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SOME ASPECTS OF THE EXTERNAL MORPHOLOGY OF
LARVAL OWLFLIES (NEUROPTERA: ASCALAPHIDAE),
WITH PARTICULAR REFERENCE TO
ULULODES AND *ASCALOPTYNX*

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INTRODUCTION

It is widely known and accepted among evolutionary biologists that the selective pressures upon the immature stages of an organism may be very different from those upon the adult form. This principle is especially true of the endopterygote (holometabolous) insects: in these, there can be seen a nearly complete dissociation of the larva from the adult, manifested both biologically and morphologically. Thus it often happens that phylogenies based upon features of the immature endopterygote insect differ sharply from those constructed from the adult; ideally, both kinds of information should be available to and utilized by the taxonomist.

The Neuroptera** is thought to be the most generalized and primitive endopterygote order, and as such is considered to include forms that are closest to the common ancestor of all Endopterygota. Such families as Sialidae, Corydalidae and Raphidiidae express their primitive phylogenetic positions by the relatively small degree of biological and morphological divergence exhibited between larva and adult. Other families and complexes of families within the Neuroptera, notably the superfamily Myrmeleontoidea (ant lions and their relatives), are highly specialized, possessing larval forms that in no way resemble the adults. The larvae of most myr-

*Parts of this paper are adapted from a thesis submitted to the Department of Biology at Harvard University in partial fulfillment of the requirements of the PhD degree.

**This term is used in the wide sense, including suborders Megaloptera, Raphidioidea and Planipennia.

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meleontoid insects are cryptic in habits and coloration and often difficult to rear to adulthood. For these reasons, few have been reliably associated with adult forms, so taxonomic and phylogenetic studies have necessarily been based primarily upon the morphology of preserved imagos. In the myrmeleontoid family Ascalaphidae, larval-adult associations have been achieved for only five or possibly six of 65 described genera (MacLeod, 1970). Additionally, all of these published associations are within one of the two ascalaphid subfamilies, the Ascalaphinae; no neuroptyngine (=ascaloptyngine) larva has been formally described, despite the fact that nearly one third of ascalaphid genera are contained in the latter subfamily (Weele, 1908).

Only a few authors have made serious attempts to bring biological information about the immatures to bear upon the problems of phylogeny within the Neuroptera in general and Ascalaphidae in particular. The first of these was Hagen (1873), who described sixteen larval "types" within the Ascalaphidae and correctly assessed the taxonomic importance of numerous larval characters, but failed to establish strong evidence for larval-adult relationship in most cases. Navás (1914, 1915), like Hagen, stressed the importance of such larval features as the number and distribution of lateral abdominal scoli (extensions), particularly in separating the split-eyed (Ascalaphinae) from the entire-eyed (Neuroptynginae) ascalaphid subfamilies. However, his papers are crudely illustrated and suffer from the same (if not more) uncertainty of larval identity as do Hagen's; it is by no means certain or even likely that his assignment of several larvae to the subfamily Neuroptynginae is correct. Withycombe's work (1925) is far more ambitious, important, and accurate, assembling a large body of behavioral, physiological and morphological data on immature Neuroptera. Since he was not seeking evolutionary relationships within families like the Ascalaphidae but rather among all neuropteran families, Withycombe did not usually require or attempt species-level identifications. Finally, MacLeod (1964) produced a thorough, well-reasoned and superbly illustrated work on Neuroptera of a scope similar to that of Withycombe's but emphasizing comparative morphology of the larval head capsule rather than behavior and physiology. This is the first work to figure in detail the head capsule of an ascalaphid larva of the genus *Ululodes* [*U. quadrimaculata* (Say)] and to document, by rearing an adult association of a neuroptyngine ascalaphid larva [*Ascaloptynx appendiculatus* (Fabricius)]. Unfortunately, MacLeod's excel-

lent study remains unpublished, with only small parts appearing in abbreviated form in his 1970 paper on fossil neuropteran larvae.

A significantly larger number of authors have concerned themselves with evaluating the evolutionary relationships within and among neuropteran families through analysis of adult morphology and wing venation. The most important works of this type include the broad-based studies of Tillyard (1916, 1926), Adams (1958) and Shepard (1967) and the ascalaphid monographs of McLachlan (1871), Weele (1908), Navas (1913) and Orfila (1949). Papers of more limited scope on the immatures of particular ascalaphid species will be discussed in the concluding section of this study.

It is my intention eventually to re-assess the evolutionary patterns within the family Ascalaphidae, based upon morphological, behavioral, and life-cycle information pertaining to the immature stages of as many species as possible. Work toward this end was initiated in a comparative study of eggs, egg barriers (repagula) and early larval habits of two North American owlflies, *Ululodes mexicana* (McLachlan) and *Ascaloptynx furciger* (McLachlan), representing both ascalaphid subfamilies (Henry, 1972). The purposes of the present paper are (a) to provide formal generic and specific descriptions of the larvae of the above-named species, (b) to summarize key morphological differences between them and among other described forms, and (c) to suggest a tentative list of evolutionarily significant larval characters defining the ascalaphid subfamilies. The description of *Ascaloptynx furciger* is particularly useful as the first, to my knowledge, published description of a neuroptyngine (entire-eyed) owlfly larva.

Papers on the behavior and life history of *Ululodes mexicana* and *Ascaloptynx furciger* are in preparation.

ACKNOWLEDGEMENTS

Much of the larval material assembled for this study was collected while I was a graduate student at Harvard University, Cambridge, Massachusetts. Collecting trips were financed by a three-year National Science Foundation Pre-Doctoral Fellowship, a Harvard University Richmond Fellowship, and grants from the Committee on Evolutionary Biology (NSF Grant GB 27911, Reed Rollins, Harvard University, Principal Investigator). Later trips to examine material in European museums and to collect living ascalaphid larvae from Europe were arranged through an NSF Institutional Grant at The George Washington University, Washington, D.C.

Living and preserved specimens were lent or given to me by Drs. Robert E. Silberglied and Thomas Hlavac (Museum of Comparative Zoology), M. A. Kolner and F. F. Hasbrouck (Arizona State University, Tempe), and James A. Slater (University of Connecticut); to these individuals I express great appreciation. In addition, warm thanks are extended to: Nancy F. Henry, for invaluable collecting assistance in the field and moral support at home; Mr. Vincent Roth of the Southwestern Research Station, for his advice on my field work in Arizona; M. Professeur A. Haget (Université de Bordeaux) for helpful suggestions pertaining to my collecting trips in France; and Drs. C. W. Rettenmeyer, C. W. Schaefer, and J. A. Slater (University of Connecticut) for their constructive comments on the manuscript.

Special thanks are extended to my colleague, friend and former advisor Professor Frank M. Carpenter, who has been consistently encouraging and helpful to me in my work on the Neuroptera.

METHODS AND MATERIALS

Ascalaphid larvae are extremely difficult to find in the field, even with intensive litter-sifting efforts. For this reason, field-laid eggs of the two owlfly species were collected, using techniques outlined in a previous paper (Henry, 1972). Eggs of *Ascaloptynx furciger* and *Ululodes mexicana* were found in abundance during August and September in the Chiricahua and Peloncillo Mountains, within a 25 mile radius of the Southwestern Research Station of the American Museum of Natural History (SWRS) in southeastern Arizona. Elevations of egg sites ranged from 1500 to 1800 meters (see Henry, 1972). Larvae hatching from these egg masses were maintained in 15 × 60 mm plastic petri dishes, one insect per dish, on a substrate of sterile sand (*U. mexicana*) or dried leaves of oaks native to Arizona egg sites (*A. furciger*). Each isolated larva received a letter and number designation and its movements, molts, etc., were recorded in chart form. Some dishes with larvae were kept in a one cubic foot wooden cabinet with regulated photoperiod but unregulated temperature regimen; others occupied a constant temperature and photoperiod Precision Scientific/GE Model 805 incubator. Temperature in the first chamber ranged from 30°C in the "day" to 22°C at "night;" the incubator was set for a constant 29°C. Light period was normally maintained at LD (light/dark) 16:8 hours.

Newly hatched larvae of both species were fed single live *Drosophila melanogaster* (Meigen) and *D. hydei* (Sturtevant) daily for the first week. They were later fed twice a week with first and second instar nymphs of *Blattella germanica* (Linn.). Each late third (last) instar ascalaphid was fed an adult female *B. germanica* roach once a week.

Larvae in various stages of development were killed in and initially fixed and injected with Bouin's solution. After 12 to 24 hours, specimens were transferred to 70 percent ethanol or, for mild clearing of sclerotized structures, to Weaver's dissection and preservation fluid: 2 parts 40% formalin, 1 part glacial acetic acid, 8 parts chloral hydrate, and 29 parts distilled water. When greater clearing was required, warm 10 percent potassium hydroxide or Nesbitt's solution (Nesbitt, 1945) proved adequate. Very small specimens and structures were run through dehydrating solutions of alcohol and xylene and mounted in Damar on depression slides. Observation, dissection and figuring of specimens involved use of a Wild M5 stereoscopic dissecting microscope equipped with integral camera lucida, and various Bausch and Lomb compound microscopes fitted with 10 × 10 micrometer eye-piece grids.

Most of the methods outlined above apply equally well to the collection, rearing, preservation and observation of other ascalaphid immatures used incidentally in this study, including an unidentified species of *Ululodes* from central Florida and *Ascalaphus libelluloides* (Schäffer) from south-central France. Large numbers of viable eggs of the latter European species were found on low herbiage clothing rugged hillsides near the Aveyron River outside the village of Penne, in the French district of Tarn-et-Garonne.

EXTERNAL MORPHOLOGY

The characteristics that define larvae of the extant Ascalaphidae and that set this family apart from other myrmeleontoid taxa like Psychopsidae, Nymphidae, Myrmeleontidae, Nemopteridae and Stilboterygidae* have been discussed at length in the works of Withycombe (1925) and MacLeod (1964, 1970). These include (a) posterior margin of the head capsule strongly cordate, (b) pres-

*Larvae of this peculiar Australian and South American family are not sufficiently known to permit confident comparisons; immatures of Psychopsidae, Nymphidae and Nemopteridae are also poorly known.

ence of three true teeth on each mandible, (c) presence of seven lateral stemmata, one ventral and six dorsal, on each distinctly raised ocular tubercle, (d) lack of any pronounced prolongations of other specializations of the cervix, (e) presence of ten to nineteen pairs of finger-like or spatulate setose extensions called scoli, laterally fringing the thorax and abdomen, (f) ventral or lateral location of the spiracles of abdominal segments 3-8 and occasionally of all eight pairs of abdominal spiracles, and (g) fusion of the tibia and tarsus on each metathoracic leg. None of these features uniquely characterizes ascalaphid larvae to the exclusion of other myrmeleontoid families. For example, seven pairs of stemmata is typical of all Myrmeleontoidea except Psychopsidae (5) and possibly Nymphidae (6 in the larva of *Nymphes* sp.), while scoli are totally absent only in psychopsids and nemopterids. Additional characteristic ascalaphid features are shared with one to several other myrmeleontoid families: metathoracic tibio-tarsal fusion with all Myrmeleontidae and probably Stilbopterygidae (McFarland, 1968); simple cervical morphology with most nymphids, psychopsids and stilbopterygids; three mandibular teeth and raised ocular tubercles with many Myrmeleontidae and perhaps all Stilbopterygidae; and cordate head margin and spiracle pattern with a few nymphids. However, only owlflies display all of the above character states together in an unmistakable *gestalt*.

Ascalaphid larvae share with all other Myrmeleontoidea (a) a heavily sclerotized, roughly quadrate head capsule displaying a unique anteriorly-positioned, vertically oriented tentorium linking one pair of pits ("anterior" ones) on the dorsum with another pair of pits ("posterior" ones) on the venter (see figures 3 and 6, TAP and TPP); (b) robust, inwardly curved jaws with mandibular-maxillary sucking specializations typical of all planipennian Neuroptera; (c) relatively small, multisegmented, filiform antennae, each with enlarged scape and inconspicuous pedicel, usually originating from a small antennal tubercle; (d) labium distally divided into two large palpmere-like prelabia, each bearing a short, usually 3-segmented* palp (figures 3B and 6B, Plb, Prlb and Plp); (e) stout, ovoid body with varying tendencies toward dorso-ventral flattening, consisting of a thorax and 9-segmented abdomen bearing at

*2-segmented in some Nemopteridae and 4-segmented in *Psychopsis elegans*, according to MacLeod (1964).

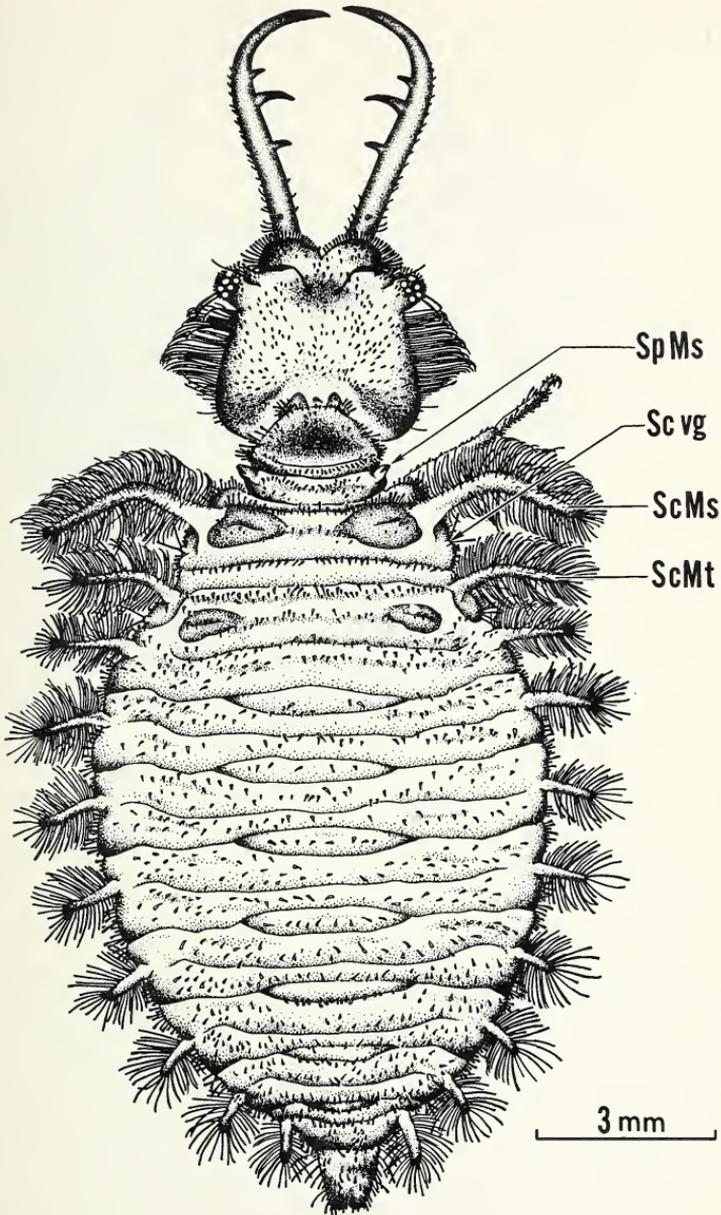


Figure 1. *Ululodes mexicana*, mature third instar larva. ScMs = mesothoracic scolus, ScMt = metathoracic scolus, Scvg = vestigial mesothoracic scolus, SpMs = mesothoracic spiracle.

its tip a retractile, tubular tenth segment that functions as a spinneret; (f) short, powerful walking legs; and (g) dolichasterine (trumpet-shaped) setae of diverse morphology over part or most of the body surface (figure 8). Like most Planipennia, ascalaphid larvae pass through three instars prior to pupation.

LARVA OF *ULULODES MEXICANA* (McLachlan)
(Refer to figures 1-4)

GENERIC DESCRIPTION: *Ululodes* Currie.

The following description is based upon examination of nearly 100 third instar specimens of *Ululodes mexicana* reared from egg to adulthood, together with 13 reared larvae of an unidentified species of *Ululodes* from Florida and two preserved third instar specimens representing a third unidentified species of the genus from Pima, Arizona. The generic diagnosis is also based on information presented in two excellent works: first, that of MacLeod (1964), describing the morphology of the head capsule and cervix of *Ululodes quadrimaculata* (Say) from Illinois, and secondly, that of McClendon (1902), describing the third instar larva of *Ululodes senex* Burmeister (described as *U. hyalina* Latreille) from Texas. I have chosen to follow the terminology used by MacLeod (1964, 1970).

Length: just prior to pupation, 13-19 mm, not including jaws.

Head: trapezoidal, approximately as wide as or slightly wider than long, broadest posteriorly and tapering evenly anteriorly; dorso-ventrally flattened but much thicker behind than in front. Cordate postero-lateral (occipital) margins. Labral margin (LmM) narrow and very strongly bilobed with a single wide deep notch at midline; labral lobes bulbous. Dorsum flat medially and convex laterally; ventral surface strongly convex with excavated antero-lateral margins permitting retraction of jaws beneath ocular tubercles (excv). Surface texture mildly rugose due to slightly raised bases of setae. Ocular tubercles (OT) large, prominent, approximately cylindroid but very slightly tapered distally and flattened dorso-ventrally; ventral stemma somewhat reduced in size compared with dorsal stemmata. Antennal tubercles (AT) prominent, cylindrical, nearly half length of ocular tubercles, appressed closely to bases of latter. Number of flagellomeres variable, usually 11 or 12, with tip of antenna projecting far beyond end of ocular tuber-

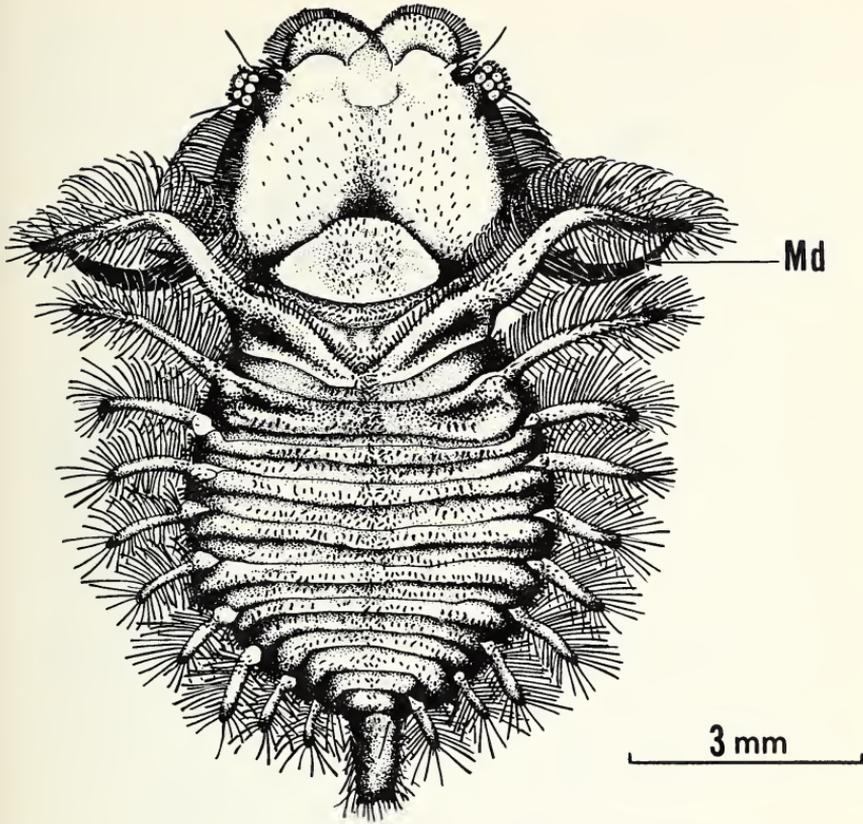
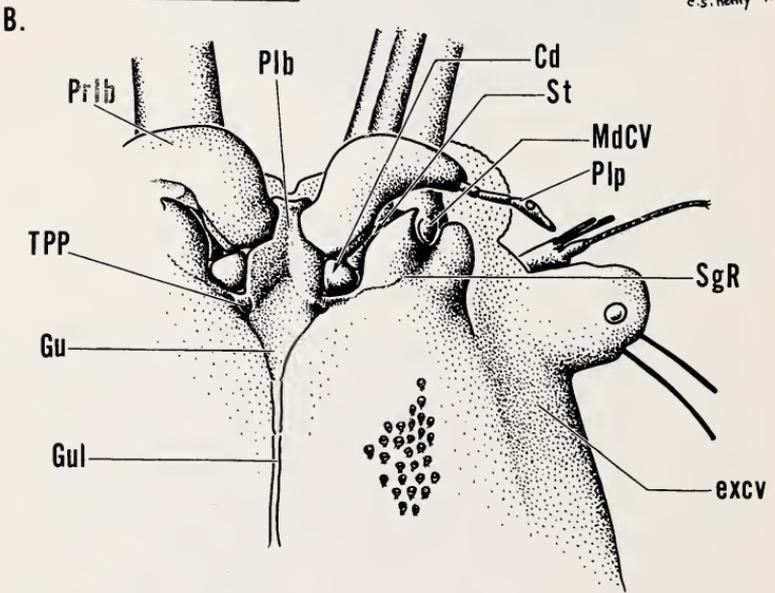
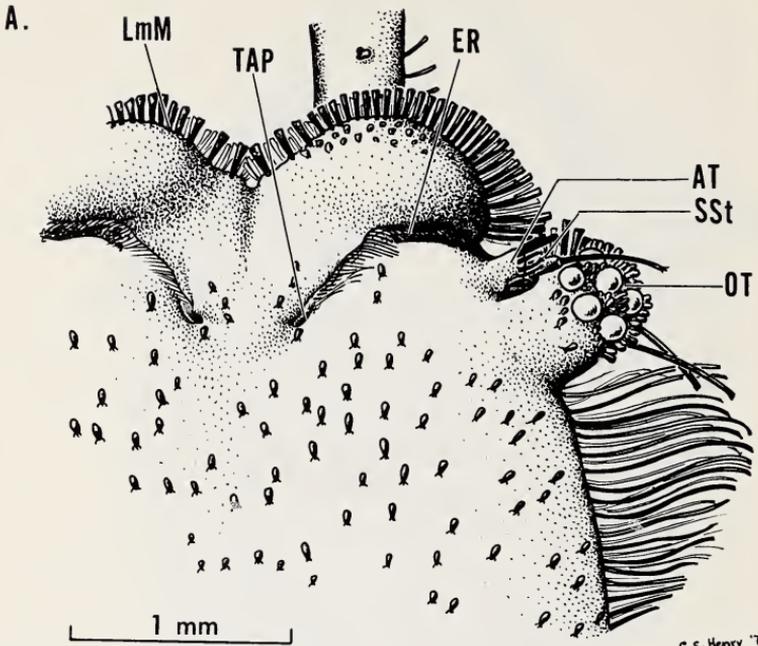


Figure 2. *Ululodes mexicana*, immature third instar larva with jaws in "trap" position. Md = mandible.

cle. Jaws falcate, smoothly tapering, and significantly longer than head capsule; they show a strong upward tilt in lateral view and are capable of being opened to an angle of 270 degrees or more (figure 2). First tooth always placed proximad of midpoint of mandible; central tooth much larger than the other two teeth and markedly curved; distal tooth unambiguously the smallest of the three and situated closely adjacent to central tooth. Ventral mandibular condyle (MdCV) positively contained within robust U-shaped socket formed from anterior ends of subgenal ridge (SgR — see figure 3B), the medial arm of which overgrows and nearly hides maxillary stipes (St). Postlabium (Plb) flask-shaped in outline



with very large, crescent-shaped, distally tapered prelabial lobes (Prlb) arising quite close to one another from sides of "neck" of postlabium. Terminal palpimere of labial palpus (Plp) nearly as long as first and second combined.

Body: elliptical in outline and not prominently flattened when mature. Prothoracic notum small, sclerotized, convex, roughly elliptical to triangular in outline and nearly twice as broad as long, bearing no scoli or tubercles. Remainder of body lightly sclerotized except for a pair of oval plates situated laterally in tergum of the mesothorax and a second smaller pair similarly located in metathorax. Lateral margins of each thoracic and abdominal segment (except terminal segments 9 and 10 of abdomen) prolonged into a pair of unflattened, finger-like setigerous scoli, ten pairs in all. Each mesothoracic scoli (ScMs) fully as long as head capsule, inclined forward basally and reflexed backward at its mid-point. Metathoracic scoli (ScMt) two-thirds as long as mesothoracic ones, less sharply reflexed; remaining 8 pairs of abdominal scoli straight, shorter than thoracic ones, and becoming gradually smaller toward rear. Minute pair of vestigial scoli (Scvg) present behind and slightly ventral to primary pair on both meso- and metathorax. Mesothoracic spiracles (SpMs) very large, borne dorso-laterally on cone-shaped sclerotized tubercles behind prothorax; all other spiracles smaller, ventro-laterally located, one pair for each of the first eight abdominal segments.

Chaetotaxy: Dense, double fringe of very long serrate setae present on lateral margins of head capsule and peripherally on all scoli. Single primary row of shorter, distally flared, serrate dolichasters (as in figure 8-a) closely set along entire anterior labral margin. Each ocular tubercle with still shorter, tightly packed dolichasterine setae over most of its distal surface, with two very large subequal setae projecting backward from the posterior outer margin. Antennal tubercle bearing a group of three (very rarely, four) slender, smooth setae with apical stellate enlargements (SSt and figure 8-d)

Figure 3. [opposite page] *Ululodes mexicana*, details of head capsule of mature third instar. A = anterior dorsal aspect, B = anterior ventral aspect. AT = antennal tubercle, Cd = maxillary cardo, ER = epistomal ridge, excv = lateral excavation, Gu = gular area, Gul = gular line, LmM = labral margin, MdCV = ventral mandibular condyle, OT = ocular tubercle, Plb = postlabium, Prlb = prelabial lobe, Plp = labial palp, SgR = subgenal ridge, SSt = stellate-tipped seta, St = maxillary stipes, TAP = anterior tentorial pit, TPP = posterior tentorial pit.

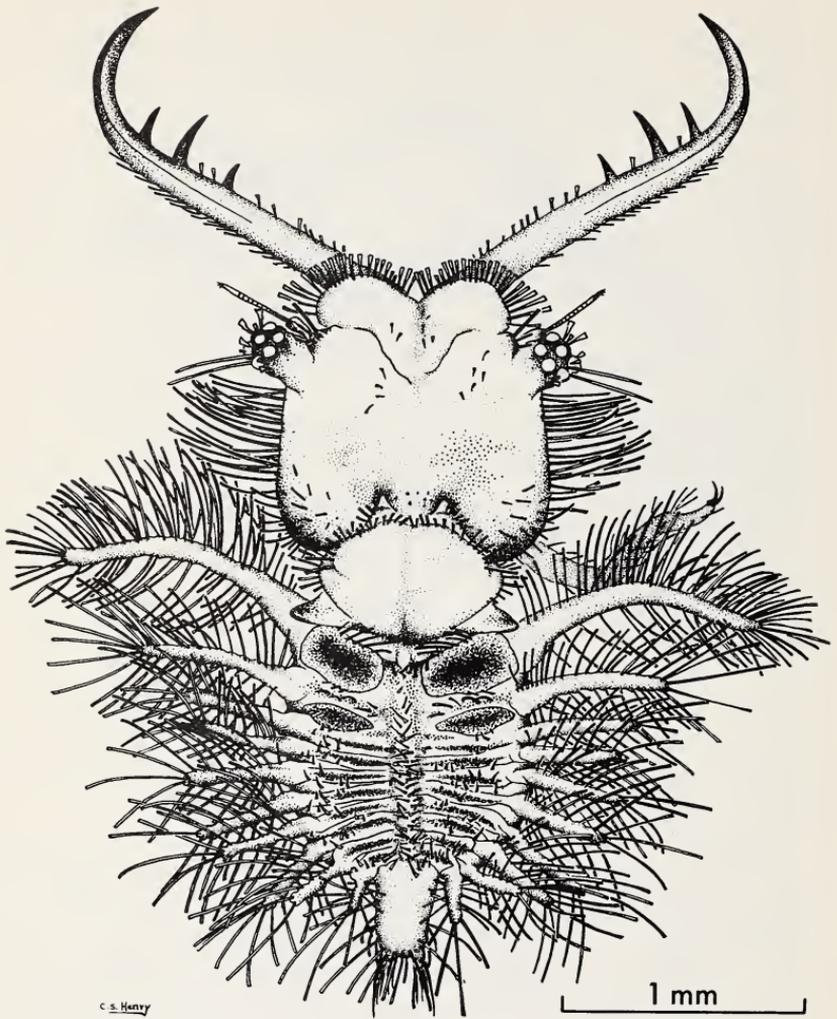


Figure 4. *Ululodes mexicana*, first instar larva at hatching.

that contact antenna scape, flanked anteriorly by two (very rarely, three) stout serrate setae and posteriorly by an enlarged dolichaster; a few other, smaller dolichasters may also be present on surface of the tubercle. Dorsum of head and body more or less clothed with small to medium sized dolichasterine setae; ventral surfaces bear more profuse, smaller dolichasters that are shaped like goblets (figure 8-c). Thick mat of very fine, tangled threads also present over entire dorsum of larva, including dorsal surfaces of all setal fringes on head and scoli. Four of five pairs of stout, tooth-like digging setae present terminally on ninth abdominal segment.

SPECIES DESCRIPTION: *Ululodes mexicana* (McLachlan), new larval association.

Measurements: Length of mature larva, 14.60-18.75 mm, mean length = 16.00 mm. Length of head capsule, 3.30-3.78 mm, mean = 3.54 mm; width of head capsule, 3.40-3.90 mm, mean = 3.60 mm.

Chaetotaxy: Setae composing fringes on lateral margins of head capsule and edges of scoli showing tendency toward gradual distal thickening with truncate tips (figure 8-a); not lanceolate. Ocular dolichasters projecting well beyond edges of stemmata and easily visible from above. Dolichasters on dorsal surface of head abundant, fairly evenly distributed, and cavate (figure 8-b-2); never peg like (figure 8-b-1) or confined to occipital lobes. Dolichasters on dorsal body surface of the flared and curved type (figure 8-a), rarely parallel sided or pointed.

Pigmentation: Head with prominent but diffuse oval to heart-shaped spot of dark pigmentation centered just behind (but encompassing) anterior tentorial pits (TAP). Labral lobes, antennal tubercles, and tips of ocular tubercles also darkly pigmented. Occipital lobes noticeably more pale than the rest of the head capsule. Prothoracic notum without obvious pattern of pigmentation.

ONTOGENETIC VARIATION:

The first instar *Ululodes* larva (figure 4) differs considerably from the mature larva. The head capsule is more quadrate than trapezoidal. The antenna is more than twice the length of the ocular tubercle, bears 12 or 13 flagellomeres, and emerges from a poorly defined tubercle. The jaws are only slightly falcate, and the proximal tooth rather than the distal tooth is the smallest of the three. All setae are relatively longer and less numerous than in mature larvae: the central dorsal aspect of the head capsule in particular is nearly

devoid of setae in all forms studied. A single stellate seta rather than three (or four) is found on each antennal tubercle, flanked by (usually) one large stout seta anteriorly and one posteriorly. Terminal digging teeth on abdominal segment nine are lacking.

The second instar larva is intermediate between first and third instars with respect to most ontogenetically variable morphological features. Three stellate setae are borne by each antennal tubercle.

The generic discussion applies equally well to the species *U. mexicana*. It is considerably more difficult to distinguish among species in the first instar than in later instars, although the morphology of the long setae bordering the head and covering the body and scoli seems to separate first and second instar *U. mexicana* larvae from those of at least one undetermined species from Florida. Additionally, consistent differences in the pigmentation patterns of the dorsum of the head capsule can be found in early instars. However, other setal patterns uniquely characterizing mature *U. mexicana* larvae are absent or unreliably present in younger individuals.

LARVA OF *ASCALOPTYNX FURCIGER* (McLachlan) (Refer to figures 5-7)

GENERIC DESCRIPTION: *Ascaloptynx* Banks.

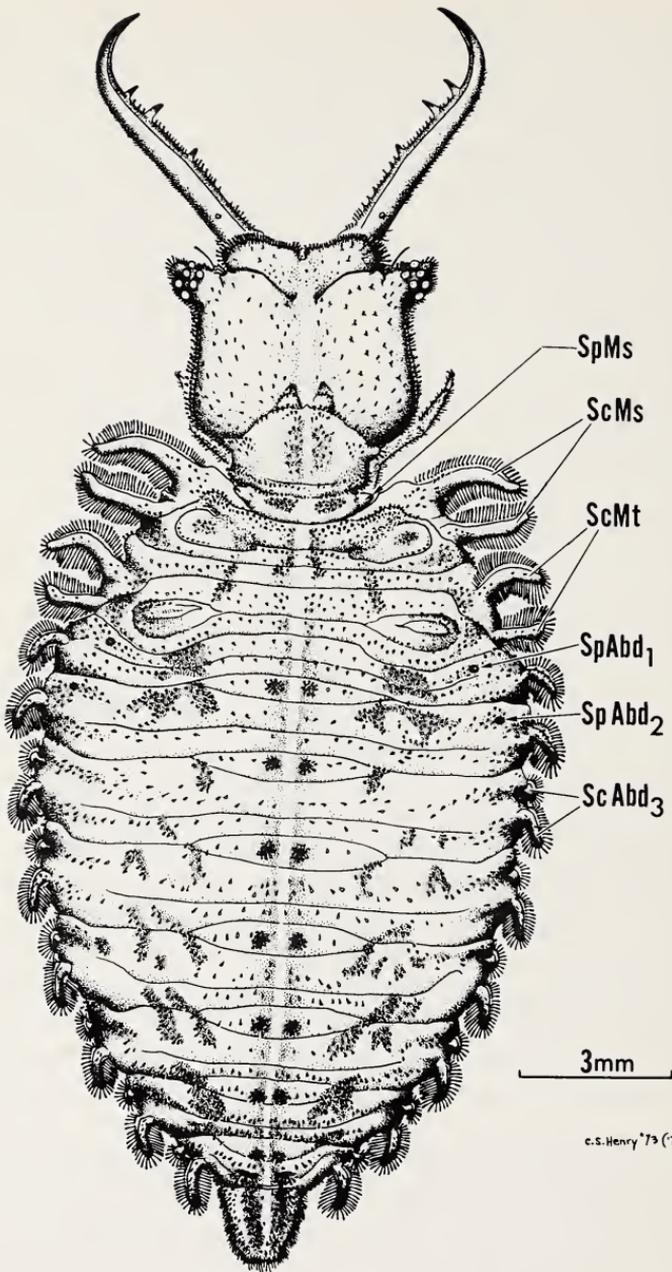
The following description is based upon examination of 67 third instar larvae reared from field-collected eggs that were morphologically matched with eggs obtained from females of *Ascaloptynx furciger*. *A. furciger* is the only species of the genus that has been sighted or collected from the vicinity of the egg collecting sites in the Chiricahua Mountains. Two additional specimens of an unidentified larva from Pima, Arizona that can be assigned with confidence to the genus on the basis of morphology were also available for comparison. In addition, the two figures published by Peterson (1953) are almost certainly of *Ascaloptynx* larvae, although the drawings are too schematic to contribute much morphological information.

Length: just prior to pupation, 16-22 mm, not including jaws.

Head: quadrate, slightly wider than long, slightly broader posteriorly than anteriorly but basically parallel sided; strongly flattened dorso-ventrally but thicker behind than in front. Moderately cordate postero-lateral (occipital) margins. Labral margin (LmM) wide and weakly bilobed with a narrow tubercle-flanked notch at

midline widening into a broad shallow central indentation; labral lobes dorso-ventrally flattened. Dorsum flat, ventral surface moderately convex with no lateral excavations for mandibles. Surface texture mildly rugose due to slightly raised bases of setae. Ocular tubercles (OT) large, prominent, unflattened, and tapering distally, each bearing a setigerous tubercle antero-laterally; ventral stemma somewhat reduced in size compared with dorsal stemmata. Antennal tubercles (AT) very small and inconspicuous compared with ocular tubercles, parallel sided to pedunculate, at least twice as broad as long. Antenna approximately three-fourths the length of ocular tubercle, bearing a variable number of flagellomeres (usually 12 or 13). Jaws only slightly falcate and significantly longer than head capsule, parallel sided to the level of proximal mandibular tooth and then tapering smoothly toward apices; they show a slight upward tilt in lateral view and are capable of being opened to an angle of 180 degrees. All teeth short and stout: proximal tooth smallest and situated barely basad of mandibular midpoint, central tooth largest and closely adjacent to distal tooth. Ventral mandibular condyle (MdCV) bounded medially by a very large curved arm formed from the anterior end of the subgenal ridge (SgR), but not contained laterally except by a low bump (see figure 6B); medial arm not appreciably overlapping stipes (St). Postlabium (Plb) broad, quadrate, articulating at its antero-lateral corners with widely separated prelabial lobes (Prlb) that are nearly straight and only slightly tapered distally; penultimate palpmere of labium medially constricted and longest of the three "segments" (Plp).

Body: elliptical in outline and not prominently flattened when mature. Prothoracic notum small, sclerotized, nearly flat, roughly pentagonal in outline and broader than long, bearing a pair of prominent setigerous tubercles at its antero-lateral corners. Remainder of body lightly sclerotized except for a pair of large oval tergal plates placed laterally on mesothorax and metathorax and a third pair of much smaller plates on eighth abdominal tergum. Body laterally fringed by 12 pairs of primary and six pairs of secondary (smaller) setigerous, dorso-ventrally flattened scoli: meso- and metathorax each bearing two pairs of primary scoli (ScMs and ScMt), with anterior pair curving gently posteriad and posterior pair curving anteriad; abdominal segments one through eight each bearing one pair of basally constricted and posteriorly directed primary scoli; additional pair of much smaller mushroom-shaped



secondary scoli present on abdominal segments three through eight immediately anterior to each primary pair (ScAbd). Anteriormost pair of body scoli longest, measuring half the length of head capsule; primary scoli become progressively smaller posteriorly, then subequal from first to eighth abdominal segments. Mesothoracic spiracles (SpMs) very large, borne dorso-laterally on cone-shaped sclerotized tubercles behind prothorax; all other spiracles smaller, those of first two abdominal segments dorso-lateral (SpAbd 1 & 2), remaining six pairs ventro-lateral.

Chaetotaxy: Dense fringe of serrate dolichasters present on lateral and labral margins of head capsule and peripherally on ocular tubercle, prothoracic shield and tubercle, ninth abdominal segment, and all scoli; longest on scoli, lateral margins of labral lobes and anterior margins of ocular tubercles. Antennal tubercle bearing a group of three small slender setae with apical stellate enlargements (SSst and figure 8-d) that contact antennal scape, flanked anteriorly by one to several stouter, serrate setae. Dorsum of head and body more or less covered by complex but minute scale-like setae (Scl and figure 8-e) interspersed with medium-sized dolichasters, the latter aggregated into pairs of tight clumps (one pair per segment) on middorsal surfaces of abdominal segments one through seven; setae nearly absent from midline of body. Ventral surface of body uniformly and thickly clothed with small, sharply flared dolichasters which become more peg-like or lanceolate on head capsule. A single long, lanceolate seta present on ventral surface of each trochanter; other, shorter lanceolate setae profusely present on ninth abdominal sternum, nearly obscuring the five terminal pairs of tooth-like digging setae.

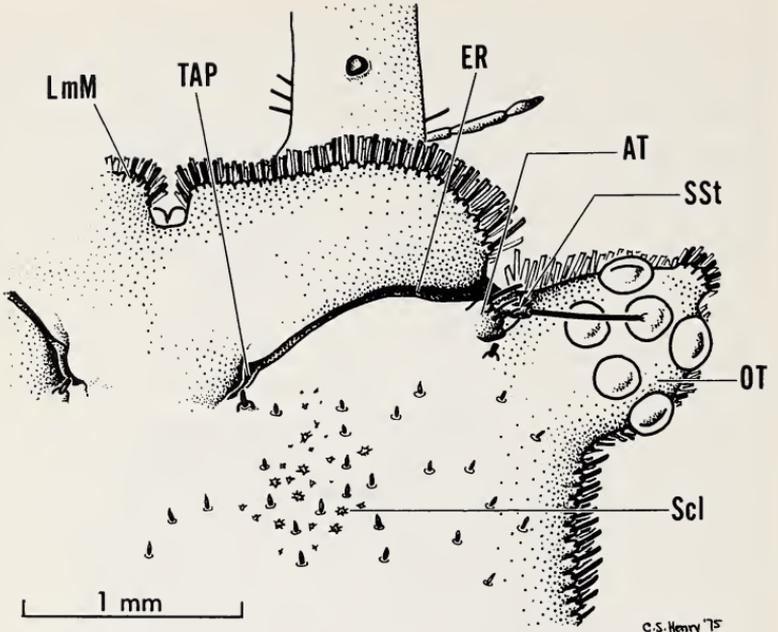
SPECIES DESCRIPTION: *Ascaloptynx furciger* (McLachlan), new larval association.

Measurements: Length of mature larva, 16.80-21.80 mm, mean length = 19.25 mm. Length of head capsule, 4.00-4.50 mm, mean = 4.35 mm; width of head capsule, 4.37-4.90 mm, mean = 4.57 mm.

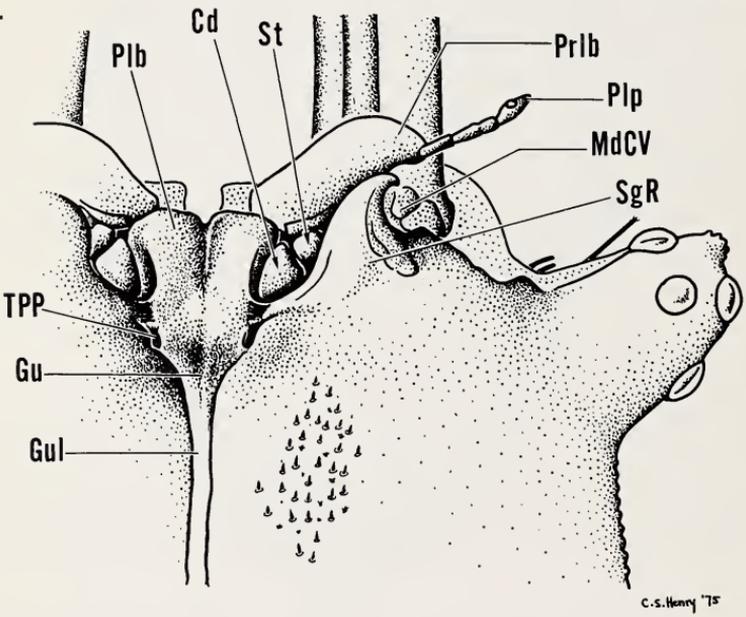
Chaetotaxy: Dolichasters on lateral margins of head capsule short and stout; those on dorsal aspect of head with closed tips.

Figure 5. [opposite page] *Ascaloptynx furciger*, mature third instar larva. ScAbd₃ = scoli of third abdominal segment, ScMs = mesothoracic scoli, ScMt = metathoracic scoli, SpMs = mesothoracic spiracle, SpAbd_{1 and 2} = spiracles of abdominal segments one and two.

A.



B.



Setae on anterior and distal margins of primary scoli stout and flared (figure 8-a); postero-basal setae on each scolus are longer, sharp-tipped, and more nearly plumose than serrated (figure 8-f). Non-scale-like setae mostly dark pigmented except all pale on labral margin and predominantly pale on margins of body scoli; several to most dolichastes on anterior distal half of anteriormost scolus prominently darkened.

Pigmentation: Head uniformly dark brown, entire body light brown to reddish brown; darker tints present dorsally in cuticle beneath clumps or thick patches of setae. Overall dorsal pattern exhibits longitudinal medial stripe, transverse segmental bands, and mid-lateral patches that strongly suggest the venation of a small dead leaf.

ONTOGENETIC VARIATION:

The first instar *Ascaloptynx* larva (figure 7) differs from the mature larva in several obvious respects. The ocular tubercle is pedunculate and nearly ovoid rather than tapered and bears a poorly developed setigerous secondary tubercle. The antenna is relatively large, projecting well beyond the tip of the ocular tubercle, but arises from a "tubercle" that can be identified as such only by the presence of stellate-tipped setae; nine flagellomeres are typically present rather than 12 or 13. The jaws are not falcate and bear relatively long mandibular teeth. Primary body scoli show little dorso-ventral flattening and no tendency toward basal constriction; the secondary scoli are inconspicuous and resemble small tubercles. All setae are relatively longer, less numerous, and of fewer morphological types than in mature larvae: the distally flared dolichaster predominates, and no minute scale-like setae are present. Two stellate setae rather than three are more likely to be found on each antennal "tubercle," with stout serrate setae usually absent from this structure. Terminal digging teeth on abdominal segment nine are also lacking.

The second instar larva more nearly resembles the third than it does the first, although its antennae are still relatively large and the ocular tubercle remains somewhat pedunculate. Additionally, constriction of the bases of the abdominal scoli is not so marked as it will become in the mature larva.

Figure 6. [opposite page] *Ascaloptynx furciger*, details of head capsule of mature third instar. A = anterior dorsal aspect, B = anterior ventral aspect. Scl = scale-like seta; other labels as in figure 3.

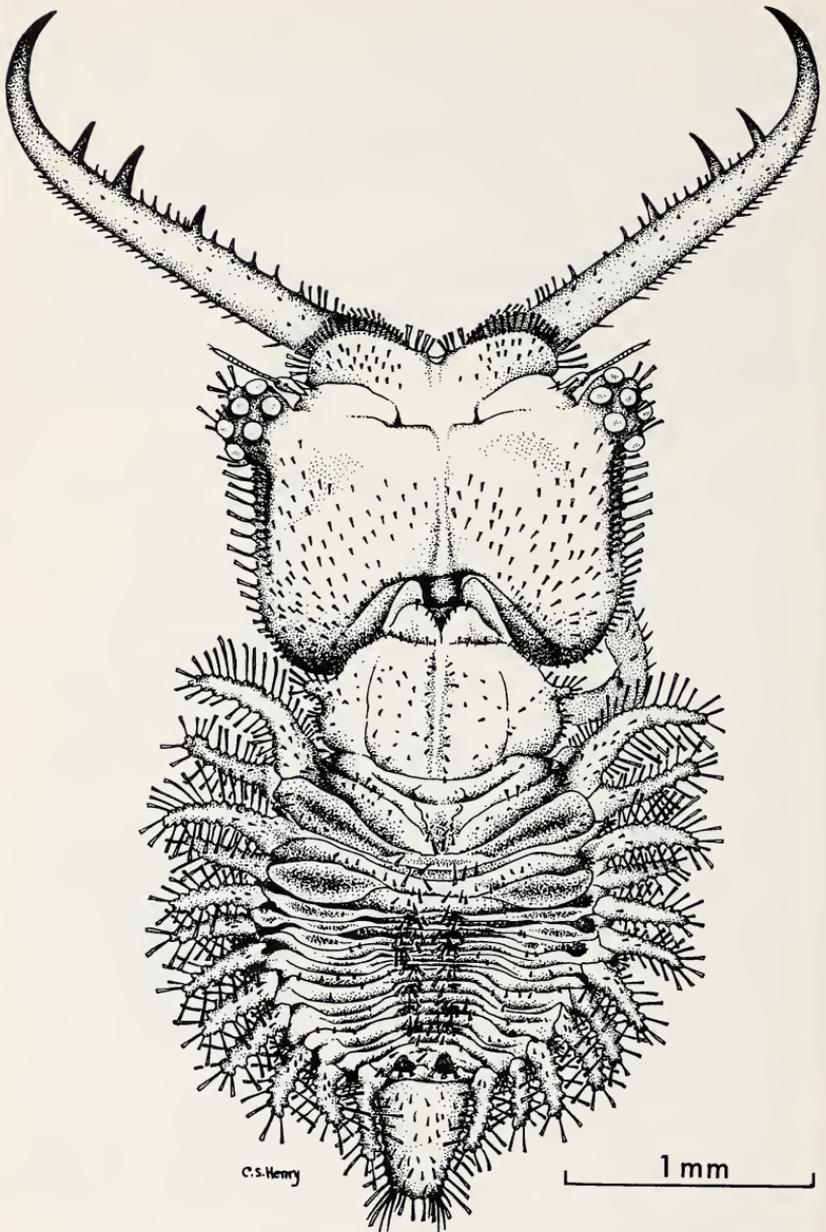


Figure 7. *Ascaloptynx furciger*, first instar larva at hatching.

DISCUSSION

Works on the morphology and biology of the immatures of Ascalaphidae other than *Ululodes* and *Ascaloptynx* include those by Westwood (1888) and Ghosh (1913) on the Asian genus *Helicomitus* McLachlan; Froggatt (1900, 1902) and Tillyard (1926) on the Australian forms *Acmonotus* McLachlan and *Suhpalacsa* Lefebvre; Gravely and Maulik (1911) on the Asian *Pseudoptynx* Weele; and Brauer (1854), Zaki (1917), Rabaud (1927), Withycombe (1925) and Rousset (1973) on various European species of *Ascalaphus* Fabricius. Xambeu (1904), Fraser (1922), Withycombe (1925), von Someren (1925) and Wheeler (1930) have contributed valuable notes on true ascalaphid larvae of uncertain taxonomic affinities. Purely morphological works on the family and general phylogenetic treatments of higher groupings within the Neuroptera have been mentioned in the introductory section of this paper.

Morphological features of owlfly larvae that have been thought to be of special evolutionary and taxonomic importance include the shape of the head capsule, the form and dentition of the jaws, the details of the ventral mandibular articulatory structure, the size, number and degree of flattening of the lateral body scoli, and the placement of the first two pairs of abdominal spiracles (Hagen, 1873; MacLeod, 1964, 1970). To this list may be added the shape and width of the labral margin (LmM), the relative size and shape

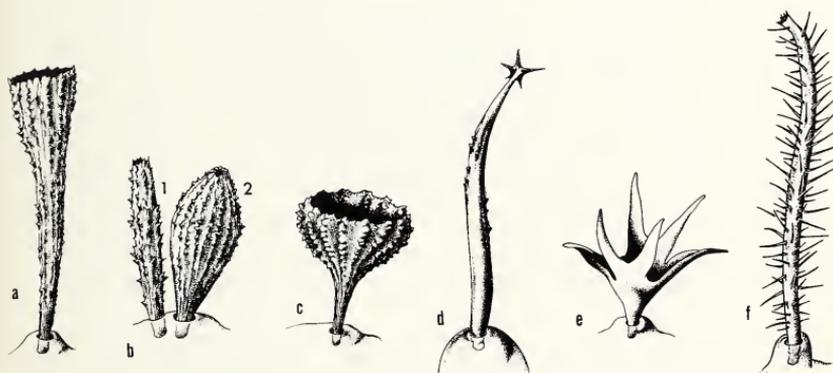


Figure 8. Ascalaphid setal types. a = typical dolichaster, b = clavate dolichasters, c = goblet-shaped dolichaster, d = stellate-tipped seta, e = scale-like seta, f = plumose seta.

of the antennal and ocular tubercles (AT and OT), the morphology of the labium (Plb and Prlb), the shape of the pronotum, and the structure and placement of setae — particularly those located peripherally and on the ocular and antennal tubercles and those forming distinct dorsal patterns.

There is some evidence from both adult and larval morphology that the Nymphidae of Australia is closer to the ancestral taxon leading to the Ascalaphidae (and to the closely related Stilbopterygidae) than any other myrmeleontoid family (Withycombe, 1925; Tillyard, 1926; and MacLeod, 1970). Thus, many of the features of certain described larvae within the Nymphidae, particularly of the Oligocene ? *Pronymphes* sp. and the extant *Nymphes* spp. (MacLeod, 1970), are thought to represent shared specializations of the ascalaphid-nymphid (*et al.*) evolutionary branch and hence to typify the generalized condition in the Ascalaphidae. In addition, the generalized condition is presumed by MacLeod (1970) to predominate in the Oligocene fossil ascalaphid larva *Neadelphus protae* MacLeod; I have carefully examined and figured the specimen from which MacLeod wrote his description, and I can attest to the nearly perfect state of its preservation in amber (figure 9).

It may be suggested tentatively, then, that generalized character states in owlfly larvae could include quadrate head with weakly cordate posterior margin (*Nymphes* and *Pronymphes*); long, non-falcate jaws bearing subequal teeth (*Neadelphus*); simple and loose ventral articulation of the mandible against a medial strut of the anterior terminus of the subgenal ridge (*Nymphes*); a dorsal and ventral series of unflattened, finger-like setigerous scoli of short to moderate length (*Pronymphes*); and all abdominal spiracles oriented co-linearly on the sides of the body (*Neadelphus* and *Pronymphes*). In addition, like *Neadelphus*, the primitive larva should probably display a wide, weakly bilobed labral margin, small antennal tubercles, cylindroid ocular tubercles, postlabium with broad anterior margin, ellipsoidal pronotum bearing small lateral tubercles, and relatively unmodified setae of moderate length clothing most body surfaces.

According to the above criteria, we may state that the genus *Ululodes* is a generalized one with respect to its unflattened scoli, cylindroid ocular tubercles and ventrally situated (and linear) abdominal spiracles. However, in certain major respects, it is highly specialized. First, the *Ululodes* larva shows no obvious

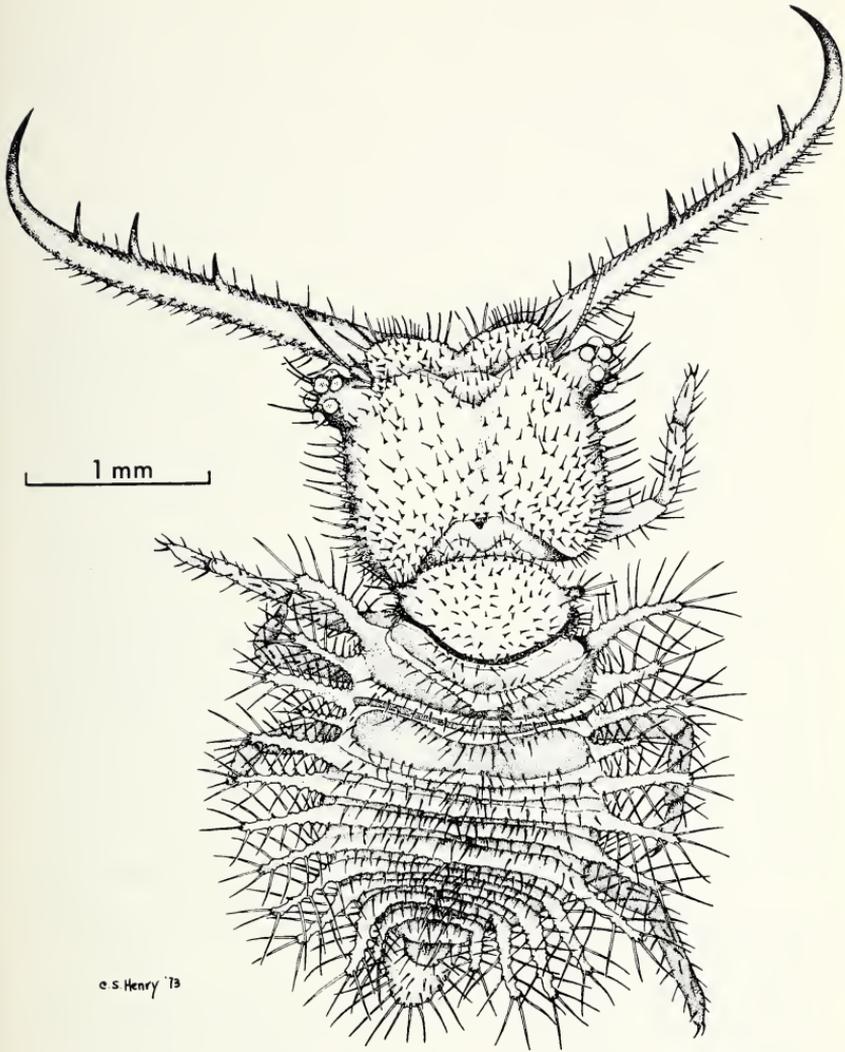


Figure 9. *Neadelphus protae* MacLeod. Baltic Amber (Oligocene). MCZ.

trace of the ventral series of body scoli; it is characterized by ten lateral extensions, all presumably dorsally derived. Secondly, it lacks any trace of pronotal tubercles. Thirdly, it has relatively much larger antennal tubercles and longer antennae than our hypothetical generalized ascalaphid. Fourthly, the setae situated laterally on the head, peripherally on the scoli, and postero-laterally on the ocular tubercles are longer than one would expect to find in a generalized form. Finally, it is characterized by a constellation of specializations associated with its method of prey capture. The strongly falcate, long-toothed and upwardly tilted jaws, the trapezoidal, strongly cordate head with concomitantly small postlabium and narrow bilobed labral margin, the ventro-lateral excavations of the head capsule, and the massive bifurcate socket that receives and tightly locks the ventral mandibular condyle are all secondary expressions of the ability of the *Ululodes* larva to draw its jaws far back alongside the body in the 270 degree "trap" position.

Ascaloptynx appears to have retained a more generalized complex of feeding-related head and jaw adaptations than has *Ululodes*. In addition, the double row of scoli has been retained from the mesothorax to the end of the abdomen, except for abdominal segments one and two. However, the two series of scoli have moved into a common horizontal plane, losing their dorsal and ventral relationship to one another; this must be considered a derived characteristic. Correlated with co-planar location of all scoli is dorso-ventral flattening of the *Ascaloptynx* larva, particularly evident in the extreme flattening of the head capsule and of each thoracic and abdominal scolus: this is also a specialization. Additional derived traits include the scale-like setal modifications and, presumably, the dorsal location of the first and second pairs of abdominal spiracles.

To assess the significance of generalized and specialized traits of *Ululodes* and *Ascaloptynx*, one must compare these genera to other described ascalaphids of known subfamilial affinity. From such an analysis emerges the view that many of the specializations of the *Ululodes* larva are, as previously mentioned, related to its method of prey capture: in this respect it most closely resembles the Indian form *Pseudoptynx* (Gravely and Maulik, 1911) among the Ascalaphinae. Larvae of other split-eyed types like *Ascalaphus*, *Acmonotus* (Froggatt, 1902), *Suhalacsa* (Tillyard, 1926), *Helicomitus* (Westwood, 1888; Ghosh, 1913) and some unidentified

Australian and African forms in my possession* display the more widespread and plesiomorphic pattern of head and mouthpart morphology characteristic of *Ascaloptynx*. Several additional specializations of *Ululodes* seem to be unique to the genus (or to its tribe, Ululodini, confined to the New World): for example, ventral scoli, entirely lacking in *Ululodes*, are retained on the meso- and metathoraces of all known ascalaphine types and on a number of anterior abdominal segments in *Ascalaphus*, *Helicomitus* (Ghosh, 1913), and several distinct but unidentified species from South Africa and Australia. Other features that are more extreme in *Ululodes* than in other Ascalaphinae include the length of the anteriormost body scoli, the prominence of the antenna and its tubercle, the degree of reduction in the size of the prothoracic tubercles, and the length of lateral head and body setae. On the other hand, *Ululodes* shares with all other known Ascalaphinae such plesiomorphic traits as cylindroid body scoli and relatively unflattened head capsule; prominent, cylindrical ocular tubercles of the *Ululodes* type are also characteristic of most ascalaphines, but *Pseudoptynx* (Gravely and Maulik, 1911) is exceptional in possessing a somewhat flattened, nearly sessile ocular area. Finally, the positioning of abdominal spiracles presents an ambiguous picture in the subfamily. Spiracles are placed ventrally in *Ululodes* and in the extinct genus *Neadelphus*. However, a tendency can be noted in *Ascalaphus* (figure 10) that becomes more pronounced in several Australian and African forms toward lateral or even dorsal placement of the first pair of abdominal spiracles; in extreme cases, the second pair may also be involved in this dorsal migration, although never to the same extent as the first.

Comparison of the *Ascaloptynx* larva with two unidentified Central American neuroptyngines in my possession** suggests that extreme dorso-ventral flattening of the head and scoli may be a universal specialization within the New World Neuroptynginae that is perhaps least developed in *Ascaloptynx*. In conjunction with this flattening, all three types bear "dorsal" and "ventral" series of scoli together in a common plane; the number of scoli in each series is also constant within the group, insofar as our limited sample permits us to generalize. Other specializations shared by

*All Australian owlflies are ascalaphines.

**A description of these forms is in preparation.

the known New World forms include prominent dorsal placement of the first and second pairs of abdominal spiracles and modification of some setae to form pigmented scales; in this latter respect, they all resemble an arboreal African larva tentatively assigned by Withycombe (1925) to the neuroptyngine genus *Tmesibasis* McLachlan, which is described as possessing conspicuous swatches of white scale-like setae on its otherwise dark body. On the other hand, those aspects of New World neuroptyngine head and mouthpart morphology that are functionally associated with prey capture fit the generalized pattern seen in most ascalaphines. However, one of the Central American forms shows a slight modification of the ventral mandibular articulation that may be associated with its proven ability to open its jaws slightly beyond 180 degrees. This tendency toward a *Ululodes* type of specialization is much more completely expressed in Withycombe's "*Tmesibasis*" just mentioned. The plesiomorphic complex of head features, then, may not be any more characteristic of Neuroptynginae than it is of Ascalaphinae.

In summary, it appears that we are dealing here with two genera, *Ululodes* and *Ascaloptynx*, that seem to have acquired numerous specializations independently of one another and of other Old World members of their respective subfamilies. In view of the distinctiveness of the New World owlfly fauna (Weele, 1908; Orfila, 1949), it is probably safe to assume that the American radiations of both subfamilies are old ones and that many of the basic traits that ancestrally defined the subfamilies have been partially obscured or modified. Thus, it is extremely difficult, given the present state of our knowledge, to separate unequivocally the larvae of split-eyed owlflies from those of entire-eyed ones. Equally difficult is assessing which of the two subfamilies displays the more specialized complex of larval traits. We have seen that feeding-related adaptations of the head and mouthpart region are of the same basic, generalized sort in the majority of known representatives of both subfamilies, with presumably independent evolution of the specialized constellation of characters at least twice in the Ascalaphinae and once in the Neuroptynginae. Other evidence presented in this paper suggests that the placement and degree of flattening of the body scoli may be more reliable indicators of subfamily affinity than head features: known neuroptyngines have flattened scoli with the secondary series coplanar with the primary series, while ascala-

phines display cylindroid scoli with the secondary abdominal scoli, when present, situated beneath the primary extensions. However, we may be dealing with specializations of the New World neuroptyngines that do not characterize the subfamily as a whole: were one analogously to base his conclusions solely upon New World ascalaphines, he might wrongly interpret the extreme specializations of the *Ululodini* (10 scoli, 270 degree jaw trap position, etc.) as basic larval features of all split-eyed owlflies. In addition, I have seen bizarre unassociated larval ascalaphids from South Africa that bear flattened co-planar scoli on the thoracic segments and two complete series of non-co-planar cylindroid scoli on the abdominal segments!

Spiracle placement also seems to be intimately associated with scoli evolution and can be more easily understood in this context. Examination of many different ascalaphid forms has convinced me that the ancestral condition in the family is lateral placement of all abdominal spiracles between a fully-developed dorsal and ventral series of scoli. Ventral location of spiracles, as in *Ululodes*, results from retention of the dorsal scoli only — or, as in *Ascaloptynx* and its American relatives, perhaps from dorsal migration of the ventral scoli of abdominal segments three through eight to positions immediately behind the dorsal ones. Dorsal location

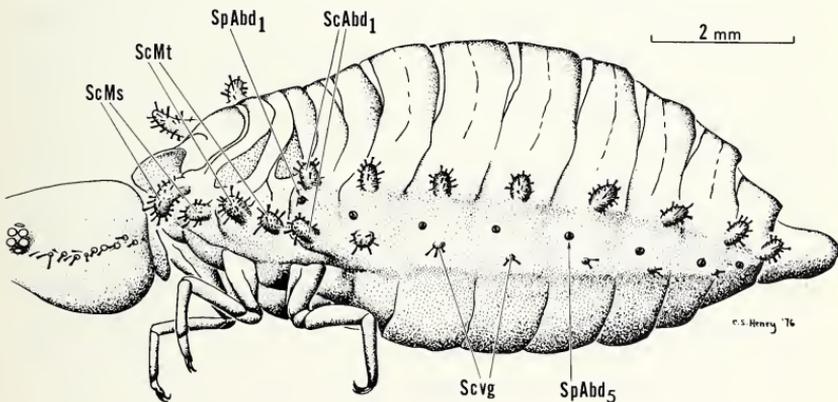


Figure 10. *Ascalaphus libelluloides*, lateral aspect of body of mature third instar larva. Scvg = vestigial abdominal scoli of ventral series; other labels as in figures 1 and 5.

of spiracles, as seen on the first and second abdominal segments of known neuroptyngine larvae, can be thought of as a consequence of total loss of the dorsal scoli of these segments. Support for this view of spiracle placement can be found in the European genus *Ascalaphus* (figure 10) and in several African and Australian forms already mentioned, in which intermediate stages in the loss of the anteriormost dorsal abdominal scoli can be seen to be correlated with dorsad migration of the associated spiracle. However, none of these ascalaphine forms carries this tendency to the second abdominal segment: here, the situation is exactly the opposite of that seen in Neuroptynginae, since the ventral rather than dorsal scoli suffer reduction (figure 10, Scvg). Note that acceptance of the above interpretation of scoli/spiracle evolution forces us to accept the larger ("primary") scoli on abdominal segments three through eight in New World neuroptyngines as derivatives of the ventral rather than dorsal series; this view gains additional support from the relative shapes of the various scoli in *Ascaloptynx* (figure 5), but compels us to consider the "primary" abdominal scoli of ascalaphines and neuroptyngines as non-homologous.

A final point concerns the chaetotaxy of the various larvae and some associated behavior patterns. None of the known neuroptyngines is a debris carrier: protective coloration is achieved through the presence of cuticular or epidermal pigments and clumps of colored, often scale-like setae. The one larva of possible neuroptyngine affinities that has been described in the literature, "*Tmesibasis*" from Africa, shares with *Ascaloptynx* and its Central American relatives similar pigmented setal scales (Withycombe, 1925). On the other hand, littering of the dorsum is widespread in the Ascalaphinae, having been described in such distantly related forms as *Ululodes*, *Ascalaphus* (Brauer, 1854; Withycombe, 1925); and personal observation), *Helicomitus dicax* (Ghosh, 1913), and several unassociated Australian species. It may be that the absence of littering may simply be correlated with arboreal or leaf-associated habits: several primarily arboricolous or litter-dwelling ascalaphines apparently remain naked (Westwood, 1888; Froggatt, 1902; Gravely and Maulik, 1911; Fraser, 1922; and Tillyard, 1926), as do a number of unassociated forms resembling bark, lichens and green leaves (von Someren, 1925; Withycombe, 1925; Wheeler, 1930). However, the possibility remains that the ability to place and secure items of sand or debris on the body has evolved entirely

within the subfamily Ascalaphinae, with the Neuroptynginae pursuing a different evolutionary route toward setal specialization.

From the preceding discussion we may conclude, tentatively;

(a) Ascalaphines show varying tendencies toward loss of the ventral scoli, while neuroptyngines retain the ventral scoli as the primary series on the abdomen.

(b) As a result of scolus modifications, full dorsal placement of the first and second pairs of abdominal spiracles has occurred in Neuroptynginae but not Ascalaphinae.

(c) Only ascalaphines systematically litter the dorsum with sand or debris — though not all species within the subfamily possess the ability.

As more of an impression than established fact, I suggest that the Ascalaphinae share with the hypothetical ancestral type a larger number of plesiomorphic larval character states than do the Neuroptynginae. Retention of primitive traits does not require close relationship between ascalaphines and ancestral ascalaphids. In fact, such a relationship is unlikely in view of indisputably derived adult features like the divided compound eye and specialized cervix (Shepard, 1967) of the Ascalaphinae. Data presented in the present work point to the many difficulties in deriving either larval type from the other; it is more convincing to invoke long separate evolutionary histories for the two subfamilies. In keeping with such an interpretation, it should be noted that the oldest known fossil ascalaphid larva, *Neadelphus protae*, is easily assignable to the subfamily Ascalaphinae (MacLeod, 1970). Another paper, by Adams (1958), adds further support to our interpretation by pointing to the impossibility of deriving the venational pattern of the Ascalaphinae from the highly specialized venation of known neuroptyngines. It is hoped that greater efforts will be made by future workers to associate, by rearing or other valid means, immature and adult ascalaphid material. A peripheral benefit of such efforts will be the accumulation of valuable information on the biology of these insects that will add additional pieces to the puzzle of their evolutionary history.

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A NEW EXOCRINE GLAND IN *NOVOMESSOR*
(HYMENOPTERA: FORMICIDAE) AND ITS POSSIBLE
SIGNIFICANCE AS A TAXONOMIC CHARACTER

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INTRODUCTION

The genus *Novomessor* is comprised of only three species: *N. albisetosus*, *N. cockerelli* and *N. manni*. The first two species are rather common in the Southwestern United States and Northern Mexico (CREIGHTON 1950, 1955), and the latter has been collected along the Pacific coast of Mexico (KANNOWSKI 1954).

The forms of *Novomessor* were originally described as *Aphaenogaster*, and recently W. L. Brown (1974) suggested that they should be placed back in that genus. He pointed out that "the characters supposed to distinguish the two genera are not very strong when one considers the whole world fauna of this complex". Brown's arguments were especially supported by his reexamination of *Novomessor manni* Wheeler and Creighton (1934) and *Aphaenogaster ensifera* Forel (1899), which he found to be synonymous. He concluded his reasoning by stating "...the example of *A. ensifera* and *N. manni* may help to alert myrmecologists to the kind of change to be expected of a worldwide reclassification. One of the changes in status resulting from this study is of course the return of *cockerelli* and *albisetosus* to their original generic assignment in *Aphaenogaster*".

In the course of a comparative study of communication mechanisms in *Novomessor*, we discovered a new complex exocrine gland. Since this gland is a very distinct character, it should be given considerable weight in the future taxonomic assessment of the species possessing it.

MATERIAL AND METHODS

Live specimens of *N. albisetosus* and *N. cockerelli* were collected in southern Arizona near Portal. For histological investigations the

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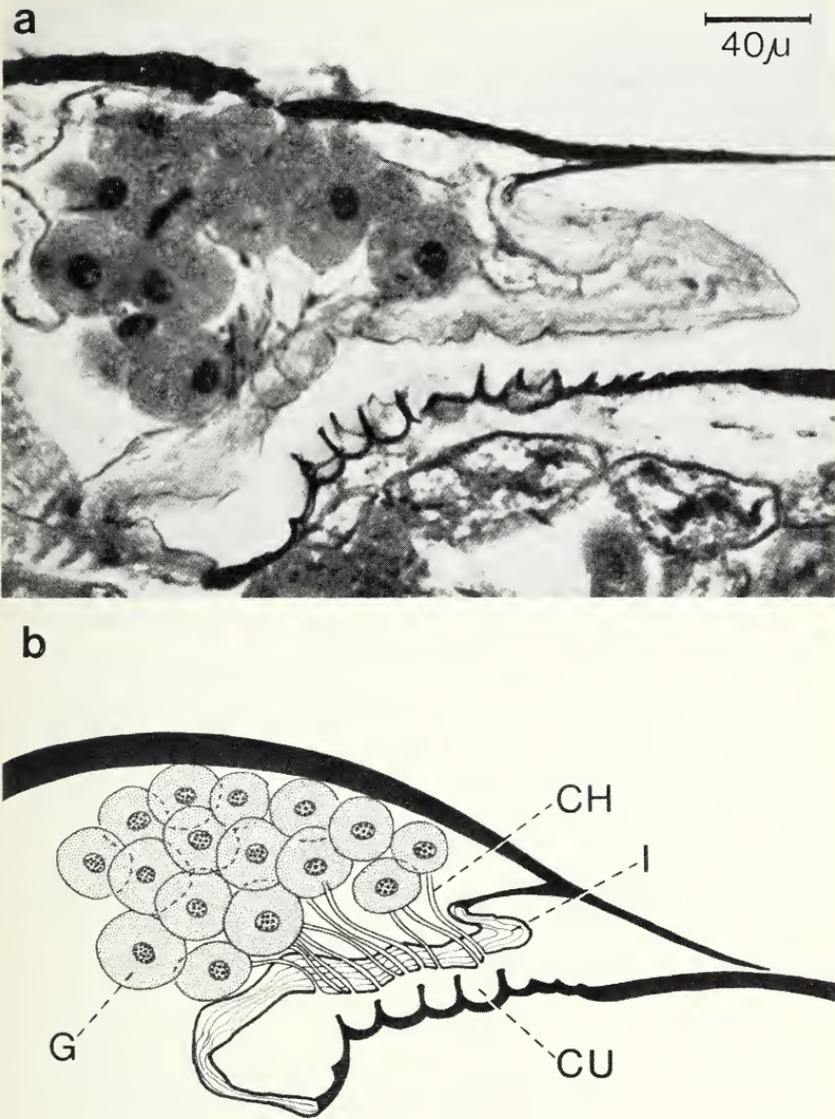


Figure 1

a) Sagittal section through the third and fourth tergite of a *N. albisetosus* worker.
b) Schematic drawing of the histological section, showing the glandular cells (G), the glandular channels (CH), the cuticular cup structure (CU), and the intersegmental membrane (I) between the third and fourth segment.

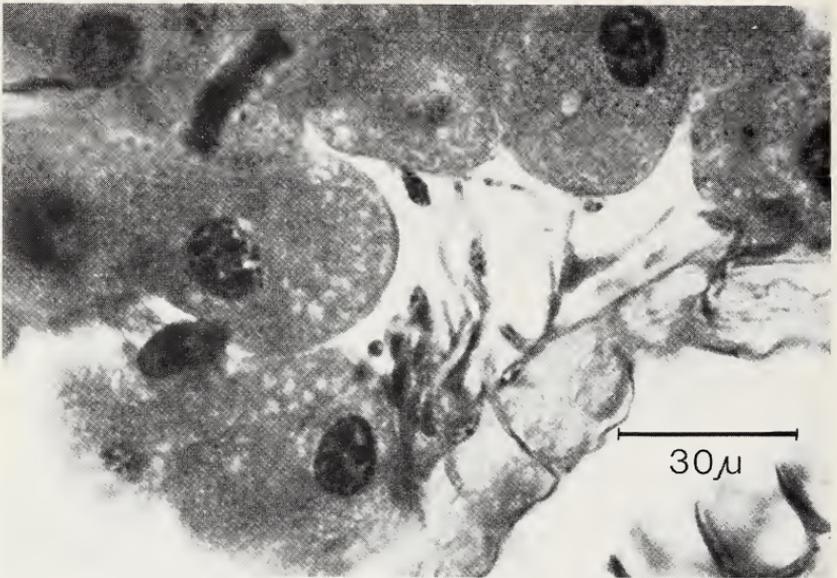


Figure 2. Sagittal section through the tergal gland complex, showing the channels that open through the intersegmental membrane.

ants were fixed in alcoholic Bouin (Dubosq Brasil), embedded in Methyl Methacrylate and sectioned $8\ \mu$ with a Jung Tetrander I microtome (RATHMAYER 1962). The staining was Azan (Heidenhain). The SEM pictures were taken with an AMR 1000 A Scanning Electron Microscope. For comparative morphological studies of cuticular surface structures we used dry specimens of the ant collection of the Museum of Comparative Zoology of Harvard University.

RESULTS

Whenever we dug up a nest of *N. albisetosus* we noticed a very repugnant odor. The same odor can be released when the gaster of a *Novomessor* worker is crushed. First we assumed that the substance originates either from the poison gland or the Dufour's gland or the hindgut, yet after all these organs were removed from the gaster the abdominal residue still exuded the odor strongly. Next we dissected segment by segment. In this way we finally determined that the odor was emanating from the third and fourth

Table 1. Species of ants which have been checked for the presence or absence of the cuticular cup structure. Except where noted, all ants that were looked at were workers.

With Structure:

Novomessor albisetosus Mayr (workers, males, and females)

Novomessor cockerelli Andre (workers, males, and females)

Ocymyrmex picardi Forel

Without Structure:

Aphaenogaster crocea
subsp. *sicula* Emery

A. ensifera Forel*

A. famelica F. Smith

A. flemingi M. R. Smith

A. fulva Roger

A. gibbosa Latreille

A. laevior Emery

A. lamellidens Mayr

A. longiceps F. Smith

A. loriae Emery

A. mariae Forel

A. miamiana Wheeler

A. obsidiana var. *epirotos* Emery

A. osimensis

Aphaenogaster pallida

subsp. *finzii* Muller

A. phalangium Emery

A. poultoni Crawley

A. praedo Emery

A. pythia Forel

A. rudis Emery

A. sagei Forel

A. sardoa Mayr

A. spinosa Emery

A. splendida Roger

A. subterranea Latreille

A. swammerdami Forel

A. texana Emery

A. tennesseensis Mayr

A. testaceopilosa Lucas

Aphaenogaster tipuna Foral

A. treatae Forel

A. uinta Wheeler

A. weigoldi Viehmeyer

Stenamma brevicorne Mayr

S. diecki Emery

S. manni Wheeler

S. schmittii Wheeler

Pheidole dentata Mayr

P. (Ischnomyrmex) longipes F. Smith

Tetramorium sericeiventre Emery

Ocymyrmex weitzckeri Emery

O. weitzckeri var. *arnoldi* Forel

Cataglyphis albicans var. *cubica* Forel

Cataglyphis bicolor Fabricius

C. viatica Fabricius

Messor aciculatus Smith

M. aegyptiacus Emery

M. barbarus Linne

M. capitata Latreille

M. luebberti Forel

M. meridionalis André

M. sanctus Forel

M. striaticeps André

M. barbarus structor Latreille

Veromessor andrei Mayr

V. lariversi M. R. Smith

V. pergandei Mayr

*Brown (1974) has shown that *Novomessor manni* Wheeler & Creighton is a synonym of this species.

tergal segment. From these results we hypothesized that a gland might exist between the third and fourth tergite, and which apparently cannot be spotted under a dissecting microscope. We therefore conducted a series of histological investigations which finally confirmed our suspicion. Workers of *N. albisetosus* and *N. cockerelli* possess two large glandular complexes, located bilaterally under the third tergite (Fig. 1). One complex consists of approximately 50 single glandular cells, each of which sends an individual channel through the intersegmental membrane between the third and fourth tergite (Fig. 2). The external openings of these channels are closely associated with a series of cuticular "cups", which are located at the apical end of the dorsal surface of the fourth segment. Under the dissecting microscope the arrangement of the series of cups looks like a netlike structure, but the SEM pictures clearly reveal the hexagonal shape of the individual cups which are arranged like the cells of a honeybee comb (Fig. 3). Normally this part of the fourth tergite is tightly overlapped by the third tergite, and only by pulling the segments apart is the structure exposed. We assume that the cups serve as repositories for the glandular secretions. When the substance is needed the ant exposes this area and the chemical evaporates. Indeed, the odor can be released simply by pulling the third and fourth tergite slightly apart. These tergal glands with the associated cuticular cup structure are found not only in the worker caste but also in queens and males (Fig. 4). In addition males of *N. albisetosus* and *N. cockerelli* were found to possess a similar glandular complex located bilaterally under the fourth tergite. The glandular channels open through the intersegmental membrane between the fourth and fifth segment. The cuticular cup structure at the fifth segment is, however, much less conspicuous than that at the fourth segment.*

In general, there appear to be no distinct differences in the tergal glands and the cup structures of *N. albisetosus* as opposed to *N. cockerelli*. Although we did not have fixed specimens of *A. ensifera* (= *N. manni*), the investigation of dried specimens in the systematic collection of the Museum of Comparative Zoology revealed that the

*Another, previously undescribed exocrine glandular complex was found in workers and queens of *N. albisetosus* and *N. cockerelli* ventrally at the fourth segment. The glandular channels open through the membrane near the cloaca. We are currently investigating the function of this gland.

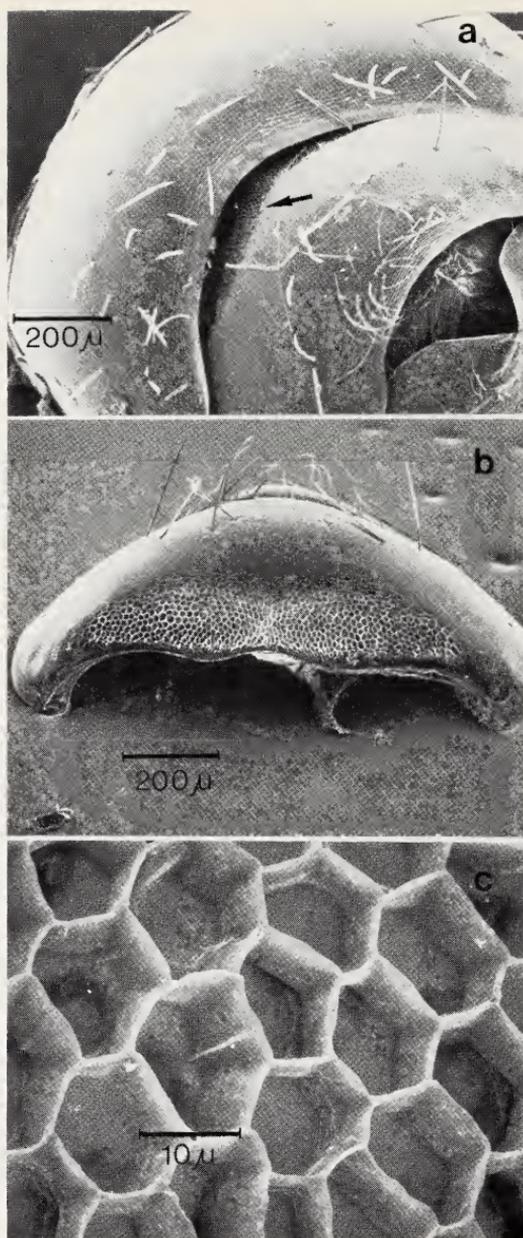
cup structure is missing in this species. Furthermore we surveyed 32 species of *Aphaenogaster* and 4 species of *Stenamma*, and in none of them could we find the cup structure (Tab. 1). An additional histological study of two *Aphaenogaster* species (*A. texana*, *A. rudis*) confirmed the absence of the tergal glands. It thus seems reasonable to suppose that the absence of the cup structure also indicates the absence of the tergal glands.

Although none of the investigated forms of *Aphaenogaster* and *Stenamma* possess the cup structure, we found a very similar cuticular structure in *Ocymyrmex picardi* (tribe Ocymyrmecini). This came as a surprise, because the species is taxonomically not at all close to *Novomessor*. In *Ocymyrmex* the structure is also located on the dorsal surface of the fourth tergite (Fig. 5).

The "cups" do not have the same approximate hexagonal shape and they appear to be not as deep as those of *Novomessor*. Since we could not obtain fixed specimens, we are unable to say if the structure is also associated with tergal glands.

DISCUSSION

With the possible exception of *Ocymyrmex picardi*, where a similar net-like structure was found at the fourth tergite, the newly discovered exocrine tergal glands seem to be restricted to the two species *Novomessor albisetosus* and *N. cockerelli*. They are absent in *A. ensifera* (= *N. manni*) and in all other investigated species of *Aphaenogaster*. Our findings seem therefore to support Brown's contention that *N. manni* should be reclassified as a species of *Aphaenogaster*. On the other hand, the existence of a large and rather complex exocrine gland associated with a particular cuticular structure in *N. albisetosus* and *N. cockerelli* (the type species of *Novomessor*) may argue against the assignment of the genus *Novomessor* to the synonymy of *Aphaenogaster*. It is clear that the repugnant odor, released by disturbed ants of *N. albisetosus*, originates from these tergal glands. We believe that the secretion's function is defense, although our experiments have not yet identified the kind of enemies against which the substance is directed. Only little is known about the natural product chemistry of *Novomessor*. Vick *et al.* (1969) found a series of hydrocarbons in *Novomessor cockerelli*, but they did not attempt to identify the glandular source of these substances. However, they discuss rather vaguely the discovery of new abdominal glands: "A very large



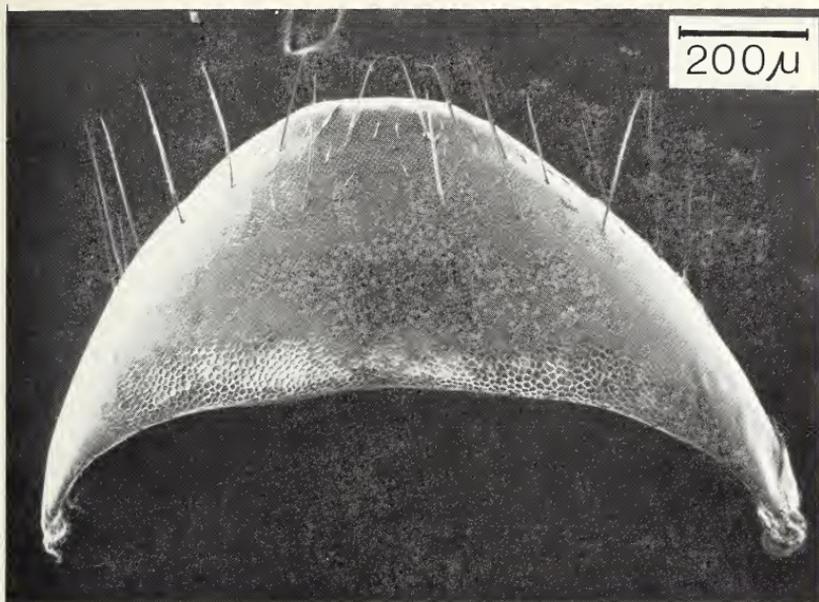


Figure 4. The SEM picture of the fourth tergite of a male of *N. albisetosus*.

glandlike structure, which we call the 'dorsal gland', occupied the dorsal part of the gaster above the digestive tract. It varied in size, but often it extended from the posterior to the anterior end of the gaster and from side to side. It was composed of countless small round yellow globules apparently connected by what may be glandular tissue". But then they write: "It is possible that what appeared to be glandular tissue was not that and the dorsal gland might be some type of fat body arrangement". Our histological investigation did not reveal any glandular type which would fit the description of the 'dorsal glands'. We believe that Vick *et al.* have indeed described the fat body tissue, but then it is hard to understand how the fat body can be mistaken for a new 'dorsal gland'.

Figure 3 (opposite)

- a) SEM picture of the gaster of a *N. albisetosus* worker. The third tergite is slightly lifted and the net-like cup structure can be seen on the surface of the fourth tergite.
- b) Separated fourth tergite with the cup structure fully exposed.
- c) The SEM close up picture shows clearly the hexagonal cups.



Figure 5. SEM picture of a dried specimen of a *Ocymyrmex picardi* worker showing the net-like cup structure.

Even more confusing is the description of additional 'anal glands'. Vick *et al.* write: "In addition, there were several glands or reservoirs which we call the 'anal glands', that opened dorsally near or into the cloacal opening. Each of these glands was composed of a few linearly arranged globules that became progressively smaller distally from their attachment near the anus. No other glandular tissue was seen attached to them and distally they seemed to float free in the haemolymph". This description does not at all fit the glandular complex we discovered ventrally at the last abdominal segment, but it is a rather accurate description of the ovaries.

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BEHAVIORAL ECOLOGY OF THE "EDGE EFFECT"
IN *SCHIZOCOSA CRASSIPES* (ARANEAE: LYCOSIDAE)¹

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INTRODUCTION

The "edge effect" is the phenomenon of increased variety and density of organisms at ecotones (i.e., transitions between two or more diverse communities, such as between forest and grasslands), and is well-known in birds (Beecher, 1942; Johnson and Odum, 1956) as well as in insects and spiders (Luczak, 1966; Luczak and Dabrowska-Prot, 1966; Dabrowska-Prot and Luczak, 1968; Luczak, 1968; Edgar, 1971; Dr. R. Blanke, personal communication). Such community junctions are narrower than the adjoining communities, although they may have considerable linear extent. Additionally, ecotones contain organisms from each of the overlapping communities, as well as the "edge" species, those organisms restricted to, or spending most of their time in, the transition zone (Odum, 1959).

While studying the behavioral biology (Aspey, 1974, 1975, 1976a,b) and environmental physiology (Aspey, Lent, and Meeker, 1972) of several wolf spider (lycosid) species, I found abundant numbers of these spiders in restricted areas at the forest-meadow interface. From a practical point of view, the ability to predict locations of large spider populations facilitated collection for laboratory studies. However, identifying those aspects of the environment or of the spider's behavioral biology that determine

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the edge effect poses interesting considerations. For example, possible ecological and behavioral variables include: (1) availability of food organisms; (2) weather parameters such as temperature and humidity; and (3) social behavior and organization of the animals. With regard to food availability, Luczak and her colleagues (Dabrowska-Prot, Luczak, and Tarwid, 1966; Luczak, 1966; Luczak and Dabrowska-Prot, 1966; Dabrowska-Prot and Luczak, 1968) observed high densities of lycosids at the forest-meadow interface and attributed such spider concentrations to the presence of large prey (i.e., mosquito) populations.

With regard to environmental parameters, Nørgaard (1951) demonstrated that microclimate is an important factor in separating two related lycosid species having different habitat and environmental tolerances. Using mark and recapture techniques in the field, Kuenzler (1958) found evidence of individual home ranges in *Lycosa* spp., and activity levels within these limited areas were positively correlated with temperature and humidity. Hallander (1967) considered courtship in relation to habitat selection in *Pardosa chelata*, and found temperature thresholds to be important for courtship display to occur. Finally, in a comprehensive study on habitat selection and distribution of 15 wolf spider species on coastal sand dunes, Almquist (1973) found daily or seasonal changes in weather often resulting in migration. Almquist (1973) concluded that habitat selection was fundamentally controlled by those microclimatic and vegetational conditions satisfying the spiders' temperature and humidity requirements. Thus, while lycosids exhibit certain physiological tolerances to extremes of environmental conditions (Aspey et al., 1972), they select their habitat, in part at least, on the basis of microclimate.

With regard to social behavior, Gillette (1968, 1972) has implicated a variety of seemingly non-environmental factors affecting aggregation in the locust, including social determinants in desert locusts (Gillette, 1973). Although eusociality is not known to exist in spiders (Wilson, 1971), there are "social" spiders, as reviewed by Kullmann (1968) and Shear (1970). With the exception of reproductive behavior, little is known about the sociobiology of wolf spiders, and an examination of the social behavior of lycosids may provide additional insight into the edge effect in these animals. To this extent, the present paper examines the frequency of inter-individual encounters among adult *Schizocosa crassipes*

in the natural habitat, and discusses those behavioral and ecological factors which may contribute to making this animal an edge species.

METHODS

Individuals of the brush-legged wolf spider, *Schizocosa crassipes* (Walckenaer), were observed as they interacted in the natural habitat at Stroud's Run State Park, Athens Co., Ohio, USA. Adults of both sexes are approximately the same size (body length = 7-10 mm, carapace width = 3-4 mm, leg span = 27-30 mm), although striking sexual dimorphism exists. For example, the female's variegated, patterned brown coloration contrasts with the male's black coloration and gray/white band down the midline of the cephalothorax and abdomen. Molting to the adult occurs in late May, at which time the males develop conspicuous tufts of black hairs on the tibiae of the forelegs with smaller brushes on the patellae.

These small, ground-dwelling spiders are distributed throughout the eastern United States within the Deciduous Forest Formation, and have been recorded as far West as Nevada (Fitch, 1963). In the present study, *S. crassipes* were found in abundance on leaf litter at the forest-meadow interface in an area approximately 2×15 m, half of which was shaded and half exposed to sunlight.

Observations were conducted continually from 1100-1600 hours every other day for 14 days during May 19-31, 1973, and air temperature was recorded during each observation period. I moved systematically around the study area every 10 min, waiting 5 min after each move before resuming observations. Thirty-five hours in the field resulted in 17.5 hr of recorded observations and totalled 1050 one-minute observation periods. Protocol was recorded on a battery-powered tape-recorder, and included the number and sex of all conspecifics crossing within 1 cm directly in front of a male observation spider every minute. An earlier criterion of any spider approaching another within 3-5 cm, regardless of direction, was discarded because so many spiders were involved that accurate counts could not be taken.

An observation spot was approximately 60 cm in diameter arbitrarily divided into 12 sectors with the perimeter corresponding to the face of a clock. Following each move around the field, data recording began with my position taken as 6 o'clock, and observa-

tions continued clockwise every minute. This procedure, coupled with systematically moving about the field, helped to representatively sample the spider population.

RESULTS AND DISCUSSION

In the natural habitat a given male *S. crassipes* encountered an average of four conspecifics per minute, which included one female and three males (Fig. 1). A Kruskal-Wallis one-way analysis of variance (Siegel, 1956) indicated that air temperature fluctuated significantly during a given observation session, which lasted 6 hours ($H = 14.07$, $df = 5$, $p < .02$, two-tailed). Correspondingly, the greatest number of individuals were encountered at 1300 hours which coincided with the highest mean air temperature (19.4°C). Although the mean number of females encountered by a given male observation spider did not vary with time, the mean number of males encountered varied significantly from 1100 to 1600 hours ($H = 15.75$, $df = 5$, $p < .01$, two-tailed).

This disparity in the sex ratio may be due to: (1) greater numbers of males to females; or (2) greater activity on the part of the males. Field data from nearly 800 *S. crassipes* collected in the same area during 1970-1973 indicated that the male:female ratio was approximately 50:50. It appeared, therefore, that the divergent sex ratio observed during inter-individual encounters reflected motility differences between the sexes. Laboratory analysis of isolated and socially grouped males and females supported this hypothesis in that males exhibited up to 10 times more locomotory activity than females (Aspey, unpublished observations).

Similar motility differences between male and female *Pardosa pullata* and *P. prativaga* have been reported by Richter, den Hollander, and Vlijm (1971), as well as for *Lycosa (Pardosa) lugubris* in the field (Dr. S. W. F. van der Ploeg, personal communication). In *P. amentata*, Vlijm, den Hollander, and Wendelaar Bonga (1970) considered high levels of male locomotory activity as inherent to the male's age and/or related to the egg sac carrying phase of the females. For *S. crassipes*, the greater activity of the males is partially attributed to their frequent foreleg Tapping (Aspey, 1974), since females do not exhibit such behavior. Whereas most females remained motionless throughout the observation period, males were rarely stationary.

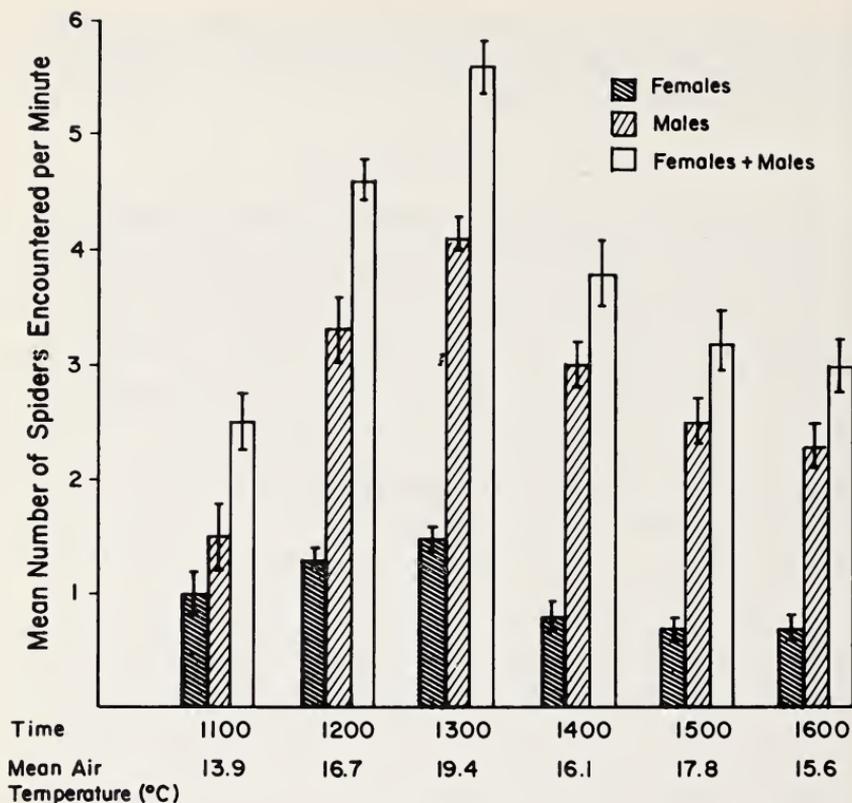


Fig. 1. The mean number of individual conspecifics crossing within 1 cm in front of adult male *Schizocosa crassipes* in the natural habitat on 7 days during May 19-31, 1973, from 1100-1600 hours. Each "Females + Males" histogram bar at each hour interval represents the mean number of spiders observed during 175 one-minute observation periods.

These differences in motility were consistent with the sexually dimorphic coloration and patterning in *S. crassipes*. To illustrate, the relatively stationary mottled brown female camouflages well with the surrounding leaf litter. In contrast, the males stand out prominently in the natural habitat, actively announcing their presence to conspecifics using a variety of visual (Aspey, 1976a, b) and acoustic (Rovner, 1975) signals. Apparently, fewer natural pressures have existed favoring camouflage for the males since their activity would have revealed their location regardless of pro-

tective coloration. In fact, selection pressures in *S. crassipes* have obviously favored conspicuous males given their extensive behavioral repertoire during male-male and male-female interactions.

Of the ecological and behavioral factors previously mentioned that possibly determine the edge effect, food availability in *S. crassipes* seems the least prominent. Although Luczak and her colleagues attributed high concentrations of lycosids at the forest-meadow interface to large populations of mosquitos, other investigators (Clark and Grant, 1968; Dabrowska-Prot and Luczak, 1968) showed that the introduction of wandering spiders above normal densities in field enclosures resulted in increased cannibalism among the spiders without proportionately greater effects on the prey species. Although a food-dependent factor may operate in making *S. crassipes* an edge species, high concentrations of prey species were not obvious in the study area, and the elaborate behavioral displays of the males appear to minimize intraspecific cannibalism. Instead, field observations suggest that microclimate is a controlling factor in determining high densities of spiders.

The natural edge habitat where *S. crassipes* was found in abundance could be divided into sunny and shaded portions. Although the spiders were restricted to a margin approximately 2 m wide, predictions as to whether they would be found in the sunny or shaded area could be made by knowing the previous day's rainfall and temperature. When temperature was high and rainfall infrequent, the spiders were found almost exclusively in the shaded area. This area provided for regulation of temperature during prolonged heat spells, as well as for sources of moisture trapped under leaf litter. Spiders were found in the sunny region following a day of rain or when temperatures were cooler. It appears, therefore, that *S. crassipes* relocate in their microenvironment according to weather conditions.

Finally, with regard to social behavior, laboratory observations of grouped *S. crassipes* have indicated that some form of social attraction exists. In groups of five spiders, three or four spiders at any point in time aggregate, maintaining inter-individual distances of 3-5 cm (Aspey, 1976b). Similarly, in the field *Pardosa* spp. have been observed to maintain a "mobile territory" (i.e., inter-individual distance) of approximately 7.5 cm in diameter (Dr. B. Vogel, personal communication). Although the basis for this aggregation is unknown, silk draglines may provide the stimu-

lus that keeps the spiders together, since Dijkstra (1975) found that both male and female *P. amentata* prefer areas where draglines of both sexes have been laid. This preference for areas having silk of both sexes present may explain why females remain in the aggregation. Males remain in such areas due to a sex pheromone(s) presumably contained in (on) the female's silk (Kaston, 1936; Hedgekar and Dondale, 1969; Richter, Stolting, and Vlijm, 1971). Furthermore, frequent displays and interactions by males would contribute to reduce locomotion into surrounding areas. On one hand, *S. crassipes* are attracted to one another and frequently interact, encountering an average of four conspecifics per minute. On the other hand, displays occurring during male-male agonistic interactions may serve to space individuals so that no spider intrudes on the personal space of another (Aspey, 1976b).

The edge effect in *S. crassipes* appears influenced by complex interactions among ecological and behavioral variables. Although food availability and environmental conditions may initially attract spiders to an edge habitat, predictions concerning the location of large spider populations within the habitat seem more influenced by microclimatic variables. Furthermore, social attraction among conspecifics maintain an aggregation within the restricted region. Thus, a delicate balance of social attraction modulated by definite inter-individual spacing interacts with ecological variables to produce the phenomenon of the edge effect in *S. crassipes*.

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THE MYRMECOPHILOUS BEETLE
GENUS *ECHINOCOLEUS*
IN THE SOUTHWESTERN UNITED STATES
(LEIODIDAE; CATOPINAE)*

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The genus *Echinocoleus* and the species *E. setiger* were described by Horn (1885) from two specimens from an unspecified locality in Arizona. Jeannel (1936) placed the genus in the subfamily Nemadinae and the tribe Nemadini based on a statement by Hatch (1933, p. 191) who had not seen specimens. Jeannel also placed the species *Dissochaetus arizonensis* Hatch in the genus *Echinocoleus*, which he would not have done had he seen specimens of either. Peck (1973) after seeing the types of both genera, placed *Echinocoleus* in the tribe Ptomaphagini and subtribe Ptomaphagina of the subfamily Catopinae, and reviewed what little was known of the genus.

Recently, Dr. D. E. Foster (Entomology Section, Agricultural Sciences, Texas Tech University, Lubbock, Texas) collected a series of *Echinocoleus* from nests of *Pogonomyrmex* harvester ants in west Texas. These specimens prompted me to study this interesting myrmecophilous beetle genus as part of a projected series reviewing the systematics and evolutionary biology of the Catopinae of North America.

The methods, terminology, and format of this paper follow those of my previous studies (Peck 1973, 1976). Dried and pinned specimens were relaxed for 24 hours by soaking in a small dish of distilled water with two drops of liquid detergent, and were then dissected under 70% alcohol. Drawings were made of structures on temporary slide mounts or embedded in glycerine jelly.

Genus *Echinocoleus*

Echinocoleus Horn, 1885, p. 136. Type species *E. setiger* by monotypy, type seen, in MCZ.

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Diagnosis. Shape widely oval or "limuloid", elytra with long semi-erect golden hairs, mesosternal keel absent. These characters plus the habit of living with *Pogonomyrmex* and *Novomessor* ants in the southwestern U. S. distinguish this genus from other Ptomaphagini (keys to the genera are in Peck, 1973, 1976).

Description of genus. Length 1.9-2.8 mm. Width 1.4-1.8 mm. Color pale yellowish to reddish brown. Form widely oval, 1.4-1.9 times as long as wide; flattened (figs. 1-3). Head compressed, closely retractile onto thorax; surface smooth, with short, or short and long hairs; eyes large. Maxillary palpi with last segment conical, shorter than preceding segment. Antennae short, not reaching beyond middle of pronotum when laid back; all segments except first three transverse; club somewhat flattened, composed of last eight segments, which uniformly increase in width, so that XI is widest; segment VIII shorter than but as wide as VII and IX. Pronotum widest slightly before base; 1.7 to 2 times as wide as long; sides regularly arcuate; hind angles drawn out but rounded; hind margin straight in middle; striae present or absent on disc; covered with recumbent short or recumbent short and semi-erect long hairs. Elytra widest at base, 1.0-1.2 times as wide as long; external apical angles rounded, hind margins truncate; sutural angles sharp in male and female; striae somewhat oblique to suture, more transverse away from suture; dense vestiture of short, recumbent hairs and about 10 longitudinal rows of long, semi-erect golden hairs (fig. 4). Flight wings fully formed and apparently functional. Mesosternum with evident midline but lacking median carina. Mesocoxae slightly separated; metacoxae contiguous. Mesepimeron of Ptomaphagina type, trapezoidal. Legs short, flattened; capable of being closely adpressed to body; all tibiae with comb of short equal spines on summit; protarsi expanded in males, distinctly or indistinctly narrower in females; mesotarsi not expanded in either sex; all tarsi five segmented. Aedeagus in side view blunt at base, gradually tapering to narrow tip; style of internal sac long, thin, twisted, with detached basal bulb; in dorsal view narrowing gradually toward tip, tip a blunt point; setae present or absent on aedeagal tip; parameres long, thin, lying close to aedeagus, with three apical setae. Genital plates twice as long as broad, with abundant long hairs at orifice; median spiculum gastrale elongate, projecting one half length beyond anterior end of genital plates. Spermatheca with narrow posterior, and with crest on larger swollen twisted anterior end.

Distribution and biology. The genus contains three species, two described below as new. The species are known to occur only in the Sonoran and Chihuahuan desert and adjacent arid regions of the southwestern United States in Arizona, New Mexico, and Texas (and probably in adjacent Mexico). All detailed collection data suggest that the species live in nests of *Pogonomyrmex* "harvester" and *Novomessor* ants. The limuloid or turtle-like body form indicates that the beetle has some need for a defensive design against the host ants. We may guess that the beetle is a synoekete, being generally ignored or indifferently tolerated by the ants. We may also guess that the beetles scavenge waste materials in the nests, because catopine beetles are generally scavengers. Dr. Foster has observed the beetle larvae most often in the presence of ant brood, and notes that both larvae and adults seem to be free living, with no phoretic association with the ants.

Observations and label data suggest that adult beetles occur more frequently and are easiest to collect in the cooler months when the ants are less active. My experiences with many painful stings received in opening *Pogonomyrmex* nests in the summer in Texas and Mexico convinced me that this is the wrong time of year. Additional records of species distribution and observations of behavioral association with the ants are needed.

Larvae of two species of beetles have been recovered from harvester ant nests. They are modified from the usual elongate shape of catopine larvae into very broad, flat forms with abundant, large, and thick setae. These larvae have been deposited in the MCZ.

The record of *Echinocoleus* from a *Pogonomyrmex* nest at Selma, Alabama (Peck, 1973) was in error. The specimen is a *Ptomaphagus* of a species unknown to me. This alone reinforces the need for additional study of the catopine beetles in the nests of harvester ants.

Echinocoleus setiger Horn

Echinocoleus setiger Horn, 1885: 136. Lectotype here designated as male in MCZ (Horn colln.) bearing red label printed "Lectotype" and with the handwritten number "2995," and a small white label "Ari". Type series consists of one other specimen, a female, bearing a blue-green label "Paratype, 2995," MCZ (Horn colln.). Both seen. Type locality: "Arizona."

Diagnosis. The species is distinguished by its larger size, more transverse pronotum with fine distinct striae and semi-erect coarse hairs, fine elytral striae, and spermathecal shape. It occurs in grass-

land or woodland habitats, and is associated with *Novomessor* ants.

Description. Body color dark brown. Size 2.5-2.7 mm long; 1.7-1.9 mm wide; 1.4 times as long as wide, widest across pronotum. Pronotum 1.7-1.8 mm wide; 1.9-2.1 times as wide as long. Elytral width across scutellum tip 1.1-1.2 times greater than elytral length from scutellum tip. Head and pronotum as well as elytra with stiff semi-erect golden hairs. Pronotal striae distinct. Elytral striae finely spaced, about 5 per 0.1 mm. Aedeagus (figs. 5 and 6), with narrower tip in dorsal view, without terminal setae or down-curved tip in side view. Spermatheca with elongated crest on anterior globular bulb (figs. 7-9).

Variation. No variation is noted.

Additional material examined. Arizona. Cochise County. Huachuca Mountains, Miller Canyon, W. M. Mann coll., 1 male pinned with *Novomessor albisetosus* (Mayr) (my determination), USNM. Huachuca Mountains, Garden Canyon, 13 Nov. 1910, W. M. Wheeler, W. M. Mann colln., 1 male pinned with *Novomessor albisetosus* (my determination), USNM. Graham County. Galiuro Mountains, 22.5 (= 22 May), Hubbard and Schwarz coll., 1 female, USNM. Pinal County. Oracle, 5000 feet elev., 11 March 1919, W. M. Wheeler, 1 female pinned with two *Novomessor albisetosus* (F. G. Werner determination), MCZ.

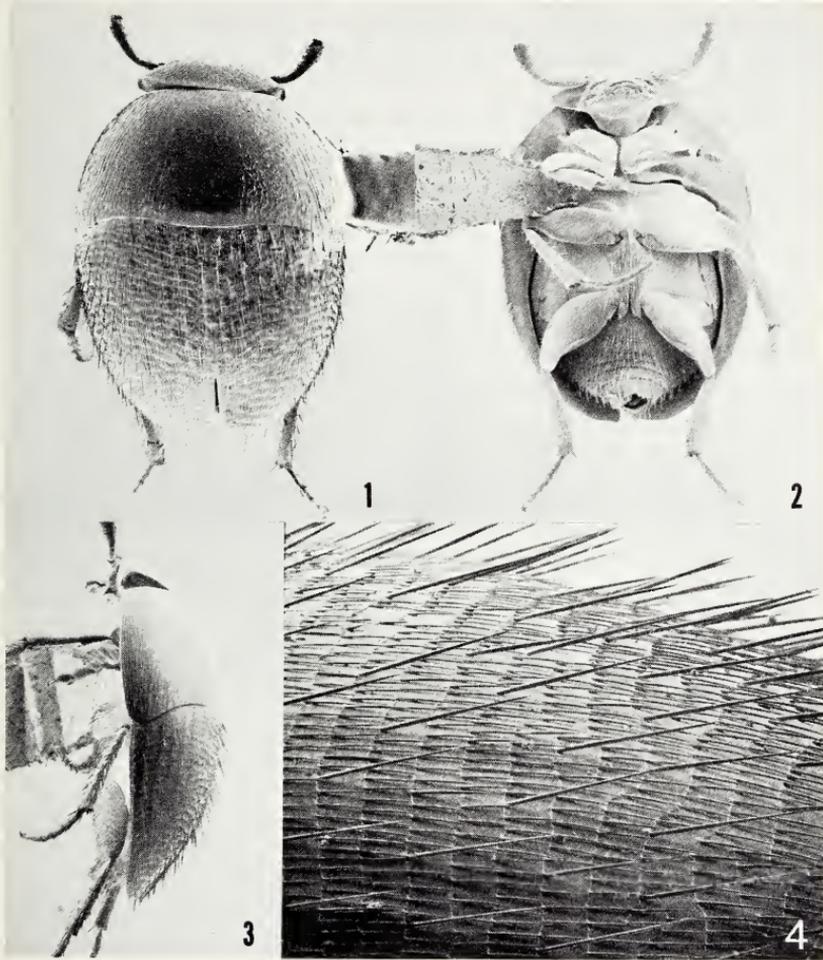
Biology. The collection data show that the beetle occurs with *Novomessor albisetosus* (Mayr) ants. Brown (1974) has indicated that the proper generic assignment of the ant may be *Aphaenogaster*. These ants range across much of the arid southwestern US and adjacent Mexico (Creighton, 1950, 1955; Wheeler and Creighton, 1934), and so might the beetle. Since the ants occasionally nest under stones (Creighton, 1950), the beetles might be found there without the need of digging into the ants' nests. The ants occur most frequently on the lower slopes of desert mountain ranges (Creighton, 1950), and the beetle records suggest an affinity for a higher elevation Sonoran desert woodland or grassland rather than a lower elevation desert shrub habitat. Although some of the above specimens were taken by W. M. Wheeler with *Novomessor*, nothing is mentioned about the presence of these beetles in his revision of this ant genus (Wheeler and Creighton, 1934).

***Echinocoleus sonorensis* sp. n.**

Holotype male in MCZ (no. 32309). Type locality: Arizona, Pima County, Tucson. Type data: 1.iv.1970, P. Ritchie *et al.*, in

nest of *Pogonomyrmex rugosus* Emory, a harvester ant (F. G. Werner determination). Paratypes: One male and one female with same data (SBP colln.).

Diagnosis. The species is distinguished by its larger size, more transverse pronotum without distinct striae or semi-erect coarse hairs, and more widely spaced elytral striae. The species is found in lower elevation Sonoran desert shrubland habitats, in association with *Pogonomyrmex* ants.



Figures 1-4. SEM photomicrographs of *Echinocoleus sonorensis*. 1-3. Dorsal, ventral, and lateral views respectively. 4. Lateral view of elytra showing long, semi-erect hairs.

Description. Body color pale; golden brown. Size 2.5-2.8 mm long; 1.6-1.8 mm wide; 1.5-1.6 times as long as wide; widest across pronotum. Pronotum 1.8-1.9 mm wide; 1.8-1.9 times as wide as long. Elytral width across scutellum tip 1.2-1.3 times greater than elytral length from scutellum tip. Head and pronotum without, but elytra with, stiff and semi-erect golden hairs; fine recumbent setae on all dorsal surfaces except polished pronotal disc. Pronotal microsculpture and striae absent. Elytral striae coarsely spaced, about 2 per 0.1 mm. Genital plate and spiculum gastrale as in figure 10. Aedeagus tip wider (fig. 11), without down-curved tip in side view. Spermatheca unknown; damaged in dissection of the unique female.

Variation. No variation is noted.

Etymology. The name refers to the arid grassland and shrub desert region of Arizona and adjacent parts of Mexico.

Biology. The beetle is known to occur only with *Pogonomyrmex rugosus* Emory, one of the harvester ants. Dr. Floyd Werner (personal communication) reports that the specimens were taken in a nest of this ant in the upper half meter. The nest was excavated to a depth of about 3 meters, and contained more than 22,000 workers. This nest was similar in structure to that excavated in Maricopa County, Arizona, and reported by Wildermuth (1931) as a nest of *P. barbatus*, but which was most likely a nest of *P. rugosus*. The host ant ranges over much of the arid southwestern US and adjacent Mexico (Creighton, 1950; Cole, 1968) and so might the beetle. One highly modified larva was taken in April with the adults in the upper part of the nest (deposited in MCZ). The ants usually nest in stony soil in open deserts (Creighton, 1950) and the general vegetation in the vicinity of Tucson is an open lower elevation Sonoran shrub and cactus desert.

***Echinocoleus chihuahuensis* sp. n.**

Holotype female and allotype male in California Academy of Sciences. Type locality: Texas, Culberson County, 5.5 mi N Pine Springs (west Dog Canyon, 5300-5400 ft. elev., in Guadalupe Mountains National Park). Type data: 2.x.1975, D. E. Foster collector, in nests of *Pogonomyrmex maricopa* Wheeler (Foster determination). Paratypes: ten with same data, and three with same data but 9.vi.1974 (deposited in MCZ, Texas Tech, and SBP collections).

New Mexico. San Miguel County. Las Vegas, A. Fenyés, three females pinned with *Pogonomyrmex maricopa* (my determination), MCZ, CAS.

Diagnosis. The species is distinguished by its smaller size, less transverse pronotum lacking striae but possessing stiff semi-erect hairs, medium fine elytral striae, downward curved aedeagus tip in lateral view, and shape of the spermatheca. The species is found in upper elevation Chihuahuan desert grassland-woodland habitat, in association with *Pogonomyrmex* ants.

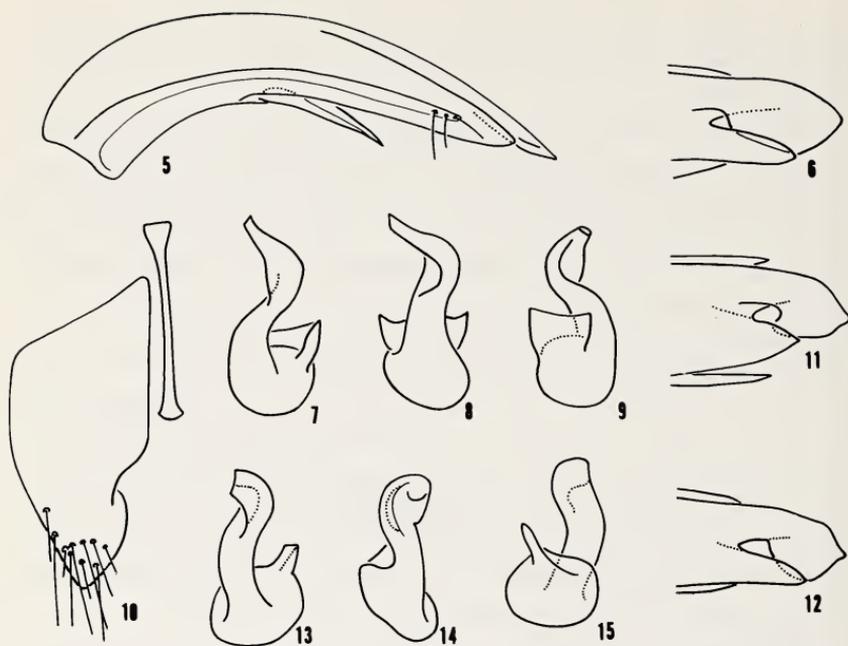
Description. Body color brown. Size 1.9-2.3 mm; 1.4-1.5 mm wide; 1.3-1.5 times as long as wide, widest across pronotum. Pronotum 1.7-1.8 times as wide as long. Elytral width across scutellum tip 1.0-1.1 times elytral length from scutellum tip. Stiff semi-erect hairs on head, prothorax, and elytra. Pronotal striae absent but very fine and light microsculpture present. Elytral striae distinct, about three per 0.1 mm. Aedeagus tip narrower (fig. 12), with terminal setae, and downcurved tip in side view. Spermatheca with shorter crest on flattened anterior bulb (figs. 13-15).

Variation. No variation is noted.

Etymology. The name refers to the arid grassland and shrub desert region of Texas and New Mexico and adjacent parts of Mexico.

Field notes. The type habitat (in Culberson Co.) is a shrub and cactus desert. The dominant plant is perennial broomweed, *Xanthocephalum sarothrae* (Pursh) Shinnars. The beetles were collected here by digging laterally into the ant nests from the side of a small ravine, and aspirating the ants and beetles as they appeared.

Biology. The beetle is probably widespread in nests of the harvester ant, *Pogonomyrmex maricopa* Wheeler, throughout much of the Chihuahuan region. The ant itself has a wider range in the arid southwest (Creighton, 1950; Cole, 1968). Dr. Foster has provided the following additional observations. Beetle larvae have been found in ant nests only at depths of over two feet, and larvae are usually in the presence of ant brood. Both larvae and adults appear to be free living, and no contact with the ants or trophallaxis or phoresy has been observed. There appears to be a single generation per year, with eggs being deposited early in the spring, mature larvae appearing by early September, and the winter passed as an adult. Additional careful study of the habits of the beetle is needed.



Figures 5-15. Structures of *Echinocoleus*. 5. *E. setiger*, holotype, lateral view of aedeagus. 6. *E. setiger*, holotype, dorsal view of aedeagus tip. 7, 8, and 9. *E. setiger*, three views of spermatheca, from Galiuro mountains, Arizona. 10. *E. sonorensis*, right genital plate and spiculum gastrale, holotype. 11. *E. sonorensis*, holotype, dorsal view of aedeagus tip. 12. *E. chihuahuensis*, allotype, dorsal view of aedeagus tip. 13, 14, and 15. *E. chihuahuensis*, holotype, three views of spermatheca.

PHYLOGENY, SPECIATION, AND ZOOGEOGRAPHY

The genus is a specialized offshoot of a New World *Ptomaphagus* (*Adelops*) ancestor which has taken up a life of myrmecophily, with all the behavioral and morphological specialization that this implies and requires (Wilson, 1971). The spermatheca suggests that the genus is derived from the *consobrinus* species group of *Ptomaphagus*. One species within this group, *P. texanus* Melander, occurs today in *Pogonomyrmex* nests at Austin, Texas (Peck, 1973). Another myrmecophilous catopine genus, *Synaulus*, is a North African derivative of an Old World *Ptomaphagus* (*Ptomaphagus*) ancestor.

A phylogenetic interpretation of characters in *Echinocoleus* as a genus, with the *Ptomaphagus consobrinus* species group as the comparative sister group, leads to an interpretation of the following

generic characters as apotypic; the limuloid shape, the lack of a mesosternal carina, and the long, semi-erect hairs. These are obvious adaptations to myrmecophily. Other characters vary between the species and are judged to proceed from a plesiotypic to an apotypic state as follows: long dorsal hairs on all dorsal surfaces to on elytra only; pronotal striae present to absent; elytral striae from closely spaced to widely spaced; aedeagus tip from narrow to broad in dorsal view; color dark brown to light brown; and spermatheca crest from narrow to elongate. Comparison of these states with data given in the species descriptions leads to the conclusion that *E. sonorensis* possesses the greatest number of apotypic characters, *E. chihuahensis* possesses a mixture of pleisotypic and two intermediately apotypic characters, and *E. setiger* possesses all but one character in a pleisotypic condition. A parsimonious splitting sequence is determined by that involving the fewest convergencies (Ball, 1976). Thus, *sonorensis* is the sister group of the stock that gave rise to the other two species. In this scheme the reduction of pronotal striae, coarsening of elytra striae, and pronotal broadening have each occurred twice.

Using this phylogenetic interpretation, applying the zoogeographic and evolutionary clues of Darlington (summarized by Erwin, 1970: 184), and considering known and surmised paleobotanic and paleoclimatic conditions, I propose the following scenario of sequential events.

1. The aridity of the southwest increased in the second half of the Tertiary. Grasslands and thorn scrub desert areas developed in the Miocene, especially in the rain shadows of the developing mountain ranges (Axelrod, 1958; Cohn, 1965). Since I know of no speculation of the subject, I suggest that *Pogonomyrmex* and *Novomessor*, both comparatively primitive myrmecine ant genera came to occupy these developing arid habitats at this time. The ants were already present because *Pogonomyrmex*, *Aphaenogaster*, and *Messor* (interpreted by Creighton (Wheeler and Creighton, 1934: 360) as *Pogonomyrmex*) occur in the Upper Oligocene Florissant shale of Colorado (Carpenter, 1930).

2. The increasing aridity of the late Pliocene and especially of the Pleistocene led to development of part of the already existing southwestern Madro-Tertiary Geoflora into the diverse and distinct Sonoran desert vegetation (Axelrod, 1958).

3. A species of *Ptomaphagus* in the *consobrinus* group invaded

Pogonomyrmex ant nests in the developing Pliocene Sonoran desert, became isolated and, under selective pressures applied by ants, differentiated into *Echinocoleus*.

4. This early *Echinocoleus* extended its range eastward into higher elevation grassland and woodland habitats and eventually into the Rio Grande River drainage and the developing Chihuahuan desert. The lack of similarity in the vegetation of the two deserts show they have been isolated by intervening regions of forest, woodland, or grassland since the start of Tertiary regional aridity.

5. The ancestral *Echinocoleus* separated into a lower elevation *sonorensis* ancestor and a higher elevation *setiger-chihuahuensis* ancestor, and the first proceeded to differentiate more rapidly than the second, probably through ant-applied selective pressures.

6. The separation of the woodland-grassland range of *setiger-chihuahuensis* into an eastern (Texas-New Mexico) *chihuahuensis* ancestor and a western (Arizona) *setiger* ancestor occurred during a Pleistocene glacial when extensive conifer forests occupied the north-south trending mountainous region of eastern Arizona and western New Mexico (Martin and Mehringer, 1965). The forest extended south to the Sierre Madre Occidental at the western edge of the Mexican Plateau. In at least the last glacial this forested barrier was unsuited for *Pogonomyrmex* and thus for *Echinocoleus*, and it was probably similarly unsuited in earlier glacials. During these glacials, the Sonoran desert was diminished in size and pushed closer to the Gulf of California, and the Chihuahuan desert was reduced to lower elevation regions of the Rio Grande drainage (Wells, 1966). This greater separation of arid Sonoran and Chihuahuan regions is known to have caused range separation, divergence, and formation of species pairs in many groups of arid-land insects (Cohn, 1965; Howden, 1969).

7. The western *setiger* ancestor shifted, into an occupation of *Novomessor* ant nests.

8. The three isolated stocks of *Echinocoleus* then differentiated into the three present species.

9. Since the last glacial maximum, some of the species of *Pogonomyrmex* have expanded from either or both of their contracted Sonoran or Chihuahuan refugia to their presently continuous and overlapping ranges, covering most of the southwestern US. *Echinocoleus* came to occupy their present non-overlapping ranges following the ants' readjustments to the present, post-glacial climatic-vegetational conditions.

I hope that this hypothetical series can be further tested with additional information on yet unknown species, and on additional distributional and host data for the known species.

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THE SPIDER GENUS *TINUS* (PISAURIDAE)*

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This paper is the third in a series of generic revisions of the pisaurids of the western hemisphere. It represents the first attempt to bring together all published information with the results of an extensive examination of all available collections of the genus. For those workers who are particularly interested in the fauna of the continental United States, *Tinus* is one of four pisaurid genera found in the area. *Dolomedes* and *Pisaurina* were revised earlier (1973 & 1972 resp.) and *Trechalea* is in progress.

Unfortunately there are no published accounts of the natural history of any *Tinus* species. Based on a few labels with *T. nigrinus* specimens and the author's sketchy observations, it seems that the habitat is quite similar to *Dolomedes*, i.e. on the faces of rocks and tree trunks, and in trash or vegetation near the margins of bodies of fresh water. The female carries the spherical egg sac in a typical pisaurid manner by holding it with the chelicerae and a thread from the spinnerets. The egg sac is white, opaque or translucent when new, and usually darkens to a brownish color with age. Only nursery webs for *T. nigrinus* and *T. ursus* are known, and their descriptions are given in the Natural History sections of each species.

The superficial body shape, eye patterns, and biology of *Tinus* suggest an affinity with *Dolomedes*. There is also a superficial resemblance to *Thaumasia*; but whether *Tinus* might be a subgenus of the latter as Gertsch suggests (1940) is a matter that must await a revision of that genus. In any case, *Tinus* is clearly a group distinct from all other pisaurids studied and is strictly limited in its distribution to southern North America, from the southwestern United States southward to Costa Rica in Central America.

Too little is known about the genus to confidently trace its phylogeny, but the apparently restricted distributions of four of the seven species suggests the kind of stream isolation situation described earlier for *Dolomedes* (Carico, 1973).

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I am also grateful to Herbert W. Levi for his review of the manuscript, and his help in obtaining type specimens. Lynchburg College provided publication expenses.

Tinus F. Pickard-Cambridge

Tinus Pickard-Cambridge, F., 1901, Biol. Centrali-America, 2:310. Type by monotypy, *Tinus nigrinus* F. Pickard-Cambridge.

Description. *Carapace:* moderately high, longer than wide. *Eyes:* posterior row moderately recurved, PE subequal and larger than AE, PME closer to each other than to PLE; anterior row slightly procurved, AME larger than ALE and closer to them than to each other, ocular quadrangle wider at top than at bottom and higher than height of clypeus. *Sternum:* lanceolate, about as long as wide. *Chelicerae:* moderately robust with three promarginal, three retro-marginal teeth on fang furrow. *Legs:* spinose, unmodified, III shortest, I, II, IV subequal. *Abdomen:* longer than wide, greatest width at the middle, slightly overlaps posterior edge of carapace. MALE. *Pedipalp:* median apophysis spatulate, membranous, usually white, directed anteriorly; *conductor* conspicuous, spatulate, directed anteriorly, located laterally; *embolus* long, slender, coiled 3-5 times; *tegulum* membranous, screw-shaped with 3-6 lamellae visible; *tibial apophysis* arises dorsally, bends retrolaterally, sometimes bifid with a dorsal spur. FEMALE. *Epigynum:* pair of lateral hemispherical elevations, median elevation present or absent. *Internal copulatory apparatus:* variable.

Note: Body conformations and eye characteristics among the various species are quite uniform and offer few useful diagnostic characters. The different relative overall sizes of some species, measured in carapace length, is an obvious exception.

The dorsal color pattern of most species also offers little help because of the variability within each species and the overlapping of the characteristic features of the pattern. A "typical" color pattern can be exemplified by that of *Tinus peregrinus* (Fig. 2). The cara-

pace has a median dark band with a submarginal, variably distinct, light band. The dorsum of the abdomen has a median dark band with a characteristic outline, notably a deep indentation on each side, bordered by a light band which is lightest in the indentations of the median band.

The following descriptions of each species, therefore, will not deal with the details of those features shared by most species. Characteristics of the genitalia are the most useful for identification. No attempt was made to distinguish juveniles because of the lack of adequate material.

UNCERTAIN SPECIES

Dolomedes minor Banks, 1898, Proc. California Acad. Sci., 3rd series, 1(7):277, pl. 17, fig. 6. Bonnet, 1959, Bibliographia Araneorum, 2:1534. *D. minoratus* nomen novum, Roewer, 1954, Katalog der Araneae, 2(a):133. Type localities in Mexico are: San Jose del Cabo, Sierra San Lazaro (Baja California del Sur); Guaymas (Sonora); Tepic (Nayarit). All of Banks' specimens were destroyed in the Great San Francisco Earthquake. From his description of the abdomen and figures of the male and female genitalia, it is clear that this is a *Tinus*. It is not certain whether it is *T. peregrinus*, as I stated earlier (1973), or *T. nigrinus* which also is probably found in the area. Only specimens from all his localities will help resolve the problem. If *D. minor* should prove to be synonymous with *T. peregrinus*, then the latter name will be invalidated.

KEY TO ADULTS OF SPECIES OF *TINUS*

1. Males 2
- Females 6
2. Length of the carapace less than 4.0 mm; carina on the anterior-medial margin of the chelicerae *Tinus minutus*
- Length of the carapace more than 4.0 mm; no carina on chelicerae 3
3. Conspicuous, curved, dorsal spur arising from the bifid tibial apophysis 4
- Tibial apophysis not bifid 5
4. Three lamellae on tegulum (Fig. 12) *Tinus tibialis*
- Six lamellae on tegulum (Fig. 16) *Tinus palictus*

5. Three lamellae on tegulum; median apophysis small, not expanded distally (Fig. 10) *Tinus peregrinus*
 Five lamellae on tegulum; median apophysis large, expanded distally (Fig. 8) *Tinus nigrinus*
6. Length of carapace less than 4.2 mm 7
 Length of carapace more than 4.2 mm 8
7. Pair of conspicuous oval atria in epigynum (Fig. 30); carapace length more than 3.3 mm *Tinus ursus*
 No conspicuous oval bursal openings present in epigynum (Fig. 24); carapace length less than 3.3 mm *Tinus minutus*
8. Median elevation of epigynum absent (Fig. 20)
 *Tinus peregrinus*
 Median elevation of epigynum present 9
9. Median elevation of epigynum about half width of epigynum; lateral elevations widely separated (Fig. 26)
 *Tinus prusius*
 Median elevation of epigynum distinctly less than half width of epigynum; lateral elevations not widely separated
 10
10. Median elevation of epigynum widely separated from lateral elevations (Fig. 22) *Tinus tibialis*
 Median elevation of epigynum not widely separated from lateral elevations 11
11. Bursa copulatrix extends from its anterior origin into area of epigynum (Fig. 29) *Tinus palictus*
 Bursa copulatrix extends from its anterior origin to about midway in epigynum (Fig. 19) *Tinus nigrinus*

Tinus nigrinus F. Pickard-Cambridge

Figures 1, 8, 9, 18, 19: Map 1

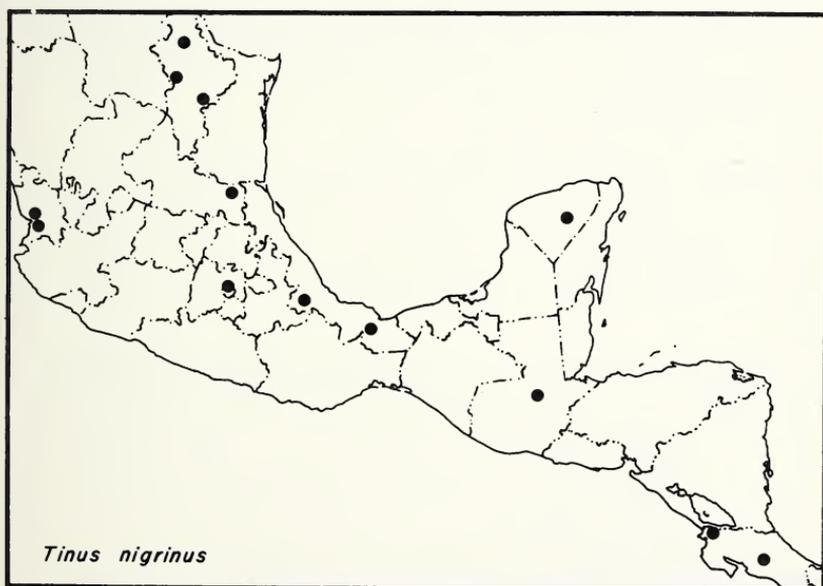
Tinus nigrinus F. Pickard-Cambridge, 1901, Biol. Centrali-America, no. 2:304, 310, 311, pl. 30, figs. 8, 8a, 8b, 9. Male holotype and female paratype from Guatemala in British Museum (Natural History), examined. Simon, 1903, Hist. nat. Araignées, 2:1045. Roewer, 1954, Katalog der Araneae, 2(a):142. Bonnet, 1959, Bibliographia Araneorum 2(5):4622.

Diagnosis. The male palpus of this species shares only with *T. peregrinus* the narrowed tip of the conductor, but is distinguished from the latter by a distinctly larger median apophysis and a small, distinct tubercle on the prolateral medial margin of the cymbium.

The epigynum of both *T. nigrinus* and *T. palictus* share the similar characteristic of a small, free, anterior median elevation. The length of the bursae copulatrix, as seen ventrally, provides the surest separation of the females of these two species.

Description. *Carapace:* average length of males 6.4 mm (6.0-7.9, N=4), average length of females 5.73 mm (4.5-6.7, N=18); broad, dark, median band; light submarginal bands. *Legs:* (1-2-4)-3. *Abdomen:* median band with typical shape (Fig. 1). **MALE.** *Pedipalp:* (Figs. 8, 9) *tibial apophysis* broad, arises apically on dorsal side, bends laterally, terminates in two tubercles; *conductor* narrowed apically; *median apophysis* rounded, conspicuous, semitransparent, widest apically; *tegulum* with 5 distinct lamellae; *cymbium* with distinct tubercle on polateral margin near base of conductor. **FEMALE.** *Epigynum:* (Fig. 18) *lateral elevations* hemispherical, broadly in contact; *median elevation* free, anterior to lateral elevations. *Internal copulatory apparatus:* (Fig. 19) *bursae copulatrix* located in anterior half of epigynum; *fertilization tubes* series of conjoined, transparent, flexible lamellae, coiled around a central core.

Natural History. Biological data are almost completely absent from labels with museum specimens. The only reference is to



Map 1. Distribution of *Tinus nigrinus* F. Pickard-Cambridge.

"sweeping stream vegetation" and the occasional mention of a stream name. I have collected this species in Nuevo Leon while searching for *Dolomedes*. Like *Dolomedes* it is found among rocks along the stream, perched head down but higher from the water. One female with an egg sac was taken from a sheet web under a boulder. Broken emboli in the female copulatory apparatus and the absence of emboli from some palpal organs indicate that the embolus is often broken during copulation.

A gravid female and egg sacs are with two collections from northern Mexico, dated respectively late September and early August. An egg sac is in a Costa Rican collection dated February.

Distribution. Eastern Mexico from Nuevo Leon and Nayarit southward to Costa Rica.

Material examined. Six males, 40 females, 20 immatures.

Tinus peregrinus (Bishop)
Figures 2, 10, 11, 20, 21; Map 2

Thaumasia peregrinus Bishop, 1924, Bull. New York State Mus., 252:62-63, pls. 36, 37. Female holotype from Hot Springs, Arkansas in the New York State Museum, examined. Bishop and Crosby, 1936, Ent. News, 47:243-244. Gertsch and Davis, 1940, American Mus. Novitates, 1059:14.

Tinus peregrinus-Gertsch, 1940, (rev. ed. Comstock, 1912, Spider Book), pp. 622, 631, 633, figs. 707, 708. Kaston, 1953, How to Know the Spiders, p. 137.

Thaumasia peregrina-Roewer, 1954, Katalog der Araneae, 2(a)141. Bonnet, 1959, Bibliographia Araneorum, 2:4416.

Diagnosis. For a comparison between the male palpus of this species and *T. nigrinus*, which it most closely resembles, see the diagnosis of the latter species. The epigynum of the female lacks the median elevation, but may have a dark area between the lateral elevations which might represent the rudiments of the median elevation.

Description. *Carapace:* average length of males 5.04 mm (4.3-5.5, N=8), average length of females 6.49 mm (5.0-7.8, N=8); broad, dark, median band; light submarginal bands. *Legs:* (4-2-1)-3. *Abdomen:* median band with typical shape (Fig. 2). *MALE. Pedipalp:* (Figs. 10, 11) *tibial apophysis* broad, arises apically on dorsal side, bends laterally and terminates in two tubercles; *conductor* narrowed apically; *median apophysis* rounded, inconspicuous, not distinctly widest apically, white; *tegulum* with 3 distinct lamellae; *cymbium* with elevation on prolateral margin near base of conductor. FE-

MALE. *Epigynum*: (Fig. 20) *lateral elevations* hemispherical, broadly in contact; no *median elevation* present, median concavity between anterior areas of lateral elevations. *Internal copulatory apparatus*: (Fig. 21) *bursae copulatrix* small, located in central area of epigynum; *fertilization tubes* distinct, relatively short, composed of convolutions located in ventral area of epigynal cavity.

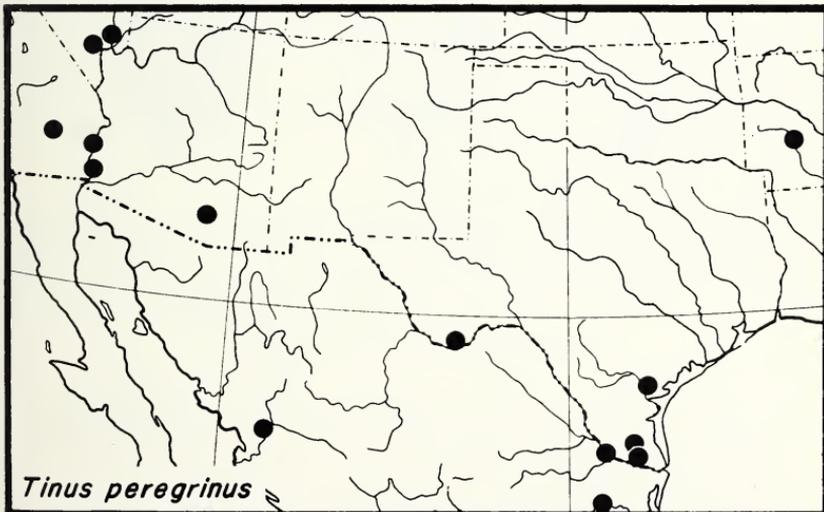
Natural History. The labels with the museum specimens provided little information. An occasional reference to a stream and a single collection from the wall of a mine near water is all that is provided. The author has collected adults from southern Texas, where they were found near bodies of water, which is a similar habitat to that of *Dolomedes*.

Egg sacs are in collections from Arizona and Texas, dated late July and early August.

Distribution. Southwestern United States from southern California and Nevada through southern Texas to Missouri, and in northern Mexico from southern Sonora to Nuevo Leon.

Material examined. Fifteen males, 52 females, and 34 immatures.

Note: The state of the type locality, Hot Springs, Arkansas, may be in error. Arkansas seems to be outside the normal range for this species. There are other specimens from Hot Springs, Texas, which is within the range. It is suggested, then, that Texas may be the actual state of the type specimen.



Map 2. Distribution of *Tinus peregrinus* (Bishop).

Tinus tibialis F. Pickard-Cambridge
Figures 3, 12, 13, 22, 23

Tinus tibialis F. Pickard-Cambridge, 1901, Biol. Centrali-America, no. 2:310, 311, pl. 30, figs. 10, 10a, 10b, 11. Male holotype and female paratype from Cuernavaca, Mexico in British Museum (Natural History), examined. Roewer, 1954, Katalog der Araneae, 2:142. Bonnet, 1959, Bibliographia Araneorum, 2:4622.

Diagnosis. Only *T. tibialis* and *T. palictus* have a bifid tibial apophysis with a conspicuous, dorsal spur. The two are distinguished by the number of lamellae on the tegulum; three for *T. tibialis* and six for *T. palictus*. The epigynum alone has a small, hood-like median elevation that arises from a large atrium which widely separates the median from the lateral elevations.

Description. *Carapace:* length of one male 5.5 mm, length of one female 6.0 mm; broad, dark, median band; light submarginal bands. *Legs:* (4-2-1)-3. *Abdomen:* median band with typical shape (Fig. 3). *MALE. Pedipalp:* (Figs. 12, 13) *tibial apophysis* arises dorsally and divided into two distinct parts, one part a dorsal curved spur, knobbed on tip, and a flattened part which bends laterally; *conductor* broad apically; *median apophysis* rounded, conspicuous, semitransparent, widest apically; *tegulum* with three distinct lamellae; *cymbium* with no distinct elevations on prolateral margin. *FEMALE. Epigynum:* (Fig. 22) *lateral elevation* hemispherical, not in contact with each other; small hood-like *median elevation* arises from large median cavity located anterior to lateral elevation. *Internal copulatory apparatus:* (Fig. 23) *bursae copulatrix* large, occupying space in posterior and anterior part of epigynal area; *fertilization tubes* looped, relatively short, located in posterior region of epigynal area.

Natural History. No data available.

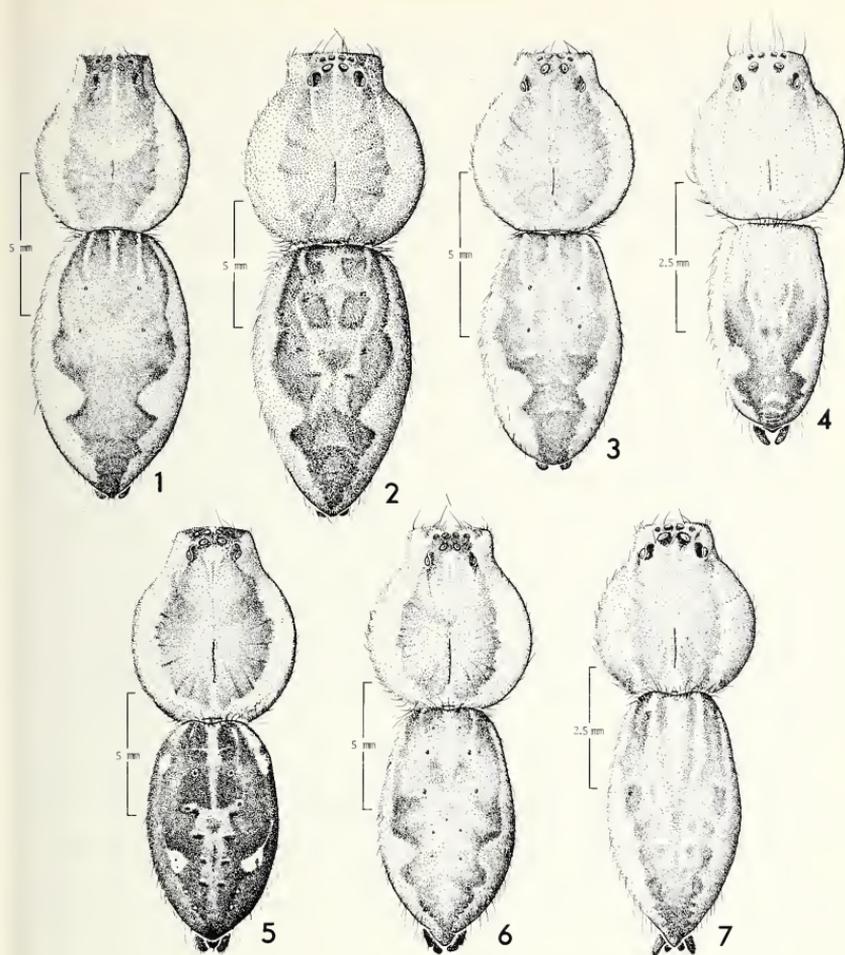
Distribution. Known only from type locality.

Material examined. One male, two females.

Tinus minutus F. Pickard-Cambridge
Figures 4, 14, 15, 24, 25; Map 3

Tinus minutus F. Pickard-Cambridge, 1901, Biol. Centrali-America, no. 2:31, 311, pl. 30, fig. 12. Female holotype from Teapa, Tabasco, Mexico in the British Museum (Natural History), examined. Roewer, 1954, Katalog der Araneae, 2(a): 142. Bonnet, 1959, Bibliographia Araneorum, 2(5):4622.

Diagnosis. This is the smallest species in the genus with the male carapace length less than 3.5 mm and the female carapace length less



Figures 1-7, Dorsal color patterns of females of species of *Tinus*, Fig. 1, *T. nigrinus* F. Pickard-Cambridge. Fig. 2, *T. peregrinus* (Bishop). Fig. 3, *T. tibialis* F. Pickard-Cambridge. Fig. 4, *T. minutus* F. Pickard-Cambridge. Fig. 5, *T. prusius* n. sp. Fig. 6, *T. palictus* n. sp. Fig. 7. *T. ursus* n. sp.

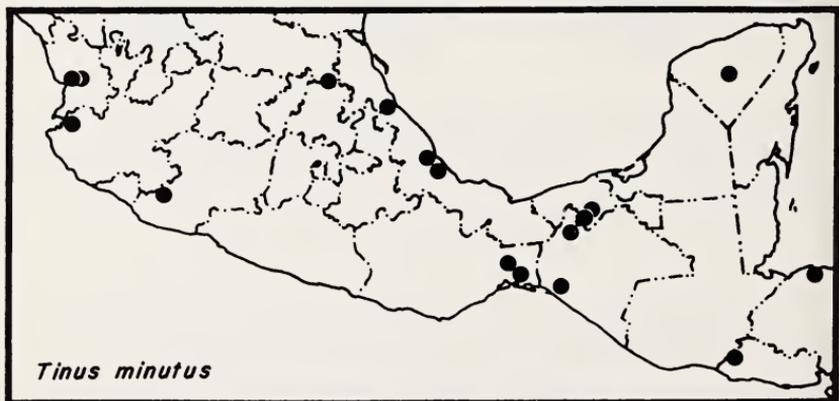
than 3.2 mm. The male palpal tibia has two small tubercles laterally near the margin. The internal copulatory apparatus of the female is relatively large, especially the bursae. Both sexes have a distinct carina on the anterior face of each chelicera.

Description. *Carapace:* average length of males 2.99 mm (2.7-3.4, N=8), average length of females 2.89 mm (2.6-3.1, N=8); broad dark median band; narrow light submarginal bands. *Legs:* (1-2-4)-3. *Abdomen:* median band with typical shape, paler anteriorly; pair of converging longitudinal light stripes (Fig. 4). **MALE.** *Pedipalp:* (Figs. 14, 15) *tibial apophysis* broad, arises apically on dorsal side, bends laterally, terminates in a single acute apex; small, acute tubercle near apical tibial margin, prolaterally and retrolaterally; *conductor* broad; *median apophysis* broad, white, mostly hidden behind conductor; *tegulum* with 2 distinct lamellae; *cymbium* with obscure elevation on prolateral margin. **FEMALE.** *Epigynum:* (Fig. 24) *lateral elevations* hemispherical, broadly in contact or opposed; *median elevation* hood-like, indented or rounded posteriorly, in contact with lateral elevations. *Internal copulatory apparatus:* (Fig. 25) *bursae copulatrix* very large, occupying most of epigynal area; *fertilization tubes* flattened, large, closely appressed against bursae.

Natural History. No data available.

Distribution. From the Mexican states of Nayarit and San Luis Postosi southward to Guatemala and El Salvador.

Material Examined. Thirty-four males, 41 females, 15 immatures.



Map 3. Distribution of *Tinus minutus* F. Pickard-Cambridge.

***Tinus prusius* new species**

Figures 5, 26, 27

Types. A female holotype, a female paratype, and seven juveniles from Prusia, Chiapas, Mexico, April-May 1942, collected by H. Wagner, in the American Museum of Natural History.

Etymology. The name is derived from the name of the type locality.

Diagnosis. Both female types have a distinctly dark dorsum with an obscure median dark band and white spots (Fig. 5). The epigynum has a large median hood-like elevation which separates the lateral elevations.

Description. *Carapace:* length of holotype 7.6 mm (paratype damaged); broad dark median band; broad light submarginal bands extend laterally almost to margin; clypeus dark except for median white spot. *Legs:* paratype 4-2-1-3 (holotype has first pair missing); color generally dark with light areas on dorsal surfaces of femora, light annuli on segments distal to patella. *Abdomen:* quite dark dorsally and laterally; median band obscure; pair of large white spots anteriorly, and posteriorly (approximately at indentations of median band); two pairs of small white spots posteriorly; median serrated light area posteriorly. *Epigynum:* (Fig. 26) *lateral elevations* widely separated, *median elevation* elevated, broad, emarginated posteriorly, hood-like. *Internal copulatory apparatus:* (Fig. 27) *bursae copulatrix* small, arising from posterior part of median elevation; *fertilization tubes* small, looped tightly against spermatheca.

Natural History. No data available.

Distribution. Known only from the type locality.

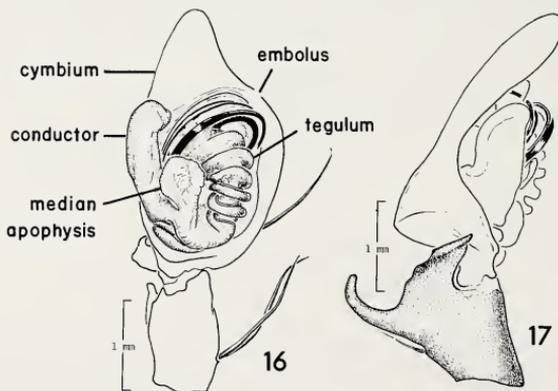
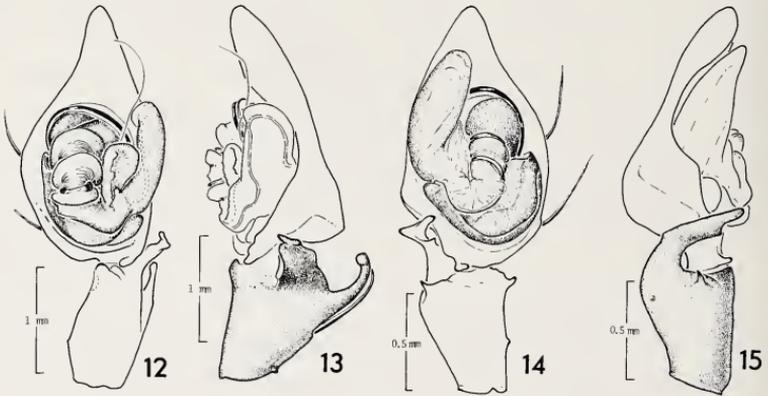
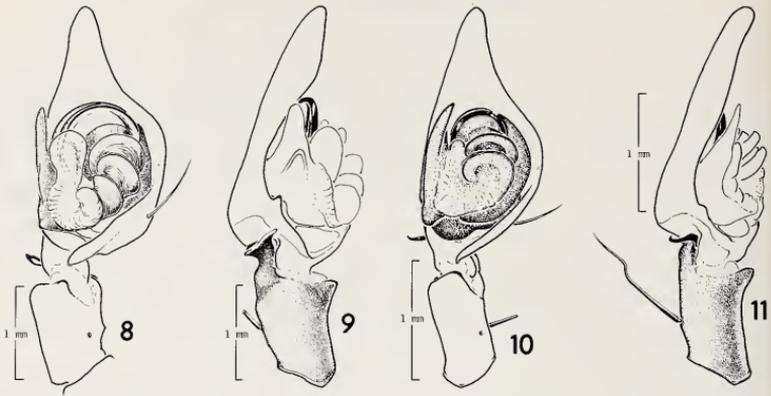
Material Examined. Two females, seven juveniles (type collection). Males unknown.

***Tinus palictlus* new species**

Figures 6, 16, 17, 28, 29

Types. A male holotype and a female paratype from Palictla, San Luis Potosi, Mexico, 1-5 Sept. 1946, collected by C. M. Bogert, in the American Museum of Natural History.

Etymology. The name is derived from the name of the type locality.



Diagnosis. See the diagnosis of *T. tibialis* for a comparison with the similar male palpus. The epigynum and internal copulatory apparatus resembles most that of *T. peregrinus*, and one should consult the diagnosis of the latter species for a comparison.

Description: Carapace: length of male 7.1 mm, length of female 7.3 mm; broad, dark, median band; wide, submarginal light bands. *Legs:* (2-1)-4-3. *Abdomen:* median band with typical shape (Fig. 6). *MALE. Pedipalp:* (Figs. 16, 17) *tibial apophysis* arises dorsally, divides into two distinct parts, one part a dorsal curved spur, other flattened part bends laterally; *conductor* broad, curved apically; *median apophysis* rounded, conspicuous, semi-transparent, widest apically; *tegulum* with 6 distinct lamellae; *cymbium* with no distinct elevations on prolateral margin. *FEMALE. Epigynum:* (Fig. 28) *lateral elevations* large, elongated, in contact with each other; *median elevation* small, elongated, free, located anteriorly between lateral elevations. *Internal copulatory apparatus:* (Fig. 29) *bursae copulatrix* narrow, nearly parallel, arises anteriorly; *fertilization tubes* a series of conjoined transparent, flexible lamellae coiled against a central core.

Natural History. No data available.

Distribution. Known only from the type locality.

Material examined. One male, one female, one juvenile (type collection).

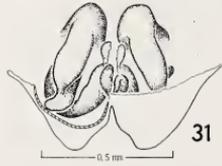
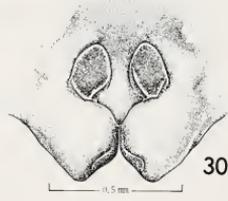
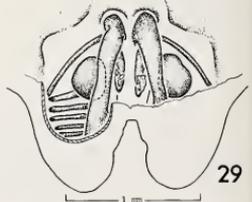
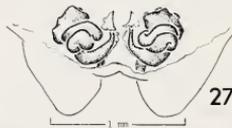
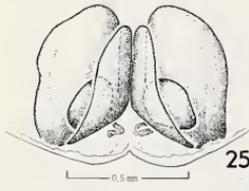
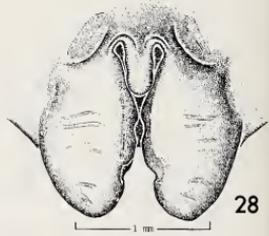
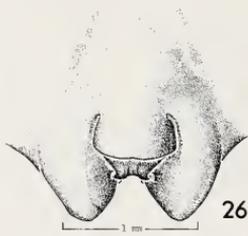
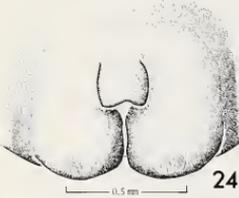
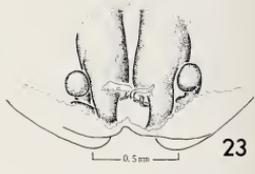
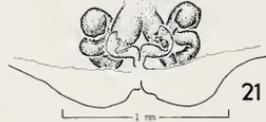
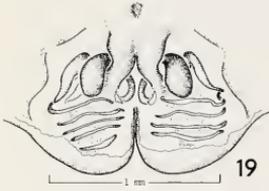
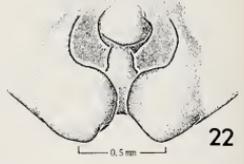
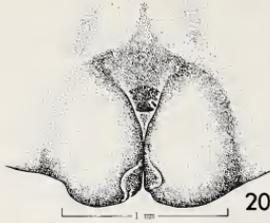
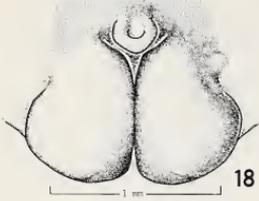
***Tinus ursus* new species**

Figures 7, 30, 31

Types. A female holotype, five female paratypes, and four juveniles from Rincón de Osa, Costa Rica, 27 February 1967, collected by Carlos E. Valerio. Holotype deposited in the Museum of Comparative Zoology, and paratypes deposited in the Museo de Zoologica, University of Costa Rica.

Figures 8-17, Male palpi of species of *Tinus*. Figs. 8-9, *T. nigrinus* F. Pickard-Cambridge, right palpus. 8, Ventral view. 9, Prolateral view. Figs. 10-11, *T. peregrinus* (Bishop), right palpus. 10, Ventral view. 11, Prolateral view. Figs. 12-13, *T. tibialis* F. Pickard-Cambridge, left palpus. 12, Ventral view. 13, Prolateral view. Figs. 14-15, *T. minutus* F. Pickard-Cambridge, right palpus. 14, Ventral view. 15, Prolateral view. Figs. 16-17, *T. palictus* n. sp., right palpus. 16, Ventral view. 17, Prolateral view.

Note the exposed embolus tip in Figs. 12 & 13. Normally it is contained in a concavity behind the conductor.



Etymology. The name is from the latin noun for bear.

Diagnosis. The length of the carapace, ranging between 3.5 mm and 3.9 mm, places its size, without overlap, between the smaller *T. minutus* and the remainder of the species which are larger. The epigynum is distinctive with a pair of oval atria.

Description. *Carapace:* average length of females 3.63 mm (3.5-3.9 N=6); broad dark median band, narrow light submarginal bands; dusky marginal band. *Legs:* (1-2)-4-3. *Abdomen:* median dark band without typical lateral, large indentations; narrow light bands within median dark bands converge posteriorly (Fig. 7). *Epigynum:* (Fig. 30) *lateral elevations* in contact; *median elevation* widest posteriorly, joined to lateral elevations, narrowed into an isthmus anteriorly which separates two large oval atria. *Internal copulatory apparatus:* (Fig. 31) *bursae copulatrix* moderately broad, arises anteriorly; *fertilization tubes* curved, relatively short.

Natural History. According to Carlos E. Valerio, his field notes for collection number CEV-366 contain the following information: ". . . adult females rolled green leaves to use as retreats. These retreats were found near the water (5-15 cm above water level). Many females had egg sacs at time of collection, holding them with the chelicerae against the sternum. Males were not found. Immatures (if the same species) had small webs located mainly in the holes of chewed up leaves . . ." (1976). A simple ovate-lanceolate leaf with serrate margins from an unidentified plant is in the collection jar. The leaf measures 4 cm × 10.5 cm and has the margins tied together to form a tube of 1.25 cm in diameter. Debris in the retreat includes spiderlings and the appendages of a single damselfly (Calopterygidae).

Distribution. Known only from the type locality.

Material examined. Six females, seven juveniles. Males unknown.

Figures 18-31, Epigyna of species of *Tinus*. Figs. 18-19, *T. nigrinus* F. Pickard-Cambridge. 18, Ventral view. 19, Dorsal view. Figs. 20-21, *T. peregrinus* (Bishop). 20, Ventral view (note base of embolus protruding from atrium). 21, Dorsal view. Figs. 22-23, *T. tibialis* F. Pickard-Cambridge. 22, Ventral view. 23, Dorsal view. Figs. 24-25, *T. minutus* F. Pickard-Cambridge. 24, Ventral view. 25, Dorsal view. Figs. 26-27, *T. prusius* n. sp. 26, Ventral view. 27, Dorsal view. Figs. 28-28, *T. palictus* n. sp. 28, Ventral view. 29, Dorsal view. Figs. 30-31, *T. ursus* n. sp. 30, Ventral view. 31, Dorsal view.

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ADULT AND IMMATURE CALVERTIELLIDAE
(INSECTA: PALAEODICTYOPTERA) FROM THE
UPPER PALEOZOIC OF NEW MEXICO AND
CZECHOSLOVAKIA*

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It is generally agreed that insects have been abundant since the Upper Paleozoic. However, occurrences of fossil insects in the Upper Carboniferous and Permian are quite rare, mainly because of the scarcity of deposition sites. Especially rare are localities that yield a diverse and well preserved assemblage sampling a large community. This is regrettable since the insects, through their enormous dispersal potential and rapid evolution, are well suited for paleobiogeographical studies, especially for comparisons on an intercontinental level. It is assumed that Paleozoic plants and insects coevolved through a close and mutual association, and that this interaction, on all levels of development, was of fundamental importance in directing evolutionary trends. Hence researches on fossil insects and plants complement each other and hold great potential for paleogeography, paleoclimatology and stratigraphy of the Upper Paleozoic, as well as for theoretical evolutionary studies in both groups.

On the entire North American continent there are at present only two localities which have yielded a rich and diverse fossil insect fauna comparable to the best Paleozoic localities of Europe and Asia: Mazon Creek, Illinois (Middle Pennsylvanian deposits equal to Westphalian C-D of the European divisions), and Elmo, Kansas (Lower Permian deposits). Concerning potentially promising regions, the Upper Paleozoic strata of New Mexico have attracted the attention of specialists in the last decade through random discoveries of fossil insects (8 specimens from the Manzanita Mountains, SE of Albuquerque, and one specimen from Santa Fe Creek, Santa Fe). Those fossils suitable for description were treated by Carpenter (1970). Since the North American West is important in spanning the gap in paleobiogeographical knowledge of the

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Paleozoic entomofauna, there is a need for a systematic search for new localities in New Mexico and other western states.

In the summer of 1975 we searched for insect fossils in the Manzanita Mountains, in a clay pit SE of Albuquerque, on New Mexico highway 10 (14 on some maps). In these deposits, presumably of late Pennsylvanian (Virgilian) age, five insects had previously been found by the paleobotanist Dr. S. Mamay (U.S. National Museum, Washington) and three were discovered by students of the Department of Geology, University of New Mexico, Albuquerque. We found 20 additional specimens but neither the composition of the insect assemblage nor the state of preservation was good enough for detailed study and the deposit was judged not worthy of extensive excavation. The material was redeposited and composed almost entirely of more resistant fragments of wings and of cockroaches, the tegmina of which are too variable in venation to be useful for taxonomic purposes.

However, on the same trip, during a visit to the University of New Mexico in Albuquerque, Dr. Barry Kues, Department of Geology, showed us and generously loaned interesting material that he found in Carrizo Arroyo, Valencia Co., about 22 miles SW of Albuquerque. The small but promising collection consists of two well preserved wings of Palaeodictyoptera (Calvertiellidae and Syntonopteridae), two Protorthoptera, and several Blattodea. The age of the Carrizo locality, judging from the plant fossils, is estimated as late Pennsylvanian (Virgilian), and this is close to the age of the two major European insect localities; the late Carboniferous (Stephanian) locality of Commentry, France, and the early Lower Permian (Upper Autunian) locality in Obora, Czechoslovakia.

This paper is concerned with the Palaeodictyoptera of the advanced family Calvertiellidae from New Mexico and from Czechoslovakia. The most notable character of the family is that many features of wing venation are suggestive of the Odonata: the simulated arculus, the "subnodal" cross veins, the general arrangement of the vein pattern, the serrated costa, the odonatoid character of the reticulation, the corrugation extended by intercalated sectors, the tendency to fuse R+M, the suppression of the CuA, and the development of simple, parallel and curved anal veins (Tillyard, 1925; Carpenter, 1943; Kukalova, 1955, 1964; Kukalova-Peck, 1974). These features do not indicate an immediate phylogenetic relationship with

Odonata, but are expressions of a genetically based "latent homology" (*sensu* de Beer, 1971); they occur independently and to lesser extent throughout the Paleoptera.

The family Calvertiellidae has previously been known only from the separated single fore and hind wings of adults. This paper describes the fore wings of a young nymphal instar and of a subimago from the Lower Permian of Obora, Czechoslovakia, and the hind wing of an adult from New Mexico, and briefly discusses the ontogenetic development of Paleozoic nymphs.

Concerning stratigraphy, the calvertiellids are distributed throughout Lower Permian strata; *Moraviptera reticulata* Kukalova was found in very early Lower Permian and *Moravia convergens* Kukalova in early Lower Permian in Czechoslovakia, and *Calvertiella permiana* Tillyard in late Lower Permian of Kansas. The specimen described here as *Carrizala arroyo* n. g. and n. sp. is the oldest known representative of the family, from the late Pennsylvanian of New Mexico. An attempt is made to identify those wing characters which tend to change successively with time, and to distinguish them from features which are more independently variable.

Adults and Pre-adults of the Calvertiellidae

Adult wings of Paleozoic Paleoptera have a straight or almost straight anterior margin and are held at right angles to the body. The nymphal wings are easily distinguishable by the characteristic "nymphal bend" at which the wing axis is turned more latero-posteriorly by the convex curvature of the anterior margin and the concave curvature of the posterior margin (figs. 1, 3, 4, 8). The wing bend was mentioned as occurring in Megasecoptera (Carpenter and Richardson, 1969; Kukalova-Peck, 1974) but was also present in Ephemeroptera (Kukalova, 1968, see figures) and in Palaeodictyoptera (Sharov, 1971, see figures; Wooton, 1972, see figures). It was probably also present in the still unknown nymphs of Paleozoic Odonata. During an individual's ontogeny, the nymphal bend becomes successively straightened (figs. 4A and B, 8) with each moult until it has completely disappeared in adult wings (figs. 2, 4C). In Megasecoptera as well as in Ephemeroptera, the nymphal bend is located in the proximal third of the wings (Kukalova, 1968, see figures; Carpenter-Richardson, 1969, see figures; Kukalova-Peck, 1974). In the calvertiellid Palaeodictyoptera and apparently

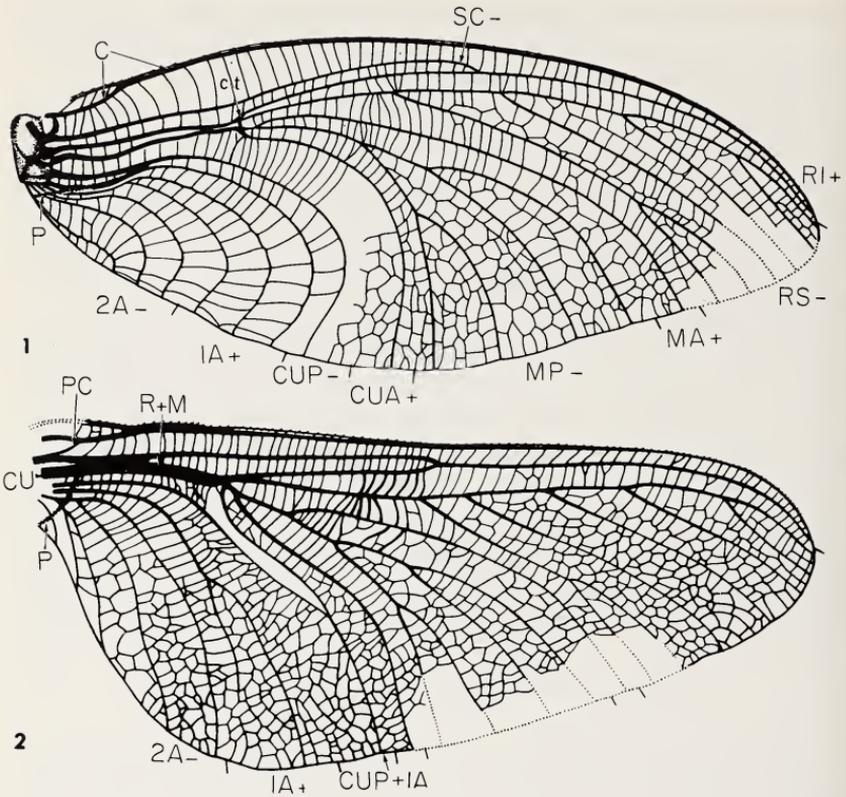


Fig. 1. *Moravia convergens*, subimaginal fore wing with highly convex anterior margin and narrowed wing tip. Lower Permian of Czechoslovakia. Original. P — anal brace.

Fig. 2. *Carrizopteryx arroyo*, n. sp., adult hind wing. Late Upper Carboniferous of New Mexico. Holotype. PC — postcostal vein; P — anal brace.

in many other nymphs with basally broad wings, the nymphal bend is limited to the distal half of the wings (fig. 3; Wootton, 1972, see figs. 1 and 2). During ontogeny, the bend is progressively shifted more distally in the older nymphal instars and in the subimagos (figs. 4A and B), until it is absent in the adult moult (fig. 4C). Thus, the angle of attachment to the body, as well as the outline of the anterior and posterior margin of the wings, changes successively and fluently, as indicated.

The nymphal wings in the Paleozoic insects are veined, articulated to the notum by pteralia, movable, and are generally considered to be functional (Sharov, 1957, 1966, 1971; Carpenter and Richardson, 1969; Kukalova, 1968; Wootton, 1972). The nymphal bend occurs only in those of the Paleoptera, the wings of which are phylogenetically bound both to be oriented laterally and to lack the ability of being flexed backwards over the abdomen. Nevertheless, the nymphal bend itself is not phylogenetically based in Paleoptera, but is adaptive. It is an alternative solution towards gaining the advantage of wing flexing, with the result that the developing wings do not impede as much the forward movement. This developed through an independent adaptation process which took place mainly in the young pre-adults (nymphs) and has nothing in common with the paleopterous or neopterous condition in the phylogenetic sense of these terms.

According to abundant fossil evidence, the fact that the immature stages of the ancestors of modern pterygotes had not solid but articulated and functional wing pads is completely contradictory to the validity of the paranotal theory, which derives the wings from the solid lateral notal expansions of the apterygotes. Were the paranotal theory correct the apparent paradox arises that the ancestral forms had hinged and complexly movable pads, while the descendants fell back to having "primitively" firmly attached wing pads, giving witness to their origin from paranota. However, the wing pads of modern nymphs were clearly secondarily immobilized and fused with the lateral margins of the terga. This adaptive process led to the more distinctively dimorphic condition between the pre-adult and adult stages in modern insects. The nymphal wing pads never had anything in common with paranotal expansions.

Moravia convergens Kukalova, young nymph

Figs. 3A-B, 4A, 6, 8

Moravia convergens Kukalova, 1964:162 (adult).

Occurrence: Lower Permian (Upper Autunian) of Obora, Czechoslovakia

Original: Specimen no. 1/1976 (obverse and reverse), deposited in the Paleontological Institute of Charles University, Prague, Czechoslovakia.

Two fore wings of a young nymph are available (actual length 9 mm, estimated full length 10.6 mm, maximum width 3.5 mm). In comparison, the length of the adult fore wing is 38 mm and the

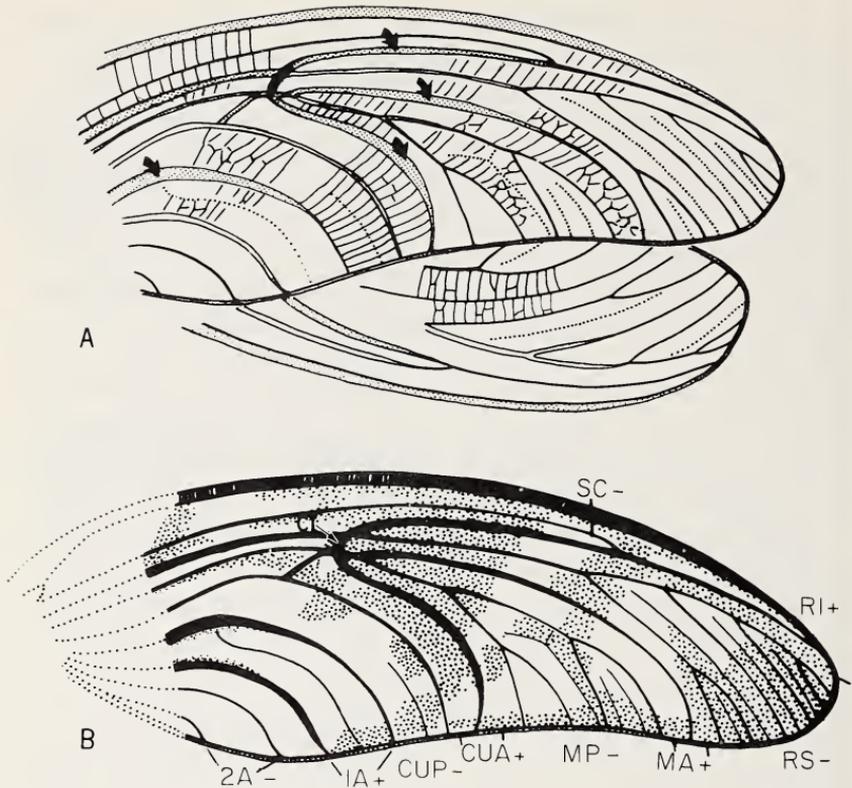


Fig. 3. *Moravia convergens*, young nymphal fore wings, with distal half curved posteriorly.

A. Actual specimen, arrows pointing to broad veinal blood sinuses.

B. Reconstructed wing pad with color pattern.

Lower Permian of Czechoslovakia. Original.

width 15 mm (Kukalova, 1964). The wings are not part of a shed cuticle, but are of a partially decomposed and redeposited dead nymph. The outlines of the next instar wings are clearly indicated inside the wing pads.

Several features of the *Moravia convergens* nymph are notably different from the characters common to all Recent pterygote nymphs and are as follows: 1) The venation is fully formed, corrugated, and cuticularized. In Recent nymphs the tubular venation

is never present, because it is secreted only during metamorphosis, shortly before the emergence of the adult or subadult. The faint ridges which indicate a simplified venation pattern on Recent nymphal wing pads are not functional veins but are residual surface structures. 2) The venation is identical with that of the adult wings. In Recent nymphs the pattern of blood channels (lacunae) which precede the veins usually approaches the pattern of adult venation only in the terminal nymphal instars. 3) The wing pads are freely articulated. In the *Moravia convergens* nymph the free attachment is indirectly proven through their easy release from the body after decomposition. In Recent nymphs, the wing pads early in development always become more or less fused together with the lateral margin of the terga, thus simulating continuous, lateral outgrowths.

As noted by Carpenter and Richardson (1969), the nymphs of Megasecoptera and Palaeodictyoptera were probably terrestrial. Equipped with identical mouthparts, they shared with the adults the same food and probably the same arboreal habitat. This finds support in the strongly cuticularized wing pads of *Moravia convergens*, armored with numerous, protruding tubercles (fig. 6). The most probable function of the tubercles is protection from abrasion. However, later in development, the cuticularized surface of the wing pads becomes thinner with an increase in size so that the subimaginal pre-adults have completely membranous wings (figs. 1, 7). The same process of thinning was observed in Paleozoic Neoptera (Protorthoptera) by Sharov (1957) and is common in Recent insects.

The wing venation of the *M. convergens* nymph has many adult characters: the tubular, corrugated venation; a well developed cross venation; recognizable intercalary sectors; and a distinct color pattern of oblique, irregular dark stripes (figs. 3, 6, 8). The prominent tubercles are restricted to young nymphs, and each carries a single hair or seta. These are arranged in rows on all veins as well as on the entire surface (fig. 6). The most notable nymphal character is the difference in the width between the convex and concave branches of the same vein-pairs. Thus, R1, MA, CuA, and both branches of 1A are conspicuously broad, much broader than their concave partners Rs, MP, CuP, and branches of 2A (figs. 3, 8). The veins are widened into broad vein-sinuses, as in some modern insects, i.e., the Embioptera. Since the present specimen is the obverse and reverse of the upper wing surface it is not known

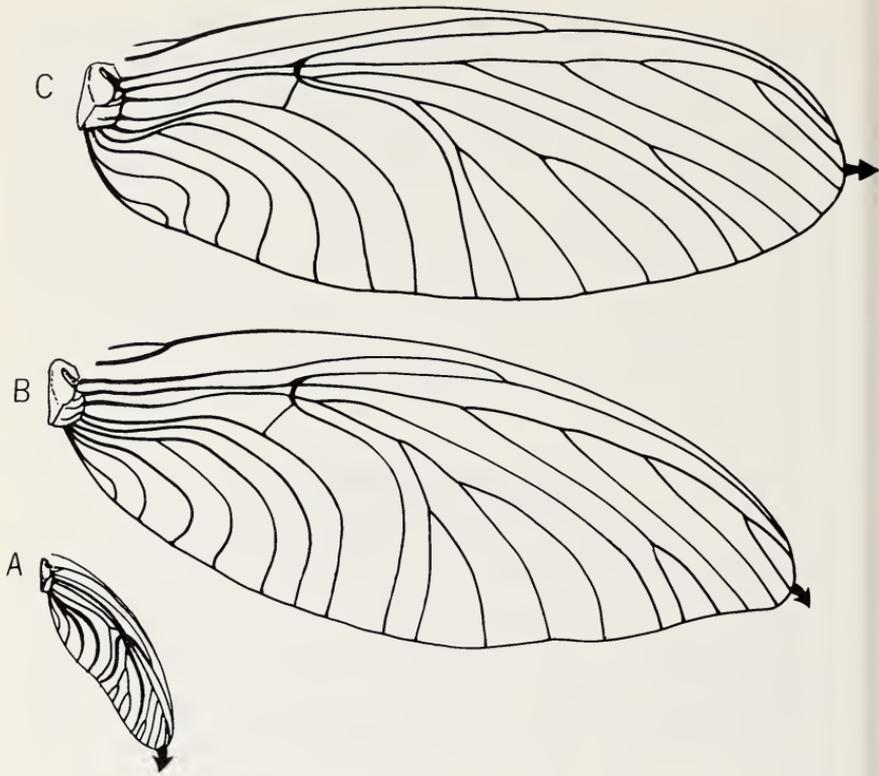


Fig. 4. Stages in the development of the fore wing in *Moravia convergens* showing changes in the longitudinal axis. A, Very young nymph; B, subimago; C, adult. Lower Permian of Czechoslovakia. Original.

whether or not the concave veins were symmetrically as broad on the lower wing surface. It should be noted that the venation of the adult wings does not show any sign of the presence of vein-blood sinuses.

Moravia convergens Kukalova, subimago

Figs. 1, 4B, 7

Occurrence: Lower Permian (Upper Autunian) of Obora, Czechoslovakia.

Original: Specimen no. 2/1976 (obverse and reverse), deposited in the Paleontological Institute of Charles University, Prague, Czechoslovakia.

The fore wing has venation identical to that of the adult (Kukalova, 1964, fig. 2) (fig. 4A), as well as almost identical dimensions (length 36 mm, width 15 mm). The subimaginal characters known in Recent mayflies, such as the opaque wing membrane and marginal hairs, could not be observed because they would be lost in the fossilization process. The subimago is distinguished from the adult by the latero-posteriorly curved wing tip. Thus, if the proximal part of the wing axis is set parallel to that of the adult fore wing, the entire anterior margin of the subimago appears to be much more convexly curved (fig. 1). However, this position of the wing is not natural, since in the living insect the wing axis in subimagoes was directed somewhat obliquely backwards as in figs. 4B-C. Because of the curved tip, the subadult wings are distinctly narrower in the apical part than the adult wings. Otherwise, there is no noticeable difference in the pteralia membrane (fig. 7), reticulation, or venation which lies outside the range of individual variation (figs. 1, 4).

The overall similarity in venation and size of the subimaginal and adult wings of *Moravia convergens* is the proof that the development was gradual and marked by only a series of moultings as in apterygotes. The number of winged subimagoes was probably more than one, judging from data on the related Megasecoptera (Kukalova-Peck, 1974).

***Carrizopteryx* Kukalova-Peck, n. g.**

Type species: *Carrizopteryx arroyo*, n. sp., Late Pennsylvanian (Virgilian) of New Mexico. The genus is monobasic and founded on the venation of a single hind wing.

Description. Hind wing: membranous, triangular, very broad in proximal half; subcostal area small; anterior margin slightly concave. Postcostal vein short; Sc terminating on R1 at mid-wing; the stems of R and M fused; flat, ribbon-like stem of Cu adjoining the R+M stem; R, M+CuA and CuP substitute a cuticular thickening of other calvertiellids by radiating from a single spot, at about the first quarter of the wing length; Rs originating shortly beyond the

"radiating spot," giving rise to 5 main branches, the first of them forked; M diverging immediately beyond the spot of radiation from CuA, and soon forking; MA simple; MP with 4 terminal branches; Cu dividing at the radiating spot into CuA and CuP; CuA simple, close and parallel to the proximal branch of MP and to CuP; CuP also simple, either close to or fused with IA posteriorly; anal veins sometimes formed, not curved distinctly backwards, not regular; IA with 2 principal branches, 2A with 4 principal branches. Reticulation not very dense, somewhat irregular; intercalated sectors short, irregular. Color pattern of irregular, dark, oblique stripes. Anal brace almost straight, crossing obliquely basal anal area from the posterior margin to the stem of R+M+Cu.

Etymology. The generic name is derived from the type locality, Carrizo Arroyo, New Mexico, and *pteryx* (Greek for wing).

Discussion. *Carrizopteryx* is the oldest calvertiellid genus and the only one known from the Upper Carboniferous. Its venation is more primitive than that of Lower Permian *Moraviptera*, *Moravia*, and *Calvertiella* in the following features: the anal veins do not differ from other less advanced Palaeodictyoptera; they are branched and lack the parallel regular arrangement and sickle-like curvature typical of the more advanced calvertiellids; the transverse, prominent, cuticular thickening of more specialized calvertiellids is replaced only by a simple contact of the veins at one terminal spot, from which the veins R, M+CuA, and CuP radiate. The fork of MP is relatively narrow and oriented more obliquely to-

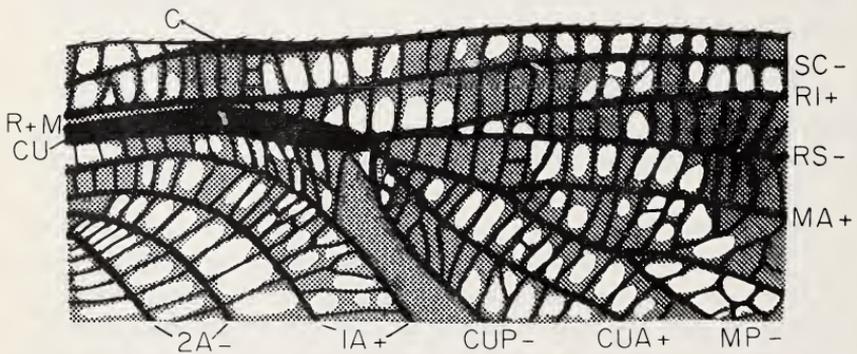


Fig. 5. *Carrizopteryx arroyo*, n. sp., portion of the hind wing showing ribbon-like cubital stem and color pattern. Late Upper Carboniferous of New Mexico. Original.

wards the posterior margin. The areas between MP-CuA-CuP are almost of equal shape and width and much less specialized than in other calvertiellids.

However, *Carrizopteryx* has a very specialized feature of its own, which is not present in either of the other calvertiellids: the fused stem of R+M with the adjoined ribbon-like Cu stem (figs. 2, 5). Fused stems of R+M repeatedly occur within the Pterygota but the combination of R+M and a ribbon-like Cu stem is rare, atypical for Palaeodictyoptera but typical for elmoid Diaphanopteroidea (a specialized group of Paleoptera able to flex their wings backwards over the abdomen while resting). However, this morphological coincidence does not express any close phylogenetic ties and is probably deeply rooted in the common genetic makeup of the Paleoptera.

***Carrizopteryx arroyo* Kukalova-Peck, n. sp.**

Figs. 2, 5

Holotype: no. 3157 (hind wing, obverse and reverse), deposited in collections of the Department of Geology, University of New Mexico, Albuquerque, New Mexico.

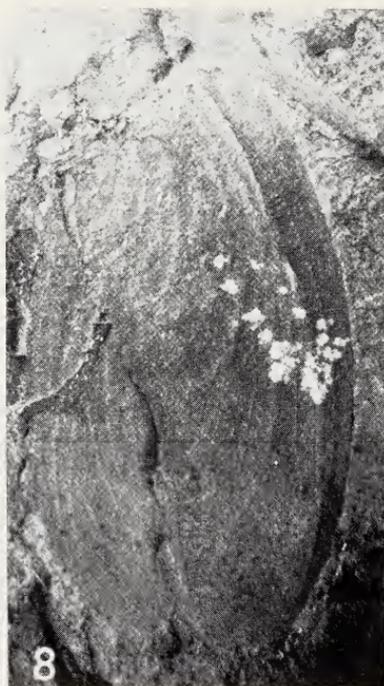
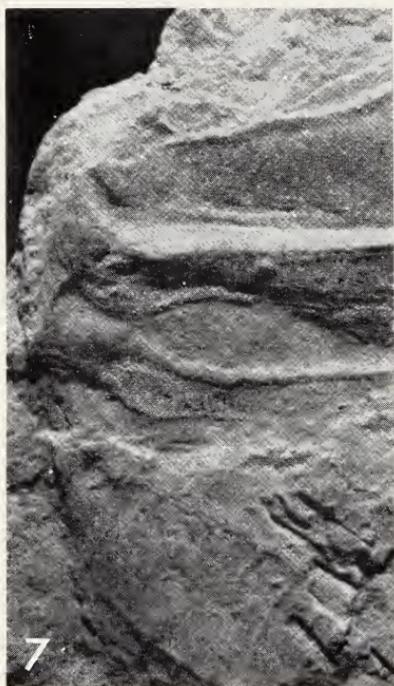
This species is based upon a well preserved adult hind wing, with the very base and the middle part of the posterior margin missing, and with a color pattern of irregular oblique stripes. The fusion of CuP and 1A posteriorly, as well as the branching of the anal veins, may be individually variable.

Description. Hind wing: length 31 mm; width 14.2 mm. Posterior margin with slight undulation between 1A and CuP and 2A; first branch of Rs originating at mid-wing; MP with two relatively narrow forks; proximal branch of MP, CuA and CuP equally distant from each other; anal veins undulating lengthwise, with a slight tendency toward a sickle-like curvature at their very tips.

Etymology. The specific name is a noun in apposition, and refers to Carrizo Arroyo, the type locality.

The Evolution of Wing Characters in the Calvertiellidae

As presently known, the occurrences of Calvertiellidae are scattered across the western half of the Northern Upper Paleozoic continent, and span a time from late Pennsylvanian (Virgilian) to late Permian (Leonard). In spite of the fact that the available ma-



terial in the field of Paleozoic insects is relatively "rich" it is obviously not sufficient for any reliable conclusions to be drawn from it. However, some hypotheses can be suggested as possible.

The calvertiellids developed from an ancestor which closely resembled *Carrizopteryx* in venation, but had separated stems of R, M, and Cu, and narrower wings. The characters of venation which appear to be potentially useful for stratigraphy are the following: the richness of ramification (the branching of venation is diminished in advanced forms); the density and regularity of reticulation (reticulation becomes larger and more cross veins are present in advanced forms); and the special features of the anal area (anal veins become simple and curved sickle-like in advanced forms). All these features developed in succession and progressively from the oldest genus, *Carrizopteryx*, to the youngest genus, *Calvertiella*.

The characters which seem to be independently variable and under the influence of mosaic evolution or of "latent homology" (sensu de Beer, 1971), are the following: the fusion and the form of the vein-stems; the degree of "discarding of the CuA" (i.e., how close CuA is shifted towards MP to function as a joined double vein). Also, the relative width of the wings is apparently independent of the stratigraphical occurrence, since *Carrizopteryx* (Virgilian) and then again *Moravia* (Upper Autunian) are conspicuously broad, while *Moraviptera* (Lower Autunian) and then again *Calvertiella* (Leonard) are moderately broad.

With the scanty information available, a more precise suggestion of the age of the strata in Carrizo Arroyo would be premature. All that can be said at present is that the general character of the venation of *Carrizopteryx* is the most primitive among the Calvertiellidae and that this may be due to an occurrence in strata older than the base of the Lower Permian.

Figures 6-8 (opposite).

Fig. 6. *Moravia convergens*, young nymph; SEM photo micrograph of the wing surface with prominent tubercles. Lower Permian of Czechoslovakia. Fig. 7. *Moravia convergens*, subimaginal fore wing base with pteralia of palaeodictyopteroid type and the anal brace. Lower Permian of Czechoslovakia. Fig. 8. *Moravia convergens*, SEM photo micrograph. Lower Permian of Czechoslovakia.

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RESPONSE STRATEGIES OF ADULT MALE
SCHIZOCOSA CRASSIPES (ARANEAE: LYCOSIDAE)
DURING AGONISTIC INTERACTIONS¹

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INTRODUCTION

This paper represents one of a series (Aspey, 1975a, b, 1976a,b,c) on the ethology and behavioral ecology of the brush-legged wolf spider *Schizocosa crassipes* (Walckenaer). Among lycosids, the adult males of this species are unusual in that they exhibit an elaborate and extensive behavioral repertoire during agonistic interactions (Aspey, 1976b). As immatures, the spiderlings exhibit a characteristic leg wave display that spaces conspecifics and presumably minimizes cannibalism (Aspey, 1975a). As adults, the males develop black foreleg brushes and exhibit the complex behaviors seen exclusively during adult male-male agonistic interactions. This display is primarily a visually-mediated communication system that preserves the personal space of adult males (Aspey, 1976c).

These spiders are found in dense abundance among leaf litter at the forest-meadow interface, and share characteristics typical of "edge" species (Aspey, 1976a). Furthermore, males are more active than females, and in the natural habitat during a given one-minute observation period, an adult male is likely to encounter three males to one female. By exhibiting one or more of the foreleg movements and/or postures comprising the behavioral repertoire, certain males drive other males away from the female while remain-

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ing in the female's vicinity. Thus, the extensive agonistic behavioral repertoire may also confer a mating advantage to those males most successful in driving other males away from the female.

Although this hypothesis has not yet been demonstrated experimentally, the males do exhibit stable, linear dominance-subordination relations among themselves when tested in the laboratory under varying social, spatial, and population densities (Aspey, 1975b, 1976b,c). Using a variety of analytical and descriptive techniques, each adult male *S. crassipes* can be classed as Dominant, Intermediate, or Subordinate in terms of the kinds and frequencies of agonistic behaviors exhibited during male-male encounters. Although the dominance classification is based on one animal's responses to an opponent (i.e., inter-individual behaviors), this study demonstrates that strikingly different response strategies are also adopted by Dominant and Subordinate spiders when intra-individual behavior sequences are analyzed

METHODS

Subjects

The subjects were 40 adult males of the ground-dwelling brush-legged wolf spider *Schizocosa crassipes* (Walckenaer) (body length = 7-10 mm; carapace width = 3-4 mm; leg span = 27-30 mm). Molting to the adult occurs in late May, at which time the males develop conspicuous tufts of black hairs on the tibiae of the forelegs, with smaller brushes on the patellae. The spiders were collected as immatures among leaf litter in early May at Stroud's Run State Park, Athens, Ohio, U.S.A., and housed individually in visually-isolated, covered plastic containers (12.5 × 7.0 × 7.0 cm) until 1 wk after the final molt. Seven to ten days after the final molt each spider was marked with nontoxic enamel paint ("Pactra 'namel," Los Angeles, CA) on the dorsal surface of the cephalothorax and/or abdomen. No detrimental behavioral effects were apparent following paint application.

All spiders were tested in four groups each of two, three, or five spiders matched into size categories of 0.5 mm increments based on adult carapace width (Hagstrum, 1971). Behavioral observations were made in various sized rectangular glass terraria (90, 180, 270, or 540 cm² floor space) having paper substrata strewn with

dried leaves. Three of the four glass walls of each terraria were shielded with white paper on the outside to minimize external visual distractions. Each terrarium was covered with glass to prevent escape and to maintain relatively constant humidity conditions ($24.5^{\circ}\text{C} \pm 1.0$ SD; 60.0% R.H. ± 2.0 SD). Water was available *ad libitum* from cotton-plugged vials, and food consisted of larvae of the yellow mealworm beetle *Tenebrio molitor* offered twice weekly. Photoperiod consisted of 16-17 hr of continuous artificial light alternated with 7-8 hr of continuous darkness.

Data Collection

Observations were conducted from early June through late July, 1973, and data collection began 5-7 days following marking of the animals. Each observation terrarium rested on a styrofoam block placed on a separate table from the recording equipment to reduce vibrations, and I was positioned 45 cm in front of the chamber. Protocol during all male-male interactions was tape-recorded and data were transcribed at a later date. Following transfer to the observation terrarium, subjects were observed for 10 consecutive days at approximately the same time. The frequencies of each behavior comprising the agonistic behavioral repertoire of *S. crassipes* during adult male-male interactions (Aspey, 1976b) were recorded continuously throughout the observation period. Since the duration of each observation period varied with the number of spiders present (with $N=2$ the observation period lasted 20 min; with $N=3$, 25 min; with $N=5$, 35 min), the data were adjusted to yield mean frequencies of each behavior per 20 min.

An interaction was considered to occur when one spider approached within 3-5 cm of another spider; data were discarded when two spiders simply passed one another without orienting or displaying to one another. An interaction was considered to continue when one spider chased or pursued a retreating spider. An interaction was considered terminated if an animal fled or was actively driven away by another spider. An interaction was considered to involve only two spiders because interactions among three or more spiders occurred only twice.

Transitional Probabilities

To determine predictable behavior sequences for individual spiders, an intra-individual transition probability matrix was con-

structured in which the preceding acts are listed as the horizontal rows and the following acts are listed as the vertical columns (Table I).

Such a matrix indicates how frequently given behaviors immediately follow or precede other specific behaviors, and similar techniques have been employed by a variety of investigators (Andrew, 1956; Altmann, 1965; Hazlett and Bossert, 1965; Delius, 1969; Wilson and Kleiman, 1974). The construction of an inter-individual transition probability matrix to determine which behaviors were exhibited by one spider in response to another's behavior is discussed in Aspey (1976b). Although procedures for constructing the intra-individual transition probability matrix of the present study are fundamentally the same as for the inter-individual transition probability matrix (Aspey, 1976b), no attention was paid in this analysis to acts performed by other spiders and their possible influence. To obtain the matrix, the complete sequence of agonistic behaviors was broken down into a series of two-act sequences. To illustrate, the four-act sequence Jerky Tapping — Following Walk — Oblique Extend — Vibrate-Thrust, provided three two-act sequences: Jerky Tapping — Following Walk, Following Walk — Oblique Extend, and Oblique Extend — Vibrate-Thrust.

To determine when any two behaviors performed by the same spider were significantly linked beyond chance expectation, the method developed by Andrew (1956) and employed by McKinney (1961) and Wilson and Kleiman (1974) was used. Two behaviors were considered significantly linked if the difference between the observed and expected values was greater than three times the square root of the expected value. In other words, the square root of the observed value was estimated as the standard error of the expected value, and a difference of more than three times the standard error between the obtained and expected totals was regarded as significant with a deviation of 2.58 times the standard error corresponding to $p < 0.01$ level of significance. With large samples the distribution was the same as for chi-square; however, Andrew's method was not restricted by the assumptions of chi-square, namely it: (1) did not assume independence of each variable; (2) allowed expected frequencies of zero; and (3) allowed expected frequencies for five or fewer in more than 20% of the cells. Therefore, Andrew's method had the same power as chi-square but allowed for the analysis of infrequently occurring behaviors, and did not assume that all

Table I: Transitional probabilities of agonistic behaviors occurring during intra-individual sequences in adult male *Schizocosa crassipes*. Underlined transitions departed significantly ($p < 0.01$) from the null order model. List of abbreviations: Ap = Approach; FA = Front Approach; FW = Following Walk; Cs = Chase; MA = Mutual Avoid; Rt = Retreat; Rn = Run; Ct = Contact; WA = Wave and Arch; PW = Prolonged Wave; JT = Jerky Tapping; HE = Horizontal Extend; OE = Oblique Extend; VE = Vertical Extend; UD = Up-Down; VT = Vibrate-Thrust. Consult Aspey (1976b) for a complete description of each behavior.

Following Behaviors

Initial Behaviors	Ap	FA	FW	Cs	MA	Rt	Rn	Ct	WA	PW	JT	HE	OE	VE	UD	VT	Total	N	
Ap	(-)	.020	.000	.011	.032	.028	.049	.006	.062	.118	.001	.428	.081	.063	.044	.037	.020	1.000	2172
FA	.000	.000	.000	.000	.143	.143	.143	.024	.071	.190	.024	.000	.071	.238	.000	.071	.024	1.000	42
FW	.000	.000	.043	.043	.000	.014	.007	.029	.071	.000	.657	.050	.029	.000	.021	.036	1.000	140	
Cs	.020	.000	.020	.190	.030	.070	.020	.030	.110	.000	.310	.010	.020	.000	.010	.160	1.000	100	
MA	.000	.000	.000	.000	.000	.000	.000	.000	.333	.000	.667	.000	.000	.000	.000	.000	1.000	3	
Rt	.294	.000	.059	.012	.000	.000	.000	.012	.235	.000	.294	.000	.047	.000	.024	.024	1.000	85	

variables were necessarily independent. Underlined transitions in Table I indicate those behaviors linked to one another which departed significantly ($p < 0.01$) from the null order model. Negative linkages are marked (-), indicating that certain behaviors occurred less frequently than expected by chance.

RESULTS

Transitional Probabilities

A total of 3,525 adult male-male agonistic interactions were recorded in the laboratory that included 14,109 behavioral acts. The original 20 agonistic behaviors were found to be better represented by 16 behavior categories, and the rationale for this consolidation is discussed in Aspey (1976b). When the data were cast into a 16×16 matrix, the occurrence of significant deviations from expected frequencies suggested a probabilistic structure to the intra-individual agonistic behavior sequences (Table I). Of 256 possible linkages from a 16×16 matrix, 37 occurred more frequently than expected by chance, while 30 occurred less frequently. With regard to only the foreleg movements and postures exhibited during agonistic interactions (Aspey, 1976b), a wider variety of subsequent behaviors occurred during intra-individual sequences than during inter-individual behavioral responses. For example, during intra-individual sequences, an average of 5.6 different agonistic behaviors followed a given foreleg movement or posture beyond chance levels, while only 2.6 different behaviors followed a given foreleg movement or posture during inter-individual encounters (Aspey, 1976b).

Sequential Behaviors of Dominant and Subordinate Spiders

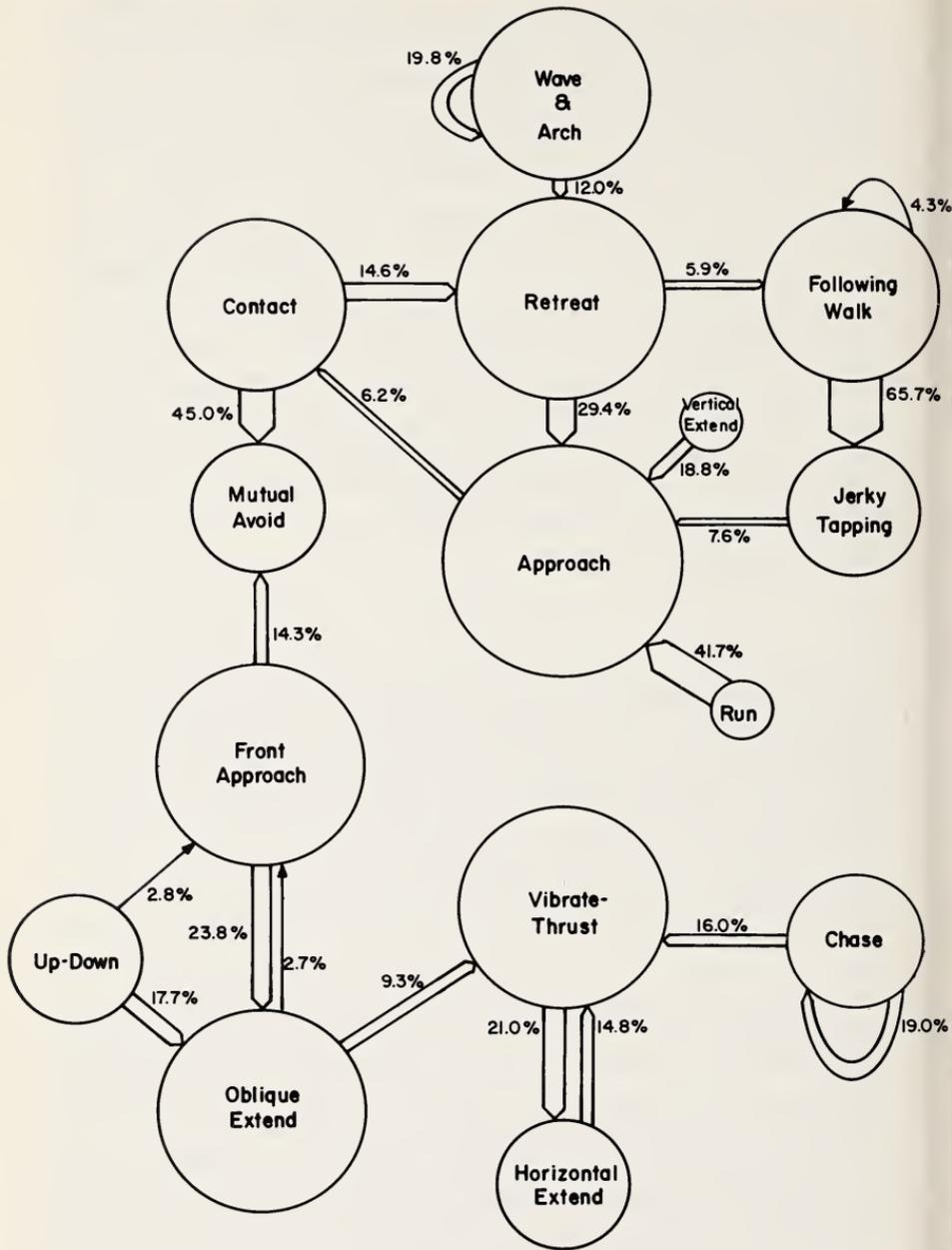
Since adult *S. crassipes* could be characterized as Dominant or Subordinate on the basis of the kinds and frequencies of agonistic behaviors exhibited during male-male interactions (Aspey, 1975b, 1976b), profiles of Dominant and Subordinate spiders were constructed using intra-individual behavior sequences. Although the original dominance classifications of the spiders utilized responses from one spider toward another, this method of characterizing Dominant and Subordinate spiders emphasized behavioral sequences exhibited by individual spiders.

Intra-individual behavioral sequences are diagrammed separately for the 16 Dominant spiders (Figure 1) and 16 Subordinate spiders (Figure 2). Dominant spiders were characterized by those agonistic behaviors comprising Factor I (Approach/Signal) and Factor II (Vigorous Pursuit) of Aspey's (1976b) factor analytic classification. Subordinate spiders were characterized by Run, Retreat, and Vertical Extend, those behaviors comprising Factor III (Run/Retreat) of Aspey's (1976b) factor analysis of the agonistic behavioral repertoire. A comparison of the original 20 behaviors displayed by Dominant and Subordinate spiders revealed that Dominant spiders exhibited a wider variety of behaviors linked together (15 out of a possible 20) than did Subordinate spiders (10 out of 20). Thus, these results indicate that Dominant and Subordinate spiders can not only be reliably identified on the basis of responses made by conspecifics toward them during agonistic interactions (Aspey, 1976b), but also by the response strategy exhibited during intra-individual behavior sequences.

DISCUSSION

A transition probability matrix of agonistic behaviors exhibited during adult male-male interactions in *S. crassipes* indicated that a wider variety of responses followed any given behavior by a single spider during intra-individual sequences than during inter-individual encounters (Aspey, 1976b). However, examination of Table I revealed that some of the sequential responses appeared inconsistent (e.g., Run or Vibrate-Thrust following the performance of Horizontal Extend; Run or Front Approach following the performance of Vibrate-Thrust). Horizontal Extend and Vibrate-Thrust are signal and active pursuit behaviors, routinely followed by some form of retreat during inter-individual encounters (Aspey, 1976b). However, if an animal exhibited Horizontal Extend or Vibrate-Thrust, seemingly aggressive behaviors, why would it suddenly retreat immediately after performing such a behavior?

Further analysis examining each specific spider indicated that some spiders were consistently Dominant over all partners, while others were consistently Subordinate to every partner. For example, Dominant spiders not only performed Horizontal Extend or Vibrate-Thrust more frequently, but also continued to exhibit Vigorous Pursuit behaviors if an initial encounter with a conspecific



did not result in that animal's retreating. If Subordinate spiders performed Vibrate-Thrust or Horizontal Extend, they then reverted to retreating, avoidance behaviors. When transition probabilities were examined separately for Dominant and Subordinate spiders, striking differences in response strategies were evident. Although eight Intermediate spiders were also identified (Aspey, 1976b), a meaningful kinematic diagram of their intra-individual response strategy could not be constructed with so few spiders. However, Intermediate spiders were typically approach-oriented, and made Contact preliminary to resolving rank differences with Dominant opponents. With Subordinate opponents, Intermediate spiders exhibited Oblique Extend, the only time a foreleg posture characteristic of Dominant spiders was exhibited (Aspey, 1976b).

If these intra-individual behavior sequences reflect a spider's responsiveness to its own behavior (i.e., feedback), then Dominant spiders exhibit the potential for more versatile response strategies during agonistic interactions than Subordinate spiders, presumably allowing greater flexibility when responding to conspecifics. Hazlett and Estabrook (1974a,b) also reported similar results regarding the response behavior of winning animals. Thus, Dominant and Subordinate spiders can not only be reliably identified on the basis of responses made by conspecifics toward them during agonistic interactions, but also by the response strategy exhibited during intra-individual behavior sequences.

ACKNOWLEDGMENTS

I gratefully acknowledge Dr. Jerome S. Rovner, Department of Zoology and Microbiology, Ohio University, for his helpful guidance and encouragement throughout all phases of this research, as well as for his useful discussions of the material. Dr. H. Dijkstra and Dr. S.W.F. van der Ploeg, Free University, Amsterdam, The Netherlands, kindly offered helpful discussion and commented on

Fig. 1. [opposite] Transitional probabilities during intra-individual behavior sequences in Dominant adult male *Schizocosa crassipes*. Arrows connecting the agonistic behaviors represent significant linkages ($p < 0.01$) between and among the behaviors. The relative thickness of the arrows indicates the percent of time one agonistic behavior followed another. The relative size of each circle represents the number of different behaviors significantly linked with that behavior. Descriptions of the behaviors are given in Aspey (1976b).

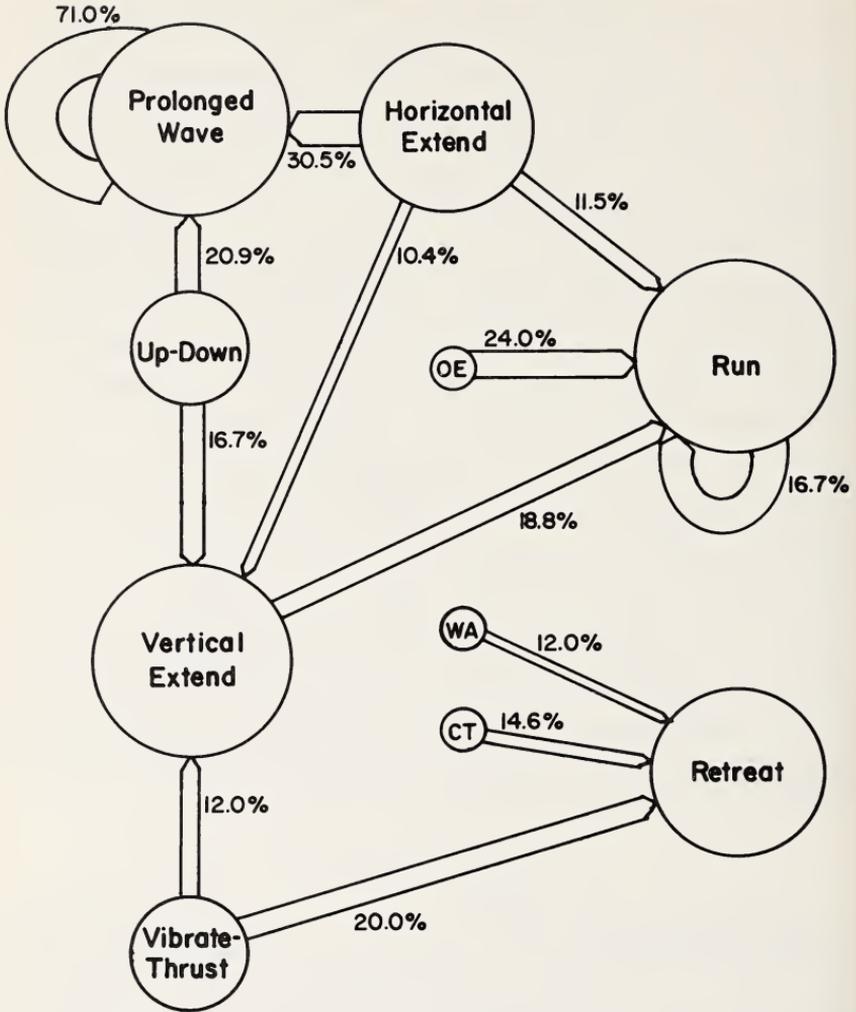


Fig. 2. Transitional probabilities during intra-individual behavior sequences in Subordinate adult male *Schizocosa crassipes*. Arrows connecting the agonistic behaviors represent significant linkages ($p < 0.01$) between and among the behaviors. The relative thickness of the arrows indicates the percent of time one agonistic behavior followed another. The relative size of each circle represents the number of different behaviors significantly linked with that behavior. List of abbreviations: OE = Oblique Extend; WA = Wave and Arch; CT = Contact. Descriptions of the behaviors are given in Aspey (1976b).

the material. Dr. B. A. Hazlett, Department of Zoology, University of Michigan, Ann Arbor, and Dr. K. Nelson, Bodega Bay, California, provided valuable criticisms for improving earlier drafts of this work.

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DISCOVERY OF A MAJOR WORKER IN
CAMPONOTUS BRANNERI (MANN), A NEW
COMBINATION (HYMENOPTERA: FORMICIDAE)

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As entomologist to the Stanford expedition to Brazil, in 1911, W. M. Mann discovered in the environs of Abunã, on the upper Madeira river, Rondônia Territory, several workers of a bizarre-looking Formicine ant, at once distinguished by the peculiar head shape: the occiput is drawn out into a long, narrow neck. Supposing to deal with a species characterized by a strictly monomorphic worker caste, Mann described these specimens as *Dendromyrmex branneri*, but admitting at the same time that it represented a very aberrant form in an otherwise strikingly homogeneous group.

To my knowledge, this species has never since been collected again. So it came as a surprise when I received among ant material recently collected at Humaitá, Amazonas State, Brazil (about 400 km NE of Abunã, further down the Madeira river), by the expedition of the Zoology Department of the "Faculdade de Ciências Médicas e Biológicas de Botucatu, S.P.," led by Dr. Virgílio Pereira da Silva, two workers of the same species associated with the hitherto unknown soldier or major worker. The latter proved that *branneri* is definitely not a *Dendromyrmex* but a true *Camponotus*, representing another of the handful of spectacular species which this genus possesses in the western part of the Amazonas river drainage.

Thanking Dr. Virgílio Pereira da Silva for letting me keep this interesting material, I give in the following a diagnosis of the soldier of *C. branneri*, redescribe the worker, and add a comment on the subgeneric allocation of the present species.

Note on measurements. TL, for total length of body, is the summed length of head with closed mandibles, diagonal length of thorax (see WL), and axial length of petiole and the remainder of the normally expanded abdominal segments; HL, for head length, is the

*Father Kempf died while attending the International Congress of Entomology in Washington, on 20 August 1976. [Editor]

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maximum perpendicular distance between two parallels drawn through the anteriormost and posteriormost point of head capsule in full-face view; HW, for head width, is the maximum width of head in full-face view including the compound eyes whenever they are laterally protruding; IFW, for interfrontal width, is the maximum distance between the outer borders of frontal carinae; SL, for scape length, is the chord length of the antennal scape, excluding the narrowed basal neck and the articular condyle; EyL, for eye length, is the maximum diameter of the compound eyes; WL, for Weber's length of thorax (or trunk), is taken in side-view diagonally from the anterior descending face of pronotum (cervix excluded) to the most posterior point of thorax situated postero-inferiorly on the so-called metasternal angle; HFL, for hind femur length, is the maximum length of the hind femur.

Camponotus branneri (Mann), new combination
(Figs. 1-4)

Dendromyrmex branneri Mann, 1916:488-489, Pl. 6, fig. 47(worker; Brazil, Rondônia Territory: Abunã). Emery, 1925: 173 (catalog). Borgmeier, 1927:161 (catalog). Kempf, 1972: 95 (catalog).

Soldier (undescribed). Measurements in mm: TL 13.0; HL 3.43; HW 2.77; IFW 0.97; EyL 0.61; SL 2.67; WL 3.85; HFL 3.49.

Color ferruginous; mandibles, antennal scapes and gaster darker than rest of body and appendages. Integument basically smooth and shining with the following exceptions: mandibles finely shagreened and opaque on basal half; dorsum of head including clypeus densely punctate and opaque, the sculpture becoming more superficial and rather reticulate-punctate on posterior vertex; occiput, posterior half of sides of head and anterior half of gular surface; occipital corners practically smooth and shining; antennal scape finely shagreened, subopaque, thorax superficially reticulate-punctate to reticulate-striolate on propodeum and mesopleura; femora and tibiae indistinctly and superficially reticulate-striolate; petiole with the anterior and posterior surfaces transversely and the lateral surfaces obliquely striolate; gastric terga and sterna nearly smooth with fading and very superficial transverse striolae. Anterior margin of clypeus, front, vertex, occiput, gular surface of head, thorax, anterior and lateral surfaces of petiole, and gaster with scattered, pale standing hairs which are always shorter than maximum diam-

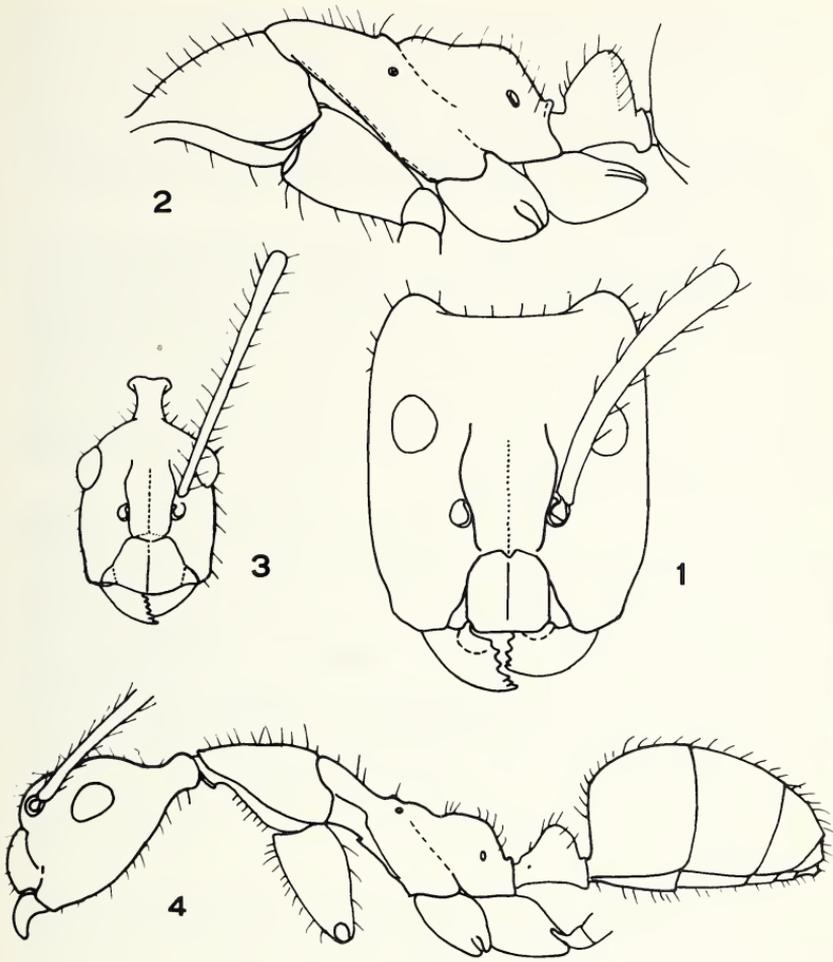
eter of eyes; hairs on scapes and legs evenly scattered, absent on mesial surface of fore femora, somewhat shorter than those of body, mostly oblique; funicular segments with very short and scattered standing hairs. Fine appressed pubescence on mandibles, antennae, sides and gular face of head, sides of pronotum, legs and gaster.

Head as shown in fig. 1. Mandibles with the infero-lateral border carinate, the chewing blade with 6 teeth, the basal tooth small, offset or retracted. Median apron of clypeus gently convex in both directions, with a weak sagittal carina which on the posterior fourth becomes an impressed sulcus. Frontal sulcus faint, fading out before the posterior end of frontal carinae. Antennal scapes feebly compressed and prismatic at basal half. Second funicular segment shorter than first and third. Eyes rather flat. Antennal socket removed from posterior corner of median apron of clypeus by a distance which slightly exceeds its own diameter. Thorax as shown in Fig. 2. Mesothoracic spiracle protuberant. Metanotum dorsally exposed, projecting as a transverse welt. In profile, the depression in front of metanotum and on anterior third of basal face of pronotum is very shallow. Tibiae and first tarsomeres not conspicuously compressed nor broadened. Petiole. (Fig. 2) with the peak transversely submarginate.

Worker. Measurements in mm: TL 8.9-9.0; HL 2.10-2.15; HW 1.33-1.38; IFW 0.54; EyL 0.46; ScL 2.67; WL 3.29; HFL 3.08-3.23.

Color and sculpture as in soldier, but nearly the entire mandibles, the gular surface of head, the drawn-out and necklike occiput, and the fore legs are smooth and shining throughout; reticulate-punctate sculpture on anterior part of dorsum of head more superficial. Pilosity likewise as in soldier, except for the presence of fringing erect hairs on sides of head; hairs on scapes more abundant and more erect; erect hairs present on median stripe of clypeus.

Head as shown in Fig. 3; note the parallel-sided head, slightly constricted in front of convex and protruding compound eyes, and the long, narrow, stalked occiput which is drawn-out in a necklike fashion. Antennal socket removed from posterior corner of median apron of clypeus by a distance which is subequal to its own diameter. Sagittal carina present on clypeus, posteriorly blunt and low, but not impressed as a sulcus. Thorax as in soldier (Fig. 4) but more slender and strongly constricted at level of mesothorax. Both the mesonotum and the anterior third of propodeum have a distinct, saddle-shaped impression. Mesepisternum terminating above in



Camponotus branneri (Mann)

Fig. 1. Soldier, head in full-face view. Fig. 2. Soldier, thorax and petiole in side-view.
Fig. 3. Worker, head in full-face view. Fig. 4. Worker in side-view.

a sharp ledge which appears in side-view as a small tooth. Petiole relatively longer and lower, its peak rounded, not transversely marginate.

Specimens examined: 1 soldier and 2 workers from Brazil, Amazonas State, km 20 of Humaitá-Porto Velho Road, April 10, 1975, Virgílio Pereira da Silva, Daniel Z. Araujo & Aldo J. P. Dillon leg. (WWK n. 11926).

Variation. The worker specimens diagnosed above disagree from Mann's description of the type in having six mandibular teeth instead of five, and in lacking a longitudinal carina on frontal area. The first difference is probably due to an oversight by Mann, since the basal mandibular tooth is very small and offset, and hidden under the clypeus when the mandibles are firmly closed. At any rate, there is no doubt about the conspecificity between the types of *branneri* and the present specimens.

Discussion. The striking and curious dimorphism shown in head shape between soldiers and workers (see Figs. 1 and 3), the latter possessing a stalked necklike occiput — to my knowledge a unique feature for a *Camponotus* — the shape of the thorax in which the metanotum is dorsally exposed and projecting as a transverse welt both in soldiers and in workers, the transversely impressed and saddle-shaped basal face of propodeum, separate *branneri* from all other species-groups and/or subgenera of the Neotropical region.

It is hard to point out any closer relationship to any one of the other groups, and even more difficult to derive *branneri* from any one of them.

The soldier head, which is elongate, parallel-sided, and more heavily sculptured dorsally in front, together with the rather smooth integument of the remainder of the body, reminds one of the more orthodox members of subgenus *Pseudocolobopsis*, but the latter lack the standing hairs on scapes and legs, and their thorax is much more compact.

The impressed dorsal profile of thorax of *branneri* resembles superficially that of *Myrmosphincta*, but in the latter group the soldier head is not elongate-rectangular, the clypeus anteriorly not impressed, and the metanotum, when exposed dorsally, is deeply sunk in between the mesonotum and the propodeum, if not reduced to a mere transverse sulcus.

One could try to derive *branneri* from the larger, shinier and more slender members of the *Tanaemyrmex*-group, especially from those

which have workers with elongate heads and drawn-out yet not necklike occiput, but even these have as a rule bristly pilosity and their soldiers show a head shape completely different from that of *branneri*, *Pseudocolobopsis* and a few *Myrmaphaenus*.

Following Emery's logic in establishing avowedly artificial subgeneric cuts in order to handle with more ease the enormous wealth of species in *Camponotus*, *branneri* would certainly qualify for separate subgeneric rank. However, I prefer to leave it as an isolated, highly distinctive species with uncertain relationship to the already recognized subgenera.

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FORAGING PATTERNS OF HALICTID BEES AT FLOWERS OF *CONVOLVULUS ARVENSIS*¹

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INTRODUCTION

An animal may acquire food in one of three general ways: 1) it may move through the environment in search of food, independently of other animals utilizing the same resource; 2) it may avoid other animals, resulting in an evenly spaced distribution of animals (Ricklefs, 1973; Chapter 18); or 3) it may forage with other animals in single or mixed species groups. Group foraging has recently been described for a variety of animals: ants (Bernstein, 1975), bats (Heithaus, Opler, and Baker, 1974), and birds (Cody, 1971; Ward, 1965). Since the acquisition of food is a likely determinant of an animal's ability to survive and reproduce, the strategy used is probably a result of natural selection for individuals which forage most efficiently.

Few studies have been conducted to investigate the foraging strategies of bees. This information is essential to understanding pollen flow and the general pollination biology of natural vegetation and agricultural crops. Kalmus (1953) found that visual and olfactory cues are important in the mutual attraction of honeybees at dishes of sugar syrup, resulting in non-independent foraging. Frankie, Opler, and Bawa (1974) reported that males of *Centris sp.* commonly forage over the forest canopy in Costa Rica in groups of up to 300 bees. Charles D. Michener (pers. comm.) has observed bees (families Colletidae and Anthophoridae) foraging on flowers of the bush *Chrysothamnus sp.* in apparent aggregations. He has observed that while one or two bees might be at a clump of bushes at any time, large numbers seemed to appear, more or less simultaneously, at the bushes, and after a time most of them left more or less suddenly. These bees seemed to be foraging in groups, not independently from one another. In this paper quadrat censusing techniques

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are employed to determine the foraging patterns of sweat bees (Halictidae) gathering pollen and nectar from bindweed (*Convolvulus arvensis*) flowers.

METHODS

All observations were made at dense floral arrays of bindweed (*Convolvulus arvensis*) on Campus West, The University of Kansas, Lawrence. Several acres of bindweed surrounded the test areas. Observations were made of the three prime bee visitors to the bindweed flowers: *Agapostemon texanus*, *Augochlorella striata*, and *Lasioglossum (Dialictus) sp.*, all sweat bees of the family Halictidae. The species of *Lasioglossum* were difficult to discriminate in the field, so it is possible that data for more than one species of *Lasioglossum* were pooled under the designation *Lasioglossum sp.* Honeybees, bumblebees, butterflies, and moths were also observed visiting bindweed flowers for food.

The following methods were used to determine the temporal patterns of the bees within the bindweed patch. Eleven test quadrats, each 1m^2 ($1 \times 1\text{m}$), were delimited by string in the bindweed population. The number of halictids (individual species were not distinguished) on flowers within quadrats 1-3 on June 30, 1974, and quadrats 4-7 on July 2, was recorded every two minutes from about 0830 to 1030 h. Counts of each of the three halictid species were made every 3 minutes at quadrats 8-11 on July 3, again between 0830 and 1030 h. At the end of each day's observations the number of flowers within each quadrat was recorded.

The spatial patterns of halictid bees were tested employing the following methods. A $12 \times 6\text{m}$ rectangular study area, near the edge of several acres of bindweed, was delimited by string. A random numbers table (Rohlf and Sokal, 1969) was used to determine the coordinates of the southwest corner of 32 0.25m^2 ($0.5 \times 0.5\text{m}$) sample quadrats within the study area. Each of the quadrats was delimited with string in late afternoon on July 4. At 0915, 0955, and 1045 h on July 5 the number of bees within each of the 32 quadrats was recorded.

The chi-square test of goodness of fit was employed to test the null hypothesis that the temporal and spatial data approximate Poisson distributions, the expectation if the bees are dispersed at random. The G-test was applied to 2×2 tables to test whether the presence and absence of species pairs at bindweed are dependent on each other.

Table I. Quadrat census data obtained on June 30, and July 2 and 3.

Quadrat	Test Date	Number of Samples	Sample Interval (min)	Mean No. Bees (\bar{X})	Coefficient of Dispersion ^a	X^2 ^b	X^2 _{0.05} ^c	No. Flowers
1	6/30	64	2	1.156	1.05	2.16	5.99	131
2	6/30	64	2	1.422	1.11	6.49*	5.99	158
3	6/30	64	2	0.969	1.05	1.13	5.99	97
4	7/2	61	2	1.639	0.69	3.82	5.99	219
5	7/2	61	2	0.410	1.09	3.35	3.84	37
6	7/2	61	2	1.164	1.04	3.30	5.99	198
7	7/2	61	2	0.951	0.86	1.09	3.84	139
8	7/3	42	3	1.214	1.23	1.53	5.99	130
9	7/3	42	3	0.810	1.34	0.19	3.84	94
10	7/3	42	3	0.881	1.12	4.92*	3.84	121
11	7/3	42	3	0.333	1.12	2.17	3.84	83

a C.D. = $\frac{S^2}{\bar{X}}$

b Result of chi-square test; (*) indicates statistical departure from expectation, $P < 0.05$

c Critical values of chi-square distribution for 1 degree of freedom - 3.84, and 2 d.f. - 5.99

RESULTS

Bindweed plants grow along the ground, often forming dense tangled mats, and produce white or pinkish funnellform flowers. On test days anthesis began at about 0715 h and most flowers were fully open by 0800 h. Nectar was produced at the base of the corolla and pollen was slowly dehiscid by the 5 anthers during the morning. The flowers wilted in the early afternoon.

Halictid bees began visiting the bindweed before 0800 h and continued until nearly 1130 h when most of the nectar and pollen was depleted. During the first and last half hour of the foraging periods visits were infrequent. Censusing was conducted from about 0830 to 1030 h when halictid activity was generally high (Fig. 1).

The number of bees per quadrat is the Poisson variable for both the temporal and spatial quadrat sampling experiments. If the observed frequencies closely fit the expected Poisson distribution with the same mean (\bar{x}), indicating the bees are randomly dispersed over the flowers, then it can be assumed that the bees are foraging

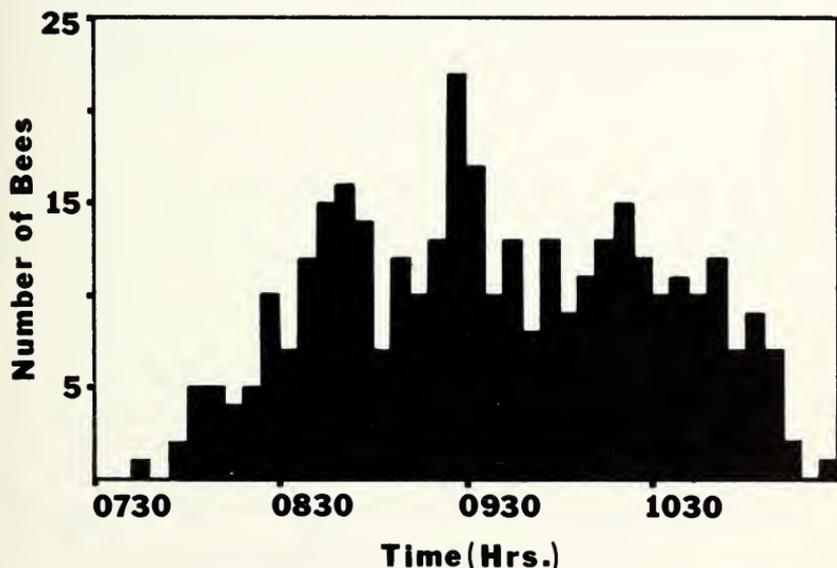


Fig. 1. Visitation frequency of Halictid bees to quadrates 4-7 (data pooled) between 0730 and 1130 h, July 2. Each bar is the sum of bees during three consecutive censuses.

independently of each other. In this case the coefficient of dispersion, $C.D. = \frac{s^2}{\bar{x}}$, (Sokal and Rohlf, 1969) will approximate 1 ($\mu = \sigma^2$ for the Poisson distribution). If, on the other hand, the observed distribution of bees per sample departs significantly from the expected Poisson distribution and $C.D. < 1$ or > 1 then the bees can be assumed to be evenly distributed over the flowers or foraging in groups (either single or multiple species groups), respectively.

Temporal patterns — Counts taken at the eleven quadrats were tested against the expected Poisson distribution, based on the observed sample means, to determine the temporal patterns of the halictids (individual species samples taken at quadrats 8-11 are pooled for purposes of this analysis). The sample means are correlated with the number of flowers within the same quadrats (Fig. 2). In fact, flower density appears to be an excellent predictor

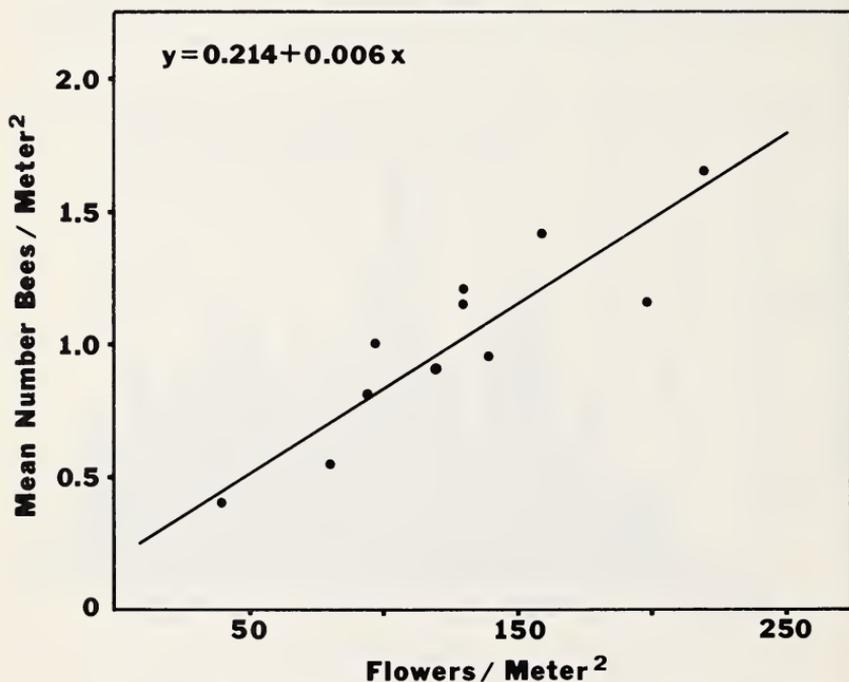


Fig. 2. Regression of mean number of bees per meter² as a function of number of flowers per meter². Dark circles represent data from 11 quadrats; data from Table I.

of mean bee density ($Y = 0.214 + 0.006 X$; the slope is significantly different from zero; F - test, $P < 0.001$).

The null hypothesis of random dispersion of the halictids was rejected (chi-square test; $P < 0.05$) for only two of the eleven frequency distributions (Table 1). In both cases, C.D. > 1 . Also, analyses of individual species data taken on July 3 (quadrats 8-11) show no association of individuals of the three possible species pairs (G - test on 2×2 tables; $P > 0.05$ for each comparison). The data indicate that the halictid species are primarily foraging at bindweed independently of one another; however, it is possible that the bees may also exhibit clumped dispersal patterns indicating a multiple halictid species group foraging strategy.

Samples of the three halictid species at quadrats 8-11 were obtained to determine the temporal patterns of individual halictid species. All twelve frequency distributions (4 distributions for each species) were not significantly different (chi-square test; $P > 0.05$) from the expected Poisson distributions. The bees appear to forage independently of conspecifics.

Spatial patterns — The data obtained during three tests on July 5 are not significantly different from the three respective expected frequency distributions. These data indicate, again, that the bees are distributed at random and foraging independently of each other.

DISCUSSION

The temporal and spatial data indicate that *Agapostemon texanus*, *Augochlorella striata*, and *Lasioglossum (Dialictus) sp.* forage at bindweed flowers as individuals, independently of one another. The bees appear not to forage in single or multiple species groups, nor are the patterns repulsed as might be expected for organisms utilizing the same resource in the same time and space. Bee numbers per area increased linearly with flower density (Fig. 2) indicating that even at the highest bee densities encountered in this study the threshold distances between individuals were not met (Ricklefs, 1973). If bee density were increased, the threshold of bees' individual distance would be reached, perhaps resulting in repulsed spatial and temporal patterns.

The possibility still remains that species associations occur among the bees, and that the spatial and temporal patterns are other than random. This is because the results obtained using

quadrat sampling techniques are influenced by the size of the quadrat (Pielou, 1969). It would have been desirable in this study to use larger sample quadrats in addition to those employed. This was not done because pilot studies indicated that as quadrat size increased, it became increasingly difficult to accurately count the bees in a very short period of time.

Other studies suggest that animal foraging patterns vary according to resource distribution and abundance. Michener's observations (pers. comm.) of seemingly clumped bee patterns, were made in a semi-desert area of southern California at a very sparse resource, *Chrysothamnus* bushes. Two strategies are exhibited by the ant, *Veromessor pergandei*, depending on food abundance (Bernstein, 1975). When food is abundant the ants forage independently, but when food is scarce they forage in groups. Some birds forage in flocks when food is uniformly distributed and scarce (Cody, 1971). Heithaus et al. (1974) found that some bats lap only a small portion of the nectar during a flower visit, thereby maintaining an abundant resource. These bats forage independently.

In the present study, bees were observed foraging at very dense arrays of *C. arvensis* flowers. The abundance and uniformity of the resource were maintained by the continuous replenishment of pollen and nectar. Pollen was dehiscid during much of the bees' foraging period (personal observation), and unpublished data provided by R. W. Thorpe suggest that nectar may be continuously secreted from time of anthesis until late morning. As suggested by Cody (1971) for birds, independent bee foraging may be favored at an abundant resource, such as the *C. arvensis* patch. However, the bees' foraging patterns may vary in response to different resource patterns or different bee densities.

Further investigations, using similar and different censusing techniques, are needed to elucidate bee foraging patterns in relation to resource patterns. Studies of several bee species may suggest some general patterns.

ACKNOWLEDGMENTS

I thank M. D. Breed, C. D. Michener, T. P. Snyder, and B. L. Waddington for helpful suggestions on the manuscript. Thanks also to R. W. Thorpe, University of California, Davis, for permitting me to see unpublished data.

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This issue (volume 83, number 1) marks the beginning of a new era for *Psyche*.

During the 102 years of its existence, the journal has been printed by some form of letterpress, starting with hand-set type, followed by Monotype and finally Linotype. Dramatic improvements in recent years in photo-offset lithography, combined with the difficulty of maintenance of letterpress equipment, have led the Editorial Board of *Psyche* to adopt offset printing for the journal. The Lexington Press, in the Town of Lexington, Massachusetts, will continue to be our printer, as it has for the past 17 years.

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Frank M. Carpenter, *Editor*

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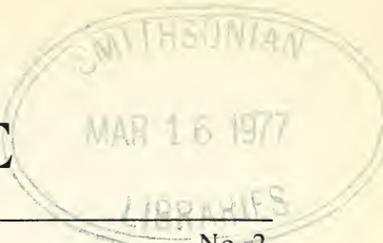
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THE SOCIAL ORGANIZATION OF MALE POPULATIONS OF *CENTRIS PALLIDA* (HYMENOPTERA, ANTHOPHORIDAE)*

BY JOHN ALCOCK

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This report is one in a series of papers on the reproductive behavior of the solitary bee *Centris pallida* Fox. Elsewhere we have shown that males of this species exhibit a behavioral dimorphism in mate-location strategies, with some males flying low over the ground searching for virgin females about to emerge and other males hovering around the borders of emergence sites as well as by flowering trees (Alcock et al., 1976; in press). The patrollers excavate virgin females from their emergence tunnels and then copulate with them; hoverers secure mates by pursuing air-borne virgins which they capture in flight.

Our earlier studies left unanswered several questions about the spatial organization of male populations of this bee, including

- 1) Do patrolling males exhibit loyalty to a particular portion of an emergence site and if so, for how many days?
- 2) How much area do patrollers examine?
- 3) Do males that hover remain at a particular aerial station for any length of time?

Almost nothing is known of the behavior of male solitary Hymenoptera with respect to the size of the territory or home range of individuals and the duration of time males spend on a territory or home range (Alcock et al., in prep.). After following a large sample of marked bees from the start of the emergence season to its conclusion, I am able to provide information on the social structure of male populations of *C. pallida*, especially with reference to the degree of site tenacity and degree of territoriality shown by hovering and patrolling males.

*Manuscript received by the editor October 4, 1976

MATERIALS AND METHODS

This study was conducted from April 30-May 31, 1976 at two locations separated by about 0.7 km in the floodplain of the Salt River about 4 km south of Saguaro Lake, north of Mesa, Arizona. Both emergence sites were open areas with well-packed soil ranging from sand to clay in composition. These areas had a sparse covering of grasses with scattered shrubs (*Ambrosia deltoidea*) and were bordered by mesquite (*Prosopis* sp.) and palo verde (*Cercidium* spp.) trees.

In order to follow the history of individual males, bees were captured with an insect net and given an identifying color combination of enamel paint marks on the dorsum of their thorax. Marking did not appear to disrupt the behavior of the bees seriously as most individuals quickly resumed their activities prior to capture. Six samples of patrolling males ($N = 153$) were collected and marked at Site 1 between April 30-May 15. Three samples totalling 76 males were taken at Site 2 from May 19-May 23. In addition, 47 hovering males were marked at Site 1 from May 1-17 as well as 20 copulating males; at Site 2, 41 copulating males were captured and marked (all copulating males were believed to have been patrolling prior to copulation).

Data on marked bees was gathered by censusing the study site on a daily basis from 30 April to 31 May with four exceptions (on two of the four days there was little or no male activity because it had rained heavily the night before). During the period from 0800-1030 my assistants and I tried to recapture as many marked males as possible; sometimes when a male was seen on the ground digging it was not necessary to capture the bee in order to identify it. A map was made of Site 1 and the points where several bees were captured and recaptured were recorded on the map. In other cases, the distance between successive sightings of a male were paced off to collect information on the approximate length of movements by known individuals.

RESULTS

Home ranges of patrolling males

In large emergence sites dozens to hundreds of males may be present in the period from 0800-1030 cruising rapidly within a few cm of the ground. The patrolling males are not distributed

Table 1

Recapture data on samples of marked males of *Centris pallida*.

	Number Marked	Number Recaptured on Another Day
Patrolling Males		
Study Site 1	153	83 (54%)
Study Site 2	76	58 (76%)
Copulating Males		
Study Site 1	20	13 (65%)
Study Site 2	41	26 (63%)
Hovering Males		
Study Site 1	47	18 (38%)

evenly; it is not uncommon for a location 10 m² to have several dozen males swirling over it while an adjacent area of equivalent size has fewer than ten individuals. The samples of males were taken for marking from limited areas (rarely covering more than 20 m² and usually less) where males were relatively abundant. Follow-up searches on subsequent days were concentrated in these areas and they quickly revealed that many marked individuals returned day after day to the same limited portion of the total emergence site. A large majority of the marked patrolling males were seen again on at least one other day (Table 1) and for the population as a whole, the average interval between the day of capture and the day of last sighting was 3.44 days (Fig. 1). Because patrolling males tend to return to the same area but do not defend it they can be said to possess home ranges (patrolling males ignore other flying males but will fight intensely for a specific digging site containing a pre-emergent female).

If we analyze the recapture frequencies of patrolling and copulating males in Site 1 vs. Site 2 (lumping copulating males with patrollers because copulating males had been patrolling prior to their capture *in copula*) we find that patrollers were significantly more likely to have been recaptured after marking in Site 2 than Site 1 ($X^2 = 6.61$, d.f. = 1, $P < .01$). This difference probably reflects higher mortality experienced by males in the first study area. There were two heavy rains accompanied by unusually cold weather

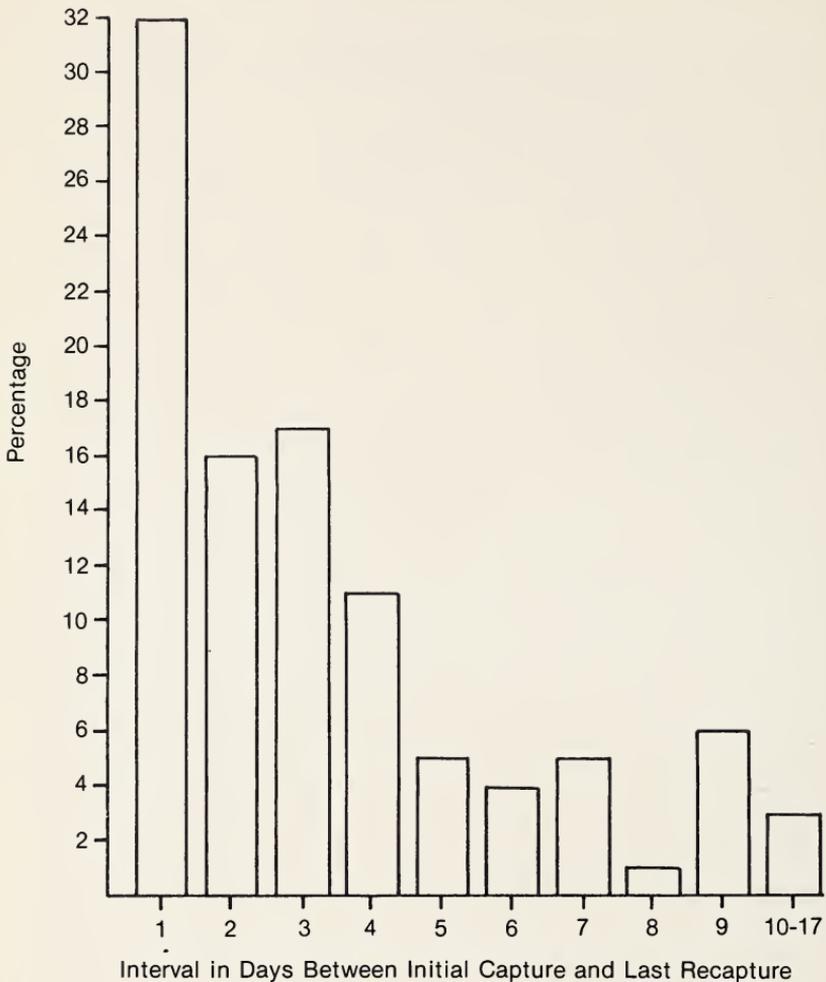


Fig. 1. Data on the duration of occupation of a home range by males initially captured while patrolling an emergence site and then marked and released.

in early May. Because males spend the night in shallow burrows and under rocks they run the risk of becoming drenched during rains. Judging from the matted thoracic hairs of survivors observed after the rains, many males did become soaked and this may have caused mortality in some cases.

Efforts to determine the size of home ranges of individual males were hindered by the great rapidity with which the bees flew over

the ground when searching for digging sites. It was impossible to determine the color combination of flying males and it was difficult to capture them as well. Often a marked male was seen close up (while digging) or was captured only once or twice during the morning flight period over emergence areas. Nevertheless, a considerable number of males were seen frequently in the same general area over a period of days. The positions of twelve of these males were plotted on maps of the study sites for periods of 2-9 days of observation; these individuals covered areas roughly 8-46 m² (\bar{x} = 18 m²; s.d. = 12.5 m²). This seemed to be the typical pattern although we have records of eight males that were seen at two separate centers of emergence about 25-35 m apart. Three additional males moved back and forth several times between locations that were separated by at least 80 m. Finally, at least some males moved permanently from one emergence area to another distant one, with five males found patrolling sites 60-100 m from the point of their capture and two others patrolling about 200 m from where they were taken initially.

To repeat, the very large majority of males that were recaptured were never found outside an area of about 50 m² around the point of original capture. Those males known to patrol two searching areas and those known to have moved large distances make up a very small minority of the total recaptured males. Thus although the activity in a large emergence area appears chaotic and random, in reality the region is divided into a large number of broadly overlapping home ranges with individual males systematically patrolling small portions of the total available searching area.

The behavior of hoverers

At Site 1 males were found hovering a few cm above the ground centered in depressions or openings surrounded by short desert shrubs under a meter in height, as well as close to the ground around the edges of mesquite trees, and at all altitudes in flowering palo verde trees. Those males hovering at low aerial stations in and around emergence sites were present primarily during the peak hours for emerging females (0830-1100). Males hovering at or near flowering trees were present throughout the day although there may be a slight decline after the period of female emergence (Fig. 2).

Hovering males continually leave their aerial station to pursue passing insects, usually for a few seconds only, before returning

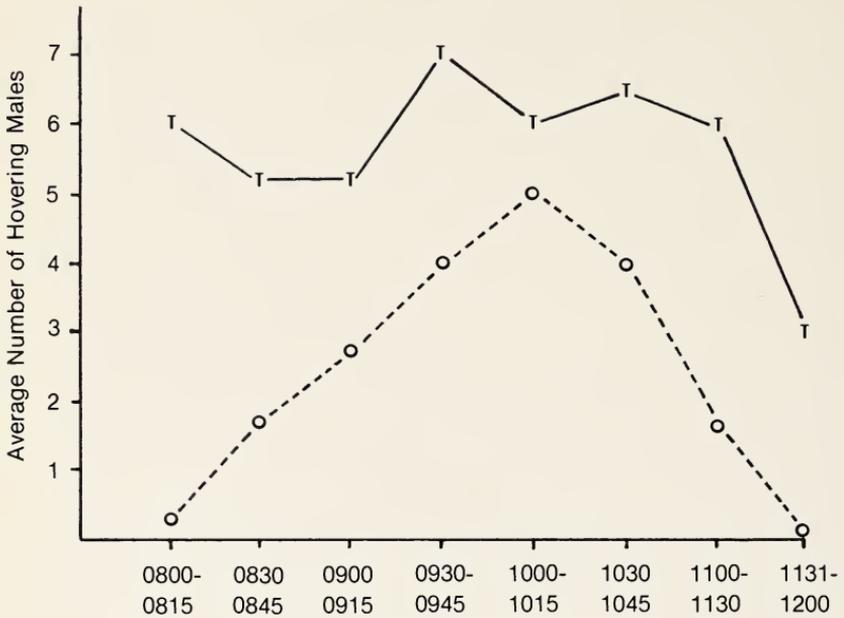


Fig. 2. The average number of males seen at different times in the morning hovering in and around a flowering palo verde tree (solid line) and close to the ground near small bushes and by the edge of a mesquite tree along a census strip through an emergence site (dotted line). Each point represents 2-4 counts (mean = 3.2) with the censuses made between 30 April - 3 May, 1976.

to their hovering point. Conspecific males that come within a meter or two of a hoverer are usually pursued and I saw a few aggressive interactions with butting and very brief midair grappling bouts. These males might be considered territorial because of these rare aggressive events and the fact that hoverers are spaced a meter or more apart. Nevertheless, as noted in an earlier paper (Alcock et al., in press), the spatial distribution of hovering males may result from a generally passive dispersal of individuals into available hovering areas rather than from the active, vigorous defense of chosen aerial stations. Many of the male-male pursuits probably involved attempts by the pursuer to determine if the passer-by were a receptive female.

Hovering males were significantly less likely to be recaptured than males that had been patrolling prior to initial capture and marking (Table 1; $X^2 = 5.02$; d.f. = 1; $P = 0.025$). In addition,

the interval between marking and last sighting for those males captured while hovering was only 2.62 days. Included in these results are four males that were hovering when first captured but which later switched to become patrollers. (A small minority of all marked males, $N=20$, exhibited the capacity to patrol and to hover, frequently doing both on the same day, patrolling in the early morning and later hovering.) Thus unless hovering males experienced a much higher rate of mortality than patrollers (which seems unlikely), one must conclude that these males were more likely to move long distances from day to day. This is not to say hoverers completely failed to exhibit site tenacity. Hovering males were continuously present at their aerial stations for several hours, while patrolling males often appeared only at irregular intervals in their searching ranges. Moreover some hoverers did return to a general area, and often a specific site, over a period of days. One male appeared at a specific location among the branches of a palo verde for four days running; another maintained a low aerial station by a creosote bush for five consecutive mornings. These males were, however, definitely the exception to the rule.

DISCUSSION

Males of the bee *C. pallida* are unusual in exhibiting two very different techniques of mate-location (patrolling and hovering), although one or the other of the two patterns is associated with a great many species of Hymenoptera (e.g. Evans, 1966; Frison, 1917; Linsley, 1965; Rozen, 1958; Shinn, 1967) including various other species of *Centris* (Frankie & Baker, 1974; Raw, 1975). The coexistence of these two divergent strategies in a single species appears related to the great variation in size of males of *C. pallida*. Size influences the ability of males to claim digging sites in competition with other males (Alcock et al., in press). Thus large males patrol and dig, small males hover. As I have shown in this paper, these two activities are linked with different tendencies to defend space against conspecific intruders and to return to a particular location. These differences are discussed below.

The pattern of short-term (several hours) residence at an aerial station or perch associated with apparent defense of the area (or at least non-overlapping distributions of males) is not unique to *C. pallida*. These traits occur in such unrelated solitary Hymen-

optera as the oaxaeid bee *Protoxaea gloriosa* (Cazier & Linsley, 1963; Linsley & Cazier, 1972; Alcock, pers. obs.) and a number of philanthine wasps (Alcock, 1975). The question arises for all these species, why should a male remain in an area for a period of hours, holding the site exclusively, only to abandon it completely, taking up residence at distant sites on subsequent days? The key to this problem may lie in the very low frequency of mating by the hovering/perched males mentioned above. Judging from the extreme rarity of observed copulations, a waiting male in these species has almost no chance of encountering a receptive female, no matter where he chooses to hover or to perch. Thus the value of a vast array of potential waiting sites must be nearly equivalent (i.e. close to zero). Given the equivalence of many sites it is not surprising that males often shift their hovering/perching sites from day to day (probably selecting an unoccupied suitable location that happens to be near the male at the moment). Shifting would also be promoted by a "musical chairs effect". If there are many males present, it is likely that a bee would find his old waiting site taken when he arrived to reclaim it on the following day. It may not pay to fight over an occupied site if there are many other equally good unoccupied places nearby. The result would be continual shifting of males as they avoided one another, taking whatever hovering/waiting site that happened to be open to them. When conspecifics are rare, hoverers might be expected to show more site tenacity because they would be less likely to find their previous day's hovering station occupied when they reached it on the next day. At Study Site 2, there were very few hoverers present and these appeared in the same aerial stations several days running. A male that has claimed a site might defend it to avoid the time costs of shifting to a new one and because it costs so little to defend it. A new arrival, finding the site taken, would have very little motivation to contest ownership because of the abundance of equally good waiting locations nearby.

In contrast to the weak territoriality and low site tenacity shown by hovering *C. pallida*, males of this species and others that patrol emergence areas ignore one another when searching the emergence site, yet show a stronger site attachment than hoverers. The persistence of home ranges in patrolling *C. pallida* almost certainly stems from the clumped nature of the resource, emerging virgin

females. Within a large emergence area there are patches from which a relatively large number of females emerge over a period of days. For example in Study Site 2, one area of about 10 m² produced a large proportion of the total copulations we observed at this location. The tendency of patrolling males to return to these areas of higher-than-average productivity is clearly adaptive, although the underlying basis for the ability to locate such sites is not known (perhaps males are attracted to sites that would attract nesting females, or perhaps males can judge from the abundance of digging males or numerous contacts with females that a particular location is superior and deserving of continuing inspection). The failure of males to defend searching areas is almost certainly a function of the high density of fellow searchers which would make defense of any but the smallest area extremely costly in terms of time and energy. Indeed, males become aggressive only when digging at a spot potentially containing a buried virgin female, repelling competitors from an area a few cm² around their body (Alcock et al., 1976; in press).

SUMMARY

Males of the bee *Centris pallida* that patrolled emergence sites in search of emerging females possessed highly overlapping home ranges of 10–25 m². Marked patrollers were found in the same general area for an average of 3.4 days. Males that hovered at spots while waiting for receptive females to fly near them possessed weakly defended non-overlapping territories a few m² in size. Marked hoverers rarely returned to a specific hovering site and averaged only 2.6 days from the date of capture to time of last sighting. Relatively long-term occupation of a home range may be adaptive for patrollers because of the clumped distribution of emerging females. In addition the high density of male competitors would make defense of a large area difficult and energetically expensive. Relatively short-term occupation of a hovering territory may be adaptive for hoverers because there are many potential hovering sites, all of which have the same low value to a male. This reduces competition for any one site making its defense feasible; at the same time, the low probability of mating

at a hovering site means that a male gains no particular advantage by returning to a specific location day after day.

ACKNOWLEDGMENTS

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RESPIRATORY SIGNIFICANCE OF THE THORACIC AND
ABDOMINAL MORPHOLOGY OF THREE CORIXIDAE,
DIAPREPOCORIS, *MICRONECTA*, AND *HESPEROCORIXA*
(HEMIPTERA: HETEROPTERA: HYDROCORISAE)*

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A. INTRODUCTION

The Corixidae are an extremely successful and abundant family of Hydrocorisae (aquatic Heteroptera). The more than 500 living species of corixids were grouped by Hungerford (1948) into six subfamilies; more recently Popov (1971) has recognized only three subfamilies, the Diaprepocorinae, Micronectinae, and Corixinae. The Corixinae, which include four of Hungerford's subfamilies, have been extensively investigated; they consist of approximately 30 genera, occur throughout the world, and range up to 16 mm. in length. Morphological and physiological studies are almost totally lacking, however, for representatives of the other two subfamilies. The Micronectinae are nearly worldwide in distribution but members of their three genera are very small (1.5-6.0 mm.) and difficult to dissect. The Diaprepocorinae consist of a single rare genus, *Diaprepocoris*, which occurs only in Australia, Tasmania, and New Zealand.

The mode of respiration in the Corixinae has been studied by many workers, including Hagemann (1910), Ege (1918), Popham (1960) and Parsons (1970). Like most Hydrocorisae, the Corixinae use "air-bubble" respiration and depend upon atmospheric air, which they carry in air stores on their bodies. The parts of the air stores which are exposed to the water can extract dissolved oxygen from the water by acting as "physical gills" (Thorpe 1950). The stored air is not a true plastron (*sensu* Thorpe 1950) because it is of considerable volume and must be periodically renewed at the surface of the water.

The air-bubble mode of respiration is reflected in the gross morphology of *Hesperocorixa* (Corixinae; Parsons 1970, 1974). In the present study the respiratory morphology of this corixid is

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compared with that of representatives of the other two subfamilies, whose respiration has never been investigated. The fine structure of the hydrofuge hairs and of the metathoracic and first abdominal spiracles, which has not yet been studied in any of the Corixidae, is also compared in *Hesperocorixa*, *Micronecta* (Micronectinae), and *Diaprepocoris* (Diaprepocorinae).

The Corixinae differ markedly from other Hydrocorisae in many morphological features. Their unusual characteristics include the very complex mesothoracic scolopophorous organ ("Hagemann's organ" of many authors), the modified mesothoracic and metathoracic epimera, the elongation of the pronotum and the posterior margin of the head, the metathoracic "air trough", and the unusual position of the metathoracic and first abdominal spiracles (Parsons 1970, 1974). These characteristics are compared in representatives of all three subfamilies, and their phylogenetic implications are discussed, below.

B. MATERIALS AND METHODS

Observations were made on *Hesperocorixa interrupta* (Say) from Massachusetts and Ontario, *Diaprepocoris zealandiae* Hale, from New Zealand, and *Micronecta sedula* Horváth, from Fukuoka, Japan. The insects, preserved in ethanol or Bouin's fluid, were dissected in 80% ethanol under a stereoscopic microscope.

For examination under the scanning electron microscope, specimens were transferred, through decreasing concentrations of ethanol, to distilled water. They were then mounted on aluminum stubs with silver Electrodag and kept briefly in distilled water until they were freeze-dried in an Edwards Speedivac-Pearse Tissue Drier, Model 1. They were coated with 20-40 nm of gold in an Edwards Vacuum Evaporator, examined under a Cambridge Stereoscan, Model 2A, and photographed with Kodak Verichrome Pan 120 roll film.

C. AIR STORES

I. Hydrofuge hairs

The distribution of the air stores in living specimens of *Hesperocorixa* was described in an earlier study (Parsons 1970). There are, to my knowledge, no similar descriptions of the air stores of *Diaprepocoris*, and Leong (1961) mentions those of *Micronecta* only briefly. Although only preserved specimens of all three corixids

were available for the present study, the location of their air stores can be deduced from their morphology, particularly the distribution of hydrofuge hairs on the body. These hairs, which are clearly visible under the scanning electron microscope, can conveniently be divided into two categories according to their length.

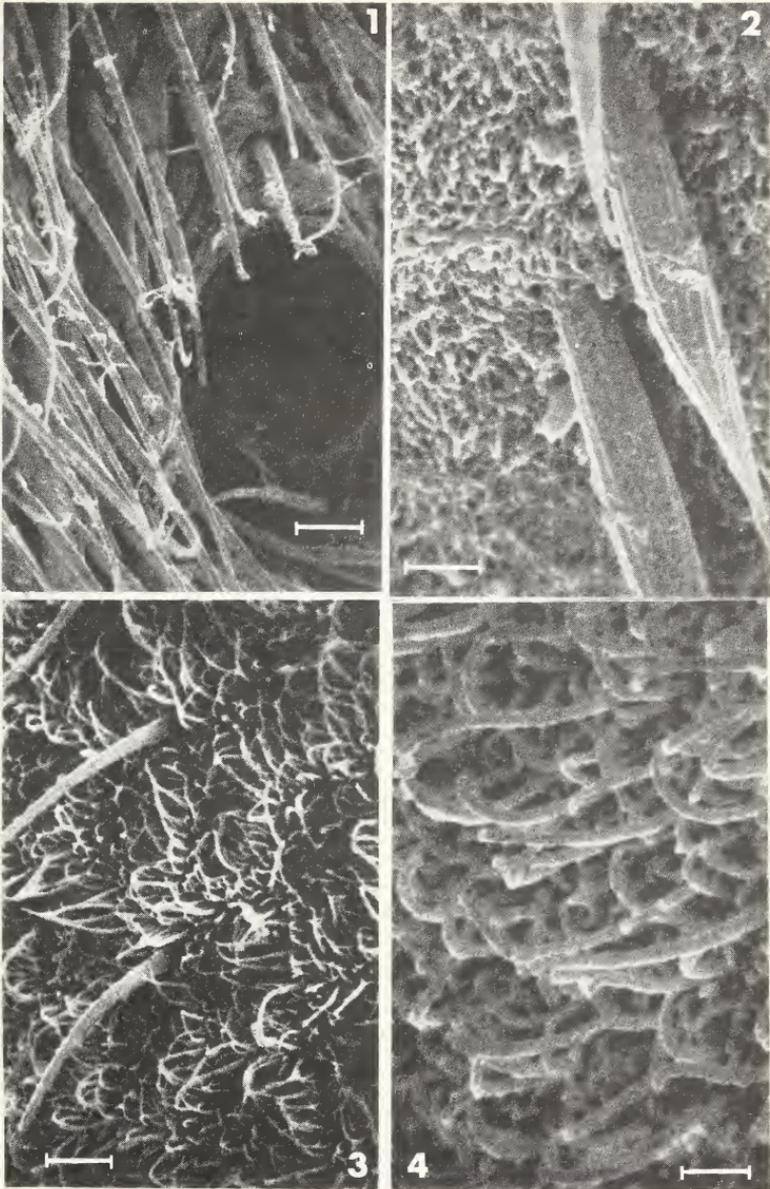
The *long hairs* (Figs. 1-3) range from 20 to 70 μm in length and are shorter in *Micronecta* (20-40 μm) than in the other two corixids. They are from one to five μm in diameter basally, and taper terminally. In *Diaprepocoris* and *Hesperocorixa* most, if not all, of the long hairs bear spiral grooves (Figs. 1 and 2); although those of *Micronecta* may have similar grooves they were not visible in any of the photomicrographs. When closely-packed, as on the abdomen of *Hesperocorixa* (Fig. 1), the long hairs are capable of holding a relatively thick air layer or "macroplastron" (term of Thorpe and Crisp 1949).

The *short hairs* (Figs. 2-4), unlike the long ones, are visible only under the scanning electron microscope and are much more densely packed. They range from two to ten μm in length and from 0.35 to 0.55 μm in diameter, and their tips are strongly curved. In many photomicrographs of *Micronecta*, and in occasional ones of *Hesperocorixa*, the short hairs have the appearance shown in Fig. 3; they resemble low arches, with several branch-like ribs, rather than separate hairs. It is not clear whether these arches are artifacts caused by the clumping of the tips of short hairs during preparation for the scanning electron microscope, or whether they represent a different type of hydrofuge structure.

II. Ventral Air Store

The ventral surfaces of the thorax and abdomen are covered with hydrofuge hairs in all three corixids. The ventral abdominal surfaces bear closely-packed long hairs which are approximately 9 to 23 μm apart in *Micronecta* and 13-18 μm apart in *Diaprepocoris* and *Hesperocorixa*. A conspicuous, thick ventral abdom-

Figs. 1-4. Hydrofuge hairs; tops of figures are anterior. Fig. 1. *Hesperocorixa interrupta*; long hairs on ventral surface of third abdominal segment in region of left third abdominal spiracle (right side of figure). Scale line = 10 μm . Fig. 2. *Diaprepocoris zealandiae*; short hairs and parts of three spirally-grooved long hairs on external surface of corium of forewing. Scale line = 5 μm . Fig. 3. *Micronecta sedula*, short hairs and parts of three long hairs on ventral surface of right prothoracic epimeron. Note arched appearance of most short hairs. Scale line = 5 μm . Fig. 4. *H. interrupta*; short hairs on ventral surface of right prothoracic epimeron. Scale line = 2 μm .



inal air layer is visible in living specimens of the latter (Parsons 1970). The third abdominal spiracles (Figs. 5-7, S3) and the spiracles posterior to them are located among the hairs in all three insects. In *Diaprepocoris* (Fig. 5) a longitudinal sulcus lies medial to these spiracles on the third through seventh abdominal segments.

Micronecta, unlike the other two insects, possesses short hairs as well as long ones on the ventral abdominal surface. The short hairs are more sparsely distributed medially than laterally, and on the fifth and more posterior abdominal segments they end approximately 10 μm from the lateral edge of the body, which is devoid of hairs. Leong (1961) mentioned the presence of "fine hairs" and a silvery ventral air layer on the abdomen of *Micronecta* sp.

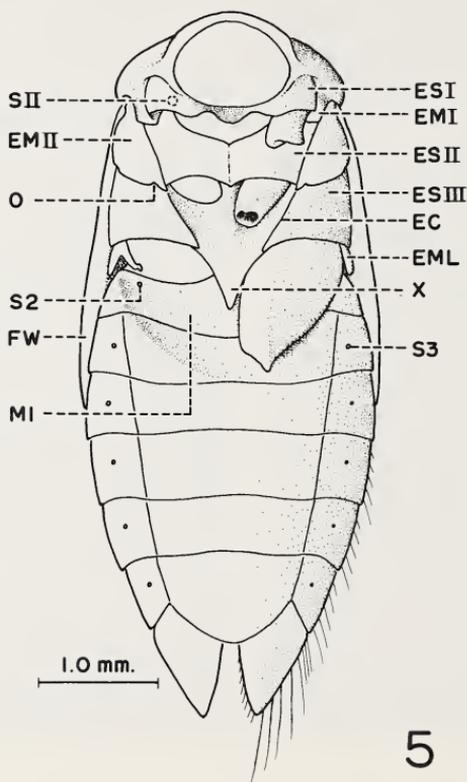


Fig. 5. *D. zealandiae*, ventral view. Head and legs removed; coxae and long setae shown only on right side of figure. Mesothoracic spiracle (S II) concealed by prothorax.

The anteroventral portion of the abdomen is concave on each side of the midline, forming a pair of *metacoxal indentations* (Figs. 5-7, MI) which accommodate the metacoxae and contain the second abdominal spiracles (S2). The metacoxae of living *Hesperocorixa* are surrounded by an air layer which extends into the metacoxal indentations (Parsons 1970). In all three corixids the ventral and posterodorsal surfaces of the metacoxae bear closely-packed long hairs, but these hairs are lacking on the anterodorsal coxal surfaces and on the metacoxal indentations in which they lie. The air in the indentations of *Hesperocorixa*, and presumably in those of the other two insects, must be retained by the close apposition between the coxae and the abdomen rather than by hydrofuge hairs.

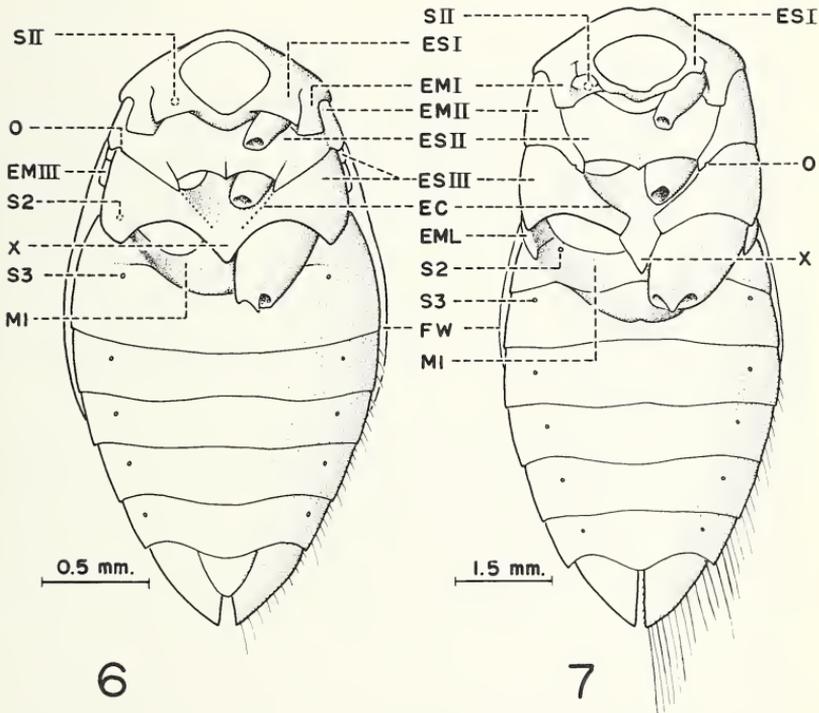


Fig. 6. *M. sedula*, ventral view, prepared as in Fig. 5. Second abdominal spiracle (S2) concealed by lobe of metathoracic episternum. Efferent channel (EC) of metathoracic scent gland, indicated by dotted lines, lies beneath exoskeleton.

Fig. 7. *H. interrupta*, ventral view, prepared as in Fig. 5.

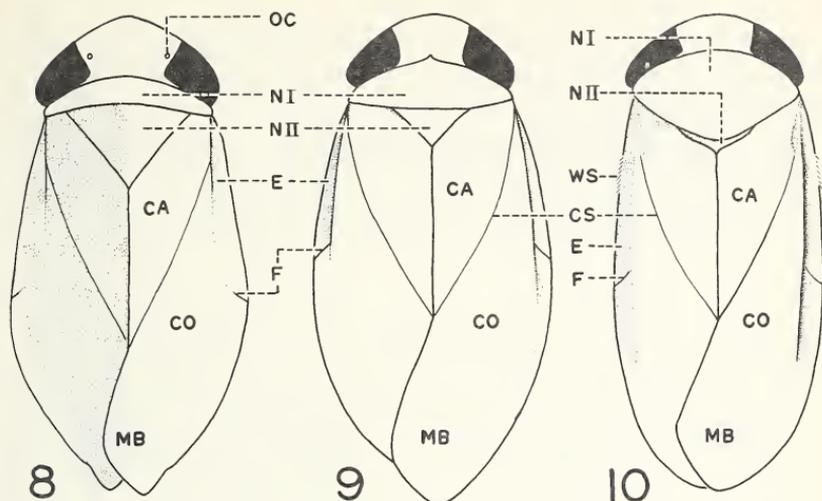
In all three corixids the exposed ventral surfaces of the prothorax and pterothorax are covered with densely distributed short hairs. Although long hairs are also present on the thorax, they are usually farther apart than on the abdomen and are entirely absent in some areas. Long hairs are rarer on the ventral thorax in *Diaprepocoris* than in the other two insects, and they are shorter than those on the abdomen. In *Corixa* (Corixinae; Thorpe 1950) and *Hesperocorixa*, however, the thoracic long hairs are longer than the abdominal ones. The ventral thoracic air layer is easily visible in living *Hesperocorixa* (Parsons 1970); the presence of hydrofuge hairs on the ventral thorax of the other two corixids indicates that they possess a similar, although perhaps thinner, air store in this region.

III. Supra-alar Air Store

In *Diaprepocoris* almost all of the exposed surface of the forewing bears hydrofuge hairs (Fig. 8, stippling on left). The clavus (CA), corium (CO) and membrane (MB) are covered with densely-packed short hairs which extend nearly to the lateral edge of the wing. The clavus and corium also bear long hairs which are 20 to 30 μm apart (Fig. 2). The extreme lateral edge of the corium lacks hairs, the bare strip being widest (approximately 0.2 mm) posterior to the nodal furrow (Fig. 8, F). The embolium (E), unlike that of the other two corixids, is not sharply differentiated from the rest of the corium and is indented only anteriorly, approximately half way to the nodal furrow.

In *Micronecta* (Fig. 9) and *Hesperocorixa* (Fig. 10) the embolium is more sharply differentiated and most of the exposed surface of the forewing lacks hydrofuge hairs. Living specimens of *Hesperocorixa* have an air layer (Fig. 10, stippling on left) on the strongly-indented embolium, on the anterior part of the claval suture (CS) and on the portion of the clavus which is overlapped by the pronotum (N I) (Parsons 1970). All these regions have a pruinose texture and are covered with short hairs and occasional long ones in *Hesperocorixa*. The hairs on the embolium extend well posterior to the nodal furrow. Anterior to the furrow they reach to the lateral edge of the wing, but posterior to the furrow they end a short distance medial to the lateral edge.

Micronecta has an even less extensive supra-alar air store (Fig. 9, stippling on left). The corium and clavus bear thick setae, up to

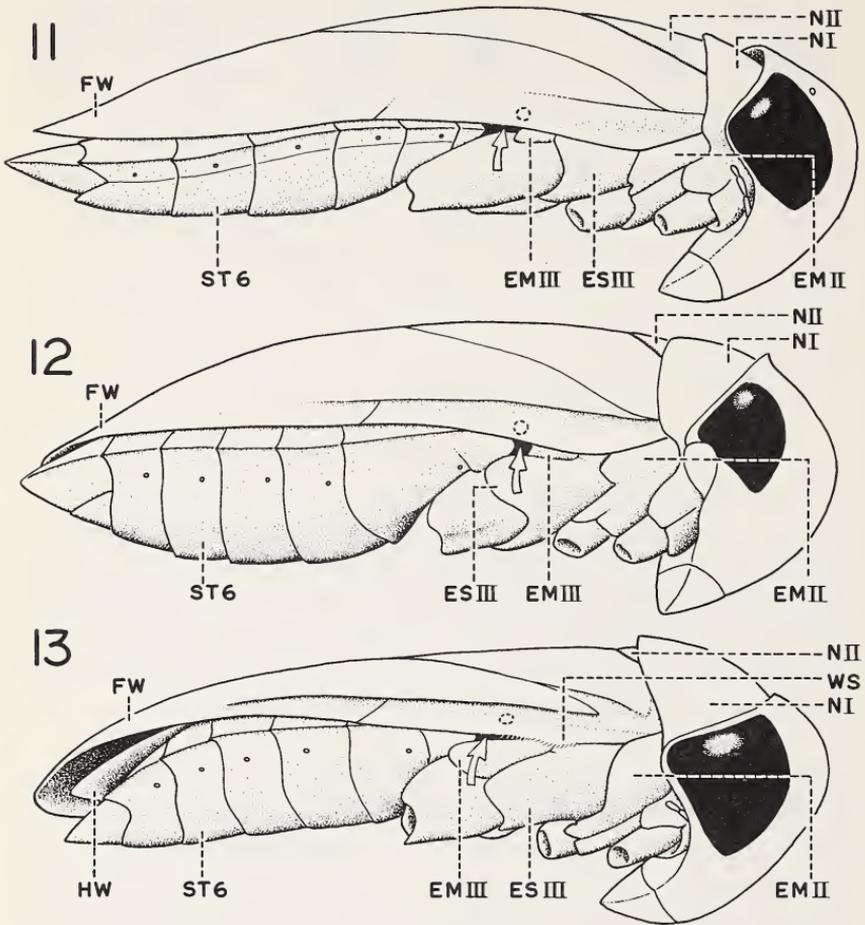


Figs. 8-10. Dorsal views; extent of exposed dorsal air stores indicated by stippling on left half. Fig. 8. *D. zealandiae*; exposed air stores on mesonotum (N II) and most of forewing. Fig. 9. *M. sedula*; exposed air store confined to anterior portion of embolium (E) and anteriormost part of claval suture (CS). Air on mesonotum is concealed by pronotum (N I). Fig. 10. *H. interrupta*; exposed air store on forewing more extensive than in Fig. 9 but much less extensive than in Fig. 8. Air on mesonotum mostly concealed by pronotum.

15 μm in length, which are spaced too far apart (500-600 μm) to retain air. Only the embolium (E), the anteriormost part of the claval suture (CS), and the part of the wing beneath the pronotum (NI) have short hydrofuge hairs. On the embolium, which is less indented than in *Hesperocorixa*, they extend only as far posteriorly as the nodal furrow. The extreme lateral edge of the embolium bears short hairs only at the level of the mesothorax. Posterior to this level the lateral edge lacks hairs; at the nodal furrow they end approximately 80 μm from the lateral edge.

IV. Cervical Air Store

In the Corixidae, unlike other Hydrocorisae, the posterior and lateral parts of the head are flattened and form flanges which overlap the prothorax (Figs. 11-13). The cervical space is filled with air which is directly continuous with the ventral air store and is exposed to the water along the posterior edges of the head (Parsons 1970).



Figs. 11-13. Lateral views. Long setae on lateral abdomen omitted; legs removed distal to coxae. Arrow indicates gap through which ventral air store communicates with subalar air store, which contains the abdominal spiracle (broken circle). Fig. 11. *D. zealandiae*. Fig. 12. *M. sedula*. Fig. 13. *H. interrupta*.

In all three corixids studied here the part of the pronotum which is overlapped by the head bears hydrofuge hairs which help to retain the air store. In *Hesperocorixa* this area, unlike the exposed part of the sclerite (Figs. 10 and 13, N I), has a pruinose texture similar to that of the embolium of the wing. The scanning electron microscope shows that in *Diaprepocoris* and *Micronecta* the exposed posterior parts of the pronota (Figs. 8, 9, 11, and 12,

N I) lack hydrofuge hairs while the anterior parts, which lie beneath the head, are covered with closely-packed short hairs. Long hairs are also present in the posteromedial part of the overlapped region in both insects. A curious feature of this region is that in both *Diaprepocoris* and *Micronecta* the localized spots at which muscle fibers attach on the pronotum are devoid of hydrofuge hairs externally.

V. I-II Air Store

Although all Hydrocorisae carry some air between the prothorax and mesothorax, this air space is greatly enlarged, in *Hesperocorixa*, by the very long pronotum (Parsons 1970). The I-II air space contains the mesothoracic spiracle (Figs. 5-7, S II). In all three corixids the spiracle is somewhat smaller than the metathoracic one and lies ventrolaterally in the intersegmental membrane, just ventromedial to the prealar bridge of the mesothorax. In *Hesperocorixa*, in which the spiracle is large enough to be examined under the stereoscopic microscope, it is covered by a "sieve-plate" similar to that of the metathoracic spiracle (see p. 161).

The I-II air store is directly continuous with the ventral thoracic and supra-alar stores. Its dorsal portion differs in the three insects. In *Hesperocorixa* (Fig. 10) the long pronotum (N I) conceals almost all of the mesonotum (N II). The latter has a pruinose texture like that of the hydrofuge parts of the forewings. The air on the mesonotum is largely concealed, although it is exposed along the posterior margins of the pronotum.

In *Diaprepocoris* (Fig. 8) the pronotum is quite short and covers only the anteriormost part of the mesonotum. The exposed part of the latter (N II), however, has long and short hydrofuge hairs like those on the dorsal surface of the forewings. It probably bears an extensive air layer which is fully exposed to the water, rather than only partly exposed as in *Hesperocorixa*.

The pronotum of *Micronecta* (Fig. 9) is longer than that of *Diaprepocoris* but shorter than that of *Hesperocorixa*, and does not cover the posteromedial tip of the mesonotum. The scanning electron microscope shows that the exposed portion of the mesonotum, unlike that of *Diaprepocoris*, lacks hydrofuge hairs. The overlapped anterior part, however, is covered with short hairs except laterally and posterolaterally, in the groove which holds the anteromedial margins of the forewings.

VI. Subalar Air Store

In all three insects the forewings are fully developed and extend to the tip of the abdomen (Figs. 11-13). All the *Hesperocorixa* examined had fully developed hindwings (Fig. 13, HW) and flight muscles. All specimens of the other two corixids, however, had vestigial indirect flight muscles and short hindwings. The latter extended to the level of the fourth and fifth abdominal tergites in *Diaprepocoris* and *Micronecta* respectively.

Hesperocorixa, like most Hydrocorisae, carries air beneath the forewings. The large subalar air store is exposed along the edges of the forewings posterior to the level of the mesothoracic epimeron, and the amount of exposure is increased when *Hesperocorixa* bends the abdomen ventrally on the thorax (Parsons 1970).

Leong (1961) reported the presence of a subalar air store in *Micronecta* sp., and *Diaprepocoris* almost certainly possesses one. The scanning electron microscope shows that in both insects the ventral surfaces of the clavus and corium bear short, densely-packed hydrofuge hairs. In these two insects the ventral margin of the forewing (Figs. 5 and 6, FW) projects laterally, beyond the edge of the body, as far posteriorly as the anterior abdominal segments. The short hydrofuge hairs extend onto the exposed, ledge-like ventral edge of the wing in both insects. In *Micronecta* they extend all the way to the lateral edge, while in *Diaprepocoris* they cover only the medial half of the exposed portion.

In *Hesperocorixa* the ventral edge of the wing does not project as far laterally as in the other two corixids. At the level of the metathorax the extreme dorsolateral edge of the embolium bears a patch of very long, curved setae (Figs. 10 and 13, WS), and immediately ventral to the posteriormost setae there is an extensive gap between the edge of the wing and the edge of the body (Fig. 13, arrow). In living specimens the subalar, supra-alar, and ventral air stores communicate with each other along this gap and for some distance posterior to it (Parsons 1970). The subalar and ventral abdominal air stores also appear to communicate with each other along the posterolateral margins of the abdomen, which bear long setae (Fig. 7, right side of figure).

The amount of communication between the subalar and supra-alar stores cannot be determined in the other two corixids without living specimens. Like *Hesperocorixa*, however, both *Diaprepocoris* and *Micronecta* possess a large space between the fore-

wing, the metathoracic epimeron, and the anterolateral part of the abdomen (Figs. 11 and 12, arrow) which allows the subalar air store to communicate with the ventral one. The two air stores probably also communicate along the posterior part of the abdomen, which bears lateral setae (Figs. 5 and 6, right sides of figures).

D. PTEROTHORAX

I. Typical Hydrocorisae

The pterothorax of typical Hydrocorisae has been described in previous publications (Parsons 1970, 1974) and will be only briefly summarized here.

The mesothoracic (Fig. 14A, EM II) and metathoracic episternum (ES III) form flat evaginated lobes laterally, posteriorly, and pos-

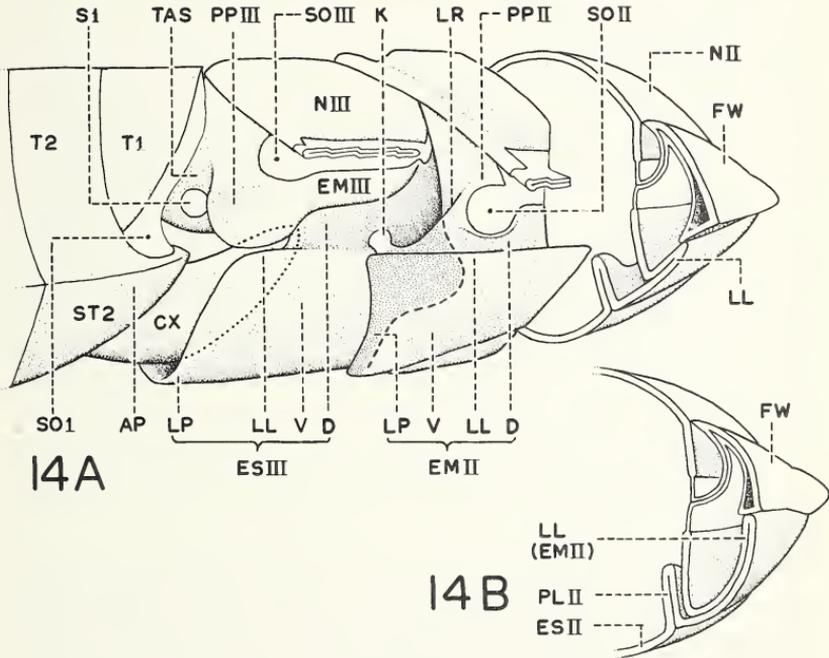


Fig. 14A and B. Diagrammatic lateral views. (A) Pterothorax and anterior abdomen of typical Hydrocorisae. Mesothorax cut transversely, wings removed posterior to transverse cut. Heavy broken line indicates position of lateral intersegmental boundary, concealed by external wall of mesothoracic epimeron (EM II); heavy stippling indicates intersegmental air store, which contains metathoracic spiracle (concealed in this view). (B) Anterior mesothorax, cut as in Fig. 14A, showing how lateral epimeral lobe (LL) is modified in *M. sedula* and *H. interrupta*.

teromedially. The *lateral lobes* (LL) subdivide each pleurite into dorsal and ventral portions. The dorsal portions (D) of the pleurites are vertical and concealed by the forewings; the ventral portions (V) are more horizontal and are exposed to the water. The *posterior lobes* (LP) of both pleurites are continuous with the lateral ones. The posterior lobe of the mesothoracic epimeron overlaps the metathoracic episternum, whose posterior lobe overlaps the metacoxa (CX).

The posterolateral corner of the mesothoracic epimeron bears a knob-like process (Fig. 14A, K) which fits into a depression on the costal margin of the forewing, anchoring it against the edge of the lateral epimeral lobe. The subalar air space between the forewing and the body is enlarged lateral to the vertical, dorsal portions of the mesothoracic epimeron and metathoracic episternum, which are indented on the body.

The mesothoracic postalar bridge projects laterally into the subalar space forming a collar-like *postalar projection* (Fig. 14A, PP II). A double-walled *lateral ridge* (LR) of the mesothoracic epimeron runs from the postalar projection to the wing-anchoring knob. The postalar projection encircles the membrane of a mesothoracic *scolopophorous organ* (SO II) either partially, as in Fig. 14A, or completely. The function of this paired sense organ, and of its homologues on the metathorax (SO III) and first abdominal segment (SO I) has been debated. Larsén (1957) believed them to be equilibrium perceptors. More recently, however, experimental evidence has indicated that the mesothoracic scolopophorous organs of *Notonecta obliqua* (Notonectidae; Arntz 1972) and *Corixa punctata* (Corixinae; Prager 1973) and the mesothoracic and metathoracic organs of *Nepa cinerea* (Nepidae; Arntz 1975) are sensitive to sound.

The boundary between the mesothorax and metathorax curves sharply anteriorly into the mesothoracic region in the lateral part of the body (Fig. 14A, heavy broken line). In some Hydrocorisae this lateral intersegmental boundary forms a prominent, flap-like invagination which grows anteriorly during postecdysial development (Parsons 1974). A lateral intersegmental air space (heavy stippling), which is posteriorly continuous with the subalar air space, is formed between the invaginated boundary and the lateral ridge of the mesothoracic epimeron. It is ventromedially continuous with a much smaller ventral intersegmental air space which lies dorsal to the posterior epimeral lobe.

The *metathoracic spiracle* (concealed in Fig. 14A) is located anterior to the intersegmental boundary in all Hydrocorisae which have been examined thus far (Parsons 1974). It lies on the mesothoracic epimeron, and usually opens onto the lateral intersegmental or ventral intersegmental air space (Positions 1 and 2, respectively, of Parsons 1974). It is thus concealed externally by the lateral ridge or posterior lobe of the mesothoracic epimeron. In *Hesperocorixa* and *Notonecta*, however, the spiracle lies immediately adjacent to the mesothoracic scolopophorous organ, on the dorsal, vertical part of the epimeron, and opens directly onto the subalar air space (Position 3 of Parsons 1974).

II. *Diaprepocoris*

Of the three corixids examined, *Diaprepocoris* shows the least modification of the typical plan diagrammed in Fig. 14A. The lateral lobe of the mesothoracic epimeron (Fig. 15, LL) is relatively narrow and projects laterally and somewhat dorsally, as in typical Hydrocorisae, rather than curving sharply dorsally, as in *Micronecta* and *Hesperocorixa* (Fig. 14B). Thus the costal margin of the wing lies farther ventrally on the body than in the latter two insects.

Posterior to the wing-anchoring knob of the mesothoracic epimeron, the margin of the forewing fits into a horizontal groove (Fig. 15, W) on the metathoracic episternum. The homologies of this groove are uncertain. Unlike the wing-holding devices on the metathoracic episterna of *Micronecta* (Fig. 16, W) and *Hesperocorixa* (Fig. 17, W), it lies far ventral to, rather than at the level of, the metathoracic coxal process (Fig. 18, PR), and appears externally as a groove rather than as a ridge. In addition, it does not form the ventral boundary of a well-developed "air trough" such as that of *Hesperocorixa* (Fig. 17, AT). In the latter, both the epimeron and the episternum of the metathorax are strongly indented in the region of the pleural sulcus (PL III). In *Diaprepocoris*, as in most other Hydrocorisae, only the dorsal portion of the episternum and a small portion of the epimeron are indented in this region (Fig. 15).

The boundary between the mesothorax and metathorax is marked dorsally by the second phragma (Fig. 18, 2PH). Ventral to the mesothoracic scolopophorous organ (SO II) the boundary bends sharply anteriorly and then curves posteromedially onto the ventral surface of the body. The portion of the boundary

which bends anteriorly forms a short projection internally (II-III); this flap, which is similar to the intersegmental projection of *Aphelocheirus* (Aphelocheiridae; Parsons 1974), partially conceals the base of the metathoracic spiracular trachea. The metathoracic spiracle (Figs. 15 and 18, S III) lies immediately below the scolopophorous organ in the dorsal part of the mesothoracic epimeron, immediately anterodorsal to the intersegmental boundary. The fine structure of the spiracle and sense organ are described on pp. 161 and 164.

Unlike *Micronecta* and *Hesperocorixa*, *Diaprepocoris* possesses a lateral epimeral ridge, which runs from the wing-anchoring knob to the postalar region (Fig. 15, LR). The ridge is much less pronounced than its homologue in typical Hydrocorisae (Fig. 14A) and, unlike the latter, is not high enough to conceal the metathoracic spiracle externally or to create a lateral intersegmental air space. Thus the spiracle, like those of *Micronecta* and *Hesperocorixa*, opens directly onto the subalar air space.

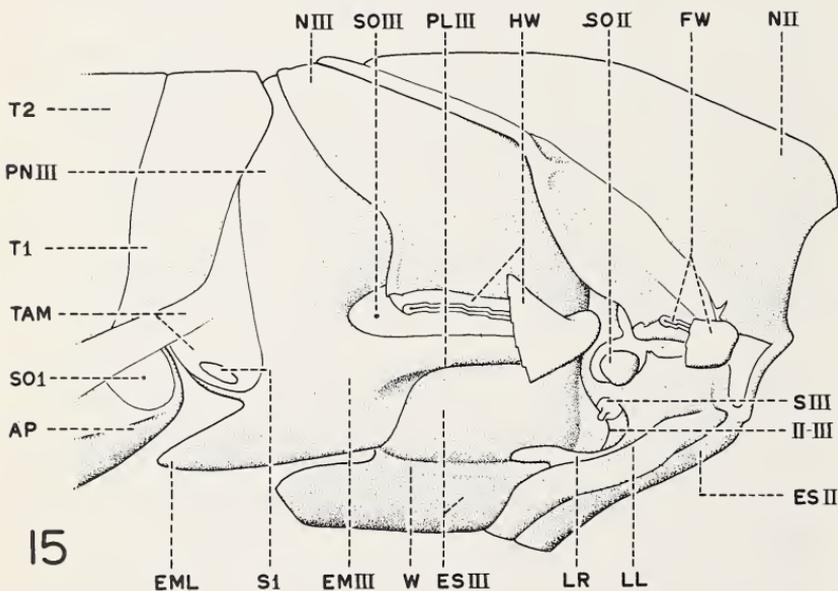


Fig. 15. *D. zealandiae*; lateral view of pterothorax and anterior abdomen. Wings and coxae removed.

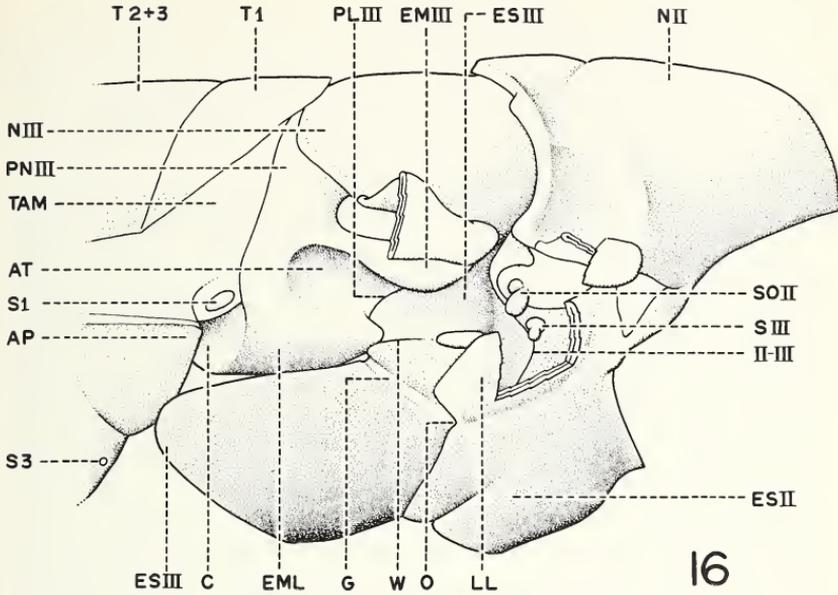


Fig. 16. *M. sedula*; lateral view of pterothorax and anterior abdomen. Wings and coxae removed; portion of lateral lobe (LL) of mesothoracic epimeron cut away to reveal structures shown in Fig. 26.

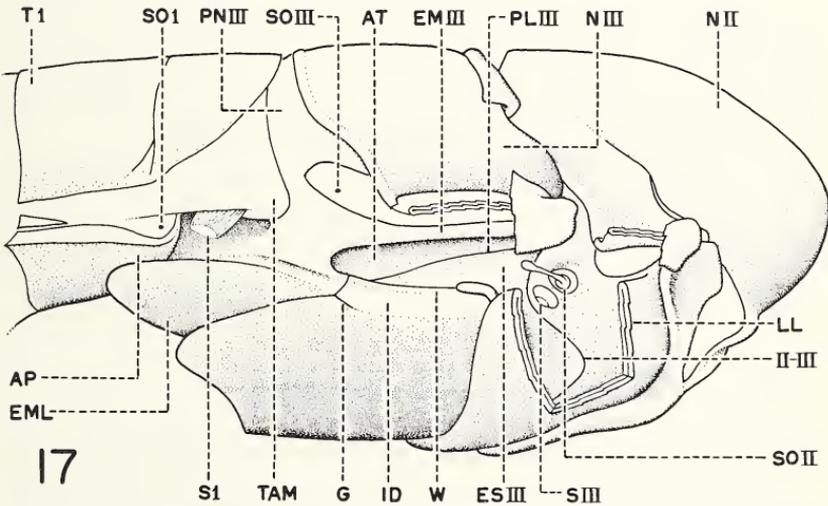


Fig. 17. *H. interrupta*; lateral view of pterothorax and anterior abdomen. Wings and coxae removed; portion of lateral lobe (LL) of mesothoracic epimeron cut away to reveal structures shown in Fig. 27.

III. *Micronecta* and *Hesperocorixa*

Two previous papers (Parsons 1970, 1974) have described the ways in which the pterothorax of *Hesperocorixa* differs from that of the typical Hydrocorisae. *Micronecta* shares these characteristics to a greater extent than does *Diaprepocoris*.

The mesothoracic epimeron of *Micronecta* and *Hesperocorixa* is considerably different from that of *Diaprepocoris* and the typical Hydrocorisae. It possesses no lateral epimeral ridge, and its lateral lobe (Fig. 14B, LL), which is greatly widened, curves strongly dorsolaterally rather than projecting laterally and only slightly dorsally (compare Figs. 14A and 14B). In both corixids the edge of the lobe (Figs. 16 and 17, LL) extends dorsal to the level of the metathoracic spiracle (S III) and reaches nearly to the level of the mesothoracic scolopophorous organ (SO II). The costal margin of the forewing (Fig. 14B, FW), which rests on the edge of the lateral lobe, lies farther dorsally on the body than in *Diaprepocoris*. Thus on the mesothorax the ventral part of the subalar air space is bounded by the lateral lobe (LL) rather than by the forewing.

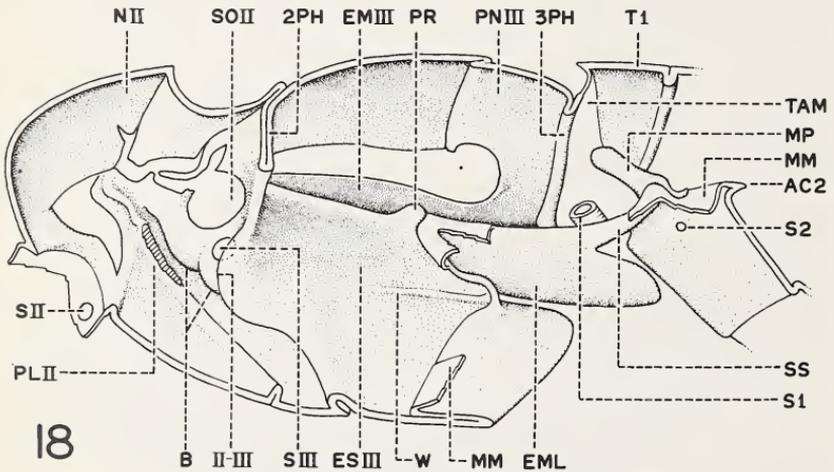


Fig. 18. *D. zealandiae*; internal view of pterothorax and anterior abdomen, cut parasagittally lateral to mesocoxa. Cross-hatched cut edge of mesothoracic pleural ridge (PL II) indicates base of pleural apophysis (removed). Metacoxa and soft tissues removed; part of metacoxal membrane (MM) cut away to show sclerotized strip (SS) and inner wall of metathoracic epimeral lobe (EML). First abdominal spiracular trachea (S I) emerges from spiracle lying in thoracico-abdominal membrane lateral to sclerotized strip.

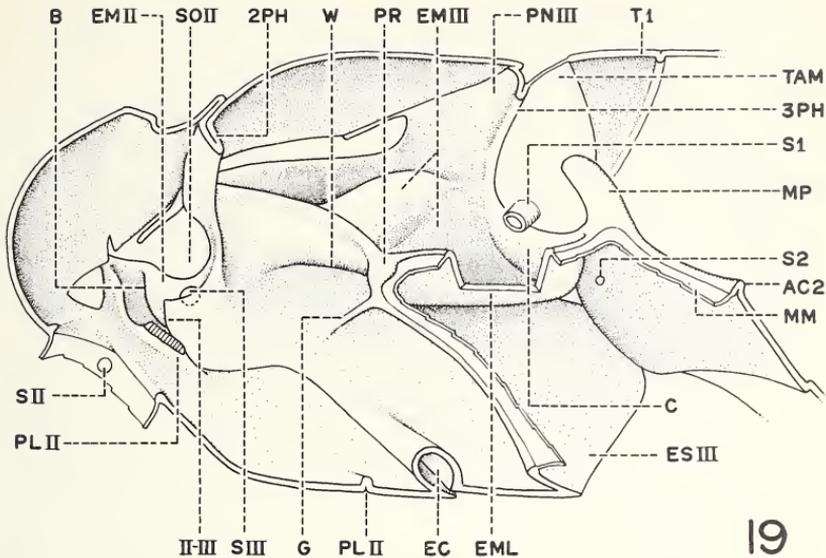


Fig. 19. *M. sedula*; internal view of pterothorax and anterior abdomen, cut parasagittally lateral to mesocoxa. Cross-hatched cut edge of mesothoracic pleural ridge (PL II) indicates base of pleural apophysis (removed). Metacoxa and soft tissues removed; part of inner wall of metathoracic epimeral lobe (EML) cut away to show indented portion (C) of outer wall of lobe.

The lateral lobe is so wide that its base (Figs. 19 and 20, B) lies immediately lateral to the mesothoracic pleural apophysis (Fig. 14B, PL II; Figs. 19 and 20, cross-hatched part of PL II). In mature specimens of both corixids the base of the lobe adheres closely to the pleural apophysis and can be dissected away from it only with difficulty. In *Micronecta* the base of the lateral lobe is marked by a groove, on the external surface of the epimeron, which extends posteriorly as far as the ostiole of the metathoracic scent gland (Fig. 16, O). The mesothoracic pleural sulcus of *Hesperocorixa*, like that of *Diaprepocoris*, is complete and extends from the mesothoracic coxal process to the pleural wing process. In *Micronecta*, however, the sulcus is incomplete and can be clearly distinguished only in the region of the pleural apophysis (Fig. 19, cross-hatched portion of PL II).

All three corixids possess a metathoracic scent gland and a paired efferent system which carries the secretion from the dorsal surface of the metasternal xiphus (Figs. 5-7, X) to an ostiole at the posterior

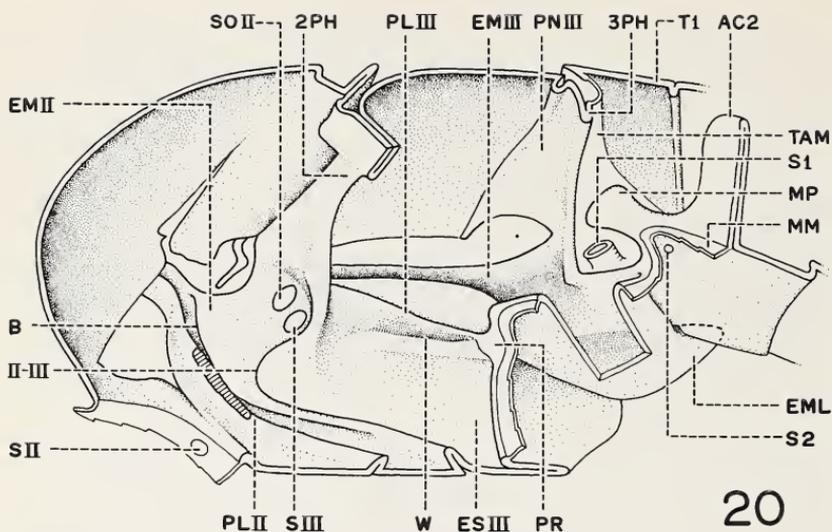


Fig. 20. *H. interrupta*; internal view of pterothorax and anterior abdomen, cut parasagittally lateral to mesocoxa. Cross-hatched cut edge of mesothoracic pleural ridge (PL II) indicates base of pleural apophysis (removed). Metacoxa and soft tissues removed; part of inner wall of metathoracic epimeral lobe (EML) removed to show outer wall of lobe.

edge of each mesothoracic epimeron. In *Hesperocorixa* and *Diaprepocoris* the ostiole (Figs. 5 and 7, O) lies posteromedially on this sclerite. The edge of the epimeron which is immediately lateral to it lacks hydrofuge hairs and resembles the "evaporating surface" of *Gelastocoris* (Gelastocoridae; Parsons 1960). In *Micronecta* the ostiole occurs far more laterally on the epimeron, at the posterior end of the lateral epimeral lobe (Figs. 6 and 16, O). The edge of the epimeron which lies lateral to it possesses hydrofuge hairs and is triangular, its apex pointing posteriorly.

The efferent canals leading to the ostioles also differ in the three corixids. In *Hesperocorixa* and *Diaprepocoris* the canals are deep, open channels which extend anteromedially on each metathoracic episternum (Figs. 5 and 7, EC). They have a similar form in such other Hydrocorisae as *Gelastocoris* (Parsons 1960), *Ilyocoris* (Naucoridae; Staddon and Thorne 1973) and *Notonecta* (Notonectidae; Staddon and Thorne 1974). In *Micronecta*, however, the canals are not externally visible on the metathoracic episternum; they are closed ducts which lie immediately beneath the surface of

the exoskeleton. These ducts (indicated by dotted lines, Fig. 6) open onto the intersegmental groove (Fig. 19, EC), between the metathoracic episternum and the mesothoracic epimeron, which leads to the lateral ostiole.

In *Hesperocorixa* the subalar space external to the metathoracic pleural sulcus (Fig. 17, PL III) is enlarged by a pronounced, horizontal, trough-like indentation (AT) which extends from the intersegmental boundary to a level posterior to the metathoracic coxal process. This "air trough" is formed by both the dorsal portion of the metathoracic episternum and the ventral portion of the metathoracic epimeron. It is bounded ventrally by a pronounced ridge (W) which appears to represent the anterior part of the episternal lateral lobe. The costal margin of the forewing fits closely against this ridge, closing off the air trough ventrally. The raised episternal ridge performs the same wing-holding function as does the horizontal episternal groove of *Diaprepocoris* (Fig. 15, W) but, unlike the latter, extends anteriorly from the coxal process (Fig. 20, PR) rather than lying far ventral to it (Fig. 18). In *Hesperocorixa* a possible homologue of the episternal groove of *Diaprepocoris* is a short groove (Fig. 17, G) which lies posteroventral to the wing-anchoring ridge, at the posteroventral edge of an indented region (ID) of the episternum. On this indentation the ventral thoracic air layer is greatly thickened. Unlike the rest of the exposed episternum, the indentation lacks long hydrofuge hairs and is covered only with short ones.

In *Micronecta* the metathoracic air trough is less well-developed. Anteriorly it is formed only by the recessed dorsal portion of the metathoracic episternum (Fig. 16, ES III). The anterior part of the epimeron (EM III) is entirely convex, like that of *Diaprepocoris* and typical Hydrocorisae, rather than partially concave as in *Hesperocorixa*. Only the portion of the epimeron which lies at the level of the coxal process is concave, forming the posterior part of the air trough (AT).

The episternal wing-holding mechanism of *Micronecta* consists of a low horizontal ridge (Fig. 16, W) which, like its more pronounced homologue in *Hesperocorixa*, forms the ventral boundary of the air trough. Ventral to this ridge is a deep groove (G) which runs obliquely anteromedially and ends at the ostiole of the metathoracic gland (O). This groove may be homologous with the wing-holding groove of *Diaprepocoris*. Its function is difficult

to determine. It may serve as an "evaporating area"¹ for the secretion which emerges from the ostiole; unlike the smooth "evaporating surfaces" on the mesothoracic epimera of *Hesperocorixa* and *Diaprepocoris*, however, the groove of *Micronecta* bears short hydrofuge hairs similar to those on the rest of the ventral portion of the episternum.

In both *Hesperocorixa* and *Micronecta* the lateral boundary between the mesothorax and metathorax projects anteriorly, as in *Diaprepocoris*. In *Micronecta* it forms a flap-like internal projection (Fig. 19, II-III) which overlaps the trachea of the metathoracic spiracle (S III); the flap is similar to, but longer than, that of *Diaprepocoris*. Externally the lateral intersegmental boundary of *Micronecta*, like that of *Diaprepocoris*, forms a faint line (Fig. 16, II-III) which reaches anteriorly only as far as the level of the spiracle S III). In *Hesperocorixa* the boundary projects farther anteriorly, beyond the level of the spiracle (Fig. 17) and forms only a low ridge, rather than a flap, internally (Fig. 20, II-III).

The metathoracic spiracles of both *Hesperocorixa* and *Micronecta* lie on the mesothoracic epimeron, anterodorsal to the intersegmental boundary and ventral to the mesothoracic scolopophorous organ. The fine structure of the spiracle and sense organ are described on pp. 161 and 164.

E. THORACICO-ABDOMINAL REGION

I. Typical Hydrocorisae

The typical structure of the lateral thoracico-abdominal region of Hydrocorisae is diagrammed in Figs. 14A and 21. The metathoracic epimeron (EM III) is relatively smaller than the mesothoracic one and has a quite different shape. Anteriorly, beneath the hindwing, it is narrow; in the postalar region it broadens and joins the metathoracic postnotum forming a large, lateral postalar projection (PP III). The metathoracic scolopophorous organ (SO III) lies anterodorsal to the projection.

Posteromedial to the postalar projection, and separated from it by a pronounced fold, is a roughly triangular structure (TAS) which has been termed the "*thoracico-abdominal sclerite*" (Parsons

¹Although this term is not appropriate when applied to underwater insects, it is retained here because of its general use in the literature on terrestrial Heteroptera.

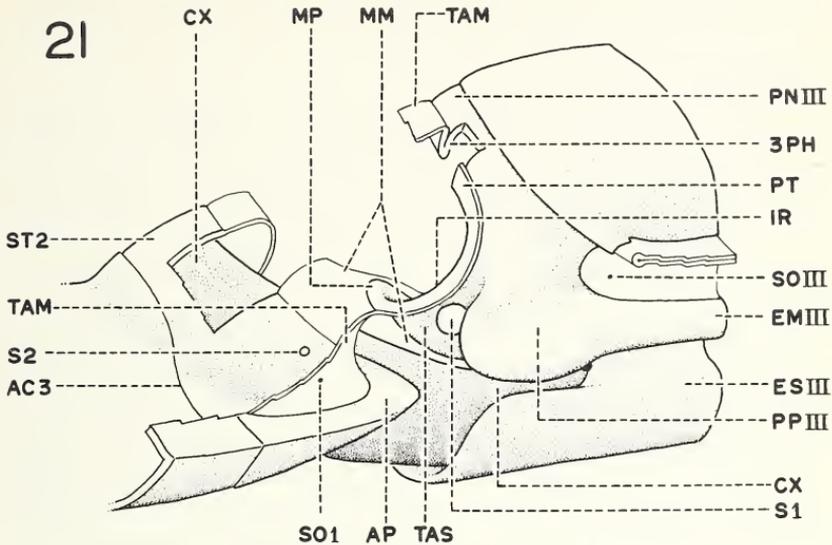


Fig. 21. Diagrammatic lateral view of thoraco-abdominal region of typical Hydrocorisae. Hindwing, soft tissues, and abdominal tergites removed; thoraco-abdominal membrane (TAM), which attaches to posttergite (PT) and lateral wall of intersegmental ridge (IR), mostly removed.

1970). The sclerite is recessed on the body and usually contains the *first abdominal spiracle* (S 1) which thus opens onto an enlargement ("first abdominal spiracular chamber", Parsons 1970) of the subalar air space.

In an earlier study (Parsons 1970) I could not determine whether this sclerite is thoracic, abdominal, or a combination of both. Further investigation of a wider variety of Hydrocorisae has strongly indicated that the "thoraco-abdominal sclerite is a recessed, posterior part of the metathoracic epimeron, and that in most Hydrocorisae the first abdominal spiracle, like the metathoracic one, has moved from the intersegmental region into the more anterior segment (Parsons 1972a).

The ventral portion of the sclerite, to which the metacoxal membrane attaches (Fig. 21, MM), is weakly evaginated in such Hydrocorisae as *Belostoma* (Belostomatidae), *Nepa* (Nepidae), *Ambrysus* (Naucoridae) and *Pelocoris* (Naucoridae). The evagination is much larger and more prominent in the Corixidae examined here (Figs. 22-24, EML). This suggests that the evaginated portion is a

supracoxal lobe, homologous with the supracoxal lobe of the mesothoracic epimeron which was described in a previous paper (Parsons 1974).

The boundary between the thorax and abdomen is less clearly marked than that between the mesothorax and metathorax. The low third phragma (Fig. 21, 3PH) is anteriorly continuous with the metathoracic postnotum (PN III) and possesses a short posterior wall, the posttergite (PT; *sensu* Snodgrass 1935). The phragma represents the first abdominal antecosta, while the posttergite represents, according to Snodgrass, the anterior part of the first abdominal segment. Thus the membrane which attaches to the posttergite is the *functional thoracico-abdominal membrane* (TAM) rather than the morphological one (Parsons 1970).

The lateral part of the phragma is continuous with a low internal ridge (Fig. 21, IR) which runs along the posteroventral edge of the thoracico-abdominal sclerite. The ridge, which is here interpreted as the thoracico-abdominal boundary, becomes indistinct posteromedially. It can be traced as far as a process (MP), of variable size and shape, from which one or more dorsoventral muscles arise. The muscles attach dorsally on the first abdominal tergite, suggesting that the process is a part of the abdomen which is fused with the posteriormost part of the metathoracic epimeron. The process may be separated from the rest of the abdomen by the functional thoracico-abdominal membrane (Fig. 21), as in *Ambrysus* (Parsons 1970), *Belostoma* (Parsons 1972a) and *Diaprepocoris* (Fig. 22), or it may be fused with the abdomen, as in *Notonecta* (Parsons 1971), *Micronecta* (Fig. 23) and *Hesperocorixa* (Fig. 24). When fused with the abdomen its crest is medially continuous with the second abdominal antecosta (Figs. 23 and 24, AC2).

The first abdominal segment, unlike the more posterior ones, is incomplete laterally. Its tergite (Fig. 14A, T1) is separated from its sternal portion by the functional thoracico-abdominal membrane, which usually contains the first abdominal scolopophorous organ dorsolaterally (Figs. 14A and 21, SO 1). The lateral portion of the reduced first abdominal sternite is represented by at least part of the process MP (Fig. 21). The medial portion of the sternite may be entirely membranous and incorporated into the metacoxal membrane (Fig. 21), as in *Belostoma* and *Ambrysus*, or may be represented by a narrow sclerotized region anterior to the crest of the second abdominal antecosta, as in *Notonecta* (Parsons 1971),

Ranatra (Nepidae; Parsons 1972a), and the Corixidae examined here.

The sternite and tergite of the second abdominal segment are joined laterally (Fig. 14A). The anterolateral part of the segment projects anteriorly forming an *abdominal projection* (Figs. 14A and 21, AP) upon which the edge of the forewing rests. The second abdominal spiracle, like the more posterior ones, is much smaller than the first abdominal one and lies in the ventrolateral part of the segment (Fig. 21, S2).

All three of the corixids examined here differ from the typical plan in three major respects: (1) the evaginated lobe of the metathoracic epimeron is much larger than in other Hydrocorisae, (2) the metathoracic postalar region does not form a strong lateral projection, and (3) the first abdominal spiracle lies in the functional thoracico-abdominal membrane rather than in the metathoracic epimeron. The three insects differ mainly in the shape of the metathoracic epimeron and in the way in which it is joined to the anteroventral part of the abdomen.

II. *Diaprepocoris*

The posterior part of the metathoracic epimeron of *Diaprepocoris* is diagrammed in Fig. 22. Unlike the thoracico-abdominal sclerite of typical Hydrocorisae (Fig. 21, TAS) it is not recessed on the body; its external wall is directly continuous with the postalar bridge, which does not project strongly laterally. The posterior part of the subalar membrane contains a small sclerite (SO III) which probably forms an attachment for the scolophore of a metathoracic scolopophorous organ.

The epimeron forms a large, two-walled ventral lobe (Figs. 18 and 22, EML) which extends posteroventrally from the metacoxal process (Fig. 18, PR; Fig. 22, heavy black dot). The metacoxal membrane (MM) attaches along the free dorsal edge of the inner wall of the lobe. The inner (medial) and outer (lateral) walls are joined anteriorly, ventrally, and posterodorsally; their apposed surfaces adhere closely to each other and are difficult to separate. The dorsal opening into the lobe extends from the coxal process to a point (Fig. 22, P) approximately midway between the level of the third phragma (3PH) and the anterior edge of the abdominal projection (Figs. 15 and 22, AP). Posterior to Point P the lobe projects posteroventrally, as a blind sac, ending just ventral to the anterior edge of the abdominal projection.

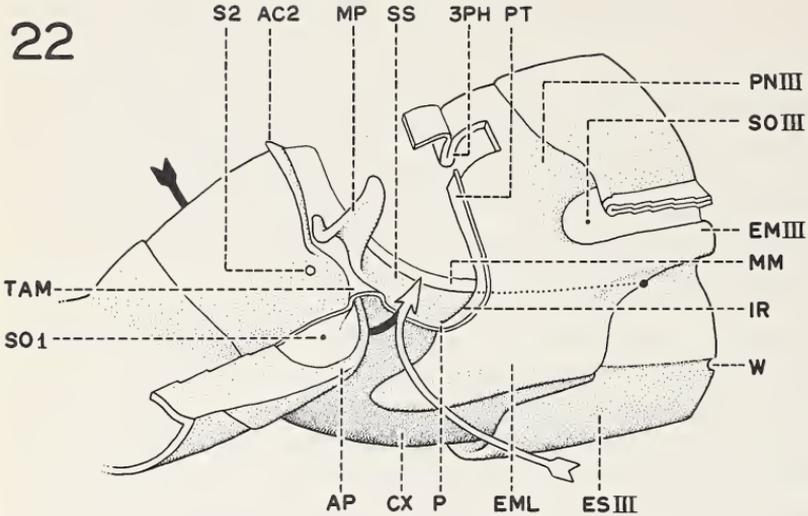


Fig. 22. *D. zealandiae*; semi-diagrammatic lateral view of thoraco-abdominal region, prepared as in Fig. 21. Thoraco-abdominal membrane (TAM, mostly removed) attaches along posttergite (PT) and lateral edges of intersegmental ridge (IR) and sclerotized strip (SS). Heavy black dot indicates position of coxal process; heavy dotted line indicates dorsal edge of inner wall of metathoracic epimeral lobe (EML). Head of arrows indicates position of first abdominal spiracle (removed) in thoraco-abdominal membrane; spiracle communicates with ventral air store (white arrow) and with air store surrounding metacoxa (black arrow).

The intersegmental boundary (Fig. 22, 3PH) is transverse in the dorsolateral part of the body. At the level of the opening into the epimeral lobe the boundary bends abruptly posteroventrally, forming a low internal ridge (IR). The ridge adheres to the inner wall of the lobe, obscuring the posterior part of the opening. Only mature specimens were available for this investigation; quite possibly the opening is not obscured in newly-moulted individuals.

At Point P the epimeral lobe becomes continuous with a narrow sclerotized strip (Fig. 22, SS) which runs posteromedially and ends in a muscle process (MP). All but the most ventral, posterolateral edge of this strip is concealed externally by the functional thoraco-abdominal membrane (Fig. 15, TAM; membrane mostly removed in Fig. 22), which attaches along this edge. The first abdominal spiracle (Figs. 15 and 18, S1) lies in the thoraco-abdominal membrane immediately lateral to the sclerotized strip. The anteromedial edge of the strip is more dorsal than the posterolateral edge and

provides an attachment for the metacoxal membrane (Figs. 18 and 22, MM). Although the intersegmental boundary is not indicated by any definite landmark on the sclerotized strip, comparison of *Diaprepocoris* with *Micronecta* (Fig. 23, IR) and *Hesperocorixa* (Fig. 24, IR) strongly suggests that the boundary runs lengthwise along the structure, paralleling the attachment of the thoracico-abdominal membrane.

The muscle process (Figs. 18 and 22, MP) which lies at the posteromedial end of the sclerotized strip projects anterodorsally. A large muscle attaches to its anterior face and extends dorso-medially to the medial portion of the first abdominal tergite. This suggests that at least the anterior portion of the process represents the first abdominal segment, and that the thoracico-abdominal boundary passes anteromedial to its base.

The muscle process, unlike that of *Micronecta* (Fig. 23) or *Hesperocorixa* (Fig. 24) is separated, by a membrane, from the anteroventral portion of the abdomen. An irregularly shaped medial arm of the process articulates flexibly with the anterior wall of a low second abdominal antecosta (Fig. 22, AC2); this narrow anterior wall appears to represent a reduced first abdominal sternite. The rest of the muscle process is separated, by a narrow strip of the thoracico-abdominal membrane, from the part of the abdomen containing the second abdominal spiracle (S2). The latter region lacks a second abdominal antecosta and appears to consist only of the second abdominal segment. Laterally it forms the abdominal projection (AP). The dorsal portion of the thoracico-abdominal membrane, which attaches to the abdominal projection, contains the sensory membrane of the first abdominal scolopophorous organ (SO I). This sense organ, like the metathoracic one (SO III), was not examined here; the small sclerite to which its scolophore probably attaches does not appear to be unusually modified.

III. *Micronecta*

The metathoracic epimeral lobe and the second abdominal spiracle of *Micronecta*, unlike those of *Diaprepocoris* and *Hesperocorixa*, are concealed ventrally by the metathoracic episternum (Fig. 6, ES III), whose posterior lobe is longer than in the other two insects. As in *Diaprepocoris*, the epimeral lobe (Figs. 19 and 23, EML) is a two-walled structure lying posteroventral to the metathoracic coxal process (Figs. 19, PR; Fig. 23, heavy black dot). The lobe differs from that of *Diaprepocoris*, however, in the shape of the

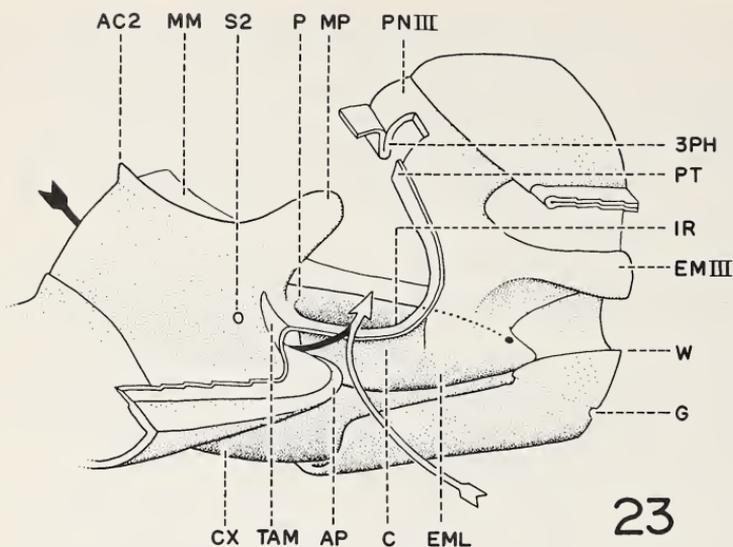


Fig. 23. *M. sedula*; semi-diagrammatic lateral view of thoraco-abdominal region, prepared as in Fig. 21. Heavy black dot indicates position of coxal process; heavy dotted line indicates dorsal edge of inner wall of metathoracic epimeral lobe (EML). Head of arrows indicates position of first abdominal spiracle (removed) in thoraco-abdominal membrane (TAM); spiracle communicates with ventral air store (white arrow) and with air store surrounding metacoxa (black arrow).

outer wall and in the extent of the dorsal opening between the inner and outer walls.

The anterior portion of the outer wall of the lobe is dilated on the body (Fig. 23, EML) and resembles a weakly-developed postalar projection. Immediately anterolateral to the metacoxal process it forms a short anterior extension which fits against the wing-anchoring ridge (W) of the episternum. The posterior portion of the outer wall (C) is strongly indented on the body. The convex internal surface of this indented portion adheres to the inner wall of the lobe but elsewhere the two walls, like those of *Diaprepocoris*, are separated by a distinct lumen. The dorsal opening into the epimeral lobe extends all the way to the base of the muscle process (MP) rather than ending anterior to the process as in *Diaprepocoris* (compare Point P, Figs. 22 and 23). Thus the posterior part of the lobe lies much closer to the abdominal process (AP) than in *Diaprepocoris*.

The thoracico-abdominal boundary is marked dorsally by the third phragma (Fig. 23, 3PH). The lateral part of the phragma becomes continuous with a low ridge (IR) which bends postero-medially. The bending is less abrupt than in *Diaprepocoris* and the intersegmental ridge does not adhere to the inner wall of the epimeral lobe like that of *Diaprepocoris*. It extends along the dorsal edge of the outer wall of the lobe as far as Point P. The narrow, flange-like external wall of the ridge is continuous with the posttergite of the third phragma and forms, like the latter, an attachment for the thoracico-abdominal membrane (TAM). The first abdominal spiracle (Figs. 16 and 19, S 1) lies in the thoracico-abdominal membrane immediately dorsal to the narrow flange. Although the spiracle is clearly visible under the stereoscopic and scanning electron microscopes, neither of these techniques revealed whether *Micronecta* possesses metathoracic or first abdominal scolopophorous organs.

Posteromedial to Point P the intersegmental boundary appears to lie anterior to the base of the muscle process. The process (Fig. 23, MP) is larger and flatter than that of *Diaprepocoris* and is separated from the second abdominal segment only laterally. Medially its crest is directly continuous with the second abdominal antecosta (AC2), and its anterior and posterior surfaces thus appear to represent the first and second abdominal segments respectively. As in *Diaprepocoris* a muscle arises on its anterior surface and attaches dorsomedially on the first abdominal tergite.

IV. *Hesperocorixa*

The metathoracic epimeral lobe of *Hesperocorixa* was described and termed the "thoracico-abdominal sclerite" in a previous paper (Parsons 1970), but its homologies were not clear until the present investigation.

The lobe (Fig. 24, EML) is relatively larger, both dorsoventrally and anteroposteriorly, than its homologues in *Diaprepocoris* and *Micronecta*. Its outer wall is anteriorly dilated and has a short anterior extension which fits against the wing-anchoring ridge of the episternum (W), as in *Micronecta*. From this extension a horizontal groove extends posteriorly along the outer wall; the edge of the forewing fits into this groove, which divides the outer wall of the lobe into dorsal and ventral portions. The ventral portion (EML; "thoracico-abdominal lobe" of Parsons 1970) is convex

along its entire length; the dorsal portion, which is concealed by the wing, is convex anteriorly but deeply recessed posteriorly (C). The recessed portion lies closely against the inner wall of the lobe, and the apposed surfaces of the two walls ("vertical plate" of Parsons 1970) become secondarily fused in mature specimens.

Because of the close apposition of the two walls, the full extent of the dorsal opening into the lobe is visible only in newly-moulted insects. As in *Micronecta*, the opening extends posteriorly as far as the base of the abdominal muscle process (Fig. 24, MP). An earlier publication (Parsons 1970) has described how the posterior part of the opening becomes secondarily closed off in mature specimens.

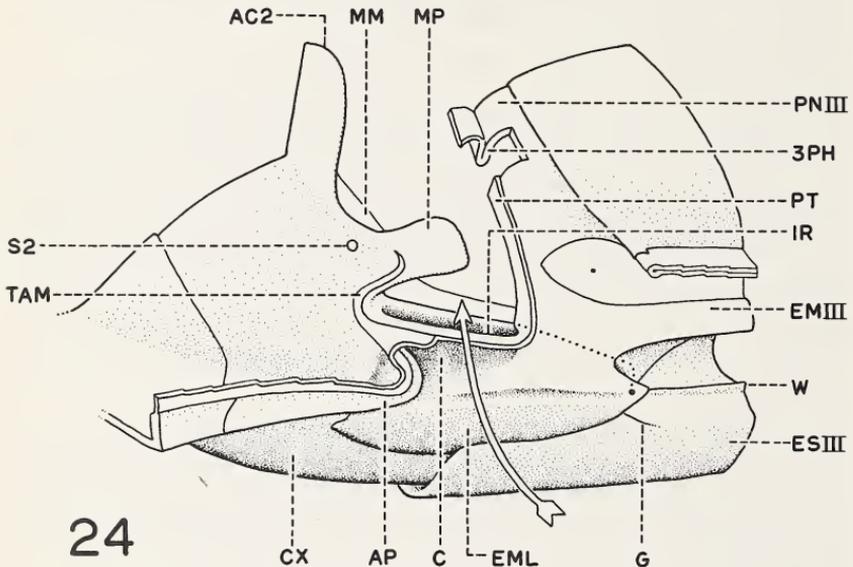


Fig. 24. *H. interrupta*; semi-diagrammatic lateral view of thoraco-abdominal region, prepared as in Fig. 21. Heavy black dot indicates position of coxal process; heavy dotted line indicates dorsal edge of inner wall of metathoracic epimeral lobe (EML). Head of arrow indicates position of first abdominal spiracle (removed) in thoraco-abdominal membrane (TAM); spiracle communicates with ventral air store (white arrow) and with supra-alar air store.

The thoracico-abdominal boundary follows the same course as in *Micronecta*. The transverse third phragma (Fig. 24, 3PH) extends as far as the level of the dorsal opening into the epimeral lobe (heavy dotted line). The boundary then bends abruptly posteriorly, forming a right angle, rather than a gradual curve as in *Micronecta*, and runs along the dorsal edge of the outer wall of the lobe in the form of a low ridge (IR). The thoracico-abdominal membrane (TAM) attaches along the narrow external wall of the ridge and contains the first abdominal spiracle (Figs. 17 and 20, S 1).

The intersegmental ridge extends as far as the base of the muscle process (Fig. 24, MP). The process is larger and more rectangular than its homologue in *Micronecta* but resembles it otherwise and bears a similar muscle attaching dorsomedially on the first abdominal tergite. As in *Micronecta* it is incompletely separated from the second abdominal segment and its crest is laterally continuous with the second abdominal antecosta (AC2). The antecosta, unlike that of *Micronecta* and *Diaprepocoris*, forms a large, raised apodeme just lateral to the muscle process; the anterior face of the apodeme provides an extensive surface for the attachment of the very large ventral longitudinal muscle of the first abdominal segment.

Although the relationship of the epimeral lobe to the abdomen is very similar in *Micronecta* and *Hesperocorixa*, the two insects differ in one major respect. In *Micronecta*, as in *Diaprepocoris*, the posterior part of the lobe does not contact the abdominal process; the two structures are separated by a narrow space in *Micronecta* and by a much larger gap in *Diaprepocoris* (Figs. 22 and 23, black arrows). In *Hesperocorixa*, however, the vertical posterior edge of the lobe fits into a groove on the ventral surface of the abdominal process (Fig. 24). The two structures fit so closely together that there is little, if any, space between them. This close fit creates a barrier between the first abdominal spiracle of *Hesperocorixa* and the air layer which surrounds the metacoxa (see p. 172).

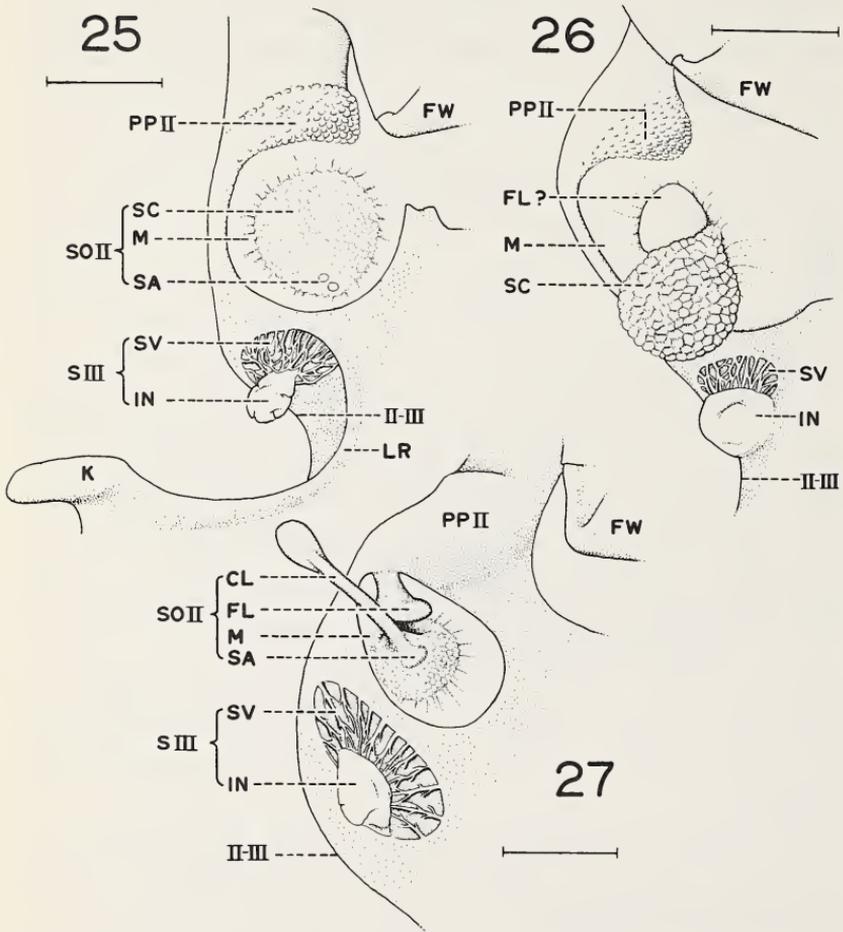
F. METATHORACIC AND FIRST ABDOMINAL SPIRACLES

I. Metathoracic spiracle

In all three corixids the orifice of the metathoracic spiracular trachea is covered by a *sieve-plate* and an *integumental region*

(terms of Parsons 1972b). In the metathoracic spiracles of *Belostoma* and *Ranatra*, which also have these two components, the integumental region bears the ecdysial opening and is lined by epidermis, while the sieve-plate lacks an underlying cellular layer (Parsons 1972b).

The sieve-plate (Figs. 25-27, SV) is composed of branching and anastomosing trabeculae (Figs. 28 and 29) which are connected, by short struts, to an internal membrane. The fine structure of



Figs. 25-27. Mesothoracic scolopophorous organs (SO II) and metathoracic spiracles (S III), oriented as in Figs. 15-17. Fig. 25. *D. zealandiae*; scale line = 100 μ m. Fig. 26. *M. sedula*; scale line = 50 μ m. Fig. 27. *H. interrupta*; scale line = 150 μ m.

the latter was clearly observed only in *Hesperocorixa* (Fig. 28); it bears very narrow, slit-like openings which are pinnately arranged on an otherwise solid surface. The arrangement of the openings is similar to that on the inner membranes of the mesothoracic, metathoracic, and eighth abdominal spiracles of *Belostoma* (Parsons 1972b, 1973). The openings appear, however, to be considerably narrower, and the metathoracic sieve-plate less porous, in *Hesperocorixa* than in *Belostoma*.

The integumental region (Figs. 25-27, IN) lies ventral to the sieve-plate. It is definitely at the margin of the plate in *Hesperocorixa* and *Micronecta* and is either marginal or very acentric within the plate in *Diaprepocoris*. Its size, relative to that of the sieve-plate, is largest in *Micronecta* (Fig. 26) and smallest in *Hesperocorixa* (Fig. 27). It forms a prominent knob in *Micronecta* and *Diaprepocoris* (Fig. 25) but is flatter in *Hesperocorixa*. In all three corixids the integumental region is covered with irregular folds (Fig. 29) which conceal the position of the ecdysial opening.

II. First Abdominal Spiracle

The first abdominal spiracle of all three genera is larger and much more permeable than the metathoracic one. Its longest dimension, compared with that of the metathoracic spiracle, is approximately $135\ \mu\text{m} : 90\ \mu\text{m}$ in *Diaprepocoris*, $45\ \mu\text{m} : 35\ \mu\text{m}$ in *Micronecta*, and $320\ \mu\text{m} : 275\ \mu\text{m}$ in *Hesperocorixa*. In *Diaprepocoris* and *Micronecta* it lacks a sieve-plate and integumental region; the spiracular trachea attaches directly to a round or oval opening in the thoracio-abdominal membrane (Figs. 15 and 16, S 1) and its orifice is not modified in any way.

In *Hesperocorixa* (Fig. 30) the orifice of the spiracular trachea lacks an integumental region and is encircled by a collar-like network of trabeculae which branch and anastomose like those on the sieve-plate of the metathoracic spiracle. Unlike the latter, however, the trabeculae lack an inner membrane and surround the tracheal orifice rather than cover it. The spiracle is thus as widely open as its less elaborate homologues in *Diaprepocoris* and *Micronecta*. The first abdominal spiracle of *Hesperocorixa* is similar to those of *Belostoma* and *Ranatra* (Parsons 1972b) except that in those two Hydrocorisae the trabeculae cover, rather than surround, the tracheal orifice.

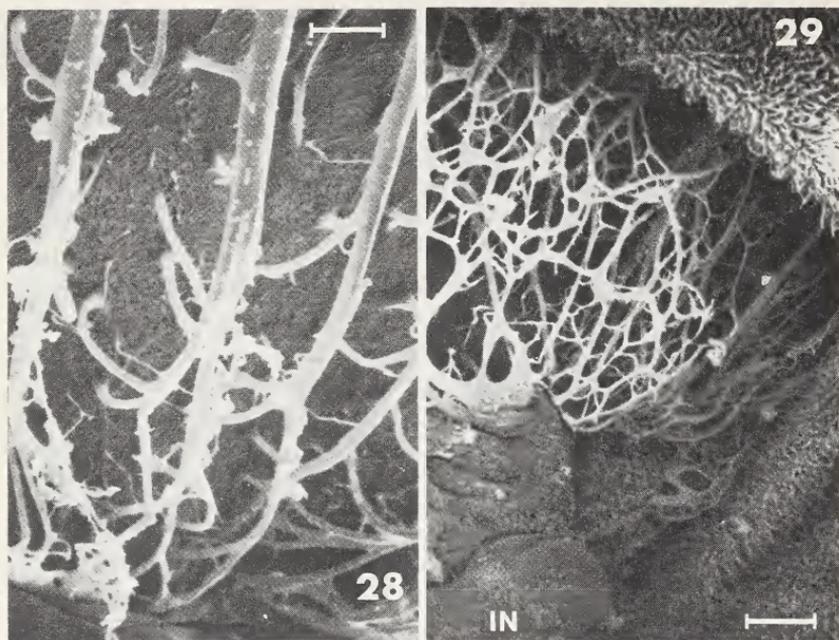


Fig. 28. *H. interrupta*; detail of external surface of sieve-plate on right metathoracic spiracle. Branching trabeculae are connected by short struts to an inner membrane which bears pinnately-arranged narrow slits. Dorsal margin of integumental region appears at extreme lower left. Top of figure is dorsal, right side is anterior. Scale line = 10 μ m.

Fig. 29. *D. zealandiae*; external surface of anterodorsal part of metathoracic spiracle, oriented as in Fig. 25. Sieve-plate bears branching trabeculae; inner membrane is too deep to be visible. Surface of mesothoracic epimeron (upper and lower right) is covered with short hydrofuge hairs. IN = integumental region of spiracle, with irregular folds. Top of figure is dorsal, right side is anterior. Scale line = 10 μ m.

G. MESOTHORACIC SCOLOPOPHOROUS ORGAN

The mesothoracic, metathoracic, and first abdominal scoloporous organs of most Hydrocorisae consist of a sensory membrane which bears a very small sclerite for the attachment of a two-celled scolophore (Larsén 1957). In the Corixidae, however, the mesothoracic scoloporous organ, unlike the metathoracic and first abdominal ones, bears a large sclerite, which is modified in different ways in the three forms here examined.

All three corixids possess mesothoracic sensory membranes with radially arranged low folds (Figs. 25-27, M). In *Hesperocorixa* (Fig. 27) the membrane is oval and completely surrounded by sclerotized areas; in the other two corixids it is round and anteriorly continuous with the subalar membrane. The postalar bridge dorsal to it (Figs. 25-27, PP II), which forms only a weak lateral projection, is covered with flattened, scale-like structures in *Micronecta* (Fig. 31) and *Diaprepocoris* (Fig. 32); similar scales were not observed in this region in *Hesperocorixa*.

The sclerite of the scolopophorous organ is most elaborate in *Hesperocorixa*. The "Hagemann's organ" of Corixinae has been described by many authors including Popham (1961), who believed it to be a pressure receptor, and Prager (1973), who found it to be sensitive to sound. Both these authors studied *Corixa punctata*, whose mesothoracic scolopophorous organ closely resembles that of *Hesperocorixa interrupta*. In both these Corixinae the sensory membrane bears a flask-shaped body (Fig. 27, FL) and a larger club-shaped structure (CL) whose base is considerably larger than its apex. The flask-shaped body ("B¹" of Popham 1961; "flaschenförmiger Körper" of Prager 1973) lies in the posterodorsal part of the sensory membrane and appears to contact the sclerotized rim of the scolopophorous organ. Immediately anteroventral to it lies the base ("B²" of Popham; "Basis" of Prager) of the club-shaped structure. Popham, who studied the sense organ histologically, stated that the flask-shaped and club-shaped bodies are joined; the scanning electron microscope shows that they are at least in very close contact.

The base of the club-shaped structure bears a pronounced knob (Figs. 27 and 33, SA) to which the scolophore attaches internally (Popham 1961). A narrow shaft joins the base to the dilated tip ("Kolben" of Prager 1973) of the club-shaped body, which extends, posteriorly and somewhat dorsally, beyond the rim of the sensory membrane and lies lateral to the metathorax. Popham (1961) believed that accidental flooding of the lateral subalar air space causes the club-shaped body to rotate until its tip touches the postalar projection (Fig. 27, PP II), thus warning the insect against tracheal flooding. Prager (1973) did not comment upon this hypothesis.

Popham (1961) described the club-shaped structure of *Corixa* as being covered with hydrofuge cuticle. The scanning electron microscope shows that in *Hesperocorixa* both the club-shaped and the flask-shaped bodies are covered with short, densely-packed projections with rounded tips. The projections are approximately 0.2 to 0.5 μm in diameter and give the surfaces of these structures a granular appearance. The base of the club-shaped body has a distinctive pattern; its granular surface is subdivided, by low grooves, into hexagonal facets (Fig. 33). This pattern was not observed elsewhere on the scolopophorous organ.

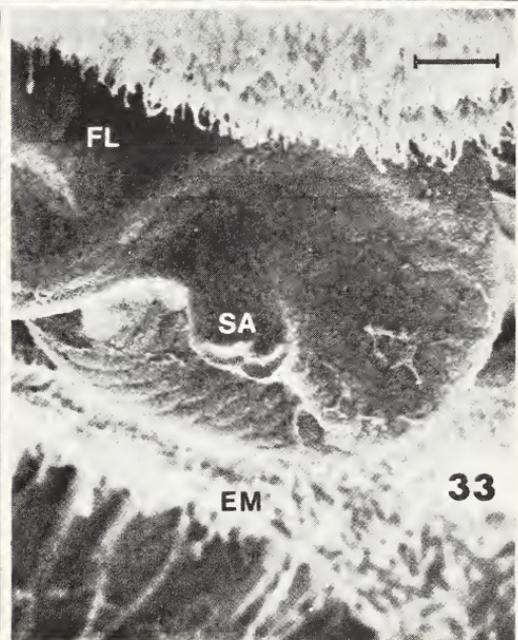
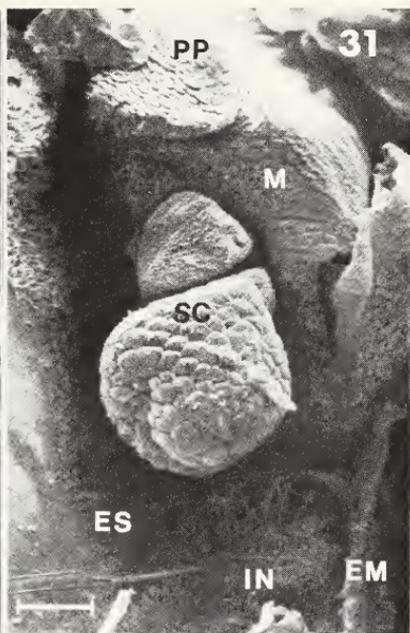
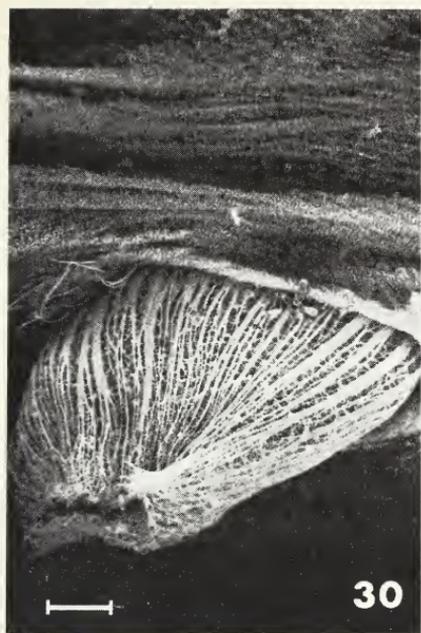
The mesothoracic scolopophorous organ of *Diaprepocoris* is considerably simpler than that of *Hesperocorixa*. The sensory membrane bears a central, roughly spherical sclerite (Figs. 25, SC; Fig. 32), which is darkly pigmented and approximately 100 μm in diameter. It projects laterally and somewhat ventrally from the

Fig. 30. *H. interrupta*; collar-like network of trabeculae surrounding orifice of right first abdominal spiracle, located in thoraco-abdominal membrane (top of figure). Spiracle lacks an inner membrane and is widely open. Top of figure is dorsal, right side is anterior. Scale line = 50 μm .

Fig. 31. *M. sedula*; right mesothoracic scolopophorous organ and metathoracic spiracle, oriented as in Fig. 26. Sensory membrane (M) of scolopophorous organ and wall of mesothoracic epimeron (EM) have been damaged at right side of figure. Bulb-shaped sclerite (SC) of sense organ bears hexagonal pattern; possible homologue of flask-shaped body of *Hesperocorixa* lies immediately dorsal to it. Spiracle possesses prominent integumental region (IN); sieve-plate lies immediately dorsal to it. Mesothoracic postalar projection (PP) bears flattened scales. ES = metathoracic episternum. Top of figure is dorsal, right side is anterior. Scale line = 20 μm .

Fig. 32. *D. zealandiae*; sclerite of right mesothoracic scolopophorous organ, oriented as in Fig. 25. A small portion of the sensory membrane is visible between the sclerite and the mesothoracic postalar projection (PP), which bears flattened scales. Note granular appearance of sclerite and pentagonal or hexagonal arrangement of grooves on its surface. Arrowheads indicate probable sites at which two cells of scolophore attach internally. Top of figure is dorsal, right side is anterior. Scale line = 20 μm .

Fig. 33. *H. interrupta*; base of club-shaped sclerite of right mesothoracic scolopophorous organ, showing granular appearance and hexagonal pattern of grooves. Scolophore attaches on internal surface of knob (SA) on base; shaft of club-shaped sclerite extends posteriorly (left side of figure) from site of scolophore attachment. Specimen has been tilted ventromedially, concealing sensory membrane. FL = part of flask-shaped body. EM = mesothoracic epimeron. Sieve-plate of metathoracic spiracle appears at lower left. Top of figure is dorsal, right side is anterior. Scale line = 20 μm .



membrane and bears, on its ventrolateral surface, two small smooth areas (Fig. 25, SA; Fig. 32, arrows) which probably represent the points at which the cells of the scolophore attach internally. The rest of its surface is covered with small rounded projections, similar to those observed in *Hesperocorixa*, which give it a granular appearance, and it has a pattern of pentagonally or hexagonally arranged grooves (Fig. 32). This pattern, along with the attachment of the scolophore, suggests that the entire structure is homologous with the base of the club-shaped body of *Hesperocorixa*. *Diaprepocoris* appears to possess no counterpart of the flask-shaped body or of the shaft and tip of the club-shaped body of *Hesperocorixa*.

Micronecta, however, shows a possible homologue of the flask-shaped body. In the posterodorsal part of the sensory membrane lies a roughly spherical structure (Fig. 26, FL?; Fig. 31) whose surface has a granular appearance but no hexagonal pattern. Its position suggests that it is the counterpart of the flask-shaped body of *Hesperocorixa*. Posteroventral to it lies a larger, bulb-shaped body (SC) which attaches to the sensory membrane by means of a narrow neck. The bulb-shaped body has a hexagonal pattern, and is probably homologous with the spherical body of *Diaprepocoris* (Fig. 25, SC) and with the base of the club-shaped body of *Hesperocorixa*. The grooves between the hexagons are deeper than those on the apparently homologous structures, and the surface of the bulb-shaped body is smooth rather than covered with granular projections. There is no distinctive feature to mark the attachment of the scolophore.

H. DISCUSSION

I. Mode of Respiration

The presence of air-bubble respiration in the subfamily Corixinae has been demonstrated by numerous physiological and behavioral studies which were mentioned in a previous publication (Parsons 1970). Similar data are lacking, however, for the Diaprepocorinae and Micronectinae except for a brief note concerning *Micronecta* sp. (Leong 1961). The following discussion of respiration in *Diaprepocoris* and *Micronecta* is therefore based almost entirely upon the morphology of preserved specimens and has yet to be confirmed or disproved by experimental evidence.

The air stores in *Diaprepocoris* and *Micronecta* appear to be at least as substantial as those of *Hesperocorixa*. All three insects possess large concealed air stores (subalar, cervical, and I-II) as well as an extensive ventral air layer which, being exposed to the water, is presumably able to obtain dissolved oxygen. *Diaprepocoris* is smaller than *Hesperocorixa* and has additional exposed air layers on the mesonotum and on most of the forewing, rather than only on the emboliar region. *Micronecta* has the advantage of very small size and, consequently, a large surface in proportion to its volume. *Diaprepocoris* and *Micronecta* thus appear to be at least as capable as *Hesperocorixa* of utilizing dissolved oxygen.

Thorpe and Crisp (1949) grouped aquatic insects with hydrofuge hairs into four categories, ranging from Group I (those with true plastral hairs) to Group IV (those with hairs which merely protect them against accidental wetting). Thorpe (1950) placed *Corixa* (Corixinae) in Group III, members of which must come to the surface at intervals to obtain atmospheric air and which are buoyant rather than heavier than water. Insects of Group III often possess a double hair pile, with a "macroplastron" of long hairs and a much thinner "microplastron" of short hairs (Thorpe and Crisp 1949). *Hesperocorixa*, like *Corixa*, clearly belongs in this category.

The similarity of the long and short hairs of *Hesperocorixa* to those of *Diaprepocoris* and *Micronecta* strongly suggests that all three insects have a similar mode of respiration. Leong (1961) and Wróblewski (personal communication) note that *Micronecta* periodically comes to the surface of the water for air although, according to Wróblewski, it can remain submerged during times of strong wave action, presumably utilizing dissolved oxygen during these occasions. Wróblewski also points out that *Micronecta* requires well-aerated aquaria. Although I could obtain no behavioral information on *Diaprepocoris*, the presence of a macroplastron of long hairs on its ventral abdominal surface would indicate that it is an air-bubble insect rather than a true plastral insect.

The Corixinae, unlike other Hydrocorisae, renew their air stores by contacting the surface of the water anterodorsally and taking in the atmospheric air beneath the long pronotum and the flange-like posterior edge of the head. To my knowledge it is not known whether the Deaprepocorinae and Micronectinae share this method of obtaining air or whether they contact the surface of the water with the tip of the abdomen, like most Hydrocorisae. Although the

latter method is possible it is, in my opinion, more probable that they contact the surface anterodorsally. *Diaprepocoris* and *Micronecta* resemble *Hesperocorixa*, and differ from other Hydrocorisae, in the presence of an air store beneath the posterodorsal margin of the head. All three insects also possess an air store on the mesonotum. Both air stores would tend to increase the buoyancy of the anterodorsal part of the body in *Diaprepocoris* and *Micronecta*, and if this region contacted the water surface the air could pass directly into these two air stores. Wróblewski (personal communication) has pointed out that the posterior margin of the head of *Micronecta* is raised at the midline (Figs. 9 and 12), forming a funnel-like space through which atmospheric air might enter. It is possible that *Diaprepocoris* can contact the water surface anywhere along its dorsal surface, owing to the buoyancy of its extensive supra-alar air store. *Notonecta* (Notonectidae), which also has a large supra-alar air store, contacts the water surface posteroventrally rather than dorsally. However its ventral air store, unlike that of *Diaprepocoris*, is held by hydrofuge hairs which are much longer than those on the forewing, and its ventral surface is thus more buoyant than its dorsal surface.

In *Hesperocorixa* the atmospheric air which enters the cervical and I-II air spaces is moved posteriorly, along the emboliar and ventral air stores, by the middle and posterior legs (Parsons 1970). Both these air stores are exposed to the water and can obtain dissolved oxygen. The ventral and supra-alar air stores communicate with the subalar one along the lateral edges of the abdomen and at a gap (Fig. 13, arrow) between the forewing and the metathoracic epimeral lobe (Parsons 1970). Thus the subalar air store, in which the metathoracic and first abdominal spiracles lie, can receive both atmospheric oxygen and dissolved oxygen. The subalar spaces of both *Diaprepocoris* and *Micronecta* could receive oxygen in a similar manner. In both insects this air store communicates with the exposed ones at least along the gap in the region of the metathoracic epimeron (Figs. 11 and 12, arrow) and quite probably along the abdomen as well. It is also possible, however, that either or both of these insects contact the atmosphere posteroventrally and take air directly into the subalar air store, as does *Ambrysus* (Naucoridae; Parsons 1970).

Popham (1960) believed that oxygen enters the tracheal system of *Corixa* chiefly through the first abdominal spiracles. This also

appears to be the case in *Hesperocorixa*, *Diaprepocoris*, and *Micronecta*. The capacity of a spiracle to inhale oxygen depends upon its porosity and size and its degree of communication with a well-oxygenated air store. In all three corixids the first abdominal spiracle is larger than the other spiracles, faces onto an enlarged part of the subalar space, and is widely open, lacking any sort of modification (*Diaprepocoris* and *Micronecta*) or bearing only a highly porous collar (*Hesperocorixa*, Fig. 30).

The more posterior abdominal spiracles, although they face directly onto the well-oxygenated ventral abdominal air layer, are much smaller than the first abdominal one and lie in a region of less metabolic activity. The mesothoracic spiracle communicates broadly with both the I-II and ventral thoracic air stores, and Parsons (1970) believed it to be a major inhalant spiracle in *Hesperocorixa*. This now appears to be unlikely. In *Hesperocorixa* it possesses a sieve-plate with an inner membrane, and in all three corixids it is considerably smaller than the first abdominal spiracle. The fine structure and porosity of the mesothoracic spiracles of the three corixids, however, has yet to be investigated by means of the scanning electron microscope. The metathoracic spiracle is smaller and much less porous than the first abdominal one in all three insects. It is covered by a sieve-plate which, at least in *Hesperocorixa*, limits its porosity (Fig. 28).

The inhalant function of the first abdominal spiracle is reflected not only in its fine structure but in the gross morphology of the region surrounding it. It lies in an enlarged part ("first abdominal spiracular chamber", Parsons 1970) of the subalar air space. When the spiracle lies within the metathoracic epimeron, as in most Hydrocorisae (Fig. 21), the relatively small portion of the epimeron which surrounds it is recessed on the body, forming the spiracular chamber. In the Corixidae, however, the spiracle lies in the thoraco-abdominal membrane and its spiracular chamber is formed by the modification of the greatly enlarged metathoracic epimeral lobe which lies ventral to it.

All three corixids possess a gap, between the forewing and the body, which leads directly into the spiracular chamber (Figs. 11-13 and 22-24, white arrows). Through this gap the spiracle can receive oxygen from the ventral air layer on the exposed parts of the epimeral lobe (Figs. 22-24, EML) and abdominal projection (AP); in *Hesperocorixa*, and quite probably in the other two insects as

well, the exposed supra-alar air store also communicates, at the gap, with the spiracular chamber.

The way in which the epimeral lobe is modified to form the spiracular chamber differs in the three corixids. In *Diaprepocoris* (Fig. 22) the dorsal part of the lobe does not extend as far posteriorly as in the other two insects. The spiracular chamber is thus formed by the large space between the abdominal projection and the posterodorsal wall of the lobe. This space can receive oxygen not only through the gap beneath the forewing (white arrow) but from the air store surrounding the metacoxa (black arrow). In *Micronecta* (Fig. 23) and *Hesperocorixa* (Fig. 24) the dorsal part of the lobe extends posterior to the level of the spiracle (position of spiracle indicated by heads of arrows in Figs. 23 and 24). If the outer wall of the lobe were dilated, as in *Diaprepocoris*, the spiracular chamber would be reduced in size. In both *Micronecta* and *Hesperocorixa*, however, the outer wall of the lobe is recessed (Figs. 23 and 24, C) immediately ventral to the spiracle, forming an enlargement of the subalar space. The spiracular chamber of *Micronecta* communicates, albeit narrowly, with the air which surrounds the metacoxa (Fig. 23, black arrow). In *Hesperocorixa*, however, the posterior edge of the epimeral lobe lies closely against the ventral surface of the abdominal projection, creating a barrier between the spiracular chamber and the metacoxa (Parsons 1970). In this respect *Hesperocorixa* differs from the other two corixids.

II. Phylogenetic Implications

According to Popov (1971) the ancestral stem of the Corixidae gave rise to six subfamilies, three of which survive at the present time. The Diaprepocorinae arose somewhere near the boundary between the Triassic and Jurassic, the Micronectinae during the Jurassic, and the Corixinae during the second half of the Cretaceous. Popov (1971) placed considerable emphasis on three plesiomorphic features of the Diaprepocorinae, the presence of ocelli, the short pronotum, and the relatively undeveloped embolium of the forewing.

The condition of the pronotum and embolium appear to have respiratory as well as phylogenetic significance. In *Hesperocorixa* and, to a lesser extent, in *Micronecta*, the lengthened pronotum increases the size of the I-II air store and the buoyancy of the anterodorsal part of the body. In *Diaprepocoris* these functions are

performed by the hydrofuge hairs on the mesonotum rather than by lengthening of the pronotum. The presence of a long, strongly indented embolium appears to be related to the size of the partial supra-alar air store on that region. The embolium is longer and more sharply indented in *Hesperocorixa* (Fig. 10), in which the air layer extends beyond the nodal furrow, than in *Micronecta* (Fig. 9), in which the air extends only to the furrow. In *Diaprepocoris* the supra-alar air store covers nearly all of the forewing rather than being confined mainly to the embolium, and the latter is only weakly indented (Fig. 8).

Two previous works (Parsons 1970, 1974) have discussed the ways in which the pterothorax of *Hesperocorixa* differs from that of most other Hydrocorisae. Popov's (1971) views on the phylogeny of the three living subfamilies are supported by the fact that *Micronecta* shares more of these pterothoracic characteristics than does *Diaprepocoris*. In all three corixids the metathoracic spiracle faces directly onto the subalar air store rather than being concealed by a high lateral epimeral ridge (Fig. 14A, LR) as in most other Hydrocorisae. *Diaprepocoris*, however, possesses a low epimeral ridge (Fig. 15, LR) while the other two corixids lack the ridge entirely. All three insects possess a weakly developed, rather than a prominent, mesothoracic postalar projection and a modified mesothoracic scolopophorous organ. The latter is simplest in *Diaprepocoris* (Fig. 25) and most complex in *Hesperocorixa* (Fig. 27). *Diaprepocoris* differs markedly from the other two corixids in the shape of its mesothoracic lateral epimeral lobe, which resembles that of most other Hydrocorisae (Fig. 14A) rather than being widened and strongly curved dorsally (Fig. 14B). The metathoracic air trough is also poorly developed in *Diaprepocoris*; it is more pronounced in *Micronecta* (Fig. 16, AT) and is most highly developed in *Hesperocorixa* (Fig. 17, AT).

The thoracico-abdominal region of all three corixids differs from that of typical Hydrocorisae in the large size of the metathoracic epimeral lobe and in the location of the first abdominal spiracle in the thoracico-abdominal membrane rather than in a recessed part of the epimeron. The three insects differ, however, in the shape of the metathoracic epimeral lobe (Figs. 22-24, EML), in the length of its dorsal opening, and in the way in which the first abdominal spiracular chamber is formed. In the latter two features *Micronecta* bears more resemblance to *Hesperocorixa* than to

Diaprepocoris. The degree of continuity between the first abdominal spiracular chamber and the air layer surrounding the metacoxa also differs in the three insects; it is greatest in *Diaprepocoris* (Fig. 22, black arrow), more limited in *Micronecta* (Fig. 23, black arrow) and very limited or absent in *Hesperocorixa* (Fig. 25).

Finally, the anterolateral part of the abdomen shows variation. All three corixids possess well-developed muscle processes (Figs. 22-24, MP), but that of *Diaprepocoris* is separated from, rather than fused with, the rest of the abdomen. Both *Diaprepocoris* and *Micronecta* lack the strongly developed condition of the second abdominal antecosta which is present in *Hesperocorixa* (Fig. 24, AC2).

Summary. 1. Representatives of the three subfamilies of Corixidae were examined. Although data on the respiration of *Diaprepocoris* (Diaprepocorinae) and *Micronecta* (Micronectinae) are lacking, the morphology of preserved specimens suggests that they use air-bubble respiration like *Hesperocorixa* (Corixinae). The structure of the forewings and intersegmental regions and the distribution of the hydrofuge hairs indicate that all three insects possess air stores on the ventral surfaces of the abdomen and thorax, beneath the forewings, between the head and prothorax, between the prothorax and mesothorax, and on the forewings. *Diaprepocoris*, unlike the other two insects, has an exposed air layer on the mesonotum and a supra-alar air layer covering nearly all of the forewing.

2. *Hesperocorixa* obtains atmospheric oxygen by periodically contacting the water surface anterodorsally, taking air into the air spaces beneath the head and pronotum. It appears likely that *Diaprepocoris* and *Micronecta* share this mode of behavior. All three insects can also obtain dissolved oxygen by means of the "physical gill" effect of their exposed air stores.

3. Of the three corixids examined, *Diaprepocoris* shows the fewest pterothoracic modifications and *Hesperocorixa* shows the most. The mesothoracic epimeron of *Diaprepocoris* is not widened like that of the other two insects, and *Diaprepocoris* lacks a specialized metathoracic "air trough". The mesothoracic scolopophorous organs of all three corixids differ from those of other Hydrocorisae. Those of *Diaprepocoris* and *Micronecta* possess one and two large sclerites respectively while that of *Hesperocorixa* has two sclerites

which form an elaborate "Hagemann's organ". The efferent system which leads from the metathoracic scent gland is different in *Micronecta* than in the other two corixids.

4. In typical Hydrocorisae the first abdominal spiracle lies in the posterior part of the metathoracic epimeron. In the three corixids, however, it lies in the thoracico-abdominal membrane, and the posterior part of the metathoracic epimeron is enlarged into a lobe ventral to it. The shape of the lobe differs in the three insects and affects the communication between the spiracles and the air stores. The lobe is least complex in *Diaprepocoris* and most complex in *Hesperocorixa*.

5. In all three corixids the metathoracic spiracle lies in the mesothoracic epimeron and faces directly onto the subalar air store. It is smaller than the first abdominal one and, unlike the latter, is covered by a "sieve-plate" which appears to limit its porosity. The large first abdominal spiracle lacks a sieve-plate and appears to be the main site of inhalation in all three insects. It is unmodified in *Diaprepocoris* and *Micronecta* and is encircled by a trabecular collar in *Hesperocorixa*.

6. The present investigation supports the views of Popov (1971) on the phylogenetic relationships among the three living subfamilies of Corixidae.

EXPLANATION OF ABBREVIATIONS

The Roman numerals I, II, or III after an abbreviation indicate prothoracic, mesothoracic, or metathoracic structures respectively; an Arabic number following an abbreviation indicates the abdominal segment to which the structure belongs. The following abbreviations are used:

AC	Antecosta
AP	Abdominal projection
AT	Air trough of metapleuron
B	Base of mesothoracic lateral epimeral lobe
C	Indented portion of metathoracic epimeral lobe
CA	Clavus of forewing
CL	Club-shaped sclerite
CO	Corium of forewing

- CS Claval suture of forewing
CX Metacoxa
D Dorsal region of mesothoracic epimeron or metathoracic episternum
E Embolium of forewing
EC Efferent channel of metathoracic scent gland
EM Epimeron
EML Lobe of metathoracic epimeron
ES Episternum
F Nodal furrow of forewing
FL Flask-shaped sclerite
FW Forewing
G Groove on metathoracic episternum
HW Hindwing
ID Indented region on exposed part of metathoracic episternum
- IN Integumental region of metathoracic spiracle
IR Intersegmental ridge between thorax and abdomen
K Wing-anchoring knob of mesothoracic epimeron
LL Lateral lobe of mesothoracic epimeron or metathoracic episternum
LP Posterior lobe of mesothoracic epimeron or metathoracic episternum
LR Lateral ridge of mesothoracic epimeron
M Sensory membrane of mesothoracic scolopophorous organ
MB Membrane of forewing
MI Metacoxal indentation
MM Metacoxal membrane
MP Muscle process
N Notum
O Ostiole of metathoracic scent gland
OC Ocellus
P Posterior end of dorsal opening into metathoracic epimeral lobe
PL Pleural ridge or sulcus
PN Postnotum
PP Postalar bridge and/or postalar projection
PR Metathoracic coxal process

PT	Posttergite
S	Spiracle or spiracular trachea
SA	Attachment of scolophore
SC	Sclerite of mesothoracic scolopophorous organ
SO	Site of scolopophorous organ
SS	Sclerotized strip
ST	Sternite
SV	Sieve-plate of metathoracic spiracle
T	Tergite
TAM	Functional thoracic-abdominal membrane
TAS	Thoracico-abdominal sclerite
V	Ventral region of mesothoracic epimeron or metathoracic episternum
W	Wing-anchoring ridge or groove of metathoracic episternum
WS	Setae on lateral edge of forewing
X	Xiphus of metathoracic sternum
2PH,	
3PH	Second phragma, third phragma
II-III	Lateral boundary between mesothorax and metathorax

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THE ADAPTIVE VALUE OF POLYMORPHISM
IN AN ALPINE ANT,
FORMICA NEORUFIBARBIS GELIDA WHEELER*

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INTRODUCTION

Organisms that inhabit alpine tundra must be able to survive and reproduce under extreme environmental conditions. Most of the year the weather is cold, windy, and the ground covered with snow. As the snow melts in the spring, the ground becomes saturated with water and there is considerable run-off. Summers are short and characterized by frequent rains, high solar radiation, and extreme temporal and spatial variations in humidity. Animals that remain on the tundra year round can be expected to have acquired habits and associated structures which enable them to overcome the difficulties of these high altitude conditions.

Of the tundra ant species, *Formica neorufibarbis gelida* is the most abundant and often the only ant species inhabiting the alpine tundra of the Colorado Rockies. According to Gregg (1963), it is the most cold tolerant of all the ant species found in Colorado. Additional adaptations include the ability to nest under rocks (which provide protection from temperature and humidity extremes) and the relatively rapid production of a single brood (from eggs to adult workers and sexual forms) within the short summer season (Taussig, 1962).

During preliminary observations on the ecology of this subspecies, I noticed color differences in the thorax of foragers—some were brownish-black and others red. Both types were found within every colony observed. The foragers with red thoraxes also appeared to be larger in body size than those with darker thoraxes. The possibility that either color or size polymorphism might be associated with adaptation to tundra environments stimulated the work presented in this paper.

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METHODS

The general ecology and thorax color of *F. neorufibarbis gelida* were examined at several different alpine tundra sites on the east slope of the Rockies during the summers of 1975 and 1976. Intensive study and data collections were from a single tundra site, Niwot Ridge, located approximately 20 miles northwest of Boulder, Colorado. This area is supervised by the Institute of Arctic and Alpine Research, University of Colorado, and therefore relatively undisturbed by human activities.

Weekly visits were made to the Niwot Ridge study site between June 21 and August 10, 1976. Records were kept of the number and color of foragers, type of food collected, the times of day when foraging took place and where the foragers searched for food. Developmental stages of the brood were observed by turning over rocks near midday, when the brood is brought to the surface of the nest.

Samples of 20 foragers each were taken from various different foraging heights (ground, flowers, and shrubs of heights ranging from 20 cm to one meter) and at different times of the day. Because several environmental factors, including light intensity, temperature and humidity, change in a regular fashion with time of day when the effects of the sun are not obscured by clouds, all collections were made on cloudless days. The samples of foragers were then taken to the laboratory, the color of each individual noted, and its head width measured with a Lietz eyepiece micrometer.

RESULTS

More than 85% of the food collected by the colonies on Niwot Ridge consisted of liquid material from plants. From the beginning of the season through peak flowering time, most of the food was nectar from flowers, primarily that of *Acomastylis rossii*. Later in the season, major foraging activity occurred on the stems of plants, where the ants sucked liquids from the area around the axil. Of the other types of food collected, seeds comprised less than 5% and dead insects about 10% of the diet. Regardless of the abundance of food, once the brood had matured, all foraging ceased for the season.

Head width measurements of foragers with red thoraxes and of those with dark thoraxes were plotted according to frequency

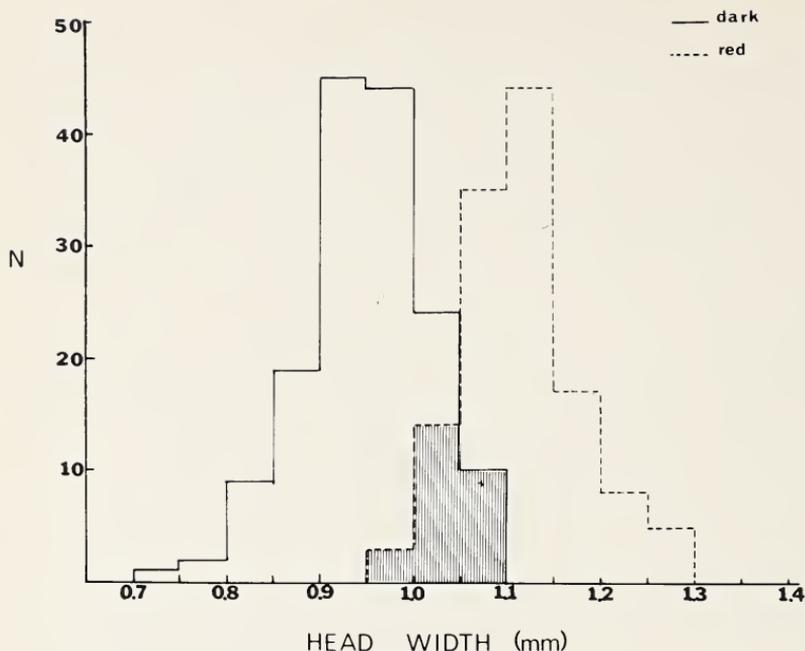


Figure 1. Frequency distribution of forager head width. The solid line is of 154 foragers with dark thoraxes; the dotted line is of 126 foragers with red thoraxes. The population appears to be dimorphic for both color and size.

of size classes. These are shown in Figure 1. A total of 280 individuals are represented, with 154 dark and 126 red. Mean head width of the dark forms is 0.944 ± 0.067 ; of the red forms, 1.111 ± 0.065 mm. A t-test of the two means indicates the differences are highly significant ($p < 0.005$); the population is dimorphic for both color and size.

The mean head width for each sample of 20 individuals was calculated and tested for degree of correlation with foraging height at which the sample was collected and time of day. No significant correlations were found to exist between foraging height and head width. There was, however, a significant positive correlation between mean head width and the time of day that the sample was collected. This relationship is shown in Figure 2. The correlation coefficient, 0.848, is significant at $p < 0.005$.

Because no correlation was found between forager size and foraging height (which should reflect different temperatures and humidities at a given time of day), the observed change in forager size and color with time of day is likely to be the effect of changes in the amount of solar radiation. This interpretation is strengthened by the fact that all of the samples taken in June, when light intensity is lower than in later months (Taussig, 1962), lie below the line of best fit.

DISCUSSION

Each colony of *F. neorufibarbis gelida* consists of a mixture of both red and dark foragers, the red tending to be larger in size than the dark. As foraging progresses through the morning, the proportion of large, red foragers increases. It seems likely that the small, dark forms have an advantage early in the day, in that they are able to warm up more quickly so that foraging can begin. As solar radiation increases throughout the morning, the advantage shifts to the larger, red forms because a larger body tends to heat up more slowly and the red color probably reflects more solar radiation than would a dark color. A colony made of both forms of foragers is able to withstand greater variations in solar radiation and therefore utilize more foraging hours per day than a colony containing only one form or the other. The lower foraging limit of this subspecies is about 12°C soil surface temperature (Taussig, 1962); the upper limit is not known because foraging has never been observed to cease during the heat of midday. Taussig (1962) reports active foraging at a soil surface temperature of 52°C.

Both small body size and dark color are characteristics of other high altitude insects and considered adaptations to cold temperatures (Mani, 1962). Another characteristic is that the activities of these insects are usually restricted to cold temperatures and they actually show a drop in activity during midday (Mani, 1962). The colonies of *F. neorufibarbis gelida*, however, were never observed to decrease their foraging activities during high environmental temperatures, a feature perhaps due to the presence, in these colonies, of not only the small, dark individuals typical of alpine environments, but also the large, red individuals.

It is concluded from this study that the color and size differences observed in *F. neorufibarbis gelida* enable each colony to utilize a greater range of environmental conditions for foraging than if

they were of a single size and color. The resultant increase in number of foraging hours each day enables a colony to quickly raise a brood to maturity within the very short summer season in alpine tundra environments.

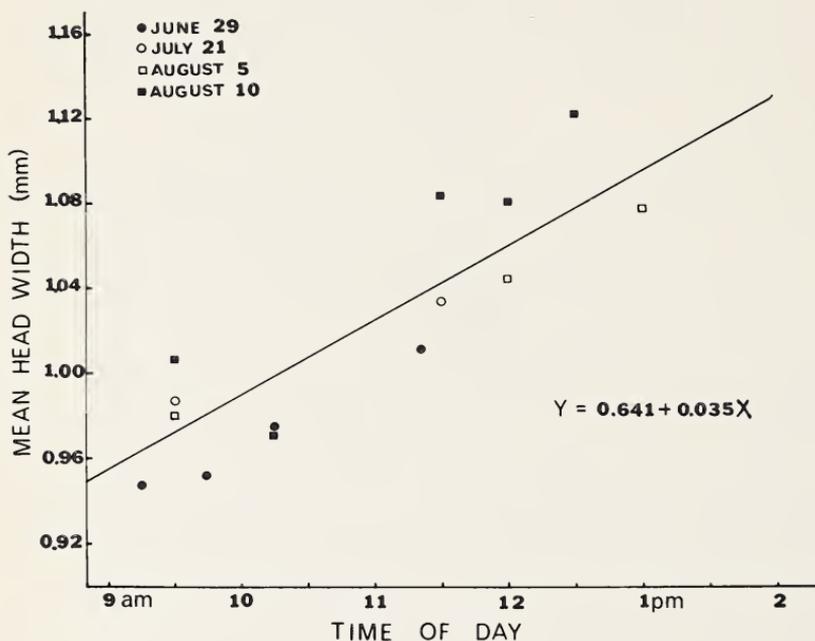


Figure 2. The mean head width of each sample of foragers shown as a function of time of day the sample was taken. Each point is the mean of 20 individuals in a sample. The correlation coefficient, $r = 0.848$, is significant at $p < 0.005$.

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A NEW ARGENTINE GENUS OF THERIINI
(HYMENOPTERA, ICHNEUMONIDAE)*

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Recent fieldwork in subtropical humid forests of Salta and Corrientes Provinces of north Argentina has revealed a new genus of the anomalonine ichneumonid tribe Theriini (as defined by Townes, 1971, p. 155) and therein most closely related to the Palearctic and Indo-Papuan genus *Heteropelma* Wesmael.

Stangepelma, new genus

(Figures 1-5, Map 1)

Clypeus: median $2/3$ of apical margin practically truncate. *Mandible*: lower tooth about $1/3$ as long as upper. *Occipital carina*: joins base of mandible. *Frons*: with a high vertical lamella between antennal sockets. *Mesoscutum*: without a transverse suture before scuto-scutellar groove. *Scutellum*: in dorsal view gently convex laterad and weakly concave on median $1/3$; in profile weakly convex. *Postpectal carina*: complete. *Propodeum*: of normal shape, gaster attached only a little above hind coxae; pleural carina absent so that propodeum is not distinctly separated from metapleuron. *Fore coxa*: without a transverse carina on ventral surface. *Mid tibia*: with one apical spur. *Hind femur*: clavate, its basal half very long and slender, 0.04 as deep as length of femur, and its apical half abruptly swollen, 0.11-0.12 as deep as length of femur. *Hind tarsus*: basitarsus 1.8-1.9 as long as segments 2-5 of hind tarsus; second segment in male with a weak depression below just beyond middle. *Tarsal claws*: not pectinate, those of front and mid tarsus with an approximately 90 degree bend just beyond middle, those of hind tarsus with a 100 degree bend at middle and a lobe at base. *Wing venation*: intercubitus joins cubitus basad of second recurrent vein by about 1.0 (male)-

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1.5 (female) the length of intercubitus; nervellus intercepted between its upper 0.33 and 0.40; metacarpella with a series of 6-7 widely spaced hamuli.

TYPE SPECIES: *Stangepelma argentinum*, new species.

DISCUSSION: Within its tribe *Stangepelma* shows special affinity to *Heteropelma* Wesmael and *Tanypelma* Townes, with which it shares such characters as a high lamella between the antennal sockets, a complete postpectal carina, and sharply bent hind tarsal claws. From the foregoing genera, it differs in its single mid tibial spur, basally very slender and apically inflated hind femur, second male hind tarsal segment with a weak depression below (*Tanypelma* has no depression, *Heteropelma* a flattened and impressed area), and by having a distal series of 6-7 widely spaced hamuli (12-18 closely spaced hamuli in *Heteropelma* and *Tanypelma*). The single mid tibial spur is a feature shared among Theriini only by the eastern Palaearctic *Brachynervus* Uchida¹ and *Brachynervus* also resembles *Stangepelma* because it has only 7 widely spaced metacarpellan hamuli. However, *Stangepelma* and *Brachynervus* do not seem closely related, since *Brachynervus* has many features which set it off from all other theriines (mesoscutum with a transverse suture before scuto-scutellar groove, postpectal carina absent, occipital carina joining hypostomal carina instead of mandibular base, intercubitus far basad of second recurrent vein, and propodeum globose with its apex raised away from the hind coxae so that the gastric socket is distant from the hind coxae). Apart from the features already mentioned, *Stangepelma* agrees almost perfectly with Townes' (1971, p. 158) description of the Palaearctic and Indo-Papuan *Heteropelma* but shows the following additional differences from the eastern Nearctic *Tanypelma*: apex of clypeus truncate instead of weakly convex, lower tooth of mandible 0.3 as long as upper instead of only a little shorter than upper, scutellum gently instead of strongly convex, front and middle tarsal claws with a 90 degree bend instead of with a moderately strong curve, and nervellus intercepted definitely above instead of near the middle.

¹According to Gauld (1976, p. 28), the Malaysian *Heteropelma perornatum* Cameron "sometimes has the inner tibial spur very reduced and although it appears to have a single spur on the mid tibia, two are in fact present."

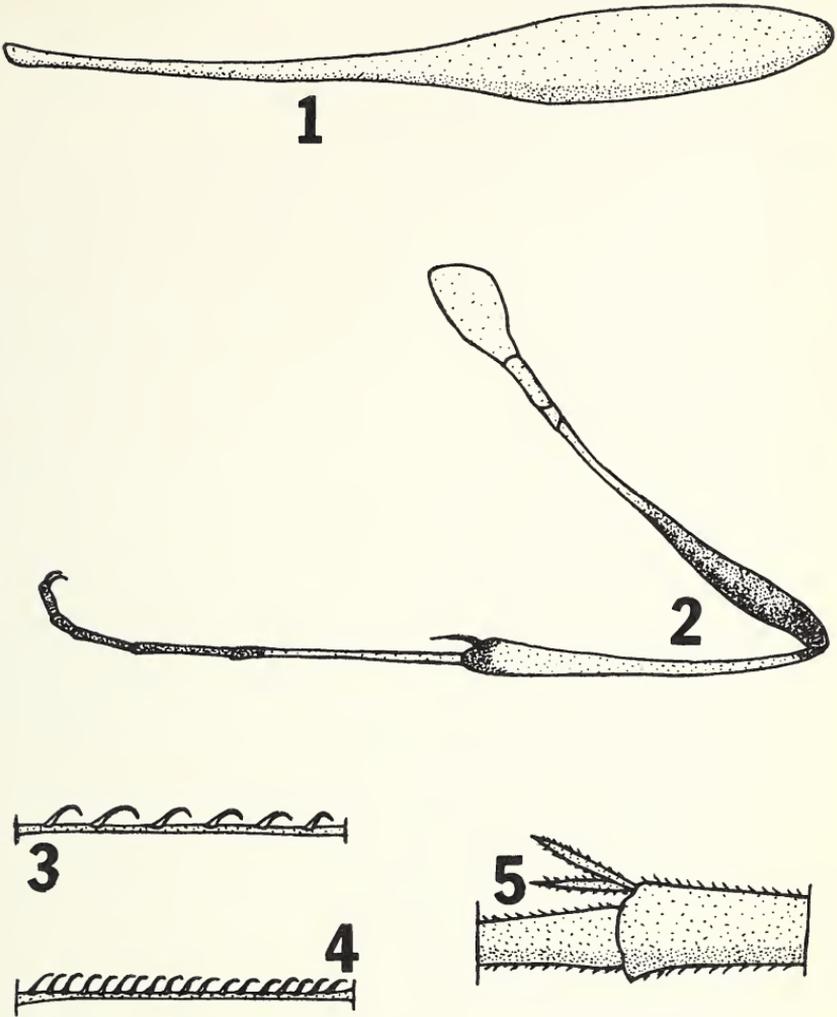


Fig. 1. *Stangepelma argentinum* n. sp., female holotype. Lateral view of hind femur. Fig. 2. *Stangepelma argentinum* n. sp., female holotype. Anterior view of left mid leg, showing color pattern and single mid tibial spur. Fig. 3. *Stangepelma argentinum* n. sp., female holotype. Metacarpellan hamuli. Fig. 4. *Tanypelma fulvicorne* Townes, female. Metacarpellan hamuli. Fig. 5. *Tanypelma fulvicorne* Townes, female. Apex of mid tibia and base of mid basitarsus, showing the two mid tibial spurs.

Therion Curtis, with several undescribed Argentine species, is the only other genus of Theriini currently known from the Neotropics. It differs from *Stangepelma* in having two mid tibial spurs, an incomplete postpectal carina, and hind tarsal claws curved at less than 90 degrees.

GENERIC NAME: For Dr. Lionel A. Stange of the Instituto Miguel Lillo, who collected the holotype of *Stangepelma argentinum*.

***Stangepelma argentinum*, new species**

Holotype: female, ARGENTINA (*Salta*: 1 km. Oe. Aguas Blancas, 11 August 1976, L. A. Strange, C. C. Porter). (Tucumán).

Paratype: male, ARGENTINA (*Corrientes*: Las Marías, ca. Gdor. Virasoro, 7 November 1971, C. Porter). (Porter).

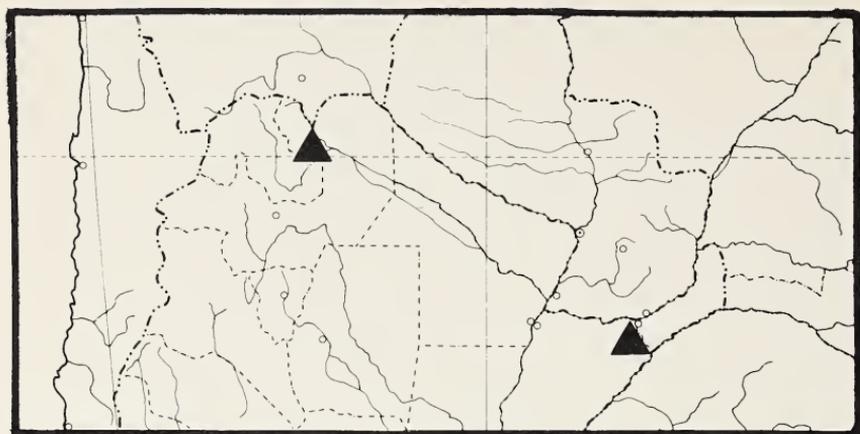
FEMALE: *Color*: antenna black with a yellow blotch on scape below; head and mesosoma shining black with yellow on basal 2/3 of mandible, labrum, clypeus, face, frontal orbit to slightly above antennal socket, for a short distance on vertical orbit, on most of temporal orbit (becoming very narrow above), broadly on lateral swellings of scutellum, briefly on base on tegula, and on most of subalarum; first gastric segment shining piceous black; second segment shining piceous black on tergite and brownish yellow on sternite; and succeeding segments shining pale brown, becoming more or less dusky dorsad and more yellowish ventrad; fore leg pale yellow with considerable light brown on apical 2/3 of femur, especially below, a little brown on base of tibia, brown on much of third tarsomere, and dark brown on tarsomeres 4-5; mid leg pale yellow with dark brown, becoming more yellowish anteriorly, on about apical 2/5 of femur, a little brown on base and apex of tibia, and dark brown on tarsomeres 2-5 and tip of 1; hind leg with coxa shining black above and yellow below; trochanter, trochantellus, and femur shining black with yellow below on extreme base of trochanter, yellow grading apically into brownish below on trochantellus, a little piceous below on basal half of femur, and tibia and tarsus dull black with yellow on sub-basal 1/5 of tibia below; wings hyaline with a slight brownish tinge and the stigma dark brown except for a small whitish area at base.

Length of fore wing: 8.1 mm. *Flagellum*: elongate and practically filiform, first segment 5.0 as long as deep at apex, second segment 2.1 as long as deep at apex. *Face*: 1.4 as high as wide at

anterior tentorial pits, 1.8 as wide at level of antennal sockets as at anterior tentorial pits; with large, strong, mostly adjacent or subadjacent to a little sparser punctures. *Clypeus*: on each side subapically with a broad, weakly defined swelling. *Temple*: moderately receding behind eye; at its upper 1/4 about 0.56 as long as eye in lateral view. *Pronotum*: with a broad and foveolate dorsal submarginal groove; its lateral surface smooth and polished for some distance behind epomia but with coarse longitudinal wrinkles toward hind margin. *Mesoscutum*: notauli strong, apically confluent, reaching about 9/10 the length of mesoscutum; surface throughout with strong, subadjacent to a little sparser punctures. *Mesopleuron*: on most of its dorsal 1/3 with strong longitudinal wrinkling but on ventral 2/3 generally smooth and polished with numerous well spaced small punctures that become progressively denser rearward. *Metapleuron*: with strong reticulate wrinkling like that of propodeum; submetapleural carina low, defined only on about basal 2/3. *First gastric tergite*: 8.2 as long as wide at apex. *Ovipositor*: sheathed portion 0.6 as long as apical depth of gaster.

MALE: differs from female as follows: *Color*: scape entirely black; no yellow on frontal orbit; yellow on temporal orbit limited to a short line near mid-height of eye; scutellum entirely black; tegula entirely black; second gastric segment almost entirely black; and succeeding gastric segments darker than in female, blackish dorsal and becoming dull yellowish brown ventrad; front femur rather dark brown below and postero-dorsally on apical 3/4 and with yellow staining longitudinally between the dark zones; fore tarsus with weak brown staining on fourth segment and dark brown only on fifth; mid femur uniformly black on a little more than apical half; mid tibia dark brown on basal 1/8 and again on apical 1/3; about apical 1/3 of mid basitarsus dark brown; hind femur with dull yellow to piceous below on basal 1/2, which is brightest close to base and again on a fairly broad, dorsally prolonged area just before mid length.

Length of fore wing: 7.4 mm. *Flagellum*: first segment 4.7 as long as deep at apex, second segment 2.3 as long as deep at apex. *Face*: 1.6 as high as wide at anterior tentorial pits, 1.4 as wide at level of antennal sockets as at anterior tentorial pits. *Clypeus*: subapical lateral swellings more strongly defined than in female and occupying all but median 1/4, which is depressed between



Map 1. Northern Argentina, showing distribution of *Stangepelma argentinum*.

them. *Temple*: at its upper 1/4 only about 0.36 as long as eye in lateral view and more strongly receding behind eye than in female. *Mesoscutum*: notauli reaching about 8/10 the length of mesoscutum; punctures even sharper and denser than in female, largely adjacent. *First gastric tergite*: 8.7 as long as wide at apex.

TYPES: The female holotype will be deposited at Tucumán, Argentina in the collection of the Instituto Miguel Lillo of the Universidad Nacional de Tucumán. The male paratype will be retained in the collection of Charles C. Porter at 301 North 39th Street, McAllen, Texas.

FIELD NOTES: The female holotype was netted among roadside weeds in bright sun. The type locality is in Selva Chaqueña, a subtropical deciduous forest which in northeastern Salta and Jujuy Provinces of Argentina forms a transition between the lowland Dry Chaco scrub to the east and the mostly evergreen Selva Tucumano-Boliviana at the base of the Andes to the west.

The male paratype comes from Selva Paranense, a humid evergreen subtropical forest characteristic of northeastern Argentina and adjoining Paraguay and Brasil.

Since almost 1,000 km. of Dry Chaco, unsuitable for moisture loving ichneumonids, separate the Selva Paranense and the north-west Argentine humid forests, the present day range of *Stangepelma* in Argentina probably is disjunct. In this respect, *Stange-*

pelma agrees with numerous other north Argentine humid forest insect genera, such as the ichneumonids *Epirhyssa*, *Acrotaphus*, *Rhinium*, *Tretobasis*, *Megajoppa*, *Cryptojoppa*, and *Macrojoppa*, the lepidopterous *Morpho*, and the pseudostigmatid zygopteron *Mecistogaster*, which enter Argentina only in the northwest and northeast, where they often are represented by closely allied or identical species. Evidently in the not distant past, perhaps during a Pleistocene glacial maximum, conditions were wetter than at present and humid forest biota ranged uniformly across the north of Argentina.

ACKNOWLEDGEMENTS

The holotype of *S. argentinum* was collected during fieldwork subsidized by the author's current U. S. National Science Foundation Grant (DEB 75-22426). I obtained the male paratype during a visit to the estate of Srs. Pablo, Arturo, and Adolfo Navajas Artaza at Establecimiento Las Marías near Gobernador Virasoro in Corrientes Province of Argentina. I am grateful for the hospitality of the Navajas Artaza, which made possible collecting in this unusually rich and little known area.

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A NEW GENUS AND SPECIES OF CONIOPTERYGIDAE
(NEUROPTERA) FROM NEW MEXICO*

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A single male specimen of an undescribed genus of Coniopterygidae was collected in a blacklight trap in Las Cruces, New Mexico. The specimen keys out to the genus *Helicoconis* Enderlein of the subfamily Aleuropteryginae in Meinander's (1972) key, but genitalic studies show the need for a new generic designation. Because the genitalia of this new genus differ from all known genera of Coniopterygidae, it is difficult to make comparisons, but for descriptive purposes, the genitalia are compared to those of *Helicoconis*. The structures referred to here as ectoprocts are probably equivalent to the ectoprocts of *Helicoconis* but may represent other structures.

Bidesmida new genus

This genus so far contains only the type species and is apparently most closely related to *Helicoconis*, which is widely distributed in the Holarctic Region and Africa.

Male-Head capsule with unsclerotized area on frons, including antennal sockets. Maxillary and labial palps long and slender; last segment of palps only slightly broader than preceding segments. Scape and pedicel about twice as long as broad.

Forewing with R4+5 superficially resembling an anterior branch of M. M bearing several small setae. Two in the middle of the wing only slightly more prominent than the rest. Bases of setae not enlarged and M not appreciably narrowed between setae.

Plicaturae present on abdominal segments 3-7.

Male genitalia apparently formed from elements of eighth, ninth and tenth segments. Ninth segment forming a closed ring.

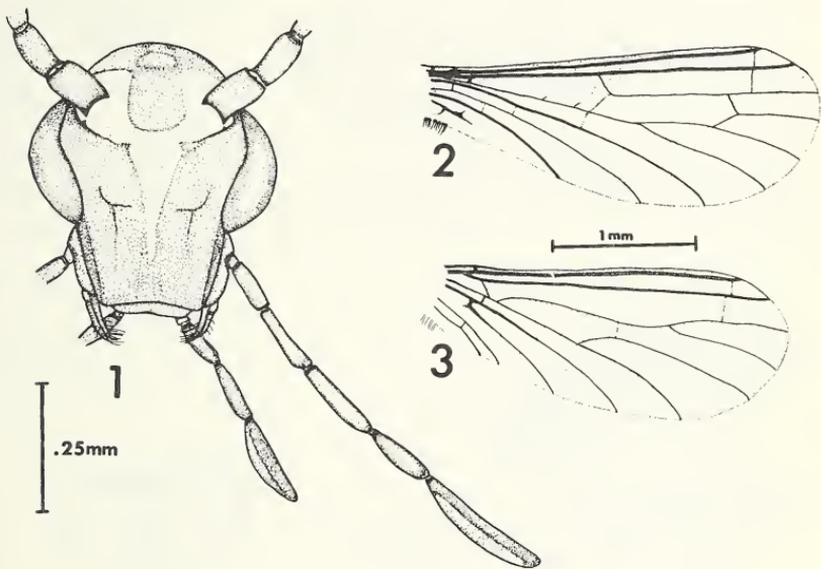
*This paper (No. 76-7-70) is published with the permission of the Director of the Kentucky Agricultural Experiment Station and is based on research performed in partial fulfillment of the requirements for the PH.D. degree in Entomology.

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Eighth segment represented by a sclerotized plate forming the of M. M. bearing several small setae. Two in the middle of the ectoprocts apparently represent elements of tenth segment and perhaps part of the ninth as well (Meinander 1972).

Type-species: *Bidesmida morrisoni* n. sp.

Bidesmida is similar to *Helicoconis* in wing venation and in having plicaturae on abdominal segments 3-7. *Bidesmida* differs from *Helicoconis* in having the eighth sternum strongly sclerotized and forming the venter of the genital capsule, the ectoprocts being fused distally, and the parameres being fused with the ectoprocts.

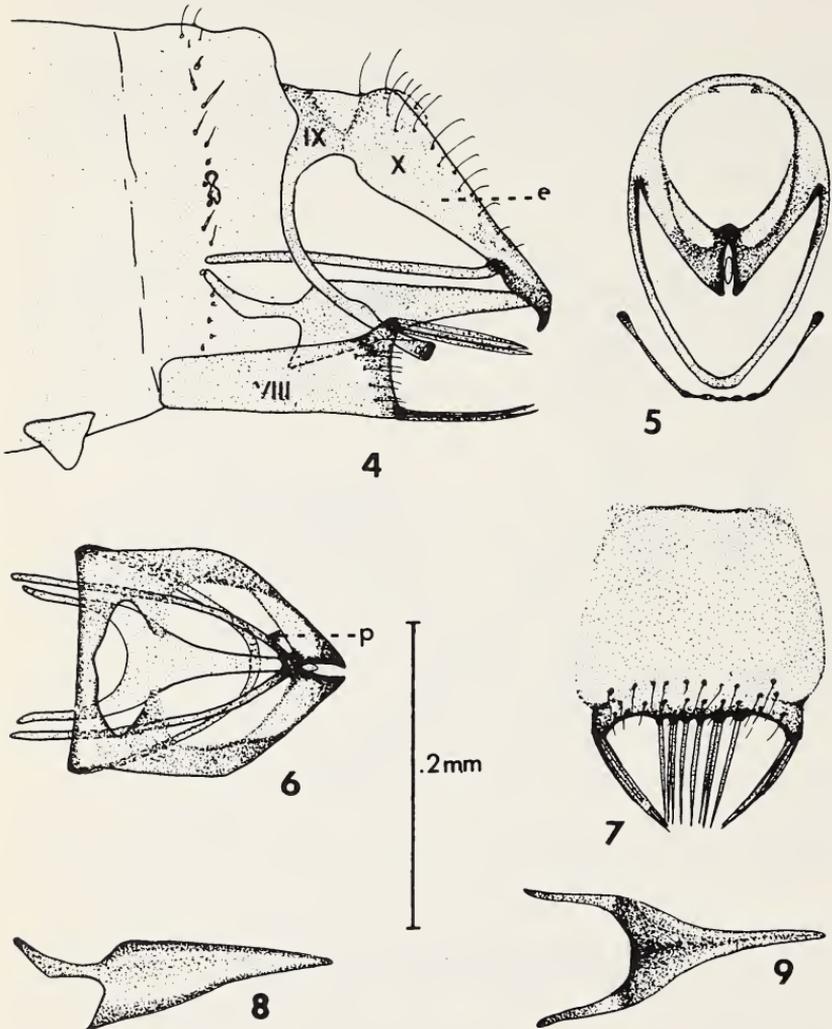


Figures 1-3. *Bidesmida morrisoni*, n.sp. Fig. 1, anterior view of head. Fig. 2, front wing. Fig. 3, hind wing.

***Bidesmida morrisoni* new species**

Male-Head capsule (Fig. 1) with large unsclerotized area on frons, including antennal sockets, and extending ventrally in a tapering tongue to near clypeus. A sclerotized area extending down from vertex into this unsclerotized area. Eyes large. Palpi long and slender. Last segment of palpi only slightly broader than

preceding segments. Antennae 26 segmented. Scape and pedicel about twice as long as broad. Second and third flagellar segments smallest of antennae, one and one-half times as long as broad. Remaining flagellar segments larger, twice as long as broad except terminal segment three times as long as broad.



Figures 4-9. *Bidesmida morrisoni*, n.sp. Fig. 4, lateral view of genitalia (e = ectoprocts). Fig. 5, caudal view of genitalia (p = parameres). Fig. 6, dorsal view of genitalia. Fig. 7, ventral view of eighth sternum. Fig. 8, lateral view of penis. Fig. 9, ventral view of penis.

Wings(Figs. 2-3) hyaline without dark spots or pattern. R4+5 of forewing superficially resembling an anterior branch of M. Forewing 2.7 mm long and hindwing 2.3 mm long. Both wings about 0.8 mm wide at widest part.

Male genitalia (Figs. 4-9) ninth segment forming a closed ring becoming a narrow band ventrally, fused with ectoprocts dorsally. A weakly sclerotized dorsal area may indicate limits between ninth segment and ectoprocts. Ectoprocts extending posteriorly with distal ends fused medially. Parameres long, fused with ectoprocts posteriorly. Penis formed of two rods fused posteriorly to form a tube. No hypandrium or styli evident. Eighth sternum strongly sclerotized and forming ventral portion of genital capsule. A row of heavy spines along posterior margin of eighth sternum and a group of several large spines on postero-lateral angles. An additional double row of smaller spines just anterior to posterior margin.

Holotype male: Las Cruces, New Mexico, blacklight trap, November 30, 1975, W. P. Morrison. Holotype deposited in USNM.

Female and immature stages unknown.

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LYCOSID SPIDERS ON ARTIFICIAL FOLIAGE: STRATUM CHOICE, ORIENTATION PREFERENCES, AND PREY-WRAPPING¹

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The majority of lycosid spiders neither spin webs for prey capture nor hunt actively, but spend most of their time waiting for prey at a resting site (Cragg, 1961; Edgar, 1969). In this regard, those lycosids that inhabit the herbaceous stratum resemble the aerial web-weaving spiders. As does a web, the foliage substratum provides a waiting site, a medium for transmission of vibratory stimuli produced by prey, and a surface on which capture is performed (Rovner and Knost, 1974). In the present study we used artificial foliage to examine stratum choice in *Lycosa punctulata* Hentz and *L. rabida* Walckenaer, which usually are found in the herbaceous stratum of fields, and in *Schizocosa saltatrix* (Hentz) and *S. crassipes* (Walckenaer), which typically are found on the leaf litter of forest floors. We also studied body orientation preferences shown by individuals of the first three species when they rested at an elevated site on the artificial foliage. The significance of a preference for vertical orientation was hypothesized with regards to equalizing proprioceptive input, minimizing energy expenditure, facilitating prey detection, and improving concealment from predators. Finally, we observed post-immobilization prey-wrapping to determine if this behavior is an adaptation for retention of captured prey by spiders dwelling in the herbaceous stratum, as hypothesized by Rovner and Knost (1974).

METHODS

Sokal and Rohlf (1969) was the source of all parametric statistical analyses. All means are accompanied by their standard deviation.

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Spiders were collected in Athens Co., Ohio, USA, and maintained under conditions described previously (Rovner and Knost, 1974). Adults of each species were examined during their natural season, i.e., when adults were abundant in the field. Studies were conducted in glass terraria ($0.2 \times 0.4 \times 0.2$ m high) containing cardboard leaves with controlled surface areas and slopes. A 50-mm styrofoam layer on the bottom was covered with 5 mm of white sand, the latter being an inert substratum (Greenquist, 1975). Two cotton-stoppered vials provided drinking water. Cardboard plants, 0.18 m high and a mean width of $21 \text{ mm} \pm 6.0$ (range = 10–30 mm), were inserted into the styrofoam so that the tops reached within 10 mm of the glass lid. Three foliage designs were used (Fig. 1):

Compound Design. This consisted of a vertical axis with one to four "leaf" projections coming off at 60° relative to the horizontal when viewed from an edge perspective. The surface area of the 60° slopes equaled the surface area of the vertical blades. There were nine to eleven "plants" per terrarium.

$60^\circ/90^\circ$ Simple Design. Individual vertical and 60° blades such that the surface area of the vertical slopes equaled that of the 60° slopes; ten vertical and nine 60° blades per terrarium.

60° Simple Design. All blades positioned at 60° ; eleven or twelve blades per terrarium. When viewed from a surface rather than an edge perspective, all the blades (or leaves) of all three designs pointed directly upward.

The relative humidity in the terraria averaged $94\% \pm 3.8$ and was maintained by a 250-ml bowl filled with cotton and distilled water. The high humidity minimized the possibility of a vertical gradient which otherwise might have influenced site selection, although Greenquist (1975) found that a difference of medium vs. high humidity levels ($< 65\%$ vs. $> 85\%$) had no effect on stratum preference in *L. punctulata*. Temperature within the terraria averaged $26.7^\circ \pm 4.5$. The hygrometer and thermometer were housed in a terrarium identical to the test terraria but without foliage and spiders. Photoperiod was not controlled. Leaf litter was placed in the bottom of several terraria of the woodland-dwelling *S. saltatrix* to see if this influenced stratum preference.

Individual experiments were conducted from 9 to 14 days with one spider ("solo") or three individually marked spiders of the

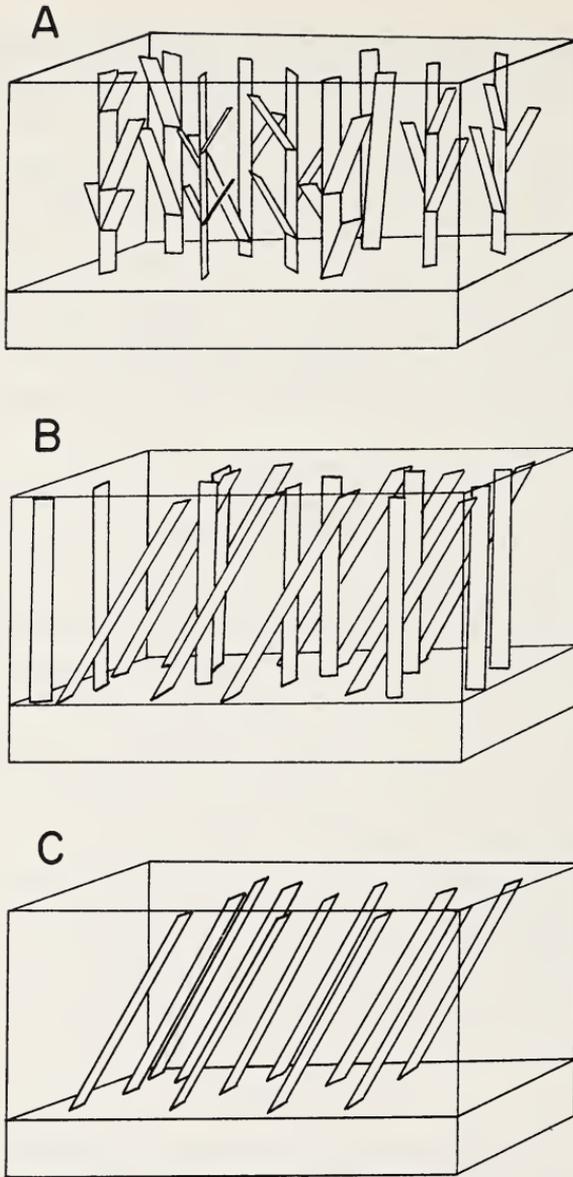


Fig. 1. Foliage designs used to study stratum choice and orientation preferences in lycosid spiders. (Water bowls and vials are not shown.) (A) Compound Design. (B) 60°/90° Simple Design. (C) 60° Simple Design.

same sex ("trio") in each terrarium. We observed the animals four times daily for 6 days at 3-hour intervals between 0900-1800. They were fed on the seventh day, and observations resumed on the eighth day. At each observation, the spider's height (from the center of the cephalothorax to the terrarium base), the slope of the resting site, and the orientation of the body relative to the blade or leaf axis were recorded. When cannibalism or death occurred (eleven cases) during trio experiments, replacement was made with equivalently marked animals. Five unmated females built egg sacs during the experiments; however, this did not influence stratum preference (paired-comparisons test with arcsine transformation; variation due to egg sac, $F_{s(1,4)} = 0.323$ NS; variation among individuals, $F_{s(4,4)} = 1.892$ NS).

RESULTS

Stratum choice. — The differences in time spent on foliage vs. on the ground were significant among the four lycosid species (one-way ANOVA with arcsine transformation; $F_{s(3,56)} = 31.189$, $P < 0.001$). *L. punctulata* (12 females, 4 males) averaged 24.4% of the recorded position on the foliage ($n = 832$); *L. rabida* (5 females, 13 males) averaged 41.1% ($n = 989$); *S. crassipes* (3 females, 15 males) averaged 1.2% ($n = 595$); and *S. saltatrix* (13 females, 7 males) averaged 9.1% ($n = 1022$). An a posteriori STP-test revealed no significant difference in preference between the two *Lycosa* spp. *S. saltatrix* had significantly greater herbaceous preference than *S. crassipes* ($P < 0.05$) and significantly less than the *Lycosa* spp. ($P < 0.001$). *S. crassipes* is omitted from the following analyses due to its very low tendency to rest on the foliage.

Stratum choice by *L. punctulata* and *S. saltatrix* was not affected by variation in foliage design or animal density; however, the tendency to spend time on the foliage in *L. rabida*, while not affected by foliage design, was significantly greater at solo density (Table I). Data on the individuals of these three species are available in Greenquist (1975).

The presence of leaf litter in some of the terraria of *S. saltatrix* did not affect stratum preference for any foliage design (paired-comparisons test; Litter variation, $F_{s(1,2)} = 1.370$ NS; Foliage variation, $F_{s(2,2)} = 1.142$ NS). This suggested that these spiders (and probably *S. crassipes*) would not seek the artificial foliage when

Table I. Effect of spider density and foliage design on stratum choice in three lycosids. Individuals were grouped according to density and foliage design. An arcsine transformation was performed on the % of readings in which each spider was on the foliage. The mean % of each group was analyzed with two-way ANOVA without replication for solo vs. trio densities and for Compound vs. 60°/90° Simple vs. 60° Simple foliage designs.

Species	Source of variation	df	Mean square	F_s
<i>Lycosa punctulata</i>	Density	1	94.72	1.52 NS
	Foliage design	2	19.50	0.31 NS
	Error	2	62.27	
<i>Lycosa rabida</i>	Density	1	570.38	48.76*
	Foliage design	2	23.62	2.02 NS
	Error	2	11.70	
<i>Schizocosa saltatrix</i>	Density	1	0.001	0.00 NS
	Foliage design	2	7.07	0.15 NS
	Error	2	46.03	

* $P < 0.05$

the leaf litter, characteristic of their natural habitat, was not available in the experimental terraria.

Orientation preferences. — Leaf slope preference was analyzed by chi-square; we assumed that random preference would result in an equal number of positions recorded on vertical and 60° slopes. *L. punctulata* had a significant preference for the 60° slope over the vertical slope on the compound foliage design; *L. rabida* and *S. saltatrix* showed no preference on this foliage design (Table II). *L. punctulata* was found on the vertical slope more often than on the 60° slope when housed with the 60°/90° Simple Design. *L. rabida* and *S. saltatrix* preferred the 60° slope in this case.

We assumed that random selection of upper vs. lower surfaces on the 60° slopes would result in an equal number of positions recorded for each surface. Chi-square analysis indicated that all three species showed a significant preference for the upper surface on all three foliage designs (Table II).

The orientation of the spider within the plane parallel to the surface on which it rested was recorded as the angular difference between the blade (or leaf) axis and the spider's body axis. This

Table II. Total numbers of resting sites recorded in three lycosid species on different surfaces of three foliage designs. Chi-square (df = 1) values for (a) 60° slope vs. vertical and (b) upper vs. lower surfaces of 60° slopes are given.

	Compound Design		60°/90° Simple Design		60° Simple Design	
	Upper	Lower	Upper	Lower	Upper	Lower
<i>Lycosa punctulata</i>	28	1	16	0	102	7
		8.100**		6.480*		
(a)					82.798***	
(b)	25.138***		16.000***			
<i>Lycosa rabida</i>	70	9	59	3	124	19
		0.006 NS		3.846*		
(a)					77.098***	
(b)	47.101***		50.581***			
<i>Schizocosa saltatrix</i>	14	1	19	0	32	4
		0.034 NS		5.538*		
(a)					21.778***	
(b)	11.267***		19.000***			

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

was measured clockwise to the nearest 30° interval, with 0° = facing directly upward (Fig. 2). Two-way ANOVA was used to determine angular preferences within species and differences among species. There was a significant difference in preference within species ($F_{s(11,22)} = 13.943$, $P < 0.001$), indicating that individuals had a preferred orientation on the artificial leaf. There was no difference, however, in angular preference among species ($F_{s(2,22)} = 0.752$ NS). Orientation to 180° (= facing directly downward) was significantly greater for the three species than to all other angles (a posteriori STP-test, $P < 0.001$). Orientation to 0° (directly upward) was significantly greater than to all other angles except 180° ($P < 0.01$). Orientation to 180° was significantly greater than to 0° ($P < 0.05$). Spiders were not found to orient differently on the 60° and vertical slopes (paired-comparisons test; *L. punctulata*, $F_{s(1,11)} = 2.560$ NS; *L. rabida*, $F_{s(1,11)} = 1.016$ NS; *S. saltatrix*, $F_{s(1,11)} = 1.194$ NS).

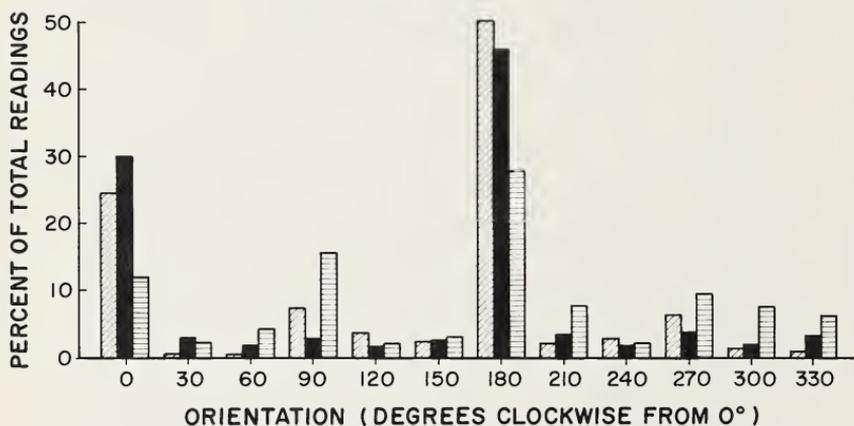


Fig. 2. Body orientation when resting on artificial foliage in *Lycosa punctulata* (obliquely hatched bar) ($n = 203$), *L. rabida* (solid bar) ($n = 399$), and *Schizocosa saltatrix* (horizontally hatched bar) ($n = 93$). 0° = facing directly upward.

Since the predominant orientation in the three species was vertical (0° and 180°), there was the possibility of the data being biased due to the spider's grasping the edges of the vertically positioned leaves with its right or left tarsal claws. Therefore, we conducted additional experiments in four other terraria, using female *L. rabida*. Each of these terraria was subdivided into five,

equal-size compartments by parallel cardboard sheets placed vertically (two terraria) or at an oblique (60°) angle (two terraria). These sheets extended the full width and height of the terraria, and were held in place by strips of masking tape along the side and bottom edges. Thus, each of the twenty spiders lived in a compartment with a narrow horizontal floor, two tall broad cardboard walls, and narrow glass sides and top. (These lycosids cannot climb glass.) Observations were made on 11 days, four times per day, as above.

Under these conditions, the spiders were recorded on the cardboard walls in 91.9% of the 834 total positions recorded; i.e., they usually were at an elevated location. In the oblique wall condition, 95.5% of the 448 positions were on the wall providing an upper surface; i.e., the spider rarely adopted a position on the undersurface of the overhanging wall.

Of the 750 positions recorded on walls, under both vertical and oblique wall conditions, 21.7% were noted in which the spider held onto the top edge (the only available edge) of the cardboard. Most of these (69.3%) involved a 90° or 270° body orientation, since the edge-holding spider typically used the tarsal claws of the four legs of the right or left side to secure the hold.

Most (78.3%) of the wall positions adopted were on the broad surface. Here, in the absence of an edge cue, 43.4% of the positions were 0° (22.3%) or 180° (21.1%), i.e., facing directly up or down. The next most common orientation on the broad surface (18.6%) was with the body parallel to the ground, i.e., at 90° or 270° . No significant differences between the orientation preferences of the spiders on these broad surfaces and the spiders on the artificial foliage were found (paired-comparisons test with arcsine transformation; $F_{s(1,11)} = 1.014$ NS).

PREY-WRAPPING

Methods. — Prey-wrapping behavior was examined in the artificial foliage terraria after prey were withheld from the spiders for up to 8 days. Prey items that either singly or in multiples of three or four would approximate the size of the spider's body were chosen to maximize prey-wrapping in the *Lycosa* spp. (Rovner and Knost, 1974). *L. punctulata* were given crickets (*Gryllus* sp. and *Nemobiinae*); *L. rabida* were fed grasshoppers (*Cyrtacanthacridinae*). On several occasions, when prey-wrapping occurred

on the foliage, the spider was chased from the prey with a soft brush to determine if the prey item was attached to the substrate and if the spider returned to the prey. *S. crassipes* and *S. saltatrix* were fed plant bugs (Miridae), thirty to forty bugs being placed in each terrarium. Multiple captures of up to six prey occurred, which should have stimulated prey-wrapping (ibid.).

Sod (with vegetation intact) from the habitat of *L. rabida* was placed in a $0.5 \times 0.26 \times 0.3$ m high glass terrarium and brought into the laboratory. After prey were captured in the home cage of an individual of this species, the spider was coaxed onto the grass of the terrarium, where it came to rest, still holding its prey. Observation periods for prey-wrapping studies lasted 2 hr.

Results. — Prey transport was common in all four species and usually occurred before the prey were immobile. Immobile prey occasionally were transported from the ground into the foliage by all species except *S. crassipes*. Spiders transported prey with the chelicerae and walked with the body raised up; nevertheless, large prey often dragged on the ground.

None of the species used silk to immobilize the prey. In the two *Lycosa* spp., females exhibited from one to five separate bouts (and males only one bout) of post-immobilization wrapping during the 2-hr observation period in response to single large prey and multiple captures of small prey. While *L. punctulata* wrapped in a counter-clockwise direction, *L. rabida* wrapped 65.3% of the time in a clockwise direction. *L. rabida* held prey in the chelicerae during the first wrapping bout for an average of 1.6 ± 1.21 revolutions. Consequently, as the spider wrapped, the prey beneath it pivoted around with the spider. The spider then released the prey and continued to pivot above it for the rest of the bout. Holding the prey in this manner while wrapping rarely occurred during subsequent bouts, only appearing if those bouts were preceded by excessive prey manipulation with the palps, and never lasted as long as it had in the original bout. *L. punctulata* never held prey in this manner while wrapping. Other details of wrapping resembled the description of Rovner and Knost (1974) and are provided in Greenquist (1975). Wrapping never occurred in *S. crassipes* (four females, nine males) nor *S. saltatrix* (fifteen females, nine males).

L. rabida was examined under the semi-natural conditions of a terrarium containing field sod. Here, with the spiders holding

onto blades of tall grass, prey-wrapping was slower than it had been on the broader, flat surfaces of the artificial foliage terraria (one-tailed t -test; $t_{(46)} = 2.922$, $P < 0.01$). When the spiders were driven 90 mm or more from the feeding site (with a soft brush), they returned after as much as 2.5 min later in four out of six cases, and resumed feeding on the prey package still attached to the grass. On two occasions they came back by a different route than the one by which they had left. On another occasion a spider carried wrapped prey for 33 mm, dropped it (when touched by the brush), and continued on for another 85 mm. After 72 sec the spider returned to the drop site, although it did not find the prey, which had fallen to a point 30 mm below.

DISCUSSION

Stratum choice.—The selective advantage for any species to carry on a major portion of its activity in a specific micro-habitat is that this prevents interspecific competition. Kuenzler (1958) found that vertical stratification separates *L. rabida* from the ground-dwelling lycosids. The same would be true later in the year when *L. punctulata* replaces *L. rabida* in the herbaceous stratum. The results of our laboratory study support the idea of differential use of two strata by lycosids. The herbaceous stratum-dwelling *Lycosa* spp. spend significantly more time resting on the artificial foliage than the two *Schizocosa* spp., which are found in nature on woodland floors.

While overall habitat selection was found to depend on the ability of various lycosid species to withstand desiccation (Cherrett, 1964), the importance of the physical form of features within a lycosid's habitat in determining their micro-habitat distribution was emphasized by the field studies of Duffey (1962, 1966) and the work of Richter (1970). We found that our lycosids spend dissimilar amounts of time, depending on species, in different strata under conditions of uniformly high relative humidity and minimal (if any) temperature and light gradients. Thus, our data provide laboratory support for the idea that a preference for structural features within the habitat can play an important role in the micro-habitat distribution of wandering spiders.

In our experimental terraria (Fig. 1) foliage design had no effect on stratum choice (Table I). Density (solo vs. trio) had an effect only in *L. rabida*, the reason for which we do not know. (Unlike

L. punctulata, most of our *L. rabida* were males, which may tend to wander more and to interact agonistically at trio density, thereby spending less time resting at an elevated foliage site. This is only a guess.)

Orientation preferences. — Leaf slope preferences on the artificial foliage were not consistent among and even within the species, some spiders being located most often on a 60° slope, others most often on a vertical surface (Table II). These data, as well as the readiness of control spiders to rest on both 60° and vertical broad surfaces, suggest that there possibly is no preference for oblique vs. vertical leaves as resting sites in these lycosids.

There was a definite preference, however, for upper- rather than undersurfaces of sloping (60°) leaves (Table II). Similarly, control spiders on the broad surfaces rarely rested while holding onto the undersurface of a 60° cardboard wall. An inverted position likely provides less secure "footholds" for resting or for chasing prey in these webless spiders. It also is less suitable for the critical act of pouncing on the prey, since the spider would have gravity working against it.

Most aerial web-weaving spiders orient in a face-down position while resting in their webs (Eberhard, 1967). Orientation preferences also were shown by our lycosids on sloping or vertical surfaces, the spider most often adopting a vertical position. As with web weavers, a vertical position possibly yields optimum "clawholds" with the least amount of energy expenditure while waiting for prey. On artificial foliage, the most common resting position for lycosids, like that of web weavers, was facing directly downward. On a broad surface, the vertical orientation was again predominant, although the lycosids here faced up as often as down. Either way, equivalent input from the proprioceptors of the right and left sides is achieved, which may be the primary determinant of this orientation.

Visual and mechanical prey-detection by wandering spiders resting in the herbaceous stratum probably are enhanced by vertical orientation on stems or grass blades, since this aims the spider in one of the two main directions from which crawling prey are most likely to approach. Kuenzler (1958) noted that crawling prey are the primary food of lycosids.

A preferred vertical orientation on grasses and other plants may have influenced selection for the bold stripes running length-

wise on the two *Lycosa* spp. found in this stratum, since such markings would provide cryptic coloration. Ground-dwelling lycosids lack such bold, anterior to posterior, striped patterns.

The next most common orientation on artificial foliage and on broad surfaces was perpendicular to the vertical one, i.e., 90° or 270° (when 0° = facing up). In such a horizontal position on a sloping or vertical surface, the spiders were holding primarily by the tarsal claws of the upper four ipsilateral legs. For some reason, positions intermediate between vertical and horizontal are less satisfactory for long-term resting postures on elevated surfaces. It may relate to the effective use of the inwardly curving tarsal claws for securing a grip or to a tendency to prefer similar proprioceptive inputs from four ipsilateral legs as the next best condition to that provided by the bilaterally symmetrical input of a vertical orientation. All things considered, it is likely that vertical orientation would predominate in the field, where stems and the edges of grass blades provide largely vertical grasping sites for the claws that would add to the laboratory-demonstrated preference for a vertical position.

Prey-wrapping.—Our data supported Rovner and Knost's (1974) hypothesis that post-immobilization wrapping of prey by wandering spiders is an adaptation for successful feeding in the herbaceous stratum. This behavior did not occur in our ground-dwelling *Schizocosa* spp. Wrapping prevents prey loss from elevated sites when the cheliceral grip is relaxed during feeding, grooming, or a startle response, since wrapping always includes attachment of the prey to the site. Furthermore, when we forced spiders to leave immobilized prey, they were able to return to the site. Obviously, wrapped (i.e., attached) prey are far more likely to be recovered at an elevated site than are non-wrapped. Since the spiders sometimes returned by a route different from that taken when chased away, they were not depending on draglines to relocate the prey. They may have used kinesthetic orientation, or visual orientation, or both (Görner, 1966).

Rovner and Knost (1974) also suggested that wrapping by lycosids might serve to free the spider for subsequent attacks on additional prey, as occurs in web weavers. Our data did not support this idea. Subsequent captures were never observed in which the spider returned to the original prey at a previous site, as was also noted to be the case in *Cupiennius salei* (Melchers, 1963). Ap-

parently, in contrast to web-dwellers, which are likely to detect a prey while still handling a previous one (Eberhard, 1967) and which spend prolonged periods at fixed sites (in their webs), the retention of prey at a site for future use after additional captures is of little value to a wandering spider.

SUMMARY

When housed in terraria, *Lycosa punctulata* and *L. rabida* spend significantly more time on artificial foliage than do *Schizocosa crassipes* and *S. saltatrix*. Such data provide laboratory support for the idea that a preference for structural features within the habitat plays a role in the micro-habitat distribution of wandering spiders. Our lycosid species prefer upper rather than lower surfaces as rest sites, and we suggest that upper surfaces are coincidentally more suitable for prey capture. On broad, steep surfaces our species most often adopt a vertical orientation, facing directly up or down. On artificial foliage, vertical orientation likewise predominates, with a significant preference here for a face-down position, i.e., the position also typical of web-weaving spiders. We suggest mechanisms, one of which may underlie this orientation preference. Coincidentally, prey detection by wandering spiders that are at rest in the herbaceous stratum may be facilitated by a vertical orientation. Our observations on post-immobilization prey-wrapping indicate that wrapping not only enables wandering spiders to retain prey while feeding at an elevated site, but also insures the recovery of immobilized prey when the spider momentarily flees and then returns to the feeding site.

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A TECHNIQUE FOR OBSERVING THE BEHAVIOUR OF SMALL ANIMALS UNDER FIELD CONDITIONS*

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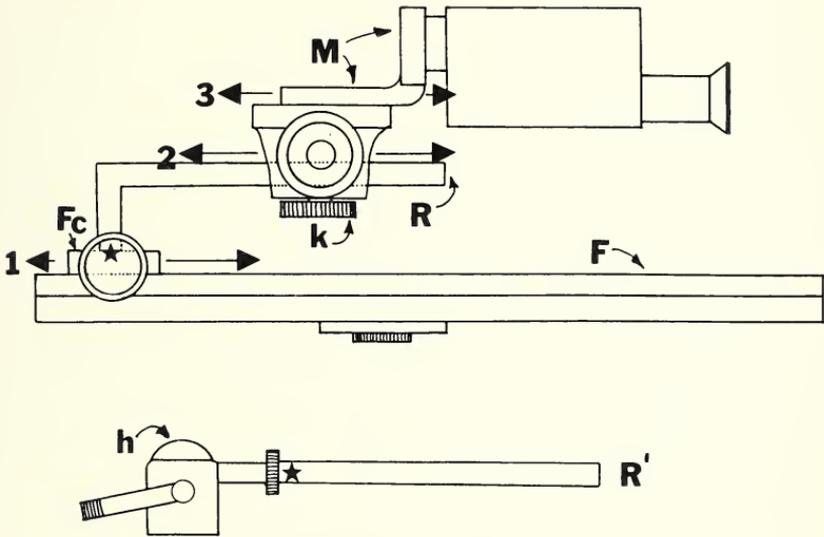
Small animals are difficult to observe under field conditions, and arthropods of less than 10 mm body length are particularly difficult subjects. When such animals are making complex movements with small parts of their body (mouth parts, reproductive organs) some device is needed to augment direct vision. One solution to the problem is to use the zoom optics of a movie camera equipped with close-up devices (Robinson & Robinson, 1972). Recently, however, one of us (M.H.R.) studied the behaviour of *Drosophila*-sized flies that associate with orb-web spiders and spend long periods standing on the spider's body. To find out what the flies were doing there it was essential to see them in close-up and be able to watch them, for long periods, under field conditions. Watching them through the macrosystem of a movie camera gave insufficient magnification. We solved the problem by adapting a stereo-binocular microscope for horizontal viewing. We feel that this adaptation has a wide variety of potential applications in field ethology. It may be a re-invention but is worth describing here.

MAKING THE MICROSCOPE ADAPTER

Essentially the adaptation consists of making a mount that enables the microscope to be used on a camera tripod, for horizontal viewing and with a greatly extended focussing range. Any microscope can be used that consists of a subassembly comprising the optical and focussing systems that is clamped onto a vertical column on the base subassembly. The optical/focussing subassembly is simply detached from the conventional base and attached to a specially made horizontal column mounted on a tripod. All that is needed is a length of steel rod the same diameter as the support column on the original base. The rod has then to be modified to fit onto a tripod. This can be done in several ways depending on

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the degree of engineering sophistication that is available. Two methods are shown in Figure 1; many others are perfectly feasible. The length of the rod determines the extent of the coarse focussing that is made possible by simply sliding the microscope assembly along the rod before using the rack-and-pinion focussing of the subassembly. Unwelcome vibrations may occur if too long a rod is used.



EXPLANATION OF FIGURE

1, 2 and 3. *arrowed: focussing facilities. 1. Focussing available on camera focusing rail (F). 2. Focussing available on microscope mounting rod (R); this is obtained by slackening knob (k) that normally attaches microscope to its stand. 3. Focussing available by rack-and-pinion focussing of microscope subunit (M).

Two methods of mounting microscope carrying rod to tripod are shown. In main diagram, R is bent at right angles and the starred end is drilled and tapped to take the standard camera attachment bolt on the focusing rail at Fc. The detail below shows an alternative: R', a straight rod, is drilled and tapped to attach to a ball-and-socket camera mount (h) that attaches at Fc.

We find that even greater flexibility of use is possible if the microscope is attached to a rod carried on a photographic focussing rail rather than one directly attached to a tripod head. With an extra-long focussing rail (45 cm, for instance) it is possible to put the tripod down once, close to the subject, and be sure that enough focussing range is available to bring the subject in focus without again moving the tripod. This can be critical in circumstances where movements of the vegetation in which the tripod is standing can cause the subject to flee or cease normal activity.

Using the device requires practice. A wide variety of adjustments are available through the pan-and-tilt head of the tripod, and through the rack-and-pinion of the focussing rail and microscope focussing system. Use of a tripod with an elevator head that is reversible further extends the scope of the device. Depth of field is slight even at very low powers of the microscope but continual focus adjustment is not difficult or distracting. Viewing with one's hands resting on the focussing wheels of the microscope helps one to acquire a habit of keeping a moving object in focus. It is possible to use one eyepiece for viewing and have a camera permanently attached to the other. This helps immensely in obtaining action photographs of transitory behavioural events.

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CTENOBETHYLUS (BETHYLIDAE) A NEW SYNONYM
OF IRIDOMYRMEX (FORMICIDAE, HYMENOPTERA)¹

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In 1939, in a paper describing several new genera and species of Baltic Amber Hymenoptera, C. T. Brues erected *Ctenobethylus succinalis* gen. et sp. nov. for a single specimen of what he took to be an apterous female bethylid. I recently chanced upon this description, and was immediately struck by the ant-like habitus of the type as portrayed in Brues' fig. 7. It was also noted that the figure showed only 12 antennomeres, although Brues had made a diagnostic point of claiming "13-jointed" antennae for his genus.

My suspicion that the type of *C. succinalis* is actually a worker ant of the dolichoderine genus *Iridomyrmex* was confirmed when it was sent for my study. The specimen has the legs folded up so as to obscure the waist, which explains why Brues did not see the petiolar scale. In the preparation as it now stands, however, the scale is partly visible in a left-side view, although it is covered with a white film. The specimen also has 12-merous antennae, and in fact closely corresponds to small-sized workers of *Iridomyrmex goepperti* with which I have compared it directly.

Although I have not seen the type of *I. goepperti*, I compared 11 worker specimens of this commonest of all Baltic Amber ants lent from the Museum of Comparative Zoology collection. (*I. goepperti* made up over half of the more than 10,000 Baltic Amber ants determined by W. M. Wheeler at one time or another; see Wheeler, 1914: *op. cit. infra*, p. 8.) These specimens and the *C. succinalis* type meet very well the available descriptions of *I. goepperti*. The formal synonymy is:

¹A Report of Research from the Cornell University Agricultural Experiment Station. Research supported by National Science Foundation Grant DEB75-22427.
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Iridomyrmex goepperti

Hypoclinea göpperti Mayr, 1868, Beitr. Naturk. Preuss. 1: 56, pl. 1, fig. 3-7; pl. 3, fig. 42-46, worker, queen, male.

Iridomyrmex goepperti: Wheeler, 1914, Schrift. Phys-ökon. Ges. Königsberg, 55: 90-91, worker.

Ctenobethylus succinalis Brues, 1939, Ann. Entomol. Soc. Amer. 32: 261-263, fig. 7, ♀ (*recte* worker). Type: Museum of Comparative Zoology, Harvard University, No. 7666. NEW SYNONYM.

Brues' figure errs in omitting the spurs, present one on each tibial apex, and also in showing the trunk as without an impressed metanotal groove; actually, this groove is distinctly though modestly impressed in the type.

I. goepperti is left in *Iridomyrmex* for the time being, although this genus is almost surely a diphyletic assemblage. The Indo-Australian species, including the type species of *Iridomyrmex*, *I. purpureus* (= *I. detectus*), differ from the New World members (*I. humilis* group) in that they lack Pavan's apparatus (with gland) at gastric sternites IV and V. The status of the Baltic Amber *Iridomyrmex* with respect to this character has not been determined, because the few samples available to me have the underside of the gastric apex obscured by films. As already stressed by Wheeler, *I. goepperti* lacks a distinct epistomal (frontoclypeal) suture and frontal triangle, conditions atypical for *Iridomyrmex* (and for ants in general). It is likely also that the living species of *Iridomyrmex* divide further into groups on the basis of proventricular anatomy, position of compound eyes, larval morphology, karyotype, and perhaps other characters. If some of these groups represent different genera, as seems likely, we do not know yet how the divisions will cut, or what genus-level names are available.

The "*Iridomyrmex* Problem" is an exceptionally complex one, calling for nothing less than a full-scale revision of the Tapinomini. Until that revision can be made, the genus *Iridomyrmex* is best left as it stands, and *Ctenobethylus*, with type and sole species *C. succinalis*, is its *new synonym*.

In recent correspondence with E. O. Wilson and H. E. Evans, I learned that they had jointly examined *Ctenobethylus succinalis* several years ago, and tentatively considered it to belong to *Iridomyrmex*, but they did not complete the study. I am grateful

for their opinions, but since the present study was made independently, they should not be held responsible for my conclusions. F. M. Carpenter has my thanks for the improved preparation and the loan of the *C. succinalis* type.

A NEW SPECIES OF *PLATYTHYREA*
(HYMENOPTERA; FORMICIDAE) FROM COSTA RICA¹

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A new species of *Platythyrea* was found in the Field Museum insect collections too late to be included in Brown's (1975) revision of the genus. Eleven workers were collected by Dr. John Wagner and Dr. John Kethley from berlesates at the La Selva Field Station of the Organization for Tropical Studies in Costa Rica. A formal description is offered herewith. Measurements are as defined in Brown (1975:3).

***Platythyrea prizo* n.sp.**
(Figs. 1-3)

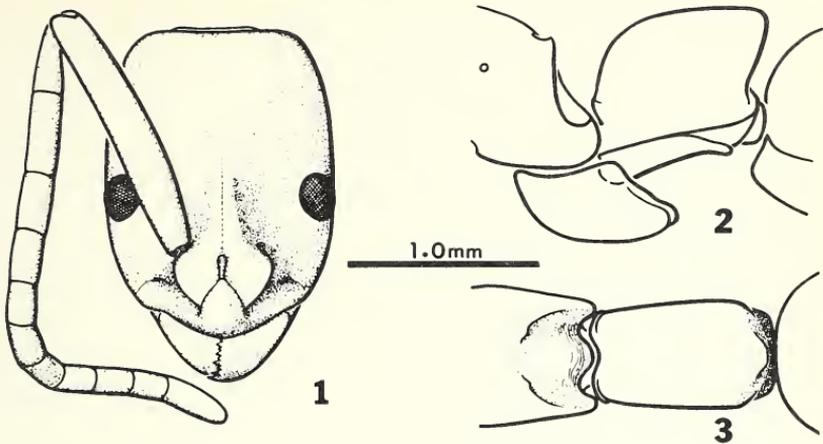
Holotype worker: TL 7.54, HL 1.68, HW (behind eyes) 1.21 (CI 72), greatest diameter of eye 0.31, W across frontal lobes 0.28, scape L 1.50, ML 0.25, WL 2.66, forefemur L 1.60, forefemur maximum W 0.42 (W/L 26%), petiolar node dorsal view L 0.88, W 0.60 mm.

Paratype workers: (10 from berlesate) All very close in size. Smallest and largest workers: HL 1.64, 1.72; HW 1.15, 1.23 (CI 70, 71.5); ML 0.23, 0.23; scape L 1.40, 1.47; greatest diameter of eye 3.0, 3.1; WL 2.58, 2.70 mm. At least one worker has 11, rather than 10 teeth on the mandible. Two ants from the same collection have 1-2 vestigial ocelli. Otherwise I detect no variation in sculpture, color or shape (aside from 1 callow worker).

Mandibles (fig. 1) subtriangular, outer border straight at mid-length, gently convex at each end; masticatory border with large apical tooth and 9 smaller teeth, larger and smaller teeth alternating, but the series as a whole decreasing in size toward the basal border. A fine sulcus runs over the dorsal mandibular surface from near

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Figs. 1-3. *Platythrea prizo* n. sp., worker. Fig. 1, head and right antenna in full-face dorsal view. Fig. 2, petiole and adjacent structures, side view. Fig. 3, same, dorsal view.

the articulation anteroventrad to the outer border. Palpal formula 4,4; all palpi short and slender, do not reach posteromedial rim of buccal cavity. Head (fig. 1) moderately long, sides gently convex, parallel. Posterior border of head weakly convex in full face dorsal view. The frontal lobes are approximated, their fused carinae trailing caudad as a prominent rounded ridge that blends into the curvature of the mid-vertex. Frontal triangle reduced to clearly defined narrow cuneiform depression surrounded by frontal lobes. Frontal sulcus, a fine impressed line anterior but effaced caudad, continues to within 0.30 mm of back of head. Middle of clypeus broadly swollen; free clypeal margin arcuate with a narrow apron. Posterior clypeal border separated from frontal lobes by distinct V-shaped sulcus. Eyes suboval, only slightly convex; on dorso-lateral surface of head slightly anterior to midlength (anterior edge of eye 0.30 mm from mandibular insertion). Eye covered with extremely fine short erect pubescence.

Antennae long and slender. In full face view scape extends beyond occiput by 0.30 mm, when held straight back. Length of first 3 funicular segments 0.34, 0.43, 0.30 mm. Segments 2-10 regularly decrease in length to 0.20 mm. Apical segment flattened, narrowly rounded, length 0.40 mm. Funicular segments vary little in width; all about 0.16 mm.

Pronotum seen from full dorsal view with anterior surface (above neck) and humeri evenly and broadly rounded; sides gradually become less convex and converge as they continue caudad; slightly concave where they overlap the mesopleura. Posterior edge of pronotum forming a broad U with gently divergent arms. Promesonotal suture impressed and probably flexible. Remainder of trunk seen from above with parallel sides, narrower than pronotum (maximum pronotal W 1.06 mm, maximum propodeal W 0.78 mm). Slight impressions in the sides are evident at the promesonotal suture, and somewhat more distinctly at the level of the metathoracic spiracles. Declivity of propodeum shallowly concave from above. In side view the dorsal profiles of mesonotum and propodeum are flat for the most part, but gently convex at each end and with broad feeble impressions fore and aft of the metaspiracle. Pronotal dorsum tilted ventrad from mesonotum; dorsal profile gently convex, meets nearly vertical anterior face in broadly rounded corner. Sides of pronotum are inclined dorsomesad and insensibly merge with dorsum, except near promesonotal suture where there is a distinct corner. At this juncture the ventral edge of the pronotum is strongly impressed mesad (around procoxal articulations) and the sides become inclined slightly dorsolaterad. The mesopleuron in side view is subtrapezoidal and clearly outlined by concave sutures (weaker along dorsal edge). Metapleuron indicated by vague sulcus running from dorsal edge of a deep pit behind metaspiracle to ventral edge of propodeal spiracle and dorsal edge of metapleural gland. Metapleural gland bulla not enlarged, meatus partially occluded by dense appressed hairs. Opening of propodeal spiracle circular. Dorsum of propodeum broadly curved into declivity, but the curve interrupted on each side by a short tooth (fig. 2). Lateral margins of declivity concave in side view, sharp only along dorsal half. From behind, the declivity is subtriangular, concave (fig. 3).

Legs long and slender. Forefemur only slightly incrassate (W/L 26%). Hind femur L 1.80 mm (W/L 20%). Hind tibia L 1.55 mm. Oblique conical setae on flexor surfaces of tarsi sparse and minute. Middle teeth of tarsal claws very small and difficult to see. Middle and hind tibiae with paired spurs, lateral spurs slightly shorter. All spurs pectinate. Flexor surface of proximal end of basitarsus of hind leg with weak depression opposite tibial spurs.

Petiolar node as in Figs. 2 and 3. Seen from the side, the anterior and posterior surfaces are subparallel, anterior surface shorter, curving broadly into dorsal surface. Dorsal profile gently convex; posterodorsal corner distinct, narrowly rounded, unarmed. Posterior outline in perfect profile gently convex, but face slightly concave. In dorsal view, node distinctly longer than wide (maximum W/maximum L 0.64). Base of node at anterior end square and narrower (0.50 mm); sides weakly convex and diverging slightly to 64% of length, then curving mesad. Viewed from the front, sides of node convex, widest at midheight, smoothly joining convex dorsal surface except near posterior edge, where juncture is slightly angular.

Dorsum of postpetiole wider than long (L 0.90 mm, W 1.12 mm), evenly rounded anteriorly in both directions (figs. 2 and 3). Acrotergite of second gastric segment with narrowly triangular stridulatory file. Sternum of postpetiole truncate in front, underhanging insertion. Tergum of second gastric segment longer than broad (L from apex of file 1.30 mm, W 1.15 mm), and much longer than sternum (L excluding acrosternite 0.40 mm). Gaster bent strongly ventrad at this segment. Gaster markedly constricted in both views between postpetiole and second segment. Pygidium very convex dorsad and caudad, apex of ventral edge subacute. Sting well developed.

The whole body has the usual pruinosity, and dense, finely reticulate-punctate ground sculpture. Superimposed larger punctures are scattered over most of the head, trunk, petiole, and first 2 gastric segments; they are coarser on the petiole, anterior ends of meso- and metapleura, and posterodorsal corners of propodeum. These superimposed punctures are smaller and more numerous than in most *Platythrea* species. Fine transverse rugules present on lower half of declivity of propodeum. Erect hairs on masticatory borders of mandibles, anterior edge of clypeus, posterior surface of first coxae, pygidium, and hypopygium. Very short, sparse, fine oblique hairs seen on gaster in some lightings.

Head, trunk, petiole, and gaster dully shining, uniformly dark reddish brown; appearing black to naked eye. Legs, antennae and mandibles lighter, castaneous brown. Appendages get lighter and yellower more distad so that terminal tarsomeres and antennomeres are bright yellow gold. Frontal lobes rimmed with black, and frontal depression darker than surrounding frontal lobes.

Queen and male unknown.

Holotype and paratypes from La Selva Field Station (Heredia Province) Sarapiquí District, Costa Rica, 10°26' N - 83°59' W, on the Rio Puerto Viejo. Collected by J. Wagner and J. Kethley. Field Museum collection #73-292, taken from 100 cc of berlesate of light brown duff from root mat around grass-like plant (8 workers); #73-299, from 100 cc of berlesate of root duff from epiphytic garden (2 workers); #73-295, from berlesate of buttress duff with soil, El Sura trail (1 worker). Holotype and 4 paratypes in the Field Museum, Chicago; remaining paratypes in Museum of Comparative Zoology, Cambridge, Massachusetts; British Museum (Natural History), London; and W. W. Kempf collection, Brasilia.

In comparison with other neotropical species, *P. prizo* is more slender, especially in its appendages (pronotal W/hind femur L of smallest worker 0.60, or largest worker 0.59), and it is the only known New World species with toothed mandibles. It bears some affinity to *P. zodion* in shape of the petiolar node and trunk, but differs in much larger body size and in conformation of the head (Brown 1975, figs. 34-36).

P. prizo appears to belong to the *clypeata* group (see Brown, 1975:50-52; Forel, 1911:378-379; and Wheeler, 1922:59-60), which until now included only Old World species. It has a similar frontal lobe structure, mandible shape, dentition, trunk shape, and the same palpal formula as this group. The petiolar node is most similar to that of *P. clypeata* (see Brown, figs. 23 and 24), but the posterior face in *P. prizo* is not so strongly concave, nor is the posterodorsal edge emarginate; the subpetiolar process is more like that of *P. gracillima* (see Brown, fig. 29). *P. clypeata* is also smaller (WL 2.30 mm), with an unarmed propodeum. *P. prizo* differs even more from *P. gracillima* and *P. bidentata*.

Prizo is a form of the Greek verb meaning "to saw". It is used here arbitrarily as a noun in apposition, in reference to the serrate mandibles that clearly separate this species from other New World *Platythyrea*.

Note on *Platythyrea strenua*: This species was described by Wheeler and Mann (1914, Bull. Am. Mus. Nat. Hist. 33: 6-7, fig.1) from material taken in a rotten log at Diquini, Haiti. No further records are known until two collections were made on the Sierra de Baoruco, Prov. Pedernales, Republica Dominicana during

February 1975 by W. L. and D. E. Brown. The collections were both made from small colonies found under limestone slabs in pine forest (*Pinus occidentalis*) with some form of everlasting prominent in the understory (*Gnaphalium* or a related species in Compositae: Inuleae) along the road from Cabo Rojo to the Alcoa bauxite mines. The first collection was made at Km 28, elevation about 1200 m, and the second at Km 33 (1500 m). Although special attention was paid to the rotten wood microhabitat in 3 weeks of intensive collecting all over the Dominican Republic, no *P. strenua* were found anywhere else in the country.

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STRUCTURE AND RELATIONSHIPS OF THE UPPER CARBONIFEROUS INSECT, *EUCAENUS OVALIS* (PROTORTHOPTERA: EUCAENIDAE)

BY FRANK M. CARPENTER¹ AND EUGENE S. RICHARDSON, JR.²

In 1885 S. H. Scudder described as *Eucaenus ovalis* a Pennsylvanian (Upper Carboniferous) insect preserved in a concretion from the Francis Creek Shale in northeastern Illinois. Subsequently, a few additional specimens of the same insect were described by Melander (1903) and Handlirsch (1906a, 1911) from the same beds. Unfortunately, none of these specimens were sufficiently well preserved to give a satisfactory concept of the insect. In recent years, however, and for the most part through the activities of local amateur collectors, a surprisingly large number of specimens of *ovalis*, many of them well preserved, have been found in spoil heaps of strip mines dug to coal just beneath the shale (see Richardson and Johnson, 1971). As a result, *Eucaenus ovalis* is now one of the two or three best known Upper Carboniferous insects from anywhere in the world. The present account is based on a study of all the specimens of the species at present available.³

For the opportunity of examining new material, previously unstudied, we are grateful to the following individuals, who have collected the specimens and loaned them to us: Mr. Frank A. Greene, Coal City, Illinois; the late Mr. Levi Sherman, formerly of Des Plaines, Illinois; Mr. and Mrs. Francis Wolff, Port Charlotte, Florida; Mr. Lanny Morreau, Normal, Illinois; and

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the late Jerry Herdina (formerly of Berwyn, Illinois), whose collection has subsequently been donated to the Field Museum of Natural History.

Examination of previously studied specimens, including types, has been made possible through the courtesy of the curatorial staff of the following institutions: Illinois State Museum, Springfield, Illinois; National Museum of Natural History, Smithsonian Institution, Washington; and the Peabody Museum, Yale University. The extensive series of unstudied specimens and of types in the Field Museum of Natural History has been essential for our investigation.

Order Protorthoptera Handlirsch, 1906⁴

Family Eucaenidae Handlirsch

Eucaenidae Handlirsch, 1906a, p. 709; 1906b, p. 164; 1919, p. 52; 1920, p. 161.
Teneopteridae Richardson, 1956, p. 56

This family embraces a single genus, which in turn is known from but a single species. We suggest that the following characters are significant on the family level. Fore wing coriaceous; costal area wide; SC, R1 and main stem of RS close together, parallel; all major veins arising near base; RS pectinate; CUP strongly concave, aligned in part with the anal furrow; anal area small. Hind wing membranous. Head slender, antennae long, setaceous, most of the segments alike; mandibles dentate; maxillary palpi very long; eyes small but prominent; prothorax long and broad, covered posteriorly with heavily sclerotized pronotum; legs similar; femora stout, tibiae slender, tarsi with 5 tarsomeres; abdomen no longer than thorax plus head; 11th segment with very short cerci; some or all abdominal segments with posteriorly directed lateral lobes; females with short ovipositor; femora, tibiae, and thoracic tergites prominently sculptured.

Handlirsch's several definitions of this family emphasized what he took to be blattoid characters of its single genus, *Eucaenus*. Richardson's definition of the family Teneopteridae was based

⁴We are including in this order the species variously assigned by some students of fossil insects to the orders Paraplecoptera and Protoblattodea, as well as those in the order Protorthoptera (s.s.). The reasons for this treatment have been summarized by Carpenter (1966, pp. 51-55).

on what we now recognize to be two abnormally preserved individuals of the same genus. Our reasons for placing these families in synonymy and our understanding of the relationships of the Eucaenidae will be brought out in the following discussion. The family is known at present only from the ironstone concretions of the Francis Creek Shale of Grundy, Will, and Kankakee Counties, Illinois.

Genus *Eucaenus* Scudder

Eucaenus Scudder, 1885, p. 325; Handlirsch, 1906a, p. 710; 1906b, p. 165; 1911, p. 359.

Teneopteron Carpenter, 1943, p. 359; Richardson, 1956, p. 46.

Since only one genus is known in the family and only one species in the genus, generic characteristics can be stated only in general terms, especially in view of the variation in venation with in some species of Protorthoptera (see Carpenter, 1966, p. 73). In all probability the extent of branching of RS and M will provide the best source of generic differences in the wings and the forms of the prothorax and legs for the body differences.

Type-species: *Eucaenus ovalis* Scudder.

Eucaenus ovalis Scudder

Eucaenus ovalis Scudder, 1885, p. 325, pl. 29, fig. 4; Handlirsch, 1906a, p. 710; 1906b, p. 165, pl. 16, figs. 17, 18; 1911, p. 359, figs. 36-41; 1920, p. 162, fig. 112.

Eucaenus mazonus Melander, 1903, p. 188-190, pl. 6, fig. 3, pl. 7, fig. 10; Handlirsch, 1906a, p. 710; 1906b, p. 165, pl. 16, fig. 19; *not* 1911, p. 32, fig. 32.

Eucaenus attenuatus Melander, 1903, p. 190, pl. 6, fig. 4, pl. 7, fig. 11; Handlirsch, 1906a, p. 710; 1906b, p. 165, pl. 16, figs. 20, 21.

Eucaenus minor Handlirsch, 1911, p. 361-362, figs. 40, 41.

Teneopteron mirabile Carpenter, 1943, p. 17-20, fig. 5, pl. 5, fig. 4; Richardson, 1956, p. 45-52, figs. 26-30.

Fore wing (figure 1): length, 19-24 mm.; width, 7-8 mm.; oval, with broadly rounded apex, rounded front margin and very slightly rounded hind margin; wing membrane coriaceous, apparently with a faint reticulation of ridges. Costal area broad, broadest at about mid-wing, somewhat narrowed basally; costal veinlets oblique, numerous, probably more than 30; SC nearly straight, slightly arched away from the costa, terminating on costa at about 4/5 of wing length; RI parallel and close to SC, its termination not definitely known, but a few distal branches

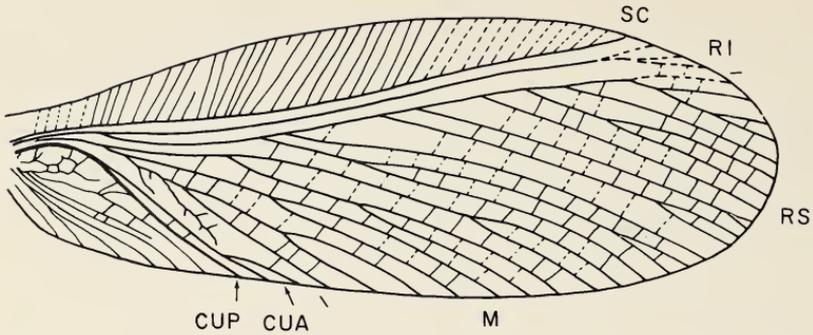


Figure 1. *Eucaenus ovalis*. Drawing of fore wing, based mainly on the Greene specimen, G75, and the Sherman specimen, W57, with details from other specimens mentioned in the text. The veins indicated by broken lines are not clearly discernible in any specimen. SC, subcosta (-); RI, first radius (+); RS, radial sector (-); M, media (\pm); CUA, anterior cubitus (+); CUP, posterior cubitus (-).

are indicated in some specimens; RS with 6-8 (possibly more) pectinately arranged branches, arising at irregular intervals, the first one at about $1/3$ of wing length, some of them bifurcating once or twice; M well developed, not so extensive as RS, forking at about the level of origin of RS into two main branches, each with 4 or 5 terminal branches arising by secondary and usually tertiary dichotomous branching; CU a strong vein basally, dividing below the origin of RS into CUA and CUP, the former weakly convex, with little or no branching, the latter strongly concave; anal veins weak and irregular. Cross veins numerous but weak, not aligned across veins.

Hind wing: only the basal part along the front margin and the apical area are known; costal area narrow, distal part of RS dichotomously branched.

Body structure (figure 2): total body length ranges from 29-32 mm. Head about 3.8 mm long, maximum width (across eyes) 2.5 mm; mandibles dentate; antennae about 10 mm long, the first 3 segments a little broader than the others, which are about 0.2 mm wide and a little more than 0.5 mm long; total number of segments about 20. Maxillary palpi 7 mm long, apparently consisting of 4 segments; the basal segment very short (about .7 mm), the 2nd and 3rd segments about 2.5 mm long, and the

4th, 1.3 mm long and much thinner than the others.⁵ Head narrowed posteriorly; between the head and the pronotal shield is a demarcated region (1.8 mm wide and 1.5 mm long), which, because of its heavy sclerotization, we consider to be part of the prothorax, rather than the cervix; pronotal shield elongate-oval, about 5.5 mm long and 3.8 mm wide, with the sides only slightly curved and with the maximum width at the posterior half; the pronotal shield is very heavily sclerotized. Mesothorax about 5.5 mm wide and 4 mm long; metathorax about 5.4 mm wide and 3 mm long. All legs are short and similar in form. The fore femur is 4 mm long and 2 mm wide, with a curved front margin; the tibia is 3.8 mm long, and the tarsus, 1.6 mm long; four tarsomeres are distinct and there is a suggestion of a fifth. The meso- and metathoracic legs are similar to those of the prothorax, except for slight differences in the lengths of the femora.

The abdomen averages about 14 mm long, the precise length depending on the amount of contraction of the segments: the width of the first few segments is 5.4 mm and that of most of the others, 4.5 mm. The cerci are very small, only about 1 mm long, but they appear to consist of 3 or possibly 4 segments. The female has a short, external ovipositor, 3.4 mm long, and definitely not extending beyond the end of the abdomen.

The integument of this insect is strongly sclerotized and has a distinctly rugose sculpturing, similar to that of many existing Orthoptera; the sculpturing covers the femora and tibiae, and is especially well developed on the thorax.

Type: no. 38142, National Museum of Natural History, Washington. Scudder saw only the obverse part of this specimen (marked "a"); the reverse part (marked "b"), now in the National Museum, is much better than the one Scudder studied, and we have been able to expose the head and prothorax, which were unknown to Scudder. The total length of the body is 30 mm.

The type of *E. mazonus* Melander, no. U.C. 9242 in the Walker Museum, University of Chicago [now in Field Museum] shows nothing to distinguish it from *ovalis*. Melander stated that the

⁵In specimen no. PE 20790 the 4th segment of the palpus shows faint traces of division into 6 or 8 segments. However, since such palpal segmentation is unknown in the insects, we believe this apparent segmentation in the fossil is associated with the process of preservation.

diagnostic feature was the shape of the "scapular" vein (R1), which formed an opposing curve to the costa. He was led to conclude from Scudder's drawing that R1 in *ovalis* was parallel to the costa. However, Scudder's account in this respect was incorrect and the reverse of the *ovalis* type shows clearly the opposing curvature of the costa and of R1. The total length of the body of the type of *mazonus* is 29 mm. In this connection, we should note that the Yale University specimen that Handlirsch (1911) identified and figured as *mazonus* (YPM 51) is not even a eucaenid. The specimen consists of parts of the hind wings and body, the front wings being completely absent. The fore femur, correctly drawn by Handlirsch, is long and slender, unlike that of *ovalis*. The venation of the hind wing of *ovalis*, as previously noted, is very little known, but what is known is very different from that of the Yale specimen identified by Handlirsch as *mazonus*. This represents a small species, incidentally, with a body-length of only 19 mm.

E. attenuatus Melander (1903), in our opinion, is also *ovalis*. The type specimen, no. 4749 in the Eagan collection of the Chicago Academy of Sciences, has not been found there at this time. However, Melander's description fits *ovalis* perfectly. He considered the specimen distinct from *ovalis* because his specimen did not possess the "median keel" on the last abdominal segments, as described by Scudder in his account of the type of *ovalis*. However, the "keel" is the ovipositor, now known to be characteristic of *ovalis* females. The type of *attenuatus* was stated by Melander to have a body length of 28 mm. Handlirsch (1906a) identified a specimen in the National Museum of Natural History (no. 38828) as *attenuatus*. He obviously never saw the type of *attenuatus*; his specimen is clearly *ovalis*, though it appears somewhat smaller than usual because it lacks the head and part of the prothorax. A second specimen (no. 33827) which Handlirsch (1906a) also identified as *attenuatus* is not even a eucaenid. The venation is not preserved, but there is a long, exerted ovipositor, extending far beyond the end of the abdomen. As noted above, the ovipositor in *Eucaenus* is very short and does not extend beyond the tip of the abdomen.

Eucaenus minor Handlirsch (1911) was based on a fragmentary specimen (YPM 47) in the Yale University Collection. Handlirsch considered it a separate species or "at least a variety" of

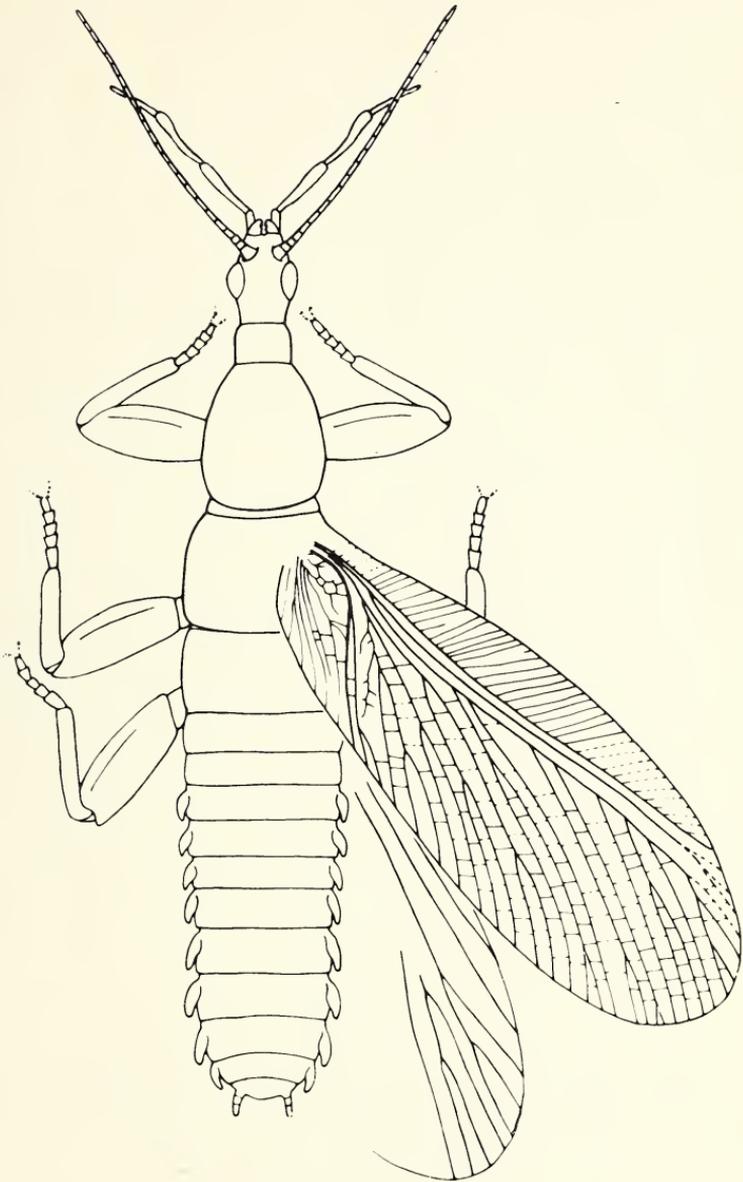


Figure 2. *Eucaenus ovalis*. Composite drawing based on specimens mentioned in the text. All structures shown are present in at least one specimen, except for those represented by broken lines. See figures 3 and 5.

ovalis. Only the basal parts of the wings are preserved and their venation, so far as discernible, is like that of *ovalis*; the wing length is 22 mm.

Teneopteron mirabile Carpenter (1943) is clearly a synonym of *ovalis*. In the type specimen (Illinois State Museum, no. 14887) the fore wings were outstretched, but only the costal area and R1 were preserved, so that the wings appeared as elongate elytra. A somewhat similar specimen, now in the Field Museum (PE 967), showing a little more wing surface below R1 than the type but still looking elytriphorous, was described by Richardson in 1956. Enough of the wings and body structure is preserved in these two specimens to show that they are *ovalis*.

As a final comment on the systematics of the species that have been described in *Eucaenus*, we should point out that two additional insects placed by Handlirsch in that genus do not in fact belong to the Eucaenidae: *E. rotundatus* and *pusillus*. The type of the former, no. 38153, National Museum of Natural History, could not be found there. However, Handlirsch's description (1906a), even as revised by him in 1911, states that RS had only three branches and that CUA was very extensively branched. This is precisely the opposite of the condition in the Eucaenidae. *E. pusillus* (1911), based on specimen YPM 52 in the Yale collection, is a small insect, about 15 mm long. We are unable to perceive the venational details shown in the left fore wing of Handlirsch's figure (1911, p. 43) but we do note that the costal area is very narrow; in addition, the fore femur is long and slender, not at all like that of the Eucaenidae. These two species are clearly Protorthoptera but their family positions are certainly obscure and for the present they should be listed as in the Protorthoptera, family and genus indet.

Specimens of *Eucaenus ovalis* studied

We have been able to examine twenty-one specimens of *ovalis* in the course of this investigation. For convenience of reference, we include here an annotated list of these:⁶

⁶The following are the localities to which reference is made in the list of specimens. Mazon Creek: the bed of the stream, 4 miles west and a mile north of Coal City. Coal City: strip mines 1 to 2 miles north of Coal City. Pit Eleven: strip mine in Will and Kankakee Counties, 3 to 5 miles south of Braidwood.

1. National Museum, No. 38142. Mazon Creek. Holotype of *ovalis*. Female; general form of entire insect but with few details preserved; prothorax and head have now been exposed; ovipositor distinct. Fore wing length 22 mm; body length, 30 mm.

2. National Museum, No. 38810. Mazon Creek. Mentioned by Handlirsch (1906a) but not described or figured. Female; shows shape of fore wing clearly, though venation is indistinct; fore and middle femora, cerci, ovipositor and distal part of hind wing well preserved.

3. National Museum, No. 38820. Mazon Creek. Mentioned by Handlirsch (1906a) but not figured or described. Male; entire insect shown but poorly preserved; head and prothorax now exposed; prothoracic shield very clear.

4. National Museum, No. 38828. Mazon Creek. Identified by Handlirsch (1906a) as *attenuatus* Melander. Male; poorly preserved but with enough wing and body structures for identification.

5. Peabody Museum, No. YPM 47. Mazon Creek. Holotype of *E. minor* Handlirsch; very poor, fragmented specimen but determination as *ovalis* virtually certain.

6. Peabody Museum, No. YPM 48. Mazon Creek. Mentioned by Handlirsch (1911). Female; very poor preservation; costal veinlets fewer than usual.

7. Peabody Museum, No. YPM 49. Mazon Creek. Mentioned by Handlirsch (1911). Very poor preservation of entire specimen, with only vague outlines of body and wings.

8. Peabody museum, No. YPM 50. Mazon Creek. Very poor specimen showing entire insect; hind femora and cerci distinct.

9. Illinois State Museum, No. 14887. Coal City. Holotype of *Teneopteron mirabile* Carpenter. Male; poorly preserved and fragmentary but shows abdomen well, especially the lateral lobes on some of the posterior segments.

10. Field Museum, No. PE 976. Coal City. Described by Richardson as second specimen of *T. mirabile*. Female; poor preservation and fragmentary, but shows hind femora, tip of hind wing, ovipositor and general abdominal segmentation.

11. Frank Greene collection, No. G75. Pit Eleven. Excellent preservation of entire insect except end of abdomen; wings and body particularly good, including head, with antennae, eyes, palpi; prothorax, femora and tibiae clearly preserved.



Figure 3. *Eucaenus ovalis*. Photograph of the Greene specimen, G75 (reverse), under oblique lighting. Note distinct region between head and pronotal shield. Length of fore wing, 20 mm. Compare with figure 4.



Figure 4. *Eucaenus ovalis*. Photograph of anterior part of the Greene specimen, G75, under balanced light, without shadows, showing details of head and prothorax. Lettering: e, compound eye; a, antenna; p, palpus; s, pronotal shield. Length of head, 3.8 mm.

12. Levi Sherman collection, No. W57. Probably Pit Eleven. Female; exceptional preservation of many details; fore wing venation faint, but basal part of wing very clear; also cross veins in distal part of fore wing, base of antennae, mandibles, all femora and ovipositor. Costal area with relatively few veinlets.

13. Wolff collection, No. 243. Preservation poor; abdomen missing but some good details of thorax, especially prothorax; head in hypognathous position.

14. Wolff collection, No. 653. Female; very incomplete specimen but excellent for anal area of fore wing; hind femora and ovipositor good.

15. Morreau specimen. Pit Eleven. Very poor preservation but determination as *ovalis* virtually certain.

16. University of Chicago, No. U.C. 9242 (at Field Museum). Mazon Creek. Holotype of *E. mazonus* Melander. Male; preservation poor, but shows femora, tibiae and tarsi.

17. Field Museum, No. PE 20790. Pit Eleven. Entire insect; abdomen not preserved, wings folded back and venation jumbled; head and thorax excellent: head, antennae, palpi, prothorax and legs. Cross veins clear in several areas of fore wings.

18. Field Museum, No. PE 31959 (Herdina 417). Pit Eleven. Male; preservation fair of head, prothorax and wings.

19. Field Museum, No. PE 32038 (Herdina 476). Coal City. Very poor preservation but enough to permit identification.

20. Field Museum, No. PE 32065 (Herdina 212). Pit Eleven. Male; preservation only fair, but prothorax very good.

21. Field Museum, No. PE 32067 (Herdina 213). Pit Eleven. Male; entire insect faintly and poorly preserved; no details of body.

Since no one specimen gives a satisfactory concept of this insect, a composite drawing is included in figure 2. The general habitus of the insect, as drawn, is based on the Frank Greene specimen, (G75; see photographs, figures 3 and 4), and details have been added from other fossils, as follows, the numbers referring to the specimens in the foregoing list: head (including eyes, maxillary palpi, antennae, mandibles), 11, 12, 17; prothorax, 3, 11, 12, 13, 17; rest of thorax, 11, 12, 17; fore wings, 2, 11, 12, 14; hind wing (fragments only), 2, 10; legs, 2, 8, 10, 11, 12, 14, 16, 17; abdomen, 2, 9, 10, 11, 12; cerci, 2, 8; ovipositor, 2, 10, 12, 14. All structures shown in the figure are preserved in one or more

of the fossils studied, with the exception of the few veins shown in broken lines.

Discussion of the Structure of *Eucaenus ovalis*

Head. The head of *ovalis* was presumably opisthognathous and it is so preserved in several specimens; however, it is also shown in a prognathous position in a few fossils, notably Greene G75. There seems to be nothing unusual about the antennae or compound eyes, but the long palpi (presumed to be the maxillary pair) are remarkable. They are exceptionally clear in two specimens (Greene G75 and PE 20790). Such long palpi are very unusual among existing Pterygota. In the orthopteroids, comparable palpi occur in a few species of Gryllacridoidea, especially of the family Stenopalmatidae; so far as known these are wingless and live in rotting wood or are subterranean.

Thorax. The prothorax is the most conspicuous and peculiar part of the thorax. Between the head and the pronotal shield there appears to be a separate, strongly sclerotized segment, which we have interpreted simply as the anterior part of the prothorax. This could conceivably be a sclerotized cervical region, although we are not aware of any such structure in existing insects. It is worthy of note in this connection that a considerable number of Upper Carboniferous Protorthoptera, not especially close to the Eucaenidae, have similar sclerotized regions, although they have not been discussed in the literature.

The pronotal shield shows considerable variation in shape among the specimens studied but a significant part of this diversity is apparently due to the nature of the preservation of the individual specimens. In some instances, the pronotum is obviously different in shape in the counterparts of the same fossil. Handlirsch stated (1911) that the pronotum of the male was comparatively smaller than that of the female, but we have found no reliable evidence for that conclusion.

Wings. The fore wings are distinctly oval in shape; combined with the form of the costal area, this is one of the major characteristics of the insect. The number of costal veinlets is quite variable, as noted above; the costal area of the wings in figures 2 and 3 is based on the Greene specimen G75, which has about the maximum number. The veinlets presumably continue for the full length of the costal area, though the distal part of the area is not satis-

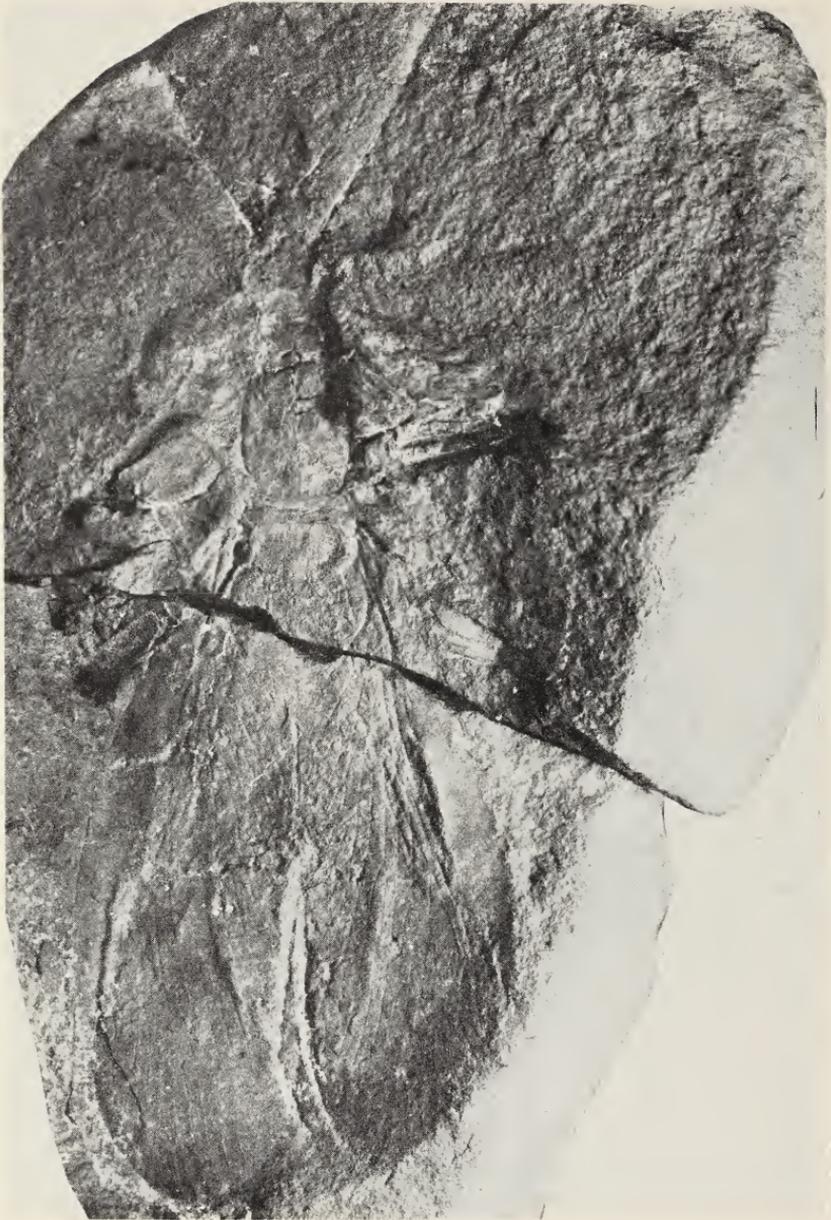


Figure 5. *Eucaenus ovalis*. Photograph of Field Museum specimen, PE 20790. Length of fore wing, 23 mm. Compare figure 6.



Figure 6. *Eucaenus ovalis*. Photograph of anterior part of Field Museum specimen, PE 20790, showing details of head and prothorax. Lettering as in figure 4.

factorily preserved in any specimen; ordinarily that part of the wing is preserved near the edge of the ironstone nodule, where some weathering and discoloration have taken place. Handlirsch's interpretation of the venation of the fore wing of *ovalis*, as represented in his "reconstruction" (1911, p. 360) is obviously incorrect in many respects. RS and M are much more extensively branched than he represented, and CUA has only a small distal fork, instead of being extensively branched as he has shown. Also, the anal area is somewhat longer than he assumed. Handlirsch's second "reconstruction" (1920, p. 162) is even worse; the branches of RS are represented as arising dichotomously, not pectinately as he originally (and correctly) showed. However, it should be borne in mind that since none of the specimens that Handlirsch studied showed the fore wing venation clearly enough for an accurate drawing to be made, his figure was mostly conjectural. The cross veins in the wing are very faint at best and it is not surprising that Handlirsch made no reference to them in his descriptions; they are visible, however, in several areas of the wings in two specimens (Sherman W57 and Wolff 653), and in all probability they were quite uniformly distributed over the wing surface in the living insect.

The hind wing of *ovalis* is unknown except for a few terminal branches of RS near the wing apex. Handlirsch's reconstruction

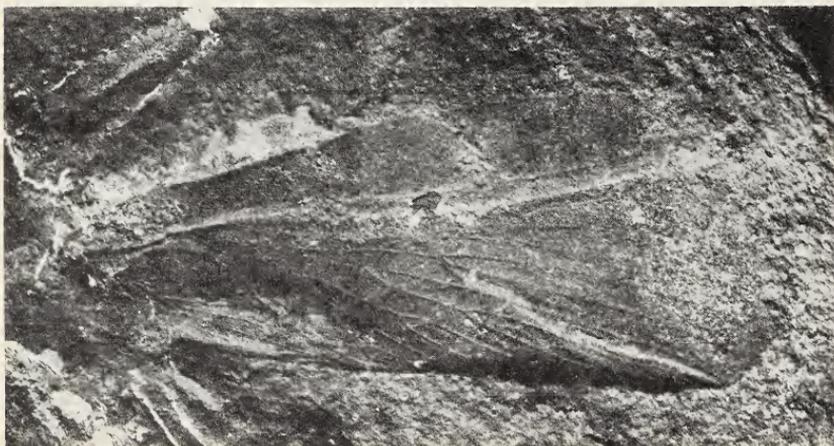


Figure 7. *Eucaenus ovalis*. Photograph of the Levi Sherman specimen, W57, fore wing only, showing anal area and branching of media and cubitus. length of wing as shown, 15 mm.

of the hind wing (1911, 1920) is either entirely imaginary or based in part on his supposed specimen of *mazonus* (YPM 51), which, as noted above, is not even a eucaenid.

Abdomen. This is of moderate size and not apparently flattened. The cerci are surprisingly short for a protorthopteron, in most of which they are very prominent structures. The small lobes on the sides of the more posterior segments (and perhaps all segments) resemble comparable structures in other Upper Carboniferous insects; they were noted by Handlirsch (1911, p. 361) in one of the Yale University specimens and are especially clear on most segments of the specimen in the Illinois State Museum (type of *T. mirabile*). The ovipositor is short, ordinarily not quite reaching the end of the abdomen; this is also unusual for a protorthopteron.

Affinities of the Eucaenidae

The relationships of the Eucaenidae are difficult to determine, mainly because we know so little about other Protorthoptera with which they might be compared. About 80% of all described Protorthoptera from the Upper Carboniferous are based on fore wings alone or even on fragments of the wings. Fortunately, the Mazon Creek nodules generally preserve insects with some body parts included, although overlapping of the fore and hind wings usually obscures the abdomen to some extent, as well as the details of the venation. A general survey of the Protorthoptera known from the nodules shows that a substantial number of species are characterized by a prolongation or some other elaboration of the prothorax—certainly a much higher percentage of the known species than occurs in other deposits. However, the nature of the wing venation indicates that at least some of these prothoracic modifications have developed independently within isolated lines of evolution.

There are two families of Protorthoptera from the Francis Creek nodules that appear to show similarities to the Eucaenidae in both prothoracic structure and venation: Cheliphlebiidae and Gerapompidae. Handlirsch consistently placed them close to his Eucaenidae. From both of these families the Eucaenidae differ in having the costal area much broader and in having SC, R1 and the stem of RS close together and parallel. Virtually nothing is



Figure 8. *Eucaenus ovalis*. Photograph of abdomen of specimen no. 14887 in Illinois State Museum, Springfield (type of *T. mirabile*). Arrows point to some of the lateral lobes. Length of abdomen as shown, 9 mm.

known about the body structure of these two families except for the enlargement of the prothorax. There are no other Upper Carboniferous families that seem to be close to the Eucaenidae.

Scudder (1885) placed *Eucaenus* in the neuropteroid section of the Palaeodictyoptera, an order to which he arbitrarily assigned all Paleozoic insects. Handlirsch (1906a, 1906b) recognized its orthopteroid affinities and included it in his new order Protoblattoidea, which he considered an annectant group between the Palaeodictyoptera and the true Blattaria. Since our present knowl-

edge of the Palaeodictyoptera eliminates them from consideration as ancestral to any existing order, especially the orthopteroid groups, assignment of *Eucaenus* to the Protorthoptera seems most reasonable. Attempts (e.g., Sharov, 1968) to divide the Protorthoptera into orders or suborders (as the Paraplecoptera, Protoblattodea, and Protorthoptera, leading to the Plecoptera, Blattaria, and Orthoptera, respectively), seem to us to be very premature. The assumption that the orthopteroids of the Upper Carboniferous had already evolved into lines leading to these three orders is most improbable and certainly unjustified on the basis of available evidence; it is much more likely that the Paleozoic orthopteroids, especially those of the Upper Carboniferous, were evolving in many directions. Unfortunately, since most Paleozoic orthopteroids are known to us now chiefly by wings or wing-fragments, we are unable to discern what those directions were. When we know as much about the structure of most other Paleozoic families of the orthopteroids as we do of the Eucanidae, we will be much better qualified to unravel their evolutionary lines.

Eucaenus ovalis presents a good example of the necessity for a knowledge of body structures in evaluating the affinities of Paleozoic insects. On the basis of its wings, this insect was considered by Scudder, Handlirsch and others to be a primitive roach. We now know that it was a specialized insect, with totally unexpected adaptive modifications and with body structures that remove it from any position leading to the roaches. It provides another illustration (Carpenter, 1971) of the diversity achieved by the insects of the Upper Carboniferous period.

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PREDATION AS A SELECTION FACTOR IN THE
MATING STRATEGY OF THE JUMPING SPIDER
PHIDIPPUS JOHNSONI
(SALTICIDAE, ARANEAE)

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INTRODUCTION

Predation risks are often considered to be a major selection pressure related to the courtship and mating behavior of animals (Emlen, 1973; Morris, 1956; Richards, 1927; Strong, 1973). The importance of this factor in the mating strategy of a salticid spider, *Phidippus johnsoni* (Peckham and Peckham), will be considered here. In this species, each individual male has at his disposal three alternative mating tactics (Jackson, 1977). The one used depends on the female's maturity and whether she is inside or outside her nest. Nests are silk structures that the spider constructs under rocks and in other rather dimly lighted locations. These are occupied during inclement weather, at night, during molting and oviposition, and at other times. When the male encounters an adult female outside her nest, he performs a form of visual courtship (type 1), consisting of various postures and movements performed in front of the facing female. A form of non-visual courtship (type 2) is employed when the female is encountered inside her nest, consisting of various forms of shaking and plucking on the silk of the nest. If the female is a subadult, the male may construct a second chamber on her nest and cohabit until she matures. Observations will be presented, implicating certain spiders of the family Gnaphosidae as predators of *P. johnsoni*. These incidences of predation occur while the salticids are at their nests and during courtship.

P. johnsoni is a common, euryecious salticid species in western North America. Often other organisms are found associated with nests of this species, both ones that are occupied by *P. john-*

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soni at the time and ones that are not. Various gnaphosid species are among the most frequent nest associates. Occasionally dead *P. johnsoni* are found inside their nests. On two occasions, both in the Wind River Range of the Rocky Mountains, a gnaphosid, *Drassodes neglectus* (Keys), was found inside a nest with a dead *P. johnsoni* female. In each case, the salticid was dry, had ruptures in the cuticle that resembled fang wounds, and had the appearance of having been consumed by another spider. In one case, the nest contained a *P. johnsoni* egg case. The silk around the eggs had been pulled away, but the eggs had not been eaten. *P. johnsoni* tend to be 10 to 12 mm in length, and the gnaphosids were of comparable size. These observations suggested that large gnaphosids prey upon *P. johnsoni* in their nests and perhaps consume the eggs as well. Further observations were carried out in the laboratory, using another gnaphosid species, *Herpyllus hesperolus* (Chamberlin). This species was a common nest associate of *P. johnsoni* in the Coastal Range of California, which was more accessible from my laboratory in Berkeley.

METHODS

Three sets of observations were carried out: *H. hesperolus* encountering *P. johnsoni* inside their nests, *P. johnsoni* males encountering *H. hesperolus* occupying the nests of *P. johnsoni* females, and *P. johnsoni* males encountering empty nests of both *P. johnsoni* females and *H. hesperolus*. The latter were included in order to determine whether *P. johnsoni* males can discriminate between the two types of nests.

Both the salticids and the gnaphosids were collected from habitats near the San Francisco Bay in California. They were maintained individually in 10 cm long plastic cages, built according to the design described by Jackson (1974), that provided a continual supply of house flies (*Musca domestica*) and moisture. Both mature and immature gnaphosids were used. Although *P. johnsoni* almost always constructed nests during the first day of occupancy of their cage, the gnaphosids built much less frequently, primarily just before molting. Each spider was used in only one observation, except for the paired observations on each male in the nest discrimination experiment; and each time the spider (and nest) used was chosen randomly, using a random

numbers table. All observations were made between one and four hours after the lights came on in the laboratory.

INTERACTIONS BETWEEN *HERPYLLUS HESPEROLUS* AND
PHIDIPPUS JOHNSONI FEMALES INSIDE THEIR NESTS

After oviposition, *P. johnsoni* females tend to remain in their nests with their eggs; and each *P. johnsoni* in this set of observations had eggs in her nest. Observation began when a *H. hesperolus* was taken from its cage and introduced through a hole in the cage of the *P. johnsoni*. Once the *H. hesperolus* touched the nest, observation continued for 15 min.

During one of the five observations, the *P. johnsoni* slowly departed her nest and approached the gnaphosid that was walking past the nest, approximately 2 cm away. When 1 cm from the *H. hesperolus*, the *P. johnsoni* leaped on the gnaphosid and subsequently consumed it. The *H. hesperolus* was 8 mm, and the *P. johnsoni* was 11 mm. The other four gnaphosids had body lengths greater than that of the salticids, approximately 15 mm compared to 10 to 11 mm in each case. In each of these observations, the *H. hesperolus* walked onto the nest, and the *P. johnsoni* responded with various behavioral elements that have been previously described in detail for interactions between conspecific males and females at nests (Jackson, 1976). These will be briefly described again here.

Pull on Nest. With the tarsi of her first pair of legs in contact with the inner dorsal surface of the nest the female moves her legs ventrally, pulling the dorsal layer of silk until it contacts the ventral layer.

Bump. The female rapidly extends her legs, causing her cephalothorax to hit the inner dorsal nest surface.

Stab. With her tarsi oriented toward the silk, the female rapidly moves her first pair of legs ventrally. As her tarsi hit the silk, pin-point bulges are made temporarily in the silk.

Strike. The female's elevated first pair of legs are rapidly moved forward and downward, such that the tarsi contact the substrate or the other spider. This behavior was performed with the *P. johnsoni* standing in the nest door, facing outward. Doors are slit-shaped openings in the nest through which the spider enters and departs.

All four *P. johnsoni* pulled the nest and struck at the gnaphosids. One bumped and another stabbed. Each *P. johnsoni* also walked and turned frequently inside the nest. In three cases, the *H. hesperolus* ran away from the nest after the *P. johnsoni* struck. In one case, this was after 3 min in contact with the nest; contact was for between 15 and 30 sec in the other two cases. For the remainder of the observation period, in each of these cases, the *P. johnsoni* remained inside the nest and the *H. hesperolus* remained at the other side of the cage.

During one observation, the *H. hesperolus* killed and consumed the *P. johnsoni* after 18 min on the nest. Intermittently, the gnaphosid inserted its fangs into the silk and pulled on the nest by raising its cephalothorax. Eventually, a hole was torn through the nest. The *P. johnsoni* repeatedly struck at the gnaphosid through the hole. Suddenly, the *P. johnsoni* walked rapidly through the nest, with the *H. hesperolus* following a parallel path on the outer nest surface. Arriving at the nest door, the *P. johnsoni* began to depart the nest, but at the moment when its anterior cephalothorax was only barely out the nest door, the *H. hesperolus* leaped from the top of the nest and hit at the carapace of the *P. johnsoni* with its extended fangs. With its body and legs arched over the *P. johnsoni*, the *H. hesperolus* made repeated predatory attacks, consisting of rapidly and briefly lowering its cephalothorax, with fangs open, making contact with the carapace of its victim. The *P. johnsoni* made several strikes at the enveloping *H. hesperolus*, but soon it became relatively immobile, with its forelegs raised. After 30 sec, the *P. johnsoni* was motionless, presumably dead or paralyzed. The *H. hesperolus* pulled with its fangs inserted in the silk in the vicinity of the door, eventually ripping the nest open somewhat. Approximately 1 min later, the gnaphosid inserted its fangs into the prey's carapace near the junction of the legs and began to feed.

INTERACTIONS BETWEEN *PHIDIPPUS JOHNSONI* MALES AND
HERPYLLUS HESPEROLUS THAT OCCUPY NESTS OF *PHIDIPPUS*
JOHNSONI FEMALES

P. johnsoni females with eggs were forced from their nests. When *H. hesperolus* were placed in the cages, they soon entered and remained inside the nests with the eggs. The next day a *P.*

johnsoni male was introduced through a hole in the cage. Once the *P. johnsoni* responded to the *H. hesperolus*, observation was continued for 15 min. In six of the seven observations, the *P. johnsoni* touched the nest, whereupon he began to perform type 2 courtship. Since the elements of this type of courtship have been described in detail elsewhere (Jackson, 1976), only brief descriptions of the major elements will be provided here. *Probe*. The first pair of legs are moved alternately forward and backward, with the tarsi in contact with the nest.

Vibrate. The tarsi of the first pair of legs are always in contact with the silk; the other legs may or may not contact the nest. A series of extremely rapid, low amplitude, dorsal-ventral movements are performed, which have the appearance of a sudden, faint blurring of the spider and the silk in his vicinity.

Grip Vibrate. The spider vibrates while his fangs are inserted into the silk.

Tug. While gripping the silk with his fangs, the spider moves his cephalothorax alternately dorsally and ventrally, over a distance of a few millimeters.

Since the result of each interaction was different, each will be related briefly.

1. As the *P. johnsoni* courted, the *H. hesperolus* departed by the opposite door and ran away.
2. The *H. hesperolus* remained inactive as the *P. johnsoni* courted. After the male entered the nest, the gnaphosid departed by the opposite door and ran away.
3. The *P. johnsoni* entered the nest after courting, with the *H. hesperolus* remaining mostly inactive. Once inside the nest, the gnaphosid began to walk, whereupon the *P. johnsoni* departed the nest and backed away. When 3 cm from the nest, the *P. johnsoni* turned 180° and ran away.
4. As the *P. johnsoni* probed at the nest door, the *H. hesperolus* approached, whereupon the *P. johnsoni* backed away 1 cm. For one min the two spiders stood motionless, facing each other, the gnaphosid partly out the nest door. Suddenly, the *P. johnsoni* turned 180° and ran, with the *H. hesperolus* making a brief dash toward the male, covering a distance of 1 cm before stopping then returning to the nest.
5. As the *P. johnsoni* courted on the nest, the *H. hesperolus* began to walk and turn actively inside the nest. When the *P.*

johnsoni suddenly began to run, the *H. hesperolus* ran out the door and onto the nest, circled the *P. johnsoni* from behind, and arched its body and legs over the facing salticid. The *P. johnsoni* struck repeatedly, and the gnaphosid's fangs were extended. As the *P. johnsoni* slowly backed off the nest, with its first pair of legs raised, the *H. hesperolus* slowly followed, with arched body, until reaching the edge of the nest. When 6 cm from the motionless gnaphosid on the nest, the *P. johnsoni* turned 180° and ran away.

6. As the *P. johnsoni* courted at one door, the *H. hesperolus* departed from the opposite door and ran across the nest toward the salticid. Simultaneously, the *P. johnsoni* turned 180° and ran. The *H. hesperolus* overtook the salticid 1 cm from the nest, circled its victim, with its body arched, and repeatedly hit the salticid with its extended fangs. After standing with its first pair of legs raised for approximately 30 sec, the *P. johnsoni* became immobile, whereupon the *H. hesperolus* inserted its fangs into the side of the carapace and fed.

In a related species, *Herpyllus blackwalli*, Bristowe (1958) noted that the fangs are usually buried at the junction of the legs on the side of the prey, consistent with the present observations on *H. hesperolus*. He described the predatory behavior of another gnaphosid, *Drassodes lapidosus*, in great detail, noting the extremely rapid speed with which the spider moved, arching of the body, and circling the prey. In this species, a band of silk is laid over the prey's legs as the predator circles, something not witnessed for *H. hesperolus*. Another point of interest is that in Bristowe's observations, *D. lapidosus* preyed, in the laboratory, on a number of other spider species of comparable size, although he did not stage interactions with salticids. Remember that the spiders found with dead *P. johnsoni* in the field were a species of *Drassodes*.

During the observation in which the *P. johnsoni* did not touch the nest, the *H. hesperolus* was standing in the nest door, facing outward, apparently motionless. The *P. johnsoni* faced the *H. hesperolus*, while 7 cm away, and slowly approached. When 3 cm away, the *P. johnsoni* began to back slowly; and when 5 cm away, a 180° turn was made, then the *P. johnsoni* walked rapidly away. A possible interpretation is that the *P. johnsoni*

recognized the gnaphosid visually, since salticids are known to have highly developed visual abilities (Land, 1972).

Incidentally, after these observations, the gnaphosids were kept for one week in the cages with the *P. johnsoni* nests and eggs. However, the eggs remained undamaged, lending no support to the hypothesis that gnaphosids prey on *P. johnsoni* eggs.

NEST DISCRIMINATION

Each *P. johnsoni* male used in these observations was exposed to an empty nest of a *P. johnsoni* female and an empty *H. hesperolus* nest on successive days. Half were exposed to *P. johnsoni* nests first, the other half were exposed to *H. hesperolus* nests first, and the spiders were assigned to the two groups randomly. On the day before the observations, nest occupants were removed. No nests contained eggs. The nests of *H. hesperolus* were similar in shape and size to the nests of *P. johnsoni*; but they differed substantially in silk texture; and they were more transparent. Each nest was used in only one test. The *P. johnsoni* male was introduced into the cage through a hole, and observation continued for 15 min after the spider touched the nest.

During both type 1 and type 2 courtship, as well as during conspecific aggressive interactions, the abdomens of *P. johnsoni* males twitch in a characteristic manner (Jackson, 1976), that is not seen in other contexts. The abdomen of each male twitched while he was on the empty nest of a *P. johnsoni* female, but not while he was at the nest of a *H. hesperolus* (McNemar, $X^2 = 4.1667$, $P < 0.05$). In addition, each male performed two elements of type 2 courtship, probing and tugging, while at the empty *P. johnsoni* nest. Two males vibrated at the *P. johnsoni* nests, and none vibrated at the *H. hesperolus* nests; however, these frequencies were not significantly different. Males of other species of spiders are reported to show elements of courtship behavior when they touch the silk of conspecific females (Dondale and Hegdekar, 1973; Hollander, *et al.*, 1973; Kaston, 1936).

The *P. johnsoni* males remained on *P. johnsoni* nests for longer time periods than on *H. hesperolus* nests (Table 1) (Wilcoxon, one tailed test $P < 0.05$). Courtship at the empty *P. johnsoni* nests lasted 1 to 7 min. Three males entered the *P. johnsoni* nests. Two of these also entered the *H. hesperolus* nests, these

Table 1. Time (min) that six *Phidippus johnsoni* males remained in contact with empty nests, during 15 min tests. See text for further details.

		Male						
		1	2	3	4	5	6	Mean
Type	<i>Phidippus johnsoni</i>	15	7	3	3	2	11	6.83
of								
Nest	<i>Herpyllus hesperolus</i>	1	0.5	0.5	0.25	0.5	12	2.46

accounting for the two longer residences at gnaphosid nests (Table 1). Inside nests, the spiders alternately groomed, walked about, and remained inactive.

Evidently, *P. johnsoni* males discriminate empty nests built by conspecific females from those built by *H. hesperolus*. Upon encountering gnaphosid nests, they did not court, and usually they remained only briefly.

DISCUSSION

There is little information available concerning the predators of *P. johnsoni*. Pompilid wasps are known to take other *Phidippus* species as larval food (Dorris, 1970; Kaston, 1948; Kurczewski and Kurczewski, 1968; Muma and Jeffers, 1945). Once an acroserid fly pupated from a *P. johnsoni* I collected, and acroserids are known to parasitize other *Phidippus* (Evert Schlinger, personal communication). No doubt there are many predators of *P. johnsoni* for which there are simply no published reports. Reports of the stomach contents of vertebrates are generally of little use in determining the predators of particular spider species or groups, since the spiders are not identified.

Almost universally, *P. johnsoni* males have bright red abdomens. Although the abdomens of immatures and adult females may be dully marked, in many cases they are bright red, orange, or gold. In the laboratory and at exposed locations in the field, such as on the surface of rocks, these spiders tend to be rather conspicuous. There is no evidence that their coloration is aposomatic, although information concerning this is limited. They

do not taste bitter or noxious to humans (personal observation). When standing motionless on the ground, *P. johnsoni* tend to be rather inconspicuous, and their coloration may contribute to their crypticity in these circumstances, since many plants close to the ground have brightly colored leaves of size, shape, and color comparable to the abdomen of a *P. johnsoni*. In addition, since there is evidence that salticids possess color vision (Kaestner, 1950), the abdominal markings may have a communicatory function during type 1 courtship.

Although it has frequently been suggested that during animal courtship and mating the participating individuals are exposed to greater predation than at other times, data to support this contention are rare. Schaller (1972) observed an African lion prey on a courting reedbeek. Predators (Walker, 1964) and parasitoids (Cade, 1975) of some Orthoptera are attracted to male calling songs. The swarming flights of some Diptera, which can be interpreted as courtship, may be attended by heavy predation (Downes, 1969; Syrjamaki, 1966). Observations of this sort at least demonstrate that predation occurs on courting animals, but they are not sufficient to show that predation risks are elevated by courtship and mating.

However, the arguments suggesting this hypothesis are rather convincing. Often it has been argued or implied that a mating or, especially, a courting individual is more conspicuous to predators (Emlen, 1973; Morris, 1956; Platnick, 1971; Richards, 1927). During type 1 courtship, *P. johnsoni* males tended to be highly conspicuous to human observers, while they gestured with their forelegs and danced in front of females. When provided vegetation and rocks, courting and mating pairs showed no tendency to seek cover (Jackson, 1976), courting and copulating sometimes on the tip of a grass blade or the top of a rock. Species that remain relatively motionless during copulation may reduce their conspicuousness; however, copulating pairs of *P. johnsoni* were not motionless. While standing on the female's dorsal surface, the male applied his paired copulatory organs, on the pedipalpi, one at a time to the female's copulatory openings on the ventral side of her rotated abdomen. In addition to the movements involved in switching palps, the male engaged intermittently in postmount courtship, consisting of various stroking and tapping motions (Jackson, 1976).

Two additional factors may be important in increasing the predation risks of courting and mating animals. In many species, a pair *in copula* probably finds it more difficult than usual to escape a predator, given that it has been detected. The other factor is that courtship and mating may be rather demanding tasks for the nervous systems of the participants. This may decrease the probability that the participants will detect the approach of a predator and respond in time to escape. Casual observations on *P. johnsoni* indicated that, when a pair was involved in courtship or mating, they were less responsive to movements of the observer. This was especially true of males.

It will be predicted that predation presents a greater risk to *P. johnsoni* courting and mating outside nests, compared to those courting and mating at nests. This is part of a more general hypothesis that individuals inside nests are subject to less predation than ones outside nests. The predicted safety is relative, not absolute, since the data presented here implicate certain large gnaphosid spiders as predators on *P. johnsoni* in their nests. Occupancy by *H. hesperolus* of the nests of *P. johnsoni* females and subsequent predation on courting *P. johnsoni* males might be a case of aggressive mimicry (Wickler, 1968), in a limited sense. It would be of much interest to verify that this behavior occurs in the field. Also, it would be of value to attempt to evaluate whether this particular advantage to the gnaphosid is great enough to constitute a significant selection pressure favoring occupancy of *P. johnsoni* nests. Other factors are certainly possible, since organisms such as isopods and anystid mites also occupy *P. johnsoni* nests, and for these the predatory function is very unlikely. In considering the importance of this type of predation for *P. johnsoni* males, it should be noted that the proportion of *P. johnsoni* nests, in the field, occupied by large gnaphosids is less than one per cent (unpublished data). In addition, males evidently discriminate between *P. johnsoni* and *H. hesperolus* nests.

In conclusion, the following are some ways in which the spider's nest may provide relative safety from predation:

1. The silk of the nest may form a physical barrier between the occupant and the predator.
2. The silk of the nest may provide a sensory barrier, both visual and chemotactic, between the occupant and the predator. Preda-

tors not adapted to respond to the nest *per se* may fail to detect the occupant.

3. The nest may provide the occupant with an early-warning device, in effect forming an extension of the spider's tactile sensory system.

4. The nest may put the occupant in a highly defensible position with respect to many predators. Usually there are only two nest doors. This may be the only or easiest way for many predators to gain access to the occupant. Some of the responses shown by females to courting males, such as pulling the door and striking, are apparently effective defense against some predators. Such behavior was used during the interactions with gnaphosids; and in the majority of cases, the *P. johnsoni* survived the encounter with the predator.

SUMMARY

P. johnsoni males may court and mate with females either inside or outside their nests, employing a different type of courtship in each circumstance. Although predation probably presents a greater risk to pairs courting and mating outside rather than inside nests, the difference is evidently relative, not absolute. Large gnaphosid spiders were found to occupy *P. johnsoni* nests containing dead *P. johnsoni* in the field. Laboratory observations implicate the gnaphosid spider *Herpyllus hesperolus* as a predator of *P. johnsoni* females while they occupy their nests. Other observations implicate *H. hesperolus* as a predator of *P. johnsoni* males that court at the nests of *P. johnsoni* females occupied by *H. hesperolus*. *P. johnsoni* can discriminate between empty *P. johnsoni* nests and empty *H. hesperolus* nests, courting at the former and remaining only briefly at the latter.

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DEFENSIVE ADAPTATIONS OF SOME NEOTROPICAL
LONG-HORNED BEETLES (COLEOPTERA,
CERAMBYCIDAE): ANTENNAL SPINES,
TERGIVERSATION, AND DOUBLE MIMICRY

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The large and diverse beetle family Cerambycidae is well-represented in the neotropical region, and contains numerous examples of species with interesting and often bizarre defensive adaptations. These include examples of cryptic coloration, defensive use of mandibles, body spines, death feigning, unpalatability coupled with aposematism, and Müllerian and Batesian mimicry. Linsley (1959a, 1959b, 1961) has reviewed the subject of structural and behavioral defense adaptations, protective coloration and mimicry in this family (see also Chemsak and Linsley, 1970, Funke, 1957). We here report field observations on three new and unusual cases of defensive adaptations of these beetles, made during 1976 on Barro Colorado Island, Panama Canal Zone.

Antennal spines.

Both sexes of *Hammaticherus batus* (Linnaeus) have elongate recurved spines on segments 3-6 of their antennae (Figure 1A). These downward-projecting lateral extensions, located at the distal end of the segments, are sharply-pointed, with the inner edge of each point continuing basally as a concave, knife-like ridge (Figure 1B). Other members of the genus have similar spines, and, since their distribution among the basal segments differs from species to species, they have been employed as taxonomic characters within the genus. Such spines as occur on the body and appendages of cerambycids and other insects have often been assumed, in general, to be defensive in function (Edmunds, 1974, Linsley, 1959a, 1961), but there are few accounts of the ways in which spines are actually employed.

Upon being grasped transversely with the fingers, *Hammaticherus batus* extends its head slightly, flailing the antennae back-

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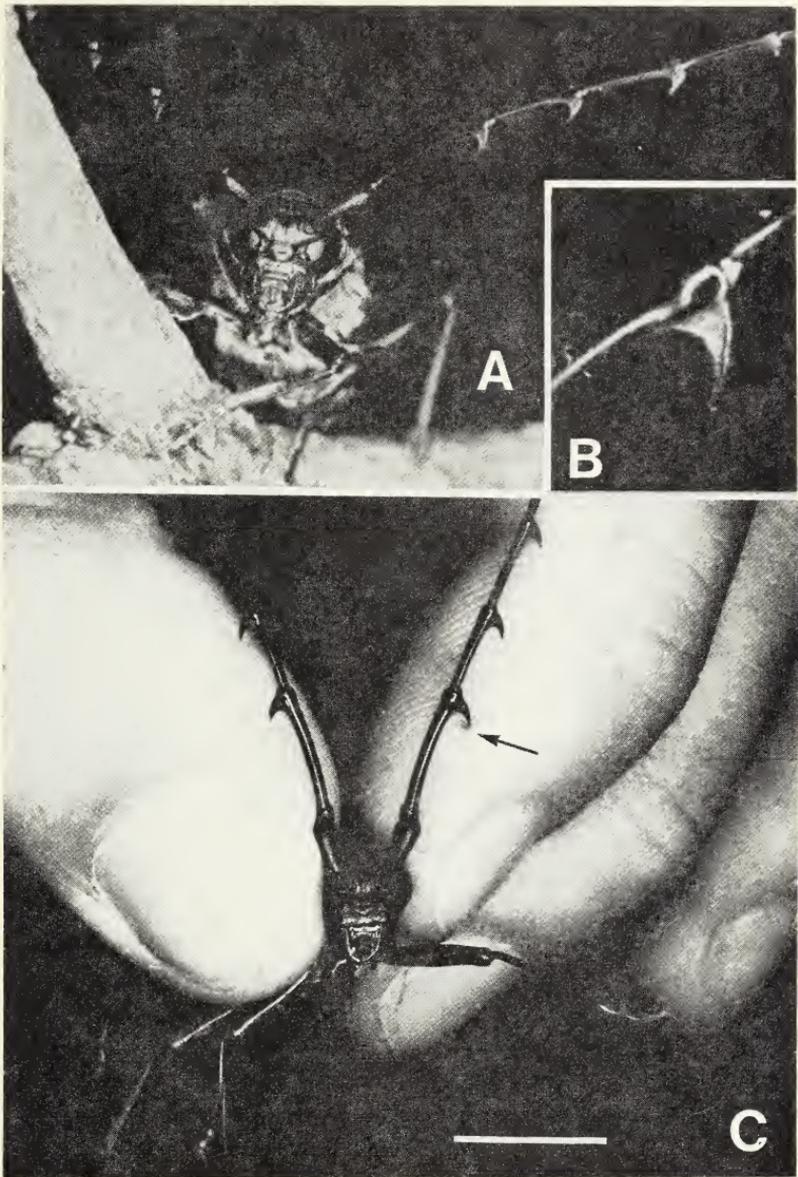


Figure 1. *Hammaticherus batus*: antennal defense. A, note antennal spines on segments 3-6; B, spine of segment 3, enlarged; C, spine in use: the beetle pulls its head downward, setting the spines in the skin and drawing blood (arrow) from the forefinger. [scale, 1C = 1 cm.]

wards and downwards, so that the pointed processes come into contact with the skin. The head is then withdrawn tightly against the prothorax and rotated from a prognathous to a hypognathous position, deeply setting the antennal hooks. They are sharp enough to penetrate the skin, causing surprise, sudden pain and occasionally drawing blood (Figure 1C). Presumably a predator that grabbed one of these beetles would be similarly surprised, possibly injured, and might immediately drop the intended prey. The hoods withdraw easily from the skin once the body of the beetle has been released.

The antennae of cerambycids are the longest known in the Coleoptera, both in an absolute sense and in relation to body size. Unlike the antennae of many other beetles, they are fully exposed and are often too long to be concealed in prothoracic grooves or other receptacles. Conceivably the use of antennae in defensive behavior is most likely to occur in insects the antennae of which are so large or so long that the alternative of concealment is no longer an option. We know of no other instance in which the antennae of an insect are used defensively.

Tergiversation.

When first seen, *Oreodera glauca* (Linnaeus) (Figure 2) appears to be a light-colored, wedge-shaped insect with two conspicuous legs directed "anteriorly." The banded antennae appear to arise from a broad, distinct "head" bearing short horns. The entire effect is an illusion; the real head is located at the other end of the body.

This illusion is achieved by a combination of color pattern and resting posture. The false "head" consists of the apices of the elytra, which are separated from the basal regions by a transverse, darkly pigmented line. False constrictions in the "cervical" region and elsewhere are produced by dark lateral markings. The true pronotum and head are somewhat darker in color and not easily recognized as such. The most important postural adaptation is the positioning of the antennae, which serve two different functions. At the true head, the enlarged antennal bases cover the compound eyes, which otherwise would be visible and would destroy the reversed effect. The antennae are held closely along the sides of the body, and emerge from beneath the elytral apices, where they appear to arise from the false head. Finally, the third

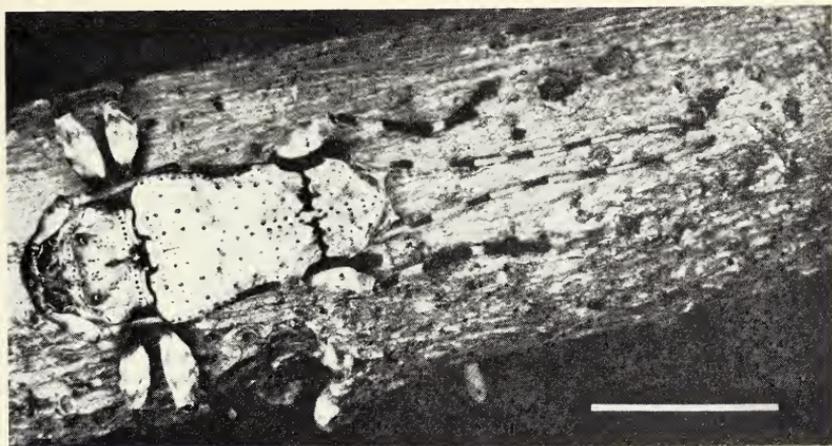


Figure 2. *Oreodera glauca*: tergiversation. The insect appears headed toward the right, but in fact it is oriented in the opposite direction. [scale = 1 cm.]

pair of legs is directed in such a way as to appear to be a first pair, an effect enhanced by the first and second pairs of legs which are grouped together at the true pronotum. The total effect is of a rather nondescript insect headed in a direction that is the reverse of its true orientation.

Predators are well-known to attack insects at the head end, often using the eyes of the prey for orientation. False eyespots and other patterns employed by prey to redirect the attack to less vital regions afford them the opportunity to escape, and are common in many insects, especially Lepidoptera. Their adaptive significance has been experimentally confirmed on several occasions, most notably by Blest (1957). Such eyespots, and other features so employed, have been aptly termed "deflection marks." We here employ the term "tergiversation" (literally, "to turn the back") to refer to the complete illusion of reversed orientation. Tergiversation is variously defined as "the desertion of a direction or of a cause, . . . an equivocation, . . . a subterfuge, . . . an evasion, . . . a turning of the back, as in flight." We feel that tergiversation is a more general term, which includes the behavioral components as well as pattern elements, and emphasizes the complete effect, rather than the parts (such as deflection marks) that produce it. Incidentally, *Oreodera glauca* has no distinctive eyespots or deflection marks at all!

Double mimicry.

The third and final example of a defensive adaptation involves mimicry. Mimicry is highly developed in the Cerambycidae (e.g., Gahan, 1913; Shelford, 1902, 1916), and has been well-reviewed by Linsley (1959a, 1959b, 1961). We here draw attention to *Acyphoderes sexualis* Linsley, a cerambycid that appears to mimic two different groups of stinging Hymenoptera, wasps and ants.

At rest, and especially when walking about, *Acyphoderes sexualis* (Figure 3A-3C) bears a striking resemblance to a large ponerine ant, such as *Paraponera clavata*. The resemblance is produced by the following adaptations: The antennae are short (for a cerambycid) and are moved in an antlike manner. The elytra are abbreviated and swollen at the base, enlarging the apparent thorax. The hindwings are heavily infuscated and are *not* folded beneath the elytra at rest, but rather are clipped in place by the elytra on the abdominal dorsum, where they are tightly twisted along the petiolate basal part, and expanded apically to produce the effect of a large dark gaster. The beetle's behavior convincingly adds to the resemblance of a ponerine ant. Upon being grasped, the beetle makes stinging movements with the abdomen. Since the abdominal apex is quite hard and sharp, the sensation of an impending sting is quite effective. Moreover, like many ponerine ants, the beetle stridulates when handled.

Upon taking flight, the appearance of the beetle changes suddenly to that of a wasp (Figure 3D-3F). For a moment the dark hindwings are raised at an angle to the body, and the "petiole" and "gaster" are slightly reduced in apparent size. The petiole now appears very thin, and the gaster more bulbous. This appearance is retained during flight, when the wasplike effect is enhanced by the hanging legs. The "wasp" is seen momentarily upon landing, just before the hindwings are again clipped in place by the elytra and the "ant" suddenly reappears.

There are many different wasp species that could potentially serve as models, especially the numerous and aggressive dark polybiines, such as *Polybia rejecta*. The beetle is therefore presumed to be a "group mimic" of large, dark ponerine ants and medium-sized, dark vespid wasps, two of the most abundant, conspicuous, aggressive, and best-defended insects in neotropical rain forests, including Barro Colorado Island. We have no information as to the palatability of the beetle.

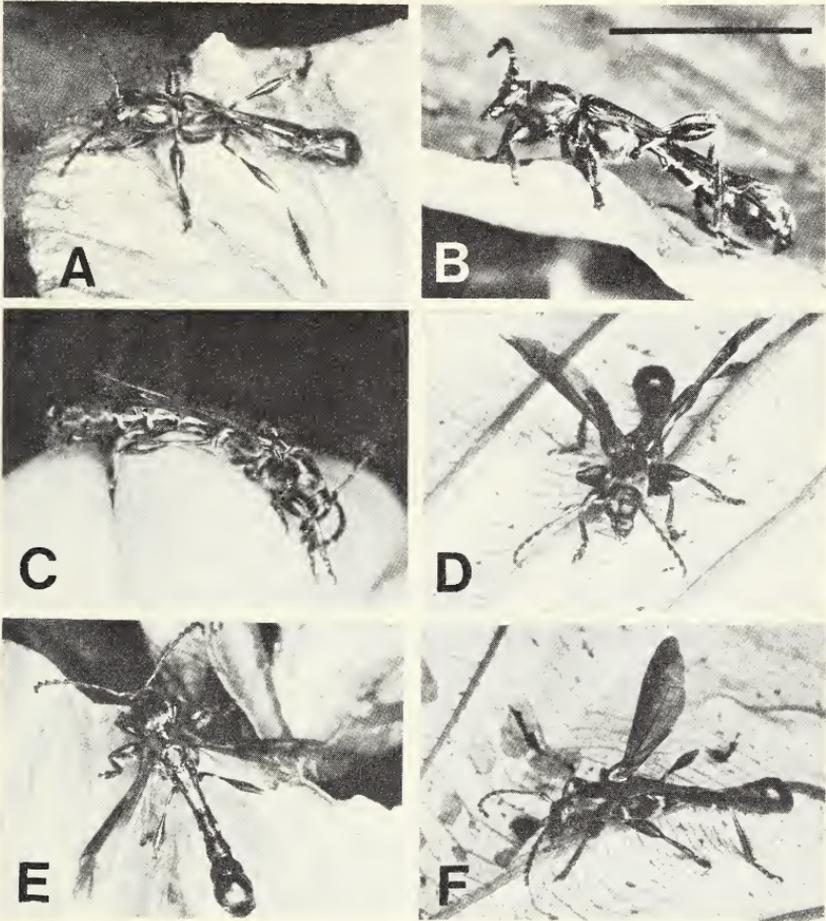


Figure 3. *Acyphoderes sexualis*: double mimicry. A-C, ant mimicry; D-F, wasp mimicry. [scale, 3B = 1 cm.]

Acyphoderes sexualis is one of the most effective mimetic insects we have ever encountered. When we offered the living, hand-held specimen to numerous visitors to the research station, the effect, without exception, was initial sudden withdrawal and surprise at our handling of it. We suggest the term "double mimicry" for cases in which a single insect resembles two distinct models at different times. This is *not* the same as "dual mimicry," in which the two sexes of a species mimic different models, a situation

that also occurs in the remarkable beetle family Cerambycidae (ref. in Linsley, 1959b).

We thank E. G. Linsley and John A Chemsak for determination of the beetles, the Smithsonian Tropical Research Institute for use of facilities, and Nancy Hinnebusch for typing the manuscript. Specimens have been deposited in the National Museum of Natural History, Smithsonian Institution.

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STUDIES ON NEOTROPICAL POMPILIDAE
(HYMENOPTERA). X.
SUPPLEMENTARY NOTES*

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The neotropical region contains a rich and exciting fauna of pompilid wasps, reviewed in a very preliminary way by Banks (1946, 1947). It was my original intention to expand upon and improve Banks' treatment, and toward this end I initiated a series of papers covering small segments of the fauna (Evans, 1965-1973b; see bibliography). The difficulties proved so great that I now propose to conclude this series with the present paper. The types of a great many species are in Europe or in South America, and even a recent trip to Buenos Aires was (due to a variety of unforeseen circumstances) unproductive from this point of view. Furthermore, at least three Latin American countries have recently passed laws making the exportation of specimens difficult. Hence it seems to me wise to leave the field to a younger person with more time, money, and fortitude than I possess.

The present paper includes species description and distributional notes supplementary to various papers in this series and also to my revision of the Mexican and Central American Pompilinae (Evans, 1966b). References to the previous 9 papers in this series are included in the bibliography.

Mystacagenia albiceps Evans

I described *Mystacagenia* in 1973b to include three species, each known from a single female. Thus, the discovery of a single additional specimen is of interest. This is a female *M. albiceps* which agrees closely with the type of that species although from a very different locality. It was collected by M. Alvarenga at Jacareacanga, Para, Brazil, in December, 1968 [Canad. Nat. Coll., Ottawa]. The type is from near Marcapata, Peru.

*Manuscript received by the editor January 26, 1977.

Anoplius (Arachnoproctonus) cteniphagus new species

Holotype. — ♀, MEXICO: VERACRUZ: Fortin de las Flores, 3350' elevation, 20 Aug. 1967 (R. E. Leech) (Wasp dragging stunned ctenid spider, *Ciupinnius foliatus* P.—C. ♀) [Canad. Nat. Coll., Ottawa].

Description of female type. — Length 20 mm; fore wing 18 mm. Black, pubescence wholly dark and with strong bluish reflections; wings dark brown, with bluish reflections. Head clothed with long, dark hair, including clypeus and scape; thorax also with dense, rather long, dark hair on dorsum and pleura, propodeum especially densely hairy; coxae strongly hairy, femora with somewhat shorter and sparser hairs; first tergite densely hairy anteriorly, tergites 2-3 with some short hair, 4-5 more densely hairy, 6 with dense, stout bristles; all sternites moderately hairy. Clypeus $2.5 \times$ as wide as its median height, with a large, arcuate median emargination. Middle interocular distance $0.55 \times$ head width; inner eye margins strongly convergent above, upper interocular distance only $0.72 \times$ lower interocular distance. Ocelli in a very compact triangle, ocello-ocular line $1.5 \times$ postocellar line. Antennae extremely long and slender, third segment $1.5 \times$ as long as upper interocular distance. Pronotum short, very broadly angulate behind; postnotum a narrow transverse band; propodeum sloping evenly in profile, median line not impressed. Front basitarsus with 3 pecten spines, the spines about twice as long as width of tarsus. Marginal cell removed from wing tip by much less than its own length; second submarginal cell rhomboidal, $1.8 \times$ as wide as high; third submarginal cell slightly wider and higher than second, narrowed by about half above.

Remarks. — Known only from the type. Dr. Leech sent me this specimen several years ago, and I have held it hoping additional specimens would come to light. None have, but I felt the species worth describing because of the unusual prey record. The dense hair and emarginate clypeus suggest *Lophopompilus*, but because of the angulate pronotum I think it more likely that the species belongs in *Arachnoproctonus*. Its closest relative may be *echinatus* Fox, known from northern South America north to Costa Rica. However, *echinatus* is a somewhat smaller

and much less hairy species with the clypeal emargination much less pronounced.

Genus EPIPOMPILUS Kohl

I reviewed the neotropical species of this genus in 1967; subsequently, I reviewed the species occurring in the Australian region (1972). This is an archaic genus with a southern hemisphere distribution. Some of the Australian and New Guinea species have unusual structural features, such as the loss of either the first or third intercubital vein, leaving only 2 submarginal cells. I describe below the first American species with only two submarginals, a brilliantly colored species from Jamaica. Two new species from Bolivia are also described, and *E. nigribasis* is reported from the West Indies for the first time. The number of neotropical species now stands at 16; 33 are known from the Australian region.

Epipompilus jamaicensis new species

Holotype. — ♀, JAMAICA: Hardwar Gap, 4000', 29 July, 1966, (Howden & Becker) [Canad. Nat. Coll., Ottawa].

Description of type female. — Length 5.8 mm; fore wing 5.1 mm. Head ferruginous except occiput black, mouthparts largely straw-colored; thorax and propodeum ferruginous except black ventrally, including propleura and extreme lower parts of meso- and metapleura; abdomen fuscous, except tergites 2 and 5 each with a pair of large white spots; antennae dull ferruginous, darkened at each joint; legs varicolored, coxae black and straw-colored, femora dark brown, blotched with straw, tibiae and tarsi brown, hind tibiae annulated with straw near base. Wings mainly hyaline, fore wing with a brown band crossing wing at basal vein and a broader band at marginal cell, apex of wing with a whitish bloom; hind wing slightly infuscated apically. Clypeus broadly emarginate. Malar space slightly shorter than width of mandibles at their base. Front narrow, middle interocular line $0.53 \times$ head width; upper and lower interocular lines subequal; eyes densely hairy; ocelli in a flat triangle, postocellar line $1.2 \times$ ocello-ocular line. Third antennal segment $0.48 \times$ upper interocular line. Postnotum a very narrow transverse band; slope of propodeum low and even, median line not impressed. Front femora not swollen,

measuring $2.9 \times$ as long as wide; tibiae wholly without spines. Fore wing with transverse median vein considerably basad of origin of basal vein; radial vein strongly angled at junction of second intercubital vein (first intercubital absent, resulting in a very long first submarginal cell); second submarginal cell slightly wider than high; hind wing with transverse median vein erect, forming a right angle with anal vein, meeting media far basad of origin of cubitus; anal lobe extremely small.

Remarks. — This striking form resembles mostly closely the Central American species *insolitus* Evans and *delicatus* Turner. It differs not only in the possession of only two submarginal cells, but also in having the head ferruginous, the postnotum extremely short, and the tibiae wholly without spines.

Epipompilus quinquenotatus new species

Holotype. — ♀, BOLIVIA: Santa Cruz: Est. Experimental Gral. Saavedra, 7 July 1973 (C. Porter, L. Stange, E. Demarest) [Inst. Miguel Lillo, Tucumán, Argentina].

Description of type female. — Length 9.6 mm; fore wing 7.0 mm. Head black, except palpi dark brown, mandibles rufotestaceous on apical two-thirds, scape with a large white spot on upper surface apically; thorax and propodeum entirely rufous except propleura black; abdomen black except for large paired white spots on tergites 2 and 5 and a median white spot on 6; legs variegated, coxae mainly black but with some white apically, middle and hind pair rufous basally; femora black except front and middle pair streaked with rufous; tibiae black except front pair rufotestaceous on inner surface, middle and hind pair spotted with white near base; tarsi fuscous. Fore wings strongly twice-banded, a broad band crossing wing at basal vein and another at marginal cell, membrane tinged with yellowish basally and between the two bands, at tip of wing more whitish; hind wing subhyaline, slightly darker apically. Clypeus broadly concave apically. Malar space about $0.4 \times$ as long as width of mandibles at their base. Front narrow, middle interocular distance $0.55 \times$ head width; upper interocular distance $1.1 \times$ lower interocular; eyes densely hairy; postocellar line $1.3 \times$ ocello-ocular line. Third antennal segment $0.54 \times$ upper interocular distance. Postnotum medially about half as long as metanotum; slope of

propodeum low and even, median line not impressed. Front femora not swollen, $2.9 \times$ as long as wide; hind tibiae with scattered minute spines which do not protrude above the coarse pubescence. Fore wing with transverse median vein slightly beyond origin of basal vein; radial vein nearly evenly arcuate; second submarginal cell $1.25 \times$ as wide as high, third submarginal cell $1.5 \times$ as wide as its maximum height; hind wing with transverse median vein strongly oblique, meeting media well basad of origin of cubitus; anal lobe very small.

Allotype. — δ , same data as type [Inst. Miguel Lillo, Tucumán, Argentina].

Description of allotype male. — Length 5.6 mm; fore wing 5.0 mm. Head black except lower inner orbits white, clypeus white except mediobasally, mouthparts mainly straw-colored; thorax and propodeum shining black, finely punctate, pronotum with a broad white band along posterior margin, mesoscutum and scutellum with median white spots; abdomen black, shining, a pair of large white spots on tergite 2 barely connected medially; antennae dark brown below, black above; front coxae straw-colored except black on basal 0.2, front legs otherwise ferruginous except tarsi becoming fuscous apically; middle legs ferruginous except basal third of coxae and all of trochanters black, outer side of tibiae and all of tarsi fuscous, spurs whitish; hind coxae black except apical third white, trochanters black, femora ferruginous suffused with black; tibiae black with a white basal spot; spurs fuscous; tarsi fuscous, segments 2–4 broadly annulated with white. Wings hyaline, apical third of fore wing faintly clouded. Clypeus $1.9 \times$ as wide as high, emarginate apically. Middle interocular distance $0.60 \times$ head width; inner eye margins diverging above; vertex forming an even arc above eye tops. Postocellar line $1.1 \times$ ocello-ocular line. Eyes not hairy. Front shining, uniformly punctate. First four antennal segments in a ratio of 11:4:7:8, segment three $1.7 \times$ as long as wide. Pronotum subarcuate behind; mesoscutum shining, uniformly punctate; scutellum with finer and closer punctures; postnotum dorsally about as long as metanotum; propodeum with median line well impressed. Claws weakly dentate except front pair bifid, outer claws of front tarsus strongly curved; hind tibiae with numerous spines extending above the coarse pubescence. Fore wing with basal and transverse median veins interstitial, other venational

features as in female. Subgenital plate tapering to a sharp point, somewhat hirsute, as figured for *delicatus* Turner by Evans, 1966b, Fig. 63. Genitalia also like those of *delicatus* (Ibid, Fig. 60) except parameres more elongate, equal in length to parapenial lobes and digiti.

Paratypes. — 1 ♂, same data as type and allotype; 2 ♀♀, 15 ♂♂, same data except various dates Jan., Feb., Aug.-Oct. 1973-74 (Malaise trap, Porter & Stange) [Inst. Miguel Lillo, Mus. Comp. Zool., Coll. C. C. Porter].

Variation. — The female paratypes resemble the type closely, but in both the spots on tergite 5 are narrowly connected medially. The males vary in length from 3.5 to 6.0 mm. The pale spot on the scutellum is present in all males, but that on the mesoscutum is reduced or absent in the smaller specimens. The spots on tergite 2 are very small in several males and entirely absent in two; but one male has a broad, pale band on tergite two and small spots on tergite three. Leg color is also somewhat variable.

Remarks. — The females run to *delicatus* Turner in my 1967 key, but differ from that species in the narrower front and in lacking any trace of rufous on the abdomen, as well as in several other details of color pattern. The males run to the couplet separating *delicatus* Turner and *tucumanus* Evans but the genitalia differ from either of those species and the pattern of white spots is distinctive.

***Epipompilus morosus* new species**

Holotype. — ♀, BOLIVIA: Santa Cruz: Est. Experimental Gral. Saavedra, Sept. 1973 (C. Porter & L. Stange, Malaise trap) [Inst. Miguel Lillo, Tucumán, Argentina].

Description of type female. — Length 9.0 mm; fore wing 7.7 mm. Head black except lower front and face rufous, fading to testaceous at the clypeus, malar space, and mandibles; palpi light brown; scape rufotestaceous, flagellum dull rufous, annulated with fuscous at joints; thorax black except ivory-white as follows: collar, streaks at extreme lower sides and at posterior lobes of pronotum, extreme posterior angles of propodeum; abdomen shining black, marked with whitish as follows: large lateral spots on tergite 2, small spots on 3, spots of irregular shape on 4-6, large spots on sternite 2 connected medially; front legs

bright rufous except coxae mostly black, tarsi weakly infuscated; middle and hind legs black except coxae white at apices, tibiae spotted with white near the base, spurs whitish. Wings hyaline, fore wings with a weak band at the basal vein and a weak spot at the second and third submarginal cells. Clypeus arcuately concave. Malar space $0.6 \times$ as long as width of mandibles at their base. Front broad, middle interocular distance $0.61 \times$ head width; upper interocular distance $0.94 \times$ lower interocular; eyes densely hairy; postocellar line twice the ocello-ocular line. Third antennal segment $0.48 \times$ upper interocular distance. Pronotum moderately long, broadly angulate behind; postnotum a very narrow band; propodeum sloping evenly in profile. Front femora $2.6 \times$ as long as wide; hind tibia with only very minute spines. Fore wing with transverse median vein located very slightly basad of basal vein; radial vein strongly angulate at second intercubital vein; maximum width of third submarginal cell $1.45 \times$ that of second submarginal; hind wing as in preceding species.

Remarks. — This species is known only from the type, which is quite unlike any other species of the genus. It is a member of the *azteca* species-group, and will run to couplet 5 of my 1967 key, separating *inca* Evans and *jocosus* Evans. The wing venation is very similar to that of those two species, but the banding is much weaker; there are important differences in body color from both species. *E. inca* is a larger species, with the postocellar line only $1.6 \times$ the ocello-ocular line and the postnotum more broadly exposed, while *E. jocosus* has the postnotum concealed dorsally and the tibiae more evidently spinose.

Epipompilus tucumanus Evans

I described this species in 1967 from a series from Argentina as well as one female from Venezuela. A single female was collected in Bolivia by Porter, Stange, and Demarest, at Buena Vista, Dept. Santa Cruz, 8–26 July, 1973 [Coll. C. C. Porter].

Epipompilus nigribasis (Banks)

I have reported this very small species from Panama, Colombia, and Brazil. In the Canadian National Collection there is a pair from Canuaru, Pernambuco, Brazil, collected in April, 1972, by M. Alvarenga. Porter and Stange have also collected this

species Malaise traps in Bolivia: 2 ♂♂, Est. Experimental Gral. Saavedra, Aug. 1973 and Jan. 1974. I am also able to report the species from the West Indies for the first time: 1 ♂, Bar del Isle, St. Lucia, Lesser Antilles, 20 Oct. 1935 (H. E. Box) [British Museum (Natural History)]. Thus three species of this genus are now known from the West Indies: *nigrbasis* (Banks), *jamaicensis* Evans, and *pulcherrimus* Evans.

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PROSTHOPORUS, A NEW BOLIVIAN GENUS OF THE
SUBTRIBE LYMEONINA (HYMENOPTERA,
ICHNEUMONIDAE)

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Since 1973 I have been conducting a Malaise Trap survey of Hymenoptera at the Bolivian government's Agricultural Experiment Station near General Saavedra in the Department of Santa Cruz. Ing. Oscar Terán and Ing. José Rocavado of the Comisión Nacional del Estudio de la Caña y del Azúcar generously pointed out a protected remnant of subtropical wet forest for safe installation of my traps and have supervised retrieval of samples at monthly intervals. The Committee for Research and Exploration of the National Geographic Society awarded grants for the summers of 1973-'75 which covered travel and equipment expenditures incurred during this project. More recently, a U.S. National Science Foundation Grant (No. DEB 75-22426) has provided funds for technical assistance in sorting and preparation of the thousands of Hymenoptera so far accumulated by the trap survey.

I have completed identification of the ichneumonids trapped at General Saavedra during 1973-'74 and among this material find a remarkable new genus belonging to the Subtribe Lymeonina of the Tribe Mesostenini. This genus now is described so as to make it available for inclusion in a phænologic and biogeographic study of the Saavedra ichneumonid fauna which I am preparing for publication at a later date.

Prosthopor new genus

Length of fore wing: 9.0 mm. *Body:* slender. *Front:* without a median horn or carina, smooth and shining with some weak shagreening. *Clypeus:* moderately large, in profile basad gently convex with highest point a little before middle and apicad flattened to slightly concave and without a median tooth or tubercle.

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Mandible: 2.5 as long as wide at middle, lower tooth strong but distinctly shorter than upper tooth. *Temple*: in dorsal view flat and abruptly receding, in profile at its upper 0.3 about 0.21 as long as eye. *Occipital carina*: gently curved, fading out below a short distance before joining hypostomal carina. *Malar space*: 0.40 as long as basal width of mandible. *Pronotum*: upper margin weakly swollen; epomia only weakly suggested. *Notaulus*: fine and sharp, reaching 0.4 the length of mesoscutum. *Mesopleural fovea*: in the form of an isolated shallow pit located well in front of mesopleural suture and not connected to it by a horizontal groove. *Sternaulus*: very weak and shallow, faintly traceable for about half the distance to middle coxa. *Postpectal carina*: defined only for a short distance laterad, its median section absent. *Metanotum*: its hind margin without a projection on each side of postscutellum, the part below the hind margin long, gently sloping, and not wrinkled. *Propodeum*: elongate, gently and evenly arched in profile and without a sharply discrete apical face; spiracle short-oval, 2.0 as long as wide; basal trans-carina sharp throughout and practically straight; no apical trans-carina or cristae; entire surface behind basal trans-carina covered with dense, regular transverse wrinkles which are finer basad and coarser apicad. *Hind coxa*: its base shallow with a short horizontal groove next to attachment. *Front tibia*: in female moderately swollen and with some unusually strong, sparse spine-like setae in addition to the normal dense vestiture of fine setae. *Front tarsus*: in female with fourth segment deeply bilobed at apex. *Wing venation*: areolet moderately large, rectangular and nearly parallel-sided, about 0.6 as high as section of second recurrent vein above bulla, about 1.7 as wide as high, receiving second recurrent vein well before middle; second intercubitus weak and medially effaced; ramellus absent; postnervulus intercepted at its upper 0.25; nervulus 0.3 its length antefurcal; nervellus intercepted at its upper 0.4; apical half of mediella strongly arched; brachiella absent; axillus close to hind margin of wing and converging to hind margin apically. *First gastric segment*: elongate and almost parallel-sided; its spiracle situated definitely in front of the middle at about basal 0.39 of tergite; without a lateral tooth at base; without longitudinal carinae, except for basal vestiges of the dorso-lateral carinae; postpetiole 0.58 as wide apically as long from spiracle to apex; apex of first sternite far distad of spira-

cle, at a point about 0.5 the distance between spiracle and apex of tergite. *Second gastric tergite*: thyridium subcircular; surface with short, sparse setae. *Ovipositor*: sheathed portion 0.94 as long as hind tibia; slender, moderately compressed; dorsal valve on tip smooth, without notch or nodus; ventral valve on tip with very strong, inclivously oblique to vertical ridges and produced into a lobe that partially encloses the upper valve.

TYPE SPECIES: *Prosthopor terani* new species.

DISCUSSION: *Prosthopor* may be separated from all other genera of the Tribe Mesostenini by the following combination of characters: occipital carina terminates below a little before hypostomal carina; sternaulus faint and only traceable on basal half of mesopleuron; whole propodeum behind basal trans-carina with regular transverse striae; areolet rectangular, 1.7 as wide as high; brachiella absent; first gastric tergite elongate, parallel-sided, and with spiracle situated at basal 0.39; ventral valve of ovipositor partly overlaps dorsal valve on tip. The position of the first tergite spiracle is unusual. Most Mesostenini have this spiracle behind the middle of the tergite while only a few have it at or slightly before the middle. In *Prosthopor* the spiracle is located farther basad than in any other mesostenine genus known to me.

Townes (1969, p. 141–145) provides a tentative subtribal classification of the mesostenines. Within his framework, *Prosthopor* shows affinity to the Subtribe Gabuniina in position of the first tergite spiracle, structure of the ovipositor tip, and in the somewhat inflated female front tibia. However, the foregoing are adaptive characters possessed independently by numerous Mesostenini that parasitize wood boring beetle larvae and *Prosthopor* differs substantially from the Gabuniina by having the lower mandibular tooth shorter than the upper and by its deeply bilobed female fourth front tarsomere. Otherwise, *Prosthopor* runs easily in Townes' subtribal key to couplet 17 which differentiates between the Lymeonina and Ceratocryptina. Here it will go unequivocally to neither subtribe as now defined but agrees with the Lymeonina in most features except for the rectangular areolet which is "much wider than high" as in Ceratocryptina. For the present, I consider *Prosthopor* a lymeonine but agree with Townes (1969, p. 141) that some of the currently recognized subtribes of Mesostenini "are doubtless partly artificial and even-

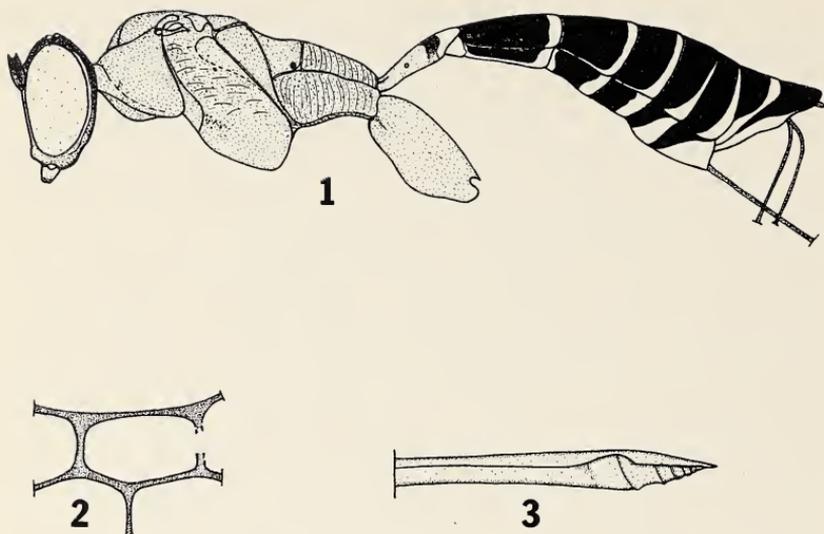


Fig. 1. *Prosthoporos terani* n. sp., female holotype. Lateral view of body showing color pattern and habitus.

Fig. 2. *Prosthoporos terani* n. sp., female holotype. Areolet.

Fig. 3. *Prosthoporos terani* n. sp., female holotype. Lateral view of apex of ovipositor.

tually will have to be redefined”.

GENERIC NAME: *Prosthoporos* comes from the Greek adverb *prosten*, “before, in front of”, and the Greek noun *poros*, “pathway” or “pore”. It was chosen in reference to the basal position of the first gastric spiracle in this genus.

1. *Prosthoporos terani* new species

(Figs. 1-3)

Holotype: female, BOLIVIA (*Santa Cruz*: General Saavedra, Estación Experimental Agrícola, November 1973, in Malaise Trap, C. C. Porter). (Gainesville).

FEMALE: *Color*: scape shining black with considerable brown staining below; pedicel black with brown on apex and below; flagellum black with a broad, ventrally incomplete white band that reaches from apical third of fourth through most of tenth segment and with some dull brownish below on eleventh to last

segments; mandible white, grading through pale brown into black on apical third; head white on much of clypeus, much of face, and on a broad, ventrally interrupted orbital ring, with pale brown to orange brown on a large median occipital blotch behind ocellar triangle, on and between antennal sockets, on much of median field of face except above, in clypeal suture, medially on apex of clypeus, in much of malar space, on apical $1/3-1/2$ of lower half of temple, and on most of postocciput, as well as with shining black on most of front, on much of vertex and occiput, and apically on upper half of temple; mesosoma shining pale red with some very obscure whitish staining, especially on scutellum, tegulae, subalarum, speculum, mesosternum, and apicad on lower metapleuron; first gastric tergite shining pale red except for a broad white crossband on its apical fifth and an even wider, somewhat irregular black area just preceding the white band; the following tergites black with complete white apical bands on 2-7 and a medially interrupted white apical band on 8; fore and mid legs pale red to yellowish red on tibiae and tarsi, with a little dusky apicad on third tarsomere and with fourth and fifth tarsomeres blackish; hind leg with coxa, trochanter, trochantellus, and femur pale red, tibia yellowish red with slight dusky staining at base and becoming blackish on most of apical third, and tarsus white with blackish on about basal sixth of first segment, on apical half of fourth, and on all of fifth segment; wings hyaline.

Flagellum: segments 1-9 a little compressed with 10 and following somewhat thickened and then attenuate toward tip, the first segment 6.1 as long as deep at apex. *Face*: mat and finely granular with mostly well spaced, medium-sized shallow punctures. *Temple*: smooth and shining with small, sparse punctures.

Mesoscutum: smooth and polished with only a few tiny, scattered punctures that are best developed anteriorly. *Mesopleuron*: prepectal carina reaches dorsad to about opposite upper 0.40 of hind margin of pronotum; no ridge on prepectus opposite lower hind corner of pronotum; surface smooth and shining on most of upper third, on speculum, and on the numerous but finely punctate prepectus but becoming mat with delicate irregularly longitudinal wrinkling on most of lower $2/3$. *Lower metapleuron*: dully shining with very fine oblique wrinkling and micro-shagreening and scattered tiny, obscure punctures emitting moderately long but mostly well spaced setae.

First gastric tergite: smooth and shining with faint micro-reticulation, especially on postpetiole, and some sparse, shallow, medium-sized punctures emitting well spaced setae. *Second gastric tergite*: shining with well developed micro-reticulation and some moderately numerous, large but very shallow punctures emitting well spaced setae. *Succeeding tergites*: 3 similar to 2; 4 and following with progressively smaller, more numerous punctures and denser, largely overlapping setae.

MALE: unknown.

TYPES: The unique holotype will be deposited in the Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Services, Gainesville, Florida.

HABITAT NOTES: The type locality is a patch of subtropical wet forest on an ecotone between the Chaco Húmedo and Selva Amazónica biotic provinces, which interdigitate near Santa Cruz, Bolivia where the drainage systems of the Paraná and Amazon Rivers come into close contact. This is a semi-evergreen plant community that dries out markedly during the winter months of July and August but which mainly is composed of hygrophile species, such as palms, cecropias, and giant-leaved epiphytic philodendrons.

SPECIFIC NAME: For Ing. Oscar Terán of the Comisión Nacional del Estudio de la Caña y del Azucar, who made possible the Malaise trap survey at General Saavedra.

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THE FIRST WORKERLESS PARASITE IN THE
ANT GENUS *FORMICA* (HYMENOPTERA:
FORMICIDAE)

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Abstract. *Formica talbotae* Wilson, a member of the *microgyna* group and the first proven workerless parasite in *Formica*, is described here. The species is known from Michigan, Iowa, and North Dakota. The discovery of *talbotae* completes the inferred evolutionary progression within *Formica* from independent existence through temporary parasitism to permanent, workerless parasitism.

During her exhaustive survey of the ant fauna of the Edwin S. George Reserve of Michigan, an effort previously unparalleled in North America, Mary Talbot has uncovered a surprising number of rare and undescribed species. One of the most significant is the species to be described below, a member of the *Formica microgyna* group which to the best of my knowledge is the first adequately documented example of a workerless parasite in this large Holarctic genus.

***Formica talbotae* Wilson, new species**

Diagnosis (queen). A small species even for the *microgyna* group, characterized further by the following combination of traits: subquadrate head; smoothly rounded anterior clypeal border; thick petiolar node with relatively thick, rounded crest; short (0.05–0.08 mm), dense standing pilosity over all of body and appendages, including scape; many of the hairs on the thoracic dorsum, propodeum, petiole, and fore coxae spatulate. So far as known, *talbotae* is exclusively a workerless parasite of *Formica obscuripes* Forel.

Relationships. During the study I examined specimens of all of the *microgyna* group species for which sexual forms are known. Most of those known from workers solely were also examined, but are in any case considered probably distinct on the basis of the possession of a worker caste alone. The closest species is *F. dirksi* Wing, which differs in the queen caste by its slightly larger size; much longer, less frequently spatulate pilosity; and more rounded head shape. *F. spatulata* Buren is also close but its queen

is distinguished by a much shorter pilosity; rounded, tapering head shape; much sparser pilosity; and the certain existence of a worker caste.

Holotype queen. Head width, across and including the compound eyes, 1.12 mm; head length, exclusive of mandibles, 1.21 mm; scape length 1.17 mm; total body length approximately 4.8 mm. Most of the diagnostic features have been illustrated in Figure 1. Body medium brown, with sides of pronotum light brown; appendages mostly light, almost light yellowish brown.

Edwin S. George Reserve, Livingston Co., Michigan; 16 August 1971; collected by Mary Talbot, series no. 71-45, in a nest of *Formica obscuripes*.

Other series. Fifteen paratype queens from the holotype nest series varied in head width 1.12-1.18 mm (mean 1.15 mm). Queens in five additional nest series from the type locality (collection dates: 25 June 1969, 29 June 1970, 17 September 1970, 18 September 1970, 29 July 1974) were closely similar to the holotype nest series in size and other characteristics. All were collected in nests of *F. obscuripes* (see Talbot, 1977).

An additional series of *F. talbotae* queens was examined from Lakeside Laboratory, Milford, Iowa; they had been taken from a nest of *Formica obscuripes* by R. L. King (accession no. 485, 13 July 1952). These are closely similar in all traits to the holotype nest series; for example, the head width of 8 specimens was 1.12-1.17 mm (mean 1.15 mm). A third series from the University of North Dakota Biological Area, Grand Forks Co., North Dakota (P. B. Kanno's leg., 3 August 1971) was assigned to *talbotae*. These queens differed from the Michigan series in having somewhat denser pilosity and being slightly larger (head width of 5 queens was 1.18-1.19 mm). They were also collected in a nest of *F. obscuripes*.

Males. Males in the holotype nest series and other collections from the E. S. George Reserve are distinguished from males of other *microgyna* group species by pilosity traits paralleling those of the queens: the hairs are short (0.05-0.08 mm) and dense on both the body and appendages, with many on the occiput, mesonotum, and propodeum blunt to spatulate. Head width of 10 individuals in the holotype nest series was 1.12-1.29 mm (mean 1.22 mm).

Type deposition. The holotype and many paratypes are in the Museum of Comparative Zoology, Harvard University, while paratypes from the holotype nest series have been deposited in the U.S. National Museum and Los Angeles County Natural History Museum.

Discussion. In their recent review Letendre and Huot (1972) note that the *F. microgyna* group is exclusively Nearctic, its various species occupying a total range from central Mexico north to British Columbia and east to Quebec and the Carolinas. As W. M. Wheeler (1904) first showed in the case of *F. difficilis*, the tiny queens enter the nests of other species of *Formica*. These host colonies either lack queens of their own at the outset or else lose them subsequently, by means still unknown. The offspring of

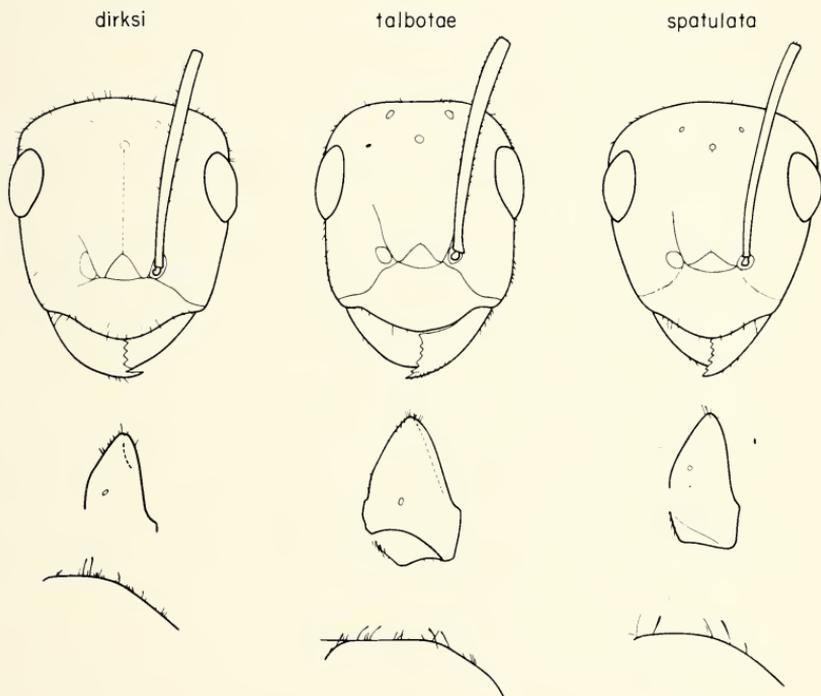


Figure 1. Frontal view of head and side views of basal propodeal face and petiolar scale of queens of *Formica dirksi* Wing (holotype), *F. talbotae* Wilson (holotype), and *F. spatulata* Buren (paratype).

the parasite queen are ordinary in size and behavior in comparison with other *Formica*, and they gradually supplant the host workers until a pure, newly independent parasite colony comes into existence. In short, most of the species of the *microgyna* group appear to be temporary social parasites.

Wing (1949) described *F. dirksi* from a single queen found in the nest of a *Formica fusca* (form "*subaenescens*") colony in northern Maine. Because of the absence of *microgyna*-group workers, he suggested that it might be a workerless social parasite. This may well be true, especially in view of the similarity now revealed between *dirksi* and *talbotae*. However, *talbotae* is the first well documented example of a workerless parasite in the genus. Both W. F. Buren and I have searched through extensive series of *F. obscuripes* containing queens and males of *F. talbotae* without finding a single *microgyna*-group worker, nor were such workers found in the North Dakota mixed series. In one thorough survey of a mixed nest in Michigan, Talbot (1977) found only workers of *F. obscuripes*. It is reasonable to conclude, therefore, that either *talbotae* is entirely workerless or else its worker caste is so scarce as to restrict it to a state of permanent social parasitism.

Thus the significance of *F. talbotae* is that it completes the evolutionary sequence within *Formica* from complete independence through temporary social parasitism to permanent social parasitism, with an apparent total loss of the worker caste. It is worth noting also that so far as known other *microgyna*-group species, including *dirksi*, parasitize members of the *fusca*, *neogagates*, and *pallidefulva* groups of *Formica*, whereas *talbotae* is associated with a member of the *rufa* group. This difference may prove significant with reference to the extreme state of social parasitism achieved by *talbotae*, although the data are still too few to establish host specificity with any degree of confidence.

ACKNOWLEDGMENTS

I wish to thank Mary Talbot, William F. Buren, and Paul B. Kannotski for supplying me with the specimens described here, Akey C. F. Hung for providing data on the Iowa series, and David R. Smith for the loan of the unique holotype of *F. dirksi*. The study has been supported by National Science Foundation Grant no. BNS73-00889.

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THE NATURAL HISTORY OF THE
WORKERLESS ANT PARASITE
FORMICA TALBOTAE

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Abstract: The ant *Formica talbotae* Wilson is a workerless social parasite of the *microgyna* group, which forms mixed colonies with the host ant *Formica obscuripes* Forel. Queens produce males and females only and there is also no worker brood of *F. obscuripes* in the parasitized colonies. The small alates have a long flight period stretching from mid-June to late September, with flights taking place on every suitable morning when the temperature is above 71° and rising, when the sun is shining, and when there is no appreciable wind. Flights are best between 78° and 83°F. Once up on plants, alates are reluctant to return to the nest so some flights, under poor conditions, are long drawn out. Flights are sparse, usually only 10 to 75 alates taking off in a day. Sometimes there is a small swarming reaction, with females loitering on plants above the nest while males fly about until they find them and mate.

Formica talbotae Wilson is the only known workerless social parasite of the genus *Formica* (Wilson, 1977). The queens live in colonies of the thatching ant, *Formica obscuripes* Forel, and produce winged males and females all through the summer. Since all of the brood in such a colony is that of the parasite (a few *F. obscuripes* males may be produced and are probably the result of worker-laid eggs), it is assumed that the small fertilized females enter colonies which lack queens or in some unknown manner bring about the death of any queen which may be present.

E. O. Wilson (1977), who described *F. talbotae*, reports that this small member of the *microgyna* group has also been found at Spirit Lake, Iowa, by Robert L. King and near Grand Forks, North Dakota, by Paul B. Kannoński.

The *F. talbotae* colonies presented here were associated with five colonies of *F. obscuripes* on the Edwin S. George Reserve, Livingston County, Michigan. This is near the eastern margin for the distribution of the host ant, which is essentially a prairie form. *F. obscuripes* finds an excellent habitat on the Reserve since there are open, sloping fields which are sandy and well drained. Mounds are numerous in some fields, a condition necessary for the existence of such a parasite as *F. talbotae*.

The parasites were first detected on June 25, 1969, when small males were seen coming from a nest of *F. obscuripes* near the end of the flying season of the latter species. In 1970 two more mixed colonies were located and all three were studied during the summer. By 1971 the two smaller colonies had disappeared, but the thriving one was watched until it was dug on August 16, 1971. By this date a fourth colony had been discovered, and it produced males and females until the end of the season but was not present in 1972. The fifth colony was found in July of 1974 and was still vigorous at the end of that year. During these years a great many nests of *F. obscuripes* were checked but no more parasitized colonies were recorded. Mixed colonies must be relatively short-lived since no worker pupae of either species were ever found. Thus a colony would become weak and depopulated as its *F. obscuripes* workers were killed during foraging or died of old age.

The first colony found ("cherry nest") was the smallest. Its mound was under the shading branches of a large choke cherry tree and was partly overgrown by trailing blackberry. This was an abnormally shaded location and the extensive overgrowth indicated a weak colony. The "cedar nest" was 25 yards away at the base of a red cedar tree. Its thatch was mostly dried cedar leaves and was almost flat. It was not overgrown and received good morning and evening sun. The "field nest" (the nest dug) was again 25 yards away and formed a rough triangle with the first two. It was the largest, had a good mound of thatch, and occupied a typical habitat. It lay in a high, sunny field of Canada bluegrass (*Poa compressa* L.) with numerous forbs, such as wild bergamot (*Monarda fistulosa* L.), daisy-fleabane (*Erigeron strigosus* Muhl.), orange hawkweed (*Hieracium aurantiacum* L.), yarrow (*Achilles millefolium* L.), mullein (*Verbascum thapsus* L.), and goldenrod (*Solidago* spp.). Grass circling the mound was tall; and it, together with a small shrubby elm, a bergamot, and a goldenrod plant, gave climbing support for flying ants and furnished flickering shade for the mound during early morning and late afternoon. The fourth colony was almost as small as the "cherry nest." It lay in a lower field about 160 yards from the first three and was almost completely overgrown with trailing blackberry. The fifth colony, 12 yards beyond in the same field, was almost as large as the colony dug. Thus all five colonies

were in one part of the Reserve, and the only evidence that there might be more was the finding of an alate female a mile away.

Development of brood. Larvae and a few alate pupae were already present when observations began on June 3. Larvae were found all summer until August 16 and pupae until September 18. Adult alates were taken first on June 16, but they must have been in the nest slightly before this for the initial flight occurred on that date. The last flight seen was on September 20, but a few alates were still in the nest on October 1 when observations ceased. There was a steady production of alates all summer and brood was always abundant. Larvae and pupae were kept together in the lower parts of the central thatch or in soil chambers below or to the sides. No worker brood of either species was found.

Population count. On August 16, 1971, the largest colony was dug with the help of three friends, and an attempt was made to collect all the inhabitants. After the digging, thatch and soil were again sorted for possible overlooked brood, and for the next two weeks workers were captured along trails and outposts until there were no more. On the outside, the nest had a cone of thatch 9 inches high in the center and 17×17 inches in diameter. Around this a grassy ring made the total nest area 30×30 inches. Thatch extended down 17 inches beneath ground surface level. The first larvae and pupae were 10 to 14 inches down in the thatch, and more were located deeper in the thatch and in the soil beneath it to about 30 inches. Around the sides, more chambers with brood were present in the soil, beginning at 14 inches. No brood was below 30 inches, although at 35 inches there were still more galleries going down and ending blindly. All of the side chambers were in a diameter of 26 inches.

F. obscuripes workers totaled 4,620, a fairly small population for this species. N. A. Weber (1935) counted 16,481 workers in a nest and said that this was not a complete count. R. L. King (1950) estimated over 50,000 workers in a large colony.

All ten dealate females of *F. talbotae* were in the central thatch and 87% of the winged males and females were there also. The nest contained 593 adult alates of which 263 were females and 330 were males. There were 1,127 pupae and 288 larvae, making a brood total of 1,415. Most of these were in chambers in the soil (78% of the pupae and 80% of the larvae). This distribution may have been influenced by the extremely dry condition of the thatch and upper soil.

The 2,018 ants (adult plus brood) revealed in the digging in mid-August were only part of the production for the year since flights had been going on since June 16. If only 20 to 25 flew a day on a possible 30 to 35 favorable days, then 600 to 800 had already escaped, giving approximately 2,600 to 2,800 as the total estimated population. If 44% of these were females, then 1,100 to 1,200 females might have left this nest in 1971 if it had not been dug.

Flights. Since the ants had a long flying season, flights were not watched constantly. After the flight pattern was determined, they were checked at various times during the summer to determine that adult alates were being produced constantly and that flying took place on each day that weather permitted. Flying ants were seen to leave the nest on 48 days.

The "field nest" gave the earliest record for a flight (6-16-71). In 1970 it ran out of alates by September, but the "cherry" and "cedar" nests both had flights on September 20 and had a few males in the nest as late as October 1. This gave a possible flying season of about 100 days. If two-thirds of these had proper weather for flying, there could have been 75 flight days in a season. This extended flight period is in marked contrast to that of the host species *F. obscuripes*, which has its flights within a period of approximately 30 days (during June), and in that time individual colonies may have 5 to 16 flights (Talbot, 1972).

Flights were tedious to watch because the small males and females were inconspicuous and because many flights were sparse and prolonged, with only a few ants coming up on plants at a time. Often there were only one to 16 alates on plants above the nest and from 10 to 15 males and from 6 to 12 females moving about on the mound. They were most abundant on the nest or on plants above when flying conditions were submarginal, and they were encouraged to come out but not to fly just before the temperature was high enough or when the sky darkened or temperature dropped. One peculiarity of the alates was their reluctance to return to the nest once they had climbed plants and were ready to fly. This sometimes lengthened flights and once, when conditions did not improve, 3 males were still hanging onto grasses at 4:30 p.m. Flying rate was often very slow. A mean of one ant flying a minute was usual and 3 or 4 a minute constituted a good flight. Sometimes 2 to 8 minutes elapsed between the takeoff of 2 ants.

Since flights were generally sparse, the releasing of 75 alates constituted a good flight. Some were larger but some involved as few as 10 to 30 alates.

The longest flights occurred after a cold night when the temperature rose slowly because the day was hazy or when conditions were not quite ideal. One, watched continuously, lasted one hour and fifty minutes. On that day the temperature kept hovering between 70° and 71°F. Conversely, flights could be quite short. One lasted only 39 minutes because, after a heavy fog, the sun warmed rapidly to 85° and flying stopped. In this time 10 males and 8 females flew and one mating was seen. Another flight was cut short in 13 minutes.

Flights began at varying times in the morning, depending on how cold the night had been and how quickly the mound and air warmed. The earliest flight seen began at 6:30 a.m. and the latest at 10:30 a.m. (E.S.T.). Males and females could come out on the mound when the temperature rose above 57° and could begin to climb at 68° to 70°. A few have been seen to fly at 69° to 71° but few flew before the temperature reached 72° or above, and the best flying took place between 78° and 82°. None was seen to fly above 85°. When mound surface reached 84° to 85°, alates no longer came to the surface. (Unless otherwise stated, all temperatures were taken 10 inches above the ground, at about the height from which ants flew.)

Various other factors beside temperature determined time and length of flight. Rain, darkening sky, or swaying grasses could stop or prevent a flight. One stopped at 7:45 a.m. because of a strong wind and decreasing light, although temperatures were favorable. One lasted until 11:45 a.m. and finally dragged to a close when gathering clouds caused the air temperature to drop to 70°. When conditions were submarginal, it was sometimes hard to tell when flight ended because a few alates would stay on the nest; and occasionally, at long intervals, one would climb and fly. Such a flight could last into the afternoon.

One day males and females came out of the mound at 64° to 66° but did not climb because, although the temperature reached 72°, it fluctuated between this and 62°, going up and down rapidly with passing clouds. On another day the "cedar nest" had a flight but the other two did not, for different reasons. At the "cherry nest" shade kept the temperature too low. "Field nest" alates

in the sun had adequate warmth, but a wind kept the plants in almost constant motion. Ants at the "cedar nest" could fly because they were in the sun and because they could climb the cedar trunk to take off, thus avoiding moving plants.

Both males and females could fly from grasses, but females often preferred the more stabile stalks of monarda or goldenrod. Sometimes they climbed rapidly with wings half spread and flew immediately. More often they came up slowly, stopping several times before reaching a plant tip from which they would fly after a brief fluttering of wings.

Females tended to loiter for a longer time than did males and so set up conditions for swarming on a miniature scale. Swarming was considered to exist when males, instead of flying off, flew among the plants, lighting on one stem after another, until they found females with which to mate. This did not take place on all flights. One typical swarm occurred on August 25, 1970, at 78°. When first seen, 10 females were standing on plants and 8 males were flying among them. One male united with a female and then moved off fluttering its wings; 3 others walked rapidly, with a jerking motion, among stems. One found a female and mated for a half minute. Then 2 others were seen mating. Other males and females joined the group. Males flew up and down among the plants, then lit on stems to find females. When females were in excess, they seemed to be waiting until males found them. This was a very low grade swarm but, aside from numbers involved and the fact that it took place over the nest, it was essentially like the ground swarms of *F. obscuripes*, which have been reported from the Reserve (Talbot, 1972), and still more like the small swarms which took place over the nest of *Formica dakotensis* Emery (Talbot, 1971).

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THE FUNCTIONAL ANATOMY OF THE MESOTHORACIC
LEG OF THE WATERSTRIDER, *GERRIS REMIGIS*
SAY (HETEROPTERA)*

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INTRODUCTION

Gerris remigis is a heteropteran which spends most of the time on the surface of flowing streams. On the surface of the water it moves by rowing, during which the meso- and meta-thoracic legs, especially the former, sweep powerfully backwards pushing against the surface film of the water (Darnhofer-Demar, 1968). In order to stand, the animal needs a large area of contact with the surface. Both standing and rowing require that these legs extend laterally consequently they differ from the more or less vertically orientated legs of most other insects, including many terrestrial Heteroptera. In a recent review of the evolution of Heteroptera, Popov (1971) discussed the divergence of the coxae in the infraorder Leptopodidomorpha — of which the Gerridae are members — in order to move on the surface of the water. It thus seemed interesting to compare these legs with those of Heteroptera having a different life style. Those Heteroptera whose mesothoracic legs have already been studied in sufficient detail are *Gelastocoris oculatus* (Parsons, 1960) and *Belostoma flumineum* (Segal, 1962). Since these two insects belong to the Hydrocorisae, and since *Gerris* belongs to the Amphibicorisae, *Gelastocoris* and *Belostoma* are not closely related to *Gerris*. Nevertheless, they provide an interesting comparison, especially since *Gelastocoris* is littoral, *Belostoma* is totally aquatic and *Gerris* is surface-living.

The primary purpose of this study, therefore, was to explore the modifications of the mesothoracic leg in terms of the external anatomy, musculature and pattern of innervation and to relate

*Note added in proof: In a recently published paper, N. M. Andersen includes a brief description of the functional anatomy of the mesothoracic leg of *Gerris lacustris* which accords well with that presented here for *Gerris remigis*. [Vidensk Meddr dansk naturh Foren, 1976, 139:337-396.]

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this both to other Heteroptera and to the mode of locomotion of *Gerris remigis*.

MATERIALS AND METHODS

Animals were collected from local streams in western Massachusetts. Mesothoracic anatomy was studied by conventional dissections of specimens preserved in 70% alcohol. Nerves were traced in animals which had been injected with a 1% solution of methylene blue in Insect Ringer (Becht, Hoyle and Usherwood, 1960) shortly before they were killed.

RESULTS

Skeleton of the Leg

The mesothoracic leg consists of the usual five segments, but some have become highly modified. The coxa, the most proximal segment, is about 2.5 mm long. In comparison with the coxae of most insects (Snodgrass, 1935) the gerrid coxa has rotated so that the coxal dorso/ventral axis of most insects has become the anterior/posterior axis in the gerrid coxa (Fig. 1a, b). The proximal two thirds of the coxa lies within the coxal groove in the mesothoracic cavity (Fig. 2). The base of the coxal groove is formed by the sternum and the lateral walls consist of the supra-coxal lobes of the well developed epimeron and episternum. The anterior end of the coxa is attached to the pleuron by a heavily sclerotized region, the pleurocoxal attachment, and the posterior

TABLE I

MESOTHORACIC MUSCLE NOMENCLATURE AS USED BY LARSÉN (1945), GUTHRIE (1961) AND DARNHOFFER-DEMAR (1969).

Guthrie <i>G. lacustris</i>	Darnhofer-Demar <i>G. lacustris</i>	Larsén <i>G. rufoscutellatus</i>
52	M. mesonoto trochanteralis	46 M. nototrochanteralis
52	M. mesopleurotrochanteralis	47 M. pleurotrochanteralis
53	M. mesonototrochantinalis	41 M. nototrochantinalis
54	M. mesonotomerocoxalis	40 M. notocoxalis
	M. mesocoxa - trochanteralis lateralis	50 M. coxa - trochanteralis lateralis

(distal) end leaves the thorax by a circular opening close to the metathorax. The lateral wall of this opening is formed by the supracoxal lobes. The coxal groove and small, backwardly projecting opening severely restrict coxal movement. The only possible movement is a rotation about the anterior/posterior axis between the pleurocoxal attachment and the opening. The proximal coxal rim has a medial trochantin and a lateral apodeme on to which muscles 40 and 41, respectively, insert. The distal third of the coxa is outside the body cavity and is more rounded than the proximal two thirds.

The next segment, the trochanter, is also highly modified. It is a little shorter and rather slimmer than the coxa (Fig. 3). The medial proximal rim is extended into several large apodemes on to which muscles 46 and 47 insert. Muscle 50 inserts on a smaller lateral apodeme. The trochanter articulates with the coxa by means of a dicondylic joint. This forms the axis about which muscles 50 and 46 plus 47 act antagonistically and is in the dorso/ventral plane. As the trochanter leaves the coxa, it makes a sharp, right-angled turn so that the surface which was medial in the proximal part of the segment is the posterior surface in the distal part of the segment (Fig. 1d).

The femur is fused directly to the trochanter and so has no independent movement. It consists of a simple cylinder, a little longer than 1 cm. The femoro-tibial joint has been described in great detail by Darnhofer-Demar (1973) and is a simple hinge. The tarsus is two-segmented and has two, backwardly directed, subapical claws. The exposed parts of each segment are covered with a variety of sensory hairs (Weber, 1930; Lawry, 1973), which are doubtless of importance in orientation during courtship (Wilcox, 1972) and capture of prey (Murphy, 1971).

Muscles

The mesothorax is by far the largest segment of the body, occupying about one third of the length of the body. Its musculature has already been described in detail by Larsén (1945), for *G. rufoscellutus*, and by Guthrie (1961) and Darnhofer-Demar (1969) for *G. lacustris*. For convenience it will here be described briefly for *G. remigis*. For reasons of historical precedence and to facilitate comparison of gerrids with other Heteroptera, Larsén's numbering system is used here. A comparison of nomen-

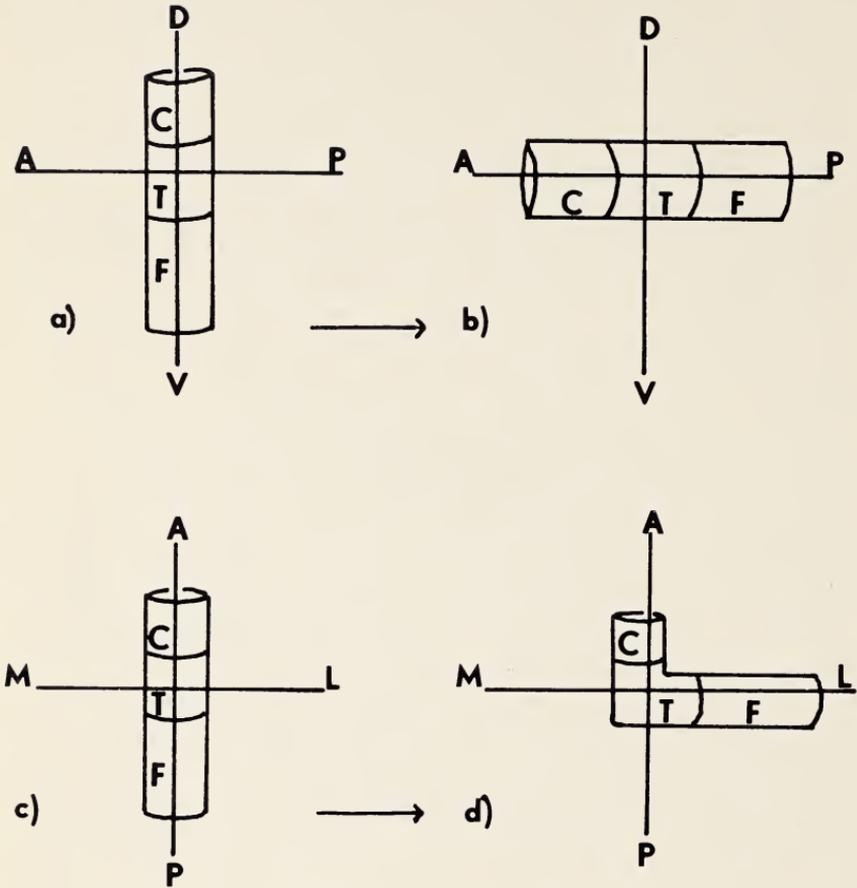


Figure 1: Diagram to illustrate the orientation of the gerrid leg with reference to the simple cylinder shown in (a). Reorientation of the coxal axis causes the dorso-ventral axis of the leg to become the anterior/posterior axis (b). The trochanteral bend causes the anterior/posterior axis of the distal part of the leg (c) to become the medio/lateral axis (d). (b) and (c) represent the same leg but viewed from a 90° shift so that the medio/lateral axis can be seen in diagram (c).

- | | | | |
|---|----------|---|------------|
| A | anterior | M | medial |
| C | coxa | P | posterior |
| D | dorsal | T | trochanter |
| F | femur | V | ventral |
| L | lateral | | |

The orientation symbols used in this diagram are used similarly in succeeding diagrams, unless otherwise stated.

clature used by these three workers is given in table 1.

Since in New England, adult *G. remigis* are usually wingless, only wingless animals were used in this study. Both direct and indirect flight muscles are lacking in the wingless animals and rather few muscles remain (Fig. 4), as follows:

Muscle 40 (*M. nototrochantinalis*) is a coxal rotator. It originates near the mid-line of the mesotergum and inserts directly on the trochantin, a precoxal sclerite which has fused with the coxal rim.

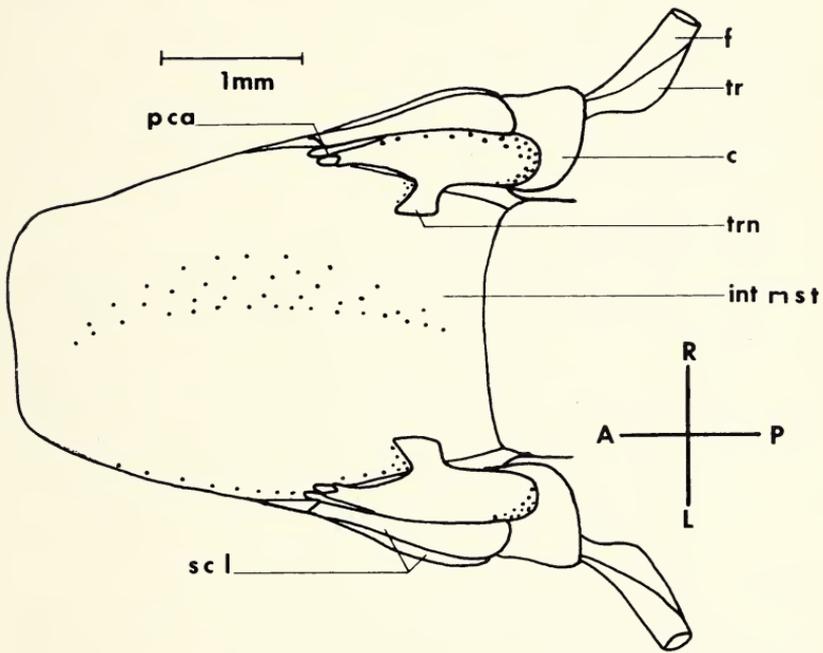


Figure 2: Internal view of the ventral exoskeleton of the mesothorax of *G. remigis* to show the relationship of the coxa to the mesothorax. The tergum and pleura have been dissected away

c	coxa
f	femur
int m s t	internal exoskeleton of the mesothorax
p c a	pleurocoxal attachment
s c l	suprocoxal lobes
tr	trochanter
trn	trochantin
L	left
R	right

Muscle 41 (*M. notocoxalis*) is also a coxal rotator and is antagonistic to muscle 40. It originates on the lateral wall of the mesotergum and inserts on an apodeme on the lateral coxal rim.

Muscle 44 (*M. furca-coxalis*) is a third coxal rotator. It is a very small muscle originating on the furca — a sternal process — and inserting on the anterior coxal wall.

Muscle 46 (*M. nototrochanteralis*). This is an extremely well developed muscle which originates on the anterior two thirds of the mesotergum and the dorsal region of the first phragma and inserts on several well developed apodemes from the medial edge of the trochanter. It is a major retractor of the leg.

Muscle 47 (*M. pleura-trochanteralis*) is also a well developed muscle. It originates on the ventral surface of the first phragma and the anterior half of the pleuron and sternum, and inserts on the same apodemes as muscle 46. It acts with muscle 46 to retract the leg.

Muscle 49 (*M. coxa trochanteralis medialis*). This muscle originates on the dorsal wall of the coxa and inserts on the same apodemes as muscles 46 and 47. It is a depressor of the trochanter.

Muscle 50 (*M. coxa trochanteralis lateralis*). This muscle originates on the ventral wall of the coxa and inserts on a flat apodeme which extends from the lateral rim of the trochanter.

It is antagonistic to muscles 46 and 47 and protracts the leg.

Muscles within the leg distal to the coxa were not considered.

Nervous System

The nervous system in *Gerris* is remarkable in being highly fused (Guthrie, 1961). All the thoracic and abdominal ganglia form a single ganglionic mass, which lies mostly in the prothorax. The three pairs of main nerves to the muscles of the mesothoracic leg arise from the more posterior region of this ganglionic mass — the region which Guthrie has identified as containing the mesothoracic ganglia. Nerve 1 sends branches to muscles 46, 40, and 41. Nerve 2 has a branch to muscle 41, but the main portion goes into the distal part of the leg and probably contains a large number of sensory fibres from the sensory receptors of the leg. Nerve 3 has branches to muscles 47, 44 and the distal part of the leg.

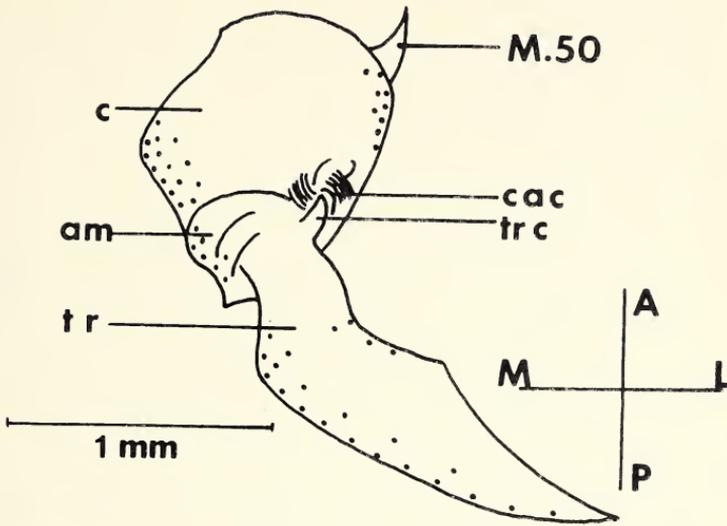


Figure 3: Right coxa and trochanter of *G. remigis* to show the articulation of the trochanter on the coxa

a m	articular membrane
c	coxa
c a c	coxal articulation for the trochanteral condyle
tr	trochanter
tr c	one trochanteral condyle, the other is directly opposite as shown in the diagram of Fig. 6.

Functions of the Muscles

The role of the coxal and trochanteral muscles can be inferred from a knowledge of their origins and insertions and of the articulations of the coxa and trochanter. These inferences have been confirmed by electrophysiological information from the muscles recorded simultaneously with monitoring of the leg movement (Bowdan, 1977).

Muscles 40 and 41 are antagonists and pivot the coxa around its anterior/posterior axis. In doing so they also lower and raise the extremities of the leg (Fig. 5). Contraction of muscle 40 rotates the coxa so that its dorsal aspect comes to lie laterally. The distal portion of the leg is lowered by this action (Fig. 5b). Contraction of muscle 41 rotates the coxa in the opposite direc-

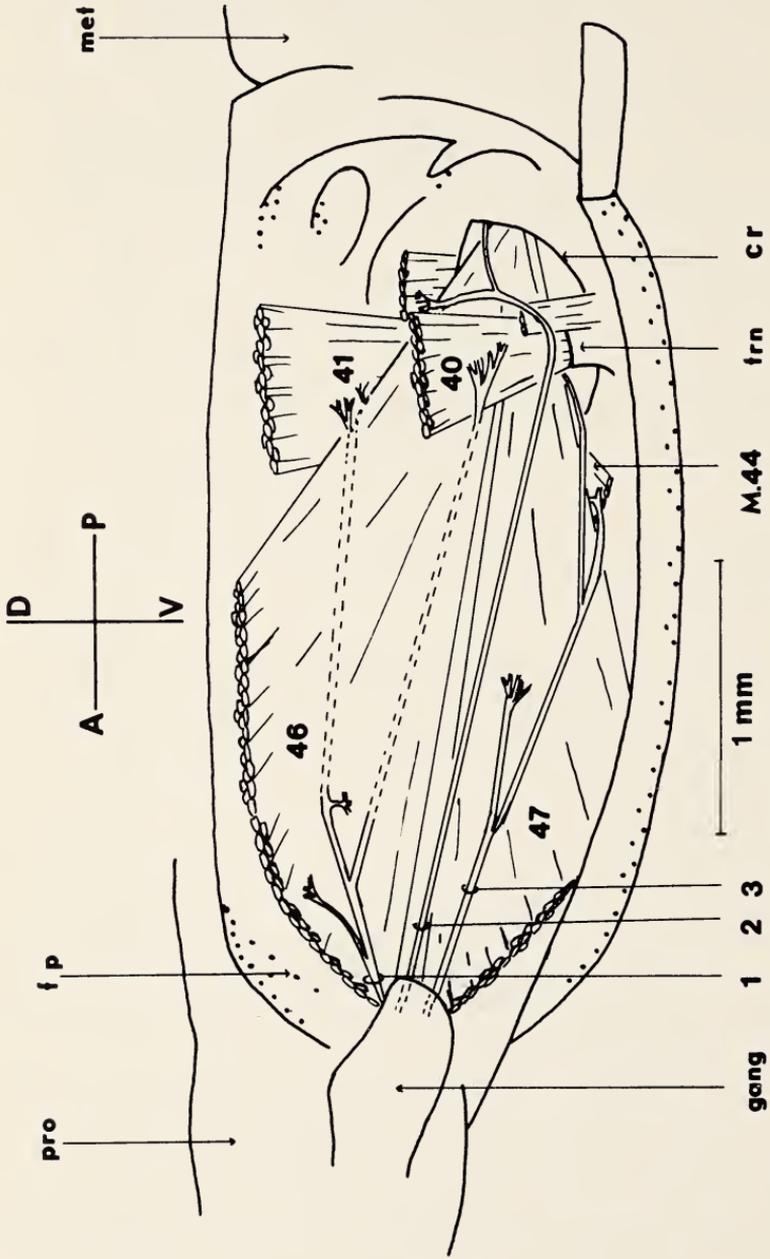


Figure 4

tion: the ventral surface of the coxa becomes lateral and the distal portion of the leg is raised (Fig. 5c). Muscles 50, and 46 plus 47 act on each side of the pivotal axis formed by the dicondylic articulation of the trochanter on the coxa (Fig. 6a). The pivotal axis is a dorso/ventral one (Fig. 6a) so the plane of movement of the leg is mediolateral (Fig. 6b). The trochanteral bend translates this into a forward and backward movement of the extremities of the leg. Contraction of muscle 50 swings the extremities forward (promotion, protraction; Fig. 6d) and contraction of muscles 46 and 47 swings them backwards (remotion, retraction; Fig. 6 c).

Thus coxal rotation can move the leg only in a dorso/ventral plane, the proximal part of the trochanter can move only in a medio/lateral plane and there are only five muscles which are important. It would seem as though the range of movement of the mesothoracic leg of *Gerris* would be very limited. In fact, however, the leg is extraordinarily versatile. It can move in a complete vertical circle, a horizontal semicircle, and any combination of the two.

DISCUSSION

Comparison with Gelastocoris and Belostoma

In gerrids the mesothoracic legs and their musculature have become so highly modified for rowing that it is of interest to compare them with those of Heteroptera with a different mode

Figure 4: Hemisection of the mesothorax of *G. remigis*, to show the major muscles and their innervation.

c r	coxal rim
gang	fused ganglionic mass
f p	first phragma
met	metathorax
pro	prothorax
trn	trochantin
40	muscle 40 M. nototrochantinalis
41	muscle 41 M. notocoxalis
44	muscle 44 M. furca coxalis
46	muscle 46 M. nototrochanteralis
47	muscle 47 M. pleurotrochanteralis
1,2,3	main mesothoractic nerve branches

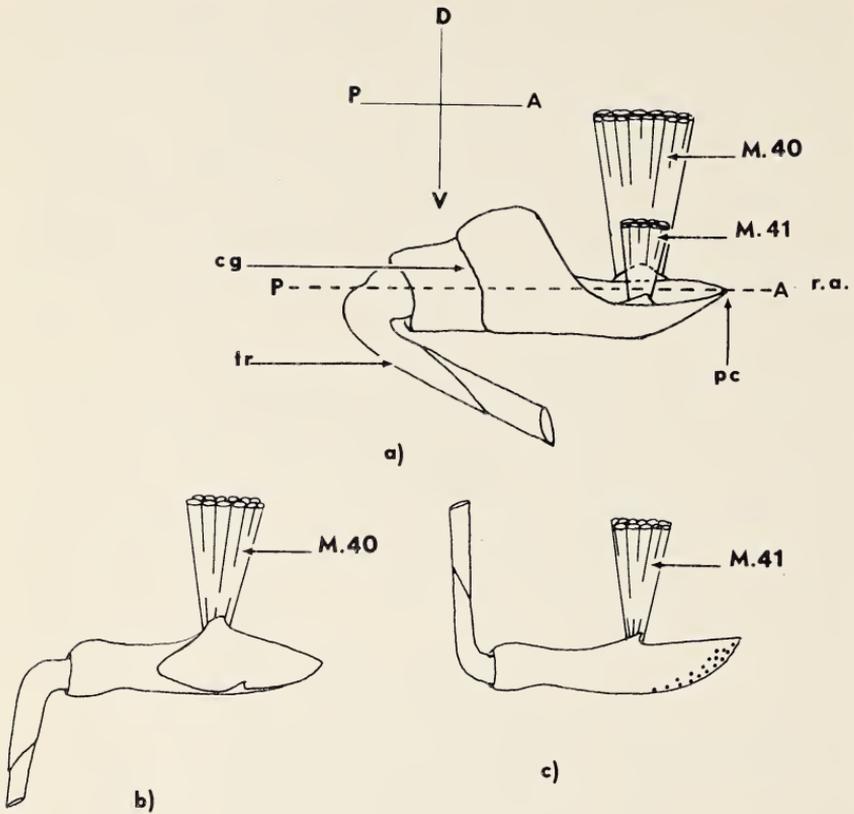


Figure 5: Lateral view of the coxa and trochanter of *G. remigis*. Diagram to illustrate the activity of muscles 40 and 41 in respectively lowering b) and raising c) the extremities of the leg.

- cg point of emergence of the coxa from the coxal groove
 pc position of the pleurocoxal attachment
 r a axis of rotation
 tr trochanter

of locomotion. Two such animals are *Gelastocoris oculatus*, the toad bug (Parsons, 1960) and *Belostoma flumineum*, the giant water bug (Segal, 1962).

The mesothoracic coxae of *Belostoma* and *Gelastocoris* are less concealed by the supracoal lobes, which are smaller than those of *Gerris*. These coxae therefore have more freedom of movement and also possess an additional coxal rotator (muscle 42). The coxae of *Belostoma* and *Gelastocoris* have rotated some-

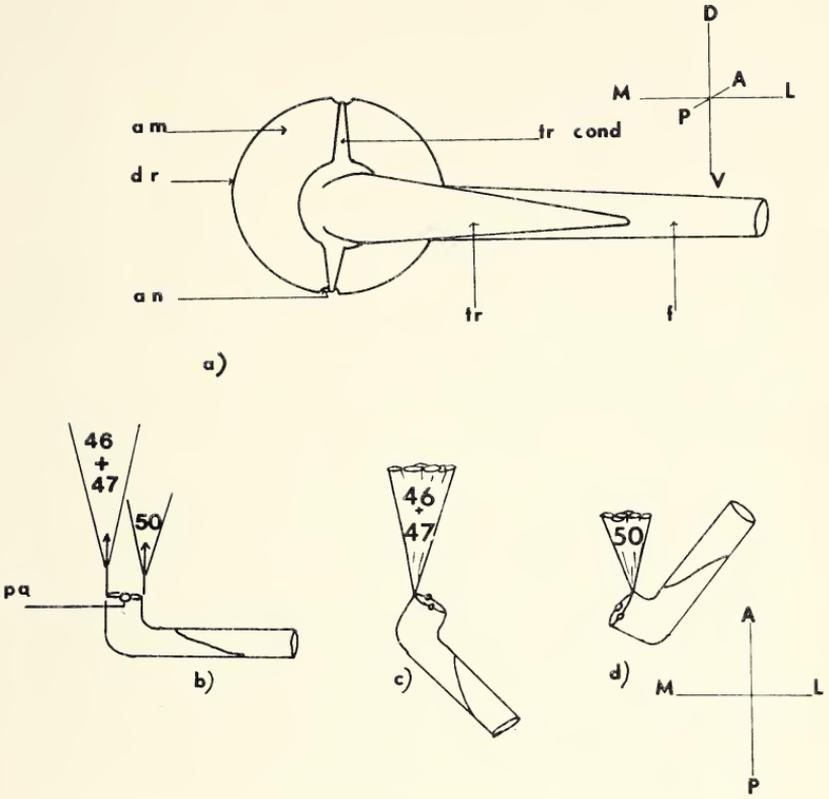


Figure 6: Diagrammatic representation of the articulation of the trochanter on the coxa, and of the actions of muscles 46, 47 and 50 on the mesothoracic leg of *G. remigis*.

- a) articulation of the trochanter on the coxa
 - a m articular membrane
 - a n coxal articular notch
 - d r distal rim of coxa
 - f femur
 - tr trochanter
 - tr cond trochanteral condyle
- b) resting position of the leg
- c) contraction of muscles 46 + 47 causes the leg extremities to go backwards (retract).
- d) contraction of muscle 50 causes the extremities to go forward (protract).

pa pivotal axis
 → direction of the major component of the muscles' force.
 Note that a) has an orientation which is different from that of b), c) and d).

what in comparison with the hypothetical plan of figure 1a, and are at an angle of about 45° from the vertical. This is in contrast with the mesothoracic coxae of *Gerris*, which have rotated so that their longitudinal axes are parallel with that of the mesothorax (Fig. 7). In addition the pleurocoxal attachments of *Gelastocoris* and *Belostoma* are medial whereas those of *Gerris* are anterior. The orientation of the coxae and the position of the pleurocoxal attachments in *Gerris* result in legs which project almost completely horizontally. In *Gelastocoris* and *Belostoma* the projection of the legs has both vertical and horizontal components. In all three insects the bend in the trochanter causes the femur to project anterolaterally.

The major change in the musculature has been the enormous development of muscles 46 and 47. In *Belostoma* these two muscles are rather small and have discrete origins, M. 46 on the lateral wall of the tergum and M. 47 on the pleural apophysis. Both insert on a single trochanteral apodeme. In *Gelastocoris* these muscles are also rather small. Muscle 46 has an origin and insertion similar to that of *Belostoma*; M. 47, however, is in two parts, one originating on the sternum, the other on the pleural apophysis. In *Gerris* these two muscles are so large as to be contiguous and it is difficult to distinguish between them; Guthrie (1961) in fact, considers them a single muscle. They originate over a wide area of the tergum, first phragma, pleuron and sternum and insert

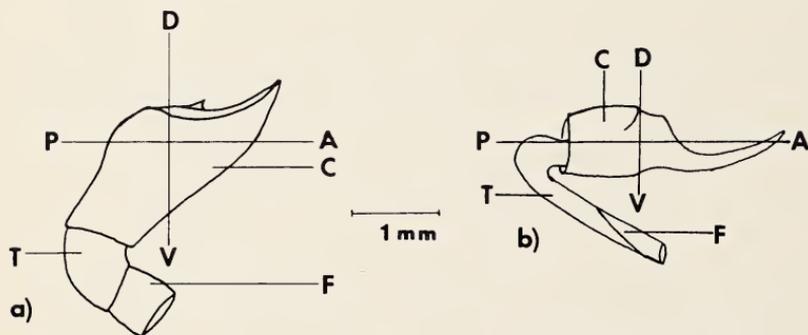


Figure 7: Coxae of the left mesothoracic legs of a) *Belostoma* b) *Gerris* to illustrate the relative positions of the coxal axes.

C coxa
F femur
T trochanter

on several long, broad, trochanteral apodemes. They effectively illustrate Hoyle's (1975) statement that powerful muscles have many points of attachment.

The reorientation of the gerrid leg about all three axes (Fig. 1), produced by the rotation of the coxa and the angle of the trochanter, has altered the functions of muscles 46/47 and 50, although they are still antagonists. The main force developed by muscles 46 and 47 in *Belostoma* and *Gelastocoris* is a vertical one, and their function is to depress the trochanter and therefore the extremities of the leg. In gerrids the main force developed is an anteriorly directed one which leads to a retraction of the leg (Fig. 6c). Muscle 50 in *Belostoma* and *Gelastocoris* raises the trochanter and the extremities of the leg. In *Gerris*, however, muscle 50 is the promotor of the leg (Fig. 6d). Muscles 40 and 41 move the leg forward and backward, respectively, in *Belostoma* and *Gelastocoris*. In *Gerris* these muscles respectively raise and lower the leg. These changes are not only the result of the rotation of the leg axis, but also of a slightly different position of the muscles themselves. In *Belostoma* the trochantin is close to the anterior margin of the coxal rim, so muscle 40 inserts anteriorly. In *Gerris* the trochantin is more posterior so that muscle 40 and 41 are in the same anterior/posterior position. Their antagonistic action is therefore across the anterior/posterior axis of the coxa. In *Belostoma* their antagonistic action is across a more mediolateral axis (Fig. 8).

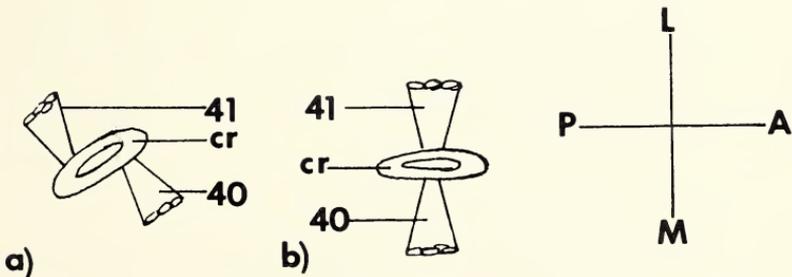


Figure 8: Diagrammatic representation of the insertions of muscles 40 and 41 in a) *Belostome* b) *Gerris*.

c r coxal rim

The mesothoracic leg of Gerris as support and oar

The modification of the coxal and trochanteral orientation of the gerrid mesothoracic leg has brought about a horizontal and lateral positioning of the leg which creates a wide base of support for the animal on the surface of the water. This orientation of the leg also rests the distal tip of the tibia and the whole of the tarsus on the surface of the water and puts the leg into a good position for the rowing stroke. If the leg had a more vertical orientation, only the tip of the tarsus would be on the surface of the water, providing a much smaller pushing area during the rowing stroke. During this stroke the leg sweeps powerfully backwards, pushing against the meniscus of the water surface (Darnhofer-Demar, 1968); such a stroke would be impossible if the leg were orientated vertically. Moreover, the greater the area of the leg resting on the water surface, the more efficient leg retraction will be in rowing. *Gelastocoris* walks on land and so a vertical orientation of the leg is a necessity. *Belostoma* swims underwater so that any orientation of the leg would push aside an equal volume of water. In *Gerris* the modification of the muscles' function follows directly from the change in orientation of the leg, and the increase in the size of muscles 46 and 47 leads to a very powerful rowing stroke so that, with a single stroke, the animal can cover a distance several times its own length (Darnhofer-Demar, 1968).

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NEW RECORDS FOR *THYREODON* FROM SOUTH TEXAS
(HYMENOPTERA, ICHNEUMONIDAE)

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Since 1973, I have been surveying the Hymenoptera of the lower Río Grande Valley of south Texas¹ and have established the presence there of *Thyreodon niger*, heretofore reported only from México and Guatemala (Townes, 1966, p. 190). Concurrently, Dr. James E. Gillaspay of Texas A. & I. University at Kingsville has loaned me for identification a series of Texan ichneumonids, containing not only additional material of *niger* but also two specimens of *T. laticinctus*, another Neotropic *Thyreodon* previously unrecorded north of México (Townes, 1966, p. 189).

The present contribution offers taxonomic and ecological notes on *niger* and *laticinctus* as well as brief discussion of the other U.S. *Thyreodon*.

Genus *Thyreodon* Brullé

The following combination of characters will separate this genus from all other New World ichneumonids:

Large to very large species, length of fore wing 16–28 mm.; apex of clypeus broadly triangular and reflexed; maxilla and labium about 0.4 as long as height of head; first intercubitus joins cubital vein far distad of second recurrent; second brachial cell with a long spurious vein that borders all or most of its hind edge; nervellus broken near upper 0.3; propodeum strongly inflated basally, so that the spiracle is situated in a deep depression; spiracle of first gastric tergite well behind middle; gaster strongly compressed.

Thyreodon is an exclusively New World genus of very large and conspicuous ichneumonids belonging to the Tribe Enico-

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spilini of the Subfamily Ophioninae. Townes (1966, p. 185-191) lists 24 species for the Neotropic Region but only three species currently are cited from America north of México (Hooker, 1912, p. 122; Muesebeck, Krombein and Townes, 1951, p. 401). Of these latter, *T. atricolor* inhabits the whole eastern U.S. and southern Canada and also has been recorded from Arizona, *T. fernaldi* is known from Colorado and Arizona, and *T. ornatipennis* from New Mexico.

T. atricolor has been reared from sphingid moths of the genera *Lapara* and *Paonias* (Hooker, 1912, p. 120-121). There are no host records for other *Thyreodon* but their large size makes it probable that they likewise attack sphingid or similar bulky lepidopterous larvae.

Many *Thyreodon* occur in subtropical or tropical forests, usually below 2000 m., but quite a few species also extend into deciduous forest, thorn scrub, savannas, and other drier habitats. Their ability to adapt to climates more arid than those favored by most ichneumonids probably explains the penetration of *T. niger* and *T. laticinctus* into the subtropical thorn scrub and semidesert of south Texas.

KEY TO THE SOUTH TEXAS *THYREODON*

1. Black with flagellum mostly yellow and gastric tergites 3-4 largely ferruginous; notaulus defined as a very shallow band of relatively fine puncto-reticulation, with a weak and appressed crest at front end; mesopleuron finely and densely punctate throughout; hind face of propodeum uniformly reticulate with only faint traces of a median channel and lateral depressions

. 1. *T. laticinctus*.

- Almost entirely black; notaulus strongly impressed and coarsely foveolate, with a conspicuously raised crest at front end; mesopleuron uniformly smooth, polished, and practically impunctate; hind face of propodeum with a deep, transversely wrinkled median longitudinal channel and two broader and shallower but also strongly trans-rugose lateral depressions, which are separated from the median channel by a pair of broad and high, mostly smooth and polished longitudinal elevations

. 2. *T. niger*.

1. *Thyreodon laticinctus* Cresson
(Fig. 1)

MATERIAL EXAMINED: 2 females, TEXAS (*Kleberg County*: Kingsville, 10 September 1972, P. W. Treptow; 30 September 1970, W. F. Granberry). (In collection of Texas A. & I. University, Kingsville, Texas).

In addition to the key characters, *laticinctus* differs from *niger* in its convex temples which in females are 0.87–1.0 as long as the eye in lateral view; differently shaped prescutellar ridge (Fig. 1); more dorsally intercepted postnervulus (lower abscissa 2.3–2.5 as long as upper); and larger size (length of fore wing 23.3–23.6 mm.).

It ranges from south Texas to Bolivia and may occur in almost any habitat from rainforest to semidesert. I have collected *laticinctus* at Tingo María, Perú in lush tropical wet forest and once observed but failed to catch it at the Bentsen Río Grande Valley State Park near Mission, Texas. It tends to fly near the ground but at great speed and thus is hard to net, in spite of its conspicuousness and exceptional size.

2. *Thyreodon niger* Cresson
(Fig. 2, 3)

MATERIAL EXAMINED: 6 females and 1 male, TEXAS (*Hidalgo County*: Bentsen Río Grande Valley State Park, 1–9 September 1976, C. C. Porter; Valley Botanical Garden at McAllen, 16–31 May 1974, C. C. Porter; *Kleberg County*: Kingsville, 27 April 1970, P. M. Kalisek, 19 September 1969, C. L. Zassow, "Site 55", 21 September 1973, Gillaspay and party; *Starr County*: Río Grande City, 2 August 1975, J. E. Gillaspay). (In Collection of Texas A. & I. University, Kingsville, Texas and Collection of Charles C. Porter, 301 N. 39th Street, McAllen, Texas.)

Niger differs from *laticinctus* in several characters besides those mentioned in the key. The temples are receding and viewed laterally measure 0.70–0.75 as long as the eye in females and 1.0 as long in males; the prescutellar ridge is of different conformation (Fig. 2); the postnervulus is more ventrally intercepted (lower abscissa 1.0–1.4 as long as upper); and the average size is smaller (length of fore wing 16.0–17.6 mm.).

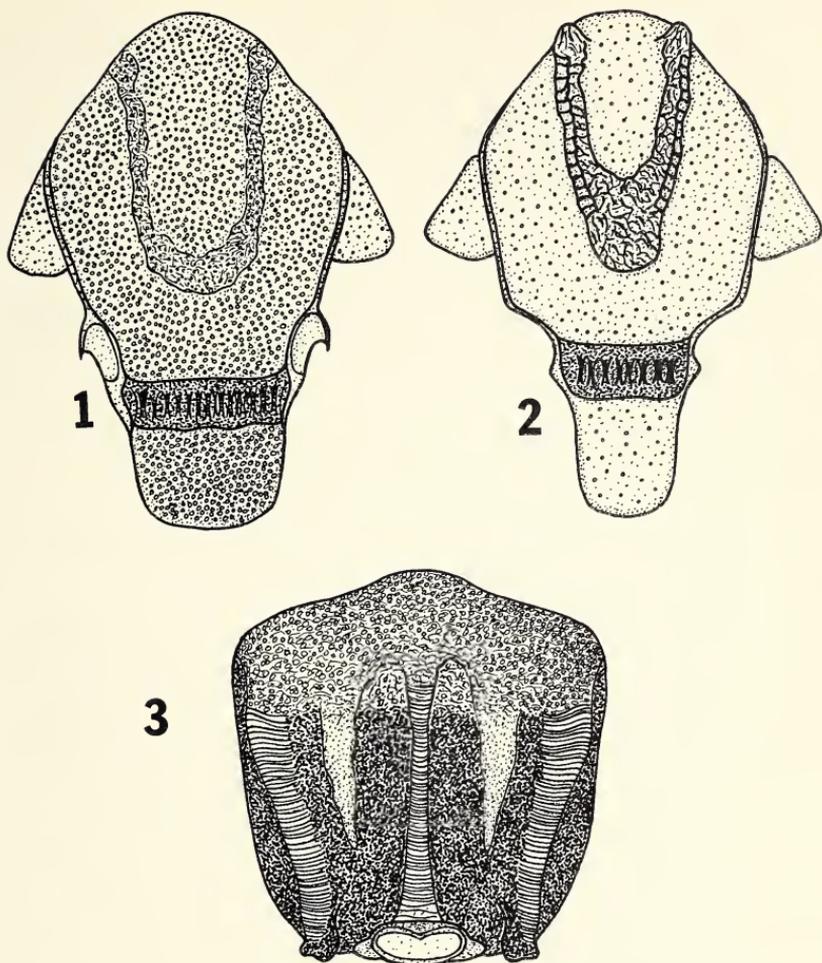


Fig. 1 *Thyreodon laticinctus* Cresson, female. Dorsal view of mesonotum showing weakly impressed and finely rugulose notauli and peculiarly modified prescutellar ridge.

Fig. 2 *Thyreodon niger* Cresson, female. Dorsal view of mesonotum, showing deeply impressed, coarsely foveolate notauli, raised crest at anterior end of notauli, and unmodified prescutellar ridge.

Fig. 3. *Thyreodon niger* Cresson, female. Posterior view of propodeum, showing the median and lateral channels.

The median channel and lateral depressions on the apical face of the propodeum are an unusual feature. Evidently, they are structures which receive the first gastric segment and the basal part of the legs, when these are elevated and folded backward. Observation of living specimens eventually may show that this has adaptive significance in oviposition, courtship, mating, or warning behavior.

Niger ranges from Kleberg County, Texas to Guatemala and has been recorded most often from México. In south Texas it inhabits semiarid scrub as well as the more humid woodlands of the lower Río Grande Valley. It flies slowly close to the ground, usually among herbaceous vegetation in partial shade of trees or shrubs. At McAllen I have collected *niger* in a grove of *Celtis lindheimeri* and at Bentsen Río Grande Valley State Park in a humid thicket dominated by *Pithecellobium flexicaule*.

Although *laticinctus* and *niger* are the only *Thyreodon* definitely recorded from Texas, ranges of the other U.S. species are such that all may enter some part of the state.

T. atricolor Olivier extends from the "Atlantic to Manitoba, Minnesota, Iowa, and Missouri in the Transition and Upper and Lower Austral Zones" and occurs also in "Kansas and Arizona" (Muesebeck, Krombein, and Townes, 1951, p. 401). Examination of material from the eastern United States shows that this species agrees with *laticinctus* in most characters studied but lacks a ferruginous band on the gaster, has the notauli a little stronger, and the propodeum very coarsely reticulate but rather shining with a pronounced median channel on the hind face (in *laticinctus* the propodeum is more finely and opaquely wrinkled with a faintly impressed postero-median channel). Eastern populations of *atricolor* show almost uniformly dark wings and body but those from Iowa west often have the head and mesosoma partly brownish and the wings more or less variegated with yellow.

I have not examined specimens of *T. fernaldi* Hooker but the literature suggests that this species may belong to the same group as *laticinctus* and *atricolor*. Because of its more or less ferruginous gastric tergites 2-5 and finely reticulate, at most faintly channeled propodeum, *fernaldi* especially resembles *laticinctus* but differs conspicuously by having "fuliginous wings, with the basal 2/3 of the anterior and a small spot on the posterior fulvous or fulvo-fuscous" (Hooker, 1912, p. 131). *Fernaldi* ranges from

Colorado and Arizona to México and thus may be looked for in west Texas.

No material of *ornatipennis* Cresson was available for study but Hooker's description (1912, p. 122) shows it to be distinctive in its almost uniformly reddish brown ground color, "fuliginous wings with a fulvo-hyaline spot extending across the middle and sometimes occupying most of the base", deep notauli, and finely reticulate propodeum with an apico-median channel. This species is known only from Orizaba, México and from an unspecified locality in "New Mexico". It also may occur in west Texas.

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LIFE HISTORY AND ECOLOGY OF *DIPLOPERLA*
ROBUSTA STARK AND GAUFIN
(PLECOPTERA: PERLODIDAE)

BY DIANA L. ASHLEY,¹ DONALD C. TARTER¹
AND WILLIAM D. WATKINS²

The purpose of this study was to describe the life history and ecology of the perlodid stonefly *Diploperla robusta* Stark and Gaufin in a small, woodland stream in Cabell County, West Virginia. No papers have been published on the life history and ecology of *D. robusta*. Ashley (1977) reported that the naiads of *D. robusta* have a TL_m^{96} pH value of 4.6. Several investigators, including Smith (1913), Needham and Claassen (1925), Claassen (1931), Frison (1935, 1942), Ricker (1949), Minshall and Minshall (1966), Tarter and Krumholz (1971), Harper (1973), and Vaught and Stewart (1974), have reported studies on the ecology of North American stoneflies.

TAXONOMY AND DISTRIBUTION

Diploperla was originally listed as a subgenus of *Perla* by Needham and Claassen (1925). Ricker (1952) considered it a monotypic subgenus of *Isogenus*. Illies (1966) gave it generic status and listed the only species as *Diploperla duplicata* (Banks). In 1974, Stark and Gaufin described *D. robusta* to replace what had been named *D. duplicata*. According to Stark and Gaufin (1974), *D. duplicata* and *D. robusta* are two distinct species.

The known range of *D. robusta* is in the eastern portion of the United States, including Kentucky, Indiana, Ohio (Stark and Gaufin, 1974), and West Virginia. According to Hissom and Tarter (1976), *D. robusta* is recorded from 20 counties in West Virginia.

MATERIALS AND METHODS

The study area is an unnamed tributary of Fourpole Creek, Cabell County, West Virginia. The county is located at 82°24'43"W

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longitude and 38°22'52"N latitude. It varies in elevation from 150.6 m at the mouth of Fourpole Creek to 355.1 m at a knob located in Salt Rock (Krebs and Teets, 1913). The tributary is 3.2 km long and 1.5 m wide. The substrate of the stream bed is gravel and sand. The riparian woodland is primarily composed of box elder, *Acer negundo* L.; red maple, *A. rubrum* L.; sugar maple, *A. saccharum* Marsh.; white oak, *Quercus alba* L.; redbud, *Cercis canadensis* L.; and hop hornbeam, *Ostrya virginiana* (Mull.) K. Koch.

Intensive and systematic field collections were made monthly between 26 April 1975 and 30 September 1976. The collections of naiads were done in ten minute sampling periods. A long handled dredge with a fine mesh net (60 threads per inch) was raked along the substrate. By kicking the substrate, the naiads were loosened from their habitat and drifted into the net, and subsequently were preserved in 10 percent formalin.

Water temperature was measured with a mercury thermometer placed near the collecting site. The following water chemistry parameters were measured with a Hach chemical kit, Model A1-36-WR: hydrogen ion concentration (pH), dissolved oxygen, total hardness, carbon dioxide, and alkalinity (carbonate and bicarbonate).

In order to determine size classes, length-frequency histograms were arranged in 1 mm groups for 320 *D. robusta* naiads. The naiads were measured by a dial vernier caliper (nearest 0.1 mm). The monthly index of growth was determined by head width which was measured for 320 *D. robusta* naiads by an ocular micrometer (nearest 0.1 mm) in a Bausch and Lomb dissecting microscope.

Naiadal food habits were determined by foregut analysis. For each month ten naiads were chosen at random. The foregut was removed by cutting off the head and making a ventral incision to the abdomen. The foregut was cut from the anterior end of the hindgut and placed on a slide with a drop of water. It was then carefully slit open and its contents emptied into the water. A Bausch and Lomb dissecting microscope was used to identify the contents. The percentage frequency of occurrence (%FO) was computed for each item and the average number of specimens with foreguts containing each item (\bar{x}) was determined.

To study the emergence pattern of *D. robusta*, the study area

was searched for adults on the wing or exuviae in the months when no naiads were found (May through July). The rocks and vegetation were checked for the shed skins of adults.

Fecundity in the adult stonefly was determined by direct counts of the ovarian eggs using a binocular dissecting microscope (Bausch and Lomb). Both ovaries were excised from 15 females (only eight contained eggs) and 241 eggs were counted. The diameters of 20 percent of the eggs from eight females were measured with an ocular micrometer (nearest 0.1 mm) under a Bausch and Lomb dissecting microscope.

The chi-square test was applied to 23 laboratory reared adults to determine any significant departure from the 1:1 ratio at the 0.05 confidence level.

RESULTS AND DISCUSSION

Stream Environment.—The average annual temperature in the tributary for the study period was 13.9 C. The monthly extremes were 5 and 22.7 C in November and August, respectively. The hydrogen ion concentration (pH) ranged from 7.5 to 8, with an average of 7.8. Dissolved oxygen concentration ranged from 4 to 15 mg/l in August and January, respectively, with a mean of 8.5 mg/l. Carbon dioxide values ranged from 5 mg/l in April, May, June, January and February to 25 mg/l in October. The mean was 18.7 mg/l. Total hardness ranged from 88.5 to 205.2 mg/l in April and November, respectively, with a mean of 135.6 mg/l. Carbonate alkalinity values ranged from 34.2 to 136.8 mg/l in April and October, respectively: the mean value was 72.7 mg/l.

Naiadal Development.—Length-frequency histograms indicated that one size class was present in the naiadal population of *D. robusta* (Figure 1). The earliest naiad was collected 30 August 1975 and measured 2.8 mm in body length. The largest naiad was found 26 April 1976 and measured 16.9 mm in body length. No naiads were found in the stream from May through July.

Frison (1935) stated that *Isoperla duplicata* (= *D. robusta*) is univoltine in Turkey Run State Park (Newby Gulch), Indiana. Minshall and Minshall (1966) did a study on two other perlodid stoneflies, *Isoperla clio* (Newman) and *Isogenus decisus* Walker and found both to be univoltine.

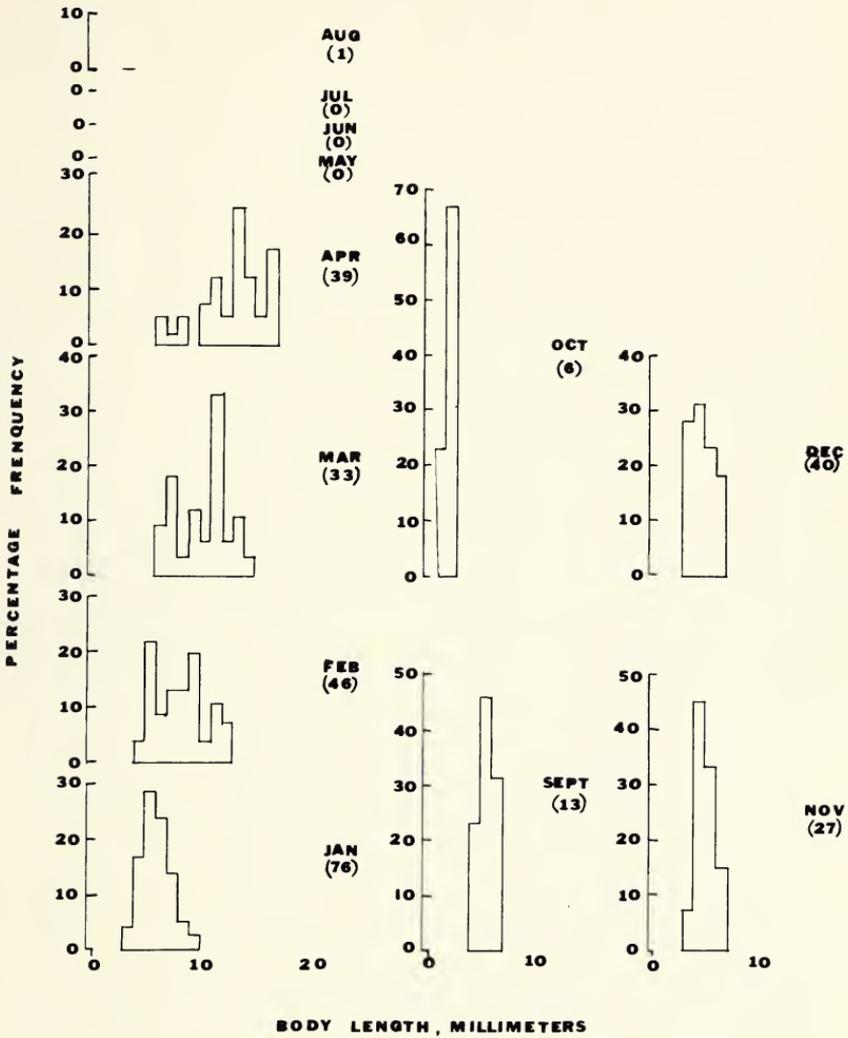


Figure 1. Length-frequencies at monthly intervals for *Diploperla robusta* naiads from a small, woodland stream, Cabell County, West Virginia. The number of naiads collected each month is given in parentheses.

Head widths of the naiads were used to show the monthly variation in growth (Figure 2). Naiads collected in March and April had a mean head width of 1.9 and 2.4 mm (maximum width), respectively. This represented the greatest growth rate, 49 percent, throughout the year. No naiads were found from May to July, and the appearance of one naiad in August, 0.62 mm head width, corroborates the theory of a new size class beginning.

From November through April, the temperature steadily increased from 5 to 15 C, corresponding to the increase in mean head widths and greatest growth rate (March to April). When the new size class appeared in August, the temperature was 22.7 C and dropped steadily until November when the previous pattern began again.

Naiadal Food Habits.—Of the 76 foreguts examined, 30 (40%) contained food and 46 (60%) were empty. Foregut analyses of the naiads of *D. robusta* indicated that dipteran larvae, primarily chironomids, ranked first in percentage frequency of occurrence in all seasons. From December through February, chironomids comprised the total foregut contents. There was an average of 5.6, 4.9, and 2.8 larvae per foregut in December, January, and February, respectively. In March and April, the naiads fed on chironomids and mayflies' (Baetidae). The chironomids averaged 5.6 and 10.8 per foregut in March and April, respectively, and the mayflies averaged 1.5 and 1.0 per foregut in March and April, respectively. No naiads were collected from May to July. When the size class was beginning in August, the single stonefly found contained no food. Likewise, from September to November, no foregut contents were found in the naiads. Many diatoms were found in the foreguts of *D. robusta* naiads. The predominant species were *Navicula* spp. and *Surirella* sp., and in smaller numbers, *Meridion* sp., *Rhoicosphenia* sp., and *Fragillaria* sp.

Frison (1935) stated that *Isoperla duplicata* (= *D. robusta*) was carnivorous but did not mention its diet. Minshall and Minshall (1966) noted that two other perlodid stoneflies were carnivorous. They reported that *Isoperla clio* and *Isogenus decisus* fed on larval chironomids and mayflies (Baetidae).

Adult Stage.—When the naiads of *D. robusta* are ready to emerge as adults, they crawl from the water to the surrounding vegetation or rocks. The emergence data were calculated by counting exuviae found on the concrete base of a bridge. Few adults were

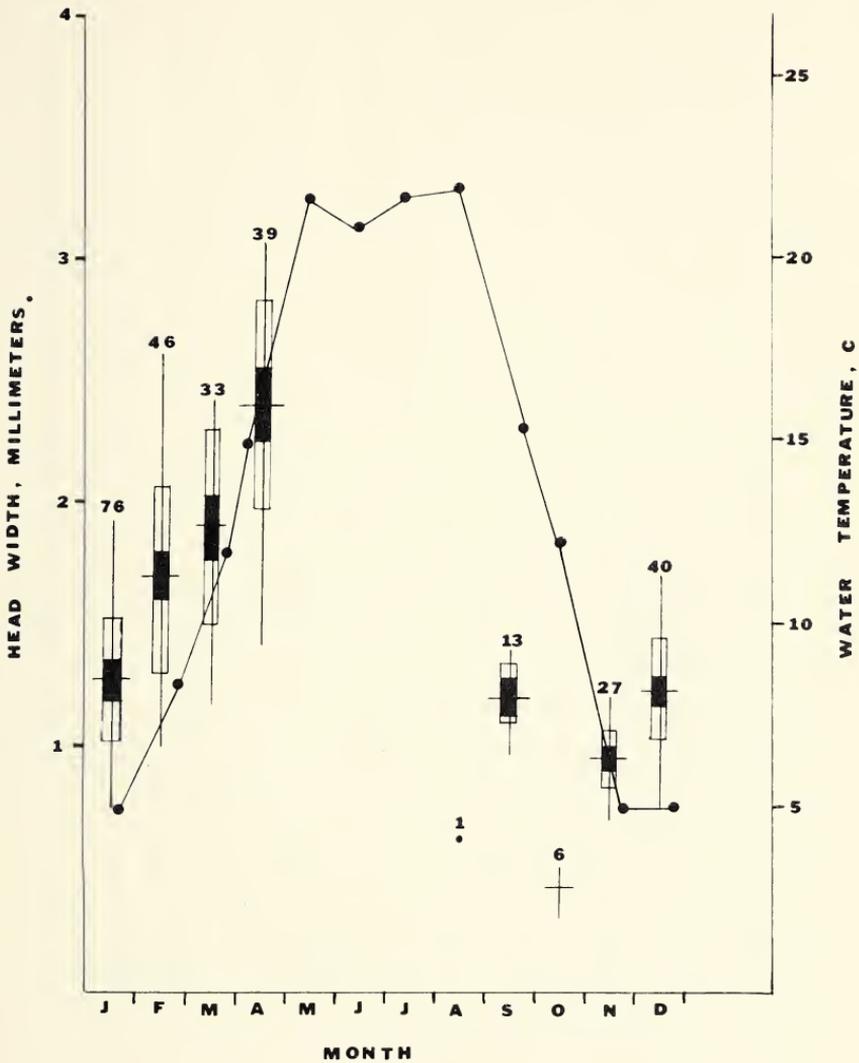


Figure 2. Monthly variation of the head widths in *Diploperla robusta* naiads from a small, woodland stream, Cabell County, West Virginia. Vertical lines = ranges, horizontal lines = means, dark rectangles = two times the standard error of the mean, larger open rectangles = one standard deviation, numbers = sample sizes, and solid lines = temperature (C).

observed. On May 11, at a temperature of 20 C, the first exuviae (19) were found at the water line and up to four feet on the wall of the bridge. One adult female was found parasitized in a spider's nest. The peak of emergence was on May 12 when 31 exuviae and three females were collected. From May 13 through 19, 51 exuviae were collected from the wall of the bridge.

Minshall and Minshall (1966) found the adults of *Isoperla clio* and *Isogenus decisus* emerged between 4:30 and 6:30 PM. Minshall and Minshall (1966) stated they found *Isoperla clio* exuviae several meters away from the stream, with the first adults collected in April, then a few in June, with a peak in April. According to Harper (1973), *I. clio* adults emerged on May 17 and lasted 20 days. He also reported on other setipalpiian Plecoptera and the emergence patterns are all similar.

The direct count of ovarian eggs of fifteen females (only eight contained eggs) resulted in a range of 4 to 60 eggs per female; the mean was 30. Seven of the females examined had ovaries containing undeveloped eggs or none at all. The eggs of *D. robusta* are spindle shaped and light, golden-brown color.

Twenty percent of the eggs from eight females had a range of 0.28 to 0.43 mm ($\bar{x} = 0.39$) in length and 0.21 to 0.32 mm ($\bar{x} = 0.27$) in diameter.

The months of May through July for two summers revealed no naiads in the stream. At this time, the stream was dried up and possibly the eggs of *D. robusta* were diapausing for 12-14 weeks. The rains of August caused the stream to be normal again and at this time the naiads, very small in size, reappeared.

Under laboratory conditions, Miller (1939) reported that the eggs of *Pteronarcys* (= *Allonarcys*) *proteus* Newman diapaused from 305 to 325 days. Diapause was apparently not obligatory since hatching was forced by high temperature. Harden and Mickel (1952) reported that the eggs of *Isoperla bilineata* (Say) oviposited in June and maintained in the laboratory did not hatch until October. The eggs of *I. clio* apparently hatch in August and September (Minshall and Minshall, 1966).

The chi-square test indicated a significant departure from the 1:1 ratio at the 0.05 confidence level. The sex ratio was based on a laboratory reared sample of 8 males and 15 females, a ratio of about 53 males to 100 females.

To determine longevity of *D. robusta*, several naiads with dark wing pads were placed in rearing cages. The average time any single adult lived was five to six days.

A male and female adult were placed in a cage together to observe mating behavior. They both died before mating occurred. Reproductive behavior was reported in two other perlodid stoneflies by Minshall and Minshall (1966). *Isoperla clio* and *Isogenus decisus* females apparently deposit their eggs directly into the water in the form of packets by dipping the tip of the abdomen while in flight.

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SWIMMING ABILITY OF NOTONECTIDAE (HEMIPTERA)

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In an earlier paper, I (Gittelman 1974) studied adaptations of fore-leg size and hind-leg lever systems for prey capture and swimming. Presently, the ability of 4 species of Connecticut *Notonecta* to swim against a current is studied as a test of predictions generated by this earlier work.

To study leg mechanics we will schematically represent a leg or leg segment (femur, tibia, and tarsus) as a simple lever with the fulcrum at the articulation between it and the structure on which it articulates. Force (F_m) is applied at the muscle insertions at the proximal end and the lever arm is the distance (R_1) from the fulcrum to where the force is applied, the resultant force (F_r) is the force generated by the lever to do work (press against water while swimming) at any given distance (R_2) away from the fulcrum and is related to the muscular force as follows:

$$F_r = \frac{R_1}{R_2} F_m$$

The ratio R_1/R_2 corresponds to the mechanical advantage. Smith and Savage (1956) compared the mechanical advantage of muscles of the forelegs of the horse (*Equus*) and a fossorial armadillo (*Dasypus*). They concluded that if the R_1/R_2 ratio is large, leg movement will be powerful though slow. If the ratio is small, it will be fast but weak.

Gittelman (1974) measured R_1/R_2 ratios in 10 species of North American Notonectidae in the genera *Notonecta* (4 spp.), *Buenoa* (4 spp.) and *Martarega* (2 spp.). The total length of the hind-leg (R_2) from the trochanter-coxa articulation to the distal tip of the tarsi (not including the tarsal claw), and the lever arm (R_1), the distance from the ventral trochanter-coxa articulation to the proximal end of the trochanter at the insertion of the depres-

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sor muscle tendon, were measured for each species of backswimmer studied. As an example of these measurements a ventral view of the proximal leg segments of the metathoracic leg of *Notonecta undulata* is included in Figure 1. In this earlier study, the mechanical advantage differed among species of different genera, with *Martarega* having the lowest and *Buenoa* the highest R_1/R_2 ratios. It was concluded that the low mechanical advantage of the former is an adaptation to living in a current. These backswimmers live in rivers and swim slowly against the water flow, maintaining their position, while feeding on immobile prey trapped in the water surface. The larger mechanical advantages found in *Buenoa* seem associated with a diet of highly mobile prey requiring the predator to accelerate rapidly in pursuit. It was concluded that the intermediate mechanical advantage exhibited by *Notonecta* represents an ecological compromise between *Buenoa* and *Martarega*. *Buenoa*, which swim below the water surface, prey almost exclusively on free-moving prey. *Notonecta* spend much of their time at the water surface and probably eat

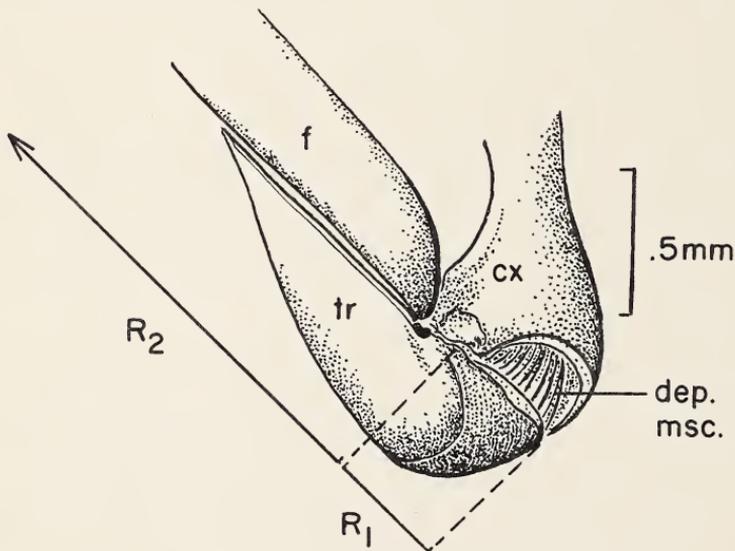


Fig. 1. Ventral view of the proximal leg segments of the right metathoracic leg of *Notonecta undulata*. tr, trochanter; cx, coxa; f, femur; dep. msc., depressor muscle; R_1 , the lever arm; R_2 , the lever (see text for explanation).

a greater proportion of prey stranded on the water film than do *Buenoa*, but less so than *Martarega*. However, since *Buenoa* and *Notonecta* are found in static water, one expects them to be more similar to each other than either is to *Martarega*, which is the case.

Significant differences between mechanical advantages of *Notonecta* spp. were found to exist. In the present Table 1 these R_1/R_2 coefficients are reproduced. The R_1/R_2 coefficient of *insulata*, the largest backswimmer, is smallest of the species studied. The coefficient of *lunata* is smaller than that of *undulata* and *irrorata*, but the latter two are not significantly different from each other. The magnitude of R_1/R_2 appears to increase with body size in all but *insulata*.

If as I proposed earlier (Gittelman 1974), low values of mechanical advantage are adaptations for low acceleration swimming (e.g. continual swimming against a current), then of these 4 species of *Notonecta*, *insulata* should be best able to swim against a current. The following is a test of this prediction.

Table 1. Measurements[#] (in mm), R_1/R_2 coefficients[#] and the maximum water current where position could be maintained of 4 species of *Notonecta* (Notonectidae). Current speeds with different letters are significantly different at the $P < 0.01$ level (2-tailed t-test). \bar{x} , mean; s, standard deviation.

Species	Body length	R_2 (leg length)	R_1 (lever arm)	R_1/R_2	Water current (cm/sec)	
					\bar{x}	s
<i>N. insulata</i>	14.50	14.93	0.458	0.031*	8.74 ^a	2.39
<i>N. lunata</i>	9.78	9.83	0.317	0.032*	4.15 ^b	1.57
<i>N. undulata</i>	11.87	11.63	0.390	0.034	6.21 ^c	2.26
<i>N. irrorata</i>	13.83	13.14	0.471	0.036	4.19 ^b	1.58

[#]data taken from Gittelman (1974).

*Significantly different from next R_1/R_2 value at $P < 0.05$ level (2-tailed t-test).

METHODS

The apparatus consisted of a plexiglass trough (7 × 32cm) within which was placed a second, "U" shaped trough with screen baffles on each end. Water was fed into the inner trough by means of a 2.4cm hose coming from a 20 l reservoir positioned 35cm above the trough. A hose from a second distilled water source kept the reservoir filled and an overflow kept the water level constant. In this way water within the hose entering the trough was maintained at a constant pressure. A clamp between the reservoir and the trough regulated the current flow. Water flow within the confined area of the U-shaped inner trough appeared to be uniform when checked with methylene blue dye. Current velocity was measured with a Gurley No. 625 Pygmy Current Meter. Water temperature was maintained between 18 and 22°C.

Insects were placed singly in the inner trough and water velocity increased until they appeared to be unable to make headway against the current. A total of 45 trials were run for each species. Trial results are given in Table 1.

RESULTS AND DISCUSSION

As predicted, *insulata* is best able to maintain its position against a current. But the ability of backswimmers to swim does not seem related to the mechanical advantage of swimming legs alone. Presumably, larger backswimmers have greater muscle volumes per unit of frictional surface, and as in Corixidae (Young 1969) swimming ability seems improved by large body size.

Notonecta insulata and *irrorata* are similar in body size but differ in hind-leg mechanical advantage and accordingly in swimming ability. The lower mechanical advantage of *insulata* favors its ability to swim against a current. Laboratory observations (Gittelman, in prep.) on the ability of these species to capture highly mobile prey (Corixidae) indicate that *irrorata*, presumably in part because of its higher mechanical advantage, is better able to make the short, quick attacks, necessary for capturing these prey.

When compared to *irrorata* and *undulata*, *lunata* has a low mechanical advantage. But due to its small size it swims only as well as *irrorata*. *N. undulata* is intermediate in body size and mechanical advantage and is intermediate in swimming ability.

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OBSERVATIONS ON THE NESTING BEHAVIOR AND
PREY OF GORYTINE WASPS IN TRINIDAD
(HYMENOPTERA, SPHECIDAE)*

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INTRODUCTION

The gorytine wasps comprise the tribe Gorytini of the sphecid subfamily Nyssoninae. They are a generalized group and all the higher Nyssoninae could have arisen from a gorytine ancestor (Bohart and Menke, 1976). Our knowledge of their ethology has been summarized by Evans (1966) and is based largely on studies in the Northern Hemisphere. Biologically these wasps are little known in the tropics or south temperate regions, although some recent observations have been made in Australia and Argentina (Evans and Matthews, 1971, 1973). The nests are mass-provisioned with Homoptera, mainly Fulgoroidea, Cicadidae, Cicadellidae, Cercopidae and Membracidae, and, in Australia, Eurymelidae, but there are few records of the prey of tropical species.

I have found a number of Gorytini nesting in Trinidad, West Indies. Several species belong to the wide-ranging genus *Hoplioides* and one to *Sagenista*, a closely related neotropical genus described by Bohart (1967). My observations provide new data on tropical species and confirm in large part what is known elsewhere of gorytine nesting behavior and prey preferences.

ECOLOGY OF NESTING SITES

Gorytine wasps nest in the ground, generally in bare, sandy soil and dig relatively shallow, normally multicellular nests. Much of Trinidad is forested or alienated for plantation crops and suitable areas for ground-nesting species are limited. All the nesting sites I found in Trinidad were in small exposed areas free from vegetation and most were in close proximity to forest.

In the foothills of the Northern Range nesting sites were found in the following areas: in lower montane rain forest in the Caura Valley, about 5 km north of Tacarigua; at the edge of a cacao plantation adjacent to similar forest in the Maracas Valley, some

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6 km north of St. Augustine; and in evergreen seasonal forest at Cumaca, about 14 km north of Sangre Grande. In both the Caura and Maracas Valleys the nesting sites were near streams. Wasps were also found nesting in the foothills of the Central Range in evergreen seasonal forest at Talparo and Mundo Nuevo, about 16 and 20 km respectively south of Arima.

In two areas nesting sites were encountered at some distance from forest. One was at St. Augustine, a residential area with many planted trees 13 km east of Port of Spain. The other was at North Post, an open windswept hillside cleared of forest on the North Coast, about 10 km northwest of Port of Spain and within 500 m of the Caribbean Sea.

Hoplisoides umbonnicida Pate

Hoplisoides umbonnicida was described by Pate (1941) as a new species based on material I sent him from Trinidad in December 1940. The type specimens, together with 3 cocoons and a specimen of the treehopper prey *Umbonia spinosa* (Fabricius) (Membracidae), are in the Academy of Sciences of Philadelphia, as are probably 2 further wasps, one with a specimen of the same treehopper prey pinned with it, which I sent Pate in March 1942.

H. umbonnicida is a medium-sized species (female 12 mm long, male 10 mm long), black but broadly marked with yellow on the head, thorax and abdomen. I first encountered it in the Caura Valley on 5 August 1938. A female burdened with a large treehopper was seen descending slowly to its nest in a narrow sandy beach deposited near a natural swimming-pool by the fast-flowing Tacarigua (or Caura) River. The nesting site was in rather coarse sand and was a true stream-side locality. The wasp appeared to drop silently out of the sky coming down ever more slowly as it lost height. Descent was more or less vertical from a height of about 2 m. Related species are known to approach the nest obliquely, slowly and from a considerable height. The wasp opened the nest quickly and plunged in precipitously with the prey. The nest was excavated and the burrow found to be oblique and no more than 10 cm long. Three cells were dug out each containing a cocoon, and the female was found in the nest with its prey in process of provisioning a fourth cell. It is possible that further cells were present with stored prey and developing wasp larvae, but they were not found.

The prey carried by the female was an adult hoplophorine tree-hopper *Umbonia spinosa*. This is the largest membracid known from Trinidad, 15 mm long, bright green with 6 vivid red longitudinal lines on the enlarged pronotum, which is drawn out dorsally into a sharp point, and bears a resemblance to a large plant thorn. It is a rare species in Trinidad, where it has only once been found feeding on indigenous woody shrubs or small trees of the genus *Inga* (Leguminosae), which do not themselves bear thorns and often occur in the understory of lower montane rain forest. The prey was actually larger than the wasp itself, and was clasped venter to venter by the female's middle legs with the head foremost and the enlarged pointed pronotum projecting downwards. Had the sand not been friable at the entrance to the nest it would have been difficult for the female to enter so rapidly with such large prey. As it was, in entering the nest the prey was displaced rearwards to the hind legs of the wasp and the sharp point of the pronotum made a clearly perceptible furrow in the sand at the nest entrance as the prey was drawn in.

Three cocoons were removed from the nest. They were ovoid, greyish, hard and smooth, rounded at the anterior end and pointed at the posterior end. Two were about 12 mm long and 5.5 mm wide and the other about 10 mm long and 5 mm wide. There were no pores in the walls of the cocoons. Female wasps emerged from the larger cocoons and a male from the smaller one, and represented the type, one of the female paratypes and the allotype respectively on which Pate based his description of *H. umbonicida*.

My second encounter with what I took to be this species was on 25 January 1942 at Talparo, where I found it nesting in the fine, friable sand on the floor of a sandpit. Several wasps were observed provisioning their nests with large membracids. They descended slowly to the closed nest entrance, which they opened quickly with the fore-legs, and disappeared from sight rapidly with their prey. Two females were captured, one with an adult of *Umbonia spinosa*. No nests were excavated. The 2 females and specimen of prey, which were sent to Pate in March 1942, came from this source.

Hoplisoides vespoides (F. Smith)

In 1973 material from Trinidad (as well as a female from Paramaribo, Surinam collected on 13 October 1938 by D. C. Geijskes)

was studied by Professor R. M. Bohart, who identified it as *H. vespoides*. These specimens were taken between 1942 and 1951 at 5 different nesting sites in the Northern and Central Ranges. Two females collected in March 1935 in Trinidad without specific locality by D. Vesey-FitzGerald are also in the Museum of Comparative Zoology, Harvard University.

On 16 May 1942 I discovered several individuals of this species nesting in a small clearing in the forest at Cumaca. The wasps were in the course of digging their nests in a flat area of friable sand at the base of a sandy bank. The fore-legs were used in digging the nest. The female came out of the entrance backwards, scraping out the sand with the fore-legs, which worked together, and sweeping it away. When disturbed the wasp rose silently into the air. Then it descended slowly to the sand near the nest, walked a few steps to the entrance with wings elevated at a strong angle to the body, entered the nest and continued digging. Three females were captured, but none were observed bringing in prey. The wasps were nesting in company with *Cerceris dilatata* Spinola and *Bicyrtes variegata* (Olivier). The former species was provisioning its nest in the sandy bank with buprestid prey, and several nests of the latter were intermingled with those of *H. vespoides*.

On 4 April 1943 I found this species nesting in the fine, loose sand on the floor of a sandpit at Mundo Nuevo. Several wasps were seen provisioning their nests. Two females were captured, both carrying adults of the large treehopper *Umbonia spinosa*. They descended slowly and silently to their nests holding the prey with their middle legs tightly clasped beneath the body and passed it to the hind legs as they entered the nest. The wasps were nesting in association with *Bembecinus agilis* (F. Smith), which was storing its nests with cicadellid prey.

I encountered on 25 December 1943 what appeared to be this species nesting in the floor of the same sandpit at Talparo, where I had found *H. umbonicida* nesting in 1942. A single female was collected, which was identified by Professor Bohart as *H. fuscus* (Taschenberg), a species described from Brazil. Pate (1941) stated, in describing *H. umbonicida*, that it was somewhat intermediate between *H. fuscus* and *H. robustus* (Handlirsch), agreeing with the former in appearance, but being apparently most closely allied to the latter. In connection with studies on other wasps, I visited the Talparo sandpit again on 26 July 1945 and noticed a single

female busily digging its nest. This individual was captured and identified as *H. vespoidea*.

Nesting sites of this species were subsequently discovered in 2 further areas. One was at North Point, where on 11 March 1949 I encountered several females provisioning their nests. I took a female carrying a large, probably 5th instar nymph of *Umbonia spinosa*. This was the only occasion on which I found a nymph and not an adult membracid being used as prey. The other site was in the Maracas Valley, where on 20 January 1951 I captured a female digging its nest in sandy soil near the Maracas River.

Hoplisoides iridipennis (F. Smith)

This is a small black species with a pair of conspicuous transverse yellow bands on the dorsum of the thorax. It ranges from Mexico to Brazil. I first encountered it at St. Augustine on 31 October 1943 when a female was observed entering its nest in a flat sandy area alongside a path. The wasp was captured and the nest excavated. The burrow was oblique and descended for about 8 cm. A single cell was found containing 3 adult tragopine treehoppers, all *Horiola picta* (Coquebert) (Membracidae). The prey was lying ventral side up and showed no sign of movement. No egg was found. *H. picta* is a widely distributed gregarious treehopper, 4.5 mm long, with dark and light brown markings. It is known as the cacao podhopper and is one of the commonest membracids associated with cacao (*Theobroma cacao* L.) in Trinidad, where it is regarded as a minor pest. Aggregations of nymphs and adults are often found feeding on the petioles of flowers and the stalks of developing cacao pods.

I next discovered this wasp on 3 June 1949 at Talparo. A female was seen flying slowly down to its nest carrying an adult darnine treehopper *Darnoides brunneus* (Germar), a smooth, olive-green, solitary species, about 5.5 mm long. The prey was clasped by the wasp's middle legs and held ventral side up, head foremost. The nest was not excavated. It was located in friable sand on the floor of the same sandpit in which *H. umbonida* and *H. vespoidea* were found nesting.

My third encounter with *H. iridipennis* was on 31 August 1949 in the Maracas Valley. A female was seen approaching its nest carrying an adult membracine treehopper *Erechtia bicolor* Walker.

The membracid, held tightly below its body by the wasp, was rather small, and I was not successful in observing prey carriage closely, but the middle legs were almost certainly used to hold the prey. The nest was unfortunately not located. *E. bicolor* is a brownish, gregarious treehopper, 4 mm long, found on mango (*Mangifera indica* L.) in Trinidad, where aggregations of adults and nymphs have been noticed feeding and causing characteristic lesions on inflorescences.

Finally, I reported (Callan, 1954) as *Gorytes* sp., a female which was almost certainly *H. iridipennis*, taken on 7 April 1944 at Cristóbal Colón, Estado Sucre, Venezuela.

H. iridipennis clearly preys on Membracidae like many other members of the genus. The 3 species of adult treehoppers recorded as prey were distinctly smaller than the wasp and several individuals are undoubtedly stored in each cell, how many is uncertain as only one nest was excavated. Two species, *Horiola picta* and *Erechtia bicolor* are gregarious, and their colonies are invariably attended by ants, mainly *Azteca*, *Dolichoderus* and *Wasmannia*, which exploit them for their honeydew. The ants evidently deter neither the gorytine wasps from capturing their prey nor the mymarid and trichogrammatid parasites, which commonly attack the eggs of these treehoppers.

Hoplisoides denticulatus (Packard)

This species is characterized by short thickened antennae and was originally described from Louisiana. It ranges widely through the United States and into Mexico. Krombein (1959) captured a female 7.5 mm long on 30 July 1958 in North Carolina with a deltocephaline nymph 5.5 mm long probably in the 5th instar (Cicadellidae).

I took a female in Trinidad at St. Augustine on 1 February 1948, which considerably extends the known distribution of the species. It was not found nesting and nothing is known of its prey in Trinidad.

Sagenista brasiliensis (Shuckard)

This is a black wasp about 10 mm in length with basally infuscate wings. Originally described as a *Gorytes*, it was transferred by Bohart (1967) to a new genus *Sagenista*, closely related to

Hoplisoides. The genus is neotropical, ranging from Mexico to southern Brazil, and comprises 6 species, most of them known only from Brazil. Nesting behavior is largely unknown, but Bohart and Menke (1976) reported "one female *Sagenista* from Rio de Janeiro (at Mus. Washington) pinned with a large adult membracid, presumably its prey."

S. brasiliensis is the only species to have been studied in the field. Williams (1928) found that it was abundant near Belém, Brazil and excavated a nest at Jabaty, about 100 km from Belém. One cell contained 6 immature fulgoroid bugs, 4 being Dictyopharidae and 2 Issidae, and in another cell were 5 adult and one immature Issidae, representing various species. A species of Flatiidae was also stored by the wasp. Williams noted that the egg was attached laterally to the thorax of the prey. The cocoons were more or less enveloped by the remains of the prey and described as "gently rounded at the fore end and more narrowed and drawn out a little, nipple-like at the base."

S. brasiliensis was collected in Trinidad in 1935 by D. Vesey-FitzGerald, as 3 males and 3 females so labelled without specific locality are in the Museum of Comparative Zoology. I first came across this rather unobtrusive species on 12 March 1945 at the 11th mile post — the highest point (550 m) — of the Arima-Blanchisseuse road. Here in typical upper montane rain forest the Northern Range is crossed by the road at a col between the summits of Mount El Tucuche and Morne Bleu. Two females, evidently searching the vegetation for prey, were taken in bright sunshine at about 1000 hours on low plants bordering the roadside. Unfortunately they were not seen capturing prey nor was the nesting site found.

I later discovered this species nesting in the Maracas Valley, where on 17 August 1949 a male and several females were collected. Little is known of the behavior of male gorytine wasps and this is the only species in which I took a male near the nesting site. A female was seen entering its nest carrying prey held tightly clasped beneath its body. A fly *Spilogona* sp. (Muscidae) was captured flying closely behind the wasp as it approached the nest burdened by its prey. Nest associates of gorytine wasps are usually Sarcophagidae, and the shadowing behavior of this satellite fly does not imply that it is an inquiline, and is of unknown significance. The nest, which was in friable sandy soil, was excavated and 2 cells found at the end of a short burrow about 6 cm long.

One cell was provisioned with 4 adult fulgoroid bugs and a single adult treehopper (Membracidae). The second cell contained 5 adult fulgoroid bugs. The prey was completely paralyzed, but capable of slight twitching movement of the legs on stimulation. A large egg about 1.0 mm long was attached for its full length ventrally at the base of the legs of one of the prey. On 31 August 1949 I visited the Maracas Valley again and took several females, one of which was carrying an adult fulgoroid bug with its ventral side up held below the body by the wasp's middle legs. The nest was not found and presumably the entrance is kept closed when the wasp is away.

On 16 September 1949 another nesting site was found in a sandy bank near the previous one in the Maracas Valley. A wasp was seen leaving its nest, which was dug out, and 3 cells, each containing a cocoon, were unearthed. As the sand crumbled readily, it is possible that they belonged to more than one nest, but this is unlikely. Attached to the cocoons by strands of fungus mycelium were the wings, eaten-out head capsules, parts of the legs, and other remains of the homopterous prey. The cocoons were ovoid, pale brown, hard and smooth, rounded at the anterior and more pointed at the posterior end, which was drawn out into a nipple-like protuberance like the distal end of a lemon. They varied in length from 9 to 10 mm and in width from 4 to 4.5 mm. No pores were present in the walls of the cocoons. Three female wasps emerged from the cocoons by biting off a cap at the anterior end leaving a rough edge.

S. brasiliensis provisions its nest almost exclusively with Fulgoroidea of various families except for a single treehopper (Membracidae), most of the prey ranging in size from about 4 to 8 mm (Table 1). Nests are multicellular and several prey, both adults and nymphs, are stored in each cell. The achilid *Koloptera callosa* was described from Panama and recorded by Fennah (1945) from Trinidad. The issid *Thionia mammifera*, and the flatids *Epormenis fuliginosa* and *Euhyloptera corticalis* were described from Trinidad (Fennah, 1945). *E. fuliginosa* is known only from the island, where it occurs commonly with related species as a minor pest on cacao and coffee (*Coffea arabica* L.). The smiliine treehopper *Ceresa vitulus* is a wide-ranging, greenish, cryptic solitary membracid, about 5 mm long, with the pronotum bearing 2 sharp humeral spines. In Trinidad it is often found on cacao and many other plants.

Table 1. Prey records for *Sagenista brasiliensis*

Species of prey	Locality	Observer
ACHILIDAE		
<i>Koloptera callosa</i> Metcalf	Trinidad	Callan
DELPHACIDAE		
<i>Punana</i> sp.	Trinidad	Callan
DICTYOPHARIDAE		
<i>Dictyophara</i> sp.	Brazil	Williams (1928)
ISSIDAE		
<i>Thionia mammifera</i> Fennah	Trinidad	Callan
<i>Thionia</i> sp.	Brazil	Williams (1928)
Spp. indet.	Brazil	Williams (1928)
FLATIDAE		
<i>Epormenis fuliginosa</i> (Fennah)	Trinidad	Callan
<i>Euhyloptera corticalis</i> Fennah	Trinidad	Callan
<i>Flatormenis</i> sp.	Trinidad	Callan
Sp. indet.	Brazil	Williams (1928)
MEMBRACIDAE		
<i>Ceresa vitulus</i> (Fabricius)	Trinidad	Callan

DISCUSSION

I have thought it best to treat *Hoplisoides umbonida* and *H. vespoidea* as distinct species. Both are listed by Bohart and Menke (1976), and Professor Bohart confirms (1976, *in litt.*) that he considers *umbonida* to be a species separate from *vespoidea*. Pate was a meticulous worker and described both sexes of *umbonida* in detail, and it seems unlikely that he would have recognized it as a new entity unless he was reasonably certain it was distinct from related species. It would be interesting, however improbable, should two similar sympatric species occur in Trinidad, nesting possibly under slightly different conditions, and both provisioning their nests, so far as known, exclusively with *Umbonia spinosa* and no other prey. Until Pate's holotype and *vespoidea* are compared, it will not be possible to resolve the problem.

Many neotropical gorytines apparently mimic social vespids of the tribe Polybiini. Pate (1941) pointed out that *H. umbonida* bears a striking superficial resemblance to the *velutina* phase of *Brachygastra lecheguana* (Latreille) — a phase now identified

with relatively newly emerged wasps. This widespread species is not found in Trinidad, but its congener *B. bilineolata* Spinola occurs commonly there. Vesey-FitzGerald (1939) reported that in Trinidad "an undetermined species of *Gorytes* which is of rare occurrence bears a very close resemblance to" a wasp which is now known as *Stelopolybia pallipes* (Olivier). This aggressive polybiine is essentially a forest species and is common in Trinidad. There is little doubt that Vesey-FitzGerald's "undetermined *Gorytes*" is the species represented by 2 specimens bearing his name in the Museum of Comparative Zoology, identified by Professor Bohart as *H. vespoides*.

Most Gorytini prey on an array of species belonging to a single homopterous family. *Hoplisoides iridipennis* is typical of its genus in taking several species of Membracidae, but *H. umbonida* and *H. vespoides* exhibit a degree of specificity in that they prey, so far as known, only on one species *Umbonia spinosa*. *Sagenista brasiliensis* preys on 6 homopterous families including Membracidae, and in this respect parallels the genus *Ochleroptera*, which is known to prey on 5 families. This provides ethological support for Bohart's separation on morphological grounds of the genus *Sagenista* from *Hoplisoides*.

Multicellular mass-provisioned nests are characteristic of Gorytini. Unfortunately the nests of only 3 species were excavated. In *H. umbonida* the burrow was about 10 cm long and 4 cells were found. Because of the large size of the prey, probably only 3 or 4 individuals are stored in each cell. In *H. iridipennis* the burrow was about 8 cm long and a single cell was found containing 3 prey. It is unlikely that this species makes unicellular nests; either this was the first cell of a series and others would be added later, or other cells were present and were not found. The 2 nests of *S. brasiliensis* that were dug out were comparatively shallow, one being only about 6 cm long. They had 2 and 3 cells respectively, and 5 prey were found in both of 2 cells that were probably fully provisioned.

The Talparo sandpit provided favorable nesting conditions for digger wasps and was exploited by numerous species. Occupying the vertical walls of the sandpit were *Trachypus petiolatus* (Spinola), *Cerceris dilatata* Spinola and *C. callani* Krombein, and nesting with *H. umbonida* and other *Hoplisoides* species in the flat sandy floor were, among others, *Tachytes*

fraternus Taschenberg, *Tachysphex inconspicuus* (Kirby), *Bembecinus agilis* (F. Smith) and *Bicyrtes discisa* (Taschenberg). A study of this complex of wasps will be published elsewhere.

Two species of Nyssonini, which are cleptoparasites of gorytine and larrine wasps, were encountered at Talparo. Three females of *Zanysson dives* (Handlirsch) were captured flying low over the floor of the sandpit and walking on the surface of the sand exploring holes or irregularities, but were not seen to enter nests. *Zanysson* is a genus known to attack *Tachytes*, and it may well be that *Z. dives* is a parasite of *T. fraternus*. A male probably of *Epinysson zapotecus* (Cresson) was also taken in the sandpit. Several members of this genus are known to be parasites of *Hoplisoides*, and it seems likely that *E. zapotecus* parasitizes one or other of the *Hoplisoides* species nesting at Talparo.

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THE LOWER PERMIAN INSECTS OF KANSAS. PART 12.
PROTORTHOPTERA (CONTINUED), NEUROPTERA,
ADDITIONAL PALAEODICTYOPTERA, AND
FAMILIES OF UNCERTAIN POSITION¹

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The three preceding parts in this series have dealt with families of Protorthoptera and Orthoptera occurring in the insect beds in Elmo, Kansas. The present paper includes a few other families of Protorthoptera, the first family of the Order Neuroptera, a new family of Palaeodictyoptera, and a series of five families that I have been unable to assign to any known order. Most of these fossils were collected in the Harvard quarry in 1927 and during the intervening fifty years I have studied them many times over in attempts to determine their relationships. It now seems advisable to describe them formally, even though some uncertainties still exist.

ORDER PROTORTHOPTERA

As our knowledge of Permian insects increases, it becomes obvious that orthopteroids were the predominant types of insects during the entire period. The Blattaria and Miomoptera were abundant as individuals and probably also as species; the Protelytroptera and Orthoptera, although not so numerous, represent very different structural and environmental divergences. The rest of the Permian orthopteroids (apart from the enigmatic Caloneurodeia) have been referred to the Order Protorthoptera — a very large, complex, and probably polyphyletic taxon (See Carpenter, 1966). It is here that the maximum diversity is found. In the Elmo

¹Partial financial support of this research is gratefully acknowledged to the National Science Foundation: Grants no. GB3970 and DEB 76-04861, F. M. Carpenter, Principal Investigator, Harvard University. I am also indebted to the authorities of the Peabody Museum, Yale University, and the Institute of Paleontology, Academy of Sciences, Moscow, USSR, for the loan of several type specimens; and to Miss Carol Robey, Radcliffe College, for assistance with the drawings.

beds alone eleven families of Protorthoptera have already been recognized, these being the following: Blattinopsidae, Strephocladidae, Stereopteridae, Toco cladidae, Liomopteridae, Demopteridae, Phenopteridae, Protrembiidae, Probnisidae, and Lemmatophoridae. Three additional families are described below.

Family *Nugonioneuridae*, new family

Insects of moderate size, with a wing expanse of about 20 mm. Fore wing: SC terminating on R1; RS arising at about mid-wing; stem of M coalesced basally with CUA, the branches of M arising abruptly from M+CUA and arching anteriorly; several anal veins present. Cross veins numerous and irregularly distributed, mostly unbranched and not forming a reticulation. The hind wing, not certainly known, is discussed below in the account of *Nugonioneura problematica*. Body unknown.

At present only the type genus is known in the family.

Genus *Nugonioneura* Tillyard

Nugonioneura Tillyard, 1937, p. 92.

Fore wing: costal margin with a small bulge basally; SC terminating on R1 just beyond the origin of RS; costal area with several oblique cross veins and the area between R1 and costal margin with several to many cross veins; RS with from 2 to 4 terminal branches; M+CUA with from 4 to 6 primary branches; CUP nearly straight, the area between M+CUA and CUP being broad; at least 4 anal veins present. Cross veins mostly straight, some oblique; wing membrane granular.

Type-species: *Nugonioneura problematica* Tillyard

Nugonioneura problematica Tillyard

Figures 1-3

Nugonioneura problematica Tillyard, 1937, p. 94, fig. 4

Fore wing: length 9.5-12 mm; width, 3-3.5 mm. Costal margin convex but with a slight concavity or straight portion near mid-wing; subcosta somewhat irregular in form, apparently with a few

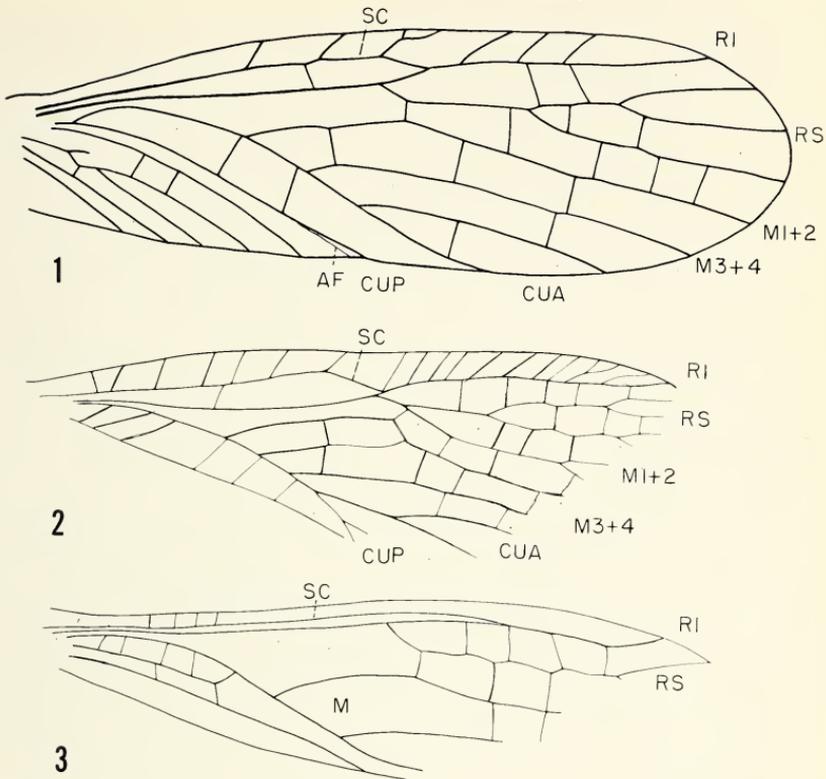
to several cross veins in the costal area; branching of RS variable; in some specimens R2+3 and R4+5 are forked but in others they are simple; branching of M+CUA also variable.² CUP is close to 1A and appears to follow the anal fold for most of its length.

Holotype: no. 15561, Peabody Museum, Yale University. As shown in Tillyard's figure, this consists of a poorly and incompletely preserved fore wing, lacking the posterior region and having most of the veins faintly preserved. I have carefully studied this specimen and I find no clear evidence that R1 is forked, as shown in Tillyard's figure; the anterior veinlet shown is almost certainly one of the several cross veins in that area. Also, M+CUA does not coalesce with RS as figured by him; there may be a short connection between these two veins, though it is not visible in any specimen.

Two additional fore wings of *problematica* are now at hand and have been used in part as the basis of the foregoing description of the genus and species. One of these, no. 5895ab, Museum of Comparative Zoology, consists of a complete and very well preserved fore wing (figure 1). It is the same size as the type and differs only in the number of branches of RS and M: R2+3 is deeply forked and there is one less terminal branch of M. However, these are the kinds of variations that usually occur within species of orthopteroids (see Carpenter, 1966). It should also be noted that in this fossil CUA is directed distally at its termination, away from CUP, not towards CUP; this is probably correlated with the absence of the terminal fork on CUA. The anal area is not sharply marked off, except for the slight indentation of the hind margin at the end of CUP. The cross veins are only faintly preserved in this fossil; in the accompanying figure only those that can positively be discerned are shown; others may be present, as indicated in the other specimens of this insect.

The second new specimen consists of an incomplete wing, no. YPM 27536, Peabody Museum, Yale University (figure 2). It is slightly larger than the other two specimens, with a length of 12 mm and width of 3.5 mm. The differences between this specimen

²It is not possible to distinguish between the branches of these two veins (M and CUA), since they do not show convexities or concavities. I have arbitrarily assumed that the last fork of M+CUA comprises CUA, and the other branches, M.



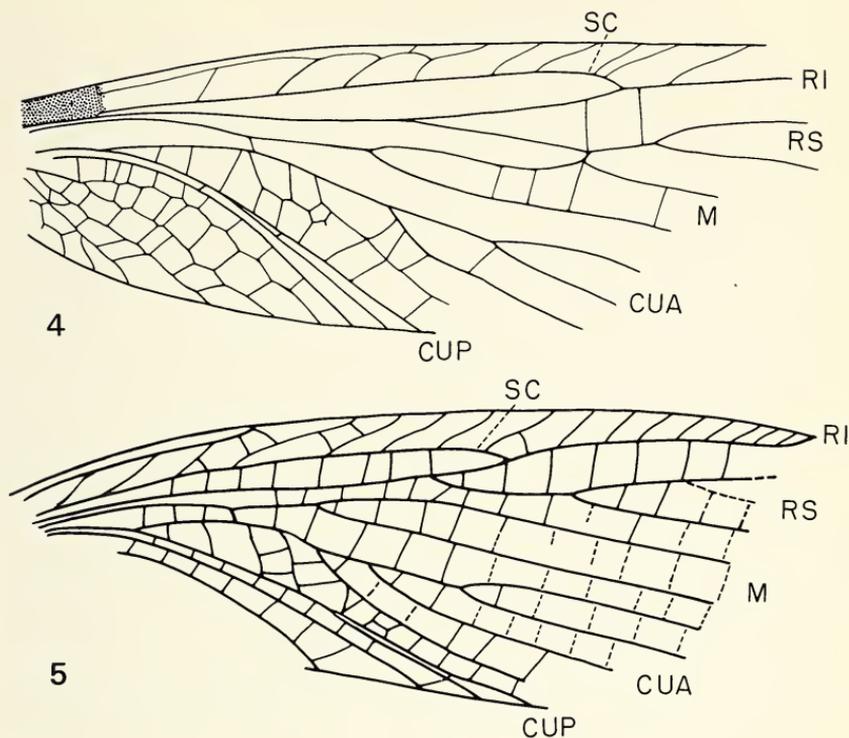
Figures 1-3. *Nugonioneura*. Fig. 1, *N. problematica*; drawing of fore wing, based on specimen no. 5895, M.C.Z. Length of wing, 10 mm. Fig. 2, *N. problematica*; drawing of fore wing, based on specimen no. YPM27536, Peabody Museum, Yale University. Length of wing, 10 mm. Fig. 3, *N. problematica* (identification uncertain); drawing of hind wing, based on specimen no. 7504, M.C.Z. Length of wing, 10 mm. AF, anal fold. The terminology of the wing veins used in all parts of this series of papers is discussed in Part 11 (Carpenter 1966).

and the others are mainly in the branching of RS and M: RS has 4 terminal branches and there are 5 terminal branches of M arising from M+CUA, as in the holotype. The cross vein between M and RS, near the origin of the latter, is very short, but this is undoubtedly an individual variation.

I see no reason to doubt that these three specimens are fore wings of one species. There is also another specimen in the Har-

vard collection which is probably this insect (no. 7504, Museum of Comparative Zoology). It is an incomplete wing, having the basic venational pattern of *problematica* but the costal and subcostal areas are very narrow. This is a feature of hind wings, at least of orthopteroid insects, and I am of the opinion that this fossil is the hind wing of *problematica*. As shown in figure 3, the costal space has the small bulge basally, as in the fore wing; SC terminates on R1 just beyond the origin of RS, which has a single fork; M+CUA gives rise to two arched branches of M; CUP is widely separated from CUA and there is a short vein, apparently formed by the alignment of cross veins in that space; 1A is remote from CUP, unlike the structure of the fore wing. The wing is not preserved beyond 1A but there is an indication that the rest of the anal area is folded back under the wing proper, an oblique line apparently marking the inner margin of the wing.

The type specimen of *Nugonioneura problematica* was one of the "puzzles" that Tillyard found in the Yale collection of insects from Elmo. He believed that it had a combination of characteristics of the Psocoptera, Hemiptera (Homoptera), Embioptera, and Protorthoptera, and finally placed it in the family Permembidae of the Order Psocoptera. *Permembia* itself, however, was and still is another puzzle: as noted below, it cannot even now be assigned with confidence to any known order. Our knowledge of *Nugonioneura* has been much improved since Tillyard's description of it, and in addition we have a much better idea of the extraordinary diversity of the Protorthoptera during the Permian than previously. Within that complex aggregation of insects, we can distinguish species suggestive of Psocoptera, Hemiptera (Homoptera), Miomoptera, Perlaria, and of course several existing orthopteroid orders. However, these possible relationships are indicated mainly by the fore wing venation, little being known about the body structure of the Protorthoptera and even less about their hind wings. In my opinion, therefore, it is futile to attempt at this time to trace the evolutionary lines within the Protorthoptera apparently leading to certain existing orders. Even less justified, I believe, is the assignment of such poorly-known fossils to the existing orders concerned. For this reason, I have placed the *Nugonioneuridae* in the Order Protorthoptera. As a member of that order, it is distinguished from other families by the coalescence of M with



Figures 4 and 5. *Opisthocladius*. Fig. 4, *O. arcuatus*, n.sp.; drawing of fore wing, based on holotype, no. 5882ab, M.C.Z. Length of wing as preserved, 13 mm. Fig. 5, *O. strictus*, n.sp.; composite drawing of fore wing, based on both wings of holotype. Length of wing as preserved, 7 mm.

CUA for most of their lengths and by the branches of M arching abruptly from M+CUA before mid-wing. No close relatives are known.

Family Tococladidae Carpenter

Tococladidae Carpenter, 1966, p.76.

This family was designated for a single genus and species, *Toco-cladus rallus* Carpenter (1966) from Elmo. Two other species, representing a new genus, are described below. One of these, *Opisthocladius strictus*, is of particular interest since it is based on a specimen that shows some details of the body structure, which has not previously been known in this group of Protorthoptera.

Opisthocladus, new genus

Fore wing: slender, apparently much as in *Tococladus*. Costal area of moderate width, its basal portion thickened and heavily sclerotized; SC ending on R1 beyond mid-wing and giving rise to several strong cross veins, some of which are at least slightly sigmoidal or which may be looped together, forming an irregular submarginal vein; oblique cross veins extend from R1 to the costal margin beyond SC; RS arising well before the end of SC, connected to or possibly coalesced with M1+2 for a short distance; M arising independently from wing base; CU forking close to wing base into CUA and CUP; CUA forming 3 or 4 long branches; CUP remote from CUA, the broad space between having several cross veins that form at least a few large cells; CUP rests in the anal fold basally, but diverges from it distally; IA very close to CUP; several other well developed anal veins. Cross veins probably as numerous as in *Tococladus*. Hind wing unknown. Body structure: head relatively large, with prominent eyes, dentate mandibles; thorax large, the segments very distinct; abdomen short, as preserved, apparently compressed; cerci unknown.

Type species: *Opisthocladus arcuatus*, n.sp.

This genus differs from *Tococladus* by having looped costal veinlets, the late origin of RS, and the longer and straighter basal portion of CUA. RS almost certainly has fewer branches than in *Tococladus*, but that is not definite, since the apical part of the wing is not preserved. The basal portion of the costal area is heavily sclerotized in *Opisthocladus*; this may have been the case in *Tococladus* also, since the basal part of the wing is unknown in that genus.

The generic name is derived from the classical Greek words *opistho-* (hinder) and *klados* (branch), and is considered masculine and singular.

Opisthocladus arcuatus, n.sp.

Figure 4

Fore wing: length (as preserved), 13 mm; width, 4.5 mm; estimated complete length (based on proportions of *Tococladus ralus*), 17 mm. Costal veinlets mostly oblique and sigmoidal; M forking just before origin of RS; CUA connected to M by a short,

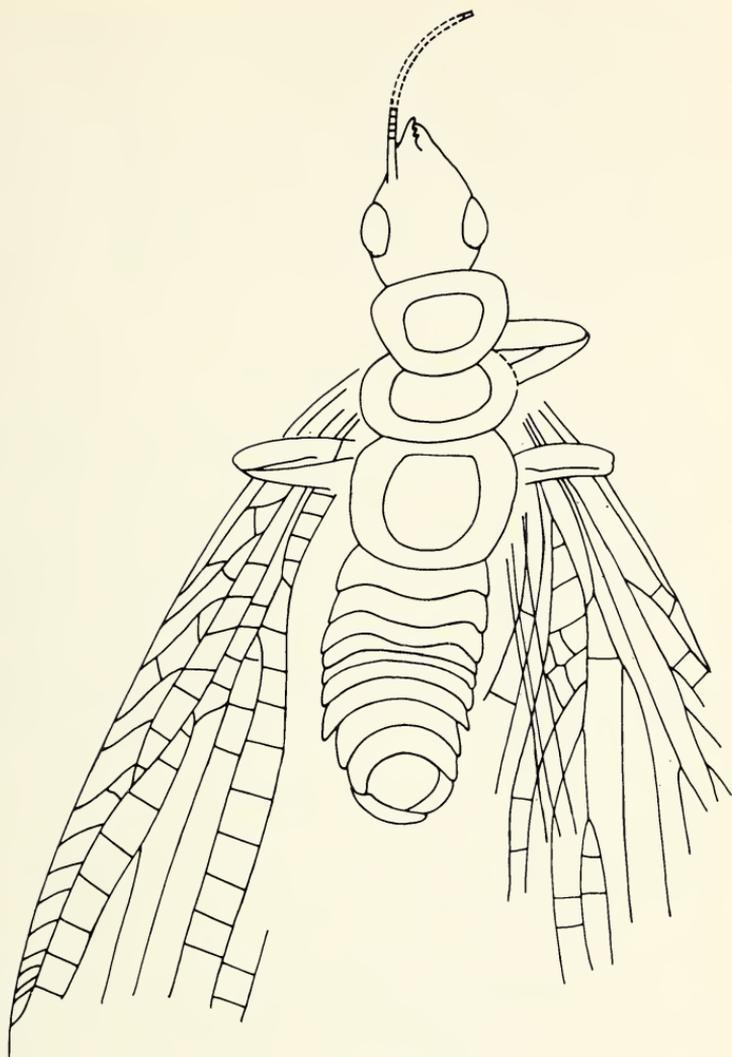


Figure 6. *Opisthocladus strictus*, n.sp.; drawing of holotype, no. 5881ab, M.C.Z.
Length of body, 13 mm.

thick cross vein; several of the cross veins between CUA and CUP forming a few large, closed cells; 2A with two deep forks.

Holotype: no. 5882, Museum of Comparative Zoology. This consists of a single fore wing, lacking about the apical quarter; the preserved portion is very clear. Whether M1+2 is actually coalesced with RS or only connected to it by a cross vein cannot be determined in the type specimen; in either case, the nature of the connection is probably subject to much individual variation, as in most other Protorthoptera.

Opisthocladus strictus, n.sp.

Figures 5 and 6

Fore wing: length (as preserved), 13 mm; estimated complete length (based on *Tococladus*), 15 mm. Costal veinlets near the base strongly sigmoidal and forming a short submarginal vein; other costal cross veins nearly straight and not looped; SC terminating on R1 at about mid-wing, only a short distance beyond the origin of RS; M and CU much as in *arcuatus*, but cross veins more definite.

Holotype: no. 5881, Museum of Comparative Zoology. This consists of a complete insect showing a dorsal-ventral view of the body, with the fore and hind wings over-lapped on each side (figure 6). Although the preservation is excellent, parts of the fore wings and virtually all of the hind wings are obscured. Figure 5 is a composite drawing of the fore wing venation based on both of the wings. The body is 13 mm long, from the tip of the mandibles to the end of the abdomen; the head is 2.5 mm long. Only fragments of the antennae are preserved; they indicate a very slender antenna, of at least moderate length. The head, seen in dorsal view (probably distorted into an abnormal, prognathous position), shows the mandibles clearly; they are relatively long and dentate. The eyes are prominent. The thoracic nota are distinct, the segments apparently not fused, and the metathorax is the largest. Little can be seen of the legs; the abdomen, as preserved, is very short, most of the segments apparently being contracted. Terminal structures on the abdomen, including cerci, cannot be discerned.

This species differs from *arcuatus* in lacking the looped costal veinlets, and in having the origin of RS closer to the end of SC

and M forked near the wing-base.

Family **Psoropteridae**, new family

Small insects. Fore wing: costal area narrow. Stem of M fused with stem of CU at base and then for a greater distance with CUA; RS unbranched; M with two branches, CUA with three; CUP unbranched; two anal veins. Longitudinal veins unusually thick and heavy but cross veins weak and thin. Wing membrane uniformly rugose, without hairs. Hind wing and body unknown.

Psoroptera, new genus

Fore wing: RS extending nearly to wing apex, unbranched; RS arising well before mid-wing; M+CUA about as long as the rest of M before its forking into M1+2 and M3+4; CUA diverging from M just before the level of the origin of RS, and forking just beyond that point; M1+2 coalesced with RS for as long an interval as the free piece of M; CUA forming three strong branches, the first arising just beyond the level of the origin of RS.

Type-species: *Psoroptera cubitalia*, n.sp.

The generic name is derived from the classical Greek words *psoro-* (scabby) and *ptera* (wings) and is considered neuter plural.

Psoroptera cubitalia, n.sp.

Figure 7

Fore wing: length, 6 mm; width, 1.8 mm. M1+2 and M3+4 un-

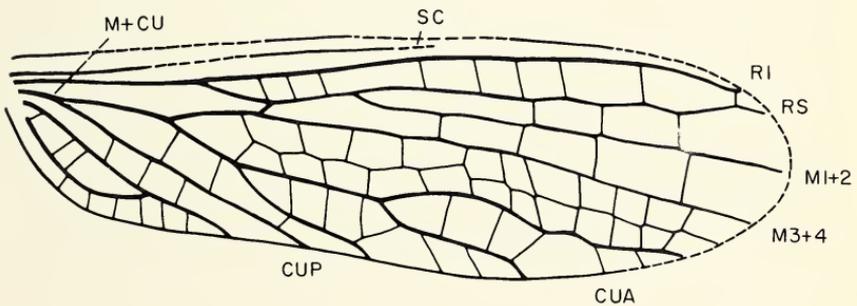


Figure 7. *Psoroptera cubitalia*, n.sp.; drawing of fore wing, based on holotype, no. 5840, M.C.Z. Length of wing, 6 mm.

branched; cross veins between M3+4 and CUA forming an irregular, double row of cells; 2A looped to 1A distally.

Holotype: no. 5840, Museum of Comparative Zoology. This specimen consists of a well preserved fore wing, complete except for small parts of the fore margin and the very apex.

Until a more nearly complete specimen is found, showing at least the hind wing, the affinities of this family will probably remain uncertain. In general, it seems protorthopterous, though the basal fusion of M with CU and CUA, the very heavy longitudinal veins, weak cross veins, and rugose membrane set it apart from all other families of Protorthoptera known to me.

Family **Heteroptilidae**, new family

Insects of moderate size. Fore wing: membranous; costal margin strongly convex; costal area very broad, broadest near mid-wing, with many straight, oblique and unbranched cross veins; subcostal area broad, with straight cross veins; R curved away from the costal margin; R1 strong, directed anteriorly and terminating on costal margin well before wing apex; RS arising before mid-wing, with several branches; M independent of R basally, forking beyond origin of RS; CU forked near base; CUA mostly straight; CUP very straight, extending to about half the wing length; 3 straight anal veins. Cross veins generally weakly developed and not numerous, except in costal area. Hind wing and body unknown.

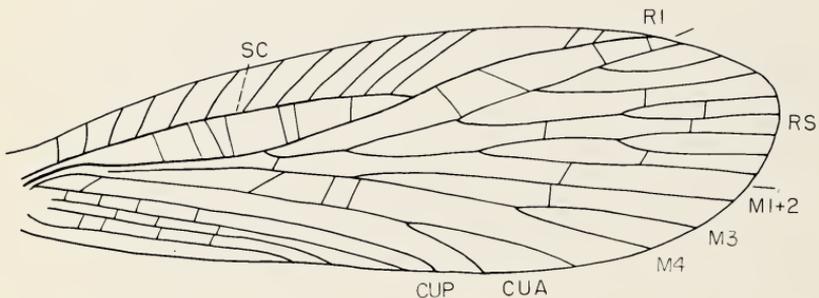


Figure 8. *Heteroptilon costale*, n.sp.; drawing of fore wing, based on holotype, no. 5878, M.C.Z. Length of wing, 15 mm.

This distinctive family is characterized by the combination of the broad costal and subcostal areas and the extension of CUP to about half the wing length, the anal area being very long and slender.

Heteroptilon, new genus

Fore wing: costal margin smoothly curved; wing broadest beyond the middle of the wing; RS with 4 primary branches; CUA with a distal fork; anal veins unbranched.

Type-species: *Heteroptilon costale*, n.sp.

The generic name is derived from the Greek words *heteros* (different) and *ptilon* (wing) and is considered neuter and singular.

Heteroptilon costale, n.sp.

Figure 8

Fore wing: length, 15 mm; width 5 mm. Costal area with about 12 veinlets; RS with 5 terminal branches; M1+2 unbranched, M3+4 forked to half its length. Cross veins as shown in figure 8.

Holotype: no. 5878, Museum of Comparative Zoology. This consists of a complete fore wing, very well preserved. The cross veins, excepting those in the costal area, are very faint. The wing membrane is irregularly wrinkled, giving the impression that it was very thin.

The venation of this insect presents no difficulty in interpretation. R1 and CUA are strongly convex, and between them are two neutral veins (\pm), obviously RS and M. I have interpreted the most posterior branch that arises from the stem RS as R4+5 but this could also be regarded as an anterior branch of M, coalesced with RS basally.

There are several unusual features of this insect. The costal and subcostal areas combined are about half the width of the entire wing, the configuration of the costal area itself is most peculiar, and the crowding of the anal veins into the elongate anal area is unique among the Protorthoptera as presently known. The position of the family in the order is therefore uncertain.

ORDER PALAEODICTYOPTERA

This order, although a prominent one in the Upper Carboni-

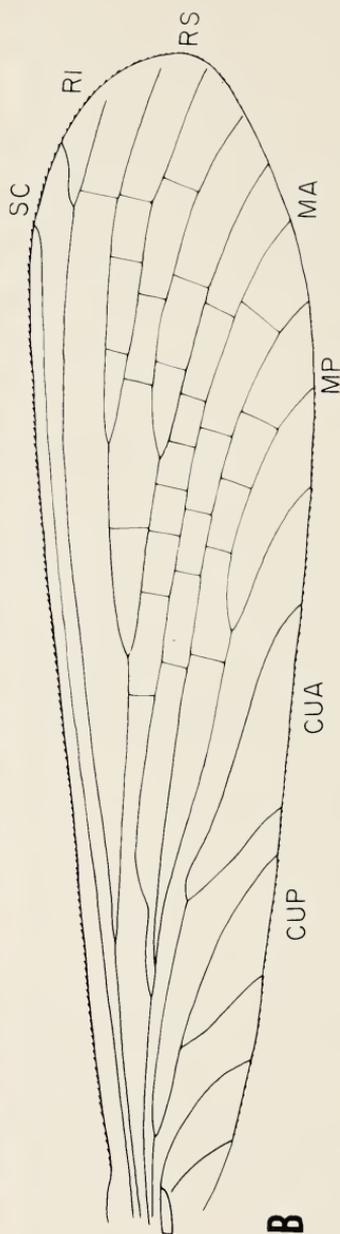
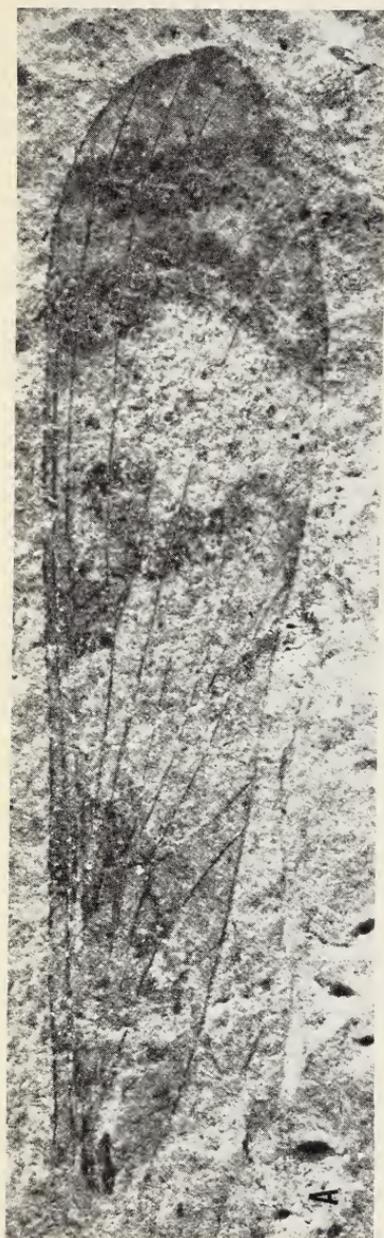


Figure 9. *Elmohoria piperi*, n.sp. A, photograph of holotype, no. 5839ab, M.C.Z. This is a composite photograph of the obverse and reverse combined. Length of wing, 15 mm. B, drawing of forewing, based on holotype.

ferous, is only sparsely represented in Permian strata. Two species have been reported from the Elmo beds.³ One of these, *Dunbaria fasciipennis* Tillyard, is a typical spilapterid. The other, *Kansasia pulchra* Tillyard, was originally described as a spilapterid (Tillyard, 1937) but has subsequently been transferred by Demoulin (1954) to the extinct order Archodonata. Although incompletely known, *pulchra* is almost certainly closely related to the species on which the order Archodonata was based (Martynov, 1931), but I do not believe that any of these insects are sufficiently distinctive to justify separation from the Palaeodictyoptera. Accordingly, I consider the Archodonata to be synonymous with the Palaeodictyoptera.

Among the fossils which I collected at Elmo in 1927 is a specimen that shows both palaeodictyopterous and megasecopterous traits. No additional specimens of this insect have subsequently been found, but I am now quite convinced that it is a representative of a new family of Palaeodictyoptera.

Family **Elmoboriidae**, new family

Fore wing: slender, at least four times as long as wide. Costal margin nearly straight; SC long, terminating a short distance before the wing apex; R1 close to and nearly parallel to SC, except distally; RS arising about $\frac{1}{4}$ wing length from base, with several branches; M forking nearly at the same level as the origin of RS; MP forking almost immediately after its origin, with 2 or 3 branches; CU forking near the base of the wing; CUA and CUP deeply forked; at least 2 anal veins. The costal margin of the wing is conspicuously serrate, the posterior margin less so. Hind wing and body unknown.

This family differs from others previously described in the Palaeodictyoptera by the elongate shape of the wing, which is broadest distally, and by the proximity of the forking of M to the first fork of MP. The family is based on the genus *Elmoboria*, described below; the genus *Oboria* Kukalova (1960), from the Permian of Moravia, apparently belongs here also.

³A third species, *Permoneura lameerei*, was doubtfully placed in the Palaeodictyoptera (Carpenter, 1931) but as pointed out below (p. 373) the unique specimen on which the species was based does not show the diagnostic features of the order.

Elmoboria, new genus

Fore wing: R1 extending almost to wing apex; RS dichotomously branched, with 4 terminal branches; MA arising slightly basad of the origin of RS, unbranched; MP3+4 deeply forked.

Type-species: *Elmoboria piperi*, n.sp.

The generic name is a combination of the names of the towns Elmo, in Kansas, and Oboria, in Moravia, both of which have important insect-bearing deposits of Permian age. The name is considered feminine and singular.

Elmoboria piperi, n.sp.

Figure 9

Fore wing: length, 15 mm; maximum width, 3.2 mm. Branches of RS about equal in length; shortly after its origin MA abruptly curves towards RS. The wing is traversed by three distinct bands of dark pigmentation and has a smaller spot nearer the base. The weak cross veins can be discerned only with difficulty.

Holotype: No. 5839ab, M.C.Z., collected at the Harvard quarry in Elmo in 1927. This consists of a complete wing, very well preserved. The distal part of the wing is on one piece of rock and the basal portion on its counterpart; photographs of these two pieces have been combined together in figure 9A to show the complete wing. The specimen is presumed to be a fore wing but since the shape of the wing is unusual for a palaeodictyopteron, we have no basis for evaluating the differences between the fore and hind wings in this new family. The insect has been placed in the Palaeodictyoptera because of (1) the remoteness of R1 from SC and the

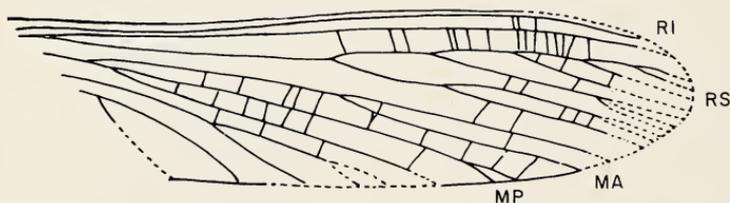


Figure 10. *Oboria longa* Kukalova, from Lower Permian of Moravia; drawing of fore wing, from Kukalova, 1960, with restoration of wing base omitted.

costal margin, (2) the wing shape, and (3) the presence of a 3-branched MP, which to my knowledge does not occur in the Megaseoptera, except for some of the highly specialized and aberrant Megaseoptera recently described by Kukalova-Peck (1975). However, the difficulty of distinguishing between the wings of the Megaseoptera and Palaeodictyoptera prevents any certainty in this assignment (see Carpenter 1963 and 1967, and Kukalova-Peck, 1975).

The species is named for the late Charles Piper of Hope, Kansas, who for more than forty years has owned the property in Elmo on which the Harvard quarry has been located, and who consistently encouraged us and assisted us in the collecting of the fossils.

The genus *Oboria* Kukalova (1960) from the Lower Permian of Moravia, originally placed in the family Spilapteridae, apparently belongs to the Elmoboriidae. The species (*longa*) on which *Oboria* was based is known from a single wing, lacking the basal and distal portions (figure 10). In view of the structure of the complete wing of *Elmobia*, I think it most probable that the wing of *longa* had a more extended base than that which Kukalova reconstructed. If that were so, the wing would have been shaped much as in *piperi*. The general venational patterns in both species, the weak and irregular cross veins, and especially the proximity of the

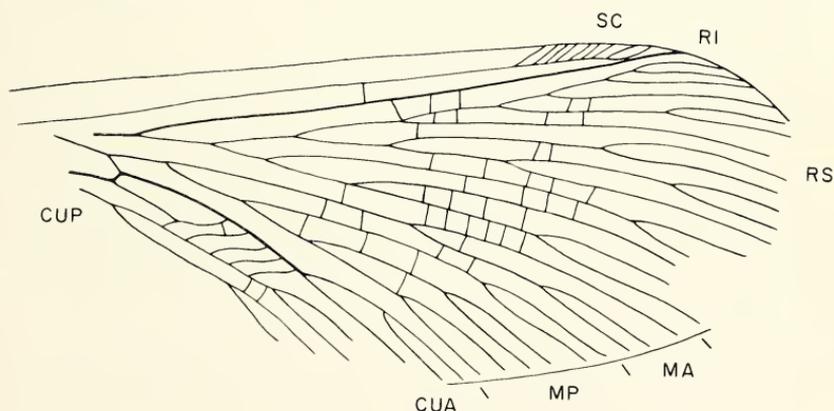


Figure 11. *Elmothone martynovae*, n.sp.; drawing of fore wing, based on holotype, no. 5585, M.C.Z. Length of wing, as preserved, 13 mm.

origin of MA to the fork of MP are indicative of family relationship. *Oboria*, however, differs from *Elmoboria* in having a more extensively branched RS and a deep fork on MA.

ORDER NEUROPTERA

The three suborders of Neuroptera (Sialoidea, Raphidioidea, and Planipennia) are first found in Permian deposits. The Planipennia have the most extensive record of the suborders in that period, with representations by three families and eleven genera. All of these Permian fossils are from the Soviet Union and/or Australia and most are from Upper Permian beds. However, specimens of two species have been described from Lower Permian deposits in the Kuznetsk Basin of the Soviet Union, although their precise position in the Lower Permian has not been determined. Until now these specimens have comprised the oldest record of the Planipennia.⁴

In the Museum of Comparative Zoology there is an incomplete wing of an ithonoid planipennian collected at Elmo in 1927. The hope of finding better specimens has deterred me from describing it over these many years, but since no additional fossils have turned up, I have decided to include a formal description of the species here. Inasmuch as the Elmo beds are part of the Lower Permian (Sumner Group), this new planipennian is at least as old as the Kuznetsk fossils. It clearly belongs to the Permithonidae.

Family Permithonidae Tillyard

Permithonidae Tillyard, 1922, p. 289; Martynova, 1961, p. 476. Synonyms: Permegalomidae Martynova, 1952, p. 201; Permopsychopsidae Riek, 1953, p. 82.

Fore wing: costal area moderately broad; costal veinlets numerous, somewhat irregular, some branched; SC terminating on RI distally or connected to it by a short cross vein; few to many cross

⁴Tillyard (1932, 1937) placed three genera of insects from the Elmo beds in the Planipennia but all have now been recognized as belonging to other orders: one (*Permobiella*), to the order Caloneurodea, and the other two (*Permoberotha* and its synonym, *Dictyobiella*), to the order Glosselytrodea (Martynova, 1962a). The latter order, although originally considered to be orthopteroid, is almost certainly closely related to the Neuroptera (Carpenter, 1964; Sharov, 1966).

veins between R and RS; RS with at least 4 primary branches; MA not coalesced with RS basally but often connected to it by a short cross vein; CUA with a distinct fork. Hind wing and body unknown.

This family is known from the Upper Permian of USSR and Australia.

Elmothone, new genus

Fore wing: costal margin straight, nearly parallel to SC; wing apex apparently broadly rounded. Costal area not as broad as in other known genera of the family; RS forking shortly after its origin and having at least 7 primary branches. M (and MA) remote from RS, forking shortly beyond the origin of RS, and with at least 7 subsequent forks; CU remote from M basally but CUA at its origin directed sharply towards M and connected to it by a short cross vein; CUP ending in a long, sigmoidal cross vein; the rest of the area between CUP and 1A having several other sigmoidal cross veins. 1A deeply forked. Cross veins in general weak and irregularly distributed.

Type-species: *Elmothone martynovae*, n.sp.

The generic name is derived from Elmo, the name of the township in Kansas in which the insect beds are located, and the generic name *Ithone*, which is feminine.

Elmothone martynovae, n.sp.

Figure 11

Fore wing: length (as preserved), 13 mm; maximum width, 5 mm; R1 very nearly straight; posterior branch of M with 4 subsequent forks. Venational details are shown in figure 11.

Holotype: No. 5585ab, Museum of Comparative Zoology.⁵ This consists of an incomplete wing, lacking about the basal quarter and part of the hind margin. The longitudinal veins, for the most part, are clearly preserved but the cross veins are indistinct, except under oblique light. The relatively narrow and uniform width of the costal area is suggestive of a hind wing. However, the hind wings are entirely unknown in the Permithonidae, and the struc-

⁵This is the fossil mentioned by MacLeod in his account of the Neuroptera of the Baltic amber (1970, p. 147).

ture of MA in *Elmothone* is not like that of the hind wings of the Ithonidae, to which the Permithonidae are apparently closely related. For this reason I consider the type of *martynovae* to be a fore wing.

The species is named for Dr. Olga Martynova of Moscow, who was on the staff of the Paleontological Institute for many years and is the author of numerous publications on fossil insects and Recent Neuroptera, Trichoptera and Mecoptera.

The genus *Elmothone* seems closest to *Permithonopsis* and *Permegalomus*, from both of which it is distinguished as follows: In *Elmothone* SC does not (apparently) terminate on R1, as has been described and figured for the other known genera of the family, although it almost touches R1 and is joined to it by a short cross vein; this is the situation in the Ithonidae. The structure of CUA in *Elmothone* is also very different from that of the other genera. In *Permithonopsis* and *Permegalomus* CUA nearly touches M but in *Elmothone* it is remote from M, although joined to it by a relatively long cross vein. Also, the area below CUA is unusually wide and is traversed by several sigmoidal cross veins. A suggestion of this condition occurs in *Permorapisma*, another member of the Permithonidae.

It is worthy of note that the Permithonidae were quite small insects, only about half the size of the existing members of the family Ithonidae.

FAMILIES OF UNCERTAIN ORDINAL POSITION

The insects described or discussed below are unusual in various respects and I have been unable to place them with confidence in any known order. Two of the species, *Permembia delicatula* Tillyard and *Permoneura lameerei* Carpenter, have already been formally described; the others, obviously belonging to very different orders, whatever they might be, are new. Having had these specimens for the past fifty years without coming to definite conclusions on their systematic positions, I have decided to describe and name them without making ordinal assignments. Related fossils present in collections from other Permian beds may ultimately be correlated with these Elmo fossils.

These "incertae sedis" insects belong to five very distinct families:

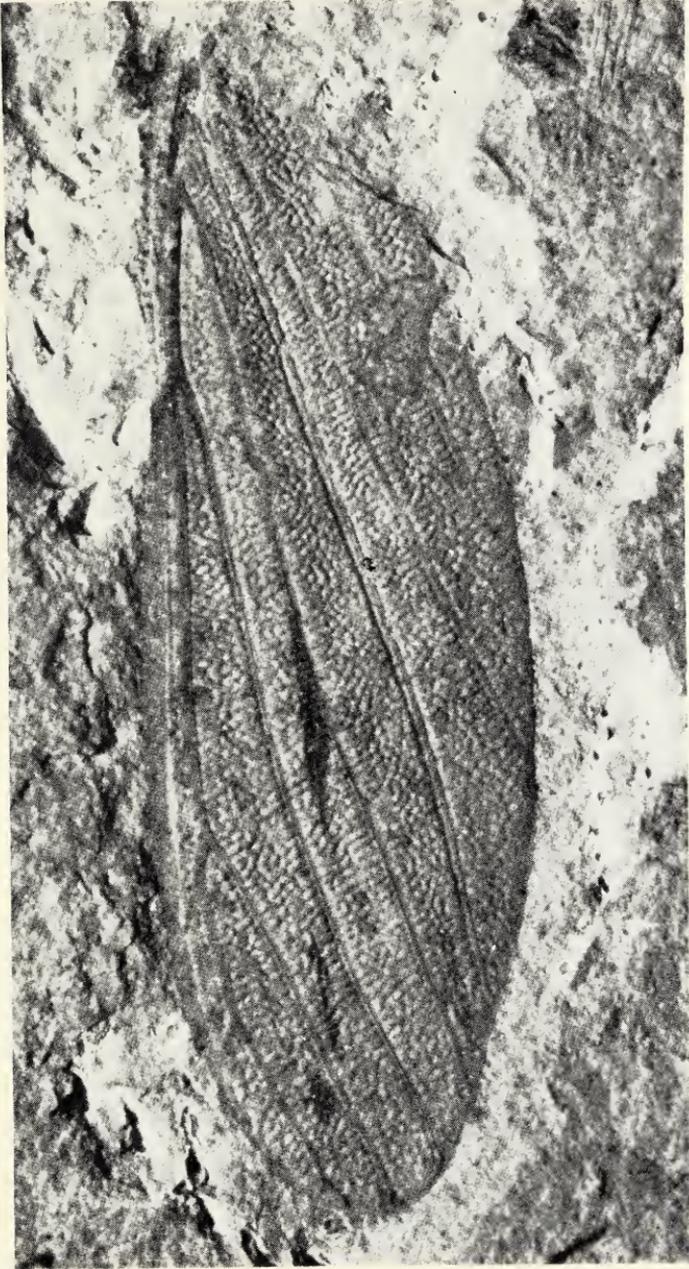


Figure 12. *Trachopteryx martynovi*, n.sp.; photograph of holotype, no. 7497, M.C.Z. Length of wing, as preserved, 13 mm.

1. Family **Trachopterygidae**, new family

Small insects. Fore wing: coriaceous; veins thick, the membrane very rough or rugose. Costa marginal, unusually thick, extending to apex of wing; the rest of the wing margin also thick, but less so; venation reduced, with all veins (except SC and possibly 1A) arising from a main stem-vein and extending in almost straight lines diagonally across the wing. Cross veins absent on most of the wing. Numerous fine setal bases on the costa and most other veins.

Trachopteryx, new genus

Fore wing: SC short, crowded between the costa and the stem-vein and terminating at about the level of the origin of MA. The other seven main veins (as interpreted below) are long but without branches.

Type-species: *Trachopteryx martynovi*, n.sp.

The generic name is derived from the classical Greek words *trachys* (rough) and *pteryx* (wing) and is considered feminine and singular.

Trachopteryx martynovi, n.sp.

Figures 12 and 13

Fore wing: length, 11 mm; width, 5 mm. RS arising about 2/3 the wing length from the base; R1 with 4 short cross veins leading

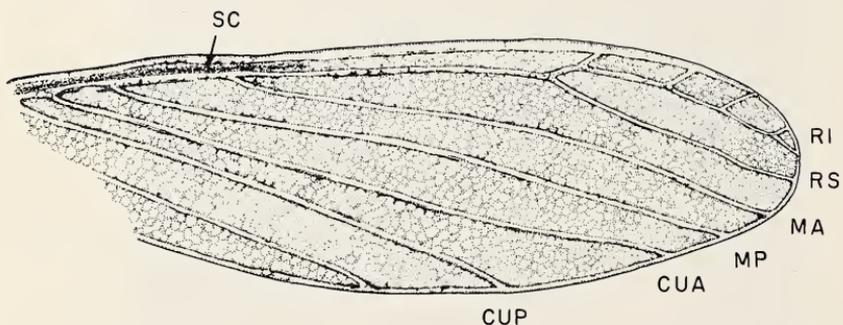


Figure 13. *Trachopteryx martynovi*, n.sp.; drawing of wing, based on holotype. Length of wing, as preserved, 13 mm.

to the costal margin beyond the origin of RS; MA arising at about $1/3$ the wing length from the base; origins of CUA and CUP close together; termination of CUA directed apically, away from CUP. The rugosity of the wing membrane is shown in figure 12.

Holotype: no. 7497, M.C.Z., collected at Elmo, 1927. The species is named for Dr. A. V. Martynov, whose field and laboratory studies on Paleozoic and Mesozoic insects of Russia, from 1922 to 1937, initiated the extensive research program in paleoentomology now being carried out by the Academy of Sciences of the Soviet Union.

As shown in the photograph (figure 12), the holotype consists of a very well preserved wing, lacking only a small piece of the posterior margin near the base. The most obvious features of this wing are the origins of most of the veins from a common stem, and the strongly rugose nature of the wing membrane.

The interpretation of the venation presented in figure 13 seems to be the most logical one, although others are possible. The convexities and concavities of the veins are distinct in the unique type, which consists of only one counterpart, the other being missing. In this specimen the main stem-vein continues as R; since this is concave, I consider this counterpart to be the reverse half, the convexities and concavities being the reverse of those as they appear on the dorsal surface of an insect's wing. In the following discussion and in figure 13 reference is made to the veins as they would appear in the reverse half.

The subcosta extends only about as far as the origin of MA and is contiguous with both C and the stem-vein; it can be discerned only with difficulty because of the rugosity of the wing membrane. The main stem-vein is convex; beyond the origin of MA the vein appears to be a normal radius (R), with an anterior branch (R1) and the posterior RS. The four remaining veins that arise from the stem, alternately convex and concave, are presumably MA, MP, CUA and CUP. The origin of the most posterior vein, 1A, is uncertain; it may arise independently or from the stem-vein.

This is a highly specialized wing and I can make no convincing suggestions regarding its ordinal affinities. So far as I am aware, none of the Neoptera have an MA which is actually convex, as in this fossil, but that *Trachopteryx* is paleopterous seems hardly credible.

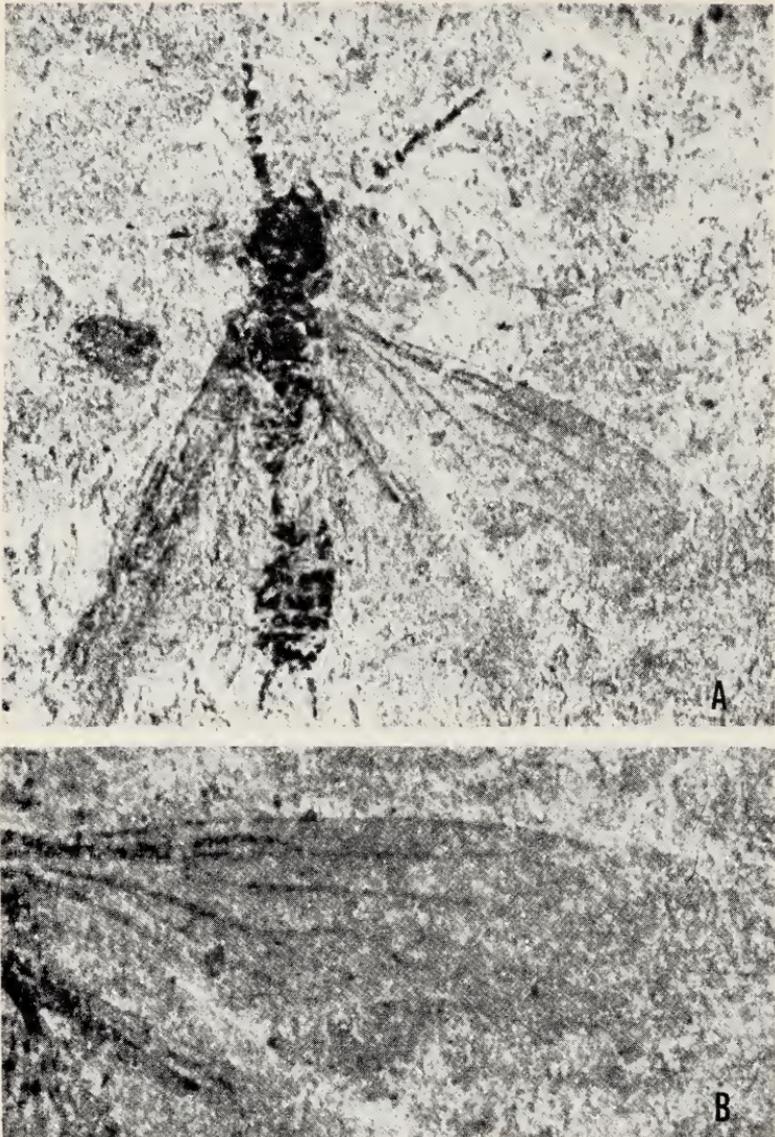


Figure 14. *Permambia delicatula*. A, photograph of holotype, no. YPM5403, Peabody Museum, Yale University. B, photograph of fore wing of type. Length of wing, 2.8 mm.

2. Family Permembaliidae Tillyard

Permembaliidae Tillyard, 1937, p. 92.

In 1928 Tillyard described, as a new genus and species, *Permembra delicatula*, a very small insect that he placed in the family Delopteridae Sellards (1909). Convinced that this family was related to the Psocoptera [Copeognatha], he transferred the Delopteridae from the Protorthoptera, where it had been assigned by Sellards, to the Psocoptera, within a new suborder, Embiopsocida. Subsequently (1937) Tillyard erected the new family Permembaliidae for the genus and also placed there the new genus *Nugonioneura*. The affinities of both these genera have remained obscure. *Nugonioneura*, now better known than previously, has been shown above to belong to the Protorthoptera, but *Permembra* still remains a mystery.

Martynov, in 1930 and unknown to Tillyard, had already placed the family Delopteridae in synonymy with the family Palaeomantidae Handlirsch (1906) and had designated the Palaeomantidae as representative of a new order, Miomoptera (1927).⁶ Subsequent studies of additional material have confirmed Martynov's conclusion on the synonymy of these families and have tended to support the recognition of the Miomoptera as a distinct, though poorly defined, order. In 1962, Martynova in a general survey of the order Miomoptera also placed the family Permembaliidae there, but with

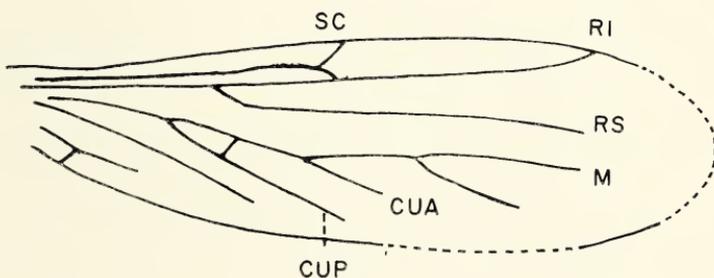


Figure 15. *Permembra delicatula*. Drawing of fore wing, based on holotype. Length of wing, 2.8 mm.

⁶For an account of the nomenclatural complexities involved in the designation of this taxon, see Carpenter, 1935, p. 105.

some uncertainty. The problem of *Permembia* results from lack of venational details in the unique specimen of *delicatula*, the species on which the genus was based. The difficulty is determining the actual, as opposed to the possible, characteristics of the genus and the family.

Dr. Kukalova experienced this in connection with her study of the Delopteridae and other Miomoptera from the Permian of Moravia (1963). Using a photograph of the type of *delicatula* that I had sent her, she concluded that Tillyard had incorrectly described and interpreted the venation, which she considered more like that of the Delopteridae than Tillyard thought. She also placed in the Permembiiidae two new genera of Miomoptera (*Permonika* and *Permonia*) from Moravia.

I have given much thought to the problem of *Permembia* since its original description and have repeatedly studied the type of *delicatula* at the Peabody Museum, Yale University, with the hope of finding some useful details previously overlooked. Only recently have I come to the conclusion that specimens of this insect are present in the Harvard collection also, though they are identifiable mainly on the basis of body structures, the venation in all specimens being more poorly preserved than that of the type. Our interpretation of the relationships of *Permembia* must therefore continue to rest for the time being on the venation of that specimen. From my examination of it, I am now convinced that Tillyard's interpretation of the venation was correct in all but minor details and that the genus *Permembia* (and of course the family Permembiiidae) cannot logically be assigned to the order Miomoptera.

The type of *delicatula* (no. YPM5403, Peabody Museum) consists of a nearly complete insect, as shown in figure 14A. One fore wing is spread out but the other three wings are folded or twisted in such a manner that their venation is not discernible. The head is relatively large and distinctly triangular in shape, markedly broad posteriorly, not globular as figured and described by Tillyard. The compound eyes are protuberant and situated posteriorly, as shown in the photograph. I certainly do not discern the three ocelli shown by Tillyard. The mandibles and palpi are not distinctive but the antennae are surprisingly thick and robust; the segments, numbering about 13, are as broad as long and subequal.

The thorax is relatively broad, the mesothorax being the largest segment. The abdomen, showing 10 distinct segments, terminates in a pair of short, segmented cerci. Several other small terminal processes, about 0.2 mm in length, are visible, but their nature is not obvious.⁷ The fore wing, which is only 2.8 mm long, was obviously very delicate and thin; this is indicated by the folded and twisted condition of the other wings of the type and of all of the wings of the specimens in the Harvard collection. The drawing of the wing of the type shown in figure 15 includes only those veins which I am confident can be seen by anyone who studies the specimen. The enlarged photograph of the wing in figure 14B shows most, if not all, of these veins. The wing is not narrowed basally as much as depicted by Tillyard. The proximal and middle parts of the wing are well preserved, especially considering the minute size of the insect, but the distal region and part of the posterior area are either broken away or simply not preserved. SC is distinct and terminates on R1 at about mid-wing. R and R1 form a straight line up to nearly the termination of R1, which is well before the apex of the wing. RS arises about 1/3 the wing length from the base and is nearly straight, diverging slightly away from R1; it is not preserved beyond the end of the level of R1 and I am unable to see any sign of its wide distal fork depicted by Tillyard or of the several branches which Kukalova mentions as probably present. M arises independently of R but apparently coalesces basally with CU; CUP diverges away first, with M+CUA continuing until near mid-wing, where M diverges anteriorly and soon forks. M is not preserved beyond the end of R1, which prevents our knowing whether or not other forks were present. Similarly, CUA is not preserved as far as the wing margin, but it is unbranched as far as it can be traced. 1A and 2A are incomplete, without branches. I have been able to distinguish only three cross veins with certainty, as shown in the figure: between SC and the costal margin, between CUP and M+CUA, and between 2A and the hind margin of the wing. I have no doubt that other cross veins were present in the wing, but I am concerned here with those that I believe can

⁷Tillyard was of the opinion that the asymmetry of these minute appendages suggested relationships with the Embioptera but in my experience most small processes on insects are asymmetrical when preserved in fossils, as a result of the softening of the cuticle.

clearly be seen. There are several features of this wing as interpreted here that resemble those of the fore wings of the Miomoptera, such as the form of SC and the coalescence of CUA with the stem of M. However, these are also features that are commonly found in many orders of insects. More important, I believe, is the apparent absence of two characteristics which occur in all known Miomoptera: the presence of 2 or 3 branches on RS and of a deep, prominent fork on CUA. Although neither RS nor CUA in the type of *Permembra* is preserved completely to the wing margin, there does not seem to be sufficient space remaining for the characteristic branching.

Rather than modify the diagnosis of the Miomoptera to accommodate *Permembra*, it seems preferable to place the genus in *incertae sedis* at the ordinal level (probably within the orthopteroid complex) until specimens showing complete fore and hind wings have been found.

Five specimens which appear to belong to this species are in the Harvard collection: nos. 7526ab, 7539ab, 7547, 7596, and 7474. All show the characteristic head shape and other body features, including the robust antennae, but in all specimens the wings are badly twisted and folded.

In this connection it is appropriate to mention *Sheimia sojanensis* Martynova (1958) from an Upper Permian deposit at Sheimo-Gora, Kuloy River Basin, Arkhangelsk Region, Soviet Union. This minute insect, with a wing-length of about 4 mm., is known only

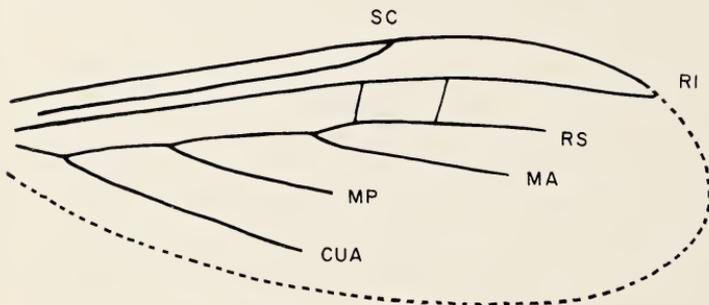


Figure 16. *Sheimia sojanensis* Martynova, from Permian of Sheimo-Gora, Arkhangelsk Region, USSR; drawing of fore wing, based on holotype, no. 1145/117, Paleontological Institute, Moscow. Length of wing, 3 mm.

by the poorly preserved holotype, which has been loaned to me for study by the Institute of Paleontology in Moscow. The general form of the body and the structure of the antennae in particular are like those of *Permembra*, but the wing venation is so different that at least family separation seems necessary. My interpretation of the venation is like that of Martynova's (1962) in most respects. However, I cannot discern the short vein that she has identified as CUP, or the vein posterior to it in her figure; and I see no trace of the basally oblique vein which her figure shows extending from R to the M+RS complex. My concept of what can definitely be seen in this wing is shown in figure 16. Although there are similarities to the venation of *Permembra*, there is one very significant difference: the absence in *Sheimia* of a free RS arising independently from R. For this reason, I do not believe that *Sheimia* can be considered at all closely related to the Permembriidae, in spite of the apparent similarities in body structure.

Martynova was of the opinion that *Sheimia* was a member of the order Embioptera and she designated a separate suborder (Sheimiodea) for it, a view that was subsequently followed by Riek (1970, p. 179). For my part, I do not believe that there is enough evidence for an embiopteran position of this fragmentary fossil to justify extending the range of the Embioptera from the Oligocene (their present earliest record), back to the Permian — an interval of about 190 million years. There is certainly no indication in the specimen of *S. sojanensis* of the thickened blood sinus (R1), or of the enlarged fore basitarsi, or even of a generalized venational pattern that might have led to that of the existing order Embioptera. It seems to me preferable, therefore, to assign the family Sheimiidae to *incertae sedis* at the ordinal level within the orthopteroid complex until additional and better preserved specimens of *Sheimia* have been found.⁸

3. Family **Apheloneuridae**, new family

Very small insects, with fore and hind wings similar, but not identical, in both size and venation. Fore wing: SC ending on

⁸I have recently examined about thirty specimens of insects, comparable in size to *Sheimia sojanensis* and from the same deposit, but none of them are even remotely related to the Sheimiidae.



Figure 17. *Apheloneura minutissima*, n.sp. Photograph of holotype, no. 7527, M.C.Z. Length of fore wing 3 mm.

costal margin at about mid-wing, also unbranched; M independent from R, with three long branches; CU dividing into CUA and CUP at wing base; CUA with a long anterior branch (CUA1) almost parallel to hind margin of wing and terminating near wing apex; CUA2 shorter; CUP nearly straight, short. Hind wing: slightly shorter than fore wing; venation similar but CUA unbranched. Cross veins weakly developed in both wings, but numerous and apparently small; antennae slender and relatively long, with many segments.

The most striking feature of this family is the nearly parallel arrangement of R, M1+2, M3, M4, and CUA1, especially in the fore wing, and the lack of branching on these veins beyond mid-wing.

Apheloneura, new genus

Fore wing: RS arising at about 1/5 of wing-length from the base; M1+2 forking about mid-way between the levels of the origins of RS and the forking of M3+4; CUA arising from CU very close to wing base. Hind wing: M1+2 arising much nearer the forking of M3+4 than to the origin of RS.

Type species: *Apheloneura minutissima*, n.sp.

The generic name is derived from the classical Greek words *aphel* (parallel), and *neura* (veins); the name is considered plural and feminine. Two species of the genus are in the M.C.Z. collection.

Apheloneura minutissima, n.sp.

Figures 17-19

Fore wing: length, 3 mm; width, 1 mm. Hind wing: length, 2.7 mm; width, 1 mm. The venational features of the holotype are shown in figure 19. CUA2 forms a straight line with the stem of CUA, and it is deeply forked.

Holotype: no. 7527, M.C.Z.; collected at Elmo in 1927. This specimen (figure 17) has all four wings, parts of the antennae, and obscure portions of the thorax and abdomen. The preservation of the fossil is remarkable considering its small size. The longitudinal veins are to be seen without difficulty, but the cross veins can be distinguished only under oblique lighting along the wing

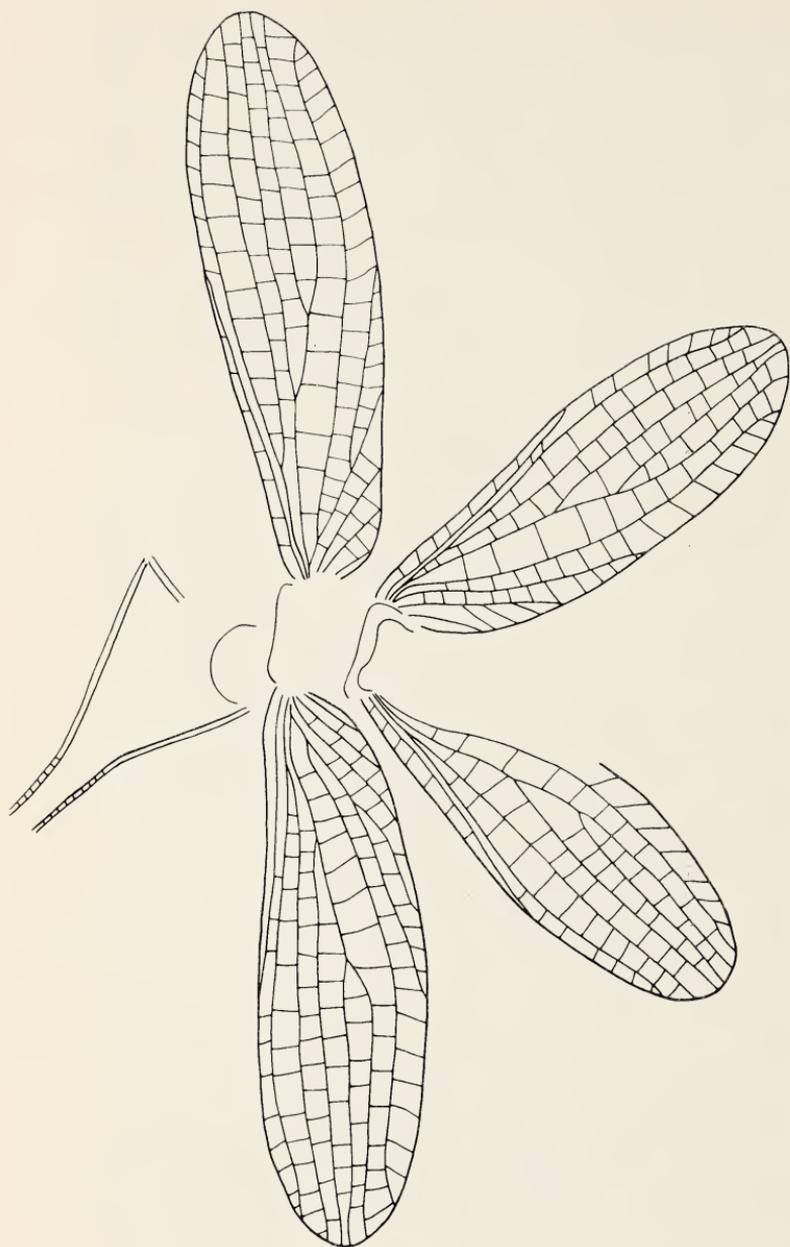


Figure 18. *Apheloneura minutissima*, n.sp.; drawing of holotype.

axis. The body is poorly preserved, showing only portions of the thorax and abdomen, and an irregular structure anterior to the mesothorax that probably consists of a small pronotum and the head, although details are not preserved. Arising from the head region is one antenna (1.2 mm long); the other antenna, although broken away from the head region, is more clearly preserved for a greater length (2.2 mm). The segments of the antennae that are visible are about twice as long as broad.

Paratype: no. 7533ab; collected at Elmo in 1932. This consists of a less clearly preserved specimen than the holotype, with one fore wing outstretched, and the others overlapping the abdomen and each other. The fore wing is 2.8 mm long and 1 mm wide. One antenna is preserved for 1 mm, and its segmentation is like that of the holotype.

In addition there is one other specimen in the collection: no. 7534, with the wings overlapping the abdomen; the fore wings are 3 mm long.

***Apheloneura amplia*, n.sp.**

Figure 20

Fore wing: length, 4.8 mm; width, 1.5 mm. Venation similar to that of *minutissima*, but RS arises somewhat nearer the wing base, CUA2 is unbranched, and CUA1 (not CUA2, as in *minutissima*) continues the straight line of the stem of CUA. Cross veins are preserved in several areas of the wing, much as in *minutissima*. The hind wing (partially preserved in paratype 7525) is apparently like that of *minutissima*.

Holotype: no. 8604 M.C.Z., collected in 1927. This consists of a very well preserved fore wing.

Two other specimens, not designated as types, are in the collection, as follows: no. 7525, showing the thorax, abdomen, and basal parts of all four wings, with the structure of CUA very clear; no. 7522, a more poorly preserved specimen with all wings overlapped.

This species is conspicuously larger than *minutissima*. The presence in the collection of three specimens, all of them of the larger size and all having the same structure of CUA1 and CUA2, shows that these are not simply over-sized specimens of *minutissima*.

I have not yet been able to reach any conclusion about the ordinal position of the Apheloneuridae. There are two obvious

features of their wings: the reduction of branches on most longitudinal veins, and the similarity of the fore and hind wings. Each of these traits has appeared quite frequently in various orders of insects, but their combined occurrence is very infrequent, at least among Recent groups. The most obvious instance is the Embioptera — which is why *Permambia* and *Sheimia*, among others, have been regarded as their close relatives. However, there are no

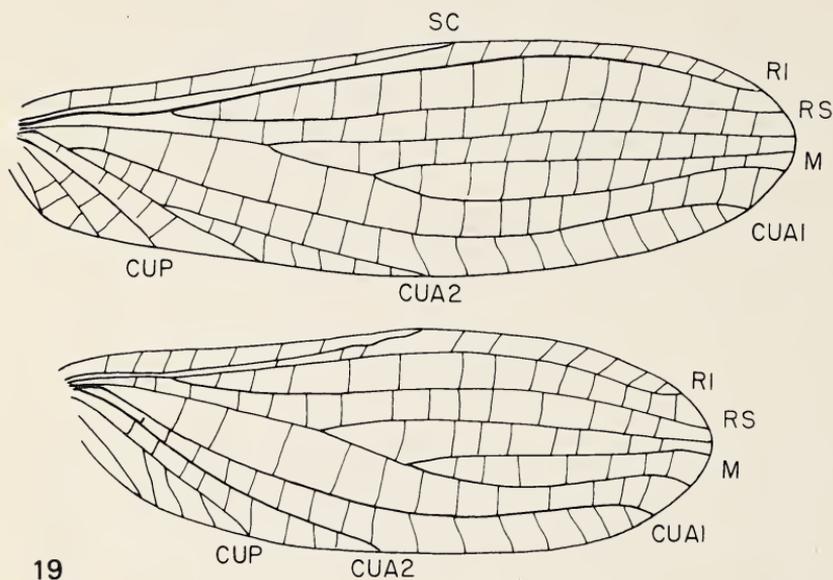


Figure 19. *Apheloneura minutissima*, n.sp.; drawing of fore and hind wings, based on holotype. Length of fore wing, 3 mm.

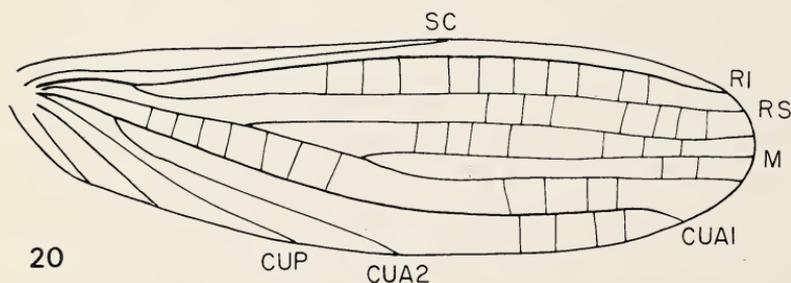


Figure 20. *Apheloneura amplia*, n.sp.; drawing of fore wing, based on holotype, no. 8604, M.C.Z. Length of fore wing, 4.8 mm.

venational details of the Apheloneuridae that suggest to me their close relationship with the Embioptera. It does seem probable, though, that the order has ultimately been derived from some aberrant protorthopterous stock, and the Apheloneuridae may well have been among the early, distant relatives of that stock.

The fore wings of *Apheloneura*, in fact, have a venational pattern much like that of the Permian Probnisidae (Protorthoptera), with the branches of RS and M reduced and CUA extending nearly to the wing apex. However, the probnisid hind wings are typically orthopterous, with a large and expanded anal fan and a distinctive venation, unlike that of the fore wings. It is the hind wing of the Apheloneuridae that induces me to withhold the family from the Protorthoptera and to place it in *incertae sedis*.

In this connection it should be noted that the Apheloneuridae are not the only Permian insects having subequal wings that show orthopteroid relationships. The Miomoptera, for example, which have a distinctive venational pattern and which are very abundantly represented in Permian beds, are in this category. There are, in fact, many similar insects, about the size of Permembidae and Apheloneuridae occurring in the Permian of Kansas, Oklahoma, and the Soviet Union, all of which are apparently orthopteroid but show remarkable diversity of structure. These have not yet been formally described, mainly because they are not clearly preserved. Until more of these small insects are better known, I believe it is advisable to leave the Apheloneuridae, along with the Permembidae and Sheimiidae, in the category of "order unknown".

4. Family **Gelasopteridae**, new family

Insects of moderate size. Fore wing: very long and slender; SC ending on costa beyond mid-wing; R1 extending very nearly to apex of wing; RS unbranched, M forked beyond mid-wing; CUA diverging at its origin towards M and connected to it by a short cross vein (or possibly a branch of M); then continuing without branches to near the apex; CUP and 1A unbranched; cross veins numerous, mostly straight. Hind wing: about as long as fore wing. Body slender, prothorax elongate.



Figure 21. *Gelasipteron gracile*, n.sp.: photograph of holotype, no. 7511ab, M.C.Z. Length of fore wing 28 mm.

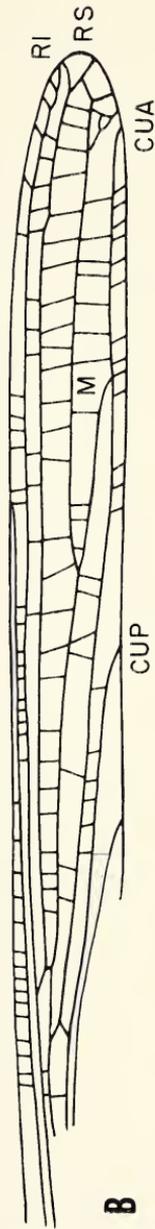
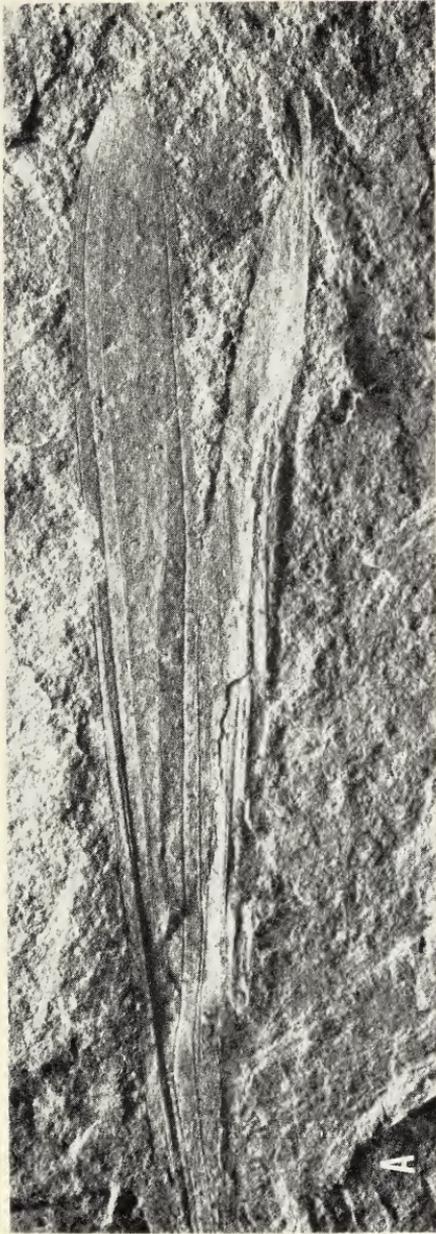


Figure 22. *Gelasopteron gracile*, n.sp. A, photograph of fore and hind wings of holotype. B, drawing of fore wing of holotype. Length of fore wing, 28 mm.

Gelasopteron, new genus

Fore wing: about ten times as long as wide; costal area only of moderate width basally; RS arising at about $1/6$ wing length from base, continuing straight and parallel to R1 for its entire length; anterior branch of M weak, terminating obscurely near the wing apex; posterior branch of M terminating on CUA.

Type-species: *Gelasopteron gracile*, n.sp.

The generic name is derived from the classical Greek words *gelastos* (ridiculous) and *pteron* (wing) and is considered neuter and singular.

Gelasopteron gracile, n.sp.

Figures 21–22

Fore wing: length 28 mm (as preserved); width 2.8 mm; estimated complete length, 30 mm. Costal margin very straight up to the apical region; base of the costal area not preserved; R1 mostly straight, curving posteriorly at the apex, as it parallels the costal margin; M forking the level of the termination of SC, the anterior branch about twice as long as the posterior one.

Holotype: no. 7511ab, M.C.Z.; collected at the Harvard quarry at Elmo in 1927. This specimen consists of a nearly complete wing and parts of others, as well as fragments of the thorax and abdomen. As shown in the photograph (figure 21), one fore wing is stretched out at right angles to the body; a second wing of the same length, presumably the hind wing of the same side, partially overlaps the fore wing basally and is twisted and rotated so that its hind margin is contiguous with the hind margin of the fore wing. The distortion of the hind wing prevents a satisfactory study of its venation; the apical part appears to be like that of the fore wing. However the long CUA, the predominate feature of the fore wing, does not seem to be present in the hind wing, and there is a suggestion of an anal fan that has been folded up under the rest of the wing.

The two wings on the opposite side of the thorax are flexed along the body, both of them folded and twisted together. The apical part (about 7 mm, labeled AP in figure 21) is bent at an acute angle to the rest of the wing, which is 20 mm long.

Little is preserved of the body. A small portion can be seen posterior to the base of the wing; this is about 6 mm long and 2

mm wide. The posterior third of this portion seems to be the first abdominal segment, but there is nothing preserved beyond that. The body anterior to the wings, presumably the prothorax, is about 10 mm long up to the edge of the piece of rock containing the specimen. This part seems to be 4 mm wide, i.e., about twice as wide as the posterior part, but about half of that width seems to consist of a pair of femora that extend along the sides of the prothorax.

The general picture derived from this curious fossil is of an insect with a long prothorax and abdomen, and with extremely long and slender fore wings, perhaps with an anal fan on the hind pair. There is some suggestion in this of a phasmatodean, but the venation of the fore wing has virtually nothing in common with that of the Triassic and Jurassic Phasmatodea described by Sharov (1968). Comparison with existing Phasmatodea is difficult since none, so far as I am aware, have normal or fully developed fore wings.

My assumption is that *Gelasopteron* is a member of the orthopteroid complex, in spite of the unbranched RS; but we will need to wait for more fossil evidence before removing the insect from the *incertae sedis* category.

5. Family Permoneuridae

Permoneuridae Carpenter, 1931, p. 124; Tillyard, 1937, p. 87; Laurentiaux, 1953, p. 425.

This family was established for *Permoneura lameerei* from the Elmo beds and placed, with some doubt, in the order Palaeodictyoptera. The unique specimen on which this species was based consisted of a single wing, which I assumed to be a hind wing because of its broad anal area. Two features of this wing were unusual: the pectinate branching of RS and the apparent anastomosis of MA with the basal branch of RS for its entire length. A third feature, the absence of CUA, was unknown in the Palaeodictyoptera.

Many different opinions have been expressed about this insect since its description. Tillyard (1937) was of the opinion that *Permoneura* was a very highly specialized offshoot of the ancestral stock of *Dunbaria* and that the loss of CUA might have been due

to abnormal development of the unique specimen on which the species was based. His final suggestion was that *Permoneura* be placed in the Spilapteridae, near *Dunbaria*. Laurentiaux (1953), on the other hand, placed it in a new order, Permoneurodea, close to the Palaeodictyoptera. Rohdendorf (1962) assigned it to the order Archodonata, which in my opinion is inseparable from the Palaeodictyoptera. Dr. Kukulova-Peck has suggested (personal communication) that the type of *lameerei* might be a hind wing of a protorthopteron. This is indeed a possibility, but none of the Protorthoptera are known to have a pectinate RS in the hind wings and none are known to lack CUA.

Inasmuch as no additional specimens of *Permoneura* have turned up in the 45 years since its description, I believe the family Permoneuridae should be placed in the category of *incertae sedis* at the ordinal level. This has the advantage of removing it from both the Palaeodictyoptera and the Protorthoptera, in neither of which it seems to belong. Its assignment to a separate order of its own seems unjustified; an order based on a single wing has no meaning.

Reexamination of the specimen of *lameerei* convinces me that although my original figure is essentially correct (1931, figure 6), it does not indicate that all the veins are concave, except for R and R1 and, apparently, the short basal piece of MA. A photograph of the counterpart of this specimen, showing the peculiarity of the venational topography, is included here (figure 23).

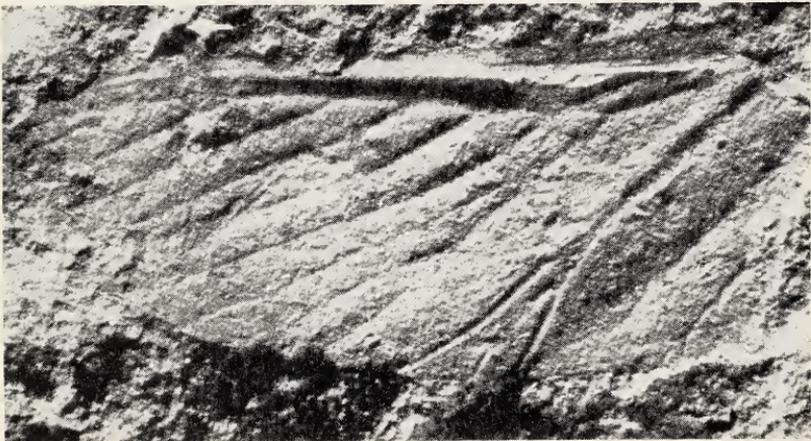


Figure 23. *Permoneura lameerei*; photograph of holotype, no. 9876, M.C.Z. Length of wing, 9 mm.

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