backwards; Rs with about six branches, MA with 2-3 branches, MP forking about five times, CuA with about four branches, CuP with one or more short branches; about eight anal veins, often forked. Cross veins few, slightly irregular. Hind wing: length 43 mm, width 15 mm.

Body structures: Head broad and short, eyes relatively small. Clypeus not known. Antennae about 15 mm long, composed of equal, long, cylindrical segments. Prothoracic lobes: about 7 mm long, with slightly undulated margin, veins about ten in number, cross veins very dense. Mesothorax about as long as metathorax.

Specimen 17-18 shows some additional body structures, which, for reasons mentioned above, I did not include into the account of this species. Fore wing: length 40.5 mm, width 11 mm; hind wing: length 41 mm, width 14.5 mm. Venation of prothoracic lobes and the wings as in *bonnieri*, except that MA in the fore wing has longer



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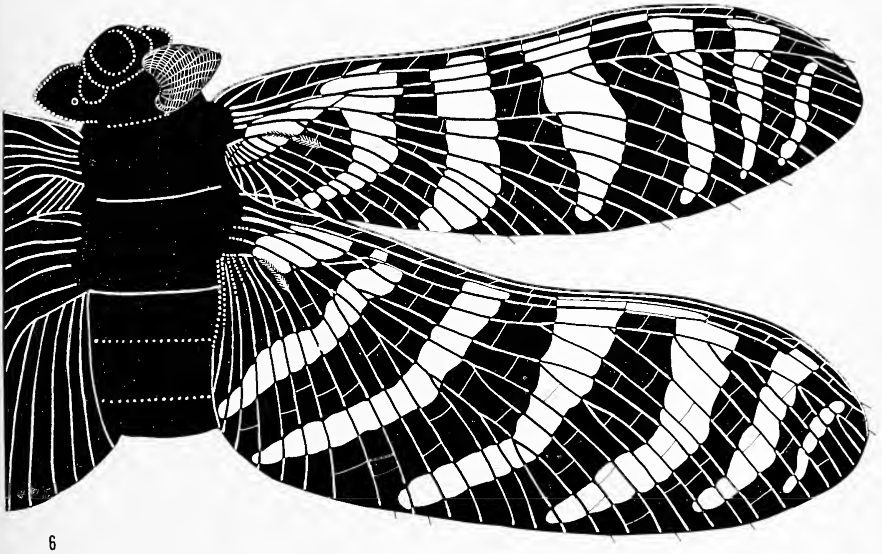

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Figure 5. *Homaloneura punctata* Brongniart; specimen 17-13. Holotype.
Figure 6. *Homaloneura joannae* Brongniart; specimen 18-5. Holotype.

and more numerous branches, and that the apical part of the anterior margin is more convex. The cuticular thickening in specimen 17-18 is very well preserved. It is as prominent as the strongest vein, R, at the base of the wing. The surface of the cuticular thickening is sculptured by transverse striae. Head: length 3.2 mm, width 5.8 mm; eye length 2 mm; clypeal length 3 mm; prothoracic lobes length about 7.5 mm. The abdomen is relatively slender, composed of very unequal segments; segments 1-3 are shorter than the following ones, segments 5 and 7 longer than segments 4 and 6. Each tergite has a distinct median line. The posterolateral angles of the tergites are prolonged.

Specimen 17-18 is spectacular in having large eyes and clypeus, and a slender abdomen. The projecting of the posterolateral angles of the tergites was probably much less in the living insects than is apparent in the fossil, as a result of the separation of the segments during preservation.

H. bonnieri is close to *elegans*, but differs in the larger dimensions, the less narrowed apical part of the wings, with a less pointed apex, and in having the denser cross venation of the prothoracic lobes.

Homaloneura punctata Brongniart
Figure 5

Homaloneura punctata **Brongniart, 1893: 319, pl. 17, fig. 13, pl. 18, figs. 3-4; Handlirsch, 1906: 108, pl. 12, fig. 4; Lameere, 1917: 147.**

This species was based upon two specimens, according to Brongniart, but only one of these was figured. In the Paris Museum collection, I was able to find only the figured specimen, this consisting of the obverse of the fore and hind wings. Since Brongniart's figure does not show some parts of the wing margin and of the vein stems, which are very helpful for the interpretation of the wings, I have prepared a new figure, which also includes some additional structures not observed by Brongniart. The following account is based upon this one specimen.

Wings equal in length, the membrane relatively thick and dark-colored; small, rounded spots distributed as shown in Figure 5; cuticular thickenings at wing base unknown. Supporting cross veins running obliquely from the stem of M to the very base of Rs. Fore wing: length 28 mm, width 8.5 mm. Posterior margin mainly lacking, but the margin seems to run parallel to the anterior one for most of its length; Rs with about five branches, the first of them forked; MA with 1-2 branches, MP forked three or four times; CuA pectinate, with 4-5 branches, sometimes forked; CuP simple.

Cross veins few, almost regular. Veins and cross veins lightly colored. Hind wing: length 28, width about 11 mm.

The venation indicates that *punctata* is related to the *elegans-bonnieri* group more closely than to the *joannae-ornata-lehmani* group, since the fore wing lacks the very oblique position of branches of CuA, and the main veins are more richly branched than in the last group of species.

Homaloneura joannae Brongniart

Figure 6

Homaloneura joannae Brongniart, 1893: 320, pl. 18, fig. 5; Lameere, 1917: 147.

Homaloneurites joannae Handlirsch, 1906: 107, pl. 12, fig. 1.

This species was based by Brongniart upon specimen 18-5, which consists of the four wings, thorax, one prothoracic lobe, and vague outlines of head and clypeus. Handlirsch (1906) erected for this species a separate genus, *Homaloneurites*, on the basis of its veins being less branched; but that genus was placed in synonymy of *Homaloneura* by Lameere (1917), who did not accept as valid the characteristics given by Handlirsch. This is a difficult problem, and it is discussed below.

Handlirsch (1906) thought that Brongniart's specimen 17-15 was *joannae* as well, this fossil being erroneously designated by Brongniart as the reverse half of the type of *ornata* (17-16). Handlirsch was right that the specimen (17-15) was not the counterpart of the type specimen of *ornata*; it is not *joannae* either, but represents an undescribed species, named below *lehmani*.

In Brongniart's account of the specimen of *joannae* there are several mistakes in venational interpretation and in the description of the color pattern; also, the hind wing and the body structures were not illustrated. The following account gives these additional details as well as a review of those noted by Brongniart.

Wings equally long, membrane relatively strong and dark, with transverse light bands. Cuticular thickening extending on A1 for a short distance as the vein curves towards the posterior margin. Supporting cross vein running obliquely from the stem of M to the very base of Rs. Fore wing: length 22.5 mm, width 5.7 mm. Fore wing broadest at the beginning of the apical third, narrowing towards the base; apex rounded, about on the wing axis; anterior margin slightly concave; postcostal area triangular and small. Rs with seven simple branches; MA forked 1-2 times; MP with a long fork; CuA with 4-5 pectinate branches; CuP simple; cubital branches very obliquely arranged; about eight simple anal veins; cross veins few and weak. Hind wing: length 25.5 mm, width 9 mm. Anterior margin more concave than in the fore wing. Anal area very much broadened just beyond the base, the inner angle of the wing nearly a right angle.

Body structures: Head apparently short and broad, with a rectangular clypeus. Prothoracic lobe: length 2.8 mm, width 2 mm; small and strongly sclerotized. Prothoracic veins about ten in number, cross veins very dense; mesothorax slightly shorter than the metathorax.

H. joannae is smaller than either *elegans* or *bonnieri* and has the wing membrane much thicker. The supporting structures in the wing are consequently less developed, the cuticular thickening extending for a very short distance on A1, and there is only one supporting cross vein as well as a few weak cross veins. These same features are present in the *ornata-lehmani* group. Convergence of several morphological features is readily seen in this series of species. The head in *joannae* is short and broad, as it is in *bonnieri*, the shape of the prothoracic lobes and the venation are as in *bonnieri*, but the small size of the insect and the more heavy sclerotization is almost as in *lehmani*. The shape of the fore wings resembles *lehmani* most closely; the lack of small twigs on the veins and the rectangular shape of the anal area of the hind wing are much as in *ornata*; the obliquely arranged cubital veins are as in *ornata* and *lehmani;* the color patern is much as in *lehmani*; the cuticular thickening as in *ornata*. From these observations, it would seem that *joannae*, *ornata*, and *lehmani* might be considered as forming a separate genus, but at the present time it seems more advisable to leave them in a single genus until more is known about other species of the family.

Homaloneura ornata Brongniart

Figure 7

Homaloneura ornata Brongniart, 1893: 321, pl. 17, fig. 16; pl. 18, figs. 6-7; Handlirsch, 1906: 109, pl. 12, figs. 5-6; Lameere, 1917: 147; Handlirsch, 1921: 136, fig. 64.

This species is based by Brongniart upon specimen 17-16, the wings of which are shown enlarged on figures 6 and 7 of plate 18. The specimen is a female, with two almost complete wings, with the abdomen showing cerci and the ovipositor, and there are vaguely preserved parts of the head and the thorax. As noted above, specimen 17-15 was erroneously determined by Brongniart as the counterpart

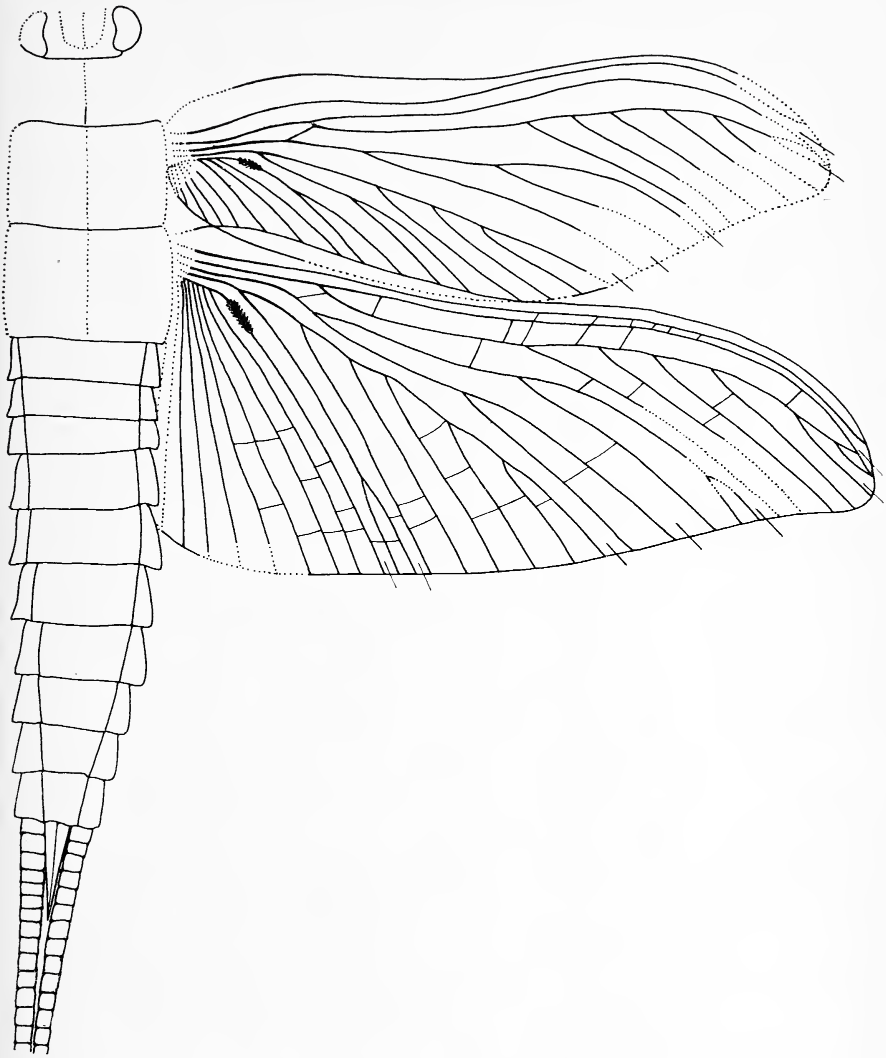

Figure 7. *Homaloneura ornata* Brongniart; specimen 17-16. Holotype.

of this specimen of *ornata*, but it is not only not the same specimen, but it is a distinct species, described below as *lehmani*.

The type specimen of *ornata* is a reverse impression, with an indistinct pattern of color on the wings. In all probability, the wing membrane was dark with transverse light bands. The first three segments of the abdomen are narrow and rather indistinct; the ovipositor, in part hidden between the cerci, has previously been overlooked. *Homaloneura ornata* was figured in reconstruction by Handlirsch (1921); the details shown by him are highly imaginary and probably incorrect; his figure, for example, shows the prothoracic lobes absent, which is almost certainly incorrect, since they are present in all other species of the genus.

Wings unequal in length, the hind pair being longer; membrane relatively strong, dark, probably with transverse light bands. The cuticular thickening strengthening A1 for a short distance at the point in which it bends towards the posterior margin; the supporting cross vein, r-m, weak, running obliquely from the stem of M to the very base of Rs. Main veins with few branches. Fore wing: length about 20 mm, width 7.5 mm; broadest shortly beyond the midwing, markedly narrowing towards the base; apex pointed, directed posteriorly; anterior margin concave at about midwing; posterior margin with a convexly curved portion just before the apex; Rs with six simple branches, MA forked 1-2 times; MP simple or with a long fork; CuA well developed, with 3-5 pectinate branches, which are obliquely arranged. CuP simple or forked; about eight simple anal veins; cross veins few and weak. Hind wing: length 23 mm, width about 10.5 mm; anal area very much expanded just beyond the wing base, the posterior margin forming nearly a right inner angle.

Body structures: Head with large, projecting eyes; clypeus apparently oval; prothoracic lobes unknown; mesothorax slightly shorter than the metathorax. Abdomen, length: 16 mm, relatively slender; tergites with projecting posterolateral angles; the segments 1-3 very short, segment 6 longer than the others; ovipositor heavily sclerotized; longitudinal lateral lines on each tergite; cerci robust, completely covered by short hair.

H. ornata belongs to the group *joannae-lehmani*, all of these being small in size with simply-marked wings. Within this genus, *ornata* shows the highest modification in the wing shape, and has the most extensively broadened hind wings.

Homaloneura lehmani, sp. nov.*

Figure 8

The holotype of this species is Brongniart's 17-15, which was figured by him in 1893 as *H. ornata*; the specimen is in the Institute of Palaeontology in Paris, where I was able to make a careful examination of it. The specimen is very well preserved and shows the complete insect with four wings and many details of body structure. It is the only specimen of Palaeodictyoptera so far found which shows the beak in a bent condition; it suggests flexibility of the sheath and the tendency for the stylets to remain together. Another unusual structure is the presence of vestigial, almost scale-like, sclerotized prothoracic lobes, completely without venation. The clypeus is probably better preserved than that in any of the specimens of Palaeodictyoptera from Commentry, and it shows the very fine parallel striations which make a continuous series of bands.

Wings subequal in length, the hind pair somewhat longer. Wing membrane relatively strong, dark, with transverse light bands. Cuticular thickening strengthening A1 for a short distance in the region of its curve towards the posterior margin. Supporting r-m cross vein weak, running obliquely from the stem of M to the very base of Rs. Main veins with many short branches. Fore wing: length 23 mm, width, 7.2 mm; broadest shortly beyond midwing, narrowing towards the base; apex pointed, the apical part curved posteriorly; posterior margin slightly convex just before apex; Rs with 6-7 pectinate, simple branches; MA forking three times; MP forking 3-5 times; CuA with 3-5 pectinate branches, often forking; CuP with two forks; cubital branches in fore wing arranged very obliquely; about 5-6 anal veins, mostly forked; cross veins few, weak. Hind wing: length 23 mm, width 9 mm. Anal area abruptly expanding just beyond the wing base.

Body structures: Head 1.5 mm long, broader than prothorax. Eyes very large, 1.5 mm long, projecting. Clypeus oval, with median ridge and about eight pairs of parallel transverse striae. Preserved length of beak 4.3 mm; prothorax narrowing anteriorly, about half the length of the mesothorax; prothoracic lobe length 2.3 mm, width 2 mm; prothoracic lobes vestigial, heavily sclerotized, cordate, the venation completely absent, but with a longitudinal median furrow, terminating just below the apex of the lobe. Mesothorax as long as metathorax. Abdomen shorter than the wings; first segment slightly

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*Named in honor of Professor J. P. Lehman, Director of the Institut de Paléontologie, Paris.

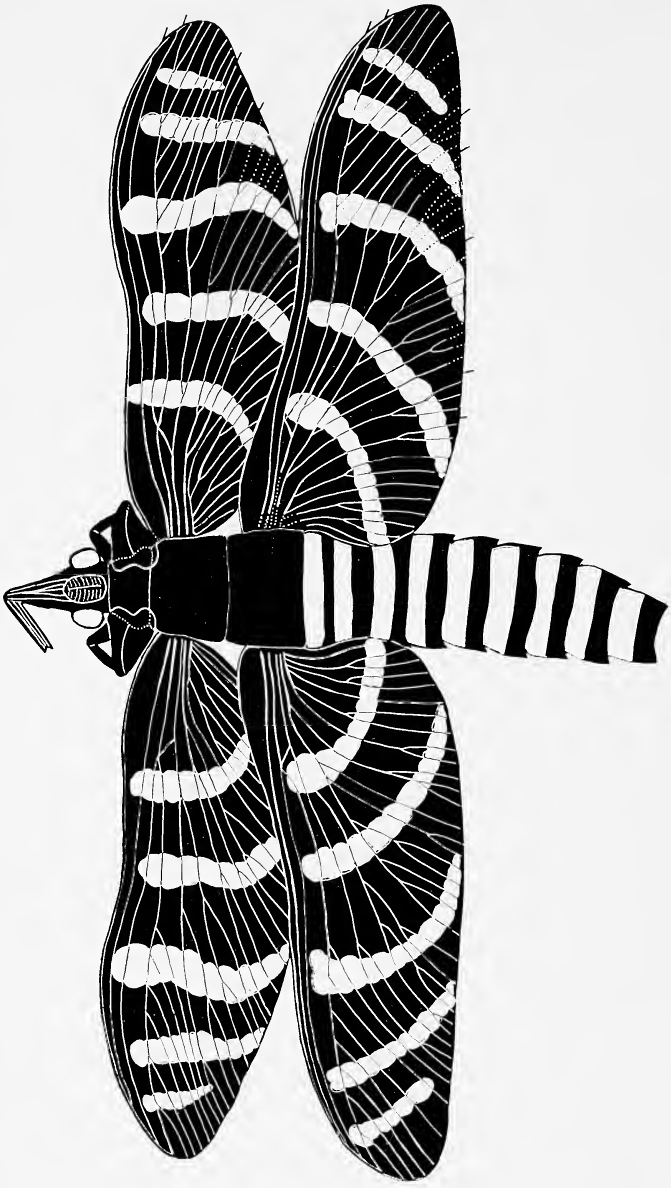


Figure 8. *Homaloneura lehmani* sp. nov.; specimen 17-15. Holotype. Prothoracic lobes are sclerotized, with their venation lost.

shorter than the following ones; posterolateral angles of tergites only slightly projecting; posterior half of tergites darkly pigmented.

This species is related to the group *joannae-ornata,* but differs in the presence of many short branches on the main veins and in the less pronounced enlargement of the hind wing, which is more similar to that of the *elegans-bonnieri-dabasinskasi* group. Within the genus this species has the most specialized prothoracic lobes, which are the smallest and most sclerotized and which, in contrast to those of other species, do not show any traces of venation.

Homaloneura bucklandi Brongniart
Figure 9

Homaloneura bucklandi Brongniart, 1893: 320, pl. 17, fig. 14; pl. 18, fig. 2; Handlirsch, 1906: 108, pl. 12, fig. 3; Handlirsch, 1919: 20; Lameere, 1917: 147.

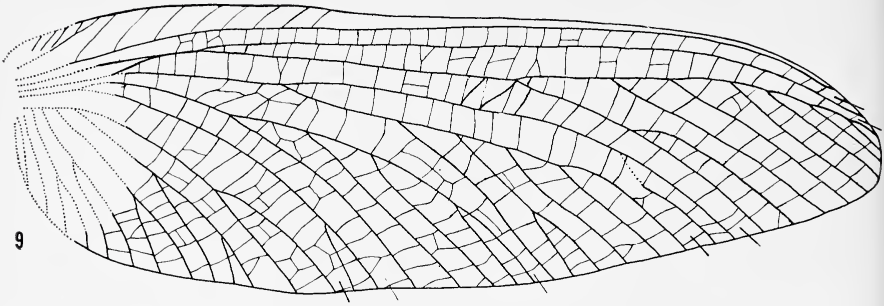
This species is based by Brongniart upon specimen 17-14 (also figured on pl. 18, fig. 2), which represents a fore wing lacking the base. The insect seems to be rather remote from all others in the genus, showing more numerous and less irregular cross veins. Unfortunately, I could not locate the type specimen in the Paris Museum. The following account is based upon the photograph made by Dr. Carpenter in 1938 and upon Brongniart's original description and Lameere's revisional study. At present, I prefer to leave *bucklandi* with the genus Homaloneura, but feel that this classification is dubious, and that this species might turn out to represent a distinct genus.

Wings probably dark; cuticular thickening unknown; supporting m-r cross vein running obliquely from the stem of M to R. Fore wing: length 29 mm, width 9 mm (according to Brongniart, p. 320); almost uniformly broad in the proximal half; anterior margin slightly concave beyond the basal third; posterior margin slightly undulated in the region of CuP and CuA; Rs with about six branches; MA with one short branch; MP with about five branches; CuA with three branches; CuP with a short fork; anal area with about 6-8 veins, mostly forked; cross veins numerous, irregular, sometimes probably with anastomoses.

H. bucklandi differs from all other species of the genus by the numerous and irregular cross veins; MA has fewer branches than *punctata* and *joannae*, and CuP has a simple fork as in *bonnieri.*

Genus *Spilaptera* Brongniart

Spilaptera Brongniart, 1885: 63; Brongniart, 1893: 337; Brauer, 1886: 110; Handlirsch, 1906: 102; Bolton, 1917: 53; Handlirsch, 1919: 20.



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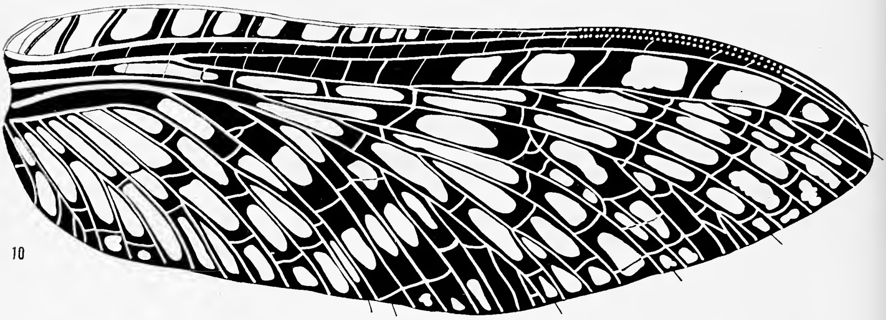

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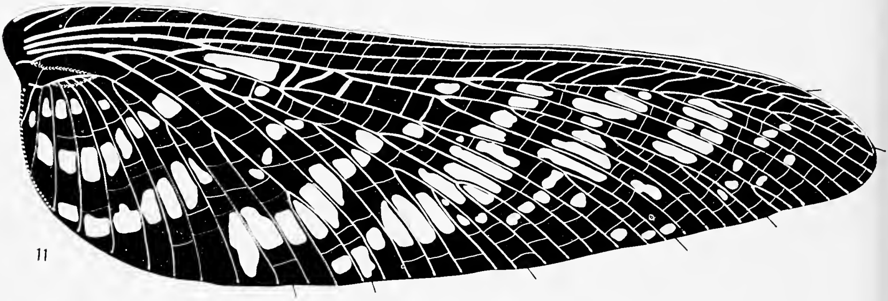

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Figure 9. *Homaloneura bucklandi* Brongniart; specimen 17-17; fore wing. Holotype.

Figure 10. *Spilaptera packardi* Brongniart; specimen 20-7; fore wing. Holotype.

Figure 11. *Becquerelia superba* Brongniart; specimen 19-1; hind wing. Holotype.

Type species: *Spilaptera packardi* Brongniart, 1885 (SD, Handlirsch, 1922).

The genus *Spilaptera* was erected by Brongniart for three species, *packardi*, *libelluloides*, and *vetusta*. In 1893, *meunieri* was added to the genus. Handlirsch (1906) made a new genus, *Epitethe* for *meunieri* on the basis of more numerous branches of the main veins, and this genus was accepted by Lameere (1917). Unfortunately, I was unable to find the type specimen of *vetusta* in the Museum and Dr. Carpenter failed to find it in 1938; for that reason I am not including *vetusta* in this paper.*

Brongniart (1893), Handlirsch (1906), and Lameere (1917) were of the opinion that Sc in *Spilaptera* does not extend much beyond the middle of the wing. This is not correct, however, as in the type species *packardi* and in *libelluloides* after removal of the covering matrix, the costa can be seen terminating near the wing apex. It has also proved possible to excavate a part of the hind wing in *libelluloides*, the hind wing not previously having been known in the genus.

The wings in *Spilaptera* are of almost equal length. Wing membrane with color markings; hind wing broader in the proximal half than the fore wing, but with a similar venation. Cuticular thickening and supporting veins missing. The anterior margin only slightly concave. R1 without terminal branches; R-Rs area broad with a series of several strong oblique cross veins; Rs with only 4-5 branches; M free from Rs; MA with several branches; MP forked several times; CuA pectinate; CuP simple or forked; cross veins few, with a tendency to make rows in the apical third of the wing.

Spilaptera resembles *Homaloneura* by having few cross veins and by the general wing structure, but it lacks both the thickenings and supporting veins. These are perhaps replaced in this genus by a few strong cross veins, which tend to be surrounded, and probably supported, by pigmented areas. The cross veins are very typical in the R-Rs area, being sigmoidal in shape in both known species, *Spilaptera packardi* Brongniart and *Spilaptera libelluloides* Brongniart.

The species of *Spilaptera* present in the Commentry shales are *S. packardi* Brongniart, 1885 and *S. libelluloides* Brongniart, 1885.

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*The small wing fragment designated by Bolton (1917: 53) as representing a new species, *Spilaptera sutcliffei,* is not recognizable even to the family level and is herein assigned to the Palaeodictyoptera incertae familiae.

Spilaptera packardi Brongniart
Figure 10

Spilaptera packardi Brongniart, 1885: 63, pl. 5, fig 1; Brongniart, 1893: 338, pl. 20, fig. 7; Handlirsch, 1906: 102, pl. 11, fig. 16.

This species is based by Brongniart upon specimen 20-7, which is a well preserved fore wing with a perfect color pattern.

Fore wing: length 53 mm, width 16.5 mm, broadest at midwing. Light spots, mostly oval in shape, occur between the cross veins as shown in figure 10. Anterior margin concave. Posterior margin parallel in the proximal half with anterior, then concave. Apical part abruptly narrowing, the apex pointed and located about on the wing axis. Postcostal area with two simple veins originating on Sc. Subcostal area broad in the proximal third, very narrow distally. R-Rs area with only about 4-5 strong cross veins in its distal half; Rs with about five very oblique simple branches; MA with four short branches; MP forked about three times; CuA with a series of about six branches; CuP simple; anal area relatively large, with about eight branches, sometimes forked. Cross veins very few, strong, mostly curved, forming rows.

S. packardi differs from *libelluloides* in its color pattern, the shape of the fore wing, the simple CuP, and the presence of fewer cross veins.

Spilaptera libelluloides Brongniart
Figure 12

Spilaptera libelluloides Brongniart, 1885: 63; Brongniart, 1893: 339 pl. 20, fig. 8; Handlirsch, 1906: 103, pl. 11, fig. 17.

This species is based upon specimen 20-8, originally consisting of part of the fore wing and a small fragment of the hind wing. After I had removed more of the matrix, all four wings, with almost complete venation, could be seen. The body, which was partially described by Brongniart (1893: 340) is insufficiently preserved for study.

Wings of equal length, with narrow dark bands, about seven in number, irregular and more concentrated in the apical part of the wing, as shown in figure 11. Anterior margin concave, the posterior margin as a whole is moderately concave and very slightly undulated. Fore wing: length 57 mm, width 21 mm, broadest at the end of the proximal third; apical part abruptly narrowing and short, the apex pointed and located on the wing axis. Subcostal area not markedly broad in the proximal third. R-Rs area with about 5-6 strong cross veins, surrounded by color markings in the distal half of the wing;

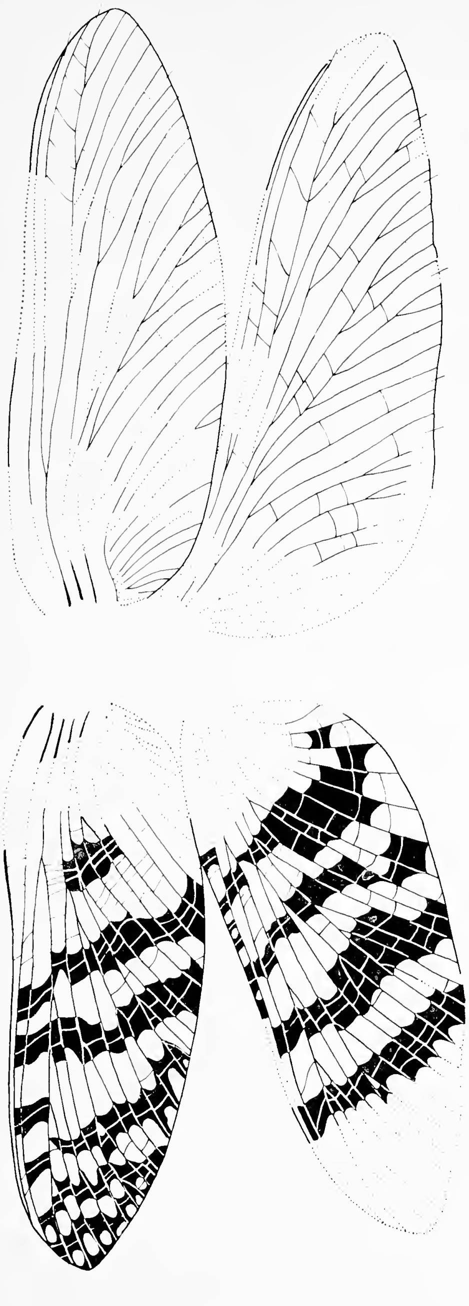


Figure 12. *Spilaptera libelluloides* Brongniart; specimen 20-8. Holotype.

Rs with about four simple branches; MA with 2-3 branches; MP forked 2-4 times; CuA with a series of four branches; CuP forming a long fork; anal area with about eight veins, mostly simple. Cross veins are not numerous and are not forming rows. Hind wing: length 57 mm, width 22.6 mm. Hind wing not much broadened, but with a rounded anal area.

S. libelluloides differs from *packardi* as previously mentioned.

Genus *Becquerelia* Brongniart

Becquerelia Brongniart 1893: 356; Handlirsch, 1906: 105; Lameere, 1917: 152.

Pseudobecquerelia Handlirsch, 1919: 24.

Type species: *Becquerelia superba* Brongniart, 1893 (SD, Handlirsch, 1906).

This genus was erected by Brongniart in 1893 for four species, *superba*, *tincta*, *grehanti*, and *elegans*. Handlirsch (1906) designated *superba* as the type species and questioned the generic position of *grehanti* and indicated his uncertainty about *elegans*, because of its fragmentary nature. In 1919, however, Handlirsch erected the genus *Pseudobecquerelia* for *elegans*, although he put it in the Palaeodictyoptera incertae sedis. Lameere (1917: 152) suggested that *grehanti* be placed in *Epitethe* Handlirsch, as previously noted, and he considered *elegans* as a true *Becquerelia*.

In this paper, *superba* and *tincta* are considered to be very closely related; they may eventually turn out to be conspecific. *Elegans* is a small fragment, but probably belongs to *Becquerelia*, as it was considered by Lameere. *Grehanti*, on the other hand, is here designated as the type species of a new genus, *Tectoptilus*. The following are the characteristics of *Becquerelia*, as they are indicated in *superba* and *tincta*; included are some features not previously noted.

Wings dark colored, with light transverse bands; cuticular thickening V-shaped, its apex on A1; anterior margin only slightly concave; postcostal area small, with a single vein. Sc long, terminating somewhat before apex; R1 with terminal branches; in the R-Rs area there are numerous long, oblique cross veins; Rs pectinate, with six branches; M fused for a long distance with the stem of Rs; MA pectinate; MP forking several times; CuA pectinate; CuP forked; cross veins numerous, simple, but somewhat irregular.

Becquerelia shows the same type of cuticular thickening as *Homaloneura elegans* and *bonnieri*, but in place of the extra strengthening cross vein between M and R-Rs, as in *Homaloneura*, MA functions as the strengthening vein by fusing with Rs at its very beginning. Except for this fusion of MA with Rs, *Becquerelia* is scarcely distinct from *Palaeoptilus*, both in venation and in coloration.

The known Commentry species of *Becquerelia* are *superba* Brongniart and *tincta* Brongniart; *elegans*, as noted above, probably belongs in this genus, but its fragmentary condition does not allow further description.

Becquerelia superba Brongniart
Figure 11

Becquerelia superba Brongniart, 1893: 357, pl. 19, fig. 1; Handlirsch, 1906: 105, pl. 11, fig. 22.

This species is based upon specimen 19-1, consisting of a well preserved hind wing with a clearly preserved color pattern.

Hind wing: length 85 mm, width 27 mm; broadest just beyond the base; anterior part of cuticular thickening running from the beginning of Cu obliquely to the bend of A1; posterior part of the thickening following A1 for some extent, then parallel to it until the bend in A1; several supporting cross veins are present between the base of MA and R + Rs; color markings forming numerous light elongate spots, arranged into about eight transverse bands; apical part of wing elongate, the apex rounded, directed posteriorly; anal area somewhat enlarged, with about 12 oblique cross veins in its distal half; Rs with six very oblique, simple branches; MA with about four long branches; MP forked about five times; CuA with a series of five long branches; CuP forked twice; anal area with nine simple branches; cross veins less numerous in the anal area, where they form rows.

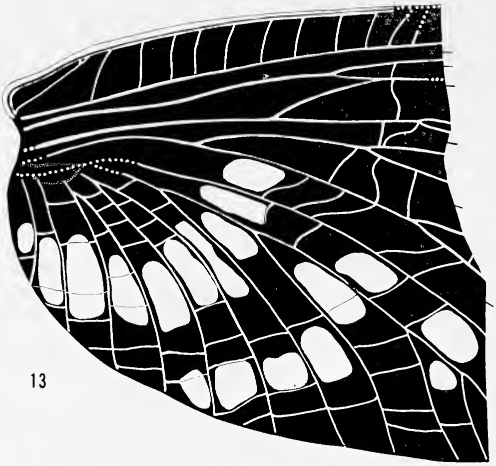
Becquerelia superba (hind wing) differs from *tincta* (basal part of fore wing) in having the first fork of MP directed more posteriorly, by the presence of long forks on the anal veins, and by the patches of additional small light spots near the base of the wing, although the latter might be an individual trait, rather than specific.

Becquerelia tincta Brongniart
Figure 13

Becquerelia tincta Brongniart, 1893: 362, pl. 20, fig. 3; Handlirsch 1906: 105, pl. 11, figs. 23-24.

This species is based upon specimen 20-3, consisting of the proximal third of a fore wing. The color pattern is not distinct.

Fore wing: length of fragment 24 mm, width 25 mm; light, elongate spots forming transverse bands; cuticular thickening apparently



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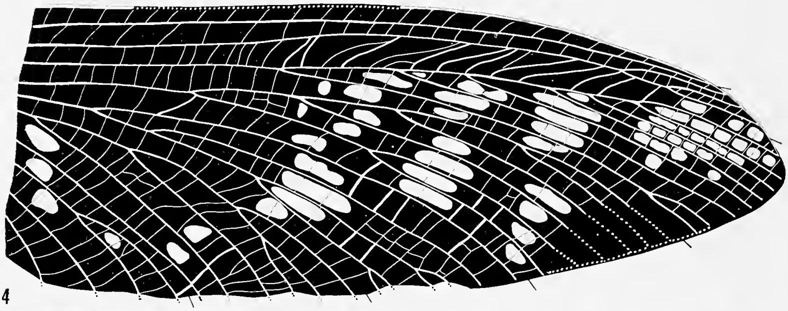

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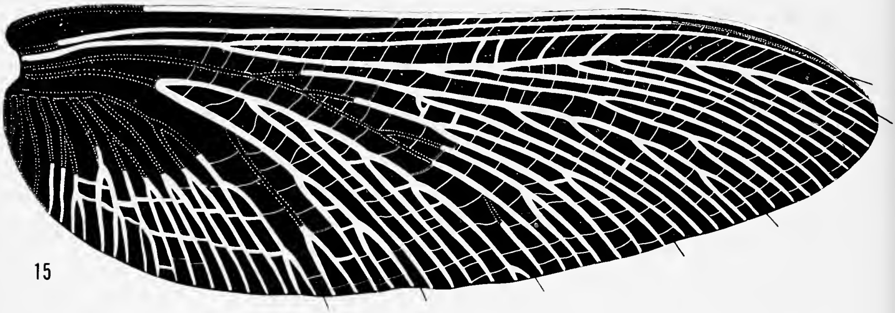

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Figure 13. *Becquerelia tincta* Brongniart; specimen 20-3; fore wing. Holotype.

Figure 14. *Palaeoptilus brullei* Brongniart; specimen 19-15; fore wing. Holotype.

Figure 15. *Epitethe meunieri* (Brongniart); specimen 19-5; hind wing. Holotype.

the same as in *superba*; wing narrowing towards the base; postcostal area triangular, narrow; subcostal area in the form of a band near the base; CuP with at least two branches; anal area large, with only five veins, but with several long forks; cross veins numerous, simple, sometimes curved.

Becquerelia tincta may be conspecific with superba, though it appears to differ in having the origin of the first fork of MP more proximal, and in having several long forks of the anal veins. The color pattern is similar to that of *Homaloneura dabasinskasi* Carpenter from the Westphalian nodules of Illinois, and of *Palaeoptilus brullei* Brongniart from the Commentry shales.

Genus *Palaeoptilus* Brongniart

Palaeoptilus Brongniart, 1893: 352; Handlirsch, 1906: 101.

Type species: *Palaeoptilus brullei* Brongniart, 1893 (OD).

This genus is montoypic, being erected by Brongniart for a single species close to *Becquerelia elegans*. The following account, which is based upon a study of the type specimen, includes more details of venation than have previously been noted.

Wings dark colored with light spots arranged in transverse bands; cuticular thickening unknown; Sc terminating somewhat before the apex; R1 with terminal branches; in the R-Rs area there are numerous long, oblique cross veins; MA is free from the stem of Rs; Rs and MA pectinate; MP forked several times; CuA pectinate; CuP forked. Anal area unknown. Cross veins numerous, simple, but somewhat irregular.

Except for the lack of fusion of MA with the stem of Rs, *Palaeoptilus* is similar to *Becquerelia*, although the shape of the cuticular thickening is not known. The general venational pattern, the cross veins, and the large R-Rs area with its oblique cross veins are reminiscent of *Epitethe*.

The type species is the only one known in the Commentry shales.

Palaeoptilus brullei Brongniart

Figure 14

Palaeoptilus brullei Brongniart, 1893: 353, pl. 19, fig. 15; Handlirsch, 1906: 102, pl. 11, fig. 15.

This species is based upon a single specimen, Brongniart's 19-15, which is a well preserved fore wing lacking the basal quarter and the posterior margin.

Fore wing: length of fragment 61 mm, width 22 mm; light spots elongate, arranged into irregular bands, more dense in the apical part; the anterior margin slightly convex in the distal half; apical part of wing not elongate, the apex moderately pointed, arranged on wing axis. Subcostal area narrow in the distal two-thirds of wing; R1 with two long terminal branches; r-rs area broad, with a series of thin, very oblique cross veins; Rs with six oblique simple veins; MA with four long branches; MP forked about three times; CuA with a series of four branches; CuP forked three times; cross veins numerous, simple, but slightly irregular.

Palaeoptilus brullei is similar to *Becquerelia superba* in having terminal branches on R1, in the broadened r-rs area with its oblique cross veins, and in the color pattern and venation, but differs in the absence of a fusion of MA with Rs.

Genus *Epitethe* Handlirsch

Epitethe Handlirsch, 1906: 103; Lameere, 1917: 150; Handlirsch, 1919: 20.

Type species: *Spilaptera meunieri* Brongniart (OD).

This genus was erected for *meunieri* on the basis of its more numerous branches of the main veins; the genus was accepted by Lameere.

Wing membrane dark; cuticular thickening unknown; the anterior margin almost straight; posterior margin slightly undulated; branches of main veins numerous, markedly parallel; Sc long, terminating shortly before apex (not terminating before midwing, as described by Handlirsch); R1 without terminal branches; MA free from Rs; Rs with seven branches; MA pectinate; MP forked several times; CuA pectinate; CuP forked several times. Anal area with many forked branches. Cross veins numerous, mostly irregular.

This genus differs from all others in the family by the pattern of dense and parallel branches of the veins; this trait and the pattern of cross veins recalls the genus *Tectoptilus* and *Palaeoptilus*. However, with the absence of other details, such as the nature of the cuticular thickening at the base of the wing, the relationship of this genus is uncertain.

Only the type species is known from the Commentry shales.

Epitethe meunieri (Brongniart)

Figure 15

Spilaptera meunieri Brongniart, 1893: 343, pl. 19, fig. 5.

Epitethe meunieri, Handlirsch, 1906: 103, pl. 21, fig. 19; Lameere, 1917: 150.

This species is based upon Brongniart's specimen 19-5, a hind wing lacking the basal part.

Wings dark, with broad, light veins and cross veins. Hind wing only moderately broadened, broadest at about the first third; length 48 mm, width 16 mm; anterior margin almost straight, posterior margin undulated; apical part relatively broad, apex rounded, located at about the wing axis; r-rs area slightly broadened, with numerous, weak and somewhat oblique cross veins; Rs with seven branches, the first being forked twice; MA with five simple, long branches; MP with six forks; CuA with a series of four long simple branches; CuP forked four times. Anal area large, with nine anal veins, most of them forked; cross veins numerous, regular, less dense in the anal area, broader and forming rows.

This species has a unique coloration among the Spilapteridae. The apparent width of the veins is probably due to the accompanying white strips along the veins, rather than to the veins themselves.

Genus **Tectoptilus** gen. nov.*

Type species: *Becquerelia grehanti* Brongniart.

The type species of this genus, *grehanti*, is known only from a single specimen, number 20-4 of Brongniart's 1893 monograph. Although he placed the species in *Becquerelia*, this assignment was questioned by Handlirsch (1906) and Lameere (1917), who referred it to the genus *Epitethe* Handlirsch. In the course of my study of the fossil, I have noted additional features which separate the insect from all genera which have been established. In the Museum collection, I have also found an unfigured specimen which seems to be conspecific with *grehanti* (figure 17). This specimen, being much better preserved than the type, contributes much information about the fore wings and certain body structures, which have been used in the following account.

Wings dark with a light pattern. Cuticular thickening Y-shaped, extending into the area of CuP and A1. Anterior margin slightly concave. The termination of R1 unknown but Rs pectinate, with few branches; MA with several branches, MP richly branched; CuA pectinate, CuP with an unusual number of branches, extending over a large area. Anal area with many branches also. Cross veins numerous, simple or rarely irregular and anastomosed; posterior mar-

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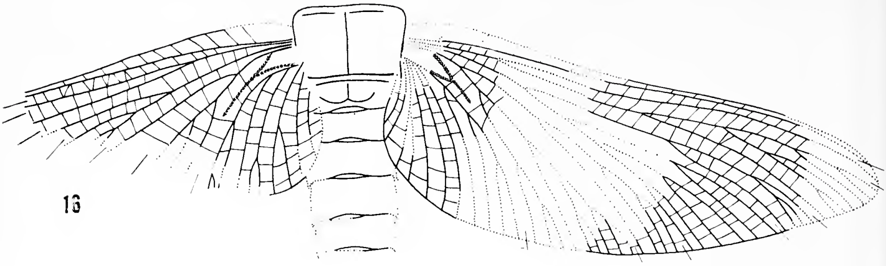
*This generic name is based on the Greek word (tekton) for a carpenter and is used in honor of Professor F. M. Carpenter, Harvard University.



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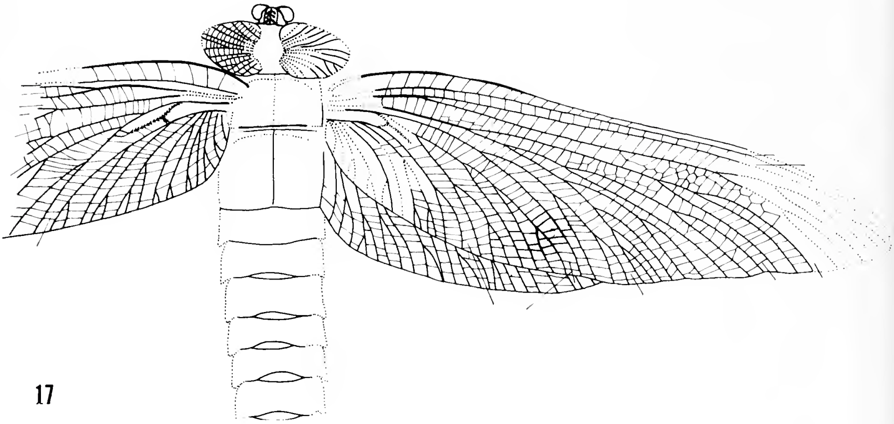

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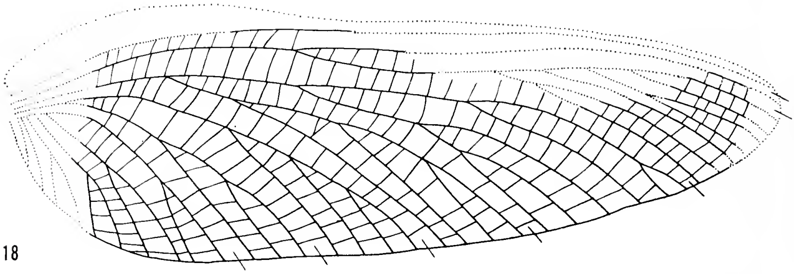

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Figure 16. *Tectoptilus grehanti* (Brongniart) ; specimen 20-4; hind wings. Holotype. Originally described as *Becquerelia grehanti* Brongniart, 1893.

Figure 17. *Tectoptilus grehanti* (Brongniart) ; undescribed specimen also in collection of Paris Institute.

Figure 18. *Spiloptilus ramondi* (Brongniart) ; specimen 19-14; fore wing. Holotype.

gin somewhat undulated. Hind wing little known, not greatly broadened.

Body structures: Head small, much narrower than the prothorax, eyes prominent. Prothoracic lobes cordate, with radiating veins and numerous cross veins; metathorax very broad, longer than the mesothorax.

This genus is apparently related to other genera of this family with numerous cross veins, such as *Palaeoptilus*, *Spiloptilus*, *Epitethe*, and *Becquerelia*. The absence of the distal part of R1 in *grehanti* prevents precise comparison with *Palaeoptilus*, and the absence of the cuticular thickening of the wing in *Palaeoptilus*, *Epitethe* and *Spiloptilus* prevents satisfactory comparison with those genera. However, the genus *Tectoptilus* differs from all other spilapterid genera in having the Y-shaped cuticular thickening, which extends between CuP and A1, and in having an unusually broad area of CuP, with many branches. This last character, as well as the fully developed MA and the presence of numerous cross veins resembles the structure of the Fouqueidae, although the other features known are spilapterid in nature. The genus *Tectoptilus*, in this way, seems to be somewhat intermediate between the Fouqueidae and the Spilapteridae. At the present state of our knowledge, it seems to be impossible to draw a strict line between these two families.

Tectoptilus grehanti (Brongniart)

Figures 16 and 17

Becquerelia grehanti Brongniart, 1893: 359, pl. 20, fig. 4; Handlirsch 1906: 106, pl. 11, fig. 25; Lameere, 1917: 152.

This species, based upon specimen 20-4, shows two hind wings, the metathorax, and five segments of the abdomen; in addition, another, previously undescribed specimen is contained in the collection of the Museum, this showing the fore wings in part, the head (with eyes and clypeus), prothoracic lobes, and the thorax and six segments of the abdomen. On the basis of the similarity of venation and the nature of the cuticular thickening, I consider this conspecific with the type of *grehanti*; this may be the specimen which Lameere (1917: 155) mentioned as an additional specimen of *Fouquea needhami* Lameere. The following account is based upon both of these specimens.

Wings: dark with light maculations; fore wing: length 58 mm, width 20 mm, broadest slightly before the midwing; narrowed in the basal part with distal part elongate; r-rs area not broadened, with dense series of slightly oblique cross veins; MA with two branches, MP richly branched, forking about eight times; CuA with three branches; CuP forking six times; anal area long and narrow, with six to eight forking branches; cross veins numerous, often curved, irregular and sometimes anastomosed. Hind wing: length 62 mm, width 24 mm, broadest at the end of the first third, with moderately rounded anal area.

Body structures: Head with reniform eyes, extending nearly to the clypeus; length of clypeus 3 mm, width 1.3 mm, rectangular in form, rounded anteriorly; transverse ridges oblique in the posterior region of the clypeus. Prothoracic lobes with about eleven veins, sometimes forked, and with numerous cross veins. Prothorax as long as the mesothorax, metathorax 1.5 times longer than mesothorax. Abdomen slenderer than metathorax, with segments 1-2 only a little shorter than the longest one, segment 3.

T. grehanti is unusual in having a very small head, the reniform eyes and the very large metathorax.

Genus *Spiloptilus* Handlirsch

Spiloptilus Handlirsch, 1906: 100.

Type species: *Graphiptilus ramondi* Brongniart (OD).

Although Handlirsch was undoubtedly correct in establishing a separate genus for *ramondi*, he was incorrect in placing it in the family Graphiptilidae; this error was made because he was under the impression that MA in *ramondi* was unbranched. The generic characters are revised here on the basis of my examination of the type specimen of *ramondi*, in which I have been able to determine more details about the structure of the Rs and anal area.

Wing: membrane dark; cuticular thickening unknown; supporting cross veins not present; anterior margin, Sc and R1 unknown; Rs diverging from R1 just beyond the first third of the wing, with a few branches, which may be forked; MA well developed, forking several times; MP with several branches; both CuA and CuP pectinate; anal area relatively small; cross veins numerous, simple, regular in form and equally distributed.

Spiloptilus differs from all other genera in the more distal origin of Rs, but detailed comparison with other genera is not possible because of the poor preservation of the type, the only known species of *Spiloptilus*.

Spiloptilus ramondi (Brongniart)
Figure 18

Graphiptilus ramondi Brongniart, 1893: 351, pl. 19, fig. 14.
Spiloptilus ramondi, Handlirsch, 1906: 102, pl. 11, fig. 14.

This species is based upon specimen 19-14, which is a badly preserved fore wing, lacking the base and the anterior margin. The venation is not clearly visible, but can be determined to some extent with the use of glycerin.

Fore wing: length 60 mm, widest at the end of the first quarter; posterior margin slightly undulated; apical part abruptly narrowed; Rs with five branches, which may be forked; MA occupying a large area, forked about five times; MP with a series of three branches; CuA with four branches, CuP forked twice; anal area relatively small, with about five branches, mostly forked. Cross veins equally distributed.

Genus *Lamproptilia* Brongniart

Lamproptilia Brongniart, 1885: 63; Brauer, 1886: 109; Handlirsch, 1906: 110; Handlirsch, 1919: 21; Laurentiaux, 1953: 422.

Type species: *Lamproptilia grandeuryi* Brongniart, 1885 (OD).

In his 1893 monograph, Brongniart added a second species, *stirrupi*, and established for the two species a separate subfamily which he termed the "Lamproptilida." Handlirsch (1906) raised this to family level on the basis of the very broad hind wings. Although this family has been accepted by subsequent workers, its close relationship to the Spilapteridae has frequently been noted. Since the body parts of *Lamproptilia* are unknown, we can base our conclusions only on the wing structure, which does not show any features justifying assignment to a separate family. Such characteristics as the broad hind wings occur in some other spilapterids in which the wings are even broader, and the form of the posterior margin of the hind wing as well as the color pattern of the wings falls well within the range of variation within the family Spilapteridae.

The species which Brongniart described as *stirrupi* is undoubtedly a spilapterid but it does not show enough of the venation to enable generic assignment; it is herein placed within the spilapterids, but without generic position.

The following are the characteristics which are suggested for the genus *Lamproptilia.* Wings: membrane dark, with a complicated color pattern, concentrated mainly in the distal half; cuticular thickening absent; wings subequal, the hind pair shorter than the front pair. Fore wing noticeably short and broad, the hind wing with pronounced convex curvature along the posterior margin between CuA and CuP; subcostal area narrow; Sc long; R1 without terminal branches; Rs long, originating in the basal third, with 2-3 branches; MA forked several times, MP somewhat more extensively branched; CuA giving rise to several branches; CuP forked several times; anal area with many forked branches.

Lamproptilia differs from all other spilapterid genera in the very broad and short wings, and in having the prominent anal-cup lobe in the hind wing. The venation, characterized by numerous cross veins, is suggestive of that of *Tectoptilus*, *Palaeoptilus*, etc.

Lamproptilia grandeuryi Brongniart

Figures 19 and 20

Lamproptilia grandeuryi Brongniart, 1885: 63, pl. 3, fig. 1; Brongniart, 1893: 345, pl. 35, figs. 7-8; Handlirsch, 1906: 110, pl. 12, fig. 8; Handlirsch, 1919: 21; Handlirsch, 1921: 137, fig. 65; Lameere, 1935: 175; Laurentiaux, 1953: 422, fig. 20.

This species was based on a single specimen (19-8), consisting of an exceptionally well preserved fore and hind wing with striking color pattern. Unfortunately, only the reverse half of the fossil could be found in the collection of the Museum; this shows the color much less clearly than the obverse, as is often the case with the Commentry insects. Fortunately, the color markings are very well shown in a photograph of the obverse made by Professor Carpenter in 1938. A drawing of the wings of this species, based on both obverse and reverse, has been published by Laurentiaux (1953, fig. 20). The following account is based upon the reverse of the type specimen.

Fore wing: length 75 mm, width 23 mm; almost oval in shape, broadest at about midwing; membrane dark, the veins and cross veins light; several oval light spots framed by dark pigmentation are distributed as shown in figure 19; anterior margin slightly concave at its middle; posterior margin undulated; apex broadly rounded. Sc long, R1 without terminal branches; R-Rs area only a little broadened with a dense series of oblique cross veins; R with only three branches, two of them forked; MA forked three times, MP six times; anal area with about ten branches, mostly forked. Cross veins mostly regular, bordered by irregular, white stripes; anastomosis of cross veins in the anal area very rare. Hind wing: length 70 mm, width 33 mm; light oval spots concentrated in the distal half and

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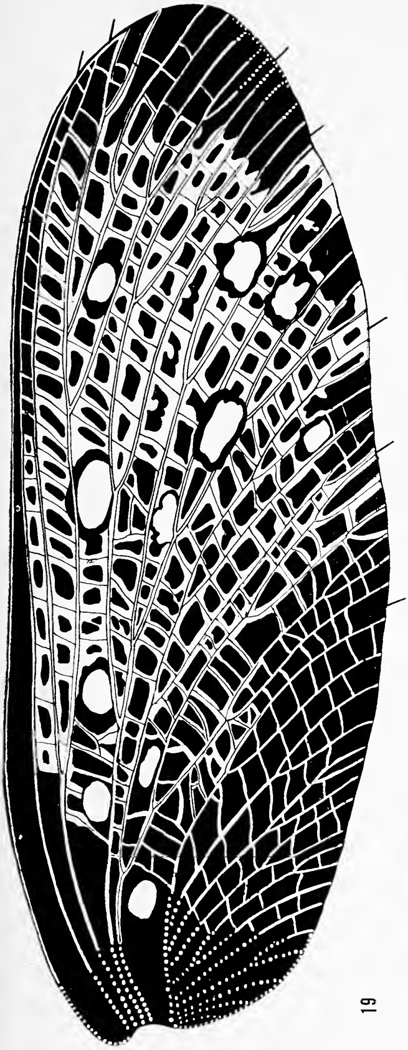
Figure 19. *Lamproptilia grandeuryi* Brongniart; specimen 19-8; fore wing. Holotype.

Figure 20. *Lamproptilia grandeuryi* Brongniart; specimen 19-8; hind wing. Holotype.



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along the posterior margin; posterior margin with a pronounced convex curve beyond CuP; anal area relatively narrow but high.

This species shows the most spectacular color pattern within the Palaeodictyoptera. The broad wings and the color pattern cause this insect to resemble superficially some of the Lepidoptera.*

Spilapteridae Gen. Inc. *stirrupi* (Brongniart)

Figure 21

Lamproptilia stirrupi Brongniart, 1893: 347, pl. 19, fig. 9; Handlirsch, 1906: 110, pl. 12, fig. 9; Handlirsch, 1919: 21; Laurentiaux, 1953: 422.

This species was based on a small fragment of a fore wing (specimen 19-9). The venation shows few features for generic assignment. The wing fragment is 72 mm long and 23 mm wide.

Family Fouqueidae Handlirsch

Fouqueidae, Handlirsch, 1906: 98; Lameere, 1917: 103; Lameere, 1917: 30.

Type genus: *Fouquea* Brongniart, 1893.

Handlirsch established this family for forms with richly branched venation and with a "reticulation recalling the Dictyoneuridae." He also associated the family with the Graphiptilidae, Spilapteridae and Lamproptiliidae. Lameere (1917: 103) called attention to the relationship between Fouqueidae and Spilapteridae, and later (1917: 30) he noted the possibility of the spilapterids being ancestral to the Dictyoneuridae (i.e., Stenodictyopteres of Brongniart). Lameere (1917: 154) considered the type genus *Fouquea* to be especially close to the genus *Rhabdoptilus*.

The family Fouqueidae is known only by fore and hind wings, in none of which are the basal portions satisfactorily preserved. The venational pattern is inseparable from that of the Spilapteridae (including the Lamproptiliidae), but is very different from that of the Graphiptilidae (including the genus *Rhabdoptilus*). The fouqueids can be differentiated from the spilapterids only by the presence of a dense pattern of prominent cross veins, which are mostly curved and often anastomosed and which extend over almost the entire area of the wings. This pattern of cross veins is very different from the true archedictyon of the Dictyoneuridae.

The wings are about equal in length, the hind pair broader in the basal parts. Venational pattern like that of the spilapterids, but

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*Forbes (1943) actually considered Lamproptilia to be holometabolous, related to the Neuroptera, Mecoptera, Lepidoptera, etc.

the cross veins strong, dense, curved and often anastomosed. The fore wing with the anterior margin almost straight. Sc long, R1 simple; Rs with 4-6 terminal branches; MA with at least two branches; MP branched several times; CuA and CuP with at least two branches; several anal veins. The hind wings have a venation like that of the fore wings. Both pairs of wings are usually marked by clusters of rounded spots. The body structures are entirely unknown.

As noted above, the family Fouqueidae is related to the Spilapteridae and especially resembles those genera of spilapterids which have many cross veins, such as *Epitethe*, *Tectoptilus*, etc. There seems to be a tendency in the Fouqueidae for MA and CuA to be less branched than in the Spilapteridae and for CuP, on the other hand, to be more branched. The cuticular thickening near the wing base, which is so distinctive in some of the Spilapteridae, is only doubtfully present in the Fouqueidae; none of the specimens which I examined has the wing base clearly preserved. However, it does seem to be visible in Professor Carpenter's photograph of the type of *Fouquea needhami* Lameere, one of the two fossils which I could not find in the Paris Museum.

Fouquea is the only genus of the family known from the Commentry shales; the genus *Neofouquea* Carpenter (1967) from the Westphalian of Illinois, also appears to belong here.

Genus *Fouquea* Brongniart

Fouquea Brongniart, 1893: 372 (*pro Oustaletia* Brongniart, 1885: 66, *nec Oustaletia* Trovessart, 1885: 66); Handlirsch, 1906: 98; Lameere, 1917: 154.
Archaecompsoneura Meunier, 1909: 41; Meunier, 1909: 137.

Type species: *Fouquea lacroixi* Brongniart, 1893 (SD, Handlirsch, 1906).

The genus *Fouquea* was erected by Brongniart for *lacroixi* and *sauvagei*. In 1909, Meunier described *Archaecompsoneura superba*, which was synonymized by Lameere (1917: 154) with *Fouquea*; in the same paper, Lameere added two more species to *Fouquea*, *comstocki* and *needhami*, figures of which have never been published. In my opinion, *comstocki* is a synonym of *lacroixi*, but *sauvagei* (based on specimen 19-11) is herein referred to uncertain family position in the Palaeodictyoptera because of the very fragmental condition of the type specimen. The following is a diagnosis of the genus *Fouquea*.

Wings with relatively strong membrane. Color markings usually forming clusters of rounded spots, irregularly distributed over the wings. Hind wing broader in proximal half, similar in venation to the fore wing. Cuticular thickening near the wing base probably present, although not definitely observed; oblique supporting cross veins missing. R1 without terminal branches; Rs with 4-6 branches, the first one forked; MA usually with a long fork; MP forked several times; MA originating very close to the first fork of MP; both CuA and CuP branched; several anal veins.

Neofouquea Carpenter differs from *Fouquea* in having a narrower sc-r area and in the presence of a relatively large area of reticulation along the posterior portion of the wing. The species of *Fouquea* occurring in the Commentry shales are *lacroixi* Brongniart, *superba* Meunier, and *needhami* Lameere.

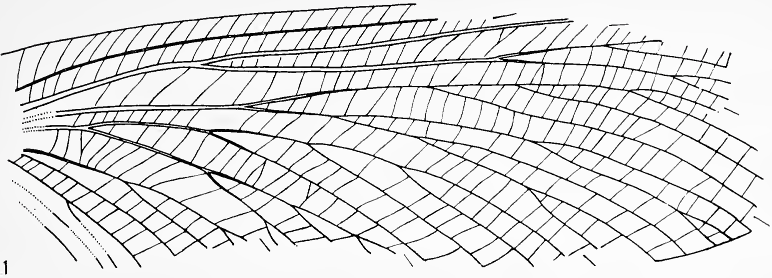
Fouquea lacroixi Brongniart
Figure 22 and 24

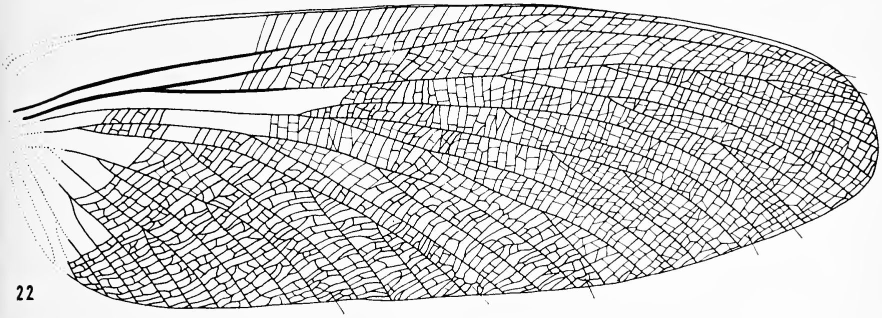
Fouquea lacroixi **Brongniart, 1893: 372, pl. 19, fig. 10; Handlirsch, 1906: 98, Lameere, 1917: 154.**

Fouquea comstocki **Lameere, 1917: 155 (New synonymy).**

This species was based by Brongniart on a single, well preserved hind wing, lacking the basal portion (specimen 19-10). Lameere (1917: 154) was of the opinion that *superba* Meunier was probably a fore wing of *lacroixi*, but although I know the latter species only by Dr. Carpenter's photograph (the original type not being found in the Paris Museum), I am convinced that it is a hind wing and also that it is specifically distinct from *lacroixi* (see figure 25). The type specimen of *comstocki* Lameere very probably is a fore wing of *lacroixi*, the venational pattern being almost identical, and the smaller size noted by Lameere, being insignificant as a specific character. At the present time, only the badly preserved reverse of the type of *lacroixi* (specimen 19-10) is in the collections of the Museum in Paris, but I was able to study the specimen of *comstocki*. The nature of the cross venational pattern is the same in both of these two specimens, but it seems to be a finer pattern in the hind wing. The following account of the species is based upon the photograph of the obverse and upon my examination of the reverse of the type of *lacroixi* and of the type specimen of *comstocki*.

Wings with a slightly convex anterior margin. Apical part broad, rounded, the apex directed posteriorly. Anterior and posterior margins almost parallel. Fore wing: length 49 mm, width 17 mm, equally broad except for the apical third. Subcostal area in the proximal third in the form of a band; Rs with 4-5 branches, the first forked twice; MA with a long simple fork; MP forked five





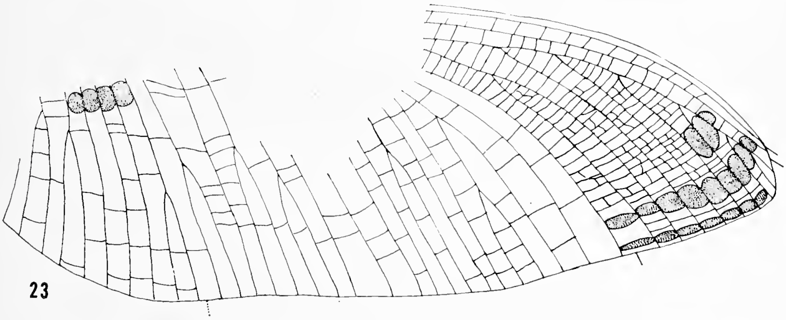
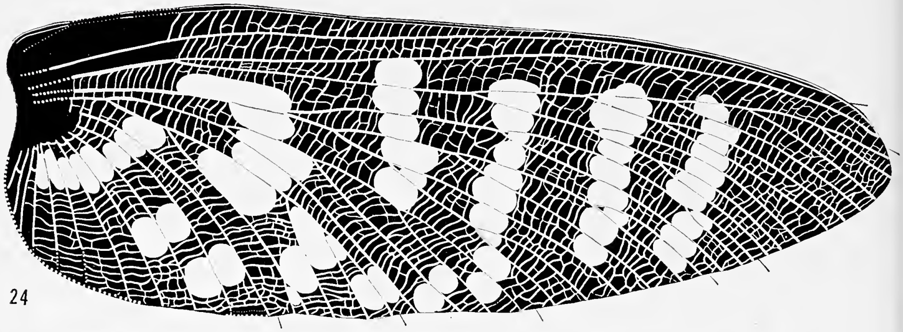


Figure 21. *Spilapteridae* inc. gen.; specimen 19-9; fore wing. Originally described as *Lamproptilia stirrupi* Brongniart, 1893.

Figure 22. *Fouquea lacroixi* Brongniart. Originally described as *Fouquea comstocki* Lameere, 1917.

Figure 23. *Compsoneura formosa* (Brongniart); specimen 19-2; fore wing. Holotype.



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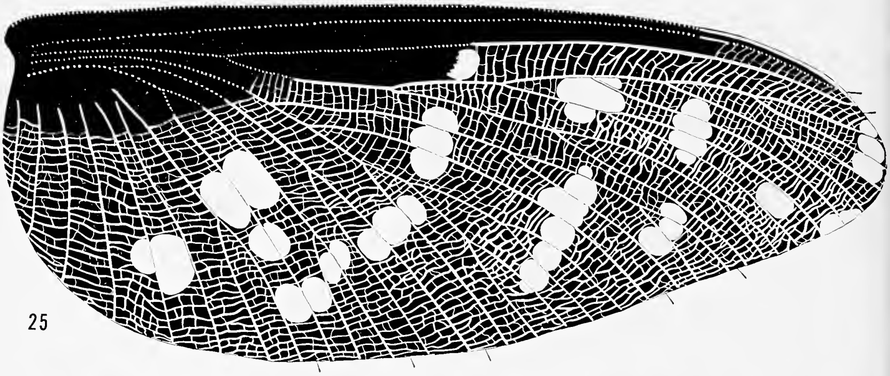

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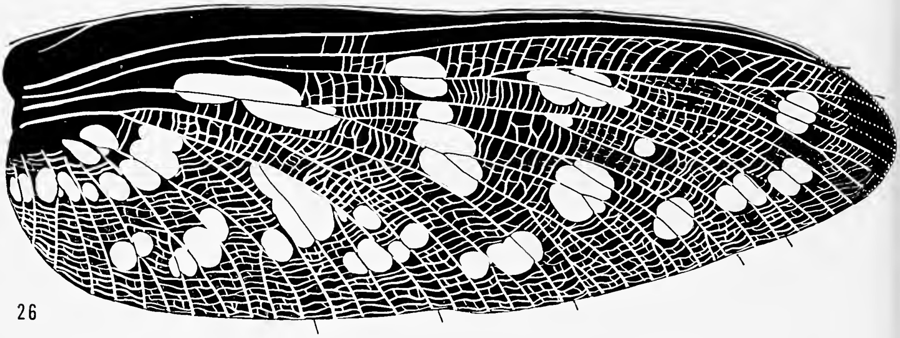

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Figure 24. *Fouquea lacroixi* Brongniart; specimen 19-10; hing wing. Holotype.

Figure 25. *Fouquea superba* (Meunier); hind wing. Holotype.

Figure 26. *Fouquea needhami* Lameere; fore wing. Holotype.

times; Cu dividing near the base; CuA with 2-3 long branches, CuP with 3-4 branches; about five anal veins, mostly forked, A1 forked twice. Hind wing: length probably 55 mm, width 18 mm (according to Brongniart). Hind wing almost uniformly broad except for the apical third; cross venation finer than in the fore wing.

The hind wing, as represented by the type specimen 19-10, differs from the fore wing described by Lameere (as *comstocki*) in having an extra branch on CuA, the second Rs branch forked, and mostly simple anal branches, the last feature being the usual one for the hind wings of spilapterids. These differences, in my opinion, are within the limits of individual variation.

Fouquea superba (Meunier)
Figure 25

Archaecompsoneura superba Meunier, 1909: 139; Meunier, 1909: 41, fig. 1; Meunier, 1909: 13, pl. 1, fig. 8; Handlirsch, 1919: 19, fig. 22.
Fouquea superba, Lameere, 1917: 154.

This species is based upon a single specimen consisting of a hind wing, lacking the anterior margin. Unfortunately, I could not locate the type specimen in the Museum, and I have had to base my account on a photograph of the fossil made by Professor Carpenter in 1938. With the exception of the cubital veins, which are indistinct, the wing venation has been worked out satisfactorily. This fossil was erroneously considered by Lameere (1917) to be the fore wing of *lacroixi*. The color pattern, shown in figure 25, is only approximate.

Hind wing: length 50 mm (according to notes by F. M. Carpenter, 1938), broadest in the proximal half; posterior margin very slightly concave in the apical third; apex slightly pointed, directed posteriorly; anal area rounded; Rs with five branches, the first forked twice; MA forked twice, MP forked five times; CuA with one branch, CuP with two branches; anal area high with about six branches; 1A forked twice.

The hind wing of *superba* differs from other species of the family in the relatively narrow cubital area, and in the small number of cubital branches; the wing itself is broader than that of *lacroixi*.

Fouquea needhami Lameere
Figure 26

Fouquea needhami Lameere, 1917: 155.

This species is based upon a well preserved specimen consisting of a fore wing, which has not been figured. Unfortunately, I was not able to find the type specimen in the Museum collection, but I have been able to use a good photograph of it made by Professor Carpenter in 1938. The venational pattern can be worked out from this photograph satisfactorily, although the color pattern given in the figure is only approximate.

Fore wing: length 55 mm, width 19 mm; anterior and posterior margins nearly parallel for the basal two-thirds of the wing; apical part slightly elongate and narrow; anterior margin very slightly concave, posterior margin convex at the CuP area; anal area moderately rounded; costal area broad at the base, abruptly narrowed distally; Rs with six branches, the first forking; MA with a long simple fork, MP with seven branches; CuA forked four times, CuP with a series of three branches; anal area with seven branches, A1 forked five times.

This species differs from all related members of the genus in having more numerous branches on Rs and in having CuA forked several times. It differs from *lacroixi* by the narrowed apical part of the wing.

The following genus, *Compsoneura,* is tentatively placed in the family Fouqueidae. As pointed out below, the absence of detailed information about the structure of the species in this genus prevents a satisfactory determination of its family affinities.

Genus *Compsoneura* Brongniart

Compsoneura Brongniart, 1893: 334 (*pro Zeilleria* Brongniart, 1885: 63; *nec Zeilleria* Bayle, 1878); Handlirsch, 1906: 104; Lameere, 1917: 149.

Type species: *Compsoneura fusca* (Brongniart) (SD, Handlirsch, 1906).

This genus was established by Brongniart for two species, *fusca* and *formosa,* both based on hind wings. It has previously been placed in the family Spilapteridae. However, in the spilapterids, both MA and CuA are usually richly branched, while CuP tends to be simple; the cross veins are usually not very numerous, and are rarely anastomosed. In the fouqueids, on the other hand, MA and CuA usually have only 1-2 branches; CuP, so far as known, is always branched, and the cross veins are very dense and very often anastomosed. The venation of *Compsoneura* seems more like that of the hind wings of the fouqueids (e.g., *Fouquea superba*) than it does that of the spilapterids; also the color pattern is very suggestive of that of *Neo-*

fouquea Carpenter, which is clearly a fouqueid. On the other hand, the cross veins, although denser than in the spilapterids, do not reach the density and strength of those of *Fouquea* and *Neofouquea.* Since I was able to find in the Museum only the type of *formosa*, a poorly preserved wing fragment, more detailed comparisons are not possible.

Wings apparently equal in length, the hind wing broader in the basal part. Color markings in the form of stripes or rounded spots; R1 without terminal branches; Rs with 4-7 branches, the first of them forked; MA usually with one branch, MP forked several times; CuA with several branches, CuP branched; several anal veins. Cross veins numerous, slightly curved, often anastomosed, denser in the distal half of the wing.

Compsoneura fusca (Brongniart)
Figure 27

Zeilleria fusca Brongniart, 1885: 63, pl. 5, fig. 2.
Compsoneura fusca Brongniart, 1893: 335, pl. 19, fig. 1; Handlirsch, 1906: 104, pl. 11, fig. 25; Lameere, 1917: 149; Handlirsch, 1919: 20.

This species was based by Brongniart on the single specimen, 19-1, consisting of almost complete hind wings, a remnant of the fore wing, and the abdomen with ovipositor and cerci. Unfortunately, the type specimen could not be found in the collection of the Museum. The following account is based upon Lameere's description and upon the photograph made by Professor Carpenter in 1938. Unfortunately, the body structures are not clearly shown in the photograph.

Hind wing: length 38 mm, width 15 mm (according to Brongniart, 1893). Hind wings short and broad, abruptly narrowing toward the apex; anterior margin almost straight; apex pointed, directed posteriorly to a slight extent; Rs with four branches, the first forked; MA probably originating near the first fork of MP, with one short branch; MP with about nine branches; CuA with one branch; CuP forked three times; about eight anal veins, mostly forked. Cross veins dense, apparently fine, often anastomosed, less abundant in the anal area.

Length of abdomen 31 mm (according to Brongniart, 1893), ending in two stout cerci, densely covered by hair; abdomen relatively narrow, composed of ten visible, subequal segments, the first and second being somewhat narrower than the others; ovipositor short, stout, and curved.

Compsoneura formosa (Brongniart)
Figure 23

Zeilleria formosa Brongniart, 1885: 63.
Compsoneura formosa, Brongniart, 1893: 336, pl. 19, fig. 2; Handlirsch, 1906: 104, pl. 11, fig. 21; Lameere, 1917: 146.

This species was based by Brongniart on specimen 19-2, which consists of a very poorly preserved fragment of a hind wing. Its assignment to *Compsoneura* was questioned by Handlirsch (1906), but Lameere accepted that position.

The hind wing is very weakly preserved, and apparently flattened, so that the branches of M and Cu cannot be clearly separated from each other. The cross veins are clearly preserved only in the apical third of the wing; in the rest of the wing only a few cross veins are visible. Nevertheless, Brongniart's assignment of *formosa* to *Compsoneura* is probably correct, since the insect shows similar patterns of cross veins and of color to that of *fusca.*

Hind wing: length 51 mm, width 19 mm. Rs with seven branches, the first forked. About eight anal veins, some of them forked. Cross veins dense and fine, often anastomosed, less abundant in the anal area.

This species differs from fusca in its larger size, in the more extensive branching of M and Cu, and in the strengthening of the costal margin by the concentration of veins there.

Family **Mecynostomatidae** fam. nov.

I am establishing this family on the genus *Mecynostomata*, represented by a single species, *dohrni* Brongniart. The type and only known specimen, which has the venation faintly preserved, was figured only roughly by Brongniart; it was subsequently incorrectly described by Handlirsch (1906), who confused the beak with a leg and referred the genus to an unidentified family in the Palaeodictyoptera. Lameere (1917) corrected some of Handlirsch's errors and noted that the genus required a separate family, although he did not propose a name for it. Lameere's description of both the body structure and the wings is very inaccurate, and his conclusions on the relationship of *Mecynostomata* to the Homoiopteridae is without real foundation.

Using glycerin on the wings to improve the visibility of the venation and a coating of ammonium chloride for the improvement of the impression of the body structures, I have been able to work out the structure of the head, with its beak, the front leg, and three

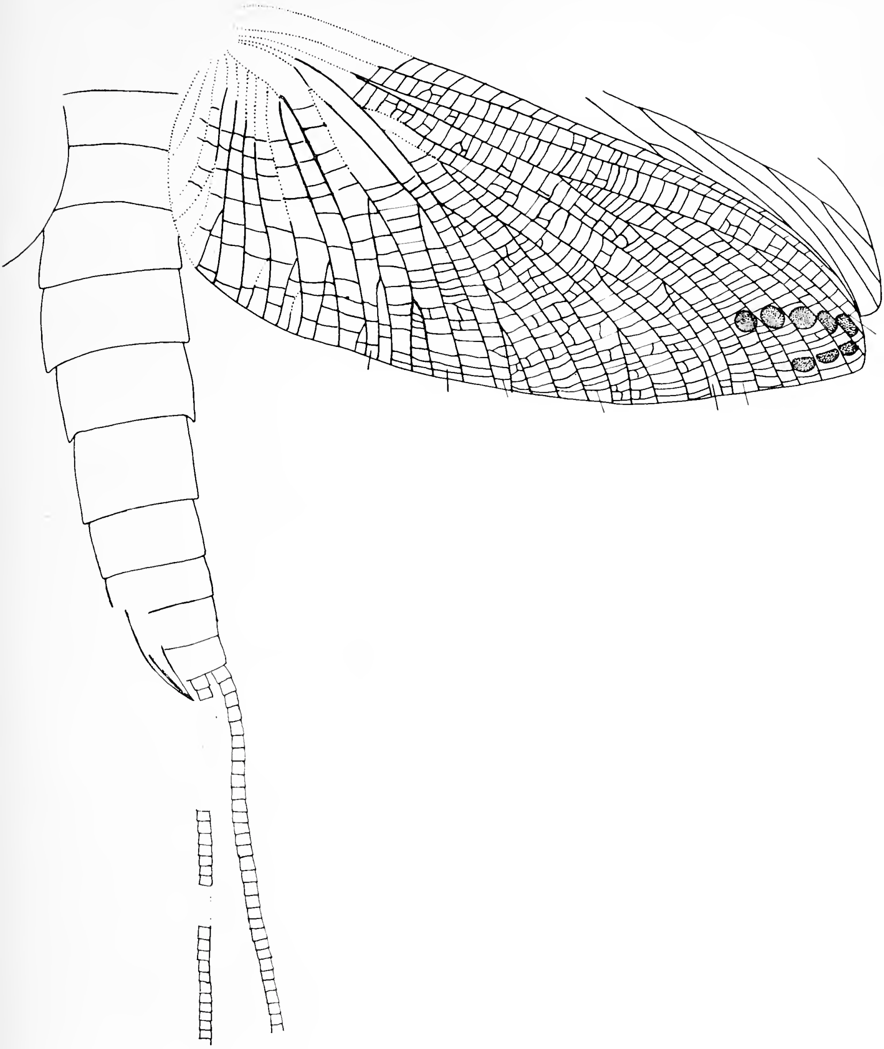

Figure 27. *Compsoneura fusca* (Brongniart); specimen 19-1. Holotype.

wings. The fore wing shows a broad subcostal area, unique among the Palaeodictyoptera, and very short Sc and Rs, both of which justify the establishment of a separate family. On the other hand, the branched MA and CuA and the nature of the cross venation are very suggestive of the Spilapteridae. In all probabliity, the Mecynostomatidae represent a specialized group derived from some spilapterid ancestors.

The structural feature which contributes most to our knowledge of the Palaeodictyoptera is the beak, which shows a long lanceolate labrum. In this specimen only, so far as known, the stylets can be seen separate from each other at the end of the beak. The outer pair of stylets are broad and shorter than the others, the inner pair are protruding distally with needle-like tips; at the same time, the terminal parts of the outer pair are slightly bent upwards, while the inner pair are completely straight. It is possible that this represents the beak in its position of actual feeding. Another feature contributed by the specimen of *dohrni* is the detailed structure of the terminal segments of the leg, showing five nearly equal tarsomeres and broadly spaced claws, with a robust arolium. The following account is different from that which has appeared in previous discussions of *Mecynostomata,* being based upon the observations which I have made on the specimen using the techniques already noted.

The wings were broad and short, almost equal in length and width; Sc short, terminating on R; subcostal area very broad in the fore wing; branches of Rs and M curving posteriorly in the fore wing; MA, MP, CuA, and CuP branched; anal area with several veins; anal area somewhat larger in the hind wing; cross veins dense, slightly irregular, sometimes anastomosed.

Body structures: Head very small, with large, conspicuous eyes. Beak long; labrum elongate; palpi long; clypeus oval. Prothoracic lobes with radiating veins and numerous cross veins. Legs relatively long; tibiae slightly longer than femur; tarsus five-segmented, with claws and arolium.

Genus *Mecynostomata* Metcalf

Mecynostomata Metcalf, 1952: 230 (*pro Mecynostoma* Brongniart, 1893: 451, *nec Mecynostoma* Graff, 1882).

Type species: *Mecynostoma dohrni* Brongniart (OD).

Brongniart originally listed five specimens in his description of *dohrni*: 37-8, 37-9, 39-10, 37-11 and 37-12. Handlirsch, in 1919,

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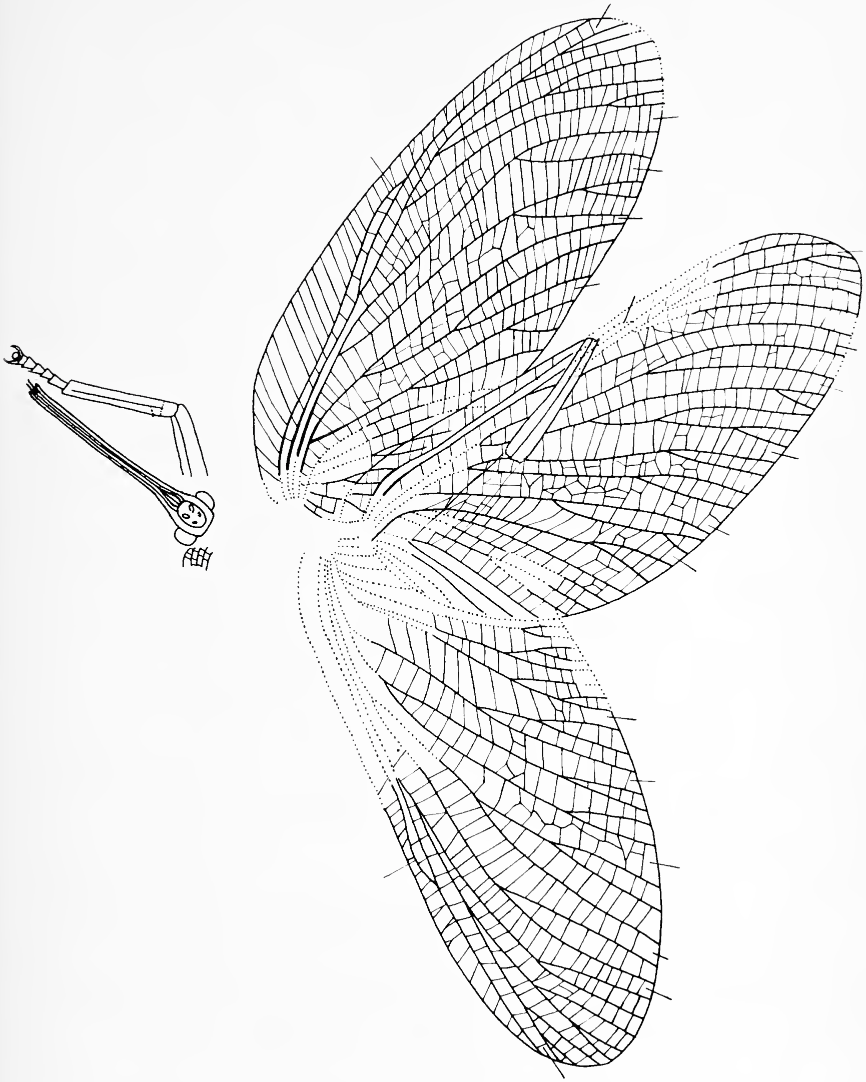
Figure 28. *Mecynostomata dohrni* (Brongniart); specimen 37-8. Holotype.



in effect designated specimen 37-8 as the lectotype of *dohrni* by placing the additional specimens in other species, as follows: 37-11 and 37-12 were placed in a distinct genus *Mecynostomites brongniarti*; 37-9 to a new genus and species *Paramecynostoma dohrnianum*; and specimen 37-10 to another new genus and species, *Pseudomecynostoma dubium*. All of these four specimens consist of wing fragments, poorly preserved and are not sufficient to permit family classification. These genera are here placed in the Palaeodictyoptera incertae familiae. The following account is based upon the lectotype specimen of *dohrni* (37-8).

Wings dark in color. Fore wings: anterior margin convex, subcostal area very broad in the basal half; Sc, R, Rs very close to each other; R and Rs bent in the apical part so as to be parallel with the anterior margin; first branch of Rs arising soon after its origin; MA weakly branched, MP with several branches; CuA forked several times, CuP sending off a few branches. Cross veins in the subcostal area long, bent and regular. In the hind wing the subcostal area is narrow, and Rs and M are not markedly curved towards the posterior margin.

The short condition of Sc apparently developed independently in several families of the Palaeodictyoptera, such as the Breyeriidae, Calvertiellidae, etc., probably in conjunction with the development of short and broad wings with numerous cross veins. It does not apparently indicate phylogenetic relationship.

Mecynostomata dohrni (Brongniart)

Figure 28

Mecynostoma dohrni Brongniart, 1893: 452, pl. 37, fig. 8; Handlirsch, 1906: 120, pl. 13, fig. 1; Lameere, 1917: 102; Lameere, 1917: 184; Handlirsch, 1919: 24, figs. 26-27; Laurentiaux, 1953: 415.
Mecynostomata dohrni, Metcalf, 1952: 230.

The lectotype specimen, 37-8, shows three faintly preserved wings, a very well preserved head, showing the clypeus, labrum and beak, with faint indications of palpi, and with almost a complete fore leg.

The clypeus is rather small in comparison with that of other Palaeodictyoptera. The labrum is elongate, lanceolate in form, a type which was quite common in the Palaeodictyoptera. The terminal parts of the inner stylets of the beak are very thin, pointed, and straight, while the outer pair is much broader, obtuse at the ends and probably flexible to some extent. The fore leg shows five well preserved tarsal segments, the first the longest; the claws are robust and the arolium is circular. For some reason, both Handlirsch and

Lameere distinguished only three tarsal segments, although five are clearly visible with the coating of ammonium chloride. The wing venation is visible in great detail only under glycerin. It was incompletely figured by Brongniart, and misinterpreted by Lameere; Handlirsch even published reconstructions of the wings, these bearing little resemblance to the actual fossil structure.

Fore wing: length 50 mm, width 21 mm. Costa sharply curved towards the base. Fore wing almost oval in shape; apex rounded, placed at about the wing axis; subcostal area abruptly broadened shortly beyond the base; Sc terminating on R just beyond midwing; Rs originating shortly before midwing, close to R1; Rs sending off five curved branches, which may be forked, the first fork originating close to the origin of Rs; MA with one, MP with 3 branches; CuA forming a long branching fork, CuP with 3 branches. Anal area with seven veins, mostly branched.

Hind wing: length 49 mm, width 23.5 mm, broadest just before midwing. The anterior margin straight, posterior margin moderately concave. The hind wing differs from the front wing in having markedly narrower costal area, in the less pronounced curvature of Rs, and the branches of M, and in having more branches on MP. Cross veins fine, dense, mostly curved, sometimes anastomosed and rather irregular.

Body structures: Head small with large conspicuous eyes. Clypeus small, oval, with two pairs of transverse ridges. Length of beak 20 mm; labrum lanceolate, reaching about one-sixth of the complete beak length. Shape of prothoracic lobes unknown, but its membrane not much sclerotized, and having radiating veins connected by numerous cross veins. Femur of fore leg 8 mm long; tibia 9.5 mm long; tarsus 3.8 mm long. The tarsus is composed of five tarsomeres, the first of them being slightly longer than the others, the last one slightly shorter than the others; claws robust, widely divergent, curved. Arolium circular, as long as the last tarsal segment. Hind leg with the tibia 15 mm long.

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The illustration on the front cover of this issue of Psyche is a reproduction of the drawing by Phillip A. Adams of an ant-lion, *Hesperoleon deflexus* Adams (Psyche, vol. 63, page 99, 1956).

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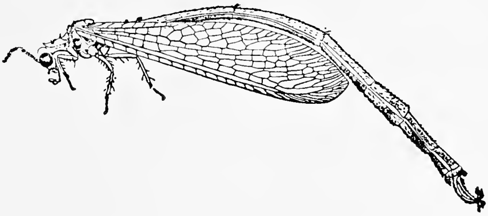

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PSYCHE

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THE MALE GENITALIA OF BLATTARIA.
1. *BLABERUS* SPP.
(BLABERIDAE: BLABERINAE)

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"Like many other genera the forms of which are variable and the specific features hard to ascertain and express, the genus *Blaberus* has been a despair to the systematist." (Rehn and Hebard, 1927). The use of male genitalia, specifically the aedeagus and preputial spines, has helped to alleviate some of the taxonomic difficulties of several species of *Blaberus*. Burmeister (1838; *in* Princis, 1946) first mentioned the preputial spines in *Blaberus trapezoideus* Burmeister and Hebard (1917) described them in *Blaberus craniifer* Burmeister and *B. atropos* (Stoll). Princis (1946) illustrated the aedeagus and prepuce of the following species of *Blaberus: giganteus* (Linn.), *trapezoideus*, *craniifer*, *atropos*, *discoidalis* Serville, *parabolicus* Walker, *anisitsi* Brancsik, and *boliviensis* Princis. Lefeuvre (1960) illustrated the genitalia of *craniifer*, Quiaoit (1961) described them for *craniifer* and *giganteus*, and McKittrick (1964) illustrated *discoidalis*.

With the exception of Princis (1946) and Lefeuvre (1960), intraspecific variations were not mentioned by the above workers. I have found considerable more variation in *Blaberus* genitalia than was indicated by Princis and Lefeuvre. In this paper I shall illustrate the male genitalia of 12 species of *Blaberus*, describe group and specific differences, including intraspecific variations, and discuss the probable evolution of the aedeagus and prepuce in this genus.

Materials and Methods

The following 5 species of *Blaberus* were available in cultures:

craniifer, *giganteus*, *parabolicus*, *atropos*, and *discoidalis*. In addition I have examined the genitalia of museum specimens of these species as well as those of *B. colosseus* (Illiger), *B. brasilianus* Saussure, *B. minor* Saussure, *B. fusiformis* Walker, *B. scutatus* Saussure and Zehntner, *B. anisitsi* Brancsik, and *B. boliviensis* Princis. Of the 14 *Blaberus* listed by Princis (1963), *assellus* (Thunb.) and *latissimus* (Herbst) were described from nymphs and are questionable species. For reasons given below, I consider *Blaberus colosseus*, which Hebard (1921) synonymized with *B. giganteus,* a valid species and *B. trapezoideus* a synonym of *B. craniifer.*

As suggested by Princis (1946) the tips of the abdomens of dried specimens were dipped in hot water for about a minute, or the specimens were placed in a relaxing chamber. Once softened, the abdomen was slit along the lateral membranes and the genitalia were removed usually without serious damage to the subgenital or supra anal plates. All specimens were treated with 10% KOH, cleared, and mounted in Permount. The hooked right phallomeres were mounted ventral side up and phallomeres L1 and L2d were mounted dorsal side uppermost. The preparations of the prepuce were spread and flattened to show the spines. This should be taken into account when examining the illustrations. Normally the prepuce partly envelopes L2d (see Fig. 121 *in* McKittrick's 1964 monograph which illustrates the folding of the prepuce in *B. discoidalis*).

Although the principal genitalic characters used are L2d and the prepuce, I have also included photographs of R2 and L1 for comparative purposes. Although these 2 phallomeres are very similar or have minor differences in all species of *Blaberus* (Figs. 1-24) they show family or subfamily differences and their inclusion should be useful in future studies of the genitalia of Blaberidae.

Wherever known I have given locality data for the illustrated specimens, and the identity of the entomologist who determined the species. The abbreviations for the sources of this material are as follows (original geographical source, if known, follows the abbreviations in the explanation of figures): (N) = Natick culture; (ANSP) = Academy Natural Sciences, Philadelphia; (MCZ) = Museum of Comparative Zoology, Harvard University; (L) = Zoological Institute, Lund, Sweden; (AMNH) = American Museum of Natural History; (USNM) = United States National Museum; (BMNH) = British Museum (Natural History). Slides of genitalia are deposited with their respective males in the above museums.

RESULTS AND DISCUSSION

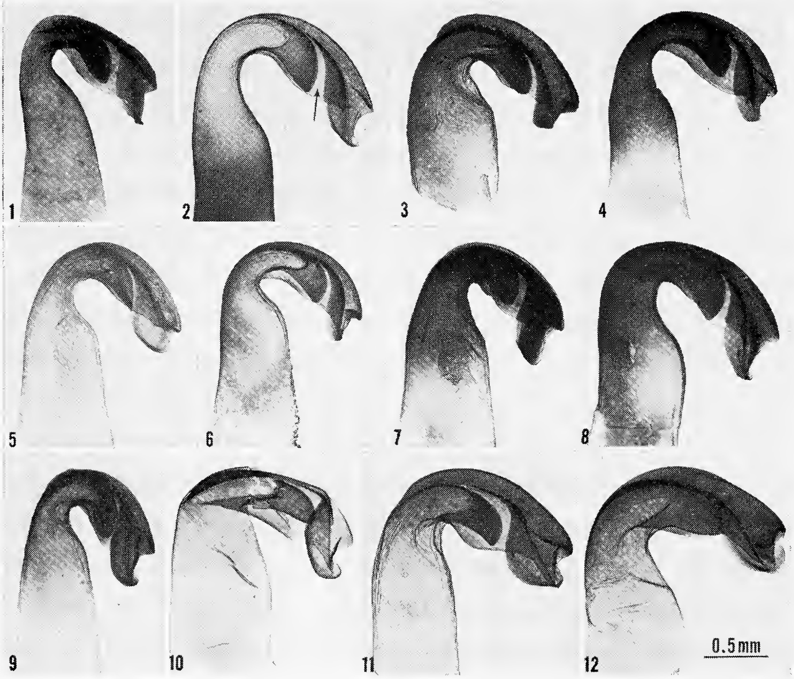
The male genitalia of Blaberidae consist of 3 main structures (McKittrick's, 1964 terminology). The right phallomere (R2) (Figs. 1-12) is a retractable hook, and all the species have a subapical incision (Fig. 2, arrow). The median sclerite (L2vm) is solidly attached (in *Blaberus* spp.) to L2d (L2 dorsal = the virga, penis, or aedeagus) (Fig. 52). The prepuce (mantle of Hebard's, 1917 terminology) is a soft, flexible membrane (Fig. 52) bearing characteristic spines, or truncate or rounded sclerotized elevations. The left side of the prepuce is solidly attached by sclerotization to the side of the L2 phallomere, whereas the right side is usually connected by a flexible membrane which permits it to fold partly around the virga. One of the sclerites (L1) (Figs. 13-24) of the left phallomere in all the species of *Blaberus* studied are more or less similar and have a heavily sclerotized cleft, noted by McKittrick (1964).

Based on body size, color, and shape of the pronotum, Hebard (1931) placed *fusiformis*, *brasilianus*, *anisitsi*, and *scutatus* in the *Brasilianus* Group of the genus. Princis (1946) divided 8 species into the *Giganteus* and *Atropos* Groups, basing his divisions on the shape of L2d and the spines present on the prepuce. He did not examine the genitalia of *minor*, *brasilianus*, *fusiformis*, and *scutatus*, but suggested that the *Brasilianus* Group, established by Hebard, probably should be included in the *Atropos* Group. As a result of my examination of the 4 species not investigated by Princis, I believe Hebard was correct in erecting the *Brasilianus* Group and I place the above 4 species in this group.

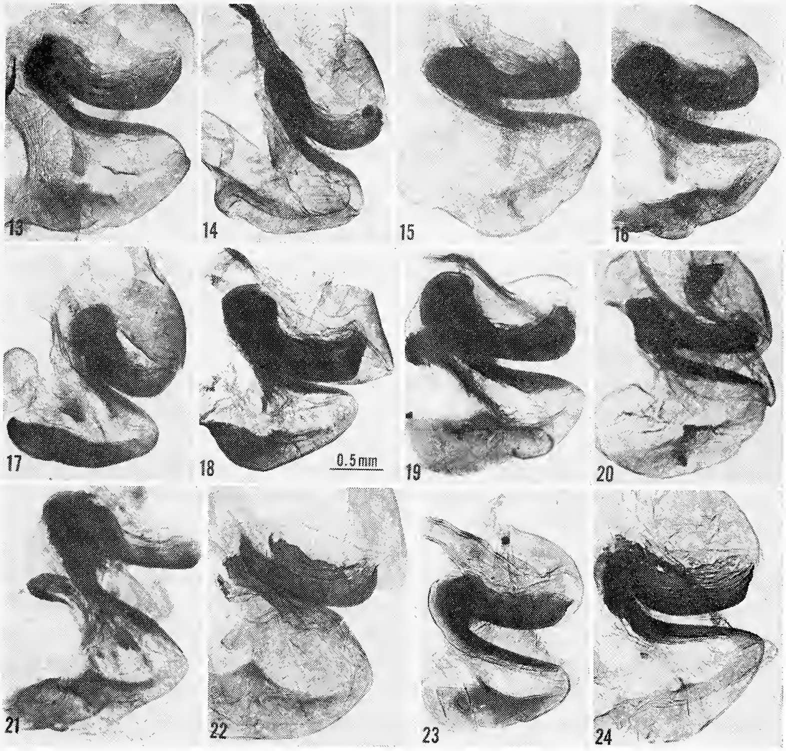
Species of *Blaberus* can be readily placed in their respective Groups, by the shape of the virga and preputial spines. However, variation is such that specific determination is often difficult. The 3 *Blaberus* Groups may be distinguished in the following key:

1. L2d recurved dorsally and slightly to the right, usually forming a hooklike structure (Fig. 52). Extending dorsally and laterally on the left, about where L2vm and L2d are solidly joined, is a sclerotized tumorlike outgrowth (Fig. 52, T). There are no large truncate elevations and all of the spines on the preputial membrane are relatively small (Figs. 28-40, 47-57, 62-74, 215) .... *Giganteus* Group.

   L2d not hookshaped. Tumorlike outgrowth on the left side absent. Prepuce with anterior truncate or rounded elevations almost always present on the left, and sometimes on the right side of the preputial membrane .... 2.



Figs. 1-12. Right hooked phallomere (R2) of *Blaberus* spp. 1-2. *Giganteus* Group. 1. *B. craniifer*. (ANSP), Juxtlahuaca Cave, Colotlipa, Mexico (det. as *B. trapezoideus* by Rehn). 2. *B. giganteus*. (ANSP), Muzo, Colombia (arrow indicates the subapical incision). 3-6. *Brasilianus* Group. 3. *B. scutatus*. (ANSP), Ceara Mirim, Rio Grande do Norte, Brazil. 4. *B. fusiformis*. (ANSP), Provincia Sara, Dept Vera Cruz, Bolivia. 5. *B. brasilianus*. (ANSP), Natal, Brazil. 6. *B. minor*. (ANSP), Mission Tacaaglé, Formosa, Argentina (det. Hebard). 7-10. *Atropos* Group. 7. *B. atropos*. (MCZ), Mexico. 8. *B. parabolicus*. (N), Ecuador. 9. *B. discoidalis*. (N), Panama. 10. *B. boliviensis*. (L), Guayaquil, Ecuador (det. Princis). 11-12. *Brazilianus* Group. 11. *B. colosseus*. (ANSP), Fyzabad, Trinidad. 12. *B.* sp. *D* (probably *colosseus*). (ANSP), St. Laurent du Maroni, French Guiana (from specimen shown in Fig. 208). (all to scale shown in Fig. 12).



Figs. 13-24. Left phallomere (L1) of *Blaberus* spp. 13-14. *Giganteus* Group. 13. *B. giganteus.* (ANSP), Muzo, Colombia. 14. *B. craniifer* (ANSP), Juxtlahuaca Cave, Colotlipa, Mexico (det. as *B. trapezoideus* by Rehn). 15-18, 22. *Brasilianus* Group. 15. *B. brasilianus.* (ANSP), Natal, Brazil. 16. *B. scutatus.* (ANSP), Ceara Mirim, Rio Grande do Norte, Brazil. 17. *B. minor.* (ANSP), Villa Ana F.C.S.F., Argentine Republic (det. Hebard). 18. *B. fusiformis.* (ANSP), Santa Cruz de la Sierra, Bolivia (det. Hebard). 19-21, 23, 24. *Atropus* Group. 19. *B. parabolicus.* (N), Ecuador. 20. *B. discoidalis* (N), Panama. 21. *B. atropus.* (N), Trinidad. 22. *B. colosseus.* (ANSP), Caparo, Trinidad (det. Hebard). 23. *B. anisitsi.* (L), (det. Princis). 24. *B. boliviensis.* (L), Guayaquil, Ecuador (det. Princis). (all to scale shown in Fig. 18).

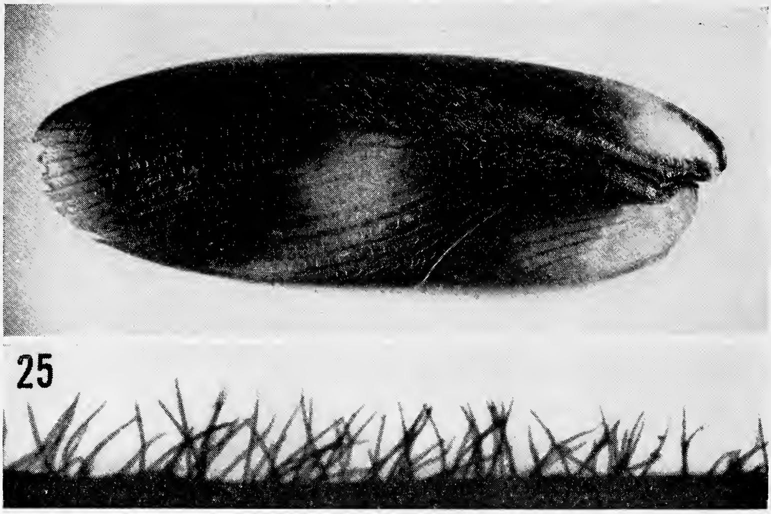
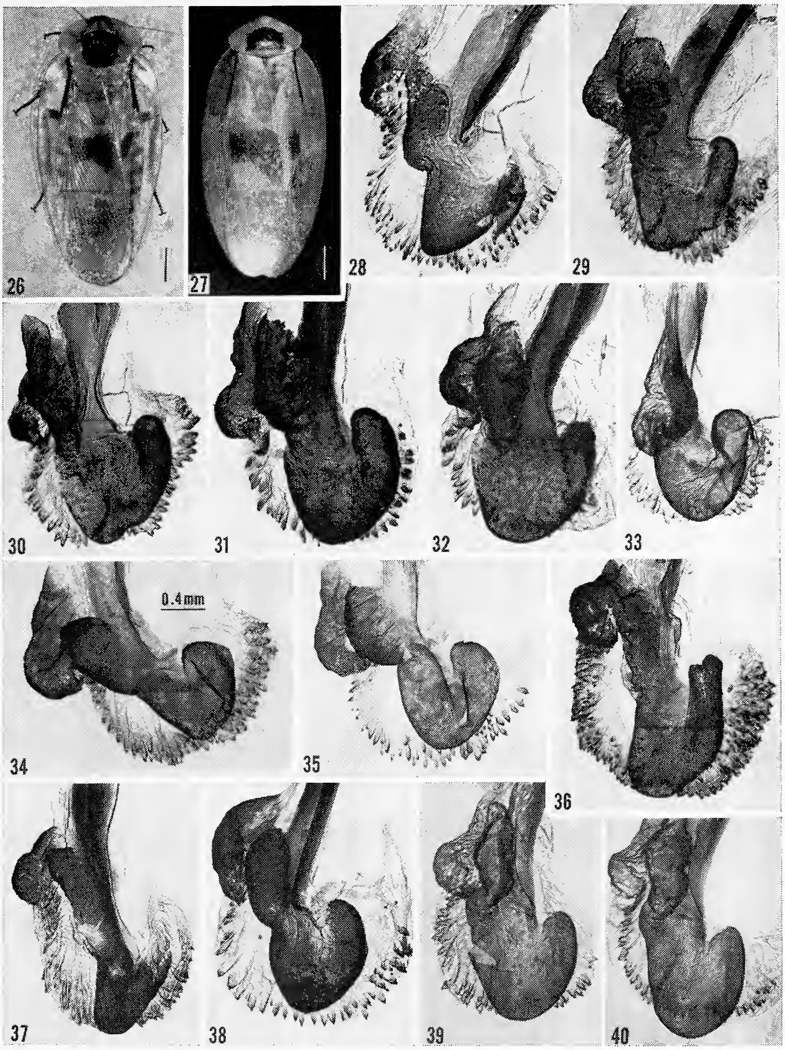


Fig. 25. Upper. Tegmen of *B. craniifer* showing the distribution of the long setae on the marginal and scapular fields. Lower. Anterior view of part of the tegmen showing the characteristic hairlike setae.

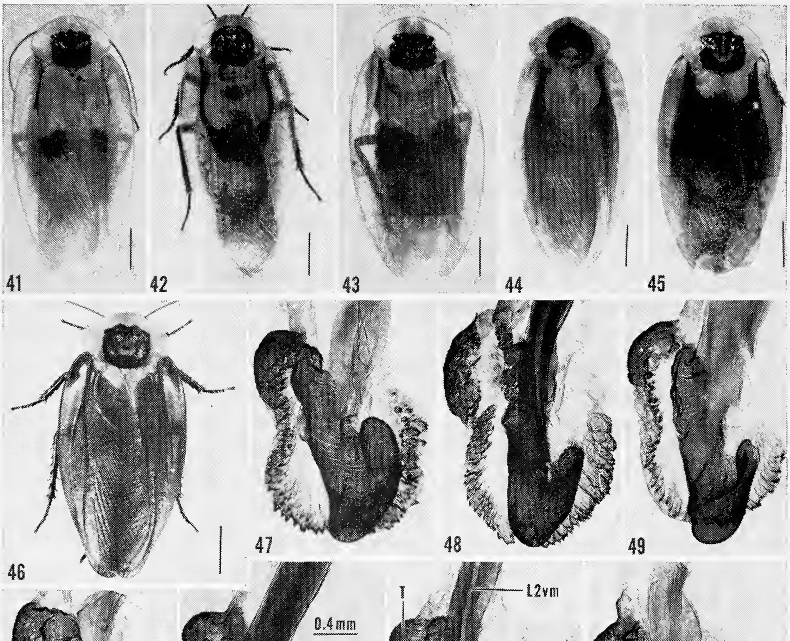
2. Anterior elevations usually rounded, present on the left and often on the right sides. Differences in size between anterior elevations on the right and left sides not great. Preputial spines numerous, usually on the left and right sides and often occur in more than a single row (Figs. 76, 77, 79-82, 84-91, 93-111, 211-214). In *colosseus* the left preputial spines usually occur in a single row (Figs. 116-129) .... *Brasilianus* Group.

Truncate or rounded elevations usually present only on the left side and generally much larger and more robust than spines on the right. Preputial spines usually less numerous than in the *Brasilianus* Group, and are often arranged (when present) in a single row on the left, and single or sometimes double or partial double row on the right. Spines on the right side usually more numerous than on the left (Figs. 133-153, 155-170, 174-198, 200, 201, 203, 204, 210) .... *Atropos* Group.

Giganteus Group. — Two species of *Blaberus* (*giganteus*, Figs. 26, 27; *craniifer*, Figs. 41-46, 58-61) belong to this group. A useful tegminal character which Princis (1946) described can be used to distinguish *B. craniifer* from all other species of the genus. In *craniifer* the marginal field and scapular field of the tegmina have diffuse projecting hairs (Fig. 25). According to Princis, no other



Figs. 26-40. *B. giganteus* (*Giganteus* Group). 26. (N). 27. (USNM), St. Jean, French Guiana (det. as *B. colosseus* by Hebard) (scale = 10 mm). 28-40. L2d and prepuce (all to scale shown in Fig. 34). 28. (USNM) (from specimen shown in Fig. 27). 29. (USNM), Cabima, Panama. 30. (USNM), Ft. Clayton, Canal Zone. 31. (AMNH), Barro Colorado Island, Canal Zone. 32. (USNM), Chilibrillo Cave, Buenos Aires, Canal Zone. 33. (USNM), Puerto Berrio, Colombia. 34-35. (ANSP), Muzo, Colombia. 36. (USNM), Atlantico, Colombia. 37. (AMNH), Colombia. 38. (AMNH), Caripito, Venezuela. 39-40. (N).



Figs. 41-57. *B. craniifer* (*Giganteus* Group). 41-46. Adult males (scale = 10 mm). 41. (USNM), Cordoba, Mexico (det. as *B. trapezoideus* by Rehn). 42. (N). 43. (USNM), Rancho Qemado, Rt. 85, Mexico. 44. (USNM), Teapa, Tabasco, Mexico. 45. (USNM), Key West, Florida. 46. (N). 47-57. L2d and prepuce (all to scale shown in Fig. 51). 47. (USNM), Mexico (from specimen shown in Fig. 41). 48. (USNM), Mexico

Blaberus has this character, although I have seen a few very minute hairs in some specimens of *B. giganteus*.

In *craniifer* the tumorlike sclerotized outgrowth on the left side of L2 extends caudally for a short distance and usually merges gradually into the border of the prepuce where small spines begin and form a fringe around the membrane. The sclerotized extension of the lateral outgrowth varies somewhat in length but is generally distinct (Figs. 47-51, 53-57, 62-64, 66-74). Exceptions are seen in Fig. 52 and 65. In *B. giganteus* there is usually little or no sclerotized extension from the tumorlike outgrowth into the preputial membrane, so that the preputial spines begin more abruptly at the outgrowth (Figs. 28-35, 38-40). Exceptions to this are shown in Fig. 36 and 37. In both species the preputial spines may occur in more than a single row, and in some individuals there may be a reduction in the number of preputial spines (Figs. 37, 65, 70, 74).

If Princis' (1946) tegminal character is valid for *B. craniifer* then I have not seen any correctly determined specimens of *B. trapezoideus*. All the specimens determined by Hebard or Rehn as *trapezoideus* (Figs. 41, 58-61) have hairy tegmina and I therefore consider them to be light forms of *B. craniifer*. The genitalia of these *"trapezoideus"* (e.g., Figs. 47, 63, 64, 66) are indistinguishable from *craniifer*. Two specimens identified as *B. trapezoideus*, received from the University Zoological Museum, Copenhagen, Denmark were actually *B. craniifer* (Costa Rica) and *B. parabolicus* (Peru). According to Princis (1946) the preputial spines of *trapezoideus* are similar to *giganteus* but are smaller and more numerous, though always clearly separated from each other. Considering the variation in size, number, and spacing of preputial spines I doubt if this character can be used to distinguish *trapezoideus* from *giganteus*. Princis also (1958) states that the pronotum of *trapezoideus* is laterally truncated with approximately parallel sides. Some individuals of our light-phased form of *craniifer* (in culture) (Fig. 42) also have the pronotum laterally truncate. It is possible that *trapezoideus* and *craniifer* are simply variants of the same species. The type localities of the 2 spp. of the

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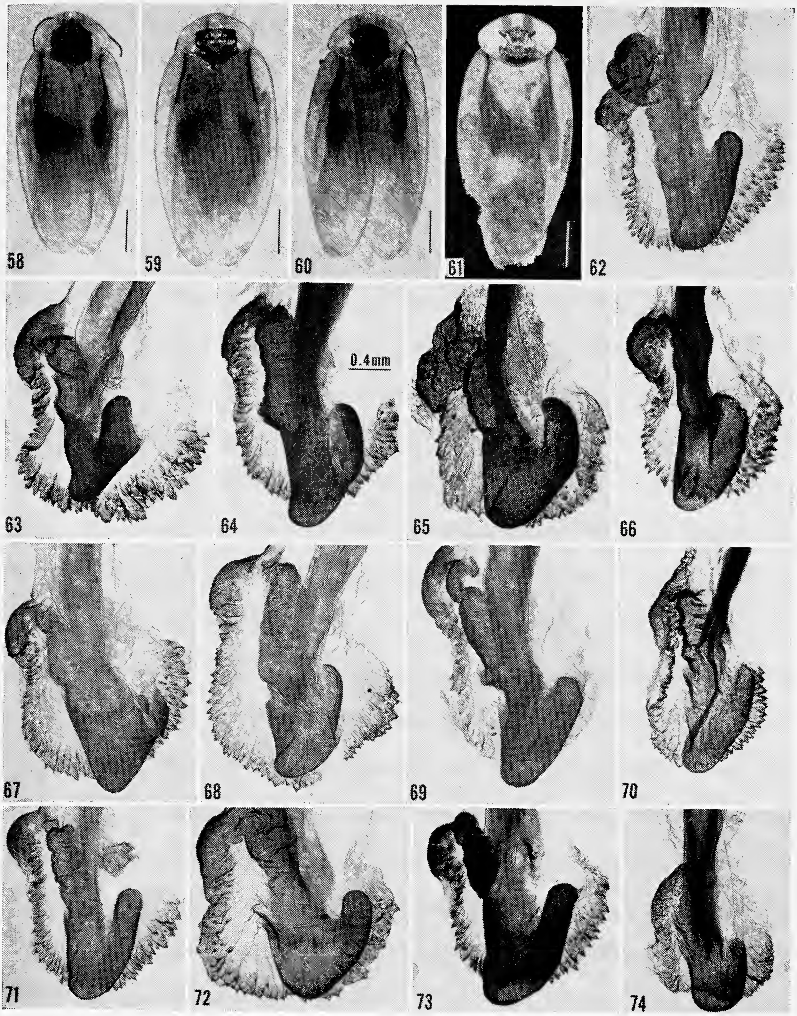
(from specimen shown in Fig. 43). 49. (USNM), Vera Cruz, Mexico. 50. (USNM), Tuxtepec, Oaxaca, Mexico (labelled *trapezoideus*). 51. (USNM), Mexico (from specimen shown in Fig. 44). 52. (MCZ), Chichén Itzá, Yucatan, Mexico. 53. (USNM), El Salvador. 54. (USNM), San Salvador, El Salvador. 55. (USNM), Benque Viejo, British Honduras. 56. (MCZ), Colón, Panama. (Abbreviations for Fig. 52. L2d = dorsal left phallomere; L2vm = ventromedial left sclerite (fused to L2d); P = prepuce; T = tumorlike outgrowth.)



Figs. 58-74. *B. craniifer* (*Giganteus* Group). 58-61. Adult males (scale = 10 mm). 58. (ANSP), Guatemala. 59. (ANSP), Vera Cruz, Mexico. 60. (ANSP). 61. (ANSP), Juxtlahuaca Cave, Colotlipa, Mexico. (These 4 males were determined as *B. trapezoideus* by Rehn, or Hebard.) 62. (MCZ), Havana, Cuba (det. Rehn). 63. (USNM), Santiago-Vegas, Cuba. 64. (ANSP) (from specimen shown in Fig. 60). 65. (AMNH), Turrialba, Costa Rica. 66. (ANSP) (from specimen shown in Fig. 61). 67. (MCZ), Havana, Cuba. 68-69. (MCZ), Colón, Panama. 70. (N). 71. (MCZ). 72. (ANSP), San Miguel, Vera Paz, Guatemala (det. as *B. colosseus* by Hebard). 73. (USNM), Florida (from specimen shown in Fig. 45). 74. (N).

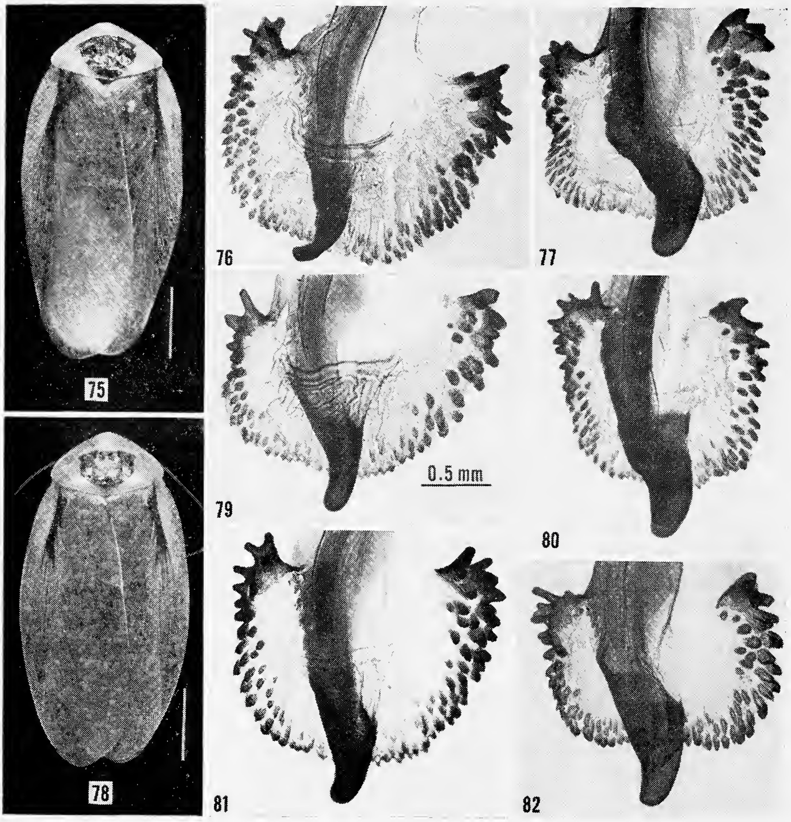
Giganteus Group are: *giganteus* — "America"; *craniifer* — Cuba. (see addendum regarding *trapezoideus*).

Although color markings are variable in several species of *Blaberus*, they are especially so in *B. craniifer*. This species is represented by light (Figs. 41-43) and dark (Figs. 45, 46) forms with intermediates (Fig. 44) connecting the extremes. Markings of light phased individuals resemble *B. giganteus* (cf. Figs. 26, 27). Lefeuvre (1960) has described some color varieties which occurred in his laboratory culture of *craniifer* and we have cultures of both light and dark forms which crossed successfully. Lefeuvre claims that rearing *craniifer* for a number of years favored the formation of an "artificial subspecies" which differed from the original in 1) coloration of the pronotum, 2) general coloration, in particular the male, and 3) the morphology of the penis and prepuce. Lefeuvre suggested that the original *B. craniifer* may have hybridized with a closely related species. The variations in *craniifer* which Lefeuvre described can be seen in museum specimens from different geographic localities. I have never seen any dark forms of *B. giganteus* comparable to dark *craniifer*.

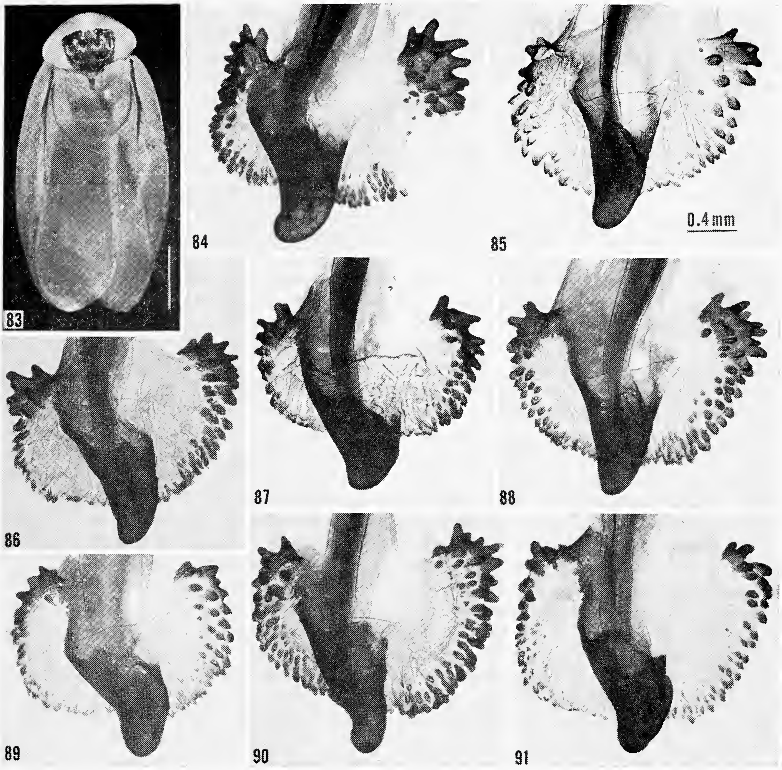
Brasilianus Group. — The 5 species in this Group, namely, *scutatus* (Fig. 75), *brasilianus* (Fig. 78), *fusiformis* (Fig. 83), *minor* (Fig. 92), and *colosseus* (Figs. 112-115), show some genitalic differences in L2d and preputial spines but variation is so great within 4 of these species (Figs. 76, 77, 79-82, 84-91, 93-111), that specific determinations, using genitalia alone, are often impossible. In some individuals of *fusiformis* (Figs. 85-87, 89, 91) and *minor* (Figs. 94-95, 100, 106) there is a marked reduction or loss of preputial spines and they may occur in a single row, usually on the left side.

Characteristic of this group is the anterior elevations which are generally fused on the right side, and are about the same size as those on the left. Rarely are the anterior spines on the right larger than those on the left (e.g., Figs. 84, 85, 88). The preputial spines decrease only slightly in size from the anterior to posterior position. When the spines are numerous and occur in more than a single row they are often closely spaced and form a more or less dense uniform fringe around the preputial membrane (e.g., Figs. 76, 77, 79-82, 88, 90, 93, 97, 99, 101, 105).

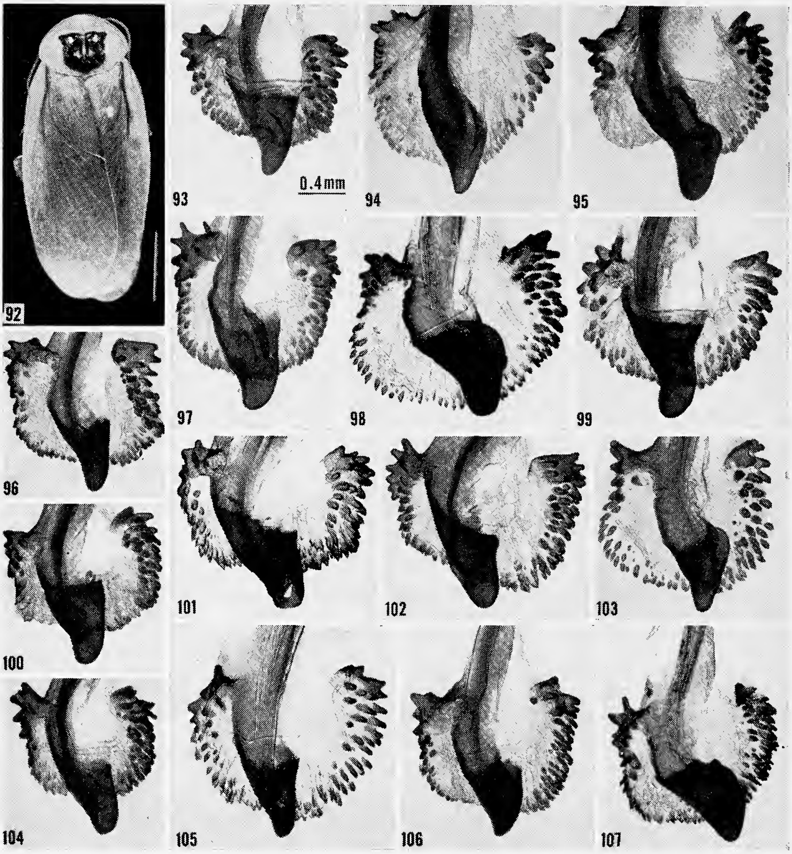
Hebard (1921, p. 148) stated, "From a study of the material in the Philadelphia collections, as well as specimens recently received from the Guianas, we are finally convinced that *B. colosseus* (Illiger) was based on a mere individual variation of *giganteus*, unworthy of nominal recognition." Princis (1963) followed Hebard and listed



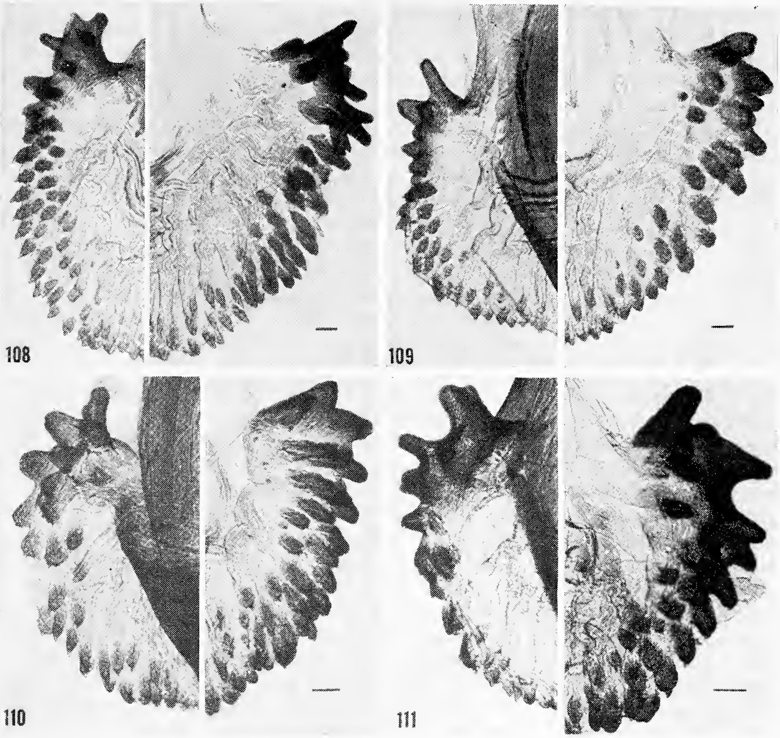
Figs. 75-82. *Brasilianus* Group. 75-77. *B. scutatus*. 75-76. (ANSP), Pernambo, Brazil (paratype of *B. scutata* var. *obscura* S. and Z.). 77. (ANSP), Ceara Mirim, Rio Grande do Norte, Brazil. 78-82. *B. brasilianus*. 78-79. (ANSP), Natal, Brazil. 80. (ANSP), Independencia, Parahybo, Brazil. 81. (MCZ), Brazil. 82. (USNM), Natal, Brazil. (Scale for adults = 10 mm; all genitalia to scale shown in Fig. 79.)



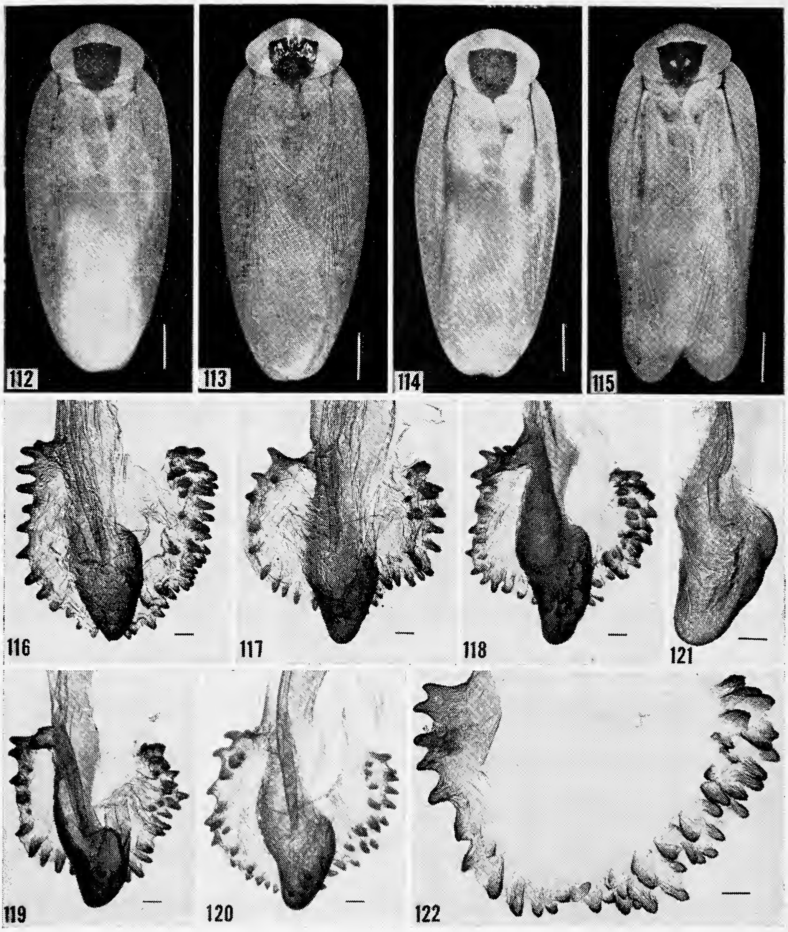
Figs. 83-91. *B. fusiformis* (*Brasilianus* Group). 83. Adult male (scale = 10 mm). (ANSP), Santa Cruz de la Sierra, Bolivia (det. Hebard). 84-91. L2d and prepuce (all to scale shown in Fig. 85). 84. (ANSP), Carumbo, Matto Grosso, Brazil (a portion of the prepuce on the right side is missing). 85. (ANSP), San Francisco, Argentina. 86. (ANSP), Provincia Sara, Dept. Vera Cruz, Bolivia (det. Hebard). 87. (ANSP), Bolivia (from specimen shown in Fig. 83). 88. (ANSP), Provincia Sara, Dept. Vera Cruz, Bolivia. 89. (ANSP), Jundiahy, Brazil. 90. (USNM), Utiariti Rio, Matto Grosso, Brazil. 91. (ANSP).



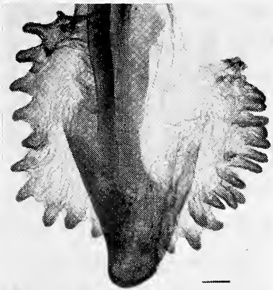
Figs. 92-107. *B. minor* (*Brasilianus* Group). 92. Adult male (scale = 10 mm). (ANSP), Argentina (det. Hebard). 93-107. L2d and prepuce (all to scale shown in Fig. 93). 93. (ANSP), Paraguay. 94. (USNM), Natal, Brazil. 95. (USNM), Brooklin, São Paulo, Brazil. 96. (ANSP), Mission Tacaaglé, Formosa, Argentina. 97-98. (ANSP), Formosa, Argentina. 99. (ANSP), Argentina (from specimen shown in Fig. 92). 100-102. (ANSP), Chaco del Santiago del Estero Bords du Rio Selado Environs D'Icaño, Argentina. 103. (ANSP), Formosa, Argentina. 104. (ANSP). 105. (ANSP), Chaco de Santiago del Estero Rio Salado, Argentina. 106-107. (ANSP), Gran Chaco, Argentina.



Figs. 108-111. *Brasilianus* Group. Right and left sides of the prepuce. 108. *B. scutatus* (from Fig. 76). 109. *B. brasilianus* (from Fig. 79). 110. *B. minor* (from Fig. 99). 111. *B. fusiformis* (from Fig. 87). (scale = 0.1 mm).



Figs. 112-122. *B. colosseus* (*Brasilianus* Group). 112-115. Adult males (scale = 10 mm). 112. (ANSP), Caparo, Trinidad. (This specimen is Fig. 4 in Hebard, 1916.) 113. (ANSP), Fyzabad, Trinidad. 114. (ANSP), Caparo, Trinidad. (This specimen is Fig. 5 in Hebard, 1916.) 115. (MCZ), Mexico. 116-122. L2d and prepuce (scale = 0.2 mm). 116. (ANSP) (from specimen shown in Fig. 112). 117. (ANSP) (from specimen shown in Fig. 113). 118. (MCZ) (from specimen shown in Fig. 115). 119. (MCZ), Mexico. 120. (USNM), Trinidad. 121-122. (ANSP) (from specimen shown in Fig. 114; L2d and prepuce have been mounted separately).



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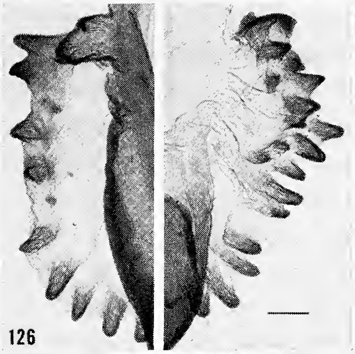

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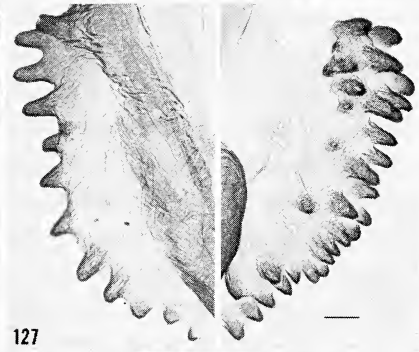

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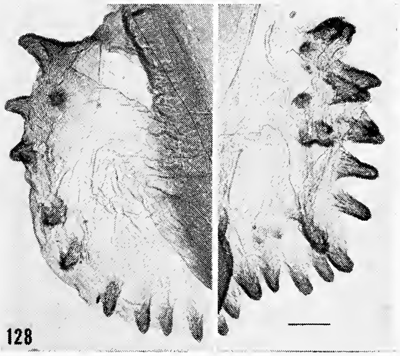

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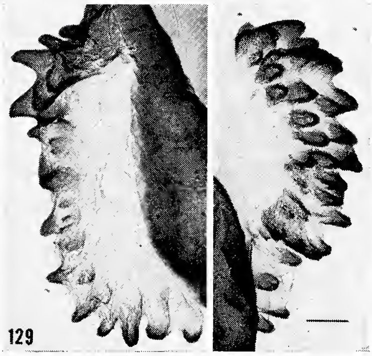

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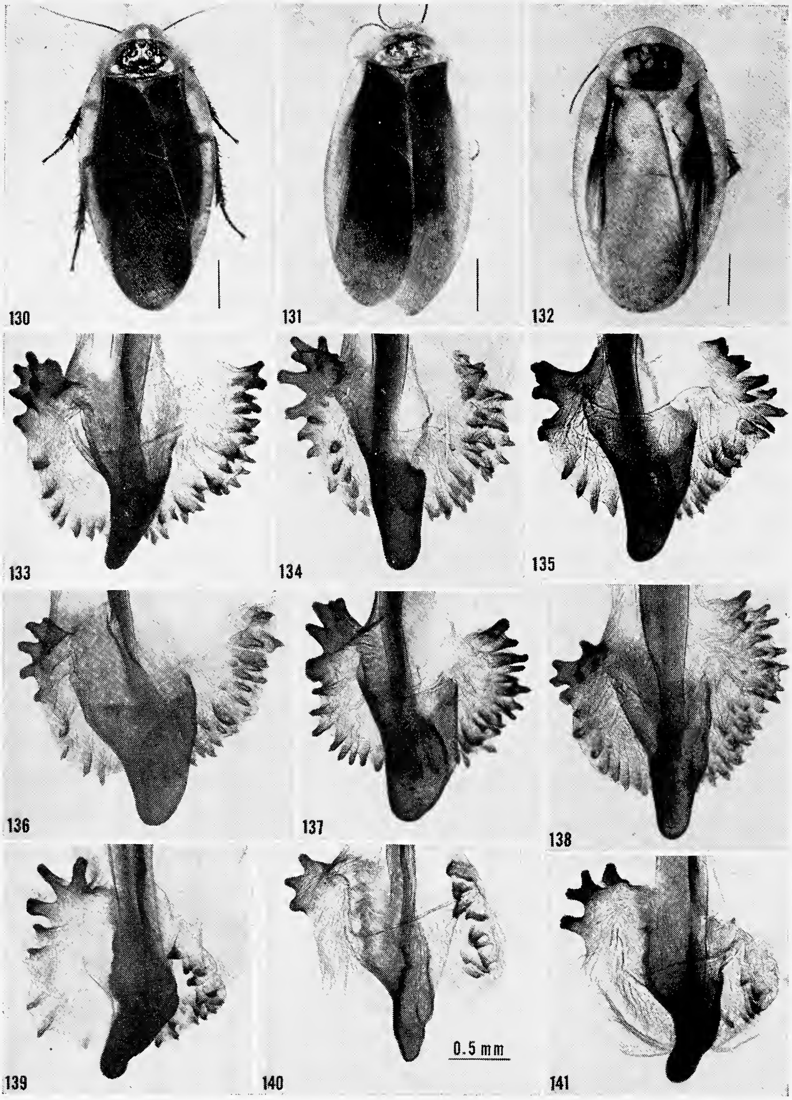
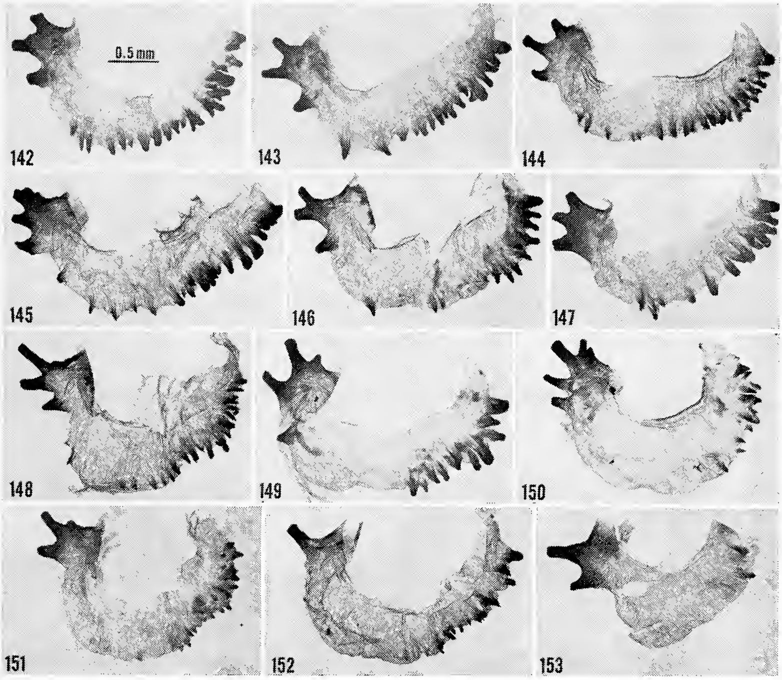
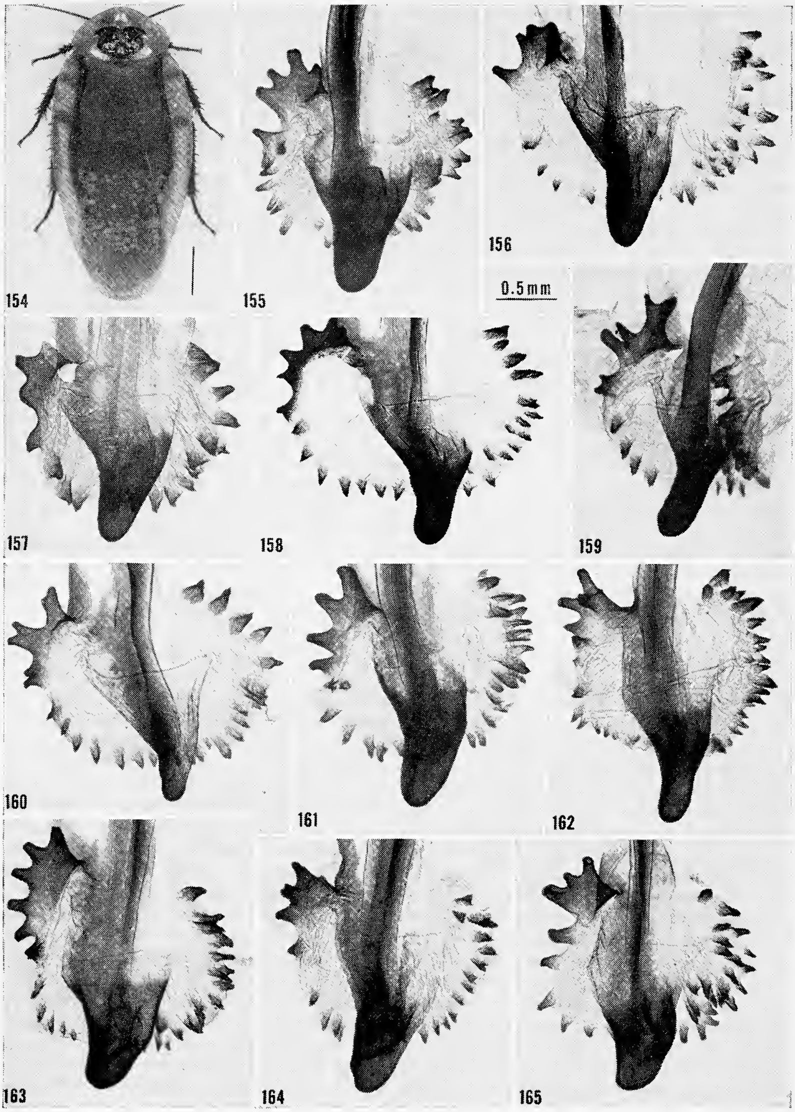
Figs. 123-129. *B. colosseus* (*Brasilianus* Group). 123. (AMNH), Trinidad. 124. (USNM), Trinidad (some of the anterior elevations on the left side are broken off). 125. (AMNH), Rancho Grande, near Maracay, Venezuela. 126-129. Right and left sides of the prepuce. 126. (MCZ) (from Fig. 119). 127 (ANSP) (from Fig. 116). 128. (ANSP) (from Fig. 117). 129. (MCZ) (from Fig. 118) (scale = 0.2 mm).



Figs. 130-141. *B. atropos* (*Atropos* Group). 130-132. Adult males (scale = 10 mm). 130. (N), Trinidad. 131. (MCZ), Mexico. 132. (USNM), Colombia (taken in quarantine on bananas at Charleston, S.C.). 133-141. L2d and prepuce (all to scale shown in Fig. 140). 133. (MCZ) (from specimen shown in Fig. 131). 134. (USNM) (from specimen shown in Fig. 132). 135. (USNM), Georgetown, British Guiana. 136-138. (USNM), Trinidad. 139-141. (N), Trinidad.



Figs. 142-153. Prepuce of *B. atropos*. From Natick culture which originated in Trinidad (all to scale shown in Fig. 142).



Figs. 154-165. *B. parabolicus* (*Atropos* Group). 154. Adult male. (N), Puraquequara, Rio Negro, Amazonas, Brazil (scale = 10 mm). 155-165. L2d and prepuce (all to scale shown in Fig. 158). 155. (AMNH), Colombia. 156. (MCZ), Napo or Marañon (Ecuador or Peru, northern Andes). (Type specimen of *Blabera armigera* Scudder.) 157. (MCZ), Upper Amazon? 158. (USNM), Gavião, Rio Negro, Amazonas, Brazil. 159. (N), Ecuador.

Blaberus colosseus as a synonym of *B. giganteus.* However, Hebard (1916, p. 292) described the prepuce of *colosseus* as follows: ". . . The surrounding mantle having the free dorsal and distal margins fringed with small blunt chitinous projections, these longer and more like short blunt teeth of a comb on the sinistral margin." This description does not fit a member of the *Giganteus* Group. I have examined the male genitalia of several specimens including some which Hebard used in his study and conclude that *colosseus* is not *giganteus.* The genitalia of *colosseus* (Figs. 116-129) differs markedly from that of *giganteus* (Figs. 28-40). *B. colosseus* phenotypically resembles *giganteus*, but it is paler in color (Hebard 1916); it is the largest member of the *Brasilianus* Group, and the only species in this group which in size, color, and markings (some individuals) resembles *B. giganteus.*

The prepuce of *colosseus* combines features of both the *Brasilianus* and *Atropos* Groups. The relatively small anterior elevations on the left side of the prepuce are not much larger than the spines on the right (Figs. 116-120, 122-129) a characteristic of the *Brasilianus* Group. However, the preputial spines of *colosseus* are all relatively large, fairly widely separated, particularly on the left side, and resemble these spines in the *Atropos* Group. With few exceptions (Figs. 184, 188) species of the *Atropos* Group have anterior truncate or rounded elevations on the left side of the prepuce that are much larger and more robust than the spines on the right side (Figs. 133-153, 155-170, 174-183, 185-187, 189-198, 200, 201, 203, 204, 210).

One specimen from Guatemala, determined as *B. colosseus* by Hebard is actually *Blaberus craniifer* (Fig. 72). Two specimens (ex Canal Zone and French Guiana) determined by Hebard as *colosseus* are *giganteus* (Figs. 27, 28). The specimens which Hebard claimed were *colosseus* came from Trinidad, Guatemala, Costa Rica, and Panama. I have seen 9 specimens of *colosseus*; 6 were from Trinidad, 2 from Mexico, and 1 from Venezuela. One specimen from French Guiana is probably *colosseus* (Figs. 208, 214). The distribution of this species must await an examination of additional material.

Atropos Group. — Five species, *atropos* (Figs. 130-132), *parabolicus* (Fig. 154), *discoidalis* (Fig. 173), *boliviensis* (Fig. 199), and *anisitsi* (Fig. 202) belong to this group.

The armament on the preputial membrane shows the greatest varia-

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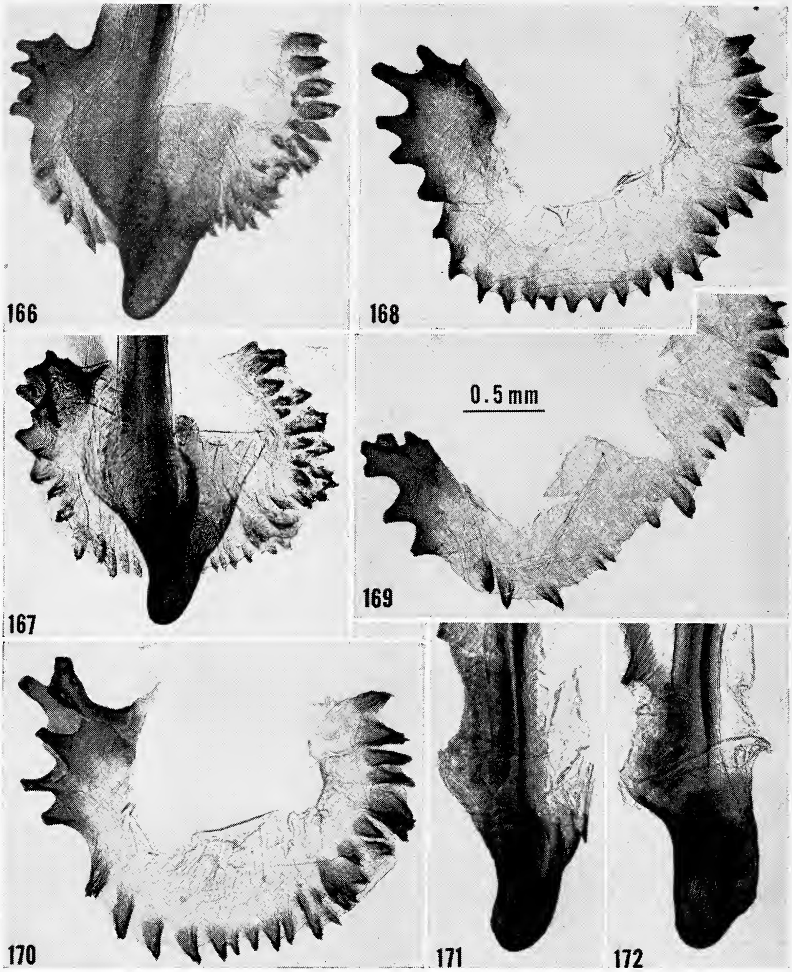
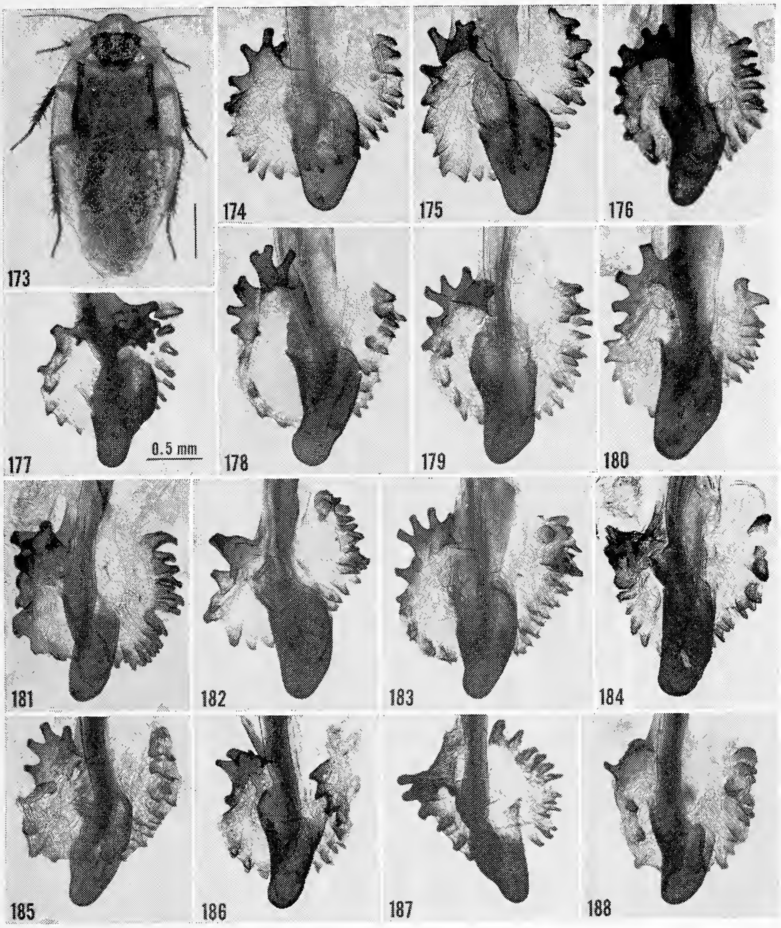
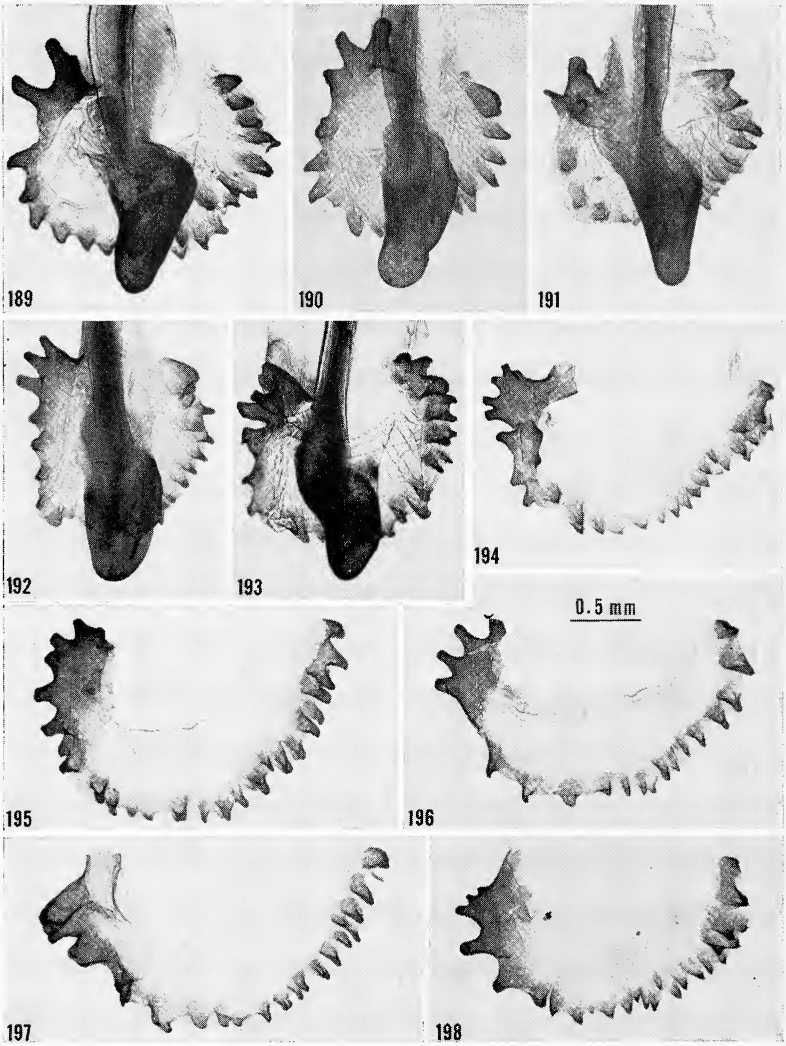
160. (N), Borba, Rio Madeira, Amazonas, Brazil. 161. (AMNH), Iquitos, Peru. 162. (AMNH), Rio Ucayali, Peru. 163. (AMNH), Moyobamoa, San Martin, Peru. 164. (AMNH), Rio Ucayali, Peru. 165. (AMNH), Rio Marañon, Peru.



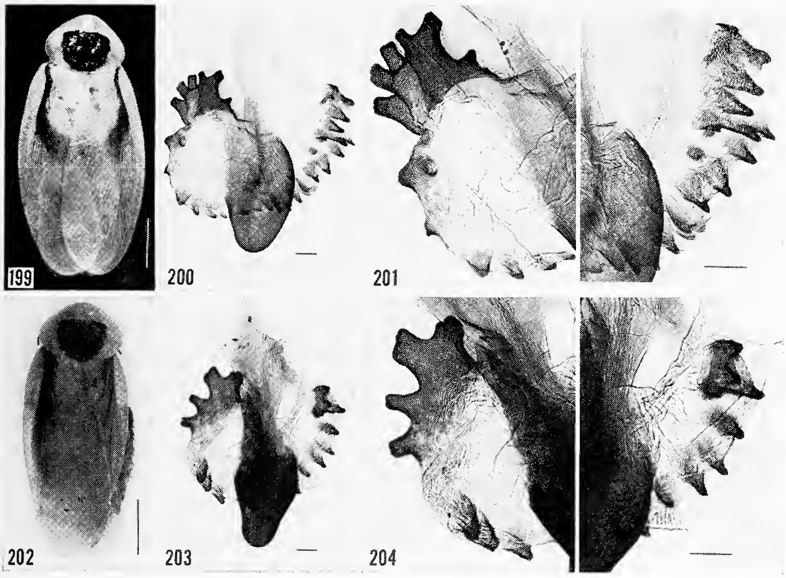
Figs. 166-172. *B. parabolicus* (*Atropos* Group). L2d and prepuce. The two structures have been mounted separately in Figs. 168-172 (all to scale shown in Fig. 169). 166-167. (USNM), South America. 168-172. (N), Puraquequara, Rio Negro, Amazonas, Brazil.



Figs. 173-188. *B. discoidalis* (*Atropos* Group). 173. Adult male (scale = 10 mm). (N), Panama. 174-188. L2d and prepuce (all to scale shown in Fig. 177). 174-175. (MCZ), Nicaragua. 176-177. (N), Panama. 178. (USNM), Pontarenas, Costa Rica. 179. (MCZ), Trinidad. 180. (AMNH), Colombia. 181. (USNM), Trinidad. 182. (MCZ), Panama. 183. (AMNH), Barro Colorado, Canal Zone, Panama. 184. (USNM), Colombia (from wild orchids at Hoboken Quarantine). 185. (AMNH), Barro Colorado, Canal Zone, Panama. 186. (USNM), British Guiana. 187. (N), Panama. 188. (AMNH), Puerto Plata, Dominican Republic.



Figs. 189-198. *B. discoidalis* (*Atropos* Group). L2d and prepuce; in 194-198, L2d has been removed (all to scale shown in Fig. 196). 189. (USNM), Ecuador. 190. (USNM), Venezuela. 191. (AMNH), Colombia. 192. (AMNH), labeled "Africa" which is undoubtedly an error. 193-197. (N), Panama. 198. (MCZ).



Figs. 199-204. *Blaberus* spp. (*Atropos* Group). Genitalia from the adult specimens shown. 199-201. *B. boliviensis.* (L), Guayaquil, Ecuador (det. Princis). 202-204. *B. anisitsi.* (L) (det. Princis). Fig. 201 and 204 are enlargements of the preputial spines of the specimens shown in Fig. 200 and 203 (scale for adults = 10 mm, for genitalia = 0.2 mm).

tion in *atropos* (Figs. 133-153). Princis (1946) stated that the truncate elevation on the left side was 3-pronged whereas Hebard (1917) stated it was 2-pronged. These elevations may vary from a single arm (Fig. 152) to one consisting of more than 5 prongs (Figs. 133, 134). More striking is the marked reduction in numbers of the smaller preputial spines in some males. This usually occurs on the left side (Figs. 139-141, 144-153) where there are few spines to begin with but a marked reduction may occur even on the right side (Figs. 141, 153). In some males the spines are completely absent from the left side (Figs. 140, 141, 147, 149-153).

In *parabolicus* (Figs. 155-170) most of the spines on the right side of the prepuce are more or less pointed. In some males there is a reduction in number of spines (Figs. 156, 169). Bruijning (1959) described the genitalia of *parabolicus* as follows: "At the extreme right of the preputium stout, rounded processes are inserted between the teeth; some of the teeth on the free margin form pairs which are squarely inserted on the margin; sinistrad the teeth are developed in blunt, stout, chitinous processes, while at the extreme left a large bi- to trilobate process is found . . ." An examination of Figs. 155-170 shows that variability is so great that it is impossible to indicate specifically the number of truncate elevations on the left side or the exact arrangement and shapes of the preputial spines on the right.

In *B. discoidalis* (Figs. 174-198) the truncate elevations on the left usually arise very close to L2vm, extend dorsally, and may even overlap L2vm (Figs. 175-180, 190). Preputial spines are more numerous on the right side, usually are somewhat truncate but sometimes are rounded or pointed at the tips. In some specimens (Figs. 195, 198) the right anterior spines, though smaller, tend to resemble the large elevations of the left side except that they are rarely fused at their bases (Fig. 195). The spines decrease in size distally on the membrane and in some individuals there is a reduction in number, usually on the left side. L2d is variable in size and shape. In a few males the large truncate elevations which are highly variable in number on the left side are poorly defined or fused together (Figs. 182, 184, 188, 191) and sometimes (Fig. 184) are reminiscent of the tumorlike outgrowth on the left side in the *Giganteus* Group.

According to Princis (1946) the preputial armament is simple and sparse in *anisitsi* (Figs. 203, 204). His drawing shows a 3-pronged truncate elevation plus 3 bluntly rounded spines on the left side and only 5 smaller pointed spines on the right. The specimen shown in Fig. 203 was the one used by Princis (Fig. 6 *in* 1946; and identified by him with reservations) but he did not remove the genitalia from the male; it differs from Princis' description in having a 4-pronged elevation on the left and more spines on the right (than he figured) terminating anteriorly in 3 spines fused at their bases (Fig. 204).

Hebard stated that the species related to *B. fusiformis* Walker ". . . are poorly understood and the description of *fusiformis* is vague. If our specimens are correctly determined it is possible that *anisitsi* is a synonym, based on material showing decided depauperation." Although Hebard included *anisitsi* in the *Brasilianus* Group, the specimen identified by Princis as *anisitsi* (Fig. 202) is clearly a member (by male genitalia, Fig. 203) of the *Atropos* Group (Princis 1946). If both Princis and Hebard are correct in their determinations *anisitsi* and *fusiformis* are obviously not the same species.

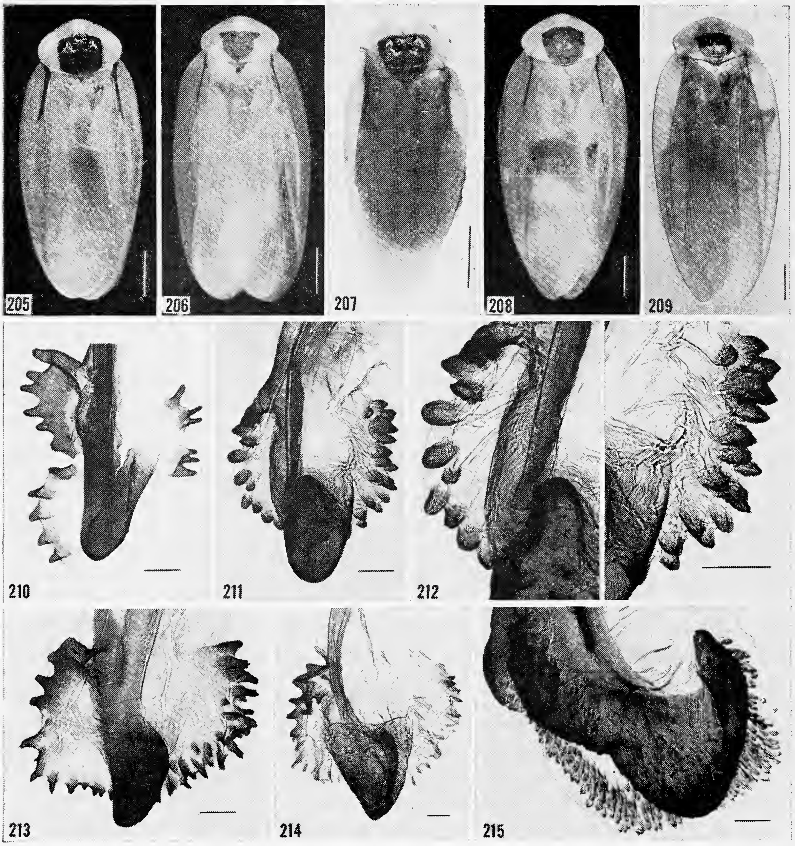
Princis (1946) compared the genitalia of *boliviensis* (Figs. 200, 201) with *anisitsi* (Figs. 203, 204). According to him the penis in *boliviensis* is more massive. The spines on the right side start with a bluntly rounded spine, are larger, more numerous and not as widely separated as in *anisitsi.* On the left side there is a 3-pronged truncate elevation followed by 10 (according to his drawing) truncate or rounded spines set fairly close together. In the specimen shown in Figs. 200, 201 (not the one illustrated by Princis), the truncate elevations on the left are at least 6-pronged. No doubt an examination of additional specimens of these 2 species would show as much intraspecific variation as occurs in other species of the *Atropos* Group.

The truncate elevations on the left side of both *anisitsi* and *boliviensis* arise close to L2vm, extend dorsally, and their genitalia closely resemble those of *B. discoidalis.*

Undetermined species. — Several museum specimens were examined whose genitalia and phenotypic appearance did not fall into the known species. These were as follows:

1-2. *Blaberus* spp. *A* (Figs. 205, 213) and *B* (Figs. 206, 211, 212). — These 2 species from Peru, except for their much smaller size, resemble *colosseus*, particularly in their slender form and pale coloration. The preputial spines of both forms (cf. Figs. 211, 213) differ from each other. The anterior elevations of the left side are not much larger than those on the right, thus resembling the prepuce of *colosseus.*

3. *Blaberus* sp. *C* (Fig. 207). — This specimen from Colombia was identified by Hebard as *B. discoidalis.* However, it is considerably smaller and more slender than is *discoidalis*, and phenotypically resembles the specimen identified by Princis as *B. anisitsi* (Fig. 202). Its genitalia (Fig. 210) are unique (and differ from *anisitsi*, Fig.



Figs. 205-215. Males of *Blaberus* spp. The genitalia are from the adult males shown. 205, 213. *Blaberus* sp. *A*. (*Brasilianus* Group) (USNM), Tingo, Maria, Peru. 206, 211, 212. *Blaberus* sp. *B*. (*Brasilianus* Group) (USNM), Tingo, Maria, Peru. (Fig. 212 is an enlargement of the right and left sides of the prepuce shown in Fig. 211.) 207, 210. *Blaberus* sp. *C*. (*Atropos* Group) (USNM), Susumuco, Colombia. (The prepuce in Fig. 210 is broken and the spines on the lower left side normally lie under L2d.) (det. by Hebard as *B. discoidalis*). 208, 214. *Blaberus* sp. *D*. (*Brasilianus* Group) (ANSP), St. Laurent du Maroni, French Guiana (det. by Hebard as *B. giganteus*). 209, 215. *Blaverus* sp. *E*. (*Giganteus* Group) (USNM), Borba, Rio Madeira, Amazonas, Brazil. (Scale for adults = 10 mm; for genitalia = 0.3 mm.)

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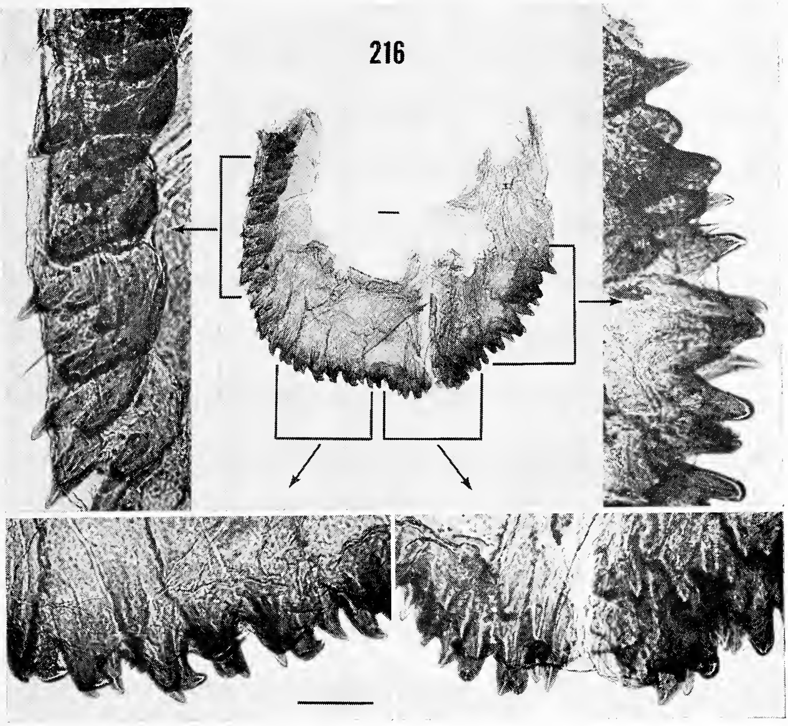

Fig. 216. Prepuce of *Blaberus* sp. (*Giganteus* Group). (MCZ), Andegoya, Colombia. Different portions (brackets) of the prepuce (center) are enlarged to show variations in the spines (scale = 0.1 mm).


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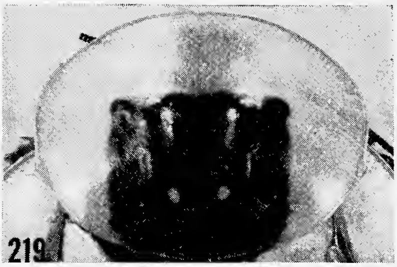
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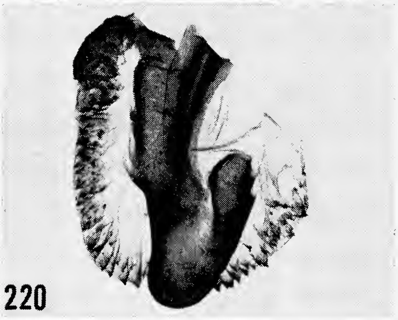
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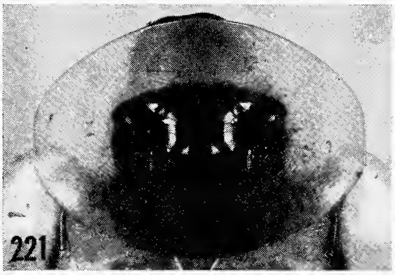
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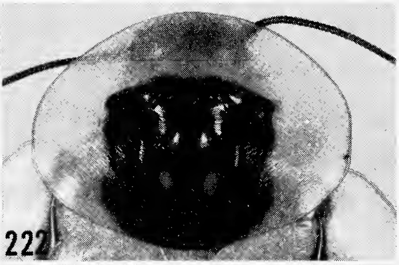
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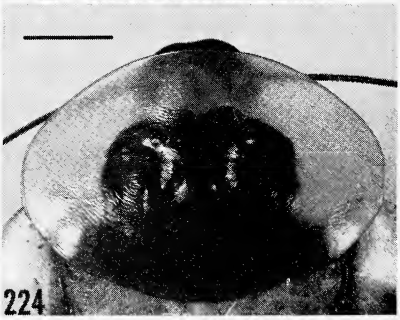
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Figs. 217-220. *Blaberus trapezoideus.* Pronotum and genitalia. 217-218. (BMNH). Paralectotype of *Blabera quadrifera* Walker. 219-220. (BMNH). Lectotype of *Blabera quadrifera* Walker. Oajaca, Vera Cruz, Mexico. 221-224. *Blaberus craniifer.* Variations in the shape of the pronotum in speci-

203) in that all of the spines bordering the prepuce are relatively large and arise from a well defined sclerotized margin; the shapes of the preputial spines also differ between these 2 specimens.

4. *Blaberus* sp. *D* (Fig. 208). — This is a species determined by Hebard as *B. giganteus* (from French Guiana) but its genitalia (Fig. 214) are that of a member of the *Brasilianus* Group. The truncate elevations on the left side of the prepuce are small and somewhat like those of *colosseus*, but the other spines are greatly reduced in size and number. This specimen is probably *colosseus* (though it is somewhat broader and more intensely colored than *colosseus* from Trinidad and Mexico, (cf. Figs. 112-115) in which the preputial spines have been greatly reduced (cf. Figs. 116-129).

5. *Blaberus* sp. *E* (Fig. 209). — This specimen is close to *giganteus* but is more slender and its general coloration is very pale. Its genitalia (Fig. 215) are massive and there are more rows of preputial spines than are usually found in *giganteus* (Figs. 28-40).

Distribution. — The species of *Blaberus* are almost entirely neotropical (Table 1). Four of the 5 species of the *Brasilianus* Group are restricted to South America; *colosseus* is more widely distributed and occurs in Mexico, Central and South America. Members of the *Giganteus* and *Atropos* Groups are found in Central and South America, and a few species occur in the West Indies, southern Florida, and Mexico.

Evolution of the aedeagus and prepuce. — I believe that the prepuce of *Giganteus* Group males which lack truncate elevations and have relatively simple, small preputial spines is the most primitive of the 3 groups of *Blaberus*. However, though the preputial spines are small they may vary in shape (Fig. 216) and some spines are reminiscent of those found in the *Brasilianus* and *Atropos* Groups. A *Giganteus* Grouplike form could have given rise to individuals of both the other 2 groups. The preputial spines of the *Brasilianus* Group are often numerous and may occur in multiple rows (e.g., Figs. 88, 90) like some individuals of the *Giganteus* Group (e.g., Figs. 36, 47, 215). In both the *Brasilianus* and *Atropos* Groups, the anterior elevations of the prepuce on the left side probably evolved from the left tumorlike outgrowth of a *Giganteus* Grouplike form. However, in the *Brasilianus* Group, the anterior elevations on the left and right sides do not differ greatly in size whereas there is a marked size difference between the elevations on the two sides in the

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mens from a laboratory culture. (Scale for pronotum [see Fig. 224] = 5 mm.; scale for genitalia [see Fig. 218] = 0.5 mm).

Atropos Group. It is of interest that in occasional specimens of *B. discoidalis* (*Atropos* Group) the anterior elevations on the left side are so poorly developed (Fig. 184) that the lateral swelling of L2d resembles the outgrowth in the *Giganteus* Group.

In Princis' (1963) linear arrangement of 14 *Blaberus* spp., the species *minor* is separated from other members of the *Brasilianus* Group by *boliviensis* and *atropos*. I would rearrange this sequence and place *minor* with *brasilianus*, *fusiformis*, and *scutatus*.

Table 1. Geographical distribution of species of *B'aberus*.

Species	Distribution[a]
Giganteus Group	
craniifer	Mexico, Guatemala, British Honduras, Honduras, Costa Rica, Panama, Venezuela, Cuba, Dominican Republic, Florida (Key West)
giganteus	Mexico, Guatemala, Panama, Colombia, Venezuela, Trinidad, British Guiana, Surinam, French Guiana, Dominican Republic (?)
Brasilianus Group	
brasilianus	Brazil
colosseus[c]	Trinidad[b], Mexico[b], Guatemala, Costa Rica, Panama, Venezuela[b], French Guiana
fusiformis	Brazil, Bolivia, Paraguay, Argentina
minor	Brazil, Bolivia, Paraguay, Argentina
scutatus	Brazil, Peru
Atropos Group	
anisitsi	Paraguay
atropos	Trinidad, British Guiana, Chile (?), Colombia[b], Mexico[b]
boliviensis	Bolivia, Ecuador[d]
discoidalis	Costa Rica[b], Dominican Republic[b], Jamaica, Cuba, Haiti, Vieques Island, Panama, Colombia, Venezuela, Trinidad, Ecuador[e], Nicaragua[b], Florida (near Key West)[f]
parabolicus	Colombia, Surinam, Brazil, Peru, Ecuador, Bolivia

[a] From Princis (1963) unless otherwise indicated; the localities for *craniifer* include those for *trapezoideus*.

[b] From present study.

[c] Localities from Hebard (1920).

[d] From Princis (1952).

[e] Princis lists Ecuador with a ?. I have seen 1 specimen (Fig. 189) from Ecuador.

[f] From A. B. Gurney (personal communication). (Record of USNM and Fla. Plant Board).

Chromosome numbers. — The diploid chromosome numbers of females of 5 species of *Blaberus* are: *giganteus*, 74; *craniifer*, 74; *atropos*, 74; *parabolicus*, 40; *discoidalis*, 38. The males have one less sex chromosome (Cohen and Roth, unpublished data). Evidently members of the *Atropos* Group have variable chromosome numbers.

Addendum: Since this paper went to press I have examined the lectotype and paralectotype of *Blabera quadrifera* Walker, which is a synonym of *B. trapezoideus* Burm. *The* pronotum of one of these specimens is illustrated by Princis (1958, p. 74). The tegmina of these 2 specimens are hairy, as they are in *B. craniifer,* and their genitalia (Figs. 218, 220) are indistinguishable from those of *craniifer* (cf. Figs. 47-57, 62-74). As for the laterally truncate pronotum of *trapezoideus* (Figs. 217, 219), the pronotal shape is so variable in light colored *craniifer* (Figs. 221-224) that this character cannot be used to distinguish the 2 species. I believe that *trapezoideus* (type locality Mexico) is the light colored form of *craniifer.* Both species were described by Burmeister (Handb. Ent. 2 (2), Berlin, 1838, p. 516). Because *B. craniifer* has been used widely as an experimental animal I select it as the valid name for this species.

SUMMARY

Based on the structure of the prepuce and aedeagus, species of *Blaberus* are placed in the following three groups: 1) *Giganteus* Group (*giganteus, craniifer*), 2) *Brasilianus* Group (*minor, brasilianus, colosseus, fusiformis, scutatus*), and 3) *Atropos* Group (*atropos, parabolicus, discoidalis, anisitsi,* and *boliviensis*).

I consider *Blaberus trapezoideus* to be a synonym of *B. craniifer,* and *B. colosseus,* formerly a synonym of *B. giganteus,* to be a valid species.

The genitalia are sufficiently distinctive to place individuals in their respective groups. However, intraspecific variation of the genitalia is so great that it is difficult and sometimes impossible to distinguish between certain species of a Group.

Three of the 5 species in the *Atropos* Group have variable chromosome numbers of 74, 40, and 38.

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THREE NEW CRETACEOUS ACULEATE WASPS (HYMENOPTERA)

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Museum of Comparative Zoology

Aculeate Hymenoptera have been known from the Mesozoic only from the Upper Cretaceous wasp *Cretavus sibiricus* (Sharov, 1957) and the ant *Sphecomyrma freyi,* known from two workers from the lower part of the Upper Cretaceous (Wilson, Carpenter, and Brown, 1967). Wasps evidently quite similar to living forms are, however, known from the Green River shales, of Eocene age (Cockerell, 1922), as are several ants, and a diversity of wasps, ants, and bees occur in Baltic Amber. Thus it has seemed probable that the Aculeata underwent a radiation in the Cretaceous, although the scarcity of fossil insects from this period has made it difficult to document this radiation.

Quite recently three fossil wasps from Cretaceous deposits have come to my attention. These do indeed indicate that the Aculeata became quite diversified before the end of the Mesozoic. One of these wasps, which I have placed in the new genus *Archisphex*, has a generalized aculeate venation but is very probably a sphecid. Only one wing is preserved, but this is in good condition and is noteworthy as the first evidence of an aculeate to be found in Lower Cretaceous deposits. A second wasp, described in the new genus *Lisponema,* is an undoubted sphecid, having a specialized wing venation strikingly similar to that of the modern genus *Spilomena* (Pemphredoninae). It is known from a headless but otherwise well preserved specimen from Cedar Lake Amber (Manitoba, Canada). Another wasp in these same deposits is a bethyloid obviously related to the cuckoo wasps, which I have placed in the new genus *Procleptes;* it is also quite well preserved although lacking most of the wings.

Thus there is now evidence that three diverse stocks of aculeates (sphecids, bethyloids, and ants) were present in the Cretaceous. *Cretavus* is usually assumed to be a scolioid (although there are certain unusual features of the wing), and eumenid wasps are known from the Eocene (Evans, 1966, p. 394). Thus we may say that representatives of three superfamilies were certainly present in the Cretaceous, two others almost certainly. These include the ancestral stocks of all the social forms, since the vespids were surely derived from eumenid stock, the bees from a primitive sphecid perhaps not greatly unlike *Archisphex*. Further discussion of phylogeny is deferred until after these specimens have been described.

My own role in these discoveries has simply been to place them in the scientific record. The Lower Cretaceous *Archisphex* was collected by R. A. Crowson of the University of Glasgow and very kindly presented to Harvard University. The two specimens from Cedar Lake, Manitoba, were collected by F. M. Carpenter, who also took a great deal of care in preparing the small pieces of amber so that the specimens could be studied in detail. These two specimens were first recognized as aculeates by Edgar Riek, of C.S.I.R.O. in Canberra, Australia, while he was sorting unworked material during a recent visit to Harvard. Various persons have advised me on the placement of these specimens, but I am particularly indebted to R. M. Bohart and A. S. Menke, who are currently preparing a revision of the genera of living Sphecidae.

Archisphex, new genus

Based on a single nearly complete fore wing (Fig. 1), the more critical features of which are as follows: costal cell present; stigma elongate, lower margin nearly straight, outer margin oblique, straight; marginal cell (cell R1) with its apex on the wing margin, not far from wing tip, and slightly appendiculate (i.e., R1 extending beyond apex of cell); three fully formed submarginal cells and three fully formed discoidal cells present (i.e., veins Rs, 2 r-m, 3 r-m, 1 m-cu, and 2 m-cu all complete), second recurrent vein (2 m-cu) curved basad so as to reach the second submarginal cell near its outer corner, first recurrent vein (1 m-cu) almost interstitial with first intercubital (Rs); major wing veins (M and Cula) reaching outer wing margin; basal vein (M + Rs) only slightly oblique, its upper terminus at some distance from stigma; transverse median vein (cu-a) oblique, reaching media (M + Cu) slightly basad of origin of basal vein; veins and stigma brown in color; wing membrane with close-set microtrichiae.

Type species: *Archisphex crowsoni,* new species

The name *Archisphex* is simply Greek for "ancient wasp" and should not influence future students toward keeping this genus in the Sphecidae if new evidence suggests that it belongs elsewhere. For the present, I do regard this wasp as probably a sphecid, largely by a process of elimination from other families plus a close approximation of the wing to certain living sphecids. These two considerations also provide a measure of certainty that *Archisphex* is an

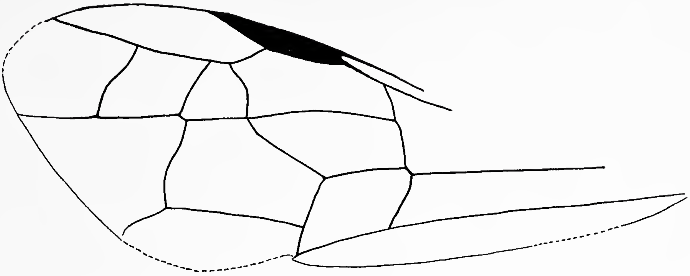

Fig. 1. *Archisphex crowsoni* n. sp., type specimen (traced from a photograph).

aculeate; a venation of this type is not approximated by any Symphyta or Terebrantia, but is very close to what might be regarded as the "basic pattern" of venation for the Aculeata. The one unusual feature, the curvature of the second recurrent vein to join the second submarginal cell, provides a major reason for placing it in the Sphecidae. However, unless the body is eventually found, it will never be possible to state unequivocally that it is a sphecid and not a very generalized scolioid, trigonalid, or representative of some extinct family of wasps.

Evidence for eliminating *Archisphex* from other living families of wasps is as follows: The full complement of veins and cells makes it improbable that it belongs in the Bethyloidea or in such families as the Formicidae, Plumariidae, or Rhopalosomatidae; the nearly erect, straight basal vein further eliminates these three families and also (and especially) the Vespoidea. All Trigonalidae known to me have a more oblique basal vein as well as modifications of the submarginal cells, also a second recurrent vein which terminates in the third submarginal. I am not familiar with any Pompilidae or Apoidea in which the second recurrent curves basad to reach the second submarginal cell. Some Scolioidea have a venation very similar to this specimen, and in the males of Anthoboscinae and Thynninae the second recurrent vein does indeed often reach the second submarginal cell. However, in both these groups, as in most Scolioidea, there is an additional vein or crease beneath the stigma (regarded as 1 r), marking off a small apical part of the first submarginal cell. There is no evidence whatever of this vein in *Archisphex,* leaving the family Sphecidae as the most likely possibility.

Within the Sphecidae there are fairly numerous genera having this basic venation. A. S. Menke has suggested that this fossil may represent a member of the Pemphredoninae, tribe Psenini, perhaps close to *Psenulus*. It is approximately the same size as living members of this genus and the venation is very similar indeed. As compared to *Archisphex, Psenulus fuscipennis* has a somewhat shorter and wider stigma, a slightly different slope to the basal and transverse median veins (but the two meet media in the same manner), a first recurrent vein which attains the inner corner of the second submarginal cell, and major veins (M and Cula) which reach the wing margin only as thin streaks. It is tempting to regard *Archisphex* as a pemphredonine, as the species to be described below, from the Upper Cretaceous, quite definitely belongs in that subfamily. However, generalized members of several other subfamilies have a venation sufficiently similar to this so that it is impossible to say that if *Archisphex* is a sphecid it is surely a pemphredonine. A basically similar venation occurs, for example, in the nysonnine genus *Clitemnestra* and in the sphecine genus *Hemichalybion* (although the latter is a much larger wasp). Little more can be said about the possible position of *Archisphex;* we can only hope that other fossils will be discovered which will eventually tie it in with greater assurance to some group of wasps.

Archisphex crowsoni, new species

Length of fore wing 5 mm; features as shown in Fig. 1. I would

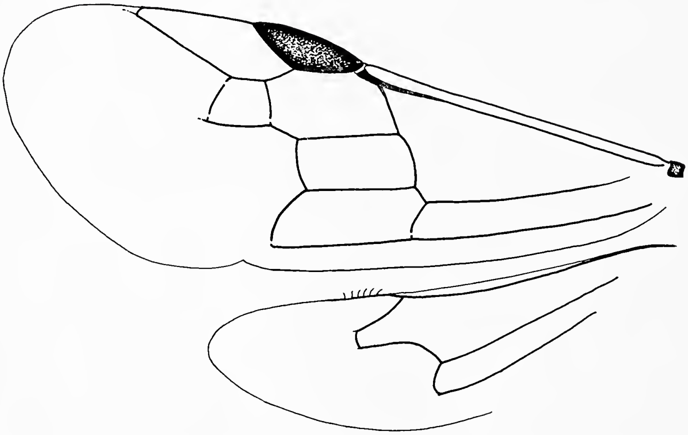

Fig. 2. *Lisponema singularis* n. sp., wings of type specimen. In the specimen, the fore wings are somewhat curled, the hind wings beneath the fore wings; they are shown here as if drawn apart and flattened.

assume that this wasp had a wing span of about 12 mm and a body length of 7-9 mm. No color pattern is evident on the wing.

Specimen from Wadhurst Clay, Quarry Hill Pit, Tunbridge, England (Lower Cretaceous).[1] Collected by R. A. Crowson in 1939; MCZ no. 6312.

Lisponema, new genus

Based on a single specimen in amber in nearly perfect condition except lacking nearly all of the head (Figs. 2, 3). The more striking features are as follows: body and legs slender, the latter devoid of spines; tibial spur formula 1-1-2; claws weakly dentate; mesoscutum large, parapsidal furrows distinct, notauli vaguely indicated; abdomen slender, sessile; fore wings with a very large stigma; marginal cell (cell R1) measured along wing margin about as long as stigma, its apex curved away from wing margin and weakly appendiculate; two submarginal cells and two discoidal cells present (veins 3 r-m and 2 m-cu wholly absent), and in general veins and cells far removed from outer wing margin; hind wing with six rather large hamuli visible, veins Rs and M not extending beyond r-m, submedian cell elongate, its outer end (cu-a) rounded up to meet media at the origin of cubitus (i.e., where M passes up to meet r-m).

Type species: *Lisponema singularis,* new species

The name *Lisponema* is an anagram of *Spilomena,* the living genus which it resembles most closely; however, it might equally well be taken to mean "smooth thread" (Greek *lispos* + *nema*), with reference to the very slender, smooth legs. This genus resembles *Spilomena* so closely that it can be uniquivocally assigned to the family Sphecidae, subfamily Pemphredoninae, and to that section of the subfamily that includes *Spilomena, Microstigmus, Ammoplanus,* and certain other genera. While the Pemphredoninae rank as one of the more generalized subfamilies of Sphecidae, these genera are considered to represent one of its more specialized elements. The specializations extend to larval characters and, in *Microstigmus,* to nest type and probable sociality (Matthews, 1968). The species of *Spilomena* are solitary wasps that nest in cavities in wood and prey upon thrips. The very close resemblance of *Lisponema* to members of this genus suggests that it, too, nested in some type of pre-existing cavities; the slender, smooth legs, in particular, indicate that it did not dig in the soil.

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[1] These relatively poorly known deposits are described by White (1928). The insect fragments from these beds have evidently not been monographed.

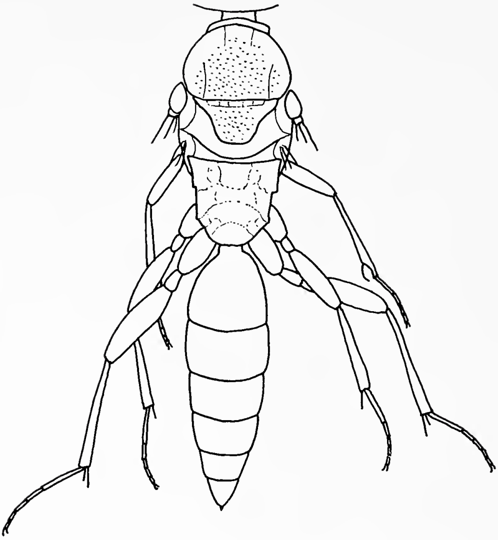

Fig. 3. *Lisponema singularis* n. sp., dorsal view of type specimen, wings omitted.

As compared to *Spilomena barberi*, *Lisponema singularis* has a slightly longer stigma, a marginal cell that curves away from the wing margin, first recurrent vein (1 m-cu) not at all interstitial with first intercubital (Rs), M and Cul separating fairly close to transverse median vein (cu-a), and, in the hind wing, a submedian cell which is longer and more rounded apically. These differences seem to me great enough to justify generic status for *Lisponema.* Some Pemphredoninae are known in which the marginal cell curves away from the wing margin (e.g. *Protostigmus*), although these differ in a number of other respects.

Lisponema singularis, new species

Length of body (without most of head, which is missing) 2.5 mm; length of forewing 1.7 mm. Body fuscous, with no evident maculations; wings hyaline, with brown veins and stigma. Features of body as shown in Fig. 3; thoracic dorsum shining and with small, close punctures; scutellum with a transverse basal groove; propodeum with reticulate sculpturing, the details of which are obscure, laterally with two small dentiform projections on each side; legs smooth and slender, as figured, the hind tibiae with some thin setae but no spines; wings as figured. Abdomen with six clearly visible segments and a small terminal projection which probably represents the subgenital plate. (I believe this specimen is a male, even though only six abdominal segments can be detected.)

Specimen in a small block of amber from Cedar Lake, Manitoba (Upper Cretaceous).[2] Collected by F. M. Carpenter, MCZ no. 6875.

Procleptes, new genus

Based on a single specimen in amber, in good condition although with some distortion and compression of the head and thorax, and with the wings absent beyond the basal fifth (Figs. 4, 5). The more striking features are as follows: mandibles rather large, with four apical teeth (but the left mandible with only three evident teeth, the basal one rather broad); palpi apparently short (but may be broken off or distorted); antennae arising far below eyes, prominently geniculate, with a long, slender scape and a somewhat longer flagellum of about 12 segments (cannot be counted precisely; both flagella lie longitudinally beneath the head and appear to be broadened and flattened on the apical two-thirds, but this may be the result of distortion); front with a strong median groove; eyes large, not hairy, ocelli well developed. Pronotum elongate, its posterior margin arcuately emarginate; mesoscutum and scutellum narrow and elongate, separated by a groove (but much compressed and distorted; parapsidal furrows and notauli not visible); propodeum with a large, acute process on each side; wings with several veins as figured; legs elongate, covered with short hairs but without spines except for a few short ones on the tarsi; tibial spur formula 1-2-2; front coxae with apical spine-like processes; claws rather large, apparently simple; basal half of abdomen broad, depressed but not evidently concave ventrally, apparently consisting of four segments as figured; apical half of abdomen in the form of a long tube, consisting of three segments, the tip of the sting protruding from the end of the apical segment.

Type species: *Procleptes carpenteri,* new species

The name *Procleptes* was chosen to suggest that this wasp may be a member of the stock which gave rise to the modern genus *Cleptes*

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[2] For a discussion of this locality and descriptions of other insects, see Carpenter *et al* (1934). Richards (1966) presents evidence that this amber is at least 72-73 million years old and probably dates from the early Upper Cretaceous, at a time when the climate of this part of Canada was mainly tropical. McAlpine and Martin (1969) give a detailed account of the occurrence of the amber and its probable origin.

(variously placed in the bethyloid family Cleptidae or in the subfamily Cleptinae of the Chrysididae). The resemblance in abdominal structure is especially close (see, e.g., the figure of *Cleptes consimilis* in Grandi, 1961, Fig. 2, no. 6). The major differences from *Cleptes* are in the mandibles, which are rather broad and 3 or 4-toothed apically, as in many Bethylidae (from which the cleptids may well have evolved), in the unusually long and slender scape, and the more prolonged head anterior to the eyes (although some of this may be the result of distortion). The elongate head and somewhat bulging eyes might suggest that this specimen belongs in the subfamily Amiseginae (variously placed in the Cleptidae or Chrysididae); however, the front has a median groove and no specialized sculpturing on the lower part, the mandibles are much broader than in any known Amiseginae, and the abdomen is relatively elongate. The abdomen is not ventrally concave nor otherwise as specialized as in

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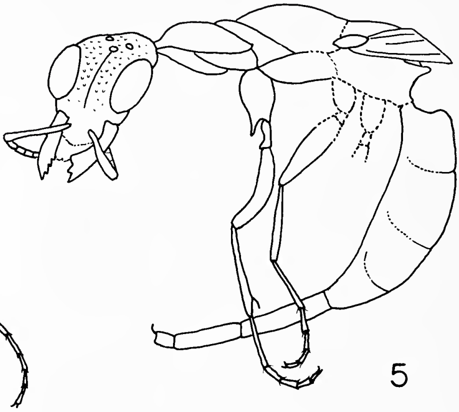

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Fig. 4. *Procleptes carpenteri* n. sp., dorsal view of type specimen. In fact the abdomen is twisted ventrally and forward, as in Fig. 5; in this figure it is shown as if it extended straight backward. Fig. 5. Same specimen, lateral view.

the true cuckoo wasps (Chrysidinae). It is unlikely that *Procleptes* was a "cuckoo" in behavior, not only because of its greater resemblance to Cleptinae and Amiseginae but because aculeate hosts must have been relatively scarce in the Cretaceous. Species of *Cleptes* have been reared from the larvae of sawflies, which may have been plentiful in the Cretaceous, since their fossil record extends back to the Triassic. Amiseginae are parasites of the eggs of walking sticks. I would assume that *Procleptes* was a parasitoid, and I suggest sawflies as probable hosts, although orthopteroids or indeed many other groups of insects cannot be ruled out as possibilities.

Procleptes carpenteri, new species

Length of body about 3.2 mm; wings apparently fully developed (although broken off near the base in this specimen). Head and thorax with a distinct blue-green cast, the integument apparently moderately thick and rather strongly punctate, the pronotum longitudinally striatopunctate; legs and abdomen black, non-metallic; body and legs covered with short, whitish hair; other details as figured.

Specimen in a small block of amber from Cedar Lake, Manitoba (Upper Cretaceous), collected by F. M. Carpenter. MCZ no. 1234.

Discussion

It comes as a considerable surprise to find such specialized wasps in the Cretaceous. The remarkable tubular development of the apical half of the abdomen of *Procleptes* is quite like that of modern species, and the unusual and much reduced wing venation of *Lisponema* is very comparable to that of some of the more specialized living Pemphredoninae. Discovery of quite a typical wing of a wasp from the lowest part of the Cretaceous, however, makes it seem less surprising to find specialized forms in the upper part of that period. The Cretaceous was, after all, a very long period, comparable in length to the entire Tertiary.

I believe that the small size of all three of these wasps is an accident of preservation rather than an indication that all the original Aculeata were small. Dr. R. A. Crowson tells me that the Wadhurst Clays in which *Archisphex* was found contain mostly small insects and fragments of larger ones; and a small piece of the wing of a large wasp might not be recognizable as such. The bits of amber from Cedar Lake, Manitoba, are all quite small and only very small insects have been preserved in them. The Cretaceous ant

Sphecomyrma, from New Jersey amber, is described as "medium-sized", while *Cretavus* is a large wasp, with a wing length of 10 mm (thus with a wing-span of about 23 mm and a probable body length of 13-18 mm). There may have been a fairly diverse fauna of Aculeata of various sizes in the Cretaceous, but it happens that the deposits considered here are chiefly favorable for preserving small species, which often happen to have reductions in wing venation and other specializations.

The diversity of Aculeata in the Cretaceous (three superfamilies certainly and two others probably, as pointed out in the introduction) suggests an origin of this group in the Jurassic. Dr. Crowson tells me that the rocks in which *Archisphex* was found contain a number of insects belonging to Jurassic proups. The Sphecidae undoubtedly diversified rapidly in the Cretaceous, as evidenced by *Lisponema* and by quite modern-looking Nyssoninae in the Eocene. *Lisponema* was surely not a ground-nester, and Baltic Amber is rich in Sphecidae which probably nested in hollow twigs and other cavities above ground (including *Passaloecus* and other genera related to *Lisponema*). If the Sphecidae arose from a scolioid ancestor one would have expected them to have been originally associated with the soil. In fact they may have been so; twig-nesters tend to occur more abundantly in forested areas and may thus become preserved in amber much more readily. The Pompilidae are sometimes regarded as a somewhat more "primitive" group on the sphecoid stem, but it is noteworthy that none are known from prior to the Oligocene (Baltic Amber) and that the fossils from that epoch belong mainly to archaic genera such as *Epipompilus.*

The radiation of the Sphecidae in the Cretaceous makes it seem very likely that the bees had their origin in this period and that they were therefore on hand to participate in the early diversification of the flowering plants. The presence of *Procleptes* in the Upper Cretaceous also suggests that a prototype for the cuckoo wasps was available to take advantage of the proliferation of the bees and wasps during the Tertiary.

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COMMENSALISM BETWEEN *RANZOVIUS MOERENS* (REUTER) (HEMIPTERA: MIRIDAE) AND *HOLOLENA CURTA* (McCOOK) (ARANEIDA: AGELENIDAE).

By Richard M. Davis and Mercer P. Russell[1]

In the spring of 1966, small red mirids were observed inhabiting the webs of *Hololena curta* (McCook), one of the most common agelenid spiders in the Los Angeles area. The insects, identified as *Ranzovius moerens* (Reuter), could be found only on the webs in two hedges of mixed honeysuckle, *Lonicera japonica*, and trumpet flower, *Clytostoma callistegiodes* in San Marino, California. This was the first report of this insect being associated with spiders, and it is one of the few examples of spider-insect associations.

These spiders are funnel-web builders, and their webs form platforms as they come out of the hedge. This horizontal sheet of silk narrows as it extends back into the hedge and forms a funnel-shaped tube of webbing up to 3 inches long which serves as the retreat of the spider where it waits for prey to enter the web. The main sheet of silk varies from a 1 × 2 inch platform to one of 8 × 8 inches, according to the maturity of the spider. These are generally three to six feet above the ground. The webs are composed entirely of dry silk, having no adhesive qualities like those of some other spiders. Some of the larger webs of this agelenid have one or two additional platforms under the main one, the spider going to any platform to capture prey. These webs are typical of agelenid spiders in bushes (Gertsch, 1949), having a network of silk lines suspended above the platform in an irregular fashion which act as trip wires, causing insects that hit them to fall onto the platform of webbing. When the confused insect falls onto the platform, the spider rushes from its funnel to attack it.

The spiders have been observed in the hedge all year round, with the young emerging in April and May. They are shy in the day, remaining in the funnel unless prey is in the web, but at night they are almost invariably seen out on the webs.

The eggs of *R. moerens* were never observed, but, judging by the criteria of Davis (1955), the ovipositor with its saw-like teeth (Fig. 1 A-B) is fully developed for placing them in plant tissue rather than on the web surfaces or on spider prey.

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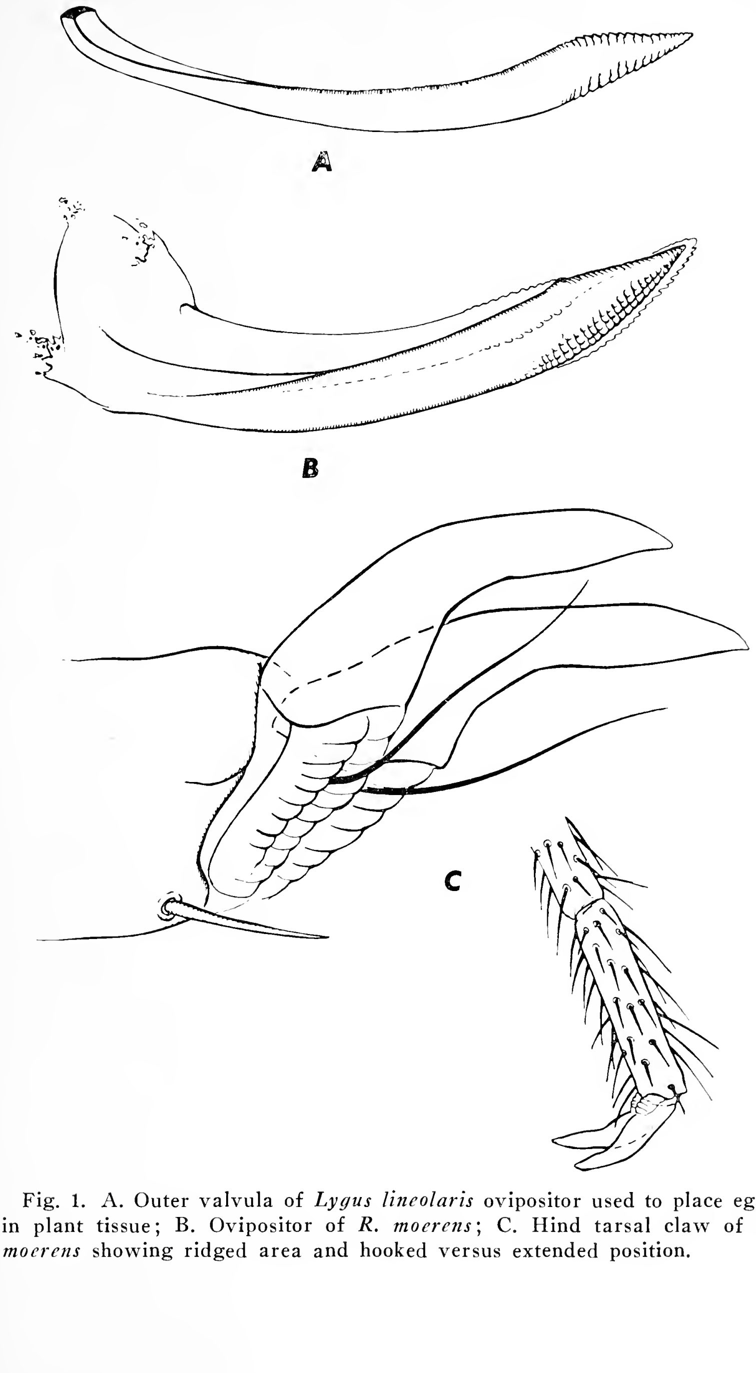

Fig. 1. A. Outer valvula of *Lygus lineolaris* ovipositor used to place eggs in plant tissue; B. Ovipositor of *R. moerens*; C. Hind tarsal claw of *R. moerens* showing ridged area and hooked versus extended position.

The first nymphs appeared in the webs in middle March (March 20, 1967, and March 18, 1968). Hatching must continue until June since large numbers of first instar nymphs were seen in the webs until that time.

The first adults were seen on May 29, 1967, and on May 3, 1968. At this time, all stages of nymphs and adults were seen on the webs concurrently. The adults were seen in the webs until September 10, 1967, and August 30, 1968. From one to as many as forty mirids occurred on a single web, depending on its size.

The mirids were active in the daylight hours, even on the hottest days, and walked or ran rapidly on the web. They appeared to move randomly over it, searching for food, and were found equally often in sun or shade. They were inactive at night, staying motionless in one place. This was possibly due to the disturbance caused by the spider being on the platform at night. The mirids were found on both sides of the web platform, and they walked and ran equally well either upright on the top of the web or inverted on the bottom. The tarsal claws (Fig. 1 C) are well adapted for this. The claw can be either held straight down, parallel to the tarsus, for walking on top of the web or turned in, almost perpendicular to the tarsus, for hanging under the web. There is also a small ridged area, at the base of the claw, which may aid in walking on top of the web or hanging from it.

The mirids did not try to avoid the spiders. They usually moved slowly across the web, their antennae moving up and down rapidly ahead of them in constant motion. One nymph was observed walking in front of an adult spider, less than one centimeter away, on the same side of the web. The spider took no notice of it. As reported by Worth (1967) in his observations on *Arachnicorus*, the nabids were in no danger of becoming stuck in dry silk webs. This was also true of the present spider-mirid association.

The hedge partially protected most of the webs from wind and rain, but the exposed part of the webs was badly damaged by these elements. The mirids moved to the part of the web back under the hedge when rain or wind started.

The insects were observed feeding on both plant and animal material caught in the webs. They fed both upright on top of the web and hanging inverted on the lower side with the beak inserted through the web. They were seen feeding on a variety of insects trapped in the webs or tied to it by the spiders. Some of the more common hosts included leafhoppers (Cicadellidae), katydid nymphs (Tettigoniidae), blow flies (Calliphoridae), and crane flies (Tipulidae).

It is likely that mirids killed and ate small insects without the spider's help. In one instance, several small flies were stunned and thrown on a web. One of the struggling flies was attacked by a mirid nymph. During the few seconds in which the mirid was fighting with the fly, the spider rushed to the scene, took the still struggling fly from the mirid, and returned to its funnel. After having seen mirids feeding on honeysuckle stamens, we placed a group of three stamens on a large web away from where any mirids were walking. Within 15 minutes, 8 mirids had gathered on top of the web and 7 on the bottom to feed on the stamens.

One possible predator was seen on a large web at night. This was a male club-footed spider (Clubionidae), several of which were seen to be active on several parts of the hedge throughout the night. The clubionid was seen on the underside of an agelenid web, along with several mirids, but apparently was scared off by the light.

LABORATORY STUDIES

Materials and Methods

In the spring of 1968, mirid nymphs were collected by tapping the web over a small glass vial. They were reared using a method modified from that of Yonke and Medler (1964), being kept individually in the laboratory in small glass cages made of 38 mm diameter glass tubing, 50 mm high, the tops of which were covered with 0.1 mm mesh plastic screen. The cages were set on a 23 × 35 cm plastic box, filled with water, out of which 10 dental wicks projected, one for each of ten cages. The cages were placed in a Thelco Model 4 (Precision Scientific Co.) growth chamber at 30°C. ± 2°C., with a 15 hour light, 9 hour dark daily photoperiod.

Table 1. Duration (days) of the nymphal stadia of 20 *Ranzovius moerens** reared to maturity. (AfterWilkinson and Daugherty, 1967)

Stadium	Range	Mean ± s	Cumulative mean age
1*	2-7*	3.8 ± 1.06	3.8
2	3-6	4.0 ± 0.98	7.8
3	3-13	5.0 ± 1.60	12.8
4	3-16	5.4 ± 1.65	18.2
5	6-12	8.1 ± 1.34	26.3
Total nymphal period	22-36	26.3	
Adult female	28-56	41.3 ± 10.96	67.6
Adult male	1-18	7.8 ± 6.12	34.1

*Reared from 1st instar nymphs collected from webs. Time in stadium 1 began with day collected.

The nymphs for laboratory rearing were considered to be first instar for the following reasons: of 81 nymphs collected from the webs and measured, none was below the size range for the first instar given in Table 1; of the 43 considered to be in the first instar group, 32 were placed in cages for rearing, and none had more than five molts to reach maturity; it is unlikely that any time was spent off the webs since the insects were unable to stay upright except on the spider silk.

Both nymphs and adults had trouble walking on a flat surface; they fell onto their backs and were unable to right themselves. Since this led initially to many deaths, webbing was added to the cages by placing an immature spider in the cage and allowing it to spin a web. The spider was then replaced by a mirid.

Daily records were kept on the number of instars, number and time of molts, the time spent in each instar, adult longevity, and type of food used.

Food used in rearing both nymphs and adults was one or more of three types. Fruit flies, *Drosophila melanogaster*, were cultured and frozen at an earlier time, then thawed before being placed in the cages. Honeysuckle stamens were taken from the hedge where the mirids occurred. Abscissed avocado flower buds, also observed as food for the mirids in the field, were collected from a tree shading the hedge.

In an effort to corroborate Bristowe's (1941) statement that the flavor of many bugs renders them immune from attack by spiders, spiders and mirids were placed together in small cages provided with water and honeysuckle stamens to see if the mirids would be eaten. Eleven such trials were carried out, using first and second instar nymphs and immature agelenids.

RESULTS

Nymphal Stages and Feeding Trials

Twenty nymphs were reared to maturity (Table 1), with measurement of nymphal development time starting on the day of collection. The average number of days spent in each instar was 3.8, 4.0, 5.0, 5.4 and 8.1 days, with completion of the entire nymphal development in an average of 26.3 days.

The males took an average of 25.6 days to complete their development while the females required an average of exactly 1 day more.

The effects of the diets on maturation are shown in Table 2. Females reared on avocado buds reached adulthood in an average of 29.3 days, 6 days longer than those fed on *Drosophila* only. A single

Table 2. Food used in rearing 20 *R. moerens* nymphs to maturity. Range, mean total nymphal period, and number reared is given for each food type.*

6 Drosophila (frozen) and 22-27 23.0

Nymphs	Food type	Range	Mean total nymphal period (days)
6	*Drosophila* (frozen)	22-29	24.5
7	Avocado flower buds	25-36	31.1
5	Honeysuckle stamens	22-27	24.8
2	*Drosophila* (frozen) and Honeysuckle stamens	22-24	23.0

*Fruit flies, *Drosophila melanogaster*, were cultured, frozen, then thawed before feeding to bugs. Honeysuckle stamens and avocado buds were collected from the study area, where they were seen being fed upon by the bugs.

female reared on a mixture of honeysuckle stamens and *Drosophila* matured like the latter group. Four males reared on avocado buds matured in an average of 32.5 days. The average was 27 days for the 2 fed *Drosophila* and 24.8 days for the 5 using honeysuckle stamens. The single male fed a mixture of the flies and honeysuckle matured in 22 days. The resulting adults were maintained on one of the three dietary regimens on which the nymphs were reared. The 8 females lived for an average of 41.3 days, while the 12 males survived for an average of only 7.8 days. The females lived for an average of 41 days on avocado buds and 44.5 days on *Drosophila.* The males averaged 12 days on Drosophila, 8.6 on honeysuckle and 5 days on avocado. The longest lived specimen was a female, reared on flies, which lived a total of 80 days; 56 of them as an adult.

On two occasions, adult female spiders were put in a dish to spin a web for rearing mirids. The webs were in poor condition, but egg sacs were constructed in the corner of each dish. The female spiders spent about 80% of their time sitting on the egg sacs, apparently guarding them. To see if the mirids would feed on these eggs, the spider was removed and one adult and two nymphal mirids were placed in each of the two dishes. No other food was added, but a wick was provided for moisture. The mirids were never observed feeding, although from time to time they would walk across the egg sacs. All had died within a week.

SPIDER PREY

In the eleven trials using first and 2nd instar nymphs in cages with immature spiders, the mirids lived for an average of 4.4 days (range 2-10 days) before being killed or eaten (eaten 9 of 11 times). Two of these were repeat trials using spiders that had eaten one bug previously, but in both cases the mirid lived only 5 days before being eaten.

Discussion

The time from the first appearance of nymphs to the first appearance of adults in the field was 70 days in 1967, and 46 days in 1968; this compared to an average laboratory development time of 26.3 days (range 22-36 days). It seems likely that growth, after hatching in early spring, is retarded by climatic conditions and/or lack of food. The first nymphs appeared before the hedge started to bloom, and the supply of insects caught in the webs was very low. As the warmer weather arrived, the hedge started to bloom and, in addition to dropping stamens in the webs, the flowers attracted a greater number of insects to the spiders' webs. The last of the first instar nymphs were seen in the field in early June and had developed to adults by the end of June. This period of less than 30 days agrees more closely with the laboratory rearing data.

Field and laboratory data agree in general on adult longevity. The period from the time the last nymph had reached maturity to the time the last adult was seen was 70 days in 1967, 60 days in 1968. Laboratory longevity for female adults averaged 41.3 days (range 13-56 days).

Only one generation occurs in this locality per year and indirect evidence indicates that overwintering occurs in the egg stage. No adults were seen in the early spring and nymphs and adults were absent from the webs from early September to mid March of the following year. Dispersal may occur in the fall, since flying was observed in the laboratory.

As previously stated by Bristowe (1941) for another arachnophilous bug, the large numbers of first instar *Ranzovious moerens* in the webs indicated that the eggs are laid in or near the webs. Since female adults possess a fully developed ovipositor, it can be further assumed that the site of oviposition was plant tissue in or near the webs.

Field observations and laboratory rearing showed that the mirids are relatively omnivorous, eating both plant and animal material. Laboratory rearing studies confirmed this when the bugs passed through five molts to maturity when fed on either of two plant sources or the insect host. The type of food used for rearing affected both the time to mature and the adult life span. Both males and females took over 5 days longer, on the average, to mature when reared on avocado buds than on either of the 2 food sources which occurred most frequently in the spider webs. The adults' life expectancy was lowest on avocado buds also; being more than halved in the case of the average male. There appeared to be little difference in the utilization of *Drosophila* or honeysuckle by either nymphs or adults.

The spider-mirid relationship appeared to be a case of commensalism, since from all indications, the mirids neither damaged nor benefited the spiders but obtained food killed by the spider or caught in its web and were provided by the spider with a substrate which afforded some protection from rain and wind as well as from predators. According to Carvalho (1954), *Ranzovius fennahi* in Trinidad was predacious on spider eggs. There are several indications that such a predacious habit did not occur with *R. moerens*: the small number of eggs laid by one agelenid spider compared to the large number (up to forty) of mirids observed in a single web, the tending of the egg sac by the spiders, and the observed feeding of the mirids on other food and not on the egg cases.

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A NEW FOSSIL SCALE INSECT (HOMOPTERA: COCCOIDEA) FROM CANADIAN AMBER

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Oligocene and Miocene ambers from the Baltic area and from Mexico have yielded more than 100 known specimens of fossil Coccoidea. However, insofar as they can be identified, these all appear to belong to extant genera. The only previously described Mesozoic coccid fossil, *Mesococcus asiatica* Becker-Migdisova (1959), is an impression, said to represent a wingless female or nymph, from an Upper Triassic deposit at Issik-Kul, Kirghiz, SSR, Soviet Union. From the published description and figure of that specimen, its assignment to the Coccoidea seems to be based upon rather inconclusive evidence as important structures, such as the antennae and mouthparts, are not preserved.

The specimen described here is preserved in amber from Cedar Lake, Manitoba. This amber is almost certainly of Upper Cretaceous age (Carpenter, *et al*, 1937; Richards, 1966).[3] The specimen is unquestionably an adult male coccid, and is in a relatively good state of preservation. The body and its appendages appear to be almost entirely intact, and the specimen is not obscured by any large external air bubbles, as in some Baltic amber coccids which I have examined. Parts of the specimen are somewhat distorted due to shriveling of the membranous portions of the integument. The venter of the head apparently is split or torn behind the ventromedial plate, and flap-like shreds of membranous integument extend beneath the head in this region. A pronounced flaw plane roughly perpendicular to the insect's body, intersects the specimen on the posterior part of dorsum of the thorax and partially obscures certain morphological details in that region. The entire venter of the insect is unobstructed, however. The left forewing extends posteriously at a slight angle to the body, and most of the details of the wing are clearly discern-

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[3] I wish to thank Dr. F. M. Carpenter, Harvard University, for providing the opportunity to study this fossil coccid.

ible. The right forewing lies directly over the abdomen making details of the dorsum of the metathorax and abdomen difficult to see. The hind wings, which in male Coccoidea are absent or reduced to very small, linear or club-like hamulohalteres, are indistinguishable in this specimen, although possibly present but obscured by the flaw plane.

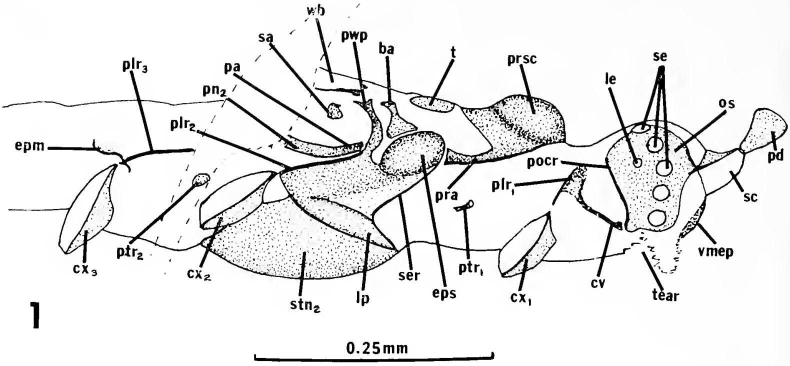
The comparative external morphology of adult male Coccoidea has been the subject of considerable research during recent years (Theron, 1958, 1960; Beardsley, 1968). Most of this work has involved study of the comparative morphology of the cephalic and thoracic sclerites in specimens which have been properly cleared and stained. Fortunately, the Cedar Lake specimen is well enough preserved that it has been possible to identify most of the integumental sclerites, thereby permitting comparison with the known adult males of extant Coccoidea. In the description which follows the terms used are largely those introduced by Theron (1958) which have been accepted, with slight modifications, by other students of male coccids.

The accompanying figures necessarily are somewhat diagrammatic. Because of distortion due to shriveling and the obscuring of certain structures by the dorsal flaw plane, it was necessary to observe all surfaces of the specimen from many angles, using different lens and light combinations, to properly delimit the integumental sclerites and other structures. It is quite possible that weakly developed sclerites which might have been seen had it been possible to clear and stain the specimen, have been overlooked.

Electrococcus, new genus

Coccoidea, presumably of the family Margarodidae (sens. lat.). Adult male characterized by small size, well-developed cephalic and thoracic sclerites, ten segmented antennae with the pedicel conspicuously enlarged, three pairs of moderately elongate slender legs and a pair of well-developed mesothoracic wings. Head well defined, separated from thorax by a distinctly constricted neck region. Ocular sclerites well developed, each bearing an anterior dorsoventral row of simple eyes, plus a single larval eye (stemma) laterally behind anterior row. With well-defined dorsomedial and ventromedial sclerites. Posterior margin of dorsum of head with a postoccipital ridge. Functional mouthparts absent; structure of tentorium not determined.

Mesothorax strongly sclerotized; with a convex prescutum separated from lateral margins of thorax by anteriolateral extensions of the scutum. Scutum without a mesal membranous area. Scutellum small, somewhat convex, approximately trapazoidal in shape, apparently separated from mesopostnotum by a moderately wide



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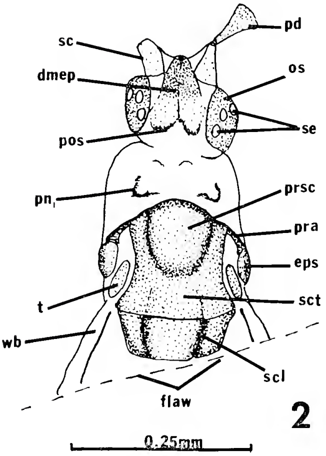

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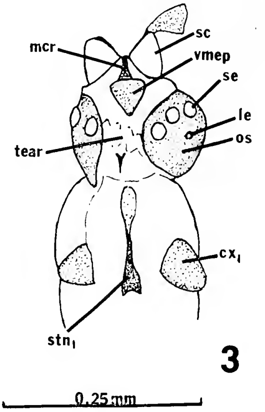

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Fig. 1. *Electrococcus canadensis* n. sp., lateral aspect of head and thorax. Fig. 2. Dorsal aspect of head and thorax. Fig. 3. Ventral aspect of head and prothorax.

membranous area. Mesosternum elongate, convex below, and rather strongly displaced posteriorly in relation to the tergites so that the mesopleurites are noticeably more inclined than in most other male Coccoidea. Sclerites of pro- and metathorax greatly reduced, as in other male Coccoidea. Two pairs of thoracic spiracular peritremes present.

Abdomen relatively elongate, slender; with eight discernible pregenital segments which become progressively narrower posteriorly. Apex of abdomen bearing a moderately elongate, apically acute, sclerotized penial sheath with a slit-like ventral opening. Structure of aedeagus not determined. Dorsal abdominal tubular duct clusters or lateral pore pockets apparently absent. Abdominal spiracles not discernible.

Type of genus: *Electrococcus canadensis*, n. sp.

Electrococcus canadensis, n. sp. (figures 1-8)

Length of specimen, excluding antennae 1.3 mm; length of forewing 0.9 mm.

Head distinctly separated from thorax by a markedly constricted neck region; lateral areas of epicranium occupied by pair of large ocular sclerites (os), each bearing an arcuate dorsoventral row of 5 simple eyes (se) anteriorly plus a single smaller larval eye (le) or stemma laterally; posterior margin of ocular sclerite thickened to form a postocular ridge (pocr), anterior margin of ocular sclerite slightly thickened above and below articulation point of antennal scape. Ocular sclerites broadly separated dorsally; dorsum of head with a definite dorsomedial sclerite (dmep) the anterior portion of which is strongly sclerotized, the posterior portion much less distinctly so; posterior margin of dorsomedial sclerite marked by a thickened postoccipital ridge (pos) which does not extend laterally to the ocular sclerites. Dorsomedial plate narrowed anteriorly, extending ventrally between antennae and onto venter of head as a narrow midcranial ridge (mcr), as far as the anterior margin of the ventromedial plate (vmep) below. Ventromedial plate approximately in form of equilateral triangle. A narrow bar-like median longitudinal sclerite of unknown relationship (possibly a cranial apophysis) on posterior portion of venter of head behind torn area. Antennae (fig. 4) about 0.54 mm. long; scape (sc) largely membranous except for longitidinal ridge-like thickening on inner face; pedicel and flagellar segments strongly sclerotized, pedicel (pd) large, trumpet-shaped; flagellar segments bearing a few scattered slender setae, and

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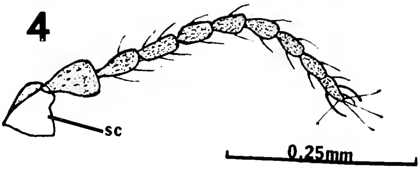

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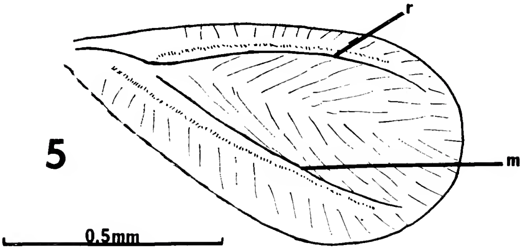

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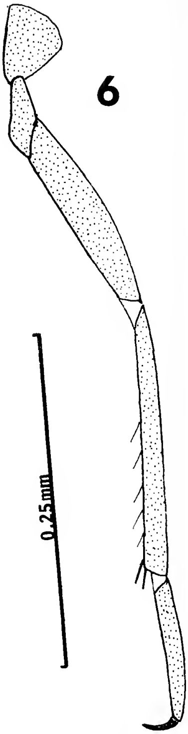

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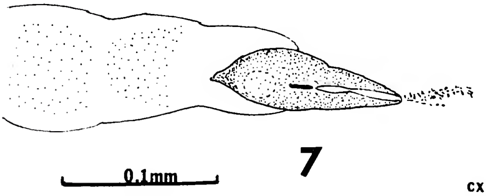

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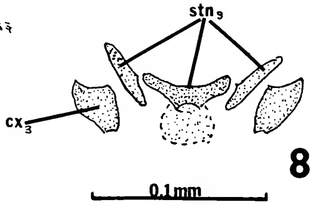

Fig. 4. Right antenna. Fig. 5. Left forewing. Fig. 6. Metathoracic leg. Fig. 7. Ventral aspect of posterior abdominal segments and penial sheath. Fig. 8. Venter of metathorax.

small dash-like reflective areas which may be sites of very short setae, or sensoria. Apical segment with 3 curved thickened digitiform setae and four long, slender, apically capitate setae.

Prothorax largely membranous; dorsum with a pair of small transverse postnotal sclerites (pn) with weak lateral anterior extension indicated; pronotal ridge apparently not developed. Propleural sclerites well defined; consisting of the propleural ridge (plr_1) and a elongate cervical sclerite (cv); these apparently not intimately fused at juncture. Anterior end of cervical sclerite apparently articulating with base of postocular ridge. Small sclerotized prothoracic spiracular peritreme (ptr_1) present in membranous area between forecoxa (cx_1) and mesepisternum. Prosternite (stn_1) well defined, narrow, elongate; anterior portion expanded into a small, nearly quadrate, less strongly sclerotized plate; posterior apex shallowly incised medially.

Prealare (pra) narrow, strongly reflexed, arising from anteriolateral extension of scutum, possibly extending as a narrow thickened band along anterior border of scutal extension to sides of scutum; no evidence of separate triangular plate at apex of prealare. Tegula (t) relatively large and elongate. Basalare sclerite (ba) large and conspicuous; small subalare (sa) discernible in membranous area just below wing base. Mesopostnotum (pn_2), except for right side, largely obscured by flaw plane in type specimen. Postalare (anterolateral arm of mesopostnotum) (pa) extending to base of pleural wing process (pwp). Mesopleural ridge (plr_2) extending almost horizontally forward from base of mesocoxa to presumed site of mesopleural apophysis just below base of pleural wing process. Mesepisternum (eps_2) well developed, with a large, oval, somewhat convex disc area dorsally; anterior part of episternum below disc weakly sclerotized; anterior margin marked by a narrow subepisternal ridge (ser). A narrow, well-defined lateropleurite (lp) present at base of episternum, apparently separated from it by a posterior extension of the subepisternal ridge. A small triangular sclerite, apparently the mesothoracic spiracular peritreme (ptr_2), behind base of mesocoxa. Mesobasisternite (stn_2) large, strongly sclerotized, convex, longer than wide; apparently not divided by a median longitudinal ridge. A pair of small, narrow, sublateral sclerites immediately behind basisternite may represent a mesospinasternite.

Metanotum not discernible in type specimen due to intersecting flaw plane. Metapleural ridge (plr_3) elongate, narrow, strongly inclined, extending anteriorly from base of hind coxa to margin of flaw plane. Hamulohalteres, if present, not discernible. Metepimeron (epm) present, consisting of a narrow posteriorly directed postcoxal ridge and small attached sclerotized patch. A very short precoxal ridge also discernible at base of metapleural ridge. A small transverse mesal metasternite (stn_3) present (fig. 8); an indefinite dark area on its posterior margin may be the metasternal furca. A pair of poorly defined, narrow, sclerotized patches, on either side of the mesal metasternite, probably represent detached portions of that sclerite, similar to those of *Steingelia* (Theron, 1958).

Forewings (fig. 5) similar to those of modern male Coccoidea. Discernible vennation includes only anterior radius vein (r) extending parallel to anterior margin, nearly to apex of wing, and media (m) extending approximately parallel to posterior margin, nearly to apex. A faint ridge-like thickening present just anterior and parallel to r and just behind and parallel to m. Wing surface with numerous fine, weakly developed fold lines, similar to, but less clearly defined than in *Matsucoccus* males (Beardsley, 1968). Legs (fig. 6) moderately long and slender; tibiae each with one or two conspicuous apical setae; tarsi apparently one-segmented; tarsal claws long, slender.

Abdomen dorsoventrally flattened, apparently largely membranous, except for venter of segments 3 to 8 which appear somewhat sclerotized. No dorsal or lateral tail-forming clusters seen. Penial sheath (fig. 7) apparently sclerotized dorsally only in area behind presumed site of anal opening. Ventral portion of sheath well sclerotized, apparently with a basal ridge and a slit-like longitudinal aperture; poorly defined dark area beyond apex of sheath possibly remains of aedeagus or endophallus.

The type specimen is in the Museum of Comparative Zoology, Harvard University (MCZ #6623).

RELATIONSHIP OF ELECTROCOCCUS TO EXTANT COCCOIDEA

Two major subdivisions of the Coccoidea are recognized by most coccid taxonomists; the more primitive archeococcids, (usually limited to the families Margarodidae and Ortheziidae) and the more specialized neococcids containing the remaining 10 or 12 generally recognized families (see Borchsenius, 1957). Among extant forms the morphologically least specialized adult males are those of the Ortheziidae and such margarodid subfamilies as the Matsucoccinae and Margarodinae (Beardsley, 1968).

The *Electrococcus canadensis* male exhibits a much greater degree of morphological specialization than do those of the more primitive

Table I. Morphological features of *Electrococcus* compared with other male Coccoidea with eyes in dorsoventral rows.

	Electrococcus	*Pityococcus*	*Steingelia*	*Phenacoleachia*	*Puto*	*Kermes*	*Coccus*
Pedicel enlarged	+	+	—	—	—	—	—
Ocular sclerites not contiguous ventrally	+	+	—	+	—	—	—
Ventromedial plate present	+	+	+	+	—	—	—
Pronotal ridge present	—?	+	+	+	+	+	+
Scutum without mesal membranous area	+	+	—	+	—	—	—
Mesosternum undivided	+	+	—	+	+	+	—
Thorax strongly slanted	+	+	—	—	—	—	—
Tail-forming pore clusters absent	+	+	—	—	—	—	—
Penial sheath bifid apically	—	+	—	+	—	—	—
Abdomen evenly tapered	+	+	—	—	—	—	—

living archeococcids. Specialized features of the *Electrococcus* male include: 1) reduction of the compound eye to a single dorsoventral row of ommatidia; 2) the strong forward inclination of the thorax; 3) the development of broad anterior extensions of the scutum which enclose the prescutum laterally; 4) the absence of dorsal abdominal tubular duct clusters; and 5) small size.

The presence of a dorsoventral row of simple eyes in adult male Coccoidea is generally interpreted as stage of reduction intermediate between the complete compound eye typical of most male archeococcids and the isolated dorsal and ventral simple eyes which are the last remaining vestiges of the compound eye in the majority of male neococcids. Among extant Coccoidea, males of six well differentiated groups (families or subfamilies) have eyes of same general type of *Electrococcus.* Of these two are specialized margarodids; *Steingelia* (Steingelinae) and *Pityococcus* (Pityococcinae) (Theron, 1958; Beardsley, unpublished). Two additional groups; *Puto* (Putoidae) and *Phenacoleachia* (Phenacoleachiidae) are morphologically and cytologically primitive neococcids (Theron, 1960; Beardsley, 1962; Brown and Cleveland, 1968), while the two remaining groups, *Kermes* (Kermidae) and some genera of the family Coccidae (Giliomee, 1967), are somewhat more specialized neococcids.

In Table I, certain morphological features of the *Electrococcus* male are compared with those of other groups having eyes in dorsoventral rows. This table is based upon direct comparison of specimens in all groups, as well as on published information. Of the groups compared, only males of *Phenacoleachia* (Theron, 1962), *Steingelia* (Theron, 1958) and the Coccidae (Giliomee, 1967) have been described in adequate detail. The evidence suggests that the *Electrococcus* male is more similar to males of *Pityococcus* than to any of the others.

The structure of the cephalic and thoracic sclerites in *Electrococcus* indicates that it is the male of a specialized archeococcid or a very primitive neococcid. The several points of similarity between this specimen and males of *Pityococcus* have led me to conclude that *Electrococcus* is probably a specialized type of margarodid, possibly related to modern Pityococcinae.

The relatively high degree of morphological specialization in the *Electrococcus* male indicates that at least the archeococcids had already undergone considerable divergence before the end of the Cretaceous, and suggests that the original divergence of the ancestors of modern Coccoidea and Aphidoidea probably occurred relatively early in the Cretaceous, or even before.

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VISUAL AND ACOUSTICAL SOCIAL DISPLAYS BY THE GRASSHOPPER *ARPHIA CONSPERSA* (ORTHOPTERA: ACRIDIDAE)[1, 2]

By Robert B. Willey and Ruth L. Willey[3]

Many species of the Oedipodinae (band-wing grasshoppers) exhibit strikingly diverse social interactions invoking visual and acoustical communication between the sexes and between individuals of the same sex (Otte, 1968, 1969).

The present paper is an account of the communication system of *Arphia conspersa* and will serve as an introduction to quantitative and experimental analyses of specific aspects of the behavior of this and other species.

LIFE HISTORY

Arphia conspersa is widespread throughout the western Great Plains from northern Mexico to the southern provinces of Canada and is found up to 11,000 feet elevation in the Rocky Mountains of southern Colorado where this study was made. We have found that these populations typically overwinter as nymphs and the eggs usually need a cold period to break diapause, implying a two-year life cycle. In the mountain areas near Gunnison, Colorado, adults have emerged consistently (1962-1968) four to five weeks after the snow has melted (June to July). The peak of abundance occurs about two weeks after the first observed emergence and the population dies out about three weeks later in most localities (Willey and Willey, 1967). In the vicinity of Boulder, however, a few adults may be found at all months of the year, even in open areas during warm days of the winter (Halliburton & Alexander, 1964).

At higher elevations such as at Gothic (9,500 feet, Gunnison Co.) and Black Mesa (9,700 feet, Montrose-Gunnison Cos.) adults pass through most of their life without coming into contact with adults

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[1] Research conducted at the Rocky Mountain Biological Laboratory, Crested Butte, Colorado; The University of Illinois at Chicago Circle; National Center for Atmospheric Research, Boulder, Colorado; and Ripon College, Wisconsin.

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of other related species, except for sparse populations of *Aeropedellus clavatus* (Acridinae). At lower elevations, *Xanthippus corallipes*, another oedipodine, is commonly sympatric with *A. conspersa*. The densest populations so far observed occur in short grass prairie parks near Los Pinos Pass (10,200 feet, Saquache Co.), Black Mesa, and Table Mesa (6,200 feet, Boulder Co.). We have counted as many as 60 males per acre, but usually the population averages fewer than 20 per acre with more or less clumped distribution. These densities would seem to be relatively low for efficiency of location of mates and may be correlated with the highly evolved signals for social communication described below.

Figure 1. Male *A. conspersa* in alert pose, Table Mesa, Boulder Co. This male also was buzzing with the right hind leg (visible as 2 faint diagonal streaks).

MATERIALS AND METHODS

Field observations entailed sitting or standing quietly in the center of a population cluster. The members of this species are unwary enough to behave normally within a few inches of the observer. Completion of behavioral sequences have been observed on our nets, clothing and boots. Notetaking and scoring an outline sheet did not disturb the grasshoppers. Climatic conditions were noted; in a few experiments temperature and wind speed were measured with recording equipment. This study is still in progress. Most observations were made of Gothic, Black Mesa, Table Mesa and Los Pinos Pass populations from 1961 to the present

Observations were also made on wild-caught and reared grasshoppers kept in a variety of cages. The most successful cage consisted of a simple plastic plant tray 8″ × 12″ filled with sand with wire screening over the top to form a "quonset". Two removable solid wooden semi-circles formed the ends. Young shoots of blue grass, rye grass, and dandelions were provided for food during the seasons when wild grasses were unavailable. A 60 or 100w bulb provided heat and light which attracted the grasshoppers into a closely interacting group.

Movements were recorded with a Camex 8 mm. reflex camera run at 16 and 32 frames per second, while sounds were recorded with a Nagra III tape system and an AKG condenser microphone (C60 with B60 power supply) equipped with a 24 inch parabolic reflector (Torngren Co.) for field recording from distances over 2 feet. Recordings were made in the laboratory without the parabola and, recently, with a Sennheiser 804 condenser microphone. Frequency response was checked with the 4000 Hz calibration tone of the Nagra. The movie film was Kodachrome II and the audiotape was Scotch 138. The audiospectrograms were produced on a Kay Electric Co. Model 675 Missile Data-Reduction Spectrograph (Missilyzer). The overall sound range of each audiospectrogram illustrated in this report was calibrated at the time of transfer to the spectrographic paper with a calibrated precision sine-square wave generator (model E-310). We also cross-checked the recorded calibration tones of the Nagra and the generator. We measured the overall amplitude of the sounds directly from the insect with a model 1551C sound level meter (General Radio Co.). The behavioral vocabulary is derived from Willey & Willey (1964), R. Alexander (1967), and Otte (1968).

OBSERVATIONS

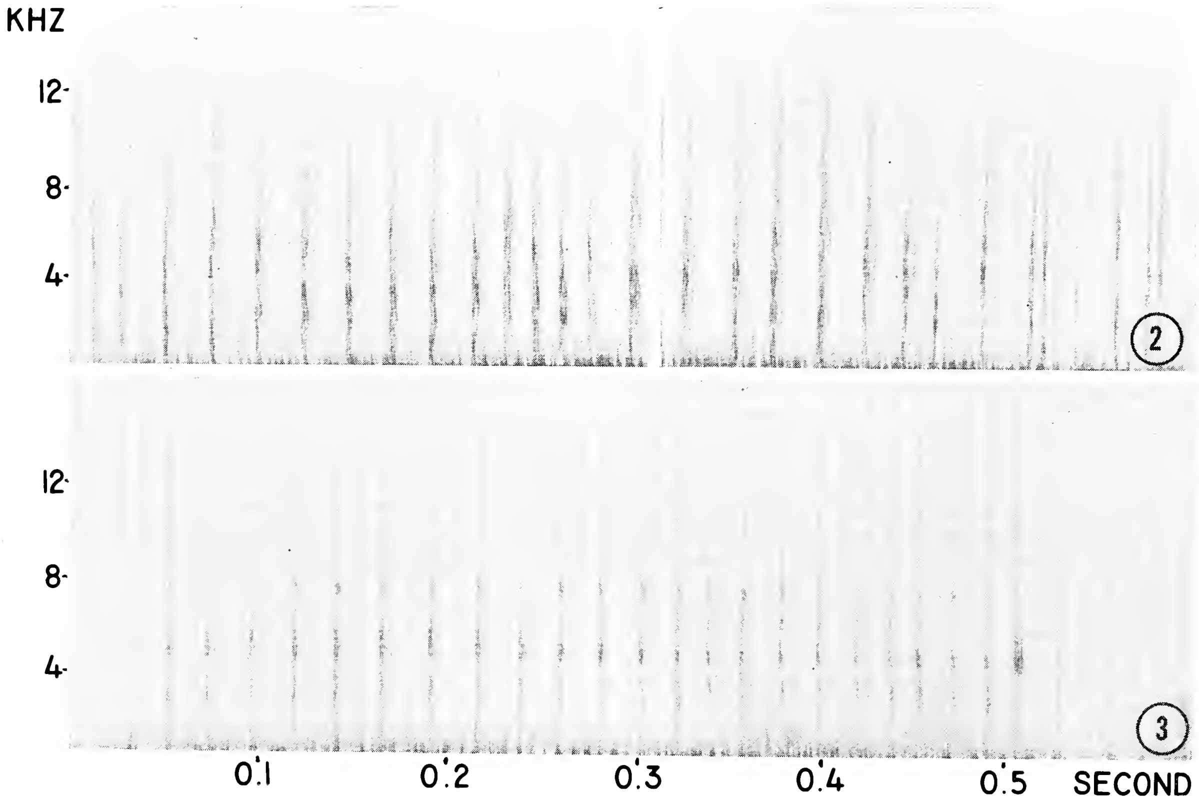
Solitary behavior

Males tend to be more active than females. They wander over the ground for distances up to 6 feet in a random path more or less determined by the microtopography. The manner of walking in males is a spurt of several complete leg movement sequences separated from the next sequence by a fractional-second pause. This spurt-walk becomes accentuated by a rapid raising and lowering of both hind legs with an open femoro-tibial angle of about 30°. One or two such flicks may occur whenever both hind legs are not in contact with the ground. The male, when approaching a high point, such as a pebble or a stick, often crawls upon it and stands in a motionless "alert pose" as in Figure 1. At this time the male is very responsive to any sudden movement or sound on the part of the observer. Usually the visible reaction to a disturbance is a slight crouch, lifting of the antennae to the vertical, closing of the femoro-tibial angle of the hind legs and lowering of the hind femora to the horizontal. The subsequent reaction is usually a leap and flight. If the male is allowed to recover from the initial disturbance, he slowly resumes the alert pose and periodically snaps the hind femora to the vertical in a flicking motion up and down, singly or together. Minor disturbances such as small insects coming too close or a grass blade touching him will cause such a flick. In fact, some flicks seem to be spontaneous during the alert pose.

Social behavior

Signals associated with social interaction are (1) spontaneous flights which are accompanied by a clicking sound (crepitation) produced by the wings, (2) simple soundless flicks of the hind legs ("femur-tipping", Otte, 1968), (3) femoro-tegminal stridulations which generate chirps, rasps, buzzes and squeals; and (4) soundless movements observed during contact between two grasshoppers which include tapping with the prothoracic tarsus, palpating with the antennae, rapid stroking with the palpi, butting with the frons, mounting by the male and, of course, genital contact. The emphasis in this paper will be placed on those signals transmitted at a distance between two or more individuals.

A signal, by our definition, must have some reaction-potential in the organism perceiving it. Our operational definition for a visual or auditory communication signal is the production of a measurable motion and/or airborne acoustical vibration by one individual followed in another individual by an action unrelated to what the latter was doing and unlikely to have occurred in the absence of the stimulation. Chemical signals could not be recorded in the present study. Frequent sounds such as mandible clicks, wing buzzes, substrate tapping with the tarsi, and tibio-tegminal clicks have produced no observable response in this species, and will not be considered in detail.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The flight crepitation.

The spontaneous aerial crepitation is a buzzing flight, which lasts one to three seconds, during which the grasshopper describes an arc one to ten feet in length and three feet in height. Males make more crepitation flights, by far, than females, which seldom are seen in flight except during the first weeks of the season. The flights by males may be repeated in a minute, but they average only one such sequence every three to four minutes at the peak of daily activity during the most active part of the short adult season. Even if disturbed, these insects usually crepitate normally. Only when disturbed a second time will they fly away relatively soundlessly. Crepitation flights are usually into the wind if there is only a slight breeze, although such flights are suppressed entirely by wind above 10 m.p.h. On the other hand, silent escape flights are usually at least 30 feet in length and often extend over several hundred feet, flying with the wind (Willey & Willey, 1967).

The sound produced by the wings during crepitation is shown in Figure 2. Each pulse is a broad spectrum click with no distinct fundamental frequency nor apparent harmonic. The highest amplitudes are in a range from 3000 to 8000 Hz and the total range of the sound is restricted by the effective frequency response of the recording system (20 to 18,000 Hz). To the human ear it is toneless and sharp. There are about 45 pulses per second and they are evenly spaced unless a change of direction or landing occurs. At these times the pulses take on an added component, appearing double, and are more closely spaced. These changes are probably due to the wings beating faster and out of phase with one another.

Male-female interaction (courtship and copulation).

The *chirp* is the primary sound generated by the male during courtship. This sound is produced by rubbing a ridge on the medial side of the hind femur on a linear series of pegs situated in both sexes on a modified intercalary vein of the tegmen. The chirp is a unitary sound probably produced by an intense pressure of the femur on the tegmen in a smooth up and down stroke cycle. As can be

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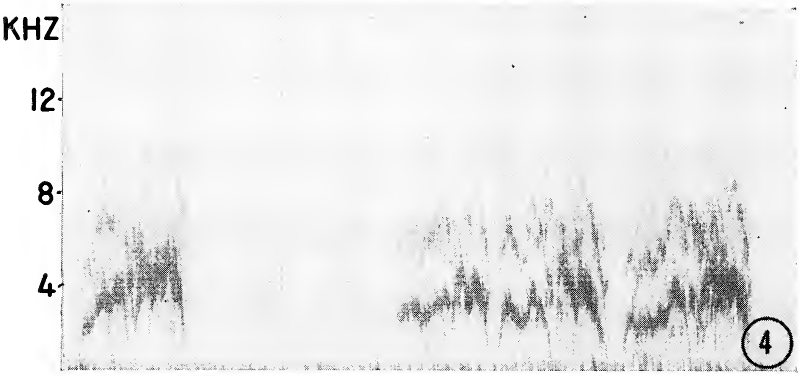
Figure 2. Field recording of beginning and ending of flight crepitation. This flight began 3 feet from the microphone, described a long arc to 10 feet away and returned to the same spot. Note the increased pulse rate (= wing beat frequncy) as the insect gains altitude. The pulse rate in mid-flight is more regular. Also note the double wave fronts as the insect lands, probably representing wings beating out of phase with one another. The break in the middle of the display = 1.8 seconds.

Figure 3. Audiospectrogram of Exakta camera re-set sounds.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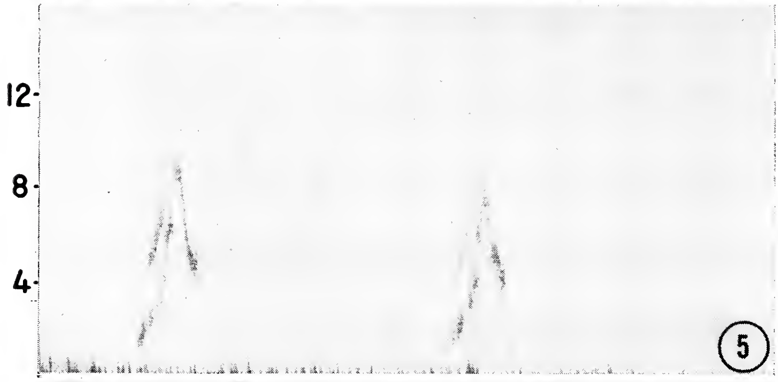
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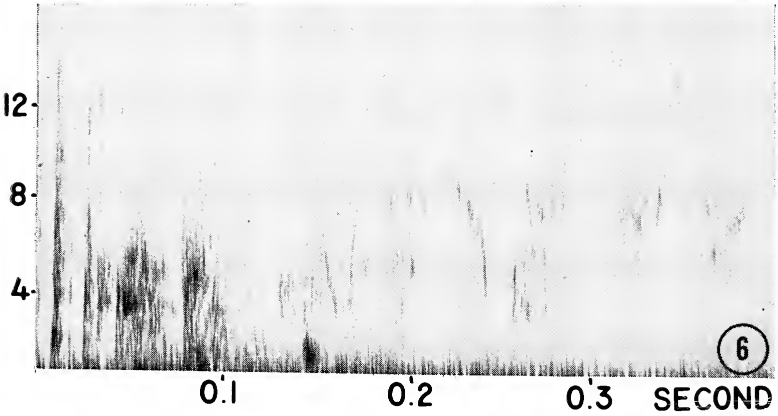
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SECOND

seen in Fig, 4, each chirp ranges to the limits of the recording apparatus but has an intense band about 500 cycles wide slurring upward and downward many times between 1500 and 5000 Hz with a duration of 40-80 msec. Each slur is probably a small multiple acoustic effect of a short series of pegs on a resonating wing and the slurring effect probably is a function of pressure, velocity, and changing strike angle of the femoral ridge as it arcs along the pegs. Additional faint overtones are observed at 7000 to 9000 Hz and 12000 to 16000 Hz. They are not likely to be heard by human ears and probably are an artifact of the spectrograph (Watkins, 1967). A sound between 3000 and 5000 Hz is usually picked up as approximating the tonal quality of the chirp. Chirps differ *inter se* in many ways and can be weak, strong, produced on the upstroke, downstroke, or both, high pitched, low pitched, etc. The average duration of a chirp is 60 msec and, when combined with other chirps in a phrase, has no standard interval. The sound intensity is difficult to measure directly, since the chirp is usually unitary and the

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Figure 4. Laboratory recording of chirps; the multiple chirps were at the beginning of a courtship sequence in which the male attempted to mount immediately, was repulsed at first, followed the female for nearly a minute giving unitary chirps and finally mounted and successfully copulated. The similarity of the peaks in the major (= fundamental) frequency band indicated that this is a single movement by both legs, either up stroke or down stroke. The "ghost" harmonics every 3-5 KHz probably indicates a basic spike pulse modulated by the number of pulses (= teeth on the intercalary vein) struck per sec/given instant (Watkins, 1967), but this must be checked further. The unitary chirp and multiple chirps were selected separately and are not in any determined time relation to each other.

Figure 5. Audiospectrogram of chipmunk (*Eutamias sp.*) alarm cry. The fundamental frequency of this complex sound seems to be 1 to 8 KHz which to human ears would average a high grasshopper chirp of 5 KHz. Since grasshoppers probably are tone deaf, the amplitude (at greater distance), great directionality of the sound, its duration, and spacing could be a good mimic of the chirp, thus causing the orientation of the two males described in the text.

Figure 6. Audiospectrogram of crepitation and squeal of two individuals in a caged population outdoors. The crepitation is separated from the squeal by two broad dark lines representing the landing of the insect on the wire netting. A smaller dark spot at about 1500 Hz represents a third impact on the wire. The squeal is difficult to reproduce clearly and is of much less amplitude than the crepitation and nearly the same as the background air noises. However, the great variation in carrier frequency shows the basic pattern. The 5 ascending major frequency peaks may represent multiple strokes, but at present we cannot ascertain how many strokes are produced nor what mechanism modulates the pulse rate frequency.

needle of a sound level meter is not deflected fully by it. However, a strong chirp seems to peak at 50 db at 4″ on the A and B scales. [All readings use a reference level of 0 db = 0.0002 microbar, alt. 9500 ft., and the scales used are those recommended by Peterson and Gross (1963) for the given sound level and frequency.]

Males can usually detect a female as a female from at least two feet and spurt-run toward her emitting separated high intensity chirps as above. Figure 7 illustrates the general schema of courtship of receptive and non-receptive females. The female "signal" seems to be an inadvertent movement such as feeding, walking, grooming or no movement at all. Her greater size probably also is a sign stimulus. The male chirps vary from pulsed phrases of one to five chirps in succession. When he has approached within one inch of the female, he typically orients by facing her directly, frons to frons. The two grasshoppers "fence" mutually with their antennae and the male continues chirping. The male then moves to the female's side and faces her thorax. He may chirp and he may even butt his frons against the side of the thorax. The male finally places a prothoracic tarsus on her metathoracic femur, pats the substrate with his hind tarsi several times very rapidly and then attempts to mount from the rear of the female. Simultaneously, there often is a train of 4-5 chirps just before mounting.

Females seem to be sexually responsive as virgins 10 days after molt and again after laying the first egg pod. However, these data are derived from females that were group-isolated as nymphs until presentation of the males and it has been shown by Highnam & Lusis (1962) that isolated females of *Schistocerca gregaria* mature more slowly. We considered a female receptive if copulation was completed. Some females actively solicited attention by males. After the short bout of antennal fencing initiated by mutual orientation and approach by both male and female, the female often turned while the male chirped, presented her side to the male, lowered the near hind leg and raised her opposite leg and both tegmina, exposing the whole abdomen. The valves of the ovipositor may open or at least move a bit. At this point three females of the total of 20 successful courtships observed fluttered the hind femoro-tibial joint against the ground but not high enough to contact the tegmen. After this the male gave his final burst of chirps and mounted. In one case, in which an old male of four weeks was involved, the female initially followed the male and patted his wing tip with a fore tarsus, while he ran away from her giving the male flutter-rasp (*q.v.*). Then he

MATING BEHAVIOR IN ARPHIA CONSPERSA

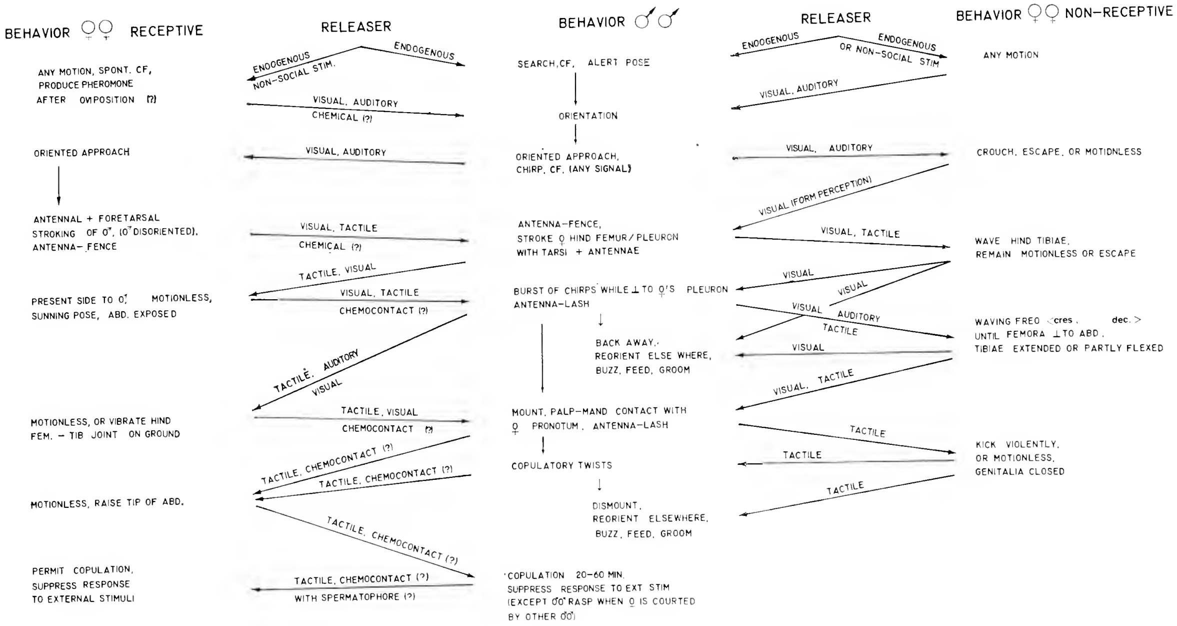

Figure 7.

suddenly oriented to her right side and chirped four times. She turned to face him and they exchanged antennal contact. She walked past him, circled clockwise and paused with her rear toward him. He ran to her front and mounted on her head. He then turned into the proper position on the female and copulated. The pair was *in copulo* for 23 minutes. This male seemed disoriented at first, and probably was not in full courting condition even though the female accepted him. However, the female seemed to be in a state of high receptivity and may have been soliciting courtship herself.

After uncoupling from the male, females often accept courtship and mounting by other males, but copulation has never succeeded during our observations, probably because the genital orifice is obstructed by the spermatophore. Under such conditions they dismount after fifteen seconds or so. Males, after they have copulated, are not usually responsive to females for 15 to 20 minutes but few males have been carefully observed in this condition. Unresponsive females show their lack of receptivity by (1) keeping closed the subgenital plate with no further evidence of resistance, (2) lowering the wings over the genitalia, (3) raising the hind femora until they point forward above the head with the tibiae stretched out above the horizontal plane and slowly waving the tibiae up and down, sometimes increasing the frequency and decreasing the amplitude until the femora are vertical and tibiae flexed, (4) kicking the male off, (5) running away and (6) flying away. It is striking how effectively the tibial waving turns off the courtship. In the field (1963) we observed one persistent male who was kicked off vigorously by a female. He returned to court again and oriented in the premounting position at the rear of the female. But when she waved the hind tibiae, he backed off and ran in another direction, chirping about four times as he went. It is possible that this is a learned response, for we have viewed many such encounters in the laboratory among naive or previously deprived males.

Male-Male Interaction

When males meet on the ground, after crepitating toward one another or during their ground level wandering, they pause at distances up to two feet apart and orient by one facing the other in an alert pose. They then crepitate, hop, spurt-run or walk to close proximity of each other. The approach is sometimes accompanied by chirping. Usually one (A) orients perpendicular to the side of the thorax of the other (B), and touches it with the antennal tips. Then (B) responds with a flutter-rasp (Fig. 9) with one or both legs, (A) answers and turns his body parallel to (B), either facing the same or opposite direction. They then generate flutter-rasps in alternation three or four times. After this sequence, if they are facing in opposite directions they walk in opposite directions, and, a few inches apart, pause in an alert pose for up to several minutes. They then crepitate in opposite directions, one first and the other a second later. If they face the same direction, they may walk parallel and flutter-rasp in several sequences before parting. We have observed in the field and more often in the laboratory that the members of some pairs seem to be of equal aggressive strength and both try to point toward the other's side. As a result, they circle around a common center and rasp in continuous alternation. Such bouts sometimes result in an attempt of one male to mount the other. This is followed with kicking by the mounted male and biting the dorsal carina of the pronotum by the mounting one. If a male tries to court another male, the signals of the courting male are usually turned off in mid-sequence by a responding flutter-rasp by the courted male. The courting male answers with a flutter-rasp and normal male-male interaction proceeds. However, males deprived of opportunities to court females for a few days will complete courtship and mount a vigorously rasping male. Indeed, the only response certain to be made by a male *in copulo* is a flutter-rasp, serving to "turn off" courtship by another male.

The flutter-rasp (Fig. 9) is produced by a rapid oscillation of the femur in contact with the tegmen. The effective sound produced is a broad-spectrum noise produced about 20 times per second whether the insect possesses one leg or two. In spectrograms of two-legged and one-legged males stridulating alternately, it is impossible to detect to which part of the sequence each belongs. Both may possess periodic double wave fronts probably produced by contact of the legs with the tegmen during both up and down stroke. Thus, as movies taken at 32 frames per second confirm, the flutter-rasp is produced by the legs moving simultaneously and in phase (if both legs are present). The burst of flutter-rasps rarely lasts more than 0.5 sec. in an active interaction and often only three or four pulses are produced, which are then answered by a similar or longer train of pulses within a tenth of a second. The frequencies are difficult to ascertain, but the fundamental tends to range between 2000 to 10000 Hz or higher with overtones at intervals of 5000 or 6000 Hz. These are the major frequencies from field recordings. The sound to the human ear is much more tonal than that of the crepitation


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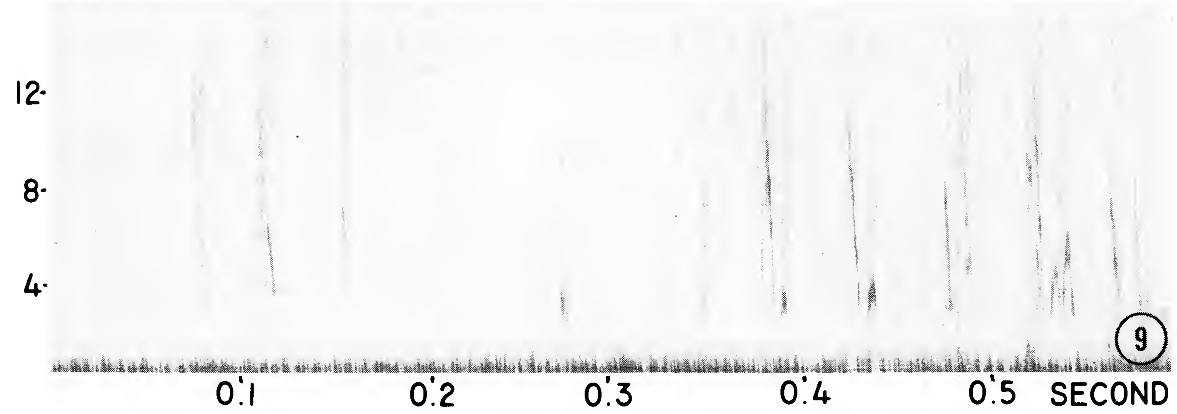
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SECOND

but much softer, blurred, and less tonal than the chirp. The amplitude is variable, but ranges from 30 to 45 db at four inches on the A scale of the sound level meter.

Other male signals.

A buzz (Fig. 8) and flutter-squeal (Fig. 6) by males have as yet no certain communicative function. However, they are made frequently enough and under such peculiar circumstances that they seem to be part of the normal male repertoire and their significance is an intriguing problem.

The buzz lasts 1 to 2 seconds with a pulse frequency of about 110-120 per second, and stops abruptly. The pulses are paired with a shorter time interval between each member of the pair than that between the pairs. The overall intensity measures 50 to 60 db at 4 inches on the B and C scale, and is loudest when the insect has its side directed to the microphone. There are several major overtones above a gliding fundamental giving a rising and falling "chord" to the first pair member and only a rising one in the second. It is likely that the pairs represent some order of up and down stroke of the femora in strong contact with the tegminal pegs. We formerly thought that the buzz of *Arphia* males was a rare sound (Willey & Willey, 1964), but it is frequently given in captivity by 3-4 week old males especially after the male has been refused by a female several times or is in isolation while other pairs nearby are courting. We have a tape of about 50 buzzes produced by 10 males during 7 minutes, each one paired with an unresponsive female in a separate mating cage (August, 1968).

So far, no female has shown any reaction to the buzz other than

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Figure 8. Field recording of entire buzz with an after-stroke resembling a very brief chirp. Note the paired nature of the strokes, sharp frequency and amplitude peaks, the even double pulse rate, increase in frequency peaks and their variability, and the abrupt beginning and ending of the song. The high frequency "ghosts" peaking at 12 to 16+ KHz probably represent an artifact of the spectrograph.

Figure 9. Laboratory recording of flutter rasp between two males. The first three pulses were delivered by a normal male using both hind legs, the train of 5 double strokes was given by a one-legged male obviously contacting the tegminal file on both up and down strokes. One of the pair of strokes is identical to that one given by the two-legged male, indicating temporal precision in deployment of the two legs making that stroke. The second of the paired strokes resembles a single pulse of the buzz in its frequency peak characteristics. There is considerable variation in the time spacing of the strokes. Again, the "harmonics" are probably largely due to spectrograph artifact based on the basic pulse repetition rate of the fundamental tone.

moving away from the sound. An anecdote from our field notes illustrates this situation. Late in the season (1964), an active male crepitated to within one foot of a female who immediately started running away from the male. She ran behind a clump of grass and lodged herself in a crevice formed by a stone so that she was hidden from the chirping male. He became "disoriented", moved a few inches in each of several directions and chirped two or three times every few seconds. Then he spurt-walked, *buzzing* at every pause. This behavior continued for 15 minutes and included two circuits. Each time he returned to the area, by about a foot, where he last saw the female. The female several times "peeked out" and, as the male approched the stone, backed in again. There seemed to be a regular decrease in the rate of the chirping and buzzing which finally ended when the male came to rest in an alert pose. After several minutes he crepitated away. We have observed a similar and normal ground behavior in the acridine *Aeropedellus clavatus,* wherein the male runs short distances over the ground, stops to buzz for several seconds, assumes a brief alert pose and then runs again.

Another peculiar aspect of the buzz is that we can "turn it on" sometimes. The reset mechanism of our Exakta camera resembles to our ears a crepitation (Fig. 3). Of 10 males in the field which were subjected to this sound (produced while one of us was lying prone about 15 inches away), five ran up to within three or four inches of the lens and then turned sideways to the camera and buzzed (Fig. 1).

We have heard the *flutter squeal* three or four times in the field. Only once was the individual which produced it positively identified. A squeal-like sound is sometimes produced by a male captured in a net or picked up by hand. In captivity, in a large flight cage, it is more frequently produced. The squeal is given when a loud crepitation by another male passes less than two feet overhead. A squeal by a captive male, with the probable cause — a crepitation immediately preceding it, is illustrated in Fig. 6. Unfortunately, the sound intensity could not be measured directly with a sound-level meter, but we infer from cross-sections of the sound made by the audiospectrograph that it is <45 db at 4 inches. The one reaction to the squeal was noted in the field where the overhead male in crepitation flight suddenly deviated about 60° and alighted seemingly prematurely near a squealing male. The landing male chirped in typical courtship manner and was answered by an intense flutter-rasp by the other male.

Finally, there is the silent raising and lowering of the legs by both sexes, nymphs and adults, which seems related to what Otte (1968) calls "femur-raising". The femora are raised relatively slowly to the vertical position and the tibiae are extended during this time about 30° to 60° from the closed position. The complete motion takes about one second and may take longer. This motion is fairly constant in detail and is a warning signal to any insect approaching. In nature, the intruder usually avoids the femur-raising insect or begins a definite social reaction. The effect of the signal, then, is to advertize that the grasshopper is not an inanimate object suitable for tasting or crawling upon. First instar nymphs exhibit this behavior as soon as they emerge from the pronymph. In captive populations this motion intergrades with the intense repulsion display of non-receptive adult females mentioned under *courtship.* Under crowded conditions, even males may begin tibial-waving and other signs of intense disturbance, but usually the warning signal does not vary much in normal interactions.

Extraneous sounds and the use of models.

Males will respond to motions other than the normal interaction noises. The human voice commonly is ignored by grasshoppers, but broad spectrum clicks and other sounds with sharp wave fronts produce definite effects in the behavior. These effects range from sudden freezing in position to flight, to assumption of the alert pose or even orientation toward the source. A chipmunk (*Eutamias sp.*) called 25 feet away while one of us was watching two males interact; they oriented to the source and ran about 12 inches toward it. Although they did not chirp, the sudden and simultaneous nature of their activity with the final pause in full alert pose, was characteristic of presocial orientation behavior. Figure 5 shows the vague resemblance of the chipmunk's alarm cry to the chirp of the courting male. The aforementioned Exakta reset buzz (Fig. 3) is another example of the ease of producing social behavior with artificial acoustic models and indicates that the acoustic and visual signals produced by the same motion are not necessarily closely linked, but rather only intensify the effect.

Males will also mount and attempt to copulate with sticks, thermometers and the rolled edges of cardboard cream cartons. However, approach sounds are seldom used to communicate with motionless objects. They seem to come upon these items by accident and proceed with the use of tactile feedback. This behavior seems to be characteristic of males between 15 and 25 days old. We are presently studying the diverse parameters of this behavior using visual and acoustic models.

DISCUSSION

Few thorough studies have been published concerning the behavior of oedipodine grasshoppers, whereas their close relatives, the Acridinae, have received more attention. Faber in 1936 and 1953 documented the behavioral repertoire of about a dozen European oedipodines with verbal descriptions but could not present oscillographic nor audiospectrographic displays. The most extensive study to date (Otte, 1968, 1969) has surveyed the social interaction of nearly 100 North American species of oedipodines and acridines, including six species of *Arphia*. However, *A. conspersa* was not described in detail. Other workers have analysed many aspects of the biology of the plague band-wing, *Locusta migratoria* and several species of the acridines *Chorthippus* and *Gomphocerus* (Faber, 1953; Haskell, 1962; Huber, 1963; and Perdeck, 1957).

R. Alexander (1967) lists nine functional categories of arthropod acoustical signals (other types of signals also could be so classified) as follows:

1) Disturbance and alarm (predator-repelling and conspecific alarming) signals.
2) Calling (pair-forming and aggregating) signals.
3) Aggressive (rival-separating and dominance-establishing) signals.
4) Courtship (insemination-timing and insemination-facilitating signals).
5) Courtship interruption (pair-reforming?) signals.
6) Copulatory (insemination-facilitating and pair-maintaining signals).
7) Post-copulatory or intercopulatory (pair-maintaining) signals.
8) Recognition (pair- and family-maintaining) signals (limited to subsocial and social species).
9) Food and nest site directives (limited to social species).

In *Arphia conspersa* only the first six categories have been observed and visual-acoustic signals are dominant in all but the sixth (copulatory) which is primarily tactile, perhaps with some contact pheromone stimuli. Fig. 7 shows a schema for courtship interaction from the flight crepitation sounds of chance encounter (onset of pair formation) through orientation, courtship chirps, to copulation. Added to these signals are the prevention of aggression signals (flutter-rasp), secondary calling signals or pair-reforming signals

(?) (buzz), alarm signals, and perhaps a tenth category, the comfort motions such as the wing buzz, wing flick, tibiotegminal click, mandible snap, etc. which could have subtle communication significance which does not involve orientation.

At this point we should discuss the relationship of the spectrogram display relative to the probable mechanisms of sound production. According to Watkins (1967), analysis of sounds by the Kay audiospectrographs must take into account the fact that pure tones (sine waves) modulated with on-off pulses whose repetition rate is more rapid than the analysing filter can discriminate will develop a definite harmonic structure. The over and under tone intervals are predictable from the pulse tone and pulse rate; Fourier analysis can predict the sound energy at each harmonic. To a degree, the original characteristics of the sound being analysed can be deducted from the harmonic structure. Likewise, if the basic tone is a spike (a very brief pulse of energy), rapid spike repetition rates fuse into harmonic intervals equal to the repetition rate added to the preceding harmonic. The greatest energy (darkest band) will be exhibited at the fundamental frequency of the repetition rate, and will be the lowest band in the trace. The femorotegminal sounds illustrated in this paper approximate the appearance of a pulsed spike repetition quite closely and this is undoubtedly related to the impact velocity of the femoral ridge on each peg of the tegminal file. On the other hand, we have no ready hypothesis for the structural basis of the flight crepitations which sometimes resemble spikes in themselves and at other portions of the spectrogram resemble the aforementioned pulse modulation which is beyond the resolving capacity of the analysing filter. Study of this problem, using oscillography and high speed cinematography is in progress.

We shall discuss the several signals of *A. conpsersa* under their presumed functional categories as listed by R. Alexander (1967) and Otte (1968).

Disturbance and alarm.

We have found the flutter-squeal (Fig. 6) commonly enough to consider it a basic stress pattern. Its neurological basis can be guessed as the outlet for an overload which brings together under stress several independent circuits, e.g., the rapid femoral flutter mechanism of the male-male interaction and the increased medial tension on the femur as it passes over the stridulatory pegs of the tegmen. Similar stridulations are produced by many acridids during capture.

In addition, the wing-flick may be a secondary alarm signal when it is not a comfort movement to rearrange the folding of the hind-wings. A startling display by both sexes of *A. pseudonietana*, mentioned briefly by Otte (1968) and observed by us in the western populations of that species, involves a sudden flicking open of the wings so that they point upward above the back with their outer surfaces mutually in contact. The wings sometimes stay open in this position for several seconds, with the brilliant red-orange disc of the hind-wings fully expanded. Grasshoppers which were approaching another individual will stop and back up or turn away when the latter performs this action. We have been able to cause the reaction with sudden probes or movements. We have noted also, as Otte has, that this action is effective against smaller insects, especially Diptera attempting to settle on the insect, and would be a good defence against tachinid and smaller asillid predators. However, in the six years in which we have studied the montane populations of *A. conspersa,* this behavior has never been evidenced by more than a very rapid flick with a duration of a few milliseconds. Only with the comparative data of *A. pseudonietana* does the potential communicative value of the wing flick become evident. Probably this prolonged exposure of the brightly colored wings is attractive to vertebrate predators, and only the large species can afford to use this as a communicative signal. *A conspersa,* for example, is so beset by avian predators in most areas that the life expectancy of whole populations is only three to four weeks (Willey & Willey, 1967). Our observations (unpublished) on *A. conspersa* in the plains of eastern Colorado indicate that these larger individuals take much longer flights, and are more conspicuous in general behavior than the montane populations. Much of the muted behavior of montane populations can be postulated as a result of extreme predator pressure.

Aggression.

The so-called "rival's song" is a common term which perhaps gives faulty perspective to the function and makeup of the male-interaction songs. Suffice it to say that the flutter-rasp serves to turn off courtship advances by a male in, at least, two well-defined instances: 1) when the courted male is alone and 2) when the courted male is part of a pair *in copulo.* In this way, aggression is prevented, conspicuous courtship interplays and fighting are mitigated and the insects are less obvious to predators. Indeed, the male flutter-rasp could be considered as forming also a courtship *interruption signal,* since the receptive female is not adversely affected by the flutter-rasp of the male *in copulo* and remains in a quiescent state.

Calling.

Here there are important questions to be asked. It is obvious that the flight crepitation performs the aggregation function which is supplied by the femoro-tegminal vibratory stridulations of the male and female Acridinae (Otte, 1968; Faber, 1953; Alexander, 1960). The crepitation by female *A. conspersa* may be equivalent to the response song of such acridines as *Chorthippus* females (Haskell, 1962). Although Faber (1953) makes much of the wing buzzes of both sexes while they are are on the ground, we have never seen that this action produces any significant reaction with *A. conspersa* and it may only be a comfort movement.

During the flight, the brightly colored hind wings flash red, orange or yellow depending on the phenotype (Willey & Willey, 1967) and the flash is arresting to human eyes. The mechanism of sound production by the wing is still open to investigation. Until very recently the best guesses suggested that the sounds were produced in a manner similar to that of a fan being snapped open and shut (Haskell, 1962). However, Otte (1968) described a possible instability of the wing membrane of loud crepitators when the wing is partially expanded which "pops" into the opposite configuration and could produce the crepitation.

The presence of the femoro-tegminal solitary buzz excites interest also, since this signal seems to duplicate the function of the flight crepitation. Such sounds in the acridines are definitely implicated in the onset of pair formation and male location. Although we have never observed anything but ignoring or evasive action by females in response to the sound, the frequency of performance by solitary or recently repulsed males makes it unlikely that the buzz is completely redundant or non-functional. Otte (1968) has reported frequent buzzing ("vibratory stridulation") for *A. sulphurea.* Only once did he hear it in *A. pseudonietana* whereas we have heard it frequently and recorded it in three populations of this species. For some, but not all, populations of *A. simplex,* he reported similar buzzes, but none have been heard at all in *A. xanthoptera* and *A. granulata.* Buzzing also was recorded for *A. conspersa,* but no details were given. Further, Otte believes that the buzz is a part of the courtship, a contention which we find not entirely satisfactory, since we find that it it predominantly given under situations of solitude, refusal or loss of visual contact (as Otte also admits). It may, then, be a dual purpose sound, evolving from a call perhaps, to a courtship interruption sound (pair-reforming). Secondly, the opportunity for field studies to turn up this sound is remote or fortuitous at best, since the signal is most frequently performed (in *A. conspersa*) during the third and fourth week just before the general drop-off in social activity and die-off in the population due to predation. Therefore, the age of any population must be considered before comparing populations or species in this respect, and caged captives or reared populations may be necessary to turn up such sounds.

The close relationship of the Oedipodinae and the Acridinae (Rehn and Grant, 1960) has significance here. Most of the Acridinae are highly specialized for emitting solitary stridulations (buzzes) as the sole, long distance male-female signalling device and usually the female is unseen. Many of the Oedipodinae, on the other hand, utilize spontaneous flight crepitation, instead, for distance communication and femoral-tegminal stridulations are less specialized and distinct interspecifically.

Courtship.

This sequence is often broken into two parts, one is the approach by the male and the other is the pre-mounting cry or Anspringlaut (Faber, 1936) produced just before the male "leaps" on the female. In *A. conspersa* the demarcation between the two songs is well marked since the approach chirp is unitary and periodically produced between or during spurts of running, but the multiple chirp (Fig. 4) is given only while the insect is standing still (near the female usually) and mounting occurs immediately thereafter unless prevented by the female's non-receptive behavior. Otte (1968) has observed the same type of demarcation in other *Arphia* species (and, by inference, also in *A. conspersa*) but feels that the multiple chirp is only an intensifier of the unitary sound as the male nears the female.

We are amassing data on males of known adult age in the field and in caged populations. It is evident so far that any or all of the acoustical signals by the male can be omitted even in successful courtships, and mounting of receptive females can be very casual — especially among older individuals. Very little is known about the signals of female receptivity, and the observed sexual presentation by the female may only be a function of propinquity. Thus far, no vestige of stridulation has been observed in females of *A. conspersa* and has rarely been reported for any other species of oedipodine. This is despite the fact that many acridine and oedipodine females (including *A. conspersa*) have a well-developed stridulatory appratus (Rehn & Grant, 1960, and this present paper). Indeed, R. Alexander (1960) reported that he had recorded the female response song in *Chortophaga viridifasciata,* an oedipodine. It is possible that virgin females in many species signal the courting males if they are at a distance or if the view of the male is obstructed. However, the probable redundancy of crepitation and response stridulation may be contributing to a selection against the weaker signal. The lack of consistent data on virgin, receptive females plus data on individual males of known age makes the courtship interaction of most oedipodines an unclear picture at best.

CONCLUSIONS

Social interaction in *Arphia conspersa* can be divided for convenience into two separate systems of communication involving specific methods of signaling: 1) communication at a distance and 2) communication during physical contact. In these grasshoppers, signaling from a distance involves visual and acoustic modalities. Signaling during contact is mainly tactile. Some chemosensory input generated by the receptive female may be present but such an explanation is not necessary for any of the observed signal-response systems.

Signals at a distance include sounds emitted by the wings under certain circumstances during flight, sounds produced by movements of the hind femora over the tegmina, and soundless but specialized movements of the hind legs during specific interaction sequences. Other sounds are emitted occasionally, such as mandible-clicking, wing-snapping, ground-scraping and -tapping, but we have never observed any evidence of meaningful reaction by other grasshoppers except avoidance reaction in the case of some wing-snapping. Most of those motions which seem to have communicative function combine a flash of bright color with a sound produced by the same motion. We are investigating the relative importance of the visual and auditory portions of the signal and have some evidence that the sound and color are intensifiers and modifiers in the several combinations such as the rasp, buzz, chirp and squeal. The resulting visual flicker plus the buzzing sound should be very attention-getting to grasshoppers in which auditory flicker fusion probably doesn't occur until pulse rate frequencies reach the order of 200/second (Haskell, 1961) and visual flicker fusion may be more than 50/second (Dethier, 1964). However, the question of flicker perception is still an open matter and grasshoppers may have even higher rates of flicker resolution (Dethier, 1964).

It is interesting, then, how visual-acoustical signals have diversified within this species. In *A. conspersa,* the basic single-pulsed sound is similar in the chirp, rasp, buzz, squeal. Each of these signals differs primarily from the others in pulse duration, intensity, and pulse rate frequency. The chirp is intense, variably spaced, multiple and with a high pulse rate frequency. The rasp is intermediate in pulse rate frequency and of lower amplitude. The squeal is a rapidly delivered short train of chirps, with a high degree of frequency variation. It is of further significance that the unitary chirp, precopulatory burst of chirps, flutter-rasp, flight crepitation, and buzz signals differ in pulse rate frequency in an ascending scale of 1, 10, 20, 45, and 100/second respectively, which indirectly indicates a Weber-Fechner-like discrimination of pulse rate frequency. If one invokes an ascending scale of specific action potential (ethologists' SAP) which is excited by this series of frequencies to produce specific behavioral patterns, then such a relationship between perception and specific choice of behavior pattern can be postulated which could be independent of the intensity of the specific stimulus. Differences in intensity of each stimulus could in turn result in complex scototaxis and phonotaxis in a manner similar to that shown in *Ephippiger spp.* (Dumortier, 1963). We are currently studying this problem in respect to the male-male interactions in several species of *Arphia.*

ACKNOWLEDGEMENTS

We are grateful for the aid of David Werner, Ruth Lewert, Allen Berlind, Gerald Mussgnug, Joyce Redemske, Melvin Shemluck, and Marianne Niedzlek, our assistants and students for at least one of the years of study. We thank Dr. Walter Roberts, Director of the National Center for Atmospheric Research and Dr. James Deardorff for enabling us to study the Table Mesa population during May and June of 1964. We also are grateful for the aid and encouragement of Professor Robert Enders, Director of the Rocky Mountain Biological Laboratories during most of the period of this research, and Professor John Corliss, Head of the Department of Biological Sciences, University of Illinois at Chicago Circle. We appreciate the helpful suggestions and encouragement of Dr. Richard D. Alexander, University of Michigan, who made, several years ago, sonograms of signals we recorded very early in the study.

SUMMARY

Arphia conspersa, an oedipodine grasshopper, is widely distributed

in western North America. The nymphs overwinter and emerge as adults soon after the snows melt. The active breeding season above 8,000 feet elevation near Gunnison, Colorado, is short and isolated temporally from that of other species which overwinter only in the egg stage.

Social communication includes silent motions of the hind legs by both sexes, as well as various frictional sounds which are produced only by the male which passes the femora over a specialized file on the tegman. Each of these patterns of movement delivers a visual and acoustic flicker stimulus which is distinct in pulse rate frequency (PRF) from all the other signals. Silent single flicks of the hind femora disclose the bright yellow (in males) or brownish yellow (in females) abdomen and serve as non-specific advertisement of presence. The sounds produced by unitary or multiple leg movements can be single *chirps* (courtship approach), multiple *chirps* (PRF up to 5/0.3 sec., probably a pre-mounting song), *flutter-rasp* (PRF=20 single or double pulses/sec., prevention of aggression among males), and *buzz* (PRF=110-120/sec., after repulsion by the female, after losing track of the female, or after hearing another courtship sequence). A *squeal* is produced in response to severe disturbance, such as capture, injury, loud multiple-pulsed sounds, etc. The brightly colored wings alone also produce pulsed sounds (PRF=45-50/sec., *crepitations*) during spontaneous flights by males and sometimes females.

Females have not yet been observed to stridulate, though they have a normal stridulatory apparatus. They reject courtship in several ways, ranging from merely closing the subgenital plate to a threat display which involves raising the hind femora past the vertical position and waving the tibiae in a slow and deliberate manner. Acceptance of the male ordinarily is passive, but active solicitation has been observed.

This wealth of definitive signals and responses makes study of species in this genus important for communication research and the evolution of communication systems in insects.

PROTOCOL (Recording and Missilyzer transfer data)[4]

Fig. 2. Crepitation = AKG microphone with parabola, distance 3 feet, Nagra input –20 db, 15 ips, sun thermometer 40°C, Gothic about 9600 feet; Missilyzer input VU = +1/+2, output VU –6/–5, ML 7.5.

Fig. 3. Clicks produced by an Exacta camera reset mechanism.

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[4] All recordings were at 15 ips, patterns normal, displays equivalent to normal speed (HH input and output), *ips* = inches per second, analysing filter bandwidth for all displays = 600 Hz.

Fig. 4. Chirp — Sennheiser 804 microphone, 3-4 in., 0 db, 15 ips, 37° incandescent lighting, grasshopper age 4 weeks from Black Mesa, recorded at Gothic at 9500 feet; Missilyzer VU in –1/0, VU out –6.5/–.5, ML 7.5.

Fig. 5. Alarm cry of a chipmunk (*Eutamias* sp.) — AKG microphone with parabola, 20 feet, –20 db, 15 ips, about 25°C (6:00 MDT), recorded at Gothic, 9700 feet; Missilyzer VU in +2/3, VU out –10/–7, ML 8.0.

Fig. 6. Crepitation and squeal — AKG microphone without parabola, 4-8 in, –10 db, 15 ips, 37° Sun, Gothic 9500 feet; Missilyser VU in +2/+3, VU out –10/7, ML 8.0, Spectrogram repeated at VU –10 five times to emphasize squeal over background (no decrease in resolution was observable).

Fig. 8. Buzz — AKG microphone with parabola, 3 feet, –20 db, 15 ips, 40°C, Gothic at 9600 feet; Missilyzer VU in +2/+3, VU out –.5/0, ML 7.5.

Fig. 9. Flutter-rasp — Sennheiser 804 microphone, 4 in. 0 db, 15 ips, 37°C incandescent lighting, grasshopper age about 4 weeks from Black Mesa, recorded at Gothic at 9500 feet; Missilyzer VU in +1.5/+2.5, VU out –6.5/–5.5, ML 7.5.

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CRETACEOUS INSECTS FROM LABRADOR.
4. A NEW FAMILY OF BEETLES (COLEOPTERA: ARCHOSTEMATA)*

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Academy of Sciences of the USSR

Through the kindness of Professor F. M. Carpenter, I have been able to study some fossil beetles from Cretaceous strata in Northern Labrador, Canada, collected by Professor Erling Dorf of Princeton University and contained in the paleontological collections of that university. The age of the deposit in which the beetles were found is early Cenomanian or very late Albian, as shown by the pollen and plant fragments (Dorf, 1967). The collection of beetles consists of eight elytra.

Four of these elytra (nos. 87272, 87274, 87275, 87276) have preserved the structure described by Rohdendorf (1961) as a furrow ("schiza"). Study of Recent beetles has shown this structure to be a process on the underside of the elytron, present only in water beetles. Functionally, it is a part of the device for keeping air in the subelytral space. Since elytra such as these are very common among schizophoroid beetles, which are numerous in Mesozoic deposits of mid-Asia (Ponomarenko, 1968, 1969), their generic affinities cannot be determined without knowledge of additional morphological details.

Two other elytra (nos. 87271 and 87278) have longitudinal striae. This sculpturing of elytra is very common and the systematic position of beetles cannot be determined satisfactorily by it. One of these elytra, however, on the basis of the shape of the elytron with an oblique base, ten rows of large punctures and a complete slender line along the sutral margin, bears a strong resemblance to the haliplid *Peltodytes*.

The two remaining elytra belong to the Archostemata. One specimen (no. 87277) belongs to the family Cupedidae. Although most Recent cupedid genera are present in the New World, this is the

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The previous parts in this series were published in *Psyche*, vol. 74, pp. 267-289, 1967.

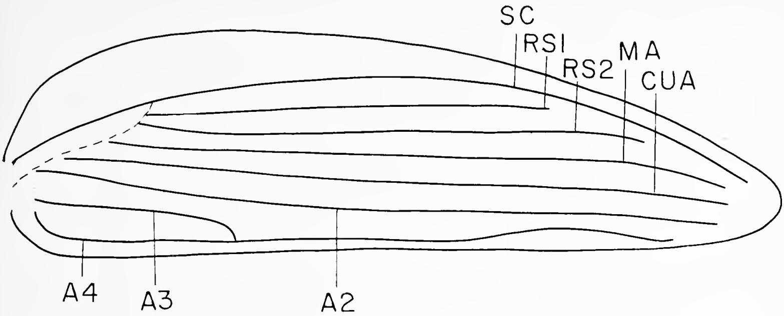

Figure 1. Elytron of *Labradorocoleus carpenteri,* gen. nov., sp. nov. Interpretation of venation based on Tshekardocoleidae.

first fossil cupedid from that region. In structure, the elytron is similar to that of *Omma* and *Tetraphalerus* (these two genera being indistinguishable on elytral structure). Modern *Omma* occurs in Australia, and *Tetraphalerus* in South America, but numerous fossils of these beetles have been found in Mesozoic deposits of Europe and Asia (Ponomarenko, 1968). The other specimen (no. 87273) from Labrador is unquestionably representative of a new family. This elytron shows a number of primitive features and is related to the Lower Permian family Tshekardocoleidae (Rohdendorf, 1944; Ponomarenko, 1963, 1969; Kukalová, 1965, 1969) from Russia and Czechoslovakia. Among the thousands of Permian and Mesozoic beetles studied by the author, there are no other members of this new family or forms intermediate between it and the tshekardocoleids.

Family **Labrodorocoleidae**, fam. nov.

This family is based on a single genus, *Labradorocoleus*, gen. nov., known only from an elytron. Elytron very convex basally, flattened to the apex, which is rounded. Epipleural (costal) space very wide in the proximal half, with several rows of large rounded cells. Venation of elytron cellulate, the principal and intermediate longitudinal veins being clearly distinguishable. Seven principal longitudinal veins present and parallel to the sutural margin. The nomenclature of these veins, based on a comparison with elytral venation of the tshekardocoleids, is shown in figure 1. A3 is very long; two rows of cells present between A3 and A4, one row of distinct cells between A4 and the sutural margin.

This new family is related to the Tshekardocoleidae by having a wide epipleural margin with several rows of cells, two Rs veins, a long A3, two rows of cells between A3 and A4, and one row

Figure 2. *Labradorocoleus carpenteri*, gen. nov., sp. nov. Photograph of holotype, Princeton University Paleontological Collections. Length of elytron, 7 mm. (Photograph by F. M. Carpenter).

between A4 and the sutural margin. It is distinguished by the complete reduction of CuP and by having all veins parallel to the elytral margin.

Labradorocoleus, gen. nov.

Type species: *Labradorocoleus carpenteri*, sp. nov.

Epipleural space narrowing to apex. The rs2-area is narrow before the middle of the elytron, with one row of cells; two rows present in the distal part of the elytron. The rest of the areas with two rows of cells. A3 more than a quarter the length of the elytron, the second row of cells in its area very short. Cells in the 24-area typically large.

This genus includes a single species from Cretaceous deposits of Canada.

Labradorocoleus carpenteri, sp. nov.

Figures 1 and 2

Epipleural space on the base with four rows of cells, with three rows in the basal third, one row in the apical third. Apical third with A4 curved forward. Cells of elytron broader than the veins. Intermediate longitudinal veins for the most part straight.

Length of elytron: 7 mm.

Holotype: No. 87273 a,b, Invertebrate Paleontology collections, Princeton University. It is a well-preserved, isolated, right elytron. The humeral part, however, is damaged, and the bases of all the veins, except the anal, are impossible to distinguish. The fossil was collected by Professor Erling Dorf in 1958, at Redmond No. 1 deposit in the Knob Lake District (near Schefferville), Labrador, Canada.

The species is named in honor of Professor F. M. Carpenter, whose courtesy and aid made possible this study.

The discovery of this beetle, with its many tshekardocoleid-like features, is very interesting. Such features were lost by all other beetles during Upper Permian time. The labradorocoleids appear to have developed the complete elytral venation independently of the tshekardocoleids and at a later time; yet this family is not interediate between the tshekardocoleids and more advanced forms like cupedids and permocupedids, for the rudimentary CuP, which is present in permocupedids, is absent in the labradorocoleids. Thus, the mechanical perfection of elytral venation was evolved in parallel with that of the permocupedid-cupedid line. In conclusion, then, the labradorocoleids arose from a tshekardocoleoid branch of archostemate beetles evolving with the permocupedid-cupedid branch, and formed with this line, a "sibling-group" in the sense of Hennig.

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TWO NEW GENERA OF DIAPRIINAE (DIAPRIIDAE, HYMENOPTERA) WITH TRANSANTARCTIC RELATIONSHIPS

By Lubomir Masner*
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Up to the present only a few species of proctotrupoid wasps have been known to have transantarctic relationships. The peculiar family Monomachidae is represented both in Australia and South America (Schulz, 1911; Riek, 1955). Among the Proctotrupidae the genus *Austroserphus* Dodd is known from Australia (subg. *Austroserphus* s.str.) and Chile (subg. *Austrocodrus* Ogloblin) (Ogloblin, 1959). In the Scelionidae, *Archaeoteleia* Masner was described with one species from New Zealand and four species from Chile (Masner, 1968). The subfamily Ambositrinae (Diapriidae) was shown to be of southern origin (Fabritius, 1968; Masner, 1969).

The two new genera of Diapriinae (Diapriidae) described below are the first known representatives of this subfamily that show transantarctic relationships. It is believed that with better knowledge of Australian and Neotropic Proctotrupoidea more examples of transantarctic relationships will be discovered. The aim of this paper is to challenge other students in this group to give some attention to this phenomenon in zoogeography.

The two genera described below are also interesting from the point of view of morphology and adaptation. In particular, the Neotropic genus from Brazil displays the highest range of morphological reduction so far discovered in the subfamily Diapriinae. The wingless females are in fact blind as their eyes are reduced to mere points and the ocelli are completely absent. In one species the antenna has only 9 segments and the tarsi are reduced to four segments. This is the first known instance of a diapriid having 4-segmented tarsi. Although these characters appear very remarkable we interpret them as adaptive modifications within a very plastic genus. Biological data are still not available and are greatly desired to understand the nature of these unique adaptations.

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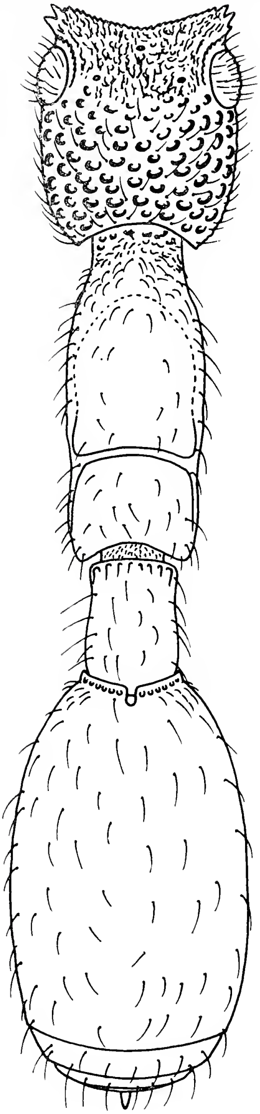

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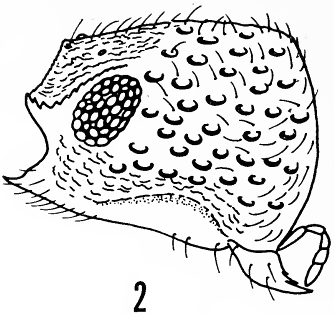

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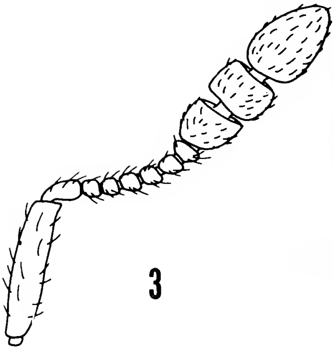

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Fig. 1. *Austropria serraticeps* n.sp. (holotype).
Fig. 2. *Austropria serraticeps* n.sp. (holotype), head (lateral view).
Fig. 3. *Austropria serraticeps* n.sp. (holotype), antenna.

Austropria gen.n.

Female. — Most of head heavily punctured; punctures dense, deep and rather large; seen from above head distinctly longer than wide; frons deeply excavated at antennal shelf, bordered with a continuous serrate crest anteriorly, the latter with largest teeth right above eyes; frons above clypeus longitudinally bulging, flanked by two smooth oblong impressions just above mandibles; eyes round, rather small, hairy, composed of large facets; ocelli small yet distinct, lateral ones closer to orbit than to median ocellus; mandibles protruded to form a beak directed almost backwards (opisthognathous); maxillary palpi 5-segmented, labial 2-segmented; antenna 11-segmented, with an abrupt 3-segmented club.

Mesosoma extensively modified due to apterism; most of the sutures obliterated or indistinct; prothorax rather large, suture dividing prothorax from mesoscutum very faint and almost invisible; mesoscutum almost flat, fused with scutellum and metanotum; suture dividing scutellum from metanotum indicated by an indistinct row of minute punctures; tegulae in the form of minute points, wings wholly absent; propodeum very long, separated distinctly from thorax by deep cleft, unarmed, flat, in same level as the rest of mesosoma; a faint suture running down from tegula to front coxa; tarsi 5-segmented; spur of front tibia unusually long.

Petiole cylindrical, slightly longer than wide; front margin of great tergite slightly elevated to form a foveolated collar, notched medially; great tergite occupying most of the length of metasoma; terminal segments very narrow, yet rather loose and not fused in a solid plate; great sternite with no fold basally.

Type species: *Austropria serraticeps* sp.n.

Austropria serraticeps sp.n.

(figs. 1, 2, 3)

Female holotype. — Sandringham, Vic., May 1928, J. C. Goudie coll. (National Museum of Victoria, Melbourne); unique.

Length 1.5 mm. Ferrugineous; antennal club, eyes and tip of metasoma black.

Head covered all over with dense silvery hairs, longer than wide (20:10), much wider than mesosoma (16:12), seen laterally longer than high (20:16); punctures on occiput, temples and genae large and deep yet less dense, not contiguous; punctures on vertex obscured by fine shagreened sculpture (between eyes); frons between antennal insertion and serrate crest almost smooth and shining, deeply concave; teeth of the serrate crest extending along the inner orbit, largest teeth just above eyes; eyes rather small, much shorter than temples (5:10); antennal socket with two little teeth directed forwards; scape finely shagreened, as long as 7 following segments combined, longer than wide (12:3), pedicel moderately oblong (4:2), segments 3-8 more narrow than pedicel, progressively shortened, as long as wide till slightly transverse, almost peniciliate; club (9-11th) abrupt, massive, progressively thickened, apical segment longest and widest, segments of club in proportions 3:4; 4:5; 7:5.5.

Mesosoma hairy like head, distinctly elongated (28:12) and constricted; prothorax dorsally with scattered punctures and tufts of hairs, distinctly neck-like protruded anteriorly; mesonotum only very slightly convex, smooth, highly polished, with only few isolated setigerous punctures; propodeum flat and almost smooth dorsally, with few scattered shallow punctures; posterior margin only slightly excavated, with no teeth or spines.

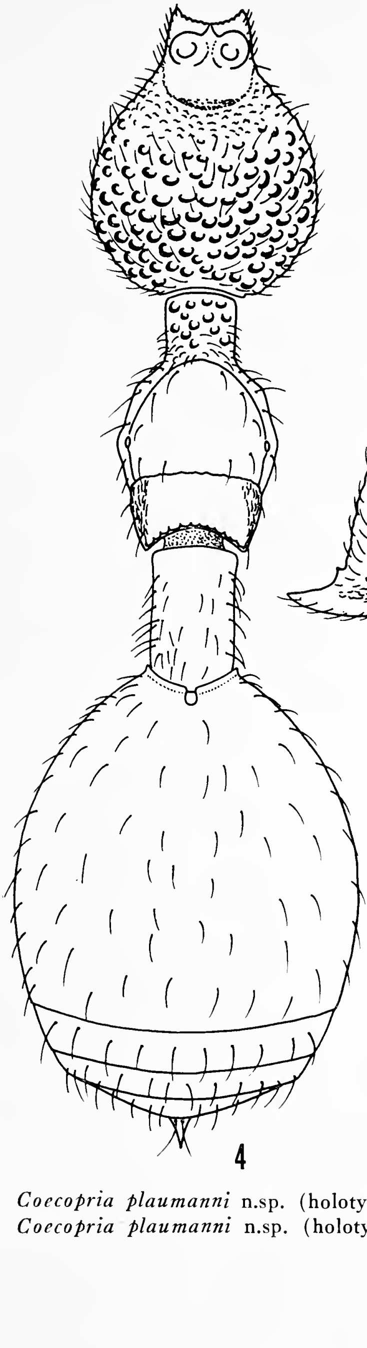
Petiole slightly elongated (10:7.5), with several indistinct longitudinal costae; rest of metasoma elongated (35:20), rather obtuse apically, with scattered hairs all over.

Coecopria gen.n.

Female. — Head heavily and evenly punctured all over, punctures deep, dense and contiguous; seen from above head either almost globose or elongated; antennal socket distinctly protruded forwards; frons more or less excavated at antennal shelf, bordered laterally (above eyes) with a ridge that tends to disappear medially; ocelli absent; eyes strongly reduced to one ommatidium point obviously devoid of function; mandibles opisthognathous, protruded backwards to form a beak; maxillary palpi reduced to an oval 1-segmented process, labial palpi appearing completely absent; antenna 9 or 10-segmented, with an abrupt 3-segmented club.

Mesoma showing different degrees of apterism in fusion of sclerites and sutures; mesoscutum always fused with scutellum and metanotum; prothorax either separated from mesothorax by a suture or fused with it; propodeum separated from thorax in two species but fused with it in one species; mesosoma almost flat above, all sclerites at same level; wings and tegulae absent but preserved as minute scales in one species; dorsal part of mesosoma either smooth and shining or punctured densely like head; tarsi 5 or 4-segmented; spur of front tibia very long.

Petiole cylindrical, elongated; front margin of great tergite slightly elevated in collar, notched medially; great sternite with longitudinal horseshoe-shaped fold with pilosity in the anterior part.



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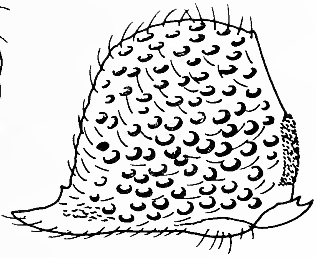

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Fig. 4. *Coecopria plaumanni* n.sp. (holotype).
Fig. 5. *Coecopria plaumanni* n.sp. (holotype), head (lateral view).

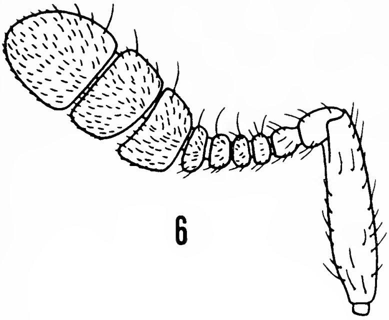
Type species: *Coecopria plaumanni*[2] sp.n.

Coecopria plaumanni sp.n.

(figs. 4, 5, 6, 7)

Female holotype. — Nova Teutonia, Santa Catarina, Brazil, October 1963, Fritz Plaumann coll. (Museum of Comparative Zoology, Cambridge, Mass., type no. 31727).

Length 1.5 mm. Light chestnut brown, metasoma darker, antennae (including club) and legs bright yellow.



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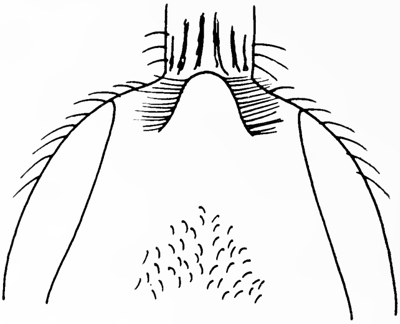

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Fig. 6. *Coecopria plaumanni* n.sp. (holotype), antenna.
Fig. 7. *Coecopria plaumanni* n.sp. (holotype), large sternite.

Head covered with dense hairs all over, almost globose if viewed dorsally but slightly longer than wide (27:22), if antennal prominence is included, longer than high (27:21), much wider than mesosoma (22:17); hind genae with little tufts of dense whitish hairs; punctures deep and dense yet not fully contiguous, particularly on occiput; vertex with fine transverse rugulosity; antennae as in fig. 6; scape and pedicel finely shagreened.

Mesosoma elongated (30:17), almost as wide as high (17:16), with long silvery hairs all over, hairs longer than those on head but less dense; prothorax clearly separated dorsally from mesothorax by suture, laterally from mesopleura by suture running down from spiracle to front coxa, neck-like constricted anteriorly and here densely hairy; mesoscutum fused with scutellum and metanotum, almost flat, wider than long (14:11), smooth and shining, with few

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[2] Named in honour of Mr. F. Plaumann in recognition of his interesting entomological collections in the Brazilian tropics.

scattered punctures; front wings reduced to minute scales; propodeum separated from thorax by a distinct suture, shining, reticulate-punctate all over; femora slightly incrassated; tarsi 5-segmented.

Petiole elongated (15:8), almost smooth and shining dorsally, with few scattered punctures, finely longitudinally striated laterally; median notch on front margin of great tergite deep and very distinct; great tergite extending to ¾ of the length of the body of metasoma (32:12), i.e. the terminal segments not particularly narrow; great sternite with horseshoe-shaped fold (with pilosity) very short, indicated only very anteriorly.

Material examined. — 9 females (paratypes in MCZ, Cambridge, and coll. L. Masner, Prague). 8 ♀♀, Nova Teutonia, Santa Catarina, Brazil, July 1959, August 1963, November 1962, all Fritz Plaumann collector. 1 ♀, Ibicare (27°09′; 51°18′) Brazil, 600 a.s.l., September 1960, Fritz Plaumann collector.

Variability. — No substantial variability encountered except for slight variation in body length (1.4-1.8 mm.).

Male. — Unknown.

Host. — Unknown.

Coecopria bella sp.n.

(Figs. 8, 9)

Female holotype. — Nova Teutonia, Santa Catarina, Brazil, July 1959, Fritz Plaumann coll. (Museum of Comparative Zoology, Cambridge, Mass., type no. 31725).

Length 2.1 mm. Head and mesosoma reddish-brown, legs and antennae honey yellow, metasoma dark brown to black, petiole brownish.

Head longer than wide (33:23), wider than mesosoma (23:17), longer than high (33:22); punctures very large and deep, contiguous; a small smooth spot above antennal insertion; hind genae with little tufts of whitish dense hairs, the same pilosity on opposite side of prosternum; crest of vertex distinct just above the single ommatidium, missing medially; scape finely shagreened, as long as 6 following segments combined, pedicel and 3rd segment slightly elongated, segments 4-7 shortened till transverse, club progressively incrassate, its first segment (i.e. 8th antennal segment) the smallest.

Mesosoma highly shining, hairy like head, constricted, slightly convex dorsally, longer than wide (37:17); all sutures fused, making mesosoma one solid body (fine suture running from prothoric spiracle down to front coxa, propodeum laterally with row of punctures indicating the former suture); punctures rather deep and dense on

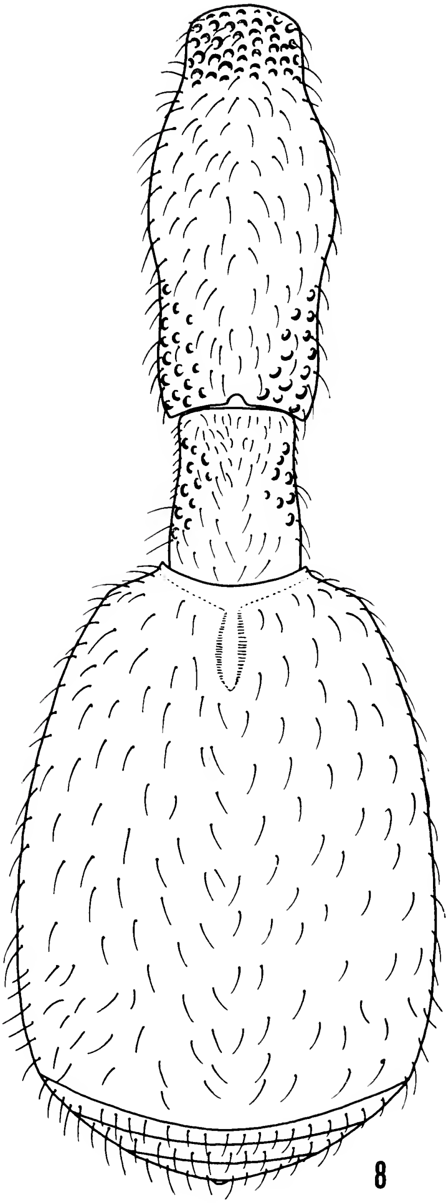

Fig. 8. *Coecopria bella* n.sp. (holotype).

neck-like constriction of prothorax but scattered and fine on rest of mesosoma; hind margin of propodeum with a delicate notch medially.

Petiole smooth and shining, with scattered fine punctures and small hairs, elongated (15:11); front margin of great tergite with very indistinct notch medially followed by impressed groove, tergite smooth, shining, hairy, occupying almost the whole body of mesosoma; the fold on great sternite very distinct, extending back to very end of sternite and here united to form a complete oval suture.

Material examined. — 3 females (paratypes, in coll. MCZ, Cambridge, Mass. and coll. L. Masner, Prague). Same data as in holotype.

Variability. — No variability encountered.

Male. — Unknown.

Host. — Unknown.

Coecopria pygmea sp.n.

(figs. 10, 11, 12, 13)

Female holotype. — Nova Teutonia, Santa Catarina, Brazil, September 1960, Fritz Plaumann coll. (Museum of Comparative Zoology, Cambridge, Mass., type no. 31726).

Length 1.1 mm. Head, scape, mesosoma and petiole amber yellow, rest of metasoma darker, flagellum and legs bright yellow.

Head covered with dense silvery hairs all over, longer than wide (17:14), wider than mesosoma (14:11), longer than high (17:12); punctures fine yet very dense, contiguous, absent only on little smooth spot just above antennal insertion; hind genae with no tuft of hairs; vertex with crest which is sharp and distinct laterally but almost missing medially; antenna as in fig. 11.

Mesosoma constricted, almost flat dorsally, longer than wide (20:11), slightly wider than high (11:9), hairy; prothorax fused with mesothorax both dorsally and laterally; mesoscutum fused with scutellum and metanotum, evenly longitudinally rugoso-punctate all over; mesepisternum distinctly separated by sutures from both prothorax and propodeum; propodeum separated from thorax by constriction and distinct suture both dorsally and laterally, of same sculpture as mesonotum; coxae and femora incrassate; tarsi 4-segmented (!), claws large (fig. 12).

Petiole slightly longer than wide (8:5), bent if seen laterally, hairy and finely punctate all over; front margin of great tergite deeply notched medially, the tergite almost bare antero-medially but densely hairy laterally and posteriorly, occupying not more than 2/3 of the

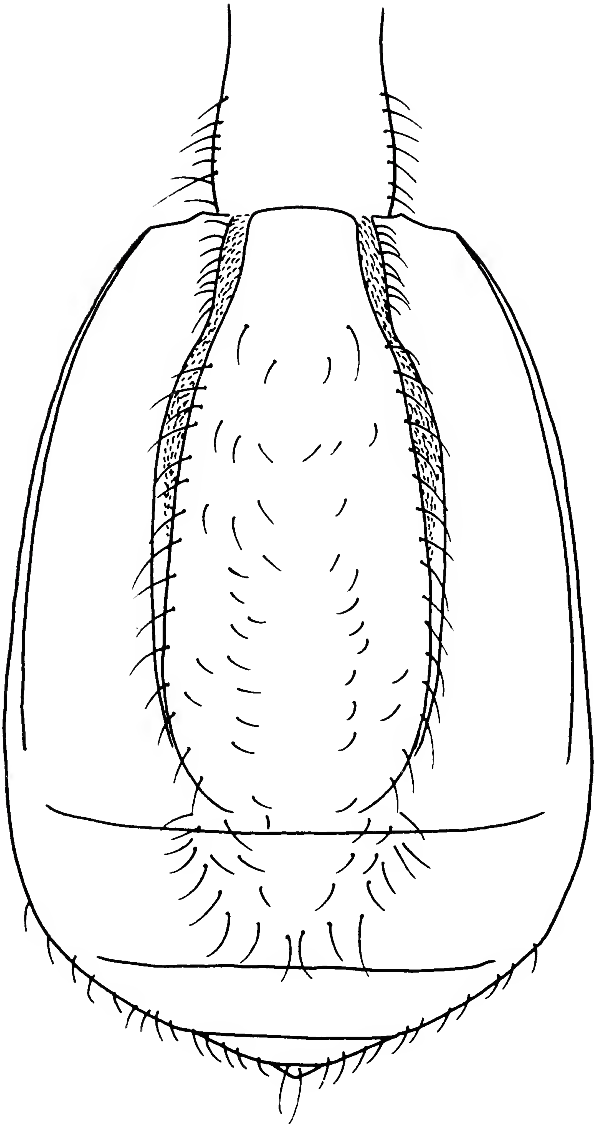

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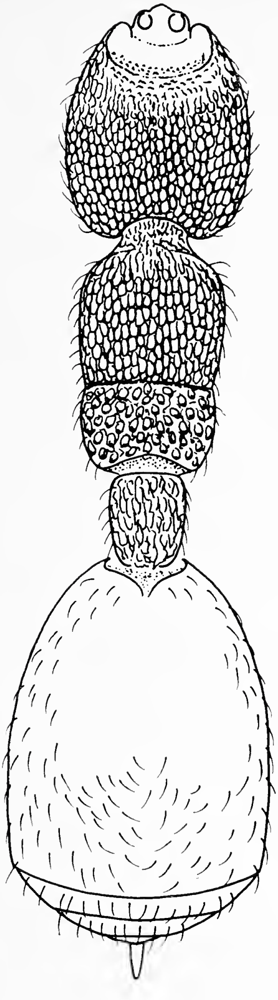
Fig. 9. *Coecopria bella* n.sp. (holotype), large sternite.



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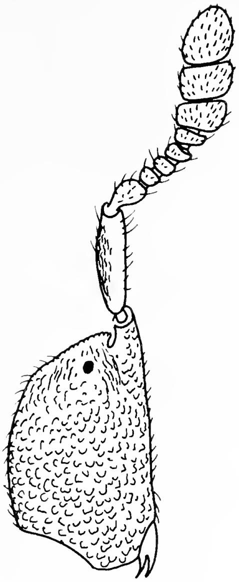

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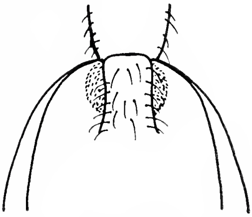

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Fig. 10. *Coecopria pygmea* n.sp. (holotype).
Fig. 11. *Coecopria pygmea* n.sp. (holotype), head and antenna.
Fig. 12. *Coecopria pygmea* n.sp. (holotype), middle leg.
Fig. 13. *Coecopria pygmea* n.sp. (holotype), large sternite.

length of the metasomatic body; great sternite distinctly protruded forwards to form a slight hump, horseshoe-shaped fold protruded backwards to 1/3 of length of the sternite, pilosity in the fold quite distinct and dense.

Material examined. — 3 females (paratypes, in coll. MCZ, Cambridge, Mass., and coll. L. Masner, Prague). 2 ♀♀, Chapeco, 27°07′; 52°36′ Brazil, 600 m.a.s.l., August 1960, Fritz Plaumann collector. 1 ♀, Erechim, 27°35′; 52°15′ Brazil, 750 m.a.s.l., July 1960, Fritz Plaumann, collector.

Variability. — Female from Erechim much paler in colour (pale yellow) with finer sculpture of mesosoma and with great tergite extending but to ½ of the length of metasomatic body.

Male. — Unknown.

Host. — Unknown.

Key to species of *Coecopria* gen.n.

1) Propodeum distinctly separated anteriorly from thorax by suture or row of deep punctures (figs. 4, 10); horseshoe-shaped fold of great sternite not extending beyond the basal 1/3 of the sclerite (figs. 7, 13) 2

— Prodeum completely fused with thorax (fig. 8); horseshoe-shaped fold of great sternite extending down to very apex of sclerite and here united, forming an oval field (fig. 9) .... *Coecopria bella* sp.n.

2) Antenna 10-segmented; tarsi 5-segmented; mesonotum almost smooth, shining, with only few scattered fine punctures; head globose (fig. 4) .... *Coecopria plaumanni* sp.n.

— Antenna 9-segmented; tarsi 4-segmented; mesonotum evenly longitudinally rugoso-punctate all over; head elongated (fig. 10) .... *Coecopria pygmea* sp.n.

DISCUSSION

Twelve genera of Diapriinae are known to have fewer than 12 antennal segments: *Solenopsia* Wasmann (Palearctic), *Bruesopria* Wing (Nearctic), *Philolestes* Kieffer (Neotropic), *Doliopria* Kieffer (Neotropic, Nearctic), *Mitropria* Ogloblin (Neotropic), *Ferrieropria* Sundholm (Ethiopian), *Solenopsiella* Dodd (Australia), *Polydiapria* Dodd (Australia), *Nanopria* Kieffer (Ethiopian), *Xanthopria* Brues (Neotropic), *Notoxopria* Kieffer (Neotropic) and *Asolenopsia* Kieffer (Neotropic).

Austropria and *Coecopria* show close ties only to *Doliopria* Kieffer and (?) *Mitropria* Ogloblin. The punctate head in *Austropria* and

Coecopria may be compared with similar structures in *Malvina* Cameron (New Zealand) and *Odontopria* Kieffer (Oriental), but this is merely due to convergence. *Austropria* is superficially reminiscent of *Psilus* Panzer (*Galesus* Haliday) but has a different structure of the terminal segments of the metasoma. *Austropria* shows no ties to any of Australian genera (? *Solenopsiella* Dodd) but does to Neotropic *Doliopria* and particularly to *Coecopria.* The latter genus is apparently closest to *Austropria,* but is also close to *Doliopria* and (?) *Mitropria* (see the key below). Among the characters considered to be common and typical for both *Austropria* and *Coecopria* the following should be emphasized: head heavily punctured, front margin of great tergite notched medially, antennae with 11 or less segments, abrupt 3-segmented antennal club, mandibles protruded to form an opisthognathous beak, high degree of apterism and reduction of mesosoma.

Key to genera related to *Austropria* and *Coecopria*

1) Head heavily thimble-like punctured, punctures rather large, deep and dense (cf. *Malvina* Cam. and *Odontopria* Kieff.) 2

— Head with no special punctulation, smooth, shining, sometimes with minute teeth anteriorly 3

2) Antenna 11-segmented; eyes well developed, ocelli present; great sternite with no fold basally; palpi 5, 2 .... *Austropria* gen.n.

— Antenna 10 or 9-segmented; eyes reduced to one ommatidium point; ocelli absent; great sternite basally with a peculiar horseshoe-shaped fold filled with pilosity, palpi 1, 0 .... *Coecopria* gen.n.

3) Vertex with a few minute teeth; anterior margin of great tergite not notched medially; mandibles hypognathous, protruded downwards to form a beak .... *Mitropria* Ogloblin

— Vertex unarmed; anterior margin of great tergite notched medially; mandibles normal and not protruded .... *Doliopria* Kieffer

If compared with each other *Austropria* is, no doubt, more plesiomorphous and less specialized than *Coecopria.* Table I illustrates this development.

Coecopria presents by itself a fine example of evolution within one genus. The most plesiomorphous is *C. plaumanni* (the type species). It has 10-segmented antenna, the propodeum clearly separated from thorax, a well developed suture between the prothorax and mesoscutum, 5-segmented tarsi and the fold on the great sternite less extended backwards. Moreover, it is the only species in *Coecopria* with rudiments of wings. *C. pygmea* is considered apomorphous for strong morphological reduction of antennae (9-segmented), tarsi (4-segmented) and suture between prothorax and mesoscutum. *C. bella* exhibits both the highest degree of reduction of mesosoma (all sutures fused) and highest specialization in the horseshoe-shaped fold of great sternite.

TABLE I

CHARACTER	*Austropria*	*Coecopria*
Antennal segments	11	10(2 spp.) or 9(1 sp.)
Maxillary palpi	5	1
Labial palpi	2	0
Eyes	only slightly reduced but functioning	reduced to one ommatidium point devoid of function
Ocelli	reduced yet well defined	absent
Propodeum	separated from thorax by deep cleavage	separated (2 spp.) or fused with thorax (1 sp.)
Suture between prothorax and mesoscutum	very faint yet developed	present (1 sp.) or fused (2 spp.)
Tarsi	5	5 (2 spp.) 4 (1 sp.)
Punctulation of head	incomplete, uneven and less dense	complete, even, the punctures contiguous
Great sternite	no specialization	horseshoe-shaped fold extending back to 1/3 of sternite (2 spp.) or down to very apex of sternite (1 sp.)

The high degree of morphological reduction on the one hand (*Austropria, Coecopria*) and the peculiar specialization of the great sternite on the other hand (*Coecopria*) are interpreted as potential adaptations to special behaviour and habitat. Unfortunately, this can be only guessed at, as no ecological or biological data are available both for *Austropria* and *Coecopria.* Particularly in *Coecopria* these adaptations are really striking and we may speculate about myrmecophylic habits in this genus. The punctulation of the head in *Coecopria* might be explained as mimicry of the host ants. The dense pilosity within the horseshoe-shaped fold on the great sternite may be explained as a source of an attractive exudate licked by ants. The formation of the mouth parts (reduction of palpi, opisthognathous mandibles) together with the strong reduction of eyes might indicate that the species of *Coecopria* are fed by ants. The absence of males in material of *Coecopria* suggests thelytoky as a possible mode of reproduction.

ACKNOWLEDGEMENTS

Thanks are extended to Dr. H. E. Evans (Museum of Comparative Zoology, Cambridge, Mass.) and Mr. A. Neboiss (National Museum of Victoria, Melbourne, Vict.) for the kind loan of material. The author is also indebted to Harvard University, Cambridge, Mass., for a grant in 1964 which enabled him to study the rich material in the Museum of Comparative Zoology.

SUMMARY

Austropria gen.n. (Diapriidae, Diapriinae) with *serraticeps* sp.n. as type-species is described from Australia (Victoria). *Coecopria* gen.n. (Diapriidae, Diapriinae) is described from Brazil, containing three new species; *plaumanni* sp.n. (type-species), *bella* sp.n. and *pygmea* sp.n.

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NORTH AMERICAN GROUND-BEETLES (COLEOPTERA, CARABIDAE, EXCLUDING CICINDELINAE) DESCRIBED BY THOMAS SAY: DESIGNATION OF LECTOTYPES AND NEOTYPES

By Carl H. Lindroth[1] and Richard Freitag[2]

Introduction

Thomas Say (1787-1834) was the founder of scientific entomology and conchology in North America. He described an immense number of insects of all orders, among the Carabidae (incl. Cicindelinae) no less than 165 species. They were included in the following eight papers:

1817. Descriptions of several new species of North American insects. Journ. Acad. Nat. Sci. 1:2. Philadelphia. pp. 19-23. (Only *Cicindela*, among the Carabidae.)

1818. A monograph of North American insects, of the genus *Cicindela*. Trans. Amer. Philos. Soc. (N. S.) 1. Philadelphia. pp. 401-426.

1823a. Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under the command of Major Long. Journ. Acad. Nat. Sci. *3*:1. Philadelphia. pp. 139-216.

1823b.[3] Descriptions of insects of the families of Carabici and Hydrocanthari of Latreille, inhabiting North America. Trans. Amer. Philos. Soc. (N. S.) *2*:1. Philadelphia. pp. 1-109.

1824. Appendix to the narrative of an expedition to the source of St. Peter's river, &c., under the command of Stephen H. Long, Major U. S. T. E. 2. Philadelphia. pp. 268-378.

1825. American entomology. II. Philadelphia. Pls. 19-36.

1828. American entomology. III. Philadelphia. Pls. 37-54.

1834.[4] Descriptions of new North American insects and observa-

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[2] Lakehead Univ., Port Arthur, Ontario, Canada.

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[3] The year of publication of this important paper is much discussed. It is often given as 1825 (e. g. by Hagen 1862-63; Leng 1929; Horn & Schenkling 1928-29), but Leconte (1859b, p. 435) is obviously right in assuming the year to be 1823. This, among other things, gives certain Say names priority over names given by Germar (1824), as expressly stated by Say himself (1834, p. 421, *Anchomenus cincticollis*).

[4] Part of Say's paper of 1834 had been printed in 1829-33 in a newspaper, "The Disseminator," and another part as a separate pamphlet, both at New Harmony, Ind. (see Leconte 1859b, p. 521). Neither can be regarded as valid publication.

tions on some already described. Trans. Amer. Philos. Soc. 4. Philadelphia. pp. 409-470.

In the present paper we have treated only the true ground-beetles. The 16 Say species of tiger beetles (subfam. *Cicindelinae*) are omitted and also 12 species described from Mexico. The remaining specific names given by Say among the Carabidae are 147 in number. Leng (1920) gives the same figure, but two of his names *(Calosoma indistinctum, Harpalus iricolor)*, listed as synonyms, are *nomina nuda.* On the other hand, *Calathus gregarius,* in Leng, was attributed to Dejean instead of to Say, and *Harpalus similis (Anisotarsus s.)* was omitted.

Of the two authors of the present paper, R. Freitag is responsible for the 5 species belonging to genus (or subgenus) *Evarthrus* among the Pterostichini, whereas C. H. Lindroth studied the remaining species with kind help, in some cases, from the following experts, who selected neotypes among their specialities:

Prof. R. T. Allen, University of Arkansas, Fayetteville, Ark., *Loxandrus rectus.*

Mr. T. L. Erwin, University of Alberta, Edmonta, Alta., *Brachinus cyanipennis* and *B. stygicornis.*

Mr. T. F. Hlavac, Harvard University, Cambridge, Massachusetts, *Clivina pallida.*

Say's descriptions were usually good, sometimes excellent *for his time.* Nevertheless, many of them, notably of course in critical genera, cannot be reliably interpreted. Unfortunately, Say's private collection was entirely destroyed after his death (Leconte 1859a, p. VI; Ord 1859, p. XIX, footnote), and a comparison with authentic Say specimens is therefore excluded (but see below). For the correctness of the present applications of his names, we are indebted primarily to John L. Leconte who, in 1859, edited "The Complete Writings of Thomas Say," with comments as to the right interpretation and taxonomic position of most Say species of Coleoptera. The Leconte Collection, in the Museum of Comparative Zoology (MCZ), Cambridge, Mass., provides a complete picture of how the Say species were interpreted by him.

In order to stabilize future use of specific names given by Say, it is highly desirable to designate type specimens. The aim of the present paper is to do so, as far as ground-beetles are concerned. It might seem, considering the total destruction of the Say Collection (see above), that a selection of neotypes would be the only solution. However, it so happened that Say distributed specimens from his own collection to at least one of his contemporaries abroad, Count

P. F. M. A. Dejean, in France. This is apparent from Dejean's famous work, "Spécies Général des Coléoptères" (Vols. I-V, 1825-31). When he wrote the first volume (1825), Dejean had not acquired contact with Say, but in the preface to Vol. 2 (1826, p. VIII) he acknowledges, in a general way, having received many Say specimens. In this, as well as in the later volumes of his work, when re-describing certain Say species, Dejean mentions that Say had sent him specimens. This is the case for the species listed in Table 1. Under many other species names, here omitted, Dejean quotes Say as the author but without mentioning specimens received from him.

One of my assistants, Mr. Reinhold Charpentier, when visiting the Muséum National d'Histoire Naturelle in Paris (MNP) in 1967, kindly undertook to study the Oberthür Collection, which includes the Dejean Collection, to search for genuine Say specimens. Dejean specimens are easily recognized by their bright green labels (see Lind-

Table 1. Say species mentioned by Dejean in "Spécies Général des Coléoptères," Parts II-V, as received from Say (modern generic names used). An * = with Say's name on the specimen.

Species	Say description	Dejean reference
Agonum decentis	1823b: 53	III.1828:107
Amara impuncticollis	1823b: 36	III.1828:466
**A. musculis*	1823b: 35	III.1828:478
**Anisodactylus agricola*	1823b: 33	IV.1829:151
A. baltimoriensis	1823b: 33	IV.1829:154
**A. caenus*	1823b: 34	IV.1829:159
A. rusticus	1823b: 32	IV.1829:157
**Anisotarsus terminatus*	1823b: 48	IV.1829:356
**Bembidion contractum*	1823b: 85	V.1831:124
**B. dorsale*	1823b: 84	V.1831: 72
**B. levigatum*	1823b: 84	V.1831:151
Calosoma luxatum	1823a:149	II.1826:197
**Carabus sylvosus*	1823b: 75	II.1826:152
**Chlaenius emarginatus*	1823b: 63	II.1826:367
Dyschirius globulosus	1823b: 23	II.1826:480
D. pallipennis	1823b: 24	II.1826:481
D. sphaericollis	1823b: 23	II.1826:480
Harpalus erraticus	1823b: 27	IV.1829:258
**H. faunus*	1823b: 28	IV.1829:254
**Lebia tricolor*	1823b: 11	II.1826:454
Olisthopus parmatus	1823b: 49	III.1828:182
**Pasimachus subsulcatus*	1823b: 19	II.1826:471
Scaphinotus bilobus	1823b: 73	II.1826: 17
**Stenolophus ochropezus*	1823b: 54	IV.1829:424
Synuchus impunctatus	1823b: 45	III.1828:469
Tachys flavicauda	1823b: 87	V.1831: 54
T. inornatus	1823b: 87	V.1831: 53

roth 1955a), and in some cases the pin bears a small additional square of the same color with "Say" or "D. Say" in Dejean's hand, or this note is added on the first label, implying that Say's name was written there twice. These specimens, belonging to species marked with an asterisk (*) in Table 1, must be accepted as authentic Say specimens and are available for selection as lectotypes. Mr. Charpentier was able to find representatives of 9 such species. Afterwards, Mr. A. Descarpentries, of the Paris Museum, was kind enough to make a complementary search for Say specimens in the Oberthür collection, and the rediscovery of three of the species *(Chlaenius emarginatus, Pasimachus subsulcatus, Stenolophus ochropezus)* was due to his efforts. For reasons mentioned below under each species, lectotypes were *not* selected for the following Say species represented in the Dejean collection: *Anisodactylus agricola, Bembidion contractum, B. dorsale, Harpalus faunus.*

Article 75 of the International Code of Zoological Nomenclature sets the following limitations and conditions for designating neotypes. They are to be designated only if no holo-, lecto-, or syntypes exist: this condition is satisfied in the present case by information given in preceding paragraphs. They are to be designated only in connection with revisory work: present designations are connected with the senior author's revisory work on the ground-beetles of Canada and Alaska (Lindroth 1961-1968), which includes almost all species of northern United States too. They are to be designated only in "exceptional circumstances," in the interests of stability of nomenclature: for reasons given in preceding paragraphs, neotypes are considered necessary to stabilize use of Say's names. Characters regarded as differentiating the taxa for which neotypes are designated are given in bibliographic references in square brackets; the reference is usually to Lth 1961-1968. Evidences are given for believing that the neotypes are consistent with what is known of the original type material (according to the descriptions and with reference to localities). And the neotypes have been marked as such for recognition, and are the property of the Museum of Comparative Zoology. The proposal to designate neotypes for Say's Carabidae is known to and approved by several of the most active specialists in North America.

ENUMERATION OF SPECIES[5]

In the following pages, all Say names given to North American Carabidae other than Cicindelinae are treated under Say's original

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[5] *Aretharea helluonis* Say (1834, p. 411) is evidently an artifact (see Lec. 1859b, p. 524; Chd. 1871, p. 287). It is omitted from the present list.

genus names but in the order of Leng's Catalogue (1920), the Leng number being given in each case.

Of 8 species, *lectotypes* (in the Paris Museum, MNP) are designated; of the remaining species, *neotypes* are designated and deposited in the Museum of Comparative Zoology (MCZ). Exceptions are 2 *nomina nuda* (names without descriptions) and 7 *nomina dubia* (names not interpretable).

In the majority of cases, a specimen in the Leconte Collection (MCZ) could have been chosen as neotype. We have, however, avoided doing this for two reasons: (1) it seemed more convenient to keep all the Say neotypes together, as a separate collection, and (2) it seemed important to designate a type locality if possible, or at least a restricted type area, and to select specimens with appropriate locality labels. Such specimens are seldom available in the Leconte Collection. This has allowed us to select specimens from as close as possible to the parts of the country from which Say's specimens came, when he gives this information.

For one species, *Patrobus longicornis*, a neotype has been selected by Darlington, 1938 (MCZ), and type localities or type areas have been designated by Lindroth (1961, 1963, 1966, 1968) for many other Say species.

134[6] *Cychrus bilobus* (1823b: 73). Type area "Missouri" or "North-Western Territory." Say's description and the later colored plate (1828: XLV: 3) do not permit a reliable separation from allied species, *cavicollis* Lec. and *fissicollis* Lec. The provenience "Missouri" (acc. to Schwarz, 1895, p. 270, probably = N Nebraska) suggests *fissicollis*, represented from Kansas and Missouri in the MCZ. "North-Western Territory," however (acc. to Schwarz, l.c.), is probably Minnesota. This is herewith designated as type area. As *neotype* I have selected a ♂ from a locality as close to Minnesota as possible: Nipigon, W. Ont. — *Scaphinotus (Nomaretus) bilobus* [Lth. 1961, p. 19].

170 *Carabus sylvosus* (1823b: 75). No type area given. Designated type loc.: Asheville, N. C. (Lth., 1961, p. 41). The interpretation of Say's name is clear from his description of the dilated palpi and the elytral sculpture. The species is geographically uniform, except in the south (see Van Dyke, 1945). In MNP is a Dejean ♂ with two of the usual green labels: (a) "sylvosus Say"; (b) "D. Say." It agrees with the present concept of the species and

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[6] The number preceding each name is the number assigned in the Leng (1920) list.

I have designated it as *lectotype.* — *Carabus sylvosus* [Lth. 1961, p. 41].

171 *Carabus serratus* (1823b: 77). No type area given. Asheville, N. C., designated as type loc. (Lth. 1961, p. 40). The interpretation of Say's name is clear from his description of the serrate elytral margin, from which his name was derived. A ♂ from the type loc. designated as *neotype.* — *Carabus serratus* [Lth. 1961, p. 40].

172 *Carabus limbatus* (1823b: 77). Type area Maryland. The application of Say's name is clear from his description of the elytral sculpture. The species has no tendency of geographical variation. A ♂ from Charles Co., Md., designated as neotype and the place as type loc. — *Carabus limbatus* [Lth. 1961, p. 35].

173 (syn.) *Carabus interruptus* (1823b: 62). No type area given. The interpretation is clear from the description of the elytral sculpture, and the synonymization with *vinctus* Weber (1801) was accepted by Say himself (1834, p. 416). A ♂ from Germantown, Penn., designated as *neotype* and the place as type loc. — *Carabus vinctus* Web. [Lth. 1961, p. 34].

176 *Carabus externus* (1823a: 150). Type area "Arkansa." Say's description of the form of prothorax and of the elytral sculpture seems sufficient for an identification. A ♀ from Little Rock, Ark., designated as *neotype* and the place as type loc. — *Calosoma externum* [Lth. 1961, p. 49].

200 *Calosoma obsoleta* (1823a: 149). Type area "Arkansa" and "near the Rocky Mountains"; apparently the Arkansas River is meant. Say's description of the sculpture and the bluish foveolae of the elytra seems to exclude other species. A ♀ from Fort Reynolds, Colo., designated as *neotype* and the place as type loc. — *Calosoma obsoletum* [Lth. 1961, p. 49].

200 (syn.) *Calosoma indistinctum.* This is a *nomen nudum*, apparently never described by Say (in spite of the quotation "1825: 151" in Leng, 1920). It was mentioned by Lec. (1845, p. 208) as being the same as *luxatum* Dej. (1826, p. 126; *nec* Say), that is *obsoletum* Say.

219 *Calosoma luxata* (1823a: 149). Type area "Arkansa," no doubt in the same sense as for *C. obsoleta,* described in the same paper. The *luxatum* group of *Calosoma (Callisthenes)* is extremely difficult and it is important to fix the properties of the true *luxatum* Say. The original patria, "Arkansa," no doubt aims at the upper parts of the Arkansas River, that is, in Colorado. According to the revision of Mrs. Gidaspow (1959, map, fig. 11, p. 312), only what

she regards as the true *luxatum* has been found in Colorado. A ♂ labeled "Douglas Spring, Routt Co., Colo." (coll. Fall) has been selected as *neotype* and the place as type loc. [Lth. 1961, p. 54].

Description of ♂ neotype. — *Chaetotaxy*. Head: 2 fix-points (setae broken) each side inside hind-margin of eye. Prothorax: all setae broken but, judging from fix-point, there have been, on each side, only 1 at hind-angle and 1 at middle laterally. (On the high variability of this character, see Lth., 1961, p. 55.) — Form of *prothorax* approximately as in Gidaspow's fig. 55; but greatest width clearly before middle and sides faintly sinuate in basal half. — *Elytra* with strong sculpture, striae regular in frontal half, tegulae subquadrate, almost flat near the suture anteriorly, becoming rounded and very convex (granulate) laterally and apically. — ♂: also 1. pro-tarsal segment with well-developed brush (as described by Gidaspow, p. 313, for a sample from Colo.). Penis apex as in a ♂ from Utah, figured by Gidaspow (fig. 166). — *Calosoma luxatum* [Lth. 1961, p. 54].

228 *Elaphrus fuliginosus* (1834: 417). Type area Pennsylvania. Say's description was based on a specimen with head and prothorax mutilated; he therefore used only elytral characters when comparing it with the European *uliginosus* F. Leconte first (1859b, p. 530) suggested identity with *cicatricosus* Lec. but in his collection (MCZ) applied the name as now unanimously used (apparently following Crotch, in Horn, 1876). Though Say's description cannot be interpreted, this practice should be retained. No specimen from Penn. could be found. A ♂, Rumney, N. H., designated as *neotype*. — *Elaphrus fuliginosus* [Lth., 1961, p. 114].

233 *Elaphrus ruscarius* (1834: 417). Type area Pennsylvania, named in the first place and designated by Lth. (1961, p. 119). The identity of Say's species seems clear from his comparison with European specimens of *riparius* L. A ♂ from Columbia, Penn., designated as *neotype* and the place as type loc. — *Elaphrus ruscarius* [Lth. 1961, p. 119].

246 (syn.) *Notiophilus porrectus* (1834: 418). No type area given. The description of the form of prothorax and the pale color of the legs confirms the view introduced by Lec. (1863) that this is a synonym of *aeneus* Hbst. (1806). A ♂ from Pennsylvania designated as *neotype* and this state as type area. — *Notiophilus aeneus* Hbst. [Lth. 1961, p. 93].

247 *Notiophilus semistriatus* (1823b: 81). No type area given. Marquette, Mich., was designated by Lth. (1961, p. 94) but, since this specimen could not be rediscovered at the MCZ, a new type

loc. is proposed below. — Say's description cannot be interpreted. His *forma typica* (nominate form), because it has "feet black," is more likely to be referred to *aquaticus* L., whereas his "Var. α," with "tibiae piceous," may be *semistriatus* auct. The "Var. β" of 1823 was later (1834) by Say separated as distinct under the name of *porrectus* (= *aeneus* Hbst.). Say's concept of *semistriatus* was thus composite and, though Lec. (e. g. 1848, p. 450) confused it with his *novemstriatus*, it seems permissable to retain the name as generally used in this century, that is, for the species with a single preapical elytral puncture and pale tibiae. Fall (1906, pp. 79, 84) reports that F. Blanchard saw "undoubtedly authentic exponents of Say's *semistriatus*" in the collections of Harris, Melsheimer and Ziegler, and that these agreed with the present concept of the species' name. — A ♂ from Fairfax, Va., with genital slide, was designated as *neotype* and this place as new type loc. (see above). — *Notiophilus semistriatus* [Lth. 1961, p. 94].

292 *Nebria pallipes* (1823b: 78). No type area given; Boston, Mass., designated as type loc. by Lth. (1961, p. 76). Say mentions the two pale frontal spots and the interpretation of his name is therefore certain. A ♂ from Monterey, Mass., designated as *neotype.* — *Nebria pallipes* [Lth. 1961, p. 76].

305 *Pasimachus subsulcatus* (1823b: 19). Type areas "Georgia and Florida." Dej. (1826, p. 471) mentions that he has received this species from Say and in MNP is a specimen (sex not determined) with one of the characteristic green Dej. labels: "subsulcatus Say, in Amer. bor. — D. Say." It agrees with Say's description, except that the "obsolete rudiments of punctures" on the elytra are virtually absent. I have designated this specimen as *lectotype*. The species is unusually variable, as described by Leng (1915, p. 566) and Bänninger (1950, pp. 495, 502). The lectotype belongs to what the latter author regards as the typical form: the inner elytral intervals are clearly indicated, nrs. 3 & 5 broader and more convex. It agrees fairly well with ex. nr. 4 in coll. Lec., whereas his exx. nrs. 1-3 belong to what Bänninger (l.c., p. 495), with some doubt, regards as sbsp. *subnitens* Csy. The lectotype also agrees with 1 ex., Sanford, Fla. (MCZ), except that, in this, the costae and punctures of elytra are better developed. Florida is herewith designated as type area. — *Pasimachus subsulcatus* [Bänninger 1950, pp. 495, 502].

331 *Clivina globulosa* (1823b: 23). No type area given. It is a *Dyschirius* belonging to a very difficult group and Say's description cannot be interpreted. The name is here applied to the commonest and most widespread member of the group, as described by Lth. (1961,

p. 154). A macropterous ♀ from Arlington, Mass., herewith designated as *neotype* and the place as type loc. ("Boston area" already designated by Lth., l.c.). — *Dyschirius globulosus* [Lth. 1961, p. 154].

339 *Clivina sphaericollis* (1823b: 23). No type area given; Rumney, N. H., designated as type loc. by Lth. (1961, p. 145). Say's description cannot be interpreted. His name is used here according to general practice, as expressed in coll. Lec. (MCZ). A ♀ from Rumney, N. H. designated as *neotype.* — *Dyschirius sphaericollis* [Lth. 1961, p. 145].

346 *Clivina pallipennis* (1823b: 24). Type loc. Egg Harbour, N. J., herewith designated; also Virginia & Florida mentioned. Though Say's description does not exclude *sellatus* Lec., it seems permissible to use his name according to general practice, that is, for the species without dorsal puncture on the elytra. A ♂ from Anglesea, N. J., designated as *neotype.* — *Dyschirius pallipennis* [Lth. 1961, p. 142].

365 *Clivina pallida* (1823b: 22). Type loc. Chinquoteague Island, Va., "under yellow pine bark." Mr. T. F. Hlavac, who is revising this group of *Clivina*, has preserved Say's name for the species characterized by slender pro-tibiae with short lateral teeth, thus separated e. g. from *rubicunda Lec. C. rufescens* Dej. has been regarded as a probable synonym of *pallida* (Lec., 1859b, p. 452) and specimen nr. 1 in coll. Lec. (MCZ), labeled "C. rufescens Dej. ? pallida Say," belongs to *pallida* Say as defined by Hlavac. Since no authentic specimen of *rufescens* Dej. is present in the Paris Museum (Lth., 1955a, p. 13), a correct application of the name may be difficult. As *neotype,* Hlavac has designated a ♂ from South Carolina (coll. Liebeck). — *Clivina pallida* [as characterized above].

383 *Clivina lineolata* (1823b: 22). No type area given; Allegheny, Penn., designated as type loc. by Lth. (1961, p. 166). Say's description could as well be applied to *sulcifrons* Putz. (1846) which, by Lec. (1859b, p. 451) and also by Putzeys himself (1866, p. 223), was regarded a synonym (see Lth., l. c.). The interpretation here made is in accordance with that of the coll. Lec. (MCZ). A ♂ (with genitalia dissected) from Allegheny, Penn., designated as *neotype.* — *Schizogenius lineolatus* [Lth. 1961, p. 66].

395 *Clivina viridis* (1823b: 21). No type area given. It is almost certain that Say described *viridis* auct. He would hardly have overlooked the coarse punctures on the disc of prothorax in *puncticollis* Dej.; and the remaining three N. American species of *Ardistomis* have striate, not seriately punctate elytra. A ♂ (genital slide made)

from Philadelphia Neck, Penn., designated as *neotype* and the place as type loc. — *Ardistomis viridis* [Lec. & Horn 1879, p. 32].

398 *Panagaeus crucigerus* (1823b: 69). Type loc. Senipuxten, Md. Say's description is conclusive. A ♂ from Surf City, N. J., designated as *neotype.* — *Panagaeus cruciger* [Lec. & Horn 1879, p. 59].

399 *Panagaeus fasciatus* (1823b: 70). No type area given. Say's description is conclusive. A ♂ from Pennsylvania designated as *neotype* and the state as type area. — *Panagaeus fasciatus* [Lec. & Horn 1879, p. 59].

408 *Bembidium inaequale* (1823a: 151). Type loc. Engineer, Missouri. Say's descriptions (also 1834, pp. 549-550) fit almost any species of subg. *Chrysobracteon* but the name has always been used as conceived by Lec., in his collection (MCZ). For geographical reasons, the typical subspecies, without lateral seta of prothorax and with strong elytral striae, must be concerned (description, see Lth., 1963, p. 234). The selected *neotype* is a true exponent of this: ♂, Mt. Pleasant, Iowa. — *Bembidion inaequale* [Lth., 1963, p. 233].

419 *Bembidium punctatostriatum* (1823b: 83). No type area given; Rumney, N. H., designated as type loc. by Lth. (1963, p. 236). Say's descriptions (also 1834, p. 436) are insufficient for a recognition but the name has always been used for the largest species of subg. *Chrysobracteon*, for instance in coll. Lec. (MCZ). A ♂ from Rumney, N. H., designated as *neotype.* — *Bembidion punctatostriatum* [Lth. 1963, p. 236].

419 (syn.) *Bembidium sigillare* (1834: 437). Type area given as "Missouri" (probably = Nebraska). This is a *nomen dubium* regarded, with doubt, as a synonym of *punctatostriatum* Say by Lec. (1859b, p. 552). The name has not been used since and there is no reason to select a neotype.

429 *Bembidium coxendix* (1823a: 151). No type area given but taken during the "Rocky Mountain Expedition"; Fort Pierre, S. Dakota, designated as type loc. by Lth. (1963, p. 243). The original description gives no clue for an identification; but, since the pale variety of the species described in 1834 (p. 436) no doubt is identical with the closely related *confusum* Hayw. (*nitidulum* Dej.), the current interpretation of *coxendix* is most probably right. A ♂ from Fort Pierre, S. D., designated as *neotype.* — *Bembidion coxendix* [Lth. 1963, p. 243].

440 *Bembidium levigatum* (1823b: 84). Type area given as "Missouri" (probably = Nebraska). The description is almost conclusive though it is peculiar that Say failed to notice the erect elytral

pubescence, unique within the entire genus. There are 2 authentic ♀♀ in MNP: (1) with two green Dej. labels: (a) "laevigata Say, in Amer. bor.," (b) "D. Say"; and (2) with two green Dej. labels: (a) "♀," (b) "Say." I have designated ♀ nr. 1 as *lectotype*. A definite choice of type area (or locality) should be postponed until specimens from Nebraska are at hand. It is not necessary to change Say's original spelling into *laevigatum*. — *Bembidion levigatum* [Lth. 1963, p. 254].

512 *Bembidium niger* (1823b: 85). No type area given; Rumney, N. H., designated as type loc. by Lth. (1963, p. 301). The name is interpreted according to coll. Lec. (MCZ). One point confirming this in Say's descriptions (also 1834, p. 437) is the very coarsely punctate, apically obsolete elytral striae. A ♂ from Rumney, N. H., designated as *neotype*. — *Bembidion nigrum* [Lth. 1963, p. 301].

577 *Bembidium postremum* (1834: 437). Type area Pennsylvania. Lec. (1859b, p. 561) first regarded *postremum* as the same as *scopulinum* Kby., which is easily understood, considering that Say described his species as smaller than *tetracolum*. However, current practice, based on Lec., according to his collection, applies the name *postremum* to the large eastern representative of the *bimaculatum* group (Lth., 1963, p. 330). There is no reason for a change. A ♂ from Allegheny, Penn., has been designated as *neotype* and the place as type loc. — *Bembidion postremum* [Lth. 1963, p. 330].

588 *Bembidium tetracolum* (1823b: 89). No type area given; Arlington, Mass., designated as type loc. by Lth. (1963, p. 331). Say's descriptions (also 1834, p. 437) are not sufficient for specific recognition in this difficult group. I have followed Lec., according to his collection (MCZ). In N. America the species is an old introduction from Europe, where it was long, incorrectly (Lth., 1957, pp. 334-335), known as "*ustulatum* L." A ♂ from Arlington, Mass., designated as *neotype*. — *Bembidion tetracolum* [Lth. 1963, p. 331].

591 *Bembidium honestum* (1823b: 82). No type area given; Water Gap, N. J., designated as type loc. by Lth. (1963, p. 248). Say's description is not decisive but it is advisable to follow Lec.'s opinion, as expressed in his collection (MCZ) where his own *basale* (1848, p. 454) was placed as a synonym. But *antiquum* Dej., referred to as another synonym by Lec. (1859b, p. 498), belongs to *chalceum* Dej. (see Lth. 1963, p. 247). A ♂ from Water Gap, N. J., designated as *neotype*. — *Bembidion honestum* [Lth. 1963, p. 248].

658 *Bembidium dorsale* (1823b: 84). Type area given as "Missouri" (probably = Nebraska). In the MNP is a ♀ with the following green Dej. labels: (a) "dorsalis Say, in Amer. Bor."; (b) "Say." There is no doubt that this is an authentic Say specimen but, unfortunately, it belongs to *variegatum* Say, auct. Say (1823b, p. 89) regarded these two species as "very closely allied" and suggested that *dorsale* might be "a mere variety" of *variegatum*. A comparison between the two descriptions (see *variegatum*, below) demonstrates, however, that Say probably had two different species before him, the ones that today pass under his two names. It should therefore be concluded that the Paris specimen was misidentified by Say and it should not be used as lectotype. A ♀ labeled Missouri has been designated as *neotype*. It belongs to the species with straight frontal furrows and the microsculpture of the forebody shallow. A definite choice of type area (or locality) should be postponed until specimens from Nebraska are at hand. — *Bembidion dorsale* [Lth., 1963, p. 359].

660 *Bembidium variegatum* (1823b: 89). No type area given; Rivervale, N. J., designated as type loc. by Lth. (1963, p. 360). The name was long used for *intermedium* Kby. and related small species of subg. *Notaphus*. Csy. (1918, pp. 139-140) correctly re-established *variegatum* as the name for the species meanwhile renamed *postfasciatum* Ham. Say gives the same size (1/5 of an inch) for *variegatum* as for *dorsale*. In his rather complete description of the two species, three pairs of characters seem to indicate that the current interpretation of his names is correct: —

	dorsale (pp. 84-85)	*variegatum* (p. 89)
(a)	"thorax green slightly tinged with cupreous"	"thorax blackish, slightly bronzed, tinged each side with green"
(b)	"elytra whitish-testaceous — two fuscous, obsolete, undulated bands behind the middle, the posterior one less definite"	"elytra black variegated with testaceous, or testaceous varied with black dots and lines"
(c)	(elytra with) "interstitial lines (= intervals) hardly convex"	(elytra with) "interstitial lines convex"

A ♂ from Rivervale, N. J., designated as *neotype* of *variegatum*. — *Bembidion variegatum* [Lth. 1963, p. 360].

694 *Bembidium contractum* (1823b: 85). No type area given; Ipswich, Mass., designated as type loc. by Lth. (1963, p. 372). Say's description is quite insufficient for a species belonging to this ex-

ceedingly difficult group. In the Paris Museum is a ♀ with small green Dejean label, with "Say" only; although it stands under the label "*contractum*" in the drawer, its character of a true representative of what Say regarded as his *contractum* may perhaps be questioned. The specimen does *not* belong to *contractum* auct. (Lth. 1963, p. 372). The wings are full (in *contractum* apparently constantly reduced) and, above all, the hind-angles of its prothorax are very poorly developed, exactly as described for *vernacula* Csy. (1885). This was regarded as a sbsp. of *constrictum* Lec. by Casey 1918 (p. 124) but it is a doubtless distinct species. In view of the incomplete labeling of the Paris specimen and also of the considerable confusion that would be created by a removal of Say's name, I have refused to designate it as lectotype. A ♂ of the "true" *contractum* from Ipswich, Mass., has been designated as *neotype.* — *Bembidion contractum* [Lth. 1963, p. 372].

705 *Bembidium affine* (1823b: 86). No type area given; Mobile, Ala., designated as type loc. by Lth. (1963, p. 376). Say's description does not exclude members of the *versicolor* group but his name has always been used for the only species with frontal furrows doubled both in front and behind. It was later described by Dej. (1831) as *decipiens* and *fallax.* A ♂ from Mobile, Ala., designated as *neotype.* — *Bembidion affie* [Lth., 1963, p. 376].

737 (syn.) *Bembidium oppositum* (1823b: 86). No type area given; Rumney, N.H., designated as type loc. by Lth. (1963, p. 383). Say mentions the laterally oblique base of the prothorax and, in 1834 (p. 439), suggests that his species belongs in (subg.) *Lopha;* the interpretation, therefore, seems certain. Lec. (1859b, p. 501) declared *oppositum* as identical with *quadrimaculatum* L., but it is now regarded as a Nearctic subspecies of this (Lth., l. c.). A ♂ from Rumney, N. H., designated as *neotype.* — *Bembidion quadrimaculatum oppositum* [Lth. 1963, p. 383].

792 *Bembidium ephippiatum* (1834: 439). Type area Indiana. Say's description is conclusive. A ♂ from Indiana (coll. Fall) designated as *neotype.* — *Tachys (Pericompsus) ephippiatus* [Hayw. 1899, p. 214].

805 *Bembidium incurvum* (1834: 440). Type area Indiana. Though Say's description of the head as "blackish-piceous" points to *incurvus* auct. rather than to the closely allied *anceps* Lec., it is by no means decisive. I have followed Lec., acc. to his collection (MCZ). A ♂ from N. Illinois (coll. Fall) designated as *neotype.* — *Tachys incurvus* [Lth. 1966, p. 416].

829 *Bembidium tripunctatum* (1834: 439). Type area Indiana.

Besides the three-punctured base of prothorax, Say mentions the presence of five elytral striae, which makes his description almost decisive. A ♂ from New Jersey designated as *neotype.* — *Tachys tripunctatus* [Lth. 1966, p. 423].

849 *Bembidium proximus* (1823b: 88). No type area given; Brookline, Mass., designated as type loc. by Lth. (1966, p. 432). The description of the prothorax ("posterior angles rectangular") fits *rhodeanus* Csy. at least as well, and also *scitulus* Lec., but I prefer to follow current practice, as expressed in coll. Lec. (MCZ). A ♀ from Brookline, Mass., designated as *neotype.* — *Tachys proximus* [Lth. 1966, p. 432].

883 *Bembidium laevum* (1823b: 88). No type area given; Arlington, Mass., designated as type loc. by Lth. (1966, p. 426). The small size ("one-twentieth of an inch") and the presence of only one impressed elytral stria, mentioned by Say, make the interpretation almost decisive. A ♀ from Arlington, Mass., designated as *neotype.* — *Tachys laevus* [Lth. 1966, p. 426].

892 *Bembidium inornatum* (1823b: 87). No type area given; Asheville, N. C., designated as type loc. by Lth. (1966, p. 436). Say's name has been associated with the North American form of subg. *Tachyta* lacking a carina inside hind-angles of prothorax. Though Say does not mention this character, the procedure may be defensible. The taxonomic position of this form is much disputed: whether a separate species (Csy., 1918), a subspecies (Lth., olim), or a form of *nanus* Gyll. not deserving a name (Lth., l. c.). A ♂, without prothoracic carina, from Asheville, N. C., designated as *neotype.* — *Tachys nanus* Gyll. [Lth., 1966, p. 436].

898 *Bembidium flavicaudus* (1832b: 87). No type area given; White Sulphur Springs, W. V., designated as type loc. (Lth., 1966, p. 441). Say fails to mention the peculiar structure of the prothorax, but color characters as well as the reported occurrence under bark seem sufficient for an identification. A ♂ from White Sulphur Springs, W. V., designated as *neotype.* — *Tachys (Tachymenis) flavicauda* [Lth., 1966, p. 441].

901 *Feronia longicornis* (1832b: 40). No type area given; Arlington, Mass., designated as type loc. by Darlington (1938, p. 158) who labeled a ♂ from the same place as *neotype.* — *Patrobus longicornis* [Lth., 1961, p. 180].

929 *Abax coracinus* (1823b: 59). No type area given; Rockeville, Penn., designated as type loc. by Lth. (1966, p. 444). The only character mentioned by Say pointing to *coracinus* auct. rather than to *cyanescens* Dej. (*foveatus* Lec.) refers to the elytral striae

being "minutely punctured"; in *cyanescens* they are virtually smooth. A ♂ from Rockeville, Penn., designated as *neotype.* — *Myas coracinus* [Lth., 1966, p. 445].

1006 *Feronia adoxa* (1823b: 46). No type area given; Mt. Wachusett, Mass., designated as type loc. by Lth. (1966, p. 467). Since Say does not mention the presence of any dorsal puncture on 3. elytral interval, as for related species of "*Feronia*" possessing it, the interpretation is almost certain. A ♂, agreeing with the type of *rejectus* Lec., from Mt. Wachusett, Mass., designated as *neotype.* — *Pterostichus adoxus* [Lth., 1966, p. 467].

1024 *Feronia honesta* (1823b: 51). No type area given; Rumney, N. H., designated as type loc. by Lth. (1966, p. 472). It is surprising that Say described the prothorax as "impunctured," which would rather suggest *blanchardi* Horn or *unicarum* Darl., from the southern Appalachians; but it seems defensible to retain Say's name for the only common and widespread species of the group, in accordance with coll. Lec. (MCZ). A ♂ from Rumney, N. H., designated as *neotype.* — *Pterostichus honestus* [Lth., 1966, p. 472].

1034 *Feronia constricta* (1823a: 147). Type loc. "Arkansa" River near the Rocky Mountains. Say's original description seems sufficient for an identification (R. F.). A ♂ from Colorado Springs, Colo., designated by R. Freitag as *neotype.* — *Evarthrus*[7] *constrictus* [Freitag, 1969, p. 158].

1044 *Feronia unicolor* (1823b: 40). No type area given. The species was interpreted from the original description and from the single specimen under this name in coll. Lec. (MCZ) (R. F.) A ♀ from Upson Co., Georgia, designated by R. Freitag as *neotype.* — *Evarthrus unicolor* [Freitag, 1969, p. 110].

1050 *Feronia heros* (1823a: 145). Type area "the Arkansa" (apparently the river). The species was interpreted from Say's original description (R. F.). A ♂ from Texas designated by R. Freitag as *neotype.* — *Evarthrus heros* [Freitag, 1969, p. 166].

1067 *Feronia sigillata* (1823b: 42). Type loc. Germantown, Penn. The name was interpreted from the original description, including type loc. (R. F.). A ♀ from Philadelphia, Penn., designated by R. Freitag as *neotype.* — *Evarthrus sigillatus* [Freitag, 1969, p. 133].

1080 *Feronia obsoleta* (1834: 424). Type area Indiana. The species was interpreted from Say's original description (R. F.). A

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[7] The senior author prefers to regard *Evarthrus* as a subgenus of *Pterostichus.*

♂ from Cades Cove, Blounto, Tenn., designated by R. Freitag as *neotype.* — *Evarthrus obsoletus* [Freitag, 1969, p. 108].

1089 *Feronia stygica* (1823b: 41). No type area given; Rumney, N. H., designated as type loc. by Lth. (1966, p. 492). The expression "basal lines (i.e. basal foveae of prothorax) double" fits *stygicus* auct. rather than *coracinus* Newn. The reported presence of only one dorsal puncture of elytra is against the situation in the entire *melanarius* group, where there are 2 (occasionally 3 or 4); it may be a case of *lapsus oculi.* A ♂ from Rumney, N. H., designated as *neotype.* — *Pterostichus stygicus* [Lth., 1966, p. 492].

1100 *Feronia moesta* (1832b: 41). No type area given; Asheville, N. C., designated as type loc. by Lth. (1966, p. 496). Concerning the earlier confusion with *superciliosus* Say, see that species. The name *moestus* has always been used for the present species. A ♂ from Asheville, N. C., designated as *neotype.* — *Pterostichus moestus* [Lth., 1966, 496].

1101 *Feronia superciliosa* (1823a: 144). No type area given but collected during the "Expedition to the Rocky Mountains." From the description this species cannot be separated from *moestus* Say; and Lec., on several occasions (1852, 1859b, 1863), regarded them as conspecific. They are, however, kept apart under the two Say names in his collection, though only ex. nr. 1 of *superciliosus* (Virginia) is the present species, nrs. 2-4 being *moestus.* Actually, the two species are very different (Lth., 1966, p. 497). Say omitted mentioning the dorsal punctures of elytra in *superciliosus,* but their absence would have excluded also *ohionis* Cki. (*purpuratus* Lec.), the only other *Pterostichus* with "purplish" elytra that could be concerned. Say's description of the prothorax fits *superciliosus* auct. much better than *ohionis.* A ♂ from Pennsylvania (coll. Fall) designated as *neotype.* — *Pterostichus superciliosus* [Lth., 1966, p. 497].

1105 *Feronia permunda* (1834: 426). Type area Indiana (not "apparently Pennsylvania," as given by Lth., 1966, p. 535). Say's description fits *atratus* Newn. equally well (for descriptions see Lth., l. c.). The interpretation is made from ex. nr. 1 under "*permundus*" in coll. Lec. (MCZ). A ♂, with genitalia dissected, from "Richland & Lawrence Co.," Wabash, Ill., designated as *neotype.* — *Abacidus permundus* [Lth., 1966, p. 535].

1108 *Feronia ventralis* (1823b: 46). Type area "Missouri" (probably = Nebraska). Closely allied to *obscurus* Say (see below) but with elytral striae evidently punctate, as mentioned by Say. A ♂, agreeing with ex. nr. 1 in coll. Lec., from Douglas Co., Kansas, designated as *neotype.* — *Pterostichus ventralis* [Lec. & Horn 1882, p. 24].

1110 *Feronia obscura* (1834: 425). Type area Indiana. The application of the name (against *ventralis* Say) seems clear from the description of the elytral striae: "not distinctly punctured, obsolete on the lateral submargin." A third species, *tumescens* Lec., has the hind-angles of prothorax much better developed. A ♂ (coll. Fall) agreeing with ex. nr. 1 in coll. Lec., from Allegheny, Penn., designated as *neotype.* — *Pterostichus obscurus* [Lec. & Horn 1882, p. 24].

1151a *Feronia submarginata* (1823b: 45). No type area given. The description is almost decisive. Whether *monedulus* Germ. (1824) is a pure synonym could not be decided. Since Say's description was published in 1823 (not 1825, as given in Leng), the name *submarginatus* Say under all circumstances has priority. A ♂ from Hope, Ark., designated as *neotype* and the place as type loc. — *Pterostichus submarginatus* [Lec. 1852, p. 246].

1161 *Feronia chalcites* (1823b: 56). No defined type area; Washington, D.C., designated as type loc. by Lth. (1966, p. 479). Say's description is not quite decisive and was interpreted according to coll. Lec. (MCZ). Say's name is older than the *chalcites* of Germar (1824; see under preceding species) and it was therefore not justified to substitute for it *sayi* Brullé (1835). A ♂ from Washington, D.C., designated as *neotype.* — *Pterostichus chalcites* [Lth., 1966, p. 479].

1162 *Feronia lucublanda* (1823b: 55). No type area given; Ithaca, N. Y., designated as type loc. by Lth. (1966, p. 482). Say's description of the depressed sides of the prothorax seems to fit this species only. A ♂ from Ithaca, N. Y., designated as *neotype.* — *Pterostichus lucublandus* [Lth., 1966, p. 482].

1162a *Poecilus fraternus* (1824: 270). Type area "North-west Territory" (probably Minnesota). The description is incomplete and cannot be interpreted. Lec. (1859a, p. 177) regarded *fraternus* as a "variety" of *lucublandus* Say but it seems wiser to treat it as a "*nomen dubium*" (Lth., 1966, p. 483) without designation of neotype.

1164 *Feronia convexicollis* (1823b: 50). Type area "Missouri" (probably = Nebraska). Say mentions that the sides of prothorax are depressed but also that they are "hardly contracted behind" whereas, in *lucublandus*, they are said to be "very little narrowed behind by a regularly curved edge." The status of *convexicollis* has been judged differently by different authors (see Lth., 1966, p. 483). In my opinion, it is not specifically distinct from *lucublandus* but may well be treated as a subspecies confined to the interior. A ♂ from Devil's Lake, N. Dakota, has been designated as *neotype* and the place as type loc. — *Pterostichus lucublandus convexicollis* [Lth., 1966, p. 483].

1167 *Feronia tartarica* (1823b: 44). No type area given. The species belongs to a difficult group (subg. *Lophoglossus*) in need of revision. Say's description cannot be interpreted but the selected ♂ neotype agrees with Lec.'s description (1852) of the ♂ meso-tibiae and with the single ♂ (orange disc) in his collection. Casey's "*tartaricus*" (1913) is different, agreeing in said respect with *strenuus* Lec.; in *haldemani* Lec., the apical process of the ♂ meso-tibia is more acute. A ♂ from Mobile, Ala., designated as *neotype* and the place as type loc. — *Pterostichus tartaricus* [Lec. 1852, p. 249].

1174 *Feronia caudicalis* (1823b: 56). No type area given; Arlington, Mass., designated as type loc. by Lth. (1966, p. 500). Say's description is not decisive, but Lec. (1859b: 480) says that he has studied specimens sent by T. W. Harris who had compared them with "Say's type." A ♂ from Arlington, Mass., designated as *neotype*. — *Pterostichus caudicalis* [Lth., 1966, p. 500].

1178 *Feronia muta* (1823b: 44). No type area given; Black Mts., N. C., designated as type loc. by Lth. (1966, p. 489). Say's description is not quite decisive and I have followed Lec.'s interpretation according to his collection (MCZ). A ♂ from Black Mts., N. C., designated as *neotype*. — *Pterostichus mutus* [Lth. 1966, p. 489].

1190 *Feronia oblongonotata* (1834: 425). Type area "North West Territory" (probably Minnesota, possibly Manitoba). The name is still used for an independent species in Leng (1920). The description is apparently based on an immature specimen and would equally well apply to *pensylvanicus* Lec., which name, if so, it would replace. In order to avoid this it is justifiable to synonymize *oblongonotatus* with *adstrictus* Eschz. A ♂ from Aweme, Man., designated as *neotype*. — *Pterostichus adstrictus* Eschz. [Lth. 1966, p. 485].

1217 *Feronia recta* (1823b: 58). No type area given. The neotype agrees with Casey's description (1918, p. 381) and also, except that it is larger, with the 7. ex. in coll. Lec. (MCZ). A ♂, with genitalia dissected, from South Carolina, designated by R. T. Allen as *neotype* and the state as type area. — *Loxandrus rectus* [Lec. & Horn 1879, p. 51].

1262 *Zabrus avidus* (1823a: 148). Type area not given but collected during the Rocky Mountain Expedition; N. Fork S. Platte Canyon, Colo., designated as type loc. by Lth. (1968). The description is by no means conclusive but the name should be used according to general practice, as expressed in coll. Lec. (MCZ). A ♂ from N. Fork S. Platte Canyon, Colo., designated as *neotype.* — *Amara avida* [Lth. 1968, p. 689].

1265 (syn.) *Amara furtiva* (1834: 429). Type area Indiana. As stated by Hayward (1908, p. 40), Say's description was apparently based upon immature specimens. Except for the color, all characters mentioned fit the species previously described by Dejean (1828, p. 509) as *exarata*, of which *furtiva* has always been regarded as a synonym. A ♂ from Wabash Valley, Richland & Lawrence Co., Ill., designated as *neotype.* — *Amara exarata* Dej. [Lth. 1968, p. 680].

1281 *Feronia obesa* (1823b: 37). Type loc. Harrowgate, Penn. Say's description is not conclusive but the name has always been used in its present sense, that is, for the only widespread species of subg. *Percosia.* As neotype I have selected a pronounced representative of the eastern form (against *diffinis* Lec.; see Lth., 1968). A ♂ from Charity Island, Mich., designated as *neotype.* — *Amara obesa* [Lth., 1968, p. 690].

1372 *Feronia musculis* (1823b: 35). Type area, coast of Virginia. Say's description, though not conclusive, fits "*musculus*" auct. In the Paris Museum is a ♂ of this species carrying four green Dejean labels: (a) "♂"; (b) "musculis Say, in Amer. bor."; (c) "D. Say"; (d) "Harpalus proletarius Melsh. St." The latter is a manuscript name never published but listed in Dej.'s Catalogues of 1833 and 1836. The Paris ♂ has been designated as *lectotype.* There is no reason to change Say's original spelling into "musculus." — *Amara musculis* [Lth., 1968, p. 706].

1385 *Feronia impuncticollis* (1823b: 36). Type area Penn., named in the first place, herewith designated. Say's description cannot be interpreted. Since the basal pore-puncture of the elytra is not mentioned, it fits not only *littoralis* Mnh. but several other members of subg. *Amara s. str.,* with pale antennal base. *A. impuncticollis,* as here conceived, and *littoralis* have been generally confused (for separating characters, see Lth., 1968, p. 730), as by Lec. and by Hayward (1908). The first specimens both in coll. Lec. and in coll. Hayward (MCZ) belong, however, to the present species and, since it is more southern in distribution, it is likely that Say's specimens from Penn. belonged to the same species. A ♂ from N. Cumberland, Penn. (coll. Fall), designated as *neotype* and the place as type loc. — *Amara impuncticollis* [Lth., 1968, p. 728].

1429 *Feronia basillaris* (1823b: 35). No type area given; Dover, Mass., designated as type loc. by Lth. (1968). The description, notably of the punctuation of prothorax and elytral striae, is conclusive. A ♂ from Dover, Mass., designated as *neotype.* — *Amara basillaris* [Lth., 1968, p. 735].

1433 *Feronia angustata* (1823b: 36). Type area "on the Missouri." Since Say had not observed the trifid pro-tibial spure, there is no character mentioned in the description that would not fit *familiaris* Dft. as well. It may be justified, in spite of this, to refer his name to that species of subg. *Zezea (Triaena)* for which it has always been used. The description of the form of prothorax seems to exclude *pallipes* Kby. A ♀ from Independence, Iowa, designated as *neotype.* — *Amara angustata* [Lth., 1968, p. 736].

1450 *Dicaelus dilatatus* (1823b: 68). No type area given in the original description but reported as Pennsylvania in Say's paper of 1825 (Pl. XXIV: 3). Neither Say's descriptions nor his figure are decisive but the name has always been used for the species defined in detail by G. E. Ball, in his monograph (1959, p. 126). A ♂ from Camp Hills, Penn., designated as *neotype* and the place as type loc. — *Dicaelus dilatatus* [Ball 1959, p. 126].

1458 *Dicaelus sculptilis* (1823b: 68). Type area "Missouri" (possibly including Nebraska). An interpretation of Say's name, on the specific level, is clear from his descriptions and the figure (1825, Pl. XXIV: 4). The species consists of three subspecies of which the nominate one was fixed by Ball (1959, p. 142) as occurring in Arkansas, Missouri, Kansas, and Oklahoma; the *neotype* was identified by him as belonging to this subspecies: ♂ from Platte Co., Missouri, designated by me; at the same time designated type loc. — *Dicaelus sculptilis sculptilis* [Ball 1959, p. 141].

1452 *Dicaelus splendidus* (1823b: 68). Type area "from the Missouri" (apparently the river). Say's descriptions (also 1825) and illustration (1825, Pl. XXIV: 1) of color are conclusive. According to Ball (1959, p. 156) there are no other constant characters than the color of the elytra separating *splendidus* from *purpuratus* Bonelli (1813), of which he regards it as a subspecies. A ♀ from Platte Co., Missouri, designated as *neotype*, and the place as type loc. — *Dicaelus purpuratus splendidus* [Ball 1959, p. 156].

1482 *Feronia gregaria* (1823b: 47) (by mistake, the species name was attributed to Dejean in Leng, 1920). No type area given; Philadelphia, Penn., designated as type loc. by Lth. (1966, p. 543). Say's description applies equally well to *ingratus* Dej. but was interpreted in accordance with coll. Lec. (MCZ). A ♀ from Philadelphia, Penn., designated as *neotype.* — *Calathus gregarius* [Lth., 1966, p. 543].

1489 *Feronia impunctata* (1823b: 45). Type loc. Germantown, Penn. Say's description seems sufficient for an identification. It is very puzzling that Dejean (1828, p. 469), from 1 ex. sent by Say, regarded *Feronia impunctata* as a synonym of *Amara familiaris* Dft. This cannot be a *lapsus calami* for *Feronia impuncticollis* (see above) because the latter was by Dejean (l. c., p. 464) synonymized with *Amara trivialis* Gyll. (= *aenea* DeG.). A ♂ from Tyngsboro, Mass., designated as *neotype.* — *Synuchus impunctatus* [Lth., 1966, p. 551].

1507 *Feronia hypolithos* (1823b: 59). No type area given; Cleveland, Ohio, designated as type loc. by Lth. (1966, p. 645). Only size and the expression "striae — irregularly punctured" suggest *hypolithos* auct., which was otherwise interpreted from coll. Lec. (MCZ). A ♂ from Cleveland, Ohio, designated as *neotype.* — *Agonum hypolithos* [Lth., 1966, p. 645].

1513 *Feronia decentis* (1823b: 53). No type area given; Marion, Mass., designated as type loc. by Lth. (1966, p. 636). Say's description of the prothorax makes it almost certain that he had the "true" *decentis* before him; the pronounced sinuation of sides in front of the denticulate hind-angles, in *sinuatum* Dej., could hardly have remained unnoticed by Say. Therefore, a pronounced *decentis s. str.* (a ♀) has been selected as *neotype.* — *Agonum decentis* [Lth., 1966, p. 636].

1518 *Feronia cincticollis* (1823b: 52). No type area given; Philadelphia, Penn., designated as type loc. by Lth. (1966, p. 640). Say's description is insufficient. His name has been interpreted according to coll. Lec. (MCZ). A ♂ from Philadelphia, Penn., designated as *neotype.* — *Agonum cincticolle* [Lth., 1966, p. 640].

1518 (? syn.) *Feronia maculifrons* (1823a: 146). Type area "Arkansa Territory." The description cannot be interpreted and the name has never been used (see Lec., 1854, pp. 43, 59; 1859a, p. 94). It should be treated as a *nomen dubium* (Lth., 1966, p. 640) and no neotype selected.

1522 *Feronia extensicollis* (1823b: 54). No type area given; Rumney, N. H., designated as type loc. by Lth. (1966, p. 625). That Say's description refers to *extensicolle* auct. can hardly be doubted. However, since this species shows considerable geographical variation (Lth., 1966, pp. 625-627) and because Say did not mention the provenience of his specimens, it is of special importance to select a type area. Lec. (1854, p. 46) regarded the eastern, Casey (1920, p. 57) the western form as the true *extensicolle.* Say's material was probably from Pennsylvania, and it is therefore advisable to follow Lec.'s opinion. A pronouncedly "eastern" specimen was designated as *neotype*: a ♀ from Rumney, N. H. — *Agonum extensicolle s. str.* [Lth., 1966, p. 625].

1523 *Feronia decora* (1823b: 53). No type area given; Arlington, Mass., designated as type loc. by Lth. (1966, p. 629). Say's description fits both *decorum* auct. and *thoracicum* Dej., but the latter, more southern species was probably not available to him. A ♂ from Arlington, Mass., designated as *neotype*. — *Agonum decorum* [Lth., 1966, p. 629].

1537 *Feronia errans* (1823a: 147). Type area not given but collected during the "Rocky Mountain Expedition"; Buena Vista, Colo., designated as type loc. by Lth. (1966, p. 616). Say's description, notably of color characters, is almost decisive. A ♀ from Buena Vista, Colo., designated as *neotype*. — *Agonum errans* [Lth. 1966, p. 616].

1540 *Anchomenus collaris* (1834: 421). Type area Indiana. There are several details in Say's description contradicting the current interpretation of his name: (a) the size is too large (7/20 of an inch, i.e. the same as given for *placidum*); (b) "body black," no mention made of the pale margins of prothorax; (c) "base of the first joint of the antennae — black-piceous," actually the entire 1. segment is rufous; (d) the prothorax is described as "subquadrate," with posterior angles "very obtuse" and basal foveae "slightly rugous"; actually the prothorax is almost circular, with obliterated hind-angles and smooth foveae. The entire description fits *melanarium* Dej. much better. In spite of this, in the interest of stability, I have followed Lec.'s interpretation, according to his collection (MCZ). A ♂ from Woodbury, N. J., designated as *neotype*. — *Agonum collare* [Lth., 1966, p. 612].

1542 (? syn) *Feronia scutellaris* (1823a: 146). No type area given but collected during the "Rocky Mountain Expedition." The description is quite uninterpretable and, though Lec. (1879, p. 56) referred it to *Agonum melanarium* Dej. (1828), before which it would then have priority, it is better to treat *scutellare* as a *nomen dubium*. No neotype should be selected.

1553 *Feronia cupripennis* (1823b: 50). No type area given; W. Roxbury, Mass., designated as type loc. by Lth. (1966, p. 591). Say's description of the color pattern is sufficient for an identification. A ♀ from W. Roxbury, Mass., designated as *neotype*. — *Agonum cupripenne* [Lth. 1966, p. 591].

1558 *Feronia nutans* (1823b: 52). Say's information "bought in New York" is of course no base for fixation of type loc.; Philadelphia Neck, Penn., designated as such by Lth., (1966, p. 617). The description, notably of the color of body and legs, as well as of the impunctate elytral striae, is almost decisive. A ♂ from Philadelphia Neck, Penn., designated as *neotype.* — *Agonum nutans* [Lth., 1966, p. 617].

1567 *Feronia placida* (1823b: 43). No type area given; Dorchester, Mass., designated as type loc. by Lth., (1966, p. 613). Say's description is by no means decisive but I have followed Lec., according to his collection (MCZ). A ♀ from Dorchester, Mass., designated as *neotype.* — *Agonum placidum* [Lth., 1966, p. 613].

1573 *Feronia obsoleta* (1823b: 57). No type area given. Lth. (1966, p. 565) designated Michipicoten, L. Superior, Ont., as type loc. but, since afterwards no specimen so labeled could be rediscovered at the MCZ, I propose to change the type loc., as below. Say's description cannot be interpreted, but Lec. (1854, p. 57) saw a specimen named by the author, and his concept, according to coll. Lec. (MCZ), should therefore be followed. By many students, including Leng (1920) and, previously, myself (1955b), *obsoletum* Say has been treated as a synonym of *Agonum bogemani* Gyll. It is, however, distinct (Lth., 1966, p. 565 a.f.). A ♂ from Bayfield, Wisc., designated as *neotype*, and the place as type loc. — *Agonum obsoletum* [Lth., 1966, p. 565].

1578 *Feronia limbata* (1823b: 49). No type area given. The interpretation is clear from Say's description. Fall (1933) has shown that *Carabus pallipes* F. (1787, p. 202) is the same species and Say's name therefore falls into synonymy. A ♂ from Camden, S. C., designated as *neotype*, and the place as type loc. — *Agonum pallipes* F. [Lth., 1966, p. 620].

1581 *Feronia punctiformis* (1823b: 58). No type area given; Philadelphia Neck, Penn., designated as type loc. by Lth. (1966, p. 622). Say's description cannot be interpreted but I have followed Lec., according to his collection (MCZ). A ♂ from Philadelphia Neck, Penn., designated as *neotype.* — *Agonum punctiforme* [Lth., 1966, p. 622].

1595 *Feronia parmata* (1823b: 49). No type area given; Wissahickon Creek, Penn., designated as type loc. by Lth. (1966, p. 553). Say's description is not decisive; I have followed Lec., according to his collection (MCZ). A ♀ from Wissahickon Creek, Penn., designated as *neotype.* — *Olisthopus parmatus* [Lth. 1966, p. 553].

1595 (syn.) *Olisthopus cinctus* (1834: 424). Type area Pennsylvania. The descriptions of both *parmatus* (1823b) and *cinctus* (1834) are uninterpretable and, to a great extent, incommensurable, containing different kinds of characters. The elytra of *cinctus* are described as unicolorous ("dull reddish-brown") but, since the size is given as virtually the same as for *parmatus* (3/10 and less than 3/10 of an inch, respectively), the name *cinctus* cannot be referred to any of the small species of the genus. Lec. (1859b, p. 537) reports that a specimen of *cinctus* was sent to him by Melsheimer and that it did not differ from *parmatus*. This was most probably an authentic Say specimen and the synonymy should be accepted. There is no reason to designate a neotype. — *Olisthopus parmatus* [Lth., 1966, p. 553].

1642 *Lebia atriventris* (1823b: 13). No type area given. Say's description of the coloration is decisive. A ♀ from Arlington, Mass., designated as *neotype*, and the place as type loc. — *Lebia atriventris* [Madge 1967, p. 153].

1643 *Lebia tricolor* (1832b: 11). Type area Pennsylvania, named in the first place, herewith designated. Say's description is conclusive. In the Paris Museum is a big ♀ (8.5 mm.) with two green Dejean labels: (a) "tricolor Say, in Amer. Bor."; (b) "D. Say." This I have designated as *lectotype*. — *Lebia tricolor* [Madge 1967, p. 156].

1655 *Lebia viridis* (1823b: 14). No type area given. Say's description refers to the brilliant metallic, greenish form of this complex species, as conceived by Madge (1967, p. 179 a.f.). To the same form belongs the designated *neotype*: ♂, Camp Hill, Penn.; the place selected as type loc. — *Lebia viridis* [Madge 1967, p. 177].

1667 *Lebia ornata* (1823b: 13). No type area given. Say's description of the elytral pattern is decisive; it refers to the northern form with small, isolated pale spots (see Madge, 1967, p. 209 a.f.)[8] and so does the *neotype*: ♀ from Wissahickon, Penn., which also is designated as type loc. — *Lebia ornata* [Madge 1967, p. 208].

1707 *Cymindis viridipennis* (1823b: 9). Type area Pennsylvania. Say's description seems conclusive; it fits the 3 ex. in coll. Lec. (MCZ), and so does the *neotype*: ♀ from Washington Co., Penn.; the place designated as type loc. — *Calleida viridipennis* [Lec. & Horn 1882, p. 55].

1712 *Cymindis purpureus* (1823b: 10). Type area "Missouri" (probably including Nebraska). Say's description seems to be conclusive. He calls the penultimate tarsal segment "bilobate" (as for *viridipennis*), which should exclude the otherwise similar *Philophuga viridis* Dej. A ♂ from Nebraska designated as *neotype*; it belongs to the blue form. — *Calleida purpurea* [Lec. & Horn 1882, p. 55].

1726 *Lebia platicollis* (1823b: 14). No type area given. A syn-

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[8] **Madge, by mistake, gives Dejean as author of *ornata* on all identification labels distributed among museum specimens.**

onym is *fuscate* Dej. (1831) but not *complanata* Dej. (1826), as assumed by Lec. (1859b, p. 446). The hind-angles of prothorax are said by Say to be "very obtuse." As a "Var. a" he describes a form with long, pale humeral spot which must be *limbata* Dej. A ♂ from Allegheny, Penn., designated as *neotype*, and the place as type loc. — *Pinacodera platicollis* [Horn 1881, p. 40].

1731 *Cymindis laticollis* (1834: 413). Type area "near the Rocky Mountains." Lec.'s first specimen as well as the one used for neotype agree with Say's description. A ♂ from Colorado designated as *neotype*, and this state as type area. — *Cymindis laticollis* [Horn 1882, p. 43].

1746 *Cymindis pilosus* (1823b: 10). No type area given. Say's description is not decisive though the "transverse" punctures on the elytra point to *pilosa* auct. as conceived in coll. Lec. (MCZ). Say's varieties α, β and γ belong to other species. A ♂ from Dorchester, Mass., designated as neotype, and the place as type loc. — *Cymindis pilosa* [Horn 1882, p. 43].

1756 *Cymindis sinuatus* (1823b: 8). Type area Maryland. The description is conclusive. A ♀ from Maryland designated as *neotype*. — *Apenes sinuata* [Horn 1881, p. 40].

1783 *Brachinus cyanipennis* (1823a: 143). Type loc. Engineer Cantonment, Missouri. This, as interpreted by Lec. in his collection (MCZ), is the species deviating from all others in North America by possessing long, erect hairs in the elytral striae (T. L. E.). A ♂ from Ames, Iowa, designated by T. L. Erwin as *neotype*. — *Brachinus cyanipennis* [erect setae of elytral depressions 2× or more as long as elytral pubescence].

1794 *Brachinus stygicornis* (1834: 415). Type area "Missouri" (possibly including Nebraska). This is an exceedingly variable species which includes also *quadripennis* Dej. (1825) and Dejean's name has priority (T. L. E.). A ♂ from South Bend, Nebraska, was designated by T. L. Erwin as *neotype*, and the place as type loc. — *Brachinus quadripennis* Dej. [tibiae and tarsi infuscate, abdomen dark brown to black].

1806 *Epomis tomentosus* (1823b: 60). Type area Pennsylvania. Say's description, e. g. of the dilated, truncate terminal segment of the palpi, seems to be conclusive. A ♀ from Pennsylvania designated as *neotype*. — *Chlaenius tomentosus* [Bell 1960, p. 103].

1814 *Chlaenius impunctifrons* (1823b: 64). No type area given. Say's description is not conclusive; I have followed Lec., according to his collection (MCZ), and Bell (1960, p. 136). A ♂ from Dorchester, Mass., designated as *neotype* and the place as type loc. — *Chlaenius impunctifrons* [Bell 1960, p. 136].

1815 (syn.) *Chlaenius circumcinctus* (1834: 418). Type area Louisiana. Say describes the irregular punctuation of the prothorax and the interpretation is certain. His name is a synonym of *perplexus* Dej. (1831), erroneously recorded from Africa (see Lth., 1955a, p. 25; Bell, 1960, p. 145). A ♂ from Louisiana designated as *neotype.* — *Chlaenius perplexus* Dej. [Bell 1960, p. 145].

1817 *Chlaenius pensylvanicus* (1823b: 66). No type area given. (The name *pensylvanicus* is a manuscript name of Melsheimer and does not necessarily imply that Say's specimens had the same provenience.) The description of color given by Say seems sufficient for an interpretation. A ♂ from Pennsylvania designated as *neotype*, and the state as type area. — *Chlaenius pensylvanicus* [Bell 1960, p. 146].

1822 *Chlaenius nemoralis* (1823b: 65). Type area Pennsylvania, Georgia, or Florida; the last-named state herewith designated. Since the strikingly dull prothorax of *nemoralis* auct. is not mentioned by Say, the description could equally well be applied to *tricolor* Dej. (1826) with which it is commonly confused. I have followed Lec., according to his collection (MCZ), and Bell (1960, p. 140). A ♂ from Winter Park, Fla., designated as neotype, and the place as type loc. — *Chlaenius nemoralis* [Bell 1960, p. 140].

1830 *Chlaenius solitarius* (1823b: 65). Type area "on the Missouri" (that is, the river). Say's description of form and punctuation of prothorax, as well as of the "polished" elytra, seems to exclude related species. A ♂ from Dubuque, Iowa, designated as neotype, and the state of Iowa as type area. — *Chlaenius solitarius* [Bell 1960, p. 111].

1838 *Chlaenius aestivus* (1823b: 62). No type area given. In Say's description, the combination of large size, narrow prothorax, and bicolored upper surface seems to exclude all other species of the genus. A ♂ from Rosslyn, Virginia, designated as *neotype*, and the place as type loc. — *Chlaenius aestivus* [Bell 1960, p. 120].

1842 *Chlaenius laticollis* (1823b: 64). Type area "Missouri" (possibly including Nebraska). Say's description is not conclusive. I have identified the species as defined by Bell (1960, p. 129). A ♀ from Tonganoxie, Kansas, designated as *neotype.* — *Chlaenius laticollis* [Bell 1960, p. 120].

1856 *Chlaenius emarginatus* (1823b: 63). No type area given. Say's remarks concerning the labrum: "deeply emarginated" and "profoundly and obtusely emarginate," make his description conclusive. In the Paris Museum is a ♂ with two green Dejean labels: (a) "emarginatus Say, in Amer. Bor."; (b) "D. Say." This I have designated as *lectotype*. Selected type loc.: White Sulphur Springs, W. Va. (MCZ). — *Chlaenius (Anomoglossus) emarginatus* [Bell 1960, p. 106].

1858 *Chlaenius pusillus* (1823b: 63). No type area given. Say's description of the deeply emarginate labrum, together with the small size, is sufficient for an interpretation. A ♂ from Franklinville, Penn., designated as *neotype*, and the place as type loc. — *Chlaenius (Anomoglossus) pusillus* [Bell 1960, p. 107].

1860 *Chlaenius lithophilus* (1823b: 62). No type area given. The small size is sufficient for the interpretation of Say's name. A ♂ from Rivervale, N. J., designated as *neotype* and the place as type loc. — *Chlaenius (Brachylobus) lithophilus* [Bell 1960, p. 137].

1862 *Oodes parallelus* (1834: 420). Type area Louisiana. Say's description is conclusive. A ♂ from Louisiana designated as *neotype*. — *Oodes (Lachnocrepis) parallelus* [Lec. & Horn 1882, p. 29].

1882 (? syn.) "*Amara* ? *grossa*" (1834: 430). Type area "N. W. Territory." Ball (1960, p. 48) pointed out that Say's description is sufficient for deciding that his species is the same as *zabroides* Lec. and that, therefore, Say's name has priority. A ♀ from Denver, Colo., designated as *neotype*, and the place as type loc. (Lth., 1968). — *Euryderus grossus* [Lth., 1968, p. 747].

1897 *Harpalus erraticus* (1823b: 27). No type area given. Say's description is almost conclusive and *retractus* Lec. seems unlikely for geographical reasons. A ♂ from Medora, Kansas, designated as *neotype*, and the place as type loc. (Lth., 1968). — *Harpalus erraticus* [Lth., 1968, p. 766].

1903 (syn.) *Harpalus viridis* (1823b: 31). No type area given. Application of Say's name is clear from his mentioning the elytral pubescence; it is a synonym of *affinis* Schrank 1781, *aeneus* Fabr. 1792, and *viridiaeneus* Beauv. 1805. A ♂ from East Boston, Mass., designated as *neotype*, and the place as type loc. — *Harpalus affinis* Schrank [Lth., 1968, p. 768].

1904 *Harpalus amputatus* (1834: 432). Type area "N. W. Territory." Say separates his species from *aeneus* F. (= *affinis* Schrank) on the nonsinuate elytral apex and his description may be regarded as decisive. A ♂ from San Luis Valley, Colo., designated as *neotype*, and the place as type loc. — *Harpalus amputatus* [Lth., 1968, p. 769].

1922 *Harpalus faunus* (1823b: 28). Type area not given. Say mentions the punctulate elytral striae which makes the interpretation virtually conclusive (see Ball & Anderson, 1962, p. 12). Apparently, his concept of *faunus* was, however, composite: a ♂ in the Paris Museum, with two green Dejean labels: (a) "Faunus Say" and (b) "D. Say," belongs to *pensylvanicus* DeG. and should not be used for lectotype. A ♂ from Pennsylvania designated as *neotype*, and the state as type area (Lth., 1968). — *Harpalus faunus* [Lth., 1968, p. 759].

1956 *Harpalus herbivagus* (1823b: 29). No type area given. The impunctate basal foveae of prothorax are mentioned in the description, and the interpretation is therefore rather conclusive. A ♂ from Rumney, N. H., designated as *neotype*, and the place as type loc. (Lth., 1968). — *Harpalus herbivagus* [Lth., 1968, p. 794].

2009 *Harpalus vulpeculus* (1823a: 30). No type area given. Say's description seems to be decisive. A ♂ from Washington, D.C., designated as *neotype*, and the place as type loc. (Lth., 1968). — *Trichotichnus vulpeculus* [Lth., 1968, p. 818].

2010 (syn.) *Harpalus iricolor* (1834: 432). This is a *nomen nudum* without formal description. Say (l. c.), by some mistake, refers to a "*Harpalus iricolor*" as described by him and being the same as *dichrous* Dej. (1829), that is, a *Trichotichnus*.

2015 (? syn.) *Harpalus iripennis* (1823b: 30). No type area given. The name has been interpreted according to coll. Lec. (MCZ) who considered it identical with his own *Selenophorus varicolor*. It is a species with strikingly large head and impunctate elytral striae; the penis is very characteristic (see Lth., 1968). *S. depressulus* Csy., a supposed synonym in Leng (1920), is a distinct species. A ♂ (with dissected genitalia) from Enterprise, Fla., designated as *neotype*, and the place as type loc. — *Selenophorus iripennis* [Lth., 1968, p. 823].

2051 *Harpalus hylacis* (1823b: 31). No type area given. Say's description of the pro- and meso-tarsi (though no correlation with sex is stated) seems to make the interpretation reliable. A ♂ from Dorchester, Mass., designated as *neotype*, and the place as type loc. (Lth., 1968). — *Gynandropus hylacis* [Lth., 1968, p. 821].

2070 *Harpalus carbonarius* (1823b: 32). No type area given. Since Say mentions the red spot on frons, the pubescence of the prosternum, and the depressed sides of the prothorax, his description must be regarded as conclusive. A ♂ from Camden, S. C., designated as *neotype*, and the place as type loc. (Lth., 1968). — *Anisodactylus (Triplectrus) carbonarius* [Lth., 1968, p. 848].

2071 *Harpalus rusticus* (1823b: 32). No type area given. The current interpretation of Say's name is somewhat dubious. The palpi are described as "reddish-brown" and the margins of prothorax are "not depressed" (both characters fitting *dulcicollis* Laf. 1841). This, however, does not provide sufficient reason for removing Say's name from the by far commonest species of subg. *Gynandrotarsus (Triplectrus)*. A ♂ from Rumney, N. H., designated as *neotype*, and the place as type loc. (Lth., 1968).—*Anisodactylus (Gynandrotarsus) rusticus* [Lth., 1968, p. 843].

2092 *Harpalus agricola* (1823b: 33). No type area given. In coll. Dejean (MNP) is a ♂ carrying three green labels: (a) "♂"; (b) "agricolus Say, in Amer. bor."; (c) "D. Say." This, without any doubt, is an authentic Say specimen. Unfortunately, it belongs to *melanopus* Hald. Say's description is not decisive. Actually, Lec. originally (1848, p. 379), used the name for *melanopus* but, in his catalogue (1863), introduced the practice followed ever since (e.g. by Horn, 1880), that is, applying the name to the species with a single pair of setiferous punctures on clypeus. It is justified, I think, to regard Say's *agricola* as a composite concept, including both species concerned, and to apply it according to present practice. Therefore, I have refused to select the Paris specimen as lectotype and have made a neotype of the "true" *agricola*. Since, in the original description, Say used "agricolus" and "agricola" as alternative spellings, the latter one, linguistically correct, should be used. A ♀ from Allegheny, Penn., designated as *neotype*, and the place as type loc. (Lth., 1968).—*Anisodactylus agricola* [Lth., 1968, p. 856].

2107 *Harpalus caenus* (1823b: 34). No type area given. In the Paris Museum is a ♀ with three green Dejean labels: (a) "♀"; (b) "caenus Say, in Amer. Bor."; (c) "D. Say." The specimen belongs to *caenus* auct. and I have labeled it as *lectotype*. Designated type loc.: Newark, N. J. (Lth., 1968).—*Anisodactylus caenus* [Lth., 1968, p. 860].

2111 *Feronia interstitialis* (1823b: 57). Type area "Missouri" or Pennsylvania. Though the elytral pubescence is not mentioned by Say, the description may be regarded as decisive. A ♂ from Camp Hill, Penn., designated as *neotype*, and the place as type loc.—*Anisodactylus (Amphasia) interstitialis* [Lth., 1968, p. 860].

2127 *Harpalus baltimoriensis* (1823b: 33). Type loc. (Say, 1834, p. 431) Baltimore, Md. The description is conclusive. After *sanctaecrucis* F. 1798 was interpreted as referring to the same species (Schaum, 1847, p. 47), Say's name has fallen into synonymy. Say consistently (also 1834, p. 431) used the spelling "baltimoriensis" and there is no reason to change this. A ♂ from Pennington Gap, Va., designated as *neotype*.—*Anisodactylus (Anadaptus) sanctaecrucis* F. [Lth., 1968, p. 839].

(Not in Leng.) *Harpalus similis* (1823b: 29). Type area North Carolina. This name, lacking in Leng (1920), has been interpreted according to v. Emden (1942, p. 541) who, apparently following a suggestion made by Lec. (1859b, p. 458), regarded it as valid name for the species afterwards described by Dejean (1829, p. 357) as *Harpalus agilis*. The selected neotype agrees exactly with Lec.'s first specimen, labeled "agilis Dej. ? similis Say" (as in his catalogue, 1863, p. 12). A ♂ from Florida designated as *neotype*. — *Anisotarsus similis* [Emd. 1953, p. 526].

2139 *Feronia terminata* (1823b: 48). No type area given. Say's description is not quite conclusive. Though his referring the species to *Calathus* (l. c.) is quite conceivable from the general habitus of the insect, the expression "posterior angles (of prothorax) subacute" is dubious. It seems, however, justified to follow general practice, as expressed in coll. Lec. (MCZ). A ♂ from Cleveland, Ohio, designated as *neotype*, and the place as type loc. (Lth., 1968). — *Anisotarsus terminatus* [Lth., 1968, p. 867].

2156 *Feronia autumnalis* (1823b: 48). No type area given. The description is insufficient and the name was interpreted from coll. Lec. (MCZ). A ♂ from Nahant, Mass., designated as *neotype*, and the place as type loc. — *Episcopellus autumnalis* [Lth., 1968, p. 813].

2163 *Feronia atrimedea* (1823b: 39). Type area "from the Missouri" (that is, the river). Say's description seems conclusive. The dilated ♂ pro-tarsi exclude *Stenolophus (Agonoderus) comma* F. and its relatives. There is no reason to change the original spelling into "atrimedius." A ♀ from Iowa City, Iowa, designated as *neotype*, and Iowa as type area. — *Bradycellus (Triliarthrus) atrimedeus* [Lth., 1968, p. 899].

2171 *Trechus rupestris* (1823b: 91). No type area given. Say's description is almost conclusive. He mentions the slightly marked hind-angles of prothorax, characteristic of *rupestris* auct., and the given color pattern is the same as in the pale form of that species (with unicolorous, rufous prothorax). To this belongs the first specimen in coll. Lec. (MCZ) and the neotype here selected agrees with it. A ♂ from Arlington, Mass., designated as *neotype*, and the place as type loc. — *Bradycellus (Stenocellus) rupestris* [Lth., 1968, p. 886].

2173 *Acupalpus debilipes* (1834: 435). Type area Indiana. Like *cinctus*, this is a dubious name. Lec. (1868), with a question mark, referred it to *parallelus* Chd., that is, the dark form of *rupestris* Say; Casey (1914) treated it as a distinct species of *Bradycellus (Stenocel-*

lus). Say's description gives no clue; the color seems too dark even for the dark form of *rupestris* and fits *lecontei* Cki. much better, but this species is excluded by the reported presence of scutellar and dorsal punctures on the elytra. The name should be treated as a *nomen dubium* and no neotype should be designated.

2174 *Stenolophus cinctus* (1834: 434). Type area Massachusetts. Say placed this species in a different genus from *rupestris*, *Stenolophus* contra *Acupalpus* (1834, p. 435), and compared it with *ochropezus* Say. The scutellar stria is said to be lacking, as is often the case in *S. humidus* Ham. which, actually, could be concerned. Lec. (1859b, p. 548), however, did not hesitate to regard *cinctus* as "a variety" of *rupestris*; Casey (1914), as a distinct species of *Bradycellus (Stenocellus)*. Say's name should be regarded as a *nomen dubium* and no neotype should be designated.

2218 *Feronia ochropeza* (1823b: 54). No type area given. In the Paris Museum is a ♂ with two green Dejean labels: (a) "ochropezus Say, in Amer. bor."; (b) "D. Say." It agrees with the general concept of *ochropezus* and I have designated it as *lectotype*. Designated type loc.: Camden, S. C. (Lth., 1968). — *Stenolophus ochropezus* [Lth., 1968, p. 911].

2238 *Trechus conjunctus* (1823b: 40). No type area given. Say's description seems sufficient for an interpretation. A ♂ from White Sulphur Springs, W. Va., designated as *neotype*, and the place as type loc. — *Stenolophus conjunctus* [Lth., 1968, p. 921].

2249 *Trechus partiarius* (1823b: 90). No type area given. Say's careful description of color and of the punctuation of the prothorax seems to exclude other species of subg. *Tachistodes* and agrees with Lec.'s concept of *partiarius* as expressed in his collection (MCZ). A ♀ from Gorham, Ill., designated as *neotype*, and the place as type loc. (Lth., 1968). — *Acupalpus (Tachistodes) partiarius* [Lth., 1968, p. 937].

2287 *Omophron tesselatum* (1823a: 152). Type loc. Elkhorn Creek, "Missouri" (= NE Nebraska). Say's description of the color pattern of the head seems to exclude other species. Say spelled the name with one "l" and so did, rightly, Benschoter & Cook (1956, p. 422). A ♂ from Kansas designated as *neotype*. — *Omophron tesselatum* [Lth., 1961, p. 12].

SUMMARY

Thomas Say described 147 species of ground-beetles (*Carabidae*, excl. *Cincindelinae*) from North America north of Mexico. His collection was destroyed, but before that he sent material of several

of his new species to Count Dejean in France. These specimens eventually, as part of the vast Oberthür collection, passed into the possession of the Muséum National d'Histoire Naturelle in Paris. Of 27 Say species mentioned by Dejean (1826-31) as received from the author, authentic specimens of 12 were found. For different reasons, 4 of these were considered not suitable, whereas of the 8 remaining species *lectotypes*, property of the Paris Museum, were designated.

For the majority of Say species, it was necessary to make *neotypes*, covering 132 of his names. All these constitute a separate collection belonging to the Museum of Comparative Zoology, Harvard University, Cambridge, Mass. As substitute for the lectotypes located in Paris, each of the 8 species concerned is represented in the MCZ by a specimen, "compared with lectotype."

Seven specific names given by Say could not be interpreted. For these no neotype was selected.

A strict acceptance of all specimens in the Paris Museum, labeled as arrived from Say, as true exponents of his species concept in every particular case, would have forced the removal of a name from one species to another within the same genus in four cases — an extremely unfortunate procedure. However, we have regarded these four Say "species" — all in critical groups — as composite, implying that the specimen sent to Dejean may well have been specifically distinct — as now understood — from the specimen(s) kept in Say's collection.

We have thus consistently retained Say's names as currently used, based on the interpretations by Leconte, according to his collection (MCZ). No changes of nomenclature have been proposed.

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ALPHABETIC INDEX OF SAY SPECIES

A NEW BOLIVIAN *TRACHYSPHYRUS* OF THE *IMPERIALIS* GROUP (HYMENOPTERA, ICHNEUMONIDAE)

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Entomologically, Bolivia is perhaps the least known part of Latin America. In 1967, when I published a monograph of the nearly 100 predominantly Andean and southern South American species of *Trachysphyrus*, I could include only two records from that country, although adjacent Perú, Chile, and Argentina were each found to be major centers of abundance and diversity for *Trachysphyrus*. In March of 1968, however, when I was able to spend a week collecting near La Paz, I discovered an abundant and conspicuous new *Trachysphyrus* belonging to the group of *T. imperialis* Haliday, as defined in my earlier study (Porter 1967, p. 275).

Trachysphyrus praeclarus n. sp.

Figure 1

Holotype: (female) BOLIVIA (*La Paz:* Cota Cota, March 4, 1968, A. García & C. Porter) (Tucumán). *Paratypes:* (21 males) BOLIVIA (*La Paz:* Cota Cota, March 4, 1968, A. García & C. Porter). (Cambridge, Ottawa, Porter, San Francisco, Townes, Tucumán, Washington).

FEMALE: *Color:* flagellum black with dull brown staining below toward apex and with a white band above on segments 5-9; scape, head, mesosoma, and gaster bright cupreous metallic, especially on head and mesosoma with bronzy-golden reflections; wings dark with brilliant metallic reflections; coxae and trochanters cupreous metallic with trochantelli becoming orange-brown on apex; fore and mid-femora bright pale orange with dark cupreous metallic staining below on about basal 1/2-2/3; hind-femur bright pale orange with some brown staining on base; tibiae bright pale orange, especially the hind-tibia with a little dusky staining on apex; tarsi mostly black. *Length of fore-wing:* 10.6 mm. *1st flagellomere:* 4.0 as long as deep at apex. *Clypeus:* low, very weakly convex in profile; apical margin practically truncate. *Malar space:* 1.1 as long as basal width of mandible. *Temple:* 0.8 as long as eye in dorsal view; gently receding. *Mesoscutum:* notauli sharp, traceable a little less than 1/2 the length of mesoscutum; surface smooth and shining with abundant, predominantly sharp, small to large punctures which are mostly subadjacent

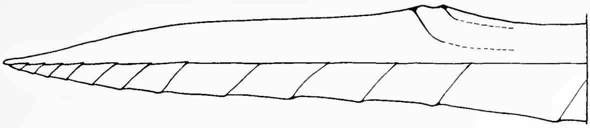

Figure 1. *Trachysphyrus praeclarus* n. sp. Lateral view of apex of ovipositor.

to in great part irregularly somewhat more widely spaced, becoming largest, densest, and with some tendency to longitudinal slurring on central lobe. *Mesopleuron:* speculum mostly smooth and polished, surface otherwise with uniform, coarse reticulate wrinkling. *Metapleuron:* with very coarse reticulate wrinkling. *Wing-venation:* areolet very large and rather high, intercubiti weakly convergent above to practically parallel, 2nd abscissa of radius 1.0-1.2 as long as 1st intercubitus; 2nd recurrent near middle of areolet; discocubitus very gently arched and sometimes slightly sinuate, with or without a stump of a ramellus; nervulus about 1/6-1/3 its length postfurcal; nervellus broken a little below middle, upper part about 1.1 as long as lower. *Propodeum:* rather short and high, basal face arched and considerably sloping behind, apical face discrete and almost vertically declivous and only about 2/3 as long as basal face; area basalis truncate behind; basal trans-carina definite but a little irregular medially, becoming obsolete laterad of areola and sharp again between spiracle and base; apical trans-carina practically absent except for the rather large, prominently projecting, bluntly cuneate cristae; median longitudinal carinae vague, areola hexagonal and a little wider than long, anteriorly elongate and strongly narrowed; lateral longitudinal carinae vague and irregular, a slight denticle at their juncture with basal trans-carina; surface with coarse reticulate wrinkling that grades basad of basal trans-carina into finer sculpture with some discrete intercalated punctures. *1st gastric segment:* postpetiole 1.5 as wide at apex as long from spiracle to apex; dorsal carinae only very faintly suggested for a short distance above and a little in front of spiracle, scarcely defining a median elevation; surface of postpetiole smooth and polished with very faint micro-shagreening and, especially laterally and apically, with rather few, small to tiny, inconspicuous, widely scattered punctures which emit short, well separated setae. *2nd gastric tergite:* smooth and highly polished with very fine, weak micro-reticulation and numerous, well spaced, tiny, superficial punctures that emit short setae which largely but not entirely fall short of the length of their interspaces. *Gaster:* moderately stout fusiform; succeeding tergites with a little stronger micro-reticulation and somewhat more abundant setae than on 2nd. *Ovipositor:* sheathed portion 0.6 as long as fore-wing; gently upcurved; nodus distinct, with a large but rather shallow notch which emits a moderately short, broad, shallow, foreward-directed fossa; dorsal valve in profile gently and directly tapering on about basal 2/3 and then with a more convex taper on apical 1/3; tip 0.24 as high at notch as long from notch to apex.

MALE: differs from female as follows: *Color:* flagellum solid black, except in many but not all specimens with a white band above on segments 13-17 to as few as 14-15; a white line on hind-orbit above; sometimes with blueish reflections, especially on gaster; mesosoma sometimes more extensively golden or greenish-golden than in female; femora and tibiae sometimes a little deeper orange than in female; ventral dark metallic areas of fore and mid-femora averaging broader than in female, occasionally extending nearly throughout and reaching farther laterad or even continuing onto dorsum for a short distance near base; hind-tibia blackish on about apical 1/8-1/6 or more behind and somewhat more narrowly so elsewhere; tarsi more intensely black, except hind-tarsus white at least above and often throughout on about apical 1/2-3/4 of 3rd segment and on all or almost all of 4th segment. *Length of fore-wing:* 9.1-11.4 mm. *1st flagellomere:* 2.9-3.2 as long as deep at apex. *Malar space:* 0.8-0.9 as long as basal width of mandible. *Temple:* 0.8-0.9 as long as eye in dorsal view. *Mesoscutum:* notauli averaging a little longer, traceable about 1/2-2/3 the length of mesoscutum; punctures averaging a little denser but mostly sparser than subadjacent. *Propodeum:* lower and longer in profile; basal face long and rather steeply sloping, apical face considerably shorter and obliquely declivous, merging more or less smoothly with basal face; basal trans-carina as in female or sometimes defined throughout or sometimes practically absent; cristae sometimes a little smaller and lower, bluntly to sharply cuneate; median longitudinal carinae, areola, and lateral longitudinal carinae often vaguer than in female; surface scarcely less coarsely reticulately wrinkled basad of basal trans-carina than elsewhere. *1st gastric segment:* postpetiole 1.0-1.1 as long as wide at apex; dorsal carinae scarcely detectable; surface of postpetiole with more numerous, widely separated, but often more generally and sometimes almost uniformly distributed, moderately small to tiny punctures which emit long and usually at least in part somewhat overlapping setae. *2nd gastric segment:* smooth and highly polished, practically without or at least with fainter micro-reticulation than in female and with abundant, well separated, small, sharp punctures emitting long setae which in great part exceed the length of their interspaces. Succeeding tergites with stronger micro-reticulation and even more numerous punctures and longer, more extensively overlapping setae.

Collections: The holotype is in the Instituto Miguel Lillo at Tucumán, Argentina. Paratypes have been deposited in the Instituto Lillo; the Museum of Comparative Zoology at Cambridge, Massachusetts; the Canadian National Collection at Ottawa; the collection of Charles C. Porter at Cambridge, Maryland; the California Academy of Sciences at San Francisco; the collection of Henry K. Townes at Ann Arbor, Michigan; and the United States National Museum at Washington, D.C.

Discussion: In its brilliantly metallic ground color, strong but dorsally unmodified epomia, large and nearly parallel-sided areolet, nearly straight 2nd recurrent, straight mediella, in having the axillus intermediate between the posterior margin of the hind-wing and the submediella, and in its elongate propodeal spiracle *praeclarus* is a typical representative of the *Imperialis* Group.

Among those subdivisions of the *Imperialis* Group proposed in my recent study of the South American *Trachysphyrus*, the present species fits best in the *Metallicus* Subgroup, a series previously unreported for Bolivia but known from Andean habitats in Ecuador, Perú, and northern Chile. However, *praeclarus* differs from my earlier diagnosis of the *Metallicus* Subgroup (Porter 1967, p. 276) both because it has the notch on the ovipositor tip a little shallower with the accompanying fossa comparatively shorter and weaker, as well as because in the female its propodeum has more strongly projecting and more wedge-shaped cristae and in form is a little shorter and higher than with most of the other species of the subgroup. Nonetheless, these are quite minor differences and there can be no doubt but that this new species belongs to the same radiation as *metallicus* and its previously described relatives.

Within the *Metallicus* Subgroup, *praeclarus* seems especially close to the Peruvian species *florezi* and *aglaus*. From *florezi* it may be distinguished additionally by the following characters: flagellum often banded with white; mesoscutum more uniformly punctate, with punctures of lateral lobes less contrastingly smaller and sparser than those of central lobe; mesopleuron except on speculum uniformly reticulately wrinkled, without a smoother area above along prepectal carina; and propodeal cristae in both sexes more wedge-shaped and more strongly projecting. Moreover, *aglaus*, which is known only in the male, differs from *praeclarus* in its more uniformly golden thorax and propodeum; dark femora and tibiae; uniformly dark hind-tarsus; more strongly receding temples; the same mesoscutal and mesopleural characters which separate *florezi* from *praeclarus*; irregularly shaped areolet with 2nd intercubitus only 0.7 as long as 1st; and shorter and higher propodeum with the apical face nearly vertical and the apical trans-carina distinct throughout.

On the infra-specific level, a striking feature of *praeclarus* is the inconstancy of its white flagellar band, which, at least in the male, is greatly variable in extent and often may be completely absent, whereas in most other species of *Trachysphyrus* the presence or absence of a pale antennal band is a stable character.

Finally, although *T. venustus* and *T. kinbergi* are the only species of the *Imperialis* Group currently reported from Bolivia in addition to *T. praeclarus*, it should be kept in mind not only that most of the other Peruvian and North-Argentine forms may be expected to occur there but also that a region so ecologically diverse and so little explored is practically certain to harbor more new species.

Habitat notes: The type locality, Cota Cota, is situated immediately above La Paz at about 4000 meters' elevation but still in a high desert environment rather than in the *puna*. Here most specimens of *praeclarus* were collected along a path bordered by a lush growth of large cactus, leguminous shrubs, and many herbaceous plants, the majority of which was in flower. During periods of sunlight many individuals of this species were seen flying swiftly in and around the tangles of vegetation but they would cease activity at once whenever the sun was obscured, even for a moment, by clouds.

Specific name: *Praeclarus* is a Latin adjective meaning "splendid" or "illustrious".

Acknowledgements: *Praeclarus* was obtained during fieldwork made possible by a National Science Foundation Grant, under which the author is Associate Investigator, awarded to Dr. Howard E. Evans of the Museum of Comparative Zoology of Harvard University. I thank also Señor Fadrique Muñoz Reyes and the personnel of the Bolivian Ministry of Agriculture for their generous collaboration during our stay in La Paz. Finally, it gives me pleasure to acknowledge the help of my friend and assistant, Señor Alberto S. García Ferrer of the Universidad Nacional de La Plata (Argentina), who collected a considerable part of the type series, including the unique female.

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COLOR CHANGE AND LIFE HISTORY OBSERVATIONS OF THE SPIDER *GEA HEPTAGON* (ARANEAE: ARANEIDAE)

By Laura Elsa Sabath*
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With the great interest in orb webs and their makers at the present time (Witt, et al, 1968; Witt, ed., 1969) any observations on webs and habits of orb weavers of genera other than the ones (*Araneus, Zygiella, Argiope* and *Uloborus*) used currently by experimenters are of interest.

Although spiders of the genus *Gea* are widespread, with species in the subtropics and tropics around the world, no studies of life history or careful web observations of any species of *Gea* have been made. Since *Gea* is believed related to the much larger *Argiope* (Levi, 1968), it was of interest to see whether *Gea* species have similar habits, as resting in the center of the web and building a stabilimentum (a zigzag swatch of silk above and below the hub), and whether they made a similar eggcase. Levi (1968) reviews our limited knowledge of *Gea* as follows: the web is vertical with a dense viscid spiral and apparently without a stabilimentum; it is probably made in low vegetation and the spider drops from it when slightly disturbed.

Material and Methods

An adult female *Gea heptagon* (Hentz) was found October 19, 1968, on her web in 10 inch (25 cm) grass of a suburban yard, Portsmouth, Virginia. She was placed in an indoor terrarium and observed until she died November 7. During this time she spun webs, fed, and made two eggsacs, from both of which spiderlings hatched.

I kept the spider in a 10 gallon (45 l) glass terrarium sealed with clear plastic wrapping. An open culture bottle with emerging fruit flies (*Drosophila*) supplied abundant food. Damp paper towels maintained high humidity. A hoop 20 cm in diameter stood on a

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*The research is a product of Public Health Service Research Grant AI-01944 to H. W. Levi, Mus. Comp. Zool., Harvard Univ., from the National Institute of Allergy and Infectious Diseases.

I thank Dr. Levi for suggesting that I observe this species, for encouragement, and for help in preparing the manuscript, and Mr. Phil Morrison of the Norfolk Museum of Arts and Sciences, Norfolk, Virginia, for photography.

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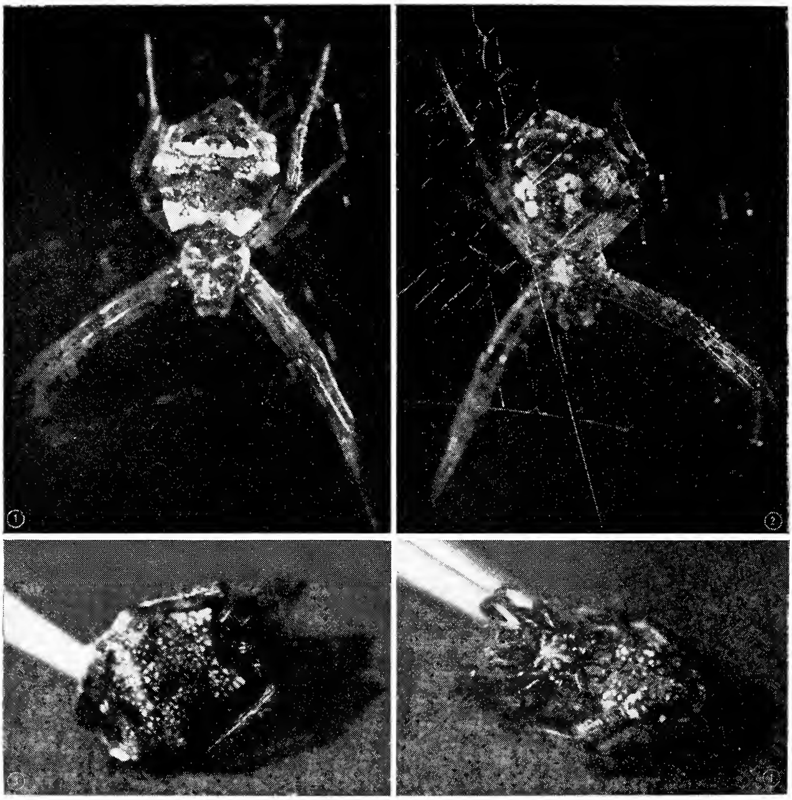


Figs. 1-4. Color change in *Gea heptagon,* total length of the spider's body is about 5.5 mm. 1. Dorsal view of female on web. 2. Ventral view of female on web. 3. Dorsal view of female after dropping from web. 4. Ventral view of female after dropping from web.

wooden leg in the center of the terrarium floor. I set the vial holding the spider at its base. The spider usually climbed upward onto the hoop where she would spin her web. I collected webs easily after the spider dropped out by removing one hoop and providing another. The terrarium sat at room temperature near a window and fluorescent lights.

Specimens used are deposited in the Museum of Comparative Zoology, Harvard University.

Observations

Dropping and Color Change. The spider dropped from her web to the ground in the yard when first approached, but soon returned. For several days in the terrarium she dropped readily on approach, but later waited until touched with forceps. On the web, especially in direct sunlight, her abdomen was mottled with areas of creamy white that contrasted with brown markings that include a dark dorsal triangle (Figs. 1-2). When she dropped to lie, legs folded, on the ground, the white areas turned instantly to brown often almost as dark as the dorsal triangle (Figs. 3-4). The white marks returned gradually over several minutes. The degree of change varied; the photographs unfortunately do not show the extremes seen.

Web. The orb web in the grass was almost vertical. The diameter of the spiral was about 13 cm; the hub was off center (Fig. 5). The webs in the terrarium were spun generally in the evening or early morning. They were not replaced nightly unless removed from the spider. Radii numbered from 25 to 33; spiral diameters varied from 10 to 12 cm. None had a stabilimentum (Fig. 5). One evening I noted a complete orb that, an hour later, was missing a 60° wedge from the lower side. Both radii and spiral were gone. Several other webs spun in captivity also were missing this wedge. In spinning the sticky spiral, the spider felt for the previous strand with leg 1, sometimes putting leg 4 on it. She used leg 4 toward the hub for putting slack into the thread.

Feeding. I observed that when feeding on a leafhopper on the web in the field, she refused to drop from the hub until nudged hard by a vial edge. In the terrarium when I blew upon a web, she shook it violently. Once when a leafhopper fell into the web, she jerked it once, then again. When the prey moved, she ran toward it; the prey froze and she turned away. I wiggled the prey with forceps and the spider jumped it. It appeared instantly covered with silk. The spider wrapped it three or four turns, cut it loose,

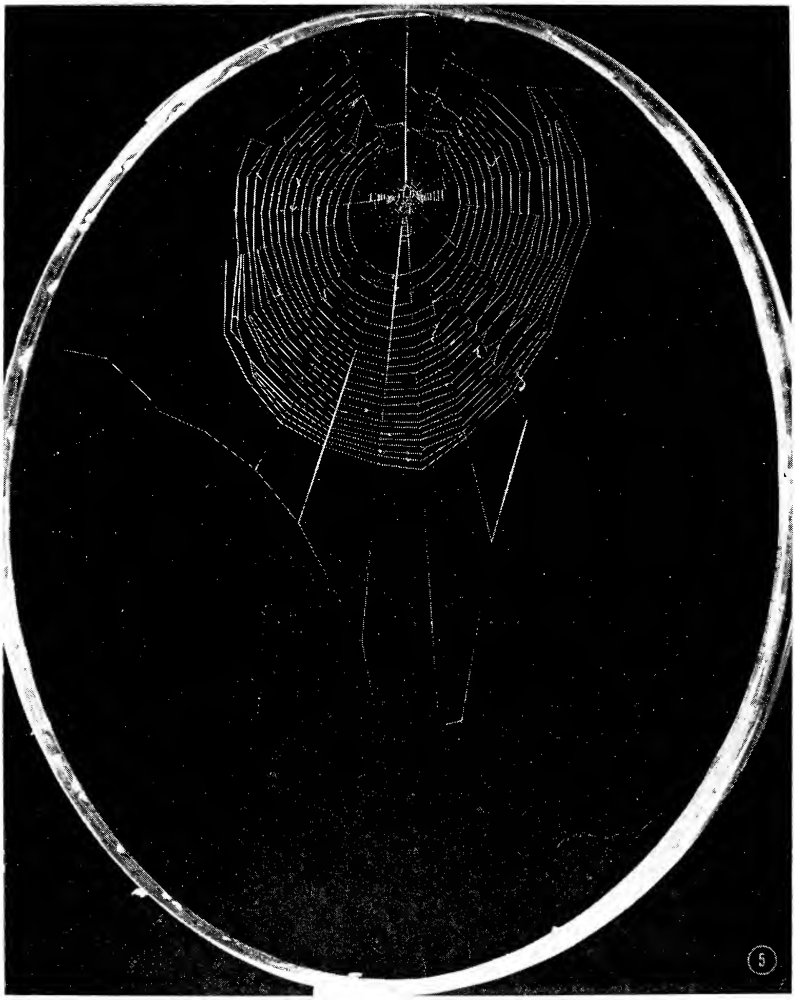


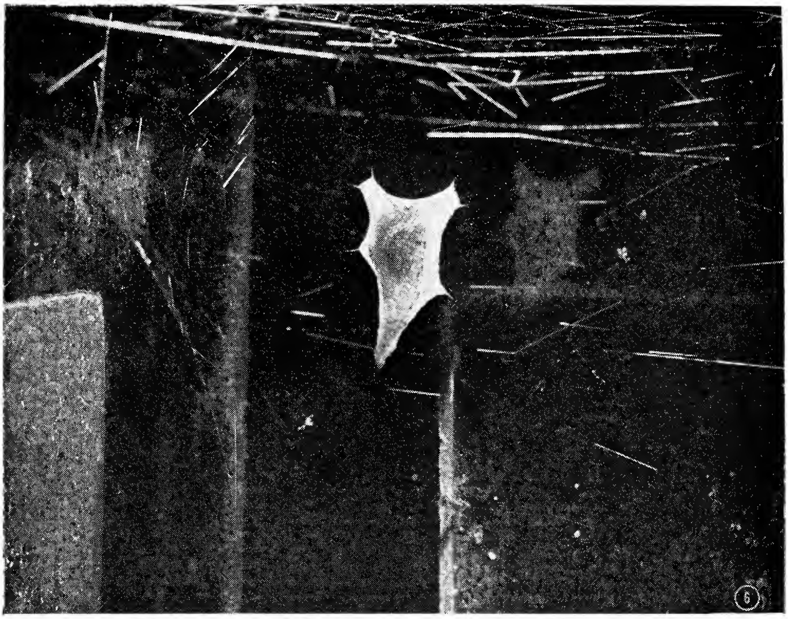
Fig. 5. Web in hoop. Tufts visible are dust. Missing sector at 12 o'clock is due to damage and partial repair. Hoop is about 20 cm across, the web 13 cm.

repaired the radii, carried the prey to the hub, wrapped it two or three more turns, and began feeding. Another day she shook the web when a leafhopper dropped into it. She ran to the prey, hesitated, then enswathed, wrapped and bit it. She returned to the hub and bobbed several times, just enough to shake the prey. She remained quietly at the hub about a minute, then returned to cut the prey loose, repaired the radii, carried the prey to the hub and began feeding. Once when the spider had completed two-thirds of the sticky spiral, a fruit fly landed in the finished portion. She ignored it, finished the web, sat on the hub about two seconds, and then went to the fly. She tore it from the web, did not repair the web, tore more web by dragging the fly to the hub, wrapped it there and began feeding. She usually threw prey remains well away from the web.

Eggsacs. I found an eggsac in an upper corner of the terrarium on the morning of October 23, about 30 cm from the web, as far from the web as space allowed. A supporting tangle web formed a thin sparse barrier around it; the sac hung inside in a hollow area about 3 cm across. The sac itself (Fig. 6) was flattened and resembled a dried broken leaf; its longest dimension was 13 mm. The more exposed side was suspended by about nine threads from the eggsac corners and one from the bulging center; the color was ivory with streaks of dark silk. Under the microscope the dark strands appeared superimposed on the sac wall; they gave the impression of camouflage. The less exposed side (facing the terrarium corner but 1.5 cm from it) was tacked to the exposed side; the seams were easily opened. This side was lighter ivory without the dark streaks. A similar eggsac was made ten days later, November 1, in another corner.

Spiderlings. The evening of November 10, 19 days after the first eggsac was made, I put it in a vial which lay under a bright light. Several hours later I noticed spiderlings emerging from breaks in the eggsac seam. With a dissecting microscope I saw those inside biting threads but did not see any silk-dissolving fluid on them. Fortyfive black-and-white spiderlings emerged (Fig. 7); no undeveloped eggs or embryos were left inside. I opened the eggsac made November 1, ten days earlier, and found 30 eggs or embryos (eggs with white leg-lines). The following day 20 hatched into translucent white spiderlings; 8 remained eggs with no sign of development; 2 were lost.

On August 25, 1968, I found 22 *Gea* in sweeping one grassy locality just south of Portsmouth (North Carolina, Camden Co.,



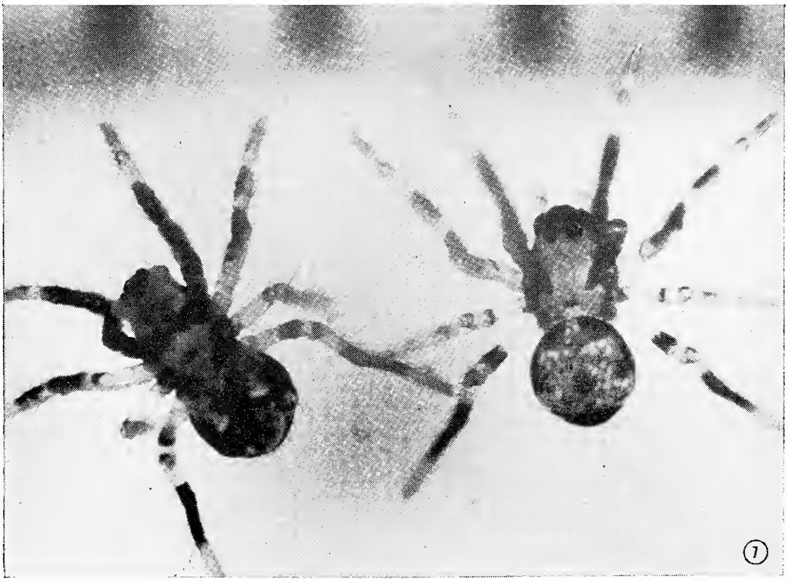


Fig. 6. Eggsac, 13 mm long.

Fig. 7. Spiderlings newly emerged from eggsac showing juvenile pattern. Bars above are 1 mm apart.

7 m.. S of South Mills). They include 2 females, 2 juvenile females, 1 male, 7 juvenile males of various sizes, and 10 small juveniles. The prolateral edge of the patella and tibia of the smallest juvenile measures a little over 0.6 mm, whereas that of the emerged spiderlings of the first eggsac average a little less than 0.5 mm. Adults measure around 2.5-3.0 mm. The smallest field juvenile is probably only one molt ahead of the emerged spiderlings. Therefore I assume that *Gea* normally emerge at this locality in the fall and presumably overwinter as juveniles. Another possibility, considering the wide range of development found in field collections, is that at least more southern *Gea* produce more than one generation per year.

Discussion

Gea heptagon makes a vertical web in grass. As in species of *Argiope,* the spider rests in the center of the web, but no stabilimentum has been observed. Unlike *Argiope,* the spider readily drops out of the web when disturbed. Most unusual is the sudden change of color when dropping from the web.

I have found reports of rapid color change in only four other spiders. Bristowe (1958, p. 264) observed the linyphiid *Floronia bucculenta* drop to the ground when disturbed and turn white abdominal areas to brown. He states that under the microscope white intestinal guanin cells contract rapidly to expose the brown body fluid when the spider is shaken; the cells take several minutes to expand again. He was told by N. L. Roberts in Australia of an araneid, *Phonognatha wagneri*, that reacts similarly. Uyemura (1957) reports color changes for the golden green tetragnathid *Leucauge subgemma* and the golden yellow theridiid *Argyria venusta* [=*Chrysso venusta*]. In both "when picked [up] or shaken strongly [out of the web]" the color breaks up into numerous star-like flecks. As in the *Gea heptagon* observed, the spiders darken instantaneously but recovery to normal takes several minutes.

Of interest also is the open sector occasionally found on the lower part of *Gea's* web. Open sectors are found in the upper part of the web of *Zygiella,* perhaps facilitating rapid descent from the retreat above it to the hub. The open sector in the web of *Gea heptagon* might also be an adaptation to the habit of dropping out of the web on disturbance.

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The illustration on the front cover of this issue of Psyche is a reproduction of the drawing by Phillip A. Adams of an ant-lion, *Hesperoleon deflexus* Adams (Psyche, vol. 63, page 99, 1956).

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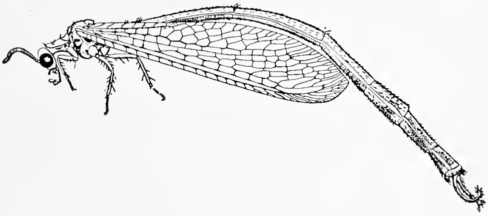

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PSYCHE

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A UNIQUE PREDATORY ASSOCIATION BETWEEN CARABID BEETLES OF THE GENUS *HELLUOMORPHOIDES* AND COLONIES OF THE ARMY ANT *NEIVAMYRMEX NIGRESCENS*.*

By Howard R. Topoff
American Museum of Natural History, New York, N.Y. 10024

This paper presents preliminary observations of a unique relationship between predatory beetles, *Helluomorphoides latitarsis* LeConte and *H. ferrugineus* Casey, belonging to the family Carabidae, and colonies of the army ant, *Neivamyrmex nigrescens* (Cresson).

Studies of interactions between these beetles and *N. nigrescens* are important because: (1) they have revealed unique predatory interactions between species of *Helluomorphoides* and colonies of *N. nigrescens*; and (2) they have increased our understanding of the role of the kinds of stimulation involved in group raiding and emigrations in army ants.

In southeastern Arizona, colonies of *N. nigrescens* are characterized by large populations, group predation, and cyclic behaviour consisting of alternating nomadic and statary phases (Schneirla, 1958). Colonies contain 150,000 to 250,000 workers and a brood population of approximately 30,000 individuals. In the study area, during the nomadic phase, raiding begins at dusk and is followed by emigrations to new nest sites. These predatory forays and emigrations are conducted on branching anastomosing chemical trails, laid down continously from the hindguts of the ants (Watkins, 1964). Worker ants maintain their positions in the columns by following these trails, and by close contact with adjacent individuals.

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*This study was supported by NSF grant GB-7602, and conducted at the American Museum of Natural History's Southwestern Research Station. I thank Miss Beverly Greenspan for her assistance as a participant in the NSF Undergraduate Research Program. I also thank Dr. George Ball for identifying the species of *Helluomorphoides*.

Manuscript received by the editor December 11, 1969

In the course of nightly studies of colony emigrations and bivouac locations, during the summers of 1966 and 1968, as many as 15 individuals of *H. latitarsis* and *H. ferrugineus* were found feeding on the booty and on the broods of *N. nigrescens*. The beetles were observed running in army ant columns or standing off to the sides of the columns, behind rocks or beneath clusters of leaf litter. During their predatory activities, beetles ran along the trails in both directions, "plowing" through the continuous two-way ant traffic. When a beetle of either species contacted a worker ant bringing booty back to her bivouac, the ant usually dropped the booty. On some occasions, if the booty was a larval or pupal individual of another ant species, the beetle immediately ate it and continued on the trail. On other occasions the beetle picked up the dropped booty, left the raiding column, and proceeded to a nearby rock. There, the beetle quickly ate the larva or pupa, returned to the column, and resumed running along the trail.

On two occasions, I observed individuals of *H. latitarsis* "forcibly" taking booty from ants. In both instances a beetle encountered an adult worker returning to the bivouac with a larva of the ant *Pheidole* sp. protruding anteriorly from her mandibles. The beetle grasped the protruding portion of the larva with its mandibles, while the worker of *N. nigrescens* was still holding the larva. The beetle then flexed its head sharply upwards, lifting both ant worker and larva, and held them off the ground for almost two seconds; the ant then released the larva and dropped back onto the ground. On the first occasion, the beetle immediately ate the larva. The second time, the beetle scampered away from the column with the larva as soon as the ant had released it.

Both species of beetles fed most intensively on nights during the nomadic phase when colonies of *N. nigrescens* emigrated with their larval broods. Individuals of *H. latitarsis*, the larger of the two species of beetles, were often observed eating as many as 28 larvae. Whenever a beetle encountered a brood cache, consisting of several hundred larvae clustered beneath a leaf at a trail junction, it fed rapidly until satiated. As the beetles consumed the ant larvae, their abdominal sclerites separated, and their abdomens swelled until they protruded considerably beyond the posterior edges of their elytra (Fig. 1).

Once beetles became associated with a colony of ants, they either fed briefly on booty or brood and then wandered off, or they remained near the colony throughout the night. In the latter case, when army

Figure 1

An individual of *Helluomorphoides latitarsis* eating pupae of *Neivamyrmex nigrescens.* Note workers biting the beetle's antenna, head, and abdomen. Other workers are removing pupae. The reference line is equivalent to 5 mm.

ant activities ceased at dawn, the beetles often entered sheltered areas beneath rocks adjacent to the ants' bivouac. Three individuals of *H. latitarsis*, marked with red dye while foraging in a column of *N. nigrescens* at night, were recovered during the following day by turning rocks adjacent to the colony's bivouac. However, no beetles have ever been found in excavated army ant nests.[1]

Six individuals of *H. latitarsis* and four individuals of *H. ferrugineus* were removed from army ant raiding columns, and maintained in the laboratory in plastic petri dishes. To observe predatory interactions between beetles and army ants, a beetle was removed from its "home" chamber, and introduced into a petri dish containing 50 adult ants and 100-200 eggs, larvae or pupae. In this situation, individuals of both beetle species fed voraciously on all developmental stages of the army ants' brood (Fig. 1). The beetles exhibited bouts of running and feeding, which were followed by periods of complete inactivity, lasting up to 20 minutes. Since the only shaded areas in the plastic chambers were beneath the inactive beetles, workers of *N. nigrescens* often deposited their brood in clusters beneath them. When the beetles again became active, they readily fed on these brood clusters.

In the confined observation chambers, each period of feeding by the beetles aroused the ants to exhibit their "alarm" reaction, which consisted of ants standing on their hind legs, opening and closing their mandibles. The ants also "attacked" the beetles by biting and stinging their antennae and legs (Fig. 1). However, these activities rarely disturbed the beetles, and although they are capable of secreting a defensive, repellent chemical (Eisner *et al.*, 1968), there was no indication that they had sprayed the ants with it.[2]

Discussion

Although many species of carabid beetles are numerous in the field study area, and routinely forage actively at night, *H. ferrugineus* and *H. latitarsis* were the only beetles found with colonies of *N. nigrescens*. Whether they encounter colonies of army ants accidentally while foraging, or actively orient towards them, is not known. Lab-

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[1] Professor Julian Watkins II has informed me that an individual of a related species, *H. texanus*, was uncovered in an excavated bivouac of *N. nigrescens*.

[2] Plsek *et al.* (1969) reported that an individual of *H. texanus*, confined in a plastic chamber with 100 workers of *N. nigrescens*, sprayed the ants that were attacking it. The repellent spray caused the ants to withdraw from the beetle.

oratory experiments by Plsek *et al.* (1969), showed that individuals of a related species, *H. texanus* (Le Conte) can follow chemical trails deposited by workers of *N. nigrescens.* In the field, army ant trails are reinforced by thousands of ants running to and from their bivouac during the course of each night's raiding. This results in the deposition of a very strong and relatively non-volatile chemical trail. If a beetle accidentally crossed a trail used by army ants during the previous night, it could run along the trail until it encountered a colony of *N. nigrescens.*

After locating a colony of *N. nigrescens*, beetles may forage in the ant columns by responding to combinations of visual, chemical, and tactual stimuli. Both species have large protruding compound eyes, which could enable them to orient visually at night. Our field observations indicate that tactual orientation is important in the beetles' foraging pattern, and is accomplished by their continuous responses to physical encounters as they "plow" through ants running to and from their bivouac.

Our field and laboratory observations of contacts between beetles and army ants, has also explicated the role of tactual stimulation in army ant group raiding and emigrations. When individuals of both species of beetles ran through raiding columns, foraging and booty-laden ants returning to their nest were repeatedly pushed aside, or knocked off their feet. Surprisingly, these ants were only momentarily interrupted by the activities of the beetles; they quickly resumed their positions on the trail, without appreciably disrupting other ants in the column.

In order to test the effect of mechanical stimulation on workers of *N. nigrescens* in the field, tactual interactions between beetles and ants were simulated by running the tip of a flexible wire probe through a column of raiding ants. Ants displaced by the moving probe were only momentarily aroused, and the column remained intact. These reactions to mechanical stimulation were then contrasted with the ants' behavior when subjected to stimuli not normally present in their nocturnal environment. Tests showed that even low intensity stimulation by light (from a headlamp) or by air currents (created by blowing) causes the running ants to disperse from the column.

The lack of significant arousal of *N. nigrescens* workers by beetles foraging in their columns, may be explained, in part, by considering the stimulus-environment characteristic of army ant colonies. Throughout their development and adult life, army ant workers live in an environment in which they are continuously stimulated by chemical and tactual interactions among all individuals in the colony. Since individual ants contact each other continually in the bivouac and in raiding and emigration columns, their thresholds of arousal for tactual stimulation may be very high. Effectively then, this low level of reactivity on the part of the ants makes the beetles' typical pattern of foraging well adapted to the physiological state of the ants. Thus, although the beetles exhibited no specific adaptations for preventing the ants from becoming aroused, they were successful predators on the army ants' brood and booty, because their contact with the ants did not result in the dissociation of the ant columns.

Although our observations represent only a preliminary study, we feel that both *H. latitarsis* and *H. ferrugineus* must be added to the list of organisms important in the biotic environment of the army ant, *N. nigrescens*. During the present study, as many as 15 individuals of *H. latitarsis* and *H. ferrugineus* were found associated with each colony of army ants, and each beetle consumed approximately 10-30 army ant larvae during every emigration. Since the nomadic phase of *N. nigrescens* lasts about 18 days, during which time colonies may emigrate up to 15 times, several thousand larvae might be consumed by the beetles during the nomadic phase of each colony. This represents a substantial degree of predation.

The queen of *N. nigrescens* lays approximately 30,000 eggs every 30-35 days. This potential increase in the size of the adult population is offset mainly by mortality of workers during the predatory raids in other ant nests, and by myrmecophiles which feed on all stages of the colony's brood. These myrmecophiles are specialized insect "guests," adapted to live within the ants' bivouac and to emigrate with the colony each night during the nomadic phase. Most myrmecophiles associated with colonies of *N. nigrescens* are flies of the family Phoridae and beetles of the family Staphylinidae. Akre and Rettenmeyer (1968) have shown that several species of these staphylinid beetles closely mimic army ant workers, and can easily follow their chemical trails. The carabid beetles, *H. latitarsis* and *H. ferrugineus*, by contrast, are not specialized myrmecophiles. We have never found them in any of the 11 army ant bivouacs excavated during the past three years, and they apparently associate with the ant colonies only at night.

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CRYPTIC SLEEPING POSTURE OF A SKIPPER BUTTERFLY, *ERYNNIS BRIZO**

By John M. Burns
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Hesperiids have seldom been observed asleep in nature. A major exception to this general statement is provided by the hesperiine *Thymelicus lineola* (Ochsenheimer), an early twentieth century accidental import from Eurasia now thriving in much of its expanding North American range (Arthur 1966; Burns 1966). The extraordinarily high density attained by colonizing populations of *T. lineola* has drawn attention even to dormant individuals. Hensel (1966) found numerous examples clinging to vegetation in early evening at Edmundston, New Brunswick, and easily sampled them by hand. I similarly sampled *T. lineola* on the evening of 24 June 1968 in a pasture at Durham, Middlesex County, Connecticut, where it abounded, although it had begun to appear in that region only five years before (Apter and Burns 1965). The sleeping skippers sat exposed on leaves, stems, and flowers of forbs and grasses, with the upper sides of the wings together above the back — a position commonly assumed by these skippers when momentarily at rest in the course of diurnal activity. There was no suggestion of concealing behavior.

In contrast to this are two observations on a native pyrgine, *Erynnis brizo* (Boisduval and Leconte), made when I was collecting genitalic differentiates of this species, and natural hybrids between them, in Texas (Burns and Gillmor, in preparation). *E. brizo* characteristically rests between diurnal flights with both pairs of wings stretched out horizontally.

In pine and scrubby oak habitat along park road P1 between Bastrop and Buescher state parks, Bastrop County, Texas, on 14 March 1967, at 1730 hours C.S.T., a flying *E. brizo brizo* male that I was pursuing abruptly flew to a dead branch on the prostrate skeleton of a shrub. The gray, barkless branch was about the diameter of a lead pencil, about half a meter above the ground, and parallel to it. The skipper lit on the ventral side of this branch and instantly embraced it by aligning its body with the branch and

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folding its wings rooflike over its abdomen in the manner of many moths. The primaries fully covered the secondaries, and the apices of the primaries extended to the dorsolateral surfaces of the branch. In *E. brizo* the upper sides of the brown primaries are partly overscaled with gray — especially distad. As a result, the skipper blended with the branch and literally looked like "a bump on a log."

The speed with which the skipper took up its sleeping position is reminiscent of a rapidly flying female of *Hesperia uncas macswaini* MacNeill seen at 3170 meters in the White Mountains, Mono County, California, by MacNeill (1964: 38): "With no apparent hesitation it turned and disappeared into the eastern side of a dense *Artemisia* bush. Immediate investigation revealed the insect sitting with closed wings four inches within the tangle of terminal twigs and leaves. At first gentle, then vigorous disturbance of that portion of the shrub evoked no visible response upon the part of the insect. The specimen was captured by vigorously tapping the main branch, causing it to fall into an open container." Unlike this *Hesperia* female, however, the *E. b. brizo* male did not become torpid at once (the late afternoon was warm and rather sunny, with thin high cloud); it energetically flew off when I tried to bottle it a minute or so after it had lit. I followed for several minutes and about two hundred meters before losing it. In this interval the skipper seemed at times to investigate briefly other low dead branches.

In juniper and scrub oak habitat on the north rim of Palo Duro Canyon, 24 kilometers south of Claude, Armstrong County, Texas, on 12 April 1968, at 1625 hours C.S.T., a flying female of *E. brizo burgessi* (Skinner) that I was pursuing suddenly settled on a gray branch of a small *Quercus mohriana* shrub that was barely beginning to leaf out. The branch was about a third of a meter above the ground and nearly parallel to it. The skipper lit on the dorsal side of the branch and at once assumed a mothlike posture as described above, except that the primaries scarcely embraced the branch. The afternoon was warm but cloudy at this time; and though the sun shone brightly again later and though some individuals in the population kept active, this female remained quiet. When she was photographed after almost an hour, her only move had been a ninety-degree rotation from the top to the side of the branch (fig. 1). She was torpid and was bottled as soon as photographs were taken.

These two strikingly similar observations — made one year and 665 kilometers apart on both sexes and two of the three major differentiates of polytypic species *E. brizo* (treated in detail by Burns

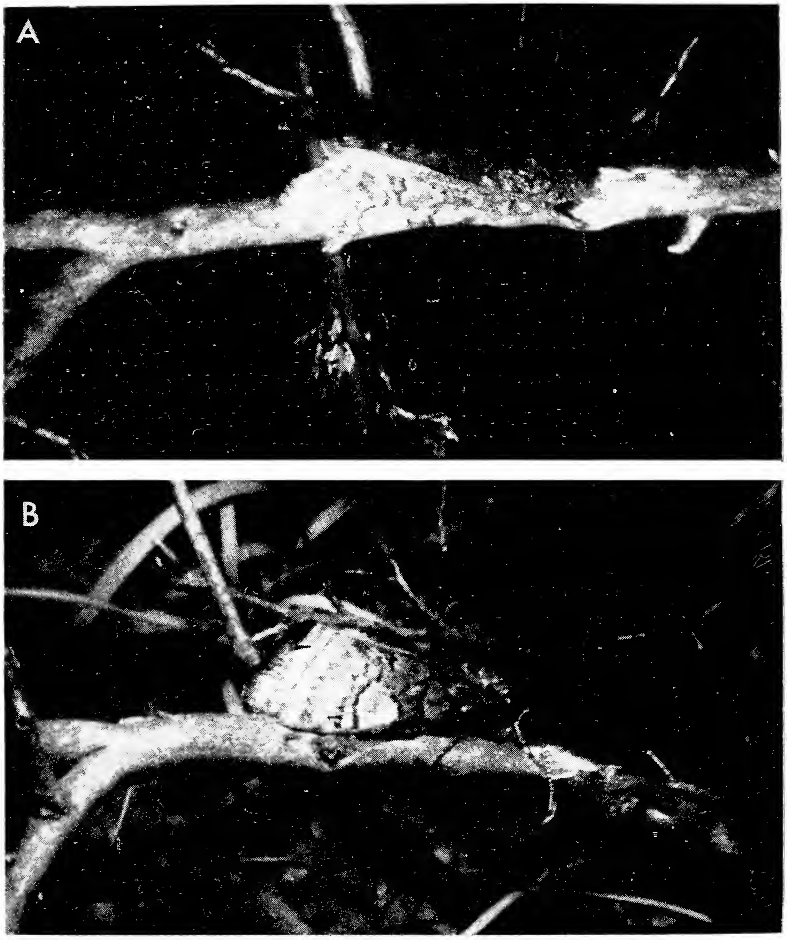

Fig. 1. Female of *Erynnis brizo burgessi* asleep on a branch of *Quercus mohriana* in Palo Duro Canyon, Texas, at 1720 hours C.S.T. on 12 April 1968. Her head is on the right. For further orientation compare fig. 2.
A. Dorsal view of female.
B. Right lateral view of female.

1964: 43-66, 195-205) — are enough to suggest strongly that this behavior is general for the entire transcontinental assemblage of populations. Wherever they occur in North America, these gray/brown skippers are primarily in scrub oak habitat and so never lack a sleeping substrate of small, low, woody (often gray) branches.

Fig. 2. The sleeping female of fig. 1 pinned and spread at a later time. Dorsal view. Her wingspread is about 38 mm.

The sleeping position of *E. brizo*, unlike that of various butterflies, affords little to no protection from weather; the skipper is exposed, but it is concealed visually from many potential predators. The cryptic posture is assumed so abruptly that a fast-moving skipper almost vanishes into a more or less static landscape.

A different but related cryptic orientation has been observed in England in *E. tages* (Linnaeus), a species that was grouped with *E. brizo* in subgenus *Erynnis* by Burns (1964: 22-28). Sleeping individuals of *E. tages* characteristically rest appressed to flower-heads of forbs, grasses, and rushes. As in *E. brizo*, the wings are roofed noctuid-style over the abdomen and distally tend to be wrapped around the sleeping substrate. The flower-heads chosen are generally dead and brown and hence closely similar in color to the skippers themselves (Trimen 1857; Frohawk 1884, 1899, [1924]: 159-161; Tutt 1905-1906: 288-289; Ford 1945: pl. XIV, fig. 4).

Acknowledgements

I thank Douglas A. Graham for his prescience in bringing a flash-equipped Brownie camera to Texas and for using it to take the photographs that appear in fig. 1. Barry I. Kiefer kindly printed these photographs and Spencer J. Berry mounted them. This research was supported by National Science Foundation grant GB 5935.

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A NEW FLIGHTLESS *DOLICHOCTIS* (COLEOPTERA: CARABIDAE) FROM SUMBAWA*

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The genus *Dolichoctis,* of the tribe Lebiini, includes a large number of small Carabidae of the Oriental-Australian area. They are characterized by size (length often *c.* 5 mm or less), by details of the mouthparts (which need not be given here — see Darlington 1968, 124), and almost always by presence of 2 minute punctures without setae on the posterior half of the third interval of each elytron. Most are arboreal, occurring often in under-story foliage of rain forest, although a few species probably occur in leaf litter on the ground. All previously known *Dolichoctis* are fully winged, so far as I know. The finding of a species in which wing atrophy has occurred is therefore of special interest. Atrophy of wings is in fact rare among all the Lebiini of the Indo-Australian islands: of 160 members of the tribe found on New Guinea, only one has reduced wings (*Nototarus papua* Darlington 1968, 186). Of course wing atrophy is very common among some other Carabidae in some other parts of the world (Darlington 1936; 1943).

Dolichoctis pedestris n. sp.

(Fig. 1)

Description. With characters of genus; form as in Fig. 1; dark brown, reflexed elytral margins, legs, mouthparts, and antennal bases brownish-yellow, antennae darker from parts of 3rd segments; reticulate microsculpture heavy and isodiametric on front, distinct and somewhat transverse on pronotum, lighter and more transverse on elytra. *Head* 0.75 and 0.73 width prothorax; 2 strong presumably formerly seta-bearing punctures over each eye. *Prothorax* subcordate; width/length 1.22 and 1.27; base/apex 0.92 and 1.02; lateral margins moderate and moderately reflexed, without setae or seta-bearing punctures; disc weakly convex, with virtually entire impressed middle line, transverse impressions obsolete, baso-lateral impressions weak, surface across base irregular but not distinctly punctate. *Elytra* short, wide; width elytra/prothorax 1.77 and 1.86 (proportions approximate, because elytra slightly spread in all specimens); apices obliquely truncate with sutural angles narrowly

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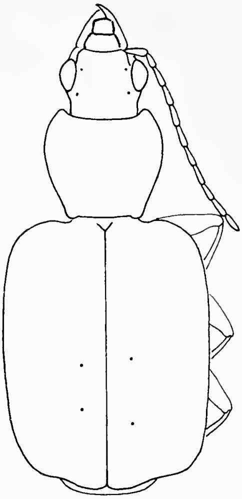

Fig. 1. *Dolichoctis pedestris* n. sp., Holotype.

rounded; striae entire, impressed, not distinctly punctate; intervals slightly convex, 3rd with 2 small impressed points without setae behind middle. *Lower surface* virtually impunctate; abdomen not pubescent. *Inner wings* reduced to vestiges less than ½ length of elytra. *Legs* slender; 4th hind-tarsal segments long, subtruncate; 5th segments without obvious accessory setae (latter probably small, weak, and mostly broken off); claws each with *c.* 4 teeth. *Secondary sexual characters:* ♂ front tarsi apparently not dilated and apparently without squamules (condition of specimens prevents certain determination of presence or absence of squamules); 1 seta each side last ventral segment in both sexes. *Measurements:* length c. 4.8-5.5; width c. 2.3-2.7 mm.

Types. Holotype ♂ (sex determined by dissection) and 3 paratypes (1 in M. C. Z., Type No. 31,675) all from "B. Aroe Hassa," Sambawa (Sumbawa), 2000-5000 ft. (about 600-1500 m), Sept., Oct. (Doherty).

Notes. The atrophy of the wings is unique in this genus, so far as I know, and loss of the lateral prothoracic setae is exceptional also. Otherwise, in Jedlicka's (1963, 356) key to East Asiatic (=Oriental) *Dolichoctis,* the present new species runs to *D. gilvipes* Dejean of the Philippines, but *terrestris* is larger, with eyes less prominent and prothorax narrower and with sides much less sinuate posteriorly; and in my (1968, 126) key to New Guinean *Dolichoctis,* it runs to couplet 2 but has the prothorax much narrower than *striata* Schmidt-Goebel and the elytra much wider and without the maculation of *microdera* Andrewes.

Atrophy of wings and loss of prothoracic setae suggest that this insect, although derived from a primarily arboreal, winged, mainly lowland stock, is adapted to a mountain habitat, perhaps to living in leaf litter on the ground in montane rain forest.

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CAVE HARVESTMEN FROM JAMAICA (OPILIONES: PHALANGODIDAE)

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Numerous islands of the West Indies are composed largely of limestone, in which many and often large caves and cave systems have developed. An abundant fauna of obligately cave-inhabiting invertebrates has been found in these caves. The checklist of Nicholas (1962) is an introduction to these interesting and highly specialized animals. Best known is the cave fauna of the largest island, Cuba. Nothing is reported of the cave fauna of the second largest island, Hispaniola. The only obligate cave inhabitant known from Puerto Rico is an amphipod (Holsinger and Peck, 1968). Two cavernicolous crustaceans, a crab and a shrimp, are reported from Jamaica (Hartnoll, 1964). The three new species of opilionids described in this paper include the first known cave-specialized terrestrial invertebrates from Jamaica.

The opilionids reported on in this paper were collected during a preliminary survey of the invertebrate fauna of Jamaican caves, undertaken in April, 1968, by Stewart B. Peck of the Museum of Comparative Zoology, assisted by Mr. Alan Fiske. In six days eight collecting visits were made to seven caves in the western half of the island. A summary report on the Jamaican cave fauna will be prepared by Mr. Peck at a later date.

The opilionids described here are all members of the family Phalangodidae, subfamily Phalangodinae; two genera are represented: *Stygnomma* with one new species, and *Cynortina* with two new species, very closely related.

The types are deposited in the collection of the Museum of Comparative Zoology. Some paratypes are deposited in the collection of the Instituto de Biología Aplicada, University of Barcelona, Barcelona, Spain.

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*I am indebted to Dr. Herbert W. Levi for placing at my disposal the specimens reported on in this paper and I gratefully thank Mr. Stewart B. Peck and Dr. Herbert W. Levi and Mrs. L. R. Levi for their assistance in preparing this manuscript. Field work by Mr. Peck supported by Evolutionary Biology Training Grant GB 3167, Prof. Reed C. Rollins, principal investigator, Department of Biology, Harvard University.

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Suborder Laniatores
Family Phalangodidae
Subfamily Phalangodinae

The author has followed the classification of Goodnight and Goodnight (1951, 1953), a modification of Roewer's system, avoiding the numerous monotypic genera of Roewer by using a combination of generic characters, some of which proved to be variable. Thus the subfamily Stygnommatinae is ignored and all its members are united in one genus *Stygnomma*. The definition of *Stygnomma* is revised below to accommodate the new species.

Stygnomma Roewer 1914

Type species by monotypy *S. fuhrmanni* Roewer from Columbia.

Phalangodids without a common eye tubercle; eyes present or not. Dorsal scute with five areas, boundaries of which are sometimes difficult to discern. First area without a median line. Tarsi of third and fourth legs without scopulae, and with simple untoothed double claws. All tarsi have a varying number of articles. Distitarsus of first tarsus with two or three articles, of second with three or four. Metatarsi of legs divided or not into astragali and calcanea. Femur of first leg normal. Endite of second coxa without a ventral projection. Secondary sexual characters of the male variable, usually expressed as increased spination of the chelicera and palpus, and enlargement of some portion of metatarsus of third leg.

We include the new species in the key made by Goodnight and Goodnight 1951.

Key to species of *Stygnomma*

1a. Spiracle clearly visible, not concealed in any degree by the fourth coxa 2
1b. Spiracle partly concealed by posterior expansion of the fourth coxa 3
2a. Eyes widely separated, and one spine between them .... *S. fuhrmanni*
2b. Without eyes and without such spine .... *S. fiskei*
3a. Spine present between the eyes 4
3b. Spine not present between the eyes 5
4a. Eyes close together, lacking development of spines on the free tergites .... *S. maya*
4b. Eyes widely separated, with some spinose development of tubercles of free tergites in the males .... *S. spinifera*
5a. Fourth coxa with large spines visible from above .... *S. spinulata*

5b. Fourth coxa without such spines 6
6a. Size about 1 mm in length, color very light .... *S. teapensis*
6b. Size about 2 mm in length, dorsum darker .... *S. annulipes*

Though several of the species reported by Goodnight, 1951, were found in caves, it is evident that the new species is the only known member of this genus that is a true cavernicolous form. This species shows a great number of structural adaptations to cave life: complete loss of eyes, minor degree of sclerotization, lighter color, and an increase in length of all appendages in comparison with related epigeic species. The remarkable length of the second pair of legs expresses the development of a tactile function in the legs of blind species. It must be recognized that these differences are due to adaptation for a cave existence, rather than to phylogenetic divergence, and are not valid to segregate this new species from the genus *Stygnomma.*

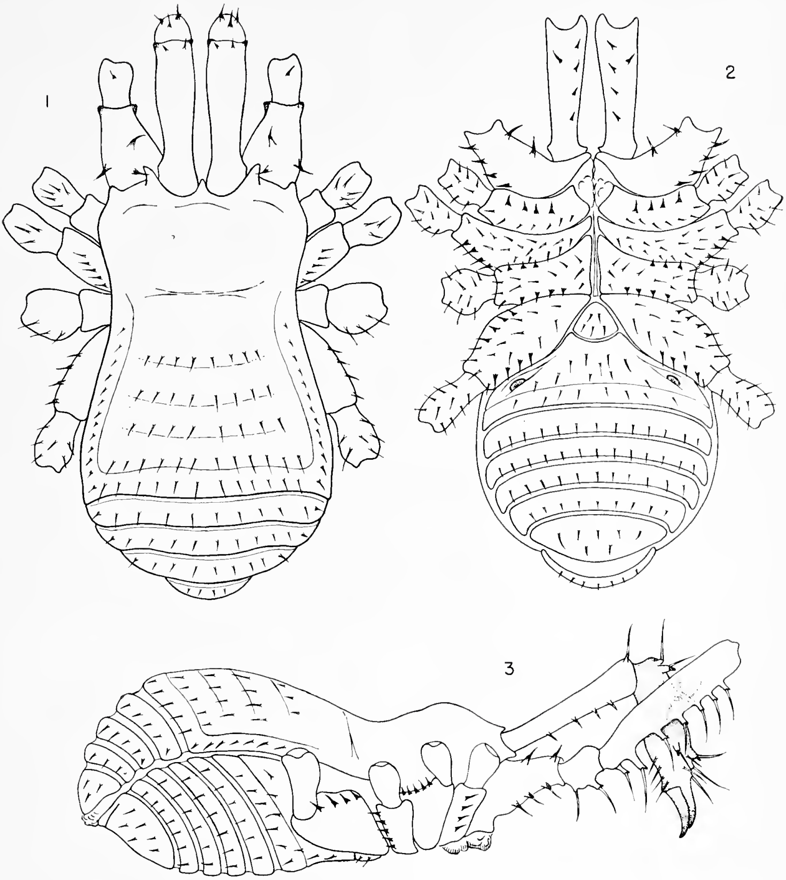
Stygnomma fiskei n. sp.

Figures 1-12

Types. Male holotype, female paratype and 1 juv. from Coffee River Cave, Auchtembeddie, 1½ miles north of Oxford, Manchester Par., Jamaica, collected 4. IV. 1968, in the Museum of Comparative Zoology.

Description. Male holotype. Total length 2.85 mm. Greatest width of body 1.78 mm. Chelicera proximal article, 1.07 mm; distal article, 1.28 mm. Palpal femur, 1.78 mm; petella, 0.86 mm; tibia, 1.40 mm; tarsus, 1.10 mm; total length 5.14 mm. Femur of first leg, 2.14 mm; total leg length 7.92 mm. Second femur, 3.50 mm; total length, 14.00 mm. Third femur, 2.42 mm; total length 9.14 mm. Fourth femur, 3.28 mm; total length, 11.88 mm.

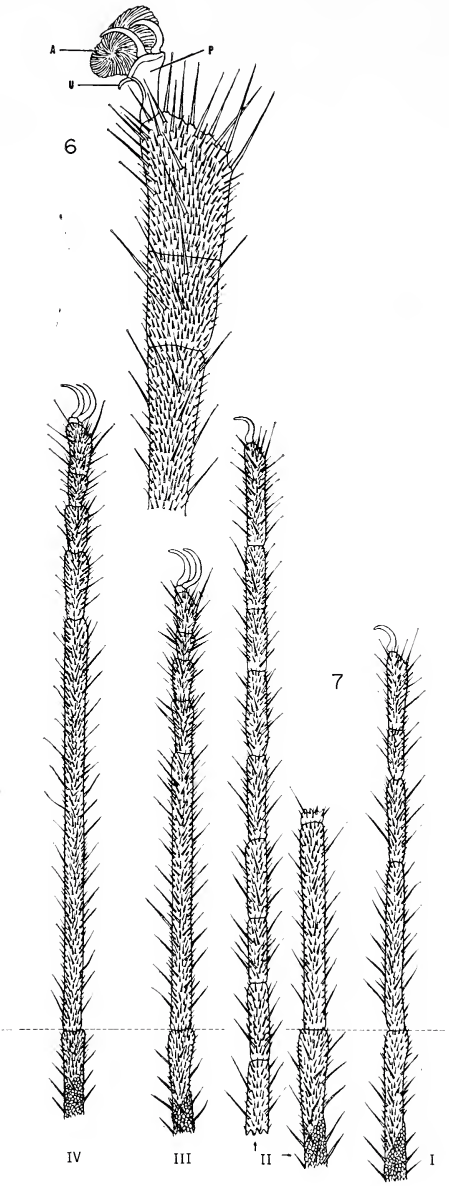
Anterior margin of cephalothorax with one lateral projection on each side, one in the middle and one close to the outer side of each chelicera (Fig. 1). Dorsum smooth, with only a few small granulations along the lateral abdominal scuta, a transverse line of small hairs on the scutum, three free tergites and anal operculum. Cephalothorax without eye tubercle. Eyes and corneal lenses absent. Abdominal scutum with five dorsal areas, except for the first, the boundaries of which are parallel to one another, but very poorly defined. Ventral surface and coxae with scattered thin hairs. Spiracles clearly visible. Hair-tipped tubercles (more or less arranged in rows), are present on the anterior and posterior margins of coxae III and IV, posterior margin of coxa II and near the anterior margin of



Figs. 1-3. *Stygnomma fiskei* n. sp., male holotype. 1. Dorsal view. 2. Ventral view 3. Lateral view.

coxa I. The endite of the second coxa without a ventral projection (Fig. 2).

Chelicera long and slender. Dorsum of proximal article smooth, but with a pair of apical tubercles; ventral surface with a row of four small tubercles. Distal article armed on dorsal surface with seven strong hair-tipped tubercles different in size and placed irregularly (Fig. 3). Base with long slender hairs. Claws curved inward. Immovable finger with 6 teeth, movable finger with 5 teeth (Fig. 4).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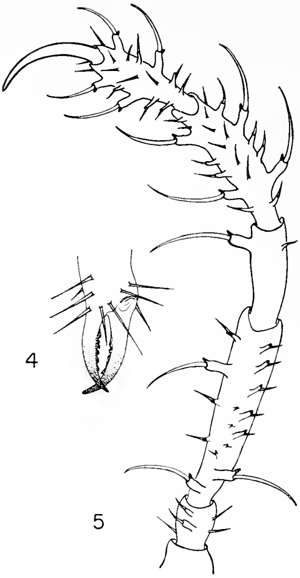
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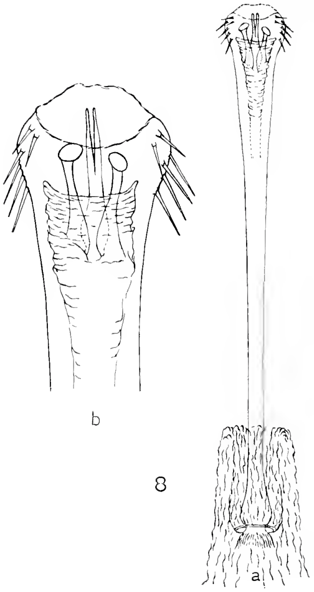

b
8
a

Palpus about twice as long as the body, armed ventrolaterally as in Fig. 5, dorsally unarmed. Tarsal claw long and curved.

Legs extremely long and slender, covered with hairs and fine granules. Metatarsi divided into astragali and calcanea. Fine granulations on legs terminate abruptly at calcaneus of metatarsus. Femur of first leg has a row of few small tubercles on the ventral surface. The fourth leg has an extremely long first tarsal article, other legs have first tarsal article longer than the remaining ones (Fig. 7). Tarsal formula: 4, 10, 5, 5. Distitarsus of first tarsus with two articles, second with four. Third and fourth tarsi of immature specimens with pretarsus (P), arolium (A) and unguiculus (U) (Fig. 6).

Body concolorous, pale yellow-orange, with venter somewhat lighter than dorsum. Appendages the same color as body, but tarsus and metatarsus lighter yellowish.

Penis long and slender. Total length, 1.40 mm. Ventral plate of penis armed as in Fig. 8a and b. Tip folded into membranous cover, and connected at two lateral projections.

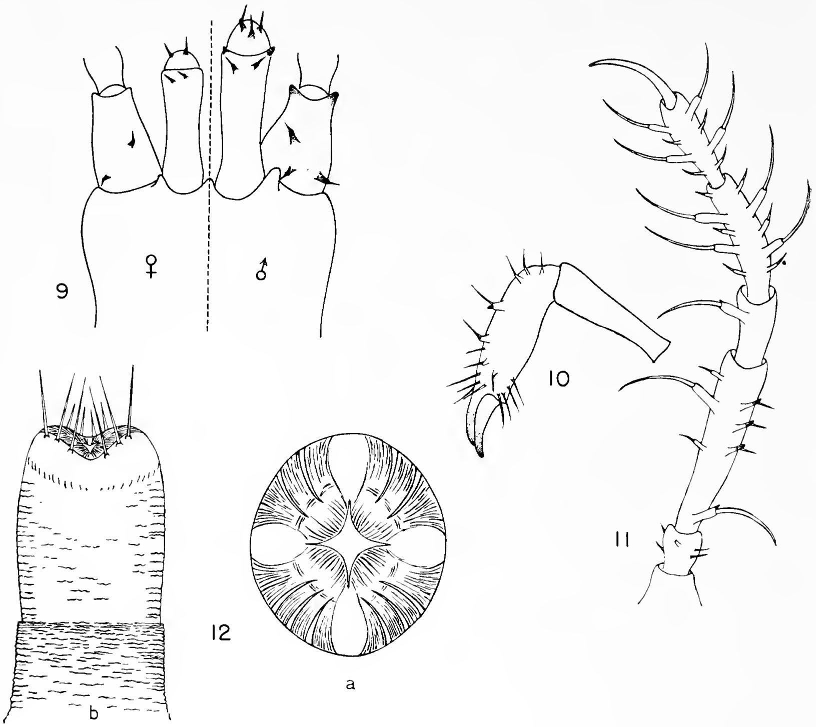
Female paratype. Total body length, 2.67 mm. Greatest width of body 1.57 mm. Chelicera proximal article, 0.78 mm; distal article, 1.28 mm. Palpal femur, 1.52 mm; patella, 0.71 mm; tibia, 1.25 mm; tarsus, 0.92 mm; total length 4.40 mm. Femur of first leg, 1.86 mm; total leg length 7.21 mm. Second femur, 3.28 mm; total length, 13.54 mm. Third femur, 2.25 mm; total length, 9.25 mm. Fourth femur, 3.21 mm; total length 11.25 mm.

Similar in appearance to male but lacking the small tubercles on the first femur. Armature of chelicera and palpus are much reduced and less prominent, as shown in Figs. 9, 10, 11. Also body and appendages are reduced in size.

Ovipositor short and enlarged. Total length, 0.70 mm. Width at widest portion, 0.60 mm. Ventral plate armed as in Fig. 12a. Apex in a frontal view shows a geometric drawing as in Fig. 12b.

Variations. Males studied showed some variability. One of the two males from Oxford Cave has the following measurements: total length, 2.75 mm; width of body, 1.72 mm; chelicera, proximal segment, 0.80 mm; distal segment, 1.10 mm. Palpal femur, 1.60 mm;

Figs. 4-8. *Stygnomma fiskei* n. sp. 4. Lateral view of cheliceral claws, male holotype. 5. Ventral view of palpus, male holotype. 6. Fourth tarsus of immature specimen. 7. Lateral view of tarsi and distal portion of metatarsi of male holotype. 8. Ventral face of penis of male holotype; a. Whole penis. b. Tip, much enlarged. (Abbreviations: A, arolium; P, pretarsus; U, unguiculus.)



Figs. 9-12. *Stygnomma fiskei* n. sp. 9. Part of anterior of dorsum showing differences between female paratype and male holotype. 10. Lateral view of chelicera, female paratype. 11. Ventral view of palpus, female paratype. 12. Ovipositor; a. Ventral view. b. Frontal view.

patella, 0.78 mm; tibia, 1.27 mm; tarsus, 0.95 mm; total length, 4.60 mm. First femur, 1.71 mm; total length, 6.78 mm. Second femur, 2.75 mm; total length, 11.60 mm. Third femur, 2.00 mm; total length, 7.70 mm. Fourth femur, 2.50 mm; total length, 10.10 mm.

There is some variation also in the armature of the chelicera and palpus. This male, in the ventrolateral surface of the femur of the palpus, has a row of only three tubercles, instead of five as does the holotype. The other male has five on the right femur and four on the left. The measurements of this specimen are about the same as of the holotype.

Diagnosis. Aside from the morphological differences due to adaptation to cave life, we can recognize the new species by the following combination of characters: spiracle clearly visible, not concealed by the fourth coxa, dorsum smooth, without any kind of granulations or spines. Eyes and corneal lenses absent. Fourth coxa normal, without large spines. Size about 3 mm.

Habitat. These animals were found on flood debris on silt banks in a side passage about 150 m from the entrance. Coffee River Cave, also called Princess Alice Cave, with a very irregular floor, carries a torrential river subject to heavy flooding. Oxford Cave is a smooth-floored, large, walk-in cave with no standing water, inhabited by abundant fauna including a large bat colony.

Records. Besides the holotype and female paratype there are two male paratypes and three immatures from Oxford Cave at the same locality.

Cynortina Banks 1909

Type species by monotypy *C. tarsalis* Banks 1909 from Costa Rica.

If one applies the limited characters for generic classification pointed out by Goodnight and Goodnight (1953), the genus *Cynortina* becomes an integration of sixteen different Roewer genera. Thus the Mexican and Central American phalangodids are divided at present into eight recognized genera.

Specimens examined possessed intermediate characters between two genera, *Cynortina* and *Sitalcina,* the only difference between them being the position of eye tubercle. It is removed from the anterior margin of cephalothorax in *Cynortina,* and not removed in *Sitalcina* (Briggs, 1968).

But, this difference is not so abrupt as once thought, because in the studied specimens, the eye tuburcle is only slightly removed from the anterior margin. On the other hand, there are no great differences between these two genera, and some characters of the examined specimens agree better with *Sitalcina,* such as tarsal formula, others with *Cynortina,* as the position of the eye tubercle. Tradition might call for the establishment of a new genus, but restricted separation of genera, as adopted by Goodnight and Goodnight (1953), does not support such division. It is thought best to place them in the genus *Cynortina* as its species range across Central America and the West Indies, while all but one species of *Sitalcina* have been found in California. Perhaps *Sitalcina* should eventually be synonymized with *Cynortina.*

The definition of *Cynortina* is revised as follows. Phalangodids with eye tubercle rounded above, unarmed or with small tubercles or spinules, usually removed from the anterior margin of cephalothorax. Eyes present or not. Dorsal scute with five areas, boundaries of which are sometimes difficult to discern. First area without a median line. First tarsus with three articles, second, third and fourth tarsi with a varying number of articles. Distitarsus of first tarsus with two articles, of second with three. Metatarsi of legs divided or not, into astragali and calcanea. Femur of first leg normal. Endite of second coxa without a ventral projection. Secondary sexual characters of the male are variable.

Cynortina goodnighti n. sp.
Figures 13-19

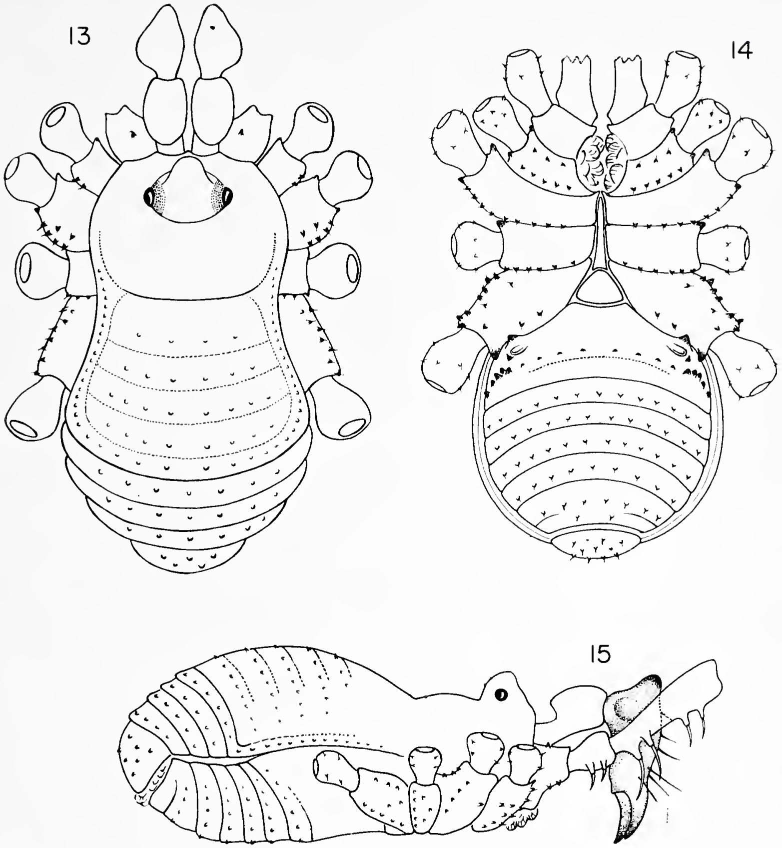
Type. Male holotype and female paratype from St. Claire Cave, 1½ miles southwest of Ewarton, St. Catherine Par., Jamaica, collected 7. IV. 1968, in the Museum of Comparative Zoology.

Description. Male. Total body length, 2 mm. Greatest body width 1.32 mm. Proximal cheliceral article, 0.51 mm; distal article, 0.70 mm. Palpal femur, 0.62 mm; patella, 0.35 mm; tibia, 0.39 mm; tarsus, 0.39 mm; total length, 1.75 mm. Femur of first leg, 0.78 mm; total leg length, 2.90 mm. Second femur, 1.10 mm; total length, 4.40 mm. Third femur, 0.85 mm; total length 3.64 mm. Fourth femur, 1.14 mm; total length, 4.48 mm.

Body pearshaped. Anterior margin of the cephalothorax without frontal or lateral projections, only slightly curved at the level of the insertion of the chelicera and palpus. Dorsum smooth, but with a row of small tubercles along the lateral margin of abdominal scutum, and transverse rows on each area and also on each of the three free tergites. Anal operculum thickly covered with tubercles. The boundaries of the five dorsal scutal areas poorly defined (Fig. 13).

Eye tubercle removed from the anterior margin of the cephalothorax, wider than long, and with a dorsal rounded cone inclined slightly forward. Eyes and corneal lenses present, situated at the base of the eye tubercle (Fig. 15).

Ventral surface with a transverse row of tubercles on each sternite (Fig. 14). Laterally, between second and third sternite, 5 to 6 big tubercles on each side, and one bigger tubercle above spiracle directed upwards. Fourth coxa with a distal-ventral tubercle, bigger than the others, near the spiracle. For this reason the spiracles, though visible, appear more or less surrounded by prominences. Rows of tubercles are present near anterior and posterior margins of coxa I and posterior margins of coxa II and III, and entire

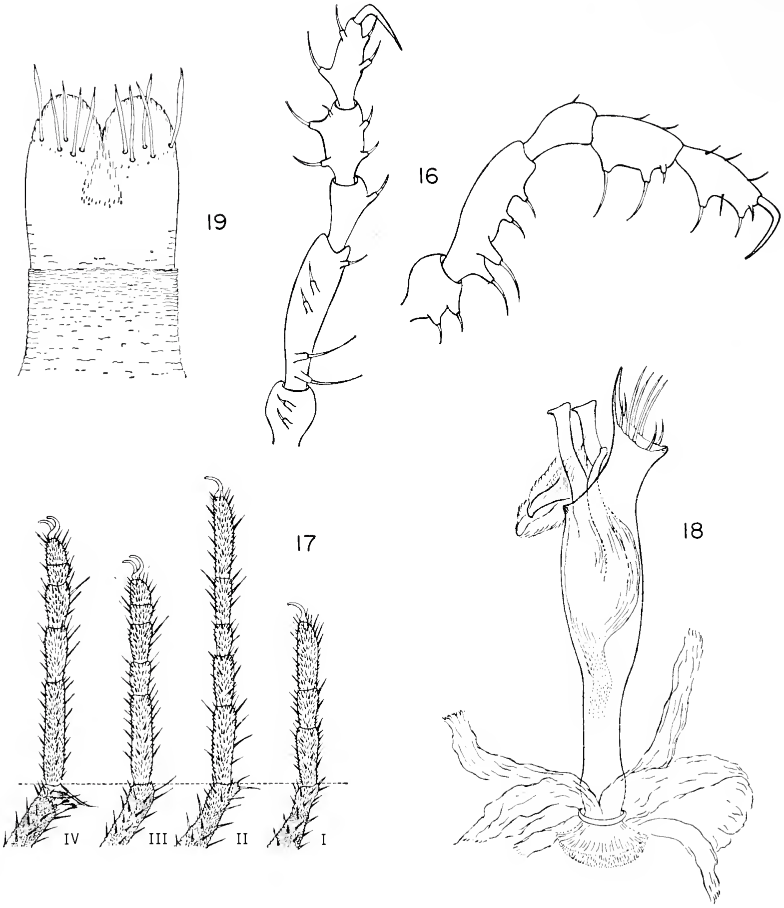


Figs. 13-15. *Cynortina goodnighti* n. sp., male holotype. 13. Dorsal view. 14. Ventral view. 15 Lateral view

surface of coxa IV is covered with bigger tubercles more or less arranged in rows.

Chelicera small, smooth except for a few hairs on the frontal margin of the distal article. Proximal article slender at the base but enlarged dorsally and distally. Distal article somewhat enlarged laterally at the base and with a large rounded elevation on the apex (Fig. 15). Palpus about the same length as the body, unarmed dorsally, armed ventrally and laterally as in Fig. 16.

Legs moderately long, clothed with thin hairs and faintly granulate. Metatarsi divided into astragali and calcanea. Fine granula-



Figs. 16-19. *Cynortina goodnighti* n. sp. 16. Ventral and lateral view of palpus, male holotype. 17. Lateral view of tarsi and distal portion of metatarsi, male holotype. 18. Lateral view of penis. 19. Ventral view of ovipositor.

tions on legs terminate abruptly at calcanea of metatarsi. Fourth metatarsus has three strong, hair-tipped tubercles, two of them directed upward, another directed downward and with a very long hair (Fig. 17). Femur of fourth leg somewhat curved. Femur of tibia of fourth leg with two apical short hair-tipped tubercles on the retrolateral margin. First metatarsus somewhat enlarged at the base.

Entire dorsum reddish brown, areas of dorsum poorly outlined, three free tergites outlined in darker reddish brown. Venter and coxae concolorous with dorsum. Chelicera and palpus lighter reddish brown. Tarsi of legs yellowish, contrasting with other leg articles, which are concolorous with the body.

Penis in lateral view shown in Fig. 18. Relatively large, and somewhat more enlarged in the middle portion. Total length, 0.64 mm. Apical portion truncate with a sharp-pointed process, and with eight setae arranged in two lateral groups of four. Basal portion encircled with a membranous process which appears subdivided in Fig. 18.

Tip simple, long and slender, and accompanied by two elongated processes, both of which appear to be folded within the penis when they are retracted.

Female. Total body length, 2.14 mm. Greatest width of body 1.42 mm. Chelicera, proximal article, 0.40 mm, distal article, 0.64 mm. Palpal femur, 0.59 mm; patella, 0.35 mm; tibia, 0.38 mm; tarsus, 0.38 mm; total length, 1.70 mm. Femur of first leg, 0.68 mm; total leg length, 2.80 mm. Second femur, 1.02 mm; total length, 4.32 mm. Third femur, 0.75 mm; total length, 3.32 mm. Fourth femur, 1.06 mm; total length, 4.42 mm.

Similar in appearance to male but lacking the large rounded elevation on the apex of the distal article of chelicera. Body somewhat large and appendages slightly shorter. Tarsal formula as in male.

Ovipositor short and thick. Total length, 0.52 mm. Distal portion provided with relatively short setae distributed as shown in Fig. 19.

Diagnosis. Unlike the related *C. pecki* this species is colored and has eyes.

Habitat. The type locality is a large, long, multi-level cave with a temporary stream and an abundant and varied fauna including a huge bat colony.

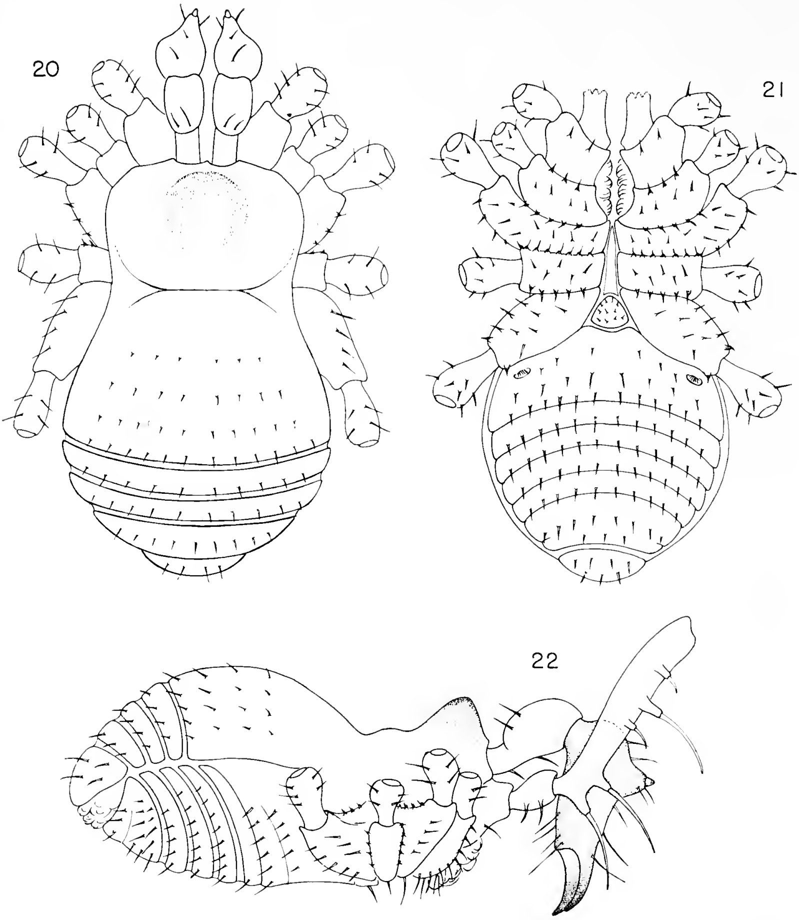
Records. This species is known only from the holotype and paratype.

Cynortina pecki n. sp.

Figures 20-26

Type. Male holotype and one female paratype from Worthy Park Cave, St. Catherine Par., Jamaica, collected 6. IV. 1968, in the Museum of Comparative Zoology.

Description. Male. Total body length, 1.61 mm. Greatest body width 1.10 mm. Chelicera, proximal article, 0.53 mm; distal article,



Figs. 20-22. *Cynortina pecki* n. sp., male holotype. 20. Dorsal view. 21. Ventral view. 22. Lateral view.

0.71 mm. Palpal femur, 0.71 mm; patella, 0.40 mm; tibia, 0.54 mm; tarsus, 0.46 mm; total length, 2.11 mm. Femur of first leg, 1.35 mm; total length, 5.00 mm. Second femur, 3.32 mm; total length, 9.14 mm. Third femur, 1.78 mm; total length, 6.17 mm. Fourth femur, 2.17 mm; total length, 8.53 mm.

Body pearshaped. Anterior margin of the cephalothorax without frontal or lateral projections, only slightly curved at the level of the insertion of the chelicera and palpus. Dorsum smooth, only with a transverse row of thin hairs in each area, each of the three free tergites and the anal operculum. Eye tubercle slightly removed from the anterior margin of the cephalothorax (Fig. 20). Eyes and corneal lenses absent. Abdominal scutum with five dorsal areas, the first without a median line, the boundaries of which are parallel to one another, but very poorly defined. Ventral surface and coxae with scattered thin hairs. Spiracles clearly visible. Hair-tipped tubercles (arranged in rows) are present on the anterior and posterior margins of coxa III. In the remaining coxae, there are some similar tubercles, but not arranged in rows. The endite of the second coxa lacks a ventral projection (Figs. 21, 22).

Chelicera has a few scattered, long hairs. Proximal article slender at the base and enlarged dorsally in the distal two-thirds. Distal article somewhat enlarged laterally at the base and with a large frontal elevation tipped with a rounded tooth (Fig. 23). Palpus almost twice as long as the body. Armed in ventrolateral view as in Fig. 23. Dorsally unarmed except for rows of long hairs. Tarsal claw long and curved.

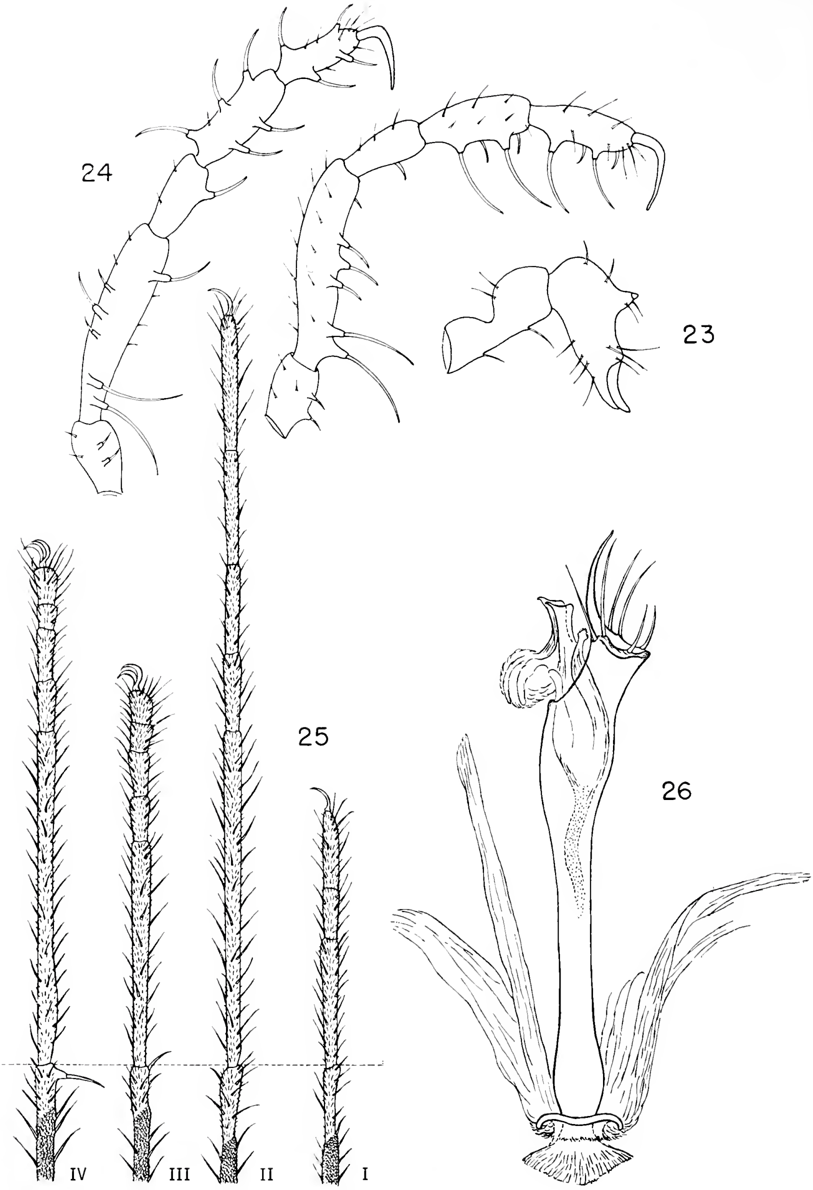
Legs extremely long and slender, clothed with hairs and finely granulate. Metatarsi divided into astragali and calcanea. Fine granulations on legs terminate abruptly at calcaneus of metatarsus. First and fourth legs have an extremely long first tarsal article, other legs have first tarsal article longer than the remaining ones (Fig. 25). Fourth metatarsus with a very long hair-tipped tubercle situated at the apex (Fig. 25). First metatarsus somewhat enlarged at the base. Tarsal formula: 3, 5, 5, 5. Distitarsus of first tarsus with two articles, second with four.

Body concolorous, pale yellow-orange, with venter somewhat lighter than dorsum. Appendages the same color as the body, but tarsus and metatarsus lighter yellowish.

Penis long and slender, in lateral view as shown in Fig. 26. Total length, 0.85 mm. Morphologically similar to that of *C. goodnighti.*

Female. Measurements of entire body and appendages are the same as of male, except the abdomen is somewhat wider. Tarsal formula as in male. Similar in appearance to males, but chelicera without the large frontal elevation tipped with a rounded tooth. Fourth metatarsus without hair-tipped tubercle on the apex, and first metatarsus not enlarged at the base. Ovipositor short and thick. Total length, 0.50 mm. Very similar to the former species.

Variations. There is no variation in the number of tarsal articles. In some of the females studied, the double claws of the third and



Figs. 23-26. *Cynortina pecki* n. sp., male holotype. 23. Lateral view of chelicera. 24. Ventral and lateral view of palpus. 25. Lateral view of distal portion of tarsi and metatarsi. 26. Lateral view of penis.

fourth tarsi are somewhat enlarged and have the inside edge sinuous.

Diagnosis. Unlike the related *C. goodnighti,* this species lacks eyes and is yellowish orange in color.

Habitat. These animals were found half-way through the cave in a chamber containing a scattering of guano. This cave has an assortment of environments along an intermittent river, reached after a 27 foot vertical descent. Abundant cave fauna is present.

Records. Eight female paratypes were collected with the holotype.

CONCLUSIONS

Of these three new species, *S. fiskei* and *C. pecki* are certainly true cavernicoles. The third, *C. goodnighti,* does not show any adaptation to cave life, and it probably is an epigeic form that has penetrated into the caves, but may be found both inside and outside of caves.

The similar appearance of *S. fiskei* and *C. pecki* is a manifestation of convergence toward a special kind of life more than of a true phylogenetic relationship. Actually *C. pecki* appears to be very closely related to *C. goodnighti.* These two species agree strongly with one another, and in spite of their different appearance, they still clearly show their relationship.

Doubtlessly *C. pecki* is the nearest form to *C. goodnighti,* but adapted to cave life. This shows itself by different adaptations, such as the increased length of appendages. The palpus has about the same length as the body in *C. goodnighti* and is almost twice as long as the body in *C. pecki.* The length of the second pair of legs in this animal is extraordinarily increased as often occurs in blind species. In *C. goodnighti* eyes are present and the retina has the characteristic black color. Eyes and corneal lenses are absent in *C. pecki*, and there are no traces of black color in retina. Sclerotization, too, apears decreased in *C. pecki.* Hair-tipped tubercles are fewer in number and less developed. The prominences surrounding the spiracles in *C. goodnighti* have disappeared in *C. pecki.*

Color of *C. goodnighti* is reddish brown, as is usual in epigeic forms. The coloration of *C. pecki* is pale yellowish, as is the tendency among the cave adapted phalangodids.

The morphology of the male genitalia is particularly pertinent to evaluation of the relationship between these forms. The penes of *C. pecki* and *C. goodnighti* are of the same type, but in *C. pecki* longer and tighter, and with a delicate appearance. In contrast, the penis of *S. fiskei* is of a very different type (Figs. 8, 18, 26).

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OBSERVATIONS ON THE PREDATORY BEHAVIOR OF THE SPIDER *HYPOCHILUS GERTSCHI* HOFFMAN (HYPOCHILIDAE)

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The primitive, relict spider family Hypochilidae[2] occurs in the United States (four species), Chile, Tasmania and China (one species each), and exhibits anatomical characters intermediate between the suborders Orthognatha and Labidognatha. Despite the obvious importance of these spiders in evolutionary studies, little has been done to clarify their behavior. Comstock (1940) briefly described the web of *Hypochilus thorelli.* Gertsch (1958) reviewed the taxonomy of the entire family, noting that while all North American members of the family make similar webs (described in detail below), *Hickmania troglodytes* (Tasmania) weaves a large sheet, up to four feet long and two feet wide, and *Thaida peculiaris* (Chile) suspends a large mesh funnel up to three feet in diameter among vegetation (Zapfe & Gertsch, 1955). The web of *Ectatosticta davidi* (China) is unknown. Hoffman (1963) described *H. gertschi* from the Appalachians and noted few differences between its web and that of *H. thorelli.* In 1964, Gertsch described *Hypochilus bonneti* from Colorado, and included excellent photographs of the upper part of the web and of the egg sacs. Kraus (1965) reported briefly on the behavior of captive West Virginia specimens of *H. gertschi* which he had transported to Germany.

This study was carried out approximately two miles north of Athens, Mercer County, West Virginia, in a typical *H. gertschi*

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[1] Study carried out under NSF Grant GB 7346 to the Evolutionary Biology Committee of Harvard University (R. Rollins, principal investigator), and Richmond Fellowship of the Dept. of Biology.

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[2] Marples (1968) recently reclassified this family: *Hypochilus* and *Ectatosticta* are left in the Hypochilidae, and *Hickmania* and *Austrochilus* are placed in their own families, Hickmaniidae and Austrochilidae, respectively. Lehtinen (1967) put each genus in its own family: Hypochilidae, Ectatostictidae, Hickmanidae (sic) and Thaididae (this last is the proper name for the family including *Thaida*, a senior synonym of *Austrochilus*). Marples' study is convincing, that of Lehtinen somewhat superficial. However, neither of these changes affects the family name of *Hypochilus*.

habitat. I have to thank Dr. and Mrs. Jeremiah Blatt for permission to use the site, and Dr. and Mrs. Carl Chapman for their hospitality. Mr. David Bard helped with the photography.

STRUCTURE OF THE WEB

Hypochilus gertschi is usually found under overhanging rock ledges. While fairly moist localities, such as stream banks, cliffs with seepage flow, etc., usually harbor a few specimens, *H. gertschi* seems to be more common in drier, sunnier locations than *H. thorelli* farther south. Hoffman (1963) commented on this, and I have observed individuals on very dry, south-facing cliffs. On two occasions, I have seen populations fully exposed to sunlight much of the day.

The web of *H. gertschi* is usually described and pictured (Hoffman, 1963; Kraus, 1965) as a "lampshade-shaped" mesh, broadly flared beneath, and attached by its smaller end to the under surface of a rock ledge. At the upper (or inner) attached end of the lampshade, a fine sheet of silk is spun over the substrate. Of all previous published references to the web, only Kraus (1965) mentioned the extensive tangle of threads extending, when the web is under a ledge, to the ground beneath, or to nearby plants.

The webs of *H. gertschi* I observed incorporated these previously described features. The size of the web is proportional to the size of the individual. Webs of large (probably penultimate instar) specimens were about 8 cm in diameter at the open end of the lampshade, and usually about 1 cm less in diameter at the closed end. The main portion of the shade consists of a close, irregular mesh (Fig. 1). The flared end of the lampshade (*A*, Fig. 2) is held taut by 10-15 double support lines (*B*, Fig. 2), attached in pairs to a roughly polygonal frame line (*C*, Fig. 2). The frame line is in turn guyed to the surrounding rock surface and to the extensive tangle below. The tangle (*D*, Fig. 2) is always cone-shaped, with the apex attached below, and the base at the frame line, when the web is placed under a ledge, or so that the plane of the lampshade walls is nearly vertical. When the webs are attached to an almost vertical surface, and the plane of the lampshade walls is nearly horizontal, the spider faces a number of problems in guying the frame line in such a way that the lampshade is held tautly flared. If a reasonably narrow crevice is used, the web can be attached to the opposite wall (Fig. 3). In cases where no such directly opposing surface is available, guy lines are run from the frame line nearly parallel to the surface to which the lampshade is attached until a protrusion in the rock, the surface of a gently sloping rock face, or some other support is reached (Fig. 4). This

Fig. 1. Lampshade portion of *Hypochilus gertschi* web seen from below, powdered with cornstarch. The spider is just above the center of the web; note the effective cryptic coloration. About 2/3 actual size.

may result in lines of extraordinary length, up to 2 m. The opposing lines from the upper side of the frame into the tangle often form a sheet in front of the lampshade part of the web. The spider occupies the center of the lampshade in a typical posture (Fig. 5) and holds the sides of the lampshade near the base with its first 2 pairs of legs. Leg pairs III and IV hold the silk sheeting spun against the substrate.

The distribution of dry and sticky silk in the web was determined by powdering the web with fine cornstarch (Fig. 1). Sticky silk is limited to the shade and its support lines, that is, while the frame line is not sticky, all the lines enclosed by it are. The sticky silk of *H. thorelli* has been described by Comstock (1940) as a hackled band consisting of a warp of four threads, the two outer ones much curled, and a broad woof with undulating edges, composed of sticky silk. This type of thread was found in a sample from the web of *H. gertschi* which also included single smooth lines on which an irregular band of sticky silk had been laid.

Comstock (1940) observed some stages of web construction in the laboratory. He found that the first part of the web was the filmy disc of silk against the substrate. This was followed by construction of the lampshade. I attempted to investigate web construction by destroying established webs and observing the manner in which the spider replaced them. Webs destroyed in late afternoon were replaced the following morning, while those destroyed in the morning were not replaced for about 24 hours. When the web was removed, the spider ran a short distance away on the rock surface. In all of the 11 cases observed, the spider returned to the old web site to build a new web. Unfortunately, web construction takes place at night, and any light on the spiders halts their activities.

PREDATORY BEHAVIOR

Remains from undisturbed webs indicate that the main items of prey are small Diptera of various families, Tipulidae, and phalangids of the genus *Leiobunum* (primarily smaller, immature individuals). In addition to these animals, abundant at the study site, experimental prey were obtained by sweeping in an adjacent field. Most of the prey obtained by this method consisted of immature Hemiptera, Orthoptera, and small beetles.

The spiders were first tested for response to prey in the non-sticky tangle below the lampshade. In all cases, the response was the same as to that of a mild threat (see below). At no time did any of the individuals studied leave the lampshade to investigate potential prey

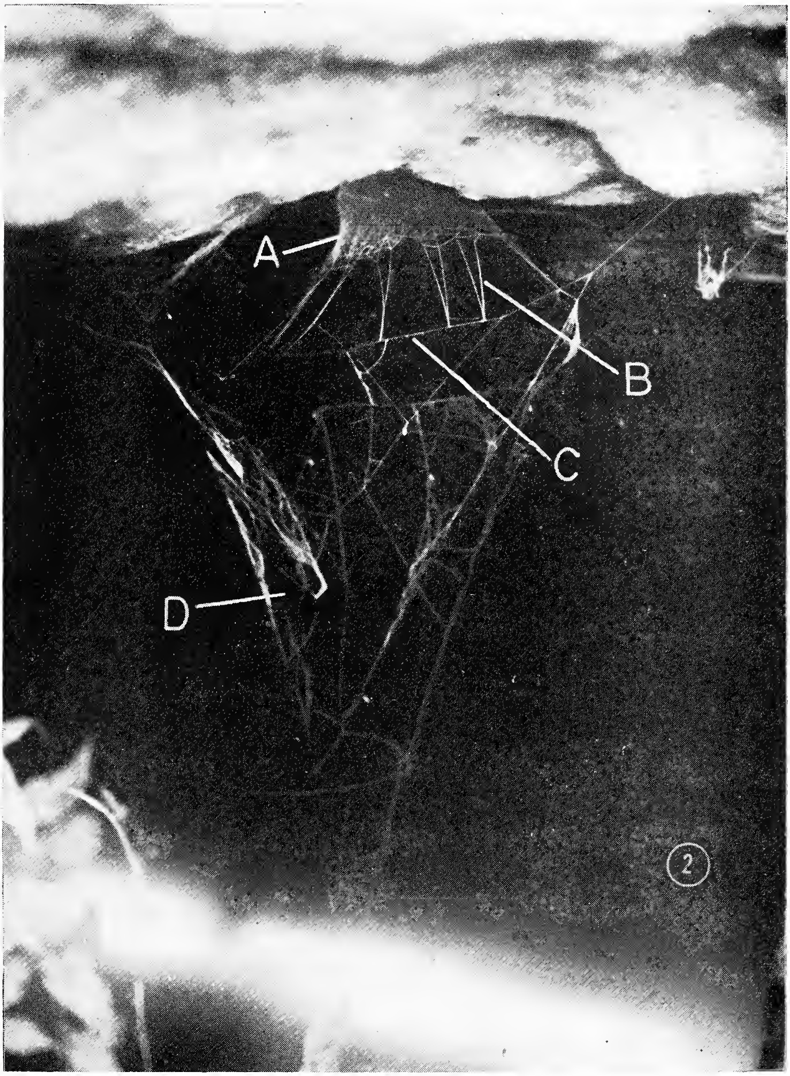
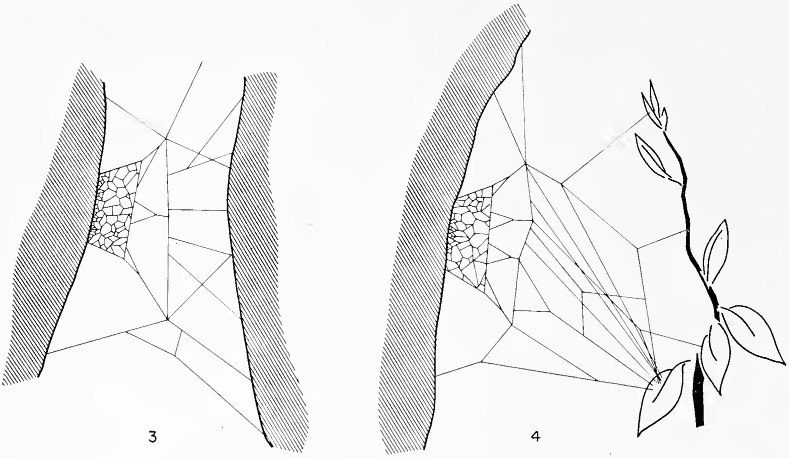


Fig. 2. Entire web of *Hypochilus gertschi* seen from the side. *A*, lampshade; *B*, support lines; *C*, frame line; *D*, tangle. Dimensions about .30 by 1 m.

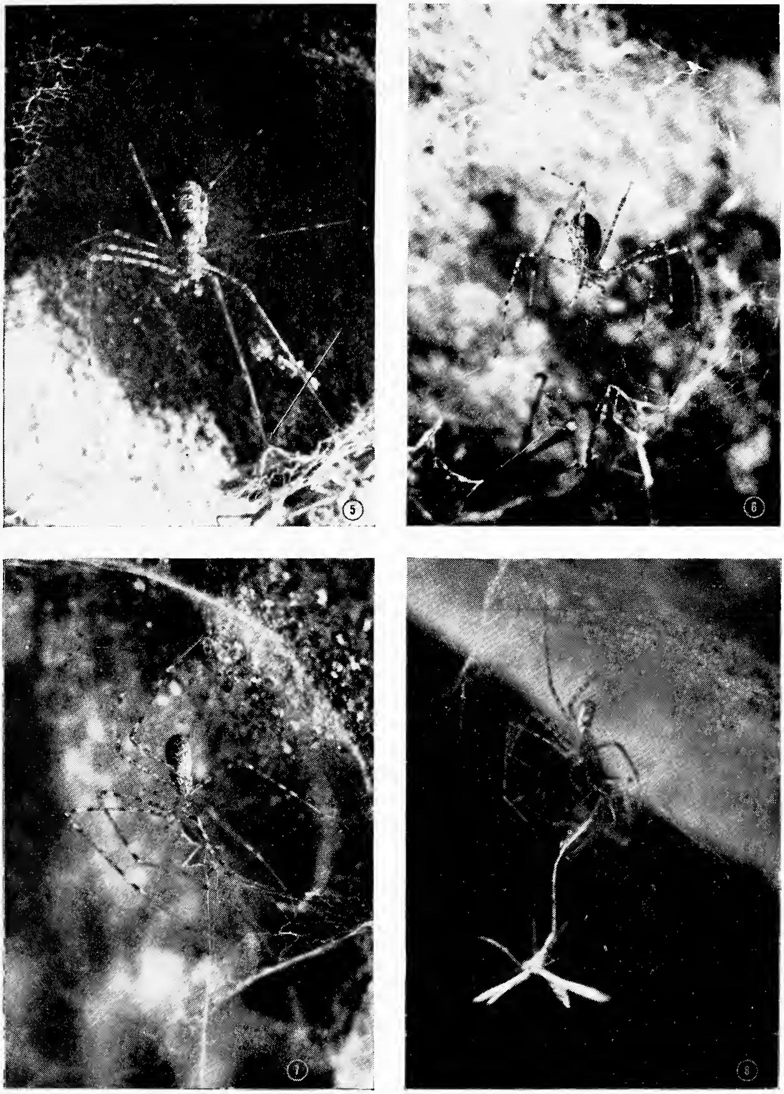


Figs. 3, 4. Webs of *Hypochilus gertschi.* Fig. 3. Web in crevice. Fig. 4. Web on nearly vertical rock face. Drawn from photos.

in the tangle, and as the silk used there is not sticky, most prey animals found it easy to escape, remaining in the tangle a maximum of 80 seconds.

The spider responded to prey only if the prey came in direct contact with the sticky silk of the lampshade. Unless the initial contact was violent, there was no visible response on the part of the spider. The continued struggles of the prey caused a "testing" of web tension by the spider, slowly flexing and extending its legs, and moving the body up and down. Presumably this allowed the spider to sense on which side of the lampshade the prey had been caught. During these motions the spider slowly turned to face the prey (Fig. 6). Up to this point any decrease in prey activity caused the spider to stop what it was doing, to resume its movements only when prey struggles began again.

Once the prey had been touched with the tarsi of the first and second legs, the actions of the spider were more or less continuous. Legs 3 and 4 grasped the opposite side of the lampshade near the base, while legs 1 and 2 pulled on the lampshade threads near the prey. From this position, the spider pulled in the side of the lampshade (Fig. 6) with a very slow, but continuous, movement. When the struggling prey came within reach of the jaws, it was palpated and bitten repeatedly. The use of silk to subdue prey was not observed. Apparently the prey was killed by a combination of biting and poison-



Figs. 5-8. Attack behavior of *Hypochilus gertschi*. Fig. 5. Position of *H. gertschi* in web. Arrow points out that first and second legs hold sides of lampshade. Fig. 6. *H. gertschi* pulling prey to lampshade center. Fig. 7. *H. gertschi* biting prey. Fig. 8. Response to a second prey; see text.

ing (Fig. 7), depending on its size. Three to five minutes after the first bites, the prey ceased its struggles.

If a second prey animal was offered to a spider feeding on one previously caught, it was usually ignored (Fig. 8), except when the spider was almost finished feeding. The spider then attacked, either holding the partially eaten remains, or allowing them to drop. If the second prey was vigorous, and as large or larger than the spider's abdomen, the first prey was merely released and held by the still-attached threads of the lampshade, while a typical attack on a second prey followed. Spiders were not seen to return to the original prey.

Feeding took up to two hours, during which time the prey was reduced to a shapeless mass. After the meal, the spiders drop the ball of remains, and many of these bits of detritus catch in the tangle below.

In some cases, when prey was brought in contact with the palpi and jaws, the spider cut the threads surrounding the prey with its fangs, and dropped the live animal out of the web. This could not be correlated with the species of prey organism or with the feeding state of the spider. The same individual prey animals were captured and fed upon by other *H. gertschi*, and such rejection behavior was observed in spiders that had not fed in at least four hours, as well as those that had just devoured prey. Twice, very active prey was ignored by spiders that had not fed during that day's study period.

The steps in *H. gertschi* predatory behavior consists of a simple sequence summarized in Figs. 9 and 10.

Escape behavior

Since the spiders responded to large, active prey in the tangle as to a mild threat, escape behavior of seven individuals was studied. A "mild threat" consisted of irregular tapping of the frame line and its supports. The primary response, as observed by Kraus (1965), was a vigorous shaking or oscillation of the body and web, as is often seen in *Pholcus phalangioides* (Pholcidae). If the threat continued, the spider moved to the side of the lampshade farthest from the intrusion, facing to the outside. Finally, five of the seven individuals used their chelicerae to cut a hole in the side of the lampshade, through which they escaped to crawl 10 cm to 1 m away from the web site. All seven returned within 20 minutes to the original web.

A "heavy threat" consisted of direct attempt to capture the individual. Upon being touched, the immediate response of the spider was to drop from the web. Usually this resulted in the spider being caught in the lower tangle, where it clumsily struggled until it could

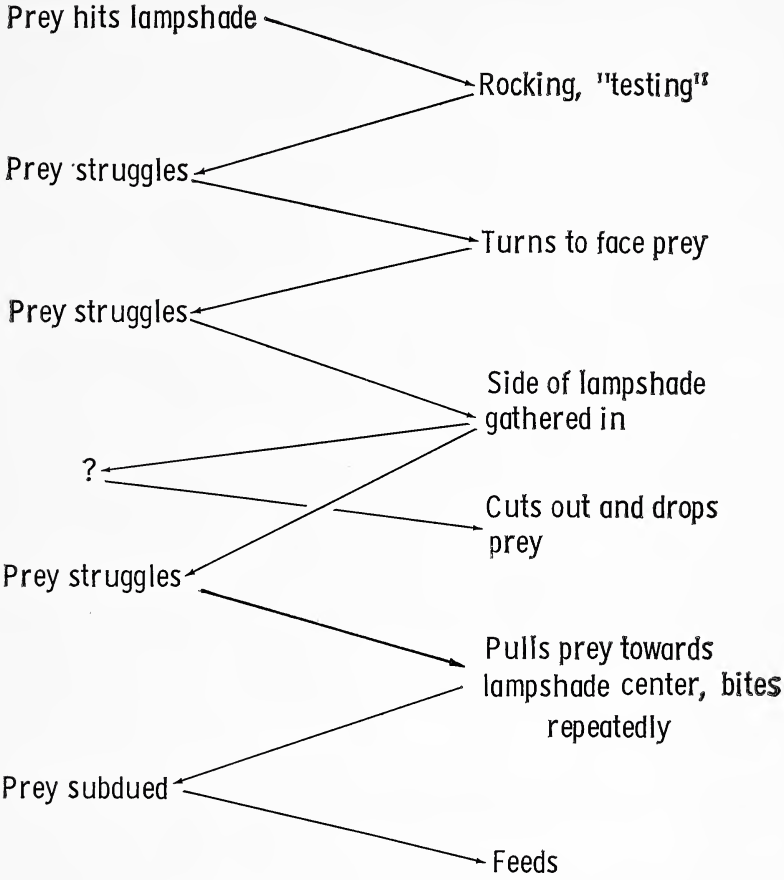


Fig. 9. Typical attack sequence of *Hypochilus gertschi.*

drop to the ground. Once on the ground, the spider remained inert with the legs drawn up over the carapace. Return to the web involved a laborious search for the attachment point of the tangle, which was then climbed until the spider could re-enter the lampshade. In two cases, escaped individuals found the webs of other individuals and attempted to climb them. When they reached the lampshade, they were repulsed by the occupant.

Discussion

According to Marples (1968), the anatomy of *Hypochilus* is the most primitive of any araneomorph spider. The web of *Hypochilus* might be considered more primitive, despite its apparent complexity, than the webs reported for other Hypochilidae. Following the scheme of Kaston (1964) the web of *Hypochilus* can easily be derived from a few capture lines extending from a silk-lined retreat. Possibly such capture lines, like those found in *Ariadna* (Segestriidae) webs, are homologous to the radial support lines of the lampshade of *Hypochilus*. The lampshade itself may represent an extension of an original silk-lined retreat. The primary function of the extensive lower tangle seems to be support of the lampshade. The more aerial webs of *Hickmania* and *Thaida* are clearly derivative and point up the long history and relict nature of the hypochilids. One is tempted to speculate that hypochilomorph orbweavers may await discovery in some remote area!

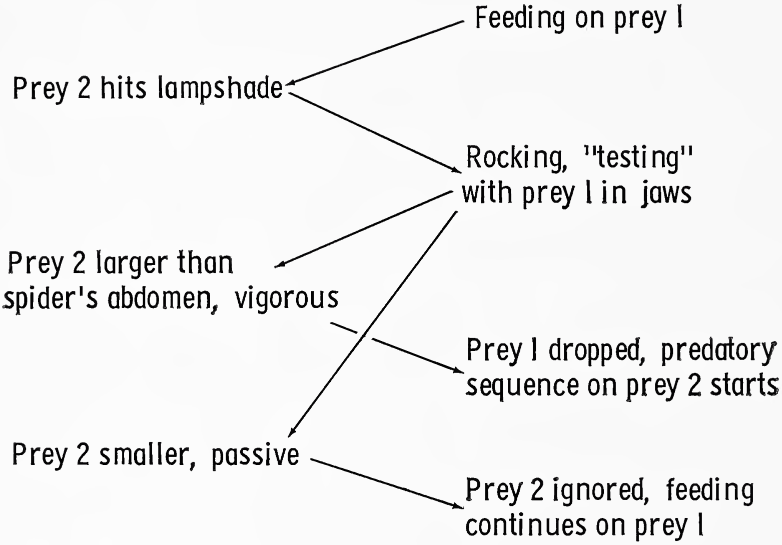


Fig. 10. Response of *H. gertschi* to a second prey.

Eberhard (1967) discussed the evolution of the use of silk as an offensive weapon, relying primarily on observations on *Diguetia*, a primitive, six-eyed, ecribellate spider. He postulated a series of steps through which spiders have come to use silk to subdue prey:

1. No web is spun, prey subdued by biting.
2. Ground webs spun, prey subdued by biting.
3. Aerial webs spun, prey subdued by biting, wrapped to prevent loss during subsequent attacks.

4. Aerial webs built, prey subdued by biting and wrapping.
5. Same as 4, but prey overcome by wrapping only.

Of particular significance is the fact that *Hypochilus*, which builds the most primitive web of those known in its primitive family, has never been observed to use silk as an offensive weapon. Instead, the extreme stickiness of the cribellate silk of the lampshade is relied on to hold prey until it can be bitten to death. *Hypochilus'* response to a second prey, before it has finished feeding on the first, clearly places it between steps two and three in Eberhard's scheme. *Hypochilus* makes an aerial web but either ignores a second prey, or abandons the first to attack the second, the sequences probably dependent on the size and activity of the second prey, and the degree to which the spider has fed on the first. In any case, behavior similar to that seen by Eberhard (1967) in *Diguetia*, in which the original prey is secured to the web by silk to prevent its loss while a second prey is attacked, does not seem to occur in *H. gertschi.*

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FOSSIL INSECTS FROM ANTARCTICA*

By Frank M. Carpenter
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The only fossil insects from Antarctica that have been formally described are two beetles, *Grahamelytron crofti* Zeuner and *Ademosynoides antarctica* Zeuner, both from a Jurassic deposit on Mount Flora, Hope Bay, Grahamland, at the northern tip of the Antarctic peninsula (Zeuner, 1959). Since these are known by isolated elytra, their family positions are obscure and conjectural at best.

Two other fossil insects from Antarctica have been reported in the literature but not named. One of these, a well preserved wing of "Permo-Carboniferous" age, was found in the Theron Mountains, near the Filchner Ice Shelf, during the Trans-Antarctic Expedition of 1955-58 (Plumstead, 1962). Unfortunately, the specimen appears to have been lost in the mail after it was consigned to Dr. Zeuner for study (personal communication, Dr. James Schopf), the only record of it being the photograph published by Plumstead. Although overlain by plant fragments, the wing was apparently well preserved and its venation could have been worked out satisfactorily from the specimen. Even the small, published photograph is sufficient to show that the insect was homopterous, although venational details are not clear enough to permit determination of family affinities.[1] Homoptera of this general type are not uncommon in Permian deposits in the Soviet Union, United States and Australia. The other specimen, a wing fragment of Permian age, was found in the Polarstar Formation of the Sentinel Mountains of Antarctica on the east slope of Polarstar Peak (Tasch and Riek, 1969). Despite the obscure nature of this fossil, Riek was led to conclude that it was a part of a homopterous fore wing, with a venation reminiscent of the family Stenoviciidae, known from the Permian and Triassic of eastern Australia and the Permian of Russia. My own, subsequent study of this specimen, made with the aid of ammonium chloride and under several different types of illumination, has revealed the presence of two additional longitudinal veins and numerous cross

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*This research has been supported in part by Grant No. GB 7308 from the National Science Foundation, F. M. Carpenter, Principal Investigator.

[1] Gressitt's suggestion (1967) that the fossil might be neuropterous is not really supportable.

veins, as well as a coarse rugosity of the wing membrane, not mentioned or shown by Riek. However, the fossil is still very fragmentary and although it might well be homopterous, its family position is most obscure.

Two additional fossil insects from Antarctica, one Jurassic and the other Permian, have been sent to me for study. Both are sufficiently well preserved to justify formal description and naming.

The Jurassic specimen is an odonate, collected from a pond deposit within the so-called Mawson Tillite on Carapace Nunatak, South Victoria Land.[2] It belongs to the suborder Anisozygoptera, which was a major one in the Jurassic Period, and to that complex of families which includes the Liassophlebiidae. The general venational pattern, the nature of the arculus, nodus and pterostigma, as well as the curvature of CuP and 1A, are very similar to those of *Liassophlebia.* There are some differences in the nature of the antenodal cross veins but, all details considered, it seems advisable to broaden our concept of the family Liassophlebiidae to include the antenodal structure of the Antarctic species, for reasons given below, rather than to establish another family. The new specimen does clearly represent an undescribed genus and species.

Caraphlebia Carpenter, new genus

This is related to *Liassophlebia,* but the hind wing has several weak antenodals in addition to the two strong, primary ones. The venation is much like that of *Liassophlebia* (see figures 1 and 3) but the cross veins between R2 and R3, proximally, are long and apparently not interrupted by transverse connections; the space between MP and CuA is very narrow; IR2 apparently arises more distally than in *Liassophlebia;* and the anal area of the wing is small. The shapes of the discoidal cell, subdiscoidal cell, CuP and 1A are very much as in *Liassophlebia.*

Type species: *Caraphlebia antarctica,* n. sp.

Caraphlebia antarctica Carpenter, n. sp.

Figure 1

Hind wing: length of wing, 40 mm; width, at level of arculus, 8 mm. Primary antenodals very well developed, the costal and subcostal elements aligned; the other antenodals weak and indistinct, but under glycerin-alcohol eleven are visible in the costal area and seven in the subcostal area, none aligned; pterostigma long and

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[2] Basaltic lavas enclosing the fossiliferous pond deposit are presently being dated by the Potassium/Argon method.

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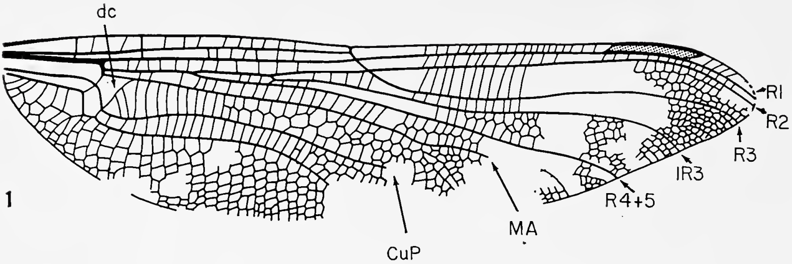

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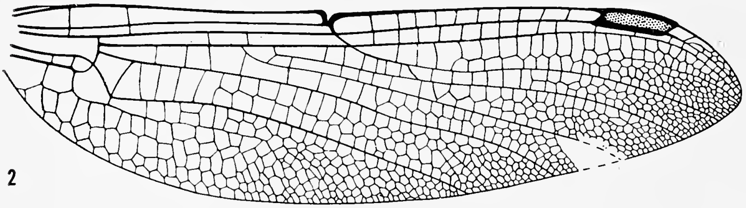

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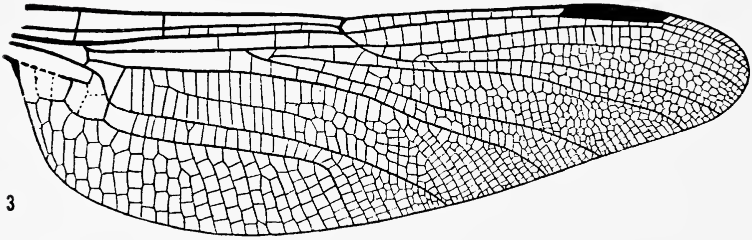

Figure 1. *Caraphlebia antarctica* n.sp. Drawing based on holotype, collected on Carapace Nunatak, Antarctica. Sc, subcosta; R1, radius; R2, R3, IR3, R4+5, branches of radial sector; MA, anterior media; CuP, posterior cubitus; dc, discoidal cell. Length of wing, 40 mm.

Figure 2. *Turanothemis nodalis* Pritykina. Drawing based on holotype (hind wing), Jurassic of Karatau, USSR (from Pritykina, 1968).

Figure 3. *Liassophlebia mirabilis* Tillyard. Drawing based on holotype (hind wing), Jurassic of England (from Tillyard, 1925).

slender; R4 + 5 arising slightly nearer to the arculus than to the nodus; other venational details are shown in figure 1.

Holotype: No. 165874, U. S. National Museum, Smithsonian Institution, Washington; found in rock forming part of the "Mawson Tillite" and collected on Carapace Nunatak, Antarctica, by H. W. Borns, Jr. and B. A. Hall.[3] The rock matrix is part of a volcanic mudflow and it includes many remains of Conchostraca, Ostracoda, and other Crustacea, as well as numerous body fragments of insects; the latter are unidentifiable even to ordinal level, though some appear to be parts of aquatic nymphs (possibly mayflies or stoneflies). The plants of the Carapace Nunatak tillite are cycads and conifers and they are indicative of Jurassic age (Townrow, 1967). This is consistent with the occurrence of the family Liassophlebiidae, which is known only from Jurassic deposits.

The specimen consists of a single wing, quite clearly but peculiarly preserved. The wing has been torn just beyond the nodus in such a way as to make it difficult to trace the subnodal vein, although its approximate position is obvious in the fossil. As a result of tearing along the posterior margin, the distal portions of the veins in the posterior half of the wing are not perfectly aligned with the basal portions, though the amount of shift is not uniform. Nevertheless, the use of large photographs has enabled the preparation of a drawing of the wing, shown in figure 1; this drawing includes only those structures that are visible in the fossil, except for the very apex, which is indicated by dotted lines. One of the peculiar features of this specimen is the preservation of the veins on the two counterparts: apparently, the convex veins are well preserved on one half and the concave veins on the other. Such a separation of the convex and concave veins can be duplicated in Recent insect wings by separating the two membranes just after the adult has developed its wings or by the use of caustic potash. Some wing veins in the fossil are only faintly indicated on the rock but they become very clear if the specimen is moistened with alcohol or glycerin-alcohol. The thin antenodals, for example, cannot be discerned unless the fossil is treated in this way. It is possible that the use of glycerin-alcohol on the specimens of *Liassophlebia,* which are in the British Museum, might also reveal the presence of faint antenodals in the costal area, since they do occur in the subcostal area (Tillyard, 1925). Even if this should prove not to be the case, the similarities between the wings of *Liassophlebia* and *Cara-*

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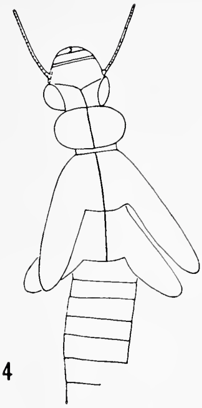
[3] For the location of this Nunatak, see Borns and Hall, 1969, p. 871, fig. 1.

phlebia are so marked that family separation of these genera seems unwarranted.

A related genus, *Turanothemis* (see figure 2), has recently been described by Pritykina from the Jurassic of Karatau (Kazakhstan) in the Soviet Union and has been assigned to a separate family, Turanothemistidae (Pritykina, 1968). In her account of this family, the author makes no comparisons with any other specific family, simply stating that it differs sharply from all other families of this series of Anisozygoptera by the presence of only the two primary antenodals in the costal area and by the form of the discoidal cell in the hind wings. However, in *Liassophlebia,* as already noted, only the two primary antenodals have been reported (Tillyard, 1925) and its discoidal cell (hind wing) has precisely the same form as that of the fossil on which *Turanothemis* is based. Since no other distinguishing characteristics of the Turanothemistidae are discernible, I consider the family Turanothemistidae inseparable from the Liassophlebiidae, which, on this basis, is known from Jurassic deposits of England, Siberia and Antarctica.

The new Permian insect, found in conchostracan-bearing beds of the Mount Glossopteris Formation, Ohio Range, is a small but well preserved nymph. Since very little is known of nymphal forms of Paleozoic insects and especially since no venational pattern is discernible in the wing pads, the ordinal affinities of the fossil cannot be determined with any degree of certainty. However, the specimen is very close to a Permian nymph, *Uralonympha* Zalessky, described from Tchekarda, in the Ural Mountains of the USSR, and similar to another, *Permoleuctropsis* Martynov, from a Permian deposit near Orenburg, USSR. The similarity of the new nymph to *Uralonympha* is especially strong in the form of the prothorax and the position of the wing pads (see figure 6). The Antarctic species is accordingly being assigned to the genus *Uralonympha*, in preference to making another separate genus that could not be satisfactorily distinguished from *Uralonympha* at the present state of our knowledge.

The ordinal position of these nymphs is conjectural. *Uralonympha* has generally been considered an immature form of a stonefly (Zalessky, 1935; Sharov, 1962) but there is an equally good possibility that it belongs to the Protorthoptera. Until a series of such nymphs has been found in association with numerous adults, the affinities of *Uralonympha* and other little-known nymphs of the Paleozoic will remain obscure. For the present, *Uralonympha* is best considered a member, *incertae sedis,* of the order Perlaria.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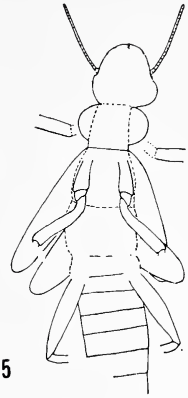
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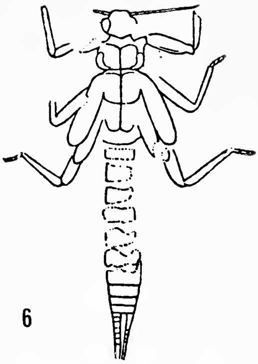
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Figure 4. *Uralonympha schopfi* n.sp. Drawing based on holotype, showing dorsal view of insect; collected at *Leaia* Ledge, Ohio Range, Antarctica.

Figure 5. *Uralonympha schopfi* n.sp. Drawing of holotype, showing ventral view.

Figure 6. *Uralonymph varica* Zalessky. Drawing based on holotype, Permian of Tchekarda, Ural Mountains, USSR (from Zalessky, 1939).

The following is a description of the nymph from the Ohio Range:

Uralonympha schopfi Carpenter, n. sp.
Figures 4 and 5

Based on a single specimen of a nymph, complete except for the last four or five abdominal segments. Length of specimen as preserved, from the clypeus to the posterior edge of the sixth abdominal segment, 8 mm; antennae slender, 2.5 mm. long, showing 21 segments, though the basal few segments are not discernible; eyes prominent, bulging, width across the eyes 0.7 mm; clypeus prominent and mandibles large; pronotum oval, 2.2 mm. wide, 1.4 mm. long; mesothorax 1.7 mm. long, metathorax 1.3 mm. long. Fore wing pad about 3 mm. long; hind wing pad 2.5 mm. long.

The pronotum resembles that of *Uralonympha* in being distinctly oval. The legs are considerably more robust than those of *Uralonympha*. The fore legs are little known but the meso- and metathoracic legs are preserved as far as the femora; they show a distinct and rather large coxa, a small trochanter and well developed femur. The dimensions of the legs and their segments are as follows: mesocoxa, 1.1 mm.; mesotrochanter, .3 mm.; mesofemur, 1.7 mm.;

metafemur, 2 mm. The abdominal segments are of equal size, 1.5 mm. long. Since the terminal portion of the abdomen is not preserved, the cerci are not included in the fossil.

Holotype: No. 165875, U. S. National Museum; collected by Dr. James Schopf, for whom the species is named (field no. ANT 67-1-a&b); it was found in a small piece of carbonaceous shale, bleached to white by weathering (*Leaia* Zone), west face, Mercer Ridge, Ohio Range, 84°50′S, 113°45′W; conchostracans and a typical *Glossopteris* flora occur in the same shale, which is considered to be late or middle Permian in age (Doumani and Tasch, 1965). The fossil is extraordinarily well preserved and if the specimen were an adult insect, the venational details would have allowed precise determination of its systematic position.

Both of the new fossils described herein are indicative of the presence of productive insect-bearing deposits in Antarctica and the excellent preservation of these particular specimens justifies further exploration of the deposits concerned, with special reference to insect remains.

ACKNOWLEDGMENTS

I am indebted to Dr. J. M. Schopf of the USGS Coal Geology Laboratory for the opportunity of studying the specimen of *Uralonympha;* to Professors Borns and Hall of the University of Maine for making available the specimen of *Caraphlebia*; to Professor Paul Tasch of the University of Wichita for certain collecting data; and to Mr. Jessa Merida of the U. S. National Museum for the loan of the specimen from the Polarstar Formation.

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A RECONSIDERATION OF THE *OXYOPES APOLLO* SPECIES GROUP WITH THE DESCRIPTIONS OF TWO NEW SPECIES (ARANEAE: OXYOPIDAE)*

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The lynx spiders, Oxyopidae, are represented by a small but diverse group of species in North America, north of Mexico. Three genera including 17 species were recorded and described from this region (Brady, 1964). Eight new species were described in the genus *Oxyopes*. Of these eight new species, six were placed in the *Oxyopes apollo* species group consisting of *Oxyopes apollo*, *floridanus*, *tridens*, *pardus*, *lynx* and *felinus*. These six species were grouped on the basis of similarities in genitalia, body structure, color pattern, and relative length of legs. With the accumulation of additional material a re-evaluation of the *apollo* group is necessary. Collections from North Carolina, Florida and Texas indicate that *O. apollo* and *O. floridanus* are conspecific. Among specimens from Arizona were included one new species and an undescribed female, both related to members of the *apollo* group. Additional Florida collections have revealed for the first time numerous specimens of a species described as *Oxyopes lanceolatus* (Walckenaer) by Chamberlin and Ivie (1944), but here considered a new species and a member of the *apollo* group.

In light of this new information a dendrogram representing the relationships of the species in the *apollo* group is shown in Text Figure 1. This comparison of the morphological features of these species takes into account their distribution as far as it is known.

Consideration of the dendrogram as a phylogeny of the species involved allows speculation and the construction of a generalized picture of the origin and dispersal routes of these North American oxyopids.

The *apollo* species group can be separated into two subgroups: A, represented by *O. apollo* and *O. artemis*; and B, represented by *O. tridens*, *pardus*, *lynx*, *cougar* and *felinus*. Both subgroups A and B have eastern and western representatives. The similarity of epigynal structure between *O. apollo* and *O. artemis* (compare figs. 47, 48 of Brady, 1964, with Figs. 13-15 of this paper) indicates a rela-

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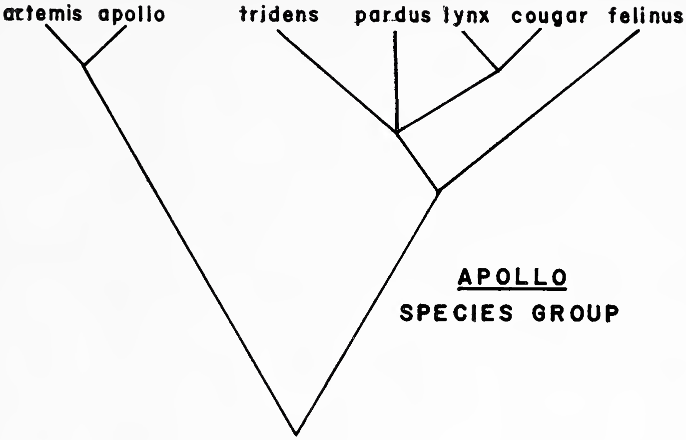


Text Figure 1. Dendrogram illustrating the hypothetical relationships of North American members of the *Apollo* species group.

tively recent common ancestry. Likewise the similarity between the palpal structure of *O. lynx* and *O. cougar* (compare figs. 66, 67 of Brady, 1964 with Figs. 9, 10 of this paper) indicate a recent linkage. In fact, the entire *apollo* species group appears to have originated in Mexico and/or Central America, perhaps after being separated via the Panamian bottle-neck from earlier South American ancestors. Expanding northward these founder populations extended into the southwestern United States on the one hand and along the Gulf Coast into Florida on the other hand.

I suggest that the exploitation of widely dissimilar ecological realms in the southwestern and the southeastern United States produced entirely different sets of selective pressures. Gene flow between the western and eastern populations would tend to be limited, and it is doubtful whether the eastern and western populations would remain conspecific for long. Exceptional cases would involve ancestral Neotropical populations that remained as a strong connecting link between east and west, or species populations that might be genetically flexible enough to meet the widely differing environments of the southern United States from east to west.

Thus, in general, the effect of expansion into North America would be to produce biological divergence and subsequent speciation in many cases. This idea would be supported if one were to find examples of closely related allopatric species in the southeast and the southwest. *Oxyopes apollo* is predominately southeastern in distribution and *O. artemis* is apparently restricted to the southwest. *Oxyopes cougar* has been found only in the southeast and *O. lynx* is from Marathon, Texas, far to the west of *O. cougar*. Better evidence for an east-west divergence influencing speciation is seen in the distribution patterns of *O. acleistus* — *O. occidens* (Brady, 1964) and the lycosids *Sosippus floridanus* — *S. californicus* (Brady, 1962). Only the effect of a geographic divergence has been emphasized until now, but *time* must be given equal consideration. Successive waves of colonization would play an important role in the process of speciation. Populations moving into North America from a southern route at different times would further complicate the evolutionary picture. Intensive and widespread collecting in Mexico and Central America will undoubetedly give clues to the temporal sequence as well as elucidate the geographic patterns of speciation in the *apollo* species group.

For collections which made this study possible I especially thank Dr. Donald C. Lowrie and Dr. W. D. Stockton of California State College at Long Beach, Dr. Howard V. Weems, Curator for the Florida State Collection of Arthropods, and Dr. Joseph A. Beatty of Southern Illinois University. These collections included the new species described here and the hypothesis concerning the effect of geographic movements on speciation of oxyopids was arrived at through a study of these collections.

I also wish to thank Dr. H. W. Levi and Mrs. Lorna Levi, who were kind enough to read the original manuscript. National Science Foundation grant number GB-13925 helped to defray expenses involved with this investigation.

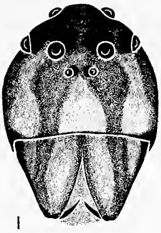
Oxyopes apollo Brady

Oxyopes helius: Bryant, 1936, Psyche, 36(4): 92, fig. 7, ♂, not *O. helius* Chamberlin.

Oxyopes apollo Brady, 1964, Bull. Mus. Comp. Zool., 131(13): 467, figs. 41, 42, 47-50, 72-75, ♀, ♂. Male holotype from Encino, Brooks Co., Texas in the American Museum of Natural History.

Oxyopes floridanus Brady, 1964, Bull. Mus. Comp. Zool., 131(13): 469, figs. 43, 44, 51, 76-79, ♀, ♂. Male holotype from Volusia Co., Florida in the Museum of Comparative Zoology. NEW SYNONYMY

Discussion. On the basis of a smaller retrolateral patellar apophysis and a denser clothing of appressed white hair over the body and legs of Florida specimens, I (1964) recognized them as a distinct species from *Oxyopes apollo* found from Tennessee to northern Mexico. Ernst Mayr (personal communication) pointed out at the time that the slight morphological differences might better be interpreted as a response to geographic conditions.



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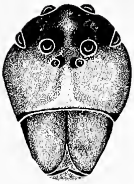

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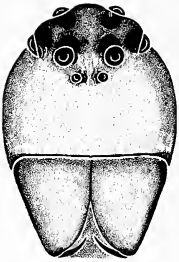

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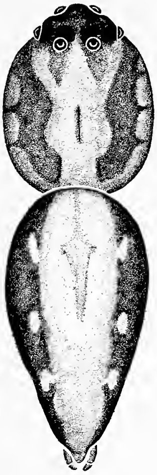

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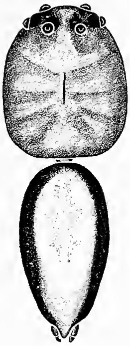

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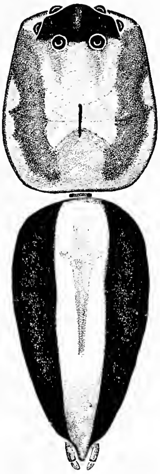

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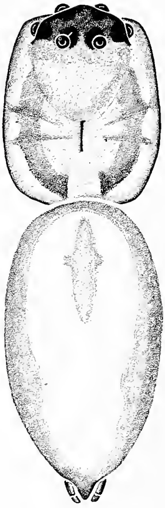

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Figs. 1-2. *Oxyopes cougar,* sp. n., female from Saufley Heights near Pensacola, Escambia Co., Florida, 8 Sept. 1945. 1. Face view. 2. Dorsal view.

Figs. 3-4. *Oxyopes cougar*, sp. n., male holotype from Saufley Heights near Pensacola, Escambia Co., Florida, 4 Aug. 1945. 3. Face view. 4. Dorsal view.

Figs. 5-6. *Oxyopes* sp., female from 12 mi. W of Portal, Cochise Co., Arizona, 13 July 1968. 5. Face view. 6. Dorsal view.

Figs. 7-8. *Oxyopes artemis,* sp. n., female holotype from 15 mi. S of Florence, Pinal Co., Arizona. 12 July 1968. 7. Face view. 8. Dorsal view.

The distribution patterns in two other groups of spiders, *Sosippus*, a lycosid genus, and the *Oxyopes acleistus* species group (see Brady, 1962 and 1964) lent credence to the idea of a distinct Florida species related to *O. apollo*. In both *Sosippus* and *Oxyopes* there are distinct species whose range does not extend beyond peninsular Florida. Also the specimens of *Oxyopes apollo* examined prior to 1964 did not exhibit much variation from Tennessee to northern Mexico.

After examination of a large series of specimens from Texas and several specimens from North Carolina, it became clear that *Oxyopes floridanus* should be considered a synonym of *O. apollo*. The size of patellar apophyses in males from Durham, North Carolina and Sinton, Texas range from that of typical Florida specimens to that of the earlier examined specimens from Texas described as *O. apollo*.

A number of specimens from Oaxaca, Mexico, smaller and much lighter in color than more northerly specimens of *O. apollo*, have epigyna or palpi identical to northern populations. These are now also considered conspecific members of this widespread species. New records for specimens of *Oxyopes apollo* examined are given below.

Natural History. In 1964 I reported *Oxyopes apollo* collected from pitfall traps in Arkansas. Specimens collected near Durham, North Carolina were also taken in pitfall traps. Although sweeping vegetation in both these regions had yielded other species of *Oxyopes, O. apollo* was not captured by this method.

Collections over a period of two years near Sinton, Texas, disclosed a very high density of *O. apollo*. Approximately 150 specimens were taken during eight collecting dates from April through September. A single day in September yielded over 50 specimens. Presumably these were taken by sweep-net. Lowrie (1969) reports *O. apollo* taken in sweeping herbaceous vegetation near Pensacola, Florida. It appears that *O. apollo* occupies dissimilar habitats or is much less abundant in different parts of its range than in others. At least in the southern sections of its range it occurs abundantly on vegetation and is taken by sweeping.

New Records. NORTH CAROLINA: Durham Co.: near Chapel Hill, 20 Sept. 1963, 0; 5 mi. E of Chapel Hill, 1 July 1964, ♂♂♀; 2 mi. S of Durham, 14 July 1964, ♂ (J. W. Berry). FLORIDA: Escambia Co.: Pensacola, 4 June 1945, ♂ (D. Lowrie). TEXAS: San Patricio Co.: 8 mi. NE of Sinton, 28 July 1959, ♂♂0, 4 Sept. 1959, 51♂♂: 9♀♀, 18 Sept. 1959, 52♂♂:6♀♀, 30 Sept. 1959, 18♂♂, 15 Oct. 1959, 3♂♂:♀, 5 Apr. 1960, 10♂♂:♀♀:300, 28 Apr. 1960, 17♂♂: ♀, 12 May 1960, 5♂♂♀, 26 May 1960, ♂♀, 12 June 1960, ♀♀:400, July 1960, 18♂♂:4♀♀:18oo, 19 Aug. 1960, 22♂♂, Sept. 1960, 35♂♂:17♀♀ (H. E. Laughlin). MEXICO, OAXACA: Jalapa, 28 Aug. 1947, ♂; Tuchitan, 30 Aug. 1947, ♂♂:9♀♀:o (H. Wagner).

Oxyopes artemis sp. n.

Figures 7, 8, 13-15

Holotype. Female from 15 mi. S of Florence, Pinal Co., Arizona, 12 July 1968 (L. D. Mikelson) in the Museum of Comparative Zoology. The specific name is a noun in apposition after the Greek goddess Artemis.

Discussion. One of the distinguishing characteristics of members of the *apollo* species group is the robust fourth legs. In other species of *Oxyopes* leg I is the longest and most powerfully developed. In those species with leg I longest the patella-tibia of a given leg is longer than any of the other leg segments and is a good indicator of relative leg length. In members of the *apollo* group, even though the patella-tibia of leg I may exceed the patella-tibia of leg IV in length, femur IV and metatarsus IV equal or exceed patella-tibia IV in length and leg IV is much the longest. For an adequate comparison of members of this group, therefore, the measurements of segments of leg I and leg IV are given below. The robust development of leg IV in species of the *apollo* group is undoubtedly related to their jumping ability and may be associated with their ecology, for example, their occurrence in rather barren areas in some cases.

Measurements. Length of three females 5.2-5.6 mm, carapace width 1.8 mm, carapace length 2.3-2.4 mm.

Width of eye rows: AME .25-.36 mm, ALE .54-.58 mm, PLE 1.03-1.08 mm, PME .54-.56 mm.

Segments of legs I and IV: femur 2.0-2.1 mm, 2.7-2.8 mm, patella-tibia 2.3-2.4 mm, 2.5-2.6 mm, metatarsus 2.1 mm, 3.1-3.2 mm, tarsus .8-.9 mm, .8-.9 mm, total length 7.2-7.5 mm, 9.2-9.5 mm.

Length of patella-tibiae: II 2.2-2.3 mm, III 1.6-1.7 mm.

Color. Female. Pattern illustrated in Figures 7 and 8. Face and chelicerae pale orange-yellow to cream. White spatulate shaped, appressed hair covering much of face and base of chelicerae. These white hairs thickest between ALE to AME, covering most of hexagonal region bounded by eyes in unrubbed specimens. An inverted T-shaped mark running from the AME to the lower edge of the clypeus is also formed by a dense alignment of these white hairs.

Carapace pale orange-yellow to cream with light brown submarginal stripes beginning in cephalic region and continuing to posterior declivity.

Dorsum of abdomen wrinkled in these specimens, pale orange-yellow with abundance of white appressed hairs giving it an ivory appearance. Indistinct brownish markings in cardiac region and along sides. Venter cream colored to ivory with abundant close-packed, flattened white hair.

Legs cream to ivory without darker markings.

Labium and endites ivory. Sternum ivory with four pairs of dark, brownish spots laterally and a single one posteriorly.

Diagnosis. *Oxyopes artemis* is most closely related to *O. apollo* among the members of the *apollo* species group (see Text Figure 1). It is readily distinguished from *O. apollo* by the structure of the epigynum (compare Figs. 13-15 of this paper with figs. 47, 48 of Brady, 1964). In *O. artemis* the epigynum is larger and relatively broader than in *O. apollo.* The much lighter color of *O. artemis* also distinguishes it from *O. apollo* throughout most of the latter's range. Specimens of *O. apollo* from Oaxaca, Mexico, however, resemble *O. artemis* in color.

Record. Arizona. Pinal Co.: 15 mi. S of Florence, 1,440 ft., 3♀♀ (L. D. Mikelson).

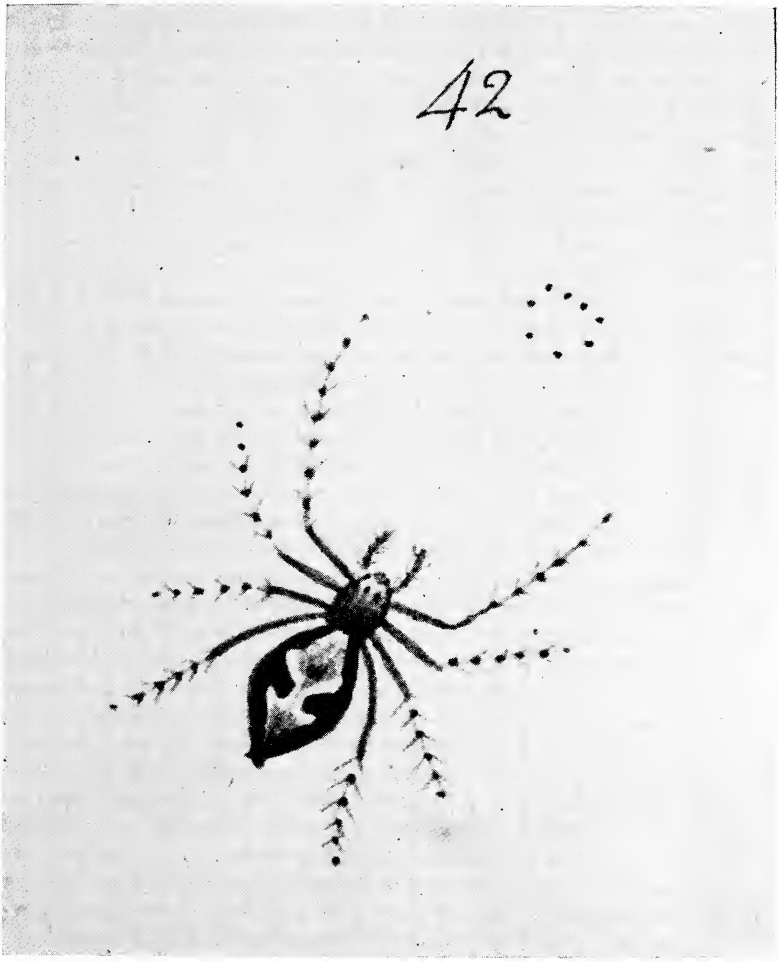
Oxyopes cougar sp. n.

Figures 1-4, 9-12

Holotype. Male from 8 mi. NW of Pensacola, Escambia Co., Florida, 18 Aug. 1945 (D. Lowrie) in the Museum of Comparative Zoology. The specific name is a noun in apposition after the Cougar.

Oxyopes lanceolatus: Chamberlin and Ivie, 1944, Bull. Univ. Utah, biol. ser., 8(5):132, figs. 180, 181, not *Sphasus lanceolatus* Walckenaer.

Discussion. Chamberlin and Ivie (1944) redescribed and figured what they considered to be the neotype of *Sphasus lanceolatus*, a name based upon Abbot's drawing number 42 in the "Spiders of the Georgia Region" (see Brady, 1964, 439-442). Figure 42 of Abbot's is not the species described as *Oxyopes lanceolatus* by Chamberlin and Ivie. Compare Text Figure 2 with Figure 2, page 429. The color pattern in Abbot's Figure 42 is close to that of *O. scalaris* Hentz, but also resembles *O. aglossus*, and *O. acleistus*. Also, if Abbot's drawings are to be considered accurate, the robust fourth pair of legs, characteristic of *Oxyopes cougar*, are not evident. Instead the first pair of legs are longer and more strongly developed as are those



Text Figure 2. Enlarged photograph of Abbot's Figure 42 in the "Spiders of the Georgia Region". Note length of first legs compared to length of fourth legs.

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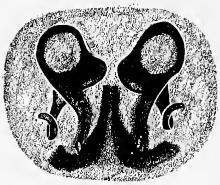

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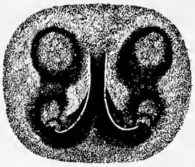

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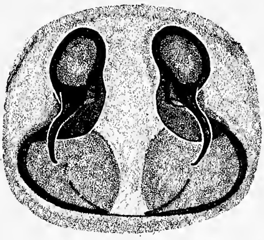

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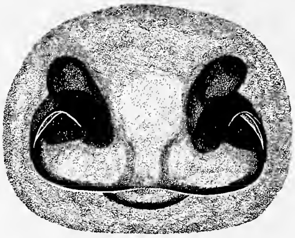

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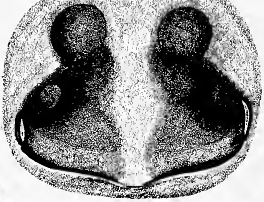

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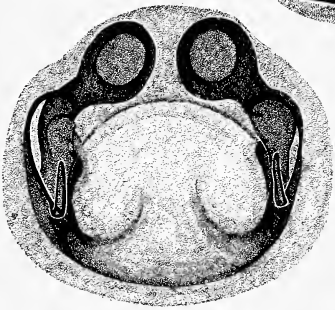

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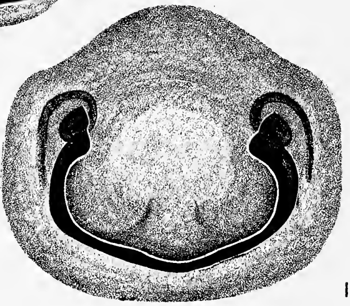

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Figs. 9-10. *Oxyopes cougar* sp. n., male holotype from Saufley Heights near Pensacola, Escambia Co., Florida, 4 Aug. 1945. 9. Left palpus, ventral view. 10. Left palpus, retrolateral view.

Figs. 11-12. *Oxyopes cougar* sp. n., female from Saufley Heights near Pensacola, Escambia Co., Florida, 8 Sept. 1945. 11. Internal genitalia, dorsal view. 12. Epigynum.

Figs. 13-15. *Oxyopes artemis* sp. n., females from 15 mi. S. of Florence, of *O. scalaris*, *O. aglossus* and *O. acleistus*. *Oxyopes lanceolatus* is best considered a *nomen dubium*.

Measurements. Length of nine males 3.4-4.0 mm, mean 3.71 mm, carapace width 1.3-1.4 mm, mean 1.36 mm, carapace length 1.6-2.0 mm, mean 1.78 mm.

Width of eye rows: AME .25-.30 mm, mean .271 mm, ALE .46-.54 mm, mean .493 mm, PLE .83-.99 mm, mean .899 mm, PME .46-.54 mm, mean .489 mm.

Segments of leg I and IV: femur I 1.5-1.8 mm, mean 1.67 mm, IV 1.6-2.0 mm, mean 1.86 mm, patella-tibia I 1.9-2.2 mm, mean 1.98 mm, IV 1.7-2.1 mm, mean 1.87 mm, metatarsus I 1.8-2.0 mm, mean 1.93 mm, IV 1.9-2.3 mm, mean 2.17 mm, tarsus I .85-.9 mm, mean .88 mm, IV .7-.9 mm, mean .79 mm, total length I 6.0-6.9 mm, mean 6.47 mm, IV 6.0-7.3 mm, mean 6.68 mm.

Length of patella-tibiae: II 1.6-2.0 mm, mean 1.79 mm, III 1.2-1.5 mm, mean 1.32 mm.

Length of 10 females: 3.9-5.9 mm, mean 5.10 mm, carapace width 1.4-1.7 mm, mean 1.57 mm, carapace length 1.8-2.2 mm, mean 2.07 mm.

Width of eye rows: AME .28-.33 mm, mean .303 mm, ALE .50-.60 mm, mean .555 mm, PLE .93-1.09 mm, mean 1.003 mm, PME .50-.60 mm, mean .555 mm.

Segments of leg I and IV: femur I 1.7-2.0 mm, mean 1.87 mm, IV 1.9-2.5 mm, mean 2.20 mm, patella-tibia I 1.9-2.3 mm, mean 2.12 mm, IV 1.8-2.4 mm, mean 2.12 mm, metatarsus I 1.6-2.1 mm, mean 1.87 mm, IV 2.0-2.7 mm, mean 2.42 mm, tarsus I .7-.9 mm, mean .75 mm, IV .7-.9 mm, mean .80 mm, total length I 5.9-7.2 mm, mean 6.68 mm, IV 6.4-8.3 mm, mean 7.54 mm.

Patella-tibiae: II 1.7-2.1 mm, mean 1.96 mm, III 1.3-1.6 mm, mean 1.45 mm.

Color. Male. Pattern illustrated in Figures 3 and 4. Face and chelicerae yellow-orange to orange-brown with faint dusky stripes from ALE to distal ends of chelicerae. Lower edge of clypeus and distal ends of chelicerae often lighter, yellowish. Iridescent scale-like hairs between ALE. Cymbia of palpi black.

Carapace yellow-orange to orange-brown, dusky along vertical sides.

Pinal Co., Arizona, 12 July 1968. 13. Internal genitalia, dorsal view. 14. Epigynum, openings to seminal receptacles plugged. 15. Epigynum of holotype tilted slightly more anteriorly than Fig. 14, seminal receptacles open.

Figs. 16-17. *Oxyopes* sp., female from 12 mi. W of Portal, Cochise Co., Arizona, 13 July 1968. 16. Internal genitalia, dorsal view. 17. Epigynum.

Dorsum of abdomen with very broad, white to cream, median stripe bounded laterally by dark brown areas. Venter yellow with two thin dusky longitudinal stripes from epigastric furrow to base of spinnerets, bordered by thin yellow stripes which are in turn flanked by dusky *or* sometimes brown color forming a very wide median stripe. Venter overlaid with scale-like iridescent hairs.

Legs yellow.

Labium dark brown, distal end lighter, yellowish. Endites yellow. Sternum yellow, periphery brown.

Female. Pattern illustrated in Figures 1 and 2. Face and chelicerae pale yellow to yellow-orange with brownish stripes beginning under ALE, widest at level of AME, and continuing to distal ends of chelicerae. White appressed hair between ALE and along sides of face. Lower edge of clypeus yellowish.

Median area of carapace yellow-orange with wide, irregular, brown stripes beginning below PLE and continuing to posterior declivity.

Dorsum of abdomen with broad median white stripe from base to tip, bounded by dark brown or black laterally. Cardiac area slightly darker than enclosing stripe. Venter with two narrow brown stripes from epigastric furrow to spinnerets, bounded by thin yellow to cream stripes which are in turn flanked by brown. Brown color sometimes filling median space between two narrow brown stripes and forming a single broad median stripe.

Legs yellow to yellow-orange with distal ends of femora and more distal leg segments with dusky bands.

Labium dark brown to black with distal end yellowish. Endites yellow-orange, dusky along outer edges. Sternum pale yellow, bordered by dark brown or black.

Diagnosis. Oxyopes cougar is very closely related to *O. lynx* from Marathon, Texas. There is a strong resemblance in the palpal sclerites and the patellar apophyses of these two species (compare Figs. 9, 10 of this paper with figs. 66, 67 of Brady, 1964). *Oxyopes cougar* is considerably smaller than *O. lynx* and the patellar apophysis and palpal structure is distinct from *O. lynx*. When the female of *O. lynx* is known, the relationship of these two species will be more clearly established.

Natural History. Oxyopes cougar was taken in pitfall traps in a Broomsedge field in Durham Co., North Carolina. Sweeping vegetation in this area did not yield any specimens. Lowrie (1969) collected moderate numbers of this species from June through September in herbaceous vegetation of a long-leafed pine (*Pinus palustris* Mill.)

woods near Pensacola, Florida. All of these specimens were taken in sweep-net samples.

Distribution. North Carolina to western Florida.

Records. NORTH CAROLINA: Durham Co., Chapel Hill Blvd., E of Co. line, 20 June 1963, ♀, 16 July 1963, ♀, 17 Apr. 1964, o (J. W. Berry). GEORGIA: Billy's Island, Okefenokee Swamp, June, 1912, ♂♀ (C. R. Crosby). FLORIDA: Escambia Co.: 8 mi. WNW of Pensacola, 20 Apr. 1945, ♂♂:300, 1 June 1945, ♂♀oo, 4 June 1945, ♀, 11 June 1945, ♂♀, 6 July 1945, ♀, 10 July 1945, ♀oo, 20 July 1945, ♀:300 27 July 1945, ♂♀, 30 July 1945, ♀o, 4 Aug. 1945, ♂♂♀o, 11 Aug. 1945, ♂♀♀:300 15 Aug. 1945, ♀o, 18 Aug. 1945, ♂o, 25 Aug. 1945, ♂, 8 Sept. 1945, ♀, 16 Sept. 1945, ♀o, 21 Sept. 1945, ♀oo, 19 June 1966, ♂, 17 July 1966, ♀oo (D. Lowrie).

Oxyopes sp.

Figures 5, 6, 16, 17

Discussion. A female *Oxyopes* from 12 mi. W of Portal was included with a number of interesting specimens from Arizona collected by L. D. Mikelson. In preliminary sorting this specimen was identified as *Oxyopes tridens* Brady. The color pattern is very similar to *O. tridens* and the epigynum resembles that species superficially. A closer examination revealed this spider to be quite different from *O. tridens*, particularly in the structure of the genitalia (compare Figs. 16, 17 of this paper with figs. 53-55 of Brady, 1964).

Three species, *O. pardus*, *O. lynx* and *O. felinus*, have males which resemble this female in coloration. The females of these three species, all of which occur in the southwestern United States, are unknown. Therefore, I think it is very possible that this solitary female belongs to one of the above species. Because *O. lynx* is so close to *O. cougar,* I suspect that the female of *O. lynx* will resemble that species. The new female described here, then, probably belongs in *O. felinus* or *O. pardus.*

Measurements. Length of female 5.4 mm, carapace width 1.7 mm, carapace length 2.3 mm.

Width of eye rows: AME .19 mm, ALE .60 mm, PLE 1.09 mm, PME .60 mm.

Segments of leg I and IV: femur, 2.0 mm, 2.4 mm, patella-tibia 2.4 mm, 2.4 mm, metatarsus 2.0 mm, 3.0 mm, tarsus .9 mm, .9 mm, total length 7.3 mm, 8.7 mm.

Length of patella-tibiae: II 2.3 mm, III 1.7 mm.

Color. Female. Pattern illustrated in Figures 5 and 6. Face and chelicerae pale yellow to cream with two dusky stripes from ALE to subdistal region of chelicerae. Eye region black.

Carapace pale yellow to cream with a pair of broad dusky stripes beginning at level of PME and continuing to thoracic declivity.

Dorsum of abdomen with wide median white stripe from base to tip, bounded by black on each side. Sides cream, mottled with black. Venter with broad, dark brown or black median stripe from epigastric furrow to base of spinnerets, bordered by narrow cream or white stripes.

Legs pale yellow to cream with dusky stripes evident on femora, particularly ventral surfaces. Other leg segments with irregular dark markings.

Labium pale yellow-brown, distal end ivory. Endites pale yellow. Sternum cream to ivory with dusky splotches at periphery and black mark posteriorly between bases of fourth coxae.

Diagnosis. This species is without doubt a member of the *apollo* group. The color pattern, epigynal structure and the long, robust fourth pair of legs ally it with these oxyopids. Since three of the southwestern species of the *apollo* group are known only from males, it is likely that this female may be conspecific with one of them. It is described here to differentiate it from *O. tridens* with which it may be confused because of a superficial resemblance. The best guess now is that this specimen represents the female of *O. pardus* or *O. felinus*.

Record. ARIZONA: Cochise Co.: 12 mi. W of Portal on Recreation Rd., 6,000 ft., ♀ (L. D. Mikelson).

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REVISIONAL STUDY OF THE ORDER PALAEODICTYOPTERA IN THE UPPER CARBONIFEROUS SHALES OF COMMENTRY, FRANCE

PART II[1]

By Jarmila Kukalova[2]
Charles University, Prague

An introductory discussion of the Palaeodictyoptera found in the Commentry shales and of the collection in the Institut de Paléontologie in Paris, as well as an account of the background of this investigation, was included in the first part of these studies. The present part deals with the following seven families: Homoiopteridae, Lycocercidae, Graphiptilidae, Breyeriidae, Eugereonidae, Archaemegaptilidae and Megaptilidae. Compared with the Spilapteridae, considered in Part I, all of these families are small, consisting of only a few genera, at least from the Commentry shales. However, they show much diversity of structure and indicate the extensive range of wing modifications which occurred in the Palaeodictyoptera, including the reduction and shortening of the hind wings. The third part of this study will deal with the Dictyoneuridae, which provide us with more information about the body structure in this order of insects.

Family Homoiopteridae Handlirsch

Homoiopteridae Handlirsch, 1906: 91; Lameere, 1917: 102; Handlirsch, 1919: 16; Handlirsch, 1921: 133.
Roechlingiidae Guthörl, 1934: 188; Kukalová, 1960: 1.
Thesoneuridae Carpenter, 1944: 10.
Scepasmidae Haupt, 1949: 42.

Type genus: *Homoioptera* Brongniart, 1893.

This family, as established by Handlirsch, included *Homoioptera* Brongniart, *Graphiptiloides* Handlirsch (1906), *Homoeophlebia* Handlirsch (1906), all from Commentry; and *Anthracentomon* Handlirsch (1904) from Belgium. Of these genera, *Graphiptiloides* (= *Graphiptilus*) is here assigned to the Graphiptilidae; *Homoeo-*

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[2] Alexander Agassiz Lecturer in Zoology, Harvard University, 1969.

phlebia has already been synonymized with *Homoioptera* by Lameere (1917, p. 151); and *Anthracentomon*, on the basis of Handlirsch's figures, is also considered a synonym of *Homoioptera.*

The present revisional study of the Commentry material has brought new aspects to the family classification of the Paleodictyoptera. The family Homoiopteridae now appears to include several genera from localities other than Commentry. Three families, Roechlingiidae, Scepasmidae and Thesoneuridae, seem to be synonymous with the Homoiopteridae; and the relationships of the Homoiopteridae with the Graphiptilidae, Breyeriidae and Lycocercidae have become more obvious.

The wings of the Homoiopteridae, as here treated, are the largest known in the Palaeodictyoptera. They are characterized especially by the following four features: (1) stems of main veins with a more or less pronounced bend in the basal third of the wings; (2) MA either simple or with very short branches and CuA always with branches (usually short ones); (3) CuA and CuP tending to be parallel to each other; and (4) a sclerotized strip with tubercles lying along the costa, just posterior to it. The cross veins are numerous, irregular and often connected.

The bending of the main veins basally is present in *Homoioptera*, *Boltopruvostia*, and to a lesser extent in *Thesoneura*; it also occurs in the related family Lycocercidae. MA is simple or has a little fork in *Homoioptera* (see left wing of the type specimen) and in *Thesoneura*; it gives rise to very short branches in *Boltopruvostia* (see *B. nigra* Kukalová, 1958). It is simple in the Breyeriidae but has a very short branch in *Graphiptilus* (type specimens of *heeri*). The branches on CuA are very short in *Homoioptera* and *Boltopruvostia*, longer in *Thesoneura* and completely reduced in Lycocercidae. In the Breyeriidae *(B. boulei)* and in *Graphiptilus* (*G. heeri*, specimen 19-12) CuA forms a short branch. The tendency for CuA and CuP to be parallel is a very persistent feature, common in all Homoiopteridae and noticeable also in some Lycocercidae *(L. pictus)*, Graphiptilidae *(Rhabdoptilus)* and some Breyeriidae *(B. barborae)*. The cross venation of Homoiopteridae and related families is very characteristic; it is readily distinguished from the more regular and rarely anastomosed venation of spilapterids and from the denser and usually relatively coarser pattern of the dictyoneurids.

From the foregoing account, it can be deduced that within the Homoiopteridae and related groups the branches of MA and CuA were in the process of reduction. The number of branches varies within the several genera of Homoiopteridae, and twigs occasionally occur in related families, in which MA and CuA are generally simple. In my opinion the families Homoiopteridae, Breyeriidae, Graphiptilidae and Lycocercidae form a phylogenetic unit, in which the Homoiopteridae represent in many respects the most primitive series. It is to be emphasized that the simple form of CuA and MA does not necessarily represent the more primitive stage, as generally believed. This hypothesis was based by Handlirsch on the assumption that the most primitive Palaeodictyoptera were the Dictyoneuridae. However, this family, except for the archedictyon, is a very advanced one, with venation very specialized and already reduced. Of course, it is very difficult to determine, in our present state of meagre information of the body structures, which of the families has the most primitive features. The geological record seems to be indicating more and more that probably all the larger families of the Paleodictyoptera were present and already well developed at the base of the Upper Carboniferous and that their representatives evolved very little during the rest of that period. As a rule within the insects, the many morphological features of wing venation do not have equal significance for classification in all families of the orders. The presence or absence of branches of MA and CuA appears to be more stable for the spilapterid group than for the homoiopterid group.

A remarkable feature, present to a more or less extent in all homoiopterid specimens I have had occasion to study [*Homoioptera*, *Boltopruvostia*, *Amousus*, *Ametretus* and *Thesoneura*], is the sclerotized strip and tubercles strengthening the costal area. It is especially marked in the largest specimens of the family, i.e., in all species of *Boltopruvostia* and in *Homoioptera gigantea.*

This family includes the largest species of Palaeodictyoptera known. The wings are of nearly equal length, the hind wings being somewhat the broader. In addition to the venational characteristics discussed above, the following should be noted: postcostal area large, with several branches included; Sc long; area of Rs small; MA simple or with short branches; MP with several branches; CuA and CuP parallel to each other; CuA with several short branches directed anteriorly (usually), CuP with several branches.

Body structures: head small, with projecting eyes and large clypeus. Prothoracic lobes with radiating veins and many cross veins, often with undulated margins. Legs longer than in Spilapteridae, with elongate tibiae. Abdomen unknown.

The family Homoiopteridae differs from the related families Lycocercidae, Breyeriidae, and Graphiptilidae in having CuA always branched and in possessing the sclerotized strip posterior to the costa. Only the genus *Homoioptera* is known from the Commentry shales. The following genera occur in other deposits: *Homoioptera* Brongniart (= *Anthracetomon* Handlirsch, 1904), Westphalian of Belgium; *Boltopruvostia* Strand, 1929 (*pro Boltonia* Pruvost, 1919) (= *Roechlingia* Guthörl, 1934, and *Ostrava* Kukalová, 1960), Westphalian of France, Westphalian C of Germany, Namurian C of Czechoslovakia. The following species appear to belong to the family Homoiopteridae but the status and relationship of the genera established for them are uncertain: *Mammia alutacea* Handlirsch, 1906, *Scepasma gigas* Handlirsch, 1911, *Amouzus mazonus* Handlirsch, 1911, and *Ametretus laevis* Handlirsch, 1911, all from the Westphalian of Illinois.

Genus *Homoioptera* Brongniart, 1893

Homoioptera Brongniart, 1893: 353; Agnus, 1902: 259; Woodward, 1906: 28; Handlirsch, 1906: 91; Lameere, 1917: 151; Handlirsch, 1919: 16.
Homoeophlebia Handlirsch, 1906: 92; Handlirsch, 1919: 16.
Anthracetomon Handlirsch, 1904: 6; Handlirsch, 1906: 93.

Type species: *Homoioptera woodwardi* Brongniart, 1893 (OD).

A few years after Brongniart described *woodwardi*, Agnus (1902) added another species, *gigantea*; this Handlirsch (1906) later made the type of another genus, *Homoeophlebia*. As pointed out by Lameere (1917), the generic separation of *gigantea* seemed totally unnecessary. Meunier (1912, p. 5) added to the taxonomic confusion by the erection of a new species, *gaullei*, in another genus *Archaeoptilus*, basing it on the *counterpart* of Agnus' type specimen of *gigantea*! Handlirsch's *Anthracetomon*, based on *latipenne* from the Westphalian of Belgium, is actually inseparable from *Homoioptera*. The following account is based on *woodwardi* and *gigantea*.

Wings relatively broad, almost identical, the hind pair being only a little broader than the fore; color markings in the form of numerous small, rounded spots. Precostal strip present (bordering the costal margin); anterior margin convex in the basal third of the wing; Rs with 3-4 branches, often forking; stem of M touching or nearly touching R near the base; M dividing near mid-wing, MA being simple and convex, MP with 3-4 branches; CuA and CuP with short branches, often originating at the same level. Anal veins 6-8 in number, sometimes forked. Cross veins often connected by numerous anastomoses, branched or forming a loose network.

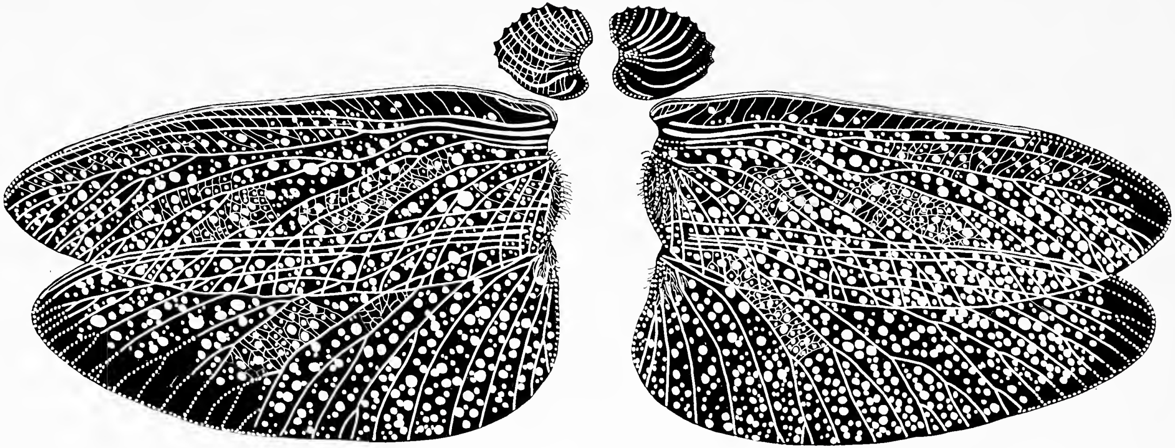


Figure 29. *Homoioptera woodwardi* Brongniart; specimen 20-10. Holotype.

Body structures: prothoracic lobes relatively small, high on prothorax, their bases relatively near to each other. Fore leg with strong femur, elongate tibia and narrow tarsus.

Homoioptera differs from the related genus *Boltopruvostia* Strand by having broader and shorter wings, smaller area of the radial sector, by more distal division of M (shortly before mid-wing), by MA being essentially simple and more convex, by CuP having fewer branches and by having a smaller anal area with less branching of the anal veins. All cross veins weak. From *Thesoneura*, *Homoioptera* differs in the more pronounced convex curvature of the main veins in the basal third of the wing and in having fewer branches on CuA.

The species included in the Commentry shales are *Homoioptera woodwardi* Brongniart and *H. gigantea* Agnus (= *Archaemegaptilus gaullei* Meunier, obj. syn.). One other species, *latipenne*, from the Westphalian of Belgium, appears to belong here, as noted above.

Homoioptera woodwardi Brongniart
Figure 29

Homoioptera woodwardi Brongniart, 1893:354, fig. 15, pl. 20, fig. 10; Handlirsch, 1906: 91, pl. 11, fig. 1; Handlirsch, 1921: 134, fig. 61.

This species was based by Brongniart on one specimen (20-10), showing the fore and hind wings, prothoracic lobes and a fragment of fore leg. The wings present a remarkable color pattern of circular dots, a pattern which occurs repeatedly in the families related to the Homoiopteridae. The shape of the prothoracic lobes probably has little taxonomic value other than at the specific level. Great variability in the shape of the lobes also occurs in the Spilapteridae. My study of the type specimen shows that the cross venation is much denser and is less regular than indicated in Brongniart's figure.

Fore wing: length 75 mm, width 27 mm. Wing membrane spotted by circular markings of varying diameters; wing uniformly broad in the proximal half, then abruptly narrowing; apex at about the wing axis; Sc, R and M almost parallel and convex at the end of the first quarter of the wing; M notably concave before the division into MA and MP; Rs with 3-4 branches, each forked several times; Rs area very small. Cross veins more simple in the areas of the subcosta, sc-r and r-rs, with much less anastomosis. A cluster of long hairs occurs at the bases of both fore wings. Hind wing: length 75 mm, width 31 mm. The sigmoidal curvature of the main veins near the base is much less pronounced than in the fore wing; anal veins only rarely forked.

Body structures: prothoracic lobes with undulated margin, their veins S-shaped, about 11 in number. Numerous anastomoses of cross veins.

Homoioptera gigantea Agnus
Figure 30

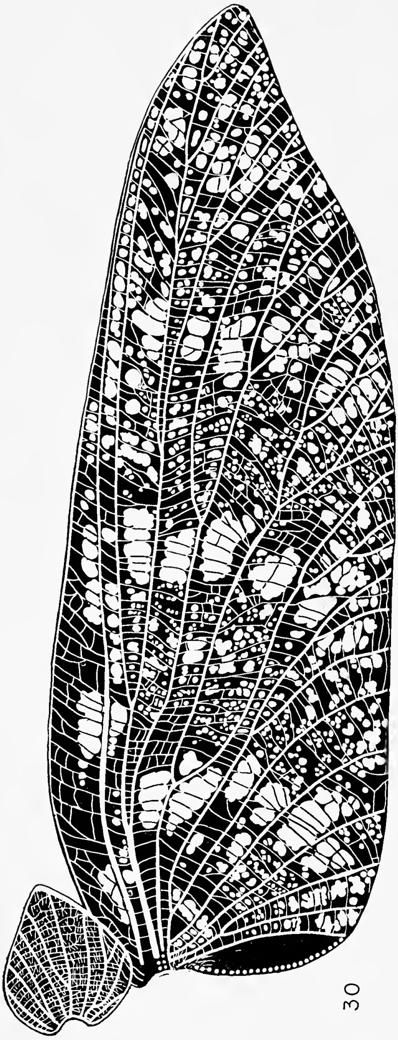
Homoioptera gigantea Agnus, 1902: 259, pl. 1; Lameere, 1917: 151.
Homoeophlebia gigantea Handlirsch, 1906: 93, pl. 11, fig. 3.
Archaeoptilus gaullei Meunier, 1910: 233, fig. 1; Meunier, 1912: 5, pl. 6, fig. 1.
Homoeophlebia gaullei Handlirsch, 1919: 16, fig. 18.

This monotypic species was based by Agnus upon a remarkably well preserved, large fore wing, with a single prothoracic lobe and vague outlines of the head, including the base of the beak, and suggestions of the thorax and a fragment of a fore leg. The reverse, as already noted, was described by Meunier (1910) as *Archaeoptilus gaullei.*

Fore wing: length 187 mm, width 65 mm. Wing membrane spotted with (1) extremely dense, small, light markings, irregularly grouped into small clusters; (2) larger spots arranged into 4 transverse bands. Wing abruptly narrowed in the apical third, with the apex pointed and falcate. Anterior margin very convex in the basal third, the posterior margin S-shaped in the apical third. Sc, R, M following the convex curvature of the anterior margin. Sc somewhat shortened; subcostal area broad in the proximal half, then very narrow; stems of R and M touching near the base; M deeply concave before division into MA and MP; Rs with about four very oblique branches, the first of them long and forked. Anal area with about seven branches, the first forked several times. Cross veins parallel and directed in different directions, with much anastomosis. Long hairs are clustered at the base.

Body structures: prothoracic lobe length 27 mm, width 24 mm, with a complete covering of long hairs. Prothoracic lobe cordate, with seven radiating veins and densely arranged, simple cross veins; margin of lobe not undulated.

This species differs from *woodwardi* by its larger size, more specialized shape of the wing with its falcate apex, the larger rs area, the contact of the stems of R and M and the smoothly curved margins of the prothoracic lobes, as well as the color pattern of the wings.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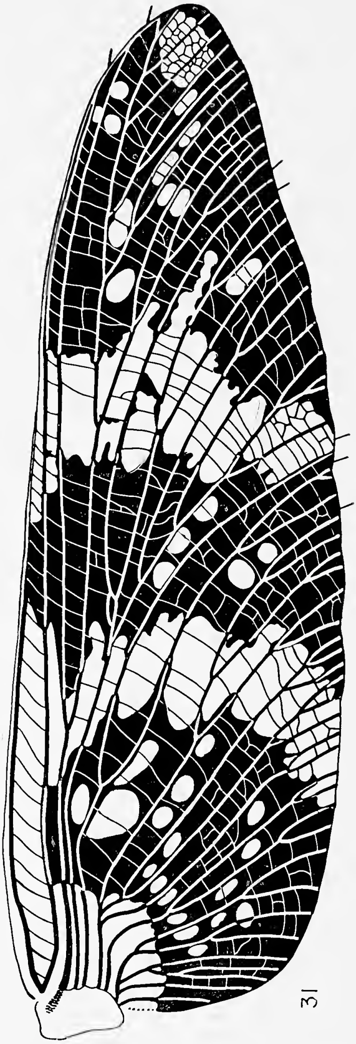
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Figure 30. *Homoioptera gigantea* Agnus; prothoracic lobe, fore wing. Holotype.
Figure 31. *Lycocercus pictus* Handlirsch; fore wing. Holotype.

Family Lycocercidae Handlirsch, 1906

Lycocercidae Handlirsch, 1906: 675; Handlirsch, 1906: 88; Handlirsch, 1921: 133; Handlirsch, 1919: 15; Lameere, 1917: 102.

Polycreagridae Handlirsch, 1906: 110; Handlirsch, 1906: 678; Handlirsch, 1921: 137.

Apopappidae Lameere, 1917: 42.

Patteiskyidae Laurentiaux, 1958: 302; Demoulin, 1958: 363.

Type genus: *Lycocercus* Handlirsch, 1906

The family Lycocercidae was established by Handlirsch for *Lycocercus* and was characterized as having more numerous branches than Lithomanteidae[3] and as having cross veins forming at least partially a dense network of the dictyoneurid type. His interpretation of the fossils on which *Lycocercus* was based is only partly correct. The cross veins of the Lycocercidae are indeed denser, more irregular and more often connected by anastomoses than in Lithomanteidae but they do not form a real network of the dictyoneurid type.

This revisional study of the type material has revealed three additional and important features for the Lycocercidae: (1) the hind wing is as long as but narrower than the fore wing; (2) the MP area is of triangular shape, with many branches; (3) the origins of MA and the first fork of MP are very close.

The following families are considered by me to be synonymous with Lycocercidae: (1) Polycreagridae Handlirsch, 1906, based on the single genus *Polycreagra* Handlirsch, 1906; this genus differs from *Lycocercus* only by having more obliquely oriented branches, with longer forks and by having Rs more richly branched. (2) Apopappidae Lameere, 1917, based upon *Apopappus* Handlirsch, 1906, which differs from *Lycocercus* by having a more regular cross venation and by having CuP somewhat richer in branches. (3) Patteiskyidae Laurentiaux, 1958, based upon the oldest palaeodictyopteron so far known, *Patteiskya bouckaerti*[4] (Namurian B, Germany), which differs from the other species of *Lycocercus* only in having M dividing more proximately; it is therefore inseparable from *Lycocercus*.

Wings about equal in length, hind pair narrower, similar in vena-

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[3] The family Lithomanteidae is here understood to include the genus *Lithomantis* Woodward (syn. *Hadroneuria* Handlirsch and *Lithosialis* Scudder), *Macroptera* Laurentiaux (syn. *Lusiella* Laurentiaux and Texeira) and *Synarmoge* Handlirsch.

[4] In the figure published by Laurentiaux (1958, figure 1) Sc is correctly drawn but the subcostal area is broader proximally and is shaped as in *Lycocercus goldenbergi*. In the figure published by Demoulin (1958, p. 359, fig. 1) the vein designated as the costa is actually the subcosta. *Lycocercus bouckaerti* is not represented by a hind wing but by a fore wing.

tion; wing membrane usually dark, with light bands and spots. Fore wings resembling hind wings in outline but with broader subcostal area. Anterior margin nearly straight, often with precostal strip; stems of main veins convex in the basal third, as in Homoiopteridae; Sc long; MA simple, curved, originating near the first fork of MP; MP with many branches, occupying a markedly triangular area; CuA simple and curved; CuP parallel to CuA, but with several branches. Anal area often large, with many branches. Cross veins fine, numerous, more or less irregular, sometimes connected.

Body structures: head small with conspicuous eyes and large clypeus. Prothoracic lobes with fan-like veins and many cross veins, often with undulated margins. Thorax broad, metathorax shorter than mesothorax; legs homonomous, not very short. Ovipositor not sculptured, stout and curved. Cerci robust, long.

The family Lycocercidae is related to the Homoiopteridae in the characteristic curvature of stems of main veins near the base, in the late division of M, in the general character of cross veins, in the presence of many small forks along the posterior margin, etc. It differs from the Homoiopteridae in the narrowed hind wing and more richly branched MP and CuP and simple CuA. Another related family is the Graphiptilidae, from which the Lycocercidae differ in the richly branched MP and CuP and the narrower hind wings.

Genera included in the Commentry shales: *Lycocercus* Handlirsch and *Apopappus* Handlirsch.

Occurrence in other deposits: *Lycocercus* Handlirsch, Namurian B, Germany.

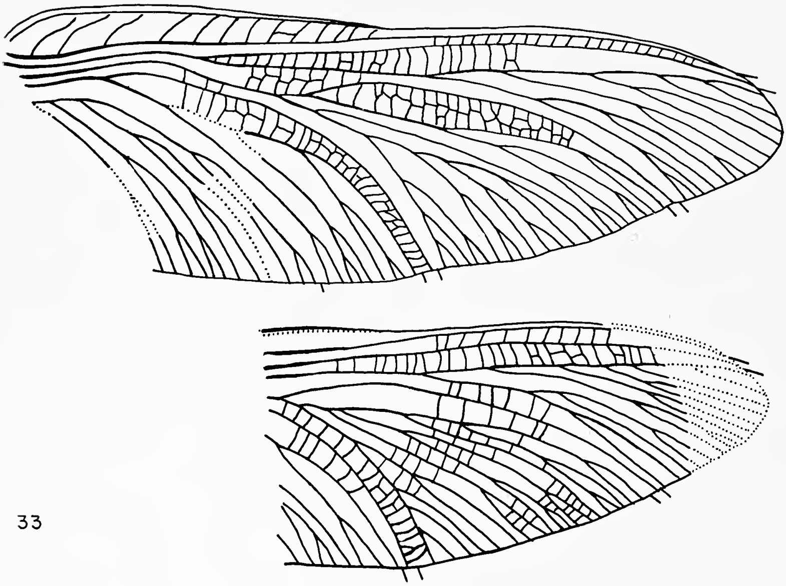
Genus *Lycocercus* Handlirsch

Lycocercus Handlirsch, 1906: 89, Handlirsch, 1919: 15; Lameere, 1917: 153. *Patteiskya* Laurentiaux, 1958: 302; Demoulin, 1958: 360.

Type species: *Dictyoneura goldenbergi* Brongniart, 1893 (SD Handlirsch, 1922).

This genus was erected by Handlirsch for *goldenbergi* Brongniart, as represented by specimen 21-1. Specimen 21-2, correctly described by Brongniart under the same specific name, was erroneously referred by Handlirsch (1906, p. 90) to a separate species *brongniarti* (Lameere, 1917, p. 153). Meunier (1911, p. 121) described *Homoioptera brongniarti*, which Handlirsch later (1919, p. 15) recognized as *Lycocercus*. The specific name having been preoccupied within the genus since 1906, Handlirsch (1919, p. 16) changed it to *Lycocercus pictus*. Though Lameere (1917, p. 153) believed that *pictus* was conspecific with *goldenbergi*, he was apparently incorrect.

Figure 32. *Lycocercus goldenbergi* (Brongniart); specimen 21-1; v = separated valves of cast cuticle. Holotype.



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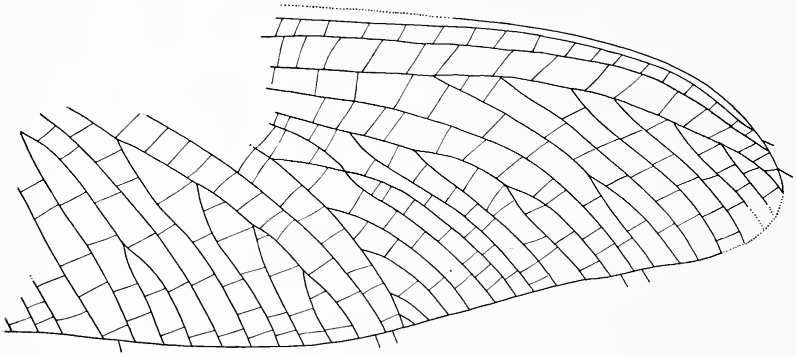

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Figure 33. *Lycocercus goldenbergi* (Brongniart); specimen 21-1; fore and hind wings. Holotype.

Figure 34. *Apopappus guernei* (Brongniart); specimen 19-3; fore wing. Holotype.

Although the differences in venation might conceivably be considered as due to individual variability and although the cross venation and color markings are almost identical, there is a marked difference in the length of the legs and probably also of the beak.

In *Lycocercus* the hind wings are like the fore wings in shape but are narrower. This assertion is based on specimen 21-2, in which the wings are preserved in their natural positions. If found isolated, a fore or hind wing can be recognized only by the width of the proximal part of the subcostal area, which is broader in the fore wings.

Fore wings unusually broad in the proximal half, shaped as hind wings. Hind wings similar but somewhat narrower. R1 simple; Rs with six branches, first of them forked; MP forked 10-20 times. Number of CuP branches variable; about 8 anal veins, mostly forked. Cross veins dense, irregular, often connected.

Body structures: beak short or long. Legs stout but not very short.

Lycocercus differs from *Apopappus* in less regular anastomosing of cross veins, smaller CuP area and in the larger number of short branches of Rs and CuP. As a whole, the venation of *Lycocercus* is much less regular. From *Polycreagra* Handlirsch (Westphalian, Illinois) it differs in the less densely branched and less obliquely oriented branches of main veins.

Species included in the Commentry shales: *Lycocercus goldenbergi* Brongniart, 1893; *Lycocercus pictus* Handlirsch, 1919.

Occurrences in other deposits: *Lycocercus bouckaerti* (Laurentiaux, 1958) of Namurian B, Germany.

Lycocercus goldenbergi (Brongniart)

Figures 32, 33, 35

Dictyoneura goldenbergi Brongniart, 1883: 265 (for additional references see Handlirsch, 1922: 39).

Lithomantis goldenbergi, Brongniart, 1893: 369, pl. 21, fig. 1, 2.

Lycocercus goldenbergi, Handlirsch, 1906: 89, pl. 10, fig. 20; Handlirsch, 1921: 138, fig. 60; Handlirsch, 1919: 15, 16; Lameere, 1917: 101; Lameere, 1917: 153; Demoulin, 1960: 1-4, pl. 1.

Lycocercus brongniarti Handlirsch, 1906: 90, pl. 10, fig. 21; Handlirsch, 1919: 15, fig. 17.

This species was based by Brongniart on specimen 21-1, one of the most remarkable Palaeodictyoptera known, and on specimen 21-2, a fragment of fore and hind wing in natural positions. Handlirsch (1922) designated specimen 21-1 as the type; specimen 21-2, which is important for showing the wing shapes, was referred by Handlirsch to a separate species, *brongniarti*, but was identified again as *goldenbergi* by Lameere (1917, p. 153).

The type specimen (21-1) has been discussed many times by various authors but of these only Brongniart and Lameere actually studied the fossil. Most interpretations are highly speculative and not worth discussing here. The fossil shows so many structures which are important for the whole order that it deserves the most detailed study. Actually, the specimen might contribute even more details than I was able to work out in my limited stay of several weeks at the Paris Museum. The following discussion is based mostly on the obverse, with the exception of the abdominal appendages, which are better preserved in the reverse. In figure 32, as usual, both obverse and reverse have been used.

The type specimen shows fragments of two twisted wings. The broad wing on the right side is a fore wing, having a broader subcostal and r-rs areas than the narrower hind wing on the left side. This conclusion was reached after noting that the second specimen (21-2, shown in figure 35), with fore and hind wings in natural positions, showed the same differences.

The body of specimen 21-1 is twisted in such a way that the thorax shows the dorsal side, while the abdomen shows the distal end in full lateral view. The head is in perfect frontal position. The insect apparently first rested with the beak oriented along the body axis; later the head became loose and shifted 90° to the left. The prothoracic lobes lifted from the pronotum and overlapped so that they are now in lateral position. Such preservation is unusual for the Palaeodictyoptera and proves beyond any doubt that (1) the prothoracic lobes were not fused together to form a pronotal shield, as claimed by Sharov (1966)[5]; and (2) that they were easily moveable. The legs of specimen 21-1 are extended on both sides of the body. All three right legs have a deep suture near the proximal end of the tibia, giving the impression of an extra segment fused with the tibia. I have observed similar sutures in *Stenodictya agnita* (Meunier) and *Stenodictya oustaleti* (Brongniart). It is of great interest that in Recent Ephemeroptera there is a marked bend in the same part of the tibia (e.g., *Ecdyonurus*). But the suture on the tibia does not seem to be present in the related orders Megasecoptera and Diaphanopterodea and not even in all Palaeodictyoptera. At any

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[5] The prothoracic lobes were attached to the pronotum by short cuticular ridges in the center of their basal part. The perfectly preserved prothoracic lobes of *Stenodictya* will be described in Part III of this series of papers.

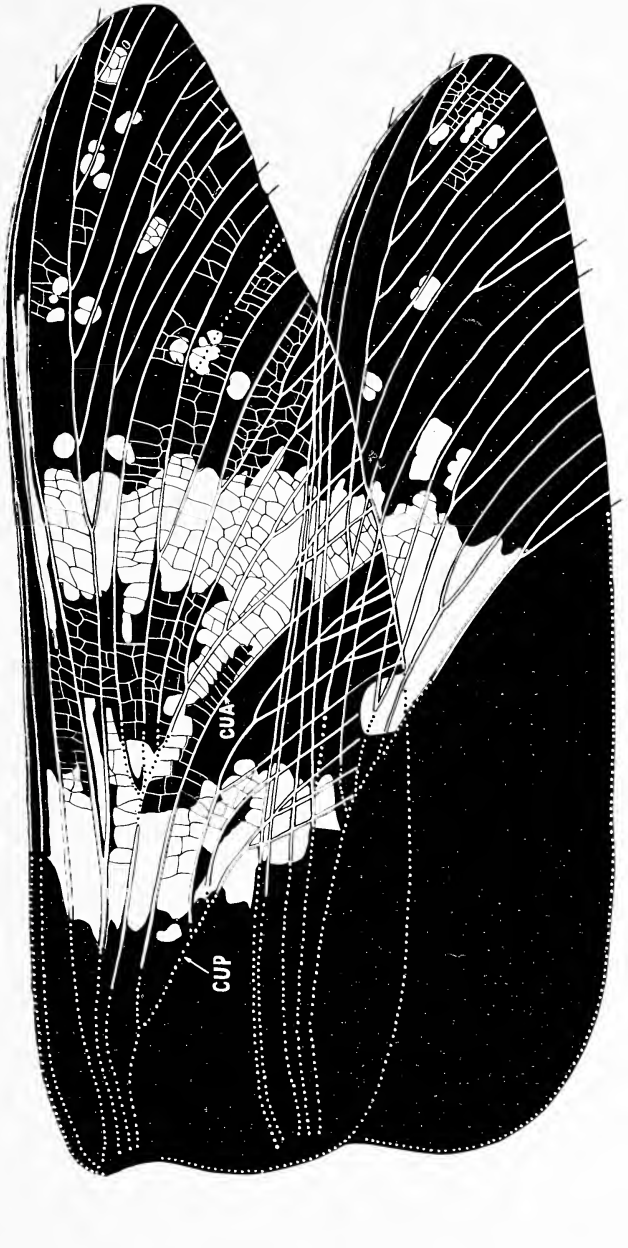


Figure 35. *Lycocercus goldenbergi* (Brongniart); specimen 21-2; fore and hind wings.

rate, the part divided by the suture makes a single piece with the tibia, so that it probably had hardly any functional significance.

The segments of the abdomen, undoubtedly because of decaying processes and distortion, show varying portions of the intersegmental membrane. The ovipositor is robust and opened widely. Between the ovipositor valves, a pair of sac-like cuticular structures appears to come from the abdomen. These have been incorrectly interpreted as gonapophyses by many authors. Demoulin (1960) considered them the evaginated cuticle of the oviduct and pointed to similar cases known in Recent Ephemeroptera after the laying of the eggs in paired large clusters (e.g., Polymitarciidae).

Above the end of the abdomen, twisted backwards, there are two structures described by Brongniart as "crochets dorsaux." Detailed examination shows that they are "attached" to the cercus. These seem like parts of a smaller and much less heavily sclerotized ovipositor and could be part of a cast cuticle. It is conceivable that the Palaeodictyoptera had an adult molt, in which case this "ovipositor" could have been part of the previously molted cuticle.

The ovipositor of *Lycocercus goldenbergi* resembles, in its broad attachment to the 9th segment, the ovipositors of certain dragonflies, such as the Zygoptera and some Anisoptera, especially those adapted for endophytic oviposition. Moreover, it resembles the ovipositor of some Diaphanopterodea (Permian of Kansas and Czechoslovakia, unpublished material) in the prolongation of the lateral margin of the 9th tergite anteriorly. The surface of the gonapophyses does not show any sculpturing, whereas in *Asthenohymen* it is armed by ridges and even stout hairs directed backwards, as in the endophytic Hymenoptera.

The following account is based on the type specimen and on specimen 21-2.

Fore wing: length 73 mm, width 25 mm, broadest in the first third. Precostal strip extending to about the middle of the wing. Posterior margin with small convexities at the end of each area. Apex directed posteriorly, rounded. Rs with about 5 branches, the first two of them more or less richly branched; MA arising occasionally distally from the first branch of MP. MP forked 11-19 times. Cu dividing near the base, CuP with 3-5 posteriorly directed branches, often forked. Anal area moderately large with veins forked many times. Cross veins fine, dense, curved, sometimes branched and connected. Hind wing fragment: length 39 mm, width 22 mm.

Basic body structures: head small, with very large clypeus having a median ridge. Beak relatively shorter than in any other known Palaeodictyoptera; length 11 mm. Labrum triangular, long. Thorax broad and robust. Mesothorax slightly longer than the metathorax and about the same length as the prothorax. Prothoracic lobes large, with fan-like veins and undulated margins. Legs stout, femur length 8.5 mm in all three pairs. Proximal end of tibia provided with a deep suture on all legs. Lengths of tibia and tarsi unknown. Abdomen relatively short and broad (length 48 mm), segments subequal, the first two being shorter than the following ones. Lateral margin of the 9th segment prolonged anteriorly. Ovipositor robust, heavily sclerotized, gonapophyses not sculptured; anterior valves arising from 8th segment, 8th sternite being shortened; 9th segment with the anterior margin concave; lateral valves much broader than the anterior ones. Cerci robust, multisegmented.

Lycocercus goldenbergi differs from the related species *bouckaerti* (Laurentiaux, 1958) of Namurian B, Germany (= *Patteiskya bouckaerti*) in the more distal division of the stem of M. From *Lycocercus pictus* Handlirsch, it differs in having shorter legs and probably also in having a shorter beak, having more numerous branches of CuP, smaller anal area; also, Cu divides more proximally and the cross venation is denser, with more numerous anastomoses.

Lycocercus pictus Handlirsch, 1919

Figures 31, 36

Homoioptera brongniarti Meunier, 1911: 121, fig. 5; Meunier, 1912: 11, pl. 7, fig. 6 (*nec brongniarti* Handlirsch, 1906).
Lycocercus pictus Handlirsch, 1919: 15, fig. 17 (*pro brongniarti* Meunier).

This species is monotypic, based by Meunier (1911) upon a specimen showing both fore wings, prothoracic lobes, vague outlines of the beak and a fore leg and part of the head. Handlirsch (1919) correctly referred this species to *Lycocercus* using the name *pictus* for it to avoid homonymy. *Lycocercus pictus* was discussed in detail by Lameere (1917, p. 153-154), who erroneously assumed it to be conspecific with *goldenbergi*. Lameere in his account described the head and beak with a clypeus similar to that of the Fulgoridae and a trace of palpus on the side. Of all these structures I was able to see only weak outlines of the beak, which seemed to be longer than in *goldenbergi*.

The prothoracic lobes are aligned by their posterior margins with the posterior edge of the pronotum, giving the appearance of a shield. This is misleading, as shown by the related species, *goldenbergi*, in which both lobes are raised up above the pronotum.

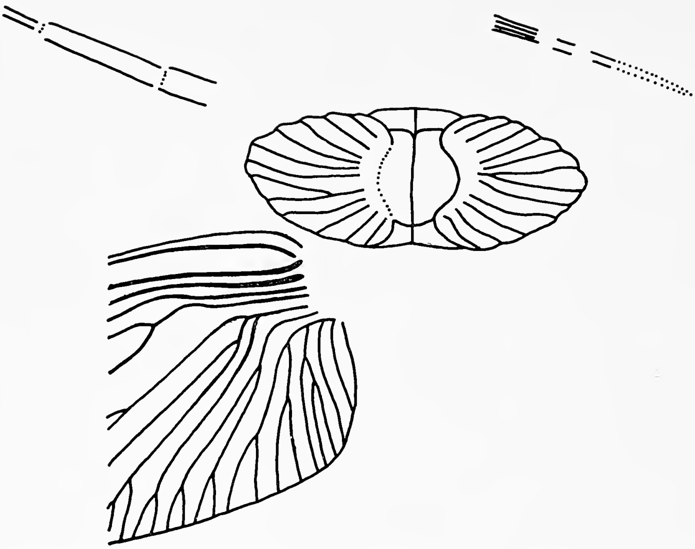


Figure 36. *Lycocercus pictus* Handlirsch; prothorax, basal part of fore wing, fragment of fore leg (l) and beak (b). Holotype.

Fore wing: 69 mm long, 22 mm broad, the wing uniformly broad in the proximal half. Anterior margin very slightly concave, posterior margin with a slight concavity also in the apical third; apex directed posteriorly, rounded. Precostal strip reaching to the end of the first third; subcostal area relatively narrow. Rs with 6 branches, mostly forked; MP forked 9 times; Cu dividing very distally, shortly before the origin of Rs; CuP as in *Homoioptera*, with a few terminal branches. Anal area very large, with 8 richly forked branches arising from separate stems. Cross veins dense, rather regular, sometimes connected.

Body structure: beak probably long (about 2.5 cm). Prothoracic lobes large, high on pronotum, their posterior margins corresponding to the posterior edge of the prothorax. Prothorax relatively long with median line. Legs longer than in *goldenbergi*, apparently with long tibia.

Lycocercus pictus differs from *goldenbergi* by the several venational traits and body structures already noted.

Apopappus Handlirsch, 1906

Apopappus Handlirsch, 1906: 100; Lameere, 1917: 149; Lameere, 1917: 103; Handlirsch, 1919: 20.

Type species: *Spilaptera guernei* (Brongniart, 1893) (OD).

This genus was erected by Handlirsch upon *Spilaptera guernei* Brongniart, specimen 19-3, because of a simple MA and CuA but it was erroneously classified with the family Graphiptilidae. Later, Lameere (1917, p. 103) suggested that *Apopappus* was a transitional form between the Spilapteridae and Ephemeroptera. Finally the same author (1917, p. 42) established for this genus a separate family, Apopappidae. With Triplosobidae, he referred this family to the Protephemeroidea because he believed that in the mp area of *guernei* there is the beginning of intercalary sectors, indicating its relationship to the Ephemeroptera.

The venation of *Apopappus* shows typical lycocercid features, such as the large triangular MP area, simple MA and CuA and fine but rather dense pattern of cross veins. The fusion of the distal branch of MP1 with the proximal branch of MP2, considered by Lameere as an intercalary sector, is in all probability an individual variation only.

Wing broad. Branches of main veins running parallel. Rs with 6 pectinate branches, most of them simple; MA arising near the first fork of MP; MP forked 9 times. CuP with a series of 6 branches. Anal area unknown. Cross veins fine, not very dense, mostly regular and simple.

Apopappus differs from *Lycocercus* in the regularly distributed branches of the main veins, in the very rich branches of CuP and in the more regular, less numerous and mostly simple cross veins.

Species included in the Commentry shales: *Apopappus guernei* (Brongniart, 1893).

Apopappus guernei (Brongniart)

Figure 34

Spilaptera guernei Brongniart, 1893: 341, pl. 19, fig. 3.

Apopappus guernei Handlirsch, 1906: 100, pl. 11, fig. 13; Handlirsch, 1919: 20; Lameere, 1917: 149.

This species is monotypic, based by Brongniart upon specimen 19-3, which I was not able to find in the collections of the Museum. This account has been made from a good photograph which Dr. Carpenter kindly placed at my disposal and which showed the venation very clearly.

As in other Lycocercidae, it is difficult to recognize the fore and hind wing if found isolated, especially if the subcostal area is missing. From the more pronounced convexity of posterior margin in the apical third and beyond the width, I believe the wing is probably the fore one.

Rs with 6 branches, the first of them with a small simple fork; MA curved as in other Lycocercidae; MP1 sending off 4 branches posteriorly, MP2 another four branches anteriorly. CuP with four simple branches, the fifth being forked several times. Cross veins tending to form rows in rs area.

Apopappus guernei is similar in the MP area to *Lycocercus pictus* but the forking of the last branch of CuP resembles the *Lycocercus goldenbergi*, specimen 21-2. The cross venation is slightly more simple and more regular than in *pictus*.

Family Graphiptilidae Handlirsch

Graphiptilidae Handlirsch, 1906: 99; Handlirsch, 1921: 136.
Rhabdoptilidae Handlirsch, 1919: 15.

Type genus: *Graphiptilus* Brongniart, 1893.

The family Graphiptilidae was erected on *Graphiptilus* but included *Apopappus* Handlirsch and *Spiloptilus* Handlirsch. The family, having been based upon an incomplete description and on a misinterpretation of the type specimens of *Graphiptilus*, represents a heterogeneous group, as treated by Handlirsch. The genus *Apopappus* belongs, in all probability, to the Lycocercidae; and *Spiloptilus*, having MA and CuA branched, has already been referred to the Spilapteridae (Kukalová, 1969). The structure of *Graphiptilus*, on the other hand, certainly justifies reference of the genus to a separate family.

Graphiptilus is known so far only from the hind wing, which is markedly and broadly triangular in form. The principal characters of its venation are the very small rs area, simple MA and CuA, and the numerous weak cross veins. Within the Palaeodictyoptera only the genus *Rhabdoptilus* and representatives of the family Breyeriidae show similar venational features.

The relationship of *Graphiptilus* to *Rhabdoptilus*, though not previously mentioned, is obvious from the similarity not only of the venation and cross venation but even of the color pattern, which seems to be a more significant feature for the Graphiptilidae and Breyeriidae than for other families of the order Palaeodictyoptera. As noted by Professor Carpenter (1967, p. 61) the small circular spots on the wings of Breyeriidae are actually cuticular thickenings on the membrane. The well preserved Commentry material of *Breyeria* shows long hairs, probably macrotrichia, in clusters at these spots; similar structures may well have been present on the wings of the Graphiptilidae.

It is to be emphasized that the hind wings of both *Graphiptilus* and *Rhabdoptilus,* though broad and therefore relatively short, do not show any sign of reduction. This fact together with the venational pattern places them far from *Lithoptilus*, which has been erroneously associated with *Rhabdoptilus* (Demoulin, 1958).

The fore wing is unknown. The hind wing is of broadly triangular shape. Anterior margin almost straight; Sc long; Rs area reduced in size, with 3-4 branches; MA simple, MP with several branches; CuA simple, CuP branched several times; several anal veins. Cross veins dense, fine, long, sometimes connected by anastomoses. Color markings usually in the form of irregularly distributed larger spots and smaller rounded spots.

The family Graphiptilidae resembles Breyeriidae in several features, already noted above, including the wing markings. The graphiptilids differ from the breyeriids in having a denser pattern of cross veins and in having the branches of the main veins obliquely oriented (not perpendicular to posterior margin, as in some breyeriids) and in having these branches closer together. Among the Breyeriidae, the less specialized genus *Stobbsia* recalls most Graphiptilidae and may turn out to belong to that family.

Two genera are included in Commentry shales: *Graphiptilus* Brongniart, 1893; *Rhabdoptilus* Brongniart, 1893.

Genus *Graphiptilus* Brongniart

Graphiptilus Brongniart, 1893: 348; Handlirsch, 1906: 99; Handlirsch, 1919: 20; Lameere, 1917: 150.

Graphiptiloides Handlirsch, 1906: 92; Handlirsch, 19-9: 16.

Type species: *Graphiptilus heeri* Brongniart, 1893 (SD Handlirsch, 1906).

This genus was erected by Brongniart for *heeri*, *williamsoni* and *ramondi*. *Ramondi* was referred by Handlirsch (1906, p. 100) to a new genus *Spiloptilus*, which has been transferred to the Spilapteridae (Kukalová, 1969); *williamsoni* was assigned by Handlirsch (1906, p. 92) to a new genus *Graphiptiloides* and placed in the Homoiopteridae. As mentioned already by Lameere (1917, p. 151) *heeri* and *williamsoni* are actually very close and they are undoubtedly conspecific; for some reason Lameere believed that *williamsoni* was based on a fore wing, though the unique type has the same wing form as *heeri*, characteristic for hind wings in this family.

A careful study of the specimens has made possible a reliable determination of the outline of the hind wings, their triangular form becoming obvious. For the relationship of *Graphiptilus* (as well as for most other Palaeodictyoptera), the cross veins are most important. Those of *Graphiptilus*, being very fine and close together, have not been observed or at any rate mentioned by previous authors.

Hind wing very broad in proximal half; wing membrane usually with many elongate spots and small circular spots. Rs with four short branches; branches of main veins obliquely oriented to the posterior margin. Anal area reaching about midwing. Cross veins fine, dense, straight, regular.

Graphiptilus differs from the related genus *Rhabdoptilus* Brongniart by its fewer branches of MP, more obliquely oriented branching of main veins and in the more regular cross venation. The color pattern differs by the shape of the elongate spots.

Only the type-species is known from the Commentry shales.

Graphiptilus heeri Brongniart

Figure 37, 38

Graphiptilus heeri Brongniart, 1893: 349, pl. 19, fig. 13, Handlirsch, 1906: 100, pl. 11, fig. 12; Handlirsch, 1919: 20; Lameere, 1917: 150.

Graphiptilus williamsoni Brongniart, 1893: 350, pl. 19, fig. 12; Lameere, 1917: 151.

Graphiptiloides williamsoni Handlirsch, 1906:92; Handlirsch, 1919: 16.

This species was based by Brongniart on a single specimen, 19-13, a hind wing without base but with a well preserved color pattern. As noted above, I consider the type of *williamsoni* (specimen 19-12) to be the same species.

Hind wing: length about 60 mm, width 27 mm, broadest at the end of the first third of the wing; light spots of diverse length are present, limited by cross veins, and in addition small round light spots irregularly distributed over the wing. Anterior margin straight, anal area moderately rounded. Apical half of wing abruptly narrowing distally, apex rounded, shifted anteriorly to the axis of the wing. R-rs area only a little broadened; anal area large with at least nine long branches reaching or extending beyond the middle of the wing; some cross veins in costal and subcostal area stronger than the others and more oblique.

The differences between specimens 19-13 (type of *heeri*) and 19-12 (type of *williamsoni*) are in the presence or absence of small forks on CuA and CuP, in one branch more or less on MP and CuP and in the relative lengths of the anal areas. None of these seem to be at the specific level.

Genus *Rhabdoptilus* Brongniart

Rhabdoptilus Brongniart, 1893: 364; Handlirsch, 1906: 88; Lameere, 1917: 102; Lameere, 1917: 154; Demoulin, 1958: 4.

Type species: *Rhabdoptilus edwardsi* Brongniart, 1893 (OD).

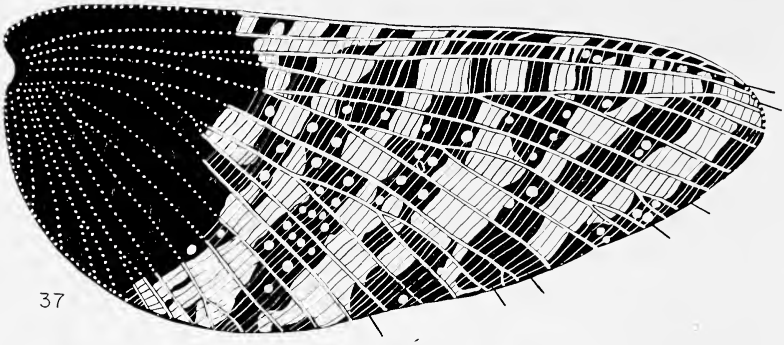
This genus is monotypic, erected by Brongniart upon a fragment of a large hind wing without base, apex or posterior margin. *Rhabdoptilus* was referred by Handlirsch first (1906) to the Lithomanteidae and later (1919, p. 15) to a separate family Rhabdoptilidae, on the basis of its parallel, dense cross venation. Lameere (1917, p. 154) associated *Rhabdoptilus* with *Fouquea* in spite of the simple MA and CuA, because the cross veins in both genera seemed to him to be very much alike. Demoulin (1958) placed *Rhabdoptilus* with *Lithoptilus* and referred both genera to Handlirsch's family Rhabdoptilidae, which he thought was near to the Breyeriidae and Thesoneuridae.

I have explained above that Handlirsch's misinterpretation of *Graphiptilus* prevented recognition of the close relationship between *Rhabdoptilus* and *Graphiptilus*, despite the marked similarity in venation, cross veins and color markings. Nevertheless, there are some differences in wing membrane characters between these genera, most probably of functional significance, as noted below.

The wing area being large, the membrane thin, and cross veins weak, the wing tends to be strengthened in several ways. First, the membrane is heavily pigmented and the pigmentation even penetrates into light spots in the form of peculiar tooth-like projections; second, the membrane between the veins is rippled, producing a corrugated effect, and the thin cross veins usually run on the ridges of the ripples. These are probably functional structures and restricted to the genus and possibly to the type species. Lameere was not correct in considering the strong conspicuous cross veins of *Fouquea* to be like those of *Rhabdoptilus*.

In *Rhabdoptilus* the hind wing is not reduced in length and all branches of the main veins are fully developed. In *Lithoptilus* the hind wing, on the other hand, is greatly reduced with branching levels of R1, Rs and M shifted distally. The cross venation of *Lithoptilus* is very dense, with numerous, coarse connections, distinctly different from *Rhabdoptilus*. For that reason I consider that Demoulin's conclusion about the relationship of these genera is insupportable. In this paper, *Lithoptilus* is referred to Eugereonidae.

Hind wing: probably broadly triangular; markings forming large, elongate and small circular light spots. Anterior margin slightly convex. Rs originating in the basal third of the wing, with several



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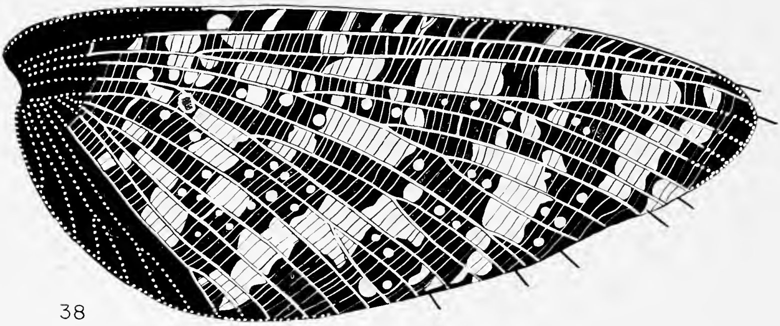

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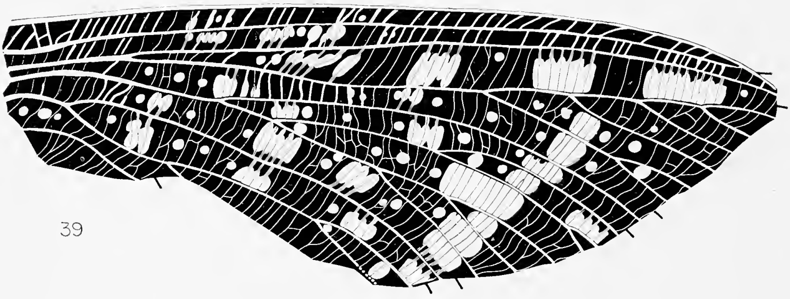

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Figure 37. *Graphiptilus heeri* Brongniart; specimen 19-13; hind wing. Holotype.

Figure 38. *Graphiptilus heeri* Brongniart; specimen 19-12; hind wing.

Figure 39. *Rhabdoptilus edwardsi* Brongniart; specimen 20-9; hind wing. Holotype.

short branches; MA simple; MP forked several times; CuA simple; CuP with few branches. Cross veins fine, dense, curved, rarely with anastomoses.

The distinctions between *Rhabdoptilus* and *Graphiptilus* have already been noted above.

Only the type species is known from the Commentry shales.

Rhabdoptilus edwardsi Brongniart

Figure 39

Rhabdoptilus edwardsi Brongniart, 1893: 365, pl. 20, fig. 9; Handlirsch, 1906: 88, pl. 10, fig. 19; Lameere, 1917: 154; Handlirsch, 1919: 15; Demoulin, 1958: 4.

This species is monotypic, being based by Brongniart upon specimen 20-9, a fragment of a large hind wing with the posterior margin missing. The preserved part of the wing is very clear and all details of venation and color pattern in the heavy pigmentation of the membrane are perfectly distinct.

Hind wing fragment: length 87 mm, width 29 mm. Light spots of diverse lengths, with rounded lateral margins, some with pigmentation penetrating into them, as shown in figure 39. Small rounded spots are numerous, irregularly distributed. R-rs area broadened; Rs with about 5 branches, first of them forked; MP forked about 5 times; CuP slightly concave near its origin, sending off several branches. Cross veins regularly distributed; in subcostal and sc-r1 areas they are not anastomosed, and they are unusually strong.

Family Breyeriidae Handlirsch

Breyeriidae Handlirsch, 1906: 95; Handlirsch, 1921: 135; Handlirsch, 1919: 18; Laurentiaux-Vieira and Laurentiaux, 1963: 173-8; Laurentiaux-Vieira and Laurentiaux, 1964: 1282-1284; Captenter, 1967: 58.

Type genus: *Breyeria* Borre, 1875.

This family was established by Handlirsch on *Breyeria* Borre, *Borrea* Brongniart and *Megaptiloides* Handlirsch; three other genera were subsequently added to the family; *Pseudoborrea* Handlirsch, *Stobbsia* Handlirsch and *Breyeriopsis* Laurentiaux.

The family is represented in Upper Carboniferous strata of England, Belgium, Holland, France, Czechoslovakia and the United States (Tennessee) but despite that record no body structures are known so far. The uniformity of the venational pattern of the Breyeriidae being obvious, it does not seem possible to recognize more than two valid genera (Kukalová, 1959, p. 311; Laurentiaux, 1964, p. 3; Carpenter, 1967, p. 61): *Breyeria* Borre and *Stobbsia* Handlirsch.

Although specimens found in deposits other than Commentry are the better preserved, the Commentry material contributes some very interesting morphological details. Both *Breyeria lachlani* and *Breyeria boulei* show clusters of long hairs, in a dense pattern and extending along the anterior part of the proximal half of the wing membrane, long hairs at the wing base, and a border of long hairs along the anterior and posterior margins of the wing. In *lachlani* clusters of hairs have been observed also arising from some of the circular light spots in the cua-cup area.

The short hairs on the wings are now well known in Palaeodictyoptera. They are common on veins and cross veins, and in some families, as Dictyoneuridae, a dense covering of hairs can be seen over the entire wing and body surfaces. Clusters of long hairs on the wing base were found also in the related family Homoiopteridae; similar hairs were noted in Archaemegaptilidae along the basal part of C, Sc and Cu. However, as far as I have been able to determine from the Commentry specimens, long hairs in clusters on the wing membrane and along the wing margin occur only in the Breyeriidae. In other Breyeriidae, outside of the Commentry deposit, traces of hairs have been described on the basal part of the costa and the posterior wing margin, as in *Breyeria barborae* (Kukalová, 1959) but the hairs themselves were not preserved. The clusters of long hairs on the wing membrane might be macrotrichia serving as sense organs, an hypothesis which seems to be supported by their presence in the light spots, which are actually cuticular thickenings of the wing membrane (Carpenter, 1967, p. 61).

Wings of large size, broad, equal in length, the hind pair broader. Sc shortened. Stems of R and M approaching or touching near the base. Branches of main veins few, widely separated from each other. CuA and MA simple; MP forked; CuP usually with a fork. Hind wings often broadly triangular in shape. Cross veins numerous, thin, irregular, often connected by anastomoses.

The family Breyeriidae seems related to the Graphiptilidae on the basis of the small rs area, simple MA and CuA, the few branches of MP and CuP, the presence of numerous long, fine cross veins and the triangular shape of the hind wings. Small circular spots frequently occur in color patterns of both groups.

Genera included in the Commentry shales: *Breyeria* Borre, 1875; *Megaptiloides* Handlirsch, 1906.

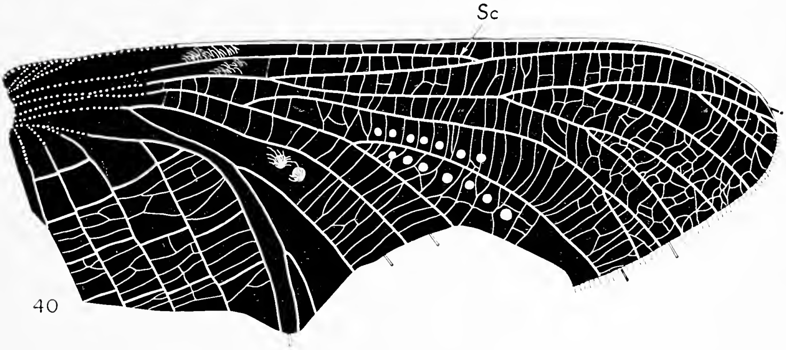
Other occurrences: *Breyeria* Borre (Westphalian-Stephanian of Europe, Westphalian of North America); *Stobbsia* Handlirsch (Westphalian of England).

Breyeria Borre

Breyeria Borre, 1875: 7; Laurentiaux, 1953: 421.
Borrea Brongniart, 1893: 378; Handlirsch, 1906: 97; Handlirsch, 1919: 18.
Pseudoborrea Handlirsch, 1919: 18.
Breyeriopsis Laurentiaux, 1949: 47-54.

Type species: *Pachytylopsis borinensis* Borre, 1875 (OD), Westphalian, Belgium.

A revised figure of the type has been published by Laurentiaux (1949, p. 50, fig. 1a and 1953, p. 42, fig. 19b). In the Commentry shales two species have been found: *Breyeria lachlani* (Brongniart, 1893) and *Breyeria boulei* (Meunier, 1910), both based on slightly damaged hind wings. Laurentiaux (1949, p. 52) considered them to be conspecific and places *boulei* as a synonym



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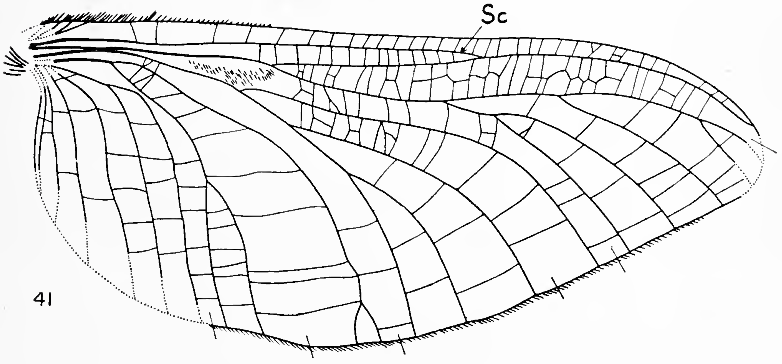

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Figure 40. *Breyeria lachlani* (Brongniart); specimen 21-9; hind wing. Holotype.
Figure 41. *Breyeria boulei* (Meunier); hind wing. Holotype.

of *lachlani.* After having removed much matrix on the specimen of *boulei* I was able to see more details of its venation, including some which are specific differences and which eliminate the possibility of the synonymy with *lachlani.*

Specimen 21-5, designated by Handlirsch (1906, p. 97) as *Megaptiloides brodiei*, is too fragmentary for definite classification. It shows dense cross veins, richly anastomosed and tending to form short intercalary sectors. The hairs along the margin are absent. Handlirsch's classification of *brodiei* into a separate genus is probably justified.

The following account is based mostly on the details already published by Laurentiaux, Laurentiaux and Laurentiaux-Vieira, Carpenter and Kukalová.

Wings subequal, hind wing being somewhat shorter and broader. Hind wing sometimes very broad in the anal third and often of triangular shape. Postcostal area triangular, with several short branches. Sc terminating far before the apex, on R; Rs with 3-6 branches, the first of them often forked. Branches of M, Cu and the anals are curved sharply toward the posterior margin. MP with 1-5 broad forks; cua-cup area often markedly broad. CuP with 1-2 forks, seldom simple. Anal area either with a series of about 5 simple branches or with a series of simple long forks. Cross veins fine, irregular, rather dense, sometimes connected by irregular anastomoses. In the anal area, there are often present stronger and straighter cross veins (in addition to the finer ones) tending to be arranged in regular rows. Circular cuticular thickenings are often present in rows in the areas of m, rs and cu.

Breyeria Borre differs from *Stobbsia* Handlirsch by having Sc ending on R and by the branches of M, Cu and the anals abruptly curving toward the posterior margin.

Species included in the Commentry shales: *Breyeria lachlani* (Brongniart), *Breyeria boulei* (Meunier); *Megaptiloides brodei* (Brongniart).

Species from other deposits: *Breyeria borinensis* (Borre) (Westphalian, Belgium); *Breyeria barborae* Kukalová (Westphalian A, Czechoslovakia); *Breyeria limburgica* Laurentiaux (Westphalian A, Holland); *Breyeria delruei* Laurentiaux (Westphalian B, France); *Breyeria vrankeni* Laurentiaux-Vieira and Laurentiaux (Westphalian B, Holland); *Breyeria rappi* Carpenter (Westphalian C, Tennessee); *Breyeria stopai* Laurentiaux and Laurentiaux-Vieira (Westphalian C, France); ?*Breyeria britannica* Laurentiaux and Laurentiaux-Vieira (Westphalian B, England).

Breyeria lachlani (Brongniart)

Figure 40

Borrea lachlani Brongniart, 1893: 379, pl. 21, fig. 9; Handlirsch, 1906: 97, pl. 11, fig. 8; Handlirsch, 1919: 18; Lameere, 1917: 157; Laurentiaux, 1949: 52.

This species was erected by Brongniart on specimen 21-9, a hind wing lacking the base and most of the posterior margin. The following account was completed after exposing additional features following the removal of substantial matrix.

Hind wing: length 65 mm; preserved width 26.5 mm. Anterior margin straight, strongly curved towards apex; apex broadly rounded. Sc terminating at the end of the second third of the length of the wing on R; Rs with 3 branches, first of them forked; MA slightly concave soon after its origin with a small fork at the end; MP probably with 2 branches extending anteriorly; CuA slightly concave in the first third of its course, CuP twice forked; anal area with 6 widely spaced branches. Cross venation dense, sometimes the cross veins connected, forming a network in the rs area. Strong, regular cross veins present in anal area. Long hairs occur in two clusters in the subcostal and sc-r areas, arising in circular, cuticular thickenings in cua-cup area and bordering the posterior margin. Small rounded cuticular thickenings forming rows between some branches.

Breyeria lachlani (Brongniart) differs from *boulei* in its denser and more reticulated cross venation and in the widely spaced anal veins, resembling those of the fore wing. It is similar to many other species, such as *delruei, vrankeni, rappi,* etc.

Breyeria boulei (Meunier)

Figure 41

Borrea boulei Meunier, 1910: 236, fig. 4; Meunier, 1912: 7, pl. 7, fig. 1.
Pseudoborrea boulei Handlirsch, 1919: 18, fig. 20.
Borrea lachlani Laurentiaux, 1949: 52.
Breyeria (*Borrea*) *lachlani* Laurentiaux and F. Laurentiaux-Vieira, 1951: 590.

This species was erected by Meunier upon a nearly complete hind wing. In comparison with all other hind wings of the genus, *boulei* does not have a very broad anal area and consequently it lacks the typical triangular shape.

Hind wing: length 59 mm, width 25 mm, broadest at about the first third of the wing length. Anterior margin, strongly curved towards the apex. Apex directed posteriorly, slightly pointed. Posterior margin as a whole convex, slightly concave in the cua-cup area and slightly convex just before the apex. Sc terminating at the end of the second third of the wing on R; Rs with 3 branches, first of them forked; MA slightly concave soon after its origin; MP with 2 branches arising anteriorly. CuA slightly concave in the first third of its course, CuP forked; cua-cup area very broad; anal area with about six parallel branches, not widely spaced. Cross veins not very dense, sometimes connected. Stronger and more regular cross veins in the anal area and also in rs and m areas. Long hairs are present in a cluster in the r-m area at the base and bordering the proximal part of the anterior margin and the whole posterior margin. Cuticular thickening in rows probably present.

Breyeria boulei differs from *lachlani* as previously indicated.

Family Eugereonidae Handlirsch

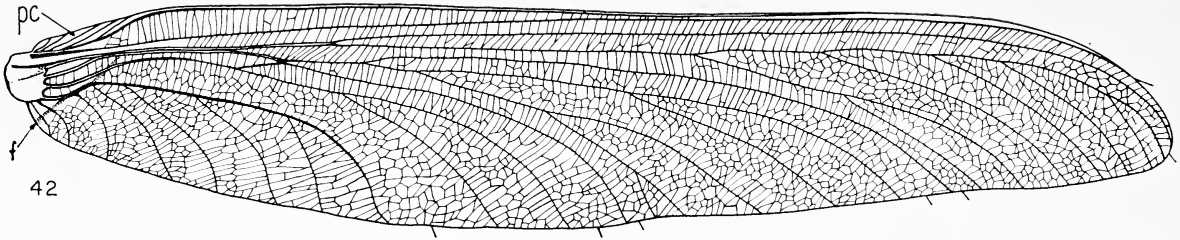
Eugereonidae Handlirsch, 1906: 388; Carpenter, 1964: 104.
Dictyoptilidae Lameere, 1917: 194.
Peromapteridae Handlirsch, 1906: 79; Handlirsch, 1919: 11; Handlirsch, 1921: 130.

Type genus: *Eugereon* Dohrn, 1866 (Lower Permian of Germany).

The family Eugereonidae has been recently (1964) reviewed by Professor Carpenter, who synonymized the Dictyoptilidae with it and discussed *Eugereon* and the Commentry genus *Dictyoptilus*. Details of that study are not repeated here. On the basis of my own studies of Commentry material, I am adding certain details on the structure of the wing base of Eugereonidae and the related family Calvertiellidae which were not included in previous papers (Carpenter 1964, Kukalová 1964). To keep the revisional study as nearly complete as possible I am including in this paper figures of all Commentry Eugereonidae (Figures 42, 43, 44, 45).

The Eugereonidae are made spectacular by the more or less pronounced reduction of the hind wings, which often (to varying degrees) differ from the fore wings in shape and venation. The tendency to reduce the hind wings apparently occurred repeatedly in families of Palaeodictyoptera. Sometimes, the hind wings are broader but slightly shorter (Dictyoneuridae, Mecynostomatidae, some Spilapteridae) while in others the hind wings are as long as the fore wings but are narrower (Lycocercidae). Extremely shortened hind wings are so far known in two families — Eugereonidae and Megaptilidae.

Within the Eugereonidae, as understood in this paper, the



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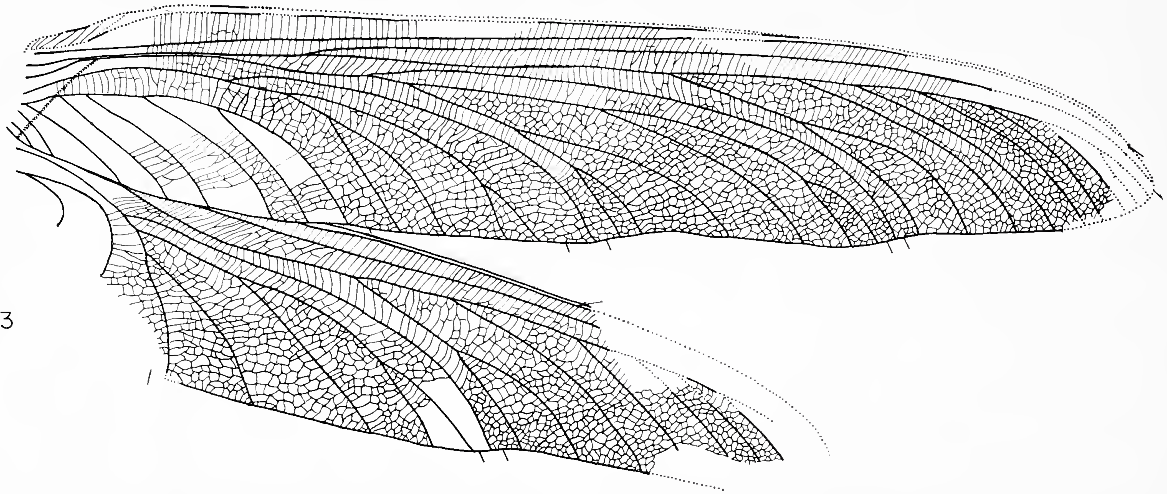

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Figure 42. *Dictyoptilus sepultus* (Meunier); fore wing. Holotype. pc = precostal area; f = furrow.
Figure 43. *Dictyoptilus peromapteroides* (Meunier); fore and hind wings. Holotype.

amount of variability in the hind wing shape and venation seems to be very great. Nevertheless, I do not consider it practical, at least at our present stage of knowledge, to separate into different families those genera in which the fore wings are much alike. In my opinion, the hind wings representing reduced structures may have been variable in form. The most modified hind wing of the Palaeodictyoptera occurs in *Peromaptera* Brongniart, the wing being very short, broad and having an extremely reduced rs area. The hind wing of *Valdeania* Teixeira is very short and broad also but the venation is similar to that of its fore wing (according to Teixeira, 1941, fig. 1). In both *Eugereon* and *Dictyoptilus* (fig. 43) the hind wing is less shortened and narrow, approximately of the same width as the fore wing; the venation is modified more in the basal third, that is in the anal and cubital areas; the rs area is relatively well developed (Carpenter, 1964). So far, I consider these differences of generic level.

Another remarkable morphological feature of Eugereonidae is the precostal area. This was mentioned for the first time by Lameere (1917, p. 160) in *Dictyoptilus sepultus* (Meunier) and later in the same species by Laurentiaux (1953, p. 423). As far as I am aware, the largest precostal area is present in both fore and hind wings of the families Eugereonidae and Calvertiellidae; a narrower precostal area occurs in the related family Archaemegaptilidae. It was probably present also in Protagrionidae.

The precostal area of the families mentioned above is comparable with that of the Orthoptera, being formed by a series of short branches coming out anteriorly from a strong costa at its very base. It continues distally, forming a long membraneous precostal strip. However, a precostal strip, not broadened basally to form a precostal area, is common in Palaeodictyoptera, being especially pronounced in the Dictyoneuridae, Lycocercidae, Homoiopteridae and some Spilapteridae. In families with the precostal area well developed, the postcostal area is completely missing.

The postcostal area, as far as I was able to observe it in the specimens, is present in all families of Palaeodictyoptera without a precostal area. Besides the Palaeodictyoptera, I was able to see it in those Megasecoptera which did not have the wings very narrowed basally. The postcostal area was first described by me in the Breyeriidae (1959) and in the Roechlingiidae (1960), under the inappropriate term "precostal area." It is formed by a short vein, often branched, arising from the very base of the costa and oriented obliquely, finally terminating again on the costa after a short distance. To avoid confusion and to emphasize the postcostal position of this area, I changed (1964) the term to postcostal area and pointed out its probable homology with the so-called costal brace of Ephemeroptera.[6] The interesting and intermediate condition between the well developed triangular postcostal area and its complete reduction and replacement by the precostal area is present in Dictyoneuridae. In this family, which has a broad precostal strip and which is very probably related to Eugereonidae and Calvertiellidae, there is only one weak postcostal vein, oriented along the wing axis and ending usually on Sc, recalling the costal brace of the mayflies more than structures in other Palaeodictyoptera.

The origin of the costal brace-postcostal area probaly goes back to the common ancestors of Palaeodictyoptera, Megasecoptera, Diaphanopterodea and Ephemeroptera. The strongly developed costal brace has been found in aquatic Permian mayfly nymphs (Kukalová, 1969) probably helping to support the obliquely oriented and independent wing pads. In adult Permian mayflies the costal brace was less developed than in the nymph and probably nonfunctional. On the other hand, the terrestrial (apparently) nymphs of Megasecoptera (Carpenter, 1969) and Palaeodictyoptera (undescribed material from Westphalian, Illinois) have a vestigial postcostal area very much as in the adults. It is possible that in ancestral palaeopterous nymphs there was a selective trend towards the ability to hold the wings in a more posterior position. The costal brace-postcostal veins possibly helped to hold the wings in this favorable position.

The other striking morphological feature of the Eugereonidae is the presence of a deep furrow crossing the anal area obliquely and ending on the stem of M. It has been found in *Dictyoptilus, Eugereon* and very probably also in *Peromaptera.* This feature is best beveloped, though not unique, in this family and apparently developed independently in the very thin wings or very large wings, so-called, in addition to Eugereonidae and is most pronouncd in the Calvertiellidae (thin wings) and Homoiopteridae (very large wings). The fuction of this furrow is very puzzling, since the wings

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[6] New and undescribed material of Calvertiellidae from the Lower Permian of Czechoslovakia shows beyond any doubt that in all known specimens of this family (including *Calvertiella,* which I had an opportunity to restudy recently) there is a well developed, large precostal area; the postcostal area is completely missing, as in the Eugereonidae. In this respect my account on Calvertiellidae (1964) has to be corrected.

of Palaeodictyoptera break off easily along this line. Thus, Calvertiellidae are usually found with the base of the anal area broken away. In Homoiopteridae the anal veins and cross veins are distinctly different before and behind the furrow, which thus forms some type of a separate basal area. The high percentage of palaeodictyopterous wings with similarly broken bases indicates the presence of the basal furrow in many families. At the present time I am not able to explain this structure.

Wings unequal in length, the fore pair being longer. Hind wings shortened, with modified venation, different from that of the fore wings. Wing membrane usually dark with very small light spots restricted to individual cells of the reticulation. Fore wings long and very narrow, with the precostal area and precostal strip present; deep furrow obliquely crossing the anal area and terminating on R; Sc terminating before apex; stems of R and M arising separately but touching for some distance beyond the base; MA simple, MP with 2-4 branches; CuA usually simple, CuP usually with one branch only. Anal area long and narrow with pectinate and widely separated veins. A very dense pattern of coarse cross veins present, often with anastomoses and sometimes forming a network.

The nearest relatives of the Eugereonidae appear to be the Archaemegaptilidae, Calvertiellidae and Protagrionidae; more distantly related are the Dictyoneuridae. All these affinities have at least partially been mentioned by previous authors (Handlirsch 1906, 1937; Lameere 1917, 1935; Martynov 1932; Tillyard and Fraser 1938; Laurentiaux 1953; Carpenter 1964; Kukalová 1964). There is also, in my opinion, a more distant relationship with another family that has markedly shortened hind wings — Megaptilidae. This family differs in having much broader and shorter fore wings, with a very large rs area but it recalls the Eugereonidae in having the branches of the main veins often arranged perpendicularly to the posterior margins; also in the simple MA and CuA, the branching of MP and in the very dense, richly anastomosing cross venation. The families mentioned above probably form a related group within the order.

Genera included in commentry shales: *Dictyoptilus* Brongniart, 1893; *Peromaptera* Brongniart, 1893.

Other genera in other deposits: *Eugereon* Dohrn, 1866 (Lower Permian of Germany; *Valdeania* Teixeira, 1941 (Stephanian, Portugal).

Genus *Peromaptera* Brongniart

Peromaptera Brongniart, 1893: 391; Handlirsch, 1906: 79; Lameere, 1917: 160; Handlirsch, 1919: 11.

Type species: *Peromaptera filholi* Brongniart, 1893. (OD)

This genus is monotypic, based upon a single specimen with fore and hind wings preserved. Unfortunately, this remarkable fossil, showing a greatly reduced hind wing with the venation modified to the highest degree among Palaeodictyopera, could not be found in the collection in Paris since I began this study. The following account is based on Lameere's revision (1917) and on photographs which Professor Carpenter made in 1938, when the specimen was in the collection.

Peromaptera was referred by Brongniart to the Dictyoneuridae. Handlirsch (1906, p. 79) erected for it a separate family on the basis of the shortened hind wing. Lameere (1917, p. 160) considered this separation as unnecessary because of the obvious relationships of the genus to *Dictyoptilus.*

From my studies of the photographs, I consider that Lameere's conclusions are correct: not only fore wing venation and cross venation but also all basal structures of the wing seem to be very similar in both *Peromaptera* and *Dictyoptilus.* The hind wing, on the other hand, is very different from that of both *Eugereon* and *Dictyoptilus,* being shorter and broader with a modified venation. But since we do not know the amount of individual and specific variation of the hind wing among the Eugereonidae and since the fore wing is almost indistinguishable from that of *Eugereon,* I do not consider it practical at this time to put *Peromaptera* in a separate family.

Fore wing narrow, broadening at the middle part. MP with few branches, CuP forked. Cross veins dense. Hind wing much broader than fore wing, extending almost to 2/3 of the fore wing length, with broad apical part. Sc probably long; sc-r area broad; Rl ending relatively far before apex; Rs originating very basally, rs area being very small; M probably dividing beyond midwing, giving rise to simple MA and forked MP; CuA simple, CuP forked; anal area probably large, extending beyond midwing. Cross venation as in fore wings, in sc-r and r-rs areas much less dense than on the rest of the wing.

Peromaptera differs from *Eugereon* and *Dictyoptilus* in the shape of the hind wing. From all other genera of Eugereonidae the hind wing differs in the extreme modification of the hind wing venation.

Species included in Commentry shales: *Peromaptera filholi* Brongniart.

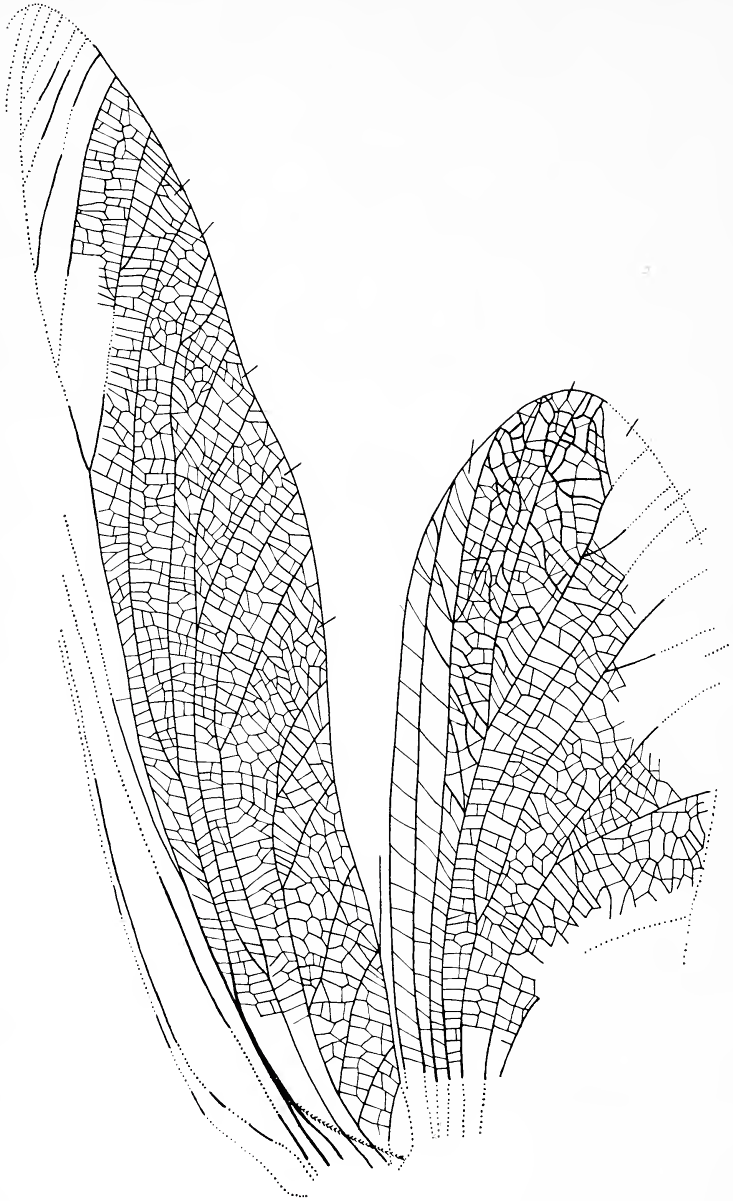


Figure 44. *Peromaptera filholi* Brongniart; fore and hind wings; Holotype.

Peromaptera filholi Brongniart

Figure 44

Peromaptera filholi Brongniart, 1883: 393, pl. 22, fig. 15; Handlirsch, 1906: 80, pl. 10, fig. 8; Lameere, 1917: 160.

This species is monotypic, based by Brongniart upon specimen 22-15, which was represented by a fore and a hind wing. For the drawing given here only the photograph was at my disposal. The base shows almost surely the stems of R and M touching as in *Dictyoptilus*. The precostal area being only fragmentary in the fossil is not so distinct. The hind wing venation unfortunately does not show convexities and concavities and has been interpreted according to Lameere (1917, p. 160).

Fore wing: length about 60 mm, width about 13 mm (according to Brongniart, 1893). Anterior margin unknown, posterior margin concave in the middle part of the wing. Subcostal area broad basally; Rs with about 7 branches, first of them forked; MA approaching the stem of Rs but not touching it; MP with two short branches; CuA independent from the stem of M but approaching it to some extent. Six anal veins.

Hind wing: length about 40 mm, width about 16 mm. Anterior margin straight; apical part shortened, apex obtusely rounded, located at about the wing axis. Rs very long, with short single branch; MP with a short fork at the end. Cu dividing proximally from M, occupying a narrow area. Anal veins far distant from each other, probably pectinate. Cross venation in hind wing with irregular thickening in the apical part.

The fore wing of *Peromaptera filholi* differs from that of all other species of Eugereonidae in the much less developed MP. The branch of CuA is probably an individual variation only, formed by the thickened reticulation which is frequently noted in the related family Dictyoneuridae. Also, CuA is simple in the hind wing. The shape of shortened hind wing recalls that of *Valdeania medeirosi* Teixeira, 1941 but the venation is completely different from that of the fore wing.

Family Archaemegaptilidae Handlirsch

Archaemegaptilidae Handlirsch, 1919: 13.

Type genus: *Archaemegaptilus* Meunier, 1908

This family, being based on a wing fragment, was erected by Handlirsch with some uncertainty as to its affinities. Lameere (1918,

p. 160), however, considered *Archaemegaptilus* related to *Dictyoptilus* (Eugereonidae).

Archaemegaptilus is known by a hind wing, which is not shortened and which has a venation similar to that of the fore wing of *Dictyoptilus.* In all genera of Eugereonidae, so far as we know, the hind wing is shortened and its venation is modified. The cross venation *Archaemegaptilus* is much coarser than in *Dictyoptilus* and forms intercalary sectors along the posterior margin, as in another related family, Calvertiellidae. Sc is almost as long as in Eugereonidae but terminates in a fork, forming thus an intermediate stage leading to an Sc which is short and which ends on R, as in Calvertiellidae. The stems of R and M are touching near the base as in Eugereonidae. The precostal area is very narrow and the wing venation less specialized than in both Eugereonidae and Calvertiellidae. In this way, *Archaemegaptilus* represents to some extent a combination of morphological features of both families being at the same time more primitive than any of them. I believe, therefore, that Handlirsch was probably correct in establishing a separate family for *Archaemegaptilus. Dictyoneurella perfecta* Laurentiaux, 1949 (Westphalian of France), should be referred to the same family, in my opinion; it is a fore wing with a long narrow precostal area, intercalary sectors and a venation and cross venation very similar to those of *Archaemegaptilus.*

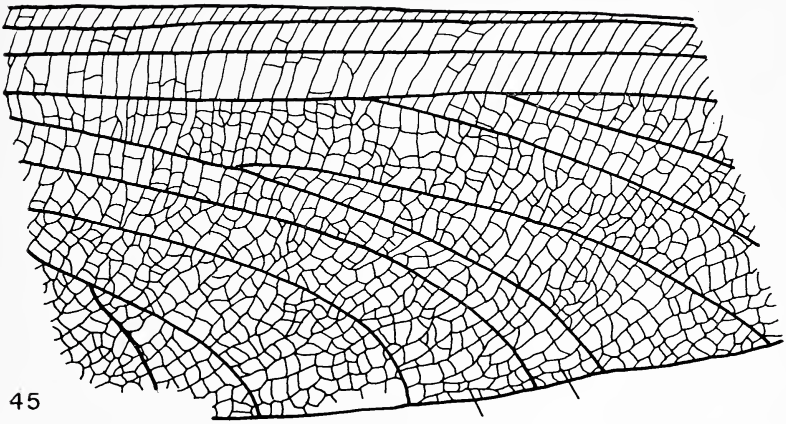
The following account is based on *Dictyoneurella* (fore wing) and the completed figure of *Archaemegaptilus* (hind wing).

Wings probably equal in length, hind pair broader. Venation in fore and hind wings alike. Wing membrane thin, with darker venation or dark with small light spots. Precostal area narrow, postcostal area completely missing. Sc more or less shortened. Stems of R and M close together or touching for some distance near base. Rs area small with few branches. MA simple, MP branched several times. CuA simple, CuP with several branches. Anal area with pectinate series of branches. Cross veins strong but not dense, forming a loose reticulation and convex intercalary sectors.

The family Archaemegaptilidae is closely related to the Eugereonidae, Calvertiellidae and Protagrionidae, from all of which it differs in its more primitive venation with independent branches and many-branched CuP.

Genus included in Commentary shales: *Archaemegaptilus* Meunier, 1908.

Genus from other locality: *Dictyoneurella* Laurentiaux, 1949 (Westphalian, France).



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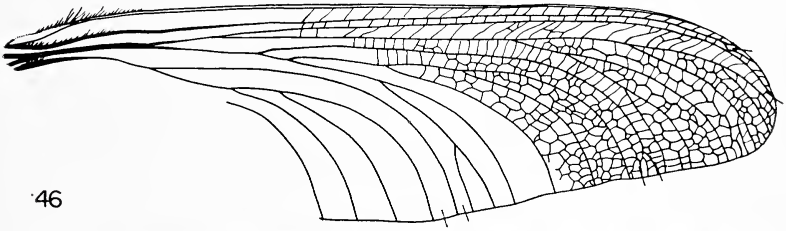

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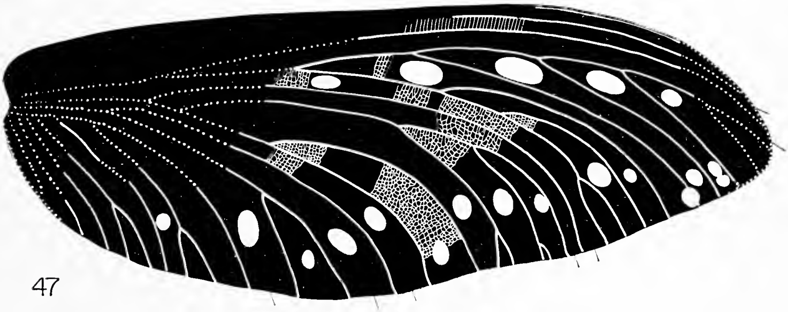

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Figure 45. *Dictyoptilus renaulti* Brongniart; fore wing. Holotype.
Figure 46. *Archaemegaptilus kiefferi* Meunier; hind wing. Holotype.
Figure 47. *Megaptilus blanchardi* Brongniart; fore wing. Holotype.

Genus *Archaemegaptilus* Meunier

Archaemegaptilus Meunier, 1908: 155; Meunier, 1908: 175; Meunier, 1909: 138; Handlirsch, 1919: 13; Lameere, 1917: 103; Lameere, 1917: 160.

Type species: *Arachaemegaptilus kiefferi* Meunier, 1908 (OD).

This genus is monotypic, based by Meunier on the reverse of a hind wing. As Lameere (1917, p. 160) correctly noted, the obverse specimen, which was apparently not seen by Meunier, is more nearly complete; it is figured here for the first time. The following account is based on both parts of the type specimen.

Hind wing: long, broadening basally. Precostal strip pronounced, broadened at the base to form a narrow precostal area; Sc slightly shortened, terminating by a fork on C and R; stems of R and M touching for a long distance just beyond the base; CuA simple, curved, not approaching the stem of M; CuP with several branches occupying a large area. Cross venation coarse, consising of cross veins connected by anastomoses, becoming a network. Intercalary sectors short.

Archaemegaptilus differs from *Dictyoneurella* by its longer Sc and denser cross venation.

Species included in the Commentry shales: *Archaemegaptilus kiefferi* Meunier, 1908.

Archaemegaptilus kiefferi Meunier

Figure 46

Archaemegaptilus kiefferi Meunier, 1908: 155; Meunier, 1908: 175, fig. 3; Meunier, 1909: 138, pl. 2 fig. 2; Handlirsch, 1919: 13, fig. 15.

Although this species was erected by Meunier on a fragment of the reverse of a hind wing, the following account is based on the obverse as well.

Hind wing: length 105 mm, width 27 mm. Anterior margin straight, slightly concave near the base, separating off a narrow precostal area. Wing broadened in the middle part of its length, narrowing behind the CuA area. Apex directed backward, rounded; C, Sc and Cu covered by long hairs near the base. M touching the stem of R, near the base, but diverging from it again; r-rs area somewhat broadened, with oblique cross veins; Rs with 3 branches, first of them forking twice; MA originating near the first fork of MP; MP forked 5 times; CuP with 4 branches. Color marking in the form of small light spots.

Archaemegaptilus kiefferi shows very similar color patterns to *Dictyoptilus sepultus* (Eugereonidae) and to *Moravia convergens* Kukalová (hind wing, Calvertiellidae). *Dictyoneurella perfecta* has dark veins very similar to those of *Calvertiella permiana* and *Moraviptera reticulata* Kukalová (Calvertiellidae).

Family Megaptilidae Handlirsch

Megaptilidae Handlirsch, 1906: 80; Lameere, 1917: 102; Handlirsch, 1921: 130.
Anaxionidae Handlirsch, 1919:19.
Lithoptilidae Handlirsch, 1922: 44.

Type genus: *Megaptilus* Brongniart, 1885.

The family was based by Handlirsch on a fragment of a large fore wing of spectacular character, showing extremely dense cross venation and a large rs area, with curved Rs branches. Professor Carpenter has kindly given me for study another (undescribed) specimen of *Megaptilus* from the Westphalian of Rhode Island, represented by a hind wing. Surprisingly enough, this hind wing turns out to be extremely shortened, reaching about only half of the fore wing length. This unexpected discovery throws more light on the obscure relationships of the Megaptilidae. The peculiar type of reduction of the hind wing venation, suggestive of some Eugereonidae (e.g., *Peromaptera*), together with a general pattern of venation and cross venation, brings this family close to the Eugereonidae - Archaemegaptilidae - Dictyoneuridae - Protagrionidae - Calvertiellidae group.

The finding of this wing of *Megaptilus* enables us to solve the systematic position of another puzzling fossil — *Lithoptilus* Lameere, from Commentry. It probably represents a shortened hind wing of the same family Megaptilidae. The following account is based on *Megaptilus* (fore and hind wings) and *Lithoptilus* (hind wing).

Wings very unequal. Fore wings large and broad, hind wing somewhat narrow, reaching only about half of the fore wing length. Branches of Rs, M and Cu in fore wing curve posteriorly. Rs area very large; MA simple, MP forked several times; CuA simple; CuP and anal area with several branches. Hind wing with a very reduced rs and mp area, with curved branches of M and Cu. Cross veins in both pairs of wings extremely dense, connected by numerous anastomoses.

The family Megaptilidae is related to the Eugereonidae, as indicated by the shortened hind wings, curved branches of the main veins, nature of the branching of MP and the presence of extremely dense cross veins with numerous anastomoses.

Genera included in the Commentry shales: *Megaptilus* Brongniart, 1893; *Lithoptilus* Lameere, 1917. No other genera are known except for an undescribed specimen of *Megaptilus* in the Museum of Comparative Zoology from the Westphalian of Rhode Island.

Megaptilus Brongniart

Megaptilus Brongniart, 1885: 61; Brongniart, 1893: 373; Handlirsch, 1906: 80; Lameere, 1917: 156.

Type species: *Megaptilus blanchardi* Brongniart, 1885 (SD Handlirsch, 1906).

This genus was established by Brongniart for three species, *Megaptilus blanchardi*, *brodiei* and *scudderi*. Handlirsch (1906, p. 98) referred *brodiei* to a new genus, *Megaptiloides*, and placed it in the family Breyeriidae; he referred *scudderi* (1906, p. 118) to another new genus, *Paramegaptilus*, and transferred it to the Palaeodictyoptera incertae familiae; and he erected a new family, Megaptilidae, for *blanchardi*.

The following account is based on the type species (fore wing) and a hind wing of *Megaptilus* species (Westphalian of Rhode Island).

Wing membrane usually dark, sometimes with light oval spots arranged in longitudinal rows. Fore wings broad and short, broadest at about the middle. Sc long, remote from C in the apical third; first branch of Rs originating before the middle of the wing, forked several times; m area much larger than cu area. Anal area relatively small, with several branches. Hind wing with obtuse apical part and with very narrowed rs and mp areas. Cross venation equally dense in both wings.

Megaptilus (hind wing) differs from *Lithoptilus* Lameere (hind wing) by Sc, R, and stem of Rs being parallel and curved, with the more dense cross venation with more anastomoses.

Species included in the Commentry shales: *Megaptilus blanchardi* Brongniart, 1885. Occurrence elsewhere: *Megaptilus* species (Westphalian, Rhode Island).

Megaptilus blanchardi Brongniart
Figure 47

Megaptilus blanchardi Brongniart, 1885: 61; Brongniart, 1893: 374; pl. 21, fig. 3; Handlirsch, 1906: 80, pl. 10, fig. 9; Handlirsch, 1921: 130, fig. 56; Handlirsch, 1919: 13.

This species was erected by Brongniart upon specimen 21-3, a large fore wing fragment. Using glycerin, I was able to work out

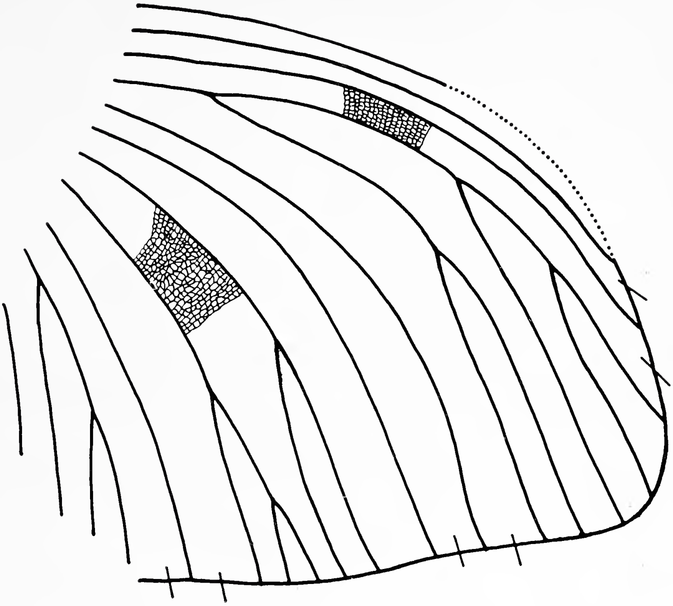

Figure 48. *Megaptilus* sp.; hind wing; Westphalian, Rhode Island.

a larger part of the anal area than shown in Brongniart's original figure.

At first, Brongniart believed that the wing of *blanchardi* belonged to the large insect's body described by him (1882) as *Titanophasma fayoli* but in 1893 (p. 374) he expressed doubt about that. Lameere (1917, p. 156) considered the small wing fragment designated as *Titanoptera maculata* Brongniart, 1893, as part of the anal area of *M. blanchardi.* Unfortunately, he did not find this fragment in the collections at the Paris Museum.

Fore wing fragment: length 144 mm, width 51 mm. Color markings light, oval, distributed along the stem of Rs between the branches and forming an irregular row in the posterior third of the wing. Wing broadest at the end of CuA, narrowing towards the base. Posterior margin concave at CuA and MA. Apex directed backwards. Subcostal area and sc-r area equally broad in the apical third; Sc, R and stem of Rs parallel and curved in the distal half; Rs with a long row of about 5 curved branches, widely distant from each other. First branch of Rs forked three times; MP forked 5 times, with widely separated branches; CuP with only one, wide fork. Branches of main veins near posterior margin S-shaped. Anal area with about 7 relatively densely arranged branches, some of them with short forks. Cross veins in sc-r area dense but simple, not connected by anastomoses.

Megaptilus blanchardi recalls *Dictyoptilus sepultus* (Eugereonidae) by its posteriorly curved veins with S-shaped tips along the posterior margin, by the fore wing broadening at the end of CuA and by the wide fork of MP. Also, the cross venation, though denser, is not very different from that of *sepultus,* either. The hind wing of *Lithoptilus boulei* (Meunier, 1908) shows the same S-shaped tips of M and Cu branches along the posterior margin as the fore wing of *blanchardi.*

Genus *Lithoptilus* Lameere

Lithoptilus Lameere, 1917: 157; Demoulin, 1958: 3.
Anaxion Handlirsch, 1919: 19.

Type species: *Lithoptilus boulei* (Meunier, 1908) (OD)

This genus was erected by Lameere (1917, p. 157) for *Archaeoptilus boulei* Meunier, 1908. Lameere noted that this genus seemed closely related to *Homoioptera,* differing only in the shorter and broader wings but he could not determine to which pair of wings the type specimen belonged. Handlirsch, noting the broad subcostal area, assumed the type specimen to be a fore wing and, having overlooked Lameere's paper, erected a new genus for *boulei, Anaxion* (Anaxionidae), which he associated with the Breyeriidae. Finally, Demoulin (1958) without seeing any of the specimens, concluded that *Lithoptilus* was based on a hind wing, vestigial as in most recent Ephemeroptera. As the closest related genus he suggested *Rhabdoptilus* and referred both genera to the Rhabdoptilidae Handlirsch. Demoulin's statement about the vestigial hind wing character of the type specimen of *Lithoptilus* is correct but there is no indication of relationship to *Rhabdoptilus.*

The systematic position of *Lithoptilus* becomes much clearer after the shortened hind wings of Eugereonidae and Megaptilidae are studied. Although *Lithoptilus* recalls some Eugereonidae by the shape of the hind wing (e.g., *Peromaptera*), the venational pattern and cross veins are most like those of *Megaptilus.* The range of variation of the hind wing shape seems to have been wide in the Eugereonidae and it probabaly was also in the Megaptilidae.

The following account is based upon the hind wing of *Lithoptilus boulei* (Meunier).

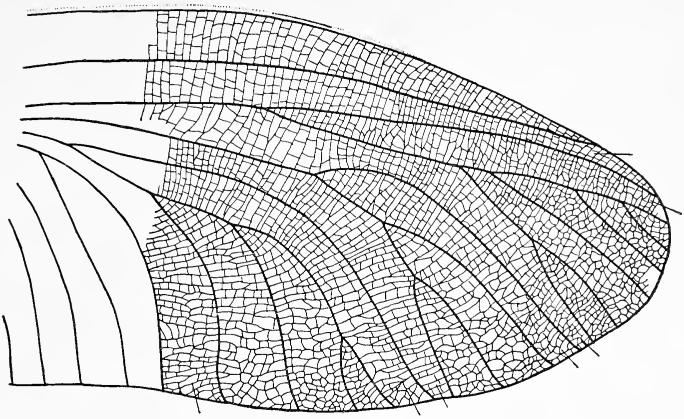

Figure 49. *Lithoptilus boulei* (Meunier); hind wing. Holotype.

Hind wing very shortened and broad, especially in the apical part. Anterior and posterior margins almost parallel. Sc long, subcostal area broad; Rs originating at about midwing; Rs area extremely small; M dividing at the level of the origin of Rs, MA simple, MP forking; Cu dividing within the first third of the wing length; CuA simple; CuP with several branches. Cross veins coarse and very dense, connected by numerous anastomoses, sometimes turning into a network.

Lithoptilus Lameere differs from *Megaptilus* (in the hind wing) by the broad subcostal area, straight Sc, R and Rs; by M dividing more distally; and by the somewhat less dense cross venation.

Species included in Commentry shales: *Lithoptilus boulei* (Meunier, 1908).

Lithoptilus boulei (Meunier)

Figure 49

Archaeoptilus boulei Meunier, 1908: 153; Meunier, 1908: 35, fig. 1; Meunier, 1909: 131, pl. 1, fig. 1.
Lithoptilus boulei Lameere, 1917: 157; Demoulin, 1958: 1-5.
Anaxion boulei Handlirsch, 1919: 19, fig. 21.

This species is monotypic, based by Meunier on a vestigial hind wing of a large palaeodictyopteron. Following the weak imprint of the veins on the matrix, I was able to work out some of the more proximal part of the type specimen.

Hind wing fragment: length 66 mm, width 40 mm. Anterior margin abruptly curved towards the apex. Posterior margin convex at the end of the anal area. Apex rounded, directed somewhat anteriorly. Subcostal and sc-r areas broad; Rl straight, Rs sending off 4 very short oblique branches, the first of them being forked. MP twice forked; CuP with a series of four branches. Anal area relatively large with long branches, perpendicular to posterior margin. Branches of M and Cu with S-shaped ends. Cross veins forming a network along the posterior part of the wing.

The broad subcostal and sc-r areas, together with straight course of Sc and R are very unusual for a hind wing. Nevertheless, the same straightening of Sc and R and broadening of sc-r area are present in the very shortened hind wing of *Peromaptera filholi* Brongniart, also.

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THE PREDATORY BEHAVIOR OF SOME ARANEID SPIDERS AND THE ORIGIN OF IMMOBILIZATION WRAPPING*

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The evolution of predatory behavior in web building spiders is a subject of considerable interest. Functionally the spider has to solve two problems immediately after prey strikes the web. It has to locate the prey and then to attack it in such a way that the prey is prevented from escaping and is subdued. The spider may then be confronted with further problems involved in freeing the prey from the web and in transporting it to a feeding or storage site. Spiders may attack solely by biting, may bite some types of prey and wrap others in silk, or may rely entirely on silk as an attack weapon. Silk may also be used, after the initial attack, at other stages in the process of prey capture. Eberhard (1967) has reviewed the possible stages in the evolution of the use of silk for attack. By comparing the uses of silk in the predatory behavior of several representatives of a number of families of web building spiders he arrived at the conclusion that immobilization by wrapping in silk is derived from post immobilization wrapping. We fully agree with his conclusions but feel that a comprehensive treatment of the subject requires a more detailed consideration of the uses of silk by araneid spiders. Araneids may use the wrapping process at four different (and in all probability, functionally distinct) stages in the prey capture sequence. Furthermore, the behavioral components of the wrapping process are not necessarily common to all four cases. If these facts are considered, the picture of the evolution of wrapping behavior by web building spiders becomes more complex than Eberhard (ibid) assumed.

This paper examines data on the predatory use of silk by *Nephila clavipes* (Linnaeus), *Argiope argentata* (Fabricius), *A. savingnyi* Levi and *A. florida* Chamberlin & Ivie, as well as other araneid spiders. In addition, we report on an experimental investigation into the functional efficiency of two basic attack strategies used by these spiders. We finally propose a scheme by which complex predatory repertoires can be derived from simpler ones by an essentially additive process.

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Terminology

Confusion can arise over the use of the terms immobilization and post immobilization. This is because the word immobile is frequently regarded as synonymous with motionless. This problem of terminology is a difficult one. Robinson (1969) used the expression restraint wrapping in preference to immobilization wrapping since restraint does not have connotations of motionlessness. However, if restraint is used as a word to qualify biting attacks, two separate effects may be confounded. Thus the bite may effect restraint simply because the prey is held in the chelicerae, whereas the addition of poison, by means of the bite, ensures a degree of immobilization after the spider releases its hold. In the interests of consistency we have decided to refer to wrapping used as a means of initial restraint as immobilization wrapping and to use "post immobilization wrapping" to designate all the forms of wrapping that occur after an initial atack by biting. This usage is not meant to imply that immobilization wrapping renders the prey absolutely motionless, or that post immobilization wrapping is applied to completely motionless prey. Immobilization wrapping does seem to *effectively* immobilize prey by preventing those forms of movement which could result in escape from the web. Similarly the immobilization bite does not necessarily render the prey motionless but does reduce the level of movements to a stage at which the spider can *safely* stop biting. Eberhard (1967, p. 177) seems to recognize this distinction without explicitly stating it. Thus, in describing the behavior of diguetid spiders, he refers to the (immobilization) bite being maintained "until the prey's struggles subsided", but also states that the prey were "usually still twitching" when the bite ceased.

Wrapping by *Nephila clavipes*

Data on the behavior of *Nephila clavipes* are derived from a recent study by Robinson & Mirick (in prep.). *Nephila clavipes* bites all prey and does not enswathe prey in silk prior to biting. Wrapping occurs in three sets of circumstances:

1. Wrapping occurs at the feeding site (the hub of the web) and is there applied to prey which have previously been treated in two different ways. All prey small enough to be pulled from the web at the capture site and carried to the hub in the jaws are wrapped on arrival at the hub. All prey which have been wrapped at the capture site (after biting) and subsequently carried to the hub in the jaws, are rewrapped at the hub. This is post immobilization wrapping at the feeding site.

2. Wrapping occurs at the capture site if the prey cannot be pulled from the web after the immobilization bite. Such prey is wrapped, cut from the web, and then transported to the hub. This is post immobilization wrapping at the capture site, type 1.
3. Wrapping occurs at the capture site *after* the prey has been freed from the web by pulling, if it is too large to be carried in the jaws. It is then carried, suspended on silk, from leg IV. This is post immobilization wrapping at the capture site, type 2.

Wrapping by *Argiope* species

The predatory behavior of *Argiope argentata* has recently been described by Robinson (1969), and further analysis is given by Robinson & Olazarri *(in press)*. Details of the predatory behavior of *A. savignyi* and *A. florida* are essentially similar (Robinson & Robinson, *in prep.*).

All the above species of *Argiope*, and many other araneids, use silk as an attack weapon, prior to biting, and in this respect their predatory behavior differs fundamentally from that of *Nephila clavipes*. The *Argiope* species also wrap prey in silk in other circumstances:

1. Prey which have been seized in the jaws and pulled from the web are subsequently wrapped at the hub (see *Nephila* 1.). Prey wrapped at the capture site but transported to the hub in the jaws are also wrapped at the hub. This is post immobilization wrapping at the feeding site.
2. Prey which have been immobilized by biting are wrapped at the capture site following the long bite. The greater proportion of lepidopteran prey is treated in this way. This is post immobilization wrapping at the capture site.
3. Prey which are carried in the jaws and become tangled in the web during transportation are wrapped and carried on silk. This is post immobilization wrapping during transportation.

Immobilization wrapping, post immobilization wrapping at the capture site, and post immobilization wrapping during transportation also occur in the case of *Araneus diadematus* (Peters 1931, 1933a, 1933b).

Two forms of immobilization wrapping occur in *A. argentata*, *A. savignyi* and *A. florida*. These differ in the initial behavioral component which has been called *throwing* (Robinson 1969). In this behavior the spider throws skeins of silk over the prey, using both legs IV to direct the throw. In one form of immobilization wrapping the spider is in contact with the prey whilst throwing, whereas in the more complex form it throws swathes of silk over the prey from a distance. In an as yet unidentified species of *Eriophora* that we have studied, the spider actually turns to face away from the prey during non-contact throwing.

The behavior of *Argiope argentata* following the wrap/short bite couplet is important to our consideration of the functional aspects of immobilization wrapping. After the wrap/short bite sequence the spider leaves the prey *in situ* and returns to the hub. Eventually, after a variable period of time, it returns to the prey, cuts it out of the web and transports it to the hub. We believe that this period during which the spider leaves the prey and returns to active monitoring of the web has important implications for the functional interpretation of immobilization wrapping.

After the long bite/wrap sequence the spider does not leave the prey *in situ* but proceeds to cut it from the web and carry it to the hub. If, however, there is already previously caught prey at the hub, the spider leaves the newly caught prey at the capture site and returns to feed on the previously caught prey. Peters (1931) notes that *Araneus diadematus* also leaves prey *in situ* if it already has prey at the hub.

Functional considerations

We have so far described araneids with one and two basic methods of attack (biting alone and biting or wrapping). In both cases there are distinct forms of employment of post immobilization wrapping. Eberhard (1967) has argued that post immobilization wrapping at the feeding site may have been the first type of wrapping behavior to appear, followed by post immobilization wrapping at the capture site. Immobilization wrapping could then be derived from post immobilization wrapping at the capture site. In terms of function Eberhard (*ibid*, p. 180) comments "wrapping may have originated as a post-immobilization process designed to free the spider for subsequent attacks".

It certainly seems reasonable to assume that post immobilization wrapping at the feeding site would ensure that the spider could make further attacks without dropping, or otherwise losing, the previously caught prey. (In fact, we have evidence that when *Nephila clavipes* omits this behavior, under the pressure of a rapid succession of prey, it can lose prey that it has already caught as it rushes to attack new prey; see page 497). Post immobilization wrapping at the capture site is another matter. In the case of *Nephila* it does not immediately free the spider to make new attacks. After such wrapping *Nephila* carries the prey to the hub and never leaves it *in situ*. Post immobilization wrapping at the capture site, by *Nephila*, must, therefore, have other functions. It certainly reinforces the immobilization achieved by the biting attack, as must post immobilization wrapping at the feeding site. There are, however, good grounds for assuming that this is not the primary function. Capture site wrapping, type 1, can be elicited by manipulating the prey, experimentally, in such a way that it cannot be pulled from the web by the spider. It is then a response to a failure of the prey removal process (Robinson & Mirick, *in prep.*). It seems reasonable to suppose that such capture site wrapping functions primarily to allow the spider to cut the prey from the web without losing it. The prey package resulting from the wrapping process is compact, partially disentangled from the viscid spiral, and securely attached to a radial web member. Eberhard (1967, p. 177) reported an instance in which a diguetid spider anchored a large prey to the web (with silk) before releasing it from the chelicerae and removing it from the web. This seems to be a functionally similar process to the capture site wrapping, type 1, by *Nephila.*

When wrapping occurs at the capture site, after the prey has been freed from the web by pulling (type 2), the function seems to be to facilitate transportation to the hub. After such wrapping the prey is carried suspended from leg IV, and not in the jaws. Both *Argiope argentata* and *Araneus diadematus* carry prey from below the hub, and above a certain weight range, on silk rather than in the jaws (Robinson 1969, Peters 1933b). In these spiders, and *Argiope savignyi*, *A. florida* and *Eriophora* sp., this carrying technique occurs after post immobilization wrapping at the capture site, type 1. All the spiders that we have studied, i.e., the *Argiope* spp., *Nephila clavipes*, and *Eriophora* sp., build webs which are inclined to the perpendicular to a greater or lesser extent. The spider rests on the undersurface of the web and almost always carries its prey along that surface, or close to it. The lower portion of the web (below the hub) is normally greater in area than the upper portion. When carrying prey from the lower portion the spider is walking against the slope. This means that prey carried in the jaws, and therefore partially beneath the spider, are in a position which potentially favors entanglement during transportation. Prey carried beneath the spider, on silk, hang away from the web and are thus much less likely to become entangled during transportation. The position is reversed in the upper part of the web. There, prey carried on silk would tend to hang awkwardly against the spider's body or legs. *Argiope argentata* does not carry prey from the upper part of the web on silk. Prey of a weight which would be carried on silk in the lower web are often carried in the jaws from the upper web. Very heavy prey, in the upper web, are moved to the hub, after wrapping, by a complex process which has been called the "derrick technique" (Robinson & Olazarri, *in press*). Thus the role of post immobilization wrapping, at the capture site, in facilitating transportation, is probably most clearly illustrated by consideration of activities in the lower part of the web. Transportation of prey with long and projecting appendages must inevitably be facilitated by the "trussing" effect of wrapping, irrespective of the means of transportation.

Once post immobilization wrapping at the capture site, type 1, has evolved it may be exploited for a further function. Prey can then be safely left *in situ* and the process of removal from the web, and transportation, can be deferred until later. If the spider already has prey at the hub it may be advantageous to return from attacks as quickly as possible, and only cut out and carry further prey when it is ready to feed upon them. This process would split up a single sequence into two shorter sub-sequences. *Nephila* does not do this but transports all prey and stores them at the hub. All the *Argiope* species that we have studied store prey, *in situ*, in the web. (Storing prey in the web may increase the danger that they will be stolen by theridiid kleptoparasites. These are frequently found in association with the webs of *Nephila clavipes* and *Argiope argentata* in Panama. The very large size of *Nephila* webs may increase the spider's difficulties in detecting the activities of the kleptoparasites and this could account for the fact that *Nephila* does not store prey in the web.)

The step from post immobilization wrapping at the capture site to attack wrapping must confer adaptive advantages. It seems improbable that these are related to the immediacy of escape prevention since the three species of *Argiope* described above, and *Araneus diadematus*, retain the immobilization bite for precisely those prey that have rapid escape potentials. (After Robinson, 1969, reported the use of the immobilization bite for non vibrating lepidopterans, as well as lepidopterans in general, we have found that this is true for several other, as yet undetermined, species of tropical araneids.) Where attack wrapping involves the prey being trapped under layers of silk thrown over it from a distance, it may enable spiders to attack prey with a diminished risk of injury to themselves. Certainly we have seen a *Nephila* lose a portion of its leg to the biting mouthparts of a katydid during a close quarters attack. In fact, *Nephila* attacks large prey with legs I and II raised off the web and flexed back, and often darts forward to make a short bite and then backs off before attacking again. A succession of short bites and retreats may thus occur.

Wrapping attacks may be initiated while the spider is actually standing on the prey. These may still protect the spider from injury since it can maintain a greater distance between itself and the prey than is possible during the more intimate bite. We feel, however, that immobilization wrapping may confer a further and very important advantage. It may help to achieve an economy of time spent away from the hub while attacking and immobilizing prey, as Robinson (1969) suggested. Any reduction in the time spent in capturing prey must enable the spider to be in a better position to respond to further prey before they can escape from the web. Additionally, if the spider is more vulnerable to predators when it is attacking prey, it would be advantageous to reduce time spent out on the web.

There is a statistically significant difference between the duration of the bite given before wrapping (in the long bite/wrap sequence) and the duration of the bite given after wrapping (in the wrap/short bite sequence). The long bite may be long simply because the spider has to wait for it to take effect before it can safely release the prey and commence wrapping. In the case of immobilization wrapping, the prey is secured before the bite is given, and the spider gives a short bite and retires to the hub to resume "monitoring" the web. The short bite may inject a smaller venom dose, or one which is slower acting. However, since the prey is wrapped, it can safely be left while the venom takes effect. The effects on living prey of the two types of bite are under investigation. There is certainly a difference in the time spent at the capture site when the spider uses the two types of attack against the same type of prey (Robinson, 1969, p. 170).

The above conclusions about function can be summarized as follows:

1. *Post immobilization wrapping at the feeding site* results in the prey being safely anchored to the web by silk. It functions to permit the spider to make further attacks without losing the prey "in hand". In effect, the spider does not have to lose time securing the prey to the web at the moment when a new prey strikes the web (i.e., when it needs to be able to make an immediate attack). That this is a correct interpretation is suggested by the fact that those prey which are carried suspended on a silk thread are *not* wrapped

at the hub, but merely attached by the transport thread, on arrival. Thus the transport thread functions as an attachment thread. Wrapped prey that are carried in the jaws do not have a transport thread and *are* wrapped again at the hub.

2. *Post immobilization wrapping at the capture site* reinforces the immobilization achieved by the poisoning bite, facilitates the removal of strongly adhering prey from the web, and enables the spider to safely store prey *in situ*. In addition, it may facilitate the transportation of large or heavy prey. The behavior of *Nephila* provides evidence for the separate functions associated with prey removal and transportation. Thus prey which *Nephila* can remove by pulling are not wrapped in the web but may be wrapped before being carried to the hub. *Argiope* only pulls very small prey from the web, and cuts out all other prey after wrapping has produced a compact prey package. The occurrence of *post immobilization wrapping during transportation* is a further example of wrapping functioning to facilitate transportation.

3. *Immobilization wrapping* effectively immobilizes prey, and compared with immobilization biting, allows the spider to attack without bringing its more vital parts into direct contact with the prey. It may thus be less dangerous than immobilization biting. Furthermore it is economical of time and this may be a very important factor.

As far as we are aware there are no araneids that do not bite after immobilization wrapping. Uloborids, on the other hand, rely exclusively on wrapping for prey immobilization (Eberhard 1967). The short bite of araneids, or at least those that we have studied, contains some poison since prey removed from the prey package after the short bite eventually become completely quiescent. It therefore seems probable that the short bite supplements the effect of the immobilization wrapping. Uloborids are all quite small spiders and it seems possible that total reliance on immobilization wrapping might be less efficient in the case of the araneids (which may rely heavily on stronger and more active prey).

The performance of *Argiope argentata* and *Nephila clavipes* confronted with a rapid succession of small prey

In the above discussion of the functional aspects of wrapping behavior we have stressed the possibility that economy of time spent in prey capture sequences may be obtained by leaving prey *in situ* after it is wrapped. We have also pointed out that this is possible as a consequence of both immobilization wrapping and post immobilization wrapping at the capture site. Economy in time spent away

Table 1.

A comparison of times spent away from the hub of the web by *Argiope argentata* and *Nephila clavipes* with *Trigona* sp. as prey.

A. Uninterrupted sequence (single *Trigona*). Prey n = 50, Spider n = 10 of each sp.

	Mean total time.	Range	Standard deviation	Standard error of mean
Nephila	70 secs.	44-108	15	2.1
Argiope	77 secs.	38-192	40	5.6

B. Ten *Trigona* per spider, arriving at 30 second intervals (see text for explanation). Data from 50 successful sequences of attack by 10 spiders of each species.

	Mean total time.	Range	Standard deviation	Standard error of mean
Nephila	30 secs.	14-65	11.8	1.7
Argiope	18.7 secs.	7-33	7.8	1.1

Times in A are for the total prey capture sequence: attack, removal from the web, transportation, storage at the hub. In B the times for *Argiope* are for attack, storage in the web and the spiders' return to the hub (since the spider omitted removal of the prey from the web and its transportation).

from the hub may be especially critical under conditions when prey arrive in rapid succession. Both *Nephila clavipes* and *Argiope argentata* deal with stingless bees (*Trigona* sp.) in predatory sequences of similar duration, see Table 1. However, *Argiope* uses immobilization wrapping whereas *Nephila* does not wrap the bees until it reaches the hub. *Agriope* has the potential of being able to omit the immediate removal of the prey from the web, and its transportation, whereas *Nephila* has not. We, therefore, decided to test the two spiders under conditions when several prey were arriving at the web in succession. To do this we allowed one bee to fly towards either a *Nephila* or an *Argiope* web every thirty seconds until ten prey had flown at the web. The *Trigona* were released from a glass tube held 18″ from the web and 6″ vertically below the spider. By having a light source behind the web we ensured that the bees would fly towards the web rather than in any other direction. The dispersion of the bees on hitting the web was approximately standardized by the constant position of the escape tube. Each of 20 well fed *Nephila* and 20 well fed *Argiope* (mature females in each case) were tested with one succession of 10 bees. We made notes of the fate of each insect and timed and noted the behavior of the spider. The results are shown in Figure 1. This reveals a basic difference in the prey

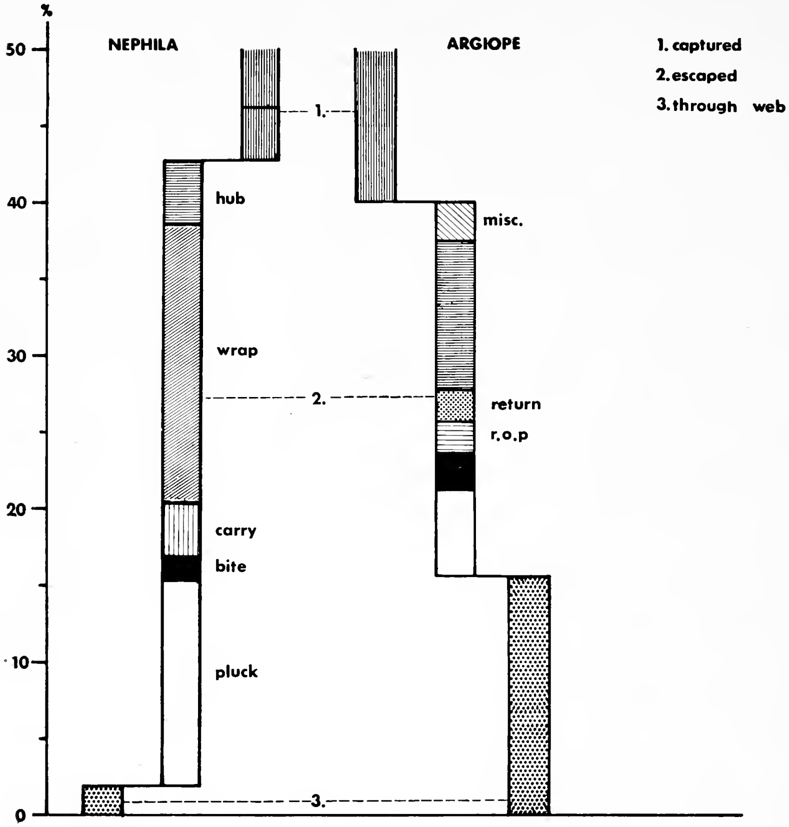
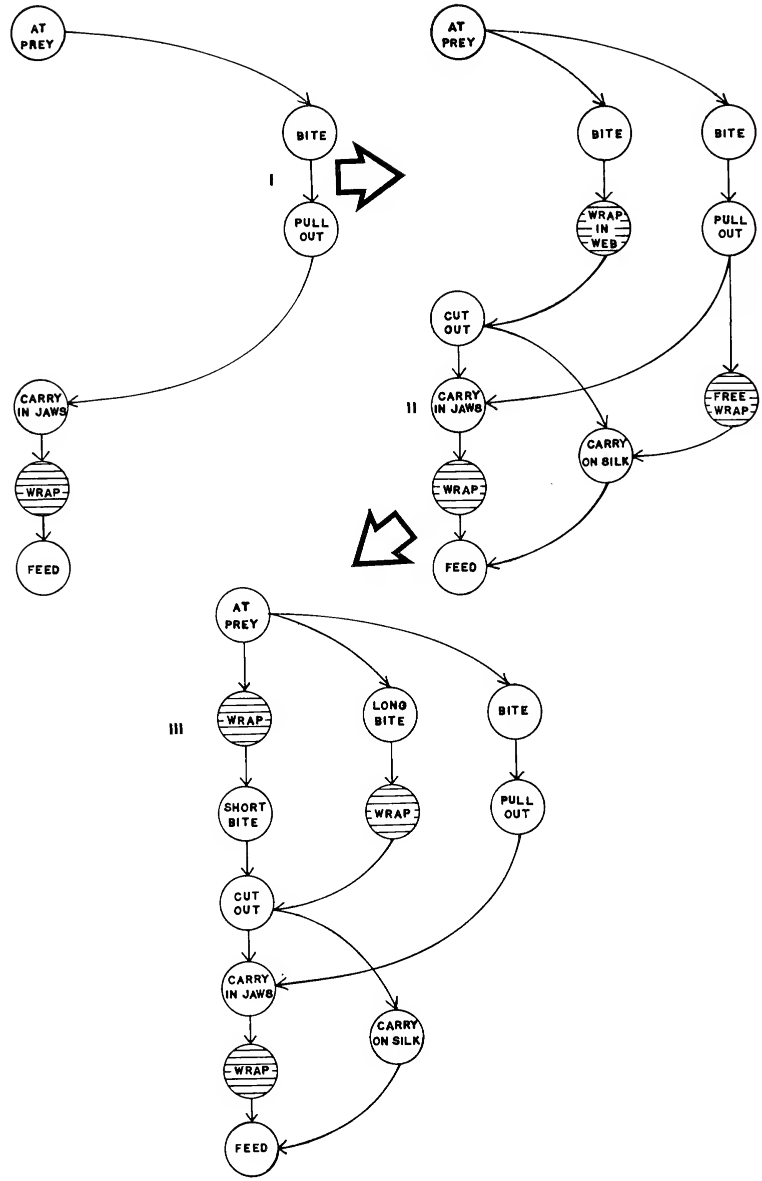


Figure 1. Stepped histograms showing, in a simplified and condensed form, the results of the experiments in which *Nephila clavipes* and *Argiope argentata* were presented with a succession of small prey. Details of the experiment are given in the text. The basal histogram (3) of each block shows the percentage of prey passing through the webs. The center histogram (2) shows the percentage escaping after hitting the web, and the behavior of the spider at the time the prey escaped. The top histogram (1) of each block shows the percentage of prey captured (reading from 100% by subtraction). In the case of *Nephila* some prey were lost after capture and these are shown in the lower part of the capture column. Number of prey presented to each species: 200.

capture efficiency of the two webs for small insects. Thus (basal columns, Figure 1), 15.5% of the *Trigona* flew straight through the *Argiope* webs, missing the viscid spiral, or touching the web momentarily. Only 2% of the *Trigona* passed through the *Nephila* webs. Since we started, in all cases, with fresh webs, this result is not likely to be biased by the effects of the prey arriving early in the sequence on the state of the web for later arrivals. In fact, in the *Argiope* results, escapes through the webs in the first five of the sequence were in the relationship 17:14 compared with escapes in the second five of the sequence.

The second columns in each graph show the number of escapes occurring after the prey were in the web and an analysis of the behavior of the spider at the time the prey escaped. *Argiope* missed only 24.5% of the prey striking the web whereas *Nephila* missed 40.5%. If we add losses through the web to these figures we find that *Argiope* lost 40%, and *Nephila* 42.5% of potential prey flying at the web. In addition, as mentioned earlier, *Nephila* incurred further losses of captured prey when it rushed into attack carrying these prey in its jaws (having omitted post immobilization wrapping at the feeding site). An additional 3.5% of prey were lost in this way. The total absolute losses for *Nephila* were thus 46%.

The fact that 15.5% of the bees passed through the *Argiope* web meant that this spider was under reduced pressure during the five minute experimental period compared with *Nephila.* However, analysis of the data shows that *Argiope* achieved a very considerable acceleration of predatory behavior under the conditions of the experiment, and became significantly faster than *Nephila* (see Table 1). A substantial part of this reduction was achieved by the omission of the cut out, carry, and wrap at hub stages and is therefore a striking illustration of the advantage of being able to leave immobilized prey *in situ*. Prey losses by *Nephila* occurred principally when it was performing activities at the hub (post immobilization wrapping and turning to resume its normal head down position). The attack phase (biting) was usually completed by the time the next prey arrived. A surprising number of escapes occurred while *Nephila* was locating the prey (i.e., at the pluck stage). These losses may be attributable to the fact that prey location did not occur at the moment of impact but was delayed by preceding activities until the prey had almost freed itself. *Argiope* was back at the hub, unencumbered by prey, when nearly half of the losses occurred. It seems quite possible that, in this case, the presence of numbers of wrapped prey in the web may complicate further prey location. We also got


I
AT PREY
BITE
PULL OUT
CARRY IN JAWS
WRAP
FEED
II
AT PREY
BITE
WRAP IN WEB
BITE
PULL OUT
CUT OUT
CARRY IN JAWS
FREE WRAP
CARRY ON SILK
WRAP
FEED
III
AT PREY
WRAP
LONG BITE
BITE
SHORT BITE
WRAP
PULL OUT
CUT OUT
CARRY IN JAWS
CARRY ON SILK
WRAP
FEED

the distinct impression, that, in at least some of these cases, the spider was ignoring newly arrived prey.

In a sense, the conditions of this experiment were purely arbitrary, and may never even be approximated under natural conditions. (We have, however, records of large numbers of social insects being caught in short periods.) The experiment does show that *Argiope* can compensate for its (for small prey) much less efficient web under certain conditions. We also believe that immobilization wrapping, and the subsequent possibility of quickly leaving the prey *in situ* is the key to this success.

Conclusion

We feel that it is possible to reconstruct the possible steps in the evolution of immobilization wrapping by considering the behavior of existing araneid spiders. This process eliminates the necessity to extrapolate from the behavior of spiders of other families which may be very distant from the line of araneid evolution. The explanation we propose below also accounts for the existence of several forms of attack behavior in some of the araneids which have developed attack by wrapping. We offer an adaptive function for each step in the process and envisage the evolution of complex predatory patterns in araneids to have been additive.

We propose the following scheme:

Stage I. All prey overcome by biting. Prey pulled from the web in the jaws and carried to the hub where post immobilization wrapping occurs. This stage is not found in any araneid whose predatory behavior is described but is represented in the behavior of *Nephila* and *Argiope* to small prey. Function of wrapping at the hub: to prevent loss of prey during subsequent attacks.

Figure 2. An additive scheme illustrating the stages in the evolution of prey wrapping by araneids as proposed by the authors. The model for each stage is simplified, behavior prior to arrival at the prey is omitted and the spider's capacity to interrupt a sequence before the *cut out* stage is not shown. The circles represent a behavioral unit and where more than one arrow leaves, or enters, a circle the behavior may be followed, or preceded, by the behaviors indicated. Stage 1 is hypothetical, but occurs as part of Stages 2 & 3. Stage 2 represents the prey capture sequences of *Nephila clavipes*, and with the omission of *free wrap* is a model of the behavior of some species of *Micrathena* and *Gasteracantha*. Stage 3 occurs in *Argiope* spp. and *Eriophora* sp., and may be typical of most "advanced" araneids.

Stage 2. (a) All prey overcome by biting. Post immobilization wrapping occurs at the capture site when the prey cannot be pulled from the web in the jaws. This stage occurs in *Nephila clavipes*. Function of wrapping enmeshed prey at the capture site: to permit the spider to safely remove its chelicerae from the prey for use in cutting it from the web. All prey stored at the hub.

(b) All prey overcome by biting. In addition to post immobilization wrapping of enmeshed prey there is wrapping of prey freed from the web by pulling. This wrapping occurs before transportation on silk. Function: to permit the safe transportation of prey too large to be carried in the jaws. This stage also occurs in *Nephila clavipes*. All prey carried to the hub for storage.

Stage 3. All prey overcome by biting. Post immobilization wrapping occurs at the capture site where it functions as in Stage 2. Additionally, after post immobilization wrapping at the capture site prey may be left *in situ* if the spider already has prey at the hub. Such wrapping acquires a new function: it enables the spider to safely store the prey at the capture site and omit immediate transportation to the hub. This stage is found in some species of *Micrathena* and *Gasteracantha*. Some prey stored in the web.

Stage 4. Immobilization biting retained for those prey which can escape rapidly from the web, other prey overcome by immobilization wrapping followed by a short bite. Immobilization wrapping similar in morphology to post immobilization wrapping at the capture site. Function of immobilization wrapping: to increase speed of prey handling, or conversely, to decrease the time spent away from the hub. Post immobilization wrapping at capture site retained for prey overcome by biting (functions: as in 3, above). Post immobilization wrapping at hub retained for small prey which can be pulled from the web, and also for others which are carried to the hub in the jaws (function: as in 2 above). Some or all of these behaviors shown by *Argiope argentata*, *A. savignyi*, *A. florida* (and probably by other *Argiope* species), also by *Araneus diadematus* (Peters 1931, 1933a) and probably many other araneids. Prey stored in web.

Stage 5. Immobilization biting retained for some prey; other prey overcome by immobilization wrapping. Immobilization wrapping of large prey includes a new behavioral component — in the early stages swathes of silk are thrown over the prey from a distance. The spider may even turn to face away from the prey whilst throwing. Function of new type of throwing: the protection of the spider from the defensive armature of the prey. Found in *Argiope* spp. also *Eriophora* sp. Prey stored in the web. Figure 2 illustrates the additive nature of this scheme.

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